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Genetic Structure of Yellow Perch Populations in Coastal Areas of Eastern Lake Michigan

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Genetic structure of yellow perch populations in coastal areas of eastern Lake Michigan

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DEDICATION

This is dedicated to all my family and friends, whom have supported me throughout my journey.

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ABSTRACT

Genetic population substructure is often overlooked because of discontinuities between management and actual population structure as in the case of yellow perch, an ecologically and economically important indigenous fish species in the Laurentian Great Lakes. A knowledge gaps pertaining to the natural history of yellow perch relates to the biological connectivity between nearshore Lake Michigan and drowned river mouth (DRM) lakes, where it remains unclear whether resident yellow perch from Lake Michigan use DRM lakes for spawning or whether DRM lakes contribute to nearshore yellow perch populations in Lake Michigan. I used DNA fingerprinting (genotyping) to explore biological connectivity between DRM lakes and nearshore Lake Michigan during autumn by: (1) comparing the genetic structure of yellow perch collected from littoral habitats among DRM lakes, and (2) comparing genetic structure of yellow perch from DRM lakes with nearshore Lake Michigan. I hypothesized that (a) yellow perch from Lake Michigan move into DRM lakes during autumn but do not spawn, (b) yellow perch from DRM lakes differ genetically from nearshore Lake Michigan and do not form a panmictic population, and (c) DRM lakes will exhibit genetic isolation by distance. Overall, yellow perch exhibited low genetic diversity. The southern DRM lakes (i.e., Muskegon, White, and Pentwater lakes) were genetically similar to each other. Lake Charlevoix was genetically different from all other sites, but most similar to nearshore northern Lake Michigan. Nearshore northern Lake Michigan was intermediate to Lake Charlevoix and southern Lake Michigan. Analysis of a subset of yellow perch from Muskegon Lake revealed that fish captured in deep-water habitat differed genetically from individuals from littoral habitat and were most genetically similar to nearshore southern Lake Michigan. Understanding yellow perch spawning stocks is important for managing and maintaining a yellow perch fishery in eastern Lake Michigan.

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INTRODUCTION

Stock delineation is an important tool for successful fisheries management (Begg et al. 1999), especially for economically important fish species. Genetic population substructure is often overlooked because of discontinuities between management and actual population structure (Kocovsky et al. 2013). Yellow perch (*Perca flavescens*) in the Laurentian Great Lakes is one such species. The yellow perch is an indigenous species in Lake Michigan that plays an important ecological and economical role throughout the region (Clapp and Dettmers 2004). In the late 1990s, yellow perch experienced dramatic declines that lead to the closing of the commercial fishery and caused great concern about maintaining a yellow perch population to sustain the recreational fishery (Clapp and Dettmers 2004). Thus, understanding yellow perch stock structure is an important piece of the successful management of this species.

Researchers have discovered that yellow perch in the eastern Great Lakes show complex patterns of genetic population stock structure (Sepulveda-Villet and Stepien 2011; Kocovsky et al. 2013; Sullivan and Stepien 2014). Great Lakes yellow perch originated from the Mississippian and Atlantic glacial refugium (Sepulveda-Villet and Stepien 2012) and exhibit low to moderate genetic diversity, which is common for freshwater fish in these post-glacial environments. However, overexploitation also has contributed to lower genetic diversity in yellow perch (Bernatchez and Wilson 1998; Sepulveda-Villet and Stepien 2012; Parket et al. 2009; Sepulveda-Villet and Stepien 2011; Sullivan and Stepien 2014). Low to moderate genetic variation also was noted in other percids such as the European perch (*Perca fluviatilis*) and ruffe (*Gymnocephalus cernua*) (Sullivan and Stepien 2014; Stepien et al. 1998, 2005). Compared to Lake Michigan, yellow perch in Lake Erie and the Huron-Erie corridor had higher levels of genetic variation, which also is consistent with walleye (*Sander vitreus*) populations located in

the same region (Sullivan and Stepien 2014). Overexploitation as well as habitat loss has led to population declines throughout much of the Great Lakes. Thus, it is important for managers to identify stock structure to design and implement proper management strategies for the recovery of this species, especially in Lake Michigan.

Many uncertainties remain regarding yellow perch genetic stock structure in Lake Michigan as well as the contribution of drowned river mouths to overall stock structure. A previous investigation in the stock structure for yellow perch in Lake Michigan suggested a separation between spawning groups of Green Bay and southern Lake Michigan (Miller 2003). Also, attempts to assign yellow perch from northern and southern Lake Michigan to their correct spawning stocks were barely more than 50% successful (Miller 2003). Adult yellow perch captured in a mark-recapture study in southern Lake Michigan may travel distances greater than 100 km, and these adult yellow perch did not exhibit spawning site fidelity but used a larger surrounding area (Glover et al. 2008). Other mark-recapture studies showed that yellow perch outside of the Great Lakes basin have travelled over 170 km (Miller 2003). Other research showed that larval yellow perch can be transported long distances in the southern basin of Lake Michigan through mass water currents, thus forming a genetically homogenous population in the southern basin of Lake Michigan (Höök et al. 2006). Clearly, there are still gaps in the knowledge of this species' life history, particularly regarding the genetic relationship with connected subpopulations. More specifically, knowledge is lacking regarding the genetic connectivity between nearshore Lake Michigan and drowned river mouth (DRM) lakes and how DRM lakes are used by yellow perch.

DRM lakes are an important link between Lake Michigan and its tributaries on its eastern shoreline. DRM lakes are influenced by both Lake Michigan water levels and riverine inputs

(Keough et al. 1999; Wilcox et al. 2002; Larson et al. 2013). These systems provide essential habitat, such as spawning sites and nursery habitat, for many fish species, including yellow perch (Chubb and Liston 1986; Jude and Pappas 1992; Darnaude et al. 2004; Janetski et al. 2013). Currently, DRM lakes are managed differently from Lake Michigan and are managed as inland lakes (Michigan Fishing Guide 2014); thus, deemphasizing the connection between DRM lakes and nearshore Lake Michigan with respect to yellow perch population structure.

The direct connectivity between Lake Michigan yellow perch populations and those in DRM lakes is not fully understood. Currently, there is conflicting evidence regarding the degree of connectivity between the two types of systems (nearshore Lake Michigan and DMR lakes). Perrone et al. (1983) found that yellow perch larvae captured in Lake Michigan before mid-June likely were hatched in a DRM lake and migrated to Lake Michigan, suggesting connectivity between the two habitats. This evidence is consistent with observations that resident yellow perch from Lake Michigan may migrate into DRM lakes during autumn, possibly for spawning (Schneider et al. 2007). However, a study on yellow perch population genetics found that yellow perch from five DRM lakes were genetically distinct from Lake Michigan (Parker et al. 2009), but did not make inference regarding the genetic structure among DRM lakes. Furthermore, there is evidence of an asynchrony in the recruitment strength of juvenile yellow perch between DRM lakes and Lake Michigan, which was not consistent with the hypothesis of strong connectivity between yellow perch populations in the two habitat types (Janetski et al. 2013). However, these studies (i.e., Parker et al. 2009, Janetski et al. 2013) focused on sampling shallow littoral habitats in DRM lakes, which could have overlooked migrant yellow perch that used deeper-water habitats in DRM lakes. The purpose of this study was to explore the genetic relationship of yellow perch between DRM lakes and nearshore Lake Michigan by: (1) comparing the genetic

structure of yellow perch collected from littoral habitats among DRM lakes during autumn, and (2) comparing genetic structure of yellow perch from DRM lakes with nearshore Lake Michigan. I hypothesized that yellow perch from (a) Lake Michigan move into DRM lakes during autumn but do not spawn (based upon Schneider et al. [2007] and Parker et al. [2009]); (b) DRM lakes differ genetically from nearshore Lake Michigan and do not form a panmictic population, and (c) DRM lakes exhibit genetic isolation by distance, as a similar pattern was shown for the round goby (*Neogobius melanostomus*) across a similar spatial scale in Lake Michigan (LaRue et al. 2011).

METHODS

Study Sites

Sample sites included four DRM lakes connected to eastern Lake Michigan, USA (Figure 1): Lake Charlevoix (7000 ha, Charlevoix Co.), Pentwater Lake (176 ha, Oceana Co.), White Lake (1049 ha, Muskegon Co.), and Muskegon Lake (1697 ha, Muskegon Co). Muskegon Lake and Lake Charlevoix are the deepest of the DRM lakes with a maximum depth of 24 and 37 m, respectively. There is evidence of hypolimnetic hypoxia in Muskegon Lake at depths greater than 5 m during summer months (Figure 2; Altenritter et al. 2013). This trend was investigated to determine temporal deep-water habitat use by yellow perch. White Lake has a maximum depth of 18 m, and Pentwater Lake is the shallowest with a maximum depth of 9 m. We also sampled two nearshore sites in Lake Michigan adjacent to Charlevoix (hereafter northern Lake Michigan) and Grand Haven (hereafter southern Lake Michigan). These Lake Michigan locations have been routinely monitored by the Michigan Department of Natural Resources (MDNR) since 1996 (Fitzgerald et al. 2004; Makauskas and Clapp 2012).

Sample Collection

Yellow perch from Pentwater, White, and Muskegon lakes were sampled in littoral habitats (depth < 2 m) via boat electrofishing during September-November 2012. Lake Charlevoix was only sampled via gill nets in depths ranging from 9 to 20 m by the MDNR during August-September 2012. To complement boat electrofishing in littoral habitats, gill netting of yellow perch also was conducted in deep-water habitats of Muskegon Lake during September-November 2012 in conjunction with gill netting for another project (see Altenritter et al. 2013), to test the hypothesis that yellow perch from Lake Michigan use deep-water habitats in Muskegon Lake during autumn. The catch data from gill netting in Muskegon Lake was used to

delineate use of deep-water habitats by yellow perch in Muskegon Lake. Yellow perch from both Lake Michigan sites (northern and southern Lake Michigan) were collected by the MDNR via trawling and gill netting during the spring (April-May) of 2013. Anal fin clips were collected from 20 yellow perch from each DRM lake and Lake Michigan site and stored in 95% ethanol for genetic analysis.

Genetic Analysis

DNA was extracted from yellow perch anal fin tissue samples using a Qiagen DNeasy kit following manufacturer's instructions (Qiagen, Valencia, CA). Population genetic structure was evaluated by examining variation in 12 microsatellite loci developed for yellow perch and walleye (*Sander vitreus*), including *Svi*4, *Svi*6, *Svi*17, *Svi*18, *Svi*33, *Svi*2, *Svi*3, *Svi*7 (Borer et al. 1999; Eldridge et al. 2002; Miller 2003; Parker et al. 2009; Sepulveda-Villet and Stepien 2012), YP6, YP16, YP13, and YP17 (Li et al. 2007; Parker et al. 2009; Sepulveda-Villet and Stepien 2012). Microsatellite loci were amplified using polymerase chain reaction (PCR) in an Eppendorf Mastercycler. The PCRs for primers *Svi*2, *Svi*7, *Svi*18, *Svi*4, YP6, YP16, YP17 contained 11.3 µL of ultra-pure water, 5 µL 5X reaction buffer, 2 µL MgCl, 2.5 µL dNTP, 0.5 µL tagged primer, 0.5 tag, 1 µL primer, 0.5 µL taq polymerase, and 2 µL DNA template. The PCRs for primers *Svi*17, *Svi*33, *Svi*6, YP13 contained 10.3 µL of ultra-pure water, 5 µL 5X reaction buffer, 3 µL MgCl, 2.5 µL dNTP, 0.5 µL tagged primer, 0.5 tag, 1 µL primer, 0.5 µL taq polymerase, and 2 µL DNA template. The PCR for primer *Svi*3 contained 9.3 µL of ultra-pure water, 5 µL 5X reaction buffer, 4 µL MgCl, 2.5 µL dNTP, 0.5 µL tagged primer, 0.5 tag, 1 µL primer, 0.5 µL taq polymerase, and 2 µL DNA template. Each primer was fluoresced with a dye, and each plate contained a negative control without DNA to detect potential PCR contamination (Miller 2003; Parker et al. 2009). A touchdown thermal cycle of 2 min at 94°C for

initial denaturation, followed by 40 cycles of denaturation (92°C, 30 s), primer annealing (1 min) temperatures of 65-55°C, 62-52°C, and 58-48°C and polymerase extension (72°C, 30 s) was used to amplify the microsatellite loci. A final extension at 72°C for 5 min was included to minimize partial strands. Amplified products were analyzed on an ABI Hitachi 3130xl Genetic Analyzer.

Statistical Analysis

Population structure was assessed using Bayesian-based clustering program STRUCTURE version 2.3.4, which uses multi-locus genotype data to investigate population structure (Pritchard et al. 2000; http://pritchardlab.stanford.edu/structure.html). Program STRUCTURE was used to assign membership of individuals to groups. Using this program, a model was used where K populations (K may be unknown) were assumed, and each population was characterized by a set of allele frequencies at each locus. Individuals in the sample were assigned based on likelihood to populations, or jointly to two or more populations if their genotypes indicated that they were admixed. Populations are assumed to adhere to Hardy-Weinberg equilibrium and linkage equilibrium (Pritchard et al. 2000). I tested for the number of true population groups in independent runs, ranging from a K=1 (panmixia) to K=6 (each sampling location as an independent population group), with 10 independent runs for each K, 100,000 replicate burn-in, and 200,000 replicates with location prior included. Optimal K scenarios were determined based on the evaluation of ΔK (Evanno et al. 2005).

Genetix version 4.05 (Belkhir et al. 2004; available at www.genetix.univ-montp2.fr/genetix/intro.htm) was used to explore population divisions and clustering with three-dimensional factorial correspondence analysis (3D-FCA). This analysis evaluated variation

within and among sites, and it clustered groups according to similarities without a priori assumptions about relationships.

GENEPOP (web version) was used to assess genotypic differentiation and pairwise F_{ST} for all pairs of populations (Raymond and Rousset 1995; available at http://genepop.curtin.edu.au/index.html). Markov chain parameters used were a dememorization of 1000, 100 batches, and 1000 iterations per batch. F_{ST} is estimated by a "weighted" analysis of variance (Cockerham 1973; Weir and Cockerham 1984)

Isolation by distance between each DRM lake was calculated by measuring the distance between the west channel entrances (i.e., the part of the channel that is in Lake Michigan). The distance between each pair of DRM lakes was graphed against its associated pairwise F_{ST} value (generated from GENEPOP).

Yellow perch catch data from gill netting in Muskegon Lake during 2012 and 2013 were analyzed to determine when fish used deep-water habitats. Sampling took place from September to December. Sampling was carried out in deep-water habitats in western Muskegon Lake.

Figure 1. Sample sites include four drowned river mouth lakes (Lake Charlevoix, Pentwater Lake, White Lake, and Muskegon Lake) and two nearshore Lake Michigan sites (N. Lake Michigan and S. Lake Michigan).

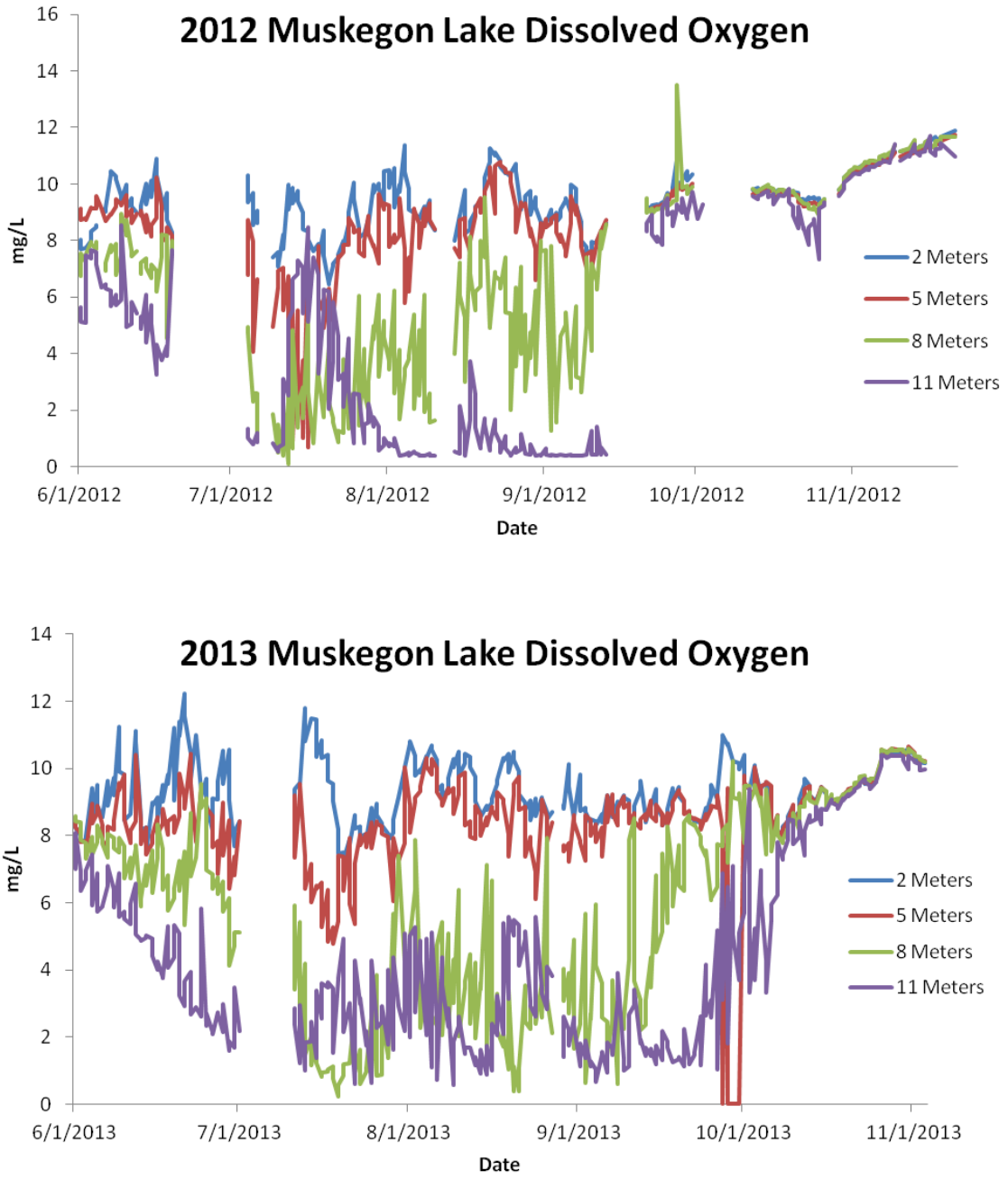


Figure 2. Dissolved oxygen concentrations at 2, 5, 8, and 11 m in Muskegon Lake from June 1 to November 1 in 2012 (top) and 2013 (bottom). Data were generated from the Muskegon Lake Buoy Observatory (http://www.gvsu.edu/wri/buoy/data-index.htm).

RESULTS

Eleven of twelve loci were polymorphic. Locus *Svi*18 was monomorphic and was therefore excluded from further analyses. A total of 140 yellow perch were genetically analyzed in this study, with an overall average total length of 19.4 cm (Table 1).

Table 1. Minimum, maximum, and mean total lengths of yellow perch used in genetic analyses at each site. Population identifications are; Musk = Muskegon Lake, Pent= Pentwater Lake, White= White Lake, S. MI= Southern Lake Michigan, N. MI= Northern Lake Michigan, Char= Lake Charlevoix.

Sampling site	Min Length (cm)	Max Length (cm)	Mean Length (cm)	N
Musk (littoral)	13.0	19.8	16.4	20
Musk (deep)	20.3	27.4	22.5	20
Pent	13.0	20.0	15.3	20
White	14.0	22.0	16.5	20
S. MI	15.9	22.1	18.5	20
N. MI	14.5	35.7	21.3	20
Char	16.5	34.0	25.1	20
Average	14.5	26.9	19.4	

STRUCTURE Analysis

Bayesian-based clustering along with delta K evaluations revealed population structure of three subpopulations (K=3), consisting of (1) Lake Charlevoix, (2) southern Lake Michigan, and (3) the three southern DRM lakes: Muskegon Lake, Pentwater Lake and White Lake (Figure 3). Northern Lake Michigan was intermediate to Lake Charlevoix and southern Lake Michigan (Figure 3). STRUCTURE clustering also showed that a subset of yellow perch captured in Muskegon Lake were genetically similar to southern Lake Michigan (Figure 3; highlighted with a black box). Thus, based on these results, Muskegon Lake was split into two groups: fish sampled from littoral habitats that were primarily resident (i.e., Muskegon Lake) fish and fish sampled from deep-water habitats in Muskegon Lake that were primarily migrants (i.e., from Lake Michigan).

Three-dimensional Factorial Correspondence Analysis

Three-dimensional factorial correspondence analysis was consistent with STRUCTURE results. Lake Charlevoix was distinct from all other sites. The southern DRM lakes were similar to each other but different from the Lake Michigan sites. Northern Lake Michigan was similar to both southern Lake Michigan and Lake Charlevoix. The deep-water habitat in Muskegon Lake was similar to southern Lake Michigan (Figure 4). Since Lake Charlevoix was substantially different from all other sites, these fish were removed and the analysis was repeated to examine patterns among the remaining sites. The result was that southern DRM lakes remained similar to each other and southern Lake Michigan and the deep-water habitat in Muskegon Lake also remained similar to each other (Figure 5). However, by removing Lake Charlevoix, northern Lake Michigan separated more clearly from southern Lake Michigan compared with the previous analysis of all sites. Finally, a separate analysis of only the southern DRM lakes was performed

to evaluate subtle patterns in genetic variation that may have been obscured in the previous analysis. This analysis suggested some definite distinction among the southern DRM lakes (Figure 6), but this separation was much finer than differences with Lake Michigan and Lake Charlevoix.

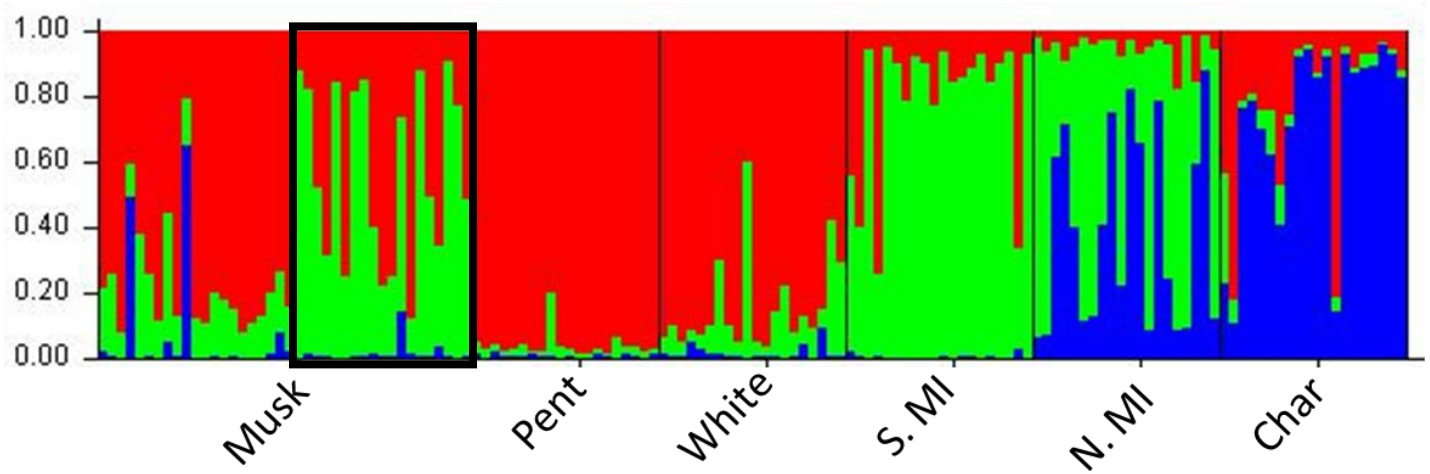


Figure 3. Estimated population structure of yellow perch from Bayesian structure analysis for K= 3 groups. Individuals are represented by thin vertical lines, which are partitioned into K colored segments representing the individuals' estimated membership fraction. The thin black lines separate sampling sites, and the black box outlines yellow perch from the deep-water habitat in Muskegon Lake. Population identifications are: Musk = Muskegon Lake, Pent = Pentwater Lake, White = White Lake, S. MI = southern Lake Michigan, N. MI= northern Lake Michigan, and Char = Lake Charlevoix. The *x*-axis represents individual fish and the *y*-axis represents proportion of an individual that belongs to a population.

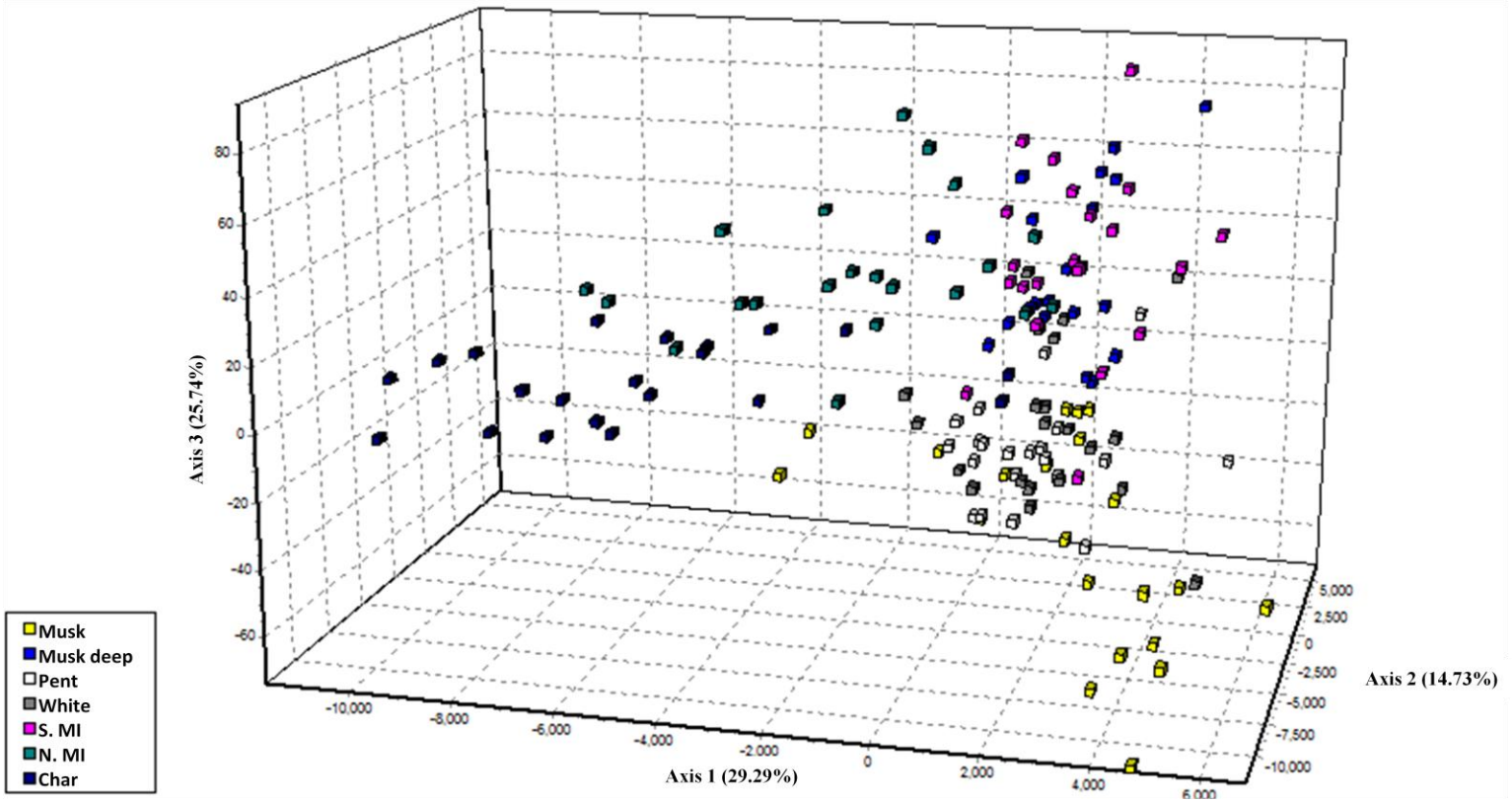


Figure 4. Three-dimensional factorial correspondence analysis of yellow perch microsatellite data. Population identifications are: Musk = Muskegon Lake (littoral habitats), Musk deep = deep-water habitat in Muskegon Lake, Pent = Pentwater Lake, White = White Lake, S. MI = southern Lake Michigan, N. MI = northern Lake Michigan, and Char = Lake Charlevoix.

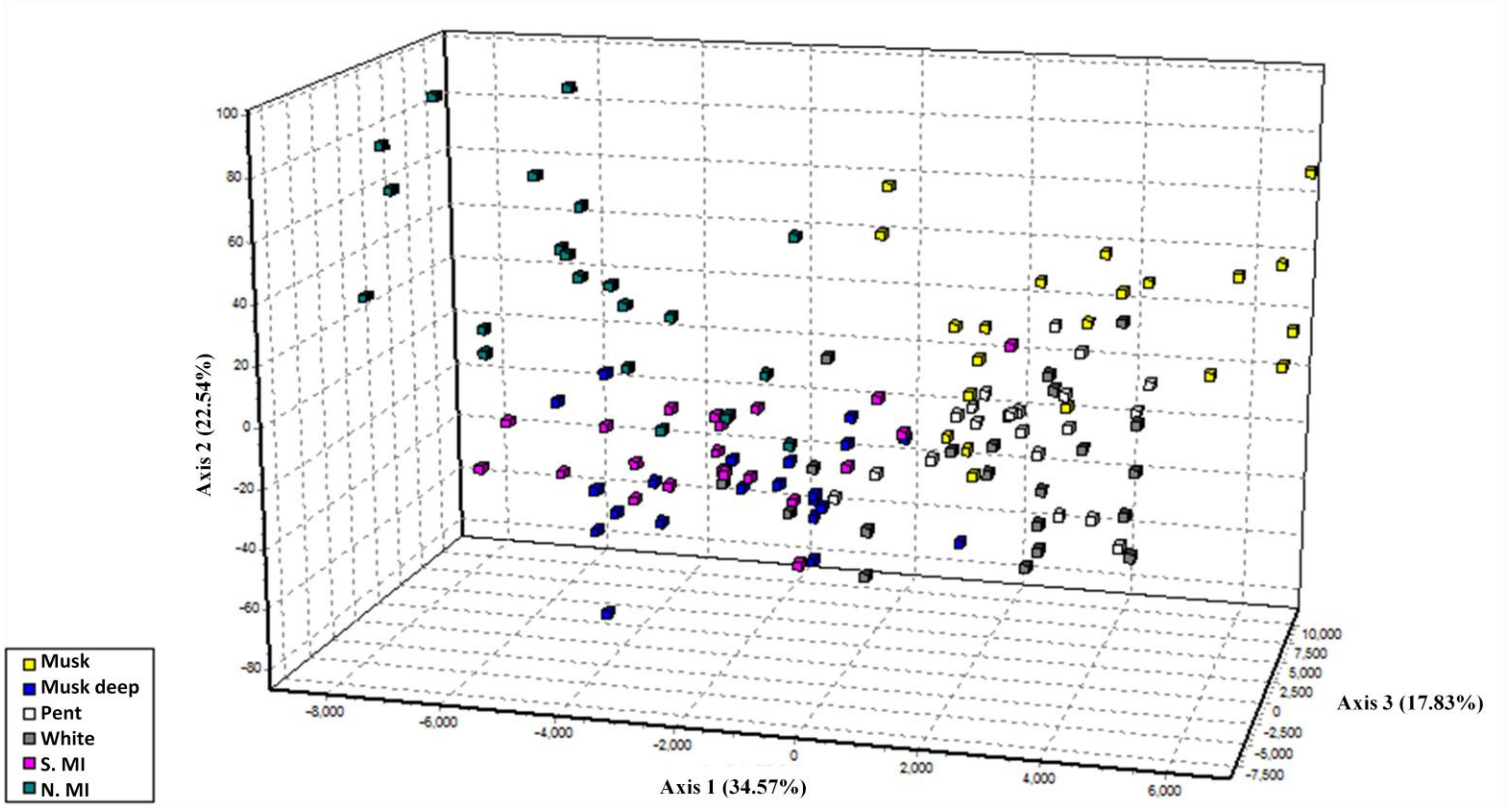


Figure 5. Three-dimensional factorial correspondence analysis of yellow perch microsatellite data. Since Lake Charlevoix was substantially different from all other sites, these fish were removed and the analysis was repeated to examine patterns among the remaining sites. Population identifications are defined in Figure 4.

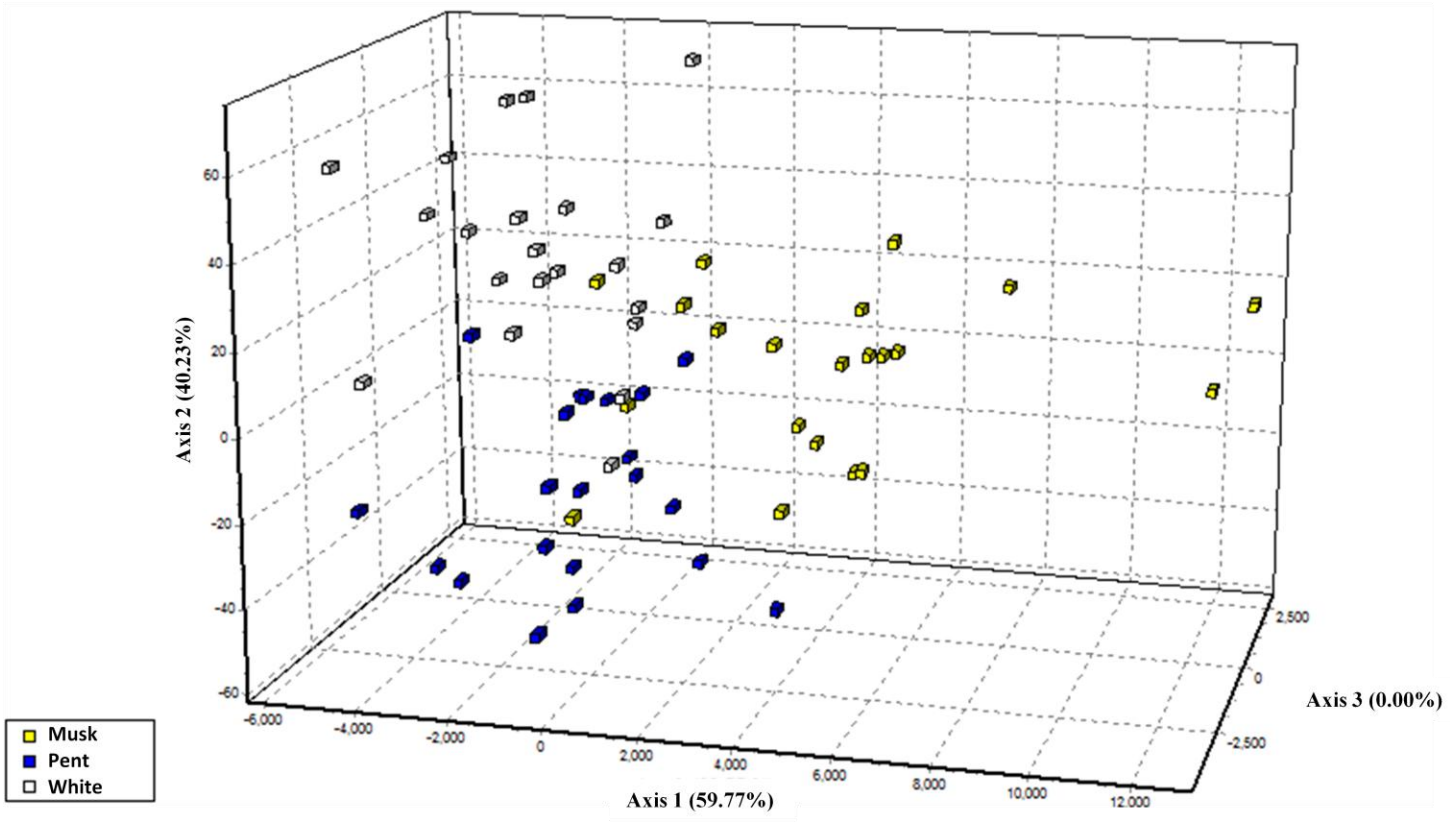


Figure 6. Three-dimensional factorial correspondence analysis of yellow perch microsatellite data. Analysis of only the southern drowned river mouth lakes was performed to evaluate subtle patterns in genetic variation that may have been obscured in the previous analysis. Population identifications are: Musk = Muskegon Lake (littoral habitats), Pent = Pentwater Lake, and White = White Lake.

GENEPOP Genotypic Population Differentiation and Pairwise F_{ST}

GENEPOP results showed significant genotypic differentiation ($P < 0.0024$) between Muskegon Lake littoral (i.e., fish sampled from littoral habitats), Muskegon Lake deep (i.e., fish sampled from deep-water habitats), southern Lake Michigan, northern Lake Michigan, and Lake Charlevoix (Table 2). Muskegon Lake littoral was not significantly different from Pentwater and White lakes ($P > 0.05$), while Muskegon Lake deep was not significantly different with the two Lake Michigan sites but differed from yellow perch in all of the other DRM lakes. White Lake was significantly different from Lake Charlevoix and northern Lake Michigan, but it was not significantly different from southern Lake Michigan (Table 2). The Lake Michigan sites were not significantly different from each other. Lake Charlevoix was significantly different from all other sites but was least different from northern Lake Michigan ($P = 0.0363$; Table 2).

Overall, pairwise F_{ST} values were low across all sites (Table 2). Average pairwise F_{ST} comparison was 0.0215. Pentwater and White lakes had the lowest pairwise F_{ST} (0.0010) followed by southern Lake Michigan and northern Lake Michigan (0.0025). Pentwater and Muskegon Lake deep had the highest pairwise F_{ST} value (0.0559) followed by Lake Charlevoix and Muskegon Lake deep (0.0539). Pairwise comparisons between the southern DRM lakes showed low genetic differentiation ($F_{ST} < 0.05$, Table 2), which was consistent with genotypic differentiation analyses.

Table 2. Pairwise F_{ST} (above diagonal) and genotypic differentiation (p-values below diagonal) for each population pair. Highest F_{ST} values are bolded. Bolded genotypic differentiation values were significantly different (P < 0.0024 with Bonferroni correction). Population identifications are defined in Figure 4.

	Musk	Musk deep	Pent	White	S. MI	N. MI	Char
Musk		**0.0454**	0.0046	0.0126	0.0233	0.0183	0.0228
Musk deep	**<0.0001**		**0.0559**	0.0171	0.0067	0.0088	**0.0539**
Pent	0.1872	0.0089		0.0010	0.0381	0.0265	0.0125
White	0.2412	0.0381	0.8895		0.0073	0.0188	0.0207
S. MI	**0.0014**	0.7431	**0.0011**	0.1753		0.0025	**0.0427**
N. MI	**0.0003**	0.1980	**0.0009**	**0.0023**	0.3192		0.0131
Char	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.0363	

Isolation by Distance

Isolation by distance was observed between the DRM lakes ($R^2 = 0.6924$; Figure 7). Muskegon Lake and Lake Charlevoix were the farthest DRMs apart and had the highest F_{ST} value (Table 3, Figure 7). Pentwater and White lakes had the lowest F_{ST} value and were the second closest DRM lakes (Table 3, Figure 7). Note that I excluded yellow perch from the deep-water habitat in Muskegon Lake deep from this analysis because they were more genetically similar to yellow perch from Lake Michigan and were considered migrants from Lake Michigan.

Table 3. Isolation by distance values for all pairs of DRM lakes. Population identifications are: Musk = Muskegon Lake (littoral habitats), Pent = Pentwater Lake, White = White Lake, and Char = Lake Charlevoix.

Population	Distance (km)	F_{ST}
Musk-White	19.31	0.0126
Pent-White	56.33	0.0010
Musk-Pent	75.64	0.0046
Pent-Char	162.54	0.0125
White-Char	273.59	0.0207
Musk-Char	294.51	0.0228

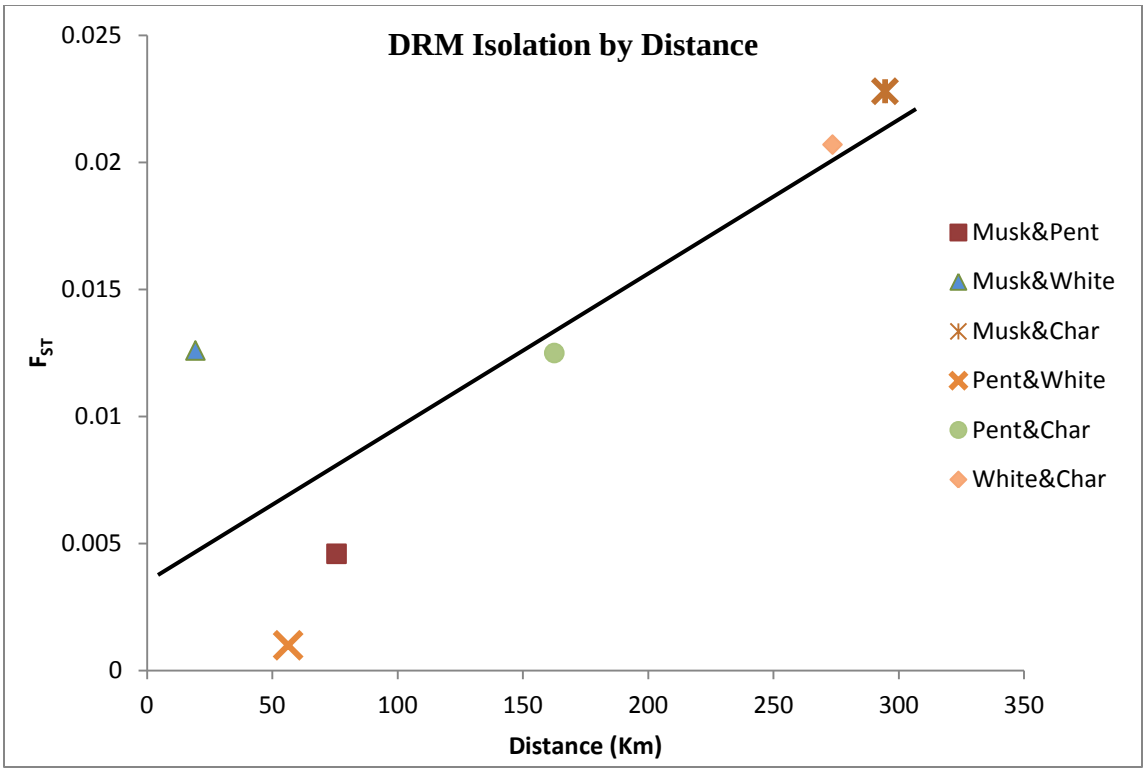
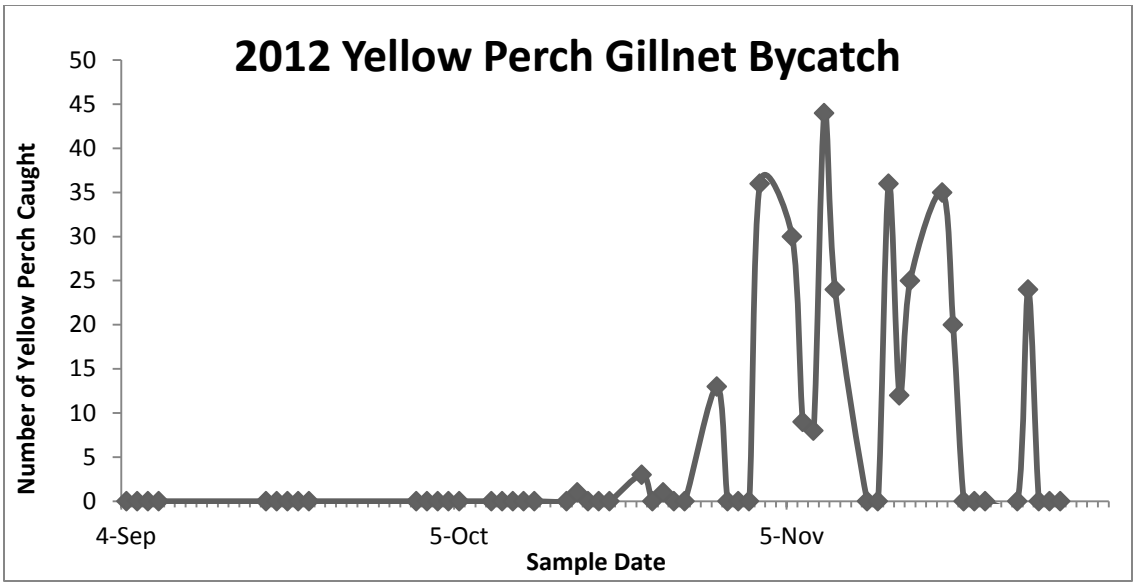


Figure 7. Isolation by distance graph for all pairs of DRM lakes. Population identifications are: Musk = Muskegon Lake (littoral habitats), Pent = Pentwater Lake, White = White Lake, and Char = Lake Charlevoix.

2012-2013 Supplementary Catch Data

Yellow perch catch data from gill netting in 2012 and 2013 revealed that yellow perch were not caught in deep-water habitats until late October/early November (Figure 8). This result is consistent with Muskegon Lake turnover (Figure 2). In 2012, gill netting began in September and the first yellow perch were caught on October 16, while the last yellow perch were caught on November 27. The highest number of yellow perch captured was 44 on November 8. In 2013, gill netting began in late September and the first yellow perch were caught on October 10, while the last yellow perch were caught on December 16. The highest number of yellow perch captured was 43 on November 8. Yellow perch total length ranged from 17 to 35 cm.



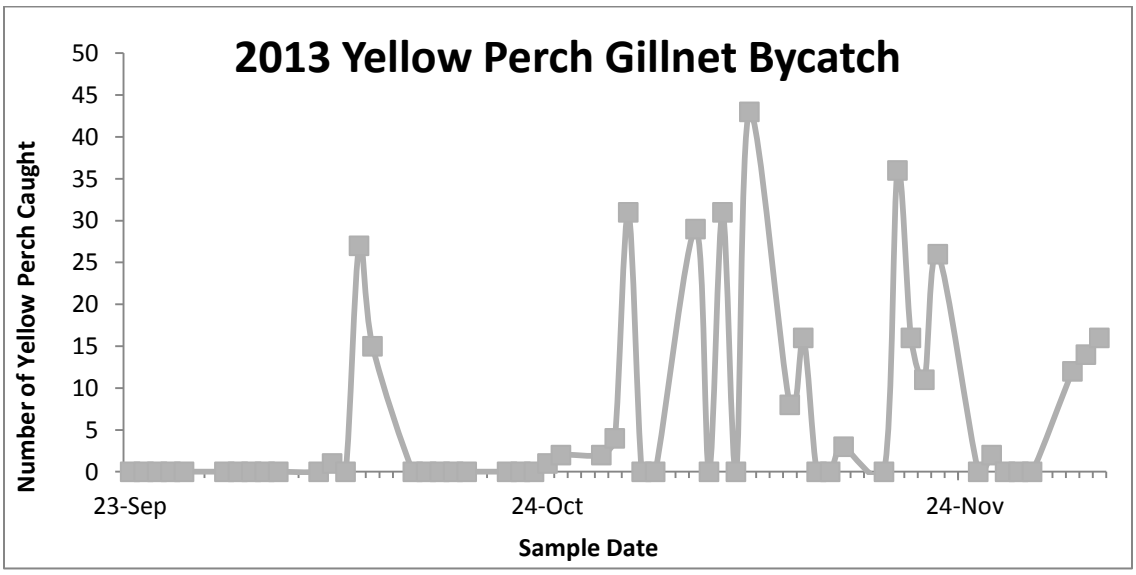


Figure 8. Yellow perch catch from gill netting in Muskegon Lake during 2012 (top) and 2013 (bottom).

DISCUSSION

The goal of this study was to explore the genetic relationship of yellow perch between DRM lakes and nearshore Lake Michigan by: (1) comparing the genetic structure of yellow perch collected from littoral habitats among DRM lakes, and (2) comparing genetic structure of yellow perch from DRM lakes with nearshore Lake Michigan. My results showed that yellow perch with a genetic fingerprint similar to Lake Michigan yellow perch were captured in a deep-water area of Muskegon Lake during autumn, which has not been previously documented (Figure 2). This evidence suggests migration of Lake Michigan yellow perch into Muskegon Lake during autumn. Because these systems have been shown to provide important habitat, such as spawning sites and nursery habitat for yellow perch (Chubb and Liston 1986; Jude and Pappas 1992; Darnaude et al. 2004; Janetski et al. 2013), potential explanations for this behavior are Muskegon Lake is being used for winter habitat or a staging area before spawning in Lake Michigan during the spring. This is an important finding because it can fundamentally change how Muskegon Lake and possibly other DRM lakes are managed for yellow perch, specifically related to harvest regulations. It is important to consider harvest of these migrant Lake Michigan yellow perch from the DRM lakes in the total harvest estimates for Lake Michigan.

This interesting result raises the question whether this migration happens in other DRM lakes because I only sampled deep-water habitats in Muskegon Lake among the southern DRM lakes. Gill netting data from Muskegon Lake suggested that yellow perch were not caught in deeper areas until late October and early November, well after the lake turned over, and resident yellow perch in littoral habitats had an opportunity to move into the deeper areas (Figures 2 and 8).

My study provides concrete evidence that the genetic structure of yellow perch in DRM lakes is distinct from nearshore Lake Michigan. This finding builds on previous research that focused on yellow perch sampled in Lake Michigan proper in an attempt to better understand their population ecology (Miller 2003; Clapp and Dettmers 2004; Glover et al. 2008). However, these studies did not explore the role of nearshore habitats in Lake Michigan such as wetlands and DRM lakes. My results also build on questions that resulted from Parker et al. (2009) because they lacked large sample sizes from DRM lakes and grouped yellow perch from multiple DRM lakes in their analysis. In addition, it has been shown that there is an asynchrony between high recruitment years in nearshore Lake Michigan and Muskegon Lake (Janetski et al. 2013). This evidence also supports our result of having distinct populations between Lake Michigan and DRM lakes.

DRM yellow perch populations were genetically isolated by distance with a clear gradient from southern to northern populations; however, this result was driven by high genetic diversity/difference of yellow perch from Lake Charlevoix relative to the other DRM lakes (Table 2; Figure 4). This relationship also was amplified by an overall low genetic diversity (e.g., low F_{ST} values) among yellow perch populations in southern DRM lakes, a finding that is consistent with past research on Lake Michigan (Miller 2003; Parker et al. 2009). Low overall genetic diversity within my study populations of yellow perch likely explained the unexpected STRUCTURE result that the southern DRM lakes were not genetically different to one another. Further investigation with three-dimensional factorial correspondence analysis (Figure 6) revealed subtle genetic differences among the southern DRM lakes. Genetic similarity among DRM lakes may also suggest that not enough time has passed post-colonization of DRM lakes to allow these DRM lake populations to become genetically isolated/distinct from each other or

their source population. Genetic analysis of more DRM lakes should be considered to fully answer questions about isolation of DRM lakes by distance, especially along the north-south gradient of eastern Lake Michigan.

Based on my study, there was no detectable genetic difference between yellow perch populations in northern and southern Lake Michigan, which coincides with findings from Miller (2003) that showed difficulty in correctly assigning Lake Michigan yellow perch to their correct northern or southern stocks. Furthermore, movement of yellow perch between southern and northern Lake Michigan is not uncommon. For example, Glover et al. (2008) discovered that adult yellow perch along the south and southeastern side of Lake Michigan travelled over 100 km.

Future studies should assess population genetic structure of yellow perch in more DRM lakes, sample both deep-water and littoral habitats, and sample across seasons. Also, the addition of more loci or the use of next generation sequencing could capture more genetic variation between Lake Michigan and DRM lakes. It also would be beneficial to better characterize the population genetic structure of yellow perch in nearshore Lake Michigan by adding sites between Grand Haven and Charlevoix. One limitation of my study was that conclusions were limited to fish sampled during autumn and temporal patterns in stock structure could not be addressed with my genetic data. For example, do Lake Michigan fish use deep-water areas of Muskegon Lake for over-wintering refugia when those deep-water areas are no longer hypoxic; or are yellow perch with genetic fingerprints similar to Lake Michigan still present in deep-water habitats of Muskegon Lake throughout the spring and early summer seasons before the lake becomes stratified and hypoxic conditions in the hypolimnion become more prevalent? Seasonal

sampling would help address knowledge gaps relating to the temporal variation of biological connectivity between DRMs and nearshore Lake Michigan.

CONCLUSION

This study provides evidence that Lake Michigan yellow perch use Muskegon Lake during autumn, which has not been shown by previous research. I found that yellow perch with a genetic fingerprint similar to Lake Michigan in Muskegon Lake during autumn after the lake turned over (i.e., no longer thermally stratified) in deep-water habitat. It is thus important for Lake Michigan yellow perch management strategies to consider Muskegon Lake and possibly other DRM lakes, which could be providing important habitats for Lake Michigan yellow perch during part of the year and account for the extra harvest of Lake Michigan yellow perch that is not currently taken into account. Future research should determine whether Lake Michigan yellow perch are migrating into other DRM lakes or whether the phenomenon I documented is unique to Muskegon Lake. Fishery managers should take into account yellow perch genetic stocks and their use of DRM lakes when determining harvest seasons and bag limits for Lake Michigan.

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