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Magnus Enbom



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Department of Wildlife, Fish, and Environmental studies

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Supervisor: Rahmat Naddafi, Dept. of Wildlife, Fish, and Environmental Studies

Assistant supervisor: Hans Lundqvist, Dept. of Wildlife, Fish, and Environmental Studies, Jan Karlsson, Umeå University

Examiner: Carin Magnhagen, Dept. of Wildlife, Fish, and Environmental Studies

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Abstract

Anadromous fish are often important vectors for nutrient fluxes between marine and freshwater ecosystems. These nutrients, termed as marine-derived nutrients (MDN), enter the stream in the form of eggs, sperm, waste and adult carcasses. Small freshwater streams often have a low primary production due to heavy shading, so these marine derived nutrients play an important role in increasing productivity of the streams food web. Pacific salmon (*Oncorhynchus spp.*) are known to contribute with MDN in the freshwaters of North America where they migrate to spawn and later die. Atlantic salmon (*Salmo salar*) and sea trout (*S. trutta*) are iteroparous, meaning that adults may return to the ocean after spawning. Therefore it is less clear if these anadromous fish can significantly contribute to spatial translocation of nutrients from the Baltic Sea to the freshwater rivers. The aim of this study was to investigate if transported nutrients incorporate into the tissues of aquatic communities and riparian plant communities. Stable isotopes were used to track marine-derived nutrients into the biota of freshwater. Field work along with laboratory analyses was done to measure the ratio of $^{13}\text{C}/^{12}\text{C}$ ($\delta^{13}\text{C}$) and $^{15}\text{N}/^{14}\text{N}$ ($\delta^{15}\text{N}$) in benthic invertebrates and primary producers (algae and riparian vegetation) collected from five streams. Two streams supported Atlantic salmon and sea trout, two streams could potentially receive other anadromous fish and one stream had a migratory obstacle. Moreover, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were estimated in tissues and eggs of reproductive individuals of Atlantic salmon and sea trout. The results from the study revealed that organisms from nearly all trophic levels are enriched with ^{15}N and ^{13}C , in the streams where Atlantic salmon spawn and the overwinter mortality occurs, indicating a significant contribution of Atlantic salmon and sea trout to nutrient dynamics of boreal stream.

Key words: Marine-derived-nutrients, Atlantic salmon, sea trout, Baltic Sea, stable isotopes

Introduction

Ecosystem services could be defined as “the benefits of nature to households, communities and economies” and the idea is that “ecosystems are socially valuable and in ways that may not be immediately intuited” (Daily 1997). It has been disputed what an ecosystem service really is, whether it is the endpoint that humans can benefit from (Boyd & Banzhaf, 2007; Wallace 2007) or the ecological mechanism behind it (Fisher and Kerry Turner 2008). However, the cycling of nutrients has been mentioned as an important ecosystem service for maintaining ecosystem functioning and resilience (Fisher & Kerry Turner, 2008; Holmlund & Hammer, 1999; Daily 1997).

According to Vanni (2002), nutrient cycling is “the transformation of nutrients from one chemical form to another, and/or flux of nutrients between organisms, habitats, or ecosystems”. De Groot et al. (2002) state that “in addition to carbon, oxygen and hydrogen, the most important nutrients are nitrogen, sulfur and phosphorous, because the availability of these elements is often a limiting factor to the growth and occurrence of life forms”. In aquatic ecosystems the focus has been on nitrogen and phosphorous because these are the nutrients that most likely limit primary producers (Vanni 2002). When speaking about nutrient cycling, one often refers to the autochthonous cycling performed by bacteria and fungi (Schlesinger 1997). However, allochthonous inputs or “nutrient translocation”, (i.e. inputs of nutrients from outside the ecosystem boundaries), could also be important in many ecosystems (Vanni 2002) and may be relatively even more important in nutrient poor systems (Jonsson and Jonsson 2003). Nutrient translocation is something that could occur across great spatial and temporal scales and could be considered as “new” nutrients which stimulates “new primary production” and increases the total amount of nutrients in the recipient ecosystem (Vanni 2002). The different role that animals play in nutrient cycling is largely dependent on degree of mobility, i.e. large animals like fish, that moves over larger distances are more likely to translocate nutrients than smaller animals like zooplankton (Vanni 2002).

In the animal kingdom there are a number of species that could translocate nutrients across ecosystems (Vanni 2002). For example, breeding colonies of seabirds contribute nutrients to nearby stream food webs by excreta, spilled food, feathers, dead chicks and abandoned eggs (Harding et al. 2004, Markwell and Daugherty 2002, Sanchez-Pinero and Polis 2000, Warham 1996). Moreover, migratory, anadromous (migrating from sea to freshwater to spawn) fish also translocate nutrients and are often important vectors of nutrient fluxes between marine and freshwater ecosystems. These nutrients are termed marine-derived nutrients (MDN) (Bilby et al. 1996) and perhaps the most known example comes from the anadromous Pacific salmon (*Oncorhynchus spp.*) (Naiman et al. 2002). In north-western North America, many species of Pacific salmon are anadromous and semelparous (they die after spawning) and up to 95% of their body mass derives from marine sources (Groot and Margolis 1991). When they migrate for spawning, these nutrients enter the freshwater stream in the form of salmon eggs, sperm, waste and adult carcasses and increase the productivity of the stream food web (Kline et al. 1990, Kline et al. 1993, Schuldt and Hershey 1995, Bilby et al. 1996, Bilby et al. 1998, , Wipfli et al. 1998, Gresh et al. 2000, Chaloner and Wipfli 2002, Chaloner et al. 2002, Schindler et al. 2003, Johnston et al. 2004). Adjacent terrestrial areas (i.e. riparian vegetation) are also enriched with MDN either via direct uptake from the roots during flooding or via activities from piscivorous predators, such as bears (Ben-David et al. 1998, Hilderbrandt et al. 1999, Helfield and Naiman 2001, Hocking et al. 2011).

When it comes to European salmonids, little research has been done. However, Elliott et al. (1997) and Lyle and Elliot (1998) studied spatial translocation of nutrients by anadromous Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta morpha trutta*) for the river Tweed in north-western England. Furthermore, Jonsson and Jonsson (2003) studied Atlantic salmon in the Norwegian River Imsa. For both river Tweed and River Imsa, MDN was incorporated into the freshwater streams (Lyle and Elliott 1998, Jonsson and Jonsson 2003). Nevertheless, the situation for the Baltic Sea is relatively unclear. Life histories of Atlantic salmon and sea trout differ from Pacific salmon in the sense that Atlantic salmon and sea trout are iteroparous (i.e. adults may return to the ocean after spawning) meaning that less nutrients would be retained in the freshwater habitat (Klemetsen et al. 2003). However, available evidence from Norwegian waters indicates that 15-60% of Kelt (i.e. postspawners) mortality occurs in freshwater habitats (Jonsson et al. 1991). Still it is less clear if Atlantic salmon and sea trout can significantly contribute to spatial translocation of nutrients from the Baltic Sea to the freshwater rivers.

The aim of this project is to investigate if transported nutrients by Atlantic salmon and sea trout incorporate into the tissues of aquatic communities and riparian plant communities. Stable isotopes were used to track MDN into the biota of freshwater. Field work along with laboratory analyses were done to measure the ratio of $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ (i.e. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in benthic invertebrates, and terrestrial and aquatic plants collected from five streams. Two streams support Atlantic salmon, two streams could potentially support other anadromous fish and one stream supports no anadromous fish since the passage is blocked by a hydropower dam.

Methods

The study was carried out in five streams during the spring of 2015, after the ice had melted but before the spring flood (Table 1).

Table 1. Overview of the studied streams, including sampling date, name of the stream, description, GPS-coordinates in SWEREF99, water temperature during sampling and an estimated water flow during sampling (Vattenwebb.smhi.se 2015). Streams with salmonids are marked with a star (*).

Date	Stream	Description	GPS coordinates	Water temperature (°C)	Est. water flow m ³ /s
28-apr-15	Vindelälven, Djupseleforsen*	Salmon spawning site	N 7234116 E 0650731	0	118
28-apr-15	Umeälven, Baggböleforsen*	Overwintering mortality site	N 7088993 E 0751852	6	660 (0,3 through old riverbed)
29-apr-15	Tuggenbäcken	Tributary with migratory obstacle	N 7154229 E 684956	0	1,45
29-apr-15	Ruskträskbäcken	Tributary	N 7194357 E 0678424	3	8,4
30-apr-15	Hjuksån	Tributary	N 7145962 E 0721988	3	13,4

The streams were distributed across the county of Västerbotten (Fig.1) and represented a gradient of possible marine input. The streams that were used in the study were Djupseleforsen (Vindelälven), Baggböleforsen (Umeälven), Tuggenbäcken (Umeälven tributary), Ruskträskbäcken (Vindelälven tributary) and Hjuksån (Vindelälven tributary). Djupseleforsen was selected because it is probably the biggest spawning site for salmon throughout the Vindelälven (Daniel Holmqvist personal communication) and Baggböleforsen was selected because it is assumed to have a high winter mortality of salmon and sea trout downstream from the hydropower station in Stornorrfors (Daniel Holmqvist personal communication). The other three streams acted as reference areas where Atlantic salmon were neither spawning nor dying. They were all tributaries, of similar size and appearance, to the bigger mountain rivers Vindelälven and Umeälven. Tuggenbäcken supports no anadromous fish because the passage is blocked by a hydropower dam, but Hjuksån and Ruskträskbäcken could potentially support other anadromous fish since they have no migratory obstacle.



Figure 1. Map of the five studied streams in the county of Västerbotten (kso2.lantmateriet.se 2015). Streams with salmonids are marked with a star (*).

The purpose of the study was to investigate if MDN transported by Atlantic salmon and sea trout were incorporated into the freshwater ecosystems. Therefore, samples consisted of riparian vegetation, algae and benthic invertebrates (Table 2). For benthic invertebrates it was desirable to get organisms from different functional feeding groups to represent the food chain, i.e. mayflies (*Baetis*, *Ephemera*, Heptageniids) are typically grazers that scrape algae from stones while stoneflies (Plecoptera) and caddisflies (Trichoptera) are typically predators which predate on other invertebrates (Merritt and Cummins 1978). The most important goal was to get the same kind of organisms of the same size for all streams to get a good comparison. However, due to seasonal scarcity this goal could not always be achieved for all streams. This also applies to algae and especially riparian vegetation for which it was hard to find the same species on all sites. In Hjuksån it was not possible to

sample primary producers due to the lack of riparian plant and algae in early spring. In addition, it was not possible to sample fish (top trophic level) in the streams because of unsuitable conditions for electrofishing. Benthic invertebrates were identified to the highest-taxonomic resolution possible, usually down to genus level. Reproductive individuals of Atlantic salmon and sea trout were taken separately during the autumn of 2013 at Stornorrfor's fish ladder when they were migrating upstream for spawning. The purpose of including them was to assess if these fish from Baltic Sea contained virtually high values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in their body and eggs.

Table 2. Overview of the samples collected for the study consisting of riparian vegetation, algae, benthic invertebrates and fish.

Samples	Type of organism
Riparian vegetation	A mix of different herbaceous plants and blueberry.
Algae	Algae
Benthic invertebrates	<i>Baetis</i> (genus) <i>Ephemerella</i> (genus) Heptageniids (family) <i>Hydropsyche</i> (genus) Plecoptera (order)
Reproductive fish	Atlantic salmon and Sea trout

Riparian vegetation was collected at the sampling sites and stored in plastic bags. Algae were collected by taking 5 large stones at each sampling site from different locations in the stream in order to achieve a good replication. These stones were later scrubbed with a tooth brush in the lab in order to remove the algae. Benthic invertebrates were collected by kicking the streambed upstream from a mesh net with the size of 200- μm . Collected invertebrates were emptied onto an enamel pan to sort out the organisms which were then stored in a cooling box for transportation to the lab (Bilby et al. 1996). The invertebrates were kept alive for 48 hours in filtered (Whatman GF/F) stream water for gut evacuation (Premke et al. 2010). Dorsal muscle tissue samples were taken from fish and were rinsed in a 10% solution of HCl to remove inorganic carbonates and then in distilled water (Bilby et al. 1996). Riparian vegetation was oven-dried at 60 degrees Celsius for 2 days (Premke et al. 2010) while algae, benthic invertebrates and fish were freeze-dried for 2 days. The samples were then ground into a powder and put into aluminum capsules until analysis. Normally the analysis could be carried out directly afterwards, otherwise the samples were stored over silica gel desiccant (Bilby et al. 2001). Mostly three samples of each organism were prepared and analyzed (Premke et al. 2010).

The analyzes were performed at SLU in Umeå with an isotope-ratio mass spectrometer and the ratios were expressed as $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (Premke et al. 2010). These values correspond to the level of enrichment or depletion compared to a standard value (Peterson and Fry 1987). For N the standard is air and for C the standard is a marine limestone called Peedee Belemnite (Peterson and Fry 1987). The values are calculated as:

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

R is the ratio of heavy isotope to light isotope. Higher values of $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ means there are higher proportions of the heavier isotope in the sample, which indicates marine origin

since marine $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ are generally heavier than freshwater $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Peterson and Fry 1987). A two-way analysis of variance (ANOVA) was performed to test the effect of stream and benthic invertebrates separately on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. This analysis was followed by a post-hoc (Bonferroni) test for multiple comparisons and for assessing the effects of invertebrate identity on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. The effect of primary producers on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values was analyzed with a two-way ANOVA that considered riparian plants and algae as main effects. Furthermore, a two-way ANOVA with fish species and egg/muscle as fixed factors was used separately for comparison of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values estimated in egg and tissue of fish parents.

Results

Benthic invertebrates

$\delta^{15}\text{N}$

$\delta^{15}\text{N}$ varied among streams and benthic invertebrates (Table 3, Fig. 2 & Fig. 3).

Benthic invertebrates in Baggböleforsen (mortality site) exhibited the highest values of $\delta^{15}\text{N}$, followed by the invertebrates in Djupseleforsen (spawning site) and Tuggenbäcken (Bonferroni test, $P < 0.001$, Table 4). There were no significant differences in $\delta^{15}\text{N}$ values of benthic invertebrates between Djupseleforsen and Tuggenbäcken ($P > 0.05$, Table 4). Among streams, Ruskträskbäcken represented the lowest $\delta^{15}\text{N}$ values for the collected invertebrates ($P > 0.05$, Table 4). Bonferroni test revealed the highest $\delta^{15}\text{N}$ values for *Hydropsyche* (Fig. 3A) and the lowest $\delta^{15}\text{N}$ values for *Ephemerella* (Fig. 2A) (Table 5, $P < 0.001$). Plecoptera (Fig. 3B), Heptageniids, and *Baetis* (Fig. 2B & 2C) had similar $\delta^{15}\text{N}$ values (Table 5, $p > 0.05$).

A strong invertebrate \times stream interaction revealed that the effects of invertebrate on the $\delta^{15}\text{N}$ values differed among streams (Table 3). Although all invertebrate showed similar trends in enrichment with ^{15}N among streams (Fig. 2 & 3), both *Baetis* and *Ephemerella* exhibited explicitly higher $\delta^{15}\text{N}$ values in streams with salmonids (Baggböleforsen & Djupseleforsen) than other streams (Fig. 2AC). For Heptageniid and Plecoptera, Baggböleforsen and somewhat Djupseleforsen had clearly higher $\delta^{15}\text{N}$ than other streams (Fig. 2B & Fig. 3B) but *Hydropsyche* exhibited almost similar values in Baggböleforsen and Hjuksån (Fig 3A).

Table 3. Two-way ANOVA testing the effects of streams and benthic invertebrates on $\delta^{15}\text{N}$ values.

Source	Type IV Sum of Squares	df	Mean square	F	p
Stream	50.3	4	12.6	109.3	< 0.001
Benthic invertebrates	37.5	4	9.4	81.5	< 0.001
Stream \times Benthic invertebrates	30.2	12	2.6	21.9	< 0.001
Error	4.8	42	0.1		

Table 4. Bonferroni test for assessing the effect of streams with and without salmonids on $\delta^{15}\text{N}$ values. Streams with salmonids are marked with a star (*).

Bonferroni post-hoc test			
Stream (I)	Stream (J)	Mean Difference (I-J)	p
Baggböleforsen*	Djupseleforsen	2.1	< 0.001
	Hjuksån	2.7	< 0.001
	Ruskträskbäcken	3.7	< 0.001
	Tuggenbäcken	2.1	< 0.001
Djupseleforsen*	Baggböleforsen	-2.1	< 0.001
	Hjuksån	0.5	< 0.01
	Ruskträskbäcken	1.5	< 0.001
	Tuggenbäcken	-0.1	1
Hjuksån	Baggböleforsen	-2.7	< 0.001
	Djupseleforsen	-0.5	< 0.01
	Ruskträskbäcken	0.9	< 0.001
	Tuggenbäcken	-0.6	< 0.01
Ruskträskbäcken	Baggböleforsen	-3.7	< 0.001
	Djupseleforsen	-1.5	< 0.001
	Hjuksån	-0.9	< 0.001
	Tuggenbäcken	-1.6	< 0.001
Tuggenbäcken	Baggböleforsen	-2.1	< 0.001
	Djupseleforsen	0.1	1
	Hjuksån	0.6	< 0.001
	Ruskträskbäcken	1.6	< 0.01

Table 5. Bonferroni test for assessing the effect of invertebrate identity on $\delta^{15}\text{N}$ values.

Bonferroni post-hoc test			
Benthic invertebrates (I)	Benthic invertebrates (J)	Mean Difference (I-J)	p
Baetis	Heptageniids	0.1	1
	<i>Hydropsyche</i>	-1.7	< 0.001
	<i>Ephemerella</i>	1.1	< 0.001
	Plecoptera	0.1	1
Heptageniids	<i>Baetis</i>	-0.1	1
	<i>Hydropsyche</i>	-1.8	< 0.001
	<i>Ephemerella</i>	.9	< 0.001
	Plecoptera	-0.1	1
Hydropsyche	<i>Baetis</i>	1.7	< 0.001
	Heptageniids	1.8	< 0.001
	<i>Ephemerella</i>	2.8	< 0.001
	Plecoptera	1.8	< 0.001
Ephemerella	<i>Baetis</i>	-1.1	< 0.001
	Heptageniids	-0.9	< 0.001
	<i>Hydropsyche</i>	-2.8	< 0.001
	Plecoptera	-0.9	< 0.001
Plecoptera	<i>Baetis</i>	-0.1	1
	Heptageniids	0.1	1
	<i>Hydropsyche</i>	-1.8	< 0.001
	<i>Ephemerella</i>	0.9	< 0.001

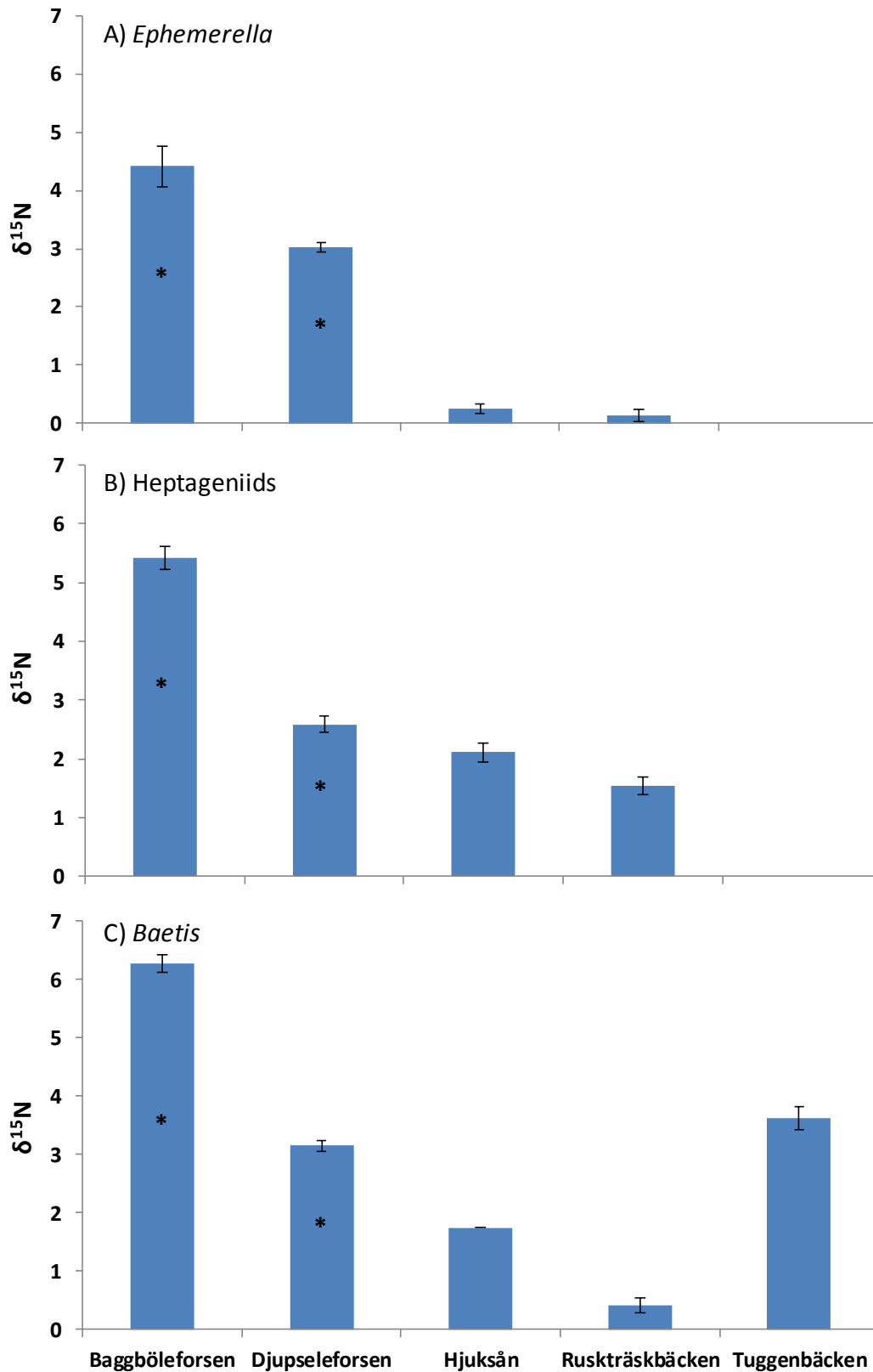


Figure 2. $\delta^{15}\text{N}$ Values (Mean \pm standard error) for *Ephemera* (A), Heptageniids (B), and *Baetis* (C) in streams. Streams with salmonids are marked with a star (*).

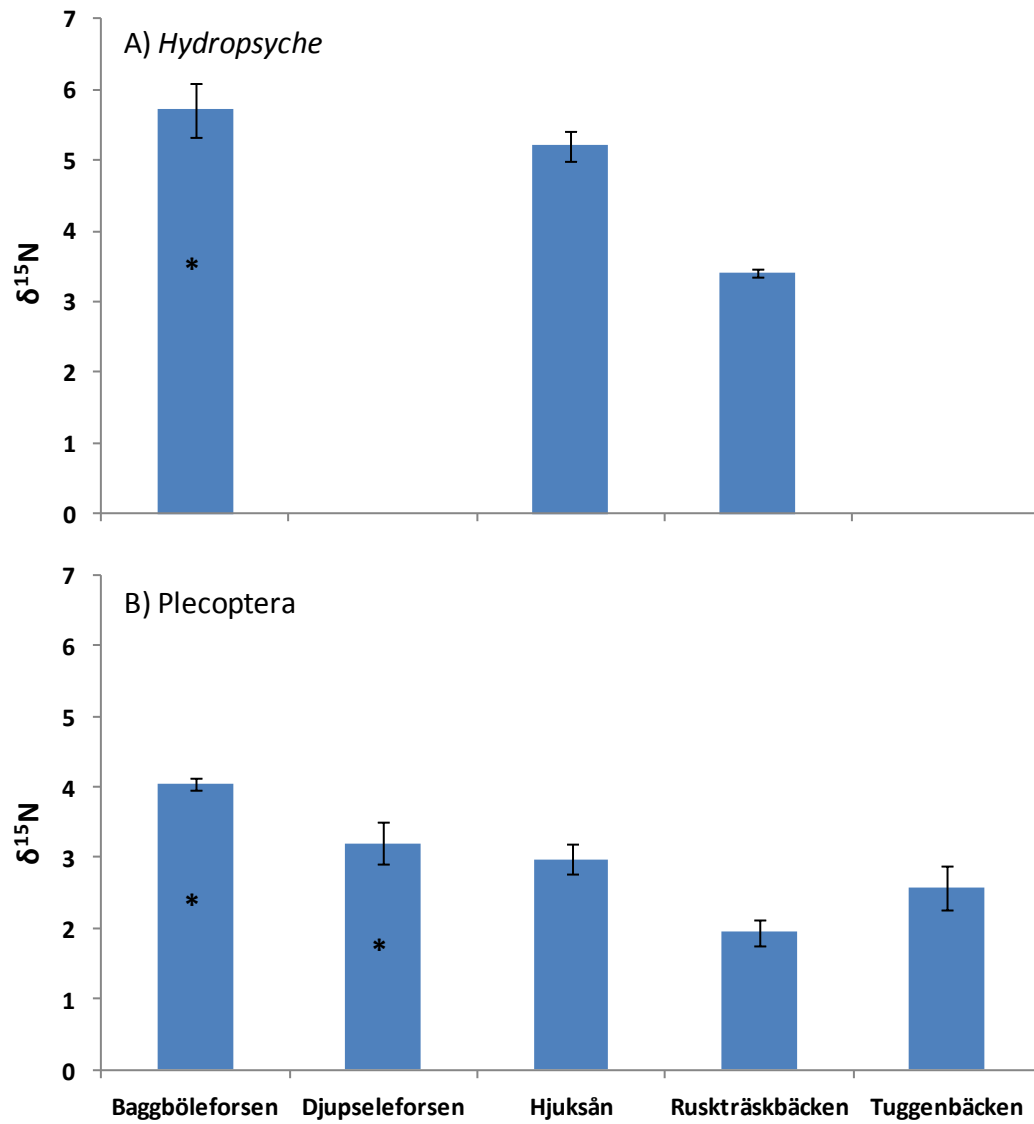


Figure 3. $\delta^{15}\text{N}$ Values (Mean \pm standard error) for *Hydropsyche* (A) and Plecoptera (B) in streams. Streams with salmonids are marked with a star (*).

$\delta^{13}\text{C}$

There were significant differences in $\delta^{13}\text{C}$ values among streams and benthic invertebrates (Table 6, Fig.4 & Fig. 5).

Benthic invertebrates in Baggböleforsen presented the highest values of $\delta^{13}\text{C}$, followed by Djupseleforsen (Bonferroni test, $P < 0.001$, Table 7, Fig.4 & Fig. 5). The invertebrates in Hjuksån, Ruskträskbäcken and Tuggenbäcken had similar values of $\delta^{13}\text{C}$ ($P > 0.05$, Table 7, Fig.4 & Fig. 5).

Heptageniids and *Hydropsyche* exhibited the highest values of $\delta^{13}\text{C}$ among benthic invertebrates (Bonferroni test, $P < 0.001$, Table 8, Fig.4 & Fig. 5). $\delta^{13}\text{C}$ values for Plecoptera were intermediate and the lowest values were observed for *Baetis* and *Ephemerella* ($P < 0.001$, Table 8, Fig.4 & Fig. 5).

The effects of invertebrate on the $\delta^{13}\text{C}$ values varied among streams, as indicated by the significant invertebrate \times stream interaction ($P < 0.001$, Table 6). Although all invertebrates showed high enrichment with ^{13}C in Baggböleforsen and Djupseleforsen (Fig. 4 & Fig. 5) mayflies (Heptageniids and *Baetis*) had higher $\delta^{13}\text{C}$ values (Fig. 4BC) and stoneflies had lower $\delta^{13}\text{C}$ values in Ruskträskbäcken than Hjuksån (Fig. 5A), respectively.

Table 6. Two-way ANOVA testing the effects of streams and benthic invertebrates on $\delta^{13}\text{C}$ values

Source	Type IV Sum of Squares	df	Mean square	F	p
Stream	391.5	4	97.9	108.5	< 0.001
Benthic invertebrates	166.2	4	41.6	46.1	< 0.001
Stream \times Benthic invertebrates	48.5	12	4.0	4.5	< 0.001
Error	37.9	42	0.9		

Table 7. Bonferroni test for assessing the effect of streams with and without salmonids on $\delta^{13}\text{C}$ values. Streams with salmonids are marked with a star (*).

Bonferroni post-hoc test			
Stream (I)	Stream (J)	Mean Difference (I-J)	p
Baggböleforsen *	Djupseleforsen	1.7	< 0.001
	Hjuksån	9.2	< 0.001
	Ruskträskbäcken	8.4	< 0.001
	Tuggenbäcken	8.0	< 0.001
Djupseleforsen *	Baggböleforsen	-1.7	< 0.001
	Hjuksån	7.5	< 0.001
	Ruskträskbäcken	6.8	< 0.001
	Tuggenbäcken	6.3	< 0.001
Hjuksån	Baggböleforsen	-9.2	< 0.001
	Djupseleforsen	-7.5	< 0.001
	Ruskträskbäcken	-0.7	0.447
	Tuggenbäcken	-1.1	0.182
Ruskträskbäcken	Baggböleforsen	-8.4	< 0.001
	Djupseleforsen	-6.8	< 0.001
	Hjuksån	0.7	0.447
	Tuggenbäcken	-0.4	1
Tuggenbäcken	Baggböleforsen	-8.0	< 0.001
	Djupseleforsen	-6.4	< 0.001
	Hjuksån	1.1	0.182
	Ruskträskbäcken	0.4	1

Table 8. Bonferroni test for assessing the effect of invertebrate identity on $\delta^{13}\text{C}$ values

Bonferroni post-hoc test			
Benthic invertebrates (I)	Benthic invertebrates (J)	Mean Difference (I-J)	p
Baetis	Heptageniids	-3.7	< 0.001
	<i>Hydropsyche</i>	-3.9	< 0.001
	<i>Ephemerella</i>	-0.1	1
	Plecoptera	-1.3	< 0.01
Heptageniids	<i>Baetis</i>	3.8	< 0.001
	<i>Hydropsyche</i>	-0.1	1
	<i>Ephemerella</i>	3.6	< 0.001
	Plecoptera	2.5	< 0.001
Hydropsyche	<i>Baetis</i>	3.9	< 0.001
	Heptageniids	0.1	1
	<i>Ephemerella</i>	3.8	< 0.001
	Plecoptera	2.5	< 0.001
Ephemerella	<i>Baetis</i>	0.1	1
	Heptageniids	-3.6	< 0.001
	<i>Hydropsyche</i>	-3.8	< 0.001
	Plecoptera	-1.2	< 0.05
Plecoptera	<i>Baetis</i>	1.3	< 0.001
	Heptageniids	-2.4	< 0.001
	<i>Hydropsyche</i>	-2.5	< 0.001
	<i>Ephemerella</i>	1.2	< 0.5

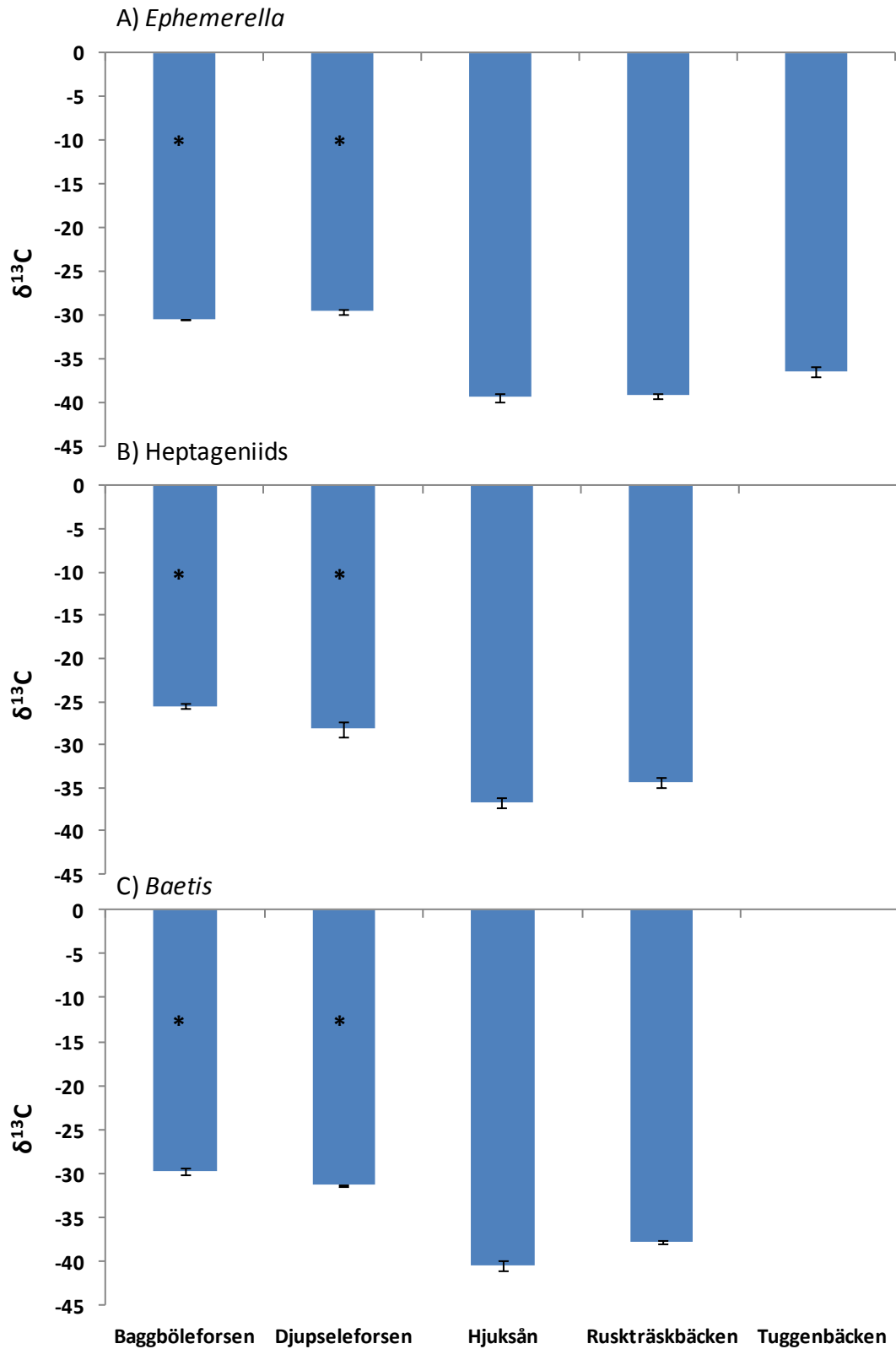


Figure 4. $\delta^{13}\text{C}$ Values (Mean \pm standard error) for *Ephemera* (A), Heptageniids (B), and *Baetis* (C) in streams. Streams with salmonids are marked with a star (*).

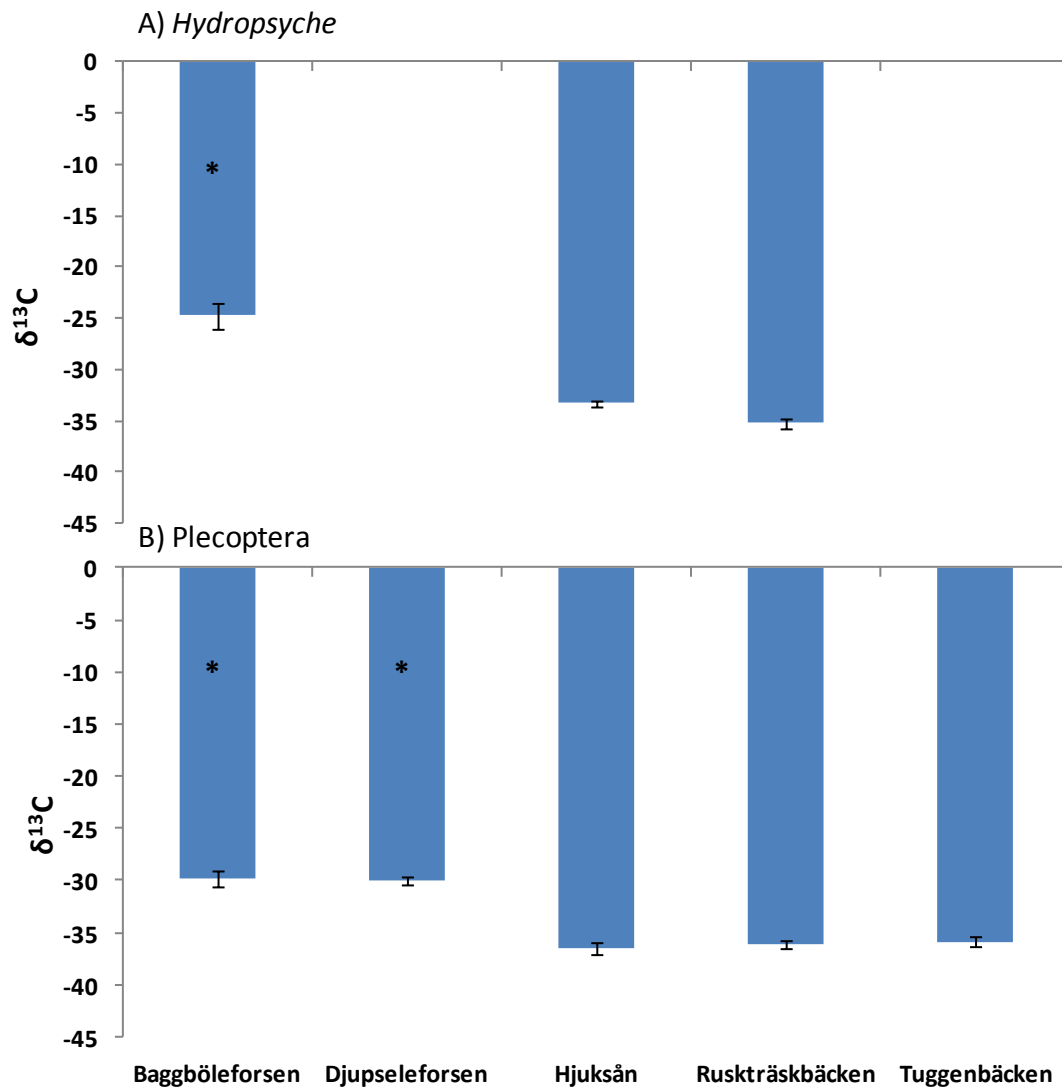


Figure 5. $\delta^{13}\text{C}$ Values (Mean \pm standard error) for *Hydropsyche* (A) and Plecoptera (B) in streams. Streams with salmonids are marked with a star (*).

Primary producers (riparian plants & algae)

$\delta^{15}N$

$\delta^{15}N$ varied among streams and primary producers (riparian plants & algae) ($P < 0.001$, Table 9, Fig. 6).

The values of $\delta^{15}N$ for primary producers were the highest in Baggböleforsen followed by Djupseleforsen (Bonferroni's test, $P < 0.001$, Table 9, Fig. 6). Primary producers in Ruskträskbäcken and Tuggenbäcken had lower $\delta^{15}N$ values than corresponding samples in the streams with salmonids ($P < 0.001$, Table 9, Fig. 6), although there was no significant difference between Ruskträskbäcken and Djupseleforsen ($P > 0.05$, Table 9).

Algae were enriched with ^{15}N more than riparian plants ($P < 0.001$, Table 9, Fig. 6). A significant stream \times primary producer interaction revealed that the effects of stream on the $\delta^{15}N$ values varied among primary producers. The difference in $\delta^{15}N$ values between Baggböleforsen and Djupseleforsen was larger in riparian plants than algae (Fig. 6AB), indicating that riparian plants absorb MDN efficiently only in mortality site where nutrients released from carcasses can penetrate into the substrate. In addition, riparian plants showed lower $\delta^{15}N$ values in Djupseleforsen than Ruskträskbäcken.

Table 9. Two-way ANOVA testing the effects of streams and primary producers (riparian plants & algae) on $\delta^{15}N$ values.

Source	Type IV Sum of Squares	df	Mean square	F	p
Stream	38.3	3	12.7	132.5	< 0.001
Primary producer	27.2	1	27.2	285.1	< 0.001
Stream \times Primary producer	9.7	2	4.8	50.1	< 0.001
Error	1.3	14	0.1		

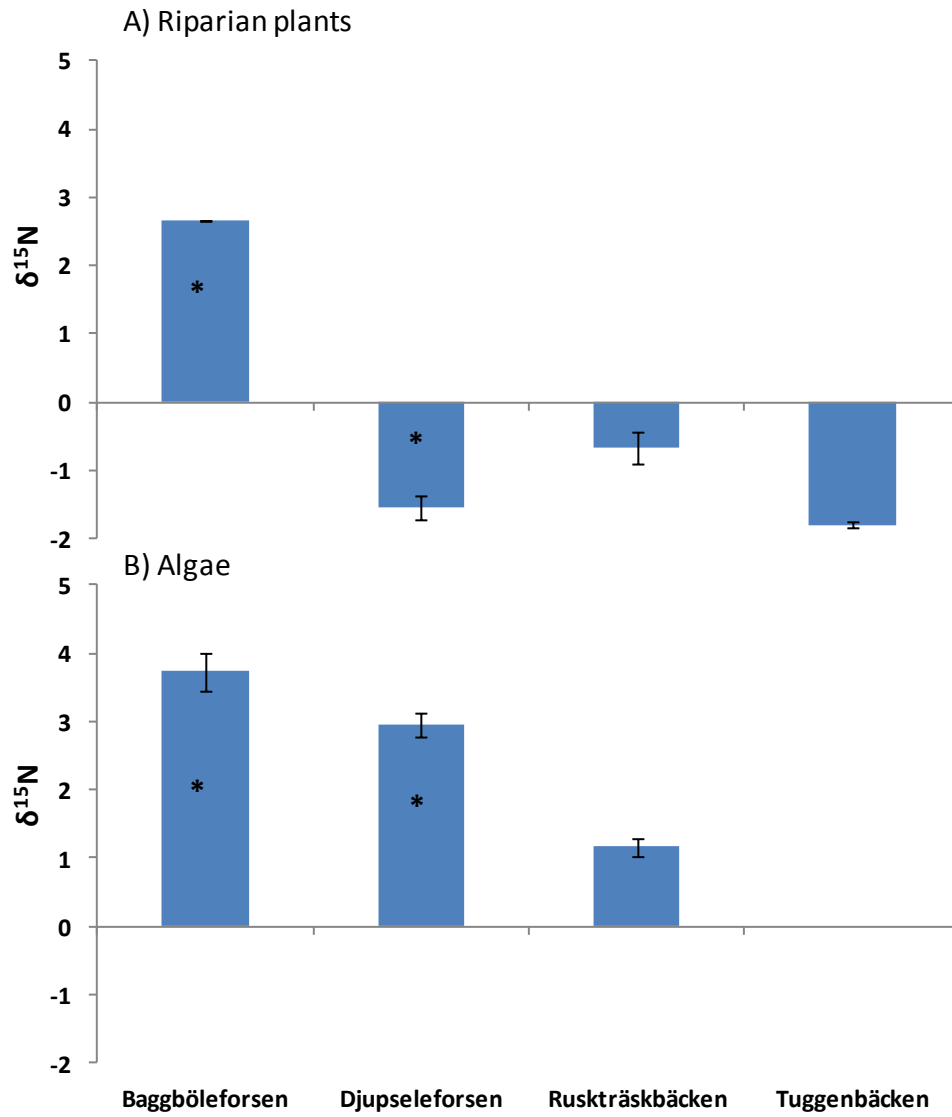


Figure 6. $\delta^{15}\text{N}$ Values (Mean \pm standard error) for Riparian Plants (A) and Algae (B) in streams. Streams with salmonids are marked with a star (*).

$\delta^{13}\text{C}$

$\delta^{13}\text{C}$ varied among streams and primary producers (Table 10, Fig.7).

The values of $\delta^{13}\text{C}$ for primary producers were the highest in Baggböleforsen followed by Djupseleforsen and Ruskträskbäcken (Bonferroni test, $P < 0.001$, Table 10, Fig. 7). Primary producers in Baggböleforsen exhibited the lowest $\delta^{13}\text{C}$ values ($P < 0.001$, Table 10, Fig. 7)

Similar to results observed for ^{15}N , algae contained higher ^{13}C than riparian plants ($P < 0.001$, Table 10, Fig. 7). The stream \times primary producer interaction was significant because the difference in $\delta^{13}\text{C}$ values between Baggböleforsen and Djupseleforsen was larger in algae than riparian plants (Table 10, Fig. 7AB).

Table 10. Two-way ANOVA testing the effects of streams and primary producers (riparian plants & algae) on $\delta^{13}\text{C}$ values.

Source	Type IV Sum of Squares	df	Mean square	F	p
Stream	22.9	3	7.6	99.9	< 0.001
Primary producer	104.2	1	104.2	1365.6	< 0.001
Stream \times Primary producer	60.9	2	30.4	398.9	< 0.001
Error	1.1	14	0.1		

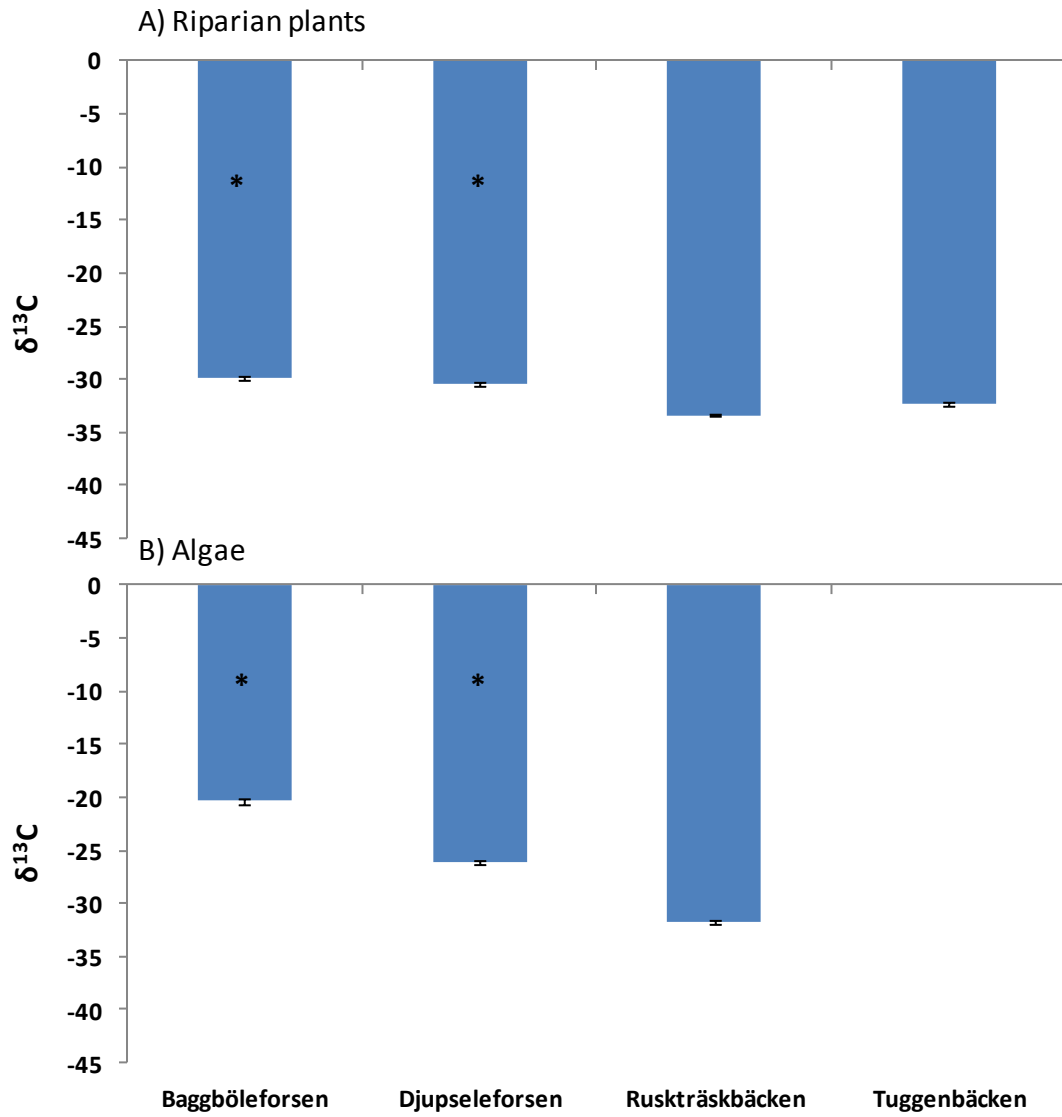


Figure 7. $\delta^{13}\text{C}$ Values (Mean \pm standard error) for Riparian Plants (A) and Algae (B) in streams. Streams with salmonids are marked with a star (*).

Reproductive fish

Both Atlantic salmon and sea trout contained high levels of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Fig. 8) in their muscle and eggs, indicating that they sequestered high amounts of MDN in their body. Atlantic salmon were more enriched with ^{15}N than sea trout ($P < 0.001$, Table 11). Fish species had no effect on $\delta^{13}\text{C}$ values of eggs and muscles ($P > 0.05$, Table 11). In Atlantic salmon, eggs were less enriched with ^{13}C and more enriched with ^{15}N than muscle ($P < 0.001$, Table 11, Fig. 8) whereas in sea trout, eggs were more enriched with both ^{15}N and $\delta^{13}\text{C}$ than muscle ($P < 0.001$, Table 11).

Fish species \times egg/muscle interactions had a strong effect on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, although their effects on $\delta^{13}\text{C}$ values were marginally significant (Table 11). The differences in enrichment with ^{15}N and ^{13}C between muscle and egg were larger in Atlantic salmon than sea trout (Fig. 8).

Table 11. Two-way ANOVA testing the effects of fish and egg & muscle on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values.

Source	Type III Sum of Squares	df	Mean square	F	p
$\delta^{15}\text{N}$					
Fish species	10.1	1	10.1	721.6	< 0.001
Egg/Muscle	3.6	1	3.6	256.9	< 0.001
Fish \times Egg/Muscle	0.2	1	0.2	10.8	< 0.05
Error	0.1	8	0.0		
$\delta^{13}\text{C}$					
Fish species	0.0	1	0.0	0.0	0.88
Egg/Muscle	9.3	1	9.3	87.2	< 0.001
Fish \times Egg/Muscle	0.5	1	0.5	5.1	0.054
Error	0.8	8	0.1		

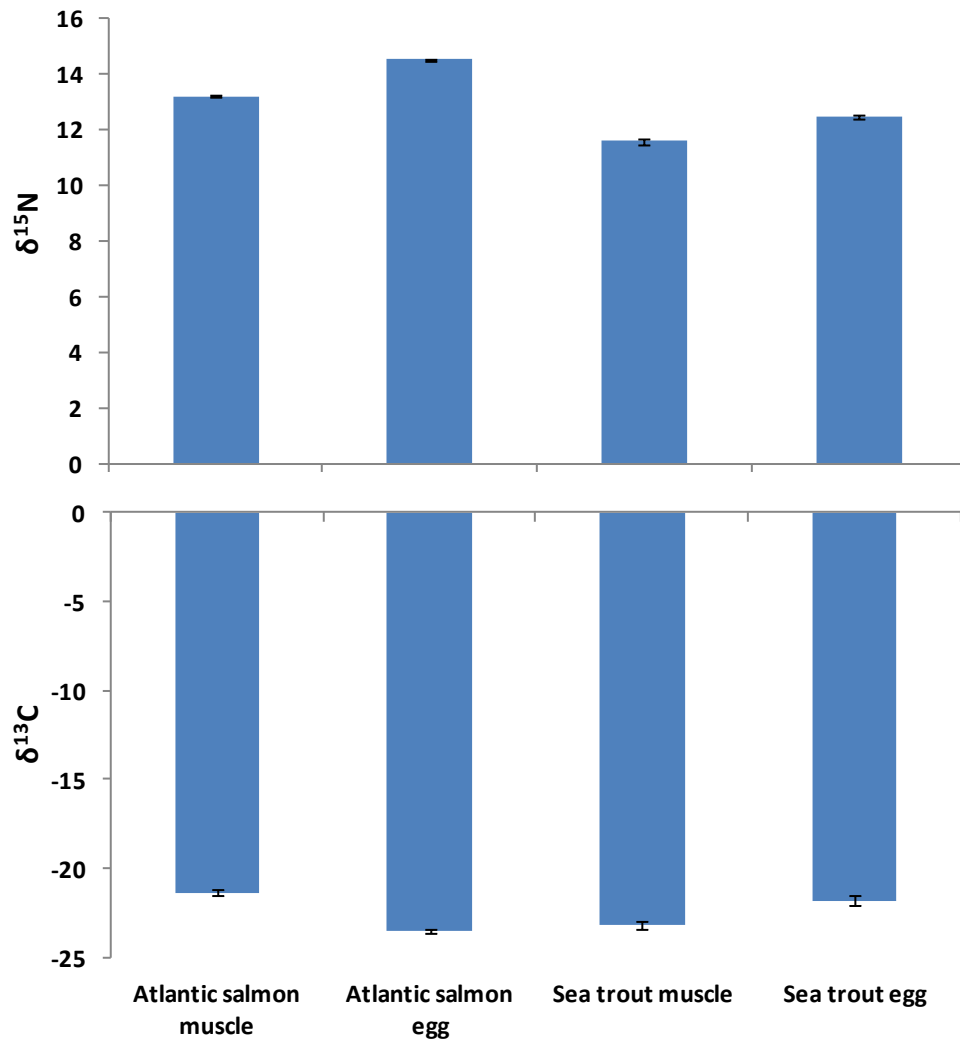


Figure 8. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (Mean \pm standard error) for Atlantic salmon and sea trout muscle and eggs.

Discussion

The results from this study showed that MDN from the Baltic Sea transported by spawning Atlantic salmon and sea trout were incorporated into the freshwater ecosystems of northern Sweden. MDN could be traced in almost all trophic levels from riparian plants to algae, benthic invertebrates and fish. This supports previous studies showing that anadromous salmonids could be important vectors for nutrient fluxes between marine and freshwater ecosystems (Bilby et al. 1996). When it comes to salmonids most of the attention so far has been directed towards the Pacific Salmon since they are semelparous and migrate in high numbers (Groot and Margolis 1991). However, recent research on Atlantic salmon living in the Atlantic ocean, has shown that they are also capable of transporting MDN into the biota of freshwater (Elliot et al. 1997, Lyle and Elliott 1998, Jonsson and Jonsson 2003). Nevertheless, the situation for the Atlantic salmon population in the Baltic Sea was until now less clear. It was uncertain if they would spawn in sufficient numbers and also if the salinity of the Baltic Sea would be enough to make MDN visible in the isotope analysis (Aarkrog et al. 1982). This study revealed that both Atlantic salmon and sea trout are able to transport a considerable amount of MDN from the sea to the streams. However, most of the MDN in the mortality site are likely transported by Atlantic salmon because a recent study demonstrated that survival rates of postspawners are 40% and 95% for Atlantic salmon and sea trout, respectively (Lundqvist et al. 2015). Interestingly, Atlantic salmon eggs were more enriched with heavier isotope of N and less enriched with the heavier isotope of C than their muscles, corresponding well to what Bilby et al. (1996) found in Pacific salmon.

In general, it was expected to see increasing levels of $\delta^{15}\text{N}$ at higher trophic levels (Peterson and Fry 1987). $\delta^{15}\text{N}$ could actually be used to estimate trophic position (Vander Zanden et al. 1999, Zanden and Rasmussen 1999, Post 2002) because for every trophic level $\delta^{15}\text{N}$ increases on average 2.4‰ (Hansson et al. 1997), which is referred to as “trophic fractionation”. $\delta^{13}\text{C}$ however, does not enrich with trophic transfer and therefore the values are the same for algae and fish (Rounick and Winterbourn 1986, Kling et al. 1992, Kelly 2000, Wipfli et al. 2011). However, for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, higher values indicate more MDN since marine N and C are generally heavier than freshwater N and C (Peterson and Fry 1987).

It was not surprising to find negative $\delta^{15}\text{N}$ values in riparian vegetation since it should be considered as normal when it comes to riparian vegetation (Bilby et al. 1996). Further, after a salmon has died, MDN most often penetrate into the substrate and are subsequently absorbed by riparian plants, either through flooding activities or via activities by piscivorous predators such as bears (Ben-David et al. 1998, Mathewson et al. 2003, Hocking et al. 2011). This could be an explanation as to why only the mortality site shows positive values of $\delta^{15}\text{N}$ for riparian plants.

$\delta^{15}\text{N}$ for Plecoptera in Hjuksån was higher than assumed. Most Plecoptera species are categorized as predators in the functional feeding group classification (Cummins and Klug 1979). However, the sampled Plecoptera of Hjuksån had a very large body size compared to the other streams and this could place them in a higher trophic position (Brose et al. 2006) and as a result their body ^{15}N could have increased (Peterson and Fry 1987).

In Tuggenbäcken, $\delta^{15}\text{N}$ values were unexpectedly high for *Baetis* and Plecoptera. One explanation could be that the sample size for Tuggenbäcken was not enough. Another possible explanation could be anthropogenic influence, i.e. sewage and land use activities

such as forestry, agriculture etc. (Stockner et al. 2000, Anderson and Cabana 2005, Jardine et al. 2009). Thus, it is possible that houses situated upstream from the sampling site in Tuggenbäcken could affect the $\delta^{15}\text{N}$ value, for example by disposing waste into the stream (Daniel Holmqvist Personal Communication). In addition, $\delta^{13}\text{C}$ values for Baetis and Plecoptera collected from Tuggenbäcken were significantly lower than values for the corresponding samples from streams supporting Atlantic salmon and sea trout, lending support to potential effect of anthropogenic sewage on $\delta^{15}\text{N}$ value in this stream. However, riparian plants in Tuggenbäcken showed the lowest $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of any of the samples collected from the streams.

Since the turnover rates of isotopes are correlated with body-mass (Post 2002) it was important to find a good timing for the sampling. When it comes to bigger organisms like fish, the isotopic signature is representative for a long period of time (Post 2002), meaning that the timing of the sampling is not very critical. But when it comes to benthic invertebrates, that have shorter turnover rates, it is more important to select the optimal time and also to sample all the streams within a short period of time to get an accurate result (Post 2002). From a turnover-rate perspective, it would have been best to sample benthic invertebrates seasonally, but due to time limitations of the study this was not possible. I decided on sampling in spring because Bilby et al. (1996) found maximum values of MDN during that season. Furthermore, the timing of sampling was after over-winter mortality when possible salmon carcasses would be fully decomposed. Spring was also the closest to spawning-time in October, and a lot of salmon fry were expected to emerge from the stream substrate (Bilby et al. 1996).

Thus, for this study one sampling occasion was considered to be enough to indicate whether or not MDN transported by spawning Atlantic salmon were incorporated into the freshwater biota. Further investigations are needed in order to test seasonal differences among organisms. Moreover, since it was not possible to find the same riparian plants for all streams there is a need for further studies. Because the results show the same trends for benthic invertebrates and algae in different streams, it is likely that MDN may also be incorporated into riparian plants.

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