ECOLOGY OF THE LEOPARD DACE *Rhinichthys falcatus* AND ITS ECOLOGICAL RELATIONSHIPS WITH THE LONGNOSE DACE *Rhinichthys cataractae*

by

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ABSTRACT

Sympatrically occuring Rhinichthys falcatus and R. cataractae were collected from four areas of the Fraser River drainage system. A life history examination of R. falcatus revealed that it is an omnivorous feeder, spawning in early July at age III and older, with some males of this age developing a permanant spawning color. Both sexes develop nuptial tubercles at age I. Females are heavier and longer than males, the greatest differences occuring at age III and older.

Field collections from a variety of defined habitats showed that R. falcatus were most numerous during daylight in water velocities of less than 1.5 ft./sec. Adults occupied primarily depths of one foot or greater, the yearling and young-of-the-year fish were most numerous in depths of less than one foot. R. cataractae were most numerous during daylight in depths of less than one foot, the adults occupying water velocities of greater than 1.5 ft./sec., while yearling and young-of-the-year fish were distributed almost equally in velocities both greater and less than 1.5 ft./sec. Both species remained unchanged in their current distribution after dark but some young-of-the-year and yearling fish of both species moved offshore to areas deeper than one foot while adult R. falcatus became more numerous at night in onshore shallows of less than one foot in depth.

Field observations on current distribution of both species were confirmed in laboratory current preference experiments in a stream tank. The preference of three size groups of both species for areas of little or no current and areas of either 1, 2, 3, or 4 ft./sec. water velocity in the stream tank were tested in 30 experiments. In all experiments but one, there was a significant difference between the ratio of R. falcatus to R. cataractae in the current areas; R. cataractae were more numerous.

Morphology and function of the airbladder of both species were analysed, and differences in volume were explained on the basis of diverging habitat selection of yearling and adult fish. The habitat divergence between yearling and older R. falcatus and R. cataractae is in accordance with Gause's contention.

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I INTRODUCTION

Rhinichthys falcatus (Eigenmann and Eigenmann) is a small river-dwelling cyprinid fish confined in its distribution to the Fraser and Columbia river systems. Although it is a common fish in both rivers, little is known about its life history. A closely related species, *R. cataractae*, also occurs in both river systems and has been collected from the same areas as *R. falcatus* in the lower Fraser River. The sympatric occurance of two congeneric species suggests a possible competitive relationship, opposing Gause's contention that closely related species cannot occupy a similar niche without one eliminating the other through competition.

The present study was iniated first to describe some of the life history features of *R. falcatus*, and secondly, to examine the comparative ecology of *R. falcatus* and *R. cataractae* in order to explain their apparent coexistence.

Published material on the life history of *R. falcatus* is scant. Eigenmann and Eigenmann first described the species in 1893. Gilbert and Everman (1895) gave a further morphological description with emphasis on nuptial tubercles. A brief and inconclusive comparative food study of *R. cataractae* and *R. falcatus* was completed by Johannes (1959).

The term habitat will be used in this investigation in reference to the physical environment of the fish, while ecological niche will be used to designate the place of the fish within its biological environment. These definitions follow closely those of Elton (1927) and Grinnell (1928), as recommended by Udvardy (1959).

II MATERIALS AND METHODS

A. Collection of Field Data.

R. falcatus and R. cataractae were collected from several areas in the Fraser River drainage system as shown in Table 1. Fish were collected in two types of seines. The first was a common beach seine, 6 ft. wide and 4 ft. high with a mesh diameter of 0.1 in. The second type of seine was equipped with a cod-end. It was 10 ft. wide, 4 ft. high, with a 0.7 in. mesh diameter in the mouth and a 0.3 in. mesh diameter in the cod-end. Both seines were operated by two men.

Two methods of seining were employed depending on the water velocity. In velocities of 2 ft./sec. or greater, the seine was spread in the water and held in position by one man. The second man stationed himself 10 to 15 ft. upstream from the seine and then moved as fast as possible to the seine while, at the same time, scuffling the bottom to dislodge fish from the spaces between stones. When the second man reached the seine it was lifted from the water. The alternative method was used in water velocities of less than 2 ft./sec. Both men pulled the seine through the water, moving with the current whenever present.

Seine hauls were made, when possible, in areas of similar water velocity and depth over a homogeneous bottom so that samples of fish collected per seine haul were restricted to certain physical environmental boundaries.

TABLE I

COLLECTION AREAS AND NUMBER OF FISH COLLECTED

		Number of Fish Collected	
		R. falcatus	R. cataractae
June 1-2/60	Fraser River, MacAllister, B.C.	38	47
June 3/60	" " Quesnel, B.C.	0	2
July 7-8/60	" " Hope-Chilliwack, B.C.	152	54
July 15/60	" " " "	83	47
July 20/60	" " " "	23	49
Aug. 16-18/60	" " " "	119	109
Aug. 29/60	" " " "	23	15
Sept. 3/60	" " " "	1003	46
Sept. 25/60	" " " "	12	83
Oct. 18/60	" " " "	123	86
Nov. 14/60	" " " "	76	0
Mar. 8/61	" " " "	48	0
Apr. 29/61	Baker Creek, Quesnel, B.C.	0	14
May 17/61	" " "	0	21
May 18/61	Fraser River, MacAllister, B.C.	31	26
May 23/61	Baker Creek, Quesnel, B.C.	0	12
June 25/61	Fraser River, Hope-Chilliwack, B.C.	396	114

B. Method of Stomach Analysis.

Fish collected between Hope and Chilliwack were utilized for stomach analysis. The contents of the anterior one third of the alimentary canal were emptied into a watch glass and identified with the aid of a binocular dissecting microscope. Food components were classified to genus where possible, and for each stomach the number of organisms in each food group was recorded and the percent volume that each food group contributed to the total individual stomach volume was estimated.

After identification, stomach contents of each fish were dried on a paper towel for five seconds and placed in a 0.25 in. diameter glass tube with one end sealed, and with a mark indicating a 2 ml. volume. One milliliter of water was added to the glass tube with a graduated syringe. This washed the stomach contents to the bottom of the glass tube. The syringe was filled with an additional milliliter of water which was then added to the glass tube until the level reached the 2 ml. mark. Displacement volume of the stomach contents was then calculated from the remaining volume of water in the syringe; the latter was calibrated to 0.01 ml.

This method also was used to determine the volume of the gonads.

C. Laboratory Experiments

1. <u>Description of Experimental Section</u>

Laboratory experiments were conducted in a stream tank, described by Northcote (1960), located at the University of British Columbia. One part of the stream tank was modified into an experimental section where all experiments were confined. The basic design, similar to that of MacKinnon and Hoar (1953), was to provide areas with and without current, for selection by experimental fish. Selection of a current area was taken as an indication of current preference.

The experimental section of the stream tank is illustrated in Figure 1. The two nozzles, connected to water pumps by flexible plastic pipes, could direct water currents into Arm A or Arm B. Two screens at each end of the experimental section separated it from the remainder of the stream tank, while a third removable screen formed a holding area where fish were held prior to each experiment. An aluminum plate was placed against the screen at the head of the non-current arm to minimize any currents created by water circulation in the stream tank. The partition separating the two arms housed an overflow drain which removed excess water added in the non-experimental section to maintain a constant water temperature. Water temperature remained between 6.5°C. and 8.5°C. during all experiments.

The bottom of each arm was sloped upwards towards the down-current end, terminating at the lip of the ramp in a downward slope (Fig. 1, side view). The upward slope was necessary to create a more uniform water velocity along the length of the current arm. The bottom of the area immediately

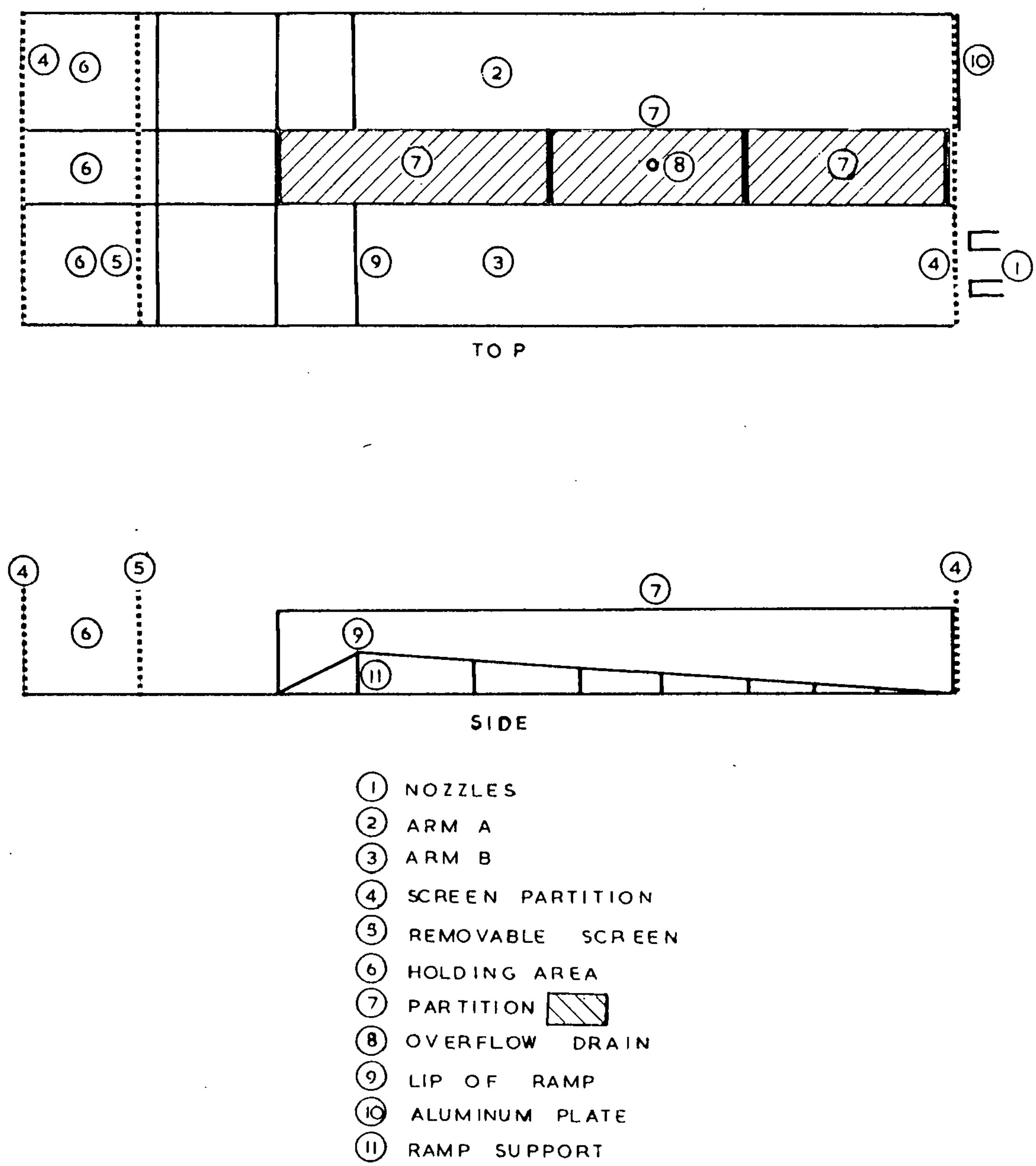

Figure 1. Experimental section of the stream tank.

below the current arms was marked off into six squares to give detailed records on the current distribution of the experimental fish.

2. Source of Experimental Fish

Experimental fish were collected from three locations. All *R. falcatus* of greater fork length than 50 mm., and approximately one half of the *R. cataractae*, were collected from the Nicola River at Merritt, B. C., on Dec. 7, 1960. The remaining *R. cataractae* were collected from Brunette Creek at New Westminster, B. C. on Nov. 4, 1960. *R. falcatus* of less than 50 mm. fork length were collected from the Fraser River between Hope and Chilliwack, B. C., on March 8, 1961.

3. Holding of Experimental Fish

Experimental fish were held in a single hatchery trough at the same temperature as that used in the stream tank. There was virtually no current in this trough although a slight turbulence occurred at one end where water was introduced. Experimental fish were fed "Clark's fish food" and frozen brine shrimp; they appeared healthy during the course of the experiments. Water temperature in the hatchery trough varied between 5 to 6.5°C. during the time that experiments were carried out.

4. Selection of Fish for Experiments

Experimental fish were selected from the trough on the basis of fork length, and were measured in a "V" shaped container submerged in the hatchery trough. Experiments were carried out on three size groups of fish: 70-95 mm., 50-70 mm., and 30-40 mm., fork length. The number and size of both species used in the experiments are shown in Table II.

The hatchery trough was divided into three compartments, with all fish originally held in the first. Prior to subjecting any size group to experiments, fish of that size group were removed from the first compartment and isolated in the second. Fish were selected in groups of ten from the second compartment and after they had been subjected to a current preference experiment, they were returned to the third. If no fish in the second compartment remained, and further tests were necessary on that size group, fish were selected from the third compartment and returned to the second. All fish of the 70-95 mm. size group were used twice and ten fish were used three times. Fish of the 50-70 mm. group were each used four times while fish in the 30-40 mm. size group were used twice.

5. Number of Experiments

Of the 12 experiments that were conducted on the 70-95 mm. size group, three tests were completed at each of four water velocities: 1, 2, 3, and 4 ft./sec. Current was measured on the lip of the ramp with a Gurly flow meter. An equal number of experiments at the same velocities were completed on the 50-70 mm. size group. Fish of the 30-40 mm. size group were tested six times, three experiments at each of

TABLE II

NUMBER AND SIZE OF FISH USED IN EXPERIMENTS

<u>70-95 mm. Size Group</u>

Total number and size of fish

Fork length (mm.)	70-75	75-80	80-85	85-90	90-95
R. falcatus	5	5	5	5	5
R. cataractae	5	5	5	5	5

Number and size of fish per experiment

R. falcatus	1	1	1	1	1
R. cataractae	1	1	1	1	1

<u>50-70 mm. Size Group</u>

Total number and size of fish

Fork length (mm.)	50-60	60-65	65-70	70-75
R. falcatus	3	3	6	3
R. cataractae	3	3	6	3

Number and size of fish per experiment

R. falcatus	1	1	2	1
R. cataractae	1	1	2	1

<u>30-40 mm. Size Group</u>

Total number and size of fish

Fork length (mm.)	30-40
R. falcatus	15
R. cataractae	15

Number and size of fish per experiment

R. falcatus	5
R. cataractae	5

two velocities: 1 and 2 ft./sec. Of the group of three experiments completed on a size group at any flow, two were made with the current in one arm while the third was completed with the current in the opposite arm.

6. Experimental Procedure

Prior to each experiment, the water pumps were started and the correct velocity was created in the selected current arm. Water currents were regulated to minimize surface bubbles and to equalize, as much as possible, water velocity along the length and width of the current arm. After the required current pattern was established, the removable screen was placed into position.

Fish were then placed into the holding area of the experimental section and held there for a 30 minute period after which the removable screen was lifted out and fish were allowed to swim into any preferred area. Observations were made at 30 minute intervals for a ten hour period following the removal of the screen. Thus 20 observations were recorded on the current distribution of the ten experimental fish. At the termination of each experiment, the current pattern was compared to the original pattern.

D. Volume Analysis of Airbladders

Seventy-five R. falcatus and 73 R. cataractae were taken from all field collections and from museum collections at the University of British Columbia. These fish were, however, restricted to the Fraser River drainages. Fish were dried on a paper towel for 15 seconds and then weighed on a Mettler precision balance accurate to 0.1 gm. Weights were estimated to two decimal places. The airbladder was then removed and the outer layer of the anterior lobe was peeled off.

The apparatus used for determining airbladder volume is illustrated in Figure 2. The needle of a 1 ml. syringe was bent at right angles and passed through a rubber stopper. The airbladder was drawn onto the needle with forceps and completely deflated by the syringe. The deflated airbladder, on the other end of the needle, was inserted into the glass tube and held in position by the rubber stopper. The rubber cap was removed from the overflow tube and water from the syphon tube was allowed to fill the glass tube and part of the graduated tube before running over the overflow tube. Water flow from the syphon tube was then halted and the overflow tube was sealed with the rubber cap. The position of the rubber cap was then adjusted until the column of water in the graduated tube reached a convenient starting mark.

The airbladder was then inflated until either minute bubbles passed out the pneumatic duct or pressure in the airbladder forced the plunger of the syringe back when pressure on it was removed. The displacement volume of the airbladder was then recorded. The position of the meniscus in the graduated tube (calibrated in 0.01 ml.) was determined with the aid of a magnifying glass.

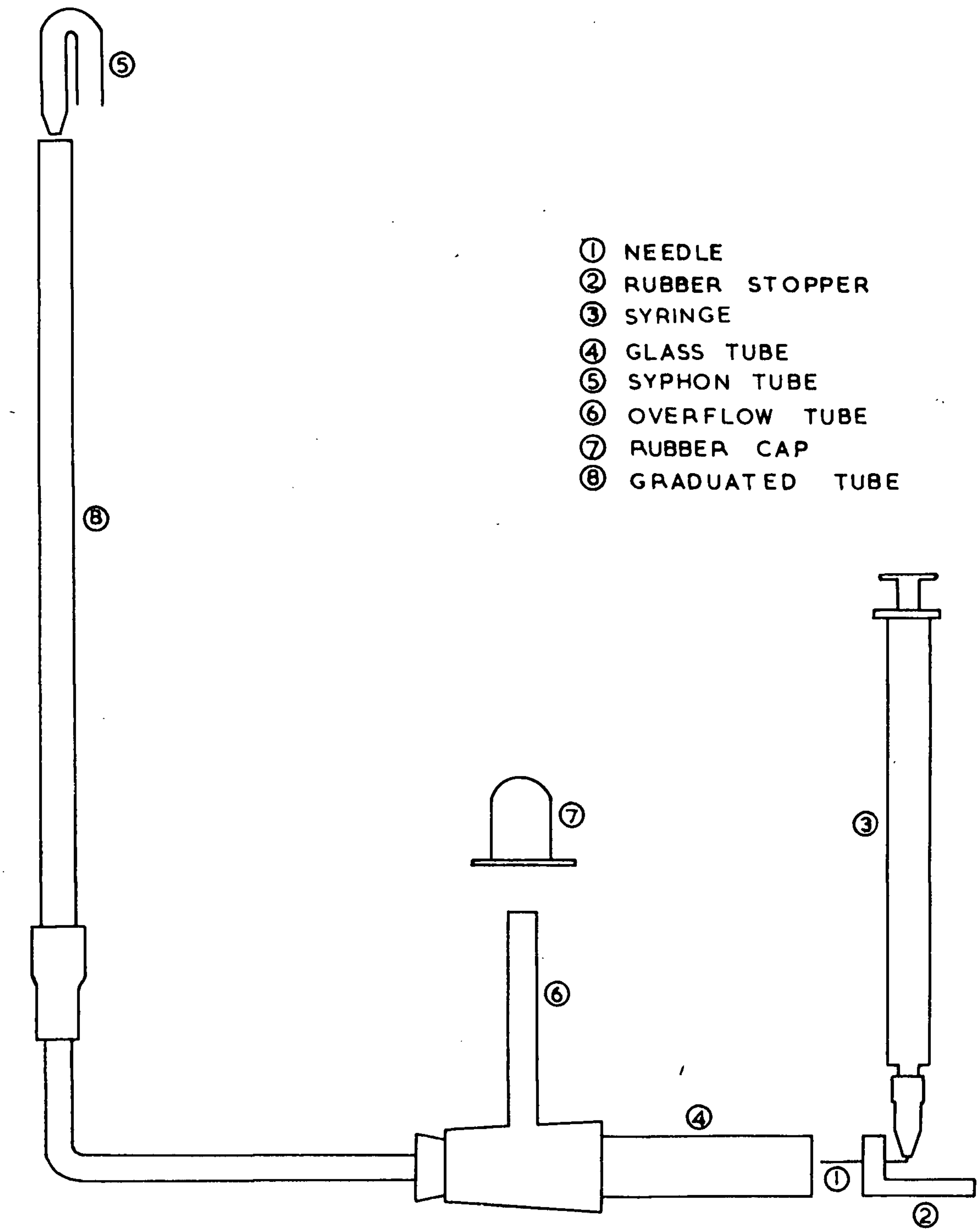

Figure 2. Apparatus for measuring airbladder volume.

III RESULTS

A. Habits of R. falcatus

1. Age and Growth

R. falcatus, collected between Hope and Chilliwack on June 2 and 5, 1961 were aged by length frequency (Fig. 3). No obvious differences in length distribution were found between sexes. Combined length frequencies of both sexes were used in age determination.

Length of fish of age I varied from 18 to 35 mm. fork length, while fish of age II varied from 45-60 mm. Fish of greater length than 62 mm. were designated as age III and older and were divided into two groups; those less than 81 mm., and those greater than 80 mm., fork length.

Growth in length and weight by sex is illustrated in Fig. 4. Fish of age 0 and age I were not sexed due to the undeveloped state of the gonads. Fish of age I and older were taken from the June 2 and 5 collections, while fish of age 0 were collected on August 15, 1960. Female fish are heavier and longer than male fish; such differences become more evident among older fish.

2. Food

Stomach contents of R. falcatus, collected in the Fraser River between Hope and Chilliwack in June, 1961 and July, 1960 were similar, as collecting times coincided with the peak spring run-off in both years. Thus the stomach contents

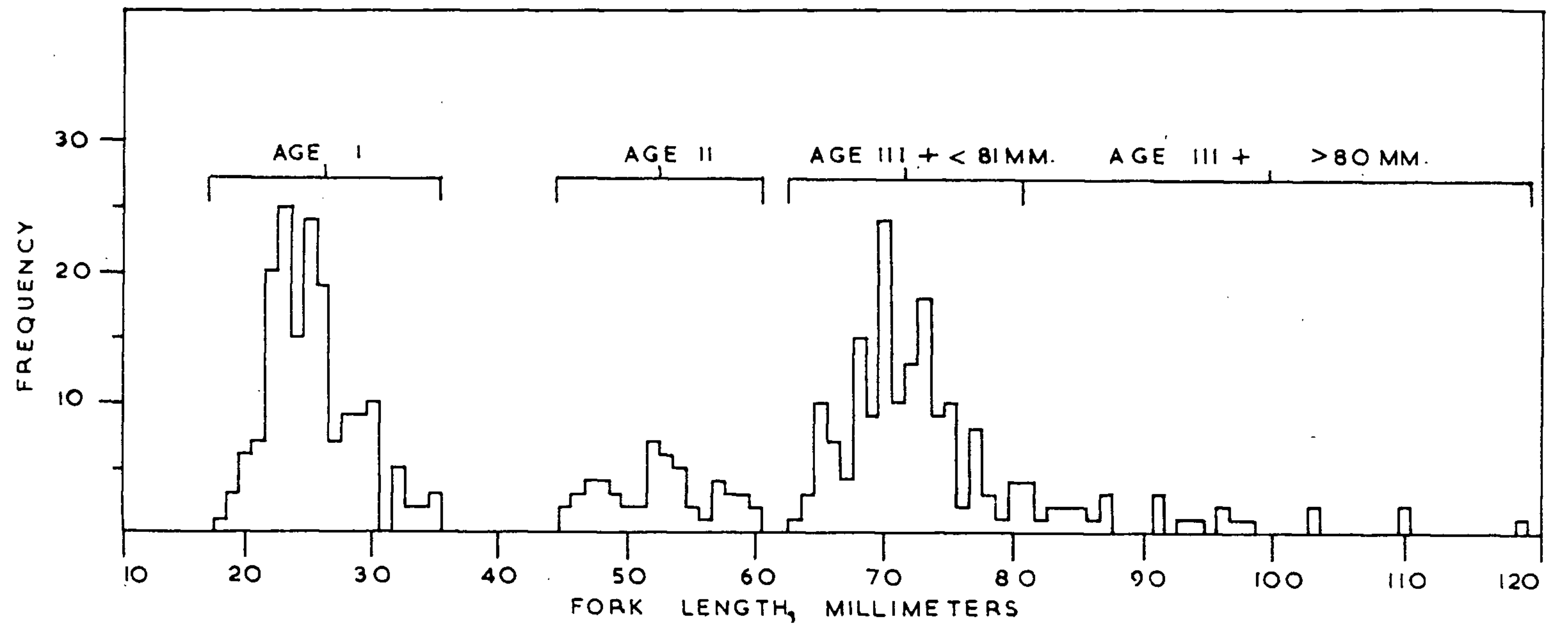

Figure 3. Length frequency of R. falcatus collected from Fraser River between Hope and Chilliwack, June 2 and 5, 1961.

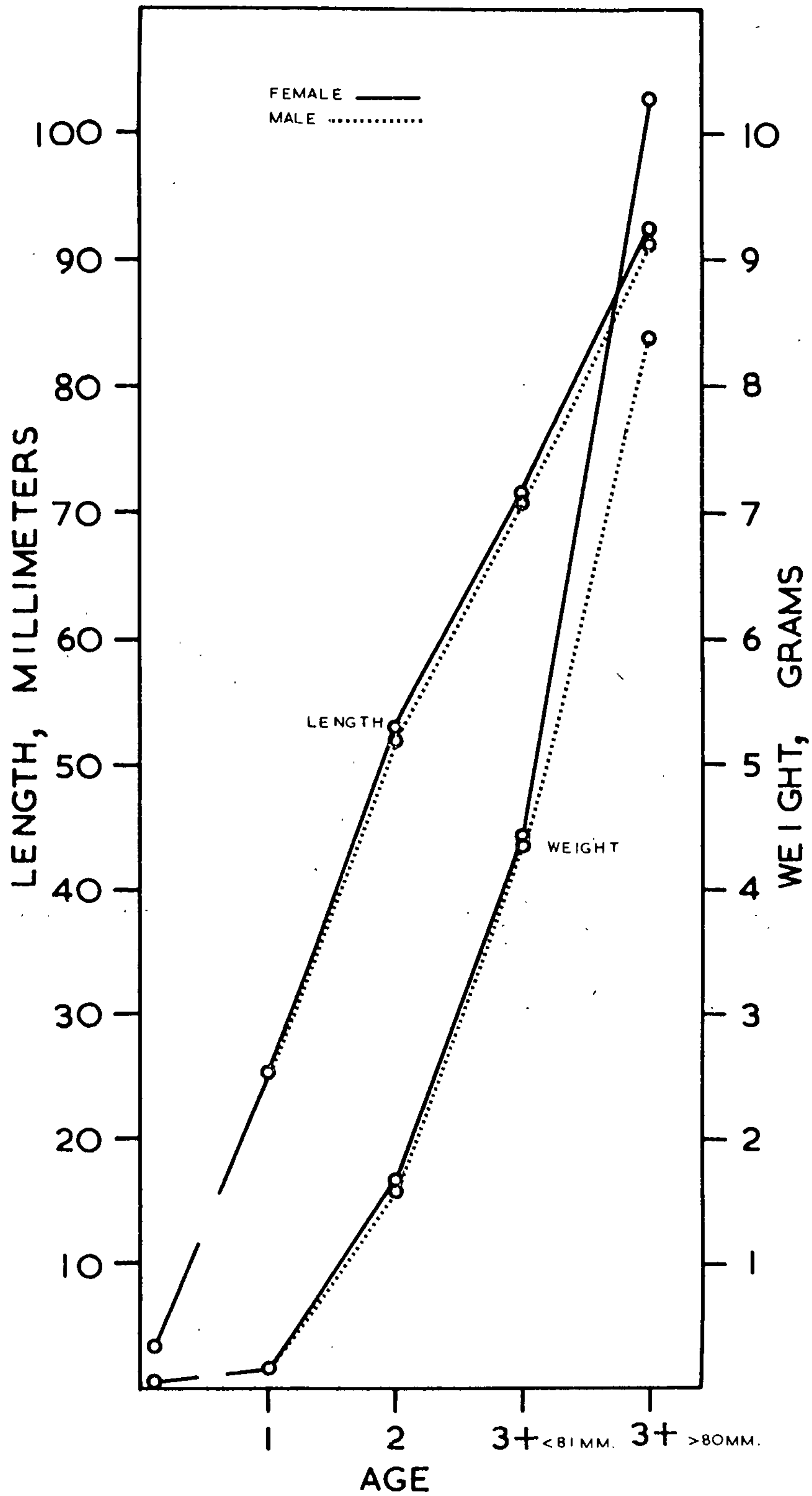

Figure 4. Growth in length and weight of <u>R. falcatus</u> from Fraser River between Hope and Chilliwack.

of fish collected in these two periods were combined. Stomach contents of fish collected in October and November, 1960 and March 1961, were also similar and were combined as shown in Figure 5.

During the spring run-off in June and July, yearling (age I) R. falcatus fed primarily (by volume) on aquatic insect larvae; Ephemeroptera and Diptera were the most predominant forms. Adult (age II and older) R. falcatus fed primarily on Lumbricus and aquatic insect larvae. Ephemeroptera and Diptera again were the dominant forms.

Lumbricus is most available as a source of food in the spring. It can be dislodged during flooding or when the ground in which it inhabits becomes inundated, the earthworms usually rest with part of their posterior ends protruding from their burrows and occasionally leave their burrows roaming over the soil surface (Campbell, 1957). On examination of a collection of R. falcatus taken from a flooded pasture, 90% by volume of the food consisted of Lumbricus.

Stomach analysis of collections taken between Hope and Chilliwack on September 3, 1960 showed that young-of-the-year (age 0) R. falcatus were feeding exclusively on aquatic insect larvae, composed mostly of Diptera (90%). Yearling and adult R. falcatus collected at this time were feeding primarily on terrestrial insects composed exclusively of winged ants.

In October, November, and March, only young-of-the-year R. falcatus were collected in the Fraser River between Hope

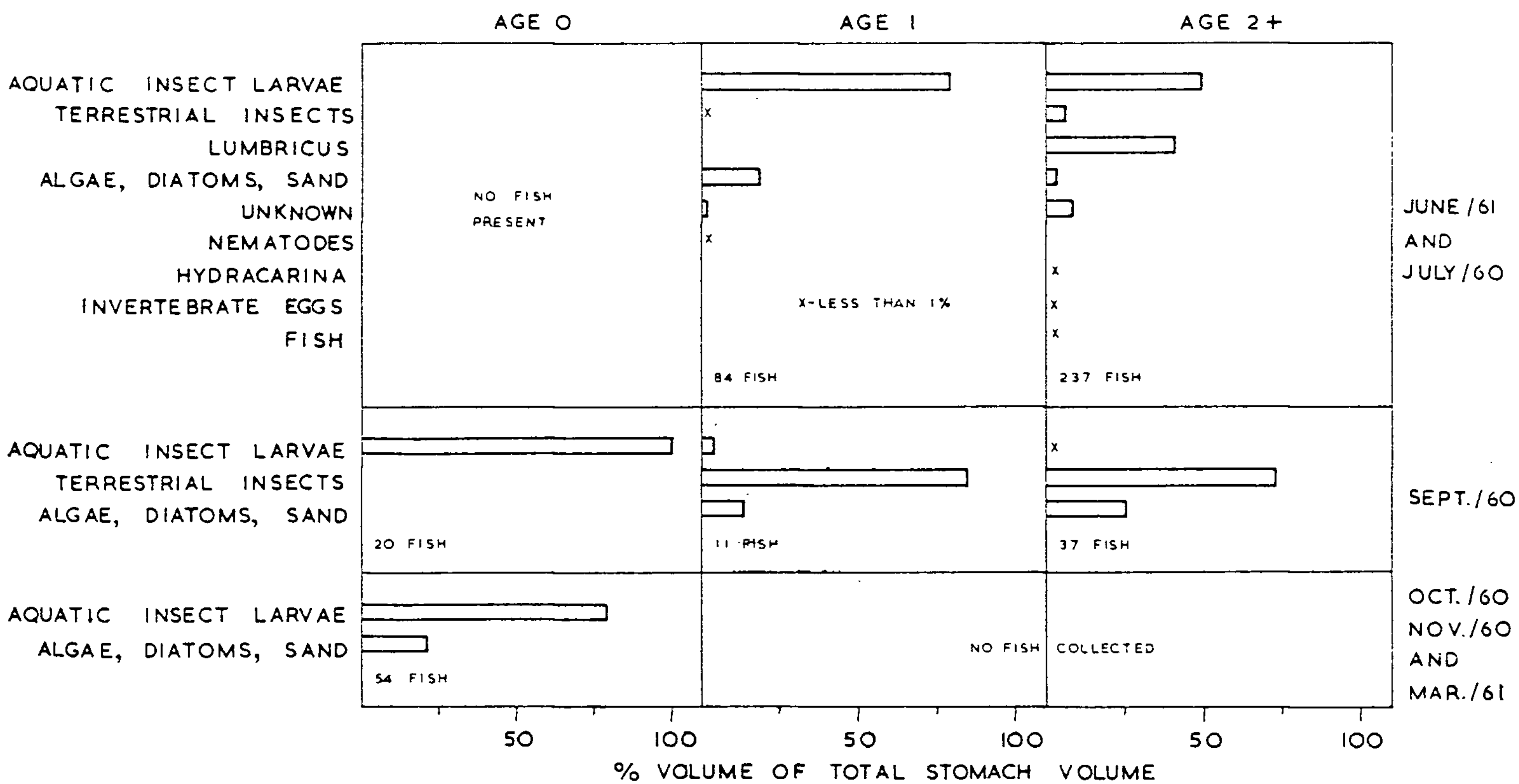

Figure 5. Stomach contents of R. falcatus collected from the Fraser River between Hope and Chilliwack.

and Chilliwack. These fish fed predominately on aquatic insect larvae, primarily Diptera.

3. Reproduction

Gonad volume was used as an indication of sexual development and maturity. Volume determination was not attempted on fish of age 0 or I, nor on male fish of less than .80 mm. fork length as the gonad volume was too small to be measured. Gonad volume and sexual development is shown in Figure 6.

Gonads of age III and older female fish increased from the June collection to the July collection which was followed by a decrease between July and September collections. A similar increase and decrease is found among age III and older males of greater length than 80 mm. The decrease in gonad volume between July and September may be attributed to spawning. Young-of-the-year R. falcatus were first collected between August 16 and 18, 1960. These fish probably had hatched some two to three weeks previous to this collection date. Gonad development of maturing fish and the appearance of young-of-the-year, suggests that the spawning period of R. falcatus occurs early in July.

Some of the male R. falcatus of age III and older are found with a distinctive spawning coloration, as described by Carl et al (1959). Not all males of this age group have such a coloration, but there is a higher percentage of colored males of fork length greater than 80 mm. (Fig. 7) This spawning coloration was observed in all seasons.

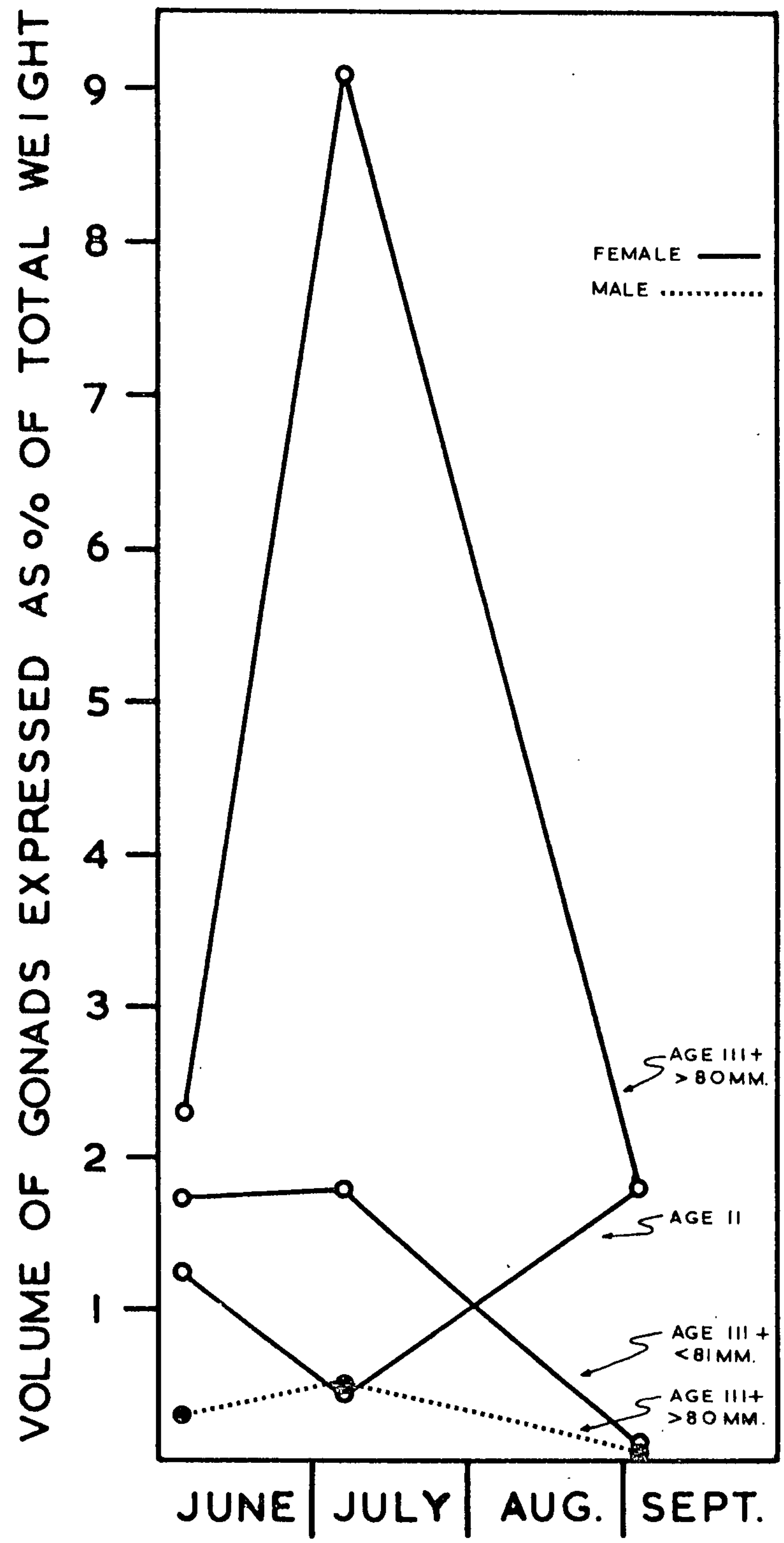

Figure 6. Gonad development of R. falcatus collected from the Fraser River between Hope and Chilliwack.

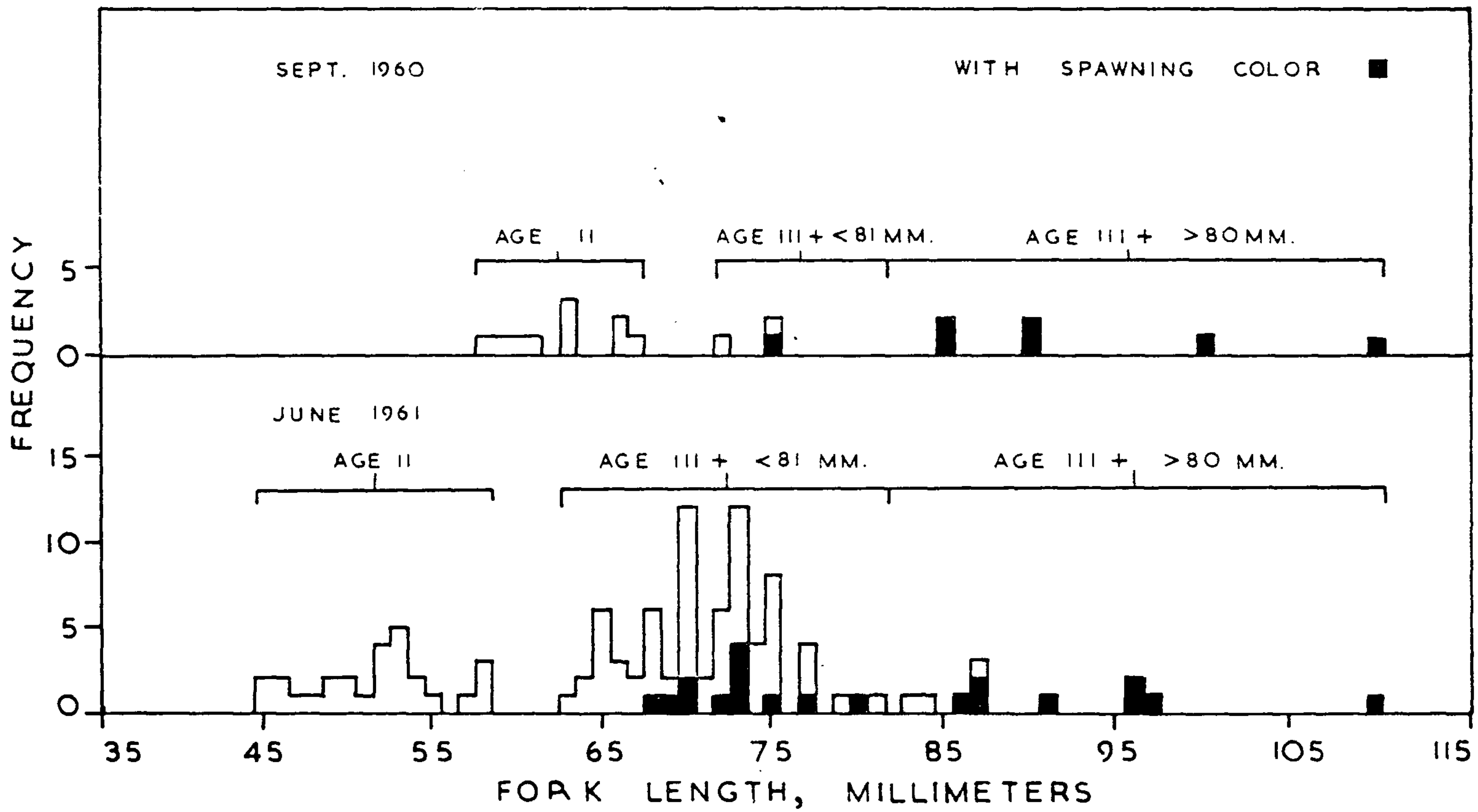

Figure 7. Length frequency of male R. falcatus with spawning color collected from the Fraser River between Hope and Chilliwack.

Age I male and female R. falcatus are found with tubercles which occur on the dorsal surface of the head and body as well as the sides of the body, with exception of the fins. Gilbert and Everman (1895) refer to these as nuptial tubercles and claim they are also present on the dorsal surface of the pectoral fin rays. Tubercles on this area were not observed on fish from the Fraser River system.

4. Parasites

Three orders of parasites were represented in R. falcatus collected between Hope and Chilliwack (G. Gibson, pers. com.). Trematoda were represented by metacercariae of Tetracotyle sp. Six fish were heavily invested with plerocercoids of the Cestoda Ligula intestinalis, while Nematoda were represented by three subfamilies. The subfamilies were: Anisakinae (contracacaecum sp.), Dioctophymidae (encysted Eustrongylides sp.), and Spiruridae (Metabronema, sp. and Rhabdochona sp.). Ligula intestinalis infections appeared to be the only serious cases of parasitism.

B. Comparative Ecology of R. falcatus and R. cataractae

Numbers of fish and corresponding ecological data from all collection areas (Table I) were utilized to describe and compare the ecology of the two species.

1. Current Distribution

Average numbers of R. cataractae and R. falcatus per seine haul in velocities less than 1.5 ft./sec. (342 seine hauls) were compared to average numbers in currents greater than 1.5 ft./sec. (101 seine hauls). The numbers of each species were recorded by size groups (young-of-the-year - age 0, yearling - age I, adult - age II and older). The difference between average numbers per seine haul of a species size group was tested statistically by a Chi square test; 0.05 was the accepted level of significance.

Adult, yearling, and young-of-the-year R. falcatus exhibit a significant difference between the two current areas and are most numerous in water velocities of less than 1.5 ft./sec. (Fig. 8). Adult R. cataractae show a significant difference in numbers between the two current areas, as they were more numerous in water velocities of greater than 1.5 ft./sec. There was no significant difference in the numbers of yearling and young-of-the-year of this species between the two current areas. These results indicate that R. cataractae in its first year or early in its second year, changes its current distribution by selecting an increased water velocity. This may account for the similarity in numbers of these two age groups in the two current areas.

2. Depth Distribution - Daylight

The analysis used for current distribution was also used for depth distribution (Fig. 9). One hundred and thirty-five seine hauls were made in depths less than 1 ft., while 125 seine hauls were made in depths greater than 1 ft. Adult R. falcatus were more numerous in depths greater than 1 ft., although the difference in numbers per seine haul between the two depth areas was not significant. Yearling R. falcatus were distributed in almost equal numbers between the two depth

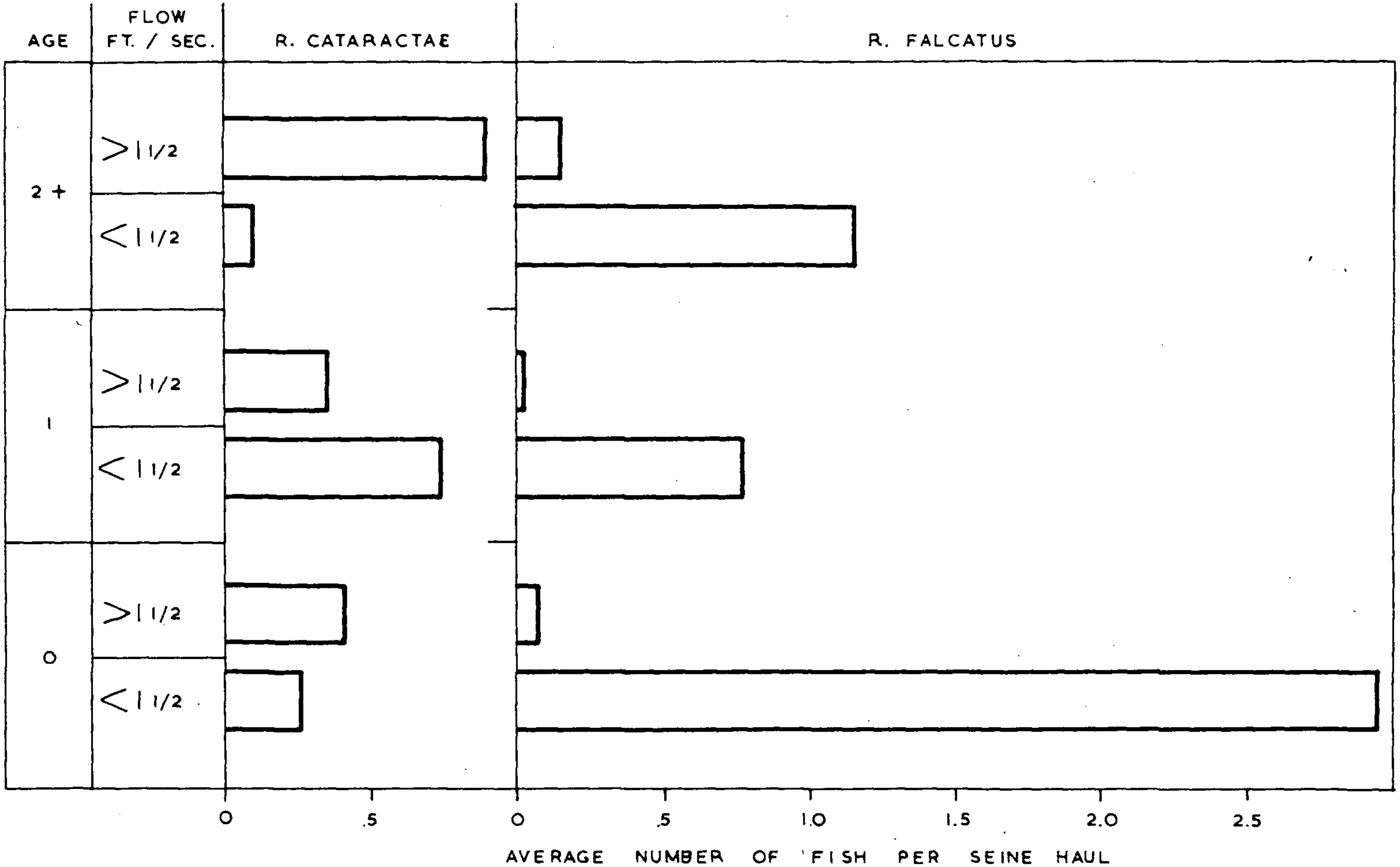

Figure 8. Current distribution of R. falcatus and R. cataractae from all collection areas (Table I).

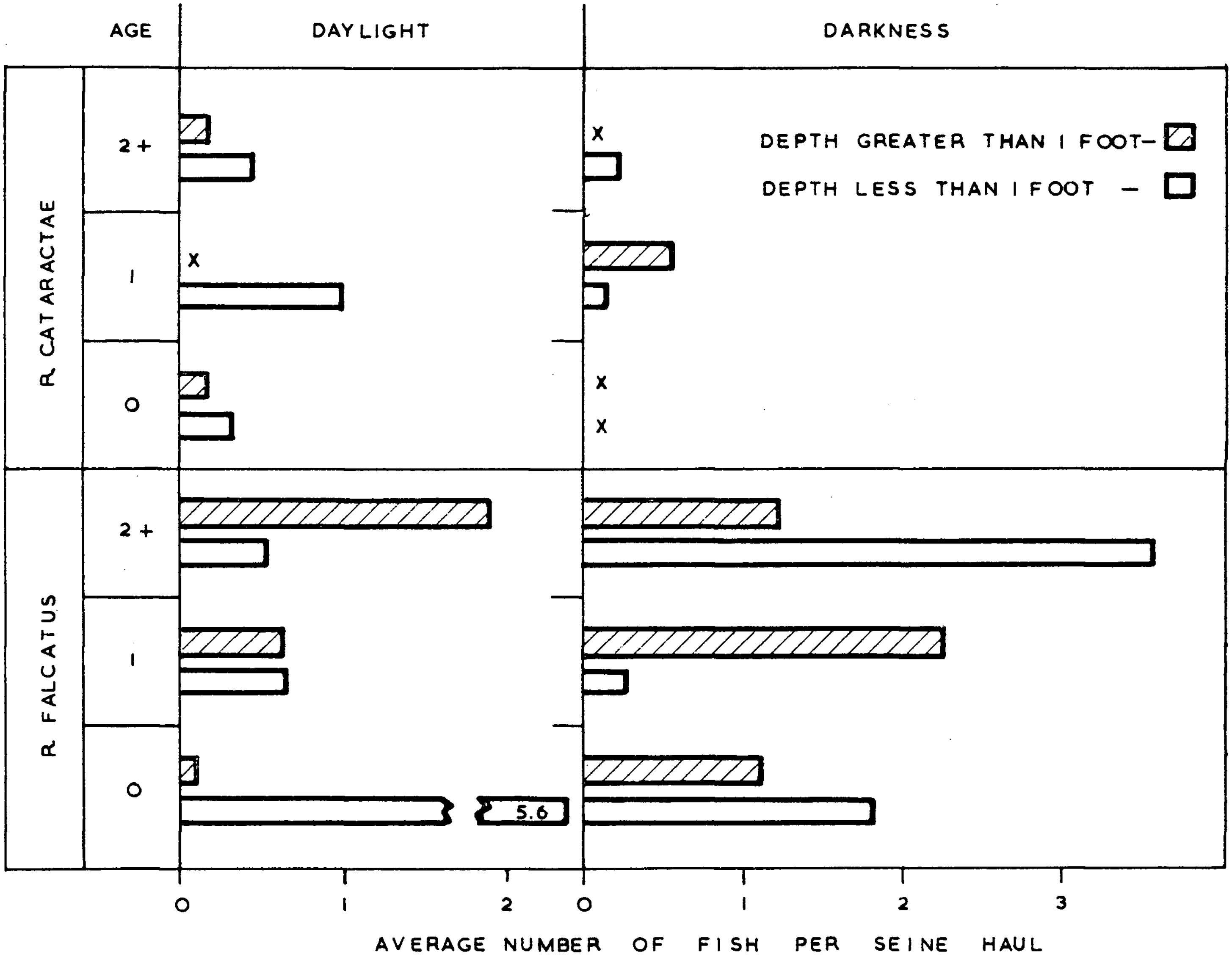

Figure 9. Depth distribution of R. falcatus and R. cataractae during daylight and at night (x-less than 0.1).

areas while the young-of-the-year of this species were more numerous in depths of 1 ft. or less. This difference was significant.

Adult, yearling, and young-of-the-year R. cataractae were more numerous in depths of less than 1 ft., but only the yearling fish showed a significant difference in this comparison.

3. Depth Distribution - Night

Only a small number of after-dark seine hauls were applicable to depth distribution analysis (27 seine hauls in depths greater than 1 ft., 28 seine hauls in depths less than 1 ft.), thus only indications can be drawn from the data.

Some young-of-the-year R. falcatus move offshore to depths deeper than 1 ft., but a larger number per seine haul were taken in shallow water. Yearling R. falcatus also exhibit an offshore movement to deeper depths, while adults, in contrast, show an onshore movement to depths of less than 1 ft. (Fig. 9).

Young-of-the-year R. cataractae, collected after dark, were too few in number to permit analysis. Yearling of this species exhibited a similar offshore movement to the yearling R. falcatus. Depth distribution of adult R. cataractae did not appear to vary between day and night.

4. Bottom Preference

Ecological data on the distribution of fish over different types of bottom was not analysed as gravel areas were usually confined to areas of water velocity and sand or silt bottoms were confined to areas of little or no current.

R. falcatus, observed in the Nicola River on December 7, 1960, were found between rocks (2-6 in. diameter) in pool areas of the river. At this time, the water was clear, with bottom areas clearly visible from shore. R. falcatus, in the Fraser River, were collected primarily on sand or silt bottoms in turbid water (water visability 4-14 in.).

In the hatchery trough, R. falcatus and R. cataractae showed a preference for darkened areas. If one half of the trough was covered with a plywood sheet, all fish would select the darkened area under the plywood. Thus it is likely that R. falcatus may select bottom cover or darkness in clear water which would result in its presence in gravel spaces in areas of little or no current. In turbid water this species may not require cover or darkness.

Field observations indicate that R. cataractae found in river areas of fast water velocities, occupied spaces between stones in both clear and turbid water, and could be dislodged only by disturbing the gravel bottom. Such a bottom selection may be necessary to inhabit a position in fast water velocities, as this species does not remain directly in the current.

5. Food of R. falcatus and R. cataractae of age 0 and I

Stomach contents of R. falcatus and R. cataractae of age 0 and I, both collected from the same areas in the Fraser River between Hope and Chilliwack, are illustrated in Figure 10. Both species of age 0 were collected together only in

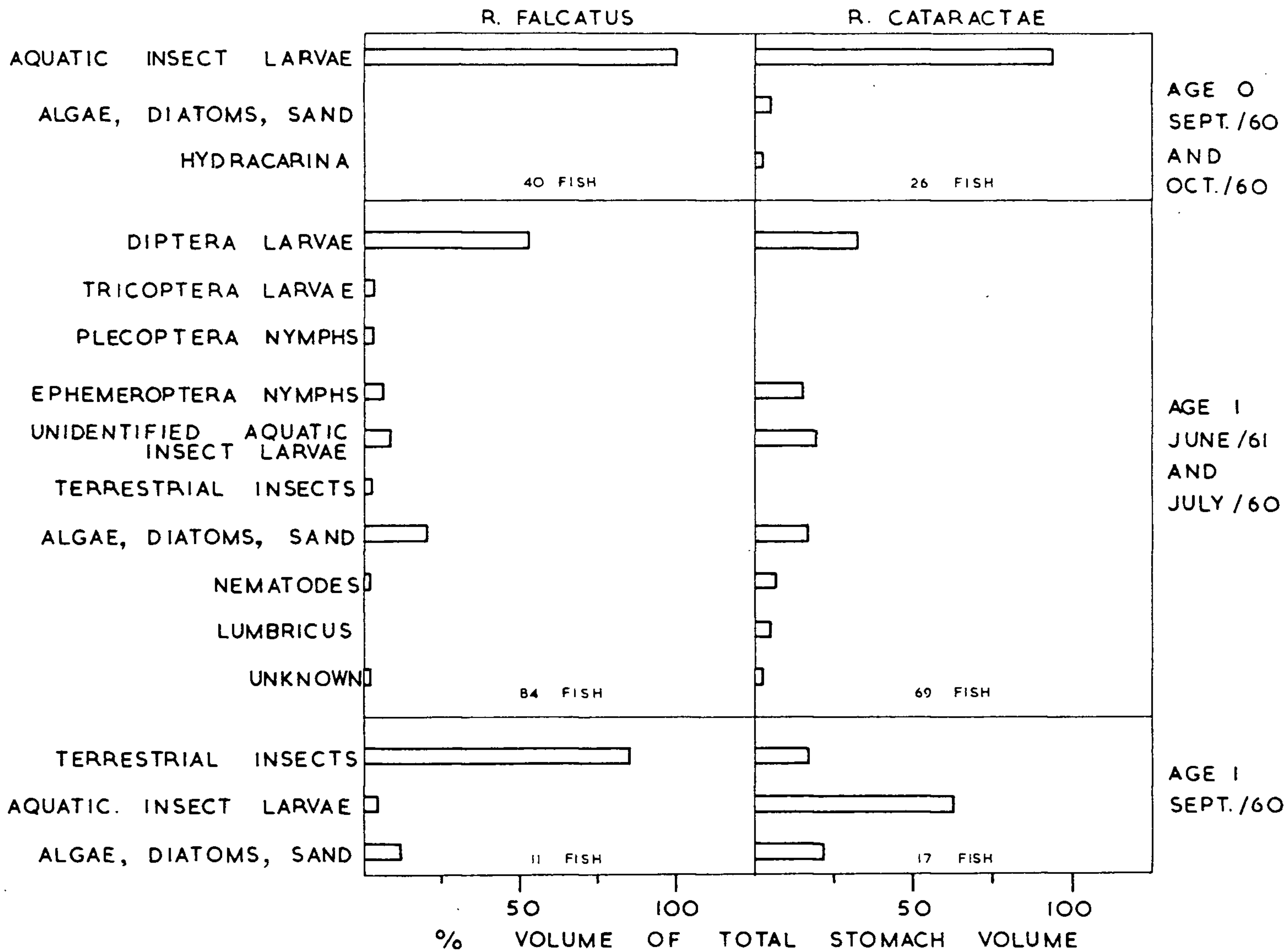

Figure 10. Stomach contents of <u>R. falcatus</u> and <u>R. cataractae</u> of age 0 and I from the same areas of the Fraser River between Hope and Chilliwack.

September and October, 1960. Food taken in each month by these fish was similar and thus combined. Diet of the two species was also similar; both relied on aquatic insect larvae as a major food source. Diptera formed 96% of the diet of R. falcatus and 82% of R. cataractae.

Yearling fish (age I) of both species fed predominately upon aquatic insect larvae during June, 1961 and July, 1960 at the peak of the spring run-off. Diptera and Ephemeroptera were the most important food items. but were taken in differing amounts by each species.

Stomach analysis of yearling fish in September, 1960 collections showed a complete divergence in diet. R. falcatus fed primarily on terrestrial insects, while R. cataractae fed primarily on aquatic insect larvae. This divergence in diet is concurrent with the divergence in habitat selection which commences in the first year (age 0) and is complete in the second (age I).

C. Stream Tank Experiments

Experiments, designed to test flow preference indicated by field ecological data were completed on three size groups of fish according to the previously described method. Experiments commenced on January 4, 1961 and terminated on March 17, 1961.

1. Ratio Analysis of Fish in Current Arm

Only the ratio of the numbers of R. falcatus to R. cataractae in the current arm were analysed. Observed ratios of the two species in the current arm at any one time is called an observation ratio. A one hour time period between observation ratios ensured independence between observations. The sum of the seven observation ratios taken for analysis from each experiment is called an experimental ratio. The sum of the three experimental ratios of a size group at any flow is called a block ratio.

(a) Block ratio analysis

Figure 11 illustrates the average number of fish in the current arm per observation. The vertical bars on this graph are proportional in area to the block ratios and thus difficulties of illustrating ratios with zero numbers are avoided.

The statistical procedure in the analysis of block ratios consisted of first a test of homogeneity on the 21 observed ratios composing the block ratio. Homogeneity was found in all block ratios. Homogeneity permitted a pooled Chi-square test to be calculated on the block ratios. The accepted level of significance was 0.05.

A significant difference was found between the numbers of R. cataractae and R. falcatus of the 70-95 mm. size group at flows of 1, 2, and 3 ft./sec. R. cataractae were more numerous in the current arm. The block ratio at the 4 ft./sec. velocity was not subjected to a Chi-square test as only one R. cataractae was observed. Attempts to enter the current arm at this flow were recorded during every other half hour period throughout the three experiments. An attempt was recorded if a fish could swim up to the lip of the current arm ramp or further. There was a significant difference in the number of attempts made by the two species to enter the

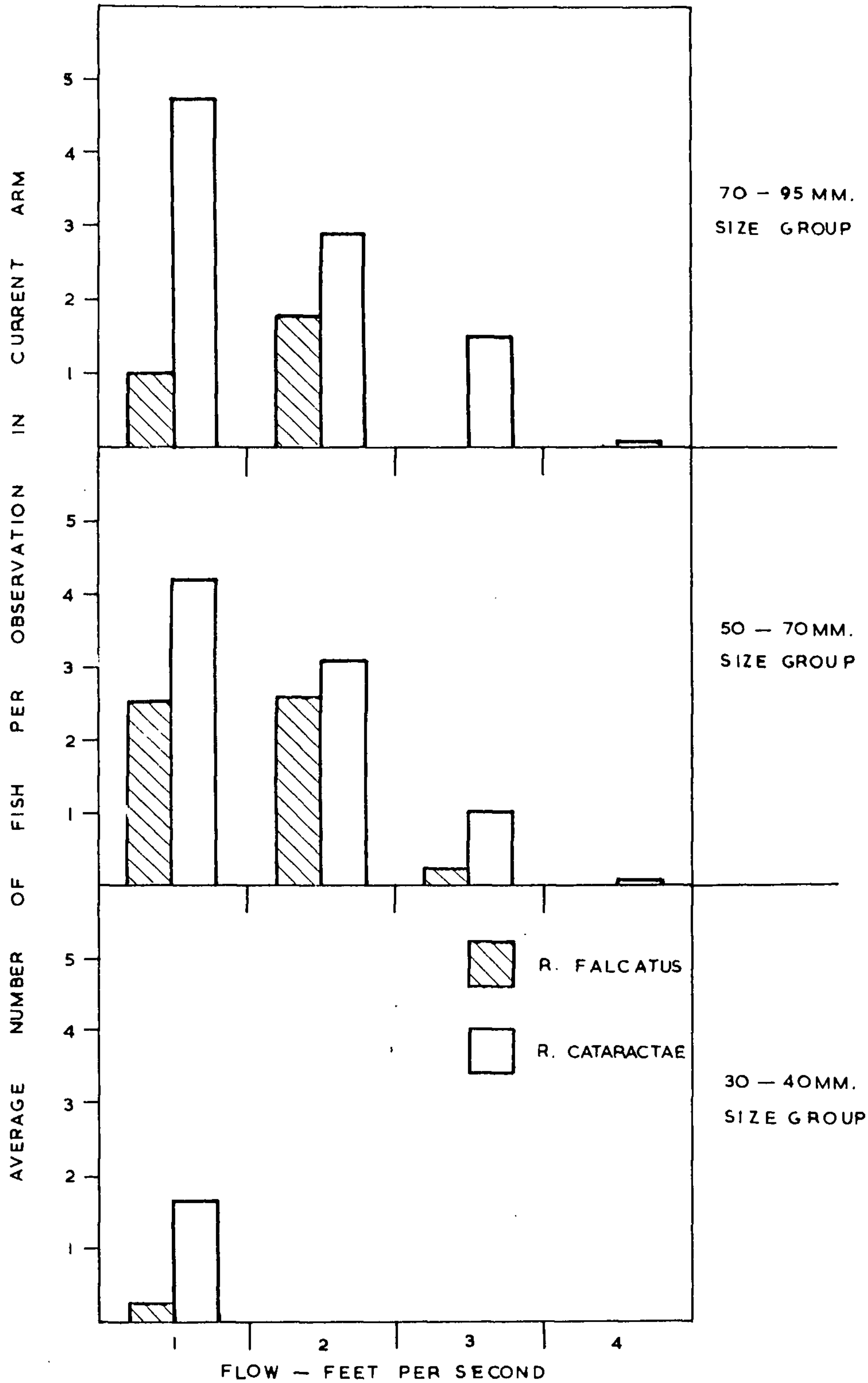

Figure 11. Flow preference of R. falcatus and R. cataractae in stream tank.

current arm at the 4 ft./sec. velocity. R. cataractae made 53 attempts while R. falcatus made only 18.

Significant differences were found between the two species with the 50-70 mm. size group at velocities of 1 and 3 ft./sec. R. cataractae were more numerous again in the current arm. At 2 ft./sec. water velocity, R. cataractae were more numerous, but the difference was not significant. At the 4 ft./sec. water velocity, one R. cataractae was noted in three observations while R. falcatus never entered the current arm. Attempts were not recorded at this velocity.

Experiments were completed on the 30-40 mm. size group at velocities of 1 and 2 ft./sec. A significant difference was found at the velocity of 1 ft./sec., R. cataractae were more numerous in the current arm. No fish were observed in the current arm at the velocity of 2 ft./sec. Attempts, recorded at both velocities, showed that for every attempt made by R. falcatus to enter the current arm, R. cataractae made ten. This ratio, at both velocities, was significantly different.

(b) Experimental ratio analysis

The presentation of data on block ratios has obscured some variation in the observed numbers of fish which becomes apparent when the experimental ratios are compared. A test of homogeneity on each of the three experimental ratios composing each block shows that these groups of experimental ratios are heterogeneous, varying by more than chance (with exception of one block - 70-95 mm. size group at 3 ft./sec).

This variation is apparent in Table III.

Two experimental ratios, one from each arm in all blocks were subjected to a homogeneity test; all were homogeneous. Therefore, the most variable ratio in a block appears to be the remaining ratio which is one of the pair of ratios in the same arm. As the two ratios conducted in the same current arm were alternated between arm A and B, the cause of the variability cannot be attributed to either arm in the experimental section, but is common to both arms.

The cause of the variation is unknown. That conditioning in the hatchery or the method of selecting experimental fish prior to each experiment could cause such variation seems unlikely. Differences in current patterns below the lip of the ramp could cause such variability. During the last experiment, such differences were noted.

The manner in which water passed over the lip of the ramp caused vertical differences in the flow pattern as illustrated in Figure 12. Water, on passing over the lip of the ramp, could either continue along the surface (Type A) or follow the bottom contour (Type B). This would affect the approach of the fish in their attempts to enter the current arm. Both species remained in contact with the bottom while swimming. With Type A current pattern, R. cataractae would not be able to detect the source of current and R. falcatus could be falsely attracted to the current arm.

If further experimental work was to be done on a similar basis as the previous experiments, one of two improved methods could be used. The first of these two methods would

TABLE III

EXPERIMENTAL AND BLOCK RATIOS OF *R. falcatus* AND *R. cataractae* IN CURRENT ARM OF STREAM TANK

Flow		1 ft./sec.			2 ft./sec.			3 ft./sec.		
Size group	Ratio	Current arm	Species R.f.:	R.c.	Current arm	Species R.f.:	R.c.	Current arm	Species R.f.:	R.c.
70-95 mm.	Experimental	A	0	28	A	17	25	A	0	11
		A	21	35	A	12	10	B	0	8
		B	0	35	B	8	25	B	0	11
	Block		21	98		37	60		0	30
50-70 mm.	Experimental	A	27	35	A	28	7	B	0	5
		B	21	33	A	17	35	B	0	6
		B	6	21	B	10	23	B	6	10
	Block		54	89		55	63		6	21
30-40 mm.	Experimental	A	5	33	A	0	0			
		B	0	2	B	0	0			
		C	0	0	B	0	0			
	Block		5	35		0	0			

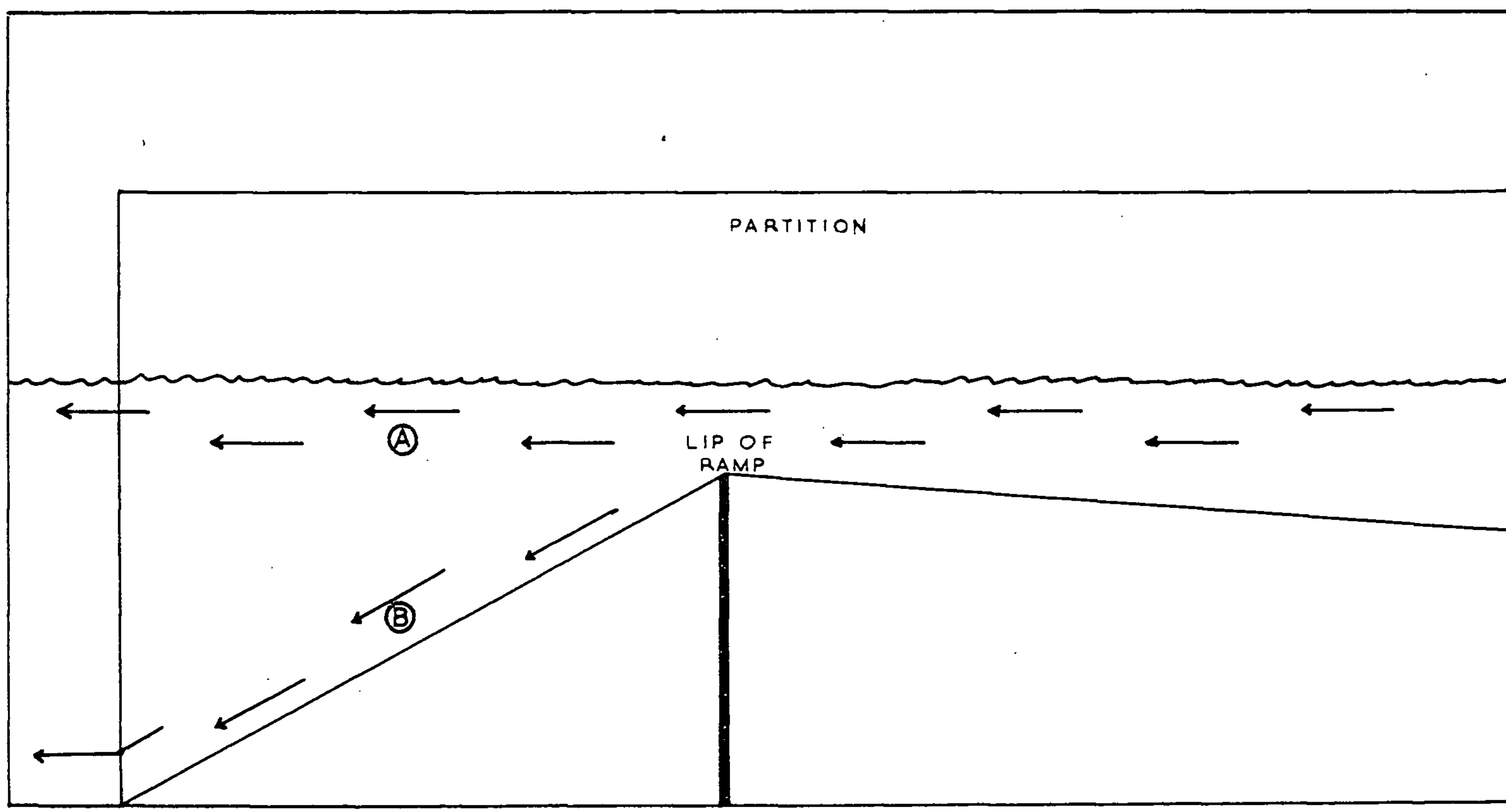

Figure 12. Two types of current patterns observed below the current arm in experimental section of stream tank.

be to introduce experimental fish and after the passage of a certain time period, a count could be made on their distribution. Then fish could be removed from their preferred areas and placed in a central area, to be released for a second time period.

The second alternative method would be to introduce experimental fish and then change the current to the opposite arm after a count was made. This method would result in a complete reversal of preferred areas.

2. Position of Fish in Relation to Current Arm

Distribution of fish in all parts of the experimental section also illustrates the difference in current preference between the two species. During the experiments, fish were found predominately in four areas; A - the current arm, B - the base of the current arm, C - the base of the non-current arm, and D - the non-current arm (Fig. 13).

There was a circular current over the unpartitioned section below the two arms. Fish, in order to swim from D to A had to move against the current as shown by the dotted arrows in Figure 13. As velocity was increased, the numbers of fish in the four areas were forced back in their position from A to D. *R. cataractae* in this analysis again exhibited a greater preference for faster water velocities than did *R. falcatus*. The number of *R. cataractae* moving out of the faster water velocity areas of A and B to the little or non-current areas of C and D were very few, when water velocities in the current arm were increased. With high water velocities,

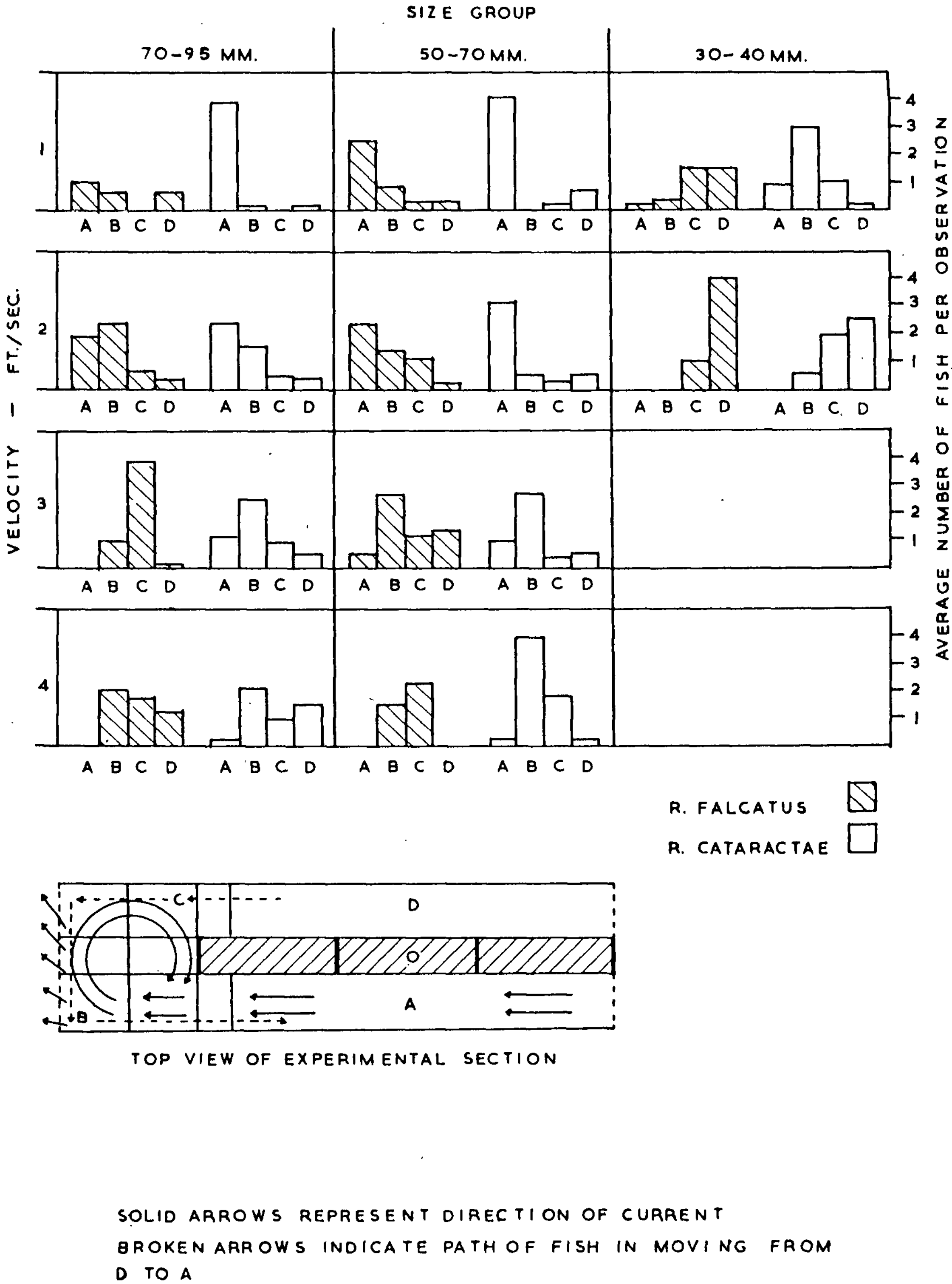

Figure 13. Position of fish in relation to current arm, A; in current arm, B; reduced current, in position to attempt to enter current arm, C; back-eddy of slight current, D; non-current arm.

R. falcatus was most numerous in the little or non-current areas of C and D.

D. Comparative Airbladder Analysis

Airbladder volume of both species is similar for fish of approximately 0.3 gm. in weight or less (Fig. 14). As *R. cataractae* increases in body weight, the airbladder volume shows little increase and appears never to exceed a volume of 0.1 ml. in fish of over 24 gms. in weight. The airbladder volume of *R. falcatus* increases greatly with increasing weight of fish, exceeding 0.4 ml. in fish of 11 gms. body weight.

Regression lines were calculated for both series of points. The regression in both cases was significant (p less than .005). The correlation coefficient (r) for *R. falcatus* was 0.95 and for *R. cataractae*, 0.44.

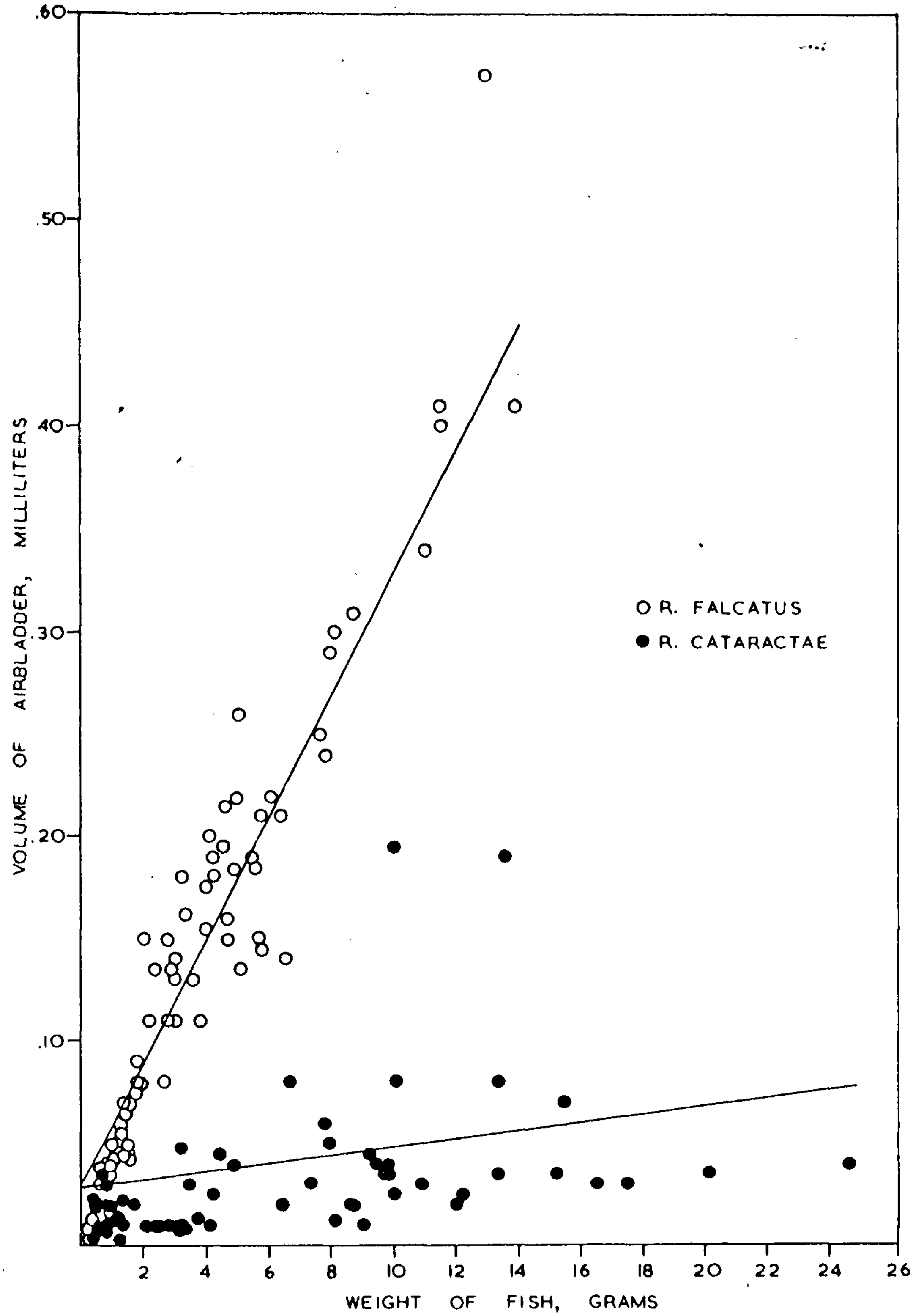

Figure 14. Comparison of the relationship between volume of airbladder and weight of fish in R. falcatus and R. cataractae.

IV DISCUSSION

A. Life History of R. falcatus

A comparative summary of the ecology and some aspects of the life history of R. falcatus and R. cataractae appears in Table IV.

The sexual dimorphism in growth rate as found in R. falcatus is also common to R. atratulus meleagris. Raney (1940) found that female fish were larger than males.

Spawning time of R. falcatus and R. cataractae is very close and it is possible that some overlap in spawning time occurs. Spawning R. cataractae have been collected in the mouth of the Coquihalla River near its entrance to the Fraser River at Hope on July 3, 1956. Spawning habitats of both species remain unknown.

The function of the tubercles in R. falcatus remains unknown. Tubercles are not, however, uncommon among species of the genus Rhinichthys. Male R. cataractae develop tubercles over most of the body and on the pectoral fin rays, but only at spawning time (Hankinson, 1923). Raney (1940) and Schwartz (1958) have described tubercles on male fish among three subspecies of R. atratulus. Raney (1940) suggests that the tubercles on the caudal peduncle of R. atratulus meleagris may assist the male in holding himself against the female during the spawning act.

The development of spawning coloration in male R. falcatus most likely functions in sex recognition as it develops at the same age as sexual maturity. Spawning coloration

TABLE IV

SUMMARY OF THE COMPARATIVE ECOLOGY OF

R. falcatus AND R. cataractae.

	R. falcatus	*R. cataractae*
Food:		
Age 0	Primarily Diptera larvae	Primarily Diptera larvae
Age 1 and older	Terrestrial insects and bottom organisms	Bottom organisms
Current:		
Age 0, Field	0-1.5 ft./sec.	Variable, 0-3 ft./sec.
Age 0, Lab.	0-0.5 ft./sec.	0.3-1 ft./sec.
Age 1 and older, Field	0-1.5 ft./sec.	Greater than 1.5 ft./sec.
Age 1 and older, Lab.	0-2 ft./sec.	1-3 ft./sec.
Depth:		
Day - Age 0	0-1 ft.	0-1 ft.
1	0-1 ft.	0-1 ft.
2 and older	Deeper than 1 ft.	0-1 ft.
Night - Age 0	0-1 ft.	?
1	Deeper than 1 ft.	Deeper than 1 ft.
2 and older	0-1 ft.	0-1 ft.
Airbladder volume:		
Age 0	Similar for both species	
1 and older	Increase in volume proportional to increase in body weight.	Little increase in volume with increasing body weight.

among males is common to the three subspecies of R. atratulus (Schwartz, 1958).

B. Ecological Significance of Experimental and Field Data

Experimental and field data show that the selection of differing water velocities results in the habitat divergence between yearling and adult fish of each species. The habitat divergence is complete when the fish is approximately a year old, and the respective habitats of each species draw further apart as the fish mature. R. cataractae selects faster water velocities with age as shown by the current preference experiments, while R. falcatus remains in slow or non-current areas.

It is difficult to determine at which time in the first year the habitat divergence becomes complete. Possibly R. cataractae begin to select slight water velocities within one or two months following hatching but many still overlap the habitat of age 0 R. falcatus. Approximately one month after hatching R. cataractae were taken in velocities from 0-1.5 ft./sec., while R. falcatus of the same age at the same time were in non-current areas.

Stream tank experiments on the 30-40 mm. size group which were approximately eight months old showed significant differences in the current preferences of the two species. Thus both species, shortly after hatching, may begin to diverge in their habitat optima probably with considerable overlap in numbers between the two habitats. The overlapping in numbers could result from the variable current preference of the young

R. cataractae, as many were collected from non-current areas with R. falcatus of the same age (age 0). When both species reach the end of their first year, the divergence in habitat optima have increased resulting in decreased overlapping of habitat ranges.

As the diet of young-of-the-year of both species is similar, competition in those areas where R. cataractae overlaps the habitat of R. falcatus could be severe. Competition cannot be assessed, however, as abundance of food is not known. Starrett (1950) found that when species of minnows entered into severe competition, the optimal food was replaced by an alternative source, One could not, however, conclude from this that competition for food does not occur when both species feed on a similar food source, as the availability of alternate food sources is unknown.

Competition between fish of both species is restricted to the area of overlap as those fish in their respective habitat optima, even though feeding on similar types of food, are feeding in different areas.

C. Ecological Significance of Airbladder Analysis

The principal function of the airbladder is hydrostatic (Harden-Jones, 1957). As the volume of the airbladder increases, the volume of the fish increases and hence the density decreases. Thus, freshwater fish with well developed airbladders of 7-10% of their total volume are able to swim easily in mid-water (Taylor, 1921; Harden-Jones, 1951). Both R. falcatus and R. cataractae have an airbladder volume less than 7% and it is likely that both species remain near or in contact with the bottom much of the time.

It would be an advantage for a bottom dwelling fish in fast water to have as great a density as possible in order to maintain position. The low airbladder volume of R. cataractae has aided this species to occupy such a habitat. As R. cataractae increases in weight, the density of the fish also increases. The increase in density is paralleled by an increase in preference for fast water velocities as the fish become larger. Airbladder volume of age 0 fish of both species is similar in accordance with their habitat similarities. The larger airbladder volume of yearling and adult R. falcatus permit it to feed on the water surface, utilizing terrestrial insects. Adult and yearling R. cataractae have not been known to feed on terrestrial insects (Johannes, 1958; Carl et al, 1959; Beckman, no date).

D. Biological Significance of Habitat Segregation

The biological significance of habitat segregation can be illustrated by Gause's contention (1934) that closely related species cannot coexist in a similar niche without one species eliminating the other through competition. This contention takes its roots from a statement made by Darwin (1859, from Harper et al, 1961). Darwin states,

> "It is the most closely allied forms - varieties of the same and related genera - which, from having nearly the same structure, constitution, and habits, generally come into the severest competition with each other; consequently each new variety or species, during the progress of its formation, will generally press hardest on its nearest kindred and tend to exterminate them."

Hutchinson (1948) has added two restrictions to Gause's contention: 1. external factors can act to limit the mixed population of coexisting species occupying similar niches, and 2. chance oscillations of environmental conditions can continually reverse the direction of competition.

Lack (1949) hypothesized that such external factors as predation and parasitism could act in such a way as to limit competition of coexisting species. Utida (1953) has demonstrated experimentally that parasitism can act in such a manner.

Gause (1934) experimented with two species of closely related ciliated protozoans, Paramecium caudatum and P. aurelia. When these two species were kept in separate cultures, both populations exhibited a sigmoid growth curve and maintained a constant population level. When both protozoans were kept in the same culture, P. aurelia eliminated P. caudatum. When a third protozoan, P. bursaria, was placed in the same culture with P. caudatum, both were able to survive and reach a state of equilibrium even when feeding on the same food. P. bursaria occupied a different part of the culture when it could feed on bacteria without competing with P. caudatum.

Other experiments by Crombie (1947), and Park (1948), in addition to those previously mentioned, have justified Gause's contention. Elton (1946) has summarized this contention for field conditions. Elton conducted a survey of ecological studies with clearly defined habitats and found that in a community there was a high percentage of genera represented by only one species. In animal communities, 86% of the genera found were represented by only one species and in plant communities, 84%.

Opposition to Gause's contention (Diver, 1936 and Cole, 1960) is concerned mainly with ecological terminology and application of mathematical models rather than with the biological basis of the principle.

In late July, at the probable time of hatching of both species, the Fraser River is near its maximum yearly discharge. Part of the surrounding land of the lower Fraser Valley becomes flooded at this time providing increased non-current areas over flooded land and gravel bars. The water is turbid (4-6 inches visability) at this time of year and the increase in water level and flooding could provide additional food sources. Such river conditions appear suitable for the survival of newly hatched fish.

It is possible at this time, with an excess of food, cover, and non-current areas, that young-of-the-year R. falcatus and R. cataractae can coexist in a similar niche for their first month (August). However, as the water level begins to drop from August until April, such favorable environmental conditions for coexistence would become scarce and interspecific competition would result and increase through the winter months. Such increased competition would result in an increasing divergence in habitat optima between the two species; as each would attempt to utilize its ecological potency (Kalleberg, 1958), and reduce the area of habitat overlap. Thus, the resulting near-complete habitat divergence at the end of the first year, allows these two congeneric species, whose ranges overlap and occur in the same river areas, to exist without entering into severe competition for those resources of their environment that are essential for their existence.

The possible coexistence of young-of-the-year R. falcatus and R. cataractae in similar niche suggests an additional exception to Gause's contention. That is, sympatrically occuring species may occupy a similar niche for a short period of their life cycle when essential environmental resources are in excess of the demand for them.

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