

Nutrient Excretion Rates of Anadromous Alewives during Their Spawning Migration

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Abstract.—Excretion is one of the processes through which anadromous fishes move marine-derived nutrients into freshwater ecosystems, but no direct estimates of nutrient excretion rates by anadromous fish exist. We estimated the mass-specific nutrient excretion rates of anadromous alewives *Alosa pseudoharengus* during their spring spawning migration into Bride Lake, Connecticut. Anadromous alewives excreted an average of 2.17 μg of phosphorus per gram of wet fish mass per hour and 24.71 μg of nitrogen. The mean N:P ratio (by mass) of nutrient excretion was 11.7. Most of the nitrogen excreted was in the form of NH_4^+ . Our results suggest that excretion by anadromous fish can affect local food webs and ecosystem function when ecosystems are relatively small and fish aggregate at high densities, such as at the peak of the spawning run.

The movement of marine-derived nutrients into freshwater ecosystems by anadromous fishes can have important consequences for local ecological processes (Durbin et al. 1979; Naiman et al. 2002; Vanni 2002; Schindler et al. 2003, 2005). Much of what is known about nutrient loading by anadromous fish is derived from research on Pacific salmon *Oncorhynchus* spp. (Schindler et al. 2003). With the exception of steelhead *O. mykiss*, Pacific salmon are semelparous, all adults dying in rearing habitats after spawning. In contrast, many species of anadromous fish, such as alewife *Alosa pseudoharengus*, are iteroparous, such that many adults return to the ocean after spawning.

The net input or export of nutrients by semelparous fishes can be modeled as the difference between nutrient inputs from adult carcasses and nutrient export by juvenile salmon (Donaldson 1969; Naiman et al. 2002; Moore and Schindler 2004). The semelparous life history of Pacific salmon allows for this simple model (net loading = adult carcass inputs – juvenile exports) because the entire mass of the carcass is assumed to be an input. This is not, however, an appropriate model for iteroparous anadromous fish species, for which nutrient inputs are represented by three separate terms: (1) adult carcasses of fish that die in the system (this includes the mass of eggs they are

carrying), (2) eggs spawned, and (3) excretion by fish that survive reproduction and return to the ocean.

Although nutrient inputs from adult carcasses and eggs are the largest input terms, direct nutrient excretion may be important in many ecosystems because it supplies forms of nitrogen and phosphorus that are immediately available for uptake (Vanni 2002). These inputs may be of particular importance in streams through which large numbers of fish migrate to reach their spawning grounds but which receive little nutrient input from carcasses and eggs. Direct nutrient excretion is commonly measured or modeled in fish (Kraft 1993; Schindler and Eby 1997; Vanni 2002; Vanni et al. 2002), but we know of no direct estimates of nutrient excretion by anadromous fish.

Here we estimate nutrient excretion by anadromous alewives during their migration to spawning grounds in Bride Lake, Connecticut. Anadromous alewives are iteroparous and spawn in coastal freshwater lakes and ponds along the Atlantic coast of North America from Labrador to the Carolinas. Spawning occurs in spring, adults spend a few weeks on their spawning grounds, and young-of-the-year (age-0) alewives spend their first summer of life in lakes or ponds before migrating to the ocean in summer and fall (Cooper 1961; Kissil 1974). Anadromous alewives were historically abundant in coastal watersheds along the Atlantic coast of North America, but they are now excluded from many watersheds by dams and the remaining populations have been in decline for the past 40–50 years (ASMFC 1999). The alewife is a species of concern across their native range and the target of restoration efforts in many states. The one available estimate of nutrient loading (Durbin et al. 1979) suggests that anadromous alewives may contribute as much nitrogen and phosphorus to freshwater ecosystems, on an areal basis, as many Pacific salmon runs.

We estimated mass-specific excretion rates of migratory alewives both because they are important in efforts to model past, present, and future nutrient loading by anadromous alewives into freshwater ecosystems and because of the potential importance of direct nutrient excretion for the small coastal streams through which alewives migrate. We made short-term and long-term estimates of the mass-specific excretion

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rates for total nitrogen and phosphorus in three separate years and the mass-specific excretion rate of $\text{NH}_4\text{-N}$ in 2 years.

Methods

Study site.—Our research was conducted at the outlet to Bride Lake in East Lyme, Connecticut, during the spring of 2004, 2005, and 2008. Bride Lake contains one of the largest remaining anadromous alewife runs in Connecticut. This lake is linked to Long Island Sound by Bride Brook, which flows 3.3 km from the outlet of Bride Lake to the sound. Bride Lake is 18.2 ha in area, has a maximum depth of 10.7 m (Kissil 1974), and had a spring total phosphorus (TP) concentration of 15.5 $\mu\text{g P/L}$ in 2005 (Post et al. 2008). The spring spawning run at Bride Lake typically begins in late March and ends in early May, alewives migrating through Bride Brook at night. The number of anadromous alewives returning to spawn in Bride Lake in the years of this study was 81,350 in 2004, 68,757 in 2005, and 73,090 in 2008 (Connecticut Department of Environmental Protection [CDEP], unpublished data; counts were made with an electronic fish counter [Smith Root SR-1601] monitored daily and calibrated against hand counts made in a weir at the entrance to the lake).

Nutrient excretion experiment.—We estimated nutrient excretion by anadromous alewives using direct measurements of nitrogen and phosphorus over a 23-h period on 6 May 2004, and 21-h periods on 26 April 2005 and 26 April 2008. Anadromous alewives were captured in a weir at the outlet of Bride Lake. We measured length and mass on a subset of the fish. We stocked 200 fish in 2004 and 120 fish in 2005 and 2008 into the circulating water holding tank of the CDEP's diadromous fish stocking truck (used to transport alewives and American shad *A. sapidissima* for restoration efforts). The mean lengths and masses of the fish used in the experiments were 260.4 mm (SD = 13.9) and 161.4 g (27.4) in 2004, 257.4 mm (17.7) and 156.0 g (37.9) in 2005, and 261.4 mm (12.1) and 163.8 g (26.6) in 2008. The holding tank was filled with approximately 4,542 L of local well water. The mean water temperature and dissolved oxygen concentrations of water in the tank were 21.3°C and 8.9 mg/L in 2004, 12.6°C and 9.2 mg/L in 2005, and 14.4°C and 4.6 mg/L in 2008. To minimize stress on the fish, water was circulated around the holding tank to create flow in which alewives could swim and school naturally. Total phosphorus and total nitrogen concentrations were measured in the tank at 0, 12, and 21 h in 2004, at 0, 6, 12, and 21 h in 2005, and at 0.5, 1, 2.5, 6, 12, and 21 h in 2008. At each sampling time, we removed around 1 L of water from the tank. We placed 120 mL of water

into acid-washed bottles for total nitrogen and total phosphorus analyses, and 120 mL of water was filtered through Whatman GF/F glass microfiber filters for analysis of $\text{NH}_4\text{-N}$. Because TN and TP were from unfiltered samples taken over a relatively long period of time they may include feces, although we did not see any obvious signs of feces in the water. We estimated average mass-specific excretion rates ($\mu\text{g P}$ or $\text{N} \cdot \text{g}$ wet mass of fish⁻¹ · h⁻¹) from the slope of the relationship between $\mu\text{g P}$ or N per gram of fish mass versus time (t_i), the P and N concentrations being standardized to the concentration of total phosphorus and total nitrogen in the tank water at the beginning of the excretion experiment (concentrations at time t_i – concentration at time t_0). The initial P and N concentrations (t_0) were 317.1 and 326.5 mg/L in 2004, 31.2 and 1,137 mg/L in 2005, and 5.8 and 330.5 mg/L in 2008. We also measured $\text{NH}_4\text{-N}$ in 2004 and 2005 to estimate the proportion of nitrogen excreted as NH_4^+ . Nitrogen and phosphorus concentrations were measured in duplicate through colorimetric analysis on an Astoria 2 auto-analyzer. We used persulfate digestion in conjunction with the automated analyzer to determine total nitrogen and total phosphorus concentrations of unfiltered samples (APHA 1998).

Previous studies have raised concerns about excretion rates measured over extended periods of time (>1 h) because these rates tend to decline when fish are not feeding (Vanni 2002). Anadromous alewives, however, do not feed during the 1–12 h required to reach their spawning grounds (it takes ~2 h for alewives to move from Long Island Sound to Bride Lake swimming at 0.5 m/s; A. W. Walters and D. M. Post, personal observation). To test the time dependence of excretion rates, we sampled at a higher temporal resolution in 2008 and then estimated hourly excretion rates for the time period between each sample (i.e., 0–0.5, 0.5–1, 1–2.5, 2.5–6, 6–12, and 12–21 h). We also conducted a replicated small-volume, short-term excretion experiment in 2008. We stocked three alewives into three oval stock tanks filled with 108 L of NANOpure water. The mean masses of the fish stocked were 155.1, 167.4, and 168.1 g, respectively. The experiment was run for 1 h. The mean initial concentrations of nitrogen was 0.038 mg/L (SD = 0.02), and the mean initial concentration of phosphorus was 7.6 $\mu\text{g/L}$ (SD = 7.6). The initial water temperature in the small-volume tanks was 18–19°C and the initial dissolved oxygen concentration was 8.6 mg/L.

Results

Nutrient concentrations increased with time in all years. The increase in mass-specific nutrient concentrations ($\mu\text{g N}$ or P/g fish) was well represented by

TABLE 1.—Relationship between time and the phosphorus and nitrogen concentrations in alewives, from experiments run in 2004, 2005, and 2008. The slope of the relationship is the mass-specific excretion rate ($\mu\text{g} \cdot \text{g fish}^{-1} \cdot \text{h}^{-1}$).

Nutrient	Year	Relationship	r^2	P -value
Nitrogen	2004	$-2.6 + 35.6 \times \text{time}$	1.00	<0.01
	2005	$-16.9 + 21.7 \times \text{time}$	0.98	<0.01
	2008	$5.5 + 16.9 \times \text{time}$	0.99	<0.01
Phosphorus	2004	$0.9 + 2.00 \times \text{time}$	0.99	<0.01
	2005	$1.9 + 2.61 \times \text{time}$	0.99	0.04
	2008	$0.25 + 1.90 \times \text{time}$	0.99	<0.01

linear models (Table 1; Figure 1), from which we estimated the mean mass-specific nutrient excretion rate for each year. Across all 3 years, the mean mass-specific excretion rate was $2.17 \mu\text{g} \cdot \text{g fish}^{-1} \cdot \text{h}^{-1}$ for phosphorus (SD = 0.384) and $24.71 \mu\text{g} \cdot \text{g fish}^{-1} \cdot \text{h}^{-1}$ for nitrogen (SD = 9.72). The highest excretion rate for phosphorus was observed in 2005 ($2.61 \mu\text{g} \cdot \text{g fish}^{-1} \cdot \text{h}^{-1}$), while the highest excretion rate for nitrogen was observed in 2004 ($35.6 \mu\text{g} \cdot \text{g fish}^{-1} \cdot \text{h}^{-1}$). There was no significant relationship between temperature and nitrogen ($n = 3, P = 0.28$) or phosphorus excretion rates ($n = 3, P = 0.62$) across the 3 years of this study. In 2004 and 2005, 73% and 77%, respectively, of the

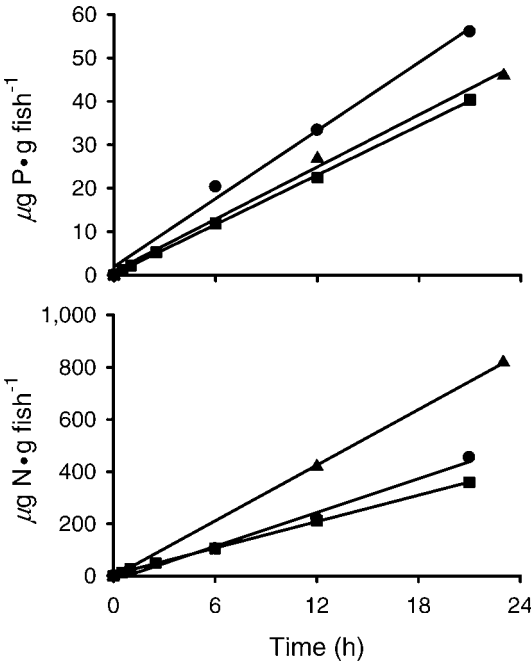


FIGURE 1.—Phosphorus and nitrogen concentrations in alewives versus time in the 2004 (triangles), 2005 (circles), and 2008 experiments (squares). The slope of each relationship (Table 1) is the mass-specific excretion rate ($\mu\text{g} \cdot \text{g fish}^{-1} \cdot \text{h}^{-1}$).

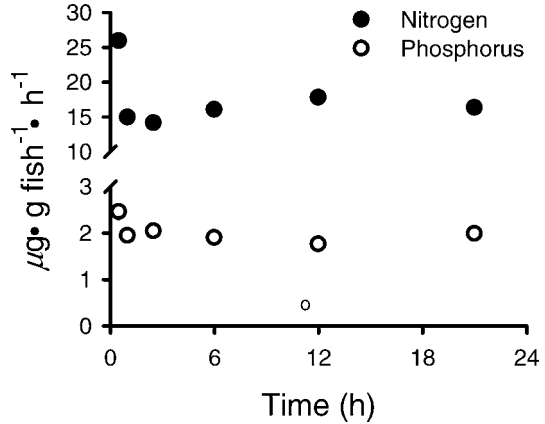


FIGURE 2.—Time dependence of the mass-specific excretion rates for nitrogen and phosphorus in alewives in 2008.

nitrogen excreted was in the form of NH_4^+ . The mean N:P ratio (by mass) of nutrient excretion was 11.7 (SD = 5.3), but it varied considerably from year to year (17.8 in 2004, 8.3 in 2005, and 8.9 in 2008).

In 2008, the mass-specific excretion rate in the stocking truck was high in the first 30 min, but it then fell to a relatively constant rate for the remainder of the experiment (Figure 2). For phosphorus, the excretion rate in the first 30 min ($2.45 \mu\text{g} \cdot \text{g fish}^{-1} \cdot \text{h}^{-1}$) was 27% higher than the mean excretion rate calculated for the remainder of the experiment ($1.92 \mu\text{g} \cdot \text{g fish}^{-1} \cdot \text{h}^{-1}$ for the period from 0.5 to 21 h) and 20% higher than the next highest period ($2.04 \mu\text{g} \cdot \text{g fish}^{-1} \cdot \text{h}^{-1}$ for the period 1–2.5 h; Figure 2). For nitrogen, the excretion rate in the first 30 min ($25.9 \mu\text{g} \cdot \text{g fish}^{-1} \cdot \text{h}^{-1}$) was 64% higher than the mean excretion rate calculated for the remainder of the experiment ($15.8 \mu\text{g} \cdot \text{g fish}^{-1} \cdot \text{h}^{-1}$ for the period from 0.5 to 21 h), and 51% higher than in the next highest period ($17.2 \mu\text{g} \cdot \text{g fish}^{-1} \cdot \text{h}^{-1}$ for the period 6–12 h; Figure 2). After the first 30 min, there was no significant decrease in mass-specific excretion rates for the remaining 21 h of the experiment (least squares regression: $P = 0.79$ for phosphorus and $P = 0.24$ for nitrogen). We found very high nutrient excretion rates in the short-term, small-volume experiments conducted in 2008. The mean excretion rates in those experiments were $5.05 \mu\text{g} \cdot \text{g fish}^{-1} \cdot \text{h}^{-1}$ for phosphorus (SD = 0.37) and $56.5 \mu\text{g} \cdot \text{g fish}^{-1} \cdot \text{h}^{-1}$ for nitrogen (SD = 5.1), resulting in a mean N:P ratio of 11.2 (SD = 1.4).

Discussion

We provide, for the first time, direct estimates of excretion for an anadromous fish during the spawning run (but see Durbin et al. 1979 for an indirect estimate

for anadromous alewife and Kraft 1993 for estimates for landlocked alewife). The mean mass-specific excretion rates of anadromous alewives ($2.17 \mu\text{g} \cdot \text{g fish}^{-1} \cdot \text{h}^{-1}$ for phosphorus and $24.71 \mu\text{g} \cdot \text{g fish}^{-1} \cdot \text{h}^{-1}$ for nitrogen) fall within the ranges reported for other fish species (e.g., Hood et al. 2005; Torres and Vanni 2007), and the mean N:P ratio (by mass) of excretion is similar to that estimated for nonpiscivorous fishes (Schindler and Eby 1997), although there was considerable year-to-year variation in the N:P of excretion.

We observed time dependence in mass-specific excretion rates in the spring of 2008. Interestingly, the time dependence appeared only in the first 30 min of the large-tank experiment (Figure 2). After the first 30 min, there was no significant decline in mass-specific excretion rates (Figure 2). We suspect that the elevated nutrient excretion rate observed in the first 30 min of the 2008 experiment resulted from handling stress. This is supported by the very high nutrient excretion rates we observed in the short-term, small-volume experiments we conducted in 2008. The mean excretion rate in the small-volume experiments was more than twice what we observed in the first 30 min of the large-tank experiments. In these small-volume experiments, alewives swam erratically, jumped out of the tanks when we approached to take water samples, and appeared lethargic when removed from the tank and released into Bride Lake. In contrast, alewives in the long-term, large-volume experiments schooled naturally and were very active when released into Bride Lake after being held in the holding tank for more than 21 h. The temperature and dissolved oxygen concentrations in the small-volume experiments ($18\text{--}19^\circ\text{C}$, 8.6 mg/L) were similar to those observed in the larger tank in the 3 years of our study ($13\text{--}21^\circ\text{C}$, $4.6\text{--}9.2 \text{ mg/L}$). Our results suggest that short-term, small-volume experiments may provide misleading nutrient excretion estimates for migratory schooling fish like alewives that do not feed during their spawning migration.

Nutrient excretion by vertebrates can have large effects on local food webs and ecosystems, particularly when ecosystems are relatively small and animals aggregate at high densities (Post et al. 1998, 2007; Vanni 2002). For many anadromous fishes, excretion represents a small contribution of nutrients to the freshwater ecosystems in which they spawn relative to other inputs like carcasses and eggs (Durbin et al. 1979; Naiman et al. 2002). However, nutrient excretion may be of considerable importance to the streams through which many anadromous fish migrate (Browder and Garman 1994) for three reasons: (1) many of the streams are small, (2) migratory anadromous fish

aggregate at high densities, and (3) the nutrients loaded into these systems by excretion are available immediately for uptake by microbes and primary producers (in contrast to those from carcasses, which must be mineralized first).

The conditions of small ecosystem size, large numbers of fish, and immediately available nutrients are all met for anadromous alewives. Most of the coastal streams in New England through which alewives migrate, including Bride Brook, are small and relatively shallow. On 26 April 2008, the average width of Bride Brook was 5 m, and the depth was 0.10–0.20 m. The number of alewives migrating through these small streams can be extremely high for short periods of time. In the 1960s, Bride Lake supported annual runs of approximately 180,000 fish (Kissil 1974). During the period of this study annual run size has ranged from a low of 69,000 in 2005 to a high of 130,000 in 2006 (CDEP, unpublished data). In many years, the majority of those fish pass within a 2–3-week period (Dalton et al. 2009). On the night of 26 April 2008, we observed approximately 18,000 alewives pass through Bride Brook in just over 8 h (the first fish were spotted at 2315 hours and the run was done by 0730 hours). With a mean migration time of around 2 h, those 18,000 alewives added 142 g of nitrogen and 12.5 g of phosphorus into Bride Brook in a single night. Finally, alewife, like other fish species, excrete inorganic forms of nitrogen (~75% of the excreted N was in the form of NH_4^+) and phosphorus, which are rapidly used by local organisms (Browder and Garman 1994). Walters and Post (in press) estimated that excretion accounts for 50% of the phosphorus and 66% of the nitrogen loaded by alewives into Bride Brook during the peak of migration. The effects of this nutrient loading by alewives have been demonstrated in previous studies: Browder and Garman (1994) saw elevated NH_4^+ concentrations during the peak alewife migration, Walters and Post (in press) showed that marine derived nutrients enter the food web of Bride Brook and other coastal streams in Connecticut, and Durbin et al. (1979) showed that nutrient loading by alewives can influence stream ecosystem functions such as leaf litter decomposition rates.

Our results raise the question of the importance of nutrient excretion for migratory fish in general. The importance of excretion by migrating fish will be influenced by the number of fish migrating, their residence time in the stream, their nutrient excretion rates, and the magnitude of other inputs. For ecosystems with semelparous fishes, nutrient excretion is not likely to be important to spawning grounds where carcass and egg inputs are very high and reasonably represent the total nutrient load (Naiman et

al. 2002). Nutrient excretion may, however, be very important for the streams and rivers through which semelparous fish migrate if those systems do not receive nutrient inputs from carcasses or eggs. For iteroparous fish species, nutrient excretion is one of three potentially important sources of nutrient inputs, and it may be of particular importance to the stream ecosystems through which anadromous alewives migrate (Durbin et al. 1979; Walters and Post in press).

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