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STRUCTURAL VARIATION AS RELATED TO THE ECOLOGY OF  
THE REDSIDE SHINER

Richardsonius balteatus (RICHARDSON)

by

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A Thesis Submitted in Partial Fulfilment of the  
Requirements for the Degree of

MASTER OF ARTS

In the Department  
of  
ZOOLOGY

The University of British Columbia

April, 1950.

*accepted:*

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ABSTRACT

R. balteatus is extremely variable in number of anal rays. Counts of over 4000 specimens from 54 localities in British Columbia varied from 10 to 21, with differences between means of different populations, different year classes and sometimes between the sexes. Variation is shown to be controlled at least partially by environmental factors during development; temperature is an important factor. A mechanism for environmental control of fin ray count is suggested. Variation also occurs in body proportions. Inflections in relative growth of body parts is demonstrated; variation in proportions of these parts is probably due to environmental control of body size at inflection. Pectoral and pelvic fins show heterogonic growth. Notes on life history are given. The spawning period varies from 7 to 10 weeks, starting between the last week of May and the second week of June. Individuals spawn at different times and probably more than once per season. Smaller fish frequent shallower water. Few fish are older than 4 years and females live longer than males. Relation of shiners to game species is discussed; shiners eat

trout fry, trout eat shiners, and shiners probably sometimes compete with trout for other food.

## TABLE OF CONTENTS

	Page
INTRODUCTION.....	1
ACKNOWLEDGEMENTS.....	3
LITERATURE ON THE SPECIES.....	4
LIFE HISTORY	
RANGE AND HABITAT.....	7
SPAWNING.....	9
EMBRYOLOGY.....	12
METAMORPHOSIS.....	15
GROWTH.....	17
SEX RATIO.....	19
MOVEMENTS.....	21
Size Differences.....	21
Night Activity.....	22
Summer Range.....	23
Winter Habits.....	23
FOOD RELATIONSHIPS.....	24
Relation to Game Species.....	24
Predation by Shiners.....	25
Predation on Shiners.....	27
Competition.....	28
Ecological Relations.....	29
STRUCTURAL VARIATION	
LITERATURE ON VARIATION IN FISH.....	31
ANAL RAY COUNTS.....	35
Counting Methods.....	35
Range of Variation.....	35

	Page
Artificial Introductions.....	36
Intra-population Variation.....	37
Summary of Adult Variation.....	38
VARIATION IN ANAL FIN BASE.....	39
Morphology of the Fin Base.....	39
Fin Base Proportion.....	41
FIN RAY FORMATION AND ECOLOGICAL FACTORS.....	43
Body Size at Ray Formation.....	43
Correlation with Temperature.....	43
Geographic Variation.....	45
VARIATION IN OTHER STRUCTURES.....	48
Relative Growth of Parts.....	48
Adult Variation in Proportions.....	49
Vertebrae.....	50
Scales.....	52
CONCLUSIONS: A POSSIBLE MECHANISM FOR ANAL	
RAY COUNT VARIATION.....	52
Evidence for Environmental Control.....	52
Possible Causes of Intra-population Variation.....	54
Hypothesis.....	55
General Application of the Hypothesis.....	58
SUMMARY.....	59a
LITERATURE CITED.....	60
APPENDICES.....	67

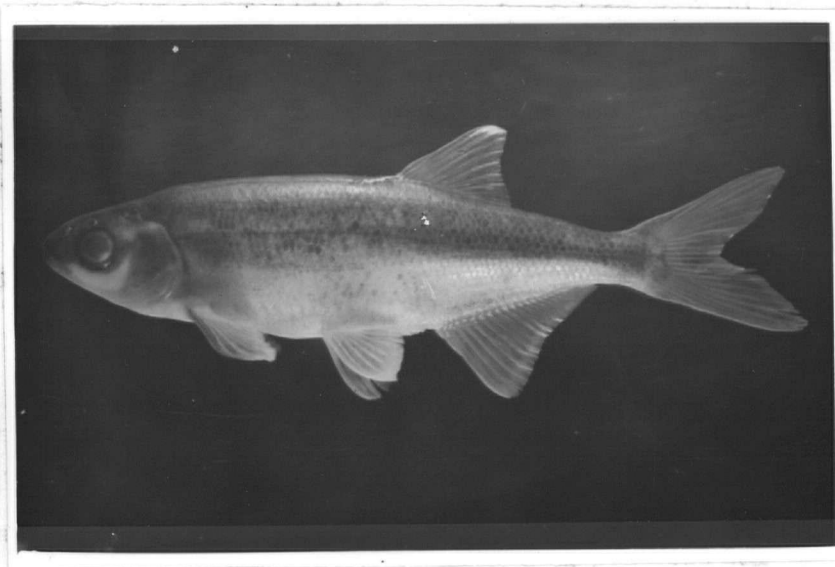


Fig.1. Adult redside shiner,  
Cottonwood lake,1949. X 4/5

## INTRODUCTION

The redside shiner Richardsonius balteatus (Richardson) <sup>(Fig. 1.)</sup> shows greater variability in number of anal fin rays than almost any other fresh-water fish which has been studied in North America. Ray counts of British Columbia specimens vary from 10 to 22. Shiners occur in dense populations in a wide variety of stream and lake types from sea level to 7300 feet. <sup>Since</sup> As large samples can be obtained from a number of different environments, the species lends itself to a study on intra-specific variation. In addition, as the fish occurs together with various species of economic value, its ecology is of practical importance. (Fig. 1 shows an adult specimen. <sup>See line 2</sup>)

The present study has been made along two lines; first, to investigate the life history and relations with certain other species, and second, to enumerate and if possible explain some of the morphological variation found. Data on life history are presented first because, although somewhat diffuse, they form a necessary background to discussion of structural variation.

Findings are based on field collections and observations made in 1948 and 1949 in various parts of British Columbia, and on experiments at the Summerland, Kaslo and

Nelson hatcheries. Collections from the Royal Ontario Museum of Zoology and various other sources were also examined. Anal ray counts and other measurements have been made on over 4000 specimens from some 54 localities.

### ACKNOWLEDGEMENTS

The guidance and enthusiasm of Dr. P. A. Larkin, and his unstinted support during collection of material for this study, have been genuinely appreciated. The assistance and advice of Dr. W. A. Clemens, who suggested the problem, is also gratefully acknowledged.

Much of the design and construction of apparatus, as well as collection of material in the field, was carried out by Arnold D. Nemetz. I am indebted to other fellow students for assistance and suggestions, particularly to the following: G. C. Anderson, W. H. Cottle, R. G. Ferguson, Craig MacPhee and T. G. Northcote.

Work during the summers of 1948 and 1949 was conducted under the auspices of the British Columbia Game Commission, and specimens from several localities were kindly submitted by personnel of that organization. Special thanks are extended to the following: Inspector C. F. Kearns, Supervisor J. Robinson, Hatchery Officer A. Higgs and Game Warden R. G. Rutherglen.

I am under obligation to W. B. Scott of the Royal Ontario Museum of Zoology, and to Dr. F. E. J. Fry of the University of Toronto. Finally, I wish to express gratitude to my wife for taking second place to this work.

## LITERATURE ON THE SPECIES

The redbase shiner has been variously placed in the genera Abramis (Cyprinus), Leuciscus and finally Richardsonius. The species was first named by Sir John Richardson in 1836. The common name has been given as Columbia river minnow, Richardson's minnow, red sided bream, shiner, lake shiner and redbase shiner. Early nomenclature of the species is dealt with by Schultz and DeLacøy (1935).

The known range of the genus Richardsonius includes British Columbia south of 56°, Washington, Oregon, and parts of Idaho, Nevada and Utah. Within this area Jordan, Evermann and Clark (1930) recognize four species largely on the basis of anal fin ray counts. They state however that many species in the group need comparison and verification, and conclude that "any arrangement of these fishes must be still wholly provisional." Schultz and DeLacøy (1935) recognize two subspecies of R. balteatus, R. b. balteatus (Richardson) in the Fraser river, Columbia river and Streams of Washington and Oregon, and R. b. hydrophlox (Cope) principally confined to the Columbia system above Snake river falls in Idaho and the Salt lake drainage in Utah. Here separation is apparently a geographic one, again based on variable anal fin ray counts. Miller and Miller (1948) state that the species is abundant in the Colorado river basin of northeast Nevada and has been recently introduced in the upper Colorado river. On the basis of anal fin ray counts, their collections fit

the description of R. b. hydrophlox with some intergrades with R. b. balteatus. A group occurs in the warm springs of southern Oregon characterized by low anal ray counts; it is recognized as R. thermophilus Evermann and Cockerell by Jordan, Evermann and Clark (1930).

In 1894 Dr. C. H. Eigenmann published ray counts of R. balteatus taken from different localities on the Fraser and Columbia systems. While there was considerable variation within single populations, there was also great variation in mean ray counts of different populations. He compared anal ray counts in the 21 genera of Atlantic Slope Cyprinids with the 17 genera from the Pacific Slope, the former having from 6 to 14 anal rays (a range of 9), but the latter varying from 7 to 22, (a range of 15). He concluded from comparison of collections from the Fraser system that the number of rays in the species, and also the range of variation, decreases with increasing altitude. He also stated without elaboration that the tendency of frequency curves of anal ray counts to be skewed to the left indicates that the number of rays is in the process of increasing.

In the same year Gilbert and Evermann (1894) denied Eigenmann's generalizations concerning lower ray counts and less range at higher altitudes, publishing counts for 30 collections with corresponding altitudes as evidence.

In 1895 Eigenmann reiterated his claims for the effect of altitude on ray count and presented more data, but denied that he intended it as a generalization for other species.

In 1897 Evermann published a table of ray counts and altitudes for seven more localities, not conforming to Eigenmann's observations. He states "At one time Dr. Eigenmann thought that a certain definite relation existed between the number of anal rays in this species and the altitude ..... In the light of fuller data Dr. Eigenmann now agrees with us that this generalization is not borne out by the facts."

Further contributions to the subject consisted of additional records of ray counts from other localities, (Evermann and Meeke 1898, Snyder 1907, Miller and Miller 1948) and distributional records which are listed in Schultz and DeLacoy (1935) (to which should be added recent works mentioned below).

Scales of Richardsonius are dealt with by Cockerell (1911a, 1911b), Cockerell and Allison (1909) and Evermann and Cockerell (1909). Occurrences in British Columbia are given by Clemens and Munro (1934), Stanwell-Fletcher (1943), and Carl and Clemens (1948). Measurements of specimens are given by Dymond (1936) and Schultz and Schaeffer (1936). Food is listed by Munro and Clemens (1937), Clemens, Rawson and McHugh (1939), Ferguson (MS) and Anderson (MS).

In summary, literature on the species comprises descriptions and changes in nomenclature, claims and denials concerning the effect of altitude on anal ray count, and limited information on the ecology of the species. Few data are available in the literature on spawning habits, growth rates or other phases of the life history.

## LIFE HISTORY

### RANGE AND HABITAT

The present study does not extend the range of the redside shiner reported in the literature. It includes 54 localities in British Columbia, distributed as follows:

Skeena river drainage	- 1
Fraser river drainage	
Driftwood valley	- 1
Caribou area	- 5
Thompson river drainage	-12
Lower Fraser valley	- 2
Columbia river drainage	
Okanagan drainage	- 8
Arrow-Kootenay drainage	- 21
Kootenai river drainage	- 4

Localities where collections were made together with pertinent information are given in Appendix I.

The species is not listed by Clemens, Boughton and Rattenbury (1945) in Teslin lake at the northern boundary of British Columbia. Cowan (1939) does not list it from the Peace river drainage, nor has it been reported authentically on Vancouver island.

Shiners occur in a wide range of habitats. Some frequent small warm, <sup>u</sup>eutrophic lakes such as Rosebud, with abundant aquatic vegetation and relatively high concentration of dissolved solids. Others are found in large cold



Fig.2. Diverse habitats occupied by shiners  
Top - Erie Pothole  
Bottom - Kaslo bay, Kootenay lake

oligotrophic lakes such as Arrow, Kootenay and Okanagan, with barren shores and little dissolved material. An extreme in low temperature tolerated by shiners was encountered in Erie Pothole, a circular pool some 200 metres in diameter and 7 metres deep, surrounded by a floating marginal mat. Throughout the summer a steep temperature gradient persisted; on 28 August 1949 the surface temperature was 21°C. and the bottom was 7°C.

The species also inhabits running water. Shiners were present among log tangles in the Inonoaklin river, where they occurred together with Kamloops trout in a surface current of one foot per second. Specimens were taken in swift current about pilings of a bridge across the Shuswap river at Grinrod; others were found in Bonanza creek, a shallow stream with gravel bottom and reedy borders.

Appendix I includes temperatures and some notes on limnological conditions. Fig. 2 illustrates the diversity of habitats occupied by shiners.

The reidside shiner is adaptable to a considerable range of physical and chemical conditions, and is one of the most successful of fresh-water fishes in British Columbia. It cohabits this area with relatively few other fresh-water species, (63 in British Columbia as against about 200 in Ontario,) and appears to fill an important niche or series of niches in a number of habitats. It has probably invaded the northern part of its range from the south through the Columbia and Fraser river systems following the retreat of the last glaciation, (Carl and Clemens 1948). Its absence

from many lakes in British Columbia is probably due not to its inability to maintain its position there, but to its failure so far to gain entrance due to geographical barriers. This contention is borne out by the explosive success of shiners introduced recently into such new localities as the Pinantan - Paul lake chain near Kamloops and many lakes in the Kootenay district. In recent years introduction has commonly occurred through release of shiners used by anglers for live bait.

#### SPAWNING

No information on the spawning habits of the red-side shiner is available from the literature. Throughout the summer of 1949 all efforts to observe spawning failed; no eggs were found despite detailed examination of the bottom and vegetation in the vicinity of young fry. Information on spawning places and dates has been inferred from other data.

A few eggs were stripped from shiners and hatched successfully under artificial conditions. Of about 1000 females tested, only 14 yielded eggs which subsequently developed. Ripe females differed in size, and were taken in a variety of habitats at varying depths and times of day. Dissection revealed quantities of unripe eggs remaining in females which had been stripped of ripe eggs. Unripe eggs were present at all times in most individuals large enough to be mature. In Rosebud lake, females with ripe eggs occurred sporadically in collections from 3 June to 22 July. The majority of males provided free-flowing milt over the same

period; dissection and flooding of testes yielded active sperms both before and after these dates.

Individuals may possibly spawn several times in a season, the production of eggs and sperms being a more or less continuous process. The small number of females with ripe eggs compared with the number with near-ripe eggs suggests that time between complete ripening of eggs and their deposition is relatively short.

Fig. 3 shows the size range of fry collected at different dates in Rosebud lake. Average hatching size is estimated from hatchery-reared specimens to be 5.0 mm. Growth rate of reared fry between hatching and absorption of yolk sac is plotted on the same figure. (Growth of hatchery specimens falls off beyond this point probably due to improper feeding.) Starting from the size of the largest fry in the earliest sample, the slope of this line is used to obtain the approximate date on which these fish were 5.0 mm. long, i.e. just hatched. The period from fertilization to hatching, estimated from experimental data as 8 days, is subtracted in order to give the date of first spawning.

No fry less than 7.2 mm. long were taken in any lake. Between hatching and reaching this length, fry are probably living on yolk reserves and are relatively inactive. (Hatching <sup>ery</sup> specimens if undisturbed remain quiescent on the bottom during the first 5 to 12 days after hatching, but subsequently swim freely near the surface.) Rosebud lake samples on 3 July and 8 August probably represent only those individuals old enough to be actively feeding; smaller fish

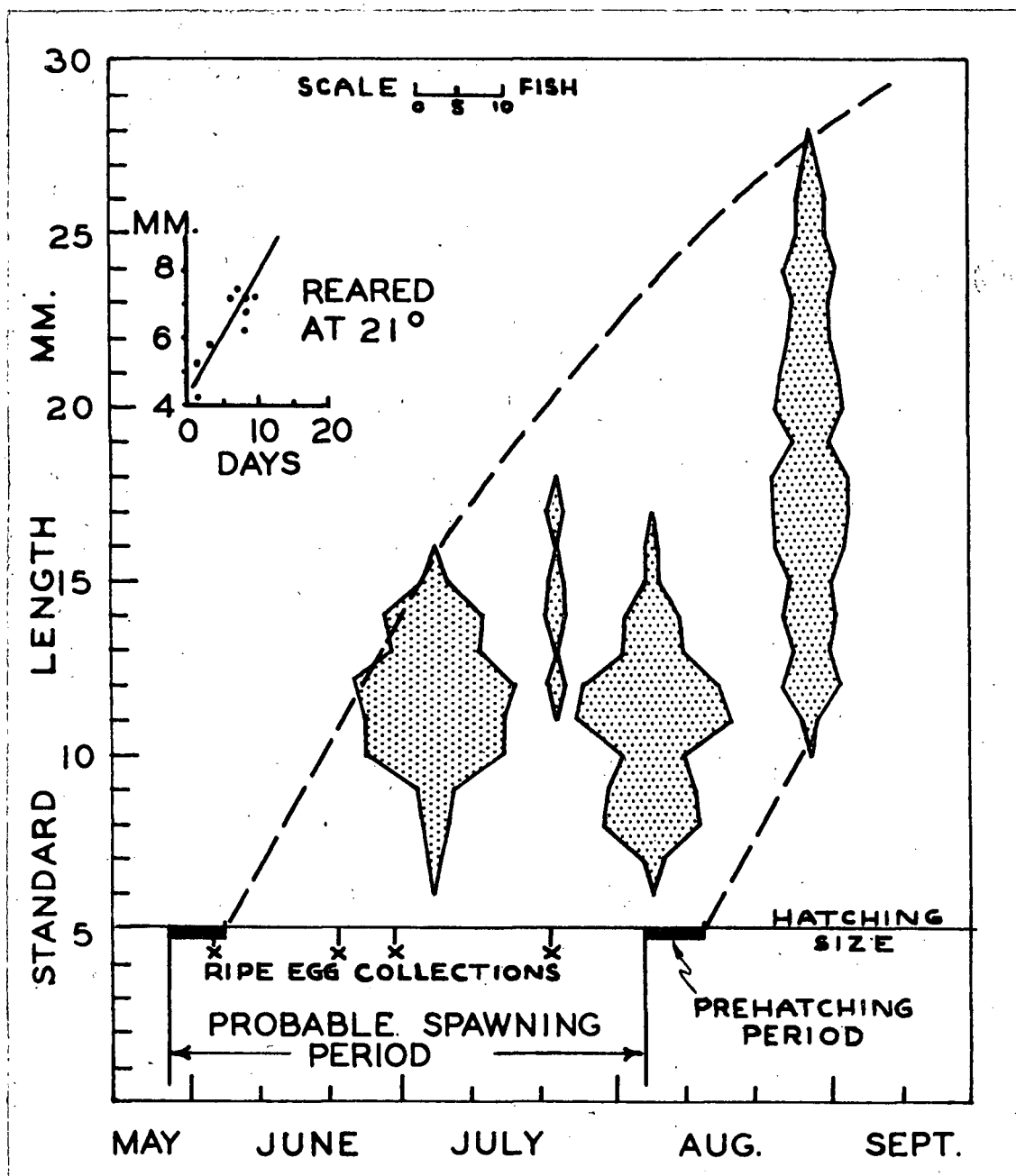


Fig. 3. Estimate of spawning period from length frequency distributions of fry, Rosebud lake, 1949.

were present in the lake but were not taken in the net. By 28 August the last fry of the 1949 year class had grown beyond minimum catchable size, so that the smallest fish in this last sample are the last hatched during the year. The last date of spawning can be estimated by running a line with appropriate slope back from the smallest fry on 28 August to give the date at hatching, and then subtracting the prehatching period.

It has been assumed that size limits in the samples were representative of those in the lake, that early growth rate of 21°C hatchery specimens equaled that of wild fry, that their prehatching periods were equivalent, that incubation periods and growth rates were equal throughout the summer, and that growth between hatching and 15.0 mm. was linear. Probably these assumptions are only approximately true, but the resultant error is considered to be small, as dates for ripe egg collections (shown in the figure) fit the estimated spawning period.

Spawning in Rosebud lake in 1949 probably extended from the end of May to the first week of August. Fry collections from Kaslo on Kootenay lake suggest that spawning at that locality was more restricted, occurring from the third week of June to the last week of July. This was reflected in a smaller size range in each year class.

Scanty data for other lakes suggest that usually length of spawning season is intermediate between that of Rosebud and Kootenay lakes. Protraction of the spawning

period is apparently the result of two factors; different individuals spawn at different times, and each individual may spawn more than once during a single season.

As no eggs were found in the wild, little can be said as to spawning localities except that they are probably near shore in protected situations. In Rosebud lake small fry were taken at many different points about the shores, usually in sheltered situations among matted vegetation. Eggs may have been deposited in the thick bottom layer of loose organic debris, or perhaps in abundant Chara beds in deeper water adjacent to shore. Small fry were observed among floating logs and about boat houses over deep water in Kaslo bay on Kootenay lake, but these may have moved out from the surrounding shore. Large numbers of fry were taken in the west arm of Kootenay lake along a sand beach with little or no submerged vegetation. The variety of habitats occupied by the shiner as well as the variety of localities in which young fry were taken suggest that spawning requirements are not rigid.

#### EMBRYOLOGY

An attempt was made to raise shiners under controlled temperature conditions during the summer of 1949 at the Kaslo hatchery. While a few eggs were hatched and the fry were kept alive for periods up to 37 days, none developed anal fin rays before death. Consequently the experiments did not contribute substantially to study of structural variation, but did provide information on early

development. Eggs were kept in baths at 9°, 12°, 15°, 18° and 21°C., supplied with a steady flow of oxygenated water. The apparatus is described in Appendix III.

In the field, eggs were squeezed from ripe females by slight pressure on the abdomen, and collected in the dry inverted top of a screw top jar. Milt from one or more males was obtained in the same manner, and mixed with the eggs. Eggs, milt and a small amount of water were swirled about and then left quiescent for a few minutes. The lid with adhering eggs was submerged gently in a pail of water and screwed onto an inverted jar underwater so as to exclude air bubbles. The jar, kept in an inverted position, could then be transported safely. The lid with adhering eggs was removed at the hatchery and placed directly into the temperature bath. Any eggs which had come loose and were free in the jar were poured out into the bath. In some cases live parents were brought to the hatchery in cans and stripped directly into the baths.

Eggs passed freely from ripe females with the application of slight pressure. They were a clear golden yellow, spherical and about 1.6 mm. in diameter. The maximum number of ripe eggs obtained from one female was about 250. The chorionic membrane enlarged, when placed in water, until it stood well away from the yolk, becoming increasingly firm and elastic. Fertilized eggs adhered even to smooth surfaces.

Milt, which streamed freely from ripe males when

only very slight pressure was applied, was white and opaque. When activated by water, sperms were discernable at a magnification of 720 diameters as minute circular bodies, exhibiting activity comparable to intense Brownian movement. Activity lasted about one minute.

Figure 4 shows a series of stages in the development of the egg. Time of development is not indicated as the series is a composite of sketches made from eggs at different temperatures on different occasions.

Figure 4 A shows an early stage in cleavage of the germinal disc. In Fig. 4B the blastoderm sits as a cloudy cap on top of the clear yellow yolk. In Fig. 4C the blastoderm is beginning to spread around the yolk, and in Fig. 4D envelopment has proceeded so that the yolk is protruding beneath as a plug. Fig. 4E shows the neural folds forming on top of the embryo, while Fig. 4F and 4G are lateral and ventral views of a later stage with optic vesicles forming.

Complete development and hatching occurred at temperatures from 12° to 21°C. In the 9° bath initial cleavage occurred, but, at 100 hours after fertilization, the germinal disc appeared as a group of irregular cells scattered on the surface of the yolk (Fig. 4H). No further development occurred at this temperature.

At later stages of development the tail bud increases in length until the embryo is curled around in a spiral within the chorion. The heart beat and blood circulation become easily visible, and periods of spasmodic motility occur.

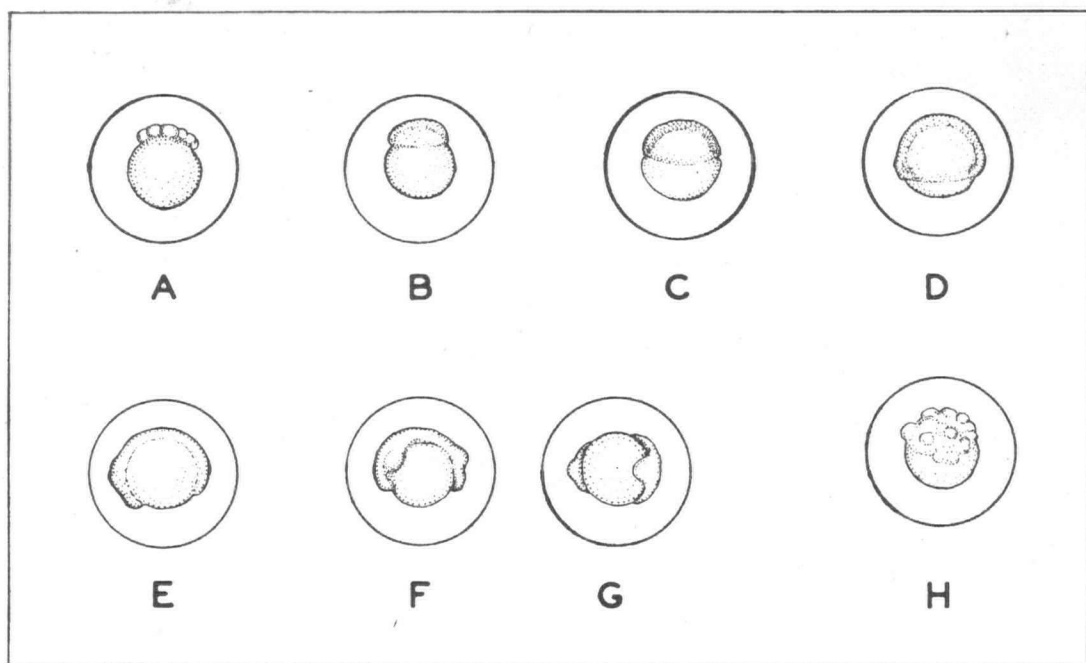


Fig. 4. Stages in development of redside shiner embryos.

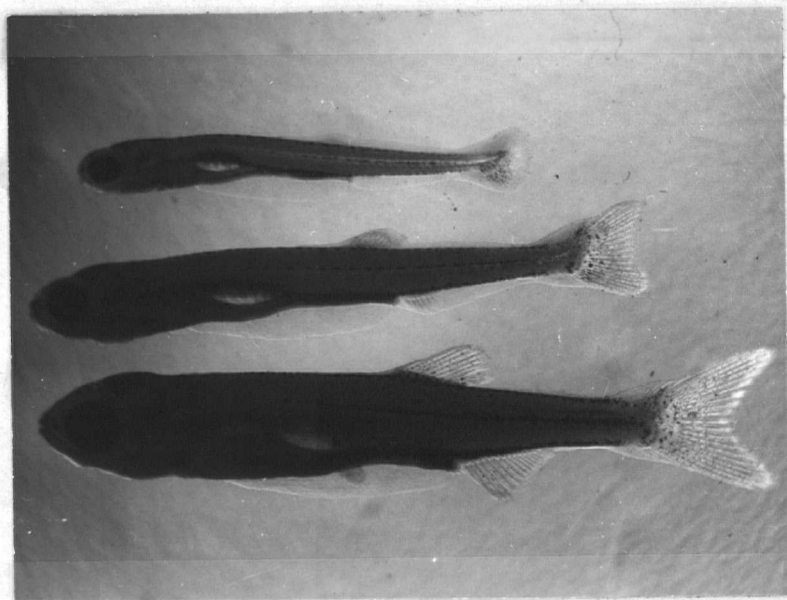


Fig. 5. Shiner larvae showing median fin fold and development of fin rays. X  $7\frac{1}{2}$  approx.

The mean number of days between fertilization<sup>2</sup> and hatching at different temperatures are summarized below. The wide difference in number of individuals hatching in different baths is probably not directly attributable to affect of temperature on viability, as the parents, the initial number and the treatment of the eggs varied.

Water temperature - Centigrade	9°	12°	15°	18°	21°
Hatching time, days	-	15	11	8	7
Number hatched	0	9	200	4	7

#### METAMORPHOSIS

In the present study metamorphosis of the embryo was studied with special reference to the development of the anal fin. Nomenclature of the stages is that suggested by Hubbs (1943). Nomenclature of the fin elements is that of Eaton (1945). Details of development of the redbside shiner from fertilization to juvenile stage appear to follow in general the course outlined for Cyprinids by Balinsky (1948).

When hatched, the larva bears a relatively small yolk sac. Within a short time the head, which is at first bent down towards the yolk sac, straightens, and the yolk is rapidly absorbed. As yolk is assimilated the larva becomes more active, leaving the bottom to swim freely for increasing periods and starting to feed. The smallest free swimming larvae (Fig. 5, top) have a median fin running from the centre of the belly around the tail and forward dorsally to a point some distance ahead of the definitive position of the

dorsal fin. This fin is interrupted only at the anus. In it no <sup>e</sup> definitive fin rays (lepidotrichia) are present, but a continual series of closely set delicate horny rays, (actinotrichia) are visible. The pectorals are present as thin leaves, but at this stage there is no trace of the pelvics or median fins. The rudiment of the air bladder is obvious.

As the larva grows, the fin fold becomes higher in the region of the dorsal, and later the anal fin (Fig. 5, centre). Concentration of tissue occurs in a strip marking the base of the fin, and definitive fin rays become visible commencing at the anterior end of each fin. The dorsal rays are fully formed before the anal. As the anal fin develops a strip of denser tissue at the fin base forms into a series of discrete masses. These appear from anterior to posterior, somewhat earlier than the fin rays, so that it is possible in a larva at this stage to distinguish a greater number of discrete basal elements than discrete lepidotrichia. At this stage the pelvic fin rudiments begin to appear as slight protuberances on either side of the median fin anterior to the anus.

As formation of the dorsal fin rays is completed and that of the anal fin rays progresses, the fin fold diminishes in width ahead of the dorsal, between dorsal and caudal, and between anal and caudal (Fig. 5, bottom). The pelvic rudiments grow rapidly and appear as little paddles without visible rays, the ventral fin fold persisting ahead of the anus.

Later the embryonic fin fold disappears. Rays appear last of all in the pelvic fins, marking the division between larvae and juvenile stages; beyond this point the individual is essentially adult in appearance.

#### GROWTH

Growth of fry during the first year has been dealt with in the discussion of spawning periods. The best method of ageing subsequent year groups was by their length frequency distributions.

Figure 6 shows lengths of fish sampled at various times during the summer of 1949 at Kaslo bay on Kootenay lake. The first collection, taken on May 29 is shown at both ends of the series to indicate the relatively slight growth occurring during the winter months. Collections from two other parts of the Kootenay lake system are shown in the same figure. The collection from Taghum, on the lower Kootenay river about four miles below Nelson, apparently indicates more rapid growth than at Kaslo, while fish from Lardeau at the north end of Kootenay lake show a slightly slower growth. Temperature observations, plankton hauls, bottom dredgings and water analysis were made during the general survey of Kootenay lake in 1949 by the British Columbia Game Commission. These indicate that the north end of the lake is colder and relatively poorer in plankton and bottom organisms than the south end and west arm. The lower Kootenay river is supplied by warm water rich in plankton, drawn off the surface of Kootenay lake along the

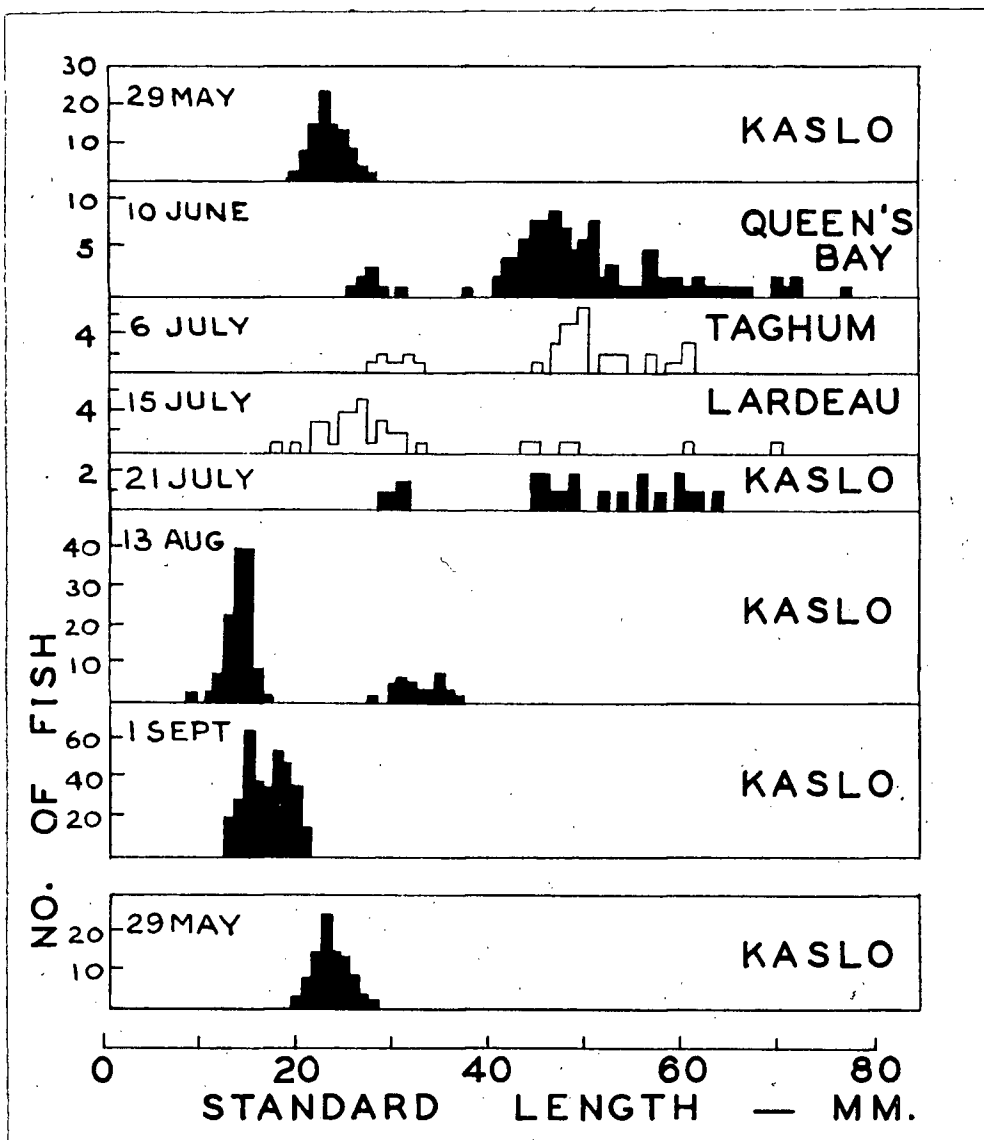


Fig. 6. Length frequency distributions of shiner collections from Kootenay lake, 1949.

shallow west arm. Apparently ecological conditions at Lardeau, Kaslo and Taghum are reflected by growth rates of shiners in these localities.

Kootenay lake shiners appeared to show the slowest growth of any populations examined. The opposite extreme was represented by fish from Pinantan lake. This body of water is highly eutrophic (Rawson 1934), with large areas of weedy shallows. Shiners are extremely abundant and many are of large size. According to the available length frequency data shiners in Pinantan lake reach an average length at the end of their second year approximately equal to the average reached by Kootenay lake shiners at the end of three years. Growth rates of the two populations are summarized below; growth in other localities studied was apparently intermediate between these two.

Estimated Mean Standard Length on Sept. 1.

	<u>Year 0</u>	<u>Year I</u>	<u>Year II</u>
Kootenay lake, Kaslo	17 mm.	34 mm.	55 mm.
Pinantan lake	27 mm.	55 mm.	75 mm.

In the younger age groups of several populations males had a greater mean size than females. Range of variation was great, and it was not possible to attribute statistical significance to the difference. However, males possibly have a higher metabolic rate than females, growing faster and dying sooner.

Ageing of the largest individuals by length frequency distribution is not possible because of the small

number of specimens. Scale reading is an unsatisfactory method of age determination as few circuli are formed each year and annuli are usually indistinct. Nevertheless, ageing by scales could probably be carried out in most populations by careful study of nuclear formations of fish spawned at the start and finish of the season. This would allow distinction between, for example, small two year olds and large one year olds.

Age determination of the largest individual taken was attempted by scale examination. This fish, taken by gill net from Rosebud lake, had a standard length of 123 mm. and a total length of 151 mm. It was in its sixth or possibly its seventh year.

The oldest class which forms an appreciable percentage of most populations is made up of fish in their fourth year, the majority of which are females.

#### SEX RATIO

There is some indication that the sex ratio is unbalanced in some populations. Of 21 samples from different localities, 12 showed sex ratios not significantly different from 50:50 at the 5% probability level. Seven localities had significantly more females than males ( $p < 0.01$  for 4 samples,  $0.02 - 0.01$  for 2 samples and  $0.05 - 0.02$  for 1 sample). Two localities had significantly more males than females ( $p < 0.01$  for 1 sample,  $0.02 - 0.05$  for the other).

There are several possible explanations for the ratios found in these samples. In many populations the

largest fish were almost exclusively females. (These individuals were probably older, rather than faster growing, as suggested in the previous section.) The same condition is reported by Cooper (1935) for the golden shiner Notemigonus crysoleucas. In this species females show greater viability, resulting in a drop in the percentage of males in older year classes. Such a factor would tend to raise the percentage of females in a sample containing all year classes.

To correct for this differential mortality it is possible in some cases to separate the sample by length frequency distribution into different year groups, and to consider the sex ratio in each year group separately. While this reduces the sample size and hence raises the probability of a given ratio being due to "chance", there still remain some samples with significantly more females even among one year olds. The preponderance of males in some samples cannot of course be attributed to higher male mortality.

There is also the distinct possibility of non-random sampling due to segregation or different behaviour of the sexes. Such a phenomenon resulting in biased sampling is reported by Heuts (1947) for Gasterosteus aculeatus. There is also the possibility that different growth rates of the two sexes coupled with selection of one size class in sampling might result in heterogenous sampling. Nevertheless, the redside shiner appears to be plastic in many environmentally controlled features, and there is strong suggestion in the literature (Eberhardt, 1943 ) that

unequal sex ratios may be produced environmentally in some fishes. Consequently, while the evidence presented here is by no means conclusive, the possibility of environmental control of sex ratio in R. balteatus should not be neglected. The species might serve as suitable experimental material for investigating the subject.

## MOVEMENTS

### Size Differences

Shiners of different sizes tend to occupy different depth zones. Frequently fry were observed close to shore in a few inches of water while adults were present only farther offshore. To demonstrate this phenomenon quantitatively a series of collections was made on Rosebud lake on 28 August 1949. A round shallow dip net of wire screening, three feet across and suspended by four wires from the end of a five foot bamboo handle, was used to sample shiners at varying depths. The unbaited dip net was lowered onto the bottom, left there for exactly sixty seconds and then drawn rapidly straight up out of the water. This procedure was repeated until an adequate sample had been obtained. Sampling was conducted in the same manner in each depth zone.

Table I summarizes the size distribution of fish caught. All fish taken in one foot of water were fry below 25 mm. in length. Very few fry were taken in two feet of water. No fry were taken in the two deeper zones, while the largest percentage of large fish was taken from the deepest zone.

TABLE I  
Standard Length of Shiners in Different Depth Zones,  
Rosebud lake, 28 August 1949

DEPTH FEET	DISTANCE FROM SHORE FEET	NO. IN SAMPLE	PERCENT OF SAMPLE IN SIZE RANGE			
			10-24mm	25-39mm	40-59mm	60-80mm
1	6	16	100	0	0	0
2	12	63	6	29	62	3
4	20	58	0	36	55	9
9	30	79	0	3	83	14

The above experiment was conducted in an area characterized by a dense growth of Chara and other aquatic vegetation. The tendency of young shiners to congregate inshore was also observed on barren beaches. Schools of small one year old shiners mixed with young suckers and squawfish, were several times observed lying in long narrow bands within ten inches of shore in Kaslo bay. This may have resulted from temperature preference of the fry. On 6 July 1949 the temperature of the water where such a band of young fish was present was 23.5°C., compared with 21.5°C. a few feet off shore. Presence of food might also account for such distribution; fry taken along a beach in the west arm of Kootenay lake were distended with copepods.

#### Night Activity.

Shiners are apparently active at night in some localities. Night seining at Kaslo and Kuskanook on Kootenay lake yielded shiners along exposed sandy beaches. In Rosebud lake on 22 July 1949, a trap suspended one foot beneath the

surface in the centre of the lake caught a large number of shiners between 11 P.M. and 8:30 A.M. The same trap caught no fish between 8:30 A.M. and noon, nor were shiners observed in the centre of the lake during daylight hours. Artificial light at midnight revealed shiners moving about off shore, but these may have been attracted or stimulated by the lights.

#### Summer Range.

During the summer of 1949, a few shiners at Kaslo bay were marked by clipping the left pectoral fin. Numbers involved were too small to be used for satisfactory population estimates. Up until June 25, 92 fish had been marked; no marking was done for the following 13 days. On July 8, a sample of 18 fish taken at the same boat house where the others had been released contained two marked individuals. This indicates that at least some of the fish were in the same vicinity where they had been taken, 13 days previously. From a total of about 200 fish marked at this location, 10 were recovered. About 40 fish were marked by clipping other fins at locations a few hundred yards from the first, but none of these was recovered. These and other similar observations suggest that shiners may sometimes frequent the same locality for considerable periods of time, returning repeatedly to the same boathouse slip or group of floating logs.

#### Winter Habits.

Scattered observations were made on winter habits of the species. In Cultus lake, shiners were readily seined

in shallow water on 25 September 1948. On 11 November 1948 no shiners were seen in their former habitats, but a school was found in the shelter of a sunken barge over deeper water. Fisheries Supervisor J. Robinson reports that shiners cannot be caught near shore on Kootenay lake during winter. In Kaslo bay, few shiners were visible about the boathouses and log booms on 7 May 1949. Shiners became increasingly numerous during the following month, perhaps moving in from deeper water.

Shiners were readily obtainable from Erie pothole throughout the summer of 1949, but Game Warden T. Rutherglen reports that the only specimens obtainable in late November 1949 were a few fry dug out of the mud near shore. On 22 November 1948 five shiners from Cultus lake were placed in an artificial pool at the north end of the University of British Columbia library grounds. During the winter the pool froze over completely. On 28 February 1949 a sample was taken of the bottom in two feet of water. This contained one shiner, alive and apparently buried in decaying leaves.

The foregoing observations suggest that during winter shiners may move into deeper water or in some localities may bury themselves in the bottom and lie dormant.

## FOOD RELATIONSHIPS

### Relation to Game Species

The relation which shiners bear to game fish is of considerable importance in British Columbia. Shiners have

been introduced recently and have multiplied enormously in several lakes which formerly contained only game species. This situation is usually viewed with alarm by sportsmen, on the assumption that shiners will seriously compete with trout for food, or that shiners will consume young trout. On the other hand in some lakes such as Snowshoe, shiners have been purposely introduced as food for game fish. The species sometimes reaches phenomenal levels of abundance. Whatever rôle they may play, shiners must exert an important pressure on the economy of many lakes.

The present study concerns only direct predation and the possibility of competition for food. Studies on competition are confined to qualitative determination of food present in samples of shiners and game species taken together. The game fish considered are the Yellowstone cut-throat Trout Salmo clarkii lewisi (Girard), the Kamloops trout Salmo gairdnerii kamloops Jordan, the mountain Kamloops trout S. g. whitehousei Dymond and the speckled char Salvelinus fontinalis (Mitchill).

#### Predation by Shiners

Consumption of trout fry by adult shiners was investigated experimentally. In 1948 three trials using young Kamloops trout fry from Summerland hatchery gave negative results. Shiners, chub and sculpins were placed for several days in a hatchery trough with trout fry; only sculpins (Cottus asper) were found to eat fry. Similar

results were obtained when an assortment of fish including shiners were confined with trout fry in an enclosure on Allison lake; only the sculpins ate fry. On 1 Sept. 1948, a seine was set in an arc out from the shore of Taylor lake, and approximately 1000 Kamloops trout fry were released inside the arc. After 10 minutes the seine was drawn in capturing a number of shiners. No fry were found in their stomachs.

In the summer of 1949, shiners from Rosebud lake were kept in a trough at Kaslo hatchery for several weeks. Kamloops trout fry were then introduced. Dead or injured fry were eaten by the shiners, but healthy fry remained alive for two days in the trough. Shiners would approach fry swimming near the surface, but would not pursue if the fry attempted to evade them. Shiners with a total length of 80 to 100 mm. ate injured fry with total length of approximately 25 mm.

On 27 July 1946 Dr. D. C. G. MacKay collected shiners from Pinantan lake following planting of Kamloops trout fry. The stomachs of eight of these preserved specimens were examined by the writer in 1950; two contained trout fry and three others contained unidentified fish remains.

Apparently shiners are capable of eating trout fry and in some instances they may do so under natural conditions. Although conditioning of the hatchery shiners may have biased results of the Kaslo experiments, it is suggested that shiners may be discouraged from attacking fry if the fry make a det-

ermined effort to escape. Trout fry poured from a hatchery can into shallow water were several times observed to lie inactive on the bottom for some minutes after release. This observation coupled with feeding experiments and the presence of freshly released fry in shiner's stomachs suggests that trout fry may be particularly susceptible to predation when they are first introduced into new surroundings.

#### Predation on Shiners

Various observations indicate that shiners are eaten by Kamloops trout, cut-throat trout and speckled char. At Nelson hatchery on 20 Aug., 1949, a number of Rosebud lake shiners, from 20 to 40 mm. long, were introduced in a circular rearing pond containing yearling Kamloops trout about 100 mm. long. Trout were seen to eat the shiners, usually swallowing them whole. Dead trout fry were also eaten by the yearlings.

Shiners occurred in the stomachs of trout from various lakes. Stomachs of the larger Kootenay lake Kamloops trout taken in 1949 contained mainly fish, usually kokanee Oncorhynchus nerka kennerlyi (Suckley) but occasionally shiners. Kamloops trout in Pinantan lake are said to feed largely on shiners; thermal stratification and severe oxygen stagnation in the hypolimnion (Rawson 1934) may force the two species into close contact. Shiners have recently entered Paul lake but have so far been reported by local residents as occurring in only a few trout stomachs. Anderson (MS) suggests shiners must reach a certain critical level of abundance before serving as trout food.

In Rosebud lake speckled char were observed chasing shiners. Two char, 10 and 12 inches long, swam back and forth in a dense school of shiners, darting at a shiner every few seconds. The shiners were apparently unconcerned, swimming within a foot of the char. No shiners were eaten during the period of observation, but injured shiners thrown on the water were immediately seized by the char.

In Cottonwood lake the shiner population apparently contains a disproportionate number of old fish. Of 37 specimens taken on five different occasions, 30 were over 80 mm. standard length and probably three or more years old. The dense population of small mountain Kamloops trout present may prey upon shiners up to a certain critical size, producing this uneven age distribution. While no shiners were found in trout stomachs from the lake, only a small percentage of the shiner population, as sampled by dip netting, was small enough to be eaten by the trout. Shiners too large to be eaten apparently live successfully alongside trout of almost the same size; the two species were frequently taken in the same dip net.

#### Competition

Table II shows the food items in stomachs of fish taken from Rosebud and Cottonwood lakes by gill net and dip net. In Rosebud lake all three species of game fish ate shiners, and the large shiners also contained small shiners. In both lakes, all food items eaten by game species were also taken by shiners. This is also true of collections of shiners

not included in Table II, taken along with speckled char fingerlings and cut-throat (or possibly Kamloops) fry in a cold stream entering Rosebud lake. Similarly collections of Kamloops trout together with shiners from South Champion lake and also from the Inonoaklin river all contained terrestrial insects plus a few lesser items.

TABLE II

Food of Shiners and Game Species Taken Together, 1949  
(Rosebud lake - 20, 21 June, 22, 23 July, 7 Aug.  
Cottonwood lake - 11 July, 16 Aug.)

	SAMPLE SIZE	NO. OF STOMACHS CONTAINING FOOD ITEM						
		Algae	Dragon- fly nymphs	Larval Diptera	Terr'l insects	Mollusca	Shiners	Misc.
ROSEBUD LAKE								
Cut-throat trout	9		1	1	7		2	1
Kamloops trout	1				1		1	
Speckled char	25		15		3	1	14	2
Redside shiner	14	6	3	2	1	3	3	1
COTTONWOOD LAKE								
Mtn. Kamloops trout	12		2	1	7	1		
Redside shiner	9		1	2	7	2		2

### Ecological Relations

In summary, shiners and game species apparently often have a definite effect on each other. It has been shown that under certain conditions shiners eat trout, trout eat shiners, shiners eat shiners and trout eat trout. In

addition shiners and young or adult Salmonids have been found to contain similar food when taken together.

Shiners may therefore be injurious to game fish production by consuming young and by competing for food of both young and old, or they may be beneficial by serving as prey for large Salmonids, converting diffuse nutrients into readily available food. They probably fill all of these roles in various habitats, environmental conditions governing the precise relationship.

Dymond (1930) has suggested that the critical factor affecting production of trout in some British Columbia lakes is the food available for the young during their first year; once trout are large enough to consume fish they are in command of an ample food supply. This situation may produce relatively small numbers of relatively large fish. From the present study it is suggested that shiners may in some cases intensify the condition outlined by Dymond, offering competition to young trout and serving as food for old trout.

The amount of contact between species of fish probably varies in different seasons. Physiological studies on the physical and chemical tolerances of each species involved might furnish evidence as to the degree of overlap of the zones occupied by each.

## STRUCTURAL VARIATION

### LITERATURE ON VARIATION IN FISH

Body proportions and the number of fin rays, vertebrae and scales are known to vary from population to population in many species of fish. In order to make taxonomic use of these characters it is necessary to be able to separate genotypic from phenotypic variation. It is therefore desirable to know which factors control phenotypic variation, and what are the mechanisms and extent of their operation.

The literature contains many <sup>appa</sup> differently contradictory results of investigations on the effect of particular environmental factors on particular meristic characters of fish. Concerning the effect of temperature on fin rays, Schmidt (1917) concluded from experimental studies on Lebistes reticulatus that higher temperatures during development of the young produced higher numbers of fin rays. Similarly Jensen (1939) finds in the plaice and the dab that the number of anal rays is directly proportional to water temperature when the larvae are small, 1°C. corresponding to 0.4 anal rays. Schultz (1927) finds a direct correlation between the highly variable anal ray count of the golden shiner Notemigonus crysoleucas and mean temperature during the spawning season.

In contrast to the foregoing, Hubbs (1922a) has demonstrated that the number of dorsal and anal rays of both Notropis atherinoides and Lepomis incisor is greater when the

developmental period is colder. Northcote (MS) shows that the average number of dorsal rays in the prickly sculpin Cottus asper increases from south to north between California and British Columbia, presumably inversely to developmental temperature.

The effects of temperature on vertebral count has been studied by several investigators. The works of Hubbs (1921, 1922a, 1922b) on Leptococcus armatus, Notropis atherinoides, Lepomis incisor, Notropis hudsonius and Notropis blennius, of Schmidt (1930) on the Atlantic cod, of Sundbom (1943) on the Norwegian herring and of Hart and McHugh (1944) on the capelin, to mention only a few, all indicates that lower temperatures tend to produce higher vertebral counts. However, Schmidt (1921) shows data for Salmo trutta which suggest that the curve of environmental temperature against vertebral count is actually V-shaped, with high counts at low and high temperatures and low counts at intermediate temperatures. Mottley (1937) also makes this suggestion.

Gabriel (1944) challenges the validity of Schmidt's conclusions and presents data on carefully controlled experiments with Fundulus heteroclitus. These show that high temperature produces fewer vertebrae, but lowering of developmental temperature below a certain point does not result in further increase of vertebrae. He concludes that differences in vertebral count at different temperatures are due to differences in temperature relations of processes controlling growth and processes controlling differentiation.

Histo-differentiation is more accelerated by high temperature than somit<sup>e</sup> separation and growth; consequently at high temperature vertebral differentiation takes place when the embryo is smaller and fewer vertebrae are formed. However, there are also genetically controlled differences in developmental rate and in the degree of temperature control. Vertebral count is therefore probably the resultant of both environmental and hereditary effects in the species studied.

There is some doubt as to the effect of temperature on vertebral count of the golden shiner Notemigonus crysoleucas a cyprinid similar in many respects to R. balteatus. Schultz = (1927) concluded that anal ray count was related to temperature during development, and yet he states that there is no significant correlation between number of anal rays and number of caudal vertebrae. Gosline (1948) gives figures suggesting that there is a tendency for the total vertebral count of the species to increase towards the north-east of its range (Texas to Maine). Hart (MS) on the other hand shows a rise in total vertebral count from north to south (between Ontario, Ohio and Florida).

Other environmental factors may affect vertebral count. Heuts (1947) lists six species of fish in which increased salinity produces higher vertebral counts. Scale count may likewise be controlled by environment; Hubbs (1922a) claims high temperatures produce high scale counts in Notropis atherinoides and Lepomis incisor, while Mottley (1934) suggests high temperature produces low scale counts

in Salmo gairdnerii. Hubbs (1941) shows that young suckers infected with parasites show a delay in time of scale formation and a concurrent rise in number of scales produced.

Part of the conflict in the foregoing examples may be due to failure to separate genetical from environmental variation; differences occurring over the geographic range of a species might show spurious correlation with a temperature gradient but actually be due to a genetic cline. However, most of the examples chosen above deal either with experimental observations or with differences between different year classes. Consequently it seems clear that in some cases environment does modify the structure of fishes.

W. R. Martin (1949) has proposed a mechanism for environmental control of body form. Log-log plots<sup>of</sup> body parts against standard length of fish are characterized by a series of "stanzas" each with a different relative growth constant. Transition from one stanza to the next is usually abrupt. The successive growth constants displayed are alike for all individuals of a species, but the body size at the point of inflection from one stanza to another is subject to environmental control. Thus one individual may enter a period of decelerated growth of a given part at a smaller size than another, and will therefore have a relatively smaller part during the remainder of its progress through the stanza. Martin showed experimentally that trout raised at higher temperatures showed faster growth rates, had larger body size at inflection from fast to slower growth of head

and fin size, and consequently had relatively larger heads and fins in later life. The direction of inflection from one stanza to the next determines whether larger body size at inflection results in relatively larger or smaller parts.

## ANAL RAY COUNTS

### Counting Methods

Anal fin ray counts were made with the aid of a binocular microscope. The last double ray of the fin has been counted as one, and the two (or rarely three) rudimentary rays ahead of the first long ray have been omitted. There are very few cases in which the ray count is in doubt, although rarely the last ray is single or an intermediate ray is split almost to its base. In general the number of divisions at the bases of the lepidotrichia have been taken as indicative of the ray count. Omission of the anterior rudimentary rays (the procedure usually followed in the literature) is not thought to have introduced an important error. The time required to count rays would be considerably increased by dissection to locate the occasional third rudimentary ray, which is relatively small. In fish in their second or higher year the last rudimentary ray is almost invariably less than half the length of the first full ray, (see Fig. 1). The first ray counted is unbranched; the remainder are split distally one or more times.

### Range of Variation

Appendix II contains anal ray counts for 54 loc-

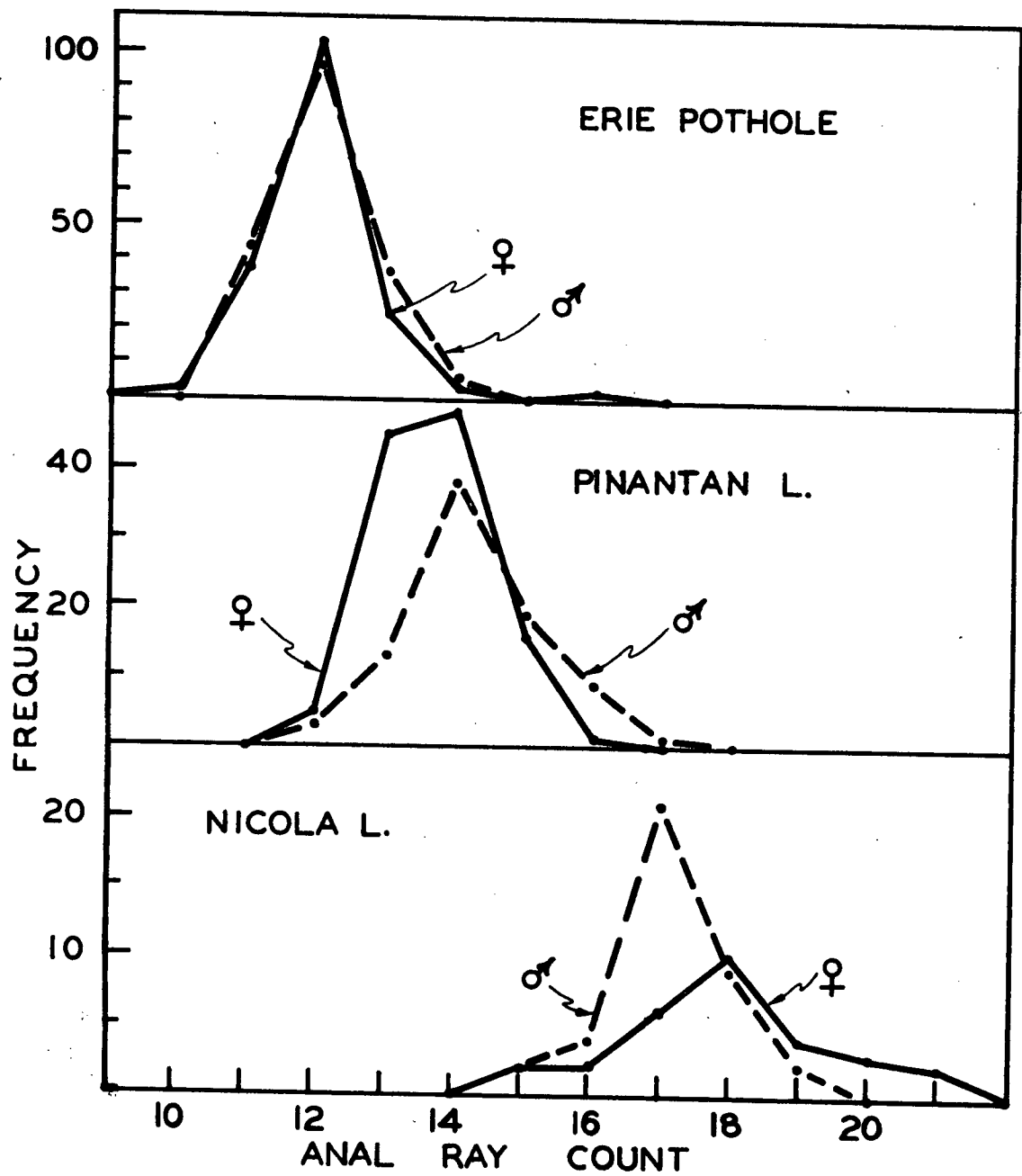


Fig. 7. Anal ray counts of shiners from three localities.

alities in British Columbia. Means varied from 12.00 to 17.44 with a range from 10 to 21. No obvious relation was apparent between ray count and altitude, latitude or drainage system. Populations separated by less than a mile differed markedly, while populations some 600 miles distant were similar. Counts from three selected localities are shown in Fig. 7. These represent the lowest and highest means obtained and one intermediate population. The range of the collections with highest and lowest means overlap by only one specimen.

#### Artificial Introductions

Ray counts were made on shiner stocks recently introduced from other known localities, and on samples from the parent populations. The species was introduced into Snowshoe lake from the Inonoaklin river by A. P. Coates in 1936, 1937 and 1938. Ray counts of samples taken from the two localities in 1949 did not differ significantly. ( $p > 0.05$ ).

According to local residents, shiners were first introduced into the Paul lake watershed in Hyas lake; they spread into Pinantan lake sometime after 1930, and from here entered Paul lake in about 1945. The mean ray count of a sample from Pinantan was significantly lower than one from Hyas ( $p \ 0.02 - 0.05$ .) Ray counts of fish from the east end of Paul lake near the creek from Pinantan lake did not differ significantly from Pinantan counts, but counts of fish from the west end of Paul (3 miles distant) were significantly lower ( $p < 0.01$ ) than those from the east end, and those from Pinantan.

An attempt at artificial introduction by the writer was unsuccessful. Shiners from Cultus lake were introduced in November 1948 into three artificial ponds on the University of British Columbia grounds. These apparently did not reproduce and were not seen after February 1949.

#### Intra-population Variation

The distributions for Pinantan and Nicola lake populations, (Fig. 7), display a striking phenomenon observed in several populations. In the former the males have a significantly higher anal ray count than the females ( $p < 0.01$ ) while in the latter the reverse is true, the females having a significantly higher mean ( $p < 0.01$ ). Females had significantly more anal rays at Queen's Bay, Kootenay lake ( $p 0.02 - 0.05$ ), while males had significantly more rays in Snowshoe lake ( $p 0.01 - 0.02$ ) and in the west end of Paul lake ( $p 0.02 - 0.05$ ). The remaining 14 collections in which the phenomenon was investigated did not show differences which were statistically significant. A possible explanation of sex differences in ray count is discussed later.

Variation in ray count was found also within single year classes. For example, Pinantan lake fry taken on 18 August 1948 showed a significant positive correlation ( $p 0.01 - 0.02$ ) between standard length and anal ray count. While in this and most other samples the larger fry had higher ray count, the reverse trend (not statistically demonstrable) was found in some samples.

Mean anal ray count also may vary from year to

year in one locality. Mean count of shiners of all sizes collected from Pinantan lake in 1946 was significantly lower ( $p < 0.01$ ) than the mean of individuals taken there in 1948. The higher mean of the 1948 sample appeared to be due largely to one year old fish, which showed a higher mean than older fish, (on the basis of size frequency distribution).

Despite annual variation found in some populations, ray counts of shiners taken by the writer at Sicamous on Shuswap lake in 1949 did not differ significantly from counts reported for the same locality by Dr. Eigenmann in 1894.

#### Summary of Adult Variation

In summary, significant differences in anal ray counts have been found between fish in different bodies of water, between recently introduced populations and their parent stock, between fish in different parts of the same lake, and between collections made in different years from the same locality. Sometimes males have significantly fewer rays than females, sometimes significantly more. Within a year class, the larger fish sometimes have significantly more rays, and possibly<sup>?</sup> they sometimes have fewer. These are strong indications that anal ray count is ~~not~~ at least partially subject to environmental control.

## VARIATION IN ANAL FIN BASE

### Morphology of the Fin Base

Schmidt (1917) and Hubbs (1922a) claim a direct relationship between vertebral count and anal ray count in certain species of fish. However, in families such as Cyprinidae the anal fin is short relative to the caudal region, and no strict serial arrangement common to fin ray and vertebral elements is apparent. Goodrich (1930) states that it is debatable whether the radials of median fins are derivatives of the axial skeleton or are special structures developed to support the fin; at any rate it is impossible in many adult Teleosts to associate each anal fin segment with a corresponding body somite, either by the musculature or innervation.

The supporting elements of the anal fin of R. balteatus were examined on specimens cleared with KOH and ultraviolet radiation, and stained with alizarin according to the methods outlined in Hollister (1934), and also on X-ray photographs of specimens. The anal fin ray elements (Fig. 8) appear in general to correspond to the figures and descriptions of Goodrich (1930). A series of long, laterally flattened plates, the proximal radial elements, project inward toward the haemal spines of the vertebrae. At the outer end each proximal element articulates with a small cylindrical and slightly tapering median radial element. This projects down and backwards, and bears on its posterior face a third still smaller distal radial element. The lepidotrichia

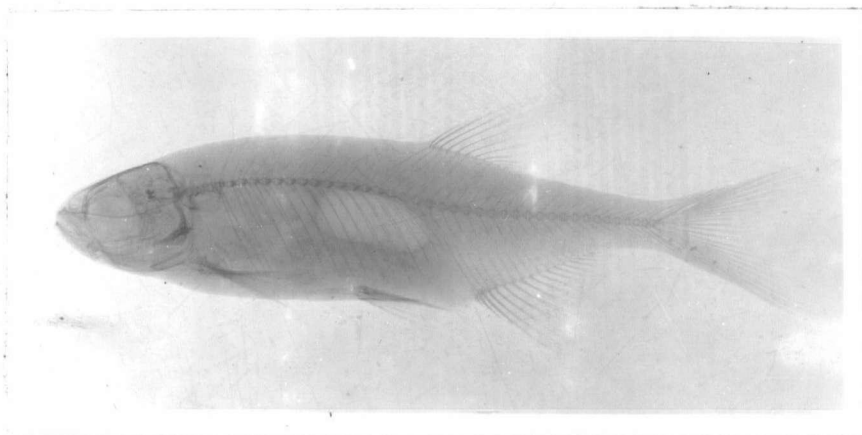


Fig.8. Print of X-ray photograph



Fig.9. Variation in anal fins of shiners  
 Top - 13 anal rays, Argenta slough  
 Bottom - 20 anal rays, S.Champion lake.

arise as two strips, straddling the junction of the proximal and median elements and uniting some distance below to form a single cylindrical anal ray. Distal to the junction of its two elements each ray is divided by a series of joints, and each of the fully developed rays, with the exception of the most anterior one, bifurcates one or more times antero-posteriorly. Anterior to the first long anal ray there is, in adult individuals, an unbranched ray about one third the length of the longest, and in addition one, or rarely two, much smaller rudimentary rays. The last two rays of the fin are united at the base.

The number of proximal radial elements does not correspond to the number of somites they occupy nor, therefore, to the number of haemal spines in the region occupied by the anal fin. There is a crowding of proximal elements especially toward the posterior end of the series. Also, the number of fin rays does not necessarily correspond to the number of proximal radial elements supporting them nor to any simple fraction thereof; there is a variable degree of fusion of proximal elements, especially at either end of the series. A typical series resulting from this crowding and fusion, taken from one of the cleared specimens, is: 18 distinguishable lepidotrichia supported by 16 distinguishable proximal radials, opposite 9 haemal spines on the vertebral column. The number of radials may be as true an index of the number of segments in the fin base as the rays, but counting fin rays rather than radials has the considerable advan-

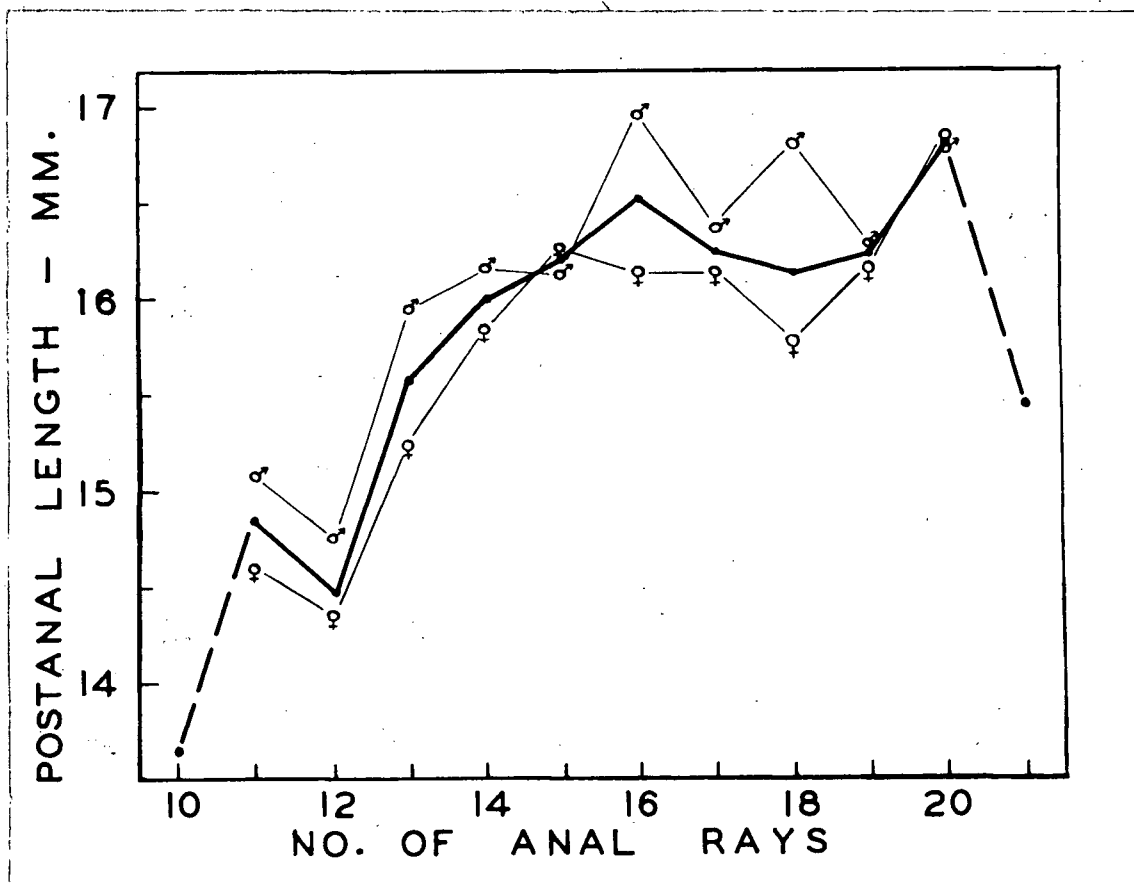


Fig. 10. Relation of anal ray count to mean postanal length (converted to preanal length of 30 mm.). 409 fish.

tage of much greater speed.

#### Fin Base Proportion

Ford (1933) and others find that vertebrae of the Caudal region tend to be the most variable in number. Though no homology between anal rays and caudal vertebrae was visible in R. balteatus, the possibility was examined that differences in anal ray count might be due to differences in length of the caudal region.

Postanal length (as defined in Appendix IV) is plotted against anal ray count in Fig. 10. In order to compare fish of different sizes it was necessary to correct for the differential growth of the two portions of the body. Each postanal length was therefore converted to the corresponding measurement at an arbitrarily chosen <sup>preanal</sup> ~~standard~~ length of 30 mm., assuming that the slope of the line of best fit for the log-log plot of postanal against <sup>preanal</sup> ~~standard~~ length of all fish, described the slope of growth of each individual (Martin 1949).

While postanal lengths of individuals with the lowest ray counts appear to be somewhat less than for those with intermediate and high ray counts, the difference is not sufficient to account for the whole range of variation of anal rays.

The proportion of the postanal region occupied by the anal fin base is next considered, and is plotted against anal ray count in Fig. 11. Clearly, fins with more

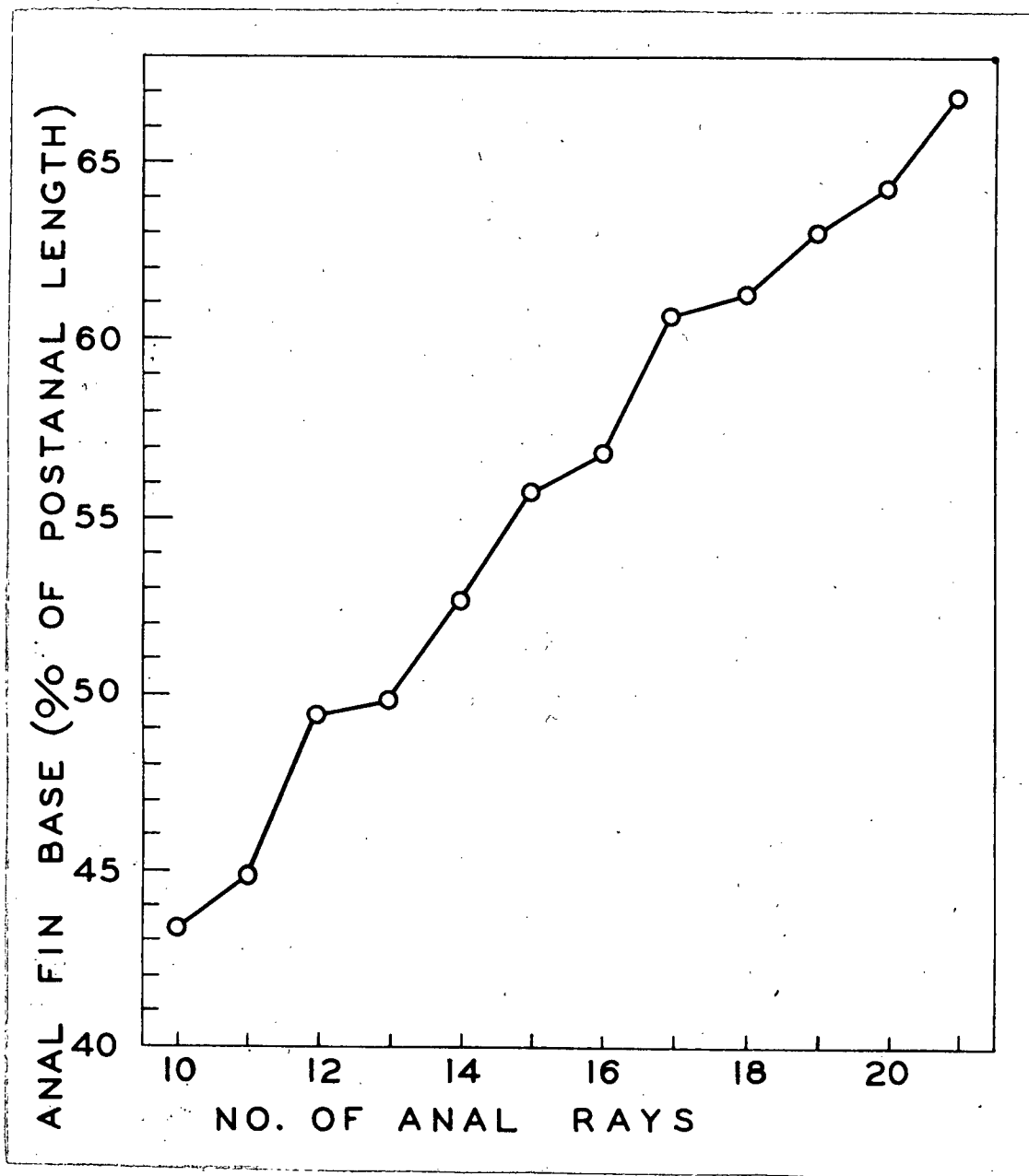


Fig. 11. Relation of anal ray count to mean length of fin base.  
113 fish.

rays generally occupy a greater proportion of the caudal region. This is also apparent in Fig. 9, which shows fish with ray counts of 13 and 20 respectively; the anal fin of the latter can be seen to extend much farther posteriorly.

Postanal length (expressed as a fraction of the standard length) was greater for males than females at <sup>almost</sup> all anal ray counts. However, considering only fish of a given ray count, there is no significant difference between sexes in the proportion of the postanal distance occupied by the fin base. Probably sex differences in postanal length are due to an inflection in relative growth of the posterior part of the body which occurs after ratio of fin base to postanal length, and also anal ray count, has been fixed. Log-log plots of postanal relative growth of 200 Erie pothole adults suggest that this inflection occurs at onset of sexual maturity in the second or third year of life. Further, postanal length of males is greater even in those populations having significantly lower male ray counts, suggesting again that sex difference in postanal length is not directly dependent on the same factor which controls anal ray counts.

## FIN RAY FORMATION AND ECOLOGICAL FACTORS

### Body Size at Ray Formation

Collections were made of fry in which the anal rays were just forming. Fig. 12 shows the number of fin rays visible in fry from different samples. In each collection there was apparently a specific size at which anal rays started to appear, but this size differed on different dates in Rosebud lake, and also between different localities. It seems unlikely that there are genetically different strains of early and late spawners, as no such condition was apparent from the spawning data already discussed. Apparently size at appearance of anal rays is subject to environmental control. The factor or factors responsible evidently affect all individuals about equally, and vary from time to time at a given locality.

Data are insufficient to decide whether size at ray formation is related to mean ray count attained, though there is some indication that fish forming rays at larger size form fewer rays. Nevertheless, environment apparently influences at least the final stage of formation of the anal fin, as it affects the time of appearance of definitive fin rays.

### Correlation with Temperature

Temperature observations at time of fry collections might be expected to furnish direct evidence on the relation of temperature to ray formation. However, sharp temperature

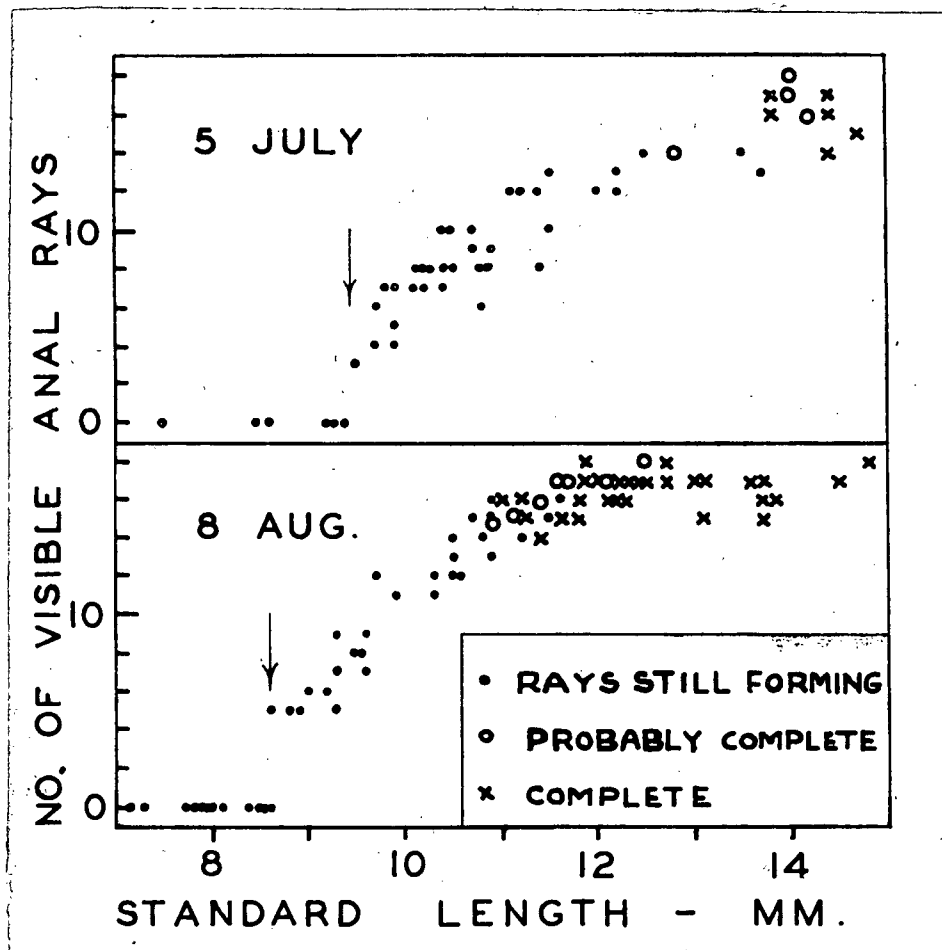


Fig. 12. Variation in size at formation of anal rays, Rosebud lake fry, 1949.

gradients frequently exist <sup>n</sup>in the environment of shiner fry, and diurnal changes may be great. Temperatures at Kaslo bay on 9 July 1949 were as follows:

Surface temperature, centre of bay - 17.9°C.

Shade side of boat house - 19.0

Sun side of boat house - 21.5

Ten inches from beach, two inches deep - 23.5

Rosebud lake temperatures were 4°C warmer on the inshore than the offshore side of a log close to shore. Gradients of 6°C within three feet in Erie pothole have been mentioned. Many other examples were noted where sharp temperature differences were set up by current, wind action or sunlight.

The mean temperature to which a group of fry were subjected could be derived only from an extensive set of observations throughout the whole diurnal<sup>n</sup> cycle in each locality studied. Such observations were not made, but the range of temperatures in which fry were moving was recorded for most collections. Table III shows collections in which anal rays were still forming. A positive correlation appears to exist between observed temperature and mean adult anal ray count.

TABLE III

Temperatures at Which Developing Fry Taken, 1949

	MEAN ADULT ANAL RAY COUNT	TEMPERATURE °C.
Erie pothole, 28 Aug., 1230 hrs.	12.08	15° - 21°
Little Shuswap lake, 4 Sept., 1030	14.90	18° - 19°
Erie lake, 16 Aug., 0900	16.01	17° - 23°
Rosebud lake, 5 July, 1300	16.09	20° - 24°
Rosebud lake, 8 Aug., 1200	16.09	23°
Middle Champion lake, 12 July, 1400	17.04	25°

#### Geographic Variation

While local differences have been shown to affect water temperature profoundly, a correlation between temperature and mean ray count, if it exists, should be apparent if a sufficient number of localities from a number of geographic areas are considered. Table IV shows mean ray counts of 51 localities in the United States from which ray counts have been recorded. These are grouped according to the average summer air temperature between June and August as given in the Atlas of American Agriculture (Baker 1936). Number of localities is indicated in brackets below each mean. Means of individual localities were each given equal weight. No comparable temperature data in sufficient detail were available for British Columbia.

TABLE IV

Mean Anal Ray Counts Within Temperature Isotherms

	AVERAGE SUMMER TEMP., JUNE-AUGUST (20 yr. average, mean of daily extremes)			
	55-60 F	60-65 F	65-70 F	70-75 F
<u>R. b. balteatus</u>	13.10 (5)	14.30 (23)	16.27 (3)	16.80 (8)
<u>R. b. hydrophlox</u>		11.42 (6)	13.40 (3)	
<u>R. thermophilus</u>		12.07 (3)		
Combined mean	13.10 (5)	13.55 (32)	14.83 (6)	16.80 (8)

A general relationship appears to exist between summer air temperature and mean ray count. In addition the lower means for R. b. hydrophlox within the same isotherms as R. b. balteatus suggests that their taxonomic separation may be justified on genetic grounds. The former group occurs at the southern extremity of the range of the genus; otherwise distribution of means forms no regular geographic arrangement except when considered relative to the irregular pattern of summer isotherms. R. thermophilus inhabits warm springs of high alkali content, and may well be a phenotypic variant.

Eigenmann (1894) claimed a negative correlation between altitude and anal ray count, as discussed previously. Probably such a general relation does exist, but is largely masked in the parts of the Columbia system from which his

opponents drew their examples. Sections of the Columbia and Snake rivers falling within the hottest summer isotherms, (in the vicinity of Walla Walla, Wash., and again in the vicinity of Nampa, Ida.) are at a higher elevation than cooler coastal areas. Hence ray count, which follows temperature, does not in these areas follow altitude.

The hypotheses of temperature controlled anal ray count fits in general the British Columbia collections. Highest ray count was found in Champion lakes, - small, shallow, rapidly warming bodies of water. Lowest ray count was found in Erie pothole, with the coldest shallow water encountered.

There is no evidence for correlation of ray count with dissolved solids. Analysis for principal dissolved solids were made on several lakes containing shiners by R. J. Waldie of the Pacific Biological Station. While calculations from the field data have not yet been made, there are indications that Rosebud lake and Erie pothole are both relatively rich in dissolved solids while varying greatly in ray count; Kootenay lake, with ray count similar to Rosebud, is relatively poor in dissolved material.

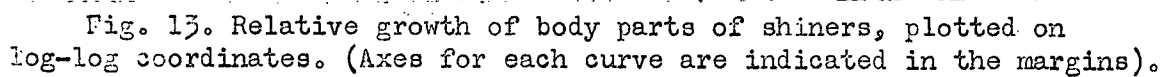


Fig. 13. Relative growth of body parts of shiners, plotted on log-log coordinates. (Axes for each curve are indicated in the margins).

## VARIATION IN OTHER STRUCTURES

### Relative Growth of Parts

Figure 13 shows growth of various parts relative to preanal length, plotted on log-log axis. Methods of measurement are listed in Appendix IV. Preanal rather than standard length was used as abscissa because postanal growth has an inflection at a preanal length of about 11.0 mm. as shown in Fig. 13. As might be predicted from Martin's hypothesis, (1949), variation is found between different populations in the proportion of postanal length, probably resulting from difference of body length at inflection as already discussed. Consequently preanal length was thought to be a better standard of reference for describing growth of parts.

Growth of a part at the same rate as growth of the whole is termed isometry. Parts growing faster than the whole are said to show tachyauxesis; parts growing slower than the whole are said to show bradyauxesis (Martin 1949). In a log-log plot of length of part against body length, the former condition results in a slope of less than  $45^\circ$ , while the latter produces an angle of more than  $45^\circ$  with the abscissa.

Eye, head, anal height and postanal length all show inflection from tachyauxesis to bradyauxesis at a preanal length of about 11.0 mm. Inflection is sharpest in eye and head growth. Postanal growth shows in addition an earlier inflection from bradyauxesis to tachyauxesis at about 7.0 mm.

A sharp inflection is seen in development of the pelvics. These appear at a preanal length of about 7.0 mm., grow rapidly until about 9.0 mm., and then inflect from extreme tachyauxesis to moderate tachyauxesis. At a later stage both pectorals and pelvics show heterosexual growth, females apparently inflecting to approximately isometric growth (isauuxesis) of these parts at a smaller size and hence having shorter pectorals and pelvics. It is possible to determine the sex of older fish by this characteristic. In old males the pectorals overlap the origin of the pelvics, and the pelvics extend posterior to the anus; in females the pectorals do not reach the pelvics, and the pelvics do not reach the posterior border of the anus.

#### Adult Variation in Proportions

Considerable variation is found, between individuals and between populations, in those structures showing inflection in growth. Examples are shown in Fig. 13 for eye, head and postanal growth. These differences are probably caused by difference in average size at inflection, perhaps due to temperature, diet or genetic effects. Differences were particularly marked in eye diameter, a measurement showing sharp inflection in growth. Eye diameters from 3.5 mm. to 4.9 mm., and head lengths from 10.1 mm. to 14.0 mm. occurred in individuals of 30.0 mm. preanal length.

Insufficient measurements were taken for detailed correlation of body proportions <sup>with</sup> to anal ray count. Eye diameter appears to show rough positive correlation with ray

count. Champion lake shiners with high ray count have statistically greater eye diameters than Erie pothole and Paul lake fish with low ray counts ( $p. < 0.01$ ); other populations studied were intermediate in mean eye diameter and ray count.

Correlation of ray count with other proportions studied is apparently not close. This is not surprising in that considerable time elapses between fixing of the anal ray count (sometime before reaching a preanal length of 6.5 mm.) and inflection of most body proportions at about 11.0 mm. The latter occurs when the fish are swimming actively and feeding; the former may occur before absorption of the yolk sac when the fish are lying inactive.

#### Vertebrae

X-ray photographs were taken of 109 shiners with anal ray counts from 11 to 20. Use of a small dental X-ray unit was kindly provided by Dr. Otto Blüh of the Physics Department, University of British Columbia. Fish were laid on holders containing 5" 7" medical X-ray film and exposed two seconds to "hard" rays at a distance of two feet.

Figure 8 shows an X-ray picture of a shiner with 37 vertebrae. Counts started at the first vertebra bearing a neural spine and included the hippural plate.

Table V gives the relation of vertebral to anal ray counts. Scatter is considerable, but there is a tendency for higher ray count to be associated with higher vertebral count. The mean vertebral count for fish with from 11 to 15 rays is significantly lower than the mean for fish with 16

to 20 rays ( $p < 0.01$ ).

TABLE V  
Vertebral and Anal Ray Counts.

NO. OF VERTEBRAE	NO. OF ANAL RAYS										MEAN
	11	12	13	14	15	16	17	18	19	20	
36	2	1	3	2	2	1					13.36
37	4	7	12	9	10	8	7	5	7	1	15.00
38	1	3	2	3	3	6	4	2	2	1	15.48
39		1									

No significant difference was found between the vertebral counts of the sexes. Similarly, the numbers of vertebrae posterior to the first proximal radial of the anal fin were similar in the sexes, (range 18 to 21, mean  $19.81 \pm 0.06$ ). This is further indication that the longer postanal length of males discussed previously is due to an adjustment occurring after segmentation is complete.

In many species of fish vertebral count has been shown to be negatively correlated with temperature. If higher temperatures produce more anal rays, it might be supposed that high ray count would be associated with fewer vertebrae. Apparently the reverse is true for R. <sup>b</sup> Balteatus. A similar condition may exist for Notemigonus crysoleucas as reported by Hart (MS).

## Scales

Counts of lateral line scales were made on 115 fish from Snowshoe lake and Inonoaklin river. These showed a variation from 54 to 67, with a mean of  $60.98 \pm 0.25$ . As in the case of vertebral count, scale count appeared to show a loose positive correlation to anal ray count within the two populations studied. Mean ray count of Snowshoe fish with 54 to 61 scales was significantly lower ( $p$  0.02 - 0.05) than those with 62 to 67.

Such a relation is in keeping with Hubbs' (1922) findings that high temperature produced both high ray count and high scale count in the minnow Notropis atherinoides.

From data in Carl and Clemens (1948), the range of variation of scales count is probably greater in R. balteatus than in all other B. C. Cyprinids, but less than in some of the Salmonids.

## CONCLUSIONS: A POSSIBLE MECHANISM FOR ANAL RAY COUNT VARIATION

### Evidence for Environmental Control

Two types of variation in body form have been considered; variation in proportions involving continuous variables which are measured, and variation in number of metameric parts involving discontinuous variables which are counted. The former included lengths of fins and relative size of different sections of the body; the latter included fin rays, vertebrae and scales.

Variation may be either genotypic or phenotypic.

It is necessary to separate the two before investigating which factors are operative in the latter. Only the problem of anal ray count variation has been examined in detail.

Considerable evidence has been presented that anal ray count is subject to environmental control. Populations in closely adjoining bodies of water may differ widely in mean ray count. No pattern is apparent in the distribution of ray counts within drainage basins or other geographic features such as might be expected if genetic clines were involved. Ray counts of recently introduced populations differ from those of their parental stock. Counts differ from year to year in one locality, and differ between large and small individuals of the same year class. Mean ray count also varies between different parts of the same lake.

On the other hand comparison of ray counts of R. b. hydrophlox with those of R. b. balteatus in comparable temperature zones suggests that a genetic cline may occur at the southern end of the range. Evidence is purely negative in the case of the Inonoaklin - Snowshoe lake transplant which produced no variation in mean ray count. Genetic differences in sex evidently can affect ray count, but the fact that males are sometimes higher and sometimes lower than females suggests that there is no simple sex-linked control of ray number.

It therefore seems apparent that among the populations studied environment plays a large part in determining anal ray count. That temperature is an important factor is

suggested by several lines of evidence. Temperature differences offer a ready explanation for the variation between times and localities already mentioned. Temperature observations at time of formation of anal rays roughly fit the observed ray counts, and mean ray counts grouped according to temperature zones are related to average air temperature during the developmental period.

#### Possible Causes of Intra-population Variation

Considerable variation has been noted in several body proportions. Sharp inflections in relative growth of these parts has been demonstrated. Probably the mechanism outlined by Martin (1949) is operative; environment controls body size at inflection to a new growth stanza and therefore governs relative size of parts during that stanza.

Significant differences in anal ray count have been found between the sexes. As either males or females may have the higher counts in different populations, simple sex-linked control of ray count seems improbable. Possibly one sex develops faster and reaches the stage at which the number of rays is determined at an earlier date than the other. (That males grow faster than females has been suggested.) If all fry in a year class developed at the same temperature, no difference between sexes would be apparent. This is the case in most populations studied. If, however, fry developed during a period of steadily rising water temperatures, the sex which developed faster would on the average

lay down rays at lower temperatures and show a lower mean ray count. If water temperatures were falling during development, fast growers would then tend to have more rays.

Lower ray count of larger individuals in a year class may also be the result of rising water temperatures, and higher ray count of larger fry the result of falling temperatures.

It seems unlikely that all intrapopulation variation is purely environmental. Though all individuals may form visible rays at the same size under given conditions, they do not all form exactly the same number of rays. Data presented for variation of R. b. balteatus and R. b. hydrophlox in comparable temperature zones suggests that the mean value about which environmental control operates is genetically determined. Similarly some degree of genetic variability is probably present within populations.

### Hypothesis

It has been shown that anal fins with relatively large number of rays occupy a relatively large proportion of the postanal region. Variation has been observed in the size at which partitioning of the postanal tissue into segments becomes visible. There is some evidence to suggest that size at which fin rays become visible is governed by temperatures, and that fish which form rays at a larger size are those which form fewer rays. The highest ray count observed was 21, and the highest number of vertebrae posterior to the

origin of the anal fin was also 21.

A hypothetical mechanism for the determination of anal ray count is offered. Two assumptions are required.

1. The number of segments into which the fin base divides is governed by the number of body somites lying adjacent to it at the time of fin segmentation.

2. Environment affects the relative lengths of the caudal region and the presumptive anal fin base at the time of segmentation.

According to this hypothesis the strip of tissue which will become anal fin initially occupies the whole ventral length of the caudal region. If the strip is broken into its definitive elements now, the maximum number of fin rays will later develop; no amount of environmental manipulation can produce more fin ray segments than there are body segments lying adjacent to them. Though in this case the segmentation of the fin base is histologically determined while the base is as long as the postanal length, the definitive rays do not form until later; by this time the caudal region has grown more rapidly than the fin base, and the base occupies less than the whole of the caudal. The consequent sliding of tail somites past fin segments produces the staggered effect seen in the adult. When fin rays and associated radial elements develop, the proportion of fin base to caudal region is "frozen" and remains relatively constant throughout life.

If, however, environmental factors delay the time

at which histological differentiation of the fin base into segments occurs, then the base will have come to occupy less than the whole caudal region. Fewer body somites will lie adjacent to the base, and fewer segments will be laid down when differentiation occurs. Development of the rays and radials will also occur later than in the first instance, so that the fin base, consisting of fewer segments, will occupy a smaller proportion of the postanal distance when "frozen".

Environmental control of the proportion of fin base to caudal length at time of segmentation, (the second assumption) might operate in several ways.

1. The temperature coefficient for growth of the two parts might vary with segmentation of the fin base occurring at a given size. If  $Q_{10}$  (temperature coefficient) for the fin base were higher than for the whole tail region, then at higher temperatures the base would be better able to keep pace with the tail and would occupy more somites at time of segmentation.

2. Another mechanism would involve fin base and tail each growing at a constant rate, with the tail growing faster. If temperature determined the size at which segmentation of the base occurred, it would affect the number of somites adjacent to the base at that time.

3. Other mechanisms might be postulated involving piracy of the preanal or other region on the fin base, so that the more delayed the segmentation was the less base

material would be available. At present the exact nature of the mechanism involved is almost entirely conjectural.

### General Application of the Hypothesis

Determination of the number of fin rays in fish by a mechanism similar to the one suggested might account for many of the apparent contradictions in the literature. It has been pointed out that low temperature apparently produces increased fin ray counts in some species but decreased counts in others. Let us suppose that the number of segments into which a presumptive fin base divides is influenced by the number of body somites adjacent to it at the time of differentiation. If the base is growing faster than the adjacent somites, any factor (such as low temperature) delaying segmentation of the fin base will produce more fin segments. If on the other hand the base is growing slower, a factor delaying segmentation will produce fewer fin segments. Similarly, if the mechanism involves different temperature coefficients for growth of fin base and body proper, then high temperature will produce more rays if fin base Q 10 is the higher, fewer rays if body Q 10 is the higher.

If in some species the fin base takes its segmentation pattern from the adjacent somites at an early stage, before any differential growth has occurred, then the number of fin rays will be governed to some extent by factors affecting the number of body somites, (e.g. temperature affecting the number of vertebrae).

Evolution of fish with short median fins from ancestors having long many-rayed fins could be postulated by the simple process of delay in time of ray differentiation. A mutation or series of mutations inhibiting ray differentiation might confer selective advantage by producing fish with improved speed or maneuverability.

This mechanism suggested is as yet hypothetical, but the available data appear to fit the hypothesis. Controlled experiments and histological sectioning are required, but difficulties encountered in artificial rearing must be first overcome. Due to its spectacular variability in anal fin ray count, R. balteatus is suggested as admirable material for further study.

## SUMMARY

1. Shiners occur in a wide variety of habitats including small warm lakes, large cold lakes, cold springs and running water.
2. The spawning period varies from 7 to 10 weeks, starting in the last week of May in some localities and the second week of June in others.
3. Different individuals spawn at different times, and one individual may spawn more than once in a season.
4. Eggs can be hatched experimentally at temperatures from 12°C. to 21°C., with corresponding mean hatching times varying from 15 to 7 days. At 9°C. eggs show initial cleavage and then die.
5. Fry lie quiescent for about a week following hatching, then swim actively in the shallow water after the yolk sac is absorbed.
6. Growth rates of different populations vary considerably. Most populations contain few individuals older than year II or III. The largest fish taken was in year V or VI.
7. Females live longer than males. Older year groups are almost exclusively females.
8. Different sizes of fish frequent different depth zones, the smaller fish occupying shallower water.
9. Shiners and game species probably affect each other considerably. Under certain circumstances shiners eat trout

fry, trout eat shiners, and shiners eat the same food as trout.

10. Great differences exist between mean anal ray counts of different populations.

11. Variation in ray count is due at least partially to environmental conditions during development.

12. Temperature is probably an important environmental factor controlling ray count.

13. There is variation in proportion of body parts between different populations. Early inflections occur in the relative growth rates of these parts. Environmental factors probably cause variation in proportions by varying body size at inflection.

14. Differences exist between body proportions of the sexes.

15. Differences exist between anal ray counts of the sexes in some populations. Males sometimes have more rays, sometimes fewer. Environmental control is suggested.

16. Anal fin rays do not appear until relatively late in development. Environment affects size at which rays appear.

17. It is suggested that the number of segments in the fin is governed by the number of body somites lying adjacent to it at the time of segmentation, and that environmental factors may control the proportion of the caudal region occupied by the fin base at this time.

18. This mechanism might account for many of the con-

tradictory reports in the literature on the affect of environment on number of fin rays in different species.

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## APPENDIX I

### Data on Shiner Collections

The geographical indices are similar to those used in the Geographical Gazetteer of British Columbia, Department of Lands. Latitude and longitude refer to the south-east corner of the quadrilateral in which the locality lies; compass references give the appropriate quarter of this area. Districts referred to are Land Districts, (for administrative purposes only). Dates following refer only to time of collection of specimens dealt with in Appendix II. Temperature readings are in Centigrade degrees; A refers to air temperature, S to surface temperature. Numbers preceding each dash refer to depths in metres. B indicates bottom. Thus 2 - 18.5 indicates that the temperature was 18.5°C. at 2 metres depth. Permanent collection numbers of specimens from the Royal Ontario Museum of Zoology are indicated by the letters R.O.M.Z.

ALLISON L. 49° 120° N.W. Expansion of Allison cr., near head, Kamloops dist. 29 Aug., 6 Sept. 1948. Temp. 5 Sept. 1949, 1030 hrs.: A-18, S-16, 1-15, 7-15, 9-12, 11-9, 12.5-8, 38B-4.5.

ARGENTA SLOUGH. 50° 116° S. W. Off Duncan r., on road to Howser, Kootenay dist. 4 June 1949. Collector I. Barrett.

ARROW LAKES. Kootenay district.

Deer Park. 49° 118° S.E. E. side Lower Arrow l. 7 June 1949.

Fosthall Ck. 50° 117° S.W. W. side Upper Arrow l. 29 July 1949.

Nakusp 50° 117° S.W. E. side Upper Arrow l. 18 July 1949.

BABINE L. 54° 126° N. W. Cassiar dist. 1947. Collector Al. Johnson.

BAPTISTE L. 50° 116° N. E. Trib. to Macaulay cr., near Edgewater, Kootenay dist. 15 June 1949. Area 34 acres, deepest 10 m., shallow shores. Collector H. Tyler.

BLUE L. (TURKEY L.) 49° 120° N. W. Expansion of Allison cr., Kamloops dist. 1948.

CARDEW L. (SHUMWAY L.) 50° 120° N.E. Expansion of Campbell cr., Kamloops dist. 4 Sept. 1949.

CHAMPION LAKES. 49° 117° S.W. Three small lakes at head of ~~head of~~ Landis cr., trib. to Champion cr., Kootenay dist. 12 July 1949. Temp. South l. 1230 hrs: S-21, Middle l. 1400 hrs.: S-25.2.

CHILLIWACK SLOUGH. 49° 121° S. W. New Westminster dist.

2 Oct. 1932. Collector W. E. Ricker. R.O.M.Z. #8581.

CHIMNEY L. 51° 121° N. W. Head of Chimney cr., Lillooet

dist. 8 Sept. 1949. Deepest 25 m. Collector Sam Mitchell.

COLUMBIA R., CASTLEGAR. 49° 117° S. W. Near mouth of

Kootenay r. 6 July 1949. Backwater near sawmill one mile

below Castlegar. Temp. 1030 hrs: S-13.5 - 15.5.

COTTONWOOD L. 49° 117° S. E. head of Cottonwood cr.,

S. E. of Nelson, Kootenay dist. 11, 14 July; 12, 16,

27 Aug. 1949. Temp. at outlet 20 June 49, 1430 hrs:

15.5. 29 June 49, 1630 hrs: 11.0. 5 July 49, 1000

hrs: 15.0. 11 July 49, 1500 hrs: 18.8. 27 Aug. 49,

1800 hrs: S-17, 14B - 11. Av. depth 13 - 14 m.

CULTUS L. 49° 121° S.W. Head of Sweltzer r., trib.

to Chilliwack r., New Westminster dist. 25 Sept. 1948

near outlet; 11 Nov. 1948 one mile W. on S. shore.

DOUGLAS L. 50° 120° S. E. Expansion of Nicola r., ca. 10

miles E. of Nicola l., Kamloops dist. 7 Sept. 1949.

DUCK L. (ELLISON L.) 49° 119° N. E. 8 miles N. E. of

Kelowna, Osoyoos dist. 6 Sept. 1949.

DUTCH L. 51° 120° N. E. One mile N. E. of junction of

North Thompson and Clearwater rivers, Kamloops dist.

27 Aug. 1946. Collector D. C. G. MacKay.

ERIE L. (BEAVER L.) 49° 117° S. E. Three miles W. of

Salmo, Kootenay dist. 16 Aug. 1949. Temp. 28 June 49,

1815 hrs: S-17. 16 Aug. 49, 0800 hrs: S - 17. 1030 Hrs:

S - 23. Lake Shallow, weed beds in centre.

ERIE POTHOLE. 49° 117° S. E. 1 3/8 miles W. of Erie l.,  
drains W. into Archibald Ck. 28 June, 5 July, 16, 28  
Aug. 1949. Temp. 28 June 49, 1750 hrs: S - 17.2. 16  
Aug. 49, 1200 hrs: S - 20.4. 28 Aug. 49, 1645 Hrs:  
A - 32, S- 31, 1 - 15, 2 - 14, 3 - 13, 4 - 9, 5 - 9,  
6 - 8, 7B - 7. Av. depth 6 - 7 m. Water stained.

GARNET VALLEY L. 49° 119° N. W. Expansion of Eneas ck.,  
Osoyoos dist. 6 July 1928. R.O.M.Z. #6203.

HYAS L. 50° 120° N. E. Drains into Pinantan l., Paul ck.  
chain, Kamloops dist. 30 July 1948. Collector G. C.  
Anderson.

INONOAKLIN R. 49° 118° N. E. Flows S. E. into Lower  
Arrow l. at Edgewood, Kootenay dist. 2 Sept. 1949.  
Murton's sawmill.

KOOTENAY L. Kootenay dist.

Campbell ck. 49° 116° N. W. Enters E. side  
Kootenay l. 2 miles N. of Kaslo. 29 May 1949.

Kaslo 49° 116° N. W. W. side Kootenay l. 45 miles  
by road N. of Nelson. 10 June 1928. R. O. M. Z. #6541.  
29 May, 21 July, 14 Aug. 1949.

Kuskanook 49° 116° S.W. E. side Kootenay l.  
near S. end. 21 July 1949.

Lardeau 50° 116° S.W. N. end Kootenay l. 15  
July 1949.

Nelson 49° 117° S.E. S. shore, West arm Kootenay l.  
26 June 1949. Boathouses.

Queen's Bay 49° 116° N.W. W. shore Kootenay l.  
immediately N. of entrance to West arm. 10 June 1949.  
KOOTENAY R. 49° 117° S.W. Drains West arm of Kootenay l.  
into Columbia r. at Castielgar, Kootenay dist.

Taghum 4 3/4 miles W. of Nelson, highway crossing of  
Kootenay r. 6 July 1949. S. shore.

Three-mile Pool Cut off from Kootenay r. by railway  
embankment. S. shore, 3 miles W. of Nelson. 24 June  
1949. Temp. 1700 hrs: S - 17.5.

LAIRD L. 49° 120° N.W. Expansion of Allison cr.,  
Kamloops dist. 4 Sept. 1948.

LITTLE SHUSWAP L. 50° 119° N.W. W. of W. end of  
Shuswap l., Kamloops dist. 4 Sept. 1949. Temp.  
E. end 1025 hrs: S - 19.

MC BAINS L. (ROSEN L.) 49° 115° S.E. 2½ miles N.E.  
of Jaffray, Kootenay dist. 1949.

NADSILNICH L. (WEST L.) 53° 122° N.W. Head of Beaverly  
cr., Nechako r., Cariboo dist. 1949.

NICOLA L. 50° 120° S.W. Expansion of Nicola r., Kam-  
loops dist. 7 Sept. 1949.

OKANAGAN L. Osoyoos dist.

North End 5 July 1928. R.O.M.Z. #6206.

Okanagan Landing 50° 119° S.E. E. side Okanagan  
l. 5 miles S.W. of Vernon. 6 Sept. 1949.

PADDY RYAN LAKES. 50° 116° N.E. 4 miles S.W. of Invermere,  
Kootenay dist. 15 June 1949. Five shallow lakes,  
sources of water for town of Invermere. Each lake 3

acres. Collector H. Tyler.

PAUL L. 50° 120° N.E. Expansion of Paul cr., Kamloops dist. W. end 3 Aug. 1949; E. end 4 Aug. 1949.

Collector G. C. Anderson.

PINANTAN L. 50° 120° N. E. Expansion of Paul cr. near head, Kamloops dist. 27 July 1946 Collector D. C. G. MacKay; 18 Aug. 1948.

PUNTCHESAKUT L. 52° 122° N.W. Expansion of Puntchesakut ck., Cariboo dist. 12 July 1949. Collector Bill Hillen.

ROSEBUD L. 49° 117° S. E. Head of Rosebud ck., Salmo r., Kootenay dist. 21 June, 28 Aug. 1949. Temp. 17 May 49, 1535 hrs: S - 16. 3 June 49, 1350 hrs: S - 19 (shade), 22 (sun). 20 June 49, 1800 hrs: S - 19 (east shore), 5 - 21 (W. shore), 19 - 12.3 - 10.8 (ascending inlet ck.). 21 June 49, 0700 hrs: 17, 0915 hrs: 5 - 18.5, 1330 hrs: S - 19(15) 28 June 49, 2010 hrs: S - 17. 29 June 49, 0815 hrs: S - 17. 5 July 49, 1215 hrs: S - 20, 24 - 28 (in protected pockets inshore). 23 July 49, 0800 hrs: S - 19, 1400 hrs: S - 23. 28 Aug. 49, 1215 hrs: A - 34 (in sun), S - 21, 1 - 19, 2 - 18.5, 4 - 18, 6 - 18, 7 - 17, 8 - 14, 9 - 13, 10 - 11, 11 - 9.5, 12 - 8.5, 13.5 - 8, 15 B - 7.

SKAHA L. (DOG L.) 49° 119° S.W. Expansion of Okanagan r., 4 miles S. of Okanagan l., Similkameen dist. 2 Aug. 1948.

SHUSWAP L. 50° 119° N.E. Head of S. Thompson r., Kamloops dist. 3 Sept. 1949. Sicamous, entrance of Mara l.

SHUSWAP R., GRINROD.  $50^{\circ}$   $119^{\circ}$  N.E.  $5\frac{1}{2}$  miles N. of  
Enderby, Kamloops dist. 3 Sept. 1949.

SLOCAN L.  $49^{\circ}$   $117^{\circ}$  N.E. Head of Slocan r., Kootenay  
dist. 10 Aug. 1949. Silverton.

SNOWSHOE L.  $49^{\circ}$   $118^{\circ}$  N.E. In Secs. 34 and 35, T p.69,  
between Inonoaklin and Whatshan cks., Kootenay dist.  
2 Sept. 1949. Temp. 1905 hrs: A - 23, S - 20, 1 - 18,  
5 - 18, 6 - 15, 7 - 11.5, 7 - 11.5, 8 - 9.5, 10 - 8.5,  
12 - 8.

SPRING L. AND TIMOTHY L.  $51^{\circ}$   $121^{\circ}$  N.E., expansion of 111  
mile ck., Lillooet dist. Autumn, 1949.

STEVENS L. (ROCK L., LAZY L.)  $49^{\circ}$   $115^{\circ}$  N.W. N.E. of  
Wasa, between Lewis and Wolf cks., Kootenay dist.  
25 July 1949. Collector J. J. Osman.

TAYLOR L.  $49^{\circ}$   $120^{\circ}$  N.W. Head of Gulliford ck., Kamloops  
and Yale dists., Merrit - Princeton road, 1948.

TETANA L.  $55^{\circ}$   $126^{\circ}$  N.E. Head of Driftwood r., Cassiar  
dist. Collector J. F. Stanwell-Fletcher. R.O.M.Z.  
#12,217.

WILLIAMS L.  $52^{\circ}$   $122^{\circ}$  S.E. Head of Williamslake ck.,  
Fraser r., Cariboo dist. 2 Aug. 1944. Collector  
G. C. Toner. R.O.M.Z. #14371.

# APPENDIX II

## Anal Ray Counts of Shiners from Localities in British Columbia.

The symbol T indicates total counts which include males, females and fish whose sex was not determined.

Counts include only adults, or collections of fry in which all the anal rays had formed.

Anterior rudimentary rays not counted; last split ray counted as one.

LOCALITY		NO. OF ANAL RAYS												NO.	MEAN
		10	11	12	13	14	15	16	17	18	19	20	21		
ALLISON L.	T						3	7	4	6	2			22	<u>16.86</u>
ARGENTA SLOUGH	♀		3	4	13	7	1	4	1					33	13.45
	♂		1	1	6	4	1							13	13.23
	T		4	5	19	11	2	4	1					46	<u>13.39</u>
ARROW LAKES															
Deer Park	T				2	12	22	22	15					73	<u>15.49</u>
Fosthall Ck.	♀			1	5	7	17	12	-	1				43	14.88
	♂			1	8	11	33	13	5	1	1			73	15.00
	T			2	13	18	50	25	5	2	1			116	<u>14.96</u>
Nakusp	♀			1	5	6	7	2						21	15.19
	♂			1	2	6	2	1						12	15.00
	T			2	7	12	9	3						33	<u>15.12</u>
BABINE L.	T				2	1	2							5	<u>15.00</u>
BAPTISTE L.	T		1	6	13	18	8	2	1					49	<u>13.73</u>
BLUE L.	T						4	6	4	1				15	<u>16.13</u>
CARDEW L.	♀					4	8	4	4	2				22	15.64
	♂		1	-	-	7	8	5	5	2				28	15.36
	T		1	-	-	11	16	9	9	4				50	<u>15.48</u>
CHAMPION LAKES															
Middle Lake	♀					1	4	12	14	14	3	3		51	17.12
	♂					1	1	7	6	5	2			22	16.86
	T					2	5	19	20	19	5	3		73	<u>17.04</u>
South Lake	♀							3	7	5	6	1		22	17.77
	♂						1	2	3	2	3	1		12	17.58
	T						8	33	56	50	25	8	1	181	<u>17.44</u>

		10	11	12	13	14	15	16	17	18	19	20	21	NO.	MEAN
CHILLIWACK SLOUGH	T							2	-	2				4	<u>17.00</u>
CHIMNEY L.	T			1	2	3	5	3						14	<u>14.50</u>
COLUMBIA R. Castlegar	T					2	4	2	1					9	<u>15.22</u>
COTTONWOOD L.	T						4	11	11	4	4	1	1	36	<u>17.00</u>
CULTUS L.															
25 Sept. 1948	♀					2	22	26	16	3				69	14.94
	♂					5	36	39	9	6				95	14.73
11 Nov. 1948	♀					2	5	12	3	4				26	15.08
	♂					1	11	7	5	-	1			25	14.80
Combined	T					29	147	184	68	20	1			449	<u>14.79</u>
DOUGLAS L.	T							9	18	13	11	1		52	<u>16.56</u>
DUCK L.	T					2	5	7	10	6	1			31	<u>15.52</u>
DUTCH L.	T					1	4	3	1					9	<u>14.44</u>
ERIE L.	T					1	1	1	2	3				8	<u>16.62</u>
ERIE POTHOLE	♀	2	38	103	25	4	-	1						173	11.97
	♂		43	96	36	5								180	12.02
	T	2	80	<del>237</del>	82	12	-	1						414	<u>12.06</u>
GARNET VALLEY L.	T			1	17	21	11	2	1					53	<u>13.98</u>
HYAS L.	T					3	8	8						19	<u>14.26</u>
INONOAKLIN R.	♀	2	10	9	8									29	12.79
	♂	1	5	10	5									21	12.90
	T	3	16	19	13									51	<u>12.82</u>
KOOTENAY L. Campbell Ck.	T					2	7	10	10	5	-	1		35	<u>16.37</u>
Kaslo, 1928	T					2	12	19	17	6	1	1		58	<u>16.35</u>
Kaslo, 1949	♀					3	5	9	9	2	1			29	16.17
	♂					2	9	7	12	1				31	16.03
	T					12	32	59	41	8	3			155	<u>16.06</u>
KUSKANOOK	T					1	1	13	11	6	1	1		34	<u>15.79</u>

		10	11	12	13	14	15	16	17	18	19	20	21	NO.	MEAN
Lardeau	T					1	11	22	4	1				39	<u>15.82</u>
Nelson	T				1	4	23	19	10	9				66	<u>15.91</u>
Queen's Bay	♀					2	5	19	16	3	1			46	16.34
	♂				1	6	13	21	12	5				58	15.90
	T				1	8	19	41	31	10	1			111	<u>16.14</u>
KOOTENAY R.															
Taghum	♀					1	2	5	6	1	1			16	16.44
	♂						6	3	6	2	1			18	16.39
	T					1	8	13	13	3	3			41	<u>16.44</u>
Three-Mile Pool	T						3	15	16	12	2	1		49	<u>16.96</u>
LAIRD L.	♀					6	24	22	49	10	6	1		118	16.47
	♂					4	10	28	20	10	5	1	1	79	16.58
	T					10	34	50	69	20	11	2	1	197	<u>16.51</u>
LITTLE SHUSWAP L.	T				4	20	20	15	-	1	1			61	<u>14.90</u>
McBAINS L.	♀			1	14	20	17	2	2					56	14.20
	♂			1	2	14	5	4						26	14.35
	T			2	18	36	22	6	2					86	<u>14.21</u>
NADSILNICH L.	T					3	2	7	5					17	<u>16.82</u>
NICOLA L.	♀					2	2	6	10	4	3	2		29	18.00
	♂					2	4	21	9	2				38	17.13
	T					4	6	27	19	6	3	2		67	<u>17.51</u>
OKANAGAN L.															
N. End 1928	T					8	10	11	5	3				37	<u>15.59</u>
Okanagan Lndg.	♀				1	5	13	11	3	1				34	15.38
	♂					4	9	2	4	1				20	15.45
	T				3	12	24	13	7	3				62	<u>15.29</u>
PADDY RYAN LAKES	T			5	20	15	7							47	<u>13.51</u>
PAUL L.															
E. End	♀				3	10	3	1						17	14.12
	♂				4	12	5	1						22	14.14
	T				17	52	20	3						92	<u>14.10</u>

		10	11	12	13	14	15	16	17	18	19	20	21	NO.	MEAN
W. End	♀	1	1	12	14	2								30	13.50
	♂			10	14	6	-	1						31	13.96
	T	2	4	56	60	19	-	2						143	<u>13.68</u>
PINANTAN L. 1946	♀		2	5	7	2								16	13.56
	♂	1	-	7	9	1								18	13.50
	T	1	2	12	16	3								34	<u>13.53</u>
1948	♀		5	45	48	16	1							115	13.68
	♂		3	13	38	19	9	1						83	14.25
	T		10	99	161	83	13	2						368	<u>13.99</u>
PUNTCHESA- KUT L.	T		3	16	35	12	3							69	<u>13.94</u>
ROSEBUD L.	♀			1	13	25	24	25	8	3				99	15.96
	♂				9	25	27	17	7	5				90	16.03
	T			1	22	50	51	42	15	8				189	<u>15.99</u>
SKAHA L.	T		3	12	12	2	1							30	<u>13.53</u>
SHUSWAP L.	T		.	3	24	28	23	7	2	1				88	<u>15.19</u>
SHUSWAP R., Grinrod	T				7	16	11	1	1					36	<u>15.25</u>
SLOCAN L.	T				2	11	14	3	2					32	<u>15.75</u>
SNOWSHOE L.	♀	1	5	29	26	24	3							88	12.86
	♂	1	-	14	25	13	5	2						60	13.20
	T	5	16	122	162	96	17	3						421	<u>12.93</u>
SPRING L. AND TIMOTHY L.	T					2	5	18	17	5	5			52	<u>16.63</u>
STEVENS L.	♀			1	3	2	1							7	14.43
	♂			3	2	2								7	13.86
	T			4	5	4	1							14	<u>14.14</u>
TAYLOR L.	T		5	14	15	3	1							38	<u>13.50</u>
TETANA L.	T				1	2	-	1						4	<u>15.25</u>
WILLIAMS L.	T				5	14	19	7	6	1				52	<u>15.96</u>

### APPENDIX III

#### Description of Constant Temperature Apparatus.



Fig. 14. Constant temperature apparatus, Kaslo hatchery.

Apparatus for rearing eggs at constant temperature was constructed at the Kaslo hatchery during the summer of 1949. Although shiner fry died after absorption of the yolk sac, the apparatus was used successfully in the rearing of Kamloops trout at temperatures from  $9^{\circ}\text{C}.$  to  $21^{\circ}\text{C}.$  (The latter temperature is apparently the highest recorded in the literature for successful hatching of trout.) Specimens so reared were preserved and have not yet been examined.

The apparatus operated satisfactorily and provided baths of oxygenated water at  $9^{\circ}$ ,  $12^{\circ}$ ,  $15^{\circ}$ ,  $18^{\circ}$  and  $21^{\circ}\text{C}.$  at  $\pm 0.4^{\circ}$ . Fig. 14 shows a general view.

Water was fed into a 10 foot length of eaves troughing suspended above the baths; excess spilled over a wall at one end, so that a constant level was maintained in the

trough. Channels of cork, glass and rubber tubing led water across from the trough into each of five galvanized pails. A thermo regulator with pilot lamp was suspended in each pail, and the desired temperature was maintained either by an immersion heater or by an electric hot-plate beneath the pail. Tubes from the bottom of each pail led to a number of baths. An electric aerator suspended above the pails was provided with tubes entering each pail; these served also as agitators which prevented unequal heating within the pails. Flow to each bath, of about 80 c.c. per minute, was controlled by a screw-type stop-cock.

Baths consisted of  $3\frac{1}{2}$ " x 6" x 12" baking dishes. Overflows were provided by glass tubing with fine metal screen covers. Baths were suspended within 24" hatchery troughs, into which the overflow from the baths passed. All metal parts were covered with aluminum paint.

Eggs were placed on a wire basket standing one inch above the floor of the bath. Shiner fry were fed plankton tows. Trout fry were fed skimmed milk and ground liver. Floors of baths were cleaned daily with a rubber syringe.

#### APPENDIX IV

##### Definition of Measurements Made on Shiners

Measurements on adult shiners were made with a vernier caliper reading to 0.1 mm., or on a steel rule marked in 0.5 mm. Measurements on fry were made with a binocular microscope containing a calibrated Whipple counting grid.

ANAL FIN BASE - Distance from origin to insertion of anal fin.

ANAL HEIGHT - Distance from origin of anal fin to tip of longest ray.

EYE DIAMETER - Antero-posterior diameter of eyeball.

HEAD LENGTH - Distance from tip of snout to posterior margin of operculum.

PECTORAL AND PELVIC LENGTHS - Distance from insertion of fin to tip of longest ray.

PREANAL LENGTH - Distance from tip of snout to origin of anal fin.

POSTANAL LENGTH - Distance from origin of anal fin to posterior margin of fleshy part of peduncle.

STANDARD LENGTH - Distance from tip of snout to posterior margin of fleshy part of peduncle.

TOTAL LENGTH - Distance from tip of snout to tip of longest caudal ray when tail compressed.