Seasonal persistence of marine-derived nutrients in south-central Alaskan salmon streams

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Abstract. Spawning salmon deliver annual pulses of marine-derived nutrients (MDN) to riverine ecosystems around the Pacific Rim, leading to increased growth and condition in aquatic and riparian biota. The influence of pulsed resources may last for extended periods of time when recipient food webs have effective storage mechanisms, yet few studies have tracked the seasonal persistence of MDN. With this as our goal, we sampled stream water chemistry and selected stream and riparian biota spring through fall at 18 stations (in six watersheds) that vary widely in spawner abundance and at nine stations (in three watersheds) where salmon runs were blocked by waterfalls. We then developed regression models that related dissolved nutrient concentrations and biochemical measures of MDN assimilation to localized spawner density across these 27 stations. Stream water ammonium-N and orthophosphate-P concentrations increased with spawner density during the summer salmon runs, but responses did not persist into the following fall. The effect of spawner density on $\delta^{15}N$ in generalist macroinvertebrates and three independent MDN metrics ($\delta^{15}N$, $\delta^{34}S$, and $\omega3:\omega6$ fatty acids) in juvenile Dolly Varden (*Salvelinus malma*) was positive and similar during each season, indicating that MDN levels in biota increased with spawner abundance and were maintained for at least nine months after inputs. Delta ^{15}N in a riparian plant, horsetail (*Equisetum fluviatile*), and scraper macroinvertebrates did not vary with spawner density in any season, suggesting a lack of MDN assimilation by these lower trophic levels. Our results demonstrate the ready assimilation of MDN by generalist consumers and the persistence of this pulsed subsidy in these organisms through the winter and into the next growing season.

Key words: Alaska; aquatic macroinvertebrate; Dolly Varden (*Salvelinus malma*); fatty acid; horsetail (*Equisetum fluviatile*); Kenai Peninsula; marine-derived nutrients; seasonal persistence; stable isotopes.

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Introduction

Organisms and material routinely move between habitats, and many of these subsidies are marked by short, intermittent periods of abundance (Polis et al. 1997, Yang et al. 2008). These pulsed subsidies—exemplified by events such as insect mass emergence (Williams et al. 1993) and mast fruiting in plants (Ostfeld et al. 1996)—are readily exploited by generalist consumers due to their ability to switch prey (Ostfeld and Keesing 2000, Sears et al. 2004) and can generate bottom-up perturbations that influence population dynamics and community structure across multiple trophic levels (Yang et al. 2008). When recipient food webs have effective storage mechanisms, the influence of pulsed resources may last far longer than the availability of the resource (Yang et al. 2008).

Annual pulses of marine-derived nutrients (MDN), conveyed to freshwater ecosystems by millions of spawning, semelparous Pacific salmon (*Oncorhynchus* spp.) in the form of eggs, excreta, carcasses, and emergent fry, are an ecologically important energy and nutrient subsidy to stream and riparian ecosystems (Gende et al. 2002, Naiman et al. 2002, Schindler et al. 2003). Where salmon returns remain abundant, MDN subsidies can have ecosystem-wide effects. Dissolved MDN, excreted by live salmon and liberated from decomposing carcasses, can boost periphyton biomass (Wipfli et al. 1998, 1999, Johnston et al. 2004) and leaf litter decomposition (Claeson et al. 2006). The presence of salmon carcasses enhances growth and development rates for taxa that scavenge carcass material (Minakawa et al. 2002, Walter et al. 2006) and is often associated with increased abundance and biomass of aquatic macroinvertebrates (e.g., Wipfli et al. 1998, 1999, Minakawa and Gara 1999, Claeson et al. 2006, Lessard and Merritt 2006). Substrate disturbance during salmon spawning, however, can offset these effects and reduce overall periphyton and macroinvertebrate biomass (Moore and Schindler 2008, Verspoor et al. 2010), especially in streams with fine sediments (Janetski et al. 2009). Growth and energy storage among stream-dwelling fishes is increased by MDN (Bilby et al. 1996, Wipfli et al. 2003, Heintz et al. 2004, Rinella et al. 2012) and the direct consumption of eggs and carcass material appears to be more important than bottom-up pathways for conveying MDN benefits (Scheuerell et al. 2007, Denton et al. 2009, Armstrong et al. 2010). MDN is transferred to the riparian environment by hyporheic processes, flooding, and terrestrial scavengers (Cederholm et al. 1989, Ben-David et al. 1998, Hilderbrand et al. 1999, O'Keefe and Edwards 2002, Quinn et al. 2009), where it enriches riparian soils (Bartz and Naiman 2005, Drake et al. 2005). Riparian vegetation can derive a substantial proportion of nitrogen from this pool (Bilby et al. 2003, Reimchen et al. 2003), which may lead to enhanced growth rates (Helfield and Naiman 2001, 2002; but see Kirchhoff 2003 and Helfield and Naiman 2003).

MDN's ecological importance is demonstrated in cases where the supply has been disrupted, such as the Columbia River basin where dams and habitat degradation have led to the prolonged depression of salmon stocks. Density-dependent mortality has been documented among juvenile Chinook salmon (*O. tshawytscha*), despite the fact that populations have been reduced to a fraction of historic levels, suggesting that nutrient deficits have lowered the carrying capacity of the Columbia River basin (Achord et al. 2003, Scheuerell et al. 2005). Recognizing the importance of MDN to salmon production, fisheries managers are adapting strategies to restore nutrient supplies to salmon-producing ecosystems (Stockner 2003, Michael 2005).

While the ecological importance of MDN has been well established, the persistence of this pulsed subsidy in riverine ecosystems has not been adequately investigated nor has a clear picture emerged from the literature. Studies tracking persistence have generally shown MDN levels to diminish in primary producers (Bilby et al. 1996, Claeson et al. 2006, Holtgrieve et al. 2010, but see Verspoor et al. 2010), macroinvertebrates (Bilby et al. 1996, Claeson et al. 2006, Walter et al. 2006, Honea and Gara 2009), and salmonid fishes (Bilby et al. 1996, Reichert et al. 2008, but see Rinella et al. 2012) over the months following salmon spawning. Additional studies that track MDN across multiple trophic levels and from a range of physiographical settings will help ecologists come to a general understanding of the factors that regulate MDN persistence in salmon streams. Studies that

rely on spatial variation in spawner abundance across multiple watersheds (e.g., Holtgrieve et al. 2010, Verspoor et al. 2010, 2011, Rinella et al. 2012) are particularly useful because they avoid the artificiality sometimes present in manipulative studies while allowing broader inferences to be drawn from the data.

The goal of this research was to better understand the seasonal persistence of MDN resources in stream food webs. To accomplish this, we examined the effect of a 27-station (in nine watersheds) gradient in spawner density on dissolved nutrient concentrations and measures of MDN assimilation in aquatic and riparian biota across three seasons. We modeled the effects of spawner density during summer and fall to examine MDN presence during and shortly after the spawning season, and during spring to indicate overwinter persistence of MDN from the previous year's spawning run. For biota, we focused our efforts on stream-resident Dolly Varden (*Salvelinus malma*), a generalist predator, due to their near ubiquitous distribution in coastal Alaskan streams; selected aquatic macroinvertebrates (both primary consumers and generalists) common in Alaska streams; and a widespread riparian plant, horsetail (*Equisetum fluviatile*).

Methods

Study sites

We collected field data at three stations in each of three watersheds within three geomorphically distinct regions on the Kenai Peninsula, Alaska ($N = 27$ stations; Fig. 1) during 2005. Streams within a given region were in relatively close proximity and were geomorphologically similar to the extent possible (i.e., similar basin area, elevation, channel slope). Each region contained two salmon streams where salmon escapement (i.e., the number of fish that escape fisheries and return to spawn) was monitored by the Alaska Department of Fish and Game (ADF&G) and one salmon-free reference stream where spawning runs were blocked by waterfalls (Table 1).

Cooper Landing area streams.—The Cooper Landing study streams are within the Kenai River basin, the Kenai Peninsula's largest watershed, which supports substantial commercial, subsistence, and sport fisheries. Sockeye are the dominant salmon, and their young rear in the watershed's many low-elevation, accessible lakes. Study streams consisted of the Russian River and Quartz Creek as salmon-bearing streams and Juneau Creek as a salmon-free reference (Table 1). These streams are in the Chugach–St. Elias Mountains ecoregion (Nowacki et al. 2001) that has a continental climate with approximately 64 cm of annual precipitation (Brabets et al. 1999). Underlying geology is primarily metamorphic, volcanic, and igneous rock (Brabets et al. 1999) and, as such, these streams had relatively low concentrations of primary nutrients. These streams have gently sloped mainstem channels that drain mixed spruce (*Picea* spp.) and birch (*Betula papyrifera*) forest with steep tributaries that drain alpine basins.

The Russian River system receives two spawning runs of sockeye salmon (*O. nerka*) each year. The early run, which averages 49,000 fish, arrives during the second half of June and the late run, which averages 87,000 fish, arrives from mid-July to mid-August (1996–2005 data; ADF&G 2006). The Russian River also receives much smaller numbers of Chinook and coho (*O. kisutch*) salmon. Quartz Creek typically receives between 1000 and 20,000 sockeye salmon that spawn from mid to late August and a small number of Chinook salmon (<100 fish) that spawn prior to the sockeye salmon (ADF&G, *unpublished data*). Juneau Creek has a waterfall ~3 km upstream of its confluence with the Kenai River which blocks salmon access to most of the basin, and all sampling stations on Juneau Creek were located above this barrier.

Homer area streams.—The Homer-area streams consisted of the North Fork Anchor River and the South Fork Anchor River as salmon-bearing streams and Happy Creek as a salmon-free reference (Table 1). This area is in the Cook Inlet Basin ecoregion (Nowacki et al. 2001) and has a climate transitional between maritime and continental with approximately 57 cm annual precipitation (Brabets et al. 1999). Streams in this area drain extensive unconsolidated glacial deposits and proglacial lake sediments (Selkregg 1974), which results in relatively high ambient nutrient concentrations. The uplands consist of rolling white spruce (*Picea glauca*) forest while riparian vegetation is typically mixed cottonwood (*Populus* spp.) and spruce along the lower alluvial
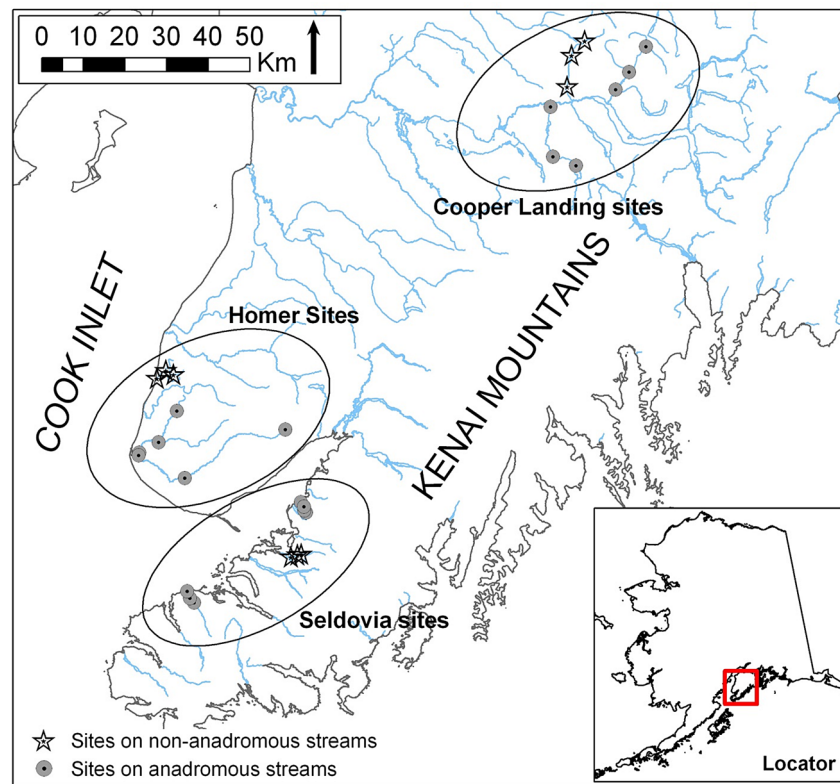
Fig. 1. Study streams and sampling stations on the Kenai Peninsula, Alaska.

stream reaches, giving way to poorly drained soils dominated by willow (*Salix* spp.) and herbaceous plants in the upper reaches. There are no significant lakes in this area, but wetlands comprise about 20% of the watershed (Mauger 2005).

On average, the Anchor River system receives runs of about 8000 of each Chinook and coho salmon plus around 2700 pink salmon (*O. gorbuscha*) (2004–2010 average; Szarzi et al. 2010). Happy Creek has no anadromous runs due to an impassible waterfall at tidewater.

Table 1. Physical characteristics and total spawner biomass for the nine study streams in three regions on the Kenai Peninsula, Alaska.

Stream	Watershed area (km²)	Length of salmon spawning (km)	Latitude (WGS84)	Longitude (WGS84)	Spawner biomass (MT)	
					2004	2005
Cooper Landing						
Juneau	146	0	−149.8961	60.5203	0	0
Quartz	322	19	−149.6852	60.5059	31	13
Russian	166	26	−149.9749	60.4782	382	222
Homer						
Happy	29	0	−151.7396	59.9359	0	0
N.F. Anchor	180	27	−151.8265	59.7766	18	21
S.F. Anchor	373	72	−151.8289	59.7711	97	123
Seldovia						
China Poot	28	0	−151.1948	59.5413	0	0
Barabara	56	11	−151.6426	59.4753	8	22
Humpy	28	6	−151.1434	59.6576	49	148

Note: MT = metric tons.

Table 2. Sampling dates for the three Kenai Peninsula study regions.

| | Sampling dates (2005) | | |
Region	Spring	Summer	Fall
Cooper Landing	6/1–6/16	8/20–9/9	10/2–10/14
Homer	5/12–5/28	8/10–8/23	10/7–10/26
Seldovia	6/22–7/8	9/8–9/21	no samples

Seldovia area streams.—In the Seldovia region, we sampled Humpy and Barabara creeks in addition to China Poot Creek as a salmon-free reference (Table 1). This area is in the Gulf of Alaska Coast ecoregion (Nowacki et al. 2001) and has a maritime climate with approximately 140 cm annual precipitation (Brabets et al. 1999). Underlying geology is primarily metamorphic, volcanic, and igneous rock (Brabets et al. 1999), giving these streams relatively low concentrations of primary nutrients. Streams in this area drain short, steep watersheds that flow directly into Kachemak Bay. Vegetation is dominated by white spruce and Sitka spruce (*P. sitchensis*), giving way to extensive alder (*Alnus* spp.) stands at higher elevations.

Humpy Creek receives a small run of chum salmon (*O. keta*) that spawn in early August and a sizeable run of pink salmon that spawn during mid to late August. Barabara Creek receives a run of pink salmon that spawn during late August. Average pink salmon escapement to Humpy and Barabara creeks based on ADF&G ground surveys is 47,300 and 4900 fish, respectively (1960–2006 average; Hammarstrom and Ford 2008). Salmon runs to China Poot Creek are blocked by a waterfall approximately 2 km above tidewater.

Field sampling

We established three sampling stations within each of the nine watersheds: one near the stream mouth, one near the geographic middle of the mainstem, and one in the upper reaches. At each station, we conducted biological sampling over a reach of approximately 150 m. Due to the lack of road access in most of the watersheds, we chose the exact sampling locations based on ease of hiking or floatplane access.

We sampled each stream in spring prior to the initiation of spawning runs, during the peak summer spawning period, and (for Cooper Landing and Homer area streams) again during the fall. Because each region differed in the dominant spawning salmon species, we shifted summer and fall sampling to ensure that summer sampling coincided with peak salmon spawning and that fall sampling coincided with a period of post-spawn carcass decomposition (Table 2). During station visits, we collected water samples for analysis of dissolved nutrient concentrations (Table 3) and collected samples of horsetail, select macroinvertebrate taxa, and Dolly Varden for biochemical analyses of MDN assimilation.

We chose the perennial horsetail as a riparian plant because it grew at or near the wetted margin of every study reach (Table 4). We gathered five individual horsetail stems from locations dispersed over the sampling reach; all stems were growing in shallow water or in saturated soil close to the stream margin.

For macroinvertebrates, we collected dominant taxa of immature aquatic insects representing two functional feeding groups, taking care to collect the same taxa across all streams in a given sampling event when possible. We collected scrapers (i.e., primary consumers; typically the caddidfly *Glossosoma* sp. or the mayfly *Drunella doddsi*) and generalists (limnephilid caddiflies *Ecclisomyia conspersa* and *Psychoglypha* sp. or the stonefly *Pteronarcella* sp.). These feeding groups were found at most stations (Table 4). We collected scrapers by hand picking them from cobbles in riffle habitats and generalists by kick netting in depositional areas.

We chose Dolly Varden as our focal fish species because they are widely distributed in the study area, occurring in salmon streams and above barriers in many salmon-free streams. We collected one to eight juvenile Dolly Varden per station per sampling event (Table 5) using minnow traps baited with salmon roe. The salmon roe was contained in perforated plastic bags to prevent consumption by trapped fish. When excess fish were captured, we retained individuals that spanned the size range observed

Table 3. Dissolved nutrient concentrations from the 27 sampling stations across three seasons.

Stream	Station	NH$_4$-N (µg/L)			PO$_4$-P (µg/L)		
		Spring	Summer	Fall	Spring	Summer	Fall
Juneau (salmon-free)	lower	4.51	4.78	3.09	0.35	0.45	0.19
	middle	2.79	3.57	2.58	0.59	0.64	0.65
	upper	1.28	2.44	2.31	0.05	0.19	0.31
Quartz	lower	0.94	39.95	8.40	1.37	8.45	2.32
	middle	0.30	3.62	2.34	1.48	2.04	1.63
	upper	0.52	4.15	6.04	2.58	1.21	2.88
Russian	lower	5.10	. . .	12.69	1.15	14.44	1.98
	middle	2.97	19.64	9.57	0.53	1.41	0.61
	upper	6.37	3.71	4.74	1.38	1.20	1.08
Happy (salmon-free)	lower	10.80	2.10	19.70	8.00	28.33	22.19
	middle	10.29	28.92	17.86	10.59	31.96	19.21
	upper	7.92	12.50	22.46	2.65	6.42	3.56
N.F. Anchor	lower	0.09	5.47	. . .	23.06	65.37	. . .
	middle	12.66	19.38	. . .	27.58	106.45	. . .
	upper	1.14	5.29	17.42	51.98	73.75	43.24
S.F. Anchor	lower	5.25	16.09	. . .	19.81	81.64	. . .
	middle	1.40	27.54	17.04	38.25	90.11	39.87
	upper	20.01	2.44	3.03	8.69	20.85	8.31
China Poot (salmon-free)	lower	1.16	4.84	. . .	0.04	0.47	...
	middle	0.70	32.99	. . .	0.04	2.23	...
	upper	0.11	1.86	. . .	0.04	0.63	...
Barabara	lower	1.93	7.19	. . .	0.60	1.09	...
	middle	0.10	4.35	. . .	0.26	2.70	...
	upper	1.49	3.45	. . .	0.16	0.41	...
Humpy	lower	1.47	1542.21	. . .	0.04	148.77	...
	middle	0.10	487.93	. . .	0.04	121.41	...
	upper	3.38	. . .	. . .	0.04	. . .	...

Notes: $N = 1$ per station and season. Seldovia-area streams were not sampled during the fall; other missing data did not meet laboratory holding times and were not analyzed.

at that station. Across all streams, fork length ranged from approximately 50 to 150 mm.

We were unable to collect all the samples we targeted. Seldovia area streams are accessible only by boat or aircraft and inclement weather prevented us from accessing this area during the fall. We did not collect horsetail during the fall sampling period because it had senesced and we expected this would alter the nitrogen isotopic composition. We found no Dolly Varden in China Poot Creek. Additional missing data are due to unavailability of some taxa at the time of sampling, missed holding times, and other logistical problems (Tables 3, 4, and 5).

We filtered water samples in the field with a syringe and 0.45-µm filter (Whatman, Maidstone, Kent, UK) and kept them cool until delivery to the lab. We kept all biological samples on ice or on liquid nitrogen in cases where field storage time exceeded several hours; in the lab, we stored samples in a −70°C ultra-cold freezer until processed. We analyzed Dolly Varden and horsetail stems individually but, because of mass constraints for analytical measurements, we analyzed composite samples of at least 10 individual macroinvertebrates. We thawed the Dolly Varden long enough to homogenize and split into subsamples for stable isotope and fatty acid analyses. All samples for stable isotope analyses (i.e., fish homogenate, horsetail stems, macroinvertebrate composites) were first oven dried (48 hours at 65°C) and pulverized. Fish homogenate for fatty acid analysis was re-frozen −70°C) until analysis.

Laboratory analyses

We used three separate biochemical measures of MDN assimilation. We measured nitrogen stable isotopes (δ^{15}N) in horsetail, scraper and generalist macroinvertebrates, and Dolly Varden, and additionally measured sulfur stable isotopes (δ^{34}S) and fatty acid composition in Dolly Varden. Delta ^{15}N has been used extensively to measure incorporation of MDN in freshwater food webs (e.g., Kline et al. 1990, Bilby et al. 1996, Chaloner et al. 2002, Scheuerell et al. 2007). Delta ^{15}N in adult salmon (typically 10–15‰; reviewed in Johnson and Schindler 2009) is enriched

Table 4. Delta ^{15}N values for horsetail and macroinvertebrates from the 27 sampling stations across three seasons.

| | | Horsetail δ^{15}N (‰) | | Macroinvertebrate δ^{15}N (‰) | | | | | |
| | | | | Scraper | | | Generalist | | |
Stream	Station	Spring	Summer	Spring	Summer	Fall	Spring	Summer	Fall
Juneau (salmon-free)	lower	2.0	. . .	4.5	2.4	4.3	2.4	3.0	1.2
	middle	1.5	1.2	3.4	1.0	0.5	3.4	2.7	1.8
	upper	0.9	2.5	...	2.9	3.4	3.1	3.4	3.9
Quartz	lower	1.9	0.5	4.6	5.5	7.0	3.6	6.0	7.9
	middle	−0.2	0.8	2.5	3.0	1.1	2.0	...	2.9
	upper	−1.2	0.9	2.6	3.6	3.5	−1.3	3.1	2.7
Russian	lower	2.0	6.5	7.2	6.1	...	5.6	6.2	7.6
	middle	5.9	5.6	5.7	4.6	8.1	4.4	5.4	...
	upper	9.5	9.5	2.9	1.4	...	3.7	7.5	5.1
Happy (salmon-free)	lower	2.6	2.0	5.6	8.0	7.5	...	...	5.6
	middle	2.6	2.6	4.3	8.1	...	2.3	...	...
	upper	0.3	3.0	...	7.1	...	3.5	4.9	2.6
N.F. Anchor	lower	...	5.0	8.3	7.0	...	6.6	6.3	2.5
	middle	1.7	5.5	...	9.5	6.5	...	...	4.9
	upper	0.0	0.8	...	...	...	...	3.7	4.0
S.F. Anchor	lower	...	3.7	7.0	8.3	...	5.4	5.5	4.9
	middle	4.4	3.4	4.6	7.2	7.4	3.9	5.9	...
	upper	3.5	4.1	4.7	4.9	5.5	...	5.3	...
China Poot (salmon-free)	lower	...	−0.3	...	...	...	0.9	...	...
	middle	...	−0.9	0.2	...	...	...	−1.9	...
	upper	−1.7	−0.9	...	−0.4	...	0.5	1.0	...
Barabara	lower	1.5	0.6	0.3	4.6	...	...	...	...
	middle	−1.4	0.3	...	−0.1	...	...	0.8	...
	upper	2.0	0.1	...	0.5	...	...	0.1	...
Humpy	lower	2.3	2.5	2.7	...	...	3.7	...	...
	middle	0.1	1.5	...	...	...	1.0	5.7	...
	upper	−0.5	...	3.6	...	...	2.1	...	...

Notes: $N = 5$ per station and season for horsetail. $N = 1$ composite sample per station and season for macroinvertebrates. Seldovia-area streams were not sampled during the fall and horsetail was not sampled at any of the stations during the fall; other missing data were due to unavailability at the time of sampling or logistical problems.

relative to freshwater sources (e.g., 0 to 9, depending on trophic level; Kline et al. 1990), creating an isotopic disparity that can be used to measure the relative contribution of marine and freshwater nutrient pools. Isotopic differences also exist between marine and freshwater sulfur (sulfate and organic sulfur) and we expected that δ^{34}S would track MDN assimilation in biota, although it has not been extensively tested for this purpose. Limited available data show δ^{34}S from adult Pacific salmon to range between 18 and 20‰ ($N = 20$; C. A. Stricker, *unpublished data*) and values in freshwater systems are typically much lower (e.g., $< −10$; Hesslein et al. 1991). Thus, both stable isotope systems have marine endmembers that are enriched in the heavier isotope, but endmember separation tends to be much larger for δ^{34}S, which is a useful characteristic for those interested in making quantitative diet estimates using mixing models as increased separation should yield higher resolution (Newsome et al. 2007). Another potential

advantage of δ^{34}S for tracking MDN is that δ^{15}N of consumer tissues reflects the nitrogen source, but it also increases with trophic level (DeNiro and Epstein 1981, Minagawa and Wada 1984), body condition, and dietary protein (Adams and Sterner 2000, Martinez del Rio et al. 2009), potentially confounding variation in diet or nutritional status with MDN assimilation. Sulfur isotopes, borne on two essential amino acids (methionine and cysteine), are a conservative diet tracer unaffected by trophic position (Hesslein et al. 1991, Barnes and Jennings 2007).

Fatty acid analysis is another method for understanding food web relationships that can be used to track MDN. Fatty acids ingested by consumers, unless directly catabolized for energy, are stored in lipid reserves with little or no modification; thus the fatty acid composition of a consumer reflects that of its food sources (Iverson et al. 2004). Production of different polyunsaturated fatty acids by freshwater (including riparian) and marine producers leads to distinct fatty

Table 5. Dolly Varden $\delta^{15}N$, $\delta^{34}S$, and $\omega3{:}\omega6$ values (and sample sizes) for the 27 sampling stations across three seasons.

Stream	Station	Dolly Varden $\delta^{15}N$ (‰)			Dolly Varden $\delta^{34}S$ (‰)			Dolly Varden $\omega3{:}\omega6$		
		Spr. (N)	Sum. (N)	Fall (N)	Spr. (N)	Sum. (N)	Fall (N)	Spr. (N)	Sum. (N)	Fall (N)
Juneau (salmon-free)	lower	...	6.2 (3)	7.8 (4)	...	−1.2 (3)	−2.2 (4)	...	4.9 (3)	2.2 (3)
	middle	...	6.2 (4)	6.5 (3)	...	−0.2 (4)	−1.2 (1)	...	3.4 (3)	2.5 (2)
	upper	6.7 (4)	7.8 (2)	...	−3.1 (4)	−2.8 (2)	...	2.2 (4)	1.8 (2)	...
Quartz	lower	11.6 (5)	11.4 (5)	...	11.1 (5)	11.5 (5)	...	8.2 (3)	10.4 (3)	...
	middle	8.4 (5)	7.9 (5)	...	0.5 (5)	0.9 (3)	...	5.1 (3)	6.2 (3)	...
	upper	9.1 (5)	7.6 (5)	7.1 (5)	0.8 (5)	−1.0 (5)	−2.0 (5)	7.5 (3)	5.4 (3)	5.8 (3)
Russian	lower	12.3 (2)	12.7 (1)	11.6 (1)	10.0 (2)	14.9 (1)	12.6 (1)	8.5 (2)	11.7 (1)	11.6 (1)
	middle	...	11.1 (1)	...	...	8.0 (1)	...	...	5.7 (1)	...
	upper	11.5 (3)	11.6 (4)	12.0 (5)	9.3 (3)	9.5 (4)	11.6 (5)	5.9 (3)	6.1 (4)	7.5 (5)
Happy (salmon-free)	lower	8.7 (3)	9.0 (2)	9.3 (3)	11.2 (3)	11.3 (2)	11.4 (3)	2.1 (3)	2.6 (2)	2.5 (3)
	middle	7.8 (6)	8.3 (5)	7.5 (5)	10.6 (6)	11.8 (5)	11.6 (5)	2.2 (2)	4.0 (3)	2.0 (3)
	upper	7.9 (3)	7.6 (6)	7.8 (5)	12.0 (3)	12.3 (6)	12.3 (5)	1.5 (3)	1.3 (3)	1.2 (3)
N.F. Anchor	lower	9.1 (2)	...	...	11.7 (2)	...	...	3.4 (2)	...	...
	middle	10.1 (3)	...	11.1 (1)	11.6 (3)	...	13.1 (1)	4.2 (3)	...	9.5 (1)
	upper	8.0 (8)	8.9 (5)	9.9 (5)	12.7 (8)	12.2 (5)	12.1 (5)	1.3 (4)	4.3 (5)	6.5 (5)
S.F. Anchor	lower	11.1 (2)	9.9 (1)	9.0 (1)	12.3 (2)	11.4 (1)	12.2 (1)	4.7 (2)	3.8 (1)	4.9 (1)
	middle	9.5 (3)	8.8 (5)	9.0 (1)	10.2 (3)	11.7 (5)	11.4 (1)	4.6 (3)	5.1 (3)	2.9 (1)
	upper	8.3 (3)	8.0 (3)	8.0 (5)	10.7 (3)	10.4 (3)	10.4 (5)	2.3 (3)	2.4 (3)	2.8 (4)
Barabara	lower	6.4 (3)	9.2 (5)	...	−1.2 (3)	3.1 (5)	...	3.5 (3)	9.7 (3)	...
	middle	4.7 (3)	5.1 (5)	...	−5.1 (3)	−4.5 (5)	...	7 (3)	5.5 (3)	...
	upper	4.9 (3)	5.1 (5)	...	−3.4 (3)	−3.6 (5)	...	5.1 (3)	5.4 (3)	...
Humpy	lower	9 (5)	10.6 (5)	...	−1.3 (5)	2.4 (5)	...	3.3 (3)	3.9 (3)	...
	middle	...	11.1 (5)	...	...	6.9 (3)	...	...	7.3 (3)	...
	upper	8.3 (5)	...	...	−2.8 (3)	...	...	3.2 (3)	...	...

Notes: Spr. = spring, Sum. = summer. Seldovia-area streams were not sampled during the fall and no Dolly Varden were found in China Poot Creek; other missing data were due to unavailability at the time of sampling or logistical problems.

acid signatures for marine and freshwater consumers (Ackman 1999, Napolitano 1999). This disparity is evident in the relatively high ratio of $\omega3$ to $\omega6$ fatty acids in marine fishes (4.7–14.4) relative to freshwater fishes (0.5–3.8) (Henderson and Tocher 1987). Likewise, $\omega3{:}\omega6$ for eggs and flesh from Chinook salmon spawning in the Anchor River ranged from 12.1–13.9 and 5.1–7.3, respectively, reflecting the marine origin of these tissues ($N = 5$; R. A. Heintz, *unpublished data*). The fatty acid signatures of freshwater fish that assimilate MDN also come to reflect the marine source, allowing for inferences regarding the contribution of MDN to consumer diets (Heintz et al. 2004, 2010, Volk 2004).

Stable isotope analyses were conducted at the U.S. Geological Survey stable isotope laboratory in Denver, Colorado. Homogenized samples were weighed into tin capsules (5 × 9 mm) and $\delta^{15}N$ and $\delta^{34}S$ were determined by continuous flow-isotope ratio mass spectrometry. Nitrogen isotope ratios were measured using a Carlo Erba NC1500 elemental analyzer (Thermo Scientific, Waltham, Massachusetts, USA) interfaced to a Optima mass spectrometer (Micromass, Manchester, UK) (Fry et al. 1992). Approximately 1–2 mg of vanadium pentoxide (V_2O_5) was added to each tin capsule as a combustion aid for the measurement of sulfur isotope ratios using an ECS4010 elemental analyzer (Costech Analytical Technologies, Valencia, California, USA) interfaced to a Thermo-Finnigan DeltaPlus XP mass spectrometer (Giesemann et al. 1994). Results are reported in δ-notation as deviations in parts per thousand (‰) relative to a monitoring gas as follows:

$$\delta X = (R_{sample}/R_{standard}) - 1 \qquad (1)$$

where X is the rare isotope (^{15}N, or ^{34}S) and R is the appropriate isotope ($^{15}N/^{14}N$ or $^{34}S/^{32}S$) ratio. Nitrogen isotopic compositions were normalized to USGS 40 ($\delta^{15}N = -4.52$‰) and USGS 41 ($\delta^{15}N = 47.57$‰) and reported relative to the internationally accepted scale, air. Sulfur isotopic compositions were normalized to NBS 127 (21.1‰) and IAEA-SO-6 (−34.05‰) and reported relative to the internationally accepted scale, V-CDT. Analytical error was ±0.2‰.

Dolly Varden fatty acid composition was measured at the National Marine Fisheries Service laboratory in Juneau, Alaska. Lipid was extracted from 0.5 to 1.0 g of wet sample homogenate using a modification of Folch's method outlined by Christie (2003). The purified lipid was spiked with C19:0 and C23:0 fatty acids which acted as an internal standard and a surrogate standard, respectively and then transesterified to fatty acid methyl esters (FAMEs). The FAMEs injected into a cyanopropyl-bonded fused silica column in a CP3800 gas chromatograph equipped with Saturn model 2200 mass spectrometer (Varian, Palo Alto, California, USA) operating in selective ion storage mode. Fatty acid concentrations were determined using five-point calibration curves for each FAME normalized to the internal standard recovery. Blank, duplicate and reference (NIST Standard reference material number 1946) sample spectra were used for QA evaluation.

Water samples were analyzed by Cook Inletkeeper's water quality lab in Homer, AK according to standard methods (APHA 2005) on a Technicon Autoanalyzer II (SEAL Analytical, Mequon, Wisconsin, USA). The phenelate method was used to determine NH_4-N (ammonium-N) concentrations and the ammonium molybdate method was used to determine PO_4-P (orthophosphate-P) concentrations.

Quantifying spawner abundance

We quantified MDN abundance as local spawner density (LSD), expressed in MT (metric tons)/km or, equivalently, kg/m. Estimates of LSD were based on ADF&G escapement monitoring for each of the salmon streams. ADF&G used weirs to census escapement to the Russian River (ADF&G 2006) and the North and South Forks of the Anchor River (Kerkvliet et al. 2008); repeated ground surveys to estimate escapement on Humpy and Barabara creeks (Hammarstrom and Ford 2008); and annual ground surveys to estimate escapement on Quartz Creek (ADF&G, *unpublished data*). We divided escapement by the length of stream used by spawning salmon, approximated from ADF&G's anadromous waters catalog (ADF&G 2005) to give stream-specific estimates of spawner densities. To account for within-stream variation in spawner abundance, we conducted several ground sur-

Table 6. Local spawner density during 2004 and 2005 at sampling stations on the nine study streams in three regions.

Stream	Station	Local spawner density (MT/km)	
		2004	2005
Cooper Landing			
Juneau	lower	0	0
	middle	0	0
	upper	0	0
Quartz	lower	2	1
	middle	0.8	0.3
	upper	0.8	0.3
Russian	lower	22	13
	middle	7	4
	upper	22	13
Homer			
Happy	lower	0	0
	middle	0	0
	upper	0	0
N.F. Anchor	lower	0.3	0.4
	middle	0.3	0.4
	upper	0.3	0.4
S.F. Anchor	lower	2	3
	middle	2	3
	upper	0.7	0.8
Seldovia			
China Poot	lower	0	0
	middle	0	0
	upper	0	0
Barabara	lower	1	3
	middle	0.4	1
	upper	0.4	1
Humpy	lower	8	23
	middle	8	23
	upper	8	23

Note: MT = metric tons.

veys over a 500-m stream reach at each salmon-bearing station and, at stations where our surveys deviated substantially from the stream-specific spawner density estimates, we adjusted spawner densities accordingly. We used year-specific average mass for individuals of each species (Hammarstrom and Ford 2008, Kerkvliet et al. 2008) to convert spawner densities into biomass.

We used 2005 salmon spawner data as predictors for MDN measures in samples collected during summer and fall. Since our spring sampling was conducted prior to the onset of the 2005 spawning runs, we used 2004 spawner data as predictors for these samples. LSD in salmon streams ranged from 0.3–22 MT/km in 2004 and from 0.3–23 MT/km in 2005 (Table 6). There is undoubtedly some error associated with estimates of LSD, but given the nearly two order of magnitude range observed across the study

Table 7. Ranking of a priori models for dissolved nutrients and stable isotopes and fatty acids in biota.

Dependent variable	Model	K	AIC_c	ΔAIC_c	w_i
log NH_4-N	intercept + LSD + region + season + (LSD × season)	10	115.59	0	0.82
	intercept + LSD + region + season	8	119.22	3.64	0.13
log PO_4-P	intercept + LSD + region + season + (LSD × season)	10	88.75	0	1.00
Horsetail $\delta^{15}N$	intercept + LSD + region	6	202.79	0	0.20
	intercept + LSD + region + season	7	202.95	0.16	0.19
	intercept + season	4	203.09	0.29	0.18
Scraper $\delta^{15}N$	intercept + LSD + region	6	208.44	0	0.55
	intercept + region	5	209.75	1.31	0.28
	intercept + LSD + region + season + (LSD × season)	10	212.08	3.63	0.09
	intercept + LSD + region + season	8	212.91	4.47	0.06
Generalist $\delta^{15}N$	intercept + LSD + region	6	205.53	0	0.49
	intercept + LSD + region + season	8	206.14	0.60	0.36
	intercept + LSD + region + season + (LSD × season)	10	207.90	2.37	0.15
Dolly Varden $\delta^{15}N$	intercept + LSD + region + fork length	7	183.13	0	0.46
	intercept + LSD + region	6	185.50	2.37	0.14
	intercept + LSD + region + fork length + (LSD × fork length)	8	185.65	2.52	0.13
	intercept + LSD + fork length	5	185.78	2.64	0.12
Dolly Varden $\delta^{34}S$	intercept + LSD + region + fork length + (LSD × fork length)	8	275.42	0	0.71
	intercept + LSD + region + fork length + season + (LSD × fork length)	10	279.19	3.77	0.11
	intercept + LSD + region	6	279.59	4.17	0.09
	intercept + LSD + region + fork length	7	280.73	5.31	0.05
Dolly Varden ω3:ω6	intercept + LSD + fork length + (LSD × fork length)	6	232.73	0	0.59
	intercept + LSD + fork length + season + (LSD × fork length)	8	234.58	1.85	0.24
	intercept + LSD + region + fork length + (LSD × fork length)	8	236.72	3.99	0.08

Notes: LSD = local spawner density. In addition to the parameters listed, all models contained stream as a random intercept. Models are ranked by AIC_c for each dependent variable and only top-performing models (i.e., those with $w_i \geq 0.05$) are shown.

streams, we feel our estimates gave relative approximations of spawner abundance with enough accuracy to meet our research objectives.

Data analysis

We defined an a priori set of linear regression models that corresponded to hypotheses regarding the influence of environmental factors on dissolved nutrient concentrations and biotic stable isotope and fatty acid signatures. We used Akaike's Information Criterion (adjusted for small sample size, AIC_c; Akaike 1973, Burnham and Anderson 2002) to rank and weight the models in the candidate set and then calculated model-averaged estimates—i.e., a weighted average of the estimates made by every model in the set—with unconditional standard errors (Burnham and Anderson 2002). We used package AICcmodavg (Mazerolle 2011) in the statistical platform R (R Development Core Team 2011) for the analyses, using each sampling event within each station as an experimental unit. Because multiple fish and horsetail samples were analyzed for each station, we averaged the data from

each at a given station on a given date (Tables 4 and 5). Dissolved nutrient data (i.e., NH_4-N and PO_4-P) required log transformation to meet model assumptions.

For Dolly Varden, our model set expressed $\delta^{15}N$, $\delta^{34}S$, and ω3:ω6 as a function of LSD (MT/km), region, fork length, season, and the interactions season x spawner abundance and fork length × spawner abundance. Our Dolly Varden model set was identical for all three dependent variables and consisted of the global model and all possible subsets of independent variables and interaction terms for a total of 25 candidate models. For macroinvertebrate $\delta^{15}N$, horsetail $\delta^{15}N$, and log-transformed dissolved nutrient concentrations, our model set expressed dependent variables as a function of LSD, region, season, and the interaction season × LSD. This model set consisted of the global model and all possible subsets of the independent variables and the interaction term for a total of nine candidate models. In addition, we included stream as a random intercept in each model to account for any stream effects. We confined interaction terms

to models where both interacting effects were also present as main effects. We included season × spawner abundance interaction terms to allow dependent variables to be constant in salmon-free streams but to vary in response to seasonal fluctuations in MDN availability in salmon-bearing streams. We included the fork length x spawner abundance interaction term because we hypothesized that larger Dolly Varden may assimilate more MDN than smaller individuals. Since we were interested in seasonal variation in the effect of spawning salmon abundance on our dependent variables, we plotted model-averaged estimates (±2 unconditional SE ≈ 95% CI) of the LSD effect (5 levels representing the observed range of LSD) for each season, holding all other predictors constant (i.e., region = Cooper Landing, fork length = 100 mm).

RESULTS

Dissolved nutrients

The best approximating models for log NH_4-N and log PO_4-P contained LSD, region, season, and LSD × season interaction (Table 7). Concentrations of both nutrients increased with spawner abundance during the summer spawning season, when point estimates of concentrations for both nutrients increased by approximately two orders of magnitude across the observed range in spawner density (i.e., 0–20 MT/km; Fig. 2). Concentrations of neither nutrient were conclusively related to spawner abundance during spring or fall (Fig. 2).

Horsetail and macroinvertebrate $\delta^{15}N$

The best approximating models for $\delta^{15}N$ in horsetail, scrapers, and generalist macroinvertebrates each consisted of LSD and region (Table 7). There was some support for season and LSD x season interactions in the lower-ranked models (Table 7), although these effects had little influence on the model estimates (Fig. 3). Across the observed range in spawner density, point estimates for $\delta^{15}N$ in generalist macroinvertebrates increased from approximately 3‰ to >6‰ in all seasons (Fig. 3). Point estimates for horsetail and scraper $\delta^{15}N$ at salmon-free stations were approximately 2‰ and 3.5‰, respectively, during summer and fall. Delta ^{15}N for both taxa increased slightly with spawner density, but the
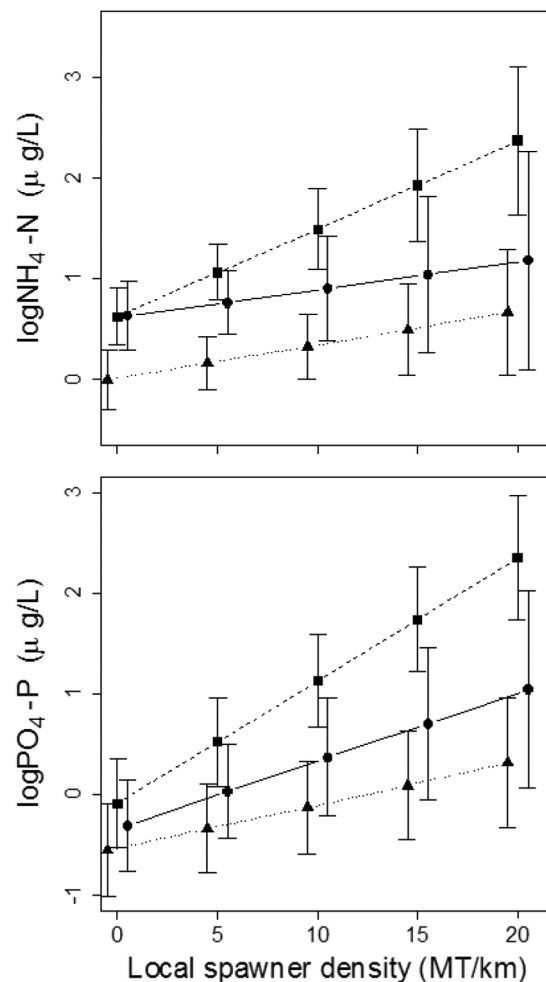

Fig. 2. Model-averaged estimates for dissolved nutrient concentrations (and 95% CI) during spring (triangles), summer (squares), and fall (circles) across five levels of local spawner density, holding region constant. MT = metric tons.

high error in these estimates made it impossible to determine if the trends were real (Fig. 3). We did not sample horsetail in the fall and we did not model scraper data from fall samples because they were found at relatively few stations during the fall and at no stations with LSD >5 MT/km.

Dolly Varden stable isotopes and fatty acids

For all three Dolly Varden MDN metrics, the effects of LSD and fork length were strongly supported by the data, and the effect of region was important for both stable isotope metrics (Table 7). An LSD × fork length interaction was
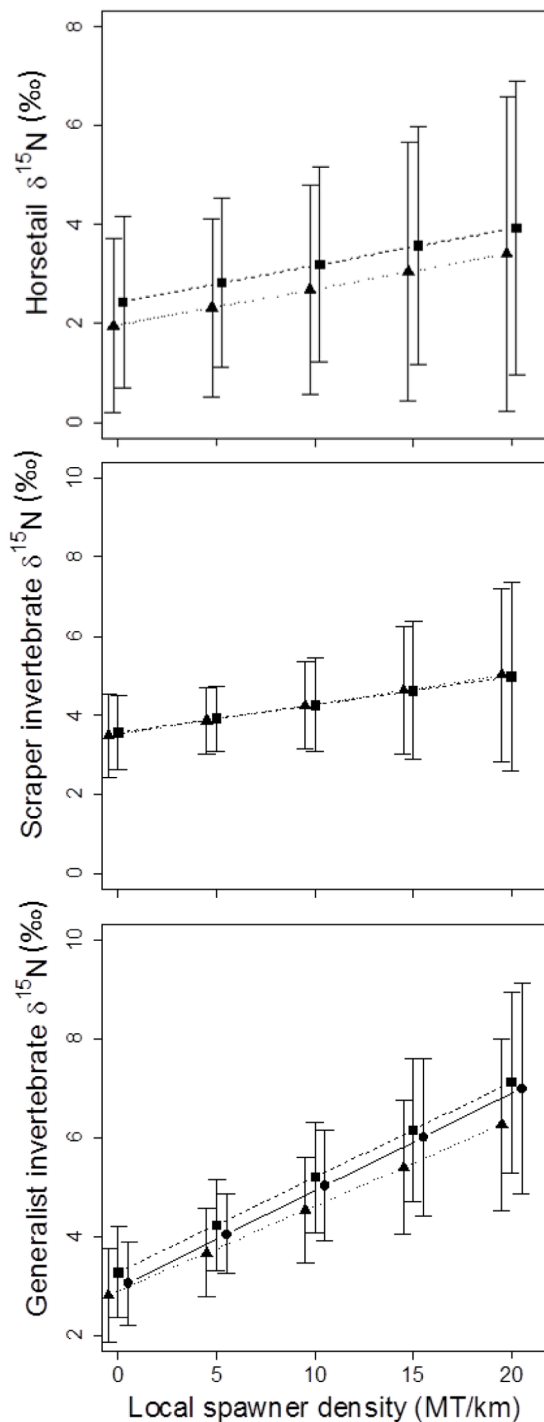
Fig. 3. Model-averaged estimates for $\delta^{15}N$ in horsetail and macroinvertebrates (and 95% CI) during spring (triangles), summer (squares), and fall (circles) across five levels of local spawner density, holding region constant. MT = metric tons.

strongly supported for $\delta^{34}S$ and $\omega3{:}\omega6$, and supported less so for $\delta^{15}N$ (Table 7). For $\delta^{34}S$ and $\omega3{:}\omega6$ there was also a small level of support for a season effect and no support for a LSD × season interaction (Table 7). The season effect had no discernible influence on the model estimates, which were essentially identical for each metric across the three seasons (Fig. 4). Across the range of observed spawner density, point estimates increased from approximately 8.2‰ to 12.3‰ for $\delta^{15}N$, from 1.3‰ to 12‰ for $\delta^{34}S$, and from 4 to 8.8 for $\omega3{:}\omega6$ during spring, summer, and fall (Fig. 4).

DISCUSSION

Ammonium-N and orthophosphate-P concentrations increased with spawner density during the summer but not during spring or fall, indicating the presence of a dissolved nutrient spike that had largely attenuated by fall sampling. Previous studies tracking dissolved nutrients have shown similar patterns (Minakawa and Gara 1999, Chaloner et al. 2002, Johnston et al. 2004, Mitchell and Lamberti 2005, Claeson et al. 2006). Delta ^{15}N in horsetail and scraper macroinvertebrates did not vary with spawner density in any season, suggesting little or no MDN assimilation by these lower trophic levels. Horsetail is capable of fixing atmospheric nitrogen (Uchino et al. 1984), while nitrate reductase activity also suggests it competes for soil nitrate (Nadelhoffer et al. 1996), making it difficult to determine the extent to which assimilated nitrogen came from the soil. Previous work showed a lack of MDN assimilation by green alder (*Alnus crispa*), also a nitrogen fixer, in contrast to three other plant species that were isotopically enriched along salmon spawning reaches (Helfield and Naiman 2002). The apparent lack of MDN assimilation by scraper macroinvertebrates contrasts previous work that showed seasonally persistent nitrogen enrichment in primary consumers (i.e., grazers) from a salmon stream relative to a non-salmon stream (Bilby et al. 1996), although the basis for this contrast is not clear.

Spawner density was an important predictor for all MDN metrics in biota and the top model for each response included this predictor. Predictions based on these models showed that
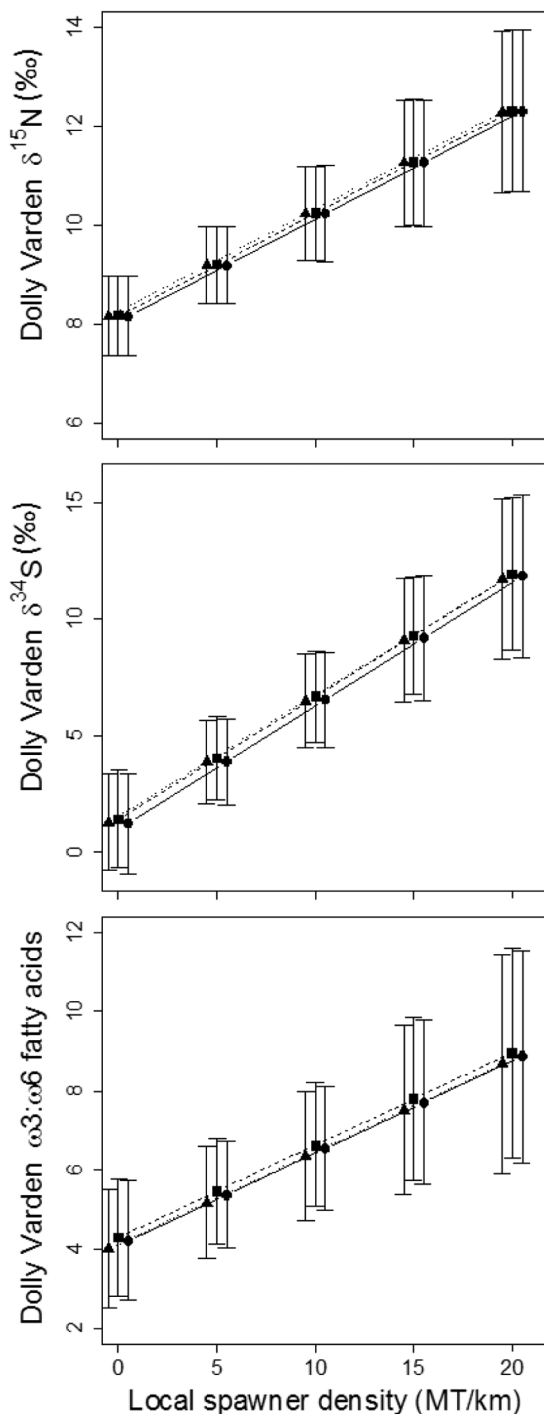
Fig. 4. Model-averaged estimates for Dolly Varden stable isotopes and fatty acids (and 95% CI) during spring (triangles), summer (squares), and fall (circles) across five levels of local spawner density, holding region and fork length constant. MT = metric tons.

generalist macroinvertebrates and Dolly Varden incorporated more MDN as spawner density increased. The evidence was particularly strong for Dolly Varden, where three independent biochemical metrics indicated assimilation of marine nitrogen, sulfur, and fatty acids. At the highest salmon abundance, point estimates for δ^{15}N in Dolly Varden (after subtracting 3‰ for trophic fractionation; Minagawa and Wada 1984) approached that of Pacific salmon (i.e., 10–15‰; Johnson and Schindler 2009). The highest point estimates for δ^{34}S, by contrast, were depleted by approximately 6‰ relative to Pacific salmon (i.e., 18–20‰; C. A. Stricker, *unpublished data*). Dolly Varden ω3:ω6 exceeded the maximum observed in salmon flesh (i.e., 7.3; R. A. Heintz, *unpublished data*), suggesting that salmon eggs (with ω3:ω6 of 12.1–13.9; R. A. Heintz, *unpublished data*) were an important dietary component (Denton et al. 2009, 2010, Jaecks 2010). Maximum δ^{15}N in generalist macroinvertebrates was substantially less than that of salmon, implying incorporation of less MDN. Our findings support the prevailing view in the literature that generalist consumers, represented in this case by Dolly Varden and macroinvertebrates, are the most likely to capitalize on and benefit from pulsed subsidies (Ostfeld and Keesing 2000, Sears et al. 2004, Yang et al. 2008).

The effect of spawner density on MDN assimilation by generalist macroinvertebrates and Dolly Varden was similar during each season measured, indicating that MDN in these taxa persisted for at least nine months following salmon spawning. Direct consumption of MDN in the form of salmon eggs and flesh has been observed for Dolly Varden (Denton et al. 2009, 2010, Jaecks 2010) and all of the generalist macroinvertebrate taxa we sampled (Piorkowski 1995, Minakawa and Gara 1999, Minakawa et al. 2002, Claeson et al. 2006, Walter et al. 2006). We hypothesize that MDN persistence in consumer tissues may be driven by one or two non-mutually exclusive mechanisms. One possible mechanism relates to low winter energetic demands and slow tissue turnover in poikilotherms in a setting where water temperatures barely exceed 0°C during the winter months. For example, tissue turnover of whitefish (*Coregonus* spp.) muscle during fall and winter was negligible, allowing the C, N, and S stable isotope

composition of summer growth to be reflected year-round (Hesslein et al. 1993, Perga and Gerdeaux 2005). Another potential mechanism is that MDN stored in the stream environment was consumed through the winter and spring. Possible direct sources of stored MDN include incubating or dead salmon eggs, salmon flesh entrained in snags or sediment, and emerging salmon fry, while possible indirect pathways include leaves, invertebrates, and microbes that have been subsidized by MDN.

An independent data set for Dolly Varden and juvenile coho salmon collected in Kenai Peninsula salmon streams showed MDN presence and associated nutritional benefits to persist through winter and into the following spring (Rinella et al. 2012). This study, together with the current study, contrasts others examining MDN persistence in aquatic consumers, which have generally shown MDN levels to decrease in the months following salmon spawning (Bilby et al. 1996, Claeson et al. 2006, Walter et al. 2006, Reichert et al. 2008, Honea and Gara 2009). However, these studies were conducted in Washington, USA streams with lower spawner densities and relatively warm winter water temperatures that would allow higher metabolic rates and tissue turnover.

Our results also show that, while spawner abundance is an important predictor, other factors contribute to variation in MDN metrics. Region was an important predictor for every MDN metric except Dolly Varden ω3:ω6, suggesting that regions have unique backgrounds upon which spawning salmon effects are superimposed. Nitrogen isotopes most clearly demonstrate this phenomenon. Scraper macroinvertebrates hold the lowest trophic position and should, therefore, most closely reflect the dissolved nitrogen pool (Cabana and Rasmussen 1996). Scraper $\delta^{15}N$ from salmon-free stations was 6.9 ± 1.5‰ (mean $\pm$ standard deviation) in the Homer region, 2.7 ± 1.5‰ in Cooper Landing, and -0.2 ± 0.4‰ in Seldovia. Understanding the basis for these regional differences is outside the scope of this study, but a few potentially additive causes stemming from differences in watershed nitrogen sources (Peterson and Fry 1987, Cabana and Rasmussen 1996) or subsequent isotopic fractionation of the nitrogen pool can be postulated. One influence may be differences in the extent of alder cover which, through nitrogen fixation, can contribute significant quantities of atmospherically-derived nitrogen (i.e., 0‰ by definition) to aquatic and riparian ecosystems (Helfield and Naiman 2002, Shaftel et al. 2012). Another factor could be differences in denitrifying potential of riparian soils, where fine-textured soils along meandering stream reaches can support high denitrification rates and, in turn, isotopic enrichment of the dissolved nitrate pool (Pinay et al. 2003). Lastly, water chemistry samples from salmon-free stations indicated that primary production may have been limited by nitrogen availability in the Homer streams (total molar N:P = 17) but not in the other regions (total molar N:P > 100), possibly leading to discriminatory assimilation of the light isotope by primary producers in the Cooper Landing and Seldovia regions (Teranes and Bernasconi 2000, Brahney et al. 2006). Similar differences in source and fractionation may explain regional differences in baseline sulfur isotopes.

Fork length was an important predictor for all three Dolly Varden MDN metrics, and model parameters indicated that MDN assimilation increased with fork length. Interactive effects were also supported, especially for $\delta^{34}S$ and ω3:ω6, indicating size-mediated differences where larger fish appeared to assimilate more MDN. This differential MDN assimilation may be due to intraspecific competition where larger individuals are better able to compete for drifting eggs and flesh. Additionally, larger individuals are released from gape limitation that may prevent smaller individuals from consuming salmon eggs (Armstrong et al. 2010). Without diet and behavioral data these explanations are speculative and further studies are required to determine the mechanism for the observed size-dependent responses.

This study demonstrated that seasonally pulsed MDN resources can persist for many months in some biota and, together with other studies (Verspoor et al. 2010, Rinella et al. 2012), suggests that salmon can have prolonged effects in ecosystems where they spawn. While MDN persisted in most taxa sampled over the three-season course of this study, we were unable to determine the full duration of its presence. This is a worthwhile research objective, since interannual persistence would help to buffer changes in

MDN availability during years of low salmon returns.

ACKNOWLEDGMENTS

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