

Incidence and phenotypic variation in alewife alter the ontogenetic trajectory of young-of-the-year largemouth bass

Mikkel Boel¹, Jakob Brodersen^{2,3}, Anders Koed¹, Henrik Baktoft¹ and David M. Post⁴

¹Section for Freshwater Fisheries and Ecology, Technical Univ. of Denmark, Silkeborg, Denmark

²Dept of Fish Ecology and Evolution, EAWAG Swiss Federal Inst. Of Aquatic Science and Technology, Center of Ecology, Evolution and Biochemistry, Kastanienbaum, Switzerland

³Div. of Aquatic Ecology and Evolution, Inst. of Ecology and Evolution, Univ. of Bern, Bern, Switzerland

⁴Dept of Ecology and Evolutionary Biology, Yale Univ., New Haven, CT 6520-8106, USA

Corresponding author: Mikkel Boel, Section for Freshwater Fisheries and Ecology, Technical Univ. of Denmark, Silkeborg, Denmark. Email: mikkelboel79@gmail.com

Decision date: 25-Jun-2018

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: [10.1111/oik.05556].

Abstract

There is increasing evidence that phenotypic variation can strongly impact community structure and ecosystem functions. Alewife *Alosa pseudoharengus* is a planktivorous fish species that strongly impact lake ecosystems. It has previously been demonstrated that phenotypic variation related to differences in life history among landlocked and anadromous alewife populations alters the strength of interactions with other species, potentially modifying its role in the community. The migration between freshwater and marine ecosystems by anadromous alewife creates seasonal differences in alewife densities, which causes lake zooplankton communities to alternate between large-body size and higher densities in the spring, and small-body size and low densities in the summer and fall. In lakes with resident (landlocked) alewife, predation from alewife modifies the zooplankton community to having low zooplankton densities and mainly small-bodied zooplankton year-round. The strong effects of phenotypic variation in alewife on zooplankton may be important for coexisting species that rely on zooplankton as a resource. Here we use estimates of growth, and direct diet and stable isotope analyses to ask if the presence- and phenotypic variation of alewife alters the ontogenetic trajectory of young-of-the-year (YOY) largemouth bass *Micropterus salmoides*, which depend on zooplankton in the early life stages. We found that both the presence- and phenotypic variation of alewife affects growth, trophic position, and diet of largemouth bass. YOY largemouth bass from lakes without alewife grew faster, switched to piscivory earlier, and reached higher trophic positions than in alewife lakes. In lakes with landlocked alewife largemouth bass grew slower and obtained a lower trophic position than those in lakes with anadromous alewife. These divergences can be explained by the strong effects of alewife on zooplankton community structure. Our results demonstrate how the strong effects of phenotypic variation can propagate through natural food webs to influence important life history transitions in other species.

Keywords: diet shifts, food web utilization, growth, largemouth bass, niche shifts, ontogeny, piscivory, size-structured predation, stable isotopes, trophic position

Introduction

The strong effect of the presence or absence species on community structure and ecosystem functions is well recognized (Brooks and Dodson 1965, Carpenter et al. 1987, Jones et al. 1994, Power et al. 1996, Naiman et al. 2002, Whitham et al. 2006). Recently studies have started to address the ecological consequences of phenotypic variation within species (Treseder and Vitousek 2001, Proffitt et al. 2005, Wimp et al. 2005, Post et al. 2008, Walsh et al. 2012, Des Roches et al. 2018). Variation within a species (phenotypic variation) can have strong direct effects upon prey communities and prey evolution and predators (Post et al. 2008; Palkovacs & Post 2009; Harmon et al. 2009; Walsh and Post 2011; Howeth et al. 2014; Brodersen et al. 2015), and strong indirect effects that propagate through the food web to alter the strength of trophic cascades and the phenotype and foraging of competitors (Post et al. 2008; Walsh et al. 2012)(Huss et al. 2014). These direct and indirect effects of phenotypic variation can create seasonal variation in prey availability (Post et al. 2008), that may have important consequences for the diet, growth and, ultimately, survival of coexisting species, particularly those that undergo pronounced seasonal ontogenetic niche shifts.

Alewife (*Alosa pseudoharengus*) are planktivorous fish, that have strong impacts on the zooplankton community (Brooks and Dodson 1965, Post et al. 2008). Across the eastern North America, there are two forms of alewife that differ with respect to life history. This phenotypic variation has effects that propagate through food webs and affects coexisting species and ecosystem functions (Post et al. 2008, Walsh and Post 2011, Walsh et al. 2012, Huss et al. 2014, Brodersen et al. 2015). Anadromous alewife spawn in and spend their first summer of life in freshwater, but then migrate to the ocean where they do most of their feeding and growth before returning to freshwater each year to spawn at around 3-4 years of age. Resident landlocked alewife spend their entire life in freshwater lakes. Many of the landlocked populations in Connecticut (and all of those under study here) are independently

evolved, after becoming isolated from anadromous ancestors around 300-450 years ago (Palkovacs et al. 2008, Twining and Post 2013). Anadromous and landlocked alewife differ in whole-body morphology, gillraker spacing and gape width, foraging behavior, and their duration of residence in freshwater (Post et al. 2008, Palkovacs and Post 2008, Jones et al. 2013). Those differences drive differences in zooplankton densities and size structure (Post et al. 2008, Palkovacs and Post 2009) and has caused evolution in life history in *Daphnia*, the dominant grazer in most lakes (Walsh and Post 2011). Lakes with landlocked alewife populations have low densities of smaller-bodied zooplankton year-round; lakes with anadromous alewife populations have zooplankton communities that cycles between higher densities of large-bodied zooplankton in the winter and spring and low densities of smaller-bodied zooplankton in the summer and fall; and lakes with no alewife population have high densities of larger-bodied zooplankton year-round (Post et al. 2008). Through the effect on zooplankton, alewife may indirectly influence the foraging behavior, growth, and survival of coexisting fish species that rely on the same resources (Neill 1975, DeVries and Stein 1992, Olson et al. 1995, Post et al. 2008).

Young-of-the-year (YOY) piscivorous fish, such as largemouth bass (*Micropterus salmoides*), undergo ontogenetic diet shifts from feeding on zooplankton, to feeding on macroinvertebrates, and finally to feeding on fish (Werner and Gilliam 1984, Olson 1996, Post 2003). The timing of these ontogenetic shifts largely depends on body size, and influences on early growth are therefore expected to affect the timing of future ontogenetic transitions (Olson 1996, Parkos and Wahl 2010). Thus, differences in zooplankton availabilities mediated by alewife (Post et al. 2008) may have profound influences on the ontogenetic trajectory and survival of coexisting fish species such as largemouth bass. The growth rate of juvenile fish in the zooplanktivorous stage is positively correlated with zooplankton availability (Persson et al. 2000, Hoxmeier et al. 2004, Milstein et al. 2006) and

competition at this early life history stage can reduce growth and survival and subsequently the recruitment of juvenile fish into the adult population (Werner 1977, DeVries and Stein 1992, Olson et al. 1995, Bystrom et al. 1998, Hjelm et al. 2000). In largemouth bass, rapid growth during the invertebrate feeding phase is critical to reaching the predatory size advantage required to reach piscivory (Olson 1996). Largemouth bass generally make the transition to piscivory during their first or second year or life (Ludsin and DeVries 1997, Post 2003), and any delays in this transition lead to loss of growth and subsequently to increased size-related predation and winter mortality (Ludsin and DeVries 1997, Post et al. 1998, Post 2003).

We hypothesize that the differences in zooplankton communities created by the presence- and phenotypic variation of alewife (Post et al. 2008) will influence the ontogenetic trajectory of sympatric YOY largemouth bass. The greater biomass and larger body-size of zooplankton prey in lakes with no alewife, compared with both lakes with landlocked- and anadromous alewife, should allow largemouth bass to grow fastest and make earliest ontogenetic shifts in this lake type. The higher density of large-bodied zooplankton in spring and early summer in lakes with anadromous alewife, though decreasing toward summer, may result in faster growth and earlier ontogenetic transitions of YOY largemouth bass in the anadromous lake type compared with landlocked lake type. These differences may be visible in the timing of the dietary niche shifts from zooplankton (pelagic food web) to macroinvertebrates (littoral food web) and ultimately in the timing of the transition to piscivory. Here we test these predictions using direct diet analyses, stable isotopes, and estimates of summer growth rates for YOY largemouth bass in lakes with landlocked-, anadromous-, and no alewife populations.

Materials and procedures:

Study Area and Lake Types

We collected YOY largemouth bass from three lakes without alewife (Black Pond, Gardner Lake, Hayward Lake), three lakes with landlocked alewife populations (Amos Lake, Pattagansett Lake, Rogers Lake), and three lakes with anadromous alewife populations (Bride Lake, Dodge Pond, Gorton Pond). Basic details of the lakes are presented in table 1. Further information and layout of their geographic location are available in Post et al. (2008). There is no significant difference in fish community composition between the lake types (Howeth et al. 2014), except that non-alewife planktivorous fish are more abundant in lakes with landlocked alewife relative to lakes with anadromous alewife (Palkovacs and Post 2008). Largemouth bass and chain pickerel (*Esox niger*) are the top predators in these systems, and bluegill sunfish (*Lepomis macrochirus*), golden shiners (*Notemigonus crysoleucas*), pumpkinseed sunfish (*Lepomis gibbosus*) and yellow perch (*Perca flavescens*) are the most common non-alewife planktivorous fishes (Palkovacs and Post 2008, Howeth et al. 2014).

Fish collection

YOY largemouth bass were collected using dip net (while snorkeling), scoop net (from boat), beach seine, and electrofishing over the period from June 4th to November 19th 2009 on four occasions in each lake. Largemouth bass were identified as YOY based on their absolute size early in the season, and their size relative to other largemouth bass late in the season (there is a large and distinct gap in size between YOY and other age classes of bass through the entire year). Lakes with landlocked alewife were sampled from day-of-year (DOY) 161 to 299 in Amos (N=48 and length: 17.8-98.0 mm); 160 to 308 in Pattagansett (N=41 and length: 19.7-82.0 mm); and 161 to 303 in Rogers (N=79 and length =17.8-60.0 mm). Lakes with anadromous alewife from DOY 164 to 300 in Bride (N=96; length: 17.4-67.0 mm); 155 to 323 in Dodge (N=70; length: 8.5-108.0 mm); and 155 to 323 in Gorton (N=57; length: 13.1-73.0 mm). Lakes with no alewife were sampled from DOY 159 to 293 in

Black (N=34; length: 15.5-107.0 mm); 159 to 323 in Gardner (N=45; length=10.0-92.0 mm); and 159 to 308 in Hayward Lake (N=41; length =13.3-89.0 mm). Upon capture, largemouth bass were euthanized and placed on ice for transport to the lab, where they were preserved at -20°C until further processing. We measured the standard length all of the fish we collected (N=511), and we haphazardly selected a subset from each lake for diet (N=221) and stable isotope analysis (N=291). The fish collection complied with Yale Institutional Animal Care and Use Committees protocol #2009-10734 and CT State DEEP scientific collector permit number SC-07015.

Stable Isotope analysis

Following Post (2002 and 2003), we used stable isotopes of nitrogen ($\delta^{15}\text{N}$) to provide evidence for ontogenetic shifts in trophic position and carbon ($\delta^{13}\text{C}$) to provide evidence for shifts in diet from pelagic to littoral food sources. Here we report isotope values in the standard δ notation where $\delta\text{X} \text{‰} = [(\text{R}_{\text{sample}}/\text{R}_{\text{standard}}) - 1] 10^3$; δX is either $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ and R is the ratio of $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$, respectively. We dried the whole body of each YOY largemouth bass, minus the head and viscera, at $45\text{--}55^{\circ}\text{C}$ for approximately 48 hours and ground it into a fine powder. Samples were analyzed using a Costech 4010 Elemental Analyzer combustion system coupled to a Thermo DeltaXP Advantage IRMS via a Thermo ConFlo III interface at Yale University. Each run included a house standard (trout muscle tissue) interspersed every 5–9 samples to correct for drift and to provide an estimate of instrumental error. Cayuga brown trout (*Salmo trutta*) was used as working standard, $\delta^{13}\text{C} = -25.1$ and $\delta^{15}\text{N} = 17.3$. The global standard was PeeDee Belemnite for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$. Lipid-corrections were applied to $\delta^{13}\text{C}$ values when C:N ratios >3.3 following (Post et al. 2007). We used herbivorous zooplankton for the pelagic baseline and periphyton for the littoral food webs and assumed a trophic fractionation of 3.4‰ for $\delta^{15}\text{N}$ and 0‰ for $\delta^{13}\text{C}$ following Post (2002). Taking the trophic levels of the respective baseline

species into account, trophic position was estimated as: trophic position = $\lambda + (\delta^{15}\text{N}_{\text{largemouth bass}} - [\delta^{15}\text{N}_{\text{pelagic}} \circ \alpha + \delta^{15}\text{N}_{\text{littoral}} \circ (1 - \alpha)]) / 3.4$, where λ is the trophic position of the organism used for $\delta^{15}\text{N}$ baseline (i.e., 1 for periphyton and 2 for zooplankton) and where α is a proportional measure of the use of littoral and pelagic food web. We calculated $\alpha = (\delta^{13}\text{C}_{\text{largemouth bass}} - \delta^{13}\text{C}_{\text{littoral}}) / (\delta^{13}\text{C}_{\text{pelagic}} - \delta^{13}\text{C}_{\text{littoral}})$ following (Post 2002) and constrained α between zero and one.

Stomach contents

We analyzed the stomach contents of five (when possible) YOY largemouth bass from each sampling date and location. These were not the same individuals we used for isotope analysis. Items in stomachs were identified to the lowest relevant taxonomic group and counted. Overall there was 20% empty stomachs in bass from lakes without alewife, increasing with the transition to piscivory. There were 4% empty stomachs in bass from lakes with anadromous- and 1% from lakes with landlocked alewife. Individuals with empty stomachs were not included in the modeled data. Prey types were evaluated as: large-bodied zooplankton (*Daphnia* spp., *Epischura lacustris*, *Mesocyclops edax*); small-bodied zooplankton (*Bosmina* spp., *Polyphemus pediculus*, *Chydorus* spp., various Copepoda, *Ceriodaphnia* spp. and *Diaphansoma* spp.); littoral macro fauna (various Chironomidae pupae and larvae, various Ephemeroptera nymphs, various Odonata nymphs, various Amphipoda, various Trichoptera nymphs, various Hemiptera nymphs, various Plecoptera nymphs and *Asellus* sp.); and juvenile fish (bluegill sunfish, yellow perch, or alewife). A standard dry mass (DM) was estimated for each type of prey item: for zooplankton DM we used estimates from Downing and Rigler (1984); for macroinvertebrates, we converted body length or head widths to DM following (Benke et al. 1999); and for fish prey we converted length to DM using a regression created with data from juvenile bluegills (Wahl and Stein 1991, Einfalt and Wahl 1997). DM of prey items was estimated from the average lengths of well-preserved

specimens from this study, and was multiplied by the number of prey in the stomach of each largemouth bass. For analysis purposes and comparison with isotope data, prey items were classified into three diet groups: pelagic prey (pelagic zooplankton), littoral prey (macro fauna and littoral zooplankton species) and fish prey (fish). Chydorus are small-bodied zooplankton that have a littoral $\delta^{13}\text{C}$ making them look like larger-bodied littoral macro fauna and YOY largemouth bass can eat them at a relatively small size (when at a low trophic level). The diets showed that Chydorus were common in the diets from the June/July samplings. Thus, there could be some confounding effect of littoral zooplankton and littoral macro fauna.

Statistical Analyses

All statistical analyses were conducted in a MCMC based Bayesian framework using JAGS (Plummer 2003), R (R Core Team 2016) and the R package R2jags (Su & Yajima 2015). This approach was chosen as it enables fitting a hierarchical version of the Gompertz growth curve and it allows between-lake type comparisons by sampling the posterior distributions of estimated parameters. For all models, this was achieved using the posterior parameter distributions to predict lake type specific mean response values for an artificial data set containing the three lake types and other covariates present in each respective model. By contrasting these predicted response values between lake types, mean lake type differences and associated 95 % credible intervals were obtained. For all models, visual assessment of the chains indicated good mixing for all parameters. To compare the growth trajectories of YOY largemouth bass in the three lake types we fitted the following hierarchical version of the Gompertz growth curve to YOY largemouth bass standard length (SL) sampled over one growth season:

$$\text{SL}_{ij} = (L_{\infty ij} * \text{LT}_{ij}) * \exp(-b_{ij} * \exp(-(c_{ij} * \text{LT}_{ij}) * \text{DOY}_{ij})) + \text{lake}_j + \varepsilon_{ij}$$

$$\text{lake}_j \sim N(0, \sigma_{\text{lake}}^2)$$

$$\varepsilon_{ij} \sim N(0, \sigma^2 * \text{DOY}_{ij}^{2*\delta})$$

In this, observation of fish length i in lake j is modelled as a function of lake type specific asymptotic length limit ($L_{\infty} * LT$), the growth rate (c), the displacement coefficient (b), the factor lake type (LT), the covariate day of year (DOY) and the residual term (ε). The asymptotic length limit (L_{∞}) and the growth rate (c) was allowed to differ between lake types (LT) whereas the term determining displacement on the x-axis (b) was assumed to constant in all lakes. A random intercept term ($lake$) was included modelling lake id as random effect with mean zero and variance σ_{lake}^2 . A variance structure allowing the variance (σ^2) to increase as a power function of DOY with exponent $2*\delta$ was included to accommodate temporal variance heterogeneity. Non-informative uniform priors were used for parameters L_{∞} , b and c and Half-Cauchy(25) priors were used for σ and σ_{lake} . The model was fitted using three chains, a 100,000 burn-in, thinning rate 100 and 1,000,000 iterations yielding 27,000 iterations for the posterior distributions of estimated parameters.

The temporal development in YOY largemouth bass trophic position (TP) between lake types was compared by fitting the following linear mixed effects model and obtain lake type contrasts from the posterior distributions:

$$TP_{ij} = \alpha + LT_{ij} + DOY_{ij} + LT_{ij} * DOY_{ij} + lake_j + \varepsilon_{ij}$$

$$lake_j \sim N(0, \sigma_{lake}^2)$$

$$\varepsilon_{ij} \sim N(0, \sigma^2)$$

In this, trophic position of fish i captured in lake j is a function of a common intercept (α), lake type (LT) and day of year (DOY) as well as the $LT*DOY$ interaction. A random intercept ($lake$) was included to model lake id as a random effect with mean zero and variance σ_{lake}^2 . Residuals (ε_{ij}) were assumed to be normal distributed with mean zero and variance σ^2 . Non-informative normal distributed priors were used for regression parameters and Half-Cauchy(25) were used for σ and σ_{lake} . The model was fitted using three chains, a 10,000 burn-

in, thinning rate 10 and 100,000 iterations yielding 27,000 iterations for the posterior distributions of estimated parameters.

The temporal development in YOY largemouth bass relative use of pelagic and littoral resources between lake types was compared in separate models for isotope- and direct diet data, modelled as pelagic proportion. In contrasting the diet composition between lake types, we focused on the pelagic-benthic proportion, excluding all piscivore largemouth bass from the dataset as fish prey could not be assigned to a food web in this study. Finally, all fish from the lake type without alewife were excluded from the analysis, as there was markedly more piscivory in these lakes (figure 5) and the data remaining data were too scarce to be modelled. We excluded 4 fish from the remaining data that had eaten prey fish from the analysis – 3 from lakes with anadromous alewife and 1 from lakes with landlocked alewife. For the isotope data subset, no lake types or fish were excluded on this account. The pelagic proportion (PP), isotopes (α) and diets separately, were compared by fitting the following beta distributed generalized additive mixed effects model (beta GAMM) to the data.

$$\begin{aligned} \text{PP}_{ij} &\sim \text{Beta}(a_{ij}, b_{ij}) \\ a_{ij} &= \Theta * \pi_{ij} \\ b_{ij} &= \Theta * (1 - \pi_{ij}) \\ E(\text{PP}_{ij}) &= \pi_{ij} \\ \text{var}(\text{PP}_{ij}) &= (\pi_{ij} * (1 - \pi_{ij})) / (\Theta + 1) \\ \text{logit}(\pi_{ij}) &= \alpha + \text{LT}_{ij} + f_j(\text{DOY}_{ij}) + \text{lake}_j \\ \text{lake}_j &\sim N(0, \sigma_{\text{lake}}^2) \end{aligned}$$

The expected values of PP observation i from lake type j ($E(\text{PP}_{ij})$) is π , which was modelled via a logit link by a predictor function containing explanatory variables of interest, i.e. the factor lake type (LT) and covariate day of year (DOY) as well as a random intercept ($lake$) with mean zero and variance σ_{lake}^2 . Variance of PP_{ij} is defined as $\text{var}(\text{PP}_{ij})$. As preliminary

data exploration indicated a non-linear effect of *DOY* on *PP*, we used lake type specific smoothing functions as indicated by $f_j(DOY_{ij})$ in the predictor function, thus one smoother per lake type was fitted. This was achieved using O'Sullivan splines (Wand & Ormerod 2008) as detailed in (Zuur et al. 2014). Diffuse normal priors were used for regression parameters α and *LT*, whereas a Half-Cauchy(25) prior was used for σ_{lake} . The model was fitted using three chains, a 10,000 burn-in, thinning rate 10 and 100,000 iterations yielding 27,000 iterations for the posterior distributions of estimated parameters. As the data contained the extreme values 0 and 1 (one observation each) excluded by the beta distribution, we employed the transformation $(PP * (N - 1) + 0.5) / N$ where *N* is number of observations prior to model fitting (Smithson & Verkuilen 2006).

Results

We found differences in growth rate (length) for YOY largemouth bass among all three lake types. The Gompertz curves and the pairwise contrast plots of lake types (Figure 1 and Table 2) supported our hypothesis that no inhibition-, intermediate- and strong inhibition of growth of largemouth bass occurs in lakes without alewife, lakes with anadromous alewife, and lakes with landlocked alewife, respectively. The growth rate of YOY largemouth bass was highest in the lakes without alewife, relative to both lakes with landlocked- and anadromous alewife. Moreover, growth rate was higher for largemouth bass from lakes with anadromous alewife compared with lakes with landlocked alewife. This indicates that the presence of alewife reduced the growth rate of YOY largemouth bass and, moreover, that this effect is stronger in lakes with landlocked alewife than in lakes with anadromous alewife.

We found that there were differences in the rate of increase in trophic position of YOY largemouth bass among all three lake types. The linear approximation and the pairwise contrast plots of the lake types (Figure 2 and Table 3) show that YOY largemouth in

lakes with landlocked alewife exhibited a lower climb in trophic level than lakes without alewife. While the contrast plots of these two lake types showed no segregation from the lakes with anadromous alewife at any time over the period, looking at the posterior distributions of slope parameters that illustrates the interaction between lake type and time (the combined effect of *DOY* and lake type on trophic position), there were no overlap in the posterior distributions (Figure 3). This illustrated that the climb in trophic position over time (the slopes) was in fact different between all three lake types. YOY largemouth bass from lakes with landlocked alewife increased in trophic position much slower than YOY largemouth bass from lakes with anadromous alewife, which had a slower increase in trophic position than YOY largemouth bass from lakes with no alewife population. Extrapolating the trends to later in the growth season, trophic position would become fully separation between the lake types in figure 2. Like growth, the rate of increase in trophic position was highest in lakes without alewife. Moreover, the rate of increase in trophic position was higher in lakes with anadromous alewife relative to lakes with landlocked alewife (Figure 2 & 3). This indicates that the presence of alewife slows down the transition of YOY largemouth bass to higher trophic positions and that this effect is stronger in lakes with landlocked alewife compared to lakes with anadromous alewife.

The isotopically illustrated differences are fully in line with the direct diet composition among lake types over time shows a clear overweight of fish prey in lakes without alewife relative to lakes with alewife. In lakes with landlocked- and anadromous alewife the diets showed a gradual decrease of pelagic prey and a short period of piscivory in August (Figure 5 A and B). The proportion of fish in the diet of YOY largemouth bass in lakes without alewife came sooner and at a smaller size, around *DOY* 197 and *SL* of approx. 33 mm, than in alewife lakes, around *DOY* 230 and a *SL* approx. 50 mm). In lakes without alewife proportion of fish increased while the proportions of littoral- and pelagic prey items

decreased; pelagic items, however, remained until the end of the period where only fish were found (Figure 5 C). The increasing piscivory in lakes without alewife coincided with several occurrences of empty stomachs, which we did not find in lakes with landlocked- and anadromous alewife.

We found no difference in the ontogenetic pattern of proportional use of pelagic-based resources by YOY largemouth bass (α) among the different lake types (Figure 4). The comparison of direct diet composition between lakes with landlocked- and anadromous alewife showed there was a shift from pelagic to littoral food items, but this trend was parallel in the two lake types and did not lead to any segregation in the contrast comparison (Figure 6). Hence, the direct diet and stable isotope do not provide any evidence for an effect of phenotypic variation in alewife on the utilization of pelagic and littoral prey by largemouth bass in lakes with anadromous and landlocked alewife.

Discussion

We found substantial influences of both presence- and phenotypic variation of alewife on growth and ontogenetic (dietary) niche shifts of young-of-the-year (YOY) largemouth bass. YOY largemouth bass grew faster and had a higher rate of increase in trophic position in lakes without alewife than in lakes with alewife, and YOY largemouth bass were only able to transition to and sustain piscivory consistently in lakes without alewife. YOY largemouth bass also grow faster and had a higher rate of increase in trophic position in lakes with anadromous alewife compare to lakes with landlocked alewife. These patterns of growth and trophic shifts are consistent with previous observations that the presence- and phenotypic variation of alewife (anadromous, landlocked and without) determines zooplankton species composition, biomass, and size structure (Post et al. 2008, Howeth et al. 2014); there are more large-bodied zooplankton in summer in lakes without alewife than in lakes with alewife, and more large-bodied zooplankton in the spring and early summer in lakes with anadromous-

than in lakes with landlocked alewife (Post et al. 2008). As zooplankton availability for most fish species is important for early growth (Persson et al. 2000, Hoxmeier et al. 2004, Milstein et al. 2006) and influences ontogenetic trajectories (Olson 1996, Parkos and Wahl 2010), our results suggest that the large effects of alewife on the zooplankton community have further affected the growth and ontogeny of YOY largemouth bass.

The higher growth rate of largemouth bass in lakes with no alewife is likely a result of the greater availability of zooplankton in spring and over the summer, providing a relative growth advantage for largemouth bass in these lakes. The abundances of large-bodied zooplankton in lakes without alewife are generally higher in spring and especially higher in summer, compared with both lakes with landlocked- and anadromous alewife (Post et al. 2008).

Finding the fastest growth and most rapid increases in trophic position in YOY largemouth bass from lakes without alewife, underlines the importance of zooplankton availability for early largemouth bass ontogeny. It suggests an important role of availability of large-bodied zooplankton in the summer months, in addition to the importance of the availability of large-bodied zooplankton in spring and early summer. Early growth differences can create positive or negative feedbacks that respectively may increase or decrease growth and survival at older ages (e.g. Olson 1996, Post et al. 1998, Mittelbach and Persson 1998, Post 2003). Fast growth in the early ontogenetic stages is crucial for reaching piscivory (Olson 1996, Parkos and Wahl 2010). This is corroborated by the faster increases in growth and trophic position of largemouth bass in lakes without alewife along with our observation that the YOY largemouth bass in these lakes made the shift to piscivory earlier and sustained it throughout the fall. This underlines the link between fast growth and obtaining a size advantage over available fish prey earlier and at a smaller size. The observed short-lived period of piscivory in lakes with landlocked- and anadromous alewife indicated that largemouth bass in these lakes had a size advantage over available fish prey for only a limited period of time, but were

unable to maintain this advantage. Therefore, the reduction in zooplankton density caused by both anadromous and landlocked alewife appears to prevent largemouth bass from sustaining piscivory in their first summer of life, which may impact their future growth and survival (Buijse and Houthuijzen 1992, Olson 1996, Ludsin and DeVries 1997). The impacts on future growth and survival of YOY largemouth bass can be expected to be greater in lakes with landlocked alewife where growth rates were the lowest and the increases in trophic position smaller than in lakes with anadromous alewife. As early growth differences can affect the ontogenetic trajectories (Olson 1996, Parkos and Wahl 2010) and ontogenetic shifts depend on gaining a size advantage over the prey (Werner 1977, Mittelbach 1981), the higher growth rate and greater rate of increase in trophic position of YOY of largemouth bass observed in anadromous compared to landlocked lakes likely results from the strong effect of anadromous alewife on the body-size and biomass of pelagic zooplankton (Post et al. 2008). Our results suggest an interspecific interaction that is mediated through a difference in zooplankton availability in the spring. This difference affects early- and future growth and results in a slower increase in trophic position in lakes with landlocked alewife, relative to lakes with anadromous alewife. Hence, we show that the life history of a dominant planktivore affects the strength of interspecific interactions.

Low zooplankton availabilities can promote an early shift to macroinvertebrate prey (Persson 1983, Persson 1986, Persson and Greenberg 1990, Wu and Culver 1992, Bystrom et al. 1998, Hoxmeier et al. 2004). In perch (*Perca fluviatilis*) the niche shift to macroinvertebrates caused reductions in growth and body condition (Bystrom et al. 1998), suggesting the premature shifts to larger prey items may have been associated with greater handling costs (Werner 1977, Mittelbach 1981). While neither stable isotope nor direct diet data indicated any clear differences in use of pelagic and littoral resources between largemouth bass from lakes with

landlocked- and anadromous alewife, diets showed that bass in lakes without alewife made and sustained the transition to piscivory from littoral- and pelagic food items more quickly than largemouth bass in lakes with alewife (Figure 5). Interestingly, bass in lakes without alewife kept pelagic zooplankton in their diets at a greater proportion longer than the other largemouth bass, which may be an effect of greater availability, as there is a higher biomass of large-bodied zooplankton in lakes without alewife (Post et al. 2008) and illustrating large-bodied zooplankton as a preference during the transition to piscivory. The isotope data showed no clear pattern of habitat shift (Figure 4). The diet data provides better taxonomic resolution for diet shifts (Layman and Post 2008), and the YOY largemouth bass in lakes with landlocked- and anadromous alewife were quite similar and showed a clear shift from pelagic to littoral food web (Figures 5 and 6).

Alewife have strong impacts on zooplankton and these impacts differ with phenotypic variation. Previous studies have shown that strong effects of zooplanktivorous fish on zooplankton size and biomass can impact the timing of ontogenetic shifts in coexisting piscivore fish. Our results corroborate this, but more importantly they show that intraspecific differences in resource use of coexisting early life history competitors can have important effects. Alewife slow the rate of growth and the transition to piscivory of largemouth bass, and these effects were greater for lakes with landlocked- than for lakes with anadromous alewife populations. The differences in growth we observed in this study, and what we know about the system, suggests that alewife competition may cause growth related reductions in survival of largemouth bass (Buijse and Houthuijzen 1992, Olson 1996, Ludsin and DeVries 1997). Additionally, early size differences may persist to older ages (Mittelbach and Persson 1998) and may result in differences in fecundity which typically correlates with as adult size (Wootton 1990). Fast growth enables reaching reproductive size at a younger age (Baylis et al. 1993), which might provide a fecundity advantage for largemouth bass in lakes without

alewife, then lakes with anadromous alewife and then lakes with landlocked alewife.

However, when reaching piscivory, the growth of predatory fish is positively correlated to planktivore biomass (DeVries and Stein 1992, Olson et al. 1995, Hjelm et al. 2000), which may compensate for reduced survival and fecundity related to slow growth in early life. Thus, competition from a planktivore, i.e. alewife, may result in adult piscivores populations with few but large individual (Werner and Gilliam 1984, Olson 1996). Taken together the growth differences established in this study may be associated with effects on future survival and translate into differences in fecundity as well as shaping the size structure and abundance of the adult population.

Only a few studies have addressed the ecological consequences of intraspecific phenotypic variation on complex trophic interactions and ecosystem function (Treseder and Vitousek 2001, Proffitt et al. 2005, Wimp et al. 2005, Post et al. 2008, Walsh and Post 2011). In our study lakes, the presence- and phenotypic variation of alewife structure the zooplankton community (Post et al. 2008, Howeth et al. 2014), drives evolutionary divergences in *Daphnia*, an important prey for YOY fishes (Walsh and Post 2011), and alters foraging morphology and behavior in competitors (Huss et al. 2014) and top-predatory chain pickerel (Brodersen et al. 2015). Here we have shown that the strong effect of the presence of and phenotypic variation in alewife on zooplankton community also alters the ontogenetic trajectory of YOY largemouth bass.

References

- Aitchison, J. 1982. The statistical analysis of compositional data. - *Journal of the Royal Statistical Society Series B-Methodological* 44: 139-177.
- Aitchison, J. 1986. The statistical analysis of compositional data. - Chapman and Hall, New York.
- Baylis, J.R. et al. 1993. Alternating life-histories of smallmouth bass. - *Transactions of the American Fisheries Society* 122: 500-510.
- Benke, A.C. et al. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. - *Journal of the North American Benthological Society* 18: 308-343.
- Brooks, J.L. and Dodson, S.I. 1965. Predation, body size, and composition of plankton. - *Science* 150: 28-35.
- Brodersen J. et al. 2015. Emergence of a novel prey life history promotes contemporary sympatric diversification in a top predator. - *Nature Communications* 6: 8115.
- Buijse, A.D. and Houthuijzen, R.P. 1992. Piscivory, growth, and size-selective mortality of age-0 pikeperch (*Stizostedion-Luciooperca*). - *Canadian Journal of Fisheries and Aquatic Sciences* 49: 894-902.
- Bystrom, P. et al. 1998. Competing predators and prey: Juvenile bottlenecks in whole-lake experiments. - *Ecology* 79: 2153-2167.
- DeVries, D.R. and Stein, R.A. 1992. Complex interactions between fish and zooplankton - Quantifying the role of an open-water planktivore. - *Canadian Journal of Fisheries and Aquatic Sciences* 49: 1216-1227.
- Downing, J.A. and Rigler, F.H. 1984. A manual on methods for the assessment of secondary productivity in fresh waters. Blackwell Scientific Publications, - Oxford, England.
- Einfalt, L.M. and Wahl, D.H. 1997. Prey selection by juvenile walleye as influenced by prey morphology and behavior. - *Canadian Journal of Fisheries and Aquatic Sciences* 54: 2618-2626.
- Hjelm, J. et al. 2000. Growth, morphological variation and ontogenetic niche shifts in perch (*Perca fluviatilis*) in relation to resource availability. - *Oecologia* 122: 190-199.
- Howeth, J. G. et al. 2014. Intraspecific variation in a fish predator affects multi-trophic lake metacommunity structure. - *Ecology and Evolution* 15: 5031-5044.
- Hoxmeier, R.J.H. et al. 2004. Growth and survival of larval walleyes in response to prey availability. - *Transactions of the American Fisheries Society* 133: 45-54.
- Huss, M. et al. 2014. Facilitation of fisheries by natural predators depends on life history of shared prey. - *Oikos* 123: 1071-1080.

- Jones, A.W., Palkovacs, E.P. and Post, D.M. 2013. Recent parallel divergence in body shape and diet source of alewife life history forms. - *Evolutionary Ecology* 27:1175-1187.
- Layman, C.A. and Post, D.M. 2008. Can stable isotope ratios provide for community-wide measures of trophic structure? Reply. - *Ecology* 89: 2358-2359.
- Ludsin, S.A. and DeVries, D.R. 1997. First-year recruitment of largemouth bass: The interdependency of early life stages. - *Ecological Applications* 7: 1024-1038.
- Milstein, A. et al. 2006. Fish larvae: zooplankton relationships in microcosm simulations of earthen nursery ponds. II. brackish water system. - *Aquaculture International* 14: 431-442.
- Mittelbach, G.G. 1981. Foraging Efficiency and Body Size - A Study of Optimal Diet and Habitat Use by Bluegills. - *Ecology* 62: 1370-1386.
- Mittelbach, G.G. and Persson, L. 1998. The ontogeny of piscivory and its ecological consequences. - *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1454-1465.
- Neill, W.E. 1975. Experimental Studies of Microcrustacean Competition, Community Composition and Efficiency of Resource Utilization. - *Ecology* 56: 809-826.
- Olson, M.H. 1996. Ontogenetic niche shifts in largemouth bass: Variability and consequences for first-year growth. - *Ecology* 77: 179-190.
- Olson, M.H. et al. 1995. Competition Between Predator and Prey - Resource-Based Mechanisms and Implications for Stage-Structured Dynamics. - *Ecology* 76: 1758-1771.
- Palkovacs, E.P. and Post, D.M. 2008. Eco-evolutionary interactions between predators and prey: can predator-induced changes to prey communities feedback to shape predator foraging traits? *Evolutionary Ecology Research*, 10, 699-720.
- Palkovacs, E.P. et al. 2008. Independent evolutionary origins of landlocked alewife populations and rapid parallel evolution of phenotypic traits. *Molecular Ecology*, 17, 582-597.
- Palkovacs, E.P. and Post, D.M. (2009). Experimental evidence that phenotypic divergence in predators drives community divergence in prey. *Ecology*, 90(2), 300-305.
- Parkos, J.J. and Wahl, D.H. 2010. Influence of Body Size and Prey Type on the Willingness of Age-0 Fish to Forage under Predation Risk. *Transactions of the American Fisheries Society*, 139, 969-975.
- Persson, L. 1983. Food-Consumption and Competition Between Age Classes in A Perch *Perca-Fluviatilis* Population in A Shallow Eutrophic Lake. *Oikos*, 40, 197-207.
- Persson, L. 1986. Effects of Reduced Interspecific Competition on Resource Utilization in Perch (*Perca, Fluviatilis*). *Ecology*, 67, 355-364.
- Persson, L. et al. 2000. Resource limitation during early ontogeny: constraints induced by growth capacity in larval and juvenile fish. *Oecologia*, 122, 459-469.
- Persson, L. and Greenberg, L.A. 1990. Interspecific and Intraspecific Size Class Competition Affecting Resource Use and Growth of Perch, *Perca-Fluviatilis*. *Oikos*, 59, 97-106.

- Plummer, M., 2003. JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling. In Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003). Vienna.
- Post, D.M. 2003. Individual variation in the timing of ontogenetic niche shifts in largemouth bass. *Ecology*, 84, 1298-1310.
- Post, D.M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*, 83, 703-718.
- Post, D.M. et al. 1998. Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality, and the recruitment of largemouth bass in a northern lake. *Canadian Journal of Fisheries and Aquatic Sciences*, 55, 2588-2600.
- Post, D.M. et al. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*, 152, 179-189.
- Post, D.M. et al. 2008. Intraspecific variation in a predator affects community structure and cascading trophic interactions. *Ecology*, 89, 2019-2032.
- Proffitt, C.E. et al. 2005. *Spartina alterniflora* genotype influences facilitation and suppression of high marsh species colonizing an early successional salt marsh. *Journal of Ecology*, 93, 404-416.
- R Core Team, 2016. R: A language and environment for statistical computing. Available at: <http://www.r-project.org>.
- Smithson, M. and Verkuilen, J., 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychological methods*, 11, 54-71.
- Su, Y.-S. and Yajima, M., 2015. R2jags: Using R to Run "JAGS". Available at: <https://cran.r-project.org/package=R2jags>.
- Treseder, K.K. and Vitousek, P.M. 2001. Potential ecosystem-level effects of genetic variation among populations of *Metrosideros polymorpha* from a soil fertility gradient in Hawaii. *Oecologia*, 126, 266-275.
- Twining, C. W. and D. M. Post. 2013. Cladoceran remains reveal presence of a keystone size-selective planktivore. *Journal of paleolimnology* 49:253-266.
- Wahl, D.H. and Stein, R.A. 1991. Food-Consumption and Growth of 3 Esocids - Field-Tests of A Bioenergetic Model. *Transactions of the American Fisheries Society*, 120, 230-246.
- Walsh, M.R et al. 2012. A cascade of evolutionary change alters consumer-resource dynamics and ecosystem function. *Proceedings of the Royal Society B-Biological Sciences*, 279, 3184-3192.
- Walsh, M.R. and Post, D.M. 2011. Interpopulation variation in a fish predator drives evolutionary divergence in prey in lakes. *Proceedings of the Royal Society B-Biological Sciences*, 278, 2628-2637.
- Wand, M.P. and Ormerod, J.T., 2008. On semiparametric regression with O'Sullivan penalized splines. *Australian and New Zealand Journal of Statistics*, 50, 179-198.
- Werner, E.E. 1977. Species Packing and Niche Complementarity in 3 Sunfishes. *American Naturalist*, 111, 553-578.

Werner, E.E. and Gilliam, J.F. 1984. The Ontogenetic Niche and Species Interactions in Size Structured Populations. *Annual Review of Ecology and Systematics*, 15, 393-425.

Wimp, G.M. et al. 2005. Plant genetic determinants of arthropod community structure and diversity. *Evolution*, 59, 61-69. Wootton, R.J. 1990. *Ecology of Teleost Fishes*. Chapman and Hall, London, UK.

Wu, L. and Culver, D.A. 1992. Ontogenic Diet Shift in Lake Erie Age-0 Yellow Perch (*Perca-Flavescens*) - A Size-Related Response to Zooplankton Density. *Canadian Journal of Fisheries and Aquatic Sciences*, 49, 1932-1937.

Zuur, A.F. et al. 2014. *A Beginner's Guide to Generalised Additive Mixed Models with R*, Newburgh, United Kingdom: Highland Statistics Ltd.

Figure Legends

Figure 1: The development in standard length (SL) over time for young-of-the-year largemouth bass, covering the study period from June 4th to November 19th (2009). Lake types are categorized as lakes with landlocked alewife (LA), anadromous alewife (AA) and without alewife (WA), respectively plot A, B and C. Standard length (mm) as a function of day of year is presented for each lake type. Raw data are given as points and model posterior mean and 95 % credible intervals as solid and broken lines. Horizontal lines indicate the posterior means and 95 % credible intervals of estimated asymptotic length limits. Pair-wise contrasts of the three lake types, plots D, E and F; periods when the distribution of standard lengths were different between lake types are signified by the horizontal zero-lines not being contained within the credible intervals of the lake type contrasts.

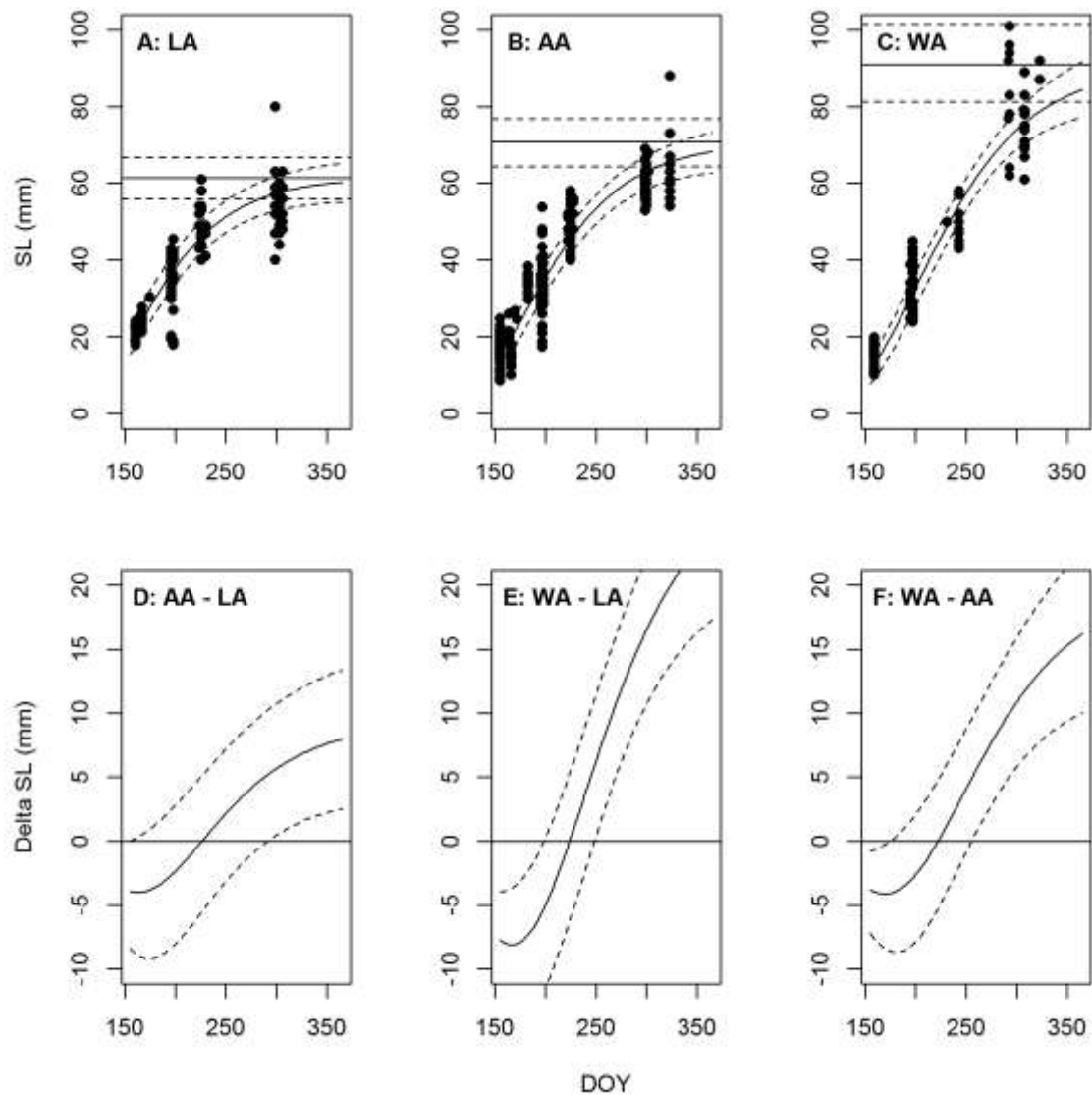


Figure 2: The development in trophic position (TP) over time for young-of-the-year largemouth bass, covering the study period from June 4th to November 19th (2009). Lake types are categorized as lakes with landlocked alewife (LA), anadromous alewife (AA) and without alewife (WA), respectively plot A, B and C. Trophic position as a function of day of year is presented for each lake type. Raw data are given as points and model posterior mean and 95 % credible intervals as solid and broken lines. Pair-wise contrasts of the three lake types, plots D, E and F; periods when the distribution of the trophic positions were different between lake types are signified by the horizontal zero-lines not being contained within the credible intervals of the lake type contrasts.

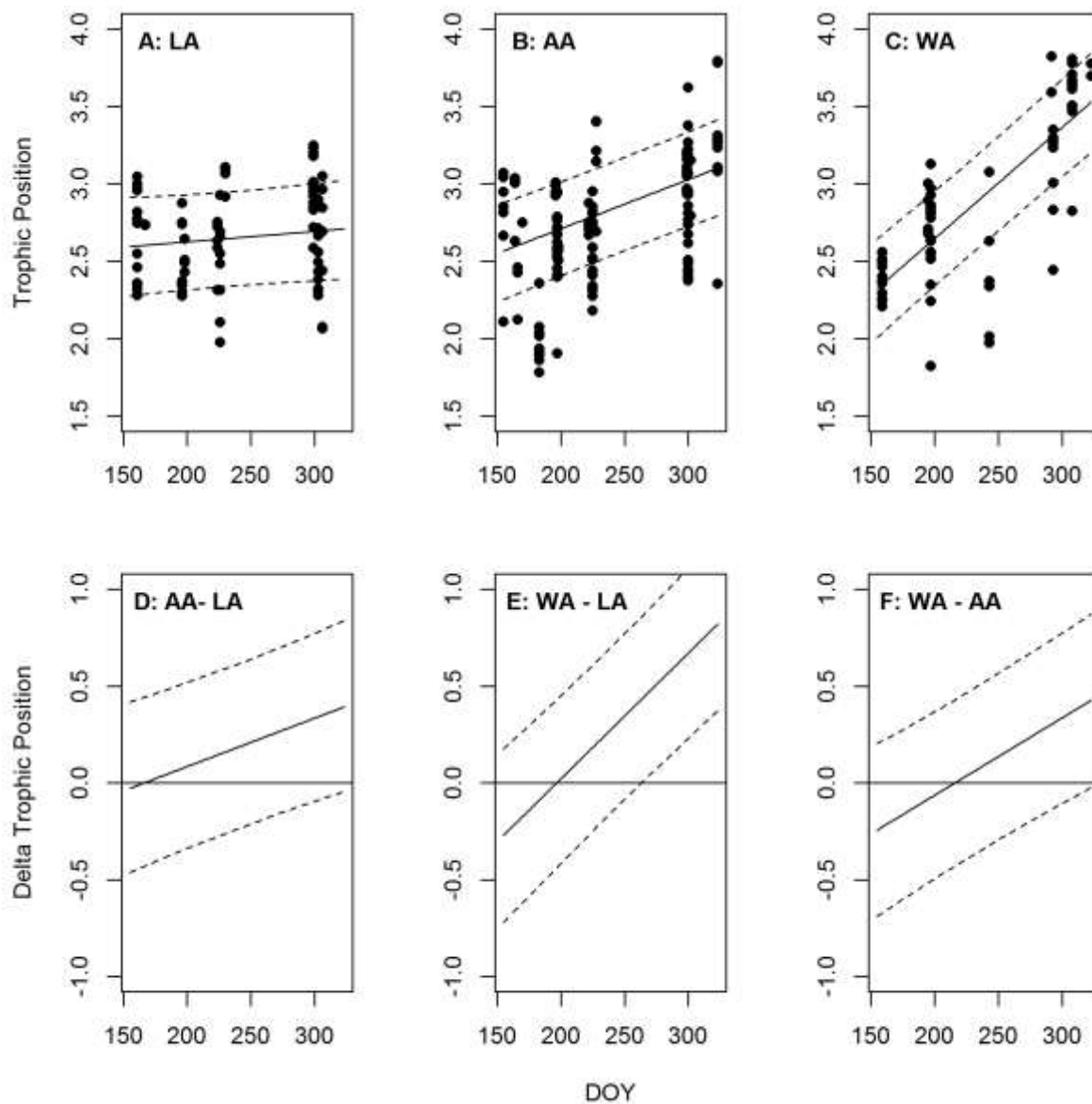


Figure 3: The linear rate of change in trophic position (TP) over time for young-of-the-year largemouth bass, illustrated by the posterior distributions of lake type specific effect of day of year (DOY), the slope parameter that illustrates the interaction between lake type and time; the estimated slope parameter for each lake type are presented as mean and 95 % credible intervals. Lake types are categorized as lakes with landlocked alewife (LA), anadromous alewife (AA) and without alewife (WA).

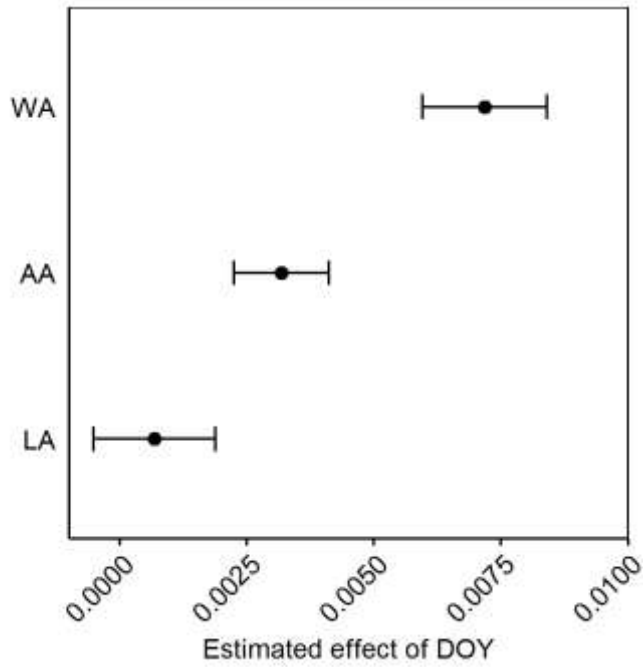


Figure 4: Temporal trends in proportional use of pelagic resources from stable isotope analysis, also referred to as δ , by young-of-the-year largemouth bass, covering the study period from June 4th to November 19th (2009). Lake types are categorized as lakes with landlocked alewife (LA), anadromous alewife (AA) and without alewife (WA), respectively plot A, B and C. Proportional use of pelagic food web as a function of day of year is presented for each lake type. Raw data are given as points and model posterior mean and 95 % credible intervals as solid and broken lines. Pair-wise contrasts of the three lake types, plots D, E and F; No lake type differences were observed in the distributions of the proportional use of pelagic food web, as indicated by there being no periods where the horizontal zero-lines were not contained within the credible intervals of the lake type contrasts.

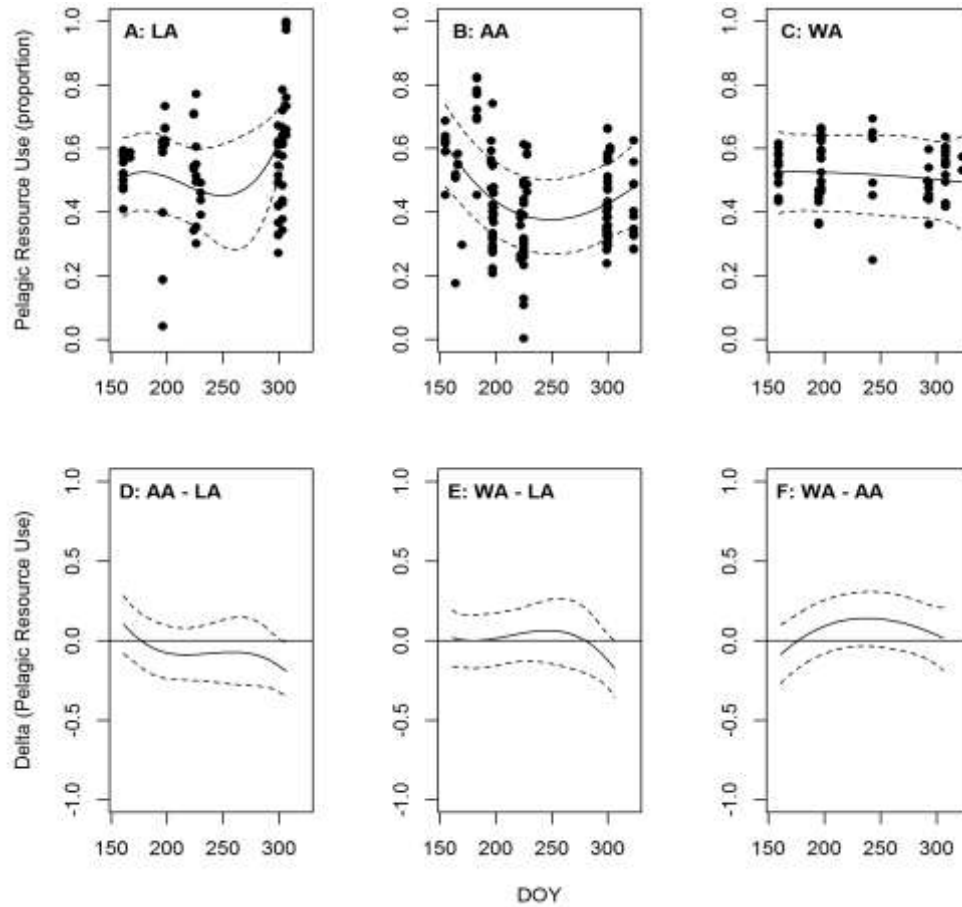


Figure 5: Generalized development of the relative proportions of the stomach contents from young-of-the-year largemouth bass; from A lakes with landlocked-, B lakes with anadromous-, and C lakes without alewife. The trends in diet (dry mass proportions) was smoothed by weighted-centered-moving-average for each lake type, and illustrated according to the food web association; pelagic prey littoral prey, and fish prey.

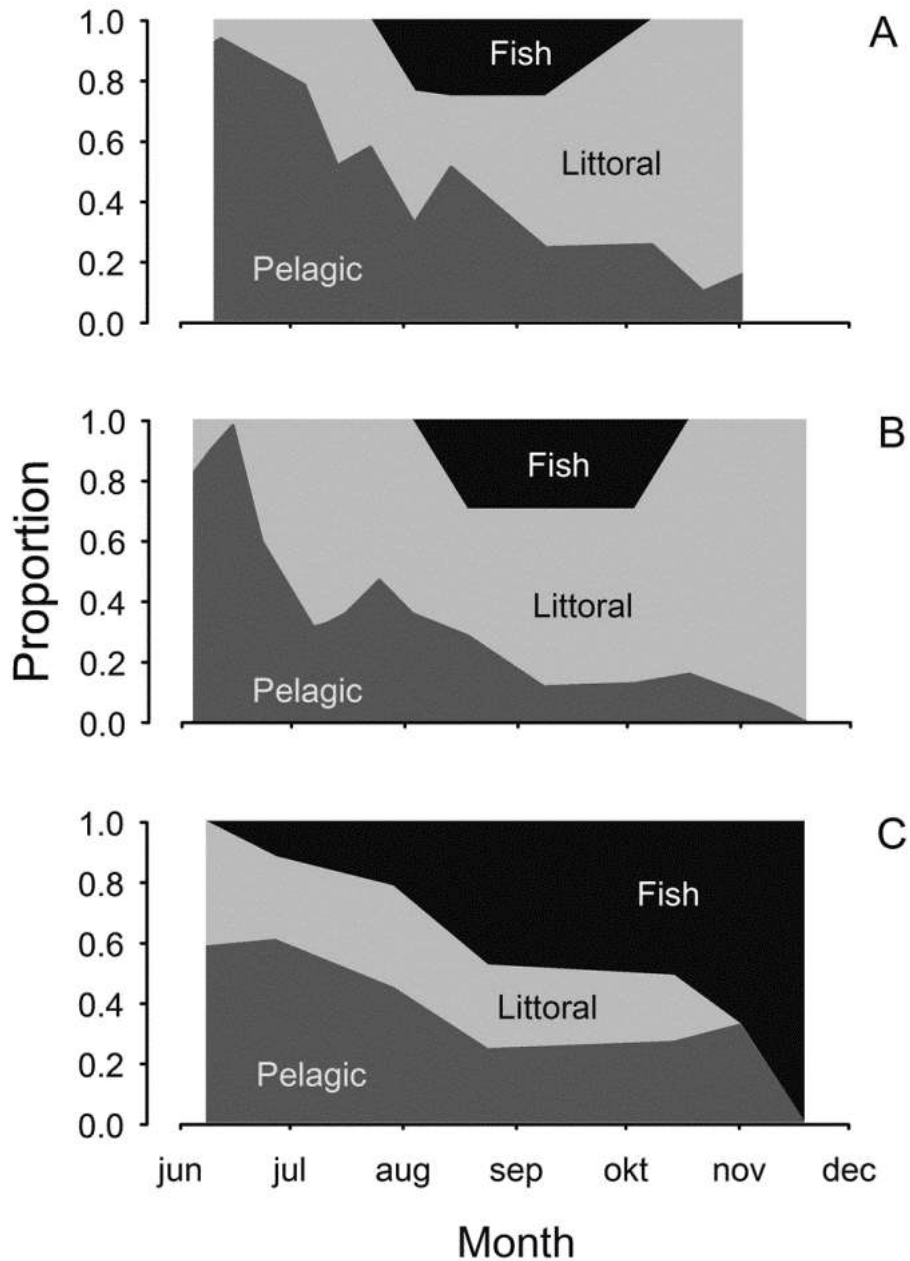


Figure 6: Temporal development in the stomach contents, represented as the proportion pelagic- relative to benthic food in diet, of young-of-the-year largemouth bass, covering the study period from June 4th to November 19th (2009). Lake types are categorized as lakes with landlocked alewife (LA) and anadromous alewife (AA), respectively plot A and B. Pelagic diet proportion as a function of day of year grouped is presented for each lake type. Raw data are given as points and model posterior mean and 95 % credible intervals as solid and broken lines. Contrast of the landlocked and anadromous lake types is presented in plot C; No lake type difference was observed in the distribution of the proportional use of pelagic food web, as indicated by there being no periods where the horizontal zero-line was not contained within the credible intervals of the lake type contrast.

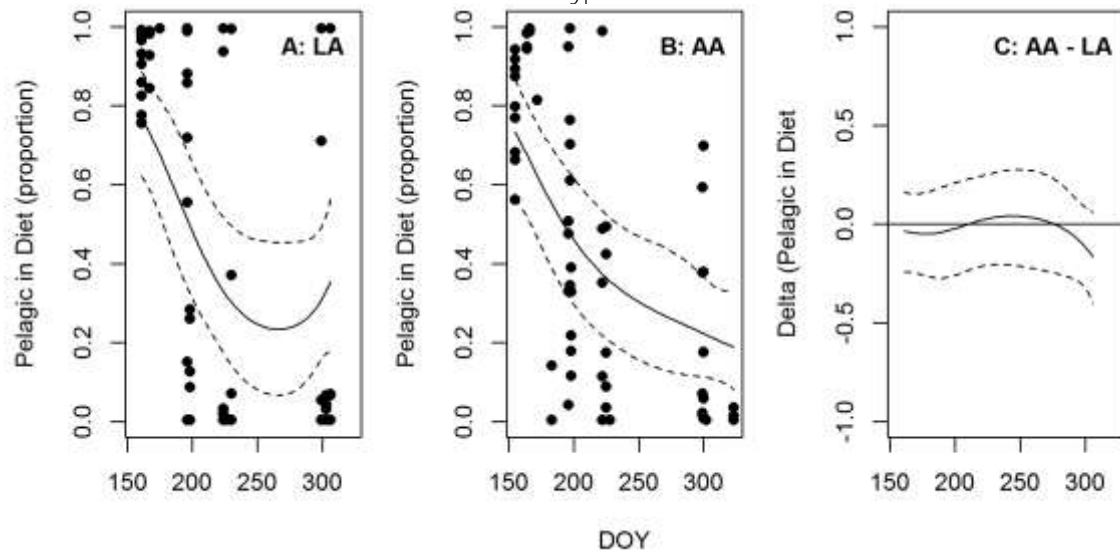


Table Legends

Table 1. Data are obtained from Post et al (2008). Lakes are categorised according to presence and life history of alewife; without alewife (WA), anadromous alewife (AA), and landlocked alewife (LA).

Name	Lake Type	Area (ha)	max depth (m)
Bride	AA	18.2	10.7
Dodge	AA	13.9	15.5
Gorton	AA	21.5	3.4
Amos	LA	42	13.7
Pattagansett	LA	49.2	10.1
Rogers	LA	106	20
Gardner	WA	194.7	13.4
Black pond	WA	30.2	7
Hayward	WA	79.6	10.7

Table 2. Parameter estimates with respect to lake types (mean and 95 % credible intervals CI) from the hierarchical Gompertz model of YOY largemouth bass standard lengths. The parameters of the growth model are presented by alewife presence and life history; without alewife (WA), anadromous alewife (AA), and landlocked alewife (LA).

Parameter description	Symbol	Lake Type	Mean	95 % CI	
Asymptotic lengths	L_{∞}	LA	61.5	56.0	66.8
	L_{∞}	AA	70.8	64.4	76.8
	L_{∞}	WA	90.9	81.3	101.4
Displacement coef	b		25.7	18.5	37.7
	c	LA	0.0198	0.0176	0.0225
Growth rates	c	AA	0.0180	0.0161	0.0203
	c	WA	0.0161	0.0142	0.0182
			0.0001		
Std. Dev.	σ		58	0.0000196	0.000579
Std.dev. Random effect	σ_{lake}		3.27	1.64	6.69
Exponent in varians structure	δ		2.03	1.71	2.35

Table 3. Parameter estimates (mean and 95 % credible intervals CI) from the linear mixed model of YOY largemouth bass trophic position (TP). The linear representations of trophic position over time are presented as intercepts and slopes by alewife presence and life history; without alewife (WA), anadromous alewife (AA), and landlocked alewife (LA) and their interaction of lake type and day-of-year (DOY).

Parameter description	Parameters	Mean	95 % CI	
Intercepts	LA	2.49	2.08	2.91
	AA	2.07	1.70	2.45
	WA	1.21	0.81	1.62
Slopes (TP*DOY)	DOY*LA	0.00068	-0.00052	0.00186
	DOY*AA	0.0032	0.0022	0.0041
	DOY*WA	0.0072	0.0060	0.0084
Std.Dev.	σ	0.30	0.28	0.33
Std.Dev. Random effect	σ_{lake}	0.24	0.11	0.50