Determining the Effects of Landlocked Alewives on Anadromous Alewife Restoration

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Abstract:

Dam removal and fish passage projects are a critical component of anadromous alewife restoration, reconnecting runs to prime spawning habitat in coastal lakes. However, landlocked alewife populations have become established in many coastal New England lakes. The effects of landlocked alewives on anadromous alewife restoration are currently unknown. This proposed research examines these effects in Rogers Lake, Connecticut. A decade-long plan to restore anadromous alewife access to Rogers Lake was recently completed, and the first spawning adults will have access to the lake in spring 2015. Rogers Lake once hosted one of the largest anadromous alewife runs in Connecticut. Thus, effective restoration could substantially bolster regional alewife production. Our specific aims are to combine juvenile density estimates with genetic assignments to determine the abundance of anadromous alewives, landlocked alewives, and anadromous-landlocked hybrids in the lake following restoration and to use otolith-based aging to determine spawning time for anadromous, landlocked, and hybrid alewives to assess the effects of spawning time overlap on rates of hybridization. We have spent two years monitoring spawning time and genetic diversity of anadromous and landlocked alewives before restored access. For the two-year duration of the proposed research, we will sample anadromous adults entering the lake and juvenile alewives in the lake to monitor abundances, spawning times, and hybridization rates. The Rogers Lake restoration project provides a unique opportunity to follow anadromous alewife recovery from its onset. This project will provide valuable information for future restoration projects where contact between anadromous and landlocked alewives will occur.

Project Description

(a) Priority RCN Topics addressed

This proposed research directly addresses **RCN Topic 7: Identify threats to NE species of greatest conservation need**. The most productive alewife spawning and juvenile rearing habitats in the Northeast occur in coastal lakes, and many of these lakes now contain landlocked alewife populations (see **Appendix 1**). This project will examine the impact of landlocked alewives on anadromous alewife restoration. This project will provide methodologies to help attain successful anadromous alewife restoration in lakes where landlocked alewives have become established.

(b) Project Location

This project will take place in **Rogers Lake (Old Lyme, CT)**. The final fishway on Mill Brook, at the outlet to Rogers Lake, was completed in 2014. With this fishway built, anadromous alewives will again have access to Rogers Lake in spring 2015, where they will encounter the landlocked alewives currently in the lake.

(c) Start and End Dates: January 1, 2016 – December 31, 2017

(d) Goal and Major Objectives

The alewife (*Alosa pseudoharengus*) can be considered a 'Jekyll and Hyde' of fisheries management. Its anadromous form was once an important fishery resource along the Atlantic Coast of North America; however, anadromous alewife populations have declined significantly, especially since the mid-1960s (Limburg and Waldman 2009, ASMFC 2012, Palkovacs et al. 2014). Abundances are now so low that the anadromous alewife is considered a Species of Concern by NMFS and was recently considered for protection under the US Endangered Species Act (ESA). In contrast, the landlocked alewife, most famous for its colonization of the Laurentian Great Lakes, is widely considered to be a harmful invasive species due to its negative impacts on water quality and native fish diversity (Stewart et al. 1981, Mills et al. 1995).

In Connecticut, where the two life history forms co-occur, the anadromous form is considered to be 'native' while the landlocked form is considered to be 'invasive' (Jacobs and O'Donnell 2002). Therefore, management efforts directed towards anadromous alewife runs focus on restoration and recovery, whereas management efforts directed towards landlocked populations focus on population control and limiting spread to other lakes. Despite being managed as a separate species, genetic data show that landlocked alewives in coastal Connecticut lakes are recently diverged from downstream anadromous populations (Palkovacs et al. 2008), and lake sediment cores show that this transition occurred at the time of widespread dam construction by the first European colonists in New England (Twining and Post 2013).

To restore anadromous fish populations throughout the state, Connecticut requires evaluation of fish passage as a mandatory part of dam relicensing on streams with anadromous fish runs (see **Appendix 2**). Many dams that are targets for restoration projects separate above-dam landlocked alewives from below-dam anadromous populations. One such project involves a series of fishways on three dams on Mill Brook, a tributary of the Connecticut River with a locally evolved landlocked population at its headwaters in Rogers Lake. When anadromous alewives had access to Rogers Lake, this system likely supported one of the largest anadromous alewife runs in Connecticut. The final fishway on Mill Brook, at the outlet to Rogers Lake, was completed in 2014 (Fig. 1). With this fishway built, anadromous alewives will again have access to Rogers Lake, where they will encounter the landlocked alewives that currently inhabit the lake.

The goal of this proposed research is to determine the impact of landlocked alewives on the outcome of anadromous alewife restoration in Rogers Lake. Our specific aims are **(1)** to combine juvenile density estimates with genetic assignments to determine the abundance of anadromous alewives, landlocked alewives, and anadromous-landlocked hybrids in the lake following restoration, and **(2)** to use otolith-based aging to determine spawning time for anadromous, landlocked, and hybrid alewives to assess the effects of spawning time overlap on rates of hybridization.

(e) Methods

Field sampling

Each spring, we will deploy a trap net at the outlet of the Rogers Lake fishway to temporary hold all anadromous adults entering the lake. Before releasing adults into the lake, we will collect information on length, weight, sex, and take a fin clip for use in genetic analysis. If anadromous adults do not reach the lake via the fishway, we will collect adults at a downstream site (Mary Steube), take data and fin clips, and truck the adults to Rogers Lake. This way, we can ensure that anadromous adults do make it to the lake to spawn during the period of this study. We anticipate 500-1000 adults will enter the lake each year during the duration of this study.

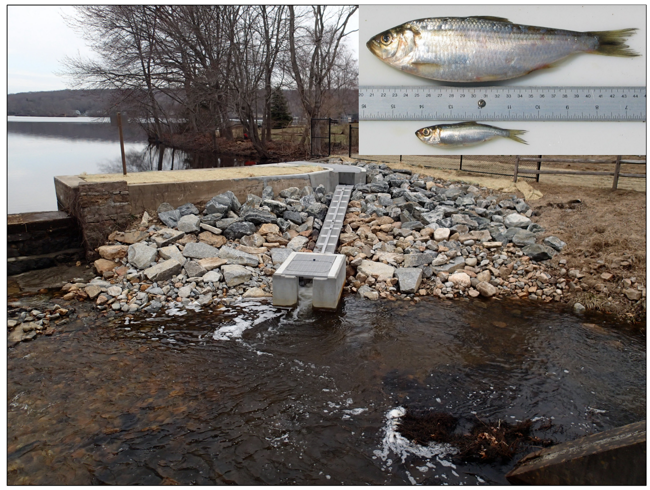

Fig. 1: A recently completed fishway will allow anadromous alewives (inset, top) from Mill Brook to once again access the spawning habitat in Rogers Lake, which is currently inhabited by landlocked alewives (inset, bottom) that were isolated in the lake when the dams were constructed.

We will purse seine Rogers Lake monthly from June – August of each year to estimate the density of juvenile alewives in the lake and to collect specimens for genetic analysis and analysis of spawn timing. Alewives will be sampled using a pelagic purse seine (Post et al. 2008). The seine (composed of 3.18-mm mesh) is 4.87 m deep and 35.36 m long and encircles an area of 100 m^2. We will conduct at least five replicate net sets in different parts of the lake to estimate density. Our goal is to collect 1000 juvenile alewives from the lake each year for genetic analysis. This sample size is necessary to detect hybridization at rates <1%. Such low levels of hybridization may be likely when anadromous alewives first recolonize the lake in relatively small numbers.

Genetic assignment

We have identified a large number of single-nucleotide polymorphism (SNP) loci in alewife and developed a panel of 96 locus-specific assays for use on a high throughput SNP genotyping system using 96.96 Dynamic Arrays and the EP1 detection system (Fluidigm Corp.). This assay panel is highly informative for alewife populations in New England and will be used for a variety of purposes, including identifying anadromous, landlocked and anadromous-landlocked hybrids in the Rogers Lake restoration project.

To generate this panel of alewife SNP loci, we used next generation DNA sequencing technology and selected 48 fish from 18 populations representative of the genetic lineages throughout the species geographic range (McBride et al. 2014, Palkovacs et al. 2014). We performed two double-digest RAD sequencing (ddRAD; Peterson et al. 2012) runs on a MiSeq instrument (Illumina Inc.). ddRAD sequencing is a genome-reduction technique that uses restriction enzymes to create DNA fragments with identical fixed endpoints for sequencing (Peterson et al. 2012). Sequencing data were processed using Stacks (Catchen et al. 2013). A total of 54 million DNA sequences were obtained from these sequencing runs, after filtering out low quality sequence reads, and a total of 33868 unique gene regions identified. Of these, 4934 genes contained exactly one SNP. SNPs were further selected for assay design using Stacks, and the 96 best assays were chosen for the final panel. We are now genotyping a much larger number of samples to estimate population-level allele frequencies (for anadromous and landlocked populations) and to determine power for assignment to life history form and for the identification of hybrids.

In order to identify hybrids, we will follow the method implemented by Hasselman et al. (2014). Using genotype data from confirmed purebred anadromous and landlocked parents (i.e., sampled in 2013 and 2014, before contact), we will first simulate genotype data for parental anadromous and landlocked alewife and various hybrid classes (F1, F2, and backcrosses) with HYBRIDLAB v.1.0 (Nielsen et al. 2006). We will then analyze the simulated data using two Bayesian methods (STRUCTURE v.2.3.3 (Pritchard et al. 2000, Falush et al. 2003) and NEWHYBRIDS v.1.0 (Anderson and Thompson 2002)) to determine the appropriate genetic admixture threshold (*Tq*) for designating juvenile specimens from Rogers Lake as either purebred anadromous, purebred landlocked, or F1 hybrids. We will then use this output to generate classification rules that will then be applied to the empirical juvenile genotype dataset to assess the frequency of anadromous, landlocked, and hybrid alewives in Rogers Lake starting in 2015. The frequency of each form (anadromous, landlocked, and hybrid) will be combined with juvenile density estimates (see Field Sampling, above) to yield estimates the total abundance of each alewife form in Rogers Lake.

Spawning time

Spawning time differences are important for whether the anadromous and landlocked populations interbreed. If there is little or no overlap in spawning time, the potential for hybridization will be minimal. If spawning time does overlap, hybridization may be likely. We will use otolith-based aging of juveniles to determine spawning time. From the sample of juvenile alewives collected from the lake each year, we will select 120 fish (targeting 40 anadromous, 40 landlocked, and 40 hybrids), previously identified based on genetic assignments. Sagittal otoliths will be removed from each fish and daily growth increments will be counted to determine hatch time for each fish. Spawning times will be estimated by adding developmental time in the egg to hatch times (Edsall 1970). We predict that anadromous alewives will spawn earlier in the year compared to landlocked alewives but that hybrids will display intermediate spawning time. Thus, the onset of hybridization – if it occurs – is expected to increase spawning time overlap, which may, in turn, further increase rates of hybridization.

(f) Measurable Products and Outcomes

The proposed research will produce both immediate outcomes that support river herring conservation and new information that will help restoration planning into the future. First, this project will enable us to track the Rogers Lake restoration project not just in terms of the number of spawning adults entering the lake but also in terms of the number of juveniles being produced. Knowing both adult returns and juvenile production will enable us to understand what life stages and habitats are limiting population growth, which is a key question for river herring recovery. Second, this project will allow us to determine whether additional restoration actions are needed to stimulate anadromous alewife recovery in Rogers Lake. For example, a large landlocked population may outcompete a small colonizing anadromous population. If so, additional management actions may be needed to jumpstart the restoration. Third, this project will help inform future restoration projects such as the one planned for nearby Pattagansett Lake (East Lyme, CT). Results of this research will be disseminated via peer-reviewed publications, presentations at regional and national conferences, direct interactions with resource managers and local stakeholder groups, and media outlets. This restoration project has already been covered by the New York Times (Nyquist 2014). The PIs have a long track record of publishing in high-quality scientific journals, presenting at conferences, and educating local stakeholders and the public.

(g) Budget

Personal Service	**Year 1**	**Year 2**	
Graduate Student Salary (for genotyping)	$5,832	$6,007	
Fringe Benefits	$146	$150	
Health Insurance	$1,295	$1,359	
Graduate Student Fees	$4,862	$5,348	
Supplies and Materials			
Genotyping	$22,000	$22,000	
Indirect Cost (26%)	$7,274	$7,321	
TOTAL AMOUNT REQUESTED	**$41,409**	**$42,185**	**$83,594**

Matching Funds			
PI salary (Palkovacs)	$24,000	$24,000	
Graduate Student Salary (for otolith aging)	$9,000	$9,000	
CT DEEP Employee Salary (for field sampling)	$9,000	$9,000	
TOTAL MATCHING FUNDS	**$42,000**	**$42,000**	**$84,000**

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Individual Qualifications

Eric Palkovacs has over a decade of experience working on river herring ecology, evolution, and conservation. He has published twelve peer-reviewed papers on river herring since 2008, including papers on population genetics and the ecology and evolution of landlocked populations. He has organized and contributed to numerous working groups including the Stock Structure Working Group (held as part of the river herring ESA Review) and the River Herring Technical Expert Working Group (organized by NMFS and the ASMFC). He has maintained active collaborations with Post and Gephard since 2005, including the Rogers Lake restoration project. He has collaborated with Hasselman and Garza since 2012 on several projects focused on applying novel genetic markers to river herring conservation and management

David Post has over two decades of experience studying fish and food webs. He has published over 25 peer-reviewed papers on river herring ecology and evolution since 2008. Post has participated in a number of regional river herring conservation and management initiatives, including advising the NFWF River Herring Program. Post lab research on river herring has been funded by the US EPA, National Science Foundation, and the CT Long Island Sound Fund. Post has collaborated with Gephard since 2004 and Palkovacs since 2005 on a number of questions related to river herring conservation, management and restoration, including studying the recovery of river herring in two lake systems, including the ongoing project at Rogers Lake.

Stephen Gephard has been working on river herring since the 1970s, studying their behavior, documenting their runs in Connecticut, managing the fisheries and advocating for their conservation. He supervises the State of Connecticut's (DEEP) Diadromous Fish Program and was instrumental in the closure of all river herring fisheries in the state in 2002, the first such statewide closure in the country. He serves on the River Herring Sub-committee of the Connecticut River Atlantic Salmon Commission, the Northeast River Herring Working Group, and the River Herring Technical Expert Working Group (NMFS/ASMFC). In 2012, he participated in the River Herring Stock Structure Working Group as part of NOAA's Endangered Species Listing Review for river herring. Gephard has been a collaborator with Palkovacs and Post on numerous river herring research projects, including projects at Rogers Lake and Bride Lake, and has co-authored several papers in respect to that work.

John Carlos Garza has over 25 years of experience in population genetic research of animals, the last 15 working primarily with marine and anadromous fishes, including salmon, trout and sturgeon. He has served on numerous working groups and expert panels related to anadromous fish management. He began working on herring in 2014, and is a member of the River Herring Technical Expert Working Group. He is a co-PI, with Palkovacs, on a collaborative project funded by the ASMFC to further develop and apply genetic stock identification methods for river herring. This collaboration has already yielded a large number of novel genetic markers and assays for use with these species.

Dan Hasselman has over a decade of experience applying genetic tools to the management and conservation of anadromous shad and river herring. Since 2008 he has published 10 peer-reviewed research articles on these species, including papers on population genetics and hybridization. He worked with Palkovacs and others to provide key genetic information to the River Herring Stock Structure Working Group as part of the river herring ESA Review. Hasselman is the Chair of the Genetics Sub-Group and serves on the Ecosystem Integration Committee of the River Herring Technical Expert Working Group and is a member of the River Herring Advisory Panel for the Mid-Atlantic Fishery Management Council.

Appendix 1: Regional applicability

A question was raised about whether landlocked alewives are found only in Connecticut and a few other locations. In fact, there is a broad geographical distribution of landlocked alewives within the range of anadromous alewife: **Maine** (Smith 1985), including a high profile conflict within the St Croix watershed (Willis 2009); **New Hampshire** (Smith 1985); **Massachusetts** (Hartel 1992); **Connecticut** (Palkovacs et al. 2008); **New York** (Smith 1970); **Pennsylvania** (Hendricks et al. 1979, Denoncourt et al. 1975, Tilmant 1999)**, Virginia** (Hocutt et al. 1986; Jenkins and Burkhead 1994), and **North Carolina** (Hasselman et al. 2014). It is unknown whether the presence of landlocked alewives is a biological obstacle to the restoration of anadromous alewives. There are socio-political concerns about this issue including the fear by some that anadromous alewives will displace landlocked alewives and that some deleterious impacts of landlocked alewives may be erroneously attributed to restored populations of anadromous alewives (Willis 2009). We know of several examples, both in Connecticut and elsewhere, where local residents have opposed alewife restoration due to misunderstandings of their ecological impact. In order to promote the restoration of anadromous alewives, the feeding ecology of the two forms and their interactions must be studied. Insofar as the results of this study will provide solid scientific data to address citizen concerns, we feel this project will greatly impact the management of the species across the Northeast.

Because virtually nothing is known about how interactions with landlocked alewives will impact anadromous alewife recovery, the River Herring Technical Expert Working Group has designated anadromous-landlocked alewife interactions as a major information gap that needs to be addressed to inform anadromous alewife recovery efforts (River Herring Technical Expert Working Group 2015). This working group was established by the National Marine Fisheries Service and the Atlantic States Marine Fisheries Commission in response to the Endangered Species Act Petition for alewife and blueback herring and has a broad geographical perspective.

In addition to informing restoration activities involving interactions between anadromous and landlocked alewives, the proposed research will inform anadromous alewife restoration across the Northeastern Region by aiding the development of new genetic tools to track restoration efforts and providing information on genetic diversity and genetic viability of newly re-established anadromous populations. A major benefit of this project that can be applied broadly across the region is the detailed tracking of the temporal sequence of alewife recovery from the onset of a newly-built fishway. This project provides a rare opportunity to observe all stages of recovery, and the lessons learned can be applied to anadromous alewife restoration across the region.

A comment by one reviewer pointed out the fact that this is only one site in only one state and questioned whether this study has regional importance. We recognize that this is only one site but feel that is a realistic constraint for a small study with limited funds. Nonetheless, science is full of examples of one-site studies that have proven valuable at regional or global scales. Certainly many of the studies of anadromous alewives, salmon, shad or catadromous eels from one Northeastern site have added to our knowledge of the species and guided management throughout the Northeast or East Coast. We believe that the lessons learned through the truly unique opportunity presented by the Rogers Lake restoration will be transferrable to watersheds across the region.

In addition to its scientific value, the Rogers Lake restoration project has direct importance for regional alewife restoration. Rogers Lake represents a critical component of the regional alewife metapopulation. Highly productive coastal lakes are critical for the regional persistence of anadromous alewives because they produce many juveniles that, through straying, help to demographically support other populations across the region. Large lakes such as Rogers therefore stabilize the regional metapopulation against ongoing threats such as bycatch in marine fisheries and climate change (Palkovacs et al 2014). Therefore, the restoration of Rogers Lake is likely to have spillover effects that directly benefit anadromous alewife recovery in nearby states that have suffered major declines such as Rhode Island, New York and Massachusetts.

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Appendix 2: Effectiveness of fishways as a restoration tool

A question was raised by reviewers about whether fishways are an effective restoration tool, in particular whether juveniles can successfully emigrate from ponds where fishways have been built. We see no evidence whatsoever that juvenile river herring that hatch in ponds upstream of dams with fishways fail to leave the pond. If that were true, we would stop building fishways because there would be no benefit to the anadromous population. We know of no instances where young of year do not leave the pond except for during some dry years in Bride Brook (East Lyme, CT) where the Town pumps its wellfields so hard that the pond drops and the outlet dries up. But in those cases, the YOY depart when the pond refills, even if in January. That pond has not suffered recent year class failure. In most cases, YOY river herring pass over the spillway to depart when it is time for them to leave. Our research shows that it is usually upon the depletion of key zooplankton prey species. There are several Connecticut sites (Mianus Pond in Greenwich, Bunnells Pond in Bridgeport, and Gorton Pond in East Lyme) where the YOY actively use the steeppass fishway to leave the pond and move downstream, and they use it readily.

YOY alewife dipnetted from Bunnells Pond Fishway during emigration.

Furthermore, landlocked alewives are physically able to leave the lakes at any time as well. The idea that somehow these fish were 'trapped' in lakes when dams were built is false. Dams without fishways prevent fish from entering lakes but not leaving lakes. Landlocked alewife populations have evolved multiple independent times in response to the absence of upstream (not downstream) movement (Palkovacs et al. 2008). Water goes over the dam, so can the fish. Dams bock upstream gene flow from returning anadromous adults. It is possible that landlocked alewives could evolve only after dams were built because the landlocked form can only prosper in the absence of anadromous alewives. The results of our research should shed some light on that hypothesis.

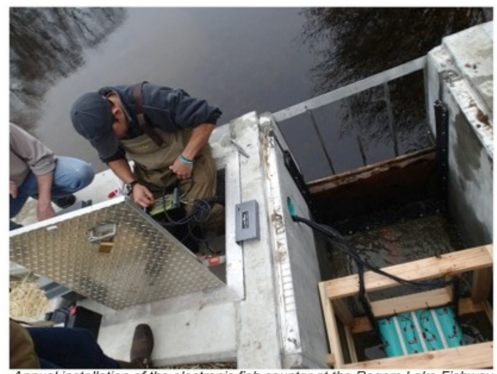
Landlocked alewives have evolved multiple morphological and ecological differences that make them distinct from anadromous alewives, including differences in gill raker spacing, gape width, prey size, and habitat use (Post et al. 2008, Palkovacs and Post 2008, 2009, Jones et al. 2012). Nonetheless, landlocked and anadromous alewives are similar enough to be very close competitors. Temporal and spatial overlap in spawning times may allow for hybridization. Understanding the interactions of the two forms will guide our expectations for alewife restoration in such watersheds and also expand our understanding of alewife reproduction and freshwater feeding ecology in general. The public is concerned about the feeding ecology of anadromous alewives when restored to a lake where they have been absence for many years. The conflict on the St. Croix River in Maine is a case study on how widespread misinformation related to such concerns can effectively block effective anadromous alewife restoration (Willis et al. 2009). Therefore, the knowledge gained through his project help managers communicate to the public about these issues, thereby helping to reduce future conflicts.

Mill Brook, which flows out of Rogers Lake) is an index stream for the CT DEEP and is carefully monitored, annually. It has an electronic fish counter at the top of the first fishway (Mary Steube Fishway) and fish are sampled from the exit trap. Count data are compiled annually and age/growth/and genetic data have been collected starting in 2015.

Electronic fish counter and weir at the exit of the Mary Steube Fishway.

The extent to which anadromous alewives can reach Rogers Lake depends on the run size. When run sizes at the first fishway exceeded 10,000, we were seeing alewives at the base of the Rogers Lake dam (before the Rogers Lake Fishway was built). Since this time, run sizes have declined severely, perhaps due to marine causes. This spring, only 134 alewives showed up at the first fishway. All fish were netted, genetically sampled, and trucked to Rogers Lake for release for this study. Trucking is not our preferred method, but it is a fallback plan that allows the study to move forward. In future years, we intend to continue to operate all three Mill Brook fishways and document passage. There will be a trap at the top of the Rogers Lake fishway so all fish that enter the lake of their own volition will be counted via another electronic fish counter and also genetically sampled. This dual approach (fishway passage and deliberate trucking if passage fails) allows us to know not only how many fish enter the lake but also *which* fish enter, enabling the identification of progeny through genetic parentage analysis.

Connecticut DEEP has great experience in run monitoring and the partnership between it and researchers from the University of California and Yale University in respect to genetics and trophic ecology, will result in much gained knowledge about landlocked-anadromous interactions, feeding ecology, restoration mechanisms and refinement of standard practices, and run monitoring.



Annual installation of the electronic fish counter at the Rogers Lake Fishway

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