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# Nutrient dynamics of an alewife migration in Nequasset Lake: Evidence and modeling efforts

A Senior Thesis

Presented to

The Faculty of the Department of Geology

Bates College

In partial fulfillment of the requirements for the

Degree of Bachelor of Science

By

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## Abstract

In the process of their annual spawning migration, anadromous alewives (*Alosa Pseudoharengus*) act as nutrient vectors. While adults import marine derived nutrients (MDNs) to their lacustrine spawning grounds, juveniles export nutrients as they emigrate seaward. Monitoring of lake water quality parameters and carbon and nitrogen stable isotopic signatures of particulate organic matter and fauna in a coastal Maine lake during two annual alewife migrations was paired with a model predicting alewife nutrient fluxes. The combination aimed to detect any current loading and predict the outcome of alewife runs of varying escapement. Water quality data were largely consistent between years and no correlation was found between nutrient or chlorophyll concentrations and daily fish passage. Stable isotope analyses were unable to concretely identify the presence of MDN's, likely due to low concentrations. Modeled adult alewife phosphorous inputs for the 2012 and 2013 migration were similar to juvenile export, while upper estimates of nitrogen contribution to the lake exceeded 75 kg . These imports currently represent an estimated 0.45% of the lakes annual N budget. Historical fish migrations, however, may have contributed as much as 12% of the annual N and 25% of the annual P load to the lake. Incorporating annual alewife flux estimates into a landscape loading model indicated that the study lake may be capable of receiving escapements of nearly 7 million (16x current) before critical water quality degradation. However, a new model describing the daily release and sequestration of lake nutrients by adult and juvenile alewife populations indicates that such annual approaches may be inappropriately blunt for water quality estimations as the result of spatiotemporal complexity in the alewife nutrient fluxes. The model additionally shows that complete nutrient import and export may be temporally separated by a month or more. This may decrease the efficiency of juvenile nutrient export. Implications for joint fishery and lake management are discussed.

# Introduction

## Overview

Anthropogenic influences on the nitrogen and phosphorous fluxes in lakes, rivers, and oceans have spurred great ecological change (Caraco 1993, Galloway 2004). Examination of sources, alterations, and fates of natural and anthropogenic nutrients hope to characterize the biogeochemical behavior of aquatic systems and how this behavior is altered by human perturbations. In the coastal rivers and lakes of New England, a portion of this perturbation has been the installation of dams and culverts that restrict the flow of water, sediments, and the passage of diadromous fish (Ligon 1995). This infrastructure impedes or occludes fish from making their annual spawning migrations. Amongst those affected are shad, river herring (alewife), white sucker and atlantic salmon. With these migratory restrictions has come a precipitous decline in populations (Lindberg and Waldman 2009, Saunders et al 2006).

There is increasing evidence to suggest that anadromous fish play an important role in the nutrient cycles of the freshwater systems in which they spawn(). Adult anadromous fish contain biomass and nutrients from the marine ecosystem that can be deposited in freshwater spawning areas via excretion, gamete release, and mortality (Walters et al 2009). These marine derived nutrients (MDNs) can make up a substantial portion of the yearly nutrient budget in some freshwater systems, though factors including migration size, lake trophic state, and subsequent juvenile (Young of the Year) survival and emigration will dictate the total flux and impact of MDNs (Kline et al 1993, West et al 2010).

This study quantifies the effects of MDN input on the nutrient budgets and ecological health of Nequasset Lake in Woolwich, ME. Stable isotope, water nutrient, and chlorophyll analyses are used in an attempt to trace the flow of MDN through the freshwater ecosystem. Modeling efforts are directed at constraining the annual nitrogen and phosphorous dynamics of the alewife migration. By incorporating increased run sizes (a predicted effect of pending improvements to the Nequasset fish ladder) into the model, future changes in net nutrient import/export may be predicted and balanced against municipal water quality demands. In addition, a daily model is developed that provides new insight into the temporal variation of MDN release in lakes.

## Alewife Ecology

Alewives are members of the *Alosa* genus, which they share with blueback herring (*Alosa aestivalis*) and other species colloquially known as shad. These fish range in length from 6-14in, weighing around 200 grams when mature, and are native to coastal waters from Florida to Nova Scotia (figure 1). They are largely planktivorous though are known to prey on fish larvae and eggs as well as small fish like cunner and sand luce when at sea (Collette and Klein-MacPhee 2002). The fish spend the majority of their life in the marine environment, but return to the freshwater lakes and ponds of their birth to spawn when they reach sexual maturity between ages 3 and 5(Loesch 1987). Tagging studies indicate that they home with great accuracy to their natal locations within these water bodies (Jessop 1994). Annual anadromous migration generally takes place between April and May, and across the state of Maine can be made up of 10 million individuals (Maine DMR



Figure 1: Natural and introduced (landlocked) range of the Alewife or River Herring. Figure from USGS. HUC stands for Hydrologic Unit Code. Brown shaded regions are native habitats while maroon regions are landlocked invasive populations. <http://nas.er.usgs.gov/queries/factsheet.aspx?SpeciesID=490>

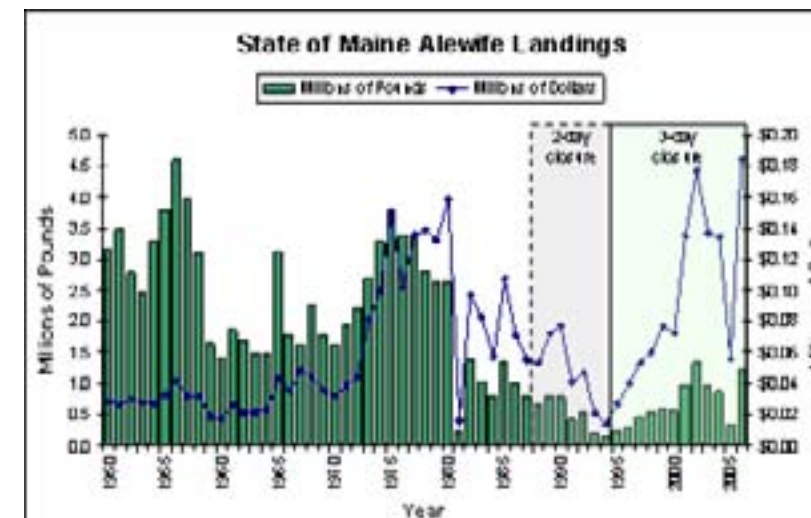


Figure 2: Decline in the Alewife fishery signals the decline in total population. Source Maine DMR 2013

and terrestrial animals like herons, eagles, and raccoons (Loesch 1987). In this way, alewives play an important role in connecting marine, freshwater, and terrestrial ecosystems (Garman and Macko 1998, Polis 1). A combination of landings reports and fishery independent fish count data compound to strongly support the notion of a widespread (eastern U.S.A. but also global) population decrease of this species (Hall et al 2012, Limburg and Waldman 2009, Marteka 2004, Meadows 2008, figure 2) in the past past two centuries and especially in the past 60 years. Maine landings may have decreased in the 1960's as the result of foreign fishing pressure by the USSR, Germany, Poland and others (Meadows 2008) and increased briefly with the Fishery Conservation and Management Act of 1976. Two and then three day per week fishery closures were later enacted by the state of Maine to aid recovery (Maine DMR 2013). As a result of continued low stock, alewife and blueback herring were listed as a species of concern in 2006 (National Marine Fisheries Service 2014). Suggested reasons for this decrease include pollution and overfishing (directly and as bycatch) as well as the reduction and degradation of spawning habitat; now only 5% of historical area (Hall et al 2011, 2012, Saunders 2006). As these fish constitute the base of many foodwebs, terrestrial and marine, their population decrease may have widespread ecological impacts (Wilson and Halupka 1995). For example, it has been suggested that the critical condition of

2013). During spawning, each female may release between 60,000 and 300,000 eggs (Kocik 2000, Mullins 1986). Many adults will die after spawning while the remainder will return to the ocean. Freshwater mortality rates are spatio-temporally variable even within small populations, and can range from 32% to 100% (Havey 1961, Kissil 1974). After hatching and feeding in freshwater, 1-5 inch alewife young, known as young of the year (YOY) will emigrate to the coast from July to October (Richkus 1975). Reaching saltwater, they are likely to spend their first year in estuaries or shallow coastal settings before joining large schools and moving offshore (but generally <100m depth) (Mullen 1986). Being iteroporous, surviving alewives may return to these same locations several more times to spawn throughout lifespans that average 5 years, with a greatest recorded age of 10(Scott 1988). Their marine life histories are not well constrained, though there is some evidence to suggest that seasonal migrations do exist (Rulifson 1987, 2012). During the well observed anadromous migrations, land and seaward, river herring serve as an important food source to other fish like striped bass, cod, trout,

New England's offshore groundfish stocks including cod and halibut may be related to a deficiency in anadromous forage fish like alewife (Licheter and Ames 2012).

The study of MDN input into freshwater systems has been carried out most extensively in the Pacific Northwest and Alaska, where annual migrations of anadromous salmon (*Oncorhynchus spp.*) have been shown to significantly increase nutrient inputs to oligotrophic streams, affecting periphyton growth and enriching local biota in  $^{15}\text{N}$  (Kline et al. 1993, Johnston et al. 2010). Alewives tend to be enriched in  $^{15}\text{N}$  and  $^{13}\text{C}$  relative to their freshwater environs and thus the nutrients they release may be tracked with stable isotopic analyses. Fewer studies have examined the effects of MDN by anadromous fishes, specifically alewife, on the Atlantic coast. These studies tend to agree with their Pacific salmon counterparts, with local biota in alewife containing waters having enriched  $\delta^{15}\text{N}$  signatures relative to reference environs (Garman and Macko 1998, Walters and Post 2009). Increases in leaf litter respiration rates, changes in the lake plankton community, and increases in the growth of local fish species have also been attributed to migratory alewives (Kissil 1974, Kircheis et al. 2004, Post et al. 2008). A study of MDN import to Bride Lake, Connecticut (West et al. 2010), indicated a substantial net import of phosphorus from the alewife migration, with alewife phosphorus constituting 23% of the lake's annual load. Modeling of historical runs indicated that this percentage may have been significantly greater (2.5x) in the 1960's with larger alewife runs.

## Study Site

Nequasset Lake is a 425 acre, oligotrophic impoundment located in Woolwich, Sagadahoc County, ME. Its watershed is 16 km long (NNE-SSW oriented), averages 3 km in width, and covers an area of 51 km<sup>2</sup> (figure 3). The watershed is over 80% forested, and 1.2% developed with the rest made up of wetland and grassland (Chiao 2013). Records indicate that the dam (with mill) and impoundment have existed since 1730 (KELT 2013). For over 100 years Nequasset Lake has served as a drinking water reservoir for the municipalities of Woolwich, Wiscasset and Bath. Geology of the area consists primarily of Ordovician age schists of the Cape Elizabeth For-

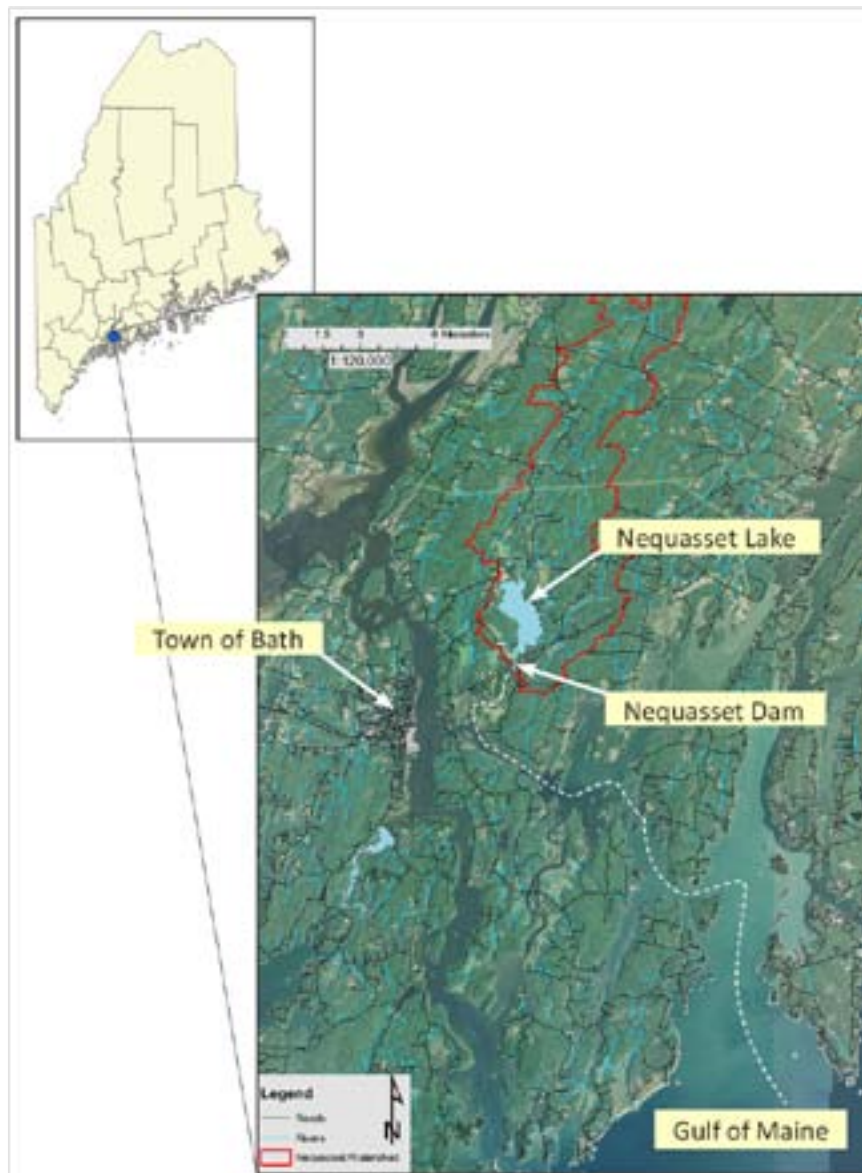


Figure 3: map of the Nequasset lake watershed. White line is a potential alewife migration route connecting the study site with the Gulf of Maine.

mation (OCE), overlain by glaciomarine deposits of the Presumpscot formation (Maine geological survey 2002).

Records from the town of Woolwich indicate that the annual alewife run provided an important form of sustenance to early settlers and townsfolk, who typically preserved the fish with salt or by smoking (KELT 2013). Recognition of the importance of upstream spawning areas on alewife population came as early as 1788, when legislation was approved to require fish passage over the dam from May to September. Today, it is estimated that only 5% of the Alewife's historical habitat is accessible due to migratory restrictions. At Nequasset dam, one of 19 other like it in the state, a commercial harvest of alewife is allowed, primarily fueled by the demand for springtime lobster bait. While the fish ladder at Nequasset is functioning and passed 30,000 fish in the summer of 2012, an effort by the community organization, Kennebec Estuary Land Trust (KELT), with financial backing from the Bath Water District, seeks to renovate the fish ladder in order to augment the annual run of alewives into Nequasset Lake. With the potential for a large increase in fish and MDN input, it is important to establish a pre-restoration baseline. Characterizing and establishing a model of nutrient cycling in the lake will help to predict potential change brought with increased MDN inputs and suggest any necessary management strategies to ensure the health of the lake and suitability of a multi-municipal drinking water supply.

## Materials and Methods

### Field Methods

#### *Fish Counts*

In order to quantify the migratory input of alewife to Nequasset Lake, a systematic fish counting program was implemented at the Nequasset fish ladder by the Kennebec Estuary Land Trust (KELT) and fish biologist Theodore Willis of the University of Maine (UMO). A 2-way stratified random sampling design after Nelson (2006) entailed volunteers engaging in two ten minute fish counts during a two-hour time period, with 7 periods (and 7 volunteers) from 6am to 8pm. From these data, fish passage was estimated for a given time interval by multiplying the mean of 10 min counts across this interval by the interval/10min. For instance, if 1,2,3,4,5,6, 7,8,9,10,11,12,13, and 14 fish were counted during 14 discrete 10 minute intervals throughout the day, total fish passage for the daily migration period (assumed to be 14hr) would be  $7.5 * (14\text{hr}/10\text{min}) = 630$ . This calculation assumes that fish do not run in the nighttime hours outside the counting period, an assumption supported by Mullens (1986) and Beltz (1975).

#### *Nequasset Lake Monitoring*

A total of 7 sample sites at 6 sample locations were chosen within the lake itself and its tributaries. The lake has 4 tributaries; Nequasset Brook (NB), Northeast Inlet (NI), George's Brook (GB), and Sucker Brook (SB). All were included in the sampling scheme (figure 4). Two sample locations at the lake's deepest part (~20m) were vertically differentiated, one at the surface (DHS), and one below the thermocline (DHD), generally around 10m depth. One site is located proximal to the dam and the fish ladder at the southern end of the lake, and is referred to as the top of dam site (TD). Each of these sites was sampled every 3 to 5 weeks from April

to October, with the exception of the TD site, which was sampled daily. With each sampling, 4L of water were collected in 4- 1L acid (5% HCl) washed Nalgene HDPE sample bottles. All bottles were rinsed 3x with sample water before filling. Samples at the DHD site were collected with a Kemmerer bottle from a boat. All samples were stored in a cooler during transport to the laboratory.

A host of data were collected with Hydrolab multimeters at each site during the course of sampling. These included temperature, dissolved oxygen (DO), specific conductivity (SpC), pH, and depth. The Hydrolabs were calibrated for SpC, pH, and %DO in the lab prior to each field use. Stream flow data were collected at the tributary sites and across the top of the dam and fish ladder. Flow rate transects were made with measurements taken at 0.5m intervals with a Global Waters impeller style flow probe. Plankton collections at DHS and DHD were performed with a plankton tow of 30in opening diameter and 147  $\mu\text{m}$  nylon mesh. The tow was pulled vertically through 3 meters of water column 3x when sampling above and below the thermocline. Hypolimnion collections were isolated from the epilimnion before removal to the surface via a drawcord installed at the midsection of the net. Samples were stored in a 125 ml acid washed HDPE bottle and frozen upon return to the lab.

## Laboratory Methods

### Sample processing

All samples collected at the Nequasset Lake study site were brought to the Environmental Geochemistry Laboratory at Bates College. Each 1L water sample was filtered through a pre-combusted GF/F filter. Filters were placed in acid washed centrifuge tubes and frozen. For each sample site on each date, 2-3 filters were reserved for chlorophyll analyses and 1-2 for stable isotope analyses. One 300 ml water subsample was taken from each sample site before filtration and was sent to Bowdoin College for nutrient analysis.

### Nutrient Analysis

At Bowdoin College, dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) were measured on a Shimadzu TOC-V analyzer with a non-dispersive infrared detector.  $\text{NO}_3^-$ ,  $\text{NH}_4^+$ ,  $\text{PO}_4^{3-}$ , and  $\text{SiO}_2$  were analyzed using methods EPA 353.2, Standard Methods 4500-NH<sub>3</sub>, and EPA 365.1, respectively, using a Smartchem automated spectrophotometer.

### Chlorophyll determination

At least two of each filter set were analyzed for chlorophyll a content. Filters were first immersed in 10ml of 90% acetone in a centrifuge tube, sonicated for 15 minutes, and left covered and refrigerated to extract for 12 hours. Immediately prior to analysis, samples were centrifuged for 15 minutes at 675g. Supernatant was transferred to a cuvette and analyzed on a Turner Designs 10-AU-005-CE fluorometer. Each sample was then acidified with 3 drops of 6 M HCl before a second reading. Pre and post acidification readings were used to calculate chlorophyll a concentration of the original sample in  $\mu\text{g/l}$  by EPA method 445 (Arrar and Collins 1997).

## $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ Analysis

At least one of each set of sample filters underwent a carbon and nitrogen stable isotope analysis of the particulate organic matter (POM) contained after filtration. Filters were oven dried. Depending on the degree of visible organic matter, somewhere between one quarter and one half of the GF/F filter was packed into a tin capsule before analysis on a Costech elemental analyzer interfaced to a ThermoFinnigan Delta V Advantage stable isotope ratio mass spectrometer via combustion (EA-C-IRMS).

## Statistical Analyses

In order to determine the statistical significance of spatiotemporal differences in lake  $\delta^{15}\text{N}$ , chlorophyll concentrations, and nutrient concentrations throughout the study the data were first tested for normality and equality of variance. If these conditions were met, then the data were analyzed with a one-way ANOVA ( $\alpha$  of 0.05) and Tukey's post hoc test. If not, data were instead analyzed with the non-parametric equivalent, the Kruskal Wallis one-way analysis of variance. Cross correlation of certain time series data sets was used to determine significant correlations across lag times. All analyses were performed using Minitab 16 statistical software.

## Modeling

In order to estimate the annual and seasonal effects of the alewife migration on the nitrogen and phosphorous dynamics of Nequasset Lake, modeling efforts are divided here into two general schema distinguished by varying timescales but underlain by very similar mechanics. The first is a model that closely follows that created by the Post Lab of Yale University, available for examination in West et al. (2010), Post and Walters (2009), and Twining et al. (2013). This model takes an annual approach to estimating the relative balance of nutrient flux by the migrating alewives and their sea-run progeny. The second schema is derived from this model but is modified to allow for the estimation of daily alewife nutrient flux. This second model is hereafter referred to as

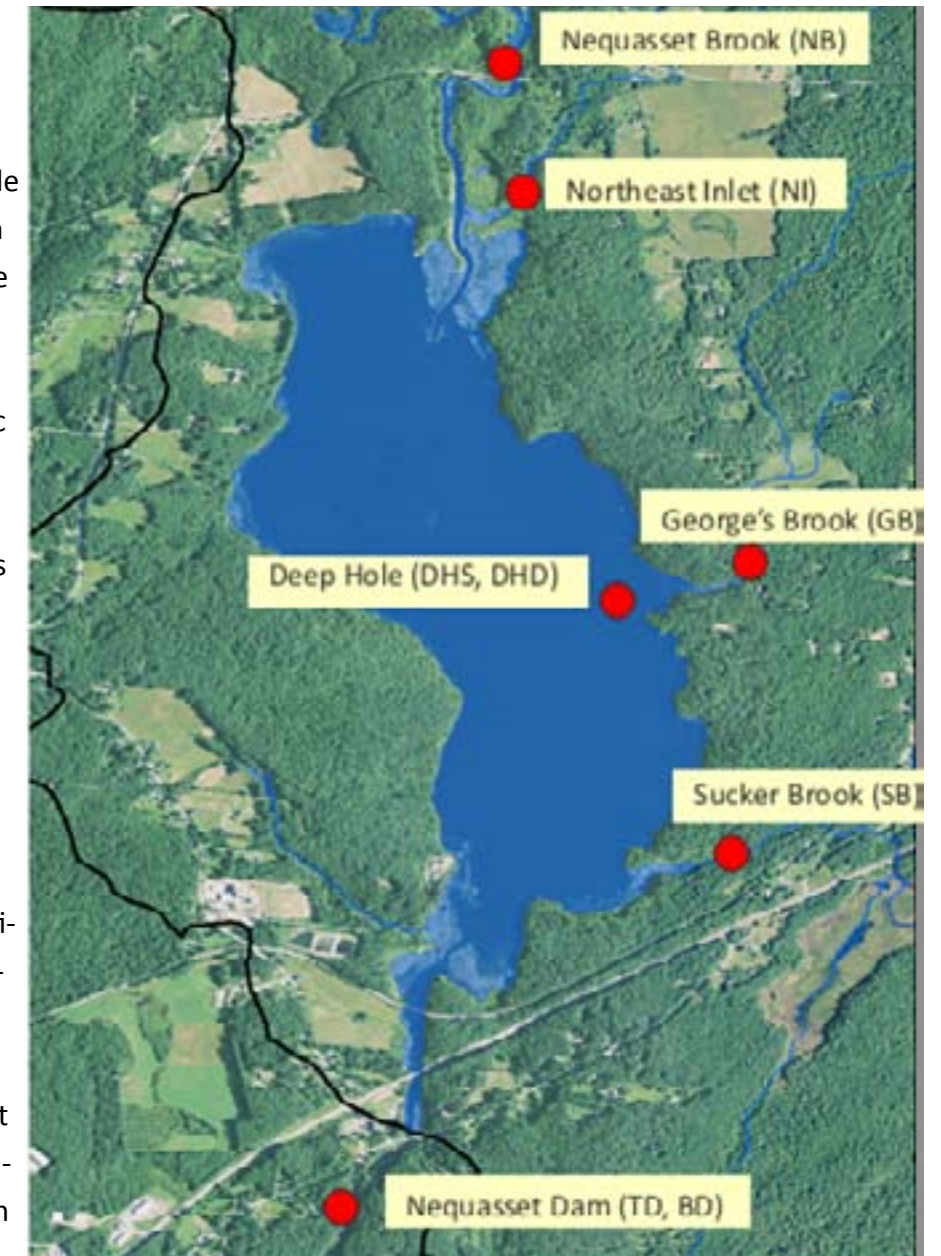


Figure 4: map of Nequasset Lake showing the locations of the 7 different sampling sites in red.

the “daily” model.

### Annual model

The annual model was closely based on that developed by the Post Lab, and specifically the iteration employed in West *et al.* 2010. Modifications have been made to the carcass loading equation to account for incomplete decomposition (discussed in daily model) and terminology has been changed in all equations to accommodate the models application to both phosphorous and nitrogen. The model uses a series of equations to determine the relative balance of nutrient imports by adults and nutrient exports by YOY. The difference between the two is the net flux. It assumes that adult imports are comprehensively accounted for by the excretion, gamete release, and mortality/carcass decomposition of adults, while YOY export is accounted for by biomass incorporation and emigration. Carcass loading per adult is calculated by the formula:

$$N_{\text{carcass}} = \mu_a * \text{mass}_a * [\text{fishnute}] * N_{\text{available}}$$

where  $N_{\text{carcass}}$  is the mass of nutrient in question released,  $\mu_a$  is the annual adult in-lake mortality rate,  $\text{mass}_a$  is the average adult fish mass (wet),  $[\text{fishnute}]$  is the concentration of nutrient in the fish carcass (% wet weight), and  $N_{\text{available}}$  is a coefficient accounting for the degree of total carcass nutrient liberation as determined by Parmenter and Lamarra (1991) with the rainbow trout *Oncorhynchus mykiss*. Given that the number of adult emigrants was not counted at Nequasset, in lake mortality rate was assumed to be identical to that measured by West *et al.* 2010 in Bride Lake, CT. Average mass was calculated from a sample of three adults taken from the upstream migrating population in 2012 from the Nequasset fish ladder. Whole fish P concentration of pre-spawning adults was taken from Durbin *et al.* (1979). Nutrient loading per fish by gamete release was determined by the equation

$$N_{\text{gametes}} = (1 - \mu_a) * 0.5 * (F_a * \text{mass}_c * [\text{nute}_c] + \Delta \text{mass}_t * [\text{nute}_t])$$

where  $N_{\text{gametes}}$  is the mass of nutrient liberated,  $F_a$  is female fecundity,  $\text{mass}_c$  is average egg mass,  $[\text{nute}_c]$  is the concentration of nutrient in each egg,  $\Delta \text{mass}_t$  is the change in mass of the testes during spawning and  $[\text{nute}_t]$  is the concentration of nutrient in the testes. Mass and nutrient content of ovaries were taken from West *et al.* (2010), as well as the relationship between female length and fecundity (in part determined by data from Kissil (1969)). The change in mass and nutrient concentration of testes was also taken from West, aided by data from Durbin *et al.* (1979). The first coefficient of the equation  $(1 - \mu_a)$  assures that fish that are already accounted for in the carcass loading determination are not also counted in gamete release, assuming that all bodily nutrients are released in the process of decomposition. The mass of nutrient liberated by excretion is calculated as

$$N_{\text{excretion}} = (1 - \mu_a) * \text{mass}_a * E_a * t_a$$

where  $N_{\text{excretion}}$  is the total mass of nutrient excreted by fish during residence in the lake,  $(1 - \mu_a)$  is used as with gametes to avoid double counting of carcass nutrients,  $E_a$  is the mass specific nutrient excretion rate as determined by Post and Walters (2009), and the average adult time spent in the lake  $t_a$  (14 days) was taken from (Kissil 1969) and was corroborated by observations by volunteers at the fish ladder. The export of nutrients by the emigration of YOY was calculated by the equation

$$N_{\text{YOY}} = B_d \text{ YOY} * [\text{nute}_{\text{YOY}}] * \text{area}$$

where  $B_d \text{ YOY}$  is a biomass density function,  $[\text{nute}_{\text{YOY}}]$  is the concentration of nutrient in whole YOY body, and area is the area of the lake. The biomass density function was calculated by way of a mesocosm experiment (West *et al.* 2010), and relates the density of YOY to the final attainable biomass density ( $\text{g}/\text{m}^2$ ) of the YOY population given a finite amount of lake productivity. This asymptotic exponential function is given as

$$B_d \text{ YOY} = a * (1 - e^{-bx})$$

where  $a$  is the value of the asymptote (max biomass density),  $b$  is the slope of the relationship between density and biomass, and  $x$  is the initial density of YOY alewives. In West *et al.* (2010) this asymptote was then adjusted from the mesocosm ( $5.4 \text{ g}/\text{m}^2$ ) to the peak midsummer YOY density observed in Bride Lake (Post *et al.* 2008). This value ( $1.6 \text{ g}/\text{m}^2$ ) was in turn used for Nequasset lake, as there were no estimates of YOY density made in this study. Constant  $b$  is equal to 2.73 (West *et al.* 2010). The annual model was run using two different coefficients for the determination of  $x$  (YOY density) as a function of escapement. The values are 6.36 YOY survived per spawner estimated by West *et al.* (2010) and 366 YOY survived per spawner, as calculated from data by Havey (1961). The first was for a smaller CT lake (Bride Lake) with higher alewife densities than Nequasset, and the second for a large Maine lake with a recovering population of lower adult density than Nequasset. Assuming that YOY survival is influenced by density, these values were used to provide upper and lower bounds for possible YOY export. Data produced using the value of 6.36 are included in scenarios labeled “YOY low” while those produced using 366 are labeled “YOY high.” Values of all model coefficients can be found in table 1.

### Daily model

The daily model takes the above described annual model, incorporates an empirically derived fish carcass nutrient elution model, modifies the growth rate curve from West *et al.*'s mesocosm experiment, and allows for the estimation of total adult imports and YOY exports on a daily basis.

Parmenter and Lamarra (1991) performed experiments to determine the total mass loss and patterns of nutrient elution by decaying rainbow trout and pintail duck in a freshwater Wyoming marsh over a ten month period. Their's appears to be one of few studies in which not only the mass but also the nutrient content of an animal carcass is detailed throughout the process of decay in freshwater. While their study was conducted in a marsh, the timeline of mass loss they observed was comparable to results from other studies tracking rainbow trout mass loss in a creek (Minshall *et al.* 1991) and bluegill sunfish in a lake (Kitchell *et al.* 1975). Minshall found that summer fish mass loss stabilized by 50 days. This finding matches nicely with the nearly asymptotic decomposition (roughly 20% dry mass remaining) found by Parmenter and Lamarra (1991) at around 60 days. Importantly, Parmenter and Lamarra (1991) indicated that the 309 day decay period measured relieved the fish of 96% of their nitrogen but only 65% of their total phosphorous. This finding is backed by results of Kitchell *et al.* (1975) who found that bluegills released only 50% of their total P. As pointed out by Sereda *et al.* (2007), this may mean that a substantial portion of fish P is incorporated into bottom sediments and is lost to the system, indicating fish as net phosphorous sinks. The figures of yearly (309 day) nutrient loss

Adult	Ma (average wet mass g)	Average length (mm)	mortality (%)	alewife nutrient content (% of wet weight)	% nutrient available from carcass	Spawner residence time (days)	Excretion rate (µg/fish/hour)	female fecundity (#eggs/female)	egg nutrient (% of wet weight)	Δtestes wet mass (g)	testes nutrient concentration (% of wet weight)
Phosphorous	116	260	56	0.42	65	14	251.2	168773	0.31	7.08	0.88
Nitrogen	116	260	56	2.49	96	14	2860.6	168773	3.3925	7.08	3.41
Source	1	1	2	2,3	4	1,2	2	2	2,3	2	2

Juvenile		YOY per spawner (low)	YOY per spawner (high)
Phosphorous	2.0	0.58	6.39
Nitrogen	2.0	2.49	6.39
Source	1	2,3	2

Table 1: coefficients used in the annual and daily alewife loading models. Organized by application to adult or YOY fluxes, and N or P. Sources: 1 is this study, 2 is West et al. (2010), 3 is Durbin (1979), 4 is Parmenter and Lamarra (1991), and 5 is Havey (1973).

calculated by Parmenter were incorporated as  $M_{available}$  coefficients into the annual model. While Parmenter used a double exponential function to model the mass loss of the carrion, he did not give an equation for the rate of nutrient loss. By using the fish mass data and percent nutrient data provided, the formulas for N and P loss (as a % of initial) were determined using a least sum squares analysis completed by the Solver function in Microsoft Excel. This function was then applied daily by assuming that 56% ( $\mu_a$ ) of daily immigrating fish (calculated from the fish run) died the day they entered the lake, marking the start of their decay. These discrete decomposing populations were then summed to determine a daily release of nutrient. Adult gamete input was assumed to take place the same day as adult immigration and excretion rate was applied to a changing adult population size dictated by the immigration and an assumed 14 day residence time.

To estimate daily YOY export, the growth equation from the West et al. (2010) microcosm experiment was modeled using the same least sum squares method as with the carcass decay equations. Data for this curve were generated using the biomass density equation to determine biomass density across a range of fish densities. Dividing the output biomass density by the input fish density, an interpolated average fish mass  $M_a$  was calculated for each population size. This fish mass was then divided by 100 days, the time from YOY birth to emigration as determined by Richkus (1975) for a Rhode Island migration in 1972. Similar figures were determined for adjacent years by Richkus(1975), and by Kissil (1969)(122 days) and Cooper (1961) (July-October). This yielded a growth rate vs density curve that was then plotted and modeled using the same exponential equation format as the biomass density curve.

To determine daily YOY population under two scenarios, the YOY:spawner ratios were multiplied by the incoming fish population and then lagged for 12 days to account for incubation and hatching time. This was estimated from a general equation relating alewife hatching time to water temperature provided by Edsall (1970) and Kellogg (1982) and the average summer water temperature measured by volunteers at the Nequasset fish ladder in 2013 (59 °F). While the annual model assumes a continuous YOY density in its estimation of biomass density, the daily model calculated YOY density dependent growth rates on a daily basis so as to account for the changing population size dictated by spawning and juvenile emigration. Net daily inputs were then calculated by subtracting the daily YOY biomass incorporation of nutrient (mass x fish nutrient concentration) from the daily input by adults. In order to estimate the short term effects of alewife nutrient release on lake nutrient

dynamics, daily nutrient fluxes were “dissolved” by dividing the flux by total lake volume in order to achieve a theoretical daily change in nutrient concentration.

### Lake Loading Response Model (LLRM)

In order to quantitatively contextualize the nutrient loading predicted by the annual and seasonal model, an estimate of the ambient landscape loading to Nequasset Lake was made using the Landscape Loading Response Model (LLRM). The LLRM is a transparent, spreadsheet based export coefficient model developed by Aecom Technology Corporation (2009). Required inputs include annual precipitation, lake area and volume, and watershed land use characteristics (including area). Calculations in the model consider atmospheric deposition, runoff, base flow, and attenuation in order to produce an estimate of the watershed nutrient yield. The model includes a small suite of empirically derived equations to make predictions about certain water quality parameters including nutrient concentrations, residence times, chlorophyll concentrations, and the probability of phytoplankton blooms. It is possible to experimentally increase the P load to the lake in the LLRM and observe the predicted effects on water quality. By noting the magnitude of load increase necessary to reach “critical” P concentrations (defined as P concentration at which probability of achieving phytoplankton concentrations > 15 ug/l reaches 10% ) the annual alewife model can then be employed to predict the escapement value at which this critical level will be reached. Precipitation data for both 2012 and 2013 were obtained for the nearby town of Bath, ME from the National Oceanic and Atmospheric Administration’s National Climate Data Center. Land use types by area for the Nequasset watershed were gathered from Chiao (2013). Rough estimates of yearly nutrient flux from the lake’s 4 tributaries were made using stream flow data collected on three to four dates in summer and fall of 2013 in each inflow coupled with nutrient concentrations from those inflows on those days. The stream flows were averaged across sampling dates and scaled to an annual estimate of water input. This volume was then multiplied by the average TDN and PO4<sup>3-</sup> concentrations to predict an annual flux to the lake. A table of export coefficients for various land use types supplied with and used in the LLRM are shown in table 2.

## Results

### Alewife migration

2013 was the second year of the volunteer based alewife count at the Nequasset fish ladder and unlike 2012, the whole of the fish migration appears to have been recorded. Counting began on April 11<sup>th</sup> and proceeded daily to June 9<sup>th</sup>. The first day of fish passage was April 30<sup>th</sup> (Figure 5). Maximum observed fish passage was on May 9<sup>th</sup> with a calculated daily run size of 9,226 individuals. This value was nearly 60% greater than the second most numerous instance of fish passage 2 days later. Numbers declined steadily thereafter, becoming small and intermittent before the end of the fish count. The last day of the count marked two days since a fish was sighted clearing the ladder. Total fish passage was counted at 5,572, and by extrapolation calculated to be



PHOSPHORUS AND NITROGEN EXPORT COEFFICIENTS FOR RUNOFF										
LAND USES		PHOSPHORUS EXPORT (KG/HA/YR)				NITROGEN EXPORT (KG/HA/YR)				
		MAXIMUM	MEAN	MEDIAN	MINIMUM	SOURCE	MAXIMUM	MEAN	MEDIAN	MINIMUM
Urban 1 (LDR)	Low density residential (>1 ac lots)	6.2	1.9	1.1	0.2		38.5	10.0	5.5	1.5
Urban 2 (MDR/Hwy)	Medium density residential (0.3-0.9 ac lots) + highway corridors	6.2	1.9	1.1	0.2		38.5	10.0	5.5	1.5
Urban 3 (HDR/Com)	High density residential (<0.3 ac lots) + commercial	6.2	1.9	1.1	0.2	Omernik	38.5	10.0	5.5	1.5
Urban 4 (Ind)	Industrial	6.2	1.9	1.1	0.2	1976,	38.5	10.0	5.5	1.5
Urban 5 (P/I/R/C)	Park, Institutional, Recreational or Cemetery	6.2	1.9	1.1	0.2	Reckhow et	38.5	10.0	5.5	1.5
Agric 1 (Cvr Crop)	Agricultural with cover crops (minimal bare soil)	2.9	1.1	0.8	0.1	al. 1980,	7.8	5.2	6.1	1.0
Agric 2 (Row Crop)	Agricultural with row crops (some bare soil)	18.6	4.5	2.2	0.3	Frink 1991,	79.6	16.1	9.0	2.1
Agric 3 (Grazing)	Agricultural pasture with livestock	4.9	1.5	0.8	0.1	Sharpley et	30.9	8.7	5.2	1.5
Agric 4 (Feedlot)	Concentrated livestock holding area	795.2	300.7	224.0	21.3	al. 1992,	7979.9	3110.7	2923.2	680.5
Forest 1 (Upland)	Land with tree canopy over upland soils and vegetation	0.8	0.2	0.2	0.0	Line et al.	6.3	2.9	2.5	1.4
Forest 2 coniferous	see below - additional sources (NH)			0.1		1998, Clark			2.5	
Forest 3 (Mixed)	see below - additional sources (NH)			0.1		et al. 2000,			2.5	
Forest 4 (Wetland)	Land with tree canopy over wetland soils and vegetation	0.8	0.2	0.2	0.0	Rohm et al.	6.3	2.9	2.5	1.4
Open 1 (Wetland/Lake)	Open wetland or lake area (no substantial canopy)	0.8	0.2	0.2	0.0	2002,	6.3	2.9	2.5	1.4
Open 2 (Meadow)	Open meadow area (no clearly wetland, but no canopy)	0.8	0.2	0.2	0.0	unpublished	6.3	2.9	2.5	1.4
Open 3 (Barren)	Mining or construction areas, largely bare soils	4.9	1.5	0.8	0.1	AECOM	30.9	8.7	5.2	1.5
Other 1	Define:	0.8	0.2	0.2	0.0	data	6.3	2.9	2.5	1.4
Other 2	Define:	6.2	1.9	1.1	0.2		38.5	10.0	5.5	1.5
Other 3	Define:	18.6	4.5	2.2	0.3		79.6	16.1	9.0	2.1

PHOSPHORUS AND NITROGEN EXPORT COEFFICIENTS FOR BASEFLOW										
LAND USES		PHOSPHORUS EXPORT (KG/HA/YR)				NITROGEN EXPORT (KG/HA/YR)				
		MAXIMUM	MEAN	MEDIAN	MINIMUM	SOURCE	MAXIMUM	MEAN	MEDIAN	MINIMUM
Urban 1 (LDR)	Low density residential (>1 ac lots)	0.050	0.010	0.010	0.001		20.00	5.00	5.00	1.00
Urban 2 (MDR/Hwy)	Medium density residential (0.3-0.9 ac lots) + highway corridors	0.050	0.010	0.010	0.001		40.00	10.00	10.00	2.00
Urban 3 (HDR/Com)	High density residential (<0.3 ac lots) + commercial	0.050	0.010	0.010	0.001		80.00	20.00	20.00	4.00
Urban 4 (Ind)	Industrial	0.050	0.010	0.010	0.001	Uttormark et	20.00	5.00	5.00	1.00
Urban 5 (P/I/R/C)	Park, Institutional, Recreational or Cemetery	0.050	0.010	0.010	0.001	al. 1974,	20.00	5.00	5.00	1.00
Agric 1 (Cvr Crop)	Agricultural with cover crops (minimal bare soil)	0.050	0.010	0.010	0.001	Mitchell et al.	10.00	2.50	2.50	0.50
Agric 2 (Row Crop)	Agricultural with row crops (some bare soil)	0.050	0.010	0.010	0.001	1989, Miller	10.00	2.50	2.50	0.50
Agric 3 (Grazing)	Agricultural pasture with livestock	0.050	0.010	0.010	0.001	et al. 1997,	10.00	2.50	2.50	0.50
Agric 4 (Feedlot)	Concentrated livestock holding area	0.100	0.030	0.030	0.001	AECOM	20.00	5.00	5.00	1.00
Forest 1 (Upland)	Land with tree canopy over upland soils and vegetation	0.010	0.004	0.004	0.001	Unpublished	100.00	25.00	25.00	5.00
Forest 2 (Wetland)	Land with tree canopy over wetland soils and vegetation	0.010	0.004	0.004	0.001	Data, some	1.00	0.50	0.50	0.05
Open 1 (Wetland/Lake)	Open wetland or lake area (no substantial canopy)	0.010	0.004	0.004	0.001	reliance on	1.00	0.50	0.50	0.05
Open 2 (Meadow)	Open meadow area (no clearly wetland, but no canopy)	0.010	0.004	0.004	0.001	runoff	1.00	0.50	0.50	0.05
Open 3 (Barren)	Mining or construction areas, largely bare soils	0.010	0.004	0.004	0.001	references	1.00	0.50	0.50	0.05
Other 1	Define:	0.010	0.004	0.004	0.001	as well	1.00	0.50	0.50	0.05
Other 2	Define:	0.050	0.010	0.010	0.001		20.00	5.00	5.00	1.00
Other 3	Define:	0.050	0.010	0.010	0.001		80.00	20.00	20.00	4.00

OTHER AREAL SOURCES										
		PHOSPHORUS EXPORT (KG/HA/YR)				NITROGEN EXPORT (KG/HA/YR)				
		MAXIMUM	MEAN	MEDIAN	MINIMUM	SOURCE	MAXIMUM	MEAN	MEDIAN	MINIMUM
from Forested Area	Deposition originating in largely forested area	0.54	0.27	0.20	0.07	Reckhow et	11.30	5.96	6.50	0.99
from Agricultural/Rural Area	Deposition originating in largely agricultural area	0.97	0.45	0.30	0.12	al. 1980,	38.00	20.98	13.10	10.49
from Urban/Industrial Area	Deposition originating in largely urban area	3.67	1.27	1.00	0.26	Dillon et al.	24.80	18.51	21.40	7.40

Table 2: Export coefficients used in the LLRM model.

41,565 alewives. Fish passage in 2013 was 36% greater than in 2012, however this figure is likely exaggerated by an incomplete (truncated) count in 2012. Total alewife harvest in 2013 was 717.5 bushels, and by assumption of 120 fish per bushel, 86,100 fish. This makes for a total run size of over 127,000 with 33% escapement. 3 adults from the 2012 fish run and 3 juveniles caught in Nequasset Lake in July of 2012 were procured from Theo Willis of USM. Wet (frozen) weights of the adults averaged 115.8 grams, while the juveniles averaged 2.0 grams. These figures were used in subsequent modeling calculations.

## Nutrient concentrations

### Top of Nequasset Dam

Data from the daily monitoring program at the top of Nequasset dam provide a time series of several nutrient species, Chlorophyll a concentrations, and the  $\delta^{15}N$  signature of particulate organic matter. The nutrient data series in 2013 contain 38 samplings across 38 days, with sampling starting 5 days before and terminating 5 days after the fish run. Phosphate levels in 2013 were below the limit of detection (<0.005 mg/l) all but two days, May 12th and May 14th, on which the concentrations were 0.0067mg/l and 0.0066 mg/l respectively (Figure 6 B1). The same sampling program in 2012 yielded detectable phosphate levels on 17 out of the 45 days, with a mean value of 0.010mg/l (standard deviation 0.007) for those detectable concentrations (Figure 6 D1). Inserting 0's for all values below the detection limit provided an average of 0.004mg/l. Ammonium levels were detectable 31 days in 2013 (Figure 6 B2) with a mean of 0.0293mg/l (stdev 0.0358), and 0.0239mg/l when inserting 0's. 2012 ammonium data (Figure 6 D2) were limited to 25 days of collection and were of de-

tectable concentration 24 days with a mean of 0.030mg/l (stdev 0.038). 2012 dissolved organic carbon (mean 5.6 mg/l, stdev 0.6), total dissolved nitrogen (mean 0.359 mg/l, stdev 0.62), nitrate + nitrite (mean 0.026mg/l, stdev 0.016), and total dissolved silica (mean 0.67 mg/l, stdev 0.51) data are included in the appendix. 2013 dissolved organic carbon (mean 4.75 mg/l, stdev 0.4), total dissolved nitrogen (mean 0.20 mg/l, stdev 0.04), nitrate + nitrite (mean 0.018mg/l, stdev 0.013), and total dissolved silica (mean 0.82 mg/l, stdev 0.6) data are also in the appendix. Mean DOC and TDN were both significantly greater in 2012 (t-test,  $p < 0.05$ ).

The Deep Hole site was sampled less frequently than the TOD in 2013. Across 6 samplings taken approximately every two weeks, surface and deep water  $PO_4^{3-}$  concentrations were detectable just once at the surface (Figure 6 B1), giving DHS waters an average of 0.0013 mg/l  $PO_4^{3-}$  (stdev .0029) when inserting 0's. Ammonium levels were more commonly detected at both sites (Figure 6 B2), with deep waters averaging 0.0075 mg/l (stdev 0.0072) and surface waters averaging 0.0049 mg/l (stdev 0.0056). Averaged combined nitrite+nitrate levels were much greater in both cases (Figure 6 B3), averaging 0.051 (stdev 0.0075) in the hypolimnion and 0.026 (stdev 0.026) at the surface. In 2012,  $PO_4^{3-}$  levels were undetectable in all surface samples but averaged 0.14 mg/l (stdev 0.34 mg/l) in the hypolimnion, with two out of six days yielding detectable levels (Figure 4 D1). Surface  $NH_4^+$  levels averaged 0.044mg/l (stdev 0.076), while deep water averaged 0.043mg/l (stdev 0.036). Surface combined  $NO_2^-$  and  $NO_3^-$  (Figure 4 D4) averaged 0.025 mg/l (stdev 0.025) while hypolimnetic waters averaged 0.070mg/l (stdev 0.044). TDN, DOC, and  $SiO_2$  did not differ significantly between the surface and deep water samples (t-test, 2 tails, unequal variances,  $p > 0.05$ ) and the averaged values of both sites were 0.25mg/l, 4.92 mg/l, and 0.86 mg/l respectively (data included in appendix).  $NH_4^+$  was the only species which had significantly different concentrations between years (t-test <0.05) at the same site, with DHD being nearly 6 times greater on average in 2012 than in 2013.

### Tributaries

In 2012, George's Brook had mean  $PO_4^{3-}$  concentrations of 0.0054mg/l (stdev 0.0037) while Northeast Inlet, Nequasset Brook, and Sucker Brook had undetectable levels in the 5 samples taken throughout the summer (Figure 6 C1). Mean  $NH_4^+$  concentrations of George's Brook, Northeast Inlet, Nequasset brook, and

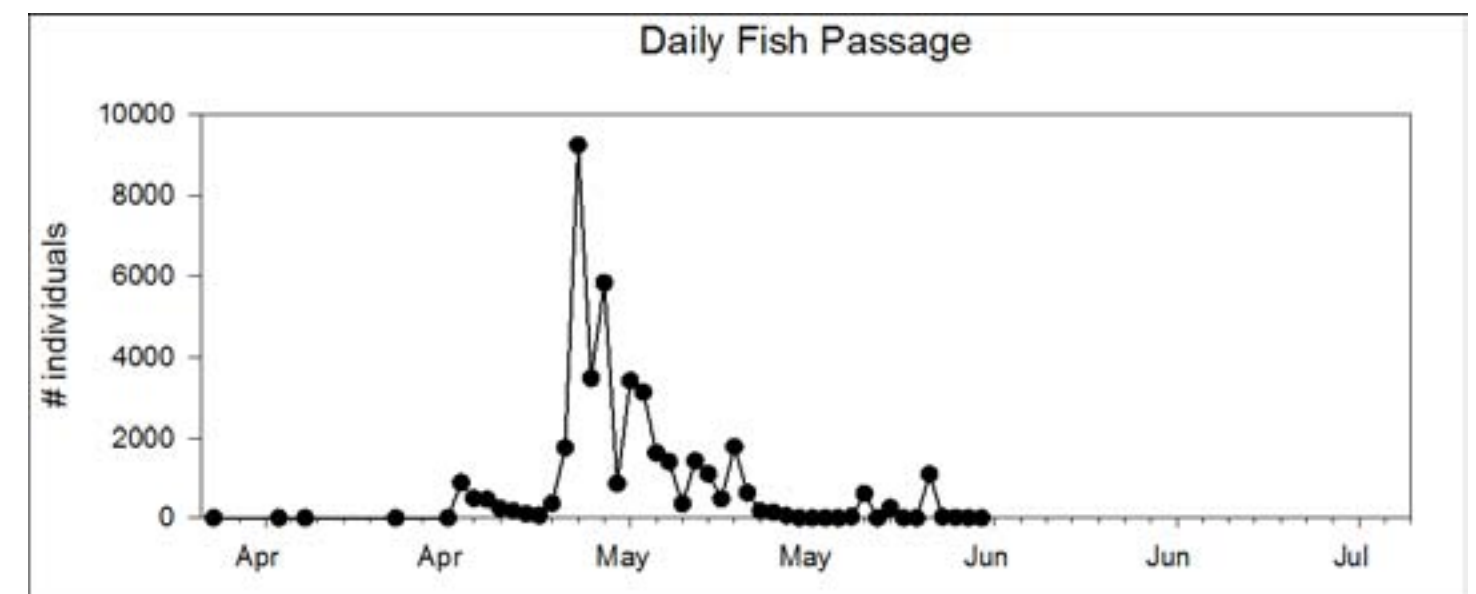


Figure 5 Estimated daily fish passage in 2013. Based on daily visual counts by volunteers.

Sucker Brook were 0.0096mg/l(stdev 0.007),0.022 mg/ (stdev 0.009), 0.029 mg/l(stdev.027), and 0.061mg/l (stdev 0.063) respectively. Combined nitrite and nitrate concentrations were 0.028mg/l (stdev 0.013), 0.048mg/l(stdev.059), 0.061mg/l(stdev0.056), and 0.048mg/l (stdev 0.030). 2013 mean PO<sub>4</sub><sup>3-</sup> concentrations were, as listed in the same site order as for 2012, 0.0048 mg/l (stdev 0.0053), undetectable, 0.0055 mg/l (stdev 0.0086), 0.0013mg/l (stdev 0.0029). NH<sub>4</sub><sup>+</sup> values were 0.0040mg/l (stdev 0.0041), 0.0060mg/l (stdev 0.067), 0.0220mg/l (stdev0.019), and 0.0039mg/l (stdev 0.0058). Combined NO<sub>2</sub><sup>-</sup> and NO<sub>3</sub><sup>-</sup> averaged 0.0190mg/l(stdev 0.0146), 0.018mg/l (stdev .0087mg/l), 0.025mg/l (stdev 0.0110) , and 0.030mg/l (stdev 0.011). Interannual differences in tributary nutrient concentrations were minimal, though PO<sub>4</sub><sup>3-</sup> was detectable 3 out of 6 samples in Nequasset brook in 2013, while there were no detectable levels any day in 2012. A decrease in TDN concentrations from 2012 to 2013 in Sucker Brook was nearly significant (t-test, p=0.05).

It should be noted that as nutrient concentrations are often near or below the detection limits (0.005 ppm), the mean values listed above and used in this analyses are likely to be underestimates. This is the result of series containing multiple values labeled only as <0.005mg/l, and necessarily being replaced with a value of 0. As an illustrative example, the series of phosphate values for Sucker Brook in 2013 were experimentally altered, changing the 5 undetectable values (out of 6 total) to arbitrary numbers below the detection limit (0.001,0.002,0.003,0.004,0.001). This alteration caused the mean concentration to change from the previously reported 0.0013 mg/l to 0.0029mg/l, an increase of 120%. While rough, this exercise shows the possibility of a substantial underestimation of nutrient concentrations under conditions where a large percentage of values are under the 0.005mg/l detection limit.

### Chlorophyll and POM stable isotopes

One way ANOVA revealed significant temporal differences in chlorophyll a concentrations at the top of dam and deep hole deep sites in 2013 (figure 7). Both sites showed significantly elevated (p<0.05) chlorophyll concentrations on May 7<sup>th</sup>. Both the sites showed a generally normal distribution about this central peak. In both cases, this peak occurs 6 days into the fish count, but on a day with no counted fish passage, 3 days prior to the single largest day of the fish run. In 2012, this trend appears to hold true for the TOD site, however a lack of data preclude an ANOVA test. Chlorophyll points on either side of the peak are also proportionately higher than in the 2013 series. At the deep hole deep sample site however, the concave down curve seen in other graphs is finished by an upward curve towards the greatest value (6.6 ug/l), outside the period of the fish run. TOD δ<sup>15</sup>N of POM in 2012 peaks on October 17<sup>th</sup>, after showing a small increase during the period of the fish run. δ<sup>15</sup>N of POM at the top of dam site in 2013 decreased substantially and nearly in unison with the cessation of the fish run. However, data does not exist long before the beginning of the run and the first data point, five days before the commencement of the run, is the second highest value. δ<sup>13</sup>C of POM data are presented for the George's Brook site in both 2012 and 2013 as they exhibit a period of enrichment (3‰ in 2012 but only 0.4‰ in 2013) that was observed at several other sites (see appendix), often concomitant with the adult alewife immigration.

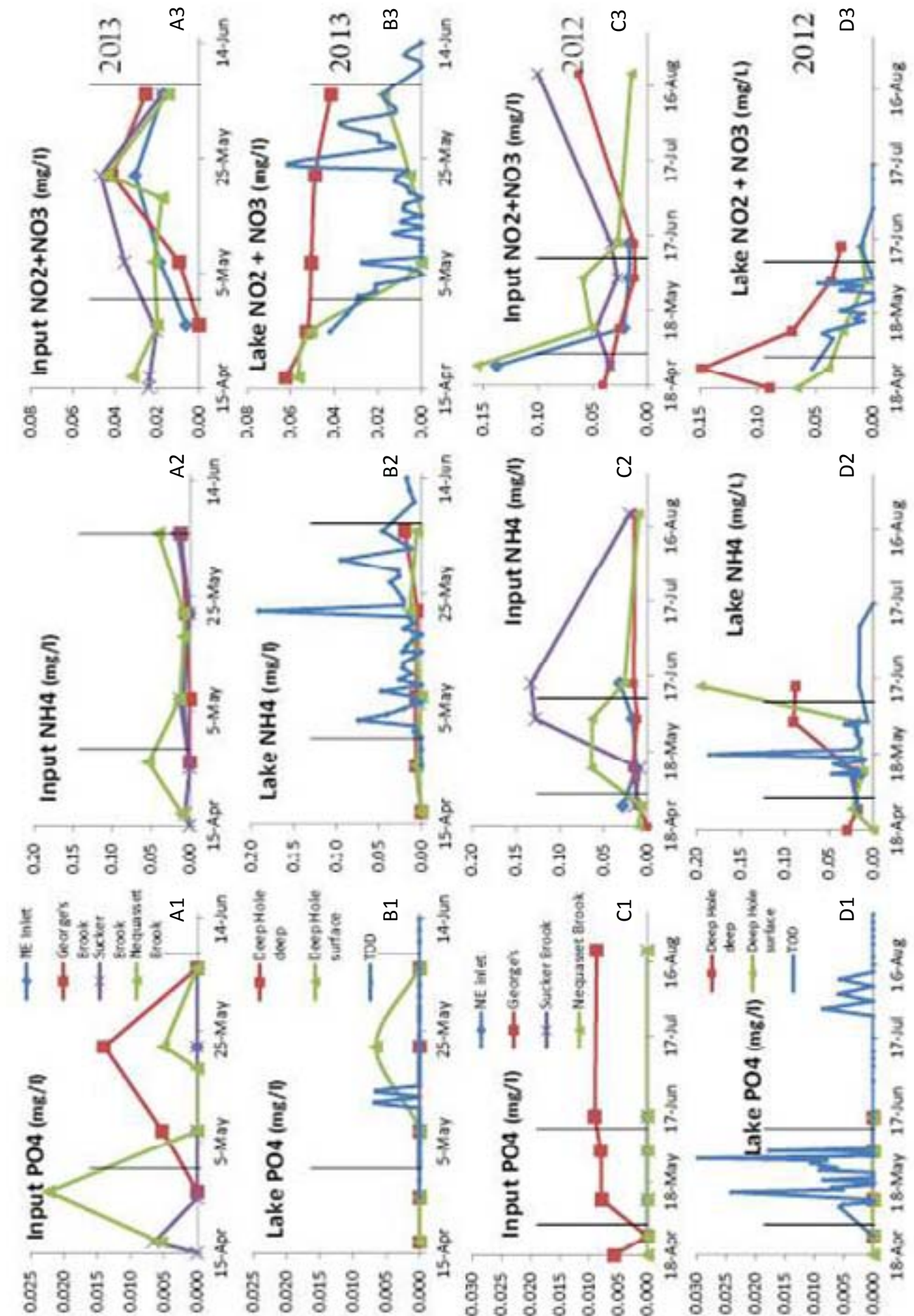


Figure 6: Nutrient concentrations of tributaries and lake in 2012 and 2011. The period of the fish run is bracketed by vertical bars.

## Annual model:

Results from the annual model are presented in both a table format and as a graphical function. The table includes a detailed breakdown of alewife component fluxes under 5 different relevant escapement scenarios. The graphical function provides insight into the net nutrient dynamics of the alewife migration across a continuous range of escapement values.

### Scenarios

#### Phosphorous

The annual model was itemized for 5 different scenarios of varying escapement: the 2013 fish run, 2013 fish run unharvested, 2012 fish run, 2012 fish run unharvested, and 1958 harvest (Table 3). Alewife escapement into Nequasset lake in 2013 totaled 41,566 individuals, of which 18,289 were predicted to spawn. Given this escapement, phosphorous loading by adult gamete release was predicted to be 1.14 kg P, adult excretion was predicted to be 1.54kg P, and adult carcass loading was predicted to liberate 4.78kg P. Theoretically adding back the total number of alewives harvested at the base of Nequasset dam in 2013 would boost escapement to 127,666 ale-

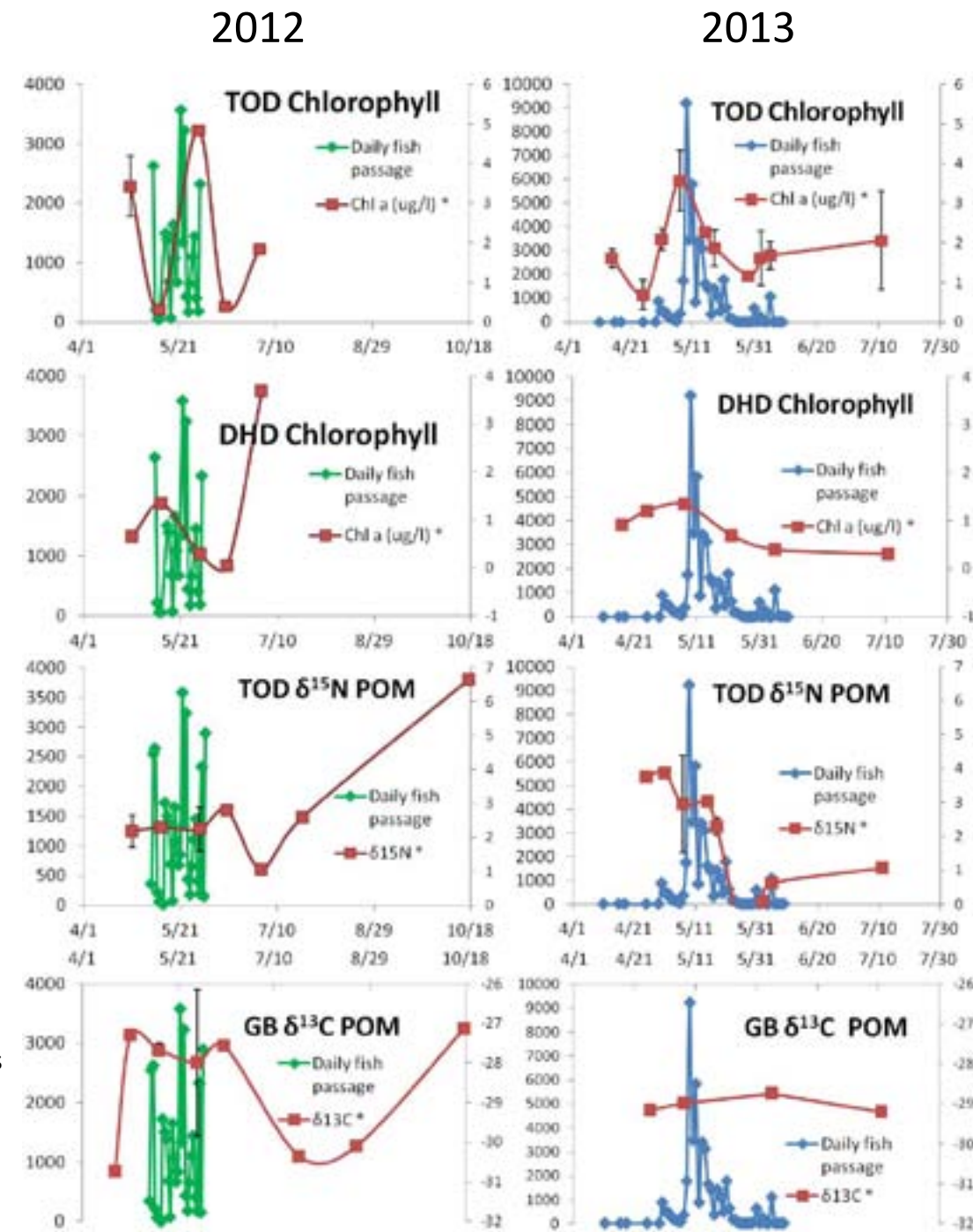


Figure 7: Chlorophyll concentrations at TOD and DHD and  $\delta^{15}N$  of POM at TOD and GB in 2012 and 2013. All underlain by daily fish passage.

wives and increase adult loading to 3.51kg P from gamete release, 4.74kg P from excretion, and 14.69 kgP from carcass loading. The 1958 scenario is based on an escapement value that is actually the number of fish known to be harvested at the Nequasset fish ladder in 1958 (Chiao 2013). This scenario, assuming an alewife escapement of 1,126,000 individuals, yielded an adult loading of 30.99kg P from gamete release, 41.82 kg P from excretion, and 129.53 kg P from carcass decay. Total adult P loading for 2013, 2013 unharvested, and 1958 is predicted as 7.47 kg P, 22.94kg P, and 202.34 kg P respectively. Total YOY export is presented for both the 6 and 336 YOY/spawner scenarios, hereafter referred to as the YOY export low and YOY export High scenarios respectively. Total YOY P export for 2013, 2013 unharvested, and 1958 was predicted as (low/high) 2.70/15.96 kg P, 6.93/15.96 kg P, and 15.85/15.96 kg P. respectively. The net annual phosphorous fluxes are the difference between adult imports and YOY exports and were calculated to be (low/high) 4.77/ -8.49 kg P, 16.01/ 6.98 kg P, and 186.48/186.38 kg P respectively. Note that the sign convention is such that positive numbers indicate net import to the lake while negative ones indicate net export. The high of 15.96kg P YOY export observed in all scenarios is the maximum theoretical P export allowed by the current biomass density equation.

#### Nitrogen

Nitrogen inputs by gamete release in the 2013, 2013 unharvested, and the 1958 scenarios were estimated at 8.49 kg N, 26.08 kg N, and 230.03 kg N respectively. N release by in lake excretion for the same scenarios were 17.58 kg N, 53.99 kg N, and 476.20 kg N. Nitrogen loading by carcass decomposition was modeled to be 61.84 kg N, 189.93kg N, and 1675.14 kg N, respectively. YOY exports were modeled to be (low/high) 11.60/ 68.52 kg N, 29.76/68.52 kg N, and 68.07/68.52 kg N. Here, 68.52 kg N is the maximum possible nitrogen given the current biomass density equation. Net flux in each scenario was (low/high) 76.31/19.39 kg N, 240.24/201.48 kg N, and 2313.3/2312.8 kg N.

#### Continuous

Results of the annual model are presented in graphical format in order to display the behavior of the system across a continuous range of escapement (Figure 8). The three lines of the graph represent the adult import, YOY export low, and YOY export high as a function of adult escapement into the lake. While the line representing adult import is linear, those representing YOY export are curvilinear as the result of the asymptot-

Scenario (Phosphorous)	Escapement	Adult Carcass	Adult excretion	Adult Gamete	YOY export (low)	YOY export (high)	Net flux (low)	Net flux (High)	Ambient P (landscape + atmospheric)	Total P loading YOY (low)	Total P loading YOY (high)	alewife % total YOY (low)	alewife % total YOY (high)
2012	30517	3.5	1.1	0.8	2.0	16.0	3.5	-10.5					
2013	41566	4.8	1.5	1.1	2.7	16.0	4.8	-8.5	555.2	560.0	546.7	0.9	-1.6
2013 unharvested	127666	14.7	4.7	3.5	6.9	16.0	16.0	7.0	555.2	571.2	562.2	2.8	1.2
1958	1126000	129.5	41.8	31.0	15.9	16.0	186.5	186.4	555.2	741.7	741.6	25.1	25.1

Scenario (Nitrogen)	Escapement	Adult Carcass	Adult excretion	Adult Gamete	YOY export (low)	YOY export (high)	Net flux (low)	Net flux (High)	Ambient N (landscape + atmospheric)	Total N loading (low)	Total N loading YOY (high)	alewife % total YOY (low)	alewife % total YOY (high)
2012	30517	45.4	12.9	6.2	8.7	68.5	55.8	-4.0	16773				
2013	41566	61.8	17.6	8.5	11.6	68.5	76.3	19.4	16773	16849.4	16792.5	0.5	0.1
2013 unharvested	127666	189.9	54.0	26.1	29.8	68.5	240.2	201.5	16773	17013.3	16974.5	1.4	1.2
1958	1126000	1675.1	476.2	230.0	68.1	68.5	2313.3	2312.8	16773	19086.4	19085.9	12.1	12.1

Table 3: Breakdown of alewife, landscape and atmospheric nutrient inputs to Nequasset Lake.

ic exponential biomass density function incorporated into the model. For phosphorous, the slope of the adult input line is 0.0002 kg, or 0.2 grams P per adult. This same slope for the nitrogen function is 0.0021kg, or 2.1 grams N for each fish immigrating to the lake. In the case of both P and N, the low YOY export scenario remains below the line of the adult import, indicating that at no escapement level will exports exceed imports. For the high YOY export curve, the point of intersection with the adult import curve represents the point of equal import/export. For phosphorous, this point lies at an escapement of 88,824, while for nitrogen, the intersection is at 32,401. All escapement lower than these x-intercepts will provide a net export of nutrient, while all escapement greater will result in a net import.

## Daily Model

### Equations

#### Growth rate

The YOY growth rate equation calculated was

$$y=0.003434+0.03948 e^{-1.2397x}$$

Where y is individual growth rate in grams/day and x is the initial YOY density in fish/m<sup>2</sup>. Regressing this model on the calculated data points yielded an r<sup>2</sup> value of 0.998.

#### Decay

Decay equations yielding the percent remaining nitrogen and phosphorous with time were structured as double exponentials, the same as the mass loss equation provided by Parmenter and Lamarra (1991). Percent remaining N was determined as

$$y= 8.7058e^{-0.0024t} + 91.2942e^{-0.0985t}$$

while the equation for percent remaining P was modeled as

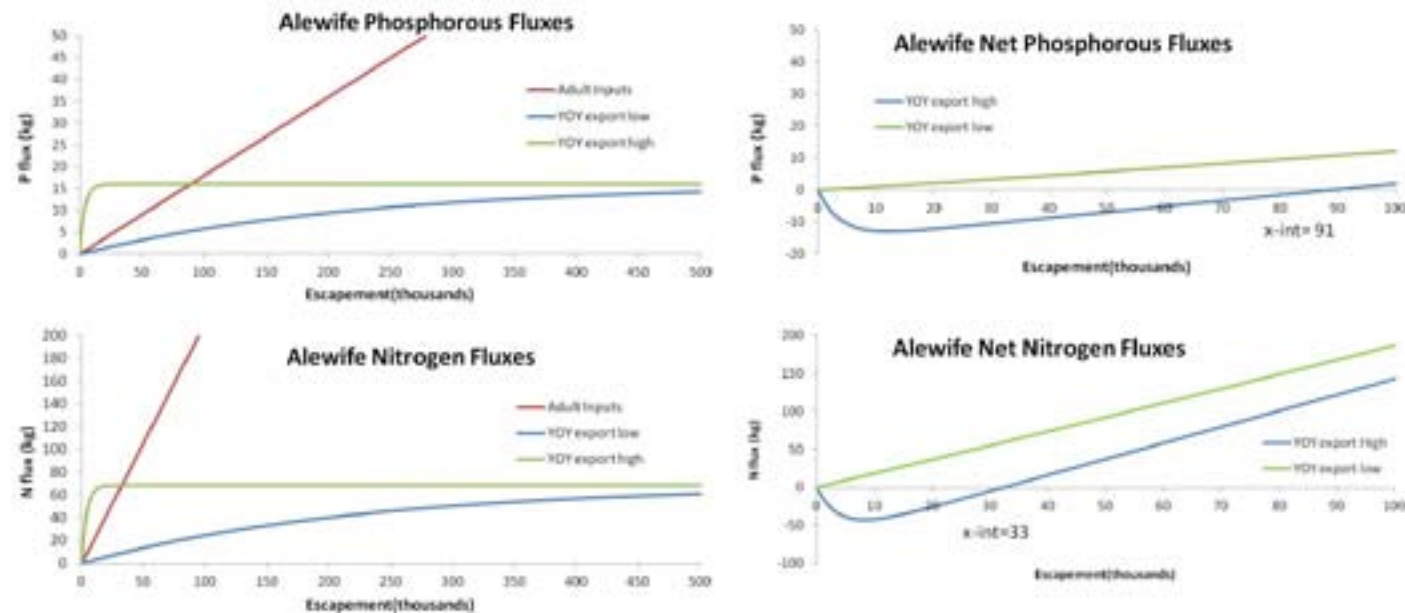


Figure 8: Annual model of nitrogen and phosphorous fluxes from the alewife migration as a function of adult escapement. At left are combined graphs of adult inputs and YOY exports. At right are net values (adult flux-YOY flux). YOY high and YOY low are scenarios discussed in the text.

$$y=51.8421e^{-0.1525t} + 48.1579e^{-0.00096t}$$

Regression of modeled data on target data yielded r<sup>2</sup> values of 0.9996 for the N equation and 0.982 for the P equation.

### Outputs

Model outputs indicate that daily adult nutrient imports begin immediately at the start of the fish run, and peak on 5/11, two days after the largest day of the fish run but ten days before the peak fish population had been achieved (figure 9A). The P flux on this day was 399 grams. The curve of daily nitrogen release peaked on 5/14 with a value of 4,166 grams. The “bell” of daily nitrogen release is generally wider than that of phosphorous, though the two curves are largely similar. Cumulative import curves for N and P have a nearly identical “s” shape, though the phosphorous curve steepens slightly before that of nitrogen. These cumulative curves begin to level off as spawned adults complete their emigration (P input 89% of total on 6/21). Total nutrient input is achieved after the last fish to have died reaches its 309 day decay limit on April 26<sup>th</sup> of 2014. In the late stages of decay (300 days after last adult emigrant for instance) the total daily P release is just over one gram, while the daily N release is 2.7 grams. Peak YOY population under the low YOY scenario was 116,864 fish, indicating a density of 0.068 fish/m<sup>2</sup> while the peak YOY population under the high YOY scenario was 6,693,604 fish with a density of 3.89 fish/m<sup>2</sup>. Minimum individual growth rates observed at these densities were 0.040 g/day and 0.0038 g/day. Community growth rates (g/day) observed at these densities were 4,642 g/day and 25,109 g/day (figure 9B). While the curve of daily growth rate is similar in both the high and low YOY scenarios, the peaks of community growth rate are at different times. While the aforementioned maximum community growth rate for the low YOY scenario is during the period of maximum population and density, the highest observed community growth rates in the high YOY scenario occurred several weeks before and after maximum density was achieved. The highest rate observed was on September 3<sup>rd</sup>, two weeks after the commencement of YOY emigration. In all cases, the net daily nutrient flux begins dominated by highly positive adult inputs, peaking on the same day as daily adult inputs, but then becomes negative for a time as YOY nutrient incorporation outpaces carcass input (figure 9C). This transition comes on May 27<sup>th</sup>/June 12<sup>th</sup> for the high YOY/low YOY phosphorous scenarios and on June 10<sup>th</sup>/June 27<sup>th</sup> (high/low). The flux in all cases then becomes positive again (Sept 25/ Sept 10) as juveniles emigrate and carcass inputs remain as the legacy of the years migration. Net cumulative nutrient fluxes begin positive in both low and high YOY export cases for both N and P though the high YOY scenarios for phosphorous becomes negative on July 2<sup>nd</sup>. Peak P accumulation is achieved on 5/26 and 6/11 (high/low) and peak N accumulation is seen on 6/9 and 6/26 (high/low).

Under the 2013 scenario, maximum daily P concentration change observed came on 5/11, with a value of  $1.45 \cdot 10^{-3}$  µg/l (ppb) or  $1.45 \cdot 10^{-6}$  mg/l assuming low YOY export (Figure 9D). Maximum daily nitrogen concentration change was predicted on May 14<sup>th</sup> with an increase of  $1.48 \cdot 10^{-2}$  µg/l or  $1.48 \cdot 10^{-5}$  mg/l. A cumulative concentration curve is also displayed, and maximum concentration achieved for P and N (low yoy export) is 0.00217 ppb ( June 7<sup>th</sup>) and 0.293ppb N (june 20<sup>th</sup>). The same curves were created for the 1958 scenario, and yielded maximum daily P increases of 0.00394 ppb, and maximum daily N increases of 0.411 ppb N. Cumulative concentration curves in the 1958 scenario yielded maximum concentration values of 0.615 ppb P and 8.24 ppb or 0.008mg/l N.

Total export by juveniles was significantly elevated in the daily model relative to the annual model as the result of a gradual release from density dependent growth with juvenile emigration, an effect predicted by West et al. (2010). This increased P and N juvenile export by nearly 10% in the YOY high scenario in 2013, and by nearly 400% in the YOY high scenario of 1958. These increases in export had the effect of decreasing net P and N flux in 1958 by 26% and 9% respectively.

## Ambient Loading

Estimates of annual load made from riparian measurements in Nequasset Brook, Sucker Brook, Northeast Inlet, and George's Brook varied widely between 2012 and 2013. Total annual P load in kilograms was estimated (from  $PO_4^{3-}$ ) to be between 101 and 153 kg (treating P levels below detection as 0 and 0.003 respectively) for 2013. Nitrogen loading was estimated from TDN concentrations to be 4,131.5 kg annually. 2012 nitrogen load was estimated by Chiao (2013) to be 22, 172 kg. Annual N and P loads as well as predicted lake nutrient concentrations were compared to those estimated by the stream flow method, and watershed attenuation values for N and P were adjusted in an attempt to minimize differences between the two estimation

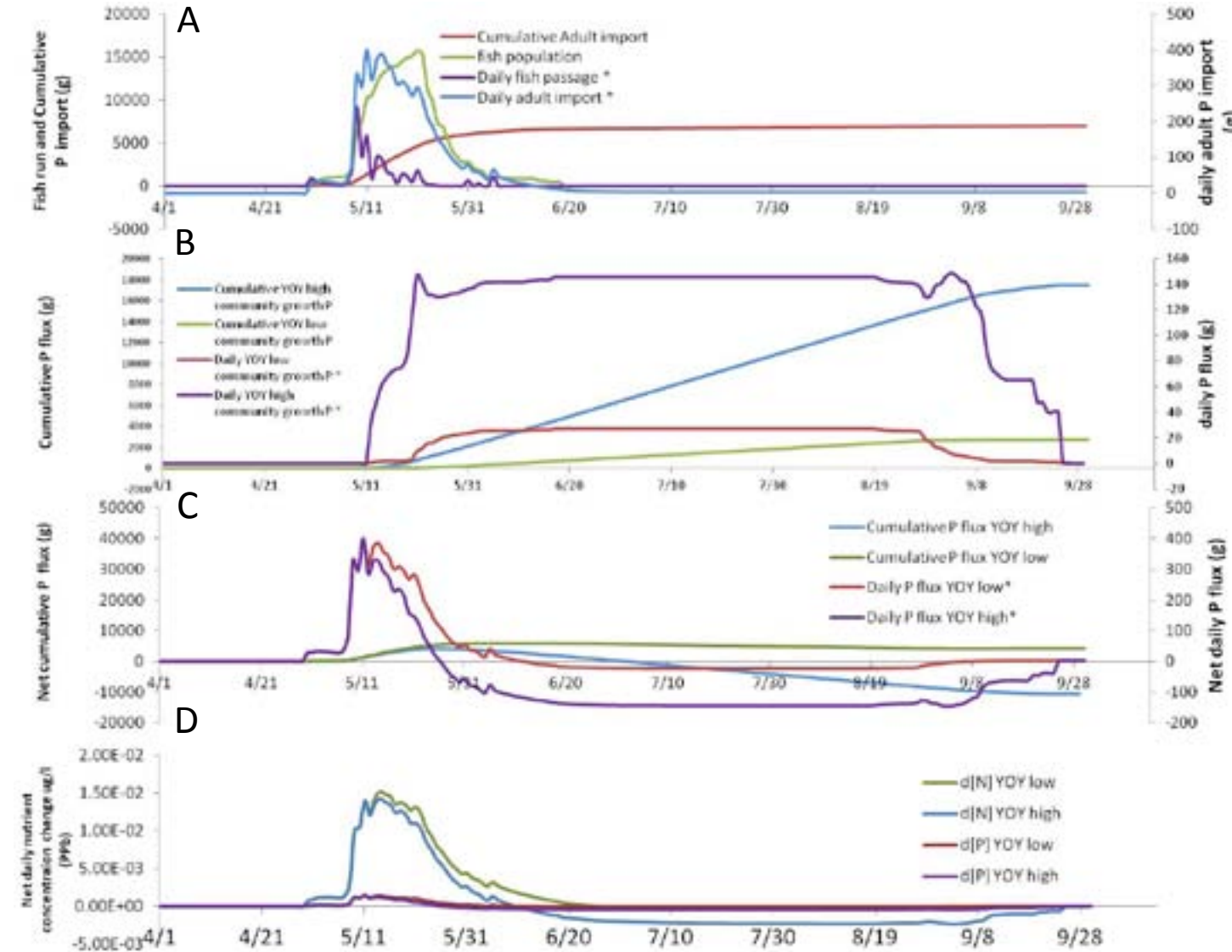


Figure 9: Daily alewife nutrient loading model. Includes adult import, YOY incorporation and export, net flux, and net flux dissolved in whole lake volume (concentration,  $d[N/P]$ )

methods. By using a phosphorous attenuation coefficient of 0.65 and a nitrogen attenuation coefficient of 1, the 2013 annual landscape nutrient load was predicted as 508 kg P and 15,748 kg N, with the estimated 2012 load being identical. Incorporating atmospheric deposition brings these figures to 555 kg P and 16773 kg N (Table 3). After including estimates of phosphate concentration in system effluent, calculated from concentrations in TOD waters, the 2013 model predicted average N concentrations of 140 ppb and average P concentrations of 8.0 ppb. These figures overestimated measured summertime  $PO_4^{3-}$  (mean 3.4 ppb among the lake sites) by 2.4 times, and underestimated mean measured in lake TDN concentration (192 ppb) by 36%. Predicted P loads may be substantially higher than measured because the model output is calibrated for total phosphorous (TP) while orthophosphate was measured in Nequasset lake. Freshwater lake ratios of TP to orthophosphate may be as high as 10:1 in some cases (Hutchinson, 1957). Given that the LLRM modeled fluxes and concentrations were “ballpark” comparable to the concentrations observed in 2012 and 2013 and riverine fluxes calculated in 2012, the figures given by the 2013 LLRM were used to contextualize predictions of alewife fluxes. The N:P ratio of this loading is 30 and is consistent with the both the riverine fluxes and in-lake ratios that generally range between 25 and 40 in Nequasset. In addition, total tributary water output in 2013 was markedly lower than in 2012 (over 6x) during the four sampling periods and this may account for the discrepancy in calculated fluxes.

The relative contribution of the alewife migration to Nequasset lakes annual nitrogen and phosphorous budget is calculated using the results of the LLRM (Table 3). In 2013, anadromous alewives were responsible for importing 4.8 kg of nitrogen, or exporting 8.5 kg in the low and high YOY scenarios, respectively. An import of 4.8 kg would amount to 0.85% of the annual load. If unharvested, the 2013 migration would have likely imported between 6.9 and 16 kg P (high/low export), corresponding to 1.2 and 2.8% of the annual P load. In 1958, assuming a historically consistent landscape loading, 25% of Nequasset's annual P budget would be attributable to marine derived nutrient transported from the Gulf of Maine by migrating alewives. Alewives contribute 12% of the annual N budget under the same circumstances. Current models indicate that the “critical” alewife escapement level (at which critical P concentrations are predicted) is roughly 6.7 million adults, or around 16x the escapement level in 2013.

## Discussion

By approaching the study of Nequasset Lake's alewife migration from both an empirical and theoretical angle, the information and insight generated proved to be more holistic than if either had been employed independently. The large dataset collected and analyzed provides important background information regarding the spatio-temporal variability of lake biogeochemistry, while the modeling exercise affords a theoretical framework for prediction and inquiry regarding difficult to observe effects.

Few statistically significant interannual changes in nutrient and chlorophyll concentrations and the carbon and nitrogen isotopic signatures of POM were observed. Exceptions include the detection of phosphate in Nequasset Brook in 2013, and a marked decrease in the ammonium concentrations in the deep hole deep site from 2012 to 2013. This indicates that the lake is relatively stable, and its low mean in-lake chlorophyll concen-

trations give it a Carlson trophic state index(CTSI) of under 40, qualifying it as an oligotrophic lake. CTSI was 33 in 2012 and 34 in 2013. Lake water N:P ratios (TDN:PO<sub>4</sub><sup>3-</sup>) averaged 35 in both 2012 and 2013, suggesting that Nequasset is phosphorous limited (Donald 2011).

The lack of statistically significant correlations between either incoming fish run or estimated in-lake alewife population and the concentrations of various nutrient species, chlorophyll concentrations, δ<sup>13</sup>C POM, and δ<sup>15</sup>N POM at any site makes it difficult to draw conclusions about any empirically evident geochemical or ecological effects of the alewife migration on Nequasset lake. Cross correlation yielded several significant results, however no consistently significant lag time appeared across nutrient species or for a single nutrient species across two years of testing. That said, there are several areas of the data that bear mention. Qualitatively, the phosphate and ammonium concentrations in 2012 and ammonium in 2013 (fig) and the TDN concentrations at TOD in 2012 (appendix) appear to be most variable at the top of Nequasset dam within the period of the fish run. Phosphate levels in 2012 are especially interesting as 65% of the samples taken had undetectable concentrations of P, but only 39% of those taken within the period of the fish run had undetectable concentrations.

Water sampling on May 31<sup>st</sup> in 2012 showed PO<sub>4</sub><sup>3-</sup> concentration at the top of the dam to be 0.018 mg/l, while the DHS and DHD sites both had undetectable levels of orthophosphate. By contrast, the three other instances in this time series where phosphate concentration data exist for all three lake sites (TOD, DHS, DHD), concentrations have been homogeneously undetectable. While regression of the difference in concentration between TOD and DHS on daily fish count was insignificant, this may be a fruitful way to analyze concentration data in more expansive data sets with more overlapping data points. If this observed elevation in PO<sub>4</sub><sup>3-</sup> was due to alewife MDN input, one would also expect to see a corresponding increase in NH<sub>4</sub><sup>+</sup> concentration, however this was not observed. Additionally, an influx of isotopically enriched NH<sub>4</sub><sup>+</sup> from fish excretion might likewise be manifested as an enrichment in <sup>15</sup>N POM, however this was not observed. Forthcoming analyses of water δ<sup>15</sup>N may be better suited to detect any enrichment. Likewise, a large spike in NH<sub>4</sub><sup>+</sup> concentration (nearly 0.2 mg/l) at TOD site in 2013 is not seen at the deep hole sites nor the tributaries but is unaccompanied by a P spike expected of an MDN input.

Significant (ANOVA p<0.05) increases in chlorophyll concentrations during the fish migration at the TOD and DHD sites were observed in 2013, and to some extent, similar patterns are observed in 2012, however a lack of data prevents statistical analysis. Operating under the hypotheses that high densities of migratory fish may increase water nutrient concentrations, one might expect to see corresponding increases in phytoplankton growth. Water chlorophyll concentrations have been observed to increase with increasing stream salmon carcass densities (Wipfli 1998) and phytoplankton blooms occurred in tank microcosm experiments with live alewives (Durbin 1979). A 1.6µg/l increase in chlorophyll concentration was measured from the first to the sixth day of the alewife migration in Nequasset lake, at which point the fish count indicates 2,783 fish had entered the lake. However, despite this observed increase, chlorophyll concentrations did not remain elevated during the migration, over the course of which alewife population increased by an order of magnitude from the sixth day (May 7<sup>th</sup>). Chlorophyll concentration increases ranging from several to approximately 20 µg/l were observed in the microsm experiment after six days, however densities there exceeded 1 fish/m<sup>2</sup> whereas

Nequasset densities, even if only including the narrowed southern area of the lake south of the railroad bridge (figure 4) would be close to 0.1 fish/m<sup>2</sup> with the fish population on day 6 of the migration.

To observe the chlorophyll increase at the TOD site as the result of increased alewife nutrient loading would not be out of the realm of possibility given results from this microcosm experiment, however the continued increase in concentrations observed in the microcosm through day 22 of the experiment suggest that Nequasset chlorophyll concentrations, if at all affected by the alewife population in this particular area, should continue to increase over a comparable period, especially as escapement vastly increases. As an additional caution, the DHD site chlorophyll data were included as they show a significant elevation of Chl a on the same day, though of much smaller magnitude (0.4 ug/l greater). The pattern and timing of the chlorophyll dynamic here is similar, however the likelihood that any significant density of alewives would be present in this more open, significantly deeper portion of lake seems much lower. That being said the, schooling behavior of the fish as well as the observation in the microcosm experiment that chlorophyll concentrations and respiration rates had returned to initial levels after approximately 2 months indicates that any effects in a large lake may be spatiotemporally very heterogeneous. As an illustrative example, if the maximum daily number of fish calculated to pass remained (9226) within the aforementioned straight below the railroad bridge (approx. 700m long by 30m wide, 1m deep), fish density on that day would approach 0.4 fish/m<sup>2</sup>. Given these scenarios, it is certainly not impossible for high alewife densities comparable to those used in the Durbin (1979) microcosms to be achieved on a large lake scale, despite calculated overall adult densities (total 2013 fish run/ total lake area) that may be over 50x less (0.02 fish/m<sup>2</sup>).

The difficulties of analyzing the underlying biological and physical mechanisms behind water quality time series is highlighted by Harris (1987). In a study of Lake Ontario employing daily sampling at many sites, advective water mass transport and wind driven convective mixing were found to be very influential on temporal changes in water quality parameters. Detailed and meaningful analyses were only allowed by high resolution sampling as decimation of the data set showed substantial biasing and aliasing. While resolution of sampling in Nequasset Lake was high at the TOD site, analyses may be limited by lack of a similarly high resolution sampling of other areas of lake. In this light, the lack of statistically significant relationships between daily fish run and water quality parameters may be the result of any of the following:

1. an inconsequentially small geochemical and biological influence of alewives on the waters surrounding the TOD site
2. a complex and non-linear relationship between alewife population and water quality parameters as the result of spatiotemporally variable fish distribution
3. incomplete consideration of variation in ambient biological and physical processes

As suggested earlier, a comparison of a given parameter at the TOD with DHS site on a high resolution time scale (limited here by a lack of data at DHS) may help to constrain background variation in water nutrient and chlorophyll concentrations and allow for the observation of a relationship between water quality parameters and alewife migration at the TOD site. Additional sampling outside of the period of the fish run would also help to constrain background variation.

### *Stable isotope Analyses:*

As with nutrient concentration data, analysis of stable isotope data suffer from the lack of a partnered control environment and/or a more detailed annual record within which this seasonal data set can be framed. The signal of POM  $\delta^{13}\text{C}$  appears to be enriched during the period of the fish run in both 2012 and 2013 in Georges Brook but may very well be the result of increased summer productivity (Terranes and Bernasconi 2000). POM  $\delta^{15}\text{N}$  at the TOD site decreases substantially with the terminus of the fish run, but is elevated before its commencement in early May. Data from the same site the previous year do not change during the period of the fish run, but increases substantially in mid-late October, perhaps representing upwelling of de-nitrified bottom water with lake turnover. Neither  $\delta^{15}\text{N}$  nor  $\delta^{13}\text{C}$  of POM are significantly correlated with daily fish run or modeled fish population. Stable isotope analyses here are in part constrained by the lack of sample replication that precludes many statistical analyses.

### MODELS

Presented with the logistical and (somewhat intertwined) analytical limitations of the collected data, models were used to predict the dynamics of alewife nutrient flux. While many important parameters used here demand customization to Nequasset lake through further research, the model outlines likely scenarios for both the annual net flux of alewife nutrients as a function of adult escapement as well as the daily release and incorporation of nutrients by adults and juveniles, respectively.

#### *Annual*

The model used for prediction of net alewife N and P fluxes was formatted in a way so as to display the uncertainty associated with the degree of juvenile alewife nutrient export. By using two figures for juvenile survivorship per adult, the goal was to isolate a range of possible export values. It is suggested by West et al (2010) that early survivorship is likely to be density dependent, and this prediction is borne out in the comparison of Bride lake, CT, and Love Lake, ME (Havey 1973) where the spawner density and #YOY/spawner are 1380 fish/ha and 6.36YOY/spawner respectively for Bride lake, and an average of 0.18 and 366 for Love lake. The “YOY export low” curve is likely to be a good lower bound as it is based on a juvenile survivorship to adult spawner ratio calculated for Bride lake (West et al. 2010), where adult alewife densities are significantly greater than in Nequasset (3000 and 100 adults/ha respectively). The YOY high scenarios is likewise an appropriate upper bound by having much lower adult densities than Nequasset.

At low escapement values (roughly 14,000; below the point of asymptotic YOY export) the degree of YOY export is largely controlled by YOY:spawner ratio, but is increasingly more affected by the asymptotic density dependent growth. In the 1958 scenario, with an escapement of over 1 million, the difference between the two scenarios (YOY high and YOY low) is negligible. This situation holds true even if the maximum biomass density is increased from 1.6g/m<sup>2</sup> (as was used in the Nequasset simulation) to 5.4 g/m<sup>2</sup>, the value found in the eutrophic Linsley Pond mesocosms (West et al. 2010). Given that the estimate derived here of “critical” escapement needed to maintain water quality is above 6 million, future work to improve model resolution may focus on the juvenile carrying capacity of the lake. This may be accomplished by a microcosm experiment as in

West et al. (2010) and may be less labor intensive than the counting or surveying of juveniles in the lake necessary to determine YOY: spawner ratios. That being said, a midsummer biomass survey would help to inform the findings of the mesocosm experiment and would better account for population depletion by predation and other stressors difficult to represent in the mesocosm.

Estimates of alewife and landscape loading indicate that at current escapement, net annual alewife inputs make up less than 2% of total annual nutrient loads. Given this relatively small input, it is unlikely that the alewife run has large ecological impacts on the system. However, the 1958 estimate of P loading exceeds 25% of the annual budget (assuming constant landscape loading through time). This figure may have been still larger before human settlement when ambient loading from landscape and atmosphere were likely to be significantly reduced. At these high percentages of total load, it is likely that the ecological effects of the alewife migration were more pronounced. Increased nutrient concentrations and algal growth as well as ecosystem <sup>15</sup>N enrichment were likely to occur as they do today in more populous alewife and pacific salmon systems (Garman and Macko 1998, Kline et al. 1993, Walters et al. 2009).

#### *Daily*

As suggested by West et al (2010), lake managers may choose to cap escapement so as to avoid importing large quantities of nutrients. While this model based approach may be a broadly effective method of alewife population and lake water quality management, it assumes a consistent nutrient load to the lake throughout the year. The reality is that the alewife migration is a pulse addition that may affect water quality parameters like phosphorous and nitrogen concentrations in a way that is distinct from the consistent background landscape loading.

The daily model created and used here takes constants and some structure from the annual model, adds daily models of carcass decay and juvenile growth rate, and outputs net daily alewife community nutrient flux. This flux is not static like the annual model and varies as a function of the number of living and dead adults as well as the number of juveniles in the lake from April to October. Naturally this makes the model sensitive to inputs regarding the timing of the alewife migration and life history, and thus harder to constrain for an individual lake. However, its output differs from the annual model in such a way as to provide insight into the daily loading of nutrients, an important factor in determining lake water quality.

While When daily fluxes were dissolved in total lake volume, both in the 2013 and 1958 scenarios, daily concentration changes remained quite low with a max of 0.0004 mg/l N in 1958. This is an order of magnitude lower than the detection limit for TDN. Uncertainty remains however in the treatment of this daily flux. Due to the spatiotemporally complex nature of the fish migration and lake hydrodynamics, it is unclear as to what volume the flux should be dissolved into. As a purely illustrative example, daily maximum alewife loading was dissolved in the estimated volume of water south of the railroad bridge in the southern “strait” of Nequasset Lake. This volume estimate was found by gauging area with Google Earth and average depth with a bathymetric map to yield a total volume of roughly 48,000 cubic meters. This exercise yielded an estimated daily concentration change of 0.0008mg/l P and 0.008mg/l N. All migrating alewives must pass through this roughly 0.75km by 2m deep section of lake, and so may be able to exert a significant and detectable influence on water

nutrient concentrations on small spatiotemporal scales. Due to the schooling behavior of these fish (Mullens 1986, Post and Walters 2009) this same phenomenon could occur throughout the spawning period.

An interesting result of the daily model is that for all scenarios run, including those for which the annual model predicted net annual export of nutrient from the lake, there is a 14 day period in which there are adult imports with no juvenile incorporation/export. This is the incubation and hatching period for the YOY. In the 2013 scenario, the day of greatest adult import lies before the first hatch. Thereafter, adult imports are tempered and often outpaced by YOY incorporation. From this result it follows that using the annual model to predict water quality parameters may be a blunt tool that overlooks important daily fluctuations in alewife nutrient input. It may be the case that where annual models predict a negligible effect on lake nutrient concentrations, daily releases (particularly in small, shallow regions of lake as in the example above) produce substantial changes in lake geochemistry and water quality parameters.

Another implication from this daily model is the temporal displacement of adult import and juvenile export. In the 2013 YOY low scenario it is over a month after the start of the fish run that juvenile incorporation outpaces adult imports and roughly three months after adult imports begin to asymptote that YOY incorporation does the same. It appears that there may be the potential here for what ecologists have called “trophic mismatch” (review by Donnelly et al. 2011), where nutrients and biomass are inefficiently transferred between trophic levels as a result of temporal disjunction in populations. In this case the transfer would be nutrients and biomass from adult to juvenile alewives. The degree of this mismatch in Nequasset Lake is likely dependent on many factors including efficiency of the microbial loop and nutrient recycling, export rates of organic matter to the hypolimnion, thermocline formation and duration, and potential for hypolimnion anoxia. These factors will be specific to different lakes. Speculatively, it may be the case that larger and deeper lakes see greater mismatch as organic matter is sequestered in the large hypolimnion while shallower, better mixed lakes see a more efficient transfer of nutrients from adult to juvenile alewives.

It would be possible to further explore these concepts if the settling /export rates of N and P in Nequasset Lake were available. This would allow for the calculation of water nutrient accumulation and therefore estimates of alewife derived nutrient concentration increase (here only presented as daily inputs divided by lake volume). It would also allow for the calculation of nutrient transfer potential between adult and juvenile alewives. For instance, one might find that as a result of phosphates settling to the hypolimnion and adsorbing to sediments, a percentage of adult enrichment is occluded from the juvenile population.

### *Feedbacks and Uncertainties*

Two potential feedbacks that are unaccounted for in the current models but that may affect its prediction are listed below

Increased lake productivity as a result of increasing escapement and nutrient influx could allow for the elevation of the density dependent growth asymptote, increasing capacity for YOY export and buffering this increased nutrient flux. While this may allow the lake to host a larger migration from an annual water quality standpoint, maximum daily increases would continue to rise.

A decrease in planktivorous fish population has been known to alter lake nutrient dynamics. By releasing large zooplankton of lower N to P ratio from grazing pressure, phytoplankton in turn transitioned from N to P limitation as more P was incorporated into zooplankton biomass (Carpenter 1992). Conversely it may be the case that increased alewife planktivory and resultant decreases in zooplankton size (confirmed by Post et al. 2008), phytoplankton communities could shift from P to N limitation. This shift could be aided by the low total N to P ratio of nutrients imported by the alewives (around 12). A shift in nutrient limitation would be likely to affect predictions about water quality and therefore maximum allowable escapement. The prediction of 6.7 million presented earlier is based on the assumption of phosphorous limitation.

### *Research Priorities*

Two aspects of the alewife loading model that are of high sensitivity (West et al. 2010) and uncertainty for Nequasset Lake are adult mortality rate and the bioenergetics of YOY growth. Determining adult mortality rate is as simple as extending the fish count to the outmigration period and is an important next step in this study. Greater adult mortality would decrease allowable escapement, while lesser mortality would increase it. Constraining the mass of nutrient exported by YOY is significantly more complex and also more difficult to quantify. Certainly the most accurate method would be to count and weigh juveniles as they emigrate, and this method has been accomplished by installing a trap at the base of the fishway (Havey 1973). However, at Nequasset Lake, the dam allows spillover and this method may not be accurate if a significant number of alewives emigrate over the dam. A joint mesocosm and biomass assay as completed in West et al. (2010) is an alternative, though it is difficult to assess the accuracy of this method. If the end goal is management of water quality, a third method would be a high resolution sampling of nutrient and chlorophyll concentrations as well as stable isotope analyses. Detection of alewife MDNs by  $\delta^{15}\text{N}$  analyses can however be confounded by enriched sources like natural fertilizers and wastewater. This strategy would likely limit management to reactionary measures and may take many years before a plan could be agreed upon.

In the face of country-wide increases in the number of river restoration and dam removal projects (Bernhardt et al. 2005), recovery of alewife populations is likely (Hall et al. 2011). With population increases will come questions regarding management practices, especially in areas where cultural eutrophication is already a major stressor on lake health. Through increased study it may be possible to establish overarching relationships and heuristics regarding alewife life history and growth ( i.e. estimating YOY biomass export as a function of adult density) that will allow managers to enact low cost strategies to jointly manage fishery and lake health. If this can be done with some degree of accuracy, managing alewife escapement may become a powerful tool for managing water quality, capable of importing or exporting nutrients from lakes and streams.



## Conclusion

Time series data of lake water nutrient and chlorophyll concentrations as well as POM stable isotope analysis displayed some intriguing patterns including elevations during the period of the fish run, though correlations with daily passage were not found. This lack of recognizable geochemical influence may be the result of low MDN concentrations and/or high spatiotemporal complexity that demands greater sampling resolution. The annual alewife loading model predicts that in 2013, an escapement of roughly 41,000 had nearly balanced P import and export while between 19 and 26kg of N were imported. Compared to results from the LLRM, this N input comprises 0.1 to 0.5% of Nequasset Lakes annual N budget. A historical escapement scenario of over 1 million individuals would have been capable of importing 25% of the lakes annual P and 12% of annual N. The LLRM and annual alewife loading model were used together to estimate that Nequasset Lake is capable of carrying an escapement of up to 6.7 million before “critical” (23ppb P) water quality degradation occurs. Results from the daily model indicate, however, that the pulse-like nature of alewife MDN input and the lag between adult import and YOY export may lead to unacceptably high P concentrations at escapements below this figure. Additionally, this lag may decrease the efficiency of nutrient transfer from adults to juveniles, depending on currently unknown nutrient settling velocities. Model estimates should be greatly improved by determination of adult mortality rates and study of YOY growth dynamics. An increase in the number of river restoration and dam removal projects in the last two decades demands further study of the geochemical and ecological effects of anadromous fish migration so as to ensure proper simultaneous management of fishery and water resources.

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