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Geographical distribution of mitochondrial DNA (mtDNA) variation in walleye, sauger, and yellow perch

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To assess its usefulness for stock identification and resolving post-Pleistocene recolonization events, mtDNA variation was examined in three economically important North American percids: walleye, sauger and yellow perch. Forty-two walleye mtDNA haplotypes were identified which could be divided into five groups that showed distinct geographic distributions. Sauger showed very little genetic variation with only four haplotypes being found across the species' range. Thirteen yellow perch mtDNA haplotypes were identified, with one haplotype predominating in all populations examined. These results suggest that mtDNA analysis will be useful for stock identification in walleye, but less so in sauger and yellow perch.

1. Introduction

There are three large percids in North America, walleye (*Stizostedion vitreum* Mitchill), sauger (*S. canadense* Smith) and yellow perch (*Perca flavescens* Mitchill), all of which are of economic importance supporting both sports and commercial fisheries (Scott & Crossman 1973, Craig 1987). The natural distribution range for each species are shown in Figs. 1, 3 and 4, respectively for walleye, sauger, and yellow perch, although all have been widely introduced into waters outside of their native range (Scott & Crossman 1973, Colby *et al*. 1979). Fluctuating yields of all three species over the last 30 years have made stock identification and manipulation (e.g. through stocking) increasingly important components of management (Laarman 1978, Rawson & Scholl 1978, Colby *et al*. 1979, Henderson & Nepszy 1990). Discrimination of walleye stocks has relied almost entirely on tagging studies (Ferguson & Derksen 1971, Wolfert & Van Meter 1978) as attempts at stock differentiation using morphological, meristic or physiological criteria have proven ineffective (Colby & Nepszy 1981). Although allozyme electrophoretic studies have generally failed to reveal substantial differentiation in local gene frequencies (Colby & Nepszy 1981), Clayton *et al*. (1974) did find that the Mdh-3 70 allele occurred in significantly higher frequencies in walleyes from the Prince Albert National Park (Central Saskatchewan) than in other western Canadian walleye populations. Recently, however, Todd and Haas (1993) were able to differentiate walleyes from Lake St. Clair and the western basin of Lake Erie using a combination of allozyme markers and physical tags.

To date, no work has been conducted on stock identification in sauger.

Tagging studies on yellow perch have revealed evidence of demic structure (Aalto & Newsome 1989, 1990), but most allozyme studies have failed to discriminate among yellow perch populations (Leary & Booke 1982, Strittholt *et al*. 1988), although Todd and Hatcher (1993) were able to discriminate yellow perch from the Mid-west from those on the east coast using protein electrophoresis. They suggested that the differences in allele frequencies between these two areas were caused by them being recolonized by yellow perch from two separate (Atlantic and Mississippian) glacial refugia following the Pleistocene glaciation. Todd and Hatcher (1993) also suggested that higher heterozygosity values in yellow perch from Lake Ontario, Oneida Lake and Lake Champlain were due to a secondary zone of contact where alleles that were fixed in each of the Mid-west and Atlantic groups had mixed.

Recent studies of freshwater fish indicate that base sequence divergence in mitochondrial DNA (mtDNA) may be useful for stock identification (Billington & Hebert 1991). Several features of animal mtDNA, such as its more rapid rate of base substitution compared to nuclear DNA, its maternal inheritance, and its smaller effective population size relative to single copy nuclear DNA markers (Moritz *et al*. 1987, Billington & Hebert 1991), facilitate an enhanced resolution in population-level studies of genetic variation using mtDNA analyses. A number of previous studies on mtDNA variation in walleye (Billington & Hebert 1988, Ward *et al*. 1989, Billington *et al*. 1992) revealed useful genetic markers that could be used to resolve post-Pleistocene recolonization events, separate some walleye stocks and serve as genetic markers for transplanted fish. Markers were also found that permitted the introgression of sauger mtDNA into walleye to be detected (Billington *et al*. 1988). Furthermore, seven mtDNA haplotypes were found in 23 yellow perch from western Lake Erie in an area where previous allozyme studies of Strittholt *et al*. (1988) had shown heterozygosity to be zero (Billington 1993).

The aim of this paper is to describe the geographical distribution of mtDNA variation in walleye, sauger, and yellow perch, and to evaluate the usefulness of mtDNA analysis for stock identification and for resolving post-glacial recolonization events in these three large North American percids.

Table 1. Sauger populations examined for mtDNA variation. Numbered site locations are shown in Fig. 3. *N* = number of fish sampled in each population.

Site	Waterbody	Location	State/Province	Year	*N*	Notes
1	Issett Lake		Manitoba	1987	1	
2	Lake Winnipeg	S. Basin-Victoria Beach	Manitoba	1990	9	
3	Lake Manitoba	S. Basin-Delta Beach	Manitoba	1990	10	
4	Lake Sakakawea		North Dakota	1989	5	
5	Missouri River	Gavins Point Dam	South Dakota	1987	7	
6	Lake Nipigon	Ombabika Bay	Ontario	1989	38	4 were hybrids with walleye
7	Abitibi River	Otter Rapids	Ontario	1990	1	Introgressed into walleye
8	Lake Simcoe	Talbot River	Ontario	1986	2	Introgressed into walleye
9	Lake St. Clair		Ontario	1986	1	
10	Lake Erie	Western Basin	Ontario	1985, 1986 1987, 1989	4	
11	Ohio River	Racine Pool	Ohio	1989	7	
12	Tennessee River	Nickerjack Tailwater	Tennessee	1993	4	
13	Tennessee River	Wheeler Tailwater	Alabama	1994	9	
14	Tennessee River	Pickwick Dam	Tennessee	1989	2	
15	Ohio River	Joppa	Illinois	1994	9	
16	Illinois River	Peoria Pool	Illinois	1995	5	

2. Methods

A total of 1 144 walleye representing 95 populations have been surveyed. Locations of most of the walleye populations surveyed were provided by Billington *et al*. (1992). Additional populations from across the range of the species have been added to the data set, including four additional populations from Saskatchewan, three populations from the Mobile Basin (Billington & Strange 1995, Billington *et al*. 1996), five populations from the Ohio River, and two populations from Lake Superior. Additional fish collected from some of the populations described by Billington *et al*. (1992) and several other locations have also been added to the data set (details of additional sample locations and sizes can be obtained from the author on request). Sixteen sauger populations (114 fish) (Table 1) and 11 yellow perch populations (103 fish) (Table 2) were also surveyed. Mitochondrial DNA analysis was performed as described by Billington and Hebert (1988). In some cases when pure mtDNA could not be obtained, total DNA was extracted using the method of Grewe *et al*. (1993) and analyzed by Southern blot analysis (Billington & Hebert 1990). All walleye were screened using ten restriction endonucleases (*Ava* I, *Bcl* I, *Bst*E II, *Cla* I, *Dra* I, *Nci* I, *Nco* I, *Sca* I, *Stu* I, *Taq* I) that have been shown to reveal polymorphisms in walleye mtDNA (Billington *et al*. 1992). In addition, examples of each haplotype were screened using 15 additional six-base recognition endonucleases (Billington & Hebert 1988, Billington & Strange 1995). Sauger were screened using nine restriction endonucleases (all as for walleye except for *Taq* I) and yellow perch were screened using eight endonucleases that revealed polymorphisms (*Apa* I, *Ava* I, *Hind* III, *Nci* I, *Nco* I, *Sca* I, *Sst* I, *Stu* I). Once again, examples of each haplotype were screened with the additional 15 six-base endonucleases that are routinely used to survey percid mtDNA (Billington & Hebert 1988, Billington *et al*. 1988, 1990, Billington 1993). Haplotypes were designated as the different composite fragment patterns observed (Billington & Hebert 1988, Billington *et al*. 1992, Billington 1993).

Differences in haplotype frequencies among populations for each species were tested for statistical significance by homogeneity χ^2-tests utilizing the Monte Carlo procedure of Roff and Bentzen (1989) with the program CHIRXC of Zaykin and Pudovkin (1993). Nucleon (haplotype) diversity (Nei & Tajima 1981) values were also calculated for each population and summarized by species. Nucleon diversity for haploid genomes (mtDNA) is analogous to heterozygosity (Nei & Tajima 1981) and ranges from zero when all specimens display the same haplotype, to 1.0 when all specimens display unique haplotypes.

3. Results and discussion

3.1. Walleye

A total of 42 walleye mtDNA haplotypes have been identified (Billington *et al*. 1992, Billington & Strange 1995, Billington, unpublished data). Due to the large size of the walleye mtDNA data set, much of which has been published in detail elsewhere (Billington *et al*. 1992, 1996), walleye mtDNA haplotype distributions have been summarized to show general distribution patterns (Fig. 1). Walleye mtDNA haplotypes can be divided into five groups that show distinct geographic distributions (Fig. 1). Three of these groups likely represent fish that spent the Pleistocene in separate glacial (A – Atlantic; B – Mississippian; and C – Missourian) refugia (Billington & Hebert 1988, Ward *et al*. 1989, Billington *et al*. 1992). The fourth group (D) represents walleye in an area that has been extensively stocked with fish from groups A and B, along with five more divergent haplotypes (36–40)

Table 2. Yellow perch populations examined for mtDNA variation. Numbered site locations are shown in Fig. 4. *N* = number of fish sampled in each population. All haplotypes shown occurred in single fish except haplotype 2 (2 fish) and haplotype 9 (5 fish); all other fish were haplotype 1.

Site	Waterbody	Location	State/Province	Year	*N*	Haplotypes
1	Grassy Lake		Wisconsin	1993	14	2
2	Illinois River	Pool 13	Illinois	1991	2	
3	Crooked Lake		Indiana	1988	13	10
4	Lake Erie	Western Basin	Ontario	1986, 1988	22	2, 3, 4, 5, 6, 7
5	Lake Huron	Bruce Peninsula	Ontario	1988	11	13
6	Lake Nippissing		Ontario	1988	1	
7	Rideau Lake		Ontario	1987	2	
8	Lake Simcoe		Ontario	1988	10	11, 12
9	Lake Ontario	Bay of Quinte	Ontario	1986	3	8
10	Oneida Lake		New York	1988	11	
11	Choptank River		Maryland	1989	14	9(5)

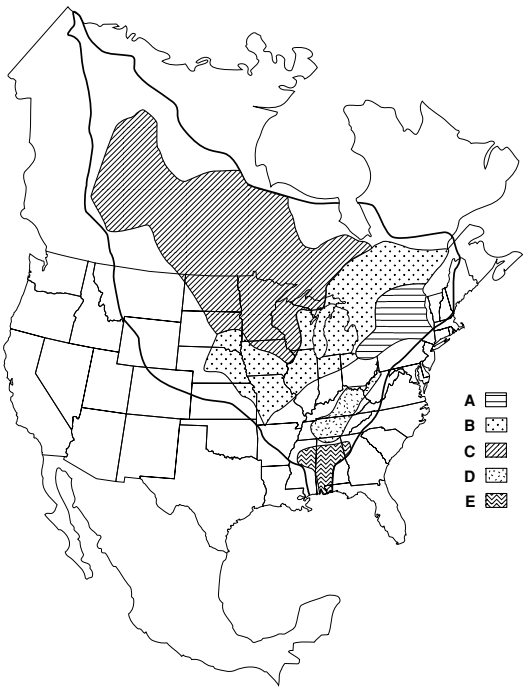

Fig. 1. Limits of the natural range of walleye (bold outline) along with generalized distribution patterns of five main walleye mtDNA haplotype groups (— A: Atlantic refugium origin. — B: Mississippian refugium origin. — C: Missourian refugium origin. — D: mixture of stocked fish of Atlantic and Mississippian refugium origin together with haplotypes thought to be typical of walleye in this region prior to stocking. — E: Mobile drainage basin haplotype).

which probably represent haplotypes that were present in the original walleye populations of this area before the rivers were impounded and stocked. The diversity of these five relic haplotypes suggests that they were not subjected to severe bottlenecks during the Pleistocene. However, it has also been difficult to quantify the genetic distances among these haplotypes and the other walleye haplotypes, as most of them were identified in Southern blot analyses and in many cases it was not possible to identify all of the smaller fragments present, or to map all of the restriction sites. The fifth group (E) of walleye, characterized by haplotype 34, are genetically very distinct (2.3% sequence divergence) and are only found in the Mobile drainage basin (Billington & Strange 1995, Billington *et al*. 1996). Genetic relationships among the four groups for which average percent sequence divergences could be calculated are shown in Fig. 2). The five relic haplotypes in group D would have genetic distances intermediate between the group B and group E fish, but their exact position cannot be determined because of the difficulty in mapping all of their small fragments.

Walleye haplotype frequencies among populations showed highly significant heterogeneity ($\chi^2 = 8\ 521$, $df = 3\ 854$, $p < 0.001$). Subdivision in walleye populations was also documented by Ward *et al*. (1989) based on mtDNA data. Nu-

Table 3. Sauger mtDNA haplotypes and yellow perch mtDNA haplotypes not previously described by Billington (1993). For sauger haplotypes, letters refer to fragment patterns described in Table 4. For perch haplotypes, letters refer to fragment patterns described by Billington (1993) or in Table 4.

Haplotype	Endonuclease and fragment pattern type							
Sauger								
	Nco I	*Dra* I	*Nci* I					
1	A	A	A					
2	B	A	A					
3	B	B	A					
4	A	A	B					
Yellow Perch								
	Nco I	*Ava* I	*Sca* I	*Apa* I	*Stu* I	*Hind* III	*Nci* I	*Sst* I
8	A	A	A	C	A	A	A	A
9	A	A	A	A	B	A	B	B
10	A	A	A	A	C	A	A	A
11	A	A	A	A	D	A	A	A
12	A	A	A	A	A	B	A	A
13	A	A	C	A	A	A	A	A

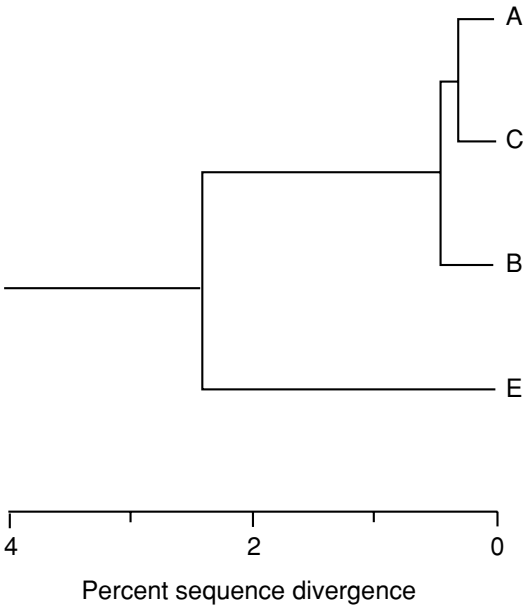

Fig. 2. UPGMA phenogram of average percent sequence divergence between four (A, B, C, E) of the main groups of walleye mtDNA haplotypes shown in Fig. 1.

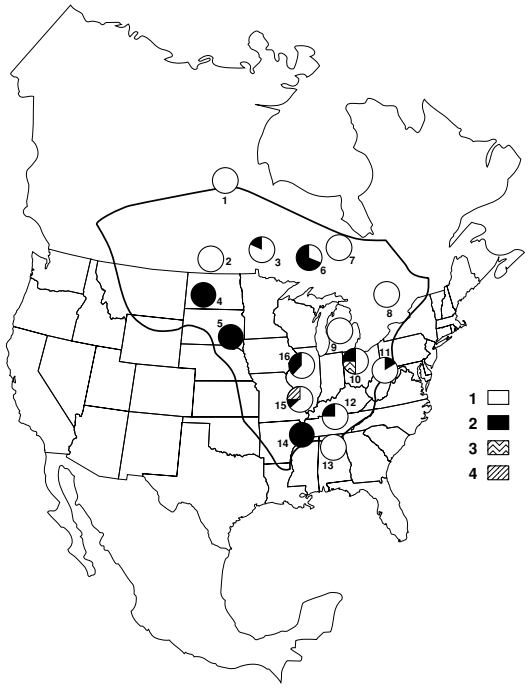

Fig. 3. Limits of natural range of sauger (bold outline) along with distribution of sauger mtDNA haplotypes. Numbers refer to sites listed in Table 1. Sauger haplotypes 1–4 are described in Table 3.

cleon diversity values for walleye ranged from 0 to 0.783, with 23 populations having zero values.

A combination of the regional geographic variation in walleye mtDNA, highly significant heterogeneity in haplotype frequencies among populations, and the fact that a number of walleye mtDNA haplotypes are found in multiple populations distributed over a limited area (Billington *et al*. 1992), suggests that mtDNA analysis will be a useful tool for stock identification in walleye management. Moreover, some of these haplotypes serve as genetic markers that allow the origin of stocked walleye to be traced (Billington *et al*. 1992).

There were also a number of instances where walleye possessed sauger mtDNA, either due to hybridization or introgression (Billington *et al*. 1988, 1992). I decided to use these data to augment the sauger data set (Table 2). Three fish identified by morphology as sauger or hybrids possessed walleye mtDNA.

3.2. Sauger

In contrast to walleye, sauger show very little mtDNA variation. Only four sauger mtDNA haplotypes were detected (Table 3, Fig. 3); these haplotypes are separated from each other by only a single restriction site. Restriction fragment patterns for the three endonucleases that revealed polymorphisms in sauger mtDNA are shown in Table 4. Sauger mtDNA haplotype 1 was the sauger mtDNA fragment pattern described by Billington *et al*. (1988, 1990). There is also no geographic structuring of the sauger mtDNA haplotypes (Fig. 3), suggesting that sauger spent the Pleistocene in a single, Mississippian glacial refuge. It should be noted that the small sample sizes for some populations might have meant that some variation went undetected. Nevertheless, their inclusion does allow a better picture of the checkerboard distribution of the two main haplotypes (1 and 2) across the whole range of the species.

Scott and Crossman (1973) note that there is still a tendency to consider sauger from the upper Missouri River as a separate subspecies (*S. c. boreum*). However, there is no evidence from the mtDNA data presented here that sauger from the upper Missouri River sites in North Dakota and South Dakota are genetically different from other sauger.

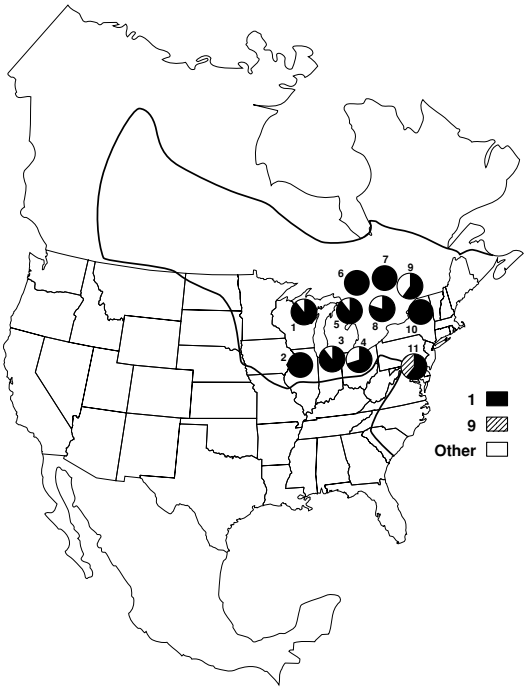

Fig. 4. Natural range of yellow perch (bold outline) along with distribution of yellow perch mtDNA haplotypes. Yellow perch haplotypes are described in Table 3. Relative frequencies of haplotypes other than 1 and 9 are also shown, but for site-specific details of these other haplotypes refer to Table 2. Numbers refer to sites listed in Table 2.

Sauger haplotype frequencies among populations showed statistically significant heterogeneity ($\chi^2 = 108.2$, $df = 45$, $p = 0.038$). However, this result should be treated with caution because sample sizes were low, resulting in a number of populations appearing to be fixed for either haplotype 1 or 2 in regions where other populations with larger sample sizes possessed both of these haplotypes. Nucleon diversity values for sauger ranged from 0 to 0.833, although nine populations had zero nucleon diversity and the highest value of 0.833 was likely affected by the small sample size for this population (population 10).

3.3. Yellow perch

Only a small proportion of the range of yellow perch has been surveyed (Fig. 4). Thirteen yellow perch haplotypes have been identified, with one haplotype (haplotype 1) predominating in all populations surveyed. Ten of the thirteen haplotypes were only observed in individual fish (Table 2), while five fish possessed haplotype 9 in the most eastern population (population 11) surveyed (Table 2, Fig. 4). One individual exhibiting haplotype 2 was found in each of populations 1 and 4 (Table 2). Yellow perch haplotypes that have not been previously described by Billington (1993) are shown in Table 3

Table 4. Fragment sizes in kilobase pairs for sauger mtDNA fragment patterns and yellow perch mtDNA fragment patterns not previously described by Billington (1993).

Enzyme	Pattern	Cuts	Fragment sizes
Sauger			
Dra I	A	3	9.06, 5.40, 2.22
	B	2	11.28, 5.40
Nci I	A	10	3.25, 2.42, 2.32, 1.80, 1.67, 1.65, 1.63, 0.74, 0.41, 0.35
	B	9	4.05, 3.25, 2.32, 1.80, 1.67, 1.65, 0.74, 0.41, 0.35
Nco I	A	2	16.13, 0.55
	B	3	9.82, 6.31, 0.55
Yellow Perch			
Hind III	B	5	7.27, 4.15, 1.93, 1.74, 1.65
Nci I	A	10	4.70, 2.65, 2.53, 2.03, 1.91, 1.35, 0.61, 0.32, 0.27, 0.24
	B	9	4.70, 3.38, 2.65, 2.53, 1.91, 0.61, 0.32, 0.27, 0.24
Sca I	C	3	8.13, 4.52, 4.01
Stu I	C	6	8.43, 3.18, 1.60, 1.35, 1.05, 1.03
	D	8	5.07, 3.18, 1.70, 1.67, 1.60, 1.35, 1.05, 1.03
Sst I	A	1	16.68
	B	2	9.47, 7.21

and fragment patterns for enzymes revealing new polymorphisms are presented in Table 4. Most haplotypes only differed from haplotype 1 by a single restriction site, except haplotypes 3 (3 sites away from haplotype 2 and 4 sites away from haplotype 1) and haplotype 9 (3 sites away from haplotype 1).

While the present data might suggest that yellow perch were limited to a single refugium, Todd and Hatcher (1993) have shown using allozyme data that both an Atlantic and a Mississippian refugium were used by yellow perch. I have yet to survey the more eastern populations examined by Todd and Hatcher (1993). Perhaps haplotype 9, found in five fish from Maryland and differing at three restriction sites from haplotype 1 fish, might be a marker of yellow perch from an Atlantic refugium, but more eastern populations will have to be surveyed to confirm this suggestion. Interestingly, in the Oneida Lake and Lake Ontario populations that Todd and Hatcher (1993) considered to contain perch with alleles typical of fish originating from both Mississippian and Atlantic refugia, haplotype 1 mtDNA predominated in Lake Ontario and was the only haplotype found in Oneida Lake yellow perch. Clearly, more research is needed to resolve the differences between the allozyme and mtDNA data sets in this species.

There was no significant heterogeneity in haplotype frequencies among yellow perch populations ($\chi^2 = 123$, $df = 120$, $p = 0.419$). Nucleon diversity values for yellow perch ranged from 0 to 0.666, with four populations having zero values, three of which had small sample sizes.

4. Conclusions

The results of this survey suggest that analysis of mtDNA variation appears to be a useful tool for stock identification and for resolving post-Pleistocene glacial events in walleye. The mtDNA data suggested that sauger used a single Pleistocene glacial refuge, but that mtDNA analysis will not be much use for stock identification in sauger, unless more polymorphisms can be found to serve as markers of local populations and until larger sample sizes can be obtained. The present data set is not sufficient to determine the number of Pleistocene glacial refugia used by yellow perch. Within the area of the Mid-west that was surveyed, mtDNA analysis would not appear to be of much use for yellow perch stock identification, as one haplotype predominates and all but two (haplotypes 2 and 9) of the other haplotypes are unique to individual fish. However, a broader geographic survey of mtDNA variation in yellow perch would likely provide more information on post-Pleistocene events for this species.

References

Aalto, S. K. & Newsome, G. E. 1989: Evidence of demic structure for a population of yellow perch (Perca flavescens). — Can. J. Fish. Aquat. Sci. 46: 184–190.

— 1990: Additional evidence supporting demic behavior of a yellow perch (Perca flavescens) population. — Can. J. Fish. Aquat. Sci. 46: 184–190.

Billington, N. 1993: Genetic variation in Lake Erie yellow perch (Perca flavescens) demonstrated by mitochondrial DNA analysis. — J. Fish Biol. 43: 941–943.

Billington, N. & Hebert, P. D. N. 1988: Mitochondrial DNA variation in Great Lakes walleye (Stizostedion vitreum) populations. — Can. J. Fish. Aquat. Sci. 45: 643–654.

— 1990: Technique for determining mitochondrial DNA markers in blood samples from walleyes. — Am. Fish. Soc. Symp. 7: 492–498.

— 1991: Mitochondrial DNA diversity in fishes and its implications for introductions. — Can. J. Fish. Aquat. Sci. 48(Suppl. 1): 80–94.

Billington, N. & Strange, R. M. 1995: Mitochondrial DNA analysis confirms the existence of a genetically divergent walleye population in Northeastern Mississippi. — Trans. Am. Fish. Soc. 124: 770–776.

Billington, N., Hebert, P. D. N. & Ward, R. D. 1988: Evidence of introgressive hybridization in the genus Stizostedion: interspecific transfer of mitochondrial DNA between sauger and walleye. — Can. J. Fish. Aquat. Sci. 45: 2035–041.

— 1990: Allozyme and mitochondrial DNA variation among three species of Stizostedion (Percidae): phylogenetic and zoogeographical implications. — Can. J. Fish. Aquat. Sci. 47: 1093–1102.

Billington, N., Barrette, R. J. & Hebert, P. D. N. 1992: Management implications of mitochondrial DNA variation in walleye stocks. — N. Am. J. Fish. Mange. 12: 276–284.

Billington, N., Strange, R. M. & Maceina, M. J. 1996: Mitochondrial-DNA analysis detects southern walleye in the Mobile Basin, Alabama. — Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 49. (In press.)

Clayton, J. W., Harris, R. E. K. & Tretiak, D. N. 1974: Geographical distribution of alleles for supernatant malate dehydrogenase in walleye (Stizostedion vitreum vitreum) populations from western Canada. — J. Fish. Res. Board Canada 31: 342–345.

Colby, P. J. & Nepszy, S. J. 1981: Variation among stocks of walleye (Stizostedion vitreum vitreum): management implications. — Can. J. Fish. Aquat. Sci. 38: 1814–1831.

Colby, P. J., McNichol, R. E. & Ryder, R. A. 1979: Synopsis of biological data on the walleye Stizostedion vitreum vitreum (Mitchill 1818). Food and Agriculture Organization of the United Nations Fisheries Synopsis 119.

Craig, J. F. 1987: The biology of perch and related fish. — Timber Press, Portland, Oregon.

Ferguson, R. G. & Derksen, A. J. 1971: Migrations of adult and juvenile walleyes (Stizostedion vitreum vitreum) in southern Lake Huron, Lake St. Clair, Lake Erie, and connecting waters. — J. Fish. Res. Board Canada 28: 1133–1142.

Grewe, P. M., Krueger, C. C., Aquadro, C. F., Bermingham, E., Kincaid, H. L. & May, B. 1993: Mitochondrial DNA variation among lake trout strains stocked into Lake Ontario. — Can. J. Fish. Aquat. Sci. 50: 2397–2403.

Henderson, B. A. & Nepszy, S. J. 1990: Yield of yellow perch in Lakes Erie and St. Clair: community associations. — Trans. Am. Fish. Soc. 119: 741–756.

Laarman, P. W. 1978: Case histories of stocking walleyes in inland lakes, impoundments, and the Great Lakes – 100 years with walleyes. — In: Kendall, R. L. (ed.), Selected Coolwater Fishes of North America. Am. Fish. Soc. Spec. Pub. 11: 254–260.

Leary, R. & Booke, H. E. 1982: Genetic stock analysis of yellow perch from Green Bay and Lake Michigan. — Trans. Am. Fish. Soc. 111: 52–57.

Moritz, C., Dowling, T. E. & Brown, W. M. 1987: Evolution of animal mitochondrial DNA: relevance for population biology and systematics. — Ann. Rev. Ecol. Syst. 18: 269–92.

Nei, M. & Tajima, F. 1981: DNA polymorphism detectable by restriction endonucleases. — Genetics 145–163.

Rawson, M. R. & Scholl, R. L. 1978: Reestablishment of sauger in western Lake Erie. — In: Kendall, R. L. (ed.), Selected Coolwater Fishes of North America. Am. Fish. Soc. Spec. Pub. 11: 261–265.

Roff, D. A. & Bentzen, P. 1989: The statistical analysis of mitochondrial DNA polymorphism: χ^2 and the problem of small samples. — Molec. Biol. Evol. 6: 539–545.

Scott, W. B. & Crossman, E. J. 1973: Freshwater fishes of Canada. — Fish. Res. Bd. Can. Bull. 184.

Strittholt, J. R., Guttman, S. I. & Wissing, T. E. 1988: Low levels of genetic variability of yellow perch (Perca flavescens) in Lake Erie and selected impoundments. — In: Downhower, J. F. (ed.), The biogeography of the Island Region of western Lake Erie: 246–257. Ohio State University Press.

Todd, T. N. & Haas, R. C. 1993: Genetic and tagging evidence for movements of walleyes between Lake Erie and Lake St. Clair. — J. Great Lakes Res. 19: 445–452.

Todd, T. N. & Hatcher, C. O. 1993: Genetic variability and glacial origins of yellow perch (Perca flavescens) in North America. — Can. J. Fish. Aquat. Sci. 50: 1828–1834.

Ward, R. D., Billington, N. & Hebert, P. D. N. 1989: Comparison of allozyme and mitochondrial DNA variation in populations of walleye, Stizostedion vitreum. — Can. J. Fish. Aquat. Sci. 46: 2074–2084.

Wolfert, D. R. & Van Meter, H. D. 1978: Movements of walleyes tagged in eastern Lake Erie. — New York Fish and Game Journal. 25: 16–22.

Zaykin, D. V. & Pudovkin, A. I. 1993: Two programs to estimate significance of χ^2-values using pseudo-probability tests. — J. Hered. 84: 152.