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SHORT COMMUNICATION

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Abstract We examined the relationship between the annual escapement of salmon and the δ^{15}N of willow (*Salix* spp.) leaves to evaluate the contribution of marine-derived nutrients (MDN) to riparian vegetation around the Pacific Northwest and Northeast regions. Foliar δ^{15}N values ranged from –3.42‰ to 4.65‰. The value increased with increasing density of carcasses up to 500 fish/km and 1500 fish/km. δ^{15}N values were variable at carcass densities below 500 fish/km. Possible factors affecting the fluctuation of δ^{15}N at reference sites are: (1) denitrification; (2) the presence of N_2-fixing trees, such as alder; and (3) agricultural runoff. δ^{15}N values at the sites with carcass densities over 500 fish/km were consistently high, while a value of δ^{15}N below zero was observed at only one site (Rusha River; $\delta^{15}N = -1.87$‰). At this site, most adult pink salmon returned to limited locations near the estuary because steeper channel gradients acted as a migration barrier, resulting in the negative δ^{15}N value. Nevertheless, we concluded that our results showed evidence of the feedback of MDN to terrestrial vegetation, although the use of the δ^{15}N value as a terrestrial end member at spawning sites is limited. If the relationship between the enrichment index, which is expressed as the values using a mixing model, and salmon abundance was estimated, the availability of MDN in riparian ecosystems could possibly be evaluated and will lead to the establishment of escapement goals.

Key words Marine-derived nutrients · Northwest Pacific region · *Salix* · Salmon carcasses · Stable nitrogen isotopes

Introduction

The role of salmon carcasses in supplying marine-derived nutrients (MDN) to freshwater ecosystems has been highlighted over the past two decades for areas of the Pacific Northwest region of North America, including southern Alaska (Cederholm et al. 1989; Gende et al. 2002; Murota 2003). MDN influence stream biota both directly and indirectly through direct feeding on the body tissue and eggs (Bilby et al. 1998) and through decomposition and uptake by bacteria and algae (Wipfli et al. 1998), resulting in alteration of the associated macroinvertebrate and fish community assemblages (Wipfli et al. 1998; Johnston et al. 2004). MDN transported to the riparian zone by flooding (Ben-David et al. 1998), hyporheic flows (O'Keefe and Edwards 2003), and wildlife (Reimchen 2000; Klinka and Reimchen 2002) can also influence nutrient dynamics in terrestrial ecosystems (Hilderbrand et al. 1999; Hocking and Reimchen 2002).

Historically, streams in Hokkaido have had natural salmon runs consisting of mass-spawning species, mostly chum salmon (*Oncorhynchus keta*) and some pink salmon (*Oncorhynchus gorbuscha*). During the 1970s, when reproduction techniques for chum salmon were established, most of the salmon for artificial fertilization and stock enhancement were captured at the mouths of catchments by fish traps and weirs, reducing natural spawning opportunities in many streams (Murota 2003). In contrast to streams in Hokkaido, natural salmon runs have been maintained in

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streams in eastern Russia (Murota 2003), and, therefore, transfer of MDN to upstream reaches by salmon has varied between Hokkaido and Russian streams. Although several studies have found positive effects of carcasses on aquatic animals and invertebrates (e.g., Nakajima and Ito 2000, 2003; Ito 2003; Yanai and Kochi 2005), information regarding the effects of MDN, especially for terrestrial ecosystems in the Pacific Northeast region of northern Eurasia is limited.

Because salmon are enriched with heavier isotopes of nitrogen (^{15}N) and carbon (^{13}C) relative to sources in freshwater and terrestrial ecosystems, MDN in energy and food web paths from salmon carcasses to other organisms can be investigated using stable isotope analyses (Kline et al. 1990; Bilby et al. 1996; Ben-David et al. 1998). In particular, the proportions of ^{15}N can be used to quantify the proportion of N derived from salmon that is contained in riparian plants and animals (Helfield and Naiman 2001; Hocking and Reimchen 2002; Mathewson et al. 2003). Koyama et al. (2005) found that the amount of MDN was positively correlated with foliar δ^{15}N. However, few studies have reported the relationship between the density of salmon carcasses and stream productivity (Johnston et al. 2004) and there is still uncertainty over the extent to which salmon carcasses are responsible for increases in productivity of riparian ecosystems (Gende et al. 2002).

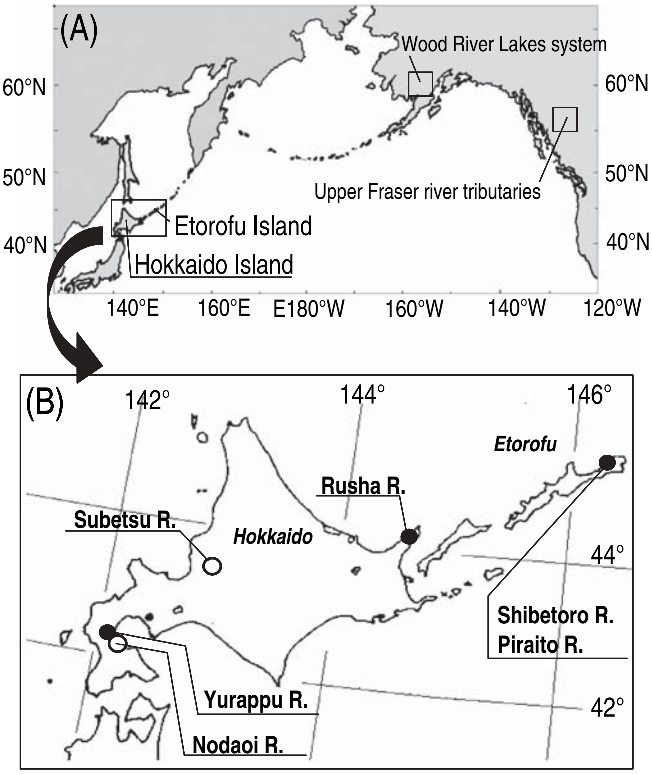

Fig. 1A, B. Map of the North Pacific rim (**A**) and location of the sampling sites in Hokkaido, Japan and the Northern Territory, Russia (**B**). δ^{15}N values in the Wood River Lake system and the Upper Fraser River tributaries were derived from literature reports. *Filled circles*, spawning sites; *open circles*, reference sites

In this study, we examined the uptake of MDN by willow (*Salix* spp.), which is common along streams in Hokkaido, Japan, and the Northern Territory of Russia. We discuss how the contributions of MDN to riparian vegetation could be evaluated by examining the relationship between salmon escapement and foliar δ^{15}N, including published δ^{15}N values in North America. This study contributes to the determination of the role of MDN in terrestrial ecosystems in Japan, Russia, and elsewhere in the Pacific rim.

Materials and methods

Study sites

A field survey was conducted in four streams on Hokkaido Island, Japan, and two rivers on Etorofu Island, Northern Territory, Russia, in 2002 and 2003 (Fig. 1B). The climate of these areas is cool and temperate (annual mean 5.5°–7.8°C), and the annual precipitation ranges from 1100 to 1300 mm, of which 50% falls as snow. We selected four streams that receive salmon carcasses (Table 1). In addition, the Nodaoi, Subetsu, and upper Yurappu were selected as reference sites for the absence of MDN; because of fish migration barriers, no spawning salmon were observed in these rivers.

The catchment landcover of four of the rivers (Rusha and Subetsu rivers in Hokkaido; Shibetoro and Piraito

Table 1. Description of the sampling sites

District	Rivers	Area (km^2)	Length of main channel (km)	Sampling site			Spawning designation	Number of willow individuals used stable isotope analysis	
				Gradient (%)	Elevation (m)	Distance from river mouth (km)		*Salix schwerinii*	*Salix udensis*
Hokkaido	Yurappu	351.8	28.5	0.5	50	15.0	Spawning	6	2
	Rusha	20.5	10.0	2.2	15	0.5	Spawning	–	4
	Upper Yurappu	351.8	28.5	0.6	65	20.0	Reference	1	2
	Nodaoi	121.5	27.2	0.7	20	4.0	Reference	5	–
	Subetsu	63.8	24.4	1.4	125	17.5	Reference	–	3
Etorofu Island[a]	Shibetoro	141.5	33.0	0.4	17	6.0	Spawning	–	3
	Piraito	37.3	16.0	0.4	10	1.0	Spawning	–	3

[a] Russian Northern Territory

rivers on Etorofu Island) was predominantly second-growth forest, while that of the Yurappu and Nodaoi rivers was agricultural. The dominant riparian vegetation along the streams was willow (*Salix* spp.), Japanese elm (*Ulmus davidiana* var. *japonica* Nakai), white ash (*Fraxinus mandshurica* var. *japonica* Maxim.), oak *(Quercus crispula* Blume), maple (*Acer mono*), and alder (*Alnus hirsuta*). The channel gradient of all study reaches in Hokkaido streams ranged from 0.5% to 2.2%, while that of the streams in Russia was relatively gentler (0.4%–0.5%; Table 1). All stream substrates were gravel bed and cobbles (median diameter range of 5–20 cm).

Sampling and analytical procedures

We collected foliage at random from the dominant willow species, silky willow (*Salix schwerinii*), within 10 m of the channel. If we could not find silky willow, we sampled from long-leaved willow (*Salix udensis*). The genetic, physiological, and habitat characteristics of these two willow species are very similar (Ohashi 2001). Therefore, we assumed that both willow species have similar metabolic processes for nutrient uptake. Foliage (five to ten leaves attached to shoots) was collected during May and June at all streams.

All willow foliage samples were dried at 60°C for 48 h, after which the foliage was ground to a fine powder. Approximately 1 mg of each sample was used for stable isotope analyses. Isotope ratios ($^{15}N/^{14}N$, expressed as $\delta^{15}N$) were measured to determine the levels of salmon-derived nutrients. We used a Finnigan MAT DELTAplus isotope ratio mass spectrometer (IRMS; Thermo Finnigan, Bremen, Germany) at the Agricultural Science Laboratory at Tohoku University. The natural abundance of ^{15}N is expressed as the per mil (‰) deviation from atmospheric N_2, the recognized isotopic standard. $\delta^{15}N$ values are calculated as:

$$\delta^{15}\mathrm{N} = \left(R_{\mathrm{sample}}/R_{\mathrm{standard}} - 1\right) \times 1000 \tag{1}$$

where R is the ratio of $^{15}N/^{14}N$ stable isotopes.

Data description

In this study, we used not only our own data, but also published data from the Pacific Northwest to evaluate the relationship between carcass density and $\delta^{15}N$ values (Fig. 1A). We used seven data for spawning sites, and five for reference (nonspawning) sites (Table 2). The main salmon species are chum and/or pink salmon in Hokkaido and Etorofu, while sockeye salmon (*Oncorhynchus nerka*) occur at three spawning sites: Forfar Creek and O’Ne-eil Creek of the upper Fraser River tributaries in British Columbia, Canada, and the Wood River Lake system of southwestern Alaska, USA. These three species are generally known for mass spawning, and several study watersheds have shown that the number of annual escapement often exceeds 10 000 fish per year (Murota 2003; Jauquet et al. 2003).

We obtained carcass densities at two spawning sites: the Yurappu River (Nagasaka and Nagasaka 2004) and the Wood River Lake system (Helfield and Naiman 2002) from published work. On Etorofu Island, the annual escapement has not been counted recently. In the 1940s, the annual escapement ranged from 9596 to 75 000 in the Shibetoro River, and from 124 to 5893 in the Piraito River (Hokkaido Fish Hatchery 1936–1945). Because these two rivers still have the largest spawning populations of pink and chum salmon in a naturally maintained reproduction system (Komiyama, personal communication), we used the average escapement for this 10-year period (1936–1945) in this study. Carcass density was evaluated by dividing the average escapement by the length of the main spawning reaches. For the remaining two sites, Forfar Creek and O’Ne-eil Creek, the carcass density was also evaluated by dividing the annual escapement by the length of the main spawning reaches derived from the literature (Johnston et al. 1997).

Results and discussion

Foliar $\delta^{15}N$ values ranged from –3.42‰ to –0.2‰ at reference sites and –1.87‰ to 4.65‰ at spawning sites (Table 2). $\delta^{15}N$ values were variable at carcass density below 500 fish/km, increasing with increasing density of carcasses up to values between 500 fish/km and 1500 fish/km (Fig. 2). The rate of increase in foliar $\delta^{15}N$ decreased with increasing carcass density over 2000 fish/km. $\delta^{15}N$ values at the sites with carcass density over 500 fish/km were consistently high, with $\delta^{15}N$ below zero at only one site (Rusha River; $\delta^{15}N$ = –1.87‰).

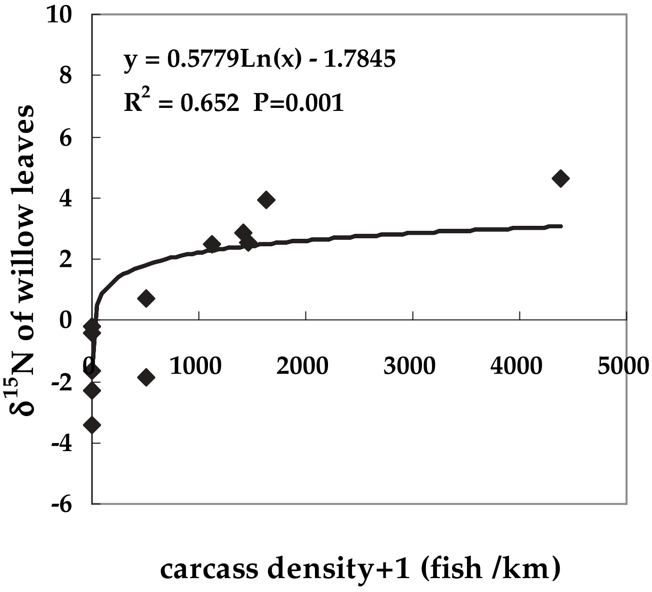

Fig. 2. The relationship between $\delta^{15}N$ of willow leaves and the density of carcasses. Carcass density is presented as the number of carcasses (or annual escapement) per kilometer of the main spawning reaches. Regression statistics: $\delta^{15}N = 0.5779 \ln$ (carcass density +1) – 1.7845; $R^2 = 0.652$; $P = 0.001$

Table 2. Comparison of published δ^{15}N values for common riparian vegetation

Species	δ^{15}N (‰)		Location	Area (km^2)	Main salmon species	Number of annual escapement	Carcass density[a] (fish/km)	Data source
	Spawning	Reference						
Willow (*Salix* spp.)	4.65		Shibetoro River, Northern Territory	141.5	Chum[b], pink[c]	9 596–75 000	5 450	This study
	2.88		Lower Piraito River, Northern Territory	37.3	Chum, pink	124–5 893	1 443	This study
	–0.09		Bivouac Creek		Sockeye[d]	762	254	Johnston et al. (1997)
	3.95		Forfar Creek		Sockeye	4 902	1 634	Johnston et al. (1997)
	2.52		O'Ne-eil Creek		Sockeye	4 371	1 457	Johnston et al. (1997)
	0.72	–3.42	Wood River Lakes system, southwestern Alaska		Sockeye	23 000–2 970 000	500	Helfield and Naiman (2002)
	–1.87		Rusha River, Hokkaido	20.5	Pink	1 000 (estimated)	100	This study
		–0.2	Lake Superior wetlands					Keough et al. (1996)
		–0.44	Nodaoi River, Hokkaido	121.5				This study
		–0.88–1.53	South Lake, Mackenzie River delta, Northwest Territories					Heckey and Hesslein (1995)
		–2.27	Subetsu River, Hokkaido	63.8				This study
Sitka spruce (*Picea sitchensis*)	0.63	–3.34	Kadashan and Indian rivers, southeast Alaska	~140 and ~57	Pink	30 000–125 000/ 200–45 000		Helfield and Naiman (2001)
Devil's club (*Oplopanax horridus*)	2.24	–0.91	Kadashan and Indian rivers, southeast Alaska					Helfield and Naiman (2001)
Salmonberry (*Rubus spectabilis*)	3.18		Warn Bay Creek, Vancouver Island, BC, Canada		Chum	3 128	782	Reimchen et al. (2003)
	0.80–2.8		Kennedy Creek, Washington, USA		Chum		10 000	Bilby et al. (2003)
	–1.13		Sydney River, Vancouver Island, BC, Canada		Chum	1 627	147	Reimchen et al. (2003)
		–4 to –1	Griffin Creek, Washington, USA		Coho[e]		100	Bilby et al. (2003)

[a] Density = escapement/channel length, or density = mean escapement/channel length

[b] *Oncorhynchus keta*

[c] *Oncorhynchus gorbuscha*

[d] *Oncorhynchus nerka*

[e] *Oncorhynchus kisutch*

One of the possible factors affecting the fluctuation of δ^{15}N in reference sites is denitrification (Mariotti et al. 1988). Denitrification activity elevates the δ^{15}N of forest soil by 5‰, and occurs more frequently in the valley floor (Koba et al. 1994; Konohira et al. 1997), resulting in higher δ^{15}N in leaves. In this study, values of the reference site were detected in riparian areas where denitrification might possibly occur but foliar δ^{15}N values have not exceeded zero. Because potential denitrification activity is accelerated by nitrate amendment as well as by anaerobic conditions, both MDN from salmon and denitrification contribute to δ^{15}N values in spawning streams (Pinay et al. 2003). Spawning salmon streams of Hokkaido are usually gravel-bed rivers with alluvial fans (Kobayashi 1968; Mayama 1993), which differ from the meandering spawning streams in southwest Alaska and Idaho that have fine sandy bottoms (particle size <0.83 mm; Garret et al. 1998; Pinay et al. 2003). Differences in soil texture and landforms also affect the occurrence of denitrification, and, therefore, it will be necessary in the future to determine the relative influence of marine-derived ^{15}N and microbial denitrification on observed δ^{15}N in riparian vegetation.

Symbiotic N_2 fixation by plants also influences N cycling in forest ecosystems (Yoneyama 2002). Although foliage and forest soil δ^{15}N from high latitudes in the northern hemisphere generally show negative values (Stewart 2001), the δ^{15}N of forest soil under nitrogen-fixing trees nears 0‰ (Yoneyama 2002). Helfield and Naiman (2002) pointed out that alder-fixed nitrogen possibly influenced MDN uptake by other plants that do not fix nitrogen, so altering their foliar δ^{15}N. Spruce δ^{15}N at alder-influenced spawning sites was similar to alder δ^{15}N, significantly decreased relative to spawning sites devoid of alders. In this study, we tried to minimize the effects of N_2 fixation on δ^{15}N values by selecting from sites with few or no alders. Because there was no information about riparian vegetation in Forfar Creek or O'Ne-eil Creek (Johnston et al. 1997), it is unclear whether there was an effect from nitrogen fixation on δ^{15}N of willow leaves in these two sites.

A difference in the salmon species is one of the factors that affect the δ^{15}N value in spawning streams. Bilby et al. (2003) suggested that low-density, lightweight spawning salmon such as coho salmon (*Oncorhynchus kisutch*) may not provide effective nutrient transfer. However, we could disregard these effects because we detected δ^{15}N values in mass-spawning salmon species in this study.

Another factor causing the elevation of δ^{15}N values, especially in Hokkaido, is agricultural runoff (e.g., Nakanishi et al. 1995; Kondo et al. 1997; Yoneyama 2002). For example, Komada et al. (1998) reported much higher δ^{15}N values in willow trees (six times; *Salix gilgiana*) for a marsh stream located near livestock production facilities. However, we did not clearly observe the effects of agricultural wastewater on the elevation of δ^{15}N values here.

The foliar δ^{15}N of the Rusha River was not as high as those of the other spawning sites examined. Owing to the steeper channel gradient in the Rusha River, most adult pink salmon return to limited locations near the estuary. Pink salmon prefer to spawn in relatively high-velocity water compared with chum salmon (Kobayashi 1968), and spawn near the estuary because the young make an immediate migration after emerging from the gravel (Kobayashi 1968). Therefore, MDN may not persist in both the stream channel and the riparian zone. In addition to this, three check dams have been constructed within 2 km of the Rusha River mouth (Takahashi et al. 2005), making it harder for salmon to migrate to upstream reaches, even though these dams have fishways. Therefore, only reaches within 1–2 km of the river mouth are used by brown bear (*Ursus arctos*) for feeding on salmon, resulting in little nitrogen uptake by riparian vegetation.

The decline in rate of increasing foliar δ^{15}N at carcass density above 2000 fish/km would represent an asymptotic effect (Bilby et al. 2001). Foliar δ^{15}N value was not determined by carcass density, but by δ^{15}N of salmon carcasses as the nutrient source and the rate of MDN contribution in nutrient uptake. Therefore, foliar δ^{15}N would not increase continuously with increasing amount of salmon carcasses; this would not represent a limitation of stable isotope analysis but a characteristic of this approach. Although another approach might need to evaluate quantitative effects of MDN on the terrestrial ecosystem, we concluded that our results showed evidence of the feedback of MDN to riparian vegetation. A limitation of this study was the lack of δ^{15}N values as terrestrial end member (i.e., δ^{15}N values representing 0% MDN) at spawning sites to evaluate percentages of MDN contribution in vegetation. Because δ^{15}N values vary at the regional scale due to other nitrogen inputs, such as precipitation and/or atmospheric deposition (Schindler et al. 2005), it is more useful to indicate the "index of ^{15}N enrichment" (Bilby et al. 2001). The availability of MDN in riparian ecosystems could possibly be evaluated if the relationship between enrichment index and salmon abundance were to be estimated, leading to the establishment of escapement goals.

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