Growth Potential and Genetic Diversity of Yellow Perch in South Dakota

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GROWTH POTENTIAL AND GENETIC DIVERSITY OF
YELLOW PERCH IN SOUTH DAKOTA

BY

ALEX J. ROSBURG

A thesis submitted in partial fulfillment of the requirements for the
Master of Science
Major in Wildlife and Fisheries Science
Specialization in Fisheries Science
South Dakota State University
2017
GROWTH POTENTIAL AND GENETIC DIVERSITY OF
YELLOW PERCH IN SOUTH DAKOTA

ALEX J. ROSBURG

This thesis is approved as a creditable and independent investigation by a candidate for the Master of Science in Wildlife and Fisheries degree and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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ACKNOWLEDGEMENTS

This thesis would not have been possible without the vast support network I have been blessed with in my family and friends (colleagues included). I would like to thank my wife, Macy, for her unwavering support throughout my schooling, patience through the stressful times of writing and analysis, and her desire to better understand my research and the profession I love. I am grateful for the guidance, support, and mentorship of my advisors Dr. Brian Blackwell and Dr. Steven Chipps. Their knowledge, patience, and dedication to my success and quality of my research have been unmatched. I extend my thanks to Dr. Bill Gibbons for allowing me the privilege of using his private ponds for my common garden research. I would also like to extend my gratitude to Dr. Justin VanDeHey, Dr. Wesley Larson, and Keith Turnquist for their contributions to the genetic analysis and assisting me in my crash course in population genetics. Thanks to my technicians Chris Seylar and Isaiah Porteous for their hard work, reliability, and day to day good humor. Our hunting/fishing talk helped keep every day enjoyable while completing the task at hand. I feel privileged to call them both friends and wish them the best in their own professional careers. Additionally, I owe many thanks to Kate Tvedt, Terry Symens, Dawn Ballegooyen and numerous other department faculty that helped to make my life as easy as possible while completing my research. I would also like to express my appreciation for the assistance provided by South Dakota Game Fish and Parks staff, particularly Todd Kaufman for his help in collecting Yellow Perch and egg skeins and Dave Lucchesi for allowing me to use the OTC microscope and teaching me to identify OTC marks in age-0 Yellow Perch. Last, but far from least, I thank my fellow
graduate students. The wealth of knowledge available in the graduate office was by far
the most valuable resource in my research. I have made numerous life-long friends in
fellow graduate students and the times spent together have been some of the best of my
life, from broomball and volleyball to trivia nights and bonfires and who can forget the
numerous intellectually stimulating “brain trust” conversations in the grad office.

This research was funded through the Federal Aid in Sport Fish Restoration
program, Project F-15-R, Study 1533, administered through the South Dakota
Department of Game, Fish and Parks. Support was also provided by the U.S. Geological
Survey, South Dakota Cooperative Fish and Wildlife Research Unit, and South Dakota
State University. Any use of trade names is for descriptive purposes only and does not
imply endorsement by the U.S. Government.
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ABSTRACT

GROWTH POTENTIAL AND GENETIC DIVERSITY OF
YELLOW PERCH IN SOUTH DAKOTA

ALEX J. ROSBURG

2017

Yellow Perch Perca flavescens represent a valued sport fish throughout their range and are an important prey species for piscivorous fishes. In South Dakota, two distinct population types of Yellow Perch have been characterized that differ in growth, survival, and recruitment patterns. Fast growth populations exhibit high growth rates, high mortality, low population density, and inconsistent recruitment. In contrast, slow growth populations are characterized by reduced growth rates, low mortality, high population density, and relatively consistent recruitment. The role of genetics in contributing to these population characteristics is currently unknown. To address these questions, I used high-throughput restriction-site associated DNA (RAD) sequencing to scan the Yellow Perch genome for genetic markers associated with population type. A combination of laboratory and field common garden experiments was used to compare relative growth and survival of age-0 Yellow Perch from the two population types. Eighteen markers that significantly differed between population types were identified through RAD sequencing; however, low allele frequency differences indicated weak support for correlation to the growth differences between populations. The laboratory and common garden experiments showed no significant differences in specific growth rates between fast and slow growth Yellow Perch populations. The results of this study indicate that population attributes are influenced more by biotic and abiotic variables within individual lakes than heritable genetic differences between population types.
CHAPTER 1
INTRODUCTION

Yellow Perch *Perca flavescens* is an important sport fish and serves as an important prey species for other piscivorous sport fishes. Because of their importance the South Dakota Department of Game, Fish, and Parks (SDGFP) manages a large percentage of South Dakota lakes for Yellow Perch in conjunction with other species. Many South Dakota lakes are managed for Walleye *Sander vitreus* and Yellow Perch while management of shallow, marginal waters is often focused on Northern Pike *Esox lucius* and Yellow Perch. In 2011, SDGFP reported that 23 small natural lakes (≤ 60 hectares) and 108 large natural lakes, encompassing over 71,000 hectares of water in South Dakota were managed for Yellow Perch (SDGFP 2014d). A goal of Yellow Perch management in South Dakota is to provide perch of a size that anglers want to harvest. Thus it is pertinent to have an understanding of the variables that effect Yellow Perch growth and population characteristics.

Yellow Perch growth patterns have been found to be highly variable across their range (Alm 1946; Carlander 1950; Pycha and Smith 1955; Henderson 1985; Post and McQueen 1994). In South Dakota, Lott (1991) characterized two Yellow Perch population types (i.e., “high quality” [fast growth] and “low quality” [slow growth]) based on growth rates, condition, size structure and relative abundance. Fast growing populations exhibit high growth rates, (mean total length [TL] at age-3 ranged from 188 mm to 227 mm), high size structure (proportional stock density [PSD] >30), high condition and sporadic recruitment that generally results in low relative abundance. Slow
growth populations exhibit low growth rates (mean TL at age-3 ranged from 107 mm to 143 mm), low size structure (PSD<30), low condition and consistent recruitment that results in high relative abundance. Fast growth populations often exhibit high natural mortality rates (few fish beyond age-3) versus slow growth populations which exhibit longer lifespans with fish often > 9 years of age (Isermann 2007).

Growth variation among Yellow Perch populations has been linked to factors such as feeding behavior, habitat use, predation, and genetics (Purchase et al. 2005; Tremblay et al. 2008; Parker et al. 2009; Cao et al. 2012). Lott et al. (1996) examined feeding habits of Yellow Perch in several natural lakes and found significant differences in relative importance values of zooplankton in perch diets. Although the size structure of Yellow Perch and size structure of zooplankton populations were correlated in South Dakota lakes, perch diets were primarily aquatic insects or small fish (Lott et al. 1998). The authors hypothesized that the difference in zooplankton size structure was a result of low abundance of planktivorous fishes that lessened the size-selective pressure on the zooplankton population. Zooplankton can be an important food source for Yellow Perch, particularly in the early life stages before the transition to benthic prey or piscivory (Mills et al. 1989, Post and McQueen 1994). Noble (1975) suggested that growth of young demersal Yellow Perch was highly correlated to mean Daphnia spp. abundance. Periods of low Daphnia spp. abundance or size structure can often be associated with high predation by planktivorous fishes. This can result in reduced Yellow Perch growth through both interspecific and intraspecific competition.

Predation pressure may alter habitat use by Yellow Perch and cause changes in morphological traits (Tremblay et al. 2008). Yellow Perch subjected to high predation
pressure have been shown to develop deeper bodies with longer dorsal spines than Perch in environments with few or no predators (Tremblay et al. 2008; Eklov and Jonsson 2007; Magnhagen and Heibo 2004). Phenotypic plasticity has also been found to be influenced by habitat structure and feeding mode for Eurasian Perch *Perca fluviatilis* (Olsson and Eklov 2005). Long-term selective pressures on fish populations can lead to genetic specialization through the process of adaptive divergence which results in differing genetic stocks within fish of the same species (West-Eberhard 2003).

Past studies have shown the potential influence genetics can have on growth and survival of Yellow Perch and other fish species. Genetic selection is widely used in commercial aquaculture settings to improve desired traits such as growth rate and disease resistance (Gjerde 1986; Hulata 2001; Wang et al. 2009; Rosauer et al. 2011; Palti et al. 2015). Other studies examining wild populations of Yellow Perch have found evidence of genetic divergence and morphological differences in perch populations even at small spatial scales (Magnhagen and Heibo 2004; Olsson and Eklov 2005; Olsson and Ragnarsson 2006). Parker et al. (2009) used microsatellites to test for genetic divergence of young Yellow Perch exhibiting morphological differences in the nearshore (deep open-water) versus wetland and littoral habitats of Lake Michigan and Saginaw Bay, Lake Huron. Comparisons of morphology, population structure, and diet led Parker et al. (2009) to conclude that differing morphologies of fish from differing habitats and lake basins were result of a combination of phenotypic plasticity and genetic divergence. In South Dakota, a 2010 study found genetic structure across 29 Yellow Perch populations with the largest genetic divergence existing between populations occurring east and west
of the Missouri River (J. VanDeHey, University of Wisconsin-Stevens Point, unpublished data).

Understanding factors influencing growth and survival of Yellow Perch in South Dakota can aid fisheries managers in making scientifically sound management decisions. To better understand the contribution of genetics to growth and survival of Yellow Perch, I developed the following objectives; 1) determine if differences in genetic structure exist between Yellow Perch populations exhibiting differing growth and survival characteristics; 2) relate any differences in Yellow Perch genetic structure and marker detection to observed growth and mortality rates; 3) determine if differences in growth and survival exist between age-0 Yellow Perch from two distinct population types reared under controlled laboratory conditions; and 4) determine if growth and survival of age-0 Yellow Perch from two distinct population types differed when reared under similar environmental conditions (i.e., common garden).
LITERATURE CITED


genotype by environment effects for cross-bred Yellow Perch families reared in communal ponds using DNA parentage analyses. Aquaculture Research 40:1363-1373.
CHAPTER 2
ASSESSING GENETIC CONTRIBUTION TO DIFFERING YELLOW PERCH GROWTH AND SURVIVAL CHARACTERISTICS IN SOUTH DAKOTA GLACIAL LAKES

INTRODUCTION

Yellow Perch *Perca flavescens* populations exhibit variable growth and survival throughout their range. Slow growing populations exhibiting high density have been commonly referred to as “stunted” and have been a focus of many studies looking to better understand the cause and possible remedies to improve growth. In Oneida Lake, New York, fast Yellow Perch growth was positively linked to *Daphnia* spp. biomass at temperatures > 13°C (Millis and Sherman 1989). Alternatively, measures of lake productivity explained about 60% of the variance in total length and wet weight of age-0 Yellow Perch collected from 10 central Alberta lakes (Abbey and Mackay 1991). Additionally, slow growing Yellow Perch populations in Canada showed higher activity rates compared to those of a faster growing population, supporting the hypothesis that activity rate is positively linked to low prey abundance and (or) prey quality (Aubin-Horth et al. 1999). Outcomes of these studies demonstrate that varying factors can affect Yellow Perch growth.

In South Dakota, Lott (1991) classified two Yellow Perch population types based on differing growth and survival characteristics; one type was classified as “high quality” (fast growing) and the other “low quality” (slow growing) populations (Figure 2-1). Fast growing populations exhibited large size structure (proportional stock density [PSD] >30) and fast growth (mean total length at age 3 [TL3] = 188 to 227 mm), sporadic
recruitment, and low abundance, while slow growth populations were characterized by reduced size structure (proportional stock density [PSD <30]) and slow growth (TL3 = 107 to 143 mm). Slow growth populations also generally have consistent high recruitment and high abundance.

Since Lott’s (1991) classification of South Dakota Yellow Perch populations, several studies have been conducted to determine factors responsible for these differences. A high percentage of the research completed has focused on feeding habits and food availability. Fisher and Willis (1997) described the early life history and feeding habits of larval Yellow Perch from two glacial lakes exhibiting the differing characteristics identified by Lott (1991). They hypothesized that growth differences could be explained by dietary differences due to prey availability and interspecific competition. Competition and zooplankton size structure models indicated that zooplankton was a limiting resource when both Yellow Perch and sunfish species (Lepomis spp.) are feeding primarily on zooplankton (Schoenebeck 2009; Kaemingk et al. 2012). Zooplankton size structure and abundance were lower in a South Dakota natural lake having a slow growing Yellow Perch population compared to a fast growing population (Schoenebeck and Brown 2010).

Differing growth and survival characteristics can also occur due to adaptive divergence, where natural selection leads to genetic change within a population (West-Eberhard 2003). Using the concept of adaptive divergence, selection is widely used in the aquaculture industry to develop strains of fast growing and disease-resistant fish to maximize production (Gjerde 1986; Hulata 2001; Wang et al. 2009; Rosauer et al. 2011). In wild populations, phenotypic plasticity and adaptive differentiation allow fish to adapt
to changing conditions and stressors such as predators, competitors, and habitat change (Magnhagen and Heibo 2004; Olsson and Eklov 2005). Long-term selection pressures can lead to genetic specialization and development of differing genetic stocks even at small spatial scales (Olsson and Ragnarsson 2006).

Past studies have relied on microsatellites to explore the relationship between growth and genetics within species. For example, Parker et al. (2009) used microsatellites to test for morphological and genetic divergence of age-1 Yellow Perch in deep open-water versus wetland and littoral habitats of Lake Michigan and Saginaw Bay, Lake Huron. Comparisons of morphology, population structure, and diet have led researchers to conclude that differing morphologies of fish from differing habitats and lake basins were the result of a combination of phenotypic plasticity and genetic divergence (Parker et al. 2009). Cao et al. (2012) used microsatellites in an aquaculture environment to compare 1-stage (no culling/random selection) and 2-stage (length-based culling [top 50% retained]) selection methods by assessing body weight of F1 Yellow Perch using microsatellite parentage assignment. The 2-stage selection methods resulted in faster growing fish exhibiting higher body weights than 1-stage selection methods. The authors concluded that 2-stage selection was more desirable and effective for Yellow Perch breeding compared with 1-stage selection in terms of improving selection efficiency and reducing costs.

In South Dakota, Yellow Perch populations exhibited genetic structure among 29 surveyed lakes, with the most pronounced genetic differentiation occurring between populations located east and west of the Missouri River (J. VanDeHey, University of Wisconsin-Stevens Point, unpublished data). While informative, this study used neutral
genetic markers (microsatellites) that reflect demographic processes such as population connectivity and genetic drift rather than adaptive differentiation (Wenne et al. 2007). Variation screened at neutral markers likely do not directly affect fitness of the individuals and therefore cannot be used to make direct conclusions about adaptive genetic differentiation (Holderegger et al. 2006). Recently, a method of genetic analysis known as restriction site associated DNA (RAD) sequencing has been developed and can be used to genotype thousands of single nucleotide polymorphisms (SNPs) across the genome; this large number of markers facilitates discovery of markers found in adaptively important genes or linked to these genes. In genome wide association studies, RAD sequencing is commonly used to identify loci that are linked to various traits or behaviors other than growth. For example, RAD sequencing was used to discover loci associated with migration behaviors in Steelhead *Oncorhynchus mykiss* (Hecht et al. 2013) and to find sex determining loci in Atlantic Halibut *Hippoglossus hippoglossus* (Palaiokostas et al. 2013).

Common garden experiments have also been used to infer whether differences in phenotypic traits are due to genetically diverged populations or phenotypic plasticity (West-Eberhard 2003). Using age-0 Yellow Perch, Heath and Roff (1987) compared growth in length between stunted and normal growing populations reared under similar environmental conditions. Although genetic attributes were not examined, they found that Yellow Perch from both populations grew at the same rate, and concluded that differences in growth in the natural populations were likely due to environmental variation. In contrast, using a common garden experiment to assess growth of four Yellow Perch populations, Rosauer et al. (2011) found that growth differed among three
populations reared in a common garden environment suggesting that growth differences were associated with different genetic stocks.

In South Dakota, the potential influences of food availability and competition on growth and survival in Yellow Perch have been well documented (Lott et al. 1996; Fisher and Willis 1997; Graeb et al. 2004). Less attention, however, has been given to examining the contribution of genetics to slow growth of populations within the state. With limited knowledge of Yellow Perch genetics in South Dakota and mixed findings in existing literature regarding the genetic influence on growth, it is uncertain whether differing population characteristics are caused by heritable genetic differences or plasticity due to environmental variation. To address this question, I developed the following objectives: 1) determine if differences in genetic structure exist between Yellow Perch populations exhibiting differing growth and survival characteristics; 2) relate any differences in Yellow Perch genetic structure and marker detection to observed growth and mortality rates; 3) determine if differences exist in growth and survival between age-0 Yellow Perch from two distinct population types reared under controlled laboratory conditions; and 4) determine if growth and survival of age-0 Yellow Perch from two distinct population types differed when reared under similar environmental conditions (i.e., common garden). If the growth and survival differences observed in fast and slow growth Yellow Perch populations are heritable traits due to adaptive differentiation I would expect to identify significant differences in genetic markers (i.e., SNPs) between population types as well as see the same growth and survival differences in perch from the two population types when reared in a common environment.
METHODS

Genomic sequencing and marker correlations to population type

Restriction site associated DNA sequencing was used to determine if genetic differences were present in Yellow Perch from fast and slow growth populations in South Dakota. Pelvic fin clips from Yellow Perch were collected from Cattail-Kettle and Waubay lakes (fast growth populations), and Enemy Swim and South Buffalo lakes (slow growth populations) and used as the source of DNA (Table 2-1, Figure 2-2). Restriction site associated DNA libraries for 48 individuals per population (n = 192) were prepared by the Molecular Conservation Genetics Laboratory (University of Wisconsin-Stevens Point) and sequenced at the Genomics Core Facility (University of Oregon). Libraries were prepared with the restriction enzyme SbfI following the methods of Ali et al. (2016) and sequenced on an Illumina HiSeq4000 (single-end 150 base pair length).

Initial data processing and single-nucleotide polymorphism discovery were conducted using the program STACKS (version 1.20; Catchen et al. 2011; Catchen et al. 2013). Single-nucleotide polymorphisms were excluded from the dataset if they were genotyped in less than 70% of individuals, had a minor allele frequency less than 0.05 in all sample populations, or were found to deviate significantly from Hardy-Weinberg expectations in more than half of the study populations (alpha = 0.05). Tests for deviations from Hardy-Weinberg expectations were conducted in GENEPOP version 4 (Rousset 2008). If a RAD tag contained more than one SNP, the first SNP in the tag was retained to reduce linkage disequilibrium. As a final filtration step, individuals that were genotyped in less than 70% of the SNPs that passed the filters discussed above were removed from further analysis. Summary statistics including differentiation among
populations \((F_{ST}; \text{Weir and Cockerham 1984})\) and inbreeding coefficients \((F_{IS})\) were calculated for each locus in GENEPOP version 4 (Rousset 2008).

An individual-based principal component analysis (PCA) was completed in the R package adegenet (Jombart 2008) using all loci to investigate patterns of population structure in the dataset. Additionally, a principal coordinate analysis based on pairwise \(F_{ST}\) values was used to visualize genetic distances \((F_{ST})\) between the four study populations. Finally, I conducted an \(F_{CT}\) (differentiation among groups) outlier test in Arlequin 3.5 (Excoffier and Lischer 2010) with populations grouped by trajectory to detect markers that displayed putative adaptive divergence between population types. Default values for all parameters and a hierarchical island model (Excoffier and Lischer 2010) were used for this analysis. Genetic data processing and analysis were conducted at the University of Wisconsin-Stevens Point in collaboration with the United States Geological Survey (USGS) Wisconsin Cooperative Fishery Research Unit.

**Laboratory growth experiments**

Age-0 Yellow Perch were collected from Reetz Lake and Enemy Swim Lake in the fall of 2014 using daytime boat electrofishing. Fish were transported to the USGS South Dakota Cooperative Fisheries Research Station at South Dakota State University in Brookings, South Dakota and placed in circular tanks (378 L) connected to a recirculating biofiltration system to acclimate to the laboratory environment.

In 2015, naturally fertilized egg skeins were collected from Reetz Lake and Enemy Swim Lake. The eggs were hatched and reared to small fingerlings (25-35mm TL) at Blue Dog State Fish Hatchery in Waubay, South Dakota. Fingerlings were
transported to the USGS South Dakota Cooperative Fisheries Research Station at South Dakota State University in Brookings, South Dakota and placed in a recirculating aquaculture system to acclimate prior to experimentation.

Laboratory growth experiments were conducted in 2014 and 2015. In 2014, a recirculating aquaculture system comprised of 24 (100 L) round tanks was used. Each tank was equipped with a center overflow to a vertical sediment settling column before returning water to a common 378 L sump. Water returned to the sump was filtered through bio-media before passing to a second compartment containing the heating and chilling units and water pump intake. Water from the sump was pumped through a large UV sterilizer and returned to the tanks. System temperature was held at 25°C ± 1°C, the optimal growing temperature for South Dakota Yellow Perch (Brown and Smith et al. 2004). Photoperiod was maintained at a 12 h light and 12 h dark cycle. Fish were allowed to acclimate to these conditions for 5 d prior to beginning the experiment.

Yellow Perch from fast and slow growth populations were placed into one of two different feeding ration treatments; satiation and maintenance (3% body weight per day). Tanks were randomly assigned for each population type-feeding ration combination to minimize bias due to location of tanks within the aquaculture system. Each tank was stocked with five age-0 Yellow Perch fingerlings of similar size (10 mm length classes) per tank (n=30 fish/population/ration). All fish were fed a ration of thawed Chironomidae larvae once daily. Fish were measured for TL (mm) and weight (g) every 14 days through 84 days. To eliminate any influence of recent feeding, fish were fasted for 24 hour before measuring TL and weight at each sampling interval (Brown and Smith 2004).
The experiment was repeated in 2015 using a vertical rack recirculating aquaculture system consisting of 30 tanks each with a volume of 38 L. Tanks were stocked with three age-0 Yellow Perch fingerlings per tank and were fed only a satiation ration \((n=45 \text{ fish/population})\) for a duration of 84 days. System temperature, photoperiod, and feed type were kept consistent with the previous year’s experiment and TL and weight were measured approximately every 14 days with a 24-hour fasting period prior to measurements.

Length-specific growth rates \((G)\) for each sampling interval (14 days) were calculated as,

\[
G = \frac{\ln(L_t) - \ln(L_i)}{t}
\]

where \(L_t\) is the mean total length (TL, mm) at time \(t\) (day) and \(L_i\) is the mean initial length at the start of the feeding trial. Weight-specific growth rate was calculated using the same equation but substituting mean weight \((W_t \text{ and } W_i; \text{ g})\) for \(L_t\) and \(L_i\), respectively. Specific growth rates from the two population types were compared across time using analysis of covariance (ANCOVA) with population as a main effect and time as a covariate. All animals used in this study were reared according to animal use and care guidelines established by South Dakota State University (Animal Welfare Assurance no. A3958-01).

Field growth experiments

In the spring of 2015 and 2016 (late April – May), naturally fertilized Yellow Perch skeins were collected using dip nets from Reetz Lake and Enemy Swim Lake. Fertilized skeins were transported to Blue Dog State Fish Hatchery in Waubay, South Dakota where they were placed in incubation racks (i.e., heath trays) and allowed to
develop to the eyed-egg stage. Eyed eggs from the two populations were stocked into separate earthen hatchery ponds and reared to small fingerlings (25 to 35 mm TL). At the end of June, small fingerlings were harvested from the ponds and transported to the USGS South Dakota Cooperative Fisheries Research Station at South Dakota State University where they were either put into a recirculating aquaculture system to begin acclimating to laboratory conditions or into aerated coolers for same day stocking into experiment ponds. A subsample of 100 fish per population was measured for TL (mm) and weight (g) to determine an initial mean TL and weight for each population.

Common garden experiments were conducted in three earthen bottom, drainable ponds during 2015 and 2016. The ponds were privately-owned, man-made impoundments consisting of gently sloping sides with a steep-faced dam at one end. Surface area of the ponds ranged from 0.13 to 0.30 ha. Maximum depths of the ponds were between 2.4 and 3.0 m. All ponds were mud bottomed and moderately covered with submerged vegetation. Other fish species present in the ponds during the study consisted primarily of Fathead Minnows *Pimephales promelas* and Brook Sticklebacks *Culaea inconstans*; Johnny Darters *Etheostoma nigrum* and Iowa Darters *Etheostoma exile* were also present in low numbers.

During 2015, ponds were stocked with age-0 Yellow Perch fingerlings from Reetz Lake (fast growth) and Enemy Swim Lake (slow growth) at equal densities for a combined rate of 320 small fingerlings per ha. Due to the low number of Yellow Perch harvested from the ponds at the conclusion of the experiment in 2015, the stocking rate was increased to 640 small fingerlings per ha in 2016, to ensure a sufficient final sample. Prior to stocking fingerlings into the first pond, one population was randomly selected to
be chemically marked with oxytetracycline hydrochloride (OTC); fish were marked in a 757 L tanks using 600 mg OTC/L. Sodium phosphate (dibasic; Na2HPO4) was added to buffer the OTC marking solution to a pH of 7.3. Water in the tanks was supplemented with pure oxygen and a silicon-based surfactant was used to reduce foaming. Yellow Perch fingerlings were immersed in the buffered OTC solution for 6 hours prior to stocking (Brown et al. 2002). The marked population was then alternated among subsequently stocked ponds to prevent any confounding effects of marking stress on Yellow Perch growth. Transportation, marking, and stocking of Yellow Perch fingerlings from a single population occurred in the same day to minimize handing stress. Populations were stocked on consecutive days during both years of the experiment.

In 2015, bi-weekly sampling began 14 days post stocking (dps), but due to low catch rates from two of the three ponds the day 14 sample data were excluded from statistical analyses. Sampling commenced at 30 dps to allow fish to reach a size that was more efficiently sampled. After 30 days, the ponds were sampled approximately every 14 days (weather dependent) using two to four cloverleaf traps placed around the perimeter of the ponds in water depths of 1.0 to 1.5 m. Traps were set in the afternoon (after 1500 h), allowed to fish overnight, and then checked between 0900 and 1100 hours the next morning to minimize stress and mortality of captured Yellow Perch. Up to 20 fish per sampling period were collected and measured from each pond to assess growth rates. Any additional Yellow Perch and bycatch captured were immediately released. At the end of the experiment (84-112 days post-stocking) the ponds were drained and fish were recovered from the catch basin using dip nets and a 6-mm knotless mesh seine. A 6-mm mesh bag seine was staked in front of the outlet of the drain pipe to catch any fish that
were flushed through the dam during draining. Collected Yellow Perch were stored in a cooler filled with pond water and transported to the laboratory where they were euthanized using a lethal dose of tricaine methanesulfonate (MS 222) then frozen for later processing.

Total length (mm) and weight (g) were recorded and sagittal otoliths were extracted for OTC mark detection for all bi-weekly sampled fish, all final harvest fish in 2015, and a subsample of 50 fish per pond in 2016. Otoliths were allowed to dry overnight before mounting concave side down to glass microscope slides using cyanoacrylate. Each slide was labeled with a unique fish identification number, pond number, and date collected. Otoliths were stored in a cool dark environment and examined for OTC marks within 24 - 48 hours of extraction to minimize mark deterioration. Otoliths were wet-sanded to expose the OTC marks with 1000-grit sandpaper (Brown et al. 2002). A Nikon Eclipse E400 compound microscope powered by a high pressure mercury lamp was used to examine otoliths for OTC marks.

Specific growth rates from the two population types were tested for normality and no transformations were used prior to comparison across time using ANCOVA. The interaction term “population X days post stocking (dps)” was included in the model to test for differences in the rate of the growth across time between the two populations. Percent survival was estimated by determining proportion of each population identified in the final sample and extrapolating those proportions to the total number of fish from the final harvest. Estimated final harvest numbers were then divided by the known stocking data to obtain a percent survival estimate for each pond. A paired t-test was used to assess differences in mean percent survival between population types.
RESULTS

Genomic sequencing and marker correlations to population type

A total of 1,717 SNPs and 146 individuals were retained for genetic analysis. Genetic structure was present among the four populations with Enemy Swim Lake showing divergence from the other three lakes (Figure 2-3). Principal coordinate analysis (PCoA) and pairwise comparison of molecular variance among populations within groups using a fixation index ($F_{ST}$) confirmed that Enemy Swim was highly differentiated from the other three study lakes. Low differentiation was observed in the Waubay, Cattail-Kettle, and South Buffalo lakes suggesting genetic similarity (Table 2-2; Figure 2-4). Low pairwise $F_{ST}$ values between Cattail-Kettle, South Buffalo, and Waubay lakes also indicated that structure was not related to population type or geography (Table 2-2). The $F_{CT}$ outlier analysis identified that 18 of the 1,717 markers differed ($P < 0.01$) between population types (Figure 2-5). However, only one of these markers, found in the NLRC3 gene coding for immune response, appeared to be highly differentiated, displaying allele frequency differences $>0.3$ among population types (Figure 2-6). The remaining 17 markers were found close to the 99% bound, indicating that the statistical support for adaptive divergence at these markers was relatively weak.

Laboratory growth experiments

In 2014, three mortalities occurred in the satiation ration treatment ($n = 2$ Enemy Swim fish and 1 Reetz fish) and two occurred in the maintenance ration treatment ($n = 2$ Enemy Swim fish), however, no tank experienced more than one mortality and the causes of the mortalities were known to have occurred from handling stress and jumping loss (fish jumped out of the tank); no unexplained mortalities occurred during the study.
Because of relatively large variation in initial TL between Reetz Lake and Enemy Swim Lake perch (difference ~39 mm), I omitted the five largest fish from Reetz Lake and five smallest fish from Enemy Swim Lake prior to data analysis. Omitting initially large and small fish from the analysis resulted in a normal distribution of sizes and helped homogenize the variance of initial mean size of Yellow Perch in each population.

For maintenance ration fish, specific growth rates ranged from 0.0005 to 0.0023 mm/mm/d in 2014 and mean growth rate was similar for Reetz Lake (0.0004 mm/mm/d) and Enemy Swim Lake fish (0.0005 mm/mm/d; F_{5,50} = 1.276, \( P = 0.28 \)). Specific growth rate based on weights ranged from -0.003 to 0.004 g/g/d and mean values were similar for Enemy Swim (0.0002 g/g/d) and Reetz Lake fish (0.0006 g/g/d; F_{5,50}=0.771, \( P = 0.57 \)). Moreover, growth in both length and weight varied similarly with time for both populations (population x time interaction; \( P > 0.05 \)).

For satiation ration fish, specific growth rate ranged from 0.0020 to 0.0080 mm/mm/d in 2014 and mean growth rate was similar between for Reetz Lake (0.0050 mm/mm/d) and Enemy Swim Lake fish (0.0048 mm/mm/d; F_{5,40} = 1.191, \( P = 0.331 \)). Specific growth rate based on weights ranged from 0.0076 to 0.0281 g/g/d and mean values were similar for Reetz Lake (0.018 g/g/d) and Enemy Swim Lake fish (0.018 g/g/d; F_{5,40} = 0.363, \( P = 0.871 \)). Again, growth in both length and weight varied similarly with time for both populations (population x time interaction; \( P > 0.05 \)).

In 2015, initial sample sizes for the laboratory tests were 45 fish per population. No mortalities occurred over the course of the trial. The mean specific growth rates based on total lengths and weights were 0.007 mm/mm/d and 0.020 g/g/d for Enemy Swim Lake and 0.006 mm/mm/d and 0.018 g/g/d for age-0 Perch from Reetz Lake. The 2015
growth rates did not differ between the two populations across time for mean specific growth rates based on total length ($F_{1,148} = 0.915$, $P = 0.34$) and weight ($F_{1,148} = 0.016$, $P = 0.89$) respectively (Figure 2-9).

**Field growth experiments**

The common garden experiment was conducted for 119 (two ponds) and 131 days (one pond) in 2015. A total of 625 Yellow Perch were examined for OTC marks with 336 fish coming from the final harvest sample. Mean specific growth rates for length and weight in 2015 were 0.010 mm/mm/d and 0.030 g/g/d for Enemy Swim Lake fish and 0.010 mm/mm/d and 0.028 g/g/d for Reetz Lake fish. No significant differences in growth rate for either length ($F_{1,24} = 0.008$, $P = 0.931$) or weight ($F_{1,24} = 0.003$, $P = 0.954$) were identified between populations (Figure 2-10).

In 2016, the common garden experiment was conducted for 84 (one pond) to 100 days (two ponds). A total of 324 Yellow Perch were examined for OTC marks with 150 fish obtained from final harvest. Mean specific growth rates for length and weight in 2016 were 0.010 mm/mm/d and 0.031 g/g/d for Enemy Swim Lake fish and 0.011 mm/mm/d and 0.035 g/g/d for Reetz Lake fish. Similar to 2015, no significant differences were noted in growth rates between populations for either length ($F_{1,24} = 0.046$, $P = 0.832$) or weight ($F_{1,24} = 0.059$, $P = 0.811$; Figure 2-11).

Mean percent survival was not significantly different between fast and slow growth populations across the two years in the pond experiments ($t = 1.57$, $df = 5$, $P = 0.177$). However, it was observed that Enemy Swim Lake fish exhibited survival
estimates greater than 90% in pond 3 during both years of the study which was much higher than the estimates from the other ponds for both years (Figure 2-12).

**DISCUSSION**

Genetic differences have been identified between populations of Yellow Perch even at small spatial scales (Grzybowski et al. 2010; Sepulveda-Villet and Stepien 2011). Studies of wild and captive fish have also found that genetic differences capable of influencing growth and survival can occur through adaptive differentiation and artificial selection processes (Gjerde 1986; Hulata 2001; Magnhagen and Heibo 2004; Olsson and Eklov 2005; Wang et al. 2009; Rosauer et al. 2011).

The results of my genetic analysis align with those from a similar genome wide association study. Gutierrez et al. (2015) found low levels of association with growth in one genetic marker out of 6,500 sequenced SNPs from 480 Atlantic Salmon *Salmo salar*. Though few SNPs were found to be associated with growth and the magnitude of the differences were relatively weak, Gutierrez et al. (2015) identified numerous markers associated with early sexual maturation and late sexual maturation, both of which can affect maximum body size and fecundity, and are of importance in aquaculture. Similar to Atlantic Salmon, sequenced SNPs from the fast and slow growth Yellow Perch populations yielded few markers associated with growth. All associations exhibited low allele frequency differences between population types, leading to the conclusion that genetics likely play a minor role contributing to observed growth and survival characteristics in South Dakota.

My combined use of laboratory and pond-based common garden experiments found that fast growing and slow growing populations exhibited no significant
differences in growth rates when reared under similar conditions. Similarly, Alm (1946) concluded that environmental factors outweighed any genetic contributions to stunting of Eurasian Perch *Perca fluviatilis* populations when populations were subjected to similar conditions in pond growth experiments. Additionally, Heath and Roff (1987) found no differences in Yellow Perch or Pumpkinseed *Lepomis gibbosus* growth between fish from stunted populations and those from non-stunted populations when subjected to similar controlled laboratory conditions.

One potentially confounding factor related to my study was that perhaps the duration of the laboratory or common garden experiments were not long enough for genetic differences to be expressed. For example, when testing the suitability of three stocks of Yellow Perch for commercial aquaculture, Rosauer et al. (2011) found a divergence in mean weights of one of three Yellow Perch populations starting around 150 days post-hatch. My study only had one growth trial run in excess of 150 days post hatch (2016; ~160 dph) suggesting that if these studies had continued longer growth differences may have emerged.

The RAD sequencing and results from laboratory and common garden experiments, paired with previous research, have lead me to conclude that observed differences in growth and survival among South Dakota Yellow Perch populations are likely phenotypic variations driven by lake specific biotic and abiotic variables. Other researchers have also shown that lake specific environmental variables influence growth rates in South Dakota Yellow Perch populations. Lott et al. (1996) found a significant negative relationship between mean relative importance (RI) values of zooplankton and Yellow Perch growth rates, and a positive correlation between perch growth rates and
mean RI of macroinvertebrates. Fishes were not a major component of Yellow Perch diets where fast growth rates and perch ≥300 mm TL were present (Lott et al. 1996). Fast growth of Yellow Perch was attributed to a diet of amphipods and corixids; whereas, corixids and amphipods were rarely consumed in slow growth populations. Zooplankton was thought to be the limiting factor in South Dakota glacial lakes when both Yellow Perch and sunfish (*Lepomis* spp.) feed primarily on zooplankton (Schoenebeck and Brown 2010). Schoenebeck and Brown (2010) hypothesized that differences in zooplankton size structure and abundance may explain observed differences in Yellow Perch growth rates between fast and slow growth populations. However, an assessment of 72 Yellow Perch populations in Ontario, Canada, determined that much of the variation in Yellow Perch growth could not be accounted for using individual environmental factors, despite the inclusion of variables identified in previous studies as linking environmental variation to life history (Purchase et al. 2005). Lake surface area was found to be the most influential environmental variable in their study, explaining approximately 20% of the variation in fork length at age-2. These researchers hypothesized that the relationship of lake surface area with Yellow Perch growth was likely due to higher species richness found in larger systems and greater diversity of prey sizes available (Purchase et al. 2005).

A new hypothesis that could explain the differing Yellow Perch population types in South Dakota involves lake productivity. Lake productivity is a well-known correlate to zooplankton and invertebrate biomass, and growth and survival rates in fish populations (Abbey and Mackay 1991; Rieman and Myers 1992; Mills and Schiavone 1982), and may explain the differences observed in South Dakota Yellow Perch
populations. I observed that lake productivity, as indexed by trophic state index (TSI, Carlson 1977) for eastern South Dakota lakes was found to decrease with increasing latitude (Figure 2-13). The relationship between TSI and latitude may be linked to higher percentage of row crop agriculture and larger watersheds in the southern Prairie Coteau resulting in a productivity gradient that may favor Yellow Perch growth in lakes farther south. Yellow Perch size at age-3 data (B. Blackwell, unpublished data) also showed a positive relationship with increasing productivity ($r^2 = 0.86; \ P < 0.001$; Figure 2-14). Together, these relationships support the hypothesis that differences in Yellow Perch growth rates are driven by an increasing productivity gradient from north to south due to differences in agricultural practices between the northern and southern regions of the Prairie Coteau (Figure 2-15).
LITERATURE CITED


Table 2-1. Lake size and population characteristics (proportional stock density [PSD], proportional stock density of preferred size fish [PSD-P], and mean total length at age-3 [TL3]) of five South Dakota Yellow Perch populations used for genomic sequencing.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Population type</th>
<th>Surface area (ha)</th>
<th>Size structure</th>
<th>Mean TL3 (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cattail-Kettle</td>
<td>fast growth</td>
<td>1,221</td>
<td>PSD = 5</td>
<td>male = 191</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>PSD-P = 0</td>
<td>female = 285</td>
</tr>
<tr>
<td>Enemy Swim</td>
<td>slow growth</td>
<td>870</td>
<td>PSD = 10</td>
<td>male = 124</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>PSD-P = 0</td>
<td>female = 166</td>
</tr>
<tr>
<td>Reetz</td>
<td>fast growth</td>
<td>350</td>
<td>PSD = 84</td>
<td>male = 180</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>PSD-P = 48</td>
<td>female = 240</td>
</tr>
<tr>
<td>South Buffalo</td>
<td>slow growth</td>
<td>724</td>
<td>PSD = 10</td>
<td>male = 121</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>PSD-P = 0</td>
<td>female = 154</td>
</tr>
<tr>
<td>Waubay</td>
<td>fast growth</td>
<td>6,289</td>
<td>PSD = 87</td>
<td>male = 233</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>PSD-P = 41</td>
<td>female = 249</td>
</tr>
</tbody>
</table>
Table 2-2. Pairwise differentiation among populations within groups using a fixation index (F_{ST}) of 1,717 markers from 146 individuals sequenced from fin clip tissue samples from fast growth (Cattail-Kettle, Waubay) and slow growth (South Buffalo, Enemy Swim) South Dakota Yellow Perch populations in 2010. An asterisk indicates statistically significant comparisons.

<table>
<thead>
<tr>
<th>Population</th>
<th>Cattail</th>
<th>Waubay</th>
<th>Buffalo</th>
</tr>
</thead>
<tbody>
<tr>
<td>Waubay</td>
<td>0.008</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Buffalo</td>
<td>0.007</td>
<td>0.011</td>
<td></td>
</tr>
<tr>
<td>Enemy</td>
<td>0.047*</td>
<td>0.038*</td>
<td>0.031*</td>
</tr>
</tbody>
</table>
Figure 2-1. Frequency of occurrence of length classes (10 mm) for age-3 Yellow Perch from fast growth (black bars) and slow growth (gray bars) populations in South Dakota.
Figure 2-2. Map depicting locations of fast growth (Cattail Kettle Lake and Waubay Lake) and slow growth (South Buffalo Lake and Enemy Swim Lake) South Dakota Yellow Perch populations used for restriction site associated DNA (RAD) sequencing.
Figure 2-3. Principal component analysis (PCA) of 1,717 markers from 146 individuals sequenced from fin clip tissue samples from fast growth (Cattail-Kettle, Waubay) and slow growth (South Buffalo, Enemy Swim) South Dakota Yellow Perch populations collected in 2010.
Figure 2-4. Principal coordinate analysis (PCoA) showing presence of genetic structure between study populations of Yellow Perch in South Dakota. Genetic differences were not correlated with population type (fast growth, slow growth) or geographic location. Black shapes indicate fast growth populations while gray shapes designate slow growth populations.
Figure 2-5. Molecular variance among groups ($F_{CT}$) as a function of observed heterozygosity/1-differentiation of 1,717 markers (SNPs) sequenced from 146 Yellow Perch from four South Dakota lakes grouped by population type (fast growth, slow growth). Outlier markers ($P < 0.01$) are indicated by gray shaded circles, dashed line represents upper 99% confidence level.
Figure 2-6. Allele frequencies of top four differentiated markers (59858_43, 37295_24, 57515_20, 112877_124) identified by molecular variance among groups ($F_{CT}$) outlier analysis for Cattail Kettle (fast growth), Waubay (fast growth), South Buffalo (slow growth), and Enemy Swim (slow growth) lakes in South Dakota sequenced from Yellow Perch fin clip tissue samples collected in 2010.
Figure 2-7. Specific growth rates based on lengths (top panel) and weights (bottom panel) of laboratory reared age-0 Yellow Perch fed a maintenance ration of Chironomids over 84 day duration during 2014. Yellow Perch were collected from Reetz Lake (fast growth; black series) and Enemy Swim Lake (slow growth; gray series), South Dakota. Error bars represent 1 standard deviation calculated for each sampling period. Dotted lines represent overall mean specific growth rate for each population.
Figure 2-8. Specific growth rates based on lengths (top panel) and weights (bottom panel) of laboratory reared age-0 Yellow Perch fed a satiation ration of Chironomids over 84 day duration during 2014. Yellow Perch were collected from Reetz Lake (fast growth; black series) and Enemy Swim Lake (slow growth; gray series), South Dakota. Error bars represent 1 standard deviation calculated for each sampling period. Dotted lines represent overall mean specific growth rate for each population.
Figure 2-9. Specific growth rates based on lengths (top panel) and weights (bottom panel) of laboratory reared age-0 Yellow Perch fed a satiation ration of Chironomids over 84 day duration during 2015. Yellow Perch were collected from Reetz Lake (fast growth; black series) and Enemy Swim Lake (slow growth; gray series), South Dakota. Error bars represent 1 standard deviation calculated for each sampling period. Dotted lines represent overall mean specific growth rate for each population.
Figure 2-10. Specific growth rates based on lengths (top panel) and weights (bottom panel) of pond reared age-0 Yellow Perch from Reetz Lake (fast growth, black series) and Enemy Swim Lake (slow growth, gray series) in South Dakota over 119 to 131 day duration of 2015 common garden growth experiment. Error bars represent 1 standard deviation calculated for each sampling period. Sampling periods lacking error bars indicate a single pond sample. Dotted lines represent overall mean specific growth rate for each population.
Figure 2-11. Specific growth rates based on lengths (top panel) and weights (bottom panel) of pond reared age-0 Yellow Perch from Reetz Lake (fast growth, black series) and Enemy Swim Lake (slow growth, gray series) in South Dakota over 84 to 100 day duration of 2016 common garden growth experiment. Error bars represent 1 standard deviation calculated for each sampling period. Dotted lines represent overall mean specific growth rate for each population.
Figure 2-12. Estimated percent survival of age-0 Yellow Perch from Reetz Lake (fast growth, black series) and Enemy Swim Lake (slow growth, gray series) populations in South Dakota from common garden experiments completed during 2015 and 2016.
Figure 2-13. Trophic state index (TSI-P) as a function of increasing latitude of five fast growth (black series) and four slow growth (gray series) Yellow Perch lakes in eastern South Dakota.
Figure 2-14. Natural logarithm of length of age-3 (TL3) Yellow Perch as a function of lake productivity (TSI-P) from four slow growth (gray series) and five fast growth (black series) lakes in eastern South Dakota (TSI values from Stukel 2003).
Figure 2-15. Mean total length (mm) of age-3 (TL3) Yellow Perch from thirteen fast growth and four slow growth lakes in eastern South Dakota shown in order of increasing latitude.
CHAPTER 3
SUMMARY AND RECOMMENDATIONS

Growth and survival patterns of Yellow Perch in South Dakota continue to be a topic of interest for fisheries researchers. A review of the literature provides recurring support for the hypothesis that growth differences are most likely the result of differing prey availability and diversity of suitable prey for the various stages of Yellow Perch growth. This study has provided support that the growth and survival differences are not likely influenced by genetic differentiation, but rather are shaped by environmental conditions such as lake productivity and prey availability.

During my thesis research I observed that lake productivity (TSI-P) values for eastern South Dakota lakes decreased with increasing latitude. It is possible that this relationship between TSI-P and latitude can be explained by differences in abundance of row crop agriculture from north to south on the Prairie Coteau. Yellow Perch growth rates (mean TL at age-3) were also negatively related to latitude in South Dakota, suggesting that lower productivity in lakes farther north on the Prairie Coteau compared to lakes in the southern coteau could be affecting prey availability and quality and, in-turn, growth and survival of Yellow Perch. This can be accentuated by increased abundance of other planktivorous fish in some lakes leading to competition for higher quality prey and reductions in growth of Yellow Perch.

My recommendations for the management and improvement of South Dakota Yellow Perch fisheries includes to focus future research on lake-specific environmental variables shown to influence growth and survival (i.e., lake productivity, predator abundance, and fish community complexity). To improve growth of Yellow perch in
slow growth lakes, I recommend managing low productivity systems for simplistic fish communities with few potential competitors for desirable prey resources and maintaining high abundances of potential predators to reduce the potential for inter- and intra-specific competition. Research on the influence of the hypothesized productivity gradient and its potential effects on Yellow Perch growth and survival may also refine the knowledge needed to improve future management strategies.