

Sea lamprey carcasses exert local and variable food web effects in a nutrient-limited Atlantic coastal stream¹

Daniel M. Weaver, Stephen M. Coghlan, Jr., and Joseph Zydlewski

Abstract: Resource flows from adjacent ecosystems are critical in maintaining structure and function of freshwater food webs. Migrating sea lamprey (*Petromyzon marinus*) deliver a pulsed marine-derived nutrient subsidy to rivers in spring when the metabolic demand of producers and consumers are increasing. However, the spatial and temporal dynamics of these nutrient subsidies are not well characterized. We used sea lamprey carcass additions in a small stream to examine changes in nutrients, primary productivity, and nutrient assimilation among consumers. Algal biomass increased 57%–71% immediately adjacent to carcasses; however, broader spatial changes from multiple-site carcass addition may have been influenced by canopy cover. We detected assimilation of nutrients (via $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) among several macroinvertebrate families including Heptageniidae, Hydropsychidae, and Perlidae. Our research suggests that subsidies may evoke localized patch-scale effects on food webs, and the pathways of assimilation in streams are likely coupled to adjacent terrestrial systems. This research underscores the importance of connectivity in streams, which may influence sea lamprey spawning and elicit varying food web responses from carcass subsidies due to fine-scale habitat variables.

Résumé : Les flux de ressources provenant d'écosystèmes contigus sont essentiels au maintien de la structure et de la fonction des réseaux trophiques d'eau douce. Les lamproies (*Petromyzon marinus*) en migration livrent un apport ponctuel de nutriments d'origine marine aux rivières au printemps, quand la demande métabolique des producteurs et des consommateurs est en hausse. La dynamique spatiale et temporelle de ces apports de nutriments n'est toutefois pas bien caractérisée. Nous avons utilisé des ajouts de carcasses de lamproie dans un petit cours d'eau afin d'examiner les variations des nutriments, de la productivité primaire et de l'assimilation de nutriments chez les consommateurs. Une augmentation de la biomasse algale de 57–71 % a été constatée immédiatement à côté des carcasses, mais des variations spatiales plus distribuées découlant de l'ajout de carcasses en plusieurs endroits pourraient avoir été influencées par le couvert végétal. Nous avons décelé une assimilation de nutriments (par l'entremise du $\delta^{13}\text{C}$ et du $\delta^{15}\text{N}$) chez plusieurs familles de macroinvertébrés incluant les heptagénidiés, les hydropsychidés et les perlidés. Nos travaux donnent à penser que les apports pourraient induire des effets localisés à l'échelle de la parcelle sur les réseaux trophiques, et que les voies d'assimilation dans les cours d'eau sont vraisemblablement associées à des systèmes terrestres attenants. Ces travaux soulignent l'importance de la connectivité dans les cours d'eau, qui pourrait influencer le frai des lamproies et produire susciter différentes réactions dans les réseaux trophiques découlant des apports de carcasses, en raison de variables de l'habitat de petite échelle. [Traduit par la Rédaction]

Introduction

Energy and nutrient flows across ecosystem boundaries can influence the structure and function of recipient ecosystems, alleviate nutrient limitation, and increase primary and secondary productivity (Vanni 2002; Polis et al. 2004; Lamberti et al. 2010). In aquatic systems, carbon, nitrogen, and phosphorus (an important subset of potential nutrient subsidies) may alleviate bottom-up constraints on productivity by facilitating in-stream production and (or) alter top-down effects if received directly by consumers (Rosemond et al. 1993; Lamberti 1996; Kiernan et al. 2010). Thus, stream production and food web structure are determined largely by resource availability and assimilation through both autotrophic and heterotrophic pathways.

The effect of nutrient subsidies varies with the magnitude and duration of the resource, as well as the environmental and community-level processes of recipient systems (Marczak et al. 2007; Zhang and Richardson 2011). Pulsed nutrient subsidies may be sporadic or pre-

dictable and large or small in magnitude but are often short lived and may alleviate nutrient limitations and stimulate productivity (Odum 1971; Yang et al. 2010; Weber and Brown 2013). Additionally, habitat variables (i.e., temperature, substrate, flow) may fluctuate across spatial and temporal scales, influencing the effects of subsidies on food web structure (Roberts et al. 2007; Kohler et al. 2012). Thus, the pathways by which nutrient subsidies are utilized are specific to the context of the recipient ecosystem.

Migratory fish are vectors of nutrients and energy, and synchronous spawning events provide resource subsidies to ecosystems that support production of their offspring. Nutrients in the form of excretion, gametes, and carcasses may influence recipient stream food webs through various pathways (Gende et al. 2002; Tiegs et al. 2011; Childress and McIntyre 2015). Subsidies may be assimilated at the base of aquatic food webs in the form of inorganic nutrients, thereby increasing algal biomass and primary productivity (Claeson et al. 2006; Kohler et al. 2008) or the production of heterotrophic

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D.M. Weaver and S.M. Coghlan, Jr. Department of Wildlife, Fisheries, and Conservation Biology, 5755 Nutting Hall, University of Maine, Orono, ME 04469, USA.

J. Zydlewski. U.S. Geological Survey, Maine Cooperative Fish and Wildlife Research Unit, and Department of Wildlife, Fisheries, and Conservation Biology, 5755 Nutting Hall, University of Maine, Orono, ME 04469, USA.

Corresponding author: Daniel M. Weaver (email: daniel.weaver@maine.edu).

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microbes (Rüegg et al. 2011). Alternatively, subsidies may enter food webs through direct consumption by consumers (e.g., macroinvertebrates and fish; Lessard and Merritt 2006; Wipfli et al. 2003; Guyette et al. 2014); therefore, nutrient response pathways vary and may be further modified by stream characteristics.

In Atlantic coastal waters, sea lamprey (*Petromyzon marinus*) spawning migrations deliver a pulse of marine-derived nutrient subsidies to freshwater streams and rivers in the spring. The decay rates of sea lamprey carcasses and subsequent water-enriching effects of nitrogen and phosphorus occur over a relatively short period of several weeks (Weaver et al. 2015). At this time, rising water temperatures and increased photoperiod stimulate primary productivity and increase the metabolic demand of consumers, including young-of-the-year fish and macroinvertebrates (Hall 1972; Gustafson-Greenwood and Moring 1990; Nislow and Kynard 2009). During this period of nutrient and energy limitation, nutrient subsidies from sea lamprey received by Atlantic coastal waters are likely to be critical in maintaining structure and function of stream food webs.

We sought to quantify the spatial and temporal dynamics of sea lamprey nutrient subsidies on primary productivity and nutrient assimilation of stream organisms. We describe and present the results of two studies: the first was a carcass-addition experiment in 2013 designed to determine temporal changes in primary productivity, which helped inform the design of a second experiment conducted in 2014 to investigate the spatial and temporal effects of nutrient subsidies in more detail. To address our objective, we sought to quantify changes in (i) stream nitrogen and phosphorus, (ii) stream nutrient limitations, (iii) spatial and temporal patterns of primary productivity attributed to sea lamprey carcass nutrients, and (iv) assimilation of nutrients among select macroinvertebrates and juvenile sea lamprey (ammocoetes).

Materials and methods

Study area

We conducted carcass-addition experiments in 2013 and 2014 in Sedgeunkedunk Stream, a third-order tributary flowing into the Penobscot River at river kilometre (rkm) 36.5 (Fig. 1, locations A (2013) and B (2014)). Two dams were removed on the stream, Mill Dam in 2008 and Meadow Dam in 2009, restoring 5.3 km and connectivity to the ocean. In subsequent years, spawning sea lamprey were regularly observed during spring in Sedgeunkedunk Stream (Gardner et al. 2012; Hogg et al. 2013). However, we selected study reaches where we observed no sea lamprey, evidence of nest building, or postspawned carcasses during our experiments.

We collected prespawning sea lamprey for carcass-addition experiments in 2013 from Veazie Dam (rkm 45.0) and in 2014 from Milford Dam (rkm 61.0) on the main-stem Penobscot River. Collection took place in May during migration, but before sea lamprey commenced nest building and spawning activities. All collected fish were measured for mass (± 0.1 g) and total length (± 1 mm) and then stored frozen at -10 °C until experimental addition.

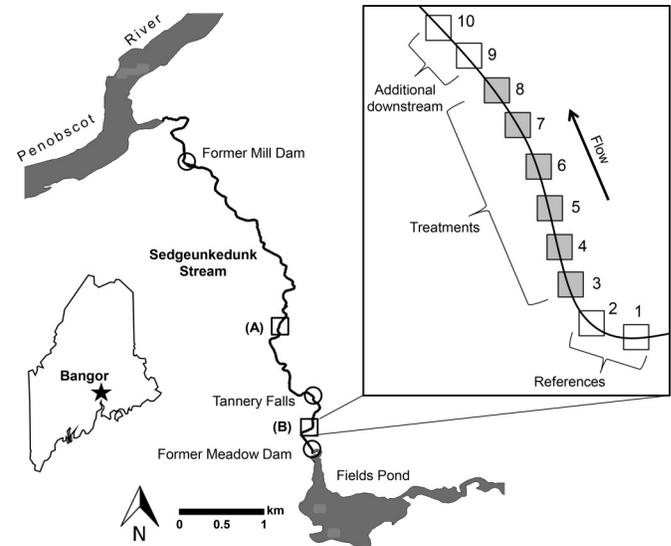
Single-site carcass-addition experiment

In 2013, we selected a 20 m reach comprising two riffle-run sequences that were similar in stream and riparian habitat (Fig. 1, location A). Fifty carcasses were placed in mesh bags and randomly assigned to one of three 2.5 cm mesh metal cages (to discourage scavengers), which were staked in the midchannel of the stream. The average individual carcass mass was 0.758 kg (± 0.023 SE); the total carcass mass added to the stream was 37.9 kg. Carcasses were deployed on 20 July 2013.

Multiple-site carcass-addition experiment

Our results from 2013 directed our experimental design for 2014. In 2014, we chose a reach upstream from the previous year (Fig. 1, location B). We delineated 10 sites along an approximately 150 m long reach (Fig. 1, inset). Each site was comprised of a riffle and subsequent run that ended at the beginning of the next riffle;

Fig. 1. Location of study reaches for experimental sea lamprey carcass addition during 2013 (A) and 2014 (B) on Sedgeunkedunk Stream, Maine. Circles indicate former or current obstacles to fish passage. Inset depicts locations of 10 sites within the experimental reach during 2014. Shaded boxes indicate sites that received additions of sea lamprey carcasses. Map source data were obtained from the United States Department of Agriculture Geospatial Data Gateway.



the average length for each site was 12 m. The two uppermost sites (1 and 2) were designated as reference sites. The following six downstream sites (3–8) were designated to receive 20 sea lamprey carcasses each (120 carcasses total). Finally, the two lowermost sites (9 and 10) received no carcasses. Carcasses were caged similar to methods described above, and the cages were anchored at the upstream-most end of each site. The average individual mass among all carcasses was 0.767 kg (± 0.02 SE); the mass added to each site averaged 15.3 kg (± 0.08 SE) and totaled 92.0 kg throughout the experimental reach. Carcasses were deployed on 25 June 2014.

The numbers of carcasses that we added to Sedgeunkedunk Stream during each experiment represent ecologically realistic densities that may be deposited after spring spawning. Mean estimates of sea lamprey spawning run densities after dam removal in Sedgeunkedunk Stream ranged from 223 to 242 (47–51 fish/km; Hogg et al. 2013). Nislow and Kynard (2009) estimated 30–136 (100–453 fish/km) spawning sea lamprey in a 300 m long reach in Fort River, a tributary to the Connecticut River, similar in width to Sedgeunkedunk Stream. Generally, however, population estimates of spawning sea lamprey throughout the northeastern United States are not well characterized.

Water chemistry

During our multiple-site carcass-addition experiment (2014), we sampled stream water for soluble nitrogen and phosphorus. Samples were taken 0.5 m from the right and left banks and from the midchannel at each of the 10 sites prior to the addition of carcasses and then after 12 h, on days 1–4, and then every other day until day 14. With the exception of our sample taken after 12 h, all samples were collected during the same time of day. Approximately 60 mL of water was filtered through 25 mm, 0.45 μ m mixed cellulose ester membranes (Millipore Corp., Billerica, Massachusetts, U.S.A.) with a syringe into an acid-washed bottle. Samples were stored frozen until analysis. Samples were analyzed for dissolved inorganic nitrogen as ammonium (NH_4^+) and nitrate (NO_3^-) by flow injection analysis (FS3000 Alpkem Flow Solution, O.I. Analytical, College Station, Texas, U.S.A.) and for total soluble phosphorus by inductively coupled plasma optical emission spectrometry (Thermo iCAP 6000,

Thermo Fisher Scientific, Marietta, Ohio, U.S.A.) by the University of Maine Analytical Laboratory and Soil Testing Service. A filtered 60 mL sample of deionized water, serving as a blank, was run periodically among sets of samples. Detection limits for ammonium and nitrate were 0.002 and 0.0005 mg·L⁻¹, respectively, and for total soluble phosphorus, the limit was 1.55 µg·L⁻¹.

Primary productivity

We used nutrient-diffusing substrates to quantify changes in algal biomass and subsequent nutrient limitation (Tank and Dodds 2003; Tank et al. 2006). Our nutrient solution treatments consisted of 0.5 mol·L⁻¹ NH₄NO₃, 0.25 mol·L⁻¹ KH₂PO₄, 0.5 mol·L⁻¹ NH₄NO₃ + 0.25 mol·L⁻¹ KH₂PO₄, and a control (hereafter referred to as N, P, N + P, and C, respectively). Solutions were amended with 2% agar and poured to the top of 60 mL polypropylene screw-cap bottles. The bottles were topped with 2.5 cm diameter, 0.7 µm glass microfiber filters (GE Healthcare Life Sciences, Pittsburgh, Pennsylvania, U.S.A.). We bored holes through the caps, which were fastened over the filters, securing them flush against the nutrient-augmented agar solution.

We constructed arrays to house diffusers using 2.54 cm polyvinyl chloride (PVC) pipe to serve as a rectangular base, with 3.8 cm angled steel slats on top. Bottles were tied by cables to the slats. In 2013, we constructed arrays that contained nine replicates of each nutrient treatment for a total of 36 diffusers per array (N = 72 total diffusers). We deployed one array in the riffle downstream of the carcasses and the other array in the riffle upstream of the carcasses. In 2014, we constructed arrays containing three replicates of each nutrient treatment for a total of 12 diffusers per array. Three arrays were deployed at each site (N = 360 total diffusers). Arrays were deployed downstream of carcasses at each site but required a minimum depth of 18 cm to become fully submerged. All arrays remained submerged throughout both experiments. The downstream distance between the added carcasses and the arrays varied but were approximately 1–2 m. We did not exclude grazing invertebrates from our nutrient-diffusing substrate arrays during both carcass-addition experiments; however, similar to Tank and Dodds (2003), we did not observe invertebrate colonization among the arrays.

Replicates of each nutrient treatment within each array were sampled at 1, 2, and 3 weeks after carcass addition as the majority of decomposition occurred during an initial 3-week period (Weaver et al. 2015). Filters were lifted gently off the bottles with forceps, placed into labeled 1.5 mL polyethylene tubes, and kept on ice in the dark. In the lab, filters were stored at -10 °C until extraction and analysis. Filters were homogenized using a 90% acetone solution and a mortar and pestle. Extracted samples were analyzed for chlorophyll *a*, corrected for pheophytin using spectrophotometry (Strickland and Parsons 1972; American Public Health Association et al. 1999) with a Thermo Aquamate spectrophotometer (Thermo Fisher Scientific, Marietta, Ohio, U.S.A.). During both years, we lost a few diffusing substrata replicates, particularly in 2014 during high flows from a spate. We analyzed chlorophyll *a* in 57 samples in 2013 and 311 samples in 2014.

Stream habitat variables

During both experiments, temperature loggers (Hobo Pendant UA-001-08, Onset, Cape Cod, Massachusetts, U.S.A.) were placed in the stream reach and retrieved at the conclusion of the experiment. Loggers continuously recorded temperature at 1 h intervals. During the multiple-site carcass-addition experiment (2014), we measured stream habitat characteristics at each of the 10 sites. We measured total stream depth and mean column velocity at 0.5 m increments along one cross-sectional transect during base flow with a top-set wading rod and Swiffer model 2100 current velocity meter (Swiffer Instruments, Seattle, Washington, U.S.A.). Percent overstory density was measured at each nutrient diffusing substrate array location with a spherical crown densiometer (model-A, For-

estry Suppliers, Jackson, Mississippi, U.S.A.), as described by Lemon (1956).

Fish and invertebrate collection

We caged individuals of a freshwater mussel, eastern elliptio (*Elliptio complanata* (Lightfoot 1786)), and juvenile sea lamprey (ammocoetes) that we sampled before and after carcass addition for analysis of nitrogen (δ¹⁵N) and carbon (δ¹³C) isotopes. Ammocoetes and eastern elliptio were collected approximately 2 km downstream of our experimental reach. Fifty ammocoetes were collected with backpack electrofishing and kept in aerated buckets prior to caging. Forty-two eastern elliptio were collected by hand. We observed no mortality during sampling and transport, and all individuals appeared to recover after capture. Ammocoetes were caged in a 0.25 × 0.25 m crate lined with fine-screened mesh filled with fine sand obtained from adjacent areas in the stream. We observed ammocoetes bury immediately into the sediment upon addition to each cage. The tops of each cage were left open and were positioned in the stream so that the top was slightly above water. Eastern elliptio were placed in submerged 0.25 m diameter circular mesh pens. Half of the individuals of each species was placed at site 2, one of the upstream reference sites, and the other half was placed at site 9, downstream of all 120 carcasses (Fig. 1). We nonselectively sampled ammocoetes prior to carcass addition, then after 3 weeks. Eastern elliptio were nonselectively sampled prior to carcass addition, then after 3 and 7 weeks. Macroinvertebrate samples representing several functional feeding groups were collected with a kicknet prior to carcass addition and then after 3 and 7 weeks at sites 1, 5, and 10 (Fig. 1). Functional groups included scrapers (Ephemeroptera: Heptageniidae), predators (Megaloptera: Corydalidae; Plecoptera: Perlidae), and collector-gatherers (Trichoptera: Philopotamidae, Hydropsychidae).

Samples of adult sea lamprey tissue were taken prior to carcass addition. After euthanasia, a 1 cm² section of muscle tissue was extracted from the left dorsolateral side of six individuals. All macroinvertebrate and fish samples were stored at -80 °C until sample preparation and stable isotope analysis.

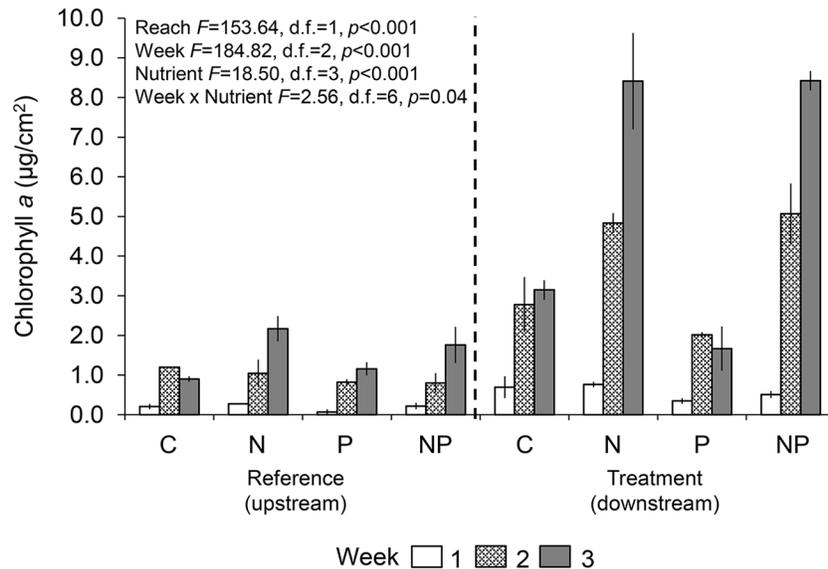
Stable isotope analysis

Stable isotope samples were prepared and analyzed at the University of New Brunswick Stable Isotopes in Nature Laboratory. Whole bodies of insects and ammocoetes and the soft body component of eastern elliptio extracted from the shell were used for analyses. Macroinvertebrate gut contents were not removed; therefore, stable isotope values reflect the whole body and food recently ingested. Samples were oven dried at 60 °C for 24–48 h and then ground into a fine powder with a mortar and pestle. Approximately 0.5 mg of each macroinvertebrate, mussel, and fish was weighed in tin capsules and combusted using a Costech 4010 Elemental Analyzer. Measurements of δ¹³C and δ¹⁵N were performed using a Delta XP continuous flow isotope-ratio mass spectrometer (CF-IRMS, Thermo-Finnigan, Bremen, Germany). Stable isotope values were expressed in parts per thousand or permil (‰) and calculated as δX = ((R_{sample}/R_{standard}) - 1) × 1000, where X is ¹³C or ¹⁵N, and R is the ratio of the heavy isotope to the light isotope (R = ¹³C:¹²C or ¹⁵N:¹⁴N sensu Jardine et al. 2003). International standards were used to calculate R_{standard} values, which included Vienna Pee Dee Belemnite for carbon and atmospheric air for nitrogen. Standard deviations of standard and sample repeats were approximately 0.1‰ or less for δ¹³C and δ¹⁵N.

Statistical analysis

We analyzed changes in chlorophyll *a* from the addition of sea lamprey nutrient subsidies from the single-site carcass-addition experiment using multifactor analysis of variance (ANOVA). Residuals did not conform to a normal distribution (Shapiro–Wilk W test; *p* < 0.05; Zar 1999); therefore, we applied a log transformation to chlorophyll *a* values, which satisfied normality assumptions. We modeled chlorophyll *a* as a function of week, nutrient treatment,

Fig. 2. Mean (\pm SE) chlorophyll *a* concentrations from nutrient-diffusing substrates among four nutrient treatments over a 3-week period upstream and downstream of sea lamprey carcass addition in Sedgeunkedunk Stream, Maine, 2013. *F* and *P* statistics are presented for a model testing for the effects of reach, week, nutrient treatment, and the interaction of week and nutrient treatment (see text for explanation).



and reach (treatment or reference) and all associated interactions. Furthermore, we determined whether carcass subsidies significantly increased chlorophyll *a* by modeling the chlorophyll *a* values of the control nutrient diffusers as a function of week and reach. Main effects and interactions were deemed significant at $p < 0.05$.

We analyzed changes in chlorophyll *a* and stream water nutrient concentrations from the multiple-site carcass-addition experiment using multifactor ANOVA. For each time period (i.e., week for chlorophyll *a* or day for stream water nutrients), we averaged response values of the two reference sites (sites 1 and 2). We then subtracted mean reference values from each of the remaining downstream sites (sites 3–10) for that particular time period. Residuals did not conform to a normal distribution (Shapiro–Wilk *W* test: $p < 0.05$; Zar 1999). We added a constant integer to each value so that negative numbers (i.e., treatments that were lower, on average, than the mean reference) were above zero. The value of the constant integer was chosen so that the lowest value was raised slightly above zero. Then, a log transformation was applied to the mean adjusted response (i.e., chlorophyll *a* or stream nutrient concentration), which satisfied normality assumptions. We modeled chlorophyll *a* as a function of site, week, nutrient treatment, and the interaction of week and nutrient treatment. We modeled stream water nutrient concentrations as a function of site and day. Time was treated as a factor in both models. We conducted post hoc pairwise tests for significant main effects.

We did not measure stream or terrestrial environmental variables continuously throughout the experiment and could not include them in the multifactor ANOVA models. We conducted a separate linear regression to analyze mean chlorophyll *a* values for each diffuser array (averaged across nutrient treatment and time) as a function of site-specific local overstory density.

Finally, we tested for spatial autocorrelation for chlorophyll *a* and stream nutrient concentrations among all treatment sites using the Mantel test. Two distance matrices were generated: one containing linear distances between each of the sites and another containing distances between our chlorophyll *a* values or stream nutrient concentrations. The Mantel test computed the correlation of the two distance matrices and then calculated 1000 permutations to generate a *p* value; *p* values less than 0.05 allowed us to reject the null hypothesis that the spatial and response distances were unrelated (i.e., no autocorrelation).

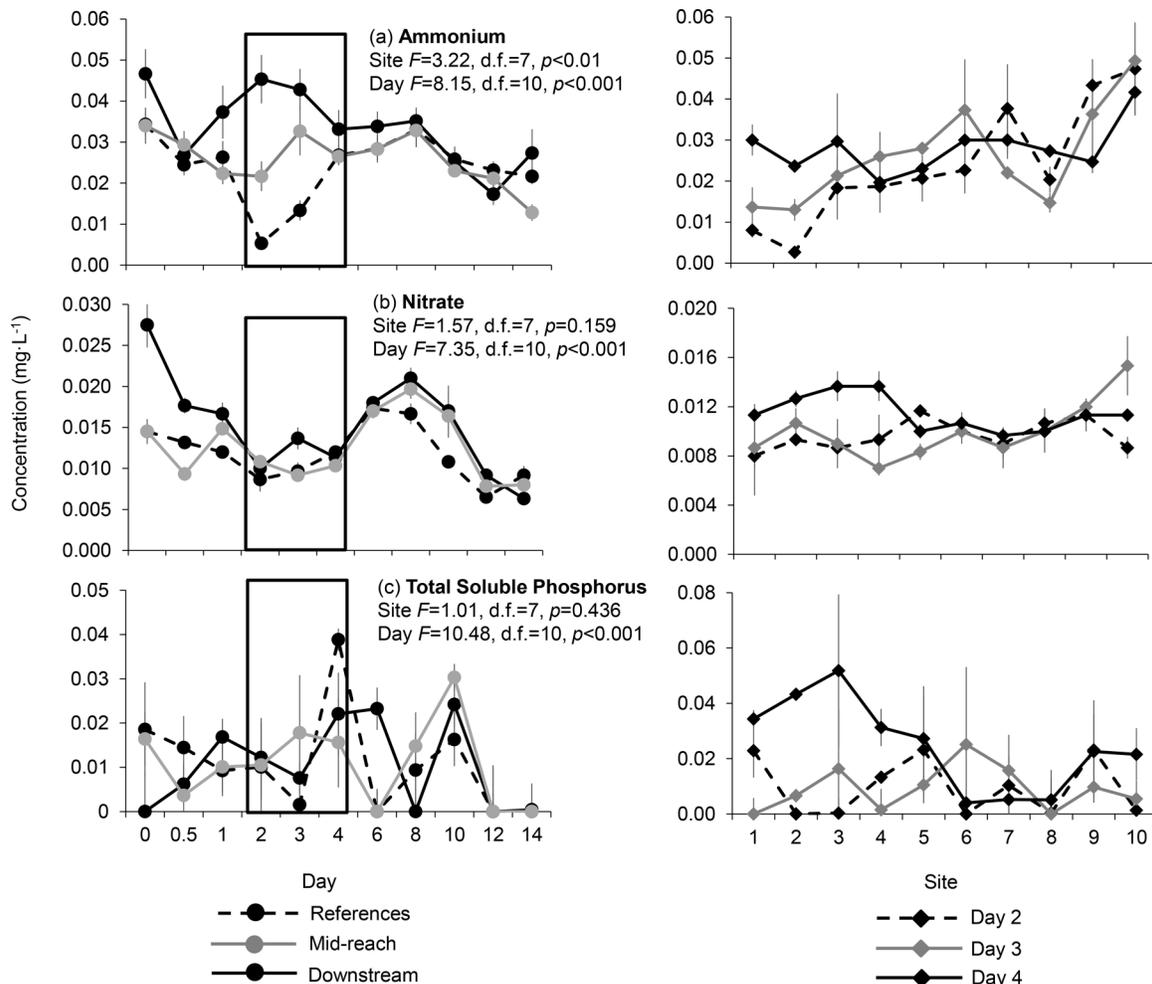
Table 1. Stream width and mean (\pm SE) total depth and water velocity along cross-sectional transects at each site and mean (\pm SE) percent overstory density among three nutrient-diffusing substrate arrays placed at each site at base flow prior to the addition of sea lamprey carcasses.

Site	Stream width (m)	Mean depth (m)	Mean velocity (m·s ⁻¹)	Overstory density (%)
1	7.5	0.20 (0.01)	0.35 (0.15)	77.8 (9.2)
2	8.0	0.20 (0.02)	0.27 (0.07)	67.1 (8.7)
3	7.2	0.23 (0.06)	0.30 (0.10)	83.7 (0.7)
4	5.3	0.23 (0.02)	0.46 (0.10)	87.5 (0.6)
5	4.8	0.23 (0.04)	0.34 (0.09)	94.1 (0.9)
6	6.6	0.27 (0.03)	0.23 (0.02)	92.7 (2.4)
7	7.9	0.22 (0.01)	0.38 (0.14)	75.0 (8.8)
8	6.8	0.24 (0.07)	0.33 (0.03)	66.7 (5.2)
9	7.8	0.24 (0.03)	0.21 (0.04)	91.0 (1.5)
10	5.4	0.21 (0.03)	0.35 (0.13)	72.6 (5.0)
Mean	6.7	0.23	0.32	80.8

We determined stream nutrient limitations during the single-site and multiple-site carcass-addition experiments from samples collected at the reference sites using a multifactor ANOVA. We modeled chlorophyll *a* as a function of week and the addition of nitrogen, phosphorus, nitrogen, and phosphorus or no nutrient addition (control). Significant main effects or interactions ($p < 0.05$) allowed us to infer nutrient limitation or co-limitation (Tank and Dodds 2003).

We analyzed mean stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) with multivariate ANOVA (MANOVA) with the Pillai's trace test to test for spatial and temporal differences in isotopic values among macroinvertebrate taxa, ammocoetes, and eastern elliptio. We modeled the isotope values as a function of stream location and week. Data were tested for multivariate normality with Mardia's test (Mardia 1970) and for homogeneity of covariance matrices with Box's *M* test. Among taxa, data were multivariate normal but did not meet the equal covariance assumption despite log transformation. The Pillai's trace test was selected because it is the most robust multivariate analysis when the assumption of equal covariance (i.e., heteroscedasticity) is not met (Johnson and Field 1993). Post hoc multiple-comparison tests were conducted for those taxa with

Fig. 3. Mean (\pm SE) ammonium (a), nitrate (b), and total soluble phosphorus (c) stream water concentrations over a 2-week period (left panels) among the average of the upstream reference sites (sites 1 and 2), two midreach sites (sites 5 and 6), and two lowermost downstream sites (sites 9 and 10) and during days 2–4 among all sites (right panels) following sea lamprey carcass addition in Sedgeunkedunk Stream, Maine, 2014. Time zero indicates samples taken before the addition of carcasses. The y-axis scales differ among nutrients. *F* and *P* statistics are presented for a multifactor ANOVA model testing for the effects of site and day (see text and Fig. 1 for site locations and descriptions).



significant stream location main effects ($p < 0.05$) to determine differences in isotopic values between the reference site (site 2) and two downstream treatment sites (sites 5 and 9). All analyses were performed with the statistical package RStudio (version 0.99.491, RStudio, Boston, Massachusetts, U.S.A.).

Results

Single-site carcass-addition experiment

Mean daily stream temperatures were $22.5\text{ }^{\circ}\text{C}$ (± 0.25 SE) and ranged from 20.0 to $26.6\text{ }^{\circ}\text{C}$. There were higher concentrations of chlorophyll *a* among all nutrient treatments downstream of the carcasses compared with upstream ($p < 0.001$; Fig. 2). Our multifactor ANOVA found differences among nutrient treatment by week, indicating that the nutrient treatments were responding differently among each sampling period from the addition of sea lamprey carcasses ($p = 0.038$). This may be due to the N and N + P treatments downstream of the carcasses, which exhibited a greater rate of change between the first and second weeks and second and third weeks compared with the rates of change upstream of the carcasses. Among control diffusers, our multifactor ANOVA found that chlorophyll *a* concentrations were 57%–71% higher downstream of carcasses compared with the upstream reference over 3 weeks ($p < 0.05$; Fig. 2).

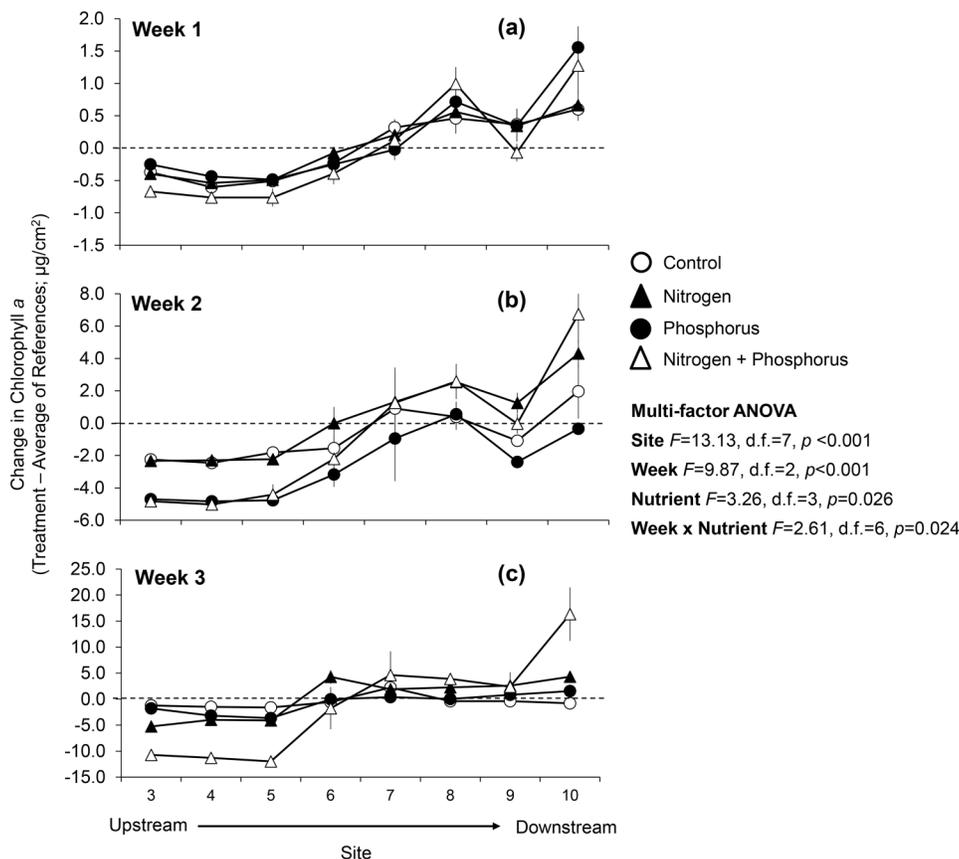
Multiple-site carcass-addition experiment

The 10 sites in our experimental reach were similar in physicochemical stream habitat variables characteristic of a third-order stream (Table 1). However, forest overstory density varied among all 10 sites. We estimated relatively higher overstory density among sites 3–6 and 9 and relatively lower overstory density among the other sites (Table 1). Our Mantel tests suggested spatial autocorrelation in that chlorophyll *a*, ammonium, and nitrate concentrations may have been influenced by adjacent sites ($p < 0.05$).

Daily stream temperature during the course of the experiment averaged $24.2\text{ }^{\circ}\text{C}$ (± 0.42 SE) and ranged from 17.6 to $29.0\text{ }^{\circ}\text{C}$. During the first week of our experiment, stream temperatures increased approximately $6\text{ }^{\circ}\text{C}$. During the second week of our experiment, a spate, from hurricane Arthur, passed through the watershed and our experimental reach. This reduced stream temperatures by an average of $8.0\text{ }^{\circ}\text{C}$ and increased mean stream velocities throughout the reach from $0.18\text{ m}\cdot\text{s}^{-1}$ (± 0.02 SE; base flow) before the spate to $0.60\text{ m}\cdot\text{s}^{-1}$ (± 0.02 SE) after the spate. Temperatures were relatively constant during the third week; however, the stream remained above base flow conditions for the remainder of the experiment.

We observed changes in stream nutrients during the course of our experiment. The multifactor ANOVA identified differences in concentrations of all three nutrients across the sampling period

Fig. 4. Mean (\pm SE) chlorophyll *a* concentrations following sea lamprey carcass addition among sites downstream of carcasses adjusted for average chlorophyll *a* concentrations from upstream reference sites from nutrient-diffusing substrates among four nutrient treatments over 3 weeks (a–c) in Sedgunkedunk Stream, Maine, 2014. *F* and *P* statistics are presented for a multifactor ANOVA model testing for the effects of site, week, and nutrient treatment, and the interaction of week and nutrient treatment (see text and Fig. 1 for site locations and descriptions).



($p < 0.001$; Fig. 3). We found differences in ammonium concentrations among sites ($p < 0.001$) but did not observe similar trends among nitrate or total soluble phosphorus. Stream ammonium concentrations at sites downstream of the carcasses increased from days 1–3 compared with the upstream reference sites (Fig. 3, left panels). We selected days 2–4 to depict nutrient patterns along all 10 sites as we expected carcasses to liberate high concentrations of nutrients during this time (Fig. 3, right panels; Weaver et al. 2015). During days 2–4, the concentrations of ammonium in stream water appear to increase linearly going downstream, with the exception of site 8. This trend becomes absent by day 8 as concentrations appear similar among sites, coincidental with increased flows and runoff associated with the spate. For comparison, we observed no directional trends in nitrate or total soluble phosphorus concentrations during days 2–4 (Fig. 3).

Chlorophyll *a* concentrations at sites 3–6 and 9 were lower than the average concentrations of the reference sites, while concentrations at sites 7–8 and 10 were higher than the average of the reference sites (Fig. 4). Results from our multifactor ANOVA show differences among all factors including site, week, nutrient treatment, and the interaction between week and nutrient ($p < 0.05$; Fig. 4). The post hoc test on the factor “site” revealed that sites 3–6 and 9 were different than sites 7, 8, and 10 for all weeks and nutrient treatments. In parallel with these trends, we found that sites 3–6 and 9 also had 20% higher overstory density than the other sites (Table 1). Chlorophyll *a* concentrations and percent overstory density among the nutrient-diffusing substrate arrays were functionally related ($p < 0.05$). Percent overstory density explained 23% of the variation in

chlorophyll *a* concentrations, and generally, we observed lower concentrations at sites with higher overstory density (Table 1).

Our multifactor ANOVA showed significant main effects of nitrogen and phosphorus on chlorophyll *a* in our reference sites for both carcass-addition experiments ($p < 0.05$). These results suggest nitrogen and phosphorus co-limitation during our experiments (Tank and Dodds 2003). Generally, samples from the N + P treatment had the highest chlorophyll *a* concentrations (Figs. 2, 4).

Adult sea lamprey used in this experiment provided an enriched isotopic signal for ^{15}N and ^{13}C (mean \pm SE; $\delta^{15}\text{N} = 12.16 \pm 0.22$; $\delta^{13}\text{C} = -17.96 \pm 0.19$) relative to the freshwater macroinvertebrates, ammocoetes, and eastern elliptio sampled. We found that differences in stable isotope values varied among taxa, attributed to subsidies delivered by carcasses as well as temporal changes in isotopic enrichment not related to the subsidies (Table 2; Fig. 5). We observed significant isotope enrichment, primarily $\delta^{13}\text{C}$, among sampled individuals of all macroinvertebrate taxa over the 3-week period (time main effect: $p < 0.05$; Table 2). Among Heptageniidae, Hydropsychidae, and Perlidae, we observed greater enrichment in stable isotope values in the treatment sites relative to the reference site (site main effect: $p < 0.05$; Table 2; Fig. 5). There was a significant time \times site interaction among Heptageniidae, suggesting that the magnitude of the treatment effect changed over time. We observed enrichment in ^{13}C among ammocoetes; however, we found no differences among reference or treatment sites. Among eastern elliptio, we observed depletion in both isotopes during the course of the experiment.

Table 2. Pillai's trace and *F* and *P* statistics from MANOVA results for macroinvertebrate taxa and *Petromyzon marinus* ammocoetes treating $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ as dependent variables in the model.

	Pillai's trace	df	<i>F</i>	<i>P</i>
Heptageniidae				
Time	1.256	4,60	25.3	<0.001
Site	0.551	4,60	5.7	<0.001
Interaction	0.730	8,60	4.3	<0.001
Hydropsychidae				
Time	0.766	4,60	9.3	<0.001
Site	0.407	4,60	3.8	0.007
Interaction	0.138	8,60	0.6	0.810
Philopotamidae				
Time	0.968	4,58	13.6	<0.001
Site	0.134	4,58	1.0	0.394
Interaction	0.289	8,58	1.2	0.301
Perlidae				
Time	0.716	4,58	8.1	<0.001
Site	0.410	4,58	3.7	0.009
Interaction	0.233	8,58	1.0	0.478
Corydalidae				
Time	0.172	4,50	1.2	0.332
Site	0.105	4,50	0.7	0.601
Interaction	0.108	8,50	0.4	0.939
<i>Elliptio complanata</i>				
Time	0.847	4,64	11.8	<0.001
Site	0.087	2,31	1.5	0.244
Interaction	0.053	4,64	0.4	0.782
<i>Petromyzon marinus</i>				
Time	0.100	2,19	1.1	0.368
Site	0.198	2,19	2.4	0.122
Interaction	0.180	2,19	2.1	0.152

Note: Values in bold indicate significant main effects or interactions at *p* < 0.05.

Discussion

We sought to quantify the spatiotemporal effects of sea lamprey carcass subsidies in an Atlantic coastal stream food web. We observed immediate downstream increases in primary productivity from carcass subsidies. Over the addition of carcass subsidies at multiple sites, we observed varying responses of stream nutrients and reduced or increased algal biomass compared with reference values. Overstory canopy density partially contributed to the patterns that we observed. The differences that we found among sites may have reflected variability associated with other environmental variables that we did not measure. We observed stable isotope enrichment among a limited group of stream consumers but did not observe increased enrichment from multiple-site carcass addition. Thus, nutrient subsidies from sea lamprey carcasses evoke largely short-term localized effects limited to areas adjacent to the carcasses, as demonstrated by Pacific salmon (Claeson et al. 2006). Furthermore, we suggest that the pathways by which nutrients are assimilated in food webs may be coupled to stream environmental variables, adjacent terrestrial systems, and flow disturbances that may alter subsidy delivery and community structure (Fisher et al. 1982; Power et al. 1988; Chaloner et al. 2004).

During our multiple-site carcass-addition experiment we found spatial autocorrelation among chlorophyll *a*, ammonium, and nitrate concentrations. Sites that were closer to each other had more similar concentrations than those farther apart. The presence of spatial autocorrelation may violate the assumption of independently and identically distributed residuals, which may inflate the type I error rate or the incorrect rejection of a true null hypothesis (Legendre 1993); therefore, we must use some caution when interpreting our ANOVA results. Our results suggest that chlorophyll *a* concentrations were, in part, driven by canopy cover. Thus, riparian vegetation at one site may also have influenced an adjacent

site. Among stream nutrient concentrations, we might expect spatial autocorrelation, as only a small portion of nutrients liberated from carcasses may be taken up and utilized by local stream organisms while the remainder flows downstream.

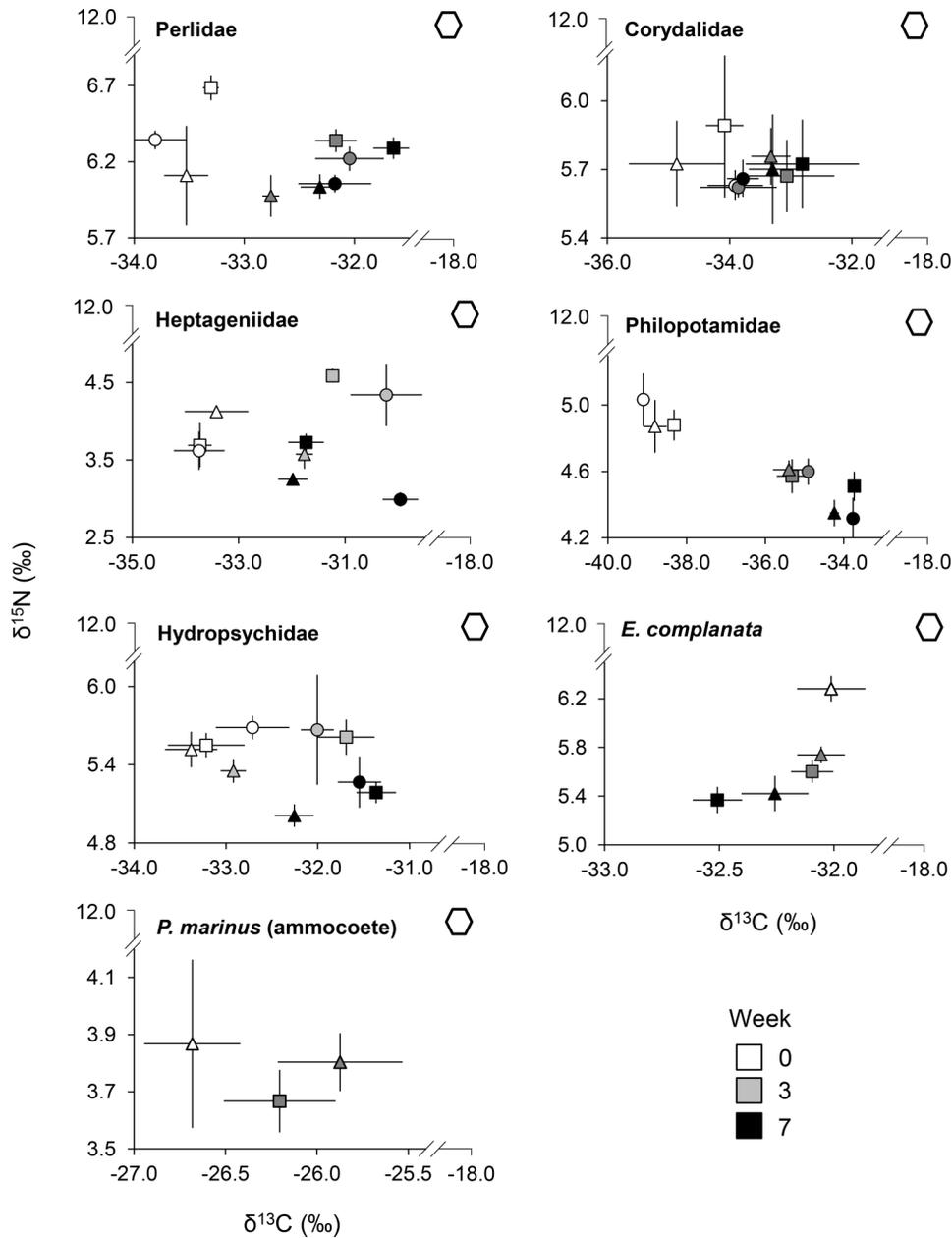
The quantitative input of nutrient subsidies to recipient systems may not correspond to concurrent responses in consumer biomass. The spatial pattern of ammonium concentrations increased from upstream to downstream (Fig. 3, right panels). However, the spatial pattern of algal biomass is partly reflective of canopy cover and light availability (Table 1; Fig. 4). A delivered pulse of nutrient subsidies may initially stimulate consumer biomass in recipient systems. A larger pulse of subsidies, however, may not elicit correspondingly larger effects. Consumer biomass may asymptote as organisms are constrained by assimilation efficiency, limited by another nutrient or resource (e.g., phosphorus), or, as our results suggest, influenced by environmental variables and habitat heterogeneity.

We found that primary productivity was co-limited by nitrogen and phosphorus in Sedgeunkedunk Stream during both experiments. Other studies have generally concluded that temperate eastern streams are phosphorus limited (Peterson et al. 1983; Newbold et al. 1983; Pringle and Bowers 1984; although see Norris 2012), while temperate western streams are nitrogen limited (Grimm and Fisher 1986; Hill and Knight 1988; Tank and Dodds 2003). Productivity can vary across climatic and geologic regions (Minshall 1978), which may explain nutrient limitations and the role that nutrient subsidies play in alleviating those limitations. The stoichiometric ratios of nutrient subsidies (e.g., N:P) may elicit varying effects on the food webs of nutrient-limited systems (Elser et al. 1996). Sea lamprey carcasses have N:P that range from 20:1 to 22:1 (Weaver et al. 2015). Therefore, sea lamprey carcass subsidies may serve to alleviate nutrient limitations in Atlantic coastal streams during the spring. The prespawn carcasses that we used in our experiments likely contain more energy and nutrients (e.g., gametes) than postspawn carcasses, as demonstrated with pink salmon (*Oncorhynchus gorbuscha*; Gende et al. 2004). Thus the prespawn carcasses that we used may have amplified concentrations of dissolved nutrients and corresponding effects on food webs.

Disturbance can influence food web structure (Sousa 1984; Ledger et al. 2008). High flows associated with a spate during 2014 may have influenced nutrient subsidy dynamics and food webs. In 2014, we observed flows three times greater than base flow conditions and high-turbidity conditions associated with the spate. High-flow disturbance events may have scoured periphyton from our nutrient diffusing substrates and reduced light availability to primary producers through swifter turbid flowing waters, which likely suppressed algal biomass (Power et al. 1988; Grimm and Fisher 1989; Hall et al. 2015). Furthermore, elevated stream flows likely accelerated carcass breakdown and nutrient liberation to a time period shorter than a few weeks (Weaver et al. 2015). Our carcasses were caged to discourage scavengers and promote retention within the experimental reach rather than allow downstream displacement, which would likely happen in a natural environment (Gende et al. 2004; Williams et al. 2010). Thus, high-flow disturbances may influence the balance between nutrient retention and transport; during high flows, transport is favored (Meyer and Likens 1979; Doyle 2005; Hall et al. 2009).

The patterns of algal biomass that we observed may exemplify the coupled relationship of streams and adjacent terrestrial systems. Sea lamprey migrate in the spring when tree canopies have just begun to fill. These fish subsequently die in late spring and early summer when canopies are completely full. Primary producers face seasonal shifts in light and nutrient limitations, while consumers face increased metabolic demands from rising water temperatures (Hall 1972; Hill et al. 2001). Stream organisms may depend upon the seasonal arrival of these nutrient subsidies. The temporal differences in executing our experiments (i.e., July 2013 versus June 2014) may have resulted in disparate food web responses;

Fig. 5. Mean (\pm SE) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotope values among six macroinvertebrate taxa and *P. marinus* ammocoetes before carcass addition (open symbols) and at weeks 3 (gray symbols) and 7 (black symbols) after carcass addition on Sedgeunkedunk Stream, Maine, 2014. The triangle symbol corresponds to site 2 (reference), the circle to site 5 (midreach), and the square to site 9 (downstream). The hexagon in the upper righthand corner of each plot is the stable isotope signature of adult sea lamprey carcasses used in this experiment (mean \pm SE, $\delta^{15}\text{N} = 12.16 \pm 0.22$; $\delta^{13}\text{C} = -17.96 \pm 0.19$). The x- and y-axes scales differ among taxa.



however, environmental conditions such as temperature, canopy cover, and nutrient limitation were similar between experiments.

Similar to other studies, we observed reduced primary productivity among sites with relatively high percentages of overstory density (Lowe et al. 1986; Hill and Knight 1988; Table 1; Fig. 4). The arrival of pulsed subsidies from sea lamprey may alleviate nutrient limitations among primary producers, thereby strengthening bottom-up effects (Lamberti 1996). Conversely, areas imposed with light limitations may have lower primary production and consumers receive the subsidy directly (Kiernan et al. 2010; Rosemond et al. 1993). Thus, nutrient subsidies may influence stream food webs disparately and depend largely upon deterministic seasonal processes and environmental characteristics of streams and adjacent riparian habitats (Chaloner et al. 2004).

We observed macroinvertebrates assimilate nutrients from sea lamprey carcasses, as demonstrated similarly with Pacific salmon carcasses (Claeson et al. 2006) and carcass analogs (Guyette et al. 2014). Nutrient subsidy assimilation among macroinvertebrates varied, likely due to differences among the functional feeding groups (Cummins 1974). Perlidae and Hydropsychidae, a predator and collector-gatherer, respectively, may have fed directly on sea lamprey tissue, whereas Heptageniidae, a scraper, may have assimilated nutrients from biofilms enriched by nutrient subsidies. Sea lamprey nutrient subsidies may be important to heptageniid mayflies during increased photoperiod and rising temperatures, which facilitate algal growth. Conversely, Lessard and Merritt (2006) found that nutrient subsidies from fall spawning salmon did not benefit heptageniid mayflies during periods of increased flows and declining photope-

riod and temperature, which reduce algal growth. We observed no assimilation among Corydalidae and Philopotamidae, a predator and collector–gatherer, respectively. Therefore the assimilation of nutrient subsidies was not equivalent across the functional feeding groups. Furthermore, the response of stream organisms to nutrient subsidies may need to be placed in the context of subsidy arrival (i.e., fish phenology) and seasonally variable environmental conditions.

Ammocoetes and eastern elliptio are both filter feeders and may assimilate nutrients from decomposing sea lamprey carcass tissue as detritus. However, we detected no enrichment in ammocoetes or eastern elliptio attributed to carcass subsidies. Conversely, eastern elliptio demonstrated isotope depletion during the experiment. We did not conduct preliminary experiments to determine the effects of caging on these two species; therefore, we cannot conclude whether the cage affected their behavior or if these species do not utilize carcass subsidies. Ammocoetes reside in silt beds and areas of slow-moving water within rivers and streams adjacent to suitable adult spawning habitat (Potter 1980), and thus it is plausible that they assimilate subsidies from adult carcasses or subsidy-enriched diatoms (Moore and Beamish 1973). In addition, ammocoetes reside in streams for up to 8 years (Beamish 1980) and may have multiple opportunities to assimilate carcass subsidies delivered to recipient streams precluding assimilation by other freshwater consumers.

Migrating fish serve as vectors of energy and nutrients among ecosystems. Many populations have declined due to pervasive damming, habitat loss, and overfishing (Saunders et al. 2006; Limburg and Waldman 2009; Hall et al. 2011), which have reduced the delivery of subsidies to resource-limited ecosystems (Polis et al. 2004). Dam removal will facilitate anadromous fish passage and restore linkages between marine and freshwater ecosystems (Hall et al. 2011; Penobscot River Restoration Trust, <http://www.penobscotriver.org/>, accessed 30 October 2015). Our results suggest that nutrient subsidies demonstrate local and variable responses that may be influenced by finer scale habitat variables. The removal of barriers facilitates the movement of spawning adults into the upper reaches of streams and watersheds (Gardner et al. 2012; Hogg et al. 2013). Therefore, carcass subsidies may evoke varying effects on food webs influenced by local habitat and land-use characteristics.

Pulsed nutrient subsidies from anadromous sea lamprey may be important for Atlantic coastal waters. The pathways by which subsidies are utilized may depend on the environmental characteristics of the recipient system. We suggest that effects from sea lamprey nutrient subsidies are relatively localized to areas adjacent to carcasses and further influenced by multiple deterministic and stochastic mechanisms. Our research adds to a growing body of knowledge that characterizes the fate and efficacy of cross-ecosystem subsidies.

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