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**Estimating Walleye (*Sander vitreus*) Movement and Fishing Mortality Using State-Space
Models: Implications for Management of Spatially Structured Populations**

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Abstract.—

Fish often exhibit complex movement patterns, and quantification of these patterns is critical for understanding many facets of fisheries ecology and management. In this study, we estimated movement and fishing mortality rates for exploited walleye (*Sander vitreus*) populations in a lake-chain system in northern Michigan. We developed a state-space model to estimate lake-specific movement and fishery parameters, and fit models to observed angler tag return data using Bayesian estimation and inference procedures. Informative prior distributions for lake-specific spawning-site fidelity, fishing mortality, and system-wide tag reporting rates were developed using auxiliary data to aid model fitting. Our results indicated that post-spawn movement among lakes were asymmetrical, and ranged from approximately 1% to 42% per year, with the largest outmigration occurring from the Black River, which was primarily used by adult fish during the spawning season. Instantaneous fishing mortality rates differed among lakes and ranged from 0.16 to 0.27, with the highest rate coming from one of the smaller and uppermost lakes in the system. The approach developed provides a flexible framework that incorporates seasonal behavioral ecology (i.e., spawning-site fidelity) in estimation of movement for a mobile fish species that will ultimately provide information to aid research and management for spatially-structured fish populations.

Keywords: movement, Bayesian inference, movement modeling, site-fidelity, state-space model, tag-recovery, walleye

Introduction

Fish demonstrate variable movement patterns and complex spatial structures among open systems that can complicate decisions related to harvest management and species conservation. Given these challenges, estimating movement rates within aquatic systems, and understanding the spatial structure of fish stocks has been an area of interest for ecologists and resource managers for decades (Hilborn 1990; Schwarz et al. 1993; Brownie et al. 1993; Schick et al. 2008; Hendrix et al. 2012; Molton et al. 2012, 2013; Li et al. 2014).

Movement dynamics of fishes are frequently evaluated using mark-recapture and/or tag-recovery studies in which individuals are uniquely marked, released, and then later recaptured live or recovered via harvest (Hilborn 1990; Brownie et al. 1993; Schwarz et al. 1993; Pine et al. 2003). Multiple models have been used to estimate movement and demographic rates from tagging studies. Common approaches assume probabilistic movement, demographic, and recapture processes (e.g., Brownie et al. 1993; Schwarz et al. 1993), or deterministic movement and demographic processes with all stochasticity arising through the sampling process (e.g., Hilborn 1990). A commonly used approach for tag-recovery data developed by Hilborn (1990) embeds a biologically meaningful but deterministic population model within a statistical estimation framework using a Poisson sampling model. More recently, extensions of the Hilborn tag-recovery model have been developed incorporating size selectivity (Anganuzzi et al. 1994), natural and fishing mortality (M and F) and tag shedding (Ω) (Aires-da-Silva et al. 2009). As such, these applications of fishery tag-recovery models contain parameters relevant to both the biology and management of fishes (e.g., M , F , Ω). These approaches, however, typically assume all variation in tag-recovery data arises as a result of sampling processes, which is likely unrealistic given that vital rates for both individual animals and populations can exhibit

considerable variation through space and time (Ogle 2009; Hansen et al. 2011; Bjorkvoll et al. 2012). Therefore, it is important to incorporate stochasticity in the underlying population model, and inclusion of both process and observation uncertainty can increase the realism of tag-recovery applications in fisheries.

A state-space model is a special class of a hierarchical statistical model for time series data that provides a rigorous approach for modeling stochastic biological and observation processes (Schnute 1994; King 2014). State-space frameworks also provide a flexible approach for tailoring biological process models to life history of a study organism (Thomas et al. 2005; Newman et al. 2014). State-space approaches have been used to estimate demographic and movement parameters in mark-recapture studies (e.g., Gimenez et al. 2007; Kéry and Schaub 2011; Holbrook et al. 2014), but have seen less application for estimating movement parameters of spatially-structured fish populations using tag-recovery data (e.g., extensions of the Hilborn model). Moreover, Bayesian applications of state-space models in fisheries provide additional flexibility by allowing one to easily constrain parameter values over realistic ranges or incorporate information from data recorded from other time periods, populations, or species through the use of informative prior distributions (Whitlock and McAllister 2009; Kéry and Schaub 2011). When data to estimate specific parameters are lacking for the population or site of interest, constraining parameters through use of informative priors acknowledges uncertainty and thus provides a more realistic alternative to the approach of assuming parameters are fixed at specific values during model fitting. Despite the strengths of the state-space frameworks for estimating movement and demographic parameters, many applications have not incorporated important aspects of fish behavioral ecology that affect within year, seasonal movement patterns of fish.

Many fish species inhabit open systems and exhibit regular seasonal or inter-annual movement patterns associated with reproductive events and movement to feeding habitats. Spawning-site fidelity is a common life-history attribute that results in nonrandom seasonal movements for a wide variety of fish species (Moyle and Cech 2004). For example, walleye (*Sander vitreus*) are a mobile species that often exhibit seasonal movements from spawning to feeding areas. However, these movement patterns can vary among systems in the extent of directed movement displayed (Rasmussen et al. 2002; DePhilip et al. 2005; Weeks and Hansen 2009), complicating fishery management for local populations. Although walleye post-spawn movement appears to be context dependent, individuals are regularly captured in the same general location during the annual spawning period, which suggests that walleye likely exhibit some degree of spawning-site fidelity (Crowe 1962; Olson and Scidmore 1962). In general, the structure of current tag-recovery models does not incorporate explicit across-year returns to a specific location or within year movement among locations, and inferences about post-spawn movements often assume perfect fidelity to spawning areas. However, allowing for variable life history rates can lead to emergent patterns among spatially structured populations that might not otherwise be detected, but that may be important for understanding movement dynamics, spatial structure, and management of walleye populations

Despite the importance of walleye as a game species, relatively few studies have quantified their movement rates (but see Rasmussen et al. 2002; Weeks and Hansen 2009; Vandergoot and Brenden 2014) due to logistical challenges as well as the limitation of analytical tools to account for complicated movement patterns. Movement of fish is an important consideration in their population dynamics, trophic ecology, conservation, and management (Landsman et al. 2011; Berger et al. 2012). As such, the goal of this study was to understand and

quantify the movement dynamics of walleye in a set of large interconnected lakes and river systems in northern Michigan. Specific objectives of this study were to: 1) develop a tag-recovery model that accounts for the biology of our study system and integrates prior sources of data to estimate movement and demographic parameters and 2) quantify movement rates for walleye in a chain-lake system in northern Michigan during 2011-2013. To accomplish these objectives we developed a state-space tag-recovery model that adapts the general framework of Hilborn (1990), described further by Quinn and Deriso (1999), to account for important movement dynamics and spawning-site fidelity observed in this system, while integrating prior data sources that allowed us to estimate important demographic and fishery parameters (e.g., fishing mortality rate) in each lake. This model was implemented in a Bayesian estimation and inferential framework, which provided a flexible approach for understanding dynamics and permitted stochasticity in both biological and observation processes generating the tag-recovery data (Gimenez et al. 2007).

Materials and methods

Study area

Michigan's Inland Waterway is an interconnected chain of lakes located in the northern Lower Peninsula that consists of four large lakes (Burt, Crooked, Mullett, and Pickerel) interconnected by a series of rivers and smaller tributaries (Figure 1). The Cheboygan Lock and Dam on the Cheboygan River and the Alverno Dam on the Black River are located at the northern portion of the Inland Waterway and restrict fish passage, and thus the system is considered closed to emigration towards Lake Huron or further upstream within the Black River (Figure 1). The lakes and rivers of the waterway are oligotrophic, provide various levels of

suitable walleye spawning substrate and prey resources, and range from 4.4 km² (Pickerel Lake) to 70.4 km² (Burt Lake) in total size (Hanchin et al. 2005a; Hanchin et al. 2005b; Herbst 2015).

The Inland Waterway was separated into five spatial strata consisting of the four lakes and the Black River, for the purpose of this study. Boundaries of the spatial strata were defined as 1) the Black River, 2) Mullett Lake including the Cheboygan River, 3) Burt Lake including Burt Lake, Indian River, Sturgeon River, and the Crooked River, 4) Crooked Lake including Crooked Lake and the Crooked-Pickerel narrows to the mid-point between Crooked and Pickerel lakes, and 5) Pickerel Lake including Pickerel Lake and the other half of the Crooked-Pickerel narrows nearest to Pickerel Lake. The divisions of these waterbodies into the specific strata were based on the four lakes, and the connecting rivers were categorized based on proximity to a specific lake and biological information gained from past walleye studies in the Inland Waterway and input from local biologists (Michigan Department of Natural Resources, unpublished data). For example, the Cheboygan River was categorized into the Mullett Lake strata because the majority of walleye captured in the river during spring sampling were collected within 150m of Mullett Lake.

Tagging and recovery data

Adult walleye, defined by expression of gametes or total length ≥ 381 mm, were captured in the spring (mid-March to early-May) during the walleye spawning season using electro-fishing, fyke nets, and trap nets throughout the Inland Waterway, 2011-2013. Following capture, walleye were marked with individually numbered, size 12 jaw tags that were affixed to their upper mandible. Tags also were labeled with a mailing address for return, and approximately half of the jaw tags affixed were \$10US reward tags to increase reporting rate. Information

recorded for each individual during tagging included location, date of initial marking, and total length (mm), and sex if gametes could be expressed.

Tag recovery data were provided to the Michigan Department of Natural Resources through a voluntary angler tag return program during the 2011-12, 2012-13, and 2013-14 angling seasons. The information collected from each tag recovery included date and location of capture. In addition to the monetary reward, project collaborators advertised the return program to the angling community through public outreach events, press releases, and signage at access points to encourage tag returns.

Model Structure

General Approach:

We developed a state-space tag-recovery model and used Bayesian estimation techniques to quantify location-specific movement and demographic parameters for walleye in the Inland Waterway. The state-space framework is a hierarchical model, which is a linked sequence of conditional probability models representing observational and ecological processes:

$$f(y | X, \vartheta_y) = \text{observation model}$$

$$f(X | \vartheta_X) = \text{ecological process model},$$

for observed data y , partially observed latent state variable X (the true quantity of interest), and parameters governing the observation (ϑ_y) and ecological processes (ϑ_X) (Royle and Dorazio 2008). In the context of modeling fish movement among spatial strata, the ecological process model represents the stochastic process that determines how many individuals are available to be caught during an angling season in a given geographic strata, which is governed by the seasonal movements and demographic parameters. In contrast, the observation model represents the

space- and time-specific probability distribution for observing y tag recoveries from a given tagging cohort given the true number of fish available for harvest (X), angling harvest, and tag-reporting processes (Figure 2). Tag-recovery model parameters associated with process and observation models and their descriptions are provided in Table 1.

Population process model:

The ecological process component of our state-space model governed the spatial-temporal dynamics of movement and survival of fish from each tagging cohort. Specifically, the number of fish from each unique release group (i.e., cohort) available for harvest on summer feeding grounds in a given year was a latent variable (X). Changes in X were modeled as a function of the number and spatial distribution of fish from that group at the previous time step and the parameters driving demographic processes of movement and apparent survival. These processes were governed by the following general model, in which fishing mortality and movement rates are year specific:

$$\begin{aligned} X_{j,l,i,t} &= R_{j,l,t} \varphi_{l \rightarrow i,t} \quad \text{when } t = j \\ X_{j,l,i,t} &= (\sum_s X_{j,l,s,t-1} \theta_{s,t-1} \psi_l) \varphi_{l \rightarrow i,t} + (\sum_{s \neq l} X_{j,l,s,t-1} \theta_{s,t-1} (1 - \psi_l) \varphi_{s \rightarrow i,t}) + \\ &\quad \left(\frac{1 - \psi_l}{4} \sum_{s \neq l} X_{j,l,l,t-1} \theta_{l,t-1} \varphi_{s \rightarrow i,t} \right) \quad \text{when } t > j. \end{aligned}$$

Here $X_{j,l,i,t}$ represents the number of fish from tagging cohort j released on spawning grounds at site l that are present and available for harvest on summer feeding grounds at site i during year t . In this study there were three release cohorts ($j = 1, \dots, 3$) at each of 5 spatial strata ($l = 1, \dots, 5$) resulting in 15 unique release groups, and three harvest recovery years ($t = 1, \dots, 3$). Moreover, $R_{j,l,t}$ represents the number of tagged fish released in cohort j at spawning site l at the start of year

t , and $\theta_{l,t}$ is the apparent annual survival rate for walleye at site l during time t . We also evaluated simpler models representing alternative hypotheses where parameter values were constrained to be drawn from the same distribution through space and/or time.

Examining state equations governing the distribution and abundance of tagged fish from each release group aids the interpretation of model dynamics. Thus,

$$\left(\sum_s X_{j,l,s,t-1} \theta_{s,t-1} \psi_l \right) \varphi_{l \rightarrow i,t}$$

represents fish from tag cohort j that survived time $t-1$ and then returned to spawn at their initial release location l at time t . This sum therefore represents the number of fish that will be available to move from their initial spawning location at time t to summer feeding grounds at site i , where $\varphi_{l \rightarrow i,t}$ is the proportion of moving from site l to site i at time t . Because a proportion of fish that survived the year at their initial release location will not exhibit spawning-site fidelity ($1 - \psi_l$), post-spawn movements of this group will originate from a site other than their initial release location. Without additional information on pre-spawn movements from this group we assumed they moved in equal numbers to all other locations:

$$\left(\frac{1 - \psi_l}{4} \sum_{s \neq l} X_{j,l,s,t-1} \theta_{l,t-1} \varphi_{s \rightarrow i,t} \right).$$

However, the proportion of fish falling into this group was relatively small because most fish exhibited strong spawning-site fidelity (see prior distributions and Results below). Moreover,

$$\sum_{s \neq l} X_{j,l,s,t-1} \theta_{s,t-1} (1 - \psi_l)$$

represents the sum of fish from tag cohort j that survived at sites other than their release location during time step $t-1$, and subsequently remained at these locations for spawning at time t (i.e.,

216 failed to exhibit spawning-site fidelity). Therefore this sum represents the number of fish
 217 available to move from their spawning location s ($s \neq l$) to summer feeding grounds at site i ,
 218 where $\varphi_{s \rightarrow i, t}$ is the proportion of the fish that make this movement. So in general if fish released
 219 at site l summer and survive at site s , where $s \neq l$, they can return to spawn at their original release
 220 location l and exhibit post-spawn movements from that site ($X_{j, l, s, t-1} \theta_{s, t-1} \psi_l \varphi_{l \rightarrow i, t}$), or they can
 221 remain and join the spawning population at site s and exhibit post-spawn movements from that
 222 site ($X_{j, l, s, t-1} \theta_{s, t-1} (1 - \psi_l) \varphi_{s \rightarrow i, t}$). Similarly, fish released at site l summer and survive at the
 223 same site, they can remain at their original release site l to spawn and exhibit post-spawn
 224 movements from this location ($X_{j, l, l, t-1} \theta_{l, t-1} \psi_l \varphi_{l \rightarrow i, t}$), or they can disperse in equal proportions
 225 to the remaining spawning sites and exhibit post-spawn movements from these sites
 226 ($\frac{1-\psi_l}{4} X_{j, l, l, t-1} \theta_{l, t-1} \varphi_{s \rightarrow i}$ for all $s \neq l$). Thus, overall the state-equation represents the number of
 227 fish from each release group that are present and available for harvest on summer grounds at site
 228 i during recovery year t . Also note that all of our models assumed the distribution of spawning-
 229 site fidelity was constant through time, whereas distributions of movement rates from spawning
 230 grounds to summering grounds were allowed to vary through time for some models.

231 Our process model assumed that all mortality occurred after fish moved to summer
 232 feeding areas. The process model also assumed all fish in a given feeding area during recovery
 233 year t experienced the same conditions and thus experienced the same apparent survival.
 234 Similarly, fishing mortality operated at the site level during summer, where fish in the same site
 235 were exposed to similar levels of fishing mortality, regardless of their unique release group.
 236 Because processes governing movement and survival dynamics (e.g., Hilborn et al. 1990;
 237 Hendrix et al. 2012) are unlikely to be deterministic, we incorporated a multiplicative process
 238 error that represented the cumulative result of stochastic variation in all mortality and tag-loss

processes. Specifically, we assumed process error was acting on total instantaneous mortality in a manner that was lake and time specific:

$$Z_{l,t} = (F_{l,t} + M + \Omega)e^{\varepsilon_{l,t}},$$

where $M = 0.3$, $\Omega = 0.1375$, $\varepsilon_{l,t} \sim N(0, \sigma_p)$, and $\theta_{l,t} = e^{-Z_{l,t}}$. Median natural mortality (M) was assumed constant at a value consistent with an average of estimates of M from walleye populations in northern Wisconsin (Hansen et al. 2011). Our base assumption for median tag shedding rate (Ω) was reflective of estimates from walleye mark-recapture studies conducted within our study area in 2001 (Hanchin et al. 2005a, 2005b). Importantly, however, realizations of both M and Ω at each site and time were random variables due to the structure of the assumed process uncertainty. Specifically, lake and time specific realizations of M and Ω come from lognormal distributions that were constant through time, where values of 0.3 and 0.1375 were the assumed medians of these distributions, respectively. This model formulation treated tag-loss as a component of instantaneous total mortality of the tagged population, and as such Z does not represent true mortality but apparent total mortality. Thus our model has no way of formally separating out components of process error related to tag-loss and true mortality, and our data do not facilitate such partitioning.

Tag-recovery observation model:

While the stochastic process model above drove movement and survival dynamics of fish from each tagging cohort, the observation model was assumed to generate observed tag-recovery data conditional on the latent tagged population at each location and recovery year. We assumed tag-recovery was a stochastic process where the number of tags recovered from each release cohort

at each site and time was conditional on fish present with tags and the parameters driving harvest and tag reporting:

$$\text{Recovery}_{j,l,i,t} \sim \text{Poisson}(\lambda_{j,l,i,t})$$

where $\text{Recovery}_{j,l,i,t}$ represented the number of walleye tags recovered at site i during time t from fish released in tag group j released at site l . The mean of the Poisson distribution for tag recoveries was determined by the number of fish available for harvest, the annual exploitation rate, and the tag-reporting rate:

$$\lambda_{j,l,i,t} = X_{j,l,i,t} \mu_{i,t} \gamma,$$

where $\mu_{i,t} = \frac{F_{i,t} e^{\epsilon_{i,t}}}{Z_{i,t}} (1 - e^{-Z_{i,t}})$ is the annual exploitation rate for walleye at site i during time t .

Because multiplicative process errors are explicit in the definition of Z in our process model, and thus implicitly included in Z in the Baranov catch equation, realized F values must also include multiplicative process errors for the leading fraction to represent the proportion of total mortality resulting from fishing. Because the model is assuming recoveries are coming from summer feeding grounds we also assume that all fish present in a given space-time combination are experiencing the same realized exploitation rate, regardless of which tag cohort they belong to or where they spawn. Reporting rate (γ) was assumed to be drawn from a distribution that was constant over space and time and was estimated using auxiliary reward tag data (see prior distributions below).

Prior distributions for model parameters:

We used existing data to develop informative prior distributions for model parameters where available, and used a diffuse prior distribution for the ϕ parameters that were of primary interest for this analysis. We used pooled catch-at-age data from walleye collected from lakes

throughout the Inland Waterway during 2011 to develop an informative prior for fishing mortality using results from a catch-curve analysis. We $\log_e$ transformed the catch curve equation to estimate instantaneous total mortality rate (Z) using linear regression (Quinn and Deriso 1999). From the catch-curve analysis $\hat{Z} = 0.542$ was the maximum-likelihood estimate of instantaneous total mortality, which has an asymptotically normal sampling distribution ($\widehat{SE}(\hat{Z}) = 0.050$). We assumed that natural mortality was constant over the catch-curve study period ($M = 0.3$) and thus $\hat{F} = 0.242$. Since linear functions of normal random variables are themselves normally distributed (Rice 2007) we used results from catch-curve analyses to derive an informative normal prior for F as a linear function of the normally distributed random variable $\hat{Z}$ (Appendix 1):

$$F_{i,t} \sim \text{Normal}(\mu = 0.242, \sigma^2 = 0.0025).$$

To avoid impossible or unrealistic draws from the prior for $F_{i,t}$, Markov Chain Monte Carlo (MCMC) sampling discarded any samples of $F_{i,t} \leq 0$ and ≥ 5 .

We lacked prior information about the magnitude of process errors, so we assumed a uniform prior over a restricted range:

$$\sigma_p \sim \text{Uniform}[0,3]$$

Although this prior is uniform, the bounds of the uniform distribution can be thought of as informative in this case because we are restricting the process error values over a relatively small numerical range. While this range is numerically restrictive, it contains all biologically plausible values of the process error; process error $\sigma_p \geq 3$ produces u-shaped distributions of apparent annual survival (θ) where nearly all individuals in the tag group survive or die (or shed tags) each year. This is biologically unrealistic for walleye in northern Michigan, thus the uniform

prior used constrains the process error standard deviation to plausible positive values while at the same time reflecting ignorance over the values of σ_p .

We used auxiliary live recaptures data derived from previously marked individuals that were subsequently recaptured during the annual (2011-2013) spring spawning sampling (i.e., electrofishing, trap, and fyke netting) and tagging operations to develop informative priors for spawning-site fidelity parameters (ψ). Specifically, the number of fish tagged on spawning grounds that were recaptured at their initial release site in subsequent years, was treated as a Binomial random variable with success probability ψ_l for site l . The conjugate prior for a Binomial parameter is a Beta distribution, and the Uniform distribution represents a special case ($\text{Beta}(\alpha = 1, \beta = 1) = \text{Uniform}[0,1]$). Moreover, using an uninformative $\text{Uniform}[0,1]$ prior for a Binomial parameter results in a closed-form Beta posterior distribution for the Binomial probability ($\text{Beta}(\alpha = x + 1, \beta = n - x + 1)$), where x = number of successes from n Bernoulli trials. Thus, we used this approach to turn the proportion of tagged fish recaptured on their original spawning release area into an informative Beta prior ($\text{Beta}(\alpha = x + 1, \beta = n - x + 1)$) for the spawning-site fidelity parameter for a given site l (ψ_l), where n represented the number of fish tagged from spawning site l recaptured on any of the spawning grounds during tagging operations for subsequent spawning seasons, and x represented the number of these fish recaptured at their original spawning ground release locations. For example, 485 walleye released on spawning grounds in Burt Lake were recaptured during tagging operations in subsequent spawning seasons, and 479 of these fish were recaptured within Burt Lake. This resulted in a $\text{Beta}(\alpha = 480, \beta = 7)$ prior for ψ_{Burt} ($\text{Beta}(\alpha = 479 + 1, \beta = 485 - 479 + 1)$). This approach was used to turn the posterior distributions from Bayesian estimation of site-fidelity parameters using live-recapture data into informative priors for spawning-site fidelity for

all sites when fitting the full state-space model: $\psi_{Burt} \sim \text{Beta}(480, 7)$, $\psi_{Mullett} \sim \text{Beta}(13, 10)$,
 $\psi_{Crooked} \sim \text{Beta}(104, 5)$, $\psi_{Pickerel} \sim \text{Beta}(16, 6)$, $\psi_{Black\ River} \sim \text{Beta}(72, 6)$.

We developed an informative prior distribution for reporting rate using data collected during high-reward walleye tagging studies conducted in Crooked, Pickerel, and Burt Lakes in 2001 and within the entire Inland Waterway in 2011 (MDNR unpublished data). The reporting rate and its variance were estimated from auxiliary data via the ratio of the recovery rate of standard tags to the recovery rate of high-reward tags assuming all reward tags were reported; these methods and assumptions are described further within Henny and Burnham (1976), Conroy and Blandin (1984), and Pollock et al. (1991). The estimate (μ) and variance of reporting rates were then used to develop an informative Beta prior for γ :

$$\alpha = \left(\frac{1 - \mu}{\text{var} - 1/\mu} \right) * \mu^2$$

$$\beta = \alpha * \left(\frac{1}{\mu - 1} \right)$$

$\gamma \sim \text{Beta}(75.257, 24.907)$.

Because we lacked prior information on movement from spawning to feeding grounds among lakes and because these were our primary targets of inference, we used diffuse priors for all ϕ parameters. Two sets of constraints must be met for the vector of movement rates away from spawning site l at time t : 1) movement rates away from a site must be bound on the interval $[0, 1]$, and 2) all movement rates leaving site l at time t must sum to one. For the vector of movement rates out of a given site at time t we used a diffuse Dirichlet distribution, which is a multivariate generalization of the Beta distribution that fulfills the necessary set of parameter constraints (Gelman et al. 2004). Thus, we specified a vague Dirichlet prior for each $\phi_{l,t}$

$\phi_{l,t} \sim \text{Dirichlet}(\alpha_{l,t})$,

where $\alpha = 1$ for all sites receiving fish from site l at time t . This effectively allocates individuals uniformly across all receiving sites at time t (Royle and Dorazio 2008). To implement this prior we simulated independent Gamma(1,1) random variables, and expressed movement rates out of site l as functions of these random variables (Royle and Dorazio 2008):

$$\beta_{l \rightarrow i,t} \sim \text{Gamma}(1,1) \text{ for all } i \text{ at time } t$$

$$\varphi_{l \rightarrow i,t} = \beta_{l \rightarrow i,t} / \sum_{s=1}^5 \beta_{l \rightarrow s,t}.$$

Model set

We developed a set of 8 models representing hypotheses of how distributions of movement (φ) and fishing mortality (F) potentially vary by location and time. In particular, our model set allowed for both site and time specific movement and fishing mortality distributions, but all models assumed spawning-site fidelity was drawn from the same lake-specific distribution over time (Table 2). The relatively short duration of this study and small number of live recaptures for fish tagged on some lakes prevented us from fitting models where the distribution of lake-specific site fidelities shifted over time. To evaluate relative support for our alternative models we used deviance information criteria (DIC; Spiegelhalter et al. 2002), which is calculated as a function of the posterior distribution of model deviance and the number of effective parameters (pD).

Model fitting and evaluation

Models were fit using OpenBUGS (Bayesian inference using Gibbs sampling) software (<http://www.openbugs.net>) called from the R2OpenBUGS package within R (R Development Core Team 2010). Samples from the posterior distributions of all model parameters were

generated using Gibbs sampling, and all analyses used three Markov Chain Monte Carlo (MCMC) chains with random starting values for model parameters. Preliminary analyses suggested all MCMC samplers converged to the posterior distributions after approximately 100,000 iterations. Thus, for each chain we used a burn-in period of 150,000 iterations that were discarded followed by 100,000 samples that were retained, resulting in posterior distributions described by 300,000 samples for each model parameter. All chains were evaluated for convergence and mixing using the Gelman-Rubin statistic (Gelman and Rubin 1992) and visual inspection of traceplots and posterior density plots for all model parameters. All computationally intensive model fitting exercises conducted for this study ran on the High Performance Computing Center cluster of the Institute for Cyber-Enabled Research at Michigan State University.

We evaluated fit of the top state-space model to tag-recovery data using Bayesian p values, which provided comparison of the posterior predictive distributions of predicted quantities with the observed tag-recovery data (Meng 1994). Specifically, we calculated a Bayesian p value for the omnibus chi-square statistic (Gelman et al. 2004), where the posterior predictive distribution of the chi-square statistic was a weighted measure of discrepancy between the predicted and observed number of total tag returns from all sites and cohorts over all posterior samples of model parameters. Goodness-of-fit evaluation based on chi-squared statistics use one-tailed tests, and as such smaller values of the omnibus chi-square statistic represent better fits of model predictions to observed data. While the omnibus chi-square statistic is a measure of fit over the entire model, we were also interested in evaluating fit of our model to tag-return data from each tagging cohort. Thus, we calculated the posterior predictive distribution for the sum of all tag returns across all sites from each specific release group and

compared this to the observed tag returns using Bayesian p values. This provided an indication of specific areas where model assumptions may have been violated or areas where the model simply did not predict the raw data well. For these cohort-specific evaluations of model fit Bayesian p values close to 0.5 represent a good fit of the model to the data, since on average the predicted values are less than or greater than the observed value with equal frequency (Whitlock and McAllister 2009).

Sensitivity and Simulation Analyses

To evaluate sensitivity of inferences to modeling assumptions and estimability of model parameters we conducted post-hoc sensitivity and simulation analyses. We evaluated effects of structural site-fidelity assumptions on parameter estimates by re-fitting the top model under assumptions of no spawning-site fidelity and perfect fidelity, respectively. To fit a model with perfect fidelity we set ψ parameters to constant values of 1 prior to model fitting via MCMC. For models with no spawning-site fidelity we removed ψ parameters from state equations and adjusted equations to reflect the assumption that at time $t+1$ fish always join the spawning population wherever they chose to summer at time t (Appendix 2).

We also evaluated sensitivity of posterior parameter estimates to assumptions about tag shedding and structure of the prior used to inform posterior distributions of F . We systematically varied assumed instantaneous tag shedding rates over small ($\Omega = 0.0377$), medium ($\Omega = 0.1375$), and large ($\Omega = 0.2357$) values to approximately reflect the range of walleye tag-loss rates reported in the primary literature (Hanchin et al. 2005; Koenigs et al. 2013; Vandergoot et al. 2012). Because our F prior using pooled catch-curve data with SD of F among lakes estimated as the $SE(\hat{F})$ (Appendix 1) could have underestimated the magnitude of spatial variation in F

among lakes in the Inland Waterway, we also fit the top model using an informative F prior developed using a hierarchical catch-curve analysis. Specifically, we conducted a linear mixed-model analysis by fitting a model with random intercepts and slopes for each site to log-transformed catch-curve data using restricted maximum likelihood and the lmer function in R. From this analysis we used the estimate and variance of the slope of $\ln(\text{catch})$ against age to develop an informative prior for F ($F \sim N(\mu = 0.134, \sigma^2 = 0.0165)$). We could not include temporal random effects in hierarchical catch curve analyses because we only had a snapshot of catch-at-age data from our study system in one sampling year (2011). To determine sensitivity of posterior inferences to assumptions about tag shedding and choice of F prior we fit all combinations of assumed Ω values and F priors using the base model structure of the top model. Lastly, we evaluated effects of ignoring process uncertainty by re-fitting our top model using a deterministic state-equation that lacked process errors.

To assess estimability of model parameters and implications of tag-release sample sizes we generated tag-recovery data from our top model and fit the model to simulated data using MCMC. We simulated tag-recovery data sets assuming all parameters and realized process errors were fixed, and the true parameter values were determined using posterior mean values from original model fitting. Specifically, we generated 100 tag-recovery data sets under 3 scenarios of tag release sample sizes: 1) tag-releases by lake and time identical to those observed during this study (Appendix 3), 2) medium sample size scenario with 2,500 tagged fish released at each lake during each release year, and 3) large sample size scenario with 5,000 fish released at each lake during each release year. For each generated data set we fit the top model using 3 chains with random starting values for model parameters, and conducted 150,000 burn-in

samples followed by 100,000 posterior samples per chain, resulting in 300,000 total posterior samples for each model parameter.

Results

Model Selection

Eight different models were fit using the walleye tag-recovery data to evaluate support for hypotheses that represented various combinations of how movement (ϕ) and fishing mortality (F) varied by location and time. The top model as indicated by DIC included distributions of spawning-site fidelity, movement, and fishing mortality rates that were location specific but constant during the three year study (i.e., lake-specific but stationary distributions; Table 2). Hypothesized models where parameter distributions were transient and changed with both spatial strata and time failed to converge and complete MCMC sampling after an entire week of running on the HPCC cluster, and thus DIC for these models are not reported. Evaluation of the top model failed to indicate lack of model fit to observed walleye tag returns using posterior predictive distribution of the omnibus chi-square statistic ($\chi^2 = 0.39, P = 0.98$). A lack-of-fit using the omnibus chi-square statistic would be indicated by large positive values (in this scenario resulting in small Bayesian p-values), thus a P-value close to 1.0 indicates close correspondence between observed and predicted tag returns. Furthermore, fit of the model to tag-return data for each of the 15 release cohorts demonstrated that posterior predictive distributions fit observed tag-recovery data reasonably well for nearly all tagging cohorts (Figure 3). The few exceptions were cohorts that had smaller numbers of observed tag recoveries (i.e., Mullett Lake cohorts 2 and 3, and Black River cohort 3), which had Bayesian p -values that deviated marginally away from the optimal value of 0.5 (Figure 3 and Appendix 3).

Demographic parameters

Walleye within the Inland Waterway exhibited asymmetrical post-spawning movement patterns. Fish from the Black River and Mullett Lake had the highest post-spawning departure rates. Of the cohorts initially tagged in the Black River and Mullett Lake approximately 46% departed to other areas for summer feeding (Table 3). Of the 46% exiting the Black River after spawning, the majority (Mean = 42%; 95% CrI: 0.21 - 0.85) moved into Mullett Lake (Table 3). However, uncertainty in post-spawn movement estimates was large for movement rates estimated for Mullett Lake and the Black River, resulting in wide credible intervals. In addition to the Black River and Mullett Lake having high departure rates, Pickerel Lake also had a large portion (approximately 35%) of the population leave after spawning. Bi-directional post-spawn movement of walleye between Crooked and Pickerel lakes occurred more frequently than other combinations of locations with ample samples sizes (i.e., excluding Mullett Lake and the Black River). Post-spawn movements of walleye from Crooked Lake to Pickerel Lake were relatively small (Mean = 5%; 95% CrI: 0.03 - 0.08), but 19% (95% CrI: 0.12 - 0.26) of fish spawning in Pickerel Lake moved to Crooked Lake during the feeding season (Table 3). Walleye cohorts initially tagged in Burt Lake had the greatest overall annual residency, with 93% (95% CrI: 0.89 - 0.96) remaining in that location throughout the year (Table 3).

The number of fish tagged and number of tag returns varied widely between locations in the watershed, and as such, the level of information provided for parameter estimation varied. A comparison of the difference between the prior and posterior distribution for fishing mortality (F) for each location (Figure 4) indicated that the tag recovery data were informative for estimating location-specific F s for most sites. Estimated fishing mortality rates from the top model with the base assumptions (i.e., system-wide catch curve derived F prior and $\Omega = 0.14$)

fell into two broad groups; the Black River, Pickerel Lake and Mullett Lake all had an estimated F between 0.16 and 0.18 (Table 4), whereas F estimates in Burt and Crooked Lakes were 0.25 and 0.27 (Table 4), respectively. The posterior distributions of F for most lakes were symmetrical and reasonably narrow (Figure 4). However, the posterior distribution of F in the Black River was asymmetrical and multimodal (Figure 4), with a 95% credible interval ranging from 0.01 to 0.30 (Table 4), suggesting that the low number of tag returns from the Black River resulted in only partial identifiability for fishing mortality at that site.

Sensitivity and Simulation Analyses

Post-spawn movement rates for Mullett Lake and the Black River were sensitive to assumptions about spawning-site fidelity in the model structure, whereas post-spawn movement estimates for other lakes were more robust. The estimated movement rates were lower for the Black River when including a data driven informative prior for spawning-site fidelity (Table 3). For example, the departure rate for the Black River was approximately 81% when precluding site-fidelity, but was much less with an estimate of 46% when the seasonal life history trait was incorporated (Table 3). Other movement rates that were influenced by incorporating a data driven site-fidelity prior were the combinations of movement rates associated with the Black River and Mullett Lake populations. Specifically, when the informative priors for spawning-site fidelity were included the estimated movement rates from Mullett Lake to the Black River increased, Mullett Lake to Mullett Lake decreased, Black River to Mullett Lake decreased, and Black River to Black River increased (Table 3). Locations with high spawning-site fidelity post-spawn movement rates that were relatively robust to assumptions about spawning-site fidelity. Burt Lake, for example, had a high site fidelity rate and there were negligible differences (< 3) in movement rates under the three scenarios (no fidelity, data driven fidelity prior, and perfect

fidelity) of site fidelity in the model structure (Table 3). However, interpretation of site-specific effects of site-fidelity assumptions is also complicated by variable sample sizes of released fish among sites (Appendix 4).

Fishing mortality and movement rates were robust to the prior distribution used for fishing mortality (F). The system-wide catch-curve derived prior distribution was less variable than the prior distribution developed using hierarchical model structures (Figure 4). Despite the increased variance for the prior on F , the model with a hierarchical prior produced fishing mortality rates that were ≤ 0.04 of the estimates produced using the catch-curve prior (Table 4). The only exception was the Black River, where the model that used the pooled catch-curve prior (i.e., with a larger mean and smaller variance for F) produced an estimate of 0.16 (95% CrI: 0.01 – 0.30), whereas the hierarchical prior estimated F at 0.02. Movement rates exhibited a similar pattern of insensitivity to the prior distribution for F , regardless of the location and assumed level of tag shedding (Table 5).

The best fit model (model 1) was robust to differing assumed values of instantaneous tag shedding rates. Fishing mortality rate estimates differed by < 0.05 in response to increasing tag shedding rates from 0.04 to 0.24 (Table 4). Changes in estimated movement rates were generally low (Table 5) in response to this range of tag shedding rates, and differed by < 0.03 among assumed values of tag shedding. The process error standard deviation was influenced more by the change in instantaneous tag shedding rates, increasing when the value for tag shedding rates (Ω) increased. The estimated process error standard deviation when using the low Ω value was 1.51 (95% CrI: 0.39 – 2.85), 1.61 (95% CrI: 0.39 – 2.86) at the base assumption of Ω , and 1.57 (95% CrI: 0.41 – 2.85) at the highest tag shedding value, illustrating the variation in process error following a change in tag shedding rate from 4% to 24%.

Tag-recovery data used to inform the model allowed for the estimation of the process error that was incorporated into the population dynamics and observation models. The posterior distribution for the process error standard deviation was approximately symmetric with a mean of 1.61 (95% CrI: 0.39 – 2.86), which differed from the uniform (0,3) distribution that was used as the prior distribution. The overall support substantially declined after modifying the structure of the best fit model to exclude process error ($\Delta\text{DIC} = 127.6$; Table 2), indicating added value for predictive purposes of including process stochasticity in the model structure.

The number of computationally-intensive model fits that completed MCMC sampling after an entire week of running on the HPCC cluster varied among simulated sample sizes, and thus the number of parameter estimates used to assess bias and estimability varied among tag-release scenarios (current = 98, medium = 89, high = 55 model fits, respectively). Fitting of state-space movement models to simulated tag-recovery data suggested robust estimation of most model parameters of interest (Appendix 4). At current sample sizes bias in most estimated movement parameters was likely minimal. The exceptions to this were movement rates within and between Mullett Lake and Black River (Appendix 4), where analyses suggested biased movement rates were likely. However, any bias in movement rate estimates approached zero as sample sizes were increased to 2,500 and 5,000, as all movement estimates approached truth at these sample sizes (Appendix 4). Simulation results also suggested that priors developed for F via sharing data across all sites may have slightly overestimated F for Mullett Lake, Pickerel Lake, and Black River at current sample sizes. However, F estimates approached truth as sample size increased for all sites except Black River.

Discussion

This study expanded upon previous extensions of the commonly used Hilborn (1990) tag-recovery model by developing a state-space formulation to accommodate spawning-site fidelity, and used the model to estimate movement and demographic rates for walleye in a lake-chain system in northern Michigan. Our approach accommodated temporal and spatial variation in demographic and movement rates (i.e., F and ϕ) by treating model parameters as random variables using Bayesian methods, and included process stochasticity to help alleviate inferential sensitivity associated with commonly used but incorrect assumptions like constant and known rates of natural mortality and tag-shedding. Moreover, the Bayesian estimation techniques used provided the flexibility to incorporate site-specific knowledge through the use of informative prior distributions while estimating demographic parameters of interest such as post-spawn movement (ϕ) and fishing mortality (F). The Bayesian approach also facilitated inclusion of prior information while accounting for uncertainty in that knowledge and thus we avoided simply assuming fixed parameter values for quantities not likely to be estimable using only tag-recovery data (e.g., spawning-site fidelity). Thus we were able to embed more realistic biological dynamics into the model structure while using existing auxiliary information to aid model fitting (Buckland et al. 2000; Buckland et al. 2007). Furthermore, this approach was complemented by formal statistical evaluation of hypotheses about structure of model parameter distributions using Bayesian model selection approaches, thus making the general approach useful under a range of biologically plausible conditions within aquatic environments.

Walleye exhibited differing post-spawning movement patterns among the five locations within the Inland Waterway. Our findings were similar to walleye in other lake-chain systems where estimated movement rates varied. In fact, walleye movement has been shown to differ widely among systems studied. For example, Rasmussen et al. (2002) found that at least half of

all walleye present at spawning could depart to another site within one week in a chain-lake system, whereas Weeks and Hansen (2009) found that the majority (82%) of walleye tagged were recaptured in the same lake. Although our study and most others evaluating walleye movement patterns have not been designed to determine factors governing movement rates, we hypothesize that walleye populations in lakes with suitable spawning substrate and abundant prey resources would not benefit from migrating great distances to spawn and/or feed. Alternatively, if spawning substrate and adequate forage are spatially separated it would be advantageous for those walleye to migrate greater distances in search of quality habitats, thereby increasing chances of juvenile survival and/or adult growth. Despite our limited ability to directly evaluate this hypothesis, the estimated walleye movement rates and the distribution of suitable spawning habitat within our study system suggests the search for desirable seasonal habitats could be an important mechanism for the observed movement rates. For example, the Black River has ample suitable spawning habitat, but marginal foraging resources, which could be the driving mechanism behind high post-spawn movement rates from the Black River to a location like Mullett Lake where prey resources are high relative to other areas in the waterway (Herbst 2015). Likewise, the poor spawning substrate but ample forage resources in Mullett Lake is likely the driving force behind it being a post-spawn recipient location from fish that spawned in the Black River. In addition, Burt Lake has resources that provide sufficient forage and spawning substrate that could explain the observed high year-round residency rates (Herbst 2015; Tim Cwalinski, Michigan Department of Natural Resources, personal communication).

The management of walleye in our study system currently assumes each lake is an independent fishery, with harvest quotas for two fisheries (spearing and angling) set separately for each lake (Tim Cwalinski, Michigan Department of Natural Resources, personal

communication). Furthermore, spring population estimates during spawning are used to set these quotas, although the spearing fishery and angling fishery occur during different time periods. The spearing harvest occurs during the spring spawning season and the angling harvest occurs during the feeding period of the year (late April to March the following calendar year). Our study illustrated that post-spawn movement among lakes can be large, leading to the potential for overexploitation or misallocation of these resources among lakes. Therefore, we recommend that combining areas within the waterway that have high exchange rates (i.e., Black River and Mullett Lake) would better align the management of walleye populations in these locations with the likely biological dynamics. Even where exchange rates are not large the disparity in population sizes could have an influence on the system wide dynamics. For example, the proportion of walleye leaving Burt Lake after spawning is small (approximately 7%); however, the relatively large population size (~ 19,500 individuals; Michigan Department of Natural Resources, unpublished data) leads to greater numbers of individuals that contribute to walleye dynamics in recipient locations that have substantially smaller populations sizes (~500 - 4,500 individuals; Michigan Department of Natural Resources, unpublished data) and therefore could buffer the level of exploitation on fish that remained in those areas. Considering the management significance of understanding seasonal habitat use and movement rates of fish populations we recommend further research to determine the mechanisms driving movement patterns.

Understanding seasonal behavioral aspects of fish ecology, such as spawning-site fidelity, can be vital when estimating movement rates and for making management and conservation decisions (Rudd et al. 2014) that are based on that knowledge. In the Inland Waterway seasonal differences in habitat use and the timing of movement could have important management implications for fish populations if they are subjected to differing levels of spatial

and/or temporal exploitation. For example, walleye populations in our study area are exposed to spearing and angling harvest that occurs on different temporal scales and that have different exploitation efficiencies. The spring spearing harvest has a high catchability, whereas, the angling harvest has a lower catchability (Hansen et al. 2000). The difference between seasonal exploitation threats combined with spawning-site fidelity and large post-spawn movements likely has implications for walleye management in our system and other lake-chains (Rasmussen et al. 2002), especially considering walleye exhibit high fidelity rates that influences seasonal residence (Crowe 1962; Olson and Scidmore 1962). The inclusion of spawning-site fidelity influenced our estimates of walleye movement rates in some areas of our study system, and live recapture data provided information that challenged traditional assumptions of perfect site fidelity in these areas (e.g., Mullett Lake). Together these results indicated the importance of accounting for seasonal movements when attempting to understand the overall spatial structure for walleye in the waterway. Specifically, these results imply that explicitly accounting for spawning-site fidelity could be important when spawning-site fidelity is low and also when spawning and feeding grounds are spatially disaggregated (e.g., Black River and Mullett Lake). The inclusion of spawning-site fidelity, however, was challenging because it required live recapture data to develop informative prior distributions. Despite this challenge, the frequency of this biological characteristic and potential for harvest season occurring at different times highlights the need for further studies that examine the extent of this seasonal pattern and the overall importance of including this life history trait when modeling annual movements and making management and conservation decisions.

Fishing mortality rates varied within the waterway, but were within the range reported for other walleye populations (Schmalz et al. 2011). Within the Inland Waterway, Burt and Crooked

lakes had the highest estimated fishing mortality rates ($F = 0.25$ and 0.27 respectively); however, neither of these rates exceeded 35%, which is commonly viewed as an upper limit reference point for safe harvest of walleye (Schmalz et al. 2011). Estimated fishing mortality rates in the other lakes and in the Black River were in the range of 0.16 to 0.18, suggesting that exploitation may not be the primary factor limiting abundance of adult walleye in these systems. The Black River estimate for F was sensitive to the assumed prior for F , which is likely a relic of small sample size of released individuals and the low number of tag recoveries. Furthermore, there was bias indicated by the simulation study was caused by the large influence of the high sample size of Burt Lake fish that dominated the prior distribution derived from the catch curve analysis. The results of the simulation study illustrated that with increased sample size the bias in estimated F became negligible, with the Black River being the only exception.

Estimates of demographic rates from fish populations can be biased because of uncertainty in the magnitude of tag shedding (Isermann and Knight 2005; Aires-da-Silva et al. 2009; Koenigs et al. 2013). For example, previous studies have generally shown that estimates of movement and fishing mortality rates are sensitive to assumed tag shedding values (Isermann and Knight 2005; Aires-da-Silva et al. 2009). Immediate or short-term tag shedding is often low for walleye ($< 0.05\%$), but long-term tag shedding for walleye is more variable and has been estimated to range between approximately 5 and 50% annually (Hanchin et al. 2005; Isermann and Knight 2005; Koenigs et al. 2013; Vandergoot et al. 2012). The insensitivity of our estimated movement rates to variable levels of tag shedding was unexpected based on results from tag-recovery studies. For example, Aires-da-Silva (2008) reported that estimates of mean movement rates for blue sharks were highly sensitive to assumed tag shedding rates, where movement varied by as much as 0.14 under the different assumed tag shedding values. Movement rates of

interest were generally robust within our best fit model, which is likely the result of our flexible model structure allowing for additional stochasticity in the instantaneous total mortality through the inclusion of process error, instead of the common assumption that total mortality is a function of tag-loss within a rigid deterministic model of movement and demographic dynamics.

Although post-spawn movement estimates were robust to most assumptions, our simulation study indicated the potential for small biases in post-spawn movement estimates for sites that had small numbers of tag releases. For example, the movement rates of fish released in the Black River and Mullett Lake that departed for Mullett Lake were biased high. Likewise, the fish released in those same two areas that departed for the Black River was biased low. These biases in movement rates were likely related to issues of a small number of individual released because these two locations had the smallest sample sizes of the locations within the waterway. Furthermore, our simulation study demonstrated that the bias in estimated movement rates for these populations tended to go to zero as the sample size increased.

In summary, this study expanded a commonly used tag-recovery modeling framework to incorporate spawning-site fidelity and additional uncertainty associated with the population dynamics processes into the model structure using a state-space framework. We used Bayesian estimation techniques to facilitate inclusion of existing information while accounting for uncertainty through the use of prior distributions. We determined that post-spawn walleye movement patterns and fishing mortality rates in the Inland Waterway were spatially asymmetrical over the study area. Furthermore, our movement and fishing mortality estimates were robust to changes in assumed rates of tag loss. Given the prevalence of open systems and organisms with complex life-history behaviors, flexible modeling frameworks that incorporate stochastic process dynamics and are readily adaptable to different species and systems are

important additions to approaches commonly used to model tag-recovery data in fisheries. State-space frameworks provide a state-of-the art framework that will permit such flexibility, and should help facilitate robust estimation of demographic parameters governing movements and mortality for mobile species (King 2014). These estimates will ultimately provide rigorous information to aid management decisions for spatially structured fish populations.

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Draft

873 Table 1: List and description of symbols that represent the parameters of the state-space tag-recovery model used to estimate
874 movement and demographic rates for walleye within the Inland Waterway.

Symbol	Description
ψ_l	Spawning-site fidelity, the proportion of individuals initially tagged on spawning grounds at site l that return to that site at the beginning of subsequent time steps to spawn conditional on having survived
$\varphi_{l \rightarrow i, t}$	proportion of individuals spawning at site l at time t that move to site i immediately after spawning.
Ω	instantaneous tag shedding rate
M	instantaneous natural mortality rate
$F_{l, t}$	instantaneous fishing mortality rate at site l during time t
$\varepsilon_{l, t}$	realized process error at site l during time t
σ_p	standard deviation of process errors
γ	tag reporting rate
θ	apparent annual survival rate

875

876

877 Table 2: Model set representing the multiple hypotheses evaluated to represent post-spawning walleye movement and demographics in
 878 the Inland Waterway, 2011-2013. Combinations of lake specific and time varying parameters for movement (ϕ), spawning-site fidelity
 879 (ψ), and fishing mortality (F) were evaluated using Deviance Information Criteria (DIC). $F(\cdot)$ is constant fishing mortality for each
 880 lake and time. The best fit model was also modified and fit without process error (*) to evaluate model support.

Model Number	Structure	DIC	Delta DIC
1	$\phi(\text{lake}), \psi(\text{lake}), F(\text{lake})$	422.9	0.0
2	$\phi(\text{lake}), \psi(\text{lake}), F(\text{time})$	432.9	10.0
4	$\phi(\text{lake}), \psi(\text{lake}), F(\cdot)$	434.5	11.6
1*	$\phi(\text{lake}), \psi(\text{lake}), F(\text{lake})$ without process error	550.5	127.6

881

882 Table 3: Location specific post-spawning movement rates (proportion*year⁻¹ with 95% credible intervals) estimated by the best fit
883 model (i.e., model 1) using three different assumptions for spawning site-fidelity (no fidelity, mark-recapture informed fidelity, and
884 perfect fidelity) and the base assumption for tag shedding rate ($\Omega = 0.14$).

Feeding Location					
Model 1: No spawning site-fidelity					
Spawning Location	Burt Lake	Mullett Lake	Crooked Lake	Pickerel Lake	Black River
Burt Lake	0.93 (0.91, 0.94)	0.06 (0.04, 0.08)	0.01 (0.01, 0.02)	0.00 (0.0, 0.01)	0.00 (0.0, 0.01)
Mullett Lake	0.05 (0.02, 0.10)	0.88 (0.61, 0.96)	0.00 (0.0, 0.01)	0.01 (0.0, 0.02)	0.06 (0.01, 0.32)
Crooked Lake	0.05 (0.02, 0.07)	0.00 (0.0, 0.01)	0.89 (0.85, 0.93)	0.05 (0.03, 0.08)	0.00 (0.0, 0.02)
Pickerel Lake	0.08 (0.04, 0.13)	0.01 (0.0, 0.04)	0.17 (0.12, 0.23)	0.73 (0.65, 0.80)	0.01 (0.0, 0.04)
Black River	0.02 (0.0, 0.06)	0.77 (0.43, 0.92)	0.01 (0.0, 0.03)	0.01 (0.0, 0.04)	0.19 (0.05, 0.54)
Model 1: Data driven informative prior on spawning site-fidelity					
Spawning Location	Burt Lake	Mullett Lake	Crooked Lake	Pickerel Lake	Black River
Burt Lake	0.93 (0.89, 0.96)	0.04 (0.03, 0.08)	0.01 (0.01, 0.02)	0.00 (0.0, 0.01)	0.01 (0.0, 0.04)
Mullett Lake	0.06 (0.02, 0.13)	0.54 (0.32, 0.91)	0.01 (0.0, 0.02)	0.01 (0.0, 0.03)	0.37 (0.03, 0.61)
Crooked Lake	0.06 (0.03, 0.11)	0.00 (0.0, 0.01)	0.82 (0.56, 0.91)	0.05 (0.03, 0.08)	0.06 (0.0, 0.32)
Pickerel Lake	0.11 (0.05, 0.17)	0.01 (0.0, 0.03)	0.19 (0.12, 0.26)	0.65 (0.51, 0.75)	0.05 (0.0, 0.18)
Black River	0.02 (0.0, 0.07)	0.42 (0.21, 0.85)	0.01 (0.0, 0.02)	0.01 (0.0, 0.03)	0.54 (0.11, 0.76)
Model 1: Perfect spawning site-fidelity					
Spawning Location	Burt Lake	Mullett Lake	Crooked Lake	Pickerel Lake	Black River
Burt Lake	0.90 (0.87, 0.93)	0.08 (0.04, 0.11)	0.01 (0.01, 0.02)	0.00 (0.0, 0.01)	0.00 (0.0, 0.01)
Mullett Lake	0.07 (0.02, 0.13)	0.83 (0.54, 0.94)	0.01 (0.0, 0.02)	0.01 (0.0, 0.03)	0.09 (0.01, 0.38)
Crooked Lake	0.06 (0.03, 0.10)	0.01 (0.0, 0.02)	0.86 (0.79, 0.91)	0.06 (0.03, 0.09)	0.01 (0.0, 0.07)
Pickerel Lake	0.10 (0.05, 0.16)	0.02 (0.0, 0.05)	0.20 (0.14, 0.27)	0.67 (0.56, 0.76)	0.02 (0.0, 0.09)
Black River	0.03 (0.0, 0.08)	0.74 (0.40, 0.92)	0.01 (0.0, 0.03)	0.01 (0.0, 0.04)	0.21 (0.05, 0.56)

885

886 Table 4: Sensitivity of fishing mortality rates (with 95% credible intervals) estimated from the best fit model (model 1) using two
 887 different prior distributions (system-wide pooled catch curve analysis and Hierarchical analysis) for fishing mortality rates and three
 888 different instantaneous tag shedding rates ($\Omega = 0.04, 0.14, \text{ and } 0.24$).

Fishing mortality rates						
Location	System-wide catch curve F prior			Hierarchical F prior		
	$\Omega = 0.04$	$\Omega = 0.14$	$\Omega = 0.24$	$\Omega = 0.04$	$\Omega = 0.14$	$\Omega = 0.24$
Burt Lake	0.23 (0.17, 0.30)	0.25 (0.20, 0.32)	0.28 (0.22, 0.34)	0.19 (0.14, 0.26)	0.23 (0.18, 0.30)	0.27 (0.21, 0.34)
Mullett Lake	0.18 (0.10, 0.30)	0.18 (0.11, 0.29)	0.20 (0.13, 0.29)	0.20 (0.09, 0.38)	0.22 (0.12, 0.40)	0.24 (0.14, 0.40)
Crooked Lake	0.25 (0.19, 0.33)	0.27 (0.21, 0.35)	0.29 (0.23, 0.36)	0.25 (0.17, 0.36)	0.29 (0.21, 0.40)	0.32 (0.24, 0.44)
Pickarel Lake	0.16 (0.10, 0.24)	0.18 (0.12, 0.25)	0.19 (0.14, 0.26)	0.13 (0.08, 0.20)	0.16 (0.11, 0.23)	0.18 (0.12, 0.26)
Black River	0.15 (0.01, 0.30)	0.16 (0.01, 0.30)	0.16 (0.01, 0.30)	0.02 (0.00, 0.06)	0.02 (0.02, 0.06)	0.02 (0.01, 0.06)

889

890 Table 5: Sensitivity of location specific mean post-spawn movement rates (proportion*year⁻¹) estimated from the best fit model
891 (model 1) using two different prior distributions (system-wide pooled catch curve analysis and Hierarchical analysis) for fishing
892 morality rates (*F*) using different assumed tag shedding rates ($\Omega = 0.04, 0.14, \text{ and } 0.24$).

Feeding Location															
System-wide catch curve <i>F</i> prior															
Spawning Location	Burt Lake			Mullett Lake			Crooked Lake			Pickerel Lake			Black River		
	0.04	0.14	0.24	0.04	0.14	0.24	0.04	0.14	0.24	0.04	0.14	0.24	0.04	0.14	0.24
Burt Lake	0.93	0.93	0.93	0.04	0.04	0.05	0.01	0.01	0.01	0.00	0.00	0.00	0.01	0.01	0.01
Mullett Lake	0.07	0.06	0.07	0.54	0.54	0.56	0.01	0.01	0.01	0.01	0.01	0.01	0.38	0.37	0.36
Crooked Lake	0.06	0.06	0.06	0.00	0.00	0.00	0.83	0.82	0.83	0.05	0.05	0.05	0.06	0.06	0.06
Pickerel Lake	0.11	0.11	0.10	0.01	0.01	0.01	0.19	0.19	0.19	0.65	0.65	0.65	0.05	0.05	0.04
Black River	0.02	0.02	0.02	0.42	0.42	0.44	0.01	0.01	0.01	0.01	0.01	0.01	0.55	0.54	0.53
Hierarchical <i>F</i> prior															
Spawning Location	Burt Lake			Mullett Lake			Crooked Lake			Pickerel Lake			Black River		
	0.04	0.14	0.24	0.04	0.14	0.24	0.04	0.14	0.24	0.04	0.14	0.24	0.04	0.14	0.24
Burt Lake	0.93	0.93	0.93	0.04	0.04	0.04	0.01	0.01	0.01	0.00	0.00	0.00	0.01	0.01	0.01
Mullett Lake	0.06	0.06	0.06	0.52	0.53	0.54	0.01	0.01	0.01	0.01	0.01	0.01	0.41	0.39	0.38
Crooked Lake	0.06	0.06	0.06	0.00	0.00	0.00	0.82	0.83	0.83	0.06	0.06	0.05	0.05	0.05	0.05
Pickerel Lake	0.10	0.10	0.10	0.01	0.01	0.01	0.18	0.18	0.18	0.67	0.67	0.67	0.05	0.05	0.04
Black River	0.02	0.02	0.02	0.40	0.41	0.41	0.01	0.01	0.01	0.01	0.01	0.01	0.57	0.56	0.55

893

894

Figure Captions

Figure 1.— Map of northern Michigan's Inland Waterway that consists of four lakes (Burt, Crooked, Mullett, and Pickerel), the Black River, and four major connecting rivers (north to south through the lakes: Cheboygan River, Indian River, and Crooked River).

Figure 2: Conceptual model depicting the process how a single cohort (e.g., Burt Lake cohort 1) is tracked through time using our tag-recovery model. For example, after the initial tagging, which coincides with the spawning period, each individual within Burt cohort 1 has the ability to move to any location within the waterway or can remain in Burt Lake. Following that post-spawn movement the individuals then experience the population and observation processes that are representative of the location they moved to after spawning. Prior to time step $t+1$, individuals either exhibit spawning-site fidelity and return to their original tagging location (i.e., Burt Lake) or remain in the location they emigrated to. Following the spawning period those individuals once again have the ability to move freely throughout the waterway.

Figure 3: Comparison of observed tag recoveries (red line) and the posterior predicted distribution of tag recoveries with Bayesian p -values for each cohort during 2011-2013.

Figure 4: Posterior (and prior) distributions of location specific fishing mortality rates (F) obtained from the best fit model with the base assumption for instantaneous tag shedding rate ($\Omega = 0.14$). The top panel (A) represents the model statement that used a system-wide catch curve analysis to develop the prior for F . The bottom panel (B) represents the model statement that used a hierarchical modeling approach for developing the prior for F .

1
2 Figure 1.— Map of northern Michigan’s Inland Waterway that consists of four lakes (Burt,
3 Crooked, Mullett, and Pickerel), the Black River, and four major connecting rivers (north to
4 south through the lakes: Cheboygan River, Indian River, and Crooked River).

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17

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19 Figure 3: Comparison of observed tag recoveries (red line) and the posterior predicted
20 distribution of tag recoveries with Bayesian *p*-values for each cohort during 2011-2013.

21

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23 Figure 4: Posterior (and prior) distributions of location specific fishing mortality rates (F)
 24 obtained from the best fit model with the base assumption for instantaneous tag shedding rate (Ω
 25 = 0.14). The top panel (A) represents the model statement that used a system-wide catch curve
 26 analysis to develop the prior for F . The bottom panel (B) represents the model statement that
 27 used a hierarchical modeling approach for developing the prior for F .

Appendix 1: The explanation for the derivation of prior distribution for fishing mortality ($\hat{F}$).

Pooled catch curve analyses provided estimates of $\hat{Z} = 0.542$ and $\hat{\sigma}_Z^2 = 0.0025$. The estimate of Z is an approximately normally distributed random variable; thus instantaneous fishing mortality is a linear function of a normal random variable ($\hat{F} = \hat{Z} - M$). From Rice (2007; pg. 59): If $X \sim N(\mu, \sigma^2)$ and $Y = aX + b$, then $Y \sim N(a\mu + b, a^2\sigma^2)$. To derive a common prior distribution for estimates of instantaneous fishing mortality we assumed $M = 0.3$; thus $a = 1$ and $b = -0.3$, and therefore $\hat{F} \sim N(\hat{Z} - M, \sigma^2) \rightarrow \hat{F} \sim N(0.242, 0.0025)$.

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Appendix 2: State equation for process model with no site fidelity used for sensitivity analyses.

This equation implicitly assumes all fish join the spawning population at time $t+1$ in the same location where they summer and survive at time t . All state-equation parameters and latent variable values, as well as their subscripts, as defined in the Methods section of text.

$$X_{j,l,i,t} = R_{j,l,t} \varphi_{l \rightarrow i,t} \quad \text{when } t = j$$

$$X_{j,l,i,t} = \sum_s X_{j,l,s,t-1} \theta_{s,t-1} \varphi_{s \rightarrow i,t} \quad \text{when } t > j$$

Draft

Appendix 3: Number of individuals released (*n*) and recovered by location and year for each of the 15 tag cohorts, which was used to inform the tag-recovery model. Cohorts 1-3 for each location correspond to the individuals tagged during spring-spawning in 2011-2013, respectively. Recovery years correspond to the annual fishing season that the fish were captured and returned. For example, cohort 1 from Burt Lake was tagged during spring-spawning in 2011 and the recovery years 1-3 correspond with the number of tagged individuals recovered and reported during the 2011-2013 fishing seasons.

Burt Lake											
cohort 1 (<i>n</i> = 5,468)				cohort 2 (<i>n</i> = 687)				cohort 3 (<i>n</i> = 2,747)			
Recovery location	Recovery year			Recovery location	Recovery year			Recovery location	Recovery year		
	1	2	3		1	2	3		1	2	3
Burt	561	281	87	Burt	-	62	24	Burt	-	-	122
Mullett	30	29	13	Mullett	-	7	1	Mullett	-	-	13
Crooked	9	7	2	Crooked	-	3	0	Crooked	-	-	11
Pickerel	1	1	0	Pickerel	-	1	1	Pickerel	-	-	3
Black River	0	0	0	Black River	-	0	0	Black River	-	-	0
Mullett Lake											
cohort 1 (<i>n</i> = 409)				cohort 2 (<i>n</i> = 54)				cohort 3 (<i>n</i> = 188)			
Recovery location	Recovery year			Recovery location	Recovery year			Recovery location	Recovery year		
	1	2	3		1	2	3		1	2	3
Burt	2	2	0	Burt	-	0	0	Burt	-	-	1
Mullett	31	13	9	Mullett	-	4	0	Mullett	-	-	17
Crooked	0	0	0	Crooked	-	0	0	Crooked	-	-	0
Pickerel	0	0	0	Pickerel	-	0	0	Pickerel	-	-	0
Black River	1	1	0	Black River	-	0	0	Black River	-	-	0

Appendix 3: (continued)

Crooked Lake												
cohort 1 (<i>n</i> = 562)				cohort 2 (<i>n</i> = 529)				cohort 3 (<i>n</i> = 614)				
Recovery location	Recovery year			Recovery location	Recovery year			Recovery location	Recovery year			
	1	2	3		1	2	3		1	2	3	
Burt	3	2	0	Burt	-	4	0	Burt	-	-	2	
Mullett	0	0	0	Mullett	-	0	0	Mullett	-	-	0	
Crooked	84	29	11	Crooked	-	74	41	Crooked	-	-	89	
Pickerel	5	3	0	Pickerel	-	3	3	Pickerel	-	-	1	
Black River	0	0	0	Black River	-	0	0	Black River	-	-	0	
Pickerel Lake												
cohort 1 (<i>n</i> = 623)				cohort 2 (<i>n</i> = 108)				cohort 3 (<i>n</i> = 326)				
Recovery location	Recovery year			Recovery location	Recovery year			Recovery location	Recovery year			
	1	2	3		1	2	3		1	2	3	
Burt	5	2	0	Burt	-	2	0	Burt	-	-	3	
Mullett	1	0	0	Mullett	-	0	0	Mullett	-	-	0	
Crooked	30	4	0	Crooked	-	2	2	Crooked	-	-	6	
Pickerel	54	26	3	Pickerel	-	10	0	Pickerel	-	-	19	
Black River	0	0	0	Black River	-	0	0	Black River	-	-	0	
Black River												
cohort 1 (<i>n</i> = 261)				cohort 2 (<i>n</i> = 99)				cohort 3 (<i>n</i> = 231)				
Recovery location	Recovery year			Recovery location	Recovery year			Recovery location	Recovery year			
	1	2	3		1	2	3		1	2	3	
Burt	0	1	0	Burt	-	0	0	Burt	-	-	0	
Mullett	24	8	5	Mullett	-	6	2	Mullett	-	-	6	
Crooked	0	0	0	Crooked	-	0	0	Crooked	-	-	0	
Pickerel	0	0	0	Pickerel	-	0	0	Pickerel	-	-	0	
Black River	2	0	0	Black River	-	0	1	Black River	-	-	3	

Appendix 4: Simulation study results determining the influence of total number of individuals released by location on movement and fishing mortality parameter estimates using posterior means from the top model as truth for model values when simulating data.

Simulated post-spawn movement rates using the actual sample size (i.e., actual number of individuals released per location using 98 simulations runs that converged).

Appendix 4: (cont'd)

Simulated post-spawn movement rates using the medium sample size (i.e., 2,500 individuals released per location using 89 simulations runs that converged).

Appendix 4: (cont'd)

Simulated post-spawn movement rates using the large sample size (i.e., 5,000 individuals released per location using 55 simulations runs that converged).

Appendix 4: (cont'd)

Simulated fishing mortality rates (F) using three different ranges of samples sizes (Actual: true number of tag releases, Medium increase: 2,500 tag releases per location, and Large increase: 5,000 tag releases per location).

Draft