EVALUATING METHODS FOR MORTALITY ESTIMATION OF LAKE ERIE WALLEYE USING ACOUSTIC TELEMETRY DATA

By

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ABSTRACT

Walleye are an important Lake Erie species with both economic and societal value to Canada and the U.S. Accurate mortality estimates are important for sustainable management of the species, especially for yield estimation and quota setting. Walleye harvest limits in Lake Erie are determined by applying a harvest control rule to the results of a stock assessment model performed by the Walleye Task Group (WTG). The WTG uses a complex statistical catch-at-age model to estimate abundance of walleye annually, incorporating fishery-dependent data from Ontario, Ohio, and Michigan, along with data from three fishery-independent gill net surveys, and assumes a natural mortality rate of 0.32. Deriving estimates of natural mortality, spatially and temporally, is challenging, but would allow for variability to be investigated and be valuable to fishery management. Acoustic detections can indicate the alive or dead status of a tagged fish at a specific point in time and space, but it is unclear how to use these data to quantify mortality of the population. There were four objectives of this dissertation: 1) Develop an estimation approach and software code for estimating mortality components for walleye in the Great Lakes based on ongoing acoustic telemetry study designs, 2) Assess the performance of the different methods and explore through stochastic simulations the sensitivity of each approach, 3) Evaluate mortality rates of Lake Erie walleye, and 4) Provide guidance on next steps for this research.

Chapter 1 addresses objectives one and two, and presents an evaluation of two different approaches to estimating mortality, a spatial and a non-spatial approach. Both approaches were evaluated using simulated data across a range of scenarios, including different study designs (receivers arranged in grids versus lines), number of receivers, and mortality levels. Accuracy and precision in mortality estimates were sensitive to assumed mortality rates and receiver

configurations; the high-density receiver grid resulted in the lowest error rates. Estimates were consistently positively biased.

Chapter 2 addresses objective three by estimating mortality rates of Lake Erie walleye using the spatial and non-spatial approaches developed for Chapter 1 and the acoustic telemetry data collected from the Great Lakes Acoustic Telemetry Observation System (GLATOS) network. We applied the spatial and non-spatial mortality estimation methods to three groups of acoustically tagged Lake Erie walleye. The total mortality rate estimated by these methods was similar to the total mortality estimated in the assessment model for Lake Erie Walleye currently used by the management agencies, yet the high reported fish harvest in the acoustic telemetry data suggests that the natural mortality rate may be lower than that assumed by the assessment model. The differences between the three tagging groups also suggests spatial differences may exist in the mortality experienced by different spawning populations. However, the poor performance of the spatial models discourage confidence in those results and inhibited inferences on the specific spatial patterns of mortality.

Chapter 3 addresses the fourth objective and provides guidance on the next steps for this line of research. The bias and performance issues in Chapters 1 and 2, particularly for the spatial models, led to the conclusion that new estimation methods are needed for using acoustic telemetry data to estimate mortality components. Accounting for the underlying movement patterns of the study species, incorporating other auxiliary data, and using a larger data set of acoustic detections may allow for a more complete spatial investigation of Lake Erie walleye mortality patterns.

This dissertation is dedicated to Mom and Dad, thanks for encouraging me to always be me.

ACKNOWLEDGEMENTS

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PREFACE

The material in chapter one has been published open access in the Canadian Journal of Fisheries and Aquatic Sciences, the full citation is: Peterson, L.K., Jones, M.L., Brenden, T.O., Vandergoot, C.S., and Krueger, C.C. 2021. Evaluating methods for estimating mortality from acoustic telemetry data. Can. J. Fish. Aquat. Sci. 78(10): 1444-1454. https://doi.org/10.1139/cjfas-2020-0417. This journal allows open access article sharing in dissertations as long as a link to the posted version along with DOI is included. The language and structure of Chapter 1 reflects the requirements of the journal, and I would also like to acknowledge my coauthors for that work. The materials in chapters two and three were also developed with the intention for publication in peer-reviewed journals, and the language used there also reflects the assistance of co-authors.

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INTRODUCTION

Lake Erie walleye (*Sander vitreus*) is a percid that is of both ecological and economic importance to the Great Lakes region. Harvest of walleye is allocated annually through a quota-management approach, using a harvest control rule in conjunction with a stock assessment model to set total allowable catch. The stock assessment model uses data collected from all the jurisdictions surrounding the lake as well as an assumed natural mortality rate to predict abundance. Management is interested in using an independent data set collected by on-going acoustic telemetry studies in Lake Erie to investigate mortality and potentially look at spatial patterns or differences in mortality between spawning populations. The goals of this dissertation are to develop an estimation approach and software code for estimating mortality of walleye in Lake Erie, assess the performance of the different methods through stochastic simulations, evaluate mortality rates of Lake Erie walleye using acoustic telemetry data, and provide guidance on the next steps for this research.

0.1 Lake Erie walleye

Lake Erie is the smallest (by volume), most biologically productive of the Laurentian Great Lakes, supporting large recreational and commercial fisheries for walleye. Walleye is a freshwater percid found in Canada and the northern United States that spawns in both riverine and lacustrine (reef) habitats, and show evidence of spawning site fidelity (Hayden et al. 2017). As an abundant terminal predator that quickly becomes piscivorous, walleye are important parts of the ecosystems they occupy. Walleye can be found in all five of the Great Lakes, and are prized by both recreational and commercial fishers from Canada and the United States. The Lake Erie Canadian commercial walleye fishery is one of the largest freshwater commercial fisheries in the world and a large recreational fishing community for walleye is found on the United States side of the lake; both are multi-million dollar industries. Walleye populations historically have fluctuated due to changes in recruitment, with corresponding fluctuations in the fishery harvest. Careful bi-national management is needed to protect both the fish populations and the economically important fisheries they support.

0.2 Acoustic telemetry in the Great Lakes

Acoustic telemetry is an electronic tagging technique that involves two components, a transmitter and a receiver. A transmitter is an electronic tag that is surgically implanted into a fish and broadcasts a series of transmissions at specified intervals. A receiver is a data logger than can be placed in the water and will receive and record the transmissions of the acoustic tags once the tag is within the detection range of the receiver. Receivers can also be manually moved (e.g., via a boat) to search for electronic tags, which is called active tracking. Acoustic telemetry studies are able to collect large amounts of location information on the tagged fish without requiring additional recaptures beyond the initial tagging. The data collected by these studies has been used to investigate movement, behavior, and population dynamics.

In 2010, the U.S. Great Lakes Restoration Initiative provided funds to the Great Lakes Fisheries Commission to support acoustic telemetry projects within the Great Lakes region. The Great Lakes Acoustic Telemetry Observation System (GLATOS) was created to bring together the network of researchers in the U.S. and Canada using acoustic telemetry. This centralized network was a way to encourage collaboration and the sharing of equipment, minimize duplication of effort, and provide a centralized database of tag detections. Over 100 projects have joined the GLATOS network, generating many scientific publications, and the tagging effort and receiver deployment continues to expand (https://glatos.glos.us/).

A number of the acoustic telemetry projects within GLATOS are focused on investigation the behavior, movement, and mortality rates of Lake Erie walleye. The two studies that generated the data used in this dissertation were titled “Identifying migration patterns and spatial ecology of a reef spawning stock of walleye in the western basin of Lake Erie” and “Understanding dam removal impacts on a formerly prolific Great Lake’s walleye population”. In these two studies alone, hundreds of walleye were tagged and hundreds of receivers deployed starting back in 2013 and 2014. Both of these projects generated millions of detections, and both had an objective to identify and compare mortality rates using this large dataset.

0.3 Mortality and the stock assessment process

Mortality estimates increase our understanding of the dynamics of a fish population. Our understanding of mortality allows scientists to predict how a population will respond to fishing pressure and changes in the environment. They also inform managers about the productivity of a stock and how much exploitation a population can reasonably sustain. Mortality, of which fishing and natural mortality are the two main components, has been studied for many different species in a variety of ways (see Siegfried and Sansó, 2009 for a review). Fishing mortality is informed by the reported catch and effort of fishers, and can be adjusted by estimates of by-catch and unreported harvest, or the catchability of the fish and the selectivity of a fishing gear. The other component of mortality, natural mortality, encompasses the remaining deaths that occur due to causes other than fishing, including predation by non-humans, disease, starvation, or old age. Natural mortality is a difficult rate to directly measure, as these ‘natural’ deaths often remain unobserved, so estimates tend to be generated from indirect measures. While many indirect measures have been developed, estimating natural mortality remains a focus of concern to the fisheries management realm.

Both fishing and natural mortality estimates are critical components of many stock assessment models. Stock assessment models are used to evaluate the status of a population, which in turn can be used to determine an appropriate management strategy for that population. While there are studies that have shown stock assessment models are sensitive to the natural mortality estimate used (Clark 1999; Williams 2002; Hewitt et al. 2007), often in practice, as is the case with Lake Erie walleye, stock assessment models assume a constant natural mortality rate across years and ages. Natural mortality is recognized to be an influential assumption in fisheries management and alternative methods for more precise estimation and an evaluation of the assumption that it is a constant value are needed.

The Walleye Task Group evaluates abundance of Lake Erie walleye using a statistical catch-at-age model that incorporates fishery effort and harvest data from both commercial and recreational fisheries as well as fishery-independent gill net surveys. These data are used to estimate fishing mortality for each of the jurisdictions, which is used with an assumed value of natural mortality (0.32) to predict abundance and apply a harvest control rule. The assumed value of natural mortality, 0.32, was generated using results from a 1991 walleye tag recapture program and has remained nearly unchanged over the past 30 years (except in 1998 where a lower value was used before returning to 0.32; Locke et al. 2005).

The assumption of a constant value for natural mortality of Lake Erie walleye has been investigated and challenged in the past, and this work looks to continue assessing that assumption. Berger et al. (2012) looked at spatially varying stock assessments for Lake Erie walleye and found evidence that spatially referenced parameters not only improved model fit but also altered the estimates of stock size. Vandergoot and Brenden (2014) used data from a Lake Erie walleye jaw tagging study to investigate region- and age-specific fishing and natural mortalities and found a decline in natural mortality with age; they recommended the Lake Erie assessment be updated to be spatially explicit and incorporate these new estimates of mortality. This dissertation continues the investigations of mortality of Lake Erie walleye using acoustic telemetry data, first by evaluating two approaches using simulated data, then empirical data, before providing recommendations for future work.

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CHAPTER 1
EVALUATING METHODS FOR ESTIMATING METHODS FROM ACOUSTIC TELEMETRY DATA

Peterson, L.K., Jones, M.L., Brenden, T.O., Vandergoot, C.S., and Krueger, C.C. 2021. Evaluating methods for estimating mortality from acoustic telemetry data. Can. J. Fish. Aquat. Sci. 78(10): 1444-1454. https://doi.org/10.1139/cjfas-2020-0417.

Abstract

Mortality rates are major determinants of long-term sustainability of exploited fish populations, yet accurately estimating these rates can be challenging. We used simulations to evaluate nonspatial and spatial modeling approaches for estimating mortality rates from acoustic telemetry detection data. Data were generated assuming different receiver configurations (grids, lines), number of receivers, and mortality levels. Relative error rates for total mortality ranged from 0% to 83% for the nonspatial model and from 1% to 141% for the spatial model. Absolute error rates ranged from 0.00 to 0.11 for the nonspatial model and from 0.01 to 0.15 for the spatial model. Accuracy and precision in mortality estimates were sensitive to assumed mortality rates and receiver configurations; the high-density receiver grid resulted in the lowest error rates. Estimates were consistently positively biased. We recommend using grid receiver configurations for mortality rate estimation from acoustic telemetry studies. The potential for biased mortality estimation from acoustic telemetry detection data should be considered during study design, particularly for those species with behavior and ecology that may result in long periods without detection.

1.1 Introduction

Mortality rate is a critical population dynamics parameter for sustainable management of exploited fish populations; despite its importance, accurately estimating mortality rates remains challenging. Tagging studies in which fish are collected, tagged with individually unique or batch tags, and released back into the system where they were captured and possibly recaptured again (perhaps several times) during future sampling events (i.e., tag–recapture studies) are among the most frequently used methods for estimating mortality rates of fish populations. Methods for estimating mortality rates from tag–recapture studies have grown in complexity, but most are extensions of two key formulations: Jolly–Seber (JS) (Jolly 1965; Seber 1965) and Cormack– Jolly–Seber (CJS) formulations (Cormack 1964; Jolly 1965; Seber 1965). With the JS formulation, parameters of interest include survival, capture probability, population abundance, and number of new individuals entering the population. The CJS formulation is a restricted version of a JS formulation and is focused only on estimating survival and capture probability. Hereafter, our discussion of tag–recapture formulations is restricted to the CJS formulation.

Tagging studies inherently yield spatial data. Individual fish are generally collected (i.e., from discrete or multiple locations), tagged, and released, after which fish disperse from the capture– tagging site. Mortality rates that tagged individuals experience also generally vary spatially because of differences in environmental conditions or where fishing activities are concentrated; consequently, overall survival of an individual depends on where that fish has been located. Also, sampling efforts to recapture tagged individuals can differ spatially. Both tag–recapture and tag–recovery (i.e., terminal recapture) frameworks for estimating mortality components have been expanded to account for the inherent spatial structure to tagging data (Royle et al. 2014; Vandergoot and Brenden 2014). In the case of tag–recapture studies, a spatial CJS framework has been proposed to include the locations of where recapture events occur and to address spatial aspects of recapture data (e.g., movement patterns of tagged individuals; spatially and (or) temporally varying mortalities), while also allowing for sample site level covariates. In recent decades, spatial CJS models have been used in a variety of applications (Hightower et al. 2001; Borchers and Efford 2008; Royle et al. 2009; Gardner et al. 2010; Raabe et al. 2014; Cooke et al. 2016; Hightower and Harris 2017; López-Bao et al. 2018).

Electronic tagging technology such as acoustic telemetry can generate large datasets of repeated observations (i.e., recaptures via transmitter detections) of tagged fish with spatial coverage that is less dependent on where fishing or assessment surveys occur. As a consequence, detections from acoustically tagged fish hold a great deal of promise for estimating mortality rates of fish populations (Kraus et al. 2018; Villegas-Ríos et al. 2020). Acoustic telemetry involves implanting or attaching an electronic tag to a fish that periodically emits a uniquely identifiable signal that is then detected and recorded on receivers (i.e., listening stations) deployed across the study area in fixed positions for up to a year or more (passive monitoring). Acoustic telemetry research can also include active monitoring in which searches for tagged fish are conducted from mobile platforms, although in large systems such as oceans or the Laurentian Great Lakes, this approach may not be an efficient means for collecting detection data. Acoustic telemetry has been used to study behavior and movement of fish in rivers (Welch et al. 2009; Perry et al. 2010), small lakes (Hightower et al. 2001), large lakes (e.g., Laurentian Great Lakes; Hayden et al. 2014; Krueger et al. 2018), and oceans (Heupel et al. 2006; Hussey et al. 2015).

Our project sought to evaluate the accuracy of estimating total mortality rates of tagged fish from acoustic telemetry detection data using spatial and nonspatial models in a large freshwater or marine system. An individual-based model was used to simulate fish movements within a system resembling Lake Erie with movement behaviors based on observed movement patterns of walleye in the lake (Kershner et al. 1999; Wang et al. 2007; Hayden et al. 2018). Detection histories of tagged individuals were simulated assuming different receiver configurations (e.g., number of receivers, spatial placement of receiver stations) and different mortality rates of tagged fish. These detection histories were then used in spatial and nonspatial CJS models to evaluate the accuracy and precision of the two models in estimating mortality rates. Our aim was to evaluate performance of the different models when applied to data generated from an acoustic telemetry study and to provide guidance regarding receiver configurations to those interested in estimating mortalities of fish populations from acoustic telemetry studies.

1.2 Methods

1.2.1 Simulation framework

Acoustic telemetry detection data were simulated in R (R Core Team 2019) using functions from the glatos package (Holbrook et al. 2017). Four components were included in the simulation framework: (1) generation of movement paths; (2) generation of electronic transmitter (hereafter referred to as “tag”) transmissions along those paths; (3) specification of receiver location; and (4) a distance function that defined the ability of the receiver to detect transmissions (i.e., detection probability). In addition, a mortality function removed fish from the simulation according to a specified mortality rate. These functions generated a spatially-explicit time series of detections similar in form to actual telemetry data, with tag detection histories for each individual fish. The simulation framework described in this study reflects ongoing acoustic telemetry work for Lake Erie walleye, coordinated by the Great Lakes Acoustic Telemetry Observation System (GLATOS; Krueger et al. 2018) but is meant to represent a more general species – large lake situation and not directly match the dynamics of walleye or the configuration of receivers in Lake Erie.

Movement generation

Detection data for 200 fish were simulated within a space that resembled Lake Erie (Figure 1.1); all fish were assumed to be released at the same time at one location in the western portion of the lake, which mimics past walleye tagging operations that have been conducted (Peat et al. 2015; Raby et al. 2018; Bade et al. 2019; Faust et al. 2019; Matley et al. 2020). Simulated fish were monitored over a period of three years. Modeled movement patterns were essentially a random walk, which is often used when modeling animal movement (Berg 1993; Turchin 1998; Humston et al. 2004). We based some of the parameters used in this simulation on the simulation framework used by Kraus et al. (2018), who evaluated different receiver grid scenarios based on the same walleye acoustic telemetry studies referenced above. Because movement characteristics of walleye in the wild were unknown, they evaluated a range of movement rates, 0.1 to 0.9 m·s–1, over a period ranging from 30 to 150 days. In our simulation, a movement rate of 0.05 m·s–1 was chosen in part due to the length of the simulation. Even at the lowest movement rate assumed by Kraus (0.1 m·s–1), movements of simulated fish could traverse the entire study system multiple times in a year, which we deemed unlikely for a system as large as that of the Great Lakes. At a movement rate of 0.05 m·s–1, the movement paths of the simulated fish more closely resembled a seasonal migratory pattern, with fish moving across the lake approximately two times during the year. This movement rate is much lower than the maximum speed measured for walleye evaluated by Peake et al. (2000) but was meant to reflect the net effect of active foraging and resting periods on movements of individual fish.

The other aspect of simulating fish movement was the turning angle. A new relative direction was randomly drawn every 100 m from a normal distribution with a mean of 0° and a standard deviation of either of 5° (100 fish) or 25° (100 fish). The two standard deviations were used to represent two groups of fish. The group with the smaller standard deviation ranged much

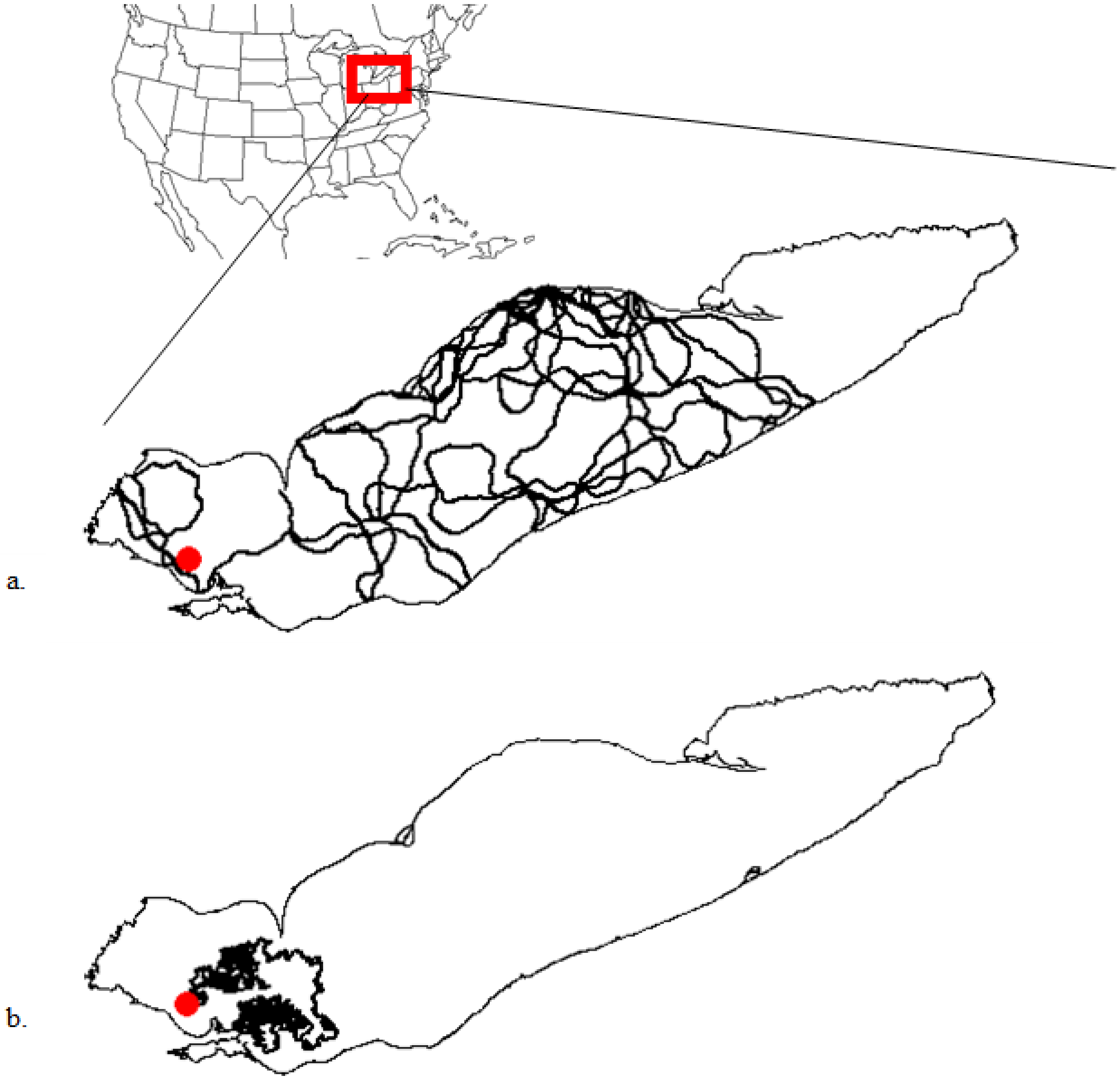

Figure 1.1 a. Movement path for a fish with a standard deviation of 5 for its turning angle. This fish would tend to be more far-ranging because it tends to continue moving in a similar direction. b. Movement path for a fish with a standard deviation of 25 for its turning angle. This fish would tend to stay closer to where it was released because it tends to turn sharply, instead of continuing in a similar direction, which results in a more circular path. Red dot is release location on Toussaint Reef.

further, as they had a greater chance of continuing to head in a similar direction to the previous time step. The group with the larger standard deviations tended to remain within a more confined area. This approach was used to reflect the idea of heterogeneity of fish movement within a population (Figure 1.1). Evidence from past tagging studies suggests some walleye spend the whole year in the western and west-central basin of Lake Erie, while others (frequently old, large walleye) move from the western basin to the eastern basin and return during the year (Wang et al. 2007; Vandergoot and Brenden 2014; Raby et al. 2018). The components of fish movement, as well as all other values used to generate simulations, did not vary over time. After release, remaining abundance of tagged fish was projected with an exponential population model where the true total mortality was one of the evaluated scenarios:

$$N_t = N_0 e^{-Z*t}$$

Fish that died during the year were randomly selected; the precise time that an individual's death occurred was drawn from a uniform distribution encompassing the entire year. When a tagged fish died, it would stop moving and disappear from the study area in the simulation. Three different instantaneous mortality rate scenarios were used: 0.1, 0.4, and 0.6.

Transmission generation

Along each of the simulated movement paths, tag transmissions were generated using tag signal specifications. We assumed that each tag transmitted approximately every minute for a duration of 5 s. Although most field studies involving Lake Erie walleye routinely used delays with longer durations, for the purpose of this study, the 1-min delay was considered sufficient. In an actual acoustic telemetry study, tag specifications are something that must be decided on by project investigators and require consideration about desired tag life and probability of tag detections to accomplish a project's objectives.

Receivers and detection generation

Whether a tag transmission was detected by a receiver depended on the assumed receiver configuration and the detection efficiency of the receivers. A detection probability function (or detection range curve) was used to represent the detection efficiency based on the distance between receivers and a tagged fish. In reality, the ability of a receiver to detect a tag transmission is highly dependent on environmental conditions (e.g., wind, waves, vegetation, ice cover, noise, and tag collisions; Kessel et al. 2014; Hayden et al. 2016), but it was beyond the scope of this research to incorporate those conditions into our simulation. The detection probability function that we used was an exponential decay function:

$$1 - \frac{1}{1 + 10^{-\beta_1 X(D-\beta_2)}}$$

where D is the distance in metres between the receiver and the transmitting tag (Figure 1.2). Under this equation, the probability of a receiver detecting the transmission of a tagged fish at a distance of 800 m was 50%. Alternatively, at distances of 400 or 1200 m, the probabilities of detection were approximately 91% and 9%, respectively. This represented "average" environmental conditions (Hayden et al. 2016; Kraus et al. 2018).

Different numbers (39 or 64 receivers) and spatial patterns (grids or lines) of receivers were used to evaluate how configuration affected model performance. Receiver lines have been used in the past to evaluate directional movement and to take advantage of choke points in rivers or lakes where a high confidence exists that fish will pass across the line at some point of the year. More recently, receiver grids have been used for more detailed information of fish movement (Kraus et al. 2018; Raby et al. 2018). For a 64-receiver grid configuration, receivers were spaced approximately 20 km apart, whereas a 39-receiver grid configuration resulted in a 25 km spacing. For the line configurations, receivers were distributed along four lines to represent lines across the basins of the study area (Figure 1.3). Locations of lines did not differ based on the number of receivers being evaluated. Rather, the 64-receiver scenario just resulted in receivers being placed closer together in the line, which lessened the chance that a fish could cross the line without being detected.

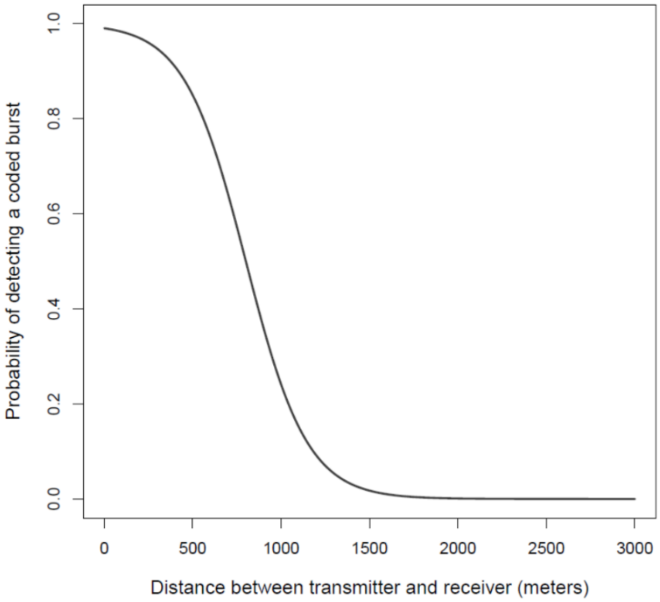

Figure 1.2. Detection range function. Shape parameters of 0.0025 and 800. At 800 meters, there is a 0.5 probability the fish will be detected.

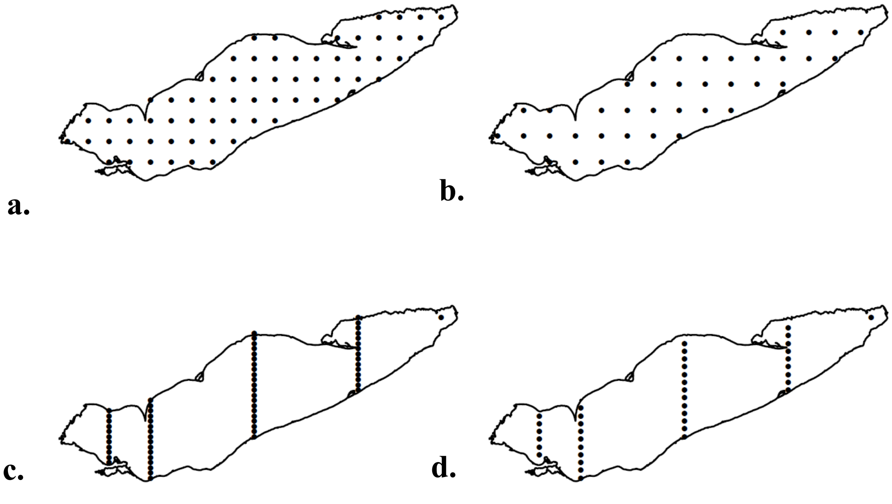

Figure 1.3. Receiver configurations. a. 64 (high-density) receivers in a grid. b. 39 (low-density) receivers in a grid. c. 64 (high-density) receivers set up in lines. d. 39 (low-density) receivers set up in lines.

The four receiver configurations combined with the three different mortality rate scenarios resulted in 12 total scenarios that were evaluated as part of this research. These 12 scenarios were replicated 10 times to evaluate the effect of the stochasticity in the simulation framework. The total amount of detections generated varied depending on the scenario, between 0.5 and 1.5 million total detections for 200 fish over three years.

1.2.2 Mortality estimation methods

Both the spatial and nonspatial models used to estimate total mortality were based on a CJS formulation (Cormack 1964; Jolly 1965; Seber 1965). As previously indicated, CJS frameworks use two parameters, survival rate (φ) and tag detection probability (p), to assign probabilities to each possible detection history (X_t). Survival rate represents the probability of an individual surviving from the previous time period to the current time period, while detection probability is the probability of a surviving fish being detected in the current time period. Both models drew inferences from the simulated acoustic telemetry data, but the structure of the two models and processing of acoustic detections differed. Both models were estimated using Bayesian inference through JAGS (Plummer 2015) executed from within R (R Core Team 2019) via the jagsUI package (Kellner 2019).

Nonspatial model

For the nonspatial model, assuming N_0 represents the number of individuals released in a tagged group, the expected number of individuals $E(X_t)$ detected at time *t* can be expressed as

$$E(X_t) = N_0 \varphi_{t=1 \to t} p_t$$

This basic structure was used for all possible detection histories. From Cormack (1964), a generalized form of the likelihood for the basic model would be

$$L \propto \prod_{t=1}^{n-1} (X_t)^{c_t} (\varphi_t)^{v_t} (p_{t+1})^{a_t+1} (1-p_{t+1})^{v_t - a_t + 1}$$

with *n* indicating the total number of time periods, *t* indicating the current time period, *c* indicating the number of tagged individuals seen for the last time at time *t*, *v* indicating the number of marked animals known to be alive (detected at least once) after time *t*, and *a* indicating the number of individuals redetected in each sample. In the model used in this study, survival was assumed constant across time periods, while detection probability was allowed to vary through time; this allowed survival and detection probability to be estimated separately in the final time step. Detection probability was allowed to vary through time because all fish paths were started in the same location in the simulation; therefore, as time passed, the receivers further away from the release spot would have increasing detection probability due to fish dispersing throughout the lake. This model also ignored the specific moments within each time period that detections occurred (i.e., all detections in a month were aggregated together). Three parallel Markov chain Monte Carlo (MCMC) chains, each consisting of 10 000 iterations, were run from random initialization values with an initial 100-iteration adaptive phase. The first 1500 saved iterations were discarded as burn-ins and the chains were not thinned. Uniform prior distributions with lower and upper bounds of 0 and 1, respectively, were assumed for survival and detection probabilities.

Spatial model

The spatial CJS model was implemented using a state–space framework. We based our approach on Gardner et al. (2010) and Raabe et al. (2014) spatial capture–recapture models. The state– space framework consisted of an observational model for the observed encounter histories of tagged fish, a state model for the "alive" state of the fish at each modeled time step, and a latent point process model that described the “activity centers” (i.e., estimated average locations) of tagged fish across the time periods. The observation model was conditional on the state model. The model was conditional on first recapture, so the initial detection was considered the first period for each individual and the state at that initial point was “alive”. This means that if a fish was never detected after release, it was excluded from the analysis (this resulted in as many as 5% of the original 200 fish being excluded in any simulation run). Subsequent states were estimated using the probability of mortality from one time period to the next. The observation model for each receiver conditional on the state model of the individual was then assumed to be drawn from a distribution informed by the point process model.

The point process model, also called the latent activity center, described the average center of a fish’s location during a sample period. This site was influenced by whether a fish was observed multiple times at a receiver as well as at what receivers it was detected during a single time step. The distance between a receiver and the estimated activity center influenced the tag detection probability for that receiver.

The formulation of this modeling approach incorporated counts of detections for each individual (i), at each receiver (*j*), during each sampling period (*t*, monthly). The observation model had encounter histories ($h(i, j, t)$) conditional on the state model ($z(i, t)$) with, as was mentioned earlier, the state in the initial time step assumed to be “alive”, and all subsequent states modeled as

$$z(i,t) \sim Bernoulli(\varphi z(i,t-1))$$

where φ was the survival probability from one time period to the next (monthly time step: $\varphi = e^{-Z/12}$). While this analysis assumed that survival was constant across space to allow a better comparison with the results of the nonspatial approach, this model could be extended to allow for spatially varying survival estimates.

This model allowed for multiple detections at any receiver during a time period. The data were count data and the observation model was conditional on the state model followed a Poisson distribution:

$$h(i,j,t)|z(i,t) \sim Pois[\lambda_0 g(i,j,t) z(i,t)]$$

where λ_0 was the baseline detection rate, or the expected number of detections when an activity center and the receiver location were identical. The function *g(i, j, t)* was a general distance function incorporating the distance between the individual activity center (*s(i, t)*) and the receiver location (*x(j)*). The distance function was a Gaussian kernel (or half-normal), a commonly used distance function used in sighting models:

$$g(i,j,t) = e^{-\frac{d(i,j,t)^2}{2\sigma^2}}$$

$$d(i,j,t) = s(i,t) - x(j)$$

where *d* was the Euclidean distance between an estimated individual activity center and the receiver, and σ was the scale parameter for the distance function. The distance function can be interpreted as the rate by which the detection probability of a specific receiver decreased as a function of distance from the estimated activity center. The location of the activity center was truncated by the specified state–space coordinates. The activity center locations were not constrained by the boundaries of the state–space itself, but by the upper and lower latitude and longitude values of the edges of the modeled system. As the modeled system was not a perfect rectangle, activity centers could be estimated in locations outside the bounds of the study system. More sophisticated modeling techniques would be needed to incorporate more complicated state–space shapes.

A random-walk approach was used for estimating activity center locations (Raabe et al. 2014) where activity center for an individual fish was informed by the location of the activity center in the previous time step. These activity centers were drawn from a normal distribution with a mean equal to the location of the activity center in the previous time step and a standard distribution, τ, which would correspond with the size of the movement of the individual between time intervals. Because we were dealing with activity centers in two dimensions, the random-walk process consisted of the following:

$$s_{x,i,t} \sim Normal\left(s_{x,i,t-1}, \tau_{x,i}\right)$$

$$s_{y,i,t} \sim Normal\left(s_{yi,t-1}, \tau_{y,i}\right)$$

where the τ values were assumed to be drawn from a beta distribution. During time periods when fish were undetected, the model had trouble estimating activity center locations, similar to what was observed by Harris et al. (2021). Like Harris et al. (2021), we modified the random-walk process in an attempt to improve model convergence due to these nondetections. The modified random-walk process included the weighted average location of the fish in the time period that it was last detected (*aa*). In other words, when fish were not detected, the random-walk process consisted of the following:

$$Fish\ not\ detected\colon s_{x,i,t} \sim Normal\left(aa_{x,i,t\ of\ last\ detection}, 50\right)$$

$$Fish\ not\ detected\colon s_{y,i,t} \sim Normal\left(aa_{y,i,t\ of\ last\ detection}, 50\right)$$

The standard deviations for the random-walk process were not able to be estimated when fish were not detected; consequently, we assumed standard deviations of 50 in cases when fish were not detected.

The first activity center for each individual fish was estimated using uniform distributions with upper and lower limits equal to the boundaries of the study area. The model-assumed detections were instantaneous for each time period and ignored the specific time at which an individual was detected within the time period. Three parallel MCMC chains, each consisting of 15 000 iterations, were run from random initialization values with an initial 100-iterations adaptive phase. Bayesian inference analyzed these models, with three chains of at least 15 000 iterations. The first 2000 saved iterations were discarded as burn-ins. The chains were thinned; each tenth iteration was saved to calculate the final statistics. Uniform distributions were assumed as priors for survival (lower and upper boundaries of 0 and 1, respectively) and τ (lower and upper boundaries of 0 and 50, respectively). A gamma distribution with shape and rate parameters of 0.1 and 0.1, respectively, was assumed for λ_0.

1.2.3 Convergence criteria

For both the nonspatial and spatial models, MCMC chain convergence for parameters was based on the potential scale reduction statistic ($\hat{R}$), which measures the stability of the Bayesian chains by taking the ratio of the average variance of the samples within each chain in the Bayesian analysis to the variance of pooled samples across all chains (Gelman et al. 2013). Ratios less than 1.1 were considered to indicate convergence. Trace plots of key parameters were also evaluated to ensure that burn-in (initial iterations that were discarded because of influence of starting values) was sufficient and as another indicator of convergence (Brooks et al. 2011).

1.3 Results

1.3.1 Convergence

For the nonspatial model, all convergence criteria were met for all parameters in all scenarios. For the spatial model, the convergence criteria were met for all mortality estimates, but the model had difficulty estimating the activity centers. Across all scenarios, over 50% of the activity centers (out of a total of 7200 activity centers per scenario) met the convergence criteria. For many scenarios, 75% of activity centers met the convergence criteria. Even though the spatial model encountered difficulties in converging on stationary distributions for activity centers, we still proceeded with analyses of results given that we assumed that mortality was spatially invariant and thus the spatial location of a fish did not affect its probability of surviving. If mortality levels did vary spatially, the model's inability to estimate activity centers would likely prove more problematic.

True mortality rate 0.1

The mortality estimates using the nonspatial model from the four scenarios and 10 replicates ranged from 0.10 to 0.18 (Figure 1.4a). The relative error of the mortality estimates ranged from 2% to 83% (Figure 1.5). The grid configuration consistently yielded more accurate estimates of mortality than the line configuration. The average mortality estimate for the grid configuration was 0.12, with the estimates ranging from 0.10 to 0.14; for the line configurations, the average mortality estimate was 0.17, with the estimates ranging from 0.15 to 0.18. Mortality estimates were more accurate with the higher number of receivers. For the 64-receiver grid configuration, the averaged mortality across all simulations was 0.11, with estimates ranging from 0.10 to 0.14. The 64-receiver grid configuration was the only configuration in which the 95% credible intervals for the mortality estimates encompassed the true mortality rate in all 10 replicates.

True mortality rate 0.4

The mortality estimates using the nonspatial model from the four scenarios and 10 replicates ranged from 0.31 to 0.49 (Figure 1.4b). The relative error of the mortality estimates ranged from 0% to 22% (Figure 1.5). The grid configuration consistently yielded more accurate estimates of mortality than the line configuration. The average mortality estimate for the grid configuration was 0.41, with estimates ranging from 0.31 to 0.48; for the line configuration, the average mortality estimate was 0.46, with the estimates ranging from 0.43 to 0.49. The average mortality estimate for both grid configurations was the same (0.41), with a range of 0.31 to 0.45 for the 39-receiver grid and 0.38 to 0.48 for the 64-receiver grid.

True mortality rate 0.6

The mortality estimates using the nonspatial model from the four scenarios and 10 replicates ranged from 0.58 to 0.71 (Figure 1.4c). The relative error of the mortality estimates ranged from 0% to 19% (Figure 1.5). The grid configuration consistently yielded more accurate estimates of mortality than the line configuration. The average mortality estimate for the grid configuration was 0.61, with the estimates ranging from 0.58 to 0.66, while for the line configuration, the average mortality estimate was 0.63, with the estimates ranging from 0.63 to 0.71. The 64-receiver grid configuration performed the best of the four scenarios, with an average mortality estimate of 0.60 and a relatively narrow range of estimates from 0.59 to 0.62. The relative error ranged from 0% to 3%.

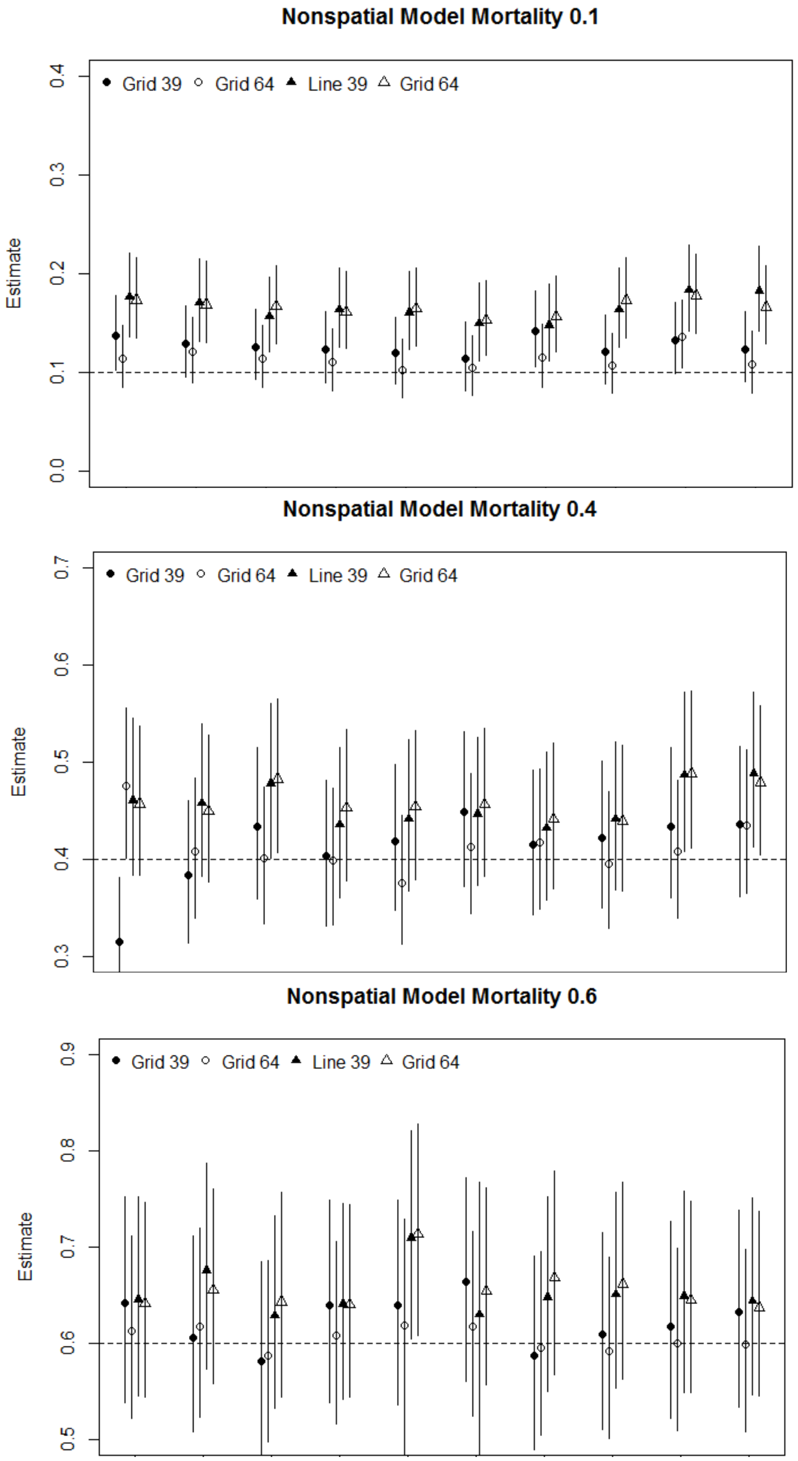

Figure 1.4. Mortality estimates using the nonspatial model from the four scenarios (grid and line, 64 and 39 receivers) for ten replicates. The point represents the estimate and the bars represent the 95% credible intervals. Circles are grids, triangles are lines, closed points are 39 receivers, open points are 64 receivers. Each of the three panels represents a different true value of mortality, 0.1, 0.4, and 0.6. All the panels have the same size y-scale.

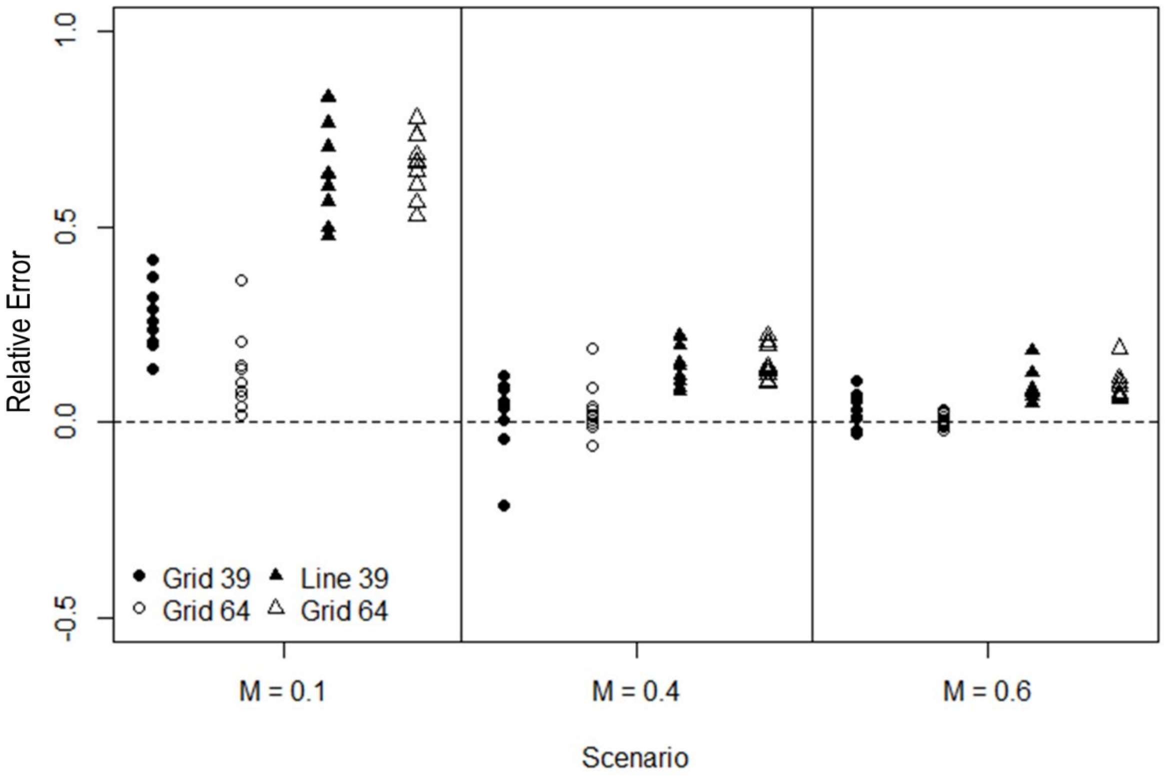

Figure 1.5. Proportional error ((observed – true)/true) for all 120 scenarios using the non-spatial estimation approach.

1.3.2 Spatial model results

True mortality rate 0.1

The mortality estimates using the spatial model from the four scenarios and 10 replicates ranged from 0.13 to 0.24, showing a consistent positive bias (Figure 1.6a). The relative error of the mortality estimates ranged from 31% to 141% (Figure 1.7). The 64-receiver grid consistently outperformed the other configurations, with an average mortality estimate of 0.15 and estimates ranging from 0.13 to 0.17. In nine out of 10 replicates, estimates from the line configuration regardless of the number of receivers were closer to the true value of mortality than the 39-receiver grid; mortality estimates for the 39-receiver grid ranged from 0.20 to 0.24 and averaged 0.21. Conversely, the 39- and 64-receiver lines resulted in average mortalities of 0.19 (range: 0.16 to 0.21) and 0.18 (range: 0.17 to 0.20), respectively.

True mortality rate 0.4

The mortality estimates using the spatial model from the four scenarios and 10 replicates ranged from 0.41 to 0.53, showing a consistent positive bias (Figure 1.6b). The relative error of the mortality estimates ranged from 1% to 32% (Figure 1.7). The 64-receiver grid configuration consistently outperformed the other configurations, with an average mortality estimate of 0.44 and estimates ranging from 0.41 to 0.46. In seven out of 10 replicates, the line configuration estimates regardless of the number of receivers were closer to the true value of mortality than the 39-receiver grid configuration. Mortality estimates from the 39-receiver grid configuration ranged from 0.47 to 0.53 and averaged 0.50. Conversely, the mortality estimates from the 39-receiver line confirmation ranged from 0.45 to 0.51 and averaged 0.48, and the mortality estimates from the 64-receiver line confirmation ranged from 0.46 to 0.51 and averaged 0.48.

True mortality rate 0.6

The mortality estimates using the spatial model from the four scenarios and 10 replicates ranged from 0.62 to 0.75, showing a consistent positive bias (Figure 1.6c). The relative error of the mortality estimates ranged from 4% to 25% (Figure 1.7). The 64-receiver grid configuration consistently outperformed the other configurations, with an average mortality estimate of 0.64 and estimates ranging from 0.62 to 0.69. In six out of 10 replicates, estimates from the line configuration regardless of the number of receivers were closer to the true mortality rate than the 39-receiver grid configuration. Mortality estimates from the 39-receiver grid con- figuration ranged from 0.64 to 0.75 and averaged 0.70. For the 39- and 64-receiver line configurations, estimates ranged from 0.65 to 0.73 and 0.66 to 0.73 and averaged 0.68 and 0.67, respectively.

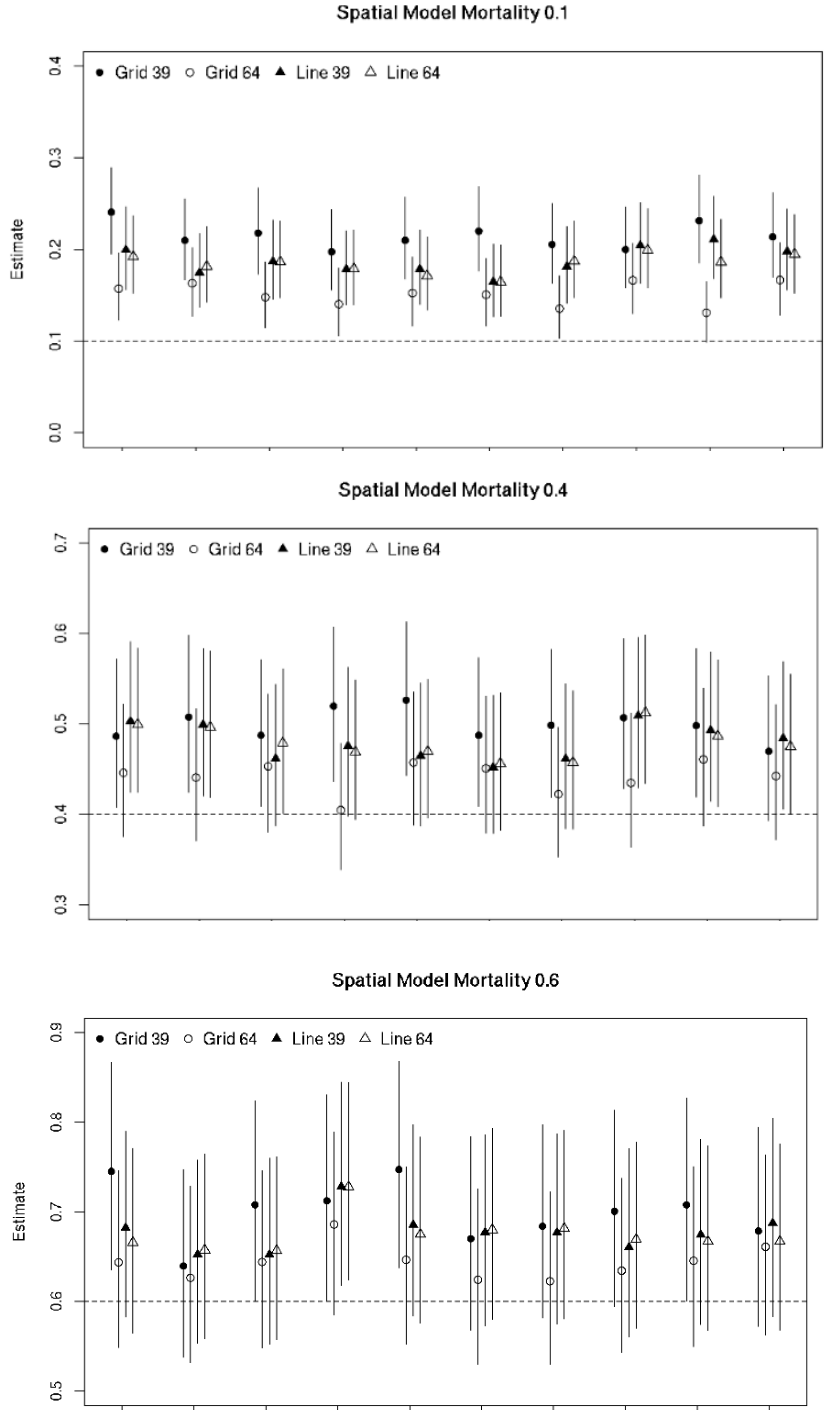

Figure 1.6. Mortality estimates using the spatial model from the four scenarios (grid and line, 64 and 39 receivers) for ten replicates. The point represents the estimate and the bars represent the 95% credible intervals. Circles are grids, triangles are lines, closed points are 39 receivers, open points are 64 receivers. Each of the three panels represents a different true value of mortality, 0.1, 0.4, and 0.6. All the panels have the same size y-scale.

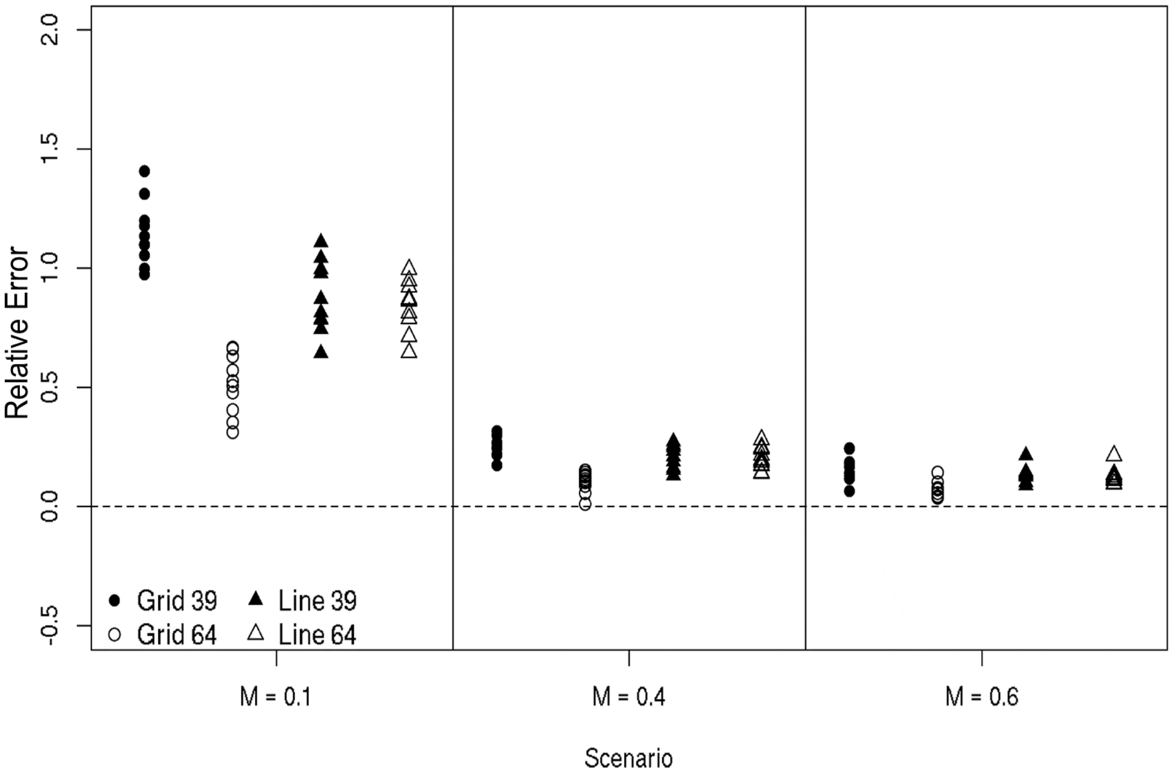

Figure 1.7. Proportional error ((observed – true)/true) for all 120 scenarios using the spatial estimation approach.

1.3.3 Comparison of nonspatial and spatial model results

The nonspatial model consistently outperformed the spatial model. Comparing the mortality estimates calculated using the spatial and nonspatial methods from the same simulated population of fish, the nonspatial mortality estimate was closer than the spatial estimate to the true mortality rate in 138 out of 140 scenarios. The average relative error for the nonspatial model was 20%, while for the spatial model, it was 38%. For mortality estimates from scenarios with a true mortality rate of 0.1, the average relative error for the nonspatial model was 43%, whereas for the spatial model, it was 84%. For a true mortality rate of 0.4, the average relative error for the nonspatial was 10%, while for the spatial model, it was 19%. For a true mortality rate of 0.6, the average relative error for the nonspatial was 6%, while for the spatial model, it was 12%.

1.4 Discussion

The nonspatial model was more accurate and precise than the spatial model when estimating total mortality using acoustic telemetry data under the conditions assumed when simulating detection data. For both spatial and nonspatial models, grids with higher densities of receivers resulted in more accurate mortality rate estimates compared with line configurations; accuracy of both approaches improved with higher assumed mortality rates. Across all evaluated scenarios, mortality estimates for both modeling approaches were greater than the true, simulated values. The positive bias that we saw across scenarios likely resulted from confounding between receiver detection probabilities and fish death, both of which result in fish not being detected.

Our observation that a high-density grid configuration of receivers resulted in more accurate and precise estimates of mortality agrees with the results of other studies that have compared the configurations for estimating movement and habitat use (Kraus et al. 2018). Regardless of whether acoustic telemetry is used for characterizing mortality or movement, estimation accuracy depends on frequent detection of transmittered individuals and successfully identifying their fates (Villegas-Ríos et al. 2020). In large lentic systems, placing receivers in lines or gates in specific areas resulted in large areas of the sys- tem for which receiver coverage is poor or non-existent and may result in fish going long periods of time without being detected. This may lead models to identifying individuals as being dead when they are actually alive and actively swimming but in areas where no detections are possible. A similar situation may arise with grid configurations with a low number of receivers because the spacing among receivers is too large. Our finding that a high- density grid configuration resulted in more accurate estimates than a line configuration is analogous to observations from other mark–recapture study evaluations that found uniform sampling effort resulting in more accurate estimates than nonuniform sampling effort (Stevens 1997). This is not meant to suggest that deployment of lines or gates of receivers are never appropriate. Receivers configured in lines would be useful for telemetry studies where the main aim was to quantify coarse-scale movements such as whether fish cross management boundaries or the occurrence of interbasin or interlake emigration (e.g., Welch et al. 2009; Kessel et al. 2014). However, when the aim is mortality estimation, as in this study, high-density grids were the better study design.

The ability to accurately estimate fish survival from acoustic telemetry detection data will depend heavily on collecting enough detection data to be able to adequately characterize the fate of tagged individuals. Consequently, the exact configuration of receivers that should be used in a study should depend on the behavior and ecology of study organisms. In this study, we simulated detection data based on movement patterns of walleye in Lake Erie. Results could change for fish that show different movement behaviors. For more mobile species, fish may be more likely to encounter receivers, which may mean that fewer receivers need to be deployed and may reduce the bias associated with the estimation approach. Conversely, for more sedentary species, the required receiver coverage may become cost prohibitive, and an alternative evaluation technique should perhaps be considered: for example, active telemetry in which searches for fish are conducted from a mobile platform (Pepperell and Davis 1999; Hightower et al. 2001) or strategically placed receivers, e.g., placing receivers at the mouths of the rivers of migrating fish or on the spawning site of a species that has a high spawning site fidelity (Binder et al. 2016; Hayden et al. 2018). Alternatively, more complex state–space models such as those that take different "states" into account may yield better estimation performance (Stich et al. 2015; Hightower and Harris 2017).

The higher density receiver configurations outperforming the low-density configurations was an anticipated result — greater sampling effort should produce more accurate estimates. As stated previously, the optimal density of receivers will be linked to the movement of the fish population being studied. In addition to fish species being sedentary and influencing results, space use by fish could influence optimal configurations as well. For example, fish that remain close to shore may be missed by receivers in open water. High-density grids and thus a higher sampling effort, especially if it can be informed by knowledge of where fish tend to be, are likely particularly important for species that show more localized movement patterns.

The true mortality rate influenced the relative error of the mortality estimation methods. The highest relative errors for both the nonspatial and spatial models across receiver configurations were when the lowest true mortality was simulated (0.1), and in all cases, these errors were overestimates of mortality. It is worth pointing out that a total mortality rate of 0.1 is likely on the lower range of mortality rates for exploited fish populations (Then et al. 2015). Relative error also obscures the consistency of the positive bias among mortality levels. The absolute error rates for total mortality for both the nonspatial and spatial model were fairly consistent across mortality rates; however, the high- density grid still resulted in lower error rates than the other receiver configurations. Positive bias may arise because both mortality estimation methods have difficulty accounting for fish that remain undetected, violating the assumption that detection was independent among sampling events and fish. Evaluating a wider range of scenarios could test this hypothesis. If this explanation is true, performance could be improved by using a higher receiver density in grids (and possibly lines) to decrease the chance of live fish remaining undetected in the study area.

This work did not evaluate the effect that the number of tags in a system has on the performance of the estimation methods. Receivers and acoustic tags are two of the main resource investments in acoustic telemetry studies. The methods described here (simulations to compare receiver configurations) could easily be extended to do a cost–benefit analysis of the trade-off between tag numbers and receiver density. By simulating different combinations of tags and receivers, the optimum study design could be identified given availability of resources.

A caveat with the results is the diagnostics of the activity center estimates. A component of the spatial model was estimating the center of activity for each individual in the population during each time step. The spatial model had difficulties estimating the activity centers for time periods when fish were not detected. Correlating activity centers from one time step to the next and using the last known detected average location of the fish alleviated some of the convergence issues, but diagnostics showed that a fraction (less than 25%) of the activity center estimates were unstable. It is possible that greater computing power and more efficient estimation algorithms than were available for this study could improve the activity center estimates. However, the difficulty with the estimation of the activity centers may always be present if instances occur when fish are not being detected. While the issues arising from non-detection could be alleviated by using a larger time step to decrease the number of non-detection instances or further restricting the assignment of activity centers, this approach would also start to diminish the amount of spatial data used in the spatial model or limit the ability to look at spatial and temporal patterns in parameters. This suggests that the spatial model may be most useful when a high number of detections exist, for example, in river systems or small lakes.

Another important caveat of this work is the major assumptions made in the simulation framework that may differ from observed acoustic telemetry studies. In our simulation framework, all fish were released in the same location all at once, the dynamics of the fish populations were not spatially or temporally varying, the detection ability of the receivers was assumed and constant, fish were constantly and consistently moving, and the tag transmission rate was more than the average transmission rate of tags commonly used. These assumptions could affect the detectability and the dynamics of the tagged individuals and thus affect the results. Future work could explore more complex simulated dynamics such as temporally and spatially varying detection and survival probability to evaluate the consequences these have on the performance of the estimation methods.

Even though the nonspatial method performed better than the spatial approach and some limitations to these models exist as described above, spatial models may be able to capture variations in demographics in ways not illustrated by this simulation study. Mortality was assumed to be constant across space in the spatial method because the focus of the study was to compare the estimates from nonspatial and spatial methods. However, the spatial method could be used to evaluate spatial survival estimates. Mortality rates have been shown to vary spatially, and studies incorporating that variability into stock assessments show the importance of spatial structure for certain fish stocks (Berger et al. 2012; Vandergoot and Brenden 2014; Langseth and Schueller 2017). Fish populations experience different mortality vulnerability as they move across a landscape, for example, due to spatially varying fishing effort. If mortality was spatially varying, a spatial model would be able to identify the dynamics that a nonspatial model would ignore. A potential middle-ground approach was used by Perry et al. (2010), who used a discrete-space multistate CJS model to estimate survival and migration of juvenile Chinook salmon, which used four potential migration routes to incorporate spatial data into their analyses. This approach could be useful particularly in river systems. The underlying simulation framework in this study did not incorporate spatial heterogeneity of population dynamics, so the additional benefits of spatial mark–recapture models may not be captured in these results.

In summary, acoustic telemetry data can be used in nonspatial and spatial models to reasonably estimate the mortality of a fish population, although some limitations occurred with regards to the performance of the spatial model. The nonspatial estimation approach outperformed the spatial estimation approach, in terms of both relative error and convergence of the model parameters. The spatial estimation approach did show promise as a mortality estimation method, and more work should be done investigating these techniques and how they perform under different acoustic telemetry study designs. When designing acoustic telemetry studies with the objective of obtaining estimates of mortality and when the study site is similarly large and the movement dynamics of the fish are unknown or considered to have low spawning site fidelity, high-density receiver grids should be used and positive bias of mortality estimates should be considered, whether using a spatial or nonspatial estimation approach, particularly if the population is expected to have a low mortality rate. The high-density receiver grid configuration consistently provided more accurate estimates of mortality and would be the recommended receiver design.

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CHAPTER 2
EVALUATING MORTALITY OF LAKE ERIE WALLEYE (*SANDER VITREUS*) USING ACOUSTIC TELEMETRY DATA

2.1 Introduction

Walleye are an important Lake Erie species with economic and societal value to both Canada and the U.S. Accurate mortality estimates are important for sustainable management of the species, especially for yield estimation and quota setting. Walleye harvest limits in Lake Erie are determined by applying a harvest control rule to the results from stock assessment modeling conducted by the Walleye Task Group (WTG). The WTG uses a complex statistical catch-at-age model to estimate annual abundance, mortality rates, and fishery characteristics (e.g., selectivity, catchability) of the walleye population; the model incorporates fishery-dependent data from the Ontario commercial, Ohio recreational, and Michigan recreational fisheries, along with data from three fishery-independent gill net surveys, and assumes a natural mortality of 0.32 (Berger et al. 2012). Walleye in the Great Lakes are known to show complex spatial structuring and movement patterns (Herbst et al. 2016; Vandergoot and Brenden 2014; Matley et al. 2020) which suggests that populations may not be experiencing natural mortality in a spatially or temporally homogenous manner as assumed by the stock assessment model. Deriving estimates of natural mortality, spatially and temporally, would allow for that variability to be investigated and be valuable to fishery management. Natural mortality of Lake Erie walleye has previously been estimated (Zhao et al. 2011; Vandergoot and Brenden 2014), but past studies have not used the higher spatial resolution, albeit smaller sample size, of acoustic telemetry data that has been collected over the past decade. Acoustic detections can indicate the alive or dead status of a tagged fish, but the methods of how to use these data to measure mortality of the population is not clear.

Acoustic telemetry studies frequently generate large datasets of repeated observations (i.e., recaptures via transmitter detections) of tagged fish with spatial coverage that is not dependent on where fishing or assessment surveys occur. Electronic tags and receivers can be used to detect a fish without physically having to recapture it and, in some cases, allow collecting additional information besides just the presence of the fish at a particular location (e.g. depth and temperature, Block et al. 1992). Electronic tagging allows a more detailed record of locations to be observed without incurring mortality or further stress to the fish after initial tagging. Consequently, detections from acoustically tagged fish hold promise for learning about fish behavior and movement. Acoustic telemetry has been used to study behavior and movement of fish in rivers (Welch et al. 2009; Perry et al. 2010), small lakes (Hightower et al. 2001), large lakes such as the Great Lakes (Hayden et al. 2014; Krueger et al. 2018, Matley et al. 2020), and in oceans (Heupel et al. 2006; Hussey et al. 2015).

Acoustic telemetry provides researchers not only with a record of a fish being alive; it provides a temporal and spatial encounter history of each individual fish. By treating these data simply as records of being detected or not detected, valuable information may be lost. Spatial models allow us to measure survival and detection probabilities along with movement probabilities within a study area (Gardner et al. 2010, Raabe et al. 2014). These spatial models can incorporate the spatial aspects of the data (e.g., movement patterns of tagged individuals), while also allowing for sample-site level covariates. In recent decades, spatial models have been used in a variety of applications (Hightower et al. 2001; Borchers and Efford 2008; Royle et al. 2009; Gardner et al. 2010; Raabe et al. 2014; Cooke et al. 2016; Hightower and Harris 2017; Lopez-Bao et al. 2018).

Considerable investment both in terms of equipment and effort in the Great Lakes basin has occurred to tag many species, including walleye, and deploy hundreds of acoustic receivers to allow better spatial management of the valuable Great Lakes ecosystem. The Great Lakes Acoustic Telemetry Observation System (GLATOS) is a network of acoustic telemetry researchers collaborating and coordinating to house the datasets generated by these studies in one place, allowing for a unique opportunity to look holistically at the data gathered for one species in one or more lakes across several different studies (Krueger et al. 2018). Inter-agency and organization coordination means a receiver deployed by one group in one area of the lake is effectively added to the full network of receivers deployed by all, thus allowing detection of tags deployed by other researchers for other projects. In Lake Erie alone, hundreds of receivers have been deployed throughout the lake, primarily in an extensive grid pattern (Figure 2.1).

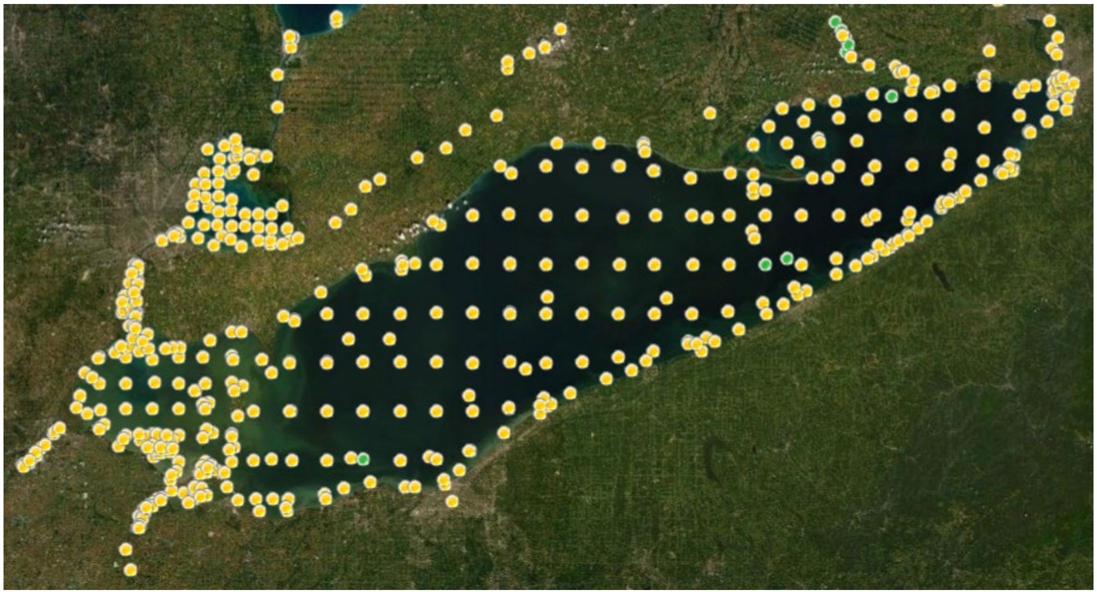


Figure 2.1. Locations of acoustic receivers present in Lake Erie and surrounding waterways in 2022. Retrieved from https://glatos.glos.us/map.

The acoustic telemetry studies that are presently ongoing for walleye in Lake Erie have the potential to yield valuable information regarding mortality rates, including comparisons among individual spawning components within the lake, provided that an estimation methodology is available that accounts for the complexity and assumptions implicit to the recovery data. Peterson et al. (2021) used a simulation framework to evaluate approaches to mortality estimation from a fixed location acoustic telemetry receiver array that mimicked Lake Erie walleye. These models can be extended for use with empirical data to provide mortality estimates of Great Lakes walleye.

Building off of the work by Peterson et al. (2021), mortality estimation approaches were applied to the Lake Erie walleye data from the GLATOS database to address three objectives: (1) estimate the total mortality of a tagged group of Lake Erie reef spawning walleye, (2) compare mortality rates between river spawning and reef spawning walleye populations in Lake Erie, and (3) evaluate whether mortality appears to be non-uniformly distributed across space and time, and whether these patterns are consistent among the different tagging groups.

2.2 Methods

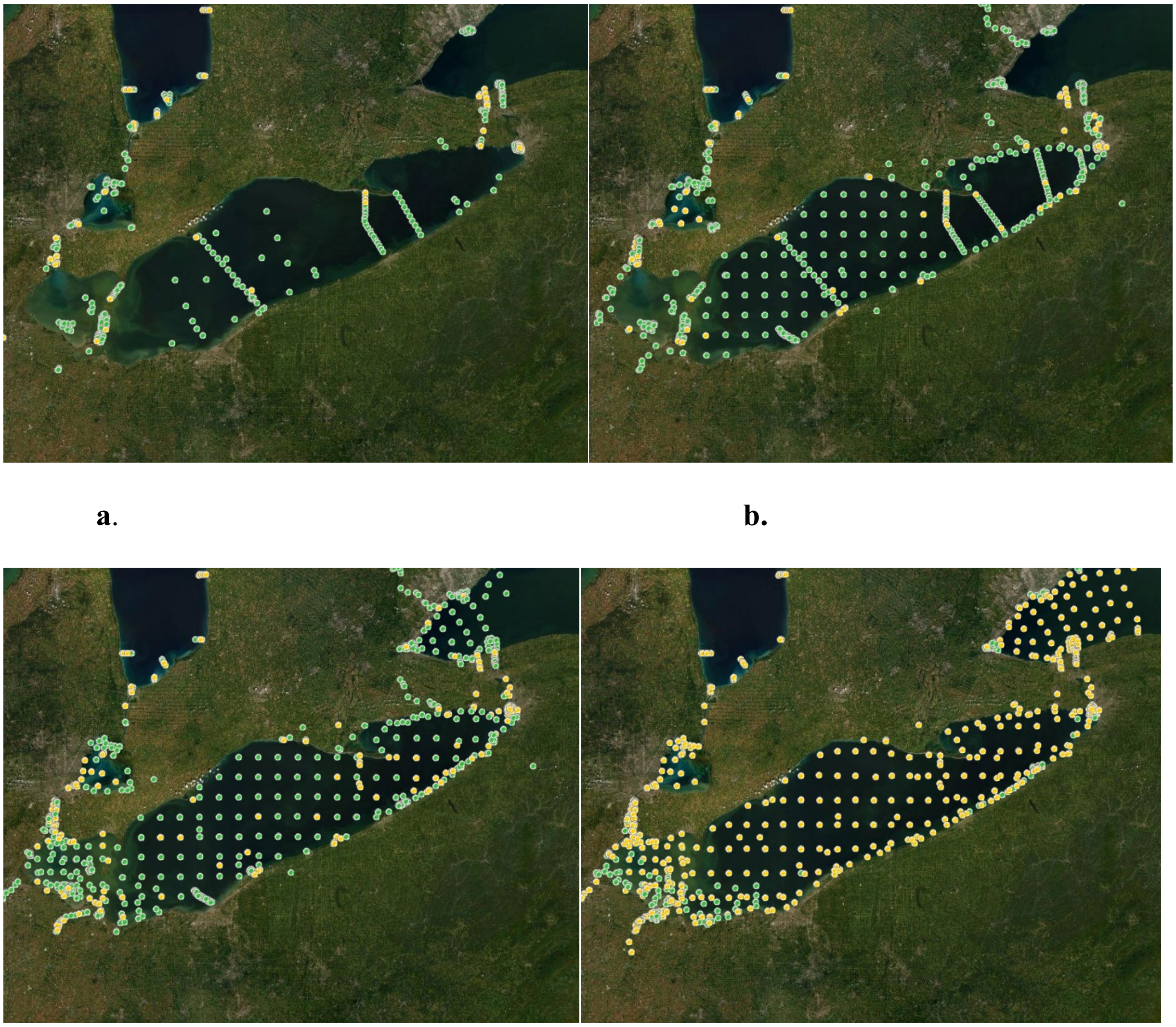
2.2.1 Data

Lake Erie is the smallest, most biologically productive of the Laurentian Great Lakes, and supports large walleye sport and commercial fisheries. Walleye is a percid that is of both ecological and economic importance to the Great Lakes region, harvested recreationally in the four states surrounding Lake Erie (Michigan, Ohio, Pennsylvania, and New York) and both recreationally and commercially in the Canadian province of Ontario.

On-going since 2010, Lake Erie walleye have been the focus of multiple acoustic telemetry studies conducted by different researchers in all areas of the lake that have led to several publications (e.g., habitat-use, Matley et al. 2020; spawning site fidelity and annual survival, Hayden et al. 2018; seasonal movements and migration, Raby et al. 2018 and Hayden et al. 2014). Two projects, one focused on tagging reproductive-age walleye in the western basin of

Lake Erie near reef spawning grounds during the spring time (walleye spawn between March and May) and one focused on tagging near the Sandusky River where walleye spawn, generated the data used in this study to investigate mortality patterns. Three groups of data generated by tagging events, one in 2016, and two tagged in 2014, were used to estimate mortality.

Receiver distributions in Lake Erie have changed through time, partially due to an increasing number of acoustic telemetry projects in the lake. If projects align their transmission frequencies, tagged fish can be detected by receivers across multiple projects linked into the GLATOS network. As a result, a fish tagged in 2014 when a more limited distribution of receivers was present in Lake Erie will still be able to be detected by receivers deployed in 2018. Between 2014 and 2020 the focus of the Lake Erie receiver network changed from one that focused on having ‘gates’ delineating basins, assisting with identifying when a fish moved from one region of the lake to another, to a large grid encompassing the entire lake (Figure 2.2). This change was determined to be a better way to investigate movement and mortality (Kraus et al. 2018, Peterson et al. 2021) but does mean that the groups of fish were experiencing different receiver configurations through time, and hence different tag detection probabilities over time.



a.

b.

c.

d.

Figure 2.2. Receiver configurations for Lake Erie in 2014 (a), 2016 (b), 2018 (c), and 2020 (d). Retrieved from *https://glatos.glos.us/map*. Yellow dots indicate the specific receiver is still currently active (as of 2022). Green dots are specific receivers that are no longer active (as of 2022).

2.2.2 Mortality Estimation Methods

A spatial and a non-spatial approach were used to estimate mortality rates for the three subsets of data, as described by Peterson et al. (2021). Modifications were made to the Peterson et al. (2021) models (described below) to accommodate differences between the simulated data used in that study and the empirical data from the GLATOS network. Both the spatial and nonspatial models were based on a CJS formulation (Cormack 1964; Jolly 1965; Seber 1965) and drew inferences from the acoustic telemetry data, but the structure of the two models and processing of acoustic detections differed. Both models were estimated using Bayesian inference through JAGS (Plummer 2015) executed from within R (R Core Team 2019) via the jagsUI package (Kellner 2019).

Non-spatial

The non-spatial model treats detections as recapture events for an individual fish in the specified time period, for our work we looked at both a monthly and seasonal time period. The non-spatial model has two major components, survival rate (1 – total mortality, or the probability of an individual surviving from the previous time period to the current time period) and detection probability (probability of a surviving fish being detected in the current time period). The model ignores the specific moments within each time period that detections occur, all detections in the time period are aggregated together. Detection probability was assumed to vary between time periods due to the impact of environmental variables.

Three parallel MCMC chains, each consisting of 22,000 iterations, were run from random initialization values with an initial 100-iteration adaptive phase. This chain length allowed the non-spatial models to meet the convergence criteria. The first 2,000 saved iterations were discarded as burn-ins based upon visual analysis of the trace plots and the chains were not thinned. Uniform prior distributions with lower and upper bounds of 0 and 1 were assumed for survival and detection probabilities.

Spatial

The spatial CJS model used by Peterson et al. (2021) was implemented using a state-space framework similar to the Gardner et al. (2010) and Raabe et al. (2014) spatial capture-recapture models to estimate survival. The state-space framework consisted of an observational model for the observed encounter histories of tagged fish, a state model for the "alive" state of the fish at each modeled time step (monthly or seasonally), and a latent point process model that described the "activity centers" (i.e., estimated average locations within a time step) of tagged fish across the time periods.

Three changes were made to the approach described by Peterson et al. (2021) and are discussed in detail below. Coefficients were added to take into account the length of time each receiver was in the water, an informative prior was used for the state variable that specified whether a fish was reported as harvested or not, and a different assumed value was used for the activity center dispersion parameter. Both the configuration of receivers and the time the receivers spent in Lake Erie changed from year to year. To consider the influence on tag detection probability these changes in receivers would have, a coefficient was added to the baseline detection probability for each receiver (the proportion of each time period the specific receiver was in the water). This changed the formulation of the model slightly. This modeling approach incorporated counts of detections for each individual (i), at each receiver (j), during each sampling period (t, monthly). The observation model ($h(i,j,t)$) was conditional on the state model ($z(i,t)$) and followed a Poisson distribution

$$h(i,j,t)|z(i,t) \sim Pois[\lambda(j,t)g(i,j,t)z(i,t)]$$

Where $g(i,j,t)$ was a general distance function incorporating the distance between the individual activity center and the receiver location and $\lambda(j,t)$ was a combination of λ_0, the baseline detection rate or the expected number of detections when an activity center and the receiver location were identical, and $r(j,t)$, the proportion of the time period the receiver was in the water.

$$\lambda(j,t) = \lambda_0 * r(j,t)$$

In the simulation study, just λ_0 was used as all receivers were simulated to have been in the water the entire study period. The state model was also assumed to be correlated through time based on survival (φ):

$$z(i,t) = z(i,t\text{-}1) * \varphi$$

The model also considered if a fish was reported as being harvested. Each acoustic tag included a number to call and alerted anglers to the $100 reward if the tag was reported, an amount judged as being a "high-reward" tag sufficient for nearly 100% rate of return (Nichols et al., 1991, Denson et al. 2002, Taylor et al. 2006, Cadigan and Brattey 2006, Vandergoot et al. 2012). Harvested tagged fish were known to be dead at a specific time, therefore we censored the state variable, labelling the state of the harvested fish as 0 (or 'dead') in all subsequent months after reported harvest. We assumed that all harvested fish were reported.

The final change from the Peterson et al. (2021) model was the assumed value for the activity center dispersion parameter in time periods where a fish was not detected. When fish were detected, the activity centers ($s_{i,t}$) were assumed to follow a random-walk, drawn from a normal distribution with a mean equal to the location of the activity center in the previous time step ($s_{i,t-1}$) and a standard deviation (τ_i) corresponding to the estimated variability in individual movements between time intervals. The two-dimensional formulation was:

$$s_{x,,} \sim Normal(s_{x,i,t-1}, \tau_{x,i})$$

$$s_{y,,} \sim Normal(s_{y,i,t-1}, \tau_{y,i})$$

During time periods when fish were undetected, the modified random-walk process included the weighted average location of the fish in the time period it was last detected (aa). In other words, when fish were not detected, the random walk process consisted of the following:

$$\text{Fish not detected: } s_{x,,} \sim Normal(\text{aa}_{x,i,t \text{ of last detection}}, 0.05)$$

$$\text{Fish not detected: } s_{y,,} \sim Normal(\text{aa}_{y,i,t \text{ of last detection}}, 0.05)$$

The standard deviations for the random walk process were not able to be estimated when fish were not detected; consequently, standard deviations of 0.05 were assumed in cases when fish were not detected. Peterson et al. (2021) used a value of 50, this proved to be larger than necessary for the empirical data. An analysis of results using a range of standard deviations showed that the reduction did not impact mortality estimates but improved model performance.

The computation needs for the spatial models were much greater compared to the non-spatial model and varied depending on the size of the data set and the time step being evaluated (monthly or seasonally), thus the size of the MCMC chains varied. For all evaluations, three parallel MCMC chains, each consisting of at least 2,000 iterations, were run from random initialization values with an initial 100-iteration adaptive phase. At least the first 1,000 saved iterations were discarded as burn-in, specific burn-in was based on a visual analysis of the trace plots, and the chains were not thinned. In addition to the informative prior used for the state variable described previously, uniform distributions were assumed as priors for survival (lower and upper boundaries of 0 and 1) and τ (lower and upper boundaries of 0 and 100), and a gamma distribution with shape and rate parameters of 0.1 and 0.1, respectively, was assumed for λ_0.

2.2.3 Spatial and temporal patterns of mortality

Two approaches were used to evaluate spatial and temporal patterns of mortality using the spatial approach described above. First, the estimates of *z(i,t)* (the state of each fish *i* at time *t*: dead or alive) were inspected for each time step and fish. The first instance of *z(i,t)* being 0 indicated a fish had died during that time period, and we used the detection data to identify the last known location of that fish. We excluded fish that were reported as being harvested in the fishery (which would also have a *z(i,t)* of 0). The distribution of these locations could suggest areas in the lake with higher natural mortality rates than elsewhere. The timing of the last detection was also used to identify seasonal periods of increased mortality.

Second, the spatial model was revised to allow mortality to vary over time. For the scenarios described above, mortality was assumed to be constant throughout the observation period. To look for evidence of seasonal variation in mortality, an additional analysis was performed in which mortality was assumed to vary among time periods (both for a one-month time step and a three-month time step). This approach has the potential to confound detection probability and mortality, particularly in the final time step.

2.2.4 Parameter convergence for non-spatial and spatial models

Trace plots of key parameters were evaluated as an indicator of convergence and to confirm burn-in was sufficient (Brooks et al. 2011). The potential scale reduction statistic was used as the other key indicator of convergence. This statistic measures the stability of the Bayesian chains by taking the ratio of the average variance of the samples within each chain in the Bayesian analysis to the variance of pooled samples across all chains (Gelman et al. 2013). Ideally, ratios less than 1.1 for all parameters of interest would indicate convergence. The activity center estimates from the spatial approach and their corresponding potential scale reduction statistic were extracted and summarized for further investigation once it became clear these estimates were not consistently meeting the convergence criteria.

2.2.5 Scenarios investigated

2016 Reef Walleye

During the April 2016 spawning season, 121 walleye were tagged on the western basin reefs of Lake Erie, these fish were active when the receivers in Lake Erie had extensive coverage using a grid configuration providing a more robust set of data than would have been available for earlier tagging years. The first subset of data used in this analysis, hereafter called 2016 Reef Walleye, included all detections from this group of fish between April 2016 and April 2020. The 2016 Reef Walleye were detected on 564 unique receivers, for a total of 6.4 million detections over 49 months (Figure 2.3 and 2.4). This group of tagged walleye included 58 females, 62 males, and 1 fish whose sex was undetermined. Total length ranged from 48cm to 79cm, with an average length of 60cm. Of the 121 walleye, 63 fish were reported as harvested.

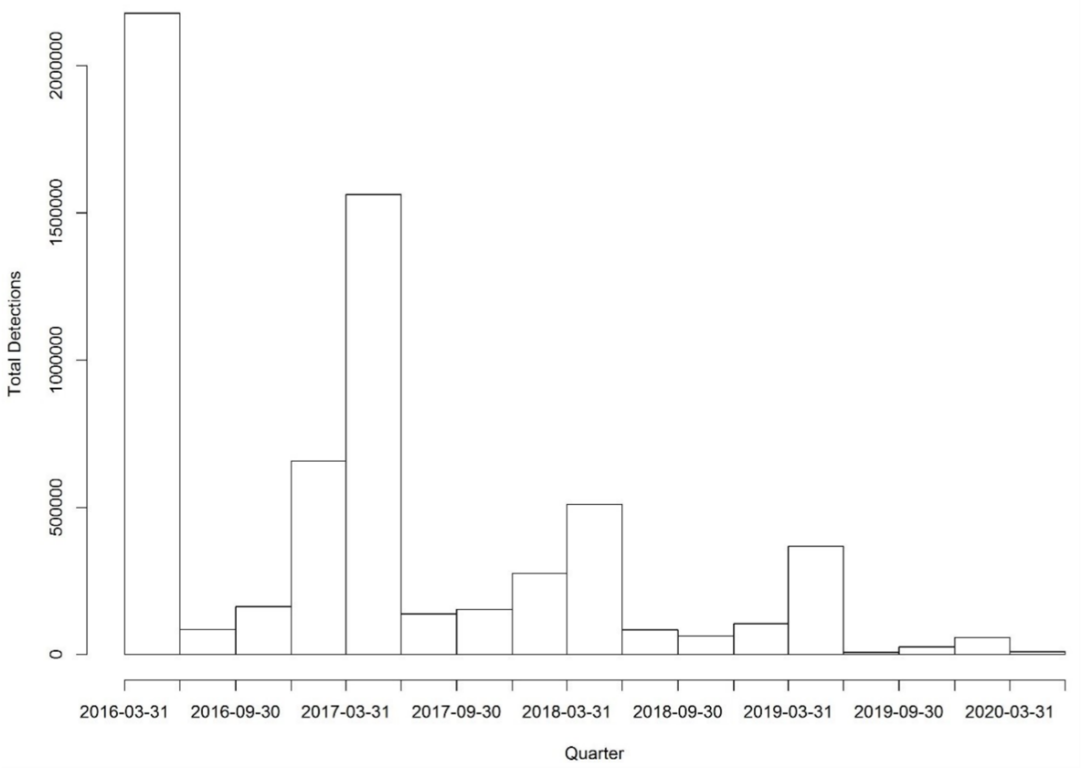


Figure 2.3. Total detections per quarter of 121 reef spawning walleye tagged in 2016. 6.4 million total detections across all quarters.

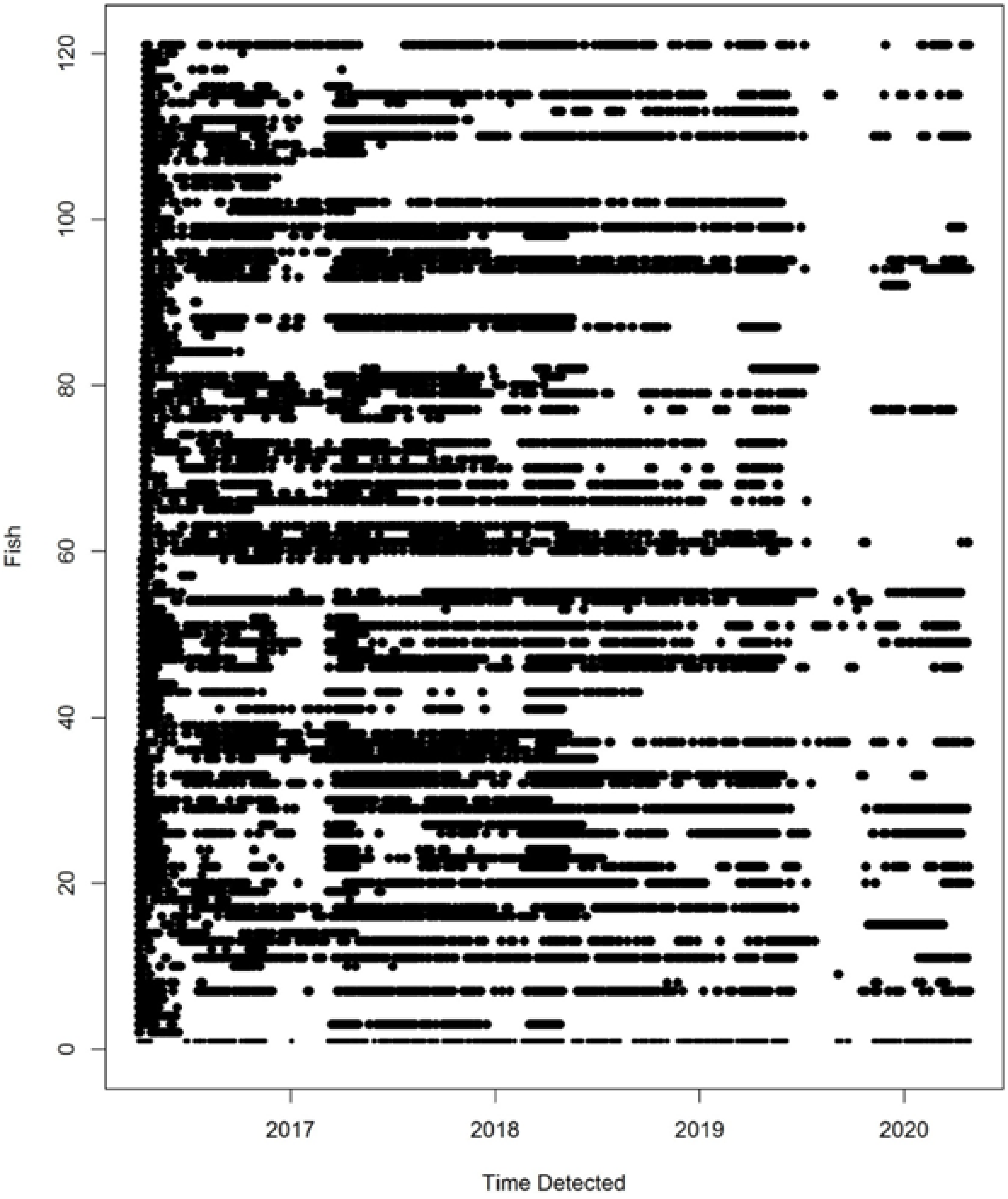


Figure 2.4. Daily detections of 121 reef spawning walleye tagged in 2016, detections range from April 2016 to April 2020, each row represents an individual fish, and each point represents an individual day in which the fish was detected at least once.

A monthly time step was compared to a quarterly time step (three months per time period); the rationale for this comparison was that the longer time step would reduce the chance that a fish that was still alive would go undetected throughout the time step, which might improve the model estimates of mortality and detection probabilities. The effect this time step had on the precision of estimates, model performance, and computation requirements was evaluated.

2014 Reef versus 2014 River Walleye

In April 2014, 84 spawning condition walleye were collected from the Sandusky River and tagged. This second subset of data, 2014 River Walleye, included all detections of the fish between April 2014 and January 2020. The 2014 River Walleye were detected on 370 total receivers, for a total of 1.5 million detections over 70 months (Figure 2.5 and 2.6). This group of tagged walleye included 44 females and 40 males. Size ranged from 42cm to 76cm, with an average length of 57cm. 25 of these fish were reported as harvested.

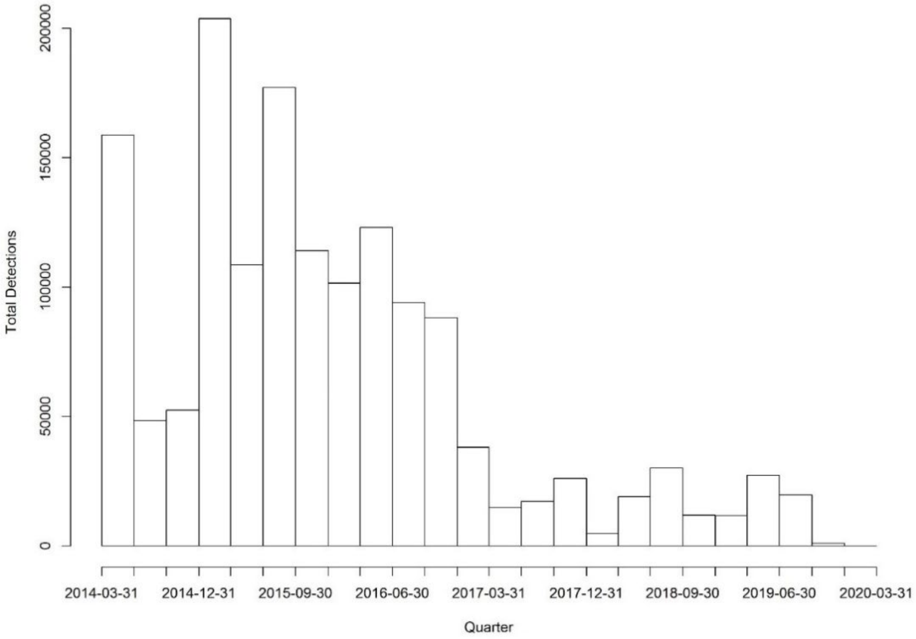


Figure 2.5. Total detections per quarter of 84 Sandusky River spawning walleye tagged in 2014. 1.5 million total detections across all quarters.

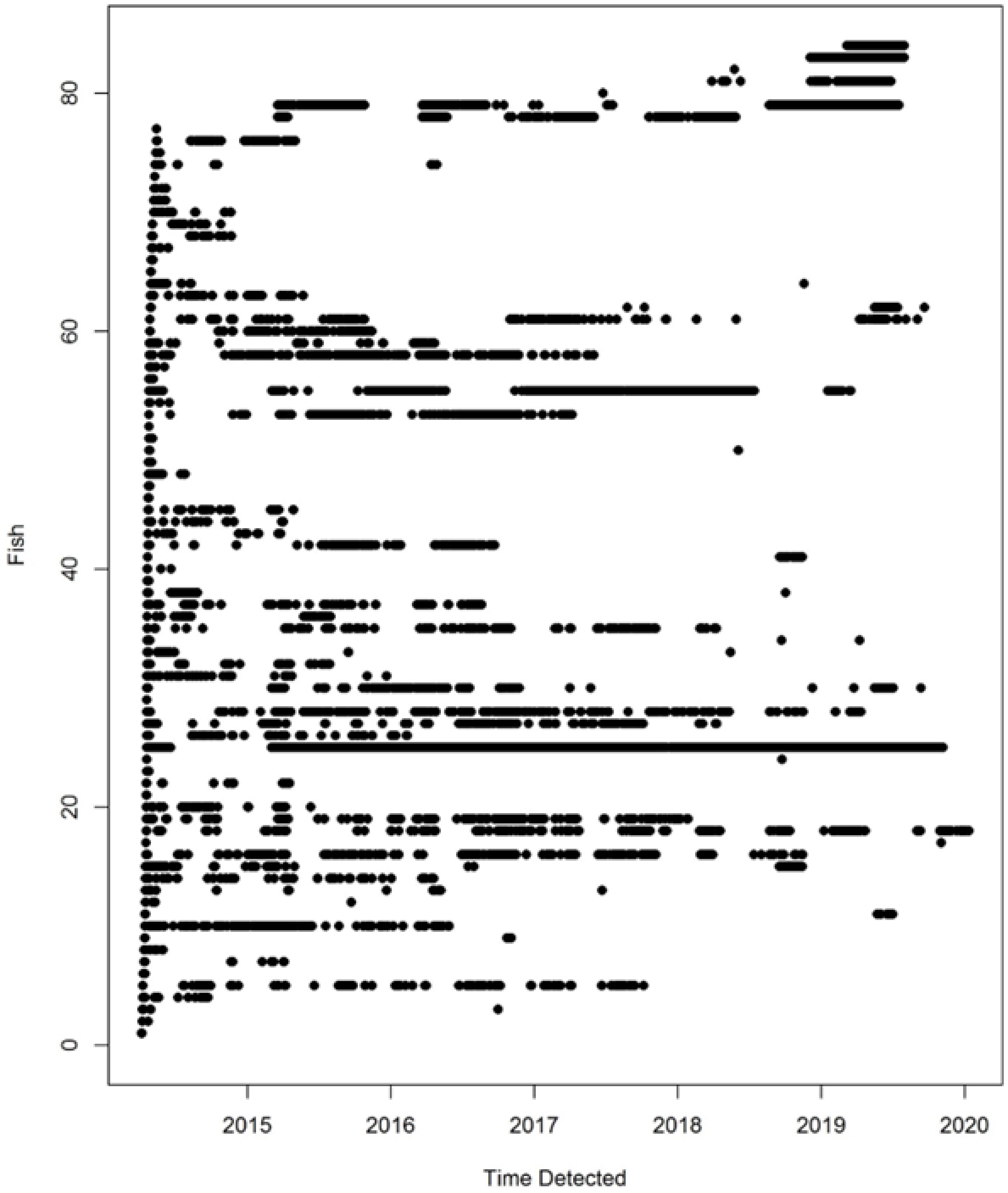


Figure 2.6. Daily detections of 84 Sandusky River spawning walleye tagged in 2014, detections range from April 2014 to January 2020, each row represents an individual fish, and each point represents an individual day in which the fish was detected at least once.

For comparison purposes, a subset of fish from the walleye tagged on the reefs was also selected. In April 2014, the same month the walleye in the 2014 River Walleye were being tagged, 51 mature walleye were captured from western basin spawning reefs and tagged. This third subset of data, called 2014 Reef Walleye, included all detections of the fish between April 2014 and May 2019. The 2014 Reef Walleye were detected on 479 unique receivers, for a total of 2.5 million detections over 62 months (Figure 2.7 and 2.8). This group of tagged walleye included 14 females and 37 males. Total length ranged from 44cm to 71cm, with an average length of 58cm. Of 51 walleye that were tagged, 27 fish were reported as harvested.

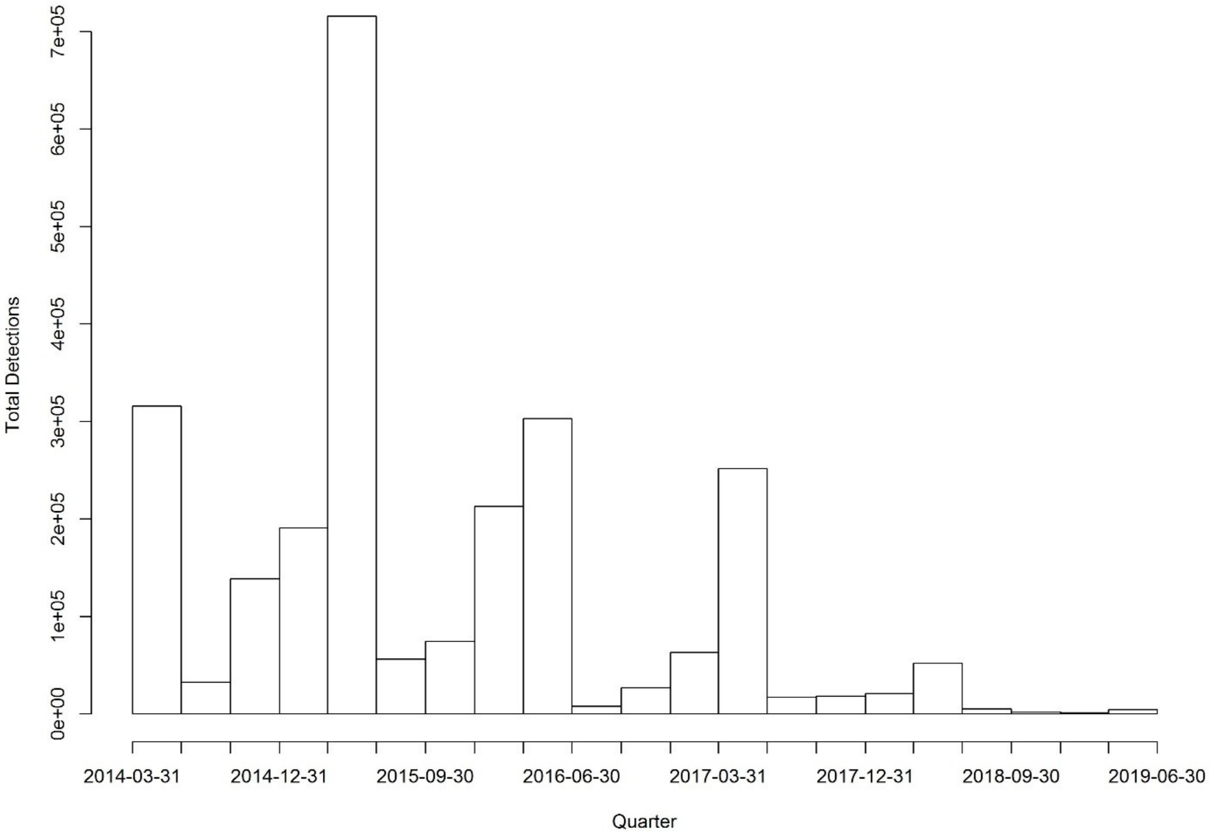


Figure 2.7. Total detections per quarter of 51 reef spawning walleye tagged in 2014. 2.5 million total detections across all quarters.

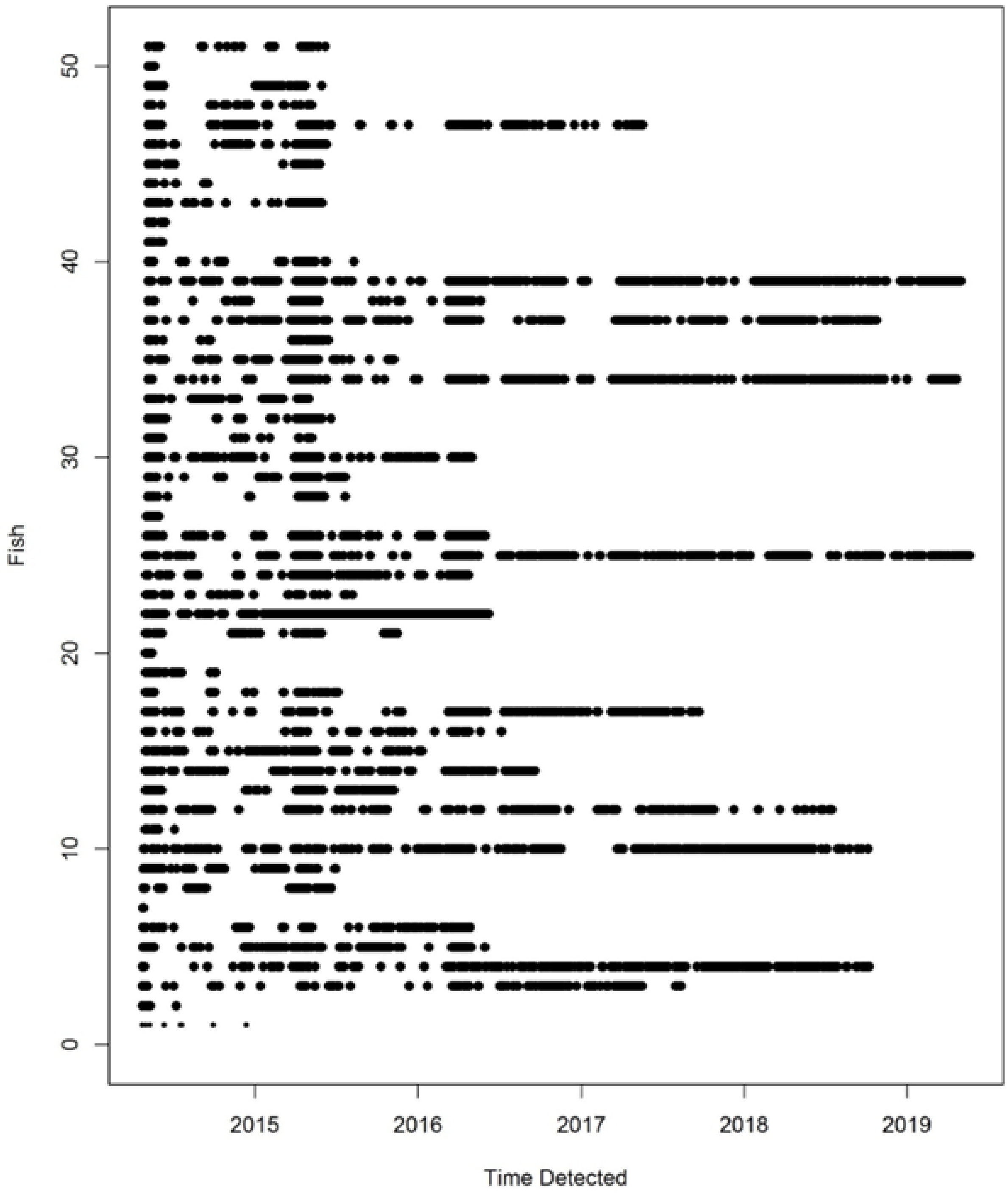


Figure 2.8. Daily detections of 51 reef spawning walleye tagged in 2014, detections range from April 2014 to May 2019, each row represents an individual fish, and each point represents an individual day in which the fish was detected at least once.

The 2014 Reef Walleye and the 2014 River Walleye were selected because both groups were tagged at similar times (April 2014) and included comparable numbers of fish (51 and 84, respectively), presumably exposing these tagged fish to similar environmental effects and the same receiver distributions throughout their period of detection. A monthly time step was also compared to a quarterly time step (three months per time period) for both groups of tagged walleye.

2.3 Results

2.3.1 Objective 1 – 2016 Reef Walleye Mortality Estimates

The non-spatial and spatial models produced similar estimates of total annual mortality for the 2016 Reef walleye tagging group, regardless of time step (Table 2.1). The spatial model estimates were slightly higher compared to the non-spatial model using the same time step, but the 95% credible intervals overlapped considerably. Similarly, the monthly time step estimates were slightly higher than the seasonal time step estimates, but the 95% credible intervals were nearly identical. Across all four scenarios, the total annual mortality estimate ranged from 0.42 (95% credible interval: 0.34, 0.52) to 0.46 (95% credible interval: 0.37, 0.55). An approximate estimate of fishing mortality for the four years in this study can be provided by the number of walleye reported as harvested by anglers: 27 (2016), 18 (2017), 9 (2018), and 7 (2019), and the annual population estimate from the spatial model that used a monthly time step. Given the estimates of total mortality and harvest rates, and assuming that total mortality is fixed through time at the estimated value, the natural mortality rates would vary from 0.21 to 0.28.

Table 2.1. Total annual mortality estimates and 95% credible intervals from the non-spatial and spatial approaches for all data sets using two time steps (1-month (monthly) and 3-month (seasonal)).

Scenario	Estimate	95% Credible Interval
2016 Lake Erie Reef		
Monthly Non-spatial	0.43	0.35, 0.52
Monthly Spatial	0.46	0.37, 0.55
Seasonal Non-spatial	0.42	0.34, 0.52
Seasonal Spatial	0.45	0.36, 0.54
2014 Reef Comparison		
Monthly Non-spatial	0.53	0.40, 0.69
Monthly Spatial	0.55	0.40, 0.71
Seasonal Non-spatial	0.51	0.37, 0.66
Seasonal Spatial	0.52	0.39, 0.68
2014 River Comparison		
Monthly Non-spatial	0.45	0.36, 0.56
Monthly Spatial	0.49	0.39, 0.60
Seasonal Non-spatial	0.40	0.31, 0.51
Seasonal Spatial	0.49	0.39, 0.60

2.3.2 Objective 2 – 2014 Reef versus 2014 River Walleye

The total annual mortality estimates were similar for both the 2014 Reef walleye and 2014 River walleye tagging groups (Table 2.1). The 2014 Reef estimates were consistently higher than the 2014 River estimates, but the 95% credible intervals of each overlapped. The spatial estimates were slightly higher than the non-spatial estimates and the monthly time step estimates were slightly higher than the seasonal time step estimates for both groups, but all credible intervals were overlapping. The 2014 Reef walleye total mortality estimates ranged from 0.51 (95% credible interval: 0.37, 0.66) to 0.55 (95% credible interval 0.40, 0.71) across the four scenarios and the 2014 River walleye estimates ranged from 0.40 (95% credible interval 0.31, 0.51) to 0.49 (95% credible interval 0.39, 0.60).

2.3.3 Objective 3 – Spatial and temporal patterns of natural mortality

For all three tagging groups, more fish were last detected (and assumed dead) in the central and eastern basins than would be expected based on the patterns of overall detections by basin (Table 2.2). For example, only 2% of all detections of 2016 Reef walleye were from the eastern basin, but 9.8% (4 of 41 fish) that were classified as dead were last detected there. In contrast, while the majority (68%) of the dead fish from this tagging group were last detected in the western basin (Figure 2.9), 80% of all detections occurred in this basin. The 2014 River group showed a similar pattern; most of the fish classified as dead were last detected in the western basin (specifically at the mouth of the Sandusky River, Figure 2.10), but the total amount of detections in the western basin was also high. The 2014 Reef group was slightly different, most of the last known locations of the fish classified as dead were in the central basin (11 out of 22) and only 11% of the total detections were in that basin (Figure 2.11).

Table 2.2. A basin-by-basin comparison of the location of fish classified as dead according to the analysis of the state variable estimates (z). The white rows contain the number of fish whose last observed location was in each basin, before the model estimated the fish to have died. The shaded rows are for comparison purposes, these are basin-by-basin breakdowns of all detections for all fish in the group.

		# fish lasted detected in basin (% fish estimated dead)		
Group	# fish estimated dead	Western Basin	Central Basin	Eastern Basin
2016 Reef	41	28 (68%)	9 (22%)	4 (10%)
	% of all detections	80%	17%	2%
20 14 Reef	22	8 (36%)	11 (50%)	3 (14%)
	% of all detections	88%	11%	1%
2014 River	58	42 (72%)	10 (17%)	6 (10%)
	% of all detections	95%	4%	1%

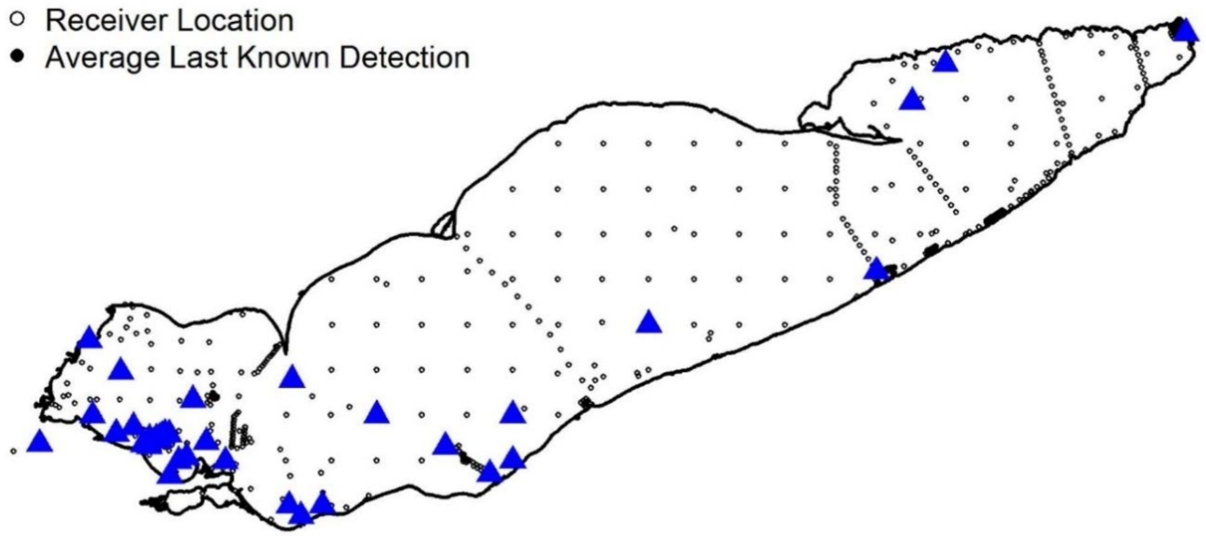


Figure 2.9. Last known location of the 41 fish in the 2016 reef walleye data classified as being dead. 28 fish were last detected in the Western Basin, 9 in the Central Basin, and 4 in Eastern Basin.

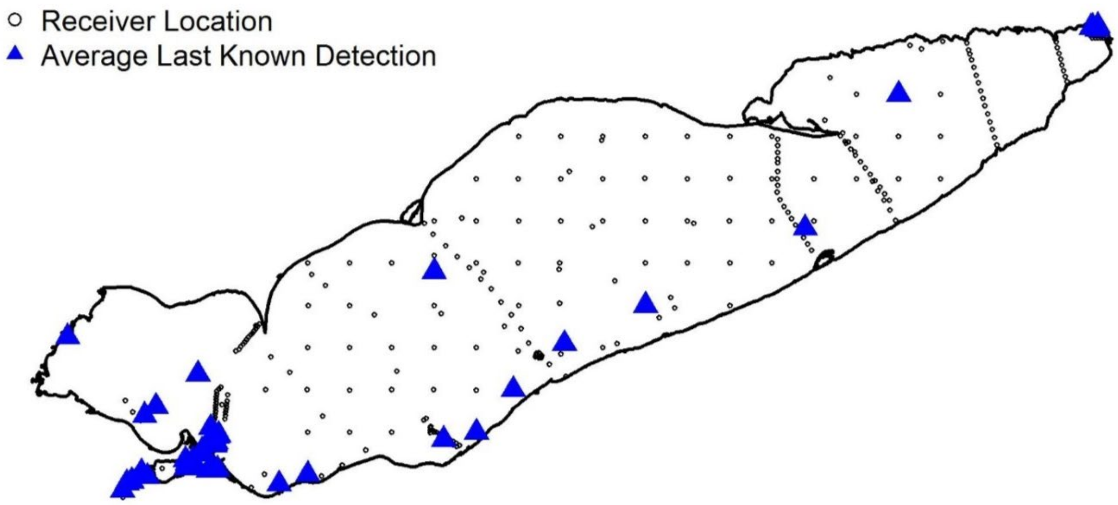


Figure 2.10. Last known location of the 58 fish in the 2014 river walleye data set classified as being dead. 42 fish were last detected in the Western Basin, 10 in the Central Basin, and 6 in the Eastern Basin.

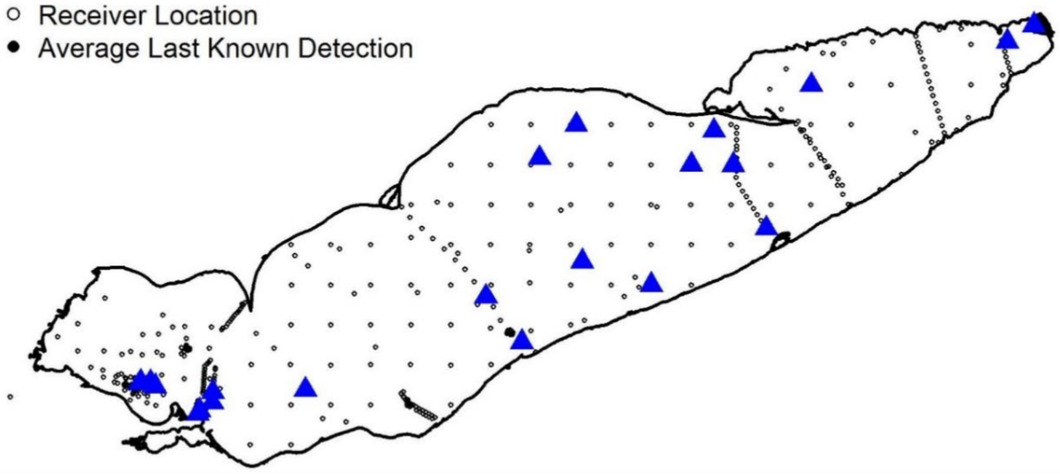


Figure 2.11. Last known location of the 22 fish in the 2014 reef walleye data set classified as being dead. 8 fish were last detected in the Western Basin, 11 in the Central Basin, and 3 in the Eastern Basin.

The seasonal patterns of when fish were last detected differed among the three tagging groups (Table 2.3). The 2016 Reef group (Figure 2.12) appeared to experience more mortality in the spring and summer (78% of last detections) compared to when all the detections took place (58% of total detections in spring and summer). The 2014 River walleye also had a higher proportion of fish last detected in the spring than would be expected based on total detections, but this group also had a slightly higher than expected amount of last known detections in the fall (Figure 2.13). The 2014 Reef walleye had most of the last known detections of presumed dead fish in the summer, more than would be expected based on the total detections (Figure 2.14).

Table 2.3. Seasonal comparison of the location of fish who experience mortality according to the analysis of the state variable estimates (z). The white rows contain the number of fish who were last observed in each season, before the model estimated the fish to have died. The shaded rows are for comparison purposes, these are a seasonal breakdown of all detections for all fish in the group.

		# fish lasted detected in season (% fish estimated dead)			
Group	# fish estimated dead	Spring (Mar-May)	Summer (June-Aug)	Fall (Sept-Nov)	Winter (Dec-Feb)
2016 Reef	41	17 (42%)	14 (34%)	5 (12%)	5 (12%)
	% of all detections	33%	25%	23%	19%
2014 Reef	22	4 (18%)	12 (55%)	5 (23%)	1 (5%)
	% of all detections	33%	27%	23%	17%
2014 River	58	25 (43%)	13 (22%)	17 (29%)	3 (5%)
	% of all detections	35%	25%	24%	17%

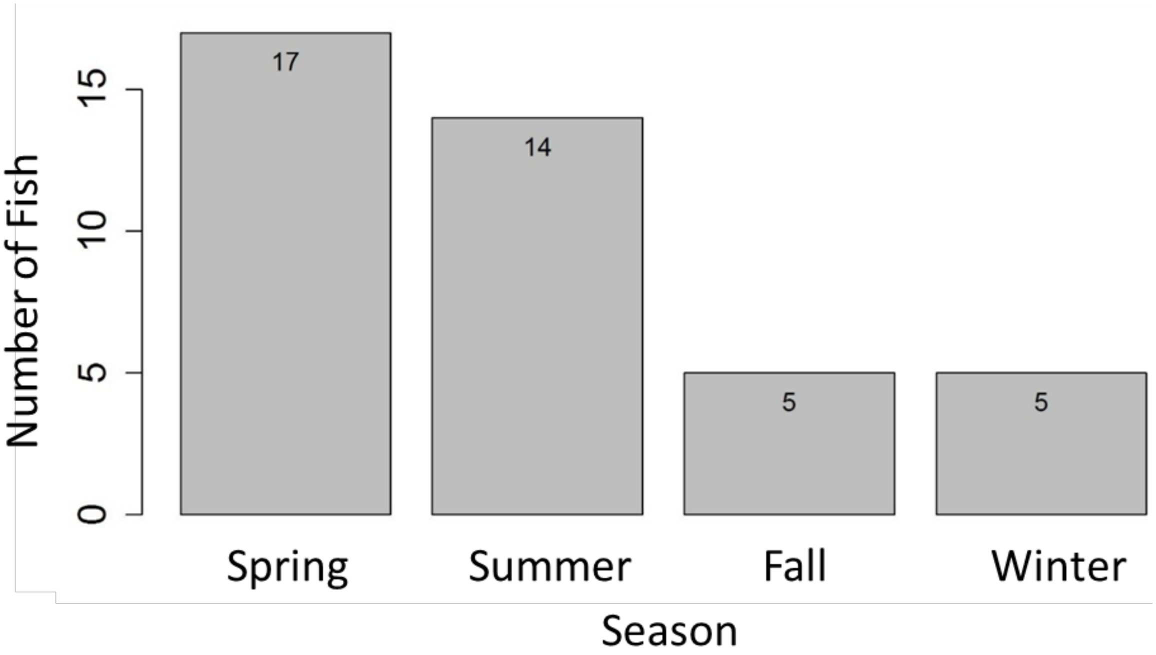


Figure 2.12. Last known detection season of the 41 fish in the 2016 reef walleye data set presumed to have died.

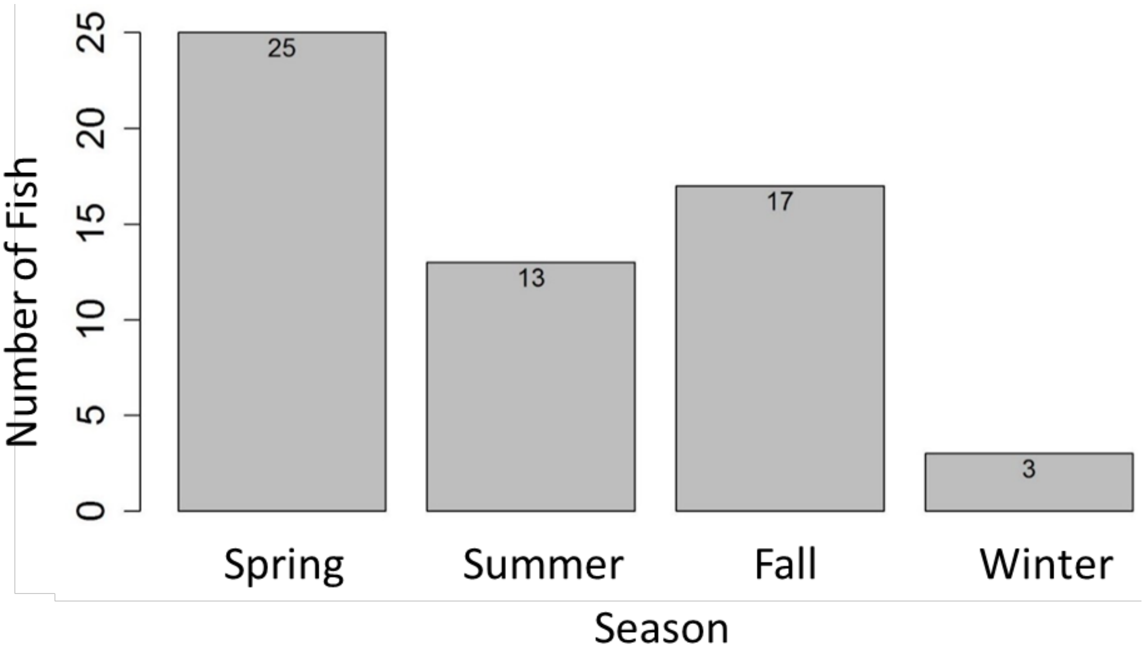


Figure 2.13. Last known detection season of the 58 fish in the 2014 river walleye data set presumed to have died.

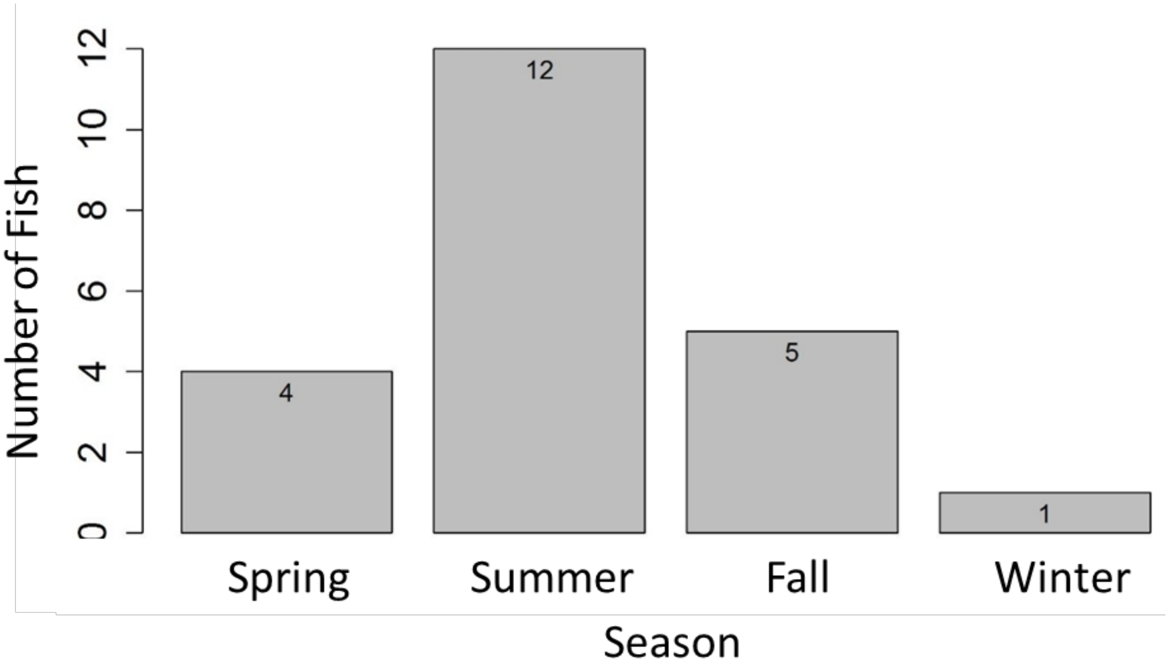


Figure 2.14. Last known detection season of the 22 fish in the 2014 reef walleye data set presumed to have died.

The model that allowed mortality to vary by month for the 2016 Reef walleye was also evaluated (Figure 2.15). Peaks of mortality (monthly mortality rate above 0.1) occurred in the late spring/early summer (May and June) every year, matching the analysis of the state estimates; however, credible intervals were large enough that the pattern was not strongly indicated. In the final year of data, additional peaks of mortality occurred in August and to a lesser extent in November. The first and final month mortality estimates were also high; however, these values tend to be biased in these types of analyses.

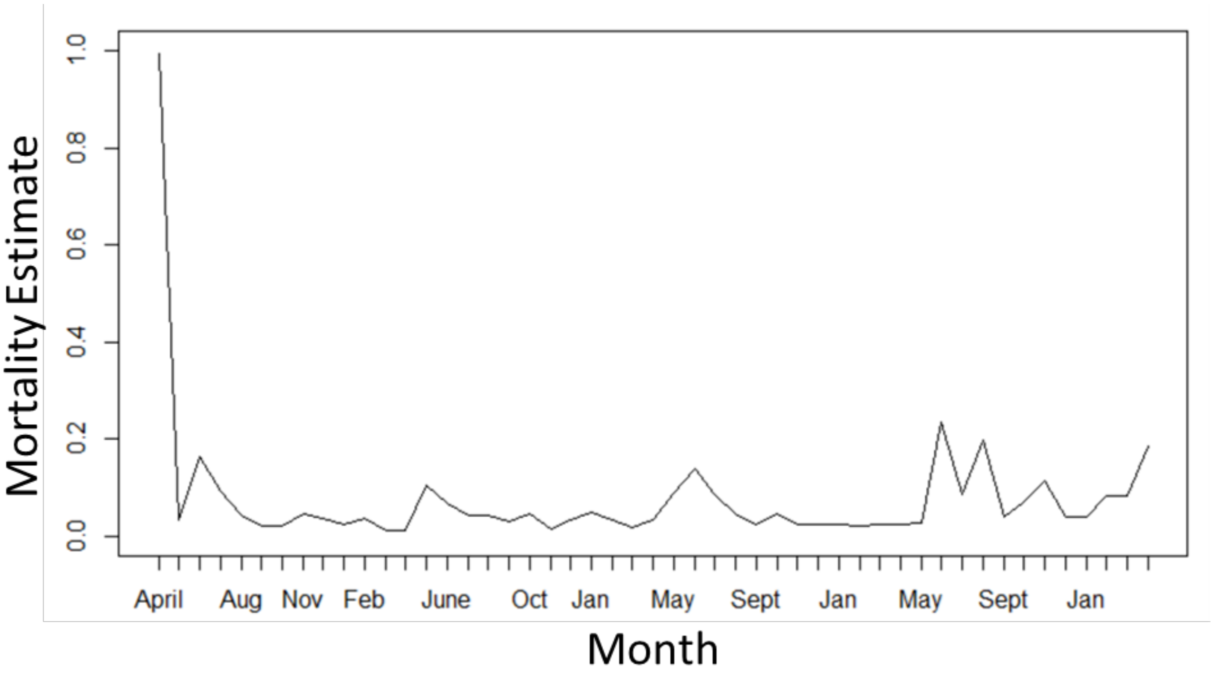


Figure 2.15. 2016 Reef walleye total mortality estimates from the spatial model where mortality was assumed to vary by month.

2.3.4 Parameter Convergence

For the non-spatial model, all convergence criteria were met for all parameters in all scenarios. For the spatial model, the convergence criteria were met for all mortality estimates, but the model had difficulty estimating the activity centers. Across all scenarios, over 63% of the activity centers met the convergence criteria, but the actual amount varied from 63% to 96% (Table 2.4). Generally, the monthly time step resulted in a higher percentage of activity center estimates meeting the convergence criteria compared to the seasonal (three-month) time step. The models had the highest percentage of converged activity center estimates when using the 2014 River Walleye: 96% of activity centers met the convergence criteria when using a monthly time step, and 85% met the convergence criteria when using a seasonal time step.

Table 2.4. Summary of convergence criteria (Rhat) values for activity center estimates from all spatial model results. Rhat values of less than 1.1 indicates convergence of parameter estimate.

Scenario	Median Rhat	# activity centers	# with Rhat < 1.1 (% of total)
2016 Lake Erie Reef			
Monthly Spatial	1.002	11,858	10,002 (84%)
Seasonal Spatial	1.001	3,872	2,440 (63%)
Vary M Monthly	1.001	11,858	10,791 (91%)
2014 Reef			
Monthly Spatial	1.001	6,324	5,607 (89%)
Seasonal Spatial	1.000	2,142	1,468 (69%)
2014 River			
Monthly Spatial	1.001	11,760	11,255 (96%)
Seasonal Spatial	1.000	3,894	3,279 (85%)

Patterns in activity center convergence

The issues we encountered with convergence of the spatial models were concerning, so we looked at additional analyses of the activity center estimates (the parameters that were driving the non-convergence) to try to diagnose the issue. Of the 11,858 individual parameter estimates for the activity centers of the 2016 Reef walleye, 1,856 (16%) of them did not meet the convergence criteria and the cause of the non-convergence was not clear. The non-converging activity centers were not aggregated in a few fish but spread across nearly all fish, 117 of the 121 fish had at least one activity center estimate that did not meet the convergence criteria. Non-detection did not lead to non-convergence, only 15% of the non-converged activity centers estimates occurred when a fish was not detected compared to the 63% of all activity centers that were estimated for time periods when a fish was not detected. The non-converging activity centers were not aggregated in time periods where a fish was not detected. Additionally, the distance the fish traveled between or within time periods was not related to the convergence of activity center locations.

2.3.5 Movement Patterns

For the spatial model, a selection of activity center estimates was investigated to see if different movement patterns occurred within the tagging groups of walleye (Figure 2.16). For the 2016 Reef walleye, the selection included fish assumed to have survived the full study period, some of which ranged across the study area during the five years at large while some tended to remain within the western (or west-central basin). Walleye movement patterns ranging across the lake aligns with the assumptions of the simulation framework used by Peterson et al. (2021) and the findings of other walleye movement studies (Wang et al. 2007; Vandergoot and Brenden 2014; Raby et al. 2018; Matley et al. 2020).

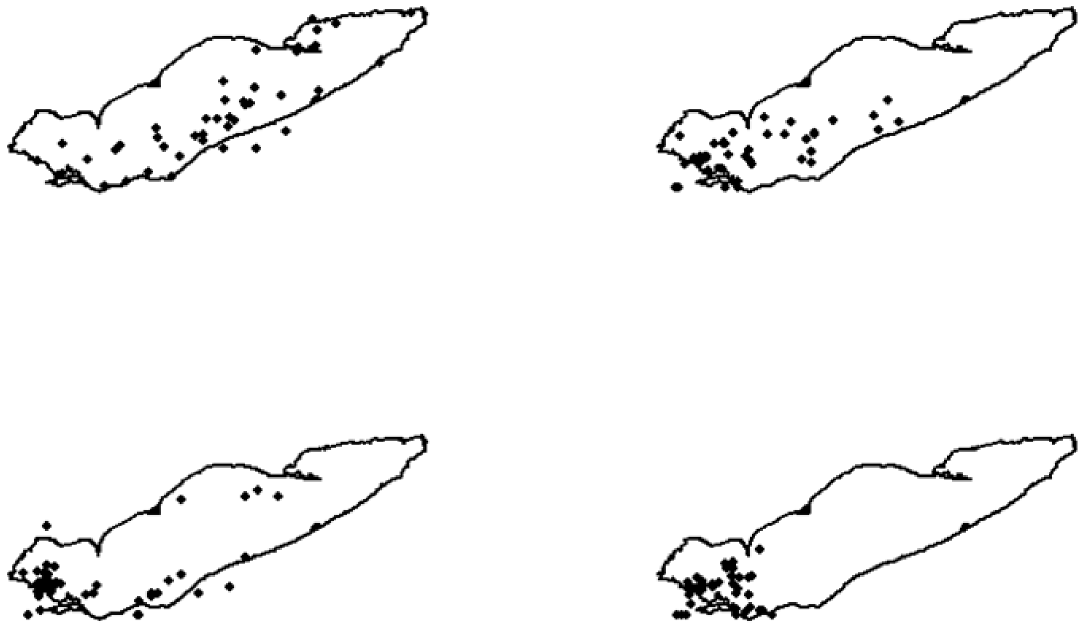


Figure 2.16. Activity center estimates for four fish from the 2016 Reef walleye data set, all four of these fish were detected throughout the entire study.

2.4 Discussion

In this study the total mortality estimates for Lake Erie walleye derived from acoustic telemetry data were similar between spatial and non-spatial approaches, although the spatial approach mortality estimates were consistently higher than the non-spatial approaches mortality estimates. While the spatial models used here had performance issues that would make us hesitate to recommend this type of model, the similarity between the estimates suggests spatial models that allow for more complex spatial and temporal assumptions about parameters are possible with more examination of the estimation issues revealed in this study. Acoustic telemetry provides details on the spatial distribution of tagged individuals and eliminates some of the drawbacks of traditional tagging, such as the need for active recapture effort and limited temporal distribution of detections, but more work is needed to develop a spatial model able to incorporate these data without performance issues.

Mortality estimates from the spatial approach were similar to the estimates from the non-spatial approach. However, the spatial model estimates tended to be slightly higher than the non-spatial model estimates, which could indicate positive bias, which both Peterson et al. (2021) and Hightower and Harris (2017) found in their simulation studies. Peterson et al. (2021) compared mortality estimates from a spatial and non-spatial approach across 140 different scenarios of receiver configurations and true mortality rates, and in 138 of those scenarios the spatial approach estimate generated positively biased estimates more so than the non-spatial approach. The activity center parameter estimates in the spatial approach were also problematic, with poor convergence in 16% of the activity center estimates using the 2016 Reef walleye dataset, 11% using the 2014 Reef data, and 4% using the Sandusky River data. Convergence issues and the potential positive bias of the spatial model used here contribute to the conclusion that more work is needed to identify a spatial modeling approach to address the issues discovered in this and previous research before its general use is justified.

More sophisticated modeling of the underlying movement patterns may improve performance. For example, Hostetter and Royle (2020) extended a spatial model similar to the one used in this research to incorporate signal rates, or the length of time between detections, into the estimation of activity centers in a separate sub-model. Their focus was not to estimate mortality, but a similar approach could be adapted to the data used in the present study. Similarly, the random walk used to estimate the activity centers could also be extended, to incorporate multiple states of movement (Franke et al. 2004; Morales et al. 2004), multiple centers of attraction (McClintock et al. 2012; Pirotta et al. 2018), or group-dynamic movement (Langrock et al. 2014). Many recent advances in movement modeling have occurred, and integrating these advances with spatial models using acoustic telemetry data could help address the performance issues (McClintock et al. 2021).

The analysis did not yield strong evidence that different components of the walleye fishery should be assessed using different mortality rates. While the mortality estimates for the 2014 Lake Erie reef spawning group of fish were consistently higher than the estimates of the 2014 Sandusky River spawning group, the differences were not large, especially relative to the uncertainty in the estimates. Once more data become available to allow for more precise estimates, this question should be revisited.

Total mortality estimates in this study were similar but slightly higher than total mortality estimates used for Lake Erie walleye management. The Walleye Task Group (WTG) uses a statistical catch-at-age model to estimate abundance of Lake Erie walleye to inform the implementation of a harvest control rule. The WTG model estimated the annual total mortality

0.40 in 2016, 0.38 in 2017, and 0.41 in 2018, and 0.42 in 2019 (WTG 2021). The estimates from this study varied between scenarios, but overall ranged from 0.40 to 0.55, higher than the WTG estimates.

While total mortality estimates were similar to those estimated from assessment models, fishing mortality estimates were higher than those derived from the assessment model. Models used here did not separate fishing and natural mortality directly. However, using an *ad hoc* approach, the fish that were reported as harvested by anglers, and the results of the spatial model using the 2016 Reef walleye, fishing mortality estimates from this analysis were consistently higher than the assessment model estimates, 0.25 versus 0.08 in 2016, 0.24 versus 0.06 in 2017, 0.17 versus 0.09 in 2018, and 0.18 versus 0.10 in 2019. Using the total mortality rate of 0.46 for 2016 Reef walleye, the natural mortality rate would range from 0.21 to 0.29 depending on the year, which is consistently less than the natural mortality rate of 0.32 assumed by the assessment model, but close to the estimate Vandergoot and Brenden (2014) obtained for age 5 and older fish for Lake Erie (range of natural mortality from 0.13 to 0.27). It is possible that the assessment models are underestimating fishing mortality because they are assuming a higher natural mortality rate than is in fact the case. Based on the limitations of these models, we do not recommend the WTG changes their mortality assumptions based on this present study.

Examination of the timing of last detections (an indicator of where and when mortality is more likely to have occurred) suggest a pattern consistent with the view that mortality was higher when walleye spawn than at other times of the year. The last detections of walleye tended to occur during the spring and summer during and immediately after spawning season. This pattern was also revealed by the model that allowed mortality to vary month to month, with peaks of mortality in May and June of every year. However, we did not see that there were more fish last seen in the western basin (which is where the bulk of spawning occurs) relative to the total distribution of detections. A finer scale mortality estimation approach might reveal unexpected hot spots outside of the spawning areas.

The primary parameter of interest, total mortality, converged consistently; however, the spatial models were not without their challenges. The non-convergence of activity centers undermines the potential of the spatial models to allow for an investigation of spatial patterns in mortality. The best performing model was the 2014 River walleye with a monthly time step, with 96% of activity centers converging; other scenarios ranged as low as 63%. A clear pattern did not occur in the non-converging activity centers, which might offer an explanation for poor convergence. Hypothesizing that the convergence issues were caused by periods of non-detection, the length of the time step was increased, and the convergence patterns investigated directly, but this approach did not support this explanation. Increasing the number of receivers or number of tagged fish to generate more detection data may not fix this issue either; because, a clear connection did not exist in our data between poor convergence and number of detections or the movement of the fish within or between time periods. It is possible that the variability in receiver coverage and distribution also influenced model performance, even with the coefficient included to take into account the amount of time the receiver was in the water. Future studies could benefit from consistent receiver numbers and locations across the study area.

Spatial model performance issues are not unique to this study. Harris et al. (2021) used a similar spatial framework to ours, except 1-dimensional, and they found activity estimates tended to drift to areas with low receiver coverage. Fischer et al. (2022) investigated a similar model formulation to the one used here using simulated data that assumed different underlying movement patterns. They found that when data were simulated based on fish movement around activity centers, matching the assumptions of the model, the model performed well. When detections were simulated from an individual-based movement model, where tag locations were based on a specified movement direction, and rate and detections were generated based on the distance between a receiver and the simulated tag locations (specifically designed to mirror the tag detection process of existing acoustic telemetry receiver arrays; Kraus et al. 2018; Peterson et al. 2021), they found low convergence for all parameters, similar to this study. Fischer et al. (2022) was able to associate the non-convergence of activity center estimates to gaps in the detection history, whereas the results presented here suggested a more wide-spread convergence issue not limited to periods of non-detection. Another limitation of this study that could have impacted convergence was the length of the MCMC chains that we were able to run for the spatial model. We did investigate running on model out to a length of 10,000 iterations and found no impact to convergence criteria or mortality estimates, but it is possible a longer chain length was needed.

In addition to the convergence issues discussed above, other important assumptions and limitations were involved in this study. Perry et al. (2012) provided an outline of the key assumptions when using acoustic telemetry data in tagging models which we believe were met with some caveats. These assumptions include aspects of study design, such that tagged fish were representative of the population, tagging does not affect survival, tag loss was minimized, and all tags were correctly identified to the individual level. The Lake Erie walleye acoustic telemetry studies took care to tag a representative subset of the Lake Erie walleye population as well as minimize post tagging mortality and using an acoustic data cleaning technique to remove erroneous detection data, before we received the dataset. However, by addressing the potential issue of environmental impacts on tagged fish by using data from fish that were tagged at similar times, we may have used a dataset that is less representative of the population compared to if we had used the full dataset. Additionally, walleye behavior likely was altered immediately post release after tagging, but due to the long term scope of this study, we assume that survival was the same between tagged and untagged individuals. Tag loss of acoustic tags is believed to have been negligible due to post release studies, but acoustic studies also rely on external tags to alert anglers to report harvest of an acoustically tagged fish. The retention of the external tags is more uncertain and could impact tag reporting. Another key assumption is that tagged individuals have the same probability of being observed, which we believe is met by the use of passive receivers (as opposed to active tracking or recapture methods). The assumption that sampling events are instantaneous was likely not met by this work, as capture histories were constricted using monthly counts of detections, not accounting for when in a month the detection occurred. While a smaller time step could have been used in the present study, we felt the monthly time step was needed to avoid long periods on non-detection, which would influence the ability of the model to estimate detection probability.

In this study, the assumption that total mortality is fixed through time was also used in order to separate the total mortality into fishing and natural mortality components. This assumption is not the current assumption of the assessment model for Lake Erie walleye, where natural mortality is assumed fixed and fishing mortality is assumed to vary through time. However, we believe this approach allowed estimation of the general range of natural mortality from these data. Future work would likely need to use more sophisticated techniques to better separate fishing and natural mortality components. Additionally, this approach assumed that the all harvest by the fishery was reported, a common assumption for high reward tags.

More sophisticated modeling techniques and use of ancillary data about the movement patterns of the study species could improve the performance of spatial models. A limitation of this work was the high computational needs required for the spatial model algorithm, it is possible that newer sampling algorithms for Bayesian inference (such as NIMBLE or STAN), would allow for fewer convergence issues. However, Fisher et al. (2022) did use NIMBLE, and its use did not improve convergence, suggesting a structural problem may exist in the model. Another approach would be to adjust the modeling technique to use more information. Klinard and Matley (2020) in their review of acoustic telemetry research discussed the drawbacks of using just detection data as the cue for mortality and suggested using additional space-use metrics (Buchanan et al. 2018; Gibson et al. 2015), such as acoustic tags equipped with pressure and acceleration sensors (Currey et al. 2015; Bruce et al. 2018), incorporating environmental data (Alos et al. 2016; Bacheler et al. 2019; Bradley et al. 2018; Melnychuk et al. 2017), or even using changes to known behavioral patterns (Alos et al. 2016, 2017) to better identify mortality events.

This work applies spatial and non-spatial mortality estimation methods to three tagged groups of Lake Erie walleye acoustic telemetry data. The results suggested the total mortality rate experienced by Lake Erie walleye was higher than the total mortality estimated in the current assessment model used by management agencies, and that the natural mortality estimate assumed by the assessment model might be too high. The differences between the three tagging groups also suggested that spatial differences in the mortality may occur among different spawning populations. Increasing spatial resolution (Fischer et al. 2022), accounting for the underlying movement patterns of the study species (Hostetter and Royal 2020; McClintock et al.

2021; Alós et al. 2016, 2017), or incorporating other auxiliary data (Lees et al. 2021) may allow for a more complete investigation of Lake Erie walleye mortality patterns.

2.5 Acknowledgements

Data used in this chapter were from two acoustic telemetry studies in Lake Erie. “Identifying migration patterns and spatial ecology of a reef spawning stock of walleye in the western basin of Lake Erie” is a joint project between the Michigan Department of Natural Resources, New York State Department of Environmental Conservation, Ohio Department of Natural Resources, Ontario Ministry of Natural Resources and Forestry, and the United States Geological Survey (glatos.glos.us/home/project/LEWAE). The objective of the study was to investigate migration patterns of walleye post spawning, spawning site fidelity rates, and to compare mortality rates for reef and river spawning walleye. “Understanding dam removal impacts on a formerly prolific Great Lake’s walleye population” was a joint project between the Ohio Department of Natural Resources and United States Geological Survey (glatos.glos.us/home/project/SRWAE). The objective of this study was to investigate the effects of the Ballville dam removal on Lake Erie walleye that spawn in the Sandusky River. These two projects did the tagging, receiver tending, and data base management. Key project members who assisted with this work include Chris Vandergoot, Richard Kraus, and Matt Faust.

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CHAPTER 3
WHERE TO FROM HERE? NEXT STEPS ON THE PATH TO LAKE ERIE WALLEYE MORTALITY ESTIMATES BASED ON ACOUSTIC TELEMETRY DATA

3.1 Introduction

The first two chapters of this dissertation addressed three objectives: 1) Develop an estimation approach and software code for estimating mortality components for walleye in the Great Lakes based on ongoing acoustic telemetry study designs, 2) Assess the performance of the different methods and explore through stochastic simulations the sensitivity of each approach to factors such as study design, and 3) Evaluate mortality rates of Lake Erie walleye. The models, while providing insights into mortality and its spatial and temporal patterns, require further development to become practical and defensible tools for stock assessment.

This chapter will review the history of using acoustic telemetry for mortality investigations, placing this work in the context of past and current research on acoustic telemetry, and highlight areas that hold promise for improving our ability to estimate mortality from acoustic telemetry data, building from the findings of this study.

3.2 History of acoustic telemetry as a tool for abundance and mortality estimation

The advent of acoustic tagging occurred in the 1950s (Trefethen et al. 1957). Acoustic tags are surgically implanted into the fish and are constantly emitting a tag-specific electronic signal that can be recorded with a date-time stamp by receivers. These receivers can be stationary or can be used to track tags actively. Acoustic tagging allows researchers to sample at a rate (receivers are detecting fish continuously) and under a level of control (receivers can be deployed in specific configurations) greater than traditional tagging studies, because no physical recapture is required to record the location of a fish. Often, the fish is also implanted with an external tag for identification by fishermen, which if reported upon capture, is another piece of information provided by acoustic tagging.

In the 1980s and 90s, the reduction in tag size coupled with the development of coded transmitter signals and the ability to process sophisticated signal patterns led to an expansion of the scope of acoustic telemetry projects. Originally, most studies involved a small number of tagged fish in an enclosed location, with researchers actively tracking tagged fish using a hydrophone and a boat. But as more fish were able to be tagged, and each could be uniquely identified, a desire to characterize larger aggregates of spawning fish than had been previously studied occurred, particularly migratory Pacific salmon (Cooke et al. 2013). These changes in available technology led to a dichotomy in acoustic tagging techniques, depending on the scope of the study. Acoustic tagging could employ active monitoring, with researchers actively moving to track tagged fish for a complete profile of movement during a specified amount of time, or passive monitoring, where receivers are deployed at a specific location and the data retrieved at a later date, recording instances of fish that have entered the detection range of the receiver.

Data obtained from active monitoring of fish with acoustic tags allowed for the development of new models to estimate population dynamics (Hightower et al. 2001). White (1983) adapted Brownie (Brownie et al. 1978) models to create a more specific case for telemetry data, where the fate of the tagged animals is known, eliminating the need to estimate a recovery rate. He assumed that a marked individual would be detected alive (moving) or dead (not moving) using active tracking. Pollock et al (1995) built upon this even further and developed a model using data collected from radio-tagged animals that allowed a recapture probability to be less than one. In 2001, Hightower et al. applied a similar approach to acoustic telemetry data to estimate both fishing and natural mortality of striped bass in Lake Gaston, North Carolina. Hightower tagged individuals and then performed active tracking, searching for the tagged individuals in the lake. They assumed they would detect an individual as alive or dead (if found in the same location on multiple surveys), and if it was not detected it was assumed to have been harvested by the fishery.

Active monitoring is a high cost way to monitor a tagged fish, requiring frequent surveys and investment of resources to get complete coverage of an area to detect the tagged fish of interest and can work well on small bodies of water; however, in the past decade a shift has occurred towards greater use of passive monitoring systems (Heupel and Webber, 2012), which produces data that are not as easily used in the models developed for active acoustic telemetry data. Passive monitoring techniques are less labor-intensive, requiring only the deployment and recovery of receivers after the initial tagging event, with the ability, in some cases, to leave receivers in place all year round. Environmental conditions can affect deployment and recovery, as well as the receiver's detection range (Heupel et al. 2006), but it still allows a researcher to gain acoustic coverage of a large area without having to physically move the receivers to find and track the fish. These passive techniques therefore lend themselves to studies on fish movement, such as spawning site fidelity, habitat use, or migration patterns (Teo et al 2013; Raabe et al. 2014). However, unless the receivers have overlapping detection ranges across the entire study area, these data lack the advantage of active tracking techniques that all tagged fish have a high probability of being observed if they are present in the study area and thus can be assumed to have been harvested if they are not observed. With increasing investment into fish tagging and passive receiver deployment an interest developed in approaches to estimate population parameters using passive telemetry data as well.

3.3 Recent developments in using acoustic telemetry for mortality estimation

In Klinard and Matley's 2020 review of acoustic telemetry studies published during 2015-2019, the most common types of articles were ecology and behavior studies, with comparatively few studies focused on estimating population dynamic parameters. The drawback of using just detection data as the cue for mortality is it tends to be difficult to distinguish among predation events, individuals that died within an array but are still detected, harvested individuals, tag expulsions, migration events, or a change in habitat use outside of the monitored area. Ways to mitigate these issues exist, such as expanding receiver coverage, refining tagging techniques to minimize tag shedding, analyzing detections for indicators that an individual has died but is still being detected (lack of movement over an extended period of time), or using external tags to encourage fishermen to report harvested individuals who have been tagged, but the risk of these problems cannot be eliminated.

To address some of these assumptions, some researchers have used study designs where the receivers are placed in arrays with overlapping detection ranges. These fine-scale receiver arrays approach the functionality of active telemetry monitoring because fish are expected to be detected if they are present in the study area, and this approach has been used to investigate mortality (Celedonia et al., 2008; Leander et al., 2021; Steel et al., 2013; Moland et al. 2019; Moore and Berejikian, 2017; Moore and Berejikian, 2022). Moore and Berejikian (2017) estimated mortality of steelhead trout using acoustic telemetry data by placing receivers along a migration path and near the mouths of the rivers and using a CJS mark-recapture model. By estimating survival through each migration segment, they were able to assume that non-detection from one segment to the next meant a mortality event. In 2022, Moore and Berejikian returned to their investigation of steelhead mortality, using a spatial mark-recapture survival model and acoustic telemetry to look at mortality of smolts encountering a bridge that extends 15 feet underwater, forming a partial barrier to migration. This narrowed focus allowed them to use a dense array of receivers to investigate mortality focused on spatial segments. Even with large arrays that are non-overlapping in detection ranges, more receiver coverage in general should improve estimates (Peterson et al. 2021; Fischer et al. 2022), likely by increasing the probability that a fish that is alive will be detected.

Overlapping arrays have also been used to separate fishing and natural mortality components, sometimes independent of using reports of harvested fish (Villegas-Rios et al. 2020). In these arrays, a fish that shows frequent movements can be assumed to be alive, if it leaves the array and is detected elsewhere it can be assumed to have emigrated, abrupt disappearances from the array are assumed to be fishing mortality events, while stationary or highly irregular movement patterns are assumed to be natural mortality events (Topping and Szedlmayer 2013; Williams-Grove and Szedlmayer 2016; Villegas-Rios et al. 2020; Currey et al. 2015; Bruce et al. 2018). This type of study design is difficult to achieve if a fish is far ranging relative to the study area and doesn't consistently aggregate, and it also requires the assumption that natural mortality will occur within the array and be detected. Williams-Grove and Szedlmayer (2016) only reported one natural mortality event of a red snapper during a two-year study period, resulting in an estimate of natural mortality that was lower than previous studies of the same population and perhaps suggesting that this assumption of detection within an array was violated.

Separating fishing and natural mortality in large systems using acoustic telemetry data has proven to be more challenging (Hightower and Harris 2017; Thortley and Andrusak 2017; Scheffel et al. 2020; MeInychuk et al. 2017). Hightower and Harris (2017) used simulations to look at different acoustic telemetry study designs to estimate mortality, and found mortality estimates from study designs of fixed receivers, even in combination with high-reward tags, tended to be biased, consistent with my findings (Peterson et al 2021, Chapter 1) and others (Fischer et al 2022). It is difficult to account for the gaps in detection in non-overlapping receiver arrays and identify unobserved mortality events. Thortley and Andrusak (2017) used an approach similar to the one we used in Chapter 1 and 2, but added additional complexity to investigate fishing and natural mortality of bull and rainbow trout acoustically tagged in Kootenay Lake. They used a Bayesian individual state-space CJS model that took into account acoustic detection probabilities, angler recaptures, spawning state, growth, and movement between sections of the lake. The complexity of the additional parameters in the model allowed them to investigate the effect spawning had on mortality, although they were constrained by the inability to directly monitor bull trout during spawning and concluded that their mortality estimates may be biased as a result.

New methods to identify movement or behavior patterns (e.g., Currey et al. (2015)'s use of tags with depth sensors; Bacheler et al. (2019) using fine-scale telemetry data to identify two to three distinct behavioral states) can also be used to better identify mortality events (Buchanan et al. 2018; Gibson et al. 2015; Bruce et al. 2018; Alos et al. 2016, 2017). Buchanan et al. (2018) used behavioral states and movement patterns to filter predation events using assumed behavioral differences between the tagged migrating Chinook salmon and their predators such as striped bass (*Morone saxatilis*). Buchanan et al. (2018) also used different model states to differentiate between routes through the various regions of their study site to better inform their survival estimates. The combination of space use and behavior patterns can better inform the state of an individual fish and improve survival estimates.

3.4 Potential avenues for Lake Erie walleye mortality estimation using acoustic telemetry

In a review by Lees et al. (2021) of mark-recapture study designs using acoustic telemetry, it was concluded that Bayesian multistate models including auxiliary data were the most appropriate framework. The work presented in Chapter 1 and 2 used relatively straight forward models, using two states, alive and dead, and no additional data beyond the acoustic data itself and reports of harvested individuals. More recent models extend this approach and include explicit models of individual movement and signal rates, introducing additional information into the estimation of location (e.g., Hostetter and Royle, 2020). Hostetter and Royle (2020) call their approach movement-assisted localization, and is a similar approach to what was used in this dissertation, except instead of time steps, their model uses the known length of time between transmissions, or a "signal rate submodel" that also incorporates missed signals, increasing the complexity of the model to take into account the information provided by tag transmissions that go undetected.

Other ways to incorporate more explicit models of animal movement and states exist that could also improve model performance. McClintock et al. (2022) reviewed a number of recent advances in animal movement modeling and the potential impact these could have on spatial modeling. They found that resource selection functions (e.g., Manly et al. 2007; Wang et al. 2019, among others), random walks to incorporate multiple states of movement (Franke et al. 2004; Morales et al. 2004), multiple centers of attraction (McClintock et al. 2012; Pirotta et al. 2018), or group-dynamic movement (Langrock et al. 2014) all had the potential to improve spatial modeling. These approaches could be incorporated to identify or include patterns of walleye movement, potentially again improving the activity center estimation component of the mortality estimation model. Extending the model to include more than two states is another avenue (Bradley et al. 2018; Block et al. 2019), such as including spawning and emigration events explicitly, or dividing the study area into distinct spatial areas (Thortley and Andrusak 2017).

Specifically for Lake Erie walleye, a relatively straightforward adjustment to the spatial model used in Chapter 2 based on the approaches outlined above could take into account whether the time period is during spawning or not spawning, and spawning site fidelity. In Chapter 2, fish movement was assumed to follow a correlated random walk, with activity center estimates (*s*) based on the location of the activity center in the previous time period:

$$s_{,\mathrm{i,t}} = s_{,i,t-1} + \tau_{,i}$$

This approach could be expanded to incorporate two states into the point process model (*m=1* not spawning, *m=2* spawning) as well as the location of the spawning site (*a*):

$$s_{,i,t} = \begin{cases} s_{i,t-1} + \tau_{,i} \ if \ m_{i,t} = 1 \\ s_{i,t-1} + B(a - s_{i,t-1}) + R(s_{i,t-1} - s_{i,t-2}) + \tau_i \ if \ m_{i,t} = 2 \end{cases}$$

Where *R* is the rotational component of the movement path, which could be set such that there tends to be direction persistence, and *B* specifies the strength of attraction towards *a*. With this formulation, the spawning sites could be specified, as well as how quickly and directly a fish will tend to head there during spawning season. During the post spawning season using this model, walleye would tend to move in a correlated random walk movement pattern similar to what we assumed for Chapter 2. This approach provides more data to the model for activity center estimation, which could minimize the estimation errors that were so prevalent as reported in Chapter 2 and improve mortality estimation overall.

Another direction to go with these models would be to simplify them, especially with regards to the spatial estimation of the activity centers. In the current approach, an activity center can be estimated at any point across a study area. Instead, a multi-state model could be used where the different regions of Lake Erie (e.g., the different management units) are used as the potential locations or states of the fish in each time period. This would reduce the complexity of the activity center estimation, potentially improving convergence, while still allowing for a coarse look at spatial patterns of mortality.

The models used in this dissertation also focused on three specific groups of tagged fish based on tagging year, representing a fraction of the full data set collected for Lake Erie walleye. This approach was used to eliminate the effects of when a fish was tagged and the distribution of receivers in the lake, but techniques could be used to incorporate multiple tagging groups into a model that takes into account the changing study design of the receiver network through time (Gimenez et al. 2007; Royle and Young 2008; Gelman et al. 2013). These data could also be combined with the extensive data sets collected by conventional tagging studies of walleye in Lake Erie (Vandergoot and Brenden 2014; Scheffel et al. 2020). The drawback to this approach is the need to make assumptions about how mortality might vary across the datasets, which would be from different time periods and regions, or estimate what that variation would look like.

Recent progress in estimation methods and software provides an opportunity for future work on mortality estimation methods to incorporate the complexities described above and to be more successful. My original research was constrained by computational challenges, each model took weeks to run with the software used, which limited the variation and complexity that could be incorporated into the model that could still be performed within time constraints. Recent estimation method and software developments since my study could alleviate some of these limitations. Some of the ideas presented here for possible next steps would not have been practical when this work was conducted, but as technology continues to improve, the opportunities for using more complex estimation estimates will expand and be capitalized on.

Lake Erie walleye management agencies desire to build upon this dissertation work to investigate alternative estimates of natural mortality that could be used in stock assessments. Acoustic telemetry could still provide that, but more research is needed to identify the appropriate model to achieve that goal. Between when this work was started and completed, much has changed. The GLATOS network in Lake Erie has expanded, covering Lake Erie in a high-density grid of receivers with non-overlapping detection ranges, papers have been published investigating the movement and behavioral patterns of Lake Erie walleye, the estimation software has improved, and a continuing interest exists in using acoustic telemetry data for mortality estimation. The next steps should capitalize on those improvements, using a larger data set of acoustic detections than used here, as well as incorporating movement information already available from walleye acoustic telemetry studies (Hayden et al. 2014; Hayden et al. 2018; Matley et al. 2020; Raby et al. 2018), in a model that explicitly incorporates the spatial information gained by acoustic telemetry studies to estimate mortality of this Lake Erie walleye.

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