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Trophic Interactions between Anadromous Juvenile Alewife (*Alosa pseudoharengus*) and Cyanobacterial Populations in a Shallow Mesotrophic Pond

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Abstract

Alosa pseudoharengus is an anadromous fish that migrates from marine to freshwaters to spawn. The early larval and juvenile forms are known to be planktivorous, where heavy feeding upon their preferred food source of large crustacean zooplankton often results in changes to composition and size structure within this trophic guild which in turn can result in shifts within the trophic spectrum and a classic trophic cascade. In this study of Lower Mill Pond, Brewster MA, we evaluated the feeding strategy of juvenile *Alosa* to determine whether juvenile alewife switches to feeding largely on cyanobacteria and whether cyanotoxins microcystin (MC) and *β*-methlyamino-L-alanine (BMAA) bioaccumulate in their muscle tissue. Within 15 - 30 days of their estimated spawning date, overexploitation of crustacean zooplankton resulted in a shift from planktivory to benthic detritivory for the majority of their life history, although this did not reduce their condition based on weight-length relationships (Log Wwt. = −5.503 + (3.101 × Log Length). Mean MC (0.003 $\mu g \cdot g^{-1}$ dwt) and BMAA (4.49 $\mu g \cdot g^{-1}$ dwt) concentrations in the muscle tissue of out-migrating juveniles were presumably derived from benthic subsidies, exporting freshwater cyanotoxins and creating a potential transfer to consumer of 0.0012 µg MC and 1.85 µg BMAA. Biodilution of MC and biomagnification of BMAA were observed. Depletion of the crustacean biomass by >95% resulted in an increase in the rotifer biomass, where Log crustacean ($\mu g \cdot L^{-1}$ dwt) = −5.642 − (7.976 × Log rotifer ($\mu g \cdot L^{-1}$ dwt), and an increase in the amount of potentially edible <50 µm cyanobacterial biomass ($r(8) = -0.676$, $p = 0.046$). A secondary cascade appears to have been maintained via invertebrate planktivory by *Chaoborus* spp.; however for a period of time edible cyanobacteria growth exceeded grazing pressure, resulting in a bloom of

edible cyanobacteria. Continued grazing resulted in a shift to larger, inedible cyanobacterial communities where late season (October) surface accumulations were observed. The mass occurrence of juvenile *Alosa pseudoharengus* appears to be coupled to the sequential increases of cyanobacterial biomass via its influence on the trophic spectrum. Overall, the rotifer biomass ($\mu g \cdot L^{-1}$) was positively correlated with MC ($pg \cdot mL^{-1}$) ($r(8) = 0.577$, $p = 0.104$), and negatively correlated with BMAA ($\mu g \cdot L^{-1}$) ($r(8) = -0.388$, $p = 0.373$) in the edible cyanobacterial fraction of the water column, although neither of these were significant.

Keywords

Cyanobacteria, Juvenile Alewife, Cyanotoxins, MC, BMAA, Bioaccumulation, Trophic Spectrum

1. Introduction

Aquatic ecosystems, including lakes, harbor community food webs, were supported by the complex interactions between a myriad of biotic and abiotic factors [1]. In temperate zones, freshwater lakes can display seasonal patterns indicative of changes in nutrient supply, community composition, relative abundance, and survivorship giving rise to diverse populations [2] [3] within a trophic spectrum [4]. The trophic spectrum concept recognizes traditional vertical models using nutrients ("bottom-up") and predator-prey relationships ("top-down), horizontal influences (trophic compensation, keystone species) and subtle resource-driven opportunistic behaviors that sculpt populations [5] [6] [7]. A frequently studied trophic spectrum within lakes involves planktivore-zooplankton-phytoplankton—nutrient source interactions [8]-[13] with many of them focusing on the anadromous alewife, *Alosa pseudoharengus* [14]-[19]. Anadromous alewife are particularly interesting, as they fulfill dual roles, acting as the planktivore [8] [14] [15] [16] as well as an exogenous source of marine-derived nutrients [20], exerting both "top-down" and "bottom-up" influence on the zooplankton and phytoplankton populations and resultant water quality conditions within a lake ecosystem [21] [22].

The phytoplankton populations within lake ecosystems are typically diverse, and can include different classes of eukaryotic algae, such as Chlorophyceae (green algae), Dinophyceae (dinoflagellates) and Bacillariophyceae (diatoms) as well as the prokaryotic Cyanophyceae (blue-green bacteria) [23]. Collectively, the cyanobacteria include upwards of 50 different genera [24], with *Microcystis* spp., *Dolichospermum* spp. and *Aphanizomenon* spp. being among the most common bloom-forming cyanobacteria encountered in New England [25]. Phytoplankton populations exhibit periodicity in response to abiotic and biotic variables [26]. The composition of cyanobacterial populations has been shown to undergo seasonal shifts in response to light, temperature and nutrient ratios [27]

[28] [29], as well as the presence of planktivores [30], other predators [31] and grazing zooplankton [11] [14], resulting in a shift from edible to inedible forms [4] creating bloom conditions. Cyanobacteria can produce toxic compounds (cyanotoxins), including dermatoxins, neurotoxins and hepatotoxins [32] [33] [34] the presence of which can vary depending on the composition of the cyanobacterial population. Cyanotoxins create risk to human health and the environment through a number of exposure pathways [35]. Within aquatic systems that support fish populations, exposure can occur via direct ingestion (dissolved and particulate forms) from the water column and/or benthic zone, as well as transfer within the food web [36] [37] [38], where the most commonly studied cyanotoxins include microcystin (MC) and its variants [36] [39] [40] [41], as well as beta-methyl-alanine amino acid (BMAA) [37].

The purpose of this study was to examine a freshwater aquatic system with populations of cyanobacteria and anadromous *Alosa pseudoharengus*, with a particular emphasis on the impacts of the juvenile stage on the lake ecology, prior to their outmigration. We wanted to 1) document the presence cyanobacteria and cyanotoxins, specifically microcystins and BMAA, within the aquatic system for the entire juvenile life history period, 2) determine whether juvenile *Alosa pseudoharengus* accumulate the cyanotoxins and at what levels, and 3) describe the trophic spectrum that links cyanobacteria with juvenile *Alosa pseudoharengus*.

2. Materials and Methods

Studied Site

Lower Mill Pond (Latitude: 41.73˚N; Longitude: −70.11˚W) is a groundwater-flooded kettle hole lake located in Brewster, MA. USA, with a maximum depth of 3.9 m, is 20.2 ha in size (550,406 m^{-3}) with a 38 day residence time during the spring months that increases to 78 days during the summer months of June to September [42]. Lower Mill Pond is the terminus of a multi-pond system that includes Walkers Pond and Upper Mill Pond, discharging into Stony Brook (**Figure 1**). Stony Brook is the site of the largest diadromous herring run in the Cape Cod North Watershed, and the fourth largest among all herring runs within the Cape and Islands watersheds [43]. The annual in-migration of adult *Alosa* spp. into Lower Mill Pond to spawn typically begins in mid to late April, peaks in early May and continues until mid-June [43] [44]. Migrating adult *Alosa* spp. were counted at the inlet to Lower Mill Pond from 5 May, 2019-1 June, 2019 [45]. The estimated Stony Brook run size over the past five years has fluctuated from 271,363 in 2014 to 104,135 in 2019. Although alewife densities were not estimated in 2019, a previous study conducted in 2014 [44] showed that juvenile alewife decreased through the summer from 111.2 m^{-3} in June to 3.62 m^{-3} in August.

Sample Collection

All samples were collected on a bi-weekly basis from May-October 2019 from the deep site (**Figure 1**). Integrated whole lake water (WLW) was collected to a

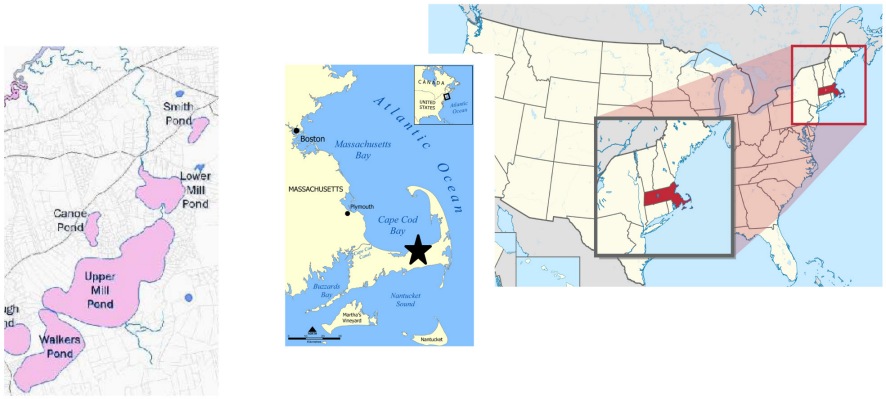

Figure 1. Map of USA, state of Massachusetts and location (black star) of Lower Mill Pond, Brewster, MA.

depth of 3 m. Subsamples were passed through a 53 μm ring net into a 125 mL darkened amber bottle, subsamples (5 mL and 20 mL) removed with a pipette and placed into darkened microvials and 20 mL HDPE vials (respectively) and frozen at −20˚C. Net plankton was collected using a Students Plankton net (15 cm diam., 53 μm mesh), lowered to a 3 m depth and pulled upwards at a rate of 0.5 $m \cdot s^{-1}$. Bloom forming cyanobacteria (BFC) and zooplankton isolates were collected following a 30 minutes separation period in a Pocket ZAPPR™ [46] device. The BFC samples were placed in 5 mL darkened microvials and frozen at −20˚C, while zooplankton samples were placed in a 10 mL vial and preserved with 0.5 mL of formalin-sucrose [47]. Bloom material was collected as a surface grab and frozen at −20˚C. A maximum of 25 specimens of juvenile alewife (YOY) were collected on four successive sampling dates (30 Aug, 10 Sep, 27 Sep and 11 Oct 2019) during their out-migration from Lower Mill Pond to Stony Brook using a dip net. Alewife was first anesthetized and then euthanized in MS-222 prior to being frozen at −20˚C. Secchi disk depth was taken using a 15 cm Secchi disk and an Aqua-Scope II. Sediment samples were collected on 13 Dec 2019 along two perpendicular transects in the open pelagic zone and at randomly selected locations in the shallow littoral zone (**Figure 1**) using a 3 m tygon tube attached to a Masterflex L/S portable peristaltic pump. Slurry samples were placed in 250 mL containers and frozen at −20˚C. Sediment samples for wet/dry weight conversions were thawed and mixed, with measured aliquots collected on pre-weighed Whatman 44 mm filters. The filters were reweighed and then placed in a drying oven for 24 hours at 60˚C, whereupon the dried samples were removed and weighed. The remainder of the sediment sample was mixed and placed into 20 mL HDPE vials.

A minimum of twelve *Alosa* specimens per sampling date were thawed and measured to the nearest millimeter using a metric ruler and weighed to the nearest 0.1 gram using an O'Haus Adventurer (0.0000 g) scale. The gut contents were obtained by inserting a hypodermic needle filled with 2 mL of Milli-Q water into the anus of the fish and gently rinsing out the contents into a petri dish.

A subsample of the gut contents was stained as needed with yellow drawing ink and then examined at 100 - 400× using light and epifluorescent microscopy filter for chlorophyll (435 nm) and phycocyanin (572 nm). The remainder of the gut rinse was placed into 1.8 mL centrifuge tubes. The fish specimen was dissected to remove the gut, and length and width were measured using a metric ruler under a dissecting microscope. The gut volume was estimated (30 Aug = 23 µL, 10 Sep = 37 µL, 27 Sep = 46 µL, 11 Oct = 68 µL) and used to calculate gut rinse dilution factors (30 Aug = 70.5, 10 Sep = 40.5, 27 Sep = 34.2, 11 Oct = 17.9). Dilution factors were applied to gut rinse concentrations of phycocyanin, microcystins and BMAA to estimate concentrations in the fish gut. The fish were skinned and muscle tissue removed from the bones to provide the muscle tissue fillets. The fillets were chopped with a razor, a subsample removed for drying and the remainder placed into a 1.8 mL centrifuge tube and macerated in the tube using a Dremel drill fitted with a Teflon pestle. Fish muscle tissue subsamples (0.5 grams) for wet/dry weight conversions were placed in pre-weighed aluminum boats, reweighed, placed in a drying oven for 24 hours at 60˚C and reweighed.

Zooplankton Analysis

Zooplankton were placed in a Sedgewick Rafter counting cell, identified [25], measured [48], and dry weight biomass estimated [49]. Entire samples were counted when less than 400 organisms were present. Samples with more than 400 organisms were subsampled and a maximum of 200 organisms were counted. Crustaceans included cladocerans (*D. pulex*, *D. ambigua*, *B. longirostris*, *E. tubicen and E. hagmanni*), calanoids and cyclopoids (*M. rubellus*, *M. varicans*) larger than 600 µm. Rotifers included *K. cochlearis*, *P. vulgaris*, *C. hippicrepis*, *S. pectinata* and *T. cylindrica* and excluded *Asplanchna* spp. Measurements were taken to the nearest micron at 40× and 100× using an Amscope biological light microscope Model XSM-40 fitted with a MU900 digital camera connected to a computer. The predator:panfish ratio was calculated using average crustacean body length and the linear regression provided by [50].

Fluorometric and Toxicological Analysis

Lake water, sediment, and gut rinse samples were prepared for fluorometric and toxicological analysis as previously reported [51] using the single freeze-thaw and triple freeze-thaw procedures respectively. Following the triple freeze-thaw procedure the entire sediment and gut rinse samples were passed through a 0.22 µm, 17 mm nonsterile nylon syringe filter to remove particulate matter prior to toxin analysis. Approximately 0.05 grams of macerated fish muscle tissue was placed in a pre-weighed 1.8 mL centrifuge tube, reweighed, whereupon 1.5 mL of Milli-Q was added and reweighed. The fish muscle tissue then was triple-freeze thawed, centrifuged at 10,000 rpm for 10 min, supernatant removed and placed into a pre-weighed 1.8 mL centrifuge tube and reweighed. Samples were concentrated, as needed, through vacuum evaporation in a Thermo Fisher Savant SPD 1010 to the desired volume. Phycocyanin concentrations were quantified using a calibrated two-channel handheld Fluoroquik fluorometer (AmiScience FQD-PC-CHL/IV-RATIO-C) for phycocyanin (PC). Toxin analysis for total

microcystins (MC) was conducted using Envirologix EP-022-HS and toxin analysis for B-N-methylamino-L-alanine (BMAA) was conducted using Eurofins Abraxis Product No. 520040. Readings were taken using a Bio-Tek Instruments Inc. El-800 Universal Microplate Reader Primary 450 nm Reference 630 nm with KC Junior software. The standard curve was calculated in Sigma Plot using a 4 parameter logistic regression. Values for all samples were reported as total microcystins (representing dissolved + particulate microcystins) and free BMAA. Recovery efficiency was estimated by spiking 500 mg of fish tissue sample with MC at 0.600 $\mu g \cdot L^{-1}$ or BMAA at 50 $\mu g \cdot L^{-1}$. The average recovery for fish muscle tissue MC and BMAA was within +/−1 standard error of 82.9% and 80.5% respectively.

Statistical Analysis and Calculations

All samples collected during the study were used for fluorometric analysis of phycocyanin (PC) except when the lowest level of detection (LoD < 1.0 $\mu g \cdot L^{-1}$) was encountered. Phycocyanin concentrations were used to calculate "inedible" cyanobacteria (>50 μm) by subtracting "edible" cyanobacteria (<50 μm) from whole lake water. Data were arc-sine and log transformed as appropriate to normalize and allow for parametric analysis. Studentized T-tests were used to determine significant difference between means. One-way analysis of variance with Tukey's post-hoc test was used to identify differences between means in more than two groups. Parametric analysis (Pearson's correlation coefficients and linear regression analysis) and non-parametric analysis (Spearman's correlation coefficients) were used to describe relationships between variables. For linear regression analysis autocorrelation (Durbin-Watson = 2.0), leverage (Studentized deleted residuals: SDR > 2) collinearity (VIF > 3), and influence (Cooks distance: $Cd > 4/n$ and Difference in Fits: DFFits = $2 \times$ sq.rt. $[(p+1)/(n-p-1)]$ where n = number of observations, p = number of variables (including the constant) were examined. Age at capture was calculated from a previously published length versus age regression for Lower Mill Pond [44], where Fork length (mm) = 31.69 + 0.17 × Age (days). Cyanobacterial biomass growth rates ($\mu \cdot d^{-1}$) were calculated from phycocyanin concentrations using the equation $(\ln PC t_1 - \ln PC t_0)/(t_1 - t_0)$ as previously described [51]. Correlation analysis was used to determine relationships between rotifer biomass (μg dwt L^{-1}) and edible cyanobacterial growth rates ($\mu \cdot d^{-1}$) [52]. Biomagnification factor (BMF) was calculated as the ratio between the cyanotoxin concentration measured in aquatic consumers and their diet [53]. Fish muscle tissue dry weight was converted to wet weight by using a factor of 0.03. All statistical analyses were conducted using Sigma Plot Version 14.

3. Results

Analysis of *Alosa pseudoharengus* catches, feeding strategy, and cyanotoxin concentrations

The mean lengths of *A. pseudoharengus* specimens significantly increased from 46 to 55 mm between 30 Aug and 27 Sep and reached a maximum of 57

mm on 11 Oct ($F(3, 70) = 47.535$ $p < 0.001$), while the mean wet weights progressively increased from 1.3 to 2.5 grams between 30 Aug and 11 Oct ($H(3) = 47.139$, $p < 0.001$), where the 11 Oct weight was significantly higher than all other sampling dates. The average estimated age at capture for the collection dates 30 Aug, 10 Sep, 27 Sep and 11 Oct were 86 days, 108 days, 136 days and 146 days respectively (Table 1). The standard weight equation (W_s) confirmed an isometric relationship, where Log Wwt = −5.503 + (3.101 × Log length), Adj. $r^2 = 0.915$, $p < 0.001$.

Investigation using light microscopy revealed that zooplankton (rotifers, nauplii copepodites, calanoids, cyclopoids and cladocerans) were absent from the gut contents of juvenile alewife. Further microscopic evaluation of the samples, with and without pigment enhancement, and under epifluorescence confirmed the presence of cyanobacteria amid an amorphous matrix. Fluorometric pigment analysis showed that phycocyanin concentrations in the gut rinse ranged from 629.2 to 1150.4 μg·L^{-1} (Table 2), being significantly higher on 30 Aug than all other sampling dates ($H(3) = 61.575$, $p < 0.001$). Toxin analysis using the ELISA technique indicated that both cyanotoxins MC and BMAA were present in the gut rinse throughout the collection period of 30 Aug-11 Oct, 2019 (Table 2). The MC concentrations were not significantly different from each other, and ranged from 2.07 to 4.62 μg·L^{-1}, while the BMAA concentrations were more variable, and ranged from 1707.77 to 9040.37 μg·L^{-1}.

Both cyanotoxins accumulated in the fish muscle tissue (μg·g^{-1} dwt), where concentrations of microcystins and BMAA (Table 3) fluctuated throughout the sampling season with mean concentrations for microcystins of 0.0026 ± 0.0005 μg·g^{-1} dwt and BMAA of 4.492 ± 0.261 μg·g^{-1} dwt. Analysis of variance of log-transformed microcystin concentrations ($F(3, 8) = 3.097$, $p = 0.089$) and BMAA ($F(3, 8) = 2.417$, $p = 0.142$) indicated that there were no significant differences in muscle tissue concentration between collection dates. The cyanotoxin muscle content (μg) varied across the sampling dates with the highest content for both MC and BMAA observed on 11 Oct, where the total microcystin content (0.0023 μg) was significantly higher than all other sampling dates ($F(3, 8) = 9.07$, $p = 0.006$) and the BMAA content (2.17 μg) was higher but not significantly different ($F(3, 8) = 3.267$, $p = 0.080$) from all other sampling dates. The contribution of the gut contents to the total cyanotoxin content varied during the sampling period (MC 20%, 13%, 19%, 6%, mean 15%: BMAA 12%, 8%, 21%, 6%, mean 12%).

Interactions between *Alosa pseudoharengus* and planktonic populations

The zooplankton biomass in Lower Mill Pond exhibited strong seasonal patterns (Figure 2) with varying distributions of the crustacean and rotifer grazers, and *Asplanchna* spp. Over the entire study period, the biomass of the crustacean and rotifer grazers were negatively correlated with each other ($r(9) = -0.818$, $p = 0.004$) where the reduction of crustacean grazers allowed for proliferation of rotifer grazers (Adj. $r^2 = 0.628$, $p = 0.004$) (Table 4). The significantly different

Table 1. Morphometric and life history characteristics of *Alosa pseudoharengus* from Lower Mill Pond. SEM indicates standard error of the mean.

Morphometric and life history characteristics									
Date	Length (mm)	SEM	*	Wet Weight (g)	SEM	*	Est. age at capture (days)	SEM	Est. spawn date
30-Aug	46	0.7	c	1.3	0.1	c	86	4	5-Jun
10-Sep	50	0.6	b	1.6	0.1	b,c	108	4	25-May
27-Sep	55	0.5	a	2.1	0.1	b	136	3	21-May
11-Oct	57	0.4	a	2.5	0.1	a	146	2	19-May

*ANOVA results indicating where groups are most similar.

Table 2. Phycocyanin (PC) and cyanotoxin (MC and BMAA) concentrations in *Alosa pseudoharengus* gut rinse. SEM indicates standard error of the mean.

Gut Rinse Concentrations									
Date	PC ($\mu g \cdot L^{-1}$)	SEM	*	MC ($\mu g \cdot L^{-1}$)	SEM	*	BMAA ($\mu g \cdot L^{-1}$)	SEM	*
30-Aug	1150.4	43.2	a	4.62	1.22	a	7822.04	1061.80	a, b
10-Sep	629.2	25.8	b	2.07	0.64	a	3346.91	539.30	a, b, c
27-Sep	702.5	19.2	b	3.90	0.05	a	9040.37	279.52	a
11-Oct	852.1	61.7	b	2.11	0.09	a	1707.77	203.60	b, c

*ANOVA results indicating where groups are most similar.

Table 3. Cyanotoxin concentrations in *Alosa pseudoharengus* muscle tissue. SEM indicates standard error of the mean.

Muscle tissue concentrations						
Date	MC ($\mu g \cdot g^{-1}$ dwt)	SEM	*	BMAA ($\mu g \cdot g^{-1}$ dwt)	SEM	*
30-Aug	0.0019	0.0002	a	5.045	0.669	a
10-Sep	0.0021	0.0007	a	4.884	0.324	a
27-Sep	0.0020	0.0004	a	3.588	0.168	a
11-Oct	0.0047	0.0010	a	4.452	0.528	a

*ANOVA results indicating where groups are most similar.

Table 4. Regression and correlation coefficients between zooplankton biomass ($\mu g \cdot L^{-1}$), cyanobacterial biomass ($\mu g \cdot L^{-1}$), microcystins ($ng \cdot L^{-1}$) and BMAA ($\mu g \cdot L^{-1}$) in Lower Mill Pond. Linear regression analysis reported as $\text{Log}\,Y = a + b \times \text{Log}X$, where X = Log All zooplankton, Log Crustacean grazers or Log Rotifer grazers and Y = Log All cyanobacteria, Log Edible cyanobacteria, Log Inedible cyanobacteria or Log Rotifer grazers. Boldface indicates significance where $p < 0.05$.

All zooplankton						
	a	b	Adj. r^2	*n*	*p*	r
All cyanobacteria	**1.593**	**1.536**	**0.607**	**9**	**0.014**	
Edible (<50 μm)	**1.511**	**1.616**	**0.634**	**9**	**0.011**	
Inedible (>50 μm)				9	0.729	0.135

Continued

Crustacean grazers						
	a	b	Adj. r^2	*n*	*p*	r
All cyanobacteria				9	0.073	−0.623
Edible (<50 µm)				**9**	**0.046**	**−0.676**
Inedible (>50 µm)				9	0.862	−0.068
Rotifer grazers	**−5.642**	**−7.98**	**0.628**	**10**	**0.004**	**−0.818**
Rotifer grazers						
	a	b	Adj. r^2	*n*	*p*	r
All cyanobacteria	**2.058**	**2.372**	**0.705**	**9**	**0.006**	
Edible (<50 µm)	**2.013**	**2.593**	**0.720**	**9**	**0.005**	
Inedible (>50 µm)				9	0.898	0.05
Edible microcystins				9	0.104	0.577
Edible BMAA				9	0.373	−0.338

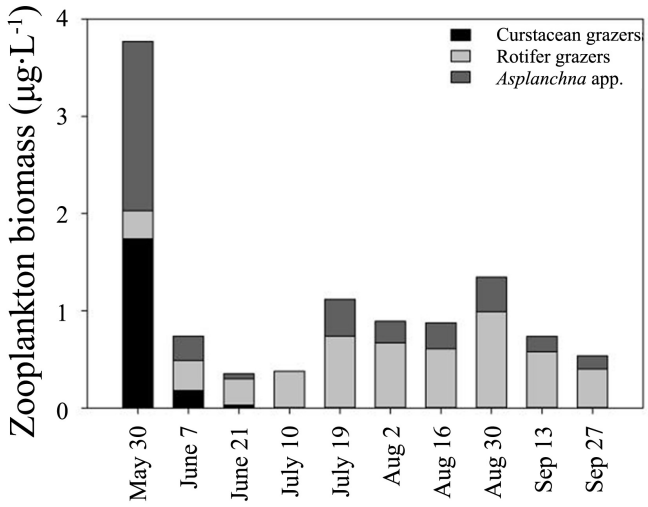

Figure 2. Distribution of zooplankton biomass (µg·L^{-1}) in Lower Mill Pond.

maximum and minimum biomass for both crustacean grazers ($F(2, 6) = 57.939$, $p < 0.001$) and *Asplanchna* spp. ($H(9) = 20.276$, $p = 0.04$) were observed on 30 May and 21 June, respectively, with both absent from the water column by 10 July. On 19 July, *Asplanchna* spp. reappeared while crustacean grazers remained absent until 27 Sep, when *B. longirostris* was once again observed. Helmeted *D. ambigua* was observed in the 30 May and 7 June samples. The biomass of the rotifer grazers increased after 10 July to a high seasonal plateau occurring between 19 July and 13 Sep, that included the seasonal maxima of 0.99 µg·L^{-1} dwt on 30 Aug.

The relative contributions of crustacean grazers and *A. priodonta* to the total zooplankton biomass were greatest on 30 May (46% and 46%), rapidly declining to the observations of 21 June (7% and 16% respectively) until they were both

absent on 10 July. The relative contribution of rotifer grazers to the total zooplankton biomass was lowest on 30 May (8%) and rapidly increased to the observations of 21 June (77%), reaching a maximum (100%) on 10 July, and remaining dominant until 27 Sep. The total crustacean biomass (excluding copepodites) was consistently dominated by the small bodied cladoceran *B. longirostris*. The mean crustacean length maxima of 0.488 mm was observed on 30 May with lengths then declining to 0.17 mm on 19 July, remaining at zero from 2 Aug to 13 Sep, until 27 Sep when an average length of 0.24 mm was noted. A positive predator: panfish ratio of 0.014 was calculated for 30 May, and was negative or zero thereafter. The cyanobacterial biomass (composed almost exclusively of *Dolichospermum planctonicum*) varied throughout the study period (**Figure 3**) with the minimum of 5.5 $\mu g \cdot L^{-1}$ on 21 June and a maximum of 70.1 $\mu g \cdot L^{-1}$ on 16 Aug. The total cyanobacterial (WLW ($F(8, 18) = 403.38$, $p < 0.001$) and edible (<50 μm ($F(8, 18) = 706.75$, $p < 0.001$)) biomass were marked by alternating significant increases and decreases between 10 July and 30 Aug, while this pattern in the inedible (>50 μm ($F(8, 18) = 7.056$, $p < 0.001$) biomass was observed between 10 July and 16 Aug. The relative contribution of the <50 μm size fraction to the WLW sample ranged from 56% - 100%, with a significant increase ($F(8, 18) = 11.182$, $p = 0.024$) of 28% from 56% to 84% between 7 June and 21 June. The greatest increase in growth rates ($\mu \cdot d^{-1}$) for the WLW (0.22 d^{-1}), <50 μm (0.21 d^{-1}) and >50 μm (0.14 d^{-1}) samples were observed on 19 July. The greatest decrease in growth rates for the WLW (−0.06 d^{-1}) and <50 μm (−0.07 d^{-1}) samples were observed on 30 Aug. A unimodal peak in the WLW and edible cyanobacterial biomass was observed between 19 July and 16 Aug, with the seasonal maxima occurring on 16 Aug. The inedible cyanobacterial biomass increased between 30 Aug and 27 Sep and surface accumulations (bloom conditions) of cyanobacteria were observed on 11 Oct. During the entire study period, linear regression analysis revealed negative casual relationships between both WLW

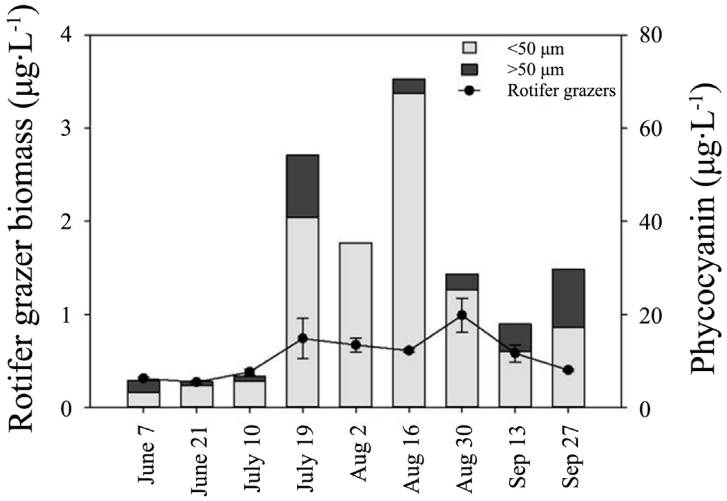

Figure 3. Distribution of rotifer grazer ($\mu g \cdot L^{-1}$), edible and inedible cyanobacterial ($\mu g \cdot L^{-1}$) biomass in Lower Mill Pond.

and edible cyanobacterial biomass and the Secchi disk depth (SDD), where SDD (m) = 2.203 − (0.838 × Log WLW biomass) (Adj. $r^2 = 0.874$, $p < 0.001$) and SDD (m) = 1.988 − (0.730 × Log < 50 biomass) (Adj. $r^2 = 0.804$, $p = 0.002$), respectively. The SDD ranged from 0.68 - 1.69 m, with the minimum SDD of 0.68 m observed on 16 Aug.

Over the entire study period there was a significant negative correlation (r(8) = −0.676, $p = 0.046$) between the biomass of crustacean grazers and edible cyanobacteria (Table 4). There were significant decreases in the crustacean grazer biomass (F(2, 6) = 57.939, $p < 0.001$) between 30 May and 21 June and a significant increase in the edible cyanobacteria biomass (F(8, 18) = 706.757, $p < 0.001$) between 7 June and 21 June. The rotifer grazer biomass increased between 21 June and 19 July concurrent with significant increases in edible cyanobacterial biomass. Rotifer grazer biomass ($\mu g \cdot L^{-1}$) and edible cyanobacteria growth rate ($\mu \cdot d^{-1}$) were positively correlated between 10 July and 16 Aug (r(4) = 0.600, p = 0.400), and negatively correlated between 16 Aug and 27 Sep (r(4) = −0.678, p = 0.322). Over the entire study period, linear regression analysis revealed that rotifer grazer biomass explained 72% of the variability in the edible cyanobacteria biomass (Table 4), where Log edible biomass = 2.013 + (2.593 × Log rotifer biomass), $p = 0.005$), whereas the converse argument explained 68.7% of the variability (Log rotifer biomass = −0.748 + (0.403 × Log edible biomass), $p = 0.007$) (Figure 4). There was a marginal positive correlation between rotifer grazer biomass and microcystins (r(8) = 0.577, $p = 0.104$), while there was a negative, but not significant correlation for BMAA (r(8) = −0.388, $p = 0.373$).

4. Discussion

Analysis of *A. pseudoharengus* catches

Juvenile *A. pseudoharengus* that were collected during their outmigration between 30 Aug and 11 Oct from Lower Mill Pond had similar lengths [17] [18] [44], weights [50] [54] [55] and age at capture [44] to those previously reported.

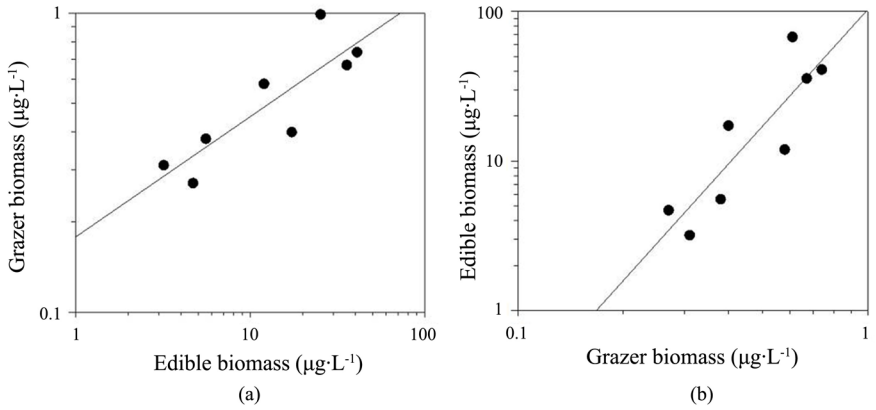

Figure 4. Linear regression analyses between rotifer grazer and edible cyanobacterial biomass: (a) "bottom-up" relationship where Log rotifer biomass = −0.748 + (0.403 × Log edible biomass) and (b) "top-down" relationship where Log edible biomass = 2.013 + (2.593 × Log rotifer biomass).

While outmigration may have begun in mid-June [55] our specimens would be considered late season migrators [54] [55]. We used the standard weight equation (W_s) to determine the condition of this population, (intercept = −5.503, slope = 3.101) which indicated that the alewife were in better-than-average condition [56]. While we used lengths that were below the suggested minimum length of 180 mm our analysis resulted in similar regression coefficients [57]. The significant increases in length ($p < 0.001$) and weight ($p < 0.001$) concurrent with an increase in estimated age suggested that there was no seasonal decline in condition [15] [54] [55] associated with the feeding strategy of juvenile alewife [19] in Lower Mill Pond. Our observation appears to agree with Rossett [44], using otolith analysis, who observed a greater last 20-day growth rate (0.0115 $mm \cdot d^{-1}$) versus the overall growth rate (0.0095 $mm \cdot d^{-1}$) in Lower Mill Pond.

Feeding strategy of *Alosa pseudoharengus*

Using microscopic and fluorometric analyses to evaluate feeding selectivity, our results suggest that juvenile alewife actively fed on cyanobacteria prior to their collections. Despite the abundance of rotifers, we did not observe rotifers (e.g empty lorica) in the alewife guts. The phycocyanin concentrations ($\mu g \cdot L^{-1}$) in the gut rinse were, on average, 33 times higher than the whole lake water (WLW), 4 times higher than the bloom-forming cyanobacteria samples (BFC's), 11 times higher than pelagic sediment and 3 times higher than littoral sediment (see **Supplemental Table S1**), which suggested selective feeding on highly concentrated material from the water column (*i.e.* BFC's) or foraging in areas of accumulations (*i.e.* littoral benthos). Differing feeding strategies based on resource availability in fish have been well documented, some being described as facultative detritivory [58] [59] [60] and ontogenetic niche shifts [17] [59] [61]. Heinrich [62] used live captured zooplankton to document a diet preference of 15-day old alewife for copepodites while noting ingestion of rotifers and algae, and Withers *et al.* [63] observed preferential feeding on the diatom *Fragilaria* over copepod eggs, nauplii, calanoids and dreissenid veligers in near-shore Lake Michigan sites. The young-of-year alewife diet (<65 mm) in Lake Ontario [16] consisted of cyclopoids, large and small cladocerans, nauplii, calanoids and dreissenid veligers. Juvenile alewife gut contents have been shown to vary seasonally [15], shifting from a preference for benthic/littoral dipteran larvae Chironomidae and Ostracoda in mid-summer to the pelagic Cladocera and Copepoda from late-summer to fall in Hamilton Reservoir, RI. The depletion of large-bodied planktonic cladocerans (e.g. Daphnidae and Calanoida) has been associated with a shift from pelagic to littoral feeding of juvenile alewife in Great Herring Pond, MA [19] [64]. Opportunistic feeding, both in terms of content and location (e.g. facultative detritivory) has been observed in other fish species [60] including the gizzard shad, *Dorosoma cepedianum* [58] [59]. Fujibayashi, *et al.* [60] used fatty acid and stable isotope analysis to determine that *Cyprinus carpio* and *Carassius* sp. fed directly upon cyanobacteria (*Microcystis* spp.). Kutkuhn [58] observed a diet consisting largely of phytoplankton (73%), composed of cyanobacteria (20%) preferentially represented by *Microcystis aerugi-*

nosa and *Anabaena circinalis*, and noted that amorphous material, thought to be organic tripton, constituted 61% of the total digestive tract contents. Changes in life stage feeding strategies (ontogenetic niche shifts) have been observed in sunfish [61] and gizzard shad [59]. Mittlebach *et al.* [61] determined that descriptive metrics of body size and age could be used to describe the subtle changes associated with ontogenetic shifts in sunfish (Centrarchidae). In an extensive study of Gizzard Shad (*Dorosoma cepedianum*) in Acton Lake, OH [59], gut and stable isotope analysis documented an ontogenetic niche shift, where feeding strategy changed from zooplanktivory to detritivory as fish aged from class "0" to adult. In contrast to the use of body size and age as ontogenetic metrics, Shaus *et al.* [59] also correlated this change in gizzard shad feeding strategy with increases in lake-wide fish biomass, suggesting resource depletion as an influencing variable. This observation is similar to the observations of class "0" alewife population in Great Herring Pond, MA [19] [64], using stable isotope analysis, where different size classes of juvenile alewife collectively transitioned from pelagic to littoral feeding, in search of other sources of prey to sustain their growth [64]. The shift in fish foraging behavior, for example cyprinids [13], towards benthic food subsidies as a result of preferred resource exploitation has been previously noted [3]. We observed a complete elimination (100%) of the preferred food source following the spawning of alewife in Lower Mill Pond. Together, these observations suggest that resource depletion could influence a change in feeding strategy, resulting in what could be termed an autogenic (self-induced) niche shift. While we cannot comment on the diet of our specimens during their first feeding and early juvenile stages, our microscopic and fluorometric analysis of gut contents from late-migrating juveniles suggest they were feeding opportunistically on cyanobacteria, via facultative detritivory, in the littoral benthic zone. It is entirely possible that ontogenetic and/or autogenic niche shifts occurred in the *Alosa* population in Lower Mill Pond during our study period, and that this behavior, if common among juvenile alewife, results in the use of benthic subsidies, thereby potentially exposing other populations to cyanobacteria. Additional research including extended temporal surveys of the rearing habitats of these populations that includes stable isotope analysis of sediments and fish tissue could confirm these dynamics.

Bioaccumulation of cyanotoxins in *Alosa pseudoharengus*

Toxin concentrations of the gut rinse supported our previous microscopic and fluorometric observation that the juvenile alewife were ingesting cyanobacteria prior to their capture. The gut rinse to whole lake water ratio (Gut:WLW) for MC and BMAA concentrations were 248X and 38,545X, respectively, and the gut rinse to sediment ratio (Gut:Sediment) for MC and BMAA concentrations were 4X and 1407X, respectively. These ratios suggest a mechanism to physically concentrate material and/or free cyanotoxins in the gut. There are limited studies reporting MC concentrations of fish gut contents [65] [66], all of which evaluated adult phytoplanktivorous silver carp (*Hypophthalmichthys molitrix*), omnivorous gold fish (*Carassius auratus*) [66] [67] and benthic omnivorous

common carp (*Cyprinus carpio*) [67]. Poste *et al.* [68] suggests that cyanobacteria present in gut contents in the silver minnow (*Rastrineobola argentea*) contributed to the observed whole fish MC concentrations. In an evaluation of BMAA transfer within aquatic food webs, Jiao *et al.* [69] notes that juvenile *H. molitrix* intestinal contents contained cyanobacteria but does not report concentrations. Our study of Lower Mill Pond, that of Lake Taihu [65] [67] [69] and Lake Chaohu [66] suggest fish feeding strategies that include ingestion of cyanobacteria [67] can result in bioaccumulation of cyanotoxins in muscle tissue.

To our knowledge, this is the first report on the concentrations of MC and BMAA in juvenile *A. pseudoharengus* muscle tissue. Juvenile specimens (<10 cm) are typically processed whole without dissection of muscle fillet [68], however a single study [66] does report that the "small" Group 1 *Coilia ectenes* (mean length 10.5 cm) had accumulated less microcystins than other larger specimens from Group 2 (mean length 18.1 cm) and Group 3 (mean length 23.4 cm), with a reported range from all three groups of 0.0 - 6.7 $ng \cdot g^{-1}$ dwt. The cyanotoxin concentrations observed in our juvenile alewife muscle tissue were within ranges reported in a global review [40], where our mean MC (0.0026 ± 0.0005 $\mu g \cdot g^{-1}$ dwt) was lower than the mean MC (0.0753 $\mu g \cdot g^{-1}$ dwt) and our mean BMAA (4.492 ± 0.261 $\mu g \cdot g^{-1}$ dwt) was slightly higher than the mean BMAA (3.55 $\mu g \cdot g^{-1}$ dwt). Adult specimens with different feeding strategies from Lake Taihu [67] of *Hypophthalmicthys molitrix* (mean MC 0.002 $\mu g \cdot g^{-1}$ dwt) and *Cyprinus carpio* (mean MC 0.003 $\mu g \cdot g^{-1}$ dwt) and Lake Chaohu [66] of *Hypophthalmicthys molitrix* (minimum MC 0.0043 $\mu g \cdot g^{-1}$ dwt) were similar to juveniles in Lower Mill Pond. Conversely, adult *A. pseudoharengus* specimens from Lake Ontario [68] reported mean MC concentrations in muscle tissue of 0.172 $\mu g \cdot g^{-1}$ dwt. The total (free + protein-bound) BMAA concentrations in the muscle tissue of juvenile filter feeding *Hypophthalmicthys molitrix* (12.9 $\mu g \cdot g^{-1}$ dwt) and *Aristichthys nobilis* (0.12 $\mu g \cdot g^{-1}$ dwt) during a cyanobacterial outbreak in Lake Taihu [69] were notably different, while the averages of seven omnivorous fish species (4.0 $\mu g \cdot g^{-1}$ dwt) and for all fish species (6.05 $\mu g \cdot g^{-1}$ dwt) were similar to our observations. In this study, there were no correlations between toxin concentration in alewife muscle tissue, with lake water concentrations or body length for either MC or BMAA. It has been noted that seasonality, feeding strategy and age could influence results [40]. We were surprised by the high concentrations of cyanotoxins in the muscle tissue of our juvenile specimens, where the apparent change in feeding strategy maximized the exposure potential to cyanotoxins. There are other lakes in this region that support migrating *Alosa* [19] [44] [45] and cyanobacterial populations [70]. Collection of juvenile *A. pseudoharengus* from additional sites during the entire period of out-migration, extending from mid-July to mid-October to further evaluate the effects of seasonality, feeding strategy and age on the bioaccumulation of MC and BMAA would be useful.

The impact of the foraging strategy of juvenile alewife on the transfer of cyanotoxins to consumers deserves additional consideration, given the importance

of this forage fish. On average, we estimated that the potential transfer to consumers (gut + muscle) was 0.0012 μg MC and 1.85 μg BMAA. The potential transfer of cyanotoxins for both MC and BMAA was greatest on 11 Oct, where MC content (0.0024 μg) was significantly greater (p = 0.006), and BMAA content (2.29 μg) was higher but not significantly different (p = 0.074) than all other sampling dates. On average, the contribution of the gut contents to the total cyanotoxin content was 15% for MC and 12% for BMAA. While human consumers could reduce their exposure potential by removing the highly concentrated gut contents prior to ingestion as compared to eating them whole [68], this option is generally not available to natural predators. We calculated biomagnification factors (BMF) [53] assuming benthic feeding strategies in either the pelagic or littoral zones. The MC BMF was 0.83 and 0.003 in the pelagic and littoral zones, respectively, while the BMAA BMF was 223.5 and 4.5 in the pelagic and littoral zones, respectively. For either feeding strategy, we observed biodilution for MC and biomagnification for BMAA. Contamination of aquatic food webs with microcystins [36] [40] has been well documented, where biodilution has typically been observed [36] with some exceptions [71]. Contamination of aquatic food webs with BMAA has not been as well documented [37], however biomagnification has typically been observed [37] with some exceptions [72]. The implications of the freshwater export of cyanotoxins in anadromous fish are largely unknown and deserve further investigation.

Interactions between *Alosa pseudoharengus*, zooplankton and cyanobacterial populations

This study has provided a unique opportunity to observe and quantify the complex and variable trophic spectrum [4] within Lower Mill Pond (**Figure 5**) using metrics that can describe trophic structure [7] [14] [73], compensation [12] [74], and cascades [8].

The presence of the juvenile *A. pseudoharengus* forced a redistribution of the zooplankton biomass (**Table 4**) from crustacean to rotifer grazers (Adj. r^2 = 0.628, p = 0.004) (**Figure 2**) via trophic compensation [12] [74], acting as a strong interactor [75] in the Lower Mill Pond food web, initiating an aquatic trophic cascade [8] [18] [76] resulting in increased relative and total edible (<50 μm) cyanobacterial biomass (**Figure 3**) in the absence of crustacean grazing pressure (r(8) = −0.676, p = 0.046). The shift from large to small crustaceans [9] [14] [77] in the presence of this vertebrate planktivore [14] [15] [17] [18] [19] [78] during the vernal period created scarcity of the preferred food source (**Figure 5**), forcing fish to forage on ever smaller zooplankters [78] until available resources were depleted. The sustained magnitude of *Alosa* biomass, absent predators as suggested by the low predator: panfish ratio [16], may have elicited the autogenic transition from planktivory to opportunistic benthic detritivory by 21 June, driven by resource availability (**Figure 5**). Without competition from large cladocerans such as *Daphnia* spp. [77], the rotifer population in Lower Mill Pond flourished between 21 June and 27 Sep, which in turn may have allowed for the proliferation of invertebrate planktivores, including *Chaoborus* spp. [77]

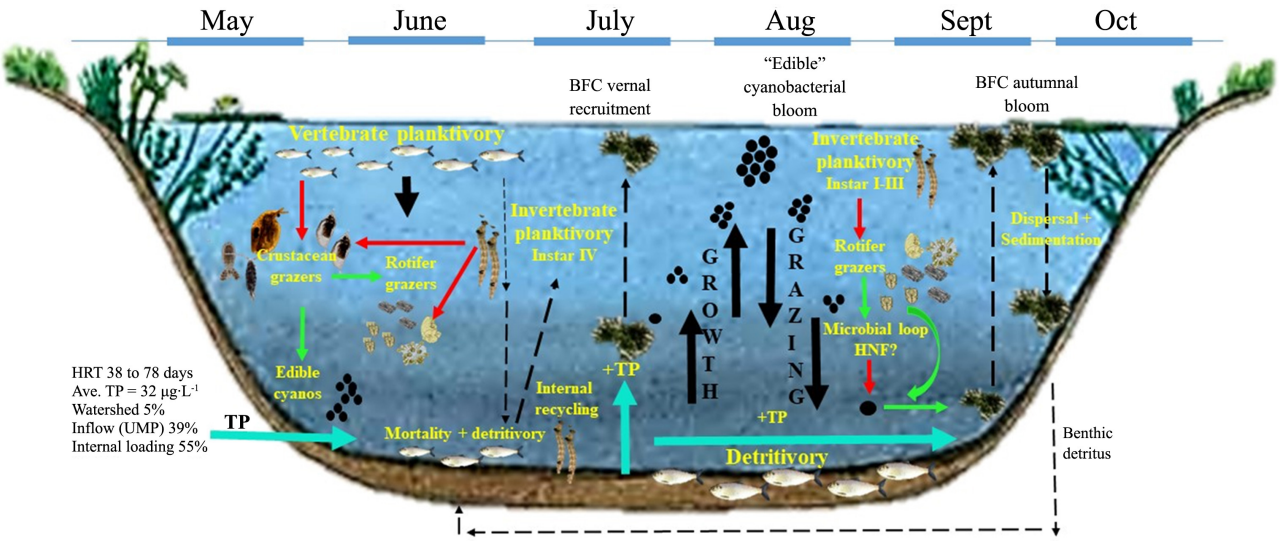

Figure 5. Diagram of the seasonal interactions between juvenile *Alosa pseudoharengus* and cyanobacterial populations in Lower Mill Pond, Brewster, MA.

and *Asplanchna* spp. (**Figure 5**). While not observed during this study, there were several indications that *Chaoborus* spp. were present, including helmeted second instar *D. ambigua* [79] [80] and predation, observed as the significant reduction in *Asplanchna* spp. biomass by 21 June ($p < 0.001$), presumably by the fourth instar of *C. punctipennis* [81] [82] prior to its emergence in June [83].

Assuming that the absence of crustacean biomass signaled the end of vertebrate planktivory, invertebrate planktivory appears to have become the dominant force structuring what remained of the zooplankton population after 21 June (**Figure 5**), where both *C. punctipennis* [81] [82] [84] and *A. priodonta* [85] [86] could have regulated species, size-structure, density and biomass. The biomass of *A. priodonta* positively covaried with that of other rotifers after 19 July ($r(8) = 0.861$, $p = 0.0276$) suggesting their predatory influence was minimal during this time. Acting as a common factor [86] we suggest that *C. punctipennis*, via ontogenetic feeding behavior, would be the dominant predator of the rotifer population in Lower Mill Pond [81] [82] [84] [87], potentially creating a secondary trophic cascade.

Over the entire study period, linear regression analysis confirmed a positive relationship between the rotifer grazer and edible (<50 µm) cyanobacterial biomass (Adj $r^2 = 0.720$, $p = 0.005$) (**Figure 4**) and all cyanobacteria (Adj $r^2 = 0.705$, $p = 0.006$), suggesting top-down control. Anticipating reciprocal patterns of trophic cascades [8], one might have expected a negative correlation [10] [88] between obligate grazers (*i.e. K. cochlearis*, *P. vulgaris* and *C. unicornis)*, and edible cyanobacteria, the latter considered algal picoplankton [10] [89]. However, rotifers can feed upon protozoans within the microbial loop including bacteria, heterotrophic nano-flagellates (HNF) [90], and ciliates [91], where HNF preferentially ingest picocyanobacteria [90]. HNF and ciliates have been proposed as forces structuring the picoplankton community [90] [92] [93]. Assum-

ing the microbial loop is embedded within the trophic spectrum of Lower Mill Pond, a cascade under the control of invertebrate planktivory (*i.e. Chaoborus*) that propagated downwards to include rotifer grazers, HNF, and picocyanobacteria (**Figure 5**) could explain the positive correlation that we observed. Conversely, linear regression confirmed a positive relationship between edible cyanobacteria and rotifer grazer biomass (Adj. $r^2 = 0.678$, $p = 0.007$) (**Figure 4**), all cyanobacteria (Adj $r^2 = 0.705$, $p = 0.006$), following a classic trophodynamic paradigm [94], commonly referred to as bottom-up control, with positive correlations between increasing trophic levels. Bottom-up control has traditionally been associated with nutrient enrichment, where documented sources in Lower Mill Pond include watershed input, inflow and internal loading [42] yet could also include juvenile *Alosa* mortality [44], transport of nutrients from sediments as a result of benthic detritivory [95] and "the Chaoborus pump" [96] (**Figure 5**). Increased biomass coupled with inefficient utilization of edible algae (<50 μm) by small planktonic herbivores, including rotifers, [14] appears to have occurred where heavy *Alosa* planktivory [14] existed.

Seasonal cyanobacterial populations and cyanotoxin concentrations

Evaluation of finer temporal patterns suggests that trophic influences successively structured the plankton biomass in Lower Mill Pond (**Figure 5**). As a consequence of *Alosa* planktivory, the relative abundance of edible cyanobacterial biomass (<50 μm/WLW%) increased to 84% by 21 June (**Figure 3**), followed by an increase in total edible cyanobacterial biomass between 10 July and 19 July, this time period with a maximum net positive growth rate [52] of 0.21 d^{-1} (**Figure 5**). This growth rate was higher than those previously reported for cyanobacteria (0.06 and 0.08 d^{-1}) [11] but similar for this size class of *Dolichospermum* spp. (0.212 d^{-1}) and for picoplankton communities (0.14 d^{-1}) [97]. The positive correlation between net growth rates in the presence of increasing obligate grazers suggests that growth rates exceeded grazing pressure during this time, consistent with the observations of Lehman and Sandgren [52]. The edible biomass maximum was observed in mid-August, similar to that found in Canadian Lakes [97], however the unimodal peak in edible biomass was somewhat abbreviated [97], as evidenced by an abrupt decline on 30 Aug, marked by a net negative growth rate of −0.05 d^{-1}. The negative correlation between net growth rates in the presence of rotifer grazers suggests that grazing pressure exceeded growth rates during this time (**Figure 5**). By the end of August, it appears that favorable conditions existed for the proliferation of the inedible cyanobacteria (>50 μm) including continued grazing pressure on the edible cyanobacteria, nutrient availability from internal recycling [44] [95] [96] and seasonal succession [2] [3] [5] [11] [98], leading to its observed seasonal maxima on 27 Sep and surface accumulations on 11 Oct (**Figure 5**).

We have previously demonstrated that for all (<50 μm, WLW and BFC) size classes of cyanobacteria, biomass was causatively related to microcystin concentration in Lake Cochichewick, Lake Attitash [46] and Lower Mill Pond [51]. During this study period, similar observations confirmed that cyanobacterial

biomass was positively correlated with microcystin concentration for all size classes ($r(27) = 0.611$, $p < 0.001$), and a marginal positive correlation ($r(8) = 0.577$, $p = 0.104$) was observed between rotifer grazers and edible microcystins. In regards to BMAA, we observed a significant negative correlation between cyanobacterial biomass and BMAA concentration for the <50 μm and WLW size classes ($r(18) = -0.521$, $p = 0.0266$), and a weak negative correlation ($r(8) = -0.388$, $p = 0.373$) between rotifer grazers and edible BMAA. This negative correlation between algal biomass (Chl-*a*) and BMAA was previously observed in Lake Winnipeg [99]. It appears that the highly significant and positive relationship between the rotifer grazer and edible cyanobacterial biomass, could have influenced the cyanotoxin concentrations, increasing microcystins and decreasing BMAA.

5. Conclusion

This study confirmed that the presence of planktivorous juvenile *Alosa pseudoharengus* in Lower Mill Pond altered the trophic spectrum, where compensation and a cascade were observed. The cascade manifested as an increase in the biomass of edible and inedible cyanobacteria, creating successive "bloom" conditions. An apparent change in juvenile *Alosa* foraging behavior towards benthic subsidies in the littoral zone facilitated the consumption of cyanobacteria, the toxins of which bioaccumulated in the fish muscle tissue. Within this portion of *Alosa* life history, we observed similar cyanotoxin concentrations to those previously reported, and concluded that MC biodiluted and BMAA biomagnified. The change in foraging behavior appears to be triggered by resource availability, and if there is a common trait amongst this forage fish, it suggests potential exposure to cyanotoxins in other freshwater resources.

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Conflicts of Interest

The authors claim no conflict of interest with this project or its outcomes.

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Supplemental

Supplemental Table S1. Phycocyanin (PC), cyanotoxin concentrations (MC and BMAA) in water and sediment (littoral and pelagic) samples, and Secchi disk depth from Lower Mill Pond. SEM indicates standard error of the mean.

Water samples													
<50 μm							WLW						
Sample Date	PC (μg·L^{-1})	SEM	MC (ng·L^{-1})	SEM	BMAA (μg·L^{-1})	SEM	Sample Date	PC (μg·L^{-1})	SEM	MC (ng·L^{-1})	SEM	BMAA (μg·L^{-1})	SEM
7-Jun	3.19	0.06	10.54	0.99	0.54	0.07	7-Jun	5.72	0.40	8.16	0.97	0.56	0.12
21-Jun	4.69	0.15	7.61	1.33	0.43	0.06	21-Jun	5.55	0.42	5.78	0.66	0.41	0.12
10-Jul	5.55	0.15	8.44	0.82	0.21	0.07	10-Jul	6.59	0.07	8.26	1.25	0.27	0.05
19-Jul	40.87	2.17	11.81	1.94	0.24	0.06	19-Jul	54.23	3.38	9.46	0.79	0.25	0.02
2-Aug	35.67	2.81	9.16	0.53	0.21	0.04	2-Aug	35.40	0.91	7.42	0.76	0.15	0.02
16-Aug	67.54	1.29	11.60	1.24	0.12	0.00	16-Aug	70.68	1.50	10.37	0.79	0.17	0.05
30-Aug	25.26	0.39	16.38	0.21	0.41	0.02	30-Aug	28.60	1.25	17.10	0.30	0.48	0.06
13-Sep	11.94	0.55	19.64	1.40	0.51	0.09	13-Sep	17.88	0.46	11.17	1.24	0.57	0.03
27-Sep	17.25	0.35	13.30	1.30	1.06	0.21	27-Sep	29.70	1.60	13.38	0.93	0.10	0.02

BFC							Secchi Disk Depth		
Sample Date	PC (μg·L^{-1})	SEM	MC (ng·L^{-1})	SEM	BMAA (μg·L^{-1})	SEM	Sample Date	SDD (m)	SEM
7-Jun	98.31	12.15	7.05	1.50	nd		7-Jun	1.69	0.004
21-Jun	18.35	1.46	7.63	1.73	nd		21-Jun	1.54	0.003
10-Jul	137.43	13.17	10.21	3.42	nd		10-Jul	1.54	0.006
19-Jul	1172.57	115.67	13.56	2.92	nd		19-Jul	1.54	0.001
2-Aug	234.87	14.75	250.00	0.00	nd		2-Aug	1.08	0.005
16-Aug	409.33	62.38	325.92	31.17	nd		16-Aug	0.68	0.007
30-Aug	249.27	29.00	32.60	4.83	nd		30-Aug	0.92	0.001
13-Sep	132.53	24.97	45.41	19.97	nd		13-Sep	0.92	0.010
27-Sep	350.97	25.73	123.26	35.81	nd		27-Sep	0.95	0.001

nd = non-detect.

Sediment samples													
Littoral Zone							Pelagic Zone						
Site	PC (μg·L^{-1})	SEM	MC (μg·g^{-1} dw)	SEM	BMAA (μg·g^{-1} dw)	SEM	Site	PC (μg·L^{-1})	SEM	MC (μg·g^{-1} dw)	SEM	BMAA (μg·g^{-1} dw)	SEM
Site #1	139.97	0.85	0.123	0.019	0.053	0.023	Site #2	94.34	0.50	0.009	0.002	0.020	0.009
Site #5	1088.93	2.52	0.544	0.173	1.445	0.440	Site #3	60.00	0.21	0.001	0.000	0.024	0.008
Site #8	234.58	0.45	1.803	0.474	2.220	0.099	Site #4	76.40	0.49	0.002	0.001	0.023	0.008
Site #9	353.27	0.88	1.159	0.103	0.299	0.022	Site #6	70.00	0.17	0.002	0.000	0.019	0.004
							Site #7	37.77	0.55	0.003	0.000	0.016	0.002