The Importance of Early Life Processes to Future Growth and Recruitment in Lake Erie Walleye

DISSERTATION

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By

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ABSTRACT

For over a century, marine scientists have sought to understand how processes operating during early life (i.e., egg and larval stages) can affect future recruitment success. These investigations have revealed that the recruitment process is complex, owing to multiple controlling mechanisms operating during different life stages. Because Lake Erie walleye, *Sander vitreus*, have life-history characteristics similar to many pelagic marine fishes (e.g., iteroparity, zooplanktivorous pelagic larvae, high recruitment variability) and recruitment of Lake Erie’s walleye population has been consistently low since 2003 for reasons that remain enigmatic, I explored the relevance of several marine recruitment paradigms to this system. Specifically, I conducted a multi-year field study (i.e., 2011-2014) and analyzed long-term data (i.e., 1994-2013) from western Lake Erie to explore if and how egg production and larval habitat quality and subsequent growth could carry over to influence future growth and recruitment to the age-0 juvenile stage, which is a good predictor of future recruitment to the fishery.

Because the quantity and quality of eggs produced has been linked to interannual variability in larval abundance, examination of egg-stage dynamics, including maternal influences and environmental conditions, provides a first look at early limitations in the recruitment process. This investigation (Chapter 2) showed that
annual egg production on open-water reefs in Ohio waters of western Lake Erie were strongly correlated with age-0 recruitment, suggesting that population regulation occurs very early in walleye. Other results from this investigation pointed to the possibility that inter-annual variation in egg production is due to density-dependent responses operating in the adult life stage.

Other evidence pointed to processes operating during the larval stage as being important to understanding inter-annual variation in recruitment. For example, I found evidence that better habitat for growth during the larval stage can translate into better recruitment to the juvenile (age-0) life stage, although a trade-off in juvenile growth appears to exist (the mean individual size of these recruits was inversely related to the density of juveniles; Chapter 3). Additionally, a lack of available high-quality zooplankton prey to larvae appeared to result in reduced individual prey consumption, larval growth rate, and subsequent recruitment to the juvenile stage (Chapter 4). I also found evidence for growth-selective mortality operating during the larval stage (Chapter 5). While it is difficult to isolate whether predation or starvation drives selective mortality, current trends in zooplankton quantity and quality and their effect on age-0 recruitment (Chapter 4) suggests that bottom-up processes play an important role in regulating walleye recruitment dynamics.

My results highlight the importance of processes operating during the early life and their implications for juvenile success. In particular, my research revealed strong linkages between egg production and age-0 recruitment as well as zooplankton quantity
and quality to larval walleye growth and subsequent age-0 recruitment. Since age-0 recruitment is an excellent indicator of the adult population two years later, mortality processes occurring during the egg and larval stage are critically important to the overall success of the population. Finally, continued investigation into how early life processes influence the recruitment dynamics of fish populations living in large lakes is likely to benefit their management as it has in marine systems for the past century.
In memory of Aubrey Wayne Noble
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CHAPTER 1
INTRODUCTION

Since the time of Hjort (1914), fisheries scientists have sought to understand how processes operating during early life stages (i.e., egg and larval) affect future recruitment success. As the risk of mortality declines exponentially with age, numerous studies on fish populations have pointed to the need to research early life stages (i.e., eggs, larvae, and in some cases juveniles), when survival rates are the lowest and most variable, in order to understand fluctuations in the abundance of adult fish stocks (see Sissenwine 1984, Anderson 1988, Houde 2008, Hare 2014 for reviews). However, understanding early life processes has proven to be difficult because multiple controlling mechanisms exist, many of which operate during different life stages (Houde 2008; Hare 2014).

Given that multiple processes operating during early life can influence recruitment, multi-scale mechanistic investigations offer the best approach for assessing drivers of recruitment (Ludsin et al. 2014). The goal of my dissertation research is to better understand how processes operating during the egg and larval stage can influence growth and eventual survival to the juvenile stage in an economically and ecologically important freshwater fish, walleye *Sander vitreus*. Limitations to recruitment during early life, including physical processes, starvation, and predation,
have previously been identified (e.g., Roseman et al. 2001; Blaxter and Hunter 1982; Cushing 1990; Ferron and Leggett 1994; Letcher et al. 1996); however, a knowledge gap exists with respect to how early life experiences and performance can carry over to affect later growth, survival and recruitment. This lack of knowledge is an important problem, because it limits our ability to understand early life population dynamics and their impacts on future growth and recruitment.

Because the quantity and quality of eggs produced has been linked to inter-annual variability in larval abundance (i.e., Houde 1987; Moodie et al. 1989), examination of egg-stage dynamics, including maternal characteristics and environmental conditions, provides a first look at early limitations in the recruitment process. Maternal characteristics of age and size affect egg quality, as older, larger females generally produce higher quality eggs that survive better (e.g., Moodie et al. 1989; Johnston 1997). Initial egg quantity also can be affected by female size (i.e., larger females produce more eggs; Bagenal 1978), but once deposited, mortality emanating from environmental conditions such as wind and wave action (e.g., Moyer 1975; Serns 1982), water temperature (e.g., Busch et al. 1975; Koonce et al. 1977), and predation (e.g., Horns and Magnuson 1981; Frank and Leggett 1984) can reduce viable egg abundances.

Several hypotheses, originating in the marine literature, seek to explain how events during the larval stage can regulate future cohort success. The growth-mortality hypothesis (GMH; Ware 1975; Shepard and Cushing 1980) predicts that as larvae
increase in size, mortality rate decreases. Large larvae are less susceptible to gape-limited predators (i.e., ‘bigger-is-better’ mechanism, Miller et al. 1988) and have greater locomotive capabilities for predator evasion (‘growth-selective predation’ mechanism, Takasuka et al. 2003, 2004) when compared to small individuals. Larvae that exhibit fast growth spend fewer days in the larval stage (i.e., ‘stage-duration’ mechanism, Chambers and Leggett 1987), essentially lowering their cumulative mortality due to predation (Leggett and Deblois 1994). Implicit to the GMH is the assumption that enhanced foraging success during the larval stage will lead to increased growth and body size (Anderson 1988). Factors that influence the overlap of larval fish and their zooplankton prey have been shown to play an important role in governing survival (e.g., Cushing 1990; Runge et al. 1999; Beaugrand et al. 2003; Castonguay et al. 2008). Cushing’s Match-Mismatch Hypothesis (MMH; Cushing 1975), which states that larval fish recruitment is driven by their degree of temporal overlap with their planktonic prey, has been the basis for a great deal of recruitment research in marine systems.

Few studies have explored the relevance of marine recruitment hypotheses in freshwater ecosystems (Miller et al. 1988; Ludsin et al. 2014; Pritt et al. 2014). This research gap is most conspicuous in the largest lakes of the world (e.g., “inland seas” such as the Laurentian Great Lakes). Many ecologically and economically important large-lake fishes have life-history characteristics (e.g., high fecundity, no parental care, lengthy planktivorous pelagic larval period, high early-life mortality) quite similar to
those of well-studied ecologically and economically important pelagic marine species (Ludsin et al. 2014; Pritt et al. 2014).

Herein, I investigate if early life habitat, prey availability, and growth carry-over to influence future growth and recruitment to the juvenile stage, testing the relevance of several marine recruitment hypotheses in the process. The central thesis of my research is that events occurring during early life stages (i.e., egg and larval) set the stage for recruitment success (or failure) in Lake Erie walleye (\textit{sensu} Ludsin and DeVries 1997). The life-history characteristics of walleye are typical of many pelagic marine fishes, suggesting similar mechanisms are likely to affect their recruitment (Ludsin et al. 2014). Additionally, age-0 recruitment, as measured in August of each year, exhibits high inter-annual variation (i.e., $>1,000$-fold; WTG 2014) with mortality rates stabilizing in the fall of their first year (WTG 2012) indicating that recruitment is strongly influenced during early life. Walleye in Lake Erie are the largest recreational fishery and second largest commercial fishery in the lake (WTG 2014), establishing them as an economically important species. As a top predator, walleye also are ecologically important through their effect on the stability and resilience of food web dynamics in Lake Erie, as well as contributing to the regulation of trophic structure (Holmlund and Hammer 1999). It is especially alarming then that age-0 recruitment has been consistently low since 2003 (WTG 2014) for reasons that remain enigmatic. To provide a better understanding of the recent decade of poor recruitment, I conducted a multi-scale, mechanistic investigation to understand how early life stages influence future
growth and survival. Toward this end, I explored processes during both the egg and larval stage over a range of space (100s of meters to 100s of kilometers) and time (days to years) scales. I used field, laboratory, experimental, and modeling approaches to address my questions. Below, I provide a synopsis of what I learned.

In Chapter 2, I examined potential early limitations in the recruitment process by calculating walleye egg production on the Ohio open-water reefs over 6 years, relating it to environmental conditions, female spawning stock biomass (SSB), and the index of age-0 recruitment. I found that egg production begins earlier in spring now than during the 1960s, with temperatures at the beginning and peak of spawning remaining unchanged. Egg production on the open-water reefs was strongly correlated with age-0 recruitment, suggesting that survival is regulated at the egg stage. Female SSB was not significantly correlated with egg production, but a negative trend was apparent. Wide inter-annual variation in egg production was observed, with density-dependent responses of fish stocks possibly responsible for the observed fluctuations. I recommend additional research into sources of density-dependence, such as limited high quality forage fish for females during the fall or limited spawning habitat in the spring, in order to better understand inter-annual fluctuations in both egg production and age-0 recruitment.

In Chapter 3, I explored whether inter-annual recruitment variability in walleye could be traced back to habitat conditions during the larval period. While Houde (1994) and Myers et al. (1997) suggested that the larval stage would be unimportant to
understanding recruitment variability in freshwater fishes (i.e., the suite of size-dependent hypotheses, such as the GMH and MMH, likely would not apply because they highlight processes operating during the larval stage; see above), I took a different perspective (that of Ludsin et al. 2014) and hypothesized that the larval growth environment would be related to future growth and recruitment variation. Toward this end, I compiled historical (i.e., 1994 – 2013) temperature and zooplankton datasets to describe the larval growth environment and then related it to age-0 juvenile growth and abundance. I found that larval-stage dynamics, as hypothesized for marine populations, appear to be important drivers of recruitment variability in large freshwater systems, demonstrating that freshwater fish can exhibit characteristics previously ascribed to marine populations. My findings suggest that for Lake Erie walleye, inter-annual differences in larval growth environment drive recruitment variability, whereas density-dependent growth regulates juvenile size.

I tested the relevance of the GMH and MMH in Lake Erie walleye to see if either hypothesis could help explain the wide fluctuations in walleye recruitment. In Chapter 4, I measured available zooplankton (prey) density and size, and larval walleye abundance and growth rate, as well as created an index of excess zooplankton, during 1994-1999 and 2011-2013. While larval walleye abundance did not differ between periods, average zooplankton density decreased by 85%. Correspondingly, walleye larvae exhibited slow mean growth rates and had low recruitment to the age-0 juvenile stage. Additionally, my findings demonstrate a mismatch between zooplankton
production and walleye consumptive demand during 2011-2013. I found measures of prey quality and quantity to explain 85-96% of the variance in recruitment, providing compelling support for the MMH occurring in a large lake ecosystem. Larval growth was not correlated with age-0 recruitment, offering little support for the GMH.

Because the carry-over effects of larval growth on juvenile survival are complex (Robert et al. 2007; Murphy et al. 2014), I further examined the GMH in walleye by empirically testing if fast growing larvae have a survival advantage in a freshwater system in Chapter 5. To do so, I examined the growth rates of the original larval population and surviving juveniles over the first 20 d of life for three different cohorts (i.e., years; 2011-2013), while also considering the duration and direction of growth-selectivity. My research provides evidence for growth-dependent mortality operating on both large and small larvae. While the direction of selection was not consistent through time, growth during all years was slow, resulting in weak recruitment. Inconsistencies in direction of selection may have been due to prevailing environmental conditions. Slow growth during the larval period during 2011-2013 is most likely due to low zooplankton prey availability (see Chapter 4).

Overall, the application of marine recruitment theory to Lake Erie walleye dynamics provided a helpful framework for understanding recruitment mechanisms. My results highlight the importance of processes operating during early life and their implications for juvenile success. My expectation is that processes, whether they be bottom-up or top-down, operating during early life are likely important in other large
lake populations, both within and outside of the Great Lakes basin. Continued investigation into how early life processes influence the recruitment dynamics of fish populations living in large lakes is likely to benefit their management as it has in marine systems for the past century.
REFERENCES


Johnston, T. A. 1997. Within-population variability in egg characteristics of walleye (Stizostedion vitreum) and white sucker (Catostomus commersoni). Canadian Journal of Fisheries and Aquatic Sciences 54:1006-1014.


Canadian Journal of Fisheries and Aquatic Sciences 53:787-801.


CHAPTER 2
EXPLORATION OF MECHANISMS REGULATING EGG PRODUCTION AND SURVIVAL IN LAKE ERIE WALLEYE

In fishes that are highly fecund, the many eggs that are produced must survive a gauntlet of potential mortality agents before successfully hatching and contributing to the larval stage. Because the quantity and quality of eggs produced has been linked to inter-annual variability in larval abundance (i.e., Houde 1987; Moodie et al. 1989), examination of egg-stage dynamics, including maternal characteristics and environmental conditions, provides a first look at early limitations in the recruitment process. Maternal age and size can affect egg quality, with old, large females generally producing high quality eggs that survive well (e.g., Moodie et al. 1989; Johnston 1997). Initial egg quantity also can be affected by female size (i.e., larger females produce more eggs; Bagenal 1978), but once deposited, mortality emanating from environmental conditions such as wind and wave action (e.g., Moyer 1975; Serns 1982), water temperature (e.g., Busch et al. 1975; Koonce et al. 1977), and predation (e.g., Horns and Magnuson 1981; Frank and Leggett 1984) can reduce viable egg abundances.

In Lake Erie, walleye (Sander vitreus) have experienced highly variable recruitment, with population regulation occurring in either the egg or larval stage
(Busch et al. 1975; Koonce et al. 1977; Zhao et al. 2009). Between 1980 and 2014, the walleye population exhibited greater than a 1,000-fold difference in age-0 recruitment (i.e., number of juveniles captured in August), with the last strong year-class occurring in 2003 (WTG 2014). Explanations for declines in age-0 recruitment strength remain elusive. While previous research has estimated walleye egg survival on the open-water reefs in western Lake Erie (e.g., Busch et al. 1975; Roseman et al. 1996; Roseman et al. 2001), none has quantified annual egg production and related it to age-0 recruitment.

Western Lake Erie is home to several spawning areas for walleye, including the Maumee, Detroit, and Sandusky Rivers as well as the Ohio open-water reef complex (Olson and Scidmore 1962). Even with such a diversity of spawning sites, it has been hypothesized that most of the walleye population spawns on the open-water reefs (Busch et al. 1975), as near-shore degradation has negatively affected tributary spawning sites (Hartman 1973; Leach and Nepszy 1976). The open-water reefs are shallow (1.5-7 m; Bolsenga and Herdendorf 1993), which make them vulnerable to wind and wave action (Roseman et al. 2001), as well as temperature reversals (Busch et al. 1975). Additionally, egg development is temperature dependent (Hurley 1972). Thus, the time spent as an egg can be prolonged, if water-warming rates stall or reverse. A prolonged egg period increases the cumulative probability of an egg being preyed upon or exposed to severe hydrologic events (Carlander et al. 1960; Wolfert et al. 1975; Roseman et al. 2006). In Lake Erie, yellow perch (Perca flavescens) and the invasive white perch (Morone americana) have been shown to be potentially important
consumers of walleye eggs (Wolfert et al. 1975; Roseman et al. 1996; Roseman et al. 2006). Because egg predator abundance increases as the spawning season progresses (Wolfert et al. 1975; Roseman et al. 2006), a low water-warming rate that slows egg development could translate into higher predation risk.

Maternal influences can directly affect the quality and quantity of eggs produced. In a laboratory setting, egg quality (e.g., size and lipid content) was found to influence survival in both the egg and resulting larvae; with eggs originating from older, larger females exhibiting higher quality and better survival (Moodie et al. 1989; Johnston 1997; Czesny and Dabrowski 1998; Johnston et al. 2007). Through computer simulations conducted using western Lake Erie walleye data, Venturelli et al. (2010) demonstrated that an increase in spawning stock biomass (SSB) and average age would elicit an increase in egg production and juvenile survival. Using field data, Madenjian et al. (1996) developed a stock-recruit model incorporating fall gizzard shad (Dorosoma cepedianum) abundance, the main diet item of adult walleye in Lake Erie, along with spring warming rate and SSB. The resulting model explained 94% of the variance in age-0 recruitment. These results imply that the size of the spawning stock and its condition entering the winter drive age-0 survival. However, Zhao et al. (2013) revisited the walleye stock-recruit relationship for Lake Erie, adding more years to the model developed by Madenjian et al. (1996), and found that fall gizzard shad biomass was no longer an important regulator of recruitment. Instead, SSB and spring warming rate were included in the best regression model, explaining 39% of the variance in age-0
recruitment (Zhao et al. 2013). Additionally, Wang et al. (2012) found weak relationships between female length and egg size among five different walleye stocks in the North American Laurentian Great Lakes, including two from Lake Erie, demonstrating only weak effects of maternal traits. Thus, our current understanding of maternal influences on egg quality and resulting age-0 recruitment in Lake Erie walleye populations remains elusive.

Herein, I examine walleye egg production on the Ohio open-water reefs in Lake Erie during 1996-1998 and 2011-2014 in an effort to decipher early limitations in the recruitment process. My first objective was to examine egg production through a series of years to see if spawning duration, water temperatures, or egg abundance varied. I also investigated if water warming rates or severe wind events influenced annual egg production. I hypothesized that that high warming rates would lead to more eggs (sensu Roseman et al. 2006), whereas high numbers of severe wind events would lead to a low number of eggs (sensu Roseman et al. 2001). Second, I tested if age-0 recruitment can be predicted from egg production on the open-water reefs. I expect egg production to vary through time, with years of low egg production leading to weak recruitment events to the age-0 juvenile stage, when recruitment is set in Lake Erie (WTG 2012). Conversely, years of high egg production could lead to either high or low age-0 recruitment, as environmental factors beyond the egg stage are also known to be important (e.g., Mion et al. 1998; Zhao et al. 2009). Finally, I tested the hypothesis that SSB of older females, drives recruitment via egg production. I predicted that years
containing an abundance of big old fat fecund female fish (BOFFFFs, sensu Hixon et al. 2013) would exhibit high egg production with the potential for strong age-0 recruitment (Venturelli et al. 2010).

METHODS

Study Site & Species

Western Lake Erie supports numerous productive walleye spawning areas and contains the highest density of walleye in the Great Lakes (Hubbs and Legler 2004). Each spring, adults typically return to their natal spawning location (Regier et al. 1969), creating geographically distinct local spawning populations (i.e., stocks), including those in the Maumee River, Detroit River, Sandusky River, and the Ohio open-water reef complex (Goodyear et al. 1982). Walleye broadcast their eggs over clean rock or gravel and neither site preparation nor parental care is provided. Hatching occurs 7 to 15 d later in April or early May, depending on water warming rates (Hurley 1972; Roseman et al 1996). Hatched embryos are pelagic, lack motility, and feed on zooplankton during the first 2-3 weeks of life. In May through early June, larvae develop into motile benthic juveniles and begin to incorporate benthos and fish into their diets (McElman and Balon 1979). In August of each year, the Ohio Department of Natural Resources-Division of Wildlife (ODNR-DOW) conducts trawl surveys across the western Lake Erie to determine the abundance of age-0 juveniles, a strong predictor of future recruitment to the fishery (WTG 2012).
Field collections

Egg collection, processing, and analysis. Walleye eggs were collected during spring in 1996-1998 and 2011-2014 on the open-water reefs located in western Lake Erie (Figure 2.1). In each year, collections began after ice-out (mid-March through mid-April), lasting until early to mid-May when spawning ceased and catches of walleye eggs were negligible. Cone, Crib, Locust Point, Niagara, Round, and Toussaint reefs (Figure 2.1) were sampled on a weekly basis. Each site was located by global positioning system coordinates and marked with an anchored buoy. Collection methods included an egg pump (1996-1998) and egg mats (2011-2014). After collection, eggs were identified based on diameter (nearest 0.1 mm) and color (Auer 1982).

An egg pump was used to estimate egg densities during 1996-1998. The egg pump consisted of a 39 kg iron sled (0.25 m wide; Stauffer 1981) attached by a flexible hose (5 cm diameter) to a diaphragm pump at the surface. The sled was towed three times per site for 2 min at about 0.5 m/s with a small (8 or 10 m hull length) research vessel following methods described in Roseman et al. (1996). Eggs and benthic debris (e.g., dreissenid mussels and shells, sand, benthic organisms) were deposited from the pump apparatus into a basket made of 10 mm mesh hardware cloth. The basket was set into a framed sluice that allowed eggs and smaller benthic materials to be washed through and collect in a sample jar. The sample was preserved in 95% ethanol.
To estimate egg density, the number of eggs in each of the three egg-pump tows per reef was counted in the laboratory. The three counts were averaged to create one single estimate of total eggs (including both dead and live eggs) per 2 min tow for each reef and date. I later converted the number of eggs per tow to number of walleye eggs per m² (see below).

Egg-mat sampling during 2011-2014 consisted of furnace filter, a common substrate used for the collection of demersal eggs (Nichols et al. 2003; Manny et al. 2007; Ivan et al. 2010). During 2011, I wrapped furnace filter around cement cinder blocks, then chained three wrapped blocks together to create a gang (total weight = ~32 kg). I positioned one gang on each reef. During 2012 – 2014, I used furnace filter set into custom-designed aluminum frames (61 X 91.5 cm) that sat flat on the lake bottom and were weighed down by 32 kg of cement. I positioned one frame at each reef. Each week, I collected all of the egg-mats, removed the furnace filter (and the associated eggs), and reset the egg-mats with new furnace filter.

In the laboratory, I processed all egg-mat samples within a 24-h window to ensure that I could accurately distinguish live from dead eggs (Roseman et al. 1996). I subsampled each egg mat by cutting out 4-8 randomly chosen squares, which represented 12.5 – 25% of the original mat (see Appendix A for details). I removed eggs from each square and identified, counted, and noted viability (i.e., dead versus alive) under a dissecting microscope. I considered eggs that showed signs of opaqueness or exhibited fungal growth as dead (Johnson 1961). For each egg mat, egg numbers from
all subsamples were used to calculate a mean density (eggs/m²) for each reef on that sample date.

To facilitate comparison of egg densities estimated by the egg pump and egg mats, I conducted a gear-comparison study during spring 2014 (Appendix A). From this analysis, I learned that total egg densities from the two gears were strongly correlated (r = -0.72, P = 0.0008; Appendix A). Owing to the strong correlation, I converted total egg pump densities collected in 1996 - 1998 into total egg-mat densities (Appendix A).

To calculate total weekly egg production for each reef in each year, I multiplied the mean number of eggs per m² by the area of that reef (Table 2.1). I summed these estimates over all sampling weeks within a year to calculate total annual egg production. Unfortunately, during 2011 and 2014, several egg-mat samples were not retrievable. During 2011, all reef samples during the week of 6 April, the week of peak egg deposition, were lost. As such, I was unable to reliably estimate egg production during that week, as well as a total deposition for the year. During 2014, the egg mat located on Round Reef was missing on 24 April, whereas the egg mat on Toussaint Reef was missing on 30 April and 8 May. To account for these losses, I used the remaining four reefs (for which we had complete mat retrieval) to calculate a mean percent of egg production that occurred during each week in 2014. Then, using the resultant week-specific estimates, I estimated the missing egg abundances using their reef-specific values.
Explanatory & Response Variables

Physical predictors. Because water warming rate has been shown to influence Lake Erie walleye egg survival (Busch et al. 1975; Wolfert et al. 1975; Roseman et al. 2006), I calculated it during the egg-production period in each year. I defined the egg-production period as the time from the first day of egg deposition until the last day an egg would be expected to hatch. To estimate this last day of hatching, I applied a temperature-dependent egg development function to the last date that I found viable eggs (Jones et al. 2003). The slope of a least-squares regression fit though the daily water temperatures, from the first day of egg deposition to the last day of hatching, was used as a proxy for the water warming rate. Daily water temperature was provided by the Collins Park Water Treatment Plant (Toledo, OH), with temperature measured at its intake pipe located at 3 m depth. Using the Collins Park data, I also noted the water temperature at which spawning began, peaked, and ended.

I calculated an index of severe wind events that occurred during the egg period, as strong winds during the egg period lead to high egg morality (Busch et al. 1975; Roseman et al. 2001). I obtained continuous wind data from the National Oceanic and Atmospheric Administration’s National Data Buoy Center, which has a station located on South Bass Island, about 20 km east of the open-water reefs. After taking a daily mean of wind velocity (km/h), I tallied the number of days that had winds sufficient to remove incubating walleye eggs into two categories: 25 to 50 km/h or greater than 50 km/h (Roseman 2000).
**Biological predictors.** To explore if total annual egg production was related to female SSB, I relied on stock assessment information provided by the Lake Erie Walleye Task Group (WTG). The WTG uses an auto differentiation model builder statistical catch-at-age stock assessment model (WTG 2001) to estimate age-specific abundance, sex ratio, rate of maturity, and mass for walleye in Lake Erie by incorporating both fishery-dependent and -independent data. Using age-specific estimates of female walleye biomass by year from the WTG, I calculated the biomass of age 7+ females (i.e., BOFFFFs; Hixon et al. 2014) for my study years.

**Biological response variable.** I used an index of age-0 juvenile abundance (number of individuals per ha; WTG 2014) as a measure of walleye recruitment. Each annual estimate of age-0 juvenile recruitment was derived from August bottom trawls conducted at 41 sites in the Ohio waters of western Lake Erie by the ODNR-DOW, with sites randomly stratified by depth strata (i.e., 0-3 m, 3-6 m, 6-9 m, and >9 m). A flat-bottom semi-balloon otter trawl with a 10.7-m head rope and 13-mm bar mesh in the cod end was employed. When loge-transformed, this index of abundance is highly correlated with adult abundance two years later (r = 0.94; WTG 2012).

**Statistical Analyses**

I used least-squares linear regression to quantify relationships between annual egg production and predictor variables (i.e., water warming and spawning stock biomass), as well as between egg production and future recruitment to the age-0
juvenile stage. I checked all data for normality and heteroscedacity before analysis, with data transformations occurring as needed. The alpha-level for statistical significance was set at 0.05.

RESULTS

The number of eggs produced in a given year and the timing of egg deposition varied during 1996-98 and 2011-2014. The total number of eggs deposited varied by year (Figure 2.2), with a 10-fold difference in egg production between the largest (1996) and smallest (2012) years. In most years, walleye spawning began during the last week of March or first week of April and ended during the first or second week of May (Table 2.2) with a 75% cumulative probability of egg deposition occurring by mid to late April (Figure 2.3). Because eggs were captured during the first week of collections in 1997, 2012, and 2014, spawning in those years may have begun earlier than collections. However, since the initial collections in 1997 and 2012 provided few eggs, I have confidence that spawning had not been underway for long. In 2014, ice prevented me from beginning the collections any earlier. Thus, I may have missed spawning activity that occurred under the ice. In 2012, spawning activity occurred before 20 March (Figure 2.3), the earliest of the seven years. In all years, spawning began between 3.3 and 7.5°C, peaked between 6.3 and 10.8°C, and ended before water temperatures reached 12°C (Table 2.2).
My hypotheses that annual total egg production would be related to water warming rate and severe wind events were not supported. Thus, while spring warming rate varied considerably among years, with a 3-fold difference found between the fastest (2013) and slowest (2012) year (Table 2.2), egg production was unrelated to water warming rate during the egg production period ($F_{1,4} = 0.11, P = 0.76$). Egg production was greater (Figure 2.2) and severe wind events (Table 2.2) occurred more frequently during the earlier period (i.e., 1996-1998) than in more recent years (i.e., 2011-2014), suggesting that low egg production in recent years was not a result of high winds.

I expected that increased egg production would stem from an increase in the biomass of BOFFFs that would lead to an increase in age-0 recruitment. I found a strong positive relationship between egg production and recruitment to the juvenile stage ($F_{1,4} = 30.0; r = 0.94; P = 0.005; $Figure 2.4). By contrast, the relationship between BOFFFs and egg production was not statistically significant ($F_{1,4}= 7.14; P = 0.06$), although a negative trend was apparent (Figure 2.5).

**DISCUSSION**

My research yielded several unexpected results for potential drivers of egg production and recruitment. For example, yearly production of walleye eggs on the Ohio open-water reef complex was strongly related to age-0 recruitment, which is surprising because of the many post-egg-deposition processes previously shown to be
important drivers of walleye recruitment in Lake Erie (e.g., Miller et al. 1988; Madenjian and Carpenter 1991; Mion et al. 1998; Roseman et al. 2005; Zhao et al. 2009). This tight relationship has several potential implications. First, the number of eggs deposited on open-water reefs is either driving lake-wide recruitment or it is a reflection of recruitment from other spawning areas. Additionally, the tight relationship between eggs and recruitment implies that recruitment is regulated at the egg stage. I also found that physical factors did not affect egg production in ways I had predicted based on previous research that showed water warming rates and wind to be important (Busch et al. 1975; Roseman et al. 2006). What might limit egg production is the biomass of BOFFFFs; while BOFFFF biomass was not significantly correlated with egg production, it did exhibit a negative trend, implying density-dependent mechanisms during spawning could be occurring.

While my results suggest that recruitment from the open-water reef either drives lake wide recruitment or is representative of recruitment among all spawning sites, we do not have stock-specific estimates of recruitment that would allow us to test this. The abundance of juvenile recruits originating from the open-water reef complex is unknown. Research is ongoing into the contribution of each of the major walleye spawning stocks in Lake Erie; however, current results are inconclusive (Merker and Woodruff 1996; Stepien and Farber 1998; Hedges 2003; Bartnik 2005; WTG 2014). Even if contributions across spawning sites were similar, survival rates of eggs and larvae may differ spatially. While eggs on open-water reefs may face higher mortality from wind
and wave scouring, eggs broadcasted in spawning tributaries could encounter high discharge rates, temperature reversals, and sedimentation from incoming spring rains, any of which can cause mortality (Humphrey et al. 2012; Mion et al. 1998). Further, predation pressure may vary across spawning grounds. Continued research into spawning stock egg deposition and resultant population contribution is encouraged, as information learned would be extremely valuable to Lake Erie walleye fishery managers who currently manage all walleye in the lake as a single stock.

My findings suggest that egg production from the reefs may be an early indicator of future recruitment to the fishery. In a laboratory setting, egg mortality is negligible once eggs reach stage-2 development, and therefore one of the first major bottlenecks for survival could be the first 50-100 hours post-fertilization (Latif 1999). However, in a field setting, walleye eggs can face mortality by both physical processes and predation, and thus why I originally predicted that a year with high egg production could lead to either high or low age-0 recruitment. Further, once hatched, larvae with limited locomotive capabilities (Houde 1969; Humphrey et al. 2012) can encounter a gauntlet of physical processes and predation pressure while foraging for food. Survivors to the juvenile stage continue to be at risk of predation. Indeed, it is incredible to think that recruitment could be set early in the egg stage when there are yet several months of unpredictable processes that walleye must endure before recruitment is measured. Therefore, I suspect that age-0 recruitment is not set in the egg stage. However, further research into alternative possibilities, such as gaining an understanding of stock specific
contributions or exploring the idea that environmental conditions conducive for egg survival are also conducive to larval survival, would help in interpreting this potential spurious correlation.

A fast spring warming rate and reduced number of severe wind events may be necessary, but not sufficient, prerequisites for a successful year-class. In 1998, 2013, and 2014, the spring warming rate was high, above 0.2°C/d, but only 1998 and 2014 had high egg production. Additionally, more severe wind events occurred during 1996-1998 than in 2012-2014, but more eggs were produced and strong recruitment occurred in the 1990s. Likely, a combination of physical and biological factors leads to successful egg deposition and hatching.

Spring water temperatures and the onset of walleye spawning have been noted for several decades. Egg collections on the open-water reefs also were conducted in 1960-1970 with an egg pump. Records from these years indicate that egg deposition began between 3.9 and 5.6°C and peaked at 7.8°C (Baker and Scholl 1971). While the temperatures of onset and peak egg production agree with the temperatures from this current study (see Table 2.2), the timing is slightly different. In the 1960s, walleye spawning usually began in the 2nd week of April (Baker and Scholl 1971). During the seven years of this study, spawning commenced either during the 4th week of March or the 1st week of April. The one to two week advancement of spawning is most likely triggered by the increased spring temperatures in the Great Lakes region (McCormick and Fahrenstiel 1999; Jones et al. 2006; Magnuson 2010). Earlier spawning, due to an
advancement of spring temperatures, also has been documented in other fishes (see Crozier and Hutchings 2014 for review), including walleye populations in Minnesota (Schneider et al. 2010).

During 2012 and 2013, only a small number of eggs were estimate to be on the reefs despite a high abundance of mature females in the population. Because Lake Erie walleye appear to demonstrate spawning-site fidelity (Regier et al. 1969; Goodyear et al. 1982), low egg numbers on the reef complex suggest that a large fraction of individuals may have skipped spawning in those years (rather than suggesting that they spawned elsewhere). Females in poor condition have been shown to skip spawning in other systems (Rijnsdorp 1990; Bunnell et al. 2005; Jørgensen et al. 2005; Rideout et al. 2000, 2005), with poor feeding conditions for females being deemed the most likely cause of skipped spawning (Jørgensen et al. 2005). Previous research has shown a positive correlation between average female walleye energetic condition and subsequent age-0 recruitment (Henderson and Nepszy 1994; Venturelli et al. 2010). Thus, one possible explanation for the reduction in egg output could be a decrease in female condition due to poor feeding conditions in 2012 and 2013. Additionally, recent increases in metabolic costs due to shorter, warmer winters (Jones et al. 2006) also could negatively affect female spawning condition (Henderson and Nepszy 1994). The warmest spring during the years that I sampled occurred in 2012, with water temperatures in March averaging 6.7°C; 1998 had the second warmest water temperature in March, averaging 3.9°C. The
unseasonably warm water temperatures in 2012 may have resulted in poor egg deposition.

Interestingly, I also found a weak, negative trend between total annual egg production and the SSB of age 7+ females (i.e., BOFFFS), suggesting the possibility of density-dependent effects existing during the adult life stage. To better investigate this possibility, I used age-0 recruitment as a proxy for egg production, due to their tight correlation in this study (see Figure 2.4), which allowed me to add more years to the analysis. Data on both age-0 recruitment and BOFFFS from 1988 until 2014 demonstrate no relationship between the two variables ($P = 0.48$; Figure 2.6) and no support for the idea that an increase in BOFFF biomass can lead to an increase in recruitment strength, as demonstrated by the lack of high recruitment values at large BOFFF biomass.

This notion counters findings from Venturelli et al. (2010), who concluded that older females drive population dynamics of western Lake Erie walleye through maternal influences on fecundity, egg size, and offspring survival rate. Our differences in findings are most likely due to changes in age composition of the population. Venturelli et al. (2010) used a dataset of Lake Erie walleye from 1947-1976 when the average age of an adult female walleye was between 3.0 and 4.4 years. During 1947-1969, 90 to 100% of the population was younger than 5 years (Shuter and Koonce 1977), and the 1960s had historically low walleye abundances (Busch et al. 1975). During 1988-2014, as little as 18% the Lake Erie walleye population was younger than 5 years with the average age of
an adult female between 4.0 and 5.8 years (WTG 2014). These recent estimates of SSB age are conservative, as the statistical catch-at-age model provides the number of mature female walleye by age until 7 years, when females are lumped into the 7+ age category (WTG 2014). Therefore, in more contemporary times, when the walleye population is larger, older, and more diverse in age structure, the contribution of BOFFFFs and their ability to drive egg and juvenile survival appears to have diminished, as the data show that the largest recruitment events occurred at low to intermediate SSB (see Figure 2.6).

Reduced egg production and recruitment at high levels of SSB suggest that density-dependent mechanisms may be at work in Lake Erie’s walleye population. Madenjian et al. (1996) found evidence for density-dependence in Lake Erie walleye, as an increase in SSB of age 5+ fish led to a decrease in recruitment to the fishery at age-2 during 1981-1993. After demonstrating that cannibalism was highly unlikely, these researchers hypothesized that intra-specific competition for food (age-0 gizzard shad) occurred during the fall or early winter between mature walleye (Madenjian et al. 1996). Additionally, intra-specific competition for good breeding areas can limit age-0 recruitment at high SSB, leading to a decrease in reproductive output (Ricker 1954). Therefore, if the open-water reefs are driving age-0 recruitment, as some researchers have hypothesized (Hartman 1973; Leach and Nepszy 1976; Busch et al. 1975), then at high SSB, spawning habitat could be limited. Because walleye exhibit site fidelity in spawning, improving nearby tributary habitat may not entice more walleye to spawn in
those locations; however, improvements could lead to an increase in egg survival, larval output, and ultimately the number of return spawners to tributaries. Additional research into density-dependent mechanisms operating within the spawning stock would aide in our understanding of variability in reproductive output and subsequent age-0 survival.

Overall, I was able to identify a strong relationship between walleye egg production and age-0 recruitment while taking into consideration water warming rates, wind events, and the biomass of BOFFFFs. I revealed that egg production now begins earlier in the spring than in the 1960s, with temperatures at the beginning and peak of spawning remaining unchanged. Egg production on the open-water reefs proved to be an excellent predictor of age-0 recruitment. Further research focused on understanding exactly if and how eggs can be limiting recruitment is needed. Additionally, wide inter-annual variation in egg production was exhibited, with density-dependent mechanisms acting on spawning adults seemingly responsible for the observed fluctuations. For this reason, I recommend additional research into sources of density-dependence, including whether high-quality prey or quality spawning habitat has become limiting. With such knowledge, our ability to better understand inter-annual fluctuations in both egg production and age-0 recruitment is likely to improve, which would benefit the ability of agencies to manage this important population.
REFERENCES


Houde, E. D. 1969. Sustained Swimming Ability of Larvae of Walleye (Stizostedion Vitreum Vitreum) and Yellow Perch (Perca Flavescens). Journal of the Fisheries Research Board of Canada 26:1647-&.


Johnston, T. A. 1997. Within-population variability in egg characteristics of walleye (Stizostedion vitreum) and white sucker (Catostomus commersoni). Canadian Journal of Fisheries and Aquatic Sciences 54:1006-1014.


Roseman, E. F. 2000. Physical and biological processes influencing the year-class strength of walleye in western Lake Erie. Michigan State University, East Lansing, MI.


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Table 2.1. Area (m$^2$) of six walleye spawning reefs in the open-water reef complex in Western Lake Erie as calculated by Bolsenga and Herdendorf (1993).
<table>
<thead>
<tr>
<th>Year</th>
<th>Duration</th>
<th>Start Temp.</th>
<th>Peak Temp.</th>
<th>End Temp.</th>
<th>Warming Rate</th>
<th>25-50 km/h</th>
<th>&gt; 50 km/h</th>
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<tr>
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<td>4/1 to 5/25</td>
<td>5.0</td>
<td>7.4</td>
<td>11.1</td>
<td>0.18</td>
<td>22</td>
<td>0</td>
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<tr>
<td>1997</td>
<td>3/30 to 5/27</td>
<td>5.0</td>
<td>6.8</td>
<td>10.6</td>
<td>0.13</td>
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<td>2</td>
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<td>4.4</td>
<td>7.5</td>
<td>11.4</td>
<td>0.21</td>
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<td>3/31 to 5/16</td>
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<td>6.3</td>
<td>10.5</td>
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<td>3/15 to 5/14</td>
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<td>10.8</td>
<td>10.0</td>
<td>0.08</td>
<td>12</td>
<td>0</td>
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<tr>
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<td>3/28 to 5/12</td>
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<td>10.4</td>
<td>0.21</td>
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</tr>
</tbody>
</table>

Table 2.2. Lake conditions during the walleye egg deposition period on the Ohio open-water reef complex in western Lake Erie during 1996-1998 and 2011-2014. Characteristics of the egg production period, including duration (i.e., from first egg captured to last egg hatched), as well as temperatures (°C) when egg deposition started, peaked, and ended are provided. The rate of water warming (°C/d), number of days when mean daily wind speed fell between 25 and 50 km/h, and the number of days the mean daily wind speed exceeded 50 km/h also are provided.
Figure 2.1. Location of six open-water walleye spawning reefs in western Lake Erie that were sampled weekly with either an egg pump (1996 – 1998) or egg mats (2011 – 2014).
Figure 2.2. Estimated number of eggs produced by walleye on Cone, Crib, Locust, Niagara, Round, and Toussaint reefs in western Lake Erie during 1996-1998 and 2012-2014.
Figure 2.3. Cumulative proportion of eggs spawned for each date during spring 1996-98 and 2011-14 in western Lake Erie.
Figure 2.4. Relationship between age-0 juvenile walleye abundance (# of individuals ha$^{-1}$) and total egg production from six open-water reefs in western Lake Erie during 1996-1998 and 2012-2014.
Figure 2.5. Relationship between total egg production from six open-water reefs in western Lake Erie and age 7+ walleye spawning stock biomass (kg) during 1996-1998 and 2012-2014.
Figure 2.6. Relationship between age-0 juvenile walleye abundance (# of individuals ha$^{-1}$) and age 7+ walleye spawning stock biomass (kg) in Lake Erie, 1988-2014. Circles indicate years during which I calculated egg production.
CHAPTER 3

LARVAL GROWTH AS A DETERMINANT OF FUTURE GROWTH AND RECRUITMENT

Understanding the processes and mechanisms that drive variability in annual recruitment has long been a goal for both marine and freshwater fishery scientists. However, because marine recruitment research has been conducted for over a century (Heincke 1878; Hjort 1914), whereas recruitment studies in freshwater systems are comparatively newer, most of the theory concerning the fish recruitment process has been derived from marine ecosystems (Ludsin et al. 2014). While the application of marine recruitment paradigms to freshwater ecosystems seems appropriate—especially for large-lake ecosystems such as the Laurentian Great Lakes, which have similar biophysical processes and fish species with life-histories similar to marine fishes (Ludsin et al. 2014, Pritt et al. 2014)—empirical studies that have tested marine-derived recruitment theory in freshwater ecosystems are relatively scarce (see reviews by Houde 1994 and Ludsin et al. 2014).

Numerous general hypotheses have been generated to explain recruitment variability and subsequent fish population dynamics in marine fishes. Among the first were the Critical Period Hypothesis, which proposes that food availability to first-feeding larvae drives cohort success (i.e., year-class strength), and the Aberrant Drift
Hypothesis, which suggests that the prevailing currents moving larvae and juveniles into suitable or unsuitable habitats determine recruitment of larvae to older life stages (Hjort 1914). During the second half of the 20th century, size-dependent processes operating during early life stages were recognized as being important drivers of recruitment variability, with slow growth/development (i.e., Stage Duration Hypothesis; Chambers and Leggett 1987) and small size (i.e., Bigger is Better Hypothesis; Miller at al. 1988) being viewed as disadvantageous. Among the multiple bases for these hypotheses is that slow growth/development during the egg and larval stage increases exposure time to predators (Chambers and Leggett 1987). In addition, small larvae, which have reduced swimming and foraging capabilities relative to larger ones (Hunter 1980; Blaxter 1986; Zaret 1980), have been shown to be more susceptible to starvation and predation than their larger counterparts (Hunter 1980; Miller et al. 1988).

While size-dependent processes appear to be important to the recruitment process of both marine and freshwater fishes (Werner and Gilliam 1984; Houde 1987; Rice et al. 1987; Miller et al. 1988), the specific processes that drive recruitment variability for freshwater fish have been suggested to differ from marine fishes (but see Ludsin et al. 2014). For example, Houde (1994) and Myers et al. (1997) compared life-history characteristics of marine and freshwater fishes. Both studies concluded that competition and predation during the juvenile period should be more important in freshwater fishes than marine fishes, owing to the former’s larger size at hatching, shorter pelagic larval period, and smaller spatial scale for recruitment variability (i.e.,
versus 500km; Houde 1994; Myers et al. 1997). Conversely, owing to these same differences, abiotic controls (e.g., temperature, currents) operating during the larval stage were hypothesized as being more important drivers of recruitment variability in marine versus freshwater fishes.

Based on these authors’ work, one might conclude that marine-derived recruitment hypotheses are not applicable to freshwater species (Janssen et al. 2014). However, Ludsin et al. (2014) suggest that the recruitment processes in large freshwater lakes (e.g., Laurentian Great Lakes) are actually quite similar to those in marine ecosystems. They note that Houde (1994) and Myers et al. (1997) focused on freshwater species that are common to small lakes and riverine environments, whereas Ludsin et al. (2014) focused on the dominant economically and ecologically important freshwater fishes of the Laurentian Great Lakes (e.g., walleye *Sander vitreus*, yellow perch *Perca flavescens*, lake whitefish *Coregonus clupeaformis*, alewife *Alosa pseudoharengus*), which have life-history traits that are similar to marine species. These traits include large inter-annual fluctuations in population size, no parental care of eggs and larvae, small size at hatch, and a prolonged planktivorous pelagic larval period (Pritt et al. 2014; Ludsin et al. 2014). In addition, large-scale (400-600 km) recruitment synchrony has been found in several Great Lakes populations (Bunnell et al. 2010; Fedor 2008), which is at scales on par with those of marine populations (Myers et al. 1997).

While Ludsin et al.’s (2014) perspective seems highly plausible, few field-based studies have actually tested the validity of marine-derived recruitment hypotheses in
large-lake ecosystems. While Houde (1994) and Myers et al. (1997) suggested that the larval stage would be unimportant to understanding recruitment variability in freshwater fishes (i.e., the Critical Period Hypothesis, Aberrant Drift Hypothesis, and the suite of size-dependent hypotheses likely would not apply because they highlight processes operating during the larval stage; see above) I took a different perspective (that of Ludsin et al. 2014) and hypothesized that the larval growth environment would be related to future growth and recruitment variation. Toward this end, I compiled historical (i.e., 1994 – 2013) temperature and zooplankton datasets to describe the variation in the larval growth environment and then relate it to age-0 juvenile walleye growth and abundance.

**METHODS**

*Study System and Species*

Lake Erie (USA-Canada) is the southernmost, shallowest, and most biologically productive of the Laurentian Great Lakes. It contains three distinct basins that differ in water temperature, phosphorus concentrations, and primary and secondary production, which tend to decrease from west to east. This study took place in the western basin (mean depth = 7.4 m) and included waters west of an imaginary line extending from Point Pelee, Ontario, Canada, to Huron, Ohio, USA (Figure 3.1).

Larval walleye are generally present in high densities during late April through early June in western Lake Erie (Roseman 2000). Walleye are pelagic as larvae, and once
the yolk sac is absorbed (around 8 mm total length (TL)), larvae feed entirely on zooplankton for three to four weeks and lack strong swimming capabilities during this time (Houde 1969; Humphrey et al. 2012). During late May to early June, larvae become motile benthic juveniles (around 21 mm TL) and begin to incorporate benthos and fish into their diets (McElman and Balon 1979). Age-0 recruitment of Lake Erie walleye exhibits high inter-annual variation (> 1,000-fold) in part due to mortality during early life stages (Busch et al. 1975; Koonce et al. 1977; Roseman 1997; Chapter 2), with the abundance of age-2 walleye being highly correlated to the abundance of young of year walleye in August ($R^2 = 0.89$, Lake Erie Walleye Task Group (WTG) 2012).

Field Collections

I gathered twenty years of data (i.e., 1994 - 2013) from western Lake Erie, which contains the highest density of walleye in the Great Lakes (Hubbs and Legler 2004). I targeted data collected during the fourth week of April through the first week of June for each year. Data included water temperature (surface) and prey (zooplankton) biomass originating from multiple sources, with sampling occurring either weekly or biweekly (Figure 3.1; Table 3.1).

Zooplankton samples were collected, preserved, and processed in a similar manner across years. Following a vertical haul with either a 64- or 153-µm mesh net (Table 3.1), samples were preserved in sugar-formalin for later identification (Pennak 1978; Balcer et al. 1984) and enumeration. For each sample, zooplankton were
counted, identified, and measured in a minimum of two subsamples until at least 150 zooplankton individuals (150 per sample method; Table 3.1) or 100 of the most abundant crustacean zooplankton taxa excluding rotifers, nauplii, and veligers (100 per species method; Table 3.1) were counted. Individual zooplankton were identified to the lowest taxonomic level in the 100-per-species method (most to species), whereas cladocerans were identified to genus and copepods were identified as calanoid, cyclopoid, harpacticoid copepodites, or nauplii in the 150-per-sample method. Zooplankton lengths from the first 20 (whole) individuals encountered in each sample were measured using an ocular micrometer (nearest 0.01 mm). Zooplankton biomass (mg/l) was estimated using abundance information and individual biomass derived from length-mass equations (Culver et al. 1985).

Previous work (Mack et al. 2012) showed that the use of different counting and collection methods in Lake Erie is unlikely to bias my estimates of zooplankton abundance and size (and hence, biomass). Mack et al. (2012) showed that the two enumeration methods (100 per species vs. 150 per sample) did not lead to differences in zooplankton abundance estimates or the precision of counts ($P > 0.05$ for both). Further, while Mack et al. (2012) found that the 64-µm mesh net was more efficient at capturing rotifers and nauplii than the 153-µm nets ($P < 0.008$), no differences in mean abundance or mean size of zooplankton were observed once rotifers and nauplii were excluded from the analysis ($P > 0.05$ and $P = 0.39$, respectively). Thus, these taxa were excluded from further analysis. Their exclusion also appears warranted because larval
walleye typically do not consume rotifers and nauplii (Mathias and Li 1982; Mayer and Wahl 1997).

**Larval Growth Environment Modeling**

I incorporated the *in situ* zooplankton biomass and water temperature measurements into a bioenergetics model to estimate the quality of the larval growth environment for walleye. Using a simple, mass-balanced energy budget (i.e., a bioenergetics model), I essentially answer the question: if a larval fish of a given size experienced an environment with a given temperature and a given zooplankton biomass, how well would it grow? We used the model to estimate the expected growth response of an individual of known size to observed habitat conditions (Mason and Brandt 1996) thus providing a measure of habitat quality (Brandt and Kirsch 1993; Goyke and Brandt 1993; Tyler and Brandt 2001). Originally, this method was referred to as Growth Rate Potential modeling (Brandt et al. 1992), and has since been used to provide a measure of habitat quality in a variety of aquatic systems (e.g., estuary: Costantini et al. 2008; large lake: Arend et al. 2011; ocean: Zhang et al. 2014).

All model equations and parameters used to estimate larval growth environment were derived from the literature and are specific to larval walleye (Kitchell et al. 1977; Madon and Culver 1993; Appendix B). Briefly, I ran a growth model for each sample site/date (see Appendix B, Tables B.1 and B.2 for model equations and parameters, respectively), assuming that (i) expected growth rate resulted from the observed
temperature and prey biomass conditions at each sampling site on each date and (ii) density-dependent foraging or feedback mechanisms do not exist (i.e., prey consumption did not alter prey biomass density). Larval growth environment is reported as gram of growth per gram of fish per day. The proportion of maximum consumption ($P$) was determined as a function of site and date-specific available prey biomass (Appendix B, Table B1). I estimated respiration rate as a function of fish size, water temperature, and activity level (Kitchell et al. 1977). I calculated Specific Dynamic Action (SDA) as a constant proportion of the assimilated energy (consumption – waste losses; Kitchell et al. 1977). I calculated waste losses (egestion and excretion) as a proportion of consumption (Kitchell et al. 1977). Given this model setup, in situ prey biomass directly affected consumption, whereas in situ temperature affected consumption, respiration, SDA, and waste losses.

I modeled both 8.5 mm and 12 mm TL larvae, as walleye begin to feed exogenously around 8.5 mm (Mathias and Li 1982) and 12 mm is a length at which larval fish are still obligate zooplanktivores. Roseman (1997) found larvae as small as 14 mm TL to have incorporated fish and benthic macroinvertebrates into their diets in Lake Erie. Additionally, in laboratory feeding experiments, Galarowicz et al. (2006) demonstrated that 20 mm TL walleye will feed upon both fish and zooplankton.

I used growth rates from field-captured fish to test the assumption that habitat quality during the larval stage (i.e., larval growth environment) was positively related to observed larval growth rate. Data on larval walleye growth rates were available for 9 of
the 20 years (i.e., 1994-1999 and 2011-2013). Larval walleye were collected on a weekly basis at 3 to 32 sites each year (mean = 19 sites). During 1994-1999, a 1 m X 2 m neuston net with a 583-µm mesh net was used to sample larvae, whereas during 2011-2013, paired 0.6-m diameter bongo nets with 500-µm mesh nets were employed. Both nets were towed in the upper 2 m of the water column at about 1m/s for 5 (1994-1999) or 10 min (2011-2013). Flow meters positioned at the mouth of each net estimated the water-volume sampled. Larvae were preserved in 95% ethanol for later identification (Auer 1982) and TL measurement (nearest 0.1 mm). The daily growth rate \( G \) of larvae was estimated with the equation, \( G = (T_{t} - T_{0})/d \), where \( T_{t} \) is the mean TL of fish on day \( t \), \( T_{0} \) is the mean TL during the prior sampling period, and \( d \) is the number of days between time \( t \) and time 0.

The Ohio Department of Natural Resources-Division of Wildlife generates an index of age-0 walleye abundance (number of individuals per ha) by conducting a bottom trawl survey during late August across western Lake Erie \( (n = 41 \text{ sites}; \text{WTG 2014}) \). I used the index of age-0 juvenile abundance to estimate recruitment, as this index has been shown to be a strong predictor of abundance at age-2 \( (R^2 = 0.89) \), at which time walleye enter the fishery (WTG 2012).

\textit{Statistical Analysis}

I averaged all larval growth environment calculations from each given week \( (n = 4 \text{ to } 45 \text{ samples per week; Table 3.2}) \) and then averaged all weeks within a given year to
arrive at an annual mean. I only considered sampling events occurring during the larval walleye season, which typically begins in the fourth week of April and ends the first week of June (Roseman 2000). Because relatively few years had zooplankton sampled during the fourth week of April, I excluded the week from the analysis. Additionally, to ensure that all years had samples collected throughout the larval period, I excluded years that lacked samples from the first and third weeks of May, as well as the first week of June. Thus, I used data collected from 1 May until 7 June from 1994-2000, 2004, 2006-2009, and 2011-2013. I calculated the growth environment for 8.5 and 12-mm larval fish, but since the magnitude and direction of results were similar across analyses of both sizes, I only discuss findings for 8.5-mm larvae. Results of the 12-mm larval analyses can be found in Appendix B.

I tested the hypothesis that the larval growth environment is related to field derived larval growth and recruitment estimates using least-squares linear regression analyses conducted on data from 1994-1999 and 2011-2013. Further, I correlated the larval growth environment with the mean size of juvenile recruits in August to determine whether the benefits of a good larval growth environment carried over into the juvenile period. Because I ran multiple tests, I used a Bonferroni adjustment of the significance level of each individual test (α = 0.05/4 = 0.0125) to maintain an overall significance level of α = 0.05.
RESULTS

The larval period provided a strong indication of future recruitment, but not future growth. Of the years considered, the number of data points per year ranged between 24 in 2000 and 2004 and 152 in 2013 (Table 3.2). I found a slightly non-significant positive relationship between larval growth environment and observed larval growth rates ($F_{1,7} = 9.23$, $P = 0.02$; Figure 3.2), demonstrating that as habitat quality (i.e., growth rate potential) increased, realized larval growth also increased. In support of my study’s central hypothesis, I found that larval growth environment was positively correlated with the age-0 juvenile recruitment index ($F_{1,13} = 9.69$, $P = 0.008$, $r = 0.65$; Figure 3.3). I found no relationship between larval growth environment and mean TL of age-0 juveniles ($F_{1,13} = 0.85$, $P = 0.36$; Figure 3.4) suggesting that larval growth did not carry over into later life stages. However, in a few years (i.e., 1994, 1998 and 1999) high catch rates of juveniles coincided with fast larval growth rates (Figure 3.2) and high-quality larval growth environment (Figure 3.3), but the resultant juveniles had short TLs (Figure 3.4). As a means to assess whether this pattern may be due to density-dependent effects on growth, I correlated age-0 walleye abundance with mean TL during August. I found a significant negative relationship ($F_{1,18} = 11.38$, $P = 0.003$, $r = -0.63$; Figure 3.5), suggesting the possibility of density-dependent growth occurring during the age-0 juvenile stage.
DISCUSSION

Larval growth environment proved to be a reasonable indicator of in situ growth rates, as well as age-0 recruitment in western Lake Erie walleye, providing evidence that larval stage dynamics can drive inter-annual variability in recruitment. The larval period also has proven to be important to recruitment in yellow perch from Lake Erie, with larvae inside the turbid Maumee River plume exhibiting greater survival to the juvenile stage than larvae outside of the river plume (Reichert et al. 2010) due to enhanced protection from predators that the plume offers (Carreon-Martinez et al. 2014).

Additionally, in Lake Michigan, zooplankton density during the early larval period has been shown to be strongly correlated to the number of juvenile yellow perch recruits (Clapp and Dettmers 2004), suggesting that larval foraging success is important to juvenile recruitment. Thus, my study adds to a growing body of evidence that recruitment variability can be driven by larval-stage dynamics in dominant economically and ecologically important freshwater fishes of the Great Lakes.

Spatial heterogeneity of available zooplankton during the larval stage may be responsible for this observed inter-annual variability in walleye recruitment. Roseman et al. (2005) found that, in general, nearshore areas in western Lake Erie provided warmer water temperatures, lower water clarity, and a higher prey density for larval walleye than offshore areas. Additionally, Zhao et al. (2009) demonstrated that in years (i.e., 1995, 1998) where walleye larvae were advected offshore in western Lake Erie, subsequent recruitment was weak, whereas in years (i.e., 1996 and 1999) where
walleye stayed in the nearshore area, subsequent recruitment was strong. My study bridges research completed by Zhao et al. (2009) and Roseman et al. (2005) by linking the importance of high-quality nursery habitat and resultant larval growth to recruitment success. Physical processes, as was originally hypothesized by Hjort (1914), may play an important role in facilitating larval location, essentially setting the stage for juvenile growth and recruitment in western Lake Erie walleye. Future research into the drivers of inter-annual variation of recruitment stemming from the larval period in walleye should include the influences of both physical processes and zooplankton availability, including tests of other marine derived hypotheses including the match-mismatch (Cushing 1975).

A uniting theme in freshwater and marine recruitment literature is the idea of growth-selective processes driving recruitment variability. In this study, I found evidence to suggest that growth-selection was occurring, where years in which larvae had access to better growth environments, and presumably grew better, higher abundances of age-0 recruits were observed. Growth- and size-selective mortality can act upon individuals via starvation and/or predation. In a few of the years, annual means of larval growth environment were less than 0, indicating a poor habitat for growth with, most likely, suboptimal prey availability, suggesting that starvation of larval fishes may have occurred. Predation of larval walleye has been documented indirectly via abundance relationships (e.g., Quist et al. 2003); however, direct evidence is lacking. Predation and starvation are both difficult to demonstrate empirically in larval fish
(Bailey and Houde 1989; Leggett and DeBlois 1994; Legler et al. 2010), although recent advances in molecular methods show promise in understanding the impact of predation (Carreon-Martinez et al. 2014). Whether mortality is acting upon walleye larvae in Lake Erie through starvation versus predation requires further investigation.

While I found a positive correlation between larval growth environment and age-0 recruitment, I also discovered a negative relationship between larval growth environment and juvenile size. At high levels of larval growth environment, only small juveniles were produced, whereas both small and large juveniles were generated at reduced levels of larval growth environment. Interestingly, large juveniles were not produced at high levels of larval growth environment. Additionally, I found a significant negative relationship between fall juvenile abundance and size, with strong year-classes exhibiting relatively smaller juveniles than weak year-classes. These results suggest that density-dependent growth is occurring during the juvenile stage. Density-dependent growth is most likely to occur in the late-larval or juvenile stage for both marine and freshwater species (Cowan et al. 2000). In freshwater systems, it has been documented for immature walleye in eight different populations, including 3 of the 5 Great Lakes (Venturelli et al. 2010), as well as for larval yellow perch in Saginaw Bay (Ivan et al. 2011). My study suggests that while growth-dependent mortality processes in the larval stage generate variability in recruitment, density-dependent effects on growth during the juvenile stage regulate size (i.e., TL). Thus, better available larval growth
environment will lead to larger larvae with subsequent higher survival of smaller juveniles.

Density-dependent effects on growth during the juvenile period can have deleterious effects on future growth and survival, as well as population dynamics. First, small juveniles are at greater risk for overwinter mortality (Post and Evans 1989; Ludsin and Devries 1997; Höök et al. 2007). For example, Venturelli et al. (2010) demonstrated that a 30 mm decrease in juvenile TL could increase overwinter mortality by about 1.5 times in walleye residing in Oneida Lake. Second, small juveniles produced in a high abundance year may take longer to recruit into the adult population (and any fisheries it supports), if poor juvenile growth is not compensated for in subsequent years. Third, fecundity is exponentially related to length for many fish species (Bagenal 1978), and as a result, small females produce fewer eggs. However, evidence exists to suggest that female length at maturity is density-independent and remains unchanged for walleye in Lake Erie (Lester et al. 2014). Therefore, fecundity in females is not affected by juvenile size, and that a small juvenile size can be compensated for in Lake Erie walleye.

In general, unless compensatory mechanisms exist, fish populations can face numerous undesirable outcomes from density-dependent juvenile growth.

Larval period dynamics, as hypothesized for marine populations, appear to be important drivers of recruitment variability in large freshwater systems, demonstrating that freshwater fish can exhibit characteristics previously ascribed to marine populations. My findings suggest that for Lake Erie walleye, inter-annual differences in
larval growth environment drive recruitment variability, whereas density-dependent
growth regulates juvenile size. By demonstrating that recruitment regulation occurs
during the larval stage in a freshwater fish, my study further erodes the barrier between
freshwater and marine research. Overall, an exchange of ideas and hypotheses between
marine and freshwater systems is justified as we continue to make headway towards an
understanding of recruitment processes and mechanisms.
REFERENCES


Fedor, S. L. 2008. Synchronous recruitment of walleye in the Great Lakes and the influence of climate on recruitment. The Ohio State University, Columbus, OH.


Roseman, E. F. 1997. Factors influencing the year-class strength of reef spawned walleye in western Lake Erie. Michigan State University, East Lansing, MI.

Roseman, E. F. 2000. Physical and biological processes influencing the year-class strength of walleye in western Lake Erie. Michigan State University, East Lansing, MI.

patterns emphasize the importance of coastal zones as nursery areas for larval walleye in western Lake Erie. Journal of Great Lakes Research 31:28-44.


<table>
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Table 3.1. Four datasets containing zooplankton biomass and water temperature information were acquired to compute larval growth environment for the years 1994-2013 in western Lake Erie. The years that each dataset spanned, size of mesh used for zooplankton collection, zooplankton counting method, number of data points obtained in a week and sampling frequency for each dataset are listed above.
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Table 3.2. Number of data points used for analysis during the first week of May (1-May) to the first week in June (1-June). A data point reflects the number of paired zooplankton and temperature samples taken in the western basin of Lake Erie on a given week. The years 2001-2003, 2005, and 2010 were excluded from the final analysis due to a low number of samples spread throughout the larval period.
Figure 3.1. Western Lake Erie sample locations for zooplankton and water temperature from four different sources that sampled during 1 May to 7 June during 1994-2013. Four datasets were used to obtain information on years, including 1994-1999 (open circles), 1995-2013 (squares), 2006-2009 (crosses) and 2011-2013 (closed circles).
Figure 3.2. Relationship between larval walleye growth rates (mm/day) and 8.5-mm larval growth environment (g/g/day) during 1 May – 7 June in Lake Erie for the years 1994-1999 and 2011-2013.
Figure 3.3. Relationship between the loge-transformed August trawl catch per hectare of juvenile walleye (age-0 recruitment, catch per unit hectare) and 8.5-mm larval growth environment (g/g/day, 1 May – 7 June) during 1994 – 2013 in western Lake Erie.
Figure 3.4. Relationship between the average total length (TL; mm) of juvenile walleye captured in August and 8.5-mm larval growth environment (g/g/day; 1 May – 7 June) during 1994 – 2013 in western Lake Erie.
Figure 3.5. Relationship between the average total length (TL; mm) of juvenile walleye captured in August and the log$_e$-transformed August trawl catch per hectare of juvenile walleye (Age-0 Recruitment; catch per hectare) during 1994 – 2013 in western Lake Erie.
CHAPTER 4

PREY QUANTITY AND QUALITY DURING THE LARVAL PERIOD REGULATES RECRUITMENT:
EVIDENCE FOR THE MATCH-MISMATCH HYPOTHESIS IN A LARGE LAKE ECOSYSTEM

The importance of processes operating during the larval stage to recruitment and subsequent cohort success has long been recognized in marine organisms, particularly for species with prolonged pelagic larval stages (Hjort 1914, Cushing 1975, 1990, Houde 1987, 1989). Several hypotheses have been generated to explain how larval size and growth can influence larval survival. For example, the growth-mortality hypothesis (GMH; Ware 1975; Shepard and Cushing 1980) predicts that as larvae increase in size, mortality rate should decrease. The rationale for this hypothesis can be explained by consideration of three related recruitment hypotheses: 1) bigger is better (Miller et al. 1988); 2) stage-duration (Chambers and Leggett 1987); and 3) growth-selective predation (Takasuka et al. 2003). Small larvae typically are more susceptible to starvation and predation (i.e., bigger is better) and endure an extended larval period (i.e., stage duration) that can increase exposure to predators. Additionally, larvae with slow growth rates are more likely to be preyed upon than faster growing larvae (i.e., growth-selective predation occurs).
Implicit to the GMH is the assumption that enhanced foraging success during the larval stage will lead to increased growth and body size (Anderson 1988). Factors that influence the overlap of larval fish and their zooplankton prey have been shown to play an important role in governing survival (e.g., Cushing 1990; Runge et al. 1999; Beaugrand et al. 2003; Castonguay et al. 2008). For example, Cushing’s Match-Mismatch Hypothesis (MMH; Cushing 1975), which states that larval fish recruitment is driven by their degree of temporal overlap with their planktonic prey, has been the basis for a great deal of recruitment research in marine systems. The MMH, as originally proposed, was mainly concerned with the temporal overlap of predator and prey. Abundance of prey was later stressed as an important consideration when examining potential matches or mismatches, as predator consumptive demand could dominate in a perfectly timed, yet low prey production year, and lead to poor recruitment (Durant et al. 2005). The additional consideration of prey abundance to the MMH is sensible as low prey availability can reduce larval survival and subsequent recruitment through increased risk of direct mortality via starvation or indirectly through predation (Frank and Leggett 1986; Rice et al. 1987; Miller et al. 1988).

While much research has tested the GMH (and its three associated hypotheses) and MMH in marine settings, with strong linkages between prey availability, larval growth, and recruitment being documented for many fish populations (e.g., Beaugrand et al 2003; Robert et al. 2007; Castonguay et al. 2008; Murphy et al. 2014), far fewer studies have explored the relevance of marine recruitment hypotheses in freshwater
systems (Ludsin et al. 2014; Pritt et al. 2014). This research gap is most conspicuous in the largest lakes of the world (e.g., “inland seas” such as the Laurentian Great Lakes). Many ecologically and economically important large-lake fishes have life-history characteristics (e.g., high fecundity, no parental care, lengthy planktivorous pelagic larval period, high early-life mortality) quite similar to those of well-studied ecologically and economically important pelagic marine species (Ludsin et al. 2014; Pritt et al. 2014). In fact, despite a growing number of early life recruitment investigations in the Great Lakes basin (Ludsin et al. 2014; Pritt et al. 2014), I am unaware of any empirical study that has explicitly sought to test the relevance of both the GMH and MMH to inter-annual recruitment variability in any Great Lakes fish population.

Toward filling this void, I explored whether the GMH and MMH could help explain inter-annual recruitment variability in Lake Erie (USA-Canada) walleye Sander vitreus, a population that 1) supports Lake Erie’s most important recreational fishery and second largest commercial fishery (Lake Erie Walleye Task Group, WTG, 2014), 2) has a lengthy (i.e., >18 d; Houde and Zastrow 1993) pelagic, planktivorous larval period similar to many pelagic marine fishes, and 3) has demonstrated high (i.e., > 1,000-fold) inter-annual fluctuations in recruitment to age-0, which is a strong predictor of future recruitment to the fishery at age 2 ($R^2 = 0.89$; WTG 2012). This population also is ideal for study because recruitment of walleye to the age-0 juvenile stage, as measured in August of each year, has been consistently low since 2003 (WTG 2014) for reasons that remain enigmatic.
To test the central hypothesis that inter-annual variability in Lake Erie walleye recruitment is driven by zooplankton availability, through its direct effect on larval growth, I compared zooplankton (prey) abundance and size, larval walleye abundance, foraging, growth rate, and juvenile recruitment between two time periods: 1) 1994-1999, a period with weak, moderate, and strong annual recruitment events; and 2) 2011-2013, a period of consistently below average recruitment events (WTG 2014). In testing the hypothesis, I also created models to best explain variation in age-0 recruitment that included indicators of zooplankton quality and quantity as well as larval growth rates to determine the level of support for the MMH and GMH in a large lake ecosystem.

**METHODS**

The study was conducted in the southern portion of the western basin of Lake Erie, which is home to several extremely productive walleye spawning areas (Olson and Scidmore 1962) and contains the highest density of walleye in the Laurentian Great Lakes (Hubbs and Legler 2004). Crustacean zooplankton and larval walleye were collected weekly during late March through mid-April at 4 to 30 sites per week (mean = 19) during 1994-1999 and 2011-2013. These are the only datasets, to my knowledge, currently available that contain information on both larval walleye and crustacean zooplankton.
**Field Collections**

Zooplankton were collected via vertical hauls with either a 153 µm (1994-1999) or 64 µm (2011-2013) mesh net. Zooplankton samples were preserved in a buffered sugar-formalin solution for later identification (Pennak 1978; Balcer et al. 1984) and counting. When processing zooplankton, a minimum of two subsamples were counted and identified until at least 150 individuals (150-per-sample method; 1994-99) or 100 of the most abundant crustacean zooplankton taxa excluding rotifers, nauplii, and veligers (100-per-species method; 2011-13) were counted (Mack et al. 2012). Individual zooplankton were identified to the lowest taxonomic level in the 100-per-species method (most to species), whereas cladocerans were identified to genus and copepods were identified as calanoid, cyclopoid, harpacticoid copepodes, or nauplii in the 150-per-sample method. Zooplankton total lengths, an indicator of zooplankton quality (Beaugrand et al. 2003), were measured on the first 20 individuals encountered, using an ocular micrometer, and later converted lengths into mm (nearest 0.01 mm).

A comparison of the zooplankton counting methods, 100-per-species versus the 150-per-sample (Mack et al. 2012), revealed no differences in the number of individuals counted or precision of counts ($P > 0.05$ for both). Further, while the 64-µm mesh net retained more rotifers and nauplii than the 153 µm mesh net ($P < 0.008$), these differences disappeared ($P = 0.39$) when rotifers and nauplii were excluded from zooplankton counts (Mack et al. 2012). Thus, I excluded these taxa from the analysis,
which also is justified given that larval walleye typically do not consume rotifers and nauplii (Mathias and Li 1982; Mayer and Wahl 1997).

Walleye were collected during daylight hours at the same sites as zooplankton, either on the same day as the zooplankton (1996-99, 2011-2013) or within 24-h of zooplankton sampling (1994-1995). During 1994-1999, a 1 m X 2 m neuston net with 583-μm mesh netting was used to sample larvae, whereas during 2011-13, paired 0.6-m diameter bongo nets with 500-μm mesh netting were employed. Nets were towed in the upper 2 m of the water column at about 1m/sec for 5 (1994-1999) or 10 min (2011-2013). Flow meters positioned at the mouth of each net provided estimates of the water volume sampled. Larvae were preserved in 95% ethanol for later identification using characteristics described by Auer (1982) and total length measurement (TL; nearest 0.1 mm). The daily growth rate (G) of larvae was estimated with the equation, 

\[ G = \frac{(TL_t - TL_0)}{t} \]

where \( TL_t \) is the mean TL of fish on day \( t \), \( TL_0 \) is the mean TL on the previous sampling day, and \( t \) is the number of days between samples. Larval walleye stomach contents were examined in 1994-1995 \( (n= 112 \) and 55 respectively) and 2011-2013 \( (n= 248, 228, \) and 174 respectively) with a dissecting microscope, noting the presence or absence of prey items to calculate feeding incidence.

The Ohio Department of Natural Resources-Division of Wildlife generates an index of age-0 walleye abundance \( (\text{no. ha}^{-1}) \) by conducting a bottom trawl survey for juveniles during late August across western Lake Erie \( (41 \text{ sites}; \text{WTG} \ 2014) \). I used the index of age-0 juvenile abundance to estimate recruitment to the fishery, as this index
has been shown to be a strong predictor of abundance at age 2 \( (r^2 = 0.89) \), at which time walleye enter the fishery (WTG 2012).

**Index of Excess Zooplankton**

To examine if zooplankton densities could be limiting to walleye production (i.e., a mismatch), I calculated an index of excess zooplankton. For a given day of zooplankton samples, I first converted zooplankton biomass (µg L\(^{-1}\)) into daily production estimates (g m\(^{-3}\) day\(^{-1}\)), using taxon specific equations (Frost 1997):

\[
\text{Eq. 1} \quad \text{COPEPOD} = 0.0386 \times [(\text{BIOM}/1000)^{0.9599}] \times (1.0860^{\text{TEMP}}); \quad n = 191, \quad r^2 = 0.98
\]

\[
\text{Eq. 2} \quad \text{BOSMINA} = 0.0587 \times [(\text{BIOM}/1000)^{0.9931}] \times (1.0685^{\text{TEMP}}); \quad n = 172, \quad r^2 = 0.99
\]

\[
\text{Eq. 3} \quad \text{DAPHNIA} = 0.0750 \times [(\text{BIOM}/1000)^{0.9548}] \times (1.0997^{\text{TEMP}}); \quad n = 168, \quad r^2 = 0.99
\]

where \( \text{TEMP} \) is the average water temperature \( (^{\circ}\text{C}, \text{depth} = 1\text{m}) \) and \( \text{BIOM} \) is the taxon specific biomass (µg L\(^{-1}\)) at each sampling location on each day (Frost 1997). Relationships among crustacean zooplankton production and biomass, and water temperature were developed from western Lake Erie data. I then calculated daily walleye consumption of crustacean zooplankton (g g\(^{-1}\) d\(^{-1}\)) using a bioenergetics model (Kitchell et al. 1977) with parameters developed for larval walleye (Madon and Culver 1993; Table 4.1, 4.2):

\[
\text{Eq. 4} \quad \text{CONSUMP} = C_{\text{max}} \times f (T) \times P
\]

where \( C_{\text{max}} \) is the maximum mass-specific feeding rate (g g\(^{-1}\) d\(^{-1}\)), \( f (T) \) is a temperature-dependent function, and \( P \) is the proportion of maximum consumption (Table 4.1). I
calculated consumption at maintenance ration (i.e., no growth was occurring) based on
the initial wet mass (g) for field captured walleye (from TL; Rose et al. 1999) by adjusting
\( P \). By doing so, I estimated the minimum amount of food necessary to maintain life. I
calculated mean maintenance consumption for walleye captured at each site, multiplied
the value by walleye density at each site (no. \( m^3 \)), and then summed the consumption
occurring at each site on each date to estimate walleye population consumption at each
site for each date (g \( m^{-3} \) day\(^{-1} \)). As a final step, I subtracted daily walleye consumption
from daily zooplankton production for each site on each date to obtain an index of
excess zooplankton. I then averaged the index of excess zooplankton by week and
averaged the weeks together to obtain a yearly index for excess zooplankton production
(g \( m^{-3} \) day\(^{-1} \)). A value less than zero would indicate that walleye consumption exceeded
zooplankton production; while a value greater than zero would indicate that
zooplankton production exceeds walleye consumption. A value at zero would indicate a
balance between walleye consumption and zooplankton production.

Statistical analyses

For the analyses, I used zooplankton density and size information only from
periods during which larval walleye were expected to be zooplanktivorous, which was
determined from field collections and varied each year (Table 4.3; overall range: late-
March to mid-June). Zooplankton density and size, as well as walleye density and the
index of excess zooplankton, were averaged first by week, with weeks averaged to
obtain one value per year. For the analysis on zooplankton size, I analyzed calanoid and
cyclopid copepods separately, and divided cladocerans into two groups (*Daphnia* spp.
and *Bosmina* spp.), as size differences between these taxa were substantial. I checked all
datasets to ensure that conditions of normality were met, and when they were not, a
transformation was applied. Walleye density, the index of recruitment, and the index of
excess zooplankton were log$_e$ transformed.

I compared the two different sampling periods (1994-1999 versus 2011-2013)
using two-sample *t*-tests to examine potential changes in zooplankton and walleye
densities as well as larval walleye growth rates, feeding incidence, and the index of
excess zooplankton. Because I ran multiple tests (*n* =5), I used a Bonferroni adjustment
of the significance level of each individual test (*α* = 0.05/5 = 0.01) to maintain an overall
significance level of *α* = 0.05.

To identify the most parsimonious predictive model of age-0 walleye recruitment
and to determine if variables associated with either the MMH or GMH were better at
explaining recruitment; I used corrected Akaike’s Information Criterion (*AIC$_c$*) (Burnham
and Anderson 1998). These analyses were conducted without 1995 in the dataset
because Roseman et al. (1996) showed that recruitment during this year was driven by
destructive high-wind events and slow spring warming rates that caused high mortality
during the egg stage (i.e., I knew *a priori* that the GMH and MMH would not be relevant
to understanding recruitment during this year). The predictors included mean larval
walleye growth rate (i.e., indicator of GMH), mean total density of crustacean
zooplankton, and mean sizes of *Daphnia* spp., *Bosmina* spp., cyclopoids, and calanoids as well as the mean index of excess zooplankton (i.e., indicator of MMH) for each year. I considered zooplankton density as a quantitative indicator of food quality and zooplankton size as a qualitative indicator (*sensu* Beaugrand et al. 2003). I considered univariate models, and models that included a mean size of an individual zooplankton taxon paired with mean zooplankton density (Table 4.4). I used least-squares linear regression to obtain coefficients of determination.

**RESULTS**

Significant changes in zooplankton availability between periods affected larval walleye growth. Mean densities of zooplankton available to larvae (i.e., prey quantity) were significantly lower in 2011-2013 than in 1994-1999 (*t*(5) = 4.42, *P* = 0.007; Figure 4.1, Table 4.5). I found a significant difference in larval walleye growth rates (*t*(5) = 2.29, *P* = 0.003) and the index of excess of zooplankton (*t*(7) = 5.56, *P* = 0.001; Table 4.5), with both greater during the 1990s. Finally, neither the densities of larval walleye (*t*(7) = 1.57, *P* = 0.159; Figure 4.2, Table 4.3) nor the feeding incidence (*t*(3) = -4.28, *P* = 0.023; Table 4.5) differed between periods.

I found several strong predictors of age-0 juvenile abundance, including four top models from AICc. Three of the four best models (i.e., ΔAICc < 2) were univariate models with *Daphnia* spp. size, calanoid copepod size, or cyclopoid copepod size, which all had very strong, positive relationships with age-0 walleye recruitment (e.g., Figure 4.3; Table
The model with the most weight included both calanoid copepod size and zooplankton density and explained 96% of the variance in age-0 recruitment (Table 4.4). Thus, all of the top models included predictors of zooplankton quality, with one model also including zooplankton quantity. The yearly index of excess zooplankton was the fifth best model (Table 4.4) and exhibited a strong, positive relationship with age-0 recruitment (Figure 4.4). Larval walleye growth rate, on its own, proved to be a poor indicator of age-0 recruitment, performing about as well as the null model (Table 4.4).

**DISCUSSION**

Recruitment to age-0 was correlated with prey quantity and quality during the larval stage, demonstrating support for the MMH in a large freshwater system. Models that contained either zooplankton density or size explained a substantial amount of variance in the index of recruitment. All relationships were strongly positive indicating that higher densities of large zooplankton available to larval fish were correlated with increases in the recruitment index. I did not find support for the GMH in this study. While growth rates were significantly lower during 2011-2013 when recruitment also was poor, overall growth by itself proved to be a weak predictor of recruitment. Previous studies in the marine literature have shown strong positive correlations between recruitment and early growth (e.g., Campana 1996; Bergenius et al. 2002; McCormick and Hoey 2004), whereas others have reported an absence (e.g., Bailey et al. 1996) or a negative relationship (e.g., van der Veer et al 1994; Ringuette et al. 2002).
Correlative methods can be severely limited in their ability to separate size-selective mortality from other sources of inter-annual variability in survivorship, which may contribute to the lack of agreement found in GMH studies that rely on correlations (Sogard 1997). Additionally, selection pressure also should be considered when testing the relevance of the GMH. Robert et al. (2007) demonstrated that under strong selection for fast growth during the larval period (i.e., early removal of slow growers by predation is occurring) poor recruitment resulted even though fast larval growth rates of survivors were exhibited. Thus, to help clarify the role of the GMH in recruitment, the severity of selection pressures should also be considered.

The most surprising finding is the significant decrease in crustacean zooplankton density between the two study periods. Similar trends in crustacean zooplankton densities are apparent in lakes Michigan, Huron, and Ontario, with the availability of spring/early summer zooplankton declining up to 90% (Graeb et al. 2004; Barbiero et al. 2009; Johannsson and Bowen 2011). My study demonstrates an 85% reduction in spring crustacean zooplankton between 1994-1999 and 2011-2013 for Lake Erie, which contrasts documented increases in crustacean zooplankton during late summer in Lake Erie, owing to its re-eutrophication (Bunnell et al. 2014, Scavia et al. 2014). Given my results, Lake Erie’s re-eutrophication (Scavia et al. 2014) may only benefit summer spawners via enhanced zooplankton prey production, not spring ones like walleye and yellow perch (*Perca flavescens*), another ecologically and economically important fish in this system.
Decreases in spring crustacean zooplankton availability to larvae could be expected to decrease due to human-driven ecosystem change. First, continued point-source phosphorus abatement programs implemented as part of the Great Lakes Water Quality Agreement has reduced nutrient input into the lake (Dolan 1993), which in turn has reduced phytoplankton production (Bunnell et al. 2014). Second, the establishment and continued spread of non-native suspension (filter) feeders (i.e., zebra and quagga mussels, *Dreissena polymorpha* and *D. bugensis*, respectively; Hebert et al. 1989; May and Marsden 1992) also has likely been reducing plankton populations in Lake Erie (Holland 1993; Nicholls and Hopkins 1993). Finally, the establishment of white perch, *Morone Americana*, which feeds on zooplankton during all life stages (Guzzo et al. 2011) and has become the most abundant fish in Lake Erie (ODW 2014) could play a role in zooplankton reduction. Future research should focus on factors influencing zooplankton quantity and quality, especially during spring when zooplanktivorous larval fish species are at large.

While zooplankton density decreased between study periods, the density of larval walleye captured remained about the same. In turn, per capita zooplankton density would be expected to decline, thus reducing encounter rates between larval predators and zooplankton prey. Given that small larvae are already disadvantaged by relatively weak locomotive capabilities (Humphrey et al. 2012) and poor visual acuity (Hairston et al. 1982), low densities of zooplankton prey would be expected to increase the vulnerability of larvae to predation and starvation mortality (Frank and Leggett
Indeed, I found a reduction in growth rates and age-0 recruitment during 2011-2013 relative to the earlier period, providing evidence for bottom-up controls dictating recruitment processes due to a decrease in the quality and quantity of zooplankton.

The sizes (i.e., quality) of preferred prey items may offset deleterious effects of reduced prey densities. For larval walleye, copepods are the preferred prey for individuals 7 – 19 mm TL (Houde 1967; Graham and Sprules 1992). Herein, mean copepod size was important in 3 of the top 4 models that explained variation in age-0 recruitment, with larger copepods leading to higher rates of recruitment. In 1997, zooplankton densities were similar to 2011-2013; however, much higher age-0 recruitment was exhibited. The quantity and quality of copepods in 1997 was large, possibly mitigating the effects of an overall reduction in zooplankton densities by increasing age-0 recruitment through more efficient energy allocation (Hunter 1980; Buckley and Durbin 2006). Generally, copepods have a higher caloric value than cladocerans (Cummins and Wuycheck 1971), but are much harder for larval fish to capture owing to their higher swimming speeds and evasive maneuvers that cladocerans lack (Kerfoot et al. 1980). Additionally, copepods are more difficult for larval fish to see due to their low width to length ratio (Mayer and Wahl 1997). As a result, larval walleye orient more frequently towards large cladocerans, but have higher capture efficiencies with small cladocerans and copepods (Mayer and Wahl 1997).

Further, copepods nearly exclusively accumulate the fatty acid docosahexaenoic acid
(DHA; Farkas 1979), which is important for neural tissue development and somatic growth (Castell et al. 1994). In a laboratory experiment, Mayer and Wahl (1997) demonstrated that larval walleye 11-17 mm TL feeding on a high density (100 organisms per liter) of mixed zooplankton taxa exhibited more rapid growth than larvae fed only cladocerans. Copepods may be the preferred prey due to their increased caloric content and DHA, but they are difficult to capture, and therefore a mixed assemblage provides larval fish with both the calories and fatty acids for rapid growth, which is important for larval survival (GMH; Miller et al. 1988). However, when numbers of zooplankton are low, I suspect that the role of preferred, large-sized, energy dense prey with high DHA content (i.e., copepods) becomes even more important and can be the difference between a poor age-0 recruitment year (i.e., 2011, 2012, 2013) and a moderate age-0 recruitment year (i.e., 1997). Additional research into the effects of zooplankton composition and size under low zooplankton density scenarios should help decipher if quality of zooplankton can mitigate mortality in larval fish.

Explaining patterns of population variability is difficult due to the multiple, interrelated causes. Recently, it has been stressed that when investigating patterns of population variability several hypotheses should be pursued (Houde 2008; Hare 2014) and that sufficient taxonomical knowledge of larval fish prey, particularly of preferred prey, should be employed (Robert et al. 2014). I also contend that temporal trends of both predator and prey are important to consider when explaining recruitment mechanisms. I considered prey availability only when larvae were zooplanktivorous,
instead of using a fixed period for each year that represented the historical timing of larval fish abundance. In doing so, I guaranteed an analysis of the temporal overlap of larval fish with zooplankton in all years, which accounted for environmental anomalies. For example, 2012 had an extremely warm spring, and the of larval walleye abundances shifted earlier by four weeks from historical records. If I had used a fixed period to examine zooplankton dynamics on larval walleye in 2012, the relationships would have been misinformed. By considering multiple hypotheses and taxonomical knowledge of prey, while also bearing in mind temporal trends, I was able to discern in 8 of the 9 years (i.e., not in 1995) that zooplankton quantity and quality regulated age-0 recruitment of Lake Erie walleye.

Recruitment to age-0 in Lake Erie walleye is heavily influenced by inter-annual variation in prey quantity and quality. My research revealed strong linkages between zooplankton quantity and quality to larval walleye growth and subsequent age-0 recruitment. Since age-0 recruitment is an excellent indicator of the adult population two years later, mortality processes occurring during the larval stage are critically important to the overall success of the population. My findings demonstrate that the Match-Mismatch Hypothesis, a marine-derived hypothesis, is applicable to a freshwater species and points to the need for more cross-fertilization of ideas between marine and freshwater scientists.
REFERENCES


Enclosures. Marine Ecology Progress Series 34:11-22.


Ohio Division of Wildlife. 2014. Ohio's Lake Erie Fisheries 2013. Ohio Department of Natural Resources, Division of Wildlife, Lake Erie Fisheries Units, Fairport and Sandusky.


Robert, D., H. M. Murphy, G. P. Jenkins, and L. Fortier. 2014. Poor taxonomical knowledge of larval fish prey preference is impeding our ability to assess the existence of a "critical period" driving year-class strength. Ices Journal of Marine Science 71:2042-2052.


\[ \text{CONSUMP} = C_{\text{max}} \times f(T) \times P \]
\[ C_{\text{max}} = CA \times W^{CB} \]

\[ f(T) = V^x \times \exp \left( \frac{x(1-V)}{2} \right) \]

\[ V = \frac{(CTM - T)}{(CTM - CTO)} \]
\[ X = Z^2 \times \left( 1 + \left( \frac{1 + 40}{Y} \right)^{0.5} \right)^2 / 400 \]
\[ Z = \ln(CQ) \times (CTM - CTO) \]
\[ Y = \ln(CQ) \times (CTM - CTO + 2) \]

Table 4.1. Model equations used to estimate larval walleye consumption (Kitchell et al. 1977).
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<td>CTM</td>
<td>Maximum temperature for consumption</td>
<td>28</td>
<td>°C</td>
</tr>
<tr>
<td>CTO</td>
<td>Optimal temperature for consumption</td>
<td>22</td>
<td>°C</td>
</tr>
</tbody>
</table>

Table 4.2. Model parameters used to estimate larval walleye consumption (Madon and Culver et al. 1993).
<table>
<thead>
<tr>
<th>Year</th>
<th>Mean Larval Length (mm)</th>
<th>Dates Used</th>
<th>Feeding Incidence</th>
</tr>
</thead>
<tbody>
<tr>
<td>1994</td>
<td>10.9 ± 4.0</td>
<td>5/2 - 5/30</td>
<td>81.2</td>
</tr>
<tr>
<td>1995</td>
<td>11.2 ± 3.5</td>
<td>5/12 - 6/5</td>
<td>85.5</td>
</tr>
<tr>
<td>1996</td>
<td>11.0 ± 3.5</td>
<td>4/24 - 6/10</td>
<td>n/a</td>
</tr>
<tr>
<td>1997</td>
<td>11.1 ± 4.8</td>
<td>4/28 - 6/10</td>
<td>n/a</td>
</tr>
<tr>
<td>1998</td>
<td>10.3 ± 2.8</td>
<td>4/14 - 5/27</td>
<td>n/a</td>
</tr>
<tr>
<td>1999</td>
<td>12.1 ± 4.2</td>
<td>5/3 - 5/28</td>
<td>n/a</td>
</tr>
<tr>
<td>2011</td>
<td>9.2 ± 0.7</td>
<td>5/4 - 5/25</td>
<td>42.8</td>
</tr>
<tr>
<td>2012</td>
<td>8.3 ± 1.1</td>
<td>3/29 - 5/1</td>
<td>9.1</td>
</tr>
<tr>
<td>2013</td>
<td>9.4 ± 1.8</td>
<td>4/22 - 5/21</td>
<td>32.2</td>
</tr>
</tbody>
</table>

Table 4.3. Characteristics of larval walleye in western Lake Erie during 1994-1999 and 2011-2013. Mean total length (mm) ± 1 SD, dates used for the analysis (i.e., when larval walleye were at large in the system) and feeding incidence (% of stomachs with food present; note: larval stomachs were not examined in 1996-1999).
<table>
<thead>
<tr>
<th>Model</th>
<th>ΔAICc</th>
<th>$w_i$</th>
<th>$R^2$ w/o 1995</th>
<th>$R^2$ w/ 1995</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.0</td>
<td>0.33</td>
<td>0.96</td>
<td>0.79</td>
</tr>
<tr>
<td>2</td>
<td>0.5</td>
<td>0.25</td>
<td>0.87</td>
<td>0.67</td>
</tr>
<tr>
<td>3</td>
<td>0.6</td>
<td>0.24</td>
<td>0.87</td>
<td>0.78</td>
</tr>
<tr>
<td>4</td>
<td>1.9</td>
<td>0.13</td>
<td>0.85</td>
<td>0.67</td>
</tr>
<tr>
<td>5</td>
<td>5.3</td>
<td>0.02</td>
<td>0.77</td>
<td>0.36</td>
</tr>
<tr>
<td>6</td>
<td>6.2</td>
<td>0.02</td>
<td>0.70</td>
<td>0.63</td>
</tr>
<tr>
<td>7</td>
<td>7.2</td>
<td>0.01</td>
<td>0.70</td>
<td>0.35</td>
</tr>
<tr>
<td>8</td>
<td>9.5</td>
<td>0.00</td>
<td>0.88</td>
<td>0.69</td>
</tr>
<tr>
<td>Null</td>
<td>12.7</td>
<td>0.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>12.9</td>
<td>0.00</td>
<td>0.40</td>
<td>0.22</td>
</tr>
<tr>
<td>10</td>
<td>13.2</td>
<td>0.00</td>
<td>0.81</td>
<td>0.51</td>
</tr>
<tr>
<td>11</td>
<td>14.9</td>
<td>0.00</td>
<td>0.22</td>
<td>0.23</td>
</tr>
</tbody>
</table>

Table 4.4. Models for predicting age-0 walleye recruitment using the Akaike Information Criterion method, ordered from best (i.e., lowest $ΔAIC_c$) to worst including $AIC_c$ weights ($w_i$). I excluded 1995 from AICc analyses because Roseman et al. (1996) showed that recruitment during this year was driven by destructive high-wind events and slow water warming rates that caused high mortality during the egg stage. For comparison, I have included $R^2$ values with and without 1995.
<table>
<thead>
<tr>
<th>Sample Period</th>
<th>Zooplankton Density</th>
<th>Walleye Density</th>
<th>Walleye Growth</th>
<th>Index of excess Zooplankton</th>
</tr>
</thead>
<tbody>
<tr>
<td>1994-99</td>
<td>16.7 ± 7.8</td>
<td>2.1 ± 2.8</td>
<td>0.4 ± 0.1</td>
<td>0.04 ± 0.03</td>
</tr>
<tr>
<td>2011-13</td>
<td>2.6 ± 0.4</td>
<td>0.5 ± 0.5</td>
<td>0.2 ± 0.1</td>
<td>0.0005 ± 0.0008</td>
</tr>
</tbody>
</table>

Table 4.5. Means and standard deviations of zooplankton density (no. L⁻¹), larval walleye density (no. 100m³), larval walleye growth (mm day⁻¹) and the index of excess zooplankton (g m⁻³ day⁻¹) in western Lake Erie during 1994-1999 and 2011-2013.
Figure 4.1. Mean crustacean zooplankton densities during the larval walleye production period in western Lake Erie during 1994-1999 and 2011-2013. Annual means were calculated by first averaging zooplankton density across sites within a week and then averaging across weeks (n= 4-7) within a year.
Figure 4.2. Larval walleye densities during the spring in western Lake Erie during 1994-1999 and 2011-2013 (top panel). Annual means (± 1 SD) were calculated by first averaging larval walleye densities across sites within a week and then averaging across weeks ($n=4$-$7$) within a year. Recruitment index for walleye from 1994-1999 and 2011-2013 (bottom panel). Index is the number of juvenile fish captured in August in Ohio waters of western Lake Erie by the Ohio Department of Natural Resources-Division of Wildlife during their annual surveys.
Figure 4.3. Relationship between log$_e$(recruitment index) and calanoid copepod size in western Lake Erie during 1994-1999 and 2011-2013. Regression line is for data excluding 1995. Note log scale used on the y-axis.

With 1995: $F_{1,7} = 25.49, P = 0.001$
Without 1995: $F_{1,6} = 40.15, P = 0.0007$
Figure 4.4. Relationship between log\(_e\)(recruitment index) and log\(_e\)(index of excess zooplankton) in western Lake Erie during 1994-1999 and 2011-2013. The regression line is for data excluding 1995. Note log scale used on x and y-axis.

With 1995: \(F_{1,7} = 3.94, P = 0.09\)
Without 1995: \(F_{1,6} = 19.58, P = 0.004\)
CHAPTER 5

LARVAL GROWTH AS A LIMITER OF RECRUITMENT

Larval survival in many fish populations is exceedingly low and conceivably predictable based on larval size. Large larvae are generally less susceptible to gape-limited predators (Miller et al. 1988) and have greater locomotive capabilities for predator evasion (Takasuka et al. 2003, 2004) than small larvae. Larvae that exhibit fast growth spend fewer days in the larval stage (Chambers and Leggett 1987). Advantages of large size also include resistance to starvation (Miller et al. 1988) and the ability to make ontogenetic diet shifts to more energetically profitable prey (Ludsin and DeVries 1997); faster growth decreases the time necessary to acquire these benefits. Given these many advantages of large size in fish larvae, one can predict that fast growth during the larval period should translate to increased survival and strong recruitment.

Empirical evidence for fast growing larvae surviving disproportionately better to the juvenile stage has been found in numerous studies (e.g., Post and Prankevicius 1987, Campana 1996; Meeken and Fortier 1996; Hare and Cowen 1997; Bergenius et al. 2002; McCormick and Hoey 2004; Buckley and Durbin 2006; Islam et al. 2010; Murphy et al. 2013). However, size-selective mortality also is not universal, nor is it always in the same direction. Some researchers have found no evidence for size-selective mortality (e.g.,
Bailey et al. 1996; Sabo and Orth 1996; Urpanen et al. 2005), whereas others have shown selection against fast growing larvae (e.g., Litvak and Leggett 1992; Pepin et al. 1992; van der Veer et al. 1994; Ringuette et al. 2002; Sponaugle et al. 2011).

Additionally, evidence exists for size-selective mortality occurring in one year, but not others within the same population (Good et al. 2001).

Although fast growth should lead to high recruitment, the relationship can be obscured in field data. In systems or years when predation pressure is low (e.g., size selectivity may be evident late in the larval period or not at all), we would not see as much of a predation-induced shift in larval size distributions, which could result in a large cohort with an intermediate mean size. In systems in which predation pressure is high (e.g. begins early, lasts for long periods), we would expect to see the size selectivity of the predators result in strong culling of the smaller, slower-growing part of the cohort. This can result in a small cohort of fish with a large mean size. Thus, field patterns could produce the counter-intuitive result of a negative relationship between mean size or growth-rate and recruitment strength.

Through the consideration of predation pressure, as measured by the selection for fast growth, one can begin to tease apart the importance of size-selective mortality in a population. For example, through the use of otoliths, Robert et al. (2007) back-calculated incremental growth over the first 20 d of life for both the original larval population and those that survived as juveniles in Atlantic mackerel Scomber scombrus. Faster growth during the larval period was found in surviving juveniles relative to the
original pool of larvae in 3 of 4 years. The one year that resulted in good recruitment, however, also included weak size-selection that began late in the larval period and lasted only a few days (Robert et al. 2007). In years when size-selection pressures (i.e., predation) were strong, slow growing individuals were culled from the population early in life or for a relatively long period (i.e., 8-16 d) and resultant recruitment was weak (Robert et al. 2007). Additional work by Murphy et al. (2014) on snapper *Pagrus auratus* demonstrated that when selective pressures are weak or absent, high recruitment will ensue, but when higher selective pressures are apparent, low to average recruitment will occur. Thus, it is also important to consider the timing and duration of selection pressures occurring during the larval stage in tandem with larval growth trajectories when considering the influence of larval growth on recruitment strength.

Herein, I tested whether larval growth-rate selection was occurring within individual annual cohorts of walleye *Sander vitreus* in Lake Erie and whether growth-rate selection predicted recruitment strength across those cohorts. I examined the growth rates of the original larval population and surviving juveniles over the first 20 d of life for three different annual cohorts. I predict that in years when slow larval growth was exhibited, weak recruitment would occur independent of size selection pressures. The combination of fast growth and weak selection pressures during the larval period would result in high recruitment, whereas strong selection pressures would lead to low recruitment despite evidence for fast larval growth (Table 5.1).
METHODS

I first determined if growth rate is directionally selected during the early life history of walleye by comparing growth rates during the first 20 d of life between recently hatched larvae and the surviving juveniles, over three years (2011-2013). Larval walleye were collected weekly from western Lake Erie from late March through May at 12 to 24 fixed sites per week (mean = 21 sites). Paired 0.6-m diameter bongo nets with 500-µm mesh netting were towed in the upper 2 m of the water column at 1 m/s for 10 min. Juvenile walleye were collected from western Lake Erie in late summer of each year by the Ohio Department of Natural Resources-Division of Wildlife (ODNR-DOW) and the Ontario Ministry of Natural Resources and Forestry (MNRF) as part of their annual assessment surveys. A bottom trawl with a 10.7-m headrope and 6.4-mm cod-end mesh was towed for 10 to 15 min at 0.8 m per sec at fixed sites across the western basin (ODNR-DOW, n = 41 sites; MNRF, n = 18). All sites were sampled once per month. Juvenile walleye captured in late July through late September were included in our analyses for each year.

Larval and juvenile walleye were measured for total length (TL; nearest 1 mm), and sagittal otoliths were removed for age and growth determination. Formation of daily increments on otoliths was previously validated in hatchery-reared walleye up to 42 d old (Parrish et al. 1994). I, therefore, determined the daily age of larvae, but not juveniles, as juveniles were 3 to 7 mos of age, based on collection times. I adhered otoliths on glass slides using thermoplastic adhesive (Crystalbond). For juveniles, I used
progressively finer lapping film (1, 3, and 9 μm) to polish otoliths until the origin, hatch mark, and daily growth rings for at least the first 20 d of life were discernible. I estimated daily growth rates (mm/d) for the entire life of captured larvae and for the first 20 d of life in juveniles.

Two different readers, without knowledge of the date and location of capture, made independent measurements on all otoliths. We immersed otoliths in oil under 50x (larvae) or 100x (juvenile) magnification and measured daily increment width along the longest axis possible using digital analysis software (NIS-Elements microscope imaging software; Nikon®). We first measured from the otolith nucleus to the hatch mark, with individual rings measured between the outer edge of the hatch mark and the outer edge of the otolith (Reichert et al. 2010). In larvae, I calculated the otolith radius as the sum of measurements from the nucleus to the outer edge, while age was determined by summing the total number of daily increments.

If the first two reads for larval otoliths were within 3 d, I arbitrarily chose the oldest read as the final age in all analyses (i.e., the read that resulted in the slower growth rate, following Ludsin and DeVries 1997 and Reichert et al. 2010). If the first two reads differed by more than 3 d, the larval otolith was aged and measured by a third reader. If no two ages were within 3 d of one another, the larval otolith was discarded (2011, n = 3; 2012, n = 4; 2013, n = 2). For larvae, the last increment to the edge of the otolith was not included in analyses, as it was not a complete day of life. Additionally, for the analyses, I only considered larvae that were ≥ 8 mm in TL, given that smaller
individuals usually contained yolk sacs and were feeding endogenously (Mathias and Li 1982). Due to low larval sample sizes, I did not include days 16-20 in our statistical analyses (Table 5.2).

For juveniles, if the first two measurements from the nucleus to day 20 on an individual otolith differed by < 12 µm (equivalent to 2-4 d of growth), I used the shortest measurement, a rule consistent with the choice of slower growth rates in the larval estimates. If the first two estimates differed by > 12 µm, then a third reader aged and measured the otolith. If no two ages were within 12 µm of one another, the juvenile otolith was discarded (2011, n = 25 fish; 2012, n = 13 fish; 2013, n = 16 fish).

Because otolith radius, as measured along the longest axis, was correlated with fish TL for larvae in 2011 (n = 132, r = 0.72, P<0.0001), 2012 (n = 54, r = 0.66, P<0.0001), and 2013 (n = 25, r = 0.87, P<0.0001), I used otolith increment width as a proxy for walleye somatic growth. However, I was unable to make inter-annual growth comparisons, given that the slope and intercept of the linear relationship between log$_{10}$-transformed TL and otolith radius differed among years (ANCOVA, P = 0.003; Figure 5.1), suggesting the presence of a growth effect (i.e., varying rates of somatic growth relative to that of the otolith). Thus, I used the biological intercept (BI) method (Campana 1990) to back-calculate length-at-age for larvae, which can eliminate this growth-effect bias. Specifically, the BI method uses an intercept-correcting approach along both X and Y axes using the following equation:

\[ L_t = L_c + (O_t - O_c)(L_c - L_0)(O_c - O_0)^{-1} \]
where $L$ is fish length at age $t$ ($L_t$), at the BI ($L_0$), and at capture ($L_c$), and $O$ is the otolith radius at age $t$ ($O_t$), at the BI ($O_0$), and at capture ($O_c$). To determine $L_0$, I used the intercept from the linear relationship between age (d) and TL (mm) from each year (2011 = 7.74 mm; 2012 = 7.57 mm; 2013 = 7.36 mm). The $O_0$ was the observed distance from the core to hatch check for each individual larva. After back-calculation, I obtained daily growth rates on individuals by subtracting the previous day’s TL from the current day’s TL (e.g., $\Delta L_t = L_t - L_{t-1}$). I averaged all individuals per day to obtain a daily average growth rate, while I took a mean of all daily averages to obtain an index of annual growth rates. I compared annual growth rates with a one-way Analysis of Variance (ANOVA) with post-hoc Tukey’s Honestly Significant Difference (HSD) test. I was unable to back-calculate juvenile TLs in the same manner because the outer edges of the otoliths were polished away such that otolith radius at capture (i.e., $O_c$) could not be measured.

I used repeated-measures ANOVA to determine the effect of age-at-capture on otolith increment width in larval fish. Previous research has suggested that the growth of survivors (i.e., juveniles) over a given age interval should be compared to the growth of the original population (i.e., larvae) from those fish captured immediately at the end of the age interval to avoid the potential effects of directional selection on growth occurring within only a few days (Meeken and Fortier 1996; Robert et al. 2007). For example, when examining day 1 – 5 growth, the growth of survivors should be compared to the growth of larvae that were 6 – 10 days old at capture. To test if larval
age influenced increment width, I designated increment widths, classified by year and 
$\log_{10}$-transformed to meet assumptions of normality and homogeneity of variance, as 
the dependent variable. Increment widths were further categorized into periods of 
early (1-5 d), middle (6-10 d) and late (11-15 d). I considered day within period as a 
repeated measure on larvae. Age-at-capture of larvae also was included in the model. I 
used Akaike’s Information Criterion to evaluate the most appropriate covariance 
structure between potentially correlated measurements. The covariance structures 
compared included first-order autoregressive, unstructured, compound symmetry, and 
variance components.

I also tested for differences between larval and juvenile growth rates within the 
same year over the first 15 d of life using a repeated-measures ANOVA. In the analysis, 
each larva was treated as an independent unit of replication for each year. Otolith 
increment widths for larvae and juveniles were $\log_{10}$-transformed to meet assumptions 
of normality and homogeneity of variances and were then divided into three age 
categories: young (1-5 d), middle (6-10 d) and old (11-15 d), and considered as repeated 
measures on an individual. For each year, I compared larval and juvenile growth 
increments in each age category to determine if significant differences in growth 
existed, suggesting the presence of selective mortality. I used Akaike’s Information 
Criterion corrected for small sample size ($\text{AIC}_c$; Hurvich and Tsai 1989) to evaluate the 
most appropriate covariance structure between potentially correlated measurements. 
The covariance structures compared included first-order autoregressive, unstructured,
compound symmetry, and variance components. For each covariance structure I examined if variance was different between larval and juveniles groups. An $\alpha$-level of 0.05 was used to judge significance in all cases; statistical procedures were performed using the MIXED and UNIVARIATE procedures in SAS version 9.3 (SAS Institute Inc., Cary, NC).

Finally, to determine if patterns in larval growth from a freshwater fish fit recruitment expectations from marine research, I also collected data on recruitment strength for our sample years. The ODNR-DOW generates an index of age-0 walleye abundance (no. ha$^{-1}$) by conducting a bottom trawl survey for juveniles during late August across western Lake Erie (41 sites; WTG 2014). I used the index of age-0 juvenile abundance to estimate recruitment to the fishery, as this index has been shown to be a strong predictor of abundance at age 2 ($R^2 = 0.89$), at which time walleye enter the fishery (WTG 2012).

**RESULTS**

Larval walleye growth rates, back-calculated using otoliths, differed among years ($F_{2,29} = 4.92, P = 0.01$). In all years, daily larval walleye growth rate declined during the first two weeks of life (Figure 5.2). Post-hoc pairwise comparisons using Tukey’s HSD indicated that the larval growth rate was greater during 2011 (0.16 ± 0.02 SD mm/d) than 2012 (0.13 ± 0.02 SD mm/d; Tukey’s HSD; $P < 0.05$); no other pairwise comparisons were significant.
I did not detect an effect of age at capture on growth rates in larval fish. When comparing the growth of larvae during 1-5, 6-10, and 11-15 d of age, I did not find significant selection occurring between ages ($F_{2,247} = 0.56, P = 0.57$). No evidence for an interaction was found between increment width (i.e., proxy for growth rate) and age at capture ($F_{5,247}= 1.13, P = 0.35$) either. Therefore, I was able to pool larval growth increments by day, regardless of their age at capture, for each year in subsequent analyses. I used the first-order autoregressive covariance structure for the analysis, which provided the best fit to these data based on an $AIC_c$ model selection procedure.

When comparing the growth achieved during the larval stage by juveniles to the growth of the original population (i.e., larvae), significant selection occurred for survival of fast-growing larvae in 2012 and 2013, and significant selection for survival of slow-growing larvae was found in 2011. In 2011, surviving juveniles were among the slowest growing larvae relative to the original population during days 6-10 ($t_{345} = 3.97, P< 0.001$) and 11-15 ($t_{345} = 2.64, P = 0.0086$; Figure 5.3A). In 2012, surviving juveniles were among the fastest growing larvae in the original population during days 11-15 ($t_{345} = 2.65, P = 0.0085$; Figure 5.3B). In 2013, surviving juveniles grew faster than the original population during days 1-5 ($t_{345} = 5.97, P< 0.0001$), 6-10 ($t_{345} = 5.34, P< 0.0001$), and 11-15 ($t_{345} = 6.52, P< 0.0001$; Figure 5.3C). I used an unstructured covariance structure with groups pooled for the analysis, chosen through a model-selection procedure.

Overall, size-selective pressures were strong in 2011 and 2013, as they began within the first week of larval life and lasted $> 10$ d. In 2012, size-selective pressures
were weak, as they began later in the larval period (i.e., day 11) and lasted only 5 d. Despite the fact that patterns in size selection direction, duration, and timing differed markedly across the three years of this study, recruitment was similar and quite low during 2011-2013 (Figure 5.4).

**DISCUSSION**

Size-selective mortality was evident during the larval period in Lake Erie walleye during three years of low recruitment. In 2011, slow-growing larvae were favored, which suggests that, while size-selective mortality is occurring, it may not be from predation. Additionally, in a year with slow-growing larvae surviving disproportionately to the juvenile stage, I would expect weak recruitment (*sensu* Chambers and Leggett 1987), which is what occurred. During 2012, weak size selection, slightly favoring the survival of fast growing larvae, occurred late in the larval period, which I would expect to result in strong recruitment (*sensu* Robert et al. 2007); however, in actuality, weak recruitment was the outcome. Finally, during 2013, there was a strong bias toward survival of fast-growing larvae beginning at 1 d of age and lasting through the first 15 d of life, suggesting high predation pressure. Recruitment during this year was weak, as would be predicted (*sensu* Robert et al. 2007).

A common assumption when estimating size-selection using larvae and juveniles collected in the same year is that both originated from the same larval population (Meeken and Fortier 1996; Hare and Cowen 1997). Because juvenile otoliths could not
be read reliably past day 42 (Parrish et al. 1994), I could not obtain hatch dates on juveniles. However, because walleye spawn once a year over a 4 to 6 week window in western Lake Erie (Roseman 2000, C. May unpublished data; Chapter 2), I can be confident that larvae and juveniles from a given year belong to the same cohort and experienced similar environmental histories during early life. Another concern is that gear selectivity may have biased results. During our study, larvae and juvenile field collection methodology was unchanged. Thus, if gear selectivity occurred, I would expect to see a similar direction and intensity of size-selection taking place in all three years. Our data do not support the idea of gear bias, in that size-selection intensity and direction differed between all years.

High turbidity levels during the larval period in 2011 may have disrupted foraging patterns for larval fish. The spring of 2011 was a wet spring marked with high discharge rates from tributaries generating low water visibility in western Lake Erie. Secchi disk readings (i.e., a measurement of water clarity) during larval fish collections in 2011 averaged 0.5 m, whereas mean Secchi disk readings for 2012 and 2013 were 1 m (C. May, unpublished data). High turbidity can affect foraging rates of fishes (Utne-Palm 2002; Pangle et al. 2012) and thus, it is conceivable that high turbidity in 2011 disrupted foraging such that a number of large larvae, which would have a high consumptive requirement to meet metabolic demands (Madon and Culver 1993), were being selectively removed from the population. Good et al. (2001) studied river-dwelling Atlantic salmon *Salmo Salar* fry across two years, each with distinct hydroclimatic
events, and found yearly differences in the direction of size-selective mortality. The authors concluded that the prevailing physical-biological features of the aquatic environment could dictate the direction of selection occurring (Good et al. 2001). Additionally, differences in the type and size distribution of predators during 2011 may explain why larger larvae were removed in that year and not in 2012 or 2013 (Bailey and Houde 1989; Takasuka et al. 2004, 2007). Regardless of the mechanism or interpretation, the low recruitment observed in 2011 was expected.

Unexpectedly low recruitment resulting from the weak selection of fast-growing larvae occurred during 2012, while preceding studies (i.e., Robert et al. 2007, Murphy et al. 2013) would have predicted strong recruitment. Previous western Lake Erie collections of larval walleye indicate that annual mean larval growth rates during 1994-1999 varied from 0.19 to 0.53 mm/d (Roseman 2000; Chapter 3; Chapter 4). Mean larval growth during this study was between 0.13 and 0.16 mm/d. Therefore, I would contend that growth during 2011-2013 was not fast, but in fact quite slow when compared to other years. In turn, poor recruitment should be and, in fact, was the result in all three years relative to the 1990s. One potential reason for the slower growth rate stems from the current lack of available larval prey (crustacean zooplankton). In 1994-1999 mean crustacean zooplankton densities during the larval period were 16.7 per L, whereas in 2011-2013 mean densities were only 2.6 per L (see Chapter 4). Additionally, the number of larval walleye stomachs with at least one prey item varied between 81-86 % in 1994-1995 (i.e., the only two years of data available), whereas in 2011-2013,
that percentage was 10-43% (see Chapter 4). With fewer available prey items, low larval consumption rates, slow larval growth rates, and resulting poor recruitment during 2011 – 2013, I have compelling evidence to support the idea that prey availability during the larval stage is the driver of poor recruitment and that size-selective mortality is a possible outcome of limited prey.

Low prey availability, and resulting slow growth, can cause mortality directly via starvation or indirectly via predation. Cannibalism in walleye from western Lake Erie is uncommon, as exemplified by the finding of walleye remains in 1 out of nearly 15,000 walleye diets (Madenjian et al. 1996). One of the most likely predators of larval walleye is the invasive white perch *Morone americana*, as its distribution overlaps with larval walleye (Lake Erie Forage Task Group 2014) and it has been found to prey on larval fish in western Lake Erie (Carreon-Martinez et al. 2014). While it is difficult to isolate whether predation or starvation drives mortality, low prey availability coupled with low walleye feeding incidences, slow growth, and poor recruitment in 2011-2013 suggests that bottom-up processes played an important role in walleye recruitment dynamics during my study years.

**CONCLUSIONS**

Recruitment in walleye is affected by growth during the larval stage. My research provides evidence of size-selective processes, operating on both large and small larvae. While the direction of selection was not consistent in my study three
years, growth during all years was slow resulting in weak recruitment. Inconsistencies in
direction of selection may have been due to prevailing environmental conditions.
Historical data on larval growth rates and environmental conditions was essential to
understanding current conditions and drivers of recruitment. Overall, the current slow
growth during the larval period is most likely due to low prey availability, which limits
survival and weakens recruitment strength.
REFERENCES


Murphy, H. M., G. P. Jenkins, P. A. Hamer, and S. E. Swearer. 2013. Interannual variation
in larval abundance and growth in snapper Chrysophrys auratus (Sparidae) is related to prey availability and temperature. Marine Ecology Progress Series 487:151-162.


Roseman, E. F. 2000. Physical and biological processes influencing the year-class strength of walleye in western Lake Erie. Michigan State University, East Lansing, MI.


Table 5.1. Conceptual diagram of recruitment outcomes from consideration of both larval growth patterns (i.e., fast versus slow) and selection pressures (i.e., strong versus weak). Only under weak selection pressures with fast growing larvae would I expect to see good recruitment.
Table 5.2. Sample size of larval and juvenile walleye used for otolith analyses across years. Note that due to low sample size, the 16 to 20d age interval was not included in analyses.

<table>
<thead>
<tr>
<th>Year</th>
<th>1-20d</th>
<th>1-5d</th>
<th>6-10d</th>
<th>11-15d</th>
<th>16-20d</th>
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</thead>
<tbody>
<tr>
<td>2011</td>
<td>47</td>
<td>130</td>
<td>118</td>
<td>52</td>
<td>9</td>
</tr>
<tr>
<td>2012</td>
<td>41</td>
<td>45</td>
<td>35</td>
<td>28</td>
<td>8</td>
</tr>
<tr>
<td>2013</td>
<td>57</td>
<td>29</td>
<td>20</td>
<td>15</td>
<td>7</td>
</tr>
</tbody>
</table>
Figure 5.1. Relationship between the log_{10}-transformed total length (TL; mm) and the log_{10}-transformed otolith radius (OR; µm) of larval walleye from western Lake Erie. Circles represent fish captured in 2011, asterisks represent fish from 2012, and squares are fish captured in 2013. Solid (2011), dashed (2012) and dotted (2013) lines represent the linear relationships for each year.

\[
\begin{align*}
2011: \log_{10}(TL) &= 0.71 + 0.16 \times \log_{10}(OR) \\
2012: \log_{10}(TL) &= 0.80 + 0.11 \times \log_{10}(OR) \\
2013: \log_{10}(TL) &= 0.67 + 0.20 \times \log_{10}(OR)
\end{align*}
\]
Figure 5.2. Larval walleye mean age-specific growth rate (± 1 SE) from western Lake Erie for 2011, 2012, and 2013.
Figure 5.3. Comparison of mean increment width at age (± 1 SE) between the original population (i.e., larvae, dotted lines) and survivors (i.e., juveniles, solid lines) for 2011, 2012 and 2013 in western Lake Erie walleye. Shaded areas represent age intervals for which larval mean increment width of juveniles differed significantly from that of larvae.
Figure 5.4. Recruitment index for walleye from 1994-2013. Index is the number of juvenile fish captured in August in Ohio waters of western Lake Erie during annual bottom trawl surveys conducted by the Ohio Department of Natural Resources-Division of Wildlife.
A COMPARISON OF ESTIMATES OF WALLEYE EGG DEPOSITION FROM TWO DIFFERENT SAMPLING GEARS ON THE OHIO OPEN-WATER REEFS IN WESTERN LAKE ERIE

Previous investigations of walleye egg deposition on the open-water reefs used suction samplers, also referred to as egg pumps (Manz 1964; Baker and Scholl 1971; Roseman et al. 1996; Roseman et al. 2001). Egg pumps are an active method of egg collection that employ a pump located on the boat that is attached via a long hose to an iron sled that is towed over the lake bottom for a specified amount of time. Egg pumps have been used to efficiently sample lake trout Salvelinus namaycush (Stauffer 1981) and lake whitefish Coregonus clupeaformis eggs (Freeberg et al. 1990) as well as to collect dreissenid mussels (Mills et al. 1999). One difficulty associated with analyzing trends in data collected from egg pumps is that, due to substrate irregularities, the area sampled by the sled is unknown (Perkins and Krueger 1994). Typically, egg deposition is reported as the number of eggs per tow time, with the number relevant only to other egg pump tows of similar type and boat speed. Therefore, it is difficult to compare egg pump tows to other egg collection methods or to calculate an estimate of egg density (e.g., number of eggs per m$^2$).
Alternatively, egg mats using artificial substrate have recently been employed to calculate egg deposition (Nichols et al. 2003; Ivan et al. 2010; Katt et al. 2012). Egg mats rest on the lake bottom and are retrieved at predetermined intervals, passively collecting eggs as they are broadcasted. Egg mats are often constructed from artificial substrates, such as furnace filter, floor buffering pads, or outdoor carpet, to mimic preferred spawning substrate (i.e., gravel and cobble, which contain numerous interstitial spaces) and provide a rough surface for eggs to adhere (Marchant and Shutters 1996; Nichols et al. 2003; Katt et al. 2012). The open-water reefs in Lake Erie are mainly composed of bedrock outcroppings, gravel, cobble, and boulders (Roseman et al. 1996). Sand and silt substrates, which surround the shallow open-water reefs, provide little protection from currents (Humphrey et al. 2012) and can bury eggs, essentially suffocating them. The objective of our study was to evaluate if the relationship between egg catches from a diaphragm egg pump and egg mats were correlated such that collections from these two methods could be standardized to a common metric for comparison purposes.

**METHODS**

Walleye eggs were collected simultaneously with egg mats and egg pump methods on the open-water reefs in 2014. Egg mats with attached buoys were set on 9 April, shortly after ice out on 6 popular spawning reefs: Niagara, Round, Crib, Toussaint, Cone, and Locust reefs (Figure A.1). Paired sampling with the egg pump occurred weekly
on 18, 24, and 30 April and 8 May. Walleye egg counts were negligible on 8 May, and therefore egg collections were ceased.

Of the 24 potential data points for comparison (paired samples from six sites across four dates), only 17 were successfully collected by both methods. The egg pump was able to collect all samples on three of the four dates. However, on 24 April, wave action prevented the pump from collecting eggs at four of the six sites. Additionally, egg mats were lost due to angler disturbance ($n = 1$ on 24 April) and wave action ($n = 2$, one each on 30 April and 8 May). We replaced egg mats on the same day they were discovered missing. Since one of the sites that the egg pump was able to sample on 24 April was also the site that anglers disturbed the egg mat, we only have data from one site on 24 April for comparison.

_Egg collections with egg-mats_

We placed furnace filter into a custom designed aluminum frame, 61 X 91.5 cm, which laid flat on the lake bottom and was held in place by 32 kg of cement weights. The frame covered the furnace filter around all four edges leaving 51 X 81 cm exposed for egg capture. We placed one egg mat per reef and replaced furnace filter each week. After collection, we returned to the lab to process the samples within a 24-hour window to ensure viability (Roseman et al. 1996). The egg mats were divided equally into $11.4 \text{ cm}^2$ squares to aide in subsampling. We randomly subsampled 4 to 8 squares, comprising 12.5 to 25% of each egg mat, for enumerating eggs. All eggs were removed and counted
from each subsample, with all squares originating from the same filter were averaged together to get a number of eggs per m$^2$ for the site.

_Egg collections with egg pump_

We conducted the egg pumping collection method at the same depth and location on each reef as egg mat deployment, typically the shallowest area of the reef. At each reef, on each sampling day, we towed a 39-kg iron sled (Stauffer 1981) attached to a diaphragm pump at the surface by a flexible hose 5 cm in diameter three times for 2-min each at a vessel speed of approximately 0.5 m/s, following methods described in Roseman et al. (1996). When possible, the iron sled was towed around the egg mat, using the egg mat buoy as a reference point.

Eggs and benthic debris (e.g., dreissenid mussels and shells, sand, benthic organisms) were deposited from the pump apparatus into a basket made of 10 mm mesh hardware cloth. The basket was set into a framed sluice that allowed eggs and smaller benthic materials to be washed through and collect in a sample jar. Water was decanted from the sample and a subsample of about 100 eggs was removed and stored in Stockard's solution (Galat 1972) for later viability categorization and classification by development stage in the laboratory. The remainder of the sample was preserved in 95% ethanol for enumeration.
Egg processing

After eggs were either picked from the egg mat or separated from benthic debris, they were identified, enumerated, categorized (i.e., alive versus dead) and developmental stage was recorded. We identified eggs based on diameter (nearest 0.1 mm) and color (Auer 1982) using a dissecting microscope. We categorized eggs that showed signs of opaqueness or exhibited fungal growth as dead (Johnson 1961). Additionally, we classified walleye eggs by developmental stage (Nelson 1968; McElman and Balon 1979). Stage-1 eggs are pre-organogenesis, stage-2 eggs show intermediate development, and stage-3 eggs are in the late embryonic stage with developed eyes, pectoral fin buds, and caudal mesenchyme rays, as well as chromatophores along the ventral line and yolk sac.

During peak egg production, the processing of all egg mats within a 24-hour window was not possible. Therefore, during these weeks we counted a minimum of two squares per mat while preserving up to six squares in Stockard’s solution for later enumeration and viability categorization. Stockard’s solution will kill the embryo immediately but will not distort the embryo or tissues (Galat 1972), and therefore we assumed that it would preserve the ability to distinguish live eggs from dead. This assumption appears valid based on results from a previous study in which we counted walleye egg samples within 24-hours of collection, and categorized them as either live or dead. We then preserved each sample in Stockard’s solution and had a technician, with no prior knowledge of the previous egg classification, count the preserved eggs
several weeks later. The categorization of eggs from < 24-hours after capture versus preserved were not significantly different for live or dead eggs (paired t-test, \( n = 9; P = 0.763 \) and 0.587 respectively).

Statistical analyses

We used separate repeated measures logistic regression models to determine the effect of gear type on the probability of collecting eggs at a particular stage (i.e., 1, 2, or 3) as well as the probability of collecting eggs that were alive or dead. Each site was an independent unit of replication for each gear type. The quasi-likelihood information criterion (QIC), a modified version of Akaike’s information criterion for generalized estimating equations (Pan 2001), was used to evaluate the most appropriate covariance structure between potentially correlated measurement taken on three sampling dates at 6 different reef sites. The covariance structures compared included independent, exchangeable, first-order autoregressive, and unstructured. An \( \alpha \)-level of 0.05 was used to judge significance; statistical were performed using the GENMOD procedure in SAS version 9.3 (SAS Institute Inc., Cary, NC).

Egg pump and egg mat samples represent measurements of a true egg density at a given time and location. True egg density is highly variable causing both measured variables to be sampled imperfectly; therefore, the resulting estimates from each sampling method contain a high degree of measurement uncertainty. Because of this, comparing sampling methods with conventional linear regression is not appropriate, as
this method accounts for uncertainty in the direction of the dependent variable, but not for the independent variable. To account for measurement uncertainty in both sampling methods and to quantify the relationship between sampling methods, we used a bivariate normal distribution and conditions relationship equation (Eq. 1; Sokal and Rohlf 1995), which estimates \( x_1 \) (egg mat densities) conditional on \( x_2 \) (egg pump densities):

\[
E(x_1|x_2) = \mu_1 + \rho \frac{\sigma_1}{\sigma_2} (x_2 - \mu_2)
\]

where, \( \mu \) is the mean of sample data, \( \sigma \) is the standard deviation of sample data, and \( \rho \) is the correlation coefficient between sample data. Before comparison, to assure the data met the assumptions of a bivariate normal distribution, we used a multivariate Box-Cox transformation on the highly skewed egg pump and egg mat density data. Box-Cox methods choose a data transformation (from a range of values) by optimizing the likelihood of the transformed data meeting three criteria: simplicity of structure, constant variance, and normality (Box and Cox 1964). The multivariate application of Box-Cox methods simultaneously optimizes normality in two variables meeting the assumptions of a bivariate normal distribution (Fox and Weisberg 2011). The conditional distribution formula is used to convert egg density estimates between sample methods on the transformed data scale, while converted data is back-transformed to the original scale. Because we are interested in standardizing the number of total eggs and live eggs, we examined relationships between total egg mat densities conditional on total
egg pump densities as well as the density of live eggs from egg mats conditional on total egg pump densities.

RESULTS

We detected strong differences between egg collection methods relative to their ability to capture eggs at different stages, as well as whether eggs were still alive. Specifically, egg mats were 5.5 times more likely (95% CI 2.4 – 12.7) to collect eggs that were alive compared to the egg pump (z = 4.02, P < 0.001). Egg mats were also twice as likely (95% CI 1.02 – 3.96) to collect eggs in stage-2 development than the egg pump (z = 2.03, P = 0.043). No differences were detected between collection method for eggs in stage-1 (z = 1.07, P = 0.285) or stage-3 (z = 0.46, P = 0.643) development. Note that we used the independent covariance structure for each of the four models given no significant improvement in model fit by using other covariance structures (ΔQIC ≥ -1.27).

After a Box-Cox transformation, total egg densities from the egg mat and egg pump were strongly correlated (n = 17, ρ = -0.72, P = 0.0008; Figure A.2). In addition, densities of live eggs from the egg mat and total densities from the egg pump were also strongly correlated (n = 17, ρ = -0.73, P = 0.001; Figure A.3). The negative direction of the correlation is due to the negative power transformation applied to egg pump densities (Table A.1), meaning that the above correlations are, in actuality, positive (Figure A.2 and A.3, top panels).
Biases in the egg sampling gear we evaluated in this study were apparent. Some of the discrepancies between the gears relative to the propensity to collect certain development stages may be related to changes in buoyancy with development. For example, dead walleye eggs become buoyant (Baker and Scholl 1971) and, as a result, are likely to be more susceptible to the egg pump as they are suspended above the substrate. Additionally, egg mortality could also be occurring through the act of sucking eggs off the lake bottom and depositing them into a basket located on the boat. The ability of the egg mat to collect twice as many eggs in stage-2 development may be due merely to the fact that the egg pump collects so many more dead eggs (i.e., eggs that either did not achieve stage-2 development or died in stage-2 development). In a laboratory setting, the majority of walleye egg mortality occurred during stage-1 development, most likely due to failed fertilization (Heidinger et al. 1997). Additionally, Latif et al. (1999) specified that the transition from stage-1 to stage-2 was a critical stage in walleye development, and that once the head and trunk of the embryo was formed (i.e., the hallmarks of stage-2 development) egg mortality became negligible. Thus, it is possible that agitation by the egg pump during the sensitive transition from stage-1 to stage-2 development killed viable embryos; however, further research into the ability of suction samplers to impact egg viability is needed.

Biases of survival created by the egg mat are unclear. Survival on the egg mats could be inflated, as the rough surface of the furnace filter may provide more protection.
from water shearing than open substrate alone (Ivan et al. 2010). Conversely, survival on egg mats could be lower than found in nature due to siltation, as we found egg mats occasionally to be saturated with sand or crushed dreissenid shells. The ability of the egg mat to influence egg predation rates is unknown, as it is possible that the mat provides protection from predators due to its myriad of interstitial spaces, or it could also attract predators due to its novelty. We are encouraged, however; by the fact that both the egg pump and the egg mat collected similar amounts of eggs in stage-3 development, suggesting that mortality from egg predation may not differ between the egg mats and the surrounding natural environment. Finally, the density estimates from egg mats should be considered conservative, as eggs have the potential to dislodge during retrieval. Since we retrieved all egg mats in the same manner, a similar proportion of eggs from each mat would have been lost (Manny et al. 2007; Katt et al. 2012).

The collection of eggs and the ability to calculate density and deposition is an important tool for fisheries managers who wish to assess temporal and/or spatial reproductive output. In comparing two different gear types, we were able to better assess their biases, determine that the relationship between egg collection gears was predictable, and establish a common metric for comparison purposes of both live and dead egg collection. The relationship between an egg pump and egg mats developed from this study can be applied to previous or future collections by an egg pump using the bivariate normal distribution (Eq. 1; Table A.1) to obtain information on egg
densities per m$^2$. In Lake Erie, the relationship will be especially helpful in relating past collections from an egg pump (Roseman 2000) to recent collections by an egg mat that were carried out in the open-water reef area.
REFERENCES


Roseman, E. F. 1997. Factors influencing the year-class strength of reef spawned walleye in western Lake Erie. Michigan State University, East Lansing, MI.


<table>
<thead>
<tr>
<th>Parameter</th>
<th>$x_1$: Total eggs</th>
<th>$x_1$: Alive eggs</th>
<th>$x_2$: Total eggs</th>
<th>$x_2$: Total eggs</th>
</tr>
</thead>
<tbody>
<tr>
<td>$x_1$ b-c power</td>
<td>0.3415</td>
<td>0.3042</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$x_2$ b-c power</td>
<td>-0.0837</td>
<td>-0.0518</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\rho$</td>
<td>-0.72</td>
<td>-0.73</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\mu_1$</td>
<td>25.24</td>
<td>12.23</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\mu_2$</td>
<td>0.62</td>
<td>0.74</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\sigma_1$</td>
<td>13.48</td>
<td>6.64</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\sigma_2$</td>
<td>0.09</td>
<td>0.07</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table A.1. Parameter values for use in the bivariate normal distribution equation when relating $x_1$ (i.e., egg mat densities; #/m2) to $x_2$ (i.e., egg pump densities; #/2-minute tow), where $\mu$ is the mean of sample data, $\sigma$ is the standard deviation of sample data, and $\rho$ is the correlation coefficient between sample data. The data underwent a Box-Cox transformation (i.e., b-c power) before parameter values were calculated.
Figure A.1. Location of six popular open-water walleye spawning reefs in western Lake Erie that were sampled with both the egg pump and egg mat weekly during the spring of 2014.
Figure A.2. Relationship between total walleye egg mat densities (#/m²) and egg pump densities (# eggs per 2-minute tow) before (top panel) and after (bottom panel) Box-Cox transformation collected from Western Lake Erie open-water reefs during spring 2014.

\[ P = 0.0008 \]
\[ \rho = -0.72 \]
Figure A.3. Relationship between live egg densities from egg mats (#/m²) and total egg pump densities (# eggs per 2-minute tow) before (top panel) and after (bottom panel) Box-Cox transformation collected from Western Lake Erie open-water reefs during spring 2014.
### APPENDIX B

#### CHAPTER 3: SUPPLEMENTAL TABLES AND FIGURES

<table>
<thead>
<tr>
<th>Equation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$E = (W^* (C - F - U - S)^<em>ED_{\text{pred}}/ED_{\text{pred}}) - W^</em> R$</td>
<td>Larval growth environment (g/g/day)</td>
</tr>
<tr>
<td>$C = C_{\text{max}} * f(T) * P$</td>
<td>Consumption (g/g/day)</td>
</tr>
<tr>
<td>$C_{\text{max}} = CA * W^{C_3}$</td>
<td>Maximum consumption (g/g/day)</td>
</tr>
<tr>
<td>$f(T) = V^* \exp \left( \lambda^*(1-V) \right)$</td>
<td>Temperature dependent function</td>
</tr>
<tr>
<td>$P = 0.7 * Z B^{0.15}$</td>
<td>Proportion of maximum consumption *</td>
</tr>
</tbody>
</table>

$$V = (\text{CTM} - \text{T}) / (\text{CTM} - \text{CTO})$$
$$X = Z^2 * (1 + (1 + 40 / Y^{0.5})^2) / 400$$
$$Z = \ln (\text{CQ}) * (\text{CTM} - \text{CTO})$$
$$Y = \ln (\text{CQ}) * (\text{CTM} - \text{CTO} + 2)$$

$$R = RA * W^{R_3} * f_6(T) * ACT$$
$$f_6(T) = V^* \exp \left( \lambda^*(1-V) \right)$$

$$S = S_{DA} * (C - F)$$
$$F = FA * C$$
$$U = UA * (C - F)$$

*Madon and Culver 1993

Table B.1. Bioenergetics model equations used to estimate larval walleye larval growth environment (Kitchell et al. 1977).
<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Value</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Parameters</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$ED_{\text{prey}}$</td>
<td>Mean energy density of prey (copepod, wet weight)</td>
<td>460</td>
<td>cal/g</td>
</tr>
<tr>
<td>$ED_{\text{pred}}$</td>
<td>Mean energy density of walleye (wet weight)</td>
<td>760</td>
<td>cal/g</td>
</tr>
<tr>
<td>$CA$</td>
<td>Intercept for maximum consumption</td>
<td>0.25</td>
<td>g/g/d</td>
</tr>
<tr>
<td>$CB$</td>
<td>Exponent for maximum consumption</td>
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<td>Dimensionless</td>
</tr>
<tr>
<td>$CQ$</td>
<td>Slope for temperature dependence of standard consumption</td>
<td>2.3</td>
<td>Dimensionless</td>
</tr>
<tr>
<td>CTM</td>
<td>Maximum temperature for consumption</td>
<td>28</td>
<td>°C</td>
</tr>
<tr>
<td>CTO</td>
<td>Optimal temperature for consumption</td>
<td>22</td>
<td>°C</td>
</tr>
<tr>
<td>RA</td>
<td>Intercept for maximum standard respiration</td>
<td>0.056</td>
<td>g O$_2$/g fish/day</td>
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<td>RB</td>
<td>Exponent for maximum respiration</td>
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<td>RQ</td>
<td>Slope for temperature dependence of standard respiration</td>
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<td>Maximum temperature for standard respiration</td>
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<td>°C</td>
</tr>
<tr>
<td>RTO</td>
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<td>°C</td>
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<tr>
<td>ACT</td>
<td>Activity multiplier</td>
<td>3</td>
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<tr>
<td>SDA</td>
<td>Specific dynamic action</td>
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<tr>
<td>FA</td>
<td>Fecal loss coefficient</td>
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<td>g/g/day</td>
</tr>
<tr>
<td>UA</td>
<td>Urinary loss coefficient</td>
<td>0.05</td>
<td>g/g/day</td>
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<td><strong>Variables</strong></td>
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</tr>
<tr>
<td>$W$</td>
<td>Wet weight of larval fish</td>
<td></td>
<td>g</td>
</tr>
<tr>
<td>$T$</td>
<td>Water temperature</td>
<td></td>
<td>°C</td>
</tr>
<tr>
<td>$ZB$</td>
<td>Zooplankton biomass (wet weight)</td>
<td></td>
<td>mg/l</td>
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</tbody>
</table>

Table B.2. Consumption model parameters from Madon and Culver et al. (1993) we used to estimate larval walleye consumption in the bioenergetics model presented in Table B.1.
Figure B.1. Relationship between larval walleye growth rates (mm/day) and 12-mm larval growth environment (g/g/day) during 1 May – 7 June in Lake Erie for the years 1994-1999 and 2011-2013.
Figure B.2. Relationship between the log$_e$-transformed August trawl catch per hectare of juvenile walleye (age-0 recruitment, catch per unit hectare) and 12-mm larval growth environment (g/g/day, 1 May – 7 June) during 1994 – 2013 in western Lake Erie.
Figure B.3. Relationship between the average total length (TL; mm) of juvenile walleye captured in August and 12-mm larval growth environment (g/g/day; 1 May – 7 June) during 1994 – 2013 in western Lake Erie.
APPENDIX C

CREATION OF A MORPHOLOGICAL INDEX OF NUTRITIONAL CONDITION

A larval fish is limited in its ability to avoid predation, starvation, and transportation to unsuitable habitat due to its small size and lack of swimming ability (Houde 1987; Pechenik 1999). Performance characteristics of individuals, such as nutritional condition, are crucial to their survival and recruitment to the population (Fuiman and Higgs 1997). Houde (1987) demonstrated how minor variations in mortality and growth schedules during the larval stage can lead to major fluctuations in recruitment by increasing instantaneous mortality of larval fish by 25% which elicited a 77% decrease in number of recruits. Variability of individual quality during the larval stage can therefore impact overall recruitment success with individuals exhibiting suitable performance characteristics having an increased probability of recruitment.

Nutritional condition is a measurement of a fish’s vulnerability to death by limitations in food (Ferron and Leggett 1994). Further, larvae in poor nutritional condition are more vulnerable to predation and starvation (Rice et al. 1987; Miller et al. 1988; Jonas and Wahl 1998). To determine whether nutritional condition is predictive of a fish’s performance and to understand how phenotypic differences impact recruitment success
of larval fish, I will create a morphometric index of nutritional condition for larval walleye.

Morphometric indices have been in use for decades to determine the nutritional condition of fishes (Theilacker 1978). These studies work under the premise that particular external body parts are more sensitive in their response to starvation than other body parts, and therefore can be analyzed by comparing measures of one part to another. Advantages to using a morphometric index include low cost, reliability in detecting condition changes, and a short relative processing time (Ferron and Leggett 1994). A nutritional condition index that is applied to wild-caught larvae must be calibrated with the condition of known laboratory-reared larvae (Ehrlich 1975; Theilacker 1978; McGurk 1985); otherwise, one would not know what a condition index means in terms of starvation and how it relates to growth. Smith et al. (2005) developed a morphometric index for juvenile largemouth bass *Micropterus salmoides* comparing morphometric characteristics between groups of fed and un-fed individuals. Using discriminant function analysis, the researchers found that a ratio of body depth to length of 0.195 can classify juvenile largemouth bass as fed (>0.195) or starving (<0.195) (Smith et al. 2005). To assess the nutritional condition of field-collected walleye larvae, I conducted a controlled laboratory experiment. My goal is to determine the effect of feeding regime on body morphometric characteristics, which then can be used to estimate nutritional condition in wild-caught fish. Ultimately, I sought to test
demonstrate that early starvation (i.e. poor nutritional condition) of larval fishes can introduce variability in recruitment success.

METHODS

To develop a nutritional condition index, a laboratory experiment was conducted to relate feeding regime to larval morphometry. Walleye eggs and milt, collected from the Maumee River during spring spawning, were reared at the Aquatic Ecology Lab in Columbus, OH. In a full factorial design (Figure C.1), larvae were randomly assigned to 1 of 3 feeding treatment groups: zero, low (4 zooplankters/L), or high (40 zooplankters/L) and to temperature treatments of either 8°C or 13°C. Zooplankton and temperature treatments reflect natural levels found in Lake Erie (Cassandra May, unpublished data). Further, work by Johnston and Mathias (1994) and Johnston (1999) demonstrate that the consumption rate of larval Walleye is not limited at a density of 40 zooplankters/L, thus I set this prey level as the high feed treatment. I chose 4 zooplankters/L as the low treatment, as this is the minimum amount of food needed for larval Walleye to remain healthy (i.e., maintenance ration; Johnston and Mathias 1994). Zooplankton was collected daily from a nearby pond to ensure a mixed natural assemblage. I selected for 600 to 1,100µm TL zooplankton by using a set of sieves to exclude rotifers and nauplii as well as large bodied zooplankton (i.e. Daphnia Magna) which larval Walleye do not typically consume (Hokanson and Lien 1986). Larval walleye density for each aquaria was 20/L, which is within the range used in previous experiments (Summerfelt 1996).
housed all aquaria in temperature-controlled rooms. Each room \((n = 4)\) contained three 65-gallon aquaria (“feeder tanks”), one for each feeding treatment. The aquaria in each room shared a common water source and had a flow-through system. These tanks were maintained at their assigned feeding level throughout the experiment by adding (or not adding) zooplankton once per day. Water quality parameters were checked daily and included temperature, dissolved oxygen, nitrate, nitrite, ammonia, pH, and turbidity. I also performed a 10% water change on a daily basis to ensure water quality through the duration of the experiment. Turbidity levels were maintained around 25 NTU to prevent cannibalism and clinging behavior (Summerfelt 1996). A surface spray was used to facilitate gas bladder inflation and reduce mortality due to non-inflation (Summerfelt 1996; Clayton and Summerfelt 2010). The overhead, indirect lighting in each temperature control room simulated the natural photoperiod during the time of the experiment, with 1 hour of increasing light at dawn and 1 hour of decreasing light at dusk. I conducted the experiment according to animal use guidelines outlined in IACUC # 2013A00000025 at The Ohio State University.

The experiment began on day 3 post-hatch, before the yolk sac was completely absorbed, when groups of 10 larvae were moved from the feeder tank to 1-L aquaria. For each feeding treatment, I had 21 replicates (i.e. 21 1-L aquaria) for a total of 63 1-L aquaria per temperature-control room. Beginning on day 3 and ending on day 9 post-hatch, I removed 3 1-L aquaria per feeding treatment per temperature replicate per day. These fish were sacrificed, imaged, and preserved. On day 10 post-hatch, I added 10
new fish to each 1-L aquaria and continued the experiment for another seven days. The experiment was repeated weekly, for 3 weeks, and ended on day 24 post-hatch. Fish were sacrificed 1 hour after feeding to ensure that consumed prey items were still identifiable in the gut tract, providing a record of how many and what types of prey items were being eaten. By sacrificing fish from each feeding treatment on a daily basis, I have a continuous series of morphological changes, allowing us to investigate the timing of morphological differences between treatments. By beginning the experiment before the yolk sac was absorbed, I ensured that food was available (or not available) to larvae as they began to feed exogenously, as there is a window of time when this occurs (i.e., 3-5 days post-hatch; Summerfelt 1996).

Measurements of standard length, total length, body depth at anus, eye diameter, caudal peduncle depth, and caudal fin length were taken using a dissecting microscope with NIS imaging software (Nikon Instruments Inc.). I chose these measurements due to their simplicity, since larval fish are still developing. I also sought a mix between starvation sensitive (e.g., body depth at anus) and insensitive (e.g., eye diameter) measures as Theilacker (1978) suggests the use of ratios with the numerator set as a starvation sensitive measurement, and the denominator as a starvation insensitive measurement to allow for detection of starvation.

Individual walleye measurements from each temperature and feeding treatment replicate were averaged together providing us with up to 3 morphometric measurements (i.e., one measurement per 1-L aquaria) per temperature and feeding
treatment per date. I conducted multivariate analyses of variance (MANOVAs) to test for morphological differences among fish. Initially, three MANOVAs (i.e., one for each prey density) were run for each temperature treatment (i.e., high and low temperature) testing for morphological differences between replicates and temperature control rooms. I found that there were significant differences between replicates, and therefore could not pool individuals together for the remaining analyses. There were no significant difference between temperature control rooms, and therefore I pooled replicates from similar rooms (i.e., 8°C and 13°C) for the remaining analyses. For each temperature treatment, a MANOVA was conducted in order to test for morphological differences due to feeding treatment and day. Finally, I conducted MANOVAs to test for morphological differences between temperature treatments.

RESULTS

Larval walleye under different feeding conditions ranged in total length from 7.4 to 10.8 mm and did not differ significantly in overall morphology due to differences in feeding treatments; however, morphology did differ significantly due to date and temperature differences. Feeding treatment did not elicit morphological differences in larval walleye from high (MANOVA; Wilk’s lambda= 0.92; F_{12,280} = 1.0; P= 0.41) and low (MANOVA; Wilk’s lambda=0.89; F_{12,288} = 1.4; P= 0.16) temperature treatments. Thus, I was unable to produce a change in nutritional condition by manipulating prey density. I did find significant morphological differences depending on the day that the
measurements were taken in both the high (MANOVA; Wilk’s lambda= 0.16; F_{6,140}= 127.1; P<0.0001) and low (MANOVA; Wilk’s lambda=0.24; F_{6,144}= 75.9; P<0.0001) temperature treatment (Table C.1). Finally, I found significant morphological differences between temperature treatments (MANOVA; Wilk’s lambda=0.33; F_{6,297}= 102.0; P<0.0001).

**DISCUSSION**

I was unable to elicit a change in nutritional condition by manipulating prey abundances in a laboratory experiment. Instead, larvae from all feeding treatments exhibited characteristics of starving larvae, even if they had access to prey. Possible reasons for failure of the experiment include issues with available prey, turbidity levels, or water source. I collected zooplankton from a nearby campus pond, and thus the prey assemblage may have differed from that found in Lake Erie. Following recommendations from the literature, I sieved prey to attain a median prey size. Imaginably, having smaller prey available, especially during the first few days of life, may have encouraged foraging. Additionally, while I aimed for turbidity levels to be near 25 NTUs, it was difficult to keep sediment in suspension for the entirety of the experiment, thus the turbidity levels ranged between 3 and 57 NTUs. The most ideal water source would have been from Lake Erie; however, due to logistical concerns, I used City of Columbus drinking water. Drinking water is highly manipulated, with added chemicals from the disinfection process (e.g., chloride) as well as for health reasons (i.e., fluoride).
While chloride was removed from the incoming water, differences in water chemistry between Lake Erie and the water source may have disrupted foraging in larval fish. All of the aforementioned issues may have acted alone or synergistically to reduce foraging in the experiment.
REFERENCES


Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval Size and


Table C.1. Means (μm) and standard deviations of larval fish traits: total and standard length, body depth at anus, and eye diameter from Maumee River larval walleye under high (13°C) and low (8°C) temperature treatments. The feeding treatments failed to provide any differences, and thus all fish were pooled by temperature treatment.
Figure C.1. Conceptualization of the experimental design, with 2 levels of temperature and 3 levels of feeding treatments (zp = zooplankton). Temperature treatments were replicated twice while feeding treatments were replicated 63 times within each temperature treatment over the course of the experiment.


Fedor, S. L. 2008. Synchronous recruitment of walleye in the Great Lakes and the influence of climate on recruitment. The Ohio State University, Columbus, OH.


Johnston, T. A. 1997. Within-population variability in egg characteristics of walleye (Stizostedion vitreum) and white sucker (Catostomus commersoni). Canadian Journal of Fisheries and Aquatic Sciences 54:1006-1014.


Ohio Division of Wildlife. 2014. Ohio's Lake Erie Fisheries 2013. Ohio Department of Natural Resources, Division of Wildlife, Lake Erie Fisheries Units, Fairport and Sandusky.


Robert, D., H. M. Murphy, G. P. Jenkins, and L. Fortier. 2014. Poor taxonomical knowledge of larval fish prey preference is impeding our ability to assess the existence of a "critical period" driving year-class strength. Ices Journal of Marine Science 71:2042-2052.


Roseman, E. F. 1997. Factors influencing the year-class strength of reef spawned walleye in western Lake Erie. Michigan State University, East Lansing, MI.

Roseman, E. F. 2000. Physical and biological processes influencing the year-class strength of walleye in western Lake Erie. Michigan State University, East Lansing, MI.


