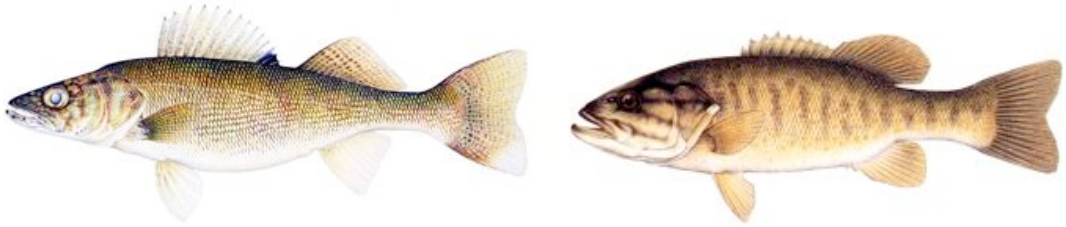
Report on the Genetic Spawning Site Stock Structure of Lake Erie Walleye, Yellow Perch, and Smallmouth Bass



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24 January 2006

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Funding Support

NOAA Ohio Sea Grant # R/L-7 "Walleye And Yellow Perch Stock Structure in the Great Lakes: A High-Resolution DNA Data Base For Fishery Management" 2004-7

Lake Erie Protection Fund #- LEPF 00-15 "Genetic Markers for Defining and Evaluating Stock Structure of Yellow Perch in Lake Erie" 2001-2004

USEPA "High-Resolution Delineation of Lake Erie Fish Populations: DNA Databases for Resource Management 2006-2008

Recent Research Presentations on Lake Erie Fishery Stock Structure by the Great Lakes Genetics Lab

2005

- Carol A. Stepien, Alexander M. Ford, and Jhonatan Sepulveda Villet. 2005. *Population genetic structure of yellow perch in the Great Lakes: a comparison with eastern North American populations* Poster presentation at the annual meeting of the Ohio Division of Wildlife held in Columbus, Ohio on Feb. 4.
- Carol A. Stepien and Rex M. Strange. 2005. *Discerning population genetic structure and geographic patterns of smallmouth bass in the Great Lakes* Poster presentation at the annual meeting of the Ohio Division of Wildlife held in Columbus, Ohio on Feb. 4.
- Rex M. Strange and Carol A. Stepien. 2005. *Genetic stock structure of walleye (Sander vitreus) in Lake Erie as inferred from mitochondrial and microsatellite loci* Poster presentation at the annual meeting of the Ohio Division of Wildlife held in Columbus, Ohio on Feb. 4.
- Carol Stepien. 2005. *An overview of walleye and yellow perch stock structure in Lake Erie, based on nuclear and mitochondrial DNA analyses* Oral research presentation to Walleye and Yellow Perch Lake Erie Task Forces at their annual meeting on Feb. 23
- James Coss and Carol Stepien 2005. *GIS Analysis of walleye and yellow perch spawning sites* Oral research presentation to Walleye and Yellow Perch Lake Erie Task Forces at their annual meeting on Feb. 23.]
- Osvaldo Jhonatan Sepulveda-Villet and Carol A. Stepien. 2005. *Yellow perch population genetics in Lake Erie* Oral research presentation to Yellow Perch Lake Erie Task Force at their annual meeting on Feb. 23.
- Rex M. Strange and Carol A. Stepien 2005. *Walleye population genetics in Lake Erie* Oral research presentation to Walleye Lake Erie Task Force at their annual meeting on Feb. 23.

- Rex M. Strange and C.A. Stepien. 2005. *Patterns of Genetic Variation Among Walleye Spawning Stocks in the Great Lakes Region* International Association for Great Lakes Research (IAGLR) annual meeting, Ann Arbor, Michigan.
- Carol A. Stepien, Alex M. Ford, and Jhonatan Osvaldo Sepulveda Villet. 2005. *Population Genetic Structure of Yellow Perch In The Great Lakes: A Comparison With Eastern North American Populations* Poster presentation at International Association for Great Lakes Research (IAGLR) annual meeting, May 2005, Ann Arbor, Michigan.
- Carol A. Stepien and Rex M. Strange. 2005. *Population Genetic Structure and Geographic Patterns of Smallmouth Bass in the Great Lakes* Oral research presentation by Carol Stepien at International Association for Great Lakes Research (IAGLR) annual meeting May 2005, held in Ann Arbor, Michigan.
- Rex M. Strange and Carol A. Stepien 2005. *Patterns of Genetic Variation Among Walleye Spawning Stocks in the Great Lakes Region* Oral research presentation by Rex Strange at American Society of Ichthyologists and Herpetologists (ASIH) annual meeting July 2005, held in Tampa, FL.
- Carol A. Stepien and Rex M. Strange. 2005. *DNA Identification of Yellow Perch Fillets from a Fish Fry: Is the Fish on Your Menu Local?* Poster research presentation by Carol Stepien at American Society of Ichthyologists and Herpetologists (ASIH) annual meeting July 2005, held in Tampa, FL. (also presented at Sea Grant colloquium at Ohio State University, August 21, 2005).
- Carol A. Stepien and Rex M. Strange. 2005. *Population Genetic Structure and Geographic Patterns of Smallmouth Bass in the Great Lakes* Oral research presentation by Carol Stepien at American Society of Ichthyologists and Herpetologists (ASIH) annual meeting July 2005, held in Tampa, FL.
- Sepulveda-Villet, Osvaldo Jhonatan, Alex M. Ford, and Carol A. Stepien. 2005. *Population Genetics Structure of Yellow Perch in the Great Lakes: A Comparison with Eastern North American Populations.* Oral research presentation by Osvaldo Jhonatan Sepulveda-Villet at American Society of Ichthyologists and Herpetologists (ASIH) annual meeting July 2005, held in Tampa, FL.
- Rex M. Strange and Carol A. Stepien 2005. *Walleye stock structure in the Great Lakes: A high resolution DNA database for fisheries management*. Poster presentation at Sea Grant colloquium at Ohio State University, August 21, 2005.
- Sepulveda-Villet, Osvaldo Jhonatan and Carol A. Stepien. 2005. *Yellow Perch Stock Structure in the Great Lakes and Beyond: Resolving Patterns using Mitochondrial and Nuclear DNA.* Poster presentation at Sea Grant colloquium at Ohio State University, August 21, 2005.
- Stepien, Carol A., Douglas J. Murphy, and Rex M. Strange. 2005. *Genetic Structure of Smallmouth Bass Populations from Nuclear DNA.* Poster presentation at Sea Grant colloquium at Ohio State University, August 21, 2005.

2004

- C.A. Stepien and W.C. Borden. 2004. *Population Structure of Smallmouth Bass in Lake Erie* Oral research presentation at 44th Ohio Fish and Wildlife Conference, Columbus, Ohio, February 6. (given by C. Stepien)

- Alex M. Ford and C.A. Stepien. *Update on Population Genetic Status of Yellow Perch in Lake Erie* The Lake Erie Yellow Perch Task Force meeting February. 2004.
- Carol A. Stepien. *Update on Population Genetic Status of Walleye in Lake Erie*. The Lake Erie Walleye Task Force meeting February. 2004.
- Alex M. Ford and Carol A. Stepien. *Population Genetic Structure of Yellow Perch (Perca flavescens) in the Great Lakes* oral research presentation by Alex Ford at the American Society of Ichthyologists and Herpetologists annual meeting held in Norman, Oklahoma, June 2004.
- Carol A. Stepien and W.C. Borden. 2004. *Population Genetic Structure of Smallmouth Bass in the Great Lakes.* Poster presentation designed and presented by Carol Stepien at the annual meeting of the Society for the Study of Evolution July 2004 held at Colorado State University, Ft. Collins, CO.

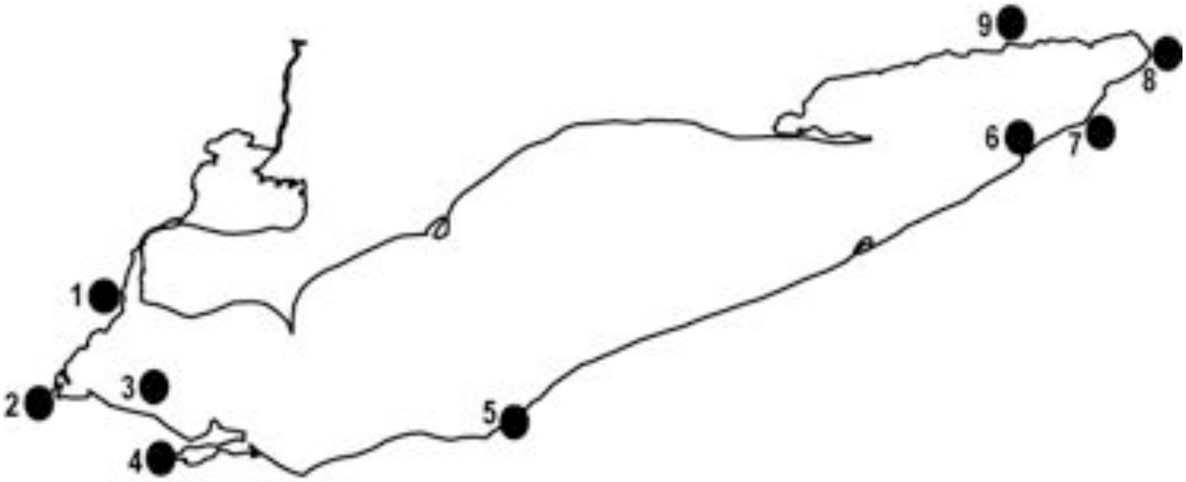
Recent and Coming Publications on Lake Erie Fishery Stock Structure by the Great Lakes Genetics Lab

- Ford, A.M. and C.A. Stepien. 2004. *Genetic variation and spawning population structure in Lake Erie yellow perch, Perca flavescens: A comparison with a Maine population*. In Proceedings of Percis III, the 3rd International Symposium on Percid Fishes, T.P. Barry and J.A. Malison, eds. University of Wisconsin Sea Grant Institute, Madison, WI. 131-2.
- Stepien, C.A. and E. Roseman. 2004. *Percid ecology: Current status and future research needs* In Proceedings of Percis III, the 3rd International Symposium on Percid Fishes, T.P. Barry and J.A. Malison, eds. University of Wisconsin Sea Grant Institute, Madison, WI . 5-6.
- Stepien, C.A., C.D. Taylor, and D.W. Einhouse. 2004. *An analysis of genetic risk to a native spawning stock of walleye Sander vitreus (Stizostedion vitreum) due to stocking in Cattaraugus Creek* In Proceedings of Percis III, the 3rd International Symposium on Percid Fishes, T.P. Barry and J.A. Malison, eds. University of Wisconsin Sea Grant Institute, Madison, WI. 93-94.
- Strange, Rex M. and Carol A. Stepien. 2005. *DNA identification of yellow perch fillets from a fish fry: Is the fish on your menu local?* Fisheries (In Review). Submitted December 2005.
- Borden, W.C., and C.A. Stepien. 2006. *Population genetic structure of smallmouth bass, Micropterus dolomieu Lacepède, in Lake Erie using mitochondrial DNA sequences and nuclear DNA microsatellites.* In Press.
- Stepien, C.A., D. Murphy, and R.M. Strange. 2006. *Broad to fine-scale genetic patterning in smallmouth bass Micropterus dolomieu across the Laurentian Great Lakes and beyond: An interplay of behavior and geography.* In manuscript. To be submitted early 2006.
- Ford, A.M., O.J. Sepulveda-Villet, and C.A. Stepien. 2006. *Population genetic structure of yellow perch (Perca flavescens) in the Great Lakes: A comparison with eastern North American populations.* In manuscript.
- *Strange, R.M., and C.A. Stepien.* 2006. *Intrinsic and Extrinsic Mechanisms underlying fine-scale population genetic structure in a vagile lacustrine fish – the walleye Sander vitreus.* In manuscript. To be submitted early 2006.

SUMMARY

The purpose of this report is to present a summary and interpretation of our research on Lake Erie spawning stock structure for walleye *Sander vitreus*, yellow perch *Perca flavescens*, and smallmouth bass *Micropterus dolomieu*. We analyzed mitochondrial (mt) DNA control region sequences and allelic variation at nuclear microsatellite loci for all three species from spawning sites in the three bathymetric basins of Lake Erie. The mtDNA marker is a maternally-inherited, single-locus genome that is passed to both male and female offspring from the egg. The nuclear DNA markers are biparentally inherited, and we tested 8 to 10 microsatellite loci per species. The sampling design included several spawning sites per basin for each species, although the sites and the sample sizes vary. Here we present in a common format levels of genetic diversity and divergence patterns among basins and spawning sites for each species, and compare and contrast them. The nuclear DNA in all of our results reveal greater patterning and increased sensitivity for evaluating fine-scale stock structure than does mtDNA. The microsatellite approach is more cost-effective and includes more loci, whereas mtDNA analyzes a single locus. The use of both is applicable for evaluating male versus female migration patterns. For all species, we found significant differences among some spawning sites in Lake Erie. Division (and management) of Lake Erie in three basins does not clearly correspond to the distribution of genetic variation among spawning groups (thus appears to be an "arbitrary" division with respect to fish population dynamics). In all three fish species – walleye, yellow perch, and smallmouth bass - the eastern basin of Lake Erie houses significantly more genetic diversity and private alleles than does the west. This appears to reflect their glacial refugia history and appears to have been maintained since by some spawning site specificity – which is greatest in the walleye. Thus, it is clear that the genetic diversity of spawning sites needs to be preserved. We found some possible influence of past stocking efforts of western Lake Erie walleye in the eastern basin. Fish from other spawning locations should not be stocked in order to conserve the genetic integrity of native fishes in Lake Erie. These studies are ongoing in our laboratory and we invite comments and questions from our agency collaborators.

Walleye Population Groups Analyzed



Western Basin

1. Huron River, MI[2]
2. Maumee River, OH[1,2]
3. Western Reef Complex – Canadian & U.S. (e.g., Touissant, Niagara, Hen Island) [1,2]
4. Sandusky Bay and River, OH[1,2]

Central Basin

5. Grand River, OH [1,2]

Eastern Basin

6. Van Buren Bay (Dunkirk), NY[1,2]
7. Cattaraugus Creek, NY[1,2]
8. Smoke's Creek, NY[2]
9. Grand River, ONT[1,2]

Data from these population groups consist of MtDNA (1) and/or microsatellite nuclear DNA (2) markers.

Statistics for Walleye Results

Table 1A. Mitochondrial DNA Diversity (Maternally Inherited) of Walleye Spawning per Lake Basin

	Gene diversity	N alleles (% of those in Lake Erie)	N unique alleles per basin (% of N alleles)
Western Basin	**0.735 +/- 0.024**	**10/15 67%**	**1/10 10%**
Central Basin	**0.713 +/- 0.064**	**04/15 27%**	**0/4 0%**
Eastern Basin	**0.738 +/- 0.024**	**13/15 87%**	**2/13 15.3%**

Interpretation: *Walleye collected from spawning sites in each of the three basins of Lake Erie have similar levels of genetic diversity in female-inherited markers. There is no appreciable evidence of population bottlenecks in any of the three basins. The major difference is that samples taken from the Central Basin have no unique mitochondrial alleles, and contain only the most common alleles that occur in Lake Erie. Our analysis includes fewer walleye from the Central Basin relative to the other basins because of the smaller number of spawning sites and historically smaller numbers of walleye spawning at those sites. Unique mtDNA alleles occur in both the west and east basins, with greatest number of unique alleles in the east.*

Table 1B. Nuclear DNA Diversity (bi-parentally inherited) of Walleye Spawning per Basin (Based on 10 Microsatellite Loci)

	Gene diversity	N alleles as % of those in Lake Erie	N unique alleles per basin
Western Basin	**0.771 +/- 0.001**	**80/90 90%**	**0**
Central Basin	**0.769 +/- 0.003**	**57/90 63%**	**0**
Eastern Basin	**0.801 +/- 0.001**	**90/90 100%**	**10/90 10%**

Interpretation: *Microsatellite variability among walleye spawning groups in the three basins is similar to the pattern observed at the mitochondrial locus. The walleye spawning groups in each basin have similar levels of genetic diversity. There is no appreciable evidence of population bottlenecks or lack of genetic diversity. However, the Central Basin has fewer alleles, and its spawning groups contain only the most common alleles. We have not analyzed as many walleye from the central basin as the other basins, due to the smaller numbers of spawning sites and numbers of walleye. Using nuclear DNA, the eastern basin has the most alleles and 10% of those are unique. Thus, all data show that the eastern basin walleye spawning groups are much more genetically variable than those spawning in the west. Since more walleye spawn in the western sites, it is particularly important to conserve genetic diversity in these eastern basin spawning groups. Stocking would be particularly deleterious in eastern basin groups, unless the genetic variability is very carefully preserved and monitored. Walleye from the western basin should not be stocked in the east.*

Table 2A. Distribution of Genetic Variability for Walleye mtDNA in Lake Erie Using Analysis of Molecular Variance (AMOVA)

Source of Variation	Percentage of Variation	Significance
Among 3 lake basins	1.54%	P < 0.0001
Among spawning sites within basins	0.49%	P < 0.0001
Within spawning sites	97.97%	P < 0.0048

Interpretation: *Most of the overall mtDNA variation in Lake Erie walleye is found within spawning sites, reflecting the large number of alleles within all samples of which most are shared among sites throughout the Lake. This is true of all fish groups in the Great Lakes, and reflects normal patterns in freshwater fishes in areas with interconnected waterways. However, the three Lake Erie basins are significantly different in their overall distributions of alleles, and spawning sites within each basin also differ significantly. These results show that Lake Erie contains separable spawning stocks of walleye and that walleye return to natal areas to spawn. In other words, Lake Erie walleye are not a single panmictic population. Fishery management should protect spawning sites for walleye in order to conserve these long-term patterns of genetic divergence.*

Table 2B. Distribution of Genetic Variability for Walleye Nuclear DNA Using Analysis of Molecular Variance (AMOVA)

Source of Variation	Percentage of Variation	Significance
Among groups (3 lake basins)	**0.001%**	**N.S.**
Among spawning sites within basins	**2.13%**	**P < 0.0001**
Within spawning sites	**97.87%**	**P < 0.0068**

Interpretation: *Most variation again occurs among individuals within spawning sites. The differences among spawning sites are significant – that is, the sites are different from each other in overall genetic composition. However, little of the observed mtDNA variation is distributed among the lake basins – showing that the concept of “basins” in fishery management is largely an artificial construct in terms of fish population groups.*

Table 3A. Mitochondrial DNA Divergences Among Walleye Spawning per Basin as Measured by *Fst*

	Western basin	Central Basin
Central Basin	***Fst*** **= 0.084** **P < 0.027****	**------**
Eastern Basin	***Fst*** **=0.005** **P < 0.072 N.S.**	***Fst*** **= 0.080** **P < 0.018****

***= significant at 0.05 level, **= significant after sequential Bonferroni correction**

Interpretation: *In this case, the central basin is significantly different from both the western and eastern basins. However, there is evidence of gene flow between the eastern and western basins, apparently due to the influence of Van Buren Bay/Dunkirk samples in our analysis. It may be that some female walleye from the Maumee River may stray to Van Buren Bay/Dunkirk to spawn, which we are currently investigating. This also may be due to stocking fish from the western basin to the eastern basin.*

Table 3B. Nuclear DNA Divergences Among Walleye Spawning per Basin as Measured by *Fst*

	Western basin	Central Basin
Central Basin	***Fst*** **= 0.002** **N.S.**	**------**
Eastern Basin	***Fst*** **=0.008** **P < 0.00001****	***Fst*** **= 0.014** **P < 0.00001****

****= significant after sequential Bonferroni correction**

Interpretation: *We found no clear genetic separation between the central and western basins, indicating possible gene flow between them. It is possible that the difference between this result and the mtDNA result may be due to male migration patterns or differential survival/success of stocked females versus males. Although the Fst values are low, differences in microsatellite composition of the eastern basin is significantly different than that in the central and western basins. Genetic divergence of eastern basin walleye is a re-occurring pattern in each of our data sets and analyses.*

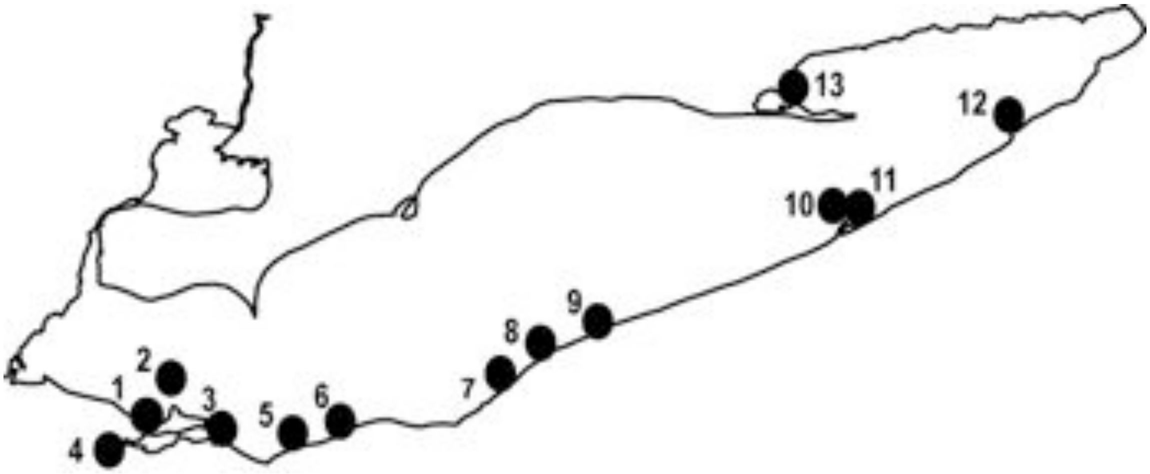
Table 4A. Matrix of Significant Differences in Microsatellite Composition among Individual Walleye Spawning Sites as Measured by *Fst*

	Huron River	W. Reef Complex	Maumee River	Sandusky River/Bay	Grand River, OH	Van Buren Bay	Cat. Creek	Smoke's Creek
West. Reef Complex	**0.061****							
Maumee River	**0.038****	**0.004**						
Sandusky River/Bay	**0.045****	**0.003**	**0.001**					
Grand River, OH	**0.033****	**0.002**	**0.001**	**0.002**				
Van Buren Bay	**0.044****	**0.011***	**0.002**	**0.001**	**0.008**			
Cattaraugus Creek	**0.032****	**0.047****	**0.048****	**0.046****	**0.037****	**0.050****		
Smoke's Creek	**0.001**	**0.027****	**0.033****	**0.031****	**0.033****	**0.031****	**0.034***	
Grand River, Ont.	**0.051****	**0.041****	**0.051****	**0.045****	**0.045****	**0.052****	**0.039****	**0.029****

***= significant at 0.05 level, **= significant after sequential Bonferroni correction**

Interpretation: *Many of the spawning populations in Lake Erie consist of genetically separable groups. There appears to be appreciable gene flow among most western basin spawning groups, especially the Maumee River, W. Reef Complex, and Sandusky River and Bay. The Central basin is quite similar to the western basin sites. However, the eastern basin sites differ from each other as well as from most western and central basin spawning sites. Walleye from Sandusky River/Bay appear genetically similar to those from the Central Basin and Van Buren Bay/Dunkirk, which may indicate gene flow among these spawning groups. Note that walleye from Cattaraugus Creek are genetically distinct from other walleye in the Lake Erie watershed despite stocking efforts that introduced fish from the Maumee River in 1996 through 2000. The genetic relationships of this group was detailed by Stepien et al. (2004).*

Yellow Perch Population Groups



Western Basin

1. Port Clinton, OH[1]
2. South Bass Island, OH[1]
3. Cedar Point, OH[1,2]
4. Sandusky, OH[1]

Central Basin

5. Vermilion, OH[1]
6. Lorain, OH[1,2]
7. Fairport, OH[1]
8. Geneva, OH[1]
9. Ashtabula, OH[1]

Eastern Basin

10. Presque Isle, PA[1]
11. Erie, PA[1]
12. Dunkirk (Van Buren Bay), NY[1,2]
13. Long Point Bay, Ontario[1]

Data from these population groups consist of MtDNA (1) and/or microsatellite nuclear DNA (2) markers.

Statistics for Yellow Perch Results

Table 5A. Mitochondrial DNA Diversity (Maternally Inherited) of Yellow Perch Spawning per Lake Basin

	Gene diversity	N alleles (% of those in Lake Erie)		N unique alleles per basin (% of N alleles)	
Western Basin	**0.139 +/- 0.056**	**04/11**	**36%**	**1/4**	**25%**
Central Basin	**0.272 +/- 0.056**	**07/11**	**64%**	**3/7**	**43%**
Eastern Basin	**0.199 +/- 0.065**	**06/11**	**55%**	**3/6**	**50%**

Interpretation: *The Yellow Perch spawning in each of the three Lake Erie basins have similar levels of genetic diversity, shown with maternally-inherited mtDNA. Yellow perch populations have lower genetic diversity than found in walleye populations, which may be due to the boom-and-bust history of yellow perch in Lake Erie. However, all Perca as well as their sister genus Gymnocephalus- the ruffe- also have low mtDNA diversity, so this is likely a characteristic of their entire group. Yellow perch spawning in the central and eastern basins have a greater number of unique alleles, and more alleles overall, than do those in the western basin. This pattern is similar to what we found for walleye.*

Table 5B. Nuclear DNA Diversity (bi-parentally inherited) of Yellow Perch Spawning per Basin (Based on 6 Microsatellite Loci)

	Gene diversity	N alleles as % of those in Lake Erie		N unique alleles per basin	
Western Basin	**0.527 +/- 0.003**	**55/80**	**69%**	**20/55**	**36%**
Central Basin	**0.549 +/- 0.003**	**48/80**	**60%**	**15/48**	**31%**
Eastern Basin	**0.544 +/- 0.003**	**43/80**	**54%**	**8/43**	**19%**

Interpretation: *Nuclear DNA results show that the genetic diversity of yellow perch in all three basins is similar, as we found with mtDNA. There is a pattern showing a slight decrease in the number of alleles from west to east, which is different than found with the mtDNA. This pattern is the opposite of what we found for mtDNA in yellow perch and for walleye using both mtDNA and nuclear DNA. The difference between the nuclear and mtDNA results for yellow perch may result from differential male vs. female migration patterns during the spawning season. This merits further investigation, which we are incorporating in our testing design.*

Table 6A. Distribution of Genetic Variability for Yellow Perch mtDNA in Lake Erie using Analysis of Molecular Variance (AMOVA)

Source of Variation	Percentage of Variation	Significance
Among 3 lake basins	**0.01%**	**N.S.**
Among spawning sites within basins	**4.19%**	**P < 0.05***
Within spawning sites	**95.69%**	**P < 0.04***

Interpretation: *Yellow perch mtDNA shows no basin-delineated structure for spawning groups. However, there is some suggestion of genetic differences among individual spawning sites. We have not performed this test with data from the nuclear DNA, because our present data set includes only one spawning site per basin. The nuclear DNA data are congruent with the mtDNA data, showing differences among some spawning sites (see 7B below).*

Table 7A. Mitochondrial DNA divergences among Yellow Perch Spawning per basin as measured by *Fst*

	Western basin	**Central Basin**
Central Basin	***Fst* = 0.013** **N.S**	**------**
Eastern Basin	***Fst* = 0.005** **N.S.**	***Fst* = 0.006** **N.S.**

***= significant at 0.05 level, **= significant after sequential Bonferroni correction**

Interpretation: *There is no discernable genetic structure distributed among the three basins for yellow perch using mtDNA. This may be a relict of disparate sampling sizes, and we are in the process of augmenting the data set. However, significant genetic differences are revealed among some of the sites (Table 8A). In contrast, nuclear DNA data showed significant differences between spawning groups in the eastern versus central/western basins (Table 7B). This may be due to differences in male and female spawning migration patterns.*

Table 7B. Nuclear DNA Divergences among Yellow Perch Spawning per Basin as Measured by *Fst*

	Western basin	**Central Basin**
Central Basin	***Fst* = 0.001** **N.S.**	**------**
Eastern Basin	***Fst* =0.002** **$P < 0.05$***	***Fst* = 0.002** **$P < 0.05$***

***= significant at 0.05 level, **= significant after sequential Bonferroni correction**

Interpretation: *In contrast to the mtDNA marker, yellow perch spawning in the eastern basin are significantly different from those spawning in the western and central basins. The differences may be due to bi-parentally inherited DNA patterns (above) versus uniparentally inherited mtDNA (Table 7A). They may also be due to our current sampling design, since we tested only a single site per basin for the nuclear DNA to date.*

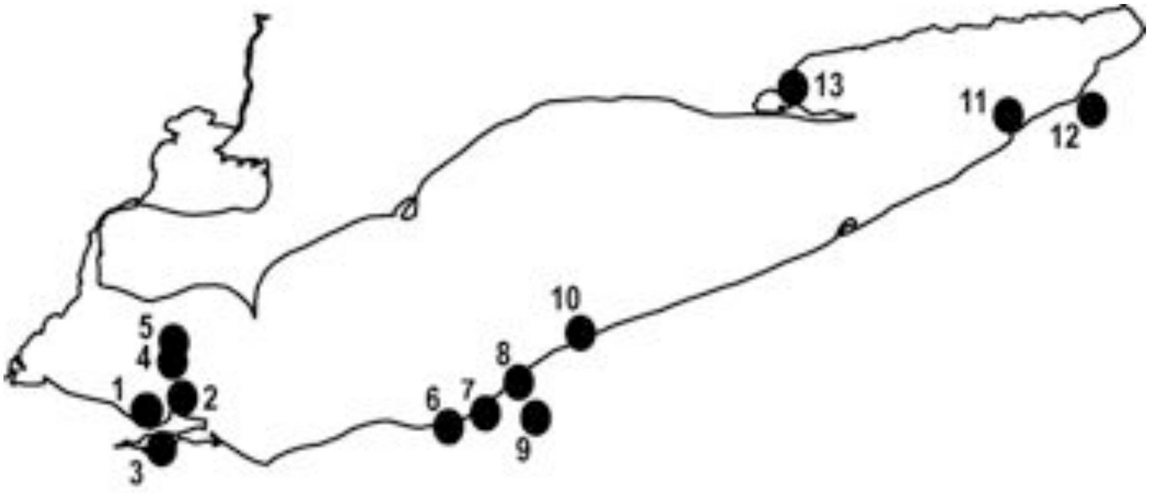
Table 8A. Matrix of Significant Differences among Individual Yellow Perch Spawning Sites as Measured by *Fst* from mtDNA Variation

	Port Clinton, S. Bass Isl.	**Cedar Point, Sandusky**	**Vermilion, Lorain**	**Cleveland**	**Fairport, Geneva & Ashtabula**	**Presque Isle, Erie**	**Dunkirk**
Cedar Point, Sandusky	**0.361****						
Vermilion & Lorain	**0.019**	**0.065***					
Cleveland	**0.019**	**0.058****	**0.028**				
Fairport, Geneva, & Ashtabula	**0.054**	**0.041**	**0.033**	**0.023**			
Presque Isle, Erie	**0.007**	**0.141****	**0.007**	**0.012**	**0.003**		
Dunkirk	**0.224****	**0.009**	**0.019**	**0.023**	**0.005**	**0.067**	
L. Point Bay	**0.248**	**0.039**	**0.040**	**0.034**	**0.023**	**0.079**	**0.026**

***= significant at 0.05 level, **= significant after sequential Bonferroni correction**

Interpretation: *We can distinguish between some spawning sites using mtDNA. The largest numbers of yellow perch tested were from Cedar Point, Cleveland, and Dunkirk. Differences seen are those that involve larger numbers of samples from widely spaced sites in different basins. It is most likely that additional differences among spawning sites would be revealed given greater sampling sizes. We are increasing these.*

Smallmouth Bass Population Groups



Western Basin

1. Port Clinton, OH[1,2]
2. Gem Beach, Sandusky, OH[1,2]
3. Sandusky Bay, OH[1,2]
4. Middle Bass Island, OH[1,2]
5. South Bass Island, OH[1,2]

Central Basin

6. Cuyahoga River, OH[1,2]
7. Chagrin River, OH[1,2]
8. Fairport Harbor, OH[1,2]
9. Grand River, OH[1,2]
10. Conneaut, OH[1,2]

Eastern Basin

11. Van Buren Bay (Dunkirk), NY[1,2]
12. Cattaraugus Creek, NY[1,2]
13. Long Point Bay, Ontario[1,2]

Data from these population groups consist of MtDNA (1) and/or microsatellite nuclear DNA (2) markers.

Statistics for Smallmouth Bass Results

Table 9A. Mitochondrial DNA Diversity (Maternally Inherited) of Spawning groups of Smallmouth Bass per Lake Basin

	Gene diversity	N alleles (% of those in Lake Erie)		N unique alleles per basin (% of N alleles)	
Western Basin	**0.533 +/- 0.037**	**7/15**	**47%**	**2/7**	**29%**
Central Basin	**0.451 +/- 0.060**	**10/15**	**67%**	**2/10**	**20%**
Eastern Basin	**0.552 +/- 0.066**	**10/15**	**67%**	**3/10**	**30%**

Interpretation: *Smallmouth bass spawning population sites exhibit similar levels of genetic diversity in the three Lake Erie basins using female-inherited markers. There is no evidence of population bottlenecks or lack of genetic diversity among these samples. Overall, smallmouth bass have less overall genetic diversity in Lake Erie than do walleye, and more than found in yellow perch. Sequence analysis revealed seven to ten mtDNA alleles per basin, with eight of those occurring in at least two basins; the remaining seven alleles were unique to a specific lake basin. As in walleye and yellow perch, overall numbers of alleles increase from west to east. All three basins had comparable numbers of unique alleles.*

Table 9B. Nuclear DNA Diversity (Bi-Parentally Inherited) of Smallmouth Bass Spawning per Basin (Based on 8 Microsatellite Loci)

	Gene diversity	N alleles as % of those in Lake Erie	N unique alleles per basin	
Western Basin	**0.511 +/- 0.001**	**50/57 88%**	**12/50**	**24%**
Central Basin	**0.518 +/- 0.001**	**44/57 77%**	**6/44**	**14%**
Eastern Basin	**0.532 +/- 0.001**	**44/57 77%**	**5/44**	**12%**

Interpretation: *Genetic diversity is comparable among lake basins using microsatellites and mitochondrial DNA. The major difference is that the western basin has twice the number of unique alleles as found in the other two basins. This is similar to what we found for yellow perch, and appear to reflect differences between female and male migration patterns.*

Table 10A. Distribution of Genetic Variability for Smallmouth Bass mtDNA in Lake Erie using Analysis of Molecular Variance (AMOVA)

Source of Variation	Percentage of Variation	Significance
Among 3 lake basins	**5.12%**	**P < 0.450**
Among spawning sites within basins	**12.10%**	**P < 0.0001**
Within spawning sites	**82.78%**	**P < 0.0001**

Interpretation: *Most of the mtDNA variation in Lake Erie smallmouth bass is distributed within sites, reflecting a large variety of individuals per site, as well as the proportion of shared alleles across the lake. Significant variation occurs among spawning sites, but does not correspond to the divisions among the basins (i.e., the basin boundaries do not correspond to real population boundaries for the fish).*

Table 10B. Distribution of Genetic Variability for Smallmouth Bass Nuclear DNA using Analysis of Molecular Variance (AMOVA)

Source of Variation	Percentage of Variation	Significance
Among 3 lake basins	**0.42%**	**P =0.1124**
Among spawning sites within basins	**2.83%**	**P < 0.0001**
Within spawning sites	**96.74%**	**P < 0.0001**

Interpretation: *Similar to the results to the mtDNA analysis, most of the genetic variance in smallmouth bass from Lake Erie occurs within spawning sites. However, there are significant differences among spawning sites as in walleye and yellow perch. The lake basin division appears arbitrary with respect to stock structure of smallmouth bass.*

Table 11A. Mitochondrial DNA Divergences among Smallmouth Bass Spawning per Basin as Measured by *Fst*

	Western basin	Central Basin
Central Basin	***Fst* = 0.105** **P < 0.009****	
Eastern Basin	***Fst* = 0.031** **P < 0.171**	***Fst* = 0.000** **P < 0.541**

***= significant at .05 level, **= significant after sequential Bonferroni correction**

Interpretation: *Divergence estimates between the eastern and western basins do not differ significantly from zero, implying that gene flow occurs between these lake-dwelling populations. However, the mtDNA haplotype assemblages from the central and western basins are markedly divergent from one another, possibly related to the fact that more than half of our central basin samples were taken from river systems and not lake habitats.*

Table 11B. Nuclear DNA Divergences among Smallmouth Bass Populations per Basin

	Western basin	Central Basin
Western Basin	-----	
Central Basin	***Fst* = 0.001** **P = 0.189**	------
Eastern Basin	***Fst* = 0.017** **P < 0.00001****	***Fst* = 0.008** **P < 0.00001****

***= significant at 0.05 level, **= significant after sequential Bonferroni correction**

Interpretation: *Divergences in allelic composition at microsatellite loci are low, but appear to reveal differences among west/central versus east. This is very similar to the pattern found in walleye and yellow perch. Thus, results from all three game fishes show that spawning groups in the eastern basin of Lake Erie are genetically distinct from those in the west and central basins. This should be reflected in management strategies.*

Table 12A. Matrix of Significant Differences in mtDNA Compositions among Individual Smallmouth Bass Spawning Sites as Measured by *Fst*

	Port Clinton	Gem Beach	Sandusky Bay	Bass Islands	Cuyahoga River	Chagrin River	Fairport	Grand River	Conne -aut	Van Buren Bay	Catt. Creek
Gem Beach	0.107										
Sandusky Bay	0.000	0.103									
Bass Islands	0.144	0.000	0.148								
Cuyahoga River	0.105	0.303*	0.141	0.292**							
Chagrin River	0.266**	0.459**	0.185**	0.474**	0.036						
Fairport	0.031	0.238**	0.036	0.284*	0.182*	0.230**					
Grand River	0.100	0.452**	0.101	0.500*	0.326**	0.431**	0.189				
Conneaut	0.004	0.221**	0.007	0.224**	0.126*	0.252**	0.084	0.240**			
Van Buren Bay	0.000	0.000	0.000	0.031	0.138*	0.286**	0.019	0.240*	0.034		
Catt. Creek	0.065	0.026*	0.076	0.256**	0.142*	0.257**	0.061	0.224**	0.069	0.071	
Long Point Bay	0.008	0.144	0.015	0.159	0.115*	0.221*	0.000	0.259**	0.000	0.000	0.065

***= significant at 0.05 level, **= significant after sequential Bonferroni correction**

Interpretation: *Divergences among lake Erie smallmouth bass populations differ widely across the Lake, possibly due to the shared number of mtDNA alleles discovered thus far. These results are consistent with the results of the AMOVA analysis (Table 10A). Genetic diversity within the smallmouth bass should be conserved at spawning sites during the spawning season.*

Table 12B. Matrix of Significant Differences in Microsatellite Compositions among Individual Smallmouth Bass spawning sites as measured by *Fst*

	Port Clinton	Gem Beach	South Bass Island	Middle Bass Island	Sandusky Bay	Cuyahoga River	Chagrin River	Grand River	Fairport Harbor	Perry	Conne-aut	Van Buren Bay	Catt. Creek
Gem Beach	0.000												
South Bass Island	0.006*	0.006											
Middle Bass Island	0.021*	0.004	0.027**										
Sandusky Bay	0.025*	0.018*	0.009	0.034*									
Cuyahoga River	0.114**	0.108**	0.077**	0.123**	0.038*								
Chagrin River	0.067**	0.058**	0.054**	0.030*	0.068**	0.178**							
Grand River	0.071**	0.060**	0.028*	0.078*	0.002	0.039	0.100*						
Fairport Harbor	0.000	0.000	0.015**	0.003	0.030*	0.124**	0.058**	0.078**					
Perry	0.007	0.009	0.011*	0.023*	0.008	0.081**	0.079**	0.033*	0.011				
Conneaut	0.014	0.018*	0.007**	0.026*	0.017*	0.087**	0.066**	0.048**	0.012	0.003			
Van Buren Bay	0.028**	0.029**	0.018**	0.040**	0.001	0.058**	0.078**	0.037*	0.030**	0.006	0.008		
Cattarau-gus Creek	0.087**	0.089**	0.058**	0.104**	0.042**	0.080**	0.165**	0.051**	0.089**	0.036**	0.040**	0.027**	
Long Point Bay	0.045**	0.056**	0.054**	0.048**	0.095**	0.201**	0.100**	0.139**	0.036**	0.051**	0.050**	0.081**	0118**

***= significant at 0.05 level, **= significant after sequential Bonferroni correction**

Interpretation: *Many of the spawning populations of Lake Erie smallmouth bass represent genetically separable groups. There appears to be appreciable gene flow among closely situated sites. It is noteworthy that the highest divergence estimates are between samples taken from riverine populations (e.g., Cuyahoga, Chagrin, Grand, and Cattaraugus) versus those taken from lake habitats. Thus, there is little exchange among lake and river spawning groups, and they have maintained separation for generations, perhaps since the Pleistocene.*