

Anadromous alewives (*Alosa pseudoharengus*) contribute marine-derived nutrients to coastal stream food webs

Annika W. Walters, Rebecca T. Barnes, and David M. Post

Abstract: Diadromous fish are an important link between marine and freshwater food webs. Pacific salmon (*Oncorhynchus* spp.) strongly impact nutrient dynamics in inland waters and anadromous alewife (*Alosa pseudoharengus*) may play a similar ecological role along the Atlantic coast. The annual spawning migration of anadromous alewife contributes, on average, 1050 g of nitrogen and 120 g of phosphorus to Bride Brook, Connecticut, USA, through excretion and mortality each year. Natural abundance stable isotope analyses indicate that this influx of marine-derived nitrogen is rapidly incorporated into the stream food web. An enriched $\delta^{15}\text{N}$ signal, indicative of a marine origin, is present at all stream trophic levels with the greatest level of enrichment coincident with the timing of the anadromous alewife spawning migration. There was no significant effect of this nutrient influx on water chemistry, leaf decomposition, or periphyton accrual. Dam removal and fish ladder construction will allow anadromous alewife to regain access to historical freshwater spawning habitats, potentially impacting food web dynamics and nutrient cycling in coastal freshwater systems.

Résumé : Les poissons diadromes établissent un lien important entre les réseaux alimentaires marins et ceux d'eau douce. Les saumons du Pacifique (*Oncorhynchus* spp.) affectent fortement la dynamique des nutriments dans les eaux intérieures et les gaspareaux anadromes (*Alosa pseudoharengus*) peuvent jouer un rôle écologique similaire le long de la côte de l'Atlantique. La migration annuelle de fraie des gaspareaux anadromes contribue, en moyenne chaque année, 1 050 g d'azote et 120 g de phosphore par excretion et par mortalité à Bride Brook, Connecticut, É.-U. Des analyses de l'abondance naturelle des isotopes stables indiquent que cet apport d'azote d'origine marine est rapidement incorporé dans le réseau alimentaire du cours d'eau. Un signal enrichi de $\delta^{15}\text{N}$, qui dénote l'origine marine, se retrouve à tous les niveaux trophiques du cours d'eau et les degrés maximaux d'enrichissement coïncident avec le moment de la migration de fraie des gaspareaux anadromes. Il n'y a aucun effet significatif de cet apport de nutriments sur la chimie de l'eau, ni la décomposition des feuilles, ni l'accumulation de périphton. Le retrait des barrages et la construction d'échelles à poissons permettront aux gaspareaux de retrouver l'accès à leurs habitats de fraie en eau douce du passé, ce qui aura potentiellement un impact sur la dynamique des réseaux alimentaires et le recyclage des nutriments dans les écosystèmes côtiers d'eau douce.

[Traduit par la Rédaction]

Introduction

Biota can play a central role in regulating the flux of energy and nutrients across ecosystem boundaries (Vanni 2002). One noteworthy example is Pacific salmon (*Oncorhynchus* spp.) that transport nutrients from marine to freshwater systems in the Pacific Northwest as a consequence of their anadromous life history (Naiman et al. 2002; Schindler et al. 2003; Thomas et al. 2003). The role of other anadromous fish, especially those of the Atlantic Ocean, is less well known. Anadromous alewife (*Alosa pseudoharengus*) ranges from North Carolina to Newfoundland (Scott and Crossman 1988) and is potentially an important source of

marine-derived nutrients to freshwater ecosystems. The one available estimate of nutrient loading by anadromous alewife in Pausacaco Pond, Rhode Island, USA, suggests that, on a per area basis, nitrogen and phosphorus loading by alewife is equivalent to that of Pacific salmon (Durbin et al. 1979).

Historically, alewives were highly abundant, but as is the case with Atlantic salmon (*Salmo salar*) and many other anadromous fish, their numbers have declined owing to dam construction and overfishing (Savoy and Crecco 1995; Atlantic States Marine Fisheries Commission 1999). Current restoration efforts across New England are attempting to reverse this trend by removing dams and constructing fish ladders. This will allow alewives to regain access to historical spawning grounds in streams and lakes, and the accompanying influx of marine-derived nutrients could impact freshwater food webs and nutrient cycling. Aquatic habitats in southern New England are moderately to highly productive, and eutrophication is a major management concern. Understanding the role of alewife-contributed marine-derived nutrients is therefore important to successfully manage restoration efforts.

In Pacific salmon systems, marine-derived nutrients have been found to have wide-ranging effects. The nutrients are

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incorporated into all levels of freshwater food webs (Kline et al. 1990; Bilby et al. 1996; Chaloner et al. 2002) and neighboring terrestrial food webs (Bilby et al. 1996; Ben-David et al. 1998). In Alaskan streams, periphyton were found to contain 50% marine-derived nitrogen at sites with a low density of spawning fish and up to 90% marine-derived nitrogen at sites with a high density of spawning fish (Kline et al. 1993). The influx of nutrients has also been found to increase algal biomass and invertebrate biomass (Wipfli et al. 1998, 1999; Johnston et al. 2004). This increase in primary and secondary production is thought to be crucial for juvenile salmon growth and survivorship (Schindler et al. 2003, 2005). In addition to providing an influx of nutrients, salmon have also been shown to play a role in the dispersal of nutrients through bioturbation of sediments during nest building (Moore et al. 2007).

It is unknown whether anadromous alewives have similar effects. The few previous studies suggest that marine-derived nutrients could also be important in the alewife system with evidence for marine-derived nutrients being incorporated into alewife predators (MacAvoy et al. 2000) and stimulating microbial leaf litter breakdown (Durbin et al. 1979). However, there are important life history differences between alewife and Pacific salmon that could mediate the response. First, alewives are smaller in size and iteroparous, while most Pacific salmon are semelparous, possibly reducing their impact as a vector of marine-derived nutrients. Second, alewives broadcast spawn in lakes instead of digging nests, possibly reducing their impact as bioturbators.

Here, we examine the effect of alewife-contributed marine-derived nutrients to coastal stream ecosystems in southern New England. We take a comparative approach examining streams with and without anadromous alewife runs. We use natural abundance stable isotope analyses to assess the incorporation of marine-derived nitrogen and carbon into stream food webs. Natural abundance isotopes can be used to trace the fate of alewife-derived nitrogen and carbon because marine organic material is enriched in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ relative to terrestrial and freshwater organic material (Kline et al. 1990; Bilby et al. 1996; Chaloner et al. 2002). We also conduct water chemistry analyses and test for changes in ecosystem rates, such as leaf decomposition and periphyton accrual. The aim is to combine estimates of nutrient loading with an understanding of the community- and ecosystem-level effects for streams.

Materials and methods

Study sites

Our research was primarily conducted at six coastal streams in New London County, Connecticut, USA. All streams flow into the Long Island Sound. We had three sites with anadromous alewife runs, Bride Brook ($41^{\circ}19'28''\text{N}$, $-72^{\circ}14'26''\text{W}$), Mill Brook ($41^{\circ}20'14''\text{N}$, $-72^{\circ}19'16''\text{W}$), and lower Pattagansett River ($41^{\circ}20'5''\text{N}$, $-72^{\circ}12'25''\text{W}$), and three reference sites that did not have alewives, Four Mile River ($41^{\circ}22'27''\text{N}$, $-72^{\circ}15'15''\text{W}$), Fall Brook ($41^{\circ}22'22''\text{N}$, $-72^{\circ}20'07''\text{W}$), and upper Pattagansett River ($41^{\circ}23'09''\text{N}$, $-72^{\circ}14'58''\text{W}$). All reference sites did not have alewife owing to a downstream barrier. One other stream without alewives, the outlet to Linsley Pond ($41^{\circ}18'53''\text{N}$,

$-72^{\circ}47'14''\text{W}$), located in New Haven County, Connecticut, was used for the leaf decomposition study in 2005.

We conducted more extensive temporal sampling at Bride Brook and Four Mile River. Bride Brook is the outlet to Bride Lake, an important spawning lake for anadromous alewife and the site of both historical (Kissel 1969) and current research (Palkovacs and Post 2008; Palkovacs et al. 2008; Post et al. 2008) on anadromous alewives. The Connecticut Department of Environmental Protection has collected daily data on the number of spawning anadromous alewives entering Bride Lake each year since 2003 with an electronic fish counter (Smith Root SR-1601). The fish counter was monitored daily and calibrated by fencing off an area at the inlet to Bride Lake and counting the alewife by hand. Four Mile River is a similarly sized stream without alewife located slightly west of Bride Brook.

Nutrient loading

The two sources of alewife-contributed nutrients to Bride Brook are excretion and carcasses. Nutrient input from excretion = excretion rate ($\text{g}\cdot\text{fish}^{-1}\cdot\text{h}^{-1}$) \times number of fish \times residence time in the stream (h). We used direct excretion rates for total nitrogen ($0.003952 \text{ g}\cdot\text{fish}^{-1}\cdot\text{h}^{-1}$) and total phosphorus ($0.00034 \text{ g}\cdot\text{fish}^{-1}\cdot\text{h}^{-1}$) calculated from Bride Brook alewives held in a circulating-water holding tank (Post and Walters 2009). We used fish swimming rate estimates ($0.5 \text{ m}\cdot\text{s}^{-1}$ measured over 5 m stretches during the spawning migration on 26 April 2008) and the length of Bride Brook (3300 m calculated from geographic information system maps) to calculate residence time of the alewife in the stream (approximately 2 h).

Nutrient inputs from carcasses = number of fish \times percent mortality in the stream \times nutrient content of fish. We used data from Durbin et al. (1979) on percent nitrogen (2.49% of wet mass) and phosphorus (0.42% of wet mass) of alewives combined with current measurements of the average wet weight of anadromous alewife (160 g) to calculate the nitrogen ($3.99 \text{ g}\cdot\text{fish}^{-1}$) and phosphorus content ($0.68 \text{ g}\cdot\text{fish}^{-1}$) of alewives. Alewife mortality in the stream was low with just one carcass or no carcasses at all added to the stream most nights (A.W. Walters, personal observation). We compared the number of carcasses in the stream before and after a large nightly spawning migration (approximately 18 000 alewives) on 25–26 April 2008 to estimate percent mortality (0.1%) in the stream. To calculate nutrient inputs on an areal basis, we estimated the area of Bride Brook by multiplying the length of Bride Brook (3300 m) by the average width of Bride Brook (5 m) (measured on 26 April 2008 from 40 transects at approximately 10 m intervals along the stream).

Water chemistry analysis

In 2005, water samples were collected every 2–3 weeks from early March until July for Bride Brook and Four Mile River. In 2006, water samples were collected in all six streams in March (prespawning run) and in April and May (peak spawning run). Two water samples were collected at each site; one was filtered through a GF/F filter and one was unfiltered. All samples were collected in acid-washed HDPE bottles and frozen. Samples collected in 2005 were analyzed for total nitrogen and total phosphorus. Samples

collected in 2006 were analyzed for total nitrogen, ammonium (NH_4^+), nitrate (NO_3^-), and nitrite (NO_2^-).

Nitrogen and phosphorus analyses were completed using colorimetric methods on the Astoria 2 flow analyzer (Astoria-Pacific International). We used persulfate digestion in conjunction with the automated analyzer to determine the total phosphorus content of unfiltered samples (American Public Health Association 1998) and the total nitrogen content of unfiltered samples (Valderrama 1981). The detection limits for NO_3^- , NO_2^- , and NH_4^+ are 0.005, 0.002, and 0.01 $\text{mg}\cdot\text{L}^{-1}$, respectively. Approximately 10% of the samples were run in duplicate for quality assurance purposes; on average, standard deviations between duplicate samples were within 0.02, 0.001, 0.003, and 0.007 $\text{mg}\cdot\text{L}^{-1}$ for NO_3^- , NO_2^- , NH_4^+ , and total nitrogen, respectively.

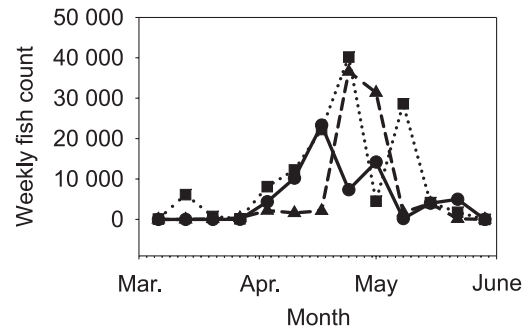
Isotope collection and analysis

We collected periphyton and aquatic insects at Bride Brook and Four Mile River every 2–3 weeks from early March until July in both 2005 and 2006. For the other four sites, periphyton and aquatic insects were collected only in 2006 and sampling occurred only at three time points: early March (prespawning run), early May (peak spawning run), and July (postspawning run).

We collected periphyton from three rocks, haphazardly selected, from a riffle section of the stream. We scraped the rocks with a toothbrush and rinsed the rocks with water. The periphyton mixture was filtered onto a precombusted CF/C filter, placed in foil, put on ice, and later frozen. Filter samples were dried at 60 °C for 48 h and a half filter was used for isotope analysis. We collected aquatic insects using a WaterMark bottom aquatic kicknet in both pool and riffle habitats. We sorted the insects in the field, placed individuals into plastic vials, put the vials on ice, and later froze them. All aquatic insect samples were identified to the family level using a 10× dissecting microscope, and macroinvertebrate functional feeding groups were designated according to Merritt and Cummins (1996). Collector-filterers collected included Hydropsychidae and Simuliidae, collector-gatherers included Ephemerellidae and Heptageniidae, shredders included Nemouridae and Taeniopterygidae, and predators included Aeshnidae, Corydalidae, Gomphidae, Lestidae, and Perlidae. For the time series graphs, we only used the most common collector-gatherer families (Ephemerellidae and Heptageniidae) and the most common predator family (Bride Brook: Lestidae, Four Mile River: Corydalidae) to reduce variation.

For isotopic analysis, we dried the samples at 60 °C for 48 h and then ground them to a fine powder using a mortar and pestle. For smaller insects, individuals were pooled (2–20 individuals) for analysis, but larger insects were run individually. Isotope analysis was performed with a ThermoFinnigan DeltaPlus Advantage stable isotope mass spectrometer at the Earth Systems Center for Stable Isotope Studies (ESCSIS) at Yale Institute for Biospheric Studies (New Haven, Connecticut). All stable isotope values are reported in the standard notation. Aquatic insect $\delta^{13}\text{C}$ values were corrected for lipids using C:N ratios using the formula $\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + 0.99 \times \text{C:N}$ from Post et al. (2007). We did not correct periphyton $\delta^{13}\text{C}$ values for lipids, as periphyton is assumed to have very low lipid content. For

Fig. 1. Bride Brook alewife spawning migration numbers for 2005 (circles), 2006 (squares), and 2007 (triangles).



aquatic insects, the local standard used was ESCSIS animal standard (trout) whereas for the filter samples, the local standard used was ESCSIS plant standard (cocoa). The standard deviation of animal standard (trout) across runs was 0.14‰ for $\delta^{13}\text{C}$ and 0.21‰ for $\delta^{15}\text{N}$ ($n = 38$). For plant standard (cocoa), the standard deviation across runs was 0.09‰ for $\delta^{13}\text{C}$ and 0.34‰ for $\delta^{15}\text{N}$ ($n = 17$).

Leaf decomposition and periphyton accrual

We measured the rate of microbial leaf decomposition for both maple (*Acer* spp.) and oak (*Quercus* spp.) leaves. For each leaf type, we placed 5 g of dry leaves into nylon bags (mesh size approximately 0.5 mm). We then placed 10 bags of each leaf type into each of two alewife streams (Bride Brook and Mill Creek) and two no-alewife streams (Four Mile River and the outlet to Linsley Pond) for 2 weeks before the alewife run (14–28 March 2005) and repeated this for 2 weeks during the alewife run (18 April – 2 May 2005). Water temperatures ranged from 3 to 6 °C (14–28 March 2005) and from 13 to 17 °C (18 April – 2 May 2005). After removing the leaf bags from the stream, we dried them at 60 °C for 48 h and reweighed the leaves.

To measure the rate of periphyton accrual, we placed ten 3 cm × 3 cm unglazed ceramic tiles into each of two alewife streams (Bride Brook and lower Pattagansett River) and two no-alewife streams (Four Mile River and upper Pattagansett River) for 2 weeks before the alewife run (11 – 25 March 2007) and repeated this for 2 weeks during the alewife run (20 April – 4 May 2007). When we retrieved the tiles, we scraped each tile with a toothbrush, rinsed the tile with distilled water, and filtered the entire mixture onto a GF/C filter. We then placed the filter on ice and froze it. We used chlorophyll *a* concentration as our measure of algal biomass. Filters were analyzed for chlorophyll *a* concentrations, corrected for pheopigments, on a Turner Designs TD-700 fluorometer (Marker et al. 1980) following US Environmental Protection Agency method 445.0.

Statistical analyses

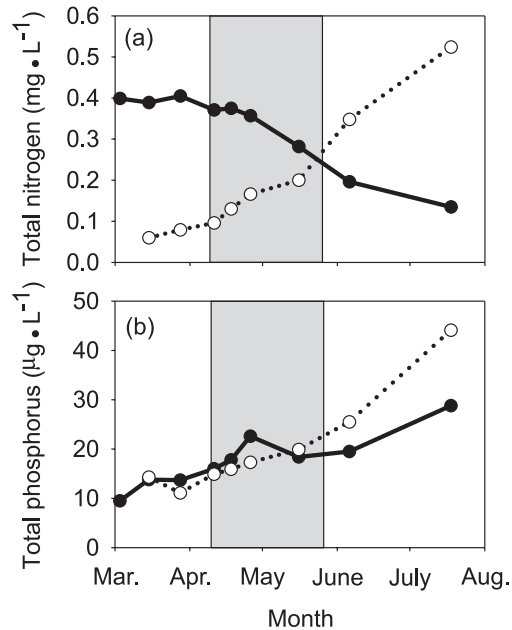
All statistical analyses were performed in R (version 2.6.0) (R Development Core Team 2008). We used analysis of variance (ANOVA) to test for effects of alewife presence and time on our $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for periphyton and collector-gatherer insects in our six streams in 2006. We only included sites if there were samples for each time point, so for collector-gatherer insects, there were only two alewife and two no-alewife streams whereas for periphyton,

Table 1. Nitrogen and phosphorus inputs by anadromous alewives to Bride Brook.

	2005		2006		2007	
	Nitrogen	Phosphorus	Nitrogen	Phosphorus	Nitrogen	Phosphorus
Total inputs (g)	817.8	94.5	1535.7	177.4	796.6	92.0
Areal inputs: total inputs/area (mg·m ⁻²)	49.6	5.7	93.1	10.8	48.3	5.6
Excretion inputs (g)	543.5	47.7	1020.5	89.6	529.4	46.5
Carcass inputs (g)	274.3	46.8	515.2	87.8	267.2	45.5
Mean daily total input (g)	11.5	1.3	19.2	2.2	11.9	1.4
Maximum daily total input (g)	101.0	11.7	190.7	22.0	147.0	17.0

Note: Inputs are calculated for the duration of the spawning run (mid-March through May). Calculations are based on the number of alewives returning to spawn (68 757 in 2005, 129 114 in 2006, and 66 975 in 2007). Areal inputs are based on an estimated area of 16 500 m² for Bride Brook.

Fig. 2. Nutrient dynamics for (a) total nitrogen and (b) total phosphorus for an alewife stream, Bride Brook (solid circles), and a no-alewife stream, Four Mile River (open circles), during spring – early summer 2005. The time period corresponding to the alewife spawning migration is shaded.



there were three of each. We assumed that each time period was independent because there was a 2 month gap between each sampling period. This is longer than the life span of many mayfly larva and sufficient time for tissue turnover in periphyton. We used the same ANOVA design to test for effects of alewife presence and time on nutrient concentrations in our six streams in 2006. We used a two-tailed Student *t* test to assess differences in ecosystem rates between alewife and no-alewife streams.

Results

Anadromous alewife spawning migration

The number of anadromous alewives returning to spawn in Brides Brook was 68 757 in 2005, 129 114 in 2006, and 66 975 in 2007. The timing of the spawning migration depends on water temperature but is fairly consistent from year to year. The first alewives appear at the end of March, with numbers peaking from mid-April to early May, and the migration is over by the end of May (Fig. 1).

Nutrient loading

The spawning migration of anadromous alewife contributes 800–1500 g of nitrogen and 90–180 g of phosphorus to Bride Brook each year (Table 1). Approximately 66% of the nitrogen is from excretion and 34% from carcasses whereas 50% of the phosphorus was from excretion and 50% from carcasses. The mean daily input was 10–20 g of nitrogen and 1.0–2.5 g of phosphorus, but there was large day-to-day variation. For example, on 5 May 2006, over 16 000 alewives passed through in one night resulting in 190 g of nitrogen and 22 g of phosphorus loaded into the system in less than 12 h.

Water chemistry

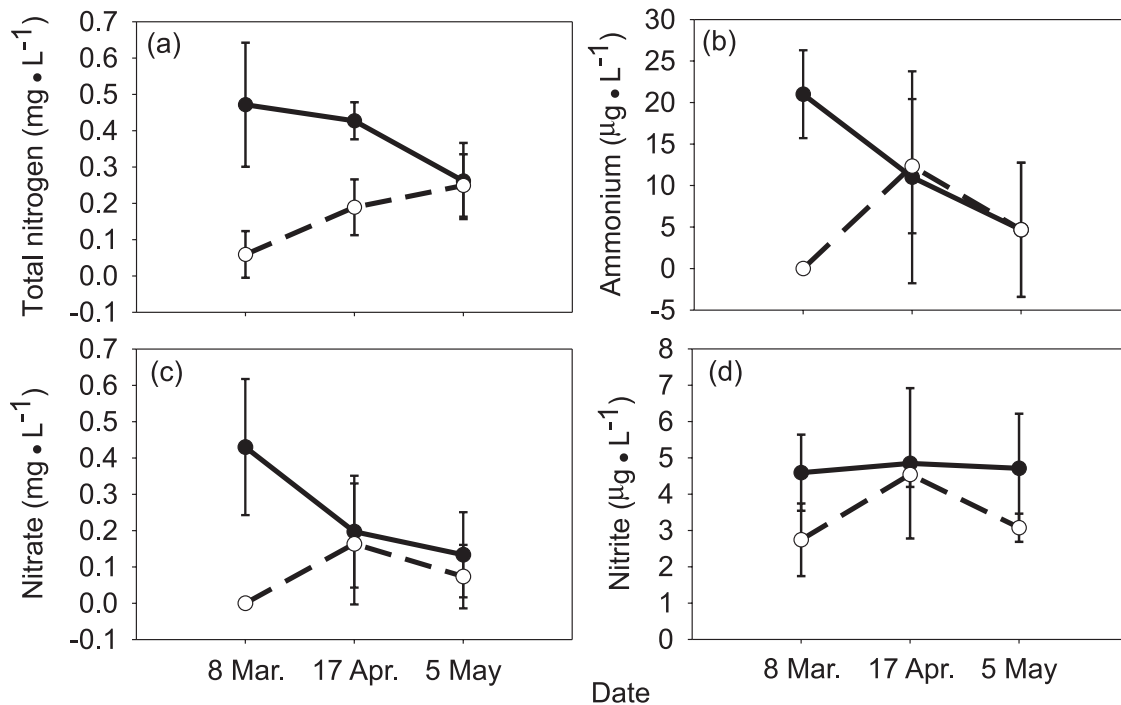
Bride Brook and Four Mile River showed opposite trends in total nitrogen dynamics; total nitrogen increased at Four Mile River whereas it decreased at Bride Brook (Fig. 2a). In contrast, the total phosphorus dynamics at Four Mile River and Bride Brook were very similar with total phosphorus increasing from March to July 2005 (Fig. 2b). When comparing nutrient levels between three alewife and three no-alewife streams in 2006, alewife streams showed significantly higher levels of total nitrogen, NH₄⁺, NO₃⁻, and NO₂⁻ (ANOVA: total nitrogen: $F_{[1,12]} = 21.9$, $p < 0.001$; NH₄⁺: $F_{[1,12]} = 11.4$, $p = 0.005$; NO₃⁻: $F_{[1,12]} = 11.6$, $p = 0.005$; NO₂⁻: $F_{[1,12]} = 7.1$, $p = 0.02$). This was, however, driven by differences before the spawning run (8 March), and there was no difference in nutrient concentrations for the time period corresponding to the peak of the spawning run (April–May 2006) (Fig. 3).

Stable isotopes

The anadromous alewives entering Bride Brook had a $\delta^{15}\text{N}$ value of 13.3 ± 0.4 and a $\delta^{13}\text{C}$ value of -18.5 ± 0.4 ($n = 13$, fish collected in both 2004 and 2005). The alewife stream, Bride Brook, had substantially enriched periphyton and aquatic insect $\delta^{15}\text{N}$ values in comparison with the no-alewife stream, Four Mile River, for 2005 and 2006 (Table 2). Within each stream, higher $\delta^{15}\text{N}$ values corresponded to presumed higher trophic positions (Post 2002). In contrast, the $\delta^{13}\text{C}$ values for the two streams were similar, although Bride Brook had slightly higher average values, particularly for predatory insects, and a greater variation in $\delta^{13}\text{C}$ (Table 2). As expected, there was little enrichment in $\delta^{13}\text{C}$ with presumed trophic position. The results were consistent between years (Table 2).

Isotopic time series at Bride Brook for 2005 show approx-

Fig. 3. (a) Total nitrogen, (b) ammonium, (c) nitrate, and (d) nitrite (average \pm 1 SD) at three alewife streams (solid circles) and three no-alewife streams (open circles) in 2006. The 8 March sampling date is before the start of the alewife run and the 17 April and 5 May sampling dates are during the peak of the run.



imately a 1.5‰ enrichment in periphyton $\delta^{15}\text{N}$ coincident with the spawning migration (Fig. 4a). Periphyton showed peak $\delta^{15}\text{N}$ values in late April, just after alewife numbers peaked in 2005 (Fig. 1). The $\delta^{15}\text{N}$ of collector-gatherer insects (the mayfly family Ephemerellidae) peaked slightly later in early to mid-May and the $\delta^{15}\text{N}$ of predatory insects (the damselfly family Lestidae) showed a broad peak in early June (Fig. 4a). At Bride Brook, there were no shifts in $\delta^{13}\text{C}$ values for the collector-gatherer or predatory insects, but periphyton $\delta^{13}\text{C}$ values increased in late April and remained elevated through mid-July (Fig. 4c). In Four Mile River, $\delta^{15}\text{N}$ decreased slightly (Fig. 4b) and $\delta^{13}\text{C}$ remained relatively constant from March to August (Fig. 4d). There was no indication of a spring increase in $\delta^{15}\text{N}$ in Four Mile River as we observed in Bride Brook.

In 2006, we expanded the study to six streams and found similar results. The $\delta^{15}\text{N}$ of alewife streams was significantly elevated for periphyton and collector-gatherers (the mayfly families Ephemerellidae and Heptageniidae) when compared with no-alewife streams (Figs. 5a and 5b) (ANOVA: periphyton: $F_{[1,12]} = 69.2$, $p < 0.001$; collector-gatherers: $F_{[1,6]} = 17.8$, $p = 0.005$). There were no significant differences in the $\delta^{13}\text{C}$ of streams with and without alewives (Figs. 5c and 5d) (ANOVA: periphyton: $F_{[1,12]} = 2.6$, $p = 0.14$; collector-gatherers: $F_{[1,6]} = 0.004$, $p = 0.95$).

Ecosystem rates

Maple leaf decomposition increased by an average of $35 \pm 3\%$ from March (prealewife run) to April–May (peak alewife run) for streams with alewife runs compared with $22 \pm 41\%$ for streams without alewife runs. Oak leaf decomposition increased by an average of $17 \pm 9\%$ from March to April–May for streams with alewife runs compared with $4 \pm$

9% for streams without alewife runs. There were only two streams in each category and these results were not significant in either case (Student *t* test: maple: $p = 0.74$; oak $p = 0.29$).

Algal production showed a similar pattern. Algal biomass accumulation increased by an average of $78 \pm 15\%$ from March to April–May for streams with alewife runs compared with $47 \pm 46\%$ for streams without alewife runs. This difference was also not significant (Student *t* test: $p = 0.50$).

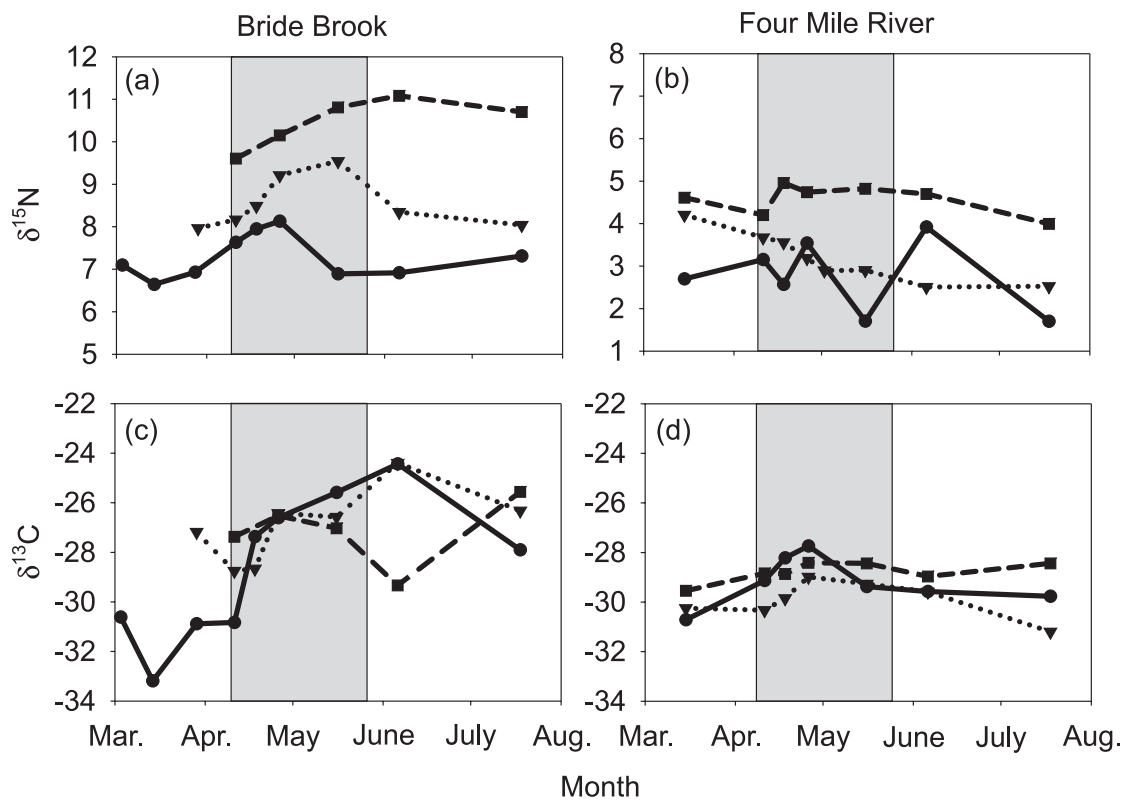
Discussion

Anadromous alewives are a potentially important source of marine-derived nutrients to coastal freshwater systems through excretion and mortality. Alewife numbers have declined over the past 50 years, but there are ongoing restoration efforts, including dam removal and fish ladder construction, to allow alewives to regain access to freshwater habitats. As a result, it is important to understand the magnitude and potential effects of alewife-contributed nutrients. Here, we measured nitrogen and phosphorus inputs into Bride Brook and explored the effects of these marine-derived nutrients on local food webs and ecosystem functioning. This influx of nutrients did not affect the water chemistry of anadromous alewife streams but was incorporated into the stream food web.

Nutrient loading into Bride Brook has decreased substantially since the 1960s because of declines in both the average body size and the number of alewives entering Bride Lake to spawn. In the 1960s, mean body mass was 220 g and the historic run size was around 180 000 alewives (Kissel 1969), resulting in approximately 3000 g of nitrogen and 360 g of phosphorus added to Bride Brook yearly. This

Table 2. Average $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for periphyton and aquatic macroinvertebrate functional feeding groups for Bride Brook and Four Mile River in 2005 and 2006.

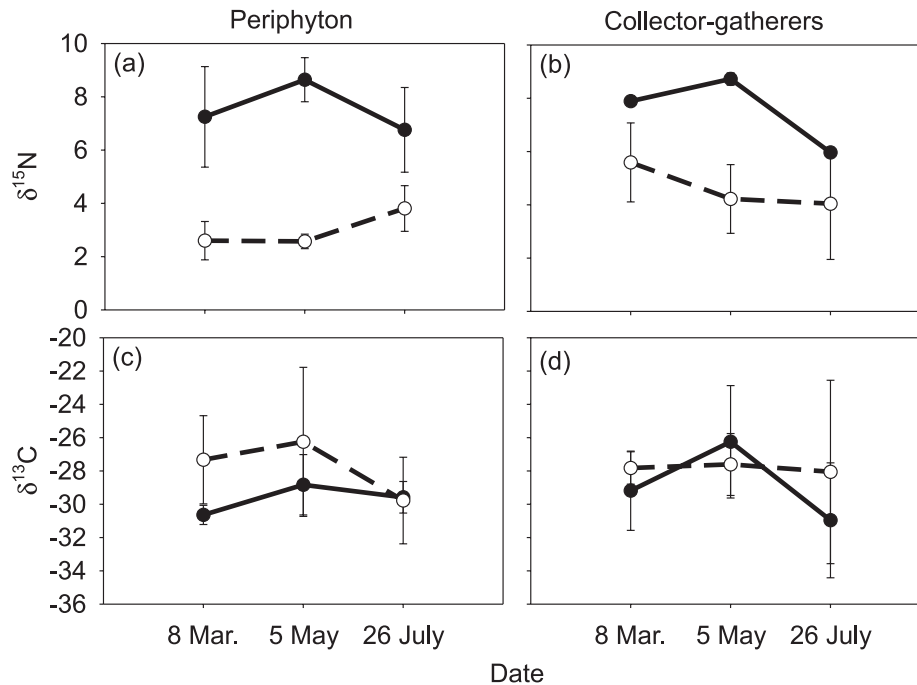
Functional group	Bride Brook (alewife)					Four Mile River (no alewife)				
	$\delta^{15}\text{N}$	SD	$\delta^{13}\text{C}$	SD	<i>n</i>	$\delta^{15}\text{N}$	SD	$\delta^{13}\text{C}$	SD	<i>n</i>
2005										
Periphyton	8.40	0.46	-29.26	2.79	6	3.63	0.64	-29.44	0.91	5
Collector-filterer	9.36	0.77	-32.63	3.48	8	3.82	0.93	-30.36	1.20	10
Collector-gatherer	8.39	0.54	-26.83	1.55	7	2.73	0.73	-30.06	1.28	14
Shredder	5.79	1.20	-32.84	2.62	3	1.34	0.57	-32.86	0.28	4
Predator	10.48	0.42	-27.18	0.99	11	4.48	0.37	-29.21	0.89	11
2006										
Periphyton	6.79	1.41	-25.91	4.03	7	2.18	0.76	-29.72	1.19	6
Collector-filterer	9.25	0.51	-31.50	4.56	3	3.62	1.14	-29.55	0.76	6
Collector-gatherer	7.65	1.07	-25.96	2.64	8	3.04	1.15	-29.56	1.03	9
Shredder	4.21	0.30	-32.62	1.83	3	1.51	0.44	-30.84	0.39	3
Predator	10.37	0.36	-23.21	0.17	3	4.77	0.48	-27.74	0.41	8

Fig. 4. (a and b) $\delta^{15}\text{N}$ and (c and d) $\delta^{13}\text{C}$ values for periphyton (circles), collector-gatherer insects (triangles), and predatory insects (squares) at (a and c) an alewife stream, Bride Brook, and (b and d) a no-alewife stream, Four Mile River, in spring – early summer 2005. The time period corresponding to the alewife spawning migration is shaded. Note that for Figs. 4a and 4b, the scale is different but the range of values is the same.

is three times greater than current estimates of alewife nutrient inputs into Bride Brook (1050 g of nitrogen and 120 g of phosphorus). Declines in Pacific salmon runs and the corresponding nutrient influx have raised concerns about the productivity of these freshwater systems and their ability to support wildlife, such as juvenile salmon (Schindler et al. 2003). These concerns are less relevant to Atlantic coastal streams that are generally more productive than Pacific streams. Also, these nutrient loading estimates are much

lower than those for Alaskan salmon streams where inputs of 90 000 – 400 000 kg of nitrogen and 11 000 – 50 000 kg of phosphorus are common (Moore and Schindler 2004). These numbers are for much larger river systems that experience high levels of carcass loading whereas alewife mortality is very low in Bride Brook. Our values are also lower than those from Durbin et al. (1979), which saw 2700 mg $\text{N}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ and 430 mg $\text{P}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ in Pausacaco Pond (Rhode Island) compared with 63.6 mg $\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ of nitro-

Fig. 5. (a and b) $\delta^{15}\text{N}$ and (c and d) $\delta^{13}\text{C}$ values (average \pm 1 SD) for (a and c) periphyton and (b and d) collector-gatherer insects at three alewife streams (solid circles) and three no-alewife streams (open circles) in 2006. For collector-gatherer insects, there are only two no-alewife streams, as no collector-gatherers were consistently found at the third site. We are also missing collector-gatherer insects for one alewife site on 8 March.



gen and $7.4 \text{ mg}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ of phosphorus for Bride Brook. The Durbin et al. (1979) study saw much higher carcass loading because it focused on a lake, which is where the majority of alewife mortality occurs. It is likely that Bride Brook receives additional nutrient inputs owing to export from Bride Lake, where there is higher carcass loading, but we were not able to quantify that input for this study.

Owing to the high nutrient content of the carcasses, small errors in our estimate of carcass loading could greatly alter the relative importance of excretion versus carcasses. We are likely underestimating the overall impacts of carcasses by not considering the nutrient export from carcasses in Bride Lake. However, we may be overestimating the impact of carcasses in the streams because it takes 1–2 weeks for nutrients to leach from the carcasses and carcasses are often scavenged by birds, moving the nutrients out of the stream (A.W. Walters, personal observation). Excretion and carcasses differ in their relative importance for phosphorus and nitrogen loading owing to differences in N:P ratios; excretion has a much higher N:P ratio (11.7) than carcasses (5.9). Excretion also provides nutrients in inorganic forms (e.g., ammonia, phosphate) that are immediately available for uptake (Vanni 2002). Excretory processes have largely been ignored for diadromous fish, although the importance of fish excretion in nutrient cycling is widely recognized (Kraft 1993; Vanni 2002; McIntyre et al. 2007). In larger systems, carcasses would quickly swamp out the effect of excretion, but for our small streams, excretion is important, especially as it supplies nutrients in a form that is highly suitable for uptake by stream organisms (Post and Walters 2009).

Water chemistry

In excretion experiments with anadromous alewife, 70%–

80% of the nitrogen excreted was in the form of NH_4^+ (Post and Walters 2009), yet we did not see an increase in NH_4^+ levels for alewife streams during the spawning run. Browder and Garman (1994) saw total NH_4^+ levels increase 10-fold in water samples from Wards Creek, Virginia, during the peak of a spawning migration of anadromous clupeid fishes (*Alosa* spp.). On peak days of the Bride Brook spawning run (5000 – 16 000 alewives passing through the stream), excretion loads 30–100 g of NH_4^+ into the stream, a loading rate of 2–6 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$. The lack of a detectable change in NH_4^+ concentrations in water samples indicates rapid removal from the water column. Mechanisms for uptake include chemical sorption onto the organic matter film of the streambed and assimilation and storage by algae and heterotrophic bacteria (Bernhardt et al. 2002; Naiman et al. 2002). NH_4^+ can also be oxidized to NO_3^- , but there was no detectable change in NO_3^- concentrations in alewife stream water samples, suggesting that the majority of NH_4^+ is undergoing biotic uptake. Data from streams across the United States suggests that uptake rates of inorganic nitrogen are high for small, shallow streams and that low to moderate inputs of inorganic nitrogen can be removed or transformed within minutes to hours (Peterson et al. 2001). Ammonia uptake rate estimates for streams in the Hubbard Brook Experimental Forest varied between 0.32 and 716 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (Bernhardt et al. 2002; Hall et al. 2002), which would make our peak day input rates (2–6 $\text{mg}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) well within the range of what a small stream can likely handle. Interestingly, total nitrogen, NH_4^+ , and NO_3^- levels are higher in March for alewife streams. Potentially, alewives are leading to higher baseline nitrogen loading, but the effects are only apparent in winter water chemistry samples when biotic uptake is low.

Previous studies in the Pacific salmon system have seen mixed effects of the spawning migration on water chemistry. Minakawa and Gara (1999) saw increases in Kjeldahl-N, NH_4^+ -N, and soluble phosphorus but no changes in NO_3^- -N whereas Bilby et al. (1996) only saw a change in NO_3^- -N. These differences could be due to a variety of factors that are known to affect nutrient uptake rates including the physical characteristics of the stream (depth, water velocity, sediment size), hydraulic processes (discharge, transient storage), and biological processes (primary productivity, community respiration) (Wollheim et al. 2001; Hall et al. 2002; Hall and Tank 2003). The lack of a consistent effect on water chemistry despite known inputs of nutrients suggests that water chemistry may be a weak method of evaluating the importance of marine-derived nutrients. A better method for assessing the incorporation of marine-derived nitrogen may be stable isotope techniques.

Stable isotopes

The natural abundance isotope data clearly show that the stream food web is incorporating marine-derived nitrogen. All organisms sampled in our alewife streams show an enriched $\delta^{15}\text{N}$ signal relative to no-alewife streams but little difference in the $\delta^{13}\text{C}$ signal. All systems drain watersheds dominated by forest cover, and therefore, it is unlikely that differences in anthropogenic nitrogen loading, in particular sources of enriched $\delta^{15}\text{N}$ (i.e., septic waste or manure), are driving the observed differences between alewife and no-alewife streams. Two of the no-alewife streams studied here almost certainly once had alewife runs that were extirpated by the construction of low head dams, which continue to disrupt alewife migrations (S. Gephart, Connecticut Department of Environmental Protection, Inland Fisheries Division, Diadromous Fish Program, P.O. Box 719, Old Lyme, CT 06371, USA, personal communication). The enriched $\delta^{15}\text{N}$ signal in the alewife streams persisted during our entire study period, indicating long-term storage of marine-derived nitrogen, which has also been seen in Pacific salmon systems (Naiman et al. 2002). However, the greatest difference in $\delta^{15}\text{N}$ values between alewife and no-alewife streams is at the peak of the spawning migration in early May.

There are two main pathways by which alewife-contributed nutrients could be incorporated into the stream food web. The first is through direct consumption of alewife carcass flesh by stream invertebrates and the second is through autochthonous and bacterial uptake of dissolved nutrients released from alewife excretion and carcass decomposition. In the salmon system, both direct consumption (Bilby et al. 1996) and indirect uptake (Kline et al. 1993) have been suggested as the primary pathway. In the alewife system, the indirect uptake pathway is more likely, as there are only a few carcasses in the stream and we have not observed macroinvertebrate activity on those alewife carcasses (A.W. Walters, personal observation). Furthermore, our time series of $\delta^{15}\text{N}$ from Bride Brook indicates that that marine nitrogen is first incorporated at lower trophic levels (periphyton) and then works its way up the food chain. This mode of transfer agrees well with the indirect uptake mechanism: first, periphyton utilizes solutes released through excretion and the decomposition and mineralization of carcass material and then the periphyton is eaten by aquatic macroinvertebrates.

An indirect uptake pathway also explains why there was no consistent shift in the $\delta^{13}\text{C}$ signature of our alewife stream food webs. If the primary pathway was through consumption, then the macroinvertebrates should have a $\delta^{13}\text{C}$ signature that reflects that of the alewife, which we do not see. However, during remineralization, the nitrogen and carbon biogeochemical pathways become decoupled and the $\delta^{13}\text{C}$ of organic matter would not necessarily be conserved (Kline et al. 1990). In this context, $\delta^{13}\text{C}$ should look like local dissolved inorganic carbon.

Ecosystem rates

Stable isotope analyses are very useful for showing the degree to which alewife resources are incorporated into aquatic food webs, but they tell us little about the effects on population, community, and ecosystem dynamics (Naiman et al. 2002; Schindler et al. 2003). Further research is needed to look at these aspects in the alewife system, although our study provides a preliminary test of the effect of anadromous alewife on ecosystem-level processes in streams. We compared leaf decomposition rates and algal production rates before and during the alewife spawning migration between streams with and without alewife. In all streams, decomposition and production rates increased owing to warmer water temperatures in April and May, but the increase was greater (although not significantly) for streams with anadromous alewife runs. The lack of a significant effect was due to a small samples size and high variability in the responses. A variety of physical and biotic factors that were not controlled for in this study can influence leaf decomposition (water temperature, leaf species, water velocity) and periphyton accrual (light availability, grazer community). Marine-derived nutrients do have the potential to impact ecosystem rates, as nitrogen and phosphorus are known to limit leaf decomposition and primary production (Elwood et al. 1981; Webster and Benfield 1986). Durbin et al. (1979) saw increased leaf litter respiration rates coinciding with the alewife spawning migration and they viewed this as the most important ecological consequence of alewife-contributed marine-derived nutrients because it releases the large amount of energy stored in leaf litter.

The impact of anadromous alewife restoration on productivity has been a concern for managers involved in anadromous alewife restoration efforts, as many of New England's aquatic habitats are at risk for eutrophication. Restoration efforts in Connecticut focus on restoring the connectivity between marine and freshwater habitats through the removal of small dams and the construction of fish ladders. The concern is that the resulting influx of fish and accompanying nutrients could exacerbate water quality issues. Our study suggests that for streams, this is unlikely to be the case. Despite a strong localized impact on the stream food web, water chemistry results show little increase in nutrient levels. Our results also suggest that managers should not rely on water chemistry samples as a method to monitor the effects of the recovery of alewife populations. Stable isotope techniques would be a more sensitive indicator of the presence of marine-derived nutrients in most freshwater ecosystems (but see Holtham et al. 2004).

Overall, the findings of this study provide further support for previous studies (Durbin et al. 1979; Garman and Macko

1998) that suggest that anadromous alewife may be an important source of marine-derived nutrients to freshwater coastal ecosystems. Despite their smaller size and iteroparous life history, our research indicates that anadromous alewives play an ecological role similar to that of Pacific salmon. Our study found that despite low to moderate nutrient input rates into the stream (nutrient loading is likely higher in the spawning lakes), there was strong evidence that alewife-contributed marine-derived nitrogen is incorporated into stream food webs. The full repercussions of this at the ecosystem level require further study, but our results suggest that alewife restoration has the potential to affect nutrient and food web dynamics in coastal freshwater systems.

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