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Carcass analogues provide marine subsidies for macroinvertebrates and juvenile Atlantic salmon in temperate oligotrophic streams

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SUMMARY

1. Anadromous fish populations entering freshwater ecosystems provide organic matter and marine-derived nutrients during spawning and subsequent mortalities of adults. Dams and other impediments to connectivity in rivers and streams have affected anadromous fish populations in many regions and prevented or reduced this influx of organic materials and nutrients.

2. This study used historical data on the timing of delivery of marine-derived nutrients; we added a carcass analogue (pellets made from the carcasses of Chinook salmon, *Oncorhynchus tschawytcha*) to simulate potential effects of restored access of anadromous fish to streams. We used stable isotopes to document the extent of nutrient incorporation of nitrogen and carbon from the carcass analogue by macroinvertebrates and juvenile Atlantic salmon (*Salmo salar*) in salmon nursery streams. We stocked four headwater streams that historically hosted spawning Atlantic salmon and sea lamprey (*Petromyzon marinus*) in Maine, U.S.A. with Atlantic salmon fry and simulated timing of nutrient addition by spawning sea lamprey in the early summer and Atlantic salmon in the autumn.

3. Macroinvertebrates and Atlantic salmon assimilated nitrogen (12–57% of total N) and carbon (21–65% of total C) from the added pellets, and the magnitude and duration of enrichment varied temporally and with macroinvertebrate functional feeding group.

4. Assimilation of nutrients from carcass analogues was both direct and indirect, and a nutrient legacy was evident in the second year of sampling. Incorporation of nutrients from the pellets at a range of heights in the food web demonstrated the potential for marine-derived subsidies to contribute to freshwater ecosystem processes in Atlantic salmon nursery streams.

Keywords: anadromous, Atlantic salmon, macroinvertebrate, marine-derived nutrients, stable isotopes

Introduction

Anadromous fish reproduce and spend their early years in fresh water, migrate to the ocean for a growth phase and return to fresh water as adults to spawn. During this spawning migration, they transport organic matter and marine-derived nutrients assimilated in the ocean into freshwater systems (Bilby, Fransen & Bisson, 1996). These carbon compounds and nutrients, which are added to freshwater ecosystems as carcasses, eggs and metabolic waste products, can be an ecologically significant contribution to the system (Cederholm *et al.*, 1999; Stockner & Ashley, 2003; Thomas *et al.*, 2003). When marine nutrient subsidies are reduced or lost, freshwater systems can be less productive (Stockner & Ashley, 2003). The restoration of anadromous fish can increase productivity in freshwater communities, especially in oligotrophic systems where productivity has declined from historical levels (Naiman *et al.*, 2002).

Most research focussing on the restoration of marine-derived nutrients has been concentrated in the Pacific Northwest and Alaska, where assemblages of anadromous fish are dominated by semelparous salmonines (Chaloner *et al.*, 2002; Claeson *et al.*, 2006; Kohler,

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Rugenski & Taki, 2008). Nutrients from semelparous Pacific salmon (*Oncorhynchus* spp.) come from the body mass of all spawners, eggs that fail to hatch and metabolic by-products while in fresh water (Wipfli, Hudson & Caouette, 1998). Most spawning events occur in the autumn, when temperature and productivity are reduced in lotic systems (Morin, Lamoureux & Busnarda, 1999; Huryn & Wallace, 2000).

Anadromous fish in eastern North America have more diverse life histories with greater variation in spawning event timing than in the west. Anadromous taxa in eastern North America include one species of salmon, Atlantic salmon (*Salmo salar*), several alosines (*Alosa* spp.), striped bass (*Morone saxatilis*), two species of sturgeon (*Acipenser* spp.), rainbow smelt (*Osmerus mordax*), Atlantic tomcod (*Migrogadus tomcod*) and sea lamprey (*Petromyzon marinus*). As Pacific salmon, Atlantic salmon spawn in the autumn; however, they are iteroparous, and adults may migrate to wintering grounds or return to the sea following spawning (Jonsson & Jonsson, 2003; Nislow, Armstrong & McKelvey, 2004; Williams *et al*., 2010). Nonviable eggs and metabolic waste are contributed to the spawning streams used by Atlantic salmon; the abundance of dead spawners retained in nursery streams is unknown (Nislow *et al*., 2004). Semelparous sea lampreys spawn in the same small streams used by salmon, and lampreys potentially contribute large amounts of organic materials and marine nutrients to these streams via dead spawners (Nislow & Kynard, 2009). This occurs in the spring or early summer, concurrent with increasing light, temperature, productivity and the emergence of salmon fry (Saunders, Hachey & Fay, 2006). The effect of sea lamprey spawning on the productivity of freshwater communities is not known (Nislow & Kynard, 2009).

Restoring subsidies of carbon and nutrients to fresh waters that have lost spawning salmon is a conservation goal in western North American rivers and streams. Experimental nutrient additions, as inorganic fertilizers (Peterson *et al*., 1993; Slaney, Ward & Wightman, 2003; Martin, Wipfli & Spangler, 2010) and fish carcasses (Giannico & Hinch, 2007; Martin *et al*., 2010), have been used to assess the effects of marine subsidies on the recovery of aquatic systems, and such nutrient supplementation has been adopted as a restoration strategy (Griswold, Taki & Stockner, 2003; Oregon Watershed Enhancement Board, 2006). Carcass analogues have been introduced as a potential mechanism to simulate the delivery of marine-derived nutrients (Wipfli, Hudson & Caouette, 2004; Kohler *et al*., 2008, 2012; Martin *et al*., 2010), and such analogues added to Pacific salmon streams have increased their productivity in a manner similar to that achieved by the addition of carcasses themselves (Wipfli *et al*., 2004; Martin *et al*., 2010).

Pathways of assimilation of marine-derived nutrients in freshwater ecosystems can be traced using stable isotopes (Kline *et al*., 1990; Bilby *et al*., 1996; Jardine *et al*., 2009; Koshino, Kudo & Kaeriyama, 2013). Relative to freshwater and terrestrial nitrogen (N) and carbon (C), marine N and C are enriched in ^{15}N and ^{13}C. Spawning anadromous fish retain their marine isotopic values because typically they do not feed after entering fresh water (Doucett *et al*., 1999; Johansen, 2001). Marine stable isotope values maintained by spawning anadromous fish thus provide a tool to trace marine-derived nutrient assimilation in aquatic and terrestrial communities.

We examined the assimilation of nutrients from carcass analogues (pellets made from carcasses of Chinook salmon, *Oncorhynchus tschawytcha*) into a variety of freshwater organisms in low-order streams typical of spawning habitat for anadromous fish in eastern North America, but without contemporary anadromous fish runs. We used the distinct N and C stable isotope values of the carcass analogues to determine the timing and magnitude of analogue nutrient assimilation by macroinvertebrates and juvenile Atlantic salmon. The primary objective was to measure the assimilation of these nutrients in the food web, with particular regard to differences in timing of analogue assimilation. We hypothesised that adding marine-derived nutrients via carcass analogues to streams would (i) increase dissolved nutrient concentrations in stream water and (ii) result in assimilation of marine-derived nutrients by macroinvertebrates and juvenile Atlantic salmon.

Methods

Study area and experimental design

We conducted this study in four headwater tributaries of Kingsbury Stream (Kingsbury Plantation township, Piscataquis County, ME, U.S.A.) in the Penobscot River basin (Fig. 1). Small dams on tributaries of the Penobscot River inhibited fish passage beginning in the late 1700s, and the first large main stem dam was built in the 1820s (Maine Department of Marine Resources & Maine Department of Inland Fisheries and Wildlife, 2007). The basin contains thousands of culverts and at least 116 dams, 24 of which are federally licensed for hydropower (Fay *et al*., 2006). These barriers greatly impede access by anadromous fish to former spawning habitat. The

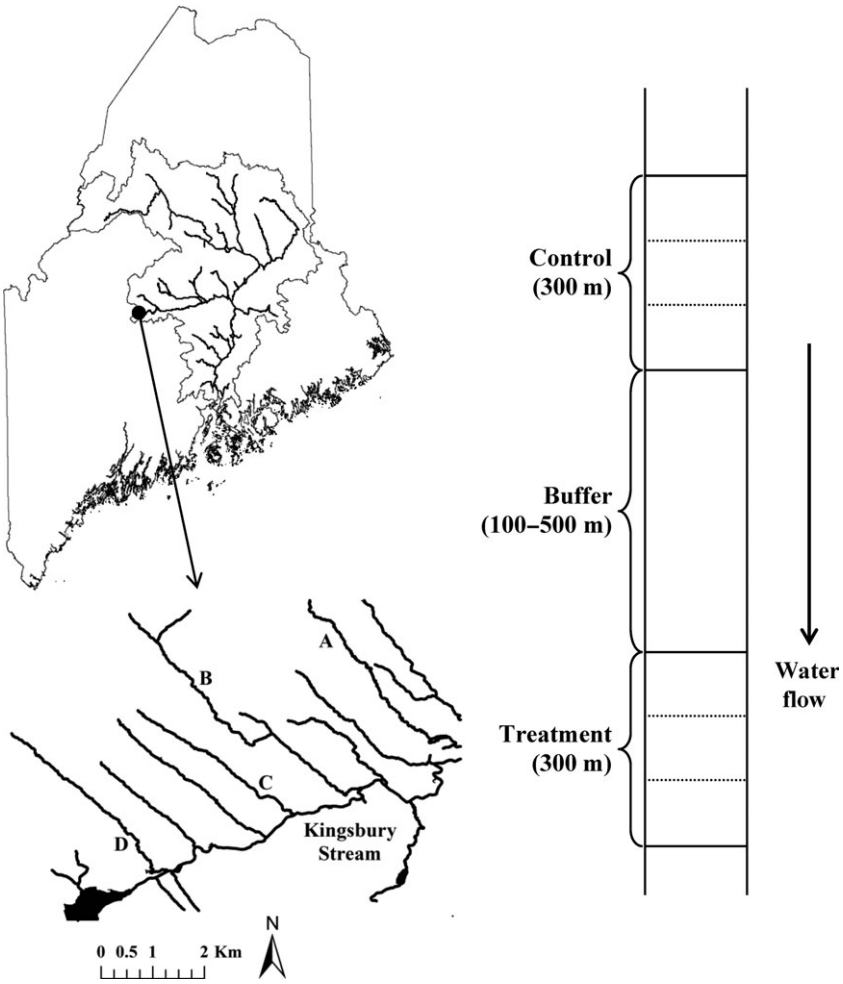

Fig. 1 Location of study sites within the Penobscot River catchment (outlined), Maine, U.S.A. Four study streams (A–D) located within Kingsbury Plantation township, tributaries of Kingsbury Stream, which flows west to east from Kingsbury Pond to the Piscataquis River (not shown). Each study stream contains a control reach, a buffer and a treatment reach.

local vegetation is mainly mixed deciduous forest, and there is a long logging history. Brook trout (*Salvelinus fontinalis*) dominate the resident fish assemblages in these streams, with blacknose dace (*Rhinichthys atratulus*) at low densities.

We established an upstream control reach (300 m) and a downstream treatment reach (300 m) on each stream, with a 100–500 m 'buffer' between reaches (Fig. 1). Details of how we decided on the buffer length, based on Atlantic salmon fry movement, are given in Guyette, Loftin and Zydlewski (2013). Physical characteristics of reaches within and between streams were similar (Table 1). The gradient of each reach was measured with a laser transit (Rugby 100; Leica Geosystems, Heerbrugg, Switzerland). Substratum characterisation involved visual estimates of per cent cover of silt, sand, gravel, cobble, boulder, leaf litter and moss within 0.25 m^2 survey plots sampled in the centre of riffles at 25-m intervals. Water temperature was recorded at 5-min intervals from May through November with HOBO loggers (UA-001-64 Pendant Temp; Onset Computer Corporation, Bourne, MA, U.S.A.) submerged and anchored to the substratum in flowing water in shaded sections of each reach. Canopy cover was measured with hemispherical photography. Photographs were taken at 25-m intervals with a Canon Powershot G3 (Canon U.S.A. Inc., Lake Success, MA, U.S.A.) with a fisheye lens placed on a platform on a tripod in the centre of the stream 1 m above the water surface. Per cent openness was measured with Winphot 5.0 (ter Steege, 1996). The study streams were oligotrophic before nutrient manipulations (total dissolved nitrogen, TDN: 0.10–0.32 mg L^{-1}; total dissolved phosphorus, TDP: 4–28 μg L^{-1}), and conductivity was low (10–35 μS cm^{-1}).

Atlantic salmon marking and stocking

The otoliths of first filial generation (F1) Atlantic salmon, raised in a hatchery, were marked thermally before the eggs hatched in January and February 2010 (U.S. Fish and Wildlife Service Craig Brook National Fish Hatchery, East Orland, ME, U.S.A.). There were two groups.

Table 1 Physical characteristics in control (C) and treatment (T) reaches in the four study streams; values are reported as means with ranges in parentheses (minimum to maximum)

	Stream A		Stream B		Stream C		Stream D	
	C	T	C	T	C	T	C	T
Mean bankfull width (m)	2.9 (2.2–3.8)	3.5 (2.3–4.7)	5.4 (4.8–6.6)	5.4 (3.8–6.9)	3.9 (3.4–4.7)	3.7 (2.6–5.0)	3.8 (2.5–5.9)	5.3 (3.6–7.5)
Gradient (%)	3.8 (2.7–5.5)	3.2 (1.5–6.2)	2.9 (1.9–3.5)	2.2 (1.0–4.3)	4.6 (1.5–8.1)	3.7 (1.8–5.2)	4.4 (3.4–5.0)	3.1 (1.6–5.2)
Gravel–cobble (%)	68 (10–100)	57 (10–100)	59 (10–100)	73 (10–100)	49 (0–100)	53 (0–100)	58 (10–100)	63 (5–100)
Water temperature (°C)	13.4 (4.0–20.7)	13.9 (4.0–22.1)	14.0 (3.3–22.4)	14.3 (3.2–22.3)	13.0 (3.9–19.4)	13.8 (3.6–21.5)	13.1 (3.8–20.9)	12.7 (3.8–19.9)
Altitude (m)	334		346		306		308	
Riparian overstorey vegetation*	Fagr	Fagr	Fagr	Fagr	Fagr	Fagr	Abba	Abba
			Bepa	Tsca	Tsca	Bepa	Bepa	Fram
			Tsca				Pima	Fagr
Canopy openness (%)	33 (25–43)	27 (21–35)	35 (31–40)	36 (33–40)	34 (29–38)	29 (23–35)	30 (24–37)	29 (24–34)

*Dominant overstorey vegetation: *Fagus grandifolia* (Fagr, American beech), *Abies balsamea* (Abba, balsam fir), *Fraxinus americanus* (Fram, white ash), *Tsuga canadensis* (Tsca, eastern hemlock), *Betula papyrifera* (Bepa, white birch), *Picea mariana* (Pima, black spruce).

One group received a series of four marks in a chilled recirculating system by exposing the eggs to alternating cycles of 36 h with a 4 °C increase in temperature and 36 h at ambient temperature (1.7 °C). The second group received a series of two marks, a 72-h ambient period and a series of two more marks. The procedure used for marking otoliths in 2009 was not effective, and thermal marks on the 2009 year class Atlantic salmon were indistinguishable.

Salmon fry were stocked throughout the streams from 100 m above to 12.5 m below each control and treatment reach. Control and treatment reaches were stocked with fish from different thermally marked groups. In the 2 years prior to this study, fry stocking occurred within Kingsbury Stream, but not in our research streams. During this study, fry stocking was relocated from Kingsbury Stream to the four tributaries, and no additional fry stocking occurred within the system. Fry density in the experimental reaches was 4 m^{-2} wetted area, which is four times the typical stocking density in Maine (Fay *et al.*, 2006), to maximise the potential number of surviving fry. Unfed fry were stocked on 18 May 2009, and fed fry were stocked on 14 May 2010. The developmental index (Kane, 1988), which is 0 at fertilisation and 100 at first feeding, was approximately 93 in 2009 and 123 in 2010. Fry were distributed evenly every 12.5 m throughout control and treatment reaches.

Carcass analogue addition

The carcass analogue material was commercially produced by BioOregon, Inc. (Warrenton, OR, U.S.A.) and was derived primarily from autumn run Chinook salmon of hatchery origin from the Pacific Northwest. The 1.9-g, 1.25-cm-diameter pellets were manufactured using a cold extrusion process and were approximately 10% N, 2% phosphorus (P), 13% lipids and 56% crude protein (Pearsons, Roley & Johnson, 2007). Pellets were applied to treatment reaches (Fig. 1) at a density of 0.1 kg m^{-2} wetted channel width on 14 July and 31 October 2009 and 1 July 2010 (Fig. 2). July delivery simulated sea lamprey spawning, whereas the additions in October simulated the Atlantic salmon spawning run. The same application density was used on all dates to facilitate comparisons. Carcass analogues were placed in Vexar® 6.35-mm mesh bags, anchored to similar bags filled with rocks collected from the streambed, distributed at random throughout each treatment reach only and left in place until the pellets had dispersed. Each mesh bag was filled with approximately 800 g of carcass analogue material.

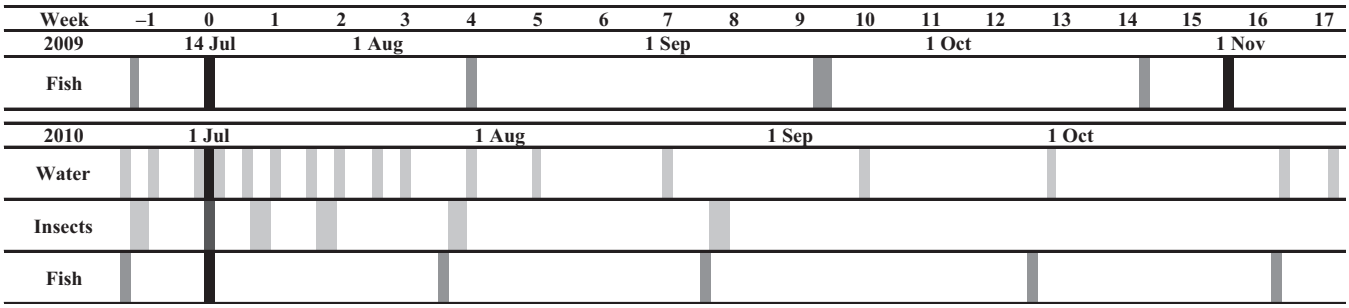

Fig. 2 Timing of carcass analogue additions (black vertical bars) and fish, water and insect sampling (grey vertical bars) in experimental streams.

Field sampling

Water samples were collected (Fig. 2) in flowing water in the centre of the stream at three locations within each control and treatment reach in 2010. Duplicate samples were collected at each location with a 60-mL syringe and filtered through 0.40-μm polycarbonate membrane filters (GE Osmonics, Minnetonka, MN, U.S.A.) with a Millipore Swinnex filter holder (Millipore Corporation, Billerica, MA, U.S.A.) into clean amber glass jars. One sample was acidified with 50% sulphuric acid and held at 4 °C prior to N analysis. The other sample was frozen (−20 °C) or held at 4 °C for <48 h prior to P analysis.

In 2010, macroinvertebrates were collected before and after analogue addition (Fig. 2) with a 500-μm D-frame kicknet at 100-m increments working from down- to upstream in each control and treatment reach. One sample from each 100-m section was compiled of three to six kicks, and larger rocks were scraped by hand in fast-flowing riffles throughout the section. Samples were rinsed with stream water, large detritus and rocks were removed, and samples were stored temporarily on ice and then at −20 °C until processing.

Juvenile Atlantic salmon were collected (Fig. 2) by backpack electrofishing conducted at 100-m increments working from down- to upstream in each control and treatment reach in 2009 and 2010. Sampling continued until a target sample size (eight to nine YOY and four Age 1 per 100-m section) was reached (usually within the first 25 m of the section). Atlantic salmon were killed individually on dry ice and stored at −20 °C in preparation for stable isotope analysis.

Laboratory analysis

Water analysis. Total dissolved nitrogen was measured with the automated cadmium reduction method after persulphate digestion (Delia, Steudler & Corwin, 1977; American Public Health Association, 1999). Total dissolved phosphorus was measured with the ascorbic acid method after persulphate oxidation (American Public Health Association, 1999). Water analyses were performed at the Sawyer Environmental Chemistry Research Laboratory (University of Maine, Orono, ME, U.S.A.). Detection limits for these analyses were determined by the laboratory (0.1 mg L^{-1} TDN and 1.0 μg L^{-1} TDP).

Sample preparation for stable isotope analysis. Macroinvertebrates were sorted and identified to genus (Peckarsky *et al.*, 1990; Merritt, Cummins & Berg, 2008). Analyses focussed on macroinvertebrates from three functional feeding groups: filter feeders: *Dolophilodes* spp. (Trichoptera: Philopotamidae), *Hydropsyche* spp. (Trichoptera: Hydropsychidae) and *Parapsyche* spp. (Trichoptera: Hydropsychidae); predators: *Hexatoma* spp. (Diptera: Tipulidae), *Dicranota* (Diptera: Tipulidae) and *Lanthus* (Odonata: Gomphidae); and the shredder: *Pteronarcys* (Plecoptera: Pteronarcyidae). Samples of *Dolophilodes* and *Dicranota* included six or more individuals. Samples of all other taxa included one to five individuals, determined by body size and availability. Gut contents of macroinvertebrates were not removed, and stable isotope values for macroinvertebrates therefore reflect the whole body and food recently consumed.

Atlantic salmon white muscle fillets (excluding bone, skin and subcutaneous fat) were dissected from individual fish with a small scalpel. Otoliths were dissected from each fish and inspected for thermal marks. All fish with indistinguishable thermal marks or those indicating movement between control and treatment reaches were excluded from the study.

Macroinvertebrate and fish muscle samples were frozen at −20 °C for 1–5 months (macroinvertebrates) or 1–17 months (fish) prior to analysis, then thawed and dried at 60 °C for 48 h and ground into a fine powder with

a mortar and pestle. Carcass analogue material was collected from a composite of pellets, dried at 60 °C for 48 h and ground into a fine powder with a mortar and pestle.

Stable isotope analysis. Approximately 0.3 mg of each macroinvertebrate, fish and carcass analogue sample was weighed in tin capsules for stable isotope analysis. The $\delta^{15}N$ and $\delta^{13}C$ values were determined with a Costech 4010 elemental analyser interfaced to a Finnigan Mat Delta Plus XP via a Conflo III, or a Thermoquest NC2500 elemental analyser interfaced to the Finnigan Mat Delta Plus mass spectrometer via a Conflo II, at the Stable Isotopes in Nature Laboratory (SINLAB, University of New Brunswick, Fredericton, NB, Canada). Stable isotope values are expressed in per mille (‰) and are calculated from the formula:

$$\delta X = \left[\left(R_{\text{sample}}/R_{\text{standard}}\right) - 1\right] \times 1000,$$

where X is ^{15}N or ^{13}C, and R is the ratio of the heavy isotope to the light isotope for the element ($R = {}^{15}N/{}^{14}N$ or $^{13}C/^{12}C$). R_{standard} values are established from International Reference Standards; the standard for N is atmospheric nitrogen (AIR), and the standard for C is Vienna PeeDee Belemnite (VPDB).

Analytical error was calculated following the recommendations of Jardine and Cunjak (2005). Precision and accuracy of stable isotope analyses were assessed with International Atomic Energy Agency standards (CH7 and N2), commercially available standards (acetanilide and nicotinamide) and SINLAB internal standards (bovine liver and smallmouth bass muscle). Standard deviations of standard repeats within analytical runs did not exceed 0.22‰ for $\delta^{13}C$ or 0.34‰ for $\delta^{15}N$. Standard deviations of sample repeats averaged 0.07‰ for both $\delta^{13}C$ and $\delta^{15}N$ and did not exceed 0.33‰ for $\delta^{13}C$ and 0.27‰ for $\delta^{15}N$.

Variability in tissue lipids can affect interpretation of stable isotope results, because lipids have more negative $\delta^{13}C$ values relative to other tissue components (Focken & Becker, 1998). Bulk tissue C : N correlates with lipid content, so C : N can be used for lipid correction (Logan *et al.*, 2008). This study used $\delta^{13}C$ values that were not lipid corrected, because there were no differences between control and treatment C : N mean values for macroinvertebrate taxa (4.9 ± 0.54 SD) or Atlantic salmon (3.2 ± 0.13 SD) based on Wilcoxon rank sum tests ($P > 0.05$) and because these corrections would not affect the interpretation of the results (Logan *et al.*, 2008).

Marine-derived nutrient assimilation. Stable isotope values were used to estimate the assimilation of analogue material (N and C) by macroinvertebrates and Atlantic salmon. We used the mass balance equation (Johnston *et al.*, 1997; Chaloner *et al.*, 2002; Claeson *et al.*, 2006):

$$\%\text{Analogue-derived nutrient} = 100(\delta X_t - \delta X_c)/(\delta X_a + (\text{TL}\delta X_e) - \delta X_c),$$

where X is ^{15}N or ^{13}C, δX_t is the stable isotope value of the organism in areas enriched with carcass analogue (treatment), δX_c is the stable isotope value of the organism in areas with no enrichment (control), δX_a is the stable isotope value of the carcass analogue, δX_e is the isotope enrichment factor per trophic level (3‰ for N, 1‰ for C; Chaloner *et al.*, 2002) and TL is the correction factor for the trophic level of the organism (assumed to be 1 for shredders, primary consumer; 1.5 for filterers, omnivore; 2 for predatory insects, secondary consumer; and 3 for Atlantic salmon; Chaloner *et al.*, 2002).

Statistical analysis

We identified treatment and temporal effects on dissolved nutrient concentrations with two-way analysis of variance (ANOVA). We identified treatment and temporal effects on mean stable isotope values ($\delta^{15}N$ and $\delta^{13}C$) for each representative macroinvertebrate taxon with multivariate analysis of variance (MANOVA). *Post hoc* pairwise comparisons at each sample date for macroinvertebrate taxa were performed on each response variable ($\delta^{15}N$, $\delta^{13}C$) with univariate ANOVA (Tukey's HSD for unequal sample sizes). We identified treatment and temporal effects on mean stable isotope values ($\delta^{15}N$ and $\delta^{13}C$) for Atlantic salmon with permutational MANOVA because assumptions of normality and homogeneity of variance were not met. *Post hoc* comparisons at each sample date for 2009 YOY, 2010 YOY and 2010 Age 1 Atlantic salmon were performed on each response variable ($\delta^{15}N$, $\delta^{13}C$) with Wilcoxon rank sum tests. We used an α of 0.05 for all analyses. All analyses were performed with the statistical package R, version 2.15.0 (R Development Core Team, 2012), with the R packages 'MASS' (Venables & Ripley, 2002), 'car' (Fox & Weisberg, 2011), 'fBasics' and the 'adonis' function in 'vegan' (Oksanen *et al.*, 2012).

Results

Temporal pattern of nutrient diffusion

Nutrient concentrations were similar (TDP: $F_{1,70} = 0.024$, $P = 0.88$; TDN: $F_{1,60} = 0.006$, $P = 0.94$) in the control and

treatment reaches in 2010 prior to analogue addition (Fig. 3). Nutrient concentrations were 405% (P) and 82% (N) greater in treatment than in control reaches 2 days after the addition (TDP: $F_{1,22} = 170$, $P < 0.001$; TDN: $F_{1,20} = 30.0$, $P < 0.001$). There was a significant interaction between treatment and date for total dissolved phosphorus until early August ($F_{8,198} = 3.04$, $P = 0.003$). Total dissolved phosphorus was 131–151% greater in treatment reaches on all sample dates until 5 August ($P < 0.001$). There were significant treatment ($F_{1,191} = 164$, $P < 0.001$) and date ($F_{8,191} = 2.12$, $P = 0.04$) effects for total dissolved nitrogen samples collected until early August, and TDN was 61–135% greater until 19 July ($P < 0.05$). No significant differences were detected on 22 July, and TDN was 85% greater on 29 July ($P = 0.02$). No significant differences between treatment and control reaches were detected for TDP or TDN after 5 August.

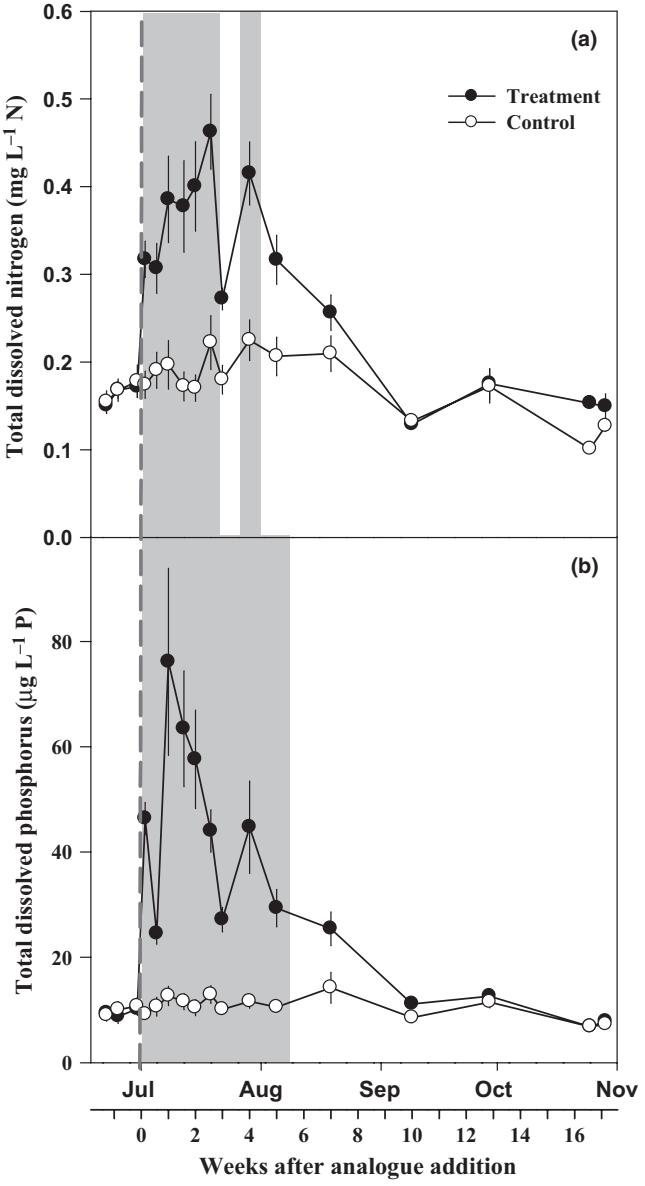

Fig. 3 Total dissolved nitrogen and total dissolved phosphorus in stream water during the 2010 sampling season. Data points shown are means ± 1 SE, pooled across all sample streams. The vertical dashed line indicates the 1 July carcass analogue addition, and the shaded regions indicate significant differences between control and treatment reaches.

Assimilation of marine-derived nutrients

The carcass analogues used in this study were isotopically enriched in ^{15}N and ^{13}C relative to the freshwater organisms collected in the absence of the analogue ($n = 5$; mean ± 1 SD: $\delta^{15}N = 11.2 \pm 0.27$; $\delta^{13}C = -19.8 \pm 0.11$; Figs 4 & 5). Macroinvertebrate taxa in treatment reaches were isotopically enriched in both ^{15}N and ^{13}C after addition of the analogues, and the degree of enrichment varied with time relative to the addition and with functional feeding group (Fig. 4). A significant interaction between treatment and date for the fine filter feeding caddisfly *Dolophilodes* (Table 2) reflected changes in the magnitude of the treatment effect over time. *Dolophilodes* (n = 4–10 per location and date) and all filterers pooled (n = 4–23) showed the greatest ^{15}N and ^{13}C enrichment 2 and 4 weeks after the addition (48–57% analogue-derived nitrogen, ADN; 61–65% analogue-derived carbon, ADC), with less enrichment after 8 weeks (39% ADN, 27% ADC; Figs 4a,d & 6a). There were significant treatment effects for the predatory cranefly *Hexatoma* and the shredding stonefly *Pteronarcys* after analogue addition (Table 2), although the effect was delayed for *Hexatoma* (Fig. 4b). *Hexatoma* (n = 3–11), and all insect predators pooled (n = 13–25) showed increasing ^{15}N and ^{13}C enrichment from 2 to 4 weeks after the addition (19–26% ADN, 24–42% ADC), maintaining this enrichment between 4 and 8 weeks (23% ADN, 38% ADC; Figs 4b,e & 6b). The shredding stonefly *Pteronarcys* (n = 5–10) showed increasing ^{15}N and ^{13}C enrichment from 2 to 8 weeks after the addition (17–22% ADN, 23–27% ADC; Figs 4c & 6c).

Atlantic salmon in treatment reaches were isotopically enriched in both ^{15}N and ^{13}C for both years and both age classes after addition of carcass analogues (2009 YOY: n = 42–48; 2010 YOY: n = 31–46; 2010 Age 1: n = 10–16; Fig. 5). There was a significant interaction between treatment and date (Table 3), and there were significant treatment effects for both years and both age classes (Fig. 5). Increased ^{15}N and ^{13}C were detected in Age 1 Atlantic salmon in treatment reaches after analogue addition (12–19% ADN, 21–40% ADC; Fig. 6f) and

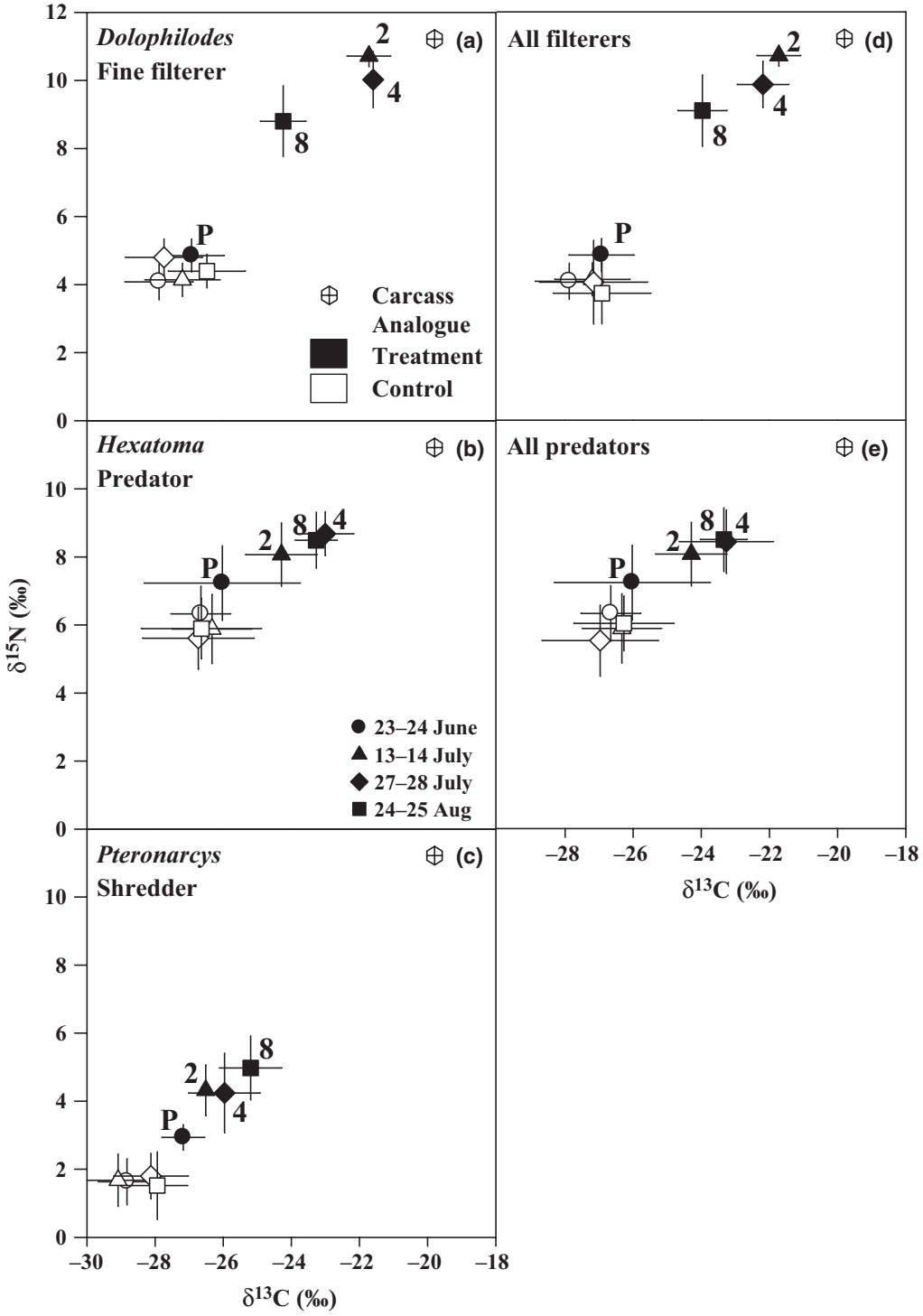

Fig. 4 2010 $\delta^{13}C$ and $\delta^{15}N$ stable isotope biplots (mean ± 1 SD) for three macroinvertebrate taxa representing different functional feeding groups: (a) *Dolophilodes*, a fine filter feeder; (b) *Hexatoma*, a predator; and (c) *Pteronarcys*, a shredder; and biplots for two macroinvertebrate functional feeding groups: (d) filterers (*Dolophilodes*, *Hydropsyche*, *Parapsyche*); and (e) predators (*Hexatoma*, *Dicranota*, *Lanthus*). Closed symbols are from treatment reaches, and open symbols are from control reaches. The crossed hexagon in the upper right corner of each plot is the stable isotope signature of the carcass analogue. Carcass analogue addition occurred on 1 July 2010. The bold letter P shows taxa sampled before the carcass analogue addition. The bold numbers show the relative time after the carcass analogue addition, in weeks. Data are pooled from all sampled streams.

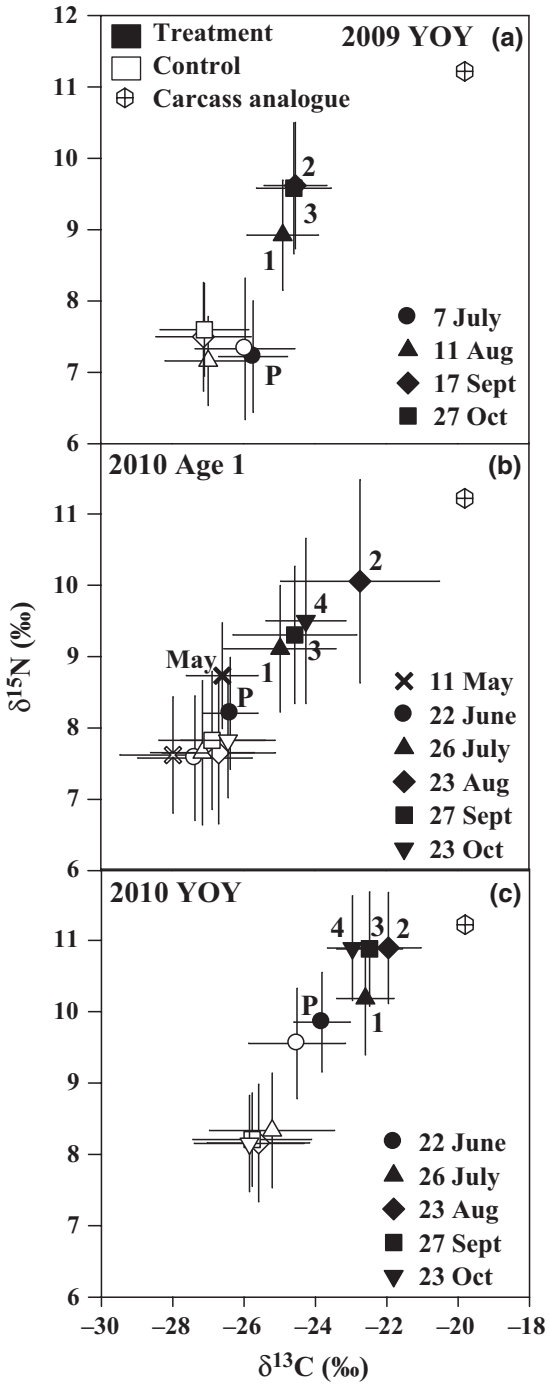

Fig. 5 $\delta^{13}C$ and $\delta^{15}N$ stable isotope biplot (mean ± 1 SD) for (a) 2009 young of the year (YOY); (b) 2010 Age 1; and (c) 2010 YOY Atlantic salmon, pooled across all four sampled streams. The individuals in plots (a) and (b) are from the same population of stocked fish. Closed symbols are from treatment reaches, and open symbols are from control reaches. The crossed hexagon in the upper right corner of each plot is the value for the carcass analogue. Carcass analogue addition occurred on 14 July 2009 and 1 July 2010. The bold letter P shows fish sampled before the carcass analogue addition. The bold numbers show the relative time after the carcass analogue addition, in months.

Table 2 MANOVA results for focal macroinvertebrate taxa where $\delta^{15}N$ and $\delta^{13}C$ are the dependent variables

	Pillai's trace	d.f.	*F*	*P*
Dolophilodes sp.				
Treatment	0.953	2,47	477.5	**<0.001**
Date	0.827	6,96	11.3	**<0.001**
Interaction	1.036	6,96	17.2	**<0.001**
Residuals		48		
Hexatoma sp.				
Treatment	0.689	2,47	52.1	**0.034**
Date	0.260	6,96	2.4	**<0.001**
Interaction	0.207	6,96	1.8	0.099
Residuals		48		
Pteronarcys sp.				
Treatment	0.815	2,46	101.6	**<0.001**
Date	0.469	6,94	4.8	**<0.001**
Interaction	0.241	6,94	2.1	0.055
Residuals		47		

Bold indicates $P < 0.05$.

in early May (9% ADN, 12% ADC), 6 months after the 2009 autumn analogue addition and before the next class of fish was stocked (Fig. 5b).

Control and treatment YOY Atlantic salmon were isotopically similar before addition of the analogues in 2009 (Fig. 5a). In 2010, isotopic values of control and treatment YOY Atlantic salmon before the addition were intermediate and much greater than in 2009 (Fig. 5c), but less than the isotopic values of YOY Atlantic salmon collected on stocking day (14 May; $n = 24$; $\delta^{15}N = 14.96 \pm 0.50$; $\delta^{13}C = -19.73 \pm 0.27$). In both 2009 and 2010, treatment fish showed a steady enrichment after the addition until September and stabilized at a similarly enriched value by October (Fig. 5a,c). The least enrichment was detected in 2009 YOY, with 13–17% ADN and 21–25% ADC (Fig. 6d). The greatest enrichment was detected in 2010 YOY, with 16–23% ADN and 31–41% ADC (Fig. 6e).

Discussion

The addition of the carcass analogues, timed to simulate sea lamprey and Atlantic salmon spawning runs, influenced stream food webs as was shown by stable isotopic enrichment in macroinvertebrates and juvenile Atlantic salmon. Similar to other enrichment studies involving carcasses and their analogues in the Pacific Northwest of the U.S.A. and Alaska (Bilby *et al.*, 1996; Johnston *et al.*, 1997; Chaloner *et al.*, 2002; Claeson *et al.*, 2006; Kohler *et al.*, 2008), our experimental findings are consistent with studies examining the contributions of marine-derived nutrients by natural populations of anadromous fish species in eastern North America (Garman &

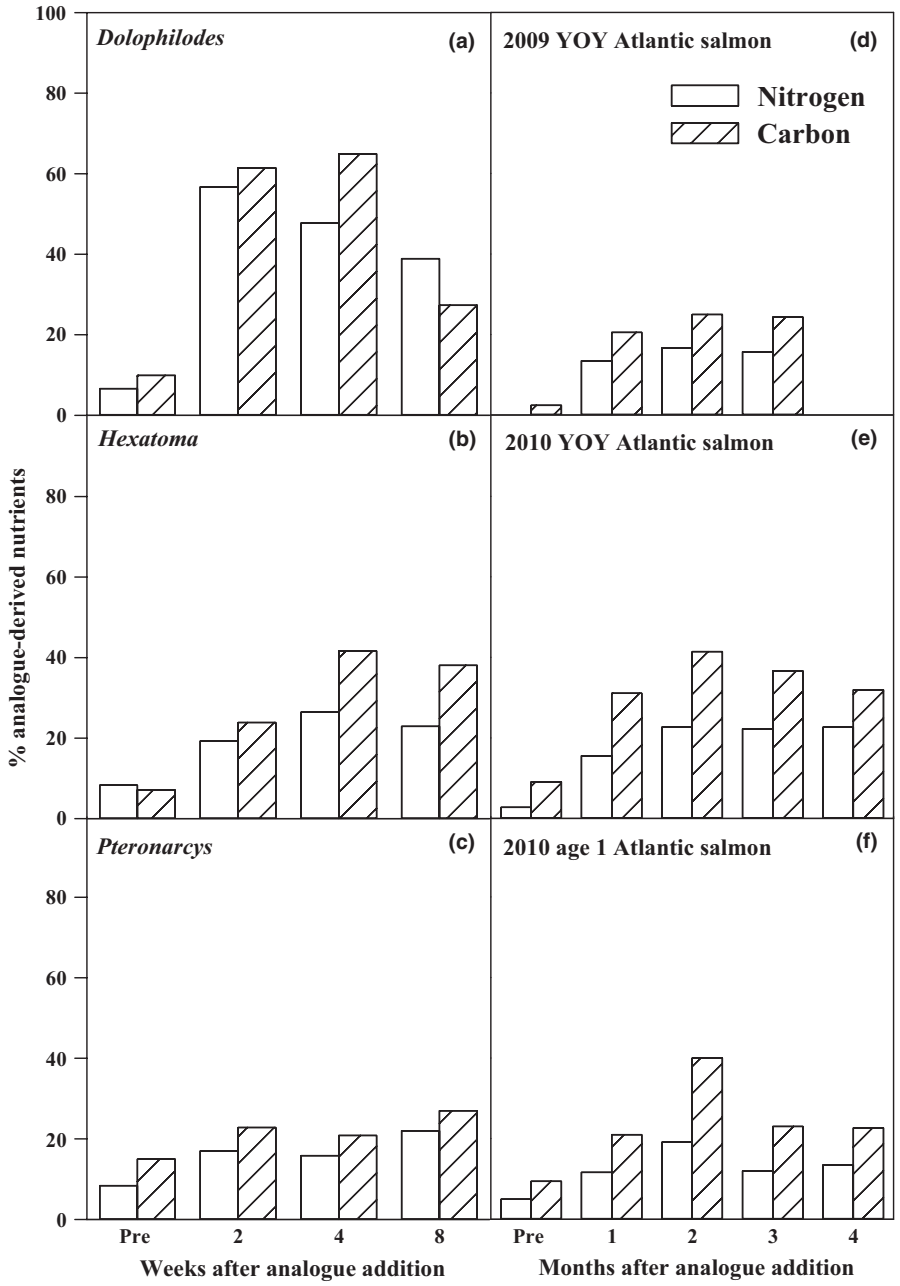

Fig. 6 Per cent analogue-derived nutrients in macroinvertebrate taxa (a–c) and fish (d–f) in treatment reaches based on stable isotope values, using the carcass analogue as the marine end member and analogous organisms in control reaches as the freshwater end member.

Macko, 1998; MacAvoy *et al.*, 2000; Jardine *et al.*, 2009; Walters, Barnes & Post, 2009).

Nutrients from carcass analogues may be easier to detect in small streams because of the lower dilution. The carcass analogues increased P and N in these oligotrophic streams, and these raised concentrations in stream water persisted for 1–2 months as the analogue broke down, dissolved and dispersed. This response is consistent with that detected in a carcass analogue treatment on the Kenai Peninsula, Alaska (Martin *et al.*, 2010); however, our results contrast with those from central Idaho, where there were no detectable changes in nutrient concentrations following carcass analogue additions (Kohler *et al.*, 2008, 2012). The loading rate (0.1 kg m^{-2}) of analogues in the present study was similar to or less than that used in Alaska and Idaho, although the discharge in the study streams in Maine was much less.

Our results suggest both direct and indirect assimilation of the carcass analogues by macroinvertebrates and that temporal changes in macroinvertebrate stable isotope values were correlated with nutrient concentrations in stream water. We did not remove the gut contents of macroinvertebrates; therefore, some stable isotope values may be artificially large in treatment reaches

Table 3 Permutational MANOVA results based on 1000 permutations for YOY Atlantic salmon in 2009 and 2010 and Age 1 Atlantic salmon in 2010 where $\delta^{15}N$ and $\delta^{13}C$ are the dependent variables

	F	*P*
2009 YOY		
Treatment	229.5	**<0.001**
Date	14.2	**<0.001**
Interaction	23.9	**<0.001**
2010 YOY		
Treatment	498.4	**<0.001**
Date	5.1	**<0.001**
Interaction	14.6	**<0.001**
2010 Age 1		
Treatment	76.0	**<0.001**
Date	11.7	**<0.001**
Interaction	1.5	0.157

Bold indicates $P < 0.05$.

because of unprocessed carcass analogue material or microbes that have assimilated nutrients from the analogue in gut contents. Net spinning caddisfly larvae (*Dolophilodes*, *Hydropsyche*, *Parapsyche*) exhibited the greatest and most rapid enrichment in both ^{15}N and ^{13}C, suggesting that these insects may have been filtering and ingesting particles of the pellets or ingesting heterotrophic microbes that had rapidly assimilated analogue nutrients. Within 8 weeks of the addition, the degree of enrichment had declined, reflecting a reduction in analogue availability. Predatory insects (*Hexatoma*, *Lanthus*, *Dicranota*) showed less and delayed enrichment in ^{15}N and ^{13}C, suggesting indirect assimilation through the food web and a slower turnover. Claeson *et al.* (2006) found delayed ^{15}N enrichment by predatory stoneflies (Plecoptera: *Perlidae* spp.); the magnitude of the enrichment was similar to that in this study, but there was no equivalent ^{13}C enrichment. We detected $\delta^{13}C$ enrichment of approximately 4‰ by predators, suggesting that the base of the food web for these macroinvertebrates contained carcass analogue material. This material probably was incorporated via heterotrophic pathways, either through direct ingestion by detritivorous and omnivorous insects or via assimilation by microbes. These enriched prey groups then became food for predatory macroinvertebrates.

Shredding insects (*Pteronarcys*) showed the least ^{15}N and ^{13}C enrichment, suggesting that nutrients in the carcass analogues were being assimilated more slowly or at a lower rate by algae and microbes on the detrital material and subsequently being ingested by these insects. Bilby *et al.* (1996) found a similar magnitude of ^{15}N enrichment in shredding insects after coho salmon (*Oncorhynchus kisutch*) runs in Washington, U.S.A., but no detectable ^{13}C enrichment. Chaloner *et al.* (2002) found a similar pattern in south-eastern Alaska with natural Pacific salmon runs; these results suggest that nitrogen and carbon were assimilated by shredders via different pathways in these systems, reflecting more autotrophic than heterotrophic assimilation at the base of the food web. Shredders process and ingest coarse particulate organic matter (CPOM), usually of terrestrial origin in forested streams, and ^{13}C enrichment by shredders in our study streams suggests that heterotrophic assimilation was dominant and that (i) carcass analogue material was being assimilated by microbes on the surface of the CPOM or (ii) the insects were ingesting some of the carcass analogue material directly.

Enrichment in nutrients derived from the carcass analogues was evident in Atlantic salmon, consistent with studies of marine-derived nutrient effects on juvenile salmonids in western North America. Comparisons of the magnitude of per cent nutrient incorporation between studies is difficult because the calculations do not adequately consider turnover rates and do not take end-member and trophic level variance into account. In a carcass analogue study from streams across the Columbia River basin, Kohler *et al.* (2012) found weak enrichment in salmonids following carcass analogue additions. Furthermore, Bilby *et al.* (1996) found more variability and a broader range of incorporation of salmon-derived N (19–46%) and C (16–61%) in resident and anadromous fish in Washington, U.S.A., than was the case for YOY and Age 1 Atlantic salmon in our study. Their system was larger (second- and third-order streams), their loading rate was greater (natural runs of coho salmon), and the streams contained a more complex fish assemblage, with five species present in systems with anadromous fish (Bilby *et al.*, 1996), in contrast to the two primary species (Atlantic salmon and brook trout) present in our study systems.

Claeson *et al.* (2006) found salmon-derived N (12–14%) and C (14–15%) assimilation in Age 1 steelhead (*O. mykiss*) in smaller streams in Washington, U.S.A.; however, there was no evidence of assimilation by YOY steelhead or resident sculpin (*Cottus* spp.). Steelhead in western North America is a close analogue to Atlantic salmon in eastern North America because both species are iteroparous; however, the results from the Washington study suggest that YOY steelhead may not feed on enriched prey (Claeson *et al.*, 2006), whereas our results suggest that the diet of YOY Atlantic salmon included enriched dietary sources. It is unknown whether the fish sampled in our study had fed directly on the analogues,

in addition to stream macroinvertebrates, although analysis of salmon growth rates following analogue addition suggests that direct ingestion of analogues is probable (Guyette *et al.*, 2013). Additionally, in our study, stable isotopes indicated that Atlantic salmon tissue retained marine-derived nutrients after the carcass analogue was no longer evident, suggesting turnover rates in the order of months.

Nutrients entering small streams may persist as a nutrient legacy (Honea & Gara, 2009). All macroinvertebrates analysed in this study were from the second year of carcass analogue additions, and the ^{13}C enrichment in *Pteronarcys* before the July 2010 addition (15‰ ADC) reflects this nutrient legacy (from the autumn 2009 addition). The effect is most readily detectable in *Pteronarcys*, a large-bodied, long-lived (2+ year life cycle) insect with longer tissue turnover rates than the small-bodied *Dolophilodes*, which completes its life cycle in 1 year. Age 1 Atlantic salmon collected in early May 2010 exhibit both ^{15}N and ^{13}C enrichment, again suggesting the presence of a nutrient legacy in the food web.

Differences between 2009 and 2010 YOY Atlantic salmon before the analogue addition can be attributed to whether the fish had been fed in the hatchery before stocking. In 2009, Atlantic salmon were stocked into the stream as unfed fry. In 2010, salmon fry had been fed a marine-based diet in the hatchery, and the resulting isotopic values for both control and treatment YOY Atlantic salmon were greater after more than a month in the stream, before carcass analogue addition. After the addition of carcass analogues, the isotopic values of control fish decreased, but remained greater than control fish in the previous year, suggesting slow tissue turnover rates (as nutrients from the hatchery were retained throughout the sampling season). Isotopic values of treatment fish increased following the addition in both years, although enrichment was greater in 2010. This greater enrichment may be due to a combination of a nutrient legacy to the food web from summer and autumn nutrient additions in 2009 and from the raised isotopic values from the marine-based hatchery diet.

Marine-derived nutrients may be incorporated into the food web at several levels, and YOY Atlantic salmon grow faster and are in better condition when such nutrients are available (Guyette *et al.*, 2013). The timing of the influx of marine nutrients is particularly relevant, given the relationship between productivity and water temperature (Morin *et al.*, 1999; Huryn & Wallace, 2000). In western North America, steelhead spawn in the spring, before water temperature has reached its summer peak, and most other Pacific salmon species spawn in the autumn, when water temperature is declining. Pink (*O. gorbuscha*) and sockeye salmon (*O. nerka*) may spawn in the summer; however, timing ranges from late July through November, and spawning does not occur typically at peak summer temperatures (Heard, 1991; Hodgson & Quinn, 2002). Although delivering subsidies of marine nutrients in the autumn may modify the stream ecosystem (Cram *et al.*, 2011), subsidies in the spring or early summer (simulating the timing of the sea lamprey spawning run), coincide with increasing light and water temperature, primary (Odum, 1956) and secondary production (Sweeney, 1984; Poff & Huryn, 1998) and Atlantic salmon growth (Thorpe *et al.*, 1989). The nutrient pulse from sea lampreys occurs when water temperature is increasing and correlates with increasing growth rates of YOY Atlantic salmon (Guyette *et al.*, 2013). Juvenile salmon body size is associated with the 'decision' to smolt (Elson, 1957; Metcalfe, 1998); a minimum body length in the autumn determines whether a salmon will continue to grow through the winter and smolt the following year or stop growth and delay smolting for 1 or more years (Thorpe *et al.*, 1989; Metcalfe & Thorpe, 1992). Greater growth rates and body sizes may influence life-history strategies and population dynamics.

The carcass analogues used in this study simulated the timing of anadromous spawning runs, but the relative N and P load differed from that expected from sea lamprey carcasses. The carcass analogues used here had a nitrogen to phosphorus (N : P) ratio of 5, which is similar to Atlantic salmon spawners (Lyle & Elliott, 1998; Jonsson & Jonsson, 2003), whereas the N : P ratio of sea lamprey is 20 (Hogg, 2012). Carcass or analogue supplementation that reflects the ecological stoichiometry of the spawning fish may affect the proportions of N and P entering the system and subsequently the nutrient limitation of the ecosystem. Nutrient amendments with the N : P ratio of sea lampreys may have a greater effect on productivity if the system is N-limited; however, a larger nutrient addition may be required to attain the same effects in a P-limited system. The nutrient supplementation matching the timing of sea lamprey spawning in this study had a positive effect on juvenile Atlantic salmon (Guyette *et al.*, 2013) and shifted macroinvertebrate community structure (Guyette, 2012); however, matching the stoichiometry of the nutrient loading with expected natural inputs based on species-specific elemental composition would enhance our understanding of the role of marine-derived nutrients in freshwater ecosystems.

There are few natural runs of anadromous fish in the eastern United States that are within an order of magnitude of historic values (U.S. Atlantic Salmon Assessment

Committee, 2005; Saunders *et al.*, 2006; Hall, Jordaan & Frisk, 2012). Restoration of these populations and their freshwater habitat is a management goal for federal, state and non-governmental organizations across the region. Recovery plans for anadromous fish involve stocking, impoundment removal, improving fish passage, and freshwater habitat remediation and restoration. This study indicates that recovery of nutrient sources, such as those delivered by returning anadromous fish, can have widespread effects on stream food webs.

The productivity of freshwater streams where anadromous fish spawned historically is enhanced by delivery of marine-derived nutrients timed to match anadromous spawning runs. Increased stream connectivity with the removal of barriers to passage may alter community structure and the flux of nutrients and energy within freshwater ecosystems, and the degree of change probably depends on the size of the spawning run. Eastern North American anadromous fish populations use a diversity of freshwater habitats; conservation of these systems will be more effective with increased knowledge and integration of anadromous fish population dynamics, delivery of marine-derived nutrients, habitat conditions and freshwater community responses.

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