



Bayesian hierarchical modeling of larval walleye (*Sander vitreus*) abundance and mortality: Accounting for spatial and temporal variability on a large river



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ABSTRACT

Larval fish are extremely variable in space and time while sampling of populations is generally restricted and incomplete. However, estimates of abundance and mortality are important for understanding population dynamics, habitat quality, and anthropogenic impacts. Acknowledging and addressing variability during sampling and data analysis are imperative to producing informative estimates. A combination of spatially and temporally distributed ichthyoplankton sampling and Bayesian hierarchical and state-space modeling was used to partition variance and estimate abundance and mortality of larval walleye (*Sander vitreus*) in the Maumee River during 2010 and 2011. System variability and degree of sampling coverage have a direct impact on the quality of abundance estimates. Small scale factors (i.e., within site and day-to-day) accounted for the most variation in larval walleye densities, therefore sampling should concentrate on capturing these sources. Bayesian state-space modeling can improve estimates by sharing information through time, properly accounting for uncertainty, and producing probability distribution based estimates. Larval fish are highly variable and difficult to sample; however, the application of Bayesian methods during the data analysis process can lead to improved estimates of abundance and informed management actions.

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Introduction

Estimates of larval fish abundance inform habitat protection, restoration (Jones et al., 2003), and mitigation of water withdrawal (Barnthouse, 2000) as well as providing insight into early life history dynamics (Mion et al., 1998). In large river systems, migratory fish larvae present a particular challenge as sampling is often restricted to relatively few replicates (Cyr et al., 1992), thereby neglecting both spatial and temporal information. Neglecting spatial and temporal coverage during sampling can lead to potentially misleading abundance estimates and uncertainty measures (Gibbs et al., 1998). Quantification of larval fish abundance is complicated due to high spatial and temporal variability (Cooper et al., 1981; Cyr et al., 1992; Snyder, 1978) driven by stochastic environmental conditions (Doyle et al., 2009), water currents (Martin and Paller, 2008; Roseman et al., 2005), time and location of spawning (McKenna et al., 2008), and larval behavior (Houde, 1969). Identifying sources of variability from the sampled data and accounting for sparse and variable data in the analysis process will ultimately lead to improved estimates of larval fish abundance.

The Maumee River, a tributary of western Lake Erie supports a distinct spawning population of migratory walleye (*Sander vitreus*)

(Merker and Woodruff, 1996; Strange and Stepien, 2007) which contributes to an important regional fishery (Gentner and Burr, 2010). The Maumee River population is part of a multi-stock system, with additional stocks reproducing in large tributaries (i.e., Detroit and Sandusky Rivers) as well as an open lake reef complex. Although these few large stocks are vital to the Lake Erie walleye population, critical information such as relative contribution from each system and patterns in annual system-specific production remain unknown. Annual estimates of larval abundance would help quantify the relative contribution of the Maumee River stock to lake-wide production and define its importance as a spawning and nursery habitat. This type of information could help guide management decisions on stock specific harvest policies and habitat restoration and protection. Additionally, abundance estimates are needed to assess the impact of larval entrainment into a coal fired power plant near the mouth of the Maumee River which may impact contribution from this system. Given the importance of larval fish production within the Maumee and other riverine spawning systems (Mion et al., 1998; Rutherford et al., 1997), it is critical to apply methods that account for the intrinsic challenges of sampling and estimating larval fish abundance.

Two data analysis methods, in particular, can help improve the estimation of larval fish abundance in large rivers. As part of the sampling process, current sample data can be evaluated with variance partitioning models, quantifying the relative importance of variation from spatial and temporal sources at multiple scales (Sims et al.,

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2006). This information can be used to inform subsequent sample allocation and ensure the capture of natural variation in the larval drift, improving sampling protocols and data quality. Post data-collection, state-space models allow for biological realism in the estimation procedure by accommodating spatial and temporal correlations in the observation and evolution processes (Harvey and Fernandes, 1989; Kery and Schaub, 2012; Wagner et al., 2013) while simultaneously accounting for spatial, temporal and process uncertainties (Cressie et al., 2009). These models limit the assumptions made about temporal trends in abundance. Although these models can be fit with traditional maximum likelihood methods, the intrinsic nature of larval fish data (i.e., sparse and variable) may necessitate a more flexible framework.

Bayesian hierarchical methods provide a framework for handling highly variable and potentially sparse larval fish data leading to improved estimates of larval abundance. These methods allow the sharing of information within groups based on an assumption of exchangeability. Exchangeability is assumed when there is a reasonable expectation that estimates (e.g., mean) among groups are related; however, there is no available information, such as a measured co-variate, to describe this relationship. The relationship between groups is then described with a higher level (i.e., global) distribution (Ntzoufras, 2009), where the individual group means are assumed to be drawn from the global group mean. During analysis, individual group means are adjusted toward the global group mean, a process called “shrinkage”. The degree of “shrinkage” depends on the strength of information in the individual and global groups. Groups with low sample size or high variation indicate less strength of information, and therefore receive a greater degree of “shrinkage” (Gelman and Hill, 2007; Gelman et al., 2014). The resulting estimates will improve as the overall estimation error is reduced while the individual groups maintain distinction (Efron and Morris, 1977). These methods are particularly beneficial in situations where portions of a data set are

limited or highly variable, as the individual groups draw strength from the ensemble. Consequently, Bayesian hierarchical methods should provide an approach to sampling and estimating abundance of larval fish in large rivers that is superior to other estimation methods.

The goal of this study is to evaluate larval walleye dynamics in the Maumee River. Specific objectives include: 1) quantifying spatial and temporal variability in larval walleye abundance to help inform sample allocation, 2) highlighting a data analysis framework to best estimate in-river abundance and mortality of larval walleye, and 3) comparing the performance of our estimation method over a range of sampling intensities along with conventional estimation methods. The results from this study will provide local information on the dynamics of larval walleye in the Maumee River and help improve larval fish sampling and estimation in other large rivers.

Methods

Study site

The Maumee River, the largest tributary by watershed area in the Great Lakes, enters Lake Erie along the southern shore of its western basin, and supports an important spawning population of walleye (Merker and Woodruff, 1996; Pritt et al., 2013) (Fig. 1). Walleye reproduction is concentrated between 25 and 30 km upstream, near Perrysburg and Grand Rapids, OH (Mion et al., 1998; ODW, 2010). After a period of incubation, larvae hatch and begin to drift downstream toward the lake during which time fish are subjected to several sources of mortality including: mechanical damage during transport, predation, and deposition in low quality habitats (Jones et al., 2003; Mion et al., 1998; Reutter and Herdendorf, 1984). The lower 12.5 km of the Maumee River is highly modified, supporting heavy shipping traffic and flows through the urbanized landscape of Toledo, OH

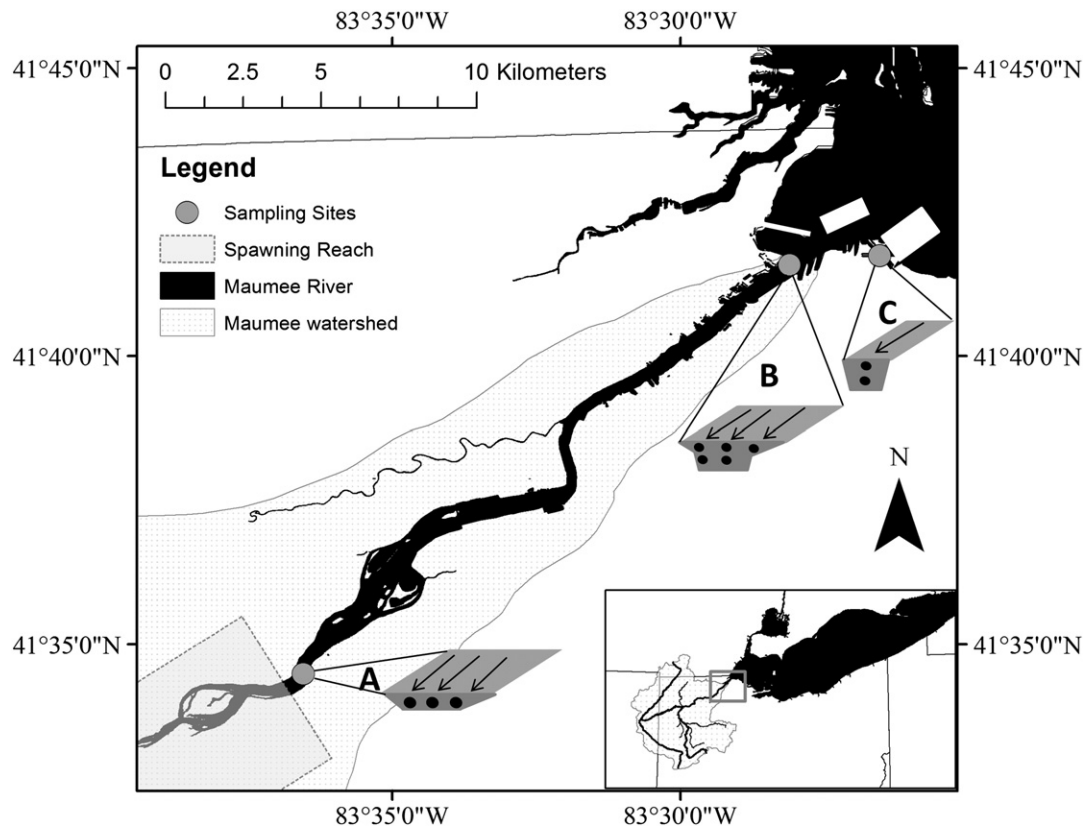


Fig. 1. Sampling area in lower Maumee River including representation of spatial distribution of larval tows at sampling sites (A, B, and C).

(Herdendorf, 1977). A coal fired power plant (i.e., the Bay Shore power plant) located near the river mouth draws cooling water directly from the river adding an additional source of mortality.

Sampling

We collected larval walleye in the Maumee River during spring 2010 and 2011 using paired ichthyoplankton bongo tows (Snyder, 1983). The bongo frame was fit with 350 μm and 500 μm mesh conical nets with 0.50 m diameter openings. Bongo nets were towed upstream at ~ 1 m/s against the current for 3–5 min depending on debris load in the river. Sample volumes were estimated with General Oceanics 2030R flow meters mounted in the mouth of each net. Larval fish were identified, following Auer (1982), and enumerated in the lab.

Larval walleye samples were collected at three sites along the river gradient, with multiple samples distributed spatially within the water column at each location (Fig. 1). The upstream site (A) was located just downstream of the lower reach of the primary walleye spawning habitat. Samples collected at this site were used to estimate the abundance of larval walleye emerging from the spawning riffles. The river is relatively shallow at site (A) with a maximum depth of less than 2.50 m. Three larval tow transects were designated at mid-depth (~ 1.25 m) spanning the river at this site. The downstream site (B) was located near the mouth of the river just upstream of the power plant water intake canal and is maintained by dredging to depths of ~ 9 m. Samples at this site were used to estimate the abundance of fish surviving downstream transport. Five tow transects were designated at this site; two near the east bank of the river (surface and mid-depth, ~ 4.50 m), two in the shipping canal (surface and mid-depth, ~ 4.50 m), and one near the shallow west bank (surface). The power plant site (C) was located just downstream of site B within the cooling water intake canal which draws water directly from the river's east bank prior to its mouth. The intake canal was ~ 4.50 m deep and ~ 65 m wide. Two tow transects were designated at this site; one at surface and mid-depth (~ 2.25 m). 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).

There were distinct differences between the 2010 and 2011 sampling protocols; changes were made in response to extreme observed temporal fluctuations in density in 2010. In 2010, samples were collected only from the downstream (B) and power plant (C) sites. In addition, samples were collected once per week with an emphasis placed on collecting many samples at each site per day (high spatial coverage and low temporal coverage). In 2011, the upstream (A) site was added and the number of samples collected per day was reduced, while two sample days were added per week (intermediate spatial and temporal coverage). Additionally, sampling was initiated early in the season at the upstream (A) site in 2011 to monitor for the start of larval hatching. This site was closest to the primary spawning grounds; and therefore, the first place larval fish would appear in the drift. Once fish were observed at the upstream location, sampling was initiated at the two downstream sites (B and C). Density was assumed to be zero at all locations until the first fish

were observed at the upstream (A) site. The total number of samples collected over each season was similar however effort was shifted from emphasizing spatial coverage in 2010 to a balance between spatial and temporal coverage in 2011 (Table 1).

Daily water measurements

The expansion of organism density to total abundance requires knowing the volume of the sampling environment (Royle, 2004), which for passively drifting larval fish in river habitats, necessitates measurements of daily system discharge. 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 (see the section on Estimating Abundance and mortality below). The Bay Shore power plant daily 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.). Power plant intake values were used in the volume expansion of daily density estimates to daily abundance in the power plant (C) sampling location (see the Estimating Abundance and mortality section below). Maumee River mean daily water temperature data were provided by NOAA's Center for Operational Oceanographic Products and Services. Data were collected from submerged temperature probes (Station ID: g10201) approximately 12.5 km upstream of the Maumee River mouth (NOAA Tides and Currents).

Larval walleye data

Within a site, each side of the bongo net was considered an independent sample on each sampled day. Sample densities between paired nets were most similar at high densities; however most of the positive catch samples (70%) were collected during periods of low density (i.e., between net average < 10 fish/100 m^3). There was no correlation observed between the two nets at low densities ($r = 0.003$), therefore the difference between nets represented small scale spatial variation and to include this in the estimate nets were treated as independent samples. Individual samples (i), were indexed within the day (j), site (k), and year (l) that they were collected. The count (n_{ijkl}) of larval walleye from each net was combined with the estimated volume of water sampled (v_{ijkl} , m^3) to calculate the density for each sample (D_{ijkl} , fish/100 m^3 , Eq. (1)):

$$D_{ijkl} = (n_{ijkl}/v_{ijkl}) * 100. \quad (1)$$

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) in evaluating variation in sampled densities and abundance estimation. Sampled larval densities for each tow location were plotted to visually examine spatial and temporal patterns in the larval walleye drift.

Quantifying spatial and temporal variability

Understanding the sources of variation within a system will help inform sampling allocation leading to improved quality of collected data. Variation in larval walleye densities collected at multiple spatial and temporal scales was partitioned using a Bayesian Poisson-lognormal ANOVA (Qian and Shen, 2007; Fig. 2). The Poisson distribution, conventionally used to model animal count and distribution data, has one parameter (λ) where the variance is equal

Table 1
Summary of sampling effort by year and site; total number of samples collected, number of days sampled, and start and end sampling dates.

| Year | Site | Samples | Days | Start | End |
|-------|-----------------|---------|------|--------|-------|
| 2010 | Downstream (B) | 138 | 9 | 13-Apr | 1-Jun |
| 2010 | Power plant (C) | 106 | 9 | 13-Apr | 1-Jun |
| Total | | 244 | 9 | 13-Apr | 1-Jun |
| 2011 | Upstream (A) | 84 | 19 | 29-Mar | 7-Jun |
| 2011 | Downstream (B) | 136 | 17 | 26-Apr | 7-Jun |
| 2011 | Power Plant (C) | 60 | 15 | 2-May | 7-Jun |
| Total | | 280 | 22 | 29-Mar | 7-Jun |

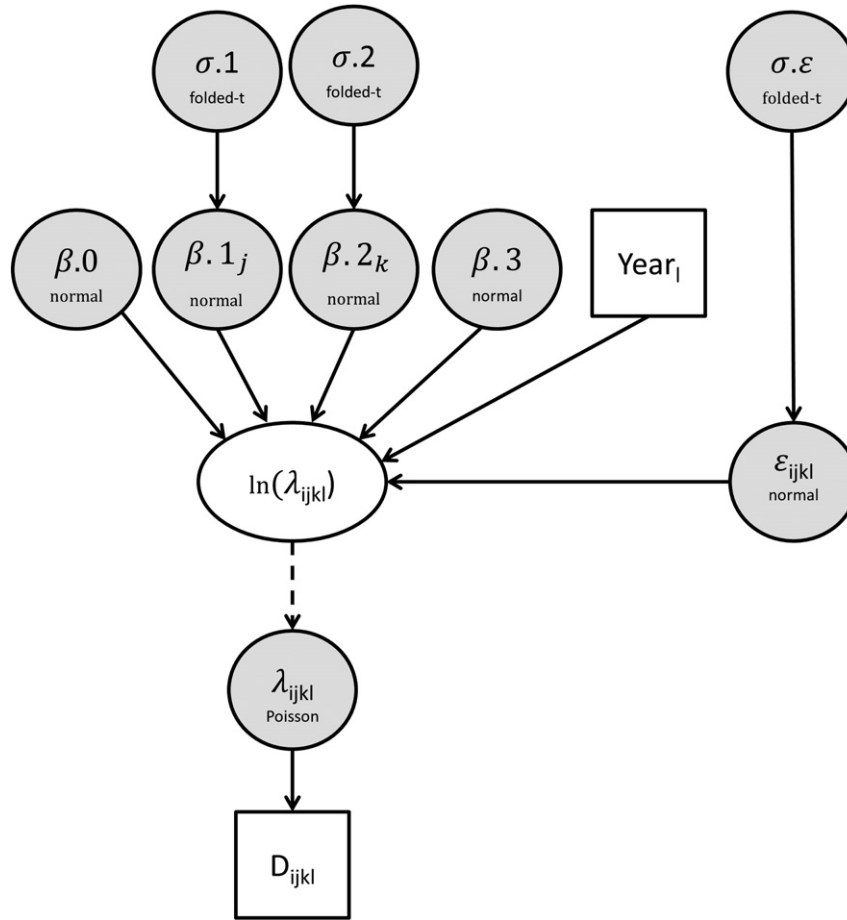


Fig. 2. A Bayesian Poisson-lognormal ANOVA directed acyclic graph displaying the relationships between model parameters and data. The data level is represented by a white box, where the model structure describing the data is represented by circles and arrows. Gray circles represent stochastic parameters which are estimated from the data based on indicated distributional assumptions. Solid arrows represent the direct parental relationships between upper (prior) and lower level parameters. The white circle represents a logical node which in this case are the natural log transformed individual sampled densities. The dashed line represents the relationship between the logical and stochastic estimates of sampled densities. The β parameters estimate the effect size of spatial and temporal levels on larval density samples, while σ hyper-priors estimate variance components.

to the mean (Eq. (2)), forming the assumption that organisms are randomly dispersed in their environment. Larval fish are often highly aggregated, breaking this assumption; however, overdispersion in the data can be accounted for in a Poisson model with the addition of an extra error parameter (ε) creating what is conventionally known as a Poisson-lognormal model (Kery, 2010; Millar, 2009; Qian and Shen, 2007; Eq. (3)):

$$D_{ijkl} \sim \text{Poisson}(\lambda_{ijkl}) \quad (2)$$

$$\ln(\lambda_{ijkl}) = \beta_0 + \beta_{1j} + \beta_{2k} + \beta_3 * year_l + \varepsilon_{ijkl} \quad (3)$$

where (i) represents individual samples, and (j) is independently sampled days (1–24), the first 8 corresponding to those sampled in 2010 and the last 16 representing those sampled in 2011. The three sites sampled are represented by (k), and year is represented by (l). The indexed β parameters ($\beta_1 \sim \text{normal}(0, \sigma_1)$; $\beta_2 \sim \text{normal}(0, \sigma_2)$; $\beta_3 \sim \text{normal}(0, 0.001)$) are the differences from the overall mean of 2010 ($\beta_0 \sim \text{normal}(0, 0.001)$) with common priors for each group. Year was included as a fixed factor given that only two years are included in the study making it difficult to estimate random effects. Extra (i.e., unexplained) variation, attributable to variation in the spatially distributed samples within sites, is accounted for with an overdispersion parameter ($\varepsilon_{ijkl} \sim \text{normal}(0, \sigma_\varepsilon)$).

Group level standard deviation priors (σ s) used low information folded- t distributions ($\sigma \sim \text{Student} - t(0, 0.001, 2)$) as described by Kruschke (2011). Finite-population standard deviations, which provide more precise estimates, were calculated for comparisons (Gelman and Hill, 2007). The standard deviation values (σ) for each level represent the proportional amount of spatial (within site and site) and temporal (day and year) variation of larval walleye densities. A larger value indicates a greater source of natural variability in the systems, and therefore greater potential source of uncertainty.

Sample data were subset to include only days within the active larval drift period which included the first and last dates that larval walleye were observed in each year. This is a simplifying assumption as larval fish may have been present at low densities outside of the “active drift” period, resulting in false zeroes (Pritt et al., 2014). However, our sampling design was not set up to address changing detectability through the season. Excluding these periods and assuming that all zeroes are true may lead to a slight overestimation of both spatial and temporal variability.

Estimating abundance and mortality

Recognizing sources of variation is an imperative step in understanding system dynamics. It is equally important to account for these sources of variation when estimating values of interest such as abundance and mortality. Individual Bayesian state-space (BSS) models

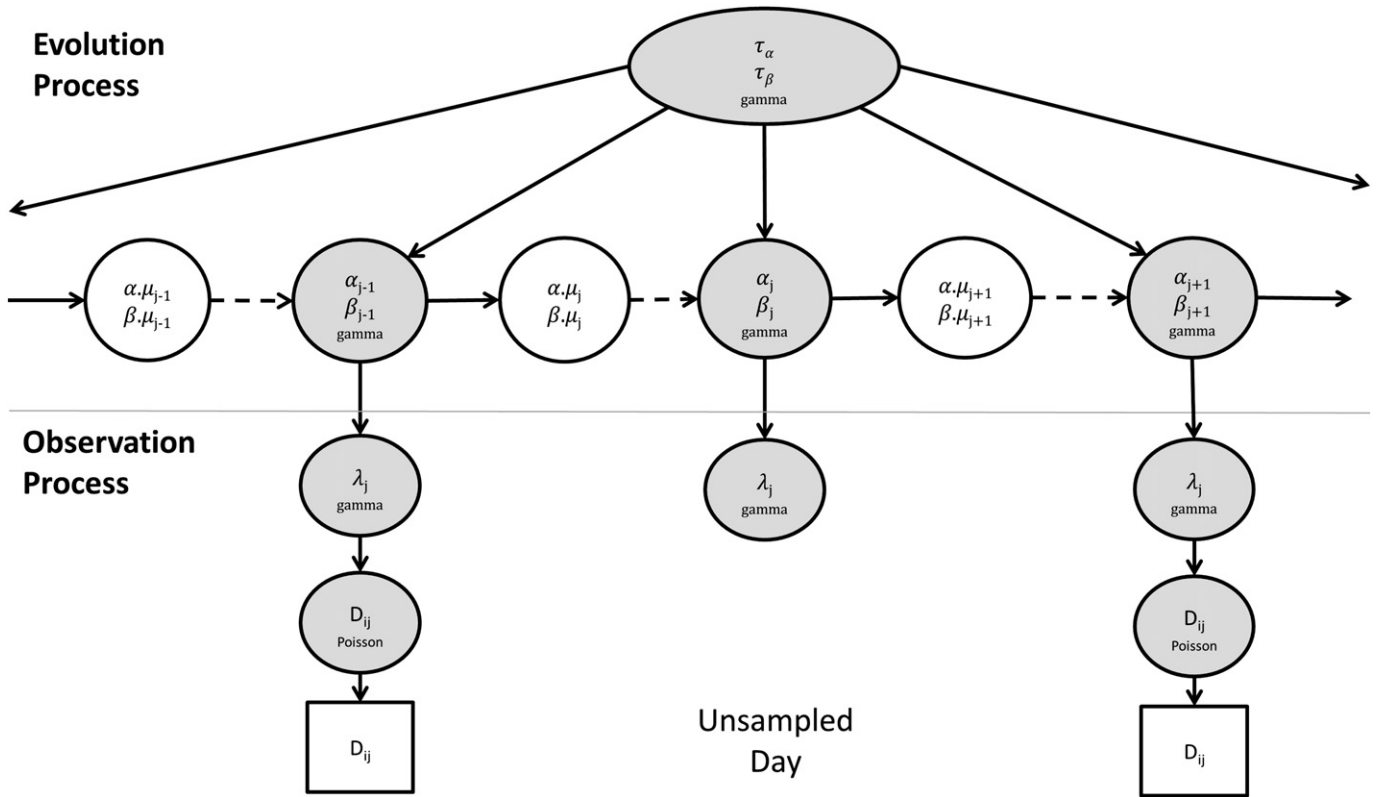


Fig. 3. A Bayesian state-space directed acyclic graph displaying relationships between parameters from the observation and evolution processes. The data level is represented by a white box, where the model structure describing the data is represented by circles and arrows. Description of parameters and connecting arrows match that of Fig. 3. The observation equation estimates daily densities from the observed data using a Poisson-gamma mixture. Information is shared between days through the evolution of α_j and β_j mean parameters. The variance of α_j and β_j parameters is governed by global hyper-parameters (τ_α, τ_β).

were used to estimate larval walleye abundance at each site and year. These models accounted for spatially aggregated distributions of larval walleye within days by using a negative binomial distribution in the form of a hierarchical Poisson–gamma mixture (Ntzoufras, 2009; Royle, 2004). A Poisson distribution was used to represent individual samples (D_{ij} ; Eq. (4)), while a gamma prior distribution described the daily mean density (λ_j ; Eq. (5)). This step represents the observation process in classical state-space modeling (West and Harrison, 1989; Fig. 3):

$$D_{ij} \sim \text{Poisson}(\lambda_j) \tag{4}$$

$$\lambda_j \sim \text{gamma}(\alpha_j, \beta_j). \tag{5}$$

Under the assumption that larval hatching was driven by a continuum of environmental factors leading to temporally related hatching events, information was shared between days. Conjugate gamma prior distributions were used to represent the shape and scale parameters (α_j, β_j) of the daily density estimates (λ_j). The prior shape and scale parameters for the α_j and β_j parameters can be expressed as mean and precision (Eqs. (6) and (7); Ntzoufras, 2009) where:

$$\alpha_j \sim \text{gamma}(\alpha \cdot \mu_j * \tau_\alpha, \tau_\alpha) \tag{6}$$

$$\beta_j \sim \text{gamma}(\beta \cdot \mu_j * \tau_\beta, \tau_\beta). \tag{7}$$

State-space models using a Poisson–gamma observation equation share information through the gamma prior parameters (Harvey

and Fernandes, 1989), where the posterior distributions of α_{j-1} and β_{j-1} are set as the prior distributions for α_j and β_j . Typically information discounting would be applied by multiplying the α_{j-1} and β_{j-1} parameters by a value between 0 and 1 which enables the loss of information as time passes (Lamon et al., 1998). However, no discount factor was applied in this study allowing the maximum amount of information to be shared between days, acknowledging that our sampling may not have completely captured the episodic and aggregated nature of larval drift patterns. A global precision hyper-prior was applied to each of the scale parameters ($\tau_{\alpha, \beta} \sim \text{dgamma}(0.1, 0.1)$), allowing the sharing of variance information among all days. This temporal sharing of information is conventionally referred to as the system or evolution process (West and Harrison, 1989; Fig. 3).

The gamma distribution representing the daily density estimates is comprised of two parameters representing shape (α) and scale (β), neither of which is ecologically meaningful. The value of interest (i.e., $mean_j$) is calculated by dividing the two parameters (Eq. (8)) returning the mean of the daily density estimate:

$$mean_j = \frac{\alpha_j}{\beta_j}. \tag{8}$$

Daily mean density estimates ($mean_j$, fish/100 m³) were expanded to daily abundance in the river (sites A and B) by multiplying it with the average daily river discharge and in the power plant intake canal (site C) by water intake values (e.g., volume units of 100 m³/day). Daily abundance estimates were summed to produce a total in-river estimate of abundance (fish/year) for each site (A, B and C). The total abundances at the three sites were used to estimate the rate of loss (i.e., mortality) between each. Three estimates of in-river mortality were calculated; *natural mortality* (A to B, Eq. (9)),

entrainment mortality (B to C, Eq. (10)), and Total in-river mortality (A to B–C, Eq. (11)):

$$\text{Natural mortality} = 1 - (B/A) \quad (9)$$

$$\text{Entrainment mortality} = C/B \quad (10)$$

$$\text{Total mortality} = 1 - ((B-C)/A). \quad (11)$$

Uncertainty in annual estimates was calculated as the 95% highest density interval (HDI) while estimates were reported as the most probable values. HDI and the most probable values provide more representative descriptions of central tendency for skewed distributions than mean and standard credible intervals based on standard deviation or quantiles. The 95% HDI represents the shortest interval that encompasses 95% of the distribution density, where the min and max of the interval have the same height or probability (Kruschke, 2011). HDIs are interpreted in the same way as standard Bayesian credible intervals, where some value has a 95% probability of occurring within the interval. The most probable value represents the peak of the distribution (i.e., mode), the value with the highest probability of occurrence.

One of the benefits of using Bayesian methods is the ability to make probabilistic comparisons. The probability that any two estimates are the same or that an estimate is above or below some threshold can be determined by calculating the area under the probability density which encompasses the interval of interest. This interval can be expressed as a discrete value or the range of overlap between two distributions. Quantifying estimates as probabilities results in a more intuitive expression of information which is beneficial in the decision making process.

Model and sampling intensity evaluation

Model performance was assessed through a simulation study, where a time series of “known” larval densities was generated and sampled. In total, nine hypothetical scenarios that included sampling different numbers of days per week and different numbers of samples within each day were evaluated. Daily densities under a subset of sampling scenarios and total annual abundance under each scenario were estimated using Bayesian hierarchical and state-space models and compared with results from more conventional estimation methods (assumption of no change between dates and linear interpolation between dates). Details on the model and sampling intensity evaluation can be found in the Electronic supplementary material (ESM) Appendix S1.

Model computation

Bayesian hierarchical and state-space models were carried out using the Markov chain Monte Carlo (MCMC) based software, OpenBUGS v3.2.2 (Lunn et al., 2009). OpenBUGS was activated (ESM Table S2) and results were summarized through the R project (R Development Core Team, 2013) based R2OpenBUGS v3.2-2.2 package (Sturtz et al., 2005). The variance partitioning model used three mixing chains including 750,000 iterations and a 500,000 iteration burn-in period per chain. Posterior samples were thinned so that 1 of every 10 iterations was used in subsequent analysis. Bayesian state-space abundance and mortality models and model evaluation scenarios (ESM Table S1) used three mixing chains each including 30,000 iterations and a 10,000 iteration burn-in period per chain thinned to 1 of every 10 iterations. Thinning was applied to reduce the influence of autocorrelation in the mixing chains and improve convergence. Convergence was assessed in both model types through visual monitoring of chain history and the R-hat statistic (Gelman et al., 2014; Gelman and

Hill, 2007). The R-hat statistic is a comparison of the weighted total and within chain variances, where convergence is assumed when the two variances are approximately proportional. This R-hat statistic indicates convergences at values <1.1, with complete convergence occurring at 1. The interpretation of the R-hat statistic is that additional iterations will not significantly improve parameter estimates at R-hat values ≤ 1.1 .

Results

Quantifying spatial and temporal variability

The larval walleye drift was dominated by early yolk sac larvae. Larval walleye were variable in both space and time (Fig. 4) with the highest density aggregations occurring in the lower portions of the water column as well as in the middle of the river channel. The degree of spatial aggregation (i.e., variation in densities) was highest at sites and years with high larval densities (sites B 2010 and A 2011). Daily fluctuations in larval densities were observed at each location and year, with distinct periods of high abundance in each (Fig. 4). The variance partitioning model showed that small scale variability (within site and day) was greater than large scale variability (site and year) (Fig. 5). The greatest variation was attributed to unexplained (within site, 2.92), a source which is derived from variation between replicate samples collected at each site and day. Daily variation (2.53) was the second highest contributor followed by site (1.10) and year (0.48).

Daily water measurements

Daily river water discharge and temperature measurements showed similar patterns between years; however, power plant water intake numbers were drastically different (Fig. 6). Although river discharge was variable, each year showed consistent periods of high discharge during April and late May with a period of low discharge in early to mid-May. Power plant water intake values were consistently high during 2010; however these numbers decreased in 2011 during the walleye drift period. Water temperature warming rates were similar between years, with overall average temperatures being slightly higher in 2010.

Estimates of abundance and mortality

At each river location and year, low abundances of larval walleye were observed early and late in the season, while the highest abundances occurred in early to mid-May (Fig. 7). Peak daily larval abundance at the upstream location (A) was 39.3 million (95% CI 33.9–44.8, May 12) in 2011. At the downstream location (B), peak daily abundance of larval fish in 2010 was 4.6 million (95% CI 2.9–6.3 million, May 10) and in 2011 was 3.1 million (95% CI 0.9–6.7 million, May 16). Peak abundance at the power plant location (C) occurred at similar times as those downstream (B) at 0.21 million (95% CI 0.07–0.37 million, May 10) and 0.15 million (95% CI 0.09–0.24 million, May 12) in 2010 and 2011 respectively. In general, unsampled days were estimated with a higher degree of uncertainty than sampled days.

In 2011, approximately 89.3 million larval walleye were produced at the upstream spawning grounds (A); however, the uncertainty (95% HDI, 71.7–144.2 million) in this estimate was high (Fig. 8). The most probable number of fish passing through the downstream location (B) in 2010 (29.5 million; 95% HDI, 12.5–84.5 million) was less than that seen in 2011 (32.2 million; 95% HDI, 20.8–52.07 million). However, uncertainty was much greater in 2010 with the probability distribution encompassing that of 2011. Resulting conclusions are that there is a 66.8% probability that abundance between years was the same, with a 9.5% probability of 2010 being less and a 23.7% probability of being greater based on the degree of distribution overlap. Annual abundance in the power plant intake canal (C) dropped between 2010 and 2011

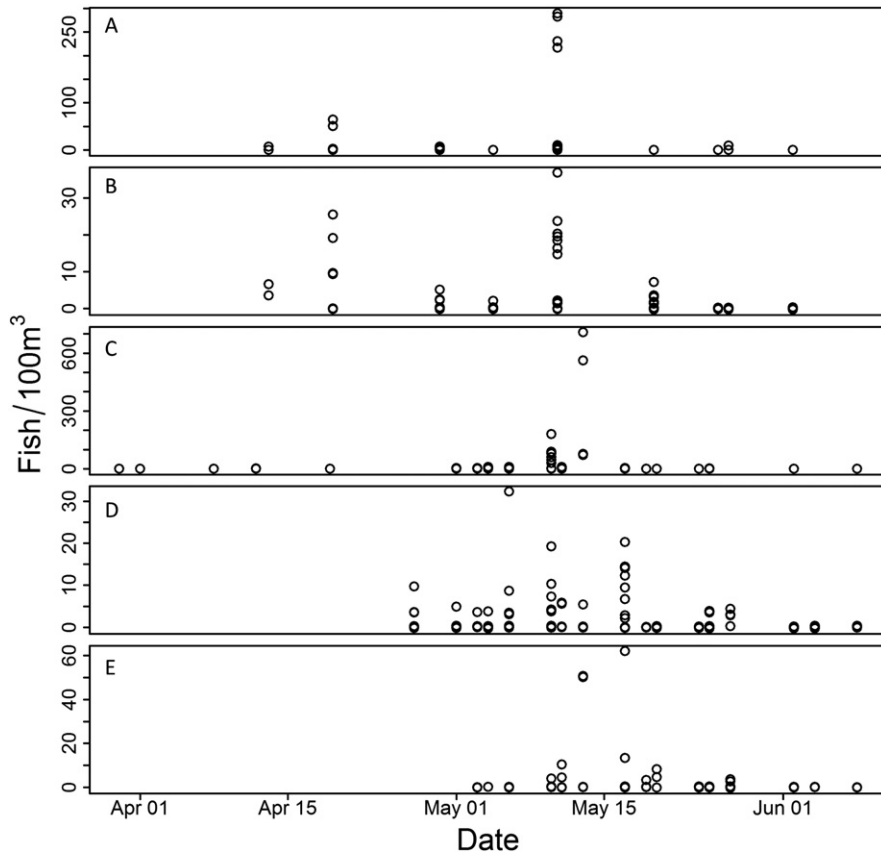


Fig. 4. Sample densities (fish/100 m³) of larval walleye displaying the observed spatial and temporal variation in the larval drift at (A) 2010 site B, (B) 2010 site C, (C) 2011 site A, (D) 2011 site B, and (E) 2011 site C. Observed densities were jittered to show overlapping values.

from approximately 2.2 million (95% HDI, 1.0–4.3 million) to 0.8 million (95% HDI, 0.5–1.3 million), resulting in a 91.8% probability that entrainment was greater in 2010.

Mean entrainment mortality and uncertainty were reduced between 2010 and 2011 from 4.5% in 2010 (95% HDI, 1.0–15.9%) to 2.18% in 2011 (95% HDI, 1.1–4.3%) (Fig. 9). These results indicate a

71.8% probability of higher entrainment mortality in 2010. In 2011, natural mortality was 66.8% however uncertainty in this estimate was high (95% HDI, 42.4%–83.5%). Entrainment did not appear to be a significant source of mortality in 2011; when combined with natural mortality, total in-river mortality increased to 67.6% (95% HDI, 43.2%–84.0%).

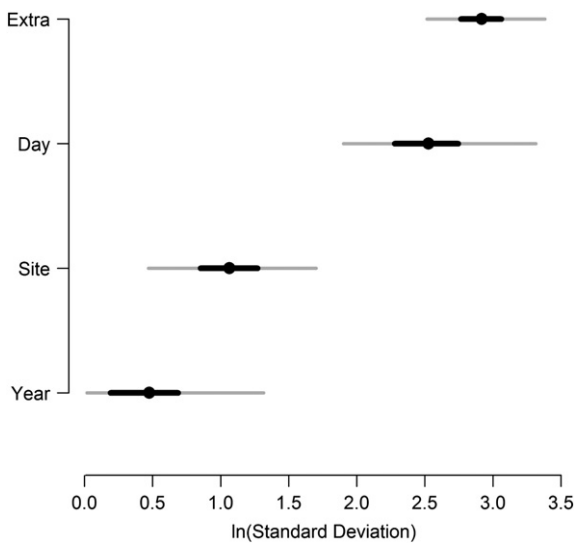


Fig. 5. Variance component estimates of larval walleye densities in the Maumee River during 2010 and 2011. Estimates are displayed as natural log transformed standard deviation of densities including contributions from year, day, site and extra (within site). Black dots represent estimated posterior means, thick black lines represent 50% credible intervals, and thin gray lines represent 95% credible intervals.

Model and sampling intensity evaluation

Accuracy and precision of daily and annual abundance estimate are highly dependent on sample data quality. The representativeness of sample data predictably decreased with decreasing sample coverage (ESM Fig. S1). Reduction in sample coverage typically led to inaccuracies in daily density estimates and underestimates of annual abundance as fewer high density values and days were included in analyses (ESM Fig. S2 and S3). Intense to intermediate sampling coverage led to reasonable estimates of daily and annual abundance. Bayesian methods typically adjusted high and low sampled densities toward the “known” population mean, improving daily estimates. All sample methods (Bayesian state-space, no change, and linear change) performed similarly under intense sampling scenarios, while variation between estimates increased as sample coverage decreased. Appropriate sampling coverage will result in reasonable estimates of mean abundance with either estimation method, while incorporating Bayesian methods will provide representative measure of uncertainty in the form of probability distributions.

Discussion

The application of Bayesian hierarchical methods when working with larval fish can improve estimates of abundance and mortality. Extreme variability in distribution and abundance coupled with the

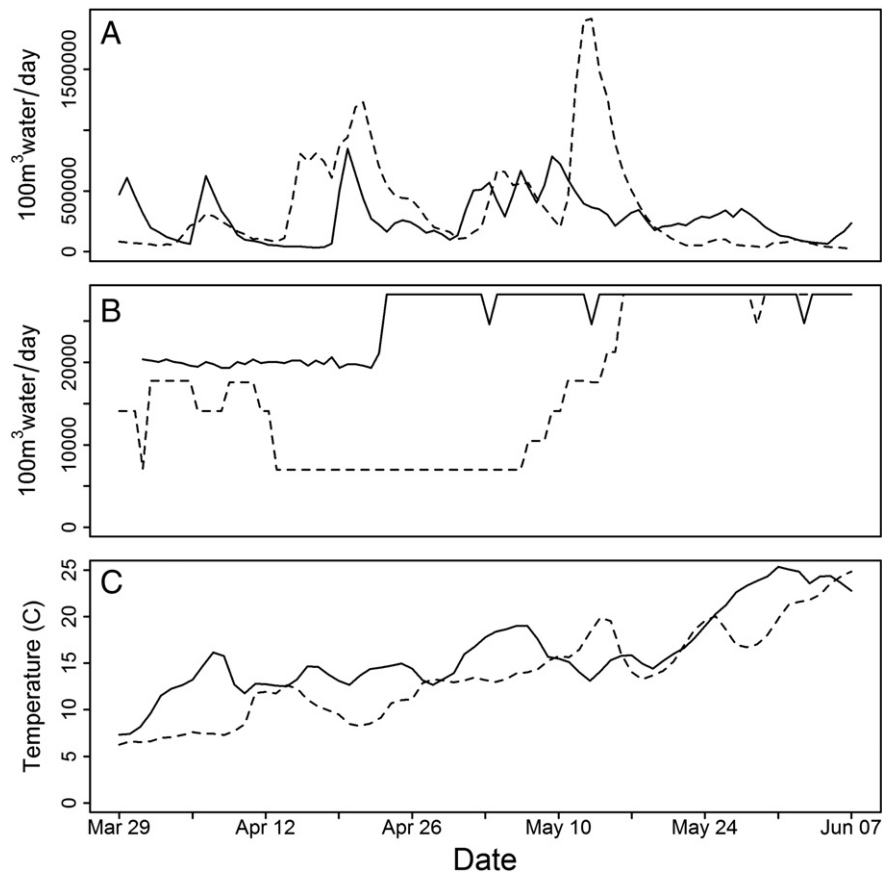


Fig. 6. Daily water flow measurements from the Maumee River (A) and Bay Shore power plant intake (B), and Maumee River water temperatures (C) collected in 2010 (solid lines) and 2011 (dashed lines). These values were used in the volume expansion of estimated daily larval densities to daily abundance and back calculation of peak larval hatches.

logistical constraints associated with larval fish sampling in large systems often leads to incomplete spatial and temporal information. However, a careful consideration of spatial and temporal patterns can improve monitoring of the species and system of interest (Oakley et al., 2003; Yoccoz et al., 2001). Specifically, variance partitioning models are a useful tool for evaluating the effectiveness of sampling protocols, and informing future sampling efforts (Larsen et al., 2001; Sims et al., 2006). Capturing natural sources of variability during the sampling process is the most important step in generating sound estimates of abundance. The application of Bayesian state-space modeling during the estimation process can partially overcome the challenges presented by restricted sampling of a variable population by sharing information among days (Gelman and Hill, 2007) and producing informative probabilistic uncertainty estimates. Coupling these approaches, when working with larval fish on the Maumee River, has led to improved sampling and estimates of abundance.

Variance partitioning models showed that small scale temporal and spatial patterns (i.e., day-to-day and within site) contributed more variability in larval fish abundance than large scale patterns (i.e., between sites and years). These small scale patterns in larval fish abundance are linked to the extreme variability in the physical conditions of the river (Thoms, 2006). For instance, extreme fluctuations in river discharge or temperature can influence walleye egg and larval survival (Crane and Farrell, 2013; Mion et al., 1998) leading to discrete peak hatching events bracketed by periods of low abundance (D'Amours et al., 2001). This relationship is exacerbated by the protracted process of walleye spawning and incubation contributing to high day-to-day variability in larval walleye abundance. Additionally,

once fish hatch and enter the drift, spatial variability of larval walleye is influenced by larval behavior (Balon, 1975, 1979) and physical conditions of the river system (Pavlov et al., 2008). Whereas at low discharge, negatively buoyant photophobic larvae concentrate lower in the water column; however at higher discharge, turbulent flows likely override these factors homogenizing larval fish distributions. Understanding the mechanisms contributing to variation is imperative to the collection of quality data and improvement of subsequent abundance estimates.

Identifying sources of variability to optimize sample allocations is an important step in improving estimates of abundance; however implementing idealized sampling protocols is often not feasible. Larsen et al. (2001) describe the major sources of variation in this study (i.e., day-to-day and within site) as interaction or ephemeral variation due to the influence of environmental conditions (i.e., discharge and temperature); the effect of which can be reduced by increasing replicate samples at these levels. Increased daily sampling will improve subsequent estimates given high day-to-day variability; however, this increase should not come at the complete neglect of within site spatial sampling. Cyr et al. (1992) provide a method for determining the appropriate number of replicate samples for monitoring larval fish abundance at a single site and the desired level of precision. When applied to data from this study (with desired precision = 0.3 CV), an across survey average of 20 replicate samples per site per day would be required. This intensive level of sampling was not feasible during our study; however we were able to improve the quality of data collected by acknowledging the proportional importance of day-to-day and within site variability and adjusting sampling between 2010 and 2011. Ultimately monitoring goals and logistical restrictions will limit the

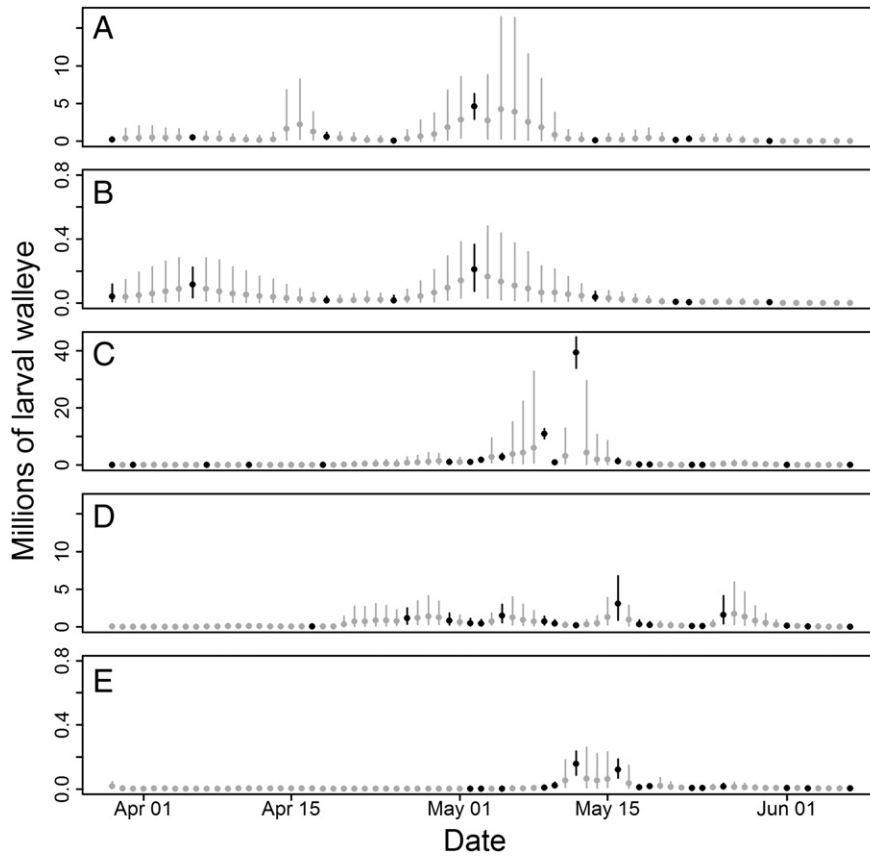


Fig. 7. Daily abundance estimates from 2010 to 2011 at (A) 2010 site B, (B) 2010 site C, (C) 2011 site A, (D) 2011 site B, and (E) 2011 site C. Dots represent posterior mean daily abundance estimates, while lines represent 95% Bayesian credible intervals. Black values are estimates of sampled days, while gray values are estimates of unsampled days.

sampling effort and precision of data collected at a single site through time, which makes the data analysis methods critical to evaluating estimates of interest.

One of the benefits of Bayesian hierarchical methods lie in the sharing of information (Gelman and Hill, 2007), which is particularly useful when working with incomplete data collected from highly

variable larval fish. Applying state-space models in a Bayesian framework allowed for the temporal sharing of larval density information, which improves on estimation made from raw data alone by compensating for days with few samples collected or high variation. For example, a day sampled with few replicates or one that displays high variation is not likely a reliable representation of the population

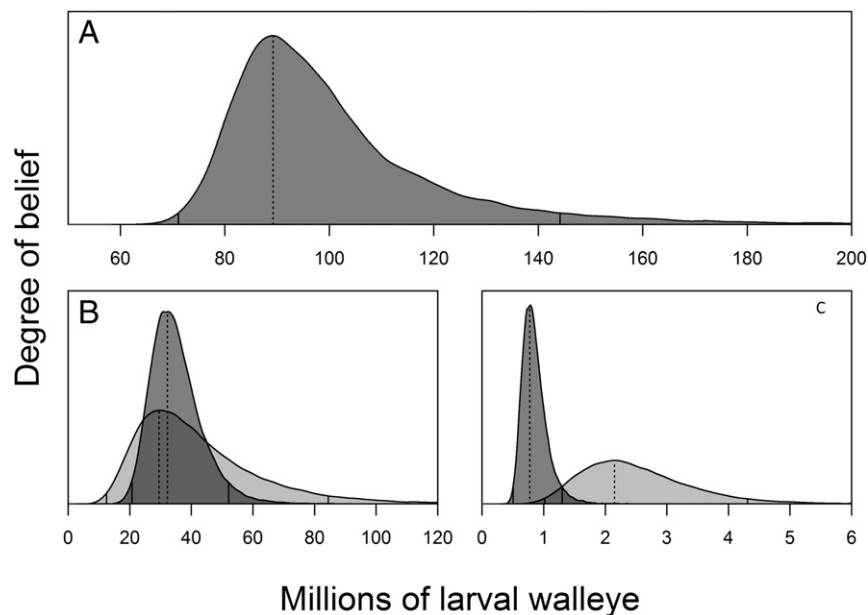


Fig. 8. Annual larval walleye abundance estimates at (A) site A, (B) site B, and (C) site C and years 2010 (light gray) and 2011 (dark gray). The distribution peak represents the most probable values (dashed lines), while the solid vertical lines designate the 95% highest density intervals.

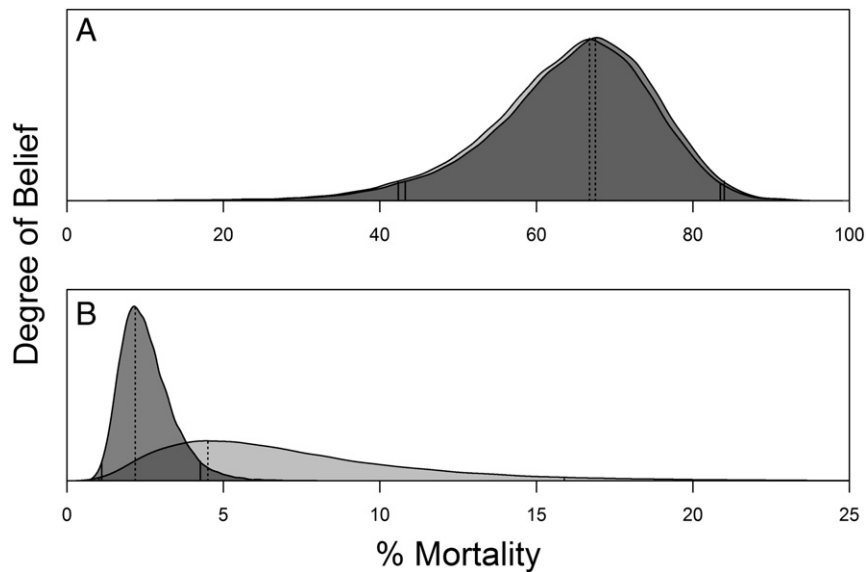


Fig. 9. Annual larval walleye mortality (%) estimates between sample sites. Natural mortality (A, light gray) represents the percent loss of fish between upstream and downstream sites, while total mortality (A, dark gray) is the percent loss between upstream and downstream sites in addition to power plant entrainment. Entrainment mortality (B) is the percent loss of downstream fish to the power plant canal, where light gray represents 2010 and dark gray 2011. Dashed lines represent the most probable values, while solid lines represent the 95% highest density intervals.

(i.e., daily density); however we can improve the estimate by making the reasonable assumption that those days close to one another are similar. The resulting estimate (mean and variance) is then adjusted. This adjustment, or “shrinkage”, is driven by strength of information (i.e., number of samples and variation) from within the group, which in our case includes the surrounding days. Our model evaluation and sampling intensity analysis highlight this improvement as mean estimates of daily densities were typically closer, and credible intervals predominantly encompassed “known” densities at intensive and intermediate sampling levels.

An additional benefit of employing Bayesian methods is the seamless propagation of uncertainty and description in the form of probability distributions. In our case, uncertainty is derived from the spatial distribution of fish, day-to-day fluctuations, and also in the estimating process itself. Systematically accounting for each source of uncertainty produces realistic estimates that engender credibility and confidence in subsequent interpretations of the data (Cressie et al., 2009). Describing uncertainty as a distribution allows for probabilistic inferences to be drawn from and between estimates. This is particularly useful when management decisions must be made, while the consequences of management options are unclear or dramatically unbalanced (Ellison, 1996).

The application of these methods in the Maumee River allowed us to draw reasonable conclusions about larval dynamics in the presence of uncertainty; particularly for larval walleye mortality. Direct entrainment occurred, but decreased from ~4.5% to ~2.2% between 2010 and 2011. Although the 2010 estimate included high levels of uncertainty, the overlap between estimates was relatively low which allowed us to conclude that there was a 91.8% probability that entrainment was higher in 2010. However, differences in abundance estimates between years at the downstream site (B) were not as clearly defined as estimates overlapped by 66.8%. Even so, we are able to conclude that entrainment mortality decreased by a probability of 71.8% from 2010 to 2011, likely due to the reduction in power plant water usage during this period. Additionally, in 2011 the impact of entrainment mortality was shown to be very low when compared to natural mortality resulting in a small increase in total mortality. Although the potential influence of power plant entrainment on larval walleye production is a

concern, the proportional influence of this factor is very small. The Maumee River's watershed has been extensively modified (Karr et al., 1985) which undoubtedly has contributed to a reduction in biological integrity (Karr and Dudley, 1981) contributing to “natural” larval mortality. From a management standpoint, these results suggest that focusing resources to improve biological integrity of the River would be a better investment due to its proportionally greater contribution to larval walleye mortality.

Annual estimates of larval walleye abundance are important in determining productivity and contribution from distinct spawning populations. Production has the potential to be highly variable as previous estimates from the Maumee River ranged from 13.4 to 24.8 million (Mion et al., 1998), far less than the 89.3 million estimated in 2011 of this study (site A). However comparing these estimates without the associated measures of uncertainty can be misleading as the sampling protocols used to generate them may be vastly different. It is clear from our model evaluation and sampling intensity analysis and the overlap in downstream estimates that the development in quality sampling protocols is imperative to assessing changes in annual abundance of larval walleye. This study occurred on a short time scale and limits our ability to generalize the importance of the Maumee River to Lake Erie walleye recruitment. However, continued monitoring and similar quantification of stock specific contributions, in this case the Detroit and Sandusky Rivers, could identify the proportional contribution from each system and help prioritize conservation and restoration of critical spawning habitat. Ultimately this type of multi-stock information would be useful in the management of harvest policies and targeted habitat protection and restoration of Lake Erie walleye as well as other migratory stocks in large systems (Stephenson, 1999). The application of Bayesian methods in this context would improve system specific estimates and benefit larger scale management objectives.

Conclusion

Larval fish, like many organisms in large aquatic systems, are inherently variable in space and time making them difficult to sample and quantify. The use of variance partitioning models led to improved sampling, estimation, and understanding of organism ecology. Larval

walleye in the Maumee River are most variable on small spatial and temporal scales within the drift. To improve the accuracy of abundance estimates of larval fish in large flashy river systems, sampling should be tailored to capture both day-to-day and within site variability. State-space models are uniquely suited to estimating organism abundance through time, especially those exhibiting irregular temporal patterns like larval walleye. Employing these techniques in a Bayesian framework helped overcome the intrinsic challenges of working with variable organisms by sharing information, propagating uncertainty, and producing distributions useful in making probabilistic comparisons.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jglr.2014.08.001>.

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