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Implications of Channel Catfish Movement in An Internationally Managed System

Ву

Henry Hansen

A THESIS

Presented to the Faculty of

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Implications of Channel Catfish Movement in An Internationally Managed System

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The largescale movements and spatial behavior of channel catfish in the Red River of the North, have direct interactions with geopolitics, anthropogenic structures, and ecosystems. Investigating the spatial dynamics and exploitation of this mobile and internationally managed fish species provides opportunities for resource managers to design evidence-based policy for the diverse interest groups that utilize the fishery. My thesis comprised two parts: 1) characterize system-wide movement and survival patterns using mark-recapture methods and acoustic telemetry and 2) project the interaction of hypothetical exploitation scenarios and alternative movement methodologies to assess the fishery from an ecosystem service flow perspective. Channel catfish were tagged with T-bar tags and acoustic transmitters to track movement patterns and quantify harvest. Approximately 40% of individuals tagged with acoustic transmitters moved into Lake Winnipeg at least once during the study. Conversely, about 30% of T-bar tag recaptures in the U.S.A. had been initially marked in Canada. A large proportion (0.89-0.97) of the individuals remained within the initial study reach where they were tagged. Fishing mortality was estimated to be less than 0.001, and natural mortality was estimated to be 0.16 across the entire system. Projection models demonstrated that trophy stages of channel catfish were highly sensitive to exploitation and were typically depleted at or below a 0.30 exploitation rate. Depletion of populations and changes in stock structure affected subregions within the Red River system differently which resulted in competing strategies

among countries and fishers from the perspective of economic valuation of harvests. We found that recruitment from areas with greatest population size appeared to buffer aspects of harvest within regions and to some extent immediately adjacent regions. Movement, regardless of methodology, was critical in supporting exploitation for regions with low recruitment. The sustainability of exploiting highly mobile fish species from an ecosystem service flow perspective hinges on the ability of fisheries management organizations to incorporate spatial variability and understand the economic consequences of exploitation for competing interests.

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CHAPTER 1 INTRODUCTION TO FISHERY MANAGEMENT CHALLENGES FOR THE RED RIVER OF THE NORTH CHANNEL CATFISH FISHERY

Quantifying the spatial behaviors and projecting the population dynamics of a fish species from a system-wide view has direct implications in managing the sustainability of a fishery and ecosystem. Fish population assessments are the primary tool to support the development of fisheries management policies. When unaccounted, the spatial and temporal variability of a fish population can bias population assessments and subsequent management policies (Cooke et al. 2016). Mobile fish populations that inhabit multiple management jurisdictions can cause competing socio-economic issues among stakeholders and result in conflict (Helfman 2007, Pracheil et al. 2012). Understanding and incorporating the spatial ecology of fishes can improve fisheries management for the fish population and stakeholders. Channel catfish in the Red River of the North are one such species that meets the above constraints.

The Red River channel catfish have been known to undertake movements greater than 500 kilometers in this system, with some individuals moving throughout the length of the basin (Aadland et al. 2005, Murray and MacDonnell 2009, Siddons et al. 2017). Some have speculated that this population's unique longevity and age at maturity provides the physiological capacity to conduct long-distance movements. The population has documented ages greater than 20 years, which are some of the oldest ages recorded for the species (MacDonald 1990, Hubert et al. 1999, Siddons et al. 2016). Stewart and Watkinson (2004) found age at maturity to be 10 years or older whereas the typical age at maturity for the species is 5 years (Hubert et al. 1999). Siddons et al. (2017) observed large catfish (>600 mm) moved greater distances than smaller individuals. Consequently, fisheries managers would like answers to the following: what are the Red River channel catfish's movement patterns and how does size and sex influence individual behavior? Additionally, how will movement patterns impact fisheries management?

Evaluation of the spatial ecology of channel catfish, requires identification and comparison of timing, direction of movement, and destinations across individuals. A review by Hubert et al. (1999) reported that channel catfish seasonal movements were often associated with spawning or overwintering, but the direction of these movements varied among populations. Riverine-specific populations exhibited both upstream and downstream movements to reach spawning or overwintering sites, whereas reservoir populations predominantly moved upstream to spawn in the river and moved downstream to the reservoir for overwintering. Lake Winnipeg is a natural "reservoir" so one would expect to see upstream movement during spring spawning and a fall downstream movement for overwintering if seasonal movement is occurring in the system.

Channel catfish that inhabit lotic systems have been known to use large rivers, connecting tributaries, and small order creeks throughout a given year (Funk 1957; Mahoney 1982; Dames et al. 1989; Pellett et al. 1998; Fago 1999). Channel catfish have also been observed in creeks moving upstream in the spring and downstream in the fall, with greater distances being travelled in the spring (Dames et al. 1989). Funk's (1957) study found native stream fish species are composed of a sedentary group and a mobile group. Another key component of Funk's study was the distinction between mobile and migratory. He conjectured the channel catfish was not migratory because there was no evidence of a large, directed movement throughout the study. Funk proposed variations in sedentary and mobile proportions could all be caused by release location, habitat preferences, and size of fish. Funk had identified channel catfish as non-migratory, but the study by Pellett et al. (1998) demonstrated that channel catfish in the Lower Wisconsin River were indeed migratory. Pellett et al. (1998) reported channel catfish migrated downstream to the Mississippi River in the fall and upstream the Wisconsin River in the spring to spawn.

Investigating the spatial ecology of freshwater fish poses unique challenges from a methodological perspective. Mark-recapture and telemetry can be used to assess the spatial ecology of fishes, but each has unique tradeoffs (Adams et al. 2012). More specifically, the bias associated with either method can affect our understanding of movement depending on the analysis implemented. One question of interest for this project is how to integrate both mark-recapture tag data and telemetry data into a single comprehensive model to provide a means to estimate system-wide mortality and movement (Hightower and Harris 2017). Previous studies have utilized a Bayesian state-space approach to develop similar models for other mobile fish populations (Raabe et al. 2013; Holbrook et al. 2014; Hightower and Harris 2017). A Bayesian state-space approach allows one to fully customize the parameters to identify biological patterns by jointly modeling a system process (e.g., ecological process) and an observation process (e.g., mark-recapture) (King 2012). The ability to customize model parameters also allows one to more readily integrate estimated parameter information into other studies, such as Leslie matrix models, discussed below.

Identifying the ecosystem services provided by an ecosystem, as well as estimating the associated values monetarily, is at the forefront of modern, environmentally focused decision making, but incorporating the spatial ecological information into these analyses is only a recent development (Bagstad et al. 2013). Costanza et al. (1997) provided the foundation on which ecosystem services is interpreted and applied, yet difficulties in estimating such values and

incorporating spatial variability have slowed adoption into mainstream management and policy making. Consequently, many studies that describe ecosystem services for an ecosystem or an organism typically give estimates that are described as likely underestimated or are location specific (Costanza et al. 1997, Postel and Carpenter 1997, Barbier et al. 2011) (Losey and Vaughan 2006, Pejchar and Mooney 2009, Vaughn 2017). Holmlund and Hammer (1999) developed a fisheries focused perspective on ecosystem services. Recently, modelling software has been developed to explore the relationships between the monetary value of ecosystem services provided by fisheries (Sharp et al. 2018). Such models are ideally suited to explore the ecosystem services in Lake Winnipeg and the Red River from a fisheries perspective as well as include the spatial behavior of the fished population. Incorporating spatial information into ecosystem-based thinking provides management and policy making officials a novel means to understanding and managing natural resources.

A cooperative management effort between the USA and Canada started in 1988 has sustained channel catfish in the Red River of the North as a trophy population and has mainly focused on recreational aspects to date for both countries. However, two policy issues are emerging for fisheries managers. First, recreational fishing harvest regulations pertaining to trophy individuals differ between Canada and the USA leading to questions about whether these differing regulations are mutually beneficial. Second, there has been substantial interest in further developing the commercial fishery in Lake Winnipeg to include more species in the multi-species quota system. Lake Winnipeg has an established commercial fishery for walleye (*Sander vitreous*), sauger (*Sander canadensis*), whitefish (*Coregonus clupeaformis*) and other species (Nicholson 2007); where fishers are allocated biomass quota rather than specific species quotas. Recent discussions among commercial fishers have expressed interest in targeting channel catfish as a commercial species now that recent legislative changes have opened such possibilities. The implications of potential regulation changes from a recreational or commercial fishing perspective could have cascading effects on the international usage of this species if the potential implications of fish movement are not included in consideration of management regimens. Now that this fishery has growing support for increased exploitation, natural resource officials would benefit from knowing monetary estimates of the ecosystem services provided by an exploited channel catfish fishery.

Investigating how potential management scenarios and fish movement may influence the population dynamics and ecosystem services of channel catfish are critical in ensuring its sustainability. The InVEST ecosystem services modelling software, a stage structured Leslie matrix model, is one approach designed to incorporate such intricacies to explore how channel catfish harvest and value changes in respect to hypothetical exploitation scenarios (e.g., Lake Winnipeg commercial exploitation) (Sharp et al. 2018). Characterizing fisheries as providers of ecosystem services as opposed to just waterbody-specific stocks, allows agencies to integrate multiple facets of a fishery into a broader understanding of fishery management decisions. Specifically, combining the 1) the spatial ecology of fisheries, 2) the population biology of the species, and 3) the value of the fisheries will provide fisheries managers a means to explore management scenarios from a system-wide perspective that reflects the unique characteristics for the population.

In summary, my research investigated implications of channel catfish spatial ecology and population dynamics regarding U.S. and Canada fisheries management regimes in the Red River of the North and Lake Winnipeg. My study consisted of two parts – 1) characterize systemwide movement and survival patterns using mark-recapture methods and acoustic telemetry

and 2) project the interaction of hypothetical exploitation scenarios and alternative movement methodologies to assess the fishery from an ecosystem service flow perspective.

My specific objectives are:

- 1. Characterize Movement Patterns using acoustic telemetry and mark-recapture methods
 - Evaluate international movement between the USA and Canada, movement through a potential barrier (movement above and below St. Andrew's Lock and Dam), and movement between ecosystems (e.g., Lake Winnipeg, Red River, Winnipeg River).
 - b. Estimate and compare survival between tagging methods
 - c. Estimate system-wide patterns of survival and movement by integrating tagging methods into a Bayesian state-space model
 - d. Identify relations of physical characteristics and movement distance
- 2. Evaluate interactions of movement and exploitation on channel catfish
 - Project the relations of different movement methodologies and exploitation scenarios
 - Evaluate the regional impacts of exploitation on stock structure, especially for trophy individuals
 - c. Investigate the impact of varying amounts of exploitation on a long-lived, slowgrowing fish species from a population perspective
 - d. Assess the economic outcomes associated with population and stock structure impacts for a mixed-use fishery

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CHAPTER 2 INTEGRATING TELEMETRY AND MARK-RECAPTURE METHODS TO ESTIMATE SURVIVAL AND MOVEMENT PROBABILITIES FOR CHANNEL CATFISH

Henry Hansen

Abstract

Channel catfish Ictalurus punctatus is considered a trophy species in the Red River of the North that can move >500 km encompassing both the United States of America and Canada. The largescale movements and spatial behavior of channel catfish have direct interactions with geopolitics, anthropogenic structures (e.g., dams), and ecosystems. Investigating the spatial dynamics of mobile fish species provides opportunities for resource managers to design policy from an ecosystem-scale perspective. The goal of this study was to characterize system-wide movement and survival patterns of channel catfish in the Red River of the North using markrecapture methods and acoustic telemetry. Channel catfish were tagged with T-bar tags and acoustic transmitters to track movement patterns and quantify harvest. A Bayesian state-space formulation of a multi-state Cormack-Jolly-Seber model was employed to estimate survival, movement, and recapture probabilities. A comprehensive model that integrated both tag types was also used to estimate natural and fishing mortality. Approximately 40% of individuals tagged with acoustic transmitters moved into Lake Winnipeg from the Red River at least once during the study. Conversely, about 30% of T-bar tag recaptures in the USA. had been initially marked in Canada. A large proportion (0.89-0.97) of the individuals remained within the initial study reach where they were tagged. Fishing mortality was estimated to be less than 0.001, and natural mortality was estimated to be 0.16 across the entire system. Linear modeling of physical characteristics revealed larger fish tended to move greater distances than smaller fish we found no correlation for sex or condition. Current management of channel catfish as a trophy fishery appears to be effective in ensuring low system-wide fishing mortality.

Introduction

Integrating the spatial dynamics of fisheries into decision making remains a challenge for fisheries management as perspectives transition from local to ecosystem scales (Berkeley et al. 2004; Ciannelli et al. 2008; Berger et al. 2017). Understanding the spatial dynamics of a fishery and incorporating that information into decision making is critical in: preventing overexploitation of fish stocks (Ying et al. 2011), maintaining social and ecological resilience, ensuring compliance and enforcement measures are successful (Canty et al. 2018), and informing tradeoffs for mixed-usage (Dichmont et al. 2013). The adoption of spatial planning and spatial stock assessment for marine fisheries has provided a pathway for decision-makers to assess the tradeoffs associated with the fishery and the ecosystem services it provides (Botsford 1997; Holmlund and Hammer 1999; Lester et al. 2009). Conversely, adoption of spatial approaches for freshwater fisheries has been slow and regulations still primarily reflect the one size fits all mentality (Carpenter and Brock 2004). The dichotomy of adoption is partly driven by the economic contributions that marine fishes provide compared to that of freshwater fishes, but the dichotomy also extends itself into fisheries science (Lynch et al. 2016, 2017). The spatial behavior of marine fishes has been more thoroughly studied than for freshwater species despite growing evidence of complex spatial behaviours of freshwater species and their interactions with geo-politics (Hogan et al. 2004), anthropogenic structures (Xie 2003) (e.g., dams), or ecosystems (Olden et al. 2010).

Specifically long-lived freshwater fish species in North America have been documented to exhibit spatial behaviours with implications to geopolitics (Pracheil et al. 2012), anthropogenic

structures (Hrenchuk et al. 2017), and ecosystems (Kluender et al. 2017) but, and they are often of recreational fishing importance. Fish with shorter life-history strategies can replace long-lived species if they are exploited (Winemiller 2005), which can catalyze the fishing down phenomenon proposed by Pauly et al. (2001). Systems that contain a long-lived species that are also a part of multispecies fisheries pose even more challenges for fisheries managers. The spatial structure of differing fish stocks within species and among species are difficult to decipher and inform at system-wide scales without a fine-scale understanding of fish movements (Cadrin and Secor 2009; Plagányi et al. 2014). The reduced costs and advancement of telemetry technology have enabled fisheries researchers to collect detailed movement information for aquatic species (Cooke et al. 2013). Similarly, traditional stock assessments have implemented mark-recapture techniques to estimate abundance and survival as well as characterize coarse movement patterns. Incorporating both the fine-scale information from telemetry and the coarse-scale information from mark-recapture into data analyses is one way fisheries researchers are exploring the system-wide implications of fish stocks (Herbst et al. 2016).

The Red River of the North (Manitoba, Canada & Minnesota – North Dakota, United States of America), hereafter referred to as the Red River, contains a population of channel catfish that have longer life spans and move greater distances than other channel catfish *Ictalurus punctatus* populations within their distribution (Hegrenes 1992; Siddons et al. 2016). Conservation and management of this international fishery as a trophy population has been a goal since 1988 (Drewes et al. 2008). Fisheries management agencies from the United States of America (USA) and Canada have coordinated to ensure similar recreational fishing management goals across political boundaries though each country has implemented different strategies. Current regulations in Canada allow the maximum daily harvest of individuals < 60 cm where possession limits are one catfish for conservation licenses and four for regular fishing licenses. Though harvest is legal for individuals for less than 60 cm in practice, the Canada reach of the Red River typically exhibits catch and release practices for recreational anglers. Minnesota and North Dakota regulations limit daily harvest to five Channel Catfish, with only one over 61 cm. Additionally, however, recent stakeholder discussions have highlighted the possibility to both further protect the trophy aspects of the recreational fishery, yet target channel catfish as a commercial species in Lake Winnipeg (Manitoba, Canada). The contradictory nature of these discussions has spatial and temporal implications that underpin the importance of understanding the spatial ecology of this species (Ciannelli et al. 2008; Donaldson et al. 2014; Cooke et al. 2016).

Long-distance movements and migrations are behavioral adaptations that can support the necessary stages of a species' life history (Milner-Gulland et al. 2011; Brönmark et al. 2013). Channel catfish, are speculated to move or migrate in association with feeding, spawning, and overwintering to increase reproductive success (Hubert et al. 1999). Multiple studies report long-distance movements across the species' range (Wickliff 1933; Funk 1957; McCall 1977; Hegrenes 1992; Peters et al. 1992). One study identified channel catfish as migratory (Pellett et al. 1998) where another study characterized channel catfish as non-migratory (Funk 1957). Despite the abundance of research on channel catfish movement, investigators have yet to identify species-wide generalizations or explain existing movement variability across distinct channel catfish populations (Hubert et al. 1999). Dames et al. (1989) found that proportions of

sedentary and mobile channel catfish populations varied greatly between rivers, where sedentary proportions could range from as high as 90% to as low as 25% per river reach. Additionally, water management structures such as locks and dams can impede the mobility of populations. Aadland et al. (2005) anecdotally reported that the 1965 Heiburg dam failure in the Red River allowed channel catfish to emigrate into new reaches upstream.

Past studies of the Red River channel catfish population have evaluated movement patterns using telemetry or mark-recapture methods, but have not combined telemetry and markrecapture data into a single comprehensive model (Drewes et al. 2008). Nor have previous studies compared how either approach and its associated methodological tradeoffs influence model parameter estimates. Hegrenes (1992) reported a maximum movement of 500 km in 27 months, but 75% of tagged individuals exhibited movements less than 16 km. Siddons et al. (2017) reported international movement did occur in the Red River system for 6% of catfish each month moving upstream from Canada to the USA, whereas only one fish was observed returning to Canada. Siddons et al. (2017) also reported greater survival rates in Manitoba (98% monthly; 95% CI = 96–99%) than in the USA (83% monthly; (95% CI = 68–92%) and speculated that the more conservative harvest regulations in Manitoba may be sustaining the trophy status of the fishery for both the province and the USA. However, their use of mark-recapture methods to evaluate movement patterns limited their ability to detect the timing, frequency, and magnitude of movement events throughout the year. The goal of this study was to characterize movement patterns of Red River channel catfish using acoustic telemetry and mark-recapture methods as three distinct transitions: 1) movement between the USA and Canada, 2) movement through a potential barrier (movement above and below St. Andrew's Lock and Dam), and 3)

movement between ecosystems (e.g., Lake Winnipeg, Red River, Winnipeg River). Objectives were to 1) compare survival and movement patterns between tagging methods, 2) estimate system-wide patterns of survival and movement by integrating data methods, 3) identify relations of physical characteristics (e.g., weight, total length) and movement distance, and 4) evaluate the scale at which channel catfish mobility is conducted.

Materials and Methods

Study Area

The study area included the Red River of the North and Lake Winnipeg (Figure 2.1). The confluence of the Otter Tail River and the Bois de Sioux River form the Red River of the North. The river forms the boundary between Minnesota and North Dakota, and it flows northward into Lake Winnipeg in Manitoba, Canada (635 km in the USA, 255 km in Canada). The river is sinuous with a low gradient, resulting in run habitat with a substrate composed of silt, clay, and sand (Brooks 2003; Aadland et al. 2005). Eight low-head dams exist in the Red River on the USA side, and additional dams exist in its tributaries. All dams on the USA side of the Red River, except Drayton Dam (near rkm 327), have been 'modernized' (modified for increased fish navigation and safety for recreational boaters). St. Andrew's Lock and Dam are situated in Lockport, Manitoba, Canada and is primarily operated to allow for boat navigation. A floodway system is also near the dam and is operated to manage annual spring flood conditions. A fish ladder is installed at the dam to facilitate fish movement.
Lake Winnipeg is the 11th largest freshwater lake on earth, with an area of 24,154 km², a maximum width of 100 km and a length of 416 km. The lake is commonly characterized as having three sections - south basin, narrows, and north basin. We partitioned the Red River and Lake Winnipeg into four geographic states for our analyses: A – Red River in the USA, B – Red River from USA border to St. Andrew's Lock and Dam (Upper Red River), C – Red River from St. Andrew's Lock and Dam to mouth (Lower Red River), D – Lake Winnipeg and Winnipeg River (Figure 2.1). Geographic states were chosen to reflect the spatial arrangement of movements across potential barriers as well as to compartmentalize the management jurisdictions of the channel catfish fishery.

Fish Tagging

We used T-bar anchor tags (Floy mfg., tags 68-B and 68-F), and V16-4H acoustic V16-4H acoustic transmitters (VEMCO; Halifax, NS, Canada) to determine the movement of channel catfish. We collected channel catfish from the Red River using hoop nets and rod-and-reel angling during the summer (May-August) 2012-2017. We baited hoop nets (seven, 0.9-m-diameter hoops) with a soybean mash. We conducted angling with $\geq 6/0$ barbless circle hooks baited with cut goldeye *Hiodon alosoides* or white sucker *Catostomus commersonii*. Sampling locations for T-bar tagging efforts were primarily in the Red River. We inserted T-bar tags under the left side of the dorsal fin, through the pterygiophores (Siddons 2015). We used tag model 68-B for fish between 200 – 500 mm and tag model 67-F for fish larger than 500 mm. We did not target channel catfish below 200 mm because smaller fish were not a preference by anglers in this system and were too small for T-bar tags. We weighed each Channel catfish to the nearest gram and measured

for total length to the nearest millimeter. Each tag contained a unique identification number, and contact phone number for anglers to report location and fate (released or harvested) of fish caught. Additional recapture data also came from our sampling effort, commercial fishers in Lake Winnipeg, Minnesota Department of Natural Resources, North Dakota Game, and Fish Department, and Manitoba Sustainable Development fisheries division monitoring.

We collected individuals for acoustic transmitter implants in similar locations as the T-bar tags and we surgically implanted V16-4H acoustic transmitters in adult (>550 mm) channel catfish. We secured transmitters to the cleithrum using surgical monofilament following Siegwarth and Pitlo Jr. (1999) to mitigate transmitter expulsion (Marty and Summerfelt 1986). Transmitters had an estimated tag life of 2435 days and were programmed with a 120-second nominal delay with an 80-160 second window. We anesthetized channel catfish using eugenol (Bowker et al. 2006) or a portable electroanesthesia system (Smith-Root; Vancouver, Washington, USA) following methods described by Smith Root (2015). We collected total length, weight, and gender for each fish.

Receiver Deployments

We installed acoustic receivers (N = 142; VR-2W & VR2Tx-69kHz VEMCO) throughout the study area during summer, 2016 (Figure 2.1). We implemented a 7 x 7 km grid design in Lake Winnipeg with a more concentrated grid of 5 x 5 km in the southern end of Lake Winnipeg. We implemented a 5 km spacing (measured down the center line of the river) from the mouth of the Red River upstream to St. Andrew's Lock and Dam, and a ten km spacing from St. Andrew's Lock and Dam upstream to the USA border. Detection radius of transmitters were expected to perform upwards of 7 km. We installed receivers on the USA side of the Red River at Drayton, ND, Halstad, MN, and Grand Forks, ND. We also installed receivers in tributaries to the Red River: Devil's Creek, Cook's Creek, Seine River, Assiniboine River (30 km spacing upstream to diversion), La Salle River, and tributaries to Lake Winnipeg: Winnipeg River and Manigotagan River as well as in distributaries from the Red River in Netley-Libau Marsh. Expected receiver battery life was estimated at 14 months. The receivers were downloaded and redeployed in summer of 2017, providing about one year of detection data. We identified path movements from detection data from fish tagged with telemetry tags and recapture locations from T-bar tagged fish to calculate movement directions.

Analysis

State Space Modelling

We employed a Bayesian state-space formulation of a multi-state Cormack-Jolly-Seber model (BSSM) to estimate channel catfish survival (ϕ), recapture probability (p), and transition (ψ) probabilities (Royle et al. 2014). We fit separate models for T-bar data and transmitter data before fitting a comprehensive model using both datasets. The comprehensive model was modified (Hightower and Harris 2017) to also estimate fishing mortality (F) and natural mortality (M). Assumptions to the BSSM include: 1) survival, transition, and capture probabilities are the same for all individuals, 2) marks are not lost and are recorded without error for all individuals and states, 3) sampling and releases are instantaneous, and 4) the population is open to deaths and births. Transition probabilities were designated between and within geographic states A-D (Figure 2.1) to assess the movement pattern objectives.

The state-space formulation is a means to identify biological patterns by jointly modeling a system process (e.g., ecological process) and an observation process (e.g., mark-recapture) (King 2012). The ecological processes for our study were specified for survival and movement transitions whereas the observation process was specified for recapture probability. Specifications of the observation and system processes can be found in the equations section (Equation 2.1, Equation 2.2, Equation 2.3, Equation 2.4). One advantage of using the BSSM is the ability to specify the transition movements between states to more appropriately match the geography of the study system which is usually not available using software designed from a frequentist approach. For example, the states in our study system are organized in a linear arrangement (e.g., movement from the USA to Lake Winnipeg cannot be achieved without first moving through the Canada portions of the Red River). Design of the system and observation processes were based on specifications presented in Holbrook et al. (2014) and modified to accommodate both tag types and system geography. Here, the transitions were designed to allow for upstream or downstream movement or staying within a state. We reasoned it was likely a catfish tagged with T-bar tags could skip geographic states because the method and frequency of recapture are far lower than the telemetry approach. The inclusion of a "skip" parameter in the T-bar tag model designated as omega (ω) is shown in Equation 2.3. Also, all parameters were estimated as constants as opposed to time-variant to simplify model design and account for non-continuity of recapture months for fish tagged with T-bar tags.

The system process likelihood and observation likelihood for both the T-bar and transmitter models were considered a categorical variable. All parameters used a uniform distribution prior from 0 to 1 except for transition parameters associated to states B and C where a Dirichlet distribution was used to keep transition probabilities for states B and C bounded between 0 and 1. The Dirichlet was needed to represent one of three possible pathways that could occur for the B or C state movement transitions since the uniform distribution can only represent one pathway. All transition parameters dependent on the Dirichlet distribution were assigned equal values, ensuring all priors reflected a uniform distribution. All models used four Markov Chain Monte Carlo (MCMC) simulations with an adaption phase of 1000, 3000 burn-in, and 10000 iterations. The T-bar tag model simulations were thinned every 10th step (every 10th sampled step of the MCMC was discarded) because of the larger dataset and subsequent runtime. The comprehensive model, using both T-bar and transmitter data, was run for an adaption of 5000, 10000 burn-in, and 100000 iterations and was also thinned every 10th step. Increased adaption, burn-in, and iterations were necessary to accommodate the larger combined data set.

Monthly time steps were used to develop capture histories for both T-bar tagged, and transmitter tagged individuals. Fish tagged with acoustic tags that were detected in multiple states during a given month were assigned the state with the highest frequency for the month. Sampling periods for fish tracked with transmitters were continuous from beginning to the end of the study. Sampling periods for T-bar tagged fish were intermittent, using only months where recreational angling and research sampling was conducted (e.g., May – October). Seasonal analyses used only fish with transmitters and weekly aggregated capture histories. Weekly aggregated capture histories were used for seasonal analysis so movement transitions could be analyzed from a finer temporal scale than the monthly aggregated models. Seasonal variation was modeled using the skip parameter because original capture states for some individuals were not adjacent to the next consecutive capture event for a season, thus a model with a skip parameter was necessary. Only individuals with non-zero detection histories for each season were used for modeling, thus numbers of individuals used to estimate parameters varied across seasons. All seasons had a single year of data except for summer which had data for 2016 and 2017. Individuals with non-zero detection histories during the summer for both years were used to estimate parameters. Credible intervals were based on 95% Highest Posterior Density Intervals (HPDI). Modeling was conducted using Program R version 3.5 (R Core Team 2018), JAGS version 4.2 (Plummer 2003), and R library CODA (Plummer et al. 2006).

Movement Distance and Physical Characteristics Modelling

We assessed total movements as a function of total length, weight, and sex using ordinary least squares regression. We selected length, weight, and sex for model parameters of the global model for two reasons: 1) size of an individual has been documented with unique movement characteristics (e.g., can move upstream of St. Andrew's Lock and Dam) (Siddons et al. 2017), and 2) physiological variations between males and females was a question of interest for fisheries managers. The review of channel catfish biology done by Hubert et al. (1999) reported male channel catfish to guard nests after spawning. We suspected that males might have shorter movement distances than females if guarding nest requires sedentary behavior after spring spawning. Length and weight are often correlated, suggesting one of the variables be dropped, but they were both included in the global model to explore if interactions were occurring with sex. We used a backward selection approach to identify the model with the most support among competing candidate models using Akaike's Information Criterion (AIC). The model with the lowest AIC and Δ AIC, coupled with greatest weight and model likelihood were our assessment criteria to identify top performing models. The analysis was performed using Program R version 3.5 (R Core Team 2018). We focused our analysis on telemetry tagged fish because we could more effectively determine the distance and direction of movements. We did not include total movement distance estimates from T-bar tagged individuals during the model selection process because their capture and recapture dates were too infrequent to provide an adequate detection path to estimate total movement distance. However, we did model T-bar movements using the top supported model for comparison once the top supported model was identified. Total movement distance for each catfish tagged with an acoustic transmitter was estimated by summarizing the lengths of each detection path per individual. Detection path lengths were calculated using the haversine formula (Sinnott 1984). We reduced cases of double detection (i.e., an individual is detected by two different receivers at the same time) to a single location before estimating distances moved. All distance data were log-transformed to meet assumptions of normality. Additional, separate linear models were implemented to explore the variability of movement distance associated with our sampling methodology as opposed to the global model set which was intended to investigate the influence of physical characteristics only. Separate models included modeling movement distance as a function of surgery time, surgeon, and relative weight (Brown et al. 1995) via linear regression. The exploration of the relationship between sampling methodology and movement distance were incorporated in our study to see

if improvements to sampling methodology could be made. Specifically, we were interested in seeing if longer surgery times, surgery experience of surgeon, or condition of the individual biased our understanding of movement.

Results

T-bar Tagging Summary

T-bar tags were implanted in 15849 channel catfish ($n_{2012} = 461$, $n_{2013} = 3478$, $n_{2014} = 8248$, $n_{2015} = 100$ 2222, n₂₀₁₆ = 1330, n₂₀₁₇ = 110) from 2012 to 2017 (Figure 2.2). Average length of marked fish was 541 mm (min. = 193, max = 1003). A total of 1078 recaptures (n₂₀₁₂ = 16, n₂₀₁₃ = 69, n₂₀₁₄ = 210, n₂₀₁₅ = 333, n₂₀₁₆ = 224, n₂₀₁₇ = 226) were recorded, resulting in a tag return rate of 7%. Anglers failed to report recapture locations for 28 individuals and tag ID numbers for 26 individuals. Recaptured fish remained at large from 0 to 1811 d with a median of 363 d and a mean of 451 d (SE ± 12 d). Movement distances ranged from 0 km to a maximum of 380 km, with a median of 8 km and a mean of 66 km (SE \pm 3 km). No movement outside of the original marking location was the most common direction of movement (n = 606, 58%); whereas, upriver movement (n = 342, 33%) was more common than downriver movement (n = 75, 7%) (Table 1). Average length of recaptured fish was 739 mm (min. = 207, max = 995). Most recaptures were reported from anglers (n = 945), but research samples (n=105), and commercial fishers (n = 27) also contributed. The harvest percentage of recaptures was approximately 6% (we documented 65 recaptured fish as harvested out of 1078). Recapture locations were reported throughout the Red River including downstream of St. Andrew's Lock and Dam (n = 539), Netley Marsh (n = 35), upstream of St. Andrew's Lock and Dam (area around city of

Winnipeg) (n = 61), Emerson, Manitoba (n = 28), and the USA portion of the river (n = 318) as well as in the Assiniboine River (n = 6), Lake Winnipeg (n = 35), and Winnipeg River (n = 1). Most fish recaptured in the USA (n = 182) and Lake Winnipeg (n = 17) were originally marked from downstream of the St. Andrew's Lock and Dam sampling area (Table 2.2). We recorded only one catfish moving from the USA to Canada. We recorded more catfish moving upstream (n = 213) past St. Andrew's Lock and Dam than moving downstream (n = 14) past the dam, though most recaptures never crossed the dam (n = 796) (Table 2.3). Recaptures also revealed fish utilizing tributaries to the study area; this includes the Assiniboine River, Sheyenne River, Buffalo River and Elm River.

Telemetry Tagging Summary

Channel catfish were tagged in the Red River downstream of St. Andrew's Lock and Dam (n = 67), Red River upstream of St. Andrew's Lock and Dam (n = 24), and Winnipeg River (n= 30) (Figure 1). Acoustic transmitters were implanted in 121 adult channel catfish (mean \pm SE length = 705 \pm 9 mm) in the summer of 2016. We censored five individuals from the dataset that were not detected after release. Tracked fish remained at large from 1 to 502 d with a median of 126 d and a mean of 187 d (SE \pm 15 d). Movement distances calculated from detection paths ranged from 0.7 km to a maximum of 1988.5 km, with a median of 38.8 km and a mean of 137.2 km (SE \pm 23.0 km). A downstream movement direction (n = 63 (54%)), was the most common direction of movement for fish tracked with telemetry. Upstream movement (n = 4 (3%)) was the least common movement observed while no movement (n = 44 (38%)) was the second largest direction of movement observed (Table 1). Most tagged fish stayed within the same river reach

if the fish was tagged in the Red River, but the downstream movement was more prevalent if a fish was tagged in the Winnipeg River (Table 2.4). Approximately 40% of all tagged fish moved into the lake at least once during the study. One individual was observed moving to the north basin of Lake Winnipeg. We did not observe upstream movement across the dam for any telemetry fish. Predominant behaviors include staying within a geographic state (n = 50), moving downstream past St. Andrew's Lock and Dam (n = 6), moving upstream to USA border (n = 2), and moving across systems from the Red River to Lake Winnipeg to Winnipeg River (n = 5)(Figure 2.3). Telemetry also revealed fish utilizing tributaries to the study area; this includes the Assiniboine River and Manigotagan River (see movement path maps in the appendix).

T-bar Model

The T-bar model had non-agreement among chains for all parameters resulting in vague parameter estimates and 95% HPDI (Table 2.55). The T-bar model estimated survival from 0.95 to 0.98 where Lake Winnipeg (ϕ_D) had the greatest survival estimate, and Upper Red River (ϕ_B) had the lowest survival estimates. Movement (ψ) within each state rather than movement between states had the greatest transition estimates. Movement within Lake Winnipeg (ψ_{DD}) had the greatest estimate among within state movement parameters (T-bar = 0.81 Cl = 0.19-1). Movement upstream across St. Andrew's Lock and Dam (ψ_{CB}) was the lowest transition estimate (T-bar = 0.09 Cl = 0.01-0.39). The USA had the greatest capture probability estimates, and Lake Winnipeg had the lowest capture probability estimates. Movement from the USA to the Upper Red River (ψ_{AB}) for the T-bar model (T-bar = 0.22 Cl = 0.1-0.40) was greater than movement from the Upper Red River to the USA (ψ_{BA}) (T-bar = 0.16 Cl = 0.02-0.40). Movement from the Lower Red River to Lake Winnipeg (ψ_{CD}) (T-bar = 0.23 CI = .05-0.54) was greater than movement from Lake Winnipeg to the Lower Red River (ψ_{DC}) (T-bar = 0.19 CI = 0.1-0.81). The omega parameter in the T-bar model was estimated to be 0.66 suggesting that if a fish were to move into a different state from its origin that it was more likely to skip a state before being recaptured. T-bar model estimated capture probabilities from 0.0 to 0.01.

Telemetry Model

Survival (ϕ) estimates ranged from 0.80 to 0.87. Despite the lack of agreement of chains for the T-bar model, patterns of parameter estimates between the telemetry model and T-bar model shared many similarities for survival and movement (Table 5). Lake Winnipeg (ϕ_D) had the greatest survival estimates, and Upper Red River (ϕ_B) had the lowest survival estimates. Movement (ψ) within each respective state rather than between states had the greatest movement estimates with Lake Winnipeg (ψ_{DD}) being the greatest (Telemetry = 0.94 CI = 0.90-0.97). Movement upstream across the dam (ψ_{CB}) was the lowest transition estimate (Telemetry = 0.004 CI = 0.0-1). Movement from the USA to the Upper Red River (ψ_{AB}) for the Telemetry model (Telemetry = 0.33 CI = 0.10-0.58) was greater than movement from the Upper Red River to the USA (ψ_{BA}) (Telemetry = 0.19 CI = 0.05-0.36). Movement from the Lower Red River to Lake Winnipeg (ψ_{CD}) (Telemetry = 0.14 CI = 0.10-0.18) was greater than movement from Lake Winnipeg to the Lower Red River (ψ_{DC}) (Telemetry = 0.06 CI = 0.03-0.08). Capture probability (p), interpreted as the probability to be detected by a receiver, ranged from 0.8 to 0.93 with Lake Winnipeg having the greatest capture probability estimates and the USA having the lowest capture estimates. Credible interval ranges for T-bar tag transition parameters were typically larger than the telemetry model with transitions from the USA (ψ AA, ψ AB) being the exception.

Comprehensive model

The combined tagging model produced similar movement patterns to the tag specific models, but the range for HPDI estimates from the comprehensive model was smaller than the separate models suggesting that the comprehensive model produced more credible estimates. Movement within each respective state was the greatest movement estimates for all three models, but HPDI's in the combined tagging model were generally less than either tag specific models (Table 2.66). The comprehensive model differed in design from the separate models because it estimated fishing and natural mortality instead of state-specific survival. The comprehensive BSSM estimated natural mortality at 0.16., resulting in a survival estimate of 0.84 for the comprehensive model. The survival estimate from the comprehensive model was similar to the telemetry model survival results, but less than the T-bar model's estimate. The comprehensive BSSM estimated fishing mortality at less than 1% which is lower than the actual harvest percentage of ~6% reported for T-bar tags. The omega parameter in the comprehensive model was 0.42 suggesting that if a fish were to move into a different state from its origin that it was more likely to move into an adjacent state as opposed to skipping a state before being recaptured.

Comparison across Seasons

Movement probability within states ranged from 0.64 to 0.98 across seasons (Table 2.77). We could not discern patterns of upstream or downstream movement across seasons (Figure 2.4), where upstream and downstream movement transitions were estimated typically less than 0.15. Upstream movement past the St. Andrews Lock and Dam was the lowest movement estimate across all seasons. Survival (ϕ) estimates ranged from 0.54 to 0.97. Lake Winnipeg (ϕ_D) had the greatest survival estimates for spring, fall, and winter while Upper Red River (ϕ_B) typically had the lowest survival estimates, except during fall when survival dropped to 0.54 in the USA Movement from the USA to the Upper Red River (ψ_{AB}) was greater than movement from the USA (ψ_{BA}) during spring, fall, and winter. Capture (p) probability estimates varied greatly across seasons. Lake Winnipeg had the greatest capture probability estimates for all seasons except winter and USA had the lowest capture estimates for all seasons. Omega parameter estimates ranged from 0.04 to 0.96 with summer and fall having greater probability of skipping to occur than spring and winter.

Physical Characteristics

Length was the best predictor of total distance moved (F(1,105)) = 7.332, p < .008, r^2 = .065, where larger fish moved greater distances (Figure 2.5) (Figure 2.6). For example, a 550 mm individual would likely travel a total distance of ~22 km while a 900 mm individual would likely travel a total distance of ~22 km while a 900 mm individual would likely travel a total distance of ~89 km. Weight was also correlated to total movement distance, but its p-value was less significant than length as a predictor. Neither length or weight explained much of the variation observed suggesting other variables need to be investigated to explain relations to movement distance. We found no correlation for sex, surgery time, surgeon, weight, or

relative weight (Figure 2.7, Figure 2.8). The relation between total movement distance and relative weight was not significant (p < 0.362) (*Figure 2.8. Scatter diagram of the natural logarithm of total movement distance ln(km) and relative weight (Wr) Red River of the North channel catfish tracked with acoustic telemetry*. Figure 2.8). The movement distance as a response to total length was also modeled for the T-bar data and showed a similar relationship to the telemetry movement distance (Figure 2.9).

Discussion

Our study demonstrated that Red River channel catfish mobility is conducted at regional scales as well as smaller localized scales. Investigating mobility with telemetry and mark-recapture information, as well as integrating these tagging methods into BSSMs allowed us to characterize different perspectives on channel catfish spatial behavior. The BSSM results demonstrated that Channel Catfish tended to exhibit state specific fidelity (remaining within the state in which they were originally tagged) more than moving among geographic states. The size of the geographic states for the BSSMs spanned from 45 river km to over 360 river km in length so state-specific fidelity is an indication of regional scale movement. Basin-wide recaptures were observed frequently with T-bar individuals reaffirming the reports of basin-wide movements documented by Hegrenes (1992) and Siddons et al. (2017). Long-distance movement activity was not restricted to lotic ecosystems; some of the farthest movements that were observed in fish tracked with telemetry occurred in Lake Winnipeg. We noted more localized movement behavior when mark-recapture results showed that no movement was the most prevalent direction observed for over half of our T-bar marking locations and that total distance moved for each tagging method revealed that mean and median distances were often much smaller than the lengths of the geographic states individuals inhabited. Additionally, median days at large for T-bar fish was approximately yearlong while the corresponding median total distance moved for T-bar fish was only 7.8 km. Low r² for both the telemetry and T-bar physical characteristic models indicate other variables besides physical characteristics are influencing total movement distance. The maximum movement distances of over 1000 km calculated for telemetry fish seems unrealistic. We consider those values as overestimates due to double detection errors that could not be completely identified and processed during data analyses.

Channel catfish in the Red River are long-lived and slow growing in respect to other channel catfish populations making larger fish more susceptible to overharvest in the presence of high fishing mortality (Hubert et al. 1999; Siddons et al. 2016). Larger individuals with longer movement distances suggest any movement between different geopolitical areas such as international boundaries (USA, Canada) or ecosystems (Red River, Lake Winnipeg) may influence population dynamics throughout the basin. Comprehensive model results estimated a very low probability of fishing mortality (0.001) for all states which is to be expected with the current management regime of a primarily catch and release fishery in Canada and conservative harvest regulations in the USA However, larger fish moving throughout the system could be detrimental to the population if individuals encounter regions with higher susceptibility to harvest. Specifically, larger female channel catfish tend to have greater fecundity than smaller individuals and the harvest of these fish could influence recruitment at regional scales (Hubert et al. 1999). Lake Winnipeg and the USA are the only two regions of the study area where large channel

catfish can be legally harvested either from commercial fishing (Lake Winnipeg) or recreational fishing (USA). Based on our BSSMs, telemetry results, and T-bar results the introduction of a Lake Winnipeg commercial fishery on channel catfish would likely increase fishing mortality in the Lake and affect mobile individuals from the lower Red River and Winnipeg River. We also noted that the recapture rate in the USA accounted for roughly a third of recaptures suggesting any changes in exploitation there could also affect canadian river reaches. The comprehensive BSSM estimated natural mortality at 0.16 system-wide, but it is hard to provide context for this estimate since natural mortality is seldom estimated for channel catfish (Hubert et al. 1999). Total mortality (natural mortality plus fishing mortality) of our study is on the lower end of annual mortality reported in Hubert et al. (1999) which ranged from 0.13 to 0.88. Additionally, our mortality estimate was lower than the mortality estimate, 0.19, in Siddons et al. (2016). Our higher survival estimate could be due to the integration of telemetry data, which provides greater recapture probability than the mark-recapture method. Comparison of T-bar, telemetry, and seasonal models suggest survival is similar between countries.

The tendency of larger fish to move farther distances would also suggest those individuals can move into other states and would be more likely to encounter more physical barriers than a smaller individual would. St. Andrew's Lock and Dam is the largest barrier to movement and potential migrations for fish in the Red River, but based on the comprehensive model, both upstream and downstream movement probabilities of channel catfish were similar to the undammed portion of the Red River (Upper Red River to the USA). Our findings suggest that upstream and downstream movement across the dam is not likely prohibited for the majority of the adult channel catfish population, though increased energy expenditure for fish to cross barriers and exposure to avian predators in the fish ladder may increase stress. Siddons et al. (2017) also reported that St. Andrew's Dam may be a partial barrier to channel catfish with a bias towards smaller individuals. An alternative reason for observed channel catfish concentrations below dams may be the increased food availability beneath dams (Santucci et al. 2005). High concentrations of channel catfish may cause increased intra-specific competition and natural mortality (Larkin 1956). The density of channel catfish may also be a driver of movement distance because T-bar tagged individuals were more commonly observed moving between states than telemetry individuals and T-bar tagging was primarily conducted near the St. Andrew's Lock and Dam area. Mahoney (1982) observed movement that was driven by spontaneous, density-dependent events, rather than discrete subpopulations on the Missouri River and some Nebraska tributaries. Density-dependent driven movement may be a means to avoid cannibalism and seek out areas with less intraspecific competition. At least for St. Andrew's Dam, there are three opportunities for channel catfish to move upstream or downstream: 1) the St. Andrew's Lock and Dam fish ladder, 2) the locks when they are in operation, or 3) the Winnipeg Floodway during flood conditions. Though not assessed quantitatively, channel catfish have been commonly observed using each of these mechanisms. Low-head dams in the USA have also been reported to restrict channel catfish movements in the Red River except during high water events (Wendel and Kelsch 1999). Similar findings have been reported in other systems (Welker 1967; Gerhardt and Hubert 1991; Butler and Wahl 2011). The removal of some low head dams on the USA portions of the Red River has been associated with new upstream occurrences of channel catfish (Aadland et al. 2005), but is unclear whether the occurrences are size specific. Our study documented recapture locations of T-bar tagged

individuals that moved upstream past multiple low-head dams in some instances likely due to the recent modifications to low head dams on the Red River to facilitate fish movement.

Channel catfish are one of the top predators in the Red River system. Density and mobility of these predators likely have strong interactions with community dynamics. Wendel and Kelsch (1999) observed greater movement activity during high water events for Red River channel catfish. Additionally, life history stage and season have been identified as variables influencing movement in other channel catfish populations (Hubert et al. 1999; Spurgeon et al. 2018). Channel catfish have been known to overwinter in deep reaches of rivers and lay dormant during winter months (Newcomb 1989), so we expected channel catfish in this system to have a stronger tendency to move in response to seasons given the latitudinal position of the system and thermal tolerance of the species. Interestingly, the movement to find overwintering and spawning habitat was not apparent from the seasonal model results but our telemetry data was limited to only a single year. The homogenous habitat characteristics of the Red River may serve to fulfill both overwintering and spawning requirements resulting in less dramatic movements between ecosystems and tributaries (Butler and Wahl 2011). Previous studies in lotic systems have reported contrasting seasonal movement behaviours for channel catfish, some have shown seasonal migration (Dames et al. 1989; MacDonald 1990; Chapman 1995; Pellett et al. 1998) while others have shown limited movement and no migratory behavior (Harrison 1953; Muncy 1957; Mayhew 1971). We could not adequately assess if the channel catfish in this study exhibited migration based on the geographic states we employed for the BSSM. Climatic driven movement, foraging driven movement, and reproduction driven movement were not evaluated

in this study but are all possible drivers of channel catfish among ecosystems (Van Eeckhout 1974).

The Red River of the North channel catfish conducted movements at regional and localized scales. Nearly half of tagged fish were observed in the river reaches they were collected in while upstream and downstream movement varied by tag type and tagging location. Channel catfish were observed moving outside of their respective reaches and traversing reaches in different countries or new ecosystems (river to the lake) and were capable of moving past low-head dams and St. Andrew's Lock and Dam. Channel catfish were also observed moving from one major river system to another (Winnipeg River to Red River). Existing fisheries management regulations for Red River channel catfish seem to be supporting overall low mortality for the trophy fishery. Marginally different harvest limits for recreational fishing regulations between the USA and Canada show similar survival though some seasonal exceptions were identified. The possibility of changing existing fisheries management regulations (e.g., targeted commercial fishing) has the potential to generate spatially explicit consequences directed at ecosystems, river basins, and geopolitical boundaries. The importance of considering the spatial ecology of a harvested species cannot be understated. The spatial understanding of channel catfish behavior varies depending on the method one applies. Our study utilized information from telemetry, mark-recapture, and comprehensive modeling to characterize channel catfish behavior. Each perspective provides opportunities to explore the variability of how movement is interpreted but also sets the stage for future research to see how these perspectives translate to management strategies. The longevity and movement characteristics for the channel catfish has direct implications with the sustainability of the fishery for both commercial and recreational

users. The harvesting of mature female catfish, in particular, can result in changes to the Red River and Lake Winnipeg ecosystems if the overall population of this apex predator is overexploited. The possibility of changing the ecosystem and its associated ecosystem services poses new questions regarding the management goals of recreational and commercial fisheries throughout the system. Designing management schemes to optimize the access and usage of this mobile fishery will ultimately determine whether the fishery maintains its trophy status in the future. How channel catfish populations are exploited inevitably shapes how the fishery will provide ecosystem services at varying spatial scales. Incorporating the spatial ecological information of channel catfish into fisheries management strategies is the first step in managing for ecosystem-scale implications of a mobile, long-lived species. Additionally, recognizing the biases associated to one's method for investigating spatial behavior (e.g., mark-recapture, telemetry) is necessary to characterize the complexity of a species' movement patterns at different spatial and temporal scales. Freshwater species and their spatial interactions with geopolitics, anthropogenic structures, or ecosystems will require fish managers to establish movement investigations as a basis for evidence-based stock management.

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Equations

Equation 2.1. Bayesian state-space model formulation of the multi-state Cormack-Jolly-Seber model used for T-bar and telemetry approaches. Where Ω_h is the hth row of the state-transition matrix Ω and θ_h is the hth row of the observation matrix θ . Subscripts t and i represent occasion and individual respectively. Z represents the latent state and Y represents the observed state.

 $\begin{aligned} Z_{i,t+1} | Z_{i,t} &= h \sim categorical(\Omega_h) \\ Y_{i,t} | Z_{i,t} &= h \sim categorical(\Theta_h) \end{aligned}$

Equation 2.2. State transition matrix and observation matrix for the T-bar tag Multi-State Cormack Jolly Seber Models. P represents capture probability, Omega (ω) represents state skipping, Phi (φ) represents survival, and Psi (ψ) represents movement probabilities. Subscripts designate geographic states in the Red River of the North Basin.

$$\Omega = \begin{bmatrix}
\phi_A (1 - \psi_{AB}) & \phi_A \cdot \psi_{AB} \cdot \omega & \phi_A \cdot \psi_{AB} \cdot (1 - \omega) \cdot \omega & \phi_A \cdot \psi_{AB} \cdot (1 - \omega) \cdot (1 - \omega) & 1 - \phi_A \\
\phi_B \cdot \psi_{BA} & \phi_B \cdot (1 - \psi_{BA} - \psi_{BC}) & \phi_B \cdot \psi_{BC} \cdot \omega & \phi_B \cdot \psi_{BC} \cdot (1 - \omega) & 1 - \phi_B \\
\phi_C \cdot \psi_{CB} \cdot (1 - \omega) & \phi_C \cdot \psi_{CB} \cdot \omega & \phi_C \cdot (1 - \psi_{CB} - \psi_{CD}) & \phi_C \cdot \psi_{CD} & 1 - \phi_C \\
\phi_D \cdot \psi_{CD} \cdot (1 - \omega) \cdot (1 - \omega) & \phi_D \cdot \psi_{CD} \cdot (1 - \omega) \cdot \omega & \phi_D \cdot \psi_{CD} \cdot \omega & \phi_D \cdot (1 - \psi_{DC}) & 1 - \phi_D \\
0 & 0 & 0 & 1
\end{bmatrix}$$

$$\Theta = \begin{bmatrix} p_A & 0 & 0 & 0 & 1 - p_A \\ 0 & p_B & 0 & 0 & 1 - p_B \\ 0 & 0 & p_C & 0 & 1 - p_C \\ 0 & 0 & 0 & p_D & 1 - p_D \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

Equation 2.3. State transition matrix and observation matrix for the telemetry multi-state Cormack Jolly Seber Models. P represents capture probability, Phi (ϕ) represents survival and Psi (ψ) represents movement probabilities. Subscripts designate geographic states in the Red River of the North Basin.

$$\Omega = \begin{bmatrix}
\phi_A (1 - \psi_{AB}) & \phi_A \cdot \psi_{AB} & 0 & 0 & 1 - \phi_A \\
\phi_B \cdot \psi_{BA} & \phi_B \cdot (1 - \psi_{BA} - \psi_{BC}) & \phi_B \cdot \psi_{BC} & 0 & 1 - \phi_B \\
0 & \phi_C \cdot \psi_{CB} & \phi_C \cdot (1 - \psi_{CB} - \psi_{CD}) & \phi_C \cdot \psi_{CD} & 1 - \phi_C \\
0 & 0 & \phi_D \cdot \psi_{CD} & \phi_D \cdot (1 - \psi_{DC}) & 1 - \phi_D \\
0 & 0 & 0 & 0 & 1
\end{bmatrix}$$

$$\Theta = \begin{bmatrix}
p_A & 0 & 0 & 0 & 1 - p_A \\
0 & p_B & 0 & 0 & 1 - p_B \\
0 & 0 & p_C & 0 & 1 - p_D \\
0 & 0 & 0 & 0 & 1
\end{bmatrix}$$

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Equation 2.4. State transition matrix and observation matrix for the Comprehensive model that included both T-bar tag and Telemetry data into the Multi-State Cormack Jolly Seber Model. P represents capture probability, Omega (ω) represents state skipping, F represents fishing mortality, M represents natural mortality, and Psi represents movement probabilities. Subscripts designate geographic states in the Red River of the North Basin.

$$\Omega = \begin{bmatrix}
\phi_A (1 - \psi_{AB}) & \phi_A \cdot \psi_{AB} \cdot \omega & \phi_A \cdot \psi_{AB} \cdot (1 - \omega) \cdot \omega & \phi_A \cdot \psi_{AB} \cdot (1 - \omega) \cdot (1 - \omega) & M \cdot (1 - \phi)/Z & F \cdot (1 - \phi)/Z \\
\phi_B \cdot \psi_{BA} & \phi_B \cdot (1 - \psi_{BA} - \psi_{BC}) & \phi_B \cdot \psi_{BC} \cdot \omega & \phi_B \cdot \psi_{BC} \cdot (1 - \omega) & M \cdot (1 - \phi)/Z & F \cdot (1 - \phi)/Z \\
\phi_C \cdot \psi_{CB} \cdot (1 - \omega) & \phi_C \cdot \psi_{CB} \cdot \omega & \phi_C \cdot (1 - \psi_{CB} - \psi_{CD}) & \phi_C \cdot \psi_{CD} & M \cdot (1 - \phi)/Z & F \cdot (1 - \phi)/Z \\
\phi_D \cdot \psi_{CD} \cdot (1 - \omega) \cdot (1 - \omega) & \phi_D \cdot \psi_{CD} \cdot (1 - \omega) \cdot \omega & \phi_D \cdot \psi_{CD} \cdot \omega & \phi_D \cdot (1 - \psi_{DC}) & M \cdot (1 - \phi)/Z & F \cdot (1 - \phi)/Z \\
0 & 0 & 0 & 0 & 1 & 0 \\
0 & 0 & 0 & 0 & 1
\end{bmatrix}$$

$$\boldsymbol{\theta} = \begin{bmatrix} p_A & 0 & 0 & 0 & 1 - p_A & 0 \\ 0 & p_B & 0 & 0 & 1 - p_B & 0 \\ 0 & 0 & p_C & 0 & 1 - p_C & 0 \\ 0 & 0 & 0 & p_D & 1 - p_D & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

Tables

Table 2.1. Comparison of direction of movement, days at large, and movement distance (km) for channel catfish tagged in the Red River of the North and Lake Winnipeg system with either T-bar mark-recapture tags or acoustic transmitters.

Tag	Direction of Move	Direction of Movement			Distance (km)
			Mean	187	137.2
	Upstream	4 (3%)	Standard Error	15	23.0
Telemetry	No Movement	44 (38%)	Median	126	38.8
	Downstream	63 (54%)	Minimum	1	0.7
	NA	6 (5%)	Maximum	502	1988.5
			Mean	451	66.0
	Upstream	342 (33%)	Standard Error	12	3.1
T-Bar	No Movement	606 (58%)	Median	363	7.8
	Downstream	75 (7%)	Minimum	0	0.0
	NA	28 (3%)	Maximum	1811	380.5

Table 2.2. Comparison of mark location to recapture location for channel catfish tagged in the Red River of the North and Lake Winnipeg system with T-bar mark-recapture tags.

		Recapture Location									
Mark Location	n	Selkirk, MB to Lockport, MB	Netley Marsh	Winnipeg	Emerson	Lake Winnipeg	Winnipeg River	U.S.A.	Assiniboine River	Not Reported	Total Recaptures
Selkirk, MB to Lockport, MB	9129	474 (64%)	29 (4%)	9 (1%)	5 (1%)	17 (2%)	0 (0%)	182 (24%)	5 (1%)	24 (3%)	745 (100%)
Netley Marsh	3365	51 (64%)	6 (8%)	0 (0%)	0 (0%)	10 (13%)	0 (0%)	13 (16%)	0 (0%)	0 (0%)	80 (100%)
Winnipeg	1594	10 (8%)	0 (0%)	49 (40%)	2 (2%)	1 (1%)	0 (0%)	57 (46%)	0 (0%)	4 (3%)	123 (100%)
Emerson	1045	2 (4%)	0 (0%)	2 (4%)	21 (47%)	1 (2%)	0 (0%)	17 (38%)	2 (4%)	0 (0%)	45 (100%)
U.S.A.	524	0 (0%)	0 (0%)	1 (2%)	0 (0%)	0 (0%)	0 (0%)	49 (98%)	0 (0%)	0 (0%)	50 (100%)
Lake Winnipeg	165	0 (0%)	1 (14%)	0 (0%)	0 (0%)	6 (86%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	7 (100%)
Winnipeg River	27	0 (0%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)	1 (100%)	0 (0%)	0 (0%)	0 (0%)	1 (100%)
Total	15849	537	36	61	28	35	1	318	7	28	1051

Table 2.3 Comparison of movement direction among mark locations for channel catfish tagged in the Red River of the North and Lake Winnipeg

system with T-bar mark-recapture tags. Direction of movement was assessed relative to mark location.

	Movement Direction of Recaptures			Days at Large					
Mark Location	Upstream	No Movement	Downstream	Not Reported	Mean	Standard Error	Median	Minimum	n Maximum
Selkirk, MB to Lockport, MB	201 (27%)	474 (64%)	46 (6%)	24 (3%)	461.04	14.11	360	0	1794
Netley Marsh	64 (80%)	6 (8%)	10 (13%)	0 (0%)	498.74	44.89	386	4	1811
Winnipeg	59 (48%)	49 (40%)	11 (9%)	4 (3%)	457.10	33.28	369	0	1173
Emerson	17 (38%)	21 (47%)	7 (16%)	0 (0%)	479.78	59.03	390	1	1180
U.S.A.	0 (0%)	49 (98%)	1 (2%)	0 (0%)	193.80	32.60	73	0	822
Lake Winnipeg	1 (14%)	6 (86%)	0 (0%)	0 (0%)	491.83	126.00	363	0	1109
Winnipeg River	0 (0%)	1 (100%)	0 (0%)	0 (0%)	69	-	-	-	-

Table 2.4. Comparison of tagging location to detection location for channel catfish tagged in the Red River of the North and Lake Winnipeg system with acoustic transmitters. The definitions for the abbreviated detected locations are as follows LRR = Lower Red River, URR = Upper Red River, LWP = Lake Winnipeg, WR = Winnipeg River, ASN = Assiniboine River, USA = United States of America portion of Red River, NA = Not available.

Detected	Upper Red	Lower Red	Winnipeg
Location	River (n = 22)	River (n = 64)	River (n = 30)
LRR	6 (27%)	28 (44%)	0 (0%)
URR	12 (55%)	0 (0%)	0 (0%)
LWP	0 (0%)	26 (41%)	20 (67%)
WR	0 (0%)	5 (8%)	10 (33%)
ASN	1 (5%)	0 (0%)	0 (0%)
USA	2 (9%)	0 (0%)	0 (0%)
NA	1 (5%)	5 (8%)	0 (0%)
UVP WR ASN USA NA	0 (0%) 0 (0%) 1 (5%) 2 (9%) 1 (5%)	26 (41%) 5 (8%) 0 (0%) 0 (0%) 5 (8%)	20 (37%) 10 (33%) 0 (0%) 0 (0%) 0 (0%)

Table 2.5. Comparison of posterior means and 95% Highest Posterior Density Intervals (HPDI) of both T-bar tag and Telemetry Bayesian state-space Multi-State Cormack Jolly Seber Models. Omega (ω) represents state skipping, P represents capture probability, Phi (φ) represents survival, and Psi (ψ) represents movement probabilities. Subscripts designate geographic states in the Red River of the North Basin.

	T	elemetry	٦	T-bar			
	Posterio	r	Posterior				
Parameter	Mean	95% HPDI	Mean	95% HPDI			
ω	0	0	0.658	0.04-0.978			
<i>p</i> _A	0.075	0.001-0.186	0.012	0.003-0.031			
p_B	0.856	0.68-1	0.003	0.001-0.006			
<i>p</i> _C	0.462	0.393-0.534	0.007	0.003-0.014			
p _D	0.932	0.883-0.976	0.000	0-0.001			
ϕ_A	0.871	0.678-1	0.950	0.839-1			
ϕ_B	0.800	0.668-0.95	0.945	0.86-1			
фc	0.870	0.831-0.905	0.995	0.982-1			
ϕ_D	0.874	0.841-0.909	0.977	0.964-0.998			
ψ_{AB}	0.330	0.096-0.577	0.217	0.097-0.406			
$\psi_{AA} = 1 - \psi_{AB}$	0.670	0.423-0.904	0.783	0.594-0.903			
ψ_{BA}	0.194	0.053-0.361	0.158	0.018-0.395			
ψ_{BC}	0.092	0.022-0.169	0.121	0-0.555			
ψ_{BB}	0.714	0.547-0.88	0.721	0.319-0.944			
ψ_{CB}	0.004	0-0.011	0.089	0.012-0.394			
ψ_{CD}	0.141	0.102-0.183	0.228	0.046-0.536			
ψ_{cc}	0.856	0.814-0.896	0.683	0.409-0.901			
ψ_{DC}	0.064	0.03-0.098	0.187	0.001-0.805			
$\psi_{DD} = 1 - \psi_{DC}$	0.936	0.902-0.970	0.813	0.195-0.999			
Table 2.6. Posterior means and 95% Highest Posterior Density Intervals (HPDI) of comprehensive (combined T-bar tag and Telemetry data) Bayesian state-space Multi-State Cormack Jolly Seber Model. Omega (ω) represents state skipping, P represents capture probability, F represents fishing mortality, M represents natural mortality, and Psi represents movement probabilities. Subscripts designate geographic states in the Red River of the North Basin.

		Posterior	
Parameter	r	Mean	95% HPDI
ω		0.419	0.321-0.518
р		0.016	0.015-0.017
F		0.001	0.001-0.001
М		0.158	0.148-0.168
ψΑΒ		0.026	0.013-0.042
ψΑΑ	= 1- ψΑΒ	0.974	0.958-0.987
ψBA		0.096	0.068-0.125
ψВС		0.017	0.006-0.028
ψВВ		0.887	0.858-0.915
ψСВ		0.041	0.034-0.047
ψCD		0.014	0.01-0.019
ψCC		0.946	0.938-0.953
ψDC		0.050	0.025-0.077
ψDD	= 1- ψDC	0.950	0.923-0.975

Table 2.7. Comparison of posterior means and 95% Highest Posterior Density Intervals (HPDI) of seasonal variations in telemetry Bayesian state-space Multi-State Cormack Jolly Seber Models. Omega (ω) represents state skipping, P represents capture probability, Phi (ϕ) represents survival, and Psi (ψ) represents movement probabilities. Subscripts designate geographic states in the Red River of the North Basin.

		Spring (n = 47)		Summ	Summer (n = 151)		Fall (n = 68)		Winter (n = 38)	
		Posterio	r	Posterior		Posterior		Posterior		
Paramete	r	Mean	95% HPDI	Mean	95% HPDI	Mean	95% HPDI	Mean	95% HPDI	
ω		0.065	0.01-0.135	0.960	0.87-1	0.863	0.555-1	0.037	0.001-0.09	
pА		0.014	0-0.041	0.029	0-0.069	0.480	0.026-0.957	0.014	0-0.043	
рВ		0.475	0.192-0.761	0.923	0.779-1	0.562	0.353-0.757	0.826	0.615-0.993	
рС		0.783	0.636-0.936	0.588	0.537-0.64	0.650	0.566-0.731	0.952	0.862-1	
рD		0.950	0.907-1	0.958	0.929-0.985	0.945	0.921-0.968	0.937	0.89-0.983	
φA		0.942	0.853-1	0.941	0.846-1	0.543	0.13-0.966	0.938	0.851-1	
φВ		0.818	0.625-1	0.888	0.784-1	0.862	0.739-0.982	0.842	0.66-1	
φC		0.904	0.813-0.988	0.915	0.889-0.94	0.919	0.876-0.958	0.904	0.79-1	
φD		0.981	0.956-1	0.891	0.855-0.925	0.969	0.95-0.985	0.966	0.932-1	
ψΑΒ		0.274	0.114-0.445	0.254	0.107-0.408	0.342	0-0.78	0.180	0.055-0.317	
ψΑΑ	= 1- ψΑΒ	0.726	0.555-0.886	0.746	0.592-0.893	0.658	0.22-1	0.820	0.683-0.945	
ψBA		0.097	0-0.278	0.321	0.184-0.47	0.053	0-0.176	0.092	0-0.251	
ψВС		0.131	0.005-0.299	0.040	0.003-0.084	0.058	0.002-0.133	0.129	0.006-0.293	
ψВВ		0.772	0.545-0.97	0.639	0.488-0.774	0.889	0.75-0.99	0.779	0.575-0.966	
ψСВ		0.042	0-0.126	0.003	0-0.008	0.008	0-0.022	0.057	0-0.153	
ψCD		0.108	0.03-0.198	0.061	0.039-0.084	0.063	0.028-0.099	0.137	0.026-0.258	
ψCC		0.850	0.727-0.953	0.937	0.914-0.96	0.929	0.889-0.965	0.806	0.665-0.944	
ψDC		0.104	0.053-0.157	0.048	0.024-0.076	0.025	0.01-0.042	0.085	0.034-0.138	
ψDD	= 1- ψDC	0.896	0.843-0.947	0.952	0.924-0.976	0.975	0.958-0.99	0.915	0.862-0.966	

Table 2.8. Comparison of Akaike's information criterion for physical characteristics and total movement distance (TMD) candidate models. K is the number of parameters estimated, AICc is the corrected Akaike's Information Criterion, Δ AICc is the difference between the model AICc and the lowest AICc among the models, AICcWt is the Akaike weights, Cum.Wt is the cumulative Akaike weight, and LL is the likelihood ratio of the model against the best model.

Model	K AICc	ΔAICc	AICcWt	: Cum.	Wt LL
log(TMD) ~ TotalLength_mm,	3 446.30	0.04	0.21	0.43	-220.03
log(TMD) ~ Weight_g,	3 446.26	0.00	0.22	0.22	-220.01
log(TMD) ~ TotalLength_mm * Sex,	5 449.14	2.87	0.05	0.82	-219.27
log(TMD) ~ TotalLength_mm + Weight_g,	4 448.35	2.09	0.08	0.76	-219.98
log(TMD) ~ Weight_g * Sex,	5 449.24	2.98	0.05	0.86	-219.32
log(TMD) ~ TotalLength_mm + Sex,	4 448.34	2.08	0.08	0.69	-219.98
log(TMD) ~ Weight_g + Sex,	4 448.28	2.02	0.08	0.61	-219.94
log(TMD) ~ Weight_g + TotalLength_mm * Sex,	6 451.32	5.06	0.02	0.98	-219.24
log(TMD) ~ TotalLength_mm + Weight_g * Sex,	6 451.39	5.12	0.02	1.00	-219.27
log(TMD) ~ TotalLength_mm * Weight_g,	5 450.40	4.14	0.03	0.94	-219.90
log(TMD) ~ TotalLength_mm + Weight_g + Sex,	5 450.43	4.17	0.03	0.97	-219.92
log(TMD) ~ 1,	2 447.73	1.46	0.10	0.53	-221.81
log(TMD) ~ Wr	3 449.32	3.06	0.05	0.91	-221.54

Figures



Figure 2.1. Study area with red line indicating Red River of the North. Geographic states are represented in black brackets and acoustic receiver locations are shown in white circles. Orange rectangle indicates St. Andrew's Lock and Dam. Only major tributaries that contained receivers are shown. Numbered boxes identify points of interest referenced in the text as follows: 1) Netley Marsh, 2) Selkirk, Manitoba, 3) Winnipeg, Manitoba, and 4) Emerson, Manitoba.



Figure 2.2. Mark and recapture locations of channel catfish tagged with T-bar tags from 2012 – 2017 in the Red River of the North system. Inset shows mark and recapture locations of channel catfish from below St. Andrews Lock and Dam downstream to the mouth of the Red River.



Figure 2.3. Examples of groups of channel catfish movement tracked by telemetry in the Red River of the North system. A – Channel catfish staying within geographic state. B – Channel catfish moving downstream past St. Andrew's Lock and Dam Dam. C – Channel catfish moving upstream to USA border. D – Channel Catfish moving across systems from Red River to Lake Winnipeg to Winnipeg River.



Figure 2.4. Arcplot showing the seasonal transition probabilities (ψ) of channel catfish tracked with telemetry within states A-D of the Bayesian state-space model. Lines arcing between states positioned above midline are defined as upstream transitions whereas lines arcing between states positioned below midline are defined as downstream transitions. Arcs that originated and end at the same state are defined as within state transitions. Thickness of the lines represent probability of transition, where thicker lines represent greater probabilities and thinner lines represent lower probabilities.



Figure 2.5. Scatter diagram of total length and natural log transformation of total movement distance of Red River of the North channel catfish tracked with acoustic telemetry. The straight line and confidence interval band represents the correlation between the natural logarithm of total movement distance ln(km) and total length (mm).



Figure 2.6. Scatter diagram of total length and total movement distance of Red River of the North channel catfish tracked with acoustic telemetry. The curved line is the backtransfomed correlation shown in Figure 5. The line represents the correlation between total movement distance (km) and total length (mm).



Figure 2.7. Comparison of surgeon linear regression model lines for the natural logarithm of total movement distance ln(km) and surgery times (s) Red River of the North channel catfish tracked with acoustic telemetry. Surgeon 2 only had one data point so was not included in the model.



Figure 2.8. Scatter diagram of the natural logarithm of total movement distance ln(km) and relative weight (Wr) Red River of the North channel catfish tracked with acoustic telemetry.



Figure 2.9. Scatter diagram of total length and total movement distance of Red River of the North channel catfish tagged with T-bar tags. The straight line represents the correlation between total movement distance (km) and total length (mm).

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CHAPTER 3 COMPETING INTERESTS FOR ECOSYSTEM SERVICE FLOWS: SIMULATING MANAGEMENT SCENARIOS FOR CONNECTED INLAND FISHERIES

Henry Hansen

Abstract

1. Conflicts in mixed-use fisheries can arise when competing interest groups (e.g., commercial fishing, recreational fishing) target the same fish populations for provisioning services. How provisioning services of exploited fish populations are distributed among interest groups can be characterized as ecosystem service flows (ESF), where ESFs of a fishery are a function of the mobility of the targeted population, spatial distribution of the fishers, and the intensity of the fishing.

2. Informing fisheries management with ESF components is a promising way to develop appropriate policy for mixed-use fisheries but is challenging to incorporate for two reasons. First, fish movement studies used to assess the spatial characteristics of the fishery can vary by methodology (e.g., mark-recapture, telemetry), affecting the understanding of fish mobility and thus ESF. Secondly, the economic valuation of the provisioning services and the methodology used to assess value varies by interest group and by the size of the fish harvested.

3. We modeled the interaction of hypothetical exploitation scenarios and alternative movement methodologies for a long-lived, mobile fish species by using stage-structured Leslie matrix models. Our study organism, channel catfish *lctalurus punctatus*, is a trophy sportfish in the Red River of the North, but also a species of commercial interest in Lake Winnipeg. The study system is composed of three different fishery types, a USA recreational fishery, a Canada recreational fishery, and a Canada commercial fishery that all utilize the channel catfish population for provisioning services. 4. Trophy stages of channel catfish were highly sensitive to exploitation and were typically depleted at or below a 0.30 exploitation rate. Depletion of populations and changes in stock structure affected subregions within the Red River system differently which resulted in competing strategies for each fishery from the perspective of economic valuation of harvests.
5. We found that recruitment from areas with greatest population size appeared to buffer aspects of harvest within regions and to some extent immediately adjacent regions. Movement, regardless of methodology, was critical in supporting exploitation for regions with low recruitment. The sustainability of exploiting highly mobile fish species from an ecosystem service flow perspective hinges on the ability of fisheries management organizations to incorporate spatial variability and understand the economic consequences of exploitation for competing interests.

Introduction

The science of ecosystem services is starting to embrace the concept that such services are not always bound to a single location (site-bound) (Costanza et al. 1997), but instead can flow and disperse (Bagstad et al. 2013). Burkhard et al. (2014) described ecosystem service flows as the spatially explicit routing of an ecosystem service source to beneficiaries. Ecosystem service carriers (e.g., matter, information, energy) are the means to provide benefits from the source locations to the use locations of the ecosystem that allow ecosystem service flows to function (Bagstad et al. 2013). Access to, and contact with, ecosystem service carriers that provide benefit to people are identified as provisioning benefits (Bagstad et al. 2013). Fish biomass has been identified as an "ecosystem service carrier" (Bagstad et al. 2013), but to our knowledge, very few fisheries are managed from an ecosystem service carrier perspective and seldom managed from an ecosystem-based management standpoint (Holmlund and Hammer 1999; Pope et al. 2016). Instead, fisheries, and particularly inland fisheries, are often managed from a "one size fits all" approach that is reactive in design and often does not prioritize sustainability of the fisheries or resilience of the ecosystems (Carpenter and Brock 2004). The challenge associated with ecosystem-based management is that ecosystem service flows are typically derived from, or are a function of, open-access or common pool resources. Common pool services are often vulnerable to the "tragedy of the commons" phenomenon which can have large-scale effects on socio-ecological systems (Abbott and Wilen 2011). The vulnerability of common pool resources is driven by two characteristics: 1) rival, meaning the quantity of service decreases with use, and 2) non-excludable, meaning the resource can be used by anyone (Fisher et al. 2009). Fisheries are an example of a resource that is both rival and non-excludable, where the harvest of the resource depletes its services supplied and access to the fishery is often shared among multiple interest groups (Costello et al. 2008; McWhinnie 2009). Therefore, it is paramount to understand the mechanisms that influence the rival and non-excludable characteristics of inland fisheries, so management from an ecosystem service carrier perspective is more attainable.

Ecosystem service flows are inherently spatial and the spatial scale on which an ecosystem service flow can function influences human-ecosystem interactions at both ecological and geopolitical scales (Hein et al. 2006). The inequity of an ecosystem service flow can introduce competing resource interests and thus generate conflicts (Bullock et al. 2011). Fish species that use large spatial-scales to complete their life histories (e.g. salmon migration) are more routinely being studied from a spatial perspective to inform fisheries and ecosystem

management initiatives but also to mitigate fishery conflicts (Cooke et al. 2013; Donaldson et al. 2014; Young et al. 2018). The provisioning services generated by a fishery encompasses some of the most contentious conflicts between fishing interests (e.g., commercial vs recreational) that can limit long-term sustainability prospects (Pauly et al. 2002; Worm et al. 2009; Spijkers et al. 2018). For example, recreational fishing has been identified as a contributor to declines in fish stocks (Coleman et al. 2004), but usually to a lesser extent than commercial fishing and is generally more localized to inland waters (Cooke and Cowx 2004; Winfield 2016). The variety of conflicts that may arise between the two practices poses challenges for fisheries management organizations when developing policy intended to govern each practice. These challenges may be especially true when each practice has contrasting perspectives on the extent to which harvest is allocated (or whether harvest should occur at all) and how much each practice contributes to the local economy (Arlinghaus and Cooke 2009). Recreational and commercial fisheries typically use fish stocks in a consumptive manner where catch, harvest, or both can be quantified and then scaled by economic metrics (Pereira and Hansen 2003). Fisheries management organizations now also incorporate valuation methods for commercial and recreational fisheries to bridge the gap of the economic asymmetries seen in mixed-use fisheries. Understanding the spatial extent and intensity of harvest provides fisheries management organizations the foundation to assess fisheries from an economic perspective and an opportunity to enact evidence-based decisions for spatially-explicit policy.

The successful implementation of ecosystem-based management for fisheries depends on understanding the spatial extent of socio-ecological interactions (Pikitch et al. 2004; Katsanevakis et al. 2011; Nunes et al. 2015; Ansong et al. 2017). Management of freshwater fish species may be particularly difficult in ecosystems with competing harvest demands across multiple political jurisdictions (Pracheil et al. 2012). Adoption of biotelemetry methods into fisheries science are revealing more complex spatial behaviors of both marine (Wilson et al. 2015; Torre et al. 2017) and freshwater fish species (Pellett et al. 1998; Pracheil et al. 2009; Hrenchuk et al. 2017) suggesting that management organizations need to incorporate the spatial scale on which a given fish stock's life-history operates (Olsen et al. 2012; Pracheil et al. 2012). Similarly, uncovering how connectivity of inland ecosystems provides movement corridors for different life-stages of fish is critical in understanding fundamental population dynamics (Spurgeon et al. 2018). There are very few examples of fisheries management that have examined the nexus of mixed-use fisheries using both spatial ecological information and valuation approaches (Abbott 2014). Furthermore, exploration of alternative management approaches from an ecosystem-service flow perspective of inland fisheries are also absent in the literature, but some marine fisheries examples exist (Martin et al. 2016; Owuor et al. 2017). Exploring how one's understanding of movement can influence the outcomes associated with fisheries management scenarios is critical in informing fisheries policy.

The Red River of the North-Lake Winnipeg system (Minnesota and North Dakota, United States of America; Manitoba, Canada) is one inland system that holds a fish species (channel catfish *lctalurus punctatus*) that exhibits large-scale spatial movements and is included in a mixed-use fishery. We set out to incorporate a comprehensive evaluation of alternative management approaches for an ecosystem service flow perspective using channel catfish that may be subjected to varying management regimes depending on their specific location within the system. The goal of this study was to present an assessment of the channel catfish fishery concerning movement, exploitation, and valuation as a means to initiate understanding the implications of potential fisheries management scenarios. We specifically asked: 1) how do different movement methodologies interact with exploitation to affect the allocation of ecosystem service flows (status quo evaluation), 2) what are the regional impacts of exploitation on stock structure, especially the trophy portion of the ecosystem service flow, 3) how does a long-lived, slow-growing fish species respond to varying amounts of exploitation from a population perspective, and 4) what are the economic outcomes associated with these impacts for a mixed-use fishery? We answered these questions by parameterizing a stage-structured Leslie matrix model to reflect 1) the population dynamics of the species, 2) the geographical subregions and spatial ecology of the species, and 3) potential exploitation scenarios specific to the predefined fishery subregions.

The Case Study

Study Area

Our study area encompassed the Red River of the North and Lake Winnipeg (hereafter RRLW). The Red River of the North (hereafter Red River) flows north approximately 885 km, with 635 km in the United States and 255 km in Canada, then empties into Lake Winnipeg (Fig. 1). Our focal subregions in this study include the Red River in the United States of America (USA) (subregion 1), the Red River in Canada from the border downstream to St. Andrews Lock and Dam (subregion 2), the Red River from St. Andrews Lock and Dam downstream to Lake Winnipeg (subregion 3), and Lake Winnipeg (subregion 4). Each subregion has unique characteristics associated with the movement of channel catfish (Chapter 2) and how the fishery is used. For example, commercial fishing only takes place in Lake Winnipeg, while recreational fishing takes place across all four subregions, albeit under somewhat different management.

Fisheries Management Conflict

A cooperative management effort between the USA and Canada started in 1988 has sustained this international fishery as a trophy population, but has mainly focused on recreational aspects to date. However, two policy issues are emerging for fisheries managers. First, recreational fishing harvest regulations do differ between Canada and the USA leading to questions about whether these differing regulations are mutually beneficial. Current regulations in Canada allow the daily harvest of individuals < 60 cm where possession limits are one catfish for conservation licenses and four for regular fishing licenses; whereas, Minnesota and North Dakota daily harvest regulations limit harvest to five Channel catfish, with only one over 61 cm. Second, there has been substantial interest in further developing the commercial fishery in Lake Winnipeg. Lake Winnipeg has an established commercial fishery for walleye (Sander vitreous), sauger (Sander canadensis), whitefish (Coregonus clupeaformis) and other species (Nicholson 2007); where fishers are allocated biomass quota rather than specific species quotas. Channel catfish have not historically been targeted as a commercial fish because species brought to market had to be sold through the Freshwater Fish Marketing Corporation (FFMC); channel catfish were generally not included in the quota system. However, channel catfish caught by commercial fishers could be harvested and sold at the dock to local fishing communities. Changes in regulation of the Lake Winnipeg commercial fishery in 2017 removed FFMC as the sole wholesale purchaser and distributor of commercial fish products for Manitoba. The current policy now allows individual to apply for and obtain dealer licenses to purchase and distribute

commercial fish products in Manitoba. Recent discussions among commercial fishers have expressed interest in targeting Channel catfish as a commercial species. The implications of these potential regulation changes could have cascading effects on the international usage of this species as a commercial and recreational fish if the potential implications of fish movement are not included in consideration of management regimens. Therefore, understanding the potential source-sink dynamics within and among connected subregions via the interaction of subregion specific exploitation was the basis for incorporating exploitation in our study.

Channel Catfish Biology

Channel catfish in the RRLW system typically have longer long-life spans and move greater distances than other channel catfish populations (Hegrenes 1992; Siddons et al. 2016). Siddons et al. (2016) reported individuals at ages up to 27 years, with ages > 20 being common. Fecundity of a channel catfish increases with age and total length, but populations are variable (Hubert et al. 1999). Fecundity of channel catfish in the Red River is currently unknown, but other populations have reported egg production to range from 1000 − 60,000 eggs per female annually or equivalent to about 15% of the total body weight of a mature female (Hubert et al. 1999). Growth of channel catfish in the Red River system is slow compared to other populations observed in lower latitudes of their distribution; Von Bertalanffy parameter estimates for channel catfish in the lower Red River were L∞= 1161 (95% confidence interval: 1018-1305) and K= 0.061 (95% confidence interval: 0.045-0.077) (Siddons et al. 2016). Very little is known about recruitment and associated density-dependent relationships of stocks and recruits for channel catfish in the Red River system but modeling the implications of recruitment and its dispersal is foundational in determining sink-source dynamics in an exploited system.

Methods

Population Projection Analysis

We created a stage-structured Leslie matrix model (Leslie 1945; Caswell 2001) using the fisheries model for ecosystem services from InVEST modeling software (Sharp et al. 2018). We parameterized aspects of life-history and survival for channel catfish in the Red River system using three age classes (juvenile, mature, and trophy) for female catfish. The InVEST model was designed to incorporate stage-specific movement matrices into the population modelling process at each time step and calculate geographic subregion population sizes and harvest until equilibrium. We modeled fish movement under either the assumption that no movement occurred across subregions (none), or that fish movement was described by 1) a Bayesian state-space model (BSSM), 2) a geographic information systems (GIS) analysis of fish tagged with acoustic transmitters, or 3) a mark-recapture analysis of fish tagged with T-bar tags (MR). We then modeled exploitation (i.e., harvest) scenarios including 1) status quo (as a base comparison), 2) increased harvest in the Lake Winnipeg commercial fishery, 3) increased recreational harvest in the United States, and 4) combined increased harvest for recreational and commercial interests combined (Both).

Input Parameters and Model Optimization

The InVEST model requires stage-specific inputs for survival, vulnerability to fishing, maturity, and duration as well as subregion-specific inputs for survival, exploitation fraction, and larval dispersion (Table 3.1). We populated survival for mature and trophy individuals from estimates derived in the comprehensive Bayesian state-space model (Chapter Two). We populated

juvenile survival from Ricker catch curve rates estimated by Siddons (2015) for channel catfish in the Red River system. We assumed all stages were fully vulnerable to harvest to reflect the system-wide vulnerability. We set juvenile stages as immature where older stages were set to fully mature. We assumed the following total lengths for each stage; juveniles were from 0 to 609 mm, matures were from 610 mm to 914 mm, and trophies were > 914 mm (Hegrenes 1992). Duration of each stage (juvenile = 12.2 years, mature = 13.2 years; trophy = 1.6) was determined by Siddons (2015).

Subregion-specific inputs for survival were constant across subregions because the BSSM approach (Chapter 2) and the Ricker catch curve mortalities from Siddons (2015) estimated natural mortality as constant across the system. We manipulated the fraction of the exploited population in our exploitation scenarios, but for the status quo model, we used the fishing mortality estimate from BSSM (Chapter 2). How and where newly produced recruits distribute spatially is not currently known in the RRLW system. Therefore, we proportionately allocated larval dispersal (allocation of each time step's recruits to subregions) based on population estimates for each subregion of the Red River by Siddons (2015). Larval dispersal was calculated differently for subregions 1 -3 compared to subregion 4 based on the availability of information. Subregions 1 -3 were allocated larval dispersal percentages based on reach length and a population density of < 200mm fish from Siddons (2015). No information on spawning, population densities, or other larval studies have been conducted on Lake Winnipeg, so we assumed the dispersal of larval fish from geographic subregion 3 to geographic subregion 4 would be best represented by extrapolating larval distribution using the movement transition of T-bar tagged fish from subregion 3 to subregion 4 from Siddons (2015). The InVEST model can

incorporate recruitment in four different ways: Beverton-Holt, Ricker, Fecundity, or Fixed Recruitment. We used fixed recruitment because we had insufficient data to infer recruitment using the other methods. However, we iteratively adjusted the recruitment parameter in the status quo, no movement model (the null model) until population estimates from the InVEST Model were within ~5% of estimated population sizes for regions 1, 2, and 3 based on estimated catfish density from Siddons (2015) as a means to at least optimize the estimates reflected from previous population information (Ding et al. 2014). Siddons (2015) subregion estimates for female channel catfish in the Red River are as follows: subregion 1 = 1,891,665, subregion 2 = 1,003,329, and subregion 3 = 2,823,266. We ultimately fixed recruitment at 560000 individuals across the RRLW system for each time step.

Inclusion of movement

Mark-recapture and telemetry are commonly used to investigate movement for inland fisheries management (Bonar et al. 2009; Adams et al. 2012). These techniques have inherent assumptions and bias which may be a confounding factor in determining typical movement behavior and harvest dynamics (Gerking 1959). For example, without knowing the locations and amount of effort performed by recreational anglers, it is difficult to contextualize sampling bias associated with mark-recapture results. Similarly, a sampling of individuals with transmitters may also be biased to more mobile individuals depending on the gear used. Both approaches can inform mortality and movement estimates but have traditionally been implemented individually and seldom modeled together despite demonstrated advantages to combining methods (Pollock et al. 2004; Hightower and Harris 2017). The recent adoption of Bayesian methods has provided a means to employ mark-recapture and telemetry methods in tandem to evaluate movement patterns of fishes with reduced bias (Adams et al. 2012; Cooke et al. 2013). Depending on the methodology one takes to assess fish movement, whether it be markrecapture, telemetry or a comprehensive approach, the understanding of fish movement for the population will likely be different. Here, we had the opportunity to explore how incorporating movements from varying techniques may or may not provide similar information regarding connectedness of a fish population that is known to move large distances. Empirical studies of channel catfish in the RRLW system have used mark-recapture (MR) techniques with T-bar tags, geographic information systems (GIS) techniques with telemetry tags, and a comprehensive approach using Bayesian state space models (BSSM) (Chapter 2, Siddons et al. 2017).

Movement was incorporated into the InVEST model by parameterizing stage-specific migration matrices that reflected sink-source movement of the population across geographic subregions. We utilized four movement methodologies to model alternative perspectives of channel catfish spatial ecology (Table 3.2). The "none" movement perspective assumed movement did not occur between geographic subregions but only occurred within geographic subregions. We included the "none" perspective as a base comparison for the remaining movement methodologies. We derived the BSSM perspective from Chapter 2 where movements within and among geographic subregions were populated from the comprehensive telemetry and T-bar model. We derived the MR perspective from quantifying the proportional number of fish tagged with T-bar tags that moved among geographic subregions. Specifically, we tallied the number of individuals that stayed within each geographic subregion and the number of individuals that moved from each geographic subregion into a new geographic subregion. We calculated the percentages for each specific geographic subregion transition by dividing the number of

individuals observed by the total number of individuals tagged in the study. Like the MR perspective, the GIS perspective utilized similar analysis procedures to identify proportional movements of channel catfish among and within geographic subregions but differed by using individuals marked with telemetry tags. Movement of fish tagged by T-bars was assumed to take the minimum movement distance path from mark location to recapture location and were aggregated to each specific geographic subregion transition to calculate percentages. During population simulations, each perspective was applied to all three life-stages, so movement did not vary by stage because our analyses were limited to population perspective as opposed to the stage-specific resolution.

Modeling of Exploitation Scenarios

Exploitation is defined as the proportion of the population vulnerable to harvest that is harvested (Sharp et al. 2018). Part of our goal was to understand how movement may influence populations should harvest regulations change from the status quo to something more liberal. Therefore, we modeled three specific scenarios to assess the interaction between movement and subregion-specific exploitation. Scenarios were designed to reflect plausible harvest regimes for the subregions in our study area (Table 3.3). We designed a USA recreational fishing scenario for the USA portion of the Red River (subregion 1), commercial fishing scenario for Lake Winnipeg (subregion 4), and a combined exploitation scenario of both commercial and recreational fishing scenarios (subregion 1 and 4) to assess the effect of incremental exploitation of channel catfish in relation to movement methodologies. We modeled increments of exploitation in 10% intervals, starting with 10% and increasing to 100%. We assumed subregions not being specifically evaluated in a given scenario had an experimental exploitation increment the same as the status quo (Table 3).

Applying valuation

We used willingness to pay values for recreationally harvested channel catfish and for mature and trophy population sizes for the recreational fisheries as a proxy to project maximum potential value of each recreational fishery. Valuing the USA and Canada's recreational fishery potential for mature and trophy individuals is a means to gauge the catch and release fishing aspect of a trophy fishery from a recreational angling perspective. Willingness to pay values were based on the length of a single harvested channel catfish and averaged across life stages (Cole 2018). The average willingness to pay value were as follows: \$14.93 (CAD) for a juvenile catfish, \$27.16 (CAD) for a mature catfish, and \$31.80 (CAD) for a trophy channel catfish. Willingness to pay values for recreational catfish change based on the frequency of capture for an angler, but were not modeled for this study. We used estimated sold at Lake Winnipeg dock market prices of \$1.00 (CAD) per kilogram for commercial valuation of harvests. Since, commercial angling operations typically fish without the consideration of catch and release practices but rather fish in whatever capacity maximizes economic return from an allotted quota, valuation of total projected populations where not considered in this study. Average weights used to calculate value for each commercially harvested channel catfish were: 0.743 kg for a juvenile, 5.728 kg for a mature, and 10.627 kg for a trophy individual.

Results

Interaction of movement and status quo exploitation

Model results for the status quo scenario and each movement perspective (Figure 3.2) demonstrate movement influences subregion population sizes. Specifically, movement tended to homogenize subregion population sizes even though recruit dispersal varied greatly among subregions. The null model approximated contemporary population estimates where we had such information so, we have some means to think the other models will reflect some aspect of reality. The Null, BSSM, MR, and GIS models with a status quo exploitation all came to equilibrium at time step 57 and had root mean squared errors (RMSE) as follows: 71,147, 515,116, 1,665,726, and 1,428,875. The models that incorporate movement suggest a connected population where especially Lake Winnipeg (subregion 4) benefits from the connection. Lake Winnipeg had the lowest recruitment for the system, but all movement methodologies projected the Lake Winnipeg population greater than the null movement model. Some specific distinctions among movement models were also identified. The BSSM movement model resulted in a lower subregion 1 population size and a larger subregion 4 population compared to the null movement model. The MR movement model which projected approximately 50% of fish from subregion 2 would move to subregion 1 per time step resulted in USA having the highest subregion population in the system. Conversely, the GIS movement model which projected approximately 50% of fish from subregion 3 would move to subregion 4 per time step resulted in Lake Winnipeg having the highest subregion population in the system.

Effect of movement and exploitation interaction on population size

Increasing exploitation decreased the population of the exploited subregion and had varying effects on abundance in unexploited regions across movement models and exploitation scenarios (e.g., USA, commercial, and both). The population of subregion 1 under the USA exploitation scenario declined exponentially with increasing exploitation and was similar across movement models (Figure 3.3). The associated harvest of subregion 1 tended to reach an asymptote around an exploitation rate of 0.50 across movement models. The inclusion of BSSM, MR, or Null movement models showed a gradual decrease in subregion 2's population and harvest as exploitation in subregion 1 increased. Alternatively, the GIS movement model projected increasing declines in populations across all subregions as follows: subregion 2 declined by 37%, subregion 3 by 14%, and subregion 4 by 18%. The GIS movement model was the only movement perspective to project the population of subregion 4 as the most abundant subregion.

The population in subregion 4 under the commercial exploitation scenario also declined exponentially with increasing exploitation, but the decline was more evident under the GIS movement models (Figure 3.4). The associated harvest of subregion 4 tended to asymptote for all movement models except for the GIS model where the harvest saw an exponential decline at and above a 0.30 exploitation rate. Exploitation of subregion 4 saw slight or no decreases in population levels or harvest across all other subregions.

The Both exploitation scenario showed declines in exploited and unexploited subregion population sizes (Figure 3.5). Exploitation characteristics among exploited subregions were

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similar to the USA and the commercial exploitation scenarios, but exploitation in subregions 2 and 3 tended to reflect the patterns in the USA exploitation scenario rather than the commercial exploitation scenario. Subregion 3 was projected to contain the largest subregion population for the system across all movement models when exploitation increased beyond 0.3.

Effect of movement and exploitation interaction on stock structure

Our models generally showed an increasing exploitation rate decreased the population of the trophy and mature individuals within exploited subregions and shifted prevalence of mature and trophy stages to unexploited subregions. The magnitude of this effect depended on the movement perspective and exploitation scenario. Additionally, the sensitivity of a trophy or mature population decreases depended on the movement perspective and the exploitation scenario. Percent changes do not reflect overall population sizes – just the proportion of mature/trophy fish within the subregion (Figs. 6 - 9).

The no movement models showed declines in mature and trophy fish at low levels of exploitation (0.10 - 0.2) for exploited subregions increased for the Both and USA scenarios (Figure 3.6). Mature stages were slightly less sensitive than the trophy stages to increasing exploitation rate, but both stages experienced almost complete depletion by an exploitation rate of 0.20 in exploited subregions — the commercial scenario projection near 0% mature and trophy individuals at exploitation rates of 0.10. Unexploited subregions remained unaffected among exploitation scenarios with subregion 3 accounting for most of the mature and trophy individuals in the system, which is expected when no movement is occurring between subregions.

The BSSM movement perspective showed that mature and trophy stages also had strong declines as exploitation increased but the exploitation rate for complete depletion of mature stages occurred at an exploitation rate of about 0.50 for the both and commercial exploitation scenarios (Figure 3.7). Trophy stages were still prone to complete depletion by 0.20 demonstrating that trophy stages were still more sensitive to exploitation than the mature stages. The BSSM movement perspective did show a relatively stable trend of mature and trophy proportions among unexploited subregions because exploited subregions did not account for large proportions of the system wide population, especially for the commercial exploitation scenario resulted in subregion 1 containing the most amount of mature and trophy fish instead of subregion 3 reported in the Both and USA exploitation scenarios.

The MR movement perspective showed dramatic shifts in which subregion contained the most mature and trophy stages throughout the system under the Both and USA exploitation scenarios (Figure 3.8). Mature and trophy individuals were less sensitive to exploitation than the BSSM movement models, with full exploitation of matures occurring at 1.0 exploitation and trophy individuals occurring at 0.4. Proportion of mature and trophy individuals in unexploited regions tended to increase at similar rates with subregion 3 being slightly more responsive. Large increases in mature and trophy proportions depended on initial proportion of subregion 1. Low initial proportion of mature and trophy individuals in the commercial scenario resulted in the greatest amount of stability between unexploited subregions for both mature and trophy

stages. The commercial scenario also reported the highest subregion 1 population proportion for mature and trophy individuals (83 – 85%) across all movement and exploitation scenarios.

The GIS movement perspective showed the greatest influence on unexploited subregions for Both and commercial exploitation scenarios (Figure 3.9). Increasing exploitation in subregion 4 resulted in an increasing proportion of mature and trophy stages in unexploited subregions for the Both and Commercial scenarios but resulted in stable conditions of unexploited subregions for the USA scenario. Again, for the Both and Commercial exploitation scenario, mature stages were less sensitive to exploitation than the trophy stages. Complete depletion of mature stages occurred at an exploitation rate near 1.0 while depletion for trophy stages occurred near 0.30. The proportion of mature and trophy stages in subregion 4 was highest in the GIS movement perspective under a USA exploitation scenario in comparison to the none movement, BSSM movement, and MR movement models. Complete depletion of the mature and trophy stages occurred near 0.20 for the USA exploitation scenario.

Effect of movement and exploitation interaction on values of a mixed-use fishery

Valuation among the USA recreational fishery (subregion 1), the Canada recreational fishery (subregions 2 and 3), and the Canada commercial fishery (subregion 4) typically showed that maximum value of mature and trophy stages occurred at low exploitation rates. Juvenile stages typically had near constant economic values across exploitation rates for the USA recreational fishery (Figure 3.10). Movement methodologies had a greater influence on the valuation of stages for the Canada recreational fishery than the other fisheries (Figure 3.11). Value of the commercial fishery peaked with an GIS movement model and either a Commercial or Both

exploitation scenario (Figure 3.12). Economic values were similar between recreational fisheries and the commercial fishery even though different valuation metrics were used. Constant economic values were most prevalent for commercial exploitation scenario for the USA fishery and the USA exploitation scenario for the Canada commercial fishery. The mature stages showed the greatest variation in economic value across fisheries and movement methodologies. Mature stages showed greater economic value in the recreational fisheries compared to the Canada commercial fishery.

Visualization of the BSSM – commercial exploitation scenario at an exploitation rate of 0.20 (maximum value obtainable for the commercial exploitation scenario) demonstrates the disparity between commercial harvest and recreational fisheries potentials (Figure 3.13). Recreational harvest values were similar but less than commercial harvest values. The potential value of the Canada recreational fishery was valued at almost 13 million CAD which, is 1300 times greater than the highest economic return possible for commercial exploitation in Lake Winnipeg.

Discussion

Our case study has highlighted one example of how ecosystem service flows might be considered under complex socio-political contexts. Herein, we assessed scenarios of how conflicting consumptive and potentially non-consumptive uses of channel catfish might influence aspects of their population dynamics in the entire RRLW system. These scenarios encompassed the current management regulations among all political purviews as well as modeled a range of potential outcomes under various methods to assess population

connectivity among subregions and across a suite of harvest rates. Our results showed that movement and exploitation do have subregion specific interactions that affect populations, stock structure, and fishery valuation. We also showed that the stability of unexploited subregions depends on the location and stability of recruitment. For example, a USA exploitation scenario, which is the furthest subregion from the suspected largest source of recruitment (subregion 3), tended to have greater impact on the stock structure and population of its adjacent subregion than the commercial exploitation scenario which was adjacent to subregion 3. Subregion 3 seems to act as a buffer to some extent for the mixed-use fishery. If we consider the perspective of mobile fishes as ecosystem service flows, our models suggest that at a fundamental level, consistency of recruitment, recruit dispersal, and subregion population movement have the ultimate bearing over how channel catfish can deliver provisioning services in a system. The extent and type of exploitation that occurs for harvestable individuals dictates how the provisioning service will be used. Connectivity throughout our subregions was a key factor in allowing the recruitment deprived subregion 4 to have exploitable numbers of channel catfish. The inclusion of movement did have a considerable influence over the population and stock structure of subregions that had little recruitment and larval dispersal. All three movement models projected different population sizes across subregions. The variation between subregion populations associated to each movement model demonstrates that differences in movement methodologies will impact one's understanding of system wide movement and population dynamics. Fish populations vary in their ability to withstand fishing mortality and our models showed how both subregion population size and stage structure would be impacted by exploitation. The long-lived and slow growing nature of the channel catfish in the RRLW system is likely the driving force behind the trophy fishery's

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sensitivity to exploitation. Similar findings have shown that long-lived and or larger fish species are more susceptible to overfishing and subsequent fishery collapse in marine (Roberts 2002) and freshwater environments (Allan et al. 2005). That is not to say that sustainable exploitation can not be obtained but rather achieving sustainable exploitation carries risk that may lead to fishery closures (Hilborn et al. 2006), or in this case an elimination of a trophy recreational fishery.

Our case study only investigated the provisioning aspects of the ecosystem service flow, but the fishery as an ecosystem service flow can and does provide regulating and cultural services throughout the study area. The channel catfish in this system is the apex predator and thus likely serves as a top-down control for the system. Exploitation of this ecological niche could have broader ecosystem repercussions if overharvested, regarding biodiversity and stock structure of other species (Frank et al. 2005). The channel catfish are also of importance to first nations people, but their use of channel catfish has not been quantified or estimated for value at this time. The inequity of ecosystem service capacity of subregions and inadequate flow of ecosystem services among subregions to satisfy ecosystem service demands is a fundamental component of the common pool dilemma. Our exploitation scenarios showed that beneficiaries of ecosystem service flows typically go beyond the exploited subregion suggesting that cooperative management among stakeholders would reduce the negative consequences associated to rivalness (Bagstad et al. 2013).

The challenge for resource managers especially those that prioritize ecosystem service goals is how to manage at varying spatial scales to achieve biologically realistic outcomes to satisfy socio-economic demands (Haddon 2010). Our study area has multiple scales to consider for management: geopolitical (Canada and USA), ecosystem (Lake Winnipeg and Red River), and connectivity (above St. Andrews Lock and Dam and below). Each scale has a different composition of stakeholders, ecosystem services capacity, and ecosystem services demand. The extent these services interact between or among scales only adds complexity to managing from an ecosystem service perspective (O'Higgins et al. 2010). For example, the Both exploitation scenario implied equal, incremental harvest for subregion 1 and subregion 4. The model does not account for the broader impacts associated with each type of fishing which does inevitably affect bycatch differently (Davis 2002) and potentially the associated ecosystem services (Davies et al. 2009). Subregion 1's harvest was only comprised of recreational fishing thus angling gear and effort would greatly differ from the harvest practices of subregion 4 which was comprised of only commercial fishing. The USA anglers typically use rod and reel angling which allows for greater survival probability for bycatch species than the gill nets typically used by commercial anglers in Lake Winnipeg. Unintentional mortality of other species can cause community shifts in localized areas of ecosystems (Crowder and Murawski 1998). We assumed in our models that harvest was defined as removing the fish from the system but in practice, recreational fishing often reflects catch and release behavior. The propensity to catch and release individuals causes an interesting dynamic for the fishery because individuals do not necessarily need to be harvested to maintain their value (Figure 3.13). This disparity among stakeholders contributes to the greater problem of managing mixed-use fisheries. The question becomes - how do decisionmakers best compare and prioritize the use of fish? There are compelling arguments among all stakeholders whether channel catfish should be used for food or for sport and each has unique socio-economic costs and benefits (Edwards 1990). Furthermore, there is a philosophical
difference between commercial fishing and recreational angling where commercial fishers only value fish if it is harvested whereas recreational anglers can value fish whether it is harvested or released.

The willingness to pay values were developed for channel catfish in Nebraska (Cole 2018). Willingness to pay for channel catfish in the Red River system is likely much higher since the Red River fishery maintains a trophy status and attracts international anglers while Nebraska does not. The willingness to pay for channel catfish in the Red River system has not been assessed. Commercial values for channel catfish were taken from typical sold at dock prices as opposed to Manitoba market prices because channel catfish are currently not sold beyond local fishing communities. Spatial and temporal dynamics of willingness to pay across distributions of sport fish species has received little attention in the literature. Similarly, market prices for inland freshwater commercial fisheries are much more difficult to obtain compared to marine stocks. One should expect that willingness to pay and commercial prices for channel catfish varies across the system but are inevitably linked by the quality of the supply and the type of demand for the fishery. For example, if the channel catfish population were to lose its trophy status the willingness to pay for the species would go down, but it is not clear how a decrease would affect each subregion. Alternatively, if the channel catfish were to maintain its trophy status, the price per fish would increase for commercial harvest, but that does not necessarily mean the largest individuals would be the preferable size for consumers. For example, the walleye fishery in Lake Winnipeg exhibits different price per kilogram depending on the size of the individual, where 'jumbo' walleye is worth less per kilogram than 'medium' and 'large-sized' categories. The

valuation aspect of our study could be greatly expanded upon and put the ecosystem service flows into a broader context for other mobile and sought after fisheries species.

The equilibrium method has been criticized for being too liberal for estimating catch levels because it assumes all catch levels are sustainable (Hilborn and Walters 1992; Haddon 2010), but in our study even the biases of an equilibrium-based model showed trophy stages were sensitive to exploitation and prone to complete depletion at low exploitation rates. Modelling the dynamics of recruitment was not a part of this study but would be crucial in understanding how resiliency of specific subregions could affect the movement and exploitation interactions we reported. We would strongly suggest fisheries managers to incorporate thoroughly studied estimates of stock-recruits when applying our approach to one's system. We also assumed for our model that stages had equal vulnerability to harvest though in application, fisheries managers can enact stage or length specific regulation to change vulnerability. Our model is limited to incorporate vulnerability at a system level rather than at a subregion scale. Future research could explore how unique length-based regulations could affect the interaction of movement and exploitation for this trophy fishery. Furthermore, we assumed movement rates among stages were equal based on chapter 2. Movement studies of juvenile catfish have not been conducted for this system and could provide very different system dynamics than the assumption we made for our models. The assumptions of larval dispersal have a similar bearing. Larval fishes in lotic systems depend largely on flow regimes to determine recruitment location. The presence of water management structures near the most productive subregions could influence the spatial variability of recruits and larval fishes alike. The slow-growing but longlived aspects of the channel catfish allow this species to reach trophy status more so than other

populations within its distribution. The consistency of recruitment and low exploitation are necessary for the population to maintain its trophy status based on our models.

The concept of priority-area conservation has gained recent attention for the protection of ecosystem services with biodiversity hotspots serving as ideal targets (Buchanan et al. 2011; Edgar et al. 2014). One might consider extending this concept for long-lived mobile species in aquatic systems to ensure recruitment and low exploitation are achieved. The concept emphasizes the identification of areas of ecosystem service capacity and areas of ecosystem services demand (Verhagen et al. 2017). Subregion 3 typically provided the most capacity regarding population and recruits suggesting that this subregion would benefit from conservation measures to ensure the sustainability of recruitment across the system. Protected areas for aquatic systems are more commonly seen in marine systems but their effectiveness to help sustain mobile and wide-ranging species such as sharks show promise for the broader ecosystem (Knip et al. 2012). Another option to consider is "swimway" management, where management of the fishery is based on the spatial characteristics of the exploited population (Pracheil et al. 2012). Flyway management is a success story of managing an exploited species based on its spatial characteristics (Nichols et al. 1995), yet fisheries managers are slow to adopt such policy for lotic fishes that exhibit spatial behaviors that operate outside of individual fisheries management areas. Future studies directed at modeling the population dynamics of fisheries after the introduction of a protected area or swimway management would provide valuable insight on the current management of inland fisheries and counter the traditional perspectives of the one size fits all approach commonly seen for inland fisheries (Carpenter and Brock 2004).

Ecosystems and their associated services and service flows are unique to their respective systems. The incorporation of spatial characteristics information regarding ecosystem service flows is a critical first step before managers can optimize planning and policy for such services. Accounting for both short-term and long-term supply of ecosystem service flows also needs prioritization for management to ensure human benefits are allocated within the bounds of the ecological integrity of a system (Burkhard et al. 2014). The adoption of an ecosystem services perspective for fisheries is intended to provide a more comprehensive view of how exploitation affects socio-ecological systems as a whole. Realizing that the sustainable harvest does not equate to stable ecosystem services poses new challenges and opportunities for inland fisheries. We were able to show that where all life-stages are equally vulnerable to harvest typically results in the complete loss of mature and trophy stages at less than 0.30 exploitation across exploitation scenarios in exploited regions. Additionally, we showed that recruitment deprived regions such as Lake Winnipeg completely depend on the emigration from recruitment rich regions such as the Red River below St. Andrew's Lock and Dam. The onset of fishing down the food chain perspective has been identified in marine fisheries along with inland fisheries (Pauly et al. 2001, 2002). Rivalness will always be a characteristic of common pool resources, especially if the resource is mobile and interacts with multiple stakeholders. Thus, sustainability focused fishery goals should also account for the rivalness of the system when it comes to maintaining viable populations for a mixed-use fishery. Analyzing the role of stakeholders, their relationships, and their use characteristics (e.g., use, manage, or impair ecosystem services) is necessary to allow for equitable access to ecosystem services (Felipe-Lucia et al. 2015). The sensitivity of the slower growing channel catfish to exploitation suggests risk-averse options may maximize the economic return of both recreational and commercial angling and mitigate for the rivalry of the ecosystem service flows. The importance of identifying the mechanisms that support the longevity of ecosystem services and their flows is critical for ensuring management goals are capable of satisfying the multitude of users that depend on our limited and complex aquatic resources.

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Tables

Table 3.1 Biological and system parameters for stage-structured Leslie-matrix model of channel catfish in the Red River of the North and Lake Winnipeg system. Subregions represent the following areas of the study system: 1) USA portion of the Red River, 2) the Canada portion of the Red River above St. Andrews Lock and Dam, 3) the Canada portion of the Red River below St. Andrews Lock and Dam, and 4) Lake Winnipeg.

Stage Class	Sub-region Survival				Vulnerability	Maturity	Duration in
	1	2	3	4	to Fishing	Watanty	Stage
Juvenile (x < 24")	0.887	0.887	0.887	0.887	100%	0%	12.2
Mature (24" > x < 36")	0.842	0.842	0.842	0.842	100%	100%	13.2
Trophy (x > 36")	0.842	0.842	0.842	0.842	100%	100%	1.6
					_		
System Event	Region Specific Parameters						
Exploitation	0.001	0.001	0.001	0.001			
Larval Dispersal	0.340	0.162	0.482	0.017			

Table 3.2 Movement methodology matrices of channel catfish movement in the Red River system. Matrix values represent sink-source dynamics for channel catfish within and among subregions which are classified as follows: 1) USA portion of the Red River, 2) the Canada portion of the Red River above St. Andrews Lock and Dam, 3) the Canada portion of the Red River below St. Andrews Lock and Dam, and 4) Lake Winnipeg. Movement methodology matrices are abbreviated as follows: Bayesian state-space model (BSSM), mark-recapture of Tbar tags (MR), and geographic information systems analysis of telemetry data.

Sink- Source	Regions					
BSSM	1	2	3	4		
1	0.974	0.096	0	0		
2	0.026	0.887	0.041	0		
3	0	0.017	0.946	0.05		
4	0	0	0.014	0.95		
MR T-bar	1	2	3	4		
1	0.98	0.451	0	0		
2	0.02	0.463	0.267	0		
3	0	0.085	0.699	0.125		
4	0	0	0.034	0.875		
GIS Telemetry	1	2	3	4		
1	0.567	0.095	0	0		
2	0.433	0.619	0	0		
3	0	0.286	0.475	0		
4	0	0	0.525	1		

Table 3.3 Hypothetical exploitation scenarios simulating possible harvest regimes of specific subregions in the Red River of the North system and Lake Winnipeg. Experimental exploitation is the proportion of the population harvested in the exploited region. The Both scenario is a combination of the commercial and USA exploitation scenario. Subregions represent the following areas of the study system: 1) USA portion of the Red River, 2) the Canada portion of the Red River above St. Andrews Lock and Dam, 3) the Canada portion of the Red River below St. Andrews Lock and Dam, 3) the Canada portion of the Red River below St.

Scenario	Experimental Exploitation	Exploitation Increments	Regions Exploited
Status Quo	0.001	NA	1 - 4
Both	0.1 to 1	0.1	1&4
Commercial	0.1 to 1	0.1	4
USA	0.1 to 1	0.1	1

Figures



Figure 3.1 Study area with red line indicating Red River of the North. Subregions are represented in black brackets and acoustic receiver locations are shown in white circles. Orange rectangle indicates St. Andrew's Lock and Dam. Only major tributaries that contained receivers are shown.



Figure 3.2 Visualizations of channel catfish population projections in the Red River of the North and Lake Winnipeg system under a status quo exploitation scenario. Individual graphs represent differing movement methodologies used to assess channel catfish movement in the system. Abbreviations for movement methodologies are as follows: for no movement (None), Bayesian state-space model (BSSM) movement, mark-

recapture of T-bar tags (MR) movement, and geographic information systems (GIS) analysis of telemetry data movement. Populations were projected using a stage structured Leslie matrix model. Red line indicates system wide population while remaining colors indicate subregion populations. Subregions represent the following areas of the study system: 1) USA portion of the Red River, 2) the Canada portion of the Red River above St. Andrews Lock and Dam, 3) the Canada portion of the Red River below St. Andrews Lock and Dam, and 4) Lake Winnipeg. Black horizontal lines indicate expected population values associated to Red River subregions 1 – 3 from Siddons (2015) where the top line is population of subregion 3 (2,823,266 individuals), middle line is population of subregion 1 (1,891,665 individuals) and the bottom line is population of subregion 2 (1,003,329 individuals).



Figure 3.3 Visualizations of a hypothetical USA exploitation scenario (only subregion 1 is undergoing increasing exploitation) on channel catfish in the Red River of the North and Lake Winnipeg system. Individual graphs represent differing movement methodologies used to assess channel catfish movement in the system. Movement abbreviations are as follows: for no movement (None), Bayesian state-space model (BSSM) movement, mark-recapture of T-bar tags (MR) movement, and geographic information systems (GIS) analysis of telemetry data movement. Solid

color lines represent subregion population size and textured lines indicate number of individuals harvested for each subregion. Subregions represent the following areas of the study system: 1) USA portion of the Red River, 2) the Canada portion of the Red River above St. Andrews Lock and Dam, 3) the Canada portion of the Red River below St. Andrews Lock and Dam, and 4) Lake Winnipeg.



Figure 3.4 Visualizations of a hypothetical commercial exploitation scenario in Lake Winnipeg (only subregion 4 is undergoing increasing exploitation) on channel catfish in the Red River of the North and Lake Winnipeg system. Individual graphs represent differing movement methodologies used to assess channel catfish movement in the system. Movement abbreviations are as follows: for no movement (None), Bayesian state-space model (BSSM) movement, mark-recapture of T-bar tags (MR) movement, and geographic information systems (GIS)

analysis of telemetry data movement. Solid color lines represent subregion population size and textured lines indicate number of individuals harvested for each subregion. Subregions represent the following areas of the study system: 1) USA portion of the Red River, 2) the Canada portion of the Red River above St. Andrews Lock and Dam, 3) the Canada portion of the Red River below St. Andrews Lock and Dam, and 4) Lake Winnipeg.



Figure 3.5 Visualizations of a hypothetical exploitation scenario occurring in the USA portion of the Red River and Lake Winnipeg (only subregions 1 and 4 are undergoing increasing exploitation) on channel catfish in the Red River of the North and Lake Winnipeg system. Individual graphs represent differing movement methodologies used to assess channel catfish movement in the system. Movement abbreviations are as follows: for no movement (None), Bayesian state-space model (BSSM) movement, mark-recapture of T-bar tags (MR) movement, and

geographic information systems (GIS) analysis of telemetry data movement. Solid color lines represent subregion population size and textured lines indicate number of individuals harvested for each subregion. Subregions represent the following areas of the study system: 1) USA portion of the Red River, 2) the Canada portion of the Red River above St. Andrews Lock and Dam, 3) the Canada portion of the Red River below St. Andrews Lock and Dam, and 4) Lake Winnipeg.



Figure 3.6 Comparison of proportional population changes for mature and trophy stages of channel catfish in the Red River of the North and Lake Winnipeg system. Individual graphs represent differing exploitation scenarios while no movement (None) is occurring between subregions. Left plots represent the Both exploitation scenario where subregions 1 and 4 are undergoing increasing exploitation, center plots represent the commercial exploitation scenario where subregion 4 is undergoing increasing exploitation, and right plots represent the USA exploitation

scenario where subregion 1 is undergoing increasing exploitation. Subregions represent the following areas of the study system: 1) USA portion of the Red River, 2) the Canada portion of the Red River above St. Andrews Lock and Dam, 3) the Canada portion of the Red River below St. Andrews Lock and Dam, and 4) Lake Winnipeg.



Figure 3.7 Comparison of proportional population changes for mature and trophy stages of channel catfish in the Red River of the North and Lake Winnipeg system. Individual graphs represent differing exploitation scenarios while Bayesian state-space movement (BSSM) is occurring between subregions. Left plots represent the Both exploitation scenario where subregions 1 and 4 are undergoing increasing exploitation, center plots represent the commercial exploitation scenario where subregion 4 is undergoing increasing exploitation, and right plots represent the USA

exploitation scenario where subregion 1 is undergoing increasing exploitation. Subregions represent the following areas of the study system: 1) USA portion of the Red River, 2) the Canada portion of the Red River above St. Andrews Lock and Dam, 3) the Canada portion of the Red River below St. Andrews Lock and Dam, and 4) Lake Winnipeg.



Figure 3.8 Comparison of proportional population changes for mature and trophy stages of channel catfish in the Red River of the North and Lake Winnipeg system. Individual graphs represent differing exploitation scenarios while mark-recapture (MR) is occurring between subregions. Left plots represent the Both exploitation scenario where subregions 1 and 4 are undergoing increasing exploitation, center plots represent the commercial exploitation scenario where subregion 4 is undergoing increasing exploitation, and right plots represent the USA exploitation

scenario where subregion 1 is undergoing increasing exploitation. Subregions represent the following areas of the study system: 1) USA portion of the Red River, 2) the Canada portion of the Red River above St. Andrews Lock and Dam, 3) the Canada portion of the Red River below St. Andrews Lock and Dam, and 4) Lake Winnipeg.



Figure 3.9 Comparison of proportional population changes for mature and trophy stages of channel catfish in the Red River of the North and Lake Winnipeg system. Individual graphs represent differing exploitation scenarios while GIS analysis of telemetry fish movement (GIS) is occurring between subregions. Left plots represent the Both exploitation scenario where subregions 1 and 4 are undergoing increasing exploitation, center plots represent the commercial exploitation scenario where subregion 4 is undergoing increasing exploitation, and right

plots represent the USA exploitation scenario where subregion 1 is undergoing increasing exploitation. Subregions represent the following areas of the study system: 1) USA portion of the Red River, 2) the Canada portion of the Red River above St. Andrews Lock and Dam, 3) the Canada portion of the Red River below St. Andrews Lock and Dam, and 4) Lake Winnipeg.



Figure 3.10 Heat map of valuation of the USA recreational fishery for channel catfish in the Red River of the North and Lake Winnipeg system based on the willingness to pay metrics estimated by Cole (2018). Values are calculated by multiplying the number of individuals harvested from population projections by the associated stage specified willingness to pay estimate. Values are organized by exploitation scenario and exploitation rate where Both exploitation scenario models subregions 1 and 4 are undergoing increasing exploitation, the commercial exploitation scenario is where subregion 4 is undergoing increasing exploitation, the USA exploitation scenario is where subregion 1 is undergoing increasing exploitation, and status quo exploitation is where all subregions exhibit current exploitation of 0.001. Values are separated by population/ fish stage and movement methodology used to assess movement of channel catfish within and among the fishery. Movement methodology abbreviations are as follows: no movement (None), Bayesian state-space model (BSSM) movement, mark-recapture of T-bar tags (MR) movement, and geographic information systems (GIS) analysis of telemetry data movement. Value is in log₁₀ form of Canadian dollars.



Figure 3.11 Heat map of valuation of the Canada recreational fishery for channel catfish in the Red River of the North and Lake Winnipeg system based on the willingness to pay metrics estimated by Cole (2018). Values are calculated by multiplying the number of individuals harvested from population projections by the associated stage specified willingness to pay estimate. Values are organized by exploitation scenario and exploitation rate where Both exploitation scenario models subregions 1 and 4 are undergoing increasing exploitation, the commercial exploitation scenario is where subregion 4 is undergoing increasing exploitation, the USA exploitation scenario is where subregion 1 is undergoing increasing exploitation, and status quo exploitation is where all subregions exhibit current exploitation of 0.001. Values are separated by population/ fish stage and movement methodology used to assess movement of channel catfish within and among the fishery. Movement methodology abbreviations are as follows: no movement (None), Bayesian state-space model (BSSM) movement, mark-recapture of T-bar tags (MR) movement, and geographic information systems (GIS) analysis of telemetry data movement. Value is in log10 form of Canadian dollars.



Figure 3.12 Heat map of valuation of the Canada commercial fishery for channel catfish in the Red River of the North and Lake Winnipeg system based on the sold at dock price metrics. Values are calculated by multiplying the number of individuals harvested from population projections by the associated stage specified willingness to pay estimate. Values are organized by exploitation scenario and exploitation rate where Both exploitation scenario models subregions 1 and 4 are undergoing increasing exploitation, the commercial exploitation scenario is where subregion 4 is undergoing increasing exploitation, the USA exploitation scenario is where subregion 1 is undergoing increasing exploitation, and status quo exploitation is where all subregions exhibit current exploitation of 0.001. Values are separated by population/ fish stage and
movement methodology used to assess movement of channel catfish within and among the fishery. Movement methodology abbreviations are as follows: no movement (None), Bayesian state-space model (BSSM) movement, mark-recapture of T-bar tags (MR) movement, and geographic information systems (GIS) analysis of telemetry data movement. Value is in log10 form of Canadian dollars.



Figure 3.13 Bar graph of projected values for harvest and potential harvest (recreational only) of mature and trophy fish in each fishery with a commercial exploitation scenario set at an exploitation rate of 0.20 (maximum value commercial fishery can produce from harvest) and a Bayesian state-space movement perspective. Values are in Canadian currency where recreational fisheries are based on willingness to pay metrics and commercial values are based on sold at dock price metrics.

Supplementary Material

Documentation of Leslie matrix models for the fisheries model, version 3.5.0, from the InVEST modeling software (Sharp et al. 2018).

$$N_{a,s,x,t} = \left\{ egin{array}{ccc} \left(N_{a,s,x,t-1}Mig^x_{a,s,x} + \sum_{x'
eq x} N_{a,s,x',t-1}Mig^x_{a,s,x'}
ight)P_{a,s,x} &+ Rec_{s,x,t} & if a = 0 \ \left(N_{a-1,s,x,t-1}Mig^x_{a-1,s,x} + \sum_{x'
eq x} N_{a-1,s,x',t-1}Mig^x_{a-1,s,x'}
ight)G_{a-1,s,x} & if 1 \le a \ + \left(N_{a,s,x,t-1}Mig^x_{a,s,x} + \sum_{x'
eq x} N_{a,s,x',t-1}Mig^x_{a,s,x'}
ight)P_{a,s,x} \end{array}
ight\}$$

Stage Structured population model – where $N_{a,s,x,t}$ is the number of individuals of age a (A = maximum age) of sex s in area x at the start of time step t; and $_{Sa-1,s,x}$ is survival from natural and fishing mortality from age a-1 to a for each sex and area; $Rec_{s,x,t}$ is recruitment of new individuals/number of offspring; $Mig_{a,s,x}^{x}$ is the proportion of individuals of age a sex s that migrate from area x' to area x (or the proportion that remain in the area if x' = x). Survival from natural and fishing mortality is defined as:

$$S_{a,s,x} = surv_{a,s,x}\left(1 - Ex_x * V_{a,s}
ight)$$

Where surv_{a,s,x} is survival from natural fishing mortality from age *a* to *a* + 1. for each sex and area; Ex_x is exploitation, which is the proportion of the population vulnerable to harvest that is actually harvested; and V_{a,s} is vulnerability to harvest by age and sex. Harvest is assumed to occur at the beginning of the year, prior to mortality from natural causes. Note that there is no *A* (maximum age) for stage-structured models because the models are designed to capture all of the life stages. $G_{a,s,x}$ is the probability of surviving from natural and fishing mortality and growing into the next stage for each sex and area; and $P_{a,s,x}$ is the probability of surviving from natural and fishing mortality and staying in the same stage for each sex and area.

 $G_{a,s,x}$ is a function of survival from natural and fishing mortality ($S_{a,s,x}$ as defined above, except now expressed as per unit time (e.g. day) rather than per year) and stage duration, D_a :

$$G_{a,s,x} = rac{{S_{a,s,x}}^{D_a} \left({1 - S_{a,s,x}}
ight)}{{1 - S_{a,s,x}}^{D_a}}$$

 $P_{a,s,x}$ is also a function of survival from natural and fishing mortality and stage duration; it is defined as:

$$P_{a,s,x} = S_{a,s,x} rac{1-S_{a,s,x}^{~~D_a-1}}{1-S_{a,s,x}^{~~D_a}}$$

CHAPTER 4 CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

The previous two chapters highlight the importance of investigating and understanding the spatial behavior of a mobile fish species. The Red River, like many rivers, is a dynamic network system that provides fundamental services for adjacent ecosystems and humans. How such services are distributed among ecosystems and humans varies across space and time. Understanding how species within rivers, in this case channel catfish Ictalurus punctatus, move and thrive in a complex space is just the beginning when informing the distribution of services and how services should be shaped by fisheries policy. Movement of channel catfish throughout the Red River has implications regarding geo-politics, anthropogenic structures, and ecosystems. The implications are emboldened by the fact that the Red River probably supports the top trophy channel catfish fishery in the world. My thesis comprises two themes, chapter 2 characterized channel catfish movement from multiple methodologies and chapter 3 demonstrated how movement could interact with exploitation. Each chapter has associated conclusions, management suggestions and future research needs, described in the sections below. The following sections should be prefaced by the notion that management and future research need not be done in isolation, to the contrary, management and future research should be conducted cooperatively across fisheries managers throughout the system. Management of channel catfish is just one opportunity out of many in the Red River system to optimize a management process for a mobile inland fishery.

Chapter 2

Conclusions

Mark-recapture and telemetry data provided us with a unique opportunity to understand channel catfish movement from two different methodologies. Each method provided different resolutions of information but still shared many similarities regarding the spatial behavior of channel catfish. We documented movement of channel catfish in excess of more than 500 kilometers both upstream into the Red River and downstream into the north basin of Lake Winnipeg. The direction of movement varied between methods, where the upstream movement was more prevalent for t-bar tagged individuals and downstream movement was more prevalent for transmitter tagged individuals, but no movement direction was prevalent among both methods. Proportionately more fish were observed moving from Canada to the U.S.A. based on the t-bar tags than transmitter tags, but more transmitter tagged individuals were observed using Lake Winnipeg than the t-bar tags. Additionally, 67% of the fish tagged in the Winnipeg River moved into Lake Winnipeg. Bayesian state-space models (BSSM) for each method showed similarities across movement parameters with movement transitions among geographic states being less common than movement transitions within geographic states. Combining methods into a single BSSM showed expected patterns of mortality where fishing mortality was estimated to currently be less than 0.001, and natural mortality was estimated to be 0.16 across the entire system. Linear modeling of physical characteristics showed that larger fish move greater distances but does not explain much of the variation. Overall, individual channel catfish exhibited either localized scale movement or regional scale movement. Localized scale movement was most common in the Selkirk to Lockport area and the U.S.A. Regional movement destinations were typically the U.S.A. or Lake Winnipeg.

Management Suggestions

1. Develop fisheries policy for international cooperative management

Currently, cooperative management of the Red River system lacks the means to pass international scale regulations for the fishery; this means legislation occurs piece-meal fashion at the discretion of the stakeholder. The absence of international scale regulation processes for the fishery is counter-intuitive to the previous and current research on the movement capabilities for the channel catfish, where interactions between movement and exploitation can occur at regional scales. Movement information from chapter 2 demonstrated high proportions of tagged channel catfish from the lower Red River moved either into Lake Winnipeg or into the U.S.A. (depending on the method). Channel catfish movement frequently occurs across international and interstate boundaries and ecosystems. The interagency working group for the Red River currently strives to meet goals of the fishery cooperatively but enforced regulations and policy timelines do differ among entities. For example, one of Minnesota's regulation processes can take 18 months to introduce a change to fishery regulations where North Dakota's regulation process has a rotating regulation cycle of every even year. Manitoba has separate regulation timelines for recreational and commercial fishing where recreational changes typically follow a 2 year cycle while commercial regulations need a 5 year warning before quota changes can be made. Additionally, the public forum components of each regulation process are intended only for the state's residents, instead of soliciting feedback from the area in which the regulation will affect all stakeholders. Furthermore, cooperation for the fishery is done so on a voluntary basis with no means of oversight among stakeholders; this means any entity can implement new regulations on the channel catfish without soliciting or incorporating any input from other stakeholders in the system. Pracheil et al. (2012) suggested

the possibility of initiating swimway oriented management areas that would reflect the spatial behavior of managed fish species, especially for mobile, long-lived species. Managing from the spatial behavior of a species has been successfully implemented through the flyway management system for migratory waterfowl species in North America (Nichols et al. 1995). Implementing an international swimway management process (ISMP) is a means to foster systemwide regulations in an expedited manner for each entity. Specifically, the ISMP would require each entity to mutually agree on a single regulation timeline (e.g., annually, biannually, etc.) so fisheries managers and associated regulating bodies can enact system-wide regulations in a synchronized fashion. The ISMP would also have some form of governance to allow cooperating entities to hold each other accountable for non-agreed upon regulations. A hypothetical example of this management suggestion would be to allow commercial fishing for the entirety of the Red River. Without an ISMP, the questions to consider are 1) what regulation processes would need to be navigated for each entity, 2) how long would each process take, 3) would the regulations for each entity be enacted at the same time and 4) how would differing opinions on the regulation change be settled? The implementation of an ISMP could provide an efficient, system-wide means of introducing regulation by channeling the previous questions into a timely policy framework. In its simplest form, the ISMP would operate in the following: a new regulation is proposed, subjected to public forum throughout the system, and either accepted or rejected by the deciding individuals of each cooperating entity all in accordance of the agreed upon timeline. The inequity of fisheries is introduced when the common-pool resource is not cooperatively managed but this dilemma can be prevented with cooperative management and an effective, scalable policy. The Great Lakes Fishery Commission is one example of binational cooperation of international fisheries and invasive species management that demonstrates the benefits of cooperative policy making and management actions.

 Develop and institute channel catfish population monitoring and spatial stock assessment

The mark-recapture efforts led by the University of Nebraska-Lincoln (UNL) has resulted in over 15,000 catfish marked since 2012, and over 1,000 recaptures. The data from the mark-recapture efforts have allowed UNL researchers to investigate fundamental population dynamics questions for channel catfish in the Red River, but the answers to these questions are not static. Supporting, developing, and continuing monitoring efforts by using mark-recapture is one of the simplest means of detecting change related to the channel catfish and the greater ecosystem. Monitoring of the channel catfish population through mark-recapture allows managers to evaluate growth, estimate absolute abundance, and to track harvest all from a spatial perspective. Mark-recapture can also provide a means to identify stocks within the Red River system (Cadrin et al. 2014). Channel catfish have been observed in many of the tributaries to Lake Winnipeg, this includes but not limited to the Red, Assiniboine, Saskatchewan, Winnipeg, Manigotagan, Dauphin, and Pidgeon Rivers (Stewart and Watkinson 2004). Each tributary could be contributing to the total abundance of channel catfish found in Lake Winnipeg but it is not clear to what extent that contribution may be. Additionally, the mark-recapture effort should be conducted from an international perspective, separate t-bar tag colors and IDs for Manitoba, Minnesota, and North Dakota would provide a far more comprehensive understanding of channel catfish population dynamics. At a minimum, general population monitoring (not using mark-recapture) should be conducted at a systemwide scale to detect natural variations of the population as well as detect changes associated to regulations. Capitalizing on joint-efforts (every 5 years) currently conducted by the Minnesota Department of Natural Resources and North Dakota Game and Fish would be an appropriate way to incorporate this suggestion.

Research needs

- 1. Investigate relationships of channel catfish spatial behavior to hydrology
 - Anecdotal reports suggest channel catfish abundance and their susceptibility to angling increases downstream of St. Andrews Lock and Dam after rain events in the summer. Additionally, Wendel and Kelsch (1999) and Aadland et al. (2005) reported movement associated with highwater or flood events. Our physical characteristics modeling performed poorly to explain variation, but one hypothesis that could be tested is the influence of hydrological events on total movement distance. Investigating the distance and direction of movement associated with hydrologic events could provide managers the information to understand the timing and frequency of international movements. The hypothesis can be further expanded to investigate hydrological influence on movements conducted at modernized and unmodified dams throughout the Red River system.
- 2. Assess if the channel catfish are migratory
 - Our seasonal analyses were conducted at a relatively large spatial scale and with limited sample sizes and time to detect migration. Pellett et al. (1998) identified migratory and homing behavior in channel catfish in Wisconsin. Investigating the spatial behavior of Red River channel catfish at a smaller spatial scale could help managers determine if the population is migratory. The transmitters used in our study last up to five years which could provide enough temporal scale to detect a migration. Detecting migratory behavior has direct implications for fisheries management and policy.

- 3. Evaluate system-wide movement characteristics of juvenile individuals
 - Our telemetry equipment limited us to use only individuals larger than 550 mm. Individuals less than 550 mm make up the majority of the population yet our understanding of their movement is known only from the mark-recapture perspective. Understanding juvenile movement would provide managers with a comprehensive view on stage-specific movement. If this research were completed, the comprehensive model designed in Chapter 2 could be reanalyzed from a stage-specific perspective. Specifically, running the comprehensive BSSM separately for juveniles, mature, and trophy individuals would provide a finer resolution understanding of how movement varies among stages.
- 4. Investigate size-based mobility of catfish through anthropogenic structures on Red River
 - Our results showed that channel catfish are capable of swimming upstream and downstream of St. Andrews Lock and Dam, but no study has evaluated whether the movements occurred through the locks, the fish ladder, or the floodway (during high water). Investigating the physical pathways in which channel catfish move across St. Andrews Lock and Dam would allow fisheries managers to identify areas where channel catfish are susceptible to excessive mortality. For example, pelicans congregate in and around the fish ladder to forage which may increase mortality for individuals trying to move upstream. Similarly, pelicans and anglers both target fish below low-head dams which may also increase mortality for individuals unable to surpass the barrier. Drayton dam is the last dam on the Red River that has not been modernized for fish passage. Investigating the before and after modernization affects on fish passage would

provide fish managers a better understanding of how low-head dams impair movement across species.

- 5. Assess apex predator role of channel catfish
 - The channel catfish is the apex predator in the Red River system, but no studies have investigated the foraging preferences for the species. The movement capabilities for the species would suggest that its generalist foraging behaviors must encompass the prey species found in both the river and Lake Winnipeg. Investigating the foraging preferences of channel catfish, especially among different stages and habitats (e.g., river, lake, marsh) would provide better insight into what ecological interactions are critical for the recruitment of juveniles and food preferences for trophy individuals.
- 6. Identify spawning habitats for adult channel catfish
 - Netley-Libau marsh was the densest area sampled for juvenile fish by Siddons (2015). Anecdotal reports suggest the marsh acts as a nursery area for channel catfish and that is why the abundance of channel catfish below St. Andrews Lock and Dam is much higher in relation to other reaches in the system. Investigating fine-scale movement patterns for adult channel catfish to pinpoint spawning grounds would be critical information for ensuring consistent recruitment for the population.

Chapter 3

Conclusions

Modeling the exploitation scenarios across alternative movement methodologies for a longlived mobile fish species provided us insight on how a trophy population could respond to harvest in spatially explicit areas. The Red River system is composed of three different fishery types, a U.S.A. recreational fishery, a Canada recreational fishery and a Canada commercial fishery that all utilize the trophy channel catfish population for provisioning services and our results showed how different exploitation scenarios would affect different fisheries. Additionally, our models showed that different movement methodologies affect subregion population sizes and the homogeneity of populations from a system-wide perspective. Trophy stages of channel catfish were highly sensitive to exploitation and were typically depleted at or below a 0.30 exploitation rate. Depletion of populations and changes in stock structure affected subregions within the Red River system differently from the perspective of economic valuation of harvests, meaning that each separate fishery had a different exploitation rate and different stage to exploit to maximize economic return. We found that recruitment location and location of recruitment dispersal ultimately determines the strength of the interaction of movement and exploitation among subregions. The largest assumption we made for our model was that exploitation was not affecting recruitment. Depending on where the recruitment is located and where the mature individuals come from, our model would likely produce different results if empirical evidence on stock-recruitment relationships were incorporated. The sustainability of channel catfish from an ecosystem service flow perspective hinges on the ability of fisheries management organizations to incorporate spatial variability of fisheries and understand the economic consequences of exploitation for competing interests. More importantly, fisheries management organizations must be cognizant of how subregion-specific exploitation could affect stage structure, population size, and economic output among other subregions.

Management Suggestions

1) Do not include channel catfish into the multi-species quota

A multi-species quota system for managing fisheries catch levels is challenging to maintain sustainably at its best (Sanchirico et al. 2006) and ecologically unpredictable at its worst (Copes 1986; Dupont and Grafton 2000). An individual quota system whether it be for a single stock or multiple species is designed to generate maximum economic returns for fishers, but the biological outcomes of the system largely depend on the specified total allowable catch (Dupont et al. 2005; King 2007). An underestimate of total allowable catch results in an underutilization of the fishery, where an overestimate of total allowable catch could result in overfishing and in some instances complete stock collapse (King 2007). The level at which a total allowable catch is specified ultimately forces fishers to prioritize certain species and sizes of individuals. Preferences on caught fish can and usually results in discards of individuals to maximize economic return for fisherman (Poos et al. 2010). The extent to which discards are returned to the water and the mortality associated to discards is largely unknown for current Lake Winnipeg commercial species, but it is understood that the practice occurs frequently (Lake Winnipeg Quota Review Task Force 2011). The absence of data related to discards as well as by-catch data for Manitoba's three largest commercial fisheries are some of the issues that have resulted in its classification as "one of the most poorly managed fisheries in the world" according to the Monterey Bay Aquarium's Seafood Watch® program (Driscol 2015; "Manitoba's lake fisheries need improving" 2015). Chapter 3 demonstrated the potential of trophy channel catfish's susceptibility to overexploitation and stock collapse in Lake Winnipeg if commercial fishing were increased. Including channel catfish into the current design of the multi-species quota system

would likely mean the channel catfish population would not be sustainably harvested and could put the trophy status of the population at risk.

2) Institute synchronized commercial and recreational monitoring of channel catfish harvest

Monitoring programs can be costly endeavors but are one of the only ways to regularly collect a variety of information for an ecosystem (Olsen et al. 1997). The Lake Winnipeg Quota Review Task Force outlined a series of monitoring programs for Lake Winnipeg walleye and sauger, these include: a commercial fisheries harvest and effort program, an index gill netting program, commercial catch sampling program, a fishers' logbook program, offshore small fish trawling program, a recreational sport fishing survey, and a comprehensive domestic (subsistence) survey (Lake Winnipeg Quota Review Task Force 2011). At a minimum, a hybrid assortment of those programs should be implemented to assess the commercial and recreational harvest of channel catfish throughout the system. Minnesota and North Dakota fisheries agencies currently cooperatively coordinate creel surveys for channel catfish in the USA. Expanding the surveys into Canadian waters would provide a system-wide perspective of channel catfish exploitation. The priority of synchronized monitoring should be on how channel catfish are harvested by recreational and commercial fishermen throughout the system. Without a systemwide perspective on fundamental harvest aspects of the fishery, expected impacts of regulation changes may not reflect the scale at which actual impacts transpire. Additionally, the data from a system-wide harvest monitoring program could provide insight on ecosystem change if the monitoring program is done from an adaptive approach, specifically being implemented in a long-term manner and is designed with statistical analyses in mind (Lindenmayer and Likens 2009). A collaborative monitoring program among all fisheries management agencies should be

the foundation on which international cooperative management bases current and future regulations for the channel catfish fishery.

Research Needs

- 1) Evaluate Ecosystem Services of Channel Catfish Fishery
 - Chapter 3 described how the ecosystem services of the Red River channel catfish flow from a provisioning perspective for a mixed-use fishery, but my work has merely scratched the surface on how an ecosystems service approach can be applied (Holmlund and Hammer 1999). Broadly speaking an ecosystem service can provide the following services: regulating, provisioning, cultural, and aesthetic. Each service can in theory disperse across an area, allowing services to move from source locations to beneficiaries via a carrier (e.g., channel catfish) (Bagstad et al. 2013). There are many aspects of ecosystem services that one could pursue for research but there are some key questions that directly relate to management of the fishery that have not been explored. The first topic to explore is what is the willingness to pay value for the channel catfish in the Red River system. Manitoba recreational anglers have a profound appreciation for the trophy class catfish but fisheries managers have not quantified the fisheries value in a comparable metric to other fisheries. Additionally, evaluating and monitoring the willingness to pay for the fishery would also give managers the ability to detect trends in recreational angling interest. The second topic to consider is mapping ecosystem service flows to a finer scale than my work in chapter 3, which only modeled flow from the fish to the angler. One could investigate how the ecosystem services provided to the angler are translated to local economies. For example, if an angler were to fish downstream of St. Andrews Lock and Dam, how would this individual's catch and harvest of channel

catfish translate to expenses in Selkirk, and furthermore which stores and businesses were the expenditures allocated to (e.g., guide services, lodging, fuel, groceries)? Additionally what time of year would the expenditures occur for businesses that depend on the fishery and how would angler expenditures change based on angler's residency? Exploring the second topic has the potential for fisheries managers to have a performance metric regarding the status of the fishery but also a metric to understand dynamics of angler recruitment and retention. The last topic to consider is evaluating the other ecosystem services provided by the channel catfish fishery. The channel catfish is the apex predator of the Red River and its tributaries and arguably the apex predator for Lake Winnipeg as well but no one has investigated how the species regulates the community and stock structure of prey species. Additionally, the cultural and aesthetic values of a fishery are engrained in the Icelandic, Metis, and First Nations communities in Manitoba but no one has investigated how the communities value channel catfish from either a cultural or aesthetic perspective.

- 2) Assess Channel Catfish Biology
 - Hubert et al. (1999) provided a review on channel catfish biology and management in North America. Many of the fundamental biological aspects of channel catfish have not been evaluated for the Red River population, but appear to be different than in other populations. Hegrenes (1992) and Siddons (2015) have investigated questions related to channel catfish biology, these include age and growth, gonadal development, and sexual maturity. But there are many other biological questions that could be investigated to help fisheries managers. The following priority questions (pertaining to fisheries management) remain for Red River channel catfish: 1) does age or length determine maturity, 2) how does fecundity change with size of a female, 3) how does a north-

flowing river affect the timing of spawning, 4) what are the habitat requirements for juvenile and mature fish, 5) do channel catfish reproduce every year? There is an infinite number of research questions one could consider for channel catfish, but the previous five questions are essential in understanding the mechanisms for population dynamics.

- 3) Assess stock-recruitment throughout the watershed
 - No study has investigated the stock-recruitment relationships of channel catfish throughout the system. The density of juvenile catfish was highest near Netley-Libau marsh, but many other parts of the system have never been sampled, especially tributaries to the Red River. Hubert et al. (1999) reported juvenile catfish might utilize tributaries of reservoirs for spawning. Similarly, Spurgeon et al. (2018) found large-river tributaries comprise of individuals from multiple smaller order tributaries. Both findings suggest mixing of recruits can occur in river habitats. Fisheries managers would benefit from understanding where and to what extent recruitment takes place across the system. Also, understanding the temporal variation in recruitment across the system would allow for a better understanding of population dynamics and movement throughout the system.
- 4) Estimate channel catfish population sizes
 - Siddons (2015) provided coarse population estimates for portions of the Red River in Canada. Estimating population sizes for the U.S.A. and Lake Winnipeg would provide context for developing better insight on the resilience of the population to varying exploitation rates. The precision of population size estimates will remain coarse unless a strong effort in mark-recapture is conducted. Regulating the fishery in the absence of absolute abundance information for either recreational or commercial fishery poses risks for overfishing if exploitation is expected to increase. Additionally, not knowing

specifically how many trophy individuals are in the system limits fisheries managers

from knowing the quality of the population regarding its trophy fishing status.

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APPENDIX

Appendix A. Length-frequency diagrams of channel catfish tagged in 2012 – 2017 with markrecapture T-bar tags and channel catfish tagged with telemetry in 2016 and 2017



Figure A – 1 Length frequency diagram of channel catfish marked with T-bar tags from 2012 -

2017.



Figure A -2 Length frequency diagram of channel catfish recaptured with T-bar tags from 2012

- 2017.



Figure A -3 Length frequency diagram of channel catfish marked with acoustic transmitters in 2016 and 2017

Appendix B. Maps of channel catfish detection paths tagged with transmitters from acoustic receivers downloaded in 2017. Maps are organized by transmitter number, shown in the top right corner of each map. Red line indicates detection path with black triangles indicating direction. Receivers are indicated as blue point while orange triangles indicate receivers that detected tagged catfish.



Catfish Movement Line for transmitter: A69-9001-17874





Catfish Movement Line for transmitter: A69-9001-17876



Catfish Movement Line for transmitter: A69-9001-17877



Catfish Movement Line for transmitter: A69-9001-17878



Catfish Movement Line for transmitter: A69-9001-17879



Catfish Movement Line for transmitter: A69-9001-17880



Catfish Movement Line for transmitter: A69-9001-17881



Catfish Movement Line for transmitter: A69-9001-17882


Catfish Movement Line for transmitter: A69-9001-17884



Catfish Movement Line for transmitter: A69-9001-17885



Catfish Movement Line for transmitter: A69-9001-17887







Catfish Movement Line for transmitter: A69-9001-17890



Catfish Movement Line for transmitter: A69-9001-17891



Catfish Movement Line for transmitter: A69-9001-17892



Catfish Movement Line for transmitter: A69-9001-17893



Catfish Movement Line for transmitter: A69-9001-17894



Catfish Movement Line for transmitter: A69-9001-17895



Catfish Movement Line for transmitter: A69-9001-17896



Catfish Movement Line for transmitter: A69-9001-17897



Catfish Movement Line for transmitter: A69-9001-17898



Catfish Movement Line for transmitter: A69-9001-19139



Catfish Movement Line for transmitter: A69-9001-19140



Catfish Movement Line for transmitter: A69-9001-19141



Catfish Movement Line for transmitter: A69-9001-19142



Catfish Movement Line for transmitter: A69-9001-19143



Catfish Movement Line for transmitter: A69-9001-19144



Catfish Movement Line for transmitter: A69-9001-19145



Catfish Movement Line for transmitter: A69-9001-19146



Catfish Movement Line for transmitter: A69-9001-19147



Catfish Movement Line for transmitter: A69-9001-19148



Catfish Movement Line for transmitter: A69-9001-19149



Catfish Movement Line for transmitter: A69-9001-19150



Catfish Movement Line for transmitter: A69-9001-19151



Catfish Movement Line for transmitter: A69-9001-19153





Catfish Movement Line for transmitter: A69-9001-19157



Catfish Movement Line for transmitter: A69-9001-19159



Catfish Movement Line for transmitter: A69-9001-19161



Catfish Movement Line for transmitter: A69-9001-19163



Catfish Movement Line for transmitter: A69-9001-19164



Catfish Movement Line for transmitter: A69-9001-19165



Catfish Movement Line for transmitter: A69-9001-19166


Catfish Movement Line for transmitter: A69-9001-19167



Catfish Movement Line for transmitter: A69-9001-19168



Catfish Movement Line for transmitter: A69-9001-19169



Catfish Movement Line for transmitter: A69-9001-19170



Catfish Movement Line for transmitter: A69-9001-19171



Catfish Movement Line for transmitter: A69-9001-19172



Catfish Movement Line for transmitter: A69-9001-19173



Catfish Movement Line for transmitter: A69-9001-19174



Catfish Movement Line for transmitter: A69-9001-19175



Catfish Movement Line for transmitter: A69-9001-19176



Catfish Movement Line for transmitter: A69-9001-19177



Catfish Movement Line for transmitter: A69-9001-19178





Catfish Movement Line for transmitter: A69-9001-19180









Catfish Movement Line for transmitter: A69-9001-19184



Catfish Movement Line for transmitter: A69-9001-19185



Catfish Movement Line for transmitter: A69-9001-19186



Catfish Movement Line for transmitter: A69-9001-19187



Catfish Movement Line for transmitter: A69-9001-19188



Catfish Movement Line for transmitter: A69-9001-19189











Catfish Movement Line for transmitter: A69-9001-19195



Catfish Movement Line for transmitter: A69-9001-19196









Catfish Movement Line for transmitter: A69-9001-19643



Catfish Movement Line for transmitter: A69-9001-19644



Catfish Movement Line for transmitter: A69-9001-19646



Catfish Movement Line for transmitter: A69-9001-19647


Catfish Movement Line for transmitter: A69-9001-19648









Catfish Movement Line for transmitter: A69-9001-19652



Catfish Movement Line for transmitter: A69-9001-19653













Catfish Movement Line for transmitter: A69-9001-19659







Catfish Movement Line for transmitter: A69-9001-19665





Catfish Movement Line for transmitter: A69-9001-19667







Catfish Movement Line for transmitter: A69-9001-19670



Catfish Movement Line for transmitter: A69-9001-21078



Catfish Movement Line for transmitter: A69-9001-21079





Catfish Movement Line for transmitter: A69-9001-21081









Catfish Movement Line for transmitter: A69-9001-21086







Appendix C. 2017 Fate exploration map of channel catfish tagged with acoustic transmitters where dots represent approximate last detected location of each individual. Color indicates number of unique receivers detected up until last detection.



Figure C – 1 Map of last known detections of channel catfish tagged with acoustic transmitters in 2017

Appendix D. 2018 Results from live tracking for fish tagged with acoustic transmitters from

St. Andrews Lock and Dam downstream to Lake Winnipeg

Table D –1 Detections from live tracking efforts in 2018 shown with initial tagging information. Drifts were conducted from Lockport Dam to Lake Winnipeg. Drifts were conducted as follows: Lockport Dam to River Kilometer 19 on July 24th, 2018, River Kilometer 19 to Lake Winnipeg on July 27th, 2018, Lockport Dam to River Kilometer 24 on August 6th, 2018, and River Kilometer 24 to Lake Winnipeg on August 9th, 2018. Cells highlighted in red are transmitters that were detected twice across drifts. Transmitters with "NA" for species were individuals that did not match any tag IDs in the Tagging Data Spreadsheet maintained by DFO, downloaded August 21, 2018. Twenty-five unique individuals were detected from live tracking: 7 channel catfish, 2 walleye, 2 lake sturgeon, 11 bigmouth buffalo, and 3 NAs

Date	Time	Tag ID Full	Species	Tagging Site	Date Tagged
7/24/2018	11:23	A69-9001 #19660	Channel Catfish	Red River	4-Jun-16
7/24/2018	11:23	A69-9001 #25534	NA	NA	NA
7/24/2018	11:45	A69-9001 #17724	Walleye	Red River	3-May-17
7/24/2018	11:45	A69-9001 #17895	Channel Catfish	Red River	14-Jun-16
7/24/2018	11:56	A69-9001 #19662	Lake Sturgeon	Red River	3-Jun-16
7/24/2018	12:09	A69-9001 #17877	Channel Catfish	Red River	11-Jun-16
7/24/2018	12:32	A69-9001 #19651	Channel Catfish	Red River	2-Jun-16
7/24/2018	12:49	A69-9001 #19653	Channel Catfish	Red River	2-Jun-16
7/24/2018	12:50	A69-9001 #14996	Bigmouth Buffalo	Red River	22-Jun-17
7/24/2018	13:35	A69-9001 #14994	Bigmouth Buffalo	Red River	20-Jun-17
7/24/2018	13:45	A69-9001 #14991	Bigmouth Buffalo	Red River	20-Jun-17
7/24/2018	14:54	A69-9001 #14990	Bigmouth Buffalo	Red River	20-Jun-17
7/24/2018	15:01	A69-9001 #14982	Bigmouth Buffalo	Red River	19-Jun-17
7/24/2018	15:01	A69-9001 #19225	Bigmouth Buffalo	Seine River	6-Jun-16
7/24/2018	15:15	A69-1601 #65011	NA	NA	NA
7/24/2018	15:15	A69-1601 #65127	NA	NA	NA
7/24/2018	15:46	A69-9001 #14983	Bigmouth Buffalo	Red River	13-Jun-17
7/24/2018	15:46	A69-9001 #14986	Bigmouth Buffalo	Red River	19-Jun-17
7/24/2018	15:46	A69-9001 #20020	Bigmouth Buffalo	Seine River	10-Jun-16
7/24/2018	16:05	A69-9001 #15800	Bigmouth Buffalo	Red River - US	16-Jun-17
7/27/2018	10:22	A69-9001 #19319	Bigmouth Buffalo	Red River	26-Jun-17
7/27/2018	11:26	A69-9001 #19658	Channel Catfish	Red River	4-Jun-16
8/6/2018	10:09	A69-9001 #14994	Bigmouth Buffalo	Red River	20-Jun-17
8/6/2018	11:00	A69-9001 #16524	Lake Sturgeon	Red River	22-Jun-17
8/6/2018	11:09	A69-9001 #19660	Channel Catfish	Red River	4-Jun-16
8/6/2018	11:34	A69-9001 #19175	Channel Catfish	Red River	10-Jun-16
8/6/2018	11:36	A69-9001 #17895	Channel Catfish	Red River	14-Jun-16
8/6/2018	11:37	A69-9001 #19662	Lake Sturgeon	Red River	3-Jun-16
8/6/2018	11:47	A69-9001 #25534	NA	NA	NA
8/6/2018	12:01	A69-9001 #17877	Channel Catfish	Red River	11-Jun-16
8/6/2018	12:30	A69-9001 #19651	Channel Catfish	Red River	2-Jun-16
8/6/2018	12:50	A69-9001 #19653	Channel Catfish	Red River	2-Jun-16
8/6/2018	13:31	A69-9001 #14991	Bigmouth Buffalo	Red River	20-Jun-17
8/6/2018	14:40	A69-1602 #27160	Walleye	Red River	8-May-18
8/9/2018	13:51	A69-9001 #20020	Bigmouth Buffalo	Seine River	10-Jun-16

Table D – 2 Catfish last detected via the receiver network in the Lower Portion of the Red River (Lockport Dam to Lake). Individuals with low numbers of unique receivers and detections are suspected to be mortality events. Individuals highlighted in orange are catfish detected once during live tracking and individuals in red were detected twice during live tracking. Only 1 catfish detected during live tracking is not present in this table.

Transmitter	Last Detection	# of	Last Reseiver Name	# of Unique
		Detections	Last Receiver Name	Receivers
A69-1601-19667	3/25/2017 5:17	1	Red rkm 24	1
A69-9001-17874	8/9/2016 4:25	124	Red rkm 14	7
A69-9001-17877	10/3/2016 10:26	1994	Red rkm 39	3
A69-9001-17880	4/8/2017 19:12	7644	Red rkm 14	7
A69-9001-17888	4/30/2017 19:12	95	Cooks Creek	8
A69-9001-17892	6/28/2016 16:39	40	Red rkm 34	8
A69-9001-17894	6/20/2016 20:38	7	Red rkm 34	2
A69-9001-17898	7/9/2016 1:09	465	Red rkm 14	2
A69-9001-19175	10/3/2016 10:28	16428	Red rkm 39	2
A69-9001-19176	7/19/2016 7:41	1006	Straight Creek	5
A69-9001-19178	7/17/2016 12:04	480	West Channel Red River	8
A69-9001-19179	7/10/2017 6:40	2169	Red East Channel	9
A69-9001-19182	6/29/2016 23:46	20	West Channel Red River	1
A69-9001-19184	6/22/2016 22:11	225	Devils Creek	4
A69-9001-19186	6/21/2016 12:58	659	Red rkm 14	3
A69-9001-19188	7/6/2016 15:08	374	Red rkm 9	2
A69-9001-19189	6/25/2017 23:21	175	Red rkm 9	2
A69-9001-19191	7/1/2016 16:23	3	Red rkm 9	1
A69-9001-19192	6/16/2016 20:21	68	Red rkm 4	2
A69-9001-19193	6/20/2016 23:57	1	Red rkm 9	1
A69-9001-19195	11/10/2016 15:46	1126	Red East Channel	9
A69-9001-19642	6/27/2016 8:58	541	Red East Channel	4
A69-9001-19643	7/6/2016 12:52	69	Devils Creek	2
A69-9001-19644	6/25/2017 8:22	432	Red East Channel	1
A69-9001-19645	6/12/2016 20:36	1	Red rkm 9	1
A69-9001-19647	6/7/2016 9:09	22	Red rkm 4	3
A69-9001-19648	6/24/2016 4:07	255	Straight Creek	2
A69-9001-19649	9/8/2017 2:18	4063	Cochrane Lake	51
A69-9001-19651	10/1/2016 8:10	5201	Red rkm 34	29
A69-9001-19652	7/25/2016 8:16	9390	Cooks Creek	2
A69-9001-19653	8/3/2017 11:33	8507	Morrison Lake	7
A69-9001-19655	6/13/2016 5:59	13	Cooks Creek	1
A69-9001-19656	6/30/2016 13:04	219	Red East Channel	6
A69-9001-19657	6/4/2016 0:35	2	Red rkm 14	1
A69-9001-19658	11/13/2016 0:22	1695	Red rkm 9	7
A69-9001-19660	6/3/2017 2:05	2828	Red rkm 34	7
A69-9001-19661	6/4/2016 4:46	1	Red rkm 14	1
A69-9001-19665	6/27/2016 18:23	31	Red rkm 14	4
A69-9001-19669	10/7/2016 13:16	6120	Red rkm 24	4
A69-9001-19670	6/15/2016 6:30	9	Red East Channel	2
A69-9001-19671	7/1/2016 2:29	1	Red rkm 9	1
A69-9001-21078	6/24/2016 4:08	180	Devils Creek	3
A69-9001-21080	3/29/2017 12:57	15622	Red rkm 14	3
A69-9001-21087	6/27/2016 17:20	103	Red rkm 14	6
A69-9001-21088	7/5/2016 12:51	39	2nd East Channel Red River	1


Figure D – 3 2018 Lower Red River Live Tracking Detections for Bigmouth Buffalo



Figure D – 4 2018 Lower Red River Live Tracking Detections for Channel Catfish



Figure D – 5 2018 Lower Red River Live Tracking Detections for Lake Sturgeon



Figure D – 6 2018 Lower Red River Live Tracking Detections for Not Available/No Tag Match



Figure D – 7 2018 Lower Red River Live Tracking Detections for Walleye

Appendix E. JAGS code for Bayesian State-Space Models and script code to run models in R

R Code E – 1 Telemetry model & and script code to run model

```
model {
  # Priors - survival and recapture for each state
  for(r in 1:4){
    phi[r] ~ dunif(0,1)
    p[r] ~ dunif(0,1)
  }
  #priors for "end" transistions
  psia ~ dunif(0,1)
  psid ~ dunif(0,1)
  # Create input vector for dirichlet distribution
  alpha[1] <- 1
  alpha[2] <- 1
  alpha[3] <- 1
  # Bound inside transitions by 1
  psib[1:3] ~ ddirch(alpha[1:3])
  psic[1:3] ~ ddirch(alpha[1:3])
  # Likelihood
  for (i in 1:M)
    z[i, first[i]] <- y[i, first[i]]</pre>
  for (t in (first[i] + 1):TS){
    z[i, t] ~ dcat(ps[z[i,t-1],])
    y[i, t] ~ dcat(po[z[i,t],])
    }
  }
    # State Transition Matrix
    ps[1,1] <- phi[1] * (1-psia)
    ps[1,2] <- phi[1] * psia
    ps[1,3] <- 0
    ps[1,4] <- 0
    ps[1,5] <- 1-phi[1]
    ps[2,1] <- phi[2] * psib[1]
    ps[2,2] <- phi[2] * psib[3]
    ps[2,3] <- phi[2] * psib[2]
```

```
ps[2,4] <- 0
ps[2,5] <- 1 - phi[2]
ps[3,1] <- 0
ps[3,2] <- phi[3] * psic[1]
ps[3,3] <- phi[3] * psic[3]
ps[3,4] <- phi[3] * psic[2]
ps[3,5] <- 1 - phi[3]
ps[4,1] <- 0
ps[4,2] <- 0
ps[4,3] <- phi[4] * psid
ps[4,4] <- phi[4] * (1-psid)
ps[4,5] <- 1 - phi[4]
ps[5,1] <- 0
ps[5,2] <- 0
ps[5,3] <- 0
ps[5,4] <- 0
ps[5,5] <- 1
```

Observation matrix - state vs state where ind was seen

```
po[1,1] <- p[1]
po[1,2] <- 0
po[1,3] <- 0
po[1,5] <- 1-p[1]
po[1,4] <- 0
po[2,1] <- 0
po[2,2] <- p[2]
po[2,3] <- 0
po[2,4] <- 0
po[2,5] <- 1-p[2]
po[3,1] <- 0
po[3,2] <- 0
po[3,3] <- p[3]
po[3,4] <- 0
po[3,5] <- 1-p[3]
po[4,1] <- 0
po[4,2] <- 0
po[4,3] <- 0
po[4,4] <- p[4]
po[4,5] <- 1-p[4]
```

```
po[5,1] <- 0
     po[5,2] <- 0
     po[5,3] <- 0
     po[5,4] <- 0
     po[5,5] <- 1
}
#Script Code
#load libraries
library(tidyverse)
library(rjags)
library(runjags)
library(mcmcplots)
capt.hist <- readRDS("data/capt-hist.rds")</pre>
first <- readRDS("data/first.rds")</pre>
M = nrow(capt.hist) # Number of unique inds
TS = ncol(capt.hist) # Maximum number of time steps
data <- list(y = capt.hist, first = first, M = M, TS = TS)</pre>
z = matrix(NA, M, TS)
for (i in 1:M) {
  for (t in first[i]:TS) {
     z[i, t] <- capt.hist[i, t]</pre>
     if(z[i,t]==5) z[i,t]=z[i,t-1]
  }
  z[i,first[i]]=NA
}
znew = z
ynew = y
inits = list(
  list(psia = .3, psid = .1,
     p = c(.05, .9, .2, .1),
     phi = c(.6, .5, .5, .9),
     psib = c(.2, .6, .2),
     psic = c(.2, .6, .2),
     z=z,
     znew = znew),
   list(psia = .1, psid = .02,
      p = c(.01, .6, .6, .8),
```

```
phi = c(.9, .9, .7, .8),
      psib = c(.1, .8, .1),
      psic = c(.6, .3, .1),
      z=z,
      znew = znew),
   list(psia = .6, psid = .05,
      p = c(.1, .5, .8, .97),
      phi = c(.5, .7, .9, .5),
      psib = c(.9, .05, .05),
      psic = c(.1, .4, .5),
      z=z,
      znew = znew),
   list(psia = .9, psid = .2,
      p = c(.07, .99, .45, .5),
      phi = c(.7, .3, .8, .2),
      psib = c(.05, .05, .9),
      psic = c(.3, .05, .65),
      z=z,
      znew = znew)
)
```

parameters <- c("phi","psia","psib","psic","psid","p","z","znew","ynew")</pre>

#pull model into R

jm = jags.model("JagsModel.R", data, inits = inits, n.chains = 4, n.adapt = 100)

#burn in update(jm, n.iter = 3000)

#generate chains
cs = coda.samples(jm, parameters, n.iter = 20000)

summary(cs)
mcmcplot(cs)

mcmcplot(cs,parms = c("p[1]", "p[2]","p[3]","p[4]","psia","psid", "phi[1]", "phi[2]", "phi[3]", "phi[4]", "psib[1]", "psib[2]", "psib[3]", "psic[1]", "psic[2]", "psic[3]"))

```
model {
  # Priors - survival and recapture for each state
  for(r in 1:4){
    phi[r] ~ dunif(0,1)
    p[r] ~ dunif(0,1)
  }
  #priors for "end" transistions
  psia ~ dunif(0,1)
  psid ~ dunif(0,1)
  # Create input vector for dirichlet distribution
  alpha[1] <- 1
  alpha[2] <- 1
  alpha[3] <- 1
  # Bound inside transitions by 1
  psib[1:3] ~ ddirch(alpha[1:3])
  psic[1:3] ~ ddirch(alpha[1:3])
  #skip parameter
  omega ~ dunif(0,1)
  # Likelihood
  for (i in 1:M){
    z[i, first[i]] <- y[i, first[i]]</pre>
    for (t in (first[i] + 1):TS){
      z[i, t] ~ dcat(ps[z[i,t-1],])
      y[i, t] ~ dcat(po[z[i,t],])
    }
  }
  # State Transition Matrix
  ps[1,1] <- phi[1] * (1-psia)
  ps[1,2] <- phi[1] * psia * omega
  ps[1,3] <- phi[1] * psia * (1-omega) * omega
  ps[1,4] <- phi[1] * psia * (1-omega) * (1-omega)
  ps[1,5] <- 1-phi[1]
  ps[2,1] <- phi[2] * psib[1]
  ps[2,2] <- phi[2] * psib[3]
```

```
ps[2,3] <- phi[2] * psib[2] * (omega)
ps[2,4] <- phi[2] * psib[2] * (1-omega)
ps[2,5] <- 1 - phi[2]
ps[3,1] <- phi[3] * psic[1] * (1-omega)
ps[3,2] <- phi[3] * psic[1] * (omega)
ps[3,3] <- phi[3] * psic[3]
ps[3,4] <- phi[3] * psic[2]
ps[3,5] <- 1 - phi[3]
ps[4,1] <- phi[4] * psid * (1-omega) * (1-omega)
ps[4,2] <- phi[4] * psid * (1-omega) * omega
ps[4,3] <- phi[4] * psid * (omega)
ps[4,4] <- phi[4] * (1-psid)
ps[4,5] <- 1 - phi[4]
ps[5,1] <- 0
ps[5,2] <- 0
ps[5,3] <- 0
ps[5,4] <- 0
ps[5,5] <- 1
```

Observation matrix - state vs state where ind was seen

```
po[1,1] <- p[1]
po[1,2] <- 0
po[1,3] <- 0
po[1,5] <- 1-p[1]
po[1,4] <- 0
po[2,1] <- 0
po[2,2] <- p[2]
po[2,3] <- 0
po[2,4] <- 0
po[2,5] <- 1-p[2]
po[3,1] <- 0
po[3,2] <- 0
po[3,3] <- p[3]
po[3,4] <- 0
po[3,5] <- 1-p[3]
po[4,1] <- 0
po[4,2] <- 0
po[4,3] <- 0
po[4,4] <- p[4]
```

```
po[4,5] <- 1-p[4]
po[5,1] <- 0
po[5,2] <- 0
po[5,3] <- 0
po[5,4] <- 0
po[5,5] <- 1
}
```

```
#Script Code
#load libraries
library(tidyverse)
library(rjags)
library(mcmcplots)
library(dclone)
library(doParallel)
```

```
n.cores <- 4
timings <- vector('numeric', 6)</pre>
```

```
capt.hist <- readRDS("floy-Run1/Data/floy-capt-hist.rds")
first <- readRDS("floy-Run1/Data/floyfirst.rds")</pre>
```

```
M = nrow(capt.hist) # Number of unique inds
TS = ncol(capt.hist) # Maximum number of time steps
```

```
data <- list(y = capt.hist, first = first, M = M, TS = TS)</pre>
```

```
z = matrix(NA, M, TS)
for (i in 1:M) {
    for (t in first[i]:TS) {
        z[i, t] <- capt.hist[i, t]
        if(z[i,t]==5) z[i,t]=z[i,t-1]
    }
    z[i,first[i]]=NA
}
inits = list(
    list(psia = .3, psid = .1,
        p = c(.05, .9, .2, .1),
        phi = c(.6, .5, .5, .9),</pre>
```

```
psib = c(.2, .6, .2),
     psic = c(.2, .6, .2),
     z=z,
     #
           znew = znew,
     omega = .9),
  list(psia = .1, psid = .02,
     p = c(.01, .6, .6, .8),
     phi = c(.9, .9, .7, .8),
     psib = c(.1, .8, .1),
     psic = c(.6, .3, .1),
     z=z,
     #
           znew = znew,
     omega = .95),
  list(psia = .6, psid = .05,
     p = c(.1, .5, .8, .97),
     phi = c(.5, .7, .9, .5),
     psib = c(.9, .05, .05),
     psic = c(.1, .4, .5),
     z=z,
     #
           znew = znew,
     omega = .97),
  list(psia = .9, psid = .2,
     p = c(.07, .99, .45, .5),
     phi = c(.7, .3, .8, .2),
     psib = c(.05, .05, .9),
     psic = c(.3, .05, .65),
     z=z,
     #
           znew = znew,
     omega = .89
)
```

params <- c("phi","psia","psib","psic","psid","p", "omega")</pre>

stopCluster(cl)
time.taken <- proc.time() - timer
timings[3] <- time.taken[3]</pre>

summary(m2) # mcmcplot(cs)

mcmcplot(m2,parms = c("p[1]", "p[2]","p[3]","p[4]","psia","psid", "phi[1]", "phi[2]", "phi[3]", "phi[4]", "psib[1]", "psib[2]", "psib[3]", "psic[1]", "psic[2]", "psic[3]", "omega"))

caterplot(m2)

saveRDS(m2, file="floy-Run1-cs.rds")

R Code E – 3 Comprehensive Model JAGS code & script code to run model

model {

```
# Priors for fish mortality, natural mortality and capture probability
F ~ dunif(0,2)
M ~ dunif(0,2)
Z <- F + M
phi <- exp(-Z)
p ~ dunif(0,1)</pre>
```

```
#priors for "end" transistions
psia ~ dunif(0,1)
psid ~ dunif(0,1)
```

```
# Create input vector for dirichlet distribution
alpha[1] <- 1
alpha[2] <- 1
alpha[3] <- 1</pre>
```

```
# Bound inside transitions by 1
psib[1:3] ~ ddirch(alpha[1:3])
psic[1:3] ~ ddirch(alpha[1:3])
```

```
#skip parameter
omega ~ dunif(0,1)
```

```
# Likelihood
for (i in 1:n){
    z[i, first[i]] <- y[i, first[i]]
    for (t in (first[i] + 1):last[i]){
        z[i, t] ~ dcat(ps[z[i,t-1],])
        y[i, t] ~ dcat(po[z[i,t],])</pre>
```

```
}
}
```

State Transition Matrix

ps[1,1] <- phi * (1-psia) ps[1,2] <- phi * psia * omega

```
ps[1,3] <- phi * psia * (1-omega) * omega
ps[1,4] <- phi * psia * (1-omega) * (1-omega)
ps[1,5] <- M*(1-phi)/Z
ps[1,6] <- F*(1-phi)/Z
ps[2,1] <- phi * psib[1]
ps[2,2] <- phi * psib[3]
ps[2,3] <- phi * psib[2] * (omega)
ps[2,4] <- phi * psib[2] * (1-omega)
ps[2,5] <- M*(1-phi)/Z
ps[2,6] <- F*(1-phi)/Z
ps[3,1] <- phi * psic[1] * (1-omega)
ps[3,2] <- phi * psic[1] * (omega)
ps[3,3] <- phi * psic[3]
ps[3,4] <- phi * psic[2]
ps[3,5] <- M*(1-phi)/Z
ps[3,6] <- F*(1-phi)/Z
ps[4,1] <- phi * psid * (1-omega) * (1-omega)
ps[4,2] <- phi * psid * (1-omega) * omega
ps[4,3] <- phi * psid * (omega)
ps[4,4] <- phi * (1-psid)
ps[4,5] <- M*(1-phi)/Z
ps[4,6] <- F*(1-phi)/Z
ps[5,1] <- 0
ps[5,2] <- 0
ps[5,3] <- 0
ps[5,4] <- 0
ps[5,5] <- 1
ps[5,6] <- 0
ps[6,1] <- 0
ps[6,2] <- 0
ps[6,3] <- 0
ps[6,4] <- 0
ps[6,5] <- 0
```

Obsvation matrix - state vs state where ind was seen

po[1,1] <- p po[1,2] <- 0 po[1,3] <- 0 po[1,4] <- 0 po[1,5] <- 1-p po[1,6] <- 0

ps[6,6] <- 1

```
po[2,1] <- 0
po[2,2] <- p
po[2,3] <- 0
po[2,4] <- 0
po[2,5] <- 1-p
po[2,6] <- 0
po[3,1] <- 0
po[3,2] <- 0
po[3,3] <- p
po[3,4] <- 0
po[3,5] <- 1-p
po[3,6] <- 0
po[4,1] <- 0
po[4,2] <- 0
po[4,3] <- 0
po[4,4] <- p
po[4,5] <- 1-p
po[4,6] <- 0
po[5,1] <- 0
po[5,2] <- 0
po[5,3] <- 0
po[5,4] <- 0
po[5,5] <- 1
po[5,6] <- 0
po[6,1] <- 0
po[6,2] <- 0
po[6,3] <- 0
po[6,4] <- 0
po[6,5] <- 0
po[6,6] <- 1
```

}

#Script code #load libraries library(tidyverse) library(rjags) library(mcmcplots) library(dclone) library(doParallel)

```
n.cores <- 4
timings <- vector('numeric', 6)</pre>
```

```
capt.hist <- readRDS("ATF-capt-hist.rds")
first <- readRDS("First.rds")
last <- readRDS("Last.rds")
capt.hist[capt.hist == 0] <- NA</pre>
```

```
# #try smaller dataset
# capt.hist <- capt.hist[100:130,]
# first <- first[100:130]
# last <- last[100:130]</pre>
```

```
n = nrow(capt.hist) # Number of unique inds
TS = ncol(capt.hist) # Maximum number of time steps
```

```
data <- list(y = capt.hist, first = first, last=last, n = n)</pre>
```

```
z = matrix(NA, n, TS)
for (i in 1:n) {
    for (t in first[i]:last[i]) {
        z[i, t] <- capt.hist[i, t]
        if(z[i,t]==5) z[i,t]=z[i,t-1]
    }
    z[i,first[i]]=NA
}</pre>
```

```
inits = list(
    list(psia = .3, psid = .1,
        p = .5,
        F = runif(1, min=0, max=2),
        M = runif(1, min=0, max=2),
        psib = c(.2, .6, .2),
        psic = c(.2, .6, .2),
        z=z,
        omega = .9),

list(psia = .1, psid = .02,
        p = .8,
        F = runif(1, min=0, max=2),
        M = runif(1, min=0, max=1),
        M = runif(1, min=0, max=1),
```

```
psib = c(.1, .8, .1),

psic = c(.6, .3, .1),
```

```
z=z,
     omega = .95),
  list(psia = .6, psid = .05,
     p = .1,
     F = runif(1, min=0, max=2),
     M = runif(1, min=0, max=2),
     psic = c(.1, .4, .5),
     z=z,
     omega = .97),
  list(psia = .9, psid = .2,
     p = .45,
     F = runif(1, min=0, max=2),
     M = runif(1, min=0, max=2),
     psib = c(.05, .05, .9),
     psic = c(.3, .05, .65),
     z=z,
     omega = .89
)
params <- c("F", "M","psia","psib","psic","psid","p", "omega")</pre>
## fit with parJagsModel
timer <- proc.time()</pre>
cl <- makePSOCKcluster(n.cores)</pre>
parJagsModel(cl = cl, name = 'res', file = "Jags-comp.R", data = data, inits = inits,
       n.chains = 4, n.adapt = 5000)
```

```
time.taken <- proc.time() - timer
timings[3] <- time.taken[3]</pre>
```

```
summary(m2)
# mcmcplot(cs)
```

```
mcmcplot(m2)
```

```
caterplot(m2)
```

```
saveRDS(m2, file="comp-Run1-cs.rds")
```

Appendix F. Bayesian State-Space Modelling Diagnostic Plots for Parameters using the

'mcmcplots' package from R programming language





Diagnostics for p[1]



heration

Diagnostics for p[2]



Diagnostics for p[3]



Diagnostics for p[4]



Diagnostics for phi[1]



Diagnostics for phi[2]



Diagnostics for phi[3]



Diagnostics for phi[4]



Diagnostics for psia



Diagnostics for psib[1]



Diagnostics for psib[2]





8000

4000

Diagnostics for psib[3]

П

14000







Diagnostics for psic[2]



Diagnostics for psic[3]


Diagnostics for psid

Figure F – 2 T-bar Model Diagnostic Plots



Diagnostics for p[1]



Diagnostics for p[2]



Iteration

Diagnostics for p[3]



Diagnostics for p[4]



Diagnostics for phi[1]







heration

Diagnostics for phi[3]



Diagnostics for phi[4]



Diagnostics for psia



Iteration

Diagnostics for psib[1]



Diagnostics for psib[2]



1 8000

ï

10000

Iteration

Т

12000

6000

T.

4000

Diagnostics for psib[3]

14000















Diagnostics for psid

Diagnostics for omega





Figure F – 3 Comprehensive Model Diagnostic Plots

323



Diagnostics for M













Diagnostics for psib[2]



















Diagnostics for psid





Diagnostics for omega