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ECOLOGY AND TAXONOMY OF HYBRIDIZING CYPRINID FISHES FROM UPPER AND LOWER KANANASKIS RESERVOIRS, ALBERTA

by

GEORGE A. BUTCHER

A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled ECOLOGY AND TAXONOMY OF HYBRIDIZING CYPRINID FISHES FROM UPPER AND LOWER KANANASKIS RESERVOIRS, ALBERTA submitted by GEORGE A. BUTCHER in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

ABSTRACT

Principal components and canonical variates analyses of hybridizing *Couesius plumbeus* (lake chub) and *Rhinichthys cataractae* (longnose dace) from Upper and Lower Kananaskis Reservoirs, Alberta, using 21 morphological characters, revealed two parental groups bridged continuously by an intermediate hybrid group. This morphological overlap between the hybrids and the parental species indicates that it is not always possible to positively identify 'pure' parental individuals from the Kananaskis. Neither backcross nor hybrid F2 individuals could be identified from the analyses, although the Kananaskis *R. cataractae* showed effects suggestive of introgression, relative to known *R. cataractae* from widespread Alberta localities. *R. cataractae* has also declined in numbers relative to *C. plumbeus* since last studied in 1961. *C. plumbeus* does not show similar effects suggestive of introgression.

C. plumbeus, *R. cataractae*, and their F1 hybrids were electrophoretically examined for five different protein systems. Only the serum prealbumen bands proved to be a reliable biochemical marker for the distinction of the two species. F1 hybrids can be identified by the presence of both parental prealbumen bands.

The effectiveness of the species' reproductive isolating mechanisms was studied in Lower Kananaskis Reservoir. Segregation in spawning time and habitat was not apparant. There was complete overlap in the spring spawning

period of the two species, and habitat isolation was absent in all areas studied except one inlet stream. Artificial crosses of the species, examination of hybrid sex products, and life history data showed no effective postmating isolation. The existence of distinct species' specific mating behaviors was not confirmed. However, ethological isolation is inferred to be important in minimizing this hybridization. Hybrid fertility was not experimentally confirmed.

All of the recognized environmental factors which facilitate the dissolution of species' isolation appear to be important in causing this hybridization. This includes environmental disturbance, paucity of spawning areas, species introductions, and rarity of one parental species. It does not appear possible to single out any of these factors as having the major role in facilitating hybridization.

PREFACE

"That old and true method of Natural History - observation - must ever have a large share in the study of living things. Together they are omnipotent; disjoined they become impotent fetishes. Biology of today, as we are beginning to realize, has not too much laboratory but too little of living Nature."

C.O. Whitman (1902)
Biological Farm.
Biol. Bull. Mar. Biol. Lab.,
Woods Hole 3: 214-224.

ACKNOWLEDGMENTS

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Unfailing field assistance was provided by Martin T. Weckerle for which I am most grateful. I also wish to thank the Cochrane boys, Jim, Les, and John for their enthusiastic, voluntary assistance in both laboratory and field.

The hospitality extended to me by the staff of the Kananaskis Environmental Science Centre (University of Calgary) contributed immeasurably to this research. I thank Dr. Gordon Hodgson and Linda Jones for providing the superb living accommodations and laboratory space as well as the generous use of Centre equipment. It was a pleasure to receive laboratory assistance at the Centre from Drs. Chris Whitely, Peter Wallis, and John Corbin, and Mr. Dennis Jacques. I thank especially Dr. Allan Legge for his refreshing discussions, humour, and sage advice.

Environment Canada (Inland Water Directorate), Calgary, performed the water quality analyses.

Mr. J. Abelseth, Calgary Power Ltd. provided data on reservoir levels and assisted by winching the truck from

numerous mud-holes and welding our boat trailer in the field.

I owe thanks to Mr. Wayne Roberts (UAMZ) for the loan of specimens in his care, the loan of the Museum's calipers, and his efficient cataloguing of specimens on short notice.

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I am grateful to Dr. Alan Wells for his invaluable assistance with various computer programs and statistical procedures, and for his insightful discussions on fish systematics. Dr. Jan Vrbik, University of Calgary, also assisted me through the morass of multivariate statistical computer programs.

Dr. J.R. Nursall was responsible for supervision of this study in the Department of Zoology, University of Alberta: his assistance and criticisms were always valuable. I wish to thank the members of my committee, Drs. B. Heming, J.C. Holmes, J.S. Nelson, and M.V.H. Wilson for their criticisms, interest and assistance at various stages of my research.

I am indebted to Dr. Brian Hammond (Environment Alberta) both for his assistance as a funding supervisor and for his friendship through difficult times. To Mr. Fraser McConnel, my solicitor, I owe thanks for his adroit actions

in preventing the escalation of the petty to the ridiculous.

Finally, I acknowledge a debt of gratitude to Diane who sacrificed innumerable weekends and evenings to my pursuit, and who suffered what seemed to be an almost interminable stay in Edmonton.

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I. GENERAL INTRODUCTION

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, 1969) following secondary contact - poses interesting problems and makes contributions to several levels of study, ranging from systematics and evolution 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 which discriminate the parental species (Hubbs, 1955). However, the wild-caught hybrid individuals are not always strictly intermediate between that of the 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 parental variants is additionally complicated by the possible presence of backcrosses and further hybrid generations. These difficulties have been largely ignored in most previous taxonomic investigations. The inadequacy of traditional hybrid index statistical techniques (Smith, 1973) may have contributed to this situation. Multivariate statistical

techniques have been advanced to overcome these problems of hybrid identification, by maximizing the separation of parental taxa, and by revealing the possible presence of backcrosses (Colgan *et al.*,1976; Smith, 1973). Such claims have not yet been subjected to intense scrutiny.

Apart from a purely morphological identification of hybrid individuals, the taxonomist is presented with the possibility of discriminating hybrids using single isoenzyme characters. This offers a second set of data with which to test the initial identification.

At the evolutionary level of study, two hybridizing populations may be expected to undergo observable and statistically significant evolutionary changes if hybrid fertility occurs (i.e., fusion or character displacement). The investigator is presented with the problem of determining the magnitude and direction of such changes if they exist. Such an approach can contribute to our understanding of evolution, but only with the availability of adequate past specimens from the area of hybridization.

At the ecological level, it is necessary to determine if and how 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. Also, the long-term viability of hybrid individuals has implications for the strength of competitive interactions between the species in

an area of hybridization. Accumulating evidence suggests that hybrids succeed in environments where competition from parental phenotypes is weak (Moore, 1977).

Disturbance of the aquatic environment, either naturally or man-induced, is a primary cause of fish hybridization (Hubbs, 1955). The escalating manipulation of our lakes and rivers for reservoirs and other development purposes poses a threat to the integrity of the resident fish species. At the practical level then, hybridization studies improve our understanding of how environmental changes directly affect species, and may contribute to the mitigation of effects of future development.

Several problems at these levels were undertaken in this study of hybridization between Couesius plumbeus (Agassiz) and Rhinichthys cataractae (Valenciennes) in Upper and Lower Kananaskis Reservoirs, Alberta. At the taxonomic level, this study presents the first multivariate statistical analyses of external morphological data; it examines hybrid variability and investigates the possibility of hybrid fertility. In so doing, the effectiveness of multivariate techniques to yield such information can be practically evaluated. To corroborate the hybrid identification by morphology, an electrophoretic analysis of the population was initiated. The possibility of phenotypic changes in the Kananaskis population, evolving over 17 years of known hybridization, is also examined. The ecology of spawning populations, the effectiveness of the isolating

mechanisms, and the results of artificial cross experiments are described in order to ascertain the causes of hybridization. As a consequence, this research provides the first thorough reproductive and life history data for these species from Alberta.

II. STUDY SITE

The Upper and Lower Kananaskis Reservoirs are located approximately 50 km south of the confluence of the Kananaskis and Bow Rivers, and within 5 km of the headwaters of the Kananaskis River at the continental divide (Fig. 1). Both reservoirs cover original mountain lake basins. The Upper Lake was the first to be modified with the construction of two hydroelectric dams (Interlakes) in 1936 and 1942. The Lower Lake was impounded in 1955, by the Pocaterra Dam. A detailed description of the history of hydroelectric development and the storage characteristics of these reservoirs is provided by Nelson (1962).

Water is stored during the spring and summer run-off and released through the fall and winter to generate electricity. The Upper Reservoir is the last to be filled and the first to be drawn down. Both reservoirs follow the same annual cycle of level fluctuations: extreme high in October and extreme low in April. The amount of water drawn down in late winter is regulated according to the amount of snowfall accumulation. Thus, the amplitude of reservoir level fluctuations may be quite variable from year to year and may differ between the two reservoirs.

The surface area of the Lower Reservoir varies from 283 hectares at low supply level to 648 hectares at full supply level. The surface area of the Upper Reservoir varies from 633 to 855 hectares (data from Nelson, 1962). The extensive area of flooded shoreline is littered with the stump and

Figure 1. Map of Upper and Lower Kananaskis reservoirs (1 cm = 0.55 km). The stars in each reservoir mark positions of water quality sampling stations. Fish sampling sites are marked with dots and site numbers (corresponding to the numbers in Appendix Tables 1. and 2.). The inset photo is copied from a Landsat I false color image shot on 5 October 1972, at an altitude of 920 km and processed by the Canada Centre for Remote Sensing, Ottawa. The image format centre is Lat.N. 51°15', Long.W. 155°00' and corresponds to the National Topographic Survey (Canada) Map 820.


Kent Creek
LK8
Smith-Dorrien Creek
Pocaterra Dam
LK9
LK7
Invincibile Creek
LK6
N
N
LK5
Lower Kananaskis Reservoir
LK4
LK3
Calgary
Upper and Lower Kananaskis Reservoirs
LK2
Boulton Creek
Interlakes Dam
RACEWAY
Kananaskis River
UK7
UK8
Common Bay
LK1
S.E. Arm
UK6
UK5
S.W. Arm
Twin Falls
Interlakes Stream
UK3
Dam
UK1
UK4
UK2
Sarrail Creek
Upper Kananaskis Reservoir

root remnants of trees removed prior to dam construction. The Government of Alberta began partial removal of stumps and roots in June, 1978. The substrate of this 'fluctuation' zone consists of unconsolidated gravel and boulders interspersed with large areas of thick eroded silt (Plate 8). The only benthic fauna to utilize this 'fluctuation' zone are the chironomids (Fillion, 1963).

In the spring, as the reservoirs fill, the spawning fish are presented with flooded shoreline areas and with upstream areas of original inlet creeks. By the time spawning commences in late May (suckers) or early June (cyprinids), the presumed original spawning beds have been flooded.

All inlet streams of the Upper Kananaskis Reservoir flow unrestricted in their natural beds. The flow of Boulton Creek and Invincible Creek into the Lower Reservoir has remained unchanged since pre-impoundment days. However, due to dam construction, Smith-Dorrien Creek and the diverted Kent Creek, which formerly drained into the Kananaskis River, now drain into the Lower Reservoir. All four streams flow unregulated with spring and summer run-off.

The original outlet flow (at the extreme south end of the Lower Reservoir), from the Upper Lake into the Lower Lake, has been reduced to seepage through the earthfill dam (here designated as Interlakes Stream). Similarly, the man-made outlet of the Upper Reservoir into the Lower Reservoir at Interlakes Dam is controlled so that there is

no flow during the spring and summer (i.e., from end of drawdown in April, to its recommencement in October).

III. PAST STUDIES

Previous pre- and post-impoundment studies on the limnology, productivity, and fishes of the Upper and Lower Kananaskis Reservoirs were reviewed by Nelson (1962) in order to establish the chronology of biological changes. Nelson deduced that both *C. plumbeus* and *R. cataractae* were introduced to the Upper and Lower Kananaskis Reservoirs as bait fishes, probably from Bow River populations (*R. cataractae* probably in the 1930's; *C. plumbeus* probably in the late 1950's). The occurrence of hybridization between these two species in Upper Kananaskis Reservoir was noted by Nelson (1962). The external morphology of hybrids from Upper Kananaskis Reservoir was described by Nelson (1966). The hybrids from both reservoirs were later examined using osteological characters and a hybrid index technique (Nelson, 1973). One juvenile specimen appeared to be intermediate between the majority of hybrids and one parental phenotype.

Hybridization between *C. plumbeus* and *R. cataractae* has been noted in several localities outside Alberta (Simon, 1946, in Wyoming; Hubbs and Lagler, 1949, in Lake Superior; Taylor, 1954, in Michigan), but without the substantiating evidence provided by Nelson (1966, 1973).

Identification of *C. plumbeus* x *R. cataractae* hybrids by numerical taxonomic or electrophoretic techniques has not been reported. Additionally, the reproductive ecology of the Kananaskis populations has not been studied.

IV. FISH SAMPLING

METHODS

Fish were collected between May 10 and August 29, 1977, from Upper and Lower Kananaskis Reservoirs and between May 1 and July 27, 1978, from Lower Kananaskis Reservoir.

C. plumbeus, and R. cataractae and their hybrids were sampled from the reservoirs proper, using monofilament gillnets (18 mm, 26 mm, and 38 mm stretch mesh), beach seines (8 mm mesh), dipnets, and baited minnow traps. This variety of sampling methods assured the capture of all sizes of specimens. Sampling sites are shown in Figure 1 and site descriptions provided in Appendix Table 1 and Table 2. The relative abundance of the hybridizing species was established for all localities. Data on depth, substrate type, and distance from shore were recorded for all captures. The study of the breeding biology of the cyprinids in 1978, involved intensive sampling of only the Lower Reservoir. The Upper Reservoir presented boat access problems in the early spring.

Inlets of Lower Kananaskis Reservoir were electroshocked (Smith-Root Electroshocker Model VII) beginning in late April 1978, when the majority of the reservoir was ice-covered (95%). A beach seine was stretched across each inlet stream mouth and the stream was electroshocked and the bottom disturbed downstream into the seine (refer to Plate 7). Smith-Dorrien Creek, Boulton Creek, Kent Creek, and the original outlet stream of Upper

Kananaskis Lake (here designated as Interlakes Stream) were sampled in this manner. As spring run-off increased, it became impossible to sample inlet streams (except Interlakes Stream), and gillnets were placed across the stream mouths and minnow traps placed along the edges.

Standard length and sex were recorded for all fish sampled. A representative sample was returned to the laboratory for weighing, gonad and scale removal, and preservation in 10% formalin. Samples of the two species and their hybrids were deposited in the University of Alberta Museum of Zoology (UAMZ).

GENERAL CATCH RESULTS

Cyprinid catch data from 1977 and 1978 for Upper and Lower Kananaskis Reservoirs are summarized in Appendix Tables 1 and 2. Capture method, locality, date, depth, and numbers of specimens are provided.

The ratios of parental species to hybrid individuals captured in each year were as follows: 1977, 133 C. plumbeus to 7 R. cataractae to 1 putative C. plumbeus x R. cataractae; 1978, 174 C. plumbeus to 12 R. cataractae to 1 putative C. plumbeus x R. cataractae. A total of 56 putative hybrids were captured in 1977 and a total of 9 putative hybrids were captured in 1978. A disproportionate cyprinid species' ratio in favour of C. plumbeus was also recorded by Nelson (1962). He found C. plumbeus to be 4.0 to 5.6 times as numerous as R. cataractae in gillnet catches for Lower

and Upper Kananaskis Reservoirs, respectively. Results of the present study (*C. plumbeus* 14 - 19 times as numerous as *R. cataractae*) may indicate an increase in the disproportion of species' numbers over the intervening 17 years. It is not known if *C. plumbeus* is numerically increasing, or if *R. cataractae* is numerically declining.

Suspected cyprinid hybrids were captured throughout both reservoirs and were not concentrated in a limited number of locations. Relatively large hybrid capture numbers (Appendix Table 1 and Table 2) at certain sites are due to more intensive sampling at these sites. Hybrids were captured alone and with individuals of each species. Capture of the hybrids was both infrequent and unpredictable.

The cyprinids sporadically swarmed in large schools with juvenile suckers over recently flooded inshore areas. The schools were observed only in midsummer on sunny days when the water temperature exceeded 15°C; schooling did not occur on cloudy, windy, or cool days. The majority of the large seined collections came from the infrequent occasions on which such large schools were observed. Hybrids were often collected from such schools. Except for these occasions, the cyprinids generally remained offshore. The mixed schools were involved neither with reproduction (since they occurred after spawning) nor with feeding (since the flooded areas are assumed not to have a developed bottom fauna). The reasons for this mixed schooling remains unstudied.

V. LIMNOLOGY

INTRODUCTION

Changes in environmental factors can trigger fish hybridization (Hubbs, 1955). The modification of a lake to a reservoir is accompanied by an obvious annual change in surface water elevation and basin morphometry. This change may directly affect fish spawning habitat so that miscegenation results.

Less visible are the possible indirect effects of changes in water quality and the thermal regime. Small changes in these factors may upset the competitive balance existing between the species and result in a disproportion of one species (a possible precursor to hybridization). An altered temperature regime may affect the timing of species' spawning activities thereby destroying a temporal barrier to reproductive isolation. Changes in these environmental factors may contribute to what Anderson (1949) termed the "hybridization of the environment" (Anderson, 1949).

Apart from accurate water level statistics, there are only few and rudimentary limnological data available for Upper and Lower Kananaskis Lakes prior to impoundment (Rawson, 1937, 1948; Miller, 1954; Thomas, 1955).

The purpose of this section is to: 1) document the degree of water level fluctuations; 2) document present water chemistry and temperature conditions; and 3) to speculate as to whether the latter have undergone significant changes since impoundment.

METHODS

Physico-chemical parameters were measured mid-monthly during June, July, and August, 1977, from three depths (surface, mid-depth, and 1 m off bottom) at one sampling station on each of the Upper and Lower Kananaskis Reservoirs (Fig. 1). The water samples were shipped within 24 hours to Environment Canada, Inland Waters Branch, Calgary, Alberta, for analysis of alkalinity, color, pH, residue (non-filterable), turbidity, total Kjeldahl nitrogen, total phosphorus, and total carbon. Water quality samples were not taken during the summer of 1978. Water temperature profiles were recorded when water samples were collected, and also sporadically through the summer. The dates on which water temperature profiles were taken from Lower Kananaskis Reservoir in 1977, are as follows: May 9,17, 31; June 20,29; July 15; Aug. 8,16; Sept. 3,17. Water temperature was measured at 1 m intervals using a Y.S.I. telethermometer. Reservoir elevations were provided by Calgary Power Ltd.

RESULTS AND DISCUSSION

Results of the water quality analysis for Upper and Lower Kananaskis Reservoirs are presented in Appendix Tables 3 and 4. Most of these water quality parameters are reported for the first time from these reservoirs.

Both reservoirs have similar basic pH values. These do not appear to have changed since last studied by Fillion (1963) and Nelson (1962). According to Nelson, no pH change

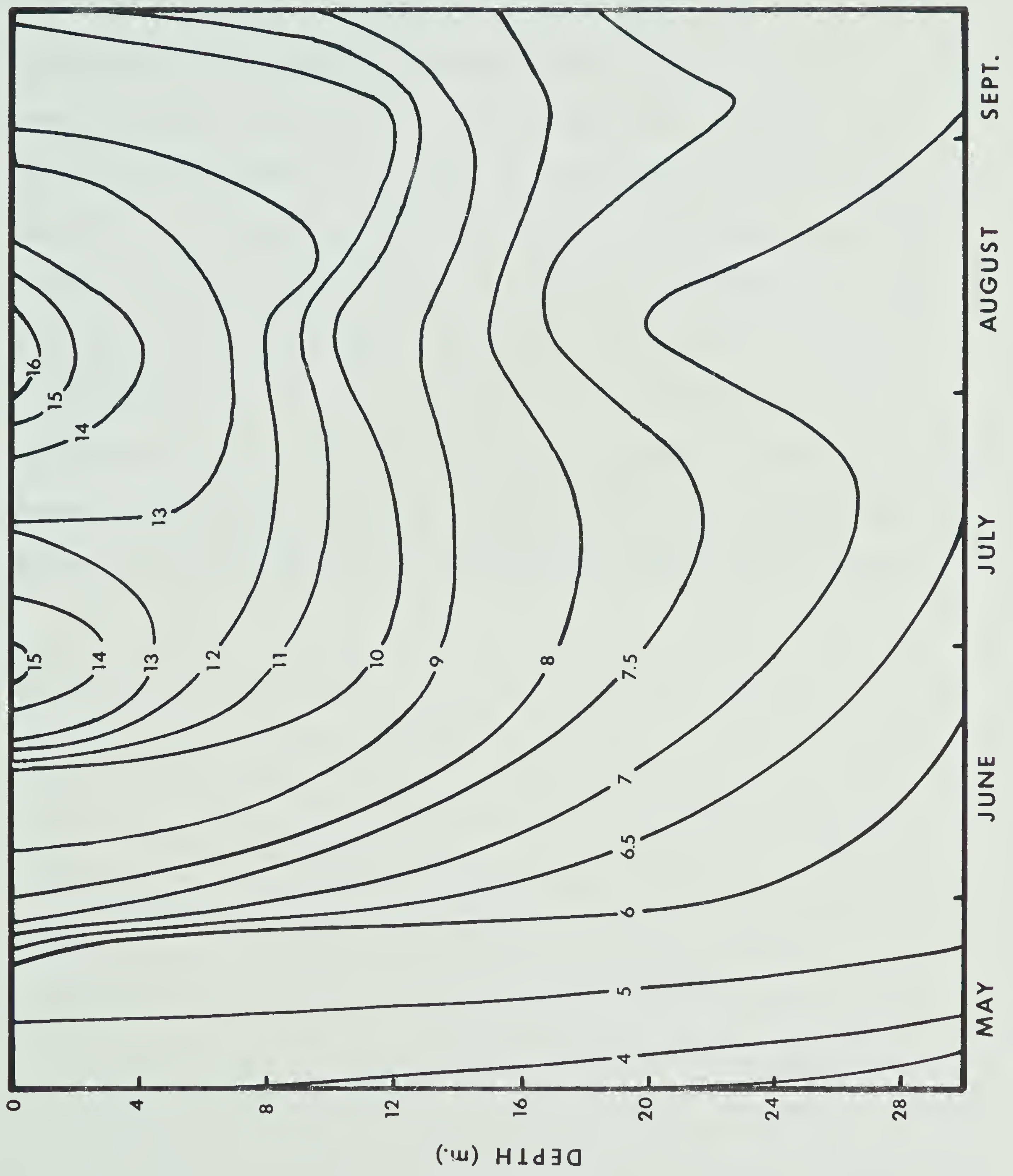
accompanied construction of Lower Kananaskis Reservoir.

Specific conductance values are high for each reservoir as a result of spring run-off. The values for the Lower Kananaskis Reservoir are consistently higher than those of the Upper Reservoir, a trend shown by Fillion. Inorganic carbon values are also higher for the Lower Kananaskis Reservoir.

The remaining parameters - color, residue, turbidity, nitrogen, phosphorus, and organic carbon - show no difference between the reservoirs. An examination of all the above parameters does not reveal any change attributable to reservoir construction. Both reservoirs are characterized by the clarity and nutrient-poor state expected for that of the original lakes.

Spring and summer isotherms from Lower Kananaskis Reservoir, 1977, are shown in Figure 2. These were constructed from the water temperature profile data. Additional temperature data from 1978, are provided in Appendix Table 5. Some thermal stratification occurs during the summer. There have been no thermal changes since the studies by Nelson and Fillion. This probably represents the original thermal situation in the Lower Lake for the spring and summer months. Since Calgary Power Ltd. does not lower the level of Upper Kananaskis Reservoir in the summer, there is no unnatural input of cool hypolimnetic waters into the Lower Reservoir in the summer. There is no reason to believe that the water temperature cue for spawning has been

Figure 2. Spring and summer, 1977 isotherms (in °C) from the water quality sampling site, Lower Kananaskis Reservoir.


DEPTH (m.)
0
4
8
12
16
20
24
28
MAY
JUNE
JULY
AUGUST
SEPT.
4
5
6
6.5
7
7.5
8
9
10
11
12
13
14
15
13
14
15
16

altered. However, the effects of hypolimnetic input from Upper Kananaskis Reservoir during fall drawdown on fish biology remains unstudied.

Annual water level fluctuations for 1977 and 1978, are shown graphically in Figures 3 and 4 for Upper and Lower Kananaskis Reservoirs, respectively. There is much unpredictability in water level from year to year; the amount of drawdown is adjusted according to the amount of snowfall accruing through the winter. Of more importance, there is significant annual variation in water levels at spawning time: in Upper Kananaskis Reservoir a 0.6 m difference and in Lower Kananaskis Reservoir a 2.0 m difference. These differences are enough to radically alter shoreline characteristics from year to year. Permanent spawning areas cannot be established under this regime.

Figure 3. Annual water level fluctuations in the Upper Kananaskis Reservoir during 1977 and 1978. Elevation is given as above sea level. Data provided by Calgary Power Ltd.

Upper Kananaskis Reservoir

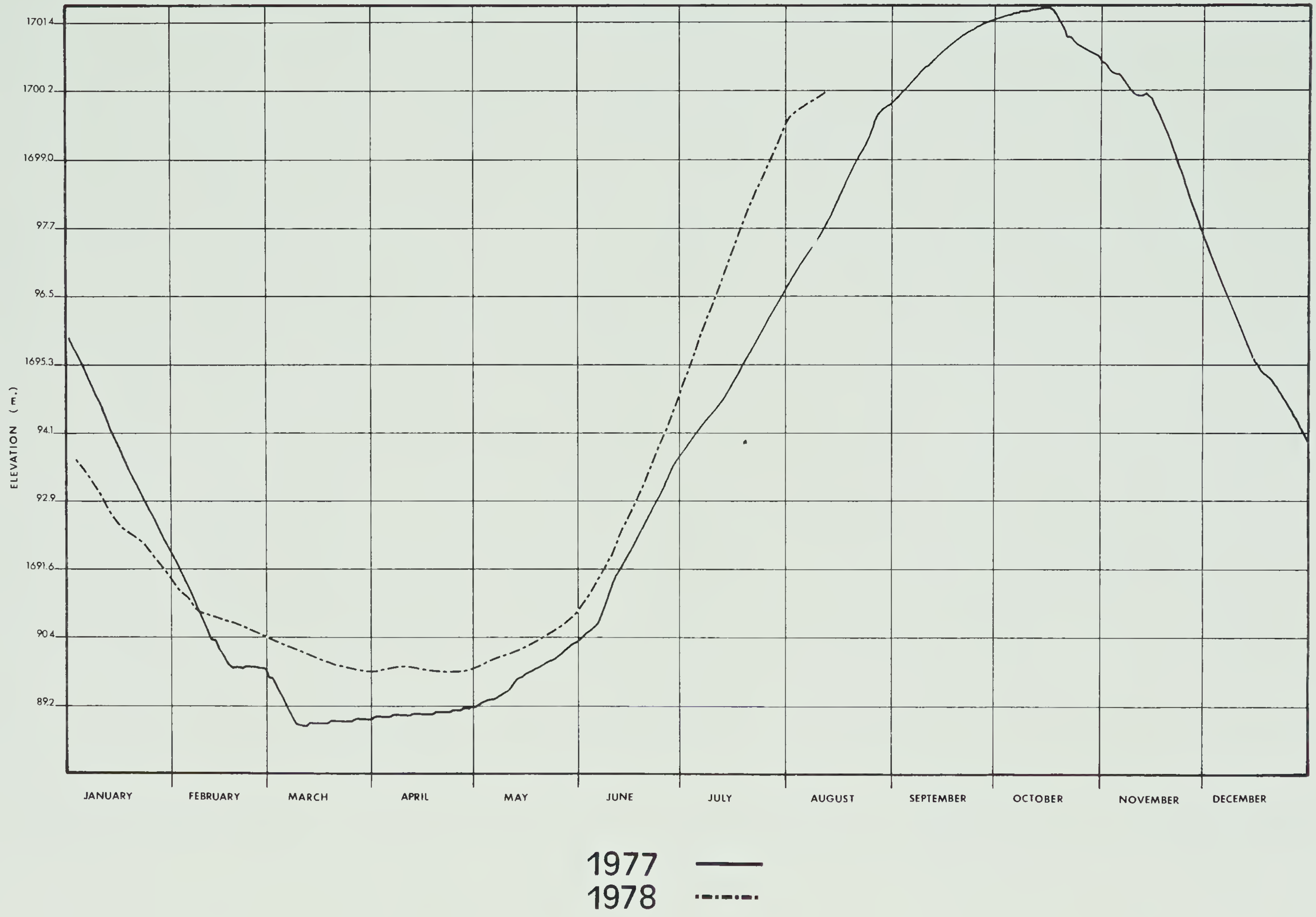
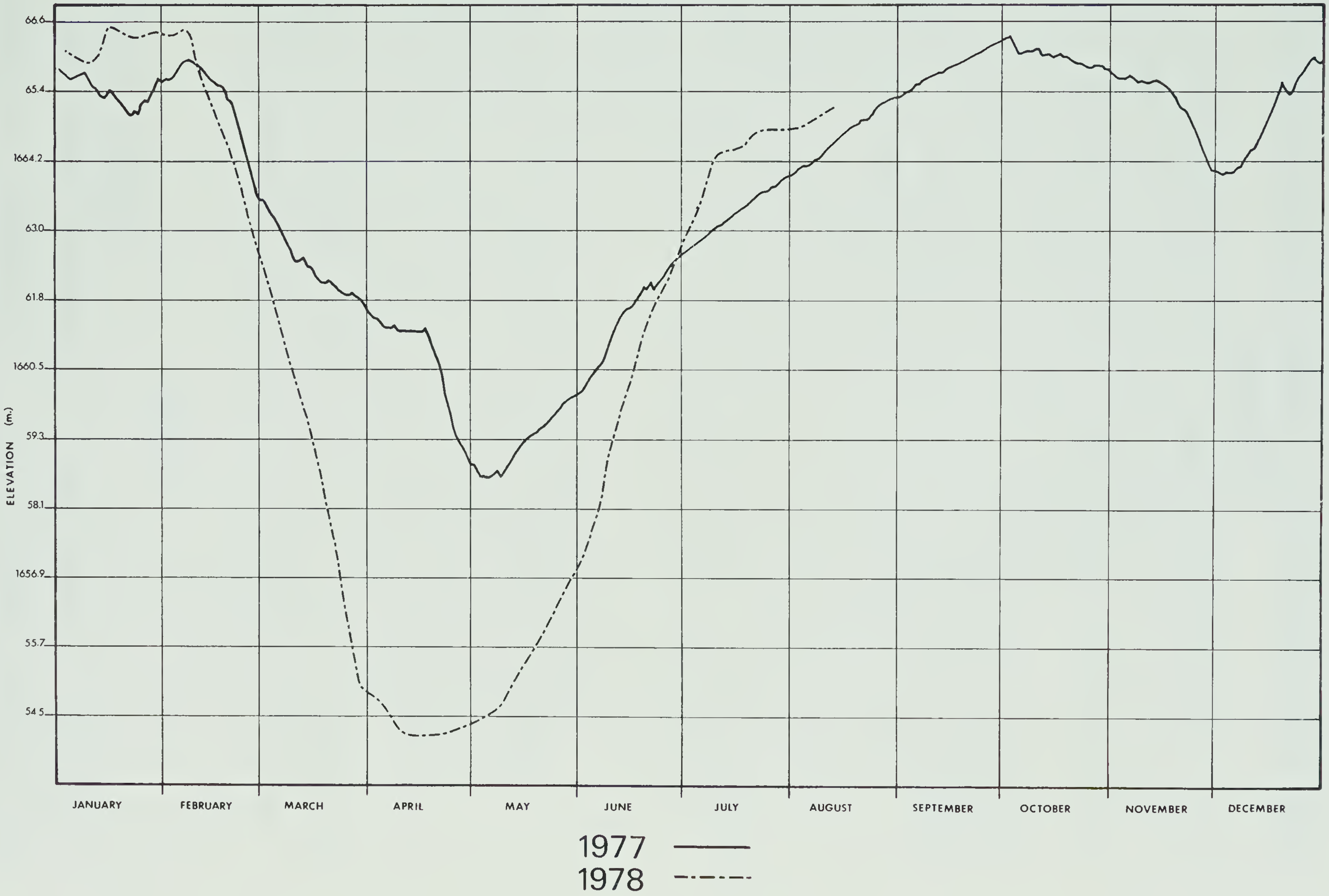


Figure 4. Annual water level fluctuations in the Lower Kananaskis Reservoir during 1977 and 1978. Elevation is given as above sea level. Data provided by Calgary Power Ltd.

Lower Kananaskis Reservoir



VI. IDENTIFICATION OF HYBRIDS USING MULTIVARIATE ANALYSIS

INTRODUCTION

Although the Kananaskis cyprinid hybrids were identified and morphologically examined by Nelson (1966, 1973), including analysis by hybrid index, there have been no numerical taxonomic studies attempted.

The advantages of multivariate statistical techniques relative to traditional methods have been reviewed by Smith (1973). Of singular importance is elimination of the necessity to prejudge hybrid or parental origin of the specimens. This is of particular value when hybrids are variable and hybrid fertility is possible. In such cases, it may be impossible to discriminate hybrids from parental individuals.

This section of the study describes principal components and canonical variates analyses of numerous morphological characters of both hybrids and parental individuals. The methods do not require assumptions as to the identity of any Kananaskis specimens. Hybrid variability, possible hybrid fertility, and the effects of hybridization over time on the populations are described.

METHODS

SPECIMENS EXAMINED

The external morphology of representative Kananaskis specimens was compared to: 1) that of museum specimens from Alberta localities where hybridization is presumed not to

occur; and to 2) that of museum specimens collected from these reservoirs in previous years.

All Kananaskis specimens examined in the morphological studies were deposited in the University of Alberta Museum of Zoology (UAMZ numbers 4145-4201).

There was a collecting bias in the field directed equally toward the less common specimens, i.e., typical *R. cataractae* and all putative hybrids. Typical *C. plumbeus*, being highly abundant, were randomly collected. A random sample of 137 specimens was chosen from the field collections of each reservoir, irrespective of sex and presumed identity, and were used in the analyses (designated here as the Kananaskis specimens). The sex ratio for the entire Kananaskis sample was 62 females to 75 males.

Fifty *C. plumbeus* and fifty *R. cataractae* were selected from widespread Alberta localities in UAMZ collections encompassing several drainage systems (designated here as the Alberta specimens). These control specimens were selected such that the size (standard length) range was similar to that of the Kananaskis specimens. The catalogue numbers, locations, and sex ratios of these collections are given in Table 1. Unfortunately, due to the scarcity of large male *R. cataractae* in the UAMZ collections, the sex ratio of Alberta *R. cataractae* was predominantly female. The sex ratio for the entire Alberta sample was 73 females to 27 males.

Past collections of *C. plumbeus* from Upper and Lower

TABLE 1. Locations and University of Alberta Museum of Zoology catalogue numbers for Alberta control specimens of *Couesius plumbeus* and *Rhinichthys cataractae*.

Species	Locality	Lat. N/Long. W	UAMZ#	Number of Specimens Examined
C. plumbeus	Brazeau Reservoir	52°57' 115°35'	566	8
	Red Deer River	52°19' 113°06'	3326	8
	Abraham Reservoir	52°16' 116°23'	3350	8
	Little Smokey River	54°44' 117°10'	1654	8
	Pothole Creek	49°25' 112°54'	3843	8
	Winefred River	56°02' 110°36'	3451	2
	Bare Creek	49°14' 110°00'	3231	3
	McIvor River	58°18' 118°03'	3418	3
	N. Saskatchewan River	52°25' 116°04'	3325	2
Total sex ratio of 27 ♀:23 ♂				
R. cataractae	N. Saskatchewan River	52°16' 116°23'	3381	7
	N. Saskatchewan River	53°30' 113°34'	2044	2
	N. Saskatchewan River	52°16' 116°23'	3322	1
	Graburn Creek	49°38' 110°01'	1620	7
	Cutbank River	54°43' 118°32'	3903	2
	Horse River	56°43' 111°23'	3435	2
	Abraham Reservoir	52°16' 116°23'	3369	5
	Gregoire River	56°29' 110°48'	3414	6
	Pothole Creek	49°25' 112°54'	4000	2
	Pothole Creek	49°25' 112°54'	3843	5
	Bare Creek	49°14' 110°00'	3231	5
	Willson Creek	51°49' 115°13'	3873	4
	Wapiti River	55°08' 118°18'	269	1
	Pinto Creek	54°58' 119°28'	272	1
Total sex ratio of 46 ♀:4 ♂				

Kananaskis Reservoirs were subjected to morphological study to determine any effects of hybridization over time. The 1961 collection of 11 C. plumbeus from Upper Kananaskis Reservoir (UAMZ 863) were analyzed. Twenty-five C. plumbeus were examined from the 1969 collections (UMAZ 2706, 2707, 2518) and 25 from the 1973 collections (UAMZ 3345, 3346) including specimens from both Upper and Lower Kananaskis Reservoirs. Only specimens within the size range of the Kananaskis specimens were selected.

Past Alberta collections of R. cataractae in the UAMZ holdings were few and contained only small specimens beyond the size range comparable to the Kananaskis specimens. These were deemed inadequate for comparison to recent Kananaskis collections. Thus, it was only possible to study the effects of hybridization over time on C. plumbeus.

CHARACTERS USED

The following 21 morphological and meristic characters were recorded for all 298 specimens. These were chosen because all were good descriptors of the fishes' shape and because some are known (Nelson, 1966) to be efficient discriminators of the parental species and of the putative hybrids. Counts and measurements follow the descriptions and diagrams in Hubbs and Lagler (1964) except as otherwise defined. Measurements were made using needle point dial calipers, read to the nearest 0.1 mm. Microscope magnification was used when required. Abbreviations for each

character follow in parentheses.

1. standard length (SL)
2. head length (HL)
3. orbit length (OL)
4. snout length (SN)
5. interorbital width (IN) - (the least fleshy width of the interorbital)
6. head depth at nostril (HDN) - the distance from the nostril downward to the ventral contour of the head.
7. head width at eye (HWE) - the greatest dimension from one lateral side of the head to the other lateral side on a line below the orbits.
8. mouth length (ML) - (length of upper jaw)
9. mandible width (MAN) - (width of gape)
10. snout overhang (SOV) - the distance from the tip of the snout along the midline to the most anterior portion of the lower jaw.
11. frenum width (FRE) - the distance between the grooves separating the upper jaw from the snout.
12. isthmus width (IW) - the distance between the gill membranes at point of attachment to isthmus.
13. body width at dorsal fin origin (WDO) - the maximum distance from one lateral side of the body to the other lateral side on a line below the dorsal fin origin.
14. snout to dorsal fin origin (SDO) - (pre-dorsal length)
15. caudal peduncle length (CP)
16. snout to anus (STA) - distance from the tip of the snout to the anal opening.
17. pectoral fin origin to anus (PTA)
18. depth of caudal fin fork (CF) - the distance from the apex of the caudal fork outward to a straight line connecting the tips of each outstretched caudal fin lobe.

19. number of lateral line scales (LS)
20. number of scales from dorsal fin origin along diagonal to lateral line (ALS) - (number of scales above lateral line).
21. number of scales around caudal peduncle (CPS)

This is the order in which the characters were used in all following morphological analyses.

Ratios were specifically avoided in order to eliminate problems with allometry and compounded variance (Marr, 1955; Atchley _et al._, 1976). Multivariate analyses were run with untransformed data and square-root transformation, since size differences could lead to vectors not being coplanar (Pimental, 1976). Frenum width for known _C. plumbeus_ was always 0.00, and since several other characters also had values < 1.0, a logarithmic transformation of the data set was inappropriate. The effectiveness of using transformed data was assessed.

These 21 characters were chosen from an original 31 characters because of their significant contribution toward group discrimination. The 10 characters discarded prior to in-depth analysis included: mouth to eye length (distance from corner of the mouth along midline to a vertical line marking the anterior margin of the orbit), cheek depth, dorsal fin origin to pelvic fin origin, dorsal fin height, anal fin height, pelvic fin axillary process (absence, presence), number of gillrakers, number of pectoral rays, number of anal rays, and number of dorsal rays.

Some of these characters, e.g., dorsal fin origin to

pelvic fin origin, number of gillrakers, and number of fin rays were discarded because they were ineffective at group discrimination. The rest were removed because they were confounding sources of variation. The characters, mouth to eye length, and cheek depth could not be accurately measured, pelvic fin axillary process could not be accurately scored, and the fin height characters are sexually dimorphic (Wells, 1978). Since each sex was not separately analyzed, characters of known sexual dimorphism were eliminated.

STATISTICAL TECHNIQUES

Principal Components Analysis

Principal components analysis (PCA) (Morrison, 1967; Cooley and Lohnes, 1971; Pimental, 1976) was used to display patterns of morphological similarity of individuals from mixed species' populations with hybrids, relative to populations without hybrids. 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, within the data. The plot of the specimens on the first three components will usually display a great amount of the total variance within the data set.

PCA scores were calculated from the character correlation matrix using the Clustan 1C computer program (Wishart, 1975) for the following two separate data sets: 1)

all 137 Kananaskis specimens; and 2) 100 control Alberta specimens. The projection scores of the specimens in the two data sets were plotted against the first and second axes and also against the second and third axes. Untransformed and square-root transformed data were analyzed. The assumption of a single multivariate normal population for a PCA has been ignored for these reasons: 1) no statistical inferences were drawn from these analyses; and 2) departures from normality are not thought to invalidate the results (Dudzinski *et al.*, 1975).

Canonical Variates Analysis

The same two data sets (untransformed and square-root transformed) were subjected to canonical variates analysis (CVA) in order to quantify the relationship between individuals (Pimental, 1976). This method requires the *a priori* identification of two or more known groups within the data set. Axes are calculated which maximally separate these groups while minimizing the within-groups 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 BMD 07M computer program (Dixon, 1973) was used to assess the relationship between the Kananaskis specimens (the *a priori* unknown group) and the control Alberta specimens (the *a priori* known group). The canonical scores were plotted against the first canonical axis and graphed as

frequency histograms. An examination of further canonical axes did not discriminate more groups than was revealed by the first canonical axis.

In addition to correct a priori identification, CVA assumes a multivariate normal distribution with equal variance-covariance matrices. A Bartlett's test of homogeneity of dispersions (DERS program; Bay, 1969) on the two known groups showed a significant difference between the matrices ($F = 2.6$, $F_{.05}(210,29352) = 1.00$). However, it is generally held that CVA has sufficient robustness, so that departures from the assumptions will not be serious (Pimental, 1976).

RESULTS

PRINCIPAL COMPONENTS ANALYSIS

The principal component scores for the Alberta specimens, calculated using untransformed data, were plotted against the first three axes (Fig. 5). The results confirm the initial identification of 'pure' specimens representing the two species, with no morphological intermediates.

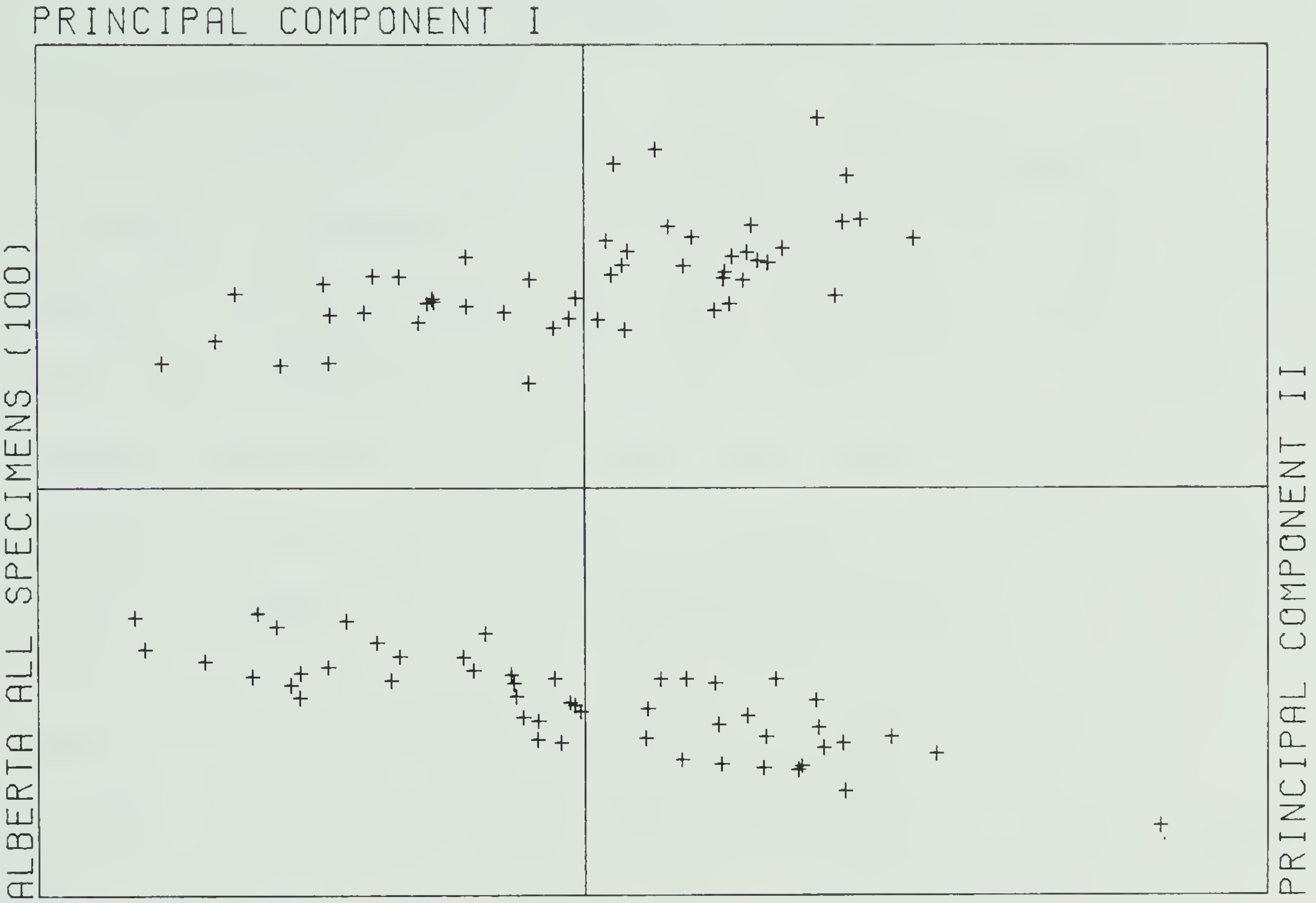
Component I represents overall size differences among the specimens, ranging from small on the left to large on the right. Component II represents between-species discrimination and Component III represents the largest component of within-species variation (perhaps due to sexual dimorphism or population differences). The variation expressed by the three components represents 91.3% of the

Figure 5. PCA Using Untransformed Data; Frenum Included

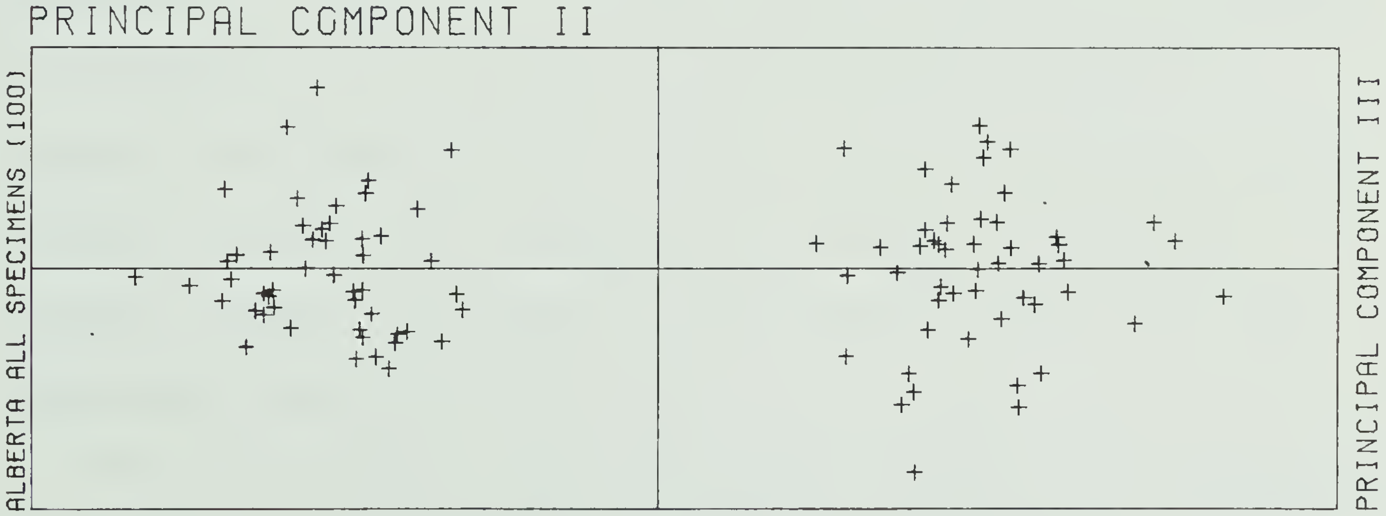
A. Plot of first and second principal component scores for Alberta, 'control' specimens. *Couesius plumbeus*, top cluster; *Rhinichthys cataractae*, bottom cluster. Component I = 59.4% of total variation in 21 character correlation matrix; Component II = 28.3% of variation.

B. Plot of second and third principal component scores for Alberta 'control' specimens. *R. cataractae* on left; *C. plumbeus* on right. Component III = 3.5% of variation.

A.


PRINCIPAL COMPONENT I
ALBERTA ALL SPECIMENS (100)
PRINCIPAL COMPONENT II

B.


PRINCIPAL COMPONENT II
ALBERTA ALL SPECIMENS (100)
PRINCIPAL COMPONENT III

variance in the total data matrix. Investigation of additional components would have been redundant. A summary of the computer results on which these plots are based, is given in Appendix Table 6.

The principal component scores for all Kananaskis specimens, calculated using untransformed data, were plotted against the first three axes (Fig. 6). The projection of scores on components I and II show the elongate clusters, as expected from the control group, but with a dissimilar bridging of the two species' clusters. The specimens of this bridge represent the putative hybrid specimens. The absence of larger hybrid specimens from the Kananaskis sample accounts for the clear discrimination between the two species' clusters to the right of the origin. Large hybrids were available in the collections, and if included in the analysis would presumably occupy this space.

The variation expressed by the three components represents 91.5% of the variance in the total data matrix. The difference in % variation represented by component I between the Alberta group (59.4%) and the Kananaskis group (66.4%) is due to the difference in range of standard lengths between the Alberta group (4.1-11.0 cm) and the Kananaskis group (3.4-12.3 cm).

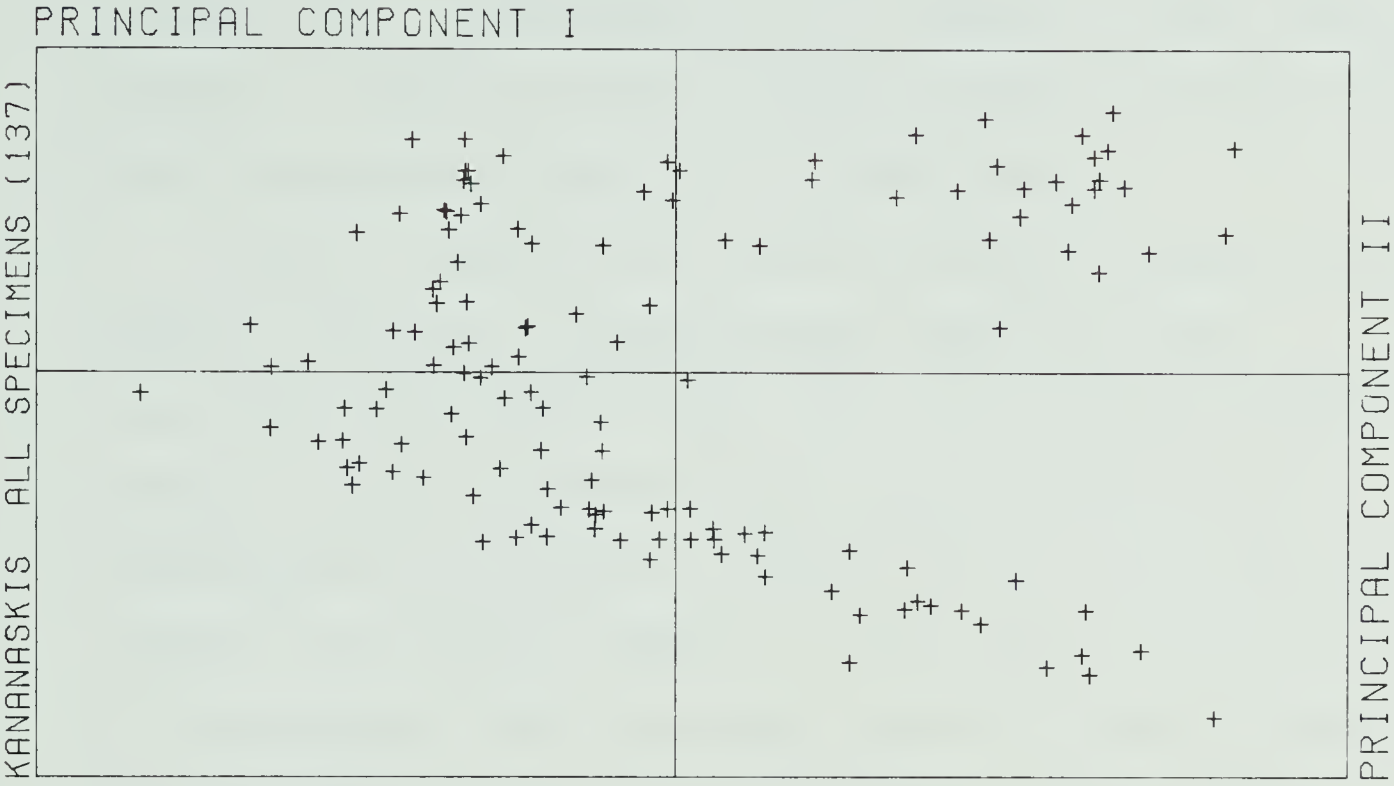
The intervening hybrid complex, shown on the Kananaskis projection of the second and third axes, obscures discrimination between the two species. This analysis provides evidence that the putative hybrids are not all

Figure 6. PCA Using Untransformed Data; Frenum Included

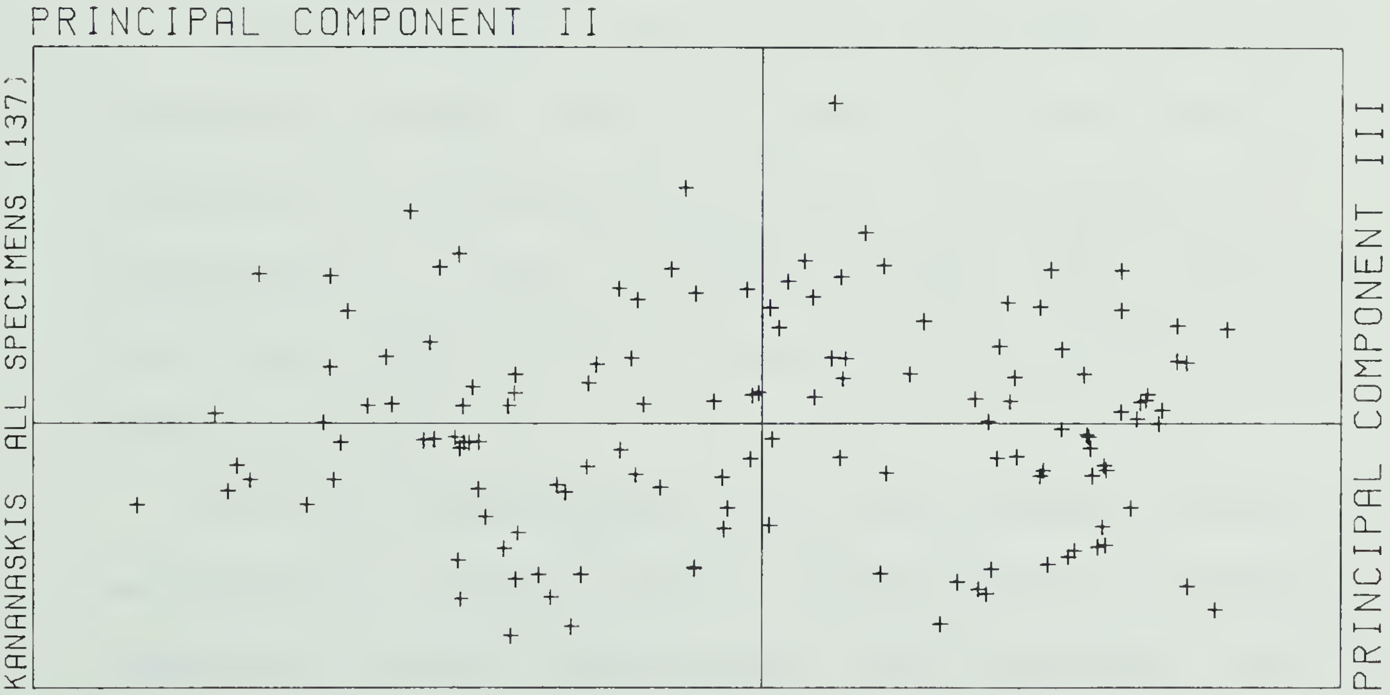
A. Plot of first and second principal component scores for all Kananaskis specimens. *Couesius plumbeus* -like specimens towards bottom; *Rhinichthys cataractae* -like specimens towards top, with a hybrid complex bridging the 2 species clusters. Component I = 66.4% of variation.

B. Plot of second and third principal component scores for all Kananaskis specimens. *C. plumbeus* -like towards left; *R. cataractae* -like towards right. Component III = 4.9% of variation.

A.


PRINCIPAL COMPONENT I
KANANASKIS ALL SPECIMENS (137)
PRINCIPAL COMPONENT II

B.


PRINCIPAL COMPONENT II
KANANASKIS ALL SPECIMENS (137)
PRINCIPAL COMPONENT III

strictly intermediate. They cover the entire phenotypic range between the parentals suggesting mixed genetic origins, i.e., backcrossing of F1 hybrids to each parental species. A summary of the computer results on which these plots are based is given in Appendix Table 7.

Similar analyses were again performed separately on Alberta specimens, and Kananaskis specimens using square-root transformed data. The resulting plots were similar to those generated using untransformed data. Transformation produced a slightly better discrimination between the smallest members of each species, but produced no new insights. The Kananaskis parental species remain continuously bridged to the same degree by the hybrid complex. Computer results for these analyses are summarized in Appendix Tables 8 and 9.

CANONICAL VARIATES ANALYSIS

The relationship between the Kananaskis specimens including hybrids, and the Alberta 'control' species can be expressed in a quantitative manner by a frequency distribution of their canonical scores. The results of a CVA using untransformed data with the full character set are given in Figure 7.

The two distributions for each Alberta species are separated by a large gap of approximately 14 standard deviations between their means. The Kananaskis specimens form a continuous distribution with no gap between the

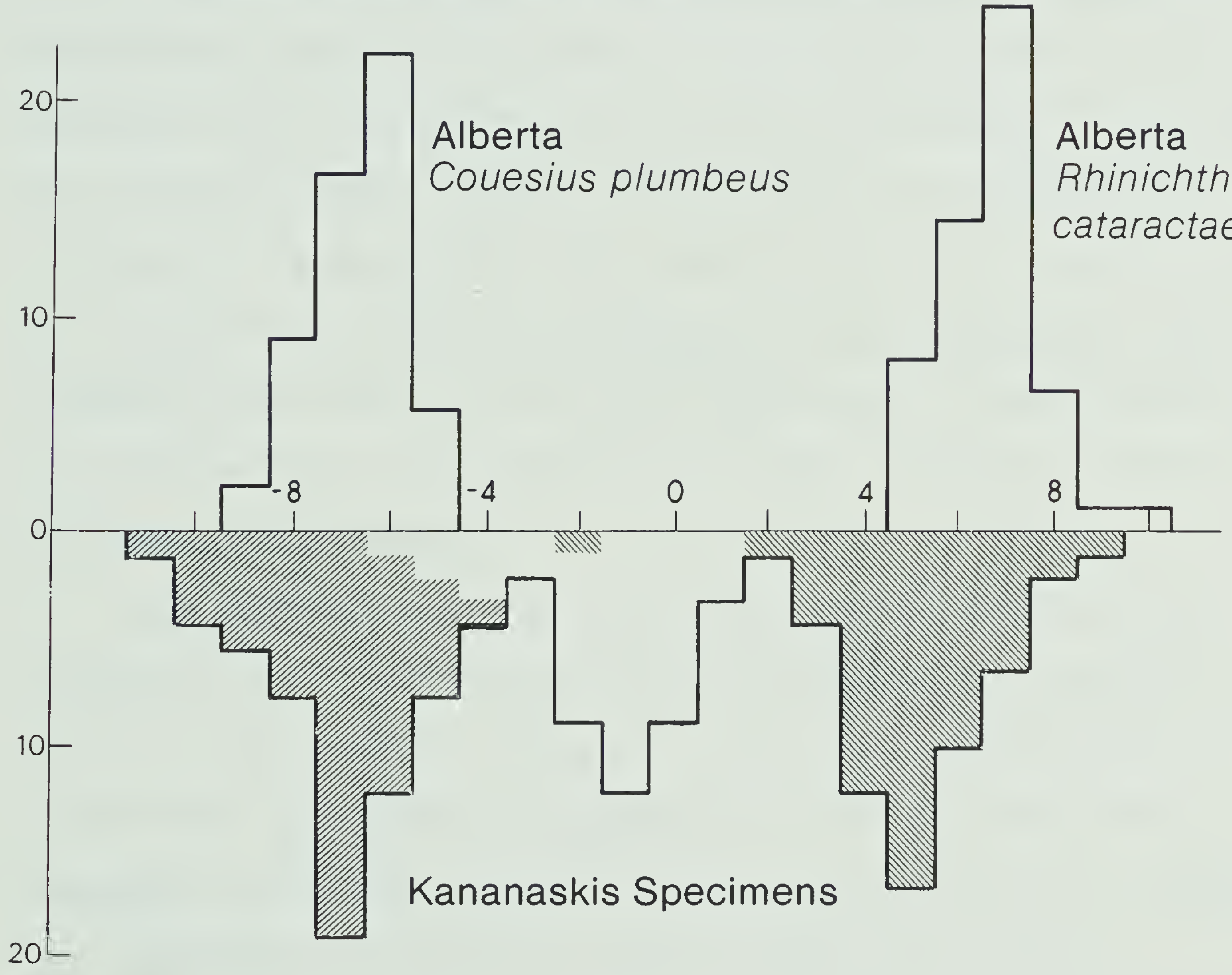
Figure 7. CVA Using Untransformed Data; Frenum Included

Frequency histograms of canonical scores on first canonical axis of specimens from Alberta 'control' group (upper histogram) and Kananaskis group (inverted histogram). Alberta species formed 2 *a priori* known groups; all Kananaskis specimens ran as *a priori* unknown groups. Units on x-axis are in standard deviations; y-axis is number of specimens. Initial field identifications of Kananaskis specimens are shaded as follows:

▨ *Couesius plumbeus*

□ *C. plumbeus X R. cataractae*

▧ *Rhinichthys cataractae*



Untransformed Data, Frenum Character Included

typical parental species.

The apparent trimodality of the Kananaskis distribution was confirmed using Cassie's (1963) graphic method of polymodal frequency separation ($\underline{X}^2$ test for goodness of fit, $\underline{X}^2 = 25.0$; d.f. = 15, $P > 0.05$). The two outer modes of Kananaskis specimens are composed of the corresponding typical parental species. The intermediate mode is composed of the hybrid complex. Although the majority of sampled Kananaskis hybrids fall into the intermediate group, as expected for F1 hybrids, the specimens intermediate between the parental modes and the hybrid mode are of contentious origin. It appears from this analysis that the variance of the typical Kananaskis *C. plumbeus* and *R. cataractae* modes (taken as the far left and far right modes, respectively) are greater than the variances of their respective Alberta control distributions.

The shading patterns in the Kananaskis distribution represent the initial field identifications of specimens, prior to the analysis (Fig. 7). All specimens initially identified as "good" *C. plumbeus* fell within the outer *C. plumbeus* mode. All specimens initially identified as "good" *R. cataractae* , except one, fell within the outer *R. cataractae* mode. A re-examination of this one misidentified *R. cataractae* specimen confirmed its hybrid appearance. Most specimens, initially identified as putative hybrids, were classified in an intermediate position by the CVA. However, several putative hybrids fell within the outer *C. plumbeus*

mode. A re-examination of these putative hybrids (with a canonical score > -3.0) revealed the absence of any frenum in all specimens, suggesting an initial misidentification.

The 12 characters contributing most to species' separation in this CVA are given in Table 2 (along with their coefficients and constants for the discriminant functions and their F ratios). The remaining 9 characters with F values > 1.0 contributed little to the discrimination and could have been eliminated from the analysis. The frenum was the most discriminating character with a high F value (F = 1048.10). The computer results for this analysis are summarized in Appendix Table 10.

It should be recalled (see Methods) that abundant C. plumbeus were randomly collected, whereas all R. cataractae and all putative hybrids captured were kept in the field collections (specimens were identified in the field as putative hybrids by their possession of a partial frenum). The objection might be raised that the formation of the intermediate peak on the histogram is an artifact of selective collecting of hybrids. It is true that the relative number of typical C. plumbeus in the population is far greater than indicated by the histogram. However, it is unlikely that the distinctiveness of the intermediate hybrid group was exaggerated since only a random sample of the field collections was analyzed. Moreover, the distinctiveness of this group relative to C. plumbeus was likely minimized since possible backcross individuals (in

TABLE 2. The 12 most discriminating characters in a CVA using untransformed data, including frenum. Characters are in order of decreasing importance with F ratios (1, 98 df) for inclusion and coefficients and constant for canonical variables (1st canonical axis).

Rank	Character	F	Coefficient
1	FRE	1048.10	-6.65
2	OL	60.69	30.74
3	IW	41.81	-12.41
4	HWE	14.27	7.88
5	CF	13.24	6.08
6	STA	12.09	-2.29
7	HL	3.18	-3.10
8	CP	2.00	-1.76
9	CPS	1.53	-0.07
10	ML	1.41	9.14
11	SN	1.06	5.88
12	ALS	1.05	0.09
			Constant -1.97

the direction of *C. plumbeus*) were collected more rigorously than typical *C. plumbeus*.

Although the frenum character is an efficient discriminator, its removal from the analysis does not seriously affect the results. The CVA histogram using untransformed data without the frenum character shown in Figure 8, is essentially identical to the histogram in Figure 7. Again, there appears to be greater variance in the modes of the typical Kananaskis parental species compared to the control distributions. The computer results for this analysis are summarized in Appendix Table 11. The 12 most discriminating characters in this analysis are given in Table 3. A comparison of Tables 2 and 3 illustrates that CVA is heavily weighted to a dependence on only a few characters.

The results of a CVA using square-root transformed data, with frenum character in the data set, are given in Figure 9. Transformation of the character data results in increased discrimination between the two species. The means of the two Alberta species' distributions are separated by approximately 23 units of standard deviation. Although an intermediate hybrid mode remains, its mean is 2 standard deviations to the left of strict intermediacy (toward *R. cataractae*). This is due to a heavy weighting on the transformed frenum character ($F = 3893.55$) (Table 4). The troughs between the hybrid and parental modes are spread thinner along the first canonical axis than seen previously.

Figure 8. CVA Using Untransformed Data; Without Frenum

Frequency histograms of canonical scores on first canonical axis of specimens from Alberta 'control' group (upper histogram) and Kananaskis group (inverted histogram). Alberta species formed 2 *a priori* known groups; all Kananaskis specimens ran as *a priori* unknown groups. Units on x-axis are in standard deviations; y-axis is number of specimens.

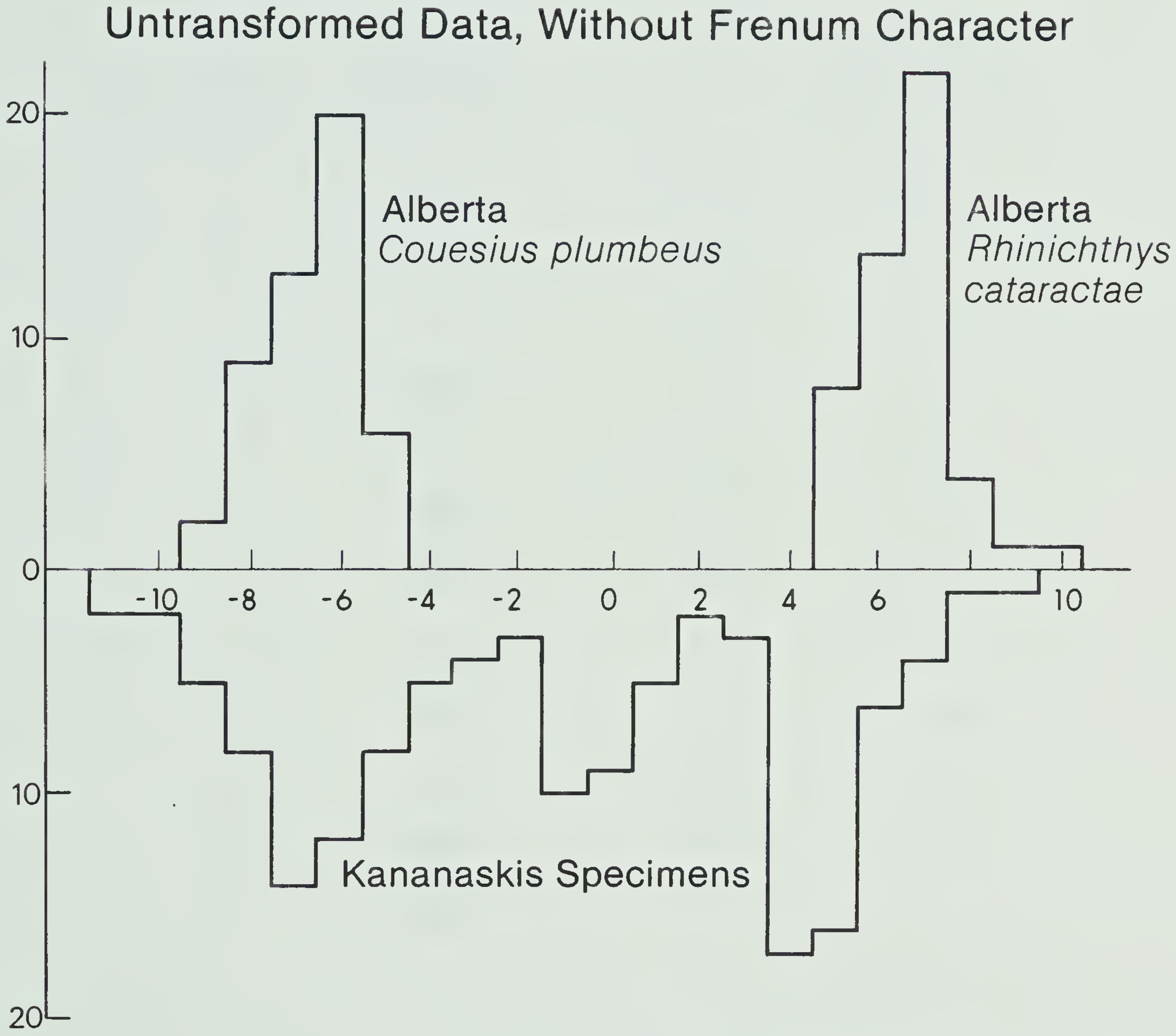

Untransformed Data, Without Frenum Character
20
10
0
10
20
-10
-8
-6
-4
-2
0
2
4
6
10
Alberta
Couesius plumbeus
Alberta
Rhinichthys cataractae
Kananaskis Specimens

TABLE 3. The 12 most discriminating characters in a CVA using untransformed data, without frenum. Characters are in order of decreasing importance with F ratios (1, 98 df) for inclusion and coefficients and constant for canonical variables (1st canonical axis).

Rank	Character	F	Coefficient	
1	IW	682.35	-13.53	
2	OL	207.69	32.87	
3	CF	13.65	6.93	
4	PTA	12.92	0.04	
5	HL	8.41	-3.66	
6	HWE	8.00	8.88	
7	ML	4.95	11.59	
8	CP	3.30	-2.07	
9	CPS	1.58	-0.08	
10	STA	1.52	-2.04	
11	MAN	0.84	-4.48	
12	HDN	0.51	-2.58	
			Constant	-1.06

Figure 9. CVA Using Square-root Transformed Data; Frenum Included

Frequency histograms of canonical scores on first canonical axis of specimens from Alberta 'control' group (upper histogram) and Kananaskis group (inverted histogram). Alberta species formed 2 *a priori* known groups; all Kananaskis specimens ran as *a priori* unknown groups. Units on x-axis are in standard deviations; y-axis is number of specimens.

Square-root Transformed Data, Frenum Character Included

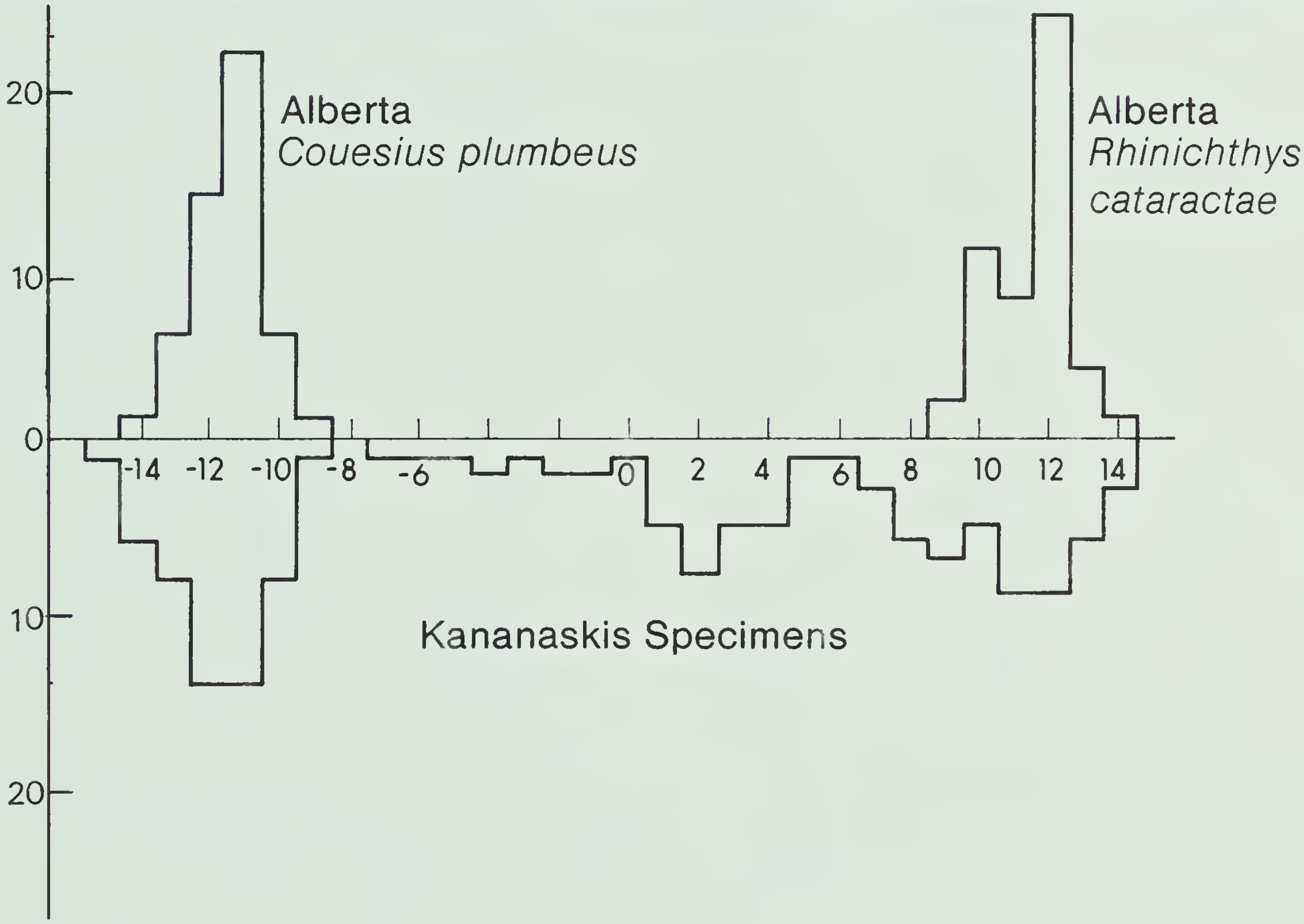


TABLE 4. The 12 most discriminating characters in a CVA using square-root transformed data, including frenum. Characters are in order of decreasing importance with F ratios (1, 98 df) for inclusion and coefficients and constant for canonical variables (1st canonical axis).

Rank	Character	F	Coefficient	
1	FRE	3893.55	24.36	
2	OL	49.30	-26.72	
3	IW	20.49	10.31	
4	CF	17.34	-9.33	
5	HWE	13.12	-13.82	
6	STA	7.94	14.96	
7	SOV	3.98	5.82	
8	CP	3.10	3.46	
9	SN	2.72	-12.63	
10	ALS	1.63	-0.13	
11	PTA	1.39	-9.24	
12	SDO	1.15	7.68	
			Constant	6.39

This indicates that there may be specimens which cannot be accounted for as either good parentals or F1 hybrids.

Unlike the results with untransformed data, the CVA using transformed data does not show as great a difference between the variances of the typical Kananaskis species' modes and the variances of the Alberta control species' distributions. Computer results for the CVA using transformed data are summarized in Appendix Table 12.

Have the two Kananaskis species been modified by this hybridization relative to the 'control' specimens? If it is assumed that the Kananaskis parental modes (Fig. 7) end at the troughs (tails of the mode) next to the hybrid mode, it becomes apparent that: 1) the Kananaskis parental species have greater variances than the 'control' species; and that 2) the means of the Kananaskis species' modes are shifted toward each other, relative to the means of the 'control' species' distributions. This leads to speculation that the cause of this could be backcrossing between hybrids and parentals, i.e., introgression (sensu Mayr, 1969).

CVA- VARIANCE TESTS

The differences in variance were investigated in order to determine if this could be a reliable indicator of introgression. It is known that the CVA procedure minimizes the within-group variance of the a priori known group, at the expense of the variance of the unknown group (Pimental, 1976). To determine how this affected the variances, the

known and unknown groups were switched: the assumed Kananaskis parental species (without presumed hybrids) were run as the *a priori* known group. The results of Variance Test I (Fig. 10) show a far narrower variance for the Kananaskis parentals, relative to the Alberta parentals, than previously seen (Table 5). Thus, the variance of the *a priori* unknown group cannot be directly compared to the variance of the *a priori* known group. The difference in variance (Fig. 7) is an artifact of CVA procedures.

What then is an accurate estimate of the Kananaskis species' variance which can be compared to the Alberta species' variance arrived at in the original CVA (Fig. 7)? Are the Kananaskis species' variances significantly different from the Alberta species' variances? The variance for the Kananaskis parentals from Test I are not truly representative because: 1) the Kananaskis group is the *a priori* unknown group; and because 2) there is little difference between the variances of the Alberta and Kananaskis groups in Test I, even though the Kananaskis variances are being minimized - indicating that the Kananaskis variances are wider than the Test I estimates.

Variance Test II (Fig. 11) was performed in order to improve the variance estimate for the Kananaskis groups. All specimens of the same species were pooled into two groups irrespective of membership in the Alberta or Kananaskis groups. This was done to relate each specimen to all other specimens of the same species irrespective of group

Figure 10. Variance Test I. Untransformed Data; Frenum Included.

Frequency histograms of canonical scores on first canonical axis of presumed pure specimens of Kananaskis species without hybrids (upper histogram) and Alberta 'control' group (inverted histogram). Kananaskis specimens formed 2 *a priori* known groups; Alberta species ran as *a priori* unknowns. Units on x-axis are in standard deviations; y-axis is number of specimens.

Variance Test I

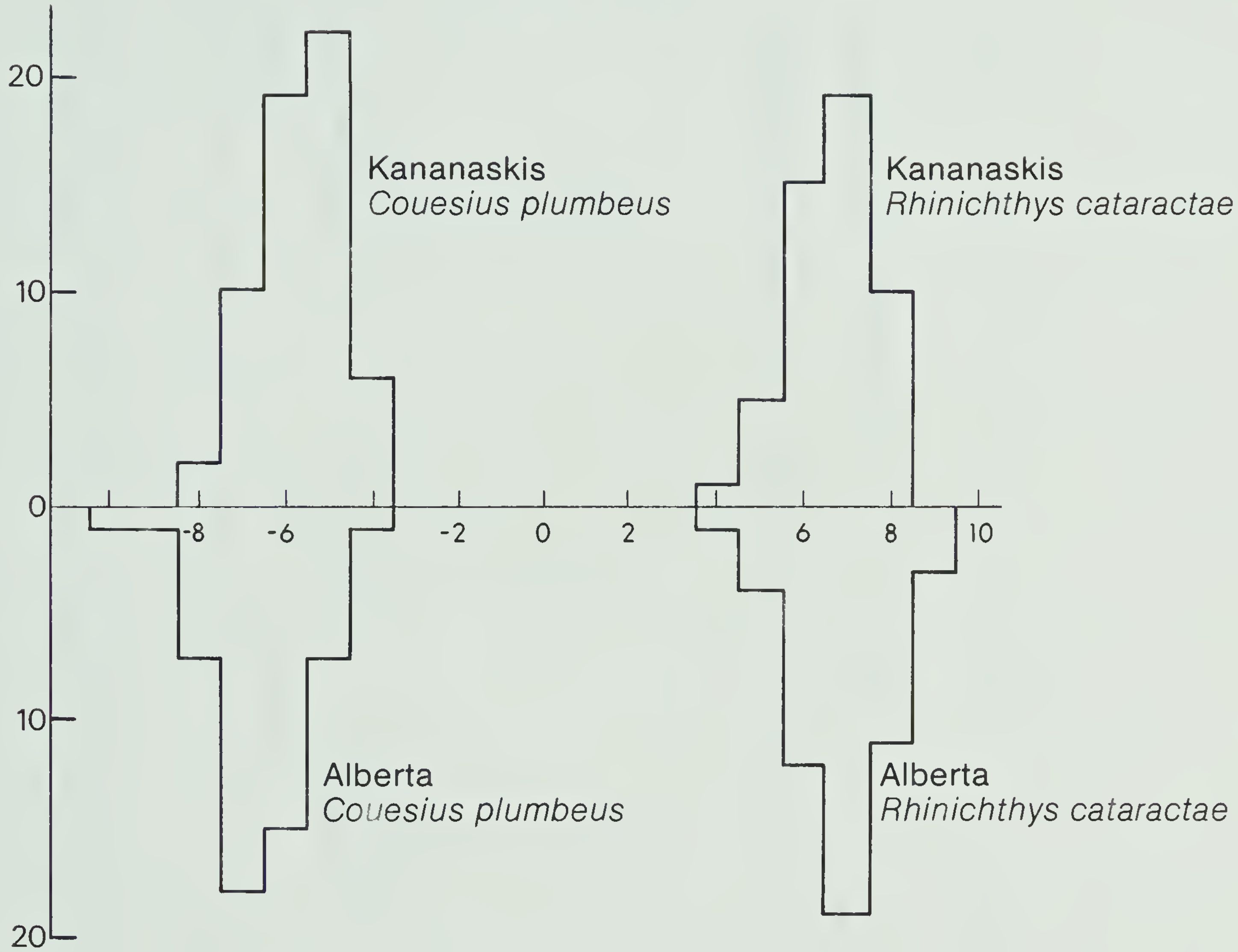


TABLE 5. A comparison of variance estimates for the 2 species from Kananaskis and Alberta groups.

	Kananaskis		Alberta	
	C. plumbeus	*R. cataractae*	*C. plumbeus*	*R. cataractae*
Original CVA (Fig. 7)	3.21	1.95	0.90	1.07
Variance Test I	0.96	1.03	1.27	1.09
Variance Test II	0.92	1.39	0.71	0.89

Tests for significance of differences between Alberta and Kananaskis species' variances:

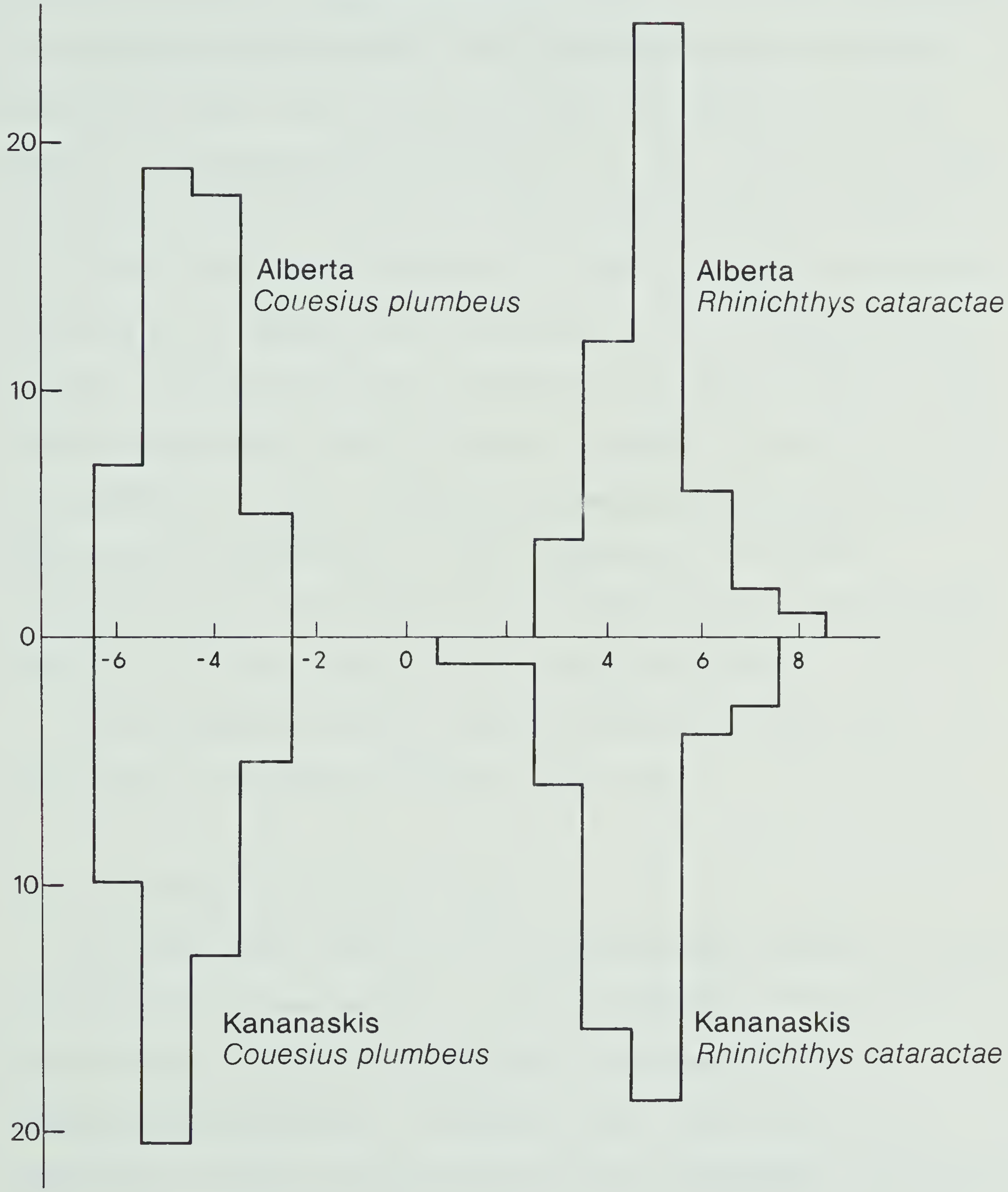
C. plumbeus $F = \frac{0.92}{0.71} = 1.30; \quad F_{.05\ (49,49)} = 1.67, \; P > 0.05.$

R. cataractae $F = \frac{1.39}{0.89} = 1.56; \quad F_{.05\ (49,49)} = 1.67, \; P > 0.05.$

Figure 11. Variance Test II. Untransformed Data; Frenum Included.

Frequency histograms of canonical scores on first canonical axis of presumed pure specimens of Kananaskis species without hybrids (upper histogram) and Alberta 'control' group (inverted histogram). Kananaskis and Alberta groups of same species were combined to form 2 *a priori* known groups; there was no unknown group. Alberta and Kananaskis specimens are separated as upper and lower histograms.

Variance Test II



membership. The two groups were run in a CVA as *a priori* knowns. No *a priori* unknowns were included. Once computed, the canonical scores of the Kananaskis group were separated from the Alberta group and plotted (Fig. 11). The variances of the Kananaskis species' distributions were calculated separately from the Alberta species' distributions. The results of Variance Test II show that the variances of the Kananaskis parental groups are not significantly different ($P > 0.05$) from the variances of their respective controls (see Table 5). There does not appear to be a significantly greater variability in the Kananaskis parentals than in the Alberta parentals, which could be ascribed to introgression. It is unsafe to draw conclusions concerning introgression from direct comparisons of the variances of species' canonical score distributions. The CVA must be manipulated in order to obtain comparable variance estimates.

The computer results for both Variance Tests are summarized in Appendix Tables 13 and 14.

CVA - COMPARISON OF GROUP MEANS

To avoid the confusion and difficulties associated with performing variance tests, it may be simpler to compare group means in order to determine the presence of introgressive effects. It appears that there has been a significant shift of the Kananaskis *R. cataractae* group mean away from the control mean (Figs. 7, 8, 9) ($X^2 = 31.8, P < 0.05$). The mean of the Kananaskis *C. plumbeus* group is

similar to the control group mean (Figs. 7, 8, 9) ($\underline{X}^2$ = 13.1,P > 0.05). The shift of Kananaskis *R. cataractae* toward the hybrid group may indicate: 1) the presence of backcrosses to *R. cataractae*; or 2) phenotypic changes in *R. cataractae* due to hybrid fertility, i.e., introgression. Conversely, this would indicate an absence of phenotypic change in Kananaskis *C. plumbeus*.

CVA - PAST COLLECTIONS

The group means of the canonical score distributions for typical *C. plumbeus*, collected in 1961, 1969, 1973, and 1977, were compared (Fig. 12) to determine if this Kananaskis species had been modified by introgressive hybridization over time. The temporal distributions of canonical scores indicates a significant shift in means in 1961, 1969, *C. plumbeus* toward *R. cataractae* and a return shift in 1973, 1977, toward the control group mean. There is a significant difference between the control distribution and the 1961 Kananaskis distribution ($\underline{X}^2$ = 31.0, P < 0.05), no significant difference between the 1961 and 1969 Kananaskis distributions ($\underline{X}^2$ = 3.9, P > 0.05), no significant difference between the 1969 and 1973 Kananaskis distributions ($\underline{X}^2$ = 2.9, P > 0.05), and a significant difference between the 1973 and 1977 Kananaskis distributions ($\underline{X}^2$ = 58.8, P < 0.05). One specimen in the 1969 UAMZ collection is revealed to be of hybrid origin. The computer results for this analysis are given in Appendix

Figure 12. CVA of Past Collections of Kananaskis *Couesius plumbeus*. Using Square-root Transformed Data; Frenum Included.

Frequency histograms of canonical scores on first canonical axis of specimens from Alberta 'control' group 1977 (upper histogram) and Kananaskis groups, 1961, 1969, 1973, 1977 (inverted histogram). Alberta group formed *a priori* known group; all Kananaskis specimens ran as *a priori* unknowns. Units on x-axis are in standard deviations; y-axis is number of specimens. Sample size and group centroid are shown for each collection.

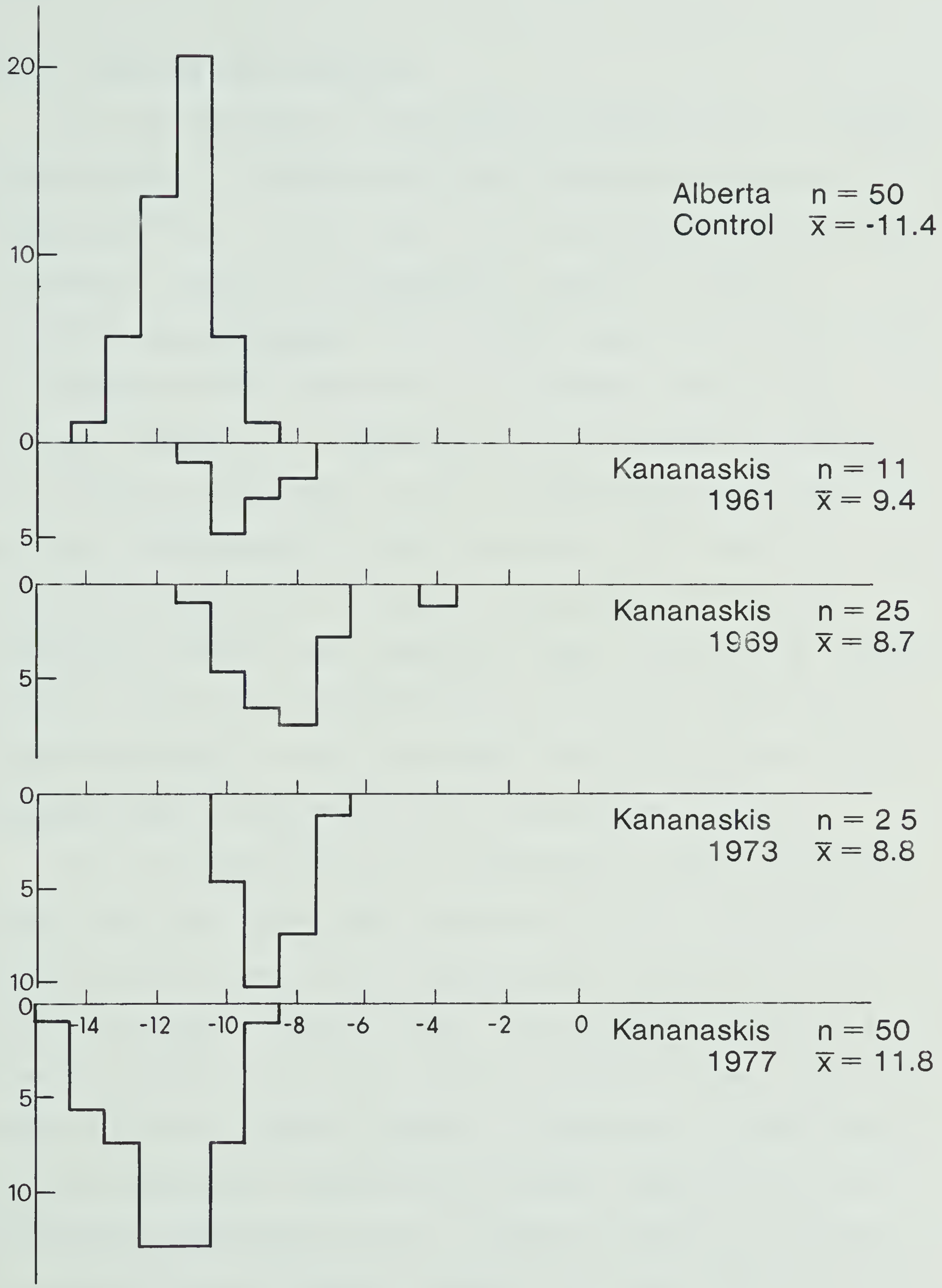

20
10
0
5
0
5
0
5
10
0
5
10
-14
-12
-10
-8
-6
-4
-2
0
Alberta Control n = 50 x̄ = -11.4
Kananaskis 1961 n = 11 x̄ = 9.4
Kananaskis 1969 n = 25 x̄ = 8.7
Kananaskis 1973 n = 2 5 x̄ = 8.8
Kananaskis 1977 n = 50 x̄ = 11.8

Table 15.

PCA - INTRA-GROUP VARIATION

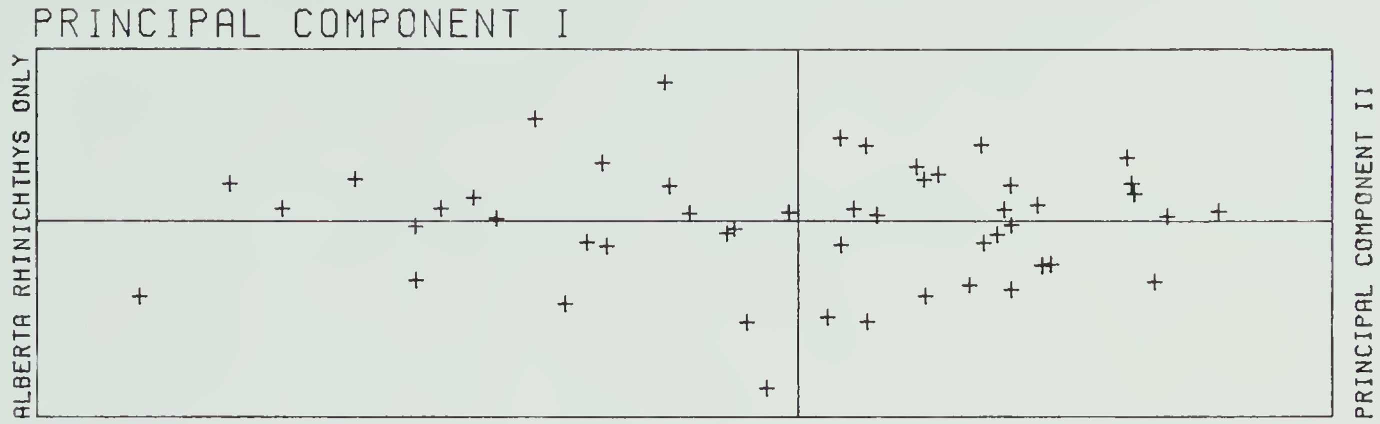
It was necessary to determine if either sex or unknown inter-population differences were confounding species' discrimination. To test this, two PCAs were performed: one on Alberta 'control' C. plumbeus; another on Alberta 'control' R. cataractae. The results shown in Figures 13 and 14 demonstrate that there are no subgroups within each species' cluster. An examination of the sex and population membership of each point in the clusters did not reveal any pattern attributable to these variables. PCA was not performed separately on typical individuals of the two Kananaskis species. The reason for this was that CVA results indicate that it is impossible to positively discriminate some individuals of the Kananaskis parental species from variant hybrid individuals on a morphological basis.

It is unlikely that the inclusion of individuals from Upper and Lower Kananaskis Reservoirs in the Kananaskis groups would increase the within-groups variability and reduce species' discrimination. The previous inclusion of diverse populations in the Alberta groups did not result in such subgroups reducing species' separation. In addition, the two Kananaskis populations analyzed (Upper and Lower Kananaskis Reservoirs) have a probably similar and recent Bow River origin. Computer results for these analyses are summarized in Appendix Tables 16 and 17.

Figure 13. PCA of Alberta *Rhinichthys cataratae* alone. Using Square-root Transformed Data; Frenum Included.

A. Plot of first and second principal component scores. Component I = 77.5% of variation; Component II = 6.2% of variation.

B. Plot of second and third prinicpal component scores. Component III = 4.9% of variation.


PRINCIPAL COMPONENT I
ALBERTA RHINICHTHYS ONLY
PRINCIPAL COMPONENT II

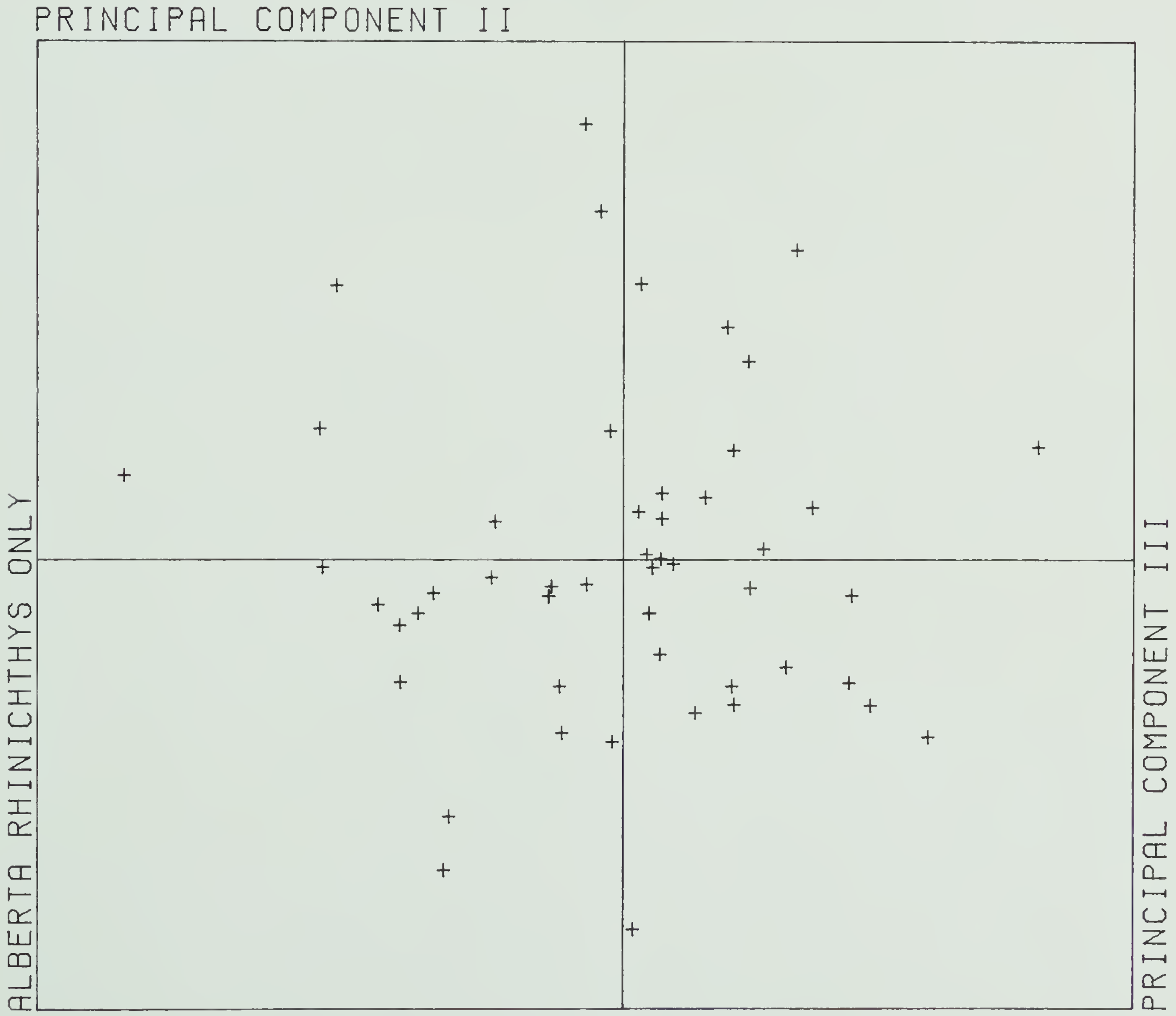
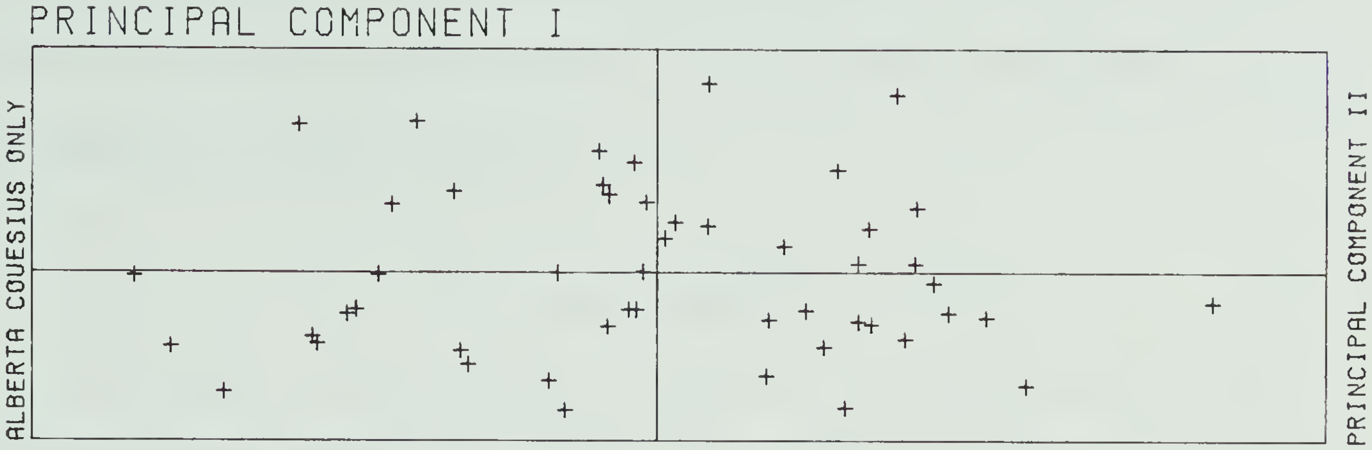
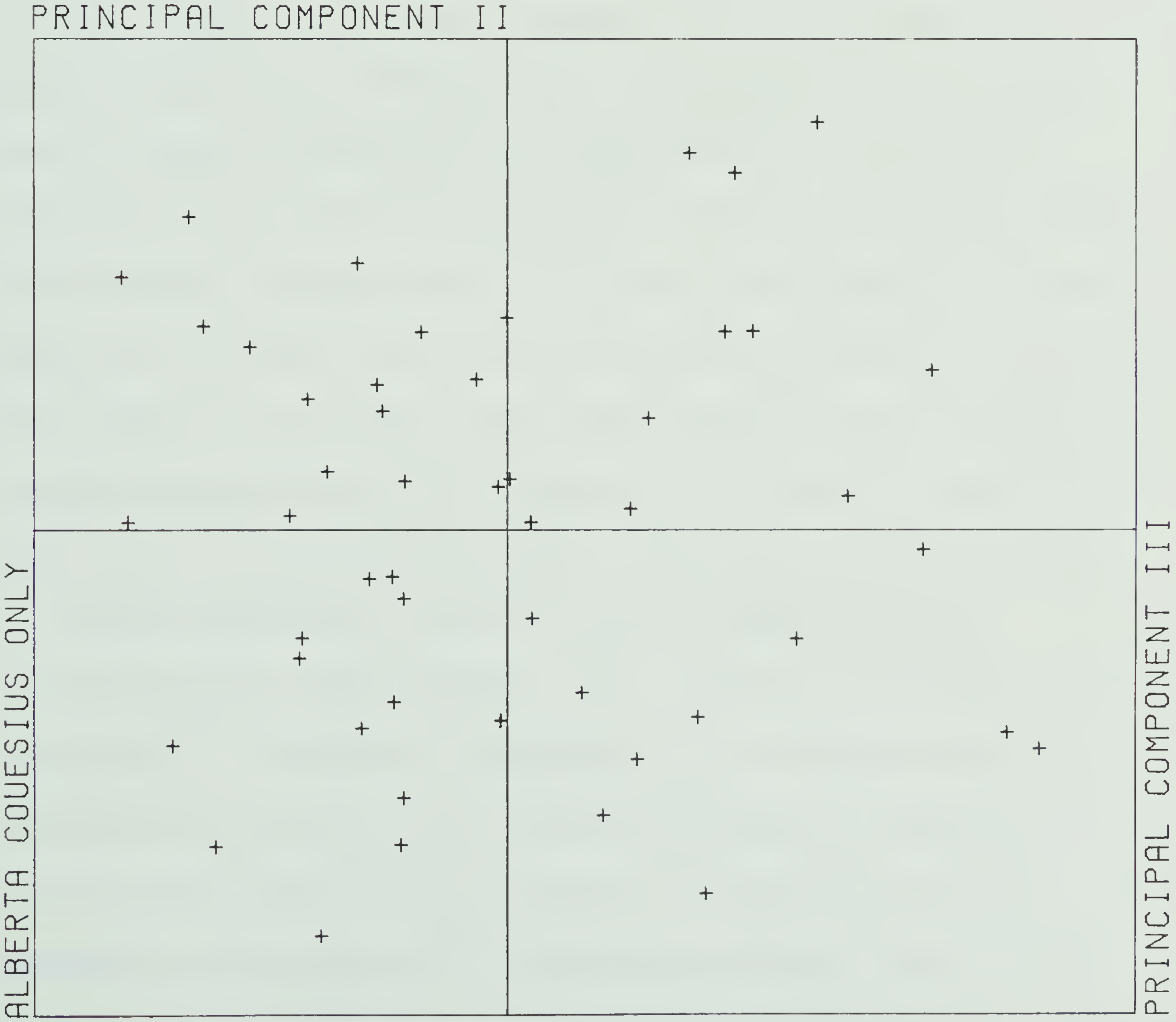

PRINCIPAL COMPONENT II
ALBERTA RHINICHTHYS ONLY
PRINCIPAL COMPONENT III

Figure 14. PCA of Alberta *Couesius plumbeus* alone. Using Square-root Transformed Data; Frenum Included.

A. Plot of first and second principal component scores. Component I = 72.0% of variation; Component II = 6.6% of variation.

B. Plot of second and third principal component scores. Component III = 5.2% of variation.


PRINCIPAL COMPONENT I
ALBERTA COUESIUS ONLY
PRINCIPAL COMPONENT II


PRINCIPAL COMPONENT II
ALBERTA COUESIUS ONLY
PRINCIPAL COMPONENT III

A listing of actual character values for all specimens used in all above multivariate statistical analyses is given in Appendix Tables 18-23.

DISCUSSION

Central to most modern studies of fish hybridization has been the desire to reach a conclusion on the fertility of hybrids from an analysis of morphological data. This stems from the assertion by Hubbs (1955) that not only are F1 hybrids intermediate between their parental species, except for some features reflecting hybrid vigor, but they are also of the same order of variability as are the parental species. Subsequently, when wild-caught hybrids showed increased degrees of morphological variability relative to the parental species, several types of hybrids were reported to be fertile without experimental evidence (Hubbs and Strawn, 1957). More recently, Schueler and Rising (1976) have stated that when individuals representing F2 or backcross generations are present, the hybrid population is found to be more variable than the parental populations.

The assumption of low F1 hybrid morphological variability has been proven false when the morphology of lab-reared F1 hybrids is compared to the morphology of lab-reared controls of the parental species. Hubbs and Strawn (1957) found the artificial F1 hybrids between _Etheostoma spectabile_ and _Percina caprodes_, from the San Gabriel River, were more variable in all characters analyzed

than their parental controls. Greenfield and Greenfield (1972) found that artificial F1 hybrids between *Gila orcutti* and *Hesperoleucus symmetricus* were not strictly intermediate between the parental species; rather the distribution of hybrid index values for known hybrids filled the intervening space between the parental species' distributions. Neff (personal communication, 1977) analyzed numerous morphological characters from 2 separate groups of artificial F1 hybrids (*Lepomis cyanella* x *L. macrochirus* and *Notropus whipplei* x *N. spilopterus*). Using CVA and PCA, she found greater variation in the known F1 hybrids than in the parental groups. This would preclude the confidant identification of backcrosses (if they were present) from hybrid individuals. Without knowing the genetic history of the hybrids in the above cases, one would have identified non-intermediates as backcrosses or F2 individuals under the erroneous assumption of low F1 hybrid variability.

It is likewise not possible to decide on *C. plumbeus* x *R. cataractae* hybrid fertility or to positively identify backcross individuals from the multivariate analyses of Kananaskis cyprinids performed in this study. Non-intermediate, putative hybrid individuals in the trough region of the Kananaskis CVA distribution could represent F2 hybrids, variant F1 hybrids, or backcross individuals.

Smith (1973) using PCA found lone hybrids occupying the area between strict intermediacy and one parental type. These were identified as backcross individuals. Without

knowing the variance of the F1 hybrids, such a conclusion is uncertain.

It may be possible to determine F1 hybrid variance from a morphological study without resorting to the study of artificial F1 hybrids. This may be possible given a large phenotypic distance between parental distributions, and a large hybrid sample forming one intermediate distribution and two smaller non-intermediate distributions toward the parental types. In this idealized case, the variability of the intermediate F1 hybrid group would be established and a backcross interpretation would be warranted for non-intermediate individuals. The results of my study do not reveal such backcross distribution peaks. Moreover, the F1 variance cannot be known with such a continuous phenotypic bridging. In a study where the hybrids bridged the gap to one species and not to the other, a backcrossing interpretation would be warranted, without the need to show F1 variance.

This continuous distribution of hybrids bridging _C. plumbeus_ and _R. cataractae_ indicates that it is not always possible to positively identify 'pure' individuals of the Kananaskis parental species. This strengthens the need to objectively classify all individuals in an area of hybridization relative to known control specimens from areas where hybridization is not known to occur.

It is also possible to use the control specimens as an objective standard against which to compare the morphology

of specimens collected over a long time period in a hybridizing area. If the area is not a stable hybrid zone (*sensu* Moore, 1977) the following alternatives of evolutionary change may be observed over time: 1) a trend toward fusion of the species by introgression - recognized by a progressive increase in hybrid frequency, skewing of parental distributions toward each other, or an increasing variance of parental distributions relative to the control distribution; 2) a strengthening of species' isolating mechanisms and character displacement - recognized by a progressive decrease in hybrid frequency, skewing of parental distributions away from each other, and no increase in parental variance; 3) extirpation of one species by competitive exclusion and hybridization; or 4) continued low level hybridization as long as the environment remains modified.

Jones (1973) observed the effects of thirty years of hybridization on the toad species, *Bufo americanus*, and *Bufo woodhousii*, in this manner. Hybridization with introgression can be best recognized temporally relative to known control groups. This would appear to be a rewarding approach for studies of fish hybridization, provided adequate past collections are available. In my study there were only sufficient *C. plumbeus* in past collections for morphological comparisons.

Three approaches were used to determine if the Kananaskis populations had changed due to hybridization.

First, the greater variances of the Kananaskis groups compared to the variances of the control groups suggested the effects of introgression. However, using the Variance Tests (I and II), this difference was found to be a property of CVA which obscured the equality of variances between the Kananaskis and Alberta groups. There has been neither an increase nor a decrease in population variance, evidence that neither introgression nor character displacement has occurred. Comparisons of variances (of CVA distributions) is not a preferred indicator of morphological change due to introgression.

The second approach was to compare the position of the Kananaskis group mean (1977) to that of the Alberta group mean, separately for each species. The analysis revealed no difference in the positions of the means for C. plumbeus, but a definite shift in the Kananaskis R. cataractae group mean away from the control mean toward the hybrid mode. This evidence suggests that Kananaskis R. cataractae has been morphologically changed due to hybridization.

The third approach was to determine if the modes of the two Kananaskis parental species were moving toward each other relative to the controls (introgression) or receding from each other (character displacement). The mode of canonical scores for Kananaskis C. plumbeus (presumably pure parental types) does reveal a shift in 1961, and 1969 means toward R. cataractae away from the control C. plumbeus distribution. Subsequently in 1973, 1977, a shift back

toward the control group mean occurred. The shift in means may indicate the initial effects of introgression followed by character displacement. However, this seems implausible for such a short time span. Without investigating the fertility potential of the hybrids by experimental means, this remains speculation. It is also reasonable to attribute the morphological shifts to selection by some unknown environmental changes through the intervening 17 year period.

In summary, there is no clear evidence of introgressive effects of hybridization upon Kananaskis C. plumbeus. However, Kananaskis R. cataractae does show a morphological change suggestive of introgression, or the presence of backcrosses. It is also possible for this difference in means to be a result of population variation due to the Founder Effect (sensu Mayr, 1969). Further evidence, especially from breeding tests, is required to test this hypothesis. Apart from this slight change, there does not appear to be a significant trend toward breakdown of the species' integrity.

Both R. cataractae and individuals of hybrid origin have remained at low frequencies during the past 17 years. Although the rate of hybridization has remained at a low level, there is some evidence of a trend toward extirpation of R. cataractae from the reservoirs (alternatives 3 and 4 from above).

This study has assessed the relative importance of the

morphological characters of *C. plumbeus* and *R. cataractae*. Nelson's (1966) finding that the best hybrid discriminators are from the head , i.e., frenum width, snout length, isthmus width, and orbit length has been confirmed. Future workers may find the canonical coefficients and constants given in Tables 2-4 to be valuable in classifying putative hybrid specimens.

VII. ELECTROPHORETIC IDENTIFICATION OF HYBRIDS

INTRODUCTION

Electrophoretic results can provide a second set of data to test the hypothesis of hybrid origin of certain specimens based on morphological criteria. The advantage of electrophoresis over a purely morphological analysis is that the genetic contributions from each parent may be detected in a single individual.

Nyman (1970) has listed all possible types of protein patterns found in fish hybrids, reflecting simple codominant expression of allelic genes. Hybrid protein patterns can be: 1) identical to one or the other parental species; 2) a complete summation of the two species; 3) a partial summation; or 4) the hybrid pattern and the two parental species' patterns can all be identical. For a protein to be a useful discriminator of hybrids, it must be present in a high frequency as a variant form in each parental species. The hybrid then, inherits a summation of the parental banding patterns (Reinitz, 1977). The confirmation of "hybridity" in this study was an empirical search for such hybrid specific biochemical markers.

METHODS

Adult _C. plumbeus_, and _R. cataractae_ and their putative, wild hybrids were collected from Lower Kananaskis Reservoir during the summer of 1978 for electrophoretic examination. Specimens from outside the system were not

examined. Adult fish of comparable age were chosen in order to exclude electrophoretic variation due to developmental differences.

To ensure that individuals representing the parental species were 'pure', the same 21 morphological characters used for PCA and CVA were measured, and the canonical scores calculated. Individuals with canonical scores within one standard deviation unit of the control parental means (from the multivariate morphological analysis Fig. 7) were used to represent 'pure' parental types.

Only hybrids with intermediate canonical scores (in the presumed F1 portion of the Kananaskis distribution on the first canonical axis, Fig. 7) were electrophoresed. Putative hybrids, with canonical scores intermediate between the parental species and the presumed F1 mode (possible backcrosses) were unfortunately not available in either a fresh or frozen state necessary for electrophoresis. The progeny of the experimental crosses had not reached sufficient size to permit electrophoretic examination.

Protein extracts were obtained from blood sera and skeletal muscle of the same specimens. Blood sera were obtained from live fish in the laboratory by severing the caudal peduncle, withdrawing the blood into heparinized capillary tubes, and spinning down the corpuscles in a Hematocrit centrifuge for 4 min.. The corpuscles were discarded and the pure sera frozen at -5.0°C. The fish were then frozen.

Skeletal muscle samples from all frozen fish were electrophoresed within six weeks of collection. Fish skeletal muscle, frozen more than a few days, has been found to be readily extractable, and muscle proteins quite stable under frozen storage (Utter et al., 1974).

One cc of the frozen dorsal musculature from each specimen was ground in a glass tissue grinder with an equivalent volume of distilled water. The creamy muscle homogenate was then centrifuged for 15 min. at X20,000 g in a Dupont Ultracentrifuge. The resulting clear supernatant was stored frozen at -5.0°C. Frozen samples of this supernatant gave identical electrophoretic patterns to freshly prepared ones and they were used as convenience dictated.

The number of typical parental specimens and hybrid specimens used for the electrophoresis of the two tissue types is given in Table 6.

Vertical polyacrylamide disc gel electrophoresis was performed at room temperature with a Buchler power supply (set on constant current) using the techniques described by Davis (1964) and Smith (1969). Seven percent polyacrylamide gels were made without sample or spacer gels according to a recipe modified from Clarke (1964) (refer to recipe in Appendix). A cold, continuous tris-glycine buffer (pH 8.3) was used for the electrode buffer in order to minimize column heating.

It was found experimentally that 8 μl was the optimal

TABLE 6. List of proteins examined in specific tissues. Numbers of fish specimens analysed for each protein is given. R - *R. cataractae*; C - *C. plumbeus*; H - *C. plumbeus* x *R. cataractae* hybrid. LDH: lactate dehydrogenase; GPD: glycerophosphate dehydrogenase; MDH: malate dehydrogenase.

Proteins	Serum	Muscle	Replicates		
LDH		X	15C	9R	3H
αGPD		X	8C	8R	2H
MDH		X	3C	2R	2H
Serum protein	X		14C	12R	5H
Muscle protein		X	14C	12R	5H

amount of extract of both tissue types for electrophoresis. An equal volume of a 40% sucrose solution was mixed with the sample extract. The entire solution was then layered between the top of the gel surface and the less dense buffer above. All samples were applied within 5 min..

One ml of 0.001 percent Bromophenyl Blue in water was added to the upper reservoir as a tracking dye. Simultaneous electrophoresis of 9 gels was begun with a current of 1.5 mA/tube for the first 10 min. to prevent undue diffusion of the sample. This was increased to 4.0 mA/tube for the remainder of the run once the tracking dye was 2 mm into the gel. Electrophoresis was completed in approximately 75 min. when the tracking dye had reached the end of the gel. Only the anodic portion of the samples was studied.

Gels were stained with amido black 10B (1 gm in 100 ml of 7% acetic acid) for one hour to discern the general

protein patterns of both the sera and muscle extracts from the two species and their hybrid. Destaining was accomplished in the same apparatus using a 7% acetic acid wash solution with a current of 10 mA/tube. Destaining was complete in 60-90 min..

Specific enzymes, lactate dehydrogenase (LDH), ∝-glycerophosphate dehydrogenase (∝-GPD) and malate dehydrogenase (MDH) were visualized using the staining procedures of Shaw and Prasad (1970). However, the gels used to separate these enzymes were not run with the recommended electrode buffers. Rather, the gel pH was adjusted closer to the stain pH by immersing the gels in the appropriate stain buffer for 15 min. prior to staining.

Gels were stored in test tubes containing 7% acetic acid and were photographed (Kodak Plus-X film) directly in the destaining tubes with no liquid interface using diffused back lighting.

RESULTS

The polymorphic banding pattern of muscle LDH was identical in all individuals of each species and hybrids that were tested (Fig. 15, #1). The appearance of three muscle LDH isozyme bands in this study is contrary to the results of Clayton and Gee (1969) who found five muscle LDH isozyme bands in both _Rhinichthys_ _atratulus_ and _R. cataractae_ collected in Manitoba. The species were distinguished by the occurrence of a variant muscle LDH in

Figure 15. Acrylamide gel electrophoretic patterns of muscle and serum tissues from *Rhinichthys cataractae* (R.c.), *Couesius plumbeus* (C.p.) and their F. hybrid (CxR) sampled from Lower Kananaskis Reservoir, 1978.

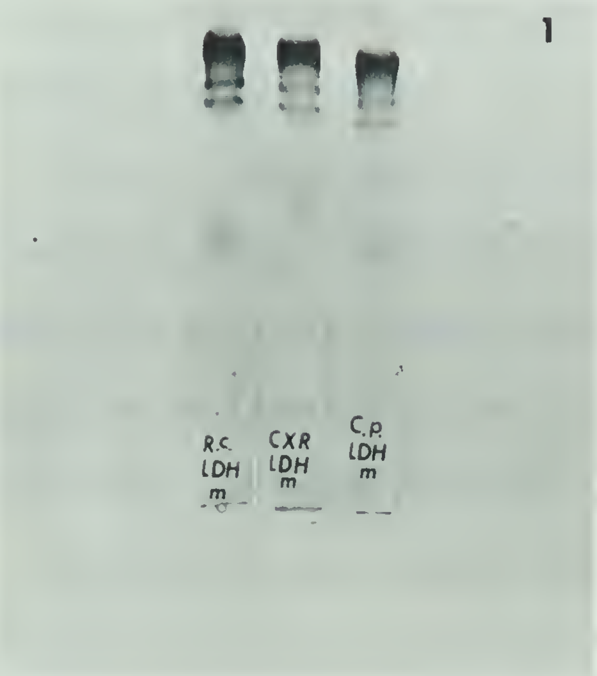
1 - muscle myogen extract stained for lactate dehydrogenase (LDH)

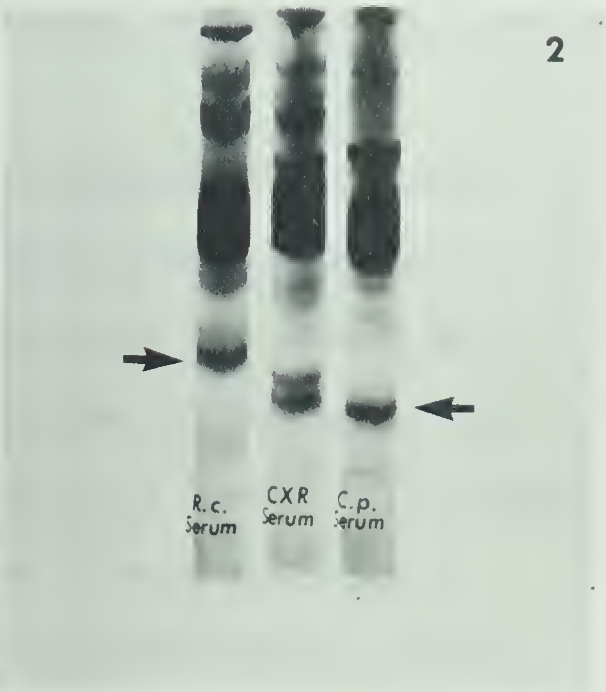
2 - serum proteins stained with amido black, a general protein stain. Arrows indicate the 2 variant forms of prealbumen.

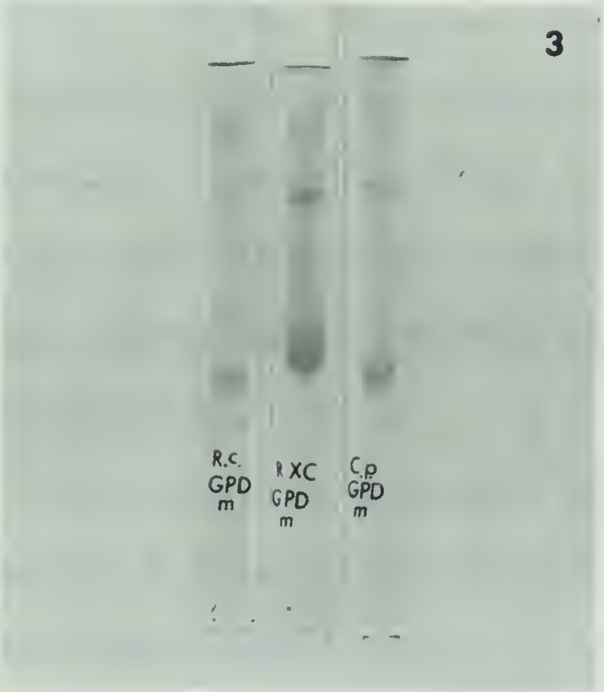
3 - muscle myogen extract stained for α glycerophosphate dehydrogenase (GPD)

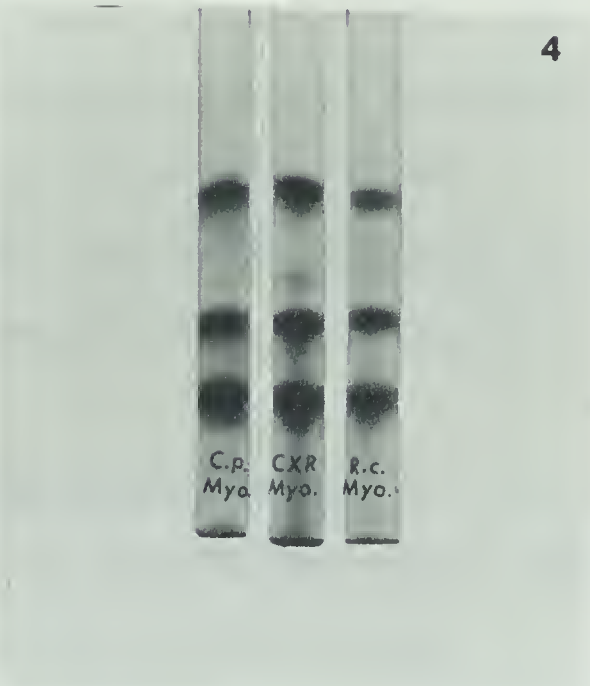
4 - muscle myogen extract stained with amido black, a general protein stain.

Anode is towards the bottom.


1
R.c. LDH m
CXR LDH m
C.p. LDH m


2
R.c. Serum
CXR Serum
C.p. Serum


3
R.c. GPD m
R XC GPD m
C.p GPD m


4
C.p. Myo.
CXR Myo.
R.c. Myo.

R. cataractae. Although our techniques differed, it is likely that my results are misleading. Given a longer electrophoretic running time, the large, most-cathodal band may have resolved into three bands of differing mobility, thereby producing a five band pattern. This was not tested in this study.

Muscle GPD (Fig. 15, #3) was polymorphic in each parental species and the F1 hybrids. Each possessed identical variant forms. Muscle MDH was expressed as a single nonvariant band with equivalent electrophoretic mobilities in each parental species and their F1 hybrids.

Muscle myogen phenotypes have been touted as an efficient method to identify hybrid individuals between other species (Tsuyuki and Roberts, 1965; Aspinwall and Tsuyuki, 1968). This was not the case in this study. All individuals of each species and all hybrids had identical three band patterns (Fig. 15, #4) for muscle extract visualized with amido black. There was some variation in the faint minor bands between the species but these were not reproducible.

The banding patterns of serum proteins for the two species differ in the possession of dissimilar, fast moving prealbumen bands (Fig. 15, #2). All specimens of R. cataractae tested, were characterized by the front band of slower anodal mobility, whereas C. plumbeus was characterized by a faster variant. All 'pure' F1 hybrids tested, were characterized by the possession of both bands,

i.e., a summation of the parental bands. These bands clearly defined a difference between the species. Although there are probably similar differences in the slowest bands, these were not investigated. The differences in banding patterns were independent of sex and were repeatable with several subsamplings of the same tissue of one individual. Electrophoretic phenotypes were not observed in the major bands of the two species' serum protein patterns.

Serum proteins appear to be influenced by environmental factors e.g., diet and physiology. It is unlikely that this could be a confounding variable in this study since the fish were sampled from the same reservoir, at the same time of the year, and presumably matured under the same conditions.

DISCUSSION

Electrophoretic serum protein analysis indicates that putative _C. plumbeus_ x _R. cataractae_ hybrids possess two prealbumen bands. These correspond in electrophoretic mobility to the single prealbumen bands of each of the parental species. This substantiates the morphological and reproductive evidence of hybridization between _R. cataractae_ and _C. plumbeus_.

Different hybrid specific protein patterns have been similarly described in only two other North American cyprinid hybrids: redside shiner (_Richardsonius balteatus_) x peamouth chub (_Mylocheilus caurinum_ (Aspinwall and Tsuyuki, 1968), and longnose dace (_Rhinichthys cataractae_) x

blacknose dace (*R. atratulus*) (Clayton and Gee, 1969).

Any *R. cataractae*, *C. plumbeus* or F1 hybrid specimens from Lower Kananaskis Reservoir could be classified as such solely by their serum phenotype. It would seem reasonable to assume that this is true for other populations of these species. Thus it should be possible to test the purity of sympatric *C. plumbeus* and *R. cataractae* populations and to confirm F1 "hybridity" by the use of this single biochemical character.

Nyman (1970) compared the efficiencies of electrophoretic and morphological techniques in detecting natural fish hybrids. He found that electrophoresis was more reliable in identifying F1 hybrids, but that the two methods were equally inefficient in identifying F2 hybrids. This is a result of the almost complete dominance of one parent's genes over the other, in the F2. However, Nyman did find 4 out of 32 protein systems in F2 hybrids (*Salmo salar* x *S. trutta*) possessing distinct banding patterns. A thorough electrophoretic survey should be undertaken by future workers in order to test the hypothesis of introgression between *C. plumbeus* and *R. cataractae* in Lower Kananaskis Reservoir.

VIII. REPRODUCTIVE ISOLATING MECHANISMS

GENERAL INTRODUCTION

Hybridization results from the dissolution of the reproductive isolating mechanisms which formerly preserved the integrity of the species' gene pools. An understanding of which isolating mechanisms are inoperative can suggest the environmental factors which facilitated the hybridization.

Reproductive isolation between sympatric C. plumbeus and R. cataractae populations has not been previously studied. In fact, published material on the breeding biology of these species is scant. The reproductive habits of R. cataractae have been comprehensively described only from Manitoba (Bartnik, 1970). The most comprehensive report for C. plumbeus is from Saskatchewan (Brown, 1969). However, it should be noted that according to Wells (1978), the Kananaskis C. plumbeus are of the 'dissimilis' morphological form while Brown's population consisted of the 'plumbeus' form. Whether there are significant biological differences between these forms is not presently known.

This section of the study investigates the effectiveness of the species' premating and postmating isolating mechanisms through ecological field studies and artificial crossing experiments. Ecological and life history data for the Kananaskis cyprinids are presented for the first time.

STUDY OF PREMATING ISOLATION

INTRODUCTION

Premating isolating mechanisms prevent the wastage of gametes and are thus more efficient than postmating isolating mechanisms. Premating isolation involves the reduction of contact between the species (i.e., spatially and temporally) and the reduction of interspecific mating by species' specific behaviors. The latter, ethological isolation, has been found to be generally more important than the other isolating mechanisms (Littlejohn, 1969).

The purpose of this section is to determine the following biological characteristics: 1) extent of differences in spawning habitat and spawning time between the two species; and 2) degree of interspecific mate preference.

METHODS

Temporal Isolation

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

ripe - eggs near maximal size; cream colored; extruded only under firm finger pressure.

fully ripe - eggs at maximal size; golden colored;

extruded spontaneously due to handling by experimenter.

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

The peak time in which fully ripe females were present in the Lower Kananaskis Reservoir was compared between the two species.

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

The third method was also quantitative. This involved measuring the mean diameter of 10 ova per sample female using needle point dial calipers under magnification (read to the nearest 0.01 mm). The grand mean of ova diameters from all sample females was graphed over time.

Fish sampled from three different locations on Lower Kananaskis Reservoir were used for all three methods and were included in the graphic analysis, irrespective of origin. The three locations were: Interlakes Raceway, mouth of Boulton Creek, and Common Bay. The purpose of pooling locations was to generate a large sample size, and to give a general picture of the spawning period for the entire Lower Reservoir, without specific site variability. Time

limitations prevented an in-depth study of spawning periods on Upper Kananaskis Reservoir. The occurrence of diel (temporal) isolation was not investigated.

Habitat Isolation

The concurrent abundance of the two species and their putative hybrids at the sampling sites was monitored using all capture techniques throughout the spawning period. Catch data were reviewed to see if there was habitat segregation by depth, current or substrate.

Behavioral Isolation

Several ripe males and females of each parental species, captured between May 26 and June 5, 1978, were returned alive to the laboratory and were kept in separate tanks. On June 6, 1978, the following reciprocal, interspecific matches were established for observations of behavioral interactions and mating:

Tank A *C. plumbeus* - 4 females
R. cataractae - 2 males
Tank B *C. plumbeus* - 3 males
R. cataractae - 2 females

Two ripe male hybrids captured on June 7, 8, 1978, were put into the same aquaria with three ripe female *C. plumbeus* on June 10, 1978:

Tank C *R. cataractae* x *C. plumbeus* hybrids 2 males

C. plumbeus - 3 females

All aquaria were kept in a controlled environment chamber which replicated the reservoir's light and temperature regime. The three 20 l tanks were started at 10°C on June 6, 1978, and increased to 14°C by June 15, 1978,(similar to the temperature rise in the reservoir). The photoperiod was a constant 15.5 hours of daylight (0600-2130 hr). Throughout the holding period, fish were fed TetraMin flakes and frozen brine shrimp.

Descriptions of breeding colors and tubercle patterns were made for each sex of the two species immediately after capture, and upon return to the laboratory. Color photographs were taken.

RESULTS

Temporal Isolation

Spawning at different times of the year constitutes an important deterrent to interspecific breeding in sympatric fish species. At present, there exist only a few records of spawning times for *R. cataractae* and *C. plumbeus* from widespread localities across Canada (Scott and Crossman, 1973). What are the spawning times of these species in Lower Kananaskis Reservoir? To what extent is temporal isolation operative?

Temperature appears to be the single, most important factor inducing spawning in these two species, as is true for most temperate, freshwater fishes. Ahsan (1966) showed

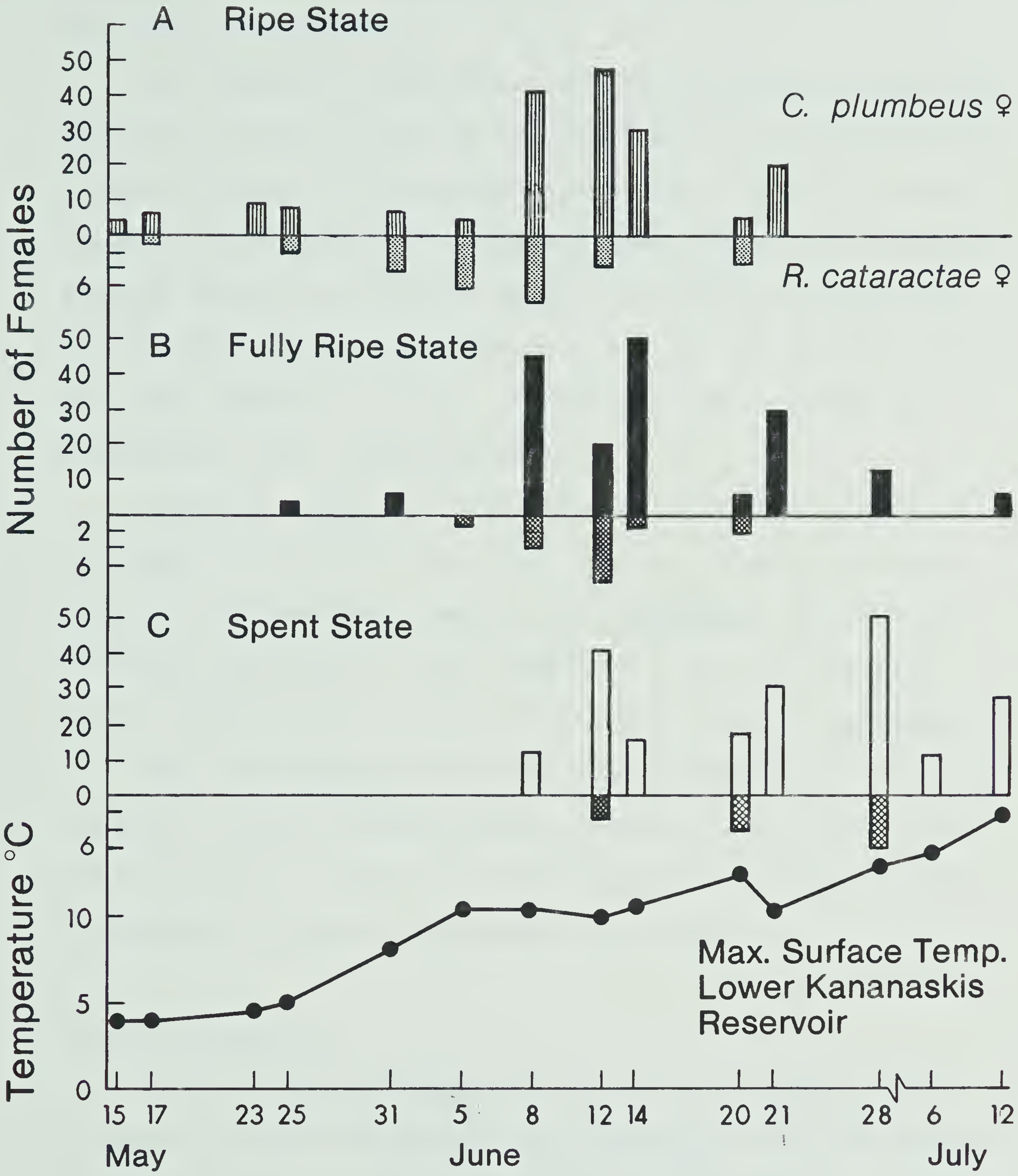
that temperature was the dominant regulator of the spermatogenetic activity of male C. plumbeus. Females, judged to be in a fully ripe state, were first collected in late May and early June after the rapid increase in surface water temperature from 5°C, May 25 to 10°C, June 4, 1978. Data from at least two years would be required to show a strict correlation of temperature with initiation of spawning.

Neither R. cataractae nor C. plumbeus were observed to undergo spawning migrations up any of the flowing inlets to the Lower Kananaskis Reservoir. Thus, it was not possible to use timing of spawning migrations as a measure of temporal isolation.

A meaningful measure of temporal isolation is overlap in the time of fully ripe females 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 Figure 16 and in Appendix Table 24.

Fully ripe females of the two species were present for the first three weeks in June, 1978, during the height of spawning. C. plumbeus females outnumbered R. cataractae females in all three different gonad states. Fully ripe male C. plumbeus similarly outnumbered fully ripe male R. cataractae. The first male C. plumbeus with freely flowing milt was captured May 17; the first such male R. cataractae was captured May 18, 1978. The last fully ripe male C.

Figure 16. Change in female gonad maturity for *Couesius plumbeus* and *Rhinichthys cataractae*, sampled from Lower Kananaskis Reservoir, during the 1978 spawning period. Maximum surface temperatures (mercury thermometer) are also presented.


A Ripe State
C. plumbeus ♀
R. cataractae ♀
B Fully Ripe State
C Spent State
Number of Females
Temperature °C
Max. Surface Temp.
Lower Kananaskis
Reservoir
50
40
30
20
10
0
6
2
5
15
17
23
25
31
5
8
12
14
20
21
28
6
12
May
June
July

plumbeus and R. cataractae were captured July 11 and June 29, 1978, respectively.

The results of the second method, involving changes in the actual gonad weight of the females of each species are shown in Figure 17 and Appendix Table 25. There is complete overlap in the period of maximum gonad weight (or spawning period) between the curves of the two species. Similarly, the results of the third method (Fig. 18 and Appendix Table 26) show synchrony between the species for a period of maximum ova size (spawning period).

Spawning activities were not actually observed due to the depth at which it occurred. However, gillnet capture records indicate that numbers of C. plumbeus increased in the early morning and late afternoon, over the spawning sites. Comparable data are not available for R. cataractae.

It is not known if the two species spawn at different times of the day. These results indicate that, apart from diel isolation, there is little temporal isolation between the species in Lower Kananaskis Reservoir.

Habitat Isolation

There is little known of the type of spawning habitat selected by the two species. R. cataractae probably spawn in riffles over a gravel bottom (Scott and Crossman, 1973), and C. plumbeus are known to spawn either along lakeshores or in streams (Geen, 1955) amid large rocks (Brown et al., 1970). The intention of this portion of the study was to determine

Figure 17. Change in gonadosomatic values (gonad weight/body weight%) of female *Couesius plumbeus* (upper graph) and female *Rhinichthys cataractae* (lower graph) sampled from Lower Kananaskis Reservoir during the 1978 spawning period. Points on hatched line represent sample means of gonadosomatic values, bars represent sample standard deviations and lines represent range of sample values. Sample range and standard deviation are not given when $n < 5$.

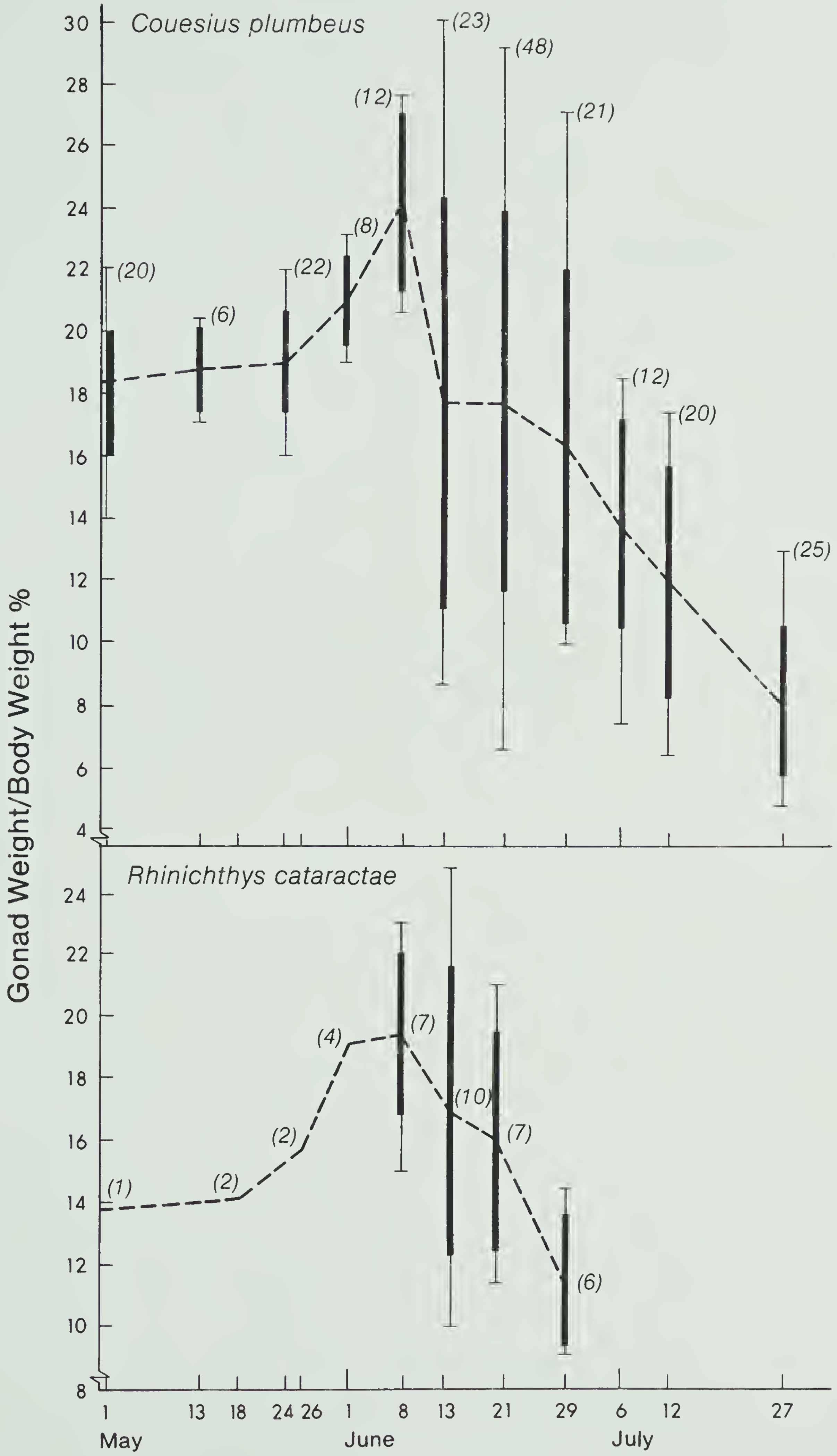
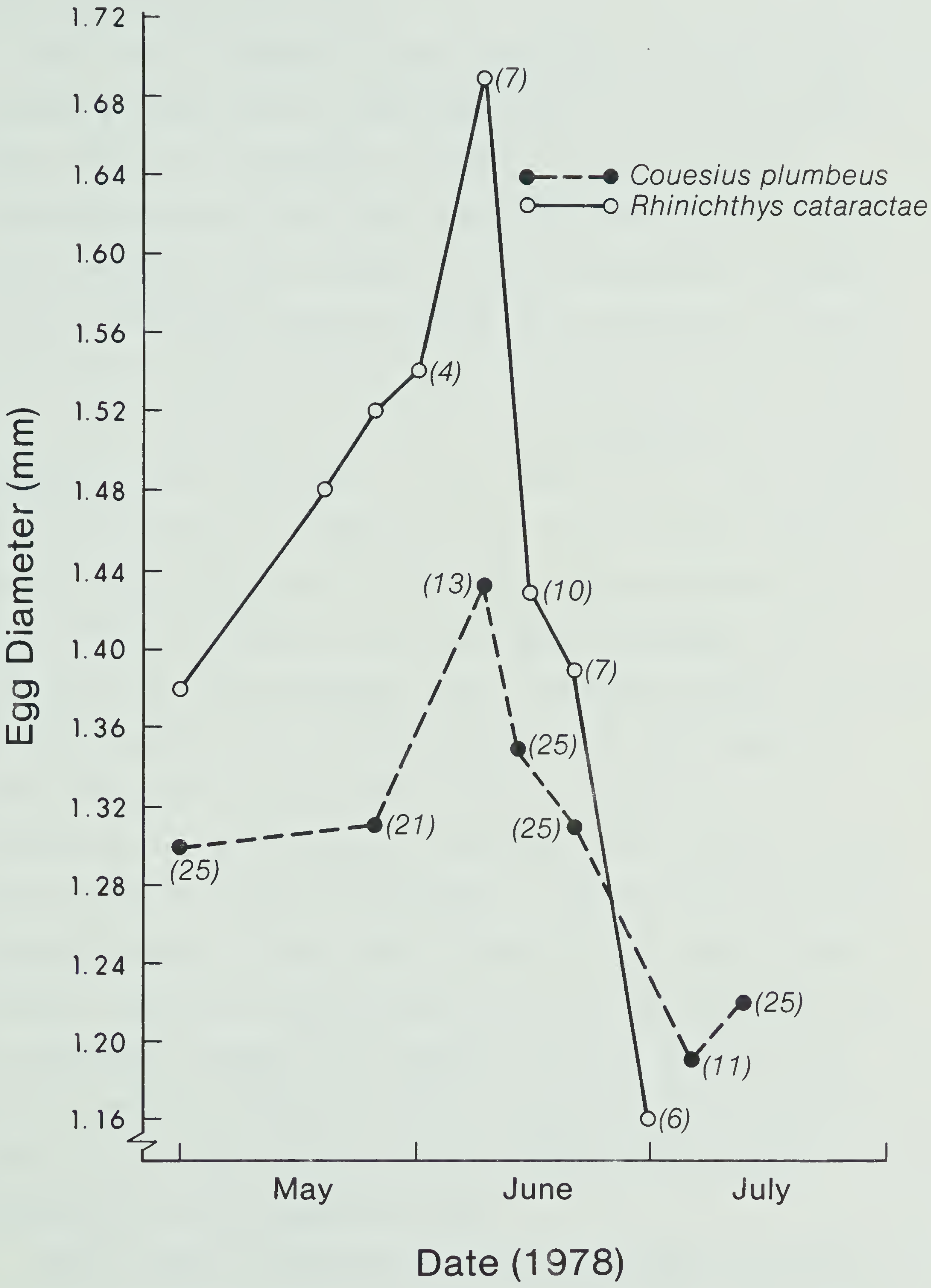

Couesius plumbeus
Rhinichthys cataractae
Gonad Weight/Body Weight %
30
28
26
24
22
20
18
16
14
12
10
8
6
4
(20)
(6)
(22)
(8)
(12)
(23)
(48)
(21)
(12)
(20)
(25)
24
22
20
18
16
14
12
10
8
(1)
(2)
(2)
(4)
(7)
(10)
(7)
(6)
1
13
18
24
26
1
8
13
21
29
6
12
27
May
June
July

Figure 18. Trends in mean ova diameter during spawning period for *Couesius plumbeus* and *Rhinichthys cataractae*, Lower Kananaskis Reservoir, 1978. Sample size in parentheses (not presented if n = 1).

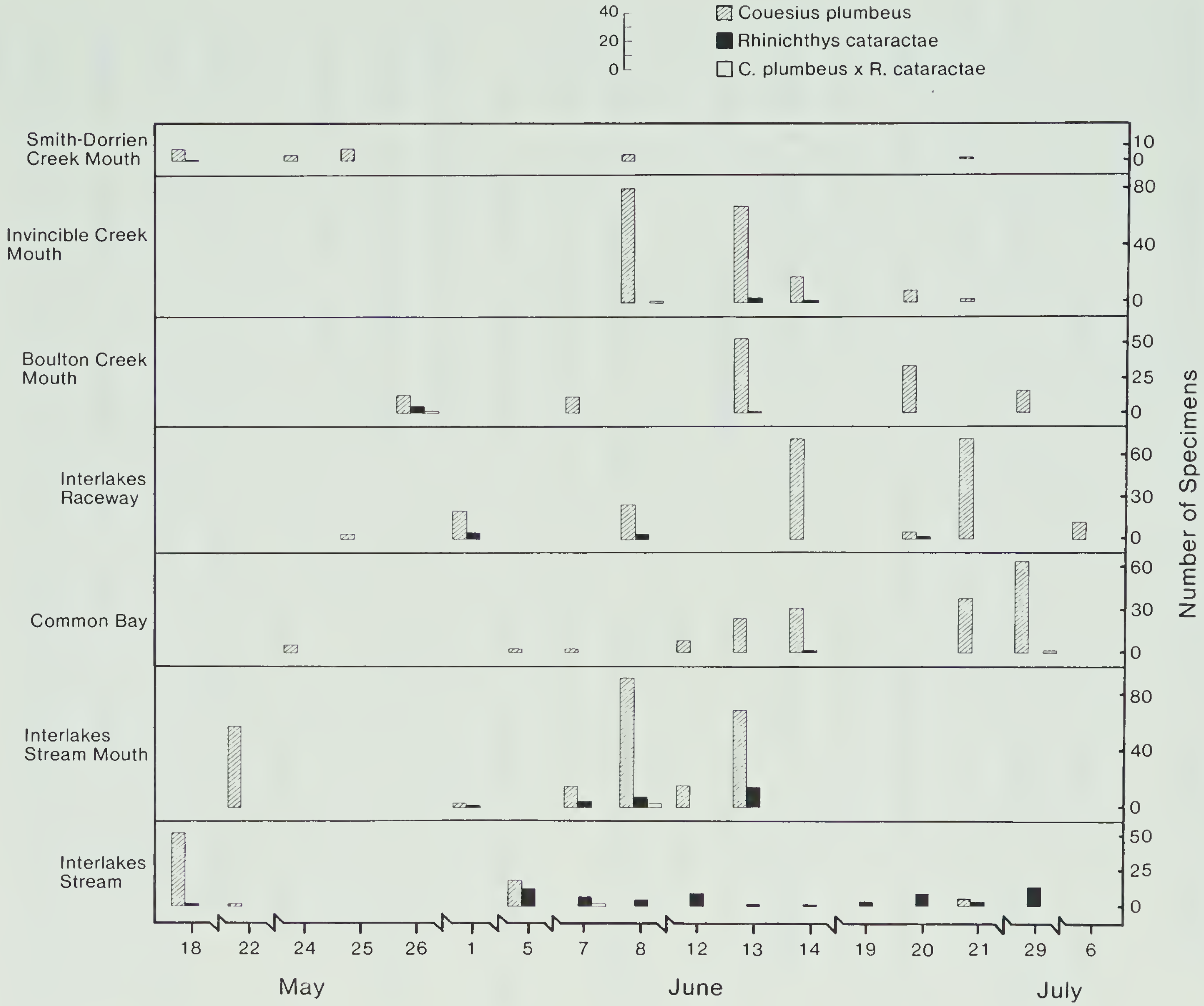

1.72
1.68
1.64
1.60
1.56
1.52
1.48
1.44
1.40
1.36
1.32
1.28
1.24
1.20
1.16
Egg Diameter (mm)
(7)
Couesius plumbeus
Rhinichthys cataractae
(4)
(13)
(10)
(7)
(25)
(21)
(25)
(25)
(25)
(11)
(6)
May
June
July
Date (1978)

the degree of habitat segregation between these species in Lower Kananaskis Reservoir.

The inlet streams of Lower Kananaskis Reservoir were carefully monitored from when they were still ice-covered until the end of spawning in order to observe species' spawning movements and areas occupied. Due to spring-time access problems, the streams of Upper Kananaskis Reservoir were not similarly studied. There was no observed spawning migration of either species into Smith-Dorrien Creek during May, June, or early July. Only a few C. plumbeus and one R. cataractae were gillnetted at the mouth of the creek during this period (Fig. 19; Appendix Table 27). Neither species were captured upstream of the mouth. Electroshocking the creek (Plate 7) yielded migrating Salmo gairdneri, and baited minnow traps captured small Salvelinus malma (< 10 cm standard length). The current velocity of Smith-Dorrien Creek increased rapidly from 0.8 m/s on April 30 to a torrential 2.5 m/s on June 8 (Appendix Table 28) due to the spring melt. It became impossible to sample this creek for cyprinids except in the lower reaches at the mouth. High current velocities probably make this creek unsuitable for the cyprinids during their spawning season. There may be some shoreline spawning by the two species in the flooded inlet at the mouth of this creek, although my limited collections do not indicate this.

There were no observed spawning migrations of either species within Kent Creek, or in the vicinity of its mouth.

Figure 19. Catch data for adult *Couesius plumbeus*, *Rhinichthys cataractae*, and their putative hybrids from 7 selected sampling sites, Lower Kananaskis Reservoir. The time interval shown includes the period of maximal spawning activity for these species in 1978. Actual numbers of individuals caught by gillnets, minnow traps, and seines are shown by size of histograms.


40
20
0
▨ Couesius plumbeus
■ Rhinichthys cataractae
☐ C. plumbeus x R. cataractae
Smith-Dorrien Creek Mouth
Invincible Creek Mouth
Boulton Creek Mouth
Interlakes Raceway
Common Bay
Interlakes Stream Mouth
Interlakes Stream
10
0
80
40
0
50
25
0
60
30
0
60
30
0
80
40
0
50
25
0
Number of Specimens
18
22
24
25
26
1
5
7
8
12
13
14
19
20
21
29
6
May
June
July

The creek is steep and swift during the spawning season (> 2.0 m/s; Appendix Table 28), with little suitable spawning habitat. The mouth area of this creek was not extensively sampled (Appendix Table 1), and it may be used by one or both species for spawning.

Cyprinid spawning migrations were not observed during June in Invincible Creek due to its swift current (Appendix Table 28), and silty nature (Secchi disc = 5 cm, June 8, 1978). Fully ripe individuals of each species were captured in the silty outfall of the creek beyond its mouth during the peak spawning period (Fig. 19). Although C. plumbeus outnumbered R. cataractae, the two species appeared to be spawning in a common area without habitat segregation. The capture of one putative hybrid at this site on June 8 might suggest that miscegenation has occurred here.

No spawning individuals of either cyprinid species were found migrating up Boulton Creek in May or June, 1978. Intensive collecting effort up the Creek from its mouth to the edge of the forest did not yield a single cyprinid. Individuals of each species in spawning condition were captured beyond the mouth of Boulton Creek and nearby vicinity (Fig. 19 and Appendix Table 1). An overlap of the species' spawning habitats near Boulton Creek mouth may be indicated by the capture of one hybrid specimen on May 26, 1978.

The outfall of Boulton Creek is often extremely silty due to intermittent rainstorm run-offs and increased melt

flow (see Secchi disc results, Appendix Table 18). This factor is also the case in Invincible Creek and may abet the interspecies hybridization occurring in both locations.

The substrate over which the spawning C. plumbeus individuals were captured was silty mud of a uniform fine texture. This was not original lake bottom but part of the reservoir's littoral flood plain. The flooded meandering bed of Boulton Creek presented the only original pre-reservoir substrate. Capture rate did not appear to rise with increasing proximity to the original creek bed. P. cataractae were captured here in disproportionately greater numbers than in other nearby shoreline areas of equal small size.

Mature cyprinids were common within the confines of Power Plant Raceway (Interlakes Dam). There was no flow of water through the Power Plant during May, June, or July; however, there was a small flow of runoff via a drainage conduit. The raceway forms a deep trench into the original lake basin and the resultant thermal stability may be attractive to the spawners. Fully ripe males and females of each species were captured within the raceway on June 8, 1978, without any observed habitat segregation (Fig. 19; Appendix Table 1). The substrate was a uniform mixture of large boulders (mean diameter 0.3 m) over gravel.

The south end of Lower Kananaskis Reservoir was the most extensively collected area on the entire reservoir. A gently flowing stream (Interlakes Stream), the original

outlet for the Upper Kananaskis Lake (Plate 8) with riffle habitat eminently appropriate for R. cataractae, emptied into the reservoir in this area. Its flow was controlled so that it did not increase with spring run-off beyond the suitability for spawning habitat. Under present reservoir conditions, this stream flows across an extensive area of exposed mudflats, which are progressively flooded as the reservoir level rises in the spring (Fig. 20).

The mouth of Interlakes Stream is constantly receding relative to the advance of Common Bay. The following dynamic habitat types were sampled at this end of the reservoir prior to and during the cyprinid spawning season.

1) Interlakes Stream - was sampled as one habitat in its entirety from source to mouth, wherever the latter occurred.

2) Interlakes Stream Mouth - the immediate vicinity of the entrance of Interlakes Stream into Common Bay was sampled as one habitat wherever it occurred.

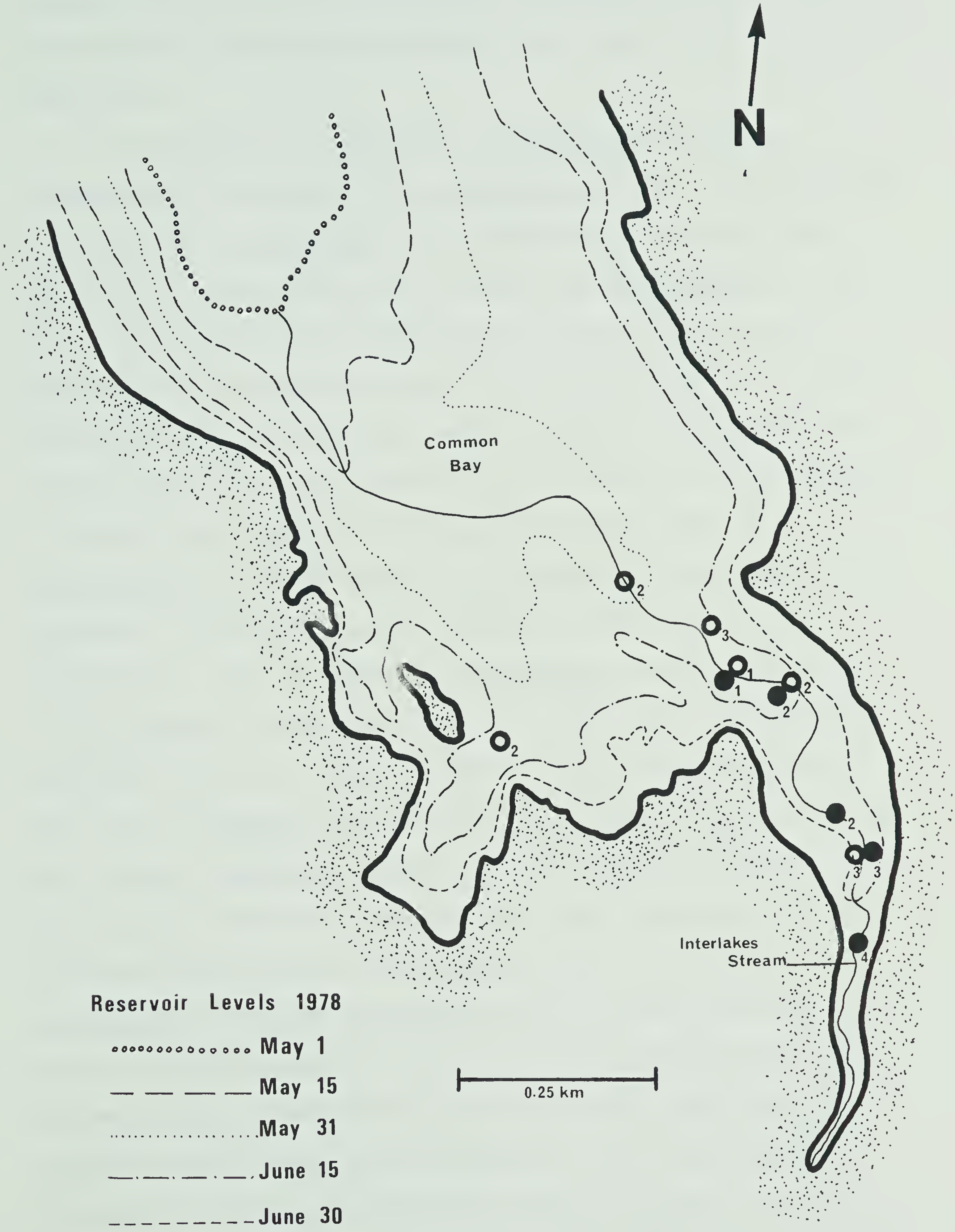
3) Common Bay - an area at least 100 m beyond the mouth of Interlakes Stream was sampled as one habitat.

The sampling sites for each habitat type were continuously moving upstream (southwards) as the reservoir filled, but the position of each habitat type remained fixed relative to the others. The types of fish occupying each moving habitat could then be compared.

C. plumbeus was abundant in the deeper waters of Common Bay, but only one hybrid and one R. cataractae were captured. The C. plumbeus captured here appeared to be spawning in the absence of R. cataractae. The substrate

Figure 20. Extreme south end of Lower Kananaskis Reservoir showing the approximate progression of shoreline changes during the summer, 1978, filling of the reservoir and the consequent flooding of Interlakes Stream (1 cm = 0.07 km). Common Bay is designated as the open water beyond the mouth of Interlakes Stream. The capture location of fully ripe and/or spent individuals of each species are presented for selected dates as follows:

○ *C. plumbeus* 1 - June 8
2 - June 12, 13
3 - June 20, 21
● *R. cataractae* 1 - June 8
2 - June 12, 13
3 - June 19, 20
4 - June 29


N
Common Bay
2
3
1
1
2
2
2
2
3
3
4
Interlakes Stream
0.25 km
Reservoir Levels 1978
May 1
May 15
May 31
June 15
June 30

ranged from gravel in the flooded Interlakes Stream bed to silty mud on the flooded mudflats in a depth of 2.5 to 3.6 m (Fig. 19).

In contrast to Common Bay, Interlakes Stream was predominantly occupied by _R. cataractae_ during the May, June 1978 period. _C. plumbeus_ were occasionally captured here (Fig. 19). A low population of adult _R. cataractae_ of both sexes remained in the diminishing length of the stream throughout the spawning period and likely spawned here. The substrate of the stream was highly variable, ranging from large patches of silt and detritus in areas of slow current to gravel and boulders in the riffle areas. Most _R. cataractae_ were sighted and captured among rocks (10 cm mean diameter) in riffles under a depth of less than 15 cm. Presumably, this is where _R. cataractae_ were spawning. The 52 _C. plumbeus_ captured on May 18, 1978, were mainly small immature specimens (mean standard length 34.3 mm) as were the two _C. plumbeus_ captured May 22, 1978, (17 mm and 25 mm SL). The _C. plumbeus_ captured in the stream on June 5, 1978, were larger specimens (mean SL 63.5 mm) including one fully ripe male and several ripe females (Fig. 19). The _R. cataractae_ specimens captured on the same date were all larger females (mean SL 58.3 mm), some of which were ripe. Spawning among these fish was not observed, nor were any females sufficiently ripe on June 5, 1978, for spawning. Intensive sampling of the stream did not yield further _C. plumbeus_ specimens until June 21, 1978, when two fully ripe

males were collected (70.0 and 72,0 mm SL) at the peak of the spawning period. In late June the reservoir level had flooded approximately half of the Interlakes Stream length within the S.E. Arm. These two C. plumbeus males were found 15 m upstream of the mouth and likely represent exploratory movements, but not a typical pattern. Their presence does suggest the possibility of interspecific spawning with the resident R. cataractae females. Spawning was not observed at any time in Interlakes Stream.

The Interlakes Stream mouth habitat was intermediate between the other two habitats in terms of the simultaneous presence of C. plumbeus and R. cataractae males and females in fully ripe and spent spawning conditions (Fig. 19; Appendix Table 1). There was no noticeable habitat separation between the two species. They were captured in the same gillnets over a substrate ranging from gravel, in the original stream bed, to silt on the flooded mudflats. The depth of the water ranged from 1.7 to 2.6 m. There was a slight, but continual current of < 1.0 m/s at the mouth of the creek. Thus, it was impossible to determine if the species segregated themselves according to current regimes. One C. plumbeus x R. cataractae hybrid specimen was captured on June 8, 1978, along with individuals of the two species.

C. plumbeus numerically outnumbered R. cataractae in the Interlakes Stream mouth habitat. However, both are represented in an intermediate frequency relative to the C. plumbeus -dominated deeper waters of Common Bay and the R.

cataractae -dominated riffle habitat of Interlakes Stream. Partial habitat isolation is achieved in the latter two habitats, but not in the intermediate habitat where the rising reservoir level brings the two species into contact.

It is reasonable to hypothesize that *C. plumbeus* spawners, in maintaining their spawning proximity to the stream mouth, advance into the newly flooded lower reaches of the stream. Here, *R. cataractae* maintain their spawning positions over the gravel and cobble rock of the flooded stream bed. Where habitat segregation occurred in the south end of the Lower Reservoir, *C. plumbeus* presumably spawned offshore in a depth of 2.0 - 3.0 m over a barren silt substrate while *R. cataractae* are inferred to spawn in very shallow riffles of slight current amid cobble-sized rock.

Behavioral Isolation

Behavioral blocks to hybridization form a final line of premating defense in the event of habitat and temporal overlap between reproducing species. However, Hubbs (1961) noticed that while a behavioral barrier to miscegenation occurs in an area where species have been sympatric for a long time, these behaviors may break down in areas where they have recently come together.

Little information concerning reproductive behaviors of the two species is available. *C. plumbeus* neither builds a nest nor guards the eggs, whereas *R. cataractae* may both establish a territory and guard the nest (McPhail and

Lindsey, 1970). Nests of *R. cataractae* were not found in the intensively sampled Interlakes Stream where *R. cataractae* was inferred to spawn in the absence of *C. plumbeus*. Nest guarding behaviors were not observed in members of *R. cataractae*, although some site specificity was indicated. When disturbed from one area, they would invariably be observed returning to the same site. Turning over the rocks and sieving the substrate in such locations did not yield eggs or nests. Nest-guarding adults were not observed when the flooded portion of Interlakes Stream in the S.E. Arm was observed underwater using S.C.U.B.A. on June 28 and July 12, 1978.

Laboratory, aquaria-held fish showed no meaningful behavioral differences when held in the reciprocal, interspecific matchings as opposed to conspecific situations. Neither mating behaviors nor aggressive interactions were observed at any time. Individuals of each sex of each species, while held in tanks, displayed similar fright behaviors and escape responses.

The male hybrids and female *C. plumbeus* in Tank C were not observed to elicit mating behaviors and tank breeding did not occur. When autopsied on June 28, the females had regressed gonads suggesting that tank conditions were inappropriate for breeding. Although the male hybrids were of equivalent size to the females, they reacted more vigorously to tank disturbance, swam faster, and dominated the feeding by rapidly snatching up the food.

The existence of distinct species' specific breeding behaviors in C. plumbeus and R. cataractae cannot be confirmed in this study. Their isolative value remains unknown. However, it is possible to evaluate species' differences in breeding coloration and nuptial tubercles (Plates 1-6). These differences may provide criteria for favoring conspecific mates. The results of this comparison (Table 7, Plates 1-6), reveal many species' differences, which may act to increase the species' reproductive isolation. Similarly, there are many morphological differences between the species, especially in head characters (previously discussed in text) of potentially high isolative value, assuming such characters are used for mate recognition. Confounding these differences is that in each species smaller males mate with larger females. Thus, mate selection on this criterion would not disfavour interspecific matings.

Without successful, controlled mating experiments, these hypothesized isolating factors remain untested speculations.

DISCUSSION

Temporal isolation may be inoperative in preventing hybridization in Lower Kananaskis Reservoir (although diel isolation was not investigated). There is total overlap in the period of fully ripe females between the two species. The peak of the spawning period for each species occurred in

TABLE 7. Comparison of Breeding Coloration and Nuptial Tubercles. Refer to Plates 1-6.

Couesius plumbeus	*Rhinichthys cataractae*
MALE	MALE
- vivid red patch at pectoral fin base, spreading posteriorly. No coloration at bases of pelvic or anal fins.	- vivid red-orange patches at bases of pectoral, pelvic and anal fins.
- red patch on top of opercle.	- no red patch on top of opercle.
- may have red pelvic axillary processes, if these are present.	- red pelvic axillary processes.
- small red patch at corners of mouth.	- red-orange patch at corners of mouth - (upper mandible may be entirely colored while lower mandible is less extensively colored.
- no coloration near isthmus.	- red-orange color scattered beneath gills at isthmus.
- all fin rays, membranes without color.	- all fin rays, membranes may have a red-orange tinge.
- fine white tubercles on dorsal surface of pectoral rays.	- fine white tubercles on dorsal surface of head (may extend posteriorly to origin of dorsal fin) and on dorsal surface of pectoral rays. (Tubercles usually restricted to head only).
- always brighter red coloration than females.	- usually brighter red coloration than females.
FEMALE	FEMALE
- red patch at base of pectoral fin, spreading posteriorly.	- may have a small red-orange patch at base of pectoral fin.
- red patches at top of opercle and at corners of mouth (on cheek) may be present.	- no red patch on top of opercle, or on cheek at corner of mouth.
- fin rays, membranes without coloration.	- all fin rays, membranes usually with a red-orange tinge.
- color patches are yellow to light red, never vivid red.	- color patches are orange-red.
- fine tubercles may be present on dorsal surface of head and posteriorly to dorsal origin.	- tubercles not present.

mid-June at approximately 10°C and ended prior to July in 1978: spawning did not continue into late August in either 1977 or 1978 as has been reported for Kananaskis cyprinids by McPhail and Lindsey (1970) and Scott and Crossman (1973) (probably based on Nelson's 1965 observation of ripe females being found on 8 August in 1961).

Previous reports have shown different temperature responses for the two species. R. cataractae in Manitoba reached a spawning peak on May 16 at 15°C in Mink River (Bartnik, 1970) and during mid-July at 15°C in Lake Winnipeg (Gee and Machniak, 1972). Kuehn (1949) reported that R. cataractae in Minnesota spawned from late June through August. Brazo et al. (1978), found the peak spawning period for Lake Michigan R. cataractae to be late June and early July at 14-19°C. C. plumbeus have spawned in the Montreal River, Sask. in early May at 4-8°C, Lac la Ronge, Sask. in mid-June at 10°C (Brown et al., 1970), and Lac Saugay, Que. in early June at 19°C (Scott and Crossman, 1973). These may be population differences.

There appears to be no effective habitat isolation between the species. They swarm in mixed schools over the mud flats at Pocaterra Dam in the summer and were captured together at spawning time along the shoreline and at the mouths of all inlet streams. However, habitat isolation was achieved by spawning R. cataractae migrating alone in modest numbers into Interlakes Stream. Presumabley no other inlet stream offered the appropriate current, temperature, and

substrate regimes to allow species' segregation. There are no other reports in the literature outside Kananaskis of such close habitat sharing between *C. plumbeus* and *R. cataractae*.

Satisfactory evidence regarding the strength of the behavioral barrier between the two species is lacking in this study. However, the failure of the other possible isolating mechanisms, and the low frequency of hybrids, suggests that with *C. plumbeus* and *R. cataractae*, as with most species (Mayr, 1969), ethological isolation is of primary importance. Differences in morphology, color, tuberculation, and the suggested territoriality of *R. cataractae* (McPhail and Lindsay, 1970) are possibly involved. Ethological barriers are also inferred to be of major importance in maintaining species' identity in hybridizing populations of *Catostomus commersonii* and *C. macrocheilus* (Nelson, 1968).

STUDY OF POSTMATING ISOLATION

INTRODUCTION

Postmating isolating mechanisms involve the reduction of hybrid survival and the reduction of gene flow through the hybrids. Effective postmating isolation is not a general characteristic of sympatric species (Littlejohn, 1969) as it is not open to the operation of natural selection.

The purpose of this section is to determine the importance of postmating isolating mechanisms in maintaining

species' distinctness. The mortality and viability of artificially reared hybrid embryos is compared relative to that of parental embryos. Certain life history characteristics of wild-caught hybrids are compared to those of the parental populations in order to assess their relative survival success under natural conditions.

METHODS

Hybrid Embryo Mortality

Embryo mortality experiments were conducted in a controlled environment chamber commencing June 8 and terminating July 1, 1978, with the final hatching of all embryos. Fully ripe adults, caught in Lower Kananaskis Reservoir using gillnets, dipnets, and seines were returned to the laboratory where they were stripped of eggs or milt. Some adults were held in aquaria for as long as two days prior to stripping, while waiting to collect the parental type with which they were crossed. Fertilization procedures were adapted from Davis (1953) and Strawn and Hubbs (1956).

No attempt was made to extract the same number of eggs for all crosses. Each cross received the maximum number of eggs which could be expressed from the female. The fertilized eggs of each cross were placed in separate glass finger bowls and each was covered with a fine Nitex mesh (36 meshes/cm^2). As many as three finger bowls of the same cross type were submerged into the same 20 l aquarium. This procedure allowed simultaneous experiments to be run without

the danger of accidental interchange of embryos.

Once hatching began, each cross was separated into its own aquarium. All aquaria were held at a constant temperature of 15ºC and were constantly aerated. There was no continuous water flow into the aquaria, rather the water was changed approximately every five days. Chemical fungal retardants were not used.

There was a total of 21 crosses (9 homospecific crosses, 11 heterospecific crosses, and 1 cross of two F1 hybrid individuals). Each cross involved different parents. Hybrid and parental crosses were treated identically. Prior to hatching, eggs of all crosses were examined once every 24 to 36 hours. Dead embryos, identified by their opaque, white color, were counted daily and discarded using a pipette. When hatching began, the crosses were examined twice daily and the number of hatched fry recorded. A mean hatching date was determined for each cross. Hatching time data were analyzed using a single classification analysis of variance (Sokal and Rohlf, 1969) and a Duncan's multiple range test (Zalik, 1977).

The diameters of 15 embryos (five days post-fertilization) from four crosses (the two parental cross types and the two reciprocal hybrid cross types) were measured under a microscope using needle-point dial calipers (read to the nearest 0.1 mm). Egg diameter data were analyzed using a single classification analysis of variance (Sokal and Rohlf, 1969) and a Duncan's multiple range test

(Zalik, 1977).

The % pre-hatching mortality results for all crosses were arcsin transformed (Zalik, 1977,) and analyzed using a single classification analysis of variance (with unequal sample sizes) (Sokal and Rohlf, 1969).

Hybrid Inviability

Immediate Post-hatching Survival

The products of all four artificial cross types were reared beyond the hatched fry stage in several 8 l aquaria. Space limitations necessitated the pooling of replicates from the same cross type. All aquaria were held under the conditions of a constant 15°C temperature, continual aeration and water changes as needed. The developing fry were fed Liquifry, TetraMin baby fish food, and live zooplankton from Lower Kananaskis Reservoir.

The number of live fry 4 days post-hatching was recorded for each cross type replicate and the data were analyzed using a single classification analysis of variance (Sokal and Rohlf, 1969). Thereafter, the number of live fry was recorded once per month until 3 November, 1978. These long-term survival data were not statistically analyzed but simply compared to determine if any differences existed in survivorship beween the cross types in the first months of life.

Long-term Survival and Life History Characteristics

The success and long-term viability of the wild-caught putative hybrids was compared to that of the two parental species by their age, growth, and length-weight data.

Age was determined by scales, read under magnification independently by two people. Where disagreement occurred, the readers conferred until a consensus was reached. Scales were removed from preserved fish in the small area above the lateral line and below the dorsal midline in front of the dorsal fin. Thirty-six putative hybrids with intermediate canonical scores (in the presumed F^1 portion of the Kananaskis CVA distribution) were aged. Aging by the scale method was corroborated using the graphic method of polymodal separation of length frequencies (Cassie, 1963).

Growth rates of these representatives of the hybrid group and the two typical parental species were calculated by plotting the mean size at each age, as derived from the scale analysis, against age-class. Growth rates were then estimated from regressions of logarithms of length on age-class. An analysis of covariance was performed on the same data using the SPSS computer program (Nie *et al.*, 1975). This provided an objective method of determining significant differences between regression lines.

Length-weight relationships for the same subsamples of the three groups were determined according to the methods of Ricker (1971). The relationship was described by a regression of logarithm of length on logarithm of weight. An

analysis of covariance was performed on these data using the SPSS program.

Female fecundity was determined for 25 *C. plumbeus*, 20 *R. cataractae*, and 7 hybrids. All ova from one female were spread evenly in a dish divided into quadrats; only one quadrat was actually counted. This value was multiplied by four to give the total number of ova. The fecundity relationship was described by a regression of logarithm of ova number on logarithm of standard length for *C. plumbeus* and *R. cataractae*. The hybrid sample size was too small to generate a meaningful regression.

RESULTS

Hybrid Embryo Mortality

Successful artificially induced hybridization may confirm the origin of putative hybrids. It can also provide insight into the relative degree of selection against hybrid cross products. The hypothesis of equal hatching success between hybrid crosses and parental crosses was tested (Table 8).

Each of the heterospecific crosses suffered 100% pre-hatching mortality in one replicate, as did the only hybrid backcross replicate. All replicates of the homospecific crosses had some hatching. However, there is no significant difference in pre-hatching mortality between the four different cross types, excluding the hybrid backcross ($P > 0.05$, Table 9). Given only one hybrid backcross

TABLE 8. Hatching results for experimental crosses, 1978, at 15°C. C - *Couesius plumbeus* R - *Rhinichthys cataractae*
H - *C. plumbeus x R. cataractae* F_1 Hybrid

	Heterospecific Crosses										
	♂ C x ♀ R				♀ C x ♂ R						
Date Started	19 June	19 June	19 June	19 June	13 June	13 June	16 June	8 June	20 June	20 June	20 June
No. Started	181	90	90	205	500	438	373	200	123	400	220
No. Hatched	128	0	73	156	227	326	0	7	49	177	48
% Pre-hatch Mortality	29.3	100.0	18.8	23.9	54.6	25.6	100.0	96.5	60.2	55.8	78.2
$\bar{x}$ Hatch Time (days)	10.0	-	10.0	11.0	9.5	10.0	-	10.0	10.0	9.5	10.0
% 4 Day Post-hatch Mortality	98.4	-	2.7	7.0	1.3	0.6	-	0	8.2	42.3	100.0
No. Alive 4 Day Post-hatching	2	0	71	145	224	324	0	3	45	102	0

	Homospecific Crosses									Hybrid Backcross
	C x C					R x R				♂ H x ♀ C
Date Started	13 June	13 June	8 June	20 June	20 June	19 June	19 June	20 June	20 June	8 June
No. Started	280	380	240	240	136	43	90	246	115	62
No. Hatched	59	98	38	219	94	12	17	84	33	0
% Pre-hatch Mortality	78.9	74.2	84.2	8.8	30.9	72.1	81.1	65.9	71.3	100
$\bar{x}$ Hatch Time (days)	9.0	9.0	9.5	9.0	8.5	13.0	12.0	12.0	11.0	
% 4 Day Post-hatch Mortality	3.4	3.0	0	49.3	3.2	0	5.9	28.6	6.1	
No. Alive 4 Day Post-hatching	57	95	38	111	91	12	16	60	31	

TABLE 9. % Pre-hatching Mortality. Single classification analysis of variance with unequal sample sizes. The single replicate of the hybrid backcross suffered 100% pre-hatching mortality and was not included in this analysis.

Arcsin Transformed Data

Crosses				ANOVA TABLE				
CC	♂C♀R	♀C♂R	RR					
62.7	32.8	47.6	58.1	Source of Variation	SS	df	MS	F
59.5	90.0	30.4	64.2	Among Crosses	743.6	3	247.9	0.59
66.6	25.7	90.0	54.3	Within Crosses	7185.6	17	422.7	
17.3	29.3	79.2	57.6	Total	7929.2	20		
33.8		50.9		$F_{.05(3,17)} = 3.2$				
		48.3						
		62.2		P > 0.5				

% 4 Day Post-hatching Mortality. Single classification analysis of variance with unequal sample sizes.

Arcsin Transformed Data

Crosses				ANOVA TABLE				
CC	♂C♀R	♀C♂R	RR					
10.6	82.7	6.6	0.0	Source of Variation	SS	df	MS	F
10.0	0.0	4.4	14.1	Among Crosses	449.4	3	149.8	0.20
0.0	9.5	0.0	32.3	Within Crosses	12479.0	17	743.1	
44.6	15.3	0.0	14.3	Total	12928.4	20		
10.3		16.6		$F_{.05(3,17)} = 3.2$				
		40.6						
		90.0		P > 0.5				

replicate, it is not possible to make any conclusions on the sterility of hybrids. I suspect the eggs used in this cross were not fully ripe.

Hybrid crosses hatch as successfully as do control crosses. On the basis of this experiment, hybrid embryo mortality cannot be operative as a postmating isolating mechanism.

There is a significant difference in hatching times for cross types ($F = 28.0$, $F_{.05}(3,14) = 3.34$). The hatching times for pure R. cataractae embryos and pure C. plumbeus embryos are significantly different from all other cross types . The hatching time for embryos of the two reciprocal hybrid cross types are not significantly different (latter results from Duncan's test). Mean hatching time for pure C. plumbeus crosses is 9.0 days: relatively short compared to pure R. cataractae at 12 days. The hatching times of the heterospecific crosses are intermediate: male C. plumbeus x female R. cataractae cross, 10.5 days; female C. plumbeus x male R. cataractae, 9.8 days. This may show a trend for the hybrids to develop at rates similar to that of their maternal controls, as reported by Hubbs and Strawn (1957).

Hybrid fertilized egg sizes are also intermediate between the parental values (Table 10). There is a significant difference in embryo sizes for cross types ($F=26.9$, $F_{.05}(3,56) = 2.76$). Pure C. plumbeus embryos are significantly smaller than embryos from the other three cross types, which are not significantly different from each

other in size (latter results from Duncan's test). There may be a causal relationship here, i.e., the larger *R. cataractae* egg requiring a longer development time than the smaller egg of *C. plumbeus*.

Hybrid Inviability

It is probable that hybrids are occasionally produced in nature by an accidental mechanism such as drifting sperm. In a natural environment, as opposed to a modified environment, these individuals may be at a selective disadvantage and may die prior to reproducing. The hypothesis that artificially produced hybrids of Kananaskis origin were not selected against was tested.

Immediate Post-hatching Survival

Percent 4 day post-hatching mortality results (Table 9) show no significant difference ($P > 0.05$) between the replicates of the four cross types. The highest percent mortality is in two heterospecific cross replicates: more than twice the highest percent mortality recorded for the homospecific crosses. There appeared to be no difference between the cross types in the number of highly deformed individuals that contributed to these mortality figures.

The results of the four month rearing experiment (Table 11) show unexpected differences in viability between the cross types. All *R. cataractae* control cross individuals died between two and three months after hatching. No other cross type suffered total mortality during the rearing

Table 10. Diameters of Eggs (5 days post-fertilization) for each artificial cross type.

Cross Type	No. of Eggs	mean diameter(mm)	Std. Deviation
C C	15	2.03	0.08
C♀ R♂	15	2.28	0.12
R♀ C♂	15	2.23	0.11
R R	15	2.35	0.08

TABLE 11. Survival of offspring from experimental crosses over a 4 month period (post-hatching). Some replicates of the same cross type were lumped together for economy during rearing as indicated. Survival values for each time period are given as absolute number of live individuals. The mean hatching date for all crosses is taken as June 27, 1978. R:- *R. cataractae;* C:- *C. plumbeus.*

Cross Type	Replicates (identified by no. hatched)	No. lumped 4th day Post-hatching	Survival (days post-hatching)			
			35	65	91	124
♀C ♂C	59, 98, 38	190	131 (55.1)	102 (46.3)	64 (35)	62 (34.3)
	219, 94	202	137 (41.4)	127 (39.6)	104 (35.2)	82 (30.1)
♀R ♂R	17, 12	28	24 (65.5)	0	0	0
	84	60	0	0	0	0
	33	31	0	0	0	0
♀R ♂C	73	71	62 (67.2)	12 (23.9)	9 (20.6)	8 (19.3)
	156	145	0	0	0	0
	128	2	0	0	0	0
♀C ♂R	227	224	183 (63.9)	142 (52.3)	99 (41.3)	56 (29.8)
	326	324	260 (63.3)	83 (30.3)	74 (28.5)	67 (26.9)
	7	3	0	0	0	0
	49, 177	147	137 (51.1)	78 (36.0)	33 (22.5)	30 (21.4)
	48	0	0	0	0	0

period. The hybrid cross of *R. cataractae* maternal descent also suffered 100% mortality in two of its three replicates in the first month of rearing.

In contrast, the hybrid cross of *C. plumbeus* maternal descent had higher viability success with 100% mortality in only two of its five replicates. There were no complete die-offs in either replicate of the *C. plumbeus* control cross.

The results suggest disproportionate selection against *R. cataractae* control specimens and hybrids of *R. cataractae* maternal descent under artificial conditions.

Long-term Survival and Life History Characteristics

a) Age

The presence of five age-classes in the *C. plumbeus* sample is indicated by scale annuli. The lengths of the fish at each annulus formation are presented in Table 12. Separation of polymodal length frequencies by probability coordinates verified the presence of five age-classes (Fig. 21). A chi-square test showed no significant differences ($P > 0.05$) between the observed and expected normal distributions of length frequencies in each of the age-classes. There is close correspondence between the results of the two methods. The size ranges at each age, determined by the scale method, fell within the size ranges at each age determined by the polymodal probability method. Bruce and Parsons (1976) found no spawning *C. plumbeus* from Labrador older than 4+ years. However, Brown (1969) found

TABLE 12. Length distribution of the age-groups of *Couesius plumbeus* from May 1, 1978 sample, Lower Kananaskis Reservoir (n = 137). (Numbers in parentheses represent the % of each age-group in each length range.)

Standard Length Interval (cm)	Age-group and Sex									
	0		1		2		3		4	
	M	F	M	F	M	F	M	F	M	F
1.0-1.9	1(50)									
2.0-2.9	1(50)									
3.0-3.9			7(30)	8(36)						
4.0-4.9			11(48)	8(36)		1(4)				
5.0-5.9			5(22)	5(23)	4(11)	7(25)				
6.0-6.9				1(5)	14(38)	9(32)				
7.0-7.9					16(43)	10(36)				
8.0-8.9					3(8)	1(4)	4(50)	5(42)		
9.0-9.9							4(50)	7(58)		1(25)
10.0-10.9									1(100)	2(50)
11.0-11.9										1(25)
Subtotals	2	0	23	22	37	28	8	12	1	4

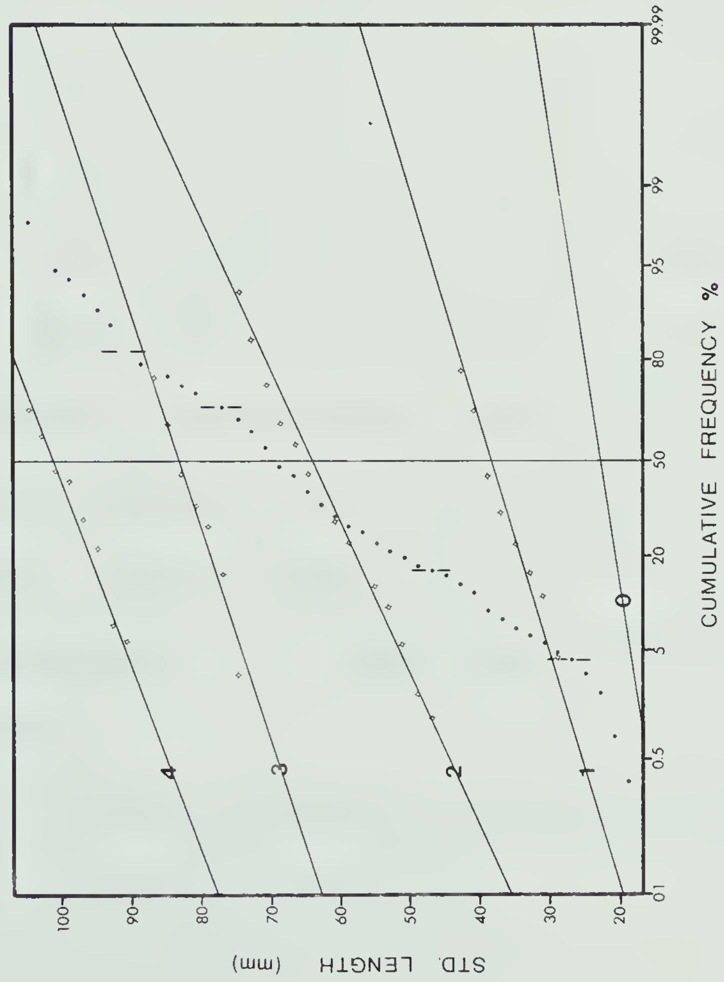
Figure 21. Graphic separation of polymodal length frequencies by probability coordinates for:

A. 343 *Couesius plumbeus* from Lower Kananaskis Reservoir. χ^2 test for departure from normality ($\chi^2 = 19.90$; $\chi^2_{.05(43df)} = 55.7$, $P > 0.05$).

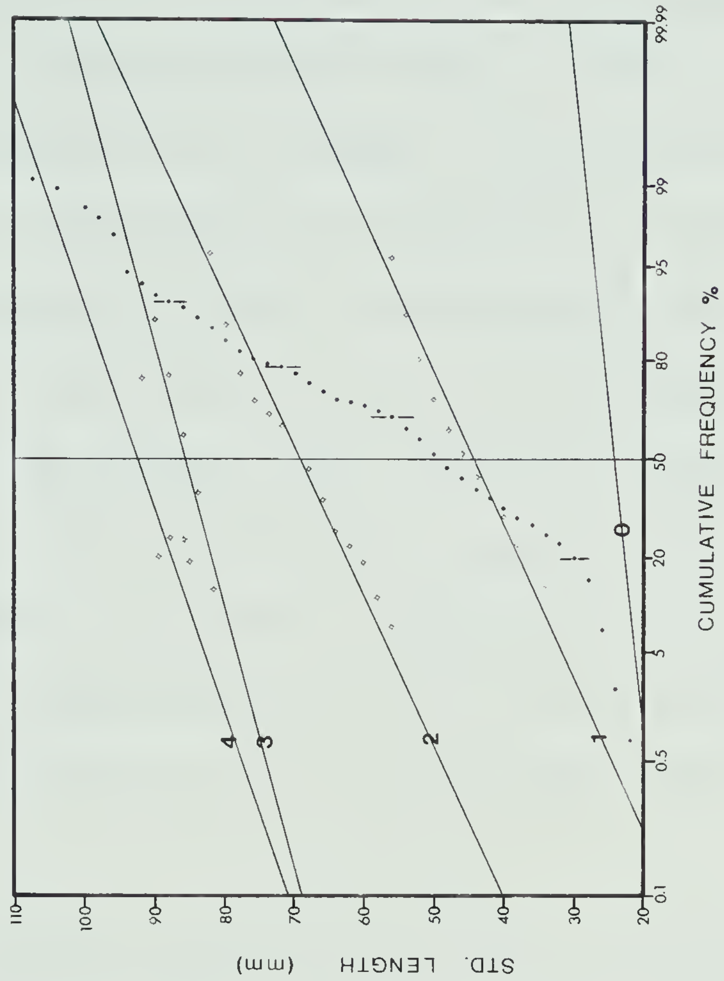
B. 241 *Rhinichthys cataractae* from Lower Kananaskis Reservoir. χ^2 test for departure from normality ($\chi^2 = 3.32$; $\chi^2_{.05(40df)} = 55.8$, $P > 0.05$).

Numerals are age-class designations. Solid dots are total cumulative frequencies and starred circles are cumulative frequencies within size groups.

A. COUESIUS PLUMBEUS



B. RHINICHTHYS CATARACTAE



spawning *C. plumbeus* 5 years and older in Saskatchewan.

Six age-classes are indicated for *R. cataractae* from scale annuli. The lengths of the fish at each annulus formation are represented in Table 13. Separation of polymodal length frequencies by probability coordinates revealed the presence of only 5 age-classes (Fig. 21). However, this is likely due to the low frequency of older 5+ *R. cataractae*. A chi-square test showed no significant differences ($P > 0.05$) between the observed and expected normal distribution of length frequencies in each of the age-classes. Six age-classes have also been reported from Lake Michigan populations of *R. cataractae* (Brazo *et al.*, 1978).

Four age-classes are indicated for the hybrid sample by counts of the scale annuli (Table 14). Although age-class 0 hybrid individuals were available they are not included in the analysis. No hybrid individuals were older than 4 years and there were no male hybrids older than 3 years. The hybrid sample is small ($n= 36$) and contains mostly small hybrids in the younger age-classes. The low frequency of hybrid individuals precludes age verification by polymodal probability method. Age analysis has not been previously reported for *C. plumbeus* x *R. cataractae* hybrids.

b) Growth Rates

Growth rates of the two species and the hybrids are described by the following equations:

C. plumbeus $\log L = 0.513 + 0.147T$

TABLE 13. Length distribution of the age-groups of *Rhinichthys cataractae* from 1977, 1978 collections, Lower Kananaskis Reservoir (n = 131). Numbers in parentheses represent the % of each age-group in each length range.

Standard Length Interval (cm)	Age-group and Sex											
	0		1		2		3		4		5	
	M	F	M	F	M	F	M	F	M	F	M	F
1.0-1.9												
2.0-2.9	2(100)	2(100)	6(40)									
3.0-3.9			6(40)	9(64)								
4.0-4.9			2(13)	5(36)	7(33)	6(25)						
5.0-5.9			1(7)		12(57)	11(46)						
6.0-6.9					2(10)	4(17)	9(82)	4(14)				
7.0-7.9						3(12)	2(18)	11(39)				
8.0-8.9								10(36)		2(17)		
9.0-9.9								3(11)	1(100)	9(75)		
10.0-10.9										1(8)		1(100)
Subtotals	2	2	15	14	21	24	11	28	1	12	0	1

TABLE 14. Length distribution of the age-groups of *Couesius plumbeus* x *Rhinichthys cataractae* hybrids, from 1977, 1978 collections, Lower Kananaskis Reservoir (n = 36). Numbers in parentheses represent the % of each age-group in each length range.

Standard Length Interval (cm)	Age-group and Sex									
	0		1		2		3		4	
	M	F	M	F	M	F	M	F	M	F
1.0-1.9										
2.0-2.9										
3.0-3.9			2(40)							
4.0-4.9			3(60)	3(100)						
5.0-5.9					10(83)	6(75)				
6.0-6.9					2(17)	2(25)	2(40)	1(100)		
7.0-7.9							3(60)			
8.0-8.9										
9.0-9.9										1(50)
10.0-10.9										
11.0-11.9										1(50)
Subtotals	0	0	5	3	12	8	5	1	0	2

C. plumbeus x *R. cataractae* log L = 0.494 + 0.124T

R. cataractae log L = 0.425 + 0.145T

where L = standard length, T = age-class and the regression coefficients equal the instantaneous growth rates. Data from each sex were pooled to calculate the regression for each species.

C. plumbeus appears to have the fastest growth rate. The growth rates for *C. plumbeus* were determined from Saskatchewan (Brown *et al.*, 1970) using the Peterson method and from Labrador (Brazo *et al.*, 1978) using back calculations. Thus, their results are not directly comparable to those in this study.

Comparison of the regression lines by inspection reveals that *R. cataractae* has the slowest growth rate for fish younger than 3 years. The hybrids have a generally intermediate growth rate between the parental species, but after 3 years age it declines below the growth rate of *R. cataractae* (Fig. 22). If the growth rates are extended back beyond the Y-axis to include all growth in the first year, it appears that the hybrid growth rate initially exceeds that of the two parentals. The hybrid offspring of the experimental crosses also showed a faster growth rate than that of the parental offspring. This apparent decline in the hybrid growth rate may suggest the accumulative effects of some selective disadvantage.

However, an analysis of covariance (Nie *et al* ., 1975) was performed to test for significant differences between

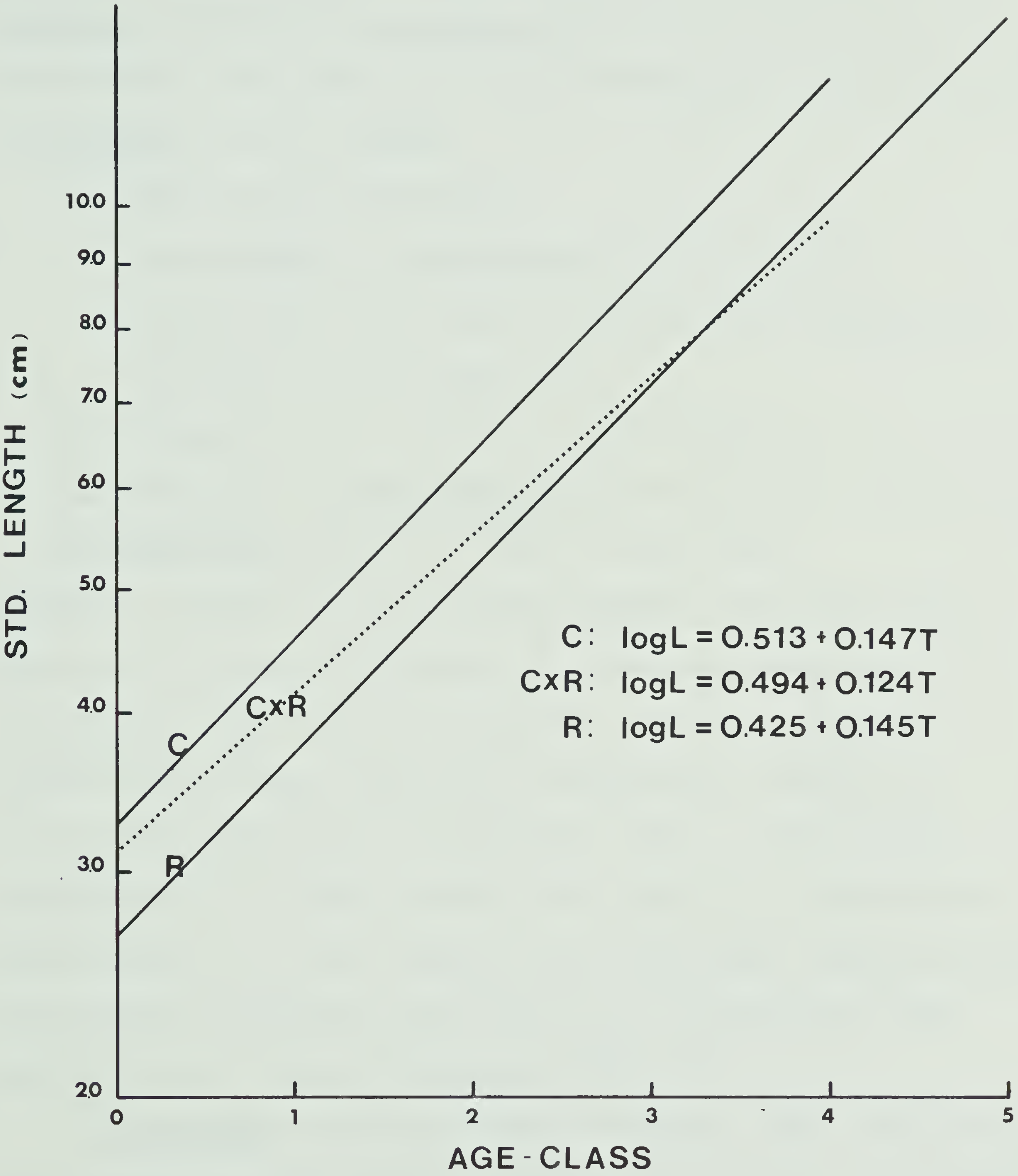
Figure 22. Growth rate regressions for:

C - 140 *Couesius plumbeus* (r = 0.90)

R - 130 *Rhinichthys cataractae* (r = 0.91)

C x R - 36 *C. plumbeus* x *R. cataractae* hybrids (r = 0.93)

from Lower Kananaskis Reservoir.


STD. LENGTH (cm)
10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
0
1
2
3
4
5
AGE - CLASS
C
CxR
R
C: logL = 0.513 + 0.147T
CxR: logL = 0.494 + 0.124T
R: logL = 0.425 + 0.145T

the regressions (Appendix Table 29). Statistically, there is no significant difference ($P > 0.05$) between the slopes of the three regression lines: there is significant difference ($P < 0.05$) between the intercepts of *R. cataractae* and *C. plumbeus* and between *R. cataractae* and the hybrid but no significant difference ($P > 0.05$) between the intercepts of *C. plumbeus* and the hybrid.

c) Length-Weight Relations

C. plumbeus, *R. cataractae* and the hybrid populations each approximate isometric growth, as described by the equations:

C. plumbeus $\log W = -1.781 + 3.064 \log L$

C. plumbeus x *R. cataractae* $\log W = -1.725 + 2.813 \log L$

R. cataractae $\log W = -1.899 + 3.120 \log L$

where W = weight and L = standard length. Data from both sexes were pooled. Comparison of the three length-weight regressions (Fig. 23) by inspection reveals no apparent differences between the three populations. Analysis of covariance between the regressions shows no significant differences ($P > 0.05$) between the slopes but significant differences ($P < 0.05$) between the intercepts. Length-weight regressions calculated separately for the sexes of each population are given in Appendix Table 30.

C. plumbeus from Saskatchewan (Brown, 1969) are heavier for any given length ($\text{Log} = -3.00 \times 10^{6} + 3.20 \text{ Log } L$) than the Kananaskis *C. plumbeus*. Additionally, *C. plumbeus* from Labrador (Bruce and Parsons, 1976) weigh less for any given

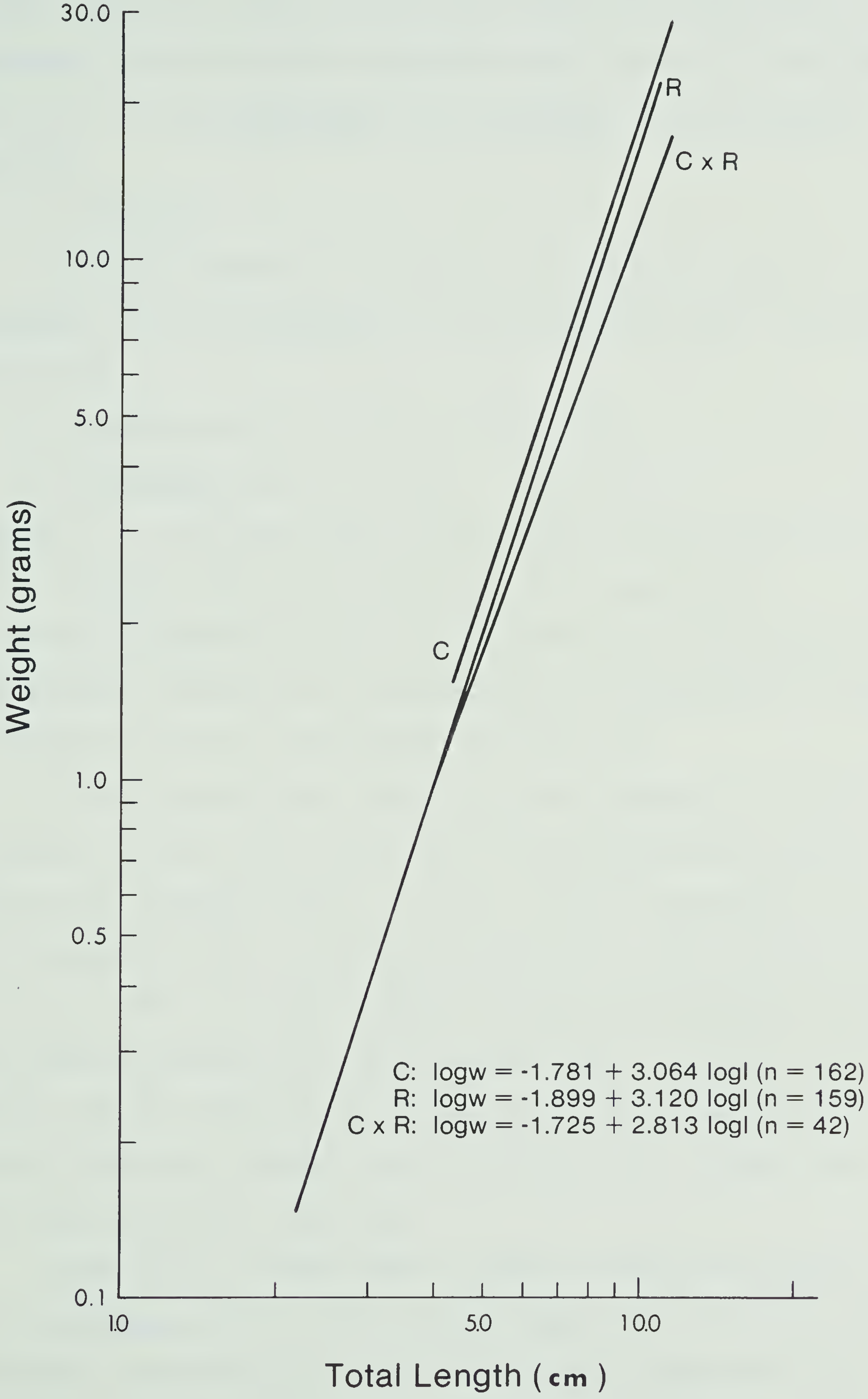
Figure 23. Length-weight regressions for:

C - 170 *Couesius plumbeus* (r = 0.96)

R - 157 *Rhinichthys cataractae* (r = 0.99)

C x R - 33 *C. plumbeus* x *R. cataractae* hybrids (r = 0.98)

from Lower Kananaskis Reservoir.


30.0
10.0
5.0
1.0
0.5
0.1
Weight (grams)
R
C x R
C
C: logw = -1.781 + 3.064 logl (n = 162)
R: logw = -1.899 + 3.120 logl (n = 159)
C x R: logw = -1.725 + 2.813 logl (n = 42)
1.0
5.0
10.0
Total Length (cm)

length ($\log W = -1.88 + 2.88 \log L$) than the Kananaskis *C. plumbeus*. Length-weight regressions have not been previously reported for *R. cataractae* or *C. plumbeus* x *R. cataractae* hybrids.

d) Fecundity

The relationship of fecundity to standard length for *C. plumbeus* and *R. cataractae* can be described by the following equations:

C. plumbeus $\log F = 0.673 + 2.534 \log L$

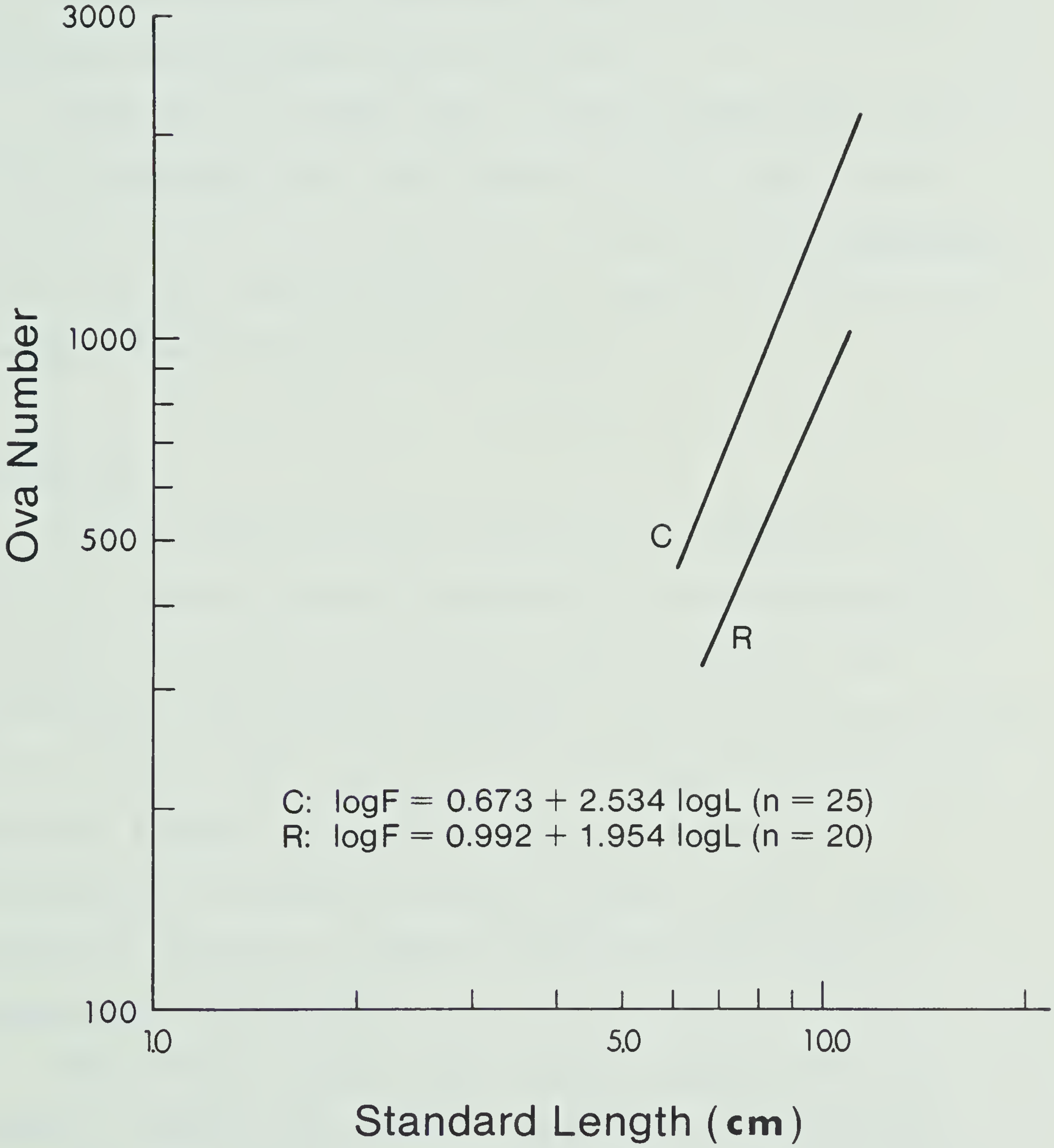
R. cataractae $\log F = 0.922 + 1.954 \log L$

Analysis of covariance shows significant differences ($P < 0.05$) between these regressions in both slopes and intercepts (Appendix Table 29). The fecundity regressions of the parental species are presented as a contribution to our knowledge of their life histories (Fig. 24).

Of the seven adult, female hybrids examined, four had regressed gonads with very small, indistinguishable eggs. These were captured July 27, 1977, and were probably in a post-spawning state. Another post-spawning hybrid female (SL = 62 mm) had 92 ova. Two hybrid females were captured during the spawning season: one was captured June 16, 1977, (SL = 96 mm) and was fully spent with only 38 ova remaining; the other female was captured May 26, 1978, (SL = 114 mm) and was fully ripe with 1038 ova.

Brown *et al*. (1970) gave a range of 450-2450 eggs for 20 *C. plumbeus* with a total length range of 9.0-13.2 cm. The fecundity regression for this Saskatchewan population was

Figure 24. Fecundity regressions for 25 *Couesius plumbeus* (C) (r = 0.80) and 20 *Rhinichthys cataractae* (R) (r = 0.70) from Lower Kananaskis Reservoir.


3000
1000
500
100
Ova Number
C
R
C: logF = 0.673 + 2.534 logL (n = 25)
R: logF = 0.992 + 1.954 logL (n = 20)
1.0
5.0
10.0
Standard Length (cm)

Log F = -3.243 + 3.096 log L. Additionally, Bruce and Parsons (1976) gave a range of 573-1158 eggs for 10 *C. plumbeus* with a fork length range of 9.2-11.2 cm. The fecundity regression for this Labrador population was Log F= -0.441 + 3.356 log L. The number of eggs for *C. plumbeus* in this study ranged from 380-2316 eggs for 25 fish with a standard length range of 6.1-11.2 cm.

Brazo *et al*. (1978) gave a range of 870-9953 eggs for 33 *R. cataractae* from Lake Michigan with a total length range of 7.4-11.7 cm. The number of eggs for *R. cataractae* in this study ranged from 364-1121 eggs for 20 fish with a standard length range of 6.6-10.0 cm.

DISCUSSION

Embryo mortality tests revealed no difference in hatching success between homospecific and heterospecific crosses. The artificial backcross was a failure, but conclusions as to hybrid fertility from one replicate would not be sound. Also, there was no difference in long-term survival between artificially produced hybrids and individuals of parental species origin. In fact, hybrid offspring survived in aquaria better than did pure *R. cataractae* individuals.

Wild-caught hybrids have similar growth rates and attain a similar age structure compared to the parental species. Also, there is no statistical difference between the length-weight relationships of the hybrids and the

parental species. The life history data suggest that the hybrids may not be facing excessive competition from the parental species. Thus, neither gametic mortality nor hybrid inviability are operative barriers preventing hybridization between C. plumbeus and R. cataractae.

Hybrid gonads were not examined histologically, but the hybrid gonads did not appear to be deformed or superficially different from those of the parental species. Fully ripe male and female hybrids were captured and exuded sex products similar to individuals of the parental species. Hybrid sperm was observed microscopically and found to be motile. Hybrid eggs appeared to be of similar shape and condition as parental eggs. Additionally, it is not known experimentally if hybrids are sterile, but it can be inferred from the results of the morphological analysis that at least the barrier is low. Introgression does not appear to put the species' status in peril. The sex ratio of the hybrids was biased toward males.

IX. GENERAL DISCUSSION

The occurrence of this hybridization between *C. plumbeus* and *R. cataractae* does not alter the systematic position of these two species within cyprinid genera that are generally held to be distantly related. Fish hybridization in areas of environmental disturbance no more imperils the generic or specific status of the animals involved than do the multitude of possible artificial crosses (Hubbs, 1961). The fact that these two types of cyprinid remain distinct in most other localities of their range overlap confirms the recognition of the two types as distinct species (*sensu* Mayr, 1969).

Certain recognized environmental factors, which facilitate the dissolution of species' reproductive isolating mechanisms (Hubbs, 1955; Mayr, 1969), all appear to be important in causing hybridization between *C. plumbeus* and *R. cataractae* in Lower Kananaskis Reservoir.

1) Environmental Disturbance; Paucity of Spawning Areas

Disturbance of the environment is often alluded to as the most frequent cause of hybridization of both plants and animals (Mayr, 1969; Anderson, 1949, 1953; Hubbs *et al*., 1943; Sibley, 1961; Mecham, 1960). However, its method of operation has not been demonstrated in any rigorous way.

The Lower Kananaskis Reservoir is a disturbed environment in terms of the annual level fluctuations associated with filling and lowering. The change from a lake to a reservoir may indirectly contribute to hybridization.

Spawning species may be brought together because flooding causes the loss and reduction of originally distinct spawning habitats. Also, with variability in drawdown levels from year to year, there is unpredictability in normal shoreline features which could be used for new spawning sites. Without predictable flooding during the spawning season, it is likely that species' habitat segregation breaks down.

C. plumbeus is an adaptable species which can lake spawn and undergo spawning migrations up rivers and streams (Brown *et al.*, 1970). *R. cataractae* probably prefers spawning in riffles (Scott and Crossman, 1973). With the possible exception of *R. cataractae* moving into Interlakes Stream, neither species underwent spawning migrations up inlet streams. Although each species has a preference for inlet stream spawning, it appears that the streams are unavailable (except Interlakes Stream) during the spawning season due to fast currents and low temperatures. (Why the unflooded portions of Interlakes Stream were not utilized more for spawning by the two species, remains unknown.) It is likely that the two species have been restricted to spawning along the shoreline and at stream mouths since their initial introduction to the lakes. Reservoir construction could neither have caused nor altered this spawning relationship with inlet streams. Lower Kananaskis Lake was equally depauperate in appropriate spawning areas, as the Reservoir is today.

However, while spawning habitat segregation was possible under original, predictable lake conditions, fluctuating reservoir levels may have disrupted this tenuous segregation. Evidence provided in this study indicates that rising reservoir levels at Interlakes Stream mouth brought together fully ripe individuals of each species. Hybridization may result because of the action of an hypothesized difference between the two species in their reaction to advancing water levels. *C. plumbeus*, in maintaining their depth distribution and their proximity to the stream mouth, advance into the newly flooded lower reaches of the stream. Here, *P. cataractae* maintain their positions relative to the stream perhaps due to spawning territoriality, as cited by McPhail and Lindsey (1970). This series of events may be inferred to occur at the other stream mouths where habitat segregation is not so apparent. The generality of this model requires verification from other reservoirs where these species are sympatric.

Without pre-impoundment information on where the species were spawning or whether hybridization occurred, it is difficult to evaluate the contribution of reservoir construction to fish hybridization. Environmental impact statements must provide these data to rigorously assess both the beneficial and adverse effects of future reservoir construction.

2) Species Introduction; Rarity of One Parental Species

Nelson (1966) advanced the idea that the two species were introduced as live bait into the original Kananaskis Lakes; *R. cataractae* prior to 1936 and *C. plumbeus* prior to 1961 (in the late 1950's). The introduction of one or both species to a new environment appears to be one of the many precursors to hybridization (Hubbs *et al.*, 1943; Hubbs, 1961; Greenfield and Greenfield, 1972). The effects of introduction will depend upon the abundance of each species, their genetic similarity, and the strength of the species' isolating mechanisms.

In Lower Kananaskis Reservoir, the introduction of *C. plumbeus* has successfully resulted in development of a large population size. Introduced *R. cataractae* have not adapted as well and have attained a small population size relative to that of *C. plumbeus*. *R. cataractae* are possibly beyond the margin of their normal habitat range in Lower Kananaskis Reservoir, which is without abundant riffle habitat. In Lower Kananaskis Reservoir, this low frequency of *R. cataractae* relative to *C. plumbeus* is a contributing factor to hybridization. In the absence of appropriate mating stimuli, individuals of the less common species may have no alternative but to respond to inappropriate stimuli from individuals of the abundant species (Mayr, 1969). Hybridization has long been attributed to a disproportion in the abundance of species (Hubbs *et al.*, 1943; Mecham, 1960; Stebbins, 1959). Whether *R. cataractae* will mate with *C. plumbeus* in the absence of conspecific mates is unknown.

Such mating did not occur during the mating tests conducted in this study.

3) Overview of Environmental Factors

Given the absence of appropriate historical information on the ecology and abundance of these two species, it is not possible to single out one of the above factors as having the major role in facilitating hybridization.

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Plate 1. Male *Couesius plumbeus* captured at height of spawning period, mid-June, 1978, from Lower Kananaskis Reservoir.

Plate 2. Female *Couesius plumbeus* captured at height of spawning period, mid-June, 1978, from Lower Kananaskis Reservoir.

Plate 3. Male *Rhinichthys cataractae* captured at height of spawning period, mid-June, 1978, from Lower Kananaskis Reservoir (Interlakes Stream).

Plate 4. Female *Rhinichthys cataractae* captured at height of spawning period, mid-June, 1978, from Lower Kananaskis Reservoir (Interlakes Stream).

Plate 5. Adult male hybrid, *Couesius plumbeus* x *Rhinichthys cataractae*, captured at height of spawning period, mid-June, 1978, from Lower Kananaskis Reservoir.

Plate 6. Top: *Couesius plumbeus* (male)

Middle: *Couesius plumbeus* x *Rhinichthys cataractae* hybrid (male)

Bottom: *Rhinichthys cataractae* (male)

All specimens captured in 1977, Lower Kananaskis Reservoir.

Plate 7. Electroshocking the lower reaches of Smith-Dorrien Creek near its mouth on Lower Kananaskis Reservoir, early May, 1978 (looking east).

Plate 8. Interlakes Stream at south end of Lower Kananaskis Reservoir (looking south), in early June prior to cyprinid spawning peak. This illustrates Interlakes stream habitat before it is flooded with the rising reservoir level.

APPENDIX TABLE 1. Summary of cyprinid catch data from Upper and Lower Kananaskis Reservoirs, 1977. Size of gillnet mesh given in mm followed by number of hours set (in parentheses).

				Numbers of Specimens Captured		
Capture Site Description	Date	Method of Capture	Depth	*C. plumbeus*	*R. cataractae*	Putative Hybrids
UPPER KANANASKIS RESERVOIR						
UK1 - East Bay near main dam	May 25	Gillnet 26 mm(24)	4.5 m	9		
UK1 - East Bay near main dam	May 27	Gillnet 26 mm(48)	2.0 m	2		
UK2 - mouth of Sarrail Cr.	June 14	Gillnet 26 mm(24)	3.5-5.5 m	27	4	
UK2 - mouth of Sarrail Cr.	June 16	Gillnet 26 mm(48)	6.0-7.0 m	7		1
UK2 - mouth of Sarrail Cr.	June 21	Gillnet 18 mm(24)		10		
UK2 - mouth of Sarrail Cr.	June 29	Gillnet 26 mm(43)	4.5-6.5 m	29	7	
UK3 - E. shore; 300 m N of rocky pt. in East Bay	May 27	Gillnet 26 mm(24)		1		
UK5 - mouth of Kananaskis R.	June 21	Gillnet 26 mm(23)	3.0-4.0 m	6		1
UK5 - mouth of Kananaskis R.	July 21	Seine		10		
UK7 - inlet to Interlakes penstock	July 21	Seine		182	1	
UK7 - inlet to Interlakes penstock	Aug. 9	Seine		378	2	7
UK8 - N. shore; midway from Interlakes to Kananaskis R.	July 21	Seine		1		
LOWER KANANASKIS RESERVOIR						
LK1 - extreme S. end of reservoir	May 10	Gillnet 26 mm(24)	3.0 m	9	1	
LK1 - extreme S. end of reservoir	May 11	Gillnet 26 mm		4		
LK1 - as above & off E. shore	May 27	Gillnet 18 mm(31)	1.5-2.5 m	8		
LK1 - extreme S. end of reservoir	June 2	Gillnet 18 mm		12		
LK1 - as above & mouth to S.E. Arm	June 14	Gillnet 26, 18 mm(27)		74	4	1
LK1 - as above & mouth to S.E. Arm	June 15	Gillnet 18 mm(26)	2.0-4.0 m	11		
LK1 - as above & mouth to S.E. Arm	June 15	Gillnet 26 mm(26)	2.0-4.0 m	22		
LK1 - as above & mouth to S.E. Arm	June 23	Gillnet 26 mm(19)	4.0-6.0 m	23		
LK1 - as above & mouth to S.W. Arm	June 23	Gillnet 26, 18 mm(18)		8		
LK1 - as above & mouth to S.W. Arm	June 23	Seine		75		
LK1 - as above & mouth to S.W. Arm	June 24	Gillnet 26, 18 mm(21)	5.5-6.0 m	41		
LK1 - as above & mouth to S.E. Arm	July 6	Gillnet 26, 18 mm(20)	5.8 6.5 m	54		
LK1 - as above & mouth to S.W. Arm	July 8	Seine		522		2
LK1 - as above & mouth to S.W. Arm	July 15	Seine		28		
LK1 - as above & near campsites W. shore	July 21	Seine		998	17	13
LK1 - as above & near campsites W. shore	July 27	Gillnet 26 mm(21)	4.5 m	28		
LK1 - as above & mouth to S.E. Arm	Aug. 9	Gillnet 26, 18 mm(22)	8.0 m	50		

APPENDIX TABLE 1. Continued

Capture Site Description	Date	Method of Capture	Depth	Numbers of Specimens Captured *C. plumbeus*	*R. cataractae*	Putative Hybrids
LOWER KANANASKIS RESERVOIR						
LK2 - E. shore; N. of Boulton Cr.	June 3	Gillnet 26, 18 mm(24)	2.0 m	13		1
LK2 - E. shore; N. of Boulton Cr.	June 14	Seine		14		
LK2 - E. shore; N. of Boulton Cr.	June 15	Gillnet 18 mm(26)		40		
LK2 - E. shore; N. of Boulton Cr.	June 16	Gillnet 18 mm(25)		7		
LK2 - E. shore; N. of Boulton Cr.	June 22	Gillnet 26 mm(24)	2.0-2.6 m	7		
LK2 - E. shore; N. of Boulton Cr.	June 24	Gillnet 26 mm(22)	4.0-5.0 m	11		
LK2 - E. shore; N. of Boulton Cr.	July 27	Seine		110		
LK2 - E. shore; N. of Boulton Cr.	July 27	Seine		3		2
LK4 - E. shore; near cottages	July 27	Seine		530	149	2
LK4 - E. shore; near cottages	July 27	Seine		3		
LK5 - mouth of Muskeg Cr.	June 1	Gillnet 26, 18 mm(29)	2.5-12 m	24	1	
LK6 - mouth of Invincible Cr.	June 1	Gillnet 26 mm(28)	2.0 m	18		
LK6 - mouth of Invincible Cr.	June 27	Gillnet 26, 18 mm		11		
LK7 - mouth of Smith-Dorrien Cr.	May 17	Gillnet 26, 18 mm(25)	2.0 m	5		
LK7 - mouth of Smith-Dorrien Cr.	May 18	Gillnet 18 mm(24)	3.0 m		1	
LK7 - mouth of Smith-Dorrien Cr.	June 9	Gillnet 26 mm		2		
LK7 - mouth of Smith-Dorrien Cr.	July 11	Seine		62		
LK8 - mouth of Kent Cr.	July 11	Seine		199		2
LK8 - mouth of Kent Cr.	July 11	Seine		62		
LK8 - mouth of Kent Cr.	July 20	Seine		732	94	12
LK9 - flats N. of Pocaterra Dam	July 11	Seine		1227	95	12
LK9 - flats N. of Pocaterra Dam	July 27	Seine		1271		
LK9 - flats N. of Pocaterra Dam	July 27	Seine		29		
LK9 - flats N. of Pocaterra Dam	Aug. 8	Seine		344		
Interlakes P.P. Raceway	June 16			97	5	

APPENDIX TABLE 2. Cyprinid captures, Lower Kananaskis Reservoir, 1978.
(LK1 Stream = Interlakes Stream)

Date 1978	Location	Capture Method	Depth	Substrate	*Couesius plumbeus*						*Rhinichthys cataractae*						*C. plumbeus* x *R. cataractae*		
					Sex	Total	Not Ripe	Ripe	Fully Ripe	Spent	Sex	Total	Not Ripe	Ripe	Fully Ripe	Spent	Total	Not Ripe	Ripe
May 1	Common Bay (E. shore)	seine	0.3 m	fine silt	♀	250	250				♀	3	3						
					♂	161	161				♂	4	4						
May 7	Smith-Dorrien Cr. Mouth	minnow trap	1 m	sandy silt	♂	1													
May 9	Common Bay (E. shore)	minnow trap	0.5 m	silt	♂	1													
May 13	LK1 Stream	seine	0.4 m	sandy silt	♀	6	5	1											
					♂	2													
May 15	LK1 Stream	seine	0.2 m	fine silt	♀	3		3											
May 16	Smith-Oorrien Cr. Mouth	gillnet 18, 26 mm (28.5)	1 m	silt	♀	3	3												
May 17	Smith-Dorrien Cr. Mouth	gillnet 26 mm (24)	1.25 m	silt	♀	1	1												
					♂	1			1										
May 18	Smith Dorrien Cr. Mouth	gillnet 18, 26 mm (22)	1.25 m	silt	♀	6		6			♀	1		1					
					♂	2													
May 18	LK1 Stream	seine	< 0.5 m	mud	♀	3	3				♀	1	1						
					♂	5					♂	1							
					jeuv.	44													
May 22	LK1 Stream	seine		silt	jeuv.	2													
May 22	LK1 Stream Mouth	seine	0.1 m	silt	♀	1	1												
					jeuv.	57													
May 23	Common Bay	gillnet 18, 26 mm (22.5)	10 m	silt	no Cyprinidae captured														
May 24	Common Bay	gillnet 18, 26 mm (24)	4 m	silt	♀	6		6											
May 24	Smith-Dorrien Cr. Mouth	gillnet 18, 26 mm (24)	1 m	silt & gravel	♀	4	1	3											
May 25	Interlakes Raceway	gillnet 18 mm (23)	15 m	boulder	♀	3	1	2											
May 25	Smith-Dorrien Cr. Mouth	gillnet 18, 26 mm (22)	5 m	silt	♀	9	9												
May 26	Smith-Dorrien Cr. Mouth	gillnet 18, 26 mm (25)	1.3 m	gravel	no Cyprinidae captured														
May 26	Boulton Cr. Mouth	gillnet 18, 26 mm (20)	1-3.0 m	silt, stumps	♀	9		6	3		♀	3	1	2			♀ 2	1	1
					♂	3			3		♂	2							
May 27	Smith-Dorrien Cr. Mouth	gillnet 18, 26 mm (22)	1-3.0 m	silt & gravel	no Cyprinidae captured														
May 27	Boulton Cr. Mouth	gillnet 18, 26 mm (24)	1-3.0 m	silt	♀	1		1											
June 1	Interlakes Raceway	gillnet 26 mm (29)	1.1-3.2 m	boulder	♀	15	7	3	5		♀	4		4					
					♂	5													
June 1	LK1 Stream Mouth	gillnet 18 mm (27)	1.2 m	silt	♀	3		2	1		♂	1							
June 1	Kent Cr. Mouth	gillnet 18, 26 mm (52)	1-3.0 m	gravel	♀	2		2											
June 5	LK1 Stream	seine, dipnet	0.1 m	boulder & silt	♀	9	4	5			♀	10	3	6	1				
					♂	9			2		jeuv.	2							
June 5	LK1 Common Bay	gillnet 18, 26 mm (19)	17.5 m	silt	♂	2			2										
June 7	LK1 Common Bay	gillnet 18 mm (48)	17 m	silt	♂	2			2										
June 7	Boulton Cr. Mouth	gillnet 26 mm (48)	1.5 m	silt	♀	10													
					♂	1													
June 7	LK1 Stream	seine, dipnet	0.05-0.5 m	boulder & silt							♂	5			4		♂ 2	1	1
											2 - sex unknown								
June 7	LK1 Stream Mouth	gillnet 26 mm (22)	2.8 m	silt	♀	11	1	4	6		♀	3		2	1				
					♂	4			3		♂	1							

APPENDIX TABLE 2. Continued.

Date 1978	Location	Capture Method	Depth	Substrate	*Couesius plumbeus*						*Rhinichthys cataractae*						*C. plumbeus* x *R. cataractae*		
					Sex	Total	Not Ripe	Ripe	Fully Ripe	Spent	Sex	Total	Not Ripe	Ripe	Fully Ripe	Spent	Total	Not Ripe	Ripe
June 8	LK1 Stream	dipnet		cobble rock							♀	1		1					
											♂	1							
June 8	LK1 Stream Mouth	gillnet 26 mm (25)	2.0 m	silt	♀	94	21	24	36	13	♀	7		6	1		♂ 2	1	1
					♂	7													
June 8	Interlakes Raceway	gillnet 18 mm (28)	5 m	boulder	♀	5		3	2		♀	2			2				
					♂	20			9		♂	1			1				
June 8	Invincible Cr. Mouth	seine	< 1.0 m	silt	♀	31	22	9									♂ 1		1
					♂	26			20										
					jeuv.	24													
June 8	Smith-Dorrien Cr. Mouth	gillnet 18 mm (26)	4.0 m	silt & gravel	♀	4		3											
					♂	1													
June 12	LK1 Stream	dipnet	0.2 m	cobble rock							♂	4			4				
											4 - sex unknown								
June 12	LK1 Stream Mouth	gillnet 18 mm (10)		gravel	♀	10		3		7									
					♂	4			4										
June 12	LK1 Common Bay	gillnet 26 mm (10)	3.7 m	silt	♀	8		6		2									
June 13	LK1 Stream	minnow trap	0.3 m	sand							♀	1		1					
June 13	LK1 Stream Mouth	gillnet 18 mm (13)	1.8 m	gravel	♀	30(12 state unknown)			13	5	♀	13		2	8	3			
					♂	39			12										
June 13	LK1 Common Bay	gillnet 26 mm (6)	3.7 m	silt	♀	23		5	3	15									
June 13	Boulton Cr. Mouth	gillnet 18, 26 mm (18)	2.1 m	silt	♀	51	6	32	1	1'	♀	1		1					
					♂	4			3										
June 13	Invincible Cr. Mouth	seine		silt	♀	7	2	2	3		♀	1	1						
					jeuv.	61					♀	2	1	1					
June 14	LK1 Stream	minnow trap	0.3 m	silt							♂	1	1						
June 14	LK1 Common Bay (SW)	gillnet 26 mm (30)	[illegible] m	silt	♀	31	2	1	23	5	1 - sex unknown								
June 14	Interlakes Raceway	gillnet 26 mm (20)	2.5-5.0 m	boulder	♀	71	2	31	27	11									
June 14	Invincible Cr. Mouth	gillnet 18 mm (24)	1.8 m	sand	♀	12					♀	1			1				
					♂	6			6										
June 19	LK1 Stream	dipnet	0.1 m	cobble rock							♀	1			1				
											♂	2	1		1				
June 20	LK1 Stream	dipnet	0.2 m	cobble rock							♀	7		3	1				
											♂	2							
June 20	Interlakes Raceway	gillnet 18 mm (25)	2.5 m	boulder	♀	4	2	[illegible]			♀	1				1			
June 20	Boulton Cr. Mouth	gillnet 26 mm (17)	2.0 m	silt	♀	29	[illegible]	3	7	17									
					♂	3			3										
June 20	Invincible Cr. Mouth	gillnet 26 mm (15)	2.3 m	silt	♂	8			6										
June 21	LK1 Stream	minnow trap & dipnet	0.1 m	cobble rock	♀	1	1				♀	2	1						
					♂	4					♂	1							
June 21	LK1 Common Bay	gillnet 18, 26 mm (16)	3.6 m	gravel & silt	♀	30	1	2	9	18									
					♂	8			6										

APPENDIX TABLE 2. Continued.

Date 1978	Location	Capture Method	Depth	Substrate	*Couesius plumbeus*						*Rhinichthys cataractae*						*C. plumbeus* x *R. cataractae*		
					Sex	Total	Not Ripe	Ripe	Fully Ripe	Spent	Sex	Total	Not Ripe	Ripe	Fully Ripe	Spent	Total	Not Ripe	Ripe
June 21	Interlakes Raceway	gillnet 26 mm (23)	5.5 m	boulder	♀	69	17	17	22	13									
					♂	2			1										
June 21	Invincible Cr. Mouth	seine	0.2	silt	♀	2		1											
June 21	Smith-Dorrien Cr. Mouth	gillnet 18, 26 mm (20)	2.4-4.0 m	silt & gravel	♀	1													
June 21	Midpoint off Interlakes	gillnet 18 mm (18)	20.0 m	silt	no Cyprinidae captured														
June 21	Kent Cr. Mouth	gillnet 18 mm (22)	5.0 m	gravel	♀	2	2												
June 29	LK1 Stream	minnow trap & dipnet	0.1 m	cobble rock							♀	6				7			
											♂	9			7				
June 29	LK1 Common Bay	gillnet 18, 26 mm (28)	1.8-2.4 m	gravel	♀	55	1		12	42							♂ 1	1	
					♂	9			5										
June 29	Boulton Cr. Mouth	gillnet 18, 26 mm (27)	2.4-3.0 m	silt	♀	15(4 state unknown)			1	10									
July 6	Interlakes Raceway	gillnet 26 mm (7)	6 m	boulder	♀	12				12									
July 6	LKL Common Bay	gillnet 18, 26 mm (7)	4.4 m	silt	no Cyprinidae captured														
July 12	LK1 Common Bay	gillnet 18, 26 mm (19)	4.0 m	silt	♀	13			5	8									
					♂	1			1										
July 12	Interlakes Raceway	gillnet 18, 26 mm (19)	6.5 m	boulder	♀	20			2	18									
July 27	LK1 Common Bay	gillnet 26 mm (19)	4.0-6.0 m	silt	♀	8				8									
July 27	Interlakes Raceway	gillnet 26 mm (3.5)	8.8 m	boulder	no Cyprinidae captured														
July 27	Pocaterra Dam flats	seine	0.3 m	gravel	♀	20				20							♂ 1	1	
July 27	Smith-Dorrien Cr. Mouth	seine	0.3 m		♀	23				23									

APPENDIX TABLE 3. Water quality data, Upper Kananaskis Reservoir (1977). S - surface; M - mid-depth; B - 1 m off bottom; N.A. - not available.

PARAMETER	June 20			July 15			August 15		
	S	M	B	S	M	B	S	M	B
Total Alkalinity (mg/1 $CaCo_3$)	83.9	84.4	84.6	83.0	85.0	86.0	79.0	84.0	85.0
Color	5	5	5	5	5	5	5	5	5
pH	8.3	8.2	8.0	8.3	8.1	8.1	8.5	8.1	8.0
Residue, Non-filterable (mg)	15	15	15	15	15	15	15	15	15
Specific Conductance (us/cm)	173	177	174	N.A.	N.A.	N.A.	155	166	167
Turbidity (JTU)	1.4	1.2	2.8	1.5	2.5	3.5	1.5	3.1	2.0
Dissolved Nitrogen (NO_3NO_2 mg/1 N)	0.02	0.05	0.05	0.03	0.05	0.05	0.01	0.06	0.01
Total Kjeldahl Nitrogen (mg/1)	0.28	0.21	0.23	0.10	0.10	0.10	0.10	0.10	0.10
Total Phosphorus (mg/1)	0.007	0.005	0.009	0.014	0.005	0.010	0.003	0.005	0.009
Total Organic Carbon (mg/1)	4	5	4	1	3	1	2	1	1
Total Inorganic Carbon (mg/1)	17	17	18	19	19	20	17	19	19

APPENDIX TABLE 4. Water quality data, Lower Kananaskis Reservoir (1977). S - surface; M - mid-depth; B - 1 m off bottom; N.A. - not availabe.

PARAMETER	June 20			July 15			August 15		
	S	M	B	S	M	B	S	M	B
Total Alkalinity (mg/l $CaCo_3$)	102.0	104.0	101.0	103.0	103.0	100.0	104.0	107.0	103.0
Color	< 5	< 5	< 5	< 5	< 5	< 5	< 5	< 5	< 5
pH	8.4	8.3	8.3	8.6	8.2	7.9	8.5	8.3	7.9
Residue Non-filterable (mg)	15	15	15	15	15	15	15	15	15
Specific Conductance (us/cm)	217	232	218	N.A.	N.A.	N.A.	216	230	218
Turbidity (JTU)	1.6	2.2	2.8	1.5	1.5	2.5	1.5	2.5	2.0
Dissolved Nitrogen (NO_3NO_2 mg/l N)	< 0.01	0.03	0.02	0.01	0.01	0.02	< 0.01	0.03	0.02
Total Kjeldahl Nitrogen (mg/l)	0.27	0.21	0.27	< 0.10	0.10	< 0.10	< 0.10	< 0.10	< 0.10
Total Phosphorus (mg/l)	0.006	0.007	0.013	0.010	0.006	0.005	0.005	0.008	0.013
Total Organic Carbon (mg/l)	4	3	6	1	2	2	3	3	3
Total Inorganic Carbon (mg/l)	21	22	21	24	24	23	23	24	23

APPENDIX TABLE 5. Temperature profiles of Lower Kananaskis Reservoir, 1978. Taken using a YSI telethermometer at Water Quality Sampling Site.

Depth (m)	Temperature °C		
	May 18	June 8	June 29
0	3.0	10.5	13.0
1	4.0		13.0
2	4.0		12.6
3	4.0	8.8	11.6
4	4.0		11.2
5	4.0		10.5
6	4.0	7.1	9.9
7	3.8		9.0
8	3.5		8.4
9	3.4		7.7
10	3.4		7.5
11	3.4		7.3
12	3.3	6.0	7.0
13	3.2		6.9
14	3.1		6.9
15	3.0	5.1	6.4
16	2.9		6.2
17	2.9		6.1
18	3.0	5.0	5.9
19	3.0		5.9
20	3.0		5.9
21		5.0	5.9
24		4.5	5.8
25			5.5

APPENDIX TABLE 6.

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ALBERTA ALL SPECIMENS (100)                 PRINCIPAL COMPONENTS ANALYSIS - CLUSTAN 1C

NUMBER OF CASES =   100
NUMBER OF BINARY VARIABLES =     0          (UNTRANSFORMED DATA)
NUMBER OF NUMERIC VARIABLES =   21

NUMERIC MEANS AND STANDARD DEVIATIONS       VARIABLE MINIMUM VALUE      MAXIMUM VALUE

   1          7.2409         1.4340             1          4.3000          11.0000
   2          1.7565         0.3337             2          1.0300           2.7100
   3          0.3299         0.0864             3          0.1800           0.5700
   4          0.5926         0.1791             4          0.2700           1.0000
   5          0.5907         0.1215             5          0.3400           0.9600
   6          0.5604         0.1241             6          0.2900           0.8700
   7          0.8187         0.1781             7          0.4500           1.3200
   8          0.4321         0.0953             8          0.2500           0.7200
   9          0.5906         0.1371             9          0.3000           0.9100
  10          0.1184         0.0949            10          0.0000           0.3000
  11          0.1890         0.1986            11          0.0000           0.5700
  12          0.4265         0.2826            12          0.0700           0.9800
  13          1.0150         0.2361            13          0.5000           1.9900
  14          3.7543         0.7397            14          2.2200           5.8400
  15          1.7702         0.3736            15          0.9400           2.5500
  16          4.5683         0.9460            16          2.6000           7.4300
  17          2.9569         0.6750            17          1.5800           5.1900
  18          0.5628         0.1435            18          0.2400           0.8900
  19         65.0900         4.1734            19         58.0000          74.0000
  20         12.3700         1.3078            20          9.0000          15.0000
  21         25.9200         3.0309            21         21.0000          33.0000
EIGENVALUES

 12.48   5.95   0.74   0.55   0.34   0.25   0.19   0.11   0.07   0.06   0.05   0.05   0.04   0.03   0.03   0.02
  0.02   0.01   0.01   0.01   0.00


PERCENTAGE VARIANCE

 59.41  28.31   3.53   2.60   1.61   1.20   0.92   0.51   0.36   0.30   0.25   0.23   0.19   0.13   0.12   0.10
  0.09   0.06   0.04   0.03   0.02


CUMULATIVE VARIANCE

 59.41  87.72  91.25  93.85  95.46  96.66  97.57  98.08  98.44  98.73  98.98  99.21  99.41  99.54  99.66  99.76
 99.85  99.91  99.96  99.98 100.00

EIGENVECTORS - BY RO*S

VECTOR  1

0.279 0.277 0.148 0.204 0.245 0.274 0.272 0.249 0.258 0.117 0.051 0.085 0.242 0.280 0.272 0.276 0.270 0.241
0.037 0.010 0.028

VECTOR  2

-0.040 0.022-0.339 0.270-0.188 0.017-0.030-0.164 0.147 0.361 0.396 0.382-0.020-0.019 0.022-0.065-0.085-0.057
 0.273-0.277 0.354

VECTOR  3

-0.001-0.051 0.012-0.116 0.006 0.078-0.048-0.001-0.051-0.119 0.012-0.037 0.231 0.009-0.016-0.004 0.074-0.216
 0.711 0.566 0.160

FIRST   3 FACTOR SCORES
                                                                           S 67     -6.154  1.644  0.284
S   1     4.145 -2.872 -0.505    S 34       6.051 -2.940 -0.962    S 68     -7.059  1.398 -1.080
S   2    -0.071 -2.394  0.522    S 35       5.279 -2.749 -0.247    S 69     -2.476  2.113  0.266
S   3    -4.879 -2.168 -0.270    S 36       4.513 -3.350 -0.184    S 70     -4.204  1.934  0.306
S   4    -1.593 -1.603  0.121    S 37       1.381 -2.103 -0.247    S 71     -4.235  1.407 -0.067
S   5     1.135 -2.766  0.225    S 38      -0.692 -2.778 -0.323    S 72     -5.049  1.381  1.545
S   6     2.405 -3.050 -0.113    S 39      -3.181 -2.123 -0.747    S 73      0.792  1.769 -0.028
S   7    -3.039 -1.847 -0.801    S 40      -4.721 -2.035 -0.542    S 74     -2.561  2.066  0.327
S   8    -1.152 -2.060  1.132    S 41       3.767 -3.075  0.115    S 75     -0.835  1.182  0.334
S   9    -0.307 -2.815 -0.289    S 42       1.154 -2.434  2.304    S 76     -1.889  2.031  0.371
S  10    -1.069 -2.299  0.813    S 43       4.009 -2.338  0.593    S 77     -2.716  1.850 -1.311
S  11    -4.725 -2.310 -0.058    S 44       3.710 -3.116 -0.378    S 78      4.766  3.001 -0.268
S  12    -0.950 -2.533  0.566    S 45       3.327 -2.106  0.395    S 79      3.034  2.544  0.979
S  13    -7.352 -1.778 -0.772    S 46       4.466 -2.814 -0.558    S 80      3.206  2.517 -0.607
S  14    -0.155 -2.369  0.367    S 47       2.853 -2.513  0.026    S 81      2.859  2.637 -1.452
S  15    -6.332 -1.909 -1.239    S 48       2.370 -2.617 -0.723    S 82      2.303  1.991 -0.743
S  16    -0.693 -2.574  0.903    S 49       0.025 -2.463  0.388    S 83      2.449  2.348  0.012
S  17     4.054 -2.646  1.810    S 50       2.295 -2.148 -1.115    S 84      2.610  2.588  0.283
S  18     1.813 -2.101 -0.843    S 51      -0.052  2.124  0.605    S 85      4.337  2.153  1.089
S  19     3.110 -3.095  1.025    S 52      -0.815  2.333 -0.250    S 86      4.474  2.969  0.123
S  20     3.162 -2.740 -0.464    S 53      -1.254  1.964  0.514    S 87      2.787  2.325  0.331
S  21    -4.255 -1.969  0.436    S 54      -3.489  2.371  0.648    S 88      1.770  2.487  0.610
S  22    -5.133 -1.525 -0.889    S 55      -4.314  2.285 -0.866    S 89      2.476  2.416  1.622
S  23    -5.535 -2.079  0.972    S 56       4.542  3.484 -0.675    S 90      0.734  2.497  0.086
S  24    -7.513 -1.421 -0.297    S 57       1.517  2.916  0.422    S 91      0.558  2.388  1.421
S  25     1.734 -3.008  0.193    S 58       2.932  2.931  0.324    S 92      3.457  2.680 -0.341
S  26    -0.406 -2.098  0.185    S 59       0.604  3.615  0.608    S 93      2.553  2.066 -0.379
S  27    -1.109 -2.155 -0.369    S 60       4.044  4.124 -0.324    S 94      0.465  2.760 -0.426
S  28    -1.962 -1.865 -0.912    S 61       1.307  3.773  0.369    S 95      0.843  2.645 -1.725
S  29    -1.789 -2.008 -1.089    S 62      -2.451  2.082 -0.207    S 96     -0.152  1.897 -2.542
S  30    -3.942 -1.460  1.521    S 63      -1.900  2.560  1.534    S 97     -0.426  1.797 -1.695
S  31    -5.451 -1.379 -0.491    S 64      -3.024  2.363  1.838    S 98      0.336  1.885 -1.528
S  32    -3.425 -1.702  0.777    S 65      -3.624  1.961  1.282    S 99      1.918  2.807 -1.298
S  33     9.843 -3.740 -0.084    S 66      -5.815  2.173 -0.279    S100      5.672  2.788  0.083
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APPENDIX TABLE 7.

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KANANASKIS  ALL SPECIMENS (137)                    PRINCIPAL COMPONENTS ANALYSIS - CLUSTAN 1C
NUMBER OF CASES =  137
NUMBER OF BINARY VARIABLES =    0                   (UNTRANSFORMED DATA)
NUMBER OF NUMERIC VARIABLES =   21

NUMERIC MEANS AND STANDARD DEVIATIONS       VARIABLE MINIMUM VALUE      MAXIMUM VALUE

  1        7.4072        1.9825           1         3.4000          12.3000
  2        1.7632        0.4117           2         0.9000           2.6900
  3        0.3419        0.0951           3         0.1800           0.6000
  4        0.5959        0.2058           4         0.2200           1.1100
  5        0.5976        0.1584           5         0.3100           1.0500
  6        0.6171        0.1974           6         0.2800           1.1000
  7        0.8950        0.2665           7         0.4000           1.5800
  8        0.4772        0.1638           8         0.2300           0.9600
  9        0.6323        0.2000           9         0.2600           1.0500
 10        0.1104        0.0958          10         0.0000           0.3700
 11        0.1746        0.1833          11         0.0000           0.6200
 12        0.3923        0.2401          12         0.0800           0.9200
 13        1.0393        0.3338          13         0.4400           1.7800
 14        3.8056        1.0151          14         1.8000           6.2600
 15        1.7936        0.4759          15         0.7500           2.8800
 16        4.7460        1.3369          16         2.1900           8.1500
 17        3.0867        0.9467          17         1.3500           5.7200
 18        0.5325        0.1482          18         0.2100           1.0000
 19       65.4234        3.5143          19        59.0000          73.0000
 20       12.9927        1.2217          20        10.0000          16.0000
 21       25.9854        2.7813          21        21.0000          32.0000
EIGENVALUES

 13.94   4.26   1.02   0.56   0.33   0.20   0.14   0.10   0.08   0.06   0.06   0.05   0.05   0.04   0.03   0.02
  0.02   0.01   0.01   0.00   0.00


PERCENTAGE VARIANCE

 66.36  20.31   4.87   2.68   1.55   0.96   0.66   0.50   0.39   0.31   0.30   0.25   0.24   0.17   0.13   0.10
  0.08   0.06   0.04   0.02   0.02


CUMULATIVE VARIANCE

 66.36  86.67  91.53  94.21  95.76  96.72  97.38  97.88  98.27  98.58  98.88  99.13  99.37  99.54  99.68  99.78
 99.86  99.93  99.96  99.98 100.00

EIGENVECTORS - BY ROWS

VECTOR  1

 0.260 0.264 0.144 0.244 0.246 0.258 0.263 0.250 0.262 0.173 0.115 0.148 0.259 0.262 0.255 0.262 0.255 0.216
 0.007-0.068 0.065

VECTOR  2

-0.104-0.036-0.387 0.179-0.166 0.059-0.013 0.001 0.061 0.337 0.422 0.379-0.037-0.074-0.086-0.084-0.121-0.195
 0.189-0.279 0.385

VECTOR  3

 0.052 0.015 0.006-0.018 0.050-0.027-0.019 0.015-0.006-0.685-0.028-0.068-0.003 0.037 0.031 0.027 0.032-0.022
 0.826 0.501 0.204

FIRST   3 FACTOR SCORES

S   1     6.445  2.416 -0.487     S 47    -2.826  2.453 -1.171     S 93    -2.898 -0.808  0.196
S   2     6.093  1.320 -1.915     S 48    -2.903  2.614  0.126     S 94    -2.185 -2.105  0.178
S   3     4.649  2.691 -0.796     S 49    -2.686  2.191 -0.037     S 95    -2.665 -2.158 -0.118
S   4     3.005  2.916  0.141     S 50    -3.834  2.060 -0.441     S 96    -1.738 -1.476 -1.653
S   5     5.708  2.193  0.732     S 51     4.138 -3.046  0.553     S 97    -1.066 -1.989 -0.165
S   6     5.022  2.399 -0.223     S 52     6.695 -3.558  1.445     S 98    -4.417 -1.148  0.585
S   7     5.846  3.089  0.602     S 53     7.741 -4.427 -0.768     S 99    -5.659 -0.693 -0.603
S   8     6.024  2.798  0.237     S 54     5.959 -3.870  0.105     S100    -1.121 -1.371 -0.646
S   9     7.889  1.805  1.174     S 55     3.518 -2.924  1.089     S101     0.280 -1.726 -1.479
S  10     4.075  2.374 -0.094     S 56     4.413 -3.217 -0.766     S102    -0.965 -0.987  1.310
S  11     5.469  2.488 -0.973     S 57     2.545 -2.266  1.510     S103    -2.023  0.617  0.446
S  12     6.792  1.571  0.251     S 58     2.700 -3.098  0.022     S104    -2.354 -0.310  0.225
S  13     6.287  3.383  0.918     S 59     1.357 -2.607  0.198     S105    -0.038 -1.731  0.484
S  14     6.096  2.506 -1.152     S 60     0.625 -2.129  1.634     S106    -0.984 -0.613  1.495
S  15     4.968  2.032  1.130     S 61     2.555 -3.715 -0.392     S107     0.251 -0.071  1.303
S  16     0.777  1.726 -0.322     S 62    -0.710 -2.134 -1.302     S108    -1.807 -0.437  1.264
S  17    -2.160  1.871 -0.306     S 63    -1.061 -1.806 -1.186     S109    -2.527  0.099  1.124
S  18    -0.956  1.651 -1.620     S 64    -1.970 -1.941 -0.881     S110    -2.859  0.398  1.233
S  19    -3.015  1.440 -1.508     S 65    -0.945 -1.760 -2.026     S111    -3.363  1.097  0.493
S  20     1.270  1.665  0.034     S 66    -1.149 -1.735  0.301     S112    -3.927  0.559  3.086
S  21     3.486  3.094 -1.553     S 67    -1.549 -1.712 -1.034     S113    -3.070  0.344  1.575
S  22     4.471  3.294 -1.776     S 68    -4.572 -1.204  0.399     S114    -5.123  0.161  0.935
S  23     2.058  2.756  0.215     S 69    -2.801 -1.564 -1.443     S115    -3.311  0.911  1.530
S  24     6.024  2.388 -0.117     S 70     3.330 -3.025 -0.528     S116    -4.637 -0.855  1.202
S  25     5.647  1.593 -1.576     S 71     3.371 -2.485  2.051     S117    -4.036 -0.206 -0.795
S  26     2.009  2.513 -0.436     S 72     5.855 -3.621 -0.529     S118    -3.262  1.194  0.995
S  27     0.037  2.240 -1.264     S 73     5.909 -3.049  1.426     S119    -4.615 -0.445 -1.365
S  28     4.533  1.744  0.755     S 74     1.351 -2.031  0.363     S120    -1.829 -0.978 -0.241
S  29    -2.918  2.497 -0.388     S 75     1.070 -2.057 -0.172     S121    -1.185 -0.030  0.286
S  30    -2.861  2.617  1.103     S 76    -2.411 -1.216 -0.400     S122    -3.352  0.111 -0.134
S  31    -2.907  3.023  0.957     S 77     2.295 -2.786  0.187     S123    -2.682 -0.045 -0.325
S  32    -2.966  2.039 -0.495     S 78     0.612 -1.993 -0.614     S124    -3.935 -1.258 -1.433
S  33    -3.146  1.652  0.460     S 79     0.292 -2.126 -0.224     S125    -3.102 -0.515  2.274
S  34    -3.206  2.110  1.489     S 80    -0.267 -1.780  0.164     S126    -5.647  0.091 -0.964
S  35    -2.881  0.932 -0.465     S 81    -1.751 -2.093 -0.169     S127    -7.469 -0.249 -0.505
S  36    -4.439  1.819  0.227     S 82     1.244 -2.335  0.791     S128    -1.341  0.779  1.848
S  37    -3.655  3.021  0.813     S 83     4.917 -2.657  0.658     S129    -2.152  0.224  1.379
S  38     3.210  2.284 -1.206     S 84     0.737 -2.309 -0.139     S130    -2.921  0.015  0.308
S  39     6.208  2.889  0.011     S 85    -0.279 -2.384 -0.149     S131    -4.163 -0.447 -1.379
S  40    -0.368  2.355  0.482     S 86    -0.154 -2.121 -1.670     S132    -3.612  0.539  0.647
S  41    -0.294  0.889 -1.428     S 87    -3.802 -0.902  0.641     S133    -5.940  0.638  0.639
S  42     0.134  2.622  1.480     S 88    -4.980 -0.866 -0.480     S134    -1.970 -0.233 -0.994
S  43    -2.367  2.810  0.289     S 89     5.157 -3.779 -0.637     S135    -2.056  0.601 -0.310
S  44    -3.170  2.093 -1.339     S 90     3.707 -2.977 -0.169     S136     4.688  0.606  1.421
S  45    -1.955  1.685 -1.383     S 91    -4.501 -1.430 -0.579     S137    -0.744  0.416  0.270
S  46    -0.043  2.733  0.057     S 92    -3.488 -1.331 -1.937
```

APPENDIX TABLE 8.

```
ALBERTA ALL SPECIMENS (100)                      PRINCIPAL COMPONENTS ANALYSIS - CLUSTAN 1C

NUMBER OF CASES =   100
NUMBER OF BINARY VARIABLES =     0
NUMBER OF NUMERIC VARIABLES =   21               (SQUARE-ROOT TRANSFORMED DATA)

NUMERIC MEANS AND STANDARD DEVIATIONS          VARIABLE MINIMUM VALUE      MAXIMUM VALUE

   1         2.6773         0.2713                 1             2.0736           3.3166
   2         1.3192         0.1277                 2             1.0149           1.6462
   3         0.5696         0.0745                 3             0.4243           0.7550
   4         0.7610         0.1168                 4             0.5196           1.0000
   5         0.7645         0.0789                 5             0.5831           0.9798
   6         0.7439         0.0845                 6             0.5385           0.9327
   7         0.8994         0.0998                 7             0.6708           1.1489
   8         0.6534         0.0724                 8             0.5000           0.8485
   9         0.7632         0.0908                 9             0.5477           0.9539
  10         0.3054         0.1593                10             0.0000           0.5477
  11         0.3055         0.3103                11             0.0000           0.7550
  12         0.6117         0.2299                12             0.2646           0.9899
  13         1.0007         0.1169                13             0.7071           1.4107
  14         1.9280         0.1936                14             1.4900           2.4166
  15         1.3227         0.1445                15             0.9695           1.5969
  16         2.1256         0.2247                16             1.6125           2.7258
  17         1.7081         0.1991                17             1.2570           2.2782
  18         0.7439         0.0976                18             0.4899           0.9434
  19        65.0900         4.1734                19            58.0000          74.0000
  20        12.3700         1.3078                20             9.0000          15.0000
  21        25.9200         3.0309                21            21.0000          33.0000
EIGENVALUES

 12.62   5.87   0.73   0.52   0.32   0.23   0.19   0.09   0.08   0.06   0.05   0.05   0.04   0.04   0.03   0.02
  0.02   0.01   0.01   0.01   0.00


PERCENTAGE VARIANCE

 60.11  27.97   3.48   2.49   1.51   1.10   0.89   0.43   0.39   0.31   0.26   0.22   0.20   0.20   0.12   0.10
  0.09   0.05   0.04   0.03   0.02


CUMULATIVE VARIANCE

 60.11  88.08  91.57  94.06  95.57  96.67  97.55  97.98  98.37  98.68  98.94  99.16  99.36  99.56  99.68  99.78
 99.87  99.92  99.96  99.98 100.00

 EIGENVECTORS - BY ROWS

 VECTOR  1

 0.278 0.276 0.144 0.210 0.246 0.273 0.271 0.249 0.259 0.119 0.033 0.087 0.248 0.279 0.271 0.276 0.269 0.240
 0.039 0.009 0.030

 VECTOR  2

 -0.035 0.024-0.343 0.261-0.184 0.020-0.036-0.164 0.141 0.353 0.404 0.382-0.015-0.015 0.023-0.060-0.078-0.068
  0.276-0.282 0.355

 VECTOR  3

 -0.005-0.045 0.011-0.101 0.004 0.074-0.048 0.005-0.044-0.125 0.005-0.031 0.196 0.006-0.020-0.009 0.067-0.189
  0.710 0.594 0.159

 FIRST   3 FACTOR SCORES

 S   1      0.148  2.197  0.574     S 35      4.225  1.996  1.071     S 68      1.929 -2.063 -0.303
 S   2     -0.632  2.421 -0.305     S 36      4.313  2.681  0.140     S 69      3.111 -3.021  0.995
 S   3     -1.070  2.102  0.462     S 37      2.854  2.264  0.262     S 70      3.194 -2.633 -0.486
 S   4     -3.416  2.662  0.566     S 38      1.863  2.435  0.571     S 71     -4.236 -2.124  0.504
 S   5     -4.348  2.641 -0.959     S 39      2.539  2.361  1.596     S 72     -5.372 -1.874 -0.799
 S   6      4.353  2.990 -0.585     S 40      0.910  2.547  0.025     S 73     -5.827 -2.322  1.076
 S   7      1.577  2.647  0.530     S 41      0.745  2.466  1.380     S 74     -8.293 -1.804 -0.179
 S   8      2.925  2.622  0.413     S 42      3.369  2.360 -0.203     S 75      1.856 -2.944  0.211
 S   9      0.747  3.502  0.619     S 43      2.543  1.767 -0.213     S 76     -0.190 -2.090  0.161
 S  10      3.926  3.709 -0.295     S 44      0.615  2.081 -0.424     S 77     -0.900 -2.137 -0.389
 S  11      1.398  3.560  0.428     S 45      0.972  2.542 -1.714     S 78     -1.763 -1.960 -0.936
 S  12     -2.313  2.218 -0.266     S 46      0.005  1.949 -2.543     S 79     -1.595 -1.999 -1.143
 S  13     -1.733  2.679  1.511     S 47     -0.253  1.886 -1.676     S 80     -3.924 -1.554  1.561
 S  14     -2.902  2.656  1.782     S 48      0.484  1.815 -1.474     S 81     -5.659 -1.479 -0.479
 S  15     -3.576  2.273  1.241     S 49      1.981  2.733 -1.226     S 82     -3.350 -1.765  0.606
 S  16     -6.105  2.586 -0.350     S 50      5.371  2.477  0.178     S 83      8.831 -3.336 -0.175
 S  17     -6.484  2.116  0.259     S 51      4.045 -2.685 -0.555     S 84      5.743 -2.669 -1.005
 S  18     -7.614  1.835 -1.118     S 52      0.034 -2.042  0.606     S 85      5.084 -2.503 -0.303
 S  19     -2.356  2.253  0.259     S 53     -4.996 -2.274 -0.250     S 86      4.389 -3.153 -0.185
 S  20     -4.237  2.233  0.270     S 54     -1.431 -1.689  0.116     S 87      1.573 -1.990 -0.292
 S  21     -4.239  1.759 -0.111     S 55      1.179 -3.013  0.304     S 88     -0.483 -2.760 -0.324
 S  22     -5.197  1.736  1.542     S 56      2.483 -2.953 -0.176     S 89     -3.030 -2.211 -0.740
 S  23      0.960  1.709 -0.043     S 57     -2.951 -1.961 -0.301     S 90     -4.839 -2.261 -0.487
 S  24     -2.426  2.272  0.271     S 58     -0.951 -2.090  1.153     S 91      3.730 -2.650  0.168
 S  25     -0.648  1.226  0.336     S 59     -0.147 -2.932 -0.298     S 92      1.122 -2.636  2.128
 S  26     -1.744  2.064  0.371     S 60     -0.882 -2.352  0.826     S 93      3.963 -2.157  0.610
 S  27     -2.577  2.066 -1.377     S 61     -4.800 -2.379 -0.020     S 94      3.654 -3.009 -0.416
 S  28      4.565  2.710 -0.301     S 62     -0.787 -2.645  0.617     S 95      3.345 -1.990  0.406
 S  29      3.060  2.502  0.958     S 63     -8.015 -1.936 -0.722     S 96      4.350 -2.600 -0.511
 S  30      3.193  2.319 -0.629     S 64      0.053 -2.332  0.395     S 97      2.912 -2.340  0.045
 S  31      2.879  2.527 -1.461     S 65     -6.802 -2.301 -1.128     S 98      2.478 -2.474 -0.715
 S  32      2.387  1.941 -0.761     S 66     -0.503 -2.600  0.944     S 99      0.183 -2.516  0.400
 S  33      2.529  2.294 -0.060     S 67      3.965 -2.553  1.763     S100      2.418 -1.964 -1.134
 S  34      2.663  2.422  0.312
```

APPENDIX TABLE 9.

```
KANANASKIS  ALL SPECIMENS (137)              PRINCIPAL COMPONENTS ANALYSIS - CLUSTAN 1C

NUMBER OF CASES =   137
NUMBER OF BINARY VARIABLES =    0            (SQUARE-ROOT TRANSFORMED DATA)
NUMBER OF NUMERIC VARIABLES =   21

NUMERIC MEANS AND STANDARD DEVIATIONS      VARIABLE MINIMUM VALUE     MAXIMUM VALUE

  1         2.6979        0.3595              1          1.8439          3.5071
  2         1.3190        0.1535              2          0.9487          1.6401
  3         0.5792        0.0804              3          0.4243          0.7746
  4         0.7611        0.1296              4          0.4690          1.0536
  5         0.7664        0.1011              5          0.5568          1.0247
  6         0.7760        0.1222              6          0.5292          1.0438
  7         0.9358        0.1391              7          0.6325          1.2570
  8         0.6815        0.1137              8          0.4796          0.9798
  9         0.7855        0.1241              9          0.5099          1.0247
 10         0.2932        0.1567             10          0.0000          0.6083
 11         0.3134        0.2774             11          0.0000          0.7874
 12         0.5988        0.1841             12          0.2828          0.9592
 13         1.0066        0.1623             13          0.6633          1.3342
 14         1.9339        0.2569             14          1.3416          2.5020
 15         1.3275        0.1773             15          0.6660          1.6971
 16         2.1575        0.3027             16          1.4799          2.8548
 17         1.7369        0.2654             17          1.1619          2.3917
 18         0.7229        0.1000             18          0.4583          1.0000
 19        65.4234        3.5143             19         59.0000         73.0000
 20        12.9927        1.2217             20         10.0000         16.0000
 21        25.9654        2.7813             21         21.0000         32.0000
EIGENVALUES

 13.83   4.24   1.01   0.57   0.30   0.24   0.20   0.13   0.10   0.07   0.06   0.06   0.05   0.04   0.03   0.02
  0.02   0.01   0.01   0.00   0.00


PERCENTAGE VARIANCE

 65.87  20.19   4.79   2.69   1.44   1.16   0.94   0.62   0.46   0.33   0.30   0.27   0.24   0.18   0.14   0.11
  0.10   0.06   0.04   0.02   0.02


CUMULATIVE VARIANCE

 65.87  86.06  90.85  93.55  94.99  96.15  97.08  97.71  98.18  98.52  98.81  99.09  99.33  99.50  99.65  99.76
 99.86  99.92  99.96  99.98 100.00
EIGENVECTORS - BY ROWS

VECTOR  1

 0.263 0.265 0.152 0.244 0.250 0.259 0.264 0.252 0.262 0.166 0.058 0.133 0.261 0.265 0.258 0.265 0.258 0.221
 0.005-0.064 0.059

VECTOR  2

-0.087-0.020-0.379 0.183-0.150 0.063-0.010-0.010 0.072 0.321 0.446 0.389-0.027-0.059-0.072-0.069-0.103-0.175
 0.203-0.272 0.397

VECTOR  3

 0.052 0.010 0.031-0.023 0.058-0.025-0.014 0.007-0.010-0.045-0.011-0.073-0.014 0.034 0.023 0.025 0.031-0.027
 0.812 0.542 0.166

FIRST   3 FACTOR SCORES

S  1     6.033  2.286 -0.518     S 47    -2.886  2.657 -1.309     S 93    -2.783 -1.071  0.187
S  2     5.788  1.257 -1.878     S 48    -2.951  2.784 -0.030     S 94    -1.920 -2.269  0.306
S  3     4.453  2.442 -0.763     S 49    -2.669  2.390 -0.154     S 95    -2.473 -2.387  0.025
S  4     7.271  2.607  0.151     S 50    -4.006  2.292 -0.549     S 96    -1.502 -1.744 -1.637
S  5     5.368  1.980  0.806     S 51     4.257 -2.787  0.554     S 97    -0.751 -2.130 -0.100
S  6     4.849  2.372 -0.284     S 52     6.450 -3.010  1.418     S 98    -4.561 -1.510  0.680
S  7     5.522  2.938  0.535     S 53     7.295 -3.797 -0.779     S 99    -6.292 -1.320 -0.539
S  8     5.669  2.655  0.172     S 54     5.826 -3.408  0.106     S100    -0.806 -1.480 -0.052
S  9     7.286  1.881  1.125     S 55     3.709 -2.642  1.103     S101     0.458 -1.785 -1.394
S 10     4.019  2.374 -0.173     S 56     4.508 -2.950 -0.784     S102    -0.759 -1.094  1.314
S 11     5.200  2.351 -1.018     S 57     2.775 -2.171  1.468     S103    -1.836  0.803  0.429
S 12     6.384  1.585  0.234     S 58     2.945 -2.927  0.061     S104    -2.141 -0.189  0.199
S 13     5.842  3.034  0.894     S 59     1.691 -2.582  0.255     S105     0.338 -1.501  0.548
S 14     5.686  2.257 -1.114     S 60     0.964 -2.134  1.673     S106    -0.722 -0.431  1.508
S 15     4.803  2.016  1.120     S 61     2.809 -3.583 -0.302     S107     0.604  0.215  1.304
S 16     0.990  1.623 -0.346     S 62    -0.407 -2.329 -1.262     S108    -1.528 -0.491  1.277
S 17    -2.140  1.972 -0.283     S 63    -0.760 -1.992 -1.144     S109    -2.410  0.146  1.100
S 18    -0.798  1.733 -1.647     S 64    -1.760 -2.248 -0.819     S110    -2.739  0.566  1.223
S 19    -3.033  1.645 -1.532     S 65    -0.639 -1.929 -2.031     S111    -3.389  1.240  0.418
S 20     1.413  1.643  0.101     S 66    -0.827 -1.851  0.356     S112    -3.996  0.734  3.097
S 21     3.407  2.929 -1.581     S 67    -1.283 -1.917 -0.997     S113    -2.973  0.549  1.590
S 22     4.272  3.026 -1.796     S 68    -4.827 -1.706  0.493     S114    -5.481  0.222  0.963
S 23     2.094  2.678  0.209     S 69    -2.773 -2.044 -1.374     S115    -3.292  1.103  1.475
S 24     5.656  2.202 -0.092     S 70     3.557 -2.811 -0.494     S116    -4.849 -1.107  1.275
S 25     5.371  1.453 -1.492     S 71     3.563 -2.308  2.078     S117    -4.337 -0.558 -0.731
S 26     2.124  2.505 -0.505     S 72     5.744 -3.161 -0.540     S118    -3.228  1.412  0.919
S 27     0.205  2.333 -1.361     S 73     5.804 -2.607  1.403     S119    -4.941 -0.728 -1.337
S 28     4.434  1.716  0.780     S 74     1.674 -2.039  0.355     S120    -1.751 -1.117 -0.180
S 29    -2.971  2.654 -0.512     S 75     1.410 -2.069 -0.156     S121    -0.881  0.197  0.268
S 30    -2.915  2.800  0.967     S 76    -2.217 -1.416 -0.373     S122    -3.322  0.257 -0.114
S 31    -3.028  3.191  0.859     S 77     2.559 -2.716  0.228     S123    -2.531  0.108 -0.337
S 32    -3.014  2.192 -0.560     S 78     0.962 -1.997 -0.572     S124    -4.099 -1.670 -1.342
S 33    -3.210  2.025  0.413     S 79     0.666 -2.146 -0.162     S125    -3.139 -0.674  2.328
S 34    -3.283  2.339  1.431     S 80     0.049 -1.973  0.217     S126    -6.298 -0.436 -0.987
S 35    -2.870  1.096 -0.420     S 81    -1.481 -2.287 -0.041     S127    -6.766 -0.516 -0.434
S 36    -4.748  2.035  0.176     S 82     1.593 -2.319  0.853     S128    -1.108  0.980  1.758
S 37    -3.880  3.218  0.463     S 83     4.940 -2.234  0.509     S129    -1.971  0.402  1.367
S 38     3.259  2.287 -1.281     S 84     1.099 -2.307 -0.075     S130    -2.955 -0.130  0.315
S 39     5.653  2.799 -0.063     S 85     0.051 -2.535 -0.060     S131    -4.266 -0.475 -1.374
S 40    -0.206  2.493  0.402     S 86     0.201 -2.250 -1.613     S132    -3.652  0.615  0.591
S 41    -0.128  0.733 -1.415     S 87    -3.887 -1.329  0.661     S133    -6.530  0.755  0.634
S 42     0.263  2.620  1.468     S 88    -5.401 -1.488 -0.404     S134    -1.735 -0.052 -0.944
S 43    -2.373  2.966  0.161     S 89     5.301 -3.365 -0.628     S135    -1.868  0.803 -0.349
S 44    -3.274  2.256 -1.412     S 90     3.904 -2.733 -0.082     S136     4.644  0.967  1.344
S 45    -1.874  1.777 -1.416     S 91    -4.607 -2.052 -0.464     S137    -0.432  0.651  0.219
S 46     0.064  2.716  0.014     S 92    -3.497 -1.730 -1.900
```

APPENDIX TABLE 10.

(UNTRANSFORMED DATA)

ALBERTA GROUPS B,C   A PRIORI KNOWN GROUPS
KANANASKIS GROUP K   A PRIORI UNKNOWN GROUP

```
BMD07M - STEPWISE DISCRIMINANT ANALYSIS
HEALTH SCIENCES COMPUTING FACILITY. UCLA

NUMBER OF VARIABLES     21

NUMBER OF GROUPS         3

NUMBER OF CASES IN EACH GROUP     50     50   -137

PRIOR PROBABILITIES          0.3333    0.3333    0.0

MEANS

            GROUP
                B             C             K
VARIABLE
   1        7.15397       7.32797       7.40723
   2        1.78279       1.73019       1.76320
   3        0.26040       0.39940       0.34189
   4        0.70420       0.47600       0.59591
   5        0.53920       0.64220       0.59759
   6        0.56920       0.55160       0.61707
   7        0.80920       0.82819       0.89496
   8        0.39660       0.46760       0.47722
   9        0.64080       0.54040       0.63226
  10        0.20020       0.03660       0.11036
  11        0.37800       0.0           0.17460
  12        0.68940       0.16360       0.39226
  13        1.01180       1.01820       1.03934
  14        3.74819       3.76039       3.80563
  15        1.80159       1.73879       1.79357
  16        4.45959       4.67719       4.74598
  17        2.84779       3.06599       3.08666
  18        0.54220       0.58340       0.53255
  19       67.70000      62.48000      65.42336
  20       11.54000      13.20000      12.99270
  21       28.39999      23.43995      25.98540

STANDARD DEVIATIONS

            GROUP
                B             C             K
VARIABLE
   1        1.20343       1.64019       1.98241
   2        0.27055       0.37300       0.41177
   3        0.03511       0.06306       0.09507
   4        0.15776       0.11019       0.20576
   5        0.08439       0.13140       0.15843
   6        0.11082       0.13673       0.19742
   7        0.18149       0.17590       0.26548
   8        0.07361       0.10177       0.16181
   9        0.12911       0.12704       0.20003
  10        0.05957       0.03140       0.09581
  11        0.08256       0.0           0.18330
  12        0.12494       0.06818       0.24006
  13        0.19179       0.27532       0.33377
  14        0.63780       0.83550       1.01490
  15        0.33823       0.40690       0.47599
  16        0.78056       1.08340       1.33665
  17        0.54326       0.77528       0.94653
  18        0.15064       0.13442       0.14819
  19        3.60978       2.87309       3.51408
  20        1.14666       0.85714       1.22171
  21        2.00000       1.41652       2.78118

SUMMARY TABLE

 STEP        VARIABLE         F VALUE TO          NUMBER OF        U-STATISTIC
NUMBER   ENTERED  REMOVED   ENTER OR REMOVE   VARIABLES INCLUDED

   1        11                1048.0564              1              0.0855
   2         3                  60.6921              2              0.0526
   3        12                  41.8057              3              0.0366
   4        18                  13.2400              4              0.0322
   5        16                  12.0925              5              0.0283
   6         7                  14.2701              6              0.0247
   7        15                   2.0021              7              0.0242
   8        21                   1.5313              8              0.0238
   9         8                   1.4173              9              0.0234
  10         2                   3.1769             10              0.0226
  11         4                   1.0547             11              0.0223
  12        20                   1.0476             12              0.0221
  13         5                   0.4029             13              0.0220
  14         6                   0.2517             14              0.0219
  15        19                   0.3814             15              0.0218
  16        14                   0.1477             16              0.0218
  17         1                   0.3141             17              0.0217
  18        17                   0.2501             18              0.0216
  19         9                   0.1970             19              0.0216
  20        13                   0.0726             20              0.0215
  21        10                   0.0078             21              0.0215

EIGENVALUES

   45.42906    0.00021    0.00010    0.00006    0.00004    0.00003    0.00003    0.00001    0.00001
    0.00001    0.00000   -0.00000   -0.00000   -0.00000   -0.00000   -0.00001   -0.00001   -0.00004
   -0.00006   -0.00008   -0.00014

CANONICAL CORRELATIONS

    0.98917    0.01436    0.01001    0.00769    0.00640    0.00582    0.00532    0.00371    0.00233
    0.00230    0.00140    0.00062    0.00073    0.00145    0.00194    0.00236    0.00184    0.00593
    0.00795    0.00899    0.01178

COEFFICIENTS FOR CANONICAL VARIABLE

ORIGINAL       1
VARIABLE
   1        0.73743      10       0.54233      19       0.02392
   2       -3.10259      11      -6.65249      20       0.09340
   3       30.74434      12     -12.40804      21      -0.06532
   4        5.87615      13       0.28944      CONSTANT
   5       -2.18694      14      -1.26575               -1.36546
   6       -2.27820      15      -1.75560
   7        7.87478      16      -2.28810
   8        9.13718      17       0.69463
   9       -2.31158      18       6.07684
```

```
X = FIRST CANONICAL VARIABLE
Y = SECOND CANONICAL VARIABLE

GROUP      B  MEAN COORDINATES  -6.672  -0.000

CASE     X       Y     CASE     X       Y     CASE     X       Y     CASE     X       Y     CASE     X       Y

  1   -7.426   1.295    11   -8.343   0.011    21   -5.135   2.219    31   -6.984   1.549    41   -6.406  -1.583
  2   -6.656   0.285    12   -5.900   0.450    22   -5.012  -1.373    32   -6.936   0.022    42   -5.003  -0.057
  3   -6.997  -0.670    13   -6.718  -0.079    23   -7.305  -2.108    33   -7.160   0.503    43   -5.561  -0.043
  4   -6.181   0.443    14   -6.318   1.346    24   -5.536   0.292    34   -6.571   0.607    44   -6.642  -0.281
  5   -6.171  -0.372    15   -6.884   0.838    25   -6.678   0.397    35   -6.076   1.475    45   -6.817   0.357
  6   -7.548   0.406    16   -5.305   0.616    26   -7.558  -0.917    36   -8.939   0.101    46   -7.347  -1.241
  7   -7.714   0.708    17   -5.216   0.941    27   -4.743   0.126    37   -6.748   0.162    47   -5.643  -1.278
  8   -7.222   0.938    18   -5.010   0.281    28   -7.449  -0.424    38   -7.234  -1.538    48   -6.448  -0.888
  9   -6.908  -1.008    19   -6.463   1.785    29   -7.386  -0.120    39   -7.543  -0.346    49   -5.855  -2.812
 10   -9.817  -0.348    20   -5.684  -0.033    30   -7.028   1.469    40   -7.022   0.048    50   -8.318  -0.032


X = FIRST CANONICAL VARIABLE
Y = SECOND CANONICAL VARIABLE

GROUP      C  MEAN COORDINATES   6.672  -0.000

CASE     X       Y     CASE     X       Y     CASE     X       Y     CASE     X       Y     CASE     X       Y

  1    5.974   0.655    11    7.467  -0.144    21    5.316  -0.714    31    5.718   0.886    41    6.123   2.021
  2    5.855  -0.553    12    8.773  -0.209    22    5.473  -1.131    32    5.954   1.068    42    6.173  -0.594
  3    6.543   0.723    13    7.601   0.762    23    6.924  -0.576    33    9.316  -0.320    43    7.938   0.557
  4    6.278  -0.476    14    6.767  -0.837    24    5.424   0.597    34    6.378  -0.362    44    7.210   0.212
  5    6.788  -0.098    15    5.840   0.003    25    6.171   1.239    35    7.760   0.124    45    7.330  -0.004
  6    7.062  -0.735    16    7.675  -1.122    26    5.473   0.374    36    8.071  -1.654    46    7.613   0.435
  7    6.224  -0.395    17    6.802   0.115    27    7.167   1.034    37    6.419   0.665    47    7.131   0.219
  8    6.203  -0.599    18    6.773   0.279    28    5.991  -0.613    38    6.056  -1.703    48    6.624   2.179
  9    7.514  -0.648    19    8.036   0.104    29    7.209   0.226    39    5.803   0.622    49    5.831  -0.597
 10    7.148  -1.171    20    7.338   0.662    30    5.450  -1.400    40    5.617   0.650    50    5.303   0.659


X = FIRST CANONICAL VARIABLE
Y = SECOND CANONICAL VARIABLE

GROUP      K  MEAN COORDINATES   1.242  -0.020

CASE     X       Y     CASE     X       Y     CASE     X       Y     CASE     X       Y     CASE     X       Y

  1   -7.162   1.898    11   -4.718   3.172    21   -8.053  -0.773    31   -5.905  -2.755    41    1.986   0.403
  2   -2.992   0.007    12   -5.740   2.086    22   -9.183  -0.914    32   -4.489  -0.591    42   -4.526  -0.311
  3   -5.739   1.023    13   -5.932   1.165    23   -6.554  -1.441    33   -3.706  -0.380    43   -4.912   0.747
  4   -5.295   3.130    14   -7.537   1.067    24   -7.257  -2.000    34   -4.035   0.001    44   -5.240   0.424
  5   -5.259   3.124    15   -5.254   1.046    25   -6.170  -2.621    35   -1.509  -2.383    45   -3.656  -0.338
  6   -5.774   2.075    16   -3.689  -2.030    26   -5.433  -0.987    36   -2.975  -0.441    46   -6.234  -0.801
  7   -4.741   2.779    17   -3.482   0.001    27   -5.777   0.080    37   -4.307   0.007    47   -4.566   2.626
  8   -6.172   4.622    18   -3.771  -1.221    28   -5.340  -0.524    38   -5.163  -0.177    48   -4.456   3.246
  9   -4.399   1.481    19   -3.505  -0.183    29   -3.687  -0.866    39   -7.183   0.781    49   -3.489   0.612
 10   -7.115  -0.569    20   -4.377  -2.526    30   -3.731  -1.214    40   -6.559   0.098    50   -4.705  -1.180

 51    7.524   0.180    61    9.339   1.037    71    7.361  -2.441    81    7.381   0.865    91    6.216   0.557
 52   10.442   4.510    62    8.939   1.232    72   11.242   2.535    82    6.931  -0.931    92    5.087   0.302
 53    9.947   0.150    63    7.464  -1.914    73    7.337  -5.740    83    6.406   2.488    93    4.377  -1.100
 54    9.705   1.136    64    7.649  -0.038    74    7.192  -2.400    84    8.237  -2.470    94    6.834  -1.112
 55    5.986   0.718    65    7.140  -0.724    75    8.671  -1.055    85    7.997   0.113    95    6.376  -0.240
 56    8.513   1.997    66    5.878  -1.780    76    5.249  -1.089    86    7.345   0.012    96    6.848  -4.115
 57   10.519   3.328    67    5.516  -0.057    77    7.060   0.544    87    7.178   3.851    97    7.367  -0.428
 58    8.457   1.665    68    5.704  -0.408    78    7.014  -2.508    88    4.616  -0.376    98    5.391   0.866
 59    9.162   1.200    69    5.466  -0.558    79    5.948  -1.468    89    6.157   5.341    99    5.171  -0.458
 60    9.018   0.624    70    8.112   1.306    80    7.017  -1.684    90    4.671  -0.311   100    7.434  -0.038

101    4.166   2.352   111    0.597   2.722   121    1.142  -1.577   131    1.624   3.655
102    1.966  -3.466   112    0.824   2.908   122   -0.484   0.976   132    0.778   0.724
103   -1.254  -1.511   113   -0.138  -0.125   123   -0.470   0.173   133    0.386  -1.872
104    2.159  -0.849   114    1.470  -1.427   124    4.121  -1.563   134   -0.550  -0.162
105    4.750   0.078   115   -0.442  -0.130   125    3.516  -2.910   135   -0.477   0.762
106    1.953  -0.148   116    6.141  -0.346   126    1.120  -0.109   136   -0.864   0.106
107    0.732  -1.794   117    2.828   1.633   127    3.415  -0.364   137    1.449  -0.568
108    2.373   0.648   118    0.511  -1.131   128    0.772  -0.757
109    2.156  -0.575   119    1.744   0.727   129    0.017  -0.789
110    0.671  -0.215   120    4.625   1.901   130    1.421  -0.088
```

APPENDIX TABLE 11.

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BMD07M - STEPWISE DISCRIMINANT ANALYSIS
HEALTH SCIENCES COMPUTING FACILITY, UCLA

NUMBER OF VARIABLES     20                      (UNTRANSFORMED DATA: WITHOUT FRENUM CHARACTER)

NUMBER OF GROUPS         3                       ALBERTA GROUPS R,C = A PRIORI   KNOWN GROUPS
                                                 KANANASKIS GROUP K = A PRIORI UNKNOWN GROUP
NUMBER OF CASES IN EACH GROUP     50     50   -137

PRIOR PROBABILITIES          0.3333     0.3333     0.0

MEANS                                                     STANDARD DEVIATIONS

          GROUP                                                     GROUP
             R             C             K                             R             C             K
VARIABLE                                                  VARIABLE
   1      7.15397       7.32797       7.40723                1      1.20343       1.64019       1.98241
   2      1.78279       1.73019       1.76320                2      0.29055       0.37300       0.41177
   3      0.26040       0.39940       0.34189                3      0.03511       0.06306       0.09507
   4      0.70920       0.47600       0.59591                4      0.15776       0.11019       0.20576
   5      0.53920       0.64220       0.59759                5      0.08439       0.13140       0.15843
   6      0.56920       0.55160       0.61707                6      0.11062       0.13673       0.19742
   7      0.80920       0.82819       0.89496                7      0.18149       0.17590       0.26648
   8      0.39660       0.46760       0.47722                8      0.07361       0.10177       0.16381
   9      0.64080       0.54040       0.63226                9      0.12911       0.12704       0.20003
  10      0.20020       0.03660       0.11036               10      0.05957       0.03140       0.09581
  11      0.68340       0.16360       0.39226               11      0.12494       0.06818       0.24006
  12      1.01180       1.01820       1.03334               12      0.19179       0.27532       0.33377
  13      3.74815       3.76039       3.80563               13      0.63780       0.83550       1.01490
  14      1.80155       1.73879       1.79357               14      0.33825       0.40690       0.47599
  15      4.45955       4.67719       4.74598               15      0.78056       1.08340       1.33665
  16      2.84775       3.06599       3.08066               16      0.54326       0.77528       0.94653
  17      0.54220       0.58340       0.53255               17      0.15064       0.13442       0.14819
  18     67.70000      62.48000      65.42336               18      3.60978       2.87309       3.51408
  19     11.54000      13.20000      12.99270               19      1.14666       0.95714       1.22171
  20     28.39995      23.43995      25.98540               20      2.00000       1.41652       2.78118


SUMMARY TABLE

 STEP       VARIABLE          F VALUE TO        NUMBER OF        U-STATISTIC
NUMBER   ENTERED  REMOVED   ENTER OR REMOVE  VARIABLES INCLUDED

   1       11                 682.3484            1               0.1256
   2        3                 207.6850            2               0.0400
   3       16                  12.9175            3               0.0352
   4       17                  13.6468            4               0.0308
   5        7                   7.9979            5               0.0284
   6        2                   8.4068            6               0.0260
   7        8                   4.9519            7               0.0247
   8       14                   3.3039            8               0.0238
   9       15                   1.5234            9               0.0234
  10       20                   1.5802           10               0.0230
  11        9                   0.8384           11               0.0228
  12        6                   0.5101           12               0.0227
  13        1                   0.3401           13               0.0226
  14       13                   0.4472           14               0.0225
  15        4                   0.3802           15               0.0224
  16       12                   0.3908           16               0.0223
  17       18                   0.2473           17               0.0222
  18        5                   0.1301           18               0.0222
  19       19                   0.0769           19               0.0222
  20       10                   0.0051           20               0.0222

EIGENVALUES

   44.14084    0.00020    0.00006    0.00006    0.00004    0.00002    0.00001    0.00001    0.00000
    0.00000    0.00000    0.00000   -0.00000   -0.00000   -0.00001   -0.00001   -0.00003   -0.00006
   -0.00007   -0.00014

CANONICAL CORRELATIONS

    0.98886    0.01399    0.00791    0.00751    0.00624    0.00495    0.00385    0.00292    0.00181
    0.00156    0.00120    0.00116    0.00054    0.00166    0.00326    0.00367    0.00531    0.00710
    0.00843    0.01164

COEFFICIENTS FOR CANONICAL VARIABLE

ORIGINAL      1
VARIABLE
   1       1.02256      11     -13.52920
   2      -3.65928      12       0.52514
   3      32.67485      13      -1.14467
   4       2.57182      14      -2.07262      CONSTANT
   5      -2.05047      15      -2.04261                  -1.05693
   6      -2.57757      16       3.04182
   7       8.88427      17       6.92533
   8      11.59242      18       0.01675
   9      -4.48015      19       0.03252
  10      -0.41036      20      -0.08498
```

```
   X = FIRST CANONICAL VARIABLE
   Y = SECOND CANONICAL VARIABLE

GROUP       R  MEAN COORDINATES  -6.577   0.000

 CASE     X       Y     CASE     X       Y     CASE     X       Y     CASE     X       Y     CASE     X       Y

   1   -7.273  -1.271    11   -8.156   0.045    21   -5.003  -2.277    31   -6.843  -1.361    41   -6.220   1.735
   2   -6.176   0.039    12   -5.486   0.016    22   -5.231   1.594    32   -6.831  -0.063    42   -4.971   0.027
   3   -6.873   0.674    13   -6.302   0.401    23   -7.399   2.372    33   -7.108  -0.556    43   -5.278   0.282
   4   -5.925  -0.219    14   -6.491  -1.592    24   -5.697  -0.562    34   -6.567  -0.613    44   -6.591   0.123
   5   -6.043   0.526    15   -6.895  -1.043    25   -6.347  -0.234    35   -5.834  -1.369    45   -6.760  -1.122
   6   -7.287  -0.430    16   -5.316  -0.756    26   -7.049   1.489    36   -8.921  -0.220    46   -7.301   3.213
   7   -7.488  -0.718    17   -5.550  -1.427    27   -4.529   3.108    37   -6.553   0.088    47   -5.600   1.272
   8   -6.874  -0.790    18   -5.006  -0.486    28   -7.733  -0.187    38   -7.084   1.490    48   -6.873   0.498
   9   -6.777   0.558    19   -6.214  -1.798    29   -7.463  -0.003    39   -7.628   0.329    49   -5.346   2.843
  10   -9.854   0.116    20   -5.859  -0.187    30   -6.516  -0.375    40   -6.372  -0.067    50   -8.342  -0.032


   X = FIRST CANONICAL VARIABLE
   Y = SECOND CANONICAL VARIABLE

GROUP       C  MEAN COORDINATES   6.577  -0.000

 CASE     X       Y     CASE     X       Y     CASE     X       Y     CASE     X       Y     CASE     X       Y

   1    6.193  -0.164    11    7.353   0.076    21    5.137   0.516    31    5.563  -0.837    41    5.963  -2.066
   2    5.826   0.597    12    8.921   0.553    22    5.940   1.245    32    5.766  -1.226    42    6.225   0.602
   3    6.724  -0.289    13    5.552  -0.708    23    6.890   0.786    33    9.046   0.166    43    7.686  -0.711
   4    6.239   0.645    14    6.432   0.636    24    5.342  -0.720    34    6.143   0.154    44    7.113  -0.316
   5    6.747   0.056    15    5.591   0.248    25    6.193  -1.045    35    7.563  -0.125    45    7.823  -0.008
   6    6.371   0.623    16    7.543   1.181    26    5.288  -0.490    36    7.905   1.058    46    7.558  -0.543
   7    6.149   1.004    17    6.700  -0.244    27    7.086  -1.049    37    6.223  -0.766    47    7.372   0.074
   8    6.047   0.476    18    6.760  -0.340    28    5.436   0.555    38    5.766   1.363    48    6.541  -2.165
   9    7.639   0.784    19    8.153   0.082    29    7.019  -0.336    39    5.691  -0.307    49    5.767   0.657
  10    6.927   1.046    20    7.737  -0.460    30    5.145   1.117    40    5.458  -0.791    50    5.173  -0.338


   X = FIRST CANONICAL VARIABLE
   Y = SECOND CANONICAL VARIABLE

GROUP       K  MEAN COORDINATES   1.228  -0.026

 CASE     X       Y     CASE     X       Y     CASE     X       Y     CASE     X       Y     CASE     X       Y

   1   -6.179  -0.598    11   -3.400  -1.715    21   -3.197   0.430    31   -6.228   2.287    41   -2.766   0.036
   2   -1.947   1.173    12   -4.943  -1.178    22   -4.450   1.316    32   -4.636   0.296    42   -4.578   0.101
   3   -5.169  -0.135    13   -4.367   0.873    23   -6.147   3.077    33   -3.754   0.031    43   -4.877  -0.921
   4   -4.068  -1.683    14   -7.160  -0.572    24   -7.204   1.753    34   -4.171  -0.346    44   -5.352  -0.737
   5   -4.342  -1.935    15   -4.631  -0.654    25   -6.330   2.307    35   -1.737   1.306    45   -3.713   0.179
   6   -5.300  -1.493    16   -3.789   1.372    26   -5.334   1.389    36   -3.053   0.285    46   -5.703   1.235
   7   -3.338  -1.714    17   -3.663  -0.404    27   -5.415   0.268    37   -4.355  -0.061    47   -5.463  -3.042
   8   -4.898  -3.238    18   -3.923   0.376    28   -4.640   1.305    38   -4.595   1.568    48   -4.340  -3.114
   9   -4.190  -0.602    19   -3.766  -3.321    29   -3.581   0.847    39   -6.876  -0.746    49   -3.703  -1.018
  10   -6.017   1.064    20   -5.357   2.413    30   -3.742   1.374    40   -6.463  -0.354    50   -4.495   0.765

  51    7.013  -0.811    61    9.343  -1.062    71    6.530   1.619    81    7.316  -0.484    91    6.138  -0.425
  52   10.435  -4.492    62    9.051  -0.919    72   11.318  -2.484    82    6.592   0.718    92    5.866  -0.205
  53    9.817  -0.267    63    7.314   1.642    73    6.524   4.424    83    6.178  -2.644    93    3.920   0.706
  54    9.245  -1.737    64    7.624   0.258    74    6.355   2.071    84    7.610   1.375    94    6.446   0.339
  55    5.523  -1.308    65    7.282   1.298    75    8.499   0.453    85    7.735  -0.363    95    5.904  -0.354
  56    6.398  -2.218    66    5.445   1.442    76    4.885   0.743    86    6.696  -0.576    96    6.662   4.203
  57   10.712  -3.058    67    5.332   0.641    77    6.714  -0.946    87    7.183  -3.447    97    7.139   0.623
  58    8.207  -1.386    68    5.573   0.451    78    6.247   2.023    88    4.427   0.844    98    5.273  -1.204
  59    9.009  -1.407    69    5.130   0.066    79    5.264   0.761    89    7.966  -5.657    99    5.030   0.479
  60    8.630  -0.600    70    7.810  -1.607    80    6.682   1.416    90    3.625  -1.263   100    7.313   0.233

 101    5.602  -0.803   111    0.773  -2.730   121    1.032   1.426   131    1. 26  -0.926
 102    1.247   2.736   112    0.846  -2.937   122   -0.346  -0.831   132    1.050  -0.527
 103   -1.210   1.545   113   -0.485  -0.324   123   -0.667  -0.362   133   -0.032   1.195
 104    1.670   0.143   114    1.398   1.303   124    3.878   1.223   134   -3.964  -0.400
 105    4.613  -0.065   115   -0.550  -0.066   125    3.391   2.645   135   -1.312  -1.846
 106    2.610   1.026   116    5.612  -0.165   126    0.703  -0.254   136   -0.259   0.175
 107    0.310   1.203   117    4.024  -0.498   127    3.135   0.215   137    1.167   0.341
 108    1.103  -2.201   118   -0.080   0.383   128    0.473  -0.140
 109    2.327   1.174   119    1.444  -1.121   129    0.273   0.474
 110    0.600   0.384   120    5.556  -0.953   130    1.767   0.275
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APPENDIX TABLE 12.

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BMD07M - STEPWISE DISCRIMINANT ANALYSIS
HEALTH SCIENCES COMPUTING FACILITY, UCLA

NUMBER OF VARIABLES      21                          (SQUARE-ROOT TRANSFORMED DATA)
                                                     ALBERTA GROUP  R,  - A PRIORI  KNOWN GROUP
NUMBER OF GROUPS                                     KANANASKIS GROUP K - A PRIORI UNKNOWN GROUP

NUMBER OF CASES IN EACH GROUP      50     50  -137

PRIOR PROBABILITIES          0.3333    0.3333    0.0

MEANS                                                STANDARD DEVIATIONS

           GROUP                                              GROUP
             R             C             K                      R            C            K
VARIABLE                                             VARIABLE
   1        2.66435       2.68370       2.66794         1       0.21032      0.30886      0.15127
   2        1.31066       1.30778       1.31102         2       0.11130      0.14244      0.15346
   3        0.86612       0.83002       0.87029         3       0.03492      0.05023      0.08038
   4        0.84676       0.84548       0.81168         4       0.03656      0.08085      0.12351
   5        0.73133       0.74711       0.76644         5       0.03875      0.08334      0.10110
   6        0.75605       0.73687       0.77665         6       0.07431      0.09371      0.12218
   7        0.43673       0.50487       0.46941         7       0.10318      0.09696      0.13410
   8        0.62193       0.67942       0.64146         8       0.05595      0.07455      0.11166
   9        0.78616       0.74006       0.76548         9       0.03273      0.08603      0.12401
  10        0.44147       0.16883       0.55422        10       0.07057      0.05089      0.15672
  11        0.07098       0.0           0.11118        11       0.06424      0.0          0.27740
  12        0.42600       0.19657       0.59685        12       0.07688      0.08028      0.18407
  13        1.01116       1.00013       1.03057        13       0.07686      0.13467      0.16230
  14        1.32883       1.32734       1.43394        14       0.16705      0.21828      0.25694
  15        1.33882       1.30530       1.42755        15       0.12356      0.15414      0.17723
  16        2.11335       2.14733       2.15755        16       0.17026      0.25466      0.30266
  17        1.67554       1.73868       1.71608        17       0.16183      0.22569      0.26542
  18        0.72502       0.75876       0.72233        18       0.13462      0.06846      0.05993
  19       17.73000      16.44000      16.42336        19       3.00378      2.87309      1.51409
  20       11.74036      13.20000      12.16270        20       1.14660      0.85714      1.22173
  21       23.39997      21.43395      25.77640        21       2.00000      1.41652      2.78118


SUMMARY TABLE

STEP       VARIABLE          F VALUE TO        NUMBER OF          U-STATISTIC
NUMBER  ENTERED  REMOVED   ENTER OR REMOVE  VARIABLES INCLUDED

   1       11                 3473.5440            1                0.0246
   2        3                   46.0991            2                0.0163
   3       12                   20.4659            3                0.0134
   4       16                   17.3352            4                0.0111
   5       15                    7.3433            5                0.0105
   6        7                   13.1377            6                0.0092
   7       10                    4.7551            7                0.0088
   8       18                    4.1029            8                0.0085
   9        1                    2.4704            9                0.0083
  10       17                    1.1845           10                0.0081
  11        4                    2.7102           11                0.0079
  12       20                    1.0217           12                0.0078
  13       14                    1.1475           13                0.0077
  14       19                    0.6022           14                0.0076
  15       13                    0.6334           15                0.0075
  16        2                    0.5743           16                0.0075
  17        6                    0.3067           17                0.0075
  18        8                    0.2305           18                0.0074
  19        5                    0.0619           19                0.0074
  20       21                    0.3556           20                0.0074
  21        9                    0.0431           21                0.0074

EIGENVALUES

  113.52116    0.40010    0.00114    0.00017    0.00010    0.00007    0.00005    0.00003    0.00002
    0.00001    0.00001    0.00001    0.00000   -0.00000   -0.00000   -0.00000   -0.00002   -0.00003
   -0.00004   -0.00011   -0.00116

CANONICAL CORRELATIONS

    [illegible]    0.01744    0.01182    0.01116    0.00931    0.00838    0.00736    0.00576    0.00412
    0.00307    0.00242    0.00137    0.00121    0.00067    0.00126    0.00180    0.00391    0.00555
    1.00667    0.01016    0.01249

COEFFICIENTS FOR CANONICAL VARIABLE

ORIGINAL       1
VARIABLE
   1       -1.15737        10         5.82133        19       -0.04416
   2       -3.57468        11        24.85063        20       -0.11204
   3      -25.71770        12        10.31279        21        0.01309
   4      -12.52638        13         2.05011      CONSTANT
   5       -2.11184        14         7.66213                   6.3876
   6        3.10362        15         3.45773
   7      -11.42156        16        14.75759
   8       -1.11473        17        -9.24000
   9       -1.56777        18        -3.32716


      X = FIRST CANONICAL VARIABLE
      Y = SECOND CANONICAL VARIABLE

GROUP       R  MEAN COORDINATES  11.439  -0.000

 CASE     X        Y     CASE     X        Y     CASE     X        Y     CASE     X        Y

   1   12.178    0.009    11   12.504    0.544    21   10.240    1.825    31   11.279    1.356    41   11.606   -0.286
   2   12.492    1.142    12   11.679    1.249    22    9.515   -2.174    32   11.806   -0.702    42    9.582    0.503
   3   12.393    0.223    13   12.608   -0.544    23   11.642   -1.213    33   12.053    0.051    43   11.057    0.683
   4   11.187    0.344    14   10.036   -1.089    24   10.173   -1.603    34   10.899   -0.080    44   11.622    0.552
   5   11.108   -0.608    15   11.777   -0.908    25   12.099    0.869    35   11.257    0.964    45   11.311    0.232
   6   12.129    0.486    16    9.759    0.023    26   12.777    0.505    36   13.228    0.032    46   12.136   -0.671
   7   12.954    0.925    17    9.103   -1.004    27    9.776    0.824    37   11.572    0.132    47    9.977   -0.258
   8   12.338    0.498    18   10.158   -0.731    28   11.578   -1.005    38   12.432   -0.205    48   10.437   -2.049
   9   11.470    0.232    19   11.802    1.506    29   11.907    0.149    39   12.063   -1.067    49   10.295   -0.041
  10   13.950   -1.434    20   10.267   -0.594    30   12.293    2.669    40   11.643   -0.675    50   11.992    0.404


      X = FIRST CANONICAL VARIABLE
      Y = SECOND CANONICAL VARIABLE

GROUP       C  MEAN COORDINATES -11.439  -0.000

 CASE     X        Y     CASE     X        Y     CASE     X        Y     CASE     X        Y

   1  -10.572    1.462    11  -11.522    0.016    21  -10.277   -0.680    31  -10.598    0.198    41  -11.067   -1.758
   2  -11.447   -0.608    12  -13.291    1.630    22  -11.749   -0.697    32  -10.663    0.210    42  -10.812    0.458
   3  -10.286    1.587    13   -9.548   -0.456    23  -11.847    1.173    33  -13.736    0.192    43  -12.850   -0.111
   4  -11.392    0.408    14  -11.567   -1.965    24  -10.557    0.950    34  -11.249   -0.753    44  -12.478    0.559
   5  -12.594   -0.114    15  -10.620    0.457    25  -11.008   -0.129    35  -12.162   -0.295    45  -12.260    0.593
   6  -11.989    0.319    16  -12.459   -0.557    26  -10.497   -0.815    36  -13.275   -0.634    46  -11.788   -0.699
   7  -11.069    0.244    17  -11.830    0.552    27  -11.838    0.583    37  -10.689   -0.487    47  -11.503   -0.329
   8  -11.137    0.577    18  -11.315    1.984    28  -10.838   -0.633    38  -10.415   -1.807    48  -11.055   -0.320
   9  -12.202    1.388    19  -12.734    2.271    29  -11.681   -0.506    39  -10.622    1.145    49  -10.874   -0.838
  10  -12.062   -0.308    20  -12.585   -0.293    30  -10.446   -0.903    40  -11.039    1.266    50   -9.463   -2.735


      X = FIRST CANONICAL VARIABLE
      Y = SECOND CANONICAL VARIABLE

GROUP       K  MEAN COORDINATES  -0.460   0.236

 CASE     X        Y     CASE     X        Y     CASE     X        Y     CASE     X        Y     CASE     X        Y

   1   13.672    1.496    11   12.500    3.613    21   12.363   -0.822    31   10.336   -2.562    41    4.297   11.385
   2   10.292    2.817    12   12.006    1.800    22   14.428   -1.183    32    8.701   -1.219    42    9.523   -0.446
   3   11.940    0.037    13   13.419    2.172    23   11.239   -0.916    33    8.943    1.472    43    9.532    0.856
   4   13.149    2.602    14   14.049   -1.680    24   12.345   -0.825    34    8.686    1.500    44   10.354   -0.010
   5   12.172    0.913    15   12.004    1.083    25   10.751   -0.613    35    6.054   -0.498    45    8.270    0.381
   6   12.580    0.884    16    8.385   -1.521    26   11.013    1.247    36    7.339   -0.477    46   12.757    0.730
   7   11.734    0.642    17    8.905    0.233    27   11.188    0.383    37    8.822    0.848    47    6.803   -2.299
   8   13.376    3.005    18    8.049   -0.799    28   11.416    1.791    38   11.298    2.637    48    8.966    0.441
   9   11.120    1.937    19    7.986   -1.505    29    8.719    0.117    39   12.518    1.596    49    7.383    0.131
  10   13.140    1.491    20   10.597   -0.701    30    8.259    0.087    40   11.160   -0.246    50    8.400   -2.076

  51  -12.779   -2.098    61  -13.599    0.852    71  -12.267   -3.151    81  -11.214   -0.195    91  -11.309    0.193
  52  -13.578    2.474    62  -13.110    0.043    72  -15.565    0.498    82  -11.696   -0.697    92  -10.394   -0.969
  53  -14.514    0.211    63  -11.866   -1.290    73  -12.326   -4.251    83  -10.793   -0.984    93   -9.715   -3.938
  54  -14.535   -0.937    64  -12.219   -0.305    74  -11.895   -1.560    84  -13.134   -3.409    94  -11.035   -3.556
  55  -11.199   -2.864    65  -10.758   -0.746    75  -12.480   -0.100    85  -12.531   -0.557    95  -10.752   -3.124
  56  -11.097   -0.771    66  -10.586   -3.106    76   -9.670   -2.787    86  -11.624   -1.105    96  -10.544   -0.426
  57  -14.445    1.987    67  -10.166   -0.685    77  -12.161    0.913    87  -11.699    2.701    97  -11.643   -1.509
  58  -13.150   -1.665    68  -10.699   -0.567    78  -12.306   -4.750    88   -9.538   -2.319    98   -9.832   -1.690
  59  -13.590    0.273    69  -10.801   -4.371    79  -10.858   -4.053    89  -13.243    1.981    99   -9.822   -2.362
  60  -13.766   -1.513    70  -12.187   -0.875    80  -11.732    0.518    90   -9.971   -5.538   100  -11.257   -3.163

 101    0.543    7.147   111    3.699    4.662   121    1.305    1.047   131   -0.908    2.458
 102   -5.317   -3.785   112    2.141    4.414   122    4.129    4.829   132    2.843    4.643
 103    4.133    1.903   113    2.713    0.574   123    2.322    0.809   133    1.625   -0.725
 104   -1.850   -0.395   114    1.440    2.248   124   -6.540    0.846   134    3.226    0.857
 105   -3.619    0.831   115    3.629    2.053   125   -2.673    1.820   135    1.733   -4.496
 106    2.631    1.689   116  -11.434   -2.657   126   -6.916   -3.918   136    6.731    3.111
 107    1.192    0.625   117    2.372    9.711   127   -4.381    0.616   137    1.201    1.337
 108   -8.711   -6.107   118    1.842    0.480   128    1.891    3.587
 109    1.334    5.903   119   -2.448    1.916   129    3.618    2.930
 110    2.623    3.079   120   -0.482    7.592   130    0.918    2.458
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APPENDIX TABLE 13.

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BMD07M - STEPWISE DISCRIMINANT ANALYSIS                    VARIANCE TEST I
HEALTH SCIENCES COMPUTING FACILITY, UCLA
                                                  KANANASKIS GROUPS X.Y = A PRIORI KNOWN GROUPS
                                                     ALBERTA GROUPS R.C   A PRIORI UNKNOWN GROUPS
NUMBER OF VARIABLES    20

NUMBER OF GROUPS        4

NUMBER OF CASES IN EACH GROUP    59     50    -50    -50

PRIOR PROBABILITIES          0.2500    0.2500    0.0       0.0

MEANS

            GROUP
               Y             X             C             R
VARIABLE
    1      0.87168       0.86792       0.85360       0.84808
    2      0.23557       0.20462       0.22794       0.24505
    3     -0.36346      -0.56616      -0.40403      -0.58841
    4     -0.30946      -0.14116      -0.33436      -0.16079
    5     -0.20691      -0.24558      -0.20177      -0.27382
    6     -0.24981      -0.17176      -0.27233      -0.25316
    7     -0.05630      -0.02597      -0.09168      -0.10347
    8     -0.33758      -0.30891      -0.34039      -0.40956
    9     -0.24246      -0.15231      -0.27944      -0.20264
   10     -1.60772      -0.70548      -1.67149      -0.72127
   11     -0.70369      -0.19656      -0.82020      -0.16901
   12      0.00597       0.03224      -0.00768      -0.00297
   13      0.57717       0.56787       0.56420       0.56731
   14      0.25410       0.25592       0.22761       0.24747
   15      0.67417       0.68027       0.65766       0.64218
   16      0.49459       0.46047       0.47195       0.44602
   17     -0.25022      -0.29969      -0.24566      -0.28367
   18     63.77965      66.35999      62.46000      67.70000
   19     13.54237      12.06000      13.20000      11.54000
   20     23.74576      20.65999      23.43999      28.39999

STANDARD DEVIATIONS

             GROUP
                 Y           X
VARIABLE
    1        0.12260     0.11720
    2        0.10620     0.09785
    3        0.08647     0.09042
    4        0.13115     0.12814
    5        0.11803     0.11626
    6        0.12541     0.14476
    7        0.12856     0.13816
    8        0.11814     0.16812
    9        0.13564     0.12890
   10        0.68346     0.17321
   11        0.13532     0.12552
   12        0.13943     0.14261
   13        0.12060     0.11605
   14        0.12349     0.11611
   15        0.12581     0.12468
   16        0.13812     0.13540
   17        0.12869     0.11479
   18        2.87118     3.41520
   19        1.02254     0.93461
   20        1.61451     1.83625

                 C           R
VARIABLE
    1        0.10240     0.07721
    2        0.09588     0.07464
    3        0.07006     0.06070
    4        0.10456     0.10390
    5        0.09307     0.07160
    6        0.11350     0.08763
    7        0.09421     0.10327
    8        0.09610     0.08573
    9        0.10525     0.09319
   10        0.57843     0.15004
   11        0.17224     0.08300
   12        0.11862     0.08590
   13        0.10043     0.07710
   14        0.10833     0.08736
   15        0.10570     0.08126
   16        0.11661     0.08962
   17        0.10263     0.12691
   18        2.67304     3.60978
   19        0.85714     1.14060
   20        1.41652     2.00000

SUMMARY TABLE

STEP                                 NUMBER OF
NUMBER
       VARIABLE        F VALUE      VARIABLES     U-STATISTIC

   1      11          406.3784          1           0.2084
   2       3          184.9675          2           0.0755
   3       4           93.0830          3           0.0402
   4      17           17.5393          4           0.0344
   5      20            7.0158          5           0.0322
   6      10            6.4062          6           0.0303
   7       5            6.8454          7           0.0284
   8      19            6.1198          8           0.0268
   9      12            1.7658          9           0.0263
  10       9            1.7741         10           0.0258
  11       7            0.3297         11           0.0257
  12       6            0.2095         12           0.0257
  13      15            0.0371         13           0.0257
  14      13            0.1659         14           0.0256
  15       1            0.0922         15           0.0256
  16       2            0.0656         16           0.0256
  17       8            0.0398         17           0.0256
  18      14            0.0244         18           0.0256
  19      16            0.0194         19           0.0256
  20      18            0.0040         20           0.0256

EIGENVALUES

   38.12546    0.00014    0.00008    0.00005    0.00004    0.00002    0.00001    0.00001    0.00000
    0.00000   -0.00000   -0.00000   -0.00000   -0.00001   -0.00001   -0.00002   -0.00002   -0.00004
   -0.00008   -0.00013

CANONICAL CORRELATIONS

    0.98714    0.01187    0.00873    0.00676    0.00611    0.00409    0.00290    0.00246    0.00121
    0.00041    0.00071    0.00123    0.00150    0.00297    0.00320    0.00390    0.00500    0.00650
    0.00892    0.01148

COEFFICIENTS FOR CANONICAL VARIABLE -

ORIGINAL      1
VARIABLE
   1      -4.61422          11      -4.94494       CONSTANT
   2       2.62533          12       6.00267                 7.85577
   3      18.59300          13       5.68418
   4     -20.79883          14       0.72079
   5       7.78173          15      -5.37419
   6       1.94627          16       0.78835
   7      -1.97851          17       7.30075
   8       0.41967          18      -0.00254
   9      -5.37530          19       0.29560
  10      -0.83583          20      -0.18583

   X = FIRST CANONICAL VARIABLE
   Y = SECOND CANONICAL VARIABLE

GROUP      R  MEAN COORDINATES  -6.898   0.584

 CASE     X       Y    CASE     X       Y    CASE     X       Y    CASE     X       Y

   1   -6.699   0.444   11   -8.713  -0.712   21   -5.941  -1.311   31   -6.549  -0.615   41   -6.614   2.217
   2   -7.618  -0.067   12   -5.312  -0.421   22   -4.279   2.209   32   -6.275   1.769   42   -7.411  -0.192
   3   -6.312  -0.461   13   -7.196   0.077   23   -5.234   1.738   33   -6.576   0.982   43   -7.198   0.670
   4   -6.428  -0.185   14   -6.140  -0.396   24   -5.094  -1.744   34   -6.358   1.542   44   -6.357   1.695
   5   -7.599   0.651   15   -6.613  -0.145   25   -4.661  -0.096   35   -6.232   0.213   45   -6.324   2.109
   6   -7.502   0.954   16   -7.467  -0.073   26   -6.114   1.152   36   -7.783   0.577   46   -8.120  -0.185
   7   -8.135   0.567   17   -6.838  -0.013   27   -5.516   0.252   37   -5.690   2.249   47   -7.649  -0.519
   8   -6.718   0.866   18   -6.728   1.380   28   -7.098   1.191   38   -7.928   1.186   48   -7.616   0.506
   9   -7.503   0.449   19   -7.681   1.433   29   -6.522   1.115   39   -7.101   1.395   49   -8.012   0.751
  10   -9.440  -0.732   20   -6.482   1.553   30   -6.276   0.977   40   -7.252   0.069   50   -6.933   1.262

   X = FIRST CANONICAL VARIABLE
   Y = SECOND CANONICAL VARIABLE

GROUP      C  MEAN COORDINATES   6.602   0.456

 CASE     X       Y    CASE     X       Y    CASE     X       Y    CASE     X       Y

   1    6.651   2.116   11    6.511   0.916   21    6.146  -0.094   31    6.737  -0.490   41    6.386   1.645
   2    7.467   0.735   12    6.415   1.033   22    6.450   1.330   32    6.129  -0.604   42    9.604  -1.551
   3    7.724   0.563   13    5.596   1.766   23    8.066   2.766   33    7.423  -0.354   43    5.635   1.355
   4    6.054   1.147   14    6.730   3.113   24    7.068   0.793   34    5.143  -0.821   44    6.144  -0.599
   5    8.170   1.303   15    7.672   0.707   25    7.335  -1.102   35    5.657  -0.241   45    5.933  -0.791
   6    7.040  -0.051   16    7.603   1.070   26    6.109  -0.881   36    6.567   0.395   46  [illegible] [illegible]
   7    6.735   1.417   17    7.464  -1.063   27    5.603  -1.430   37    4.535   0.047   47  [illegible] [illegible]
   8    6.526  -0.134   18    7.205  -0.799   28    5.758  -1.331   38    5.607   1.655   48  [illegible]  1.311
   9    8.277   0.426   19    9.075   1.559   29    5.361  -0.122   39    6.727  -1.283   49    6.637   0.032
  10    7.343   2.771   20    5.277  -0.469   30    6.060   0.587   40    6.699   0.014   50    4.475   1.406

   X = FIRST CANONICAL VARIABLE
   Y = SECOND CANONICAL VARIABLE

GROUP      X  MEAN COORDINATES  -6.645  -0.000

 CASE     X       Y    CASE     X       Y    CASE     X       Y    CASE     X       Y

   1   -7.133   0.233   11   -7.336  -0.761   21   -8.316  -1.384   31   -8.306  -0.567   41  [illegible] -0.475
   2   -4.970   0.265   12   -5.561   1.526   22   -7.969   1.709   32   -6.147  -1.012   42   -7.045  -1.406
   3   -7.219   0.165   13   -7.561   1.334   23   -7.729  -0.154   33   -6.256  -0.701   43   -6.916  [illegible]
   4   -7.342   0.169   14   -8.426  -0.122   24   -6.962   0.657   34   -6.962   0.071   44   -5.783  [illegible]
   5   -5.656  -0.956   15   -6.764  -0.539   25   -5.513   1.569   35   -4.773   0.217   45   -7.137  [illegible]
   6   -7.307  -0.893   16   -5.599  -0.407   26   -6.251  -0.743   36   -4.127   0.270   46   -6.216   1.560
   7   -7.222   0.176   17   -7.531   0.355   27   -6.167  -1.343   37   -7.174   0.665   47   -5.397  [illegible]
   8   -7.097  -0.914   18   -6.164  -1.927   28   -5.391   0.172   38   -5.948   0.714   48  [illegible] [illegible]
   9   -5.556   2.318   19   -7.058   0.679   29   -6.580   0.572   39   -7.256  -0.071   49   -7.116   1.007
  10   -7.291   0.992   20   -5.907   1.176   30   -6.716  -1.206   40   -5.609  -0.699   50   -4.306  -0.365

   X = FIRST CANONICAL VARIABLE
   Y = SECOND CANONICAL VARIABLE

GROUP      Y  MEAN COORDINATES   5.632  -0.000

 CASE     X       Y    CASE     X       Y    CASE     X       Y    CASE     X       Y    CASE     X       Y

   1    5.537  -2.748   11    7.531   0.202   21    4.814   0.102   31  [illegible]  0.166   41    6.846  -1.664
   2    6.880  -1.376   12    6.113  -0.250   22    6.006  -0.335   32    6.431   0.621   42    4.767  [illegible]
   3    6.736   0.214   13    5.351   0.618   23    3.542  -1.717   33    5.054   0.957   43  [illegible]  1.359
   4    5.959  -2.157   14    6.884  -0.136   24    5.256   1.141   34    5.717   1.505   44    4.655   0.494
   5    6.031   0.772   15    6.521   0.180   25    4.664   0.976   35    6.455  -0.644   45    5.337  [illegible]
   6    4.943  -0.637   16    5.017   1.299   26    3.796   0.065   36    5.210  -1.000   46  [illegible] [illegible]
   7    7.091  -0.476   17    5.185   0.673   27    7.112   0.761   37    5.196  -1.652   47    5.676  [illegible]
   8    6.378   0.864   18    6.513   0.163   28    4.886  -0.541   38    7.311   0.458   48    5.173  [illegible]
   9    5.495  -1.506   19    5.692   0.374   29    4.540   0.524   39    6.253  -1.296   49    7.525  [illegible]
  10    5.127  -0.714   20    5.462  -0.306   30    6.630   0.622   40    3.751   0.603   50    5.684   1.095

  51    6.603   0.106
  52    4.409   1.215
  53    5.285   0.519
  54    5.040  -0.152
  55    5.031   1.796
  56    5.761   0.516
  57    4.947   1.391
  58    3.636  -1.476
  59    4.719  -0.074
```

APPENDIX TABLE 14.

VARIANCE TEST II

ALL GROUPS INCLUDED IN A PRIORI KNOWN GROUPS
ALBERTA + KANANASKIS COUESIUS   X C
ALBERTA + KANANASKIS RHINICHTHYS   R

```
BMD07M - STEPWISE DISCRIMINANT ANALYSIS
HEALTH SCIENCES COMPUTING FACILITY, UCLA

NUMBER OF VARIABLES     20

NUMBER OF GROUPS         2

NUMBER OF CASES IN EACH GROUP   100   100

PRIOR PROBABILITIES          0.5000    0.5000


MEANS

          GROUP
             R          X   C
VARIABLE
   1      7.41294     7.70294     7.55794
   2      1.83799     1.78589     1.81194
   3      0.26930     0.41720     0.34325
   4      0.73279     0.50649     0.61964
   5      0.56569     0.65719     0.61144
   6      0.64099     0.57960     0.61029
   7      0.90029     0.89279     0.89654
   8      0.46360     0.48430     0.47395
   9      0.68979     0.58359     0.63669
  10      0.20700     0.04430     0.12565
  11      0.67280     0.18390     0.42835
  12      1.07649     1.06789     1.07219
  13      3.88455     3.92376     3.90416
  14      1.83959     1.84309     1.84134
  15      4.72894     4.91253     4.82074
  16      3.01018     3.25906     3.13462
  17      0.53059     0.59989     0.56524
  18     66.95999    63.10999    65.03499
  19     11.78000    13.36000    12.57000
  20     28.51999    23.53999    26.01000


STANDARD DEVIATIONS

          GROUP
             R          X   C
VARIABLE
   1      1.66178     1.88311
   2      0.36070     0.39275
   3      0.04695     0.07025
   4      0.18852     0.12825
   5      0.12711     0.14718
   6      0.19186     0.15365
   7      0.26072     0.23686
   8      0.16928     0.10818
   9      0.17755     0.16099
  10      0.06916     0.03153
  11      0.16087     0.06654
  12      0.28760     0.10031
  13      0.86752     0.94266
  14      0.41949     0.44467
  15      1.14151     1.24249
  16      0.77960     0.90604
  17      0.14240     0.14409
  18      3.57012     2.96153
  19      1.06912     0.95895
  20      1.92526     1.48677

SUMMARY TABLE

 STEP      VARIABLE        F VALUE TO        NUMBER OF         U-STATISTIC
NUMBER  ENTERED  REMOVED  ENTER OR REMOVE  VARIABLES INCLUDED


   1      11              799.3086             1                0.2005
   2       3              348.4276             2                0.0724
   3       2               40.2512             3                0.0601
   4      20               16.7103             4                0.0554
   5       9               13.0501             5                0.0519
   6      17               14.4820             6                0.0482
   7       8               10.6967             7                0.0457
   8       1                3.5381             8                0.0449
   9      13                1.7921             9                0.0444
  10      15                1.8769            10                0.0440
  11      10                2.3929            11                0.0435
  12      19                1.0922            12                0.0432
  13       5                1.0253            13                0.0430
  14       6                0.3441            14                0.0429
  15       7                0.3990            15                0.0428
  16       4                0.2467            16                0.0427
  17      14                0.1369            17                0.0427
  18      12                0.0326            18                0.0427
  19      16                0.0060            19                0.0427
  20      18                0.0012            20                0.0427


EIGENVALUES

   22.42146    0.00015    0.00007    0.00003    0.00002    0.00002    0.00001    0.00001   0.00000
    0.00000    0.00000    0.00000   -0.00000   -0.00000   -0.00000   -0.00001   -0.00002  -0.00002
   -0.00005   -0.00011


CANONICAL CORRELATIONS

    0.97843    0.01229    0.00831    0.00566    0.00478    0.00465    0.00301    0.00233   0.00177
    0.00120    0.00107    0.00086    0.00040    0.00152    0.00193    0.00310    0.00422   0.00438
    0.00683    0.01052



COEFFICIENTS FOR CANONICAL VARIABLE

ORIGINAL      1
VARIABLE
   1      -1.05486        11      -4.18479      CONSTANT
   2      -2.91379        12       0.12874               0.34593
   3      31.49019        13       1.48315
   4      -1.21377        14       0.26699
   5       2.81261        15      -0.75618
   6      -1.09111        16       0.01936
   7       0.58412        17       4.41864
   8       6.64307        18      -0.00058
   9      -2.05565        19       0.08826
  10      -4.03406        20      -0.17955


X = FIRST CANONICAL VARIABLE
Y = SECOND CANONICAL VARIABLE

GROUP      R  MEAN COORDINATES  -4.711   0.000

CASE    X       Y     CASE    X       Y     CASE    X       Y     CASE    X       Y     CASE    X       Y
       ALBERTA RHINICHTHYS 1-50
  1  -5.042  -0.847    11  -6.600  -0.455    21  -4.392  -1.681    31  -5.344  -0.512    41  -4.557   2.003
  2  -5.141  -1.252    12  -3.746  -0.346    22  -2.505   0.505    32  -4.284   0.658    42  -4.816  -0.449
  3  -5.038  -0.270    13  -4.842   0.909    23  -4.333   1.167    33  -5.055   0.554    43  -4.769  -0.049
  4  -4.107  -0.697    14  -4.751  -0.816    24  -3.243  -0.017    34  -4.931  -0.557    44  -5.425   0.651
  5  -4.485  -0.068    15  -4.368   0.270    25  -4.152  -0.497    35  -5.050   0.124    45  -5.011   0.874
  6  -5.765  -0.293    16  -4.338  -1.057    26  -4.549   0.692    36  -7.050  -0.607    46  -5.219   1.327
  7  -6.235   0.034    17  -4.516  -0.477    27  -3.267  -0.044    37  -4.463   0.831    47  -4.604   0.515
  8  -4.877   0.008    18  -3.196   0.511    28  -5.328  -0.223    38  -5.772   0.931    48  -5.125   0.150
  9  -5.321   0.100    19  -5.315  -1.311    29  -5.521   0.591    39  -5.873  -0.038    49  -5.385   1.843
 10  -7.867   0.618    20  -4.407  -0.711    30  -5.170  -0.126    40  -5.248   1.012    50  -6.266  -0.761
       KANANASKIS RHINICHTHYS 51-100
 51  -5.687  -1.619    61  -4.799  -1.372    71  -7.372  -1.178    81  -4.970   1.139    91  -1.249  -2.235
 52  -2.889  -0.618    62  -4.243  -0.073    72  -6.610   0.470    82  -1.704  -0.319    92  -3.914  -0.675
 53  -5.210   0.122    63  -4.819   0.582    73  -6.305   0.169    83  -1.762   0.040    93  -4.734  -1.479
 54  -5.340  -0.389    64  -6.210   1.116    74  -5.915  -0.358    84  -4.652  -0.537    94  -4.289  -1.278
 55  -4.583  -1.776    65  -4.795   0.280    75  -4.905   0.308    85  -1.927   1.061    95  -3.014   0.325
 56  -5.323   0.772    66  -3.394   0.249    76  -4.647   1.154    86  -2.599  -0.431    96  -5.199  -0.676
 57  -4.692   0.347    67  -4.209  -1.845    77  -4.174   0.878    87  -4.729  -0.697    97  -5.041  -0.690
 58  -5.410   0.039    68  -3.635   0.556    78  -4.234   1.138    88  -4.309   2.218    98  -3.553  -0.725
 59  -4.317   0.086    69  -3.493  -0.503    79  -3.322   0.855    89  -6.917  -0.755    99  -3.737  -0.740
 60  -5.389   1.333    70  -4.013   1.403    80  -3.700   0.686    90  -4.783   0.407   100  -3.749   0.701


X = FIRST CANONICAL VARIABLE
Y = SECOND CANONICAL VARIABLE

GROUP      C  MEAN COORDINATES   4.711   0.000

CASE    X       Y     CASE    X       Y     CASE    X       Y     CASE    X       Y     CASE    X       Y
       ALBERTA COUESIUS 1-50
  1   4.998   0.905    11   5.158  -0.075    21   3.546  -0.087    31   3.553  -0.513    41   5.623  -1.261
  2   4.366   1.041    12   6.097   0.484    22   3.705   0.257    32   3.486  -0.793    42   4.712   0.557
  3   4.832  -0.687    13   3.698  -0.479    23   4.570   0.906    33   6.740   1.292    43   4.657  -1.081
  4   3.711   0.092    14   5.188   0.510    24   3.155  -0.248    34   4.386   0.084    44   4.638  -0.957
  5   5.218   1.699    15   4.097   0.012    25   5.124  -0.897    35   4.961  -0.385    45   4.976  -0.360
  6   5.053   0.949    16   5.532  -0.065    26   3.580  -0.897    36   5.722   1.833    46   6.141  -0.983
  7   4.294   0.764    17   4.653  -1.061    27   4.012  -1.534    37   3.727  -1.178    47   5.352  -0.025
  8   4.041  -0.279    18   5.017  -0.628    28   3.765   0.087    38   4.516   2.352    48   4.299  -0.791
  9   5.651   0.574    19   6.254   0.643    29   4.449   0.018    39   3.656  -0.348    49   4.451   0.869
 10   5.063   1.563    20   4.757  -1.207    30   3.309   0.456    40   3.402  -0.175    50   4.859  -0.889
       KANANASKIS COUESIUS 51-100
 51   4.256  -0.702    61   6.985   0.127    71   4.294   2.593    81   5.093  -1.382    91   3.883  -0.987
 52   6.444  -1.697    62   6.076   0.324    72   6.401  -0.689    82   4.743  -0.263    92   3.999  -0.517
 53   6.522   0.081    63   5.080   0.515    73   3.317   3.799    83   4.505  -0.998    93   3.238   0.464
 54   5.319  -1.301    64   5.313   0.300    74   4.843   2.158    84   5.550   0.517    94   4.768   0.210
 55   4.688   0.221    65   5.669   0.735    75   6.150  -0.045    85   5.216   0.904    95   4.501   0.139
 56   5.206  -0.880    66   4.093  -0.355    76   3.651   1.840    86   4.810  -0.001    96   4.738   2.612
 57   5.954  -2.341    67   3.509  -0.150    77   5.030   1.454    87   3.482  -2.815    97   5.256  -0.093
 58   6.169  -0.021    68   3.811   0.567    78   4.206  -1.171    88   1.216   0.763    98   3.383  -1.062
 59   5.468  -1.428    69   4.552   0.124    79   3.773   0.674    89   4.711  -2.692    99   3.805   0.166
 60   5.136  -0.320    70   5.453  -0.922    80   4.439   1.750    90   3.278  -0.196   100   5.622   0.171
```

APPENDIX TABLE 15.

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BMD07M - STEPWISE DISCRIMINANT ANALYSIS -                (SQUARE-ROOT TRANSFORMED DATA)
HEALTH SCIENCES COMPUTING FACILITY, UCLA
                                                          ALBERTA GROUPS B,C    A PRIORI KNOWN GROUP
NUMBER OF VARIABLES     21                           EAST KANANASKIS GROUP K    A PRIORI UNKNOWN GROUP
                                                          (1961,1969,1973)
NUMBER OF GROUPS         3

NUMBER OF CASES IN EACH GROUP      50     50    61

PRIOR PROBABILITIES          0.3333    0.3333    0.0

MEANS                                                 STANDARD DEVIATIONS

          GROUP                                                 GROUP
            B             C             P                         B             C             P
VARIABLE                                              VARIABLE
   1      2.66695       2.63970       2.53777            1      0.23032       0.33486       0.28635
   2      1.11066       1.30778       1.23886            2      0.11130       0.14244       0.12435
   3      0.50912       0.61002       0.59400            3      0.03492       0.05023       0.04710
   4      0.93170       0.68526       0.65463            4      0.03650       0.08095       0.07171
   5      0.73133       0.73711       0.73626            5      0.05875       0.08338       0.08290
   6      0.75085       0.73667       0.69002            6      0.07431       0.09171       0.07807
   7      0.93173       0.90437       0.91367            7      0.10318       0.03818       0.08699
   8      0.62695       0.67982       0.63890            8      0.05993       0.07455       0.06581
   9      0.75110       0.73006       0.70093            9      0.08273       0.08613       0.08465
  10      1.04145       0.18803       0.18434           10      0.37057       0.03099       0.08634
  11      0.61030       0.0           0.00232           11      0.08424       0.0           0.01811
  12      0.32196       0.31053       0.50360           12      0.07688       0.00020       0.07521
  13      1.00130       1.00018       0.90047           13      0.01606       0.13487       0.11889
  14      1.62883       1.52737       1.81575           14      0.16765       0.21823       0.21307
  15      1.31108       1.10989       1.24377           15      0.12468       0.13814       0.13788
  16      2.13335       2.14733       2.00634           16      0.13026       0.25466       0.24424
  17      1.67354       1.71663       1.61281           17      0.16531       0.22569       0.22940
  18      0.72902       0.75871       0.70894           18      0.11462       0.09846       0.07370
  19     67.76030      62.44033      63.98360           19      3.60978       2.87304       3.31361
  20     11.46000      13.23033      12.29508           20      1.14660       0.85714       0.93082
  21     28.33999      21.43355      24.11475           21      2.03000       1.41652       1.78977


SUMMARY TABLE

 STEP     VARIABLE           F VALUE TO        NUMBER OF          U-STATISTIC
NUMBER  ENTERED  REMOVED   ENTER OR REMOVE  VARIABLES INCLUDED

   1       11                3893.5463            1                0.0216
   2        3                  49.2061            2                0.0183
   3       12                  20.4375            3                0.0134
   4       19                  17.3352            4                0.0111
   5       16                   7.3403            5                0.0103
   6        7                  13.1077            6                0.0092
   7       10                   3.4754            7                0.0085
   8       15                   3.1029            8                0.0083
   9        5                   2.4704            9                0.0083
  10       17                   1.3885           10                0.0081
  11        4                   2.7162           11                0.0079
  12       20                   1.6267           12                0.0078
  13       14                   1.1475           13                0.0077
  14       18                   0.6022           14                0.0076
  15       13                   0.6034           15                0.0076
  16        2                   0.5743           16                0.0075
  17        6                   0.3067           17                0.0075
  18        8                   0.2005           18                0.0074
  19        9                   0.0643           19                0.0074
  20       21                   0.0556           20                0.0074
  21        1                   0.0431           21                0.0074

EIGENVALUES

  131.32118    0.00030    0.00014    0.00013    0.00010    0.00007    0.00003    0.00001    0.00002
    0.00001    0.00001    0.00001    0.00000   -0.00000   -0.00000   -0.00000   -0.00002   -0.00003
   -0.00004   -0.00010   -0.00016

CANONICAL CORRELATIONS

    0.99628    0.01744    0.01182    0.01114    0.00781    0.00733    0.00710    0.00576    0.00412
    0.00387    0.00242    0.00247    0.00124    0.00317    0.00120    0.00100    0.00091    0.00555
    0.00067    0.01016    0.01249

COEFFICIENTS FOR CANONICAL VARIABLE

ORIGINAL      1
VARIABLE
   1       -1.15737        10        5.62133        19       -0.04418
   2       -3.58406        11       24.36063        20       -0.11204
   3      -16.71770        12       10.31279        21        0.01909
   4      -12.42598        13        2.06011      CONSTANT
   5       -2.11104        14        7.64213                  6.38768
   6        3.03162        15        3.45776
   7      -13.82356        16       14.91759
   8       -3.81073        17       -9.24000
   9       -2.88777        18       -9.12718


    X = FIRST CANONICAL VARIABLE
    Y = SECOND CANONICAL VARIABLE

GROUP       B  MEAN COORDINATES  11.439  -0.000

  CASE     X       Y    CASE     X       Y    CASE     X       Y    CASE     X       Y

    1   12.178   0.009   11   12.904   0.544   21   10.240   1.825   31   11.279   1.350   41   11.606  -0.248
    2   12.492   1.142   12   11.679   1.249   22    9.515  -2.174   32   11.600  -0.702   42    9.582   0.503
    3   12.393   0.223   13   12.008  -0.544   23   11.642  -1.213   33   12.053   0.031   43   11.057   0.633
    4   11.187   0.344   14   10.036  -1.089   24   10.173  -1.603   34   10.899  -0.380   44   11.622   0.552
    5   11.108  -0.608   15   11.777  -0.403   25   12.399   0.869   35   11.257   0.404   45   11.311   0.232
    6   12.129   0.466   16    9.759   0.021   26   12.777   0.505   36   13.228   0.012   46   12.136  -0.671
    7   12.954   0.425   17    9.109  -1.004   27    9.776   0.924   37   11.572   0.132   47    9.977  -0.250
    8   12.338   0.498   18   10.158  -0.731   28   11.578  -1.005   38   12.432  -0.205   48   10.437  -2.049
    9   11.470   0.232   19   11.802   1.506   29   11.907   0.149   39   12.003  -1.007   49   10.235  -0.041
   10   13.950  -1.434   20   10.267  -0.534   30   12.293   2.669   40   11.643  -0.075   50   11.142   0.404


    X = FIRST CANONICAL VARIABLE
    Y = SECOND CANONICAL VARIABLE

GROUP       C  MEAN COORDINATES -11.439  -0.000

  CASE     X       Y    CASE     X       Y    CASE     X       Y    CASE     X       Y

    1  -10.572   1.462   11  -11.322   0.016   21  -10.277  -0.930   31  -10.533   0.179   41  -11.077  -1.754
    2  -11.447  -0.608   12  -13.291   1.630   22  -11.747  -0.697   32  -10.063   0.210   42  -10.012   0.458
    3  -10.286   1.587   13   -9.548  -0.456   23  -11.447   1.173   33  -13.736   0.192   43  -12.850  -0.111
    4  -11.392   0.406   14  -11.567  -1.965   24  -10.557   0.950   34  -11.247  -0.733   44  -12.478   0.357
    5  -12.594  -0.114   15  -10.620   0.457   25  -11.008  -0.129   35  -12.162  -0.275   45  -12.260   0.313
    6  -11.989   0.319   16  -12.459  -0.557   26  -10.497  -0.315   36  -13.275  -0.634   46  -11.703  -0.677
    7  -11.069   0.244   17  -11.830   0.552   27  -11.333   0.583   37  -10.609  -0.437   47  -11.533  -0.329
    8  -11.137   0.577   18  -11.315   1.384   28  -10.348  -0.633   38  -10.415  -1.107   48  -11.055  -0.120
    9  -12.202   1.388   19  -12.734   2.271   29  -11.641  -0.506   39  -10.622   1.145   49  -10.374  -0.538
   10  -12.062  -0.308   20  -12.585  -0.293   30  -10.446  -0.303   40  -11.033   1.266   50   -9.451  -2.715


    X = FIRST CANONICAL VARIABLE
    Y = SECOND CANONICAL VARIABLE

GROUP       P  MEAN COORDINATES  -8.845  -3.844

  CASE     X       Y    CASE     X       Y    CASE     X       Y    CASE     X       Y    CASE     X       Y

    1  -10.204  -0.378   11   -8.523  -3.075   21   -7.417  -3.246   31   -8.714  -3.883   41   -7.673  -3.690
    2  -10.556  -2.022   12   -8.232  -3.675   22   -7.422  -4.320   32   -8.035  -4.246   42   -8.372  -3.489
    3  -10.331  -1.441   13   -9.024  -1.518   23   -8.360  -4.404   33   -9.165  -4.235   43   -9.666  -3.342
    4   -8.007  -2.984   14   -9.827  -1.468   24   -8.682  -3.785   34   -4.377   0.272   44   -8.733  -5.036
    5   -8.199  -3.479   15  -10.148  -9.340   25   -7.892  -4.646   35   -6.387  -4.663   45   -8.122  -4.343
    6   -9.796  -3.389   16   -8.270  -4.080   26   -9.131  -4.657   36   -7.243  -3.074   46   -8.012  -4.862
    7   -9.136  -2.243   17   -9.993  -3.164   27   -9.629  -3.491   37   -9.307  -4.508   47   -9.850  -3.043
    8  -10.085  -3.047   18   -9.103  -2.951   28   -8.454  -3.081   38   -9.772  -4.503   48   -9.760  -4.070
    9   -9.738  -1.746   19  -10.051  -1.372   29  -10.767  -2.780   39   -9.267  -3.803   49   -9.226  -4.786
   10   -8.947  -3.331   20   -8.470  -4.699   30   -8.695  -2.729   40   -9.320  -3.195   50   -9.215  -6.332

   51   -8.794  -6.278   61   -8.269  -4.217
   52   -8.976  -4.811
   53  -10.179  -4.645
   54   -9.073  -6.925
   55   -9.131  -5.565
   56   -8.219  -4.657
   57   -7.502  -4.364
   58   -7.521  -3.960
   59  -10.286  -5.600
   60   -8.925  -5.007
```

APPENDIX TABLE 16.

```
ALBERTA RHINICHTHYS ONLY
                                                PRINCIPAL COMPONENTS ANALYSIS - CLUSTAN 1C
NUMBER OF CASES =    50
NUMBER OF BINARY VARIABLES =    0
NUMBER OF NUMERIC VARIABLES =   21              (SQUARE-ROOT TRANSFORMED DATA)

NUMERIC MEANS AND STANDARD DEVIATIONS       VARIABLE MINIMUM VALUE      MAXIMUM VALUE

  1        2.6650        0.2303              1         2.1213            3.0822
  2        1.3307        0.1113              2         1.0583            1.5166
  3        0.5091        0.0350              3         0.4243            0.5745
  4        0.8367        0.0965              4         0.6245            1.0000
  5        0.7320        0.0588              5         0.5831            0.8307
  6        0.7509        0.0743              6         0.5916            0.9055
  7        0.8937        0.1032              7         0.6708            1.0630
  8        0.6270        0.0600              8         0.5000            0.7211
  9        0.7963        0.0827              9         0.6000            0.9381
 10        0.4419        0.0706             10         0.2646            0.5477
 11        0.6110        0.0693             11         0.4359            0.7550
 12        0.8268        0.0769             12         0.6557            0.9899
 13        1.0013        0.0969             13         0.7810            1.1747
 14        1.9289        0.1677             14         1.5906            2.2204
 15        1.3361        0.1297             15         1.0000            1.5362
 16        2.1034        0.1903             16         1.6793            2.4352
 17        1.6795        0.1658             17         1.2728            1.9698
 18        0.7290        0.1046             18         0.4899            0.9055
 19       67.7000        3.6100             19        60.0000           74.0000
 20       11.5400        1.1466             20         9.0000           14.0000
 21       28.4000        2.0001             21        25.0000           33.0000
EIGENVALUES

 16.28   1.31   1.02   0.79   0.52   0.26   0.20   0.12   0.09   0.08   0.07   0.06   0.06   0.04   0.04   0.02
  0.02   0.01   0.01   0.00   0.00


PERCENTAGE VARIANCE

 77.51   6.22   4.86   3.74   2.47   1.22   0.96   0.56   0.42   0.40   0.35   0.28   0.27   0.21   0.19   0.11
  0.09   0.07   0.05   0.02   0.02


CUMULATIVE VARIANCE

 77.51  83.72  88.59  92.33  94.80  96.02  96.98  97.54  97.97  98.36  98.71  98.99  99.26  99.47  99.65  99.76
 99.84  99.91  99.96  99.98 100.00
 EIGENVECTORS - BY ROWS

 VECTOR  1

  0.245 0.242 0.226 0.240 0.240 0.238 0.238 0.240 0.241 0.234 0.212 0.232 0.226 0.243 0.236 0.243 0.238 0.208
  0.033 0.015 0.076

 VECTOR  2
 -0.033-0.015 0.000-0.087 0.025 0.051-0.049 0.017-0.009-0.094 0.166-0.041 0.089-0.024-0.069-0.051 0.038-0.210
  0.569 0.501 0.558


 VECTOR  3

 -0.049 0.056-0.054 0.063 0.003-0.068 0.031-0.033 0.030 0.080 0.165-0.009-0.113-0.076-0.058-0.019-0.082 0.162
 -0.648 0.673 0.106


 FIRST   3 FACTOR SCORES

 S  1    -0.072  0.193 -0.322     S 26    -1.870  0.707  1.455
 S  2    -1.010 -0.211 -0.140     S 27    -3.453 -1.561 -0.268
 S  3    -1.569  0.180  0.043     S 28     5.481 -1.136 -1.921
 S  4    -4.475  0.091 -2.293     S 29     3.297  0.736 -0.775
 S  5    -5.679 -1.103 -1.586     S 30     3.766 -0.827 -0.097
 S  6     5.667  0.128  0.309     S 31     3.300 -1.300 -0.322
 S  7     1.982  0.845  1.244     S 32     2.673 -1.204 -0.197
 S  8     3.697  0.353 -0.017     S 33     2.879 -0.384 -0.777
 S  9     1.096  1.504 -0.753     S 34     3.193  0.271  0.016
 S 10     5.129  0.751 -0.893     S 35     5.057  1.261  0.334
 S 11     1.861  1.093 -0.657     S 36     5.169  0.558  0.397
 S 12    -2.818 -0.455 -0.215     S 37     3.302 -0.042 -1.119
 S 13    -1.934  2.738  0.711     S 38     2.194  0.943  0.077
 S 14    -3.893  2.020 -1.093     S 39     2.847  1.516 -0.211
 S 15    -4.815  0.499 -0.941     S 40     0.911  0.268 -0.575
 S 16    -7.701  0.279  0.265     S 41     0.712  1.639 -0.895
 S 17    -8.485  0.748  0.692     S 42     3.904 -0.804  0.248
 S 18    -9.846 -1.421 -0.396     S 43     3.085 -0.215  2.719
 S 19    -2.887  1.159  1.936     S 44     0.714 -0.439 -0.157
 S 20    -5.318  0.277  0.422     S 45     1.114 -1.922 -0.036
 S 21    -5.692 -0.057  0.812     S 46    -0.412 -3.206  0.541
 S 22    -6.601  0.656 -0.162     S 47    -0.704 -1.941  0.826
 S 23     1.266  0.145  1.729     S 48     0.510 -1.837  1.716
 S 24    -3.121 -0.372 -1.063     S 49     2.001 -1.419 -0.747
 S 25    -0.888 -0.118  2.176     S 50     6.448  0.219 -0.039
```

APPENDIX TABLE 17.

```
ALBERTA COUESIUS ONLY
                                                     PRINCIPAL COMPONENTS ANALYSIS - CLUSTAN 1C
NUMBER OF CASES =    50
NUMBER OF BINARY VARIABLES =    0                    (SQUARE-ROOT TRANSFORMED DATA)
NUMBER OF NUMERIC VARIABLES =   21

NUMERIC MEANS AND STANDARD DEVIATIONS       VARIABLE MINIMUM VALUE     MAXIMUM VALUE

  1        2.6897         0.3089             1            2.0736            3.3166
  2        1.3078         0.1425             2            1.0149            1.6462
  3        0.6300         0.0503             3            0.5292            0.7550
  4        0.6853         0.0809             4            0.5196            0.8485
  5        0.7971         0.0834             5            0.6083            0.9798
  6        0.7369         0.0937             6            0.5385            0.9327
  7        0.9050         0.0970             7            0.7071            1.1489
  8        0.6798         0.0746             8            0.5196            0.8485
  9        0.7301         0.0870             9            0.5477            0.9539
 10        0.1688         0.0909            10            0.0000            0.3606
 11        0.0            1.0000            11            0.0               0.0
 12        0.3966         0.0803            12            0.2646            0.6164
 13        1.0002         0.1349            13            0.7071            1.4107
 14        1.9271         0.2183            14            1.4900            2.4166
 15        1.3093         0.1582            15            0.9695            1.5969
 16        2.1479         0.2547            16            1.6125            2.7258
 17        1.7367         0.2257            17            1.2570            2.2782
 18        0.7588         0.0885            18            0.5831            0.9434
 19       62.4800         2.8734            19           58.0000           70.0000
 20       13.2000         0.8572            20           11.0000           15.0000
 21       23.4400         1.4168            21           21.0000           26.0000
EIGENVALUES

 15.13   1.38   1.08   0.73   0.55   0.44   0.21   0.12   0.10   0.06   0.05   0.04   0.03   0.02   0.02   0.01
  0.01   0.00   0.00   0.00   0.0


PERCENTAGE VARIANCE

 72.04   6.57   5.16   3.49   2.60   2.11   1.01   0.56   0.47   0.29   0.23   0.19   0.15   0.12   0.10   0.06
  0.04   0.02   0.01   0.01   0.0


CUMULATIVE VARIANCE

 72.04  78.61  83.77  87.27  89.86  91.98  92.99  93.55  94.01  94.31  94.54  94.73  94.87  94.99  95.09  95.15
 95.20  95.22  95.23  95.24  95.24
EIGENVECTORS - BY ROWS

VECTOR  1

 0.255 0.254 0.248 0.251 0.253 0.251 0.252 0.246 0.252 0.177 0.0   0.190 0.220 0.255 0.249 0.254 0.250 0.241
 0.043 0.026-0.006

VECTOR  2

 0.006-0.025-0.005-0.055-0.019 0.032-0.017-0.014-0.042-0.246 0.0  -0.073 0.117 0.010 0.017 0.014 0.029 0.014
 0.690 0.648 0.127

VECTOR  3

 -0.061 0.026 0.071 0.037 0.033-0.036 0.037-0.044 0.017 0.272 0.0   0.052 0.000-0.065-0.088-0.054-0.059-0.007
 -0.230 0.196 0.893

FIRST  3 FACTOR SCORES

S  1     4.036 -0.913 -2.034     S 26    -0.140  0.037  0.264
S  2    -0.080  1.023 -1.824     S 27    -0.704 -0.729  1.351
S  3    -4.715 -0.496 -1.343     S 28    -1.636 -1.499  1.032
S  4    -1.497  0.023  1.075     S 29    -1.389 -1.911  1.282
S  5     0.896  0.676 -1.146     S 30    -3.756  2.158  0.814
S  6     2.454 -0.510 -1.578     S 31    -5.419 -0.876  0.304
S  7    -2.925 -1.268  0.929     S 32    -3.168  1.168  1.807
S  8    -0.837  1.735  0.180     S 33     8.932 -0.408  1.004
S  9    -0.251 -0.496 -0.338     S 34     5.962 -1.573  1.585
S 10    -0.784  1.257  1.006     S 35     5.337 -0.607  0.609
S 11    -4.362 -0.009 -0.951     S 36     4.491 -0.129  0.767
S 12    -0.684  1.120  1.006     S 37     1.868 -0.633  0.739
S 13    -7.669 -1.007 -0.537     S 38    -0.365 -0.494  0.251
S 14     0.377  0.732  0.569     S 39    -3.058 -1.069  0.079
S 15    -6.821 -1.653 -1.080     S 40    -4.867 -0.555 -0.226
S 16    -0.287  1.578  2.063     S 41     4.195  0.143  0.047
S 17     3.901  2.537 -1.012     S 42     0.896  2.698 -1.099
S 18     1.827 -1.441 -1.588     S 43     4.222  0.941  1.908
S 19     2.963  1.474 -0.540     S 44     3.500 -0.708 -0.991
S 20     3.296 -0.666 -0.237     S 45     3.463  0.644  0.114
S 21    -4.149  0.980 -0.938     S 46     4.737 -0.549 -0.859
S 22    -5.336 -0.978  0.668     S 47     3.293  0.150 -0.437
S 23    -5.634  2.112 -0.089     S 48     2.751 -1.021 -0.639
S 24    -8.253 -0.020  0.224     S 49     0.211  0.506 -1.429
S 25     2.101  0.402 -0.808     S 50     3.087 -1.877  0.046
```

APPENDIX TABLE 18. Alberta control *Couesius plumbeus*; Raw character values, n = 50.

ALBERTA CONTROL COUESIUS PLUMBEUS N 50

601A	[illegible]	2.08	0.44	0.54	[illegible]	[illegible]	1.07	0.55	0.63	0.05
0.0	[illegible]	1.12	5.00	2.24	6.09	4.15	0.72	64.00	12.00	21.00
602A	7.50	1.71	0.39	0.45	0.61	0.56	0.84	0.47	0.53	0.0
0.0	0.17	0.96	3.87	1.77	4.93	3.32	0.55	66.00	13.00	22.00
603A	5.40	1.28	0.34	0.32	0.49	0.39	0.62	0.36	0.36	0.03
0.0	0.11	0.69	2.76	1.26	3.37	2.12	0.42	62.00	13.00	21.00
604A	6.50	1.55	0.36	0.42	0.63	0.58	0.76	0.46	0.50	0.02
0.0	0.11	0.86	3.34	1.40	4.31	2.83	0.51	65.00	12.00	26.00
605A	6.10	1.82	0.42	0.50	0.68	0.56	0.83	0.53	0.57	0.0
0.0	0.12	1.00	4.19	1.96	5.25	3.64	0.57	64.00	13.00	23.00
606A	8.20	1.98	0.43	0.53	0.73	0.66	0.98	0.54	0.63	0.04
0.0	0.15	1.21	4.30	1.81	5.58	3.83	0.59	62.00	13.00	21.00
607A	6.00	1.43	0.37	0.38	0.56	0.50	0.71	0.37	0.46	0.02
0.0	0.10	0.77	3.16	1.39	3.94	2.58	0.46	60.00	12.00	25.00
608A	7.00	1.71	0.38	0.45	0.60	0.52	0.76	0.44	0.48	0.03
0.0	0.13	0.90	3.58	1.67	4.43	2.82	0.53	67.00	14.00	24.00
609A	7.30	1.71	0.42	0.48	0.68	0.51	0.81	0.46	0.53	0.01
0.0	0.10	1.14	3.78	1.73	4.63	2.93	0.51	60.00	13.00	23.00
610A	6.90	1.56	0.40	0.46	0.64	0.49	0.77	0.40	0.49	0.02
0.0	0.13	1.05	3.61	1.59	4.49	3.05	0.56	64.00	14.00	25.00
611A	5.30	1.29	0.35	0.39	0.47	0.39	0.63	0.35	0.39	0.03
0.0	0.12	0.76	2.76	1.16	3.38	2.10	0.46	61.00	14.00	21.00
612A	6.60	1.62	0.42	0.45	0.62	0.51	0.81	0.45	0.49	0.01
0.0	0.13	1.06	3.52	1.53	4.39	2.81	0.61	63.00	14.00	25.00
613A	4.30	1.05	0.28	0.30	0.40	0.29	0.50	0.31	0.30	0.01
0.0	0.11	0.55	2.22	1.01	2.60	1.58	0.36	59.00	13.00	22.00
614A	7.20	1.64	0.41	0.48	0.67	0.56	0.80	0.42	0.55	0.03
0.0	0.21	1.03	3.75	1.82	4.44	2.93	0.66	63.00	14.00	24.00
615A	4.60	1.15	0.30	0.30	0.44	0.35	0.57	0.35	0.35	0.0
0.0	0.08	0.64	2.43	1.12	2.89	1.73	0.34	58.00	12.00	22.00
616A	6.90	1.64	0.42	0.45	0.65	0.55	0.81	0.43	0.49	0.02
0.0	0.17	1.06	3.47	1.79	4.28	2.78	0.59	62.00	15.00	26.00
617A	9.50	2.01	0.46	0.55	0.76	0.72	1.02	0.51	0.68	0.02
0.0	0.19	1.35	4.63	2.36	5.91	3.94	0.67	70.00	14.00	23.00
618A	8.40	1.81	0.42	0.52	0.70	0.63	0.83	0.46	0.63	0.05
0.0	0.11	1.16	4.21	2.25	5.07	3.34	0.71	64.00	11.00	22.00
619A	8.90	1.92	0.46	0.53	0.80	0.66	0.93	0.53	0.62	0.04
0.0	0.10	1.20	4.58	2.15	5.65	3.88	0.66	66.00	14.00	23.00
620A	9.00	1.96	0.45	0.62	0.75	0.66	1.01	0.53	0.69	0.04
0.0	0.18	1.17	4.37	2.18	5.55	3.60	0.67	61.00	13.00	23.00
621A	5.60	1.36	0.31	0.36	0.48	0.42	0.64	0.37	0.43	0.01
0.0	0.12	0.68	2.88	1.41	3.51	2.14	0.47	64.00	14.00	22.00
622A	5.00	1.32	0.32	0.35	0.50	0.37	0.65	0.36	0.39	0.0
0.0	0.11	0.67	2.60	1.28	3.11	1.86	0.41	60.00	12.00	25.00
623A	4.90	1.18	0.30	0.32	0.46	0.35	0.58	0.35	0.35	0.01
0.0	0.08	0.59	2.58	1.10	3.23	2.03	0.53	65.00	15.00	23.00
624A	4.30	1.03	0.28	0.27	0.37	0.31	0.52	0.27	0.32	0.0
0.0	0.07	0.50	2.28	0.94	2.68	1.63	0.34	61.00	13.00	24.00
625A	8.20	1.93	0.43	0.49	0.69	0.58	0.86	0.53	0.60	0.02
0.0	0.27	1.22	4.06	1.97	5.15	3.37	0.70	62.00	14.00	22.00
626A	7.10	1.70	0.37	0.44	0.64	0.57	0.80	0.47	0.56	0.03
0.0	0.17	1.08	3.58	1.73	4.47	2.96	0.54	63.00	13.00	24.00
627A	6.90	1.68	0.40	0.44	0.61	0.52	0.88	0.43	0.53	0.04
0.0	0.16	0.96	3.43	1.55	4.35	2.83	0.49	60.00	13.00	25.00
628A	6.50	1.56	0.38	0.43	0.56	0.47	0.75	0.38	0.49	0.02
0.0	0.17	1.05	3.23	1.57	4.19	2.72	0.54	59.00	12.00	25.00
629A	6.70	1.55	0.40	0.47	0.60	0.43	0.76	0.40	0.49	0.04
0.0	0.14	1.03	3.32	1.63	4.17	2.79	0.49	58.00	12.00	25.00
630A	5.60	1.40	0.33	0.37	0.52	0.42	0.66	0.36	0.42	0.02
0.0	0.12	0.84	2.95	1.30	3.60	2.28	0.41	68.00	14.00	25.00
631A	5.00	1.22	0.32	0.30	0.45	0.36	0.60	0.30	0.38	0.02
0.0	0.13	0.76	2.55	1.15	3.14	2.16	0.44	62.00	12.00	24.00
632A	6.00	1.46	0.35	0.36	0.51	0.43	0.69	0.39	0.44	0.03
0.0	0.13	0.78	3.07	1.42	3.71	2.43	0.44	64.00	14.00	26.00
633A	11.00	2.71	0.57	0.72	0.96	0.87	1.32	0.72	0.91	0.13
0.0	0.23	1.72	5.84	2.55	7.43	5.19	0.89	60.00	14.00	24.00
634A	9.90	2.47	0.50	0.66	0.85	0.73	1.11	0.62	0.77	0.10
0.0	0.26	1.34	5.11	2.22	6.56	4.21	0.76	58.00	13.00	25.00
635A	9.50	2.22	0.49	0.63	0.81	0.76	1.12	0.58	0.73	0.09
0.0	0.25	1.34	4.80	2.11	6.28	4.20	0.77	62.00	13.00	24.00
636A	9.00	2.28	0.48	0.62	0.82	0.65	1.06	0.62	0.70	0.05
0.0	0.19	1.25	4.69	2.06	6.10	4.06	0.73	60.00	14.00	24.00
637A	8.00	1.90	0.40	0.56	0.73	0.54	0.92	0.51	0.61	0.09
0.0	0.20	1.17	4.05	1.91	4.92	3.05	0.61	62.00	13.00	24.00
638A	7.10	1.60	0.39	0.49	0.60	0.52	0.78	0.44	0.52	0.03
0.0	0.15	1.02	3.74	1.66	4.82	3.21	0.53	58.00	14.00	23.00
639A	6.00	1.48	0.33	0.37	0.52	0.43	0.69	0.40	0.47	0.04
0.0	0.09	0.80	3.12	1.49	3.79	2.50	0.49	59.00	13.00	23.00
640A	5.50	1.36	0.31	0.37	0.49	0.38	0.56	0.36	0.38	0.01
0.0	0.07	0.70	2.81	1.17	3.56	2.35	0.46	60.00	13.00	23.00
641A	9.30	2.16	0.50	0.56	0.77	0.70	0.99	0.54	0.62	0.05
0.0	0.35	1.10	4.77	2.20	5.70	3.90	0.69	62.00	14.00	23.00
642A	7.50	1.72	0.40	0.46	0.62	0.57	0.83	0.46	0.54	0.0
0.0	0.19	1.99	3.90	1.80	4.92	3.30	0.58	68.00	14.00	23.00
643A	8.80	2.23	0.45	0.63	0.79	0.73	1.05	0.62	0.65	0.10
0.0	0.20	1.09	4.60	2.08	5.55	3.67	0.72	65.00	14.00	26.00
644A	8.90	2.18	0.43	0.61	0.79	0.73	1.00	0.64	0.66	0.04
0.0	0.13	1.15	4.51	2.18	5.65	3.75	0.60	61.00	13.00	22.00
645A	8.60	2.00	0.43	0.58	0.72	0.73	0.94	0.59	0.68	0.09
0.0	0.15	1.11	4.32	2.23	5.39	3.49	0.78	67.00	13.00	24.00
646A	9.40	2.16	0.48	0.65	0.79	0.75	0.97	0.59	0.68	0.07
0.0	0.26	1.08	4.82	2.33	5.74	3.61	0.85	63.00	13.00	22.00
647A	8.60	2.10	0.45	0.60	0.70	0.64	0.93	0.60	0.57	0.05
0.0	0.27	1.10	4.41	2.01	5.51	3.48	0.76	65.00	13.00	23.00
648A	8.40	1.98	0.40	0.58	0.72	0.63	0.96	0.58	0.63	0.07
0.0	0.23	1.03	4.40	1.84	5.34	3.49	0.71	61.00	13.00	22.00
649A	7.50	1.72	0.40	0.44	0.62	0.57	0.85	0.47	0.54	0.01
0.0	0.18	0.97	3.84	1.79	4.94	3.36	0.53	65.00	13.00	22.00
650A	8.40	1.93	0.45	0.55	0.75	0.63	0.88	0.51	0.59	0.10
0.0	0.38	1.11	4.23	2.07	5.17	3.32	0.76	61.00	12.00	23.00

APPENDIX TABLE 19. Alberta control *Rhinichthys cataractae*; Raw character values, n = 50.

```
ALBERTA CONTROL   RHINICHTHYS CATARACTAE   N 50
 401A      7.50    1.73    0.25    0.69    0.55    0.54    0.75    0.40    0.62    0.17
    0.37   0.71    1.01    3.78    1.92    4.45    2.84    0.52   70.00   12.00   27.00
 402A      7.00    1.68    0.24    0.68    0.55    0.57    0.75    0.38    0.62    0.17
    0.41   0.58    0.92    3.46    1.89    4.15    2.55    0.45   67.00   11.00   28.00
 403A      6.70    1.68    0.24    0.63    0.51    0.56    0.68    0.35    0.57    0.18
    0.37   0.57    1.02    3.41    1.69    4.29    2.82    0.43   68.00   12.00   27.00
 404A      6.00    1.46    0.23    0.52    0.47    0.45    0.61    0.32    0.50    0.12
    0.30   0.57    0.83    3.09    1.43    3.61    2.24    0.35   74.00   10.00   26.00
 405A      5.50    1.35    0.21    0.49    0.44    0.45    0.62    0.29    0.46    0.12
    0.28   0.52    0.77    2.85    1.48    3.36    2.20    0.30   67.00    9.00   27.00
 409A      8.50    2.30    0.32    1.00    0.69    0.71    0.96    0.48    0.88    0.29
    0.57   0.84    1.27    4.48    2.05    5.24    3.44    0.78   67.00   11.00   31.00
 410A      7.50    2.05    0.24    0.83    0.58    0.56    0.81    0.43    0.76    0.28
    0.51   0.68    1.00    4.01    1.76    4.78    3.09    0.69   69.00   13.00   29.00
 411A      8.10    2.04    0.29    0.87    0.63    0.63    0.87    0.47    0.83    0.26
    0.50   0.81    1.16    4.28    1.90    5.02    3.15    0.76   71.00   12.00   28.00
 412A      7.10    1.89    0.28    0.77    0.54    0.61    0.79    0.37    0.69    0.22
    0.45   0.72    1.00    3.74    1.84    4.34    2.73    0.65   73.00   11.00   32.00
 415A      8.60    2.23    0.29    0.94    0.65    0.66    0.90    0.50    0.85    0.30
    0.52   0.86    1.22    4.39    2.10    5.51    3.63    0.66   70.00   10.00   33.00
 416A      7.40    2.06    0.25    0.81    0.55    0.59    0.80    0.44    0.71    0.26
    0.47   0.77    1.00    3.90    1.85    4.58    2.81    0.69   73.00   11.00   31.00
 417A      6.20    1.54    0.26    0.56    0.47    0.49    0.65    0.32    0.54    0.18
    0.36   0.59    0.92    3.19    1.54    3.89    2.49    0.45   67.00   11.00   27.00
 419A      6.30    1.53    0.26    0.59    0.47    0.52    0.74    0.37    0.60    0.13
    0.41   6.67    0.89    3.26    1.53    4.02    2.56    0.41   70.00   13.00   33.00
 426A      6.00    1.44    0.22    0.51    0.45    0.47    0.63    0.35    0.50    0.11
    0.27   0.64    0.99    3.07    1.49    3.57    2.42    0.40   74.00   12.00   30.00
 427A      5.80    1.39    0.20    0.50    0.41    0.45    0.59    0.32    0.53    0.12
    0.30   0.59    0.85    3.14    1.35    3.64    2.42    0.39   73.00   12.00   25.00
 428A      5.00    1.29    0.20    0.46    0.39    0.36    0.52    0.26    0.42    0.10
    0.25   0.50    0.61    2.56    1.29    2.85    1.62    0.36   66.00   11.00   30.00
 429A      4.00    1.21    0.18    0.41    0.37    0.36    0.50    0.26    0.40    0.08
    0.20   0.46    0.72    2.53    1.11    2.94    1.88    0.31   65.00   12.00   30.00
 431A      4.50    1.12    0.19    0.39    0.34    0.35    0.45    0.25    0.36    0.07
    0.19   0.43    0.62    2.56    1.00    2.82    1.66    0.24   63.00   10.00   26.00
 441A      6.10    1.68    0.22    0.63    0.50    0.50    0.67    0.35    0.54    0.17
    0.39   0.55    0.84    3.30    1.38    3.69    2.32    0.42   64.00   13.00   31.00
 443A      5.60    1.41    0.22    0.52    0.46    0.41    0.60    0.26    0.46    0.16
    0.28   0.53    0.78    2.89    1.42    3.36    2.15    0.36   67.00   12.00   28.00
 444A      5.60    1.40    0.21    0.48    0.43    0.42    0.58    0.29    0.47    0.12
    0.27   0.45    0.81    2.91    1.34    3.52    2.27    0.36   64.00   12.00   28.00
 446A      5.00    1.40    0.23    0.47    0.44    0.42    0.48    0.29    0.44    0.12
    0.25   0.49    0.72    2.78    1.26    3.09    1.88    0.32   72.00   13.00   25.00
 433A      7.10    1.79    0.29    0.72    0.61    0.61    0.85    0.38    0.69    0.18
    0.42   0.79    1.19    3.66    1.76    4.65    2.92    0.60   63.00   13.00   29.00
 434A      6.00    1.50    0.26    0.55    0.42    0.50    0.59    0.36    0.56    0.17
    0.28   0.64    0.99    3.16    1.52    3.74    2.45    0.46   70.00   11.00   26.00
 435A      6.80    1.75    0.26    0.64    0.51    0.55    0.73    0.36    0.59    0.19
    0.40   0.63    1.03    3.53    1.72    4.30    2.81    0.49   63.00   14.00   26.00
 436A      6.40    1.69    0.26    0.63    0.48    0.50    0.67    0.34    0.50    0.17
    0.42   0.70    0.83    3.31    1.62    4.11    2.57    0.51   66.00   13.00   29.00
 440A      6.00    1.51    0.25    0.56    0.46    0.50    0.63    0.34    0.52    0.16
    0.30   0.55    0.82    3.09    1.52    3.80    2.44    0.52   64.00   10.00   27.00
 449A      8.90    2.19    0.32    0.97    0.66    0.78    1.04    0.49    0.81    0.28
    0.42   0.88    1.38    4.80    2.23    5.44    3.56    0.63   71.00   10.00   26.00
 450A      8.50    1.90    0.27    0.80    0.58    0.69    0.91    0.45    0.68    0.22
    0.38   0.77    1.27    4.38    2.31    5.28    3.56    0.69   72.00   12.00   29.00
 451A      8.30    2.03    0.29    0.80    0.60    0.67    1.06    0.44    0.72    0.26
    0.45   0.79    1.28    4.48    2.11    5.20    3.46    0.66   66.00   11.00   28.00
 452A      8.50    1.98    0.30    0.76    0.58    0.61    0.99    0.43    0.73    0.25
    0.37   0.80    1.17    4.35    2.36    5.12    3.32    0.70   64.00   10.00   30.00
 453A      8.20    1.86    0.30    0.78    0.60    0.68    0.90    0.45    0.72    0.21
    0.39   0.75    1.09    4.29    2.21    5.05    3.35    0.57   65.00   11.00   27.00
 454A      8.20    1.93    0.29    0.79    0.59    0.65    0.92    0.46    0.68    0.23
    0.38   0.76    1.28    4.37    2.07    5.15    3.44    0.54   68.00   11.00   28.00
 455A      8.00    1.92    0.29    0.80    0.61    0.60    0.97    0.45    0.73    0.25
    0.40   6.83    1.18    4.17    2.04    4.91    3.20    0.68   69.00   12.00   29.00
 456A      8.90    2.12    0.33    0.84    0.64    0.72    1.11    0.52    0.81    0.24
    0.45   0.76    1.27    4.68    2.10    5.70    3.88    0.53   69.00   13.00   30.00
 457A      8.70    2.20    0.28    0.86    0.65    0.77    1.10    0.50    0.81    0.29
    0.45   0.84    1.27    4.65    2.33    5.40    3.47    0.61   67.00   12.00   31.00
 458A      8.20    1.95    0.30    0.78    0.65    0.66    0.95    0.48    0.70    0.23
    0.39   0.76    1.27    4.40    2.04    5.18    3.47    0.55   70.00   11.00   28.00
 459A      7.70    2.00    0.28    0.80    0.60    0.66    0.97    0.44    0.68    0.21
    0.44   0.67    1.13    4.16    1.97    4.93    3.23    0.40   68.00   12.00   30.00
 460A      8.10    1.90    0.27    0.77    0.62    0.70    1.00    0.45    0.73    0.22
    0.40   0.75    1.19    4.23    2.12    5.04    3.34    0.48   72.00   13.00   29.00
 461A      7.50    1.77    0.27    0.68    0.56    0.55    0.91    0.42    0.68    0.20
    0.35   0.71    1.09    4.00    1.95    4.70    3.05    0.46   68.00   11.00   30.00
 462A      7.40    1.79    0.28    0.68    0.57    0.59    0.86    0.43    0.62    0.19
    0.37   0.63    0.98    4.01    1.88    4.81    3.15    0.42   73.00   12.00   30.00
 463A      8.10    2.06    0.28    0.93    0.58    0.65    1.10    0.47    0.82    0.26
    0.46   0.83    1.14    4.16    2.19    4.92    3.16    0.82   69.00   12.00   26.00
 464A      7.80    2.00    0.27    0.88    0.58    0.61    1.00    0.48    0.77    0.27
    0.46   0.77    1.04    4.02    2.14    4.81    2.95    0.77   63.00   14.00   28.00
 465A      7.40    1.90    0.26    0.82    0.55    0.53    0.84    0.38    0.63    0.23
    0.42   0.68    0.95    3.98    1.80    4.60    2.96    0.56   68.00   11.00   28.00
 466A      7.40    1.89    0.26    0.83    0.55    0.53    0.87    0.40    0.69    0.22
    0.41   0.77    1.00    4.10    1.72    4.59    2.96    0.66   64.00   10.00   27.00
 467A      7.10    1.81    0.24    0.75    0.53    0.55    0.79    0.38    0.65    0.20
    0.34   0.69    0.86    3.64    1.81    4.72    2.59    0.65   60.00   10.00   25.00
 468A      7.00    1.80    0.25    0.72    0.51    0.51    0.80    0.42    0.62    0.19
    0.31   0.68    0.81    3.55    1.76    4.52    2.58    0.65   62.00   11.00   27.00
 469A      7.20    1.79    0.26    0.78    0.54    0.53    0.86    0.40    0.66    0.24
    0.33   0.80    0.99    3.66    1.84    4.54    2.73    0.64   60.00   12.00   27.00
 470A      7.80    1.97    0.26    0.84    0.56    0.58    0.96    0.45    0.69    0.25
    0.35   0.73    0.90    4.07    2.04    5.12    3.02    0.76   68.00   10.00   28.00
 471A      9.50    2.26    0.32    0.95    0.68    0.82    1.13    0.51    0.80    0.27
    0.42   0.98    1.24    4.93    2.30    5.93    3.60    0.80   69.00   12.00   30.00
```

APPENDIX TABLE 20. Kananaskis typical *Couesius plumbeus*; Raw character values, n = 50.

```
KANANASKIS   APPARANT COUESIUS PLUMBEUS
601          16.20    2.31    0.49    0.67    0.82    0.78    1.18    0.64    0.86    0.05
      0.0     0.25    1.62    4.95    2.48    6.57    4.52    0.72   65.00   14.00   24.00
602          12.10    2.57    0.58    0.75    0.92    0.89    1.32    0.75    0.88    0.11
      0.0     0.22    1.78    6.10    2.72    7.63    5.31    0.85   68.00   14.00   25.00
603          12.30    2.69    0.60    0.79    1.05    1.02    1.58    0.70    1.00    0.07
      0.0     0.26    1.75    6.26    2.75    8.15    5.72    0.84   61.00   13.00   22.00
604          11.50    2.48    0.55    0.76    0.91    0.87    1.26    0.71    0.94    0.06
      0.0     0.22    1.55    5.38    2.88    7.27    4.97    0.90   60.00   15.00   27.00
605          10.00    2.21    0.50    0.61    0.83    0.77    1.10    0.58    0.78    0.05
      0.0     0.32    1.46    5.16    2.33    6.38    4.40    0.71   65.00   15.00   26.00
606          10.60    2.35    0.51    0.72    0.85    0.79    1.20    0.69    0.83    0.04
      0.0     0.26    1.38    5.25    2.40    6.74    4.47    0.78   61.00   13.00   24.00
607           9.80    1.97    0.50    0.60    0.79    0.71    1.07    0.55    0.70    0.05
      0.0     0.12    1.21    4.73    2.28    5.86    3.90    0.77   70.00   13.00   27.00
608           9.50    2.06    0.52    0.60    0.78    0.75    1.13    0.54    0.76    0.03
      0.0     0.28    1.27    4.85    2.11    6.08    4.20    0.71   63.00   14.00   24.00
609           8.70    2.02    0.48    0.58    0.73    0.62    1.07    0.53    0.70    0.05
      0.0     0.19    1.20    4.32    1.97    5.42    3.52    0.62   64.00   14.00   24.00
610           8.20    1.85    0.46    0.57    0.65    0.60    1.04    0.49    0.69    0.03
      0.0     0.22    1.10    4.12    1.92    5.10    3.27    0.65   68.00   15.00   26.00
611           9.60    2.15    0.52    0.61    0.78    0.67    1.11    0.55    0.71    0.04
      0.0     0.20    1.26    4.93    2.20    6.11    4.14    0.71   62.00   14.00   21.00
612           7.40    1.68    0.44    0.48    0.64    0.47    0.92    0.49    0.58    0.03
      0.0     0.17    0.99    3.74    1.70    4.69    3.16    0.54   62.00   12.00   22.00
613           7.00    1.72    0.43    0.49    0.62    0.55    0.88    0.45    0.52    0.04
      0.0     0.17    0.91    3.59    1.84    4.42    2.78    0.50   60.00   13.00   25.00
614           6.60    1.55    0.40    0.43    0.58    0.47    0.75    0.44    0.48    0.02
      0.0     0.15    0.92    3.27    1.56    4.26    2.86    0.54   62.00   13.00   23.00
615           6.90    1.59    0.41    0.44    0.60    0.56    0.78    0.48    0.50    0.05
      0.0     0.20    1.03    3.46    1.84    4.47    3.01    0.63   61.00   11.00   22.00
616           7.10    1.66    0.40    0.49    0.64    0.57    0.79    0.43    0.52    0.05
      0.0     0.22    0.94    3.52    1.78    4.47    2.87    0.54   65.00   14.00   24.00
617           7.00    1.60    0.36    0.46    0.63    0.44    0.75    0.42    0.49    0.05
      0.0     0.17    0.97    3.45    1.80    4.32    2.80    0.57   61.00   13.00   24.00
618           5.30    1.32    0.32    0.32    0.46    0.31    0.60    0.37    0.35    0.01
      0.0     0.11    0.60    2.70    1.35    3.33    2.18    0.37   66.00   14.00   23.00
619           6.00    1.47    0.38    0.43    0.50    0.49    0.64    0.40    0.49    0.0
      0.0     0.25    0.86    3.09    1.44    3.75    2.35    0.51   60.00   13.00   23.00
620          10.00    2.19    0.50    0.67    0.80    0.71    1.08    0.59    0.74    0.10
      0.0     0.24    1.32    4.95    2.49    6.19    4.22    0.74   63.00   13.00   22.00
621           9.80    2.23    0.48    0.67    0.80    0.72    1.09    0.66    0.76    0.11
      0.0     0.17    1.23    5.00    2.53    6.53    4.61    0.61   69.00   15.00   26.00
622          11.00    2.44    0.53    0.76    0.97    0.76    1.31    0.71    0.93    0.10
      0.0     0.22    1.57    5.38    2.52    7.03    4.95    1.00   62.00   13.00   24.00
623          11.00    2.53    0.52    0.84    0.82    0.92    1.26    0.72    0.99    0.07
      0.0     0.27    1.48    5.60    2.55    7.76    4.77    0.90   66.00   15.00   27.00
624           8.50    1.93    0.44    0.58    0.72    0.62    1.00    0.54    0.64    0.06
      0.0     0.16    1.15    4.44    2.38    5.38    3.63    0.60   66.00   13.00   25.00
625           8.20    1.93    0.46    0.59    0.68    0.56    1.01    0.53    0.60    0.08
      0.0     0.17    1.24    4.40    2.04    5.32    3.56    0.62   64.00   13.00   25.00
626           6.40    1.54    0.37    0.43    0.50    0.42    0.73    0.40    0.47    0.05
      0.0     0.21    0.75    3.41    1.53    4.23    2.78    0.50   64.00   13.00   24.00
627           9.20    2.10    0.46    0.56    0.78    0.65    1.08    0.50    0.72    0.08
      0.0     0.15    1.32    5.01    2.07    6.05    4.39    0.65   66.00   13.00   22.00
628           7.70    1.80    0.44    0.55    0.74    0.69    1.00    0.46    0.64    0.07
      0.0     0.25    1.30    3.59    2.12    4.82    3.43    0.51   63.00   13.00   23.00
629           7.70    1.76    0.40    0.55    0.67    0.59    0.93    0.46    0.65    0.07
      0.0     0.25    1.26    3.92    1.94    4.96    3.38    0.61   63.00   14.00   23.00
630     [illegible]   1.72 [illegible] 0.51   0.64    0.55    0.85    0.46    0.55    0.07
      0.0 [illegible] 1.18    4.93    1.92    4.83    3.34    0.70   66.00   13.00   24.00
631     [illegible] [illegible] 0.40 [illegible] 0.63  0.46    0.46    0.42    0.52    0.08
      0.0     0.17    0.69    3.44    1.76    4.14    2.66    0.47   64.00   14.00   21.00
632           6.30    2.00    0.43    0.55    0.76    0.69    0.96    0.53    0.65    0.09
      0.0     0.18    1.18    4.31    2.00    5.34    3.56    0.66   67.00   14.00   23.00
633          10.80    2.25    0.47    0.70    0.87    0.75    1.14    0.62    0.79    0.09
      0.0     0.34    1.72    5.49    2.86    6.39    4.30    0.94   67.00   13.00   25.00
634           7.70    1.80    0.45    0.56    0.71    0.69    1.00    0.47    0.68    0.07
      0.0     0.21    1.15    3.94    2.07    4.87    3.33    0.65   63.00   14.00   24.00
635           7.00    1.80    0.43    0.51    0.66    0.50    0.90    0.50    0.60    0.05
      0.0     0.14    1.17    3.93    1.73    4.97    3.43    0.51   63.00   14.00   23.00
636           7.60    1.77    0.42    0.54    0.60    0.55    0.84    0.45    0.62    0.09
      0.0     0.16    1.09    3.86    1.93    4.80    3.29    0.62   61.00   12.00   21.00
637           5.90    1.26    0.31    0.38    0.43    0.43    0.65    0.37    0.41    0.01
      0.0     0.12    0.72    2.87    1.24    3.43    2.21    0.55   69.00   13.00   23.00
638           4.70    1.15    0.30    0.27    0.41    0.39    0.60    0.33    0.38    0.0
      0.0     0.15    0.68    2.50    1.22    3.05    1.93    0.37   62.00   14.00   25.00
639          11.50    2.51    0.54    0.69    0.90    0.87    1.32    0.60    0.89    0.06
      0.0     0.26    1.50    5.80    2.07    7.52    5.36    0.80   62.00   13.00   22.00
640          10.00    2.22    0.48    0.70    0.79    0.87    1.15    0.55    0.87    0.10
      0.0     0.37    1.39    5.24    2.22    6.51    4.39    0.67   61.00   15.00   23.00
641           5.40    1.35    0.34    0.33    0.40    0.38    0.64    0.36    0.32    0.0
      0.0     0.15    0.59    2.62    1.36    3.35    2.14    0.40   62.00   14.00   23.00
642           5.80    1.42    0.35    0.39    0.45    0.43    0.67    0.39    0.40    0.01
      0.0     0.19    0.68    2.89    1.42    3.64    2.27    0.48   60.00   12.00   22.00
643           6.00    1.45    0.34    0.40    0.51    0.50    0.68    0.38    0.46    0.02
      0.0     0.23    0.73    3.13    1.43    3.85    2.63    0.47   69.00   12.00   22.00
644           6.50    1.51    0.38    0.48    0.54    0.48    0.77    0.43    0.48    0.05
      0.0     0.24    0.85    3.24    1.62    4.12    2.64    0.54   64.00   15.00   21.00
645           6.30    1.54    0.39    0.45    0.50    0.48    0.68    0.42    0.45    0.03
      0.0     0.21    0.85    3.21    1.43    4.08    2.66    0.48   60.00   16.00   24.00
646           6.50    1.55    0.41    0.45    0.56    0.52    0.79    0.40    0.53    0.04
      0.0     0.13    0.90    3.38    1.50    4.60    2.65    0.55   60.00   12.00   25.00
647           7.10    1.70    0.42    0.47    0.58    0.54    0.82    0.47    0.54    0.05
      0.0     0.19    0.91    3.61    1.93    4.35    2.82    0.57   63.00   14.00   24.00
648           5.40    1.22    0.32    0.34    0.44    0.42    0.62    0.35    0.41    0.02
      0.0     0.15    0.67    2.73    1.28    3.26    2.06    0.38   65.00   15.00   24.00
649           4.40    1.03    0.31    0.25    0.39    0.35    0.54    0.29    0.35    0.0
      0.0     0.16    0.62    2.24    1.05    2.81    1.80    0.34   64.00   13.00   23.00
650           6.80    1.53    0.42    0.46    0.58    0.56    0.83    0.48    0.52    0.05
      0.0     0.28    0.99    3.43    1.81    4.20    2.87    0.57   65.00   12.00   23.00
```

APPENDIX TABLE 21. Kananaskis typical *Rhinichthys cataractae;* Raw character values, n = 50.

```
KANANASKIS  APPARANT RHINICHTHYS CATARACTAE
401         10.[illegible] [illegible] [illegible] 1.91 [illegible] [illegible] [illegible]
      0.52   0.66   1.62   5.30   2.52   6.59   4.10   0.59  67.00  11.00  27.00
402          9.70   2.41   0.37   1.00   0.79   1.10   1.31   0.81   0.97   0.27
      0.46   0.74   1.40   5.00   2.27   6.61   4.04   0.75  59.00  12.00  28.00
403          8.70   2.24   0.31   0.94   0.70   0.89   1.26   0.75   0.87   0.31
      0.48   0.88   1.52   4.62   2.01   5.96   3.94   0.58  64.00  12.00  29.00
404         10.70   2.61   0.35   1.11   0.81   1.08   1.47   0.96   1.05   0.37
      0.57   0.90   1.60   5.71   2.49   7.15   4.53   0.71  67.00  12.00  31.00
405          9.80   2.25   0.34   0.91   0.76   0.93   1.36   0.81   0.94   0.32
      0.50   0.90   1.64   4.88   2.48   6.33   4.29   0.54  69.00  13.00  27.00
406          9.60   2.26   0.31   0.92   0.71   0.85   1.19   0.79   0.93   0.26
      0.46   0.73   1.52   5.03   2.36   6.36   4.18   0.54  65.00  12.00  31.00
407          9.60   2.18   0.33   0.97   0.73   0.94   1.32   0.82   0.96   0.29
      0.50   0.87   1.65   5.00   2.30   6.35   4.38   0.61  71.00  11.00  30.00
408         10.00   2.30   0.31   0.97   0.71   0.85   1.20   0.83   0.94   0.28
      0.56   0.87   1.61   5.10   2.41   6.53   4.39   0.79  67.00  12.00  32.00
409         11.20   2.49   0.36   1.10   0.90   1.02   1.40   0.82   1.03   0.26
      0.51   0.88   1.67   5.76   2.84   7.05   4.53   0.85  69.00  13.00  31.00
410          8.90   2.10   0.28   0.83   0.70   0.91   1.31   0.66   0.93   0.17
      0.50   0.78   1.27   4.78   2.28   5.92   3.66   0.59  66.00  12.00  30.00
411          9.40   2.19   0.29   0.97   0.68   1.02   1.32   0.79   0.93   0.25
      0.54   0.79   1.54   4.85   2.39   6.07   3.96   0.72  65.00  11.00  28.00
412         10.90   2.44   0.35   1.02   0.86   0.96   1.28   0.80   0.99   0.27
      0.49   0.82   1.46   5.60   2.65   6.99   4.55   0.72  68.00  12.00  27.00
413          9.60   2.51   0.35   1.06   0.80   0.91   1.32   0.88   0.89   0.32
      0.62   0.91   1.37   5.14   2.47   6.39   3.98   0.64  70.00  12.00  32.00
414         10.00   2.43   0.31   1.01   0.75   0.92   1.26   0.89   0.98   0.36
      0.46   0.87   1.40   5.33   2.50   6.75   4.29   0.53  62.00  12.00  29.00
415          9.70   2.33   0.31   0.98   0.70   0.88   1.17   0.79   0.88   0.26
      0.45   0.74   1.47   5.10   2.38   6.33   4.00   0.58  70.00  13.00  28.00
416          7.20   1.76   0.30   0.72   0.55   0.74   0.97   0.50   0.70   0.17
      0.31   0.67   1.13   3.65   1.90   4.72   2.93   0.51  64.00  13.00  29.00
417          5.80   1.57   0.21   0.64   0.48   0.55   0.71   0.40   0.56   0.20
      0.29   0.47   0.75   3.00   1.40   3.59   2.01   0.45  63.00  14.00  28.00
418          6.30   1.68   0.26   0.64   0.48   0.52   0.82   0.40   0.66   0.17
      0.30   0.57   0.94   3.22   1.57   4.21   2.66   0.52  61.00  12.00  27.00
419          5.30   1.47   0.19   0.58   0.44   0.52   0.65   0.43   0.51   0.12
      0.23   0.46   0.72   2.86   1.26   3.40   2.01   0.39  60.00  13.00  26.00
420          7.50   1.82   0.27   0.75   0.57   0.71   0.98   0.48   0.74   0.27
      0.34   0.65   1.09   4.05   1.97   5.14   3.16   0.56  67.00  11.00  25.00
421          8.50   2.12   0.31   0.88   0.63   0.87   1.26   0.46   0.66   0.27
      0.43   0.89   1.47   4.41   2.05   5.53   3.52   0.49  62.00  11.00  31.00
422          9.00   2.09   0.33   0.89   0.71   0.95   1.28   0.51   0.93   0.31
      0.48   0.92   1.43   4.93   2.17   5.95   3.85   0.48  63.00  10.00  30.00
423          7.90   1.95   0.28   0.82   0.61   0.75   1.15   0.38   0.79   0.28
      0.39   0.72   1.25   4.11   1.94   5.30   3.39   0.48  71.00  11.00  26.00
424         10.20   2.47   0.36   1.08   0.84   0.92   1.31   0.60   1.01   0.32
      0.50   0.85   1.51   5.27   2.50   6.51   4.12   0.54  69.00  11.00  26.00
425          9.60   2.41   0.37   1.00   0.78   1.04   1.29   0.57   0.97   0.32
      0.45   0.82   1.38   5.09   2.24   6.57   4.33   0.67  61.00  12.00  27.00
426          7.80   1.93   0.29   0.74   0.59   0.68   1.06   0.48   0.80   0.23
      0.41   0.66   1.26   4.14   2.02   5.18   3.35   0.57  67.00  11.00  29.00
427          7.10   1.64   0.27   0.61   0.51   0.61   0.95   0.42   0.67   0.15
      0.33   0.65   1.22   3.77   1.74   4.70   3.13   0.38  66.00  10.00  26.00
428          9.20   2.23   0.32   0.89   0.69   0.88   1.23   0.66   0.90   0.25
      0.47   0.77   1.38   4.87   2.19   6.28   4.03   0.69  69.00  13.00  27.00
429          5.40   1.41   0.24   0.53   0.42   0.46   0.67   0.35   0.51   0.12
      0.27   0.50   0.73   2.93   1.29   3.49   2.00   0.41  65.00  12.00  31.00
430          5.40   1.43   0.22   0.53   0.41   0.44   0.66   0.33   0.56   0.12
      0.29   0.48   0.75   2.83   1.31   3.50   2.13   0.47  72.00  12.00  29.00
431          5.20   1.44   0.21   0.54   0.41   0.47   0.72   0.31   0.56   0.16
      0.28   0.59   0.82   2.89   1.17   3.55   2.07   0.34  72.00  12.00  26.00
432          5.50   1.50   0.24   0.52   0.43   0.46   0.63   0.35   0.50   0.12
      0.27   0.51   0.73   2.81   1.48   3.40   2.10   0.36  63.00  13.00  30.00
433          5.60   1.44   0.21   0.53   0.40   0.44   0.64   0.30   0.48   0.14
      0.27   0.40   0.74   2.94   1.41   3.58   2.19   0.41  68.00  13.00  27.00
434          5.40   1.45   0.18   0.50   0.43   0.46   0.69   0.31   0.52   0.13
      0.28   0.38   0.75   2.90   1.27   3.46   2.23   0.39  70.00  14.00  29.00
435          5.70   1.54   0.28   0.55   0.47   0.42   0.75   0.33   0.52   0.13
      0.23   0.38   0.75   3.04   1.39   3.76   2.27   0.28  62.00  14.00  27.00
436          4.70   1.27   0.22   0.42   0.40   0.42   0.61   0.29   0.43   0.09
      0.23   0.41   0.71   2.50   1.18   2.92   1.89   0.25  67.00  13.00  27.00
437          5.10   1.35   0.20   0.47   0.43   0.41   0.63   0.28   0.45   0.14
      0.26   0.44   0.70   2.65   1.22   3.17   1.96   0.36  69.00  12.00  32.00
438          8.50   2.03   0.32   0.82   0.60   0.78   1.10   0.51   0.77   0.24
      0.43   0.68   1.30   4.60   2.14   5.79   3.80   0.69  63.00  11.00  31.00
439         10.20   2.45   0.33   1.04   0.77   1.01   1.34   0.63   1.05   0.28
      0.51   0.80   1.50   5.41   2.28   6.66   4.25   0.65  68.00  11.00  31.00
440          7.00   1.66   0.26   0.55   0.52   0.59   0.91   0.40   0.65   0.16
      0.30   0.65   1.11   3.76   1.75   4.53   2.96   0.37  69.00  12.00  29.00
441          7.10   1.79   0.29   0.67   0.59   0.62   0.85   0.42   0.67   0.18
      0.32   0.08   1.05   3.54   1.79   4.42   2.65   0.48  63.00  11.00  26.00
442          7.10   1.78   0.31   0.72   0.52   0.62   0.91   0.42   0.67   0.22
      0.35   0.72   1.02   3.72   1.64   4.46   2.69   0.46  72.00  13.00  29.00
443          5.80   1.51   0.22   0.54   0.42   0.53   0.66   0.35   0.52   0.16
      0.28   0.52   0.77   2.98   1.45   3.56   2.17   0.46  68.00  12.00  31.00
444          5.50   1.40   0.20   0.52   0.42   0.48   0.56   0.32   0.49   0.15
      0.25   0.49   0.72   2.85   1.38   3.35   1.90   0.44  62.00  12.00  28.00
445          6.00   1.62   0.26   0.61   0.44   0.51   0.68   0.37   0.51   0.16
      0.28   0.53   0.76   3.20   1.39   3.95   2.51   0.49  62.00  12.00  27.00
446          7.00   1.66   0.25   0.68   0.50   0.65   0.91   0.44   0.71   0.20
      0.40   0.67   1.00   3.52   1.78   4.49   2.48   0.47  68.00  12.00  28.00
447          5.50   1.42   0.19   0.55   0.41   0.45   0.61   0.30   0.48   0.14
      0.24   0.50   0.76   2.86   1.34   3.38   2.93   0.44  64.00  11.00  29.00
448          5.60   1.45   0.23   0.47   0.48   0.47   0.58   0.35   0.51   0.12
      0.26   0.46   0.68   2.86   1.41   3.42   2.11   0.41  69.00  11.00  30.00
449          5.70   1.46   0.22   0.54   0.43   0.48   0.67   0.35   0.52   0.12
      0.24   0.48   0.75   2.97   1.39   3.50   2.22   0.45  67.00  12.00  29.00
450          5.00   1.31   0.19   0.46   0.40   0.42   0.61   0.32   0.47   0.09
      0.21   0.51   0.69   2.72   1.22   3.21   1.91   0.38  66.00  12.00  27.00
```

APPENDIX TABLE 22. Kananaskis suspected hybrids *Couesius plumbeus* x *Rhinichthys cataractae*; Raw character values, n = 37.

KANANASKIS SUSPECTED HYBRIDS COUESIUS PLUMBEUS X RHINICHTHYS CATARACTAE (1977)

501	7.60	1.72	0.43	0.46	0.61	0.71	1.00	0.52	0.69	0.0
0.21	0.40	1.08	4.00	1.89	4.69	2.85	0.63	60.00	13.00	22.00
502	7.10	1.69	0.32	0.55	0.62	0.60	0.79	0.46	0.52	0.0
0.03	0.35	0.83	3.68	1.81	4.61	3.00	0.60	69.00	14.00	25.00
503	6.30	1.63	0.29	0.54	0.51	0.50	0.72	0.36	0.51	0.09
0.22	0.41	0.80	3.26	1.44	4.16	2.63	0.48	68.00	13.00	25.00
504	6.20	1.58	0.31	0.51	0.48	0.52	0.69	0.41	0.50	0.03
0.08	0.32	0.82	3.19	1.55	3.86	2.52	0.49	67.00	13.00	24.00
505	8.10	1.70	0.43	0.51	0.64	0.57	0.85	0.47	0.54	0.10
0.04	0.31	1.05	4.04	2.17	4.95	3.28	0.51	66.00	14.00	23.00
506	7.10	1.52	0.39	0.45	0.59	0.54	0.77	0.42	0.55	0.03
0.21	0.38	1.10	3.63	1.79	4.56	3.19	0.50	70.00	14.00	25.00
507	7.60	1.82	0.33	0.64	0.66	0.68	0.89	0.47	0.65	0.11
0.17	0.35	1.02	3.88	1.87	4.87	3.23	0.49	69.00	14.00	26.00
508	6.60	1.66	0.29	0.53	0.58	0.58	0.78	0.40	0.55	0.08
0.0	0.31	0.81	3.43	1.38	4.05	2.67	0.52	67.00	15.00	27.00
509	6.20	1.52	0.33	0.43	0.53	0.52	0.73	0.38	0.48	0.02
0.18	0.22	0.86	3.15	1.50	3.92	2.48	0.39	70.00	13.00	26.00
510	6.10	1.48	0.25	0.50	0.52	0.46	0.67	0.39	0.47	0.07
0.16	0.24	0.81	2.97	1.48	3.79	2.37	0.40	69.00	14.00	26.00
511	5.80	1.29	0.28	0.45	0.45	0.51	0.61	0.30	0.46	0.05
0.20	0.29	0.94	2.73	1.23	3.44	2.28	0.38	67.00	13.00	29.00
512	5.70	1.30	0.24	0.40	0.48	0.42	0.63	0.33	0.45	0.05
0.17	0.27	0.67	2.78	1.19	3.34	2.17	0.42	73.00	16.00	28.00
513	5.80	1.44	0.26	0.48	0.49	0.45	0.67	0.35	0.48	0.07
0.16	0.36	0.81	2.98	1.39	3.58	2.35	0.43	69.00	15.00	26.00
514	4.80	1.17	0.25	0.40	0.40	0.37	0.54	0.26	0.36	0.03
0.15	0.22	0.57	2.38	1.19	3.00	1.93	0.35	69.00	14.00	23.00
515	5.60	1.35	0.25	0.44	0.45	0.47	0.65	0.32	0.47	0.06
0.18	0.33	0.72	2.95	1.36	3.51	2.31	0.47	70.00	14.00	28.00
516	4.90	1.22	0.34	0.33	0.44	0.42	0.72	0.25	0.40	0.03
0.0	0.22	0.74	2.49	1.07	3.00	2.00	0.39	68.00	15.00	24.00
517	5.60	1.26	0.34	0.35	0.43	0.46	0.58	0.29	0.40	0.0
0.24	0.14	0.70	2.83	1.30	3.50	2.27	0.36	62.00	13.00	26.00
518	5.60	1.39	0.24	0.52	0.40	0.49	0.69	0.34	0.45	0.10
0.12	0.32	0.68	2.86	1.31	3.61	2.24	0.45	70.00	13.00	27.00
519	5.20	1.23	0.26	0.34	0.42	0.40	0.58	0.26	0.38	0.0
0.06	0.20	0.69	2.59	1.27	3.20	2.20	0.40	60.00	13.00	25.00
520	6.70	1.60	0.41	0.45	0.54	0.48	0.80	0.38	0.50	0.0
0.20	0.27	0.87	3.53	1.52	4.15	2.73	0.52	62.00	14.00	27.00
521	6.70	1.69	0.33	0.56	0.58	0.56	0.82	0.43	0.58	0.07
0.15	0.39	0.84	3.57	1.45	4.45	2.78	0.52	67.00	13.00	25.00
522	5.80	1.41	0.23	0.43	0.48	0.45	0.69	0.32	0.44	0.06
0.18	0.26	0.76	2.93	1.44	3.58	2.23	0.45	61.00	15.00	28.00
523	6.10	1.43	0.25	0.43	0.54	0.47	0.71	0.38	0.53	0.04
0.13	0.32	0.82	3.00	1.50	3.88	2.53	0.45	62.00	14.00	27.00
524	5.60	1.35	0.33	0.36	0.48	0.44	0.68	0.29	0.42	0.0
0.02	0.15	0.71	2.85	1.40	3.56	2.26	0.36	60.00	13.00	23.00
525	6.00	1.42	0.36	0.40	0.51	0.49	0.70	0.32	0.48	0.0
0.10	0.21	0.77	3.07	1.49	3.87	2.46	0.38	71.00	15.00	27.00
526	4.40	1.20	0.23	0.26	0.38	0.33	0.50	0.29	0.35	0.0
0.0	0.23	0.57	2.27	1.01	2.81	1.73	0.37	64.00	12.00	24.00
527	3.40	0.90	0.24	0.22	0.31	0.28	0.40	0.23	0.26	0.01
0.02	0.10	0.44	1.80	0.75	2.19	1.35	0.21	63.00	14.00	23.00
528	7.20	1.76	0.31	0.55	0.47	0.58	0.79	0.41	0.60	0.06
0.16	0.20	0.80	3.57	1.85	4.49	2.86	0.36	72.00	13.00	29.00
529	6.70	1.65	0.31	0.50	0.57	0.51	0.68	0.43	0.49	0.05
0.18	0.30	0.68	3.35	1.59	4.20	2.48	0.39	69.00	14.00	27.00
530	6.00	1.49	0.32	0.44	0.48	0.46	0.70	0.39	0.52	0.0
0.17	0.32	0.71	3.10	1.46	3.71	2.28	0.41	67.00	13.00	25.00
531	5.50	1.33	0.26	0.39	0.42	0.49	0.62	0.32	0.39	0.02
0.06	0.23	0.59	2.86	1.42	3.21	1.94	0.40	63.00	12.00	21.00
532	5.60	1.34	0.27	0.41	0.46	0.45	0.57	0.34	0.41	0.03
0.16	0.24	0.82	2.93	1.29	3.49	2.25	0.42	68.00	13.00	27.00
533	4.30	1.11	0.25	0.33	0.38	0.32	0.46	0.23	0.32	0.05
0.09	0.26	0.48	2.21	1.08	2.65	1.55	0.28	67.00	14.00	26.00
534	6.50	1.62	0.27	0.54	0.52	0.49	0.71	0.39	0.52	0.12
0.14	0.34	0.76	3.42	1.51	4.25	2.73	0.50	60.00	14.00	25.00
535	6.00	1.58	0.25	0.52	0.43	0.50	0.62	0.55	0.64	0.12
0.09	0.44	0.76	3.04	1.48	3.90	2.48	0.52	65.00	13.00	25.00
536	10.00	2.41	0.42	0.82	0.86	0.91	1.20	0.71	0.95	0.15
0.35	0.44	1.42	5.21	2.31	6.47	4.27	0.39	72.00	12.00	27.00
537	6.90	1.56	0.31	0.53	0.54	0.64	0.86	0.41	0.63	0.13
0.12	0.38	0.95	3.44	1.73	4.39	2.76	0.60	69.00	12.00	25.00

APPENDIX TABLE 23. Past Kananaskis *Couesius plumbeus*, Raw Character values, n = 61.

PAST KANANASKIS COUESIUS PLUMBEUS

196101	5.70	1.57	0.34	0.40	[illegible]	0.47	[illegible]	[illegible]	[illegible]	[illegible]
0.0	0.12	0.73	[illegible]	1.63	[illegible]	[illegible]	[illegible]	[illegible]	13.00	[illegible]
196102	6.20	1.63	0.39	0.45	0.66	0.56	0.31	0.45	0.55	0.0
0.0	0.24	1.04	4.07	2.01	5.13	3.48	0.61	70.00	13.00	25.00
196103	8.50	1.93	0.40	0.53	0.68	0.62	0.86	0.51	0.57	0.01
0.0	0.27	1.84	4.35	1.96	5.45	3.66	0.73	65.00	13.00	23.00
196104	6.00	1.60	0.35	0.43	0.55	0.50	0.74	0.43	0.49	0.03
0.0	0.31	0.86	3.53	1.59	4.07	2.40	0.55	63.00	13.00	24.00
196105	6.30	1.53	0.34	0.40	0.50	0.49	0.60	0.37	0.45	0.02
0.0	0.28	0.77	3.19	1.54	3.81	2.40	0.55	64.00	13.00	26.00
196106	7.00	1.65	0.37	0.46	0.56	0.52	0.71	0.43	0.52	0.01
0.0	0.26	0.81	3.59	1.65	4.34	2.90	0.58	61.00	12.00	24.00
196107	6.00	1.57	0.36	0.42	0.52	0.54	0.70	0.41	0.52	0.02
0.0	0.23	0.77	3.38	1.50	4.17	2.57	0.56	60.00	13.00	27.00
196108	5.80	1.41	0.34	0.40	0.45	0.48	0.61	0.36	0.48	0.0
0.0	0.17	0.71	3.09	1.34	3.73	2.39	0.47	56.00	13.00	22.00
196109	5.50	1.35	0.32	0.36	0.44	0.44	0.50	0.36	0.41	0.0
0.0	0.18	0.64	2.75	1.36	3.33	2.02	0.44	58.00	12.00	22.00
196110	5.30	1.24	0.31	0.33	0.41	0.39	0.51	0.34	0.37	0.0
0.0	0.16	0.57	2.71	1.33	3.37	2.11	0.35	62.00	14.00	21.00
196111	4.00	1.27	0.29	0.32	0.38	0.34	0.46	0.34	0.32	0.0
0.0	0.17	0.54	2.59	1.10	3.06	1.91	0.36	65.00	13.00	23.00
196901	6.30	1.48	0.34	0.43	0.56	0.42	0.63	0.39	0.49	0.06
0.0	0.24	0.89	3.05	1.57	3.73	2.33	0.45	60.00	12.00	21.00
196902	4.00	1.13	0.32	0.29	0.38	0.35	0.50	0.31	0.36	0.01
0.0	0.16	0.59	2.45	1.22	2.86	1.71	0.39	67.00	12.00	23.00
196903	5.60	1.34	0.32	0.35	0.51	0.45	0.64	0.35	0.45	0.01
0.0	0.15	0.72	2.75	1.35	3.47	2.08	0.45	61.00	11.00	23.00
196904	5.20	1.30	0.32	0.35	0.43	0.39	0.59	0.33	0.39	0.04
0.0	0.21	0.67	2.51	1.21	3.22	2.09	0.42	64.00	11.00	22.00
196905	6.10	1.47	0.33	0.41	0.52	0.45	0.61	0.37	0.46	0.05
0.0	0.25	0.77	3.11	1.47	3.71	2.36	0.49	72.00	11.00	25.00
196906	6.30	1.52	0.37	0.44	0.50	0.45	0.65	0.40	0.48	0.06
0.0	0.23	0.80	3.11	1.58	3.65	2.49	0.52	69.00	12.00	22.00
196907	5.40	1.30	0.32	0.37	0.46	0.40	0.56	0.36	0.41	0.04
0.0	0.20	0.65	2.65	1.38	3.19	2.00	0.45	63.00	12.00	23.00
196908	5.40	1.35	0.36	0.40	0.47	0.42	0.57	0.37	0.36	0.05
0.0	0.20	0.67	2.70	1.23	3.26	1.98	0.48	58.00	12.00	20.00
196909	5.70	1.42	0.33	0.42	0.48	0.42	0.59	0.38	0.45	0.06
0.0	0.27	0.70	2.93	1.26	3.50	2.21	0.47	64.00	11.00	21.00
196910	5.30	1.32	0.30	0.35	0.43	0.37	0.51	0.31	0.40	0.04
0.0	0.20	0.64	2.66	1.32	3.23	2.01	0.42	59.00	12.00	20.00
196911	5.20	1.27	0.29	0.35	0.45	0.36	0.54	0.34	0.36	0.03
0.0	0.24	0.60	2.66	1.32	3.22	1.99	0.42	67.00	11.00	21.00
196912	5.10	1.19	0.31	0.34	0.45	0.37	0.55	0.32	0.40	0.01
0.0	0.26	0.61	2.67	1.25	3.17	2.01	0.46	61.00	12.00	23.00
196913	5.50	1.38	0.33	0.38	0.44	0.39	0.57	0.37	0.41	0.03
0.0	0.23	0.66	2.79	1.31	3.50	2.17	0.45	62.00	13.00	22.00
196914	5.20	1.25	0.30	0.34	0.43	0.34	0.50	0.32	0.42	0.04
0.0	0.20	0.65	2.69	1.29	3.31	2.19	0.44	67.00	12.00	23.00
196915	6.80	1.61	0.37	0.48	0.57	0.51	0.75	0.43	0.56	0.07
0.0	0.29	0.83	3.65	1.52	4.25	2.66	0.53	66.00	14.00	23.00
196916	6.20	1.44	0.36	0.42	0.54	0.48	0.70	0.37	0.49	0.05
0.0	0.23	0.79	3.17	1.41	3.85	2.50	0.47	66.00	13.00	26.00
196917	5.60	1.40	0.30	0.39	0.47	0.43	0.60	0.35	0.43	0.05
0.0	0.20	0.65	2.77	1.35	3.45	2.19	0.44	62.00	12.00	21.00
196918	5.10	1.25	0.34	0.34	0.41	0.41	0.55	0.34	0.39	0.0
0.0	0.17	0.55	2.57	1.28	3.11	1.92	0.41	67.00	12.00	22.00
196919	5.10	1.26	0.29	0.35	0.43	0.40	0.56	0.35	0.42	0.04
0.0	0.17	0.64	2.53	1.25	3.16	2.04	0.41	62.00	11.00	19.00
196920	5.50	1.35	0.33	0.39	0.46	0.40	0.58	0.37	0.43	0.06
0.0	0.23	0.71	2.70	1.32	3.41	2.13	0.45	60.00	13.00	23.00
196921	5.00	1.26	0.30	0.34	0.43	0.39	0.54	0.33	0.38	0.01
0.0	0.25	0.62	2.44	1.26	3.03	1.85	0.41	54.00	12.00	23.00
196922	5.10	1.28	0.33	0.39	0.44	0.39	0.56	0.36	0.38	0.03
0.0	0.22	0.60	2.65	1.21	3.13	1.91	0.36	64.00	12.00	22.00
196923	4.60	1.09	0.26	0.31	0.43	0.35	0.51	0.32	0.35	0.03
0.02	0.18	0.57	2.36	1.08	2.88	1.73	0.37	63.00	12.00	22.00
196924	5.00	1.21	0.35	0.31	0.43	0.37	0.50	0.32	0.37	0.04
0.0	0.25	0.60	2.55	1.30	3.01	1.89	0.40	64.00	14.00	23.00
196925	4.80	1.15	0.29	0.34	0.41	0.37	0.49	0.30	0.34	0.03
0.0	0.16	0.65	2.44	1.17	2.96	1.82	0.35	59.00	11.00	21.00
197301	7.70	1.86	0.45	0.55	0.64	0.55	0.72	0.46	0.52	0.06
0.0	0.33	0.90	4.03	1.78	4.85	3.18	0.59	57.00	13.00	22.00
197302	7.70	1.84	0.45	0.55	0.63	0.50	0.76	0.50	0.55	0.06
0.0	0.32	0.96	3.92	1.81	4.79	3.13	0.53	61.00	12.00	25.00
197303	8.00	1.88	0.43	0.56	0.67	0.60	0.80	0.54	0.63	0.08
0.0	0.34	1.06	4.16	1.87	5.11	3.52	0.58	65.00	12.00	26.00
197304	6.40	1.56	0.38	0.43	0.58	0.45	0.69	0.43	0.47	0.05
0.0	0.25	0.81	3.38	1.56	4.00	2.59	0.50	65.00	11.00	24.00
197305	7.40	1.68	0.39	0.46	0.57	0.55	0.70	0.41	0.50	0.07
0.0	0.32	0.90	3.74	1.78	4.53	2.95	0.55	63.00	14.00	24.00
197306	6.20	1.43	0.37	0.40	0.55	0.45	0.63	0.37	0.47	0.05
0.0	0.23	0.80	3.22	1.54	3.85	2.40	0.45	64.00	11.00	23.00
197307	7.00	1.68	0.41	0.48	0.61	0.49	0.68	0.43	0.49	0.07
0.0	0.26	0.88	3.48	1.74	4.30	2.73	0.54	69.00	12.00	21.00
197308	7.60	1.71	0.41	0.48	0.62	0.60	0.75	0.47	0.60	0.05
0.0	0.32	0.98	3.98	1.95	4.68	3.13	0.60	65.00	13.00	25.00
197309	5.40	1.33	0.32	0.36	0.50	0.44	0.56	0.35	0.41	0.03
0.0	0.23	0.75	2.73	1.22	3.40	2.13	0.39	67.00	13.00	24.00
197310	6.10	1.48	0.36	0.39	0.56	0.46	0.67	0.36	0.46	0.04
0.0	0.26	0.80	3.25	1.51	3.88	2.53	0.41	66.00	11.00	22.00
197311	7.40	1.73	0.43	0.50	0.62	0.54	0.80	0.46	0.52	0.06
0.0	0.29	1.08	3.82	1.74	4.80	3.25	0.57	63.00	12.00	23.00
197312	8.70	1.91	0.42	0.54	0.70	0.63	0.84	0.50	0.60	0.06
0.0	0.35	1.20	4.37	2.25	5.31	3.59	0.66	68.00	14.00	24.00
197313	8.80	2.04	0.47	0.57	0.76	0.64	0.94	0.56	0.66	0.07
0.0	0.38	1.32	4.70	1.99	5.79	4.03	0.60	65.00	12.00	23.00
197314	8.80	2.00	0.41	0.59	0.75	0.70	0.91	0.56	0.71	0.07
0.0	0.39	1.15	4.61	2.20	5.90	4.12	0.72	65.00	11.00	27.00
197315	8.60	2.01	0.43	0.62	0.79	0.66	0.85	0.57	0.65	0.07
0.0	0.38	1.05	4.59	2.07	5.42	3.45	0.66	70.00	12.00	26.00
197316	8.90	2.01	0.46	0.57	0.70	0.64	0.84	0.53	0.67	0.07
0.0	0.39	1.21	4.72	2.01	5.69	3.92	0.69	66.00	13.00	24.00
197317	9.00	2.04	0.43	0.59	0.77	0.63	0.93	0.56	0.67	0.06
0.0	0.36	1.20	4.63	2.20	5.82	4.11	0.75	73.00	12.00	25.00
197318	8.70	2.11	0.44	0.61	0.77	0.66	0.87	0.58	0.70	0.09
0.0	0.48	1.18	4.36	2.13	5.46	3.62	0.75	60.00	13.00	22.00
197319	6.40	1.70	0.34	0.42	0.59	0.44	0.71	0.44	0.53	0.03
0.0	0.28	0.93	3.26	1.59	4.12	2.42	0.46	62.00	13.00	25.00
197320	5.80	1.32	0.32	0.38	0.51	0.40	0.59	0.34	0.44	0.03
0.0	0.23	0.75	2.91	1.44	3.53	2.32	0.42	64.00	13.00	24.00
197321	5.10	1.22	0.30	0.34	0.44	0.37	0.49	0.32	0.38	0.02
0.0	0.21	0.59	2.68	1.20	3.16	2.00	0.39	63.00	12.00	23.00
197322	5.00	1.24	0.28	0.32	0.44	0.36	0.50	0.34	0.37	0.02
0.0	0.19	0.62	2.62	1.25	3.10	1.96	0.38	70.00	12.00	26.00
197323	11.20	2.53	0.53	0.71	0.90	0.81	1.15	0.68	0.67	0.10
0.0	0.48	1.46	5.58	2.68	7.20	4.96	0.81	67.00	14.00	22.00
197324	9.80	2.20	0.48	0.62	0.86	0.75	0.98	0.58	0.76	0.10
0.0	0.40	1.26	5.24	2.25	6.56	4.64	0.79	64.00	11.00	21.00
197325	8.90	2.05	0.42	0.57	0.74	0.66	0.85	0.55	0.63	0.08
0.0	0.34	1.16	4.70	2.09	5.75	3.94	0.66	71.00	12.00	24.00

APPENDIX TABLE 24. Summary of changes in female gonad maturity for both *Couesius plumbeus* and *Rhinichthys cataractae* and surface water temperature during spawning period, 1978, Lower Kananaskis Reservoir. These data were extracted from total catch data in Table 2 in Appendix.

Date	*C. plumbeus*			*R. cataractae*			Temperature
	Ripe	Fully Ripe	Spent	Ripe	Fully Ripe	Spent	°C
May 15, 16	3						4.0
17, 18	6			1			4.0
23, 24	9						4.5
25, 26	8	3		2			5.0
27	1						
May 31, June 1	7	6		4			8.2
June 5	5			6	1		10.5
6							10.5
7, 8	44	44	13	9	4		10.0
12, 13	48	20	41	4	8	3	10.5
14	32	50	16		1		12.5
19, 20	15	7	17	3	2	4	10.5
21, 22	20	31	31				
28, 29		13	52			5	13.0
July 6			12				13.7
12		7	26				16.0

APPENDIX TABLE 25. A. Data summary for female *R. cataractae* Gonadosomatic Index values (GSI), Lower Kananaskis Reservoir, 1978.

Date	n	$\overline{X}$	s_D	Range
May 1	1	13.8	-	-
May 18	2	14.1	-	12.6 - 15.6
May 26	2	15.6	-	14.9 - 16.2
June 1	4	19.1	0.3	18.8 - 19.5
June 8	7	19.4	2.6	15.0 - 23.0
June 14	10	17.0	4.6	10.0 - 24.8
June 20	7	16.0	3.5	11.4 - 21.0
June 29	6	11.4	2.1	9.1 - 14.4

APPENDIX TABLE 25. B. Data summary for female *C. plumbeus* Gonadosomatic Index values (GSI), Lower Kananaskis Reservoir, 1978.

Date	n	$\overline{X}$	s_D	Range
May 1	20	18.4	2.2	14.0 - 22.0
May 13	6	18.8	1.4	17.1 - 20.4
May 24, 25	22	19.0	1.6	16.6 - 22.0
June 1	8	21.0	1.4	19.0 - 23.2
June 8	12	24.2	2.9	20.6 - 27.6
June 13	23	17.7	6.6	8.7 - 30.1
June 21	48	17.7	6.1	6.7 - 29.2
June 29	21	16.3	5.6	9.9 - 27.1
July 6	12	13.7	3.3	7.4 - 18.4
July 12	20	11.9	3.6	6.4 - 17.3
July 27	25	8.1	2.3	4.8 - 12.9

APPENDIX TABLE 26. Summary of ova diameter statistics for both *Couesius plumbeus* and *Rhinichthys cataractae* from Lower Kananaskis Reservoir, 1978.

Date	Single Values (mm)	n	$\overline{X}$ (mm)	s_D	Range
Couesius plumbeus					
May 1		25	1.30	0.11	1.01 - 1.48
May 24		21	1.31	0.07	1.17 - 1.39
June 8		13	1.43	0.07	1.31 - 1.53
June 13		25	1.35	0.23	0.95 - 1.88
June 21		25	1.31	0.23	0.88 - 1.70
July 6		11	1.19	0.15	0.94 - 1.36
July 12		25	1.22	0.16	0.88 - 1.46
Rhinichthys cataractae					
May 1	1.38	1			
May 18	1.48	1			
May 26	1.52	1			
June 1		4	1.54	0.05	1.49 - 1.60
June 8		7	1.69	0.05	1.62 - 1.78
June 14		10	1.43	0.27	0.91 - 1.68
June 20		7	1.39	0.26	0.88 - 1.69
June 29		6	1.16	0.22	0.96 - 1.48

APPENDIX TABLE 27. Summary of catch data for *Couesius plumbeus* (C), *Rhinichthys cataractae* (R) and their putative hybrids (H) from 7 different selected habitats on Lower Kananaskis Reservoir. All samples of these species taken during the time period of maximal spawning activity in 1978 are listed below.

	Habitat Locations						
Sampling Date	LK1 Stream (Interlakes Stream)	LK1 Stream (Interlakes) Mouth	LK1 Common (Interlakes) Bay	Interlakes Raceway	Boulton Cr. Mouth	Invincible Cr. Mouth	Smith-Dorrien Cr. Mouth
May 18	C-52, R-2						C-8, R-1
22	C-2	C-58					
24			C-6				C-4
25				C-3			C-9
26					C-12, R-5, H-1		
June 1		C-3, R-1		C-20, R-4			
5	C-18, R-12		C-2				
7	R-7, H-1	C-15, R-4	C-2		C-11		
8	R-4	C-101, R-7, H-2		C-25, R-3		C-81, H-1	C-5
12	R-8	C-14	C-8				
13	R-1	C-69, R-13	C-23		C-55, R-1	C-68, R-3	
14	R-1		C-31, R-1	C-71		C-18, R-1	
19	R-3						
20	R-9			C-4, R-1	C-32	C-8	
21	C-5, R-3		C-38	C-71		C-2	C-1
29	R-14		C-64, H-1		C-15		
July 6				C-12			

APPENDIX TABLE 28. Lower Kananaskis Reservoir inlet stream surface temperatures (^{o}C, Hg thermometer), approximate current speeds (calculated from timed passage of a floating object over 10 m) and Secchi disc readings. CPL:- data from Calgary Power Ltd., flow station.

Date	Smith-Dorrien Creek		Kent Creek		Invircible Creek		Boulton Creek		LK1 Stream	
April 28	5.5		5.0				3.0			
29	4.5									
30	6.0	0.9 m/s					3.0			
May 1									7.0	0.5 m/s
7	5.5									
10									4.4	
13									4.0	0.7 m/s
15	3.3	1.0 m/s								
16	4.0								7.0	
22									8.0	
25	4.9 - mouth 3.3 - upstream 1.7 m/s		2.7							
26	3.8					1.0 m/s	5.0	Secchi = 0.2 m		
30			2.5							
31									4.0	
June 1							4.5			
5							3.5		17.5	
7	6.5							Secchi = 0.3 m	16.5	0.2 m/s
8	4.3	2.5 m/s	3.8	2.0 m/s	4.0 Secchi = 0.05 m	1.4 m/s				
9			64 cfs (CPL)							
12					12.5		8.2	Secchi = 0.4 m	10.5	0.2 m/s
13						Secchi = 0.04 m				
20	5.2									
21	4.8		7.2	2.2 m/s	12.0					

APPENDIX TABLE 29. Analysis of Covariance of Viability Regressions.

A. Growth Rate Regressions (Fig. 23 in text)

		F	$F_{.05(df\ 1,\ \alpha)}$	
R. cataractae + *C. plumbeus*	slope	0.017	3.84	$P > 0.05$
	intercepts	21.20	3.84	$P < 0.05$
R. cataractae + Hybrid	slope	2.27	3.84	$P > 0.05$
	intercepts	4.68	3.84	$P < 0.05$
C. plumbeus + Hybrid	slope	2.83	3.84	$P > 0.05$
	intercepts	0.407	3.84	$P > 0.05$

B. Length-Weight Regressions (Fig. 24 in text)

		F	$F_{.05(df\ 1,\ \alpha)}$	
R. cataractae + *C. plumbeus*	slope	0.86	3.84	$P > 0.05$
	intercepts	48.66	3.84	$P < 0.05$
R. cataractae + Hybrid	slope	0.19	3.84	$P > 0.05$
	intercepts	13.69	3.84	$P < 0.05$
C. plumbeus + Hybrid	slope	0.91	3.84	$P > 0.05$
	intercepts	14.62	3.84	$P < 0.05$

C. Fecundity Regressions (Fig. 25 in text)

		F	$F_{.05(df\ 1,\ 41)}$	
R. cataractae + *C. plumbeus*	slope	12.959	4.08	$P < 0.05$
	intercept	6.878	4.08	$P < 0.05$

APPENDIX TABLE 30. Length-weight regression summary.

Species & Sex	Sample Size	Correlation Coefficient	Regression Equation
C x R combined ♀ & ♂	42	0.980	$\log w = \bar{1}.725 + 2.813 \log \ell$
C x R ♂ only	24	0.975	$\log w = \bar{1}.759 + 2.858 \log \ell$
C x R ♀ only	18	0.986	$\log w = \bar{1}.698 + 2.774 \log \ell$
C combined	162	0.962	$\log w = \bar{1}.781 + 3.064 \log \ell$
C ♂ only	65	0.957	$\log w = \bar{1}.710 + 2.967 \log \ell$
C ♀ only	97	0.962	$\log w = \bar{1}.782 + 3.072 \log \ell$
R combined	159	0.985	$\log w = \bar{1}.899 + 3.120 \log \ell$
R ♂ only	62	0.959	$\log w = \bar{1}.955 + 3.239 \log \ell$
R ♀ only	94	0.992	$\log w = \bar{1}.885 + 3.093 \log \ell$

Disc Gel Acrylamide Electrophoresis Recipes

1 N HCl

21.55 ml conc. reagent (36.0%) to 250 ml

Stock A	Stock C	Catalyst
pH 8.9		
48 ml 1 N HCl	70 g Acrylamide	2.8 g to 1000 ml
36.6 g THAM (TRIS)	1.84 g Bis	Ammonium Persulfate
0.23 ml TEMED	to 250 ml (H_2O)	
to 100 ml H_2O		

Small Pore Gel

5 ml A   10 ml C   5 ml H_2O 20 ml catalyst

gel stock good for 4000 runs.

Buffer

6.0 g THAM (TRIS)

28.8 g Glycine

to 1000 ml (H_2O)

pH 8.3

- dilute to 1/10 strength for run
- ignore for various enzyme systems

Destain

50:50:10 methanol:H_2O:glacial acetic acid

Storage

7% Acetic Acid

Tracking Dye

0.1 g Bromophenyl Blue to 1000 ml (H_2O)

Dept Copy

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NAME OF AUTHOR GEORGE A. BUTCHER

TITLE OF THESIS ECOLOGY AND TAXONOMY OF HYBRIDIZING CYPRINID FISHES FROM UPPER AND LOWER KANANASKIS RESERVOIRS, ALBERTA

DEGREE FOR WHICH THESIS WAS PRESENTED MASTER OF SCIENCE

YEAR THIS DEGREE GRANTED SPRING, 1979