Diets and Growth of Age-0 Walleye in a Recently Recovered Population

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Abstract

Most fishes undergo ontogenetic diet shifts, progressing from small to larger prey as they grow. The availability of suitable prey throughout early ontogeny can influence growth, survival and ultimately, year-class strength. Simultaneously, due to their numeric abundance and high mass-specific consumption rates, young fish can serve as influential consumers and thereby affect abundance of various prey. The walleye *Sander vitreus* population in Saginaw Bay, Lake Huron, recently recovered and is now entirely supported by natural reproduction. Recovery coincided with a dramatic decline of alewife *Alosa pseudoharengus*, a preferred prey of walleye. Thus, we are uncertain what primary prey now support production of young life stages of this recovered walleye population. To this end, we collected young (larval and later-stage young of year) walleye in Saginaw Bay and characterized their growth, diets and cumulative consumption using bioenergetics models. Young walleye progressed from feeding entirely on zooplankton as larvae in April to feeding almost entirely on fish by September. Based on bioenergetics analyses, fish were the most important prey for young walleye cohorts. Shiners *Notropis* spp., along with invasive rainbow smelt *Osmerus mordax* and round goby *Neogobius melanostomus*, were the primary fish prey. In contrast, yellow perch *Perca flavescens*, an important prey for adult walleye in Saginaw Bay, were largely absent in young walleye diets. Young walleye growth rates were similar to rates observed in other systems, but lower than growth rates previously observed in Saginaw Bay when alewife were abundant and the density of walleye was low.

Keywords: Saginaw Bay; larval fish; feeding ecology; ontogenetic shifts

Introduction

Marine and freshwater piscivorous fishes ontogenetically shift from consumption of zooplankton as larvae to reliance on large invertebrates and ultimately fish (Fuiman, 1994; Mittelbach and Persson, 1998). The shift to piscivory depends on both individual fish growth and prey availability (Wu and Culver, 1992). Young fish must not only forage successfully, but their desired prey also needs to be sufficiently abundant to sustain their continued morphological and physiological development (Mittelbach and Persson, 1998). The ability to capture prey is especially important for early-life growth and can enhance survival and promote recruitment success (e.g., Wu and Culver, 1992; Fullerton et al., 2000; Höök et al., 2007). However, diet ontogeny and age-0 growth tend to be highly variable across ecosystems and populations within certain fish species (Roseman et al., 2005; Hoxmeier et al., 2006).

Walleye, *Sander vitreus*, an ecologically and economically important piscivore indigenous to the Laurentian Great Lakes, shift to piscivory during the first year of life (Maloney and Johnson, 1957; Graeb et al., 2005; Galarowicz et al., 2006). As top piscivores, walleye exert top-down pressure on food webs with potential to influence forage fish populations and community structure (He et al., 2015). In recent decades, the Great Lakes have undergone considerable food web changes as reduced nutrient loading coupled with species introductions have led to spatio-temporal restructuring of food webs (Bunnell et al., 2014; Kao et al., 2014; Turschak et al. 2014; Ivan et al. 2014). These food web changes have contributed to altered diets for a number of piscivorous fish populations, including adult walleye (He et al., 2015; Pothoven et al., in press). In particular, Lake Huron has experienced dramatic changes in forage fish species composition and abundance with the collapse of the alewife *Alosa pseudoharengus* population (Riley et al., 2008), declining rainbow smelt *Osmerus mordax* and gizzard shad

Dorosoma cepedianum populations, and the invasion of round goby *Neogobius melanostomus* (Madenjian et al., 2013; He et al., 2015). Adult walleye in Lake Huron and Saginaw Bay (a shallow productive embayment of Lake Huron) previously relied on alewife as an important prey (Haas and Schaeffer, 1992; Fielder and Thomas, 2006), but have now shifted to other prey including round goby and young yellow perch *Perca flavescens* (Roseman et al., 2014; He et al., 2015; Pothoven et al., in press).

Coincident with these changes in prey resources, walleye populations in Lake Huron and Saginaw Bay have dramatically increased. The Saginaw Bay walleye population was previously supported via stocking, but is now entirely naturally reproducing and has been declared recovered by the Michigan Department of Natural Resources (Ivan et al., 2014; Johnson et al., 2015). The recovery of Saginaw Bay walleye appears to be strongly related to the crash of the Lake Huron alewife population (Fielder et al., 2007). Alewife was likely limiting walleye recruitment through competition and/or direct predation of young life stages (Fielder et al., 2007). However, a more abundant walleye population may now exert high predation pressure on other fishes. In particular, studies of adult walleye diets have raised concerns that walleye predation may now be reducing survival of young yellow perch and leading to a suppressed population of this recreationally and commercially targeted species (Fielder and Thomas, 2014; Pothoven et al., in press).

Most recent studies of walleye diets in Lake Huron have focused on adults (e.g., Roseman et al., 2014; He et al., 2015; Pothoven et al., in press). However, seasonal trophic interactions of age-0 walleye have received less attention, even though this is a critical period for understanding recruitment success of piscivores (Mittelbach and Persson, 1998), including walleye (Ivan et al., 2011). Walleye generally transition from zooplanktivory to benthivory to

piscivory during their first year of life (Matthias and Li, 1982; Graeb et al., 2005; Galarowicz et al., 2006). A temporally detailed analysis of walleye diet ontogeny may reveal mechanisms of early-life success leading to their population resurgence and help fisheries managers understand which food-web components are supporting walleye recruitment. Finally, due to their numerical abundance and high mass-specific metabolic and consumption rates, young fish may exert a disproportionally high predation pressure (e.g., Hewett and Stewart, 1989). While predation by adult walleye may contribute to the control of Saginaw Bay's yellow perch population, age-0 walleye may also be an important predator on yellow perch. Such an interaction is plausible as age-0 walleye consume yellow perch in other systems (Maloney and Johnson, 1957; Smith and Pycha, 1960; Priegel, 1970).

Bioenergetics modeling has been extensively used to evaluate linkages between piscivores and their prey (e.g. Schaeffer et al., 1999; Madenjian et al., 2011). We employed this approach, together with temporally detailed collections of young walleye cohorts, to integrate larval and juvenile (i.e., age-0) diets and growth rates to understand predation pressure by young walleye and mechanisms contributing to their early-life success. Our objectives were (1) to evaluate larval and age-0 temporal growth rates and (2) to quantify, through diets and bioenergetics modeling, which prey groups are supporting young walleye growth in Saginaw Bay.

Methods

Sampling design

During 2009 and 2010, we collected young walleye as one component of a comprehensive assessment of multiple environmental stressors on Saginaw Bay, a shallow, eutrophic

embayment of Lake Huron. We sampled larval fish at 9 sites approximately weekly from April through June, and we sampled juvenile fish at 5 sites approximately monthly from April through November (for more details on sampling design see Pothoven et al., 2014; Roswell et al., 2014; Sesterhenn et al., 2014; Fig. 1). Concurrent with larval and juvenile fish sampling, we measured surface water temperature (within 0.5 m of surface) with a handheld thermometer. Saginaw Bay is generally vertically well-mixed at most sites throughout the year.

Larval walleye

We collected larvae during daytime sampling using two types of ichthyoplankton nets; a bongo sampler and a neuston net. The bongo sampler consisted of two 0.5 m diameter, 1.5 m long nets (333-µm and 700-µm mesh), that were paired together on one frame. The neuston net consisted of 1000-µm mesh netting mounted on a 2 m x 1 m frame. We attached flow meters (General Oceanics) to the mouth of each net to estimate filtered water volume. We towed the nets behind the research vessel individually at approximately 4.6 km/h for 5 min. At each site, we conducted a surface (top of net ~ 0.5-1.0 m below surface) and an oblique bongo tow. For the oblique tow, we deployed the net at approximately 1 m above the bottom and gradually decreased the tow depth while towing to sample the entire water column. Samples were concentrated and placed in 95% ethanol upon collection.

In the laboratory, we sorted samples and used a dissecting microscope (Olympus SZ2-1 LST, 20X magnification) and attributes detailed in Auer (1982) to identify larval walleye. To measure the total length (to 0.1 mm) of each larvae, we used the dissecting microscope mounted with a Micrometrics camera and Image J open-source image analysis software. Lengths were initially not corrected for possible shrinkage (see below). To analyze diets of larvae, we

removed the digestive tract and extracted diet contents for examination under a compound microscope (Leica DM1000, 40X magnification). We counted diet items, identified prey to general taxonomic groups (*Bosmina*, *Daphnia* spp., Copepoda, naulii, veliger, other zooplankton). Due to low numbers of larval walleye, larvae were combined into three size-groups with similar sample sizes to examine diets, i.e., 9-10 mm, 11-12 mm, and 13+ mm. To estimate larval walleye age, we removed otoliths from larvae and adhered them to a slide. Using the compound microscope, we counted daily incremental growth rings and estimated ages (in days) as described in Sesterhenn et al. (2014).

Age-0 walleye

To collect juvenile walleye, we towed a 7.6 m semi-balloon bottom trawl with a 13 mm mesh cod liner at approximately 4.6 km/h for 10 min. During each month of sampling, we conducted 1 – 5 trawls per site. Upon collection, fish were sorted to species, placed in bags with water, and put on ice in coolers. When we returned to shore, we froze fish samples in -20 $^{\circ}$C freezers. Subsequently, we measured total length (to 1 mm) and wet weight (to 0.01g) of all young walleye. Age-0 and age-1 walleye were separated, using total length, based on divisions in distributions of length-frequency data (Pothoven et al., 2014).

To evaluate diets of age-0 walleyes, we removed contents from the fish stomachs, identified, and counted all diet items under a dissecting microscope (whole invertebrates and partial invertebrates with heads attached were counted). Stomach contents were dried at 70°C for 3 days and total dry weight of food was recorded for each walleye. Fish prey were identified to species where possible using bony structures to aid in identification (Traynor et al., 2010). We measured lengths of all measureable fish prey in walleye stomachs, and we used Image Pro

imaging software to measure lengths of up to 20 prey per invertebrate taxon per fish. We estimated dry biomass of each prey type using measured lengths and published length-mass regressions (see Roswell, 2011; Electronic Supplementary Material (ESM) Table S1). We then used these biomass estimates to estimate the proportion of each prey type in the diet of each fish and multiplied these proportions by measured total diet dry mass to determine total mass of each prey type in the diet of each fish.

Data Analysis and Bioenergetics Analysis

We compared monthly growth rates of age-0 walleye by calculating instantaneous growth in mass (G) between sampling occasions. We estimated the slope between two consecutive months by calculating the difference in natural log of mean total mass over the number of days between sampling.

Based on dry biomass, we summarized diets of age-0 walleye into seven categories, zooplankton (cyclopoid and calanoid copepods, *Daphnia* spp., and *Diaphanosoma* spp.), predatory cladocerans (*Bythotrephes longimanus* and *Leptodora kindtii*), benthic invertebrates (primarily Chironomidae or Amphipoda), round goby, rainbow smelt, shiners (primarily emerald shiners *Notropis hudsonius*), yellow perch, unidentified fish, and other fish (primarily gizzard shad). We fit linear regressions between walleye length and individual fish prey lengths to examine length relationships between age-0 walleye and the three main fish prey they consumed, i.e., round goby, rainbow smelt and shiners. We used an ANCOVA (after testing for homogeneity of slopes; covariate, walleye total length; factor, species of prey) to compare the size of prey consumed across species.

We used a bioenergetics approach to model total annual prey consumption by young walleye during 2009 and 2010 at a daily time-step using published walleye metabolic parameters (Madon and Culver, 1993; Johnston, 1999). Input parameters included monthly field-derived values for temperature, energy densities of walleye (Pothoven et al., 2014; Sesterhenn et al., 2014) and their prey (ESM Table S2), monthly walleye mass (this study), and monthly proportional diet biomass (this study). We linearly interpolated daily temperature, proportional diet composition, walleye energy density, and mean walleye mass between dates.

We started to track walleye growth on day of year 124 and 123 in 2009 and 2010, respectively, and assumed they would start exogenous feeding at this time (initial length, 9 mm; initial wet mass 0.0034 g calculated from equation in Sesterhenn et al., 2014). For each time stanza, we adjusted the p-value (proportion of maximum daily consumption) to match observed change in mass and energy content using an automated iterative process. We lack information on larval walleye energy density and instead assumed that larval walleye have the lowest energy density observed for juvenile walleye, 2762 J g^{-1}. Larval walleye growth rate was set as 0.3 mm/d based on average observed growth rates and would thus transition from larvae to juveniles at a length of 20 mm (or 0.0948 g) (Auer, 1982) after 38 days of growth.

During the larval period, walleye consumed exclusively zooplankton prey and we used parameters from Johnston (1999) to model their consumption. After the transition to juvenile stage, we used parameters from Madon and Culver (1993) to model walleye bioenergetics. We used measures from Pothoven et al. (2014) and allowed walleye energy densities to vary seasonally, while prey energy densities were assumed to be fixed (see ESM S2).

Prey consumption supporting growth and production of young fish can be expressed in terms of mass or energy supporting growth of an individual that survives from hatch to the end

of the first growing-season. Alternatively, prey consumption can be expressed in terms of mass or energy supporting production of an entire cohort, accounting for loss of individuals over time through mortality. We calculated proportional contribution of prey categories using four approaches (i.e., contribution to individual and cohort growth based upon mass and energy). We lacked estimates of larval and juvenile walleye mortality rates specific to Saginaw Bay for the cohort analysis. Moreover, model- and field-derived estimates of mortality rates are highly variable. Initially, for simplicity we assumed a larval and juvenile instantaneous mortality rate (Z) of 0.01 d^{-1}. Mortality rates of young fish likely decrease as individual size increases (McGurk 1986). Thus, we also calculated cohort consumption assuming size-dependent mortality. Specifically, we used the individual-mass relationship presented in McGurk (1986) and assuming that dry mass is 20% of wet mass (W; g), $Z=8.64\times10^{-4} W^{-0.85}$. We applied this relationship for individuals with a wet mass less than 0.125 g (Z>0.005 d^{-1}), as we did not want to extrapolate too far beyond the size data McGurk (1986) used to build the relationships. Once young walleye exceeded this size threshold, we set Z=0.005 d^{-1}.

Results

Despite a high level of sampling effort (514 total net tows during April-June) and success collecting a large number of larvae of other species (e.g., yellow perch, lake whitefish *Coregonus clupeaformis*), we only collected 73 larval walleyes in both years combined. The first walleye larvae of the season were captured on May 6, 2009 and on April 20, 2010. During both years, larval walleye were present in ichthyoplankton tows until early June. Mean larval lengths were 10.7 mm and 9.7 mm during 2009 and 2010 respectively. Based on otolith incremental age estimation, across both years the mean ± SE larval growth was 0.29 ± 0.03 mm d^{-1} (n=64), which

corresponds to 0.32 mm d^{-1} when accounting for 10% shrinkage in ethanol (Foley et al. 2010). Due to low catches of larval walleye, we did not estimate separate larval walleye growth rates by annual, weekly or daily cohorts.

During 2009 and 2010, we collected 1,496 age-0 walleyes in bottom trawls. Mean total lengths of age-0 walleyes increased throughout the summer in both years (Fig. 2). During 2009, age-0 walleyes grew through November, but during 2010, growth halted between September and November (Fig. 2). Monthly mean lengths were greater for each month during 2010 than 2009; however, daily instantaneous growth in mass (G) was greater for all months during 2009 than 2010 (Table 1). G decreased from July through November in both years as temperatures cooled (Table 1, Fig. 2).

Larval walleyes exclusively consumed zooplankton, and juvenile walleyes transitioned ontogenetically from zooplanktivory to piscivory throughout their first year of life. The proportion of larvae with stomach contents was 0.61 and 0.31 during 2009 and 2010, respectively. Larvae began exogenously feeding at approximately 9 mm total length (TL), and larger larvae (>11 mm TL) consumed a greater number of diet items. Larval walleye consumed a variety of taxa including cladocerans, copepods and dreissenid veligers. They consumed more dreissenid veligers in 2009 while copepod nauplii were more dominant in 2010. However, given low samples of exogenously feeding larval walleye we present diet summaries combined across the two years for April-June (Fig. 3).

Age-0 walleye were piscivorous during all months when they were collected. However, zooplankton (mostly calanoid copepods, *Daphnia* spp. and *Diaphanosoma* spp.) and predatory cladocerans (mostly *Bythotrephes*) made up a larger proportion of diets during July and August than later in the season; whereas by September age-0 walleye were almost exclusively

piscivorous (Fig. 4). Benthic macroinvertebrates, primarily chironomids, were mainly eaten in July and August, and never accounted for more than 20% of the diet biomass. Piscivorous walleye primarily consumed shiners, rainbow smelt and round goby. Contrary to expectations, yellow perch were not an important prey for age-0 walleye (in total two yellow perch were identified in 1,187 walleye stomachs that contained food). Diets were similar between the two years, but benthic invertebrates and rainbow smelt were more abundant in age-0 walleye diets during 2009 and round goby and shiners were more important during 2010.

Age-0 walleye displayed strong size-based consumption of the three dominant fish prey with larger walleye consuming larger fish prey (Fig. 5). However, at a given length, walleye tended to consume smaller round goby than shiners or rainbow smelt (ANCOVA, $F_{1, 90}=42$; $p<0.001$). On average, total lengths of round goby in juvenile walleye stomachs were 33% of the total length of the walleye that consumed them, while lengths of shiners and rainbow smelt were 46% and 49% of walleye, respectively. However, if mean prey length (adjusted for walleye length) of each of these species in the diet was converted to a corresponding dry weight, the average sized (by weight) shiner in the diet was twice (51 mm, 0.18 g) that of round goby (35 mm, 0.09 g) and rainbow smelt (49 mm, 0.08 g).

Bioenergetics estimates suggest that consumption of fish prey primarily supported growth and production of young walleye in Saginaw Bay (Table 2). The importance of fish prey was evident regardless of whether consumption was calculated in terms of mass or energy and regardless of whether calculated for an individual or entire cohort of young walleye. In particular, shiners were an important prey during both years, while rainbow smelt was also important during 2009 and round goby was important during 2010. Yellow perch was not an important prey source for walleye during either year.

Discussion

We quantified growth and diets of walleye through their first growing season in Saginaw Bay, Lake Huron during 2009 and 2010 and determined that multiple prey resources supported early-life success of this population. During both years, walleye grew continuously through the summer, and in 2009 they grew through November. Growth rates likely slowed in the fall due to decreased temperatures; however, age-0 walleye in Saginaw Bay do not seem to be particularly vulnerable to overwinter mortality (e.g., Madon and Culver, 1993; Pothoven et al., 2014). Warmer temperatures during 2010 may have caused earlier larval emergence and faster growth during the summer. In total, young walleye growth rates during 2009 and 2010 were much lower than growth rates during earlier time periods. For instance, during the 1980s and 1990s when age-0 walleye routinely reached a minimum mean length in excess of 200 mm by October, compensatory density-dependent reductions in walleye growth were less likely because energy-rich alewife were still abundant in Saginaw Bay and young walleye densities were much lower than today (Ivan et al., 2011). Growth rates of young walleye during 2009 and 2010 appeared to be similar, or slightly below average statewide growth rates in Michigan lakes (180 mm by the end of age 0; Fielder and Thomas, 2006). This reduced growth rate might be expected given that reduction in growth is consistent with previously stated goals for walleye recovery in Saginaw Bay (Fielder and Thomas, 2014). Historic (1912-1940) growth rates in Saginaw Bay were also likely below the average growth rate for lakes in the State of Michigan (Fielder and Baker, 2004).

Feeding success during the larval period is critical for survival and year-class formation (Devries et al., 1998; Hoxmeier et al., 2004). The larval walleye transition to feeding at approximately 9 mm was consistent with previous studies (e.g., Mathias and Li, 1982). Larval

walleye consumed zooplankton from a range of different sizes and taxonomic groups, which is also consistent with previous studies (Hokanson and Lien, 1986; Mayer and Wahl, 1997). Cladocerans were a relatively important part of the diet for larvae 9-13 mm long, but only accounted for about 4% of the prey eaten by larvae 13-19 mm. The shift away from cladocerans is somewhat surprising, considering that cladocerans are generally considered a preferred prey that enhances growth and survival for walleye larvae (Mayer and Wahl, 1997; Hoxmeier et al., 2004; McDonnell and Roth, 2014). By contrast, the very small prey nauplii and dreissenid veligers accounted for a large fraction of walleye larvae diets, especially for fish 11-19 mm. In general, such small prey are thought to be unprofitable and are avoided by walleye larvae (Mathias and Li, 1982; Mayer and Wahl, 1997; Hoxmeier et al., 2004). The numeric importance of veligers and nauplii in diets could indicate a bottleneck of larger zooplankton prey available for walleye and other fish in the early spring in Saginaw Bay. The relatively high incidence of empty walleye larvae stomachs (56%) suggests that food resources might have been limited during this period as well. Interestingly, veligers were also an important food source for larval yellow perch in Saginaw Bay (Roswell et al., 2014); and consumption of veligers may simply reflect use of an easily accessible food resource (e.g., Withers et al., 2015).

Age-0 piscivores, including walleye, are generally expected to undergo an ontogenetic progression from eating zooplankton to eating macroinvertebrates and then fish (Mittelbach and Persson, 1998; Galarowicz et al., 2006). In Saginaw Bay, zooplankton decreased in the diets of age-0 walleye as they grew and were largely replaced by fish rather than macroinvertebrates. In fact, macroinvertebrates never accounted for more than 20% of the diet in any given month. Other studies suggest that benthic macroinvertebrates are most important in age-0 walleye diets when there are inadequate numbers and sizes of prey fish (Priegel, 1970; Graeb et al., 2005;

Galarowicz et al., 2006). Age-0 walleye might also delay the shift to benthivory if zooplankton are abundant (Hoxmeier et al., 2004) or if benthic macroinvertbrates are not abundant (Jackson et al., 1992). Competition for benthic invertebrates in Saginaw Bay could be intense in the summer, and age-0 yellow perch largely did not undergo an expected shift from zooplanktivory to benthivory in Saginaw Bay (Roswell et al., 2014). Formerly, the mayfly *Hexagenia* spp. would have served as an additional large macroinvertebrate prey, but their abundances in Saginaw Bay remain severely reduced relative to historical levels (Siersma et al., 2014).

The energetically favorable switch to piscivory (Galarowicz and Wahl, 2005; Galarowicz et al., 2006) was expected for age-0 walleye (e.g., Knight et al., 1984; Hartman and Margraf, 1992) and overall, first year growth was mainly supported by consumption of fish. Age-0 walleye had incorporated fish into their diets by July when fish accounted for 39% and 58% of the diet biomass in 2009 and 2010 respectively. By September each year, fish accounted for at least 94% of the diet. The shift to piscivory requires the availability of appropriately sized prey (Mathias and Li, 1982; Mittelbach and Persson,1998; Persson and Brönmark, 2002). The primary fish eaten were soft-rayed fish, including shiners, rainbow smelt, and round goby. Age-0 walleye, especially those greater than 100 mm TL, prefer to consume soft-rayed fishes if they are available (Wagner, 1972; Schneeberger, 2000; Galarowicz et al., 2006). Shiners and rainbow smelt compose a considerable proportion of age-0 walleye diets in Lakes Erie and Michigan (Knight et al., 1989; Hartman and Margraf, 1992), consistent with our observations in Saginaw Bay. Availability of these preferred prey likely contributed to low observed consumption of spiny-rayed yellow perch by age-0 walleye.

Our bioenergetics analysis could have overestimated the overall importance of fish to young walleye production because the juvenile walleye were larger than those used to develop

the bioenergetics parameters (Madon and Culver, 1993). Specifically, applying the Madon and Culver (1993) model to larger juveniles likely overestimated their consumption because as walleye grow, the ACT activity multiplier should decrease. This in turn, would inflate the importance of fish prey supporting walleye production, and underestimate the importance of zooplankton. However, to our knowledge, no other bioenergetics model is available for use with late stage juvenile walleye. Furthermore, based on re-analysis of model runs using lower ACT multipliers, we do not believe this discrepancy would change the conclusion, that overall, growth of young walleye cohorts is supported mainly by consumption of fish.

Walleye as small as 37 mm were found with fish in their stomachs and the size of fish eaten increased linearly with walleye length. Jackson et al. (1992) suggested that this linear relationship between walleye length and prey fish length indicated that the onset of piscivory depended more on the availability of suitable-sized fish prey than on walleye size. Mittelbach and Persson (1998) found that the size of fish eaten by different piscivore species varied little when standardized for piscivore length, indicating that prey size variation was due to piscivore length. However, we found that an age-0 walleye of a given length ate smaller round goby than rainbow smelt or shiners, indicating that the suitable lengths of prey for a given sized walleye can also differ by prey species. This relationship could have energetic implications if a particular prey was not readily available for some reason, especially if shiners were not available, given that the mass of a shiner eaten by a walleye of a given length is twice that of a rainbow smelt or round goby.

Even though production of age-0 yellow perch is high in Saginaw Bay (Fielder and Thomas, 2014), we found almost no age-0 yellow perch in age-0 walleye stomachs. Based on studies in other systems, age-0 yellow perch can be the dominant prey for age-0 walleye, and

walleye growth and recruitment success is linked to their availability (Maloney and Johnson, 1957; Forney, 1966; Carlander and Payne, 1977). However, age-0 yellow perch are not necessarily eaten by age-0 walleye (Priegel, 1970; Pelham et al., 2001; this study). One reason yellow perch might not be eaten by age-0 walleye is if suitable sizes of other prey are more available (Pelham et al., 2001). The main fish prey eaten by age-0 walleye was 33%-49% of walleye length, whereas the mean length of age-0 yellow perch was always >61% of the mean age-0 walleye length during July-November in both years (Pothoven et al., 2014). Yellow perch and walleye larvae appeared in the bay at roughly the same time and initially grew at roughly the same rate (Roswell et al., 2014), so walleye might not have been able to achieve a large enough size advantage over yellow perch to prey on them during their first year in the lake. Moreover, as suggested above, soft-rayed fishes are often preferred prey for young walleye (Wagner, 1972; Schneeberger, 2000; Galarowicz et al., 2006) and may have served as a buffer for predation pressure directed at young yellow perch.

Overall, age-0 walleye growth in Saginaw Bay was supported largely by fish, mainly native shiners as well as invasive rainbow smelt and round goby. Interestingly, the nearly complete disappearance of the invasive alewife appears to have led to increased recruitment for age-0 walleye (Fielder et al., 2007), but the resurgent walleye population appears to be highly dependent on two other invasive species for their success during their first year in the lake. Walleye dependence on invasive fish prey might reduce predation demands on other valuable fish such as yellow perch, but at the same time, complicates management strategies to lessen the harmful impacts of invasive species within the ecosystem.

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Table 1. Monthly mean mass and instantaneous growth in mass (G) of age-0 walleye. Note that G values were calculated based on change in mean mass from age-0 walleye collected the previous month.

Year	Month	n	Mean mass (g)	G (d^{-1})
2009	July	464	1.255	
	August	164	3.199	0.043
	September	359	7.477	0.030
	October	184	13.419	0.017
	November	70	15.173	0.004
2010	July	70	2.432	
	August	107	6.052	0.027
	September	85	17.957	0.025
	November	43	16.859	-0.001

Table 2. Bioenergetics-based estimates of consumption (% biomass and % energy) of prey supporting growth of an individual age-0 walleye and cohort of walleye from hatch through November in 2009 and 2010 in Saginaw Bay. "Other fish" category includes both rare identified fish species and unidentified fish. Cohort consumption was determine using two methods, one using a constant mortality rate ($Z=0.01$ d^{-1}) and one using an individual mass based mortality rate (see methods for further details).

		Individual		Cohort $Z=0.01d^{-1}$		Cohort $Z=f(mass)$	
		%Mass	%Energy	%Mass	%Energy	%Mass	%Energy
2009	Zooplankton	8	5	15	9	11	7
	Predatory zooplankton	3	1	4	2	4	2
	Benthic invertebrates	5	4	7	6	6	5
	Round goby	9	8	7	7	8	7
	Shiners	21	27	17	23	19	25
	Rainbow smelt	22	20	21	20	21	20
	Yellow perch	2	2	1	1	1	2
	Other fish	31	32	29	32	30	32
2010	Zooplankton	8	5	15	9	11	7
	Predatory zooplankton	3	1	4	2	4	1
	Benthic invertebrates	1	1	2	1	1	1
	Round goby	25	22	21	19	23	20
	Shiners	43	53	39	49	41	51
	Rainbow smelt	3	2	3	3	3	3
	Yellow perch	1	1	1	1	1	1
	Other fish	16	16	16	17	16	16

Figure captions

Fig. 1. Map of larval and juvenile walleye sampling locations in inner Saginaw Bay, Lake Huron in 2009-2010. Open squares represent sites for larval sampling only, whereas closed circles represent sites where both trawling and larval sampling took place.

Fig. 2. Mean surface temperatures (solid lines) and total lengths (TL) of individual larval (circles) and age-0 (✘'s) walleye collected in Saginaw Bay, Lake Huron during (a) 2009 and (b) 2010. Dashed lines connect mean monthly TL.

Fig. 3. Percentage of prey by count in stomachs of larval walleye from Saginaw Bay, Lake Huron in 2009-2010. All larvae < 9mm TL had empty stomachs. The "other" category consisted of Diptera, *Leptodora*, Ostracoda, and larval fish. Sample size above each bar is the number of walleye stomachs examined that contained food.

Fig. 4. Diet composition of age-0 walleye based on dry mass in stomachs in Saginaw Bay, Lake Huron during (A) 2009 and (B) 2010. Sample size above each bar is the number of walleye stomachs examined that contained food.

Fig. 5. Relationships between the total lengths of age-0 walleye and the total lengths of three species of prey fishes found in their stomachs in Saginaw Bay, Lake Huron in 2009-2010.

Total length (mm)

Mean temperature (°C)

Day of Year

a) 2009

b) 2010