Examination of walleye (*Stizostedion vitreum*) stocks , using morphometrics and meristics, biochemical genetic analysis and standard rate of oxygen consumption

by

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A thesis
presented to the University of Manitoba
in partial fulfillment of the
requirements for the degree of
Master of Science
in the
Department of Zoology

Winnipeg, Manitoba, 1990

ISBN 0-315-63225-9

EXAMINATION OF WALLEYE(Stizostedion vitreum) STOCKS, USING MORPHOMETRICS AND MERISTICS, BIOCHEMICAL GENETIC ANALYSIS AND STANDARD RATE OF OXYGEN CONSUMPTION

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ABSTRACT

Stocking endeavors to replenish depleted walleye stocks, *Stizostedion vitreum* (Mitchill), have led to the mixing of various walleye stocks. Stocking procedures have also employed the rearing of fingerling walleye in ponds and stocking these fish into lakes without considering the effect the pond environment might have on the developing walleye. The purpose of this study was to provide information on whether or not different walleye stocks could be distinguished and to determine if walleye, reared under pond conditions, were the same or different from native lake walleye. Walleye were collected from three lakes in Manitoba (Falcon, Manitoba and Dauphin) and one lake in Saskatchewan (Crean) and fingerlings from Falcon, Manitoba, and Crean lakes were reared in ponds at the Methley Beach Research Station at Dauphin Lake. Three techniques: meristic and morphometric analysis, biochemical genetic analysis, and standard oxygen consumption were used to examine walleye stock differences. Meristic and morphometric differences indicated the four lake stocks have adapted independently to their respective lakes. Differences among stocks reared under similar pond conditions indicated that genetics may be involved in determining meristic traits. Examination of differences between pond reared walleye and native lake walleye showed that brood stock selection could play an important role in determining phenotypes. Biochemical genetic analysis of malate dehydrogenase and isocitrate dehydrogenase indicated that the gene frequencies of these two enzymes were useful in differentiating the four walleye stocks in this study. Gene frequencies remained constant in the pond reared walleye if selection of brood stock was random. Standard oxygen consumption tests of walleye fingerlings, raised under similar conditions, also indicated significant differences among stocks. All three techniques indicated that the walleye stocks examined in this study were distinct from one another. Examination of meristic counts suggests that lake reared walleye are different from pond reared walleye. This implies that stocking procedures should take into account

differences among lakes walleye stocks and that mixing of stocks may not be in the best interest of stock enhancement (indicated by differences in stock genetics and oxygen consumption). Also brood stock should be selected so that the walleye genome and phenome of the entire lake is represented in the offspring.

ACKNOWLEDGEMENTS

I would like to extend my sincerest gratitude to my supervisor Dr. William Franzin for his guidance and support throughout this study.

The research of this thesis was part of a walleye rehabilitation project by the Department of Fisheries and Oceans Canada, and was made possible with the assistance and cooperation of many individuals at the Freshwater Institute. I would like to thank all of them, especially:

Dr. M. Giles, who allowed me to use his oxygen respirometry system and aided in the calculation and interpretation of the results of the oxygen consumption tests.

Dr. J. Clayton and especially his technician Mr. R. Lillie, who allowed me to use their laboratory facilities for electrophoretic analysis and provided helpful suggestions whenever problems occurred.

Mr. C. Day, for his help in field work and statistical analysis and Mr. J. Babaluk, for help in analyzing the walleye opercular bones for ages.

I would also like to thank fellow graduate students, Karen Broughton and Tom Johnston, and summer students, Janis Klapecki and Wayne Hiltz, for assistance in field work and moral support. Thanks also goes to my family and friends for their patience and understanding throughout the various phases of this study.

I am also grateful to the Department of Natural Resources, Manitoba for supplying walleye eggs from the Swan Creek and Whiteshell hatcheries, and allowing me to gill net walleye in Falcon lake, Lake Manitoba, and Dauphin lake. Thanks also goes to the park staff at the Prince Albert National Park, Saskatchewan for allowing us to collect eggs and fish at Crean lake.

I gratefully acknowledge financial support from the Department of Fisheries and Oceans, Canada through a research stipend.

Finally I extend my greatest appreciation to my supervisory committee, Dr. W.G. Franzin, Dr. M. Giles, Dr. G.E.E. Moodie, and Dr. C. Jay for their helpful comments and patience in reviewing this thesis.

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COMPARISONS OF OXYGEN CONSUMPTION RATES AMONG THREE JUVENILE STOCKS OF WALLEYE FROM FALCON AND MANITOBA LAKES IN MANITOBA AND CREAN LAKE, SASKATCHEWAN

INTRODUCTION

Stock differentiation is an important concept in fisheries management. Stocks need to be identified, characterized and managed as separate entities. Too often, fish from different lakes are used for stocking into lakes with depleted fish stocks without considering the repercussions of these acts. First, in order to identify stocks, a definition of a stock must be established. A genotypic stock is a population of fish maintaining and sustaining Castle-Hardy-Weinberg equilibrium for a particular character in each generation (Booke, 1981 and Altukhov, 1981). If genotypic stock characterization is not possible then a phenotypic stock may be recognized and defined as a group, or population, of fish maintaining characteristics which are expressed in one or more ways depending on the type of environment they inhabit (Booke, 1981). Ricker (1972) defined the term stock as a group of fish spawning in a particular lake or stream at a particular season. These fish do not interbreed to any substantial degree with any other group spawning in a different place, or in the same place at a different season. Other terms may be used in the place of stock, such as race, tribe, population, subpopulation or subspecies (Ihssen, et al., 1981). The main idea of the stock definition is to show that fish species are subdivided into local populations and that there are genetic differences between local populations which are adaptive (MacLean and Evans, 1981).

Because walleye (*Stizostedion vitreum vitreum* (Mitchill)) is an important fish to both commercial and sport fisheries, many walleye stocking programs are currently underway. Mixing of stocks is now occurring because of stocking procedures in which walleye are spawned from one lake, the eggs are hatched in a hatchery and then the larvae are stocked into different lakes. Little thought has been devoted to considering whether these introduced fish will perform as well in a new environment as in their native lake, or if they will produce less fit offspring if the two stocks interbreed. Few studies of walleye stock differences have been conducted. Shcherbukha (1972) found significant

morphological differences among three species of the genus *Stizostedion* in the Dnieper-bug estuary in the Soviet Union. Uthe and Ryder (1970) in a study of muscle myogen polymorphism and morphometrics in five walleye stocks found differences among stocks using electrophoresis but did not find differences in the morphometric measurements. This may be due to the fact that they took very few measurements and used ratios. Billington et al. (1989), Clayton et al. (1971), who studied large geographic areas, and Paragamian (1988), who studied a small geographic area, have found biochemical genetic differences among walleye stocks. The hatchery and pond environments may have an effect on fish. These conditions may change the characteristics of the walleye even before they hatch, causing larvae to develop differently from the parental stock (Tåning, 1952).

Various techniques may be used to determine and describe stock differences (Ihssen, et al., 1981). Tarby (1981) studied oxygen consumption in one walleye stock. Colby and Nepszy (1981) describe various techniques including biochemical genetics, morphology, and parasites, employed to find biological differences among walleye stocks. The purpose of this thesis was to determine if there are differences among stocks of walleye from four different lakes, Falcon Lake, Lake Manitoba, Dauphin Lake in Manitoba and Crean Lake, Saskatchewan (Table 1). Crean Lake, Falcon Lake, and Lake Manitoba have been used frequently as sources of walleye eggs for stocking, while Dauphin Lake has been the recipient of huge inputs of walleye larvae from Crean Lake. The techniques employed in this study were morphometrics, meristics, oxygen consumption and biochemical genetic analysis. This study also examines differences and similarities between pond-raised fingerlings and their parental lake stocks and among three of the stocks of fingerlings raised under similar conditions of the pond environments.

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
Dauphin[c]	51° 15'	99° 46'	519.3 km^2	260 m	3.5 m	2.1 m	silty clay	no	eutrophic	northern pike, suckers 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

GEOLOGICAL HISTORY

The geological history of the lakes in this study also has important bearing on the adaptation of walleye to the lakes in which they live. All four lakes were at one time or another joined by Glacial Lake Agassiz as the glaciation of the Wisconsin period receded (Elson, 1967) . Walleye probably entered into Lake Agassiz from the upper Mississippi River refuge (McPhail and Lindsey, 1970; Crossman and McAllister, 1986). The Missouri River refuge would have been another possible point of entry, however McPhail and Lindsey (1970) state that walleye are not native to the upper Missouri system.

As the glacial lake began to recede and move northward, Crean lake would have been the first of the four lakes to become isolated and Falcon separated soon after (approximately 9000 B.P.). Dauphin lake and Lake Manitoba remained as a part of Glacial Lake Agassiz for a much longer period of time. Separation of these two lakes would probably have occurred at about 8000 B.P. according to the maps of Elson (1967). Accordingly one might expect Crean walleye stock to be the most different from the other three stocks and Dauphin and Manitoba walleye stocks might be the most similar.

FORWARD

This thesis has been written in the paper style format with three sections. Each section has its own introduction, methods, results, and discussion with a general discussion concluding the thesis. Initial studies conducted on pond competition between Crean and Manitoba larvae are discussed in Appendix 1.

MERISTIC AND MORPHOMETRIC ANALYSIS OF FOUR WALLEYE LAKE STOCKS AND THREE WALLEYE POND STOCKS

Introduction

Morphometrics and meristics have been used in many studies to determine differences among fish stocks (for recent examples see: Beacham et al., 1988; Blouw et al., 1988; Bowering, 1988; Carscadden and Leggett, 1975; Peden et al., 1989; Shcherbukha, 1974; Swain and Holtby, 1989; and Todd et al., 1981). Different types of analysis performed on morphometrics and meristics can indicate if stocks are different from each other and which traits are important in determining these differences.

Martin (1949) and Tåning (1952) recognized the variability of fish morphology and conducted various experiments to determine how different environmental conditions could affect fish morphology. The problem encountered using morphometric and meristic characteristics in stock delineation studies is that these traits are affected by both the environment and the genetic makeup of a fish. Tåning (1952) found in his experiments with brown trout that meristics were affected mostly by temperature and to a lesser extent, by oxygen and carbon dioxide concentrations. Blouw et al. (1988) also found meristic variation among Atlantic salmon stocks and found that some of these differences were due to environmental effects such as temperature. Tåning also noted that most of the meristic traits became fixed before the eggs hatched. Therefore, one may expect that differing environmental conditions to which fish may be exposed in individual lakes may produce variation in phenotypes. This also may indicate that eggs hatched in a hatchery might develop differently than if they were hatched in a lake. A genetic component also has been found to play an important role in meristic and morphometric variation. Tåning (1952) found that some traits, such as number of vertebrae were controlled to a greater extent by genetic factors than by environmental conditions. Taylor and McPhail (1985) and Murray

and Beacham (1989) in their studies with coho and chum salmon, found heritable genetic components in morphological and meristic characters.

This section describes meristic and morphological variation among four native walleye stocks and examines the effects of rearing fingerlings from these stocks in a common pond environment.

Methods and Materials

Adult walleye were collected using trapnets or gillnets. Sixty walleye were taken from a spawning run at Crean Lake in 1988. One-third of the fish sampled from Falcon Lake were sampled from a spawning run in 1988; the rest were gill-netted during the summer of 1989 to obtain a total of 60 fish. Because some of these fish were much smaller than those caught in other lakes, all fish smaller than 145 mm were omitted from analyses leaving a sample of 50 fish from Falcon Lake. Fish were collected from Lakes Manitoba and Dauphin with gillnets; 60 from Lake Manitoba in summer and fall, 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 in a hatchery at the former DFO Methley Beach Research Station at Dauphin Lake. 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. Lake Manitoba larvae also were obtained from the Swan Creek hatchery in May 1988. All larvae were raised to fingerlings (60-120 mm) in separate one hectare ponds at the Methley Beach Research Station, close to Dauphin Lake. Sixty fingerlings each of Crean Lake, Falcon Lake and Lake Manitoba stocks were taken from the rearing ponds during pond drainage and frozen for later meristic analysis. A list of the numbers of fish sampled and types of examinations made on each stock are shown in Appendix 2A.

Morphological measurements (Table 2) and meristic counts (Table 3) were made with the naked eye on partially thawed fish. Due to the small size (40-70 mm) of fingerlings from the Manitoba and Falcon stocks; meristic counts were taken with the aid of a dissecting microscope and morphometric measurements were omitted. Mean values of meristic counts and standardized morphometric measurements for lake and pond walleye stocks may be found in Appendix 2B and 2C respectively.

All counts and measurements (using digital calipers read to the nearest 0.1 mm) were done on the left side of the fish. Ages were determined (Appendix 2D) using the left opercular bones according to the methods of Campbell and Babaluk (1979).

The sex of each adult walleye was recorded and the possibility of sexual dimorphism was considered for both meristic and morphological traits. Pond stock fish were not sexed because of difficulties in sex determination. Growth rates and condition of the adult stocks also were examined using ANCOVA .

Meristic data of both lake and pond stocks were analyzed using univariate and multivariate techniques. Variability within stocks was checked using chi-square analysis on year classes. Univariate Chi-square analysis and Mann-Whitney U tests, were performed on each trait to determine or check for differences in distribution of counts and differences between means among populations respectively. Data were pooled for chi-square analysis in cases where frequencies of counts were under five. Canonical discriminant function analysis was used to separate stocks by examining all meristic data simultaneously. Class means were plotted for canonical vectors one, two, and three.

Since fish exhibit allometric growth, in which body proportions are correlated to the absolute size of the individual fish (Gould, 1966), raw morphological 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

Table 2 List of morphological measurements, assigned abbreviations and method reference

Measurement	Abbreviation	Method
Total length	TL	Hubbs & Lagler, 1958
Fork Length	FL	Hubbs & Lagler, 1958
Standard length	SL	Hubbs & Lagler, 1958
Predorsal length	PRDL	Hubbs & Lagler, 1958 except to the first dorsal spine, not ray
Interdoral space	IDS	Distance between the 1st & 2nd dorsal fins
Postdorsal length	PDL	distance from posterior 2nd dorsal fin to end of veterbral column
Prepelvic length	PPVL	tip of snout to anterior base of pelvic fin
Preanal length	PAL	posterior pelvic finbase to anterior anal finbase
Caudal peducle length	CPL	Hubbs & Lagler, 1958
Caudal peducle depth	CPD	Hubbs & Lagler, 1958
Body depth	BD	Hubbs & Lagler, 1958 taken behind the third spine of the 1st dorsal fin
Head length	HL	Hubbs & Lagler, 1958 to opercular spine tip, not membrane
Head depth	HD	Hubbs & Lagler, 1958
Snout length	SNL	Hubbs & Lagler, 1958
Upper jaw length	UJL	Hubbs & Lagler, 1958
Premaxilla length	MXL	Lindsey, 1962 similar to maxilla measurement
Premaxilla width	MXW	Lindsey, 1962
Lower jaw length	LJL	Lindsey, 1962
Orbit diameter	OD	Hubbs & Lagler, 1958
First Doral fin length	D1L	measured at the third spine
First dorsal finbase length	D1BL	Hubbs & Lagler, 1958
Second dorsal fin length	D2L	Hubbs & Lagler, 1958

...Cont'd

Table 2 (cont'd)

Measurement	Abbreviation	Method
Second dorsal finbase length	D2BL	Hubbs & Lagler, 1958
Pectoral fin length	PCL	Hubbs & Lagler, 1958
Pelvic fin length	PVL	Hubbs & Lagler, 1958
Anal fin length	AL	Hubbs & Lagler, 1958
Anal finbase length	ABL	Hubbs & Lagler, 1958
Superior Caudal lobe length	SCL	end of the vertebral column to the tip of upper caudal fin lobe
Inferior caudal lobe length	ICL	end of the vertebral column to the tip of lower caudal fin lobe
Gill raker length	GL	Lindsey, 1962

Table 3 List of meristic counts, assigned abbreviations and method reference

Trait	Abbreviation	Method
First dorsal fin rays	D1FR	spines counted
Second dorsal fin rays	D2FR	first two spines included, also last branched rays
Anal fin rays	AFR	first two spines included, also last branched rays
Pelvic fin rays	PVFR	Hubbs & Lagler, 1958
Pectoral fin rays	PFR	Hubbs & Lagler, 1958
Lateral line scales	LLS	Hubbs & Lagler, 1958
Caudal fin rays	CFR	Hubbs & Lagler, 1958
Upper gill rakers (first arch)	GRU	Hubbs & Lagler, 1958
Lower gill rakers (first arch)	GRL	Hubbs & Lagler, 1958

variable, 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 average mean of SL for all fish from all four stocks. This form of adjustment is similar to that used by Skulason et al. (1989), using the least squares regression form of the allometric equation to calculate the allometric coefficient b:

$$\log VAR = \log a + b (\log SL_i).$$

Allometric coefficients from separate stock regressions were compared using analysis of covariance.

Morphological data were inspected for normality using the Kolomogorov D statistic (SAS, 1982) before any analysis was performed. 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 morphometric variables showed significant stock differences and between which stocks these differences existed. Canonical discriminant function analysis was performed on morphometric data in a manner similar to that used for meristic data. The raw canonical coefficients of the 37 meristic and morphometric variables were examined to determine which were the most important for discriminating among stocks (Appendix 2E) 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) and are measures of dissimilarity among groups (Sneath and Sokal, 1973). Discriminant analysis was performed on the four stocks to check if individual fish could be classified to their respective lakes based on a subset of ten fish from each of the four lake stocks. These tests also were performed on the meristics of pond stocks and combined lake and pond stocks.

Results

Approximately equal numbers of male and female fish were examined from each lake stock and no sexual dimorphism was found in either meristic or morphometric measurements. This observation was in agreement with Scott and Crossman (1973) who also reported no sexual dimorphism among walleye. Growth rates (Table 4) and condition (Table 5) of the adult stocks indicated significant differences among stocks. Figure 1 indicates that both Falcon and Manitoba lake stocks were faster growing stocks than Crean and Dauphin lake stocks. ANCOVA of the weight-length relationship indicates significant differences in condition among stocks, although these differences were not great (Figure 2). Meristic data with the exception of lateral line scales, were not normally distributed because meristics are discrete variables (Blouw et al., 1988) and have few classes. Lateral line scale counts had a wider range of variation and therefore more classes. Non-parametric univariate tests were used to analyze the meristic data. In addition, canonical discriminant function analysis, a parametric test, was used on the meristic data because multivariate tests have been found to be considerably robust even for non-normal data (Mardia, 1971; and Sneath and Sokal, 1973). Morphometric data were normally distributed, allowing parametric tests to be used.

Table 6 shows the actual ranges of meristic counts for both lake and pond stocks. Lateral lines scales and caudal fin rays showed that the Falcon walleye stock had higher counts when compared to Crean stock. Few differences were found between Crean and Manitoba lake and pond stocks. The Falcon lake and pond stocks however, were quite different from each other with pond fish showing a shifted, lower range in counts for the traits first dorsal rays, lateral line scales and caudal fin rays.

Univariate Meristic Analysis

Test for within stock variability indicated that the variation among year classes was

Table 4 Comparison of growth rates using ANCOVA with age as the covariate.

Stock	Slope	r^2 fit to regression	Intercept	Standard Error of slope	Tukey'sTest[a]
Crean	0.026	0.246	2.344	0.008	*
Dauphin	0.030	0.508	2.465	0.005	*
Falcon	0.078	0.666	2.221	0.007	F-D,F-C
Manitoba	0.067	0.662	2.311	0.007	M-D,M-C

a Comparisons between lakes using Tukey's studentized range test are significant at the 0.05 level. Single letter indicates comparisons between lakes are significant, * indicates all comparisons to this lake are significant.

Table 5 Comparison of condition using ANCOVA with $\log_{10}$ standard length as the covariate.

Stock	Slope	r^2 fit to regression	Intercept	Standard Error of slope	Tukey's Test[a]
Crean	2.930	0.980	-4.595	0.054	*
Dauphin	2.829	0.761	-4.252	0.206	*
Falcon	3.136	0.963	-5.157	0.089	*
Manitoba	3.021	0.933	-4.802	0.108	*

a Comparisons between lakes using Tukey's studentized range test are significant at the 0.05 level. Single letter indicates comparisons between lakes are significant, * indicates all comparisons to this lake are significant.

Figure 1 Plot of the age-length relationship of walleye from Falcon Lake, Lake Manitoba, Dauphin Lake, and Crean Lake

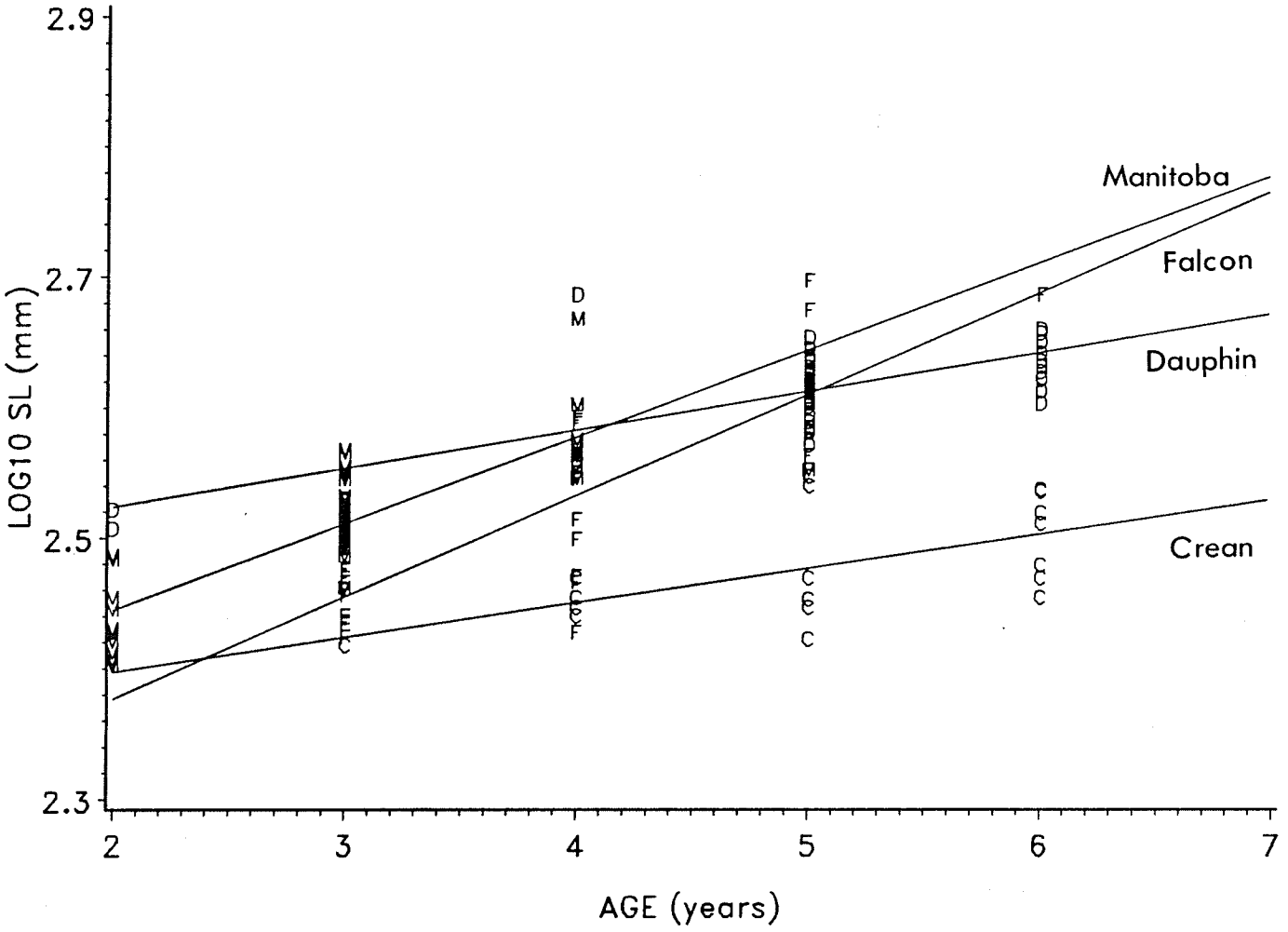

2.9
2.7
2.5
2.3
LOG10 SL (mm)
2
3
4
5
6
7
AGE (years)
Manitoba
Falcon
Dauphin
Crean

Figure 2 Plot of the length-weight relationship of walleye from Falcon Lake, Lake Manitoba, Dauphin Lake, and Crean Lake indicating fish condition

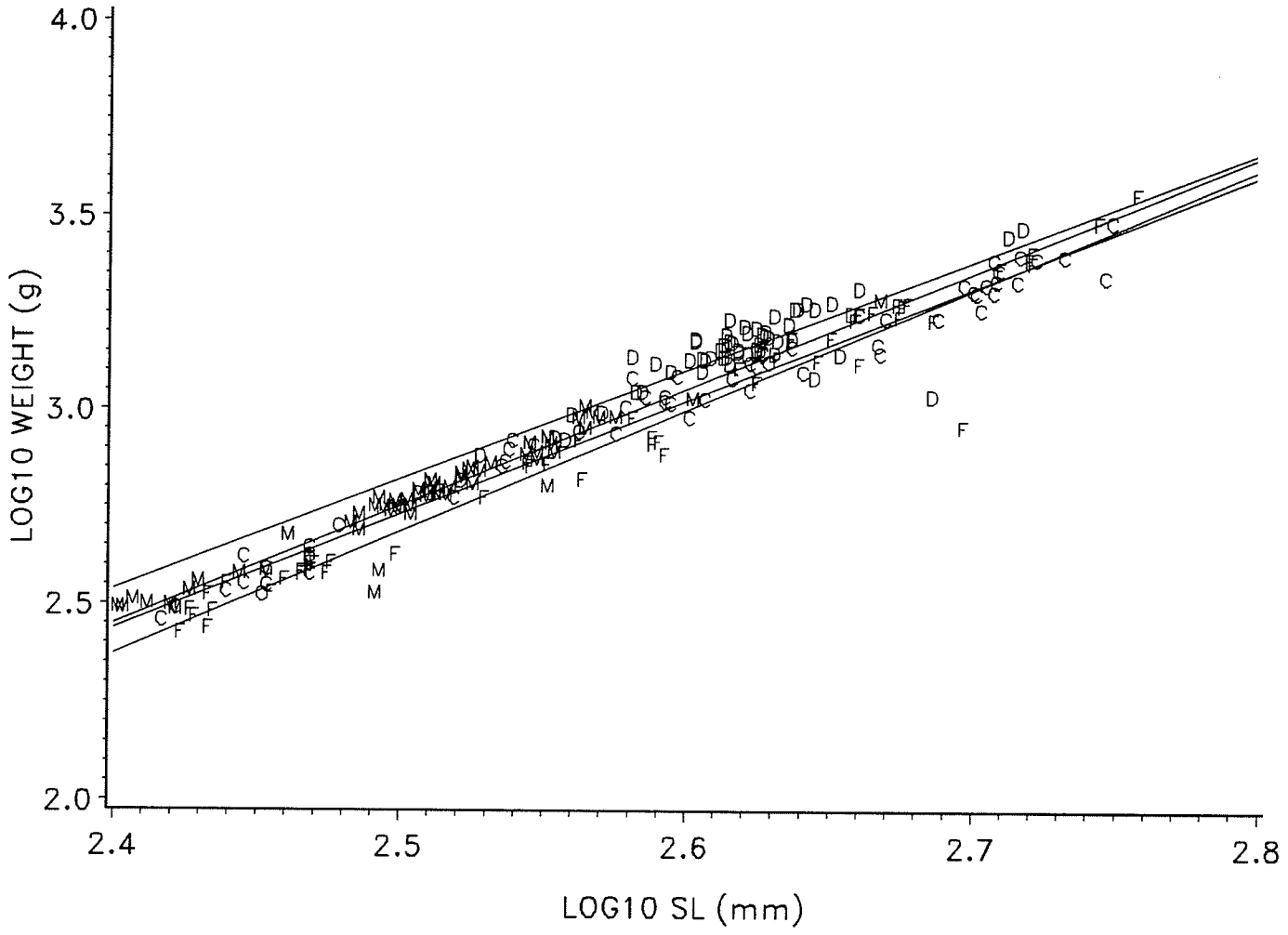

4.0
3.5
3.0
2.5
2.0
LOG10 WEIGHT (g)
2.4
2.5
2.6
2.7
2.8
LOG10 SL (mm)

Table 6 Comparison of frequency and geographic variation in counts of meristic traits for lake and pond walleye stocks

	lake					pond				
D1FR	12	13	14	15	16	12	13	14	15	16
FALCON	-	17	28	5	-	4	27	26	2	-
MANITOBA	1	15	35	7	2	-	10	43	7	-
DAUPHIN	-	8	36	15	2					
CREAN	-	9	38	13	2	-	3	36	20	1

	lake							pond						
D2FR	15	19	20	21	22	23	24	15	19	20	21	22	23	24
FALCON	-	-	2	15	26	7	-	-	1	7	25	13	14	-
MANITOBA	-	-	10	23	19	6	1	-	1	1	15	23	20	-
DAUPHIN	1	-	12	27	17	4	-							
CREAN	-	-	2	27	29	4	-	-	-	13	26	19	2	-

	lake							pond						
AFR	12	13	14	15	16	17	18	12	13	14	15	16	17	18
FALCON	-	2	4	26	16	2	-	-	-	4	11	27	17	-
MANITOBA	-	-	6	31	19	3	1	-	-	-	8	31	20	1
DAUPHIN	1	5	22	23	10	-	-							
CREAN	-	-	7	31	21	3	-	-	1	1	18	36	4	-

. . . Cont'd

Table 6 (cont'd)

	lake							pond						
PFR	11	12	13	14	15	16	17	11	12	13	14	15	16	17
FALCON	-	2	-	6	29	12	1	-	-	2	18	29	11	-
MANITOBA	-	1	2	17	39	1	-	-	-	-	7	34	18	1
DAUPHIN	1	-	1	11	36	12	-							
CREAN	-	-	-	5	50	7	-	-	-	-	12	41	7	-

	lake																	
LLS	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96
FALCON	-	-	-	-	1	-	-	2	2	6	9	5	8	5	5	4	1	-	2
MANITOBA	-	-	-	-	1	1	4	6	8	8	13	6	6	4	1	1	1	-	-
DAUPHIN	-	-	1	-	-	3	4	2	6	9	6	7	5	5	5	4	1	-	-
CREAN	-	-	-	2	3	3	8	7	12	10	7	5	4	-	-	-	-	-	-

	pond																
LLS	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95
FALCON	2	3	-	2	5	10	2	9	2	4	9	3	3	1	1	3	-	1
MANITOBA	-	1	2	1	3	5	6	5	8	10	4	4	3	3	1	3	1	-
CREAN	-	-	5	3	6	5	7	7	5	7	4	5	4	5	-	-	-	-

	lake							pond						
CFR	14	15	16	17	18	19	21	14	15	16	17	18	19	21
FALCON	-	-	4	35	9	1	1	-	9	16	25	7	2	-
MANITOBA	-	-	2	54	4	-	-	-	4	7	44	5	-	-
DAUPHIN	1	1	5	47	6	-	-							
CREAN	-	1	13	42	6	-	-	-	1	2	54	3	-	-

. . . Cont'd

Table 6 (cont'd)

GRU	lake		pond	
	2	3	2	3
FALCON	44	6	50	10
MANITOBA	37	23	41	19
DAUPHIN	52	8		
CREAN	48	14	52	8

GRL	lake				pond			
	6	7	8	9	6	7	8	9
FALCON	3	10	36	1	-	15	42	3
MANITOBA	-	14	44	2	1	9	42	8
DAUPHIN	-	13	41	6				
CREAN	2	26	33	1	2	10	46	2

insignificant. Several significant differences ($p \leq 0.05$) among the four lake stocks studied were indicated by results of Chi-square and Mann-Whitney U tests (Table 7). First dorsal fin rays were useful for separating Falcon walleye from the other walleye stocks. The Dauphin Lake stock exhibited unique differences in the number of anal fin rays. The Lake Manitoba stock showed distinctions in the meristic traits: pectoral fin rays and upper gill rakers. Lower gill rakers separated the Crean stock walleye from the other walleye stocks. Lateral line scale counts showed the greatest variability and distinction among stocks. Considering all meristic traits, Falcon and Crean stocks were the most different from each other and Dauphin and Manitoba stocks were the most similar.

Analysis of meristic counts among pond reared stocks also indicated some significant differences (Table 8). Crean and Manitoba stocks showed the most numerous differences, however a large number of significant differences between Crean and Falcon, and Falcon and Manitoba also were found. Anal finray counts were important in separating Crean stock from the other stocks. Pectoral fin rays, as in adult fish, were important for distinguishing Lake Manitoba stock. No significant differences were found among counts of lateral line scales and lower gill rakers and very little difference among counts of upper gill rakers indicating that these characters seemed to be most influenced by the common environment. First and second dorsal finray counts and anal finray counts maintained separation and showed the greatest variability and distinction among all three pond stocks. Comparisons of meristics between lake and pond stocks (Table 9) also were made using univariate statistics. The Falcon lake and pond stocks were the most different from each other, whereas the two Crean stocks were the most similar to each other. Anal finray counts exhibited significant differences between lake and pond pairs in all stocks whereas upper gill rakers and first dorsal fin rays exhibited little or no difference.

Multivariate Meristic Analysis

Only individual fish for which there were complete sets of observations were used in multivariate meristic analyses (Pimentel,1979), accounting for differences in sample sizes

Table 7 Results of the Chi-square (upper asterisks) and Mann-Whitney U tests (lower asterisks) for the native adult 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 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 9 Results of Chi-square (upper asterisks) and Mann-Whitney U tests (lower asterisks) for native adult populations 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		**	**	**				
		**	**	**	*			

for the different stocks in some of the analyses (discriminant function analysis). Canonical discriminant function analysis of meristic data demonstrated significant differences among the walleye stocks. Examination of the raw canonical coefficients (Appendix 2F) indicated that all eight meristic variables were important for discriminating among native walleye stocks (Figure 3). Mahalanobis distance values indicated that Lake Manitoba walleye were more similar to Crean and Falcon stocks than to Dauphin Lake walleye (Table 10). Table 11, showing Mahalanobis distances among pond stocks, indicated that Falcon and Manitoba pond stocks were most similar to each other. Three dimensional plots of the results of canonical discriminant function analysis could not be done because there were only three classes (resulting in calculation of only two canonical vectors), but the multivariate test statistic indicated the ponds were significantly different from each other (Hotelling-Lawley trace = 0.788, F = 8.230, degrees of freedom = 16, $p \leq 0.0001$). Canonical discriminant function analysis (Figure 4) showed that lake and pond stocks may be clearly distinguished from one another and Mahalanobis distance values (Table 12) indicated that the Crean lake and pond stocks were the most similar and the Falcon lake and pond stocks were the most different.

Classification of individual adult fish into native lake stocks based on meristic counts showed an average of 46.88 % were correctly classified (Table 13). Examination of pond stocks showed an average of 64.52 % were correctly classified (Table 14) and an average of 47.11 % of the lake-pond stocks were classified into the correct pond or lakes (Table 15).

Univariate Morphological Analysis

Allometric coefficients from pooled regressions (Table 16) of the four stocks were used because no significant differences were found among stocks (Reist, 1986). Results of morphological data analyses using ANOVA on adjusted variables are shown in Table 17. ANOVA indicated that the morphological variables: TL, FL, PRDL, PDL, PPVL,

Figure 3 Plot of discriminant function analysis centroids of meristic counts of the four native lake walleye stocks on three canonical vectors. Hotelling-Lawley trace = 0.505, F = 4.524, degrees of freedom = 24, $p \leq 0.0001$

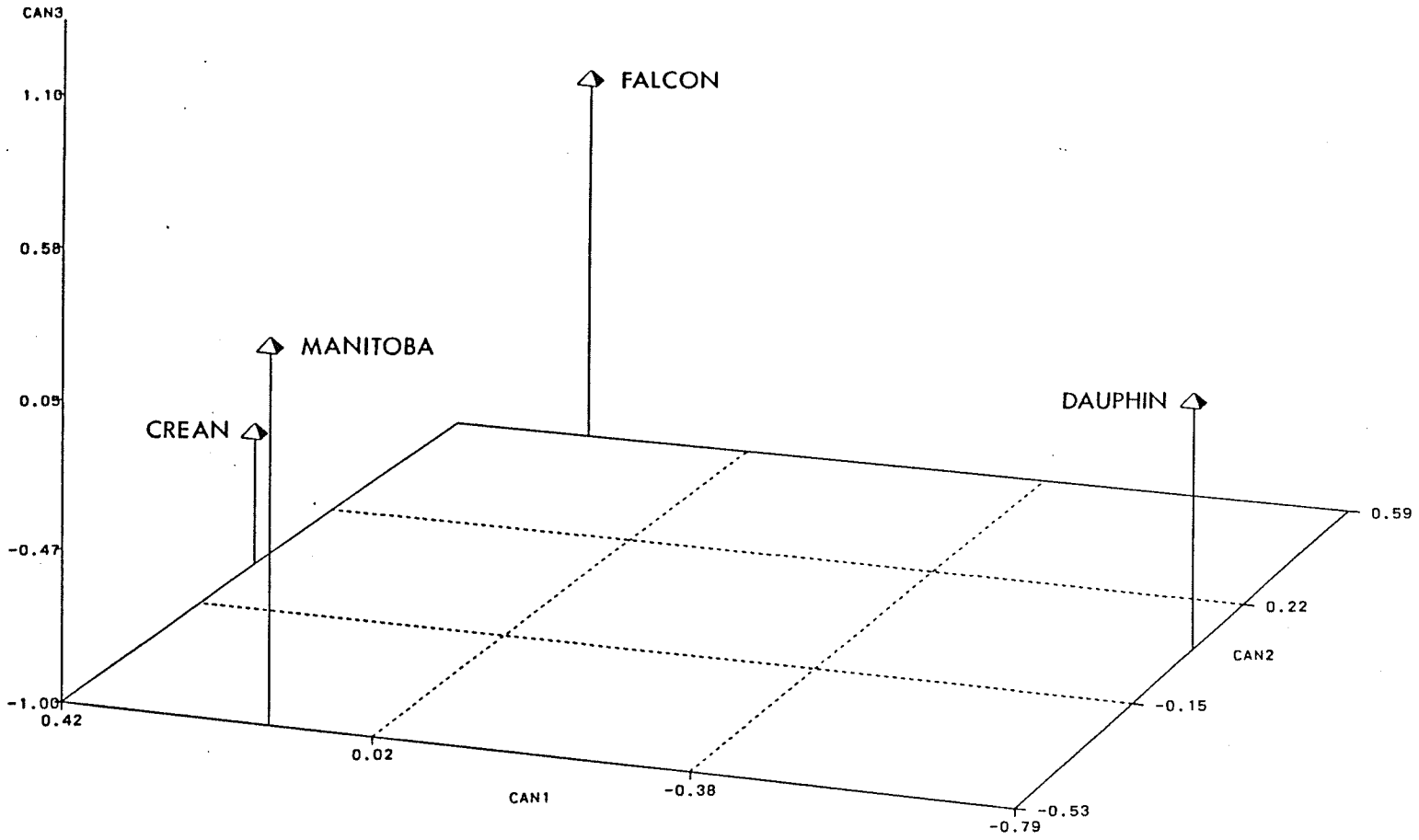

CAN3
1.10
0.58
0.05
-0.47
-1.00
FALCON
MANITOBA
CREAN
DAUPHIN
0.42
0.02
-0.38
-0.79
CAN1
0.59
0.22
-0.15
-0.53
CAN2

Table 10 Matrix of Mahalanobis distances (D^2) between centroids of meristics for walleye lake stocks (see Figure 3 for test statistics)

	Crean	Dauphin	Falcon
Dauphin	1.18		
Falcon	1.12	1.25	
Manitoba	1.01	1.27	1.06

Table 11 Matrix of Mahalanobis distance (D^2) between centroids of meristics for walleye pond stocks (see text for test statistics)

	C pond	F pond
F pond	1.76	
M pond	1.56	1.24

Figure 4 Plot of discriminant function analysis centriods meristic counts of the three lake and pond walleye stocks on three canonical vectors. Hotelling-Lawley trace = 1.03, F = 8.592, degrees of freedom = 40, $p \leq 0.0001$

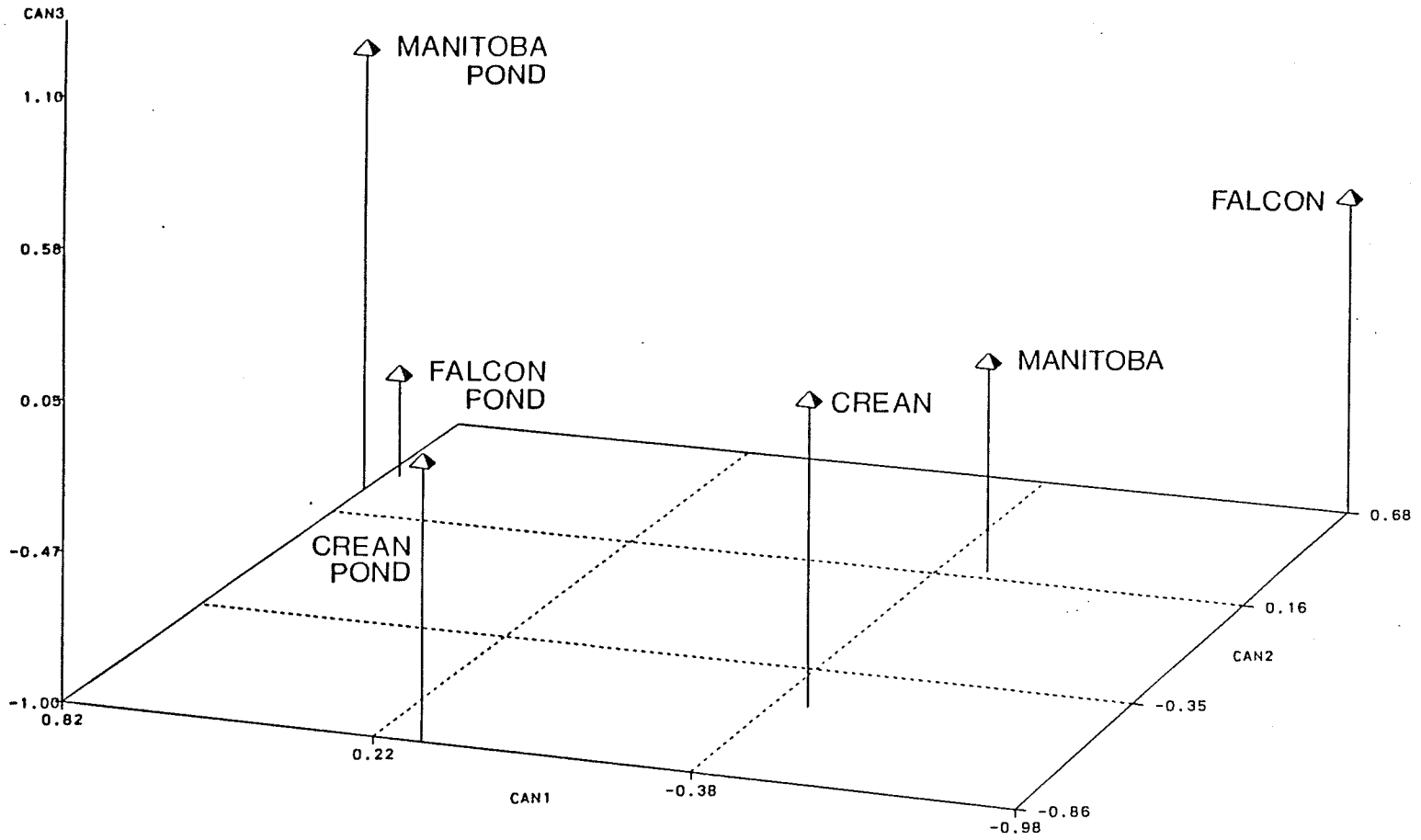

CAN3
1.10
0.58
0.05
-0.47
-1.00
MANITOBA POND
FALCON POND
CREAN POND
CREAN
MANITOBA
FALCON
0.82
0.22
-0.38
-0.98
CAN1
0.68
0.16
-0.35
-0.86
CAN2

Table 12 Matrix of Mahalanobis distances (D^2) between centroids of meristics for lake and pond walleye stocks (see Figure 4 for test statistics)

	Crean p	Falcon p	Manitoba p	Crean	Falcon
Falcon pond	1.59				
Manitoba pond	1.55	1.29			
Crean	1.07	1.71	1.69		
Falcon	1.94	1.97	1.95	1.46	
Manitoba	1.39	1.54	1.63	1.21	1.18

Table 13 Classification of native walleye 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
$\overline{X}$	46.88 %					

Table 14 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
$\bar{X}$	64.52 %				

Table 15 Classification of walleye lake stocks 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
$\bar{X}$	47.11 %							

Table 16 Allometric coefficients from pooled regressions performed on walleye morphometric variables of Crean, Manitoba, Dauphin and Falcon (see Table 2 for trait abbreviations)

Trait	Allometric Coefficient	r^2	F value	Significance
TL	0.932	0.982	12505.24	0.0001
FL	0.951	0.981	11970.33	0.0001
PRDL	0.935	0.949	4280.19	0.0001
IDS	0.773	0.241	72.88	0.0001
PDL	0.992	0.901	2075.36	0.0001
PPVL	0.932	0.784	830.56	0.0001
PAL	1.103	0.929	3006.73	0.0001
CPL	0.933	0.931	3075.31	0.0001
CPD	0.981	0.914	2447.73	0.0001
BD	1.079	0.895	1958.96	0.0001
HL	0.922	0.955	4830.49	0.0001
HD	0.886	0.705	547.73	0.0001
SNL	0.836	0.921	2676.96	0.0001
UJL	0.959	0.925	2817.95	0.0001
LJL	0.872	0.941	3625.84	0.0001
MXL	1.010	0.441	180.49	0.0001
MXW	0.931	0.839	1195.14	0.0001
OD	0.743	0.759	722.11	0.0001
IW	1.075	0.888	1807.38	0.0001
D1L	0.729	0.756	647.60	0.0001
D1BL	1.019	0.922	2705.54	0.0001
D2L	0.738	0.793	858.98	0.0001
D2BL	0.945	0.932	3151.24	0.0001
PCL	0.917	0.869	1364.07	0.0001
PVL	0.791	0.902	2097.67	0.0001
AL	0.768	0.790	842.06	0.0001
ABL	0.920	0.882	1706.79	0.0001
SCL	0.739	0.801	853.62	0.0001
ICL	0.748	0.806	878.28	0.0001
GL	0.772	0.568	300.73	0.0001

Table 17 Analysis of Variance (ANOVA) of morphometric variables of the four walleye lake stocks (degrees of freedom=3)

Trait[a]	Type III Sum of Squares	r^2	F value	Significance	Tukey's Test[b]
TL	739.38	0.03	2.56	0.0560	C-M[c]
FL	752.37	0.03	2.72	0.0456	n.s.[d]
PRDL	104.20	0.02	1.63	0.1833	n.s.
IDS	253.76	0.08	6.70	0.0002	D-F,D-C
PDL	55.13	0.01	1.04	0.3746	n.s.
PPVL	469.82	0.04	3.04	0.0297	C-M
PAL	2315.47	0.18	16.30	0.0001	F,C-D
CPL	292.52	0.08	6.43	0.0003	F-C,F-M
CPD	125.12	0.21	19.95	0.0001	D,F-M
BD	1651.14	0.25	25.01	0.0001	D,F
HL	82.73	0.02	1.63	0.1832	n.s.
HD	16.44	0.003	0.24	0.8677	n.s.
SNL	25.37	0.06	4.80	0.0029	C-M,C-F
UJL	210.74	0.12	9.88	0.0001	D-F,D-C,M-F,M-C
MXL	275.19	0.09	7.19	0.0001	C
MXW	34.76	0.24	23.71	0.0001	D-F,D-C,M-F,M-C
LJL	92.40	0.07	5.35	0.0014	M
GL	54.09	0.17	15.98	0.0001	C,F-M
OD	54.60	0.14	12.22	0.0001	D-C,D-M,F-M
D1L	99.03	0.04	2.67	0.0487	n.s.
D1BL	840.52	0.10	8.68	0.0001	F
D2L	441.11	0.19	17.29	0.0001	C
D2BL	105.78	0.03	2.48	0.0620	C-D
PCL	546.24	0.18	14.75	0.0001	C

...Cont'd

Table 17 (cont'd)

Trait[a]	Type III Sum of Squares	r^2	F value	Significance	Tukey's Test[b]
PVL	367.72	0.18	16.26	0.0001	C
AL	1168.37	0.36	41.91	0.0001	C,F
ABL	394.95	0.19	17.92	0.0001	C
SCL	1595.81	0.33	35.22	0.0001	C,D-F
ICL	1416.01	0.31	31.50	0.0001	C,F

a: Abbreviations as listed in Table 2

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

c: Letter indicates walleye stock: C=Crean, D=Dauphin, F=Falcon, M=Manitoba

d: Tukey's test indicates there are no significant differences between lakes

HL, HD, D1L, and D2BL were similar among walleye stocks. Crean stock walleye were most different from the other three walleye stocks. Head and fin length measurements indicated the most significant differences among stocks. The most important head measurements were: UJL, MXL, MXW, and GL. All fin measurements except for D2BL showed equally important differences among stocks. In general, Crean walleye had the smallest body part measurements and Manitoba walleye had the largest measurements of body part lengths adjusted to a standardized standard length. A general comparison of the different stocks at a similar standard length would be as follows: walleye from Crean Lake have small head parts but large head depths, long gill rakers, and shorter fins; Falcon walleye have long premaxillae, short gill rakers, long pelvic and pectoral fins and slender body depths; walleye from Dauphin Lake have the largest interdorsal spaces, very wide premaxillae, large eyes and greater body and caudal peduncle depths; and Lake Manitoba walleye have the longest total lengths, the largest mouths (longest snout lengths and longest upper and lower jaws), and smallest eyes.

Multivariate Morphological Analysis

Figures 5 and 6 show the canonical discriminant plot of individual fish for the original 37 variables and the selected 21 variables respectively. Thirteen morphometric variables (PRDL, CPD, BD, SNL, UJL, MXL, MXW, LJL, OD, AL, ABL, SCL, GL) were selected as most important and all eight meristic counts were used in further multivariate analysis. The canonical discriminant plot of morphometric data (Figure 7) showed that Crean walleye were quite distinct from the other three stocks. Dauphin and Falcon walleye also were well separated groups, while Manitoba stock was intermediate. Meristic and morphological data were combined, analyzed and class means plotted on three canonical variables (Figure 8). The combination of morphometrics and meristics clearly distinguishes the different stocks, providing better separation between Manitoba and Dauphin walleye. These results indicate that the four lake stocks are significantly different from one another in form. Mahalanobis distance values indicated that Dauphin

Figure 5 Plot of individual fish from four stocks using discriminant function analysis of meristic counts and morphometric measurements for 37 traits. Hotelling-Lawley trace = 5.393, F = 7.174, degrees of freedom = 443, $p \leq 0.0001$.

Crean = cross, Falcon = flag, Dauphin = square, Manitoba = diamond

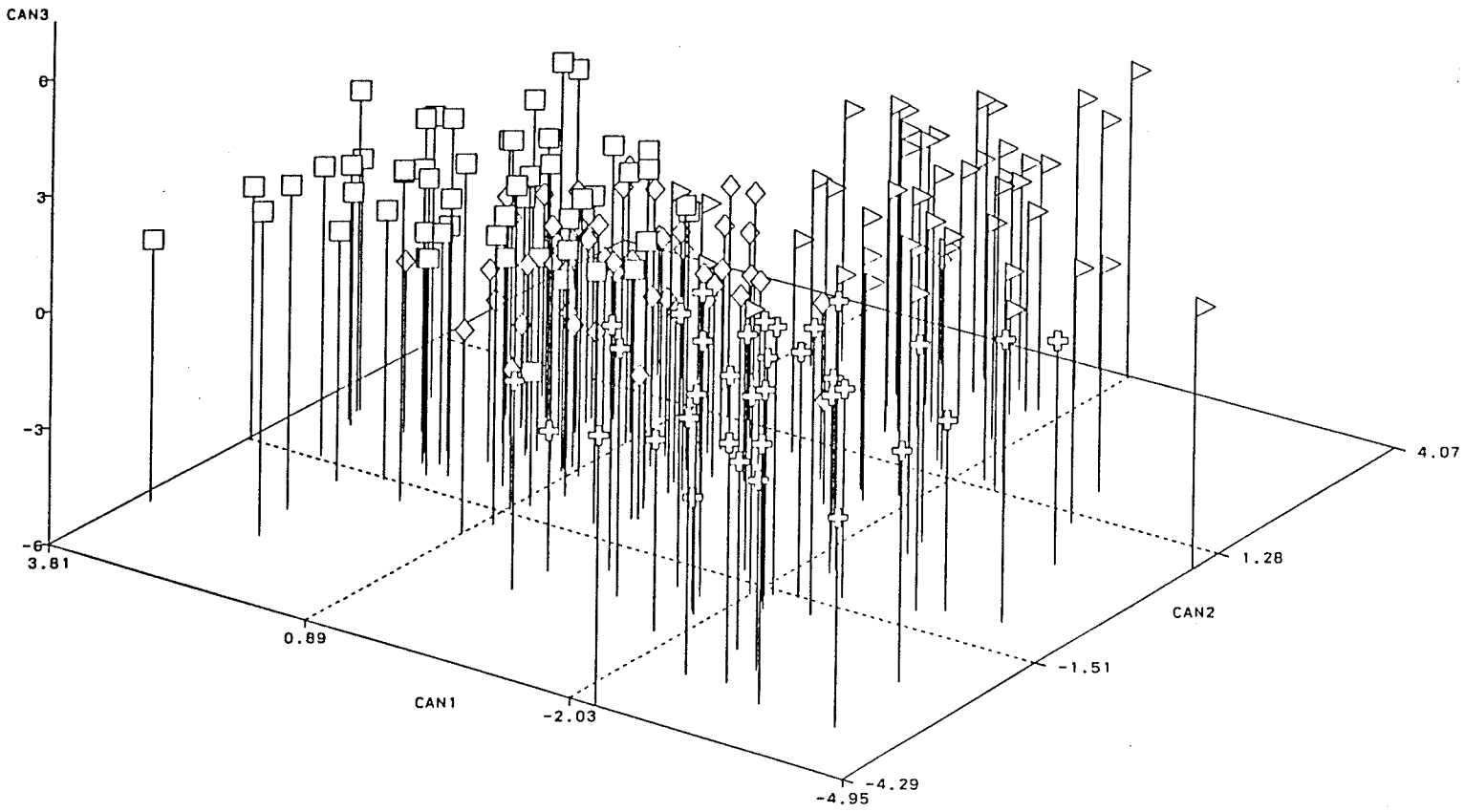

CAN3
6
3
0
-3
-6
3.81
0.89
-2.03
-4.95
CAN1
-4.29
-1.51
1.28
4.07
CAN2

Figure 6 Plot of individual fish from four stocks using discriminant function analysis of meristic counts and morphometric measurements for 21 traits. Hotelling-Lawley trace = 3.907, F = 11.453, degrees of freedom = 63, $p \leq 0.0001$.

Crean = cross, Falcon = flag, Dauphin = square, Manitoba = diamond

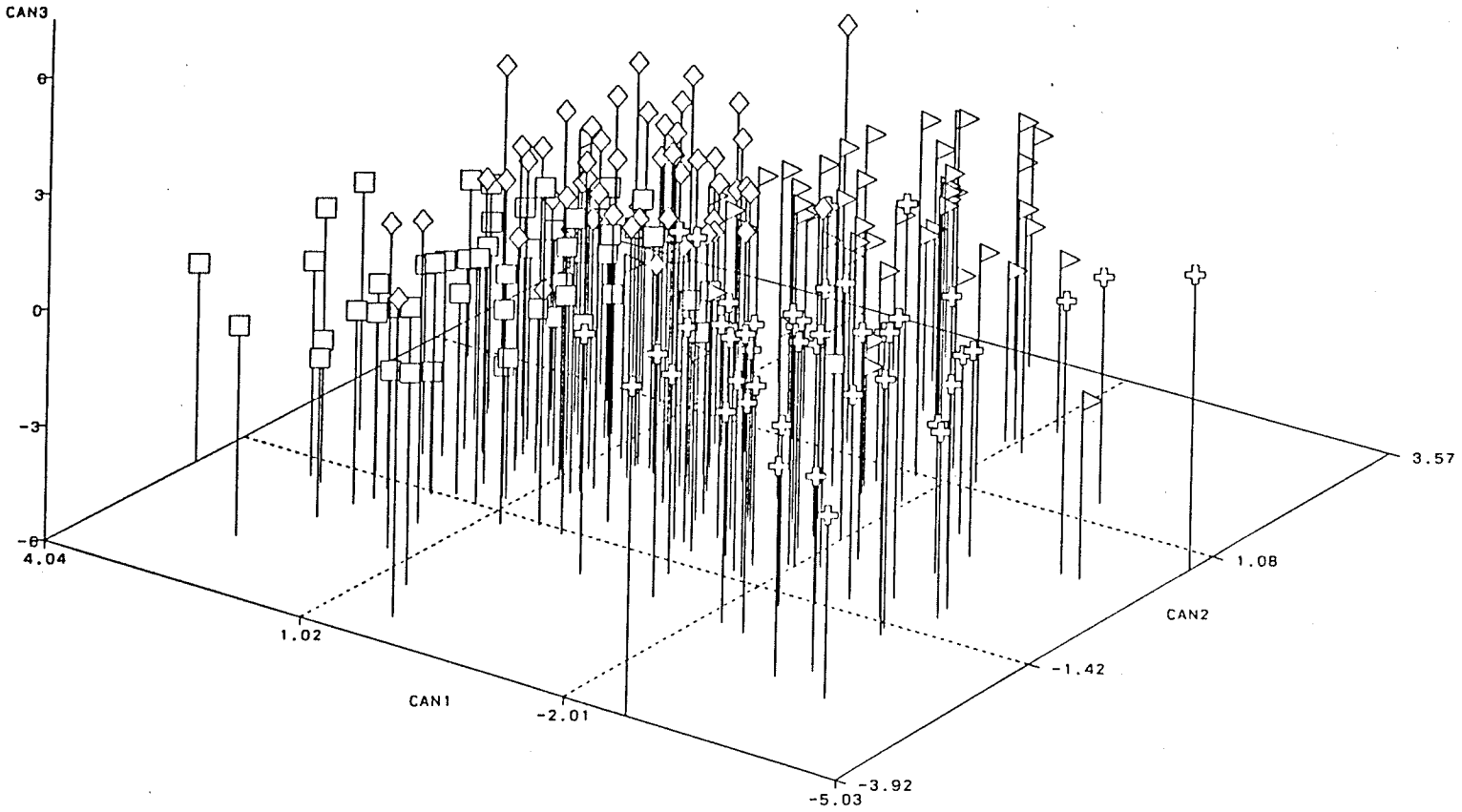

CAN3
6
3
0
-3
-6
4.04
1.02
-2.01
-5.03
CAN1
-3.92
-1.42
1.08
3.57
CAN2

Figure 7 Plot of discriminant function analysis centroids of morphometric measurements of four native lake walleye stocks on three canonical vectors. Hotelling-Lawley trace = 3.302, F = 16.650, degrees of freedom = 39, $p \leq 0.001$

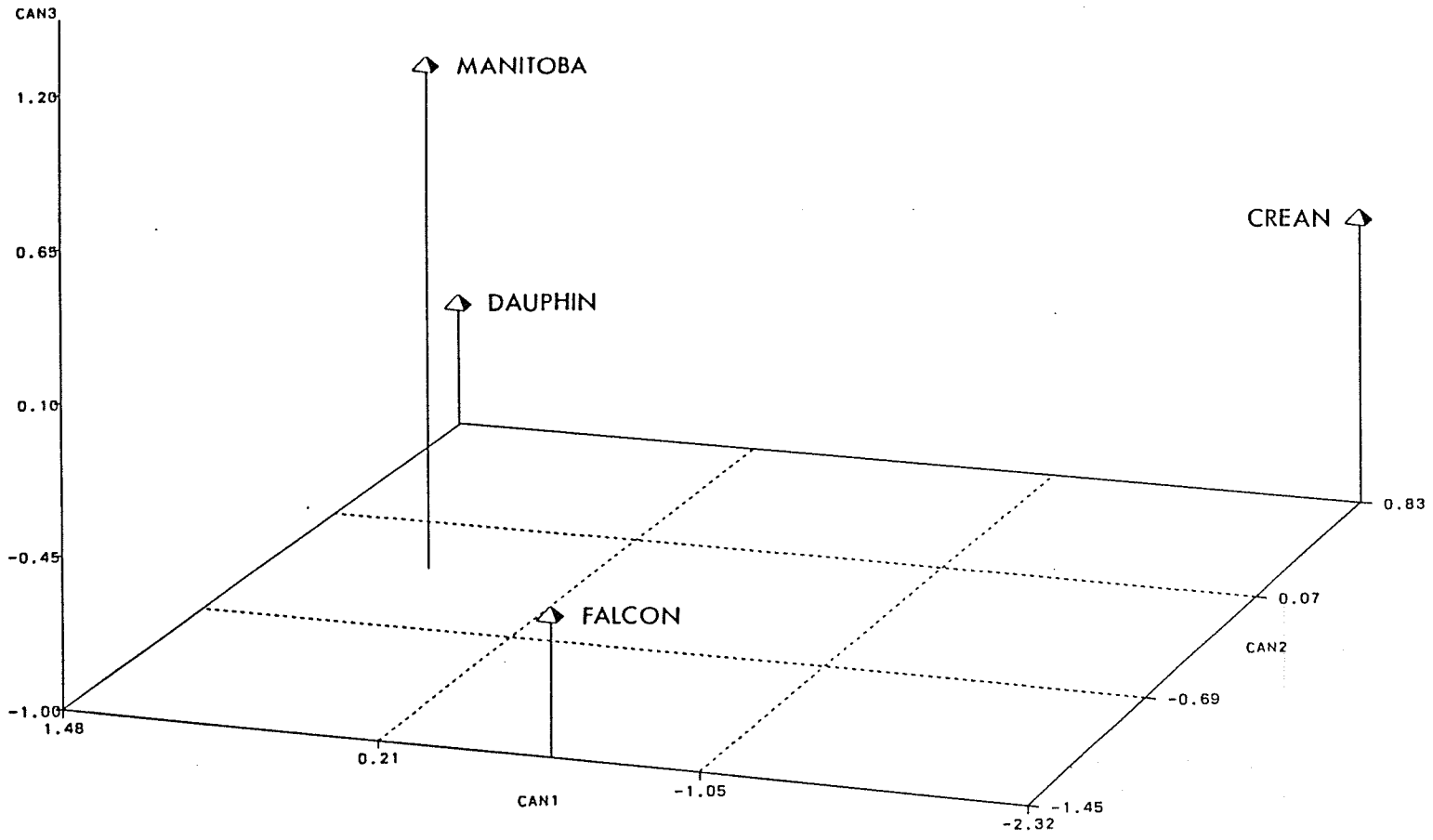
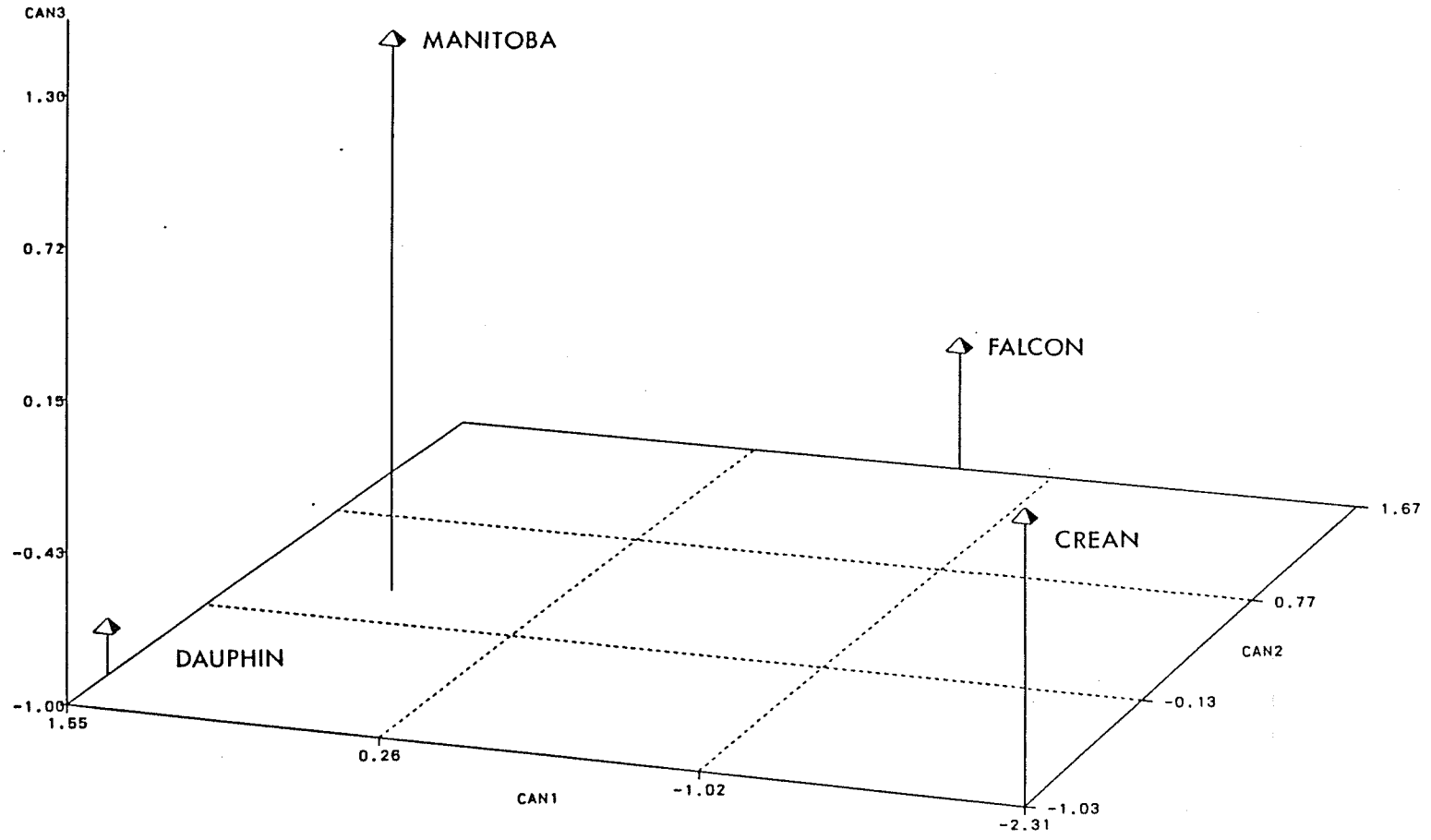

CAN3
1.20
0.65
0.10
-0.45
-1.00
MANITOBA
DAUPHIN
FALCON
CREAN
1.48
0.21
-1.05
-2.32
CAN1
0.83
0.07
-0.69
-1.45
CAN2

Figure 8 Plot of discriminant function analysis centroids of meristic counts and morphometric measurements of the four native lake walleye stocks on three canonical vectors. Hotelling-Lawley trace = 3.907, F = 11.453, degrees of freedom = 63, $p \leq 0.0001$


CAN3
1.30
0.72
0.15
-0.43
-1.00
MANITOBA
FALCON
CREAN
DAUPHIN
1.67
0.77
-0.13
-1.03
-2.31
CAN2
1.55
0.26
-1.02
CAN1

and Crean stocks were the most different and Manitoba and Dauphin stocks were the most similar (Table 18). Results of analyses using combined meristic and morphometric variables confirmed significant differences among lake stocks and Mahalanobis distance values gave results similar to morphometric data alone (Table 19).

Classification of individual fish to stock of origin using morphometric measurements gave better results than meristic counts (Table 20), but the combination of meristics and morphometrics resulted in the highest number of fish being classified into the correct walleye stocks (Table 21).

Discussion

Meristics

The general trend among the samples of the four lake stocks was for higher counts and a greater range of counts for Falcon stock and lower counts and a narrower range for Crean stock. This was particularly well demonstrated by lateral line scale counts. Falcon stock ranged from 82 to 96, whereas Crean stock range from 81 to 90. This trend also was seen in pectoral and caudal fin ray counts. Manitoba and Dauphin stocks have counts intermediate to Crean and Falcon stocks. Martin's studies (1949) indicated that body tissues which develop slowly, develop into a greater number of elements before segments are fixed, ie. higher counts. The opposite to this was found in slower growing walleye stocks, Dauphin and Crean stocks had lower meristic counts. Conversely, rapid growth tends to prevent the differentiation of as many elements (Barlow, 1961). This, however was not the case with Falcon stock which had the highest counts for many of the meristic traits. It is possible that the growth rates are important for setting meristic characters early in life.

Egg size is another possible reason for the differences in meristics among stocks. It was observed in the field that Crean eggs and larvae (437 $\pm$ 38 larvae/ml) were much smaller than the other three walleye stocks (221 + 41 larvae/ml). Crean walleye

Table 18 Matrix of Mahalanobis distances (D^2) between centroids of morphometrics for walleye lake stocks (see Figure 7 for test statistics)

	Crean	Dauphin	Falcon
Dauphin	3.84		
Falcon	2.99	2.99	
Manitoba	3.44	1.89	2.24

Table 19 Matrix of Mahalanobis distances (D^2) between centroids of meristics and morphometrics for walleye lake stocks (see Figure 8 for test statistics)

	Crean	Dauphin	Falcon
Dauphin	3.97		
Falcon	3.23	3.28	
Manitoba	3.61	2.26	2.74

Table 20 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
$\bar{X}$	82.11 %					

Table 21 Classification of walleye lake stock meristics and morphometrics using discriminant analysis

Stock	% correctly classified	No. classified into lake				
		Crean	Dauphin	Falcon	Manitoba	Total
Crean	97.87	46	0	0	1	47
Dauphin	83.93	1	47	2	6	56
Falcon	86.00	2	2	43	3	50
Manitoba	85.96	1	6	1	49	57
$\bar{X}$	88.44 %					

generally had lower meristic counts. Brown (1987) found that walleye larvae from larger eggs had a faster rate of formation of hypural bones and caudal fin rays. Ali and Lindsey (1974) found with medaka that larger eggs resulted in larvae with more anal rays than smaller eggs.

Although differences of mean values of the eight meristic traits were small, univariate tests indicated that meristic traits are useful in distinguishing different walleye stocks. Carscadden and Leggett (1975) studying spawning populations of American shad and Blouw et al. (1988) studying Atlantic salmon were able to distinguish among stocks using strictly meristic characters. Pectoral fin rays and lateral line scales were the most useful in univariate tests for distinguishing among stocks in the present study.

Canonical discriminant function analysis of meristic traits also indicated significant differences among stocks. The large number of misclassified individual fish to lakes using discriminant function analysis shows however that meristic counts were not particularily good for classification of individual walleye into stocks. This does not mean that meristic characters should be ignored because they may be influenced to a lesser extent by environment than are morphometric measurements (Beacham et al.,1988). Leary et al (1985) determined high heritabilities for meristic traits such as anal, dorsal, and pelvic rays and vertebrae indicating the value of using meristic traits as tools for stock identification.

Although no trends could be established among pond raised walleye stocks, univariate tests indicated differences among stocks. The first and second dorsal fin rays and lateral line scales had the greatest weight in differentiating the pond stocks. Although grown under similar pond conditions (Falcon and Manitoba in 1989 and Crean in 1987) only two meristic traits, lateral line scale and upper gill raker counts converged among the three stocks. Although the three walleye stocks were raised under similar conditions in the ponds, each stock was hatched in a different hatchery. Different water temperatures (Tåning, 1952) and light conditions (MacCrimmon and Kwain, 1969) during egg and larvae development may effect meristic counts and this may have influenced the results of these experiments. Furthermore, it is possible that selection occurred during the choosing

of parents during spawning particularily in the case of Lake Manitoba stock. Sampling of Lake Manitoba stock was done during the summer when one would expect the various lake stocks to be mixed. The Manitoba pond stock was taken from a spawning run at Swan Creek, so this sample may not be indicative of the whole lake walleye phenome. The small sample sizes of both pond and lake samples or the mixed selective effects of hatchery and pond rearing conditions also may confound these types of experiments.

Morphology

Results from both univariate and multivariate analyses of morphological measurements indicated that the four walleye stocks are significantly different from each other. Studies by Beacham (1985) on pink salmon, Swain and Holtby (1989) and Taylor and McPhail (1985) on coho salmon, also identified separate stocks using morphometrics. Growth rate also may have an effect upon morphometric development. Falcon and Manitoba lake stocks exhibited faster growth than Crean and Dauphin stocks. One explanation for the difference in growth rates is due to the heavy exploitation of walleye in Lake Manitoba, Falcon Lake and Dauphin Lake. Also, Dauphin and Manitoba are warmer lakes, closer to the optimal temperature of walleye which would promote faster growth. This may partially account for Crean walleye having the smallest body parts and Manitoba walleye having the largest. Martin (1949) found that fish with slower growth had smaller heads, eyes, maxillas and fins, similar to the results in this study Manitoba walleye, fast growing, had small eyes. Loch (1974), working on whitefish, found that fish with faster growth had smaller heads but larger fins, as was also found in Falcon walleye which had longer fins.

It can be concluded that the four lake stocks are different from each other in both meristic counts and morphometric measurements. Rearing of these stocks under similar pond conditions did not eliminate these differences, indicating that the differences among stocks were not entirely due to different lake environments. This study also showed that hatchery and pond rearing may effect the development of eggs and fingerlings and significantly change the meristic counts of the pond reared stocks from the parental stocks.

BIOCHEMICAL GENETIC ANALYSIS OF WALLEYE STOCKS USING MALATE DEHYDROGENASE AND ISOCITRATE DEHYDROGENASE ENZYMES

Introduction

Electrophoretic analyses of fish tissues have been used extensively to determine differences among fish stocks (Allendorf and Phelps, 1981; Beacham, et al., 1988; Casselman, et al., 1981; Clayton et al., 1974; Edds and Echelle, 1989; Northcote et al., 1970). Electrophoresis is used to determine the genotype of different enzymes from the enzyme phenotype (electrophoretic bands) (Utter et al., 1986). This tells something about the genetic makeup of an individual because enzymes are proteins formed through transcription and translation of DNA by RNA. Differences in the occurence (presence or absence) or frequency of allelles of different enzymes indicates whether different stocks are genetically the same or different at the genetic loci coding for the enzymes.

Because most enzyme activity is strongly affected by temperature, exposure to different temperatures of different lakes may result in selection for different isozymes of an enzyme which may perform better at different temperatures (Moon and Hochachka, 1971 and Philipp et al., 1981). Shaklee et al. (1977) found there were changes in the levels of activity of different enzymes from green sunfish acclimated to different temperatures and Hines et al. (1983) found that different allele frequencies corresponded to different thermal adaptations of largemouth bass.

Clayton et al. (1971), in studies of genetic variation in walleye, found significant differences among populations for the gene frequencies of alleles coding for malate dehydrogenase enzymes. The two multigenic enzyme systems chosen for the present study, malate dehydrogenase and isocitrate dehydrogenase, are found in the mitochondrial matrix and are involved in the citric acid cycle of the second stage of respiration

(Lehninger, 1982). Malate dehydrogenase also has been found to be a regulatory enzyme with roles in lipogenesis, glucogenesis and the transport of reducing power into mitochondria during aerobic metabolism (McReynolds and Kitto, 1970).

The present study followed the distributions of genetically determined phenotypes of malate dehydrogenase (Clayton et al., 1971) and isocitrate dehydrogenase (Tretiak, unpublished data) in walleye stocks. Gene frequencies of fingerling walleye, raised in ponds, were compared to those of parental stocks to ascertain if a change in environment (hatchery and pond rearing) or selection of parents would effect the gene frequency of progeny.

Methods and Materials

White muscle samples for MDH electrophoretic analysis were taken from the caudal peduncle on the right side of the fish (see Appendix 2A for list of adult and pond raised fingerling walleye sampled for electrophoretic analysis). A portion of liver was sampled for IDH electrophoretic analysis. Both tissues were frozen in an aqueous solution of sucrose, 85.6 g/liter and nicotinamide adenine dinucleotide (NAD), 300 mg/liter, in 1.5 ml polypropylene microcentrifuge tubes (Clayton el al., 1971) using a 1:3 to 1:4 g tissue per ml of NAD solution. Frozen samples were stored at -12^{o} C for up to one year prior to electrophoresis.

Samples were thawed, homogenized at room temperature and then centrifuged at 15,600 G for 15 minutes. Aliquots of the supernatant were subjected to starch-gel electrophoresis at 160 volts for two hours at 4-5^{o} C using the micro technique of Tsuyuki et al. (1966). The starch and electrode buffers were 0.002 and 0.04 M citric acid respectively. Both buffers were adjusted to pH 6.1 with N-(3-amminopropyl) morpholine. Gels were stained for MDH using the method of Clayton and Gee (1969) except 87 ml instead of 94 ml of 0.15 M diethanolamine were used and malic acid was substituted for lactic acid. IDH gels were stained using the staining methods by Harris

and Hopkinson (1976) with the following modifications: 40 ml of bicine buffer, pH 8.5 was substituted for the Tris/HCL buffer, 60 mg sodium isocitrate instead of 20 mg, 2.0 ml of $MgCl_2$ instead of 15 ml, 1.2 ml of NADP (10 mg/ml), 0.8 ml NBT (10 mg/ml) instead of MTT and 0.24 ml of PMS (D. Tretiak, Freshwater Institute, unpublished data). MDH phenotypes were classified according to Clayton et al. (1971) and IDH phenotypes were classified according to a model devised by D. Tretiak. Finished gels were stored in destaining fluid of methanol, water and acetic acid (5:5:1 ratio) and refrigerated. 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). Chi-square analyses were performed to test for differences within and among lake and pond stocks.

Results

Malate Dehydrogenase

MDH electrophoretic analyses revealed that gene frequencies differed among the four lakes (Table 22). Crean Lake had a higher b_1 gene frequency, Lake Manitoba and Dauphin Lake had higher b_2 gene frequencies and Falcon Lake had a higher higher b_3 gene frequency. No significant differences ($p \geq 0.05$) were found between observed and expected numbers of MDH phenotypes within lakes and ponds. Significant differences ($p < 0.001$) were found among phenotypes between lake pairs with the exception of Manitoba and Falcon lakes (Table 23).

No differences were found in comparisons of pond reared and native lake fish except for Falcon pond stock which was significantly different from its parental lake stock (Table 24). To further test this difference, electrophoretic analysis was performed on Falcon walleye samples from 1987, raised in the Bishop Grandin ponds in Winnipeg. Chi-square analysis of lake and 1987 pond stocks indicated no significant difference suggesting that genetic truncation resulting from chance parental selection at spawn taking was responsible for the differences observed in 1989. Significant differences were found between MDH

Table 22 Distribution of malate dehydrogenase 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 fromCastle-Hardy-Weinberg law) and confidence limits for B_2 frequency

Location	Number of fish	Phenotype						X^2	p	Gene Fequency			99 % confidence limit[d] for B_2 frequency
		B1B1	B1B2	B1B3	B2B2	B2B3	B3B3			b_1	b_2	b_3	
Crean Lake[a]	417	150	6	204	0	0	57	33.32	n.s.[c]	0.556	0.143	0.302	0.004-0.041
		(155.9)	(3.7)	(194.5)	(0.02)	(2.3)	(60.6)						
Crean Pond	30	13	1	14	0	0	2	0.32	n.s.	0.683	0.017	0.300	0.002-0.223
		(14.0)	(0.7)	(12.3)	(0.01)	(0.3)	(2.7)						
Lake Manitoba	68	1	0	1	21	33	12	0.21	n.s.	0.022	0.551	0.427	0.385-0.708
		(0.03)	(1.6)	(1.3)	(20.6)	(32.0)	(12.4)						
Manitoba Pond	60	0	2	0	15	34	9	1.02	n.s.	0.017	0.550	0.433	0.409-0.648
		(0.02)	(1.1)	(0.9)	(18.1)	(28.6)	(11.3)						
Dauphin Lake[b]	109	0	5	1	56	31	16	4.09	n.s.	0.027	0.679	0.294	0.590-0.761
		(0.1)	(4.4)	(1.9)	(50.4)	(43.0)	(9.2)						
Falcon Lake	60	0	1	1	16	24	18	0.88	n.s.	0.017	0.475	0.508	0.352-0.591
		(0.02)	(1.0)	(1.0)	(13.5)	(29.0)	(15.5)						
Falcon Pond 1989	60	0	0	0	33	22	5	0.11	n.s.	0.000	0.733	0.267	0.619-0.824
		(0.0)	(0.0)	(0.0)	(32.2)	(23.5)	(4.3)						
Falcon Pond 1987	16	0	0	1	4	9	2	0.39	n.s.	0.031	0.531	0.438	0.298-0.753
		(0.02)	(0.53)	(0.43)	(4.51)	(7.44)	(3.07)						

a Clayton et al., 1974

b Tretiak, 1983 unpublished data

c not significant

d Mainland et al., 1956

Table 23 Chi-square analysis of MDH phenotypes of comparisons between lake stocks

Stocks	Number of fish	Degrees of Freedom	X^2	p
Falcon-Dauphin	60-109	2	12.2	**
Falcon-Manitoba	60-68	2	2.8	n.s.
Falcon-Crean	60-417	2	337	**
Dauphin-Manitoba	109-68	2	10.6	**
Crean-Dauphin	417-109	2	428	**
Crean-Manitoba	68-417	2	390	**

** significant at $p \leq 0.001$
n.s. not significant, $p \geq 0.05$

Table 24 Chi-square analysis of MDH phenotype comparisons between lake and pond stocks

Stocks	Number of fish	Degrees of Freedom	X^2	p
Falcon-Falcon pond 1989	60-60	2	15.32	**
Falcon-Falcon pond 1987	60-16	2	2.28	n.s.
Manitoba-Manitoba pond	68-60	2	0.922	n.s.
Crean-Crean pond	417-30	2	2.067	n.s.

** significant at $p \leq 0.001$
n.s. not significant, $p \geq 0.05$

phenotype frequencies of all three pond stocks (Table 25). However, when these same comparisons were made using the 1987 Falcon pond samples, significant differences were only found between Falcon and Crean stocks.

Isocitrate Dehydrogenase

No significant differences were found between observed and expected numbers of IDH phenotypes within any group (Table 26). This indicates that the different phenotypes of both MDH and IDH occurred in the proportions expected by the Castle-Hardy-Weinberg equation. Gene frequencies between the "fast" and "slow" alleles were similar among groups except for the Falcon pond stock which exhibited a significantly higher "fast" gene frequency ($p < 0.001$). IDH allele frequencies from Falcon Lake walleye differed significantly from those in walleye from Crean Lake and Lake Manitoba stocks (Table 27).

Chi-square analysis indicated no significant differences between lake and pond stocks (Table 28). No significant differences in IDH phenotypes were found (Table 29) between the various pond comparisons.

Discussion

Malate Dehydrogenase

MDH phenotypes yielded clear distinctions between stocks except for Falcon and Manitoba stocks. The differences in MDH allele frequencies among lakes may be due either to evolution under different environmental conditions or genetic drift from an original Lake Agassiz stock. Of the four lakes studied, Crean and Falcon lakes are separated by the greatest distance in latitude and exhibit the greatest differences in gene frequencies. These observations support the separation of these stocks based upon the Mahalanobis distance values calculated from meristic counts and morphometric

Table 25 Chi-square analysis of MDH phenotypes of comparisons between pond stocks

Stocks	Number of fish	Degrees of Freedom	X^2	p
Falcon, 1989-Manitoba	60-60	3	12.6	**
Falcon, 1989-Crean	60-30	2	39.6	**
Crean-Manitoba	30-60	1	60.1	**
Falcon, 1987-Manitoba	16-60	2	0.10	n.s.
Falcon, 1987-Crean	16-30	1	34.0	**

** significant at $p \leq 0.001$

n.s. not significant, $p \geq 0.05$

Table 26 Distribution of isocitrate dehydrogenase 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 S frequency

Stocks	Number of fish	Phenotype FF	Phenotype FS	Phenotype SS	X^2	p	Gene frequency F	Gene frequency S	99 % confidence limit[b] of S frequency
Crean Lake[a]	38	10	19	9	0.001	n.s.	0.51	0.49	0.340-0.642
		(9.9)	(19.0)	(9.1)					
Crean Pond	20	4	10	6	0.002	n.s.	0.45	0.55	0.339-0.748
		(4.1)	(9.9)	(6.0)					
Lake Manitoba[a]	50	12	23	15	0.144	n.s.	0.47	0.53	0.398-0.659
		(11.0)	(24.9)	(14.0)					
Manitoba Pond	57	19	25	13	0.380	n.s.	0.56	0.45	0.328-0.577
		(17.9)	(28.7)	(11.5)					
Falcon Lake	59	37	11	11	7.900	n.s.	0.72	0.28	0.181-0.397
		(30.59)	(23.79)	(4.62)					
Falcon Pond 1989	51	22	21	8	0.304	n.s.	0.64	0.36	0.241-0.493
		(20.9)	(23.5)	(6.6)					
Falcon Pond 1987	9	5	2	2	1.11	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

Table 27 Chi-square analysis of IDH phenotypes of comparisons between lake stocks

Stocks	Number of fish	Degrees of Freedom	X^2	Level
Crean-Manitoba	38-50	2	0.45	n.s.
Crean-Falcon	38-59	2	14.06	**
Falcon-Manitoba	59-50	2	17.05	**

** significant at $p \leq 0.001$
n.s. not significant, $p \geq 0.05$

Table 28 Chi-square analysis of IDH phenotypes of comparisons between lake and pond stocks

Stocks	Number of fish	Degrees of Freedom	X^2	Level
Crean-Crean pond	38-20	2	0.39	n.s.
Manitoba-Manitoba pond	50-57	2	0.88	n.s.
Falcon-Falcon pond 89	59-51	2	6.88	n.s.

n.s. not significant, $p \geq 0.05$

Table 29 Chi-square analysis of IDH phenotypes of comparisons between pond stocks

Stocks	Number of fish	Degrees of Freedom	X^2	Level
Crean-Manitoba	57-20	2	1.37	n.s.
Crean-Falcon, 1989	51-20	2	5.12	n.s.
Falcon, 1989-Manitoba	51-57	2	1.40	n.s.
Falcon, 1987-Crean	9-20	2	3.75	n.s.
Falcon, 1987-Manitoba	9-57	2	1.92	n.s.

n.s. not significant, $p \geq 0.05$

measurements in Table 19 which indicates a large genetic distance between Crean and Falcon. Differences in latitude may be related to changes in the number of heating and cooling degree-days, length of growing season, average temperatures and photoperiod and it is possible that fish may become adapted to any or all of these changes. Temperature may effect enzyme activity and involve the production of different enzymes or forms of an enzyme which function at the temperature to which the organism is adapted (Somero and Hochachka, 1971). Variations in enzyme allele frequency related to differences in water temperature and latitude have been reported for many species of fish including creek chubs (Kent and Hart, 1976), largemouth bass (Hines et al., 1983 and Philipp et al.,1985), salmonids (Moon and Hochachka, 1971), and green sunfish (Shaklee et al., 1977). In each case, stocks separated by latitude and adapted to different temperatures were found to have different gene frequencies.

Although Lake Manitoba and Dauphin Lake have many features in common, ie. latitude, temperature, water depth (Crowe, 1980 and Heise, 1985), their walleye stocks still exhibit significantly different frequencies for MDH alleles. Thus the expectation that they would exhibit similar allelic frequencies in the MDH isozymes was not realized. Mitochondrial DNA analysis, however, found differences unique to these two lakes from all other lakes sampled across Ontario, Manitoba and, Saskatchewan (Billington et al. (1989). Possibly genetic drift and/or chance differences in gene frequencies of the present samples are responsible for this observation and Lake Manitoba and Dauphin Lake walleye are indeed different stocks.

The difference in MDH phenotype frequencies between Falcon pond fingerlings and Falcon Lake parental stock probably reflects problems in sampling. Since the results of the 1987 pond samples indicate no difference between lake and pond samples, the change in gene frequency may have resulted from parental selection during spawn taking. Genetic truncation may have occurred in 1989 by sampling a small proportion of the population as spawning stock thereby changing the gene frequency of the Falcon pond fingerlings. It is also possible that because the confidence interval of B_2 allele of MDH for Falcon lake-

pond almost overlaps each other, the difference between them was caused by sampling error. The change in lake-pond gene frequencies could also reflect the method of spawn taking. Pooled gamete mating (the method used in this study) in rainbow trout was found to produce offspring which deviated significantly in genotypic diversity from the parents (Gile and Ferguson, 1990).

All three pond stock MDH phenotype frequencies were significantly different from each other indicating rearing under similar environments in the shallow, warm ponds did not introduce selection for any particular MDH phenotype. Adaptation to a particular environment may take generations to accomplish and therefore was not seen in this experiment.

Isocitrate Dehydrogenase

The two putative alleles of IDH, "F" for fast and "S" for slow, occurred in almost equal proportions in the lake and pond stocks with the exception of Falcon Lake and pond stocks. These results were similar to those of Paragamian (1988) who also found close to equal proportions between what he called B1 and B2 IDH alleles. The significant differences found between lakes (except between Crean and Manitoba) indicated that IDH may be a good enzyme with which to differentiate walleye stocks, particularly Falcon walleye. The fact that Falcon Lake stock was the only one of the four stocks from a PreCambrian Shield lake, whereas the other three lakes were in Mesozoic and glacial till deposit plains (Dept. of Energy, Mines and Resources, 1970), may have had an influence on the difference in gene frequencies.

No significant differences were found between pond and parent lake stocks and no significant differences were found among pond stocks. This indicates that the Falcon pond fingerlings have become more similar to the other fingerling stocks, possibly through environmental selection.

This study indicated the enzymes MDH and IDH were useful in identifying Crean and Falcon walleye respectively from other walleye stocks. Comparisons among pond stocks for MDH indicated that these stock differences remained even when fish were reared under similar pond conditions, but results of IDH analysis indicated the opposite, where differences among stocks were either eliminated due to similar rearing conditions or changed due to parental selection during spawn taking. Comparisons between respective lake and pond stocks indicated the gene frequencies of pond reared fingerlings had not deviated from the parental stock.

COMPARISONS OF OXYGEN CONSUMPTION AMONG THREE JUVENILE STOCKS OF WALLEYE FROM FALCON, MANITOBA AND CREAN LAKES

Introduction

Oxygen consumption rates have been determined for various species, particularily trout, in attempts to understand fish energetics (Beamish, 1964b; Cech et al., 1985; Moss and Scott, 1961; Sullivan and Smith, 1982; Tarby, 1980). These tests may have some predictive value as to the ecology of the fish in its environment. Subsequently, energetics studies may serve to illustrate the biological adaptations utilized by a species or stock to cope with different biotic or abiotic factors in the environment (Sullivan and Smith, 1982).

Stock or strain differences have been identified for a variety of biochemical and physiological processes in fish (Hines et al., 1983; Koehn et al., 1971 and Leary et al., 1984). Demonstration that many of these differences are genetically based suggests they reflect adaptations to specific environmental conditions. Changes in most biochemical and physiological activities are supported by changes in the rate of oxygen consumption (Danzman et al., 1988 and Klar et al., 1978) and it might be expected that stocks of fish from different environments would exhibit differences in oxygen consumption rates when compared under standardized conditions.

Little work in this area of study has been done on walleye. Tarby (1980) did some initial work on walleye resting and swimming oxygen consumption rates and Beamish and MacMahon (1988) examined the effect of feeding on baseline oxygen consumption. In the present study, three juvenile walleye stocks were tested to see if different stocks exhibit different rates of oxygen consumption. Because these walleye stocks were grown under similar pond environments, any differences found might be attributed to a genetic basis of adaptation to original lake environments.

Methods and Materials

Live walleye fingerlings were taken from the Methley Beach rearing ponds (water temperature 23° C) using trap nets. Fish were transported to the Freshwater Institute in Winnipeg and acclimated to either 10° C or 16° C for three weeks. All fish were kept at a constant day/night cycle of 12 and 12 hours. Fingerlings were fed live fathead minnows (*Pimephales promelas*) during the summer months and frozen minnows during the winter months. Some walleye contracted diseases and/or fungus infections as a result of a combination of tank stress and exposure to wild minnows. Walleye and minnows were treated with pickling salt and a 250 ppm formaldehyde solution as disease control methods. Fish were given one month to recover before being used in experiments.

Fish were starved for 24 hours before being used in experiments to reduce oxygen demand from food digestion (Brett and Groves, 1979). The closed vessel respirometry apparatus (M. Giles, unpublished method) consisted of a battery of 990 ml jars for larger fish (8-35 grams) and for small fish (1.0-4.0 grams), 300 ml jars. This gave ratios of water volume to fish weight of 28 ml/g to 123 ml/g for larger fish and 200 ml/g to 300 ml/g for small fish. Temperature of the water bath was kept constant. Fish were kept in the dark and allowed 24 hours to acclimate while receiving a constant flow of oxygenated water into the jars. The water supply was then turned off and the decline in dissolved oxygen tension was monitored using one ml water samples withdrawn at one hour intervals. Oxygen tension of the water samples was determined with a digital acid-base analyzer and a thermostated E5046 oxygen electrode. Water temperature and barometric pressure were recorded midway through the test. Tests started in the morning and continued until the fish expired, after which fish were weighed and frozen.

Oxygen consumption tests were run over a period of time and number of fish weights at 10° C (Appendix 3A) and 16° C (Appendix 3B). Because fish reduced their oxygen consumption rates as oxygen levels in the jars declined, values from the first half of the experiments (before the inflection point) were used in calculations. Linear regression of

oxygen concentrations versus time yielded a slope used in an equation to calculate oxygen consumption as milligrams/hour/kilogram (see Appendix 3C and 3D for detailed calculations). Oxygen consumption rates were plotted using linear regression of log oxygen consumption (milligram/hour) versus the log weight. Duplicate tests were run in two cases to check for accuracy of oxygen tests. Analysis of covariance (using log milligrams/hour of oxygen vs log weight) was used to test for stock differences in oxygen consumption rates using weight as the covariate and stock as the classification variable. Slopes of the oxygen consumption rates for the different stocks were first examined to see if they were parallel. If they were parallel, analysis of covariance was run again to test Ho: if the stocks had the same oxygen consumption rate, by testing the differences in slope and intercept.

Adjustment of oxygen consumption measurements due to microbial respiration was unnecessary, since oxygen consumption in blanks (trials in which the respiratory jar contained only water) was negligible.

Lethal residual oxygen levels were measured at the time when the fish stopped respiring. Comparisons using t-tests were made among the different stocks, between seasons, between different water temperatures for the same sized fish and between large and small fish.

Results

Oxygen Consumption

Results of the oxygen consumption experiments at 10^{o} and 16^{o} C are shown in Tables 30 and 31 respectively. Comparisons among stocks using ANCOVA (Table 32) were made by matching fish weights because the stocks examined had a narrow range in weights. Oxygen consumption rates of walleye from Crean, Manitoba, and Falcon lake acclimated to 10^{o} C in the weight range of 1.5-2.0 grams were not significantly different ($p \geq 0.05$). Walleye from Lake Manitoba and Falcon Lake, tested at 16^{o} C demonstrated a

Table 30 Oxygen consumption rates of three stocks of walleye from tests run on fish of different size ranges, at different times of the year, at 10° C

Stock	Number of Fish	Size Range (grams)	O_2 Rates (mg/h/kg) Mean ± St.D.	r^2 fit of regression	p
Crean, winter	17	9.3-37.7	51.4 ± 10.0	0.74	0.0001
Crean, summer	5	24.2-35.7	80.4 ± 10.6	0.36	0.289
Crean, summer	5	1.5-2.0	144.3 ± 14.3	0.73	0.065
Manitoba, winter	9	7.3-9.3	67.7 ± 8.9	0.48	0.039
Manitoba, summer	10	7.2-10.5	77.5 ± 8.8	0.50	0.023
Manitoba, summer	19	1.5-2.3	140.1 ± 8.8	0.70	0.0001
Falcon, winter	11	6.4-23.6	51.5 ± 6.1	0.89	0.0001
Falcon, summer	18	2.6-13.3	82.9 ± 8.7	0.95	0.0001
Falcon, summer	11	1.4-2.1	151.2 ± 9.3	0.87	0.0002

Table 31 Oxygen consumption rates of three stocks of walleye from tests run on fish of different size ranges, during the summer, at 16° C

Stock	Number of Fish	Size Range (grams)	O_2 Rates (mg/h/kg) Mean ± St.D.	r^2 fit of regression	p
Crean	4	28.5-41.9	87.6 ± 16.5	0.43	0.348
Crean	7	12.6-15.2	99.3 ± 8.5	0.31	0.190
Manitoba	9	1.4-1.9	254.7 ± 16.8	0.84	0.0005
Falcon	4	29.3-61.1	99.1 ± 14.8	0.86	0.070
Falcon	9	1.3-1.8	211.7 ± 22.0	0.36	0.091

Table 32 Comparison of oxygen consumption rates using analysis of covariance. Log weight is the covariate and stock is the classification variable

Stock	Size	Temperature (°C)	Slope	Standard error of slope	Intercept	Type III S.S. F value	P value
Crean	1.5-2.0	10	0.860	0.130	3.202	2.01	0.1559
Falcon			0.883	0.128	1.862		
Manitoba			0.855	0.115	1.403		
Falcon	1.5-2.0	16	0.858	0.208	1.912	17.79	0.0008
Manitoba			1.254	0.189	3.113		
Crean	9.0-23.6	10	0.865	0.140	1.389	1.45	0.2467
Falcon			0.823	0.104	1.346		
Crean	28.5-41.9	16	0.731	0.455	-0.800	2.61	0.1812
Falcon			0.827	0.396	-0.705		
Difference between seasons for the same sized fish							
Falcon winter	8.5-12.2	10	0.462	0.168	0.630	117.6	0.0001
Falcon summer			0.956	0.153	1.819		
Manitoba winter	7.3-10.9	10	0.654	0.298	1.232	3.53	0.0830
Manitoba summer			0.711	0.268	1.289		
Crean winter	21.0-30.5	10	0.745	0.242	1.549	60.7	0.0001
Crean summer			1.003	0.209	1.907		
Difference between water temperatures for the same sized fish							
Falcon	1.1-2.1	10	0.785	0.136	1.942	83.8	0.0001
		16	0.914	0.122	2.072		
Manitoba	1.4-2.2	10	0.720	0.119	1.391	298.7	0.0001
		16	1.250	0.13	3.117		

significant difference in oxygen consumption rates (Figure 9).

Results of comparisons of Crean and Falcon stocks, in the weight range of 9.0 g - 23.6 g, at 10^{o} C in February, 1988 and the weight range of 28.5 g - 42.9 g, at 16^{o} C in April, 1988, indicated no significant difference at either temperature ($p \geq 0.05$). Significant seasonal effects ($p \leq 0.0001$) were found for both Crean and Falcon stocks (eg. Figure 10). Significant differences ($p \leq 0.0001$) in oxygen consumption rates between acclimation temperatures (10^{o} and 16^{o} C) for both Manitoba (eg. Figure 11) and Falcon stocks at weights of 1.5-2.0 g were also found.

Results of duplicate tests run on Crean walleye in February, 1988 and on Manitoba walleye in September, 1989 were similar (Appendix 3A). This indicates that data from the oxygen consumption tests were reproducible. Also, smaller fish had higher oxygen consumption rates than larger fish in any stock.

Lethal Residual Oxygen Levels

Significant differences were found between the following stocks, Crean and Falcon at 10^{o} C and between Falcon and Manitoba at 10^{o} and 16^{o} C for fish of 1.5-2.0 g. No difference was found between Crean and Manitoba stocks at 10^{o} C (Table 33).

The lethal residual oxygen levels of small and large fish were also found to be different (Appendix 3E). Large fish expired sooner than small fish except in the case of the Crean stock when small fish died considerably sooner than large fish. No difference was found between experiments conducted in different seasons.

Discussion

Oxygen Consumption

Standard oxygen consumption (Beamish and Mookherjii, 1964) was used for the assessment of stock differences in oxygen consumption rates of Falcon, Manitoba and Crean walleye stocks. Spontaneous activity was minimized by acclimation. Dark

Figure 9 Comparison of oxygen consumption rates of Falcon (log O_2 Cons. = 1.912 + 0.858 log wt, r^2 = 0.34) and Manitoba (log O_2 Cons. = 3.11 + 1.25 log wt, r^2 = 0.84) stocks at 16° C using ANCOVA. Dotted lines indicate 95 % confidence intervals.

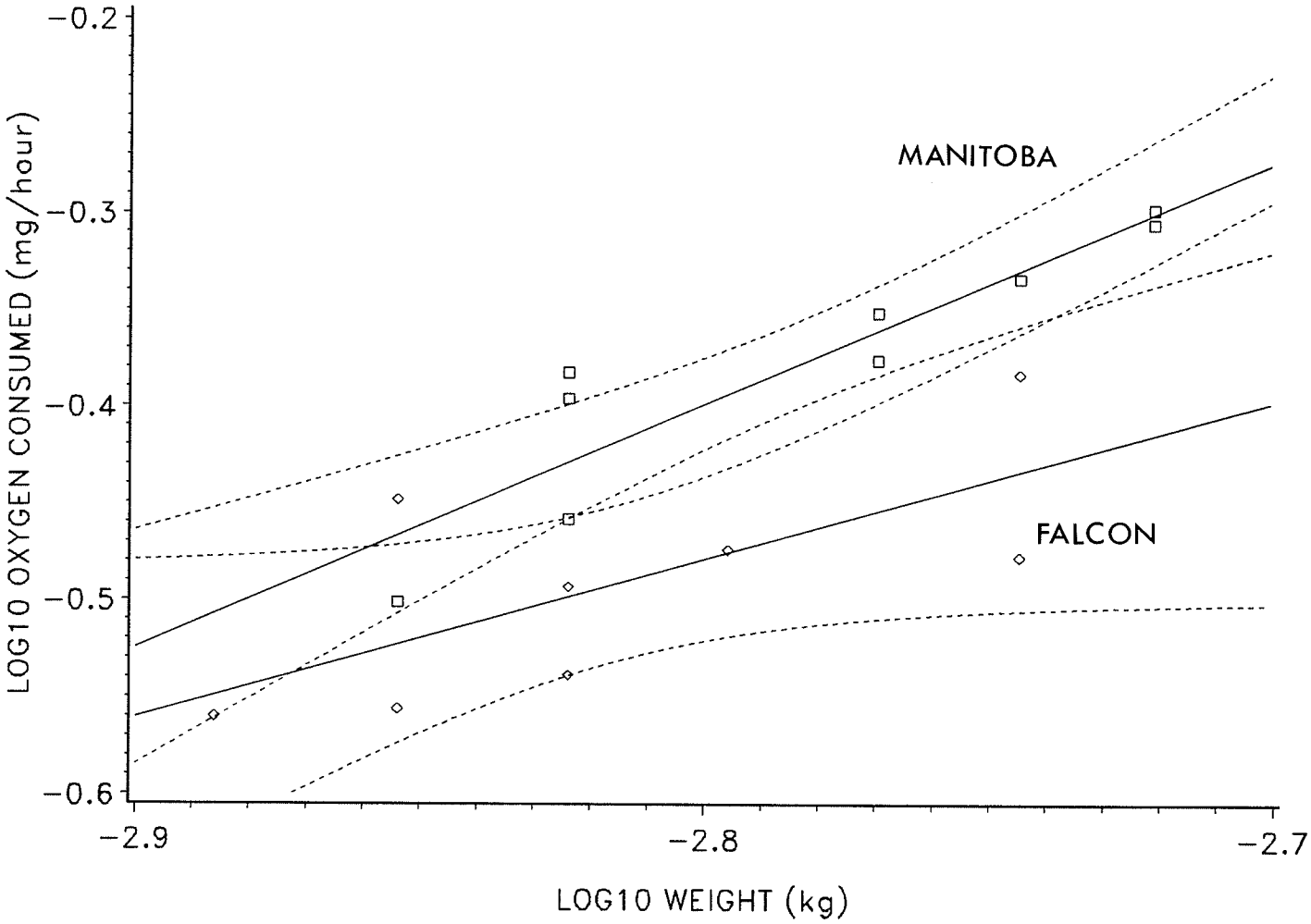

−0.2
−0.3
−0.4
−0.5
−0.6
LOG10 OXYGEN CONSUMED (mg/hour)
MANITOBA
FALCON
−2.9
−2.8
−2.7
LOG10 WEIGHT (kg)

Figure 10 Comparison of winter (log O_2 Cons. = 0.630 + 0.462 log wt, r^2 = 0.32) and summer (log O_2 Cons. = 1.819 + 0.956 log wt, r^2 = 0.87 oxygen consumption rates of Falcon stocks at 10^o C using ANCOVA. Dotted lines indicate 95 % confidence intervals.

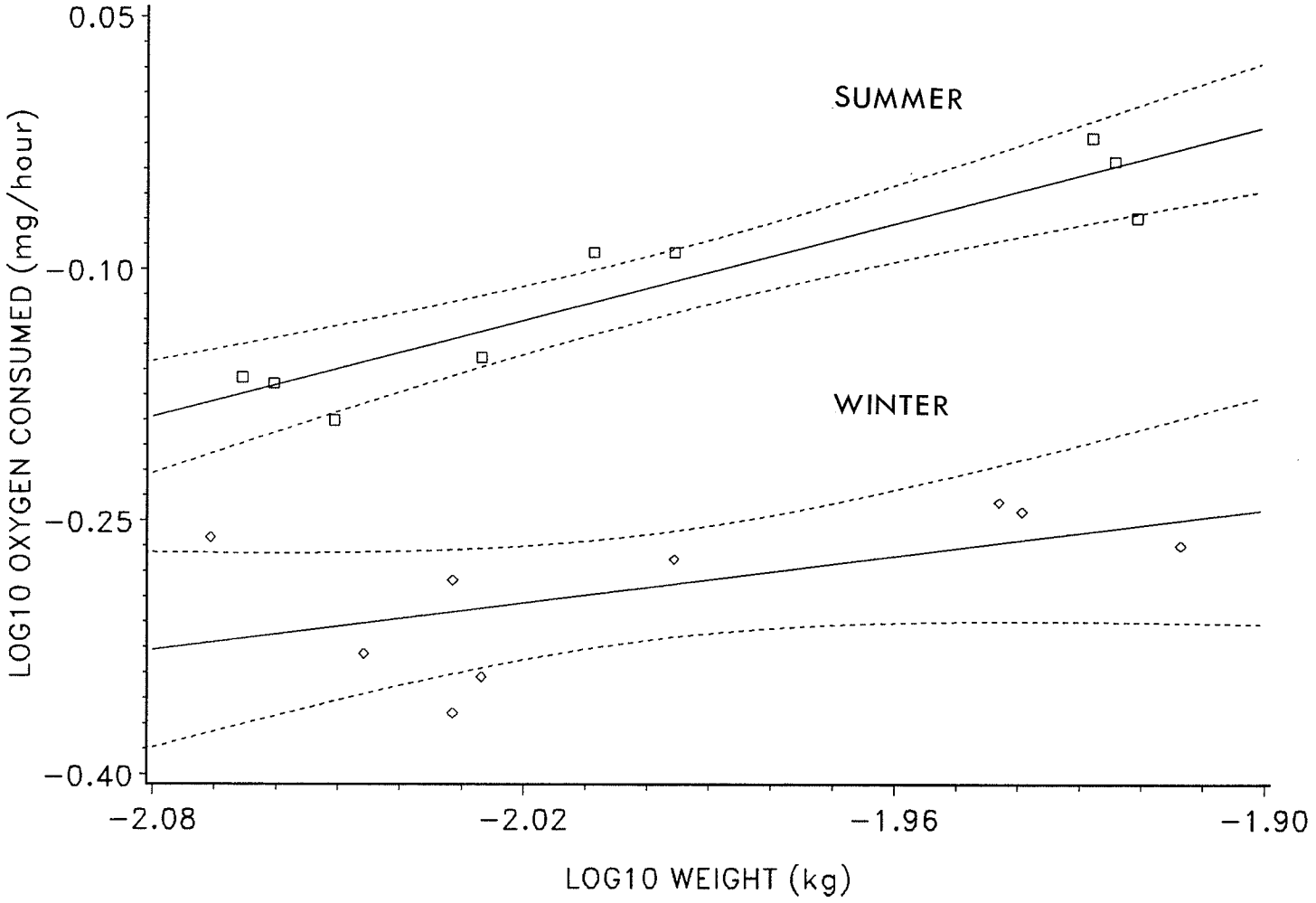

0.05
−0.10
−0.25
−0.40
LOG10 OXYGEN CONSUMED (mg/hour)
SUMMER
WINTER
−2.08
−2.02
−1.96
−1.90
LOG10 WEIGHT (kg)

Figure 11 Comparison of oxygen consumption rates of Manitoba walleye stock at 10^{o} C (log O_2 Cons. = 1.391 + 0.720 log wt, $r^2 = 0.79$) and 16^{o} C (log O_2 Cons. = 3.117 + 1.250 log wt, $r^2 = 0.84$) at 10^{o} C using ANCOVA. Dotted lines indicate 95 % confidence intervals.

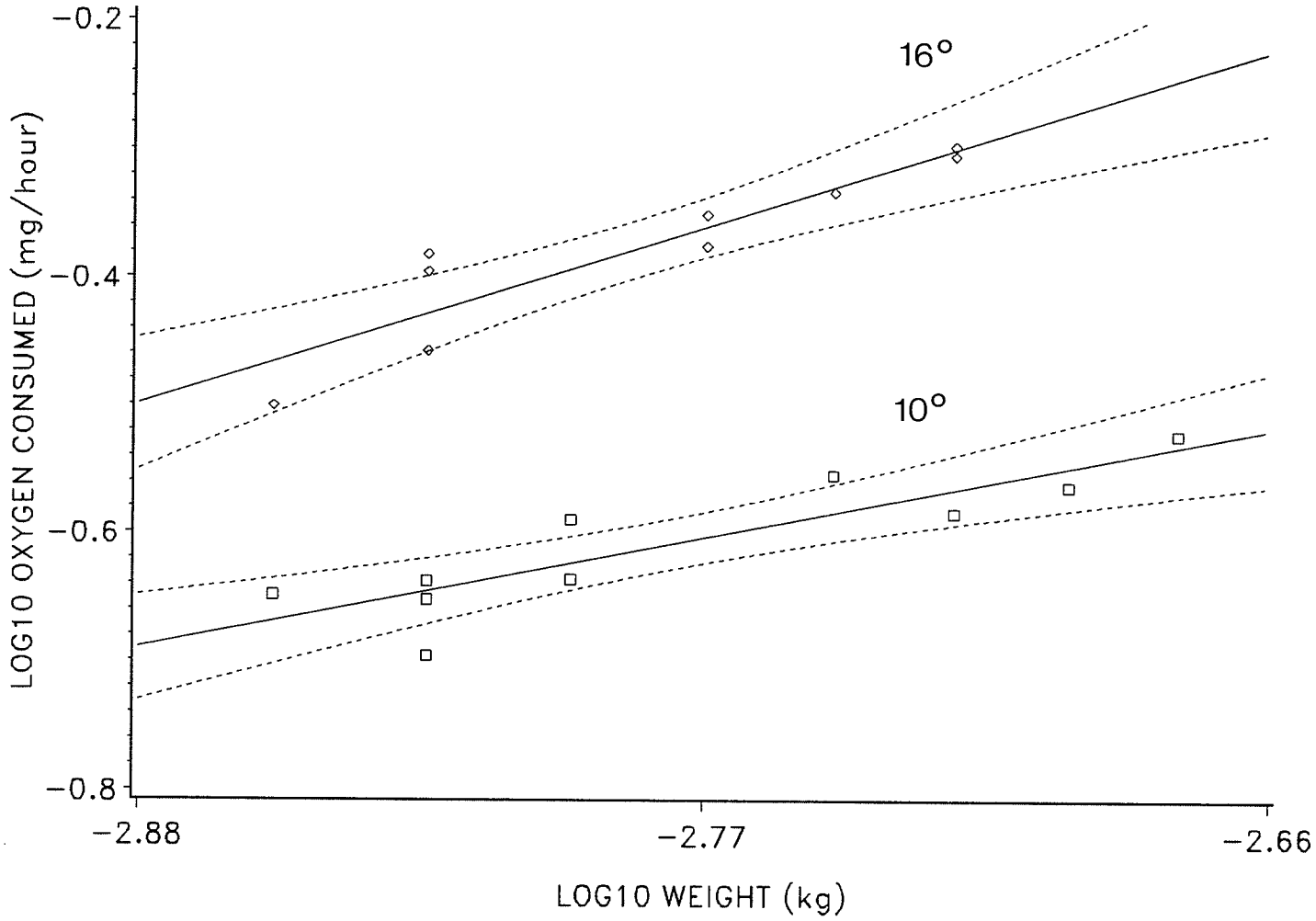

−0.2
−0.4
−0.6
−0.8
LOG10 OXYGEN CONSUMED (mg/hour)
16°
10°
−2.88
−2.77
−2.66
LOG10 WEIGHT (kg)

Table 33 Comparison of residual lethal rates using t-tests

Stock	Number of fish	Size	Test and acclimation temp.	Mean mg/kg	Standard error	P value
Crean	5	1.5-2.0	10	19.140	1.531	0.001
Falcon	14			13.057	0.779	
Crean	5	1.5-2.0	10	19.140	1.531	0.341
Manitoba	6			16.617	1.897	
Falcon	14	1.5-2.0	10	13.057	0.779	0.051
Manitoba	6			16.617	1.897	
Falcon	6	1.5-2.0	16	16.333	0.657	0.011
Manitoba	5			20.240	1.100	
Falcon	3	28.5-40.1	16	18.233	2.491	0.375
Crean	3			15.367	0.874	
Difference between seasons for Manitoba stock of the same sized fish						
Winter	8	7.2-10.5	10	19.188	0.684	0.076
Summer	8			15.563	1.763	
Difference between water temperatures for the same sized fish						
Manitoba	6	1.5-2.0	10	16.617	1.897	0.138
	5		16	20.240	1.100	
Falcon	6	1.5-2.0	10	13.200	1.219	0.047
	6		16	16.333	0.657	

acclimation alleviated most interference from activity and made it possible to distinguish between swimming and resting fish due to the higher oxygen consumption rate of active fish. Results from fish that appeared to be active, as evidenced by abnormally high oxygen consumption rates, were eliminated from the data set.

Because oxygen consumption is weight dependent, comparisons among stocks had to be done by matching weights. Therefore, comparisons of oxygen consumption rates in this study were limited due to the lack of size conformity among stocks. Oxygen consumption rates of pond reared fingerlings (1.5-2.0 g) from Crean Lake, Falcon Lake and Lake Manitoba were not significant at 10^{o} C. The similarity of oxygen consumption rates among stocks at 10^{o} C may be due to the fact that 10^{o} C is a temperature that all walleye stocks experience in fall and spring. Manitoba and Falcon stocks were significantly different from each other at 16^{o} C. At this temperature, Lake Manitoba walleye were consuming more oxygen than the walleye from Falcon Lake. The ecological significance is unknown, but a possible explanation may be that because Lake Manitoba is a shallow lake, water temperatures would either be cold in winter or very warm (+25^{o} C) in summer. Therefore, Lake Manitoba walleye would be exposed to moderate temperatures for only short time periods in spring and fall in comparison to Falcon walleye. The average summer temperatures of Falcon Lake are probably closer to 16^{o} C allowing these walleye to be better adapted to this temperature.

Larger fish of Crean and Falcon stocks (9.0-42.9 g) were examined at 10 and 16^{o} C. Crean and Falcon stocks both occur in lakes which are deeper and colder than Lake Manitoba. These fish should be adapted to respiring in cooler waters. Oxygen consumption rates of both small and large fish of these two stocks showed no difference indicating both stocks are equally adapted within this temperature range.

The data from this study indicated that juveniles of different walleye stocks had different rates of oxygen consumption. Because these three fingerling stocks were raised under similar conditions, genetic factors probably were the major contributors to these differences. The adaptation of native parental lake stocks to their particular lakes may have

led to certain biochemical changes by selection or changes in enzyme activity in response to prevalent temperature regimes (Shaklee et al., 1977). These adaptations may have been fixed in the genome and passed on to their offspring. Oxygen consumption rates could not be obtained for adult walleye in this study.

If the walleye stocks could have been tested at warmer temperatures, particularly at their optimum temperature, 21-23^{o} C (Hokanson, 1977) further differentiation among stocks might have been possible. Walleye stocks in Manitoba and Dauphin lakes are subjected to warmer water conditions than walleye from Falcon and Crean lakes. Testing at warmer temperatures and larger sizes (adults) may lead to further differentiation between stocks from these two groups of lakes.

Seasonal changes in oxygen consumption rates of Manitoba, Crean and Falcon stocks were examined in February and June/July. In all three cases, oxygen consumption rates were found to be significantly different between seasons, with winter rates being lower than summer rates in spite of constant light and temperature regimes. These results indicate an endogenous seasonal difference in oxygen consumption rates similar to Brett's work on salmonids (1979) but further experiments would be required to verify this in walleye. Even though temperature and light are known to influence internal seasonal cycles of fish (Beamish, 1964d; Brett, 1979; Evans et al., 1962; and Wells, 1935), fish exposed to continuous light have been shown to continue to exhibit cyclic patterns in their oxygen consumption (Spencer, 1939). The findings of this study corroborate the work of these authors.

Walleye were found to have significantly different oxygen consumption rates at 10^{o} and 16^{o} C. Work by Anderson et al. (1980) on *Notropis lutrensis* showed similar results of higher oxygen consumption rates at higher temperatures. An increase in temperature causes an increase in metabolism which in turn causes an increase in demand for oxygen (Beamish, 1964c).

Differences in oxygen consumption rates were seen between small and large juvenile walleye. Studies of largemouth bass, channel catfish and bluegill (Moss and Scott, 1961)

and goldfish (Beamish and Mookherjii, 1964) have shown similar results. This may be due to a higher growth rate during the immature stage of fish. This is illustrated by the works of Wells (1935), Sullivan and Smith (1982), Beamish (1964b), and Beamish and Mookherjii (1964) which show that fish metabolic rates decrease with increasing size.

The variability of rates of oxygen consumption among fish of the same weights within a stock (as shown by standard deviations in Appendix 3A and 3B), is due to various factors. Fish stocks have been shown to have different isozyme frequencies of many different enzymes, many of which are involved in the respiratory pathways. Different isozymes, adapted to different temperatures may lead to different rates of oxygen consumption (Anderson et al., 1980). Sex of the fish may also play some role in determining oxygen consumption rates. Cech et al., (1985) found that male mosquito fish had a higher rate of mortality at extreme hypoxia than females. Female mosquito fish however, are larger than male fish and require more oxygen in absolute terms. Beamish (1964d) however, found similar rates between male and female fish with maximum oxygen consumption at spawning times.

Time taken for experiments may cause variation in oxygen consumption rates because most experiments lasted from five to 24 hours. Changes in the rates of metabolism and oxygen consumption have been found to be dependent upon the time of day the fish is active and feeding (Brett and Groves, 1979; Clausen, 1936; Moss and Scott, 1961; and Spencer, 1939). The effect of this diurnal activity on metabolic rate was increased metabolism at dusk and at dawn and decreased metabolism during the daytime. This was not assessed in the present study.

Fish health also effects the results of oxygen experiments. Since it was not possible to tell whether fish chosen for the oxygen experiments were feeding regularly, these fish may have been in poor health. Poor health results in fish which are easily stressed, giving rise to poor oxygen assimilation and consumption (Beamish, 1964a; Coche, 1967; and Moss and Scott, 1961). Brett (1962) presented evidence from studies on salmonids that standard metabolism steadily decreased as fish starve.

Lethal Residual Oxygen Levels

According to the data of this study, Falcon walleye fingerlings were best adapted to survive at lower oxygen levels. Both Crean and Manitoba walleye died at significantly higher oxygen levels than Falcon walleye. Manitoba walleye live in a warm, shallow lake where summer mixing would probably keep the lake oxygen saturated. Falcon lake is a cooler, deep lake with well developed stratification, preventing summer mixing which may limit oxygen levels. Therefore Falcon stock may be adapted to survive at lower oxygen levels than Manitoba stock. Since the temperatures at which the fish were tested were temperatures to which all stocks are regularly exposed, it is possible that real differences in lethal residual oxygen levels would not be apparent until fish were tested at warmer temperatures.

Temperature may have an effect on lethal oxygen levels. Falcon stock, 1.5-2.0 grams, expired at significantly higher oxygen tensions at 16^{o} C than at 10^{o} C. Manitoba stock, however, showed no difference between temperatures. Other gases or metabolic by-products, which were not measured, may have had an effect on the lethal oxygen levels.

Size and health also may be important in resistance to low oxygen levels. Small walleye from Falcon and Manitoba stocks were found to expire at lower oxygen levels than large walleye. These results are contrary to Shepard's (1955) findings that small brook charr tended to be less resistant to oxygen lack than large fish. Crean walleye used in my experiments were approximately three times larger than those of Falcon and Manitoba stocks. Possibly the size and condition of Falcon and Manitoba fish played some part in their lower resistance to oxygen lack.

This study indicates differences in oxygen consumption rates among walleye stocks may be genetic. Further studies of oxygen consumption rates and lethal residual oxygen levels need to be conducted at greater size ranges and warmer temperatures to verify this possibility.

GENERAL DISCUSSION

Three separate techniques were used to study differences among four stocks of walleye. There is some merit to attempt to relate results of the different methods. The Falcon lake stock was analyzed using canonical discriminant function analysis to determine linkages between either MDH or IDH and meristic data (Appendix 4A and 4B respectively). The canonical vector plots of both MDH and IDH indicate that there are groupings according to genetic phenotypes, but the test statistics indicate that these differences are not significant (probably due to the small sample size). Rubec et al. (in press) found correlation between MDH banding patterns and anal fin ray counts in two species of beaked redfish (*Sebastes* sp.). *Sebastes fasciatus* had lower anal fin ray counts and a higher MDH-A^2 allele frequency, while *Sebastes mentella* had higher counts and a higher MDH-A^1 allele frequency. Leary et al. (1984) found significant differences in meristic counts of rainbow trout, with fish having no phosphoglucomutase (Pgm1-t) expression having higher meristic counts than fish expressing Pgm1-t.

Correlation between biochemical analyses and oxygen consumption was also tested (Appendix 4C) but again no significant results were found. Anderson et al. (1980) made an attempt to determine if genic variation at the MDH locus (which is active in the respiratory pathway) was translated into differences in whole animal metabolic rates such as oxygen consumption in the red fin shiner (*Notropis lutrensis*). But, as in the present study, variations in MDH genotypes were not significantly reflected in oxygen consumption. Some studies have been able to find correlations between genetics and oxygen consumption. Danzmann et al. (1988) found that oxygen consumption rates decreased as the number of heterozygous loci decreased in rainbow trout and Klar et al. (1979) found differences in rainbow trout swimming performance for different LDH B phenotypes.

It is possible that certain enzyme systems such as Pgm1-t and LDH are more

important to physical and physiological parameters. Further study of physiological functions and enzymatic genetics of walleye is required.

This study clearly illustrates the differences among the four walleye stocks. Fish with different morphometric and meristic characters adapted to unique environmental conditions may or may not fare as well if placed in a dissimilar environment. The biochemical genetic study clearly indicated that the stocks are distinct and since it is not known what effect MDH and IDH enzymes have on the overall fitness of walleye, placing walleye with various gene frequencies for these enzymes in different environmental conditions may not be in the best interest of stocking. Oxygen consumption rates and lethal residual oxygen bioassays of walleye raised under similar conditions suggests that the walleye stocks may have physiological adaptations to their particular lake environments. Because this part of the study was conducted only on fingerlings, it is not possible to predict differences among adults of the four stocks. However, because fish are generally stocked into lakes at the fingerling stage, the difference in oxygen consumption rates still would be important.

It is clear from this study and previous studies (Allendorf and Phelps, 1980; Edds and Echelle, 1989; Krueger and Menzel, 1979; Reisenbichler and McIntyre, 1977; and Ryman and Stahl, 1980) that fish raised in hatchery or pond situations were genetically different from the parental fish. For example, wild steelhead trout had the highest survival in streams, whereas hatchery trout had the highest survival in hatchery ponds (Reisenbichler and McIntyre, 1977). Differences in agonistic behavior were found between juvenile coho salmon reared under identical conditions, indicating a genetic basis for this difference (Swain and Riddell, 1990). Gile and Ferguson (1990) showed that different types of mating crosses effect genotypic diversity in rainbow trout. Pooled gamete mating (the method used in the present study) 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. This indicates that greater care needs to be taken in

selecting parents to insure that a wide spectrum of the parental variation is shown in the offspring if they are to be released into natural lakes.

The hypothesis of this thesis, that walleye from Falcon, Manitoba, Dauphin, and Crean lakes are separate distinguishable stocks is validated by this study. The important findings of this thesis are as follows:

The four adult walleye stocks differ from one another in morphometrics, meristic counts, MDH and IDH isozyme patterns, and oxygen consumption rates as follows:

	Crean	Dauphin	Falcon
Dauphin	meristics morphology MDH		
Falcon	meristics morphology MDH, IDH lethal O_2	meristics morphology MDH	
Manitoba	meristics morphology MDH	meristics morphology MDH	meristics morphology IDH O_2 rates lethal O_2

Juvenile walleye, grown in similar pond environments, were found to be significantly different in mersitic counts from their parental stocks. Thus rearing in hatchery and pond environments had a different effect upon the development of fish than a natural lake environment although the mechanisms giving rise to these changes are at present unknown.

This study provides results that indicate walleye stocks should be managed as separate units and that introduction of stocks into other than native waters could result in adverse changes in the gene pool of the native populations as has been shown for other fish populations (Krueger and Menzel, 1979; and Reisenbichler and McIntyre, 1977). Protocols for artificial spawning of walleye should be established so that a large proportion of the genome of the particular lake is represented in the offspring. Hatchery and pond rearing conditions, ie. water temperature, should be kept as close to lake conditions as possible since it is known that different factors such as meristic counts are determined in the early developmental stages of fish.

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Appendix 1 Experiments conducted in Methley research ponds in 1988

Experiments to determine if Crean and Manitoba walleye could be grown together in ponds or if one stock would out compete the other stock were conducted in the Methley research ponds during the summer of 1988. These experiments were initiated because Crean larvae were stocked into Dauphin Lake in an attempt to rehabilitate the Dauphin Lake walleye population, but it was not known how the Crean larvae would fare in competition with Dauphin larvae. Because Dauphin Lake walleye larvae could not be obtained, Lake Manitoba larvae were used to represent a comparable local stock.

40,000 larvae of both stocks were placed into each of four ponds. Samples of 200 (determined from Mainland, 1956) were taken at two week intervals throughout the summer from June to August in order to determine if equal numbers of Crean and Manitoba walleye were present at all times, and if they were not, at what period of time did one stock out-compete the other stock. Electrophoretic analysis of samples, using the B_1 allele as a marker, determined whether the walleye were Crean or Manitoba.

Analysis indicated from the first sample that only Manitoba walleye were present in the ponds. These results were due to stocking Crean larvae six days later (May 19, 1988) than Manitoba larvae (May 13, 1988) because of the later spawning date of Crean walleye. Because Crean larvae were stocked into the ponds at the time Manitoba larvae were starting to feed, it is possible that the Crean larvae served as the first food source available to the Manitoba larvae. Unfortunately the facilities were not available to delay the hatching of Manitoba eggs in order that the two stocks could be placed simultaneously in ponds so that competition could be observed.

Appendix 2A List of walleye from various lakes and the techniques performed on them

Stock	Fish	Year	No. of Fish	Technique
Crean	adult	1988	62	morphology and meristics
	fingerlings	1987	60	morphology and meristics
		1987,88	30	oxygen consumption
		1974	417	biochemical genetics (Clayton et al., 1974)
Manitoba	adult	1989	60	morphology and meristics
		1989	60	biochemical genetics
	fingerlings	1989	60	meristics
		1987,89	42	oxygen consumption
		1989	60	biochemical genetics
Dauphin	adult	1988	61	morphology and meristics
			109	biochemical genetics (Tretiak, unpublished data 1983)
Falcon	adult	1988	21	morphology and meristics
		1989	29	morphology and meristics
		1988,89	60	biochemical genetics
	fingerlings	1989	60	meristics
		1987,89	53	oxygen consumption
		1987	16	biochemical genetics
		1989	60	biochemical genetics

Appendix 2B Means, standard deviations, standard errors and ranges for meristic traits of the four lake and three pond stocks of walleye

Meristic Trait	No. of Fish	Mean Count	Standard Deviation	Std. Error of Mean	Range
			FALCON LAKE		
D1FR	50	13.76	0.62	0.09	13-15
D2FR	50	21.76	0.74	0.10	20-23
AFR	50	15.24	0.82	0.11	13-17
PFR	50	15.04	0.90	0.13	12-17
LLS	50	89.52	2.77	0.39	82-96
CFR	50	17.22	0.79	0.11	16-21
GRU	50	2.12	0.33	0.05	2-3
GRL	50	7.70	0.61	0.07	6-9
			LAKE MANITOBA		
D1FR	60	13.90	0.75	0.10	12-16
D2FR	59	21.41	0.95	0.12	20-24
AFR	60	15.37	0.80	0.10	14-18
PFR	60	14.62	0.67	0.09	12-16
LLS	60	87.60	2.44	0.32	82-94
CFR	60	17.03	0.32	0.04	16-18
GRU	60	2.38	0.49	0.06	2-3
GRL	60	7.8	0.48	0.06	7-9
			DAUPHIN LAKE		
D1FR	61	14.18	0.69	0.09	13-16
D2FR	61	21.11	1.16	0.15	15-23
AFR	61	14.60	0.92	0.11	12-16
PFR	61	14.92	0.84	0.10	11-16
LLS	58	88.21	3.08	0.40	80-94
CFR	60	16.93	0.63	0.08	14-18
GRU	60	2.13	0.34	0.04	2-3
GRL	60	7.88	0.55	0.07	7-9

... Cont'd

Appendix 2B (cont'd)

Meristic Trait	No. of Fish	Mean Count	Standard Deviation	Std. Error of Mean	Range
			CREAN LAKE		
D1FR	62	14.13	0.69	0.09	13-16
D2FR	62	21.56	0.67	0.08	20-23
AFR	62	15.32	0.74	0.09	14-17
PFR	62	15.03	0.44	0.06	14-16
LLS	61	86.01	2.28	0.29	81-90
CFR	62	16.85	0.60	0.07	15-18
GRU	62	2.22	0.42	0.05	5-3
GRL	62	7.53	0.59	0.07	6-9
			FALCON POND		
D1FR	59	13.44	0.68	0.09	12-15
D2FR	60	21.53	1.03	0.13	19-23
AFR	60	15.98	0.87	0.11	14-17
PFR	60	14.82	0.77	0.10	14-17
LLS	60	86.57	3.91	0.50	78-95
CFR	59	16.61	1.00	0.13	15-19
GRU	60	2.17	0.38	0.05	2-3
GRL	60	7.8	0.51	0.07	7-9
			MANITOBA POND		
D1FR	60	14.0	0.53	0.07	13-15
D2FR	60	22.00	0.90	0.11	19-23
AFR	60	16.23	0.70	0.09	15-18
PFR	60	15.22	0.67	0.09	14-17
LLS	60	86.4	3.42	0.44	79-94
CFR	60	16.83	0.67	0.09	15-18
GRU	60	2.32	0.47	0.06	2-3
GRL	60	7.95	0.59	0.08	6-9

... Cont'd

Appendix 2B (cont'd)

Meristic Trait	No. of Fish	Mean	Standard Deviation	Std. Error of Mean	Range
			CREAN POND		
D1FR	60	14.32	0.60	0.08	13-16
D2FR	60	21.17	0.81	0.10	20-23
AFR	60	15.68	0.70	0.09	13-17
PFR	60	14.92	0.56	0.7	14-16
LLS	60	85.18	3.12	0.40	80-91
CFR	60	17.0	0.39	0.5	15-18
GRU	60	2.13	0.34	0.04	2-3
GRL	60	7.8	0.55	0.07	6-9

Appendix 2C Means, standard deviation, standard error of mean and range of morphological traits of walleye stocks adjusted to a standardardized length of 350 mm

CREAN LAKE

Morph. Trait	No. of Fish	Mean (mm)	Standard Deviation	Std. Error of Mean	Range
TL	62	417.0	7.58	0.96	372.9-426.6
FL	62	393.6	7.28	0.92	352.2-402.6
PRDL	62	111.8	5.17	0.65	97.8-123.1
IDS	62	14.9	3.00	0.38	7.78-24.50
PDL	62	62.8	2.77	0.35	56.5-68.6
PPVL	62	114.9	3.97	0.50	108.0-126.9
PAL	62	125.3	5.35	0.68	108.3-135.7
CPL	62	80.2	3.38	0.43	72.5-87.4
CPD	62	27.1	1.47	0.19	22.5-30.0
BD	62	73.3	4.61	0.58	62.5-81.8
HL	62	100.6	2.00	0.25	93.0-103.5
HD	62	53.2	6.46	0.82	13.4-77.5
SNL	62	28.3	1.17	0.15	25.80-30.6
UJL	62	45.6	1.41	0.18	40.7-49.6
MXL	62	37.6	1.75	0.22	32.04-41.3
MXW	62	10.0	0.60	0.08	8.11-11.4
LJL	62	57.5	2.28	0.29	52.3-62.7
OD	62	15.9	1.29	0.16	13.2-19.1
D1L	47	45.6	3.54	0.51	27.4-50.9
D1BL	62	103.5	5.07	0.64	88.4-115.8
D2L	60	42.2	3.16	0.41	33.0-50.9
D2BL	62	80.1	2.71	0.34	69.8-84.7
PCL	42	52.1	3.48	0.54	41.2-57.6
PVL	61	56.6	2.5	0.32	50.4-52.7
AL	57	46.0	3.43	0.45	38.7-52.7
ABL	62	47.1	2.46	0.31	40.8-53.3
SCL	48	62.6	4.70	0.68	40.8-53.3
ICL	47	61.7	5.16	0.75	48.5-72.0
GL	62	10.1	1.30	0.16	5.0-12.2

Appendix 2C (cont'd)

MANITOBA LAKE

Morph. Trait	No. of Fish	Mean (mm)	Standard Deviation	Std. Error of Mean	Range
TL	58	421.8	3.82	0.50	413.6-431.2
FL	58	398.1	3.69	0.48	391.0-410.1
PRDL	58	112.4	2.98	0.39	104.9-121.4
IDS	58	14.3	4.08	0.39	5.7-23.7
PDL	58	62.4	3.65	0.48	53.0-71.4
PPVL	58	118.3	3.09	0.41	110.9-125.7
PAL	58	126.5	5.53	0.73	113.2-137.3
CPL	58	79.9	3.61	0.47	71.7-86.6
CPD	58	27.7	1.00	0.13	24.8-30.0
BD	58	74.9	3.61	0.47	62.9-82.6
HL	58	102.2	2.58	0.34	95.7-108.9
HD	58	53.1	2.38	0.31	46.9-58.9
SNL	58	29.1	1.15	0.15	26.7-31.5
UJL	58	47.8	1.28	0.17	45.5-50.3
MXL	58	39.7	5.84	0377	15.5-43.9
MXW	58	10.6	0.54	0.07	9.2-11.7
LJL	58	58.8	1.50	0.20	55.0-62.4
OD	58	15.4	1.05	0.14	12.8-17.6
D1L	57	47.3	2.77	0.37	38.8-54.3
D1BL	58	102.0	4.84	0.64	90.1-112.6
D2L	57	45.8	2.05	0.27	39.8-50.5
D2BL	58	79.0	3.61	0.47	68.6-86.8
PCL	55	56.0	2.24	0.30	51.0-62.0
PVL	57	59.3	2.24	0.26	55.4-64.5
AL	58	51.7	2.86	0.37	44.7-58.0
ABL	58	44.0	2.98	0.39	36.8-51.7
SCL	57	65.9	3.05	0.40	59.8-75.9
ICL	57	68.3	3.44	0.45	59.0-76.9
GL	58	9.5	1.02	0.13	4.2-10.9

... Cont'd

Appendix 2C (cont'd)

DAUPHIN LAKE

Morph. Trait	No. of Fish	Mean (mm)	Standard Deviation	Std. Error of Mean	Range
TL	61	420.3	12.80	1.64	343.1-432.6
FL	61	396.4	122.07	1.54	321.9-405.2
PRDL	61	110.5	4.82	0.62	85.9-118.5
IDS	61	13.0	3.38	0.43	4.2-21.4
PDL	61	63.1	5.55	0.71	46.1-90.3
PPVL	61	115.4	12.16	1.56	30.1-129.7
PAL	61	129.7	9.00	1.15	30.1-129.8
CPL	61	81.1	4.13	0.53	64.2-88.6
CPD	61	28.6	1.49	0.19	22.7-31.1
BD	61	78.2	5.25	0.67	60.7-91.6
HL	61	101.1	5.98	0.67	81.3-137.1
HD	61	52.5	5.27	0.67	44.3-82.9
SNL	61	28.6	1.61	0.21	21.2-32.0
UJL	61	47.6	4.40	0.56	38.9-77.5
MXL	61	39.9	1.82	0.23	32.9-43.2
MXW	61	10.9	0.91	0.12	5.6-12.5
LJL	61	57.6	2.77	0.35	47.9-63.0
OD	61	16.7	1.31	0.17	10.5-18.9
D1L	59	47.3	3.50	0.45	37.4-54.2
D1BL	61	104.0	7.1	0.91	78.6-117.7
D2L	61	45.1	3.27	0.42	35.9-54.1
D2BL	61	78.2	4.97	0.64	53.2-88.0
PCL	61	56.1	3.09	0.39	44.7-63.2
PVL	61	59.5	2.98	0.38	49.6-64.7
AL	61	51.2	2.87	0.37	41.5-57.7
ABL	61	44.0	2.75	0.35	37.3-48.6
SCL	59	69.9	3.66	0.48	61.4-76.9
ICL	60	68.1	3.22	0.42	58.0-74.7
GL	61	9.0	0.84	0.11	7.2-11.1

... Cont'd

Appendix 2C (cont'd)

FALCON LAKE

Morph. Trait	No. of Fish	Mean (mm)	Standard Deviation	Std. Error of Mean	Range
TL	50	418.9	12.55	1.77	344.0-434.3
FL	50	394.1	12.94	1.83	322.4-406.3
PRDL	50	111.2	5.15	0.73	88.5-121.5
IDS	50	16.0	3.73	0.53	7.2-28.7
PDL	50	63.7	4.35	0.61	51.6-72.2
PPVL	50	114.9	5.16	0.73	92.0-130.0
PAL	50	120.6	7.00	1.00	103.5-131.9
CPL	50	82.9	4.46	0.63	61.2-89.7
CPD	50	26.6	1.76	0.25	22.1-30.5
BD	50	70.7	5.15	0.73	52.7-80.1
HL	50	101.1	4.68	0.66	81.6-112.1
HD	50	53.1	3.56	0.50	44.9-61.0
SNL	50	29.1	1.31	0.18	24.6-31.6
UJL	50	46.0	2.20	0.31	37.7-50.1
MXL	50	40.4	3.39	0.48	31.1-47.2
MXW	50	10.1	0.67	0.09	8.3-11.7
LJL	50	57.1	2.86	0.40	48.2-62.7
OD	50	16.3	1.19	0.17	12.6-19.5
D1L	48	46.8	4.24	0.61	37.8-52.9
D1BL	50	99.0	5.30	0.75	80.5-110.9
D2L	48	44.6	2.99	0.43	37.6-52.9
D2BL	50	79.2	3.37	0.48	70.4-86.6
PCL	50	56.2	4.90	0.69	47.7-67.6
PVL	50	59.6	3.40	0.48	50.4-68.3
AL	50	49.5	3.40	0.48	41.2-55.6
ABL	50	45.1	2.64	0.37	38.3-50.5
SCL	50	67.8	4.12	0.58	54.4-78.0
ICL	50	65.9	3.63	0.51	58.2-73.5
GL	50	8.8	1.01	0.14	6.5-10.4

Appendix 2D Average ages of the four native lake stocks

Stock	No. of fish	Average Age (years)	Standard Deviation	Range of ages
Falcon	50	6.64	4.21	3-19
Manitoba	60	3.02	0.91	2-8
Dauphin	61	5.15	1.15	2-10
Crean	62	8.92	3.73	3-22

Appendix 2E Raw canonical coefficients from canonical discriminant function analysis. Large positive and negative values indicate meristic and morphometric variables which are important in determining stock differences. See Tables 2 and 3 for trait abbreviations

Trait	Canonical Vector 1	Canonical Vector 2	Canonical Vector 3
TL	-0.035	0.027	-0.004
FL	0.027	-0.011	-0.028
PRDL	-0.147	-0.065	-0.068
IDS	-0.064	0.029	-0.013
PDL	-0.005	-0.017	0.064
PPVL	0.015	0.016	-0.016
PAL	0.043	-0.023	0.010
CPL	-0.026	0.014	0.023
CPD	0.275	-0.218	0.014
BD	0.117	-0.130	0.054
HL	-0.042	0.021	-0.034
HD	-0.034	0.002	0.057
SNL	-0.138	0.310	0.150
UJL	0.135	-0.015	-0.024
MXL	0.100	0.225	0.023
MXW	0.480	-0.452	-0.201
LJL	0.022	-0.020	-0.165
OD	-0.162	0.013	0.417
D1L	-0.055	0.037	-0.039
D1BL	-0.027	0.004	0.018
D2L	0.036	0.036	-0.015
D2BL	-0.004	-0.089	0.019
PCL	-0.056	0.030	0.020
PVL	-0.037	0.042	0.097
AL	0.171	0.082	-0.001
ABL	-0.207	-0.112	0.113

... Cont'd

Appendix 2E (cont'd)

Trait	Canonical Vector 1	Canonical Vector 2	Canonical Vector 3
SCL	0.070	0.063	0.100
ICL	0.012	-0.001	-0.084
D1FR	-0.145	0.011	0.124
D2FR	-0.016	0.327	0.026
AFR	0.049	0.240	-0.672
PFR	0.038	-0.096	0.276
LLS	0.053	0.124	0.057
CFR	-0.116	0.303	0.086
GRU	0.356	-0.479	-0.825
GRL	0.367	0.283	0.241
GL	-0.112	-0.194	-0.321

Appendix 3A Oxygen consumption rates of four juvenile walleye stocks for experiments conducted at 10^{o} C

Test Date	Number of Fish	Stock and Year	Size Range (g)	O_2 Rates (mg/h/kg) Mean ± St.D.
Feb.12. 1988	9	Crean, 1987	9.3-37.7	50.5 ± 7.9
Feb.15, 1988	8	Crean, 1987	9.3-29.5	52.3 ± 12.5
Feb.17, 1988	11	Falcon, 1987	6.4-23.6	51.5 ± 6.1
Feb.19, 1988	9	Manitoba, 1987	7.3-9.3	67.7 ± 8.9
June 14, 1988	5	Crean, 1987	24.2-35.7	80.4 ± 10.6
June 16, 1988	5	Crean, 1987	1.5-2.0	144.3 ± 14.3
June 30, 1988	10	Manitoba, 1987	7.2-10.5	77.5 ± 8.8
July 2, 1988	10	Falcon, 1987	2.6-13.3	85.7 ± 10.0
July 25, 1988	8	Falcon, 1987	2.9-12.0	79.4 ± 5.5
Sept. 15, 1989	8	Manitoba, 1989	1.5-2.0	144.0 ± 8.3
Sept. 17, 1989	5	Manitoba, 1989	1.5-2.0	134.5 ± 6.5
Sept. 25, 1989	5	Falcon, 1989	1.4-1.8	159.1 ± 4.6
Sept. 27, 1989	6	Falcon, 1989	1.1-2.1	144.6 ± 6.4
Oct. 12, 1989	6	Manitoba, 1989	1.5-2.2	147.8 ± 11.4

Appendix 3B Oxygen consumption rates of four juvenile walleye stocks for experiments conducted at 16^{o} C

Test Date	Number or Fish	Stock and Year	Size Range (g)	O_2 Rates (mg/h/kg) Mean ± St.D.
April 11,17 1989	4	Crean, 1987	28.5-41.9	87.6 ± 16.5
April 11,13 1989	7	Crean, 1988	12.6-15.2	99.3 ± 8.5
April 15, 1989	4	Falcon, 1987	29.3-42.9	99.1 ± 14.8
Sept. 6, 1989	5	Manitoba, 1989	1.4-1.7	249.5 ± 22.1
Sept. 11, 1989	6	Falcon, 1989	1.4-1.8	193.4 ± 18.8
Sept. 13, 1989	3	Falcon, 1989	1.3-1.8	231.7 ± 21.4
Oct. 15, 1989	4	Manitoba, 1989	1.7-1.9	266.1 ± 3.1

Appendix 3C Sample calculations for oxygen consumption rates.

First water oxygen solubility was corrected for temperature and barometric pressure (1). Linear regression was performed using time (changed to a fraction) and oxygen level of the sample of water (M. Giles, personal communication). The slope of the line was divided by 155 (saturation level of oxygen in water) and multiplied by the corrected oxygen solubility number (2). This number was multiplied by the volume of water in the jar of the particular fish (3) and divided by the weight of the fish to get the resulting oxygen consumption rate expressed as mg/hour/kg (4).

For example, a fish at 10^{o} C with weight = 23.6 g, water volume = 963.7 ml, slope = 19.38, barometric pressure = 731 mm Hg and water vapor pressure at 20^{o} C = 17.5

(1) 11.277 mg/L x (731 mm Hg-17.5 mm Hg) /760 mm Hg = 10.84 mg/L

(2) (19.38)/155 x 10.84 mg/L = 1.355 mg/L/hour

(3) (1.355 mg/L/hour) x 0.9637 L = 1.306 mg/hour

(4) (1.306 mg/hour)/0.0236 kg = 55.339 mg/hour/kg

Appendix 3D Slope, intercept and standard errors of slopes calculated from oxygen consumption experiments at 10° C

Date	Stock and Year	Slope	Std. Error (Slope)	Intercept	r^2 fit to regression	p
Feb.12. 1988	Crean, 87	0.844	0.132	1.443	0.85	0.0001
Feb.15, 1988	Crean, 87	0.819	0.279	1.393	0.59	0.016
Feb.17, 1988	Falcon, 87	0.758	0.088	1.229	0.89	0.0001
Feb.19, 1988	Manitoba, 87	0.847	0.335	1.509	0.48	0.039
June 14, 1988	Crean, 87	0.545	0.424	1.201	0.36	0.289
June 16, 1988	Crean, 87	1.379	0.483	3.202	0.73	0.065
June 30, 1988	Manitoba, 87	0.887	0.317	1.658	0.49	0.023
July 2, 1988	Falcon, 87	0.917	0.076	1.721	0.99	0.0001
July 25, 1988	Falcon, 87	0.916	0.035	1.721	0.82	0.014
Sept. 15, 1989	Manitoba, 89	0.824	0.190	1.680	0.76	0.005
Sept. 17, 1989	Manitoba, 89	0.823	0.225	1.642	0.82	0.035
Sept. 25, 1989	Falcon, 89	0.971	0.162	2.122	0.92	0.009
Sept. 27, 1989	Falcon, 89	0.953	0.097	2.028	0.96	0.0006
Oct. 12, 1989	Manitoba, 89	1.007	0.209	2.144	0.85	0.009

Slope, intercept, and standard errors of slopes calculated from oxygen consumption experiments at 16° C

Date	Stock and Year	Slope	Std. Error (Slope)	Intercept	r^2 fit to regression	p
April 11,17 1989	Crean, 89	0.897	0.737	1.784	0.43	0.348
April 11,13 1989	Crean, 88	0.868	0.573	1.748	0.31	0.190
April 15, 1989	Falcon, 89	0.518	0.144	1.328	0.87	0.070
Sept. 6, 1989	Manitoba, 89	1.310	0.702	3.264	0.54	0.159
Sept. 11,13 1989	Falcon, 89	0.858	0.437	1.912	0.36	0.205
Oct. 15, 1989	Manitoba, 89	1.065	0.153	2.600	0.96	0.012

Appendix 3E Lethal residual oxygen levels of juvenile walleye stocks at 10° C

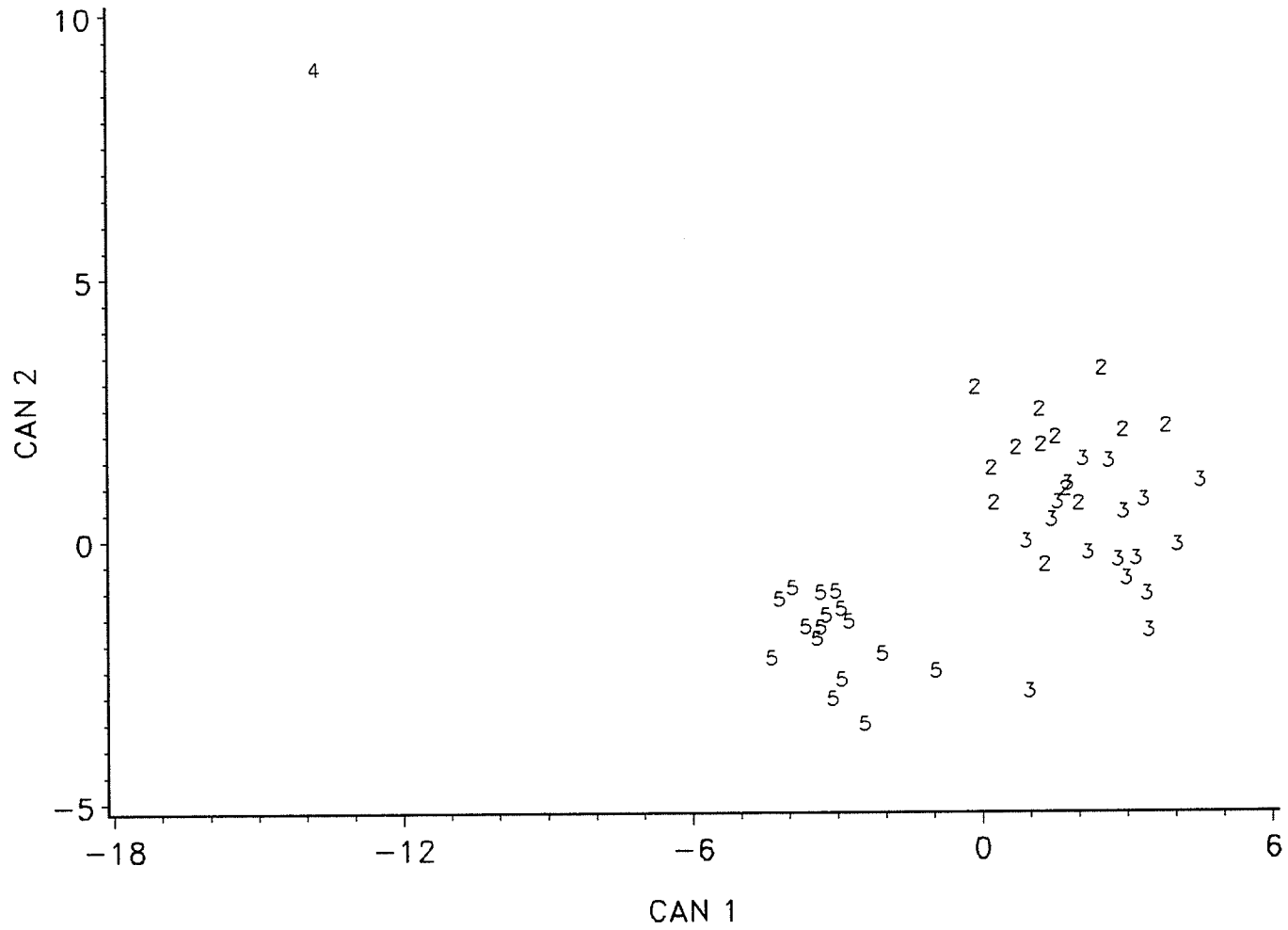
Test Date	Number of Fish	Stock and Year	Size Range (g)	Lethal O_2 Levels (mg/kg) Mean ± St.D.
Feb. 17, 1988	11	Falcon, 1987	6.4-23.6	23.2 ± 5.9
Feb. 19, 1988	10	Manitoba, 1987	7.3-9.3	19.6 ± 1.9
June 14, 1988	7	Crean, 1987	23.7-35.7	11.1 ± 2.0
June 16, 1988	5	Crean, 1987	1.5-2.0	19.1 ± 3.4
June 28, 1988	8	Falcon, 1987	7.6-11.6	11.8 ± 3.4
June 30, 1988	10	Manitoba, 1987	7.2-10.5	15.7 ± 4.3
July 2, 1988	5	Falcon, 1987	8.7-13.3	21.3 ± 1.9
July 2, 1988	5	Falcon, 1987	2.6-3.6	25.8 ± 2.0
July 25, 1988	6	Falcon, 1987	8.6-12.0	18.0 ± 2.6
July 25, 1988	5	Falcon, 1987	2.9-4.4	25.9 ± 3.5
Sept. 17, 1989	6	Manitoba, 1989	1.5-2.0	16.6 ± 4.6
Sept. 25, 1989	6	Falcon, 1989	1.4-1.8	13.2 ± 3.0
Sept. 27, 1989	8	Falcon, 1989	1.1-2.1	12.9 ± 3.1
Oct. 25, 1989	4	Manitoba, 1989	1.5-2.3	8.5 ± 3.4

Lethal residual oxygen levels of juvenile walleye stocks at 16° C

Test Date	Number of Fish	Stock and Year	Size Range (g)	Lethal O_2 Levels (mg/kg) Mean ± St.D.
April 11, 1989	4	Crean, 1987	13.0-14.2	17.9 ± 1.2
April 11,17 1989	9	Crean, 1987	28.5-41.9	17.1 ± 2.7
April 13, 1989	9	Crean, 1988	12.6-15.2	18.4 ± 2.2
April 15, 1989	4	Falcon, 1987	29.3-42.9	17.5 ± 3.8
Sept. 6, 1989	5	Manitoba, 1989	1.4-1.7	20.2 ± 2.5
Sept. 11, 1989	6	Falcon, 1989	1.4-1.8	16.3 ± 1.6

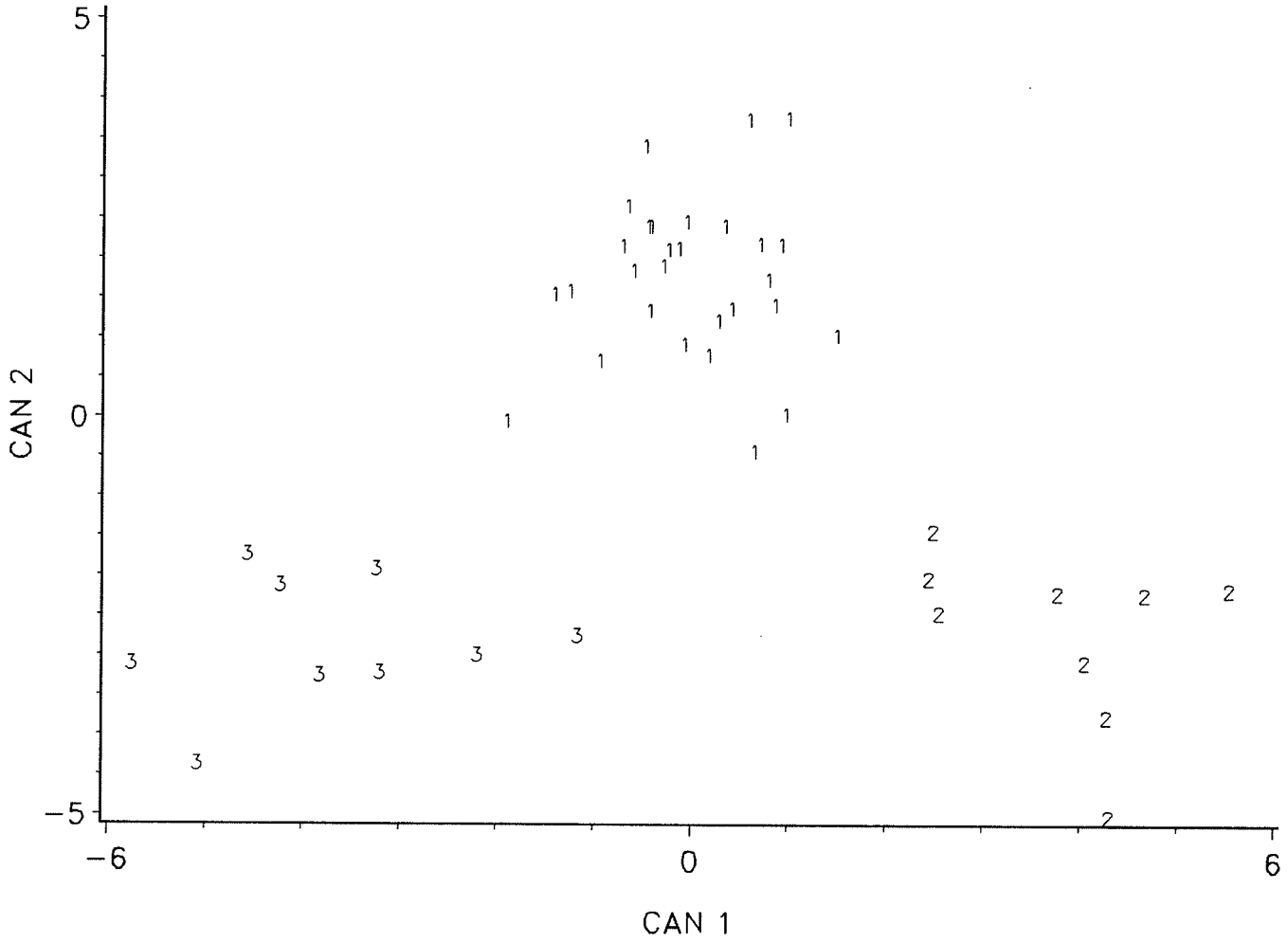
Appendix 4A Comparison of Falcon walleye using meristic counts and morphometric measurements and biochemical genetic analysis of MDH using canonical discriminant function analysis. Hotelling-Lawley trace = 18.368, F = 0.938, degrees of freedom = 111, $p \leq 0.605$

2 = C2C2, 3 = C3C3, 4 = C1C3, 5 = C2C3


10
5
0
−5
CAN 2
−18
−12
−6
0
6
CAN 1

Appendix 4B Comparison of Falcon walleye using meristic counts and morphometric measurements and biochemical genetic analysis of IDH using canonical discriminant function analysis. Hotelling-Lawley trace = 10.892, F = 1.030, degrees of freedom = 74, $p \leq 0.509$

1 = FF, 2 = FS, 3 = SS


5
0
−5
CAN 2
−6
0
6
CAN 1

Appendix 4C Comparison of oxygen consumption rates and biochemical genetic analysis of malate dehydrogenase (MDH) and isocitrate dehydrogenase (IDH) at 10° C using analysis of covariance with weight as the covariate and MDH and IDH phenotypes as the classification variables

Stock	Size range	No. of fish	Type III SS		R-square	Standard error
			F value	P value		
Falcon						
MDH & IDH	1.1-1.8	11	0.25	0.783	0.575	0.044
MDH	1.1-2.1	12	2.89	0.123	0.824	0.041
Crean						
MDH	10.8-15.2	13	0.85	0.457	0.162	1.296
IDH	10.8-15.2	13	0.24	0.789	0.054	1.420
Manitoba						
MDH	7.2-10.4	10	0.85	0.473	0.606	0.937
IDH	7.5-10.5	9	0.37	0.565	0.425	0.960