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Yellow Perch Genetic Stock Structure in Eastern Lake Michigan: What is the Importance of Drowned River Mouth Lakes?

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Dedication

I dedicate this thesis to my wife (Audrey) and family who have given me emotional and financial support through this process. Thank you!

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Abstract

Habitat heterogeneity has the possibility of structuring populations. Even in connected landscapes, there can be cryptic structuring of populations that coincides with landscape features that limit gene flow or select for different phenotypes within a species. Yellow perch (*Perca flavescens*) is an economically and ecologically prominent fish in the Laurentian Great Lakes. In the Lake Michigan basin, yellow perch reside in nearshore Lake Michigan, including drowned river mouths (DRMs, lake-like habitats that link tributaries to Lake Michigan). The goal of this study was to understand whether yellow perch populations are structured in eastern Lake Michigan by the connected DRM lake habitats. Specifically, I tested whether DRMs and Lake Michigan are distinct genetic stocks of yellow perch and which habitats those stocks occur in throughout the year. To do so, I genotyped yellow perch at 14 microsatellite loci collected from 10 DRMs in both deep and littoral habitats during spring, summer, and fall and two nearshore sites in Lake Michigan (spring and fall) during 2015-2016. I found that all DRMs are genetically distinct from nearshore Lake Michigan. My data also suggest that Lake Michigan yellow perch likely use DRM deep habitats during the fall season, based on how deep-habitat DRM yellow perch from fall cluster with Lake Michigan yellow perch. I also found weak but significant genetic structuring between DRMs. These results are consistent with previous studies and angler accounts of yellow perch. Fisheries managers should take into account this population structure when setting fishing regulations in DRM systems.

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Chapter 1

Introduction

Understanding population genetic structure is crucial for conservation and management of fisheries. The importance of conserving genetic and phenotypic diversity has long been recognized in fisheries management (Begg et al., 1999; Stephenson, 1999) and research continues to support genetic data being incorporated into fisheries management plans (Hilborn et al., 2003; Schindler et al., 2010, 2015). Since habitat heterogeneity can structure populations, understanding cryptic stock sorting is especially important when valuable fish species reside in complex connected habitats (Brenden et al., 2015; Wilson et al., 2016).

Yellow perch (*Perca flavescens*) is an economically and ecologically valuable fish species in the Laurentian Great Lakes. Yellow perch suffered dramatic declines in recruitment in the late 1980s (Marsden and Robillard, 2004) and have since remained at a much lower abundance in Lake Michigan than historically (Clapp and Dettmers, 2004). Yellow perch across the Great Lakes (and specifically within Lake Erie) are not made up of a single, panmictic population, but rather show complex patterns of genetic structuring (Sepulveda-Villet and Stepien, 2011; 2012). In Lake Michigan, genetic and movement analyses suggest stock divisions among the northern, southern, and Green Bay basins (Miller, 2003; Glover et al., 2008). Gaps in our knowledge persist, however, regarding the stock structure of yellow perch in certain regions, particularly nearshore eastern Lake Michigan and its connecting water bodies.

Drowned river mouths (DRMs) are a unique feature along the eastern shoreline of Lake Michigan that may affect the population structuring of fish. DRMs are protected, lake-like

habitats that connect tributaries to Lake Michigan (Janetski and Ruetz, 2015). They receive inputs of water and nutrients from both the tributary and Lake Michigan (Wilcox et al., 2002) and are more productive systems than nearshore Lake Michigan (Höök et al., 2007; Janetski and Ruetz, 2015). Yellow perch reside in both DRMs and Lake Michigan proper; recruitment dynamics, morphometrics, movement studies, and genetic evidence all suggest that DRMs may represent distinct populations (i.e., stocks) from Lake Michigan. Recruitment dynamics of yellow perch in a DRM (i.e., Muskegon Lake) were found to be asynchronous with patterns in nearshore Lake Michigan (Janetski et al., 2013). Morphological differences in yellow perch were found between fish captured in Lake Michigan and DRM wetlands (Parker et al., 2009). Genetic studies suggest that yellow perch from nearshore Lake Michigan are genetically divergent from those in DRMs (Parker et al., 2009; Wesolek, 2014); however, it is still unclear whether these are distinct populations given the spatial and genetic coverage of those studies. Most recently, otolith microchemistry revealed that yellow perch in Lake Michigan exhibit different life histories (Schoen et al., 2016): resident wetland fish, a Lake Michigan resident that returns to wetlands once each year, and transient that spends its juvenile years (~1-3) in the wetland before migrating to reside in Lake Michigan.

Anglers have reported that during autumn and winter "Lake Michigan" yellow perch enter DRMs, based on their catch of large-bodied lighter colored yellow perch (G. Chorak, personal observation). These reports are supported by the transient life histories yellow perch exhibit (Schoen et al., 2016). However, it is unclear whether these yellow perch are in fact from a separate Lake Michigan genetic population and when they reside in DRMs. It is possible DRMs are used as spawning sites for Lake Michigan yellow perch similar to how Lake Erie yellow perch use the Huron-Erie corridor (Sullivan and Stepien, 2014). It has been suggested that

yellow perch from Lake Michigan may migrate into DRMs to overwinter and possibly spawn (Schneider et al., 2007; Seites, 2009; Tonello, 2012; Schoen et al., 2016).

Purpose

The purpose of this study was to better understand yellow perch populations in eastern Lake Michigan. Specifically, I wanted to test whether there was cryptic population structuring of yellow perch in this region by connected DRM lakes.

Scope

This study aimed to better understand yellow perch population genetic structuring and specifically, yellow perch structuring in eastern Lake Michigan. The scope of this research includes yellow perch in Lake Michigan and the Great Lakes basin. However, it is possible the findings here could be applied to other fish species in similar connected water bodies.

Assumptions

When designing my sampling, I assumed that yellow perch in the littoral habitats of DRM lakes would represent DRM resident yellow perch. I also assumed that if Lake Michigan yellow perch were coming into DRM lakes that they would seek out habitats most similar to Lake Michigan. Therefore, I assumed that Lake Michigan fish would be captured in deep habitats of DRM lakes, where the water temperatures are more similar the Lake Michigan (i.e., cooler) than in littoral habitats. Further, the genetic analyses that were performed assume that the 14 microsatellite loci used here are neutral and that all populations are in Hardy-Weinberg equilibrium (HWE).

Hypotheses / Research Questions

This study aimed to answer three questions. 1) Are DRM yellow perch divergent from Lake Michigan yellow perch? Based on genetic evidence (Parker et al., 2009; Wesolek, 2014), I hypothesized that genetic divergence of yellow perch would be detected between DRMs and nearshore Lake Michigan. 2) If so, do Lake Michigan yellow perch use DRMs during specific seasons? Given angler accounts and genetic evidence from a single DRM lake (Wesolek, 2014), I hypothesized that Lake Michigan yellow perch are using the deep-water habitats of DRMs at least during the fall and, based on Schoen et al. (2016), into the spring. 3) Are yellow perch populations in DRMs distinct from each other? I hypothesized that DRM divergence would follow an isolation by distance (IBD) pattern (Wright, 1943), where DRMs that are farther apart will be more divergent from each other. By answering these questions, I aimed to inform the overall question: do DRMs shape the genetic structuring of yellow perch populations in eastern Lake Michigan?

Significance

Since the decline of yellow perch in the Laurentian Great Lakes and specifically the Lake Michigan basin, researchers have been interested in all aspects of yellow perch life history and biology in this region. Yellow perch was once a commercial fishery that has since been halted due to low population sizes. Understanding population genetic structure is crucial for conservation and management of fisheries, and research continues to support that genetic data should be incorporated into fisheries management plans (Hilborn et al., 2003; Schindler et al., 2010; Schindler and Hilborn, 2015). Harvest limits for yellow perch in DRMs are higher than for Lake Michigan (50 vs. 35/day; MDNR 2016). If Lake Michigan yellow perch are using DRM habitats at any point during the year, then they have the potential to be harvested at a higher rate

than what is allowed in Michigan waters of Lake Michigan. My study has the potential to better inform management when setting yellow perch harvest limits in DRMs.

Definitions

DRM -- Drowned river mouth - The end of a tributary where it empties into a large lake (e.g., Lake Michigan) and at that outflow the tributary widens and deepens forming a lake-like habitat.

HWE -- Hardy-Weinberg equilibrium - A steady state populations are in when no evolutionary processes are taking place in them (i.e., random mating, no mutation, no selection, no genetic drift, and no gene flow).

IBD -- Isolation by distance - A pattern where populations become more genetically separate as they become more geographically separate.

Microsatellite - A repeat motif containing 3-5 nucleotides tandemly repeated. These repeats are polymorphic among individuals and populations and are neutral (i.e., not under selection).

Chapter 2

Literature Review

Natural History of Yellow Perch (*Perca flavescens*)

In this section, I will cover the natural history and general biology of yellow perch. The yellow perch occupy a wide range of environments, from freshwater wetlands and lakes to brackish water estuaries (Jenkins and Burkhead, 1993). Yellow perch often move in schools in deeper water during the day, move towards shore at dusk, and disperse to sit on bottom after dark for the night (Becker, 1983). At dawn, yellow perch reassemble into schools and move back to deeper water (Becker, 1983). The yellow perch is mostly found in littoral habitat, under the cover of aquatic vegetation during the summer season (Jenkins and Burkhead, 1993) and in the deepest areas of the lake during the winter months (Becker, 1983; Jenkins and Burkhead, 1993). The yellow perch is heavily fished in the Laurentian Great Lakes, and catch is often highest during the winter near where outflows empty into the Great Lakes (Hubbs and Lagler, 1958).

Yellow perch can tolerate low dissolved oxygen concentrations much better than many other fishes (Becker, 1983). Hypoxia for most fishes and yellow perch is defined as <2 mg/L of dissolved oxygen (Roberts et al., 2009). However, yellow perch have been shown to tolerate dissolved oxygen levels down to 0.07 mg/L for short periods, rates that would kill many other freshwater fishes (Becker, 1983). The yellow perch is thought to use excess oxygen in the swim bladder to survive hypoxic conditions (Becker, 1983). The yellow perch was even found to reside in areas of suboptimal oxygen to be in areas of optimal water temperature (~23.4°C;

Becker, 1983). In Lake Erie's central basin, yellow perch were found to avoid the hypoxic hypolimnion by moving horizontally or vertically from it (Roberts et al., 2009). Diets of yellow perch shifted to mesozooplankton (found higher in the water column) from benthic macroinvertabrates, which are usually consumed under normoxic conditions (Roberts et al., 2009). The yellow perch is thought to make dives into the hypoxic hypolimnion to forage (Roberts et al., 2009).

The yellow perch's diet consists of a wide range of prey and is often dependent on the available prey in a particular habitat. The yellow perch is considered a secondary piscivore and is a sight feeder (Jenkins and Burkhead, 1993). Zooplankton, the food source for juvenile yellow perch, are found in higher densities farther offshore in Lake Michigan, suggesting a better habitat for juveniles (Dettmers et al., 2005). However, fringing wetlands also have been shown to harbor many age-0 yellow perch and the macroinvertebrates they feed on (Parker et al. 2009a).

Yellow perch spawn 8-19 days in the spring (April or early May) immediately after ice-out (Becker, 1983). Yellow perch do not provide natal care to their young; egg strands are left on vegetation or woody debris (Becker, 1983). Egg strands also can be left on sand or gravel areas in shallow water (Becker, 1983), which is likely how yellow perch spawn in Lake Michigan. Once the larvae hatch, they are sedentary for 5 days while they absorb their yolk sack (Becker, 1983). In large lakes (e.g., Lake Michigan), larvae are passively carried offshore in currents, where they have a pelagic larval stage before returning to the nearshore zone (Dettmers et al., 2005). Female yellow perch grow faster and mature more quickly than males (Sepulveda-Villet and Stepien, 2011), contradicting reports by Scott and Crossman (1973) that males mature faster but have shorter life spans.

Genetic Diversity of Yellow Perch Across their Native Range

Population genetic techniques are important tools in determining stock structure and spatiotemporal distributions of fisheries (Hilborn et al., 2003; Schindler et al., 2010, 2015). As time progresses, so do genetic techniques leading to a greater understanding of fine scale structuring of species. This section will summarize the genetic studies aimed at understanding the stock structure of yellow perch in the Laurentian Great Lakes, focusing on the Lake Michigan basin.

This first method used to distinguish yellow perch genetically were polymorphic fragments known as allozymes, visualized using gel electrophoresis. Leary and Booke (1982) found allozymes to be more polymorphic in yellow perch from Vermont than in the Great Lakes region, suggesting genetic diversity is higher in the East Coast populations. Billington (1996) was able to identify 13 haplotypes of yellow perch across their range. However, all populations were dominated by a single haplotype and many of the other haplotypes only deviated by one restriction site and were unique to a single individual. Therefore, they were not able to trace the number of glacial refugia from which yellow perch recolonized. Thus, allozymes were not deemed a sufficient method for stock identification of yellow perch (Billington, 1996).

As technologies improved, new studies emerged on the genetic diversity of yellow perch. Using maternally-inherited mtDNA markers, Sepulveda-Villet et al. (2009) showed that haplotypes corresponded to the glacial refugia from which yellow perch repopulated. The Great Lakes basin was repopulated from a Mississippian refugium and the East Coast from an Atlantic refugium (Sepulveda-Villet et al., 2009). The greatest haplotype diversity was found in North Carolina and East Coast states. Diversity was relatively low in the Great Lakes, which is likely

due to population bottlenecks experienced by yellow perch in this region (Sepulveda-Villet et al., 2009).

The use of microsatellite markers led to greater refinement of yellow perch genetic relatedness. Microsatellites, unlike mtDNA haplotyping, are inherited from both parents, which allow for more detailed assignments of individuals to specific populations (or stocks). The genetic diversity across the yellow perch's range, from the upper Midwest to the East Coast, showed the most genetically diverse samples came from the East Coast (Gryzbowski et al., 2010), which supported the previous findings from Sepulveda-Villet et al. (2009) using mtDNA.

Combining both mtDNA and microsatellite techniques, Sepulveda-Villet and Stepien (2012) showed a pattern of isolation by distance and glacial refugium origins of populations in areas across the range. Overall, yellow perch displayed isolation by distance; however, this pattern did not hold at a finer spatial scale, suggesting that spawning site fidelity or habitat preference is more likely driving the distribution of fish. This is expected given there are separate spawning groups within a single water body (i.e., Lake Erie; Sepulveda-Villet and Stepien, 2011; Sepulveda-Villet and Stepien, 2012). Finally, genetic diversity was found to be higher in areas that did not undergo glaciation, such as the South Atlantic and Gulf coastal populations, both of which are isolated and very divergent from each other (Sepulveda-Villet and Stepien, 2012).

Great Lakes Yellow perch

Most modern (since the last ice age) populations of Great Lakes yellow perch can be traced back to the Mississippian refugium (including parts of western Lake Superior) with only slight contribution from the Atlantic refugium in the eastern parts of Lake Erie and Ontario (Sepulveda-Villet and Stepien, 2012). Although low genetic diversity in Great Lakes yellow perch has been attributed to bottlenecks, the Eurasian perch and closely related *Gymnocephalus*

both have low genetic diversity, so this may be a characteristic of the lineage (Sepulveda-Villet and Stepien 2011).

Lake Erie - Range wide studies have shown that yellow perch in the Great Lakes are the least genetically diverse, and low genetic diversity is problematic when trying to decipher genetic stock structure. Many of the fine scale (single lake) genetic studies have been done in Lake Erie. Those studies reported slight genetic diversity among some spawning groups in eastern Lake Erie using mtDNA haplotyping and suggested using more sensitive markers (microsatellites) may uncover diversity related to all spawning sites within the whole lake (Sepulveda-Villet et al., 2009). When 15 microsatellite loci were examined for 569 yellow perch from 13 spawning sites in Lake Erie as well as one from Lake St. Clair and one from Lake Ontario (15 sites total), most of the spawning sites in Lake Erie were found to be distinct stocks (Sepulveda-Villet and Stepien, 2011). However, some sites did not follow this pattern, and it did not seem to be related to geographic distance or management units (Sepulveda-Villet and Stepien, 2011). Sullivan and Stepien (2015) added to the previous dataset, sampling the same sites over multiple years. They reanalyzed the dataset with multiple years added to the same sampling locations to test whether there was temporal variation at spawning sites. Since the previous study sampled locations across Lake Erie and some were sampled during different years, the spatial diversity could be confounded by temporal diversity. The data before this study suggested that yellow perch likely returned to natal grounds to spawn. However, they found significant temporal diversity between years at the same site, suggesting that yellow perch may not home to their exact natal spawning site. It is also possible that because of high mortality in early life stages of yellow perch that only young from a few adults survive, which would lead to

significant changes in genetic structure at a spawning site from year to year (Sullivan and Stepien, 2015).

Kocovsky et al. (2013) used microsatellite loci and morphometrics to look at fine scale variation of the central basin of Lake Erie, an area under increasing exploitation that had not been previously studied. Yellow perch (158 individuals) were examined from four new sites in the Central basin to test whether individuals from the northern and southern shores differed genetically and morphologically. Genetic and morphometric analyses both agreed there was a clear difference between northern and southern populations, but the differences did not seem to be related to geographic distance.

Studies on Lake Erie yellow perch genetics converge on the conclusion that there must be another mechanism driving the genetic differentiation other than geographic distance. There may be barriers to dispersal or kin recognition (Sepulveda-Villet and Stepien, 2011; Kocovsky et al., 2013). Bathymetry, spawning site philopatry, and kin recognition using olfactory sensory, similar to European perch (*Perca fluviatilis*), are all hypothesis of what may be structuring populations of yellow perch in open water environments (Sepulveda-Villet and Stepien, 2011).

Lake Michigan **-** Early studies suggested that Lake Michigan yellow perch were one interbreeding population. There were no polymorphic allozyme loci found in Lake Michigan samples (Leary and Booke, 1982). Additionally, a mark-recapture study showed that up to 25% of the yellow perch were recaptured in different spawning grounds than where they were marked (Mraz, 1952). These results suggested high gene flow and low genetic diversity in Lake Michigan yellow perch.

Following a decline in yellow perch abundance attributed to an absence of recruitment in 1990, the Yellow Perch Task Group (YPTG) was formed by the Lake Michigan Committee of

the Great Lakes Fishery Commission to understand the reason(s) for this recruitment decline (Clapp and Dettmers, 2004). A study as part of the YPTG found that larval yellow perch are gape limited and that the presences of small copepods are critical for their survival (Clapp and Dettmers, 2004). As a result of the yellow perch decline and the YPTG initiative, several more studies on yellow perch were undertaken in the Lake Michigan basin. Here I will focus on the studies that assess population structure.

Two distinct stocks of yellow perch were found in Lake Michigan, one in Green Bay and one in southern Lake Michigan (Miller, 2003). A small sample of fish from northern Lake Michigan also was found to be more closely related to the southern basin than to Green Bay, suggesting that Green Bay is distinct from the rest of Lake Michigan (Miller, 2003). A hypothesis for this pattern was that lake currents dispersed larval yellow perch throughout Green Bay and Southern Lake Michigan (Miller, 2003). Yellow perch have a relatively long pelagic larval stage that may be influenced by strong offshore currents, carrying juvenile (age-0) fish far off shore. The pattern of older bigger age-0 fish farther offshore, shown by Dettmers et al. (2005), supports the idea of ocean-like currents passively dispersing fish, especially since the average currents in Lake Michigan are much faster than juvenile yellow perch can swim, so their dispersal is almost certainly at the mercy of the currents (Dettmers et al., 2005).

The lack of fine scale structure related to spawning grounds within a large region (e.g., Green Bay) also may be explained by adult movements between spawning grounds, although it is unlikely adults would travel that distance based on recapture studies (Miller, 2003). Yellow perch marked and recaptured over a 5-year period (1996-2001) showed high (35-80%) spawning site fidelity (Glover et al., 2008). However, fish strayed from all locations except between

Wisconsin and Michigan waters in the southern basin (Glover et al., 2008), supporting the findings of Miller (2003).

The eastern shore of Lake Michigan is unique in that it is characterized by outflows of rivers that are channelized where they empty into Lake Michigan, causing the river to "back-up" at the mouth and form a lake-like water body known as a drowned river mouth (DRM) lake (Wilcox et al., 2002). Since these DRM lakes have an open connection to Lake Michigan and yellow perch inhabit both, it is important to know how yellow perch use these habitats to inform management. Parker et al. (2009b) showed that yellow perch from wetlands of DRM lakes were genetically and morphologically distinct from yellow perch caught in nearshore Lake Michigan. Yellow perch from these different habitats also had different feeding strategies based on diets (Parker et al., 2009b). Otolith microchemistry analysis showed that yellow perch in connected DRM wetlands and nearshore Lake Michigan exhibit at least three different life histories (Schoen et al., 2016): resident wetland fish, a Lake Michigan resident that returns to wetlands once each year, and transient that spends its juvenile years (~1-3) in the wetland before migrating to reside in Lake Michigan.

Although there are several studies on yellow perch stock structuring throughout its range, less is known about the structuring of populations in Lake Michigan, especially related to how connected DRM lakes may shape population genetic structure of yellow perch. Studies focusing on the wetland habitats of these connected DRM lakes showed that yellow perch residing in DRM wetlands may be of a different stock than nearshore Lake Michigan (Parker et al., 2009b; Schoen et al., 2016) and that there also may be mixing of these stocks at least once a year when Lake Michigan residents use DRM wetlands (Schoen et al., 2016). However, there is still a knowledge gap surrounding the DRM lakes. The wetlands of DRM lakes sampled by those two

studies (Parker et al., 2009b; Schoen et al., 2016) are located in what is considered the tributary that feeds the DRM lake and sample sizes in Lake Michigan connected wetlands were small, partially because these studies focused on both lakes Michigan and Huron. To date, there are no studies that sampled yellow perch in the main basin of DRM lakes, which is where yellow perch fishing is most productive during the winter months (Hubbs and Lagler, 1958). Approximately 50,337 yellow perch were harvested from Muskegon lake in the winter of 2003 (Hanchin et al., 2007), which could account for up to 20% of the Lake Michigan catch of yellow perch. Therefore, the question of how DRM lakes shape yellow perch stock structure and the habitat use of those stocks remains open when it comes the main basin and outflows of DRM lakes. Answers to these questions would have a great impact on management plans in this area since DRM lakes and Lake Michigan are managed as separate water bodies.

Chapter 3

Methods

Field Sites and Sample Collections

Yellow perch were collected in both deep and littoral habitats of 10 DRMs along the eastern shore of Lake Michigan (Fig. 1). Yellow perch from deep habitats were captured using 5.08- and 7.62-cm stretch-mesh gill nets placed on the bottom in the deepest part (range = 8.4 - 20.5 m) of each DRM where dissolved oxygen was >2 mg/mL. Littoral habitats were sampled using boat electrofishing. The shoreline of each DRM was divided into 200-m transects and numbered, then three transects were selected randomly and electrofished for 20 min. If the target number of yellow perch (40 individuals) was not achieved at the randomly-selected transects, then additional transects were chosen, based on habitat (e.g., presence of submerged aquatic vegetation), to reach the target number of fish. Yellow perch were sampled from DRMs during spring, summer, and fall seasons 2015-2016, though not all lakes were sampled in every season (Table 1). Seasons were defined as: summer - when the lake is thermally stratified, fall - after turnover and before ice cover, and spring - after ice out and before thermal stratification. Yellow perch were captured in nearshore Lake Michigan adjacent to sampled DRMs by the Michigan Department of Natural Resources (MDNR) during late summer and spring seasons (2016) using gill nets and trawling as part of their bi-annual survey of yellow perch. The two sites sampled in nearshore Lake Michigan were adjacent to the furthest north DRM, Charlevoix, and the other between the two most southern DRMs, Macatawa and Muskegon (Fig. 1). I will refer to these sites as northern and southern Lake Michigan, respectively. A piece of fin was clipped from each

yellow perch that was either stored in ethanol or dried in a scale envelope. I also supplemented my sampling with yellow perch collected by Wesolek (2014) from northern and southern Lake Michigan and the deep habitat in Muskegon Lake during 2013 (see Table 1).

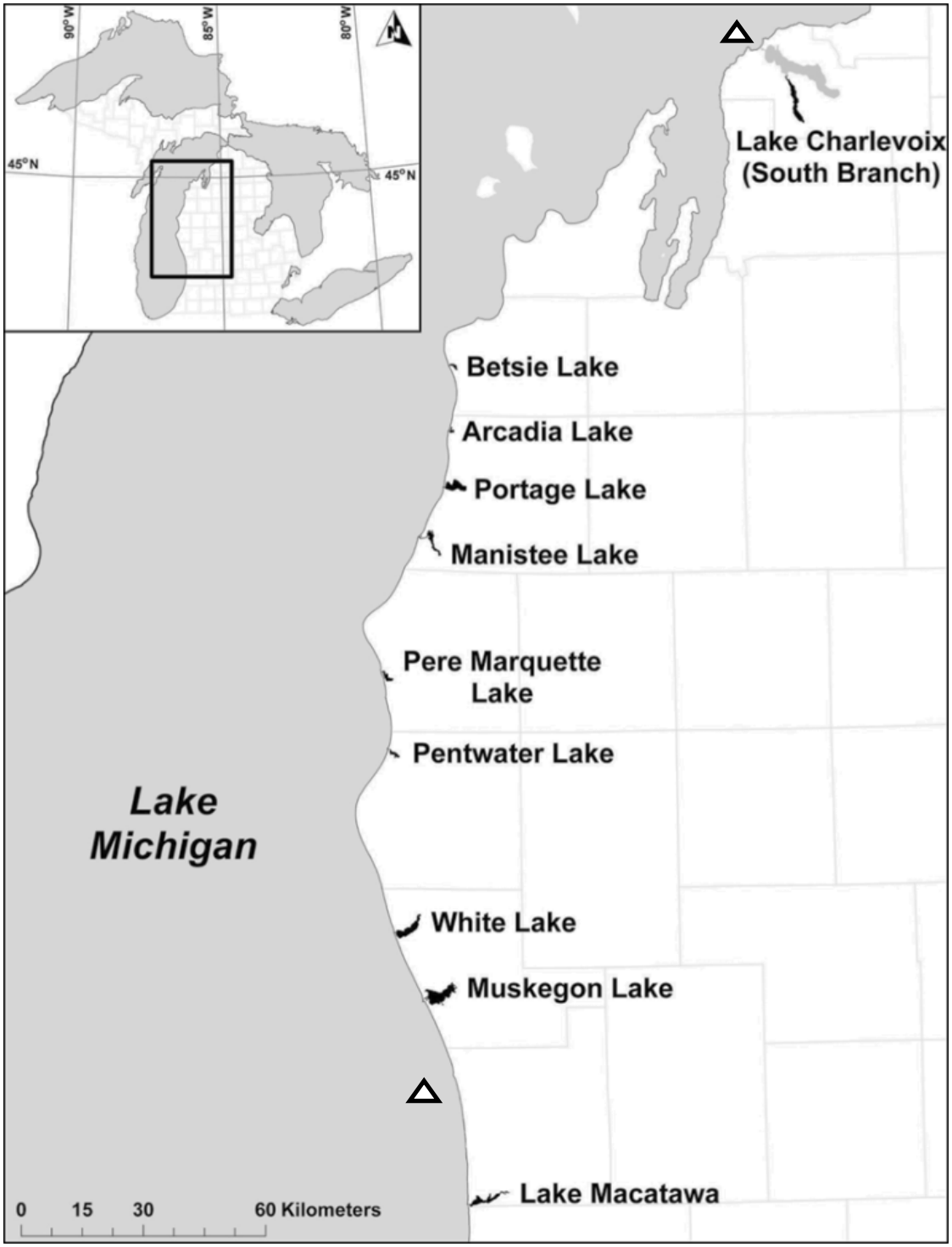


Figure 1. Map of eastern Lake Michigan showing drowned river mouth lakes sampled for yellow perch in deep and littoral habitats between summer 2015 and fall 2016. Triangles indicate the two nearshore Lake Michigan sampling locations.

Table 1. Numbers of yellow perch collected from each zone of each lake by year and season between summer 2015 and fall 2016 in eastern Lake Michigan and connected drowned river mouth lakes. "-" indicates that location was not sampled during that season, where "0" indicates that no yellow perch were collected.

Site	Season/Year	Deep/Near-Shore	Littoral	Total
Arcadia	Summer 2015	0	40	80
	Spring 2016	0	40	
Betsie	Summer 2015	0	28	55
	Spring 2016	0	27	
Charlevoix	Summer 2015	0	39	41
	Fall 2015	2	0	
Lake MI Charlevoix	Spring 2016	40	-	59
	Fall 2013	19	-	
Lake MI Grand Haven	Summer 2016	40	-	60
	Fall 2013	20	-	
Macatawa	Summer 2015	-	18	67
	Summer 2016	-	40	
	Fall 2016	9	-	
Manistee	Summer 2015	0	40	80
	Spring 2016	0	40	
Muskegon	Summer 2015	4	10	157
	Fall 2015	1	20	
	Spring 2016	0	25	
	Summer 2016	0	30	
	Fall 2016	47	-	
	Fall 2013	20	-	
Pentwater	Summer 2015	1	40	128
	Fall 2015	3	0	
	Spring 2016	0	40	
	Fall 2016	44	-	
Pere Marquette	Summer 2015	10	40	93
	Spring 2016	3	40	
Portage	Summer 2015	0	40	45
	Fall 2015	0	5	
White	Summer 2015	0	40	157
	Spring 2016	10	40	
	Fall 2016	67	-	
	Totals	340	682	**1022**

Molecular Methods

Whole DNA was extracted from approximately 4 mm^2 fin tissue using a modified method from Walsh et al. (1991). Approximately 30% volume of Chelex-100 (Sigma-Aldrich), 0.112 µg proteinase K, and ultrapure water were combined for 150 µl total extraction volume. Fin clips in extraction buffer were incubated at 76 ºC for 1 hour and 99 ºC for 10 minutes. Sixteen microsatellite markers previously developed for yellow perch (YP: Li et al., 2006; Pfla: Leclerc et al., 2000; and Mpf: Gryzbowski et al., 2010) and walleye (*Sander vitreus;* Svi: Borer et al., 1999) were amplified in each individual (Supp. Table 1). PCR was performed in 25 µl total volume consisting of 4X KCl Buffer (Thermo Sci.), 2 mM $MgCl_2$, 0.2 mM of each dNTP (New England Biolabs), 1 µM each primer (Tagged-Forward and Reverse), 1.25U *Taq* DNA Polymerase (Thermo Sci.), and ~100 ng template DNA. All amplifications started at 95 ºC for 3 minutes followed by 30 cycles of 95 ºC for 30 seconds, an annealing step for 1 minute (temperatures varied, see Supp. Table 1), and 72 ºC for 30 seconds. A final extension for 10 minutes at 72 ºC finished the amplification. The exceptions were a touchdown PCR on Svi-6 and an extra 10 cycles on Pfla-L6 (see Supp. Table 1). Microsatellites were visualized on a 3130xl genetic analyzer using HiDi chemistry (Applied Biosystems).

Data Analysis

Markers were scored blindly to their collection location in GeneMapper v5 (Applied Biosystems). I tested conformity of loci to Hardy-Weinberg Equilibrium (HWE) in Genepop v4.2 (Raymond and Rousset, 1995) using 100 batches of 1000 Markov Chain Monte Carlo (MCMC) iterations. Populations were grouped by lake and habitat within lake (deep or littoral), and loci not in HWE for more than 60% of the populations were removed from further analyses.

I performed quality control using the STRATAG package (Archer et al., 2017) in R. All samples missing 80% or more of loci were removed from further analyses. I also removed any sampling habitat (population) with less than 15 individuals to avoid sample size bias in analyses. Remaining individuals (n = 975) and loci (n = 14) were included in the statistical tests for population differentiation. Visualization of populations was performed in the Bayesian clustering program STRUCTURE v2.3.2 (Pritchard et al., 2000). Yellow perch were clustered using the admixture model and a burn-in period of 100,000 and a run time of 200,000 MCMC reps, 10 iterations at each value of K (1-17). I ran STRUCTURE both with priors where I used sampling habitat (lake/habitat in lake) as a priori population indicators and without priors. I found the most likely values of K using the ΔK method from Evano et al. (2005) calculated in STRUCTURE HARVESTER v0.6.93 (Earl and vonHoldt, 2012). I found consensus clusters across iterations of STRUCTURE by permuting and matching clusters using the large K greedy algorithm with a random input and 1000 repeats in CLUMPP v1.1.2 (Jakobsson and Rosenberg, 2007), and I used *distruct* v1.1 (Rosenberg, 2004) to draw the final STRUCTURE plots. I then performed further clustering of individuals by habitat type (deep, littoral, or nearshore) using Discriminant Analysis of Principle Components (DAPC) in the *adegenet* v2.0.1 (Jombart, 2008) package for R to test which habitat (littoral DRM or nearshore Lake Michigan) clustered closest to the yellow perch captured in the deep-DRM habitat. I calculated pairwise F_{ST} (Weir and Cockerham, 1984) between all sampling locations in STRATAG (Archer et al., 2017) to test whether sampling locations are genetically distinct. I also applied a Holm-Bonferroni sequential correction (Holm, 1979) to pairwise F_{ST} to correct for multiple comparisons. I used a Mantel test with 999 replicates in the R package *adegenet* v2.0.1 (Jombart, 2008) to test for isolation by distance (IBD; Wright, 1943). IBD was assessed using straight-line distances between DRMs through

Lake Michigan and pairwise F_{ST} of yellow perch collected only in littoral habitats of DRMs. I found PGDSpider v2.1.1.0 software (Exoffier and Lischer, 2012) especially helpful in converting between dataset formats.

Chapter 4

Results

In total, I collected DNA from 1,022 yellow perch. After filtering the data to remove populations with small sample size and individuals with missing loci, my dataset contained 975 yellow perch for analyses; 187 from deep DRM habitats, 681 from littoral DRM habitats, and 107 from nearshore Lake Michigan. I only included deep DRM habitat fish collected in the fall season for analyses (Table 1). This was because I captured few yellow perch in deep DRM habitats during spring and summer seasons; therefore, sample sizes were not sufficient to make meaningful comparisons with the other populations. Sample sizes of DRMs, both deep and littoral habitats, ranged from 39 to 84 individuals (see Supp. Table 2). In Lake Michigan, sample sizes ranged from 60 fish at the southern site to 47 fish at the northern site. Two loci (Pfla-L3 and Pfla-L4) had intense stutter in their chromatograms, which likely caused unreliable calling. These loci were ultimately excluded from analyses because they were out of HWE in more than 60% of the populations. Yellow perch collected by Wesolek (2014) were not different (based on analysis of microsatellites) from our samples (years 2013 vs. 2016, Table 1), so fish were pooled across years in the analyses reported below.

DRMs vs. Lake Michigan

DAPC clustered individuals by the location type in which they were collected, showing that divergence between DRM littoral locations and Lake Michigan is much greater than the divergence between DRM deep and Lake Michigan yellow perch (Fig. 2A.). The most

informative axis (component 1) highlights how the difference between DRM deep and Lake Michigan yellow perch is much smaller than the difference between DRM littoral and Lake Michigan yellow perch (Fig. 2 B.).

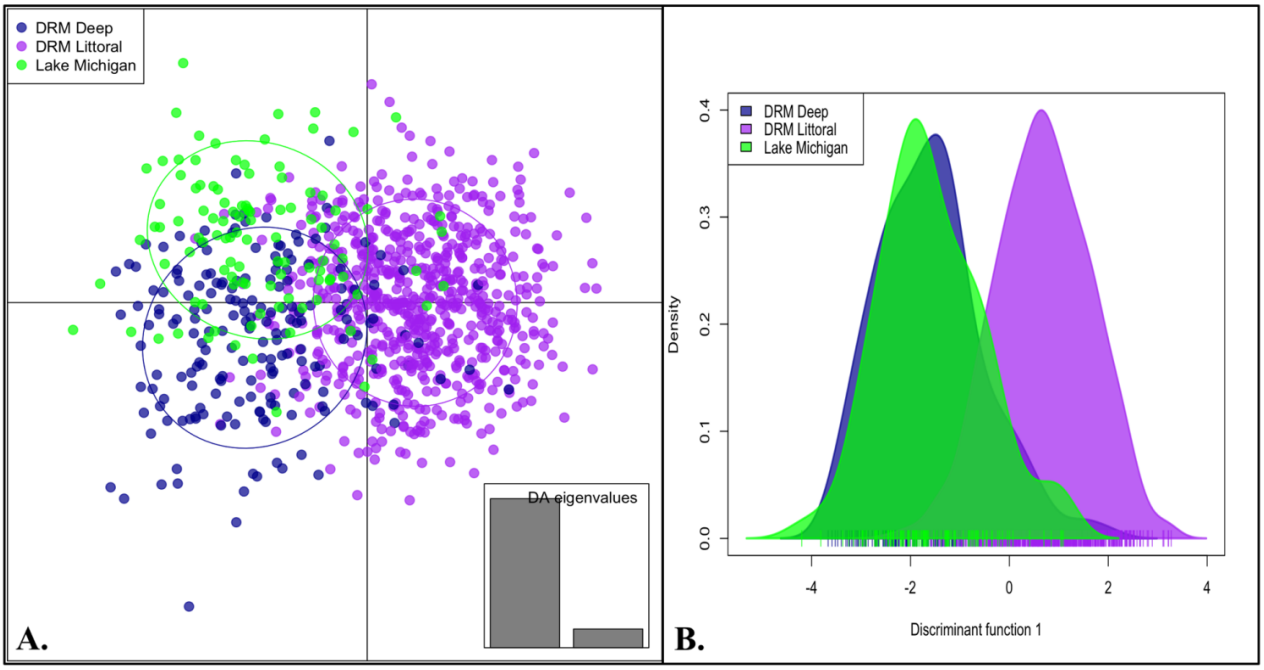


Figure 2. Discriminant analysis of principle components calculated in *adegenet* v2.0.1 (Jombart, 2008) package for R. (**A**) Plot of both discriminant function axes; each dot represents an individual, and all individuals (n = 975) are included and grouped by habitat type. (**B**) Plot of discriminant function 1, distributions include all individuals (n = 975) grouped by habitat type.

I found a similar clustering pattern in STRUCTURE analyses (Fig. 3). The Evano method (ΔK) showed the most support for K=2 (Supp. Fig. 1). At K = 2, yellow perch from DRM deep habitats cluster similar to Lake Michigan yellow perch (majority 'red' cluster), while the littoral DRM yellow perch differed (majority 'blue' cluster; Fig. 3).

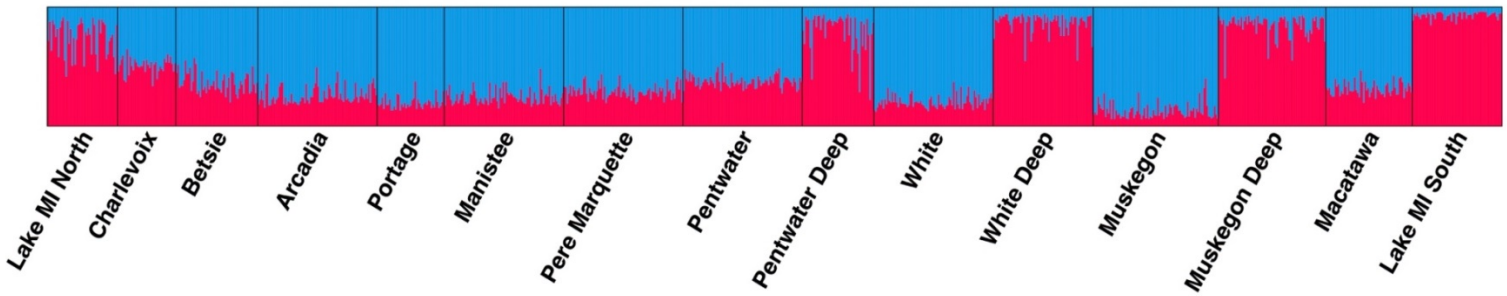


Figure 3. STRUCTURE analysis of all yellow perch (n = 975) at K = 2. STRUCTURE was run using the admixture model and a burn-in period of 100,000 and a run time of 200,000 MCMC replicates, 10 iterations at each value of K (1-17). Sampling locations listed were used as a priori population indicators. ΔK was found to be 2. Clusters were matched in CLUMPP v1.1.2 (Jakobsson and Rosenberg, 2007) and *distruct* v1.1 (Rosenberg, 2004) was used to draw the final STRUCTURE plot.

All DRM littoral locations were significantly different from both Lake Michigan sites in pairwise F_{ST} comparisons (Table 2). Yellow perch from deep-water habitat in Muskegon Lake were not significantly different from northern Lake Michigan, and yellow perch from deep-water habitat in Pentwater Lake were not significantly different from either northern or southern Lake Michigan sites in pairwise F_{ST} comparisons (Table 2). All other yellow perch from deep DRM sites were significantly different from both Lake Michigan sites. However, average F_{ST} between DRM littoral habitats and nearshore Lake Michigan was much higher (Mean and Median ≈ 0.034) than between deep DRM habitats and nearshore Lake Michigan (Mean and Median ≈ 0.005), which supports the findings of both clustering analyses. Additionally, the divergence between north and south Lake Michigan sites was small (F_{ST} = 0.008, Table 2).

Table 2. Pairwise F_{ST} comparison between all DRM littoral, DRM deep, and Lake Michigan populations. F_{ST} calculated following Weir and Cockeram (1984) in STRATAG package (Archer et al., 2017) for R using 1000 permutations. All values represent pairwise F_{ST} scores and values in bold are statistically significant ($P < 0.05$) after Holm-Bonferroni sequential correction (Holm, 1979).

FST	Arcadia	Betsie	Charlevoix	LK MI Charlevoix	LK MI Grand Haven	Macatawa	Manistee	Muskegon	Muskegon Deep	Pentwater	Pentwater Deep	Pere Marquette	Portage	White	White Deep
Arcadia	-														
Betsie	**0.008**	-													
Charlevoix	**0.022**	**0.015**	-												
LK MI Charlevoix	**0.022**	**0.019**	**0.008**	-											
LK MI Grand Haven	**0.043**	**0.037**	**0.035**	**0.008**	-										
Macatawa	**0.016**	**0.018**	**0.020**	**0.022**	**0.046**	-									
Manistee	**0.009**	**0.016**	**0.028**	**0.032**	**0.053**	**0.019**	-								
Muskegon	**0.007**	**0.011**	**0.027**	**0.030**	**0.051**	**0.009**	**0.010**	-							
Muskegon Deep	**0.027**	**0.027**	**0.025**	0.003	**0.008**	**0.030**	**0.029**	**0.031**	-						
Pentwater	**0.023**	**0.022**	**0.030**	**0.030**	**0.041**	**0.019**	**0.020**	**0.014**	**0.028**	-					
Pentwater Deep	**0.024**	**0.024**	**0.022**	0.000	0.001	**0.029**	**0.034**	**0.032**	0.000	**0.027**	-				
Pere Marquette	**0.011**	**0.014**	**0.017**	**0.018**	**0.043**	**0.007**	**0.017**	**0.009**	**0.026**	**0.021**	**0.025**	-			
Portage	**0.009**	**0.014**	**0.027**	**0.025**	**0.043**	**0.027**	**0.020**	**0.018**	**0.032**	**0.031**	**0.028**	**0.024**	-		
White	**0.011**	**0.016**	**0.025**	**0.027**	**0.049**	**0.011**	**0.015**	**0.006**	**0.032**	**0.011**	**0.031**	**0.010**	**0.021**	-	
White Deep	**0.027**	**0.028**	**0.028**	**0.008**	**0.007**	**0.029**	**0.031**	**0.030**	-0.001	**0.024**	0.001	**0.028**	**0.031**	**0.032**	-

DRMs

To test whether DRMs were genetically distinct from each other, only DRM fish collected in littoral habitats were compared. All DRMs were found to be significantly different from one another in pairwise F_{ST} comparisons. However, F_{ST} was low between all DRM lake comparisons (mean ≈ 0.017, median ≈ 0.016; Table 2). I observed a significant pattern of isolation by distance (Figure 4; R = 0.462, P = 0.001,). Yellow perch littoral DRM habitats showed a slight structuring among DRMs using program STRUCTURE (Supp. Fig. 2), supporting the results of pairwise F_{ST} comparison. However, the clusters were not clearly defined, likely due to the continuous isolation by distance pattern exhibited between DRMs.

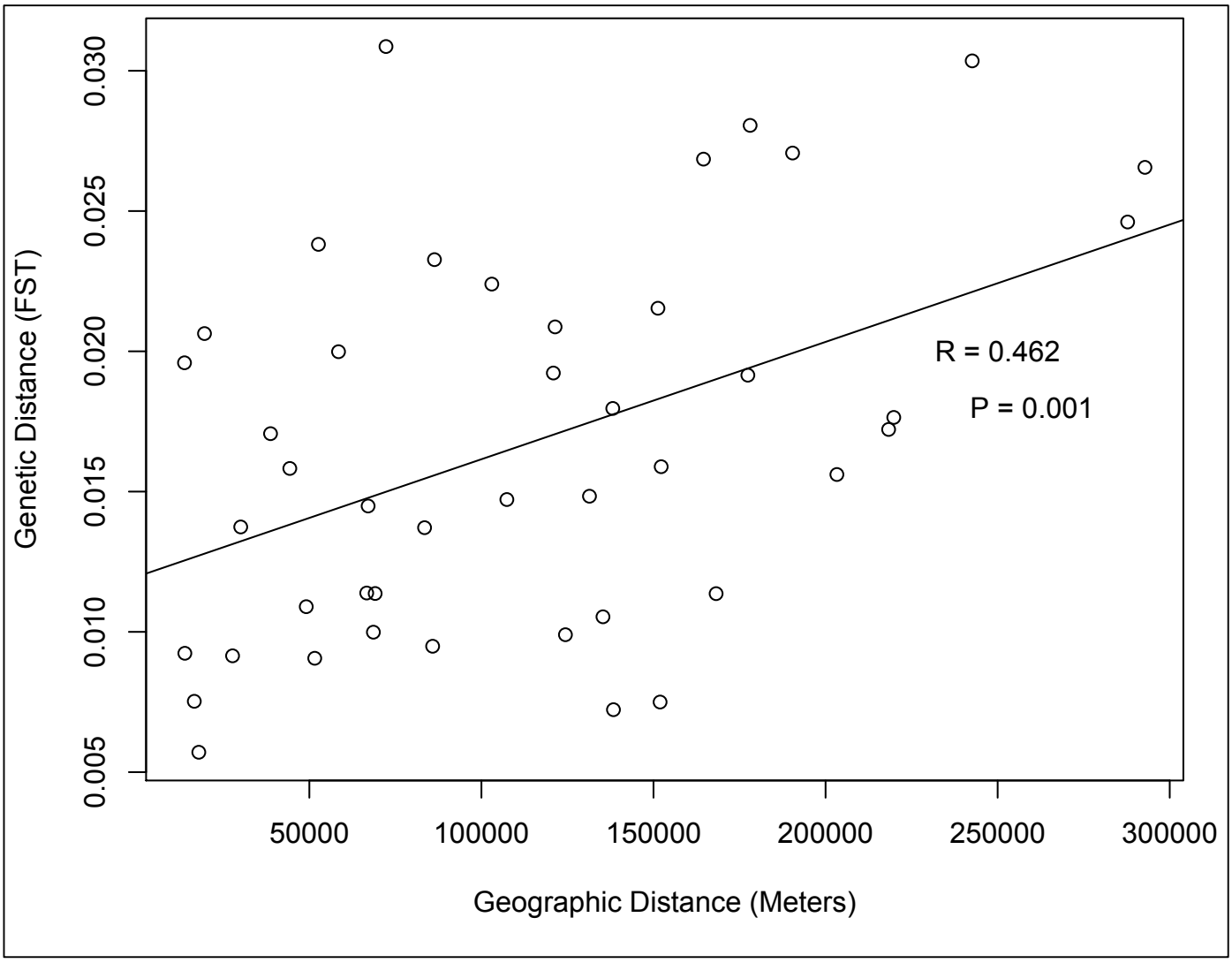


Figure 4. Mantel test using pairwise F_{ST} of all yellow perch from littoral DRMs and straight-line distance (through Lake Michigan) between drowned river mouths (R = 0.462, P = 0.001).

Chapter 5

Discussion

DRMs vs. Lake Michigan

My data showed that yellow perch in eastern nearshore Lake Michigan represent a separate stock from the littoral DRM habitats. All pairwise comparisons between DRM littoral samples and Lake Michigan were significantly different (Table 2). This claim is further supported by DAPC and STRUCTURE, because both analyses clustered DRM littoral and nearshore Lake Michigan samples separately.

From my data, it is clear there is structuring of yellow perch populations by DRMs in eastern Lake Michigan. However, given the large size of these populations, genetic drift is likely very slow, which could explain why my divergence estimates are very small. A study comparing Muskegon Lake to Lake Michigan found that Muskegon Lake experienced relatively higher water temperatures, primary production, and densities of small-bodied zooplankton than Lake Michigan (Höök et al., 2007). The environmental differences between the DRM lake and Lake Michigan contributed to healthier juvenile alewife (*Alosa pseudoharengus*) in Muskegon Lake than in Lake Michigan (Höök et al., 2007). Littoral and wetland habitats in DRM lakes also offer more cover (e.g., vegetation and woody debris) for juveniles and small-bodied fishes (see Janetski and Ruetz [2015] for description of littoral habitats in DRM lakes) compared with nearshore Lake Michigan. Reduced cover in Lake Michigan possibly leads to increased predation risk for yellow perch therefore, leading to different selective pressures occurring

between the very different habitat types of Lake Michigan and the DRMs. Future studies, including many more markers (e.g., SNPs), may be able to pick up on markers differentially selected in these populations and may yield more definitive structuring of yellow perch in eastern Lake Michigan and DRMs.

Previous studies of yellow perch reported genetic differences between northern and southern Lake Michigan. I found small divergence of northern from southern Lake Michigan (F_{ST} = 0.008, Table 2), which supports the findings of those previous studies (Miller, 2003; Gryzbowski et al., 2010; Wesolek, 2014).

Lake Michigan Migrants

When sampling yellow perch in DRMs, it was rare to catch yellow perch in both the littoral and deep locations in the same season (Table 1). Therefore, a large majority of yellow perch were captured in deep DRM habitats during fall and littoral DRM habitats during summer and spring. Once quality control was applied to the dataset, all deep DRM habitat yellow perch included in analyses were from fall (Table 1). The deep habitats of DRMs can have low dissolved oxygen concentrations during summer when thermally stratified (Altenritter et al., 2013; G. Chorak, personal observations), which is likely why I captured few yellow perch in deep DRM habitats during summer. Lake Michigan yellow perch may use southern DRM deep habitats starting in autumn, once DRMs are no longer thermally stratified, and continue to use DRMs until spring when they migrate back to Lake Michigan to spawn. It had been suggested that yellow perch from Lake Michigan may migrate into DRMs to overwinter and possibly spawn (Schneider et al., 2007; Seites, 2009; Tonello, 2012, Schoen et al., 2016). However, given the genetic divergence of yellow perch captured in littoral DRM habitats vs. nearshore Lake Michigan, the possibility that yellow perch from Lake Michigan are regularly spawning in the

DRMs with the DRM resident yellow perch seems low. Further, I did not find Lake Michigan yellow perch in either habitat of the DRMs during the spring season. My data suggest that Lake Michigan yellow perch may overwinter in DRMs but are not predominantly spawning there. Although my data focused on southern DRMs, I see no reason why Lake Michigan yellow perch would not similarly use other DRMs. I hypothesize that Lake Michigan yellow perch also use deep habitats of northern DRMs during the fall.

Although the yellow perch captured in deep DRM habitats are genetically more similar to fish from nearshore Lake Michigan than fish from littoral DRM habitats, the fact that they do not group perfectly with them in either STRUCTURE or DAPC (Fig. 2 & 3) suggests that fish from deep DRM habitats may not only represent Lake Michigan yellow perch. The majority of samples collected in the deep DRM habitat during the fall are from Lake Michigan based on how close they group as populations, but some individuals are probably DRM residents that move from the littoral habitat to the deep habitat in the fall after DRMs turnover and the hypolimnion is no longer hypoxic. Given the amount of admixture found between populations (i.e., populations are not represented by a single cluster but rather ratios of clusters in STRUCTURE; Fig. 3), it is difficult to assign individuals from deep habitats of DRMs back to either littoral or Lake Michigan populations. The admixture between these populations also makes it impossible to determine if any of the individuals are recent hybrids between DRM and Lake Michigan resident yellow perch.

DRMs

Littoral habitats of DRMs were found to be significantly distinct from one another. However, F_{ST} values were small (mean ≈ 0.017, median ≈ 0.016; Table 2), suggesting that yellow perch in DRMs either recently diverged or that moderate gene flow is still occurring

between populations. Genetic divergence between DRMs does follow a weak pattern of isolation by distance (Figure 4), suggesting that moderate levels of gene flow occur among DRM populations given that these populations have likely been separate since yellow perch recolonized the Great Lakes after the last glaciation ~80,000 - 10,000 years ago (Mandrak and Crossman, 1992). One possible mechanism of gene flow between DRM lakes is that resident DRM yellow perch move into Lake Michigan, possibly during summer to seek thermal refuge and avoid hypolimnetic hypoxia. However, resident DRM yellow perch may not be well adapted for Lake Michigan (Parker et al., 2009). Thus, once in Lake Michigan, DRM residents may eventually seek out the nearest DRM lake. If DRM residents do not return to the exact DRM lake from which they originated, then this could cause the weak isolation by distance pattern that I observed. It is also possible that gene flow between DRM yellow perch and Lake Michigan yellow perch is causing the weak structuring between DRM lakes. However, since I found greater divergence between Lake Michigan and littoral DRM habitats (mean $F_{ST} \approx 0.034$) than between DRM lakes (mean $F_{ST} \approx 0.017$), this seems less likely.

Conclusions

Understanding similar types of population structure has proved critical for the successful management of Pacific salmon in Alaska (Hilborn et al., 2003; Schindler et al., 2010) and should be considered when managing yellow perch in the Great Lakes. For example, two interesting questions that have come out of my research are: where do DRM resident yellow perch go when they are no longer found in the littoral habitats? Since there were not many resident yellow perch in the deep habitats of DRM lakes it is most probable that they are residing in areas of intermediate water depth, that we did not sample here. The second question, likely being most important to managers: are Lake Michigan yellow perch being harvested at higher rates while

residing in DRMs during fall and winter? Harvest limits for yellow perch in DRMs are higher than for Lake Michigan (50 vs. 35/day; MDNR 2016). If Lake Michigan yellow perch are using deep DRM habitats during the fall and winter, then they have the potential to be harvested at a higher rate than in Lake Michigan. Future studies should examine what proportion of yellow perch harvested by anglers in DRMs during fall and winter are from Lake Michigan.

Supplemental Tables

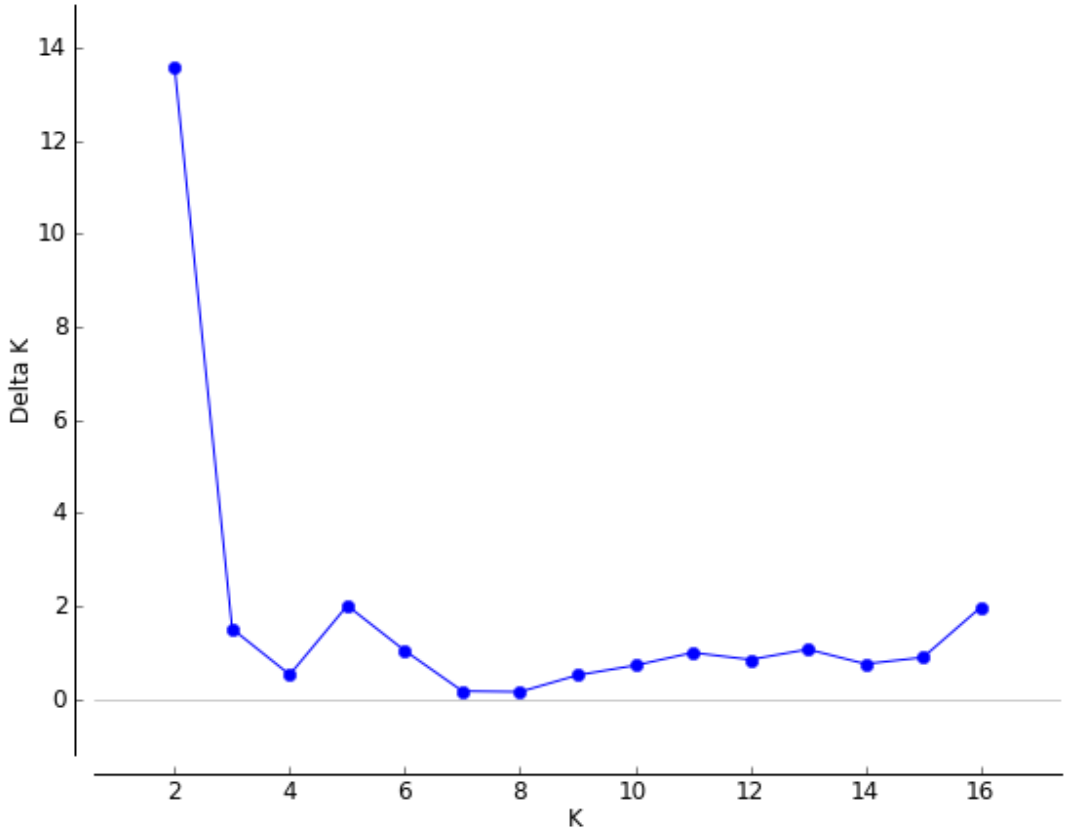
Supplemental Table 1. Summary of PCR parameters and locus statistics for 14 microsatellite loci.

Locus	Num. Genotyped	Num. Alleles	Prop. Unique Alleles	Obsvd. Heterozygosity	Expt. Heterozygosity	Annealing Temp. (ºC)	Cycles	Source
Mpf.4	956	29	0.14	0.77	0.78	54	35	Gryzbowski et al. 2010
Mpf.5	973	14	0.14	0.55	0.56	54	35	Gryzbowski et al. 2010
Mpf.6	958	10	0.00	0.54	0.55	54	35	Gryzbowski et al. 2010
Mpf.7	968	30	0.23	0.86	0.88	54	35	Gryzbowski et al. 2010
Pfla.L2	944	15	0.27	0.53	0.56	51	35	Leclerc et al. 2000
Pfla.L5	963	14	0.29	0.48	0.49	51	35	Leclerc et al. 2000
Pfla.L6	920	18	0.06	0.46	0.49	47	40	Leclerc et al. 2000
Svi.33	901	46	0.11	0.91	0.96	61	35	Borer et al. 1999
Svi.4	958	30	0.10	0.94	0.88	61	35	Borer et al. 1999
Svi.6	916	41	0.10	0.79	0.91	TD (65,55)	10@65, 30@55	Borer et al. 1999
YP41	956	8	0.00	0.54	0.54	54	35	Li et al. 2006
YP60	962	9	0.11	0.31	0.31	51	35	Li et al. 2006
YP78	956	14	0.07	0.52	0.52	54	35	Li et al. 2006
YP96	963	8	0.00	0.19	0.20	51	35	Li et al. 2006

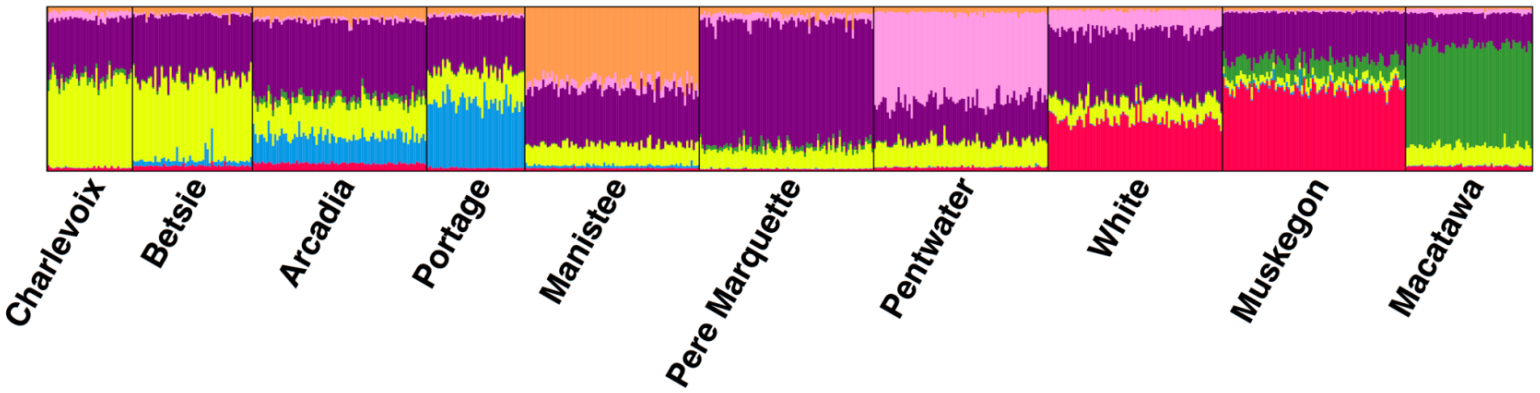
Supplemental Table 2. Summary of population differentiation statistics by population.

Strata	*n*	Avg. Samples Missing Data	Avg. Alleles/Locus	Prop. Unique Alleles	Heterozygosity
Arcadia	80	0.3571	13.43	0.229	0.608
Betsie	55	0.6429	11.64	0.289	0.621
Charlevoix	39	0.0714	9.79	0.282	0.599
LK MI North	47	7.6429	9.64	0.261	0.528
LK MI South	60	0.5	9.93	0.248	0.57
Macatawa	58	1.6429	11.64	0.242	0.596
Manistee	80	0.2857	12.21	0.199	0.624
Muskegon	84	3	14.29	0.203	0.65
Muskegon Deep	72	3.0714	11.64	0.218	0.558
Pentwater	80	0.9286	11.43	0.215	0.618
Pentwater Deep	48	1.6429	10.43	0.311	0.55
Pere Marquette	80	1.5714	12	0.195	0.578
Portage	45	1	11.36	0.305	0.63
White	80	0.3571	13.43	0.241	0.636
White Deep	67	2.7143	11.86	0.261	0.567

Supplemental Figures



Supplemental Figure 1. Delta K output from STRUCTURE Harvester for STRUCTURE analysis of all yellow perch samples (Fig. 3).



Supplemental Figure 2. STRUCTURE analysis of DRM littoral yellow perch (*n* = 681) at K = 7. STRUCTURE was run using the admixture model and a burn-in period of 100,000 and a run time of 200,000 MCMC replicates, 10 iterations at each value of K (1-12). Sampling locations listed were used as a priori population indicators. ΔK was found to be 7. Clusters were matched in CLUMPP v1.1.2 (Jakobsson and Rosenberg, 2007) and *distruct* v1.1 (Rosenberg, 2004) was used to draw the final STRUCTURE plot.

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