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HYBRIDIZATION AND PREMATING ISOLATING MECHANISMS IN *PHOXINUS EOS* AND *PHOXINUS NEOGAEUS* (OSTEICHTHYES : CYPRINIDAE) IN ALBERTA

by

MRINAL K. DAS

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL 1986

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YEAR THIS DEGREE GRANTED FALL 1986

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled HYBRIDIZATION AND PREMATING ISOLATING MECHANISMS IN *PHOXINUS EOS* AND *PHOXINUS NEOGAEUS* (OSTEICHTHYES : CYPRINIDAE) IN ALBERTA submitted by MRINAL K. DAS in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

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Supervisor

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Date.....14 October 1986

Abstract

Hybridization between northern redbelly dace (*Phoxinus eos*) and finescale dace (*Phoxinus neogaeus*) was studied in Upper Pierre Grey Lake, Alberta. Sympatric parental and hybrid populations were compared with allopatric parental populations from Cameron Lake and Tay Lake. Canonical variates and principal components analyses, using 31 morphological characters, revealed that the two parental groups were bridged by an intermediate all-female hybrid group in Upper Pierre Grey Lake. Hybrids made up approximately 33% of the individuals of the sympatric population. Neither backcross nor hybrid F2 individuals could be identified from the analyses, although the majority of hybrids were morphologically more similar to *P. neogaeus* than to *P. eos*. No clear evidence of introgressive hybridization was found in either of the sympatric parental species.

The effectiveness of the species' premating isolating mechanisms was studied in Upper Pierre Grey Lake. Segregation in spawning time and habitat was not apparent; there was a distinct overlap in the spawning period of the two species and habitat isolation was also absent. Breeding colors and behaviors did not show any significant difference between the two species; mate preference tests were not performed. The eggs of the hybrids appeared to be similar in condition to the parental eggs; however, hybrid fertility was not

experimentally confirmed.

Some of the environmental factors classically recognized as being associated with the break-down of isolating mechanisms such as rarity of one parental species and paucity of spawning areas, appear to be important in causing hybridization in Upper Pierre Grey Lake.

Acknowledgements

I express my deep gratitude to my supervisor, Dr. J. S. Nelson for his guidance, inspiration and continuing interest in this project from the beginning. The manuscript has benefited from his patient review.

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To Elizabeth Stinson, I extend my thanks for suggestions and encouragement. Discussions with Terry Smith, John Clay Bruner and Clifford L. K. Robinson helped clarify many ideas.

I wish to thank Tom Boag, Rob Stewart, Wayne Roberts and Bernie Wright for their assistance and help in the field.

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1. GENERAL INTRODUCTION

"Speciation may be considered complete when individuals of a population have acquired properties which enable them to maintain reproductive isolation from their parental species. Geographic isolation in sexually reproducing organisms is generally considered a prerequisite for the formation of these properties, which become tested when external barriers break down. The absence of adequate isolating mechanisms when populations come into secondary contact results in a fusion of the forms. The establishment of isolating mechanisms, which prevent interbreeding of sympatric populations, may thus be considered the most important aspect of speciation" (Nelson, 1968).

Interspecific and intergeneric hybridization are frequent phenomena among northern, temperate, freshwater fish species, especially the cyprinids (Hubbs, 1955). Hybridization - defined here as the successful reproduction between two species (*sensu* Mayr, 1970) following secondary contact - poses interesting problems to several levels of study, ranging from systematics to ecology and habitat management.

At the taxonomic level, putative hybrid individuals pose a methodological problem of identification. Traditionally, hybrids have been identified by their intermediacy in those characters that differ between the parental species (Hubbs, 1955). However, the wild-caught hybrid individuals are not always strictly intermediate in all characters to their

parental species. Certain morphological characters of hybrids may be identical to, or approximate those of one parental type, or they may be beyond the range of either parental type (Hubbs and Strawn, 1957). The difficulty of discriminating hybrids in a wild-caught collection from possible uncommon variants is additionally complicated by the possible presence of backcrosses and further hybrid generations. Multivariate statistical techniques have been advanced to overcome many of these problems of hybrid identification by mathematically enhancing the separation of parental taxa.

Hubbs (1955) emphasized the role of environmental factors in inducing hybridization and regarded the relatively high rate of hybridization in freshwater fishes in northern areas to be the result of the changing nature of the environment. From the ecological point of view, it is necessary to determine how different environmental factors were responsible for the dissolution of the species' reproductive isolating mechanisms. Hybridization may indicate a wide overlap in those components of the species' niches concerning habitat preferences and spawning habits.

The genus *Phoxinus* Rafinesque has been a focus of controversy involving the relationships between Palearctic and Nearctic cyprinids. In North America the genus has five species, four from the genus *Chrosomus* Rafinesque placed in synonymy with Eurasian *Phoxinus* by Banarescu (1964); but this lumping has not been readily accepted (Phillips, 1969; Stasiak, 1972; Scott and Crossman, 1973). On the basis of

comparative osteology, Mahy (1975) supported the synonymy of the American species with Eurasian *Phoxinus*. Gasowska (1979) splits the genus into three genera - *P. eos* and *P. erythrogaster* are placed in *Chrosomus*, *P. neogaeus* in *Phoxinus*, and *P. oreas* in a new genus, *Parchrosomus*. The most recent work on *Phoxinus* systematics has been done by Howes (1985), where he supported the idea of Banarescu and placed all five North American species in the genus *Phoxinus*.

While species of *Phoxinus* have been known to hybridize with species of other genera (Phillips and Etnier, 1969; Legendre, 1970; Greenfield *et al.*, 1973), most reported hybridization has been intrageneric between *P. eos* and *P. neogaeus* (Hubbs and Brown, 1929; New, 1962; Stasiak, 1972; Joswiak *et al.*, 1982). The frequency of hybridization is not consistent throughout the area of sympatry. Stasiak (1972), in an examination of collections throughout Minnesota, found very few hybrids. Greeley and Greene (1931) stated that in many localities in New York, hybrids were more numerous than either parental species. However, Greene (1935) examined 18 collections of *P. neogaeus* from Wisconsin, 15 of which also contained *P. eos*, yet not one of 857 specimens was identified as a hybrid. Hybrids have been collected in Colorado (Bailey and Allum, 1962) and Montana (Brown, 1971), although no pure *P. neogaeus* have been taken in those states. New (1962) found only female hybrids, and they tended to be intermediate in some characters but more similar to one parent in other characters. In contrast, Legendre (1970) indicated that

hybrids of both sexes exist in some Québec lakes. He concluded from a discriminant analysis that the hybrids formed Mendelian populations. Electrophoretic analysis of the specimens from one of those postulated Mendelian populations failed to detect any allozymic heterozygotes or recombinants (Joswiak *et al.*, 1985).

All these works mentioned above have been done with the populations from the southeastern area of the ranges of the two species. Paetz and Nelson (1970) first suspected hybridization between the two species in Alberta, a northwestern area of their distribution.

The purpose of this work is to study the phenomenon of hybridization between *P. eos* and *P. neogaeus* in Upper Pierre Grey Lake, Alberta. At the taxonomic level, this study presents multivariate statistical analyses of morphological data; it examines hybrid variability and investigates the possibility of hybrid fertility. The ecology of spawning populations and the effectiveness of the potential premating isolating mechanisms are described in order to ascertain the causes of hybridization. This research provides the first thorough morphological analyses and reproductive and life history data for these two species and their hybrids from Alberta and in the northwestern portion of their range.

2. STUDY AREA

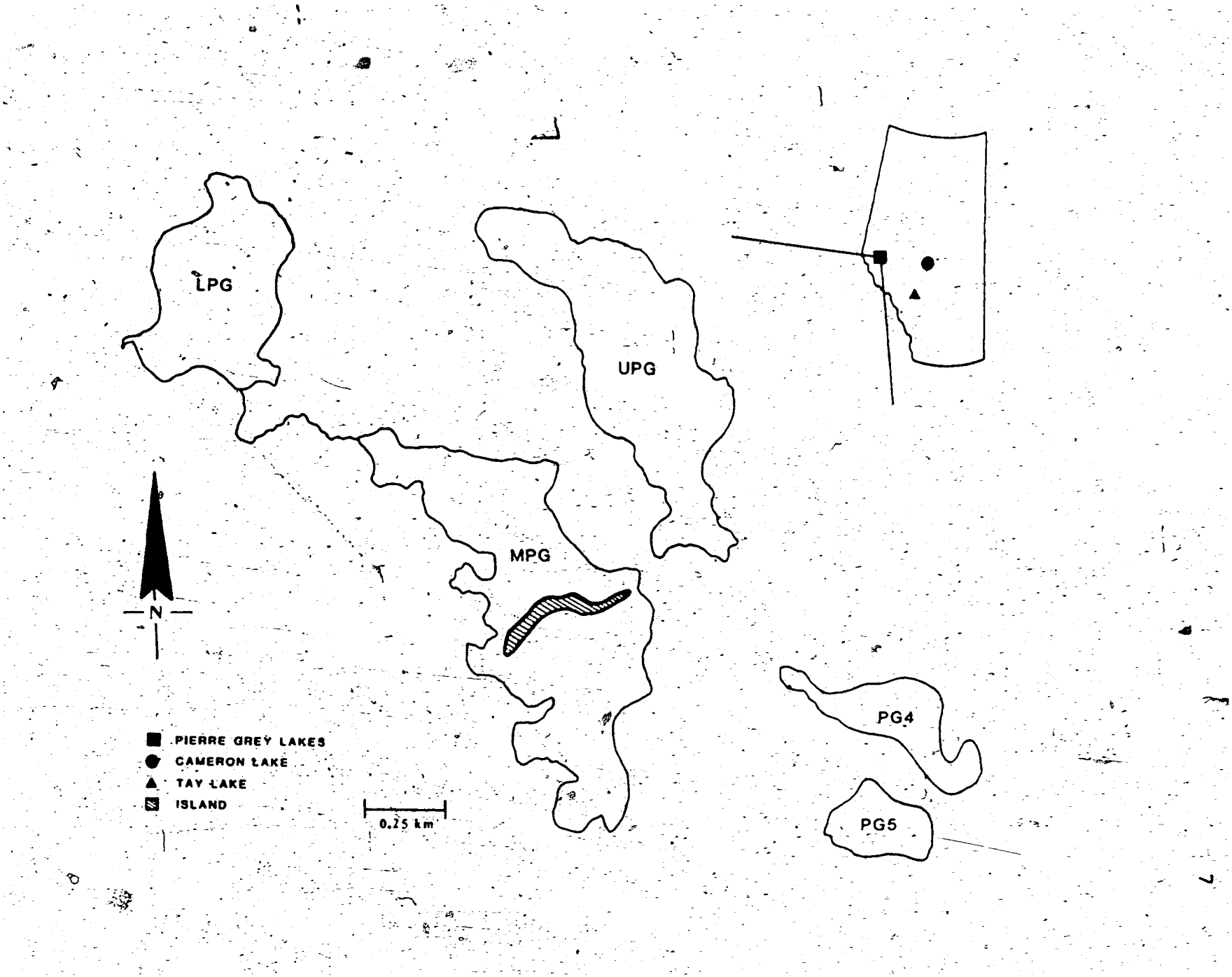
Pierre Grey Lakes are a complex of five lakes situated about 32 km east of the town of Grande Cache in the boreal forest of the foot-hills of the Rocky Mountains in western Alberta (Fig. 2.1). Three of these lakes, known as Lower (#1), Middle (#2), and Upper (#3), are managed for sport fisheries and have stocked rainbow trout (Lower and Middle) and brook trout (Upper).

The two parental species, *Phoxinus eos* and *Phoxinus neogaeus*, and their hybrids used in this study came from the Upper Pierre Grey Lake (UPG). This lake (53°54'N, 118°34'W) of 40 ha has the second largest surface area of the five lakes. Its maximum depth is 9.0 m which is the deepest of the lakes. Contours of the lake are indicated in Fig. 2.2.

The lake is surrounded by slopping banks except for the northwest and southeast corners. Surrounding banks are mainly vegetated by black spruce (*Picea mariana*) and lodgepole pine (*Pinus contorta*), with a few aspen poplar (*Populus tremuloides*) and white spruce (*Picea glauca*). The Muskeg River flows by the south end of the lake. The lake is landlocked with no distinct inlet or outlet. The emergent and submergent vegetation is very sparsely distributed along the narrow littoral zone, however, no quantitative or qualitative sampling was conducted. The bottom of the lake consists of ooze or ooze and clay (Snyder, 1972).

Surface water temperatures taken between early June and early August ranged from 11-19.5°C in 1984 and 13.5-17°C in

FIGURE 2.1. Map of the study area.
LPG = Lower Pierre Grey Lake.
MPG = Middle Pierre Grey Lake.
PG4 = Pierre Grey Lake # 4.
PG5 = Pierre Grey Lake # 5.
UPG = Upper Pierre Grey Lake.


LPG
UPG
MPG
PG4
PG5
N
PIERRE GREY LAKES
CAMERON LAKE
TAY LAKE
ISLAND
0.25 km

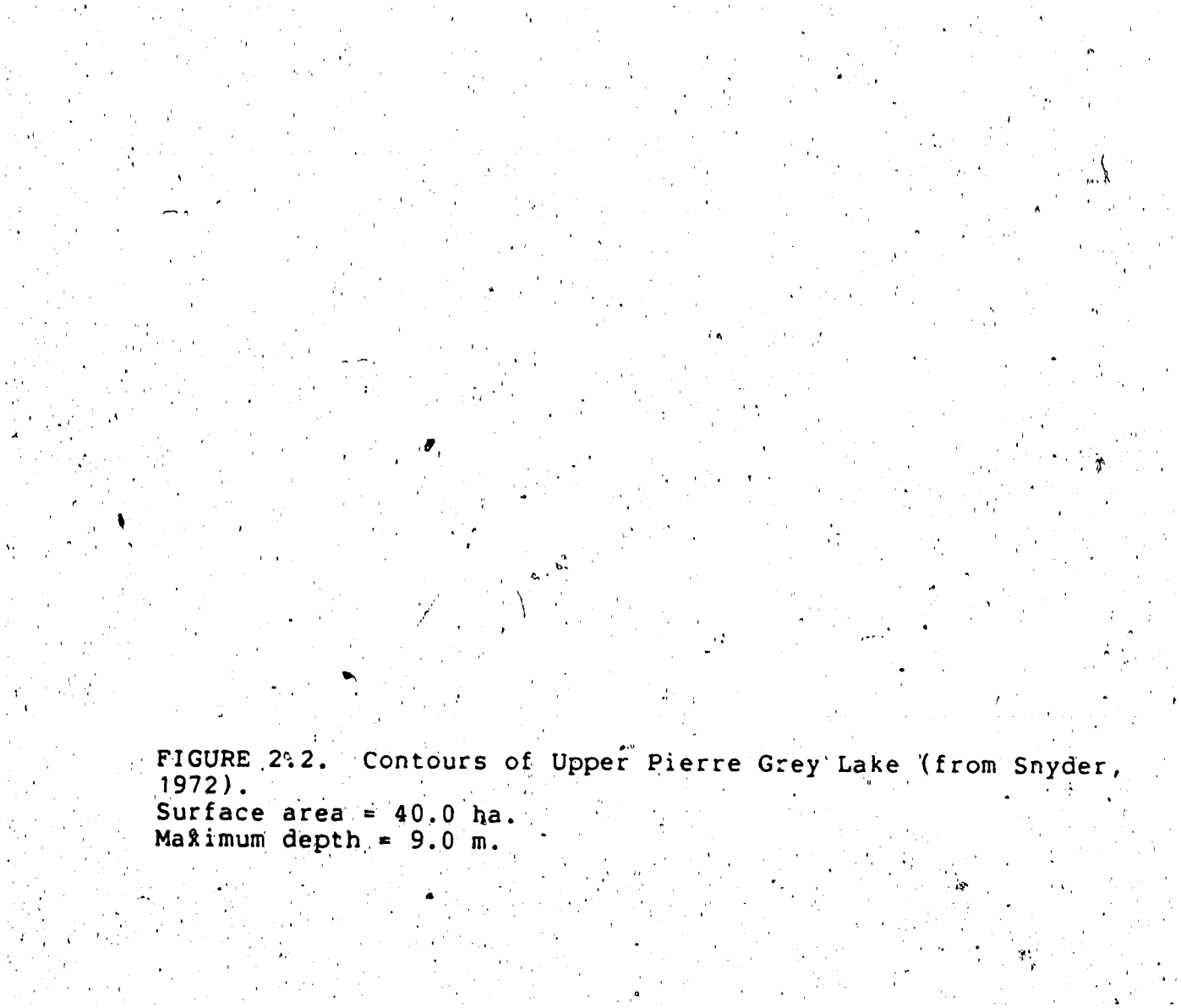
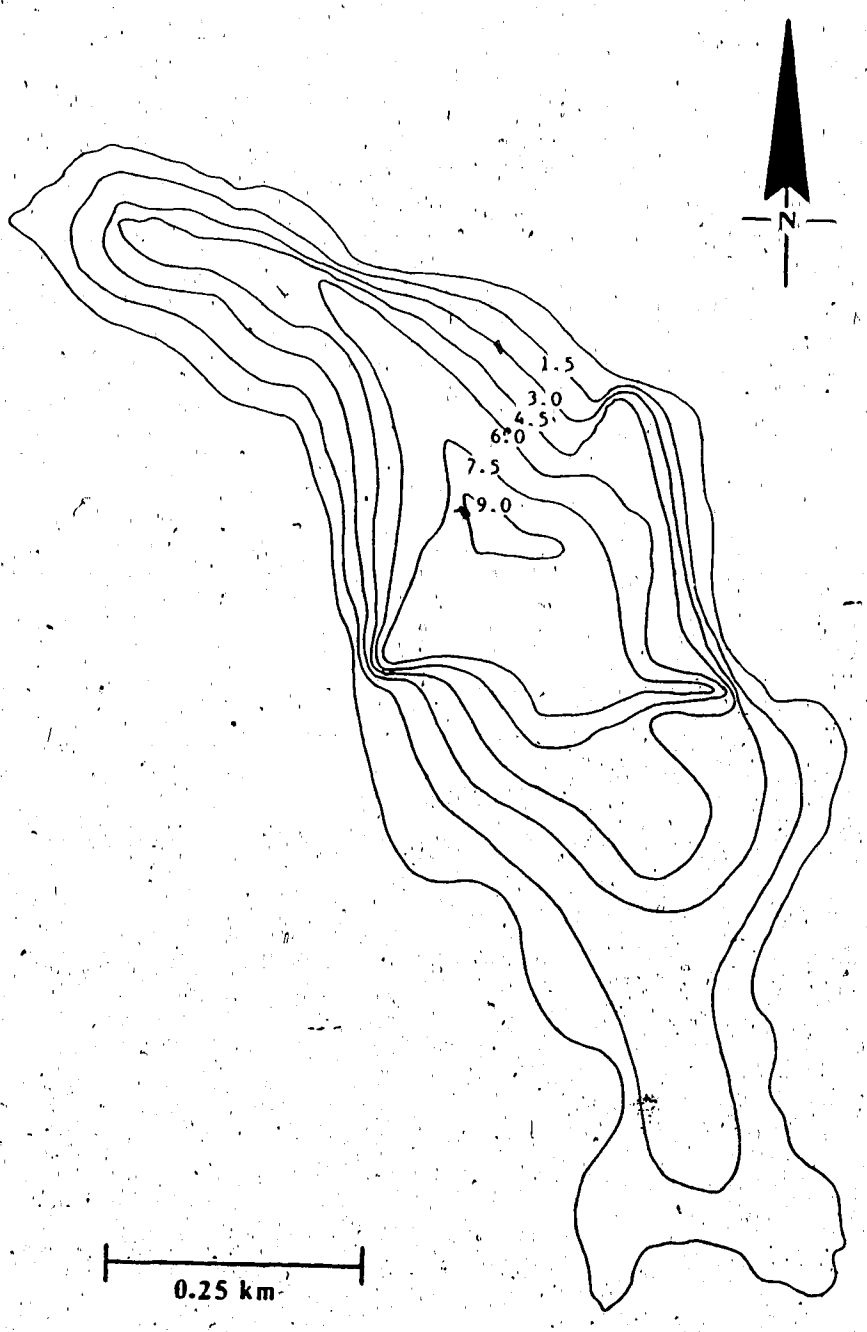


FIGURE 2.2. Contours of Upper Pierre Grey Lake (from Snyder, 1972).
Surface area = 40.0 ha.
Maximum depth = 9.0 m.


N
1.5
3.0
4.5
6.0
7.5
9.0
0.25 km

1985.

Data on some physico-chemical parameters and zooplankton and bottom fauna abundance presented here (Table 2.1) have been taken from Snyder (1972) and Turner (1981). The water of the lake is very transparent as indicated by the secchi disc data and this is supported by very low plankton density. The lake can be classified as an oligotrophic lake exhibiting very little in the way of bottom fauna, plankton and aquatic vegetation.

Brook trout (*Salvelinus fontinalis*), few white suckers (*Catostomus commersoni*), brook stickleback (*Culaea inconstans*), pearl dace (*Semotilus margarita*), northern redbelly dace (*Phoxinus eos*), finescale dace (*P. neogaeus*) and *P. eos* X *P. neogaeus* hybrids presently occur in the lake. Formerly the lake had white sucker, brook stickleback, pearl dace, northern redbelly dace and finescale dace; brook trout was introduced in 1969.

An allopatric population of each of the two parental species was collected from Alberta (see Fig. 2.1). Specimens of *P. eos* were collected from Cameron Lake which is situated in the Spruce Grove area, approximately 50 km west of the city of Edmonton. The greatest depth of the lake is about 6 m. The allopatric *P. neogaeus* were collected from Tay Lake, situated about 60 km west of the town of Red Deer and with a maximum depth of approximately 6 m. Of the three lakes, Tay Lake is the one most predominantly surrounded by a wide boggy area.

TABLE 2.1. Some physico-chemical and biological parameters of Upper Pierre Grey Lake. Data taken from Snyder (1972) and Turner (1981). The bottom fauna represents number of organisms per 25 samples taken by 15 cm Ekman dredge.

DATE	DEPTH (m)	TEMP. (°C)	pH	DISSOLVED OXYGEN (ppm)	LIGHT TRANSPARENCY (m)	SOURCE
July 30, 1968	Surface	17.1	7.8	5.6	5.8	Snyder, 1972
	8.8	15.2	7.8	5.3		
May 30, 1972	Surface	15.6	7.8	11.0	5.5	Snyder, 1972
	8.5	10.0	8.0	12.0		
June 3, 1981	Surface	14.0	8.2	10.0	7.9	Turner, 1981
	8.0	-	8.5	9.0		

	ZOOPLANKTON				BOTTOM FAUNA						
DATE	Copepods	Cladocera	Rotifera	Larval Crustaceans	Amphipods	Chironomids	Sphaeriids	Gastropods	Hirudinea	Oligochaeta	SOURCE
June, 1972	Abundant	Rare	Rare	Rare	19	85	12	18	5	3	Snyder, 1972
June, 1981	Abundant	Rare	Rare	Common	NO DATA						Turner, 1981

3. IDENTIFICATION OF HYBRIDS USING MULTIVARIATE ANALYSIS

3.1. INTRODUCTION

The advantages of multivariate statistical techniques relative to traditional methods for identifying hybrids have been reviewed by Smith (1973) and Danick and Barnes (1975). Despite these advantages, the identification of specific F2 or backcross individuals may not be possible in some cases (Neff and Smith, 1979). However, it may still be possible to identify a majority of hybrids as being of mixed genetic origin and to obtain indirect evidence of successful hybrid reproduction without resorting to time-consuming artificial cross experiments.

The existence of hybrids between *P. eos* and *P. neogaeus* has been known for more than 55 years since Hubbs and Brown (1929) first mentioned them. The first multivariate statistical approach was by Legendre (1970), who studied the hybrids from Québec by comparing them with the parental species through a discriminant function.

This section of my study describes canonical variates analysis (CVA) and principal components analysis (PCA) of various morphological characters of both hybrids and parental individuals. The methods do not require assumptions as to the identity of any UPG specimens. Hybrid variability and possible hybrid fertility are described.

3.2 METHODS

3.2.1 SPECIMENS EXAMINED

The morphology of representative Upper Pierre Grey Lake specimens was compared with an allopatric population of each of the two parental species - *P. eos* from Cameron Lake and *P. neogaeus* from Tay Lake. 3297 *P. eos*, 627 *P. neogaeus* and 1336 hybrids were collected from Upper Pierre Grey Lake during 1984 and 1985.

A random sample of 175 specimens was chosen from the collections of Upper Pierre Grey Lake, irrespective of sex and presumed identity, and were used in the analyses (designated hereafter as UPG specimens). The sex ratio for the entire UPG sample was 144 females to 31 males.

Some 40 *P. eos* from Cameron Lake (designated hereafter as Cam L specimens) and 44 *P. neogaeus* from Tay Lake (designated hereafter as Tay L specimens) were used in the analyses. The sex ratio for the Cam L specimens was 22 females to 18 males. Due to the scarcity of male specimens of *P. neogaeus*, the sex of the Tay L specimens was predominantly female (41 females to 3 males).

3.2.2 CHARACTERS USED

The following 22 morphometric and 11 meristic characters and 3 attributes were recorded for all specimens. These were chosen because most are good descriptors of the fish and some are known to be efficient discriminators of the parental

species and of the putative hybrids (New, 1962; Legendre, 1970; Stasiak, 1972; Scott and Crossman, 1973). Measurements and counts follow the descriptions and diagrams in Hubbs and Lagler (1964) except when otherwise defined. Morphometric measurements were taken using needle point *Hellos* dial calipers, read to the nearest 0.1 mm. The attributes were subjectly quantified and measured on an ordinal scale. Abbreviations for each character follow in parentheses.

MORPHOMETRIC CHARACTERS:

1. Standard length (SL).
2. Head length (HL).
3. Length of orbit (EYD).
4. Snout length (SNL).
5. Interorbital width (IOW).
6. Width between the nostrils (INW).
7. Head width (HDW).
8. Head depth (HDH).
9. Width of gape (GAPE).
10. Predorsal length (PRDOR).
11. Length of dorsal fin base (DRFINB).
12. Prepelvic length (PRPEL).
13. Preanal length (PRANAL).
14. Distance from the posterior margin of the anus to the base of the hypural plate (UROL).
15. Length of caudal peduncle (LCPD).
16. Depth of caudal peduncle (HCPD).
17. Length of dorsal fin (DORFL).

18. Length of pectoral fin (PECFL).
19. Length of pelvic fin (PELFL).
20. Length of anal fin (ANALFL).
21. Length of caudal fin (CAUDFL).
22. Length from pectoral to pelvic fin (PECPEL) - the longest straight distance between the points where the uppermost, outermost, or anteriormost ray of these fins is inserted into the body.

MERISTIC CHARACTERS:

1. Number of scales in lateral series (LATL).
2. Number of scales from dorsal fin origin along diagonal to the lateral series scale (LATTR).
3. Caudal peduncle scale count (CIRCUMPED).
4. Dorsal fin rays - divided into two variables
   a. unbranched rays (DORFR1);
   b. branched rays (DORFR2).
5. Pectoral fin rays - divided into two variables
   a. unbranched ray (PECFR1);
   b. branched rays (PECFR2).
6. Pelvic fin rays - divided into two variables
   a. unbranched ray (PELFR1);
   b. branched rays (PELFR2).
7. Anal fin rays - divided into two variables
   a. unbranched rays (ANALFR1);
   b. branched rays (ANALFR2).
8. Caudal fin rays (CAUDFR).
9. Branchiostegal rays - divided into two variables

a. rays of the left side (BRACSTEGL);

b. rays of the right side (BRACSTEGR).

10. Number of pharyngeal teeth - divided into four variables

a. number of teeth in the outer row of the left arch (PHARTLO);

b. number of teeth in the inner row of the left arch (PHARTLI);

c. number of teeth in the inner row of the right arch (PHARTRI);

d. number of teeth in the outer row of the right arch (PHARTRO).

11. Mouth angle (MOANGLE) - with the mouth closed, the angle between a straight line passing from the most anterior to the most posterior points where the upper lip touches the lower lip, and the line from the most anterior point of junction of the lips to the rear of the fish, parallel to the longitudinal axis.

ATTRIBUTES :

1. Digestive tract pattern (DIGTRACT) - from a simple S-shaped loop to an elongate tract with two crosswise coils (scale of 1 to 5) (Fig. 3.1).

2. Extension of mouth (MOEXTN) (scale of 1 to 3) - 1) not reaching a vertical through anterior margin of eye; 2) reaching up to the anterior margin of eye; 3) extending back to below anterior margin of eye (Fig. 3.2).

3. Lateral band (LATBAND) (scale of 1 to 4) - from presence of one distinct mid-lateral band to presence of two

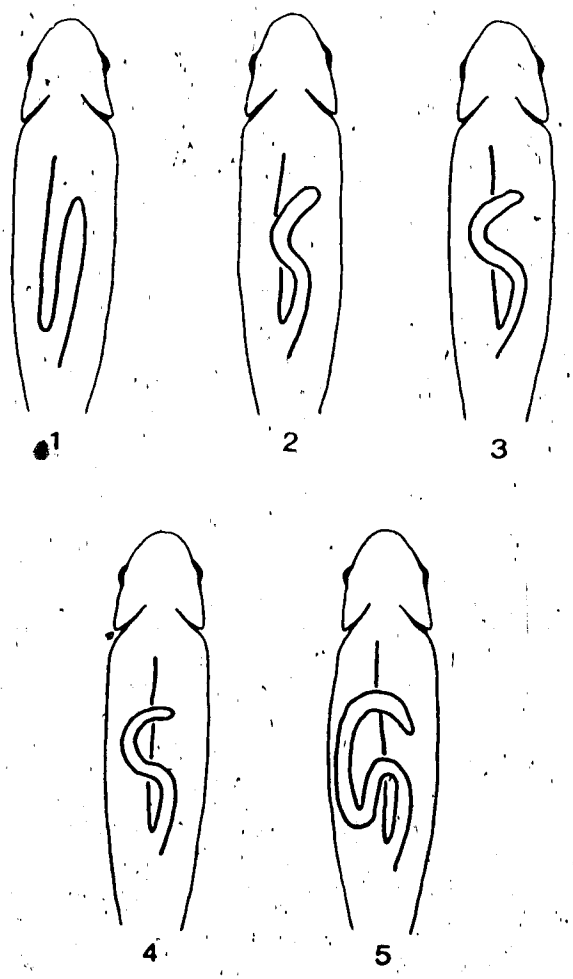


FIGURE 3.1. Digestive tract patterns.
1 = *Phoxinus neogaeus*, 2-4 = various stages of intermediacy between the parental species (state 2 was found in 22% of allopatric *Phoxinus neogaeus*), 5 = *Phoxinus eos*.

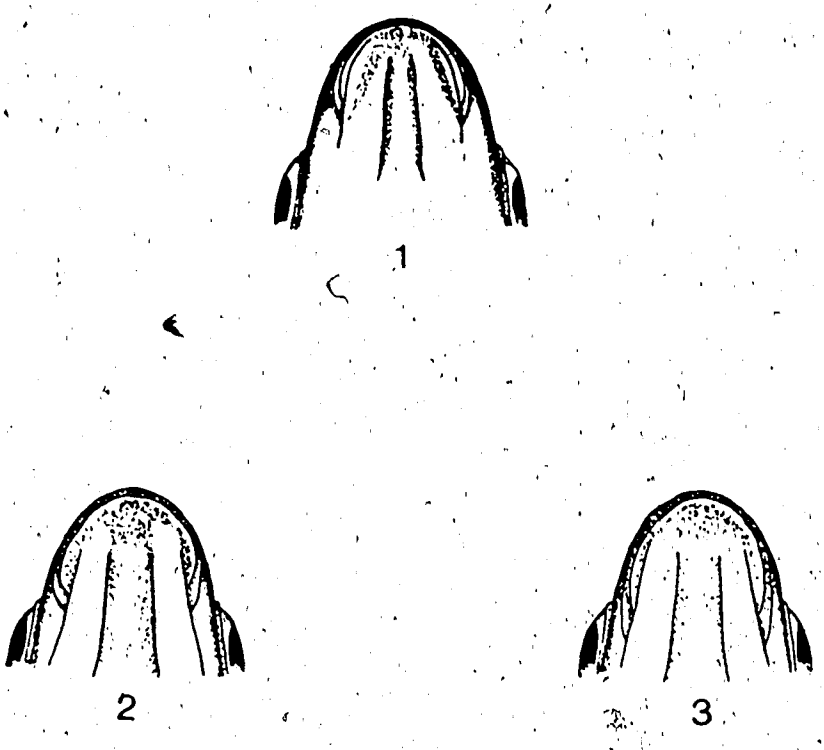


FIGURE 3.2. Extension of mouth.
1 = *Phoxinus eos*, 2 = intermediates between the parental species, 3 = *Phoxinus neogaeus*.

distinct lateral bands. Two lateral bands can be defined as one mid-lateral band beginning on snout and terminating in a basicaudal spot and another thin dorsolateral band between mid-lateral band and mid-dorsal stripe from operculum to the margin of hypural plate (Fig. 3.3).

Ratios were specifically avoided in order to eliminate problems with allometry (Marr, 1955). Atchley *et al*. (1976), Atchley and Anderson (1978), Humphries *et al*. (1981) also suggested that ratios should be avoided in morphometric studies because of effects of correlation between numerators and the denominator and because they may cause statistical and conceptual difficulties that may seriously affect conclusions. Multivariate analyses were run with untransformed and log-transformed data. Log-transformation of data stabilizes the variance.

From the original 36 characters, five meristic characters (dorsal fin rays, pelvic fin rays, anal fin rays, caudal fin rays, and branchiostegal rays) were discarded prior to in-depth analyses because they were ineffective at group discrimination.

3.2.3 CANONICAL VARIATES ANALYSIS

Two separate data sets - 1) 40 Cam L specimens and 44 Tay L specimens; 2) all 175 UPG specimens were subjected to canonical variates analysis in order to quantify the relationship between individuals (Pimentel, 1979). This

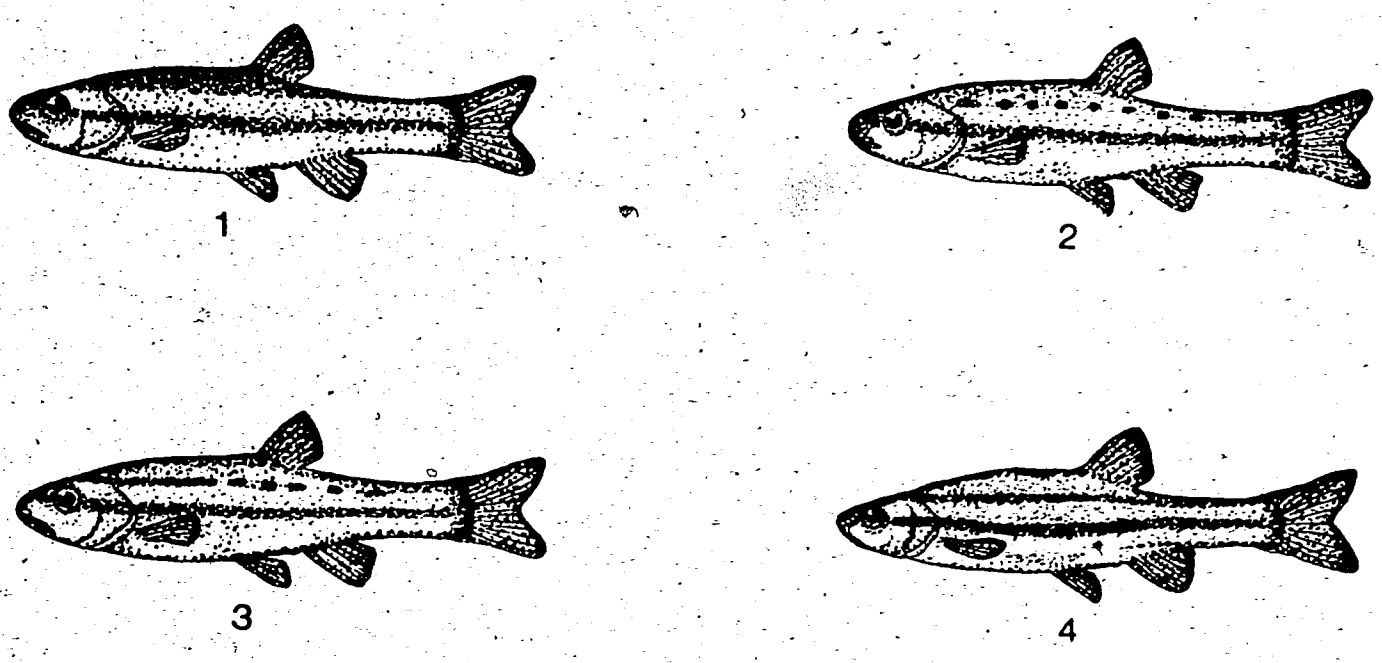


FIGURE 3.3. Lateral band.
1 = *Phoxinus neogaeus*, 2 and 3 = stages of intermediacy between the parental species, 4 = *Phoxinus eos*.

method requires the *a priori* identification of two or more known groups within the data set. Axes are calculated that maximally separate these groups while minimizing the within-group variance. Specimens of unknown origin can then be assigned a position on this axis (calculated using the discriminant function) relative to their similarity to either group.

The BMDP7M computer program (Dixon, 1983) was used to assess the relationship between the UPG specimens (the *a priori* unknown groups) and the Tay L and the Cam L specimens (the *a priori* known groups). The canonical scores were plotted against the canonical axis and graphed as frequency histograms.

3.2.4 PRINCIPAL COMPONENTS ANALYSIS

Principal components analysis (Namkoong, 1966; Morrison, 1967; Cooley and Lohnes, 1971; Pimentel, 1979) was used to display patterns of morphological similarity. This method finds the orthogonal axes through the n-dimensional character space in directions of greatest variance. The new axes provide new directions from which to view the group relationships, if any, with the data. A scatter plot of the specimens on the first two components usually displays the greatest amount of the total variance within the data set (Danick and Barnes, 1975). Computation of the principal components does not require any *a priori* assumptions about group membership.

PCA scores were calculated from the character correlation matrix using the BMDP4M computer program (Dixon, 1983) for three separate data sets. The first two data sets were the same as used in the CVA. In the third data set, 84 specimens of the two allopatric parental species and 175 specimens of UPG were used together in the analysis. The projection scores of the specimens in three data sets were plotted in simple bivariate scatter plots against the first and second axes (Principal Component I - PC I and Principal Component II - PC II). Untransformed and log-transformed data were analyzed separately.

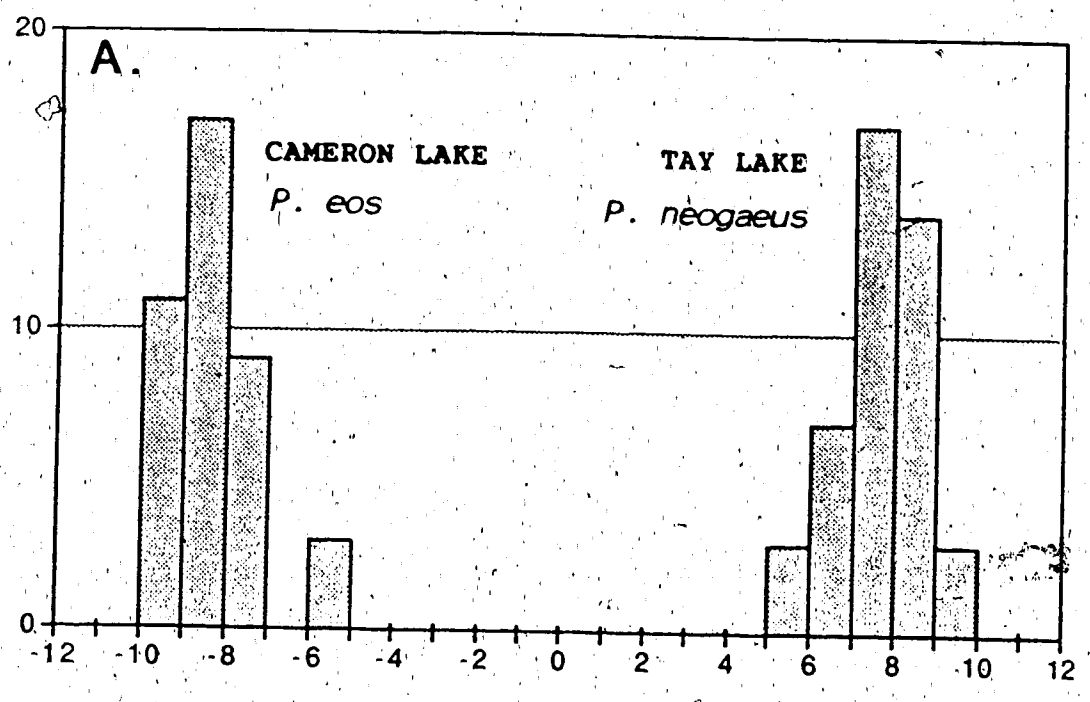
3.3 RESULTS

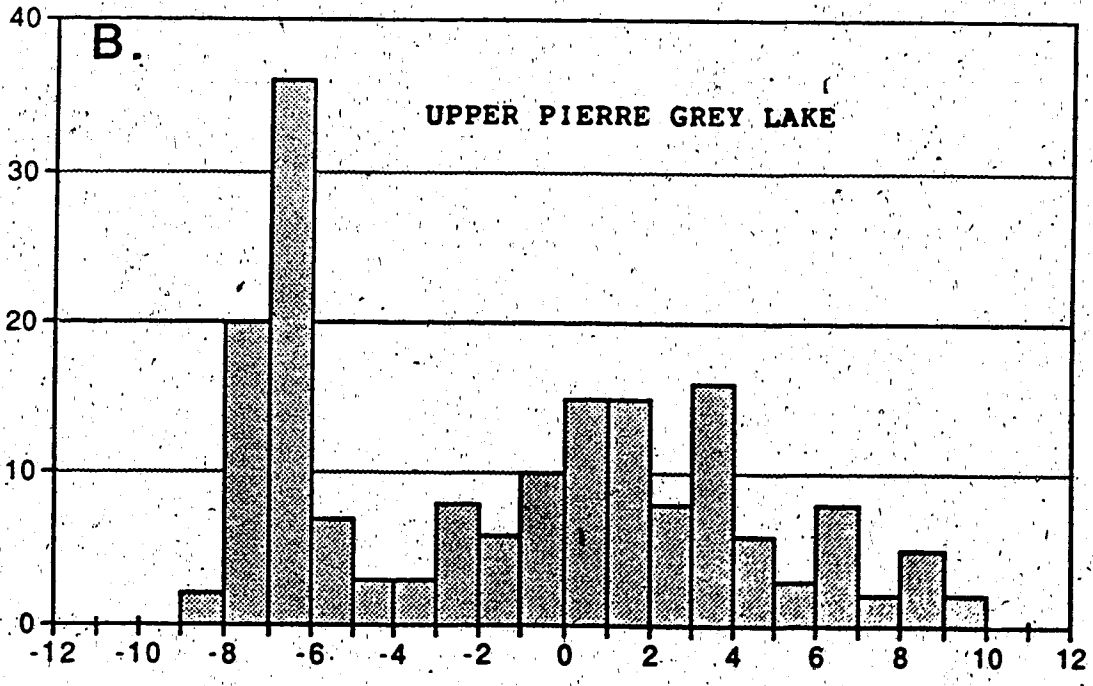
3.3.1 CANONICAL VARIATES ANALYSIS

The relationships between the UPG specimens including hybrids, and the two allopatric populations of the parental species can be expressed in a quantitative manner by frequency distributions of their canonical scores. The results of a CVA using untransformed data with the full character set are given in Fig. 3.4. The computer results for this analysis are summarized in Appendix Table 1.

The two distributions for the two allopatric species are separated by a large gap of approximately 16 standard deviations between their means. The UPG specimens form a continuous distribution with no gap between the typical parental species

FIGURE 3.4. CVA using untransformed data; MOEXTN included. Frequency histograms of canonical scores of specimens from A. Cameron Lake and Tay Lake; B. Upper Pierre Grey Lake. Cameron Lake and Tay Lake specimens formed two *a priori* known groups; all Upper Pierre Grey Lake specimens ran as *a priori* unknown groups.
x-axis = canonical scores;
y-axis = number of specimens.


A.
CAMERON LAKE
P. eos
TAY LAKE
P. neogaeus
20
10
0
-12
-10
-8
-6
-4
-2
0
2
4
6
8
10
12


B.
UPPER PIERRE GREY LAKE
40
30
20
10
0
-12
-10
-8
-6
-4
-2
0
2
4
6
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12

An apparent trimodality, which is expected from the presence of two parental species and the hybrids in the population, cannot be identified in case of UPG specimens. A small number of *P. neogaeus* (11.5%) in the sample is the reason for the low magnitude of *P. neogaeus* mode. More *P. neogaeus* could have been included in the analysis, but in that case an objection might be raised that the formation of the *P. neogaeus* peak with the greater magnitude is an artifact of selective inclusion of the species. Instead, since only a random sample of the field collections was used for the analysis, the representation of the whole population in the analysis is more natural.

All specimens initially identified as "good" *P. eos* fell within the outer *P. eos* mode. All specimens that were initially identified as "good" *P. neogaeus*, except six, fell within the outer *P. neogaeus* mode. All specimens, initially identified as putative hybrids, were classified in the intermediate position by the CVA.

All the hybrids falling into the intermediate mode are females.

The seven characters that contribute most to separation of the species in this analysis, are given in Table 3.1 (along with their F ratios, coefficients, and the constant for the discriminant functions). Due to high correlation, most of the morphometric characters contributed little to the discrimination and could have been eliminated from the analysis. The extension of mouth (MOEXTN) was the most

TABLE 3.1. The seven most discriminating characters in a CVA using untransformed data, including MOEXTN. Characters are in order of decreasing importance with F ratios (1, 82 df) for inclusion and coefficients.

Rank	Character	F	Coefficient
1	MOEXTN	1295.77	1.97
2	LATBAND	44.83	-1.14
3	LCPD	37.21	0.22
4	PHARTLO	17.2	1.28
5	DIGTRACT	11.05	-0.53
6	MOANGLE	10.73	-0.15
7	INW	6.55	1.13
			Constant 0.55

discriminating character with a high F value (F = 1295.77).

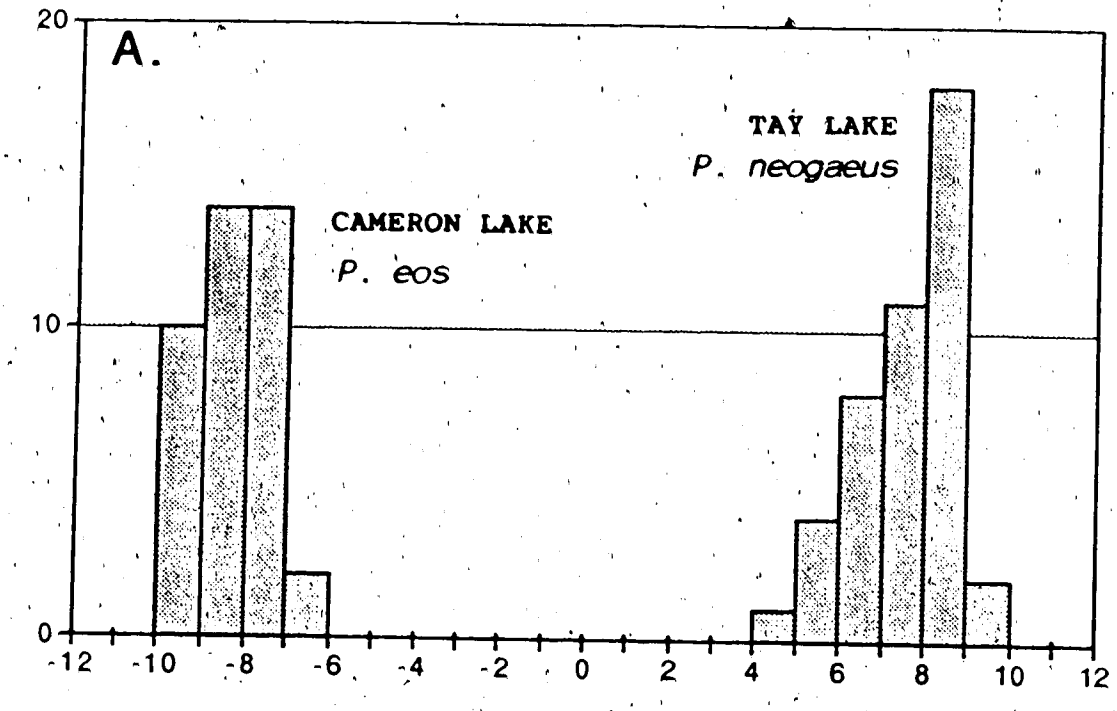
Although MOEXTN is an efficient discriminator, its removal from the analysis does not seriously affect the results. The CVA histogram using untransformed data without MOEXTN was essentially identical to the histogram in Fig. 3.4 (see Fig. 3.5). The characters contributing most to separation are given in Table 3.2. The computer results for this analysis are summarized in Appendix Table 2.

The results of the CVA using log-transformed data, with MOEXTN character included in the data set, are given in Fig. 3.6 (see Appendix Table 3 for the summary of the computer results). Transformation of the characters does not show any significant increase in the between-species discrimination. The means of the two allopatric species' distributions are separated by approximately 17 units of standard deviation. Sympatric species and the hybrids do not show any significant change either.

3.3.2 PRINCIPAL COMPONENTS ANALYSIS

The principal components scores for the allopatric populations - Cam L and Tay L specimens - were calculated using untransformed data with the full character set, and projection scores plotted against the first two axes (Fig. 3.7) (Appendix Table 4). Two clusters, reflecting both variation in size and direction of discrimination, are evident, confirming the initial identification of 'pure' specimens representing the two species, with no morphological

FIGURE 3.5. CVA using untransformed data; MOEXTN excluded. Frequency histograms of canonical scores of specimens from A. Cameron Lake and Tay Lake; B. Upper Pierre Grey Lake. Cameron Lake and Tay Lake specimens ran as *a priori* known groups; all Upper Pierre Grey Lake specimens ran as *a priori* unknown groups.
x-axis = canonical scores;
y-axis = number of specimens.


A.
TAY LAKE
P. neogaeus
CAMERON LAKE
P. eos
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-8
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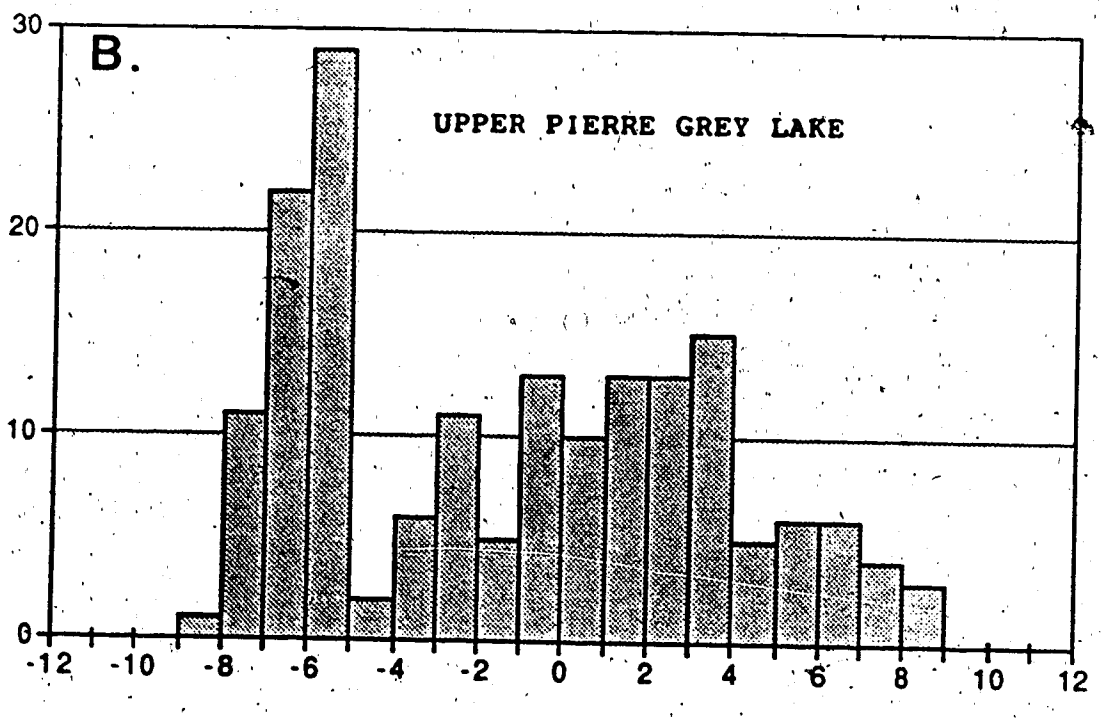
B.
UPPER PIERRE GREY LAKE
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20
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-12
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-4
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TABLE 3.2. The eight most discriminating characters in a CVA using untransformed data, excluding MOEXTN. Characters are in order of decreasing importance with F ratios (1, 82 df) for inclusion and coefficients.

Rank	Character	F	Coefficient
1	LATBAND	1197.9	-1.46
2	HL	53.68	0.4
3	MOANGLE	26.78	-0.22
4	DIGTRACT	24.11	-0.51
5	PHARTLO	15.02	1.24
6	PELFL	5.95	0.96
7	INW	5.22	1.22
8	ANALFL	4.09	-1.08
			Constant 8.15

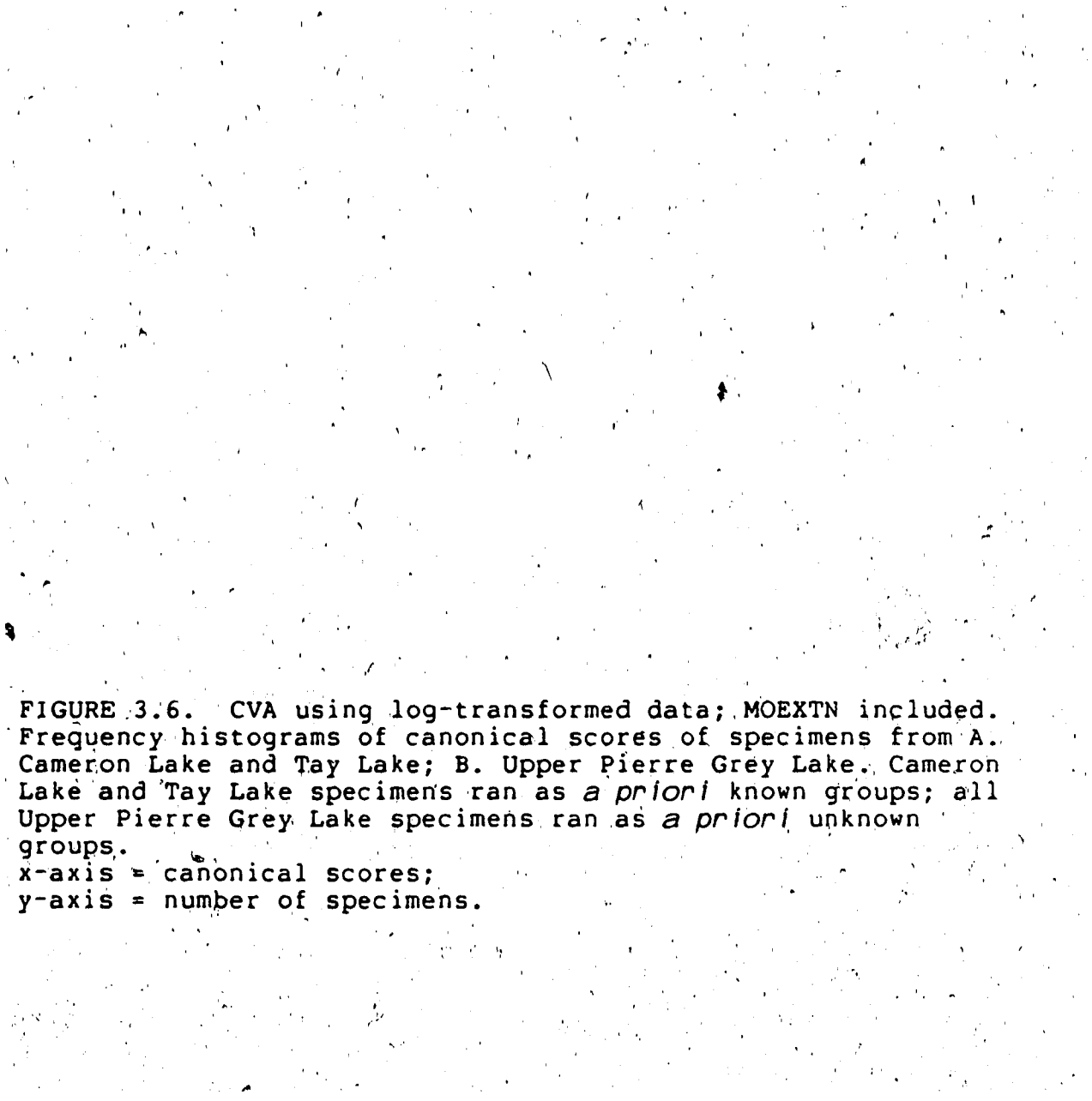
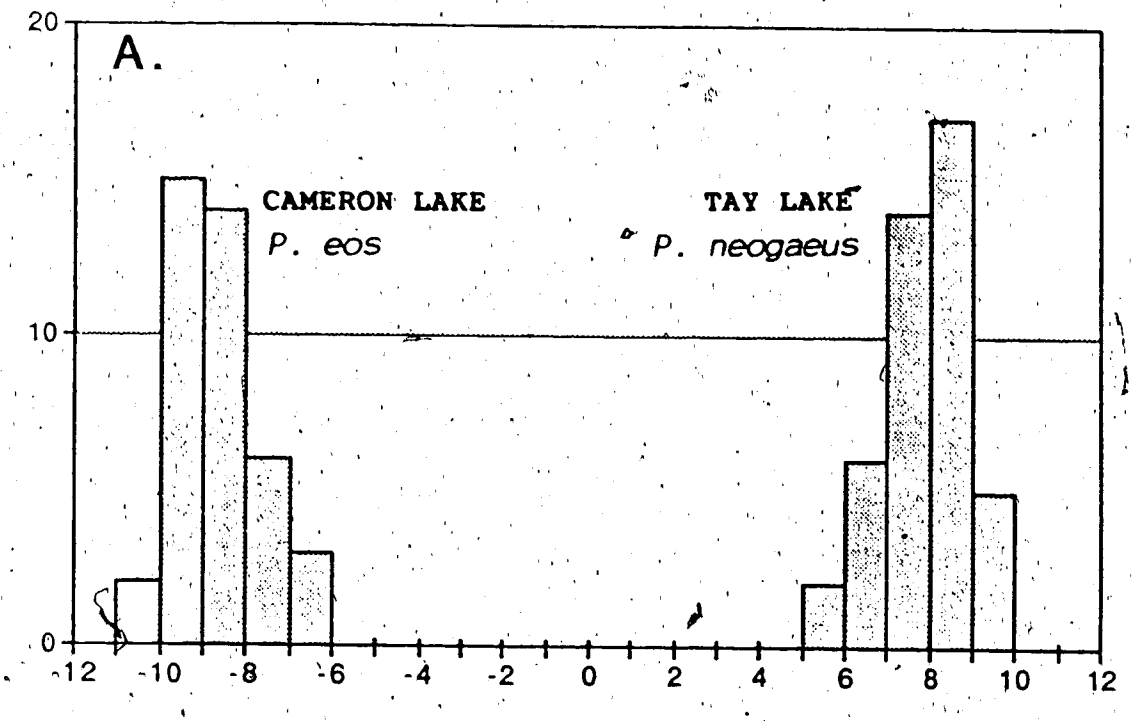


FIGURE 3.6. CVA using log-transformed data; MOEXTN included. Frequency histograms of canonical scores of specimens from A. Cameron Lake and Tay Lake; B. Upper Pierre Grey Lake. Cameron Lake and Tay Lake specimens ran as *a priori* known groups; all Upper Pierre Grey Lake specimens ran as *a priori* unknown groups.
x-axis = canonical scores;
y-axis = number of specimens.


A.
CAMERON LAKE
P. eos
TAY LAKE
P. neogaeus
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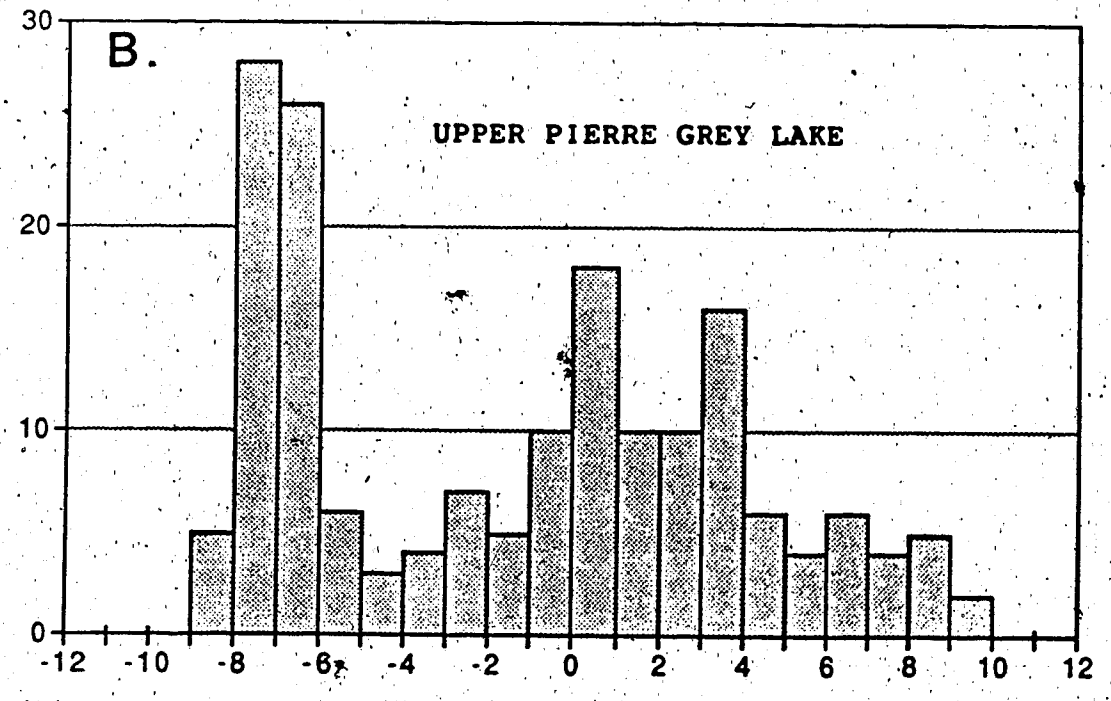
B.
UPPER PIERRE GREY LAKE
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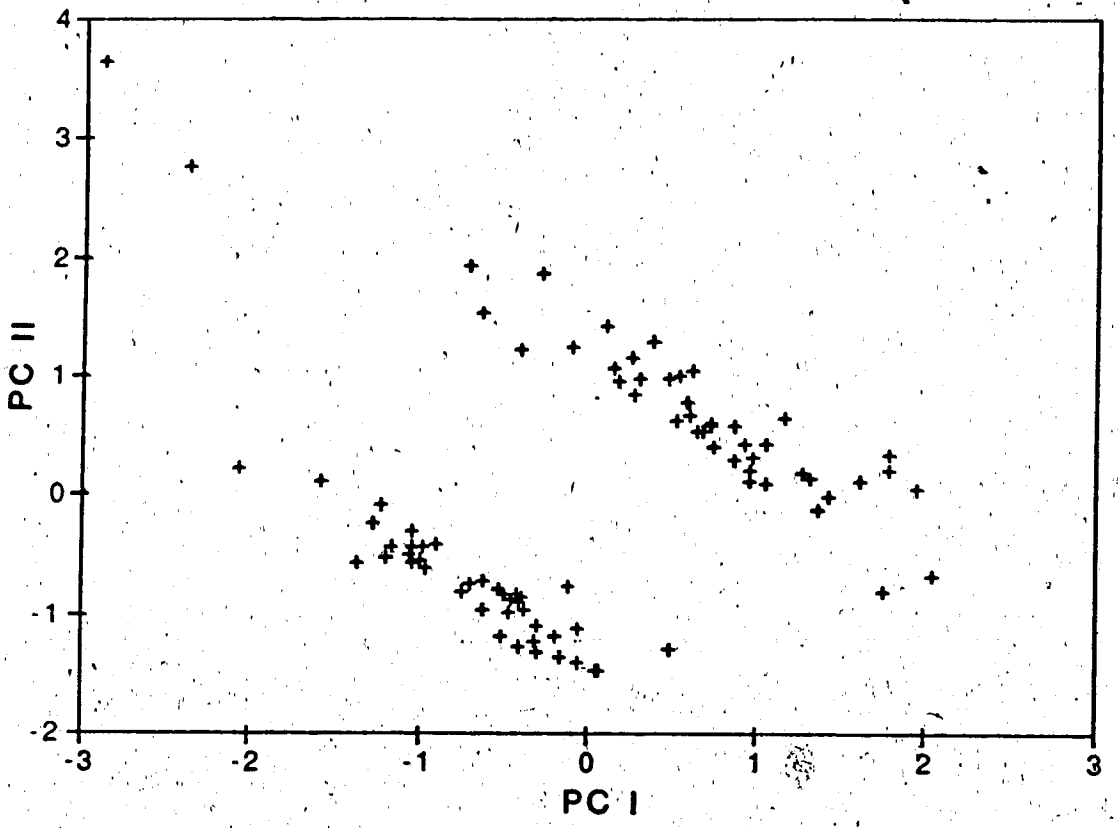


FIGURE 3.7. PCA using untransformed data; MOEXTN included. Plot of first and second principal component scores for Cameron Lake and Tay Lake specimens. *Phoxinus eos* from Cameron Lake - bottom cluster; *Phoxinus neogaeus* from Tay Lake - top cluster. Component I = 78.2% of total variation; component II = 5.5% of total variation.

intermediates. Two outliers in the plot represent two immature *P. neogaeus* males. The variation expressed by the two components represents 78.2 + 5.5 = 83.7% of the total variance in the data matrix.

The principal component scores for all UPG specimens, calculated using untransformed data including MOEXTN, were plotted against the first two axes (Fig. 3.8) (Appendix Table 5). The variation expressed by the two components represents 68.1 + 5.7 = 73.8% of the variance in the total data matrix. The projection of scores show elongated clusters with a bridge in between the two species' clusters. The specimens of this bridge represent the putative hybrids. Although the cluster representing the *P. eos* specimens is prominent, the *P. neogaeus* cluster is not very clearly identifiable. It was hypothesized that small number of pure *P. neogaeus* specimens in the population is responsible for this. To test that hypothesis, a third data set with specimens from all three localities was used in another PCA. The components scores show two distinct clusters for the two species and an intermediate cluster for the hybrids (Fig. 3.9) (Appendix Table 6). The components scores of the *P. neogaeus* specimens from UPG fall within the components scores of Tay L specimens.

This analysis also shows that the hybrids are not all strictly intermediate. They cover the entire phenotypic range between the two species suggesting backcrossing of F1 hybrids to their parental species.

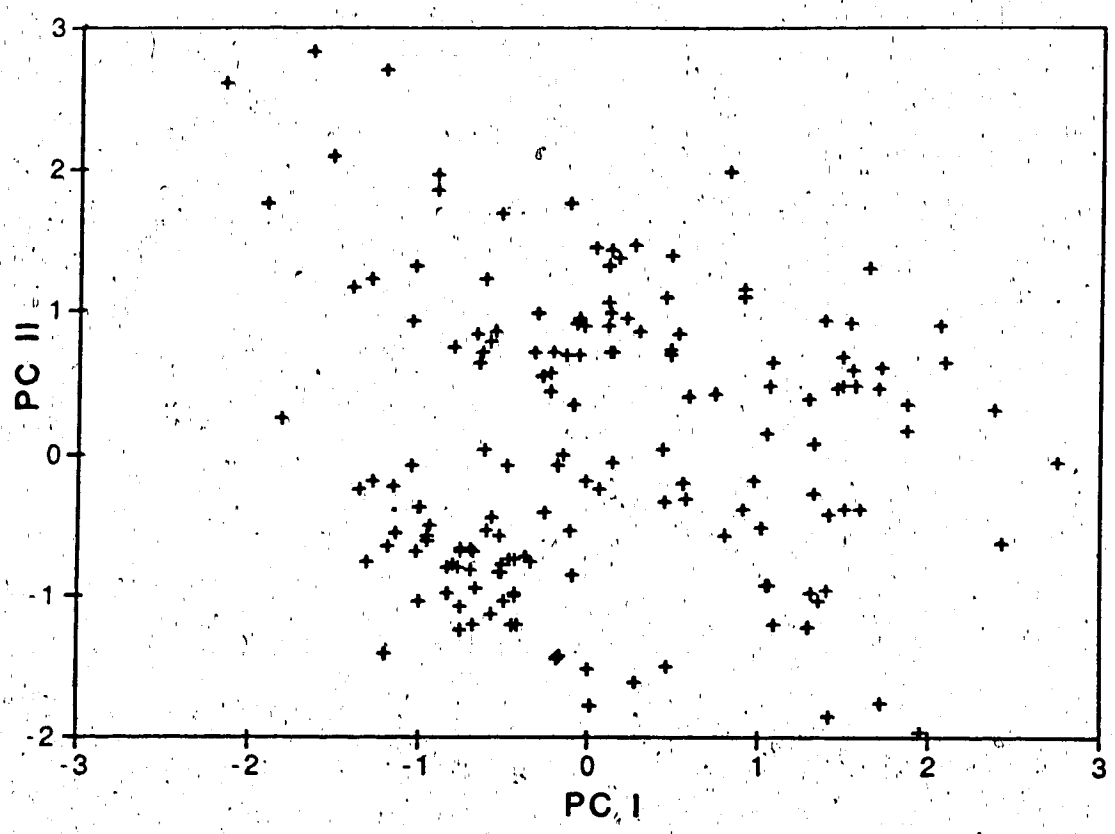


FIGURE 3.8. PCA using untransformed data; MOEXTN included. Plot of first and second principal component scores for Upper Pierre Grey Lake specimens. *Phoxinus eos*-like specimens towards bottom; *Phoxinus neogaeus*-like specimens towards top, with hybrids bridging the two species clusters. Component I = 68.1% of total variation; component II = 5.7% of total variation.

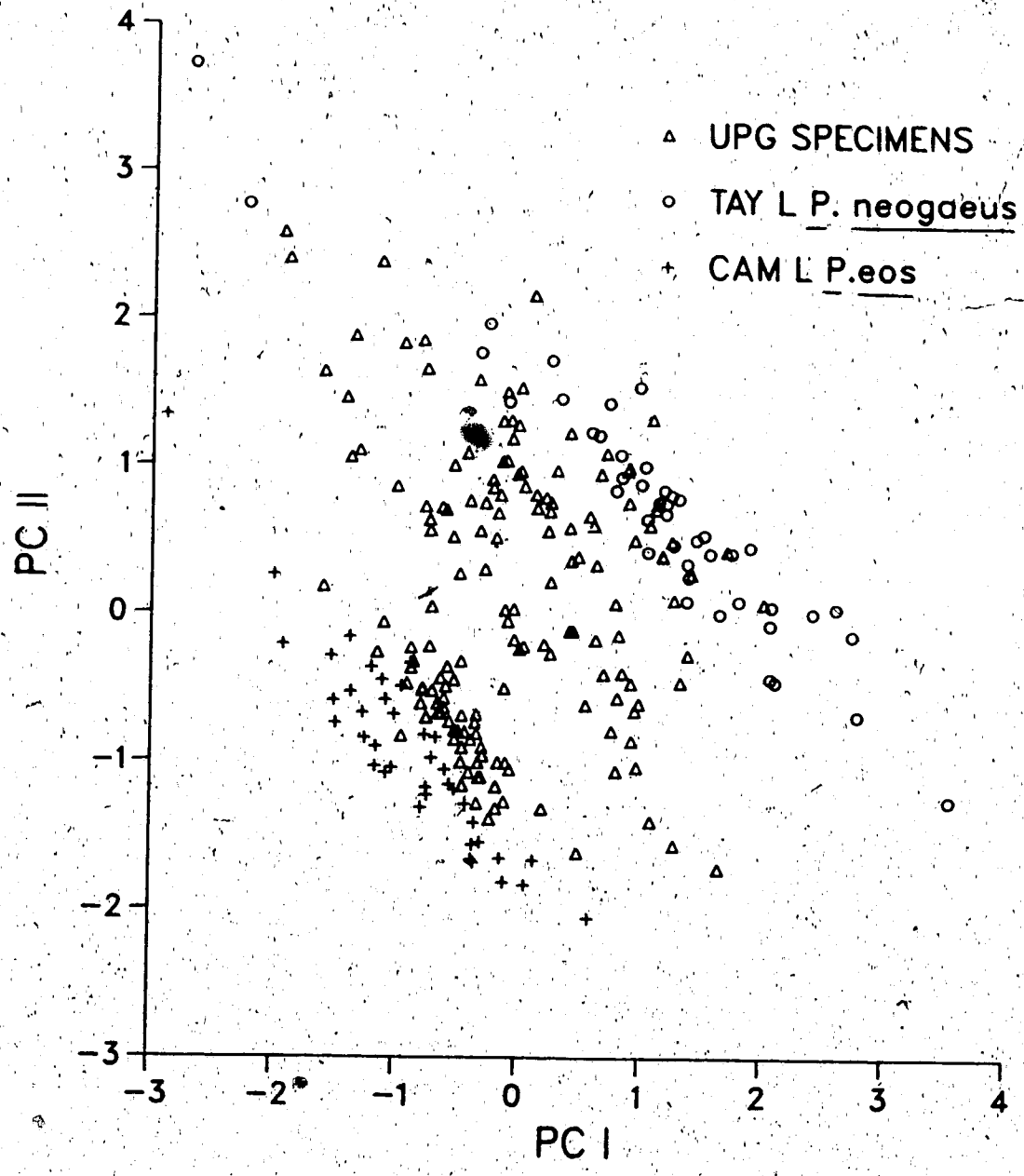


FIGURE 3.9. PCA using untransformed data; MOEXTN included. Plot of first and second principal component scores for Cameron Lake, Tay Lake and Upper Pierre Grey Lake specimens. *Phoxinus eos*-like specimens towards bottom; *Phoxinus neogaeus*-like specimens towards top, hybrids bridging the two species clusters. Component I = 69.4% of total variation; component II = 5.7% of total variation.

PCA using log-transformed data resulted in plots similar to those generated using untransformed data (Figs. 3.10, 3.11 and 3.12) (Appendix Tables 7, 8, 9). The UPG parental species remain bridged by the hybrid complex. Exclusion of MOEXTN character from untransformed and log-transformed data set did not change the results either.

The scatter plots of the PCAs discussed before (Figs. 3.7 - 3.12) display clusters oblique to components I and II. This is due to the fact that there is a distinct difference in size between the two parental species. Most of the specimens of *P. eos* are smaller than *P. neogaeus*. This size difference primarily effects the morphometric characters. CVA has also shown that most of the morphometric characters have contributed very little in the species' discrimination. According to Humphries *et al.* (1981), an increased discrimination can be attained through separate analyses of continuous and discontinuous variables. It should also eliminate artifacts caused by large size differences because the discriminators are uncorrelated within groups.

Two PCAs were computed using log-transformed morphometric characters and meristic characters and attributes separately. Bivariate scatter plots were plotted against component I of morphometrics and component I of meristics and attributes. Although the results show a better discrimination, the identification of individuals do not change (Figs. 3.13 and 3.14) (Appendix Tables 10, 11).

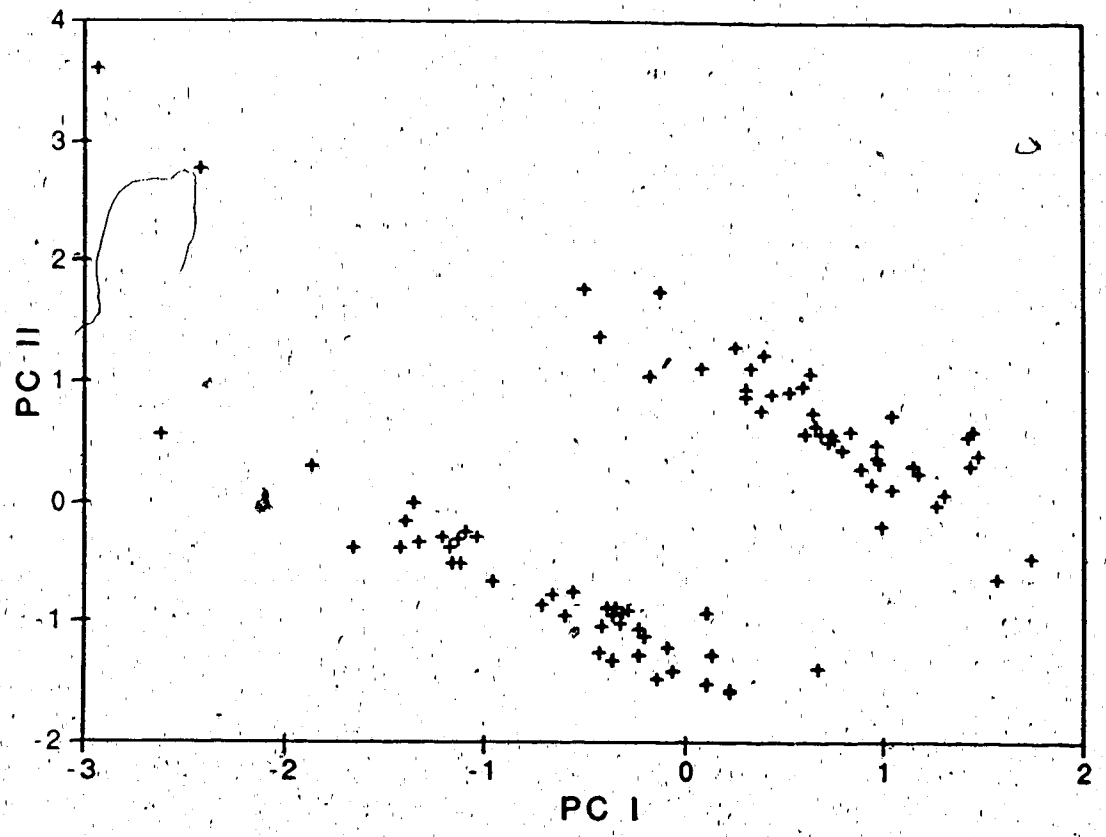


FIGURE 3.10. PCA using log-transformed data; MOEXTN included.
Plot of first and second principal component scores for Cameron Lake and Tay Lake specimens. *Phoxinus eos* from Cameron Lake - bottom cluster; *Phoxinus neogaeus* from Tay Lake - top cluster. Componet I = 78.6% of total variation; Component II = 5.5% of total variation.

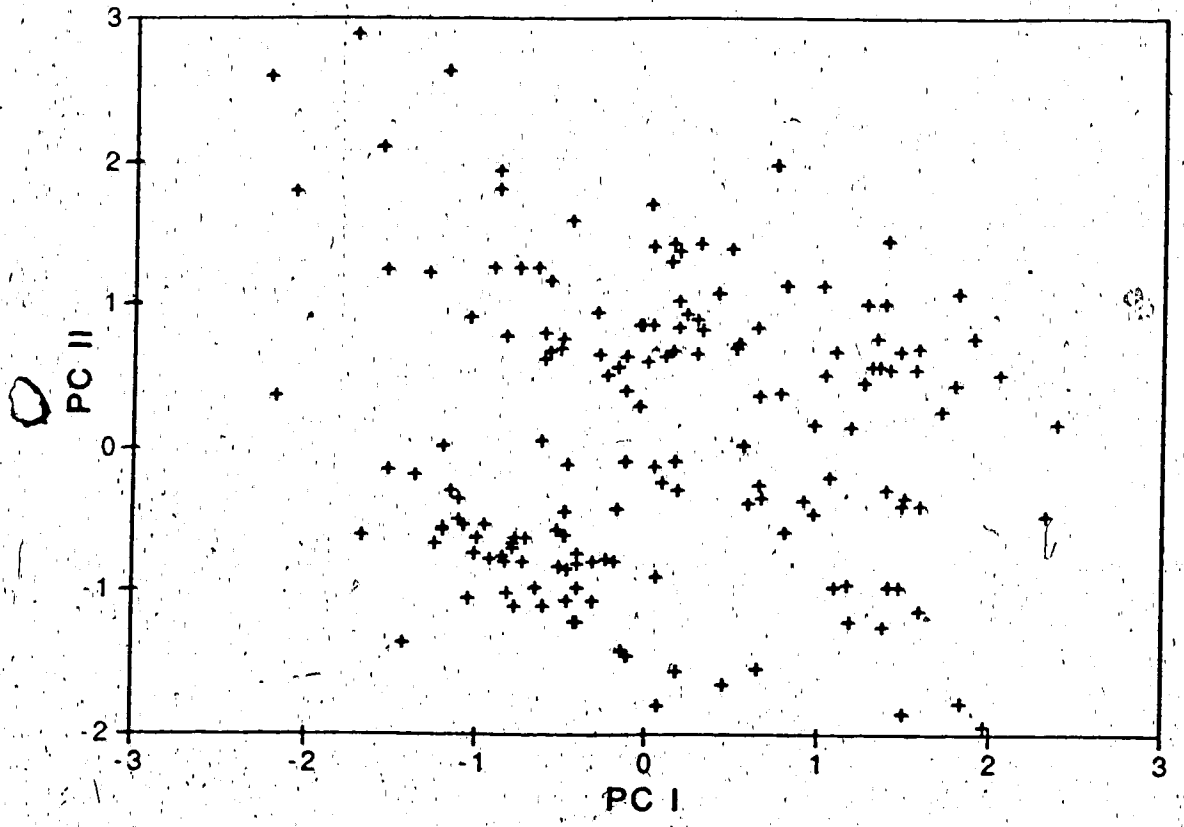


FIGURE 3.11. PCA using log-transformed data; MOEXTN included.
Plot of first and second principal component scores for Upper Pierre Grey Lake specimens. *Phoxinus eos*-like specimens towards bottom; *Phoxinus neogaeus*-like specimens towards top, with hybrids bridging the two species. Component I = 68.3% of total variation; Component II = 5.8% of total variation.

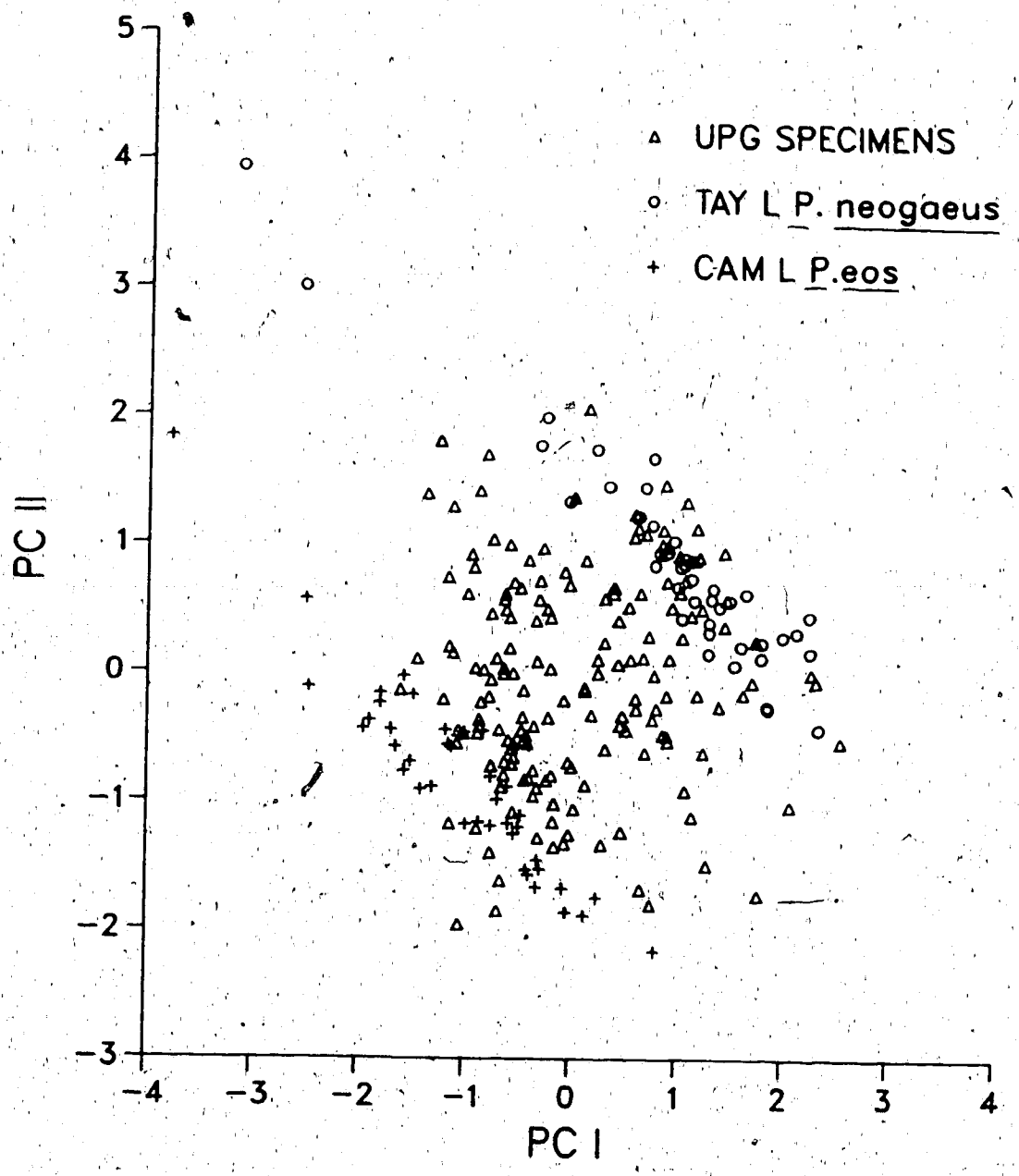


FIGURE 3.12. PCA using log-transformed data; MOEXTN included.
Plot of first and second principal component scores for Cameron Lake, Tay Lake and Upper Pierre Grey Lake specimens. *Phoxinus eos*-like specimens towards bottom; *Phoxinus neogaeus*-like specimens towards top, with hybrids bridging the two species clusters. Component I = 71.3% of total variation; Component II = 6.0% of total variation.

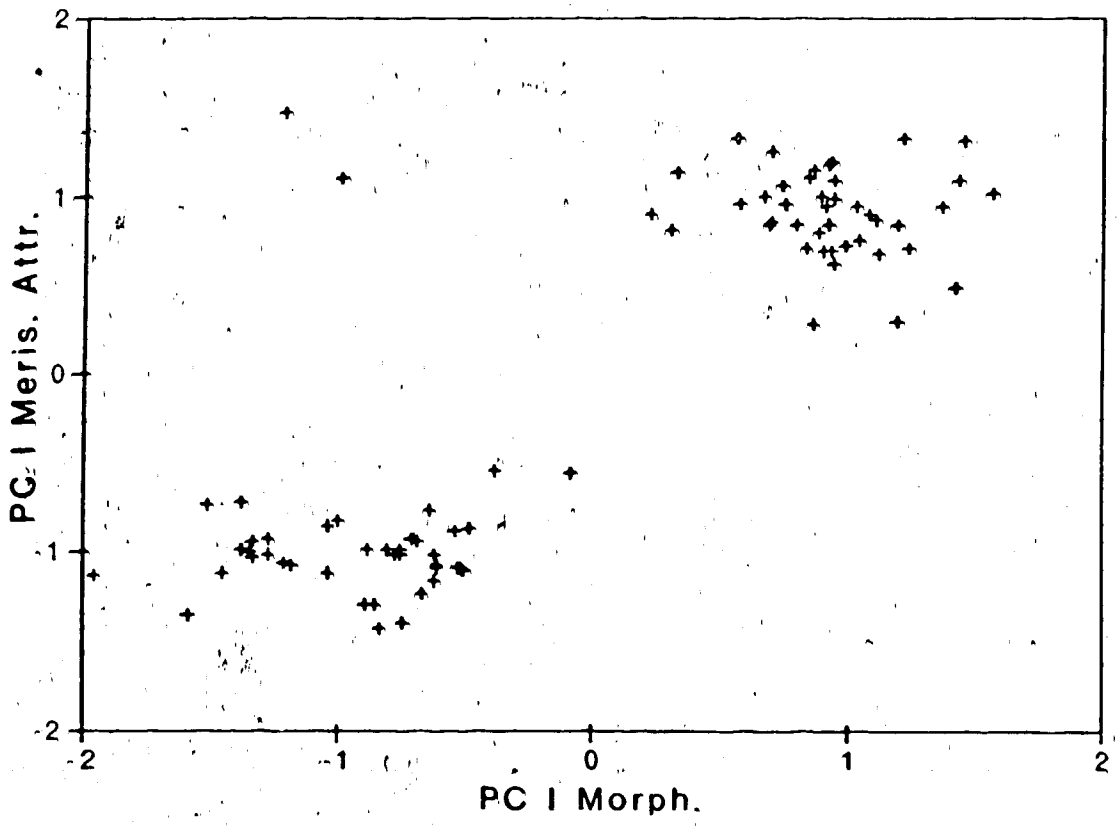


FIGURE 3.13. PCA : Morphometrics vs. Meristics and Attributes.
Plot of first principal component scores of morphometrics (x-axis) and meristics and attributes (y-axis) for Cameron Lake and Tay Lake specimens. *Phoxinus eos* from Cameron Lake - bottom cluster; *Phoxinus neogaeus* from Tay Lake - top cluster.

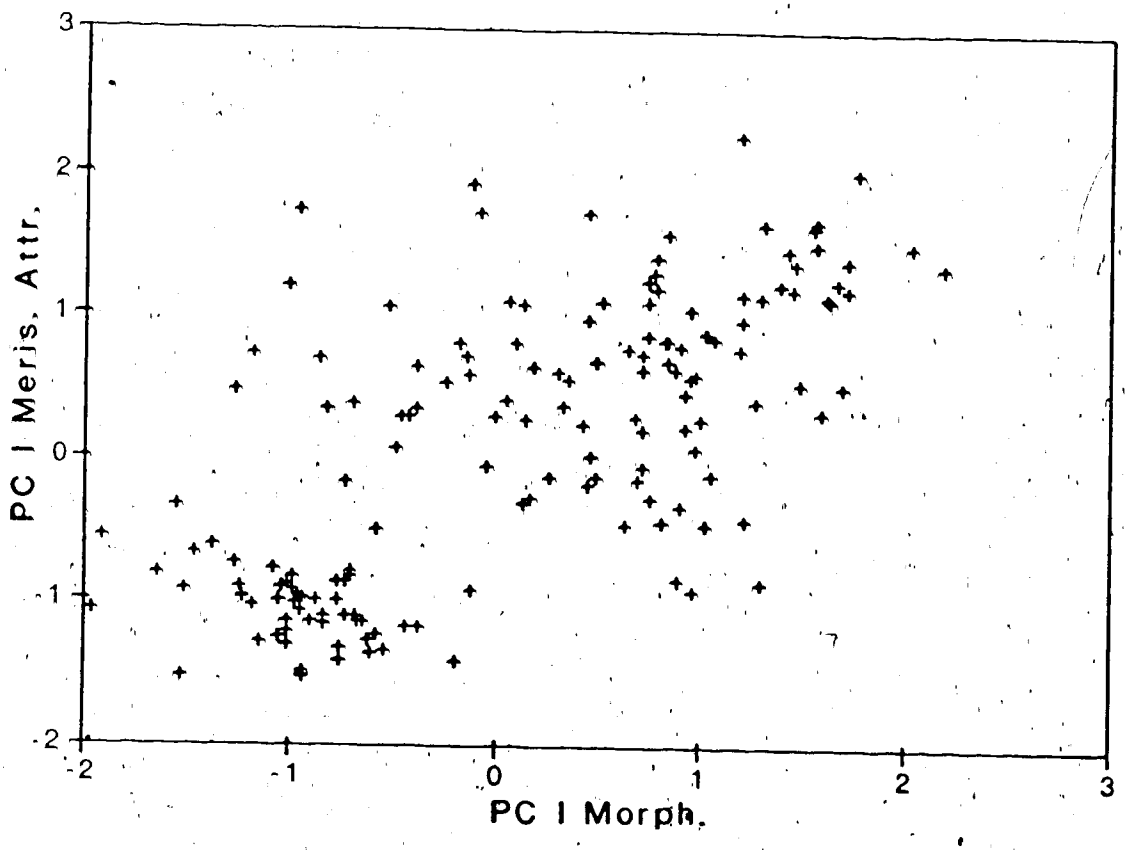


FIGURE 3.14. PCA : Morphometrics vs. Meristics and Attributes.
Plot of first principal component scores of morphometrics (x-axis) and meristics and attributes (y-axis) for Upper Pierre Grey Lake specimens. *Phoxinus eos*-like specimens towards bottom; *Phoxinus neogaeus*-like specimens towards top, with hybrids in between.

3.3.3 PCA - INTRA-GROUP VARIATION

It was necessary to determine if any unknown inter-population differences were confounding discrimination of the species. To test this, two PCAs were performed: one on the *P. eos* specimens from Cameron Lake and another on the *P. neogaeus* specimens from Tay Lake. The scatter plots of the first two components (Figs. 3.15 and 3.16) (Appendix Table 12) resulted in single species clusters without any distinct subgroups.

3.4 DISCUSSION

Identification of a natural hybrid is usually determined from evidence showing morphological and meristic intermediacy between two species. This interpretation is supported by field and experimental studies indicating that fish hybrids usually possess characteristics intermediate to parental forms (Hubbs, 1955; Weisel, 1955; Nelson, 1968; Smith, 1973).

Central to most modern studies of fish hybridization has been the desire to come to a conclusion on the reproductive success of hybrids from an analysis of morphological data.

The assumption of low F1 hybrid morphological variability has been proved false when the morphology of laboratory-reared F1 hybrids was compared with morphology of the parental species (Neff and Smith, 1979). Therefore, despite the large phenotypic variability of the UPG hybrids, it must be regarded as possible that these hybrids could be of F1 origin. It is not possible to determine the extent of

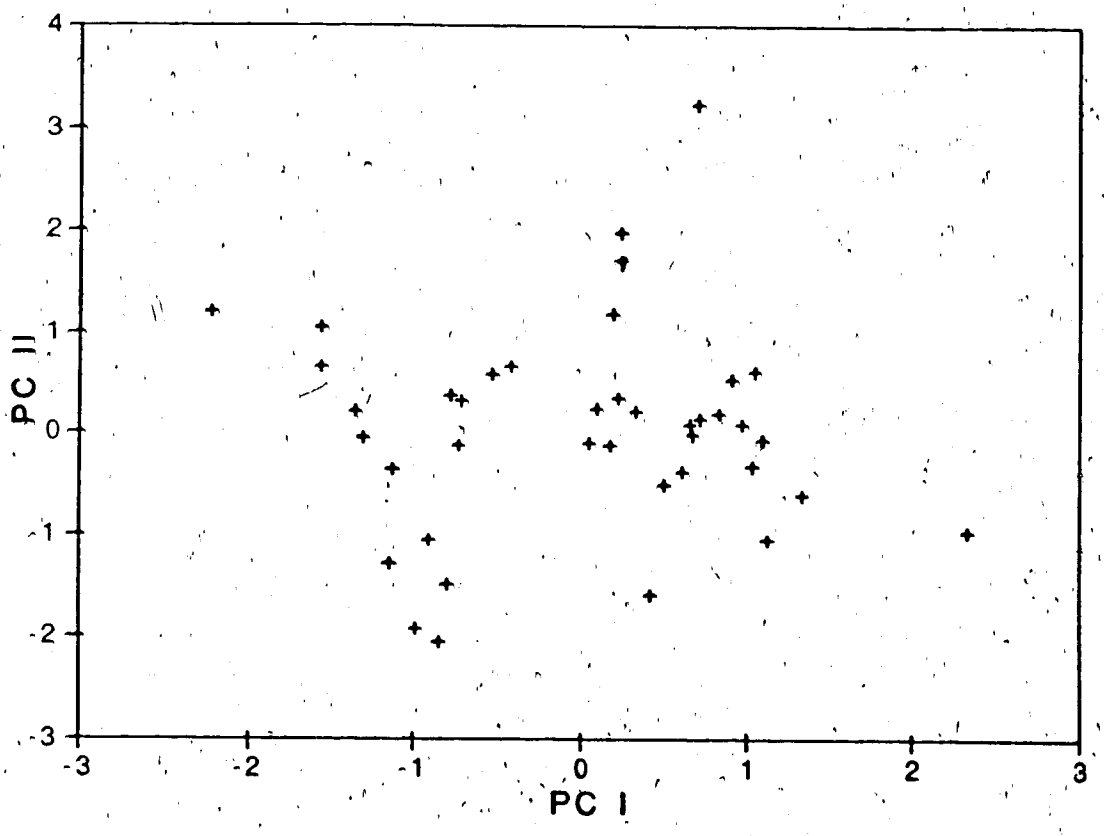


FIGURE 3.15. PCA of *Phoxinus eos* from Cameron Lake using untransformed data; MOEXTN included.
Plot of first and second principal component scores.
Component I = 59.03% of total variation; Component II = 6.9% of total variation.

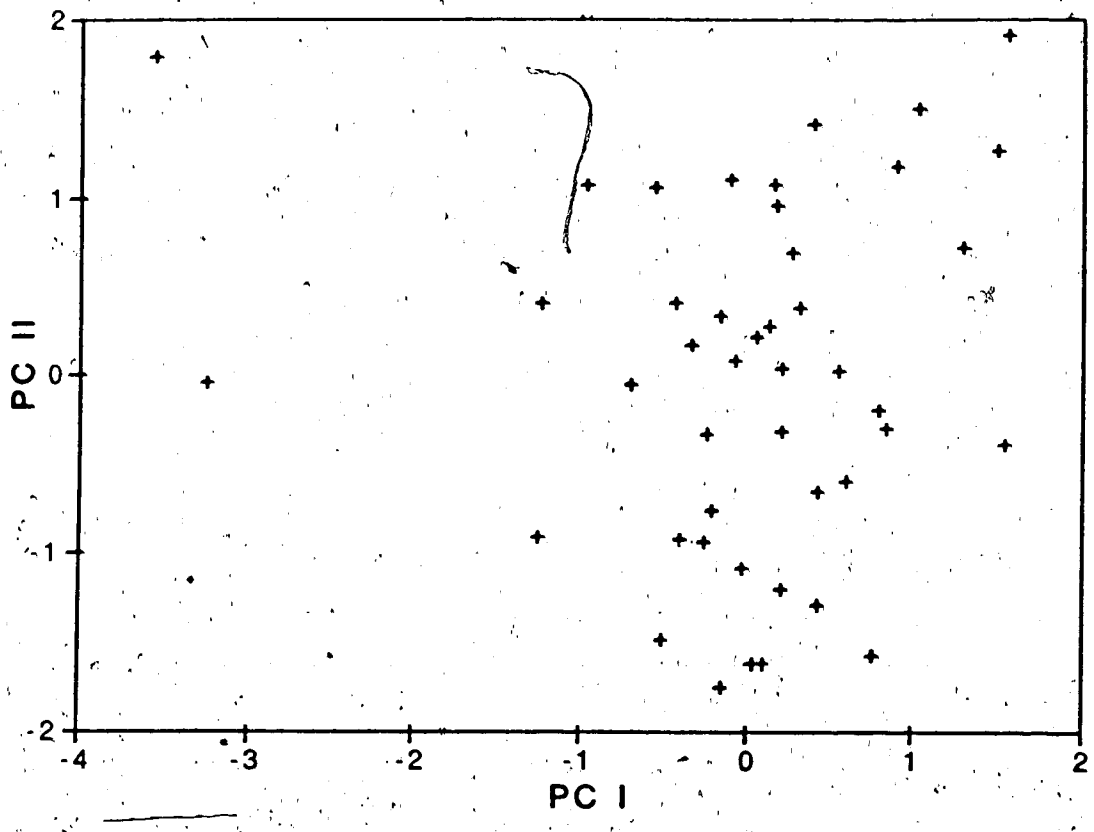


FIGURE 3.16. PCA of *Phoxinus neogaeus* from Tay Lake. Using untransformed data; MOEXTN included.
Plot of first and second principal component scores. Component I = 57.8% of total variation; Component II = 6.1% of total variation.

P. eos X *P. neogaeus* hybrid fertility or to positively identify backcross individuals from my study of multivariate analyses of the UPG specimens. Nonintermediate hybrid individuals falling between the intermediate hybrid mode and the parental modes of the CVA distributions of UPG specimens could represent F2 hybrids, variant F1 hybrids, or backcross individuals. Smith (1973) using PCA found hybrids occupying the area between strict intermediacy and one parental type. They were identified as backcross individuals. Without knowing the variance of the F1 hybrids, such a conclusion is disputable.

It may be possible to determine F1 hybrid variability from a morphological study without resorting to the study of artificial F1 hybrids. In a case where the hybrids bridged the gap to one species and not to the other, an interpretation of backcrossing could be presumed, without the need to show F1 variance (Butcher, 1980). Although the results of my study do not reveal such distinct backcross peaks or clusters, from both canonical variates and principal components analyses it is clear that the majority of the hybrid individuals are morphologically more similar to *P. neogaeus* than to *P. eos*. Discriminant distance (Mahalanobis D^2) from CVA of the untransformed complete data set shows that 77% of 91 hybrid individuals could be classified as *P. neogaeus*. New (1962) noted similar skewed similarity in hybrids from New York, Michigan, and South Dakota. Hybrids from Nebraska were all females with allozymic patterns

expected of F1 hybrids and most of them closely resembled *P. neogaeus* females (Joswiak, *et al.*, 1982). These could be explained by the fact that the interspecific crosses involve both sex combinations with the resulting hybrids more closely resembling the species of their maternal progenitor. Skewed morphological similarity of laboratory-reared F1 hybrids towards the species of their maternal progenitor has been reported in the deer mouse, *Peromyscus* (Brand and Ryckman, 1969). All-female mostly *Phoxinus neogaeus*-like hybrids from UPG support this hypothesis.

The continuous distribution of hybrids between *Phoxinus eos* and *P. neogaeus* indicates that it is not always possible to identify all 'pure' individuals of the UPG parental species. But if we compare UPG specimens with the allopatric populations from Cameron Lake and Tay Lake, it is possible to classify them.

A rather different hypothetical explanation is that the *P. eos* X *P. neogaeus* hybrids are a self-perpetuating hybrid "species" which reproduces by unusual meiotic mechanisms and are characterized by several features - all-female, occurring in the absence of at least one parent species, and outnumbering the other parent species. Dawley and Schultz (1984) found that in northern New Hampshire the hybrids are all females and occur in the presence of only *P. eos*. This explanation agrees with a well documented pattern in the poeciliid genera *Poeciliopsis* (Schultz, 1966 and 1969) and *Poecilia* (Hubbs and Hubbs, 1932). In Upper Pierre Grey Lake

both parental species are present along with the hybrids, and there is no significant difference in variance between the two UPG species and their respective allopatric groups. Of course, the number of *P. neogaeus* individuals is less than *P. eos* and the hybrids. From these facts, we may say that the UPG hybrids are not an example of ideal hybrid "species". In order to test the two hypotheses, 'maternal progenitor' and 'self-perpetuating species', specimens should be collected over a long period of time. An analysis of morphological data could then give us a clearer view of evolutionary change and which mechanism is more responsible for the production of hybrids.

Detailed studies of hybridization and introgression have been made for a few North American fresh water fishes (Hubbs and Miller, 1943; Hagen, 1967; Nelson, 1968; Greenfield and Greenfield, 1972; Butcher, 1979). Evidence for introgression in fishes is sparse, probably partially due to cryptic effects of backcrossing. Greenfield and Greenfield (1972) reported that crosses between introgressed minnows produced progeny that were indistinguishable from parental populations. There is no clear evidence of introgressive hybridization in either of the parental species in Upper Pierre Grey Lake. Further information, especially from breeding experiments and allozyme analysis, are required to test this evidence. New (1962) suggested that there is a possibility of introgression between the two species with a shift toward *P. eos*. In UPG, it appears that, even if there

is any introgression, shifting is more likely toward *P. neogaeus* than toward *P. eos*.

This study has assessed the relative importance of the morphological characters of *P. eos* and *P. neogaeus*. Future researchers may find the canonical coefficients and constants to be valuable in classifying putative hybrid individuals.

4. PREMATING ISOLATING MECHANISMS

4.1 INTRODUCTION

The break-down of the reproductive isolating mechanisms can result in hybridization. In fishes at least, premating isolating mechanisms seem to become established phylogenetically before postmating isolating mechanisms. Premating isolating mechanisms prevent the waste of gametes and are thus more efficient than postmating isolating mechanisms. Premating isolation involves the reduction of contact between the species and the reduction of interspecific mating by species-specific behaviors. It seems that when hybridization between fish species occurs, it is often the result of the disruption of these premating isolating mechanisms for which selection has occurred. Littlejohn (1969) presented arguments for such direct selection of premating isolating mechanisms.

The main objective in this part of the study is to examine some of the premating isolating mechanisms. The extent of differences in spawning time and spawning habitat between *P. eos* and *P. neogaeus* are determined. Certain life history characteristics of wild-caught hybrids are compared to those of the parental populations in the area of sympatry to assess their relative success of survival under natural conditions.

Reproductive isolation between sympatric *P. eos* and *P. neogaeus* populations has not been previously studied. The

reproductive behaviors of *P. eos* have been studied by Cooper (1935) and Hubbs and Cooper (1936) in Michigan. A more comprehensive study for *P. neogaeus* was conducted in Minnesota (Stasiak, 1972 and 1978). New (1962) stated that breeding males of both species were collected in New York in August, 1955 and June, 1958.

This section of the study investigates the effectiveness of premating isolating mechanisms (excluding mate preference tests) and some life history characteristics in the two species and their hybrids through ecological field studies. Comprehensive ecological data for the two species from Upper Pierre Grey Lake (UPG) are presented for the first time.

4.2 METHODS

4.2.1 TEMPORAL ISOLATION

The time of spawning for each of the parental species was followed using three different methods. The first method from Nelson (1968) involved a qualitative judgement on the degree of female gonad development. The following qualitative criteria were used to describe female gonad maturity:

ripe - eggs near maximum size; creamy yellow colored; extruded under firm manual pressure.

fully ripe - eggs at maximum size; golden yellow colored; extruded spontaneously while handling.

spent - few or no mature eggs extruded from body cavity; abdomen visibly sunken.

The peak time in which fully ripe female were present in UPG was compared between the two species and the hybrids.

The second method was quantitative. The spawning period for each species and the hybrids was followed by determining the percentage contribution of female gonads to body weight. Total wet body weight and gonad weight (both sides) were measured in the preserved specimens to the nearest 0.01 gm. These gonadosomatic indices (% gonad weight into total body weight) of both species and hybrids were pooled for sampling dates and plotted over the spawning period.

The third method was also quantitative, involving measuring the mean diameter of 10 ova per live female using a microscope ocular. The grand mean of ova diameters from all sample females was graphed over a period of time.

4.2.2 HABITAT ISOLATION

Selection of different areas for spawning often acts as a mechanism for reproductive isolation (Hubbs, 1961). The concurrent abundance of the two species and their putative hybrids at selected sampling sites was monitored using minnow traps throughout the spawning period in 1984. Seining could not be done due to the very soft nature of the bottom of the lake.

Elizabeth Stinson (pers. comm.), while looking at the populations of brook sticklebacks in the Pierre Grey Lakes, found that in UPG approximately 98% of the *Phoxinus* population were found from the shore up to two m depth during

June and July.

Five sampling sites (# 1 to 5) were selected (Fig. 4.1) in 1984. Eastern and northern sides of the lake could not be sampled regularly due to poor accessibility. Six baited minnow traps were used at each sampling site. Traps were set about two m apart from each other at depths of 0.5-1.0 m and 2.0-2.5 m alternately.

4.2.3 ETHOLOGICAL ISOLATION

Among the several mechanisms responsible for the prevention of interbreeding between species, ethological (behavioral) barriers to random mating often constitute the most important class of isolating mechanisms (Mayr, 1970).

Visual stimuli in terms of peculiarities in color, pattern and form are regarded as very important for discrimination among different species. Descriptions of breeding colors were made for each sex of *P. eos* and *P. neogaeus* from freshly caught fish.

4.2.4 LIFE HISTORY CHARACTERISTICS

Life history characteristics of the putative hybrid females were compared to those of the two parental species and consisted of length, weight and fecundity data.

a. LENGTH-WEIGHT RELATIONS

Length-weight relationships for 50 *P. eos*, 16 *P. neogaeus* and 30 hybrids were determined according to Bagenal and Tesch (1978). The relationships were described by a

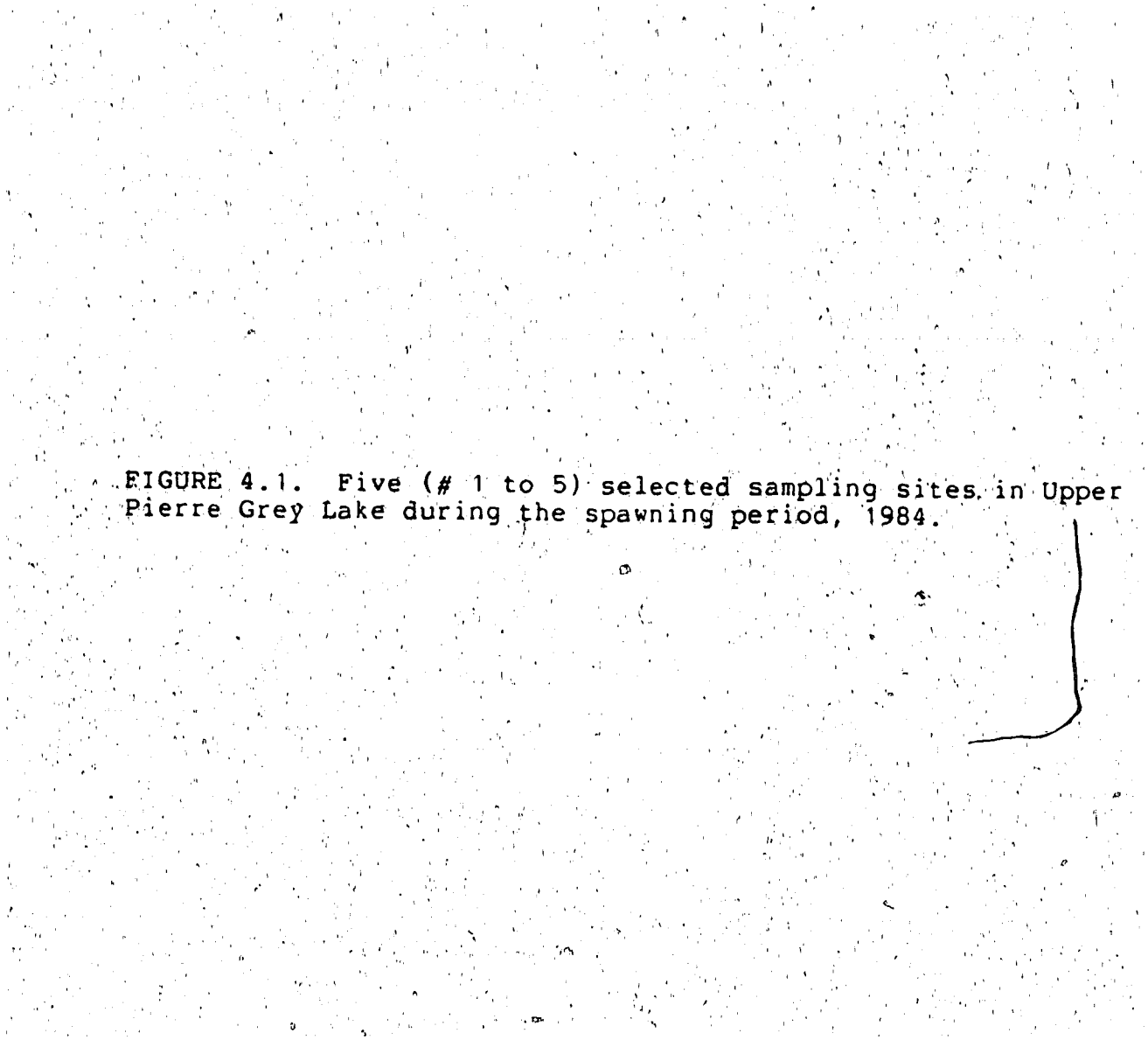
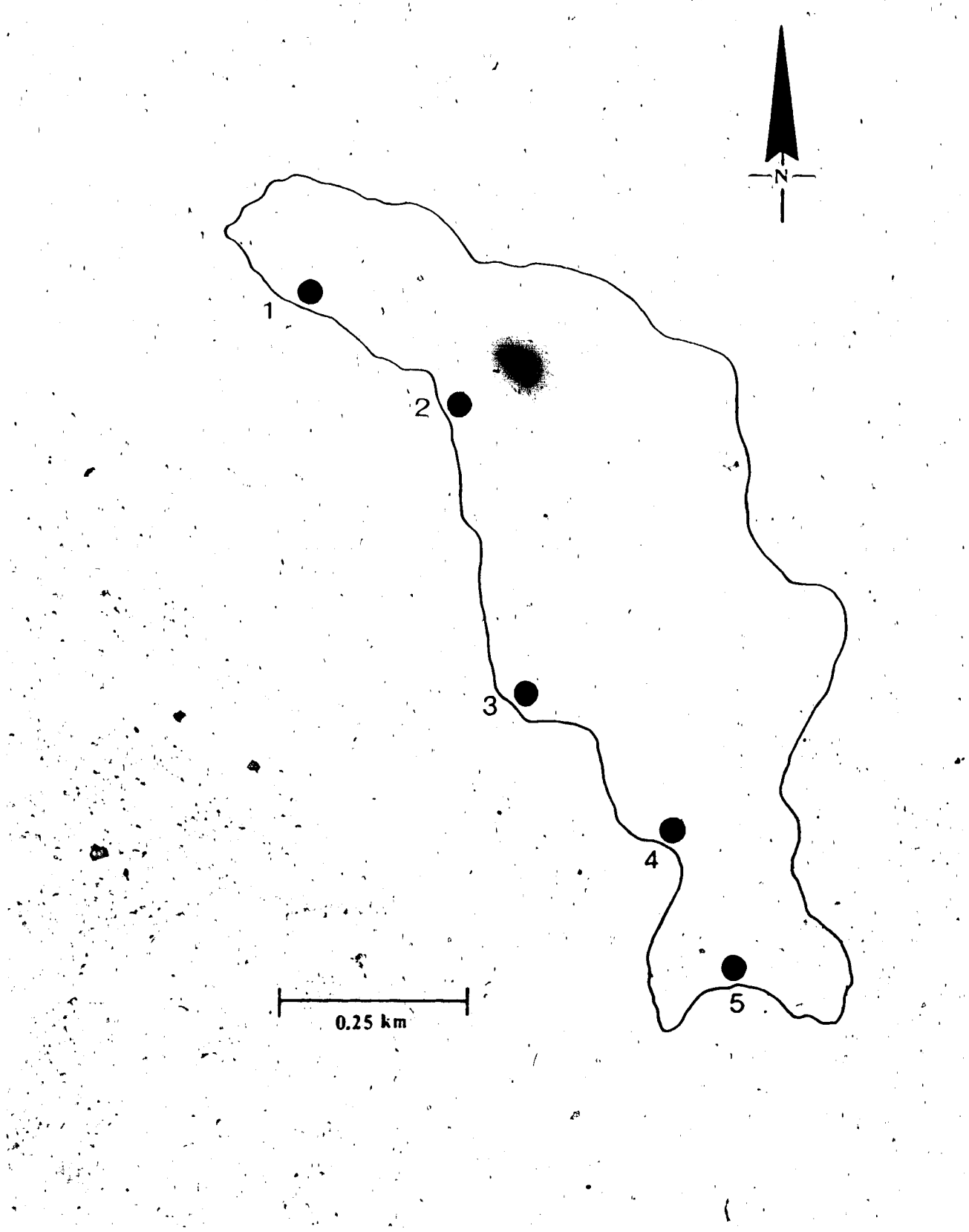


FIGURE 4.1. Five (# 1 to 5) selected sampling sites in Upper Pierre Grey Lake during the spawning period, 1984.


N
1
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0.25 km

regression of logarithm of length on logarithm of weight. The BMDP6D computer program (Dixon, 1983) was used for the regression analysis. An analysis of covariance was performed on these data using the BMDP1V computer program.

b. FECUNDITY

Several definitions of fish fecundity have been used by different researchers; there have likewise been many ways to determine it. For the purposes of this study, fecundity was defined as the number of ripening eggs found in the female. Various techniques have been used by various workers in counting fish eggs. These include direct counts, automatic egg counters, volumetric and gravimetric estimation (see Bagenal and Braum, 1978, for a summary of these).

The gravimetric subsampling method was used to determine the female fecundity of the same subsamples of the three groups. All ova from one female were divided into two equal parts by weight. Potential fecundity was measured by actual counts of all ova present in one part under a dissecting microscope. The value was multiplied by two to give the total number of ova. No attempt was made to distinguish immature from mature ova, although both kinds were clearly present in many specimens. The fecundity relationship was described by a regression of logarithm of ova number on both logarithm of standard length and logarithm of body weight using the BMDP6D program. Analysis of covariance was performed on these data using the BMDP1V program.

4.3 RESULTS

4.3.1 TEMPORAL ISOLATION

Spawning at a different time of the year constitutes an important factor for interspecific breeding in sympatric fish species. Many congeneric species are isolated only or in part by differences in time of spawning of the two species in sympatry.

What are the spawning times of the two species and the hybrids in UPG? To what extent is temporal isolation operative?

Data on the degree of maturity of gonads of these studies from 1984 and 1985 show that temperature is an important factor inducing spawning which is true for most temperate, freshwater fishes. Ahsan (1966), in discussing the relationship of environmental factors to breeding in *Coueslus plumbeus*, considered temperature to be the major factor controlling spermatogenesis.

The spawning seasons of *P. eos* and *P. neogaeus* have been studied by many workers. In Michigan, spawning activities of *P. eos* commenced in late May and extended to August as reported by Cooper (1935) and Hubbs and Cooper (1936). Breeding males of both species were collected in New York in August, 1955 and June, 1958 (New, 1962). McPhail and Lindsey (1970) reported females of *P. eos* containing large eggs caught on 24 August in "Pierre Grey Lake". Stasiak (1972) made extensive studies on the spawning season of *P. neogaeus*

in Minnesota where the spawning fish were observed in late April when the water temperature was no warmer than 11°C and on May 6-8 in waters from 13 to 18°C. Becker (1983) stated that in Wisconsin, spawning of *P. neogaeus* occurs from April to June and ripe males and females have been taken in mid-June. He also mentioned that mature females of *P. eos* were collected on June 18, 1960 from Henlock Creek (Wood County), and the spawning season extends from the later part of May into August.

A meaningful measure of temporal isolation is the amount of overlap in the time during which females are fully ripe in the spawning area (Nelson, 1968). The results of the first of the three methods, involving a qualitative judgement as to the state of female gonad maturity are presented in Figs. 4.2, 4.3 and in Tables 4.1 and 4.2.

In 1984 and 1985, females of both species and the hybrids became fully ripe at about same time. *P. eos* and hybrid females outnumbered *P. neogaeus* females in all three gonad states. Male *P. neogaeus* were very few in number and only two fully ripe males were caught in 1985. The first male *P. eos* with freely flowing milt was captured on June 4 in 1984 and on June 2 in 1985 and the last such male was captured on August 1 in 1984 and on July 29 in 1985 (Appendix Table 13, 14).

The results of the second method, involving changes in the actual gonad weight of the females, and the third method, involving ova size, are shown for 1985 in Figures 4.4 and 4.5

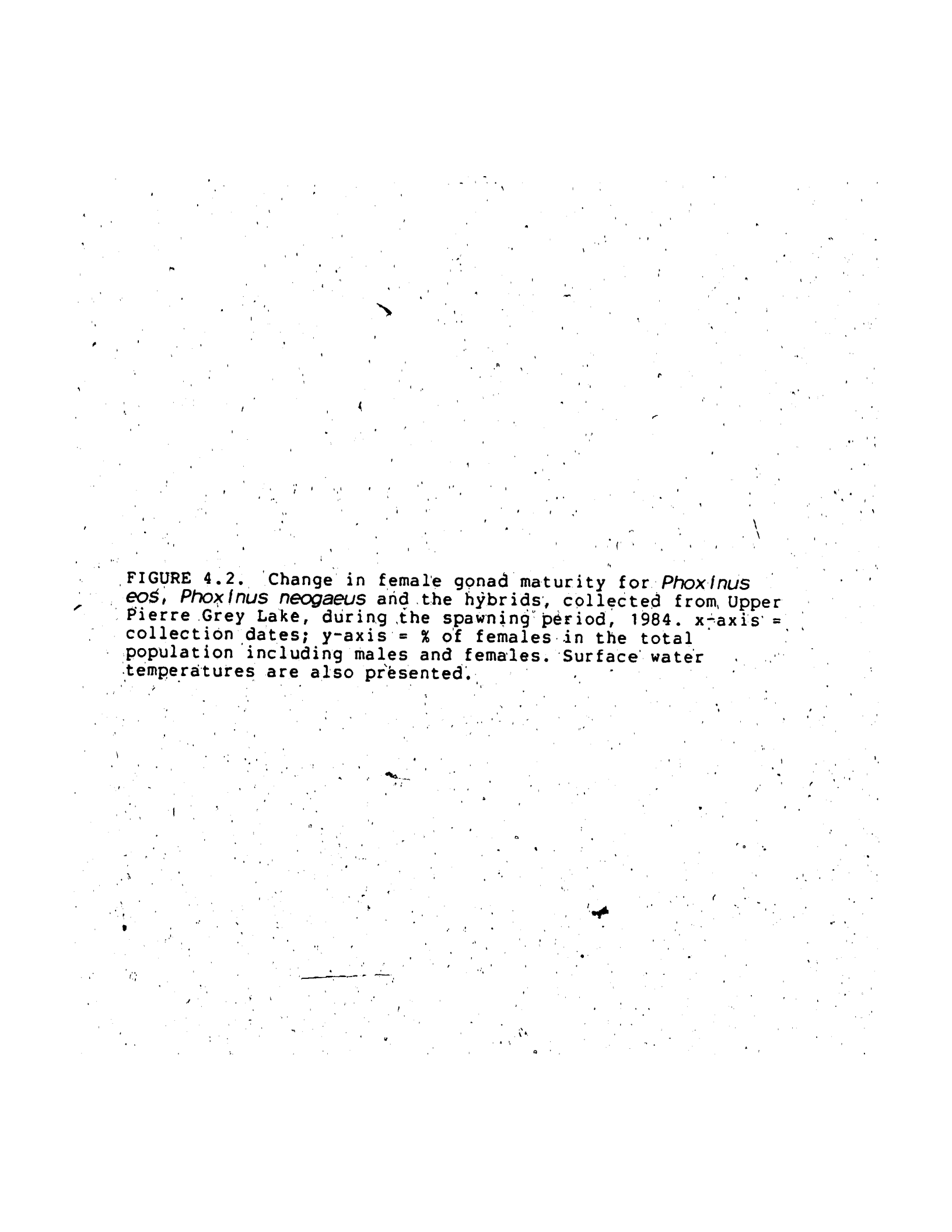
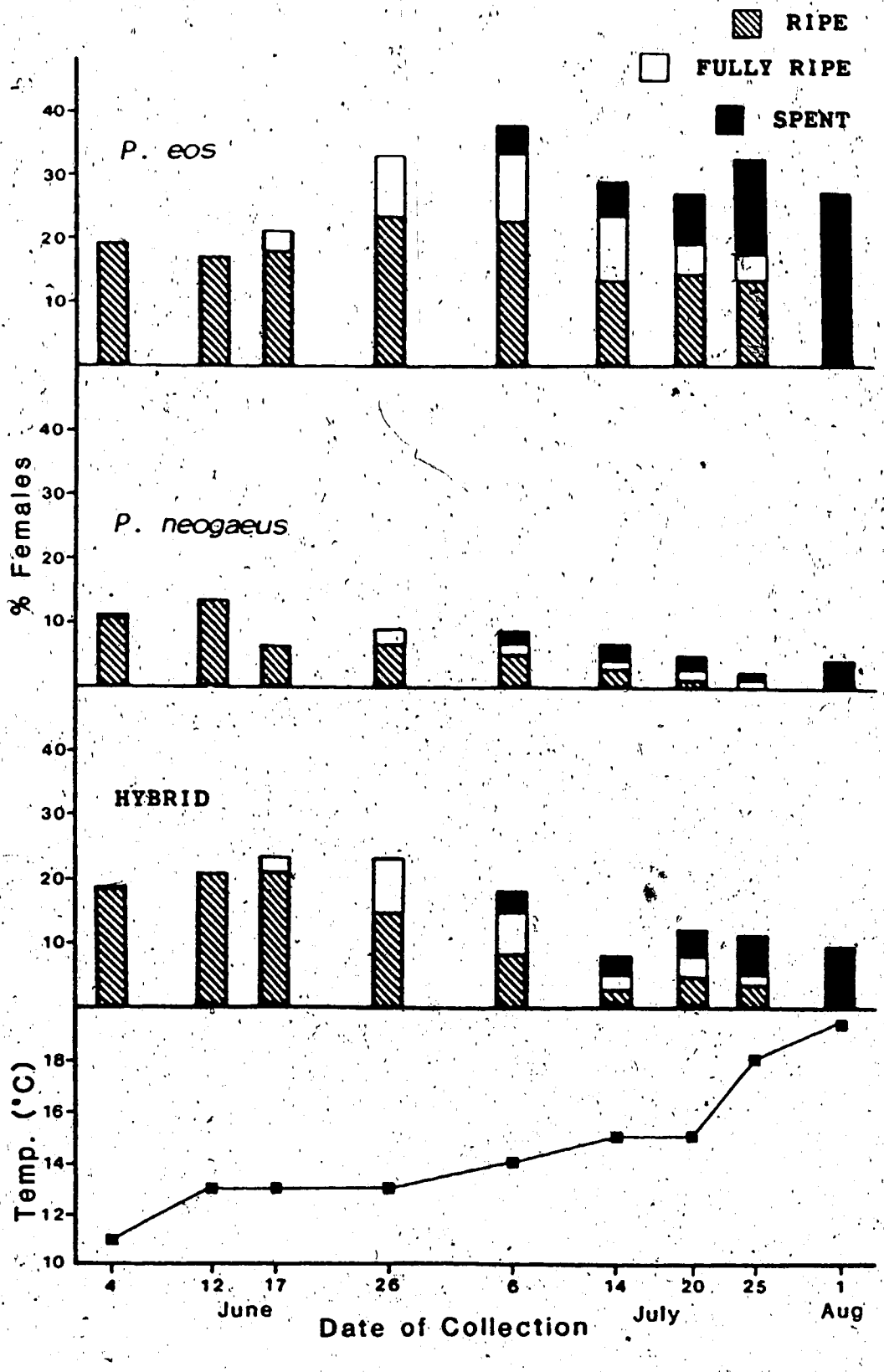


FIGURE 4.2. Change in female gonad maturity for *Phoxinus eos*, *Phoxinus neogaeus* and the hybrids, collected from Upper Pierre Grey Lake, during the spawning period, 1984. x-axis = collection dates; y-axis = % of females in the total population including males and females. Surface water temperatures are also presented.


RIPE
FULLY RIPE
SPENT
P. eos
P. neogaeus
HYBRID
% Females
Temp. (°C)
Date of Collection
June
July
Aug
4
12
17
26
6
14
20
25
1

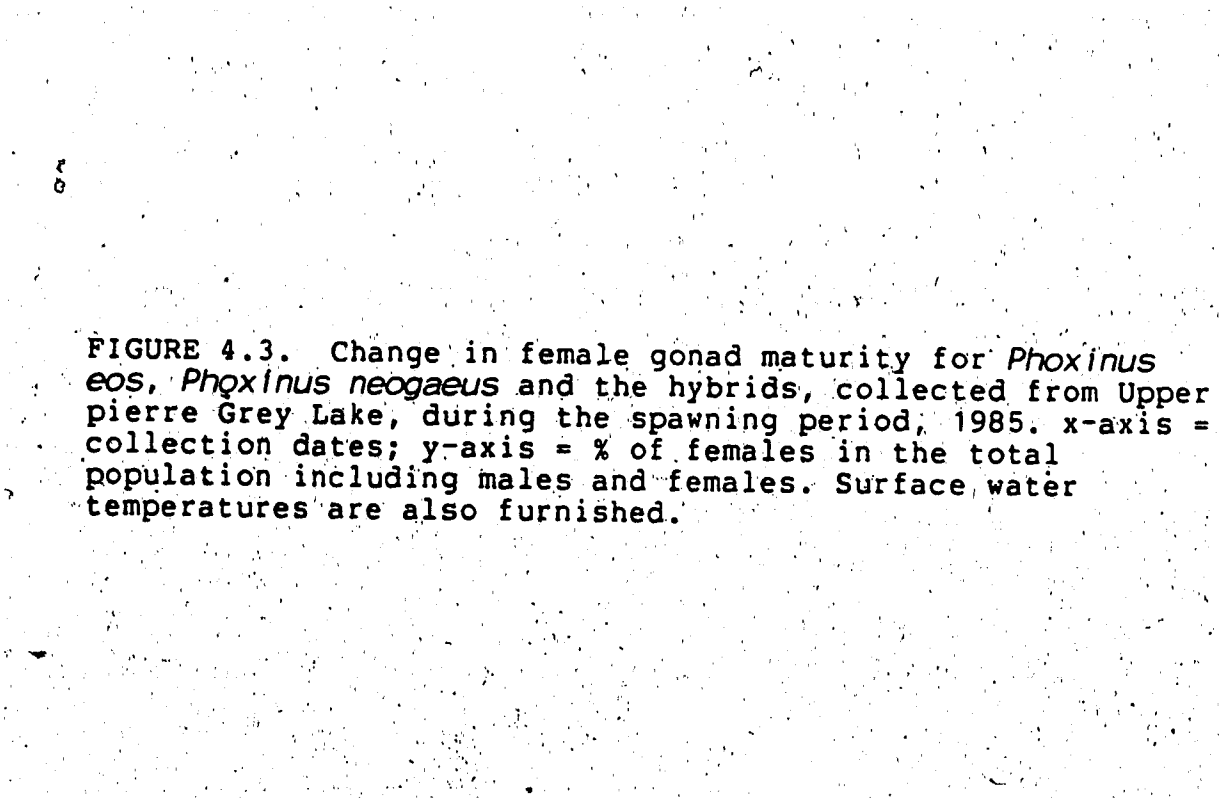


FIGURE 4.3. Change in female gonad maturity for *Phoxinus eos*, *Phoxinus neogaeus* and the hybrids, collected from Upper pierre Grey Lake, during the spawning period, 1985. x-axis = collection dates; y-axis = % of females in the total population including males and females. Surface water temperatures are also furnished.

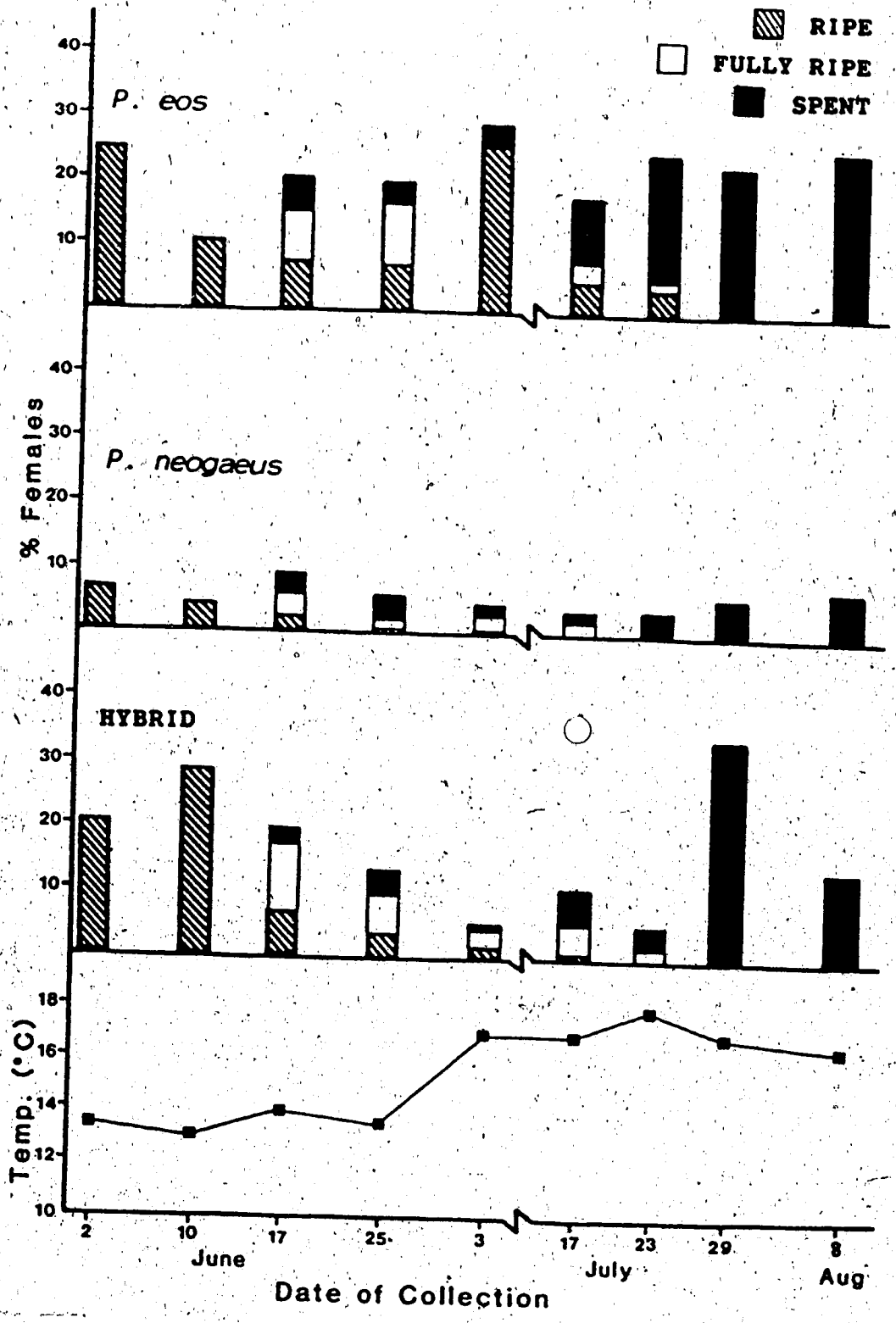

RIPE
FULLY RIPE
SPENT
P. eos
P. neogaeus
HYBRID
% Females
Temp. (°C)
June
July
Aug
Date of Collection

TABLE 4.1. Summary of changes in female gonad maturity for *Phoxinus eos*, *Phoxinus neogaeus* and hybrids (% in total population including males and females) and surface water temperatures during spawning period in 1984, Upper Pierre Grey Lake.

Date	*Phoxinus eos*			*Phoxinus neogaeus*			Hybrid			
	Ripe	Fully Ripe	Spent	Ripe	Fully Ripe	Spent	Ripe	Fully Ripe	Spent	Temp. C
June 4	13.8	0	0	11.7	0	0	19.1	0	0	11.0
June 12	17.6	0	0	13.9	0	0	20.8	0	0	13.0
June 17	18.2	2.5	0	4.8	0	0	21.6	1.9	0	13.0
June 26	24.1	9.1	0	6.2	3.0	0	14.7	8.3	0	13.0
July 6	22.9	10.7	4.4	4.7	1.5	2.4	8.2	6.4	3.5	14.0
July 14	13.9	9.9	5.5	3.6	0.5	2.3	3.1	1.8	2.9	15.0
July 20	14.4	4.9	8.3	1.8	0.7	2.0	4.9	3.1	4.3	15.0
July 25	14.0	3.7	15.2	0	0.2	1.6	4.0	1.4	6.3	18.0
Aug 1	0	0	27.5	0	0	4.0	0	0	9.6	19.5

TABLE 4.2. Summary of changes in female gonad maturity for *Phoxinus eos*, *Phoxinus neogaeus* and hybrids (% in total population including males and females) and surface water temperatures during spawning period in 1985, Upper Pierre Grey Lake.

	Phoxinus eos			*Phoxinus neogaeus*			Hybrid			
Date	Ripe	Fully Ripe	Spent	Ripe	Fully Ripe	Spent	Ripe	Fully Ripe	Spent	Temp. C
June 2	25.4	0	0	6.9	0	0	21.4	0	0	13.5
June 10	10.6	0	0	4.6	2.5	0.8	29.2	1.7	1.7	13.0
June 17	7.6	8.2	4.4	3.3	2.7	3.3	7.1	10.4	2.7	14.0
June 25	7.5	9.0	3.5	0.5	0.5	5.0	4.0	5.5	4.0	13.5
July 3	20.4	5.3	3.3	0.6	1.9	1.9	2.0	2.0	1.3	17.0
July 17	5.6	2.3	10.2	0	2.0	1.4	0.9	4.2	5.1	17.0
July 23	4.4	1.2	19.7	0	0	4.0	0	0.8	4.0	18.0
July 29	0	0	23.0	0	0	5.9	0	0	34.2	17.5
Aug 8	0	0	25.9	0	0	7.4	0	0	13.6	17.0

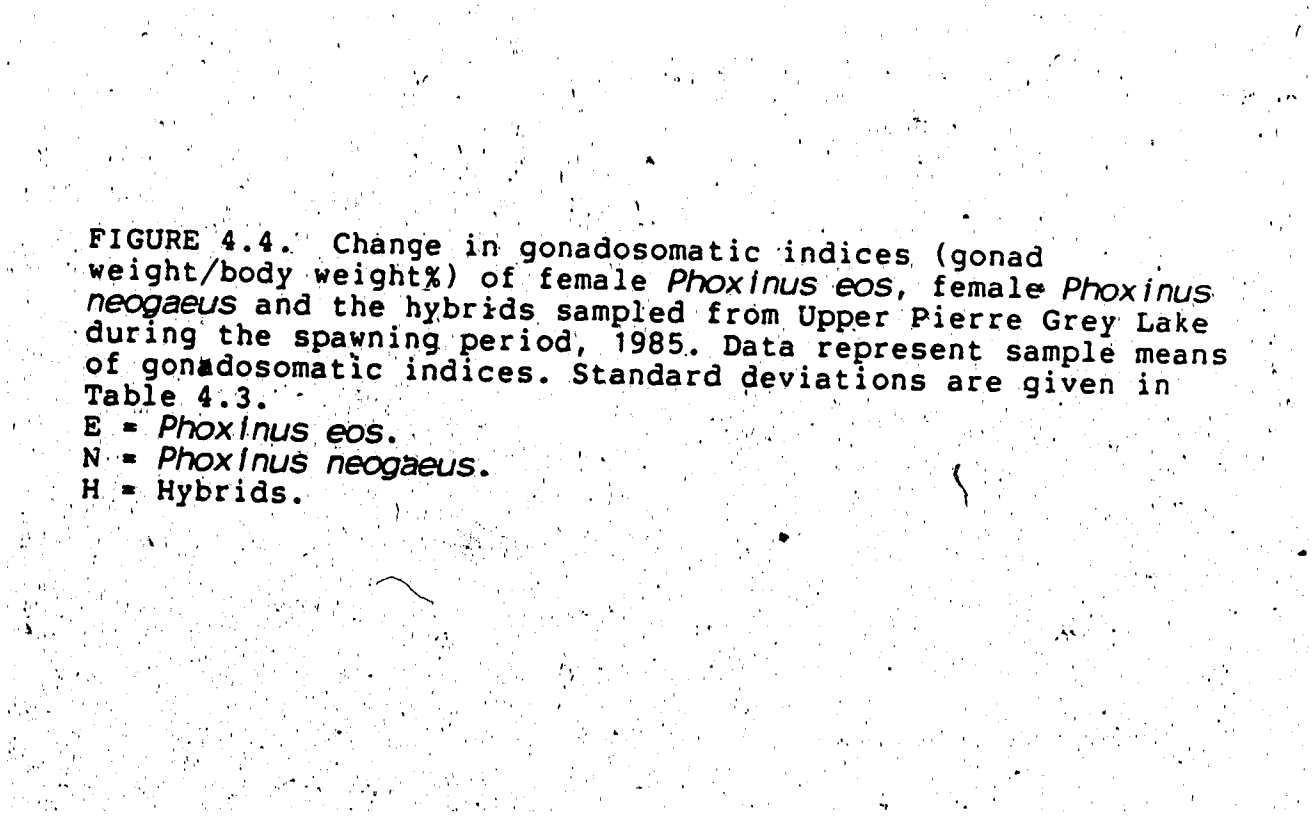


FIGURE 4.4. Change in gonadosomatic indices (gonad weight/body weight%) of female *Phoxinus eos*, female *Phoxinus neogaeus* and the hybrids sampled from Upper Pierre Grey Lake during the spawning period, 1985. Data represent sample means of gonadosomatic indices. Standard deviations are given in Table 4.3.
E = *Phoxinus eos*.
N = *Phoxinus neogaeus*.
H = Hybrids.

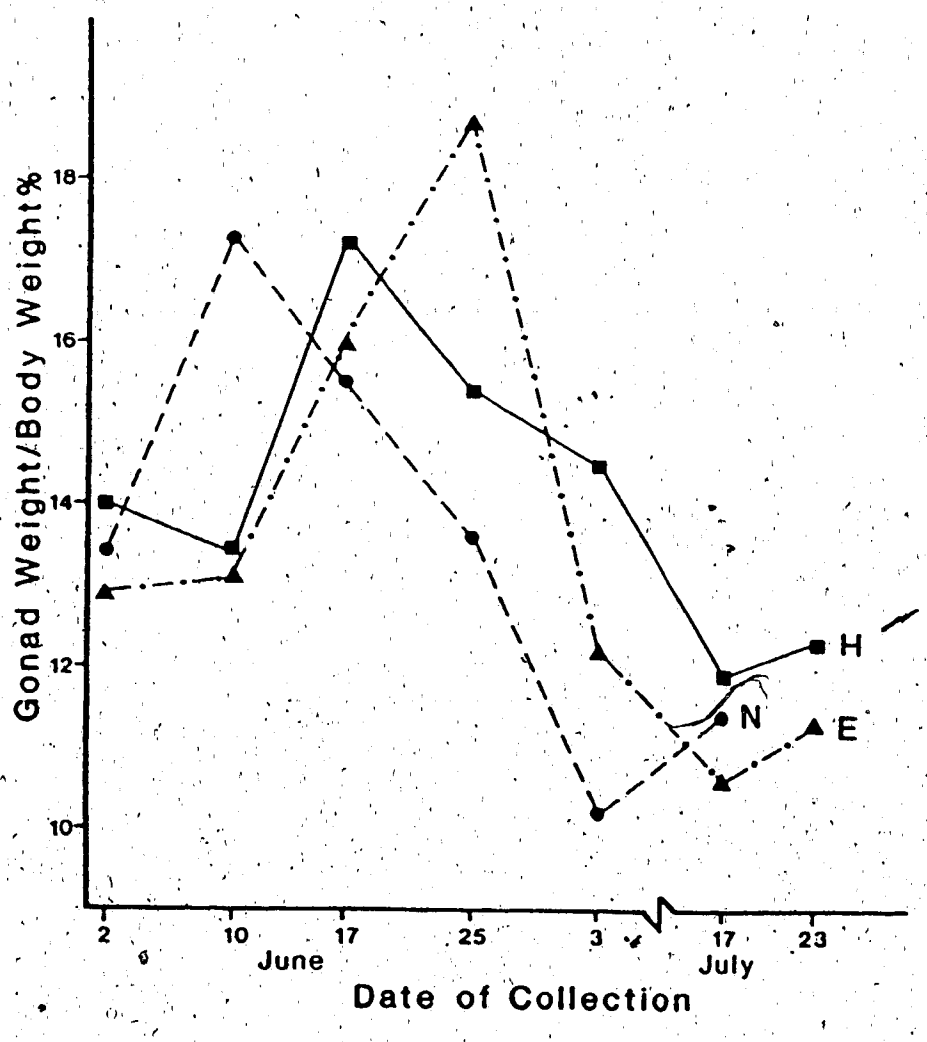
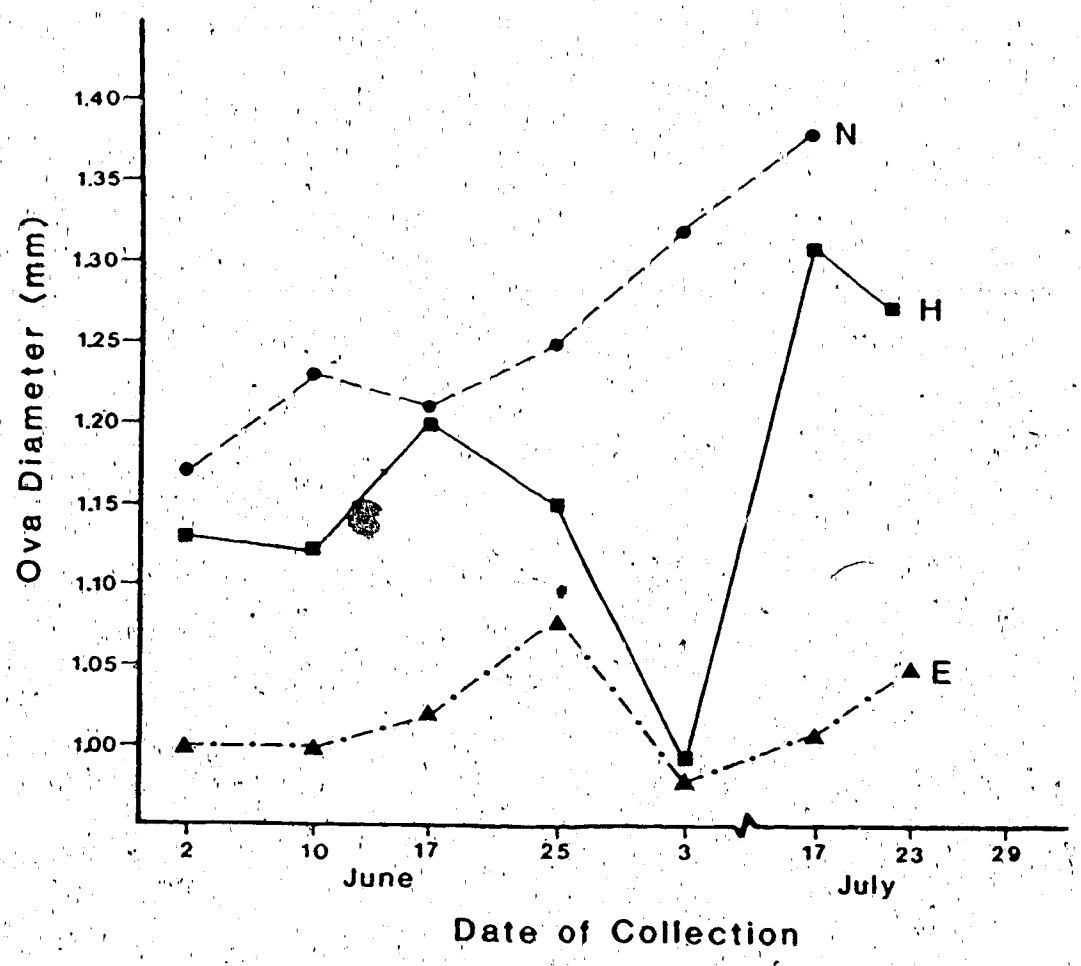

Gonad Weight/Body Weight%
18
16
14
12
10
H
N
E
2
10
17
25
3
17
23
June
July
Date of Collection

FIGURE 4.5. Trends in ova diameter during 1985 spawning period for *P. eos*, *P. neogaeus* and the hybrids from Upper Pierre Grey Lake. Data represent sample means of ova diameter. Standard deviations are given in Table 4.4.
E = *Phoxinus eos*.
N = *Phoxinus neogaeus*.
H = Hybrids.


Ova Diameter (mm)
1.40
1.35
1.30
1.25
1.20
1.15
1.10
1.05
1.00
N
H
E
2
10
17
25
3
17
23
29
June
July
Date of Collection

and Tables 4.3 and 4.4. There is a partial separation in the periods of maximum gonad weight and maximum ova size. It indicates that major spawning occurs earlier in *P. neogaeus* and the hybrids than in *P. eos*. The increase in the mean ova size in the case of *P. neogaeus* after June 17 and in the case of the hybrids after July 3 is due to the presence of only fully ripe females in the collection, although total gonad weights are less during this period.

4.3.2 HABITAT ISOLATION

There is not much known of the type of spawning habitat selected by the two species and the hybrids. *P. eos* is known to spawn on masses of filamentous algae (Cooper, 1935; Hubbs and Cooper, 1936). In *P. neogaeus*, spawning occurs in the areas covered by fallen logs or groups of branches at usually 0.5-0.9 m depth (Stasiak, 1978).

Specimens were collected from the end of May until the end of spawning period in order to observe areas occupied by the spawning individuals. The aim of this part of the study was to determine the degree of habitat segregation between the two species in Upper Pierre Grey Lake.

Catch data (Table 4.5) from five selected sampling sites do not show any significant difference in area of occurrence of the two parental species and the hybrids. Data from June 4 to August 1, 1984 are presented. During this time both species and the hybrids were common in all five sites, although number of *P. neogaeus* was much less than that of *P.*

TABLE 4.3. Data summary of gonadosomatic indices for female *P. eos*, female *P. neogaeus* and the hybrids, Upper Pierre Grey Lake, 1985.

Date	n	$\bar{x}$	SD
P. eos			
June 2	44	12.9	4.9
June 10	25	13.1	5.2
June 17	29	16.0	3.7
June 25	33	18.7	4.6
July 3	39	12.2	3.1
July 17	17	10.6	2.9
July 23	14	11.3	2.5
P. neogaeus			
June 2	12	13.4	1.8
June 10	15	17.3	4.3
June 17	11	15.5	3.6
June 25	2	13.6	-
July 3	4	10.2	-
July 17	4	11.4	-
Hybrids			
June 2	37	14.0	3.1
June 10	35	13.4	4.5
June 17	32	17.3	5.9
June 25	19	15.4	3.1
July 3	6	14.5	5.8
July 17	11	11.9	3.4
July 23	2	12.3	-

TABLE 4.4. Data summary of ova diameter for *P. eos*, *P. neogaeus* and the hybrids from Upper Pierre Grey Lake, 1985.

Date	n	$\bar{X}$ (mm)	SD
P. eos			
June 2	44	1.0	0.16
June 10	25	1.0	0.15
June 17	29	1.02	0.14
June 25	33	1.08	0.08
July 3	39	0.98	0.09
July 17	17	1.01	0.17
July 23	14	1.05	0.12
P. neogaeus			
June 2	12	1.17	0.16
June 10	15	1.23	0.14
June 17	11	1.21	0.13
June 25	2	1.25	-
July 3	4	1.32	-
July 17	4	1.38	-
Hybrids			
June 2	37	1.13	0.13
June 10	35	1.12	0.16
June 17	32	1.2	0.16
June 25	19	1.15	0.17
July 3	6	0.99	0.11
July 17	11	1.31	0.14
July 23	2	1.27	-

TABLE 4.5. Summary of catch data for *Phoxinus eos* (E), *Phoxinus neogaeus* (N) and the hybrids (H) from five selected sampling sites, Upper Pierre Grey Lake, during spawning period of 1984.

Sampling Date	Sampling Sites				
	Site # 1	Site # 2	Site # 3	Site # 4	Site # 5
June 4	E-7, N-3, H-2	E-8, N-2, H-5	E-8, N-5, H-3	E-14, N-2, H-11	E-12, N-6, H-6
June 12	E-27, N-16, H-11	E-29, N-13, H-19	E-31, N-24, H-28	E-42, N-19, H-39	E-53, N-8, H-21
June 17	E-72, N-21, H-46	E-67, N-17, H-28	E-51, N-12, H-31	E-46, N-18, H-20	E-66, N-16, H-49
June 26	E-42, N-9, H-8	E-61, N-12, H-17	E-47, N-16, H-42	E-79, N-18, H-33	E-75, N-10, H-49
July 6	E-50, N-3, H-19	E-49, N-9, H-27	E-67, N-7, H-33	E-73, N-15, H-17	E-60, N-8, H-4
July 14	E-68, N-5, H-13	E-61, N-11, H-9	E-32, N-9, H-6	E-29, N-3, H-17	E-97, N-8, H-14
July 20	E-47, N-9, H-23	E-53, N-0, H-21	E-43, N-11, H-11	E-79, N-13, H-15	E-97, N-4, H-19
July 25	E-45, N-6, H-9	E-72, N-12, H-26	E-70, N-0, H-15	E-81, N-6, H-12	E-60, N-0, H-3
Aug 1	E-59, N-0, H-7	E-63, N-0, H-2	E-37, N-0, H-1	E-62, N-9, H-15	E-72, N-8, H-18

eos and the hybrids.

Large schools were seen swimming near the surface. Fish of all sizes, including large females and males in bright breeding colors (mostly *P. eos*), were present. A dip net was used to collect individuals from a single school and results showed that each school contained members of both the parental species and the hybrids. A few young *Semotilus margarita* were also found occasionally. Adult *S. margarita* were never seen within a *Phoxinus* school.

4.3.3 ETHOLOGICAL ISOLATION

The spawning behavior of *P. eos* has been studied in Michigan by Hubbs and Cooper(1936):

"...Spawning occurs in pairs or in a group of one female and several males. The breeding males can be easily recognized by their more brilliant colors, the breeding females by the swollen abdomen, due to presence of large eggs. The great activity of female, when ready to spawn, immediately attracts the ripe males, which then persue her, in what appears to be a type of spawning courtship. The female followed closely by 1 to as many as 8 males, darts through the water for several feet as if attempting to escape. The first male to be attracted to the female, sometimes the only one, takes up a position a few inches behind and just below the female; other males joining the pursuit take up positions behind for several feet, the female darts headlong into a mass of filamentous algae, almost immediately followed by 1 or more

males. The entire spawning group appears to struggle against the obstruction offered by the entangling algal filaments. The male, when only one is involved, takes a position directly alongside the female; several males, when present, form a dense cluster about the female, each approximately parallel to the female. It is not evident whether more than one male spawns with one female at the same time. The spawning act, lasting 2 to 4 seconds, accompanied by a vigorous vibration of the bodies of the spawning fish....By careful examination, it is seen that these masses of algae contain a few (5 to 30) non-adhesive eggs, scattered through and entangled among the filaments."

Stasiak (1978) described the spawning behavior of *P. neogaeus* from Minnesota:

"...Spawning *P. neogaeus* would suddenly leave large schools and dart into depressions under cover such as fallen trees, logs, and brush. Usually one or two ripe females departed from the school, and several males aggressively chased them into cover. Females could be seen emerging from under the brush after about 15 seconds, but males ordinarily remained for up to 30 seconds before rejoining the school. Egg deposition presumably occurred at the time the fish were under the debris."

Stasiak also noted that the spawning behavior of the species in a tank was essentially similar to that observed in the field. He noted the males using their large pectoral fins to control the swimming of the females.

In UPG one or two females were occasionally observed to leave the school and swim for some cover, usually a fallen log or a small boulder; the females were almost immediately chased by more than one male. Spawning probably occurred at this time, although I was unable to observe the actual spawning act. It was also not possible to identify the females, but in most cases the males could be identified as *P. eos*.

It is well known fact that many cyprinids demonstrate some form of sexually dimorphic coloration, especially during breeding season. The general pattern is for the male to take on brighter colors, while the female remains quite drab. This situation holds true for both *P. eos* and *P. neogaeus*. During the breeding season, most members of the Cyprinidae characteristically develop rows of small epithelial projections called breeding tubercles. These secondary sex structures are usually much more pronounced on the males. Comparison of breeding coloration and tubercles of the two species has been furnished in Table 4.6. It is possible to notice the differences in breeding coloration between the males of the two species, *P. eos* being brighter than *P. neogaeus*, although not much difference exists between the females. These differences may be helpful for identifying conspecific mates, and may act to increase the species' reproductive isolation.

Within each species, females are usually larger than the males, so in each species smaller males would be expected to

TABLE 4.6. Comparison of breeding coloration and tubercles of both sexes of *P. eos* and *P. neogaeus*.

P. eos	*P. neogaeus*
MALE	MALE
1. Lower halves of dorsal, pectoral, pelvic, anal and caudal fins bright yellow.	1. Lower halves of pectoral, pelvic, anal and caudal fins light yellow.
2. A bright red lateral stripe below lower lateral band extending from edge of operculum to base of caudal fin.	2. A very light yellow lateral stripe below the lateral band extending from edge of operculum to base of caudal fin.
3. Area below red stripe and most of ventral surface bright yellow.	3. Area below yellow stripe and ventral surface creamy white.
4. Batches of tubercles at bases of pectoral and anal fins.	4. Patches of tubercles at bases of pectoral and anal fins.
FEMALE	FEMALE
1. Bases of dorsal and caudal fins orangish yellow; bases of pectoral, pelvic and anal fins yellowish in some and white in others.	1. Bases of dorsal, pectoral, pelvic, anal and caudal fins yellowish in some and white in others.
2. Area below lower lateral band with a few scattered red spots on a light yellow background in some, light yellow or white in others.	2. Area below the lateral band with a light yellow pigmentation in some and lacking any special coloration in others.
3. Ventral surface creamy white.	3. Ventral surface creamy white.
4. No tubercle present.	4. No tubercle present.

mate with larger females. Thus selection of mates on this criterion would not disfavor interspecific matings.

4.3.4 LIFE HISTORY CHARACTERISTICS

a. LENGTH-WEIGHT RELATIONS

Length-weight relationships of the two species and the hybrids can be described by the following equations:

P. eos $\log W = -4.643 + 2.931 \log L$

P. neogaeus $\log W = -4.766 + 3.00 \log L$

Hybrid $\log W = -4.391 + 2.811 \log L$

where W = total body weight and L = standard length. Comparison of the three length-weight regressions (Fig. 4.6) reveals no apparent differences between the three populations. *P. neogaeus* are slightly heavier for any given length than *P. eos*, and the hybrids have an intermediate body weight between the parental species. An analysis of covariance was performed to test for significant differences between the regressions (Table 4.7). Statistically there is no significant difference ($P>0.05$) between the slopes of the three regression lines; though there is a significant difference ($P<0.05$) between the intercepts of *P. eos* and *P. neogaeus* and between *P. neogaeus* and the hybrids, but no significant difference ($P>0.05$) between the intercepts of *P. eos* and the hybrids. Length-weight relationships for these two species and the hybrids have not been previously reported.

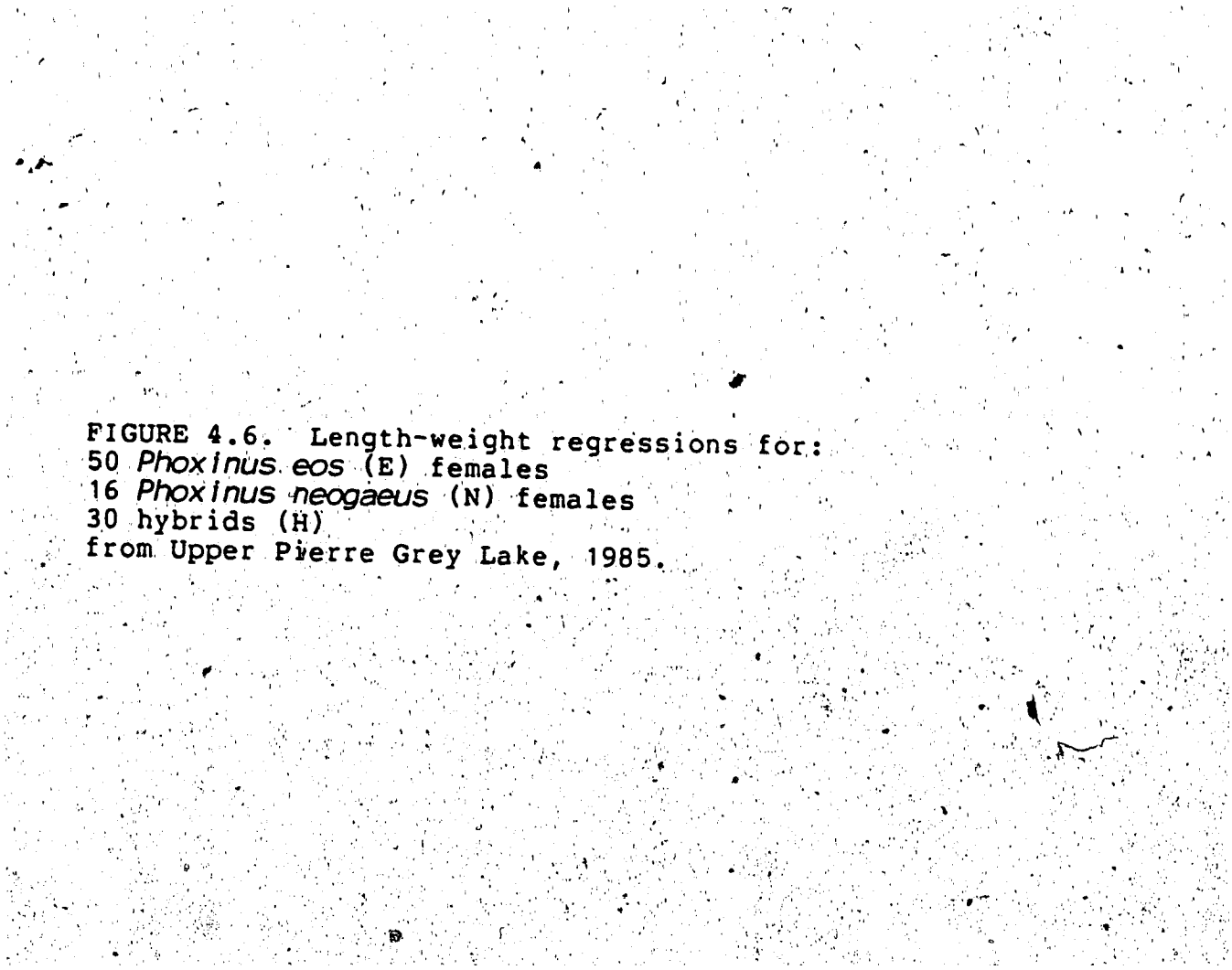


FIGURE 4.6. Length-weight regressions for:
50 *Phoxinus eos* (E) females
16 *Phoxinus neogaeus* (N) females
30 hybrids (H)
from Upper Pierre Grey Lake, 1985.

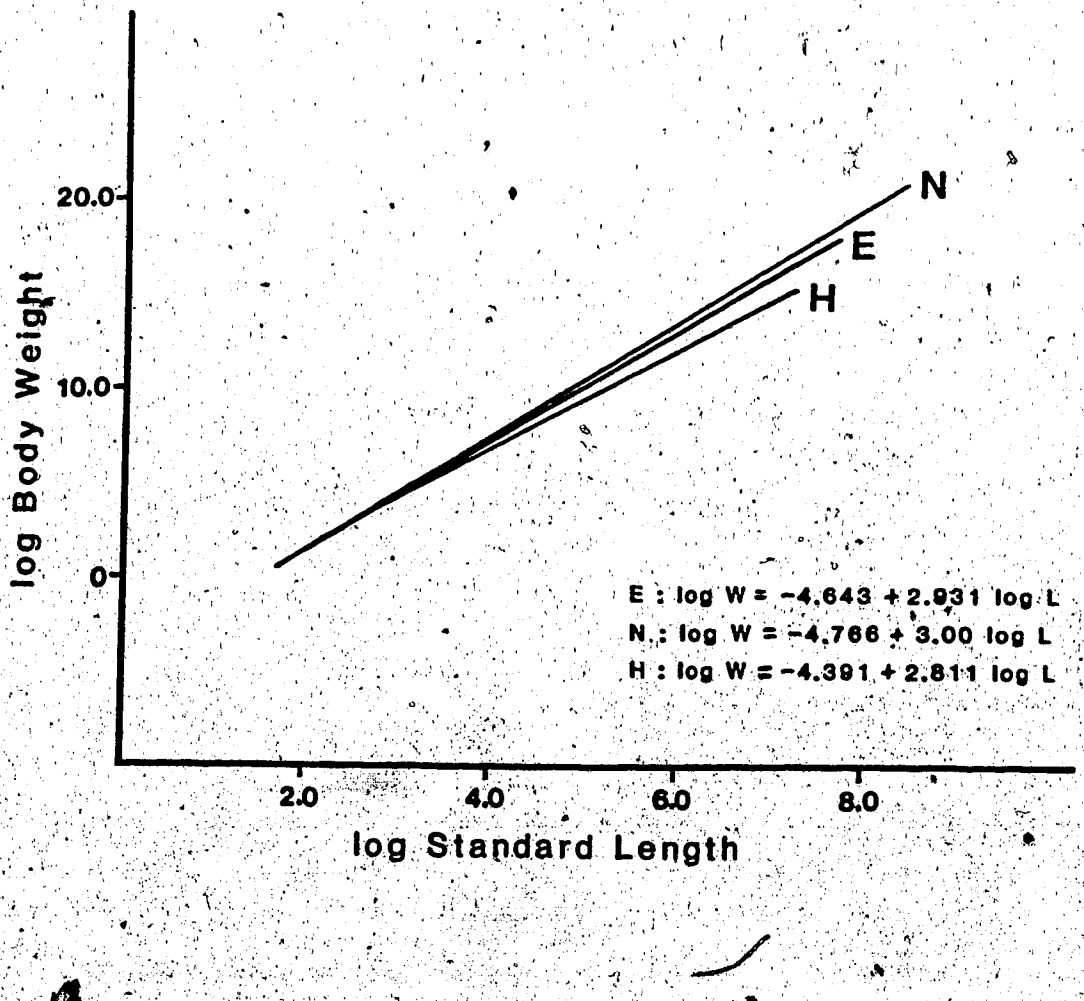

20.0
10.0
0
log Body Weight
N
E
H
E : log W = -4.643 + 2.931 log L
N : log W = -4.766 + 3.00 log L
H : log W = -4.391 + 2.811 log L
2.0
4.0
6.0
8.0
log Standard Length

TABLE 4. Analyses of covariance of length-weight, length-fecundity and weight-fecundity regressions of 50 *P. eos* females, 16 *P. neogaeus* females and 30 hybrids from Upper Pierre Grey Lake, 1985.

LENGTH-WEIGHT REGRESSIONS			
P. eos + *P. neogaeus*	intercept	5.645	$P < 0.05$
	slope	0.034	$P > 0.05$
P. eos + Hybrid	intercept	0.599	$P > 0.05$
	slope	0.002	$P > 0.05$
P. neogaeus + Hybrid	intercept	5.916	$P < 0.05$
	slope	0.026	$P > 0.05$
LENGTH-FECUNDITY REGRESSIONS			
P. eos + *P. neogaeus*	intercept	1.511	$P > 0.05$
	slope	2.058	$P > 0.05$
P. eos + Hybrid	intercept	0.061	$P > 0.05$
	slope	1.496	$P > 0.05$
P. neogaeus + Hybrid	intercept	2.384	$P > 0.05$
	slope	0.089	$P > 0.05$
WEIGHT-FECUNDITY REGRESSIONS			
P. eos + *P. neogaeus*	intercept	3.638	$P > 0.05$
	slope	6.204	$P < 0.05$
P. oes + Hybrid	intercept	1.632	$P > 0.05$
	slope	3.835	$P > 0.05$
P. neogaeus + Hybrid	intercept	1.889	$P > 0.05$
	slope	0.437	$P > 0.05$

b. FECUNDITY

The relationship of fecundity to standard length for the two species and the hybrids is described by the following equations (Fig. 4.7):

P. eos log F = -0.436 + 1.912 log L

P. neogaeus log F = 2.617 + 0.067 log L

Hybrid log F = 2.122 + 0.402 log L

where F = fecundity and L = standard length. Analysis of covariance shows no significant difference ($P>0.05$) between the three regressions in either intercepts or slopes (see Table 4.7).

The relationship of fecundity to total body weight is described by the following equations (Fig. 4.8):

P. eos log F = 2.509 + 0.931 log W

P. neogaeus log F = 2.716 + 0.039 log W

Hybrid log F = 2.683 + 0.269 log W

where F = fecundity and W = total body weight. Analysis of covariance shows no significant difference ($P>0.05$) between the three regressions in intercepts, but shows significant difference ($P<0.05$) between the slopes of *P. eos* and *P. neogaeus* (see Table 4.7). There is no significant difference between the slopes of *P. eos* and hybrids and *P. neogaeus* and hybrids.

Stasiak (1978) gave a range of 2300-6450 eggs for *P. eos* from Minnesota. Becker (1983) found 410 ripe eggs in one *P. eos* from Wisconsin. The number of eggs for *P. eos* in my study ranged from 145-1030 eggs for 50 individuals.

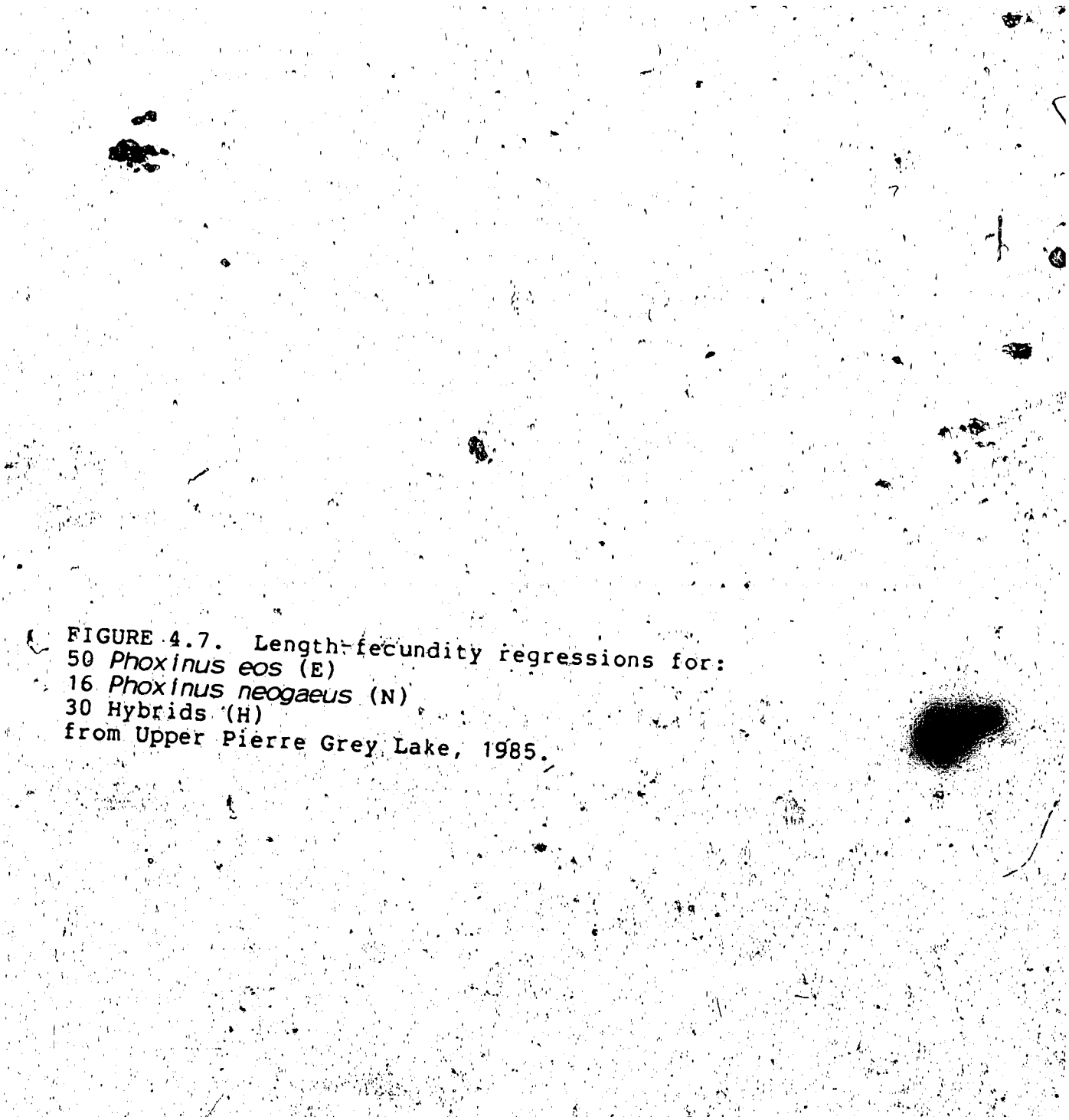
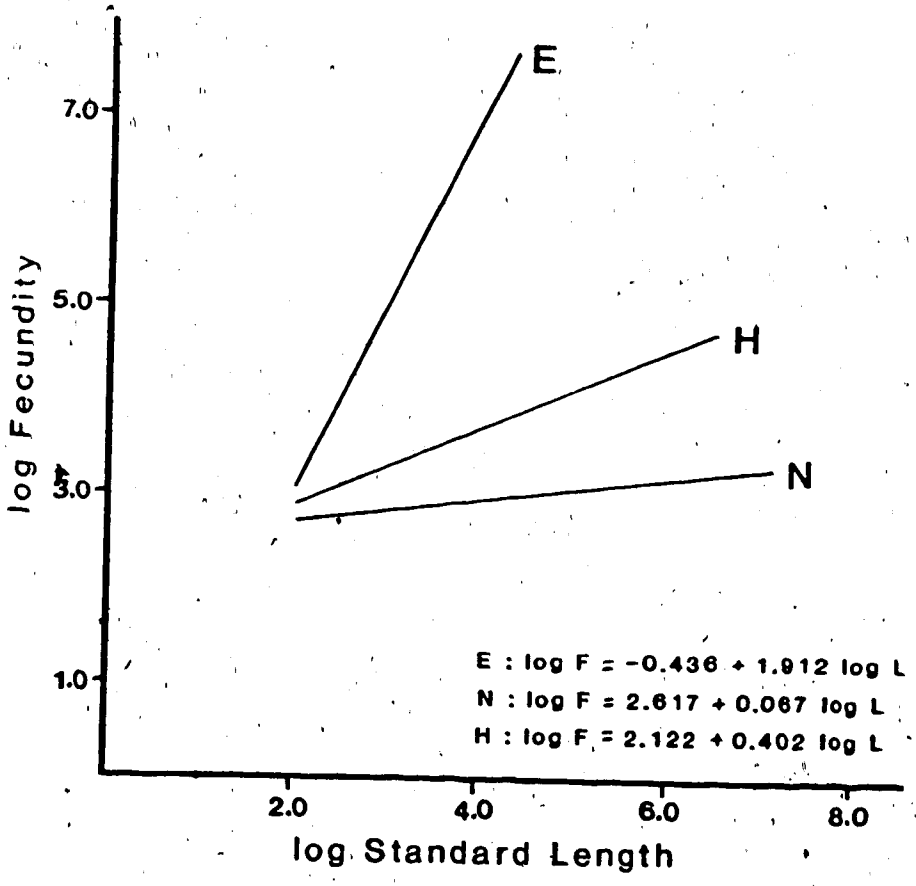


FIGURE 4.7. Length-fecundity regressions for:
50 *Phoxinus eos* (E)
16 *Phoxinus neogaeus* (N)
30 Hybrids (H)
from Upper Pierre Grey Lake, 1985.


E
H
N
7.0
5.0
3.0
1.0
log Fecundity
2.0
4.0
6.0
8.0
log Standard Length
E : log F = -0.436 + 1.912 log L
N : log F = 2.617 + 0.067 log L
H : log F = 2.122 + 0.402 log L

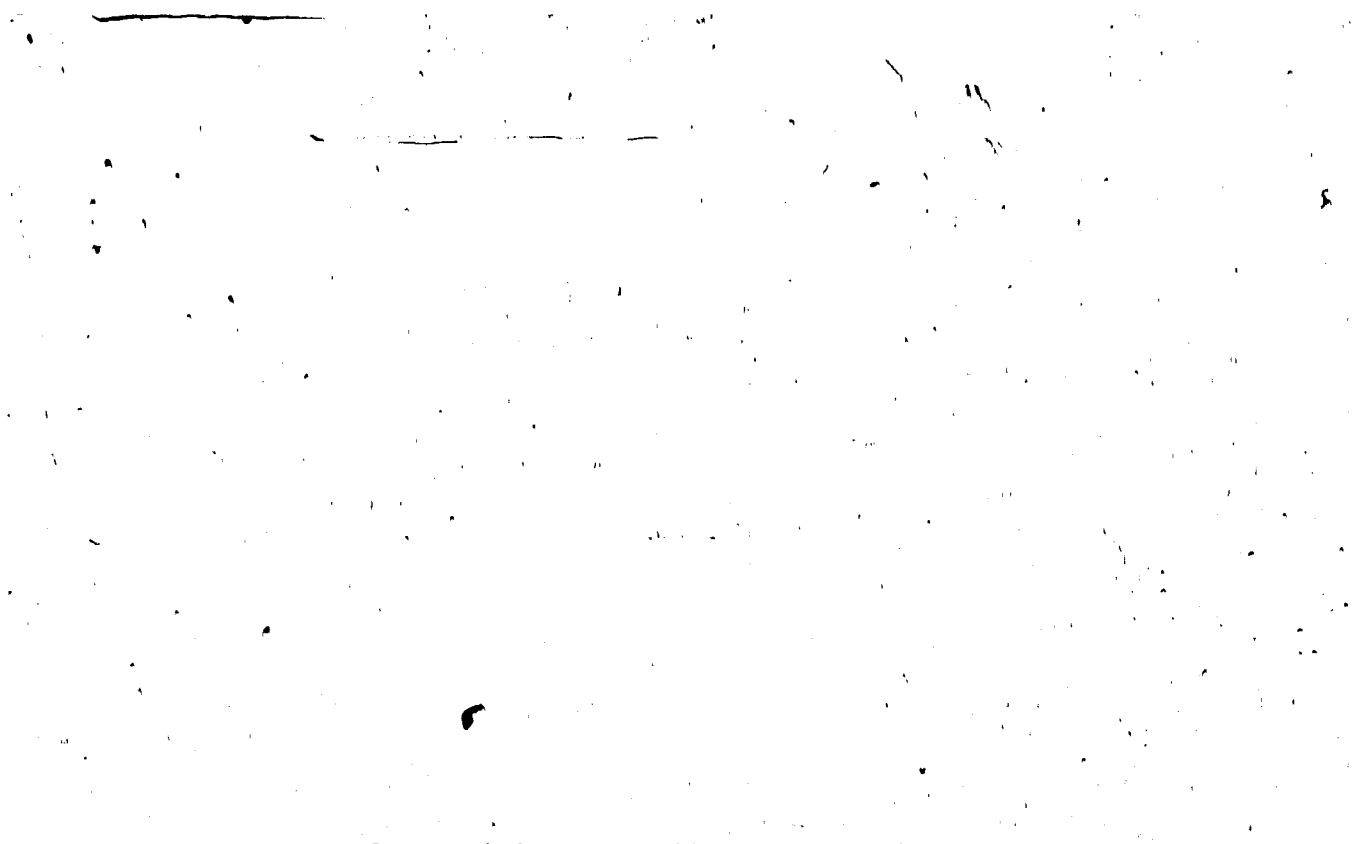
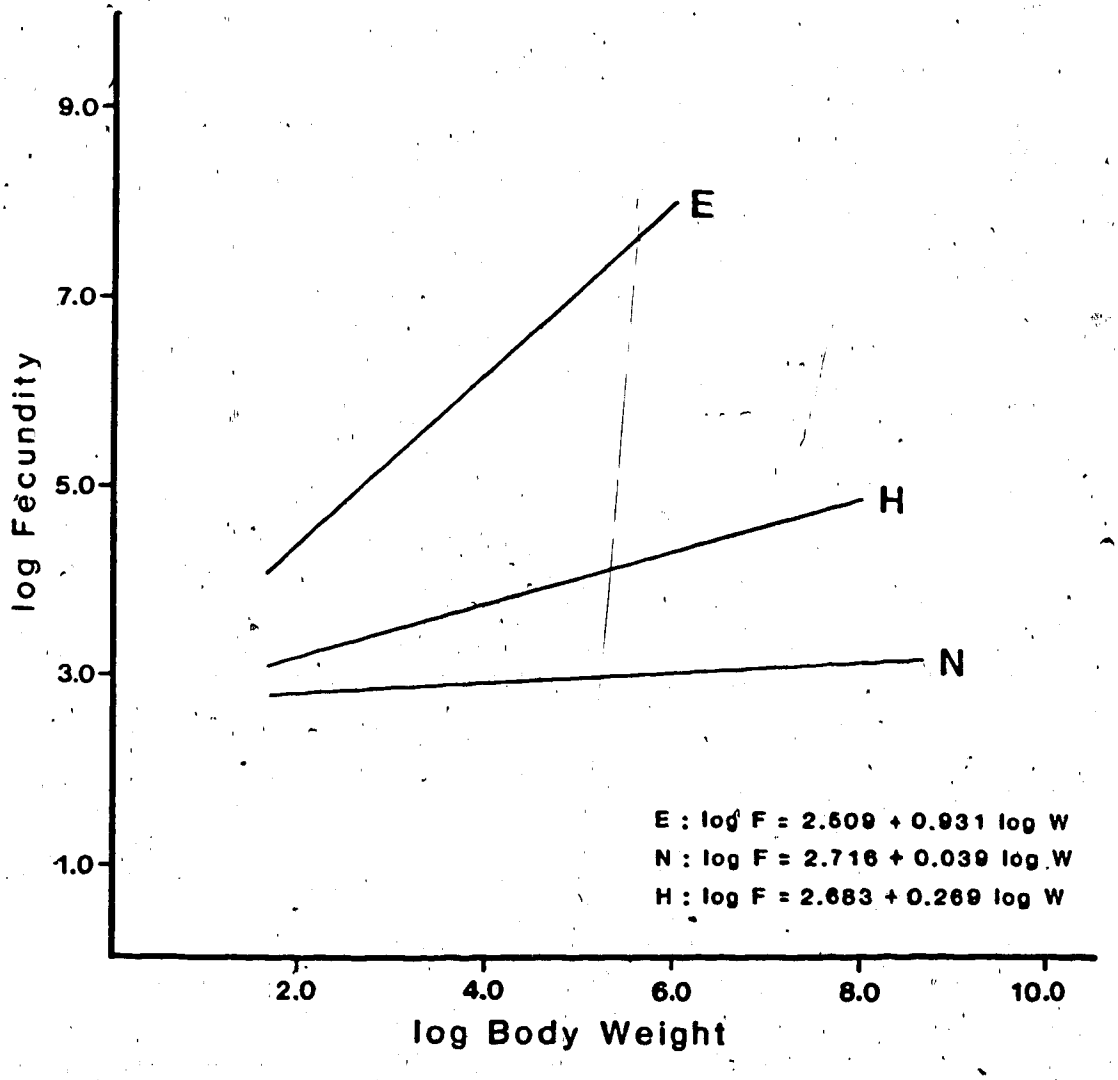


FIGURE 4.8. Weight-fecundity regressions for:
50 *Phoxinus eos* (E)
16 *Phoxinus neogaeus* (N)
30 Hybrids (H)
from Upper Pierre Grey Lake, 1985.


9.0
7.0
5.0
3.0
1.0
log Fecundity
E
H
N
E : log F = 2.509 + 0.931 log W
N : log F = 2.716 + 0.039 log W
H : log F = 2.683 + 0.269 log W
2.0
4.0
6.0
8.0
10.0
log Body Weight

Egg counts taken from 20 *P. neogaeus* from Minnesota ranged from 784-3060 (Stasiak, 1978). The number of eggs for *P. neogaeus* in my study ranged from 406-830 eggs for 16 specimens.

The ova number of *P. eos* X *P. neogaeus* hybrids has not been previously reported. The number of eggs for the UPG hybrids ranged from 292-1716 eggs for 30 fish.

4.4 DISCUSSION

There is a partial overlap in the period of fully ripe females between the two parental species,a fact that suggests that temporal isolation may not be a successful barrier in preventing hybridization in Upper Pierre Grey Lake. Although the peaks of the spawning period for the females of the two species occurred at different times (in 1985, June 10 for *P. neogaeus* and June 25 for *P. eos*), fully ripe *P. eos* males were available during all of this period. As a result, interspecific matings could be possible between *P. eos* males and *P. neogaeus* females. Rarity of *P. neogaeus* males may also facilitate this. Spawning for the two species ended by the end of July in 1984 and 1985 and did not continue into August as has been reported by McPhail and Lindsey (1970) who noted that female *P. eos* collected from "Pierre Grey Lake" on 24 August contained "eggs that though white were quite large and rather free". In Minnesota, Stasiak (1972) observed a separation of the spawning seasons between the two species where *P. neogaeus* was observed spawning in late April and

early May, but *P. eos* did not begin to spawn until early June.

It appears that there is no effective habitat isolation operating between the two species. They swarm in mixed schools near the surface along the shoreline and were captured together with their hybrids.

It was not possible to obtain satisfactory information on the effectiveness of the ethological barriers between the two species in this study. Mate preference tests with interspecific and conspecific matchings would have to be conducted in order to see if there were some basis for the existence of effective ethological isolating mechanisms. It is most likely that the breeding behavior of *P. eos* and *P. neogaeus* is similar enough to allow interspecific spawning in localities where the breeding seasons overlap.

There is no statistical difference between the length-weight relationships of the parental species and the hybrids. Fecundity and standard length and fecundity and body weight relationships do not show any marked difference either. Eggs of hybrids appeared to be similar in shape and condition to the parental eggs. Joswiak, Stasiak and Berven (1986) reported evidence of hybrid fertility by fertilizing the hybrid eggs with *P. eos* sperms. Although hybrid fertility was not tested in my study, it can be inferred from the results of the analyses of different reproductive isolations and life history characteristics that the barrier is low.

5. GENERAL DISCUSSION

In Upper Pierre Grey Lake the total *Phoxinus* population comprises approximately 55% *P. eos*, 12% *P. neogaeus* and 33% *P. eos* x *P. neogaeus* hybrids. Despite the evidence of hybridization, the taxonomic status of *P. eos* and *P. neogaeus* as separate species appears valid. If evidence shows that the two forms remain distinct (i.e., do not fuse), regardless of hybridization, the forms should be recognized as distinct species (Nelson, 1968). Fish hybridization associated with environmental disturbances no more jeopardizes the taxonomic status of the animals involved than do the many artificial crosses (Hubbs, 1961; Nelson, 1968). Although it is well known that *P. eos* and *P. neogaeus* hybridize in many areas, it is by no means the rule. No hybrids were found from 15 sympatric localities in Wisconsin (Greene, 1935). New (1962) reported collecting large numbers of both species from Line pond, New York; no hybrids have ever been identified from that locality. Legendre (1970), in examining "a collection of *P. eos* and *P. neogaeus* from Alberta", failed to identify any hybrid specimens. In Minnesota, hybrids are restricted to four eastern localities (Stasiak, 1972).

From this study, I could determine which key characters were the most useful for identification of *P. eos* and *P. neogaeus*. Extension of mouth (MOEXTN), as used by many authors in fish keys (Paetz and Nelson, 1970; Scott and Crossman, 1973), was the best single criterion for separation of the two species. Other important key characters, e.g.,

lateral band, pharyngeal teeth, digestive tract pattern, angle of mouth also contributed in the discrimination of the two species.

It may not be possible to obtain accurate estimates of the variability of the hybrids among any wild population. However, studies on the premating isolating mechanisms provided knowledge relating to overlap of temporal, habitat and behavioral isolations. Similarity in certain life history characteristics was also noted which may have contributed to the hybridization.

According to Mayr (1970), hybridization is not a random phenomenon and there are certain environmental factors which facilitate the dissolution of species' reproductive isolating mechanisms. Some of those factors, which might have some effects in causing hybridization between *P. eos* and *P. neogaeus* in Upper Pierre Grey Lake, are worth discussing.

a. RARITY OF ONE PARENTAL SPECIES

In the absence of appropriate mating stimuli, individuals of the less common species may respond to inappropriate stimuli from individuals of the abundant species (Mayr, 1970). It is already clear from the previous chapters that there is a marked difference in relative numbers of the two species in Upper Pierre Grey Lake, *P. neogaeus* constituting approximately 12% of the whole *Phoxinus* population. The extent of hybridization between *P. eos* and *P. neogaeus* in UPG is probably influenced by this disparity in sizes of the populations. The phenomenon of hybridization

often appears attributable to a difference in the abundance of the species and as a result to the failure of an individual to find a conspecific mate (Stebbins, 1959; Mecham, 1960; Nelson, 1968). Whether *P. neogaeus* does mate with *P. eos* because of absence of conspecific mates is not known. It would be desirable to conduct a study of breeding behavior, such as mate choice, between these two species.

b. LIMITED SPAWNING AREA

A limited spawning area that compels breeding individuals to mate in close proximity often results in hybridization (Trautman, 1948). Upper Pierre Grey Lake is an isolated body of water without any distinct inlet or outlet. Both the parental species spawn in a similar habitat. Therefore, it is likely that the two species are restricted to spawning along the shoreline of the lake and in close proximity, if not in the same areas.

c. ENVIRONMENTAL DISTURBANCE

Disturbance of the environment is often referred to as one of the most important causes of hybridization (Anderson, 1953; Mayr, 1970). Upper Pierre Grey Lake was chemically treated in 1969 for stocking purpose. No data were available as to the effect of the chemical treatment on the *Phoxinus* population. Without this information it is not possible to speculate on the potency of this factor as a cause of hybridization.

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APPENDIX TABLE 1.

BMDP7M – CANONICAL VARIATES ANALYSIS
UPG, TAY L AND CAM L SPECIMENS

SUMMARY TABLE

STEP NUMBER	VARIABLE ENTERED	VARIABLE REMOVED	F VALUE TO ENTER OR REMOVE	NUMBER OF VARIABLES INCLUDED	U-STATISTIC
1	46 MOFTN		1295.7678	1	0.0895
2	47 LATBAND		44.8337	2	0.0363
3	18 LCPD		37.2095	3	0.0241
4	43 PHARTRO		13.2045	4	0.0213
5	44 DIGTRACT		11.0820	5	0.0188
6	45 MOANGLE		10.7250	6	0.0169
7	8 INW		8.8488	7	0.0152

VARIABLE	COEFFICIENTS FOR CANONICAL VARIABLES 1
8 INW	1.13222
18 LCPD	0.22110
43 PHARTRO	1.26102
44 DIGTRACT	-0.53394
45 MOANGLE	-0.18088
46 MOFTN	1.88021
47 LATBAND	-1.14124

CONSTANT 0.88848

GROUP UPG

CASE	CAN V	CASE	CAN V	CASE	CAN V	CASE	CAN V	CASE	CAN V	CASE	CAN V
1	0.33	11	-7.91	21	-8.71	31	-8.73	41	-8.79		
2	-6.06	12	-7.01	22	-1.24	32	-8.86	42	.4	62	
3	3.21	13	0.80	23	-7.85	33	-8.94	43	-0.30		
4	-8.80	14	-0.80	24	-7.44	34	-8.84	44	2.78		
5	-8.02	15	0.88	25	-8.82	35	-8.83	45	-8.73		
6	-7.78	16	2.54	26	0.82	36	-7.01	46	-2.04		
7	3.21	17	-7.14	27	0.03	37	-7.87	47	1.42		
8	1.65	18	-3.20	28	-2.48	38	-8.82	48	-2.13		
9	0.18	19	1.88	29	-8.78	39	-8.87	49	-1.78		
10	-8.08	20	-7.81	30	1.44	40	-7.0.	50	-0.87		
51	1.80	61	3.89	71	-2.77	81	3.18	91	-4.82		
52	3.43	62	1.31	72	-8.86	82	2.20	92	-3.84		
53	-3.86	63	0.83	73	0.72	83	1.77	93	-0.74		
54	-7.48	64	1.31	74	-8.86	84	3.04	94	-5.01		
55	-8.48	65	1.02	75	-8.20	85	3.72	95	1.22		
56	3.30	66	2.77	76	3.88	86	0.77	96	3.87		
57	0.80	67	1.82	77	5.81	87	3.26	97	2.83		
58	-2.20	68	0.80	78	0.83	88	-1.12	98	3.34		
59	-2.76	69	3.28	79	0.32	89	-0.32	99	4.86		
60	-8.86	70	0.89	80	4.01	90	0.71	100	1.33		
101	2.80	111	-8.23	121	-8.89	131	8.81	141	-7.34		
102	4.10	112	-2.60	122	-8.04	132	8.84	142	-8.12		
103	2.88	113	-8.31	123	-7.48	133	4.33	143	-8.34		
104	3.06	114	-8.87	124	-8.00	134	-0.17	144	-8.91		
105	2.88	115	-8.82	125	-8.05	135	-1.81	145	-8.86		
106	1.72	116	-8.83	126	8.17	136	-8.82	146	-8.77		
107	0.18	117	1.88	127	8.26	137	-0.46	147	-7.37		
108	1.30	118	-1.88	128	8.01	138	-1.80	148	-8.87		
109	2.46	119	-8.80	129	8.78	139	-8.33	149	-8.82		
110	-2.12	120	-8.34	130	8.77	140	-8.33	150	-8.82		
151	-7.78	161	-8.80	171	7.86						
152	-8.71	162	-8.02	172	8.17						
153	-8.82	163	4.47	173	8.78						
154	-7.44	164	3.81	174	8.20						
155	-7.81	165	8.22	175	8.82						
156	-7.01	166	8.83								
157	-7.87	167	7.42								
158	-8.88	168	8.88								
159	-8.33	169	8.26								
160	-8.83	170	8.02								

GROUP TAYLARE

CASE	CAN V	CASE	CAN V	CASE	CAN V	CASE	CAN V	CASE	CAN V	CASE	CAN V
176	8.24	186	7.80	196	8.85	206	7.08	216	7.38		
177	8.20	187	7.08	197	8.16	207	7.48	217	8.85		
178	8.84	188	7.88	198	8.35	208	7.89	218	5.12		
179	8.14	189	8.70	199	7.88	209	8.32	219	8.11		
180	8.17	190	8.01	200	7.88	210	8.27				
181	7.73	191	8.80	201	8.82	211	8.82				
182	7.11	192	7.23	202	7.81	212	8.02				
183	8.87	193	8.18	203	8.74	213	7.84				
184	8.32	194	7.80	204	8.88	214	7.32				
185	8.28	195	8.11	205	8.86	215	7.84				

GROUP CAMERONL

CASE	CAN V	CASE	CAN V	CASE	CAN V	CASE	CAN V	CASE	CAN V
230	-8.84	240	-8.18	260	-7.80	280	-8.83		
231	-8.83	241	-8.31	261	-8.01	281	-8.88		
232	-8.86	242	-8.27	262	-8.76	282	-7.86		
233	-8.87	243	-7.86	263	-8.73	283	-8.71		
234	-8.83	244	-7.82	264	-8.86	284	-7.88		
235	-8.38	245	-8.81	265	-8.80	285	-8.77		
236	-8.83	246	-7.87	266	-8.13	286	-8.86		
237	-8.82	247	-8.22	267	-8.06	287	-8.42		
238	-7.72	248	-8.37	268	-8.88	288	-8.24		
239	-8.34	249	-7.83	269	-7.81	289	-8.80		

APPENDIX TABLE 2.

BMDP7M - CANONICAL VARIATES ANALYSIS
UPG, TAY L AND CAM L SPECIMENS

SUMMARY TABLE

STEP NUMBER	VARIABLE ENTERED	VARIABLE REMOVED	F VALUE TO ENTER OR REMOVE	NUMBER OF VARIABLES INCLUDED	U-STATISTIC
1	47 LATBAND		1187 8892	1	0 0641
2	4 ML		83 6790	2	0 0388
3	45 MDANGLE		26 7823	3	0 0288
4	44 DISTRACT		24 1127	4	0 0221
5	40 PMARTLO		15 0208	5	0 0185
6	23 ANALFL		4 0840	6	0 0176
7	22 PELFL		8 9860	7	0 0163
8	8 IRW		8 2288	8	0 0153

VARIABLE	COEFFICIENTS FOR CANONICAL VARIABLES		
4 ML	0 40882		
8 IRW	1 22247		
22 PELFL	0 86231		
23 ANALFL	-1 08648	CONSTANT	8 14972
40 PMARTLO	1 24340		
44 DISTRACT	-0 81288		
45 MDANGLE	-0 22942		
47 LATBAND	-1 48878		

GROUP UPG

CASE	CAN V	CASE	CAN V	CASE	CAN V	CASE	CAN V	CASE	CAN V
1	-1 05	11	-7 08	21	-8 86	31	-8 82	41	-1 10
2	-4 10	12	-8 36	22	-2 82	32	-8 17	42	5 28
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
4	-8 77	14	-0 24	24	-0 04	34	-8 68	44	2 80
5	-8 80	15	0 72	25	-3 19	35	-8 93	45	-8 77
6	-8 78	16	1 67	26	1 78	36	-8 67	46	-2 02
7	3 46	17	-8 73	27	8 27	37	-7 66	47	2 64
8	1 48	18	-2 78	28	0 11	38	-8 88	48	-2 07
9	-0 87	19	1 84	29	-8 24	39	-8 15	49	-0 78
10	-7 84	20	-7 36	30	-0 07	40	-8 88	50	-0 88
51	3 28	61	3 84	71	-2 30	81	3 19	91	-3 88
52	1 78	62	2 83	72	-8 33	82	1 78	92	-3 22
53	-7 87	63	-2 07	73	-0 86	83	1 83	93	0 80
54	-8 85	64	0 33	74	-8 36	84	2 81	94	0 70
55	-8 15	65	0 77	75	-3 82	85	3 03	95	3 28
56	1 03	66	2 78	76	8 03	86	-0 40	96	2 00
57	-0 82	67	1 18	77	3 37	87	1 88	97	2 18
58	-0 13	68	0 84	78	0 18	88	-0 32	98	4 12
59	-2 43	69	2 86	79	-0 28	89	0 88	99	3 83
60	-8 70	70	0 48	80	3 38	90	1 80	100	2 32
101	2 18	111	-8 86	121	-8 84	131	4 88	141	-8 62
102	4 85	112	-3 23	122	-7 88	132	3 81	142	-8 71
103	2 88	113	-8 23	123	-8 71	133	4 78	143	-8 88
104	2 36	114	-8 77	124	-7 41	134	-0 28	144	-8 01
105	3 00	115	-8 71	125	-8 74	135	-2 24	145	-4 48
106	4 15	116	-8 81	126	8 44	136	-8 34	146	-8 82
107	1 76	117	3 21	127	8 33	137	-2 74	147	-7 10
108	3 13	118	-2 37	128	3 80	138	-0 14	148	-8 77
109	8 16	119	-8 42	129	8 12	139	-8 06	149	-8 71
110	-1 20	120	-8 18	130	3 88	140	-8 27	150	-8 86
161	-8 76	161	-8 77	171	8 71				
162	-8 88	162	-8 80	172	8 44				
163	-3 19	163	8 79	173	8 12				
164	-7 06	164	3 84	174	8 84				
165	-7 28	165	8 42	175	7 76				
166	-8 47	166	7 83						
167	-7 86	167	7 82						
168	-8 33	168	8 80						
169	-8 88	169	7 21						
160	-8 81	170	8 72						

GROUP TAYLAKE

CASE	CAN V	CASE	CAN V	CASE	CAN V	CASE	CAN V	CASE	CAN V
176	8 16	186	7 82	196	8 78	206	7 28	216	8 86
177	8 86	187	8 18	197	8 86	207	8 37	217	8 32
178	7 88	188	8 88	198	8 06	208	8 46	218	8 46
179	8 37	189	8 73	199	7 83	209	7 70	219	4 78
180	7 46	180	8 74	200	8 16	210	7 18		
181	8 88	191	7 87	201	8 81	211	8 48		
182	8 02	192	7 86	202	8 38	212	8 83		
183	7 80	193	8 18	203	8 06	213	7 82		
184	8 34	194	8 18	204	8 34	214	8 12		
185	8 44	195	8 88	205	8 86	215	8 16		

GROUP CAMERON1

CASE	CAN V	CASE	CAN V	CASE	CAN V	CASE	CAN V
220	-7 84	230	-7 80	240	-7 73	250	-7 18
221	-8 78	231	-8 26	241	-8 87	251	-8 71
222	-8 26	232	-8 81	242	-8 78	252	-8 71
223	-8 17	233	-7 80	243	-8 86	253	-7 02
224	-8 76	234	-8 26	244	-8 86	254	-7 26
225	-8 78	235	-8 83	245	-8 18	255	-8 82
226	-8 26	236	-7 77	246	-7 82	256	-8 22
227	-8 76	237	-7 81	247	-8 18	257	-8 81
228	-8 20	238	-7 83	248	-8 01	258	-7 88
229	-8 45	239	-7 24	249	-7 28	259	-8 26

APPENDIX TABLE 3.

BMDP7M - CANONICAL VARIATES ANALYSIS
UPG, TAY L AND CAM L SPECIMENS

SUMMARY TABLE

STEP NUMBER	VARIABLE ENTERED	VARIABLE REMOVED	F VALUE TO ENTER OR REMOVE	NUMBER OF VARIABLES INCLUDED	U-STATISTIC
1	46 MOERTN		1299 7678	1	0 0595
2	84 LOGINM		61 7011	2	0 0336
3	47 LATBAND		43 8612	3	0 0218
4	43 PHARTRO		13 7238	4	0 0188
5	45 MDANGLE		12 8304	5	0 0160
6	44 DISTRACT		11 4348	6	0 0139

VARIABLE COEFFICIENTS FOR CANONICAL VARIABLES

43 PHARTRO	1 12709		
44 DISTRACT	-0 48004	CONSTANT	2 97291
45 MDANGLE	-0 16175		
46 MOERTN	2 10172		
47 LATBAND	-1 18254		
84 LOGINM	10 81349		

GROUP UPG

CASE	CAN V	CASE	CAN V	CASE	CAN V	CASE	CAN V	CASE	CAN V
1	-0 01	11	-8 18	21	-6 64	31	-7 23	41	-0 80
2	0 22	12	-6 82	22	-0 98	32	-6 80	42	5 04
3	2 66	13	0 30	23	-7 95	33	-5 98	43	-0 34
4	-7 55	14	-0 83	24	-7 81	34	-7 06	44	2 93
5	-6 19	15	1 18	25	-4 64	35	-6 80	45	-6 80
6	-7 81	16	2 62	26	0 44	36	-7 76	46	-2 31
7	3 37	17	-7 34	27	5 65	37	-6 36	47	1 85
8	1 83	18	-3 44	28	-3 14	38	-7 06	48	-2 69
9	0 37	19	2 19	29	-6 22	39	-6 38	49	-1 86
10	-6 74	20	-7 47	30	1 33	40	-7 38	50	-0 86
51	1 89	61	2 89	71	-2 64	81	3 19	91	-4 91
52	3 86	62	0 68	72	-7 95	82	3 29	92	-3 84
53	-3 89	63	0 96	73	0 63	83	1 22	93	-0 64
54	-7 51	64	0 84	74	-6 80	84	2 78	94	0 13
55	-6 66	65	0 72	75	-5 22	85	3 77	95	1 80
56	2 78	66	2 92	76	3 82	86	0 84	96	3 91
57	0 70	67	1 86	77	5 84	87	3 26	97	3 01
58	-2 30	68	0 78	78	0 44	88	-1 28	98	3 81
59	-2 93	69	3 06	79	0 48	89	-0 27	99	4 65
60	-7 41	70	0 91	80	4 18	90	0 81	100	1 74
101	3 17	111	-6 80	121	-7 74	131	6 36	141	-7 95
102	4 81	112	-2 29	122	-7 83	132	6 83	142	-6 86
103	3 06	113	-6 37	123	-6 09	133	4 48	143	-6 28
104	3 06	114	-6 76	124	-7 88	134	-0 18	144	-5 89
105	3 25	115	-5 48	125	-6 11	135	-2 03	145	-6 03
106	2 02	116	-6 76	126	6 17	136	-7 22	146	-7 06
107	0 12	117	2 22	127	6 80	137	-0 89	147	-7 18
108	1 81	118	-1 86	128	6 18	138	-1 85	148	-6 78
109	2 86	119	-5 86	129	7 48	139	-5 71	149	-6 48
110	-1 86	120	-5 76	130	6 80	140	-6 31	150	-7 06
151	-7 81	161	-7 86	171	7 82				
152	-6 84	162	-6 16	172	8 17				
153	-6 84	163	4 85	173	7 48				
154	-7 81	164	4 13	174	8 81				
155	-7 67	165	5 86	175	8 23				
156	-7 74	166	5 86						
157	-8 38	167	7 80						
158	-7 85	168	6 81						
159	-6 80	169	6 58						
160	-6 76	170	6 40						

GROUP TAYLAKE

CASE	CAN V	CASE	CAN V	CASE	CAN V	CASE	CAN V	CASE	CAN V
176	8 17	186	8 04	196	8 82	206	7 27	216	7 80
177	8 81	187	7 38	197	8 32	207	7 81	217	7 48
178	8 88	188	8 08	198	8 62	208	7 77	218	8 87
179	8 82	189	8 80	199	8 01	209	7 81	219	8 83
180	8 17	190	8 83	200	8 42	210	8 88		
181	8 11	191	8 03	201	8 84	211	8 78		
182	7 33	192	7 43	202	7 87	212	9 38		
183	8 90	193	8 86	203	8 30	213	7 46		
184	8 23	194	7 74	204	8 80	214	7 86		
185	8 88	195	8 28	205	8 81	215	7 83		

GROUP CAMEROWL

CASE	CAN V	CASE	CAN V	CASE	CAN V	CASE	CAN V
220	-7 83	230	-8 88	240	-7 94	250	-8 70
221	-8 74	231	-8 71	241	-8 78	251	-10 85
222	-8 21	232	-8 88	242	-8 87	252	-7 87
223	-8 71	233	-7 83	243	-8 23	253	-8 17
224	-8 80	234	-7 72	244	-8 31	254	-8 11
225	-8 00	235	-8 08	245	-8 88	255	-8 38
226	-8 85	236	-8 18	246	-8 80	256	-10 88
227	-8 00	237	-8 26	247	-8 87	257	-8 78
228	-8 43	238	-8 88	248	-8 33	258	-8 89
229	-8 85	239	-7 78	249	-8 11	259	-8 85

APPENDIX TABLE 4.

BMDP4M - PRINCIPAL COMPONENTS ANALYSIS
TAY L AND CAM L SPECIMENS
FIRST 2 FACTOR SCORES

CASE LABEL	NO	FACTOR 1	FACTOR 2
	1	1.422	-0.018
	2	1.044	0.437
	3	2.048	-0.871
	4	1.748	-0.813
	5	0.863	0.861
	6	1.318	0.162
	7	0.716	0.872
	8	0.898	0.861
	9	1.778	0.197
	10	0.374	1.278
	11	0.743	0.408
	12	1.044	0.080
	13	0.850	0.112
	14	0.857	0.264
	15	0.857	-0.188
	16	0.183	0.886
	17	0.578	0.628
	18	0.488	0.967
	19	1.801	0.126
	20	1.848	0.051
	21	1.778	0.338
	22	0.808	1.048
	23	1.262	0.177
	24	0.822	0.830
	25	0.878	0.760
	26	0.838	0.898
	27	-0.282	1.888
	28	1.384	-0.133
	29	0.101	1.414
	30	0.861	0.838
	31	0.148	1.080
	32	0.718	0.898
	33	-0.088	1.248
	34	-0.848	1.529
	35	-0.408	1.221
	36	0.827	0.828
	37	1.188	0.647
	38	0.308	0.973
	39	0.873	0.327
	40	0.261	1.188
	41	0.273	0.843
	42	-0.718	1.823
	43	-2.381	2.758
	44	-2.884	3.888
	45	0.081	-1.484
	46	-0.410	-1.288
	47	-0.287	-1.088
	48	-0.048	-1.124
	49	-0.287	-1.318
	50	-0.428	-0.837

CASE LABEL	NO	FACTOR 1	FACTOR 2
	51	-0.787	-0.802
	52	-0.182	-1.388
	53	-0.382	-0.882
	54	-0.478	-0.887
	55	-0.380	-0.847
	56	-0.462	-0.888
	57	0.073	-1.480
	58	-0.823	-0.714
	59	0.481	-1.304
	60	-0.531	-0.784
	61	-0.111	-0.784
	62	-0.088	-1.401
	63	-0.708	-0.738
	64	-0.488	-0.827
	65	-0.827	-1.178
	66	-0.885	-0.808
	67	-0.407	-0.908
	68	-0.318	-1.224
	69	-0.181	-1.182
	70	-0.835	-0.888
	71	-0.803	-0.408
	72	-1.188	-0.822
	73	-1.178	-0.427
	74	-1.048	-0.888
	75	-1.883	0.118
	76	-1.388	-0.878
	77	-1.278	-0.232
	78	-1.081	-0.304
	79	-1.228	-0.078
	80	-2.071	0.226
	81	-1.080	-0.487
	82	-0.887	-0.838
	83	-1.040	-0.433
	84	-0.881	-0.443

APPENDIX TABLE 5.

BMDP4M - PRINCIPAL COMPONENTS ANALYSIS
UPG SPECIMENS
FIRST 2 FACTOR SCORES

CASE LABEL	NO	FACTOR 1	FACTOR 2
	1	0.863	-0.190
	2	1.294	-1.227
	3	0.470	1.388
	4	-0.433	-0.866
	5	-0.486	-1.032
	6	-1.194	-1.416
	7	1.897	-0.402
	8	-1.917	2.094
	9	-0.481	-0.077
	10	-0.878	-1.212
	11	0.017	1.770
	12	-0.187	-1.422
	13	-0.828	0.705
	14	0.052	-0.242
	15	-0.087	0.886
	16	-0.883	0.777
	17	-0.747	-1.077
	18	1.723	-1.762
	19	-0.270	0.536
	20	-0.442	1.203
	21	-0.784	-0.675
	22	-0.813	0.025
	23	-1.018	-0.886
	24	-0.836	-0.802
	25	-0.888	-0.275
	26	0.100	0.888
	27	2.083	0.804
	28	-0.181	-0.015
	29	-1.012	-0.841
	30	-1.026	1.327
	31	-0.426	-0.744
	32	-0.276	-0.730
	33	-0.088	-0.853
	34	0.867	-1.508
	35	0.261	1.808
	36	-0.331	-0.781
	37	-0.461	-0.760
	38	-0.857	-0.847
	39	-0.802	-0.847
	40	0.003	-1.822
	41	1.855	-1.856
	42	1.060	0.848
	43	-1.086	0.828
	44	-0.811	1.882
	45	-0.894	-0.878
	46	1.401	-0.976
	47	1.612	-0.436
	48	0.867	-0.318
	49	-0.885	0.841
	50	-0.808	0.761
	51	1.806	-0.287
	52	0.826	0.847
	53	-0.263	-0.416
	54	-0.880	-0.883
	55	-1.348	-0.241
	56	0.484	0.735
	57	-0.231	0.438
	58	0.847	-0.218
	59	-1.291	1.232
	60	-1.818	0.285
	61	0.743	0.418
	62	0.127	0.888
	63	1.280	-1.037
	64	2.438	-0.827
	65	-0.212	0.707
	66	0.222	0.847
	67	1.330	-0.288
	68	-0.851	0.845
	69	0.442	1.108
	70	0.428	0.038
	71	0.447	-0.343
	72	-0.868	-0.878
	73	-0.237	0.888
	74	-1.209	-0.788
	75	-1.038	-0.867
	76	0.808	1.102
	77	-1.208	2.888
	78	1.047	0.131
	79	-0.883	0.852
	80	0.172	1.370
	81	0.881	0.388
	82	0.295	0.884
	83	-0.134	0.880
	84	-0.819	1.882
	85	0.120	1.438
	86	-1.801	1.760
	87	-0.082	0.852
	88	-1.383	1.178
	89	-0.817	1.221
	90	0.137	0.718
	91	1.412	-1.864
	92	-0.820	-0.877
	93	0.809	-0.404
	94	0.138	-0.858
	95	1.016	-0.816
	96	1.248	0.378
	97	-2.186	2.813
	98	-1.845	2.842
	99	0.033	1.455
	100	-0.885	0.338
	101	-0.210	0.898
	102	1.888	0.888
	103	-0.036	0.898
	104	1.081	0.486
	105	-0.810	1.886
	106	1.320	0.088
	107	-0.328	0.704
	108	0.128	0.708
	109	-0.078	0.813
	110	-0.008	-0.200
	111	-0.804	-0.834
	112	1.087	-1.202
	113	-0.424	-0.878
	114	-1.181	-0.861
	115	-1.143	-0.888
	116	-0.828	-0.838
	117	0.118	1.088
	118	-0.188	-0.078
	119	-0.804	-0.780
	120	-0.788	-1.244
	121	-0.884	-0.820
	122	-0.888	-1.044
	123	-0.878	-1.133
	124	-0.784	-0.808
	125	-1.140	-0.881
	126	0.808	1.888
	127	0.807	1.188
	128	-0.118	1.788
	129	1.488	0.488
	130	1.878	0.188
	131	0.282	1.482
	132	1.487	0.882
	133	0.108	1.328
	134	1.082	-0.821
	135	0.808	-0.872
	136	-0.833	-0.877
	137	1.044	-0.832
	138	1.313	-0.888
	139	-0.888	-0.867
	140	-0.838	-0.788
	141	-0.188	-1.448
	142	-1.278	-0.188
	143	-0.884	-0.852
	144	-0.788	-0.884
	145	-1.188	-0.236
	146	-0.804	-0.778
	147	-0.418	-1.204
	148	-1.181	-0.881
	149	-1.143	-0.888
	150	-0.887	-0.447
	151	-1.194	-1.416
	152	-0.784	-0.675
	153	-0.888	-0.275
	154	-0.836	-0.802
	155	-0.442	-1.203
	156	-0.331	-0.781
	157	-0.461	-0.760
	158	-0.848	-0.678
	159	-0.804	-0.836
	160	-0.828	-0.838
	161	-0.433	-0.888
	162	-0.888	-1.022
	163	1.871	0.472
	164	0.481	0.787
	165	1.848	1.305
	166	1.381	0.836
	167	1.781	0.462
	168	1.873	0.348
	169	2.788	-0.888
	170	1.728	0.888
	171	1.838	0.824
	172	0.888	1.888
	173	1.483	0.487
	174	2.383	0.308
	175	2.087	0.840

APPENDIX TABLE 6. BMDP4M - PRINCIPAL COMPONENTS ANALYSIS
UPG, TAY L AND CAM L SPECIMENS
FIRST 2 FACTOR SCORES

CASE LABEL	CASE NO	FACTOR 1	FACTOR 2
	1	0.648	-0.117
	2	0.970	-1.038
	3	-0.108	1.487
	4	-0.436	-0.606
	5	-0.286	-0.984
	6	-0.483	-1.187
	7	1.390	-0.277
	8	-1.348	1.878
	9	-0.030	0.028
	10	-0.286	-1.109
	11	0.493	-1.816
	12	0.198	-1.318
	13	-0.767	0.720
	14	-0.035	-0.178
	15	-0.534	-0.714
	16	-0.540	0.898
	17	-0.088	-1.012
	18	1.086	-1.604
	19	-0.318	0.858
	20	-0.176	-1.173
	21	-0.896	-0.487
	22	-0.712	0.042
	23	-0.339	-0.886
	24	-0.865	-0.365
	25	-0.529	-0.453
	26	-0.212	0.848
	27	0.884	0.888
	28	0.488	0.267
	29	-0.807	-0.477
	30	-1.416	1.466
	31	-0.636	-0.440
	32	-0.811	-0.575
	33	-0.351	-0.736
	34	-0.174	-1.321
	35	-0.104	-1.278
	36	-0.673	-0.641
	37	-0.748	-0.708
	38	-0.575	-0.370
	39	-0.855	-0.324
	40	-0.329	-1.265
	41	1.650	-1.720
	42	0.419	0.682
	43	-1.001	0.856
	44	-0.863	1.826
	45	-0.492	-0.787
	46	0.924	-0.861
	47	0.888	-0.408
	48	0.260	-0.272
	49	-0.728	0.887
	50	-0.734	0.829

CASE LABEL	CASE NO	FACTOR 1	FACTOR 2
	51	0.834	-0.178
	52	-0.218	0.804
	53	-0.470	-0.328
	54	-0.853	-0.872
	55	-1.148	-0.267
	56	0.147	0.713
	57	-0.278	0.287
	58	0.208	-0.209
	59	-1.308	1.088
	60	-1.882	0.178
	61	0.813	0.880
	62	-0.100	1.028
	63	0.886	-0.818
	64	1.330	-0.482
	65	-0.183	0.900
	66	0.043	0.868
	67	0.820	-0.148
	68	-0.801	0.887
	69	0.207	0.888
	70	-0.111	0.022
	71	0.010	-0.241
	72	-0.780	-0.008
	73	-0.841	0.816
	74	-0.852	-0.831
	75	-1.088	-0.086
	76	0.898	0.844
	77	-1.141	2.376
	78	0.784	0.068
	79	-0.276	0.748
	80	-0.842	1.181
	81	0.433	0.280
	82	0.217	0.748
	83	-0.171	0.878
	84	-0.328	1.878
	85	-0.129	1.300
	86	-1.801	1.822
	87	0.013	0.880
	88	-1.378	1.051
	89	-0.730	1.082
	90	-0.403	0.789
	91	1.283	-1.884
	92	-0.113	-0.508
	93	0.849	-0.401
	94	0.420	-0.117
	95	0.820	-0.470
	96	0.488	0.288
	97	-1.895	2.389
	98	-1.838	2.877
	99	0.418	1.224
	100	0.280	-0.214

CASE LABEL	CASE NO	FACTOR 1	FACTOR 2
	101	-0.814	0.842
	102	0.881	0.880
	103	0.288	0.780
	104	0.826	0.331
	105	-0.787	1.883
	106	1.274	0.884
	107	-0.188	0.810
	108	0.237	0.887
	109	0.137	0.804
	110	0.948	-0.226
	111	0.820	-0.782
	112	0.801	-1.867
	113	-0.088	-1.867
	114	-0.836	-0.877
	115	-0.704	-0.827
	116	-0.488	-0.810
	117	-0.108	1.033
	118	-0.087	-0.884
	119	-0.336	-0.818
	120	-0.317	-1.111
	121	-0.784	-0.813
	122	-0.488	-1.808
	123	-0.400	-1.078
	124	-0.819	-0.885
	125	-0.781	-0.820
	126	0.111	2.188
	127	-0.073	1.208
	128	-0.788	1.847
	129	1.180	0.268
	130	1.417	0.270
	131	0.018	1.828
	132	1.126	0.788
	133	-0.013	1.273
	134	0.812	-0.888
	135	0.886	-0.808
	136	-0.323	-1.010
	137	0.883	-0.887
	138	0.788	-0.784
	139	-0.885	-0.733
	140	-0.285	-0.858
	141	-0.222	-1.282
	142	-0.878	-0.233
	143	-0.282	-0.808
	144	-0.882	-0.883
	145	-0.727	-0.228
	146	-0.888	-0.811
	147	-0.161	-1.010
	148	-0.838	-0.877
	149	-0.784	-0.827
	150	-0.875	-0.870

CASE LABEL	CASE NO	FACTOR 1	FACTOR 2
	151	-0.483	-1.187
	152	-0.535	-0.487
	153	-0.528	-0.453
	154	-0.585	-0.385
	155	-0.178	-1.173
	156	-0.813	-0.841
	157	-0.748	-0.708
	158	-0.780	-0.508
	159	-0.820	-0.782
	160	-0.468	-0.810
	161	-0.438	-0.805
	162	-0.285	-0.864
	163	1.263	0.491
	164	0.261	0.891
	165	1.083	1.318
	166	0.734	1.088
	167	1.088	0.888
	168	0.847	0.488
	169	2.006	0.871
	170	1.117	0.707
	171	0.888	0.888
	172	0.113	2.186
	173	1.172	0.388
	174	1.705	0.428
	175	0.888	0.780
	176	2.086	0.851
	177	1.740	0.412
	178	2.778	-0.888
	179	2.100	-0.858
	180	1.884	0.488
	181	2.087	-0.078
	182	1.184	0.838
	183	1.138	0.783
	184	2.888	0.851
	185	0.578	1.838
	186	0.884	0.878
	187	1.846	0.881
	188	1.286	0.488
	189	1.383	0.348
	190	1.378	0.887
	191	0.848	1.207
	192	1.205	0.746
	193	1.838	0.887
	194	2.886	0.888
	195	3.537	-1.259
	196	2.732	-0.182
	197	1.308	0.778
	198	1.800	0.887
	199	1.846	0.841
	200	1.201	0.878

CASE LABEL	CASE NO	FACTOR 1	FACTOR 2
	201	1.348	0.800
	202	0.284	1.718
	203	2.081	-0.438
	204	0.828	1.077
	205	1.052	0.418
	206	0.880	1.228
	207	1.382	0.338
	208	0.238	1.488
	209	-0.328	1.782
	210	-0.054	1.431
	211	1.484	0.802
	212	1.880	0.484
	213	0.827	0.824
	214	1.513	0.532
	215	0.731	1.428
	216	0.781	0.833
	217	-0.388	1.880
	218	-2.238	2.788
	219	-2.688	3.722
	220	-0.139	-1.885
	221	-0.743	-1.228
	222	-0.878	-0.841
	223	0.081	-1.835
	224	-0.521	-1.181
	225	-0.430	-1.281
	226	-0.791	-1.212
	227	-0.376	-1.865
	228	-0.898	-1.858
	229	-0.748	-1.177
	230	-0.582	-1.188
	231	-0.367	-0.883
	232	-0.110	-1.818
	233	-0.856	-0.485
	234	0.586	-2.858
	235	-0.879	-0.238
	236	0.133	-1.886
	237	-0.354	-1.415
	238	-1.882	-0.888
	239	-0.784	-0.822
	240	-1.108	-0.852
	241	-1.028	-1.848
	242	-0.388	-1.883
	243	-0.107	-0.878
	244	-0.303	-1.847
	245	-1.814	-0.884
	246	-1.183	-0.387
	247	-1.488	-0.744
	248	-1.805	-0.882
	249	-1.825	-0.282
	250	-1.899	0.288

APPENDIX TABLE 7.

BMDP4M - PRINCIPAL COMPONENTS ANALYSIS
TAY L AND CAM L SPECIMENS
FIRST 2 FACTOR SCORES

CASE LABEL	NO	FACTOR 1	FACTOR 2
	1	1.210	0.058
	2	0.887	0.471
	3	1.741	-0.486
	4	1.673	-0.637
	5	0.628	0.560
	6	1.178	0.237
	7	0.787	0.822
	8	0.860	0.622
	9	1.477	0.304
	10	0.408	1.212
	11	0.788	0.421
	12	1.047	0.088
	13	0.928	0.186
	14	0.884	0.287
	15	0.884	-0.197
	16	0.304	0.672
	17	0.730	0.488
	18	0.828	0.908
	19	1.341	0.297
	20	1.420	0.840
	21	1.447	0.575
	22	0.821	1.057
	23	1.148	0.286
	24	0.905	0.887
	25	0.845	0.740
	26	0.894	0.848
	27	-0.123	1.748
	28	1.284	-0.040
	29	0.249	1.284
	30	0.888	0.884
	31	0.303	0.942
	32	0.745	0.868
	33	0.060	1.115
	34	-0.434	1.373
	35	-0.177	1.084
	36	0.888	0.373
	37	1.038	0.718
	38	0.432	0.884
	39	0.882	0.325
	40	0.328	1.103
	41	0.385	0.788
	42	-0.511	1.788
	43	-2.418	2.778
	44	-2.936	3.808
	45	0.231	-1.588
	46	-0.388	-1.311
	47	-0.207	-1.118
	48	0.132	-1.276
	49	-0.135	-1.473
	50	-0.214	-0.831

CASE LABEL	NO	FACTOR 1	FACTOR 2
	51	-0.713	-0.868
	52	-0.086	-1.416
	53	-0.237	-1.084
	54	-0.411	-1.044
	55	-0.282	-0.915
	56	-0.328	-1.017
	57	0.227	-1.884
	58	-0.886	-0.784
	59	0.075	-1.396
	60	-0.388	-0.852
	61	0.105	-0.831
	62	0.104	-1.526
	63	-0.662	-0.771
	64	-0.381	-0.877
	65	-0.427	-1.282
	66	-0.863	-0.886
	67	-0.380	-0.875
	68	-0.226	-1.286
	69	-0.080	-1.218
	70	-0.801	-0.838
	71	-1.048	-0.287
	72	-1.420	-0.372
	73	-1.338	-0.334
	74	-1.187	-0.809
	75	-1.888	0.308
	76	-1.881	-0.286
	77	-1.399	-0.188
	78	-1.103	-0.246
	79	-1.388	-0.018
	80	-2.813	0.666
	81	-1.122	-0.817
	82	-1.173	-0.378
	83	-1.211	-0.287
	84	-1.134	-0.321

APPENDIX TABLE 8.

BMDP4M - PRINCIPAL COMPONENTS ANALYSIS
UPG SPECIMENS
FIRST 2 FACTOR SCORES

CASE LABEL	NO	FACTOR 1	FACTOR 2
	1	1.059	-0.208
	2	1.384	-1.240
	3	0.483	1.382
	4	-0.307	-1.088
	5	-0.470	-1.059
	6	-1.422	-1.384
	7	1.505	-0.351
	8	-1.880	2.095
	9	-0.483	-0.114
	10	-0.852	-1.284
	11	0.068	-1.807
	12	-0.242	-1.420
	13	-0.575	0.883
	14	0.173	-0.283
	15	0.104	0.834
	16	-0.805	0.884
	17	-0.788	-1.098
	18	1.844	-1.778
	19	-0.238	0.805
	20	-0.424	-1.207
	21	-0.788	-0.884
	22	-0.818	0.048
	23	-1.013	-0.728
	24	-0.886	-0.827
	25	-1.111	-0.347
	26	0.183	0.842
	27	1.807	1.077
	28	0.044	-0.126
	29	-1.118	-0.484
	30	-0.808	1.251
	31	-0.307	-0.791
	32	-0.231	-0.771
	33	0.048	-0.885
	34	0.584	-1.538
	35	0.457	-1.848
	36	-0.187	-0.800
	37	-0.287	-0.733
	38	-0.479	-0.442
	39	-0.621	-0.577
	40	0.181	-1.885
	41	1.874	-1.845
	42	1.088	0.882
	43	1.044	0.908
	44	-0.873	1.835
	45	-0.718	-0.785
	46	1.473	-0.871
	47	1.488	-0.810
	48	0.880	-0.243
	49	-0.802	0.820
	50	-0.830	0.776

CASE LABEL	NO	FACTOR 1	FACTOR 2
	51	1.589	-0.388
	52	0.636	0.830
	53	-0.172	-0.633
	54	-0.778	-0.826
	55	-1.814	-0.185
	56	0.825	0.721
	57	-0.123	0.388
	58	0.853	-0.284
	59	-1.284	1.224
	60	-2.182	0.368
	61	0.787	0.378
	62	0.217	0.933
	63	1.898	-1.137
	64	2.326	-0.488
	65	-0.135	0.837
	66	0.290	0.886
	67	1.299	-0.288
	68	-0.808	0.808
	69	0.410	1.024
	70	0.881	0.013
	71	0.893	-0.397
	72	-1.083	-0.826
	73	-0.188	0.852
	74	-1.874	-0.800
	75	-1.202	0.011
	76	0.801	1.137
	77	-1.181	2.837
	78	0.871	0.170
	79	-0.481	0.772
	80	0.178	1.384
	81	0.642	0.357
	82	0.318	0.813
	83	-0.012	0.805
	84	-0.486	1.885
	85	0.140	1.427
	86	-2.073	1.782
	87	0.024	0.882
	88	-1.626	1.246
	89	-0.567	1.171
	90	0.285	0.850
	91	1.508	-1.888
	92	-0.477	-0.810
	93	0.808	-0.374
	94	0.187	-0.087
	95	0.871	-0.488
	96	1.267	0.450
	97	-2.228	2.580
	98	-1.717	2.885
	99	-0.021	1.388
	100	-0.888	0.282

CASE LABEL	NO	FACTOR 1	FACTOR 2
	101	-0.281	0.841
	102	1.888	0.888
	103	-0.044	0.885
	104	1.028	0.803
	105	-0.874	1.811
	106	1.181	0.138
	107	-0.278	0.883
	108	0.128	0.880
	109	-0.888	0.882
	110	0.088	-0.280
	111	-0.483	-0.842
	112	1.184	-1.217
	113	-0.411	-0.803
	114	-1.243	-0.889
	115	-1.200	-0.881
	116	-0.818	-0.818
	117	0.182	1.018
	118	-0.128	-0.102
	119	-0.828	-0.788
	120	-0.788	-1.281
	121	-0.888	-0.828
	122	-1.038	-1.048
	123	-0.808	-1.108
	124	-0.848	-0.748
	125	-1.187	-0.888
	126	0.741	1.882
	127	1.012	1.181
	128	0.010	1.883
	129	1.208	0.888
	130	1.723	0.288
	131	0.287	1.422
	132	1.237	0.780
	133	0.127	1.287
	134	1.172	-0.880
	135	0.784	-0.888
	136	-0.822	-1.018
	137	1.088	-0.887
	138	1.413	-0.878
	139	-0.704	-0.828
	140	-0.825	-0.778
	141	-0.112	-1.488
	142	-1.282	-0.188
	143	-0.848	-0.872
	144	-0.780	-0.882
	145	-1.188	-0.200
	146	-0.388	-0.812
	147	-0.811	-1.208
	148	-1.242	-0.888
	149	-1.200	-0.881
	150	-0.878	-0.442

CASE LABEL	NO	FACTOR 1	FACTOR 2
	151	-1.422	-1.384
	152	-0.788	-0.884
	153	-1.111	-0.347
	154	-0.888	-0.827
	155	-0.424	-1.207
	156	-0.187	-0.800
	157	-0.287	-0.733
	158	-1.083	-0.828
	159	-0.483	-0.842
	160	-0.818	-0.818
	161	-0.307	-1.088
	162	-0.470	-1.058
	163	1.417	0.881
	164	0.505	0.880
	165	1.403	1.447
	166	1.278	1.005
	167	1.867	0.884
	168	1.787	0.430
	169	2.382	0.788
	170	1.883	0.888
	171	1.387	1.011
	172	0.741	1.882
	173	1.347	0.888
	174	2.053	0.803
	175	1.886	0.763

APPENDIX TABLE 9. BMDP4M - PRINCIPAL COMPONENTS ANALYSIS
UPG, TAY L AND CAM L SPECIMENS
FIRST 2 FACTOR SCORES

CASE LABEL	NO	FACTOR 1	FACTOR 2
	1	0.868	-0.185
	2	1.136	-1.116
	3	0.013	1.389
	4	-0.320	-0.884
	5	-0.157	-1.017
	6	-0.647	-1.083
	7	1.293	-0.284
	8	1.264	1.802
	9	0.122	-0.112
	10	-0.186	-1.188
	11	0.647	-1.880
	12	0.283	-1.334
	13	-0.521	0.818
	14	0.188	-0.323
	15	-0.480	0.883
	16	-0.413	0.880
	17	0.028	-1.087
	18	1.278	-1.484
	19	-0.228	0.900
	20	-0.018	-1.287
	21	-0.548	-0.852
	22	-0.642	0.038
	23	-0.184	-0.788
	24	-0.478	-0.447
	25	-0.430	-0.487
	26	-0.025	0.888
	27	0.843	0.836
	28	-0.323	0.093
	29	-1.020	-0.472
	30	-1.278	1.283
	31	-0.888	-0.524
	32	-0.844	-0.887
	33	-0.230	-0.832
	34	-0.191	-1.384
	35	-0.088	-1.328
	36	-0.882	-0.707
	37	-0.787	-0.724
	38	-0.871	-0.414
	39	-0.678	-0.361
	40	-0.304	-1.281
	41	1.787	-1.720
	42	0.525	0.820
	43	-0.833	0.821
	44	-0.818	1.700
	45	-0.388	-0.823
	46	1.067	-0.818
	47	0.858	-0.476
	48	0.403	-0.404
	49	-0.822	0.499
	50	-0.841	0.874

CASE LABEL	NO	FACTOR 1	FACTOR 2
	51	0.798	-0.270
	52	-0.088	0.792
	53	-0.383	-0.410
	54	-0.829	-0.883
	55	-1.214	-0.206
	56	0.288	0.877
	57	-0.138	0.260
	58	0.411	-0.338
	59	-1.236	1.038
	60	-1.787	0.312
	61	0.723	0.805
	62	0.026	0.894
	63	0.746	-0.711
	64	1.286	-0.487
	65	-0.052	0.884
	66	0.186	0.767
	67	0.020	-0.186
	68	-0.830	0.853
	69	0.433	0.888
	70	0.039	-0.071
	71	0.208	-0.368
	72	-0.885	-0.486
	73	-0.446	0.472
	74	-1.172	-0.884
	75	-1.209	0.004
	76	0.705	0.918
	77	-1.028	2.284
	78	0.906	-0.038
	79	-0.063	0.807
	80	0.072	1.071
	81	0.685	0.248
	82	0.389	0.872
	83	-0.012	0.843
	84	-0.188	1.438
	85	-0.006	1.188
	86	-1.818	1.818
	87	0.188	0.882
	88	-1.388	1.005
	89	-0.228	0.898
	90	-0.186	0.886
	91	1.418	-1.818
	92	0.108	-0.838
	93	0.874	-0.488
	94	0.818	-0.217
	95	1.038	-0.884
	96	0.574	0.222
	97	-1.851	2.287
	98	-1.988	2.837
	99	0.458	1.237
	100	0.434	0.131

CASE LABEL	NO	FACTOR 1	FACTOR 2
	101	0.128	0.882
	102	0.834	0.824
	103	0.388	0.871
	104	0.718	0.282
	105	-0.882	1.487
	106	1.248	0.126
	107	0.002	0.438
	108	0.410	0.488
	109	0.278	0.768
	110	0.240	-0.288
	111	-0.438	-0.832
	112	0.888	-1.178
	113	0.114	-1.138
	114	-0.824	-0.761
	115	-0.817	-0.888
	116	-0.253	-0.966
	117	0.038	0.807
	118	0.122	-0.188
	119	-0.172	-0.812
	120	-0.210	-1.163
	121	-0.787	-0.860
	122	-0.341	-1.071
	123	-0.328	-1.148
	124	-0.440	-0.888
	125	-0.729	-0.880
	126	0.144	12.065
	127	0.009	1.192
	128	-0.883	1.888
	129	1.131	0.434
	130	1.338	0.314
	131	0.108	1.443
	132	1.085	0.774
	133	0.109	1.178
	134	0.846	-0.843
	135	1.133	-0.681
	136	-0.158	-1.127
	137	1.123	-0.788
	138	0.916	-0.858
	139	-0.485	-0.741
	140	-0.228	-0.864
	141	-0.134	-1.488
	142	-0.784	-0.271
	143	-0.134	-0.891
	144	-0.348	-0.752
	145	-0.887	-0.306
	146	-0.880	-0.688
	147	-0.058	-1.053
	148	-0.824	-0.761
	149	-0.817	-0.886
	150	-0.871	-0.414

CASE LABEL	NO	FACTOR 1	FACTOR 2
	151	-0.867	-1.083
	152	-0.848	-0.852
	153	-0.430	-0.487
	154	-0.678	-0.447
	155	-0.018	-1.287
	156	-0.882	-0.707
	157	-0.787	-0.724
	158	-0.888	-0.486
	159	-0.838	-0.832
	160	-0.253	-0.886
	161	-0.320	-0.884
	162	-0.157	-1.017
	163	1.220	0.801
	164	0.388	0.822
	165	0.873	1.472
	166	0.888	1.088
	167	1.014	0.832
	168	0.847	0.812
	169	1.728	0.287
	170	1.080	0.726
	171	0.845	1.085
	172	0.144	2.085
	173	1.118	0.880
	174	1.480	0.878
	175	0.886	0.716
	176	1.781	0.261
	177	1.486	0.887
	178	2.328	-0.426
	179	1.843	-0.272
	180	1.381	0.822
	181	1.778	0.122
	182	1.867	0.886
	183	1.017	0.838
	184	2.118	0.323
	185	0.751	1.878
	186	0.882	0.844
	187	1.834	0.888
	188	1.742	0.888
	189	1.280	0.318
	190	1.283	0.184
	191	0.618	1.223
	192	1.083	0.850
	193	0.854	1.032
	194	1.882	0.282
	195	2.230	0.483
	196	2.240	0.171
	197	1.174	0.880
	198	1.892	0.312
	199	0.883	0.871
	200	1.117	0.728

CASE LABEL	NO	FACTOR 1	FACTOR 2
	201	1.124	0.882
	202	0.222	1.785
	203	1.838	-0.253
	204	0.748	1.158
	205	1.032	0.427
	206	0.891	1.217
	207	1.280	0.282
	208	0.340	1.488
	209	-0.308	1.0774
	210	-0.032	1.388
	211	1.310	0.880
	212	1.634	0.828
	213	0.818	0.842
	214	1.328	0.863
	215	0.873	1.448
	216	0.778	0.843
	217	-0.284	1.883
	218	-2.857	3.008
	219	-3.152	3.841
	220	-0.071	-1.673
	221	-0.872	-1.158
	222	-0.805	-0.885
	223	0.128	-1.844
	224	-0.883	-1.172
	225	-0.837	-1.251
	226	-0.888	-1.178
	227	-0.317	-1.864
	228	-0.478	-1.108
	229	-0.767	-1.180
	230	-0.486	-1.200
	231	-0.420	-1.838
	232	-0.038	-1.888
	233	-1.018	-0.488
	234	0.780	-2.188
	235	-0.837	-0.480
	236	0.248	-1.743
	237	-0.310	-1.484
	238	-1.188	-0.888
	239	-0.761	-0.808
	240	-1.402	-0.440
	241	-1.318	-0.888
	242	-0.388	-1.888
	243	-0.885	-0.885
	244	-0.288	-1.823
	245	-1.138	-0.873
	246	-1.487	-0.178
	247	-1.882	-0.434
	248	-1.807	-0.368
	249	-1.806	-0.187
	250	-2.512	0.871

CASE LABEL	NO	FACTOR 1	FACTOR 2
	251	-2.486	0.112
	252	-1.808	-0.235
	253	-1.883	-0.023
	254	-1.702	-0.438
	255	-3.784	1.836
	256	-1.420	-0.806
	257	-1.876	-0.763
	258	-1.880	-0.873
	259	-1.818	-0.882

APPENDIX TABLE 10.

BMDP4M - PRINCIPAL COMPONENTS ANALYSIS
TAY L AND CAM L SPECIMENS
FACTOR 1 MORPH. AND FACTOR 1 MERIS. ATTR. SCORES

CASE LABEL	NO	FACTOR 1	FACTOR 1
	1	1.240	0.703
	2	1.120	0.671
	3	1.422	0.486
	4	1.107	0.249
	5	1.035	0.938
	6	1.195	0.635
	7	0.928	0.845
	8	0.882	0.780
	9	1.436	1.089
	10	0.847	1.067
	11	0.837	0.709
	12	0.891	0.720
	13	0.847	0.822
	14	0.938	0.891
	15	0.868	0.263
	16	0.899	0.840
	17	0.912	0.894
	18	0.885	1.145
	19	1.273	0.944
	20	1.588	1.022
	21	1.487	1.315
	22	0.937	1.182
	23	1.084	0.884
	24	0.801	0.840
	25	0.885	1.001
	26	0.830	1.178
	27	0.862	1.328
	28	1.127	0.678
	29	0.787	1.247
	30	0.757	0.954
	31	0.677	0.886
	32	0.818	0.946
	33	0.972	0.861
	34	0.221	0.894
	35	0.302	0.803
	36	0.948	0.978
	37	1.218	1.320
	38	0.746	1.055
	39	1.042	0.748
	40	0.847	1.105
	41	0.702	0.846
	42	0.827	1.135
	43	-0.887	1.106
	44	-1.218	1.488
	45	-0.504	-1.098
	46	-0.802	-1.301
	47	-0.530	-1.083
	48	-0.488	-0.881
	49	-0.760	-1.396
	50	-0.803	-0.887

CASE LABEL	NO	FACTOR 1	FACTOR 1
	51	-1.043	-1.121
	52	-0.818	-1.102
	53	-0.842	-0.887
	54	-0.778	-1.008
	55	-0.838	-0.789
	56	-0.787	-1.020
	57	-0.821	-1.082
	58	-0.788	-0.882
	59	-0.887	-0.886
	60	-0.827	-1.013
	61	-0.390	-0.840
	62	-0.813	-1.076
	63	-0.890	-0.883
	64	-0.869	-0.838
	65	-0.837	-1.428
	66	-1.192	-1.072
	67	-0.716	-0.831
	68	-0.877	-1.237
	69	-0.808	-1.084
	70	-0.884	-1.281
	71	-1.001	-0.828
	72	-1.458	-1.122
	73	-1.367	-0.891
	74	-1.218	-1.052
	75	-1.821	-0.732
	76	-1.587	-1.360
	77	-1.348	-1.002
	78	-1.041	-0.883
	79	-1.387	-0.721
	80	-1.858	-1.138
	81	-1.281	-1.020
	82	-1.337	-1.020
	83	-1.337	-0.939
	84	-1.280	-0.831

APPENDIX TABLE 11.

BMDP4M - PRINCIPAL COMPONENTS ANALYSIS
UPG SPECIMENS
FACTOR 1 MORPH. AND FACTOR 1 MERIS. ATTR. SCORES

CASE LABEL	NO	FACTOR 1	FACTOR 1
	1	0.579	0.288
	2	0.807	-0.444
	3	0.778	1.405
	4	-0.838	-1.184
	5	-0.892	-1.110
	6	-1.823	-1.826
	7	1.878	0.325
	8	-0.837	1.052
	9	-0.046	-0.084
	10	-0.766	-1.418
	11	-0.186	-1.418
	12	-0.440	-1.182
	13	-0.398	0.349
	14	0.140	-0.266
	15	-0.140	0.885
	16	-0.148	0.707
	17	-0.844	-1.246
	18	0.766	-0.819
	19	-0.183	0.809
	20	-0.813	-1.383
	21	-0.886	-0.833
	22	-0.739	-0.174
	23	-0.888	-1.223
	24	-0.778	-0.858
	25	-0.716	-0.787
	26	0.488	0.881
	27	1.847	1.824
	28	-0.500	0.857
	29	-1.847	-0.813
	30	-0.888	0.888
	31	-1.068	-0.768
	32	-0.884	-0.816
	33	-0.713	-0.828
	34	-0.863	-0.851
	35	-0.884	-1.066
	36	-1.021	-0.887
	37	-1.248	-0.806
	38	-1.289	-0.832
	39	-1.381	-0.813
	40	-1.140	-1.278
	41	1.288	-0.862
	42	0.849	1.045
	43	-0.705	0.390
	44	0.080	1.005
	45	-0.839	-1.111
	46	0.881	-0.251
	47	0.816	0.217
	48	0.463	-0.178
	49	-0.470	0.283
	50	-0.432	0.288

CASE LABEL	NO	FACTOR 1	FACTOR 1
	51	1.000	0.278
	52	0.444	0.866
	53	-0.883	-0.489
	54	-1.048	-0.806
	55	-1.818	-0.823
	56	0.830	0.814
	57	-0.008	0.282
	58	0.487	-0.125
	59	-0.831	0.339
	60	-1.811	-0.866
	61	1.029	0.870
	62	0.848	0.770
	63	0.488	0.811
	64	1.480	0.826
	65	0.081	0.805
	66	0.741	0.852
	67	0.880	0.867
	68	-0.281	0.836
	69	1.200	0.811
	70	0.036	0.402
	71	0.258	-0.140
	72	-1.488	-0.882
	73	-0.258	0.822
	74	-1.088	-1.088
	75	-1.848	-0.332
	76	1.440	1.195
	77	-0.124	1.824
	78	1.288	0.384
	79	0.323	0.384
	80	0.788	1.178
	81	0.829	0.870
	82	0.885	0.781
	83	0.291	0.888
	84	0.742	1.090
	85	0.748	1.241
	86	-1.183	0.731
	87	-0.723	0.721
	88	-1.288	0.478
	89	0.382	0.846
	90	0.186	0.834
	91	0.883	-0.837
	92	-0.128	-0.822
	93	1.048	-0.108
	94	0.806	-0.182
	95	0.878	0.888
	96	1.083	0.846
	97	-1.018	1.212
	98	-0.888	1.732
	99	1.207	1.135
	100	0.718	0.182

CASE LABEL	NO	FACTOR 1	FACTOR 1
	101	0.718	0.621
	102	1.208	1.188
	103	0.874	0.882
	104	1.182	0.788
	105	0.128	1.072
	106	1.888	0.808
	107	0.427	0.230
	108	0.818	0.484
	109	0.887	0.625
	110	0.472	-0.278
	111	0.838	-0.878
	112	0.827	-0.481
	113	-0.278	-1.188
	114	-1.023	-1.211
	115	-1.023	-1.148
	116	-0.883	-1.001
	117	0.808	1.103
	118	0.128	-0.210
	119	-0.888	-1.138
	120	-0.880	-1.481
	121	-1.233	-0.878
	122	-0.841	-1.518
	123	-1.081	-1.248
	124	-0.908	-1.121
	125	-1.182	-1.026
	126	1.184	2.284
	127	0.443	1.723
	128	-0.082	1.720
	129	1.820	1.108
	130	1.718	1.181
	131	0.838	1.884
	132	1.718	1.384
	133	0.782	1.284
	134	0.720	-0.082
	135	1.208	-0.428
	136	-0.783	-1.318
	137	1.026	-0.488
	138	0.788	-0.277
	139	-0.878	-1.008
	140	-0.[illegible]	-1.088
	141	-1.018	-1.287
	142	-0.887	-0.830
	143	-0.826	-1.282
	144	-0.777	-0.886
	145	-0.737	-0.888
	146	-1.087	-0.888
	147	-0.870	-1.138
	148	-1.023	-1.211
	149	-1.023	-1.148
	150	-1.288	-0.732

CASE LABEL	NO	FACTOR 1	FACTOR 1
	151	-1.823	-1.826
	152	-0.888	-0.833
	153	-0.718	-0.787
	154	-0.778	-0.888
	155	-0.813	-1.383
	156	-1.021	-0.887
	157	-1.248	-0.806
	158	-1.486	-0.882
	159	-0.936	-0.878
	160	-0.882	-1.001
	161	-0.839	-1.184
	162	-0.892	-1.110
	163	1.888	1.248
	164	0.818	0.828
	165	1.788	2.003
	166	1.307	1.883
	167	1.483	1.381
	168	1.388	1.217
	169	2.188	1.383
	170	1.888	1.806
	171	1.883	1.882
	172	1.184	2.284
	173	1.818	1.123
	174	2.028	1.488
	175	1.423	1.483

APPENDIX TABLE 12.

BMDP4M - PRINCIPAL COMPONENTS ANALYSIS
FIRST 2 FACTOR SCORES

CAM L SPECIMENS

CASE LABEL	NO	FACTOR 1	FACTOR 2
	1	1.107	-0.070
	2	0.040	-0.082
	3	1.054	0.614
	4	1.131	-1.052
	5	0.611	-0.378
	6	0.431	-1.893
	7	-0.417	0.844
	8	0.432	0.184
	9	0.713	3.218
	10	0.184	1.184
	11	0.728	0.141
	12	0.216	0.247
	13	0.804	0.837
	14	0.496	-0.801
	15	2.317	-0.477
	16	0.881	0.095
	17	1.332	-0.611
	18	1.028	-0.318
	19	0.088	0.251
	20	0.859	0.081
	21	0.234	1.977
	22	-0.716	0.325
	23	0.323	0.220
	24	0.883	-0.016
	25	0.721	0.148
	26	0.172	-0.121
	27	-0.779	0.372
	28	-1.304	-0.052
	29	-1.355	0.218
	30	-0.738	-0.122
	31	-1.859	1.043
	32	-1.862	0.849
	33	-1.132	-0.350
	34	-0.533	0.577
	35	-1.144	-1.271
	36	-2.210	1.202
	37	-0.916	-1.042
	38	-0.842	-2.040
	39	-0.987	-1.926
	40	-0.801	-1.483

TAY L SPECIMENS

CASE LABEL	NO	FACTOR 1	FACTOR 2
	1	0.830	-0.204
	2	0.606	-0.802
	3	1.643	-0.387
	4	0.752	-1.868
	5	0.852	0.015
	6	0.786	-0.201
	7	0.178	0.888
	8	0.206	0.040
	9	1.867	1.813
	10	0.388	1.408
	11	-0.246	-0.336
	12	0.212	-1.209
	13	0.100	-1.813
	14	0.038	-1.814
	15	-0.188	-1.782
	16	-0.817	-1.481
	17	0.094	0.221
	18	-0.074	0.084
	19	1.288	0.713
	20	1.030	1.492
	21	1.488	1.288
	22	0.196	1.063
	23	0.428	-1.291
	24	-0.288	-0.838
	25	-0.022	-1.081
	26	0.128	0.287
	27	-0.865	1.058
	28	0.433	-0.851
	29	-0.111	1.102
	30	-0.212	-0.787
	31	-0.428	0.404
	32	-0.202	-0.217
	33	-0.684	-0.048
	34	-1.222	0.408
	35	-1.252	-0.806
	36	0.258	0.883
	37	0.606	1.174
	38	-0.348	0.174
	39	0.312	0.381
	40	-0.182	0.338
	41	-0.401	-0.828
	42	-0.886	1.075
	43	-3.244	-0.044
	44	-3.858	1.800

APPENDIX TABLE 13. Summary of catch data (in % of total population) in terms of gonad maturity from Upper Pierre Grey Lake, 1984.

	Jun 4	Jun 12	Jun 17	Jun 26	Jul 6	Jul 14	Jul 20	Jul 25	Aug 1
Phoxinus eos									
male with milt	22.3	11.3	16.0	10.8	13.5	18.8	11.9	5.4	3.1
male without milt	13.8	8.9	11.8	10.2	9.3	18.0	22.9	32.1	46.2
ripe female	13.8	17.6	18.2	24.1	22.9	13.9	14.4	14.0	0
fully ripe female	0	0	2.5	9.1	10.7	9.9	4.9	3.7	0
spent female	0	0	0	0	4.4	5.6	8.3	15.2	27.5
female without egg	15.9	1.0	5.5	4.4	5.5	8.9	9.2	8.6	6.2
Phoxinus neogaeus									
male with milt	0	0	0	0	0	0	0	0	0
male without milt	0	0	0.7	0	0.6	0.7	0	0	0
ripe female	11.7	13.9	4.8	6.2	4.7	3.6	1.8	0	0
fully ripe female	0	0	0	3.0	1.5	0.5	0.7	0.2	0
spent female	0	0	0	0	2.4	2.3	2.0	1.6	4.0
female without egg	7.4	7.1	2.3	3.3	2.0	2.1	3.8	3.7	0.8
Hybrid									
ripe female	19.1	20.8	21.6	14.7	8.2	3.1	4.9	4.0	0
fully ripe female	0	0	1.9	8.3	6.4	1.8	3.1	1.4	0
spent female	0	0	0	0	3.5	2.9	4.3	6.3	9.6
female without egg	9.6	10.3	7.5	5.8	4.0	7.6	7.6	3.5	2.6

APPENDIX TABLE 14. Summary of catch data (in % of total population) in terms of gonad maturity from Upper Pierre Grey Lake, 1985.

	Jun 2	Jun 10	Jun 17	Jun 25	Jul 3	Jul 17	Jul 23	Jul 29	Aug 8
Phoxinus eos									
male with milt	2.3	12.3	13.7	19.1	24.3	6.5	5.2	0	0
male without milt	14.4	9.7	15.8	8.5	9.2	9.7	18.5	11.2	27.1
ripe female	25.4	10.6	7.6	7.5	20.4	5.6	4.4	0	0
fully ripe female	0	0	8.2	9.0	5.3	2.3	1.2	0	0
spent female	0	0	4.4	3.5	3.3	10.2	19.7	23.0	25.9
female without egg	11.0	12.7	9.3	13.5	13.8	15.3	13.7	13.3	16.0
Phoxinus neogaeus									
male with milt	0	0	0	0	0	0.9	0	0	0
male without milt	0	0	0	0	0	0.5	0.4	1.0	0
ripe female	6.9	4.6	3.3	0.5	0.6	0	0	0	0
fully ripe female	0	2.5	2.7	0.5	1.9	2.0	0	0	0
spent female	0	0.8	3.3	5.0	1.9	1.4	4.0	5.9	7.4
female without egg	6.3	4.2	2.7	11.5	5.9	12.1	6.8	2.7	2.5
Hybrid									
ripe female	21.4	29.2	7.1	4.0	2.0	0.9	0	0	0
fully ripe female	0	1.7	10.4	5.5	2.0	4.2	0.8	0	0
spent female	0	1.7	2.7	4.0	1.3	5.1	4.0	34.2	13.6
female without egg	12.1	9.7	8.7	7.5	11.8	23.2	21.0	8.5	7.4