Report for 2004CT38B: The dual influence of Alewife, Alosa pseudoharengus, on inland water quality

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Report Follows

Introduction

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 (Hrbácek et al. 1961, Brooks and Dodson 1965, Carpenter et al. 1987) and because they transport, store, and recycle large quantities of nutrients (Kitchell et al. 1975, Durbin et al. 1979, Kitchell et al. 1979, Kraft 1993, Schindler et al. 1993, Vanni 2002). 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 (Carpenter et al. 1995, Carpenter et al. 1996). 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 (e.g., Schindler et al. 1993, Vanni 2002) or, in the case of anadromous fishes such as alewife, shad, and salmon, import large quantities of new nutrients into lakes (e.g., Donaldson 1969, Durbin et al. 1979), further increasing rates of eutrophication in the lakes they inhabit.

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 growing concern by local lake associations and land owners that the recovery of anadromous herring, in particular alewife, will cause water quality problems in their 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 anadromous 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 populations of alewives. Yet, river herring were a natural part of these ecosystems for thousands of years, and are an important prey for fish, birds and mammals (Loesch 1987). 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 alewife populations, which feed year round in lakes and ponds. 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; Graham 1956). 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.

With the removal of dams and the construction of fish passages, the recovery of anadromous alewives, in some cases, will occur in systems that currently contain landlocked populations. This *secondary contact* (when two species or populations that have had time to evolve separately come back into contact) has important implications for the reestablishment of anadromous populations. Where secondary contact occurs, anadromous populations may interbreed with landlocked populations – or they may not. Reproductive isolation, or the inability of co-occurring populations to interbreed, may evolve rapidly in populations where multiple traits are under divergent selection. For example, freshwater populations of threespine sticklebacks appear to have repeatedly evolved from anadromous populations (McKinnon and

Rundle 2002). If anadromous and landlocked populations are unable to interbreed, anadromous young-of-the-year will face strong competition with well-established landlocked populations. The ability of anadromous herring to compete with landlocked herring is unclear, but there are several interesting potential outcomes when populations with distinct life histories make secondary contact after decades of separation. Because of their greater number and/or because of local adaptations to life in freshwater lakes with low zooplankton densities (a result of the intense predation), landlocked alewives may strongly out compete young-of-the-year anadromous alewives. Alternatively, if young-of-the-year anadromous alewives can hold their own, the presumed advantages of greater growth and fecundity provided by migration to the coastal ocean could enable anadromous herring to rapidly increase in abundance and effectively swamp out landlocked populations. Finally, both landlocked and anadromous alewives could coexist in lakes, either ecologically, with distinct gene pools, or as a single gene pool with some individuals displaying an anadromous lifestyle and others remaining in freshwater their entire lives. Such polymorphisms (situations in which two or more traits are expressed simultaneously in a single population) with regard to anadromy are not uncommon among temperate fishes, especially salmonids (Northcote 1967).

Project goals and accomplishments:

The general goal of this research project is to test the ecological role and evolutionary history of river herring within the context of river restoration efforts. Lines of inquiry are designed to address both basic ecological and evolutionary questions while simultaneously providing information useful to local resource managers for restoration efforts. In the first year of this research I:

1) Developed methods in collaboration with the CT DEP for artificially rearing larval anadromous and landlocked alewives for research and restoration.
2) Tested for differences in the effects of anadromous and landlocked alewives in their first summer of life on water quality in Rogers Lake,
3) Collected much of the data required to develop a general model of nutrient loading by anadromous alewives,
4) Started collecting the landlocked and anadromous alewife samples required to evaluate the evolutionary origin of landlocked populations of alewives as a first step in attempting to understand the outcome of secondary contact between anadromous and landlocked alewife populations, and
5) Started monitoring Linsley Pond, Rogers Lake and two reference lakes to gather pre-manipulation data before fish ladders are installed and anadromous alewives recover into these lakes.

Below, I outline in more detail our accomplishments of our major goals.

Larval alewife aquaculture:

Because landlocked and anadromous alewives are nearly indistinguishable to the naked eye and extremely susceptible to mortality during capture and handling, I had proposed to use hatchery-reared alewives for our experiments in 2004 and 2005. At the time, there was limited expertise to draw upon because there had been few efforts to rear alewives in the lab. One goal of this effort, conducted in collaboration with the CT DEP, the Sound School (Hew Haven's Regional Vocational Aquaculture and Agriculture High School), and Sam Chapman at the

Waldoboro Shad Hatchery in Maine, was to develop alewife aquaculture to facilitate expanded research and restoration efforts.

Results from year one – Initial efforts to rear alewives were not successful. Our failure to rear alewives in captivity was disappointing, but perhaps not surprising – alewives are notoriously difficult to work with in the lab. We have, however, learned a considerable amount about rearing alewives. One of our biggest problems was rapid fungal formation that resulted in the loss of entire broods. By the end of the spawning season, we were making progress in reducing the loss of eggs to fungal infections, and we are confident that we can produce sufficient survival next spring to conduct our experiments. Because of our failure to rear alewives in the lab, experiments in 2004 were stocked later in the summer than originally planned, using alewives approximately 35-40 mm in length. These alewives were caught using a purse seine in lakes where the only alewives we could catch were from purely landlocked or anadromous populations. The disadvantages of using wild-caught alewives are that we were not able to control the genetic variability in our sample (it was likely high in our sampled fish, but ultimately unknown), and that we were unable to stock our experimental mesocosms until later in the summer than originally planned. The advantage was that we were able to capture and stock a sufficiently high density of landlocked and anadromous alewives to conduct our experiment.

Food web effects of anadromous and landlocked alewife:

The shift from an anadromous to an entirely freshwater lifestyle is a significant ecological shift that could strongly impact the potential for anadromous and landlocked populations of alewives to affect water quality through food web effects. There are widespread reports of water quality problems associated with landlocked alewife populations, but few if any reports of water quality problems caused by anadromous alewife populations (Stephen Gephard personal communication; Maine DEP fact sheet on alewife). The difference between landlocked and anadromous populations could emerge from two sources. First, there may be phenotypic differences between landlocked and anadromous alewives, such as feeding efficiency or gill raker size and spacing, which would increase the ability of landlocked alewives to suppress zooplankton populations. Indeed, given the large impact landlocked alewives can have on the size structure of zooplankton communities (e.g., Brooks and Dodson 1965), there is every reason to believe that there is strong evolutionary pressure on foraging ability in landlocked populations. Second, differences in ecological impacts might derive from the extended period of time landlocked alewives spend in lakes and ponds. Of particular importance is the presence of landlocked alewives in the spring of the year. In contrast to anadromous alewives, which do not feed in lakes and ponds in the early spring (Moring and Mink 2002), landlocked alewives can maintain high biomass year round and actively feed as water temperature increases and zooplankton populations emerge after the winter. Even relatively low predation in the spring or early summer can “cap” zooplankton populations at low densities through the summer, while extremely high levels of predation might be required to reduce zooplankton population late in the summer (e.g., Johnson and Kitchell 1996, Post et al. 1997, Post and Kitchell 1997). This pathway for food web impacts is not possible for anadromous populations because of their out migration and represents a potentially important phenotypic difference between landlocked and anadromous alewives.

Results from year one – In 2004 I conducted an experiment in Rogers Lake to test the effects of anadromous and landlocked alewives on food web structure and water quality. The goal of this experiment was to determine if anadromous and landlocked alewives in their first summer of life would have the same or different effects on zooplankton community structure and, therefore, on water quality. In the first week of June, 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 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. Final fish densities in the fish treatments were around 4 alewives per m^2 late August; about twice the density of alewives found in Rogers Lake at the end of August 2004. Densities were higher than found in Rogers Lake because survival of stocked fish was higher than expected. After a year of research I now know that survival rates of fish > 30 mm are higher than previously assumed. In each mesocosm we monitored temperature, dissolved oxygen, total nitrogen and total phosphorous concentrations, water transparency (secchi depth), zooplankton community structure, and phytoplankton biomass.

Figure 1. Experimental mesocosms in Rogers Lake in 2004.

To date, we have fully analyzed water transparency and phytoplankton biomass. Both show similar trends. Figure 2 shows mean secchi depth in each of the three experimental treatments. While there was some tendency for greater water clarity in the no fish treatments early in the experiment, there were no significant differences among the treatments across July and August. This indicates that 1) YOY anadromous alewives have similar effects on food web structure as anadromous alewives when found at the same densities, and 2) removing these pelagic planktivores from the Rogers Lake water column has little immediate impact on water clarity. The first result needs to be confirmed with lower densities of alewives (planned for 2005) and in lakes where landlocked alewives do not presently reside. 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

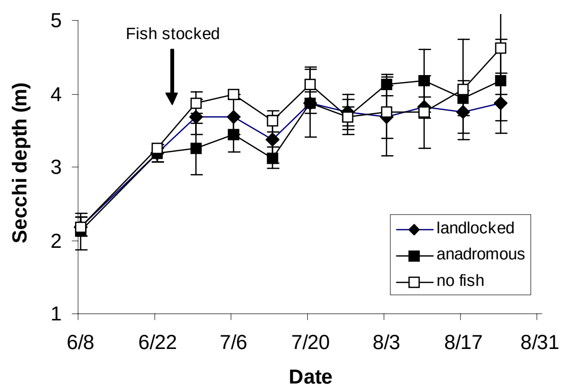

Figure 2. Secchi depth (a measure of light penetration) in the experimental mesocosms. Plotted are the mean +/- 1 standard deviation for each treatment.

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 (to this date) were *Cerodaphnia*, which are not as efficient grazers as are 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 we have observed in various lakes studied by Brooks and Dodson where alewives have recently gone extinct.

Nutrient loading model:

Direct nutrient loading is one of the multiple concerns for the reintroduction of anadromous alewives. Previous research suggests that large populations of anadromous alewives can have substantial effects upon water quality through nutrient loading (Durbin et al. 1979). The three mechanisms through which alewives may affect nutrient are 1) direct excretion of nutrients by spawning adults, 2) nutrient inputs by adult mortality and egg production, and 3) the export of nutrients by YOY alewives as they emigrate in the fall of each year (Figure 3). My goal is to produce a mass balance model to predict net nutrient addition to lakes, such as Rogers Lake, during different stages of anadromous alewife recovery. I am interested in a general model based on the trajectory of population recovery because some of the key parameters, particularly those related to YOY emigration, are likely a function of alewife density with a lake. 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 therefore will provide guidance for the management of lakes targeted for alewife restoration.

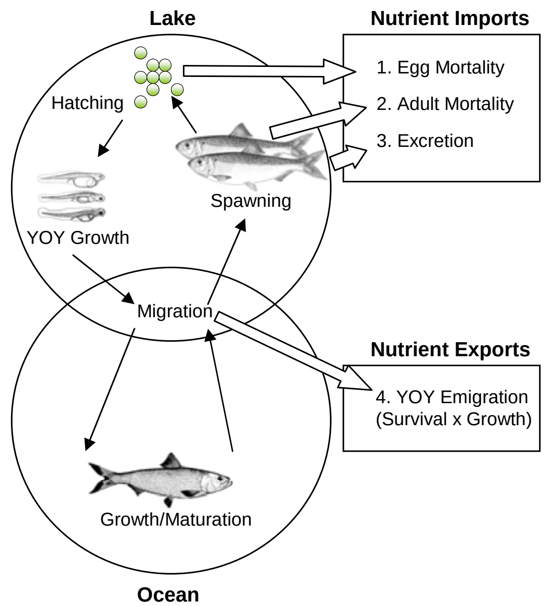

Figure 3. General life history of anadromous alewives highlighting sources of nutrient imports and exports.

Results from year one – In the spring of 2004, I worked with the CT DEP to directly measure nutrient excretion by anadromous alewives at Brides Lake, CT. 200 adult anadromous alewives were placed into the DEP's herring transportation truck (with a circulating water tank to minimize stress on the alewives) and samples were collected to measure concentrations of total nitrogen and phosphorus, nitrate, ammonia, and soluble reactive phosphorus at the beginning, middle (11hrs) and end of the experimental period (22hrs). Water for the experiment was dechlorinated water obtained from the New Haven drinking water supply. The nutrient samples have not yet been fully analyzed (I am waiting for a new nutrient autoanalyzer at Yale, expected in early November, to finish the sample analysis). This experiment will be repeated in 2005.

In addition to the amount of nutrients excreted by adults while in fresh water, the two key parameters needed to estimate nutrient loading are the number of adults entering a lake and the adult mortality rates. Adult mortality has been estimated to be around 50% in Brides Lake, CT (Kissel 1974), and a second study of adult mortality funded by the CT DEP is currently underway (Stephen Gephard, personal communication). Estimates of adult mortality are quite time consuming and these are, likely, the best estimates we will have for anadromous alewife populations. As part of the alewife restoration efforts on Rogers Lake, the CT DEP is planning to put in place a fish counter on the fish ladder. Over the course of the next several years, this fish counter should provide an accurate estimate of the number of anadromous adults entering Rogers Lake. Using allometric relationships between adult alewife size and fecundity, and estimates of the number of returning adults, we will be able to predict the mass of nitrogen and phosphorus added to Rogers Lake in eggs. Using mortality estimates (even though quite rough) we will be able to provide estimates of the mass of nitrogen and phosphorus added to Rogers Lake through adult mortality.

The mass of nutrient export by juveniles is perhaps the most important and most difficult parameter to estimate for our mass balance nutrient budget because it requires both estimates of adult immigration and of the mean size and number of YOY leaving a lake. Both the number and mean size of YOY depend, in part, upon the timing of emigration by alewives. My lab spent a considerable amount of time and effort this summer studying growth and mortality dynamics of YOY anadromous alewives in Brides Lake. We obtained estimates of densities of alewives in Brides Lakes through the summer using a purse seine that samples 100 m^2 of lake area. To increase the reliability of our estimates, sampling was conducted using replicate purse seine sets at night when alewives are higher in the water column and maximally dispersed. A subset of fish was measured to estimate length and mass. Figure 4 shows estimates of YOY alewife densities, body size and an estimate of potential phosphorus export from Brides Lakes in 2004. The final sampling date shown in Figure 4, 29 September, was the first possible date of alewife emigration from Brides Lake because there was no flow out of Brides Lake into Brides Brook between the middle of the summer and 28 September (Brides Brook was dry during that period). Densities on 29 September likely represent a "best" estimate of the number of alewives leaving Brides Lake. Sampling planned for October should further resolve emigration patters in 2004.

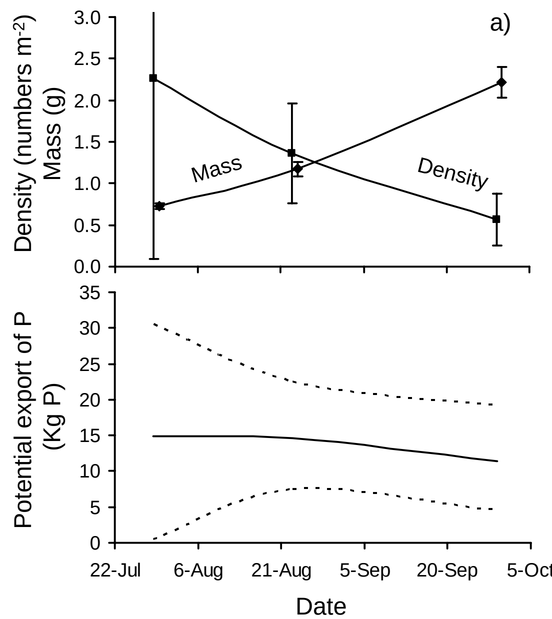

Figure 4. a) Growth, density and b) biomass trends for YOY alewives in Brides Lake, CT, in 2004. The error bars for density and mass are one standard error. Potential export of phosphorous is the product of mass times density times lake area (18.2 ha) times an estimate of percent P (0.42% of wet wt). The dotted lines provide the range biomass estimates possible based on error estimates around mass and density. Biomass, and therefore the potential for nutrient export by YOY, likely peaked near the end of August

The general model for nutrient loading is nearing completion. I have already produced a basic population model and parameterized it using general assumptions about mortality and emigration. The next step in model development is to include density-dependent feedbacks in YOY growth and survival. Preliminary analyses suggest that density dependence among YOY has the greatest potential to influence net nutrient loading.

Evolutionary origins and secondary contact:

One major 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. The origin of landlocked herring is not clear. We are collecting alewives in watersheds where both anadromous and landlocked populations are found (e.g., above and below a dam) to test two different models of the evolution of landlocked alewives. At one extreme, landlocked alewives may have evolved in just one or a few populations and humans may have spread them across the landscape. The alternative model is that landlocked alewives have evolved repeatedly in each watershed as dams eliminated access to the ocean. It is likely that aspects of both models are valid, but determining the relative importance of each mode of life history evolution is important to answering residents concerns.

Data on the evolutionary origins of landlocked alewives also provides information on the possible outcomes of secondary contact. The level of relatedness has important implications for whether anadromous populations may interbreed with landlocked populations in lakes where secondary contact may occur. If anadromous and landlocked populations are unable to interbreed, anadromous young-of-the-year will face strong competition with well-established landlocked populations which could hinder restoration efforts and exacerbate nutrient loading (competition would reduce growth rates, increase mortality rates, and reduce the export of nutrients from the lake). Alternatively, both landlocked and anadromous alewives could coexist in lakes with a single gene pool with some individuals displaying an anadromous lifestyle and others remaining in freshwater their entire lives. Both the evolutionary origins and potential outcome of secondary contact can be addressed using molecular genetic markers that provide powerful tools for reconstructing historical population processes (Avise 2000). Mitochondrial DNA (mtDNA) is commonly used to examine population differentiation and to investigate population-level genealogical relationships. Nuclear microsatellites may be used to assess genetic diversity within populations and to estimate rates of gene flow between populations.

Results from year one – In 2004 we collected landlocked alewives from > 20 populations in CT (including Rogers Lake) and expect to receive fish from the Finger Lakes, Laurentian Great lakes, and the St Crox watershed in Maine before December. We also collected anadromous alewives from about 10 populations in CT and expect to collect fish from another 10-15 populations next spring. Initial analyses are planned for the winter of 2004-2005.

Lake monitoring:

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.

Results from year one – In the summer of 2004, we initiated basic limnological sampling of Linsley Pond and Rogers Lake both to complement our experimental research in Rogers and Linsley, and to provide data on ecosystem condition prior to alewife recovery. We also started sampling two lakes, Pattaganset and Quonnipaug, which will provide reference systems against which future changes in Linsley and Rogers can be compared. In each lake, we measured zooplankton community structure (including body size), secchi depth, chlorophyll *a* concentrations, the abundance of bluegreen algae (cyanobacteria), and standard physical-chemical parameters (TN, TP, DO, temperature, etc.). TN and TP were measured in mixed epilimnetic samples taken through the summer, and will be measured from the entire water column early in the spring during spring mixis. We collected samples of the phytoplankton community, but will only enumerate phytoplankton community structure (biovolume) if the chlorophyll *a* and bluegreen algae data suggest further analyses is warranted. Sampling was conducted every two weeks from the end of May through September, and will be taken once a month when lakes are ice free from Oct. – April.