

South Dakota State University
**Open PRAIRIE: Open Public Research Access Institutional
Repository and Information Exchange**

Electronic Theses and Dissertations


2018

Walleye Fishery Ecology in Lake Oahe of the Dakotas

Eli Felts

South Dakota State University

Follow this and additional works at: <https://openprairie.sdstate.edu/etd>

 Part of the [Aquaculture and Fisheries Commons](#), and the [Natural Resources Management and Policy Commons](#)

Recommended Citation

Felts, Eli, "Walleye Fishery Ecology in Lake Oahe of the Dakotas" (2018). *Electronic Theses and Dissertations*. 2465.
<https://openprairie.sdstate.edu/etd/2465>

This Dissertation - Open Access is brought to you for free and open access by Open PRAIRIE: Open Public Research Access Institutional Repository and Information Exchange. It has been accepted for inclusion in Electronic Theses and Dissertations by an authorized administrator of Open PRAIRIE: Open Public Research Access Institutional Repository and Information Exchange. For more information, please contact michael.biondo@sdstate.edu.

WALLEYE FISHERY ECOLOGY IN LAKE OAHE OF THE DAKOTAS

BY

ELI FELTS

A dissertation submitted in partial fulfillment of the requirements for the

Doctor of Philosophy

Major in Wildlife and Fisheries Sciences

South Dakota State University

2018

WALLEYE FISHERY ECOLOGY IN LAKE OAHÉ OF THE DAKOTAS

This dissertation is approved as a creditable and independent investigation by a candidate for the Doctor of Philosophy in Wildlife and Fisheries Science and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this does not imply that the conclusions reached by the candidates are necessarily the conclusions of the Department of Natural Resources

~~Brian D. S. Graeb~~, Ph. D.
Dissertation Advisor

Date

Michele R. Dudash Ph.D.
Head, Department of Natural
Resource Management

Date

~~Dean~~, Graduate School

Date

ACKNOWLEDGEMENTS

This project was funded by the Federal Aid in Sport Fish Restoration Act Study number 1529 administered by South Dakota Department of Game, Fish, and Parks.

Additional financial support was provided by the North Dakota Game and Fish Department.

Staff of the South Dakota Department of Game, Fish and Parks and North Dakota Game and Fish Department completed the majority of the field work associated with this project. I want to especially thank Paul Bailey, Jason Barstad, Dave Fryda, Mike Greiner, Bob Hanten, Dan Jost, Jason Jungwirth, Russ Kinzer, Hilary Meyer, Kyle Potter, and Mike Smith for their efforts. I also wish to acknowledge the data used in chapters 2 and 5 of this dissertation were collected over a span of greater than 25 years by a small army of South Dakota Department of Game, Fish, and Parks employees. Ryan Johnston, Carlee Fletcher, and Dylan Gravenhof worked as technicians for this project. Many South Dakota State University students contributed to the tagging efforts involved in this study; I want to specifically acknowledge assistance provided by Nick Kludt and Matt Wagner. My dad, Craig Felts, also assisted with tagging efforts during 2014-2016. Literally thousands of anglers voluntarily reported tagged walleyes as part of this study, and I am grateful for their cooperation. Friendly reviews of select chapters in this dissertation were provided by Dan Dembkowski and Josh McCormick and greatly improved the writing and content presented therein.

A great deal of support was also provided by staff within the Department of Natural Resource Management at South Dakota State University. Kate Tvedt, Terri Symens, and Dawn Van Ballegooyen provided administrative support and were a joy to

work with. Many graduate students have passed through SDSU during my time here, and the relationships and conversations with them helped to challenge and shape my thinking about this project and science in general. Jason Breeggemann, Dan Dembkowski, David Deslauriers, Adam Janke, and David Schumann were particularly influential during my time as a doctoral student.

One of my dominant feelings as I near the completion of this degree is a profound sense of gratitude to the people who played a significant role in my development without realizing the depth of their impact. While it is impossible to recognize all those folks here, there are a few who I feel compelled to acknowledge. I had two exceptional ecology and evolution professors at the University of Wisconsin-Oshkosh who sparked my interest in population biology: Dr. Gregory Adler and Dr. Bob Stelzer. I didn't realize it at the time, but I learned everything I needed to know about fisheries biology in Dr. Adler's Population and Community Ecology class. I'm also happy to report that to this day I instinctively recoil at the use of "data" as a singular noun; data were, are, and shall always be, plural. Dr. Katie Graeb baptized me into academia, taught me how to be a scientist, and has continued to be a valued friend and mentor. Anyone who studies fisheries science at South Dakota State University owes an enormous debt of gratitude to the late Dr. David Willis, and I am personally humbled to be counted as part of the Willis Nation. While writing this dissertation I have often envisioned Dave as the editor, and I hope the content reflects this strategy.

I'd like to thank my graduate committee which consisted of Dr. Steve Chipps, and my co-advisors: Dr. Mark Fincel and Dr. Brian Graeb. Steve's research is everywhere in this dissertation, and so are lessons I learned in his outstanding Aquatic Trophic Ecology

course. Mark has been a great bridge between academia and the state agency environment and is an invaluable resource for all things Missouri River. He's pretty funny, too. Brian has influenced my development as a fisheries scientist more than any single person. He is a phenomenal teacher and I'm extremely thankful to have spent 8 years learning from him.

I thank my family who has supported and believed in me throughout this very long and sometimes frustrating process. My wife, Brandi, has not only supported me, but did so while she herself was a doctoral student. I'm not sure that I could have made it through without her by my side, but I'm forever grateful that I didn't have to find out.

CONTENTS

ABSTRACT.....	viii
CHAPTER 1: INTRODUCTION.....	1
Dissertation Content and Format	10
CHAPTER 2: INFLUENCE OF SPATIAL COMPLEXITY AND ENVIRONMENTAL FACTORS ON WALLEYE RECRUITMENT IN A LARGE MISSOURI RIVER RESERVOIR.....	15
Abstract.....	15
Introduction	16
Methods.....	18
Results.....	23
Discussion	25
References	31
CHAPTER 3: USE OF HIGH-REWARD TAGS AND DOUBLE-TAGGING TO ESTIMATE ANGLER REPORTING AND JAW-TAG LOSS RATE FOR LAKE OAHE WALLEYE	45
Abstract.....	45
Introduction	46
Methods.....	47
Results.....	50
Discussion	51
References	55
CHAPTER 4: WALLEYE MOVEMENT PATTERNS INFERRED FROM TAGGING IN LAKE OAHE.....	64
Abstract.....	64
Introduction	65
Methods.....	68
Discussion	78
References	85
CHAPTER 5: ANGLER RESPONSE TO WALLEYE POPULATION VARIABILITY IN LAKE OAHE, SOUTH DAKOTA.....	103
Abstract.....	103
Introduction	103
Methods.....	106
Results.....	109
Discussion	109

References	112
CHAPTER 6: SPATIAL VARIATION IN WALLEYE POPULATION RESPONSE TO FLOOD IMPACTS IN A LARGE MISSOURI RIVER RESERVOIR	118
Abstract.....	118
Introduction	119
Methods.....	122
Results.....	126
Discussion	128
References	136
CHAPTER 7: CONCLUSIONS.....	149
Summary.....	149
Research needs.....	151
References	154

ABSTRACT

WALLEYE FISHERY ECOLOGY IN LAKE OAHE OF THE DAKOTAS

ELI FELTS

2018

Walleye *Sander vitreus* is among the most popular sport fishes in North America and is the most sought-after fish in both South Dakota and North Dakota. Lake Oahe, a large main stem Missouri River reservoir, spans state boundaries and provides one of the most popular and productive Walleye fisheries in both Dakotas. The Walleye population of Lake Oahe has experienced wide fluctuations in abundance and size structure over the last 25 years which has caused high variability in angler use and satisfaction. Much of this variation is thought to be driven by Rainbow Smelt *Osmerus mordax*, which are the dominant prey for Lake Oahe Walleye and are characterized by erratic population dynamics. Rainbow Smelt in Lake Oahe are also prone to high entrainment rates during periods of high discharge. Twice during the last 25 years greater than 90% of the Rainbow Smelt population in Lake Oahe was lost due to high entrainment. I utilized long-term monitoring efforts by the South Dakota Department of Game, Fish, and Parks and assisted with a 5-year tagging study to research several components of the Lake Oahe Walleye fishery. Specific research areas included recruitment, movement, natural mortality, and fishing mortality of the Walleye population. I also studied the impact of Walleye population variability on angling. Throughout my research I paid special attention to spatial variation in the Lake Oahe Walleye fishery. I demonstrated that Walleye recruitment in Lake Oahe is consistent but variable and has been regulated by

density independent factors over recent decades. Analysis of tag recoveries showed that Walleye movement in Lake Oahe is related to the configuration of spawning and feeding areas and spatial structuring forms relatively isolated groups within the reservoir. I found that angler catch rates of Walleye in Lake Oahe were independent of abundance but were strongly influenced by condition with highest catch rates occurring when Walleye condition was low. I also documented spatial variation in natural and fishing mortality of Walleye following high entrainment of Rainbow Smelt during 2011. Taken together, my results add to the understanding of Walleye fishery dynamics in Lake Oahe and how those dynamics respond to highly variable climatic, hydrologic, and biotic conditions. Evidence of spatial variation in Walleye population dynamics should be particularly relevant to managers. In addition to providing guidance to management of Lake Oahe, my results are relevant to broader topics such as Walleye fishery dynamics, reservoir ecology, and spatial structuring of freshwater fish populations.

CHAPTER 1: INTRODUCTION

Fisheries management is a complex process which requires understanding of fish population dynamics as well as commercial or recreational fleet dynamics to forecast future conditions and outcomes of potential management actions. Monitoring surveys provide indices of initial conditions after which managers must predict the future status of a population and the effects of potential management actions. Such forecasting is made possible by studying the response of populations and anglers to a range of environmental conditions and management practices.

Fish populations fluctuate in abundance and size structure as a result of variable recruitment, individual growth, and survival rates. Additionally, the distribution of populations within waterbodies may change seasonally and annually due to large-scale movements. To forecast effective management practices, managers should understand which environmental factors drive the variability in these important rate functions and be aware of the range of variability in each component.

Anglers that exploit fish populations exhibit variable effort, catch per unit effort, and in recreational fisheries, harvest decisions. These variables are influenced by dynamics of the target fish population as well as social, economic, and aesthetic factors. Management actions may have indirect effects on angler dynamics (Beard et al. 2003), which must also be considered by managers. Anglers directly influence mortality of fish populations by harvest and hooking mortality, and often indirectly affect growth and recruitment through compensatory density dependence.

Walleye *Sander vitreus* is one of the most popular sport fish in North America, particularly at northern latitudes in the United States and Canada. Walleye ranks first or

second in popularity among anglers throughout their current distribution (Quinn 1992). Walleye are harvested commercially in Canada and portions of the Laurentian Great Lakes. In both Canada and the U.S., aboriginal peoples are permitted to practice subsistence fishing using spearing and netting practices. Recreational Walleye fisheries are harvest-oriented, as Walleye are prized table fare. Accordingly, overexploitation is the most common concern among managers of commercial, subsistence, and recreational Walleye fisheries (Schmalz et al. 2011). However, other components of population dynamics, including recruitment and growth, have been issues in many Walleye fisheries. More recently, researchers have identified important management implications of spatial variation in Walleye population dynamics and movement patterns in large waterbodies such as Lake Erie (Wang et al. 2007; Vandergoot and Brenden 2014).

Overexploitation has been implicated in Walleye fishery declines throughout their geographic distribution. Managers typically respond by designing regulations aimed at reducing fishing mortality. Results of this strategy have ranged from ambiguous success to abject failure suggesting management actions were either ineffective or insufficient, or overexploitation was not the primary cause of fishery decline in the first place. In Canada, Post et al. (2002) demonstrated that recreational fisheries severely depleted many high-profile Walleye fisheries, and asserted that a suite of compensatory food web processes along with insufficient reduction in angling mortality has prevented recovery of those fisheries. Walleye abundance in Lake Erie declined in the late 1960's and early 1970's, leading managers to reduce fishing mortality through implementation of a quota system (Hatch et al. 1987). This action was followed by reductions in fishing mortality and increases in Walleye abundance. However, the quota system ran concurrently with a

phosphorus abatement program which had profound impacts on the food web dynamics in Lake Erie and positively affected Walleye recruitment and growth. Therefore, it is difficult to decouple the effects of reducing fishing mortality from nutrient management, although they were likely both important in the successful recovery of Lake Erie's Walleye fishery. In Mille Lacs Lake, Minnesota, overharvest by a joint fishery (recreational and subsistence) has been implicated in the decline of the Walleye fishery. Strict harvest regulations have been imposed for the Walleye fishery on Mille Lacs Lake, but the Walleye population has shown little sign of recovery. A "Blue Ribbon Panel" of leading Walleye researchers, contracted by the Minnesota Department of Natural Resources to review the Mille Lacs Lake Walleye management, recently concluded that the declining Walleye abundance was most likely due to poor juvenile survival, rather than alternative hypotheses related to insufficient egg production (Venturelli et al. 2014).

Natural mortality of fishes is difficult to measure directly, and often paid less attention than fishing mortality. Nonetheless, natural mortality has the potential to exceed the influence of fishing mortality on total annual mortality of adult populations. Natural mortality of fishes follows a predictable overall trend with lower rates at higher latitudes. As Walleye occupy a broad range of latitudes, populations exhibit a wide range of longevity related to differences in natural mortality, with maximum ages ranging from 4 years at southern latitudes to 32 years at northern latitudes (Bozek et al. 2011). Natural mortality has been identified as a major driver of fisheries collapses for other species, such as Atlantic Cod *Gadus morhua* (Dutil and Lambert 2000), but has rarely been identified as an issue for Walleye.

Walleye recruitment ranges from non-existent (naturally) to variable, and is often the leading cause of interannual variation in population abundance and size structure. In a study of Northern Wisconsin Lakes, Hansen and Nate (2014) demonstrated that size structure of Walleye populations was more strongly driven by recruitment and growth than fishing mortality. Walleye exhibit low juvenile survivorship, high fecundity and high age at maturity, aligning them toward the “periodic” endpoint life-history strategy in the trilateral continuum for fishes proposed by Winemiller and Rose (1992). Periodic strategists are characterized by occasional exceptional year-classes carrying their population through poor years. This can be thought of as a “bet-hedging” strategy where fish spread their reproductive capacity over multiple years, betting on a big payoff within their relatively long life span (Winemiller and Rose 1992). Big payoffs for periodic strategists are typically attributed to favorable environmental conditions, rather than variation in egg production. Thus, much of the temporal variation in Walleye population structure will be related to environmental factors, and identifying principal drivers is critical to understanding Walleye population dynamics. This must be done on a system-specific basis, because environmental factors affecting Walleye recruitment vary across their geographic range and the diversity of waterbodies and biotic communities in which they occur.

Prey abundance and composition, along with adult population density are primary factors influencing Walleye growth rates (Chipps and Graeb 2011; Nate et al. 2011). Fastest growth rates and highest maximum sizes are typically observed when Walleye populations have an abundant, vulnerable pelagic prey fish, such as Cisco *Coregonus artedii* or Rainbow Smelt *Osmerus mordax* (Jones et al. 1994; Kaufman et al. 2009). In

general, growth rates are inversely related to population density. Accordingly, exploitation may have a positive effect on growth rates for adult Walleye (Nate et al. 2011).

Sustainability and quality of recreational fisheries relies upon the validity of critical assumptions regarding angler dynamics. First, recreational fisheries are assumed to be self-regulating because effort is believed to decline with stock density (Cox et al. 2002). Second, catchability is assumed to be density independent. Taken in tandem, these assumptions posit that as population density declines, anglers should catch less fish and allocate effort elsewhere. Both assumptions have been violated to varying degrees, depending on the circumstances. Post et al. (2002) attributed some of the decline of Canada's recreational Walleye fisheries to a violation of the assumption that fisheries are self-regulating. Their findings suggested angler effort may remain constant in the face of declining fishing quality, particularly when fisheries are close to human population centers (Post et al. 2002). In other situations, effort has been strongly tied to stock density (Shaner et al. 1996; Lathrop et al. 2002). Similarly, the assumption of density independent catchability seems to hold in some cases, and not in others. In northern Wisconsin lakes, Beard et al. (1997) and Hansen et al. (2000) both found Walleye population density to be a strong predictor of angler catch rates. Conversely, Forney (1980) and VanDeValk et al. (2005) each provided evidence that prey fish abundance influenced angler catch rates of Walleye more than population density. As prey fish abundance is often closely related to Walleye density, this finding suggests that catchability may not necessarily be independent of stock density.

Lake Oahe, a large mainstem Missouri River reservoir, is one South Dakota's most popular and productive Walleye fisheries, yielding average annual harvest of greater than 300,000 fish. Lake Oahe is characterized by moderate variability in terms of both total harvest and size structure. The Lake Oahe Walleye population is sustained through natural reproduction and is managed through passive harvest regulations in the form of creel and possession limits as well as length restrictions. Lake Oahe has sustained numerically high levels of Walleye harvest for decades, with little evidence of decline, but annual exploitation rate has rarely been quantified. Documented variability in the Lake Oahe Walleye fishery has been related to large environmental fluctuations, especially high discharge events in the late 1990's, and again in 2011, as well as a period of prolonged drought during the mid 2000's.

Long-term standardized sampling of fish populations and anglers of Lake Oahe provides necessary information to investigate fishery dynamics. Large-scale disturbance in the recent past provides an opportunity for field-based study of Walleye response to unusual environmental conditions. Moreover, Walleye fisheries demonstrate wide variability across their geographic range and range of habitats. Large reservoirs such as Lake Oahe represent a novel habitat for Walleye when compared to the natural lakes and rivers which dominate the Walleye literature. Study of the Walleye fisheries in Lake Oahe will provide valuable insights not only for its managers, but also to managers of Walleye fisheries in other large reservoirs.

The Walleye fishery in Lake Oahe has experienced extremes in many measures, including 5-fold variation in angling effort and total harvest, 8-fold variation in Proportional Size Distribution (PSD), and body condition that has ranged from the upper

75th percentile to among the lowest ever recorded among Walleye populations. Much of this extreme variability is linked to the interaction with Rainbow Smelt which are primary prey of adult Walleye in Lake Oahe, especially in the lower two-thirds where thermal stratification during summer months provides year-round coldwater habitat. When Rainbow Smelt abundance is high in Lake Oahe, they are the dominant item (> 85% by weight) in Walleye diets, and allow for exceptional growth rates (Graeb et al. 2008). When Rainbow Smelt abundance is low they are still utilized by adult Walleye (> 30 % by weight), but Walleye condition and growth plummet. Additionally, Graeb et al. (2008) demonstrated that Walleye survival was poor, especially for the largest fish in the population during a period of Rainbow Smelt abundance during the early 2000's.

Little study of Walleye recruitment in Lake Oahe has occurred. Nelson and Walburg (1977) documented variable year-class strength of Walleye directly after initial reservoir filling. Fielder (1992) investigated the contribution of fry and fingerling stockings in lower Lake Oahe, and factors influencing stocking success. Annual fishery surveys by South Dakota Department of Game, Fish and Parks (SDGF&P) are not designed specifically to quantify recruitment. However, age distribution of Walleye in gill net catches suggests that year-class strength remains highly variable.

Walleye growth has been studied intensively in Lake Oahe due to changes in prey abundance and composition. Graeb et al. (2008) used data collected from earlier studies (Bryan 1995; Davis 2004; Hanten 2006) on diet composition, prey energy density, and seasonal water temperature to demonstrate large differences in growth dynamics of Walleye under variable levels of Rainbow Smelt abundance. Fincel (2011) evaluated the importance of Gizzard Shad *Dorosoma cepedianum* to Walleye growth following their

establishment in Lake Oahe in the early 2000's. Results suggested that Gizzard Shad became a dominant prey item (60% by weight), and that growth rates were intermediate to those when Rainbow Smelt abundance was high versus when it was low (Fincel 2011). Although Fincel (2011) concluded that Gizzard Shad can subsidize Rainbow Smelt as Walleye prey in Lake Oahe, they appear to have been extirpated from the reservoir by 2011 due to harsh winters. Thus, Walleye growth has varied substantially over time, exhibiting fast growth when Rainbow Smelt were abundant and dominated Walleye diets, displaying moderate growth when Gizzard Shad were abundant and Rainbow Smelt were not, and slow growth when neither Rainbow Smelt nor Gizzard Shad were abundant (Fincel 2011).

Angling mortality has been quantified infrequently for Lake Oahe, but available estimates suggest that it is not sufficiently high to negatively affect the population. Graeb et al. (2008) used a mark-recapture study to estimate that angler exploitation of Lake Oahe Walleye ranged from 17% to 22% from 1999-2003. These estimates likely represent the upper end of historical exploitation rates for Lake Oahe because at that time regulations were liberalized to encourage high Walleye harvest, and Walleye were exceptionally vulnerable to angling due to depressed prey conditions. For context, simulation models by Schueller et al. (2008) suggested that Walleye populations in Wisconsin had a 0% probability of extinction when exposed to 35% annual exploitation, and that up to 61% annual exploitation could be sustained.

Total annual mortality was evaluated along with exploitation in Lake Oahe from 1999-2003, allowing for indirect estimation of natural mortality. Graeb et al. (2008) documented increased total annual mortality for Lake Oahe Walleye when Rainbow

Smelt abundance was low. Change in exploitation did not account for the magnitude of increase observed for total annual mortality, leading the authors to conclude that natural mortality had greatly increased due to lack of prey. Bioenergetics modeling provided additional support to this hypothesis, indicating that prey resources were insufficient in providing maintenance energy for Walleye after the decrease in Rainbow Smelt abundance (Graeb et al. 2008).

I am unaware of any formal study of Lake Oahe angler dynamics. Important metrics for evaluating these dynamics, such as angler effort and harvest have been collected during annual creel surveys conducted by SDGF&P since 1991. Anecdotal evidence suggested that effort increased in response to liberalized regulations and a special, discounted non-resident license during 2001. Similarly, SDGF&P biologists responded to concerns regarding the effect of reduced access on angler effort when low water levels disconnected many of the lake's boat ramps from the water.

As mentioned in the preceding paragraphs, much of Lake Oahe's dynamic nature over the past 3 decades has been a result of fluctuations in prey supply. Floods and droughts have changed both the abundance and composition of Walleye prey in Lake Oahe, which has influenced Walleye growth and mortality rates. In 2011, Lake Oahe experienced record high discharges which led to high rates of Rainbow Smelt entrainment through Oahe Dam (Fincel et al. 2016). This event represents a natural experiment which allows us to compare with, and expand upon, the natural experiment examined by Graeb et al. (2008).

My research focused on questions regarding ecology of Walleye in Lake Oahe, as well as the interaction between anglers and those fish. Available data from long-term

monitoring programs allowed me to address questions regarding how changes in environmental conditions and population demographics affect recruitment and angler catch rates of Walleye in Lake Oahe. Additionally, I assisted with a tagging study in which Walleye were marked annually from 2013-2016 and recovered by anglers from 2013-2017. This study allowed me to investigate Walleye movement patterns, as well as spatial and temporal variation of natural and angling mortality in Lake Oahe.

Dissertation Content and Format

In addition to this introductory chapter, this dissertation contains 5 research chapters (2-6) and a final conclusions chapter. I wrote using singular pronouns because I assume all responsibility for the content and conclusions of the research chapters in this form. However, this dissertation was decidedly a collaborative effort, and I anticipate publishing all 5 research chapters as peer-reviewed publications with coauthors. All chapters are formatted following the American Fisheries Society style guide.

References

- Beard, T. D. Jr., S. P. Cox, and S. R. Carpenter. 2003. Impacts of daily bag limit reductions on angler effort in Wisconsin walleye lakes. *North American Journal of Fisheries Management* 23: 1283-1293.
- Bozek, M. A., D. A. Vaccante, and N. P. Lester. 2011. Pages 233-302 in B.A. Barton, editor. *Biology, management and culture of walleye and sauger*. American Fisheries Society, Bethesda, Maryland.
- Bryan, S. D. 1995. Bioenergetics of walleye in Lake Oahe, South Dakota. M.S. Thesis. South Dakota State University, Brookings, SD.
- Chipps, S. R., and B. D. S. Graeb. 2011. Feeding ecology and energetics. Pages 303-320 in B.A. Barton, editor. *Biology, management and culture of walleye and sauger*. American Fisheries Society, Bethesda, Maryland.
- Cox, S. P. 2000. Angling quality, effort response, and exploitation in recreational fisheries: field and modeling studies on British Columbia rainbow trout lakes. Ph.D. Dissertation, University of British Columbia, Vancouver. 214 p.
- Davis, B. A. 2004. Estimating trophic position of Lake Oahe walleye using stable isotope analysis. M.S. Thesis, South Dakota State University, Brookings, SD.
- Dutil, J. D., and Y. Lambert. 2000. Natural mortality from poor condition in Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 57: 826-836.
- Fielder, D. G. 1992. Evaluation of stocking walleye fry and fingerlings and factors affecting their success in lower Lake Oahe, South Dakota. *North American Journal of Fisheries Management* 12: 336-345.
- Fincel, M. J. 2011. Productivity and trophic interactions in the Missouri River impoundments. Doctoral Dissertation. South Dakota State University, Brookings, SD.
- Fincel, M. J., W. J. Radigan, and C. M. Longhenry. 2016. Entrainment of Rainbow Smelt through Oahe Dam during the 2011 Missouri River flood. *North American*

- Journal of Fisheries Management 36: 844-851.
- Forney, J. L. 1980. Evolution of a management strategy for the walleye in Oneida Lake, New York. *New York Fish and Game Journal* 27: 105-141.
- Graeb, B. D. S., S. R. Chipps, D. W. Willis, J. P. Lott, R. P. Hanten, W. Nelson-Stastny, and J. W. Erickson. 2008. Walleye response to rainbow smelt population decline and liberalized angling regulations in a Missouri River reservoir. Pages 275-292 *in* M. S. Allen, S. Sammons and M. J. Maceina, editors. *Balancing fisheries management and water uses for impounded river systems*. American Fisheries Society, Symposium 62, Bethesda, Maryland.
- Hansen, M. J., T. D. Beard, and S. W. Hewett. 2000. Catch rates and catchability of walleyes in angling and spearing fisheries in northern Wisconsin lakes. *North American Journal of Fisheries Management* 20: 109-118.
- Hansen, M. J., and N. A. Nate. 2014. Effects of recruitment, growth, and exploitation on walleye population size structure in northern Wisconsin lakes. *Journal of Fish and Wildlife Management* 5: 99-108.
- Hanten, R. 2006. Seasonal food habits, condition, growth and distribution of Lake Oahe, South Dakota, walleye during depressed prey conditions spring 2001 to spring 2002. South Dakota Department of Game, Fish and Parks, Fisheries Division Report 07-02, Pierre.
- Hatch, R. W., S. J. Nepszy, K. M Muth, and C. T. Baker. 1987. Dynamics of the recovery of the western basin Lake Erie walleye *Stizostedion vitreum vitreum stock*. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 15-22.
- Jones, M. S., J. P. Goettl, and S. A. Flickinger. 1994. Changes in walleye food habits and growth following rainbow smelt introduction. *North American Journal of Fisheries Management* 41: 409-414.
- Kaufman, S.D., G. E. Morgan, and J. M. Gunn. 2009. The role of ciscoes as prey in the trophy growth potential for walleyes. *North American Journal of Fisheries Management* 29: 468-477.

- Lathrop R. C., B. M. Johnson, T. B. Johnson, M. T. Vogelsang, S. R. Carpenter, T. R. Hrabik, J. F. Kitchell, J. J. Magnuson, L. G. Rudstam, and R. S. Stewart. 2002. Stocking piscivores to improve fishing and water clarity: a synthesis of the Lake Mendota biomanipulation project. *Freshwater Biology* 47: 2410-2424.
- Nate, N. A., M. J. Hansen, L. G. Rudstam, R. L. Knight, and S. P. Newman. 2011. Population and community dynamics of walleye. Pages 321-374 in B.A. Barton, editor. *Biology, management and culture of walleye and sauger*. American Fisheries Society, Bethesda, Maryland.
- Nelson, W. R., and C. H. Walburg. 1977. Population dynamics of yellow perch (*Perca flavescens*), Sauger (*Stizostedion canadense*), and walleye (*S. vitreum vitreum*) in four main stem Missouri River Reservoirs. *Journal of the Fisheries Research Board of Canada* 34: 1748-1763.
- Post, J. R., M. Sullivan, S. Cox, N. P. Lester, C. J. Walters, E. A. Parkinson, A. J. Paul, L. Jackson, and B. J. Shuter. 2002. Canada's recreational fisheries: the invisible collapse? *Fisheries* 27: 6-17.
- Quinn, S. P. 1992. Angler perspectives on walleye management. *North American Journal of Fisheries Management* 12: 367-378.
- Schmalz, P. J., A. H. Fayram, D. A. Isermann, S. P. Newman, and C. J. Edwards. 2011. Harvest and exploitation. Pages 375-402 in B.A. Barton, editor. *Biology, management and culture of walleye and sauger*. American Fisheries Society, Bethesda, Maryland.
- Schueller, A. M., M. J. Hansen, and S. P. Newman. 2008. Modeling the sustainability of walleye populations in northern Wisconsin lakes. *North American Journal of Fisheries Management* 28: 1916-1927.
- Shaner, B. L., M. J. Maceina, J. J. McHugh, and S. F. Cook. 1996. Assessment of catfish stocking in public fishing lakes in Alabama. *North American Journal of Fisheries Management* 16: 880-887.
- VanDeValk, A. J., J. L. Forney, J. R. Jackson, L. G. Rudstam, T. E. Brooking, and S. D.

- Krueger. 2005. Angler catch rates and catchability of walleyes in Oneida Lake, New York. *North American Journal of Fisheries Management* 25: 1441-1447.
- Vandergoot, C. S., and T. O. Brenden. 2014. Spatially varying population demographics and fishery characteristics of Lake Erie walleyes inferred from a long-term tag recovery study. *Transactions of the American Fisheries Society* 143: 188-204.
- Venturelli, P., J. Bence, T. Brenden, N. Lester, and L. Rudstam. 2014. Mille Lacs Lake Walleye blue ribbon panel data review and recommendations for future data collection and management. Minnesota Department of Natural Resources Special Report.
- Wang, H. Y., E. S. Rutherford, A. H. Cook, D. W. Einhouse, R. C. Haas, T. B. Johnson, R. Kenyon, B. Locke, and M. W. Turner. 2007. Movement of walleyes in Lakes Erie and St. Clair inferred from tag return and fisheries data. *Transactions of the American Fisheries Society* 136: 539-551.
- Winemiller, K. O., and K. A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 2196-2218.

CHAPTER 2: INFLUENCE OF SPATIAL COMPLEXITY AND ENVIRONMENTAL
FACTORS ON WALLEYE RECRUITMENT IN A LARGE MISSOURI RIVER
RESERVOIR

Abstract

Recruitment is an important driver of fish population abundance and size structure and can be affected by a variety of density dependent and density independent factors. Walleye *Sander vitreus* populations often exhibit highly variable year-class strength which has been attributed to a suite of factors. In this study, I quantified variability in Walleye recruitment, assessed within-lake recruitment synchrony, and modeled recruitment variability for year-classes produced during 1988-2013 in Lake Oahe. Walleye recruitment exhibited low variability relative to other populations and was characterized as consistent (no missing year-classes) but variable. Over the 26 years assessed, 3 exceptionally large year-classes were produced whereas all other years were not significantly different from one another. I detected recruitment synchrony among locations within Lake Oahe, but this relationship was largely influenced by spatial synchrony of the three exceptionally large year-classes and was no longer detectable when those three year-classes were removed. Relative abundance of age-4 and older walleyes, taken as an index of spawner abundance, was a poor predictor of Walleye recruitment indicating that Walleye recruitment was regulated by density independent factors across the range of observations. Reservoir elevation change improved model fit to explain 26 % of recruitment variation and indicated that increased elevation from the previous year improved recruitment, but this effect was heavily influenced by a single

observation. I conclude that Walleye recruitment in Lake Oahe is regulated by density independent factors across the range of spawner abundance observed from 1988-2011.

Introduction

Recruitment is typically the most variable rate influencing fish population abundance and size structure (Gulland 1982; Allen and Pine 2000; Hansen and Nate 2014). Year-class strength and subsequent recruitment to a fishery can be influenced by density dependent effects on juvenile production and survival as well as many density independent abiotic and biotic factors. Spawner abundance may influence recruitment through compensatory density dependence, with high juvenile survival at low spawner abundance and low juvenile survival at high spawner abundance (Rose et al. 2001). Density independent abiotic factors affecting recruitment may include climatic variables, such as wind velocity (Busch et al. 1975), temperature (Post and Evans 1989; Madenjian et al. 1996), and precipitation (Phelps et al. 2008). Density independent biotic interactions, including interspecific competition and predation may also influence year-class strength (Nielsen 1980; Kaemingk et al. 2012).

Recruitment often varies more than other population processes for Walleye *Sander vitreus* (Nate et al. 2011) and, as a result, recruitment dynamics of Walleye have been studied across many water bodies. Relationships between stock density and recruitment have been documented (Forney 1980; Madenjian et al. 1996; Hansen et al. 1998) but may be less influential than abiotic factors and interspecific biotic interactions. Abiotic factors such as spring water temperature (Madenjian et al. 1996; Hansen et al. 1998), and wind direction and intensity (Zhao et al. 2009) have been found to influence Walleye recruitment in some situations. Additionally, biotic factors such as density of

Yellow Perch *Perca flavescens* (Hansen et al. 1998), Rainbow Smelt *Osmerus mordax* (Johnson and Goettl 1999), Gizzard Shad *Dorosoma cepedianum* (Madenjian et al. 1996), and White Crappie *Pomoxis annularis* (Quist et al. 2003) have also been found to influence Walleye year-class strength and may override abiotic drivers when present (Quist et al. 2003).

Novel habitat and unique fish communities found in reservoirs introduce additional considerations for Walleye recruitment. In the impounded Upper Mississippi River, Pitlo (2002) found that warming rate during the spawning season was the best predictor of Walleye year-class strength, similar to results from natural lakes (Hansen et al. 1998; Madenjian et al. 1996). Conversely, storage ratio was a major driver of Walleye recruitment in small Kansas reservoirs, likely because of entrainment of young Walleyes (Willis and Stephen 1987). Quist et al. (2003) found that White Crappie, which did not historically overlap with Walleye, had a negative influence on Walleye recruitment in Kansas reservoirs. Similarly, Johnson and Goettl (1999) found a negative relationship between Rainbow Smelt and Walleye recruitment in a Colorado reservoir. The diversity of factors found to affect Walleye recruitment across different water bodies and through time within water bodies underscores the importance of studying system-specific factors affecting Walleye recruitment.

Lake Oahe, a mainstem Missouri River reservoir in South Dakota is the largest and most economically important fishery within the state, generating approximately \$16 million (US) annual direct economic impact, and is nationally recognized as a destination Walleye fishery. Walleye recruitment in Lake Oahe has been studied occasionally, yet many questions remain. Nelson and Walburg (1977) reported up to 30-fold variation in

year-class strength and suspected this variability was driven by tributary flows and water temperature. Fishery managers have suspected spatial heterogeneity in Walleye recruitment within Lake Oahe, suggesting Walleye recruitment was poor on the downstream portion of Lake Oahe (Michaeletz 1986). Fielder (1992) investigated fry and fingerling stocking success in lower Lake Oahe, concluding that fry stockings were unsuccessful, and that fingerling stockings supplemented natural recruitment but that results varied by embayment and among years. Zooplankton density and temperature were suggested as potential mechanisms influencing recruitment of stocked fingerlings among years and between embayments (Fielder 1992). A recent otolith microchemistry study indicated differences in production among spawning locations by demonstrating that natal contributions were highest in tributaries (Carlson et al. 2016).

In this study, I utilized long-term standardized gill-net data collected by SDGF&P to characterize annual and spatial variability of Walleye recruitment in Lake Oahe. Further, I investigated the effect of density dependent factors, as well as density independent biotic and abiotic factors, on Walleye recruitment in Lake Oahe. Specific objectives of this study were to: 1) characterize patterns of annual recruitment in Lake Oahe Walleye as consistent (i.e. no missing year-classes) or erratic (i.e. missing year-classes) and quantify variability of year-class strength, 2) assess spatial synchrony of Walleye recruitment in Lake Oahe, and 3) assess the influence of factors hypothesized to influence Walleye year-class strength in Lake Oahe.

Methods

Study Area

Lake Oahe is the second largest of a series of six main stem Missouri River reservoirs. A remnant river reach, called the Garrison Reach, offers approximately 165 km of riverine habitat in North Dakota above Lake Oahe to the Garrison Dam near Riverdale, North Dakota. The reservoir extends downstream of the Garrison Reach to Oahe Dam, 5 miles north of Pierre, South Dakota. Lake Oahe has a surface area of approximately 145,000 ha at full pool, a mean depth of 19 m, and a maximum depth of 67 m. Numerous embayments give Lake Oahe 3,623 km of shoreline at full pool, and a shoreline development index of 27.4 (Nelson and Walburg 1977). Approximately 111,000 ha of Lake Oahe is in South Dakota, with the remainder in North Dakota. Lake Oahe is primarily operated for flood control and multiple uses, resulting in large (3.9 m mean) interannual water level fluctuations (Nelson and Walburg 1977) and low exchange rate. Lake Oahe is fed by two large tributaries in North Dakota (Cannonball and Knife Rivers) and three large tributaries in South Dakota (Grand, Moreau, and Cheyenne Rivers). Thermal stratification occurs in approximately the lower two-thirds of the reservoir from June through September.

Walleye is the most sought-after sport fish in Lake Oahe with average annual harvest exceeding 350,000 fish. Walleye were previously stocked as fry and small fingerlings in the lower third of Lake Oahe, but no stocking has occurred since 1993 (Fielder 1992). Common prey for Walleye in Lake Oahe include Rainbow Smelt, Gizzard Shad, Yellow Perch, and other warmwater prey fish species (Bryan 1995; Davis 2004; Hanten 2006; Fincel et al. 2014).

Fishery Data

Standardized gill net surveys of Lake Oahe Walleye were conducted annually during August from 1990-2015 by SDGF&P. Surveys were conducted using experimental multifilament nets measuring 91.4 m in length by 1.8 m deep with 15.2 m panels of 12.7 mm, 19.1 mm, 25.4 mm, 31.8 mm, 38.1 mm, and 50.8 mm bar mesh. Six nets were deployed at each of 9 locations (Figure 2.1) for a total of 54 nets per year. All Walleye collected during gill net surveys were measured for total length (mm) and weighed (g). Aging structures were removed from a maximum of ten fish per 25-mm length class annually. Scales were used to age Walleyes until 2001, after which sagittal otoliths were used. For Walleye less than 300 mm, otoliths were viewed whole under a thin layer of glycerol in a black dish. For fish greater than 300 mm, otoliths were cracked through the focus and charred using a propane torch prior to age estimation. Otoliths were read independently by at least two readers and age discrepancies were re-examined until both readers and a third party came to a consensus. Year-specific age-length keys were constructed using methods described by Isely and Grabowski (2007) to assign ages to Walleye collected in gill net surveys which were not aged.

Age-2 Walleye catch per unit effort (CPUE; fish per net-night) was used as an index of recruitment as Walleye year-classes were typically not fully recruited to sampling gear until this age. Annual recruitment was summarized by calculating mean age-2 CPUE across the 54 nets. Confidence intervals (95 %) were calculated for each year and I considered means different if confidence intervals did not overlap. Coefficient of variation (CV) in mean age-2 CPUE was calculated across all years to quantify variability of year-class strength. Coefficient of variation was also calculated for all years

excluding three year-classes (1991, 1995, 2009) which exhibited significantly higher age-2 CPUE than all other years.

To assess synchrony of Walleye recruitment among locations within Lake Oahe, mean age-2 CPUE was calculated at each of 9 gill net locations (6 nets per location) sampled annually by SDGF&P. Correlation analysis was conducted using Pearson's correlation coefficient including all sampling years and again excluding the three years with the highest lake wide age-2 Walleye CPUE (1991, 1995, 2009) to examine patterns in the absence of high-leverage observations. Pairwise comparisons were considered significant at $P < 0.05$.

Relative abundance of Rainbow Smelt in Lake Oahe has been monitored using deep water gill nets and hydroacoustics surveys. Deepwater gill net surveys were conducted in July from 1993 through 2000. Hydroacoustics surveys date back to 1996; equipment and analytical methods were consistent from 1996-2004, after which different equipment and analytical methods were used. The variability in sampling and quantitative methods used to index Rainbow Smelt abundance prevented rigorous quantitative analysis. The available data was used to describe broad trends in Lake Oahe's Rainbow Smelt abundance and discuss these trends in the context of Walleye recruitment during the same period.

I modeled the influence of stock abundance and several environmental variables on recruitment. Relative abundance (gill-net CPUE) of age-4 and older Walleye was treated as an index of stock abundance. End-of-month reservoir elevation (feet above mean sea level; ft msl) was obtained from the United State Army Corps of Engineers and annual elevation change (Elevation Change) was calculated as the difference in end-of-

May elevation between a given year and the previous year. Tributary inputs (Tlibs) were examined using U.S. Geological Survey stream gauge data from two large tributaries, the Grand River and the Moreau River. Mean daily flow from these rivers during January through June was summed to encompass snow thawing as well as spring and summer rains, which are thought to influence Walleye early life history in Missouri River reservoirs (Graeb et al. 2010). Temperature (Temp) was represented by mean May air temperature at the Mobridge, South Dakota Municipal Airport weather station operated by the National Weather Service. Condition of spawning stock (Condition) was calculated as the mean relative weight of age-4 and older Walleye during the previous August.

A spawner-recruit model modified by environmental variables was used to evaluate factors affecting year-class strength. I used a \log_e transformed Ricker (Ricker 1975) model to represent the spawner-recruit relationship:

$$\log_e[R] = \log_e[S] + a - bS + cX + \varepsilon$$

where recruit relative abundance (age-2 Walleye CPUE; R) is described as a function of stock relative abundance (age-4 and greater Walleye CPUE; S), density dependent recruitment (a), density dependence (b), influence of environmental variables (c) and residual error (ε). I constructed biologically meaningful combinations of environmental variables into competing models and used nonlinear regression to estimate model parameters. Models were compared using second-order Akaike's Information Criterion (AIC_c). Model pseudo- r^2 values were computed by regressing predicted against observed age-2 CPUE. All statistical analysis was conducted in program R (R Core Team 2017).

Nonlinear regression analysis was conducted using the nlstools package (Baty et al. 2015), and AIC_c was computed using the AICcmodavg package (Mazerolle 2016).

Results

Age-2 Walleye were encountered during every year from 1990-2015 in Lake Oahe. Mean age-2 CPUE ranged from a low of 1.4 fish per net night for the 2013 year-class to a high of 18.8 fish per net night for the 2009 year-class (Table 2.1). Across all years considered, average age-2 CPUE was 4.8 fish per net night and CV was 0.9. Three year-classes (1991, 1995 and 2009) were significantly larger than all others considered (Figure 2.2). Excluding these three year-classes, average age-2 CPUE was 3.4 fish per net night and CV was 0.4.

Age-2 Walleye were encountered at all 9 SDGF&P gill netting locations during every year considered, except at Cow Creek during 2006 (Table 2.1). Mean age-2 CPUE tended to be lowest at downstream locations. The maximum observed age-2 CPUE ranged from 9.8 to 36.2 fish per net-night and was lowest at downstream locations. Pairwise comparisons of age-2 CPUE among all but one location (Pollock Bay) were significantly correlated ($P < 0.05$; Table 2). Among these 8 locations, correlation coefficients ranged from 0.54 to 0.91. Only one location (Blue Blanket) was significantly correlated with Pollock Bay. Few pairwise comparisons were significant when the three largest year-classes were omitted from correlation analysis (Table 2.3). Recruitment patterns were similar among main lake locations on the downstream portion of Lake Oahe (Peoria Flats-Cow Creek, Bush's Landing-Whitlock Bay), whereas the major tributary site on the downstream end (Minneconjou) was not correlated with any other

locations. Among upstream Oahe locations, only the Grand River and Moreau River displayed similar recruitment patterns.

Rainbow Smelt abundance estimates varied erratically during 1988-2013. Gill nets indexed abundance from 1993-2000, indicating relatively high abundance from 1993-1995, considerably lower abundance during 1996-1997, and very low abundance during 1998-2000 (Figure 2.3). Hydroacoustics surveys estimated age-0 and adult Rainbow Smelt density from 1996-2013, indicating the highest abundance during 1996 and decreasing rapidly until a low in 2001 (Figure 2.3). Rainbow Smelt abundance increased after 2001 and remained moderate until rapidly decreasing during 2012-2013 (Figure 2.3).

Four Ricker stock-recruitment models incorporating annual reservoir elevation change had the most support from the data in our *a priori* model set (Table 2.4). The pseudo- r^2 values of these four models ranged from 0.26-0.27. The top model suggested a positive effect of Elevation Change, and the other three moderately supported models were additive models which all contained Elevation Change, indicating that Elevation Change was the sole explanatory environmental variable in any of those models. All other models were substantially less supported by the data. The Ricker model without environmental variables was poorly supported relative to other models (AIC Weight = 0.05) and did not explain recruitment variability (pseudo- r^2 = 0.01, Figure 2.4). Each of the three strongest year-classes occurred when annual reservoir elevation change was positive. The strongest year-class (2009) occurred following the greatest elevation change, whereas other exceptional year-classes (1991, 1995) were not well explained by elevation change (Figure 2.5).

Discussion

Walleye recruitment was consistent and year-class strength was variable in Lake Oahe from 1988-2013, as all 26 year-classes were represented with approximately 13-fold variation in strength. Recruitment variation ($CV = 0.88$) was relatively low compared to other well-studied Walleye fisheries. Nate et al. (2011) reported CV for recruitment metrics of 0.86, 1.35, and 1.29 in Escanaba Lake, Oneida Lake, and Lake Erie, respectively. Across the 26 years considered in this study, three Walleye year-classes were much larger than all others and had a large influence on results. Excluding those three year-classes, recruitment variation was quite low ($CV = 0.45$). Periodic, strong year-classes intermixed with low to moderate year-classes are characteristic of self-sustaining Walleye populations (Hansen et al. 1998; Nate et al. 2011).

I found significant correlations in age-2 Walleye relative abundance across 8 of 9 Lake Oahe locations, but subsequent analysis indicated that synchrony was limited to years during which favorable recruitment conditions were present. The three strongest year-classes across all observations were strong at nearly every location. The 2009 year-class was the most abundant across all observations at 7 of 9 locations, and among the top 5 at 8 of 9 locations. Similarly, the 1991 and 1995 year-classes were among the 5 largest observed at 8 of 9 locations. Outside of those three year-classes there was much less synchrony in age-2 CPUE across locations. I speculate that Walleye spawn successfully at many locations throughout Lake Oahe and factors affecting survival during early life history vary across these locations but abiotic conditions, such as abundant flooded vegetation due to increased reservoir elevation, have the potential to yield synchronous strong year-classes throughout the reservoir. Therefore, the broad spatial distribution of

Walleye spawning within Lake Oahe hedges the population's bets against local factors which may inhibit recruitment and reduce overall recruitment variability.

This investigation of spatial variability in Lake Oahe Walleye recruitment was limited because year-classes were not indexed until age 2. Spatial distribution of age-2 Walleye does not necessarily represent spatial distribution of Walleye production. However, age-2 distribution is indicative of distribution as year-classes approach harvestable size. Thus, although I cannot make conclusions regarding Walleye production throughout Lake Oahe, these results indicate recruitment of harvestable Walleye occurs consistently throughout Lake Oahe, contrary to previous conclusions that Walleye recruitment was limited in the downstream portions of Lake Oahe (Michaeletz 1986).

My data do not suggest a negative interaction between Rainbow Smelt and Walleye recruitment in Lake Oahe, contradicting results from inland Wisconsin lakes (Mercado-Silva et al. 2007) and a Colorado reservoir (Johnson and Goettl 1997). The authors of these studies suggested competition for zooplankton between Rainbow Smelt and larval Walleye as a potential mechanism for the negative interaction. The size and complexity of Lake Oahe likely decreases the spatial overlap between larval Walleye and Rainbow Smelt limiting their interaction. I suspect Walleye successfully spawn across a broader distribution within Lake Oahe than Rainbow Smelt because Rainbow Smelt are thermally constrained. Furthermore, zooplankton may not be a limiting resource for larval Walleye and Rainbow Smelt in Lake Oahe. Estimates of Lake Oahe zooplankton density have been intermediate relative to other temperate lakes and reservoirs (Finzel 2011) but exhibit significant spatial and temporal heterogeneity. Zooplankton "spikes"

observed during June in Lake Oahe yield densities comparable to eutrophic systems (Fincel 2011) and may free larval Walleye from interspecific competition.

Stock abundance had no apparent effect on recruitment indicating that Lake Oahe Walleye recruitment was regulated by density independent factors during the years included in this study. Strong year-classes were produced from relatively low stock sizes signaling that production has not been limiting across the range of observations. My data were not well supported by the density dependent Ricker curve, contrary to much of the literature on Walleye recruitment (Madenjian et al. 1996; Hansen et al. 1998). Cannibalism of age-0 recruits is a commonly hypothesized mechanism for compensatory density dependence at high Walleye stock sizes (Chevalier 1973; Forney 1976). Numerous diet studies have indicated that Rainbow Smelt is the dominant prey item for Lake Oahe Walleye, and cannibalism has not been documented even when Rainbow Smelt abundance was relatively low (Bryan 1995; Hanten 2006; Fincel et al. 2014). As such, cannibalism seems an unlikely mechanism for compensatory density dependence in Lake Oahe Walleye which may explain the contrast between my results and those found elsewhere.

Walleye year-class strength, as indexed by age-2 CPUE, was best explained by annual elevation change and the degree of influence exerted by elevation change depended on reservoir elevation. This variable likely explains the largest year-class in the data set, but two other large year-classes in the data were poorly represented. Water-level fluctuations have long been recognized to positively influence reservoir fish populations by increasing system productivity, spawning substrate and nursery habitat (Miranda et al. 1984; Ploskey 1986). During the mid-2000's Lake Oahe was at its lowest levels since the

1950's, and high inflows starting in 2008 raised the water level to nearly full pool during 2009. This resulted in an elevation change of 8.9 m from May 2008 to May 2009, and inundation of habitat that had been terrestrial for 10 years. Conditions during 2009 likely included a lake-wide pulse of primary and secondary productivity increasing Walleye development rates and shortening duration of vulnerable early life history stages. Furthermore, flooded terrestrial vegetation would have provided nursery habitat and decreased mortality during vulnerable early life history stages. Although fluctuating reservoir water level is a likely explanation for the historic 2009 year-class, my model greatly underestimated other large year-classes, suggesting that a positive variable was missing, or not properly represented.

All environmental variables other than annual elevation change were poorly supported by the data, but this may be an artifact of data limitations. In particular, the lack of a temperature influence was surprising given the large body of evidence for water temperature influences on Walleye recruitment (Forney 1976; Madenjian et al. 1996; Hansen et al. 1998). Relevant temperature metrics have included warming rate (Forney 1976; Madenjian et al. 1996; Pitlo 2002) and variability (Koenst and Smith 1976; Hansen et al. 1998). Water temperature data were not available for Lake Oahe, and the air temperature metric I used was likely insensitive to important water temperature characteristics. I speculate that water temperature does indeed influence Walleye recruitment in Lake Oahe, but the index of temperature used in this analysis was insufficient.

Knowledge of the factors that allow Walleye recruitment to occur in the presence of moderate to high Rainbow Smelt abundance would help managers predict whether this

coexistence will continue. If the timing of zooplankton pulses is critical in releasing age-0 Walleye from a competitive interaction with Rainbow Smelt, then climate change has the potential to alter the interaction. Although it is likely that age-0 Walleye do not completely overlap spatially with Rainbow Smelt, recruitment failure at locations where overlap occurs may destabilize and weaken lake-wide recruitment.

Walleye recruitment in Lake Oahe was regulated by density independent factors during the period of this study. However, Myers et al. (1999) demonstrated that density dependent factors regulate recruitment at low stock sizes and the results of this study should not be taken to indicate otherwise. Managers should be conscious of this fact if stock abundance declines below the levels observed in this study.

Water-level fluctuations and other unknown density independent factors were important in regulating Walleye recruitment during the period of this study, and fishery managers have little control over these factors. Lake Oahe water-level fluctuations are partially controlled by the U.S. Army Corps of Engineers, but actions are dictated by the amount of precipitation within the Lake Oahe watershed. The three main stem flood control reservoirs in the Upper Missouri River Basin (Fort Peck Reservoir, Lake Sakakawea, Lake Oahe) are given preference for water-level management on a rotating basis. I recommend that fishery managers request water level increases over previous levels during preferred years.

My summarization of Walleye recruitment in Lake Oahe from 1988-2013 indicates a stable, self-sustaining Walleye population which occasionally produces exceptionally large year-classes. Managers previously suspected poor recruitment in downstream portions of Lake Oahe and implemented supplemental stocking (Fielder

1992). However, I documented only one missing year-class at one location across all years considered which indicates that all of Lake Oahe is self-sustaining. My data and previous research (Carlson et al. 2016) suggests there may be spatial differences in year-class abundance, but the long-term monitoring data used in this study were not designed to rigorously analyze spatial differences in recruitment. Future research designed to quantify differences in year-class strength would help managers evaluate whether supplemental stocking would be helpful in augmenting local populations in regions of Lake Oahe perceived to support a lower abundance of adult Walleye.

References

- Allen, M. S., and W. E. Pine III. 2000. Detecting fish population responses to a minimum length limit: effects of variable recruitment and duration of evaluation. *North American Journal of Fisheries Management* 20: 672-682.
- Baty, F., C. Ritz, S. Charles, M. Brutsche, J. Flandrois, M. Delignette-Muller. 2015. A toolbox for nonlinear regression in R: the package nlstools. *Journal of Statistical Software* 66: 1-21. <http://jstatsoft.org/v66/i05>.
- Bryan, S. D. 1995. Bioenergetics of walleye in Lake Oahe, South Dakota. M.S. Thesis. South Dakota State University, Brookings, SD.
- Busch, W. D. N., R. L. Scholl, and W. L. Hartman. 1975. Environmental factors affecting the strength of walleye (*Stizostedion vitreum vitreum*) year-classes in western Lake Erie, 1960-1970. *Journal of the Fisheries Research Board of Canada* 32: 1733-1743.
- Carlson, A. K., M. J. Fincel, and B. D. S. Graeb. 2016. Otolith microchemistry reveals natal origins of Walleyes in Missouri River reservoirs. *North American Journal of Fisheries Management* 36: 341-350.
- Chevalier, J. R. 1973. Cannibalism as a factor in first year survival of walleye in Oneida Lake. *Transactions of the American Fisheries Society* 102: 739-744.
- Davis, B. A. 2004. Estimating trophic position of Lake Oahe walleye using stable isotope analysis. M.S. Thesis, South Dakota State University, Brookings, SD.
- Fielder, D. G. 1992. Evaluation of stocking walleye fry and fingerlings and factors affecting their success in lower Lake Oahe, South Dakota. *North American Journal of Fisheries Management* 12: 336-345.
- Fincel, M. J. 2011. Productivity and trophic interactions in the Missouri River Impoundments. Ph.D. Dissertation. South Dakota State University, Brookings, SD.
- Fincel, M. J., D. J. Dembkowski, and S. R. Chipps. 2014. Influence of variable rainbow smelt and gizzard shad abundance on walleye diets and growth. *Lake and*

- Reservoir Management 30: 258-267.
- Forney, J. L. 1976. Year-class formation in the walleye (*Stizostedion vitreum vitreum*) populations of Oneida Lake, New York, 1966-1973. *Journal of the Fisheries Research Board of Canada* 33: 783-792.
- Forney, J. L. 1980. Evolution of a management strategy for the walleye in Oneida Lake, New York. *New York Fish and Game Journal* 27: 105-141.
- Gulland, J. A. 1982. Why do fish numbers vary? *Journal of Theoretical Biology* 97: 69-75.
- Hansen, M. J., M. A. Bozek, J. R. Newby, S. P. Newman, and M. D. Staggs. 1998. Factors affecting recruitment of walleyes in Escanaba Lake, Wisconsin, 1958-1996. *North American Journal of Fisheries Management* 18: 764-774.
- Hansen, M. J., and N. A. Nate. 2014. Effects of recruitment, growth, and exploitation on walleye population size structure in northern Wisconsin lakes. *Journal of Fish and Wildlife Management* 5: 99-108.
- Hanten, R. 2006. Seasonal food habits, condition, growth and distribution of Lake Oahe, South Dakota, walleye during depressed prey conditions spring 2001 to spring 2002. South Dakota Department of Game, Fish and Parks, Fisheries Division Report 07-02, Pierre.
- Isely, J. J., and T. B. Grabowski. 2007. Age and Growth. Pages 187-228 in C. S. Guy and M. L. Brown, editors. *Analysis and Interpretation of freshwater fisheries data*. American Fisheries Society, Bethesda, Maryland.
- Johnson, B. M., and J. P. Goettl Jr. 1999. Food web changes over fourteen years following introduction of rainbow smelt into a Colorado reservoir. *North American Journal of Fisheries Management* 19: 629-642.
- Kaemingk, M. A., J. C. Jolley, D. W. Willis, and S. R. Chipps. 2012. Priority effects among young-of-the-year fish: reduced growth of bluegill sunfish (*Lepomis macrochirus*) caused by yellow perch (*Perca flavescens*)? *Freshwater Biology* 57: 654-665.

- Koenst, W. M., and L. L. Smith, Jr. 1976. Thermal requirements of the early life history stages of walleye, *Stizostedion vitreum vitreum*, and sauger, *Stizostedion canadense*. *Journal of the Fisheries Research Board of Canada* 33: 1130-1138.
- Madenjian, C. P., J. T. Tyson, R. L. Knight, M. W. Kershner, and M. J. Hansen. 1996. First-year growth, recruitment, and maturity of walleyes in western Lake Erie. *Transactions of the American Fisheries Society* 125: 821-830.
- Mazerolle, M. J. 2016. AICcmodavg: model selection and multimodel inference based on (Q) AIC (c). R Package version 2.0-4. <http://CRAN.R-project.org/package=AICcmodavg>.
- Mercado-Silva, N., G. G. Sass, B. M. Roth, S. Gilbert, and M. J. Vander Zanden. 1997. Impact of rainbow smelt (*Osmerus mordax*) invasion on walleye (*Sander vitreus*) recruitment in Wisconsin lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 64: 1543-1550.
- Michaeletz, P., B. Johnson, J. Riis, C. Stone, D. Unkenholz, and D. Warnick. 1986. Annual fisheries surveys of the Missouri River reservoirs, 1981-1985. South Dakota Department of Game, Fish and Parks, Wildlife Division Report 86-11, Pierre.
- Miranda, L. E., W. L. Shelton, and T. D. Bryce. 1984. Effects of water level manipulation on abundance, mortality, and growth of young-of-year largemouth bass in West Point Reservoir, Alabama-Georgia. *North American Journal of Fisheries Management* 4: 314-320.
- Myers, R. A., K. G. Bowen, and N. J. Barrowman. 1999. Maximum reproductive rate of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 2404-2419.
- Nate, N. A., M. J. Hansen, L. G. Rudstam, R. L. Knight, and S. P. Newman. 2011.

- Population and community dynamics of walleye. Pages 321-374 in B.A. Barton, editor. Biology, management and culture of walleye and sauger. American Fisheries Society, Bethesda, Maryland.
- Nelson, W. R., and C. H. Walburg. 1977. Population dynamics of yellow perch (*Perca flavescens*), sauger (*Stizostedion canadense*), and walleye (*S. vitreum vitreum*) in four main stem Missouri River Reservoirs. Journal of the Fisheries Research Board of Canada 34: 1748-1763.
- Nielsen, L. A. 1980. Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. Canadian Journal of Fisheries and Aquatic Sciences 37: 11-19.
- Phelps, Q. E., B. D. S. Graeb, and D. W. Willis. Influence of the Moran effect on spatiotemporal synchrony in common carp recruitment. Transactions of the American Fisheries Society 137: 1701-1708.
- Pitlo, J. 2002. Effects of environmental factors on walleye and sauger recruitment in Pool 13, Upper Mississippi River. North American Journal of Fisheries Management 22: 1021-1031.
- Ploskey, G. R. 1986. Effect of water-level changes on reservoir ecosystems, with implications for fisheries management. Pages 86-97 in G. E. Hall and M. J. Van Den Avyle, editors. Reservoir Fisheries Management: Strategies for the 80's. American Fisheries Society, Bethesda, Maryland.
- Post, J. R., and D. O. Evans. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): Laboratory, *in situ* enclosure, and field experiments. Canadian Journal of Fisheries and Aquatic Sciences 46: 1958-1968.
- Quist, M. C., C. S. Guy, and J. L. Stephen. 2003. Recruitment dynamics of walleyes (*Stizostedion vitreum*) in Kansas reservoirs: generalities with natural systems and effects of a centrarchid predator. Canadian Journal of Fisheries and Aquatic Sciences 60: 830-839.
- R Core Team. 2016. R: a language and environment for statistical computing. R

foundation for statistical computing. Vienna, Austria. URL <https://www.R-project.org/>.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Rose, K. A., J. J. Cowan Jr., K. O. Winemiller, R. A. Myers, and R. Hilborn. 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries* 2: 293-327.

Willis, D. W., and J. L. Stephen. 1987. Relationships between storage ratio and population density, natural recruitment, and stocking success of walleye in Kansas reservoirs. *North American Journal of Fisheries Management* 7: 279-282.

Zhao, Y., M. L. Jones, B. J. Shuter, and E. F. Roseman. 2009. A biophysical model of the Lake Erie walleye *Sander vitreus* explains interannual variations in recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* 66: 114-125.

Table 2.1. Relative abundance (# per gill net night) of age-2 Walleye collected during annual August gill net surveys on Lake Oahe, 1990-2015. Numbers in parentheses represent 95% confidence intervals.

Year Class	Minneconjou	Peoria Flats	Cow Creek	Bush's Landing	Whitlock Bay	Moreau River	Blue Blanket	Grand River	Pollock Bay	Lakewide
1988	0.8 (1.2)	1.8 (1.0)	1.2 (1.7)	2.0 (2.7)	3.3 (2.2)	1.5 (1.1)	3.8 (3.0)	1.7 (1.6)	2.3 (2.0)	2.1 (0.5)
1989	1.2 (1.5)	9.0 (6.2)	4.8 (10.0)	9.2 (9.6)	14.2 (7.3)	4.0 (2.4)	4.5 (3.6)	3.3 (2.7)	0.8 (1.0)	5.7 (1.8)
1990	NA	NA	NA	NA	NA	NA	NA	NA	NA	4.3 (NA)
1991	9.0 (9.6)	7.8 (6.9)	8.5 (12.3)	6.0 (4.0)	13.7 (9.6)	8.0 (4.4)	19.7 (9.6)	5.7 (5.9)	15.2 (9.1)	10.4 (2.4)
1992	NA	NA	NA	NA	NA	NA	NA	NA	NA	2.1 (NA)
1993	7.3 (9.4)	3.5 (2.2)	2.2 (2.3)	1.5 (1.4)	3.5 (2.5)	4.5 (3.5)	8.3 (4.3)	2.2 (1.5)	11.7 (5.5)	5.0 (1.4)
1994	NA	NA	NA	NA	NA	NA	NA	NA	NA	6.7 (NA)
1995	4.7 (5.0)	7.7 (4.2)	9.0 (7.0)	14.7 (6.5)	11.7 (5.7)	13.2 (5.9)	21.3 (7.4)	18.8 (9.9)	24.0 (5.6)	13.9 (2.3)
1996	4.0 (0.7)	4.7 (3.6)	3.0 (3.3)	3.2 (1.9)	4.2 (2.0)	2.7 (1.8)	3.3 (1.3)	4.7 (3.9)	1.7 (1.6)	3.5 (0.6)
1997	3.8 (3.1)	1.5 (1.1)	2.2 (2.4)	4.7 (2.5)	1.3 (2.1)	2.3 (1.1)	1.0 (1.3)	2.0 (1.5)	0.7 (0.9)	2.2 (0.6)
1998	1.7 (2.9)	2.2 (3.1)	1.2 (1.0)	0.8 (0.8)	2.0 (2.7)	0.8 (1.2)	0.8 (1.2)	1.7 (2.1)	5.3 (2.7)	1.8 (0.6)
1999	2.8 (3.2)	1.7 (1.3)	2.2 (2.2)	0.8 (1.4)	3.2 (1.2)	2.8 (1.5)	9.3 (8.6)	6.2 (6.7)	11.2 (11.0)	4.5 (1.6)
2000	0.8 (1.0)	1.2 (1.2)	0.8 (1.4)	1.0 (1.1)	2.3 (2.1)	2.0 (1.8)	2.0 (1.5)	3.3 (2.0)	16.7 (4.1)	3.4 (1.4)
2001	1.2 (1.2)	2.2 (1.7)	3.7 (7.2)	11.8 (8.4)	6.5 (1.4)	9.2 (6.8)	4.3 (5.2)	8.3 (3.8)	4.3 (5.6)	5.7 (1.6)
2002	3.3 (3.7)	2.3 (1.8)	1.7 (1.1)	5.3 (4.1)	3.5 (2.9)	1.0 (0.7)	4.5 (4.2)	5.2 (3.0)	1.0 (1.6)	3.1 (0.8)
2003	1.5 (2.2)	1.0 (0.9)	1.8 (2.3)	3.0 (1.9)	10.0 (6.3)	1.0 (0.9)	7.0 (2.7)	2.3 (2.5)	4.0 (3.3)	3.5 (1.1)
2004	0.8 (1.0)	0.7 (0.5)	0 (NA)	6.2 (3.6)	5.8 (2.6)	1.2 (1.5)	3.7 (2.2)	1.5 (1.1)	1.0 (1.6)	2.3 (0.8)
2005	1.2 (0.8)	8.2 (9.9)	5.7 (8.3)	6.5 (3.7)	11.0 (10.3)	1.7 (2.0)	3.8 (3.1)	0.2 (0.4)	10.7 (6.0)	5.4 (1.8)
2006	6.2 (11.3)	4.2 (5.6)	7.3 (7.0)	15.3 (13.1)	9.7 (12.2)	1.7 (1.4)	4.5 (5.0)	0.5 (0.6)	2.5 (2.3)	5.8 (2.2)
2007	2.2 (2.9)	0.7 (0.5)	0.7 (1.1)	10.7 (11.7)	3.3 (4.7)	1.5 (2.9)	0.7 (0.9)	1.5 (3.4)	0.8 (1.7)	2.4 (1.4)
2008	1.3 (1.3)	1.0 (1.3)	2.0 (2.4)	6.2 (5.8)	6.0 (4.1)	0.5 (0.9)	2.7 (1.7)	1.8 (1.9)	8.7 (11.3)	3.4 (1.3)
2009	17.2 (11.2)	14.0 (3.9)	9.8 (3.6)	27.0 (19.7)	21.2 (9.7)	18.7 (11.0)	19.2 (4.6)	36.2 (13.2)	5.8 (4.3)	18.8 (3.4)
2010	0.2 (0.4)	0.7 (0.9)	0.5 (0.9)	1.8 (1.2)	3.0 (3.3)	1.0 (0.9)	1.5 (1.1)	2.7 (1.4)	2.8 (2.1)	1.6 (0.5)
2011	5.2 (3.1)	1.8 (2.0)	2.2 (1.2)	3.3 (3.3)	3.0 (2.1)	5.8 (8.9)	0.5 (0.9)	2.0 (2.2)	2.0 (1.6)	2.9 (1.0)
2012	2.2 (2.8)	0.5 (0.9)	1.2 (1.2)	1.5 (1.7)	1.8 (1.5)	0.3 (0.9)	2.2 (2.2)	1.5 (1.1)	3.2 (4.7)	1.6 (0.6)
2013	0.7 (0.9)	1.0 (0.7)	0.8 (1.0)	0.5 (0.6)	1.2 (0.8)	0.5 (0.6)	3.2 (4.7)	2.3 (3.1)	2.0 (2.2)	1.4 (0.6)
					<i>Summaries</i>					
Mean	3.4	3.4	3.1	6.2	6.3	3.7	5.7	5.0	6.0	4.7
CV	1.1	1.0	0.9	1.0	0.8	1.2	1.1	1.6	1.0	0.9

Table 2.4. Rankings of *a priori* stock-recruitment models to explain variation in age-2 Walleye catch per effort in Lake Oahe between 1988 and 2013. All models included the parameters a , b , and ϵ from the Ricker stock-recruitment model. Some models included environmental variables. Table columns include K (the number of estimated parameters), ΔAIC_c (the difference in AIC_c between a model and the model with lowest AIC_c), AIC weight (relative weight of evidence for each model), and pseudo- r^2 (correlation coefficient between predicted and observed values). Elevation Change is the difference in end of May elevation in a given year from the previous year, Tribs is the sum of cumulative inflow from the Grand and Moreau rivers (two large tributaries to Lake Oahe), Condition is the mean relative weight of age-4 and older Walleye during the previous August, and Temp is average May air temperature in Mobridge, South Dakota.

Environmental variables	K	AICc	Delta AIC	AIC Weight	pseudo- r^2
Elevation Change	4	54.32	0.00	0.49	0.26*
Elevation Change + Tribs	5	56.95	2.63	0.13	0.27*
Elevation Change + Condition	5	57.25	2.93	0.11	0.26*
Elevation Change + Temp	5	57.34	3.02	0.11	0.26*
None	3	59.00	4.68	0.05	0.01
Elevation Change + Tribs + Temp	6	59.72	5.40	0.03	0.29*
Tribs	4	60.61	6.29	0.02	0.05
Condition	4	60.95	6.62	0.02	0
Temp	4	61.78	7.46	0.01	-0.03
Elevation Change + Tribs + Temp + Condition	7	62.79	8.47	0.01	0.31*
Tribs + Condition	5	63.23	8.91	0.01	0.07
Tribs+ Temp	5	63.59	9.27	0.00	0.06
Temp + Condition	5	63.91	9.59	0.00	0.01

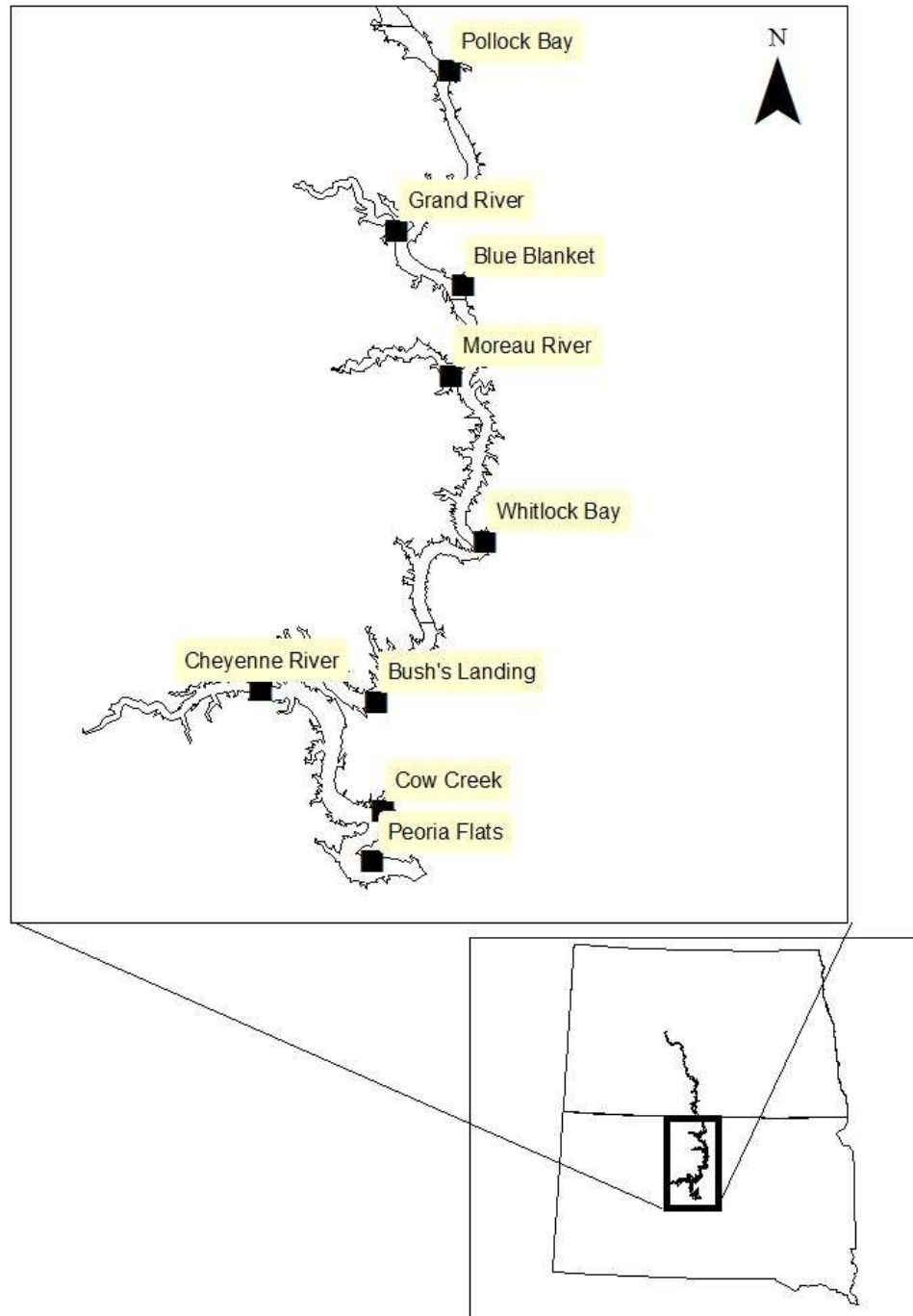


Figure 2.1. Map of SDGF&P gill net locations for standardized surveys 1990-2015.

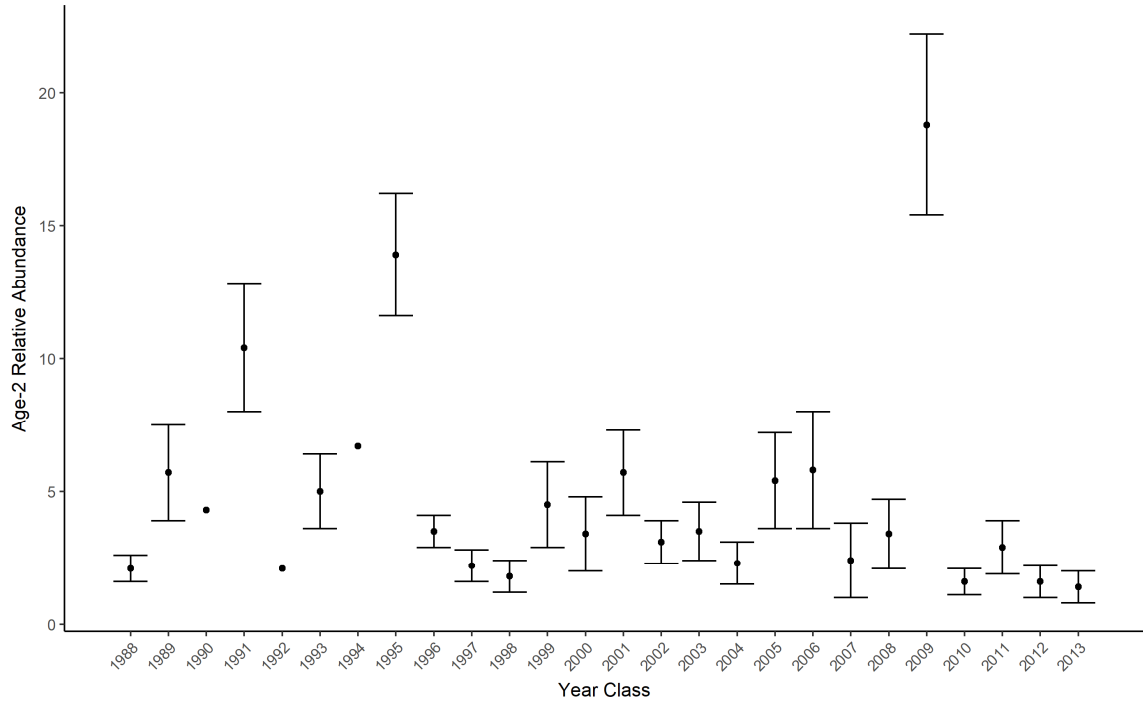


Figure 2.2. Average relative abundance (# per gill net night) of age-2 Walleye collected during annual August gill net surveys on Lake Oahe, 1990-2015. Error bars indicate 95% confidence intervals.

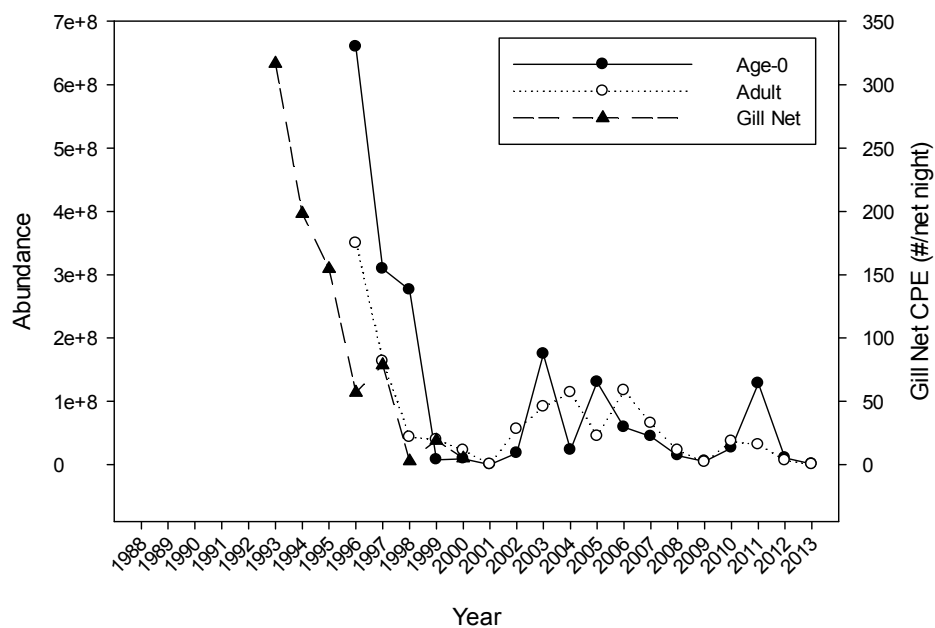


Figure 2.3. Rainbow Smelt abundance estimated by hydroacoustics (age-0 = filled circles, adult = open circles) and indexed by gill net (closed triangles), 1993-2013.

Hydroacoustics surveys occurred during July from 1996-2013. Gill net surveys occurred during August.

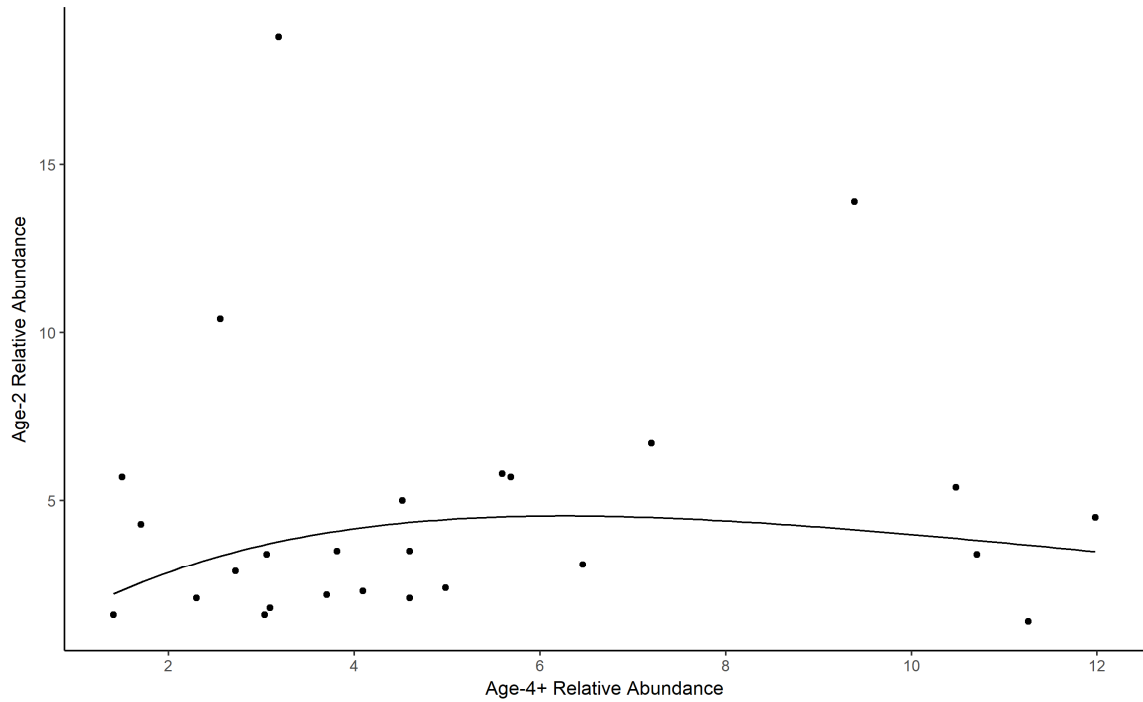


Figure 2.4. Age-2 Walleye relative abundance (# per gill net night) in Lake Oahe as a function of age-4 and older relative abundance (# per gill net night) in 1988-2013. Line represents fitted Ricker stock-recruitment model.

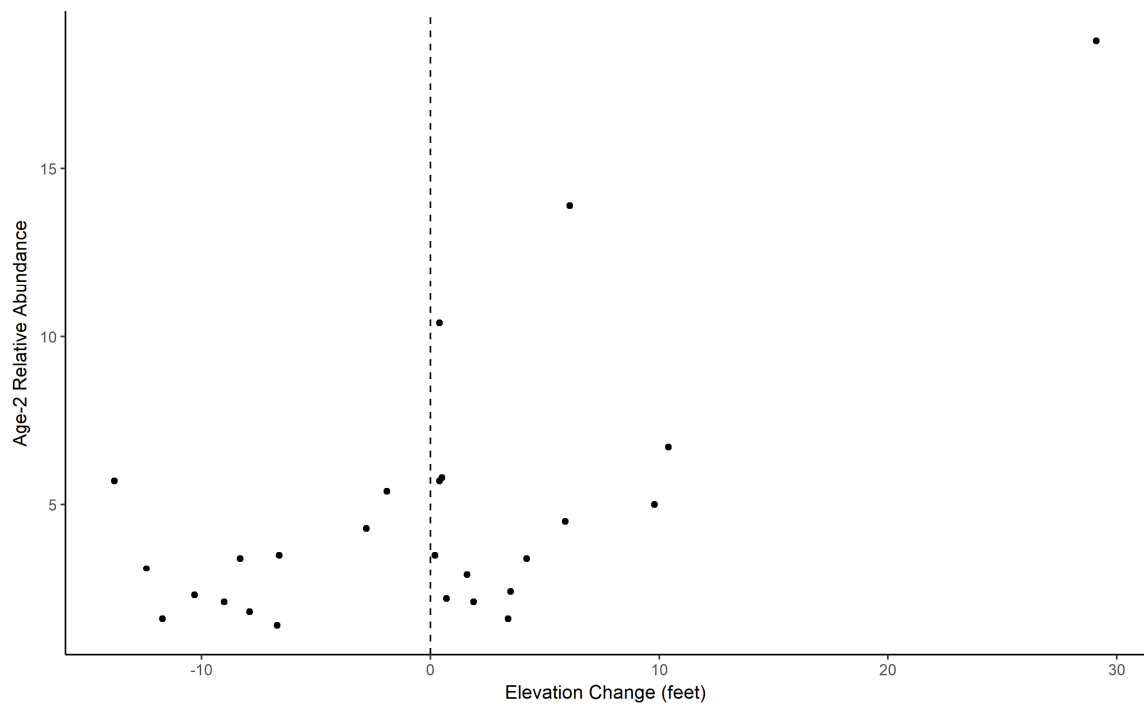


Figure 2.5. Age-2 Walleye CPUE in Lake Oahe as a function of elevation change in 1988-2013.

CHAPTER 3: USE OF HIGH-REWARD TAGS AND DOUBLE-TAGGING TO
ESTIMATE ANGLER REPORTING AND JAW-TAG LOSS RATE FOR LAKE OAHE
WALLEYE

Abstract

Tag recovery studies in which fish are marked by researchers and later recovered and reported by anglers are commonly used to estimate survival and exploitation of fish populations. Angler nonreporting and tag loss can cause estimates from such studies to be biased. I used high-reward tags and double-marking to estimate reporting and tag retention rates for Walleye *Sander vitreus* marked with Monel metal jaw tags in Lake Oahe. As a secondary mark, a dorsal spine was removed from fish tagged during the first year of the study. Estimates of reporting rate from 2013-2015 ranged from 56% to 70% but did not differ significantly among years. The aggregate estimate of reporting rate was 58%. I estimated initial (6-58 days after tagging) and chronic (1 – 3 years) tag retention rate. Initial tag retention rate was 100% then declined to 96% after 1 year, 94% after 2 years, and 83% after 3 years. Few (n=3) Walleye from the initial tagging cohort were recaptured after 4 years at large so I did not estimate tag loss after more than 3 years at large. Dorsal spine removal was clearly identifiable after as many as 3 years, indicating it is a reliable batch marking technique. These estimates of angler reporting rate and tag retention rate can be used to reduce bias of survival and exploitation estimates and add to a growing body of literature documenting these rates among a variety of fisheries and circumstances. Caution should be used in applying these estimates to other tagging studies as Walleye growth rates were slow during the study period, which likely increased tag retention rates.

Introduction

Exploitation and annual mortality rates are cornerstones of fisheries stock assessment (Ricker 1975). These metrics are commonly estimated using mark-recapture techniques (Pine et al. 2003). This approach requires many assumptions including: marked individuals are independent, marking does not cause mortality, and that marks are retained (Pollock et al. 2001). Additionally, when exploitation is estimated from angler reported tag recoveries it is often assumed that all recovered tags are reported. Some assumptions of mark-recapture techniques are realistic or can be overcome with appropriate study design, whereas others introduce significant bias and therefore must be explicitly examined to obtain accurate estimates of exploitation and total mortality.

Many researchers have found that anglers and commercial fishers do not report a large portion of the tagged fish they encounter and that marks are not retained perfectly (Cadigan and Bratney 2006; Miranda et al. 2002; Vandergoot et al. 2012; Koenigs et al. 2013; Meyer and Schill 2014). Both angler nonreporting and tag loss (Isermann and Knight 2005; Koenigs et al. 2013; McCormick et al. 2018) lead to underestimation of exploitation, which is especially problematic as this may lead managers to prescribe more liberal harvest regulations than are appropriate. As such, it is critical to account for angler nonreporting and tag loss when using mark-recapture methods to estimate exploitation rates.

Several methods have been proposed for estimating reporting and tag retention rates (Pollock et al. 2001). Reporting rate is commonly estimated using the high-reward method in which the recovery rate of standard, non-reward tags is compared to the recovery rate of high-reward tags assumed to have a reporting rate of 100%. Retention

rate is most often estimated by double marking fish and observing the number which have lost one mark during a period at large (McCormick and Meyer 2018). Estimates of reporting rate and tag retention rate are quite variable and, as such, it is important that they are directly estimated within mark-recapture studies.

Lake Oahe, USA, provides a high-profile recreational Walleye *Sander vitreus* fishery. During 2011, an extreme flood event caused high entrainment rates of Rainbow Smelt *Osmerus mordax* through Oahe Dam (Fincel et al. 2016). Rainbow Smelt are the primary prey of Walleye in Lake Oahe (Fincel et al. 2014a), and previous research indicated high natural mortality of Walleye following a similar event in 1997 (Graeb et al. 2008). As such, a multiple year mark-recapture study was initiated during 2013 to quantify Walleye mortality and exploitation in response to low Rainbow Smelt abundance and liberalized harvest regulations following the 2011 flood. This study was designed to explicitly estimate angler nonreporting and tag retention rates. I used a high-reward tagging system and double marking to estimate angler reporting and tag retention rates for jaw-tagged Walleye in Lake Oahe. The objectives of this study were to: 1) estimate angler reporting rate of tagged Walleye in Lake Oahe from 2013-2015, and 2) estimate initial and chronic tag loss rate for jaw-tagged Walleye.

Methods

Walleye tagging. – Methods designed to quantify angler reporting rate and tag loss for Lake Oahe Walleye were incorporated into a mark-recapture study that occurred throughout Lake Oahe from 2013 through 2017. Walleye tagging was conducted by personnel from North Dakota Game and Fish Department (NDGF), South Dakota Department of Game, Fish, and Parks (SDGF&P), and South Dakota State University

(SDSU) throughout Lake Oahe from 2013 through 2016. Fish were captured using trap nets, electrofishing and gill nets during March through May at 27 locations. Each Walleye was marked with an individually numbered size 12 Monel metal jaw tag manufactured by National Band and Tag Company. For Walleye less than 450 mm, jaw tags were affixed to the lower mandible bone (Figure 3.1a) and for Walleye greater than or equal to 450 mm jaw tags were affixed to the upper maxillary bone (Figure 3.1b). Tags were affixed to the jaw by piercing an incision through the flesh with a small knife, inserting the end of the jaw tag through the incision, and overlapping the ends of the tag using a pair of specialized pliers from National Band and Tag Company designed for smaller size 10 jaw tags.

Angler reporting rate. – From 2013 through 2015 Walleye were tagged with a mix of standard, non-reward tags and high-reward tags which had a value of US\$100. Approximately every 20th Walleye tagged was outfitted with a high reward tag to achieve a random distribution throughout the tagged population. Both standard and high reward tags were inscribed with a unique 5-digit number. Standard tags were also inscribed with a phone number, whereas high reward tags were inscribed “REWARD\$100” in place of the phone number. Tag returns were solicited via signage at boat launches, press releases, informational meetings, and advertisements by NDGF and SDGF&P published in regulation handbooks and on departmental websites. To discourage fraudulent reporting, physical verification of high-reward tags was required prior to paying rewards.

Reporting rates (λ) were estimated by comparing the number of standard to reward tags reported by anglers relative to the number of standard and reward tags released and assuming 100% of high-reward tags were returned (Pollock et al. 2001):

$$\lambda = \frac{S_r}{S_t} \div \frac{R_r}{R_t}$$

Where S_r is the number of standard tags released and S_t is the number of standard tags reported, R_r is the number of high-reward tags released and R_t is the number of high-reward tags reported. Variance of reporting rate was calculated using methods described by Henny and Burnham (1976):

$$Var(\lambda) = \lambda^2 * \left[\frac{1}{S_r} + \left(\frac{\lambda}{S_r} \right)^2 * \left(\frac{S_t}{R_t} \right)^2 * R_r \right]$$

This estimate of variance was used to calculate 95% confidence intervals. Reporting rates were estimated for each annual tagging cohort (2013-2015). I considered reporting rates different among years if 95% confidence intervals did not overlap.

Tag retention. - To estimate tag retention rate, Walleye tagged during 2013 were double marked with jaw tags and a dorsal spine removal. Dorsal spine removal was selected as the second mark because they have been observed to be easily distinguished longer after marking than other marks such as caudal fin clips (Koenigs et al. 2013). The 3rd dorsal spine was removed for fish tagged on the lower mandible bone and the 4th dorsal spine was removed for fish tagged on the upper maxillary bone.

Initial tag loss (6 – 58 days after tagging) was assessed by examining all Walleye captured after the start of tagging for the presence of tags and missing dorsal spines during initial 2013 tagging efforts which extended through May 31, 2013. Annual tag loss was assessed by examining all Walleye captured during subsequent years of tagging (2014-2016) and during 2017 when NDGF and SDGF&P continued to examine Walleye for marks when collecting Lake Oahe Walleye broodstock. Captured Walleyes that had a missing dorsal spine but no jaw tag were examined for physical damage to the jaw and

were tagged with a new individually numbered tag using identical methods as previously described. Because no initial tag loss was documented, I assumed this protocol prevented these fish from being counted as a tag loss again if recaptured during the same specific period. The probability of tag loss (R_{TL}) for each individual period was estimated using the equation:

$$R_{TL} = N_L/N_C,$$

Where N_L is the number of fish with a missing dorsal spine that had shed their tag and N_C is the total number of fish observed with a missing dorsal spine. This method of estimating tag loss has been described by others as the “discrete” method (McCormick and Meyer 2018). Although there are many methods for estimating tag loss, the discrete method is computationally simple relative to other methods yet produces similar results (McCormick and Meyer 2018). I estimated R_{TL} separately for fish tagged either on the upper maxillary or the lower mandible, and also for the two placements combined.

Results

From 2013 through 2015, 24,852 Walleyes were marked with standard tags and 3,908 (15.7%) of those were reported by anglers within the same year as tagging, and 1,279 Walleye were marked with high-reward tags and 334 (26.1%) of those were reported by anglers within the same year as tagging (Table 3.1). Estimated reporting rate of standard tags ranged from 56% to 70%, but confidence intervals overlapped among all years (Figure 3.2). Because no significant differences were detected among years I also analyzed 2013-2015 as a single period. From 2013-2015, 4,982 (20.0%) standard tags were reported and 442 (34.6%) high-reward tags were reported. When pooled from 2013-2015 reporting rate was estimated to be $58 \pm 5.6 \%$ (Table 3.1).

During 2013 tagging efforts, 9,132 Walleyes were double-marked with a Monel metal jaw tag and a dorsal spine removal. Of those, 6,886 were tagged on the lower mandible and 2,246 were tagged on the upper maxillary (Table 3.2). From 2013 through 2017, a total of 327 Walleye that had retained at least one mark were recaptured. Most recaptures (68%) occurred during the initial recovery period or after 1 year at large.

The dorsal spine removal was identifiable in all double-marked Walleye which had retained their jaw tag. Minimal spine regeneration was evident after multiple years at large (Figure 3.3). Additionally, evidence of deformation on the lower mandible was evident on fish that had shed their jaw tag (Figure 3.4).

During 2013, 115 Walleye were recaptured and none had shed their tag, yielding an estimate of zero for initial tag loss. Very few ($n=3$) fish tagged in 2013 were recaptured after 4 years at large. Low tag loss was observed for Walleye tagged on the bottom mandible with only 6.7% having shed their tag after 3 years at large (Table 2). Apparent tag loss for Walleye tagged on the upper maxillary was low (6.7%) after 2 years at large but estimated tag loss increased to 40.0% after 3 years at large. When all fish, including two tag placements, were pooled, tag loss was estimated to be 0% initially, 5.7% after 1 year at large, 6.3% after two years at large, and 20% after 3 years at large (Table 3.2)

Discussion

Estimated angler reporting rate (58% overall) of jaw-tagged Walleye in Lake Oahe was comparable to values reported for other tagging programs which rely on voluntary reporting from recreational fisheries. Meyer and Schill (2014) estimated a statewide reporting rate of 54.5% across species and years in a high-reward tag study

across the state of Idaho. Vandergoot et al. (2012) estimated an average tag reporting rate of 55% in Lake Erie during the initial 10 years of a long-term tagging study before finding evidence of a decline in reporting rate which they hypothesized was due to anglers becoming apathetic to the tagging program after an extended period. I found no evidence of temporal variation in angler reporting rate over the relatively short duration of this study and speculate it simply takes longer than 3 years for anglers to become apathetic to a tagging program.

Estimated tag loss rates were comparable to the lowest found among other studies which used Monel metal jaw tags to mark Walleye (Einhouse and Haas 1995; Isermann and Knight 2005; Vandergoot et al. 2012). This result was expected as this study followed recommendations from previous studies to maximize retention of jaw tags on Walleye. Vandergoot et al. (2012) compared tag retention rates among agencies using various tagging methods for Lake Erie Walleye and found the best results from the New York State Department of Environmental Conservation (NYSDEC). Methods used in this study were modeled after those used by NYSDEC, except that size-12 tags were used exclusively in this study as opposed to the size-10 tags used by NYSDEC. Einhouse and Haas (1995) and Isermann and Knight (2005) reported improved tag retention for size-12 as opposed to size-10, which prompted the exclusive use of size-12 tags in this study.

Another potential reason for the relatively low tag loss rates observed in this study was slow growth rates of Walleye during the study period. Low Rainbow Smelt abundance, as observed during this study (Fincel et al. 2014b, Meyer et al. 2015), contributes to extremely slow growth of Walleye in Lake Oahe (Graeb et al. 2008, Fincel et al. 2014a). I hypothesize fish may shed jaw tags, particularly those affixed to the

mandible, at a higher rate when experiencing fast growth rates as the tag would expand as the jaw grows. As such, my results may not apply to periods of fast growth even if identical tagging methods are used.

Apparent tag loss rate was higher for Walleye tagged on the upper maxillary after 3 years at large, but sample size after that length of time was small for both groups. As such, I am reluctant to draw strong conclusions regarding these apparent differences. Because estimates among the two groups were similar over periods with much larger sample sizes, I recommend using the pooled estimates when correcting for tag loss.

Results indicate dorsal spine removal is an effective, low-cost method for assessing chronic tag shedding of Walleye. Other low-cost methods, such as fin-clipping have been criticized because fin regeneration and natural abrasions can make accurate identification of fin clips difficult, especially after multiple years at large (Eipper and Forney 1965; Deroba et al. 2005; Guy et al. 1996). Although dorsal spine damage was commonly observed in Lake Oahe Walleye, observers were confident in distinguishing dorsal spine removal from natural damage. Flesh separating spines regenerated but very little spine regeneration was observed even after 3 years at large which helped contrast dorsal spine removal with dorsal spine damage. I recommend using dorsal spine removal as a batch marking method for Walleye and other percids such as Sauger *Sander canadense* and Yellow Perch *Perca flavescens*.

The values estimated in this study can be incorporated into estimates of exploitation and natural mortality for Lake Oahe Walleye during the same period to reduce bias associated with tag loss and angler nonreporting. If the Lake Oahe Walleye tagging program is extended into the future, I recommend the continued use of the high-

reward method to estimate annual reporting rate. Finally, I recommend replicating the tagging methods applied in this study during a period of fast Walleye growth to evaluate the influence of growth on tag loss rate.

References

- Cadigan, N. G., and J. Bratney. 2006. Reporting and shedding rate estimates from tag-recovery experiments on Atlantic cod (*Gadus morhua*) in coastal Newfoundland. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 1944-1958.
- Einhouse, D. W., and R. Haas. 1995. A preliminary examination of walleye distribution and exploitation in the eastern basin of Lake Erie using tag-recovery data. New York Department of Environmental Conservation, Division of Fish and Wildlife, Dunkirk.
- Eipper, A. W., and J. L. Forney. 1965. Evaluation of partial fin clips for marking largemouth bass, walleyes, and rainbow trout. *New York Fish and Game Journal* 12: 233-240.
- Deroba, J. J., M. J. Hansen, N. A. Nate, and J. M. Hennessy. 2005. Evaluating assumptions of mark-recapture studies for estimating angling exploitation of walleyes in northern Wisconsin lakes. *North American Journal of Fisheries Management* 25: 890-896.
- Fincel, M. J., D. J. Dembkowski, and S. R. Chipps. 2014a. Influence of variable rainbow smelt and gizzard shad abundance on walleye diets and growth. *Lake and Reservoir Management* 30: 258-267.
- Fincel, M. J., R. Hanten, H. Meyer, K. Potter and M. Smith. 2014b. Annual fish population and Angler use, harvest and preference surveys on Lake Oahe, South Dakota 2013. South Dakota Department of Game, Fish and Parks, Wildlife Division, Annual Report 14-02, Pierre.
- Fincel, M. J., W. J. Radigan, and C. M. Longhenry. 2016. Entrainment of Rainbow Smelt through Oahe Dam during the 2011 Missouri River flood. *North American*

- Journal of Fisheries Management 36: 844-851.
- Graeb, B. D. S., S. R. Chipps, D. W. Willis, J. P. Lott, R. P. Hanten, W. Nelson-Stastny, and J. W. Erickson. 2008. Walleye response to rainbow smelt population decline and liberalized angling regulations in a Missouri River reservoir. Pages 275-292 *in* M. S. Allen, S. Sammons and M. J. Maceina, editors. Balancing fisheries management and water uses for impounded river systems. American Fisheries Society, Symposium 62, Bethesda, Maryland.
- Guy, C. S., H. L. Blankenship, and L. A. Nielsen. 1996. Tagging and marking. Pages 353-383 *in* B. R. Murphy and D. L. Willis, editors. Fisheries techniques, 2nd Edition. American Fisheries Society, Bethesda, Maryland.
- Henny, C. J., and K. P. Burnham. 1976. A reward band study of mallards to estimate Reporting rates. Journal of Wildlife Management 40: 1-14.
- Isermann, D. A., and C. T. Knight. 2005. Potential effects of jaw tag loss on exploitation estimates for Lake Erie Walleyes. North American Journal of Fisheries Management 25: 557-562.
- Koenigs, R. P., R. M. Bruch, and K. K. Kamke. 2013. Impacts of anchor tag loss on walleye management in the Winnebago system. North American Journal of Fisheries Management 33: 909-916.
- McCormick, J. L., and K. A. Meyer. 2018. Sensitivity of exploitation estimates to tag loss estimation methods in Idaho sport fisheries. North American Journal of Fisheries Management 38: 170-179.
- Meyer, H., R. Hanten, K. Potter, M. Fincel, and M. Smith. 2015. Annual fish population and angler use, harvest and preference surveys on Lake Oahe, South Dakota 2014. South Dakota Department of Game, Fish and Parks, Wildlife Division, Annual Report 15-04, Pierre.
- Meyer, K. A., and D. J. Schill. 2014. Use of a statewide angler tag reporting system to

- estimate rates of exploitation and total mortality for Idaho sport fisheries. *North American Journal of Fisheries Management* 34: 1145-1158.
- Miranda, L. E., R. E. Brock, and B. S. Dorr. 2002. Uncertainty of exploitation estimates made from tag returns. *North American Journal of Fisheries Management* 22: 1358-1363.
- Pine, W. E., K. H. Pollock, J. E. Hightower, T. J. Kwak, and J. A. Rice. 2003. A review of tagging methods for estimating fish population size and components of mortality. *Fisheries* 28: 10-23.
- Pollock, K. H., J. M. Hoenig, W. S. Hearn, and B. Calingaert. 2001. Tag reporting rate estimation 1: an evaluation of the high-reward tagging method. *North American Journal of Fisheries Management* 21: 521-532.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin* 191.
- Vandergoot, C. S., T. O. Brenden, M. V. Thomas, D. W. Einhouse, H. A. Cook, and M. W. Turner. 2012. Estimation of tag shedding and reporting rates for Lake Erie jaw-tagged walleyes. *North American Journal of Fisheries Management* 32: 211-223.

Table 3.1. Summary of standard and high-reward tags released from 2013 to 2015 in Lake Oahe.

Year	Standard tags			High-reward tags			Reporting rate (\pm 95% CI)
	Released	Recovered Year 1	Recovered 2013-2015	Released	Recovered Year 1	Recovered 2013-2015	
2013	8779	1285	1809	394	99	133	58.2 \pm 11.9
2014	7291	1072	1622	424	89	163	70.0 \pm 15.1
2015	8782	1551	1551	461	146	146	55.8 \pm 9.5
Total	24852	3908	4982	1279	334	442	58.0 \pm 5.6

Table 3.2. Summary of recovery data for Lake Oahe Walleye double-marked with size-12 Monel metal jaw tags and a dorsal spine removal. Walleye were marked in two configurations: 1) tag on the lower mandible bone (Jaw_bottom) and third dorsal spine removed (Spine_3) and 2) tag on the upper maxillary bone (Jaw_top) and fourth dorsal spine removed (Spine_4).

Mark Type	Number Marked	Recaptures by years at large				
		0	1	2	3	4
Upper Maxillary						
Jaw_top+Spine_4	2,246	57	30	15	10	1
Jaw_top		0	0	0	0	0
Spine_4		0	3	1	4	0
Tag loss (%)		0.0	10.0	6.7	40.0	0.0
Lower Mandible						
Jaw_bottom+Spine_3	6,886	58	76	48	15	2
Jaw_bottom		0	0	0	0	0
Spine_3		0	3	3	1	0
Tag loss (%)		0.0	3.9	6.3	6.7	0.0
Pooled						
Jaw_tag+spine_removal	9,132	115	106	63	25	3
Jaw_tag		0	0	0	0	0
Spine_removal		0	6	4	5	0
Tag loss (%)		0.0	5.7	6.3	20.0	0.0



Figure 3.1. Placement of size 12 Monel metal jaws on (a) lower mandible of Walleye less than 450 mm, and (b) upper maxillary of Walleye greater than or equal to 450 mm.

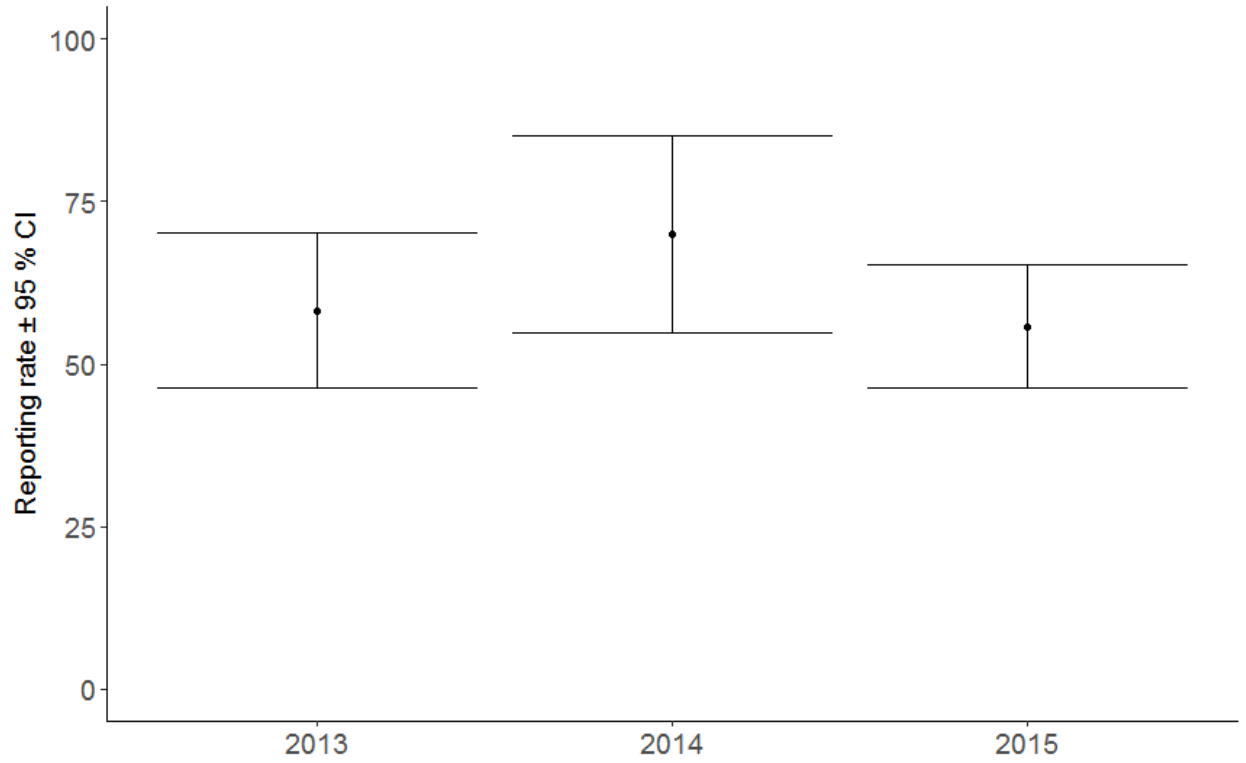


Figure 3.2. Estimated reporting rate and associated 95% confidence intervals for tagged Walleye during 2013-2015 on Lake Oahe.



Figure 3.3. Photograph of missing 4th dorsal spine after 2 years at large.



Figure 3.4. Photograph of jaw deformation on a Walleye which had shed a tag from its lower mandible bone after 1 year at large.

CHAPTER 4: WALLEYE MOVEMENT PATTERNS INFERRED FROM TAGGING IN LAKE OAHE

Abstract

Walleye *Sander vitreus* are capable of moving long distances but populations often exhibit spatial structuring within large water bodies containing multiple spawning and feeding areas. Previous research suggested Walleye inhabit specific regions within Lake Oahe, a large Missouri River reservoir. I used tag returns collected from 2013 through 2017 to quantify Walleye movement patterns among 4 regions of Lake Oahe. My objective was to characterize movement patterns of Lake Oahe Walleye and to evaluate whether isolated groups occur within the population. Walleye were primarily caught within the region where they were tagged and interregional movement typically involved fish moving in a downstream direction from the tagging location. In the upstream portion of the reservoir, Walleye inhabited the Garrison Reach of the Missouri River throughout the year, displaying a river-resident life history strategy. Walleye tagged near the confluence of the Garrison Reach and Lake Oahe exhibited a lake-resident, river-run life history strategy moving into the Missouri River to spawn before returning to the reservoir. Within Lake Oahe, Walleye tagged in large tributaries were typically recaptured at nearby reservoir locations. These fish displayed a lake-resident, river-run life history but the close proximity of spawning habitat to feeding areas resulted in relatively short movement distances. Male Walleye were more likely than females to be recaptured at or near tagging locations which I hypothesize was a result of their tendency to remain on spawning grounds longer than females. I conclude that the Lake Oahe Walleye population is spatially structured such that isolated groups occur within the

system and recommend evaluating the extent to which Walleye population dynamics vary spatially within Lake Oahe.

Introduction

Walleye *Sander vitreus* is a popular sport and commercial fish throughout its distribution in the United States and Canada, and is found in many large water bodies which contain diverse habitats. Walleye are capable of long migrations (up to 300 km; Colby et al. 1979), which are thought to be movements between feeding and spawning areas. Bozek et al. (2011) classified Walleye life histories into three categories based on feeding and spawning behavior: 1) river-resident Walleye which feed and spawn in rivers (Preigel 1970; Stevens 1990), 2) lake-resident, river-run Walleye which feed in lakes and spawn in major tributaries (Geiling et al. 1996; Hayes and Petrusso 1998), or 3) lake-resident Walleye which feed throughout lakes and move into shallow reefs or bays to spawn (Eschmeyer 1950; Raabe 2006). Thus, movement patterns within waterbodies are influenced by the distance between feeding areas and suitable spawning habitat (Colby et al. 1979; Bozek et al. 2011). For example, lake-resident, river-run Walleye of the Laurentian Great Lakes may travel long distances through deep, cold water to reach spawning tributaries (Hayden et al. 2014), whereas lake-resident Walleye often move short distances to spawn along shorelines (Bozek et al. 2011).

Within large systems, Walleye often utilize multiple spawning and feeding areas in a manner that is sufficiently isolating to create distinct stocks (Preigel 1970; Spangler et al. 1977; Jennings et al. 1996), which are identified as groups which spawn in the same location and time, and exhibit similar growth and mortality rates (Van Den Avyle 1993). The presence of multiple stocks within a population may increase resilience to

disturbance (Vandergoot and Brenden 2014), but such complexity can lead to misguided management decisions if spatial structure is not accounted for (Cooper and Mangel 1999; Smedbol and Woblewski 2002). In Lake Erie, Walleye utilize multiple spawning areas and stocks exhibit variation in movement patterns as a result of regional patterns in water temperature and prey abundance (Wang et al. 2007). Further, Vandergoot and Brenden (2014) documented regional differences in movement probability and natural mortality rates within Lake Erie, underscoring the importance of accounting for spatial variation in Walleye populations which contain multiple stocks.

Lake Oahe is a large mainstem Missouri River reservoir which supports a popular Walleye sport fishery in North Dakota and South Dakota, USA. Due to its large size and habitat diversity, Lake Oahe contains multiple, isolated Walleye spawning areas which provide the potential for all three life histories described by Bozek et al. (2011). A remnant reach of the Missouri River enters Lake Oahe at its upstream boundary and offers deep, coolwater river habitat suitable for both river-resident and lake-resident, river-run Walleye. Additionally, three large tributaries enter Lake Oahe and provide suitable habitat for lake-resident, river-run Walleye. Shallow water and warm temperature probably limit river-resident Walleye in these tributaries. Shallow embayments and reefs abound throughout Lake Oahe, providing inshore habitat for lake-resident Walleye.

Lake Oahe also exhibits spatial heterogeneity in primary productivity and water temperature which influences Walleye prey abundance and composition (Fincel 2011). In general, Lake Oahe experiences a typical reservoir pattern of primary productivity, in which primary and secondary productivity are relatively low at its furthest upstream,

riverine section due to light and nutrient limitation, then increases to a peak at the transition from riverine to reservoir habitat where the balance between nutrient concentration and light limitation is optimized, before decreasing further downstream as sediment settles out and reduces nutrient concentration (Wetzel 2002; Fincel 2011). Large tributaries also increase local productivity in Lake Oahe (Fincel 2011). Walleye consume a variety of fish and macroinvertebrate prey throughout Lake Oahe, but Rainbow Smelt *Osmerus mordax* are a dominant diet item when abundant (Bryan 1995; Davis 2004; Fincel et al. 2014a), and their distribution in Lake Oahe is limited to the lower reservoir where water thermally stratifies and maintains an oxygenated hypolimnion during summer months (Fincel 2011).

Previous research has indicated Lake Oahe Walleye inhabit particular regions throughout the year (Riis et al. 1993; Hendrickson 2005). For Walleye tagged in lower Lake Oahe (Riis et al. 1993) and in upper Lake Oahe and the Garrison Reach (Hendrickson 2005), approximately 75% of angler recoveries occurred within 30 km of their tagging location. Hendrickson (2005) also found that females traveled further and were more likely to be recaptured downstream than males. Carlson et al. (2017) assessed Walleye movement in Lake Oahe using otolith microchemistry and found considerable site residency and concluded adult Walleyes more commonly moved downstream than upstream.

Reservoir habitat, coldwater prey distribution, and previous research all indicate ecologically meaningful regions exist for Walleye in Lake Oahe. However, the extent to which Walleye from these regions mix within and among years has not been evaluated. In this study, I quantified regional patterns of Walleye movement in Lake Oahe by

analyzing recovery data from a system-wide tagging study, accounting for spatial and temporal variation in tagging and angling effort. Broadly, my objectives were to evaluate whether Walleye population dynamics should be quantified separately by region within Lake Oahe, and whether opportunities for regional management within Lake Oahe exist. My specific objectives were to: 1) quantify the relative contributions of Walleye spawning stocks within regions to Walleye harvest in other regions, 2) characterize movement patterns of Walleye from individual spawning stocks within all regions of Lake Oahe according to life-history strategies described by Bozek et al. (2001), 3) evaluate differences in pre-spawn and post-spawn movement patterns, and 4) test for differences in movement patterns among male and female Walleye.

Methods

Study Area

This study occurred on the Missouri River downstream of Garrison Dam (River Mile (RM) 1390) and upstream of Oahe Dam (RM 1072). This section of the Missouri River contains a remnant river reach called the Garrison Reach and a reservoir called Lake Oahe. The Garrison Reach consists of approximately 167 km of regulated river habitat between the Garrison Dam and Lake Oahe. The confluence between the Garrison Reach and Lake Oahe shifts as much as 54 river miles, occurring as far downstream as RM 1232 at low reservoir elevations, and as far upstream as RM 1286 at full pool (Johnson et al. 2012). Due to flow regulation, the Garrison Reach experiences a relatively flat hydrograph when compared to pre-dam conditions of the Missouri River when large peak flows occurred annually during April and June (Johnson et al. 2012). Water released through the Garrison Dam is sediment- and nutrient-starved and nearly all of the

sediment load transported through the Garrison Reach originates from tributaries and riverbed erosion within the Garrison Reach. Sedimentation occurs at the point of confluence between the Garrison Reach and Lake Oahe forming novel reservoir delta habitat (Johnson et al. 2012). Although the exact location of the delta varies, the Garrison Reach can be thought of as having two distinct habitats: an upstream section with a distinct channel containing cold, clear water, low sediment load, and low habitat diversity, and a downstream section characterized by a braided channel, relatively warm, turbid water, side channels, and floodplain connectivity (Graeb et al. 2009).

Lake Oahe consists of approximately 344 km of impounded river which creates approximately 145,000 ha in surface area. Lake Oahe has a mean depth of 19 m and a maximum depth of 67 m (Nelson and Walburg 1977). The reservoir exhibits longitudinal changes in basin morphology, water depth, and water clarity which influence primary and secondary productivity (Fincel 2011). In general, depth increases, water clarity increases, shoreline development increases, and productivity decreases from upstream to downstream.

Three large tributaries influence local productivity in Lake Oahe (Fincel 2011). The downstream portion of the reservoir thermally stratifies in the summer and maintains an oxygenated hypolimnion. The extent of thermal stratification varies annually, but is consistently documented as far upstream as Swan Creek (RM 1174). Therefore, Lake Oahe typically maintains approximately 48,000 ha of coldwater habitat during the summer.

For analysis, I defined 4 zones (Figure 4.1) within Lake Oahe based on natural habitat boundaries, coldwater prey distribution and boundaries used in the design of

monitoring programs implemented by South Dakota Game, Fish and Parks (SDGF&P) and North Dakota Game and Fish Department (NDGF). These zones include: (1) the Riverine zone (R) which approximates the upper portion of the Garrison Reach containing cold, clear sediment-starved water, (2) the Transition zone (T) which combines the lower Garrison Reach and the North Dakota portion of Lake Oahe; this region is characterized by relatively warm, turbid water, and high primary productivity, (3) Upper Oahe (UO) which encompasses two large tributaries to Lake Oahe and is characterized by intermediate primary productivity and relatively high coldwater prey abundance, (4) Lower Oahe (LO) which encompasses one large tributary to Lake Oahe and is characterized by deep, cold water, low primary productivity, and highly variable coldwater prey fish abundance. Recaptures from below Oahe Dam were treated as a separate zone (Entrained) in our analysis.

Data Collection

Walleye tagging occurred throughout Lake Oahe and the Garrison Reach annually from 2013 through 2016. Fish were captured using trap nets, electrofishing and gill nets during March through May at 27 locations thought to be Walleye spawning sites (Table 1). For each Walleye, personnel measured for total length (TL; mm), determined sex, and affixed an individually numbered size 12 Monel metal jaw tag to the mandible or maxillary bone. Each tag was inscribed with a phone number for anglers to report tags. Recapture information came from anglers who voluntarily reported tagged fish and was collected through the end of 2017. Anglers were asked to provide the tag number, date of recapture, fate of the fish (harvested, released with tag intact, released but removed tag),

and approximate location of the recovery. Recapture location was estimated to the nearest river mile of the Missouri River.

I used estimates of angler effort generated by NDGF creel surveys which are conducted every three years and were available for only one (2015) of the four years of this study (Bailey et al. 2016). Reports from NDGF summarize angler effort by three zones: Garrison Reach, Upper Missouri River, and Lake Oahe. The Upper Missouri River and Lake Oahe as described by NDGF comprised what I classified as the Transition zone, so annual estimates of angling effort (hr) from these two zones were combined and divided by their total surface area (ha) to estimate standardized angler effort (hr/ha). The Garrison Reach as described by Bailey et al. (2016) mirrored what I considered the Riverine zone, so no adjustments were needed to estimate standardized angler effort. I applied the 2015 estimates of standardized angler effort (h/ha) for the Riverine and Transition zones for all years considered in this study, thereby assuming constant angling effort in these zones.

Estimates of standardized angler effort (hr/ha) generated from SDGF&P creel surveys were available for all years of this study (Fincel et al. 2014b, Meyer et al. 2015, Potter et al. 2016). Annual reports from SDGF&P summarize angler effort by three zones: Upper, Middle, and Lower. The Upper and Middle zones comprise what was classified as Upper Oahe, so annual estimates of angling effort (hr) from these two zones were combined and divided by their total surface area (ha) to generate annual angler effort (h/ha) estimates for Upper Oahe. The Lower zone described in SDGF&P reports comprised what I considered Lower Oahe, so no adjustments were needed to estimate standardized angling effort.

Analysis

Recapture locations of tagged Walleyes were classified by zone (R, T, UO, LO, Entrained; Figure 4.1). I calculated standardized tag return rates which estimate the number of tagged Walleye from each zone expected to be recaptured within each zone if the number of Walleye tagged and the amount of angler effort applied were equal among zones. Annual tag return rates in each zone were standardized using methods similar to Wang et al. (2007) which adjust the number of tags recaptured in a given zone and year for differences in the number of tags released annually in each zone, and for differences in annual angler effort in each zone:

$$S_{ijt} = R_{ijt} \div T_{jt} \div E_{it}$$

where S_{ijt} is the standardized tag return rate for fish tagged in zone j and recaptured in zone i during year t (I used only fish tagged and recaptured during the same year for this analysis to reduce the influence of variable annual mortality rates across zones on differences in standardized tag return rate); R_{ijt} is the number of Walleye recaptured during year t in zone i which were tagged in zone j ; T_{jt} represents the number (in 1,000s) of tags released in zone j during year t ; E_{it} is the relative angling effort in zone i during year t . Relative angling effort was calculated by dividing the effort (hr/ ha) for a given zone by the effort in the Transition zone for the same year. Angling effort was quantified relative to the Transition zone because effort was consistently highest in that zone. Few tagged fish were recaptured downstream of Oahe Dam so I estimated standardized tag return rate for the Entrained category by pooling all years and all tagging zones.

Movement patterns were investigated at a finer spatial scale for Walleye tagging cohorts thought to represent spawning groups. I defined spawning groups based on

tagging location. I selected spawning groups from the six locations with the greatest number of Walleye tagged, which included one Riverine spawning group (1), two Transition spawning groups (10, 13), two Upper Oahe spawning groups (16, 17), and one Lower Oahe spawning group (24). For each spawning group, I compared recapture distributions (by river mile) between Walleye recaptured during the same calendar year as tagging (TY recaptures) and those recaptured in any calendar year different than the tagging year (DY recaptures). I hypothesized these distributions would be different because the distribution of DY recaptures would include movements during late winter and early spring when large spawning migrations are thought to occur for Walleye, whereas the distribution of TY recaptures included only post-spawn movements. I used a two-sample Kolmogorov-Smirnov test to evaluate the null hypothesis of no differences among the distribution of TY and DY recaptures within each spawning group. Comparisons were tested for statistical significance at $\alpha = 0.05$.

To test whether movement patterns differed among sexes, I compared recapture distributions of male and female Walleye from spawning groups using a two-sample Kolmogorov-Smirnov test. If TY and DY recapture distributions were found to be significantly different, this analysis was conducted separately for TY and DY recaptures from a given spawning group, otherwise all recaptures were pooled. This analysis was not conducted for Site 24 due to small sample size of females. Comparisons were tested for statistical significance at $\alpha = 0.05$. All statistical analyses were conducted using the base package in Program R (R Core Development Team 2016).

Results

From 2013 through 2016, 34,378 Walleye were tagged at 27 locations throughout Lake Oahe, and from 2013 through 2017, 8,029 of those tagged fish were recaptured by anglers and voluntarily reported with a description of recapture location. Anglers returned 5,084 tagged Walleye during the same year as tagging and 2,945 after one or more year at large. The greatest number of tags were released and returned from the Transition zone and Upper Oahe (Table 4.2). Selected spawning groups accounted for a large proportion of tagged fish within their respective zones (R = 92%, T = 76%, UO = 79%, LO = 79%).

Standardized tag return rate

Standardized tag return rates indicated Walleye were most likely to be recaptured in the same zone in which they were tagged (Table 4.3, Figure 4.2). Percentage of standardized return rate within the same zone as tagging ranged from a low of 66% for Walleye tagged in the Transition zone in 2014 to a high of 98% for Walleye tagged in Lower Oahe during 2016 (Table 4.3). Patterns were consistent for zones across years; the observed range in percentage of standardized return rate was no greater than 11% for any zone across years (Table 4.3).

Walleye tagged in the upstream zones (R, T) of Lake Oahe were recovered across boundaries more frequently than those tagged in downstream zones (UO, LO). Walleye that crossed boundaries were most likely to be recaptured in neighboring zones and movement direction varied by tagging zone. Walleye tagged in the Riverine zone composed a relatively large portion of the standardized return rate in the Transition zone across all years (19% - 26%) but had little representation further downstream (0% - 4%). Fish tagged in the Transition zone displayed some upstream movement, making up between 4% and 13% of the standardized return rate in the Riverine zone, but had a

greater influence immediately downstream in Upper Oahe where they accounted for 14% - 24% of the standardized return rate. Further downstream in Lower Oahe, Walleye tagged in the Transition zone composed 0% - 1% of the standardized return rate.

Walleye tagged in Upper Oahe and Lower Oahe composed a low percentage of standardized return rates in other zones (Table 4.3, Figure 4.2). Fish tagged in Upper Oahe rarely moved across boundaries, accounting for 0% - 7% of standardized return rate across years in all other zones. Walleye tagged in Lower Oahe made up 0% of the standardized return rate in all years for the Riverine and Transition zones, and a maximum of 2% of the standardized return rate in Upper Oahe.

From 2013 through 2016 anglers reported eight Walleye tagged in Lake Oahe from below Oahe Dam, all of which were upstream of Big Bend Dam in Lake Sharpe. All Entrained recaptures were reported from within 12 river miles downstream of Oahe Dam, and seven were recovered within one river mile below the dam. Walleye tagged in the Transition zone, Upper Oahe, and Lower Oahe were among the eight Entrained recaptures. I estimated a standardized tag return rate of 0.23 Entrained recaptures for every 1,000 Walleye tagged in the Oahe system.

Spawning groups

I found no significant differences ($D = 0.09$, $P = 0.4$; Table 4.4) between the distributions of TY and DY recaptures tagged at Site 1 in the Riverine zone. A high percentage (46.0%) of Site 1 recaptures came from the 3 river miles between the tagging location and Garrison Dam. Nearly all (97.4%) Site 1 recaptures were recovered in the Riverine zone (77.5%) or the Transition zone (19.1%). Recapture distributions of male and female recoveries varied significantly ($D = 0.25$, $P < 0.001$; Table 4.5) for Walleye

tagged at Site 1 (Figure 4.3). Females (65.6%) were recaptured more frequently than males (39.8%) from the 3 river miles between the tagging location and the Garrison Dam. Males (22.6%) were recaptured in the Transition zone more frequently than females (11.1%).

The distributions of TY and DY recaptures differed significantly (Site 10, $D = 0.15$, $P < 0.001$; Site 13, $D = 0.20$, $P < 0.001$; Table 4.4) for two Transition zone spawning groups. Recapture distributions also varied among sexes for Site 10 (TY: $D = 0.27$, $P < 0.001$; DY: $D = 0.32$, $P = 0.001$) and Site 13 (TY: $D = 0.18$, $P < 0.001$; DY: $D = 0.30$, $P < 0.001$).

For both TY and DY recaptures from Site 10, Walleye were recovered in nearly equal proportions upstream (TY = 50.0% vs. DY = 50.4%) and downstream (TY = 46.1%; DY = 46.0%) of the tagging site (Figure 4.4). However, a greater proportion of Site 10 DY recaptures (21.9%) came from RM 1269 to RM 1280 than TY recaptures (7.8%). Site 10 Male TY recaptures were more frequently recaptured upstream of the tagging location than female TY recaptures (Figure 4.4). More specifically, 48.3% of Site 10 male TY recaptures were recovered upstream of Site 10 (RM1287) to RM 1325, as opposed to 27.2% of Site 10 female TY recaptures. Differences among sexes for Site 10 DY recaptures were most evident from RM 1269 to RM mile 1325 where 73.8% of males were recovered as opposed to 48% of females.

Site 13 DY recaptures were recaptured in greater proportion than TY recaptures at the tagging location (TY = 20.1%; DY = 29.2%) and between RM 1269 and RM 1280 (TY = 10.5%; DY = 16.1%; Figure 4.5). Female Site 13 TY recaptures were recovered at the tagging location more frequently than males (25.5% vs. 16.6%). A higher percentage

of male Site 13 TY recaptures (33.8%) was recovered between RM 1269 and RM 1325 than their female counterparts (17.0%). Similar differences were observed for Site 13 DY recaptures; 48.1% of females and 23.4% of males were recaptured at the tagging location, whereas 46.3% of males and 16.3% of females were recovered between RM 1269 and RM 1325. Both TY and DY recovery patterns downstream of the tagging location were similar among sexes for the Site 13 spawning group (Figure 4.5).

I found no significant differences between the distributions of TY and DY recaptures tagged at Site 16 in Upper Oahe ($D = 0.09$, $P = 0.06$). Significant differences between the distributions of TY and DY recaptures were detected for Walleye tagged at Site 17, also located in Upper Oahe ($D = 0.12$, $P = .04$). Site 16 and Site 17 displayed somewhat similar recapture patterns (Figure 4.6; Figure 4.7), with a large percentage recaptures coming from the tagging location (Site 16 = 33.8%; Site 17 = 39.8%), and a tendency for recaptures from outside the tagging location to be recovered at a higher percentage downstream (Site 16 = 74.3%; Site 17 = 73.6%). Walleye tagged at these locations tended to not cross into Lower Oahe (Figure 4.6, Figure 4.7). Recapture distributions did not vary significantly among sexes for the Site 16 spawning group ($D = 0.11$, $P = 0.10$). Recapture distributions varied among sexes for Walleye tagged at Site 17 (TY: $D = 0.32$, $P < 0.001$; DY: $D = 0.31$, $P = 0.007$). Site 17 male and female recapture patterns differed from RM 1110 to RM 1152 where 33.3 % of females and 14.0 % of males were recaptured (Figure 4.7). Additionally, Site 17 males (41.3%) were recaptured at the tagging location more frequently than females (30.6%).

The distributions of TY and DY recaptures differed significantly for one Lower Oahe spawning group (Site 24, $D = 0.44$, $P < 0.001$). Nearly all (98.4%) Site 24 TY

recaptures were recaptured within Lower Oahe (Figure 4.8); 91 % of Site 24 TY recaptures came from within 10 river miles of the tagging location. Site 24 DY recaptures were much more likely than TY recaptures to be recovered upstream (TY = 51.7%; DY = 71.7%), and especially across regional boundaries in Upper Oahe (TY = 1.2%; DY = 20.5%).

Discussion

Throughout Lake Oahe and the Garrison Reach the majority of Walleye movement between spawning and feeding areas occurred within regions, although the rate of interregional movement varied within and among spawning regions. The distribution of tag returns relative to tag location indicates that Lake Oahe Walleye use multiple life-history strategies. The high propensity of Walleye recaptured in lake habitat but initially tagged in river habitat suggests that the lake-resident, river run is the most common strategy. Therefore, regional configuration of river spawning areas and lake feeding areas is an important driver of Walleye movement patterns in Lake Oahe. Similar to previous studies (Riis et al. 1993; Hendrickson 2005; Carlson et al. 2017), I found the majority of Walleye harvested within zones were year-long residents of those zones. Overall, there is strong evidence that the Lake Oahe Walleye population contains multiple, isolated groups which potentially experience variable population dynamics related to spatial variability in environmental conditions and angling effort.

Standardized return rates within zones were dominated by resident Walleye within all zones indicating the majority of fish do not cross regional boundaries. My results also demonstrated that if Walleye did cross regional boundaries after spawning they tended to cross into the adjacent, downstream zone. The Riverine zone was among

the most isolated in Lake Oahe. The majority of Riverine spawners remained there throughout the year, whereas spawners from other zones rarely moved into the Riverine zone after spawning. Walleye use temperature and discharge as environmental cues for spawning (DiStefano et al. 1997; Nilsson and Berggren 2000), and these cues may be altered in the Riverine zone by releases from the Garrison Dam. Similarly, suitable habitat may be scarce in the Riverine zone due to downstream impacts of the Garrison Dam on traditional spawning habitat (Zhong and Power 1996). Standardized return rates from the Transition zone and Upper Oahe both suggest that some Walleye spawn in upstream neighboring zones before moving downstream across regional boundaries. This pattern was not observed for Lower Oahe. I hypothesize Walleye that spawn in the Transition zone move into the reservoir after spawning, and that many of these fish move into Upper Oahe in search of cooler water temperatures and coldwater prey. In Upper Oahe, a high proportion of Walleye spawn in large tributaries and feed within the large embayments created by these tributaries where warmwater prey are abundant due to relatively high primary and secondary productivity (Finzel 2011). Rainbow Smelt display relatively high abundance in Upper Oahe (N. Kludt, South Dakota State University, unpublished data), and deep, stratified water offers optimal water temperatures for Walleye throughout warm summer months. Therefore, there is little incentive for Walleye that leave the Upper Oahe or Transition zone spawning areas to move further downstream than Upper Oahe.

Entrainment of Walleye through Oahe Dam was quite rare during this study. Carlson et al. (2017) found increased entrainment of Walleye during a period of high discharge through Oahe Dam, but my study occurred during a period of relatively low

discharge which was more characteristic of average conditions for Oahe Dam. Thus, although the rate of entrainment may be high during periods of extremely high discharge, my results indicate little entrainment of adult Walleye occurs during normal discharge.

Walleye tagged at Site 1, the primary tagging location within the Riverine zone, exhibited similar recovery patterns across years and displayed characteristics common to tailrace fisheries. A very low proportion of this group was recaptured in the reservoir, indicating a river-resident life history strategy (Bozek et al. 2011). Nearly half of recoveries occurred in the 3-mile river segment between the tagging location and Garrison Dam, a trend that was more exaggerated for females. Walleye and other migratory percids such as Sauger *Sander canadensis* are commonly concentrated below dams while migrating, and these areas are often easily accessible by anglers (Beamesderfer 1998; Pegg et al. 1997; Williot et al. 2002). Both of these factors likely contributed to high recovery rates directly below Garrison Dam. However, angler effort applies equally among sexes yet I observed more downstream movement by males.

I observed differences in patterns between TY and DY recaptures and between male and female Walleye tagged at Site 10 within the Transition zone. This tagging site is located at the interface between the reservoir and the Garrison Reach of the Missouri River where sedimentation and fluctuating water levels have created novel reservoir delta habitat (Johnson et al. 2012). I suspect Walleye tagged at this location express a lake-resident, river-run life history, feeding in the reservoir and moving into the delta and the lower Garrison Reach to spawn. The primary differences between TY and DY recaptures occurred downstream of the tagging location from approximately RM 1269 to RM 1280, where a greater proportion of DY recaptures occurred for both males and females. I

speculate this difference occurred because Walleye pre-spawn movement into the delta happens during late winter and early spring, at which time TY fish would not yet have been tagged. Male Walleye tagged at Site 10 were much more likely than females to be recaptured from RM 1269 to RM 1325. I hypothesize male Walleye arrive earlier and stay longer at this spawning area than females, which is consistent with observations from other Walleye populations (Eschmeyer 1950; Whitney 1958; Forney 1963; Ellis and Giles 1965). Female Walleye tagged at Site 10 were more likely than males to be recovered downstream in Upper Oahe. I suspect this result is an artifact of higher exploitation of males on spawning grounds, which are exposed to very high angling effort due to accessibility and proximity to the urban areas of Bismarck and Mandan, North Dakota (Bailey et al. 2016).

Walleye tagged at Site 13, particularly females, were much more likely than Site 10 to be recaptured at the tagging location. This tagging site is an embayment located in the upper reservoir which is formed by a small tributary. I hypothesize Walleye tagged at this location employ a lake-resident, river-run life history, moving into the tributary embayment to spawn and moving back toward the reservoir to feed. Warm water and nutrient inputs enter from Beaver Creek and contribute to relatively high productivity (Johnson 2010). Recoveries upstream of Site 13 in the same river reach where a high proportion of Site 10 Walleye were recaptured (RM 1269-1325) suggest that some Walleye enter Site 10 to spawn and then continue moving upstream in search of more, or better, spawning opportunities. Males tagged at Site 13 were much more likely than females to be recaptured upstream, which may be a result of more males moving upstream after spawning at Site 13, or because the males which continued upstream

remained in that area longer than females. Although Site 13 is located 31 river miles downstream of Site 10, a much lower proportion of recaptures came from downstream of Site 13. This result demonstrates that emigration from Site 13 is related to spawning rather than feeding.

Walleye tagged at both Sites 16 and 17 displayed high site fidelity and a tendency for movement to occur in a downstream direction. These two sites are large tributaries which enter Lake Oahe and form large embayments with relatively high water temperature and productivity (Fincel 2011). Additionally, coldwater prey inhabit these embayments during late spring and occur in nearby downstream areas within the main reservoir throughout the year (N. Kludt, South Dakota State University, unpublished data). I suspect Walleye tagged at these two locations exhibit a lake-resident, river-run life history, spawning in tributaries during the spring and either remaining in the large adjoining embayments throughout the year or moving into the main reservoir to feed on coldwater prey. In this study, I classified recaptures by river mile within the mainstem Missouri River, so measurements were insensitive to movements within these large embayments. Females tagged at Site 17 were more likely than males to be recaptured downstream, which may occur because male Walleye remain at spawning areas longer than females. It is not clear why this pattern would be observed at Site 17 and not at Site 16.

Walleye tagged at Site 24 displayed high site fidelity within the tagging year. This site was typically sampled later in the year than elsewhere and, as a result, I hypothesize Walleye tagged there had completed spawning by the time they were tagged. The extremely skewed sex ratio (male:female = 21:1) at this location also supports this

hypothesis. Therefore, fish tagged at this location likely represented Walleye which had already arrived at their feeding location. A high percentage (93%) of TY recaptures occurred during summer months (May-July), so the distribution of those returns indicates very little movement after Walleye had arrived at their feeding location. This is consistent with evidence that long distance Walleye movement is usually between spawning and feeding areas (Colby et al. 1979). A substantial proportion of Site 24 DY recaptures occurred upstream of the tagging location, often crossing into Upper Oahe. Although this result seems to suggest considerable upstream movement, there is evidence that prey abundance was extremely low in Lower Oahe during this study due to high Rainbow Smelt entrainment during 2011 (Finzel et al. 2016; N. Kludt, South Dakota State University, unpublished data), which has previously caused high mortality rates due to starvation (Graeb et al. 2008). Therefore, the observed recovery patterns may be indicative of differential mortality rates among regions rather than movement patterns.

I conclude that “lake-resident, river-run” is the most common life-history strategy for Walleye in Lake Oahe and movement patterns vary according to local configuration of spawning and feeding areas. Male Walleye were more likely than females to be recovered at or near tagging locations which I suspect was a result of males arriving earlier and staying longer at spawning areas than females. Although distance moved varied among tagging regions and a small number of fish were found to travel the entire reservoir, our results strongly suggest that Walleye in Lake Oahe do not constitute a single, intermixed population. The Riverine zone and Lower Oahe appear to be particularly isolated from the rest of Lake Oahe and present the opportunity for regional management within Lake Oahe. I recommend incorporating spatial variation into

estimates of Lake Oahe Walleye population dynamics (e.g. recruitment, growth, mortality) to evaluate whether important functional differences exist among isolated groups in Lake Oahe.

References

- Bailey, P. B., S. Gangl, and D. Fryda. 2016. Angler use and sportfishing catch survey on the Missouri River and Lake Oahe, North Dakota: April 1 through October 31, 2015. North Dakota Game and Fish Department Project F-2-R-61, Report 2.
- Beamesderfer, R. C. 1998. Management and trade in Pacific sturgeon. Pages 95-105 in D.F. Williamson, G. W. Benz, and C. M. Hoover, editors. Proceedings of the Symposium on Harvest, Trade, and Conservation of North American Paddlefish and Sturgeon. TRAFFIC North America Washington, D.C.
- Bozek, M. A., D. A. Vaccante, and N. P. Lester. 2011. Walleye and sauger life history Pages 233-302 in B.A. Barton, editor. Biology, management, and culture of walleye and sauger. American Fisheries Society, Bethesda, Maryland.
- Bryan, S. D. 1995. Bioenergetics of walleye in Lake Oahe, South Dakota. M.S. Thesis. South Dakota State University, Brookings, SD.
- Carlson, A. K., M. J. Fincel, and B. D. S. Graeb. 2017. Otolith chemistry indicates Walleye movement and entrainment in a large serial reservoir system. Fisheries Management and Ecology 24: 217-229.
- Colby, P. J., R. E. McNicol, and R. A. Ryder. 1979. Synopsis of biological data on the walleye *Stizostedion v. vitreum*. FAO Fisheries Synopsis 119, Rome.
- Cooper, A. B., and M. Mangel. 1999. The dangers of ignoring metapopulation structure for the conservation of salmonids. U.S National Marine Fisheries Service Fishery Bulletin 97: 213-226.
- Davis, B. A. 2004. Estimating trophic position of Lake Oahe walleye using stable isotope analysis. M.S. Thesis. South Dakota State University, Brookings, SD.
- DiStefano, R. J., T. P. Barry, and J. A. Malison. 1997. Correlation of blood parameters with reproductive problems in walleye in a Missouri Impoundment. Journal of Aquatic Animal Health 9: 223-229.
- Ellis, D. V., and M. A. Giles. 1965. The spawning behavior of the walleye *Stizostedion vitreum* (Mitchill). Transactions of the American Fisheries Society 94: 358-362.

- Eschmeyer, P. H. 1950. The life history of walleye, *Stizostedion vitreum vitreum* in Michigan. Michigan Department of Conservation, Bulletin of the Institute of Fisheries Research No. 3, Ann Arbor.
- Fincel, M. J. 2011. Productivity and trophic interactions in the Missouri River impoundments. Doctoral dissertation. South Dakota State University, Brookings.
- Fincel, M. J., D. J. Dembkowski, and S. R. Chipps. 2014a. Influence of variable Rainbow Smelt and Gizzard Shad abundance on Walleye diets and growth. *Lake and Reservoir Management* 30: 258-267.
- Fincel, M. J., R. Hanten, H. Meyer, K. Potter, and M. Smith. 2014b. Annual fish population and angler use, harvest and preference surveys on Lake Oahe, South Dakota, 2013. South Dakota Department of Game, Fish and Parks, Wildlife Division Report 14-02, Pierre.
- Fincel, M. J., W. J. Radigan, and C. M. Longhenry. 2016. Entrainment of Rainbow Smelt through Oahe Dam during the 2011 Missouri River flood. *North American Journal of Fisheries Management* 36: 844-851.
- Forney, J. L. 1963. Distribution and movement of marked Walleyes in Oneida Lake, New York. *Transactions of the American Fisheries Society* 92: 47-52.
- Geiling, W. D., J. R. M. Kelso, and E. Iwacheski. 1996. Benefits from incremental additions to walleye spawning habitat in the Current River, with reference to habitat modification as a walleye management tool in Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 79-97.
- Graeb, B. D. S., S. R. Chipps, D. W. Willis, J. P. Lott, R. P. Hanten, W. Nelson-Stastny, and J. W. Erickson. 2008. Walleye response to rainbow smelt population decline and liberalized angling regulations in a Missouri River reservoir. Pages 275-292 in M. S. Allen, S. Sammons, and M. J. Maceina, editors. *Balancing fisheries management and water uses for impounded river systems*. American Fisheries Society, Symposium 62, Bethesda, Maryland.
- Graeb, B. D. S., D. W. Willis, and B. D. Spindler. 2009. Shifts in sauger spawning

- locations after 40 years of reservoir ageing: influence of a novel delta ecosystem in the Missouri River, USA. *River Research and Applications* 25: 153-159.
- Hayden, T. A., C. M. Holbrook, D. G. Fielder, C. S. Vandergoot, R. A. Bergstedt, J. M. Dettmers, C. C. Krueger, and S. J. Cooke. 2014. Acoustic telemetry reveals large-scale migration patterns of walleye in Lake Huron. *PLoS ONE* 9: e114833. doi:10.1371/journal/pone/0114833.
- Hayes, D. B., and P. A. Petrusso. 1998. The role of tributaries in the sustainability of Great Lakes fisheries. *Fisheries* 23: 42-43.
- Hendrickson, J. C. 2005. Movements and population statistics of walleye in the Garrison Reach of the Missouri River and Lake Oahe, North Dakota: 1999-2004. North Dakota Game and Fish Department Report.
- Jennings, M. J., J. E. Claussen, and D. P. Philipp. 1996. Evidence of heritable preferences for spawning habitat between two walleye populations. *Transactions of the American Fisheries Society* 125: 978-982.
- Johnson, M. S. 2010. Fishes in tributaries of the Garrison Reach of the Missouri River, North Dakota. Master's thesis. South Dakota State University, Brookings.
- Johnson, W. C., M. D. Dixon, M. L. Scott, L. Rabbe, G. Larson, M. Volke, and B. Werner. 2012. Forty years of vegetation change on the Missouri River floodplain. *BioScience* 62: 123-135.
- Meyer, H., R. Hanten, K. Potter, M. Fincel, and M. Smith. 2015. Annual fish population and angler use, harvest and preference surveys on Lake Oahe, South Dakota, 2014. South Dakota Department of Game, Fish and Parks, Wildlife Division Report 15-04, Pierre.
- Nelson, W. R., and C. H. Walburg. 1977. Population dynamics of yellow perch (*Perca flavescens*), sauger (*Stizostedion canadense*), and walleye (*S. vitreum vitreum*) in four main stem Missouri River Reservoirs. *Journal of the Fisheries Research Board of Canada* 34:1748-1763.
- Nilsson, C., and K. Berggren. 2000. Alterations of riparian ecosystems caused by river

- regulation. *BioScience* 50: 783-792.
- Pegg, M. A., J. B. Layzer, and P. W. Bettoli. 1997. Angler exploitation of anchor-tagged saugers in the lower Tennessee River. *North American Journal of Fisheries Management* 17: 763-768.
- Potter, K, H. Meyer, R. Hanten, M. Greiner, M. Fincel, and M Smith. 2016. Annual fish population and angler use, harvest and preference surveys on Lake Oahe, South Dakota, 2015. South Dakota Department of Game, Fish and Parks, Wildlife Division Report 16-03, Pierre.
- Priegel, G. R. 1970. Reproduction and early life history of the walleye in the Lake Winnebago region. Wisconsin Department of Natural Resources Technical Bulletin 43, Madison.
- R Core Team. 2017. R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. <https://www.R-project.org/>.
- Raabe, J. K. 2006. Walleye (*Sander vitreus*) spawning habitat selection and dynamics in a north-temperate Wisconsin lake. Master's thesis. University of Wisconsin-Stevens Point, Stevens Point.
- Riis, J. C., B. Johnson, and C. C. Stone. 1993. Movement and exploitation of walleye, sauger and smallmouth bass in the Missouri River system in South Dakota. South Dakota Department of Game, Fish and Parks Fisheries Division Report 93-1, Pierre.
- Smedbol, R. K., and J. S. Wroblewski. 2002. Metapopulation theory and northern cod population structure: interdependency of subpopulations in recovery of a groundfish population. *Fisheries Research* 55: 161-174.
- Spangler, G. R., N. R. Payne, and G. K. Winterton. 1977. Percids in the Canadian waters of Lake Huron. *Journal of Fisheries Research Board of Canada* 34: 1839-1848.
- Stevens, A. G. 1990. Physical habitat preferences of walleye in streams in Wisconsin. Master's thesis. University of Wisconsin-Stevens Point, Stevens Point.
- Van Den Avyle, M. J. 1993. Dynamics of exploited fish populations. Pages 105-134 *in*

- Kohler, C. C., and W. A. Hubert, editors. Inland fisheries management in North America, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Vandergoot, C. S., and T. O. Brenden. 2014. Spatially varying population demographics and fishery characteristics of Lake Erie walleyes inferred from a long-term tag recovery study. *Transactions of the American Fisheries Society* 143: 188-204.
- Wang, H. Y., E. S. Rutherford, A. H. Cook, D. W. Einhouse, R. C. Haas, T. B. Johnson, R. Kenyon, B. Locke, and M. W. Turner. 2007. Movement of walleyes in Lakes Erie and St. Clair inferred from tag return and fisheries data. *Transactions of the American Fisheries Society* 136: 539-551.
- Wetzel, R. G. 2002. *Limnology*. Saunders, Philadelphia, Pennsylvania, USA.
- Whitney, R. R. 1958. Numbers of mature walleyes in Clear Lake, Iowa, 1952-3, as estimated by tagging. *Iowa State Journal of Science* 33: 55-79.
- Williot, P., G. Arlati, M. Chebanov, T. Gulyas, R. Kasimov, F. Kirschbaum, N. Patriche, L. P. Pavlovskaya, L. Poliakova, M. Pourkazemi, Y. Kim, P. Zhuang, and I. M. Zholdasova. 2002. Status and management of Eurasian sturgeon: an overview. *International Review of Hydrobiology* 87: 483-506.
- Zhong, Y., and G. Power. 1996. Environmental impacts of hydroelectric projects on fish resources in China. *Regulated Rivers: Research and Management* 12: 81-98.

Table 4.1. Walleye tagging sites in four habitat zones of Lake Oahe during 2013-2016.

Asterisks denote locations analyzed as spawning groups.

Habitat zone	Site #	Description	River mile
Riverine	1	Garrison Dam Spillway Channel*	1387
	2	Knife River	1376
	3	Stanton	1375
	4	Washburn	1355
	5	Sanger	1346
Transition	6	East Price Bluffs	1333
	7	Double Ditch	1325
	8	Heskett Station	1319
	9	Bernie's Banks	1297
	10	Huff Bluffs*	1287
	11	Eckroth Bottoms	1280
	12	Cannonball River	1269
	13	Beaver Bay*	1256
Upper Oahe	14	Cattail Bay	1245
	15	Pollock Bay	1224
	16	Grand River*	1198
	17	Moreau River*	1176
	18	Swan Creek	1174
	19	Whitlock Bay	1152
Lower Oahe	20	Sutton Bay	1135
	21	Cheyenne River	1110
	22	Little Bend	1107
	23	Okobojo Bay	1090
	24	Spring Creek*	1088
	25	Peoria Flats	1080
	26	East Shore	1074
	27	West Shore	1073

Table 4.2. Number of Walleye tagged and returned within the same calendar year as tagging from in four habitat zones of Lake Oahe during 2013-2016.

Year	Released tags				Recovered tags				
	R	T	UO	LO	R	T	UO	LO	Entrained
2013	1,180	3,070	3,972	951	150	300	701	176	2
2014	160	4,017	2,585	953	54	481	452	148	2
2015	337	4,277	3,552	1,077	159	608	632	273	4
2016	627	3,498	3,714	408	118	375	391	66	
Total	2,304	14,862	13,823	3,389	481	1,764	2,176	663	8

Table 4.3. Standardized tag return rate (number of tags returned per 1,000 tags released) and percentage of annual standardized tag return rate from four habitat zones within the Lake Oahe Walleye fishery during 2013-2016.

Angling zone	Tagging zone	2013	2014	2015	2016
Standardized tag return rate					
R	R	64.9	107.9	149.3	104.2
	T	10.3	4.9	15.6	6.7
	UO	1.1	1.5	0.6	0.0
	LO	0.0	0.0	0.0	0.0
T	R	28.0	43.8	32.6	30.3
	T	84.7	110.3	133.5	98.9
	UO	1.8	12.0	7.3	2.7
	LO	0.0	0.0	0.0	0.0
UO	R	5.2	0.0	0.0	4.7
	T	69.6	48.4	39.0	39.0
	UO	213.8	201.6	240.1	118.0
	LO	1.6	5.0	4.5	3.6
LO	R	1.3	14.9	0.0	0.0
	T	2.9	0.6	1.3	3.7
	UO	6.7	7.4	15.1	4.9
	LO	235.9	346.0	623.3	342.3
Percentage of tag return rate					
R	R	85	94	90	94
	T	13	4	9	6
	UO	1	1	0	0
	LO	0	0	0	0
T	R	24	26	19	23
	T	74	66	77	75
	UO	2	7	4	2
	LO	0	0	0	0
UO	R	2	0	0	3
	T	24	19	14	24
	UO	74	79	85	71
	LO	1	2	2	2
LO	R	1	4	0	0
	T	1	0	0	1
	UO	3	2	2	1
	LO	96	94	97	98

Table 4.4. Results of Kolmogorov-Smirnov two-sample tests for recapture distributions of Walleye recovered during the same calendar year as tagging (TY) and Walleye recovered during a different calendar year than tagging (DY) within spawning groups tagged at selected locations within Lake Oahe during 2013-2016.

Group	D	P	# of recoveries (TY)	# of recoveries (DY)
Site 1	0.09	0.40	316	127
Site 10	0.15	< 0.001	612	529
Site 13	0.20	< 0.001	970	961
Site 16	0.09	0.06	799	281
Site 17	0.12	0.04	579	185
Site 24	0.44	< 0.001	489	140

Table 4.5. Results of Kolmogorov-Smirnov two-sample tests between male and female recapture distributions of Walleye from spawning groups tagged at selected locations within Lake Oahe during 2013-2016.

Group	D	P	# of male recoveries	# of female recoveries
Site 1	0.26	< 0.001	256	106
Site 10 TY	0.27	< 0.001	511	92
Site 10 DY	0.32	0.001	470	40
Site 13 TY	0.18	< 0.001	645	306
Site13 DY	0.30	< 0.001	722	195
Site 16	0.10	0.23	927	148
Site 17 TY	0.32	< 0.001	492	83
Site 17 DY	0.31	0.007	147	37

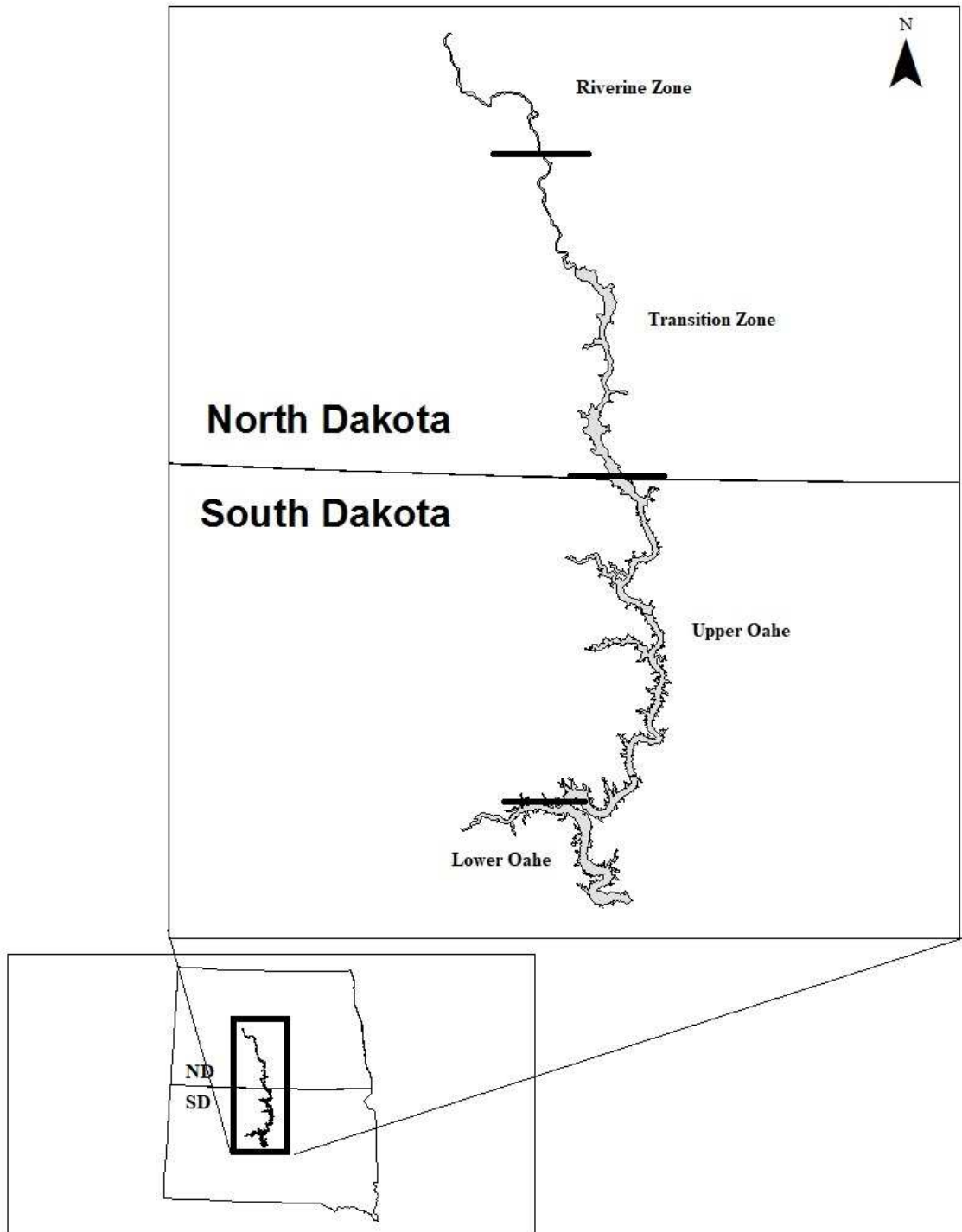


Figure 4.1. Map of Lake Oahe, North Dakota and South Dakota, and regions.

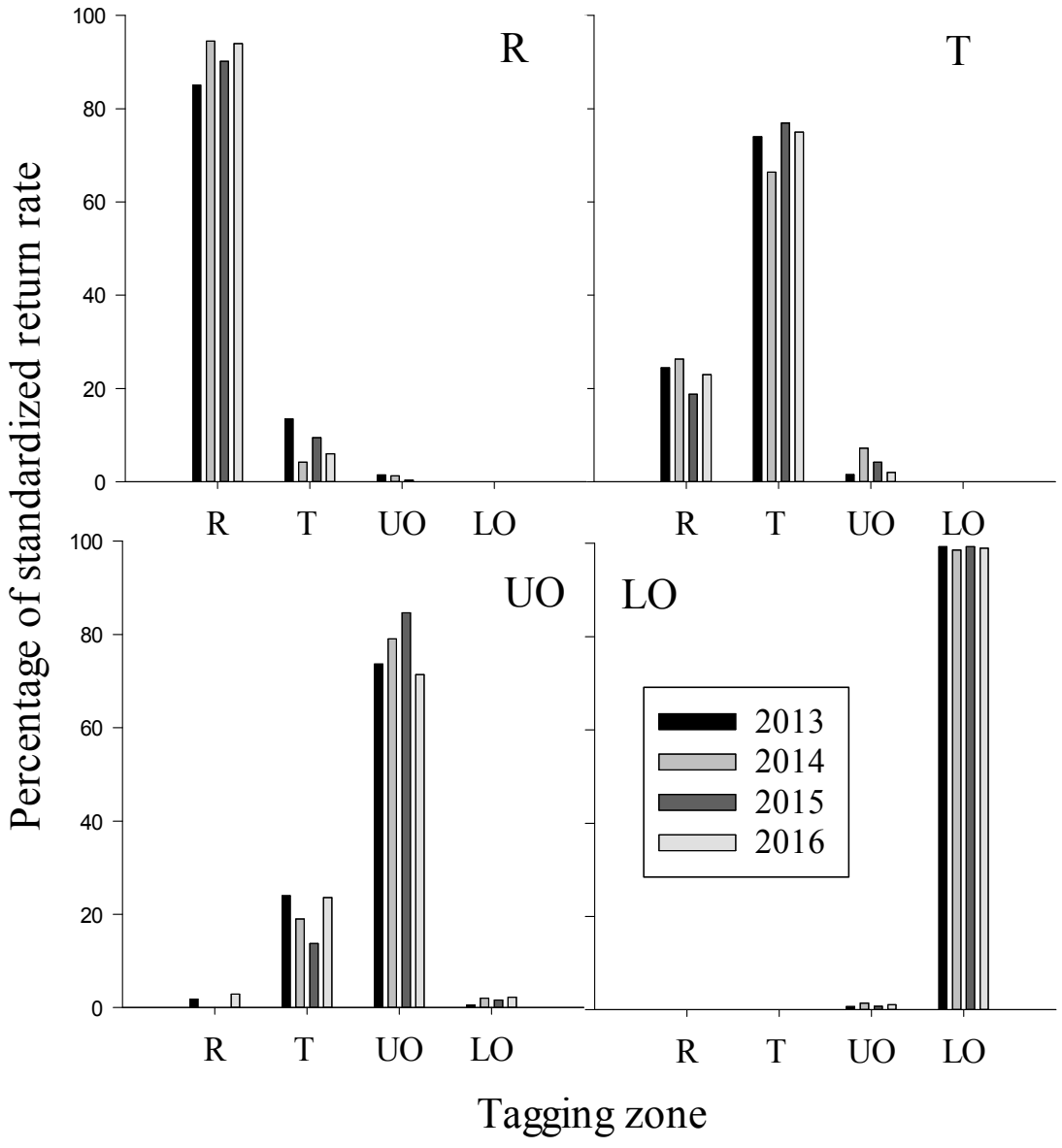


Figure 4.2. Percentage of annual standardized tag return rate (number of tags expected per 1,000 tags released) for the Walleye fisheries in zones (Riverine (R), Transition (T), Upper Oahe (UO) and Lower Oahe (LO)) of Lake Oahe during 2013-2016.

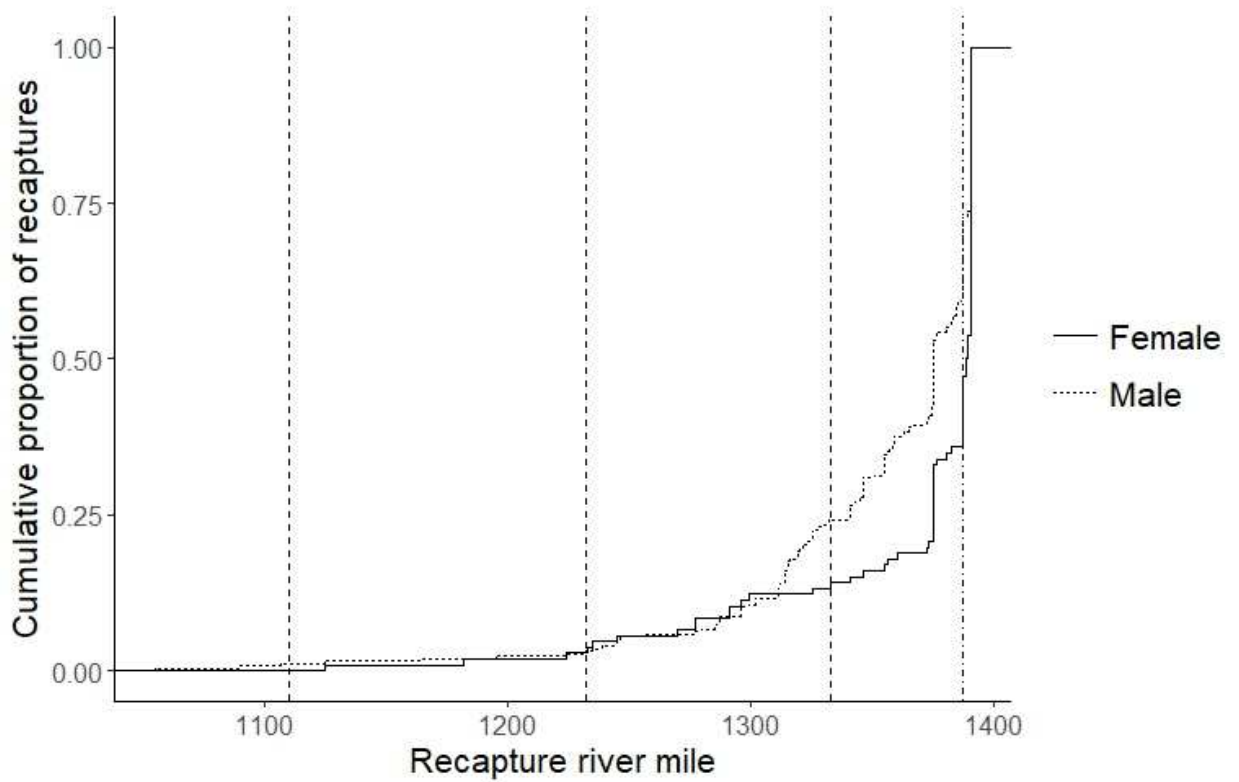


Figure 4.3. Cumulative proportion of recaptures as a function of river mile for male and female Walleye tagged at Site 1 of the Riverine zone in Lake Oahe during 2013-2016. Recaptures include 2013-2017. Vertical dashed lines represent zone boundaries, and vertical dot-dashed line represents Site 1.

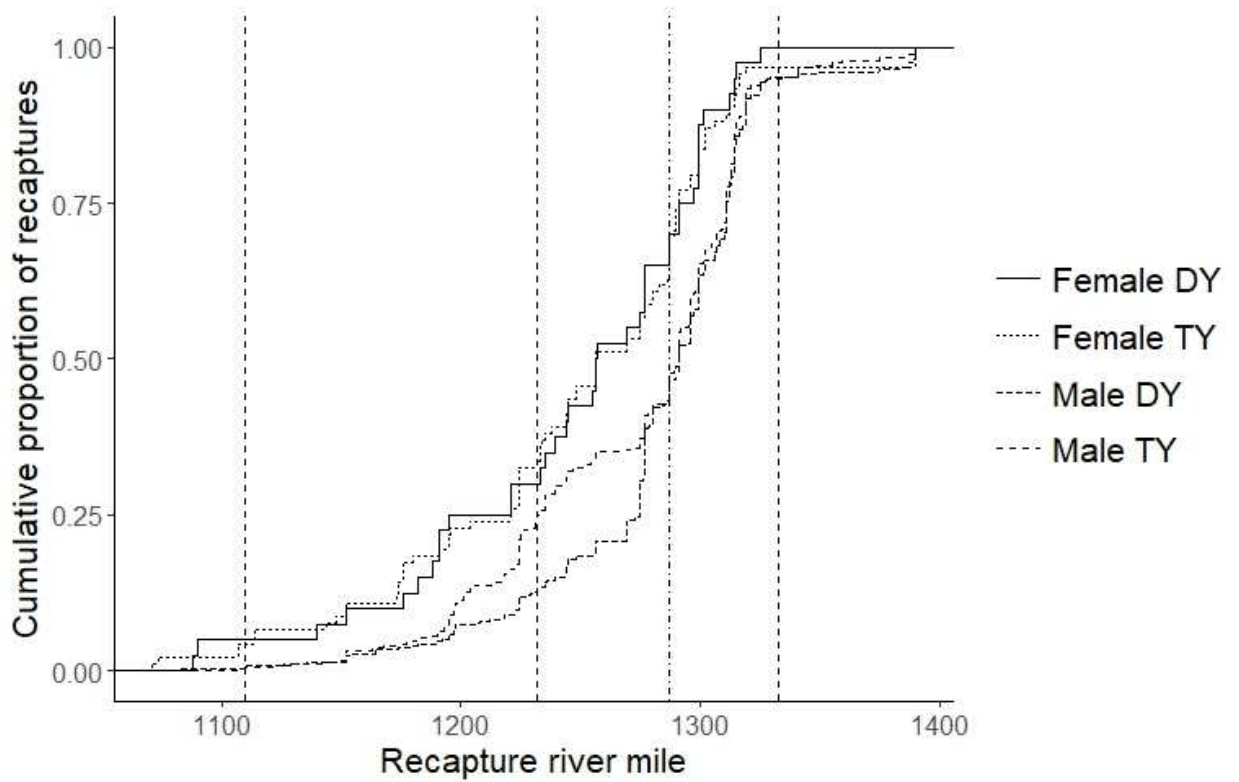


Figure 4.4. Cumulative proportion of recaptures as a function of river mile for male and female Walleye tagged at Site 10 of the Transition zone in Lake Oahe during 2013-2016. Recapture distributions are separated for fish recovered during the same calendar year as tagging (TY) and during a different calendar year than tagging (DY). Recaptures include 2013-2017. Vertical dashed lines represent zone boundaries, and vertical dot-dashed line represents Site 10.

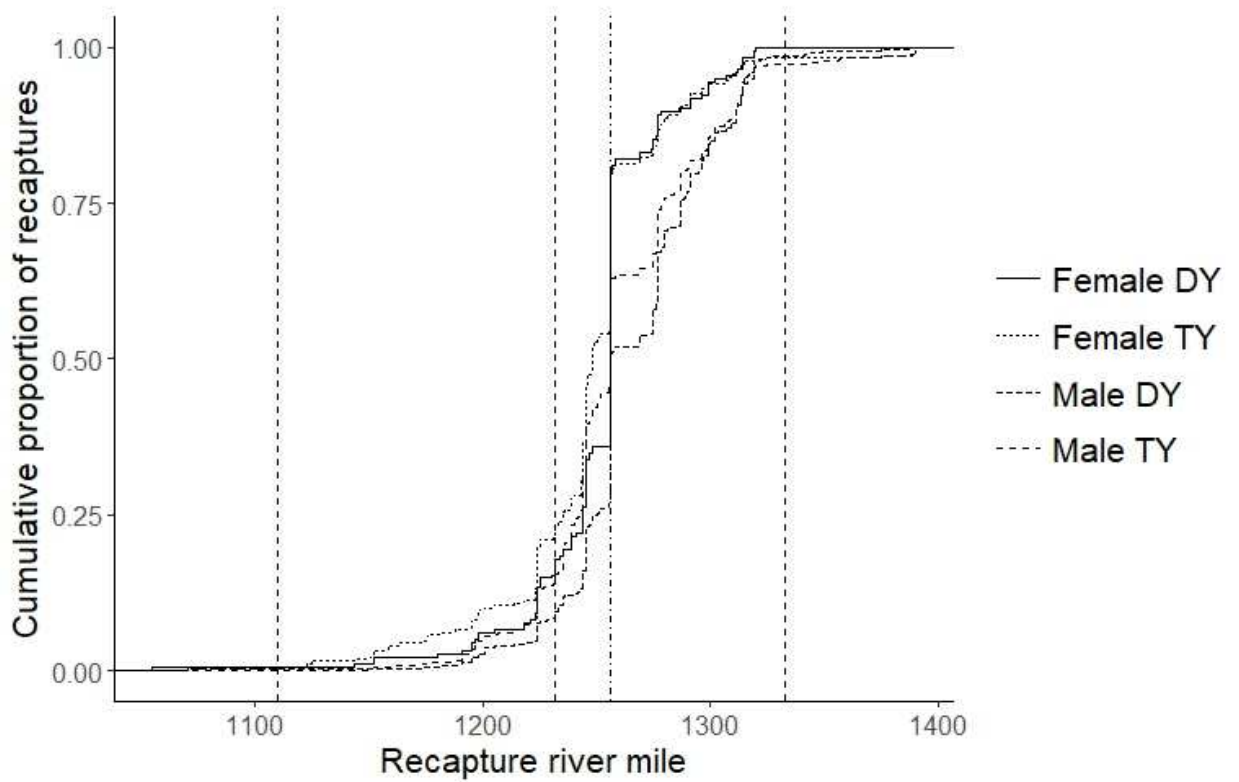


Figure 4.5. Cumulative proportion of recaptures as a function of river mile for male and female Walleye tagged at Site 13 of the Transition zone in Lake Oahe during 2013-2016. Recapture distributions are separated for fish recovered during the same calendar year as tagging (TY) and during a different calendar year than tagging (DY). Recaptures include 2013-2017. Vertical dashed lines represent zone boundaries, and vertical dot-dashed line represents Site 13.

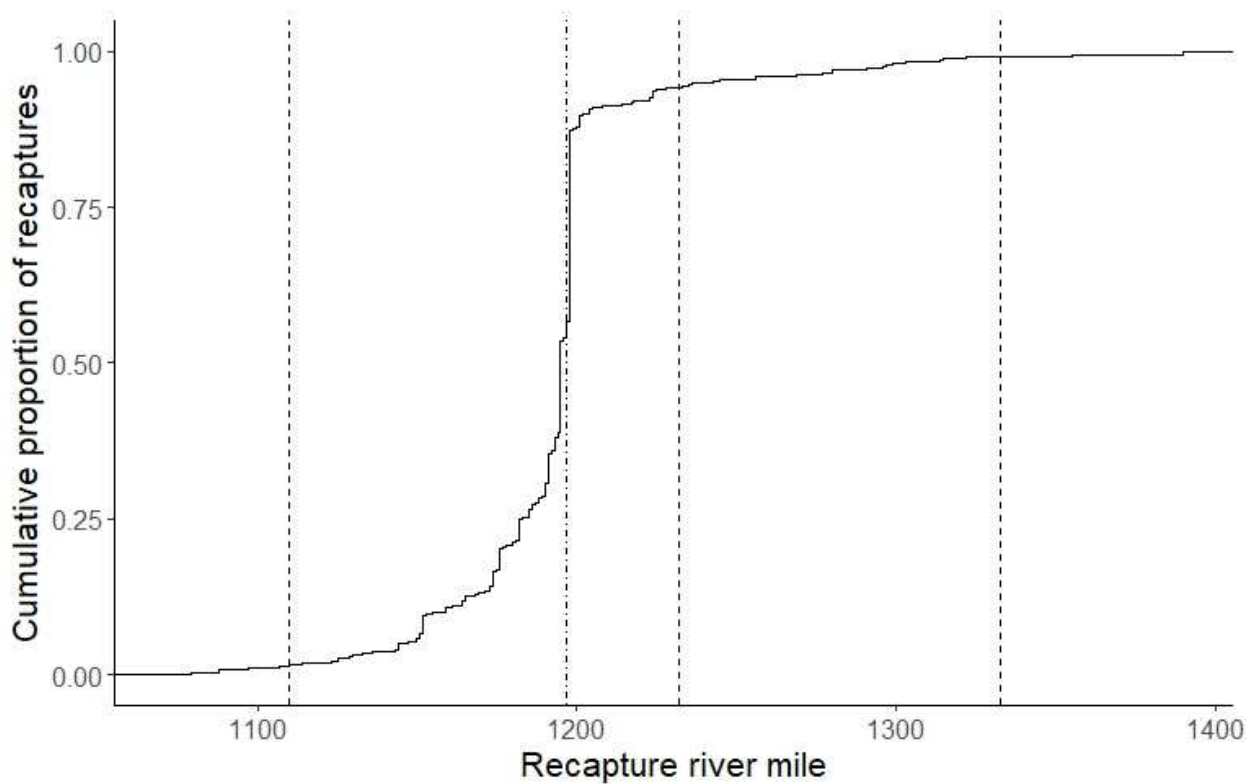


Figure 4.6. Cumulative proportion of recaptures as a function of river mile for Walleye tagged at Site 16 of the Upper Oahe zone in Lake Oahe during 2013-2016. Recaptures include 2013-2017. Vertical dashed lines represent zone boundaries, and vertical dot-dashed line represents Site 16.

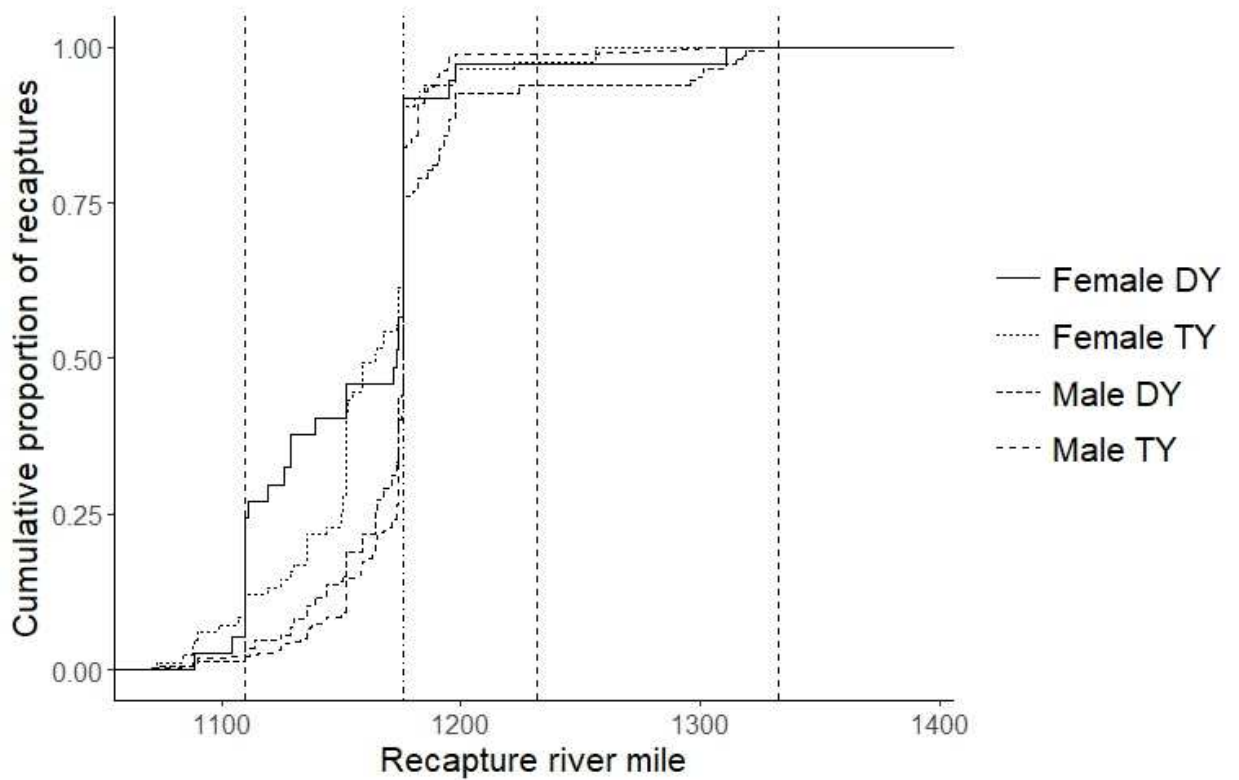


Figure 4.7. Cumulative proportion of recaptures as a function of river mile for male and female Walleye tagged at Site 17 of the Upper Oahe zone in Lake Oahe during 2013-2016. Recapture distributions are separated for fish recovered during the same calendar year as tagging (TY) and during a different calendar year than tagging (DY). Recaptures include 2013-2017. Vertical dashed lines represent zone boundaries, and vertical dot-dashed line represents Site 17.

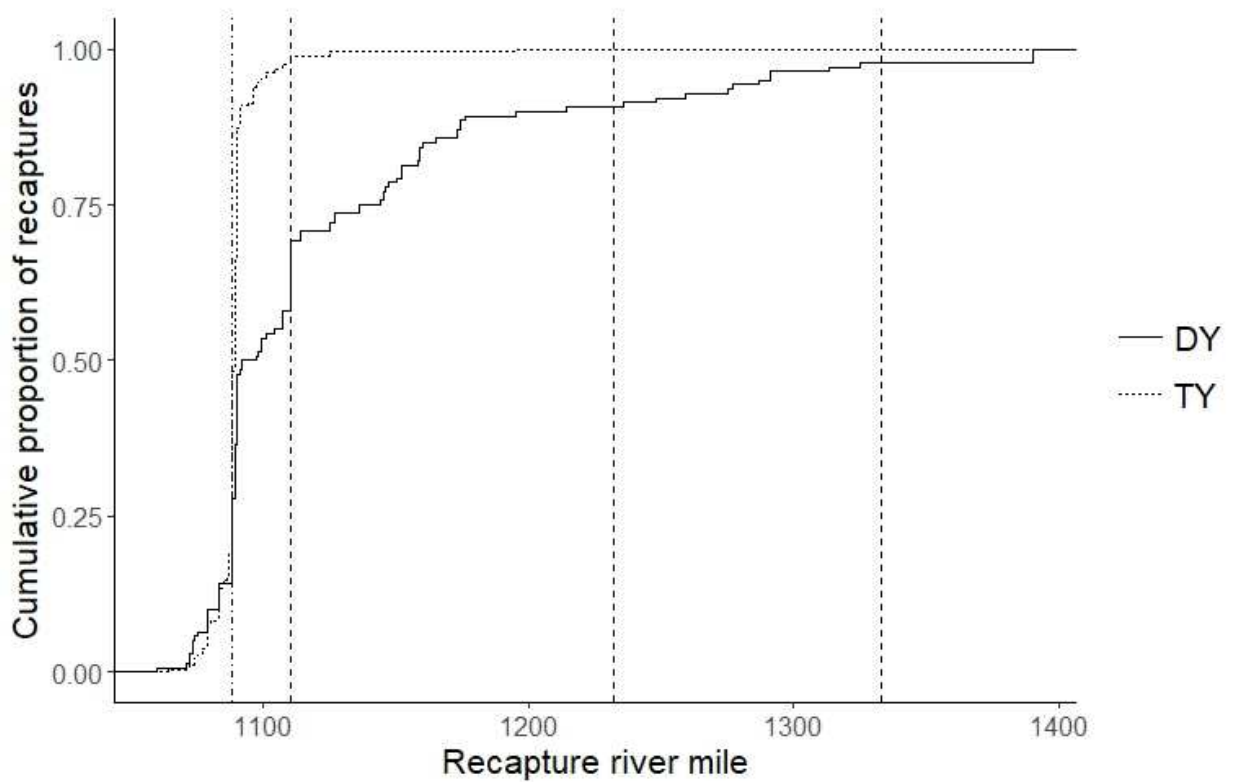


Figure 4.8. Cumulative proportion of recaptures as a function of river mile for Walleye tagged at Site 24 of the Lower Oahe zone in Lake Oahe during 2013-2016. Recapture distributions are separated for fish recovered during the same calendar year as tagging (TY) and during a different calendar year than tagging (DY). Recaptures include 2013-2017. Vertical dashed lines represent zone boundaries, and vertical dot-dashed line represents Site 17.

CHAPTER 5: ANGLER RESPONSE TO WALLEYE POPULATION VARIABILITY
IN LAKE OAHE, SOUTH DAKOTA

Abstract

The interaction between anglers and fish is an important aspect of fisheries ecology. In recreational hook-and-line fisheries, a common assumption is that catchability is constant and these fisheries are therefore self-regulating because angler catch rates decline with population density. I used creel surveys and standard population surveys to assess the relationship between angler catch rates and both relative abundance and relative weight of stock-size (250 mm) and greater Walleye *Sander vitreus* in Lake Oahe from 1992-2015. My results indicated no relationship between relative abundance and angler catch rates, but revealed a strong inverse relationship between relative weight and angler catch rates. These results indicate Walleye catchability increased as population density decreased, creating the potential for depensatory fishing mortality in Lake Oahe. Additionally, for Walleye populations that experience wide swings in prey abundance, the effect of those fluctuations precludes other factors affecting angler catch rates. My results demonstrate that an assumption of self-regulation is inappropriate for the Lake Oahe Walleye fishery and that fisheries managers have a greater opportunity to influence fishing mortality when Walleye condition is low.

Introduction

Fisheries management typically involves manipulation of habitat, biota or human users. Human users are influenced through direct or passive control of effort and the size and number of fish that may be harvested. In commercial fisheries, fishers tend to use

high efficiency gears which allow harvest rates to operate independent of stock density (Hilborn 1985). Consequently, stock density of commercially fished species is often estimated using fishery-independent methods, and effort and total harvest exerted by fishers is intensively managed. Conversely, hook-and-line angling is considered a low-efficiency gear for which catch rates are directly related to stock density, and therefore believed to be self-regulating (Deriso and Parma 1987). Thus, hook-and-line fisheries are typically open entry and harvest is managed indirectly through bag limits, possession limits, and length restrictions. In essence, recreational fisheries represent a predator-prey interaction over which managers have varying degrees of influence on both the predators (anglers) and their prey (fish). Fisheries managers may influence three components of angler behavior: effort, catch rate, and probability of harvesting captured fish.

Understanding how these aspects of angler behavior respond to fluctuating fish population abundance is important for managers to identify the degree to which a recreational fishery is self-regulating, how passive management actions indirectly influence angler behavior, and when and where passive harvest tools may be used effectively.

Angler effort is analogous to numerical response in studies of predator-prey relationships and is seldom regulated in recreational fisheries. Effort is generally hypothesized to decrease with reduced fish population abundance resulting in self-regulation. However, effort has been found, in some instances, to be influenced by density independent factors such as travel distance (Post et al. 2002) and bag limits (Cox 2000, Beard et al. 2003). If angler effort is density independent there is greater potential for depensatory fishing mortality, where per capita fishing mortality increases as fish

population abundance decreases and leads to further decline and potential collapse (Post et al. 2002). Therefore, it is important for managers to evaluate the hypothesis of density dependent angling effort. If rejected, it is critical to evaluate the density independent factors which drive angler effort and identify management strategies to influence angler effort when population abundance declines.

Angler catch rate is commonly assumed to be linear and proportional to stock density, implying that catchability is constant and density independent. If true, then a fishery will be self-regulating, even under constant angling effort, because anglers will catch less fish per unit effort as density declines. However, exceptions to both assumptions occur. Catchability may be density independent but vary due to other factors such as prey availability (Forney 1967; VanDeValk et al. 2005), water clarity (Drenner et al. 1997), and population size structure (Isbell and Rawson 1989). Inverse density dependent catchability, on the other hand, occurs when catchability increases as density decreases. Such a relationship may result from nonrandom searching by anglers and/or schooling behavior of fish (Peterman and Steer 1981, Hansen et al. 2000). This process has led to collapses in multiple commercial fisheries (Rose and Kulka 1999) and is suspected to be similarly problematic for recreational fisheries (Post et al. 2002).

Walleye *Sander vitreus* is one of the most popular sport fish in North America, particularly at northern latitudes in the United States and Canada. Walleye fisheries are harvest oriented and overexploitation is the most common concern among managers of commercial, subsistence, and recreational Walleye fisheries (Schmalz et al. 2011). In a famous example, Post et al. (2002) documented the depletion of several prominent recreational Walleye fisheries in Alberta, Canada. The causes of these declines included,

among others, density independent angling effort which remained high despite long-term declines in Walleye abundance, and compensatory mortality due to inverse density dependent catchability of Walleye.

Lake Oahe, South Dakota, United States is the largest and most economically important fishery in the state, supporting average annual harvest of over 300,000 Walleye. Annual Walleye harvest has displayed high interannual variability in recent history, presumably due to the combined effects of variation in angler effort and catch rate. Therefore, the objectives of this study were to evaluate the influence of Walleye density and density independent factors on angler catch rates and catchability of Walleye in Lake Oahe.

Methods

Study Area. - Lake Oahe is a main stem reservoir of the Missouri River in South Dakota and is one of the largest and most used fisheries in South Dakota. Fishing pressure averages approximately 500,000 angler hours per year, generating an estimated \$16 million of direct economic impact (SDGF&P 2014). On average, Walleye make up greater than 75% of the total fish harvest (SDGF&P 2014). The popularity and importance of the Lake Oahe Walleye fishery led to the establishment of annual standardized fish population and creel surveys. Walleye harvest regulations have varied over the study period and have included various combinations of minimum-length limits, maximum length (“one-over”) limits, daily bag limits, possession limits, and reduction of license cost.

Creel Survey Data. -Angler catch rate was calculated using data collected in creel surveys conducted by South Dakota Game, Fish, and Parks. Creel surveys have been

conducted annually on Lake Oahe since 1992. Creel surveys were conducted during peak open water fishing months. Duration of creel surveys varied slightly in certain years due to budget constraints and flooding. Aerial counts of boat and shore anglers were used to estimate fishing pressure, and angler interviews at access points were used to estimate catch, harvest, and trip length. Flight dates and interview dates were selected using a stratified random design with weekdays and weekend days/holidays treated as separate strata (Meyer et al. 2015). Access points for interviews were selected using a stratified random design, separating different access areas by month (Stone et al. 1994). Angler catch rate was calculated as the estimated total Walleye catch (C; number) divided by total estimated effort (f; angler hours):

$$\frac{C}{f} = \frac{\sum C}{\sum f}$$

This measure of “catch” rate includes all Walleyes captured by anglers, harvested or released.

Walleye Population Characteristics. - Walleye were sampled with gill nets annually during August in Lake Oahe. Standard gill nets are experimental multifilament nets which are 91.4-m long by 1.8-m deep and have 15.2-m panels of 12.7-mm, 19.1-mm, 25.4-mm, 31.8-mm, 38.1-m, and 50.8-mm bar mesh. Six nets were deployed at each of 9 locations throughout Lake Oahe for a total of 54 nets per year. All Walleye collected during gill net surveys were measured for total length (mm) and weighed (g). Relative abundance of stock-size (250 mm) and greater Walleye was expressed as mean catch per gill net night (#/net night) and was used as an index of Walleye density. Relative weight (W_r) of Walleye was calculated using the Walleye standard weight (W_s) equation (Murphy et al. 1990), and was taken as an index of prey availability.

Analysis. - To test the assumption that catchability is proportional and linear to Walleye density, I used a power function (Peterman and Steer 1981; VanDeValk et al. 2005), described as:

$$\frac{C}{f} = \alpha N^{\beta+1}$$

Where C is total estimated Walleye catch, f is total estimated effort, N is relative abundance of stock size and greater Walleyes, and α and β are estimated parameters. Parameters were estimated using ordinary least squares regression on the \log_e transformed form of the model:

$$\log_e\left(\frac{C}{f}\right) = \log_e\alpha + (\beta + 1) * \log_e(N)$$

The α parameter estimates catchability near the origin, and the β parameter estimates the degree to which catchability is density dependent. I used a test statistic (t^*) to test whether β differed significantly from 0:

$$t^* = \frac{\text{observed slope} - \text{specified slope}}{\text{SD of observed slope}}$$

I used a multiple regression similar to Hansen et al. (2004) and VanDeValk et al. (2005) to model the influence of prey availability on angler catch rate of Walleye:

$$\frac{C}{f} = \alpha N^{\beta+1} * X^\delta$$

Parameters were estimated using ordinary least squares regression on the \log_e transformed form of the model:

$$\log_e\left(\frac{C}{f}\right) = \log_e\alpha + (\beta + 1) * \log_e(N) + \delta * \log_e X$$

In this model, Walleye relative weight is represented by X and δ was an additional estimated parameter.

Results

From 1992 through 2015 in Lake Oahe angler catch rate of Walleye ranged from 0.32 to 2.08 fish/hour while relative abundance of stock (250 mm) and greater Walleye ranged from 5.1 to 24.6 fish/net night (Table 5.1). Regression analysis indicated no relationship between angler catch rate and Walleye relative abundance ($df = 22$, $\alpha = -0.46$, $\beta + 1 = 0.02$, $r^2 < 0.01$, $F = 0.003$, $P = 0.96$) (Figure 5.1). The β coefficient was significantly less than 0 ($H_0: \beta + 1 = 1$; $df = 22$, $t^* = -2.53$, $P = 0.02$), indicating that catchability was inversely related to Walleye relative abundance.

Mean relative weight of Walleye in Lake Oahe ranged from 78 to 94 during 1992-2015. (Table 5.1). Regression analysis suggested a strong inverse relationship between angler catch rate and Walleye condition ($df = 2, 21$; $r^2 = 0.58$, $F = 14.32$, $P < 0.01$) ($\log_e \alpha = 31.86$, $df = 21$, $t = 5.24$, $P < 0.01$) ($\beta + 1$ [Walleye relative abundance] = 0.22, $df = 21$, $t = 0.85$, $P = 0.41$) (δ [condition] = -7.4, $df = 21$, $t = -5.4$, $P < 0.01$) (Figure 5.2). A t-test of the β parameter indicated that catchability was inversely related to Walleye relative abundance when condition was held constant ($df = 21$, $t^* = -6.1$, $P < 0.01$).

Discussion

Walleye relative abundance failed to explain observed variability in angler catch rate in Lake Oahe, contrasting empirical relationships observed in several Walleye fisheries (Beard et al. 1997, Hansen et al. 2000, Newby et al. 2000). Prey availability, as indexed by Walleye relative weight, accounted for 58% of the variability in angler catch rates. Angler catch rate was inversely related to Walleye condition, indicating prey availability was more important to angling success than Walleye density. My results

corroborate VanDeValk et al. (2005) who provided evidence of an inverse relationship between prey availability and angler catch rate of Walleye in Oneida Lake, New York, and suggested the effects of prey availability are most pronounced in systems with wide swings in prey abundance. Rainbow Smelt *Osmerus mordax*, which are the dominant prey of Walleye in Lake Oahe, have experienced broad fluctuations in abundance due to entrainment during periods of high discharges through Oahe dam (Unkenholz 1998; Fincel et al. 2016).

My results indicated Walleye catchability in Lake Oahe was inversely related to density when condition was held constant, suggesting the Walleye fishery is not self-regulating and the potential for depensatory mortality exists (Post et al. 2002). Behavioral and/or habitat-mediated aggregation by Walleye coupled with nonrandom searching can lead to an inverse relationship between density and catchability (Peterman and Steer 1981, Post et al. 2002). For example, reductions in overall Walleye abundance may decrease the number of fish in aggregations but anglers could potentially locate aggregations just as easily and catch similar numbers of fish, resulting in higher per capita fishing mortality as abundance decreases. This process has been responsible for declines in commercial (Rose and Kulka 1999) and recreational (Post et al. 2002) fisheries.

The apparent inverse relationship between density and catchability may be an artifact of data limitations. Relative weight is an index which does not perfectly describe prey availability as it relates to the relationships hypothesized in this study (Liao et al. 1995). Thus, when relative weight was held constant in our models, I may have failed to accurately assess the relationship between catchability and Walleye relative abundance

when holding prey availability constant. Similarly, Walleye relative abundance is an index of density which introduces the same potential for error. Additionally, population age structure, unaccounted for in our analysis, may have affected catchability in a manner that was not independent of population density. Isbell and Rawson (1989) provided evidence that older Walleye in a population may be one-third to one-half less vulnerable to exploitation than younger Walleye. Although my data did not allow for quantification of age-specific catchability, wide fluctuations in Walleye recruitment (Chapter 2) and exceptionally high total annual mortality of large, old Walleye during periods of low Rainbow Smelt abundance (Graeb et al. 2008) in Lake Oahe mean that population age structure was highly variable over the range of observations used in this analysis. If age structures tended to be younger at lower densities, and younger fish were easier to catch, that may have created the illusion that catchability increased as Walleye abundance decreased.

References

- Beard, T. D., S. W. Hewett, Q. Yang, R. M. King, and S. J. Gilbert. 1997. Prediction of angler catch rates based on walleye population density. *North American Journal of Fisheries Management* 17: 621-627.
- Beard, T. D. Jr., S. P. Cox, and S. R. Carpenter. 2003. Impacts of daily bag limit reductions on angler effort in Wisconsin walleye lakes. *North American Journal of Fisheries Management* 23: 1283-1293.
- Cox, S. P. 2000. Angling quality, effort response, and exploitation in recreational fisheries: field and modeling studies on British Columbia rainbow trout lakes. Ph.D. Dissertation, University of British Columbia, Vancouver. 214 p.
- Deriso, R. B., and A. M. Parma. 1987. On the odds of catching fish with angling gear. *Transactions of the American Fisheries Society* 116: 244-256.
- Drenner, R. W., K. L. Gallo, C. M. Edwards, K. E. Rieger, and E. D. Dibble. 1997. Common carp affect turbidity and angler catch rates of largemouth bass in ponds. *North American Journal of Fisheries Management* 17: 1010-1013.
- Fincel, M. J., W. J. Radigan, and C. M. Longhenry. 2016. Entrainment of Rainbow Smelt through Oahe Dam during the 2011 Missouri River flood. *North American Journal of Fisheries Management* 36: 844-851.
- Forney, J. L. 1967. Estimates of biomass and mortality rates in a walleye population. *New York Fish and Game Journal* 12: 217-232.
- Graeb, B. D. S., S. R. Chipps, D. W. Willis, J. P. Lott, R. P. Hanten, W. Nelson-Stastny, and J. W. Erickson. 2008. Walleye response to rainbow smelt population decline and liberalized angling regulations in a Missouri River reservoir. Pages 275-292 *in* M. S. Allen, S. Sammons and M. J. Maceina, editors. *Balancing fisheries management and water uses for impounded river systems*. American Fisheries Society, Symposium 62, Bethesda, Maryland.
- Hansen, M. J., T. D. Beard, and S. W. Hewett. 2000. Catch rates and catchability of walleyes in angling and spearing fisheries in northern Wisconsin lakes. *North*

- American Journal of Fisheries Management 20: 109-118.
- Hansen, M.J., S. P. Newman, and C. J. Edwards. 2004. A reexamination of the relationship between electrofishing catch rate and age-0 walleye density in northern Wisconsin lakes. *North American Journal of Fisheries Management* 24: 429-439.
- Hilborn, R. 1985. Fleet dynamics and individual variation: why some people catch more fish than others. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 2-13.
- Isbell, G. L., and M. R. Rawson. 1989. Relations of gill-net catches of walleyes and angler catch rates in Ohio waters of western Lake Erie. *North American Journal of Fisheries Management* 9: 41-46.
- Liao, H., C. L. Pierce, D. H. Wahl, J. B. Rasmussen, and W. C. Leggett. 1995. Relative weight (W_r) as a field assessment tool: relationships with growth, prey biomass and environmental conditions. *Transactions of the American Fisheries Society* 124: 387-400.
- Meyer, H., R. Hanten, K. Potter, M. Fincel, and M. Smith. 2015. Annual fish population and angler use, harvest, and preference surveys on Lake Oahe, South Dakota, 2014. South Dakota Department of Game, Fish and Parks, Wildlife Division Report 15-04, Pierre.
- Murphy, B. R., M. L. Brown, and T. A. Springer. 1990. Evaluation of the Relative Weight (W_r) index, with new applications to walleye. *North American Journal of Fisheries Management* 10: 85-97.
- Newby, J. R., M. J. Hansen, S. P. Newman, and C. J. Edwards. 2000. Catchability of walleyes to Angling in Escanaba Lake, Wisconsin, 1980-1995. *North American Journal of Fisheries Management* 20: 873-881.
- Peterman, R. M., and G. J. Steer. 1981. Relation between sportfishing catchability and coefficients of salmon abundance. *Transactions of the American Fisheries Society* 110: 585-593.
- Post, J. R., M. Sullivan, S. Cox, N. P. Lester, C. J. Walters, E. A. Parkinson, A. J. Paul,

- L. Jackson, and B. J. Shuter. 2002. Canada's recreational fisheries: the invisible collapse? *Fisheries* 27: 6-17.
- Rose, G. A., and D. W. Kulka. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 118-127.
- Schmalz, P. J., A. H. Fayram, D. A. Isermann, S. P. Newman, and C. J. Edwards. 2011. Harvest and exploitation. Pages 375-402 in B.A. Barton, editor. *Biology, management, and culture of walleye and sauger*. American Fisheries Society, Bethesda, Maryland.
- South Dakota Department of Game, Fish and Parks. 2014. Fisheries and Aquatic Resources Adaptive Management System, 2014-2018: Missouri River Fisheries Management Area.
- Stone, C., J. Riis, and B. Johnson. 1994. Angler use and sport fishing harvest survey on Lakes Francis Case, Sharpe, and Oahe, South Dakota, 1992 and 1993. South Dakota Department of Game, Fish and Parks, Wildlife Division, Annual Report 94-9, Pierre.
- Unkenholz, E. G. 1998. Entrainment of Rainbow Smelt through Oahe Dam, South Dakota. 1998. M.S. Thesis, South Dakota State University, Brookings, SD.
- VanDeValk, A. J., J. L. Forney, J. R. Jackson, L. G. Rudstam, T. E. Brooking, and S. D. Krueger. 2005. Angler catch rates and catchability of walleyes in Oneida Lake, New York. *North American Journal of Fisheries Management* 25: 1441-1447.

Table 5.1. Walleye catch, angler effort, angler catch rate of Walleye, relative abundance of stock (250 mm) and larger Walleye, and mean relative weight for stock and larger Walleye in Lake Oahe during 1992-2015.

Year	Walleye catch (#)	Angler effort (hours)	Catch rate (#/hour)	Walleye abundance (#/net night)	Mean Walleye W_r
1992	393,197	1,051,330	0.37	13.4	90
1993	413,191	1,299,344	0.32	19.1	93
1994	423,527	1,189,267	0.36	17.6	94
1995	583,671	1,695,945	0.34	24.6	93
1996	675,269	1,968,525	0.34	15.3	87
1997	1,152,050	1,617,024	0.71	15.9	83
1998	2,103,666	1,781,032	1.18	15.4	79
1999	816,394	847,359	0.96	19.0	81
2000	602,288	539,188	1.12	15.6	78
2001	783,598	1,014,591	0.77	12.6	85
2002	501,958	856,059	0.59	14.4	80
2003	275,883	651,557	0.42	11.5	82
2004	354,368	660,973	0.54	15.1	87
2005	215,164	393,875	0.55	16.7	88
2006	299,535	541,432	0.55	12.9	87
2007	370,611	531,751	0.70	12.6	86
2008	517,362	718,557	0.72	12.8	87
2009	399,179	872,900	0.46	10.3	91
2010	289,346	800,728	0.36	12.4	88
2011	1,398,454	1,036,972	1.35	20.6	84
2012	1,973,850	949,690	2.08	18.5	78
2013	1,645,921	929,830	1.77	14.6	80
2014	932,381	771,419	1.21	11.7	87
2015	571,664	738,360	0.77	5.1	82

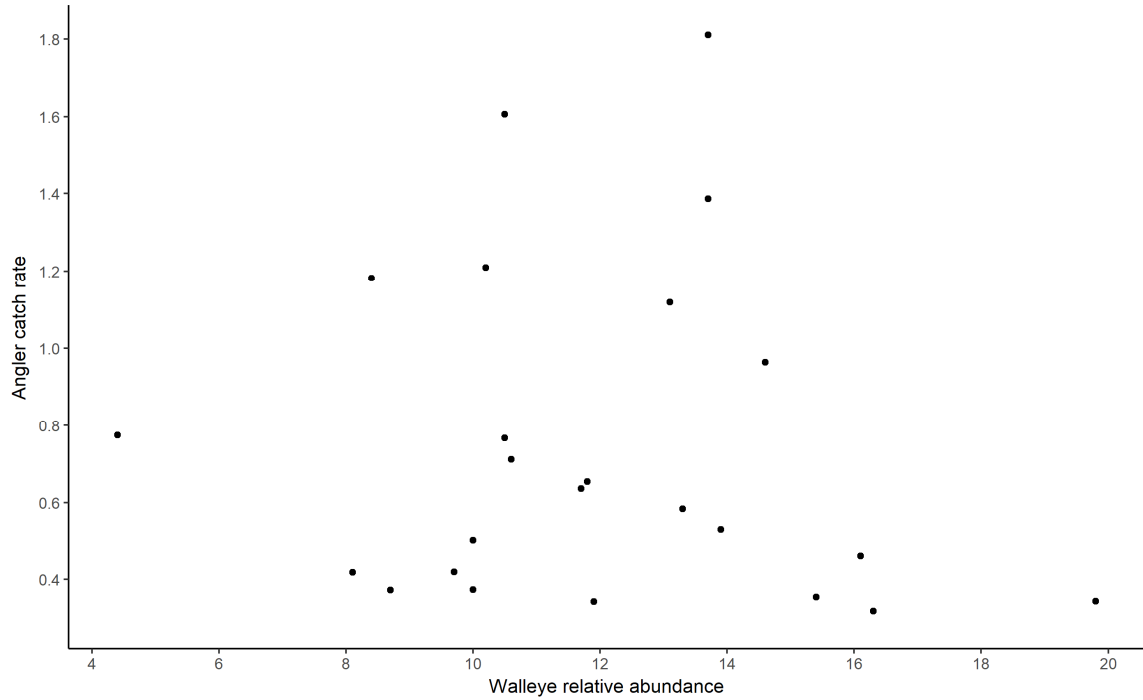


Figure 5.1. Angler catch rate of Walleye (#/hour) as a function of relative abundance of harvestable size (300 mm) and greater Walleye (#/net night) captured during gill net surveys in Lake Oahe, 1992-2015.

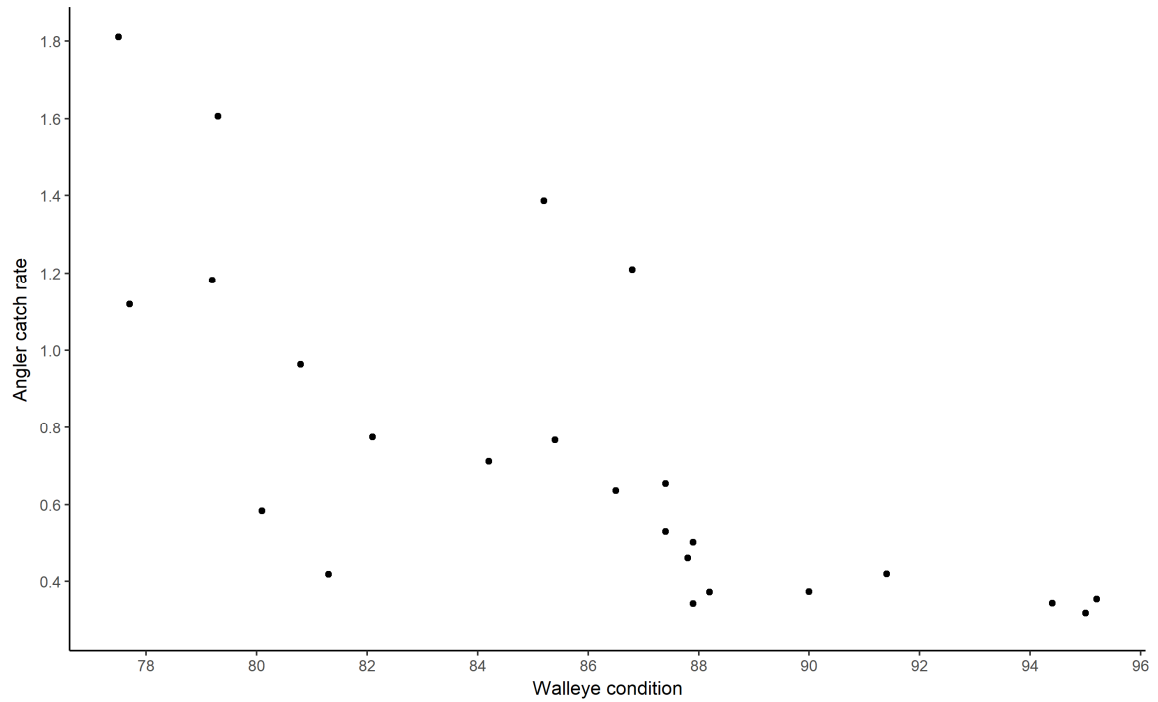


Figure 5.2. Angler catch rate of Walleye (#/hour) as a function of harvestable size (300 mm) and greater Walleye condition (mean W_r) collected during gill net surveys in Lake Oahe, 1992-2015.

CHAPTER 6: SPATIAL VARIATION IN WALLEYE POPULATION RESPONSE TO FLOOD IMPACTS IN A LARGE MISSOURI RIVER RESERVOIR

Abstract

Previous research demonstrated high mortality rates of Walleye *Sander vitreus* in Lake Oahe, a large main stem Missouri River reservoir, following high entrainment of their primary prey resource Rainbow Smelt *Osmerus mordax*. In large, open systems like Lake Oahe, spatial structuring may contribute to spatial variation of population dynamics. In 2011, a historic flood in the Missouri River contributed to high entrainment of Rainbow Smelt through Oahe Dam. A 5-year tagging study was conducted throughout Lake Oahe to evaluate: 1) Walleye population response to the 2011 flood, 2) the impact of liberalized harvest regulations enacted in response to low Rainbow Smelt abundance, and 3) the extent to which Walleye population response varied spatially within Lake Oahe. Candidate models were evaluated using an information-theoretic approach, and the top model indicated that both annual survival and exploitation varied over space and time. Within zones, annual survival was lowest during 2013 but ranged from 0.11 to 0.47 across zones. Annual survival was highest in the Transition zone, and the Transition and Upper Oahe zones exhibited large increases in annual survival from 2013 through 2015. Annual survival was lowest in the Riverine and Lower Oahe zones and displayed little or no increase through 2015. Zone-specific annual exploitation ranged from 0.15 to 0.39, and results suggested that harvest regulations were not a major driver of variation. My analysis demonstrated spatial variation in natural and fishing mortality of Walleye in Lake Oahe and provides guidance for future management during periods of low prey abundance.

Introduction

Quantifying mortality rates and distinguishing between fishing and natural mortality is important in the management of harvested fish populations. Fishing mortality is commonly the focus of monitoring efforts for heavily utilized fish populations as managers typically have more control over this component of the fishery than others. The potential for overexploitation has been well documented (Myers et al. 1997; Post et al. 2002; Morales-Nin et al. 2005; Worm et al. 2009) and protecting against this threat is often a primary management goal. Decoupling natural mortality and fishing mortality is difficult and natural mortality is often paid less attention than fishing mortality. However, these components of mortality interact, making it difficult to understand one without the other (Allen et al. 1998). Additionally, large-scale environmental disturbances have the potential to collapse fish populations through increases in natural mortality. For example, increased natural mortality stemming from poor environmental conditions contributed to the collapse of Atlantic Cod *Gadhus morhua* stocks in the norther Gulf of St. Lawrence (Dutil et al. 1999, Dutil and Lambert 2000). The interaction between natural and fishing mortality, and the potential for drastic effects of variability in natural mortality emphasize the importance of estimating both fishing and natural mortality.

In large systems, spatial variation of mortality components is common (Berger et al. 2017) and adds to the difficulty in accurately representing mortality. Spatial variation in natural mortality may result from heterogeneity in factors such as food web structure and thermal regime, and spatial variation in fishing mortality may result from differences in factors such as accessibility, catchability, and harvest restrictions. Spatial structuring of fish populations has long been recognized (Beverton and Holt 1957), but quantification

has lagged considerably due to the high amount of practical and computational effort required to model such complexity. Owing to advances in technology and statistical theory, much focus has been placed on this area recently (e.g., Berger et al. 2017). Although the leading edge of this trend has occurred in marine fisheries (Stephenson 1999, Smedbol and Wroblewski 2002, Cadigan et al. 2017, Kai et al 2017), there are also applications to large freshwater systems. For example, Vandergoot and Brenden (2014) found considerable spatial variation in population dynamics of Walleye *Sander vitreus* in Lake Erie and encouraged increased evaluation of spatial variation in mortality components within freshwater systems.

Lake Oahe is a large main stem Missouri River reservoir which supports a popular Walleye fishery in both North Dakota and South Dakota, USA. In Chapter 4, I used the results of a tagging study to demonstrate that the Lake Oahe Walleye population is spatially structured such that isolated groups occur within the reservoir. I attributed this result to proximity between spawning and feeding areas. Lake Oahe exhibits spatial heterogeneity in factors such as habitat, productivity, and thermal regime (Fincel 2011, Johnson et al. 2012) which may influence natural and fishing mortality. Additionally, Lake Oahe is subject to multi-jurisdictional management which may cause within-reservoir variation in fishing mortality. As a result, I recommended (in Chapter 4) evaluating the extent to which Walleye population dynamics vary spatially within Lake Oahe.

Rainbow Smelt *Osmerus mordax* are the primary prey resource for Walleye in Lake Oahe when abundant (Bryan 1995, Hanten 2006, Fincel et al. 2014). Record flooding of the Missouri River during 2011 led to high entrainment rates of Rainbow

Smelt through Oahe Dam (Fincel et al. 2016). In 1997, a similar flood event resulted in a shortage of prey resources yielding an imbalance between Walleye and Rainbow Smelt. Using a multiple year tagging study and bioenergetics modeling, Graeb et al. (2008) concluded that this imbalance drastically increased natural mortality rates of Walleye through starvation. However, the information used by Graeb et al. (2008) was collected from only the South Dakota portion of Lake Oahe, so these conclusions may not apply to the entire reservoir. Indeed, there are good reasons to suspect that mortality rates vary regionally within Lake Oahe. First, Rainbow Smelt are thermally limited to approximately the lower one-third of Lake Oahe during the summer months. As Walleye are not so limited (see Chapter 4), I hypothesized the effects of low Rainbow Smelt on natural mortality of Walleye would be most acute in the lower one-third of Lake Oahe where the interaction is strongest. Additionally, Lake Oahe exhibits a typical reservoir pattern of productivity, in which primary and secondary productivity are relatively low at the furthest upstream, riverine portion due to light limitation, then increase to a peak at the transition from riverine to reservoir where the balance between nutrient concentration and light limitation is optimized, before decreasing further downstream as sediment settles out and reduces nutrient concentration (Wetzel 2002, Fincel 2011). Graeb et al (2008) posited that when Rainbow Smelt abundance is low in Lake Oahe, Walleye rely more heavily on a benthic food web which is strongly linked to secondary productivity. As such, I hypothesized the effects of Rainbow Smelt on natural mortality of Walleye would be lowest near the transition from riverine to reservoir habitat in Lake Oahe.

In this study, I utilized a multiple year tag recovery study conducted throughout Lake Oahe to quantify changes in Walleye fishing mortality and natural mortality during

years following the 2011 flood. I sought to expand on previous research by investigating regional differences in population dynamics within Lake Oahe. Specific objectives were to evaluate: 1) Walleye population response to the 2011 flood, 2) the impact of liberalized harvest regulations enacted in response to low Rainbow Smelt abundance, and 3) the extent to which Walleye population response varied spatially within Lake Oahe.

Methods

Study area

Lake Oahe is a large main-stem Missouri River reservoir which extends approximately 512 river km from Riverdale, North Dakota to Pierre, South Dakota (Figure 6.1). The upper portion of Lake Oahe contains a remnant river reach called the Garrison Reach which consists of approximately 167 km of regulated river habitat. Approximately 345 km of impounded river occurs downstream of the Garrison Reach. The impounded section of Lake Oahe encompasses approximately 145,000 ha in surface area, has a mean depth of 19 m, and a maximum depth of 67 m (Nelson and Walburg 1977). The impounded section exhibits longitudinal changes in basin morphology, water depth, and water clarity which influence primary and secondary productivity (Fincel 2011). Three large tributaries also influence local productivity (Fincel 2011). The downstream portion of the impounded section thermally stratifies in the summer and maintains an oxygenated hypolimnion. The extent of thermal stratification varies annually but is consistently documented as far upstream as Swan Creek (River Mile 1174).

Lake Oahe fisheries are managed jointly by the North Dakota Game and Fish Department (NDGFD) and the South Dakota Department of Game, Fish, and Parks (SDGF&P). Walleye harvest is managed using daily bag and possession limits as well as length restrictions and differs between agencies (Table 6.1). Harvest regulations enacted by SDGF&P have changed substantially over time. During the period of this study, NDGF harvest regulations were constant and were different than those implemented by SDGF&P. During 2013, SDGF&P increased daily bag and possession limits before returning to the statewide standard for Walleye from 2014-2017.

For this study, I divided Lake Oahe into 4 zones based on differences in management authority and spatial structuring of the Walleye population (see Chapter 4). Lake Oahe is split by management authority (North Dakota and South Dakota) and then split into two zones within each state (Figure 6.1). Zones within respective states were taken to represent ecologically distinct spatial strata based on Walleye movement patterns.

Data Collection

Walleye tagging occurred throughout Lake Oahe and the Garrison Reach annually from 2013 through 2016. Fish were captured using trap nets, electrofishing and gill nets during March through May at 27 locations thought to be Walleye spawning sites. For each fish, an individually numbered size 12 Monel metal jaw tag was attached to the mandible or maxillary bone. Walleye less than 450 mm were tagged on the lower mandible and Walleye greater than or equal to 450 mm were tagged on the upper maxillary. Each tag was inscribed with a phone number for anglers to report tags. Recovery information came from anglers who voluntarily reported tagged fish and was

collected through the end of 2017. Anglers were asked to provide the tag number, date of recovery, fate of the fish (harvested, released with tag intact, released but removed tag), and approximate location of the recovery.

Data Analysis

I estimated survival and exploitation rates of mature Walleye using a Brownie et al. (1985) dead recoveries model. I excluded immature Walleye from analysis for two reasons: 1) sex could not be determined for those fish, and 2) juveniles must be treated differently in these models and doing so would have increased the complexity of this analysis. The general form of this model uses maximum likelihood estimation to estimate the parameters S , survival, and f , the probability of being killed, recovered, and reported, from tag recoveries obtained during l years from a series of tag releases occurring in k years. The model is commonly stated as:

$$R_{l,k} = N_k * f_l, \text{ when } l = k$$

$$R_{l,k} = N_k * f_l * S, \text{ when } l > k$$

Where $R_{l,k}$ is the number of tags recovered from tagging year k during recovery year l , N_k is the number of fish released during tagging year k , f_l is the recovery probability during recovery year l , and S is annual survival probability.

The general form of the Brownie et al. (1985) dead recoveries model includes several assumptions including: 1) all recovered tags are reported, and 2) marks are retained perfectly. To account for violation of these assumptions, I adjusted observed recoveries (N_k) using estimates of reporting rate and tag retention rate presented in Chapter 3 of this dissertation. To do so, it is useful to restate recovery probability, f , as:

$$f = Kc\lambda$$

Where K is the probability of being killed by an angler, c is the probability of being retrieved and λ is the probability of being reported. Furthermore, the unadjusted survival probability, \hat{S} , can be thought of as:

$$\hat{S} = r * S$$

Where r is the probability of tag retention and S is annual survival probability.

Therefore, I rearranged the above equations to express the models as:

$$\frac{R_{l,k}}{\lambda_l * c * r_{l-k}} = N_k * K_l, \text{ when } l = k$$

$$\frac{R_{l,k}}{\lambda_l * c * r_{l-k}} = N_k * K_l * S, \text{ when } l > k$$

To solve the left side of these equations I fixed c at 1, which assumes that anglers retrieved all fish that they harvested. I treated λ as known based on estimates of reporting rate from Chapter 3. I used year-specific estimates of λ during 2013 through 2015 when high-reward tags were released. For 2016-2017, I used the aggregate estimate of λ from 2013 through 2015 because no new releases of high-reward tags occurred during these years. I treat r as known based on estimates of tag retention rate reported in Chapter 3.

I constructed biologically meaningful models to evaluate whether survival (S) and exploitation rate (K) varied over time (t), among zones (z) and between sexes (sex).

Models were fit using the RMark package (Laake 2013) which uses Program R (R Core Team 2016) to implement models within Program MARK (White and Burnham 1999). Program MARK estimates model parameters using numerical maximum likelihood.

Overdispersion was assessed by calculating a variance inflation factor for the global model. The variance inflation factor was calculated as the chi-square value from the Pearson goodness-of-fit test divided by the degrees of freedom. Because the variance inflation factor indicated overdispersion ($\hat{c} = 5.51$), candidate models were evaluated using second order quasi-likelihood Akaike information criterion (QAIC_c; Burnham and Anderson 2002), and standard errors for parameter estimates were increased by the square root of the variance inflation factor.

Results

From 2013 through 2016, a total of 32,229 mature Walleye were tagged at 27 locations throughout Lake Oahe, and from 2013 through 2017, 7,378 of those fish were harvested and reported by anglers. Additionally, I estimated that 12,270 tagged Walleye would have been recovered if all tagged Walleye harvested by anglers were reported, and tags were retained perfectly (Table 6.2). Greater numbers were tagged in the Transition (14,368) and Upper Oahe (13,473) zones than in the Riverine (1,567) and Lower Oahe (2,821) zones. The tagged population was skewed toward males (male: female ratio = 4.6), and this pattern was consistent across all zones (Table 6.2).

Among my candidate model set, the model with time and zone-specific estimates of annual survival (S) and exploitation (K) had the most support from the data, and all other models had substantially less support (Table 6.3). The second most supported model, which included zone-specific estimates of annual survival and time and zone-specific estimates of annual exploitation, had a delta AIC_c value of 17.8 indicating that it had essentially no support in the data relative to the top model. Given that the top model

had an QAIC_c weight of nearly 1, all interpretations of parameter estimates were taken from the top model.

For all zones, confidence intervals for annual survival estimates during 2016 spanned from nearly 0 to 1.0, indicating poor convergence so this year was removed from consideration; further reference to annual survival includes only 2013-2015. Temporal trends in estimates of annual survival rate were similar among the Transition, Upper Oahe, and Lower Oahe zones. For each of these zones, annual survival was lowest in 2013 (0.11-0.47) and highest in 2015 (0.32-0.67; Table 6.4, Figure 6.2). Across all years, annual survival was highest in the Transition zone, where annual survival was estimated at 0.47 during 2013 and increased to 0.67 during 2015. The greatest range in annual survival occurred in the Upper Oahe zone, where annual survival increased from 0.21 during 2013 to 0.56 during 2015. The Riverine zone was among the lowest in annual survival across the 4 regions during 2013-2015 and 95% confidence intervals overlapped among all years indicating no change over time. The Lower Oahe zone was among the lowest in annual survival across all years, but did increase from 0.11 in 2013 to 0.32 in 2015.

For all zones, confidence intervals for annual exploitation estimates during 2017 approached the lower origin, indicating poor convergence so this year was removed from consideration; further reference to annual exploitation includes only 2013-2016. Temporal trends in exploitation were similar among regions with highest exploitation observed during 2013 and 2015, and lowest exploitation during 2014 and 2016 (Table 6.5; Figure 6.3). During 2013, exploitation was highest in the Lower Oahe zone, and confidence intervals overlapped among all other zones. Exploitation was lowest during

2014 for all zones, and no significant differences were apparent. Exploitation was highest during 2015 for all zones, was higher in Lower Oahe than in the Transition and Upper Oahe zones, and was lower in Upper Oahe than any other zones. Exploitation was lower during 2016 than other years and was lower in Upper Oahe than in any other zone.

Discussion

The Lake Oahe Walleye population exhibited spatial variation in natural and fishing mortality, and the observed patterns aligned with hypotheses generated using previous research of Lake Oahe food web dynamics (Graeb et al. 2008, Fincel 2011) and basic ecological theory (Wetzel 2002). The impacts of the 2011 flood were observed throughout Lake Oahe with annual survival estimated to be less than 50% in all zones during 2013. However, the magnitude of effect and timeline of recovery varied among zones. My analysis showed that Walleye in the Lower Oahe zone were most affected by low Rainbow Smelt abundance, and very low annual survival during 2015 (32%) indicates that Walleye population in this region was still struggling in 2015, four years after the flood event which so drastically reduced the Rainbow Smelt population (Fincel et al. 2016). Relative to other zones of Lake Oahe, the Transition zone appeared to support the highest survival for Walleye when conditions were the worst and had recovered to an annual survival rate of 67% by 2015.

The results of this study broadly agreed with those from a previous tagging study under similar environmental conditions in Lake Oahe following a high discharge event in 1997 (Graeb et al. 2008), but some differences were apparent following the 2011 flood. Previous tagging efforts were limited to the South Dakota portion of Lake Oahe (Graeb et al. 2008) which corresponds to the Upper Oahe and Lower Oahe zones delineated in this

study, so I limit comparisons of parameter estimates to those two zones. Following the 1997 event, initial survival (2-3 years post-flood) was lower than after chronic low prey abundance (4-6 years post-flood), and during the initial period male Walleye experienced a higher mortality rate than females (Graeb et al. 2008). Following the 2011 flood, initial survival was lowest and similar to the rates estimated 4-6 years after the 1997 event (Graeb et al. 2008), then increased substantially in the Upper Oahe zone 4 years after the flood, and also did not indicate differences in survival among sexes. A possible explanation for this discrepancy is the 2011 flood resulted in much higher discharge than during 1997, which may have resulted in greater losses of Rainbow Smelt. After the 1997 event, it may have taken longer for the imbalance between Rainbow Smelt and Walleye to become as large as what occurred only 2 years after the 2011 event. Exploitation estimates reported by Graeb et al. (2008) were lower than those from my study, but this discrepancy can largely be explained by differences in estimates of angler reporting rate. Graeb et al. (2008) used creel surveys to estimate a reporting rate of 0.77, while I used estimates generated from a high-reward tagging study which ranged from 0.56 to 0.7, with an aggregate estimate of 0.58 (Chapter 3). The high-reward method is considered among the best approaches for estimating nonreporting rates (Pollock et al. 2001), and the use of creel surveys may overestimate reporting rates if anglers inflate their responses (Graeb et al. 2008). If my aggregate rate (0.58) was used by Graeb et al. (2008), then their estimates of exploitation would have ranged from 23% to 28%, which compares closely to the estimates for Upper Oahe and Lower Oahe reported in this study.

Although Graeb et al. (2008) did not estimate survival among the two zones I defined within their study area, their estimates of survival for both zones in South Dakota

remained low up to 6 years post-flood, whereas I observed a 35% increase in survival for Walleye in the Upper Oahe zone from 2013 to 2015 (4 years post-flood). Although survival remained low in the Lower Oahe zone, an aggregated survival estimate for the two South Dakota zones would still have been higher than those reported by Graeb et al. (2008). Monitoring efforts by SDGF&P (Meyer et al. 2015; Potter et al. 2016) documented increasing abundance of pelagic coldwater prey, including both Rainbow Smelt and Cisco *Coregonus artedi*, in Lake Oahe from 2013-2015. Concurrent research (N. Kludt, South Dakota State University, unpublished data) focused on the spatial distribution of these species in Lake Oahe has shown that they primarily occupied the Upper Oahe zone during 2013-2015 and that their abundance has remained low in the Lower Oahe zone. This result may explain the substantial increase in annual survival observed between 2013 and 2015 for Walleye in the Upper Oahe zone.

Walleye tagged in the Transition zone of Lake Oahe were least affected by the cascading effects of the 2011 flood which aligns with my initial hypotheses based on the food web dynamics of Lake Oahe and basic reservoir ecology. Evidence from bioenergetics modeling (Graeb et al. 2008) and stable isotope analysis (Davis 2004) suggested that low survival rates of Walleye were primarily caused by low Rainbow Smelt abundance. Although annual survival was below 50% for Walleye tagged in the Transition zone during 2013, it was 2 to 4 times higher than any other zone and was higher than other zones during all years of the study, indicating that Walleye in this zone are less susceptible to fluctuations in Rainbow Smelt abundance than those in other zones. This result was expected because Rainbow Smelt are thermally limited to the Lower Oahe and Upper Oahe zones during the summer (Fincel 2011). Analysis of

movement patterns (Chapter 4) indicated that some Walleye tagged in the Transition zone may spend the summer in the Upper Oahe zone, so the effect of low Rainbow Smelt on this group is not negligible, but the fact that most of this group remains in the Transition zone year-round explains the relatively low impact. Reservoir ecology provides further explanation for the dampened response in the Transition zone. Primary productivity in reservoirs is a balance between light limitation and nutrient concentration (Wetzel 2002) and in Lake Oahe this trade-off is optimized in the Transition zone.

Walleye clearly prefer Rainbow Smelt when available in Lake Oahe (Bryan 2004, Hanten 2006, Fincel et al. 2014), but when Rainbow Smelt abundance is low they must utilize alternative prey. In Lake Oahe, alternative prey sources include benthic invertebrates and a suite of warmwater fish species such as Gizzard Shad *Dorosoma cepedianum*, Yellow Perch *Perca flavescens*, White Bass *Morone chrysops*, Black Crappie *Pomoxis nigromaculatis*, White Crappie *Pomoxis annularis*, and Emerald Shiner *Notropis atherinoides* (Fincel 2011; Hanten 2006; Potter et al. 2016). I speculate these alternative prey sources have higher abundance in the Transition zone than elsewhere in Lake Oahe due to its relatively high primary productivity, which buffers Walleye in the Transition zone from the impact of low Rainbow Smelt abundance.

Walleye tagged in the Riverine zone of Lake Oahe experienced low survival during this study. This zone does not contain suitable habitat for Rainbow Smelt, so their low abundance does not provide a reasonable explanation for this observation. An investigation by Schenk et al. (2014) showed the 2011 flood caused considerable channel incision in the Riverine zone, although losses of habitat complexity have occurred since the closure of Garrison Dam due to erosion, channel incision, and loss of islands and

sandbars (Schenk et al. 2014). I do not know of any survival estimates for Walleye in the Riverine zone prior to this study so it is difficult to evaluate whether the 2011 flood caused the poor survival rates of Walleye observed in this study, or if poor habitat conditions make low survival the baseline condition for Walleye in the Riverine zone.

Temporal trends in annual exploitation were similar among zones with the highest rates observed during 2013 and 2015 and the lowest rates during 2014 and 2016.

Liberalized bag and possession limits implemented by SDGF&P during 2013 may have increased exploitation rates, but exploitation within the Lower Oahe zone was among the highest during all years. Furthermore, exploitation was also relatively high across all years in the Riverine zone, where regulations were constant. Additionally, exploitation rates were highest during 2015 across all zones, after daily bag and possession limits in South Dakota had been reduced from 2013 limits. All these observations suggest that harvest regulations were not the most important drivers of exploitation rate during this study.

Although regulations, such as daily bag limits used by SDGF&P, may impact exploitation rate, their impact is also related to angler catch rates and effort (Cook et al. 2001; Radomski et al. 2001; Cox et al. 2002). Angler catch rates of Walleye in Lake Oahe are inversely related to Walleye condition (Chapter 5) which, in Lake Oahe, is closely related to Rainbow Smelt abundance (Graeb et al. 2008), and has been shown to be related to prey availability elsewhere (Porath and Peters 1997). I speculate that Walleye in Lower Oahe had high catchability relative to other zones throughout this study due to low prey availability which contributed to persistent, high exploitation. Similarly, I posit that increases in coldwater prey abundance (N. Kludt, South Dakota

State University, unpublished data) or increased warmwater prey production (Potter et al. 2016) contributed to relatively low exploitation in the Upper Oahe zone during 2015 and 2016. Analysis of movement patterns demonstrated that a large proportion of the Walleye tagged in the Riverine zone inhabit the Garrison Dam Tailrace. Tailrace fisheries commonly experience high exploitation rates due to ease of access and concentration of fish (Beamesderfer 1998; Pegg et al. 1997; Williot et al. 2002), and I hypothesize these factors explain the high exploitation rates observed during this study.

Spatial differences in natural and fishing mortality within Lake Oahe provide guidance for future management, particularly during periods of low Rainbow Smelt abundance. Within North Dakota, the Transition zone exhibited relatively high survival and fast recovery following the 2011 flood, indicating that changes in management, such as the liberalized harvest regulations implemented by SDGF&P following both the 1997 and 2011 floods, would not be prudent for that zone. The Riverine zone exhibited poor survival which did not change during this study. As this zone is unlikely to be affected by low Rainbow Smelt abundance, further investigation into the mechanisms driving low survival is needed to guide future management. Nonetheless, movement patterns and variability among the Riverine and Transition zones within North Dakota offer the opportunity for regional management.

Within South Dakota, the Lower Oahe zone exhibited low survival and showed little sign of recovery through 2015. Additionally, analysis of movement patterns (Chapter 4) suggest that almost no fish from other zones of Lake Oahe moved into this region, during periods of low Rainbow Smelt abundance. In other words, help is not on the way for the Lower Oahe zone. Given these circumstances, the liberalization of

harvest regulations by SDGF&P was appropriate for the Lower Oahe zone. In addition to increasing daily bag and possession limits, I also recommend the removal of the one-over 508 mm size restriction for the Lower Oahe zone during periods of low Rainbow Smelt abundance. Previous research (Davis 2004; Graeb et al. 2008) showed that large fish are more acutely affected by low Rainbow Smelt abundance. Those results along with the extremely low survival rates documented by this study and Graeb et al. (2008) indicate that exploitation of Walleye is compensatory under those conditions and will have no effect on total annual survival (Allen et al. 1998). However, my estimates for the Upper Oahe zone, along with analysis of movement patterns (Chapter 4), indicate that this is likely not true throughout the entire South Dakota portion of Lake Oahe, as survival increased rapidly in the Upper Oahe zone during this study. Additionally, my analysis of movement patterns (Chapter 4) indicated that approximately 20% of Walleye harvested by anglers in Upper Oahe were tagged in the Transition zone, which means that management actions taken by SDGF&P would affect the Transition zone group described in this study. Given these considerations, I recommend that SDGF&P implement liberalized bag limits for Walleye in the Lower Oahe zone but not in the Upper Oahe zone when Rainbow Smelt abundance is low.

The results of this study demonstrate the complexity which arises from spatial structuring of fish populations within large, open systems, and underscores the importance of understanding such complexity to better inform management decisions. In addition to reinforcing the conclusions made by Graeb et al. (2008), this study revealed important spatial differences in the Lake Oahe Walleye population response to the 2011 flood, which resulted in refined recommendations for management and future research.

Spatial structuring is common in fish populations (Beverton and Holt 1957; Vandergoot and Brenden 2014; Berger et al. 2017), and I recommend that managers and researchers account for this important feature and continue to refine techniques which account for it when quantifying dynamic rate functions such as recruitment, growth, and mortality.

References

- Allen, M. S., L. E. Miranda, R. E. Brock. 1998. Implications of compensatory and additive mortality to the management of selected sportfish populations. *Lakes and Reservoirs Research and Management* 3: 67-79.
- Beamesderfer, R. C. 1998. Management and trade in Pacific sturgeon. Pages 95-105 in D.F. Williamson, G. W. Benz, and C. M. Hoover, editors. *TRAFFIC North America. Proceedings of the Symposium on Harvest, Trade, and Conservation of North American Paddlefish and Sturgeon*. Washington, D.C.
- Berger, A. M., D. R. Goethel, P. D. Lynch, T. Quinn II, S. Mormede, J. McKenzie, and A. Dunn. 2017. Space oddity: the mission for spatial integration. *Canadian Journal of Fisheries and Aquatic Sciences* 74: 1698-1714.
- Beverton, R. J. H., and S. J. Holt. 1957. *On the dynamics of exploited fish populations*. Fisheries Investment Series 2. 19. UK Ministry of Agriculture and Fisheries. Chapman and Hall, London.
- Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson. 1985. *Statistical inference from tag-recovery data – a handbook*. 2nd edition. U.S. Fish and Wildlife Service, Washington DC.
- Bryan, S. D. 1995. *Bioenergetics of walleye in Lake Oahe, South Dakota*. M.S. Thesis. South Dakota State University, Brookings, SD.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd edition. Springer-Verlag, New York.
- Cadigan, N, E. Wade, and A. Nielsen. 2017. A spatiotemporal model for snow crab (*Chionoecetes opilio*) stock size in the southern gulf of St. Lawrence. *Canadian Journal of Fisheries and Aquatic Sciences* 74: 1808-1820.
- Cook, M. F., T. J. Goeman, P. J. Radomski, J. A. Younk, P. C. Jacobson. 2001. Creel limits in Minnesota: a proposal for change. *Fisheries* 26: 19-26.
- Cox, S. P., T. D. Beard, Jr., and C. Walters. 2002. Harvest control in open-access sport fisheries: hot rod or asleep at the wheel? *Bulletin of Marine Science* 70: 749-761.

- Davis, B. A. 2004. Estimating trophic position of Lake Oahe walleye using stable isotope analysis. M.S. Thesis, South Dakota State University, Brookings, SD.
- Dutil, J. D., M. Castonguay, D. Gilbert, and D. Gascon. 1999. Growth, condition, and environmental relationships in Atlantic cod (*Gadus morgue*) in the northern Gulf of St. Lawrence and implications for management strategies in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 1818-1831.
- Dutil, J. D., and Y. Lambert. 2000. Natural mortality from poor condition in Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 57: 826-836.
- Fincel, M. J. 2011. Productivity and trophic interactions in the Missouri River impoundments. Doctoral Dissertation. South Dakota State University, Brookings, SD.
- Fincel, M. J., D. J. Dembkowski, and S. R. Chipps. 2014. Influence of variable rainbow smelt and gizzard shad abundance on walleye diets and growth. *Lake and Reservoir Management* 30: 258-267.
- Fincel, M. J., W. J. Radigan, and C. M. Longhenry. 2016. Entrainment of Rainbow Smelt through Oahe Dam during the 2011 Missouri River flood. *North American Journal of Fisheries Management* 36: 844-851.
- Graeb, B. D. S., S. R. Chipps, D. W. Willis, J. P. Lott, R. P. Hanten, W. Nelson-Stastny, and J. W. Erickson. 2008. Walleye response to rainbow smelt population decline and liberalized angling regulations in a Missouri River reservoir. Pages 275-292 *in* M. S. Allen, S. Sammons, and M. J. Maceina, editors. *Balancing fisheries management and water uses for impounded river systems*. American Fisheries Society, Symposium 62, Bethesda, Maryland.
- Hanten, R. 2006. Seasonal food habits, condition, growth and distribution of Lake Oahe, South Dakota, walleye during depressed prey conditions spring 2001 to spring 2002. South Dakota Department of Game, Fish and Parks, Fisheries Division

- Report 07-02, Pierre.
- Johnson, W. C., M. D. Dixon, M. L. Scott, L. Rabbe, G. Larson, M. Volke, and B. Werner. 2012. Forty years of vegetation change on the Missouri River floodplain. *BioScience* 62: 123-135.
- Kai, M., J. T. Thorson, K. Piner, and M. Maunder. 2017. Spatiotemporal variation in Size-structured populations using fishery data: an application to shortfin mako (*Isurus oxyrinchus*) in the Pacific Ocean. *Canadian Journal of Fisheries and Aquatic Sciences* 74: 1765-1780.
- Laake, J. L. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. ASFC Processed Rep 2013-01, 25 p. Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service, Seattle WA.
- Meyer, H., R. Hanten, K. Poter, M. Fincel, and M. Smith. 2015. Annual fish population and angler use, harvest and preference surveys on Lake Oahe, South Dakota, 2014. South Dakota Department of Game, Fish and Parks, Wildlife Division Report 15-04, Pierre.
- Morales-Nin, B., J. Moranta, C. Garcia, M. P. Tugores, A. M. Grau, F. Riera, and M. Cerda. 2005. The recreational fishery of Majorca Island (western Mediterranean): some implications for coastal resources management. *ICES Journal of Marine Science* 62: 727-739.
- Myers, R. A., J. A. Hutchings, and N. J. Barrowman. 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. *Ecological Applications* 7: 91-106.
- Nelson, W. R., and C. H. Walburg. 1977. Population dynamics of yellow perch (*Perca flavescens*), Sauger (*Stizostedion canadense*), and walleye (*S. vitreum vitreum*) in four main stem Missouri River Reservoirs. *Journal of the Fisheries Research Board of Canada* 34: 1748-1763.
- Pegg, M. A., J. B. Layzer, and P. W. Bettoli. 1997. Angler exploitation of anchor-tagged saugers in the lower Tennessee River. *North American Journal of Fisheries Management* 17: 763-768.

- Pollock, K. H., J. M. Hoenig, W. S. Hearn, and B. Calingaert. 2001. Tag reporting rate estimation: 1. An evaluation of the high-reward tagging method. *North American Journal of Fisheries Management* 21: 521-532.
- Post, J. R., M. Sullivan, S. Cox, N. P. Lester, C. J. Walters, E. A. Parkinson, A. J. Paul, L. Jackson, and B. J. Shuter. 2002. Canada's recreational fisheries: the invisible collapse? *Fisheries* 27: 6-17.
- Potter, K, H. Meyer, R. Hanten, M. Greiner, M. Fincel, and M Smith. 2016. Annual fish population and angler use, harvest and preference surveys on Lake Oahe, South Dakota, 2015. South Dakota Department of Game, Fish and Parks, Wildlife Division Report 16-03, Pierre.
- Porath, M. T., and E. J. Peters. 1997. Use of walleye relative weights (W_r) to assess prey availability. *North American Journal of Fisheries Management* 17: 628-637.
- Radomski, P. J., G. C. Grant, P. C. Jacobson, and M. F. Cook. 2001. Visions for recreational fishing regulations. *Fisheries* 26: 7-18.
- R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. URL <https://www.R-project.org/>.
- Schenk, E. R., K. J. Skalak, A. J. Benthem, B. J. Dietsch, B. K. Woodward, G. J. Wiche, J. M. Galloway, R. A. Nustad, and C. R. Hupp. 2014. Geomorphic change on the Missouri River during the flood of 2011. U.S. Geological Survey Professional Paper 1798-I, 25 p.
- Smedbol, R. K., and J. S. Wroblewski. 2002. Metapopulation theory and northern cod population structure: interdependency of subpopulations in recovery of a groundfish population. *Fisheries Research* 55: 161-174.
- Stephenson, R. L. 1999. Stock complexity in fisheries management: a perspective of emerging issues related to population sub-units. *Fisheries Research* 43: 247-249.
- Vandergoot, C. S., and T. O. Brenden. 2014. Spatially varying population demographics and fishery characteristics of Lake Erie walleyes inferred from a long-term tag

- recovery study. *Transactions of the American Fisheries Society* 143: 188-204.
- Wetzel, R. G. 2002. *Limnology*. Saunders, Philadelphia, Pennsylvania, USA.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from Populations of marked animals. *Bird Study* 46: 120-139.
- Williot, P., G. Arlati, M. Chebanov, T. Gulyas, R. Kasimov, F. Kirschbaum, N. Patriche, L. P. Pavlovskaya, L. Poliakova, M. Pourkazemi, Y. Kim, P. Zhuang, and I. M. Zholdasova. 2002. Status and management of Eurasian sturgeon: an overview. *International Review of Hydrobiology* 87: 483-506.
- Worm, B., R. Hilborn, J. K. Baum, T. A. Branch, J. S. Collie, C. Costello, M. J. Fogarty, E. A. Fulton, J. A. Hutchings, J. Simon, O. P. Jensen, H. K. Lotze, P. M. Mace, T. R. McClanahan, C. Minto, S. R. Palumbi, A. M. Parma, D. Ricard, A. A. Rosenberg, R. Watson, and D. Zeller. 2009. Rebuilding global fisheries. *Science* 325: 578-585.

Table 6.1. Harvest regulations for Walleye in portions of Lake Oahe managed by North Dakota Game and Fish Department (NDGF), and South Dakota Department of Game, Fish and Parks (SDGF&P), 2013-2017.

Time period	Daily Limit	Possession Limit	Length Restrictions
<i>NDGF (Riverine and Transition Zones)</i>			
2013-2017	5	10	None
<i>SDGF&P (Upper Oahe and Lower Oahe Zones)</i>			
2013	8	24	1 over 508 mm; maximum 4 over 381 mm
2014-2017	4	8	1 over 508 mm

Table 6.2. Number of tags released, and the estimated number harvested under perfect tag reporting and retention among regions and sexes for Walleye tagged in Lake Oahe from 2013-2016.

Tagging Year	Number Tagged			Estimated Number Harvested		
	Male	Female	Total	Male	Female	Total
<i>Riverine Zone</i>						
2013	515	116	631	176	55	231
2014	71	49	120	28	25	53
2015	202	91	293	102	54	156
2016	356	167	523	150	75	225
Total	1,144	423	1,567	456	209	665
<i>Transition Zone</i>						
2013	2,150	646	2,796	931	340	1,271
2014	3,534	356	3,890	1,646	179	1,825
2015	3,323	927	4,250	1,770	488	2,258
2016	2,197	1,235	3,432	681	420	1,101
Total	11,204	3,164	14,368	5,028	1,427	6,455
<i>Upper Oahe Zone</i>						
2013	3,549	400	3,949	1,151	98	1,249
2014	2,095	229	2,324	740	72	812
2015	2,677	870	3,547	968	344	1,312
2016	3,164	489	3,653	583	91	674
Total	11,485	1,988	13,473	3,442	605	4,047
<i>Lower Oahe Zone</i>						
2013	619	83	702	222	28	250
2014	715	40	755	234	9	243
2015	1,017	32	1,049	493	20	513
2016	269	46	315	83	14	97
Total	2,620	201	2,821	1,032	71	1,103

Table 6.3. Model comparison for models used to estimate annual survival (S) and exploitation (K) of Walleye from a tag recovery study on Lake Oahe conducted from 2013-2017. Models are described in terms of second order quasi-likelihood Akaike information criterion (QAIC_c), the difference from the QAIC_c values of the top model (Δ QAIC_c), model weight (QAIC_c weight), and model deviance. Table show only top 10 models; candidate models not shown had no support in the data.

Model	K	QAIC _c	Δ QAIC _c	QAIC _c weight	Deviance
S(time*zone) K(time*zone)	36	11438.8	0.00	0.997	54.10
S(zone) K(time*zone)	24	11456.7	17.84	1.34E-04	95.98
S(time*zone) K(time)	21	11456.9	18.07	1.19E-04	102.22
S(zone*sex) K(time*zone)	28	11462.6	23.81	6.73E-06	93.95
S(time*zone) K(time*zone*sex)	56	11462.9	24.06	5.94E-06	38.05
S(time*zone) K(time*sex)	26	11464.2	25.38	3.07E-06	99.52
S(zone) K(time*zone*sex)	44	11480.9	42.06	7.34E-10	80.12
S(time*zone*sex) K(time*zone)	52	11483.4	44.52	2.15E-10	66.53
S(zone*sex) K(time*zone*sex)	48	11486.1	47.26	5.45E-11	77.30
S(zone) K(time)	9	11486.2	47.34	5.25E-11	155.51

Table 6.4. Zone-specific annual survival estimates (S) and associated confidence limits during 2013-2015 for Lake Oahe Walleye.

Zone	Year	S	Lower 95 % Confidence Limit	Upper 95 % Confidence Limit
Riverine	2013	0.23	0.16	0.30
Transition	2013	0.47	0.43	0.51
Upper Oahe	2013	0.21	0.18	0.23
Lower Oahe	2013	0.11	0.07	0.16
Riverine	2014	0.39	0.28	0.51
Transition	2014	0.53	0.50	0.56
Upper Oahe	2014	0.45	0.41	0.49
Lower Oahe	2014	0.26	0.22	0.32
Riverine	2015	0.32	0.24	0.42
Transition	2015	0.67	0.62	0.71
Upper Oahe	2015	0.56	0.50	0.62
Lower Oahe	2015	0.32	0.25	0.39

Table 6.5. Zone-specific annual exploitation estimates (K) and associated confidence limits during 2013-2016 for Lake Oahe Walleye.

Zone	Year	K	Lower 95 % Confidence Limit	Upper 95 % Confidence Limit
Riverine	2013	0.27	0.23	0.30
Transition	2013	0.23	0.22	0.25
Upper Oahe	2013	0.24	0.23	0.26
Lower Oahe	2013	0.32	0.29	0.36
Riverine	2014	0.24	0.18	0.30
Transition	2014	0.19	0.18	0.20
Upper Oahe	2014	0.18	0.17	0.20
Lower Oahe	2014	0.19	0.17	0.22
Riverine	2015	0.39	0.34	0.45
Transition	2015	0.32	0.30	0.33
Upper Oahe	2015	0.27	0.25	0.28
Lower Oahe	2015	0.39	0.36	0.42
Riverine	2016	0.32	0.28	0.36
Transition	2016	0.25	0.23	0.26
Upper Oahe	2016	0.15	0.14	0.16
Lower Oahe	2016	0.27	0.22	0.32

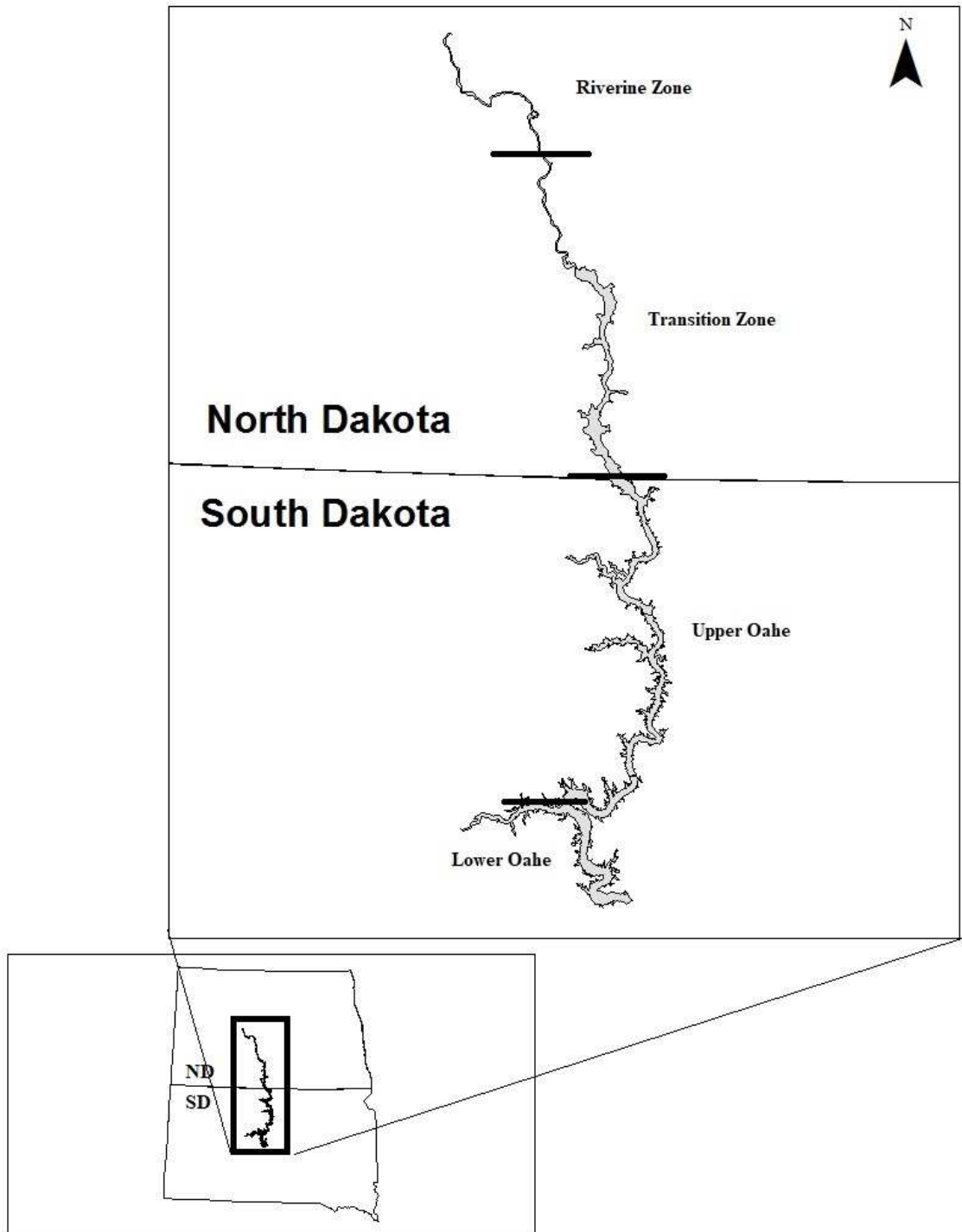


Figure 6.1. Map of Lake Oahe and zones.

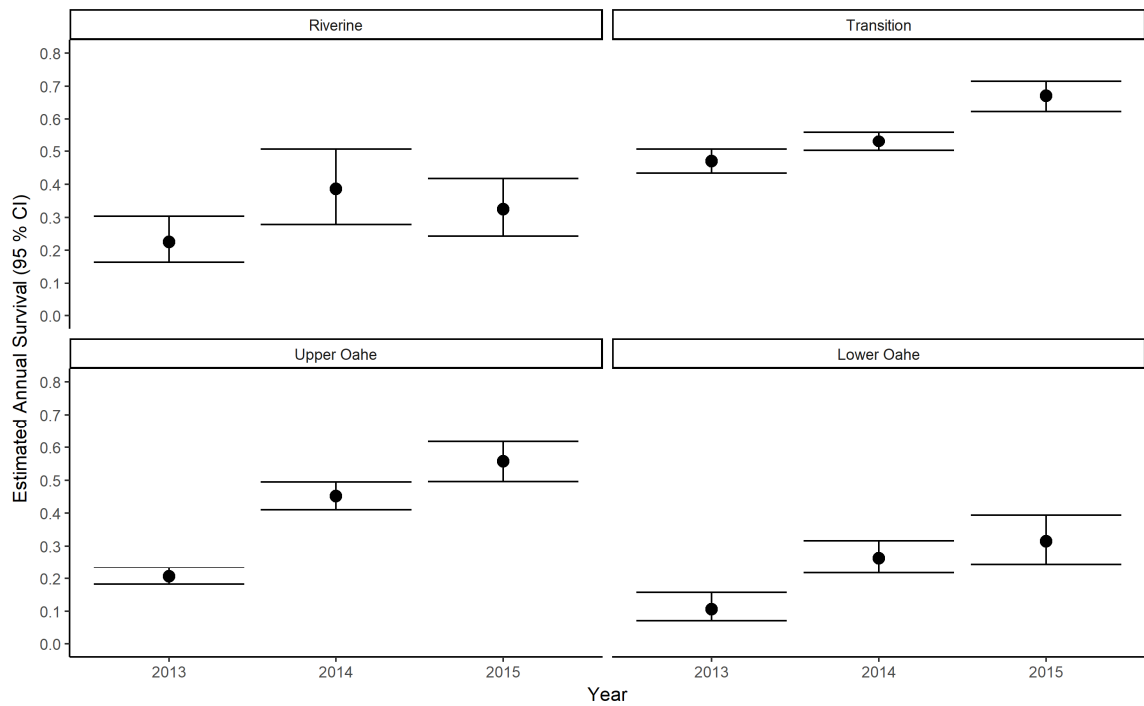


Figure 6.2. Zone-specific annual survival estimates (S) and associated confidence limits during 2013-2015 for Lake Oahe Walleye.

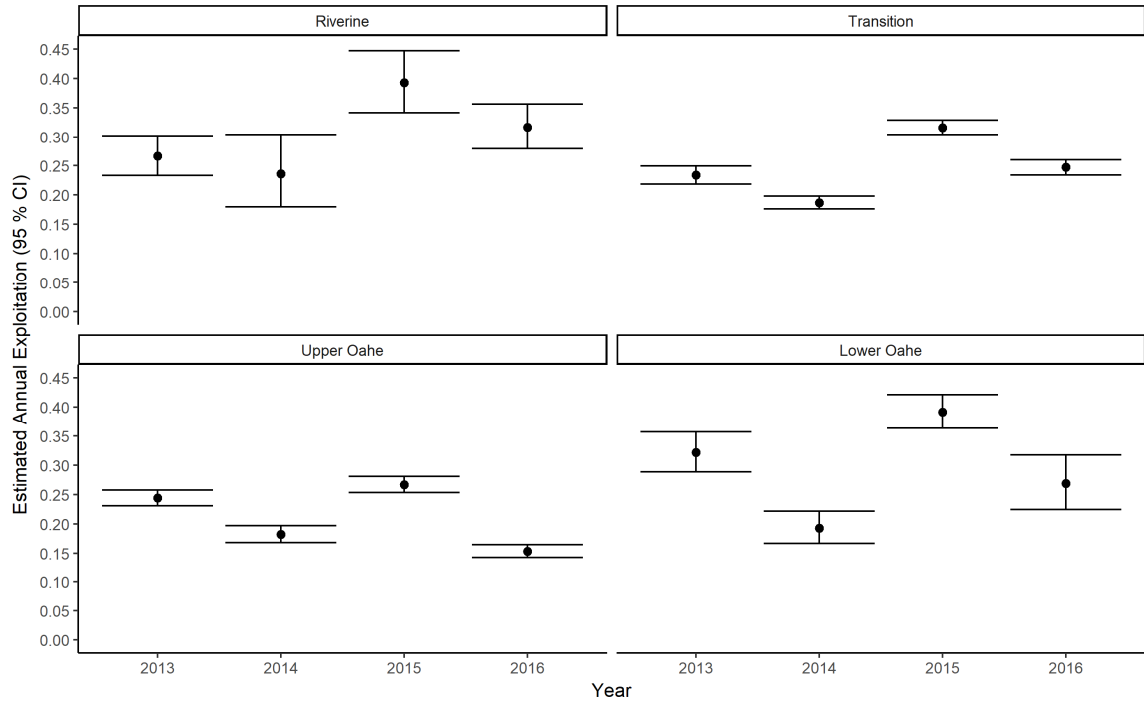


Figure 6.3. Zone-specific annual exploitation estimates (K) and associated confidence limits during 2013-2016 for Lake Oahe Walleye.

CHAPTER 7: CONCLUSIONS

Summary

The research presented in this dissertation covered several facets of the Lake Oahe Walleye fishery and contributed to the broader topics of Walleye population ecology and spatial variation of fish population dynamics. My findings complement and expand upon previous research which investigated Lake Oahe Walleye movement patterns (Riis et al. 1993; Hendricksn 2005; Carlson et al. 2017), population response to shifts in prey abundance (Graeb et al. 2008; Fincel et al. 2014), and spatial variation in the ecology of Lake Oahe (Fincel 2011; Carlson et al. 2017). My investigations of Walleye recruitment and angler catch rates represent advances in topics on which little previous research was focused in Lake Oahe.

Evidence from 26 years of standardized annual monitoring demonstrated that Walleye recruitment in Lake Oahe has been consistent and that variation in year-class strength has been driven by density independent factors. Previously, managers suspected Walleye recruitment was inconsistent in the lower portion of Lake Oahe, but my analysis showed that nearly every year-class during a 26-year period was present throughout Lake Oahe. The rapid increase in water level which occurred from 2008 through 2009, after many years of drought and low water levels, likely contributed to record-high Walleye recruitment during 2009. Overall, my analysis of Walleye recruitment in Lake Oahe indicates that variation in abundance and size structure is largely driven by mortality and growth rates.

Analysis of movement patterns showed that the Lake Oahe Walleye population is spatially structured, with most fish occupying one zone throughout an entire year. The

Lower zone of Lake Oahe, downstream of the confluence with the Cheyenne River was particularly isolated. Multiple life-histories, related to the configuration of spawning and feeding areas (Bozek et al. 2011), were present but the “lake-resident, river-run” strategy was most common for Lake Oahe Walleye. Perhaps the most important implication from this analysis was that the Lake Oahe Walleye population contains multiple, isolated groups which potentially experience variable population dynamics.

The impacts of the 2011 flood were experienced throughout the Lake Oahe Walleye population, but there was considerable spatial variation in the magnitude and duration of impact. Annual survival was as low as 0.11 during 2013 and in some zones did not increase from 2013 to 2015. By contrast, annual survival was as high as 0.47 during 2013, and in some zones exhibited a substantial increase from 2013 to 2015. Despite the implementation of liberalized harvest regulations by the South Dakota Department of Game, Fish, and Parks during 2013, my results indicated that harvest regulations are not a primary driver of exploitation rate in Lake Oahe. Under the extremely low annual survival rates observed for some zones and years of this study, exploitation of Walleye is almost certainly compensatory (*sensu* Allen et al. 1998), meaning that total annual survival would not increase if exploitation rate was increased.

Angler catch rates of Walleye were not related to population density. However, a strong inverse relationship between Walleye relative weight and angler catch rate was apparent. Walleye relative weight is driven by abundance of prey such as Rainbow Smelt and Gizzard Shad (Fincel et al. 2014). Therefore, this result demonstrates that angler catch rates of Walleye can be expected to be highest in Lake Oahe when prey abundance is low. Accordingly, the greatest potential to increase exploitation rates of Walleye

through harvest regulations exists when prey abundance is low, whereas exploitation rates are likely to be low when prey abundance is high because anglers simply do not catch many fish.

My research supported the notion that prey populations, particularly Rainbow Smelt, are primary drivers of Walleye population dynamics in Lake Oahe. The effects of those populations extend to anglers, meaning they influence the entire Walleye fishery. However, arguably the most important finding of my research was that the effects of prey populations on Walleye are variable within Lake Oahe. An additional implication of this finding is that other factors also exert variable influence on Walleye throughout Lake Oahe. These observations lead to additional questions and topics of future research.

Research needs

- 1) Annual survival was low in the Riverine zone throughout this study, but I suspect this cannot be attributed to low Rainbow Smelt abundance. Additional research is necessary to evaluate other factors, such as poor habitat quality, which potentially cause low annual survival in this zone, and to assess whether the low survival observed during this study was a result of the 2011 flood or if it is simply the baseline condition.
- 2) The two studies which have quantified survival and exploitation of Walleye in Lake Oahe occurred during periods of low Rainbow Smelt abundance. A long-term tagging program, in which Walleye are tagged annually throughout Lake Oahe, would provide a better understanding of Walleye mortality components over a range of conditions.

- 3) Recruitment was evident throughout Lake Oahe, but the data used were not particularly well-suited to evaluate spatial differences in recruitment. Future research designed to evaluate spatial variation of Walleye recruitment would provide a better understanding of Walleye recruitment dynamics in Lake Oahe.
- 4) Walleye relative weight has served as an early indicator of problems for the Lake Oahe Walleye population. An important question is at what point does low prey abundance shift from causing poor growth rates to causing mortality? Walleye condition in Lake Oahe has tended to be at one of two extremes, so it is difficult to predict population response at intermediate values. Laboratory experiments in which fish were starved while body condition was monitored were conducted for Atlantic cod *Gadhus morhua* (Dutil and Lambert 2000). Similar experiments for Walleye could be conducted to estimate the relationship between relative weight and mortality.
- 5) Population demographics present during this study were somewhat limiting to analysis. Tagged Walleye were primarily small (< 450 mm) Walleye, and the sample population was heavily skewed toward males, especially in the Lower zone. Male Walleye are simply more vulnerable to sampling techniques, so samples are likely to be skewed, but it seems possible to achieve a better representation of females under different circumstances. I suspect that by 2013, many of the large Walleye in Lake Oahe, which are disproportionately female, had died because of low prey abundance. It is worth noting that the model which best fit the data in Chapter 6 contained sex-specific estimates of exploitation but was heavily penalized for the number of parameters. However, because the

candidate set of models only included sex-specific models across all zones, the lack of information for females in the Lower Oahe zone affected model evaluation across all zones.

References

- Allen, M. S., L. E. Miranda, R. E. Brock. 1998. Implications of compensatory and additive mortality to the management of selected sportfish populations. *Lakes and Reservoirs Research and Management* 3: 67-79.
- Bozek, M. A., D. A. Vaccante, and N. P. Lester. 2011. Walleye and sauger life history Pages 233-302 *in* B.A. Barton, editor. *Biology, management, and culture of walleye and sauger*. American Fisheries Society, Bethesda, Maryland.
- Carlson, A. K., M. J. Fincel, and B. D. S. Graeb. 2017. Otolith chemistry indicates Walleye movement and entrainment in a large serial reservoir system. *Fisheries Management and Ecology* 24: 217-229.
- Dutil, J. D., and Y. Lambert. 2000. Natural mortality from poor condition in Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* 57: 826-836.
- Fincel, M. J. 2011. Productivity and trophic interactions in the Missouri River impoundments. Doctoral Dissertation. South Dakota State University, Brookings, SD.
- Fincel, M. J., D. J. Dembkowski, and S. R. Chipps. 2014. Influence of variable rainbow smelt and gizzard shad abundance on walleye diets and growth. *Lake and Reservoir Management* 30: 258-267.
- Hendrickson, J. C. 2005. Movements and population statistics of walleye in the Garrison Reach of the Missouri River and Lake Oahe, North Dakota: 1999-2004. North Dakota Game and Fish Department Report.
- Riis, J. C., B. Johnson, and C. C. Stone. 1993. Movement and exploitation of walleye, sauger and smallmouth bass in the Missouri River system in South Dakota. South Dakota Department of Game, Fish and Parks Fisheries Division Report 93-1, Pierre.