# The dual influences of Alewife, Alosa pseudoharengus, on inland water quality: nutrient fluxes and food web effects

## Basic Information

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| **Title:** | The dual influences of Alewife, Alosa pseudoharengus, on inland water quality: nutrient fluxes and food web effects |
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| **Principal Investigators:** | David M Post |

## Publication

# CT INSTITUTE OF WATER RESOURCES:  Annual Report 2005-2006 Project Summary

## BASIC PROJECT INFORMATION

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| **FocusCategories** | water quality, nutrients, ecology |
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## PROPOSALS AND AWARD

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| Dalton | Christopher | B.S. | EEB |

## PUBLICATIONS

| | |
|---|---|
| Journal Article | Palkovacs, E.P., and D. M. Post. In prep. Anadromy, landlocking, and the evolution of feeding morphology and prey selectivity in the alewife. To be submitted to Ecology |
| Journal Article | Post, D.M., E. P. Palkovacs, and S. A. Dodson. In prep. Size selective predation by alewives: a classic ecological system revisited. To be submitted to Ecology |
| Journal Article | Post, D.M., A. Walters, and S Gephart. In prep. Nutrient loading by anadromous alewives: contemporary patterns and implications for restoration efforts. To be submitted to Canadian Journal of Fisheries and Aquatic Sciences |
| Journal Article | Post, D.M., E. P. Palkovacs. In prep. The in and out of nutrient loading by anadromous fishes. To be submitted to Ecology. |
| Journal Article | Walters, A. and D. M. Post. In prep. Influence of nutrient loading by alewives on a coastal Connecticut stream. |
| Journal Article | Dalton, C.M., D. M. Post, D. Ellis. In prep. Extent and impact of Double-crested Cormorant predation on anadromous alewives in Bride Lake, Connecticut |

## NOTABLE ACHIEVEMENTS, AWARDS, RECOGNITION

# Project Status Report:
# The dual influence of Alewife, Alosa pseudoharengus, on water quality

## A) Problem and Research Objective

*Problem statement* – Zooplanktivorous fishes, such as the alewife, *Alosa pseudoharengus*, can have profound impacts on lake water quality, both because they strongly affect the biomass and size structure of zooplankton communities and because they transport, store, and recycle large quantities of nutrients. High densities of zooplanktivorous fishes can seriously exacerbate the symptoms of eutrophication by extirpating populations of large bodied zooplankton, such as *Daphnia* spp., which could otherwise hold phytoplankton biomass to levels well below those established by phosphorus limitation alone. Water quality can be further degraded by zooplanktivorous fishes as they redistribute nutrients within a lake, for example by moving nutrients from benthic to pelagic regions of the lake where the nutrients can promote algal growth or, in the case of anadromous fishes such as alewife, shad, and salmon, import large quantities of new nutrients into lakes, further increasing rates of eutrophication.

River restoration efforts in CT (and throughout New England) aimed at removing dams or adding fish ladders to existing dams will once again provide access for river herring to lakes and ponds along the Atlantic coast. There is considerable concern by local lake associations, landowners, and resource managers that the recovery of anadromous river herring, in particular alewives, will cause water quality problems in coastal lakes. At the same time, EPA restrictions on total daily loads of nutrient pollutants are increasing pressure to limit non-point source nutrient pollution. The addition of river herring to this mix causes lake managers to cringe when they consider the potential new nutrient vector, and lake residents become resistant to restoration efforts when they see images of algal blooms and fish die-offs that occur in lakes with landlocked alewives (alewives that spend their entire life in freshwater). Some stake holders also worry that restored anadromous alewife populations will become landlocked (although most just think they are ecologically the same).

Alewives were a natural part of these ecosystems for thousands of years, and are an important prey for fish, birds and mammals. Furthermore, it is not clear that anadromous herring have the same impacts upon water quality as landlocked populations. Young-of-the-year anadromous alewives are resident in lakes for just a few months, and adults on spawning runs probably do not feed (although this is not well documented). These factors could reduce the impact of anadromous alewives on food web structure as compared to landlocked alewives, which feed year round in lakes and ponds and have caused water quality problems in the Great Lakes, which they invaded in the past century. Likewise, the life history shift from an anadromous to an entirely freshwater lifestyle represents a significant ecological shift, with important implications for body size, abundance, and foraging efficiency (e.g., landlocked alewives typically grow to just half the maximum body size of and mature one to two years earlier than anadromous alewives). Such changes in life history traits could diminish or exacerbate the influence of alewife populations on food web structure and lake water quality, but, to date, there has been very little research on this topic.

*Objectives* – My objectives were to test the ecological role and evolutionary history of river herring within the context of river restoration efforts. I have:

1) Addressed the effects of anadromous and landlocked alewives in their first summer of life on water quality in Linsley Pond, where access for alewives was restored in the spring of 2006, and Rogers Lakes, where restoration of river access is planned for the spring of 2008.
2) Addressed the magnitude of nutrient loading by anadromous alewives in lakes with existing anadromous alewife populations and provided a nutrient-loading model to estimate nutrient loading by anadromous alewives during population growth after river restoration. This model will allow managers to minimize nutrient loading within the context of population recovery through adaptive management of adult alewife passage through planned fishways.
3) Evaluated the population genetics of landlocked and anadromous alewives in Connecticut as a first step towards understanding the evolutionary origin of landlocked populations.
4) Started monitoring Linsley Pond, Rogers Lake and four reference lakes to gather pre-manipulation data before fish ladders are installed and anadromous alewives recover into these lakes. Anadromous alewives entered Linsley Pond in the spring of 2006 for the first time in over 100 years.

## B) Methodology

***Objective 1*** **–** I addressed the effects of anadromous and landlocked alewives in their first summer of life on water quality using a set of mesocosm experiment in Rogers Lake (summer of 2004) and Linsley Pond (summer of 2005). These lakes were chosen because they were, at the time, sites of planned river herring restoration efforts and represent the two types of lakes that are subject to river herring restoration efforts: lakes with landlocked alewives (Rogers Lake) and lakes without any alewives (Linsley Pond). Linsley Pond has since been restored and anadromous alewives entered the lake in the spring of 2006.

In Rogers Lake, I compared the food web effects of landlocked alewives to the food web effects of anadromous alewives at a fish density similar to that observed naturally in Rogers Lake. I compared landlocked to anadromous alewives in Rogers Lake because planned restoration efforts would slow anadromous alewives to “invade” this lake that already contains a health population of landlocked alewives. In the summer of 2004, I raised twelve experimental mesocosms (2 m diameter, 6 m deep; Figure 1) through the water column of Rogers Lake to fill them with natural lake water. In these mesocosms, I stocked four replicates with 15 (4.8 $m^{-2}$) young-of-the-year (YOY) anadromous alewives (mean length = 41 mm), four with 15 YOY landlocked alewives (mean length = 40 mm), and retained four as a no fish treatment. Fish were stocked on 24 June and the experiment was ended in late August. In each mesocosm I monitored temperature, dissolved oxygen, total nitrogen and total phosphorous concentrations, water transparency (secchi depth), zooplankton community structure, and phytoplankton biomass. This experiment asks the question: “what effect would

Figure 1. Experimental mesocosms in Rogers Lake in 2004.

replacing landlocked alewives with anadromous alewives have on summer food web and water quality?”

In Linsley Pond, I stocked two replicate experimental mesocosms at 7 different densities of anadromous alewives (0, 0.32, 0.64, 1.27, 2.55, 5.1 and 10.19 alewives $m^{-2}$) to simulate the food web effects of anadromous alewives at different densities on a lake that currently contains no alewives. Fish were stocked in mid June. Again, in each mesocosm I monitored temperature, dissolved oxygen, total nitrogen and total phosphorous concentrations, water transparency (secchi depth), zooplankton community structure, and phytoplankton biomass. This experiment asks the question: “which densities of YOY anadromous alewives will cause noticeable changes in summer food web structure and water quality?” This experiment had the secondary benefits of providing me with data on the form of density dependent growth and mortality in YOY anadromous alewives, which is important for developing nutrient loading models.

***Objective 2*** – Direct nutrient loading is one of the multiple concerns for the reintroduction of anadromous alewives. I addressed the magnitude of nutrient loading by anadromous alewives in Bride Lake and developed a generalized alewife nutrient loading model estimate nutrient loading by anadromous alewives during population growth after river restoration. This model will help us understand *when* in the restoration process and under which environmental conditions alewives might serve as net sources or sinks for nutrients, and provide an adaptive management framework for managers to minimize nutrient loading within the context of population recovery.

The nutrient loading model (for simplicity I present only the phosphorous model here) is described in the most general terms as:

$$\text{Net P loading} = (P_{adults} + P_{eggs} + P_{excretion}) - P_{juv} \qquad (1)$$

Where $P_{adults}$ is the mass of phosphorus loaded into the lake by adult mortality, $P_{eggs}$ in the mass of phosphorus loaded into the lake by inputs of eggs, and $P_{excretion}$ is the mass of phosphorus loaded into the lake through direct excretion of phosphorus by adults during their residence in the freshwater ecosystem. $P_{juv}$ is export of phosphorus by juvenile fish as they emigrate from the ecosystem.

The mass of phosphorus loaded by adults ($P_{adults}$) is modeled as:

$$P_{adults} = n_a \bullet \mu_a \bullet mass_a \bullet p_a \qquad (2)$$

where $n_a$ is the number of adults, $\mu_a$ is the adult mortality rate, $mass_a$ is the average mass of the adults (wet weight) entering the lake (and therefore includes the mass of egg), and $p_a$ is the concentration of phosphorus in adults (g P / g wet weight). The number of adults ($n_a$) was either estimated directly for estimates of net nutrient loading into Bride Lake, was used as a dynamic variable to look at patterns of net nutrient loading across a range of adult densities, or determined by the demographic model used to predict patterns of population growth during restoration. The in lake adult mortality rate ($\mu_a$) was estimated from data on adult immigration and emigration taken at the Bride Lake fish counter. Adult mass ($mass_a$) was estimated directly from fish entering Bride Lake or as an output of the demographic model. Adult phosphorus content ($p_a$) as measured directly for Bride Lake anadromous alewives (see below).

The mass of phosphorus loaded by eggs ($P_{eggs}$) is modeled as:

$$P_{eggs} = (1-\mu_a) \bullet n_a \bullet m_a \bullet mass_e \bullet p_e, \qquad (3)$$

where $m_a$ is the fecundity of each adult (female fecundity divided by 2; assumes a 1:1 sex ratio), $mass_e$ is the mass of each egg, and $p_e$ is the concentration of phosphorus in each egg (g P / g wet weight). Egg mass ($mass_e$) and $p_e$ were measured in 10 anadromous alewives taken at the entrance of Bride Lake in early May of 2004 and April of 2005. Fecundity ($m_a$) was estimated as a function of fish mass ($mass_a$) based on the relationship $m_a = 1321 \bullet mass_a - 31628$ ($n=24$, $t=3.91$, $r^2 = 0.41$, $p < 0.01$) derived from data in (Kissil 1969) and from fish sampled in 2004 and 2005. The $1-\mu_a$ term was included because we assume that all of the P contained in a fish remains in the lake when that fish dies ($mass_a$ is the mass of fish entering the lake). Thus, $P_{adult}$ includes $P_{eggs}$ for each adult that dies and the $1-\mu_a$ term was included to avoid double counting $P_{eggs}$ from adults that die.

The mass of phosphorus loaded through direct excretion ($P_{excretion}$) is modeled as:

$$P_{excretion} = (1-\mu_a) \bullet n_a \bullet mass_a \bullet E_a \bullet t_a, \qquad (4)$$

where $E_a$ was the excretion rate of adults (g P / g wet weight / day) and $t_a$ was the time spend in freshwater by spawning adults. Again, the $1-\mu_a$ term was included because we assume that fish that die contribute all of their P to the lake. Excretion is only important for fish that survive spawning and leave the system. Rates of excretion were estimated experimentally at Bride Brook in the spring of 2004 and 2005.

The mass of phosphorus exported by YOY or juvenile alewives was modeled as:

$$P_{yoy} = n_{yoy} \bullet mass_{yoy} \bullet p_{yoy}, \qquad (5)$$

where $n_{yoy}$ and $mass_{yoy}$ are density dependent functions and $p_{yoy}$ is the concentration of phosphorus in each YOY (g P / g wet weight). Here, the number of YOY ($n_{yoy}$) was modeled as: $m_a \bullet n_a \bullet (1- \mu_b - \mu_d \bullet m_a \bullet n_a)$ where $\mu_b$ is a density independent mortality rate and $\mu_d$ is the density dependent mortality rate that depends upon the initial number of eggs spawned ($m_a \bullet n_a$). The mass of YOY leaving the lake ($mass_{yoy}$) was modeled as: $b_0 + b_1 \bullet \exp(-b_2 \bullet m_a \bullet n_a)$ where $b_0$, $b_1$, and $b_2$ are parameters of a negative exponential growth curve such that growth depends upon the initial number of eggs spawned ($m_a \bullet n_a$). The form of $n_{yoy}$ and $mass_{yoy}$ were estimated from mesocosm experiments performed in Linsley Pond in the summer of 2005 (see figures below). These two density dependent can also be combine to produce a relationship between $P_{yoy}$ and $m_a \bullet n_a$ (the total number of eggs spawned) that approximates the Beverton-Holt stock recruit model used by Moore and Schindler (2004) and Post et al. (in prep) to model net nutrient loading. $p_{yoy}$ was measured in YOY alewives caught in Bride Lake in the falls of 2004 and 2005.

Table 1 presents the major variables and parameters. There are a few variables that are still under study but for which values are expected by August of 2006.

Table 1: Parameters and sources for the alewife nutrient-loading model.

| Trait | Value | Notes |
|---|---|---|
| Egg mass ($mass_e$) | 0.00012 g | 1,2 |
| Egg P content ($p_e$) | Still to be measured | 1 |
| Adult fecundity ($m_a$) | $1321 \bullet mass_a - 31628$ | 1,2 |
| Adult numbers ($n_a$) | Variable | 1 |
| Adult mass ($mass_a$) | 160 g | 1,4 |
| Adult P content ($p_a$) | 0.42% | 3 |
| Adult mortality rates ($\mu_a$) | 50-60% | 1,2 |
| Adult excretion rates ($E_a$) | $2.3\ \mu g\ g^{-1}\ hr^{-1}$ | 1 |
| Adult time in system ($t_a$) | ~2-4 weeks | 1,2 |
| YOY mass ($mass_{yoy}$) | $f(m_a, n_a, t_{yoy})$ | 1 |
| YOY P content ($p_{yoy}$) | 0.43% | 1 |
| YOY numbers ($n_{yoy}$) | $f(m_a, n_a, t_{yoy}) \bullet m_a \bullet n_a$ | 1 |

[1] This study
[2] Kissil 1974
[3] Durban et al. 1979
[4] Average wet mass of adult alewives returning to spawn in 2004 and

***Objective 3*** – One of the concern expressed by lake associations and lake property owners is that the restoration of anadromous herring population will provide a mechanism for the establishment of new local landlocked populations of alewives. This concern derives from the strong effects of landlocked alewives on zooplankton community structure and water quality in lakes across North America. Because the origin of landlocked alewives is not clear, I am conducting a molecular genetics study of alewives across Connecticut and New England. This analysis will be based on mitochondrial DNA (mtDNA) and microsatellite. Sample analysis is underway and will be completed in the fall of 2006.

**Objective 4** – In 2004, I started monitoring Linsley Pond, Rogers Lake and four regional reference lakes to gather pre-manipulation data before fish ladders are installed and anadromous alewives recover into these lakes. Anadromous alewives entered Linsley Pond in the spring of 2006 for the first time in over 100 years. A fish way is planned for Rogers Lake in the fall of 2007. In all of these lakes I monitored temperature, dissolved oxygen, total nitrogen and total phosphorous concentrations, water transparency (secchi depth), zooplankton community structure, and phytoplankton biomass.

## 3) Principal Findings and Significance

***Objective 1*** – Data from the 2004 mesocosm experiment in Rogers Lake have been analyzed. Data from the 2005 Linsley Pond mesocosm experiment have not been fully analyzed. In the Rogers Lake mesocosm experiment, there was some tendency for greater water clarity (Figure 2) and algal biomass (data not shown) in the no fish treatments early in the experiment, there were no significant differences among the treatments across July and August in both phytoplankton biomass and Secchi depth (Figure 2). There were some differences in zooplankton community structure among all three treatments, but these differences were subtle and did not cascade to an effect on algal biomass and water quality measures. These results indicate that YOY anadromous alewives have similar effects on food web structure as landlocked alewives when found at the same densities. In lakes such as Rogers Lake where landlocked alewives already reside, these results suggest that the replacement of landlocked alewives with anadromous alewives will not worsen water quality through food web effects. The second result, that there was no increase in water clarity in the no fish treatments, may appear paradoxical, but is expected given the current structure of the Rogers Lake zooplankton community. There are no large zooplankton in Rogers Lake because of the intense predation in zooplankton by landlocked alewives. By filling the mesocosms with Rogers Lake water, and therefore the Rogers Lake zooplankton community, there was little scope for large zooplankton (particularly large bodied *Daphnia*) to invade the bags, increase grazing pressure, and increase water clarity. Mean cladoceran length in our bags was 0.4 mm (s.d. = 0.1 mm) on 22 June. By the end of August the mean cladoceran length had declined to 0.3 mm (0.12) and 0.24 mm (0.05) in the landlocked and anadromous treatments, respectively, while mean cladoceran length had increased to only 0.54 mm (0.18) in the no fish treatment. The largest zooplankton found in the no fish treatments were *Cerodaphnia*, which are not as efficient a grazer as the much larger *Daphnia* spp. The limited impact of fish exclusion on water quality, in this case, is a short term effect – over a few to several years a lake without alewives would be invaded by *Daphnia* and water clarity would increase, as I have observed in other of my study lakes that do not contain any alewives.

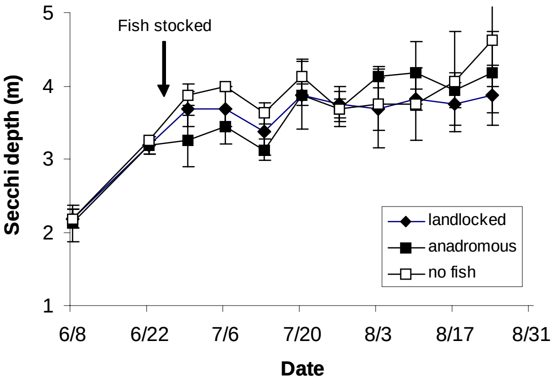

Figure 2. Secchi depth (a measure of light penetration) in the experimental mesocosms. Plotted are the mean +/- 1 standard deviation for each treatment.

***Objective 2*** – I now have a fully functional nutrient loading model. Key results revolve around how net nutrient loading changes as adult abundance and resulting YOY densities influence nutrient export by YOY alewives. Furthermore, estimates of loading are quite sensitive to adult mortality rates. The experiments performed in Linsley Pond in 2005 showed that YOY growth and mortality are density dependent (Figure 3). My results indicate that 1) at very high levels of adult returns (levels seen only in well-established runs) alewives load very large quantities of nutrients 2) at low levels of adult returns (1000s to 10000s) net nutrient loading is relatively low and there can even be a net export of nutrients when adult returns are low and YOY growth is high.

Nutrient excretion experiments performed in the spring of 2004 and 2005 provide, for the first time, an estimate of nutrient loading through direct excretion by an anadromous fish (Table 1). Estimates of the mass specific excretion rate were similar in both years.

Adult mortality rates are a key parameter for the nutrient-loading model. In collaboration with the CT DEP we estimated the adult mortality rate for anadromous alewives spawning in Bride Lake in the spring of 2005. Our estimate of mortality, around 60%, was similar to the estimate of around 50% found in Bride Lake by Kissel (1974).

***Objective 3*** – My work on the evolutionary origins of landlocked alewives is ongoing and results are expected by the fall of 2006.

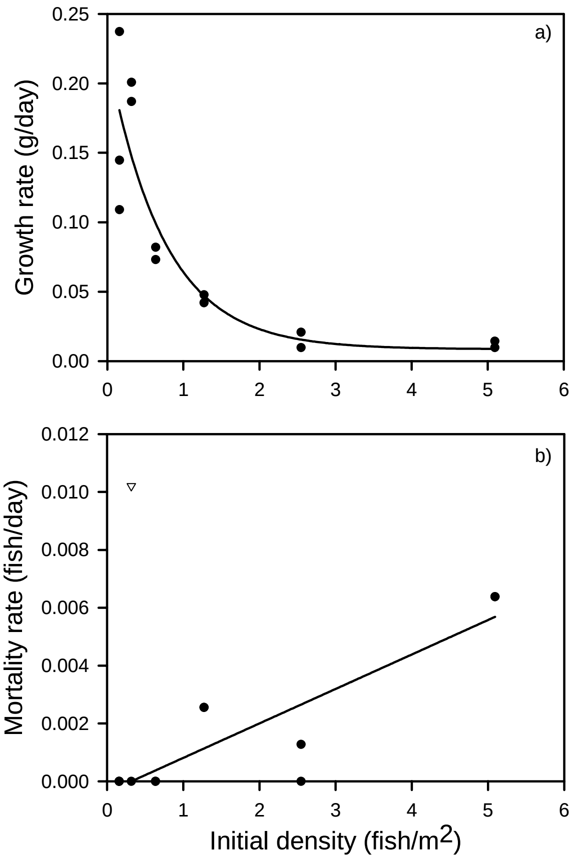

Figure 3. Patterns of density dependent growth (a) and mortality (b) from the Linsley Pond mesocosm experiment.

***Objective 4*** – The long-term goal is of this research is to evaluate the influence of recovering anadromous alewife populations on ecosystem function at the whole lake scale. Most of the work outlined in this proposal represents intermediate steps towards understanding the mechanisms through which effects of alewives could be manifest. In Rogers Lake and Linsley Pond, CT we have the opportunity to directly observe the effects of recovering alewives as fish ladders are put into those watersheds during the next year or two. Of particular interest are the contrasting current conditions of Rogers Lake and Linsley Pond: Rogers Lake has a resident population of landlocked alewives while Linsley Pond appears to have no current alewife population (although alewives were resident in the lake as recently as the 1960; Brooks and Dodson 1965). Effects of these restoration efforts will emerge over the next decade or more, but pre-manipulation data is essential to understand changes manifest at the whole lakes scale.

I am now in the third year of monitoring Linsley Pond, Rogers Lake, and four other regional reference lakes. The fish way installed below Linsley Pond will allow me to test the effects of anadromous alewives on ecological interactions in a lake that contained no alewives before the reintroduction. In the spring of 2006, over 3000 alewives passed the Branford Supply Ponds fish way and over 600 entered Linsley Pond. I expect to see effects on Linsley Pond this summer or next.