Quantification of variability, abundance, and mortality of Maumee River larval walleye (Sander vitreus) using Bayesian hierarchical models

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Quantification of Variability, Abundance, and Mortality of Maumee River Larval Walleye (*Sander vitreus*) Using Bayesian Hierarchical Models

by

Mark R. DuFour

Submitted to the Graduate Faculty as partial fulfillment of the requirements for the Master of Science in Biology (Ecology Track)

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December 2012
An Abstract of

Quantification of Variability, Abundance, and Mortality of Maumee River Larval Walleye (*Sander vitreus*) Using Bayesian Hierarchical Models

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The estimation of abundance is complicated by factors contributing to spatial and temporal variability. Many organisms are highly variable across both of these scales, thereby violating assumptions of conventional abundance estimation methods. Larval walleye in the Maumee River are extremely variable; however estimates of abundance and mortality are important in understanding anthropogenic impacts on this spawning group and their role in Lake Erie walleye recruitment. Bayesian hierarchical models were used to quantify spatial and temporal variability, and estimate abundance and mortality within the river while accounting for spatial and temporal uncertainty. We sampled larval walleye at the river mouth and in the intake canal of a water-cooled power plant in 2010 and at an additional upstream site near the spawning grounds in 2011. Temporal variability and uncertainty was greater than spatial variability at all sites and years during the study. Daily abundance at each site and year was related to patterns in river discharge and temperature. Larval walleye abundance decreased in a downstream fashion, with an estimated annual natural mortality rate of 63.7% in 2011. Downstream (B) and power plant abundance (C) varied between years leading to a decrease in power plant entrainment mortality from 2010 to 2011, 11.1 to 2.8% respectively. Total in-river
mortality was estimated at 64.8% when entrainment mortality was included. Quantifying sources of variability lead to an adjustment in sampling protocol, which increased precision in estimated values. Bayesian hierarchical models provided an optimal framework for understanding sources of variability and estimating larval fish abundance and mortality in this large river system.
I dedicate this work to my father who encouraged me to pursue a career based on my interests.
Acknowledgement

I would like to thank my committee for their assistance in completing this work. I am especially grateful to my advisor, Dr. Christine Mayer, for providing this opportunity and allowing me to follow my interests. Many thanks go out to Dr. Craig Stow for his patience and quantitative guidance. I also want to thank Dr. Edward Roseman for his constructive comments and contributions of larval fish knowledge throughout this process. I am also very grateful for the participation of Dr. Jonathan Bossenbroek.

This work would not have been possible without the help of fellow lab mate Jeremy Pritt. Many have helped in the collection and processing of samples, which at times was grueling and tedious, including; Peter Bichier, Jason Ross, Mike Kuebbeler, Robert Mapes, Bianca Sanders, Sarah Panek, and Corey Becher. Special thanks go out to the University of Toledo – Lake Erie Center staff who helped overcome many unforeseen circumstances.

Finally, I would like to acknowledge the consistent and continued encouragement provided by my family, past and present. I also want to thank my wife, Allison, for her unwavering commitment and support.
Contents

Abstract .................................................................................................................................................. iii
Acknowledgements ............................................................................................................................ vi
Contents .................................................................................................................................................. vii
List of Tables .......................................................................................................................................... ix
List of Figures ......................................................................................................................................... x
1 Introduction ........................................................................................................................................... 1
  1.1 Bayesian Methods ......................................................................................................................... 3
  1.2 Maumee River Larval Walleye ...................................................................................................... 5
  1.3 Objectives ........................................................................................................................................ 5
2 Methods ............................................................................................................................................... 6
  2.1 Site Description .............................................................................................................................. 6
  2.2 Sampling Protocol ......................................................................................................................... 8
  2.3 Daily Water Measurements .......................................................................................................... 11
  2.4 Data Structure .............................................................................................................................. 13
  2.5 Larval Drift Patterns ..................................................................................................................... 13
  2.6 Variance Partitioning .................................................................................................................... 14
  2.7 Abundance and Mortality Estimates ............................................................................................. 15
  2.8 Model Summary and Analysis ....................................................................................................... 18
3 Results .................................................................................................................................................. 20
  3.1 Sampling Overview ....................................................................................................................... 20
<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.2 Daily Water Measurement Summary</td>
<td>22</td>
</tr>
<tr>
<td>3.3 Larval Drift Patterns Summary</td>
<td>23</td>
</tr>
<tr>
<td>3.4 Variance Partitioning Estimates</td>
<td>25</td>
</tr>
<tr>
<td>3.5 Abundance and Mortality Estimates</td>
<td>27</td>
</tr>
<tr>
<td>3.5.1 Daily Larval Walleye Abundance</td>
<td>27</td>
</tr>
<tr>
<td>3.5.2 Annual Larval Walleye Abundance</td>
<td>28</td>
</tr>
<tr>
<td>3.5.3 Annual Larval Walleye Mortality</td>
<td>30</td>
</tr>
<tr>
<td>4 Discussion</td>
<td>31</td>
</tr>
<tr>
<td>4.1 Abundance and Variance Partitioning Models</td>
<td>31</td>
</tr>
<tr>
<td>4.2 Maumee River Larval Walleye Ecology</td>
<td>33</td>
</tr>
<tr>
<td>5 Conclusion</td>
<td>40</td>
</tr>
<tr>
<td>References</td>
<td>42</td>
</tr>
</tbody>
</table>
List of Tables

2.1 Model summary including model types, data sources, and outputs of interest

3.1 Summary of sampling effort by year and site

3.2 Numbers of walleye captured by year and site, including size descriptions and first and last encounters

3.3 Summaries of daily water measurements over the period of study

3.4 Estimates of spatial and temporal variation by year and site

3.5 Model estimates of annual abundance and mortality by year and site
List of Figures

1-1 Description of posterior probability distribution interpretation.........................4
2-1 Key locations in the lower Maumee River including primary walleye spawning reach and sampling sites.........................................................8
2-2 Description of key sampling sites in the lower Maumee River.........................10
2-3 Daily water variable measurements over the period of study.........................12
2-4 A graphical display of the variance partitioning model.................................15
2-5 A graphical display of the abundance estimation model................................17
3-1 A description of the range of larval walleye stages observed in the Maumee River during the period of study.........................................................22
3-2 Annual average densities of spatially distributed larvae at each tow location, site, and year.................................................................24
3-3 Daily average sample densities from each site and year..............................25
3-5 Temporal and spatial variance estimates for each site and year....................26
3-6 Daily larval walleye abundance estimates from each site and year................28
3-7 Annual larval walleye abundance estimates from each site...........................29
3-8 Annual larval walleye mortality estimates..................................................30
Chapter 1

Introduction

Many basic and applied ecological questions require the accurate and precise description of organism abundance over broad spatial and temporal scales (Stewart-Oaten et al. 1995, Gibbs et al. 1998, Kery et al. 2005, Royle et al. 2007). Systematic sampling can provide a picture of an organism’s abundance but natural complexities and logistical restraints set the limit of feasible sampling causing this picture to be incomplete. Further, as the scale of description and natural variability escalates the picture of abundance becomes increasingly fuzzy. Therefore, fuzziness, or uncertainty, is an inherent component of sampling organismal abundance and should be acknowledged and accounted (Regan et al. 2003, Cressie et al. 2009). Abundance modeling has been widely applied using N-mixture models in situations that assume population closure (Royle 2004, Kery et al. 2005, Ver Hoef and Jansen 2007, Joseph et al. 2009). Unfortunately many organisms of interest do not adhere to closed population assumptions on feasibly measurable scales.

Aquatic systems exacerbate the challenges of abundance modeling especially in small ephemeral species or life stages that exist over large spatial and short temporal scales. In particular, the distribution and abundance of larval fish is highly variable (Cyr 1992).
Their variability is affected by strong relationships between stochastic environmental variables (Crane 2007, Doyle et al. 2009), time of spawning (McKenna et al 2000), and larval developmental rates and survival (Blaxter 1992). Heterogeneous habitat availability and variable physical factors such as currents contribute to uneven spatial distributions of larval fish (Roseman et al. 2005, Martin and Paller 2008, Zhao et al. 2009). Some larval fish have shown the ability to influence their locations through vertical migrations (Houde 1969, Cooper et al. 1981). The combination of these factors causes uneven spatial and temporal distributions and often highly aggregated pockets of larval fish making precise descriptions of abundance especially difficult.

In addition to high variability, the logistics of larval fish collection often results in sparse sampling on both the spatial and temporal scales. The presence of sparse data, in turn creates a need to estimate (i.e. fill in the gaps) prior to examining patterns in time or space (Mion et al. 1998). This is in part due to the large scales that populations exist within, and the cost and physical restrictions of sample collection and processing. Because of these complications, system specific sampling protocols should be designed to maximize the efficient collection of quality data. Additionally, most larval studies rely on relative (density) rather than absolute abundance which can be misleading in situations where the concentration of fish is related to the amount of water in the environment. This requires the expansion of density estimates by environmental volume generating total abundance (Royle 2004). Studying larval fish in dynamic habitats has many natural and practical challenges.

Despite these difficulties, the estimation of larval fish abundance remains an important part of both basic and applied fish ecology research. Basic research continues
to ask questions about the influence of biological and environmental stressors on larval abundance, growth, and mortality (Blaxter 1992, Houde 1997), with the ultimate goal of understanding how these interactions influence recruitment variability (Miller et al. 1988, Crowder et al. 1992, Houde 2008). Applied research often focuses on larval fish presence and abundance to support habitat protection and restoration (Jones et al. 2003), mitigation of water withdrawal (Kelso 1979, Barnhouse 2000), and more recently the prediction of climate change impacts (Ficke et al. 2007). The importance of these topics and the challenges of larval quantification (i.e. high temporal and spatial variability, sparse data, and volume expansion) necessitate a flexible approach to estimate values of interest (i.e. abundance and mortality) while producing reliable measures of uncertainty.

1.1 Bayesian Methods

Bayesian methods provide a framework for handling variability while producing estimates with explicit measures of uncertainty (Ellison 1996, Ellison 2004). Additionally, Bayesian hierarchical methods allow for natural complexities to be incorporated into models as conditional relationships (Wilke 2003). The added structure and conditional framework allows the variability at multiple levels (i.e. space and time) to contribute to the uncertainty in all estimated values (i.e. abundance and mortality) (Clark 2003, Clark 2005). The integration of abundance estimation into a Bayesian framework allows for flexibility in spatial and temporal relationships of dynamic organisms, removing the need to assume population closure. Consequently, Bayesian hierarchical models provide a practical approach to estimating larval fish abundance in large, complex systems.
In addition, Bayesian methods produce estimates that can be directly integrated into the decision making process (Ellison 1996). Bayesian theory regards probability as the degree of belief in an observation. Uncertainties in estimates are expressed as posterior distributions that explicitly demonstrate changing degree of belief over a range of possibilities (Figure 1-1). This presentation format has an intuitive appeal and assists in the effective communication of scientific knowledge to all members of society, positively influencing management and policy decisions.

Figure 1-1: The plot of the posterior probability distribution represents a varying degree of belief over a range of possibilities. The most probable value occurs at the peak of the probability distribution, with degree of belief decreasing at higher and lower values.
1.2 Maumee River Larval Walleye

Quantifying larval walleye abundance in the Maumee River provides a prime case study for the application of these methods. Maumee River walleye are one of several spawning groups (Todd and Haas 1993, Merker 1997, Strange and Stepien 2007) that contribute to the Lake Erie population, which sustains a 1.3 billion dollar fishery (Getner and Burr 2010). The Maumee River is the largest tributary to Lake Erie (Herdendorf 1990) and experiences high variability in environmental conditions (Richards 1990). Additionally, larval walleye abundance in the Maumee River is impacted by power plant entrainment near the mouth (Ager et al. 2008). Consequently, accurate information on larval abundance will be valuable in the management decision making process for determining harvest rates, initiating habitat protection and restoration, and mitigation of anthropogenic impacts.

1.3 Objectives

The objectives of this study were to: (1) quantify temporal and spatial variability in the Maumee River larval walleye drift in order to increase sampling efficacy; (2) incorporate temporal and spatial uncertainty into estimates of daily and annual abundance at three key sites along the river (upstream, downstream, and power plant); and (3) differentiate magnitudes of natural and anthropogenic mortality in the river.
Chapter 2

Methods

2.1 Site Description

Lake Erie is a eutrophic system generating one of the most productive fisheries in the Great Lakes region (Rawson 1952). The Maumee River is one of the largest tributaries of the Great Lakes entering Lake Erie along the southern shore of its western basin. The river’s watershed (~17,000 km$^2$) is heavily impacted by agriculture resulting in high levels of sediment and nutrient inputs (Moorehead and Bridgeman 2008). The river experiences extreme variable discharge, especially during the spring, due to a vast network of ditches designed to keep agricultural fields drained (Richards 1990). The lower 12.5 km of the Maumee River is highly modified flowing through the urbanized landscape of Toledo, OH. This section supports heavy shipping traffic, as a channel has been dredged and is maintained at ~9 m deep by the U.S. Army Corp of Engineers (Herdendorff 1977).

Each spring adult fish migrate into the Maumee River to reproduce (Hartman 1973, Trautman 1981). Suitable substrate for walleye reproduction begins about 25 km upstream near Perrysberg, Ohio (Mion et al. 1998, ODW 2010). Upstream migration of
fishes is blocked by the Providence Dam located in Grand Rapids, Ohio, approximately 55 km upstream (Figure 2-1). Walleye reproduction is concentrated between these two locations (ODW 2010). Walleye are lithophilic broadcast spawners laying demersal eggs in the substrate that hatch after a period of incubation. The incubation period is driven by the temperature at which eggs are fertilized, and water warming rates there after, with warmer temperatures hastening the hatching process (Smith and Hokanson 1974). During this period eggs are vulnerable to multiple sources of mortality including; extreme temperature fluctuations, mechanical damage and redeposition in unsuitable habitats from high water flows, and direct predation. Directly after hatching larvae rise into the current and begin to drift down stream toward the Lake, during which time larval fish are subjected to additional natural in river mortality similar that of the egg stage (Herdendorf et al. 1977, Snyder 1978, Mion et al. 1998). A coal fired power plant located at the river mouth draws cooling water for its generating system, where larval fish are drawn into the system adding an additional source of anthropogenic (entainment) mortality (Ruetter and Herdendorf 1977, Ager et al. 2008). Some fraction of the walleye produced in the river survives transport to the mouth and are exported to Lake Erie.
2.2 Sampling Protocol

To estimate larval walleye abundance and distribution larvae were collected from sites in the Maumee River using ichthyoplankton tows with paired bongo nets (Nielsen and Johnson 1983) fitted with 350 and 500 µm mesh. Sample volumes were estimated with General Oceanics 2030R flow meters mounted in the mouth of each net. Bongo nets were towed in an upstream direction against the current for 3-5 minutes depending on debris load in the river. Samples from each paired net were euthanized with a lethal dose of FINQUEL MS-222 and preserved in 70% ethanol. Larval walleye from individual samples were identified and enumerated in the lab following keys in Auer (1982).
Larval walleye samples were collected at three key sites along the river gradient, with multiple samples distributed spatially at each site (Figure 2-2). The upstream site (A) is located just downstream of the lower reach of primary walleye spawning habitat. Samples collected here were used to estimate the abundance of larval walleye emerging from the spawning riffles. The river is relatively shallow here with a maximum depth of less than 2.5 m. Three larval tow transects were designated at mid-depth across the river at this site. The downstream site (B) is located at the mouth of the river prior to the power plant water intake canal. Samples taken here were used to estimate the abundance of fish surviving downstream transport. The river channel is maintained by dredging to depths of ~9 m at this site. Five tow transects were designated at this site; two near the east bank of the river (surface and mid-depth), two in the shipping canal (surface and mid-depth), and one near the west bank (surface). The power plant site (C) is located just downstream of site B within the cooling water intake canal, which draws water from the river’s east bank. The intake canal is ~4.5 m deep and ~65 m wide. Two tow transects were designated at this site; one at surface and mid-depth. Samples were collected primarily during daylight hours in the spring (March-June) to target the walleye hatch (Cooper et al. 1981, Mion et al. 1998).
In 2010, samples were collected from only the downstream (B) and power plant (C) sites. Sampling took place once per week from mid-April through early June. During each sampling day, larval tows were performed at each of the 5 designated tow transects at the downstream site (B). These tows were then duplicated resulting in 10 tows and 20 individual samples per day. Sampling at the power plant (C) was also performed once per week. Two tows were taken, one at the surface and one at mid depth. These tows were quadrupled resulting in 8 tows and 16 individual samples per day.
In 2011, the upstream site (A) was added near the first major spawning riffles allowing us to determine the rate of loss (i.e. natural mortality) occurring during the downstream drift. Temporal sampling effort was increased to 3 days per week at all 3 sites. Samples were collected from late March through early June. Spatial sampling was decreased as replicate tows were dropped at each designated tow transect. Samples were collected from all of the designated tow transects (3 upstream, 5 downstream, and 2 power plant canal) once per week. Additionally, two tow transects were sampled from each site on the remaining two days per week. Individual samples decreased at the downstream site (B) from 20 to 10-4 per day, and at power plant canal (C) from 16 to 4 per day.

2.3 Daily Water Measurements

Mean daily river discharge (water volume/day) was provided by the USGS National Water Resources website (USGS Water Resources). Data were collected from the National Stream Quality Accounting Network Station 04193500 located in Waterville, Ohio approximately 40 km upstream of the river mouth. These values were used in the volume expansion of daily density estimates to daily abundance at upstream (A) and downstream (B) sampling locations in the Maumee River. Bay Shore power plant water intake values (water volume/day) were provided by FirstEnergy Corp. which measured the volume of water taken in and used in the generator cooling facility (personal communication, FirstEnergy Corp.). Reduced intake values relate do a reduction in energy production. Power plant intake values were used in the volume expansion of daily density estimates to daily abundance in the power plant (C) sampling location.
Maumee River mean daily water temperature data were provided by NOAA’s Center for Operational Oceanographic Products and Services. Data was collected from submerged temperature probes (Station ID: g10201) approximately 12.5 km upstream of the Maumee River mouth (NOAA Currents and Tides). Water discharge and temperatures (Figure 2-3) were used to explain daily patterns in abundance.

Figure 2-3: Daily water variable measurements (river discharge, power plant intake, river water temperature), that may influence patterns in larval walleye abundance and mortality
2.4 Data Structure

Within a site, each individual sample was considered spatially independent on each sampled day. Although individual samples from bongo nets were collected from one tow location, there was low correlation between paired nets when larval fish densities were in middle to low ranges. Only at very high densities did we see a strong relationship between paired samples. The majority of all samples were collected at low to middle densities. Individual tows \( (i) \) were indexed within the day \( (j) \) collected. The count \( (n_{ij}) \) of larval walleye from each tow were combined with the estimated volume of water sampled \( (v_{ij}) \) to calculate a density for each sample \( (D_{ij}, \text{fish}/100 \text{ m}^3, \text{Equation 1}) \).

Equation 1

\[
D_{ij} = \frac{n_{ij}}{v_{ij}}
\]

Larval fish densities were rounded to the nearest whole number creating discrete count based data. This facilitated the use of count based probability distributions (e.g. Poisson, negative binomial) in variance partitioning and abundance estimation.

2.5 Larval Drift Patterns

Spatial patterns in larval densities was visually examined by plotting the averages of samples collected from tow locations at each site and year. Temporal patterns in larval densities was visually examined by averaging samples on each day at each site and year \( (\overline{D}_j) \). The relationships observed in the plotting of raw data were used to inform the structure of the abundance estimation model.
2.6 Variance Partitioning

Spatial and temporal variability were partitioned using a Bayesian Poisson analysis of variance (ANOVA) (Qian and Shen 2007, McCarthy 2007, Kery 2010) which allowed me to determine which source of variation was greater (Figure 2-4). A Poisson distribution and log link function were used to model individual sample densities \(D_{ij}\), while \(\alpha\) represented the global mean density, \(\mu_j\) represented daily differences from the global mean (temporal), and \(\varepsilon_i\) represented the extra variation (spatial) in the data. A low information normal prior was used to represent the global mean \(\alpha\). Daily differences \(\mu_j\) and extra variation \(\varepsilon_i\) also used low information normal priors; while variances at each of these levels used uniform hyper-priors \(\sigma^2_\varepsilon, \sigma^2_\mu\). These variance values represent the within (spatial) and among (temporal) day variation, respectively (Qian and Shen 2007). The larger value will indicate a greater source of natural variability in the systems. Low information priors contribute minimal influence on the estimated values outside of distributional structure. A low information normal prior generally has a mean of zero and an extremely wide standard deviation signifying little strength in prior knowledge. A uniform prior is similar to a low information prior in that it initially considers each value within a set interval to have equal probability of occurrence. In situations where there is no relevant prior information these types of distributions are used, allowing the data to dominate the estimates.
Variance Partitioning Model

\[ \log(\lambda_{ij}) = \alpha + \mu_j + \varepsilon_{ij} \]

\[ D_{ij} \sim \text{dpois}(\lambda_{ij}) \]

Figure 2-4: This graphical display of the variance partitioning model shows how the distinct parts interact. The outputs of interest are the measure of temporal variation (\(\sigma^2_{\mu}\)) which estimates the variation in daily estimates (\(\mu_j\)) from the overall mean (\(\alpha\)), and spatial variation (\(\sigma^2_\varepsilon\)) which measures the extra variation not explained by time (\(\sigma^2_\mu\)).

2.7 Abundance and Mortality Estimates

I used a dynamic Bayesian hierarchical model to estimate larval walleye abundance (Figure 2-5). This model accounted for spatially aggregated distributions of larval walleye by using a negative binomial distribution in the form of a hierarchical Poisson-gamma mixture. The Poisson-gamma mixture is used when count data are spatially aggregated, exhibiting more variation than can be accounted for by the Poisson distribution alone (McCarthy 2007, Ntzoufras 2009, Yelland 2008). Individual samples (\(D_{ij}\)) were drawn from a Poisson distribution while the daily mean density (\(\lambda_j\)), was drawn from a gamma prior. Under this structure the individual samples follow a negative
binomial distribution which accounts for an uneven distribution of larval walleye within the drift (Royle and Nichols 2003, Royle 2004, Joseph et al. 2009). Under the assumption that larval hatching was driven by a continuum of environmental factors leading to temporally related hatching events (Stewart-Oaten et al. 1995), information was shared between days creating a dynamic hierarchical model (Figure 2-5). Parameters \((\alpha_j, \beta_j)\) from the daily density estimates \((\lambda_j)\) were drawn from a normal prior distribution which included a daily autoregressive process where parameters from adjacent days were allowed to share information with one another (Yelland 2008, Kery 2012). Parameter \((\alpha_j, \beta_j)\) distributions were censored to keep values within a reasonable range above zero. Days with more samples and/or less variation provided stronger information and had a greater influence on the surrounding daily estimates (Gelman and Hill 2007). Low information gamma hyper-priors were applied to the variance of the daily mean hyper-parameters \((\sigma^2, \alpha_j^2, \beta_j^2)\). The mean daily value with extra variation \((\text{mean}_j)\) is calculated by dividing the two parameters \((\alpha_j, \beta_j, \text{Equation 2})\) returning the mean of the daily density estimate \((\lambda_j)\).

\[
\text{Equation 2} \quad \text{mean}_j = \frac{\alpha_j}{\beta_j}
\]
Figure 2-5: This graphical display of the abundance estimation model shows the flow of information. Higher level parameters ($\lambda_j$, $\alpha_j$, $\beta_j$, $\sigma^2$) within a day are estimated from the data ($D_{ij}$). The information in the higher level parameters is shared between days to estimate unsampled days, and adjust estimates of sampled days. Days with stronger information (i.e. more samples and/or less variation) will have a greater influence on surrounding days.

Daily mean density estimates ($mean_j$, fish/100 m$^3$) were expanded to daily abundance in the river (sites A and B) by multiplying with the average daily river discharge (100 m$^3$/day) and in the power plant intake canal (site C) by water intake values (see Daily Water Measurements section above) (Royle 2004). Daily abundance estimates were summed to produce an annual estimate of abundance (fish/year) for each site (A, B, and C). The annual abundances at the three sites were used to estimate the rate of loss (i.e. mortality) between each. Three estimates of mortality were calculated; in-river (A to B), power plant (B to C), and total (A to B+C) (Equation 3, 4, 5,
respectively). Bayesian methods allow for the propagation of variability (i.e. spatial and temporal) through the model resulting in an unbiased measure of uncertainty in the estimated values.

Equation 3: \( \ln - \text{river mortality} = 1 - (B/A) \)

Equation 4: \( \text{Power plant mortality} = 1 - (C/B) \)

Equation 5: \( \text{Total mortality} = 1 - \left( \frac{B+C}{A} \right) \)

2.8 Model Summary and Analysis

Variance partitioning and abundance and mortality estimate models were run for each site and year sampled resulting in 7 total individual models (Table 2.1). Each model type had distinct outputs of interest. Each of the 5 variance partitioning models returned estimates of spatial and temporal variation for each site and year. Each of the 2 abundance models returned daily and annual abundance estimates for each site and year. Additionally, they also calculated mortality estimates within years. A total of 24 outputs of interest were generated from 7 individual models.
Table 2.1: Model summary including model types, data sources, and outputs of interest.

<table>
<thead>
<tr>
<th>Model Type</th>
<th>Year</th>
<th>Site</th>
<th>Spatial</th>
<th>Temporal</th>
<th>Variation</th>
<th>Abundance</th>
<th>Mortality</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variance Partitioning</td>
<td>1</td>
<td>2010 Downstream (B)</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Power plant (C)</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>2011 Upstream (A)</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>Downstream (B)</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>Power plant (C)</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| Abundance & Mortality Estimates | 1    | 2010 Downstream (B) | x       | x        | x          |           |           |
|                                |      | Power plant (C)    | x       | x        |            |           |           |
|                                | 2    | 2011 Upstream (A)  | x       | x        |            | x         | x         |
|                                |      | Downstream (B)     | x       | x        | x          |           |           |
|                                |      | Power plant (C)    | x       | x        |            |           |           |

Bayesian hierarchical models and subsequent analyses were carried out using the Markov chain Monte Carlo (MCMC) based software, OpenBUGS (Lunn et al. 2009). MCMC methods circumvent the need to analytically calculate parameter values from conjugate distributions by estimating posterior distributions based on conditional relationships within the model. Variance partitioning models used three mixing chains each including 500,000 iterations, and a 200,000 iteration burn-in period. Posterior samples were thinned so that 1 of every 50 iterations was used in subsequent analysis. This was done to reduce the influence of autocorrelation in the mixing chains.

Abundance estimation models also used three mixing chains each including 55,000 iterations and a 5,000 iteration burn-in period with no thinning. Reduction in iterations and thinning was allowed by a more rapid convergence of mixing chains in the abundance models. Stationarity was assessed in both model types through visual monitoring of chain history.
Chapter 3

Results

3.1 Sampling Overview

In 2010, each site (B and C) was sampled a total of 9 days between April 13 and June 1 (Table 3.1). A total of 244 samples were collected over this period with more than half of those taken at the downstream site (B). In 2011, sampling was adjusted through the addition of an upstream site (A), decrease of number of samples per day, and an increased number of days sampled. A total of 22 days were sampled between March 29 and June 7. Sampling was first initiated at the upstream site (A), and commenced at downstream sites (B and C) as larval walleye appeared in the drift. A total of 280 samples were collected in 2011, with 84, 136 and 60 collected from sites A, B, and C respectively.

Table 3.1: Summary of sampling effort by year and site.

<table>
<thead>
<tr>
<th>Year</th>
<th>Site</th>
<th>Samples</th>
<th>Days</th>
<th>Start</th>
<th>End</th>
</tr>
</thead>
<tbody>
<tr>
<td>2010</td>
<td>Downstream (B)</td>
<td>138</td>
<td>9</td>
<td>13-Apr</td>
<td>1-Jun</td>
</tr>
<tr>
<td>2010</td>
<td>Power Plant (C)</td>
<td>106</td>
<td>9</td>
<td>13-Apr</td>
<td>1-Jun</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>244</td>
<td>9</td>
<td>13-Apr</td>
<td>1-Jun</td>
</tr>
<tr>
<td>2011</td>
<td>Upstream (A)</td>
<td>84</td>
<td>19</td>
<td>29-Mar</td>
<td>7-Jun</td>
</tr>
<tr>
<td>2011</td>
<td>Downstream (B)</td>
<td>136</td>
<td>17</td>
<td>26-Apr</td>
<td>7-Jun</td>
</tr>
<tr>
<td>2011</td>
<td>Power Plant (C)</td>
<td>60</td>
<td>15</td>
<td>2-May</td>
<td>7-Jun</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>280</td>
<td>22</td>
<td>29-Mar</td>
<td>7-Jun</td>
</tr>
</tbody>
</table>
A total of 827 walleye were captured in 2010 with a majority of those fish coming from the downstream site (B) (Table 3.2). The total number of walleye captured increased in 2011 to 841; however the majority of the catch came from the upstream site (A). Larval walleye captured in the river were predominately of the yolk sac stage, with very few fish captured from later stages (Figure 3-1). However we did notice some differences between years, as larval walleye in 2010 were slightly larger and further developed than in 2011 (Table 3.2, Figure 3-1).

**Table 3.2:** Numbers of walleye captured by year and sample site, including size descriptions and first and last encounters.

<table>
<thead>
<tr>
<th>Year</th>
<th>Site</th>
<th>N</th>
<th>N – measured</th>
<th>Mean TL (mm)</th>
<th>SD TL (mm)</th>
<th>First Encouter</th>
<th>Last Encouter</th>
</tr>
</thead>
<tbody>
<tr>
<td>2010</td>
<td>Downstream (B)</td>
<td>694</td>
<td>193</td>
<td>8.5</td>
<td>0.62</td>
<td>13-Apr</td>
<td>26-May</td>
</tr>
<tr>
<td>2010</td>
<td>Power Plant (C)</td>
<td>133</td>
<td>133</td>
<td>9.1</td>
<td>0.87</td>
<td>13-Apr</td>
<td>19-May</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>827</td>
<td>326</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2011</td>
<td>Upstream (A)</td>
<td>695</td>
<td>695</td>
<td>6.9</td>
<td>0.51</td>
<td>11-Apr</td>
<td>24-May</td>
</tr>
<tr>
<td>2011</td>
<td>Downstream (B)</td>
<td>83</td>
<td>82</td>
<td>7.3</td>
<td>0.92</td>
<td>26-Apr</td>
<td>26-May</td>
</tr>
<tr>
<td>2011</td>
<td>Power Plant (C)</td>
<td>63</td>
<td>61</td>
<td>8.5</td>
<td>0.84</td>
<td>9-May</td>
<td>26-May</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>841</td>
<td>838</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 3-1: A description of the range of larval walleye stages observed in the Maumee River during sampling, 2010 to 2011. a) Early yolk sac larvae were observed predominantly in 2011 at upstream and downstream locations. b) Later stage yolk sac larvae were observed predominately in downstream and power plant locations during 2010 and power plant locations during 2011. c) Post yolk sac larvae were rarely observed in the Maumee River drift during 2010 and 2011.

3.2 Daily Water Measurement Summary

Water flow and temperature values differed between years. All discharge metrics (min, mean, max, and SD) were greater in 2011 than 2010 (Table 3.3). Stability and volume of water moving through the system may have an impact on larval fish behavior.
and survival. Power plant water intake volumes were also different between years, with the min and mean intake through the season in 2011 being less than 2010. The max intake was the same, but due to reduction of intake volume through the season, SD was greater in 2011. These numbers changed as First Energy responded to low energy demand during the larval walleye drift period, by shutting down some coal fired generators, thus reducing the cooling water demand. Most water temperature metrics (min, mean, and max) were slightly higher in 2010 than 2011, which may have impacted timing of spawn and larval hatch/developmental rates. Variability in temperature was slightly greater in 2011, but the magnitude did not appear to be a major factor in survival.

Table 3.3: Annual summaries of river discharge and power plant intake volumes (100 m$^3$/day$^{-1}$), as well as river water temperatures ($^\circ$C) over the period of study.

<table>
<thead>
<tr>
<th></th>
<th>Year</th>
<th>Min</th>
<th>Mean</th>
<th>Max</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>River Discharge</td>
<td>2010</td>
<td>34,741</td>
<td>301,797</td>
<td>846,515</td>
<td>204,669</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>51,378</td>
<td>464,436</td>
<td>1,915,669</td>
<td>428,857</td>
</tr>
<tr>
<td>Power Plant Intake</td>
<td>2010</td>
<td>19,330</td>
<td>24,344</td>
<td>28,232</td>
<td>4,117</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>6,976</td>
<td>12,996</td>
<td>28,232</td>
<td>6,888</td>
</tr>
<tr>
<td>River Water Temp</td>
<td>2010</td>
<td>7.32</td>
<td>16.15</td>
<td>25.34</td>
<td>4.39</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>6.25</td>
<td>13.68</td>
<td>24.82</td>
<td>4.90</td>
</tr>
</tbody>
</table>

3.3 Larval Drift Patterns Summary

Plotting averaged sample densities demonstrated the distinct patterns that occur in the Maumee River larval walleye drift. Larval walleye appear to be spatially aggregated within the middle of the water column (Figure 3-2). The degree of spatial aggregation was highest at sites and years with high larval densities (sites B 2010 and A 2011). Within each sampling site, higher average densities of larval fish were observed in the
lower portions of the water column as well as in the middle of the river channel compared to the river edges. These results strongly influenced the use of the negative binomial distribution (Poisson-gamma) in the description of spatial variation. Dramatic daily fluctuations in larval densities were seen at each location and year, with distinct periods of high abundance in each (Figure 3-3). Although daily densities were highly variable, there does appear to be some association between adjacent days, which led to the incorporation of an autoregressive relationship in abundance models.

**Figure 3-2:** Annual average densities of spatially distributed larvae at each tow location, site, and year. Dot size represents the relative density of larval fish at each location. Depths and transects correspond to locations outlined in Figure 2-2.
3.4 Variance Partitioning Estimates

Partitioning of variance indicates that at each site and year temporal variability was greater, as most probable values and uncertainty were consistently larger than spatial variability (Table 5, Figure 3-5). However, in 2011 uncertainty in the temporal variation was reduced by decreasing spatial sampling within days and increasing the number of days sampled, capturing more of the natural temporal variability. Also, temporal and spatial variability behave differently on a longitudinal scale in the river. In 2011, temporal variation decreased from site A to site B while spatial variability increased, indicating a more homogeneous mixture of larval fish downstream. These results indicate that, in general, temporal variability is a greater source of uncertainty and that redistribution of sampling effort was successful in reducing this without negatively affecting the capture of spatial uncertainty. Also, because of the high degree of temporal
variation seen upstream (A), further increased temporal sampling may be needed to
precisely characterize abundance at this site.

Table 3.4: Estimates of spatial and temporal variation by year and sampling site,
presented as the logged standard deviations from the variance partitioning
models. Most probable values (highest point on distribution), and 95% highest
density interval (HDI) demonstrate magnitude and uncertainty
associated with sources of variability.

<table>
<thead>
<tr>
<th>Year</th>
<th>Site</th>
<th>Spatial Variation (log SD)</th>
<th>Temporal Variation (log SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Most Probable Value</td>
<td>95% HDI</td>
</tr>
<tr>
<td>2010</td>
<td>Downstream (B)</td>
<td>4.4</td>
<td>2.9 - 6.2</td>
</tr>
<tr>
<td>2010</td>
<td>Power plant (C)</td>
<td>2.3</td>
<td>1.6 - 3.5</td>
</tr>
<tr>
<td>2011</td>
<td>Upstream (A)</td>
<td>1.6</td>
<td>1.2 - 2.6</td>
</tr>
<tr>
<td>2011</td>
<td>Downstream (B)</td>
<td>2.2</td>
<td>1.7 - 3.4</td>
</tr>
<tr>
<td>2011</td>
<td>Power plant (C)</td>
<td>2.0</td>
<td>1.3 - 3.6</td>
</tr>
</tbody>
</table>

Figure 3-5: Spatial and temporal variance estimates for each site and year. Dark gray
distributions represent spatial variation while the light gray distributions represent temporal.
The relationship between larval drift variability and environmental conditions is not fully understood, as it likely is driven by multiple interacting factors. However, in general, one may expect temporal variability to be influence strongly by environmental stability. As extreme and variable environmental factors increase (i.e. discharge and temperature) the periods of preferred conditions for spawning and egg/larval survival will decrease and become fragmented. This would translate in to discrete periods of high and low abundance as demonstrated by our sampled data (Figure 3-3). Under more stable environmental conditions, we may expect to see more consistent densities of larval fish though time. Interestingly, the opposite may be true spatially as stability in flow and temperature may allow for higher densities of fish. Lower turbulence would allow fish to select position in the drift as was seen at the downstream site (B) in 2010, leading to high aggregation (Figure 3-2). However, with only two years of data it is difficult to confirm any consistent influences on the spatial and temporal patterns.

3.5 Abundance and Mortality Estimates

3.5.1 Daily Larval Walleye Abundance

In 2011, upstream (A) larval abundance was much greater than that at other locations and years (Figure 3-6). Low numbers of larvae were produced early in the season, with a major hatching event beginning at the start of May, ending abruptly after peak daily abundance (mean, 36.97 million) in mid-May. In 2010 at the river mouth (B) there were two distinct abundance peaks, a small early peak in late April and a large peak in mid-May. In contrast, in 2011 abundance was more constant at the river mouth. While there was still a pattern of peaks and declines, the peaks were more frequent and extended
longer into May. Temporal patterns in the power plant canal (C) mirrored those downstream (B).

![Daily Abundance](image)

Figure 3-6: Daily larval walleye abundance estimates from key sample sites from 2010 and 2011. Black dots represent mean daily estimates while lines encompass the 95% credible intervals.

### 3.5.2 Annual Larval Walleye Abundance

In 2011, approximately 93.1 million larval walleye were transported from the upstream spawning grounds (A) however the uncertainty (95% HDI, 58.3 – 177) in this estimate is relatively high (Table 3.5, Figure 3-7). The number of fish passing through the downstream location in 2010 was less than that seen in 2011, approximately 20.95 and 38 million respectively. The uncertainty in 2010 annual export was greater than in 2011, likely due to the decreased temporal sampling and increased spatial aggregation. Annual abundance in the power plant intake canal (C) dropped between 2010 and 2011
from approximately 2.78 to 1.01 million respectively. This was partly due to a ~55% reduction in water intake at the power plant over the drift period.

Table 3.5: Model estimates of annual abundance and mortality by year and site. Most probable values (highest point on distribution) and 95% HDI demonstrate magnitude and uncertainty in estimates.

<table>
<thead>
<tr>
<th>Year</th>
<th>Site/Type</th>
<th>Most Probable Value</th>
<th>95% HDI</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Abundance (millions of walleye)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2010</td>
<td>Downstream (B)</td>
<td>20.95</td>
<td>10.11 - 62.07</td>
</tr>
<tr>
<td>2010</td>
<td>Power Plant (C)</td>
<td>2.78</td>
<td>1.39 - 6.82</td>
</tr>
<tr>
<td>2011</td>
<td>Upstream (A)</td>
<td>93.1</td>
<td>58.3 - 177</td>
</tr>
<tr>
<td>2011</td>
<td>Downstream (B)</td>
<td>38</td>
<td>24.4 - 65.10</td>
</tr>
<tr>
<td>2011</td>
<td>Power Plant (C)</td>
<td>1.01</td>
<td>0.64 - 2.46</td>
</tr>
<tr>
<td></td>
<td>Mortality</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2010</td>
<td>Entrainment</td>
<td>11.1%</td>
<td>1.8% - 32.0%</td>
</tr>
<tr>
<td>2011</td>
<td>Entrainment</td>
<td>2.8%</td>
<td>0.9% - 6.8%</td>
</tr>
<tr>
<td>2011</td>
<td>Natural</td>
<td>63.7%</td>
<td>26.0% - 86.0%</td>
</tr>
<tr>
<td>2011</td>
<td>Total</td>
<td>64.8%</td>
<td>28.2% - 87.3%</td>
</tr>
</tbody>
</table>

Figure 3-7: Annual larval walleye abundance estimates from key sample sites (upstream (A), downstream (B), and power plant (C)) from 2010 and 2011.
3.5.3 Annual Larval Walleye Mortality

Mean entrainment mortality and uncertainty were dramatically reduced between 2010 and 2011 from 11.1% to 2.8% respectively (Table 3.5, Figure 3-8). In 2011, the most probable values for natural mortality were 63.7% however uncertainty in these estimates was great (95% HDI, 26% - 86%). Entrainment did not appear to be a significant source of mortality in 2011, as natural mortality increase by only a small amount when entrainment was included bringing total in-river mortality to 64.8%. High levels of uncertainty in mortality estimates are caused by high natural variability in the system as well as a propagation of uncertainty in daily and annual abundance estimates.

![Figure 3-8: Annual larval walleye mortality estimates between key sites. Natural represents the percent loss of larvae between upstream (A) and downstream (B) sites, while Total is the percent loss from upstream (A) and cumulative downstream numbers (B+C). Entrainment is the percent loss of downstream larvae (B) to the power plant canal (C).](image-url)
Chapter 4

Discussion

4.1 Abundance and Variance Partitioning Models

The development of abundance models incorporating time and space is an important area of ecological study as the scale and complexity of ecological questions increases. The application of a Bayesian hierarchical model in estimating larval walleye abundance and mortality was beneficial on several accounts. The flexibility of these methods allowed us to accommodate the aggregated spatial distribution and dramatic temporal fluctuations of the larval walleye drift thereby increasing the reality of our estimates (Wilke 2003) and allowing for informative biological interpretations on daily and annual scales. The goal of ecological modeling is to mimic the study systems in a simplified form, but unless appropriate measures of uncertainty are included results can misrepresent reality (Levin et al. 1997).

When sampling larval fish quantifying uncertainty is important as they are naturally variable with multiple contributing factors. An additional benefit of the Bayesian method allowed variability in the data to propagate through the model explicitly quantifying uncertainty in estimated values (Clark 2003, 2005). Propagation of uncertainty is a
strength of Bayesian methods as the variability in data, and uncertainty in parameters and ecological processes are all expressed in the final estimates (Wilke 2003). Understanding this uncertainty can be beneficial to management agencies as they move forward in the decision making process with a complete understanding of the quality of knowledge they are working with. Additionally, the use of transparent and intuitive approaches to handling uncertainty is an important step in effectively communicating scientific results to all members of society (Bradshaw and Borchers 2000).

One potential source of uncertainty that we were not able to account for in this study, but deserves attention, is that of observation error. Conventional abundance sampling allows for the calculation of detection probabilities, that is the probability that an organism will be observed given it is present in the system. All organisms are imperfectly detected, and a detection probability allows for observed data to be corrected, more accurately representing actual abundance (Kery and Schaub 2012). The ephemeral nature of larval fish and dynamic characteristics of our system did not allow for fine scale temporal sampling, which would have been necessary to meet the assumptions in determining detection probabilities (MacKenzie et al. 2002, MacKenzie et al. 2003). However, I feel that our estimates of abundance are strong, as the temporal sharing of information buffers our daily estimates from both over and under estimation, each of which becomes more likely as organisms aggregate in space. Although, observation error is an important consideration in all abundance monitoring studies, often, due to organism ecology and system dynamics, the sampling of this process is not feasible. Additionally, the greatest source of uncertainty in my study was derived from temporal variation and the application of effort at this level was most beneficial.
Species ecology and system specific characteristics are important to consider when sampling larval fish. Partitioning variance with a Bayesian Poisson ANOVA allowed me to determine that within the Maumee River temporal variability was greater than spatial variability in the larval walleye drift and therefore a greater source of uncertainty in our estimates. In 2011 I increased the efficiency of our sampling protocol by reallocating spatial replication to temporal coverage. The increased quality of our sample data lead to a noticeable reduction in uncertainty in daily and annual abundance estimates as well as annual mortality estimates. A similar treatment of data collected from other systems, both lotic and lentic could lend insight in to the drivers of larval fish distribution and abundance substantially improving sampling methods and subsequent estimates.

4.2 Maumee River Larval Walleye Ecology

The great variability seen in organisms, especially the ephemeral stages of larval fish, is important to understand on a system specific basis to aid in effective sampling and ecological understanding. Quantification of spatial and temporal variability along the river’s gradient provided a window in to how the larval walleye drift takes place on the Maumee River, which facilitated efficient data collection and improved precision in estimates. The patterns observed on the Maumee River were incorporated into the abundance models and the results provide us a deeper look into drivers behind these patterns including organism ecology and physical system characteristics.

Within the drift, larval walleye exhibited a pattern of spatial aggregation, with higher densities found in the middle of the water column. These aggregated patterns were very evident during periods of high abundance and low discharge. As lithophilic spawners,
yolk sac larval walleye are naturally photophobic and initially have difficulty holding position in the water column (Balon 1975, Balon 1979) which may explain the propensity for higher observed densities at lower depths in the Maumee River (Houde 1969, Snyder 1978, Cooper et al. 1981). Additionally, migratory species of larval fish (i.e. walleye) have been shown to prefer areas of high current velocities (Pavlov et al. 2008), which helps explain our observations of higher densities near the theoretical thalweg at upstream (A) and downstream (B) sampling sites. Spatial aggregation may also be influenced by the physical properties of larval transport (Pavlov et al. 2008, Wolter 2008). Turbulent high flows likely disrupt spatial clumping patterns and move fish quickly downstream resulting in lower more evenly distributed densities in the drift. During lower flow periods with low turbulence, larval fish behavior may lead to increased spatial aggregation as fish select preferred drift locations. These patterns are evident at the downstream site (B), while 2010 was sampled at comparatively low discharge to 2011. Understanding of these drift characteristics were important in establishing an appropriate sampling protocol and generating accurate estimates of abundance.

The larval walleye drift periods in 2010 and 2011 (April-May) were similar to those observed in previous studies (Snyder 1978, Cooper et al. 1981, Mion et al. 1998). Walleye take advantage of the predictable seasonality of the Great Lakes region (Winemiller and Rose 1992, Winemiller 2005), spawning in the early spring as the system transitions to a more stable productive summer period. However, the discrete periods of high and low abundance and differences in the timing of peak abundance from year to year indicate that spawning success within this window is driven by stochastic
environmental conditions (Roseman 1997, Mion et al. 1998, Crane 2007, Zhao et al. 2009). Low early abundance occurred during periods of relatively high discharge (mid to late April), which may have limited the success of egg hatching due to mechanical damage or deposition in unsuitable incubatory habitats (Mion et al. 1998, Roseman 2001). Alternatively, the peak hatching events and highest abundances were observed during periods of low discharge in early to mid-May. Water temperature warming rates were similar between years, and although there was some daily variation there were no dramatic temperature changes that would reduce egg or larval survival (Smith 1974, Blaxter 1992). Peak downstream abundance occurred 6 days earlier in 2010 than 2011. This is likely a product of earlier declines in discharge, and warmer average daily water temperatures. Warmer temperatures may initiate earlier spawning and hasten egg development during incubation causing an earlier peak hatching event in 2010. In 2011, upstream (A) daily abundance patterns preceded those seen downstream (B), with peak abundance occurring 4 days prior. This gap is likely caused by higher river residence times during periods of low discharge. Although the larval walleye drift period is seasonally predictable, the daily abundance patterns are dependent on favorable environmental conditions.

Annual abundance of larval fish in the Maumee River and other systems can be used as a proxy for stock contribution, and potentially an early judge of annual recruitment. Annual upstream (A) abundance was predictably greatest as we sampled directly below the primary spawning reach. At this point larval fish surviving the hatching process were encountered prior to downstream drift, during which larvae may experience several sources of natural mortality. The estimate of approximately 93.1 million fish at the
upstream site (A) was substantially greater than previous estimates from the Maumee River (13-24 million, Mion et al. 1998). Similarly, annual downstream (B) abundance was lower in 2010 than 2011, displaying the interannual variability of walleye spawning success associated with a periodic life history strategy (Winemiller 2005). Annual power plant (C) abundance was an order of magnitude less than that downstream (B), which was also expected. The power plant canal (C) is seeded with downstream larval fish so the abundance is heavily influenced by the amount of water drawn from the river by the power plant, which on average uses an order of magnitude less than the river discharges (~24,000 to 300,000 100 m$^3$ *day$^{-1}$) over the sampled periods. Interestingly, the patterns in abundance at downstream (B) and power plant canal (C) sites moved in opposite directions between 2010 and 2011, which lead to very different estimates of entrainment mortality as discussed below. Annual estimates such as these generated over large temporal and spatial scales include a great deal of uncertainty. Displaying only point estimates of abundance without accumulated uncertainty can mislead interpretations in annual patterns.

Discrete rates of early larval fish mortality can have a substantial impact on recruitment success (Houde 1989, a et al. 1992, Houde 1997). Mortality through the larval period on average ranges from 95 to 99% between freshwater and marine systems (Houde 1994). However, larval development is a saltatory process (Kuznetsov 1972, Balon 1981) resulting in stage specific sources and rates of mortality (Houde 1997, Houde 2008), and larval walleye in the Maumee River are composed primarily of the yolk sac stage. Annual natural mortality in the Maumee River (~63.7%) was lower than conventional estimates (Houde 1994) as well as the average of previous daily estimates
from the Maumee and Sandusky Rivers (Jones et al. 2003). Much of this mortality in the Maumee River is likely attributed to predation (Letcher et al. 1996), environmental factors (Mion et al. 1998), or deposition of drifting larvae in sub-optimal bottom habitats (Balon 1981, Roseman 2001, Tuckerman 2010), especially in the highly modified lower Maumee River. Additionally, the proportion of surviving larval walleye retained in slow moving back water areas between sites is unknown and may contribute to an overestimate of in-river mortality. If lower rates of early stage mortality occur consistently in Maumee River, this could provide a significant advantage to the survival of fish produced in this system.

Anthropogenic source of mortality have shown to be substantial in many systems impacted by power plant entrainment (Kelso and Milburn 1979, Barnhouse 2000, Ager et al. 2008). In 2010 a relatively high percentage (~11.1%) of larval walleye at the river mouth were entrained in the power plant. This number dropped to approximately 2.8% in 2011, and is likely due to an interaction between power plant intake volumes and river discharge. At lower discharge, as seen in 2010, larval walleye are more concentrated (i.e. higher densities), while at higher discharge, 2011, larval walleye densities decrease.

When power plant water intake volumes are held constant, low discharge presents a situation where entrainment susceptibility is high, as the power plant draws in a high proportion of the total river discharge including high densities of larval walleye. Conversely, high discharge results in lower entrainment by the power plant. This relationship can be further manipulated by changing the volume of water taken in by the power plant, as was seen in 2011 when intake volumes dropped substantially over the walleye drift period. Total in- river mortality (~64.8%) in 2011 was not substantially
influenced by entrainment although if cooling water intake rates are not reduced during
the peak drift periods, entrainment may play a much larger role. Although entrainment
under certain environmental conditions (i.e. low river discharge and high power plant
intake volumes) can be high the ultimate influence on recruitment and stock abundance is
difficult to project (Barnhouse and Van Winkle 1988, Newbold and Iovanna 2007), as
fish encounter many more hurdles on their way to recruitment.

It is difficult to assess the overall importance of Maumee River larval walleye
mortality to annual recruitment without additional information about mortality once
exported from the river, as well as relative contributions from other spawning stocks.
However, what I can say is that a reduction in mortality at early life stages, in general,
will have a positive influence on the number of fish surviving to later life stages. Lake
and riverine spawned walleye experience very different abiotic and biotic conditions
during the early stages (Mion et al. 1998, Roseman et al. 2001). Winemiller (2005)
compares the periodic reproductive strategy to bet-hedging on a temporal scale, that is, an
individual spreads the risk of failed reproductive contribution over time by participating
in many spawning events through its life. This concept also applies to the population
level on a spatial scale. By partitioning reproduction over a diverse set of habitats, Lake
Erie walleye reduce the risk of total recruitment failure due to poor conditions in a single
habitat. At one point migratory walleye utilized greater extents of major Lake Erie
tributaries, as habitat is currently restricted in the Maumee River by the Providence Dam,
as well as many other streams (Hartman 1973). Because of the reduction in riverine
spawning habitats, recruitment is now more reliant on the success of open lake spawning
groups which may be contributing to the extremely high variability currently seen in
Lake Erie walleye recruitment (WTG 2010). Similar concurrent measures of early stage abundance and mortality from other systems used by the Lake Erie walleye spawning stock would be beneficial in understanding lake wide recruitment, while protecting and increasing habitat availability in these locations could help bolster population stability.
Chapter 5

Conclusion

My study has shown that both spatial and temporal variability are important factors to consider when sampling larval walleye in the Maumee River. Larval walleye exhibit highly aggregated spatial distributions, with most fish drifting in the lower middle water column. Temporal variability proved to be greater at all sampling locations within the river. By redistributing sampling effort in 2011 to account for temporal variability, I was able to improve the precision of abundance and mortality estimates. The level of uncertainty in our results demonstrates the difficulty in generating precise abundance estimates of highly variable organisms. Accounting for variability using Bayesian methods was beneficial, producing explicit measures of uncertainty facilitating a more transparent assessment of results.

The Maumee River larval walleye drift is dominated by the yolk sac stage. Daily abundance at all sites was related to river discharge. In 2010 and 2011, peak abundances occurred during periods of low discharge. Annual downstream (B) abundance fluctuated greatly between years indicating that contribution from the Maumee River sub-stock to lake wide recruitment is not consistent. High rates of in-river mortality were observed during 2011, however it is not understood how early stage mortality relates to late
stage survival and recruitment. Power plant entrainment mortality decreased between 2010 and 2011. This decrease was caused by the beneficial combination of environmental conditions and plant operations including; High River discharge leading to low larval fish densities, and low power plant water intake volumes over the larval walleye drift period.
References


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