Personal Statement

Alewives have nothing to do with either beer or marriage, but are a species of fish. That is usually the first thing I make clear when explaining my research to people. Most people have never heard of alewives and if they have, what they have heard is often not altogether positive. Alewives developed a bad reputation as an invasive species in the Laurentian Great Lakes. However, in their native range along the East Coast, where I work, alewives are an important keystone species and support everything from striped bass to coastal breeding birds, such as ospreys and bald eagles. East Coast alewives are in a decline that began centuries ago when colonists dammed the region's streams. Today, they are listed as a federal species of concern. Part of my job as an environmental scientist is to explain these nuances to the public. But before I launch into my full alewife spiel, I should back up and explain how I began studying alewives.

As an undergraduate, I explored environmental activism as well as environmental science before deciding to follow the latter as a career path. I joined the Student Environmental Coalition in my freshman year and led the group during my junior year. As president, I organized a regional environmental conference for over 200 students, re-established our faculty advisory board, wrote a series of op-eds for student newspaper, and created and managed a new website. I also educated my fellow students about making their daily habits around my campus more sustainable while working for the Office of Sustainability during my junior and senior years. While these positions kept me very busy, they left me feeling discouraged. I knew that none of my hours of hard work organizing letter-writing campaigns or distributing energy efficient light bulbs would ever make a meaningful difference in solving large-scale environmental issues like climate change.

As a result, I decided to focus on local environmental issues. At the end of my junior year I founded Service & Hands On Restoration Ecology (SHORE), a community service group focused on local habitat restoration projects. My work for SHORE included coastal cleanups, dune-grass planting, and invasive species removal projects around Connecticut. In these projects, I collaborated with area universities and high schools, local environmental organizations, and church groups. Through the partnerships I formed, I enabled students to engage with community members from different educational and socio-economic backgrounds who all share a common concern for local environment issues. I found this type of hands-on, local environmental work more fulfilling than my previous activism efforts because my fellow students and I could see the visible difference we were making in our community.

At around the same that I was becoming frustrated with the results of my environmental activism efforts, I joined my current ecology lab. I soon discovered a passion for scientific research while working on my undergraduate senior thesis on the ecological history of alewives in coastal Connecticut. I found that I was more interested in the underlying science behind environmental problems than in law or policy and decided to pursue my PhD in ecology.

Through my undergraduate research, I realized that I could personally contribute more to solving environmental issues through science than through advocacy. After completing my senior thesis, I presented my findings to several lake associations, municipal governments, and conservation groups based near my study sites. In the past, lakeside residents throughout Connecticut were worried about the effects that anadromous alewife restoration might cause eutrophication in their lakes. My research demonstrating that anadromous alewife were historically native in the region's lakes and that nutrient loading from fishes was minor compared to that from human activity has not only helped assuage lakeside residents' fears, but has also converted them into strong advocates for alewife restoration in their watersheds. This experience shaped me into a strong believer in the necessity of sharing my findings with the general public. I was also recently invited to serve as a scientific consultant on anadromous fish restoration projects for a major regional environmental organization. Encouraged in part by my research, this group is now collaborating with the state to build a fishway over the last remaining dam blocking anadromous fish passage in one of my case study watersheds. This opportunity to put my own research to use has been the highlight of my career as an ecologist thus far.

In my doctoral studies, I will continue to engage with the public and policy-makers as I have in the past by sharing my research findings with local citizen stakeholders, conservation groups, and regional environmental managers. I will also specifically target First Nations tribes involved in anadromous fish restoration projects in my research. I will collaborate with tribal officials in my study regions in compiling information about pre-European contact land use, anadromous fish densities, and fishing pressure. I also intend to create opportunities for tribal members to participate in the hands-on fieldwork portions of my research, including coring lakes. I will then in turn share my findings and data with my tribal collaborators.

In addition to my research-based outreach efforts, I aspire to affect positive change by training the next generation of environmental scientists and leaders. Twice a month, I teach a class on environmental history and its legacy today to a group of students at a predominantly minority (55% African American, 30% Hispanic) public high school. After meeting with my students in the classroom for a lecture and discussion, I take them out into the field where they can learn about environmental history hands on. Though my students sometimes struggle to pay attention and stay engaged in the classroom, once we get outside their brains switch on and they fire question after question at me. This experience has taught me just as much about teaching as I have taught my students about environmental history. I have learned the importance of walking my students through complex concepts piece by piece. I have also learned how to trick my students into figuring out the answers to their own questions using their existing knowledge.

In addition to my work with high school students, I have taught and mentored graduate and advanced undergraduate students while serving as a teaching fellow for a field ecosystem ecology course. In addition to leading weekly field exercises and discussion sessions, I designed and supervised a major freshwater mesocosm experiment on trophic cascades. Leading this experiment provided me with the chance to direct and manage a large collaborative research project. In addition to this class project, I also helped my students design and conduct their own independent projects. I took on the role of research advisor and provided my students with constructive criticism and suggestions on how to develop exciting, yet manageable class projects.

Since graduating from college, I have continued to stay involved with my undergraduate Environmental Studies Program by serving as an alumna mentor to students with interests in ecology and environmental science. I provide mentees with advice that includes how to get involved in research and how to find an advisor that match their interests and personality. I have especially enjoyed helping students find research areas that they are passionate about as I am about aquatic ecology. In addition to mentoring, I developed and organized a career exploration discussion series within the Environmental Studies Program, which allows undergraduates to connect with professionals in environmental careers ranging from academia to public policy to business. This has allowed me to help other students discover which path they want to take to become environmental problem-solvers.

Ecology is my passion and path to environmental problem solving. The NSF GRFP will allow me to pursue my PhD in ecology and develop into a leader in environmental science.

Summer 2009-Summer 2010
A Study in the Mechanism of Eco-evolutionary Feedback in Freshwater Systems

As an undergraduate research assistant, I worked in on several projects focused on the ways that alewife (*Alosa pseudoharengus*), an anadromous fish species, shapes its ecological communities as a keystone predator and the ways that the alewife's ecological communities have in turn influenced its evolution and foraging strategies. During summer 2009, I gained experience in the field and in the lab while gathering long-term ecological data and assisting with a survey of thirteen New England lakes in the alewife study system. In the lab I prepared and ran water samples for chlorophyll analysis, counted, measured and identified zooplankton, and prepared periphyton and fish tissue samples for stable isotope analysis. As part of routine lake sampling around southern Connecticut, I collected water and zooplankton samples, and monitored productivity, temperature, dissolved oxygen, and pH. As part of a regional lake survey assessing the impacts of alewife on other freshwater fish species that two former post-docs in the lab, conducted, I caught fish for study by electrofishing, purse seining, and gillnetting, and assisted in measuring, weighing, tissue sampling, and stomach flushing fish. During the 2009-2010 academic year, I continued working in the lab. My work as an undergraduate research assistant in the lab allowed me to become familiar with limnology fieldwork and lab techniques and prepared to undertake my own independent research in the lab.

Winter 2010-Spring 2011
The Ecological History of Two Watersheds in South Central Connecticut

In my Environmental Studies senior thesis project, I researched the ecological history of alewife (*Alosa pseudoharengus*) from pre-colonial times to present. Alewife are ancestrally anadromous, meaning they migrate from the ocean to freshwaters to spawn. However, in coastal Connecticut there are several populations of landlocked alewife, which do not migrate and are genetically, morphologically, and ecologically distinct from anadromous alewife. Previous research suggested that these landlocked populations became genetically isolated from anadromous alewife and from each other 270-500 years ago. In my senior thesis, I asked how and why these populations of anadromous alewife became landlocked and what impact this had on food web structure and nutrient cycling in the region's lakes. In this research, I used a combination of environmental history and paleoecological approaches.

My thesis work began during my junior year as a research for credit project guided by an environmental historian and my ecologist mentor. In this part of my research, I collected colonial land records and maps in search of evidence of early colonial dam construction that would have blocked anadromous fish passage in two watersheds in coastal Connecticut with landlocked alewife populations. I found ample evidence that early colonists built dams, which would have blocked runs of alewife and other anadromous fishes, on the streams in my study watersheds as well as other small alewife streams throughout coastal Connecticut [1].

After completing my historical analysis, I began my paleoecological analysis. I cored several lakes with populations of landlocked alewife and anadromous alewife. Using fossil zooplankton remains and nitrogen stable isotopes from my sediment cores, I examined the effects of alewife on food webs and nutrient cycling. Alewives are strong size-selective planktivores and mediate competition and predation in the zooplankton community. Large-bodied predatory zooplankton are unable to survive in lakes with alewife while small-bodied zooplankton are able to thrive because alewife consume their predators. I examined the morphology of *Bosmina spp.*, a small zooplankton species, as a proxy for alewife presence using both recent zooplankton tow samples and sediment core samples from the region. I found significant differences in the morphology of *Bosmina spp*. between lakes with and without alewife in both recent and core samples, which suggested that the morphology *Bosmina spp*. was highly a reliable proxy for past alewife presence in sediment cores [2]. These results also suggested that prior to colonial dam construction anadromous alewife would have been present in lakes with natural connections to the ocean throughout the coastal Connecticut region [2].

I also tested the use of nitrogen stable isotope signatures as a proxy for past anadromous alewife populations. Spawning anadromous alewives serve as a vector of isotopically-enriched, marine-derived nutrients to coastal lakes. I expected to see a decrease in nitrogen stable isotope ($\delta^{15}N$) values when colonial dams were built and began blocking fish passage and cutting off all sources of marine-derived nutrients from alewife into my study watersheds. However, instead of seeing a decrease in $\delta^{15}N$ values during this period, I saw a dramatic increase in $\delta^{15}N$ values, which continued to accelerate towards the present. This increase in $\delta^{15}N$ likely resulted from human nutrient inputs, such as animal agriculture and human sewage disposal, which are also isotopically-enriched and began to increase at the same time that anadromous fish migrations in my study watersheds ceased [3]. This suggested that colonists began to have a noticeable impact freshwater nutrient cycling soon after arriving in coastal Connecticut. My research also suggested that historical marine-derived nutrient loading from alewife and other anadromous fishes was minor compared to nutrient loading from recent human activity [3].

Summer 2011-present

The Ecological History of Freshwater Ecosystems in Coastal Connecticut

Intrigued by the results of my undergraduate research, I decided to study the effects of human land use change on ecosystem dynamics in Connecticut's coastal freshwater systems in more depth in my Master's of Environmental Science research. In addition to expanding my study from two to four lakes in the region, I analyzed nitrogen and phosphorus concentrations as well as N:P ratios in my cores to reconstruct nutrient loading over time, total carbon stable isotopes, C:N ratios to estimate terrestrial inputs into my study watersheds, and total organic carbon stable isotopes to reconstruct paleoproductivity. I am using nutrient loading models to estimate historical nutrient loading from pre-colonial times to present as well as future nutrient loading with both continued intense human land use and restored runs of anadromous fishes. My findings from this work echo those in my undergraduate research and suggest that land use change starting with Euro-American settlement in the region had major impacts on nutrient dynamics and that nutrient inputs from human activities in the past 350 years are much greater in magnitude than past nutrient inputs from anadromous fishes and other natural sources [3].

My previous research experiences have provided me with excellent preparation for my proposed doctoral work. In my undergraduate and master's research projects, I have used all of the techniques that I plan to use in my doctoral work from historical land use data collection to stable isotope analysis to nutrient loading models. I have experience carrying out limnological fieldwork, lab analyses, modeling, and paleoecological analyses as well as environmental history research and historical data analysis. My proposed research builds upon my past work and I am confident that I have developed the skills necessary to conduct it successfully.

[1] Twining, C.W. (in prep) Changes in the lakes: the ecological history freshwaters in coastal Connecticut. To be submitted to *Environmental History*. **[2] Twining, C.W.** and D.M. Post. (in prep) Cladoceran remains reveal presence of a keystone size-selective planktivore. To be submitted to *Journal of Paleolimnology*. **[3] Twining, C.W.** and D.M. Post. (in prep) Past and future ecosystem dynamics in Connecticut's coastal watersheds: linking paleoecology and nutrient loading models. To be submitted to *Limnology and Oceanography*.

When Does Nutrient Loading by Anadromous Fishes Serve as an Important Driver of Ecosystem Function in Freshwater Systems?

***Key Words**: anadromous fishes, nutrient loading, life history traits, landscape characteristics*

Anadromous fishes, which migrate from marine systems to freshwater systems to spawn, can serve as important drivers of ecosystem function by transporting substantial quantities of marine-derived nutrients to freshwater systems (1,2). Past work has examined nutrient loading by anadromous fishes on both short (3) and long time scales (4). Nearly all past studies have focused almost entirely on nutrient loading by semelparous (spawning once and dying) Pacific salmonids (*Onchorynchus spp.*) in low productivity streams and lakes that have minimal additional nutrient inputs from the landscape. However, many anadromous species are iteroparous (spawning multiple times) and many spawn in highly productive systems where nutrient loading from human activity is often significant (5,6,7). Yet, the importance of nutrient loading by anadromous fishes with alternative life history traits in regions with different landscape characteristics, such as climate and land use, remains largely unexamined (8).

Life history traits are likely to help determine the importance of various anadromous fishes as nutrient vectors and drivers of ecosystem function. For example, fishes that spawn at high densities load more nutrients on a per area basis than fishes that spawn at lower densities (8). Semelparous fishes load nutrients primarily through carcasses (1,2) while iteroparous fishes, load nutrients through a combination of carcasses, excretion, and release of gametes (7). Small fishes have higher biomass-specific nutrient excretion rates and load more nutrients per unit biomass than larger fishes (9). Anadromous fishes that spawn during dry seasons when terrestrial inputs are low and water residence times are long are likely to be more important drivers of ecosystem function than those that spawn during wet seasons (9).

Factors such as regional climate, geomorphology and land use affect the loads of other nutrient inputs from the landscape (10). Climatic and geomorphological variables, such as precipitation and watershed size, can reduce the importance of nutrient subsidies from anadromous fishes by diluting or quickly flushing inputs from fishes out of the system (11). In systems with intensive human land use, human activity can become the dominant source of nutrient inputs and serve as the main driver of ecosystem function (12,13), obscuring the effects of nutrient inputs from anadromous fishes. I propose to examine how landscape characteristics interact with fish life history traits in determining the importance of anadromous fishes as nutrient vectors and drivers of ecosystem function.

In many systems, anadromous fishes have declined at the same time that human land use has intensified. As a result, nutrient inputs from fishes have decreased at the same time that nutrient inputs from human activity have increased. Therefore, examining nutrient loading on contemporary time scales alone may underestimate the importance of anadromous fishes as nutrient vectors in the past when their inputs were higher and when inputs from human land use were lower. Here, I propose to examine how nutrient loading by anadromous fishes varies across fish life histories, across regional landscape characteristics, and through time.

Hypotheses | H1) Anadromous fishes with high densities, high post-spawning mortality, and high nutrient excretion rates load more nutrients and are more important drivers of ecosystem function than other anadromous fishes. **H2)** Nutrient loading by anadromous fishes in regions with low terrestrial inputs and long water residence time are more important drivers of ecosystem function than nutrient loading by anadromous fishes in regions with high terrestrial inputs and short water residence time. **H3)** In the past 150-350 years, nutrient loading from human land use has become a more important driver of ecosystem function than loading from anadromous fishes.

Methods | To test H1, I will use fish nutrient loading models as in West et al (7) to estimate and compare loading by two anadromous fish species, sockeye (*Onchorynchus nerkus*) and alewife (*Alosa pseudoharengus*). Sockeye and alewife differ in several key life history traits that I expect to be important determinants of the importance of nutrient loading by anadromous fishes: spawning season, spawning density, post-spawning mortality, and nutrient excretion rate.

To test H2, I will use a combination of fish and watershed nutrient loading models developed by West et al (7) to estimate and compare loading by sockeye and alewife across regions that differ in landscape characteristics. Sockeye and alewife are both distributed across regions that differ in climate, geomorphology, and land use, which are landscape characteristics that I expect to be important determinants of the importance of nutrient loading by fishes. Past research has focused on sockeye systems in Alaska and British Columbia that differ in climate and geomorphology, but all have low productivity and minimal human land use and on alewife systems in Connecticut with high productivity and extensive human land use. I will focus on collecting data from sockeye systems with higher productivity and more intensive human land use in the Columbia River basin and from alewife systems with lower productivity and less intensive land use in Maine and New Brunswick.

To test H3, I will use a combination of paleoecological and historical data to compare nutrient loading across my study systems from pre-European contact to present. I will take sediment cores from lakes in systems with sockeye and alewife. I will reconstruct past nutrient inputs using concentrations of nitrogen, diatom-inferred phosphorus levels and N:P ratios from lake sediment cores (12,13). Using $\delta^{15}N$, $\delta^{13}C$, δD, and $\delta^{34}S$ stable isotopes from sediment cores in combination with Bayesian stable isotope mixing models, I will reconstruct sources of nutrient inputs (1,2,4,11). Using C:N ratios and algal pigments from sediment cores, I will reconstruct past primary production (11). I will estimate past anadromous fish densities by calibrating paleoecological proxies for anadromous fishes with recent records of anadromous fish densities (4). I will use oral histories from Native American tribes on past anadromous fish abundances as additional estimates of past anadromous fish densities. I will then combine my historical data and paleoecological data to relate trends in anadromous fish populations and land use patterns to trends in nutrient loading and primary production (4).

Broader Impacts | Environmental managers working to restore freshwater ecosystems across North America are concerned about the dual effects of nutrient loading from anadromous fishes and human land use on ecosystem function. In the West, managers are concerned about low productivity in areas that were formerly fertilized by anadromous fishes whose passage is now blocked by dams, while in the East, managers are concerned that restoring runs of anadromous fishes will result in eutrophication. Managers throughout North America are concerned about nutrient loading and eutrophication from intensive human land use. My research will identify the fish life history traits and landscape characteristics under which anadromous fishes are likely to be important nutrient vectors. In conducting my research, I will actively engage with environmental managers, citizen stakeholders, conservation groups, and First Nation tribes involved with anadromous fish restoration. I will also directly involve First Nations tribes in my research by collecting their oral histories on past anadromous fish abundance.

1. Naiman et al *Ecosystems* 5:399-417 (2002). **2.** Schindler et al *Front Ecol Environ* 1:31-37 (2003). **3.** Donaldson, University of Washington Zoology, PhD Thesis (1967). **4.** Finney et al *Science* 290:795-799 (2000). **5.** Durbin et al *Ecology* 60:8-17 (1979). **6.** Nislow et al *Can J Fish Aquat Sci* 61:2401-2410 (2004). **7.** West et al *Can J Fish Aquat Sci* 67:1211-1220 (2009). **8.** Flecker et al *Am Fish S S* 73:559-592 (2010). **9.** Vanni *Annu Rev Ecol Syst* 33:341-370 (2002). **10.** Bremigan et al *Limnol Oceanogr* 53:1420-1433 (2008). **11.** Selbie et al *Limnol Oceanogr* 54:1733-1745 (2009). **12.** Brugam *Ecology* 59:19-36 (1978). **13.** Keatley et al *PLoS ONE* 6:e15913 (2011).