A TAXONOMIC STUDY OF CUTTHROAT TROUT, SALMO CLARKI CLARKI RICHARDSON, RAINBOW TROUT SALMO GAIRDNERI RICHARDSON AND RECIPROCAL HYBRIDS

by

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ZOOLOGY

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degree of MASTER OF ARTS

Members of the Department of Zoology

THE UNIVERSITY OF BRITISH COLUMBIA
September, 1956

ABSTRACT

Reciprocal hybrid crosses were made of cutthroat and rainbow trout and the eggs were reared under similar conditions with pure cutthroat and pure rainbow eggs. Viability of hybrid crosses was compared with viability of pure strains, and sex ratios in (offspring) were studied. Relative growth of several head and body parts was studied in the four lots of fish. Meristic comparisons, counts of teeth and pyloric caeca were made. Coloration was studied in all experimental lots of fish. Hybrid crosses were as viable as intraspecific crosses and sex ratios did not differ significantly from expected. Relative growth studies showed cutthroat had larger heads, larger head parts and deeper peduncles than rainbows. Hybrids were usually intermediate. Rainbow trout had higher scale, ray and vertibral counts than cutthroats. Contrary to most authorities, scale counts were higher on rainbows than on cutthroat. Dorsal ray counts for both hybrid lots resembled rainbow parents. Vertebral counts among hybrids tended to resemble female parents. No marked differences were found in teeth except on the hyoid bone. Pyloric caeca counts were similar in both parental lots. Coloration on rainbows was different than on cutthroats. Hybrids were intermediate in some aspects of color and in others they tended to resemble one parent. Eight samples of wild fish were examined. Several features which were distinctive in the hatchery fish were different for the two species in the wild.

ACKNOWLEDGMENTS

I wish to express my appreciation to Dr. C.C. Lindsey who helped in the selection of this problem and directed me throughout the course of the investigation. I am grateful to Dr. Larkin who criticized this manuscript and gave me help in many ways. I am particularly indebted to Mr. Frank Pells, Smith Falls Hatchery Supervisor, who generously gave a great deal of his own time to this investigation; without his cooperation this programme would not have been possible. Mr. I. Barrett kindly made hatchery facilities available for the investigation. I should like to express my appreciation to Mr. E.H.Vernon and Mr. A. H. Houston who read the manuscript.

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TABLE OF CONTENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES

LIST OF FIGURES

LIST OF FIGURES

LIST OF FIGURES

I. INTRODUCTION

Two similar species of trout inhabit the coastal waters of British Columbia. In some areas members of these two species are very easy to distinguish but fish bearing some of the distinguishing features of each species are sometimes encountered, suggesting hybridization. In order to shed some light on the nature of the differences between the two species, a detailed study of rainbow trout, cutthroat trout and their hybrids was carried out.

The history of the two types of trout is not clearly understood. Jordan and Evermann (1902) state that the American trout probably originated in Asia, from whence it extended its range through Alaska to the Columbia system. It then spread to the upper Columbia River, through Two-Ocean Pass to the Yellowstone and Missouri systems, then south to the Platte and Arkansas Rivers. They moved through the Rio Grande and Colorado to the Kern River in the Sierras and from here along the coast, past the former colonization areas on the Columbia, into the Fraser River. In the Fraser system the Kamloops trout marks one end of the extreme and the cutthroat represents the original progenitor.

Mottley (1934) suggested that during the last inter-glacial period the two species were evolving from a single salmonine stock which had been separated from the oncorhyncid stock by previous glaciation. Fresh-water colonies of the non-migratory forms fostered the distinct characters observed today. The last glaciation forced both stocks of fish south and presumably only the southern populations survived. These stocks apparently moved into a number of isolated or partly isolated areas as indicated by the large numbers of proposed species. On the west slope of the Rockies there are fourteen tentative species in the genus Salmo (Shapovalov 1941). All of these species fit into a rainbow or cutthroat series. The present experiment was set up to examine in detail the differences between representatives of the two species in the lower Fraser Valley. The following is a brief statement of the programme carried out.

The viability of the hybrids was compared to that of the pure crosses. The progeny were compared for relative growth, various meristic counts, numbers of teeth and other parts, coloration and other characters. Features that were different on the experimental fish were examined on a number of wild fish.

II. MATERIALS AND METHODS

Fish Used

The material used consisted of groups of fish reared in Smith Falls Hatchery, Cultus Lake, B.C. and collections of wild trout from the Institute of Fisheries Museum at the University of British Columbia.

In April, 1954, cutthroat and rainbow trout of both sexes were stripped at Smith Falls Hatchery. The eggs and milt were divided and four lots of fertilized eggs were cultured under similar conditions of food, temperature and light. These lots included two pure parent strains and two reciprocal hybrid crosses as listed;

K	male	X K	female	-	pure rainbow
C	"	X C	"	-	pure cutthroat
K	"	X C	"	-	hybrid
C	"	X K	"	-	hybrid

The rainbow trout stock originated in Cultus Lake. One male and one female were used for all rainbow reproductive products. The cutthroat trout stock originated in Chilliwack Lake. The rainbow males and female were both five year old fish. The cutthroat males were two years old while females were five years old.

Samples of twelve fish, from each lot, were preserved every half month for three months, except in the C male X K female cross where numbers were limited so samples of five or six fish were preserved. After three months samples were taken monthly for the ensuing nine months, following which each lot of fish was sampled once in July 1955, and once in May 1956.

In April 1956, to test the viability of hybrids, two pure strain lots and two hybrid lots were cultured using larger numbers of parents. Records were kept on egg loss, numbers of alevins hatching and on fry loss. All infertile eggs and dead alevins as well as samples of live fry were preserved.

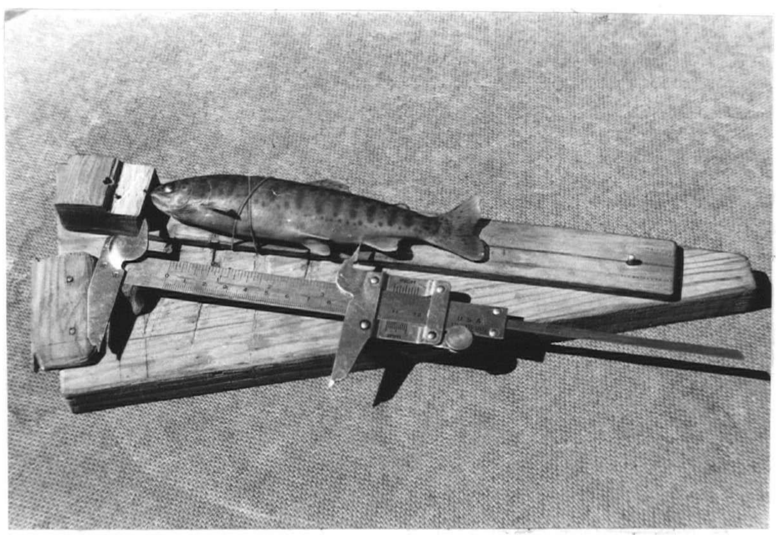
For the study of wild fish an attempt was made to obtain series of fish of comparable sizes from adjacent areas or from areas in the same river system.

Staining Procedure

Samples of hatchery reared fish, from all four lots, were stained and cleared with a technique essentially like that described by Hollister (1934). Fry one and two months old were cleared and stained. Details on clearing and staining are given in Appendix I.

Figure 1

(a) Vernier substage micrometer used to measure fish under 40 mm. fork length



(b) Vernier caliper and board used for measurement of fish from 40 mm to 150 mm. fork length

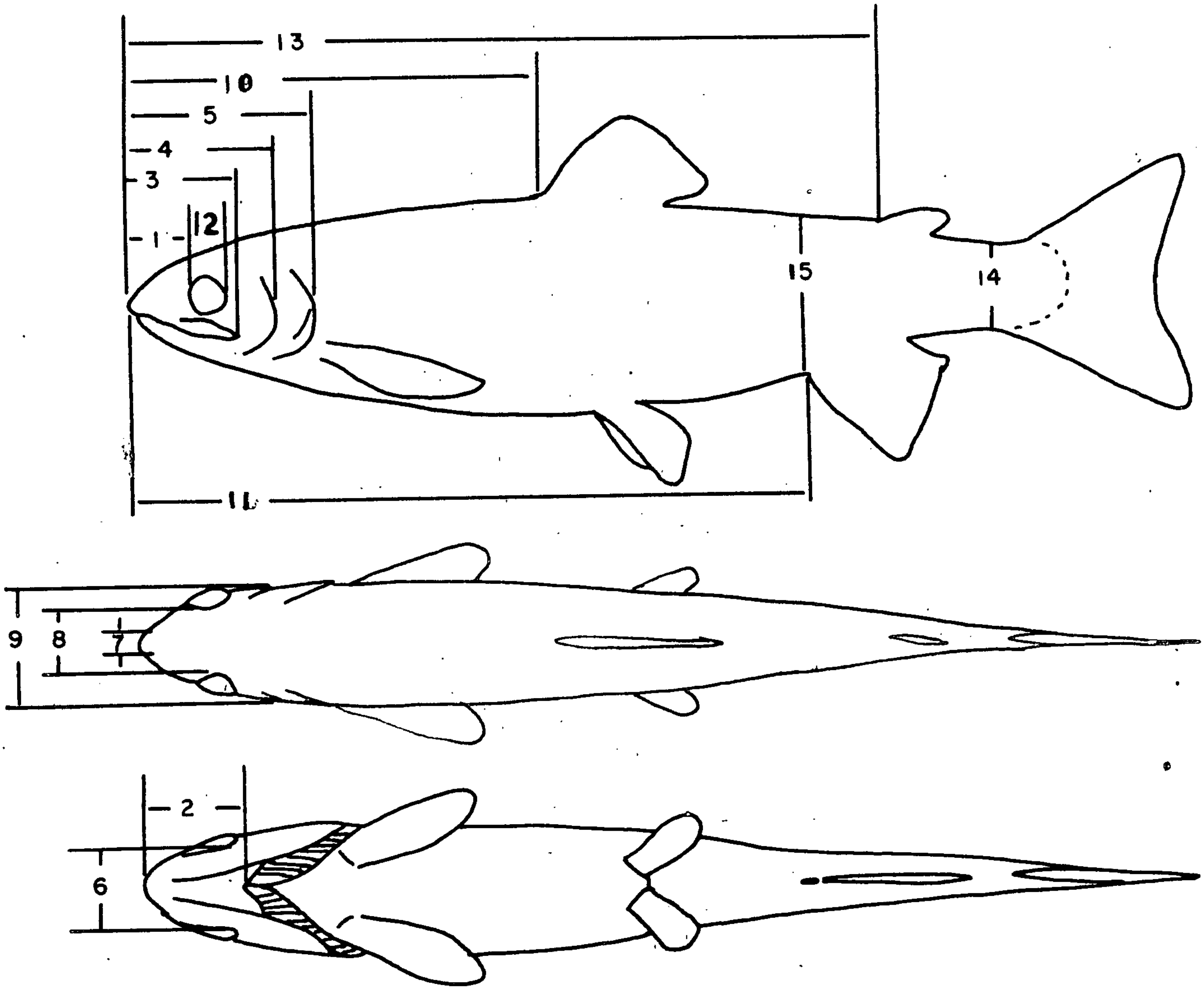


Figure 2. Measurements made on experimental fish

1. Snout length
2. Chin length
3. Maxillary length
4. Preoperculor length
5. Head length
6. Mouth width
7. Inter-nasal width
8. Inter-orbital width
9. Head width
10. Snout to dorsal origin
11. Snout to anal origin
12. Eye diameter
13. Snout to adipose
14. Peduncle depth
15. Body depth at vent

Measurements

Measurements of fish up to 40 mm. were made with a vernier substage mounted on a binocular microscope (Figure 1 (a)). Fish from 40 mm. to 150 mm. were measured on a board with vernier calipers (Figure 1 (b)), while fish over 150 mm. were measured with needle point dividers and a scale graded in mm.

The following measurements, illustrated in Figure 2, were made:

1. Snout length, distance from tip of snout to antierior margin of eye.

2. Chin length, tip of snout to median fold anteriol to branchiostegals.

3. Maxillary length, tip of snout to posterior tip of maxillary.

4. Preoperculor length, tip of snout to posterior margin of preoperculor bone.

5. Head length, tip of snout to posterior margin of operculum.

6. Mouth width, width of mouth, across lower jaw, at the posterior tips of the maxillaries.

7. Inter-nasal width, width of the snout between the nostrils.

8. Interorbital width, minimum distance between the orbits at their top margins.

9. Head width, maximum head width at posterior margin of preopercle.

10. Snout to dorsal origin, tip of snout to origin of dorsal.

11. Snout to anal origin, tip of snout to anal origin.

12. Eye diameter, anterior to posterior margin of orbit.

13. Snout to adipose, tip of snout to origin of adipose fin.

14. Peduncle depth, minimum depth of peduncle.

15. Body depth at vent, depth of body at vent.

16. Head depth, (not illustrated) depth of head at posterior margin of preopercle.

17. Amount of parr marking on the lateral line on left side of fish. Sum of the widths, at lateral line, of all parr marks.

Most of the measurements were made on samples of 150 or more fish in each of three lots. Only 95 fish were measured in the cutthroat male X rainbow female lot.

Counts

Counts of rays, scales, vertebrae and teeth were made on samples of cleared specimens from all four lots of experimental fish.

Ray counts: In the dorsal and anal all rays, including short fractional rays at the anterior of the fin, were counted. The posterior split ray was always counted as one ray. Only the caudal rays which reached the posterior margin of the fin were counted.

Scale counts: The number of oblique scale rows were counted, about eight scales above the lateral line. Most scale counts were made on cleared fish. Accurate counts of scale rows were made by scraping all the scales from the side of the fish and counting the scale pockets.

Vertebral counts: Counts of the total number of vertebrae were made on cleared fish.

Teeth counts: Counts of teeth, on all paired bones, were made on one side only (usually the right-hand side). All teeth on the tongue vomer and hyoid were counted. Pharyngeal teeth were noted, but they did not stain heavily and could not be counted accurately. Any point or ossified cone, whether joined to or free from the tooth bearing bone, was counted as a tooth.

Pyloric caeca counts: The gut was exposed and the pyloric caeca were picked and counted as they were removed.

Color Pattern

Wherever possible an attempt was made to evaluate differences in color pattern quantitatively.

Parr mark counts: Number of parr marks which crossed the lateral line on both sides of the fish.

Dorsal median "parr-like" spots: On the dorsal mid-line of the fish parr-like spots were counted and observed. The pigment forming these marks, similar to the pigment in the parr marks, lies at a deeper level in the skin than the pigment which produces the "speckle effect" on trout. For this reason they are referred to as parr-like spots.

White on dorsal fin margin: The number of white pigmented ray interspaces on the dorsal fine.

Numbers of spots on adipose fin.

Hyoid color: Hyoid color was given four arbitrary indices. Hybrid fish and parent types were grouped according to hyoid color index.

Treatment of Data

All measurements were plotted against fork length or head length on logarithmic coordinates. (Martin 1949). Where close similarity of these relationships in the two species was indicated full series of measurements were not completed. For complete series lines of best fit for each growth stanza were estimated by eye from the average values on ordinate and abcissa for each ten mm. fork length interval. While regression lines would have described the data more precisely, the technique employed was adequate for indicating major differences between the two species.

III. RESULTS

Viability and sex ratios in hybrid and intraspecific crosses.

Comparisons of viability of hybrid crosses with intraspecific crosses (Table I) indicate that rainbow and cutthroat trout can hybridize freely.

TABLE I

Viability of hybrid and intraspecific crosses in rainbow (K) and cutthroat trout (C)

Parents Male		Female	Eggs Lost	Live Fry	% Hatching
K	X	K	650	1627	71.5
C	X	K	513	1817	78.0
K	X	C	757	130	14.6
C	X	C	795	128	13.9

Eggs from both species appear to be as viable in hybrid crosses as in intraspecific crosses. The low survival of cutthroat eggs, whether fertilized by rainbow or cutthroat male, is unexplained.

Comparisons reveal no significant differences in sex ratios within lots as tested by Chi-square at the .05 probability level. (Table II).

TABLE II

Sex ratios in reciprocal hybrid crosses
and intraspecific crosses between
rainbow (K) and cutthroat trout (C)

Parents Male		Female	Sex of Offspring Male	Female
K	X	K	15	12
C	X	K	10	8
K	X	C	13	10
C	X	C	23	12

Relative-Growth Studies

Relative growth method

The analysis of relative-growth developed by Huxley (1932) and used extensively by Martin (1949) results in log-log linear relationships between body parts for given stanzas in the development of an organism. At certain stages these linear relationships are altered sharply producing inflections in the growth curves.

Relative-growth of head parts

Typical results for the type of treatment of data, given by Huxley (1932) and Martin (1949), are given in Figures 3, 4, 5 and 6. These show relative growth of snout, eye, maxillary, snout to preopercular margin and head relative to fork length for rainbow, cutthroat and two types of hybrids.

Figure 7 illustrates the approximate relationship of these parts to fork length. Figures 8, 9, 10 and 11 give relative growth of mouth width, head width and inter orbital width and fork length. Figure 12 shows the approximate relation of these parts to fork length. Figures 13, 14, 15 and 16 illustrate the relative growth of chin length, snout to dorsal origin, snout to anal origin and fork length. Figure 17 shows the approximate relation of these dimensions to fork length.

Spouth length: Snout length of fish in all four lots increases relatively quickly until the fish are about 30 mm. long, after which the snout grows at about the same relative speed as the rest of the fish. At about 150 mm. fork length, a second inflection occurs which is associated with sexual maturity.

Cutthroats have relatively longer snouts than rainbows, the differences becoming distinct around 70 mm. fork length. Hybrids appear to resemble the cutthroat lot.

Eye diameter: The eye grows relatively quickly until the fish are about 30 mm. long. The first inflection reduces the growth rate of the eye, at about 110 mm. a second inflection further reduces the growth rate. Sexual maturity has no apparent effect on the growth rate of the eye.

Figure 7 suggests that cutthroat over 150 mm. have larger eyes than rainbow of the same size. The eye size of of the hybrids appear to be intermediate.

Maxillary, snout to preopercular margin and head length: These three parts all display the same general growth phenomena as the snout and can be discussed as a group. Growth curves for these parts show one inflection, which reduces relative growth rate, in the vicinity of 30 mm. fork length. Growth rates are about the same as the body up to 150 mm., at which point sexually maturing fish show sharp inflections. The relative growth rates in these parts are increased following sexual maturity.

These head parts are larger on cutthroats than on rainbows, differences becoming apparent between 50 and 70 mm. fork length. Rainbows have a slower relative growth rate for each of these parts hence the differences become more pronounced in large fish. For fish over 80 mm. lines of best fit for hybrid lots are intermediate, length of snout to preopercular margin approximates that of cutthroat more closely than rainbow.

Mouth width: Relative growth of mouth width (Figures 8, 9, 10, 11 and 12), shows a first growth inflection which reduces growth rate at 40 mm. fork length in all lots of fish. A second inflection, apparently related to sexual maturity, occurs in the cutthroat and hybrid lots, at 150 mm.

Cutthroats have wider mouths than rainbows while hybrids are intermediate. (Figure 12).

Interorbital width: Interorbital width, (Figures 8, 9, 10, 11 and 12) shows two growth inflections in all lots of fish, the first occurs at 30 mm., the second at about 100 mm. Like other head dimensions interorbital increases relatively quickly to 30 mm. fork length. The rate of development of the interorbital is then slower until about 100 mm. fork length. At this second inflection the growth rate of the interorbital is increased. The second inflection in the growth curve of the interorbital occurs at about the same stage as the second inflection for the eye. The increase in growth rate for the interorbital space seems to compensate for the decrease in rate of eye growth, so that the lateral position of the eye is maintained.

Figure 12 indicates that cutthroats are narrower than rainbows across the interorbital. The hybrids appear to resemble the rainbows but their relation to parent types is not consistent.

Head width: Head width shows an inflection, decreasing its growth rate in all four lots of fish around 40 mm. There is a second inflection in the cutthroat lot near 100 mm. This inflection is not definite in the hybrid lots and is absent among the rainbow.

Parent fish and hybrids appear to have similar head widths until the fish reach about 100 mm., at this point an inflection occurs in the cutthroat lot and cutthroat heads appear to be wider.

Chin length: Plots of chin length on fork length, (Figures 13, 14, 15 and 16) show only one growth inflection occurring near 40 mm. fork length.

After 40 mm. the growth curves for the two species diverge. Above 125 mm. there is no overlap in chin length and this dimension clearly separates the two species. Hybrid relative growth curves are intermediate.

Internasal width and head depth: Preliminary plots of these measurements revealed no differences between rainbow and cutthroat trout. (Data not presented).

Relative growth of head parts and head: Plots of maxillary and snout length on head length (not presented here) showed no inflections. Cutthroat trout had larger head parts, relative to head size, than did rainbows.

Summary of relative growth of head parts

All head parts show one inflection at 30 to 40 mm. fork length. Growth curves for eye and interorbital widths show inflections at about 100 mm. Growth rate of the eye is reduced at this point while that of the interorbital dimension is increased. Chin length in all lots of fish shows only one inflection which occurs at 40 mm. fork length. Among sexually mature fish snout length, maxillary length, preopercular length and head length show a second inflection, at about 150 mm., resulting in an increased relative growth rate.

Cutthroats have larger heads and head parts are larger relative to head length and fork length. Figure 18 illustrates some of the major differences between the two species. In cutthroat the snout is longer and more pointed, the maxillary is longer and projects further past the eye, the distances to the preopercular and opercular margins are greater. The chin is longer, the mouth wider and the interorbital width is narrower.

Hybrid trout are apparently intermediate in most features, but resemble the cutthroat in snout length and preopercular length. Statements about hybrids are based on comparisons of the plots of head parts and the lines fitted to these by eye. Their exact relations to parental types can not be given without more discriminating methods.

Figure 3. Relative-growth of head parts and fork length for rainbow trout. (Logarithmic coordinates)

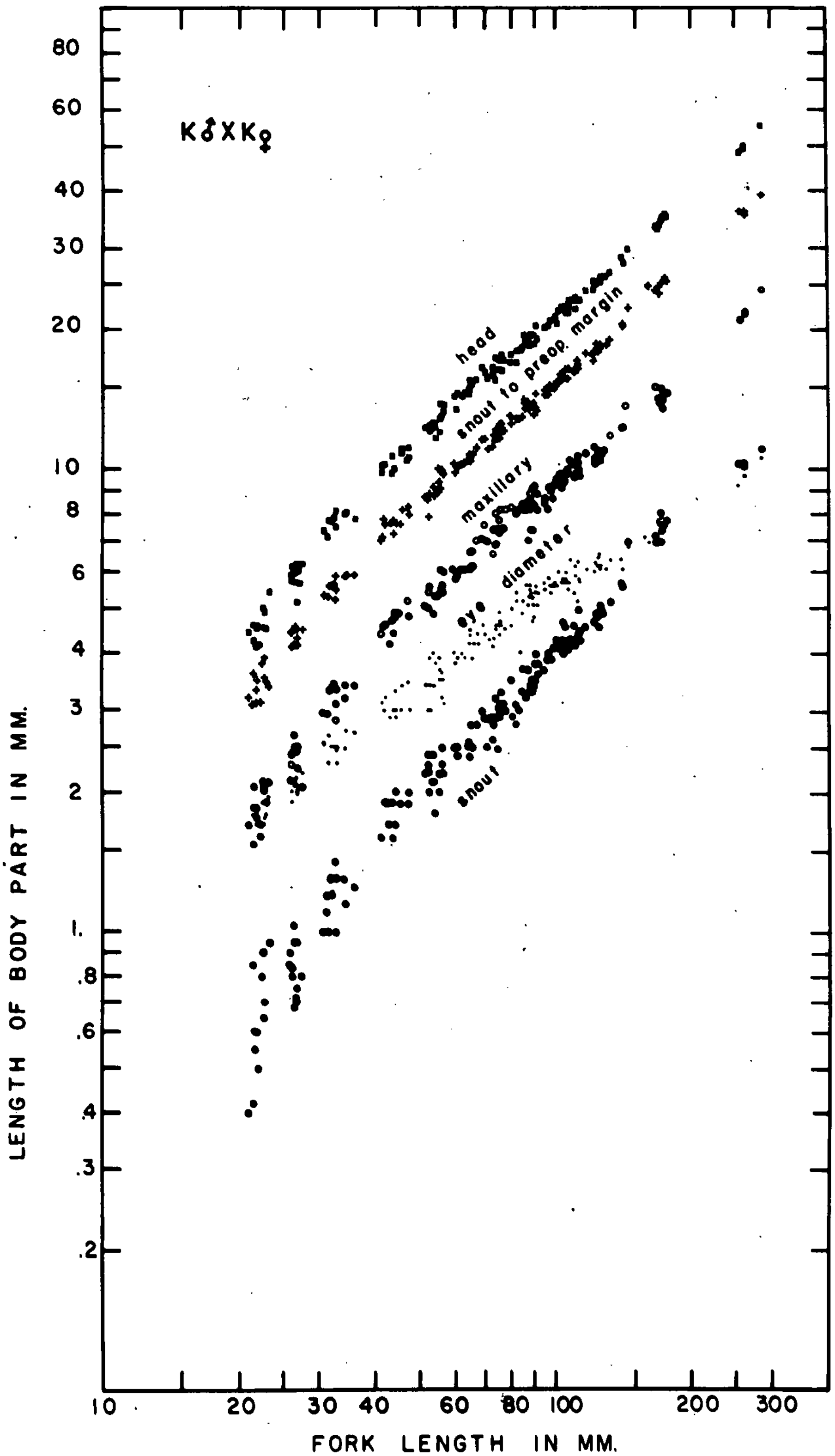
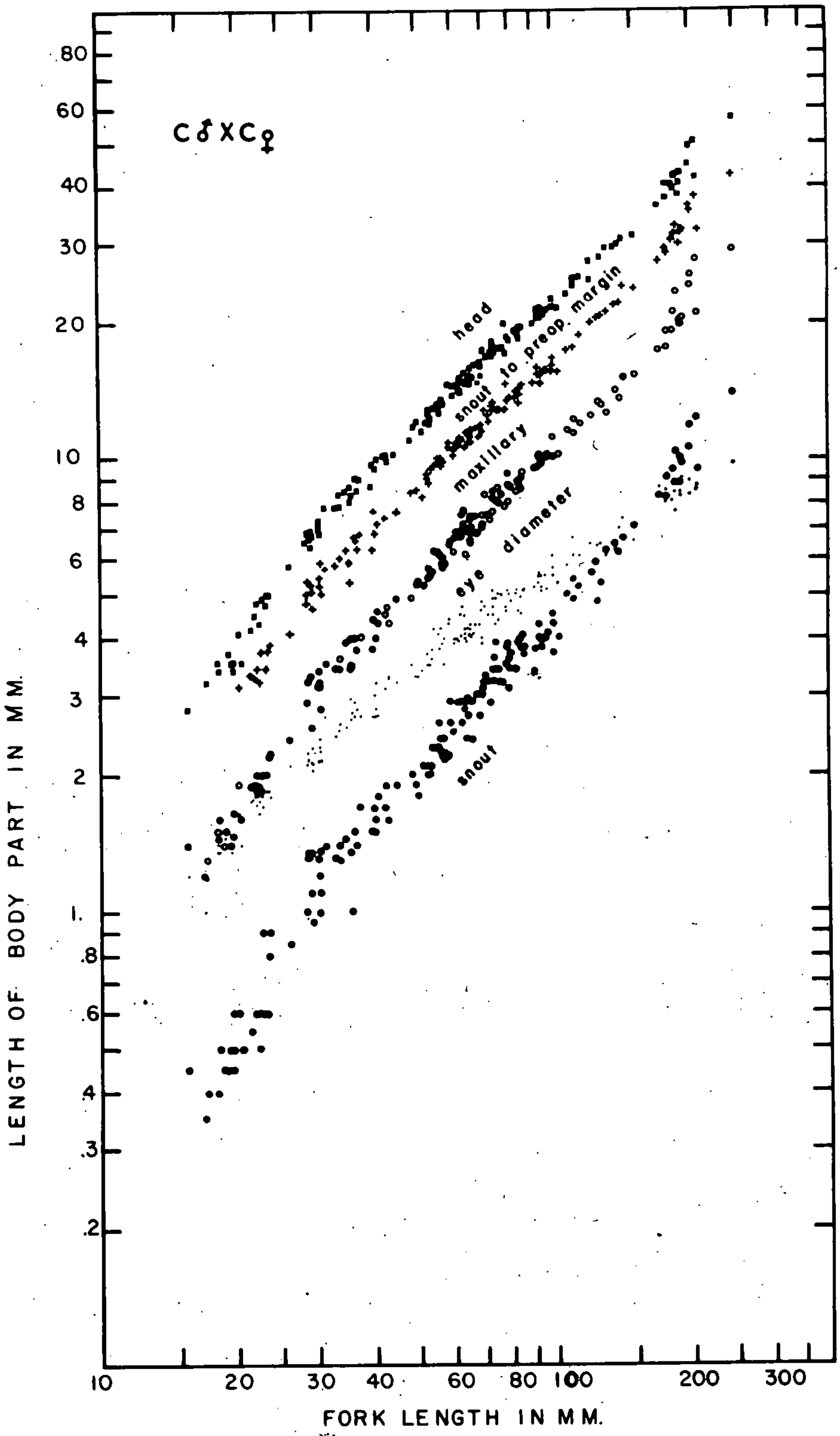

K♂XK♀
head
snout to preop. margin
maxillary
eye diameter
snout
LENGTH OF BODY PART IN MM.
FORK LENGTH IN MM.
80
60
40
30
20
10
8
6
4
3
2
1.
.8
.6
.4
.3
.2
10
20
30
40
60
80
100
200
300

Figure 4. Growth of head parts and fork length for cutthroat trout. (Logarithmic coordinates)


C♂ X C♀
head
snout to preop. margin
maxillary
eye diameter
snout
LENGTH OF BODY PART IN MM.
FORK LENGTH IN MM.
80
60
40
30
20
10
8
6
4
3
2
1.
.8
.6
.4
.3
.2
10
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30
40
60
80
100
200
300

Figure 5. Relative-growth of head parts and fork length for cutthroat male X rainbow female hybrids (Logarithmic coordinates)

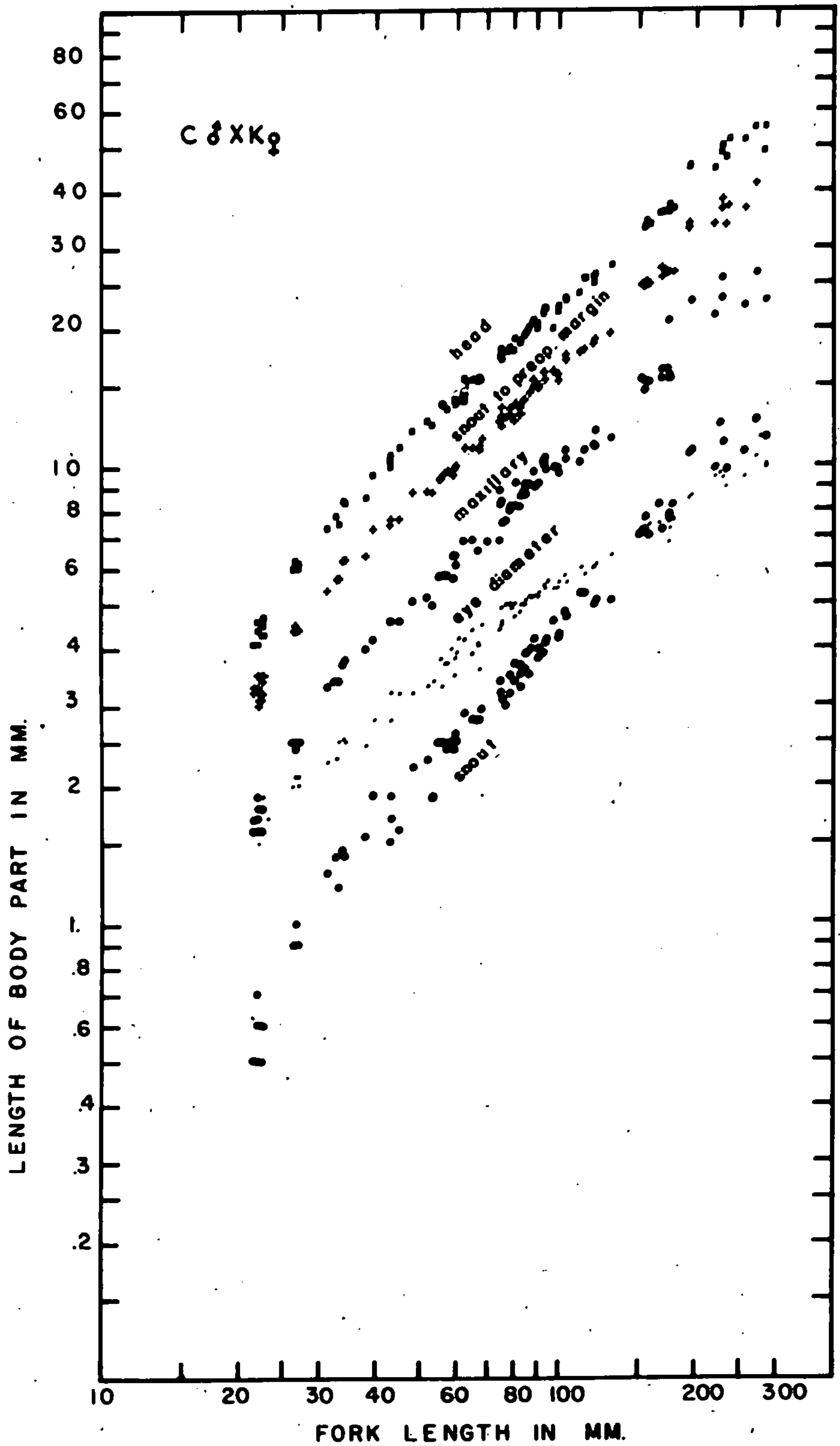
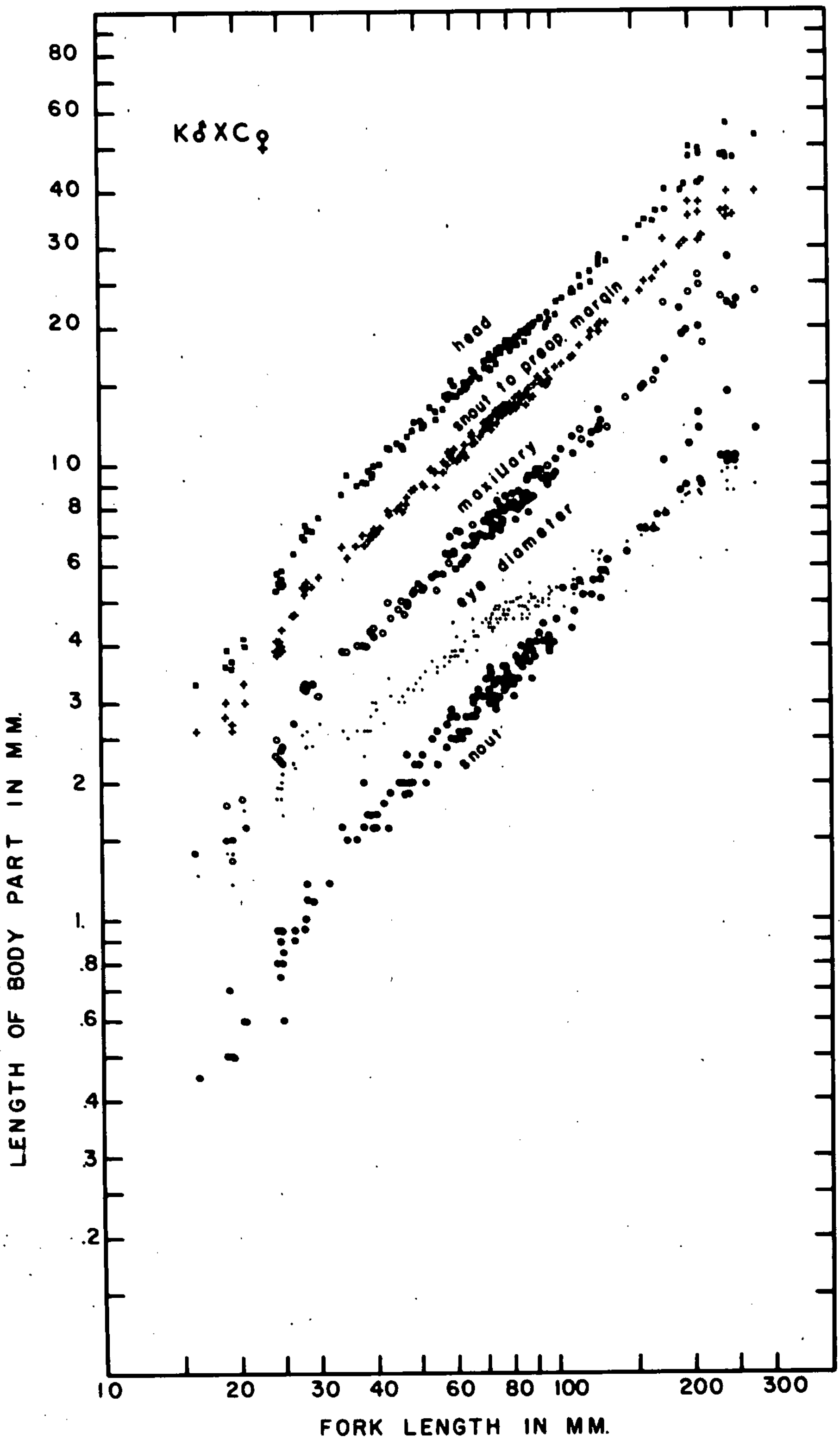

C♂XK♀
head
snout to preop. margin
maxillary
eye diameter
snout
LENGTH OF BODY PART IN MM.
FORK LENGTH IN MM.
80
60
40
30
20
10
8
6
4
3
2
1.
.8
.6
.4
.3
.2
10
20
30
40
60
80
100
200
300

Figure 6. Relative growth of head parts and fork length for rainbow male X cutthroat female hybrids (Logarthmic coordinates)



K♂ X C♀
head
snout to preop. margin
maxillary
eye diameter
snout
LENGTH OF BODY PART IN MM.
FORK LENGTH IN MM.
80
60
40
30
20
10
8
6
4
3
2
1.
.8
.6
.4
.3
.2
10
20
30
40
60
80
100
200
300

Figure 7. Approximate relation of head parts and fork length in four lots of experimental fish. Inflections at 150 mm. are due to sexual maturation. Dotted lines represent relative growth of parts on immature fish. (Logarithmic coordinates)

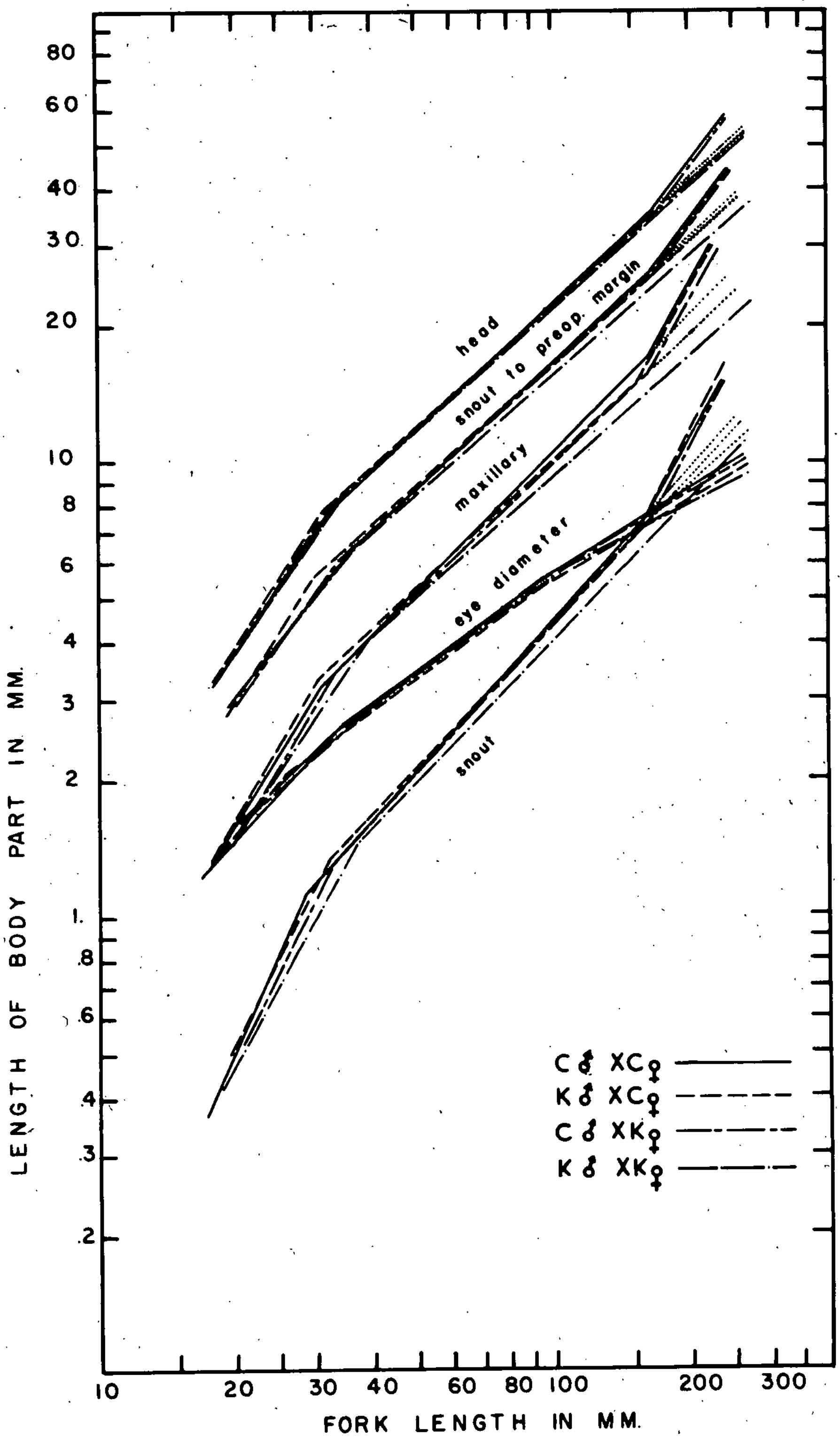
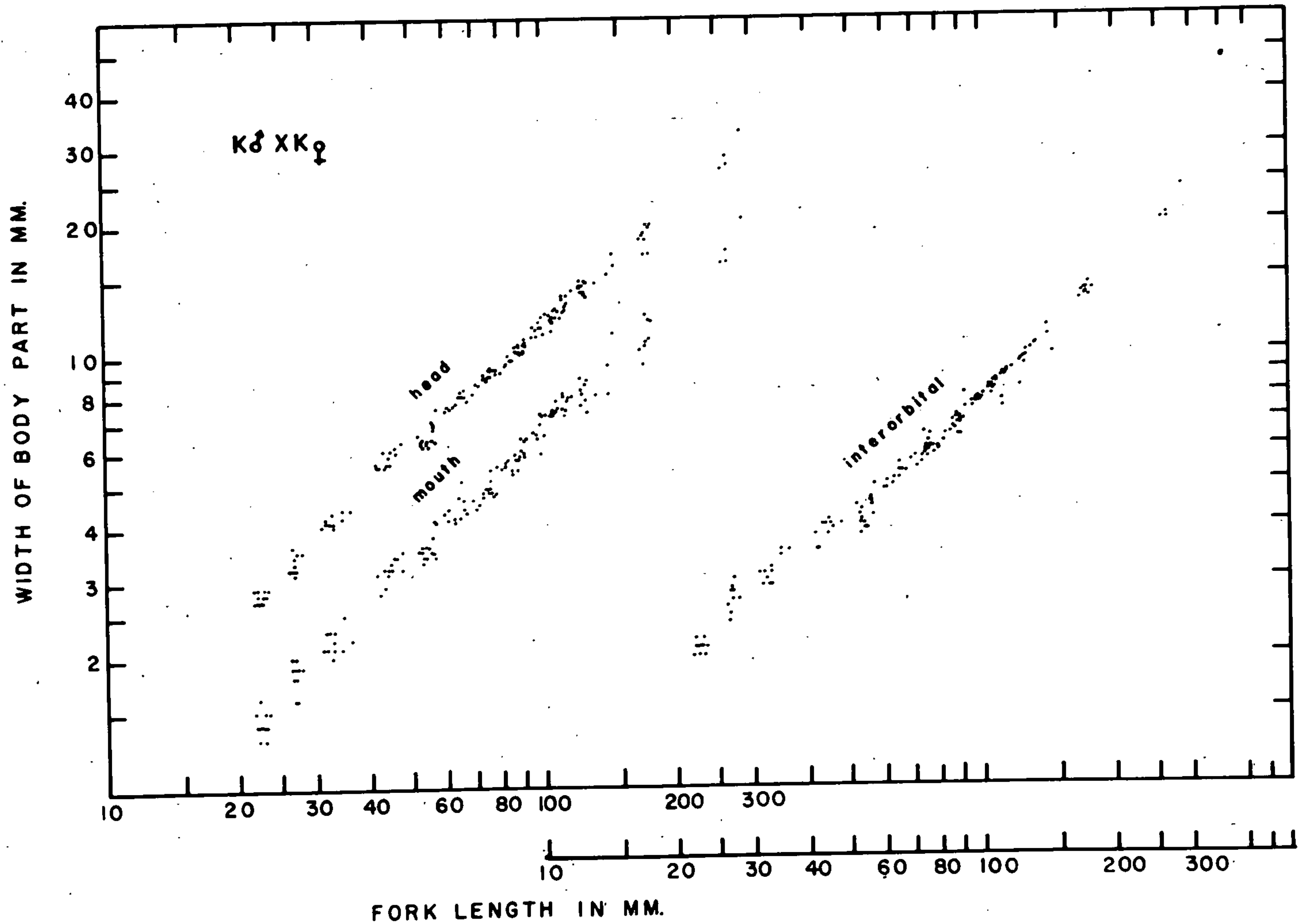

80
60
40
30
20
10
8
6
4
3
2
1.
.8
.6
.4
.3
.2
LENGTH OF BODY PART IN MM.
head
snout to preop. margin
maxillary
eye diameter
snout
C♂ XC♀
K♂ XC♀
C♂ XK♀
K♂ XK♀
10
20
30
40
60
80
100
200
300
FORK LENGTH IN MM.

Figure 8. Relative-growth of head parts and fork length for rainbow trout.
(Logarithmic coordinates)



K♂ X K♀
head
mouth
interorbital
WIDTH OF BODY PART IN MM.
FORK LENGTH IN MM.

Figure 9. Relative-growth of head parts and fork length for cutthroat trout.
(Logarithmic coordinates)

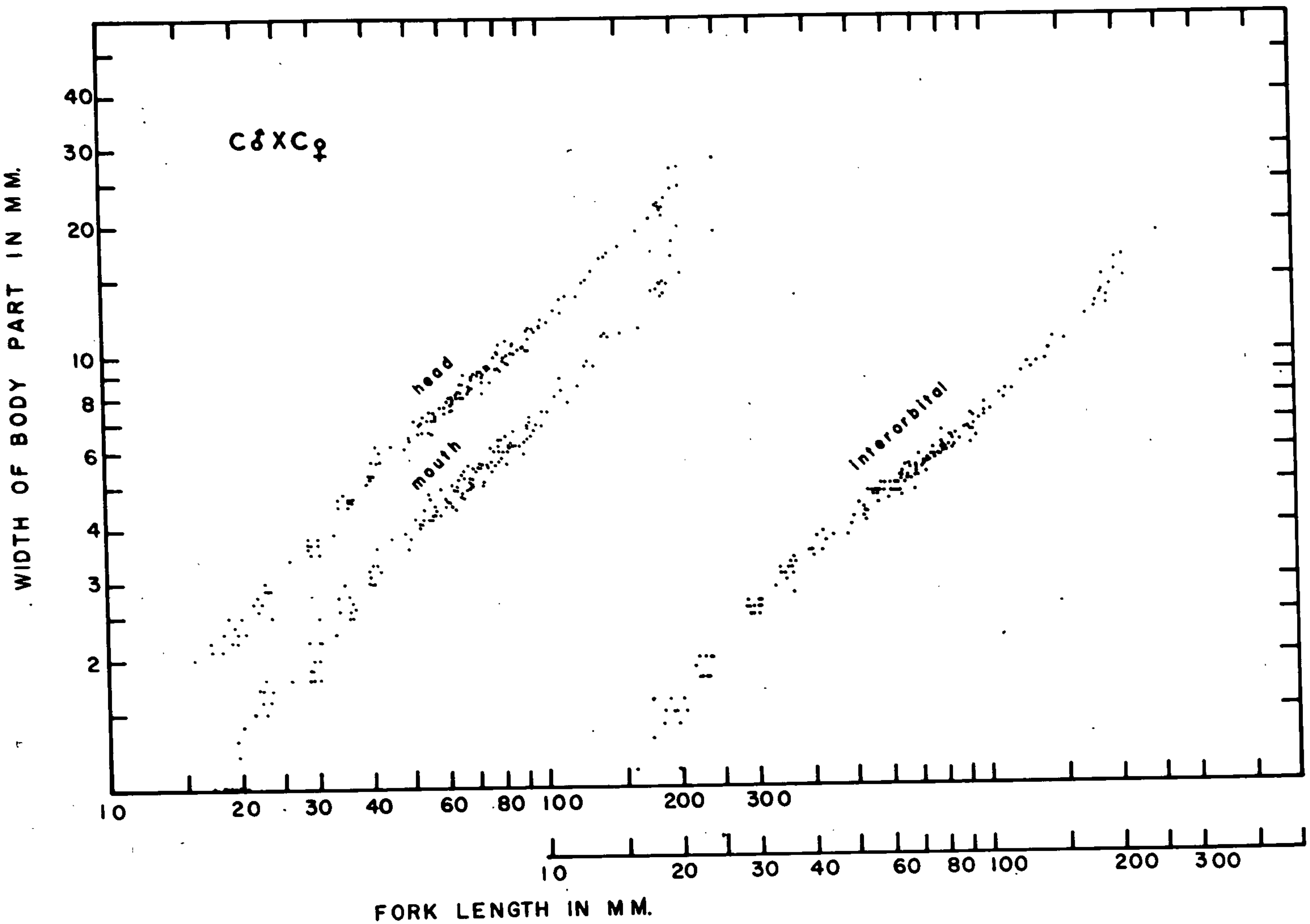

C♂XC♀
WIDTH OF BODY PART IN MM.
40
30
20
10
8
6
4
3
2
head
mouth
interorbital
10
20
30
40
60
80
100
200
300
10
20
30
40
60
80
100
200
300
FORK LENGTH IN MM.

Figure 10. Relative-growth of head parts and fork length for cutthroat male X rainbow female hybrids. (Logarithmic coordinates)

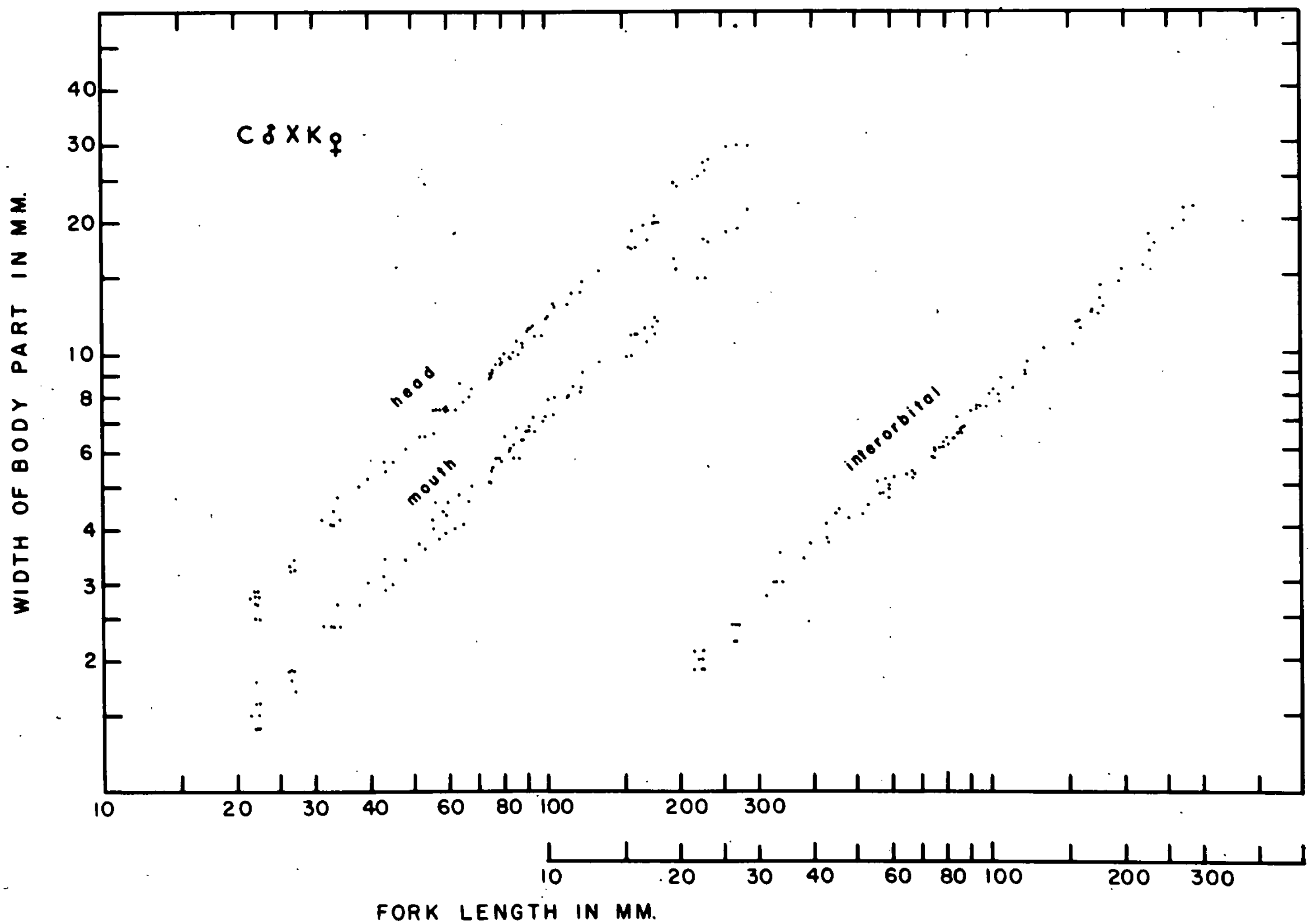
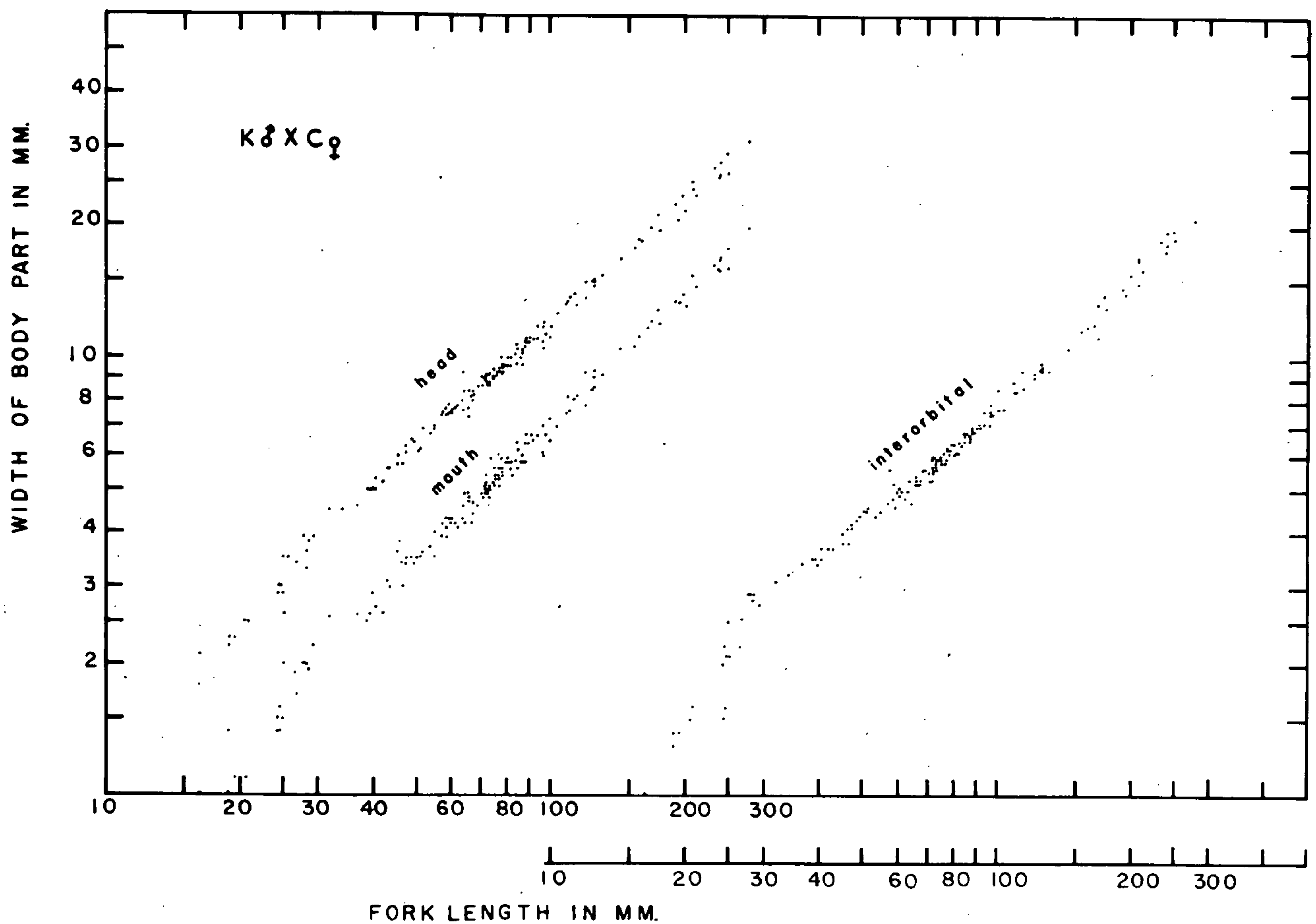

C♂XK♀
head
mouth
interorbital
WIDTH OF BODY PART IN MM.
40
30
20
10
8
6
4
3
2
10
20
30
40
60
80
100
200
300
FORK LENGTH IN MM.

Figure 11. Relative-growth of head parts and fork length for rainbow male X cutthroat female hybrids. (Logarithmic coordinates)



K♂XC♀
WIDTH OF BODY PART IN MM.
40
30
20
10
8
6
4
3
2
head
mouth
interorbital
10
20
30
40
60
80
100
200
300
FORK LENGTH IN MM.

Figure 12. Approximate relation of head parts and fork length in four lots of experimental fish.
(Logarithmic coordinates)

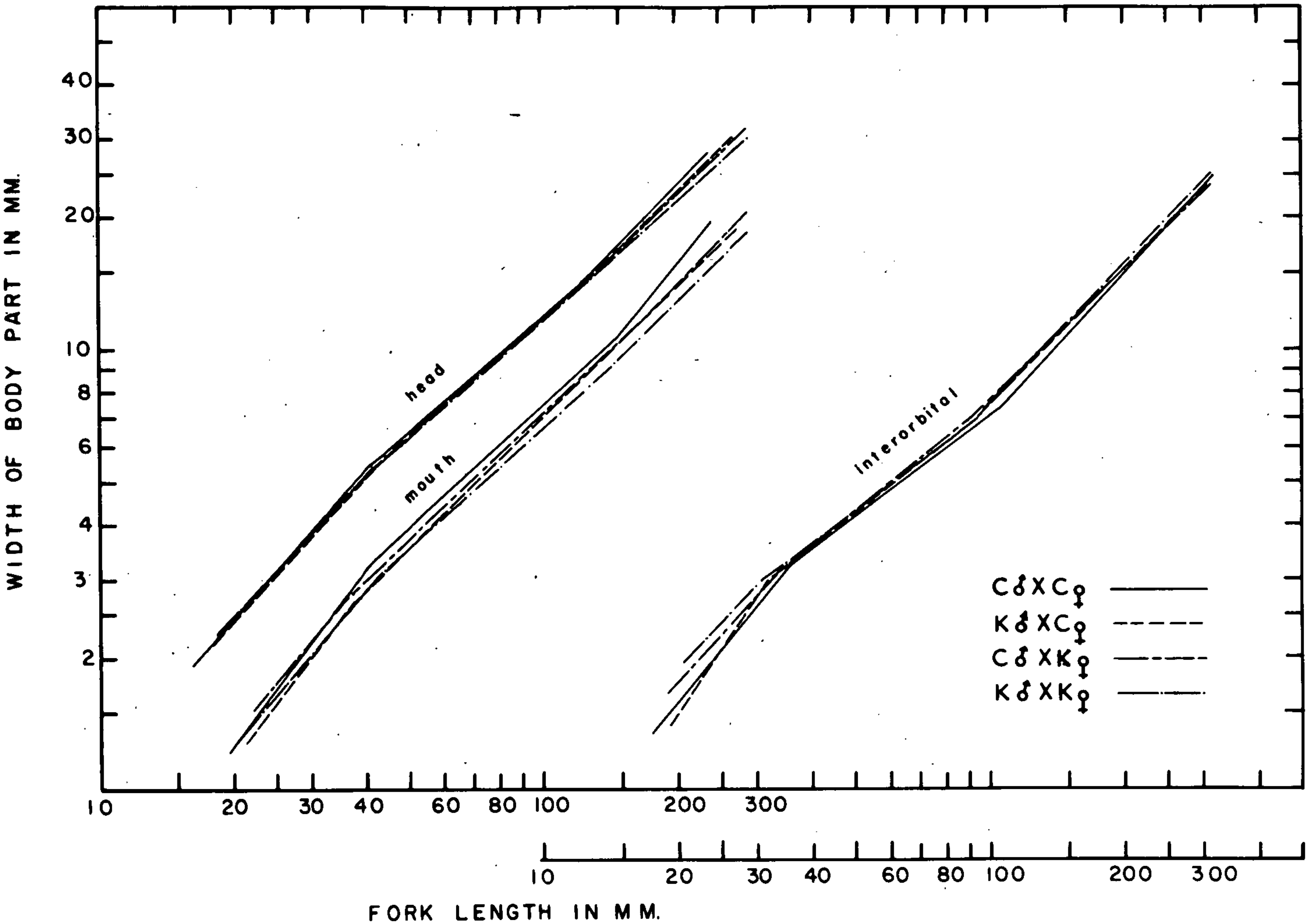
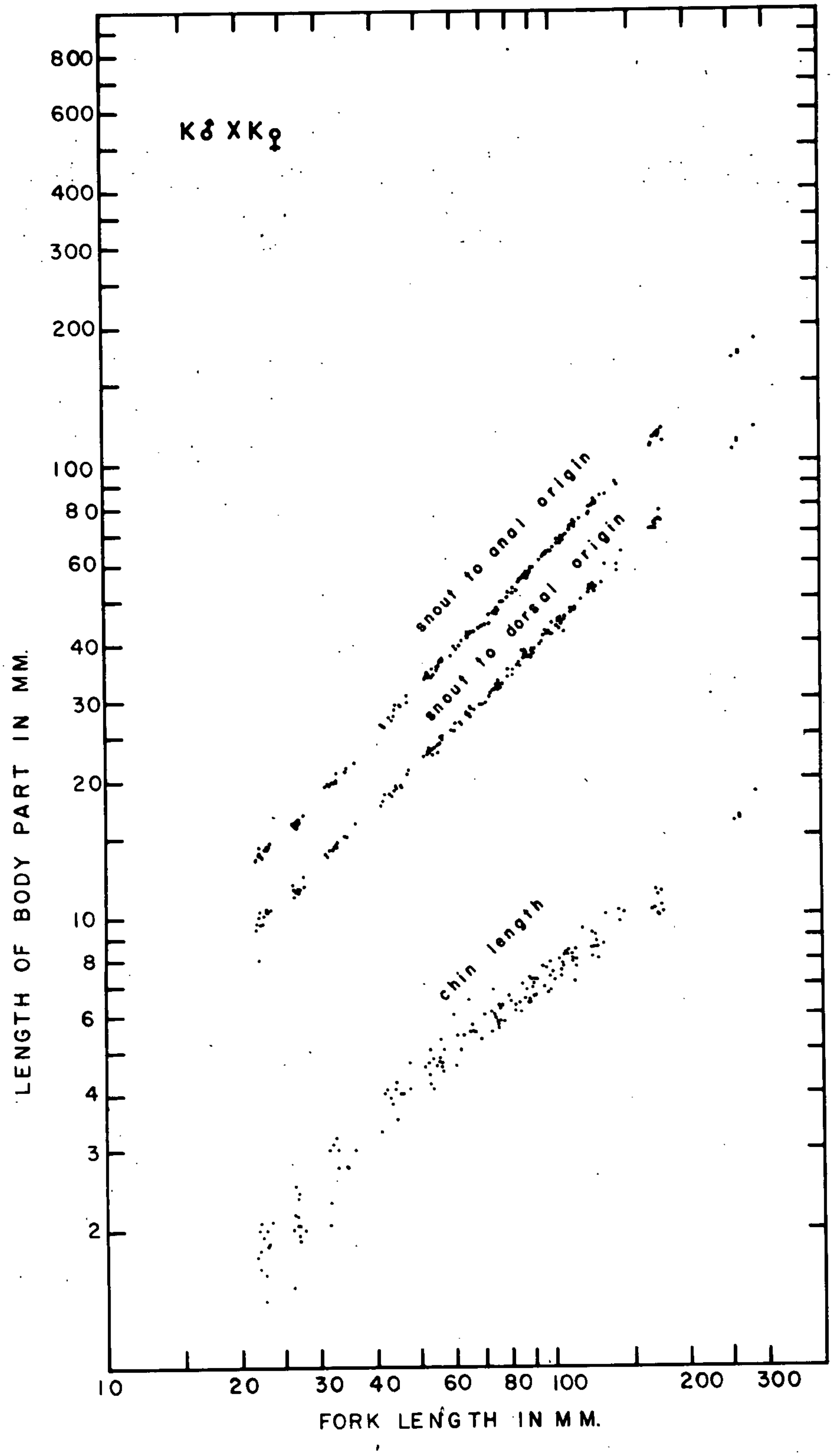

WIDTH OF BODY PART IN MM.
40
30
20
10
8
6
4
3
2
head
mouth
interorbital
C♂ X C♀
K♂ X C♀
C♂ X K♀
K♂ X K♀
10
20
30
40
60
80
100
200
300
10
20
30
40
60
80
100
200
300
FORK LENGTH IN MM.

Figure 13. Relation of head and body parts to fork length for rainbow trout. (Logarithmic coordinates)


K♂ X K♀
snout to anal origin
snout to dorsal origin
chin length
LENGTH OF BODY PART IN MM.
FORK LENGTH IN MM.
800
600
400
300
200
100
80
60
40
30
20
10
8
6
4
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2
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100
200
300

Figure 14. Relation of head and body parts to fork length for cutthroat trout. (Logarithmic coordinates)

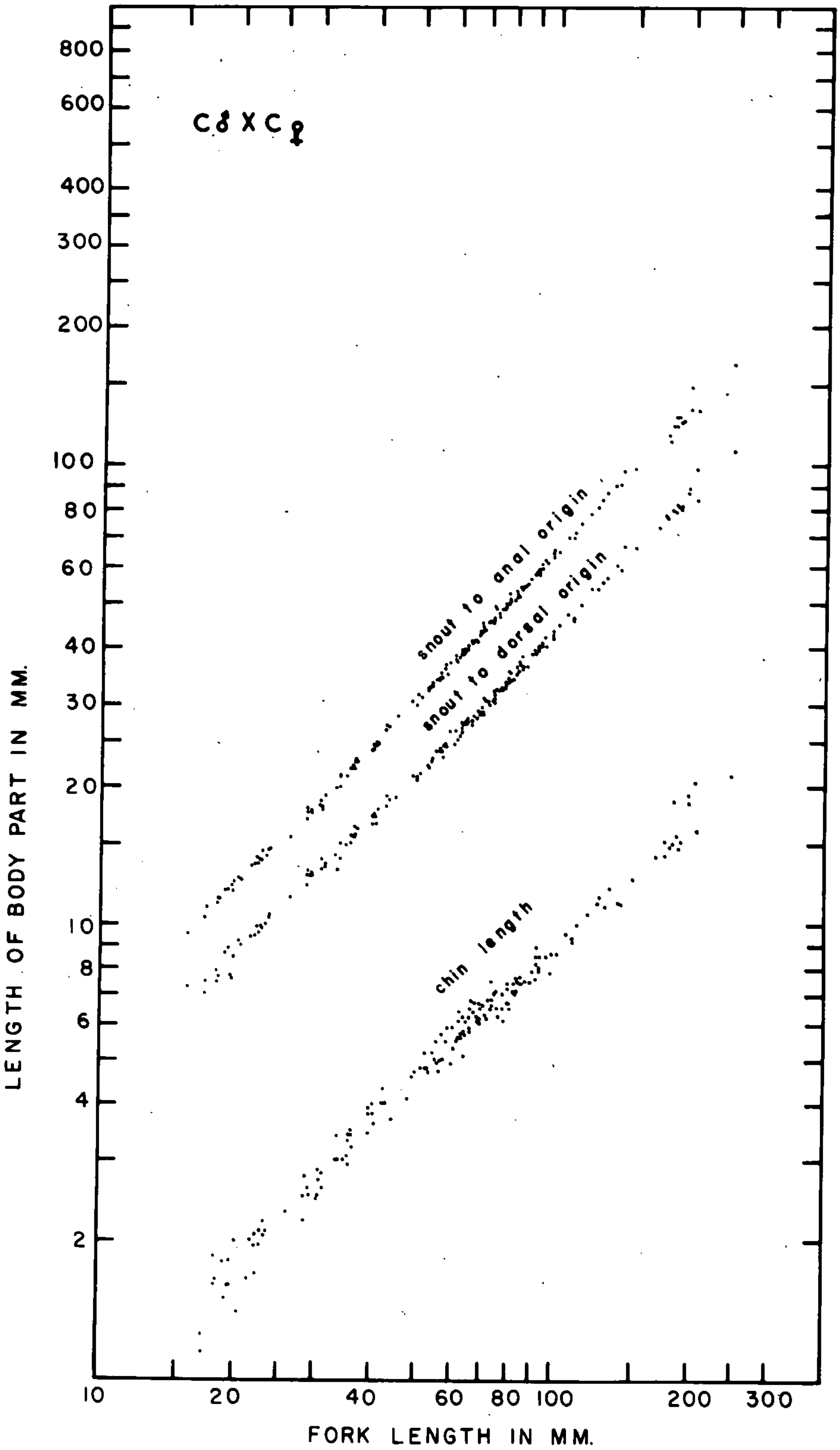
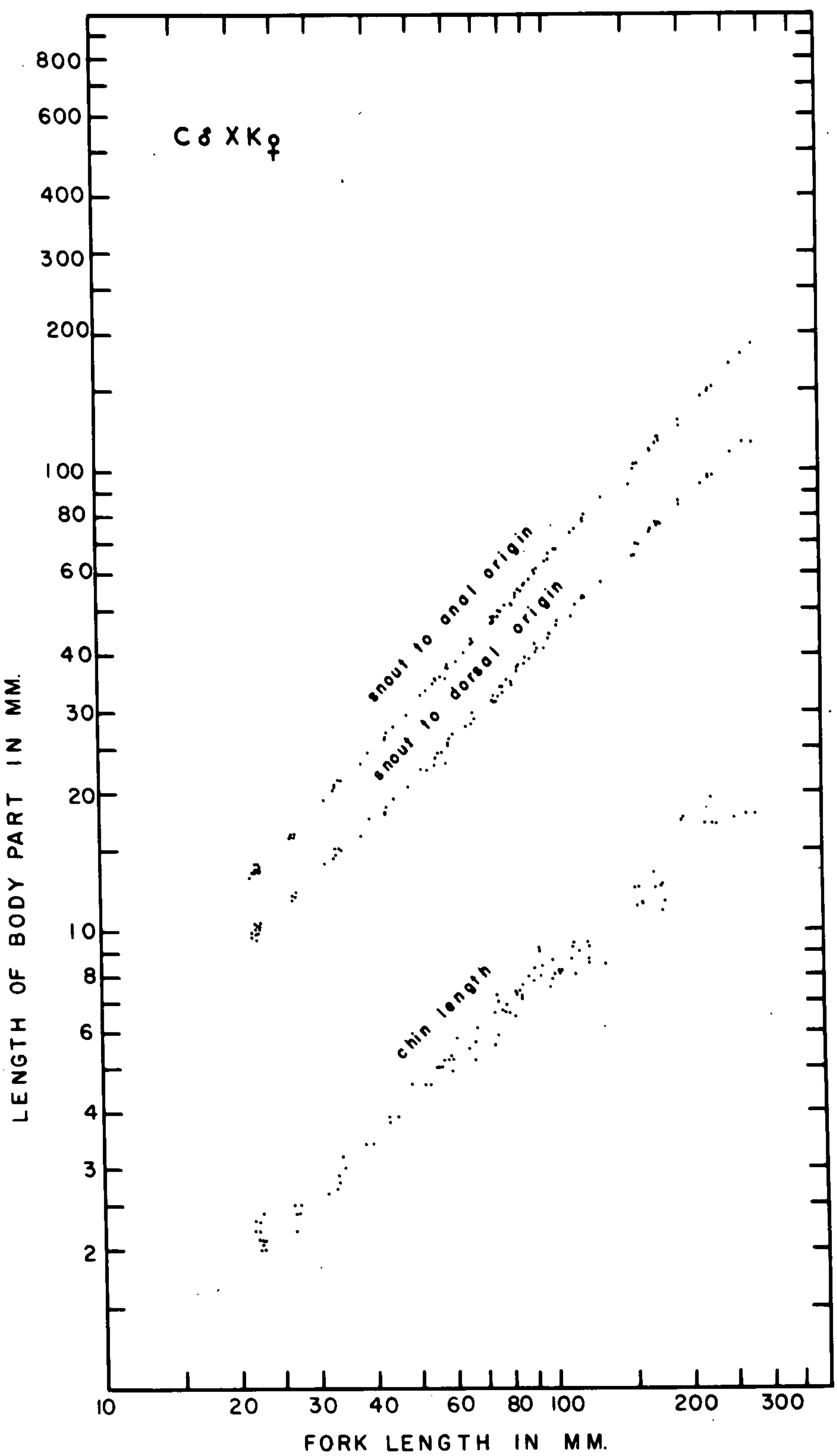

C♂ X C♀
snout to anal origin
snout to dorsal origin
chin length
LENGTH OF BODY PART IN MM.
800
600
400
300
200
100
80
60
40
30
20
10
8
6
4
2
10
20
40
60
80
100
200
300
FORK LENGTH IN MM.

Figure 15. Relation of head and body parts to fork length for cutthroat male X rainbow female hybrids.
(Logarithmic coordinates)



C♂ X K♀
LENGTH OF BODY PART IN MM.
FORK LENGTH IN MM.
snout to anal origin
snout to dorsal origin
chin length
800
600
400
300
200
100
80
60
40
30
20
10
8
6
4
3
2
10
20
30
40
60
80
100
200
300

Figure 16. Relation of head and body parts to fork length for rainbow male X cutthroat female hybrids.
(Logarithmic coordinates)

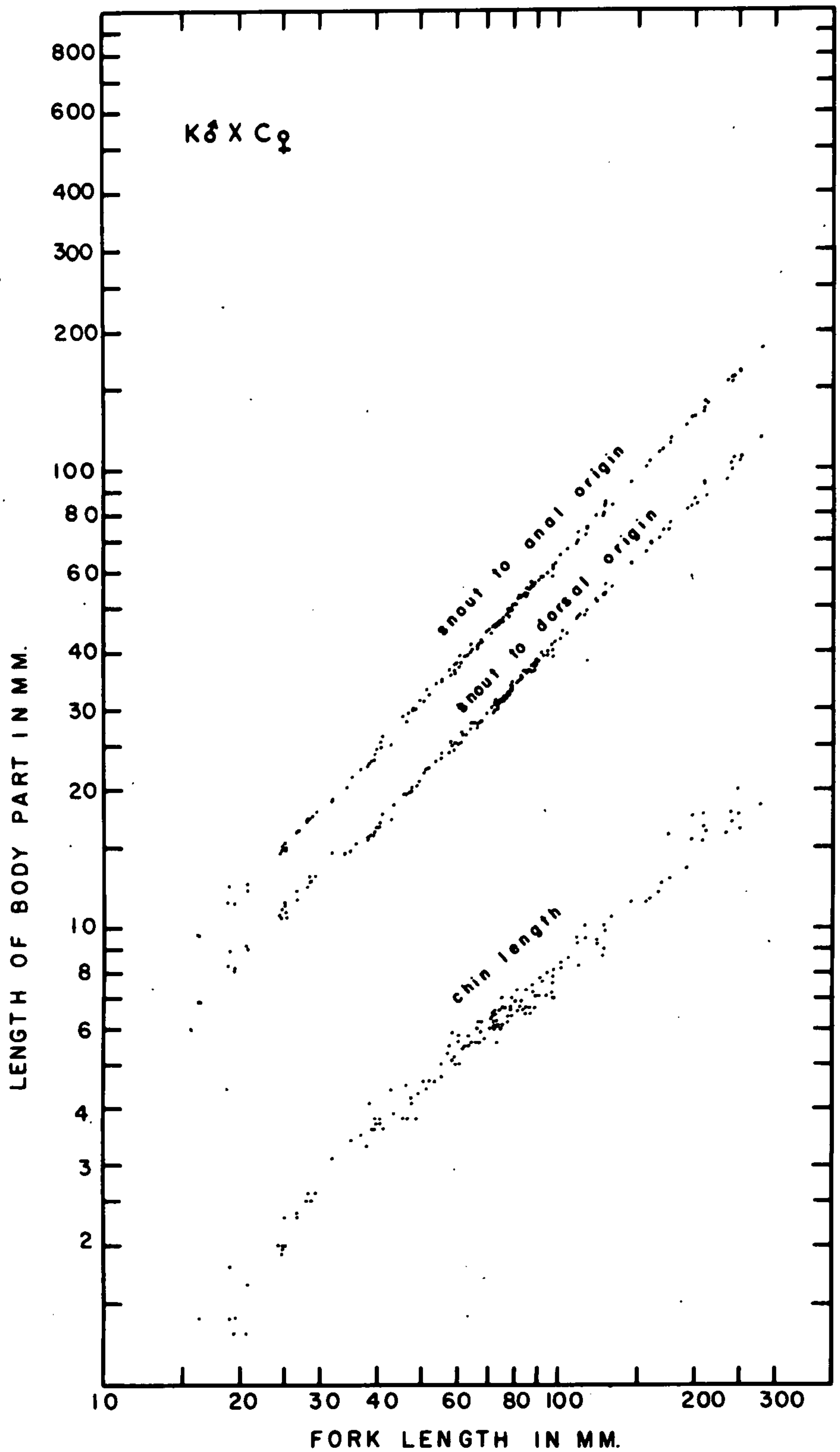
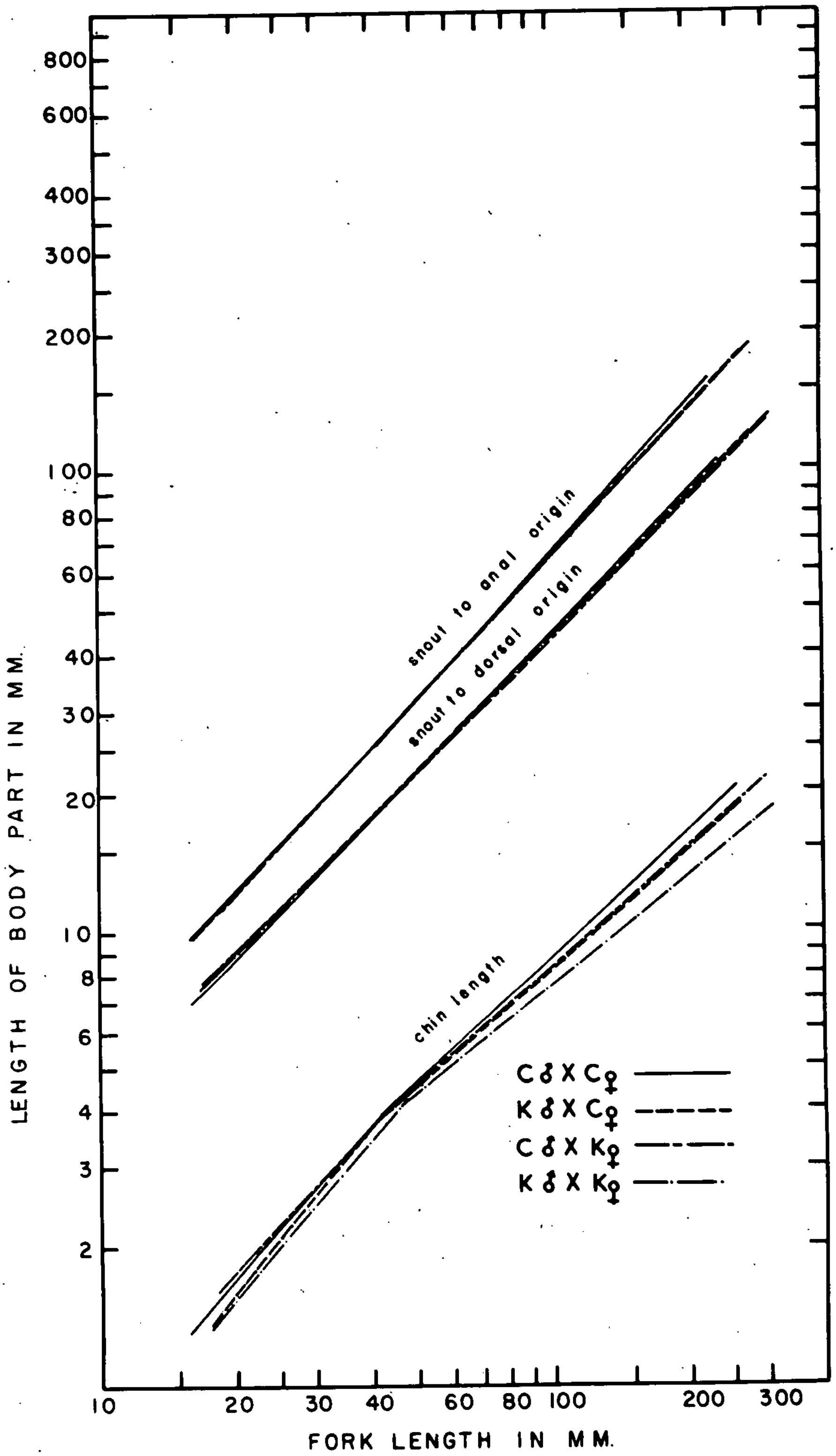

K♂ X C♀
snout to anal origin
snout to dorsal origin
chin length
LENGTH OF BODY PART IN MM.
FORK LENGTH IN MM.
800
600
400
300
200
100
80
60
40
30
20
10
8
6
4
3
2
10
20
30
40
60
80
100
200
300

Figure 17. Approximate relation of head and body parts to fork length in four lots of experimental fish.
(Logarithmic coordinates)



800
600
400
300
200
100
80
60
40
30
20
10
8
6
4
3
2
LENGTH OF BODY PART IN MM.
snout to anal origin
snout to dorsal origin
chin length
C♂ X C♀
K♂ X C♀
C♂ X K♀
K♂ X K♀
10
20
30
40
60
80
100
200
300
FORK LENGTH IN MM.

Relative growth of head parts on wild fish

Two samples of small wild cutthroat were compared with similar samples of rainbows (Figure 19). The pairs of species compared were taken together in one case, Black Creek, Vancouver Island, and from the same drainage system in the second comparison. (The Bulkley River and Lakelse River are both tributary to the Skeena River). Although the samples are small the plots of the data for pairs of species from each locality, strongly suggest that chin, maxillary, preopercular and head length are greater in cutthroats than rainbows. Only one comparison of large wild fish was made. (Figure 20,A). These fish are not directly comparable because the rainbow trout came from Fraser Lake, in the upper Fraser River, while the cutthroats were from the lower Fraser River. The sample is small but it indicates that cutthroats have larger heads and head parts. The samples of adults compared contained no spawning fish. Comparisons made between samples of the two species may be confusing if the individuals of one species are sexually mature. The spawning fish from Cowichan River (Figure 20,B) exhibit sexual dimorphism. Differences between male and female spawners has been observed in runs of Kamloops trout at Loon Lake, in the interior of British Columbia. In view of this it seems likely that spawning male rainbow trout would have head parts as large or larger than female cutthroats.

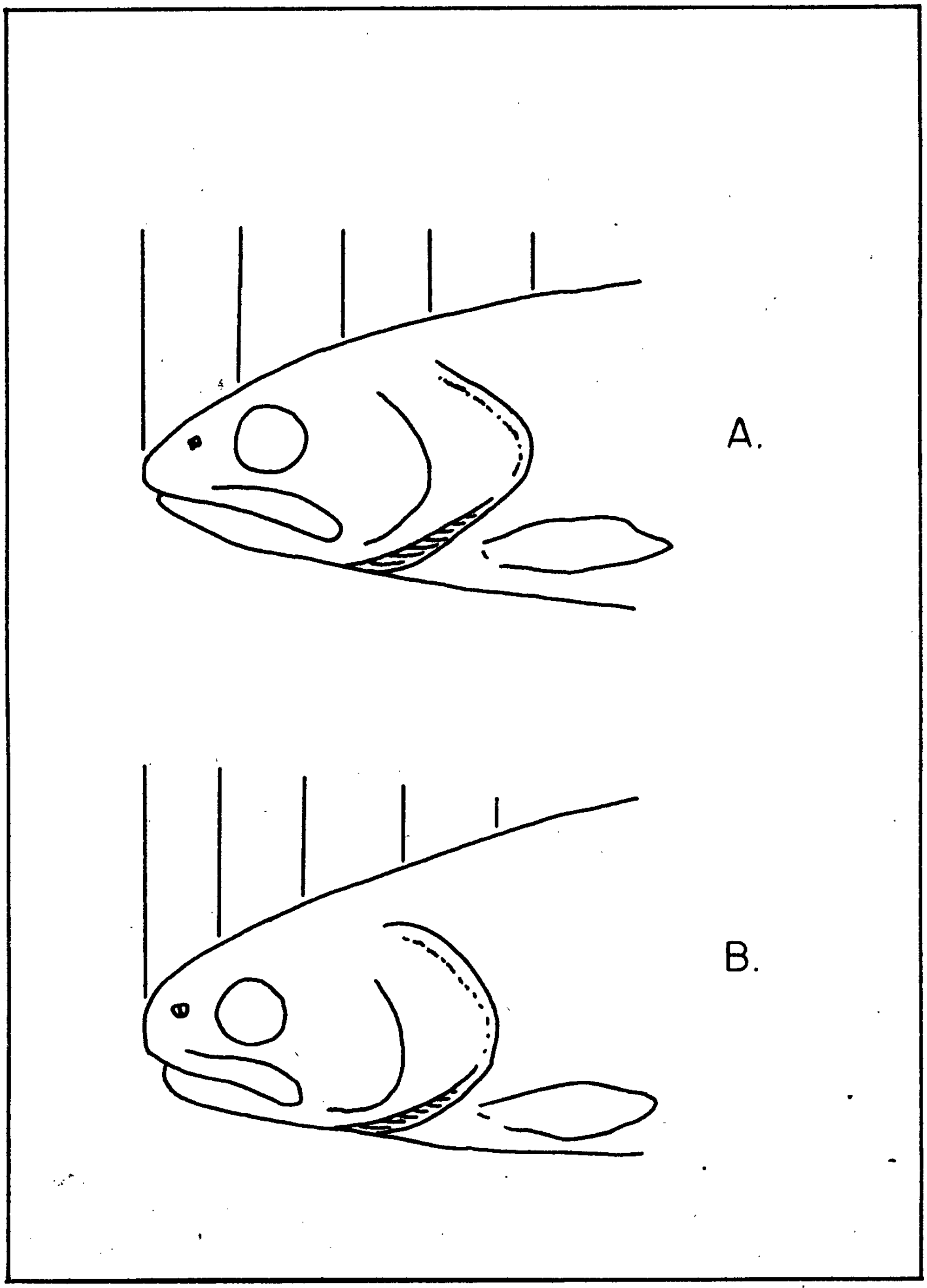


Figure 18. Drawings of immature male cutthroat (A) and rainbow trout (B). Both fish are 262 mm. long. Guide lines indicate snout length, maxillary length, preopercular length and head length.

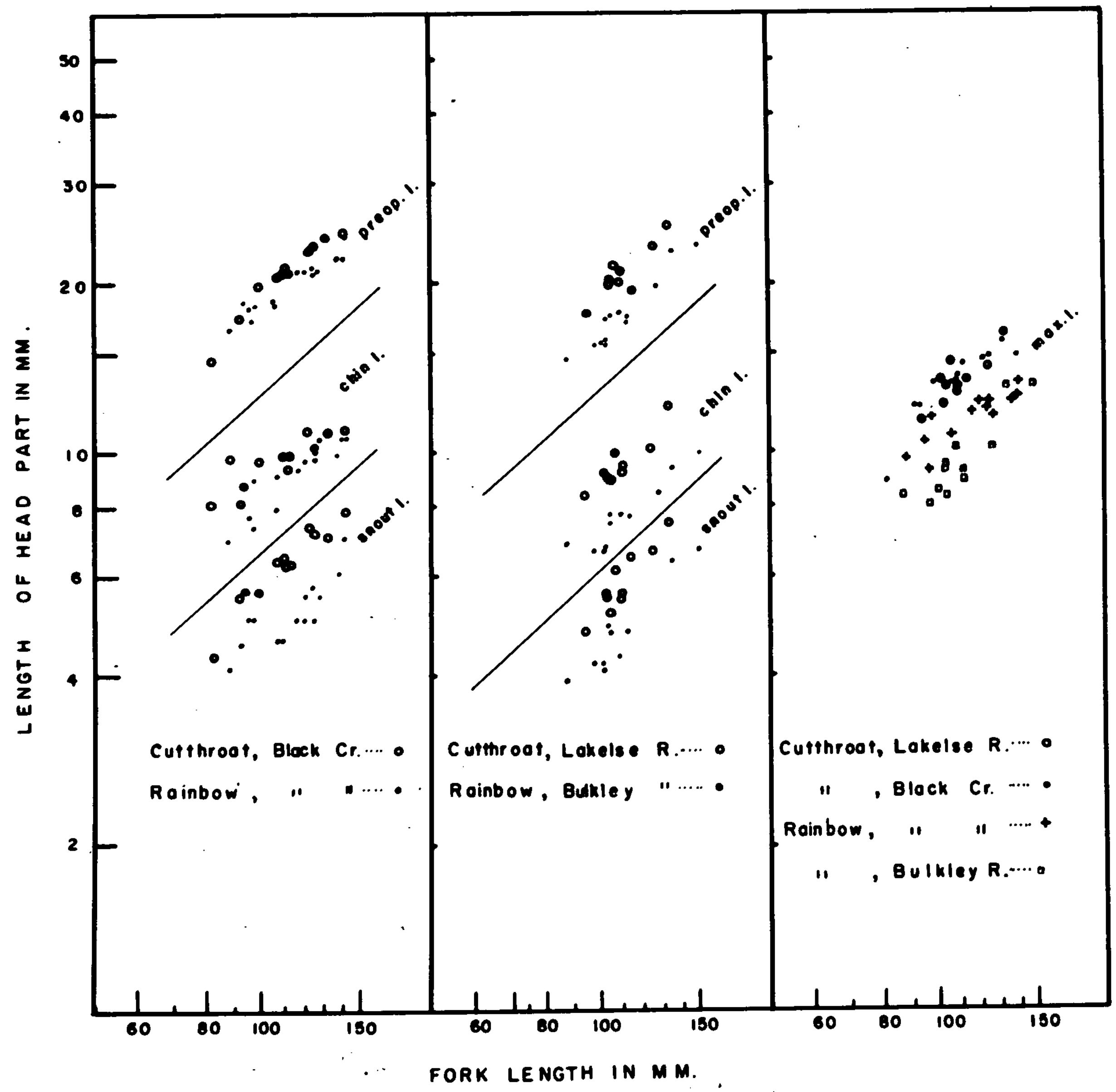


Figure 19. Relative-growth of head parts and fork length samples of wild fish. (Logarithmic coordinates)

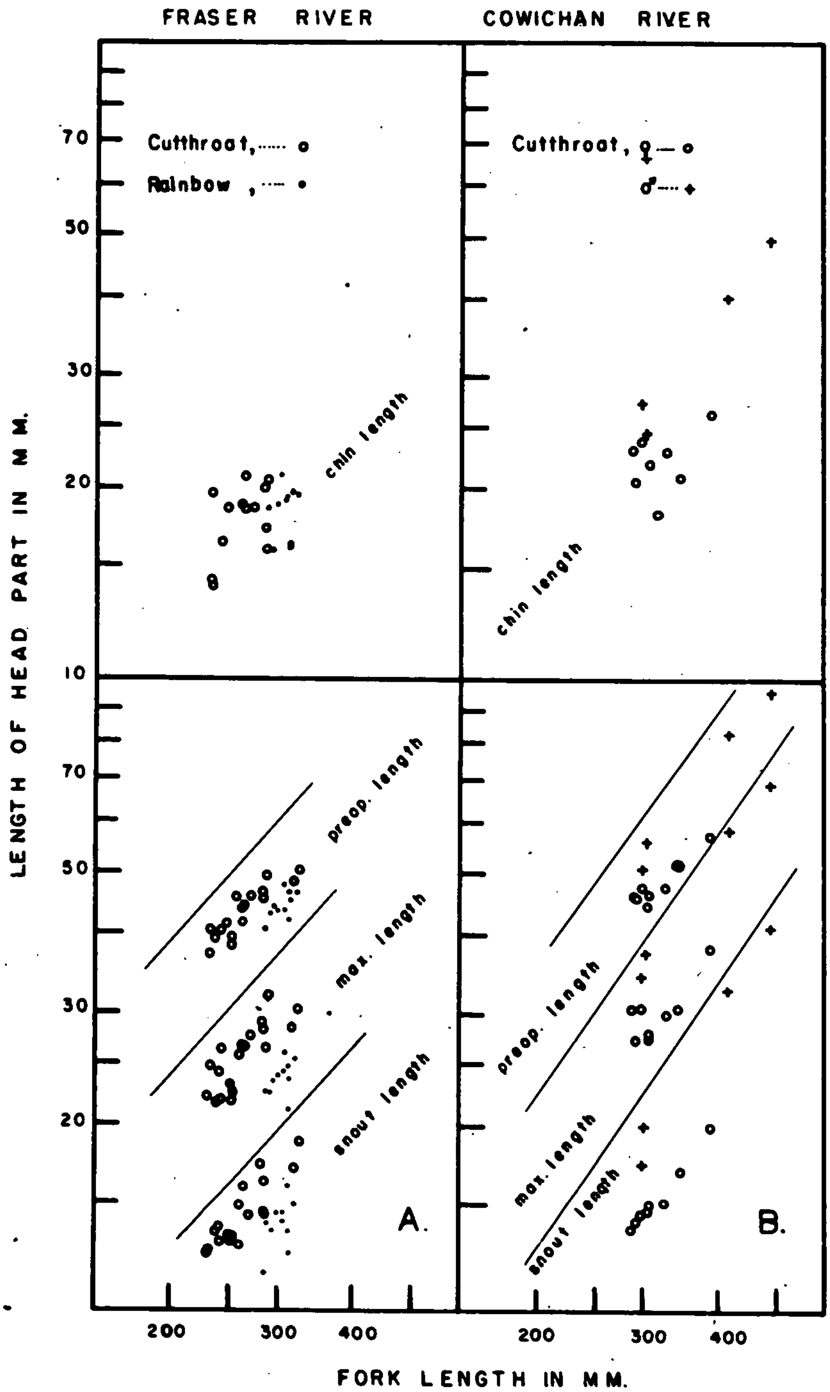


Figure 20. A. Relative-growth of head parts and fork length in samples of wild adult fish from the Fraser River system.

B. Illustration of sexual differences in cutthroat spawners from the Cowichan River. (Logarithmic coordinates)

Relative-growth of body parts

Snout to dorsal origin: No growth inflections occur in the plot of snout to dorsal length on fork length (Figures 13, 14, 15, 16 and 17).

All four lots of fish are similar.

Snout to anal origin: No growth inflections occur in the graphs for snout to anal on fork length (Figures 13, 14, 15, 16 and 17).

Snout to anal measurements are similar in all lots of fish compared.

Body depth at vent: Growth curves for body depth at vent, (Figures 21, 22, 23, 24 and 25), show a sharp inflection at 30 mm. fork length but no further inflections occur. Rate of increase in depth is rapid until the 30 mm. inflection after which the relative growth rate is reduced.

No differences are revealed, between parental type lots or hybrids, by the plots of depth at vent on fork length. (Figure 25).

Peduncle depth: Peduncle depth, in all four lots, increases rapidly until 30 mm. fork length. At this point the curve shows a strong inflection following which the growth is linear and no more inflections occur.

Cutthroat trout have deeper peduncles than rainbows and hybrid peduncles appear to be intermediate between parental types.

Snout to adipose measurements: Measurements of snout to adipose, were made on large fish but preliminary plots revealed no differences so full series of measurements were not made. No data is presented for this measurement.

Summary of relative growth of body parts

Plots of length of body from snout to dorsal and snout to anal origin revealed no growth inflections and no species differences. Measurements which were made on distance from snout to anal revealed no species differences. Body depth at vent and at peduncle, when plotted on fork length, revealed one growth inflection at 30 mm. The development of these parts was characterized by rapid growth up to 30 mm. fork length. After 30 mm. the growth rate was reduced. Peduncle depth was the only measurement which revealed a specific difference.

Meristic Comparisons

Ray Counts

Figure 26 illustrates the ray counts obtained on dorsal anal and caudal in four lots of fish.

Dorsal ray counts: these were significantly lower for cutthroat than for rainbows. ($p < .01$). To obtain these counts all rays, including short ones at the front of the fin, were counted. Mean dorsal ray counts for the four lots are:

rainbow 14.52
rainbow male X cutthroat female . 14.6
cutthroat male X rainbow female . 14.5
cutthroats 13.91

Both hybrid lots resemble the rainbow but the sample size, in the cutthroat male X rainbow female hybrid lot is small (14).

Anal ray counts: These were significantly lower for cutthroats ($p < .02$). Counts were made the same as for dorsal fin. Mean anal ray counts for the four lots are:

rainbow 14.15
rainbow male X cutthroat female . 13.8
cutthroat male X rainbow female . 14.5
cutthroat 13.47

Tests for significant differences, between hybrid lots and parent type lots, were made. The mean for one hybrid lot is intermediate and the mean for the other is greater than either parent type mean.

Caudal rays: Mean counts, for caudal rays, are the same for rainbow and cutthroat. No caudal ray counts were made on hybrids.

Figure 21. Relation of body depth at vent and at peduncle to fork length for rainbow trout (Logarithmic coordinates)

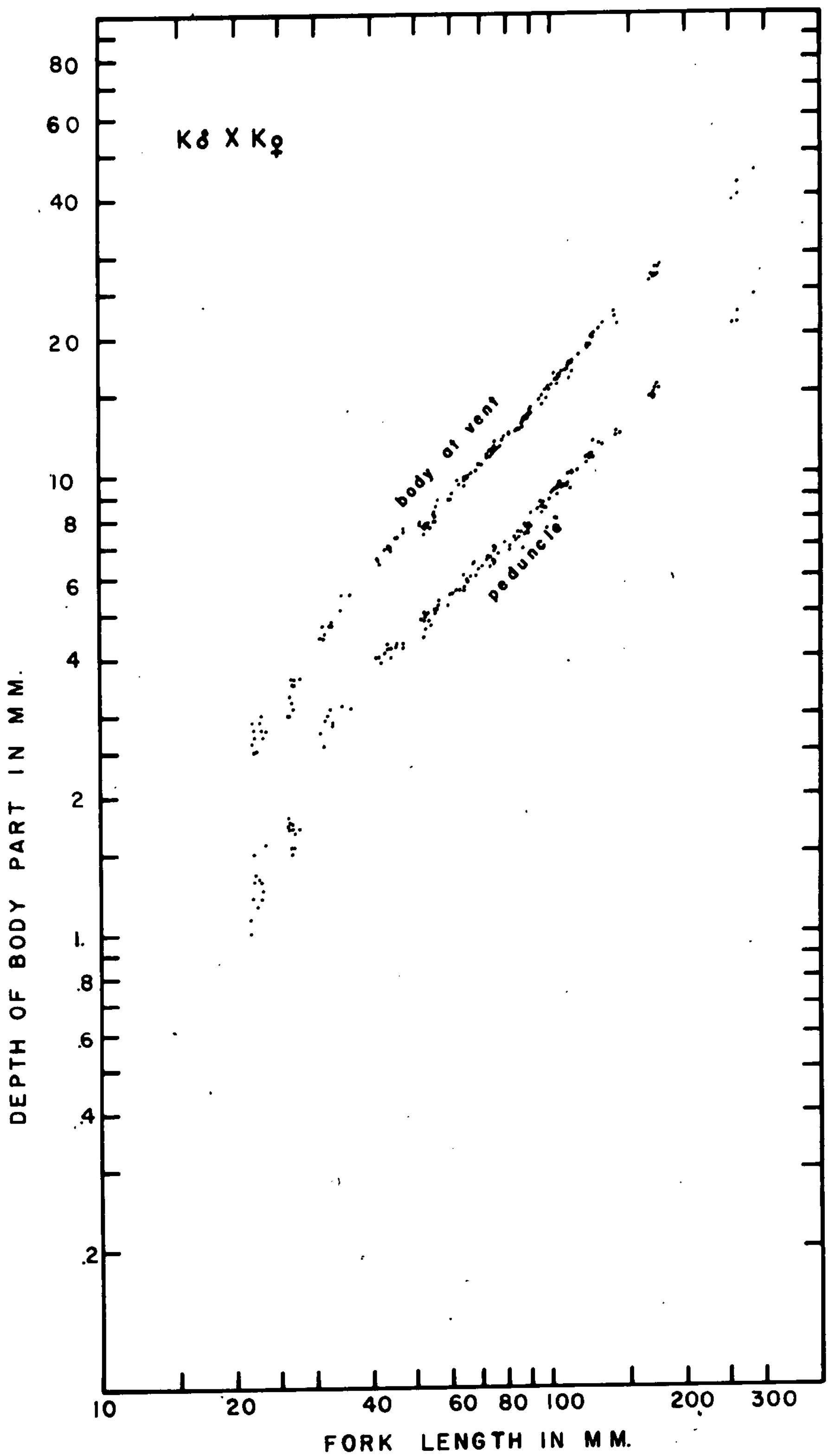

K♂ X K♀
body at vent
peduncle
DEPTH OF BODY PART IN MM.
80
60
40
20
10
8
6
4
2
1.
.8
.6
.4
.2
10
20
40
60
80
100
200
300
FORK LENGTH IN MM.

Figure 22. Relation of body depth at vent and at peduncle to fork length for cutthroat trout (Logarithmic coordinates)

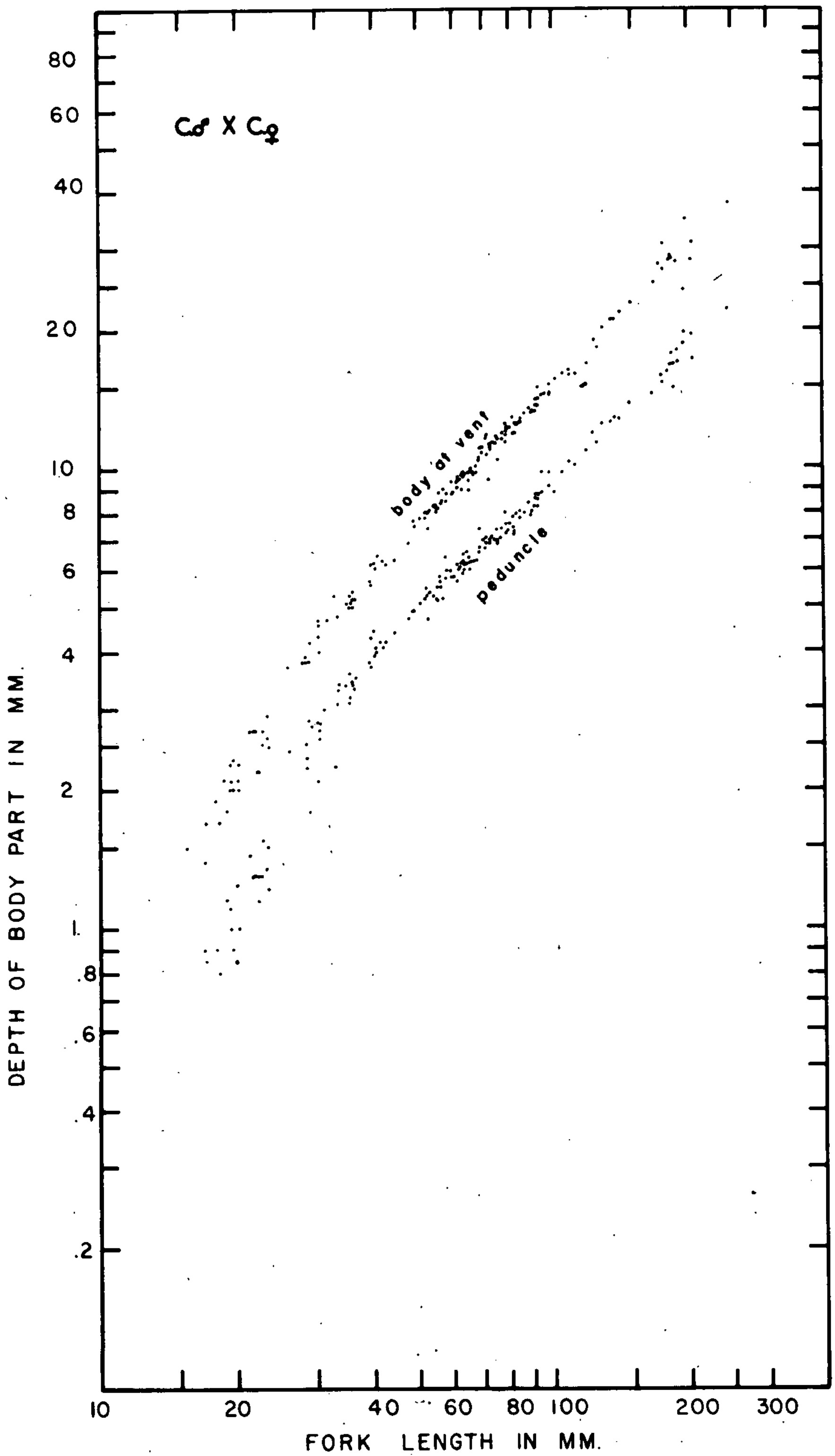

Cô X C♀
body at vent
peduncle
DEPTH OF BODY PART IN MM.
80
60
40
20
10
8
6
4
2
1.
.8
.6
.4
.2
10
20
40
60
80
100
200
300
FORK LENGTH IN MM.

Figure 23. Relation of body depth at vent and at peduncle to fork length for cutthroat male X rainbow female hybrids (Logarithmic coordinates)

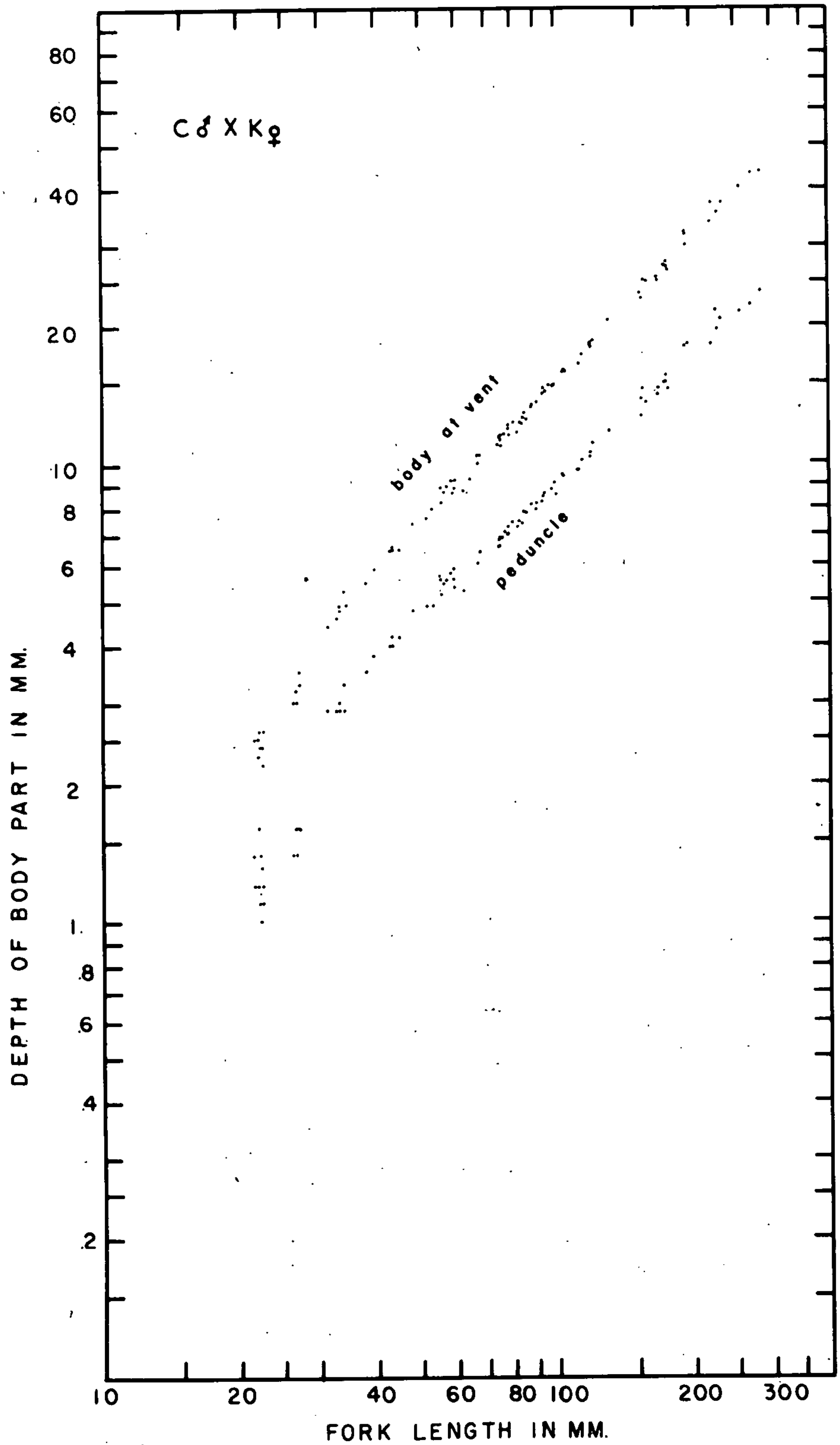

C♂ X K♀
body at vent
peduncle
DEPTH OF BODY PART IN MM.
80
60
40
20
10
8
6
4
2
1.
.8
.6
.4
.2
10
20
40
60
80
100
200
300
FORK LENGTH IN MM.

Figure 24. Relation of body depth at vent and at peduncle to fork length for rainbow male X cutthroat female hybrids (Logarithmic coordinates)

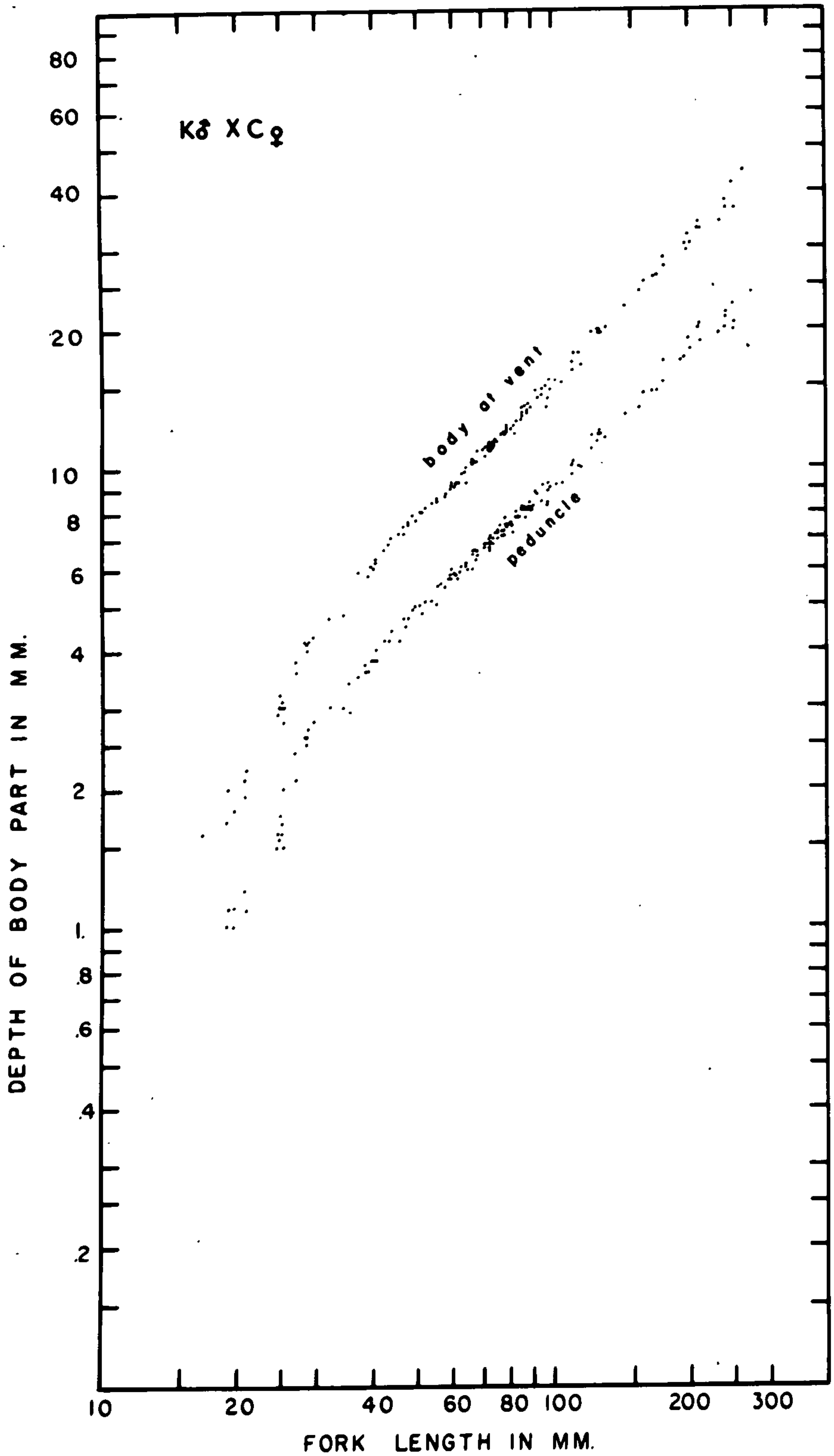

K♂ X C♀
body at vent
peduncle
80
60
40
20
10
8
6
4
2
1.
.8
.6
.4
.2
DEPTH OF BODY PART IN MM.
10
20
40
60
80
100
200
300
FORK LENGTH IN MM.

Figure 25. Approximate relation of body depth at vent and at peduncle to fork length in four lots of experimental fish
(logarithmic coordinates)

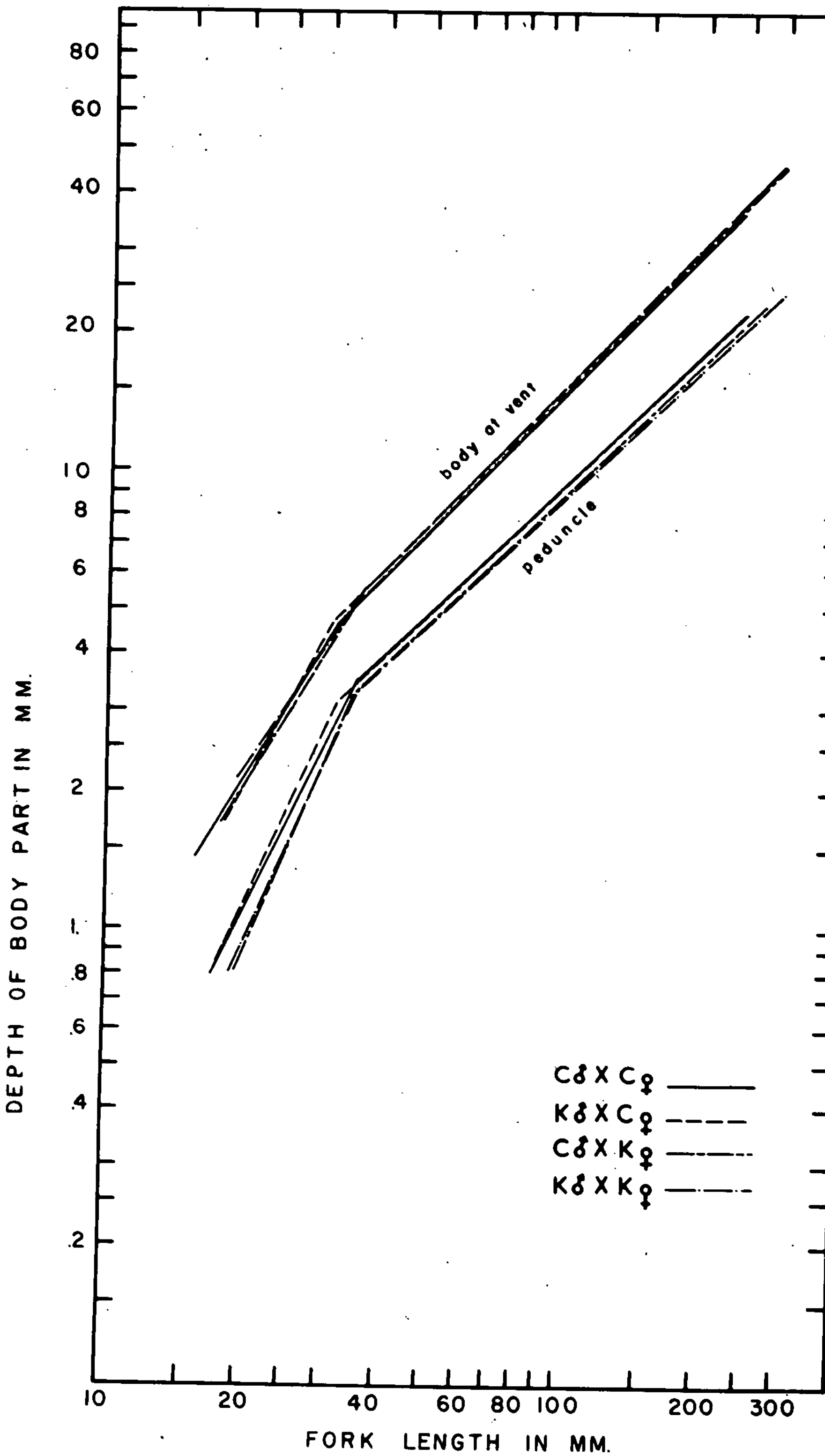
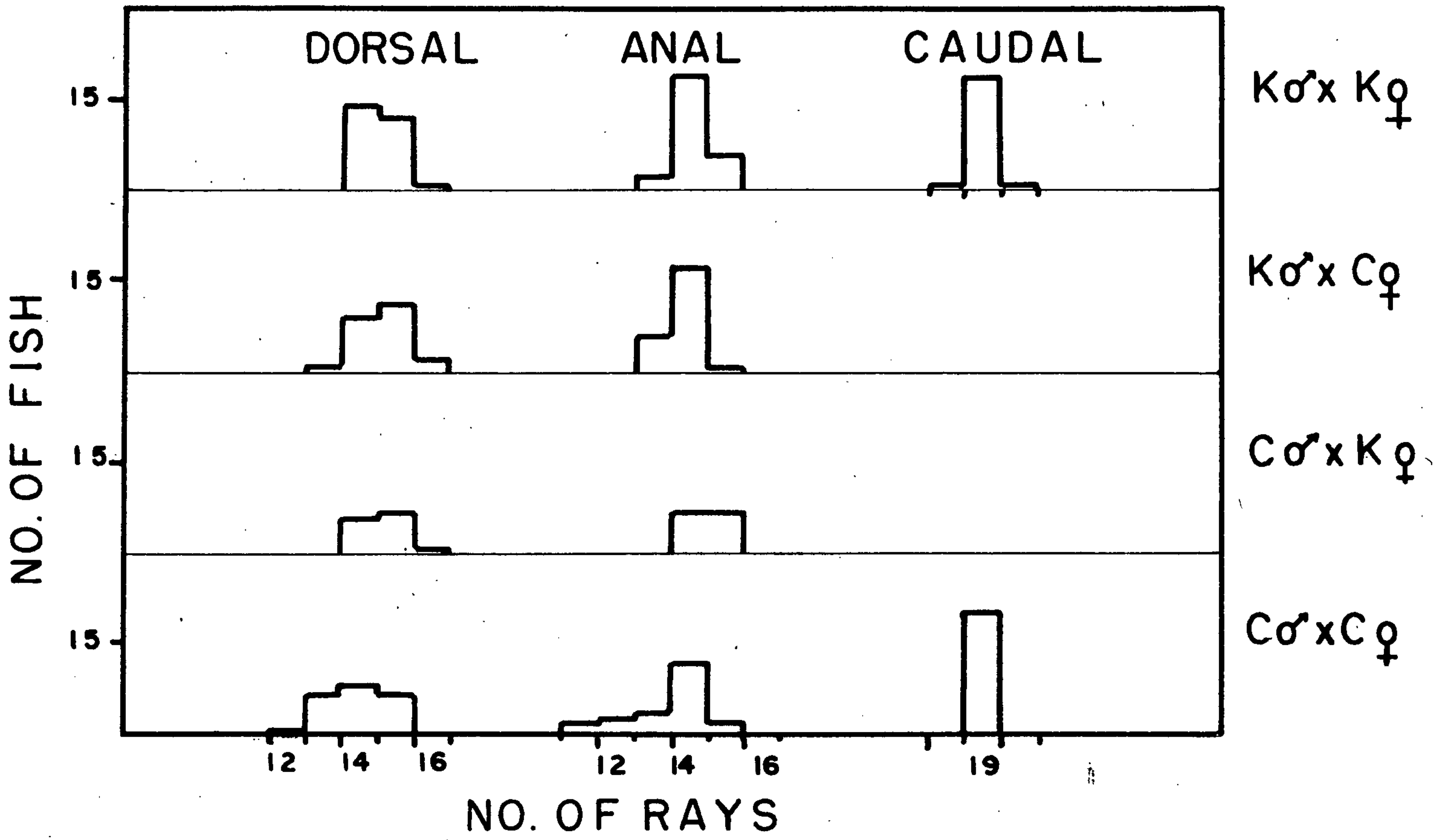

80
60
40
20
10
8
6
4
2
1.
.8
.6
.4
.2
DEPTH OF BODY PART IN MM.
10
20
40
60
80
100
200
300
FORK LENGTH IN MM.
body at vent
peduncle
C♂ X C♀
K♂ X C♀
C♂ X K♀
K♂ X K♀

Figure 26. Ray counts in four lots of experimental fish. Counts include all short rays at the anterior of the fins and the last split ray in the dorsal and anal is counted as one. Only caudal rays reaching posterior margin of the fin are counted



DORSAL
ANAL
CAUDAL
15
15
15
15
K♂ x K♀
K♂ x C♀
C♂ x K♀
C♂ x C♀
NO. OF FISH
12
14
16
12
14
16
19
NO. OF RAYS

Scale Counts

Scale counts (Figure 27), for cutthroat and rainbow were significantly different ($p < .01$). Contrary to most authorities, Neave (1943), Vernon and McMynn (Unpublished) and Carl and Clemens (1953), rainbow trout had higher scale counts than cutthroats. Scale counts were made about eight scale rows above the lateral line. Mean scale counts are given below:

rainbow	149.85
rainbow male X cutthroat female .	143.27
cutthroat male X rainbow female .	147.47
cutthroat	141.05

The scale counts in the hybrid lots appear to resemble the female parent species.

Vertebral Counts

Vertebral counts, (Figure 27,) were significantly different in rainbow and cutthroat ($p < .01$). Mean vertebral counts for the four lots are given below:

rainbow	63.54
rainbow male X cutthroat female .	61.95
cutthroat male X rainbow female .	63.55
cutthroat	61.00

Hybrid vertebral counts tended to resemble those of female parent species. This is illustrated by the fact that there is a difference between the cutthroats and cutthroat male X rainbow female hybrids in vertebral count. Tests showed a significant difference between hybrid lots. ($p < .01$)

Summary of meristic data

Rainbow trout had higher dorsal and anal ray counts than cutthroats. Hybrid dorsal ray counts resembled those of the rainbows. Anal ray counts resembled the rainbow in one lot of hybrids and were intermediate in the other lot. Caudal ray counts were the same for both species.

Rainbow scale counts were highest, hybrids were intermediate but mean scale counts resembled female parent type most closely.

Rainbow vertebral counts were higher than cutthroats, those of the hybrids resembled the female parent type.

Counts on teeth and pyloric caeca

Tooth counts

Means for tooth counts given in Figures 27 and 28 are summarized in Table III.

TABLE III

Mean tooth counts in four lots of experimental fish the same age

(Male fish are indicated first in all crosses)

	K X K	K X C	C X K	C X C
Premaxillary	7.3	8.5	8.5	7.2
Maxillary	19.65	20.95	21.4	18.59
Palatine	15.05	16.00	18.8	15.18
Dentary	15.5	18.31	19.1	17.04
Tongue	9.85	14.0	15.4	11.63
Vomer	16.8	19.81	21.2	16.70
Hyoid	0.0	0.45	0.0	4.72

Hyoid tooth counts were different for rainbow and cutthroat. Tests indicated that the other mean tooth counts, showing the greatest separation were not significantly different for rainbow and cutthroats (p.05). Hybrid lots always had higher mean tooth counts than either parental group except in the case of hyoid teeth. All rainbow trout lacked hyoid teeth. All ten cutthroat male X rainbow female hybrids lacked hyoid teeth. Six out of twenty fish in the other hybrid lot had one or two small hyoid teeth. Of twenty-one cutthroat trout examined all but two had from one to eleven hyoid teeth. It was noted that the hyoid bone appeared stronger in cutthroat than in rainbow but no measurements were made. Two-year old fish from the four experimental lots were examined for presence of hyoid teeth. Table IV gives results for hyoid teeth examinations in cleared and two year old fish.

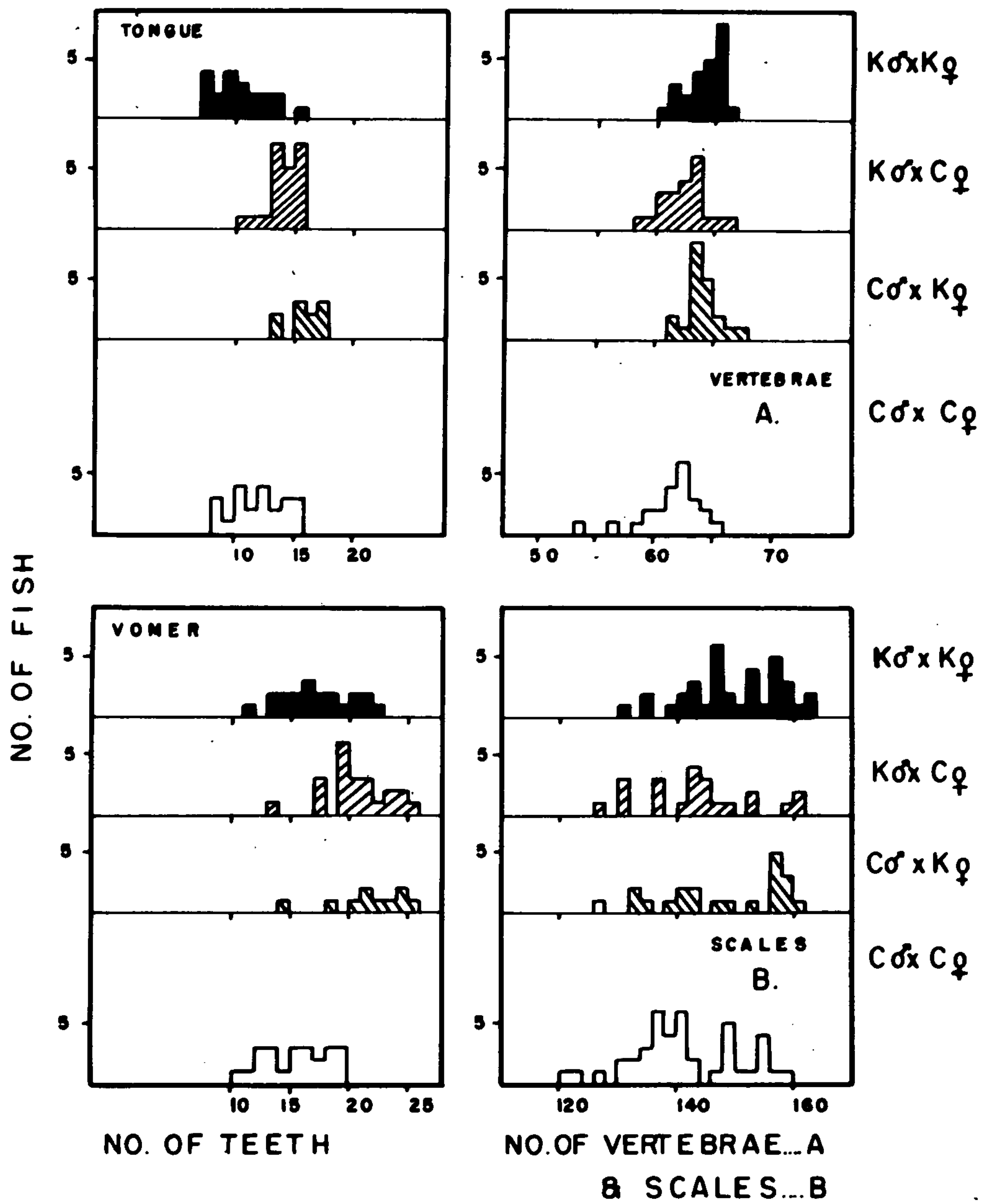


Figure 27. Number of teeth, vertebrae and scales in four experimental lots of fish.

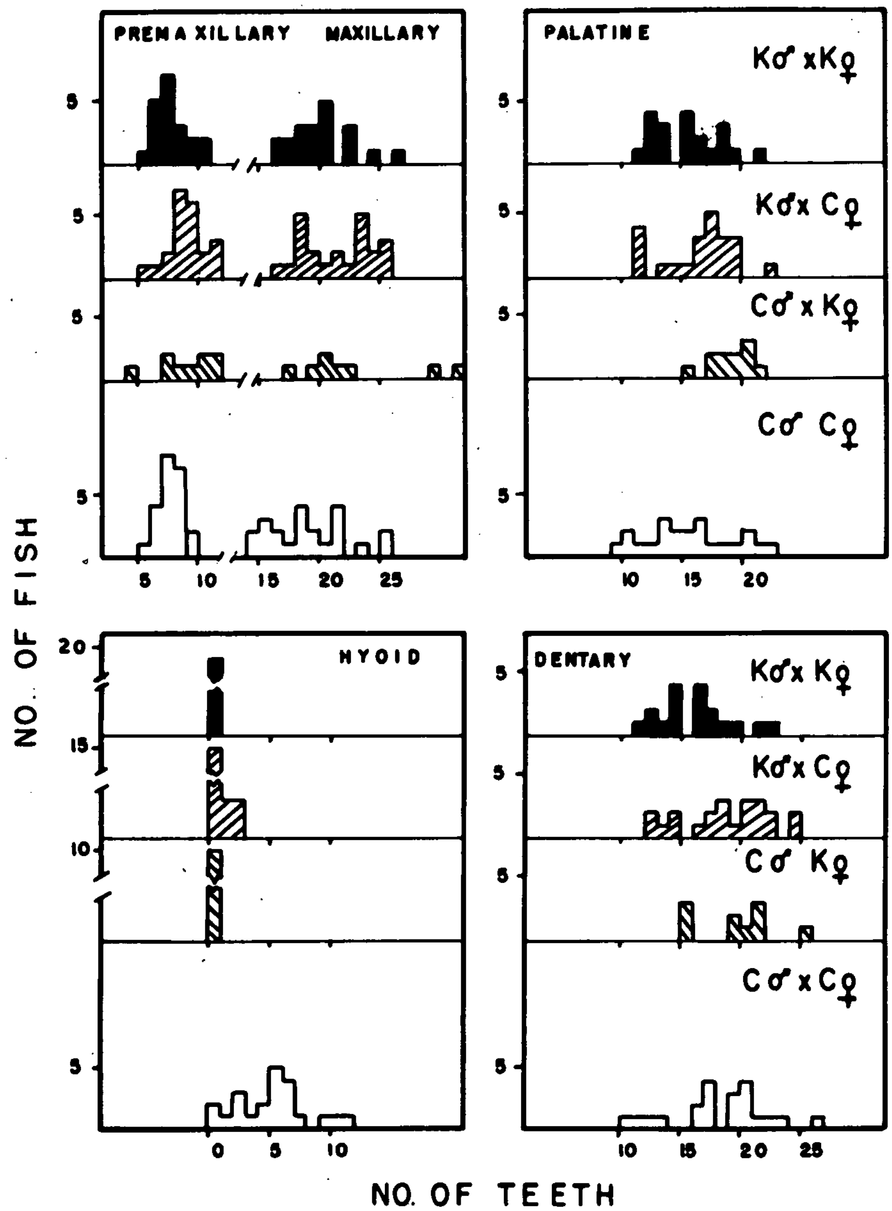


Figure 28. Number of teeth in four experimental lots of fish

TABLE IV

Occurrence of hyoid teeth in cleared 10 month old fish and in uncleared 2 year old fish

(Male fish are indicated first in all crosses)

Cross	K x K		K x C		C x K		C x C	
Teeth	Pres.	Absent	Pres.	Absent	Pres.	Absent	Pres.	Absent
Ages								
10 Mos.	0	19	6	14	0	10	20	2
2 Years	0	4	6	9	2	6	14	0
Combined	0	23	12	23	2	16	34	2

Summary of tooth counts

The only tooth counts which differed significantly for rainbow and cutthroat were those made on the hyoids. The hybrid lots had higher mean tooth counts in all cases than either parental group. The percentage of hybrids possessing hyoid teeth was intermediate, where hybrid hyoid teeth were counted they were weak and few in number. Hyoid teeth were absent in the majority of hybrids.

Tooth studies in wild fish

Ten out of 12 cutthroat adults from Cowichan River had hyoid teeth, in the other two fish it appeared that the hyoid teeth had been broken off.[1] In a sample of nineteen adult cutthroat, from the lower Fraser River and Matsqui Slough,

1. The samples of fish have been referred to as cutthroat because they possess the cutthroat characters used in field identification.

all but one had hyoid teeth. Examination of twenty-eight fish, ostensibly rainbows, from the upper Fraser and Bulkley Rivers, revealed no hyoid teeth. Counts of hyoid teeth were not made on any of these uncleared fish as many of the teeth are too small to see or detect with a needle.

Pyloric Caeca

Counts of pyloric caeca revealed no differences between rainbow and cutthroat trout. Counts on rainbow ranged from 27 to 55 with a mean of 41.9. Counts on cutthroat ranged from 30 to 57 with a mean of 42.6.

Color Patterns

Size of parr marks

Figure 29 shows the difference in size of parr marks, between cutthroat and the other three lots of fish. Figure 29 shows the frequency distributions of calculated percentages of the fork length made up by the width of parr marks which crossed the lateral line. Cutthroat had smaller parr marks than the other three lots of fish. The average percentages of parr marking on the lateral line is given below: (males are listed first in all crosses).

Cross	Average % of parr marking
K X K	28.8
K X C	27.7
C X K	27.3
C X C	23.3

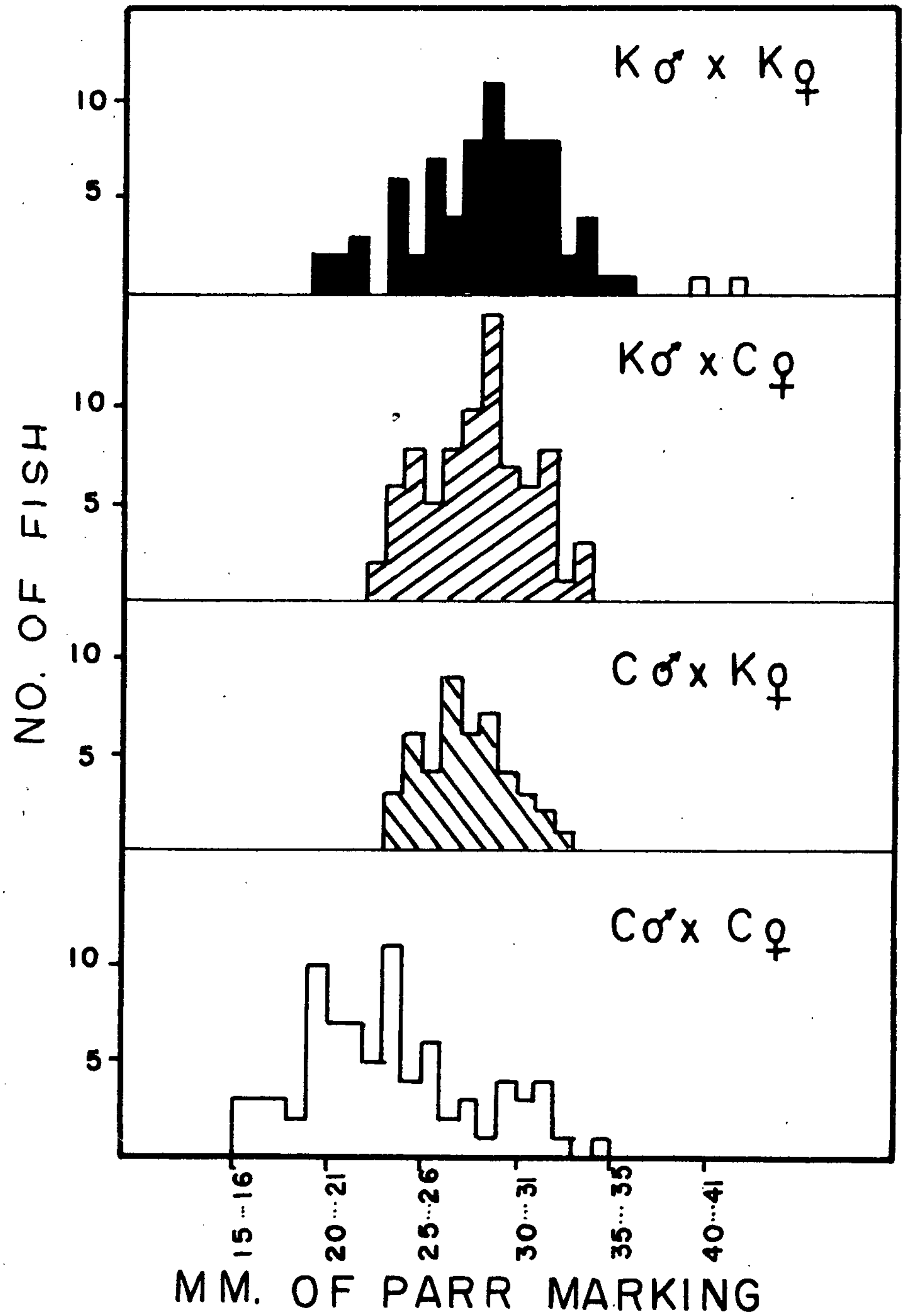


Figure 29. Sum of the width of all parr marks on the lateral line per 100 mm. fork length

Counts of the parr marks crossing the lateral line were slightly higher for rainbows. Differences in cutthroats and rainbows were due mainly to parr mark size. Examinations of limited numbers of wild fish from Black Creek indicated that rainbow trout had more parr marking on the lateral line than cutthroats.

White on dorsal

The amount of white on the margin of the dorsal fin is usually greater on rainbows than on cutthroats. Figure 30 shows plots of the number of ray interspaces that are white. The hybrid lots are intermediate between rainbow and cutthroat lots.

Adipose spots

The number of spots on the adipose is usually greater on cutthroats than rainbows. Figure 30 represents distribution of adipose spots in the four lots of fish. The difference between hybrid lots is not significant, Chi-square value 5.39, 2 D.F. Hybrids are intermediate as in dorsal coloration. No difference, in adipose spotting, could be detected in the small samples of wild fish examined.

Dorsal median parr-like spots

Counts of dorsal median parr-like spots revealed a distinct difference between the experimental rainbow and

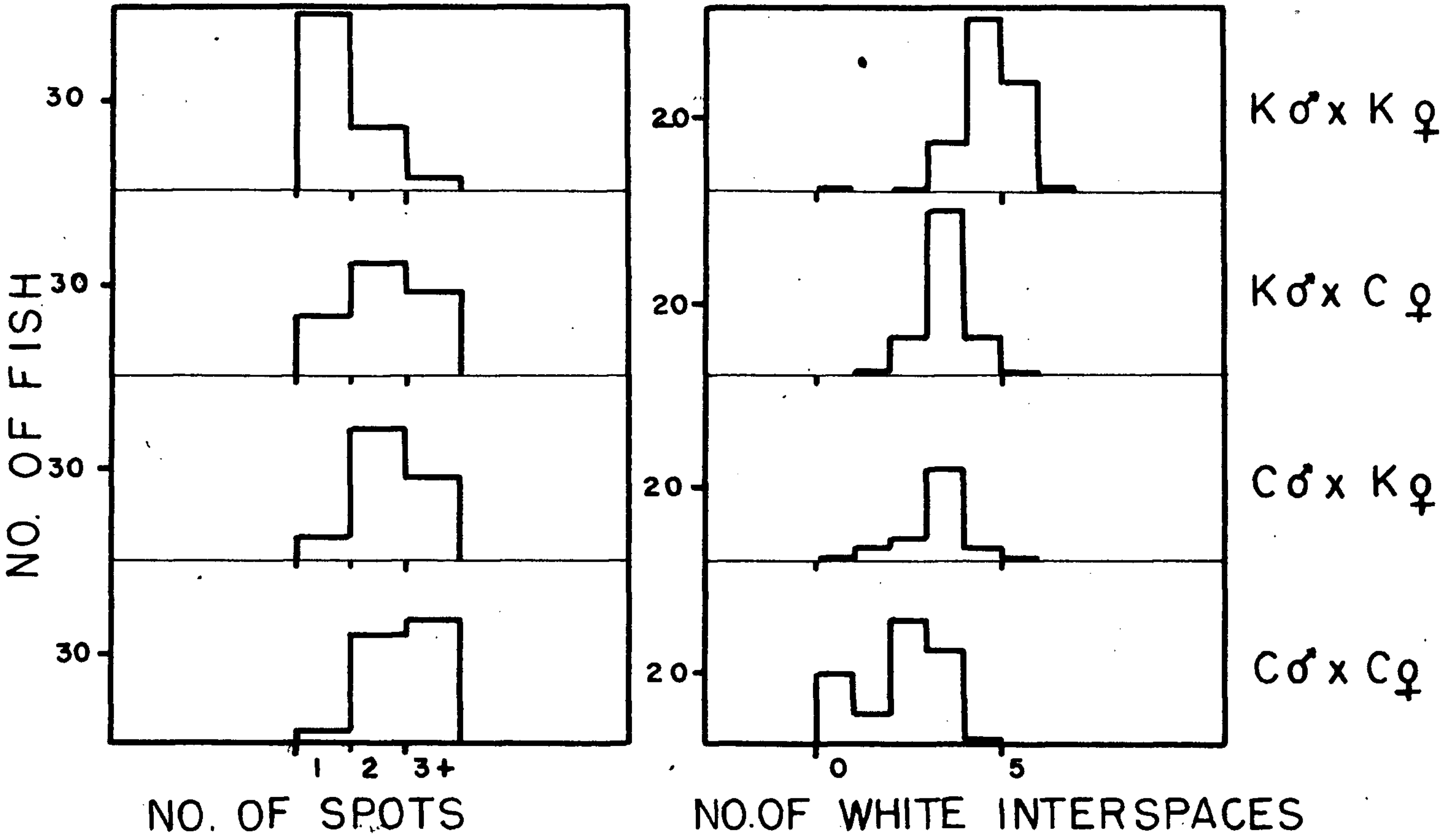


Figure 30. Number of adipose spots and the amount of white on the dorsal fin as indicated by the number of white ray interspaces

cutthroat. Figure 31 (A) shows distribution of these spots in the four lots of experimental fish. Among thirty-six cutthroat inspected only three had spots and each of these had only one spot which was ahead of the dorsal fin. All thirty-six rainbow examined had five or more dorsal median spots and most counts ranged from seven to ten. The average number of dorsal median spots was intermediate in hybrids and counts ranged from zero to ten.

Counts on wild fish (Figure 31 (B)), separated some rainbow and cutthroat populations but not others. Rainbow trout from Loon Lake, near Clinton, B.C. and cutthroat trout from Lakelse River bore the same relation to each other as did the experimental rainbow and cutthroat. The dorsal median spots revealed no differences between rainbow and cutthroat, from Black Creek, Vancouver Island. Nine out of thirteen cutthroat, from Black Creek, had two to five dorsal median spots while the number of spots on the rainbow ranged from zero to eight.

Hyoid color

The hyoid color of four lots of hatchery fish was examined while the fish were alive. The colors of the hyoids were catalogued using the arbitrary color scale on the following page.

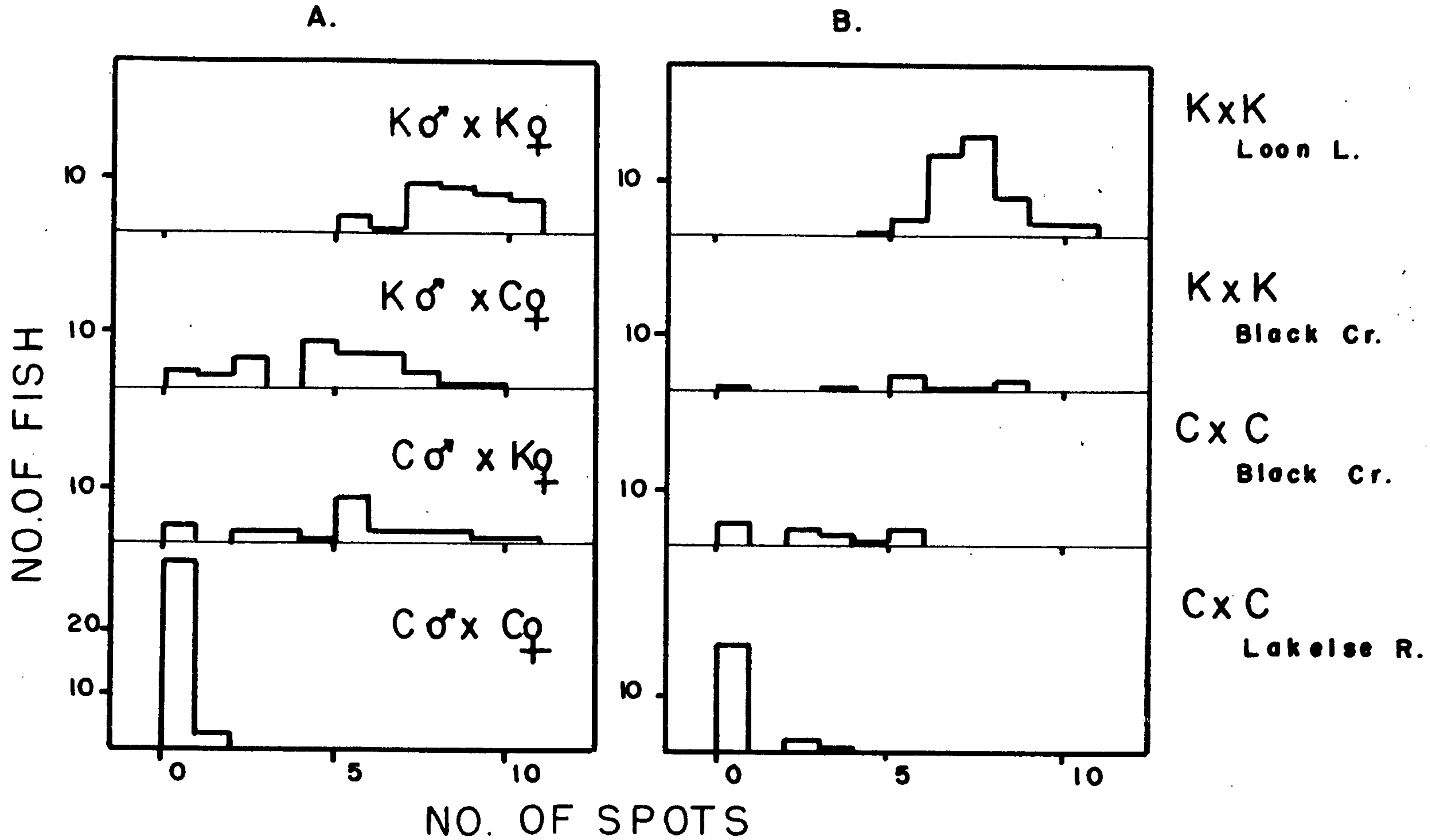


Figure 31. Number of parr-like spots on dorsal median line in experimental fish (A), and wild fish (B)

0 - no hyoid color

I - pale yellow shade

II - strong yellow with or without red spots

III - full red

Table V shows the results of the examination.

TABLE V

Hyoid color in four lots of experimental two year old fish (Males are indicated first in all crosses)

Cross	Color 0	I	II	III
K X K	4	0	0	0
K X C	2	22	8	3
C X K	3	4	13	1
C X C	0	0	0	20

Table V indicates that the cutthroat were definite in their hyoid color while in the small rainbow sample no hyoid color was present. Hybrids coloration was intermediate. The K X C hybrids are more like rainbows than the C X K lots. A Chi-square test indicated that the hybrids differed significantly. This test was made by lumping data in columns 0 and I into one total and data in II and III into a second total as shown below:

Cross	Color 0 & I	II & III
K X C	24	11
C X K	7	14

(Chi-square value 5.24 for I.D.F.)

Summary of color patterns

Measurements of the amount of parr marking revealed that cutthroats had smaller parr marks than rainbows or hybrids. Measurements, not presented, indicated that wild cutthroats had smaller parr marks.

The white margin on the dorsal was longer on rainbow trout. Hybrids were intermediate.

The cutthroats had more spots on their adipose fins. This did not apply to samples of wild fish examined.

Dorsal median spots were present on all rainbow and absent on all but three cutthroat. Rainbow from Loon Lake near Clinton and cutthroat from Lakelse River, Skeena system, bore out findings on experimental fish. Samples of fish from Black Creek, Vancouver Island, contained specimens from both species with variable numbers of dorsal median spots.

Hyoid color on experimental fish was red for all cutthroats, white for all rainbows and intermediate for hybrids.

The relation of hyoid color and hyoid teeth to other characters in wild fish.

A collection of twenty-eight fish was made in Black Creek, Vancouver Island. These fish were first separated on the basis of their hyoid color. All the fish used had bright red hyoids or no hyoid color. Of the fourteen fish, with red hyoids, two lacked hyoid teeth. An examination of other characters on these fish revealed that each had dorsal median parr-like marks and one adipose spot. One fish had very small head parts for a cutthroat. Two fish, among fourteen, without red hyoid marks, had hyoid teeth. The size of head parts and the coloration on these fish was similar to that of the rainbow. These fish indicate that some hybrid formation may have occurred, but most members of the sample fitted one species or the other, in most features, except for the intermediate numbers of dorsal median spots.

Twenty-one fish from Nine-Mile Creek, Kootenay Lake in south-eastern British Columbia were examined. The relation of hyoid teeth and hyoid color is shown below. Most of the fish had no hyoid teeth and no hyoid color. Six other fish had variably colored hyoids, three of them possessed hyoid teeth. Comparisons of relative size of head parts in lots with and without hyoid color revealed no differences in maxillary, snout and preopercular length. The evidence indicated that some hybridization had occurred.

	Teeth	
Hyoid color	Present	Absent
White	0	15
Yellow and spotty red	1	2
Red	2	1

IV. DISCUSSION

The study points up a number of differences between rainbow and cutthroat trout, in relative growth, meristics, dentition and coloration. The differences found were seldom distinct enough to separate all members of the two species. Relative-growth differences which were detected became more pronounced as the fish grew larger indicating that the growth rate rather than the point of inflection differed for the two species. Points of inflection occurred at about 30 mm. and 150 mm. These points coincide with periods of ossification and sexual maturity and results are in accord with Martin's data for Atlantic salmon (Martin 1949).

Samples of wild rainbow and cutthroat trout are often difficult to identify unless both species are taken in the same locality and compared. It is unlikely that any single set of characteristics can be used to separate the two species in all localities. This difficulty arises because trout vary in different age groups, sexes and environments. Mottley (1941) demonstrated that rainbow trout transferred from Kootenay Lake, in south eastern British Columbia, to Wilson Lake, near Nakusp British Columbia, developed larger heads. Martin (1949) was able to alter body proportions of fish by rearing them at different temperatures. Mottley (1933) reduced the lateral line scale count in trout by increasing the developmental temperature after the eyed egg stage. Table VI indicates that scale counts on both species vary in different localities due to genetic or environmental factors. Hubbs (1922) demonstrated that year classes of Notropes and Lipomis which had hatched out following lower developmental temperatures, had higher vertebral counts. Taning (1952) showed that sea trout reared at 6°C had lower mean vertebral counts than those reared either above or below this temperature. Lindsey (1953) found a positive correlation between air temperature and mean anal ray count within a given latitude and within each temperature zone a south to north increase in anal rays for Richardsonius balteatus (Richardson) Because many anatomical features vary with environmental conditions, consideration of these features alone in differentiation of closely related species may leave the systematist with only part of the picture. It has been shown that rainbow and cutthroat can hybridize freely. Hubbs (1955) states that it does not often occur among trout, but that hybridization is extremely common among Cyprinids, Centrarchids and Perches. Hubbs points out that most cases of hybridization in nature are associated with introduction of new species to an area, depletion of a species in an area or instability of the environment. Anderson (1949) states that plant hybridization also is associated with change or disturbance of habitat. In view of the fact that the trout of British Columbia live in watersheds which fluctuate violently and

TABLE VI

Number of oblique scale rows above the lateral line

on rainbow, steelhead and cutthroat trout

Species	Locality	Range	Mean	Reference
Rainbow	Cowichan River	115-130	122.3	Neave, 1943
Steelhead	" "	122-143	131.5	" 1943
Steelhead		115-159		Carl & Clemens, 1953
Steelhead	Smith Falls Hatchery	127-147	136.	Vernon & McMynn (Unpublished)
Rainbow	" "	131-163	149.8	*
Cutthroat	Cowichan River	146-177	160.4	Neave, 1943
Cutthroat	Veitch Creek	122-154	137.4	" 1943
Cutthroat		170-200		Carl & Clemens, 1953
Cutthroat	Smith Falls Hatchery	146-173	158.	Vernon & McMynn (Unpublished)
Cutthroat	" "	121-159	141.	*

* Results obtained in this investigation

which have recently been influenced by glaciation there is some reason to believe that strong mechanisms exist to keep the two species separate.

Studies of food habits of rainbow and cutthroat trout in Cowichan River (Idyll 1942) showed that cutthroat were much more piscivorous upon reaching 200 mm., than were rainbow. Idyll interprets this as evidence for selective food habits for one or both species; in any case the relationships of the two species to the rest of the habitat are different. The longer nose, wider mouth and hyoid teeth may be associated with strong fish-eating tendencies in cutthroat trout. Hartman (1954) B.A.Thesis, University of British Columbia, found that mouth size was a limiting factor with regard to size and type of food available to rainbow trout. A rough appraisal of the distribution of the two species shows that cutthroat are found with rainbow in the lower sections of large coastal streams. Rainbow occupy the upper Fraser and Thompson Rivers exclusive of cutthroat, which further indicates differences in ecological requirements of the two species. (A distinct subspecies of the cutthroat type of trout, Salmo clarki lewisi (Girard), is found in the middle and upper Columbia; Yellowstone and upper Missouri Rivers).

Anderson (1949) states that hybrid plants have intermediate coloration and structure and are at the same time probably intermediate in their habitat requirements. Such plants would not compete successfully in either parental type of habitat. The applicability of Anderson's theory to the rainbow-cutthroat problem is a matter for speculation, but such a process might account for a behavior which would prevent interbreeding.

The differences existing between rainbow and cutthroat trout appear to be anatomical and behavioral. Differences such as mouth size and dentition are probably related to the behavior of the animal. Meristic differences may not be of any direct advantage but may be the result of a particular physiological process which was selected for in the species (Hubbs 1926). In a consideration of the relationship of two closely related species ~~texomic~~ taxonomic differences such as those found in this investigation are of value as key characters but their utility is increased with a knowledge of their relationship to the habits and the ecology of the animal.

V. SUMMARY

(1) Cutthroat and rainbow trout were hybridized with no loss in viability.

(2) Sex ratio in hybrid lots did not differ significantly from the expected.

(3) Studies on relative growth revealed differences between the parental types. Cutthroats had larger head and head parts than rainbow. Hybrids were intermediate in most cases but resembled cutthroat in preopercular and snout lengths.

(4) Most body parts measured were identical in rainbow and cutthroats. Cutthroat had deeper peduncles than rainbows, hybrids were intermediate.

(5) Meristic comparisons revealed that rainbows had more vertebrae, scales and rays than cutthroat. Hybrid vertebral and ray counts resembled female parent type. Dorsal ray counts in hybrid lots resembled rainbows. Anal ray counts were intermediate in one hybrid lot and resembled rainbows in the other.

(6) Most cutthroat trout had hyoid teeth while all rainbow lacked them. Hybrids had intermediate numbers of hyoid teeth.

(7) Cutthroat trout had more adipose spots, fewer parr-like marks on the dorsal mid-line and less white on the dorsal fin margin than rainbows. Hybrids were intermediate in these color characteristics. All two year old cutthroat had red hybrids, all rainbow lacked them. Hybrid lots were intermediate in hyoid color but differed significantly from each other. Each lot resembled male parent type to a limited extent.

(8) Differences in relative size of head parts, coloration and dentition in experimental fish were apparent in several samples of wild fish examined.

(9) Some of the differences found between the two species may be related to important differences in the behavior and ecology of the two species.

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APPENDIX I

CLEARING PROCEDURE

(1) Wash fish (formalin preservation) for twenty-four hours.

(2) Hold small fish in two percent KOH and large fish in four percent KOH till post-anal vertebrae are visible. (In this work galvanized metal tags had been fastened to the fish which resulted in improper clearing).

(3) Place fish in alizarin red dye, mixed in four percent KOH, for twenty-four hours.

(4) Place in two or four percent KOH, under ultraviolet light, until tissue is nearly clear. In this experiment small fish were immediately put into a solution of nine parts two percent KOH and one part glycerine.

(5) Place in a solution of three parts glycerine and seven parts two to four percent KOH. Small fish about 30 mm. were left at this stage for about six hours. Larger fish (with tags) were left for two days because they did not clear properly.

(6) Place in solution of six parts glycerine and two or four percent KOH. Small fish were left at this stage for six hours.

(7) Place in pure glycerine for four or five days.

(8) Transfer to fresh glycerine and add a few crystals of thymol.