

Brendan J. Hicks · Mark S. Wipfli · Dirk W. Lang
Maria E. Lang

Marine-derived nitrogen and carbon in freshwater-riparian food webs of the Copper River Delta, southcentral Alaska

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Abstract After rearing to adulthood at sea, coho salmon (*Oncorhynchus kisutch*) return to freshwater to spawn once and then die on or near their spawning grounds. We tested the hypothesis that spawning coho salmon return marine N and C to beaver (*Castor canadensis*) ponds of the Copper River Delta (CRD), Cordova, southcentral Alaska, thereby enhancing productivity of the aquatic food webs that support juvenile coho salmon. We sampled three types of pond treatment: (1) natural enrichment by spawning salmon, (2) artificial enrichment via addition of salmon carcasses and eggs, and (3) ponds with no salmon enrichment. All ponds supported juvenile coho salmon. Seasonal samples of stable isotopes revealed that juvenile coho salmon, threespine sticklebacks (*Gasterosteus aculeatus*), caddisfly larvae, leeches, and chironomid midge larvae were enriched with marine N and C. The aquatic vascular plants bur reed (*Sparganium hyperboreum*), pondweed (*Potamogeton gramineus*), and mare's tail (*Hippuris vulgaris*) were enriched with marine N only. Riparian vegetation (Sitka alder *Alnus viridis* ssp. *sinuata*

and willow *Salix* spp.) did not show enrichment. Artificial additions of adult carcasses and eggs of coho salmon increased the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of juvenile coho salmon. In this dynamic and hydrologically complex coastal environment, spawning coho salmon contributed marine N and C comprising 10–50% of the dietary needs of juvenile coho salmon through direct consumption of eggs and carcass material. Invertebrates that have assimilated marine N and C yield a further indirect contribution. This perennial subsidy maintains the productivity of the ecosystem of the coho salmon on the CRD.

Keywords Stable isotopes · Marine nutrients · Dietary analysis · Coho salmon · Aquatic invertebrates

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B. J. Hicks (✉)
Centre for Biodiversity and Ecology Research,
Department of Biological Sciences,
The University of Waikato, Private Bag 3105,
Hamilton, New Zealand
E-mail: b.hicks@waikato.ac.nz
Tel.: +64-7-8384661
Fax: +64-7-8384324

Present address: M. S. Wipfli
USGS, Alaska Cooperative Fish and Wildlife Research Unit,
Institute of Arctic Biology,
University of Alaska Fairbanks,
Fairbanks, AK, 99775-7020 USA

Present address: D. W. Lang
Cordova Ranger District, USDA Forest Service,
612 N. Second Street, Cordova, AK, 99574 USA

Present address: M. E. Lang
School of Fisheries and Ocean Sciences,
University of Alaska Fairbanks—Juneau Center,
Juneau, AK, 99801 USA

Introduction

Anadromous populations of Pacific salmon (*Oncorhynchus* species) can act as an upstream nutrient pump, importing marine N and C into freshwater habitats as the semelparous adults migrate upstream to spawn and die. Spawning pink (*Oncorhynchus gorbuscha*), sockeye (*Oncorhynchus nerka*) and chum salmon (*Oncorhynchus keta*) contribute considerable amounts of marine N and C to spawning streams (Kline et al. 1990) and riparian vegetation (Bilby et al. 2003). The strength of this contribution can depend on the size of the salmon run, with greatest contribution of marine N and C in years of greatest salmon abundance (Kline et al. 1993; Schmidt et al. 1998; Finney et al. 2000, 2002). Coho salmon (*Oncorhynchus kisutch*) often spawn at lower densities in many systems than sockeye, pink, and chum salmon (Bilby et al. 2003), but can still contribute substantial amounts of marine N and C to stream food webs (Gende et al. 2002), even in regions such as western Washington (Bilby et al. 1996) where salmon runs are known to be depressed (NRC 1996; Gresh et al. 2000). This biomass of marine origin subsidizes food webs throughout the west coast of North America (Bilby et al. 1998; Heintz

et al. 2004; Minakawa and Gara 1999; Wipfli et al. 1998, 2003).

Many regions of North America have experienced reduced salmon returns, resulting in potential losses of nutrient and energy inputs of marine origin to these ecosystems (NRC 1996; Gresh et al. 2000). For example, river systems in parts of British Columbia and the Pacific Northwest of the US have seen serious declines of returning salmon (NRC 1996; Schoonmaker et al. 2003; Thomas et al. 2003). However, run sizes in most of Alaska and parts of western Canada are generally considered to be near historic levels (Baker et al. 1996; Slaney et al. 1996). The full extent to which salmon-borne nutrients influence freshwater and riparian ecosystems is not understood (Gende et al. 2002).

Marine subsidies can permeate freshwater food webs through multiple pathways. Nutrients and C released immediately upon salmon returning to streams are taken up by and stimulate lower trophic levels (Wipfli et al. 1998; Minakawa and Gara 1999). In Alaska, these lower trophic levels subsequently influence the next level of consumer up the food web (Wipfli 1997; Wipfli et al. 1999). Invertebrates and fishes also ingest marine subsidies directly, preying on salmon tissue and eggs (Bilby et al. 1998; Chaloner and Wipfli 2002; Wipfli et al. 2003). Riparian plants were also shown to sequester marine N in Washington streams (Bilby et al. 1996, 2003) and appear to benefit from the fertilization these fish provide in Alaska (Ben-David et al. 1998).

Coho salmon spawned on the Copper River Delta (CRD), Prince William Sound, southcentral Alaska, rear to adulthood at sea, and return to freshwater between September and December. Spawning takes place in the channels and ponds of the CRD in October and November each year. After spawning, the adults die and decompose in or near the freshwater rearing habitats of their juveniles. Bears (*Ursus* spp.) and other vertebrate predators and scavengers also carry spawning fish to shore, often leaving many fish carcasses scattered throughout the riparian zone (Gende et al. 2002).

The aim of this study was to determine the proportion of marine N and C transferred from adult salmon to the food webs and juvenile salmon in beaver (*Castor canadensis*) ponds of the CRD. Beaver ponds on streams can substantially increase N storage (Naiman and Melillo 1984). The CRD is hydrologically complex, with a network of beaver ponds interconnected by stream channels. The rivers of the area usually have two periods with high runoff: a spring snowmelt period and a fall rainfall period. High water can occur throughout the year, but the greatest discharges are most common in the fall months. Low-water periods usually occur in late spring and mid-summer, prior to the rainy fall period (Meyer et al. 2001). Returning coho salmon spawners have access to only a proportion of the available rearing habitat. Juvenile coho salmon on the CRD emerge in April, and are redistributed throughout the beaver ponds and other wetland habitats of the Delta during periods of high flow, including habitat that did not re-

ceive spawning adults. Beaver dams further restrict salmon access in places, but drown barriers elsewhere. Because of this complexity, some ponds receive adult coho salmon spawners naturally, while others do not. Juvenile coho salmon eventually move into most ponds, providing an ideal opportunity to compare $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ with and without spawners. Our hypothesis was that stable isotopes would reflect the annual inputs of marine C and N from spawning coho salmon to rearing habitats of their juveniles. Further, we sought to demonstrate that eggs and carcasses of adult salmon were the sources of this marine subsidy by enriching selected rearing habitats that would not otherwise have received such inputs.

Methods

Study sites

The study sites comprised nine beaver ponds located in the Mile 18 Stream drainage of the CRD southcentral Alaska ($60^{\circ}26'\text{N}$, $145^{\circ}20'\text{W}$; Fig. 1). The Mile 18 Stream system is a fourth-order coastal floodplain river with a catchment area of approximately 15 km^2 , with 21 km of stream channels and a mean annual discharge is estimated to be $7.0\text{ m}^3\text{ s}^{-1}$. The area receives approximately 380 cm of rainfall annually (Lang 2003). Wetted widths are approximately 9 m during mean summer flow and mean stream surface gradient is 1%. The substrate of the stream system is alluvium composed of sand, silt, and organic material.

Riparian habitats around the ponds were dominated by Sitka alder (*Alnus viridis* ssp. *sinuata*) and willow (*Salix* spp.), and the aquatic plant communities of the ponds included the submerged aquatic macrophytes

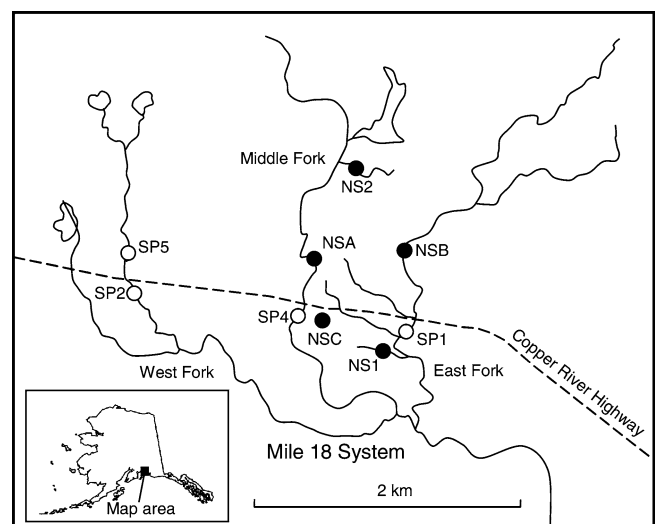


Fig. 1 Location of the study sites on the Copper River Delta, southcentral Alaska. *open circle* ponds with spawners; *filled circle* ponds without spawners

pondweed (*Potamogeton gramineus*) and mare's tail (*Hippuris vulgaris*), the emergent macrophytes bur reed (*Sparganium hyperboreum*), and rush (*Juncus mertensianus*), and sedge (*Carex lyngbyaei*) (Hulten 1968). Age-0 and age-1 coho salmon were present in all the ponds. Threespine stickleback (*Gasterosteus aculeatus*), slimy sculpin (*Cottus cognatus*), Dolly Varden (*Salvelinus malma*), and coastal cutthroat trout (*O. clarki*) were also present in some ponds (Lang 2003).

Invertebrates are also common in ponds and riparian vegetation. The taxa included caddisfly larvae (Trichoptera: Limnephilidae), which are largely detritivores, snails and slugs (Mollusca: Gastropoda; omnivores), leeches (Annelida: Hirudinea; scavengers), dragonfly nymphs (Odonata: Aeshnidae; predators), caterpillars (Lepidoptera: various families; chewing herbivores), aphid nymphs and adults (Homoptera: Aphidae; sucking herbivores), midge larvae (Diptera: Chironomidae; multiple trophic guilds), water boatman nymphs (Hemiptera: Corixidae; omnivores), and aquatic worms (Annelida: Oligochaeta; detritivores).

The ponds in the study ranged in area from 1,200 m² to 4,300 m², and had a maximum depth of 1.0–2.4 m (Table 1). Four ponds received spawners naturally, and five ponds did not. Densities of carcasses from natural spawners in ponds averaged 0.07 fish m⁻², or 0.278 kg wet mass m⁻². Food web components were sampled between July 1999 and May 2001. Additions of carcasses and eggs of mature coho salmon that had returned from the sea were made to two ponds (NSA and NSB) in five lots at weekly intervals between 1 October and 18 November 2000 (Table 1). The loading rates were designed to mimic natural rates. Fifty carcasses (total weight 194 kg wet mass) were added to pond NSA in lots of 3–16 carcasses at a time, and 100 carcasses (total weight 398 kg wet mass) were added to pond NSB in lots of 4–25 at a time (Lang 2003). The resultant total loadings were 0.219–0.276 kg wet mass m⁻² (Table 1). Egg skeins were removed from females and separated with a 2-cm mesh screen. After refrigerating for 2–3 days, 12 l of eggs were added to pond NSA as lots of 1–3 l, and 25 l of eggs were added to pond NSB in lots of 2–7 l (Lang 2003). The mean conversion factor calculated from seven weighings of 100 ml of eggs was

1.27 g ml⁻¹ (D. Lang unpublished data). The eggs were broadcast over the pond surface to give a total loading of 0.018–0.022 kg wet mass m⁻² (Table 1), which simulated the natural amount of eggs that would have been deposited by spawners at the carcass loadings used. Pond NSC received no eggs or carcasses. Growth of juvenile coho salmon was also measured in these ponds in a companion study (Lang 2003).

Sampling and tissue preparation

Samples of juvenile coho salmon, sticklebacks, invertebrates, and plants were collected between July 1999 and May 2001. Juvenile coho salmon and sticklebacks were captured each month with wire-mesh minnow traps baited with salmon eggs (Lang 2003). Submerged and emergent aquatic macrophytes, leaves of alder and willow, and selected terrestrial invertebrates were collected as they became available seasonally. Adult coho salmon and eggs were collected in November 1999 and October 2000 from ponds SP2 and SP5.

To prepare juvenile coho salmon caught in July 1999 for analysis of stable isotopes, fish were prepared both as filleted white muscle, and as whole fish with the gut removed. Thereafter, all juvenile coho salmon were processed as whole fish with the gut removed. All samples were oven dried to uniform weight at 40°C, and then ground to a homogenous powder. Caddisfly larvae were removed from their cases before drying and grinding, and individual invertebrates were combined before grinding where necessary to make a sample.

Analysis of stable isotopes

A Europa Scientific continuous flow 20/20 mass spectrometer with a triple ion-collector and ANCA SL inlet system was used to analyze stable isotopes of C and N. Small subsamples (3–6 mg) of dried, ground material were weighed with a 5-place balance, and oxidised and reduced at high temperature in the furnaces of the ANCA SL analyzer. The resultant CO₂ or N₂ stream was then analysed with the 20/20 to a precision of about

Table 1 Access of spawning coho salmon and treatment regimes of beaver ponds of the Copper River Delta, southcentral Alaska

Pond code	Pond area (m ²)	Maximum depth (m)	Received spawners naturally	Treatment		Date range of sampling
				Carcass additions	Egg additions	
SP1	1,588	1.7	Yes	Natural spawners	Natural spawning	Nov 1999–May 2001
SP2	1,394	1.0	Yes	Natural spawners	Natural spawning	July 1999–May 2001
SP4	4,298	1.5	Yes	Natural spawners	Natural spawning	July 1999–May 2001
SP5	3,147	–	Yes	Natural spawners	Natural spawning	Nov 1999–Nov 2000
NSA	704	1.2	No	0.276 kg m ⁻² added	0.022 kg m ⁻² added	July 1999–May 2001
NSB	1,779	1.1	No	0.219 kg m ⁻² added	0.018 kg m ⁻² added	July 1999–May 2001
NSC	2,023	2.4	No	No additions	No additions	Nov 1999–May 2001
NS1	1,432	1.7	No	No additions	No additions	July 2000–May 2001
NS2	1,231	1.6	No	No additions	No additions	Oct 2000–May 2001

Eggs and carcasses (wet mass) were added between 1 October and 18 November 2000. The pond naming scheme follows Lang (2003)

0.1‰ for ^{13}C and 0.3‰ for ^{15}N . The precision was maintained with reference samples of calibrated Australia National University (ANU) cane sucrose for $^{13}\text{C}/^{12}\text{C}$, and N_2 in air for $^{15}\text{N}/^{14}\text{N}$.

The ratios of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ were expressed as relative difference per mil (‰) using the equation:

$$\delta X = \left[\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1,000,$$

where $X = ^{13}\text{C}$ or ^{15}N , and $R = ^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. The ratios of ^{13}C to ^{12}C are expressed relative to PDB (Pee Dee Belemnite), for which $R_{\text{standard}} = 1.1237$ atom % ^{13}C (Craig 1957). The ratios of ^{15}N to ^{14}N are expressed relative to N_2 in air, for which $R_{\text{standard}} = 0.3663$ atom % ^{15}N (Mariotti 1983).

Data analysis

Because the number of potential food sources for juvenile salmon exceeded the number of sources that could be uniquely partitioned using C and N stable isotopic signatures, we used the IsoSource mixing model (Phillips and Gregg 2003) to determine the feasible range of dietary contributions for each food source. All possible

combinations of each source contribution (0–100%) were examined in 2% increments. Combinations that summed to the observed stable isotopic signatures of the mixture (juvenile coho salmon) within a tolerance of 0.1 were considered to be feasible solutions, from which the frequency and range of potential source contributions was determined, following the method described in detail by Phillips et al. (2005). We used eight food sources: muscle from adult coho salmon, coho salmon eggs, midge larvae, leeches, water boatman nymphs, caddisfly larvae, aphid nymphs and adults, and lepidopteran larvae. We assumed a trophic enrichment of +0.4‰ for $\delta^{13}\text{C}$, and +2.3‰ for $\delta^{15}\text{N}$, which were the increments suggested for either poikilothermic, ammonotelic, or aquatic animals (McCutchan et al. 2003). After the mixing analysis, we added the columns for the different food sources obtained from the IsoSource output file to form new variables, i.e., adult coho salmon muscle + eggs = marine, midges + leeches + water boatmen + caddisflies = freshwater invertebrates, and aphids + lepidopterans = terrestrial invertebrates. We then found the mean, 1 and 99 percentiles, and frequency histogram for each new combination to determine the range of feasible dietary contributions from those food groups (Phillips and Gregg 2003;

Table 2 Mean values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for food web components, aquatic macrophytes, and riparian vegetation of beaver ponds of the Copper River Delta excluding results for ponds NSA and NSB during and after enrichment (October 2000–May 2001)

Food web item	$\delta^{15}\text{N}(\text{‰})$						$\delta^{13}\text{C}(\text{‰})$							
	No spawners			Spawners			<i>P</i>	No spawners			Spawners			<i>P</i>
	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD		<i>n</i>	Mean	SD	<i>n</i>	Mean	SD	
Fish														
Coho adult eggs				7	14.9	0.47	–				7	–20.9	0.58	–
Coho adult muscle				11	12.9	0.57	–				11	–20.0	0.65	–
Coho adult eggs and adult muscle				18	13.7	1.14	–				18	–20.4	0.77	–
Coho juvenile	141	8.2	1.11	170	10.2	1.74	<0.001	141	–28.9	2.00	170	–26.7	2.05	<0.001
Stickleback	131	8.5	0.95	124	9.6	1.34	<0.001	131	–35.2	3.54	124	–34.9	3.41	0.499
Stickleback stomach	13	4.1	1.06	6	6.0	1.01	0.002							
Aquatic invertebrates														
Caddisfly larvae	14	2.6	2.04	29	5.2	1.23	<0.001	13	–31.2	4.12	28	–31.5	2.96	0.885
Dragonfly nymphs	31	5.5	0.86	2	5.6	0.18	0.831	31	–36.0	2.87	2	–35.0	4.78	0.631
Leech	4	6.7	1.02	5	9.3	1.35	0.016	3	–30.4	6.00	5	–29.2	4.30	0.757
Midge larvae	6	3.2	0.87	7	5.3	1.44	0.010	4	–39.6	3.05	7	–33.8	3.90	0.032
Oligochaete	2	0.6	0.47				–	2	–25.5	0.69				–
Water boatmen nymphs	7	1.8	0.32	10	1.8	0.25	0.788	5	–32.1	0.41	10	–32.5	0.73	0.286
Terrestrial invertebrates														
Aphid nymphs and adults	2	–1.3	1.20	2	0.6	1.10	0.245	2	–25.1	0.27	2	–25.9	1.21	0.466
Lepidoptera larvae	6	–0.1	1.11	4	–0.2	0.14	0.863	6	–28.3	1.21	4	–28.1	1.14	0.859
Slug	1	1.8		1	4.1		–	1	–24.7		1	–25.3		–
Snail without shell				1	–0.7		–				1	–25.2		–
Shell				1	0.7		–				1	–18.3		–
Aquatic plants														
Bur reed	4	1.9	1.71	5	4.7	2.21	0.075	4	–29.2	1.38	5	–28.6	2.83	0.721
Mare's tail	7	2.7	0.98	5	3.7	0.61	0.091	7	–29.9	1.54	5	–30.3	2.44	0.705
Pondweed	6	1.6	1.87	7	3.3	0.89	0.057	6	–30.6	1.35	7	–30.2	3.67	0.782
Rush	2	2.7	0.41	1	5.8		–	2	–28.2	0.95	1	–28.4		–
Sedge	8	4.0	2.12	7	3.4	1.64	0.592	8	–27.6	0.99	7	–27.6	0.63	0.867
Terrestrial plants														
Alder	20	–1.7	0.95	22	–1.8	0.85	0.804	20	–26.9	0.85	22	–26.5	0.72	0.066
Willow	21	–1.4	1.47	20	–1.5	1.87	0.826	21	–27.9	1.14	20	–28.3	0.89	0.195

Significance of difference (*P*) between means for ponds with and without spawners was determined by analysis of variance

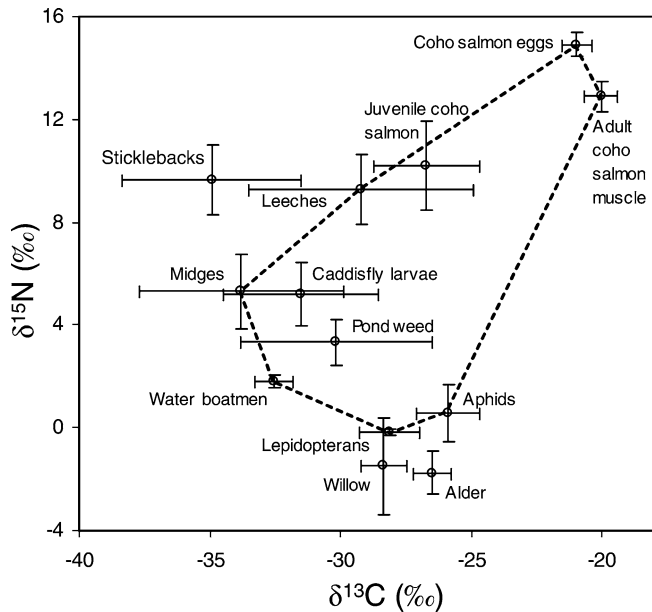


Fig. 2 Comparison of mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of food web in beaver ponds of the Copper River Delta, southcentral Alaska, which received natural coho salmon spawners. Error bars are one standard deviation. The dashed polygon connects the end members of the food of juvenile coho salmon

Phillips et al. 2005). Statistical analyses were carried out using SYSTAT version 10 and Statistica version 6.0.

Results

Stable isotope values of coho salmon

Adult coho salmon white muscle and eggs typically had high values of $\delta^{15}\text{N}$ (12–15‰) and $\delta^{13}\text{C}$ (–21 to –20‰), reflecting the marine origin of these elements

Table 3 Means and 95% confidence intervals (CI) of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of white muscle and whole juvenile coho salmon from beaver ponds of the Copper River Delta, southcentral Alaska

Pond	$\delta^{15}\text{N}$ (‰)				$F_{1,8}$	P
	White muscle		Whole fish			
	Mean	95% CI	Mean	95% CI		
SP2	12.7	2.2	12.0	2.5	0.352	0.570
SP4	10.1	2.6	10.5	1.7	0.113	0.746
NSA	7.5	0.5	7.7	0.5	0.415	0.538
NSB	8.2	0.3	8.4	1.7	0.094	0.767

Pond	$\delta^{13}\text{C}$ (‰)				$F_{1,8}$	P
	White muscle		Whole fish			
	Mean	95% CI	Mean	95% CI		
SP2	–24.9	3.3	–25.2	4.3	0.031	0.865
SP4	–28.3	5.4	–28.5	2.2	0.017	0.901
NSA	–29.2	1.2	–31.6	1.1	16.76	0.004
NSB	–31.5	0.7	–29.1	1.0	30.61	0.001

$n = 5$ for each mean, F and P statistics from analysis of variance

(Table 2). The $\delta^{15}\text{N}$ of eggs were greater than in muscle (ANOVA $F_{1,16} = 61.4$, $P < 0.001$), as were the $\delta^{13}\text{C}$ values (ANOVA $F_{1,16} = 9.55$, $P = 0.007$). For juvenile coho salmon, $\delta^{15}\text{N}$ of white muscle and whole fish was the same (Table 3). There was a difference in $\delta^{13}\text{C}$ between white muscle and whole fish in two out of four ponds, but these differences were small and inconsistent (Table 3). After this trial in July 1999, we used whole juvenile coho minus the gut rather than white muscle, which greatly sped up and simplified sample preparation. Lipids were not extracted from the samples before isotopic analysis.

Differences in stable isotopes between ponds before enrichment

The $\delta^{15}\text{N}$ of juvenile coho salmon and sticklebacks were 1.1–2.0‰ greater in ponds that received spawning coho salmon than in ponds that did not (Table 2). All ponds were included in these comparisons except for NSA and NSB after artificial enrichment. Juvenile coho salmon had mean $\delta^{13}\text{C}$ that was 2.2‰ greater in ponds with spawning salmon than in ponds without. The submerged aquatic macrophytes bur reed, rush, pondweed, and mare's tail all had higher $\delta^{15}\text{N}$ in ponds with spawners than in ponds without spawners ($P < 0.1$), suggesting that enrichment with marine N had occurred. Riparian vegetation (alder and willow) and the emergent sedge were not significantly enriched in ^{15}N ($P > 0.1$).

Stable isotopes of food webs in the different ponds

A wide variety of aquatic and terrestrial invertebrates were potential foods of juvenile coho salmon in the

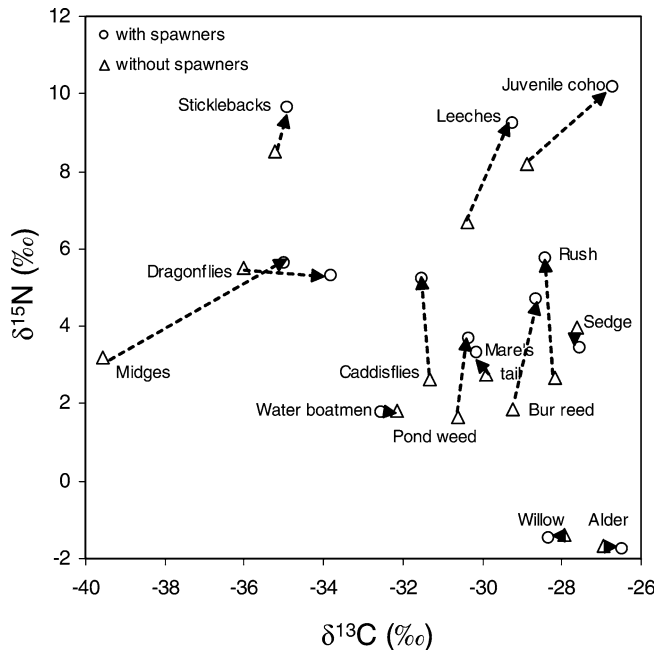


Fig. 3 Response of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in fish, aquatic invertebrates, and aquatic plants to natural coho salmon spawners in beaver ponds of the Copper River Delta, southcentral Alaska. NSA and NSB were excluded after their enrichment with carcasses of adult coho salmon and coho salmon eggs in October and November 2000. Arrows indicate the direction of the response for the same item between ponds with spawners and ponds without spawners

ponds that received spawners naturally (Fig. 2). All had lower $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values than the marine-enriched eggs and muscle of adult coho salmon. In comparison to ponds that did not receive spawners, aquatic animals in the ponds with natural spawners showed increased $\delta^{15}\text{N}$, except for dragonfly larvae and water boatmen (Fig. 3). Dragonfly larvae and water boatmen were more abundant in ponds without spawners than in ponds with spawners (Table 2).

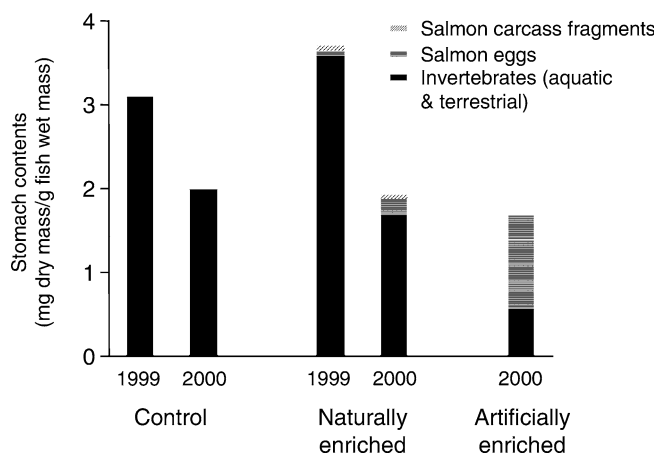


Fig. 4 Stomach contents of juvenile coho in beaver ponds of the Copper River Delta, southcentral Alaska, November 1999 and 2000

Stomach contents of juvenile coho salmon revealed they ate primarily invertebrates, but eggs were a small proportion of their diet in ponds that received spawners naturally (Fig. 4). Egg consumption was much greater in ponds that received artificial additions of eggs and carcasses.

The most plausible foods of sticklebacks from their stable isotopic signatures appeared to be midges and dragonfly larvae. Stomach samples from sticklebacks contained midges and in May 2001, stickleback stable isotopic values were compared to those of their stomach contents. There was sufficient material only for $\delta^{15}\text{N}$ analyses, so $\delta^{13}\text{C}$ analyses were not carried out. The $\delta^{15}\text{N}$ values of the sticklebacks were 3.5–5.4‰ greater than their stomach contents (mean + 4.5‰). The mean stable isotopic signature of the stomach contents with (6.0‰) and without (3.6‰) spawners was close the means for midge larvae from the same ponds (3.2‰ and 5.3‰; Table 2).

The mean $\delta^{15}\text{N}$ values of the aquatic plants pondweed, bur reed, and rush were 1.7–3.1‰ greater in ponds with spawners compared to ponds without spawners (Fig. 3), but the variability and small samples sizes rendered these differences nonsignificant (Table 2).

C and N stoichiometry

Mean N content was higher for coho salmon than for sticklebacks or most invertebrates (Table 4). Leeches, however, had a higher N content (11.0%) than other invertebrates (7.5–9.9%; ANOVA $P \leq 0.009$). Plants were typically low in N (2.0–2.3%). Carbon content was similar across all food web components, except that sticklebacks had a lower mean C content (40.7%) than whole juvenile coho salmon (44.3%; ANOVA $P < 0.001$). Among invertebrates, water boatmen had the highest C content (52.1%). Additions of N and C to ponds NSA and NSB made through the addition of eggs and carcasses were 7–8 g N m⁻² and 22–28 g C m⁻² (Table 5), assuming a water content of 80% (Stephan et al. 1985).

Response of stable isotopes to artificial marine enrichment

Juvenile coho salmon in both ponds showed enrichment in ^{15}N and ^{13}C in response to the additions of eggs and carcasses of adult coho salmon to ponds NSA and NSB in October and November 2000 (Fig. 5, Table 6). Values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ increased by 2–3‰ between these sampling periods. In contrast, juvenile coho salmon in pond NSC (control pond), which did not receive either natural spawners or artificial additions of eggs and carcasses, showed no response in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Although sticklebacks showed increased values of both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in response to the

Table 4 Carbon content of food web components, aquatic macrophytes, and riparian vegetation of beaver ponds of the Copper River Delta, southcentral Alaska

Food web item	Nitrogen content (%DW)		Carbon content (%DW)		C:N ratio
	<i>n</i>	Mean	<i>n</i>	Mean	
Fish					
Coho juvenile muscle	20	12.8	20	45.1	3.5
Coho juvenile whole	336	10.9	336	44.3	4.1
Coho adult muscle	11	14.1	11	46.8	3.3
Coho eggs	7	11.5	7	50.6	4.4
Coho adult muscle and eggs	18	13.1	18	48.2	3.7
Stickleback	296	9.8	295	40.7	4.2
Aquatic invertebrates					
Caddisfly larvae	45	7.5	43	43.4	5.8
Dragonfly nymphs	41	9.9	41	45.6	4.6
Leech	9	11.0	7	45.2	4.1
Midge larvae	18	8.7	16	43.8	5.0
Oligochaete	2	7.8	2	39.0	5.0
Water boatmen nymphs	26	9.0	24	52.1	5.8
Terrestrial invertebrates					
Aphid nymphs and adults	4	7.9	4	48.4	6.1
Lepidoptera larvae	10	8.6	10	49.0	5.7
Slug	2	9.5	2	41.0	4.3
Snail (without shell)	1	9.2	1	37.4	4.1
Aquatic plants					
Bur reed	9	2.0	9	37.5	19.0
Mare's tail	12	2.1	12	39.4	18.5
Potamogeton	13	2.2	13	35.2	16.1
Rush	3	2.0	3	42.8	21.1
Sedge	15	2.0	15	44.2	22.3
Terrestrial plants					
Alder	42	2.3	42	48.9	21.7
Willow	41	2.1	41	47.1	22.1

DW dry weight

Table 5 Contributions of N and C to ponds NSA and NSB through additions of eggs and carcasses of coho salmon in October–November 2000 estimated from N and C content (Table 4), assuming a water content of 80%

Component added	N added (g m ⁻²)		C added (g m ⁻²)	
	NSA	NSB	NSA	NSB
Coho carcass	7.8	6.2	25.8	20.5
Coho eggs	0.5	0.4	2.2	1.8
Total	8.3	6.6	28.0	22.3

additions of carcasses and eggs, these differences were not significant.

Mixing model

The IsoSource mixing model (Phillips and Gregg 2003) was used for ponds with spawners to determine the relative contribution of marine, freshwater, and terrestrial foods. For each individual food source, the IsoSource model provided distributions of stable isotopically feasible contributions to the diet of juvenile coho salmon (Fig. 6). Direct consumption of coho eggs and carcasses contributed 10–50% (1–99 percentiles, mean = 35%) of the diet of juvenile coho salmon in beaver ponds that received spawning adults naturally

(Fig. 6). The remainder of the diet came from aquatic invertebrates such as leeches, caddisfly larvae, midges, and water boatmen (16–82%, mean = 46%), and terrestrial invertebrates such as aphids and lepidopterans (0–38%, mean = 19%). Dragonfly nymphs were omitted from the mixing model analysis because although they were common in ponds without spawners, only two samples were found in ponds with spawners.

Discussion

Natural enrichment

Our study supports the hypothesis that stable isotopic composition of juvenile coho salmon rearing in ponds of

Fig. 5 Response of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in aquatic food webs in beaver ponds on the Copper River Delta to enrichment with carcasses and eggs of adult coho salmon. Means of $n=5$; eggs and carcasses were added to NSA and NSB, but were not added to NSC. Tests of significance between means for November 1999 and November 2000 are shown in Table 6

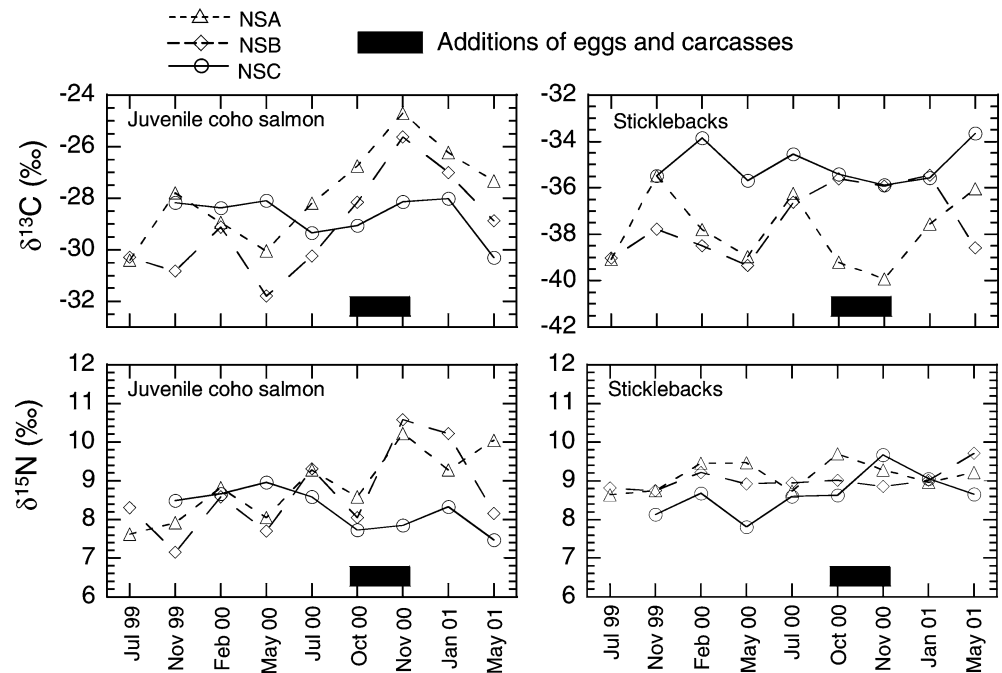


Table 6 Differences between mean stable isotope values ($n=5$ for each pond and year) for juvenile coho salmon and threespine sticklebacks in the Copper River Delta in November 1999 (before enrichment) and November 2000 (after enrichment)

Pond code	Access for spawners	Eggs and carcasses added	Test of significance between Nov 1999 and 2000			
			$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
			$F_{1,8}$	P	$F_{1,8}$	P
Juvenile coho salmon						
NSA	No	Yes	7.83	0.021	7.24	0.025
NSB	No	Yes	24.57	0.001	23.83	0.001
NSC	No	No	0.00	0.950	3.14	0.114
Threespine sticklebacks						
NSA	No	Yes	5.89	0.041	0.81	0.394
NSB	No	Yes	0.91	0.369	0.04	0.840
NSC	No	No	0.20	0.660	10.91	0.006

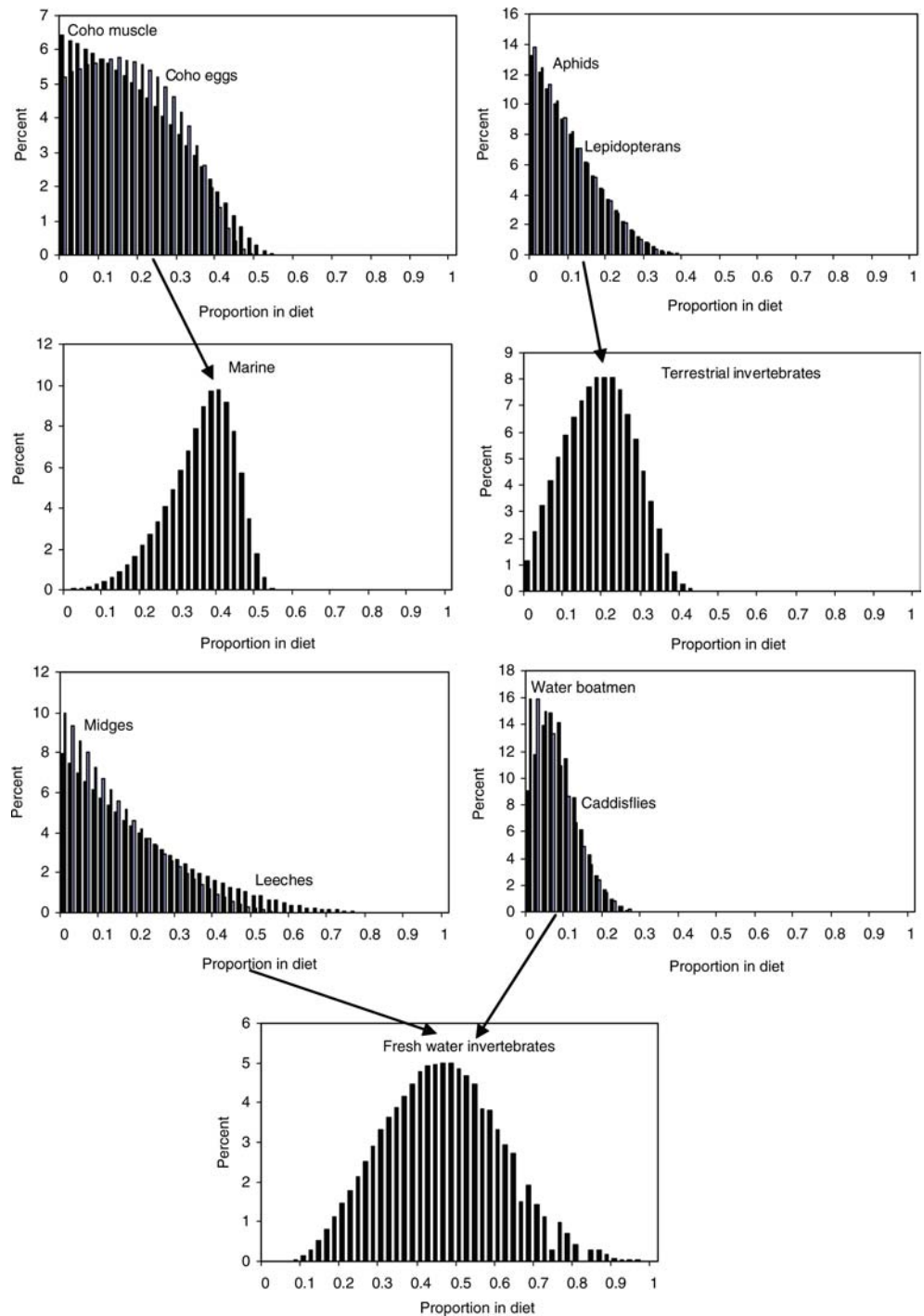
NSA and NSB were enriched with eggs and carcasses in October–November 2000. See Fig. 5

the CRD reflect assimilation of marine N and C from returning coho salmon spawners. Adult coho salmon white muscle and eggs typically had high values of $\delta^{15}\text{N}$, reflecting the marine origin of these elements. Our values for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were very similar to those previously reported lipid-normalized values (e.g., Satterfield and Finney 2002), suggesting that lipid removal was not necessary in our study. Direct consumption of eggs and carcasses of spawning adult coho salmon is of central importance to the diet of juvenile coho salmon. In addition, indirect assimilation of marine nutrients occurred through consumption of midges, caddisfly larvae, water boatmen, and leeches that were themselves enriched with marine N and C. Carcasses of spawning salmon probably increased invertebrate abundance, e.g., Wipfli et al. (1998), though we did not set out to inves-

tigate this. Inputs of marine nutrients to our study ponds mirror on a small scale the massive input of N and C from anadromous sockeye salmon in Lake Iliamna (Kline et al. 1993). However, extrapolated across the entire 80-km-wide CRD the contribution of marine-derived N and C from coho salmon spawners is potentially huge.

Most components of the aquatic food webs of the CRD, including submerged aquatic macrophytes, showed elevated $\delta^{15}\text{N}$ values in the presence of natural spawners. The magnitude of these responses (0.9–2.6‰) was slightly less than differences between streams ecosystems with and without coho salmon spawners in western Washington State (Bilby et al. 1996). In another study, juvenile coho salmon in streams with spawners had $\delta^{15}\text{N}$ values 3–5‰ greater than those in streams

Fig. 6 Frequency distributions of the contribution of individual food sources and aggregated sources (marine, freshwater invertebrates, and terrestrial invertebrates) to the diet of juvenile coho salmon in beaver ponds of the Copper River Delta that received natural coho salmon spawners



without spawners (Bilby et al. 1998). Midges in our study were the most depleted in ^{13}C of any invertebrate, which reflects the wide range of $\delta^{13}\text{C}$ that midges can have (Grey et al. 2004a, b). Sedges, the riparian trees alder and willow, and terrestrial invertebrates in our study did not show a response in $\delta^{15}\text{N}$. Riparian alder and willow had $\delta^{15}\text{N}$ values similar to riparian vegetation not influenced by coho salmon spawners in Washington State (0 to -2‰ ; Bilby et al. 2003). It is possible that contributions of marine N to alder in our study

could have been overridden by internally derived N, because alder is an N fixer. N fixation has little impact on stable isotope ratios (Bilby et al. 2003), and uses atmospheric N_2 ($\delta^{15}\text{N} = 0\text{‰}$; Kohl and Shearer 1980).

The elevation of $\delta^{15}\text{N}$ in riparian vegetation in salmon streams appears to depend on the density and species of salmon. In Washington State, the high spawner densities of chum salmon in Kennedy Creek ($22,000 \text{ fish km}^{-1}$) elevated $\delta^{15}\text{N}$ in riparian vegetation by 3‰ , whereas the lower densities of coho salmon in

Griffin Creek (260 fish km⁻¹) did not elevate $\delta^{15}\text{N}$ in riparian vegetation (Bilby et al. 2003). As mean widths of these streams are about 10 m (Kennedy Creek) and 4 m (Griffin Creek; B. Bilby, personal communication), the carcass loadings would have been about 10.2 and 0.18 kg wet mass m⁻² respectively. However, unspecified riparian vegetation was elevated $\delta^{15}\text{N}$ by +2.9‰ in Grizzly Creek, Washington State, which had coho salmon spawners (Bilby et al. 1996).

In addition to elevated $\delta^{15}\text{N}$, juvenile coho salmon and midges in our study also showed elevated $\delta^{13}\text{C}$ values in ponds with natural spawning coho salmon, reflecting the importance of carcass material as a source of energy and biochemicals such as lipids (Heintz et al. 2004). Midges are the important food of sticklebacks in our study, but the magnitude of the response of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in sticklebacks was only about half that shown by juvenile coho salmon. In addition, the $\delta^{13}\text{C}$ values of sticklebacks were 6–8‰ lower than in coho salmon in the same treatment, probably because of midge consumption. In contrast, threespine sticklebacks in Lake Iliamna had similar stable isotopic values to juvenile sockeye salmon (Kline et al. 1993).

Artificial enrichment

We demonstrated that carcasses and eggs of spawning coho salmon were the source of these marine nutrients by adding adult coho salmon carcasses and eggs to selected rearing habitats that would not otherwise have received such inputs. We achieved a response at lower carcass loadings (0.22–0.28 kg wet mass m⁻²) than in some past studies. For instance, 1.7–2.1 kg wet mass m⁻² of pink salmon was added to an unnamed stream near Margaret Creek, southeastern Alaska (Wipfli et al. 1999). However, pink salmon often have higher spawner densities than coho salmon (Bilby et al. 2003). Carcass loading rates were not given by Bilby et al. (1996), but using their spawner density range of 240–721 fish km⁻¹, assuming mean widths of 5 m for Grizzly Creek and 6 m for East Fork Creek (B. Bilby, personal communication), and mean weight of 2.83 kg for coho salmon spawners (Gresh et al. 2000), the natural carcass loadings were about 0.14–0.25 kg wet mass m⁻² in Grizzly Creek, and 0.34 kg wet mass m⁻² in East Fork Creek. In our study, inputs in the enrichment experiment contributed about half (7–8 g m⁻²) of the annual N input that was observed in a small coniferous stream (15 g m⁻²; Triska et al. 1984). Beaver dams on streams increase N storage by about 1,000 times, per linear meter of stream, compared to riffles. Nitrogen fixation can contribute 5 g m⁻² year⁻¹ (Naiman and Melillo 1984). One potential problem with our study was the broadcast method of distributing the eggs in the artificially enriched ponds, which may have increased the availability of eggs to juvenile coho salmon. In addition, salmon eggs were used as bait in the minnow

traps, and this could have contaminated the juvenile coho salmon samples. However, because tagged (i.e., previously trapped) fish were not used for stable isotopic analysis, and because eggs did not escape from the traps, we believe that this potential problem did not affect the validity of our results.

Mixing models and trophic enrichment

Mixing models applied to freshwater ecosystems inhabited by Pacific salmon in the past have viewed the contributions of various end members as single values that have not reflected the range of possible combinations that might lead to the same stable isotopic values of the assimilating tissue. IsoSource, the mixing model proposed by Phillips and Gregg (2003), does consider the range of possible combinations, but should be considered as a heuristic investigation of the relative importance of different food types (Ben-David and Schell 2001) rather than an exact determination of dietary proportions. Considering the small proportion of lipids in salmon tissue generally, (typically >5%; Ben-David and Schell 2001; Gende et al. 2002), our analysis of whole rather than lipid-extracted tissue is likely to make no difference to our conclusions.

Aquatic invertebrates were the most important foods, followed by direct consumption of marine N and C from coho salmon spawners. Terrestrial invertebrates, which were not enriched by marine nutrients, contributed a significant but lesser proportion of the diet in our study; this was an unpredicted outcome because of the low proportion of pond area covered by riparian vegetation (Lang 2003). Terrestrial invertebrates are an important food source in stream populations of rearing coho salmon, where the influence of riparian vegetation is considerable (Wipfli 1997). In streams of the Prince of Wales Island, southeastern Alaska, terrestrial and aquatic invertebrates were equally important foods (Allan et al. 2003).

Mixing models assume that C and N move through the food web in similar stoichiometry (Phillips and Koch 2002; Post 2002). Wide variations in C:N ratios, for instance, when an omnivore eats both detritus (100:1) and animal prey (6:1), can lead to incorrect interpretation of the relative contribution of different foods. In our study, however, C:N ratios of invertebrate and vertebrate foods were similar (3:1–6:1), so any resultant errors were probably small. The proximity of the C:N ratios of the juvenile coho salmon to that of their foods suggests that the trophic enrichment between a food and its consumer ($\Delta \delta^{15}\text{N}$) should be minimal, justifying our assumption of $\Delta \delta^{15}\text{N} = 2.3\text{‰}$ (McCutchan et al. 2003).

Appropriate values for $\Delta \delta^{15}\text{N}$ and $\Delta \delta^{13}\text{C}$ are of central importance to estimates of the relative contribution of different food sources, and underpins estimates of trophic level (e.g., Kline et al. 1998). A consequence of overestimating $\Delta \delta^{15}\text{N}$ and $\Delta \delta^{13}\text{C}$ is to

underestimate the proportional contribution of the relatively enriched marine sources, and to overestimate the contribution of depleted end members. Kline et al. (1993) assumed a value of 3.4‰ for $\Delta \delta^{15}\text{N}$ and 1.0‰ for $\Delta \delta^{13}\text{C}$, and thus probably underestimated the contribution of marine nutrients. The same applies to Bilby et al. (1996), who assumed a value of 3.0‰ for $\Delta \delta^{15}\text{N}$ and 1.0‰ for $\Delta \delta^{13}\text{C}$. As $\Delta \delta^{15}\text{N}$ is significantly lower for consumers of invertebrates (+1.4‰) compared to consumers of high-protein foods such as vertebrates (+3.3‰), the value of +2.3‰ suggested for McCutchan et al. (2003) for poikilothermic, ammonotelic, or aquatic consumers seems appropriate for our juvenile coho salmon, which consumed both invertebrate and vertebrate foods. We followed the same reasoning in our assumption of +0.4‰ for $\Delta \delta^{13}\text{C}$. We resisted using our measurement of $\Delta \delta^{15}\text{N}$ between sticklebacks and their stomach contents (mean enrichment +4.5‰) because this represents only one season and might not reflect the annualized value. Also, the stable isotopic composition of the stomach contents may simply reflect the ingested food that was not assimilated, and therefore not be a true reflection of the assimilated component.

Ecological significance of marine subsidies on the CRD

Faster growth of juvenile coho salmon in ponds of the CRD that naturally receive spawning coho salmon is one consequence of the marine subsidy, although this response is variable (Lang 2003). Increased growth of juvenile coho salmon also resulted from artificial enrichment with additions of carcasses and eggs to ponds that did not naturally receive spawners (Lang 2003), showing that the increased stable isotopic values resulting from these additions (Fig. 5) have ecological significance. This mirrors increased growth of age-0 coho salmon, cutthroat trout (*Oncorhynchus clarki*), and Dolly Varden (*Salvelinus malma*) in streams as a response to artificial additions of pink salmon in southeastern Alaska (*O. gorbuscha*; Wipfli et al. 2003). Increased growth can have a direct pay-off in evolutionary terms, as larger juvenile coho salmon tend to survive over winter and from smolt to adulthood better than smaller individuals (Hartman and Scrivener 1990). Marine inputs, therefore, are likely to increase inclusive fitness of rearing juveniles.

Marine inputs from coho salmon spawners contributed valuable N and C sources to almost all components of the aquatic food webs of the CRD. In this dynamic and hydrologically complex lowland environment, the benefits of the coho salmon's semelparous life history will be widely distributed. Considering the relatively low spawner density in ponds of the CRD, and the limited period of seasonal availability of eggs and carcasses, the 10–50% contribution from direct consumption is a substantial contribution to the N and C requirements of juvenile coho salmon. This range of proportions is similar to estimates for the marine contribution to the

simpler, single-channel streams in Washington State (Bilby et al. 1996), with an unknown additional amount resulting from indirect assimilation in both systems. Maintenance of this perennial marine subsidy is important in maintaining the productivity of the ecosystem of the coho salmon on the CRD.

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