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DIFFERENTIATION OF WALLEYE (*Stizostedion vitreum*) STOCKS AND COMPARISON TO THEIR POND-REARED STOCKS USING MORPHOLOGICAL AND GENETIC ANALYSES

by

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PREFACE

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Stocking endeavors to replenish depleted walleye, *Stizostedion vitreum vitreum* (Mitchill), stocks have led to the mixing of various stocks. This study was conducted for three reasons. First, to determine whether different walleye stocks were distinguishable from one another using morphometric and meristic characters, second to examine meristic differences among pond stocks and third, to compare meristic characters of native walleye stocks to pond-reared offspring. Electrophoresis also was used to examine stock differences.

Walleye were collected from three lakes in Manitoba (Falcon, Manitoba and Dauphin) and one lake in Saskatchewan (Crean). Morphological and meristic analyses indicated that each of the four lake stocks were distinct. Eggs also were collected from these lakes (with the exception of Dauphin Lake), incubated in hatcheries and reared in separate ponds at Dauphin Lake, Manitoba. Meristic characteristics of pond-reared walleye were significantly different from each other and from their corresponding native lake walleye.

Crean walleye had significantly different allele frequencies of malate dehydrogenase and Falcon walleye had significantly different allele frequencies of isocitrate dehydrogenase from the other walleye stocks. These results suggest that agencies stocking walleye should consider stock differences and use caution to prevent mixing of stocks and irreversible loss of genetic diversity.

Key words: enzyme electrophoresis; stock enhancement; fishery management

RÉSUMÉ

Brown J.G. and W.G. Franzin. 1994. Differentiation of walleye (*Stizostedion vitreum*) stocks and comparison to their pond-reared stocks using morphological and genetic analyses. Can. Tech. Rep. Fish. Aquat. Sci. 1963: v + 27 p.

Avec les opérations de repeuplement, divers stocks de dorés jaunes (*Stizostedion vitreum vitreum* (Mitchill)) se sont mélangés. L'étude présentée ici a été réalisée pour trois raisons. Premièrement, on a voulu déterminer s'il est possible de faire la distinction entre différents stocks de dorés jaunes d'après des caractères morphométriques et méristiques. Deuxièmement, on a cherché des différences méristiques entre des stocks d'élevage. Troisièmement, on a comparé les caractères méristiques de dorés jaunes indigènes avec ceux de dorés d'élevage. On a également étudié les différences électrophorétiques entre les stocks.

On a capturé des dorés jaunes dans trois lacs du Manitoba (Falcon, Manitoba et Dauphin) et dans un lac de la Saskatchewan (Crean). L'analyse des caractères morphologiques et méristiques a révélé que les stocks de chacun de ces quatre lacs sont distincts. Par ailleurs, on a récolté des oeufs dans chaque lac (sauf dans le lac Dauphin) et, après incubation dans des installations d'élevage, les poissons éclos ont été élevés dans des bassins séparés, au lac Dauphin (Manitoba) : au point de vue des caractères méristiques, on a constaté des différences significatives d'un groupe à l'autre, ainsi que par rapport aux dorés du lac d'où les oeufs provenaient.

Chez le doré jaune du lac Crean, les fréquences alléliques de la malate-déshydrogénase sont différentes dans une mesure significative; le doré jaune du lac Falcon, quant à lui, présente des fréquences alléliques de l'isocitrate-déshydrogénase différant dans une mesure significative de celles des autres stocks. À la lumière de ces résultats, il conviendrait que les organismes s'occupant de reconstituer les stocks de dorés jaunes prennent en considération les différences qui existent entre les stocks et tâchent de prévenir un appauvrissement génétique irréversible en prenant les précautions nécessaires pour éviter qu'ils se mélangent.

Mots-clés: électrophorèse enzymatique; amélioration des stocks; gestion des pêches

INTRODUCTION

Augmentation of walleye, *Stizostedion vitreum vitreum* (Mitchill), populations by stocking is important to many commercial and sport fisheries, and is the goal of extensive stocking programs throughout the species' range. Mixing of stocks has occurred because walleye often are spawned at one lake, eggs are hatched in a hatchery and the larvae are then stocked into different lakes. Little consideration has been devoted to actual or potential stock differences or the consequences of hatchery and pond rearing upon walleye. Rational stocking procedures should consider whether introduced fish (either different stocks or hatchery/pond reared fish) will perform as well in new environments as in their native lake, or if they will produce less fit offspring when stocks interbreed. Stock differences should be investigated using indicators such as morphological characters and DNA analysis before stocking programs are put into action.

Morphometric and meristic characteristics are affected by both the environment and the genetic makeup of a fish. Much of the meristic variation among brown trout and chum salmon stocks is caused by environmental effects, in particular temperature (Tåning 1952, and Murray and Beacham 1989). Meristic traits are sensitive to environmental influence throughout the entire developmental period until fixation (Lindsey and Arnason 1981). Therefore, exposure of fish to differing environmental conditions in individual lakes may produce variation in phenotypes and certain phenotypes may be associated with certain environmental conditions. Tåning (1952) also found that some traits, such as vertebral number, were controlled to a greater extent by genetic factors than by environmental conditions. Taylor and McPhail (1985) and Murray and Beacham (1989) found heritable genetic components in morphological and meristic characters of coho and chum salmon. Therefore constant exposure to a set of environmental conditions, over many generations, may cause selection for particular genes and fix them into the genome of the fish.

Because of the effect of environmental conditions upon development, eggs incubated in a hatchery may develop different numbers of meristic characters than if they were incubated in a lake. Todd et al. (1987) compared laboratory-reared ciscoes of four different species to their native parents. Morphology differed between the laboratory-reared progeny and their wild parents, and the progeny of different species were more similar to each other than each was to their parents, indicating a large environmental effect. Both Swain et al. (1991) and Taylor (1986) found significant differences in morphology between wild and hatchery-reared coho salmon. Differences were largely attributed to environment with reduced phenotypic variance in hatchery populations due to homogeneity of hatchery environments.

Genetic differences also have been found between hatchery- or pond-reared fish and natural parental stocks (Edds and Echelle 1989; Ryman and Ståhl 1980). In these cases, wild fish had the highest survival in streams, whereas hatchery fish had the highest survival in hatchery ponds (Reisenbichler and McIntyre 1977).

Some implications of walleye stock differences and methods of stock identification have been considered. Shcherbukha (1972) found significant morphological differences among three species of the genus *Stizostedion* in the Dnieper-bug estuary in Russia. Uthe and Ryder (1970) found differences among five walleye stocks using muscle myogen polymorphisms but did not find differences in morphometric measurements. This may have been due to the limited number of measurements taken and the use of ratios. Scale shape has been used to differentiate some stocks (Jarvis et al. 1978) but did not differentiate the five known stocks of walleye from Lake Erie (Riley and Carline 1982). Genetic studies conducted on mitochondrial DNA from across the walleye range in Canada (Billington et al. 1992 and Ward et al. 1989) and enzyme analyses of walleye populations from Western Canada (Clayton et al. 1974) and Lake St. Clair and Lake Erie (Todd 1990) have indicated genetic

differences among walleye stocks.

The purpose of this study was to determine whether walleye stocks from Falcon Lake, Lake Manitoba, and Dauphin Lake in Manitoba and Crean Lake, Saskatchewan could be distinguished from one another using morphometric, meristic, and electrophoretic characters. Comparisons were made among fingerlings exposed to hatchery and pond rearing conditions. Native parental lake stocks were then compared to the pond fingerlings. These comparisons were made because walleye from these lakes have been used in fry and fingerling stocking programs. Crean Lake fry have been stocked successfully into West Blue Lake (Ward and Clayton 1975 and Schweigert et al. 1977) and into Dauphin Lake (Mathias et al. 1992). A large provincial hatchery on Lake Manitoba produces large numbers of walleye fry which also are stocked into many different lakes (Manitoba Natural Resources).

MATERIALS AND METHODS

STUDY AREA

Walleye were collected from four different lakes: Falcon, Manitoba, Dauphin and Crean which are decribed in Table 1. Rearing ponds were located at the former Department of Fisheries Research Station at Methley Beach on Dauphin Lake. Each pond was 1 hectare in area and ranged in depth from about 0.5 to 2 metres.

FISH COLLECTION

The four samples of adult walleye were collected using trapnets and gillnets. Sixty walleye were taken from a spawning run at Crean Lake in 1988. One-third of the fish sampled from Falcon Lake were taken from a spawning run in 1988; the rest were gill-netted during the summer of 1989 for a total of 50 fish. Walleye were collected from Lakes Manitoba and Dauphin with gillnets; 60 from Lake Manitoba in the summer and fall of 1989 and 61 in all from Dauphin Lake in the falls of 1988 and 1989. All fish were frozen for later morphometric and meristic analysis.

Fertilized eggs from Crean Lake walleye were obtained by the Department of Fisheries and Oceans (DF0) staff in May, 1987. These eggs were incubated at the Freshwater Institute in Winnipeg. Falcon Lake and Lake Manitoba walleye larvae were obtained from Manitoba Department of Natural Resources at the Whiteshell and Swan Creek hatcheries, respectively, in May of 1989. The eggs from the three different stocks were reared to hatching under different water temperature regimes. All larvae were raised to fingerlings (40-120 mm) in separate but adjacent one-hectare ponds at Methley Beach. Attempts at raising Dauphin Lake walleye failed due to hatchery problems. Sixty fingerlings each of Crean Lake, Falcon Lake and Lake Manitoba stocks were taken from the rearing ponds during pond drainage about 60 days after hatching and frozen for later meristic analysis.

MORPHOLOGICAL VARIABLES

Both morphometric (Table 2) and meristic (Table 3) charactristics were examined on the left side of the fish. Morphometric characteristics, measured to 0.1 mm, were made with the naked eye on partially thawed adult fish (for detailed methods see Brown 1990). Ages were determined using the left opercular bones according to the methods of Campbell and Babaluk (1979). Morphometric traits of fingerlings were not assessed because of measuring difficulties due to their small size. The same meristic counts were taken from fingerling walleye as for adult walleye but due to the small size (40-70 mm) of some fingerlings a dissecting microscope was required.

The sex of each adult walleye was recorded and sexual dimorphism was examined in both meristic and morphometric traits. Pond stock fish were not sexed because of difficulties in sex determination of juvenile

fish.

GENETICS

White muscle samples for malate dehydrogenase (Mdh-3; EC 1.1.1.37) electrophoretic analysis were taken from all walleye stocks. Liver was sampled for isocitrate dehydrogenase (Idh-1; EC 1.1.1.42) electrophoretic analysis from the same fish with the exception of Dauphin Lake. Tissues were frozen according to Clayton et al. (1971).

Samples were thawed, homogenized, and centrifuged at 15,600 G for 15 minutes. Supernatant aliquots were subjected to horizontal starch electrophoresis (Tsuyuki et al. 1966). Gels were stained for Mdh-3 using the method of Clayton and Gee (1969) substituting malic acid for lactic acid. Idh-1 gels were stained using the staining method of Harris and Hopkinson (1976) with some modifications (Brown 1990). Mdh-3 phenotypes were classified according to Clayton et al. (1971) and alleles b1, b2, and b3 correspond to Mdh-3 alleles 70, 100, and 120 respectively (Ward et al. 1989). IDH phenotypes were classified according to a model devised by D. Tretiak (Freshwater Institute, personal communication) and S and F alleles correspond to Idh-1 alleles 75 and 100 respectively (Ward et al. 1989). The distribution of observed and expected (calculated according to the Castle-Hardy-Weinberg law) phenotypes as well as gene frequencies were calculated (Clayton et al. 1974).

STATISTICAL ANALYSES

Chi-square and Mann-Whitney U tests were performed on each meristic trait to determine differences in distribution of counts and differences between means among populations respectively. Data were pooled for chi-square analysis in cases where observed frequencies of counts were under five. Chi-square analysis was also used to test for different frequencies of observed electrophoretic phenotypes among lake and pond stocks.

Raw morphometric variables were adjusted to a common standard length (SL_m) to remove the effect of fish size using the equation: $AVAR = VAR\ (SL_m/SL_i)^b$ (Reist 1985 and Thorpe 1976), where AVAR is the adjusted form of a morphometric variable (VAR), SL_i is the individual standard length, b is the allometric coefficient (explaining the growth relationship between VAR and SL_i), and SL_m is the mean of all SL for all fish from all four stocks. The least squares regression form of the allometric equation was used to calculate the allometric coefficient b: $\log VAR = \log a + b\ (\log SL_i)$. Allometric coefficients from separate stock regressions were compared using ANCOVA.

One way analysis of variance (ANOVA) and Tukey's studentized range test (also called Tukey's honest significant difference test, (Day and Quinn 1989)) were used to determine which size-adjusted morphometric variables showed significant stock differences and between which stocks these differences existed. Canonical discriminant function analysis was performed on size-adjusted morphometric and meristic data. Raw canonical coefficients of the 29 morphometric variables were examined (Brown 1990) to determine which were the most important for discriminating among stocks because use of a large number of characters or variables may make a large haphazard contribution to Mahalanobis distance values (Sneath and Sokal 1973). Mahalanobis distance (D^2) values were used to summarize meristic and morphological distances between stock means (Pimentel 1979). Discriminant analysis was performed on the four stocks to determine if individual fish could be classified to their respective lakes based on a subset of ten fish from each of the four lake stocks.

RESULTS

Approximately equal numbers of male and female fish were examined from each lake stock. No sexual dimorphism was found in either meristic or

morphometric measurements, consistent with Scott and Crossman (1973).

WALLEYE LAKE STOCK ANALYSES

Morphometric analysis

Morphometric data were normally distributed, allowing parametric tests to be used. Allometric coefficients from pooled regressions (Brown 1990) of the four stocks were used in ANOVA because no significant differences were found among stocks (Reist 1986). ANOVA indicated that the morphological variables: PRDL, PDL, PPVL, HL, HD, D1L, and D2BL (Table 2) were similar among walleye stocks and did not contribute to stock differences (Table 4). Most significant differences among stocks were related to head dimensions and fin length. The most important ($p \leq 0.0001$) head measurements were: UJL, MXL, MXW, and GL. Overall, the Crean walleye stock was most different from the other three walleye stocks.

Based upon results of ANOVA and raw canonical coefficients (Table 5) of all morphometric variables (Brown 1990), thirteen morphometric variables (PRDL, CPD, BD, SNL, UJL, MXL, MXW, LJL, OD, AL, ABL, SCL, GL) were selected as the most important morphometric measurements to be used in multivariate analysis. Mahalanobis distance values indicated that walleye stocks from Crean and Dauphin lakes were the most different, while Manitoba and Dauphin lake stocks were the most similar (Figure 1). Canonical discriminant function analysis of morphometric data indicated all four stocks were significantly different ($p \leq 0.0001$) from one another. Using the raw canonical coefficients it can be seen that MXW, OD, AL, ABL, and GL were the most important along canonical vector one in distinguishing Crean from Dauphin walleye. SNL, MXW, and CPD differentiated Falcon from Crean and Dauphin walleye along vector two (Figure 2).

Classification of individual fish to stock of origin using morphometric measurements showed 82.11 % were correctly classified (Table 6). Crean walleye were correctly classified most frequently (89.58 %).

Meristic analysis

The test for within stock variability indicated that variation among year classes was insignificant, allowing all ages of adult walleye to be combined in analyses. Pelvic fin ray counts showed no variation within or among stocks (six rays) and were omitted from further analysis.

Chi-square and Mann-Whitney U tests showed several significant differences ($P \leq 0.05$) among the four lake stocks (Table 7). The Dauphin Lake stock differed significantly from the other three walleye stocks in its mean number of anal fin rays. Lake Manitoba stock was distinct in counts of pectoral fin rays and upper gill rakers. Lower gill raker counts differed significantly between Crean stock walleye and the other walleye stocks. Lateral line scale counts showed the greatest variability and distinction among stocks (Table 4). Falcon stock, for example, ranged from 85 to 96 (with one anomaly at 82) in lateral line scale counts whereas Crean stock ranged from 81 to 90 (Brown 1990).

Examination of the raw canonical coefficients (Brown 1990) indicated that all eight meristic variables were important for discriminating among native walleye stocks (Table 5). Canonical discriminant function analysis of meristic data indicated walleye stocks were significantly different from each other. Mahalanobis distance values indicated that Lake Manitoba walleye were more similar to Crean and Falcon stocks than to Dauphin Lake walleye (Figure 1). AFR, GRU, D1FR, and GRL differentiated Dauphin from Manitoba walleye along vector one while CFR, GRU, GRL, and D1FR differentiated Falcon from Crean walleye along vector two (Figure 2). Discriminant analysis indicated 46.88 % of the fish were correctly classified to stock of origin using meristic counts (Table 8).

A general comparison of the four stocks at a similar

standard length would be as follows: walleye from Crean Lake had low counts of lateral line scales, gill rakers, and caudal fin rays, small head parts but a large head depth, long gill rakers, and short fins; Falcon walleye had high counts of lateral line scales, and long premaxilla, short gill rakers, long pelvic and pectoral fins and slender body depth; walleye from Dauphin Lake had low counts of anal fin rays, largest interdorsal space, wide premaxilla, large eyes and greater body and caudal peduncle depths; and Lake Manitoba walleye had high upper gill rakers counts, longest total lengths, largest mouth parts (snout lengths and upper and lower jaws), and smallest eyes. In general Crean Lake walleye had the smallest and Lake Manitoba walleye had the largest body part measurements.

Genetic analysis

Significant departures from Castle-Hardy-Weinberg equilibrium were found for Dauphin Lake Mdh and Falcon Lake Idh-1 phenotype frequencies. This probably was due to a sampling bias. Mdh-3 gene frequencies (Table 9) differed significantly between lake stocks, except between the Falcon and Manitoba stocks (Figure 3). Crean walleye showed a significantly higher frequency of the Mdh-3^{70} allele than any other stock. Idh gene frequencies (Table 10) were similar between Crean and Manitoba stocks but differed between all other walleye stocks (Figure 3). Falcon walleye had a much higher Idh-1^{100} allele frequency than any other stock.

WALLEYE POND STOCK ANALYSES

Falcon Lake walleye eggs were incubated at an average temperature of 9.3^{o} C with a standard deviation of 2.91 for 30 days. Temperature ranged from 4^{o} to 15^{o} C. Lake Manitoba walleye eggs were incubated at an average temperature of 9.7^{o} C with a standard deviation of 2.13 for 22 days. Temperature ranged from 5^{o} to 12^{o}. Crean Lake walleye eggs were incubated at an average temperature of 9.9^{o} C with a standard deviation of 1.17 for 20 days. Temperature ranged from 9^{o} to 15^{o}.

Meristic Analysis

Univariate analyses of meristic counts of pond reared walleye indicated significant differences ($p \leq 0.05$) among stocks (Table 11) as it did among native lake stocks. Anal fin ray counts of the Crean stock differed from the other stocks. Pectoral fin rays, as in adult fish, were distinct in the Lake Manitoba stock. The lack of significant differences among pond stocks for counts of lateral line scales and lower gill rakers and very small differences for counts of upper gill rakers, suggests that these characters were strongly influenced by rearing under common pond environments. Meristics of first dorsal fin rays, anal fin rays, and upper and lower gill rakers maintained stock separation previously shown by the adult walleye stocks. Mahalanobis distances between pond stocks (Figure 1) indicated that Falcon and Manitoba pond stocks were the most similar pair. These results are similar to the Mahalanobis distance values of the adult lake stocks. Canonical discriminant function analysis (Table 5) indicated that the pond stocks were significantly ($p \leq 0.0001$) different from one another. D1FR, AFR, CRF, GRU, and GRL along canonical vector one were important in differentiating Crean walleye from Falcon and Manitoba walleye. D1FR, D2FR, PFR, GRU, and GRL along vector two distinguished Manitoba walleye from Falcon and Crean walleye (Figure 2). Classification of individual fingerlings into pond-reared stocks based on meristic counts, using discriminant function analysis, showed an average of 64.52 % could be correctly classified (Table 12).

Genetic analysis

The original differences between Mdh-3 allele frequencies of lake stocks were retained between pond stocks (Table 9). However, Idh-1 allele frequencies did not differ between any pond stock (Table 10).

LAKE AND POND STOCK ANALYSES

Meristic analysis

The fewest differences were found between the Crean lake and pond stocks. Falcon lake and pond stocks however, differed from each other in several traits with pond fish showing extended, lower ranges for counts of first dorsal rays, lateral line scales and caudal fin rays (Table 4). Anal fin ray counts indicated significant differences between lake and pond pairs in all stocks whereas upper gill rakers and first dorsal fin rays exhibited little or no difference (Table 13). Mahalanobis distance values ($p \leq 0.0001$) (Figure 1) and canonical discriminant function analysis ($p \leq 0.0001$) (Table 5) showed that lake and pond stocks may be clearly distinguished from one another. AFR and GRL were the most important traits for the discrimination of pond and lake stocks along canonical vector one. D1FR and D2FR were important along vector two and D1FR, D2FR, and PFR along vector three. These results indicated that the Crean lake and pond stocks were the most similar and the Falcon lake and pond stocks were the most different. An average of 47.11 % of the lake-pond stocks were classified into the correct pond or lake (Table 14).

Genetic analysis

Analysis of Mdh-3 gene frequencies between lake and pond stocks showed no significant differences except when data from Falcon pond 1989 was used (Figure 3). Then a significant difference was found between the Falcon lake and pond stocks ($X_2 = 15.32$, df = 2, $p \leq 0.001$) but not in 1987 ($X_2 = 2.28$, df = 2, $p \geq 0.05$). No significant differences occurred in Idh-1 gene frequencies.

DISCUSSION

Previous studies (Beacham and Murray 1986; Ali and Lindsey 1974; MacGregor and MacCrimmon 1977) found that a rapid developmental rate, due to high temperatures, resulted in fish larvae with lower meristic counts because rapid growth tends to prevent the differentiation of as many elements (Barlow 1961). A slower developmental rate, due to lower temperatures, resulted in larvae with higher counts because body tissues which develop slowly, develop into a greater number of elements before segments are fixed (Martin 1949). Examination of adult fish growth rates indicated that Falcon and Manitoba stocks had faster growth rates than Crean and Dauphin stocks (unpublished data). However, adult growth rates may be different from developmental growth rates. Walleye generally start their spring spawning run when water temperatures reach 6-7^{o} C and spawn at 7-10^{o} C at both Crean Lake (Mathias et al. 1985) and Dauphin Lake (Ken Rowes, personal communication). This indicates that the walleye eggs start their development at similar temperatures. However, Crean Lake is slower to warm up, in comparison with Manitoba and Dauphin lakes (Ken Rowes, personal communication),which may result in different developmental rates. Falcon Lake also would be a slow warming lake due to it's depth and few inflowing rivers. Falcon Lake walleye had higher counts, which fits the slower development theory, but Crean Lake walleye generally had the lowest counts. This indicated that another factor may be important in determining the number of meristic counts in Crean walleye.

Measurement of Crean walleye eggs and larvae (437 ± 38 larvae/mL indicated they were much smaller than the other three walleye stocks (221 + 41 larvae/mL) (Brown, unpublished data). Brown (1987) found that walleye larvae from larger eggs had a faster rate of formation of hypural bones and caudal fin rays which may in turn lead to a higher meristic count. Crean walleye had smaller eggs and generally had lower meristic counts, which might explain the difference in meristic counts found between Crean and Falcon walleye. Ali and Lindsey (1974) found similar results in medaka (*Oryzia latipes*) where larger eggs resulted in larvae with more anal rays than larvae from smaller eggs.

Different gene frequencies of some enzymes in the walleye lake stocks also may indicate adaptation to lake environment. Philipp et al. (1985) found that specific alleles at several enzyme loci (malate dehydrogenase-B, isocitrate dehydrogenase-B, superoxide dismutase-A, and aspartate aminotransferase-B) allele frequencies were correlated with latitude and environmental variables related to thermal regime. This suggests that these correlations may reflect adaptation to different thermal environments in largemouth bass (*Micropterus salmoides*). Northerly largemouth bass populations were best adapted to their environment as were the southerly populations adapted to their environment.

Differences in meristic counts among pond stocks may be due to the stocks being exposed to different water temperatures on different days during incubation. The Falcon and Manitoba stocks were hatched at hatcheries on the lakes from which they came, although well water instead of lake water was used. The third stock (Crean) was hatched under conditions in which the water temperature was regulated more accurately. Incubation water temperature means and ranges were similar for all three pond stocks. Therefore differences between stocks may be due to two different reasons: genetic stock differences and fluctuations in temperature at different times. Different water temperatures (Ali and Lindsey 1974) and light conditions (MacCrimmon and Kwain 1969) during egg and larval development have been shown to effect meristic counts.

Gene frequencies of Mdh-3 from the 1989 sample of Falcon pond walleye were different from the parental stock. This indicates that inadvertent selection may have occurred when parents were chosen during spawn taking. The change in Mdh-3 gene frequencies of fingerlings from adults indicated that more parents with the 100 allele were chosen. A change in hatchery stock gene frequency from that of the parental stock, and loss of genetic variability through selection of spawning stock has been documented in trout (Allendorf and Phelps 1980; Krueger and Menzel 1979; Reisenbichler and McIntyre 1977; Ryman and Ståhl 1980).

Mating method during spawn taking also has been shown to play an important role in genetic variation and therefore selection of traits. Gile and Ferguson (1990) showed that different types of mating crosses affect genotypic diversity in rainbow trout. Pooled gamete mating (the method used in this study) and full-sibling family crosses produced offspring which deviated significantly from the parents, whereas the offspring of diallel crosses did not differ. Gile and Ferguson (1990) hypothesized that the deviation of the pooled gamete crosses may be due to unequal male contributions.

Further studies are required in order to determine the basis for the differences among the four walleye stocks. This study of meristic and morphometric variation and genetic differentiation among walleye stocks provided evidence of stock specific adaptation in walleye. Stocking agencies should consider these stocks as separate entities and prevent mixing of stocks. The creation of gene flow between previously isolated populations may break up adapted gene complexes and cause a decrease in the productivity of the species (Ståhl 1988).

This study also showed that hatchery and pond rearing may affect the development of eggs and fingerlings, significantly changing the meristic counts of the pond-reared stocks from those of the parental stocks. Selection of parents during spawn taking and methods of mating used may contribute to significant differences between naturally produced and pond-reared walleye. Protocols for spawning and mating walleye should be established so that a large proportion of the genome of the particular lake stock is represented in the offspring.

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Table 1. Description of lakes from which walleye stocks were sampled.

Lake	Latitude	Longitude	Area	Elevation	Maximum Depth	Average Depth	Bottom Substrate	Stratification	Lake Type	Fisheries
Falcon[a]	49° 42'	95° 15'	15.6 km^2	327 m	26 m	14.1 m	sand, mud, clay	yes	formly oligotrophic culturally eutrophic	sports fishery walleye, whitefish, northern pike, smallmouth bass
Manitoba[b]	50° 54'	98° 32'	4,643.5 km^2	248 m	7.2 m	4.7 m	mud, sand, clay, gravel, humus	no	eutrophic	commercial fishery walleye, sauger, whitefish northern pike,suckers
Dauphin[c]	51° 15'	99° 46'	519.3 km^2	260 m	3.5 m	2.1 m	silty clay	no	eutrophic	commercial fishery walleye, northern pike
Crean[d]	54° 15'	106° 10'	119.4 km^2	524 m	32.6 m 25 % of lake exceeds 20 m	11.8 m 33 % of lake shallow	sand, silt	yes	eutrophic due to limited watershed and bogs	sports fishery walleye, northern pike

References

a McLeod, 1943

b Crowe, 1980

c Heise, 1985

d Environment Canada, 1986; Columbia, 1987

Table 2. List of morphological measurements and assigned abbreviations.

Measurement	Abbreviation
Total length	TL
Fork Length	FL
Standard length	SL
Predorsal length	PRDL
Interdorsal space	IDS
Postdorsal length	PDL
Prepelvic length	PPVL
Preanal length	PAL
Caudal peduncle length	CPL
Caudal peduncle depth	CPD
Body depth	BD
Head length	HL
Head depth	HD
Snout length	SNL
Upper jaw length	UJL
Premaxilla length	MXL
Premaxilla width	MXW
Lower jaw length	LJL
Orbit diameter	OD
First dorsal fin length	D1L
First dorsal finbase length	D1BL
Second dorsal fin length	D2L
Second dorsal finbase length	D2BL
Pectoral fin length	PCL
Anal fin length	AL
Anal finbase length	ABL
Superior caudal lobe length	SCL
Inferior caudal lobe length	ICL
Gill raker length	GL

Table 3. List of meristic counts and assigned abbreviations.

Trait	Abbreviation
First dorsal fin rays	D1FR
Second dorsal fin rays	D2FR
Anal fin rays	AFR
Pelvic fin rays	PVFR
Pectoral fin rays	PFR
Lateral line scales	LLS
Caudal fin rays	CFR
Upper gill rakers (first arch)	GRU
Lower gill rakers (first arch)	GRL

Table 4. Comparison of biological and morphological variable mean values by location and testing of significance using ANOVA and Tukey's tests. Areas are: Falcon Lake (F), Lake Manitoba (M), Dauphin Lake (D), Crean Lake (C), Falcon pond (FP), Manitoba pond (MP), Crean pond (CP). Variable abbreviations listed in Tables 2 and 3. n.s. = not significant

	Lake						
	F	M	D	C	FP	MP	CP
Biological variables							
WGT	1109.0	638.0	1458.4	1218.7	1.7	6.3	18.1
TL	418.9	421.8	420.3	417.0	61.6	85.6	132.7
FL	394.1	398.1	396.4	393.6	57.3	80.1	125.3
Meristic variables							
D1FR	13.8	13.9	14.2	14.1	13.4	14.0	14.3
D2FR	21.8	21.4	21.1	21.6	21.5	22.0	21.2
AFR	15.2	15.4	14.6	15.3	16.0	16.2	15.7
PFR	15.0	14.6	14.9	15.0	14.8	15.2	14.9
LLS	89.5	87.6	88.2	86.0	86.6	86.4	85.2
CFR	17.2	17.0	16.9	16.8	16.6	16.8	17.0
GRU	2.1	2.4	2.1	2.2	2.2	2.3	2.1
GRL	7.7	7.8	7.9	7.5	7.8	7.9	7.8

	Lake					
	F	M	D	C	p	Tukey's Test[a]
Standardized (SL = 350 mm) morphometric variables						
PRDL	111.2	112.4	110.5	111.8	0.183	n.s.
IDS	16.0	14.3	13.0	14.9	0.0002	D-F,D-C
PDL	63.7	62.4	63.1	62.8	0.375	n.s.
PPVL	114.9	118.3	115.4	114.9	0.030	C-M
PAL	120.6	126.5	129.7	125.3	0.0001	F,C-D
CPL	82.9	79.9	81.1	80.2	0.0003	F-C,F-M
CPD	26.6	27.7	28.6	27.1	0.0001	D,F-M
BD	70.7	74.9	78.2	73.3	0.0001	D,F
HL	101.1	102.2	101.1	100.6	0.183	n.s.

Table 4. Continued

	Lake					
	1	2	3	4	p	Tukey's Test
HD	53.1	53.1	52.5	53.2	0.868	n.s.
SNL	29.1	29.1	28.6	28.3	0.003	C-M,C-F
UJL	46	47.8	47.6	45.6	0.0001	D-F,D-C,M-F,M-C
MXL	40.4	39.7	39.9	37.6	0.0001	C
MXW	10.1	10.6	10.9	10.0	0.0001	D-F,D-C,M-F,M-C
LJL	57.1	58.8	57.6	57.5	0.001	M
OD	16.3	15.4	16.7	15.9	0.0001	D-C,D-M,F-M
D1L	46.8	47.3	47.3	45.6	0.049	n.s.
D1BL	99.0	102.0	104.0	103.5	0.0001	F
D2L	44.6	45.8	45.1	42.2	0.0001	C
D2BL	79.2	79.0	78.2	80.1	0.062	C-D
PCL	56.2	56.0	56.1	52.1	0.0001	C
PVL	59.6	59.3	59.5	56.6	0.0001	C
AL	49.5	51.7	51.2	46.0	0.0001	C,F
ABL	45.1	44.0	44.0	47.1	0.0001	C
SCL	67.8	65.9	69.9	62.6	0.0001	C,D-F
ICL	65.9	68.3	68.1	61.7	0.0001	C,F
GL	8.8	9.5	9.0	10.1	0.0001	C,F-M

a: Comparisons between lakes using Tukey's studentized range test are significant at the 0.05 level. Single lake letter indicates allcomparisons to this lake are significant (eg.C), other comparisons indicate differences between two lakes (eg. F-M).

Table 5. Raw canonical coefficients of meristic and morphometric variables. For abbreviations of variables see tables 2 and 3. % = percent of total variation accounted for by the discriminant axis, ** $p \leq 0.0001$

	Discriminant axis		
	1	2	3
Selected Morphometrics			
PRDL	-0.149	-0.060	0.050
CPD	0.108	0.307	-0.108
BD	0.077	0.145	-0.142
SNL	-0.038	-0.399	-0.151
UJL	0.103	0.072	0.086
MXL	0.054	-0.085	-0.064
MXW	0.342	0.692	0.120
LJL	-0.049	-0.005	0.182
OD	-0.184	-0.011	-0.621
AL	0.186	-0.094	0.102
ABL	-0.237	0.032	-0.005
SCL	0.116	-0.108	-0.047
GL	-0.256	0.136	0.298
Eigenvalue	2.088	0.864	0.351
%	63.2	26.2	10.6
Significance	**	**	**

	Discriminant axis		
	1	2	3
Lake meristic variables			
D1FR	-0.500	-0.724	-0.121
D2FR	-0.008	-0.010	0.235
AFR	0.998	-0.185	-0.076
PFR	-0.119	-0.133	0.792
LLS	0.012	0.083	-0.004
CFR	0.252	0.917	0.023
GRU	0.790	-0.989	-0.958
GRL	-0.413	0.590	-0.974
eigenvalue	0.227	0.155	0.124
%	44.8	30.6	24.5
Significance	**	**	**

Table 5. Continued

	Discriminant axis	
	1	2
Pond meristic variables		
D1FR	-1.292	0.855
D2FR	0.386	0.516
AFR	0.603	0.305
PFR	-0.206	0.657
LLS	0.075	0.072
CFR	-0.407	-0.083
GRU	0.407	0.581
GRL	0.386	0.598
Eigenvalue	0.540	0.249
%	68.4	31.6
Significance	**	**

	Discriminant axis				
	1	2	3	4	5
Lake-pond meristic variables					
D1FR	-0.272	-0.995	0.891	0.395	-0.038
D2FR	-0.059	0.437	0.567	-0.354	-0.325
AFR	1.029	0.266	0.159	0.362	0.262
PFR	0.168	-0.203	0.848	-0.716	0.155
LLS	-0.138	0.211	0.075	0.069	0.037
CFR	-0.502	-0.044	0.116	0.532	0.547
GRU	0.068	0.127	0.392	1.079	-1.946
GRL	0.706	0.326	0.270	0.928	0.573
Eigenvalue	0.441	0.292	0.149	0.094	0.054
%	42.8	28.3	14.5	9.2	5.2
Significance	**	**	**	**	**

Table 6. Classification of walleye lake stock morphometrics using discriminant analysis.

Stock	% correctly classified	No. classified into lake				
		Crean	Dauphin	Falcon	Manitoba	Total
Crean	89.58	43	1	4	0	48
Dauphin	79.66	1	47	2	9	59
Falcon	82.00	3	2	41	4	50
Manitoba	77.19	0	7	6	44	57
X	82.11 %					

Table 7. Results of the Chi-square (upper asterisks) and Mann-Whitney U tests (lower asterisks) for lake walleye populations (see Table 3 for trait abbreviations) * $p \leq 0.05$ ** $p \leq 0.01$.

Stocks	Traits							
	D1FR	D2FR	AFR	PFR	LLS	CFR	GRU	GRL
CREAN-DAUPHIN		**	**	*	**			**
		**	**		**			**
CREAN-FALCON	**			*	**			**
	**				**			**
CREAN-MANITOBA				**		**		*
				**	**	*		**
FALCON-DAUPHIN	**	**	**		*			
	**	**	**		*			
FALCON-MANITOBA		*	**	**	**		**	
		*		**	**		**	
DAUPHIN-MANITOBA			**	**			**	
	*		**	**			**	

Table 8. Classification of walleye lake stocks by meristic counts using discriminant analysis.

Stock	% correctly classified	No. classified into lake				
		Crean	Dauphin	Falcon	Manitoba	Total
Crean	36.07	22	17	9	13	61
Dauphin	53.45	9	31	10	8	58
Falcon	54.00	9	7	27	7	50
Manitoba	43.10	11	13	9	25	58
X	46.88 %					

Table 9. Distribution of Mdh-3 phenotypes (expected values in brackets) and calculated gene frequencies of lake and pond walleye stocks, chi-square (X^2) analysis of fit of data between observed and expected number (calculated from Castle-Hardy-Weinberg law) and confidence limits for Mdh-3^{100} frequency.

Stocks	Number of fish	Phenotype						X^2	p	Gene Frequency			99 % confidence limit[d] for 100 allele frequency
		70/70	70/100	70/120	100/100	100/120	120/120			70	100	120	
Crean Lake[a]	417	150 (155.9)	6 (3.7)	204 (194.5)	0 (0.02)	0 (2.3)	57 (60.6)	6.29	n.s.[c]	0.556	0.143	0.302	0.004-0.041
Crean Pond	30	13 (14.0)	1 (0.7)	14 (12.3)	0 (0.01)	0 (0.3)	2 (2.7)	0.61	n.s.	0.683	0.017	0.300	0.002-0.223
Lake Manitoba	68	1 (0.03)	0 (1.6)	1 (1.3)	21 (20.6)	33 (32.0)	12 (12.4)	0.05	n.s.	0.022	0.551	0.427	0.385-0.708
Manitoba Pond	60	0 (0.02)	2 (1.1)	0 (0.9)	15 (18.1)	34 (28.6)	9 (11.3)	1.97	n.s.	0.017	0.550	0.433	0.409-0.648
Dauphin Lake[b]	109	0 (0.1)	5 (4.4)	1 (1.9)	56 (50.4)	31 (43.0)	16 (9.2)	9.03	*[e]	0.027	0.679	0.294	0.590-0.761
Falcon Lake	60	0 (0.02)	1 (1.0)	1 (1.0)	16 (13.5)	24 (29.0)	18 (15.5)	1.66	n.s.	0.017	0.475	0.508	0.352-0.591
Falcon Pond 1989	60	0 (0.0)	0 (0.0)	0 (0.0)	33 (32.2)	22 (23.5)	5 (4.3)	0.14	n.s.	0.000	0.733	0.267	0.619-0.824
Falcon Pond 1987	16	0 (0.02)	0 (0.53)	1 (0.43)	4 (4.51)	9 (7.44)	2 (3.07)	0.74	n.s.	0.031	0.531	0.438	0.298-0.753

a Clayton et al., 1974

b Tretiak, 1983 unpublished data

c not significant

d Mainland et al., 1956

e $p \leq 0.05$

Table 10. Distribution of Idh-1 phenotypes (expected values in brackets) and calculated gene frequencies of lake and pond walleye stocks, Chi-square (X^2) analysis of fit of data between observed and expected numbers (calculated from Castle-Hardy-Weinberg law) and confidence limits for Idh-1^{75} frequency.

Stocks	Number of fish	Phenotype 100/100	75/100	75/75	X^2	p	Gene frequency 100	75	99 % confidenc limit[b] of 75 allele frequency
Crean Lake[a]	38	10	19	9	0.0012	n.s.	0.51	0.49	0.340-0.642
		(9.9)	(19.0)	(9.1)					
Crean Pond	20	4	10	6	0.003	n.s.	0.45	0.55	0.339-0.748
		(4.1)	(9.9)	(6.0)					
Lake Manitoba[a]	50	12	23	15	0.31	n.s.	0.47	0.53	0.398-0.659
		(11.0)	(24.9)	(14.0)					
Manitoba Pond	57	19	25	13	0.74	n.s.	0.56	0.45	0.328-0.577
		(17.9)	(28.7)	(11.5)					
Falcon Lake	59	37	11	11	17.03	**[c]	0.72	0.28	0.181-0.397
		(30.59)	(23.79)	(4.62)					
Falcon Pond 1989	51	22	21	8	0.62	n.s.	0.64	0.36	0.241-0.493
		(20.9)	(23.5)	(6.6)					
Falcon Pond 1987	9	5	2	2	2.25	n.s.	0.67	0.33	0.095-0.658
		(4.0)	(4.0)	(1.0)					

a Tretiak, unpublished data

b Mainland et al., 1956

c $p \leq 0.001$

Table 11. Results of the Chi-square (upper asterisks) and Mann-Whitney U tests (lower asterisks) for pond fingerlings (see Table 3 for trait abbreviations) * $p \leq 0.05$ ** $p \leq 0.01$.

Stocks	Traits							
	D1FR	D2FR	AFR	PFR	LLS	CFR	GRU	GRL
CREAN-FALCON	**	**	**			**		
	**		*			**		
CREAN-MANITOBA	**	**	**	*		*	*	
	**	**	**	**			*	
FALCON-MANITOBA	**	*		*		**		
	**	**	**					

Table 12. Classification of walleye pond stocks by meristic counts using discriminant analysis.

Stock	% correctly classified	No. classified into lake			
		C pond	F pond	M pond	Total
C pond	75.00	45	6	9	60
F pond	56.90	12	33	13	58
M pond	61.67	10	13	37	60
X	64.52 %				

Table 13. Results of Chi-square (upper asterisks) and Mann-Whitney U tests (lower asterisks) for native lake stocks versus pond fingerlings (see Table 3 for trait abbreviations) * $p \leq 0.05$ ** $p \leq 0.01$.

Stocks	Traits							
	D1FR	D2FR	AFR	PFR	LLS	CFR	GRU	GRL
CREAN-CREAN		**	**			**		
		**	**					**
FALCON-FALCON			**		**	**		
	*		**		**	**		
MANITOBA-MANITOBA		**	**	**				
		**	**	**	*			

Table 14. Classification of walleye lake and pond stocks by meristic counts using discriminant analysis.

Stock	% correctly classified	No. classified into group						
		C pond	F pond	M pond	Crean	Falcon	Man	Total
C pond	55.00	33	3	8	8	5	3	60
F pond	39.66	9	23	14	2	5	5	58
M pond	56.67	5	7	34	5	5	4	60
Crean	42.62	12	5	3	26	7	8	61
Falcon	48.00	4	5	2	6	24	9	50
Manitoba	40.68	10	1	5	6	13	24	59
X	47.11 %							

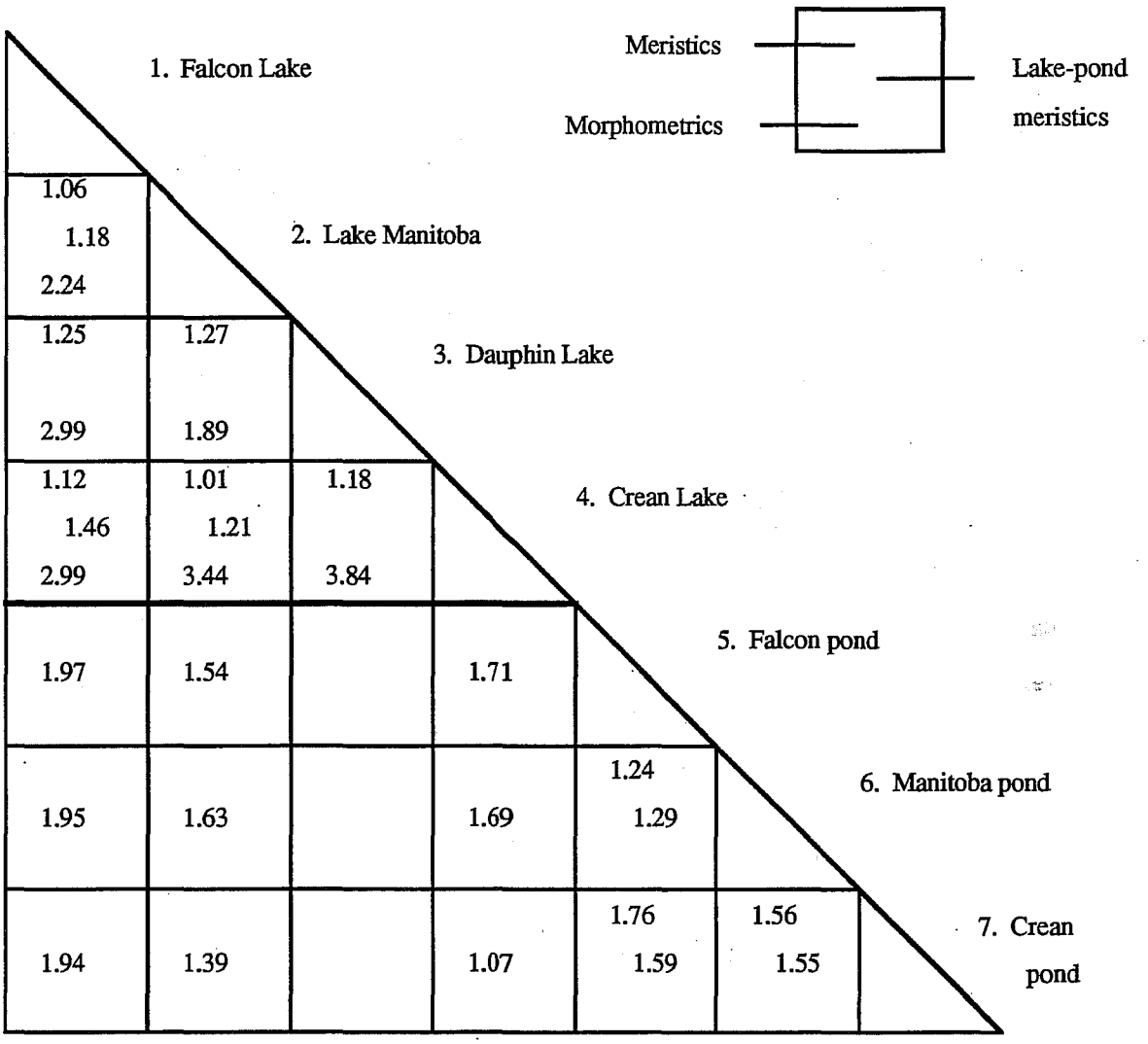

Fig. 1. Summary of Mahalanobis distances between centroids of meristics and morphometics for walleye lake and pond stocks.

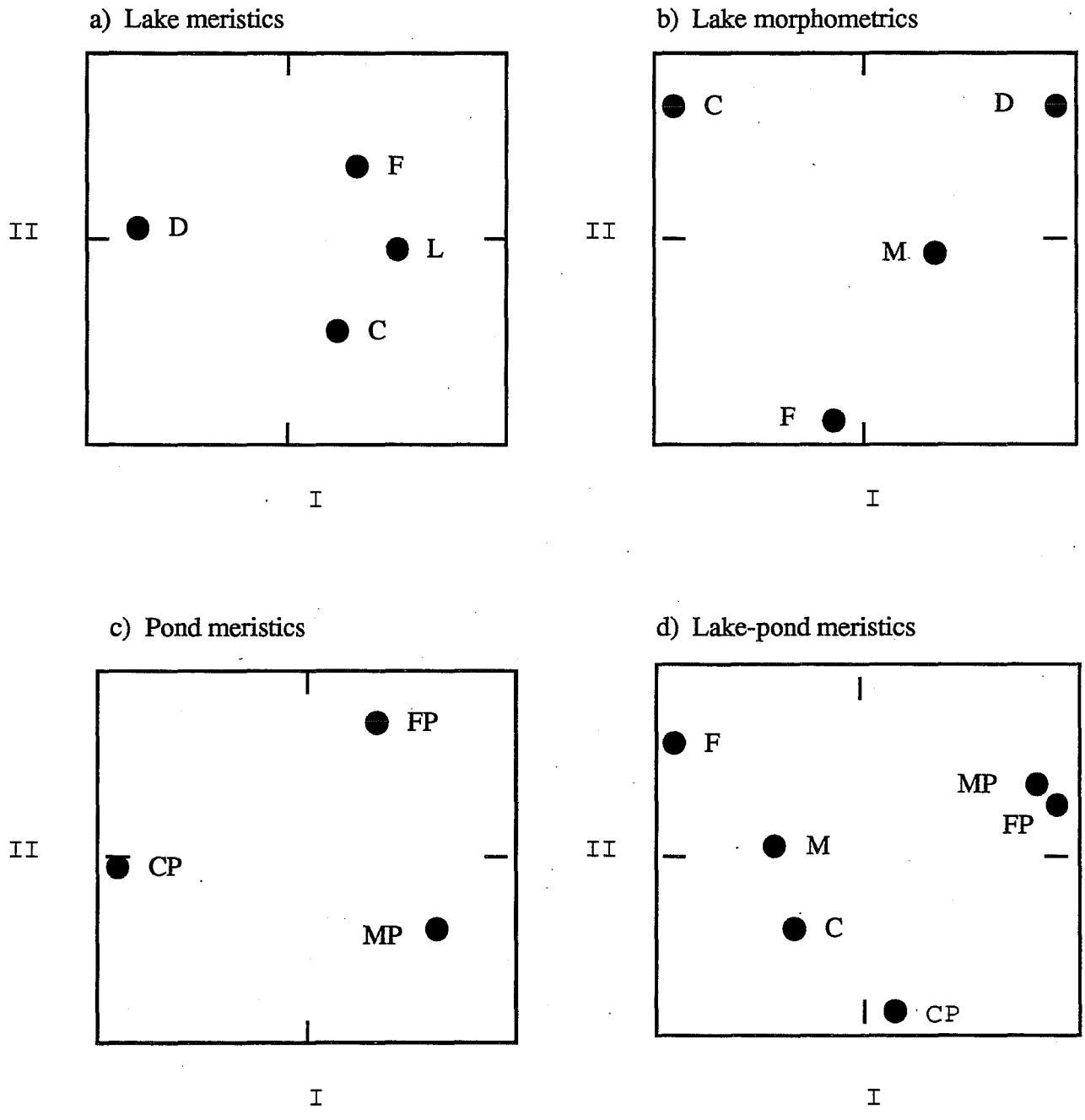

Fig. 2. Plots of canonical discriminant function analysis class means on axis one vs. axis two for walleye from lakes and ponds. Areas are: F (Falcon Lake), M (Lake Manitoba), D (Dauphin Lake), C (Crean lake), FP (Falcon pond), M (Manitoba pond), CP (Crean pond).

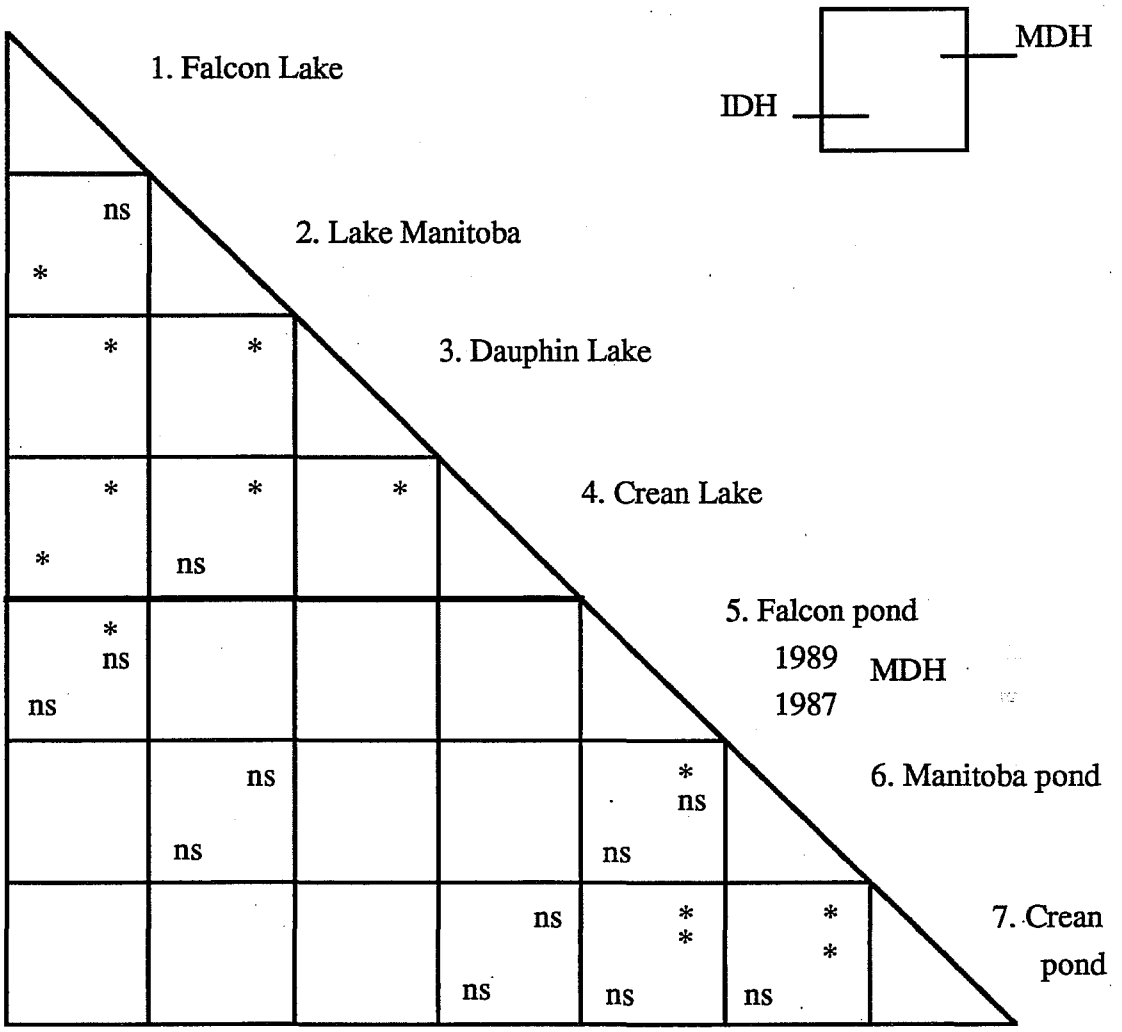

Fig. 3. Summary of Chi-square values for comparisons of Mdh-3 and Idh-1 electrophoresis of lake and pond walleye stocks. * = $P \leq 0.01$ and ns = non-significant (no Idh-1 test for Dauphin Lake).