The Effects of Seasonal Feeding Behavior of Juvenile Alewife and Blueback Herring on Piscine Growth Rate and Zooplankton Nutrient Regeneration

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Abstract

The growth rate and feeding behavior of two species of river herring: alewife (*Alosa pseudoharengus*), and blueback herring (*Alosa aestivalis*) were studied as a function of temperature and prey availability. An additional component examined the effect of predation by these river herring on the zooplanktonic community and nutrient regeneration. Zooplankton were compared between a site with, and a similar site without size selective feeding pressure of herring which determined significant differences between communities but nutrient regenerative rates were beyond the limits of detection. Additional measurements were taken from a system with a spawning herring population of alewife and blueback. A time series of zooplankton abundance, zooplankton size distribution, and temperature were determined throughout the development season (April-November) for both species of river herring. Herring were collected for determination of hatch date ranges, age class growth rates, and δ13C and δ15N analysis. Stable isotopes from skeletal muscle in herring were compared to the isotopic signature of snails (isotopically representative of littoral habitat), and mussels (isotopically representative of pelagic habitat) throughout the development season to determine changes in feeding distribution. Hatch dates and otolith growth increments allowed for the determination of change in growth rate for a variety of age classes over time. A generalized linear model (GLM) was used for significance testing between otolith increment and the determinants of temperature and prey density. Results of the GLM showed limitation to growth rate by temperature in the larval and late juvenile period for alewife and in the late juvenile period for blueback herring. Prey density showed limitation to the growth rate only for the late juvenile stages of blueback herring. δ13C showed no significant change for blueback herring over time, however, confirmed that alewife are adapting to more littoral feeding zones as the season progresses.

Introduction

Populations of the alewife and blueback herring have been heavily affected by spawning and nursery habitat loss, overfishing, and heavy pollution. Their importance as a fishery, and as prey for other major fisheries, like striped bass, has brought attention to restoring wild populations. An increasing number of dam removal projects are allowing their reintroduction into limnic spawning and nursery grounds, and there is interest in the relationships between herring and this habitat. Additionally, as average global temperatures rise, river herring species could be highly affected by changes to water temperature and prey availability, both well understood to affect piscine growth rates, which is often a determinate of survivability (Werner & Blaxter, 1980). Field observation has also suggested spatial feeding patterns of herring may shift both diurnally and seasonally as pelagic zones are first exploited of larger zooplankton to a high degree, leaving littoral plankton an increasingly important food source (Llopiz, pers. comm.). Further, size distribution, abundance, and composition of zooplankton communities are heavily altered by the strong size selective feeding pressures of herring, pushing towards fewer zooplankton, smaller size, and different dominate taxa (Brooks & Dodson, 1965). Predatory selectivity of herring for young of the year is for individuals 0.62 +/- 0.05mm (Mills et al, 1995) and due to the visual nature of picking feeding styles, which dominate in larval and juvenile
states, is likely to include larger individuals as well supported again by the findings of Brooks and Dodson (1965) which saw all large individuals eliminated by herring.

Zooplankton, as 1° consumers, are abundant, remineralizing food material into available forms for primary productivity, and connecting higher trophic levels to detrital and photosynthetic pathways. For aquatic ecosystems, primary productivity is often a determinant of all higher trophic productivity in the system. The limiting factor for primary productivity, held in delicate balance, is often nutrients, and so processes that affect cycling of macronutrients like nitrogen and phosphorous can have large effects on ecosystem structure. Particularly in freshwater habitats, phosphorous is typically the limiting nutrient (Elser et al., 1990). It is released by weathering, but also occluded by iron oxides, and immobilized by phytoplankton. One major counter to this, creating dissolved available P for primary production, is remineralization by metabolic processes of consumers like zooplankton. For this reason, they are an important target in understanding consumer driven nutrient recycling (CNR) and nutrient availabilities at ecosystem levels (Elser & Urabe, 1999). This project is an attempt to understand how zooplankton will alter nutrient regenerative rates in the ecosystem, and may also act as a determining factor for developing juvenile herring growth rates and feeding distribution.

Methods:

In this study, we compared two lakes from the local Massachusetts area: one with annually returning herring, and one without access to herring, Great Herring Pond, (Plymouth Ma, 152 ha, avg. 6.1m) (Fig. 1). Big Sandy Pond (Plymouth MA, 55 ha, avg. 5.8m) served as a control site, without herring (Fig. 2). Data from the Town of Plymouth Pond and Lakes Atlas 2015 show similar Chl α (representative of primary productivity) and similar physical characteristics apart from total phosphorous which was determined lower in the Big Sandy Pond System.

10 herring samples were examined from each of the following 5 catch dates: 06/24/15, 07/13/15, 08/03/15, 09/23/15, and 10/05/15 from GHP. All 10 individuals from 6/24/15 and 7/13/15 were alewife due to availability. Later 3 catch dates included 5 individuals from both alewife and blueback species. 3 of the most abundant snail (Planorbidae) and mussel (Anodonta) were used from catch dates 8/12/15, 9/2/15, 9/23/15, 10/12/15, and 11/04/15.

Wet weight, fork length, standard length, and species identification was recorded for the 50 individual aforementioned herring samples. Sagittal otoliths were extracted, cleaned, and prepared on a slide with immersion oil to clear. After approximately 10 days of sitting in immersion oil, otoliths were examined under light. When necessary, additional polishing with 3 µm and 30 µm metallurgical lapping film (Otolith Microstructure Preparation, 2015) was performed to make growth rings more apparent. Images of otoliths were taken and analyzed with LAS software version 4.3.0 (Leica Microsystems, Switzerland), where the number of rings was counted to determine age, and otolith increment widths were determined at each ten day interval from the nuclei.

Stable isotopic analysis for herring skeletal muscle and noncalcareous parts of collected mussels and snails was conducted for each of the total 50 herring, 15 mussel, and 15 snail samples. Although liver tissue is typically used to determine stable isotopic values over time, due to its high turnover rate comparative to muscle tissue, muscle tissue was analyzed due to the high
lipid content of herring liver, which can affect stable isotopic measurements (Otter, pers. comm.). Justification for using muscle tissue is supported by the comparatively high turnover rates in younger individuals (Peragon et al., 2001). Snails serve as a comparison to littoral predation, because they tend to feed on the detritus associated with shallower shore regions, while mussels filter feed directly from the water column and their stable isotopes tend to reflect pelagic regions. $\delta^{13}C$ is a reflection of sources of primary productivity at the base of the food web. Littoral zones tend to be $\delta^{13}C$ enriched from benthic algae and terrestrial inputs, while phytoplankton usually have lower $\delta^{13}C$ (Post, 2002).

Samples were oven dried, ground by mortar and pestle, 1-2 mg weighed, packed in tin, and submitted to the Marine Biological Laboratory stable isotopes lab (Woods Hole, MA) for both $\delta^{13}C$ and $\delta^{15}N$ samples analysis. $\delta$ values were calculated as: $1000 \times (\delta_{\text{sample}} - \delta_{\text{standard}})/(\delta_{\text{standard}}) \%$, where the standard for $^{15}N$ is atmospheric and $^{13}C$ is PDB (Pee Dee Belemnite).

Zooplankton were collected by a 5 m vertical tow with a 30-cm-diameter, 150-µm mesh net in GHP (~41.4780 N, 70.3380 W) and BSP (~41.4743 N 70.3396 W). Zooplankton were kept alive in 1.5 L bottles bubbled gently with air to prevent settling and deoxygenation.

Zooplankton collection from tows on 11/13/15 was fractioned twice by plankton splitter to produce 4 even subsamples. One quarter was sieved with 150 µm mesh, and preserved in 70% ethyl alcohol. Other zooplankton samples were kept intact until examination of relative abundances. Depending on the density of zooplankton in the sample, varying volumes of subsample, and dilutions were made to count the abundance of each of 5 dominant taxa present: Bosminidae, Daphniidae, Calanoida, Cyclopoidea, and Asplanchna, from GHP, from time intervals: 5/8/15, 5/21/15, 6/1/15, 6/8/15, 6/16/15, 6/22/15, 6/29/15, 7/7/15, 7/13/15, 7/27/15, 8/12/15, 9/2/15, 9/23/15, 10/12/15, 11/13/15 in addition to one time period from BSP, 11/13/15. Images of approximately 10 individuals of each taxa were taken from GHP from 5/8/15, 5/21/15, 6/8/15, 6/22/15, 6/29/15, 7/7/15, 7/27/15, 8/12/15, 9/2/15, 9/23/15, 10/12/15, 11/13/15 in addition to one time period from BSP, 11/13/15. Images of individuals were examined using ImageJ software (US NIH) to determine length and width characteristics.

The remaining 3 zooplankton sample fractions from each site were sieved with 150 µm nitex mesh, put into 3 sealed cylindrical 4.2 L respirometers with magnetic stirrers, and filled with water from the respective sample location, filtered with 20 µm mesh to remove phytoplankton. One control form each lake was run with all plankton removed to account for bacterial remineralization and respiration. Cores were incubated for 15.5 hours, with measurements of $O_2$ concentration taken by probe, and 60 mL water samples taken at $t=0$, 2.3, 5.5, and 15.5 hours. As water was removed from the container it was replaced, to reduce oxygenation, with filtered water from each location. Extracted sample water was syringe filtered (GF/F ashed) to remove biota, and approximately 20 mL dispensed into each of three bottles for $NH_4^+$, $NO_3^-$, and $PO_4$ analysis. The $NO_3^-$ bottle will be frozen, and those for $NH_4^+$ $PO_4$ analysis will be acidified with 20µL of 5N HCl for preservation. $NH_4^+$, $NO_3^-$, and $PO_4$ concentrations were determined by spectrophotometric analysis modified from Strickland and Parsons, 1972.

Results

By density calculations of dominant taxa (bosminidae, daphniidae, calanoida, and cyclopoidea) at sample date 11/13/15 from GHP and BSP we determined significantly different
structure by chi squared test (p < 0.00). GHP had higher cyclopid and bosminid abundances relative to BSP, which had higher abundances of daphnia and calanoid (Fig. 3). Time series calculations from GHP determined that apart from asplanchna, highest abundances occurred approximately between mid-May to mid-June. Abundances for bosminids, daphnia, calanoids, and cyclooids in the time period following mid-June to October were much lower. Asplanchna abundances however, peaked in this intermediate period (Fig. 4).

Size analysis of individuals collected on 11/13/15 from GHP and BSP determined the relative size order of dominant taxa from shortest to longest: bosminids, daphnia, calanoid, and cyclopid. Time series calculation so of GHP determined a polynomial trend in the average size of individuals from earliest to latest measurement. All taxa except asplanchna showed highest relative size at the beginning and end of measurement dates. Asplanchna showed an inverse trend. The seasonal pelagic prey availability, calculated as the density of a taxon, multiplied by the normal probability an individual would be greater than 0.6mm, BSP showed a higher prey availability than GHP as per chi square test (p < 0.00) (Fig. 5). Compared to relative abundances, abundances of prey sized individuals showed comparable trends, whereby prey size individuals were must abundant as total abundance increased for each respective species. For all except, asplanchna, abundance was greatest in the beginning of the season followed by the very end of the season (Fig. 6).

With calculated flux rates from initial and final concentrations of NH$_4^+$, NO$_3^-$, PO$_4^-$, and O$_2$, adjusted with the values of the controls, it was determined that the only significant differences in any fluxes was for PO$_4^-$ and NO$_3^-$. CO$_2$ flux, calculated as the magnitude in O$_2$ change in a 1:1 ratio, only showed significant increase for GHP. CO$_2$ flux in BSP and both GHP and BSP for NH$_4^+$ showed no significant change over the incubation period. However consultation determined that results were beyond the analytical limitations of the equipment, because concentrations fell too low for accurate reading (McHorney, pers. comm.).

Stable isotopic analysis showed that the signature of Anodonta had an average $\delta^{13}$C of -26.58 +/- 0.152, and average $\delta^{15}$N of 9.36 +/- 0.354. Planorbidae samples showed a significant linear change in $\delta^{13}$C over time (p=0.038) from -15.9 +/- 0.904 to -14.9 +/- 0.799 according to (y = 0.0143x - 620.27, $R^2$=0.823), and an average $\delta^{15}$N of 8.23 +/- 0.301 (Fig. 7). Alewife showed a significant increase in $\delta^{13}$C over time (p < 0.00) characterized linearly (y=0.0295x -1271.8, $R^2$=0.700) (Fig. 8) representative of a shift to more littoral feeding, and a significant decrease in $\delta^{15}$N over time (p=0.043) characterized linearly (y = -0.0086x + 375, $R^2$= 0.156) (Fig. 9) suggestive of lower trophic level feeding. Blueback Herring showed no statistically significant change in $\delta^{13}$C over time, with an average $\delta^{13}$C of -25.8 +/- 1.05, but had a significant linear change in $\delta^{15}$N over time (p=0.043) according to (y = 0.0084x - 341.13, $R^2$=0.673) (Fig. 10) suggestive of higher trophic level feeding. Analysis of the relative contributions of food source from the pelagic and littoral feeding zones assuming a consistent $\delta^{13}$C for pelagic zones and a $\delta^{13}$C for littoral food sources consistent with the linear change in Planorbidae, determined that by 10/5/15, alewife 3.8% diet of food sources characteristic of littoral habitat. Identical analysis for blueback herring determined an average 2.6% diet of food sources characteristic of littoral habitat.

We counted otoliths rings, and the age was subtracted from the catch date with an additional three days added to the age of the fish, assuming delayed deposition of the first ring
before feeding to determine hatch dates (Llopiz, pers. comm.). Radii were taken every ten growth increments on the longest side of the otolith to determine increment widths and relative growth rates. A comparison of hatch date to age class otolith increment width with a T-test determined a significant positive relationship for larval alewife during 0-10 and 10-20 days post hatch (dph), as well as a significant negative relationship between hatch date and otolith increment width 40-50 dph with (p = 0.0039, 0.036, and 0.00094) respectively (Fig. 11, 12, 13, 14, 15). A comparison of hatch date to age class otolith increment width determined a significant positive relationship for blueback herring during 10-20, 30-40 and 40-50 dph, as well as a significant negative relationship between hatch date and otolith increment 70-80 dph with (p = 0.0079, 0.010, 0.085, and 0.021) respectively (Fig. 16, 17, 18, 19, 20).

A comparison was made between an extreme early hatch (4/28), and extreme late hatch (6/13) for alewife (Fig. 21). Daily otolith increment deposition rates were determined for each 10 day age class from 0 to 80 days. In the following age classes where otolith increment widths were determined to be dependent on hatch date in a significant relationship, the linear trend line was used to calculate the daily otolith increment deposition for both hatch dates: 0-10 (y = 0.7685x - 32350, R²=0.3208), 10-20 (y = 0.366x - 15379, R²=0.1269), 40-50 (y = -0.5474x + 23145, R²=0.4288), and 50-60 dph (y = -0.8016x + 33855, R²=0.3115). In all other cases, the average of individual otolith increment widths of the age class was used. Total otolith radius during the 0-90 day for extreme late hatch was 2.13% lower than an extreme early hatch date. An extreme early (5/15) and late hatch (7/5/15) were also determined for blueback herring (Fig. 22). In the following age classes where otolith increment width were determined to be dependent on hatch date, the linear trend line was used to calculate the daily otolith deposition rate for both hatch dates: 10-20 (y = 0.4299x – 18090, R²=0.431), 30-40 (y = 0.6732x – 28332, R²=0.41), 40-50 (y = 0.4981x – 20941, R²=0.2114), and 70-80 dph (y = -0.5861x + 24758, R²=0.301). In all other cases, the average of individual otolith increment width of the age class was used. Total otolith radius during the 0-80 day for extreme early hatch was 12.47% lower than an extreme early hatch date.

Because both prey availability and temperature were acting at the same time upon otolith growth increment, a generalized linear model (GLM) analysis was performed to determine whether temperature or prey density had a significant relationship with growth rate in an age class. Surface temperature was calculated as the average temperature between 0.5 and 2 metres in depth from physical data collected from 18 time points from 4/10/15 to 11/13/15. A polynomial curve was fit to the seasonal data (y= -0.0013x² + 112.16x – 2 x 10⁶, R² = 0.9597) to interpolate the temperature for each date of the development season (Fig. 23). Individual daily otolith increment width, calculated as 1/10 of the 10 day otolith increment width were compared to the respective temperature and prey availability during deposition. For blueback herring, it was determined that there was a significant positive relationship between growth rate and temperature during the 50 to 60 and 60 to 70 dph age classes with slopes of 0.97 and 0.160 respectively (p= 0.0014, 0.013). Blueback herring also had a significant positive relationship with prey density for the 50 to 60 dph age class with a slope of 0.015 (p=0.00037) (Table 2). Alewive had a significant positive relationship with temperature for the 0 to 10, 10 to 20, 60 to 70, and 80 to 90 dph with slopes of 0.356, 1.421, 0.211, and 0.194 respectively (p=0.0085, 0.035, 0.0034, 0.088). There was no significant relationship between growth rate and prey density determined for any age class of alewife (Table 3).
Discussion

Analysis of community structure differences between systems with and without the selective feeding pressures of herring, agreed with previous studies, by demonstrating a tendency towards taxa and individuals with a larger size (Fig. 3, 5) (Brooks & Dodson, 1965). This was seen in the BSP site where, without size selective feeding pressure, larger taxa and individuals were in higher abundance. In GHP we saw the exact opposite: taxa with individuals tending towards smaller sizes had higher abundances.

Although the results of the nutrient regeneration experimentation proved to be statistically insignificant, it was hypothesized that we might have expected with the results of measurements of dominant taxa, abundances, and size analysis, that BSP would have shown greater nutrient regeneration rates, largely due to a higher density of individuals as well as a size distribution tending towards larger individuals and taxa. The idea that larger individuals might contribute more to remineralization is based on the Size Efficiency Hypothesis, whereby a larger size allows them to process a wider size range in materials (Brooks & Dodson 1965). If zooplankton are processing more material, they would also likely be remineralizing more.

One possible way to improve the experiments testing the relative nutrient regenerative capabilities of zooplankton from each system would be to work with a higher density of zooplankton which could produce measureable results. The experiment could also be carried out in an entirely different method, stoichiometrically. If we did an analysis of C:N:P in zooplankton, and also found the C:N:P ratio of food sources including phytoplankton and detritus, we could determine approximately how much of each nutrient would be remineralized assuming we could find literature values for relative exploitation and production efficiencies.

Results of zooplankton abundances and community still contributed to understanding of the determinates of herring growth rates. Examining zooplankton, in the form of converted prey density, based on a 0.6mm and greater size selectivity by herring, the pattern of change can be explained by seasonal temperature changes, as well as predator abundance and developmental stage. Increases to prey availability likely occur in the early season until about mid-June as temperature warms and feeding pressures remain low. Alewife hatched earlier in the season (4/28-6/13) with an average hatch date of 5/18, which suggests they would be inhibit this dramatic change in zooplankton, however feeding is considered much more aggressive in the juvenile state, usually defined as 30 days after hatch (Llopiz, pers comm.), which given the mean hatch date for alewife, would come just as the zooplankton and prey availability begin to decline. Asplanchna peaked on 9/2, after several months susceptible to exploitation by juveniles and larvae. This is possible because only a small fraction of their size distribution fell above 0.6mm or also because it may not have been a preferred prey item for herring. The other zooplankton showed increases in the last two sample dates (10/12 and 11/13) suggesting their ability to rebound as herring began to emigrate from the ecosystem. However temperatures were also cooling over this period and herring remained in the system past this date, so zooplankton recruitment may still have been somewhat inhibited.

It was expected there would be two major determinants of herring growth rate: temperature, and prey availability, which was tested with the GLM analysis. Importantly, when there was a significant positive relationship determined between growth rate and either factor, we might assume that it was limiting during that age class, otherwise, growth rate would not have
changed as the factor did. With this assumption, during larval periods and early juvenile stages for both species prey density was never limiting. Feeding intensity increases with development, which might explain why prey was not limiting during these time periods. For alewife, maximum prey density occurred during the larval period, which might also account for the lack of relationship between growth rate and prey density during this time period, but because later development stages, which occurred past the crash of zooplankton around 6/15 were not inhibited by the low prey densities during these periods, it is unlikely that the high density of prey mattered for the larvae. Only blueback during the 50 to 60 dph age class displayed a significant limitation by prey density (Table 2). The demand of food increasing positively in relationship to age class could be the cause of this limitation.

Temperature had no effect on growth rate for blueback herring in the larval or early juvenile age class, while it did for alewife in the 0 to 10 and 10 to 20 dph age classes, possibly due to the difference in average hatch dates for both species. For the 0 to 10 dph age class of alewife, the earliest hatched individuals experienced the coldest temperatures of 13.5 °C. The earliest hatched blueback started at 17.4°C, almost 4 °C higher. This could be why no significance was found for alewife in earlier age classes. Both species saw a temperature limitation in later age classes (60 to 70 and 80 to 90 dph for alewife, 50 to 60 and 60 to 70 dph for blueback herring) (Table 2, 3). Temperature during these age classes were higher, change in temperature was lower, but significance was still found. Because positive relationships were determined between growth rate and temperature even as temperature reached its maximum (25.3°C) may be an indication that thermal optimum was never reached and temperature was in fact limiting during all time intervals (Fig. 23). Previous studies however have suggested that (25.0 °C) is the preferred temperature for young of the year individuals, which was recorded as 9°C higher than mature individuals, and is likely to correspond to the thermal optimum (Otto et al, 1976).

Importantly, while we were able to determine significant relationships between growth rate and prey density or temperature during some age classes, determinations of no significance do not necessarily mean there was no limitation by either of these factors in an age class. For alewife there was a significant relationship between hatch date and growth rate 40 to 50 dph but there was no significance proven for either temperature or prey density. In blueback, there were significant relationships between hatch date and growth rate during 10 to 20, 30 to 40, and 40 to 50 dph age classes which were never explained by temperature or prey density with statistical analysis. It is possible that there was another factor affecting growth during this period, but it should be considered that for some age classes, even between early and late spawn individuals, there was only a difference of (0.51°C) (Fig. 23). Additionally, significance testing for relationships at high temperature is impaired by a low sample size because as temperature increases, variability in growth rate also increases (Houde, 1989). Likewise, after the crash of zooplankton in the early summer, prey density did not change greatly over some time intervals during which, temperatures may have been high. Changes in prey density were as small as 15 (individuals>0.6mm) m⁻³ (Fig. 6). This may not have been a large enough change, in combination with a small sample size, to determine a significant relationship. A larger sample size for each species might also contribute to establishing significance particularly since each individual may respond very differently to either factor, possibly based on their size, genetic factors, or metabolism.
Considering the feeding distribution, lack of significance to growth rate particularly in later juvenile alewife can be partially explained using δ¹³C determinations. Prey density calculations were entirely based on samples taken in pelagic regions. If there were different densities in the littoral regions, which the herring were exploiting, then it may prevent growth limitation by pelagic prey availability. Alewife had a significant change from pelagic feeding zones to a mixture of pelagic and littoral feeding based on δ¹³C. Based on the idea that size might play a role in morphological ability to feed littorally, a T-Test was performed for individuals from each catch date to determine if there was a significant relationship between standard length and stable isotopic value. No relationship was found, and we therefore assume that all alewife individuals regardless of size and likely age class transformed their diet spatially according to the same pattern. The trend towards more littoral feeding provides explanation as to why alewife did not show significant positive relationships with prey availability in later age classes. Therefore, although prey density in pelagic regions may have decreased, their shift in feeding more into the littoral habitats may have compensated for this drop. Previous studies have suggested that predatory pressures may cause zooplankton to make diel horizontal migration (DHM) due to the structural effects on feeding efficiency (Burks et al, 2001). DHM could supplement littoral prey abundances and possibly increase importance as a feeding zone. Blueback herring, showed no significant change from littoral to pelagic feeding, which offers suggestion as to why significant relationships between growth and pelagic prey availability existed. If they did not shift their feeding, more heavily into littoral zones with higher prey abundance, they could become prey limited. Still, hypothesis about littoral prey availability might be supplemented by future study.

It was determined there was only a 2% difference in total growth between alewife hatched in the extreme early season as compared to the extreme late season. This suggests that for the time period measured, the increases in larval growth for a late spawning individual may be evenly matched by hindrance to juvenile growth rate later in the season. An extreme late hatched blueback however, showed a 12% difference in size as compared to an extreme early hatched individual. If we consider that size is synonymous with survivability, then we might expect that this would act as a selective pressure on spawning and hatch date. This is however dependent that there is a significant relationship between size and survivability. Most of the juveniles used in this study were of similar age, but comparing larval growth rates between samples of later stage juvenile fish, and larvae could indicate if smaller individuals are being lost to predation and other pressures, if juveniles show larval growth increments significantly above the average for larvae.

Considering projected climate warming, and the limitations to growth rate by temperature for both species, with rising temperatures, recruitment may improve in the study region and northern reaches. Ultimately, it could result in a shift in latitudinal range as southern exceed maximum temperature tolerances and norther reaches reach minimum temperature requirements for juvenile individuals.

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counting zooplanker abundancies, and contributed funding from his Marjot Scholarship for stable isotopic analysis.

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Figure 1. Bathymetric map of Great Herring Pond, Plymouth, MA (MA Dept. of Fisheries and Wildlife, 2007). The red X indicates the approximate location of zooplankton sampling.
Figure 2. Bathymetric map of Big Sandy Pond, Plymouth, MA ((MA Dept. of Fisheries and Wildlife, 2007). The red X indicates the approximate location of zooplankton sampling.
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<td>12.8</td>
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Table 1. System characteristics for GHP and BSP (Plymouth Ponds and Lakes Atlas, 2015)
Figure 3. Densities of dominant taxa of GHP and BSP from sample date 11/13/15.
Figure 4. Zooplankton density of dominant taxa in GHP from 5/8/15 to 11/13/15, calculated as individuals m$^{-3}$. 

![Graph showing zooplankton density of dominant taxa in GHP from 5/8/15 to 11/13/15, calculated as individuals m$^{-3}$]
Figure 5. Prey density in GHP and BSP for sample date 11/13/15 (individuals>0.6mm) m$^{-3}$.
Figure 6. Prey density in GHP from 5/8/15 to 11/13/15 ((ind. > 0.6mm) m^{-3})
Figure 7. $\delta^{13}$C in for *Planorbidae* tissue collected from 8/12/15 to 11/4/15

$y = 0.0143x - 620.27$

$R^2 = 0.8229$
Figure 8. δ^{13}C for skeletal muscle tissue of alewife collected from 6/24/15 to 10/5/15.

\[ y = 0.0295x - 1271.8 \]

\[ R^2 = 0.7 \]
Figure 9. $\delta^{15}$N for skeletal muscle tissue of alewife collected from 6/24/15 to 10/5/15

$y = -0.0086x + 375$

$R^2 = 0.1554$
Figure 10. Change in $\delta^{15}$N for blueback herring collected from 8/3/15 to 10/5/15.
Figure 11. Alewife 10 day growth increment (µm) compared to hatch date for the 0-10 day age class.

\[ y = 0.7685x - 32350 \]

\[ R^2 = 0.3208 \]
Figure 12. Alewife 10 day growth increment (µm) compared to hatch date for the 10-20 day age class.
Figure 13. Alewife 10 day growth increment (µm) compared to hatch date for the 40-50 day age class.

\[ y = -0.5474x + 23145 \]

\[ R^2 = 0.4288 \]
Figure 14. Alewife 10 day growth increment (µm) compared to hatch date for the 50-60 day age class.

\[ y = -0.8016x + 33855 \]

\[ R^2 = 0.3115 \]
Figure 15. Slope of significant linear relationships between growth increment and hatch date
Figure 16. Blueback herring 10 day growth increment (µm) compared to hatch date for the 10-20 day age class.
Figure 17. Blueback herring 10 day growth increment (µm) compared to hatch date for the 30-40 day age class.

\[ y = 0.6732x - 28332 \]

\[ R^2 = 0.41 \]
Figure 18. Blueback herring 10 day growth increment (µm) compared to hatch date for the 40-50 day age class.

\[
y = 0.4981x - 20941 \\
R^2 = 0.2114
\]
Figure 19. Blueback herring 10 day growth increment (µm) compared to hatch date for the 70-80 day age class.
Figure 20. Slope of significant linear relationships between growth increment and hatch date
Figure 21. Daily otolith deposition (µm) throughout development calculated for an extreme early and late hatch alewife.
Figure 22. Daily otolith deposition (µm) throughout development calculated for an extreme early and late hatch blueback herring.
Figure 23. Surface temperature for GHP from 4/10/15 to 11/13/15, fitted with a polynomial trendline.

\[ y = -0.0013x^2 + 112.16x - 2E+06 \]

\[ R^2 = 0.9597 \]
<table>
<thead>
<tr>
<th>Age Class</th>
<th>Daily Increment vs Temp. (µm/°C)</th>
<th>Daily Increment vs. Prey Density (µm/((ind.&gt;0.6mm)/m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 to 10</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>10 to 20</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>20 to 30</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>30 to 40</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>40 to 50</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>50 to 60</td>
<td>0.970</td>
<td>0.0149</td>
</tr>
<tr>
<td>60 to 70</td>
<td>0.161</td>
<td>NS</td>
</tr>
<tr>
<td>70 to 80</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

Table 2. Results of generalized linear model analysis for blueback herring. NS indicates no significant relationship while values indicate the slope of the relationship.
<table>
<thead>
<tr>
<th>Age Class</th>
<th>Daily Increment vs Temp. (µm/°C)</th>
<th>Daily Increment vs. Prey Density (µm/((ind.&gt;0.6mm)/m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 to 10</td>
<td>0.356</td>
<td>NS</td>
</tr>
<tr>
<td>10 to 20</td>
<td>1.421</td>
<td>NS</td>
</tr>
<tr>
<td>20 to 30</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>30 to 40</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>50 to 60</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>60 to 70</td>
<td>0.211</td>
<td>NS</td>
</tr>
<tr>
<td>80 to 90</td>
<td>0.194</td>
<td>NS</td>
</tr>
<tr>
<td>100 to 110</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

Table 3. Results of generalized linear model analysis for alewife. NS indicates no significant relationship while values indicate the slope of the relationship.