

# Decomposition of sea lamprey *Petromyzon marinus* carcasses: temperature effects, nutrient dynamics, and implications for stream food webs

Daniel M. Weaver · Stephen M. Coghlan Jr. · Joseph Zydlewski · Robert S. Hogg · Michael Canton

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**Abstract** Anadromous fishes serve as vectors of marine-derived nutrients into freshwaters that are incorporated into aquatic and terrestrial food webs. Pacific salmonines *Oncorhynchus* spp. exemplify the importance of migratory fish as links between marine and freshwater systems; however, little attention has been given to sea lamprey (*Petromyzon marinus* Linnaeus, 1758) in Atlantic coastal systems. A first step to understanding the role of sea lamprey in freshwater food webs is to characterize the

composition and rate of nutrient inputs. We conducted laboratory and field studies characterizing the elemental composition and the decay rates and subsequent water enriching effects of sea lamprey carcasses. Proximate tissue analysis demonstrated lamprey carcass nitrogen:phosphorus ratios of 20.2:1 ( $\pm 1.18$  SE). In the laboratory, carcass decay resulted in liberation of phosphorus within 1 week and nitrogen within 3 weeks. Nutrient liberation was accelerated at higher temperatures. In a natural stream, carcass decomposition resulted in an exponential decline in biomass, and after 24 days, the proportion of initial biomass remaining was 27% ( $\pm 3.0\%$  SE). We provide quantitative results as to the temporal dynamics of sea lamprey carcass decomposition and subsequent nutrient liberation. These nutrient subsidies may arrive at a critical time to maximize enrichment of stream food webs.

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D. M. Weaver (✉) · S. M. Coghlan Jr.  
Department of Wildlife, Fisheries and Conservation  
Biology, University of Maine, 5755 Nutting Hall, Orono,  
ME 04469, USA  
e-mail: daniel.weaver@maine.edu

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

R. S. Hogg  
Oregon Department of Fish and Wildlife, Umatilla  
Hatchery Monitoring and Evaluation, Umatilla,  
OR 97838, USA

M. Canton  
Hollings Scholar, National Oceanic and Atmospheric  
Administration, Maine Field Station, Orono, ME 04473,  
USA

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## Introduction

Historically, many freshwaters were linked to the marine environment by spawning migrations of adult anadromous fishes and subsequent seaward migration of juveniles. Adult fish were important vectors for marine-derived nutrients transported into oligotrophic

freshwater systems and subsequently incorporated into stream and lake food webs. However, populations of many species declined or collapsed due to widespread damming, the loss of spawning habitat, and overfishing (Sheer & Steel, 2006; Saunders et al., 2006; Limburg & Waldman, 2009; Hall et al., 2011). Productivity and stream food web structure and function in resource limited aquatic systems may depend upon this annual influx of carbon, nitrogen, and phosphorus (Polis et al., 1997; Wipfli & Baxter, 2010).

Research from the Pacific Northwest is replete with examples documenting the influence of anadromous salmonines in driving nutrient and energy flows among marine and freshwater ecosystems (Cederholm et al., 1999; Gende et al., 2002). Nutrients provided by decomposing salmon carcasses have been shown to increase: (1) concentrations of nutrients in stream water (Jauquet et al., 2003; Mitchell & Lamberti, 2005; Claeson et al., 2006); (2) algal biomass (Claeson et al., 2006; Kohler et al., 2008), and conversely ecosystem respiration (Holtgrieve & Schindler, 2011; Levi et al., 2013); (3) macroinvertebrate production and density (Lessard & Merritt, 2006); (4) fish growth (Bilby et al., 1996; Wipfli et al., 2003); and (5) riparian vegetation growth (Naiman et al., 2002). These subsidies may alleviate nutrient limitations (Ruegg et al., 2011). The understanding of the role of Atlantic coast anadromous fish assemblages in altering nutrient dynamics of freshwater systems is limited, but discernible linkages between marine and freshwater systems have been established (Durbin et al., 1979; Garman & Macko, 1998; Walters et al., 2009). Food web response to nutrient subsidies in Atlantic coast systems may differ from what is observed in Pacific coast systems.

Pacific and Atlantic coast streams in North America exhibit differences that may affect the dynamics and efficacy of nutrient subsidies from anadromous fish. Pacific coast streams are generally high-gradient oligotrophic systems originating from the Rocky Mountains and Sierra Nevadas. In contrast Atlantic coast streams are generally low-gradient oligotrophic and mesotrophic systems originating from the lower-lying Appalachian Mountains. These ecoregions are characterized by distinct climates, soils, nutrient limitations, and surface land geomorphology (Omerik, 1977; Smith et al., 2003). Nutrient subsidy responses vary between ecoregions and are further

influenced by land use patterns (Tank & Dodds, 2003; Johnson et al., 2009). Whereas dams have impacted systems on both coasts, Atlantic coast systems are disproportionately impacted by historic and ongoing timber harvesting practices and acid rain pollution that have further increased environmental stress and reduced productivity, resilience, and biodiversity (Driscoll et al., 2001; Sweeney et al., 2004). Therefore, land use and watershed integrity in Atlantic coast systems are largely perturbed from intact conditions relative to Pacific coast systems and may respond to nutrient subsidies differently.

Atlantic and Pacific coast streams comprised unique anadromous fish assemblages that likely vary in net nutrient additions to freshwater systems (Nislow & Kynard, 2009; Pess et al., 2014; Weitkamp et al., 2014). Fish assemblages in Pacific coast streams largely comprised five species of semelparous salmonines *Oncorhynchus* spp. However, Atlantic coast anadromous fish assemblages contain more diverse life histories, comprised ubiquitous populations of iteroparous alosines *Alosa* spp., and striped bass (*Morone saxatilis* Walbaum, 1792), with relatively smaller spawning populations of iteroparous Atlantic salmon (*Salmo salar* Linnaeus, 1758), and rainbow smelt (*Osmerus mordax* Mitchell, 1814), and semelparous sea lamprey (*Petromyzon marinus* Linnaeus, 1758). Iteroparous species primarily supply metabolic waste and gametes to freshwater systems, but carcasses can contribute nutrients, whereas semelparous species primarily contribute relatively larger amounts of nutrients from dead spawners (Nislow & Kynard, 2009). The contrasting composition of these fish assemblages, and associated life history expressions likely influence the timing and magnitude of nutrients delivered to freshwater systems, and may preclude the direct application of trends from Pacific coast streams to Atlantic coast streams.

Sea lamprey and Pacific salmonines share traits of anadromy and semelparity, but the seasonal timing of migration suggests disparate carcass nutrient effects on stream food webs (Guyette et al., 2013). Sea lamprey spawn from spring to early summer (Beamish, 1980) compared to the majority of salmonines that spawn from fall to winter (Sumner, 1953; Quinn, 2005). Thus, sea lamprey arrival in freshwaters provides nutrient subsidies at a critical time when rising water temperatures and increasing photoperiod stimulates primary productivity and increases the

metabolic demand of consumers (Lovern, 1938; Hall, 1972, Cummins, 1974). Additionally, this coincides with the emergence of young-of-the-year fish (e.g., Atlantic salmon fry), and macroinvertebrates (Gustafson-Greenwood & Moring, 1990; Merritt et al., 2008; Nislow & Kynard, 2009), which may benefit from these nutrient subsidies.

Our objective was to characterize the temporal nutrient dynamics of decomposing sea lamprey carcasses as a first step in revealing subsidy pulses to stream ecosystems. To address our objective we sought to (1) analyze whole adult sea lamprey carcasses for elemental composition; (2) quantify temperature-dependence of concentrations of nutrients liberated from carcasses in the laboratory; and (3) quantify the decay rates (i.e., loss of biomass) of carcasses in a natural stream.

## Methods

### Fish collection

For the laboratory component of this study investigating elemental composition and temperature effects on nutrient liberation (Objectives 1 and 2), we collected pre-spawn sea lamprey during May 2010 and 2013 from Veazie Dam, the first barrier encountered by anadromous fishes migrating upstream the Penobscot River, Maine, at river kilometer (rkm) 40.0 in Penobscot County, Maine (note: Veazie Dam was removed in summer 2013; Penobscot River Restoration Trust, 2015). Collection took place during migration before sea lamprey commenced nest building and spawning activities. For the field component investigating in-stream decomposition rates (Objective 3), we collected post-spawn sea lamprey from Sedgeunkedunk Stream, a 3rd order tributary flowing into the Penobscot River at rkm 36.5 during June 2010. All collected fish were sexed and measured for mass ( $\pm 0.1$  g) and total length ( $\pm 1$  mm), then stored frozen at  $-10^{\circ}\text{C}$  until experimental deployment.

### Elemental composition analysis

Whole pre-spawn sea lamprey carcasses (7 males, 3 females,  $n = 10$ ) were processed for elemental composition. Individual carcasses were homogenized with water in a tissue grinder and oven dried at  $68^{\circ}\text{C}$  for

48 h. Samples were pulverized with a mortar and pestle then weighed out into two equivalent replicate samples. Samples were analyzed for total carbon and nitrogen by dry combustion (Leco CN-2000, St. Joseph, Michigan, U.S.A.), and for Ca, K, Mg, P, Al, Fe, Mn, Na, Zn, and Cu by dry ash mineral analysis with inductively coupled plasma optical electron spectroscopy (Thermo-Jarrell Ash ICP spectrometer, Model 975, Franklin, Massachusetts, U.S.A.) by the University of Maine Analytical Laboratory and Soil Testing Service. Results for total carbon and nitrogen were reported as a percent of dry weight and elements were reported in  $\text{mg kg}^{-1}$  of dry weight.

### Laboratory carcass decomposition and nutrient dynamics

In the laboratory, we assigned sea lamprey carcasses (9 females, 3 males;  $n = 12$ ) randomly as one of four replicates to one of three temperature treatments: 15, 20, and  $25^{\circ}\text{C}$ . Carcasses were placed into individual 15 l tanks irrigated with well water brought to each temperature using isolated heated or chilled water baths connected by a recirculating pump. A header tank for each treatment provided constant groundwater inflow at approximately  $80 \text{ ml min}^{-1}$ ; a complete water turnover within each tank occurred every 3 h. Air stones were placed inside tanks to circulate water and promote mixing. Temperature loggers (Onset, Hobo Pendant UA-001-08, Cape Cod, Massachusetts, U.S.A.) were placed inside the tanks of two replicates of each treatment and recorded temperature at one-hour intervals. During the course of this study the laboratory received no sunlight, and fluorescent lights operated on a timer lighting the room between 0700 and 1900 h. At the end of the experiment carcasses were re-measured for wet mass ( $\pm 0.1$  g).

We sampled water from the outflow of each tank prior to the addition of carcasses, at day 1, 2, and 3, then every 3 days for 45 days. Approximately 60 ml of water was filtered through 25-mm,  $0.45\text{-}\mu\text{m}$  mixed cellulose ester membranes (Millipore Corp., Billerica, Massachusetts, U.S.A.) with a filter holder and syringe into an acid washed bottle. In addition, a filtered 60 ml sample of deionized water, serving as a blank, was collected during each sampling occasion. After collection, samples were stored frozen until analysis. Samples were analyzed for dissolved inorganic nitrogen as ammonium ( $\text{NH}_4$ ) and nitrate ( $\text{NO}_3$ ) by flow

injection analysis (O.I. ALPKEM Flow Solution FS3000, College Station, Texas, U.S.A.), and total soluble phosphorus by inductively coupled plasma optical emission spectrometry (Thermo iCAP 6000, Thermo Fisher Scientific, Marietta, OH, U.S.A) by the University of Maine Analytical Laboratory and Soil Testing Service. Detection limits for ammonium and nitrate were 0.03 and 0.01 mg l<sup>-1</sup>, respectively, and 0.1 mg l<sup>-1</sup> for total soluble phosphorus.

### Natural stream carcass decomposition

Sea lamprey carcasses ( $n = 24$ ) collected from Sedgeunkedunk Stream were reintroduced on June 24 2010 consistent with the peak in post-spawning mortality we have observed in previous years. Carcasses were placed in mesh bags, caged in 1/2" mesh hardware cloth (to discourage scavengers), and distributed evenly among three 25-m reaches in the stream. Cages were anchored to secure carcasses to the substrate and prevent removal by terrestrial scavengers. Temperature loggers were placed in the stream reaches to record temperature at one-hour intervals. We sampled carcasses at days 14–17, 21, 24, 29, 32, 37, and 46. Carcasses were lifted gently from the stream with a dip-net, and debris was removed and excess water was allowed to drain, while attempting to minimize handling. Mass was measured with a hanging scale to the nearest 0.1 g. During sampling periods, carcasses that declined to  $\leq 15\%$  original body mass were removed from the stream as they largely comprised a notochord and oral disk.

### Statistical analysis

Due to low sample sizes, we used a series of nonparametric Wilcoxon Rank-Sum tests (Sokal & Rolf, 2012) to analyze for differences in elemental composition between males and females. Coefficients of variation ( $CV = SD/mean \times 100$ ; Zar, 1999) were calculated from replicate samples. Ammonium, nitrate, and total soluble phosphorus concentrations from the laboratory decomposition experiment were analyzed in a linear mixed effects model (JMP Pro version 11.0, SAS, Inc., Cary, North Carolina). Residuals did not conform to a normal distribution (Shapiro–Wilk  $W$  test:  $P < 0.05$ ; Zar, 1999); therefore, a log transformation was applied to the nutrient concentrations to satisfy normality assumptions. We

modeled nutrient concentration as a function of temperature, day, and the interaction as fixed effects, and replicate as a random effect. Finally, results from our natural stream carcass decomposition experiment were plotted as a mean proportion of initial carcass weight and tested as an exponentially declining function of time with a Kolmogorov–Smirnov goodness-of-fit test (Zar, 1999).

## Results

### Elemental composition

Our elemental composition analysis demonstrated several differences among male and female sea lamprey (Table 1). Wilcoxon rank-sum tests identified higher calcium and aluminum concentrations and lower iron concentrations in females versus males

**Table 1** Mean ( $\pm$ SE) sea lamprey length, weight, elemental concentration (% or mg kg<sup>-1</sup>), and N:P and C:N ratios from elemental composition analysis

Variable	Males Mean (SE)	Females Mean (SE)
Metric		
Length (mm)	654.1 (20.3)	568.0 (43.9)
Mass (g)	629.4 (82.2)	449.7 (97.8)
Element (%)		
N	11.1 (0.5)	11.3 (0.3)
C	55.2 (1.0)	53.6 (1.4)
Element (mg·kg <sup>-1</sup> )		
N	110,714 (14,863)	112,667 (3384)
<b>Ca</b>	<b>262 (18)</b>	<b>597 (126)</b>
K	8641 (432)	3826 (2261)
Mg	598 (26)	479 (111)
P	5830 (256)	5340 (1179)
<b>Al</b>	<b>54 (7)</b>	<b>198 (41)</b>
<b>Fe</b>	<b>280 (22)</b>	<b>181 (20)</b>
Mn	–	–
Na	3497 (277)	1662 (874)
Zn	61 (4)	81 (5)
Cu	14.5 (1.4)	12.9 (0.5)
N:P	19.0 (0.2)	22.8 (3.9)
C:N	5.1 (0.4)	4.8 (0.3)

Manganese concentrations were below detection limits ( $<2.0$  mg l<sup>-1</sup>). Bolded parameters indicate significant differences from Wilcoxon rank-sum tests ( $P < 0.05$ )

( $P < 0.05$ ). Conversely, we observed no differences in potassium, magnesium, phosphorus, and sodium concentrations, nor percent carbon and nitrogen. Nitrogen to phosphorus ratios (mean  $\pm$  SE) among all individuals were 20.2:1 ( $\pm 1.18$ ); 19.0:1 ( $\pm 0.17$ ) for males and 22.8:1 ( $\pm 3.93$ ) for females, however, this was not significantly different. Concentrations of manganese were below detection limits ( $1.0 \text{ mg kg}^{-1}$ ), in many instances reported as  $<2.0 \text{ mg kg}^{-1}$ , and therefore were excluded from analysis. Coefficients of variation between replicate samples were generally low ( $\leq 2.0\%$ ) with the exception of aluminum that ranged 2–88%.

#### Laboratory carcass decomposition and nutrient dynamics

During the laboratory experiment, temperatures in the three treatments (mean  $\pm$  SD) averaged  $15.0 \pm 1.3$ ,  $19.6 \pm 0.6$ , and  $25.5 \pm 0.8^\circ\text{C}$ , respectively. After 45 days, mean proportion of initial body mass decreased to 0.75 at  $15^\circ\text{C}$ , to 0.74 at  $20^\circ\text{C}$ , and to 0.48 at  $25^\circ\text{C}$  (Table 2). Our linear mixed effects model revealed a significant interaction between Day and Temperature among all nutrients ( $P < 0.001$ ; Fig. 1). For the main effects, Day was significant among all nutrients, and Temperature was significant for nitrate and phosphorus, but not ammonium.

Our experiment demonstrated varying liberation rates and temperature dependencies among nutrients (Fig. 1). Mean background nutrient concentrations (day 0; mean  $\pm$  SD) among all tanks were  $2.4 \pm 0.002 \text{ mg l}^{-1}$  for nitrate,  $0.027 \pm 0.003 \text{ mg l}^{-1}$  for ammonium, and  $0.042 \pm 0.0006 \text{ mg l}^{-1}$  for phosphorus. Nutrient concentrations were the most variable among temperatures from day 1–9. During this period

ammonium concentrations (mean  $\pm$  SD) were  $2.5 \pm 1.1 \text{ mg l}^{-1}$  at  $15^\circ\text{C}$ ,  $4.4 \pm 0.8 \text{ mg l}^{-1}$  at  $20^\circ\text{C}$ , and  $9.8 \pm 3.4 \text{ mg l}^{-1}$  at  $25^\circ\text{C}$ . From day 12–21, ammonium concentrations were relatively consistent for  $15^\circ\text{C}$  ( $4.2 \pm 1.1 \text{ mg l}^{-1}$ ), but lower for  $20^\circ\text{C}$  ( $3.9 \pm 1.7 \text{ mg l}^{-1}$ ) and  $25^\circ\text{C}$  ( $2.8 \pm 1.7 \text{ mg l}^{-1}$ ). Ammonium concentrations continued to decline after day 21, approaching background concentrations among all treatments. Nitrate concentrations responded to temperature differently than ammonium during the first nine days and were  $2.1 \pm 0.2 \text{ mg l}^{-1}$  at  $15^\circ\text{C}$ ,  $1.7 \pm 0.4 \text{ mg l}^{-1}$  at  $20^\circ\text{C}$ , and  $0.8 \pm 0.5 \text{ mg l}^{-1}$  at  $25^\circ\text{C}$ . After three weeks, nitrate concentrations were relatively consistent among temperatures. Total soluble phosphorus demonstrated a similar pattern among temperatures. During days 1–9 total soluble phosphorus concentrations were  $0.8 \pm 0.7 \text{ mg l}^{-1}$  at  $15^\circ\text{C}$ ,  $1.0 \pm 0.7 \text{ mg l}^{-1}$  at  $20^\circ\text{C}$ , and  $1.1 \pm 0.9 \text{ mg l}^{-1}$  at  $25^\circ\text{C}$ . The highest concentrations among all temperatures occurred at day 1 and returned to background concentrations after day 21.

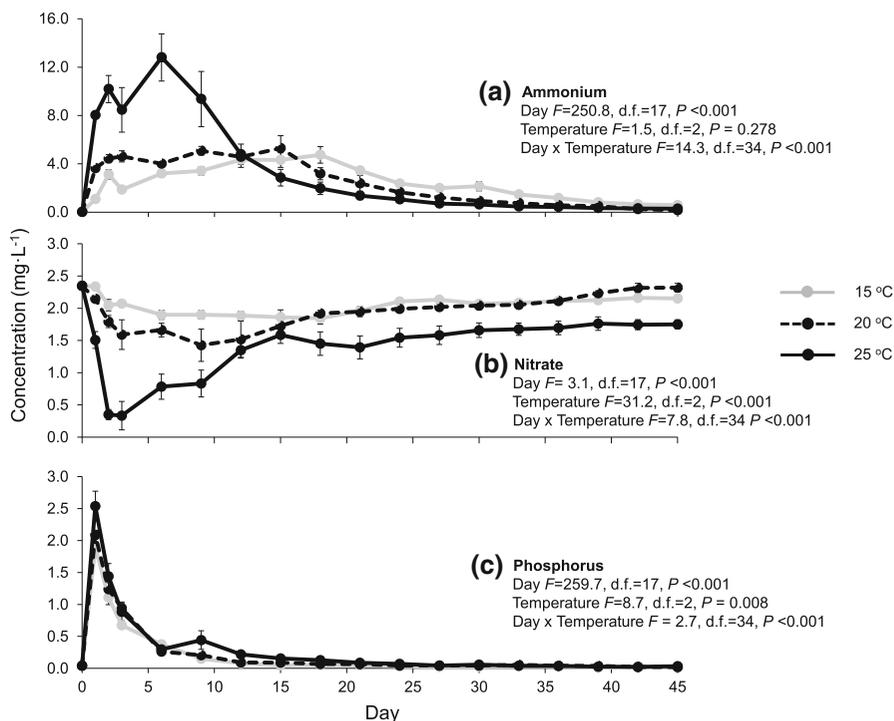
#### Natural stream carcass decomposition

Mean daily temperatures on Sedgeunkedunk Stream were  $21.8 (\pm 0.24^\circ\text{C SE})$  during our field decomposition experiment. Carcasses reintroduced into the stream averaged  $0.56 \pm 0.03 \text{ kg SE}$  prior to decomposition. Surveys of carcasses after two weeks revealed a decrease in mean proportion of initial body mass to  $0.85 \pm 0.13 \text{ SE}$  (Fig. 2). Between days 15 and 17 mean carcass proportions declined to  $0.47 \pm 0.08 \text{ SE}$ , and by day 24 mean carcass proportions were  $0.27 \pm 0.03 \text{ SE}$ . By day 32 (July 23, 2010) we had removed 9 carcasses from the stream ( $<15\%$  initial body mass), and by day 46 (August 6, 2010) only 2

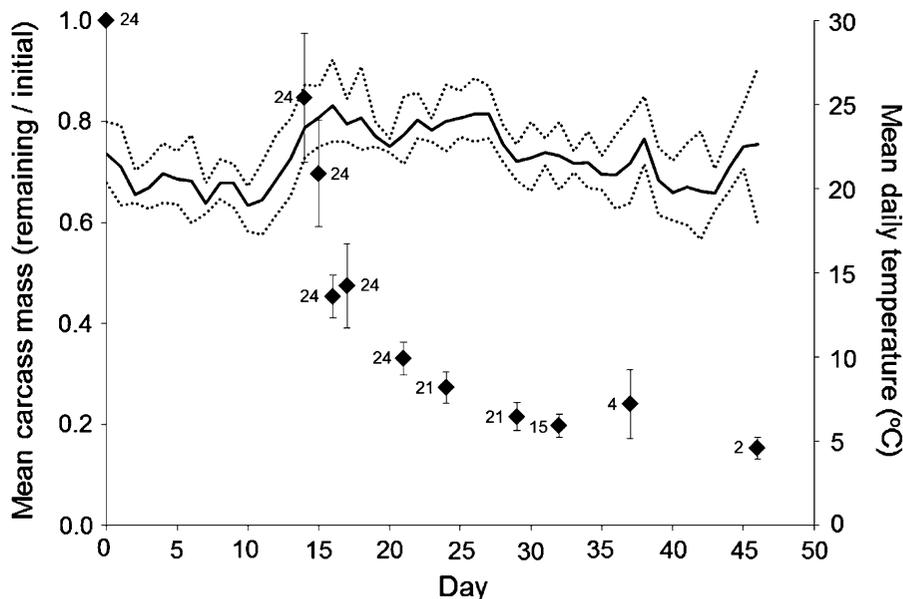
**Table 2** Comparisons of sea lamprey carcass mean ( $\pm$ SE) length and mass before and after 45 days, and average mass loss and proportion of initial mass remaining among temperature treatments

Treatment ( $^\circ\text{C}$ )	Before		After		
	Length (mm)	Mass (g)	Mass (g)	Mass loss (g)	Proportion of initial mass
15	691.3 (16.7)	758.4 (39.0)	567.0 (70.4)	191.4	0.75
20	680.0 (22.4)	786.7 (110.6)	581.2 (131.2)	205.5	0.74
25	680.3 (15.3)	772.5 (54.8)	368.5 (30.6)	404.0	0.48

**Fig. 1** Ammonium, nitrate, and total soluble phosphorus concentrations (mean  $\pm$  SE) over 45 days among 15, 20, and 25°C temperature treatments ( $n = 12$ ).  $F$  and  $P$  statistics are presented for a linear mixed effects model testing for the effects of time and temperature (see text for explanation)



**Fig. 2** Proportion of mean carcass mass (kg  $\pm$  SE) remaining of initial carcass mass over 46 days ( $n = 24$ ), mean daily temperature (degrees Celsius; *solid line*) and minimum and maximum daily temperatures (*dotted lines*) in Sedgeunkedunk Stream during June–August 2010. Numbers next to each mean indicate the number of carcasses remaining in the stream



carcasses remained above our threshold. The Kolmogorov–Smirnov goodness-of-fit test determined that the proportion of initial body mass over time among sampled carcasses followed an exponential decay ( $D = 0.292$ ;  $P = 0.25$ ).

## Discussion

We sought to quantify elemental composition, decay rates, and temperature effects on nutrient liberation from anadromous sea lamprey carcasses. In the

laboratory, nutrient liberation from carcasses was faster at higher temperatures and the majority of phosphorus and ammonium leached within one and three weeks, respectively. In a natural stream, carcasses decomposed to <30% of their original mass in 24 days. Our results suggest that conclusions drawn about changes in nutrient dynamics from anadromous fish assemblages based on studies of Pacific Northwest streams may not apply to Atlantic coast streams.

### Elemental composition

Nitrogen to phosphorus ratios of sea lamprey averaged 20.2:1 ( $\pm 1.2$  SE), whereas N:P ratios measured in salmonines vary from 5:1 to 17:1 (Stansby & Hall, 1965; Lyle & Elliott, 1998; Johnston et al., 2004; Pearsons et al., 2007; Guyette et al., 2014). Whole-body elemental composition varies among species and arises from differences in morphology, anatomy, physiology, and life history strategies (Elser et al., 1996; Tanner et al., 2000; Dantas & Attayde, 2007). Differences in N:P ratios between salmonines and sea lamprey may be due to contrasting anatomical structures. Unlike salmonines, sea lamprey lack recalcitrant scales and bone, which are sources of phosphorus that likely increase whole-body N:P ratios (Bowen, 1966; Parmenter & Lamarra, 1991). Stoichiometric differences between salmonines and sea lamprey subsidies may result in disparate available nutrient pools, leading to differences in primary productivity, consumer-regulated nutrient cycling, and community structure (Kitchell et al., 1979; Tilman, 1982; Elser et al., 1996). Expressed effects of these stoichiometric differences are context-dependent, according to biological (i.e., community structure), physical, and geological characteristics that vary between Pacific coastal streams and Atlantic coastal streams.

The individuals collected for elemental analysis were in the process of migrating up the Penobscot River and likely had not begun any spawning activity. We may expect differences in whole-body calcium, nitrogen, and phosphorous concentrations between males and females due to the synthesis of vitellogenin, a female-specific yolk precursor protein in oviparous vertebrates during maturation. Increases in plasma calcium concentrations and phosphoprotein phosphorus are associated with vitellogenesis and, for example, have been observed among female spawning cod *Gadus* spp., and rainbow trout *Oncorhynchus mykiss*,

Walbaum 1792 (Woodhead, 1968; Whitehead et al., 1978; Nagler et al., 1987). We observed higher calcium concentrations in females compared to males. However, we did not detect lower N:P ratios in females from phosphoprotein phosphorus production, compared to males, which may be due to low sample sizes (7 males, 3 females).

### Carcass decomposition and nutrient dynamics

We observed higher carcass decomposition rates in Sedgeunkedunk Stream compared to the laboratory. In the lab, carcasses decreased to 0.48–0.75 of initial body mass at the end of 45 days, whereas in the stream all carcasses decreased to <0.15 of initial body mass or had previously decreased below that proportion over the same time period. In streams, carcasses likely break down at much faster rates due to higher stream flows and associated shear stress, and abrasion and direct consumption by organisms (e.g., macroinvertebrates; Minakawa & Gara, 1999; Chaloner et al., 2002; Fenoglio et al., 2010). During our natural stream measurements of carcass decomposition (Fig. 2), there were two instances at day 16–17 and day 32–37 where we measured higher mean carcass mass remaining from a preceding measurement. We attribute these increases in mean mass to variation introduced from debris, and excess water retained by the carcasses as they were lifted out of the water. We wished to minimize handling disturbance to keep carcasses intact, therefore, we incurred this error.

The decomposition rates and enrichment effects of sea lamprey and salmon carcasses may be influenced by the seasonal timing of migration and spawning as well as biophysical processes in streams. Organic matter decomposition is faster at higher temperatures due to increased microbial and invertebrate metabolism (Cummins, 1974; Minshall et al., 1991; Young et al., 2008). The decomposition of sea lamprey carcasses during early summer is likely accelerated by higher temperatures compared to decomposition of salmon during the fall and winter. Wipfli et al., (1998) observed salmon carcasses decompose to 60% of their original mass over a three month period in average temperatures of 7.5°C, with much of that decomposition occurring initially during higher temperatures immediately post-spawn. In contrast, our study demonstrated that sea lamprey carcasses lost over 60% of initial mass in less than a month (Fig. 2). We

observed a slower decomposition rate during the first two weeks at a mean stream temperature of 20.6°C. This was followed by an accelerated decomposition rate, characteristic of exponential decay, at a mean stream temperature of 23.8°C. The abrupt increase in mean stream temperature and corresponding decrease in proportion of initial weight are a plausible explanation for the patterns we observed. Furthermore, the disparate trends in decomposition between salmon and sea lamprey may be due to differences in skeletal structure. As decomposition occurs, a large proportion of initial salmon carcass weight remains in the stream in the form of recalcitrant bone and scales comprising phosphorus and calcium (Parmenter & Lamarra, 1991), in contrast to sea lamprey that leave behind a relatively lighter cartilaginous notochord and keratinized mouth parts.

The influence of nutrient subsidies from sea lamprey carcasses likely depends upon carcass retention within the stream. Although we did not measure carcass retention within streams, literature examining the fate of post-spawning salmonines has demonstrated that a majority of carcasses are retained within streams or adjacent forests (carried by scavengers; Cederholm et al., 1989), while a proportion may be displaced downstream and accumulate in areas of slow moving water (Williams et al., 2010). To our knowledge a formalized study has not been conducted examining sea lamprey carcass retention within lotic systems; however, we suspect that downstream displacement and scavenger removal play a role. We have observed snapping turtle (*Chelydra serpentina* Linnaeus, 1758) consuming moribund sea lamprey in Sedgeunkedunk Stream; other likely scavengers would include raccoon (*Procyon lotor* Linnaeus, 1758) and crayfish (e.g., Cambaridae).

The enriching effects of carcasses on nutrient concentrations in ambient water we observed were over periods of days, in contrast to studies of salmonids in which elevated stream water nutrient concentrations persisted for several weeks or more (Minakawa & Gara, 1999; Claeson et al., 2006; Kohler et al., 2008). Wipfli et al., (2010) observed relatively high phosphorus and ammonium concentrations in stream water, persisting for four and six weeks, respectively, after salmon carcass addition compared to control reaches during the fall over temperatures that ranged 6.2–9.3°C. Water temperatures of small streams within the Penobscot Watershed may average

20°C or more during the spring at the time of sea lamprey spawner death, which correspond to ammonium and phosphorus liberation rates that persist for just one to three weeks (Fig. 1). Thus, the timing of sea lamprey migration affects the magnitude and persistence of nutrient subsidies available to stream food webs.

The patterns of nitrate and ammonium from the carcasses we observed may be explained by microorganisms present on the carcasses. Denitrification and dissimilatory nitrate reduction to ammonium (DNRA) by heterotrophic bacteria may be two plausible hypotheses explaining the trends we observed. Denitrification reduces nitrate to dinitrogen gas (N<sub>2</sub>), while DNRA reduces nitrate to ammonium (MacFarlane and Herbert 1984; Kelso et al., 1997). These processes occur under anaerobic conditions, likely occurring within carcasses and may explain the decrease in nitrate and corresponding increase in ammonium during the first three weeks of decomposition (Fig. 1). Ammonium, nitrate, and soluble phosphorus become available nutrients for other biological processes, uptake, and recycling in lotic systems.

Anadromous fish are important vectors of marine-derived nutrients to freshwater ecosystems (Gende et al., 2002; Lamberti et al., 2010). The spring timing of sea lamprey spawning is such that nutrient subsidies may arrive at a critical period of increased metabolic demand and declining primary productivity (Hall, 1972; Cummins, 1974). Thus, bioenergetic limitations of stream organisms may be alleviated at this time. Furthermore, these nutrient subsidies may increase the success of juvenile migratory and resident fishes (e.g., Atlantic salmon; Nislow et al., 1998; Nislow & Kynard, 2009; Guyette et al., 2014). In areas where sea lamprey populations are intact, these fish are likely important drivers of nutrient dynamics and an integral component of the structure and function of stream food webs.

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