

Stable isotope evidence indicates the incorporation into Japanese catchments of marine-derived nutrients transported by spawning Pacific Salmon

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SUMMARY

1. Pacific salmon (*Oncorhynchus* spp.) transport marine-derived nutrients (MDN) and organic matter to freshwater ecosystems, which enhances the productivity of North Pacific ecosystems. Relatively few studies, however, have evaluated the MDN subsidy to both the aquatic system and the terrestrial catchment simultaneously. Using stable isotope analysis, we tested how the dynamics of MDN differed between the river and adjacent riparian forest in rivers of the Shiretoko World Natural Heritage Site in eastern Hokkaido (Japan). In addition, we accounted for temporal and spatial variations in the stable isotope signatures of freshwater organisms due to the presence or absence of spawning salmon.

2. We analysed carbon and nitrogen stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of biofilm, invertebrates, fish, riparian plants and brown bear (*Ursus arctos*) in the Rusha River during the pre-spawning and spawning periods and in the Akai River (where there are no salmon). Willow leaves were collected along the 50-m transects to evaluate how far MDN are incorporated within the riparian area. We counted the number of pink salmon (*O. gorbuscha*) carcasses in riparian areas and categorised their mode of transport. In addition, we examined the stomach contents of Dolly Varden (*Salvelinus malma*).

3. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of aquatic organisms increased by 1–4‰ and 1–6‰, respectively, with the arrival of salmon spawners. Aquatic organisms incorporated 23% of their nitrogen from salmon (range: 7–46%). The diet of Dolly Varden switched from aquatic invertebrates to salmon eggs during the salmon spawning run.

4. More salmon carcasses were transported from the stream to riparian areas by flooding than by brown bears. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of blowflies (*Calliphora* spp.) and brown bears increased significantly during the spawning run. Riparian vegetation, with the exception of Manchurian alder (*Alnus hirsuta*), incorporated 25% of its nitrogen from salmon. The $\delta^{15}\text{N}$ values of riparian willow (*Salix* spp.) were correlated negatively with distance from the stream.

5. The proportion of MDN incorporated in the freshwater biota was lower than that reported for North American rivers, potentially due to the influence of dams and modification of the river environment in this Japanese example. The riparian forest incorporated a relatively high fraction of MDN, however, mainly due to the transport of salmon carcasses from the channel by brown bears and, particularly, flooding. The dynamics of salmon-derived nutrients thus differed between river and adjacent riparian zones. These results suggested the importance of linkages between freshwater and riparian ecosystems for the extent of the marine nutrient subsidy.

Keywords: brown bear, marine-derived nutrients, pink salmon, stable isotope

Introduction

Nutrients and organic matter flow from land to sea through rivers, but marine-derived nutrients (MDN) can be transported back to the land via biological vectors such as migrating salmon and seabirds (Juday *et al.*, 1932; Kline *et al.*, 1990; Ben-David, Hanley & Schnell, 1998; Harding *et al.*, 2004). Pacific salmon (*Oncorhynchus* spp.) transport potentially large amounts of MDN to natal spawning grounds during migrations (e.g. Gende *et al.*, 2002; Schindler *et al.*, 2003). For example, the phosphorus originating from sockeye salmon (*O. nerka*) carcasses accounted for 23% of the total annual input into Dalnee Lake, Kamchatka (Krokhin, 1959). Similarly, increases in the concentration of nitrogen and phosphorus in freshwater systems have been linked to the spawning of Atlantic salmon (*Salmo salar*) (Johnson & Johnson, 2003). Furthermore, researchers have documented increases in the biomass of epilithic biofilm on rocks in rivers as a result of MDN input from salmon carcasses (Wipfli, Hudson & Caouette, 1998; Chaloner *et al.*, 2004). Such increases in primary producers result in a higher biomass or growth rates of aquatic invertebrates (Wipfli *et al.*, 1998), and inputs of MDN by spawning salmon can increase secondary production of macroinvertebrates (Lessard, Merritt & Berg, 2009). Some aquatic invertebrates directly consume dead salmon tissue (Chaloner, Wipfli & Caouette, 2002a; Minakawa, Gara & Honea, 2002) and are themselves eaten by predators. Salmon eggs and tissue are also used as seasonal food resources by resident fish species (Bilby *et al.*, 1998; Denton *et al.*, 2010). For example, the growth rate of resident salmonids increases by feeding on salmon-derived resources (Scheuerell *et al.*, 2007). Thus, inputs of salmon-derived nutrients can influence stream productivity at several trophic levels.

In addition to direct effects on streams, salmon make a significant contribution to terrestrial ecosystems when their nutrients are transported onto the land. Nutrients originating from salmon carcasses are incorporated in the soil, vegetation and insects along the spawning streams (Reimchen *et al.*, 2003), thus enhancing their nutrients status (Helfield & Naiman, 2001). Brown bears (*Ursus arctos*) and blowflies (*Calliphora* spp.) are important biological vectors of MDN and affect the productivity of riparian ecosystems (Johnson & Ringler, 1979; Hilderbrand *et al.*, 1999a; Hocking & Reimchen, 2006).

A number of studies have used stable isotope analysis to evaluate the contribution of MDN from spawning salmon to aquatic and terrestrial ecosystems (e.g. Kline *et al.*, 1990; Bilby, Fransen & Bisson, 1996; Helfield & Naiman, 2001). Delta ^{15}N is an indicator of trophic height

of an organism, because the heavier nitrogen isotope accumulates by approximately 3–4‰ with each trophic transfer (Minagawa & Wada, 1984). Delta ^{13}C is an indicator of the diet and reflects the basal carbon source available in aquatic food webs (Vander Zanden & Rasmussen, 1999). Nitrogen and carbon in spawning salmon have a marine signature and contain higher proportions of the heavier isotopes of both elements than do nitrogen and carbon imported to streams from other sources (Kline *et al.*, 1990). Thus, stable isotope analysis has shown that salmon can make significant contributions of nutrients and organic matter to aquatic and adjoining terrestrial ecosystems (Bilby *et al.*, 1998, 2003; Hilderbrand *et al.*, 1999a).

Most research on MDN from spawning Pacific salmon has been conducted in North America, and much of it has evaluated the effects on freshwater and riparian ecosystems separately. The relationship between freshwater and riparian ecosystems is poorly understood in MDN cycling. For example, emerging aquatic invertebrates disperse MDN from spawning streams to riparian forests (Francis, Schindler & Moore, 2006). Riparian forest in turn provides large woody debris supporting the retention of salmon carcasses (Cederholm *et al.*, 1989; Helfield & Naiman, 2001), which are the main source of MDN for the freshwater biota. Thus, to clarify the resource subsidy from salmon, it is necessary to evaluate freshwater and riparian ecosystems and the interface between them simultaneously.

The objective of this study was to examine the responses of both the freshwater and riparian biota to the spawning migration of salmon. We compared the incorporation of salmon-derived nutrients into biofilm, macroinvertebrates, fish, riparian vegetation and brown bears using stable isotope analysis. We tried to account for temporal and spatial variations in the stable isotope signatures of freshwater organisms in terms of the presence or absence of spawning salmon. Further, to evaluate the importance of different vectors in MDN cycling, we assessed the transport of salmon carcasses and the extent of incorporation of MDN in riparian plants. Our goal was to demonstrate how the dynamics of MDN vary between the river and adjacent riparian forest.

Methods

Study area

This study took place in the Akai River (44°6'N, 145°2'E) and Rusa River (44°11'N, 145°11'E) on the Shiretoko Peninsula, eastern Hokkaido, Japan. The Shiretoko

Peninsula was designated as an UNESCO World Natural Heritage Site in 2005 because of remarkable ecosystems and biodiversity. The climate is subarctic, with an annual mean precipitation of 110 cm. There are a number of endangered and endemic species such as Blakiston's Fish owl (*Ketupa blakistoni*) and a rare violet (*Viola kitamiana*). The terrestrial vegetation is dominated by Manchurian alder (*Alnus hirsuta*), Yezo spruce (*Picea jezoensis*) and Japanese oak (*Quercus crispula*). A high density of large mammals, such as brown bear and sika deer (*Cervus nippon*), inhabit riparian areas.

Three species of Pacific salmon naturally spawn within the Shiretoko Peninsula: pink salmon (*O. gorbuscha*), chum salmon (*O. keta*) and masu salmon (*O. masou*). The spawning migration of a large number of pink salmon occurs from early September to early October in this area. Stream fish faunas are dominated by diadromous fishes, and the Dolly Varden (*Salvelinus malma*) is numerous. The Shiretoko Peninsula is the southern limit of anadromous Dolly Varden (Morita *et al.*, 2005). In many streams, however, the upstream migration of salmonids is blocked by artificial dams without fish passes. The Akai River is a small tributary (length, 10 km; mean width, 5 m; mean flow, $1.9 \text{ m}^3 \text{ s}^{-1}$; mean velocity, 0.8 m s^{-1} ; substratum, cobbles and gravel) of the Iwaobetsu River. As a reference site, we sampled a section of the stream that has no anadromous salmon. This was situated between erosion dams, with a drop of 5 m, that prevent access to the stream above (Fig. 1). The Rusha River is a typical mountain stream (length, 9 km; mean width, 9 m; mean flow, $3.5 \text{ m}^3 \text{ s}^{-1}$; mean velocity, 0.85 m s^{-1} ; substratum, cobbles and gravel) and was also sampled (Fig. 1). A large number of pink salmon, as well as a few chum and masu salmon, spawn there. The spawning run of pink salmon in this river ranged from 10 000 to 58 000 individuals from 2006 to 2008 (Yokoyama *et al.*, 2010). There are three low-head dams in the lower reaches, but salmon can migrate upstream through gaps in the dams.

Field sampling

Samples of aquatic and terrestrial organisms were collected at least once a month from July to October in both rivers in 2007, 2008 and 2009 (Table 1). On each occasion, a biofilm sample was taken from three randomly collected rocks within riffles. The upper surface of each stone was scraped with a wire brush and flushed with river water into individual plastic bottles. Aquatic invertebrates were collected by hand and by disturbing the substratum upstream of a 0.25-mm-mesh hand net in

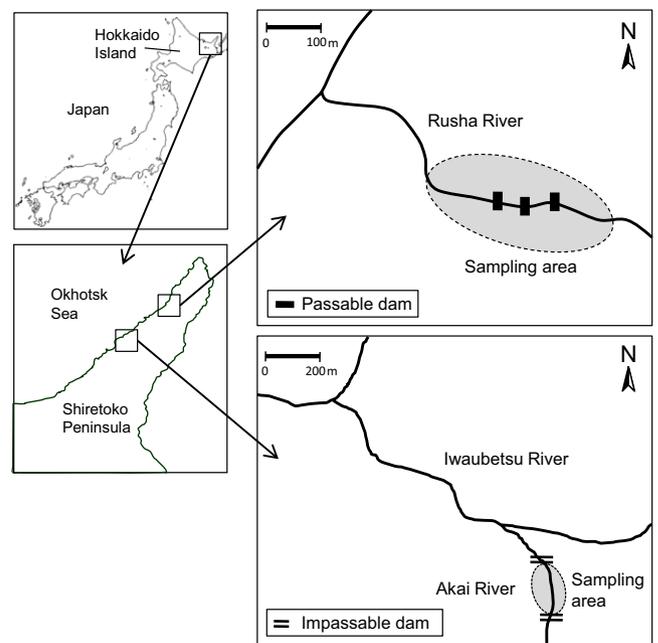


Fig. 1 Location of the Rusha and Akai Rivers in the Shiretoko Peninsula of eastern Hokkaido Island, Japan. Solid and double bars represent passable and impassable dams, respectively. Light shaded circle indicates the sampling area of both rivers.

riffles. The dominant taxa collected, representing five functional feeding groups (Merritt & Cummins, 1996), included shredders *Protonemura* sp. (Plecoptera), grazers *Epeorus latifolium* (Ephemeroptera), collector-gatherers *Orthocladius* spp. (Diptera), filter-feeders *Stenopsyche marmorata* (Trichoptera) and predators *Rhyacophila* sp. (Trichoptera). To provide sufficient mass for stable isotope analysis, three to 50 individuals of each species were combined to form one sample. Salmonids were collected monthly from each river using a back-pack electrofisher (LR-24, Smith-Root, Vancouver, WA, U.S.A.) from July to October. Salmonids were measured the fork length (nearest mm) and body mass (nearest g), and taken dorsal muscle tissue from each individual for stable isotope analysis. The stomachs of Dolly Varden were stored in 10% formalin for later analysis of their contents.

We collected terrestrial organisms from the riparian zone neighbouring both spawning and non-spawning rivers. From both rivers, foliage samples (*Parasenecio auriculatus*, *Petasites japonicus*, *Picea jezoensis*, *Salix* spp. and *Alnus hirsuta*) were collected at random from the dominant riparian vegetation within 10 m of the river on September. In addition, to evaluate the distance over which MDN were assimilated into the riparian zone in 2009, we established five transects extending perpendicularly from the river. Along each transect, we collected samples of willow (*Salix* spp.) leaves 10, 20, 30, 40 and

Table 1 Organisms sampled for stable isotope analysis from 2007 to 2009

Sample organism	Date of sampling	River		Sampling method
		Rusha	Akai	
Biofilm	July to October 2008 and 2009	○	○	Scraping surface of rocks with wire brush
Aquatic invertebrates				
<i>Protonemura</i> sp.	July to October 2007, 2008 and 2009	○	○	Collecting from riverbed with net
<i>Stenopsyche marmorata</i>		○	○	
<i>Orthocladus</i> spp.		○	○	
<i>Epeorus latifolium</i>		○	○	
<i>Rhyacophila</i> sp.		○	○	
Salmonids				
<i>Oncorhynchus gorbuscha</i>	July to October 2007, 2008 and 2009	○		Collecting with electroshocker
<i>Oncorhynchus masou</i>		○	○	
<i>Oncorhynchus masou</i> (anadromous)	September 2007	○		
<i>Salvelinus malma</i>	July to October 2007, 2008 and 2009	○	○	
<i>Salvelinus leucomaenis</i> (anadromous)	October 2008	○		
Riparian vegetation				
<i>Parasenecio auriculatus</i>	July to October 2007, 2008 and 2009	○	○	Riparian area within 10 m from the river
<i>Petasites japonicus</i>		○	○	
<i>Picea jezoensis</i>		○	○	
<i>Salix</i> spp.		○	○	
<i>Alnus hirsuta</i>		○	○	
Terrestrial invertebrates				
<i>Calliphora</i> sp.	July to October 2008 and 2009	○		Collecting with sweep net
<i>Calliphora</i> sp. (larvae)		○		Picking from surface of salmon carcasses
Mammals				
<i>Cervus nippon</i>	October 2007	○		Picking from surface of tree
<i>Ursus arctos</i>	July to October 2007 and 2008	○		Barbed-wire hair trap set up in bear trail

50 m from the edge of the river. Adult and larval blowflies were collected from the surface of salmon carcasses with a hand net. As an important herbivorous animal, hairs of sika deer were picked from riparian trees. Bear hair was sampled using a hair trap on bear trails along both river banks in the Rusha River basin, from August to October in 2007 and 2008. To reflect the most recent food sources consumed, as evidenced by stable isotope value, we used only the roots of deer and bear hair.

We counted the number of salmon carcasses transferred to the riparian forest between 22 September and 8 October (four times in total) in 2009. We investigated how far salmon carcasses were transferred from the riverbank into the riparian forest. We classified the transport of salmon carcasses onto land as by bears

(‘bear-killed’) if there were wounds to the salmon head, hump and belly, or as ‘senescent’ if the carcass was emaciated after spawning or had fungus and/or had wounds typical of fighting with other salmon. To avoid double counting the same individual, carcasses were tagged by placing a band through the gill into the mouth.

Laboratory procedure

All samples for stable isotope analysis were washed using deionised water and dried at 60 °C for at least 48 h. Biofilm samples were immersed in 1 N HCl to remove inorganic carbon before drying. Following this, the samples were ground into fine powder with a

mortar and pestle. To minimise the influence of lipid on $\delta^{13}\text{C}$ values, we extracted lipid from all samples by rinsing in chloroform–methanol solution (2 : 1). Approximately 0.5–1.5 mg of each sample was then packed into a tin cup and analysed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ by MAT252 mass spectrometry (Finnigan MAT, Bremen, Germany). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were expressed as follows:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N}(\text{‰}) = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1000 \quad (1)$$

where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ for $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$, respectively. We used the Pee Dee Belemnite and atmospheric N_2 as standards for carbon and nitrogen stable isotope analysis, respectively. The mixing model was used to estimate the contribution of MDN to their nitrogen component (Kline *et al.*, 1993; Johnston *et al.*, 1997; Chaloner *et al.*, 2002b).

$$\text{MDN enrichment (\%)} = 100 \times (\delta X_{\text{se}} - \delta X_{\text{c}}) / ((\delta X_{\text{s}} + (\text{TL} \times \delta X_{\text{e}})) - \delta X_{\text{c}}) \quad (2)$$

where δX_{se} is the isotopic ratio of the organism in areas enriched with salmon (Rusha River during spawning), δX_{c} is the isotopic ratio of the organism in areas without salmon enrichment (Rusha River before the spawning), δX_{s} is the isotopic ratio of spawning salmon, and δX_{e} is the isotopic enrichment factor of nitrogen (3.4‰; Minagawa & Wada, 1984). In the case of Dolly Varden, the δX_{c} was assigned a value typical of landlocked Dolly Varden, which reside in upstream areas of the Rusha River. TL is the trophic level correction factor (1 for herbivores, 1.5 for omnivores and 2 for carnivores).

In the stomach content analysis of Dolly Varden, we weighed (wet mass, g) and counted prey animals and classified them into four categories: terrestrial invertebrates, aquatic invertebrates, salmon eggs and sea lice (*Lepeophtheirus salmonis*). The latter is a parasite specific to Pacific salmon during its oceanic stage. To assess the stomach contents of each fish, we estimated the index of relative importance (IRI; Pinkas, Oliphant & Iverson, 1971) as follows:

$$\text{IRI} = F(N + W) \quad (3)$$

where F is the frequency of occurrence of prey in the stomach, N is the percentage by number of prey, and W is the percentage by mass of prey. We compared the condition factor of Dolly Varden between the Rusha and Akai Rivers as an index of trophic status. The condition factor (K) was calculated for each fish as follows:

$$K = 100W/L^3 \quad (4)$$

where W is body weight (g) and L is fork length (cm).

Data analyses

In this study, a BAC I experimental design (Green, 1979) was applied to detect the difference in the isotopic signature of freshwater organisms in 2008 before and after the spawning events, as well as differences between non-spawning and spawning rivers and their interaction. We defined the 'Before' as a date just before spawning of pink salmon on 3 September and 'After' as the period from 23 September (20 days after the initial spawning) to 14 October (40 days after spawning began and the last pink salmon spawning date). The Akai and Rusha are defined as 'non-spawning (Control)' and 'spawning (Impact)' rivers, respectively. We used a two-way ANOVA (two rivers \times three periods) with a Bonferroni correction to analyse for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of each organism (sample size of each sampling period = 5). In the analysis, Before/After (before or after spawning) and Control/Impact (spawning salmon present or not) are the main effects. The interaction between the presence or absence of spawning salmon and period shows whether the relationship between control and impact sites changed and thus indicates any effect of salmon. The Mann–Whitney U -test was used to assess differences in measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of terrestrial invertebrates, brown bears and riparian plants and condition factor of Dolly Varden between 'After' in the Rusha River and 'Before' in the Rusha or Akai Rivers. We used a simple correlation analysis ($\alpha = 0.05$) to test the relationship between $\delta^{15}\text{N}$ values in the willow foliage and distance from the river. All statistical analysis was performed using SPSS (version 20, SPSS Japan Inc., Tokyo, Japan).

Results

The isotopic signature of spawning salmon

The flesh of mature pink salmon and their eggs had $\delta^{15}\text{N}$ values of 10.2 and 10.8‰, respectively. Similarly, the $\delta^{15}\text{N}$ values for anadromous masu salmon and white-spotted char (*Salvelinus leucomaenis*) were $>10\text{‰}$ (Table 2), reflecting the marine signature. The $\delta^{13}\text{C}$ value of anadromous masu salmon was greater than that of other anadromous salmon.

The freshwater ecosystem

Stable isotope values of biofilm and aquatic invertebrates were higher during the spawning period in the spawning river than before spawning or in the control river (Table 2). In particular, the isotopic signature of

Table 2 The $\delta^{13}\text{C}$ (‰), $\delta^{15}\text{N}$ (‰) and MDN enrichment (%) of organisms in the Rusha and Akai Rivers in 2007–09

	Rusha River (Before)		Rusha River (After)		Akai River (Before)		Akai River (After)		MDN enrichment					
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n	MDN	enrichment	Range		
Spawner														
<i>Oncorhynchus gorbuscha</i>				-21.6 ± 0.6	10.2 ± 0.2	24								
<i>Oncorhynchus gorbuscha</i> (egg)				-22.2 ± 0.3	10.8 ± 0.3	10								
Biofilm	-16.0 ± 1.4	-1.5 ± 0.3	8	-15.9 ± 1.5	2.6 ± 0.8	8	-14.4 ± 1.2	-2.6 ± 1.4	8	-15.8 ± 1.3	-2.6 ± 0.7	8	39 ± 6.6	24–50
Aquatic invertebrates														
Shredder														
<i>Protonemura</i> sp.	-24.2 ± 1.0	-0.2 ± 0.5	8	-22.2 ± 0.4	0.4 ± 0.1	8	-24.8 ± 0.8	-0.7 ± 1.0	8	-24.6 ± 1.1	-1.3 ± 0.4	8	7 ± 1.7	3–10
Filter-feeder														
<i>Stenopsyche marmorata</i>	-21.7 ± 0.9	1.9 ± 0.1	16	-17.4 ± 1.2	4.3 ± 0.4	16	-23.9 ± 0.9	-0.3 ± 0.2	16	-25.0 ± 0.7	-0.2 ± 0.1	16	16 ± 3.0	5–21
Collector-gatherer														
<i>Orthocladus</i> spp.	-22.7 ± 2.8	-1.2 ± 1.2	12	-18.1 ± 1.2	4.8 ± 0.6	12	-24.5 ± 0.8	-1.8 ± 0.6	12	-23.0 ± 1.1	-1.5 ± 0.5	12	46 ± 1.9	29–56
Grazer														
<i>Epeorus latifolium</i>	-18.8 ± 1.4	-0.2 ± 0.7	12	-16.9 ± 0.6	3.4 ± 0.8	12	-21.4 ± 1.0	-1.9 ± 0.7	12	-23.2 ± 0.7	-2.2 ± 0.4	12	19 ± 4.3	6–31
Predator														
<i>Rhyacophila</i> sp.	-21.6 ± 1.7	1.3 ± 0.8	8	-18.1 ± 1.6	4.0 ± 0.4	8	-21.9 ± 0.8	-0.4 ± 0.3	8	-22.8 ± 0.4	0.0 ± 0.2	8	15 ± 2.2	9–20
Salmonids														
<i>Salvelinus malma</i>	-20.6 ± 0.2	10.3 ± 0.4	39	-20.4 ± 0.3	9.6 ± 0.2	32	-20.0 ± 1.1	5.0 ± 0.4	18	-21.1 ± 1.4	4.8 ± 0.8	18	31 ± 1.7	14–43
<i>Salvelinus leucomaenis</i> (anadromous)				-21.3	13.5	1								
<i>Oncorhynchus masou</i>	-21.6 ± 0.4	6.2 ± 1.1	5	-21.4 ± 0.5	7.2 ± 1.1	11				-24.3 ± 0.6	4.2 ± 0.2	5	13 ± 4.0	4–26
<i>Oncorhynchus masou</i> (anadromous)				-18.5	14.0	1								

Data: mean ± SE

biofilm and the collector-gatherer *Orthocladus* spp. suggested significant enrichment from MDN during the spawning period (Table 2). The $\delta^{15}\text{N}$ values for Dolly Varden collected in the spawning river were 5‰ higher than that in the control river both before and after spawning (Table 2). The isotopic values for masu salmon were higher during the spawning season in the Rusa River than that in the Akai River (Table 2). Thus, the marine nutrients from spawning salmon were transferred to the various freshwater species (Fig. 2).

The $\delta^{15}\text{N}$ of biofilm and all other aquatic invertebrates showed significant interactions (two-way ANOVA with Bonferroni correction; all $P < 0.001$) with Before/After spawning and Control/Impact river (Table 3). There were no significant interactions for the $\delta^{13}\text{C}$ of biofilm and aquatic invertebrates (two-way ANOVA with Bonferroni correction, all $P > 0.05$; Table 3). Dolly Varden showed no significant interaction for either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$, but great difference between rivers in $\delta^{15}\text{N}$ (two-way ANOVA with Bonferroni correction, $P < 0.001$, Table 3).

Dolly Varden fed primarily on aquatic invertebrates during the pre-spawning period in the spawning (Rusha) river (Fig. 3). However, they shifted from aquatic invertebrates to pink salmon eggs and sea lice during the spawning period. Few terrestrial invertebrates were observed in stomach contents during the sampling period (Fig. 3). In the control river, Dolly Varden primarily consumed aquatic invertebrates during July to October (Fig. 3). The condition factor of Dolly Varden in the spawning river after salmon spawning was significantly

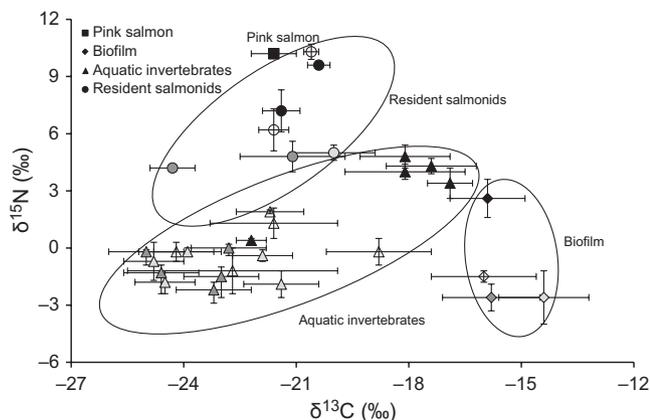


Fig. 2 Trophic shifts in freshwater biota in the Rusa and Akai Rivers from the pre-spawning to spawning periods. Different shapes reflect different trophic elements (diamond, biofilm; triangle, aquatic invertebrates; circle, resident salmonids; square, spawning pink salmon), and shading indicates the difference of time and location [open symbols: Rusa River (Before), solid symbols: Rusa River (After), heavily shaded symbols: Akai River (Before) and lightly shaded symbol (After spawning)]. Data: mean \pm 1 SE

higher than that in the control river (U -test, $P < 0.05$; Fig. 4).

The riparian ecosystem

We counted a total of 412 salmon carcasses killed by bears and 1024 senescent carcasses in the riparian area between 22 September and 8 October 2009 (Fig. 5). Almost all the senescent carcasses observed in the riparian area on 5 October had been carried there by a flood over the banks 2 days before.

Riparian vegetation collected within 10 m of the spawning river had significantly higher $\delta^{15}\text{N}$ values than vegetation collected along the control river (U -test, $P < 0.05$; Table 4). However, there was no difference in the isotopic signature of Manchurian alder between the two rivers (U -test, $P > 0.05$; Table 4). Therefore, MDN enrichment of riparian vegetation ranged between 20 and 30% at spawning sites, except for Manchurian alder, which had a lower uptake of MDN (4%). The nitrogen isotopic values of riparian willow were negatively correlated with distance from the river ($r^2 = 0.92$, $P < 0.05$; Fig. 6) in the spawning river. In contrast, in the control river, distance from the river had no effect on the $\delta^{15}\text{N}$ values of willow foliage (Fig. 6). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of blowfly (*Calliphora* spp.) larvae colonising salmon carcasses were both higher than that in the adults (U -test, $P < 0.05$; Table 4). Bear hair collected during the pink salmon spawning period ($\delta^{13}\text{C}$, -18.6‰ ; $\delta^{15}\text{N}$, 11.3‰) also indicated higher stable isotope values than that during the pre-spawning season ($\delta^{13}\text{C}$, -21.6‰ ; $\delta^{15}\text{N}$, 5.2‰). Brown bears foraging in the riparian zone derived 34% of their hair nitrogen from salmon (Table 4). In contrast to omnivorous brown bears, herbivorous sika deer had low $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($\delta^{13}\text{C}$, -26.2‰ ; $\delta^{15}\text{N}$, 3.1‰) (Table 4). These results indicate that MDN inputs altered the trophic structure of terrestrial ecosystems in the Rusa River (Fig. 7).

Discussion

Aquatic ecosystems

We found higher $\delta^{15}\text{N}$ values in biofilm during the spawning period in the Rusa River than that in the pre-spawning period. Values were also lower in the Akai River, which lacked spawning salmon. This result is consistent with other studies that have documented an increase in $\delta^{15}\text{N}$ values in biofilm during salmon spawning (e.g. Bilby *et al.*, 1996; Fisher-Wold & Hershey, 1999) or after supplementation with salmon carcasses or their analogues (Wipfli *et al.*, 1999; Kohler, Rugenski &

Table 3 Two-way ANOVA testing the effect of Before/After (before and after spawning) and Control/Impact (Rusha and Akai Rivers) on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of freshwater organisms

	River		Spawning		River \times Spawning	
	F	P	F	P	F	P
$\delta^{13}\text{C}$						
Biofilm	0.024	0.878	2.005	0.164	1.006	0.385
<i>Protonemura</i> sp.	0.495	0.491	0.629	0.545	0.275	0.763
<i>Epeorus latifolium</i>	114.511	<0.001	1.865	0.184	0.073	0.930
<i>Stenopsyche marmorata</i>	32.878	<0.001	0.456	0.641	1.724	0.207
<i>Orthocladius</i> spp.	12.946	0.002	0.063	0.939	0.562	0.580
<i>Rhyacophila</i> sp.	59.950	<0.001	2.037	0.159	2.055	0.157
<i>Salvelinus malma</i>	231.562	<0.001	0.728	0.492	0.294	0.749
$\delta^{15}\text{N}$						
Biofilm	140.670	<0.001	9.580	0.001	23.575	<0.001
<i>Protonemura</i> sp.	31.928	<0.001	5.734	0.012	6.805	0.006
<i>Epeorus latifolium</i>	124.845	<0.001	8.605	0.001	13.401	<0.001
<i>Stenopsyche marmorata</i>	200.332	<0.001	11.717	0.001	20.928	<0.001
<i>Orthocladius</i> spp.	173.646	<0.001	24.150	<0.001	17.391	<0.001
<i>Rhyacophila</i> sp.	97.449	<0.001	10.774	0.001	12.894	<0.001
<i>Salvelinus malma</i>	191.433	<0.001	1.433	0.245	0.177	0.679

Bold values: significance

Taki, 2008). However, biofilm $\delta^{13}\text{C}$ was not enriched by MDN in the Rusha River, which is consistent with the observations of Chaloner *et al.* (2002b) who concluded that marine-derived carbon is assimilated by biofilm at a lower rate than nitrogen. The carbon signature of biofilm is dominated by fixation of atmospheric CO_2 during photosynthesis (Lock *et al.*, 1984), while nitrogen is taken up from the water column (Bothwell, 1988).

Similarly, all functional feeding groups of aquatic invertebrates in the Rusha River were enriched during the salmon run. Moreover, MDN not only represent a nutritional source, but also increase the nutritional value of aquatic invertebrates, such as their energy content (Winder *et al.*, 2005). Among the invertebrates, the collector-gatherer *Orthocladius* spp. exhibited a greater enrichment in marine-derived nitrogen than other taxa. This enrichment may be due to filtering salmon particles that have been sloughed off carcasses. Interestingly, Claeson *et al.* (2006) noted an increase in the density of chironomid larvae 2 months after the addition of carcasses, which they attributed to the assimilation of MDN. Chironomids appear to use MDN more readily than other aquatic invertebrates (e.g. Wipfli *et al.*, 1999; Chaloner *et al.*, 2004; Lessard & Merritt, 2006). Because chironomids are important food for juvenile Pacific salmon (Kaeriyama, 1986), the enhancement of chironomid production (Lessard *et al.*, 2009) is likely to have a positive effect on juvenile salmon production. The transfer of MDN to aquatic invertebrates could support juvenile salmon growth and survival.

In our study, Dolly Varden fed primarily on aquatic invertebrates before the spawning season and then switched to salmon eggs. Resident salmonids often feed upon salmon eggs and carcass material when available (e.g. Reed, 1967; Bilby *et al.*, 1998; Denton *et al.*, 2010). This diet shift was associated with an increase in the condition factor of Dolly Varden in the Rusha River, as has been seen elsewhere in juvenile coho salmon (*O. kisutch*) and rainbow trout (*O. mykiss*) (Bilby *et al.*, 1998). Both the growth rate and condition factor of resident salmonids increase when they feed on eggs and salmon carcasses (Wipfli *et al.*, 2003; Lang *et al.*, 2006). The eggs of anadromous salmon are evidently an important food source for overwintering resident salmonids (Bilby *et al.*, 1998). In addition, indirect assimilation of MDN can occur through consumption of macroinvertebrates, such as mayflies and chironomids, that are themselves enriched with MDN (Hicks *et al.*, 2005). However, the $\delta^{15}\text{N}$ of Dolly Varden did not differ between pre-spawning and spawning periods, even though the Dolly Varden were feeding on salmon eggs. Dolly Varden already has a high $\delta^{15}\text{N}$ value, due to its own migration to the sea and feeding on marine organisms. The Dolly Varden in the Shiretoko Peninsula are anadromous (Umatani, Arai & Maekawa, 2008), although no other populations in Japan are migratory.

Riparian ecosystems

We estimated that brown bears transported 412 salmon carcasses to the riparian zone within a month. Earlier

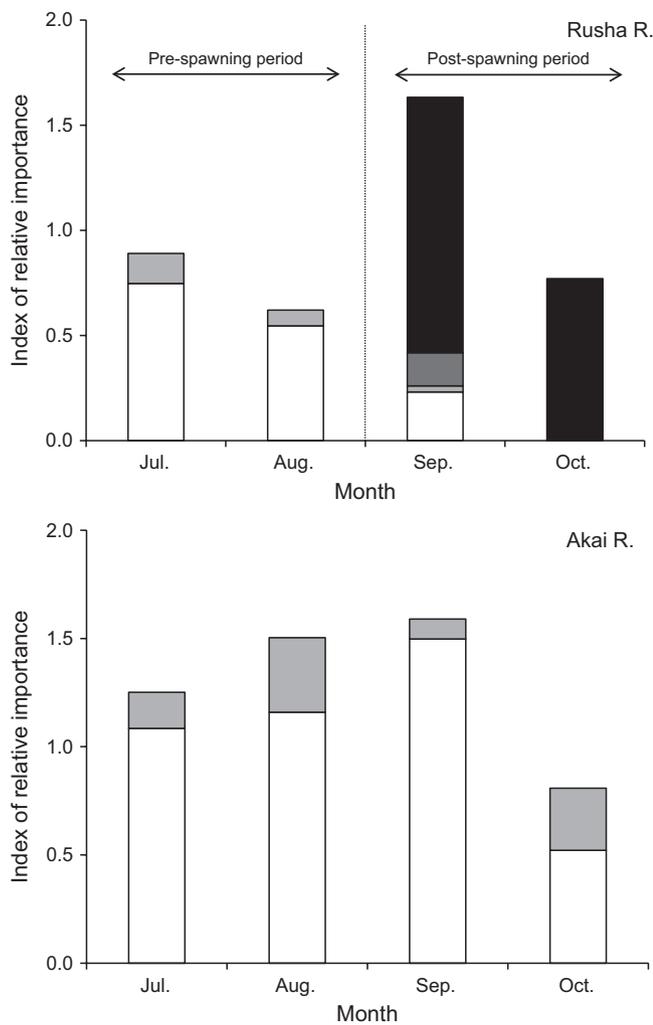


Fig. 3 The stomach contents of Dolly Varden collected from the Rusha (upper) and Akai (lower) Rivers from July to October. Food was represented by an index of relative importance (IRI; Pinkas *et al.*, 1971). Salmon eggs (solid bars), sea lice (heavily shaded bars), terrestrial invertebrates (lightly shaded bars) and aquatic invertebrates (open bars) are shown for each month. The index value (*y*-axis) was calculated as follows: $IRI = (\text{numerical composition} + \text{mass composition}) \times \text{frequency of occurrence}$.

studies demonstrated that brown bears transport MDN to terrestrial systems via their urine and faeces (Hilderbrand *et al.*, 1999a) and by physically moving salmon carcasses (Quinn *et al.*, 2009) to terrestrial habitats. For example, female brown bears transport an estimated 37 kg MDN year⁻¹ bear⁻¹ in the Kenai Peninsula, Alaska (Hilderbrand *et al.*, 1999a).

Physical processes are also important, and floods transported more than twice the numbers of carcasses into the riparian zone as were carried by bears. Ben-David *et al.* (1998) noted high $\delta^{15}\text{N}$ values in riparian vegetation associated with carcass transport by flooding. Thus, flooding probably plays an important role

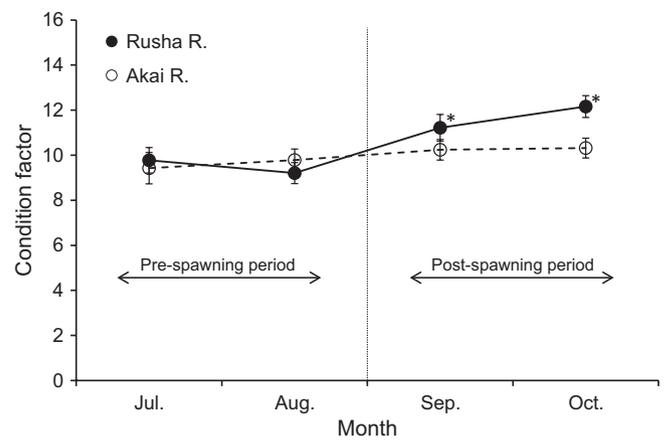


Fig. 4 Monthly change in condition factor of Dolly Varden in the Rusha and Akai Rivers during July and October. Asterisk indicates a significant *P*-value (*U*-test). **P* < 0.05. Data: mean \pm 1 SE

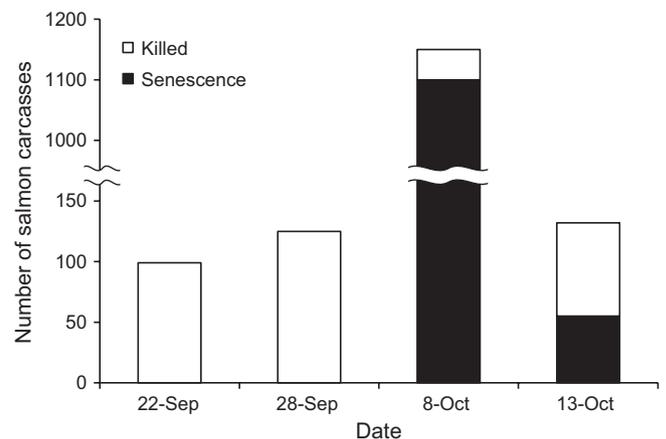


Fig. 5 Temporal change in the number of carcasses of salmon killed by bears or that died after spawning in the riparian area of the Rusha River.

in transporting salmon carcasses into riparian ecosystems.

Riparian vegetation along the Rusha River had higher $\delta^{15}\text{N}$ values than the vegetation on the Akai River (that has no migratory salmon). Further, we observed a progressive decline in $\delta^{15}\text{N}$ values in riparian willows with distance from the river, suggesting that riparian plants assimilated nitrogen from decaying salmon. Hilderbrand *et al.* (1999a) concluded that bear faeces and the decay of salmon caused by bears affect the uptake of MDN by white spruce (*Picea glauca*). In some instances, MDN are incorporated into riparian vegetation via the hyporheic zone, when nutrients from decaying salmon leach into the sediment (O’Keefe & Edwards, 2002). However, the $\delta^{15}\text{N}$ of plants may reflect microbial nitrogen processing (Schulze, Chapin & Gebauer, 1994). Furthermore, the

Table 4 The $\delta^{13}\text{C}$ (‰), $\delta^{15}\text{N}$ (‰) and MDN enrichment (%) of organisms in the riparian zones of the Rusha and Akai Rivers from 2007 to 2009

	Rusha River (Before)		Rusha River (After)		Akai River (Before)		Akai River (After)		MDN enrichment	
	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	MDN	Range
Riparian vegetation										
Herbaceous plants										
<i>Parasenecio auriculatus</i>			-29.0 ± 1.4 ^a	0.1 ± 0.6 ^a	-32.8 ± 1.1 ^a	-2.9 ± 0.6 ^b			30 ± 6.3	18–39
<i>Petasites japonicus</i>			-28.6 ± 0.3 ^a	1.6 ± 1.3 ^a	-31.8 ± 1.5 ^a	-1.5 ± 0.4 ^b			29 ± 8.7	14–48
Trees										
<i>Picea jezoensis</i>			-28.3 ± 0.2 ^a	-2.6 ± 1.3 ^a	-30.5 ± 0.9 ^a	-4.3 ± 1.1 ^b			21 ± 7.1	7–31
<i>Salix</i> spp.			-30.3 ± 1.8 ^a	0.8 ± 1.2 ^a	-30.4 ± 0.2 ^a	-1.3 ± 0.3 ^b			20 ± 2.7	6–47
<i>Alnus hirsuta</i>			-29.4 ± 1.0 ^a	-1.4 ± 0.4 ^a	-28.8 ± 1.5 ^a	-1.5 ± 0.5 ^a			4 ± 0.4	-8 to 8
Terrestrial invertebrates										
<i>Calliphora</i> spp.			-23.8 ± 0.3 ^b	9.2 ± 0.7 ^b						
<i>Calliphora</i> spp. (larvae)			-21.4 ± 1.5	13.6 ± 1.6						
Mammals										
<i>Cervus nippon</i>			-26.2 ± 1.0	3.1 ± 0.7						
<i>Ursus arctos</i>			-18.6 ± 0.2 ^b	11.3 ± 0.4 ^b					34 ± 3.0	23–45

Data: mean ± SE. Shared letters indicate no significant difference ($P < 0.05$) between periods and rivers, using Mann–Whitney U -tests.

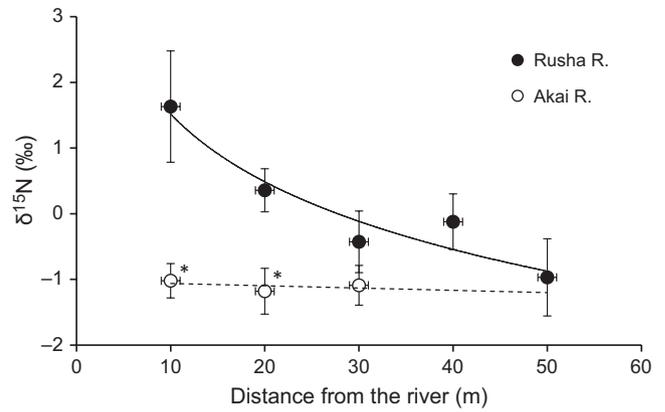


Fig. 6 Relationship between the distances (D , m) from the river and $\delta^{15}\text{N}$ values (W_N , ‰) of willow leaves in the riparian zones of the Rusha ($W_N = -1.486 \ln(D) + 4.9376$, $r^2 = 0.92$) and Akai Rivers ($W_N = -0.0035D - 1.0267$, $r^2 = 0.19$). Asterisk indicates a significant P -value (U -test). * $P < 0.05$. Data: mean ± 1 SE

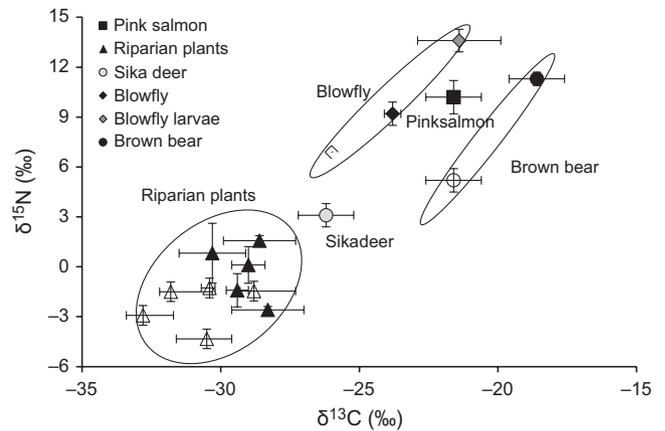


Fig. 7 Trophic structure of terrestrial biota of the Rusha and Akai Rivers in pre-spawning and spawning periods. Triangles represent riparian plants (open: Akai River, solid: Rusha River). Diamonds represent blowfly [open: pre-spawning; shaded: spawning (larvae); solid: spawning]. Circles represent terrestrial mammals (open: brown bear (pre-spawning); shaded: sika deer; solid: brown bear (spawning)). Solid square represents pink salmon. Data: mean ± 1 SE

$\delta^{15}\text{N}$ of riparian plants was more strongly affected by nitrogen fixation by alder trees than by MDN (Helfield & Naiman, 2002). Various factors influence the isotopic signature of riparian plants, so conclusions about nutrient sources must be drawn with caution.

Fly larvae had higher stable nitrogen isotopic values than adults and were more enriched than any other organism studied. In some cases, up to 50 000 individual larvae colonised a single salmon carcass (Meehan, Seminet-Reneau & Quinn, 2005). Hocking & Reimchen (2006) estimated that the biomass of dipteran larvae ranged from 38 to 195 g m⁻¹ of spawning reach, depending on the catchment and fish species. Salmon carcasses depos-

ited in riparian forest of the Rusha River certainly produced a huge number of larvae.

The increase in $\delta^{15}\text{N}$ values in bear hair following the salmon spawning season supports a shift in the diet of bear from plants to pink salmon. Hilderbrand *et al.* (1999b) noted that the $\delta^{15}\text{N}$ of brown bears feeding on salmon was higher (>10‰) than that of other bears. Taken together, these observations suggest that brown bears fed mainly on salmon during the autumn in the Rusha River basin. Brown bears are omnivorous, but generally depend primarily on plants in Hokkaido Island (Ohdachi & Aoi, 1987; Nomura & Higashi, 2000; Sato, Mano & Takatsuki, 2005). A recent study demonstrated that brown bears did not often use salmon as a food resource in eastern Hokkaido (Narita *et al.*, 2011). Our results reflect a distinctive feeding behaviour in this area among the brown bears in Japan.

The difference of MDN dynamics between the river and riparian zones

The Rusha River is characterised by coarse substrata and a high density of spawning salmon, which favours the effect of MDN on aquatic organisms (Janetski *et al.*, 2009). However, enrichment by MDN of freshwater organisms here was typically lower than that found in the better known North American examples. For instance, in natural North American streams, MDN enrichment of aquatic biota was 73% for biofilm, 40% for aquatic invertebrates (Chaloner *et al.*, 2002b) and 43% for resident salmonids (Bilby *et al.*, 1998), compared to 39, 21 and 29% in our site. In an example from north-east England, however, the contribution of MDN from spawning Atlantic salmon was apparently zero in aquatic invertebrates and 34% in juvenile salmon (Elliott, Lyle & Campbell, 1997). The lesser enrichment in the Rusha River (than in North American examples of Pacific salmon) is perhaps due to the presence of artificial structures that disrupt upstream migration by salmon, despite recent improvements to the dams (Yokoyama *et al.*, 2010). Kaeriyama & Minagawa (2008) noted that low-head dams negatively affect velocity and hyporheic flow in the Rusha River. Dams affect organic matter dynamics, water chemistry and other factors (Bunn & Arthington, 2002; Kaeriyama and Edpalina, 2004) and eliminate and/or reduce MDN input in upstream regions (Levin & Tolimieri, 2001). Furthermore, in the Rusha River, the high gradient and velocity may not allow salmon organic matter to be retained long enough to affect MDN. Large woody debris and pools play an important role in the retention of organic matter (Bilby

& Likens, 1980; Smock, Metzler & Gladden, 1989), and in the lower reaches of the Rusha River, these features are lacking due to the past deforestation. Therefore, our results suggest that dams and the fluvial environment itself affect MDN assimilation by freshwater biota.

In the Rusha River, salmon-derived MDN ranged from 20–30% of the total nitrogen in the riparian vegetation (except for alder). These proportions of MDN closely agree with other research examining the contribution of MDN to riparian vegetation near spawning streams (e.g. Helfield & Naiman, 2001; Bilby *et al.*, 2003). The transport of carcasses by brown bears and by floods is a primary route by which MDN find their way into riparian ecosystems along the Rusha River. Other vectors include emerging flies (Hocking & Reimchen, 2006) and hyporheic flow (O'Keefe & Edwards, 2002). Moreover, considerable amounts of bird faeces (gulls and hawks) are deposited in the riparian forest, resulting in another route for MDN input to the wider basin. These pathways contributed to the transport of MDN from salmon into the riparian zone at rates similar to those in North America. However, incorporation of MDN by riparian plants might also be influenced by dams. Nagasaka *et al.* (2006) reported that foliar $\delta^{15}\text{N}$ of willow collected within 10 m of the Rusha River in 2002 and 2003 was -1.87‰ , a value about 2‰ lower than we found. The passage of migrating salmon through the dams was eased in 2006, and the spawning area above the dams was thus expanded in the Rusha River. In fact, the redd capacity of pink salmon increased sixfold above the dams following improvements (Yokoyama *et al.*, 2010). These potential impacts of dams on freshwater and riparian ecosystems still persist and need more study, including the effects on spawning dynamics of anadromous salmon.

In conclusion, the dynamics of salmon-derived nutrients differ between the river and the adjacent riparian zones. Marine nutrients may not be incorporated substantially into the freshwater biota in heavily modified rivers, even if there are a large number of migratory salmon. Our study indicated an important contribution of physical and biological vectors on carcass transport, although of course these results came from a single year. These vectors play significant roles in transport of MDN from the spawning river to the riparian forest. The ecological importance of the interface between the river and the riparian forest for the cycling of marine-derived nutrients, including terrestrial predators of salmon, flooding and hyporheic flows, should be clarified in detail.

It is believed that the loss of wild salmon populations has caused a decrease in the transport of MDN to Pacific Rim ecosystems (Gresh, Lichatowich & Schoonmaker,

2000). The addition of carcass analogues, which reverses the loss of freshwater productivity, has achieved significant results in recent years (Pearsons, Roley & Johnson, 2007; Kohler *et al.*, 2008). However, these artificial nutrient supplements have different effect than the natural spawning of wild salmon (Harvey & Wilzbach, 2010; Tiegs *et al.*, 2011). Spawning salmon and their eggs are used by many aquatic and terrestrial organisms, as seasonal food resources during autumn and winter. The rehabilitation of wild salmon is significant in enhancing the productivity of freshwater and riparian ecosystems.

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