

Nutrient loading by anadromous alewife (*Alosa pseudoharengus*): contemporary patterns and predictions for restoration efforts

Derek C. West, Annika W. Walters, Stephen Gephard, and David M. Post

Abstract: Anadromous alewives (*Alosa pseudoharengus*) have the potential to alter the nutrient budgets of coastal lakes as they migrate into freshwater as adults and to sea as juveniles. Alewife runs are generally a source of nutrients to the freshwater lakes in which they spawn, but juveniles may export more nutrients than adults import in newly restored populations. A healthy run of alewives in Connecticut imports substantial quantities of phosphorus; mortality of alewives contributes 0.68 g P-fish⁻¹, while surviving fish add 0.18 g P, 67% of which is excretion. Currently, alewives contribute 23% of the annual phosphorus load to Bride Lake, but this input was much greater historically, with larger runs of bigger fish contributing 2.5 times more phosphorus in the 1960s. A mesocosm experiment in a nearby lake showed that juvenile alewife growth is strongly density dependent, but early survival may be too low for juvenile outmigration to balance adult inputs. In eutrophic systems where nutrients are a concern, managers can limit nutrient loading by capping adult returns at a level where juvenile populations would not be suppressed.

Résumé : Les gaspareaux (*Alosa pseudoharengus*) anadromes peuvent potentiellement modifier les bilans de nutriments des lacs côtiers pendant leurs migrations adultes vers les eaux douces et leurs migrations juvéniles vers la mer. Les montaisons de gaspareaux sont généralement des sources de nutriments pour les lacs d'eau douce dans lesquels ils fraient, mais, dans les populations nouvellement rétablies, les jeunes peuvent exporter plus de nutriments que les adultes n'en importent. Une montaison saine au Connecticut importe des quantités importantes de phosphore; la mortalité des gaspareaux fournit 0,68 g P-poisson⁻¹, alors que les poissons survivants apportent 0,18 g P, dont 67 % est de l'excrétion. Actuellement, les gaspareaux fournissent 23 % de la charge annuelle de phosphore du lac Bride, mais cet apport était beaucoup plus élevé dans le passé lorsque, durant les années 1960, des montaisons plus importantes de poissons plus grands fournissaient 2,5 fois plus de phosphore. Une expérience en mésocosme dans un lac adjacent montre que la croissance des gaspareaux est fortement reliée à la densité, mais que la survie au début du cycle est peut-être trop faible pour que l'émigration des jeunes contrebalance les apports des adultes. Dans les systèmes eutrophes dans lesquels les gestionnaires se préoccupent des nutriments, ceux-ci peuvent contrôler la charge de nutriments en limitant les retours d'adultes au niveau nécessaire pour que les populations de jeunes ne soient pas réduites.

[Traduit par la Rédaction]

Introduction

In coastal watersheds across New England, diadromous fish are regaining access to inland waters from which they have been barred for a century or more. The removal of dams and the installation of fishways have already reopened 250 miles of stream to diadromous fish in the state of Connecticut, USA alone. Restoration of the spatial connection between the ocean and freshwater ecosystems is a priority for diadromous fish management and conservation (Atlantic States Marine Fisheries Commission 2009). Diadromous fish

are essential components of both the freshwater and marine systems in which they reside; however, many diadromous fish species are in decline (Limburg and Waldman 2009). While species such as Atlantic salmon (*Salmo salar*) and American shad (*Alosa sapidissima*) have garnered the preponderance of public attention, ecological interactions may be most strongly influenced by less glamorous, but historically more abundant fish such as alewife (*Alosa pseudoharengus*), and blueback herring (*Alosa aestivalis*) (collectively called river herring).

Alewives are an important component of the marine and

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freshwater ecosystems in which they reside. Juvenile alewives are extremely effective size-selective predators, driving strong changes in zooplankton community structure and causing trophic cascades in their natal rearing lakes (Brooks and Dodson 1965; Post et al. 2008). Juvenile alewives are important prey for largemouth bass (*Micropterus salmoides*) and pickerel (*Esox* spp.) (Cooper 1961; Yako et al. 2000) and adults are important prey for coastal predators and piscivorous birds (Hartman 2003; Dalton et al. 2009). In the fall, juvenile anadromous alewives migrate to the ocean where they feed and grow for several years before returning to their natal systems to spawn. Although the migration of adult alewives is obstructed by even low-head dams, they will readily ascend fishways, making them a good target for restoration efforts (Havey 1961).

One consequence of reconnecting freshwater ecosystems to the coastal ocean is the reestablishment of the movement of nutrients by diadromous fish between the ocean and inland waters. While an enormous amount of research has focused on the role of Pacific salmon in loading marine-derived nutrients into freshwater ecosystems (Donaldson 1969; Bilby et al. 1996; Naiman et al. 2002), much less is known about the role of other anadromous fish as nutrient vectors, particularly those in the Atlantic Ocean. Like Atlantic salmon, alewives are iteroparous, with about half of adults surviving spawning to return to sea (Cooper 1961; Kissil 1974; Dalton et al. 2009). Inputs from carcasses, gametes, and excretion make anadromous alewives a potentially sizable source of marine-derived nutrients for the streams through which they migrate (Post and Walters 2009; Walters et al. 2009) and lakes in which they spawn. Marine-derived organic matter from alewives has been shown to be incorporated into stream invertebrates and piscivores (Garman and Macko 1998; Walters et al. 2009). The one available estimate of nutrient loading to lakes suggests that anadromous alewives may contribute considerably more nitrogen and phosphorus to freshwater ecosystems, on an areal basis, than many Pacific salmon runs (Durbin et al. 1979).

Alewife populations have changed considerably since the 1970s when Durbin et al. (1979) studied the movement of nutrients by alewives. Despite restoration efforts, alewife populations are in decline throughout much of their native range (Atlantic States Marine Fisheries Commission 2009; Limburg and Waldman 2009). Dramatic declines have been seen from 1950 to 2000 in both commercial fisheries landings and the passage of river herring through monitoring stations on fish passes (Davis and Schultz 2009). In addition to the decline in population size, the body size of alewife spawners has decreased substantially. Historically, the alewife run at Bride Lake, Connecticut, consisted of fish that were age 5 or greater, but currently, the run is dominated by smaller age 3 and 4 fish (Davis and Schultz 2009).

While Pacific salmon typically spawn in nutrient-poor lakes and streams where marine-derived nutrients are considered ecologically beneficial (Stockner 1987; Gresh et al. 2000; Naiman et al. 2002), alewives transport nutrients into and out of freshwater ecosystems that are typically quite productive. Coastal ecosystems throughout southern New England are naturally mesotrophic and are typically imbedded within a human-dominated landscape where cultural eutrophication is a persistent management concern (Brugam

1978). In this context, the restoration of anadromous alewives could exacerbate water quality problems if alewives increase net nutrient loading into the freshwater ecosystems where they spawn. This has caused concern among some local stakeholders and has the potential to delay or prevent restoration efforts in watersheds where nutrient loading is a primary water quality concern (e.g., where the US Environmental Protection Agency has mandated Total Maximum Daily Load studies for nutrient abatement).

Anadromous fish move nutrients both into and out of freshwater ecosystems, although inputs are typically more obvious and much better studied (Moore and Schindler 2004). Net loading into freshwater ecosystems is fully described as inputs due to adult mortality, gametes, and direct excretion of nutrients minus the removal of nutrients from freshwater ecosystems by juvenile fish when they emigrate. Since juvenile growth and survival in freshwater are typically density dependent (Jonsson et al. 1998), anadromous fish can export nutrients from freshwater ecosystems when at low densities and import nutrients when at high densities (Scheuerell et al. 2005). This sets up the potential for anadromous alewives to export nutrients from freshwater ecosystems early in restoration when adult densities are low and to import large quantities of nutrients as adult returns (escape-ment) increase.

Here, we evaluate the patterns of net nutrient loading by alewives over a range of population sizes. We concentrate on phosphorus, as it is generally the nutrient that limits production in the lake ecosystems in which alewives spawn (Schindler 1978). First, we estimate net alewife nutrient loading and parameterize an alewife nutrient loading model using data from an existing run of anadromous alewives in Bride Lake. We then compare the current alewife nutrient load to that in the 1960s when alewives were more numerous and larger. Next, since little is known about the actual patterns of nutrient loading during restoration, we predict the net nutrient loading for a newly restored population across a range of adult escapement. We use a local sensitivity analysis to determine which parameters are most important to the alewife nutrient loading model. Finally, we use an export coefficient model to estimate the landscape phosphorus loading to Bride Lake and Linsley Pond to place the alewife loading term in the context of the lake's nutrient budget.

Materials and methods

Study site

Our research was conducted at Bride Lake and Linsley Pond in Connecticut. Bride Lake contains an anadromous alewife population that we used to both evaluate contemporary and historic net nutrient loading by an alewife population and parameterize our general alewife nutrient loading model. Bride Lake is the site of extensive historical (Marcy 1969; Kissil 1974) and current research on alewife (Davis and Schultz 2009; Post and Walters 2009). It is located in East Lyme, Connecticut, and is linked to Long Island Sound by Bride Brook, which flows 3.3 km from the outlet of Bride Lake to Long Island Sound (see Dalton et al. 2009 for map). Bride Lake is 28.7 ha in area (based on a high-resolution areal photograph, not 18 ha, as previously reported

in Kissil (1974)), has a maximum depth of 10.7 m (Kissil 1974), and had an average summer total phosphorus (TP) concentration of 21.3 $\mu\text{g P}\cdot\text{L}^{-1}$ from 2005 to 2007. The Bride Lake anadromous alewife population was studied in the 1960s by Kissil (1974) to evaluate characteristics of the spawning population and young-of-the-year (YOY) in the lake. Since 2003, the Connecticut Department of Environmental Protection (CTDEP) has monitored the number of adults returning to Bride Lake to spawn using a blocking weir (2003–2005; Davis and Schultz 2009) and a Smith-Root SR-1601 fish counter (2005–2008). In 2005, the fish counter was also used to estimate the number of adults leaving Bride Lake. YOY alewives in Bride Lake were sampled monthly from June to August from 2004 to 2006 in a pelagic purse seine with 3.18 mm mesh. The seine was 4.87 m deep and 35.45 m long and encircles an area of 100 m^2 .

Linsley Pond is a 9.4 ha pond with a maximum depth of 13.4 m located on the border of Branford and North Branford, Connecticut. Linsley Pond flows into Pisgah Brook, which runs 3.9 km to the Branford Supply Ponds Dam and then another 1.6 km to Branford Harbor and Long Island Sound. The river linkage between Linsley Pond and Long Island Sound was severed in 1900 by the construction of the Branford Supply Ponds Dam. A fishway was built at the Branford Supply Ponds Dam in the fall of 2005. In the first year that the fishway was opened, 3123 adult alewives entered the supply ponds, and although no alewives have been confirmed in Linsley Pond to date, they are expected to reach Linsley Pond in the coming years. Excessive nutrient inputs from development and industry have led the CTDEP to develop a Total Maximum Daily Load for the watershed in 2005. The analysis found that Linsley Pond currently receives ~100 kg P annually and recommended a 43% reduction in TP inputs. In 2005, the lake had a spring TP concentration of 150 $\mu\text{g P}\cdot\text{L}^{-1}$.

Alewife nutrient loading model

Here, we present a fully described nutrient loading model for anadromous fish. With an annual time step, the general model estimates net phosphorus flux from alewives as

$$\text{Net P flux} = n_a \times (\text{P}_{\text{mort}} + \text{P}_{\text{gametes}} + \text{P}_{\text{excretion}}) - \text{P}_{\text{YOY}}$$

where n_a is the number of adults, P_{mort} is the phosphorus loaded into the lake by adult mortality, $\text{P}_{\text{gametes}}$ is the phosphorus loaded into the lake by inputs of eggs and sperm, and $\text{P}_{\text{excretion}}$ is the phosphorus loaded into the lake through direct excretion of phosphorus by adults during their residence in the freshwater ecosystem; P_{YOY} is export of phosphorus by YOY or juvenile fish as they emigrate from the ecosystem. The n_a was used as a dynamic variable to look at patterns of net nutrient loading across a range of adult densities.

The mass of phosphorus loaded per fish by adult mortality (P_{mort}) was modeled as

$$\text{P}_{\text{mort}} = \mu_a \times \text{mass}_a \times [\text{P}_a]$$

where μ_a is the adult in-lake mortality rate (per year), mass_a is the average mass of the adults (wet weight) entering the lake, and $[\text{P}_a]$ is the concentration of phosphorus in adults (grams phosphorus per gram wet weight). We used counts

of adult immigration and emigration taken at the Bride Lake outlet in 1966 and 1967 by Kissil (1974) and in 2005 by the CTDEP to estimate μ_a . Current mass_a was estimated directly from 120 sampled fish entering Bride Lake in 2004, 2005, and 2008. The mass_a from the 1960s was determined using the length of fish found by Kissil (1969) and the length–weight regression for current adult alewives in Bride Lake. The phosphorus content of unspawned adults ($[\text{P}_a]$) was taken from Durbin et al. (1979).

The mass of phosphorus loaded per fish by gametes ($\text{P}_{\text{gametes}}$) was modeled as

$$\text{P}_{\text{gametes}} = (1 - \mu_a) \times 0.5 \times (F_a \times \text{mass}_e \times [\text{P}_e] + \Delta\text{mass}_t \times [\text{P}_t])$$

where F_a is the fecundity of each female, mass_e is the mass of each egg, $[\text{P}_e]$ is the concentration of phosphorus in each egg (grams phosphorus per gram wet weight), Δmass_t is the change in mass of the testes, and $[\text{P}_t]$ is the concentration of P in the testes. The ovaries of 10 anadromous alewives taken at the entrance of Bride Lake in early May of 2004 and April of 2005 were measured for mass_e and $[\text{P}_e]$. The F_a was estimated as a function of adult length (length_a) based on the relationship $F_a = 3596 (\text{mm}^{-1}) \times \text{length}_a - 766186$ ($n = 24$, $t = 4.04$, $r^2 = 0.43$, $p < 0.01$) derived from data in Kissil (1969) and from fish sampled in 2004 and 2005. The change in mass of the testes was calculated as the mass of the testes of unspawned alewives minus the mass of the testes of spawned fish. The initial mass of testes was estimated as a function of length_a and based on the relationship $\text{mass}_t = 0.157 (\text{g}\cdot\text{mm}^{-1}) \times \text{length}_a - 28.563$ ($n = 289$, $t = 13.64$, $r^2 = 0.39$, $p < 0.01$) for fish captured at the entrance to Bride Lake in 2003 and 2006 (J.P. Davis, CTDEP Inland Fisheries Division, Eastern District Headquarters, 209 Hebron Road, Marlborough, CT 06447, USA, unpublished data). The mass of spawned testes was taken to be 5.18 g (Durbin et al. 1979). The $1 - \mu_a$ term was included because we assume that all of the phosphorus contained in a fish remains in the lake when that fish dies. Thus, P_{mort} includes $\text{P}_{\text{gametes}}$ for each adult that dies and the $1 - \mu_a$ term was included to avoid double counting $\text{P}_{\text{gametes}}$ from adults that die. We assumed a 1:1 sex ratio.

The mass of phosphorus loaded through direct excretion ($\text{P}_{\text{excretion}}$) was modeled as

$$\text{P}_{\text{excretion}} = (1 - \mu_a) \times \text{mass}_a \times E_a \times t_a$$

where E_a is the excretion rate of adults (grams phosphorus per gram wet weight per day) and t_a is the time spent in freshwater by spawning adults. Again, the $1 - \mu_a$ term was included because we assume that fish that die contribute all of their phosphorus to the lake. Excretion is only accounted for in fish that survive spawning and leave the system. The time that adult alewives spend in freshwater was set as 14 days, which corresponds to the median stay in freshwater for alewives at the time when migration peaks (Kissil 1969). Adults do not feed between migration and spawning, so all nutrients excreted during this time are of marine origin (Cooper 1961). Adults may feed in the lake between spawning and returning to the ocean but this time is generally short. The E_a was calculated with alewives entering Bride Lake (Post and Walters 2009).

The mass of phosphorus exported from the lake by YOY alewives (P_{YOY}) was modeled as

$$P_{YOY} = n_{YOY} \times \text{mass}_{YOY} \times [P_{YOY}] \times \text{area}$$

where $n_{YOY} \times \text{mass}_{YOY}$ is a density-dependent function that relates the biomass density of YOY alewives to the number of adult spawners, $[P_{YOY}]$ is the concentration of phosphorus in each YOY alewife (grams phosphorus per gram wet weight), and area is the lake area in hectares. The biomass density of YOY alewives ($n_{YOY} \times \text{mass}_{YOY}$) emigrating from the lake was calculated on an areal basis and was modeled as a function with an exponential rise-to-maximum as the number of YOY individuals increases. The form of $n_{YOY} \times \text{mass}_{YOY}$ was estimated from the mesocosm experiment performed in Linsley Pond in the summer of 2005 (see below). This density-dependent relationship reflects a decrease in growth and survival as the number of juveniles increases. The $[P_{YOY}]$ was measured in 13 YOY alewives caught in Bride Lake in the falls of 2004 and 2005.

Density-dependent growth and survival of YOY alewives

In the summer of 2005, we conducted a mesocosm experiment in Linsley Pond to estimate the density-dependent growth and survival of YOY alewives. Each mesocosm was 2 m in diameter with 6 m deep cylindrical sides of solid polyethylene. They were closed on the bottom and open to the atmosphere on top. Mesocosms were lowered to around 7 m depth and raised through the water column isolating approximately 19 m³ of water from the lake. We stocked YOY anadromous alewives from Bride Lake into the mesocosms on 12 July 2005 at densities that spanned the range of densities observed in local lakes with anadromous alewives. We had one treatment with a density of 0.32 fish·m⁻² (one fish per mesocosm) replicated three times. The other five treatments, with densities of 0.64, 1.27, 2.55, 5.1, and 10.19 fish·m⁻² (2, 4, 8, 16, and 32 fish per mesocosm), were replicated two times. Fish stocked into mesocosms had an average length of 32 mm (SD = 3.1 mm) and an average mass of 0.26 g (SD = 0.09 g). Fish were stocked at this size because fish <25–30 mm are difficult to keep alive during transport. Nitrogen and phosphorus were added to each mesocosm at a 25:1 molar ratio based on a phosphorus loading rate of 0.30 mg P·m⁻³·day⁻¹. The sides of the mesocosms were scrubbed clean of periphyton weekly. Fish were censused on 26 July and 16 August and a final count was made on 30 August when all fish were removed from the mesocosms to be measured for length and mass. One of the 0.32 fish·m⁻² treatments was omitted due to the inadvertent addition of a fish in the middle of the experiment.

We fit a negative exponential model to the growth rate of YOY alewives across stocking densities and a linear model to mortality rate across stocking densities. The relationship between initial fish density and final biomass density of YOY produced was fit with an asymptotic exponential function:

$$n_{YOY} \times \text{mass}_{YOY} = a \times (1 - e^{-b \times x})$$

where $n_{YOY} \times \text{mass}_{YOY}$ is the biomass density (grams per square metre) of YOY alewives, a is the maximum biomass density (asymptote), b is the slope of the relationship between density and biomass, and x is the initial density of

YOY alewives at stocking. Linsley Pond is more productive than Bride Lake, so we expected to obtain greater densities of YOY alewives in the Linsley Pond mesocosms than in Bride Lake. To translate the biomass from the experiment to biomass in Bride Lake, we matched a to the biomass density of YOY alewives observed in midsummer in Bride Lake for 2004 and 2005, which was 1.60 g·m⁻² (Post et al. 2008). The year 2006 was excluded because an early emigration event of YOY alewives greatly reduced their midsummer density. The initial density x of YOY alewives was converted to the number of spawners (n_a) by fitting an exponential decline between the time when eggs were spawned on 1 May and 12 July, when fish were stocked into the mesocosms. Using the number of spawners and fecundity, we can estimate the number of eggs spawned and measure the slope of the exponential decline to the time at which we were first able to estimate the population size using a purse seine, which was 30 June in 2005 and 19 June in 2006.

The mesocosm experiment provides a good estimate of the density-dependent growth of alewives larger than 30 mm in Linsley Pond, but we do not know the growth or survival of smaller alewives. The survival of alewives in Bride Lake provides a best estimate of early survival; however, early survival is likely density dependent and survival could be considerably higher at densities lower than that seen in Bride Lake. Therefore, in the estimate of potential nutrient export from Linsley Pond, we also examine the case where the survival of YOY alewives to 30 mm increases 10-fold from that seen in Bride Lake.

Phosphorus content of fish (adults, gametes, and YOY)

Phosphorus content of unspawned adult alewives and alewife testes was taken from Durbin et al. (1979). Phosphorus content of eggs and YOY was estimated by ashing dried samples in a muffle furnace followed by digestion with HCl and analysis of liberated soluble reactive phosphorus on an Astoria 2 autoanalyzer (Higgins et al. 2006).

Sensitivity analysis

We conducted a local sensitivity analysis of our alewife nutrient loading model for the current alewife run in Bride Lake to determine the relative importance of each parameter to the estimation of net nutrient flux. The sensitivity measures the percent change in the model output for a 1% change in a parameter. We varied n_a , μ_a , mass_a , $[P_a]$, F_a , mass_e , $[P_e]$, Δmass_t , $[P_t]$, t_a , and E_a by sequentially adjusting each parameter by $\pm 10\%$ and recording the centered distance estimate of the response of the net nutrient flux:

$$s_i = \frac{Y(1.1 \times p_i) - Y(0.9 \times p_i)}{0.2 \times Y(p_i)}$$

where s_i is the sensitivity of the model to parameter i , $Y(\)$ is the net nutrient flux for the given parameter set, and p_i is the parameter being adjusted (Ellner and Guckenheimer 2006). We analyzed the sensitivity of the full model to the estimated biomass density of YOY fish ($n_{YOY} \times \text{mass}_{YOY}$) with the same method, adjusting the asymptote and slope parameters by $\pm 10\%$ and recording the change to the full model.

Watershed loading model

To understand the impact that alewives are having on

their natal systems, we estimated background phosphorus loading into Bride Lake. Export coefficient models are widely used to estimate the nutrient loads from watersheds (Johnes 1996). These models use an estimate of the nutrient yield for each land-use type in a watershed to calculate the total nutrient load from the landscape (Reckhow and Simpson 1980). We used the Lake Loading Response Model, an export coefficient model that was developed for use in southern New England (AECOM Technology Corporation 2009). The Lake Loading Response Model considers water that flows overland (runoff) and subsurface (baseflow) and produces an estimate for the nutrient yield of a watershed based on precipitation, land uses, and basin characteristics. The model has been used by the CTDEP for Total Maximum Daily Load analysis of Linsley Pond, and it showed a close match to other estimates of nutrient loading (Stahl and Bolton 2005). The extent of the watershed of Bride Lake was determined using the National Hydrography Dataset and overlaid on land cover information from the 2001 National Land Cover Database to determine areal land uses (Homer et al. 2004). Although we do not have land-use information from the 1960s, the Bride Lake watershed likely has changed little due to the presence of two large prisons in the watershed.

Annual precipitation was calculated from monthly precipitation records from Middletown, Connecticut (42 km to the northwest of Bride Lake), from 1982 to 1996. Median values of loading estimates for each land use were chosen and nutrient inputs from the approximately 50 blue heron (*Ardea herodias*) individuals nesting in the watershed were included in the model. The proportion of phosphorus that makes it through the watershed to the lake, known as the phosphorus basin attenuation, was considered to be moderate due to the presence of a wetland in the basin (K. Wagner, AECOM Global Environment, P.O. Box 506, 11 Phelps Way, Willington, CT 06279, USA, personal communication (2009)). To ensure that the estimate of phosphorus loading was reasonable, the model output was entered into the equation

$$TP_{\text{lake}} = \frac{TP_{\text{in}}}{1 + 1.12(\text{year}^{-0.47}) \times \tau_w^{0.47}}$$

which estimates the lake phosphorus concentration (TP_{lake} (micrograms per litre)) using the inflow phosphorus (TP_{in} (micrograms per litre)) and the water residence time (τ_w (years)). Brett and Benjamin (2008) found this relationship to perform better than several older models relating phosphorus loading to lake phosphorus concentration. Predicted TP_{lake} was compared with measured values of TP_{lake} taken in the pelagic zone of Bride Lake during the summer months.

Results

Alewife nutrient loading model

Adult alewives contribute considerable amounts of phosphorus to Bride Lake. The values for all parameters used in the nutrient loading model are provided (Table 1). Each adult entering Bride Lake currently adds a mean of 0.46 g of phosphorus to the system. Adults that die in the system (P_{mort}) make up 83% of the total alewife phosphorus input, with each carcass contributing 0.68 g of phosphorus. Adults

that survive each add 0.18 g of phosphorus, of which 67% is excretion ($P_{\text{excretion}}$) with gametes (P_{gametes}) contributing the remainder. The P_{gametes} is split nearly evenly between males and females, as the higher phosphorus content of testes compensates for their lower mass. In the 1960s, adult alewives entering Brides Lake were larger than present-day alewives and contributed 39% more phosphorus per fish (mean of 0.64 g P·fish⁻¹). The difference in nutrient loading between the present and the 1960s is magnified when the size of the populations is taken into account. The average population returning to Bride Lake from 2003 to 2008 was nearly 90 000 fish, while in 1966 and 1967, the population averaged over 160 000 fish. As a result, the total amount of phosphorus added to Bride Lake in the 1960s was 2.5 times greater than it is today (Fig. 1).

YOY growth and survival

Growth and survival of YOY alewives in the Linsley Pond mesocosms was strongly density dependent (Fig. 2). Growth rate declined with increasing initial stocking densities as a negative exponential in the form of $Y = 0.0112 + 0.26 \times e^{-0.84x}$, where Y is growth rate (grams per day) and x is the initial density of YOY alewives stocked on 12 July 2005 ($n = 12$, $F_{2,10} = 36.57$, $r^2 = 0.89$, $p < 0.001$) (Fig. 2a). Survival declined with increasing initial stocking density. When one outlier was removed, a linear relationship between initial stocking density and daily mortality rate was found with $Y = 0.0006x - 0.0004$, where Y is the daily individual mortality rate and x is the initial density of YOY alewives ($n = 11$, $r^2 = 0.77$, $p < 0.001$) (Fig. 2b). The outlier was a treatment with two fish in which one died between days 14 and 35 of the experiment.

An asymptotic exponential function provided a good fit to the density-dependent growth of the YOY alewives, resulting in the relationship $n_{\text{YOY}} \times \text{mass}_{\text{YOY}} = 5.42 \text{ g}\cdot\text{m}^{-2} \times (1 - e^{-2.73x})$, where x is the initial stocking density of YOY alewife in the mesocosms ($n = 12$, $r^2 = 0.46$, $p < 0.01$) (Fig. 2c). After adjusting the asymptote for Bride Lake, the slope (decay constant) of the exponential decline of the YOY population in Bride Lake was found to be -0.13 day^{-1} to give an estimate of 6.39 YOY alewives surviving to 12 July (start of the mesocosm experiment) per adult spawner. After multiplying the density of fish by the area of the lake (28.7 ha), the resulting relationship between spawner density and the mass of YOY alewives in Bride Lake was $n_{\text{YOY}} \times \text{mass}_{\text{YOY}} = 2.67 \text{ kg} \times (1 - e^{-0.000061 \times n_a})$ (Fig. 1).

At the current escapement of 90 000 adults, the phosphorus export from YOY alewives is 2.66 kg and the net phosphorus input to Bride Lake by alewives is 38.6 kg. With the adult population of 162 000 found in 1960s, YOY export is expected to have been similar at 2.67 kg of phosphorus, but the net input would have been much higher with 100.8 kg of phosphorus imported to Bride Lake.

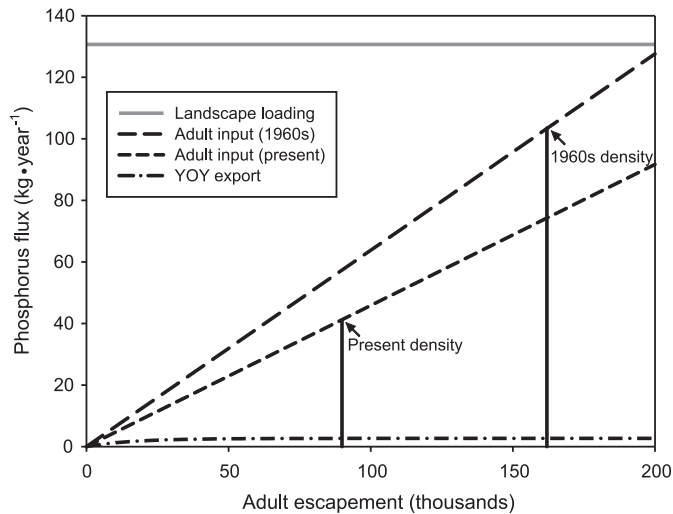
For Linsley Pond, we estimate a relationship between adult spawners and YOY biomass export of $n_{\text{YOY}} \times \text{mass}_{\text{YOY}} = 2.96 \text{ kg} \times (1 - e^{-0.000061 \times n_a})$, if early survival is the same as in Bride Lake. If the survival rate of fish less than 30 mm increased by an order of magnitude so each spawner resulted in 63.9 YOY alewives surviving to 12 July, the resulting relationship would be $n_{\text{YOY}} \times \text{mass}_{\text{YOY}} = 2.96 \text{ kg} \times (1 - e^{-0.00061 \times n_a})$ (Fig. 3). This estimate is reason-

Table 1. Parameters and sources for the alewife (*Alosa pseudoharengus*) nutrient loading model.

Trait	Value	Reference(s)
Adult numbers (n_a)	Variable	1, 2
Adult mortality rates (μ_a)	0.56·year ⁻¹	2, 3
Adult wet mass ($mass_a$)	161.5 g (present), 222.4 g (1960s)	1, 2
Adult length ($length_a$)	260 mm (present), 289 mm (1960s)	1, 2
Adult P concentration ($[P_a]$)	0.0042 g P·g fish ⁻¹	4
Adult fecundity (F_a)	$3596 \times length_a - 766\,187$	1, 2
Egg wet mass ($mass_e$)	0.00012 g	1, 2
Egg P concentration ($[P_e]$)	0.0031 g P·g egg ⁻¹	1
Δ testes wet mass ($\Delta mass_t$)	7.08 g (present), 11.60 g (1960s)	3, 5
Testes P concentration ($[P_t]$)	0.0088 g P·g testes ⁻¹	3
Adult excretion rate (E_a)	2.17 μ g P·g ⁻¹ ·h ⁻¹	6
Adult time in system (t_a)	14 days	2
YOY P concentration ($[P_{YOY}]$)	0.0058 g P·g YOY ⁻¹	1

Note: 1, This study; 2, Kissil (1974); 3, Dalton et al. (2009); 4, Durbin et al. (1979); 5, J.P. Davis (CTDEP Inland Fisheries Division, Eastern District Headquarters, 209 Hebron Road, Marlborough, CT 06447, USA, unpublished data); 6, Post and Walters (2009).

Fig. 1. Phosphorus flux to Bride Lake from alewives (*Alosa pseudoharengus*) and landscape sources across a range of adult densities. Average current (2003–2008) and 1960s (1966–1967) adult alewife escapement indicated by vertical bars.



able, as Havey (1973) found an average of 366 YOY alewife emigrants per adult spawner when adult densities were low following the restoration of an alewife population in Love Lake, Maine.

Sensitivity analysis

For the Bride Lake nutrient loading model, adult population size and adult body size (n_a and $mass_a$), which affect the input from P_{mort} , $P_{gametes}$, and $P_{excretion}$, were the most sensitive parameters, with sensitivities of 1.07 and 1.12, respectively. Adult phosphorus concentration had a sensitivity of 0.88, while adult mortality was slightly less important with a sensitivity of 0.65. The parameters for $P_{gametes}$ (F_a , $mass_e$, $[P_e]$, $\Delta mass_t$, and $[P_t]$) had little impact on the net nutrient flux, with sensitivity values of just 0.03 each. The adult time in the lake and excretion rate (t_a and E_a) each had a sensitivity of 0.12. The asymptote of juvenile biomass density (a) had a sensitivity of 0.07, while the slope param-

eter (b) had nearly no effect on the overall model at the adult densities seen in Bride Lake.

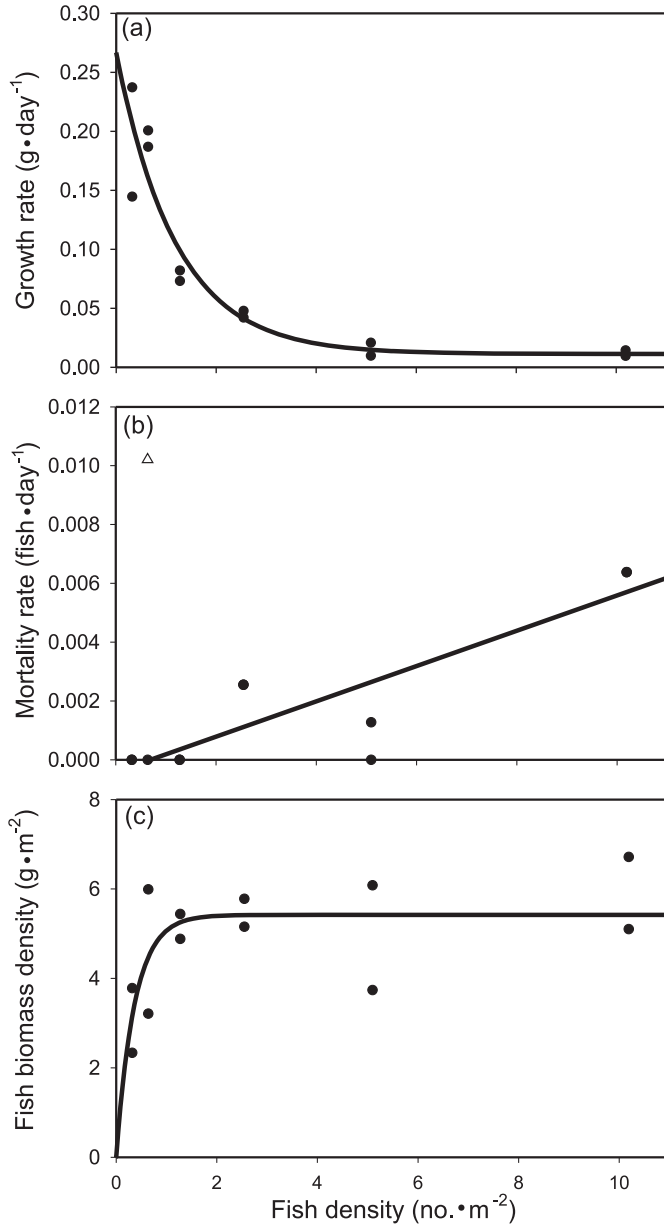
Landscape loading model

The parameters used for the lake loading response model export coefficient model are listed in Table 2. The amount of phosphorus added annually to Bride Lake from external sources (excluding alewives) was 130.7 kg (Fig. 1). Of this, 117.6 kg of phosphorus was from the watershed, 8.6 kg was directly deposited on the lake from the atmosphere, and 4.5 kg was from waterfowl. The 38.6 kg input from alewives brings our total estimated phosphorus load to Bride Lake to 169.3 kg·year⁻¹. Comparing the phosphorus concentration of Bride Lake with the Brett and Benjamin (2008) model shows that our loading estimate is reasonable but is likely an overestimate of the true phosphorus load to the lake. The Brett and Benjamin (2008) model predicted a lake phosphorus concentration of 23.6 μ g·L⁻¹, 11% greater than the observed average summer phosphorus concentration.

Discussion

The full model for nutrient loading by an iteroparous fish shows that alewives are loading substantial quantities of phosphorus to Bride Lake. Alewives currently import 23% of the total phosphorus input to Bride Lake, and this number increases to 44% for estimates from the 1960s. These numbers are relatively high compared to the phosphorus loading reported for sockeye salmon (*Oncorhynchus nerka*), which supply 3%–28% of lake phosphorus budgets in normal years, with a peak of 58% of the phosphorus budget for Lake Iliamna in a peak year for sockeye returns (Stockner 1987; Gross et al. 1998). Not surprisingly, the majority (83%) of the input from alewives is from alewives that die in the system. The nutrient input from alewives was much greater in the 1960s than at present because of both greater run size and larger body size in the 1960s than at present. Although fish were only 38% heavier and 80% more numerous in the 1960s, the combination resulted in 2.5 times greater phosphorus input by alewives in the 1960s than in the early 2000s. We do not know the size of the alewife run

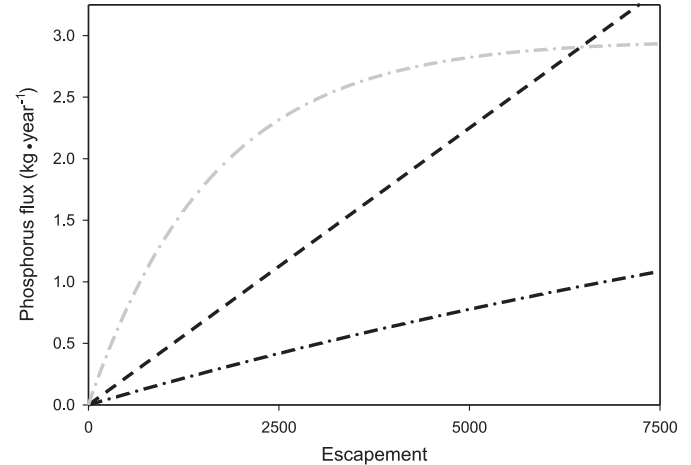
Fig. 2. Patterns of density-dependent (a) growth, (b) mortality, and (c) biomass production for alewives (*Alosa pseudoharengus*) in the Linsley Pond mesocosm experiment. The triangle in Fig. 2b was excluded from the analysis of density-dependent mortality.



before European settlement, but landscape nutrient inputs were likely considerably less (Brugam 1978) and alewife run size considerably larger, suggesting that alewives were an even more important part of the nutrient budget of coastal lakes in precolonial New England.

Based on the in-lake-survival of YOY alewives observed for Bride Lake, we believe that alewives are rarely nutrient exporters for a watershed. The growth of YOY alewives in mesocosms was strongly density dependent, but the early survival rates that we measured in Bride Lake were too low to produce a sufficient number of young to exceed the nutrient inputs of the parents. If, however, growth and survival of juveniles smaller than 30 mm are strongly density dependent, then it is possible that alewife populations could

Fig. 3. Estimated phosphorus flux due to alewives (*Alosa pseudoharengus*) in Linsley Pond following restoration. YOY export predicted from juvenile growth in mesocosms with 6.39 YOY per spawner surviving to 12 July (black dot-dashed line) and 63.9 YOY per spawner surviving to 12 July (gray dot-dashed line). Input by adults is for current fish (black dashed line). Note that axes scales differ from those on Fig. 1.



be a net exporter of phosphorus when adult populations are small. If 63.9 juveniles per adult survive to 12 July in Linsley Pond, rather than the 6.39 per adult estimated from early survival in Bride Lake, we estimate that the population will be a net exporter of phosphorus until the population reaches 6500 adults (690-ha^{-1}). Although they have not yet reached Linsley Pond, more than 3100 fish ascended the Branford fishway into the Branford Supply Ponds the first year that it opened (D.M. Post, unpublished data). If these fish had moved into Linsley Pond rather than remaining in the artificial supply ponds, we predict they would have imported 0.8 kg of phosphorus to Linsley Pond and, with good early survival, they could have exported greater than 1 kg of phosphorus. Thus, early in the recovery of an alewife population, net loading is likely to be small or even slightly negative (net export) where YOY survival and growth are high.

One possible source of bias in our estimates of nutrient export by YOY alewives is that juveniles can leave their natal lakes at different times throughout the year. The loss of some individuals early in the year may release the remaining fish from density dependence and increase the total biomass of YOY fish that emigrate from the system. For Bride Lake, Linsley Pond, and many other coastal lakes with low-gradient outlet streams, the outlet streams often go dry for most of the summer months, prohibiting emigration. In wet years and in lakes with larger outlet streams, YOY alewives can migrate to the ocean throughout the summer. Yako et al. (2002) found that alewives in lakes where they cannot emigrate throughout the year were smaller, possibly due to an increase in intraspecific competition throughout the growing season. As a result, managing flow regimes to allow alewife emigration throughout the summer may both benefit alewife populations and increase nutrient export from eutrophic systems.

In the Bride Lake model, sensitivity analysis shows that at current levels of adult escapement, parameters related to phosphorus input by adult mortality are the most important to nutrient loading. Adult escapement and adult body size

Table 2. Parameters for the Bride Lake export coefficient model.

Land use	Area (ha)	Runoff fraction	Baseflow fraction	Runoff P export (kg-ha ⁻¹ ·year ⁻¹)	Baseflow P export (kg-ha ⁻¹ ·year ⁻¹)	Notes
Low-density residential	40.23	0.40	0.25	1.10	0.010	>0.4 ha lot
Medium-density residential or highway corridors	8.28	0.50	0.15	2.50	0.010	0.1–0.4 ha lot
High-density residential or commercial	1.26	0.60	0.05	2.50	0.010	<0.1 ha lot
Institutional, cemetery, park, or recreational	66.87	0.40	0.25	1.10	0.010	
Agricultural, row crops	1.26	0.3	0.3	1.00	0.010	
Agricultural	36.45	0.3	0.3	0.40	0.010	
Upland	377.91	0.3	0.4	0.05	0.004	
Wetland/lake	55.10	0.05	0.4	0.20	0.004	
Meadow	25.65	0.15	0.3	0.20	0.004	

Note: Other model parameters: precipitation 1.3 m·year⁻¹ (Middletown, Connecticut), waterfowl 4.5 kg P·year⁻¹ (50 birds), water basin attenuation 0.8, and P basin attenuation 0.6.

have the highest sensitivities, as they are important for all input terms. Adult mortality also has a very strong impact, although considerably less than population size or body size because although an increase in adult mortality increases the phosphorus input from mortality, it decreases the input from gametes and excretion. Since adult population size, adult body size, and adult mortality are expected to vary considerably from system to system, it is important that they are accurately measured to get a good estimate of net phosphorus loading from alewives. Since the model is not very sensitive to any of the factors affecting the phosphorus load from gametes or excretion and these factors are not expected to vary greatly between lakes, these parameters are less important to measure in different systems. One exception is the time of adult residence in freshwater, which may vary considerably between lakes and could have a strong effect on the amount of excretion and the overall model if differences are on the order of weeks. Since the YOY production is a small fraction of the net nutrient flux at the current escapement levels for Bride Lake, the YOY biomass density asymptote has little effect on the overall nutrient budget. In the Bride Lake model, the slope parameter has virtually no effect, since the population is near the asymptote of YOY biomass density. In lakes that have smaller adult populations, however, this parameter is very important to the overall nutrient budget. In the projected nutrient budget for Linsley Pond, for example, the model is very sensitive to the slope parameter of the YOY export term.

Knowing the nature of the nutrient flux from alewives to coastal ponds will allow for adaptive management of alewife populations for one of two goals: minimizing nutrient inputs while allowing some alewives to spawn or maximizing alewife returns while limiting nutrient loading. In Linsley Pond, for example, managers can control the number of alewives that ascend the Branford Supply Ponds fishway. Once a run of alewives becomes established in the pond, managers could constrain the number of fish that are allowed into the pond to a point where there is nearly zero net loading or at a point where YOY export is nearly maximized. Since juvenile growth is strongly density dependent, changing the number of adults will not have a large effect on the biomass of juveniles that survive to emigrate from the pond, although

the number of juveniles will be affected. If early survival of alewives in Linsley Pond is similar to that in Bride Lake, capping the adult run at 23 000 fish (2450·ha⁻¹), the YOY biomass exported would be expected to be greater than 75% of the maximum capacity for the lake. The net nutrient input for this many fish would be 8.3 kg of phosphorus, which is less than 10% of the current phosphorus load to the pond.

The nutrient loading estimate from adult mortality that we provide is an upper estimate for the nutrient load to lakes, as some of the nutrients from carcasses can be removed from the system by mobile predators. At present, cormorants (*Phalacrocorax auritus*) are a major predator of adult alewives, responsible for as much as 48% of the alewife mortality in Bride Lake (Dalton et al. 2009). Although the birds transport much of the nutrients away from the lake as allocation to growth and reproduction or as feces, they excrete a substantial proportion of their diet back into the lake, since they remain on the lake for the majority of the day. The nutrients excreted by cormorants are not available for direct uptake by primary producers, as excretion from fish is, but feces are mineralized by microbes to available forms (Vanni 2002). Aside from mobile predators, the retention of carcasses in the lake should be high, unlike in lotic systems where water flow necessitates an explicit consideration of carcass retention (Garman 1992; Nislow et al. 2004).

We estimate that 11% of the phosphorus input from alewives is due to excretion of alewives that survive spawning. Since adult mortality is likely not instantaneous, an additional 5.9 kg of phosphorus could be excreted in the lake by fish that eventually die, bringing the total contribution from excretion to as much as 26% of the total alewife phosphorus input. This estimate closely approximates that of Durbin et al. (1979) who found that 18% of alewife phosphorus input came from excretion. The importance of inputs from metabolic processes from anadromous fish has received relatively little attention, likely because it is not important to the net energy budget of semelparous species. Recent work in Bride Brook, which drains Bride Lake, has shown that alewife excretion is an important source of nutrients for the stream (Walters et al. 2009). Although Bride Lake is many times larger than the stream, the residence time for alewives in the lake is considerably longer than in the stream, resulting

in more nutrients being excreted. Excretion from surviving alewives alone equals 3% of the external load of the phosphorus to the lake at present and would have been 5% in the 1960s. The claim of Johnston et al. (2004) that *Oncorhynchus* spp. do not excrete phosphorus when they are not feeding is not relevant to breeding individuals, whose physiology changes dramatically as they prepare to spawn (Gende et al. 2002). A recent meta-analysis shows a striking difference in nitrogen and phosphorus dynamics between natural salmon runs and artificial carcass additions (Janetski et al. 2009). The additional nutrients seen in the natural system may be coming from excretion before senescence. Since excretion is in an inorganic form that can be readily used by primary producers, it appears that excretion may be an important but often overlooked piece of the nutrient budget for anadromous fish (Post and Walters 2009).

The decline in the size of existing alewife runs has led to the listing of alewife as a species of special concern (National Marine Fisheries Service 2006). By providing passage past existing barriers, fisheries managers have the opportunity to restore fish populations and strengthen the overall anadromous alewife population. For most diadromous fish whose populations are declining, restoration would be a desirable outcome and environmental groups would rally for the demolition of dams or the installation of fish ladders. Alewives, however, face the additional obstacle of being embedded in the densely populated coast of eastern North America where the nutrients that they import are an unwelcome addition to lakes that are already eutrophic. Although this makes alewife restoration projects more challenging, alewife populations can be adaptively managed to minimize the extent of potentially harmful nutrient loading.

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