SOME FACTORS AFFECTING THE DISTRIBUTION AND ABUNDANCE OF THE CHISELMOUTH (ACROCHEILUS ALUTACEUS)

by

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ABSTRACT

Some features of the biology of Acrocheilus alutaceus were investigated with the purpose of explaining the rarity and disjunct distribution of the species in British Columbia.

Two populations were compared, one in a lacustrine environment, in which the species is often rare, the other in a riverine environment, in which the species is usually common.

Age and growth analysis of the two populations showed that in the river population growth continued for one year longer than in the lake population. Maximum age attained in both populations was 6 years.

Observations of feeding behavior in the field and laboratory suggested that the unusual lower jaw of the fish is an adaptation to scraping Aufwuchs, chiefly filamentous algae, from smooth substrates.

Analysis of diet in the two habitats showed a much more restricted diet in the river. It is concluded that the growth of the type of food consumed by Acrocheilus and the occurence of a substrate suitable for feeding will be most abundant and commonly found in warm rivers.

The temperature required for spawning by Acrocheilus is probably higher than that of other local cyprinids. This may also limit the distribution of the species.

In both habitats, diet changes with age; young fish lack the scraper-like lower jaw and eat principally insects.

Diatoms ingested with filamentous algae probably provide the chief source of nutrition. Filamentous algae undergoes little or no digestive breakdown.

The possibility of interspecific competition for food and spawning sites in the lake is discussed.

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INTRODUCTION

This study deals with a freshwater cyprinid fish which is unique with regard to its scarcity and disjunct distribution. Acrocheilus alutaceus, commonly known as the chiselmouth, occurs in three drainage systems in northwestern north America, the Fraser, Columbia, and Malheur systems (the last a closed drainage).

Acrocheilus is present in both lakes and rivers, being reported most frequently from the latter. Agassiz and Pickering first described Acrocheilus from Willamette Falls and the Walla Walla River, Oregon (Agassiz, 1955). The fish was not discovered in British Columbia until 1950, in Skaha Lake (Ferguson 1950). Since then it has been taken in a few widely disjunct localities, and usually in small numbers. The distribution of the species in British Columbia is thus unusual and the population density relative to other cyprinids present is apparently low in all localities examined.

The purpose of this study was to attempt to explain the unusual distribution and abundance of Acrocheilus in British Columbia. The approach to the problem consisted of an investigation of the general biology of the species in order to discover whether it contained any features which might explain the distribution and abundance of the species. In particular, food and feeding, feeding behavior, age, growth and spawning requirements were examined. Where possible, these were studied on a comparative basis, examining a lake environment in British Columbia where the fish is scarce, and a river environment in Washington where the fish is common. Food, spawning requirements, local distribution and fecundity of other cyprinids not showing the distribution of Acrocheilus were compared with Acrocheilus in order to see whether any differences might explain the peculiarities of the distribution and abundance of the chiselmouth.

Most data were obtained during the summer of 1965; some samples were procured on short field trips in the summer of 1964.

THE STUDY AREAS

The main study area was Wolfe Lake (lat. 49° 26' N long, 120° 59' W), near the town of Princeton, British Columbia. This lake was chosen because of its accessability and relatively small size.

Wolfe Lake is a shallow and roughly circular lake, with longest dimension 850 m, and surface area 33.6 hectares. It is the lowest of a chain of four lakes lying in a valley which was once the channel of the Similkameen River (Mathews, 1944). Wolfe Lake now drains via an outlet 1.3 km long into the Similkameen River (Fig. 1).

The west end of the lake is marshy, the margin in many parts consisting of Typha. Potamogeton is abundant in the open shallow water which is present only at this end of the lake.

The lake has been dammed in recent times, causing the water level to rise approximately 1.2 m. As a result, the west end of the lake contains many submerged dead trees and bushes. The north and south shores are steeper than the west, consequently there is little aquatic vegetation in this area. Windfallen logs are present above and below the surface.

The lake empties over a rocky sill which is in part artificial. The drop over the sill is probably an effective barrier to most species ascending the stream.

The maximum depth found in the lake was 6.4 m. Thermal stratification was established in May, but was not strongly defined in May, June, or July, the duration of the study period. Frequent wind action probably prevents the establishment of a stable stratification.

The water is stained a deep brown color and contains large amounts of seston. Cyclopoid copepods make up the bulk of the zooplankton. Filamentous algae, epiphytic diatoms, chydorids, and gammarids are present in the littoral zone.

Other fish in the lake are Ptychocheilus oregonense, (Northern Squawfish), Mylocheilus caurinus, (Peamouth Chub), Richardsonius balteatus, (Redside Shiner), Catostomus macrocheilus, (Largescale Sucker), Cyprinus carpio, (Carp), Prosopium williamsoni, (Mountain Whitefish), and Salmo clarkii, (Cutthroat Trout). The last two species are uncommon. In addition there are suckers which are tentatively classified as hybrids between Catostomus columbianus, (Bridgelip Sucker), and Pantosteus jordani, (Northern Mountain Sucker). These fish will hereafter be referred to as "hybrid suckers".

The inlet creek enters the lake at the west end. The width of the creek is seldom more than 8 m, and the maximum depth less than 1.5 m. The average cross-section is about 4 m wide by 40 cm deep, the velocity in such an area in mid-June was 1.4 - 1.8 m per second. The bottom is made up of gravel of various sizes, distributed according to the velocity at a given area. The fast, deep zones have a bottom of large (10 - 20 cm) boulders. The area immediately beyond such a deep region is composed of much smaller (5 - 8 cm) rocks. Riffles are usually pebble-bottomed. Slow back-waters are sandy-bottomed. The entire lower part of the creek, just before it enters the lake, is sandy-bottomed.

The creek water is darkly stained and contains a large amount of suspended material. The flora of the creek consists of occasional patches of filamentous algae attached to rocks and logs. A fresh water sponge is common in the deep areas. Common insects in the creek are Ephemeroptera naiads and Trichoptera larvae. The margin of the creek is densely overhung by Populus and small bushes. Beyond the ford (Fig. 1), the gradient increases and there are few slower areas in which cyprinids can be found. Fish inhabiting the creek are Rhinichthys osculus, (Speckled Dace), and Cottus rhotheus (Torrent Sculpin).

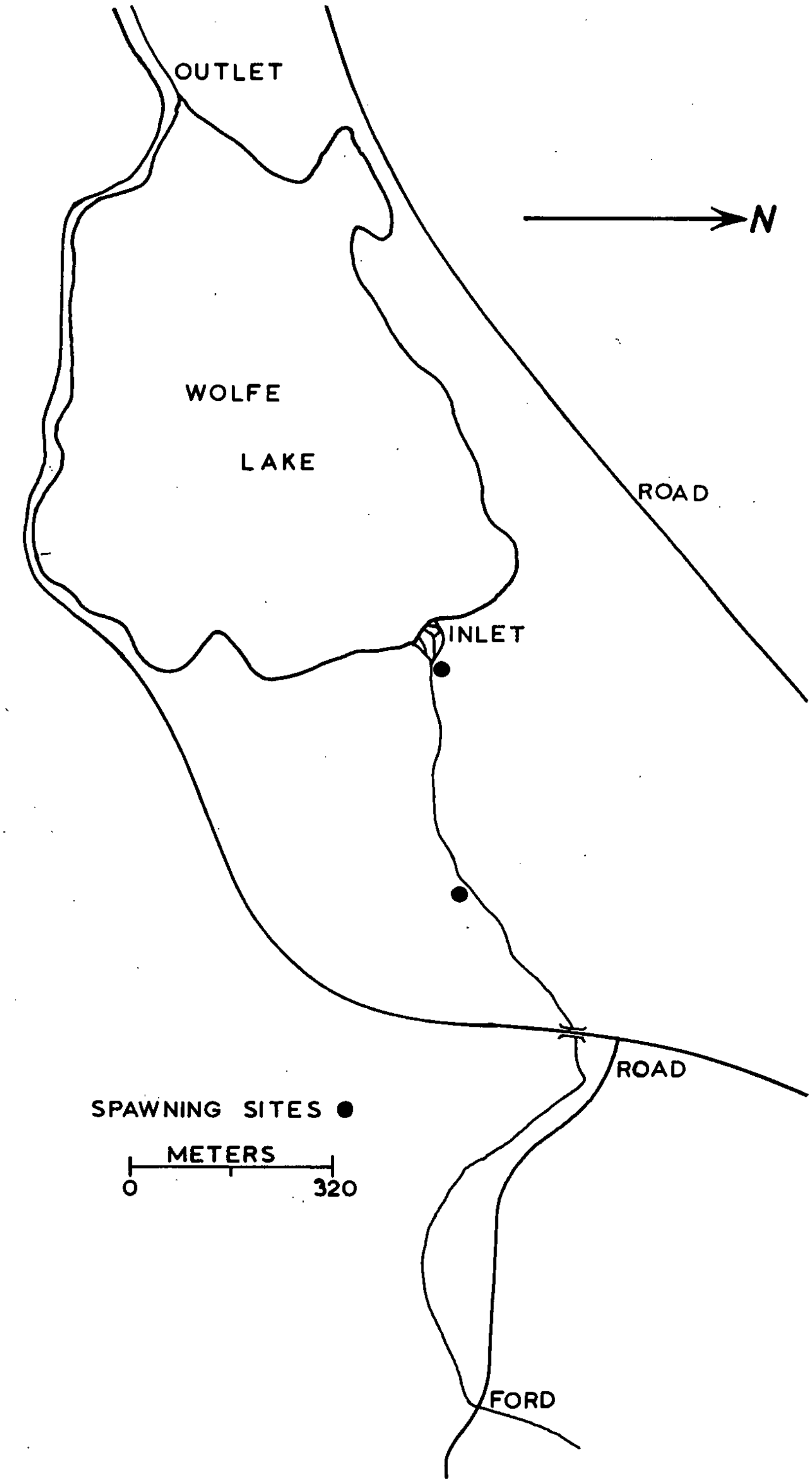


Figure 1. The Wolfe Lake study area

A sample of chiselmouths from a riverine population was obtained from the Okanogan River near the town of Brewster, Washington, U.S.A., lat. 48° 10' N, long. 119° 45' W. The fish were collected in water ranging in depth from 0 - 2 m. The bottom consisted of large (15 - 25 cm) boulders, bearing a dense growth of filamentous algae and its associated Aufwuchs. The current was swift. Juveniles were obtained from sandy-bottomed shallow back-waters. Other species in the river habitat were *R. balteatus*, *C. macrocheilus*, and *P. oregonense*. Only *R. balteatus* was more abundant than *Acrocheilus*.

Additional samples were obtained from Missezula Lake, Issitze Lake, Vidette Lake and Vaseux Lake, all in British Columbia. Small samples also were obtained from a few streams in central Washington.

THE MORPHOLOGY OF *ACROCHEILUS*

The chiselmouth has an elongate, slightly compressed body. The maximum size is reported to be 300 mm. The caudal peduncle is narrow and the tail large and flaring. The most outstanding characteristic of the fish is its mouth. The snout overhangs the mouth, which is horizontal. The lower jaw bears a sharp, nearly square edge when viewed from beneath. The sharp part of the lip consists of cornified epithelium which is sometimes slightly calcified. Internal to the fleshy upper lip is a small, hard plate upon which the lower lip bears. Young fish have a more rounded lower lip, when viewed either laterally or from below. The digestive tract is unmodified and is about twice the length of the body.

METHODS

Fecundity was estimated by a displacement method. The volume of the two ovaries was first measured by the displacement of 40% isopropyl alcohol in a graduate. The ovary was then broken up and enough eggs counted to displace one cubic centimeter of alcohol in a graduated centrifuge tube. This value was then multiplied by the total volume of the ovaries.

Chiselmouth eggs were obtained from the inlet creek of Wolfe Lake in July of 1965. Females were stripped onto plastic screens, the eggs were then fertilized and taken to the laboratory. In the laboratory the eggs were placed in gauze baskets hanging in boxes with water circulating at a constant temperature. Rearing temperatures were 12° and 18°C.

The larval fish were fed on brine shrimp nauplii and infusoria. Developing cyprinid eggs obtained directly from the spawning area in the inlet stream of Wolfe Lake, were reared in the same way.

Behavior of the fish at spawning time, and the locations of the spawning areas in the inlet stream of Wolfe Lake were observed with the aid of a face mask and snorkel.

In Wolfe Lake, adult fish were sampled for stomach contents analysis from May 7 through to July 20, 1965. Sampling was carried on 24 hours per day, but the majority of the fish were caught during the night. The data presented thus represent almost daily small samples of Acrocheilus. Samples of other species and samples of juveniles of all species were obtained in the same places and during the same period of May through July, but at less frequent intervals.

Adult fish were sampled with monofilament gillnets 2.4 m deep x 15.2 m long. Mesh size varied from 2 - 5 cm stretched.

Juvenile fish were sampled by seining or, more commonly, by poisoning with rotenone.

All specimens were initially preserved in 10% formalin, and later transferred to 40% isopropyl alcohol. Large fish were injected with formalin after capture.

For age studies otoliths were removed before fish were preserved in formalin. A transverse cut across the skull exposed the otoliths lying on each side of the brain. They were removed with forceps and stored in 50% glycerin.

For age determinations, the otolith was glued to a microscope slide, flat side down, using epoxy-resin. The slide was placed otolith down, on a glass plate which bore a paste of medium grade grinding compound and water. The otolith and surrounding resin were then ground down by rotating the slide. The progress of the grinding was frequently checked under a dissecting microscope, and the process stopped when the ground surface reached the level of greatest diameter of the otolith. The majority of otoliths treated in this way were readable (Fig. 2). Those otoliths lacking distinct annular rings were discarded.

Guts of Acrocheilus were left in the fish until the stomach content analysis was performed in the laboratory. Guts (and their contents) of species other than Acrocheilus were removed after capture, wrapped in gauze, identified and preserved in 10% formalin.

The composition of food eaten by all species was evaluated in two ways, each outlined by Hynes (1950). The volumetric method consists of the allotment of points, the total of which is based on the total volume of food in the gut. Since the stomach is very easily distended, the estimation of its degree of fullness is difficult, and only five classes of fullness are recognized: empty, $\frac{1}{4}$ full, $\frac{1}{2}$ full, $\frac{3}{4}$ full, and completely full. These conditions are given the following total number of points: 0, 5, 10, 15, 20 respectively. The points allotted on the basis of fullness are then proportioned according to the visually estimated proportions of the different food items in the gut.

The second method consists of simply listing the food items as present or absent. This method does not take into account the abundance of the items in the individual fishes.

The only departure from the methods of Hynes was that the entire

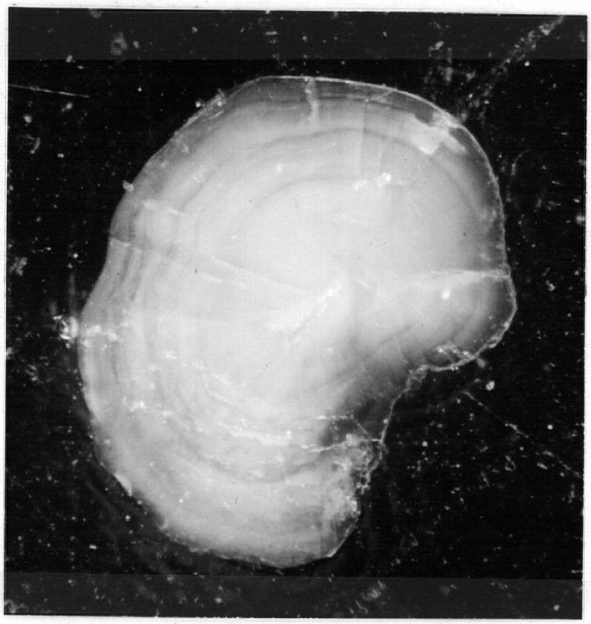


Figure 2. A ground otolith, age three years

intestinal tract rather than only the stomach, was analyzed.

The digestion of cellulose was examined by staining filamentous algae taken from different sections of the guts of chiselmouths with 75% sulfuric acid and IKI solution. This results in the cellulose membranes becoming blue. The amount of cellulose present in the cell walls of the algae was then estimated throughout the digestive tract.

Laboratory observations and photographs of feeding and other behavior were made in an aquarium measuring 145 cm long x 32 cm deep x 47 cm wide. A thick growth of filamentous algae was produced on the sides of the aquarium by continuous illumination with three 100 watt light bulbs. The observer was concealed from the view of the fish by a cloth screen and could watch the fish through a small opening. All fish observed were from Wolfe Lake. The difficulty involved in obtaining and maintaining Acrocheilus resulted in prolonged observation of only five individuals, three adults and two juveniles. One of these adults, maintained for 18 months, was the chief source of information concerning feeding behavior. Laboratory fish were fed primarily on commercially prepared trout food, although frozen brine shrimp were also used. Although given prepared food daily the fish also fed frequently on the filamentous algae growing in the aquaria.

TAXONOMY

Acrocheilus alutaceus Agassiz and Pickering is a cypriniform teleost belonging to the suborder Cypriniodei, family Cyprinidae. Acrocheilus is a monotypic genus. The occurrence of natural and artificial hybrids between Acrocheilus and the other northern Pacific slope cyprinids, Ptychocheilus oregonense, Mylocheilus caurinus, and Richardsonius balteatus, suggests that the differences among these genera may be less than their morphology would indicate.

SYNONOMY

Since a complete synonomy for <u>Acrocheilus</u> does not exist, it was considered desirable to include one in this study.

<u>Acrocheilus</u> <u>alutaceum</u>. Agassiz, L. Amer. Jour. Sci. Arts, 19, 1859:99. Willamette Falls and Walla Walla River, Ore.

<u>Acrocheilus</u> <u>alutacium</u>. Gunther, A. Catalogue of the fishes in the British Museum 1868: 7:1-512. Willamette Falls.

<u>Acrocheilus</u> <u>alutaceum</u>. Jordan, D. S. Proc. U. S. Nat. Mus., 1879: 1:69-85. John Day River.

<u>Acrocheilus</u> <u>alutaceum</u>. Jordan, D. S. in Goode, G. B. The fisheries and fishery industries of the U. S. Fishes Sect. 1 Part 3, 616-618. Willamette Falls.

<u>Acrocheilus</u> <u>alutaceum</u>. Bean, T. H. Proc. U. S. Nat. Mus., 1882: 5:89-93. Umatilla River, Walla Walla River.

<u>Acrocheilus</u> <u>alutaceum</u>. Gilbert, C. H. and B. W. Evermann, Bull. U. S. Fish. Comm., 1894: 14:169-204. Tucannon River, Grande Ronde River, Yakima River, Lower Crab Creek, Rock Island Dam, Wenatchee River, Little Spokane River, Hangman River.

<u>Acrocheilus</u> <u>alutaceum</u>. Gill, T. Smiths. Misc. Coll. 1907: 48:297-340.

<u>Acrocheilus</u> <u>alutaceum</u>. Snyder, J. O. Bull. U. S. Bur. Fish., 1907: 27: 153-189. Clackamus River.

<u>Acrocheilus</u> <u>alutaceum</u>. Snyder, J. O. Bull. U. S. Bur. Fish., 1907: 27:69-102. Sylvies River.

<u>Acrocheilus</u> <u>alutaceus</u>. Ferguson, R. G. Can. Field Nat., 1950: 64:156. Skaha Lake.

<u>Acrocheilus</u> <u>alutaceum</u>. Carl, G. C., W. A. Clemens and C. C. Lindsey. The fresh-water fishes of British Columbia. 1959: 117-119. Euchiniko River, Nazko River, Missezula Lake, Nicola Lake, Skaha Lake, Gallagher Lake, Tugulnuit Lake, Okanagan River, Windermere Lake, Wolfe Lake.

Acrocheilus alutaceum. Patten, B. G. Copeia, 1960; 1:71-73. Yakima River.

Lavinia alutacea. Girard, C. Proc. Acad. Nat. Sci. Phila. 8, 1857: 165-213.

Willamette River and tributaries.

THE BIOLOGY OF THE CHISELMOUTH

DISTRIBUTION

General Distribution

The distribution of Acrocheilus is noteworthy in that in the southern portion of its range it is a common fish, both in terms of overall distribution and of abundance relative to other species (Gilbert and Evermann, 1894). In the northern part of the range i.e. British Columbia, Acrocheilus is rare in every sense (Fig. 3). Since being found in Skaha Lake, Acrocheilus has been taken in several other lakes nearby. The nearest location to the above where chiselmouths occur is Wolfe Lake and Issitze Lake, 80 km to the west. Forty-five km to the north of these two lakes, chiselmouths are again found in Missezula Lake. Acrocheilus has not been found anywhere else in the Columbia system in British Columbia except for Windermere Lake, near the headwaters of the Columbia. In the Fraser system, chiselmouths are found in five localities. They have been taken in Vidette and Mara Lakes, which are about 90 km apart. Seventy-four km south of Vidette Lake, chiselmouths are found in Nicola Lake. The only other records of Acrocheilus in the Fraser system are from the Nazko and Euchiniko Rivers, about 600 km northwest of Vidette Lake. Many of the intervening waters have been extensively sampled in the past 15 years, so that if chiselmouths do occur in such localities they must be rare.

In British Columbia, Acrocheilus is most often found in lakes rather than rivers. In Washington and Oregon, the reverse is the case. This may be correlated with the general scarcity of slow moving, warm, fairly eutrophic

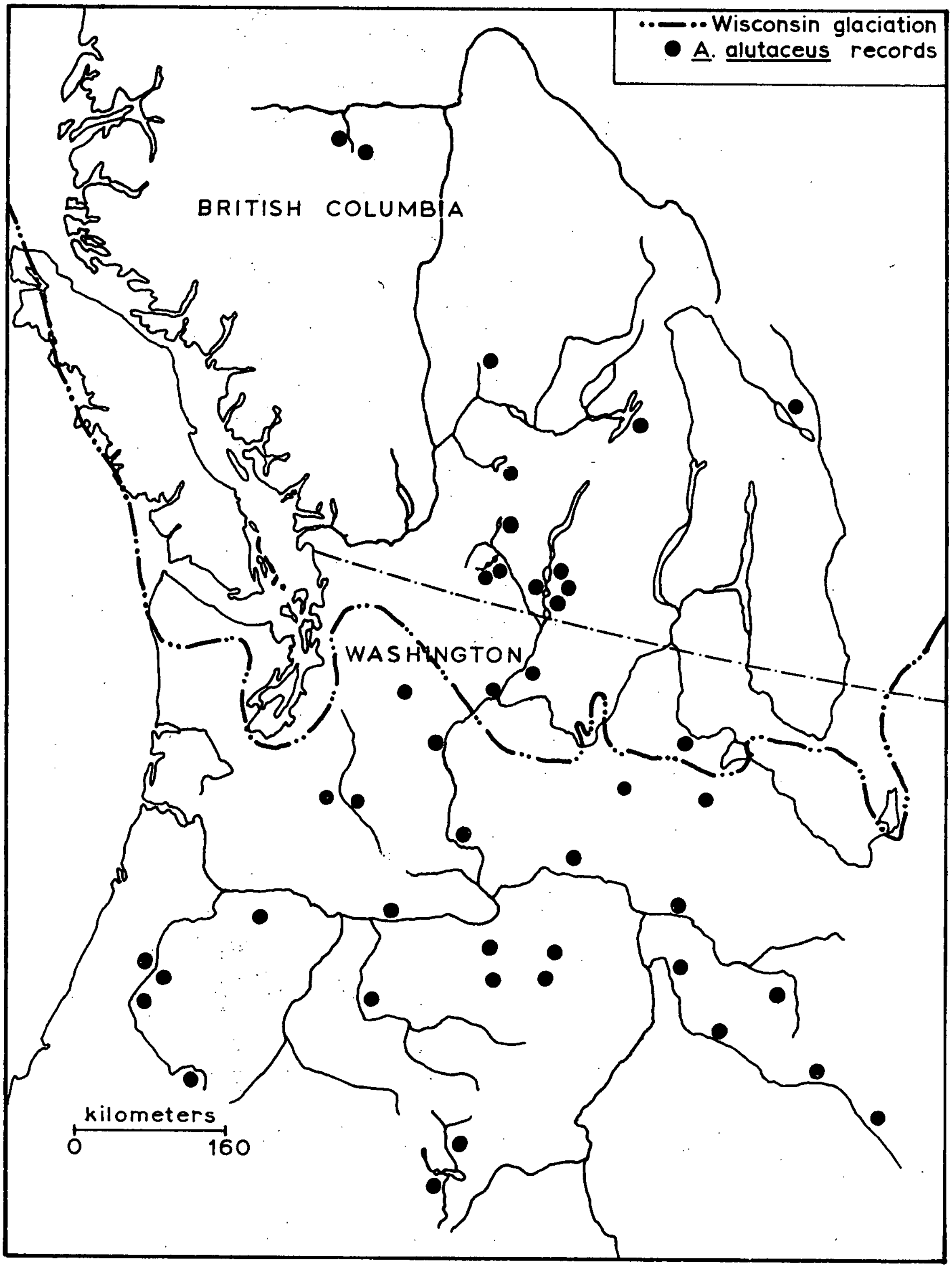


Figure 3. The distribution of Acrocheilus and the extent of recent glaciation

rivers in British Columbia as compared to Washington and Oregon.

Local Distribution and Movement in the Wolfe Lake Study Area

The local distribution and movement of Acrocheilus in Wolfe Lake were studied for two reasons. Firstly, an indication that the chiselmouth is territorial would lend weight to the conclusion based on laboratory observations that the fish are aggressive, which in turn would be of interest if intraspecific competition for food occurs. Secondly, if interspecific competition for food occurs, it is necessary to know whether the different species occupy the same micro-habitat.

In order to discover whether the chiselmouth occupies a home range, fish were individually marked at different points around the margin of the lake. The study was complicated by the spawning period which lasted from about June 10 to July 9, in 1965.

Eighty-one fish, adults of both sexes, were marked with numbered aluminum clips placed on the operculum. One hundred more were marked by clipping various combinations of fins. The maximum number of fins clipped on a fish was two. Marking was done from May 7 to June 9, 1965. Netting for recovery was conducted 24 hours per day, from May 7 to July 20, 1965. Marking was done at a variety of points around the margin of the lake. Netting for recovery was done at the points of marking and at intervening points.

Of the total marked by either method only 14 were recovered. The low recovery rate was probably due to injury sustained by the fish during gillnetting prior to initial marking. Fish brought back to the laboratory were found to be extremely susceptible to disease even following the most careful handling. Recoveries and controls held in the lake after tagging indicated that the tag itself seldom caused death.

Figure 4 indicates the movements of marked fish which were recovered. It can be seen that in the few instances where the fish were recovered prior to

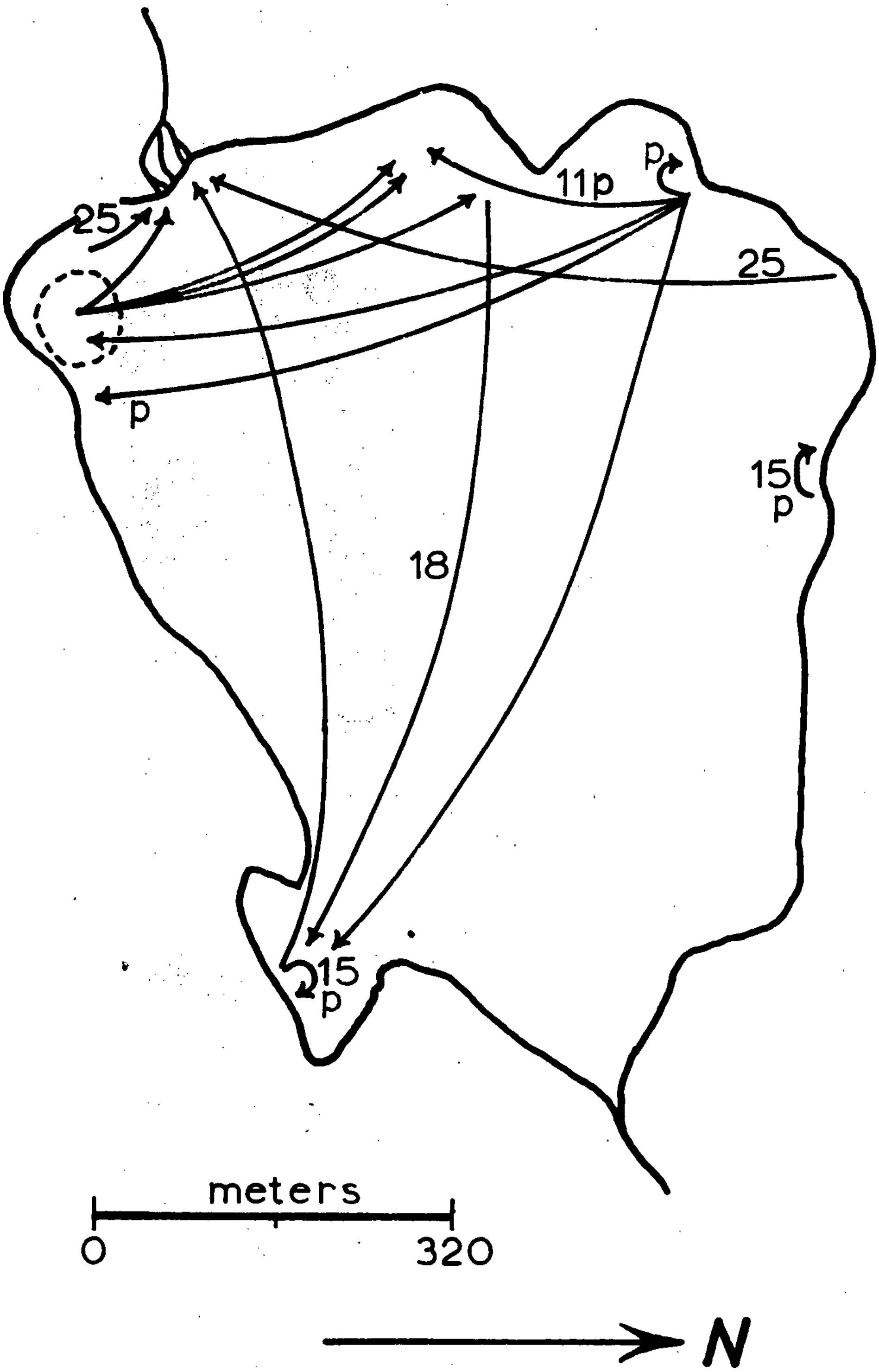


Figure 4. The movement of marked and recovered chiselmouths in Wolfe Lake. Recoveries made prior to the spawning period are indicated by "p". Numbers indicate days between marking and recapture. Lack of a number indicates a fin clip recovery, none of which were dated.

the spawning migration, the amount of movement was limited.

In order to obtain further information about the movements of chiselmouths in the lake, gillnets were set in various patterns: Nets were set perpendicular to shore with one end on or very close to shore. The depth of water was about 2 m near the shore and from 3 - 5 m at the offshore end of the net. The nets were always set with the lead line on the bottom of the lake. This was the usual arrangement of nets throughout the study period May 7 to July 20, 1965, with some exceptions to be noted. The direction of fish caught in such an arrangement was almost equally divided, that is one half the fish were going in either direction. Fish were occasionally caught together but most often appeared to be moving as individuals rather than in groups. Except for two occasions at spawning time, there was never any suggestion that Acrocheilus adults swim in schools.

On 5 occasions 4 nets were set perpendicular to shore, but off the shore. Unless set within 6 m of shore, no chiselmouths were caught. In these cases the inshore end of the net extended from the surface to the bottom of the lake. On a separate occasion an equal number of nets were set parallel to shore. Again, unless the net was within 6 m of the shore, no chiselmouths were caught. In both cases nets were set in a variety of places known to provide chiselmouths by other methods of capture.

To discover whether movement along the shore was limited, 4 nets were set parallel to each other 15 m apart and perpendicular to the shore, to which one end was attached. In such an arrangement the catch of the inner two nets was most often equal to that of the outer two. This method of net setting was carried out 4 times in 2 locations. The total catch of this as well as any other arrangement usually diminished over a period of time.

The results of the net catches indicate that the movement of adult Acrocheilus from May to July is limited in its along-shore component.

From May to July and on September 12 and 13, 1965, chiselmouths were found only around the margin of the lake, except for during the spawning period when they were in the inlet stream. On October 20, no Acrocheilus could be caught around the margin of the lake, but two were caught in deep water near the center of the lake, where they were never found earlier in the year. This suggests that in the autumn Acrocheilus either becomes very inactive or moves to deeper water.

Young chiselmouths, up to age one, were obtained by dip-netting, seining and poisoning. The fish were found in mixed schools of young P. oregonense, M. caurinus, and R. balteatus.

Acrocheilus from 2 - 4 years of age were obtained by gillnetting. They were found most often with M. caurinus, and to a lesser extent, P. oregonense of the same size.

Adult chiselmouths were caught with all of the above species plus C. macrocheilus.

On two occasions, just after the spawning period in Wolfe Lake and just prior to spawning in Missezula Lake, a large school of 50 - 100 adult chiselmouths was caught, in both cases the schools were not near the spawning area.

Local Distribution in the Okanagan River

The local distribution of adult chiselmouth in the river habitat, although examined only briefly, was different from that in Wolfe Lake. In the river adult chiselmouth were more spatially isolated from each other and from other species, as determined by gillnet catches. Adults were spaced out over the bottom and other cyprinids were rare in the area. Juveniles were caught using seines and gillnets and were found with the same species with which they occur in Wolfe Lake.

Aggressive Behavior

The significance of aggressive behavior in interspecific competition and territoriality was explained earlier. The different local distribution in the lake and river examined suggested that in the lake crowding might increase the extent of aggression to a harmful degree.

Laboratory observations of aggressive behavior were made on five individuals. Observations were made on three adult fish in the large aquarium previously described. Initially one adult was placed in the tank. After several days, another fish approximately one cm larger was introduced. The introduced fish was immediately chased by the earlier inhabitant of the tank. Whenever the newcomer approached within about 45 cm of the other, it would be driven back to the far end of the tank. While chasing, the aggressive fish would swim along side of and slightly behind the other fish. Frequently the dominant fish would bite the region behind the dorsal fin. After about 8 hours of such behavior, a glass divider was placed in the center of the aquarium and was left in place for two days. Upon removal of the divider, the relationship between the two fish was reversed, the larger fish became the dominant and pursued the slightly smaller fish when it approached within about 45 cm. The fish were left together and the behavior described above was frequently observed during the next three days. At the end of the third day, the smaller fish died, apparently due in part to an open wound behind the dorsal fin, caused by the actions of the larger fish. One other adult of similar size to the dominant was placed in the tank several days later. When the previously described behavior began to appear, the fish were permanently separated.

Two juvenile fish were placed simultaneously in an aquarium measuring 27 cm wide x 30 cm high x 50 cm long. The sizes of the fish were approximately 70 and 80 mm. The larger fish chased the smaller fish whenever it approached within about 10 cm. As in the case of the adults, chasing consisted of swimming to the side of and slightly behind the fish being pursued. Less biting was observed in the juveniles and the fish were uninjured after three days when they were separated. When placed in adjacent aquaria of the dimensions given above, one fish frequently pushed against the side of the tank where it could see the fish in the other aquarium. The fish in the second aquarium avoided the part of the aquarium closest to the other fish. This behavior was observed for five days. These fish were aged about two years, one year more than those observed schooling in the field.

Chasing was also exhibited by an adult chiselmouth towards a juvenile peamouth chub. Whenever the chub left its sheltering place, (a pane of glass set against the side of the tank), the chiselmouth pursued it. This behavior persisted as long as the fish were together, a period of 18 months.

AGE AND GROWTH

Because of the difference in abundance of <u>Acrocheilus</u> in the lake and the river, it was thought that an analysis of the age and growth of the species in these two environments might indicate whether the growth rate in the lake was reduced, thus indicating less favorable conditions.

Otoliths were used to age <u>Acrocheilus</u>, since scales showed indistinct circuli. Samples large enough for ageing by the size frequency method could not be obtained.

The otoliths were examined using epi-illumination and a black background. The usual magnification was 50X. The narrow annuli appear transparent in contrast to the whiteness of the broad intervening zones (Fig. 2). Fish in the river population having one and two annuli on their otoliths came from two distinct size classes, smallest and second smallest respectively. This was used to establish the first year mark and as evidence that the annuli do in fact represent yearly growth marks. The range of variation and sample size of these two age classes in the river population are given in Figure 5. The chief area of difficulty in interpreting ages was in the most recent part of the otolith i.e. at the margin. However the sector in which the growth rings are most compressed was generally readable. About 40% of the otoliths prepared were unreadable either because of improper mounting and/or grinding or because the annuli were not distinct enough to make a confident estimate possible. If there was any doubt as to the age of an otolith, it was not used for the growth rate estimates. Forty-one fish from Wolfe Lake and 47 from the Okanogan River were aged.

Growth curves for Acrocheilus from Wolfe Lake and the Okanogan River populations are shown in Fig. 5.

The maximum age attained in both populations is 6 years. The growth rate of the Okanogan River population is greater than that of the Wolfe Lake population; this difference is highly significant ($F = 18.35$, df 1, 83). In the lake population, females reach a greater size than males of the same age, after the age of three. It is not known whether the same holds in the river population, since sex determinations made in the field were later found to be unreliable. In Wolfe Lake, males probably spawn at age 3, females probably spawn sometimes at age 3 but usually at age 4.

PARASITISM AND DISEASE

The possibility of disease and parasitism as a factor controlling population density has been suggested by some authors (Mayr, 1963). Chiselmouths from both the lake and the river environment were examined for macroscopic parasites of the digestive tract, coelom, and integument. On this basis, the level of parasitism in Acrocheilus in both environments was lower than in any of the other cyprinids examined, and was equalled only by the sucker C. macrocheilus. The only parasites seen were small nematodes which occurred in low numbers in the intestines of a few fish. Rarely one or two leeches were attached to the roof of the buccal cavity. No chiselmouth showing obvious signs of disease were seen.

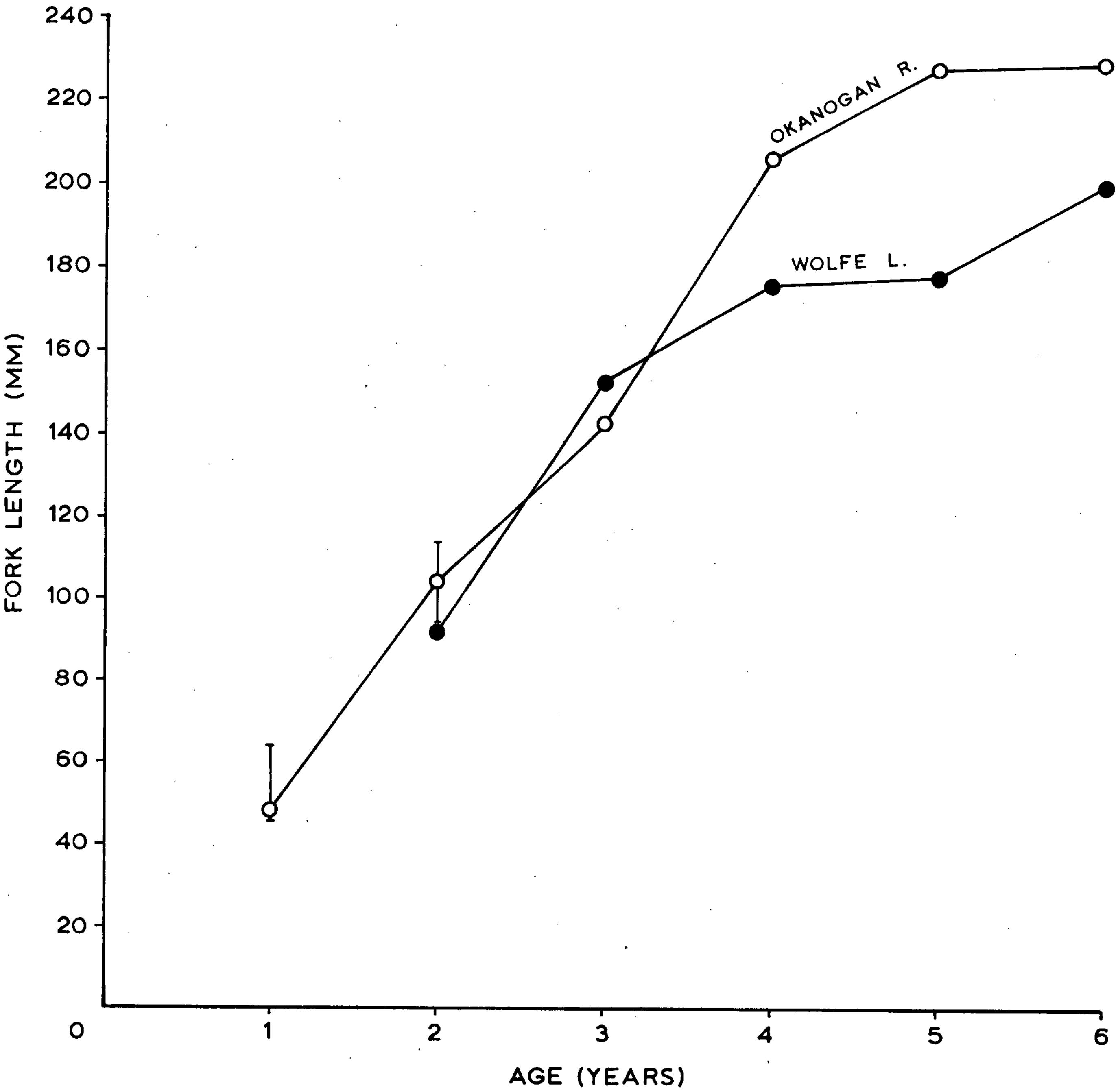


Figure 5. Growth curve of Acrocheilus in Wolfe Lake (closed circles) based on 41 fish, and in the Okanogan River (Open circles) based on 47 fish. Sexes are combined in both curves. Vertical lines indicate the range in size variation at ages one and two in the river sample; sample sizes were 10 and 19 respectively.

REPRODUCTION

The spawning habits of Acrocheilus were examined in Wolfe and to a lesser extent, Missezula Lakes, in order to see whether there were any peculiar requirements which might limit the distribution of the species in British Columbia, by preventing reproduction.

In Wolfe Lake Acrocheilus undergoes a considerable spawning migration, some fish travelling 1.5 km up the inlet stream. Chiselmouths began to congregate at the mouth of the inlet stream June 10, 1965, and became rare in the lake at this time. Ripe males were present in the lake beginning on May 28. Ripe females appeared in the inlet area June 20, at this time the surface water temperature of the inlet area at mid-day was 17.8°C.

Distribution of fish in the creek was determined by almost daily underwater observations during the spawning period. Observations were made at selected points in the lower part of the creek between the bridge and the lake (Fig. 1). On one occasion the entire creek from Issitze Lake to Wolfe Lake was examined. Gillnets were set in the creek throughout the spawning period. Due to the rapid current, these were not fully effective and permitted most fish to pass. (Fish observed between two nets were often seen to leave the area without being caught in either net.)

By June 23 chiselmouth were up to 91 m upstream from the lake, in the inlet creek. By June 26 fish had reached the ford and few or none went beyond this point. Observations of tagged fish indicated that once in the creek the fish probably remain several days, sheltering under brush piles and log jams.

The spawning migration of Acrocheilus is much more extensive than that undertaken by the other cyprinids in the lake. Both Ptychocheilus and Mylocheilus move only about 700 m upstream. The majority of the redside shiners spawn in the riffles near the lake. These cyprinids as well as C. macrocheilus spawn slightly before Acrocheilus. By July 9 fish were being caught in all parts of the lake again.

Chiselmouths in both Wolfe and Missezula Lakes did not spawn until the water temperature was approximately 17°C in 1965 and also in 1964 in Missezula Lake. This compares with minimal known spawning temperatures of 12.2°C for R. balteatus, 4.5°C for M. caurinus, and 14.0°C for P. oregonense (C. C. Lindsey, pers. comm.).

Eggs of Acrocheilus were found in two locations in the inlet to Wolfe Lake. At the upstream site, only a few scattered eggs were seen. Judging by the color, some of these were probably chiselmouth eggs. At the lower site, a large number were found at the downstream end of a narrow pool about 9 m long, 3 m wide and 75 cm deep. Water depth over the eggs was about 30 cm. One side of the pool was lined with a large tangle of dead branches and trees, the other side was a sandy bank. The eggs were adherent to a rock about 5 cm in diameter and to smaller (1 cm) stones. The bottom of the stream was devoid of macroscopic organic material either living or dead.

The egg mass was quite compact and was completely covered by a layer of 7.5 - 10 cm rocks. How the eggs are deposited in such a location is unknown. The extent to which R. balteatus fed on exposed eggs indicates that eggs deposited on the open bottom would have a low survival rate.

The eggs were eyed when discovered and the surrounding gravel contained many hatched larvae. When exposed to light and current, the larvae attempted to wriggle down into the gravel.

About 100 eggs from the lower site were sent back to the laboratory for rearing. Of these, 80 grew to an identifiable size; 14.3% of these were chiselmouths, the remainder were squawfish.

Actual spawning of Acrocheilus was not seen. Extensive observations were made, totalling many hours, both above and below the surface. As long as the observer did not approach any closer than 2 m, the fish did not seem disturbed.

Feeding and current-oriented behavior was noted but no behavior of a reproductive nature was seen. The conclusion must be either that *Acrocheilus* will not spawn when an observer is nearby, or else, as was the case with *R. balteatus* in Wolfe Lake, chiselmouths spawn at dusk or in the dark.

The mean egg count for 6 chiselmouths was 6200. This compares with a range of 5000 to 53,000 for *Ptychocheilus* (Cartwright, 1956).

Eggs when laid are a distinctive golden yellow color. Chiselmouth eggs obtained by stripping the parents hatched in the laboratory in 16 days at 12°C and in 6 days at 18°C, slightly warmer than the creek temperature at spawning time. Eggs reared at 12°C all died within 35 days of fertilization. At hatching the larvae are about 8.1 mm long. The yolk is orange-gold and elongate, running back to the anus. Chromatophores are present dorsally from between the eyes to a point midway between the dorsal fin fold and the anus. A row of chromatophores also runs along the line where the body meets the yolk sac. The following characteristics were observed which serve to differentiate *Acrocheilus* larvae from those of *Ptychocheilus*, the only other cyprinid likely to be spawning at the same time and place as *Acrocheilus* in Wolfe and Missezula Lakes:

- Blood in the heart of *Acrocheilus* is vermillion, as opposed to crimson in *Ptychocheilus*.
- *Acrocheilus* has more melanophores in the anterior-dorsal region.
- The yolk sac of *Acrocheilus* is longer, wider, rounder and reaches further forward than that of *Ptychocheilus*.
- The yolk of *Acrocheilus* is orange-gold, that of *Ptychocheilus* pale yellow.

Once the yolk has been absorbed, it is impossible to differentiate larvae of *Acrocheilus* from those of other cyprinids, until they reach a size of about 15 mm. At this size, the fish may be stained with alizarin and the fifth pharyngeal arch removed for identification by tooth count.

The pectoral fins appear very early in development, the pelvics much later. Primordia of the pelvic fins appeared in laboratory reared fish at 47 days, at 18°C. The median fin fold is still present at 63 days at this temperature.

The characteristic short, downcurved mouth does not begin to appear until the fish reaches a size of about 15 mm.

In Missezula Lake the inlet stream is cold (10.5°C) in mid-summer. Only Oncorhyncus nerka is known to spawn there. Acrocheilus spawns in an area of the lake just above the outlet. As in Wolfe Lake, chiselmouths become rare in their usual habitat during the breeding season and become concentrated in the spawning area. In two years, ripe fish have been found only in this part of the lake.

The actual area where eggs were deposited was not found. Acrocheilus were frequently observed under dense submerged and over-hanging bushes, a location in which they were never found during the non-reproductive season. Water depth in this region was 25 - 100 cm, the bottom resembled that of the spawning area in Wolfe Lake, being clean and composed of rocks from 1 - 15 cm in size. Except for the near absence of a current in the Missezula Lake spawning area, it was similar to that of the spawning area in Wolfe Lake.

Issitze Lake, above Wolfe Lake, was visited June 30, 1965, while spawning was taking place in Wolfe Lake. The inlet stream was much colder than that of Wolfe Lake, however ripe individuals of R. balteatus, P. oregonense, M. caurinus, and C. macrocheilus were found in the stream, presumably spawning. Acrocheilus was not found here nor in the lake proper. Chiselmouths were seen in the outlet stream, however, which was much warmer (17°C). Chiselmouths, adult and juvenile, were present for about 180 m downstream. It is probable that spawning occurs in the outlet. Acrocheilus was later found in the lake in September.

An observation by J. D. McPhail (pers. comm.) at Omak Creek, Washington, indicates that river populations of Acrocheilus may utilize small tributaries in which to spawn.

FOOD AND FEEDING

This aspect of the study was given special emphasis since it was considered that the unusual lower jaw of the species might be accompanied by special ecological requirements.

The Method of Feeding of Acrocheilus

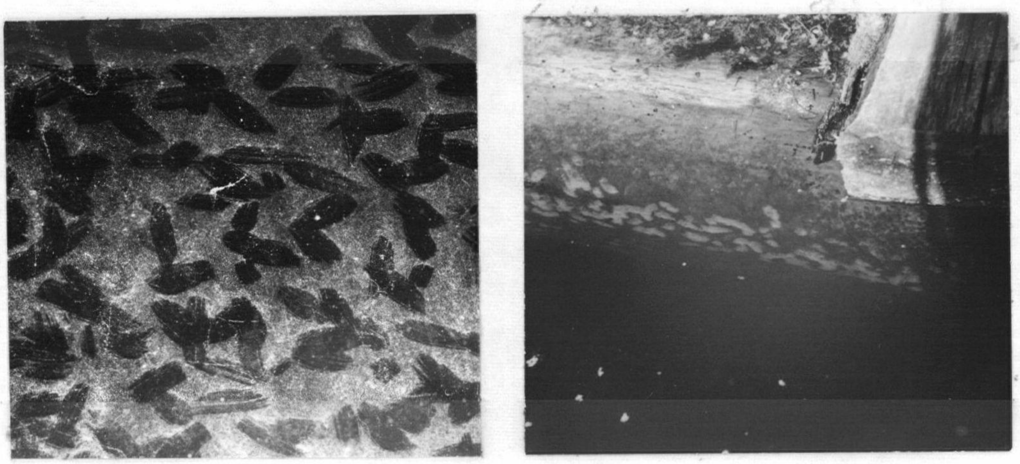
Observations in the laboratory and the field revealed that the sharp lower jaw of the adult chiselmouth is used as a scraper to remove Aufwuchs from the substrate.

When feeding in the large aquarium in the laboratory, the adult chiselmouth swims about 10 - 15 cm above the substrate. The tail is then flicked powerfully, the head is lowered and the fish slides its open lower jaw along the substrate (Fig. 6). The distance the jaw travels while scraping is short, about 2 - 2.5 cm. The fish usually swims about briefly before repeating the procedure. Only rarely did the fish scrape the substrate for a distance greater than that given above. When such prolonged scraping occurs, the fish swims along and works the upper and lower jaws together in what resembles a nibbling motion. Fish fed from vertical, horizontal surfaces of the aquarium as well as from large rocks. In all cases, the manner of feeding was similar. In the case of vertical surfaces, the fish approached the surface head-on, then tilted the body head upward to about a 45° angle before making the typical feeding movement. Alternatively, the fish would swim parallel to the vertical surface and then roll on its side to scrape.

In all cases, the feeding scrape is accomplished by a sudden flick of the tail which propels the fish against the substrate with considerable speed and results in some Aufwuchs being removed from a short section of the substrate.

In the inlet creek of Wolfe Lake chiselmouths were observed feeding in a manner quite similar to that seen in the laboratory aquarium. The fish in the creek, which were adult spawners, were continuously swimming to maintain their

Figure 6. An adult chiselmouth beginning to feed. Note feeding scrapes in the algal mat.



A B

Figure 7. Marks produced by a chiselmouth feeding on algae; A in the laboratory with algae growing on the glass about $\frac{1}{2}$ natural size. B in Wolfe Lake with the algae growing on a smooth log, about 1/10 natural size.

position; feeding therefore was intermittent. The fish would dart toward the creek bed about 10 cm beneath it, scrape material from the substrate and then resume its position-maintaining activity.

Figure 7 shows scraping marks made by *Acrocheilus* in the field and in the laboratory aquarium. A log in the creek was seen which bore many scrape marks. The log formed a spillway at a constriction in the creek, thus the velocity of the water going over it was high. It is noteworthy that *Acrocheilus* can feed in such an environment.

The Time of Feeding of *Acrocheilus*

Due to the difficulty of catching fish during daylight, it was not possible to get enough stomachs for this time period to make a reliable estimate of time of feeding. The low catch rates during daylight are thought to be a result of visual net avoidance rather than sedentary behavior during the daylight hours. This belief is supported by the fact that in turbid Wolfe Lake, the daytime catch rate was much higher than in clear Missezula Lake.

On the basis of brain morphology and the method by which *Acrocheilus* feeds, it seems very likely that it is a daylight feeder. Miller (1965) showed that in catostomids different types of feeding behavior may be correlated with development of different areas of the brain. The configuration of the brain of *Acrocheilus* resembles that figured by Miller of a visually oriented cyprinid. This is to be expected in view of the fact that *Acrocheilus* appears to locate its food visually.

The Diet of *Acrocheilus*

The diet of *Acrocheilus* was examined in the river and the lake in order to see whether the same food was utilized, and to find out whether there was any appreciable overlap in the diet of *Acrocheilus* and of other cyprinids and catostomids in the lake.

The diet of the chiselmouth changes with age (Figs. 10 and 11). No digestive tracts were examined between the stage after absorption of the yolk and a length of 20 mm. From 20 - 100 mm the chiselmouth eats large amounts of insects. Beyond 100 mm *Acrocheilus* eats plant material, chiefly filamentous algae, the percentage of which steadily increases with age (Figs. 9, 10, 11).

The change in diet can be correlated with the development of a coiled gut and a square, sharp-edged lower jaw, which becomes more pronounced with age (Fig. 8).

The Digestion of Plant Material by *Acrocheilus*

It can be seen from Tables III and IV that plant material is an important component of the diet of *Acrocheilus*. It was of interest to learn whether *Acrocheilus* is able to digest this material.

In nearly all the fish examined which contained plant material, eg. filamentous algae, it was noted that there was little or no evidence of digestive breakdown. Algae near the rectum was of the same color and condition as that at the anterior end of the stomach. The cellular contents of algae near the rectum were indistinguishable from those in the stomach.

Tests for cellulose (M. S. Weintraub, pers. comm.) were made on algae from the stomach, midgut, and hindgut. In all cases, there was no detectable reduction in the amount of cellulose along the length of the gut. In the absence of cellulose digestion, the fish would have to physically rupture the cell wall in order to utilize the cell contents. There was no evidence that this was done ~~by~~ to any significant extent.

It must be concluded then, that *Acrocheilus* derives little or no nutrition from filamentous algae, in spite of its abundance in the digestive tract.

Diatoms, which are on the average taken in volume equal to filamentous algae, are probably the chief source of nutrition. The cell wall of diatoms, although itself indigestable, contains minute pores which expose the cell contents

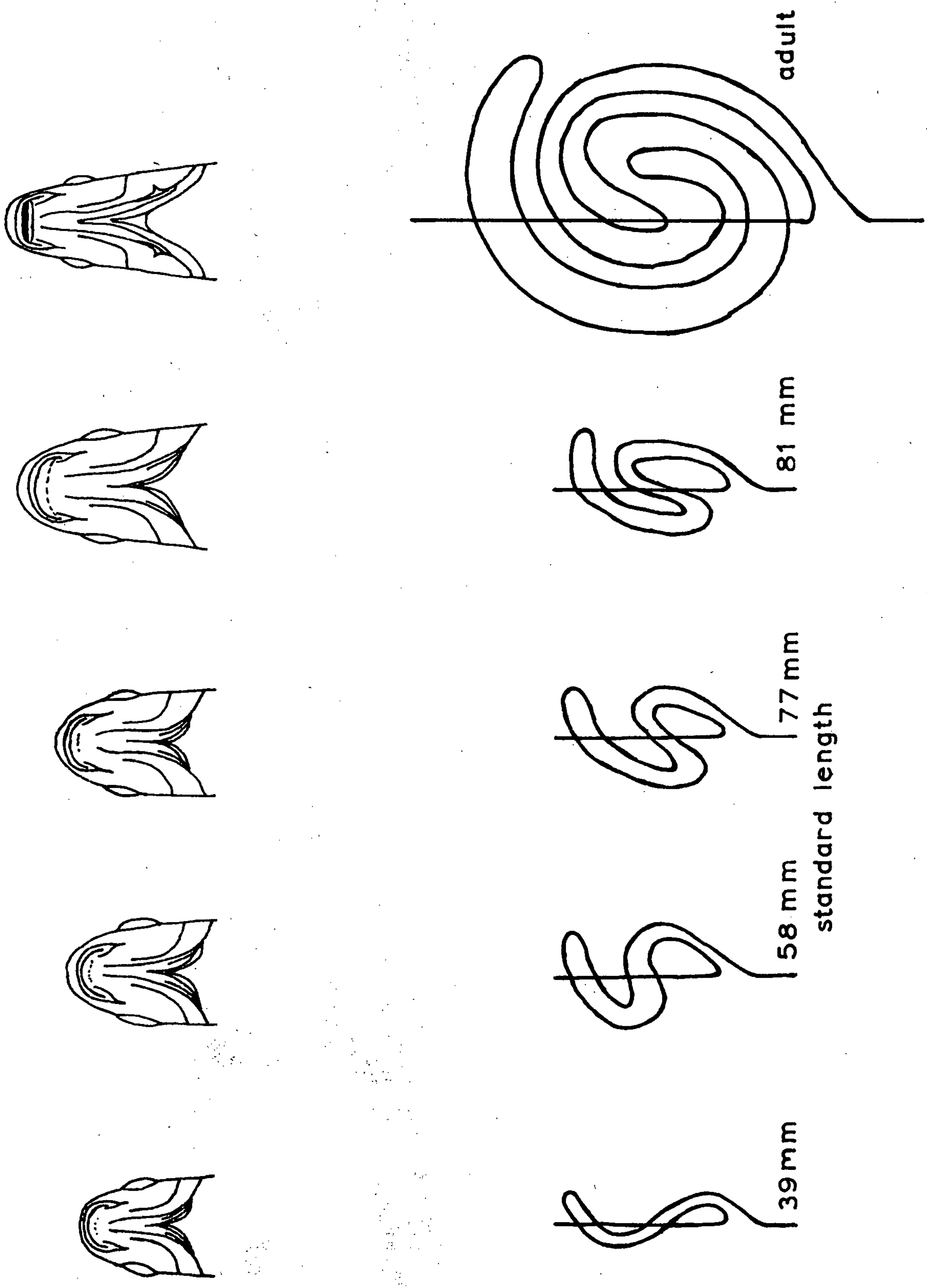


Figure 8. The ontogeny of the lower jaw and of the coiling of the intestine of Acrocheilus. Drawings are not all to the same scale.

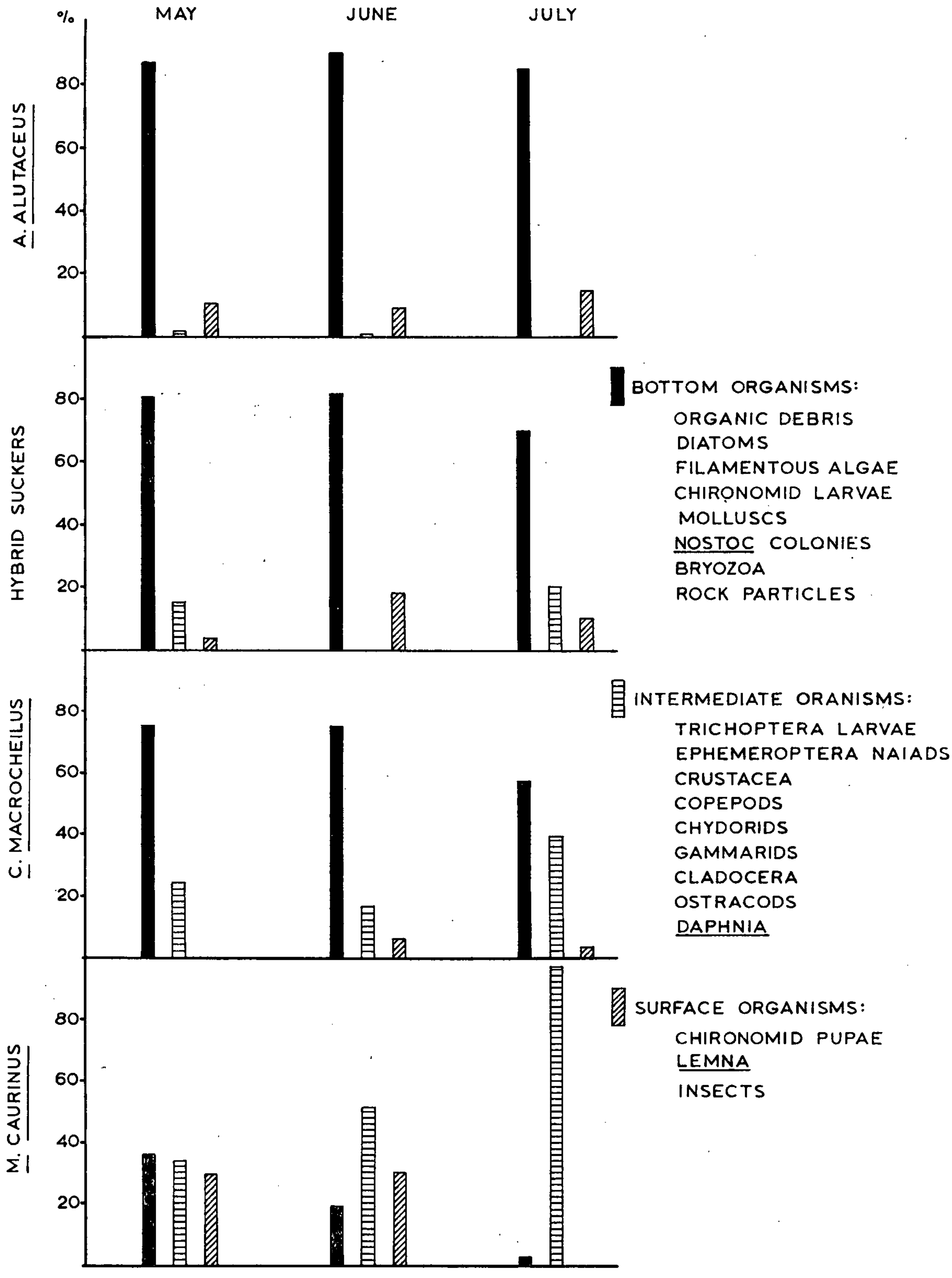


Figure 9. The diet of A. alutaceus, M. caurinus, C. macrocheilus, and hybrid suckers in Wolfe Lake. Vertical axis indicates the percent composition of food in the guts using the point method of analysis.

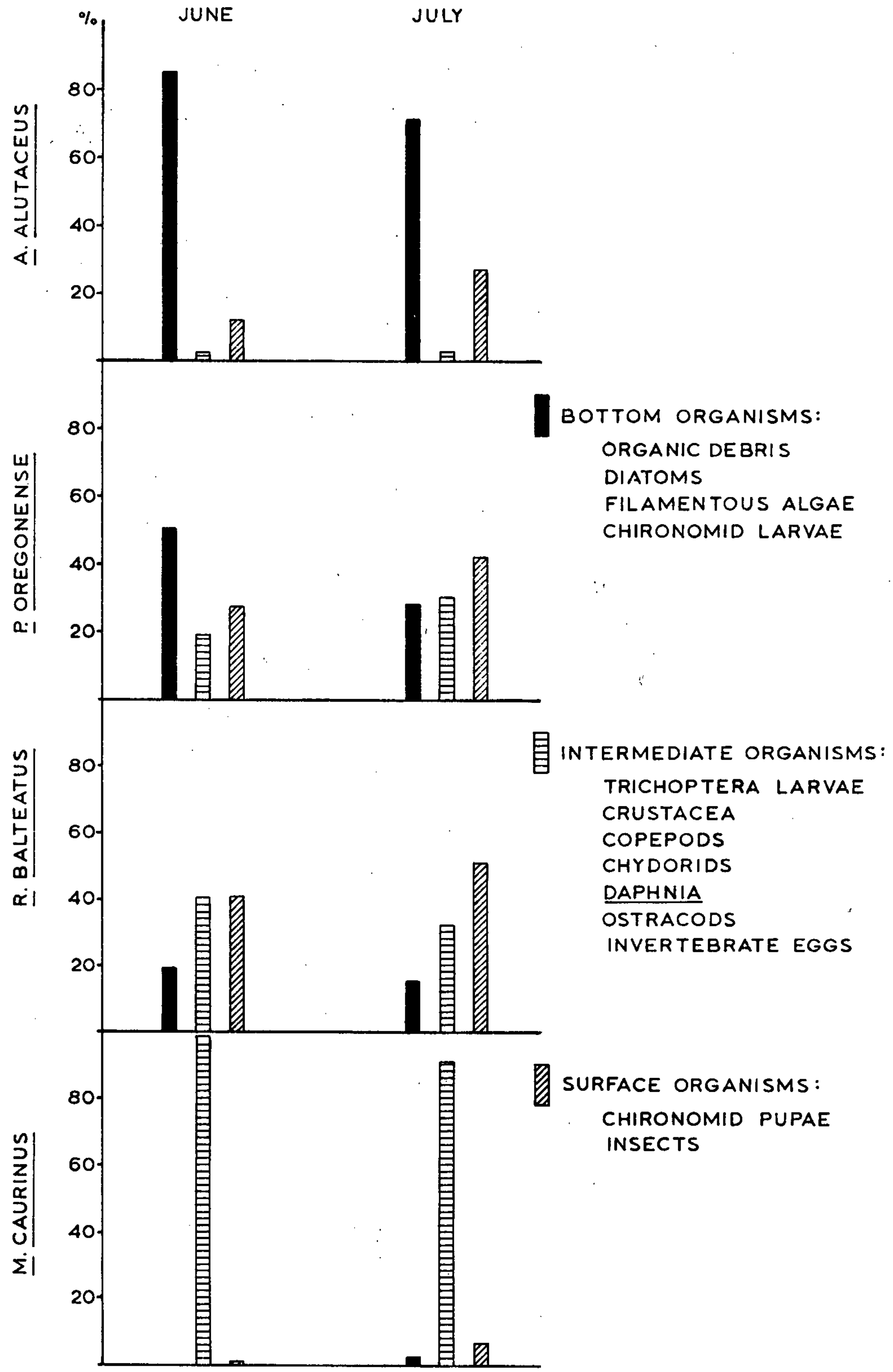


Figure 10. The diet of juvenile A. alutaceus, M. caurinus. P. oregonense, and of both adult and juvenile R. balteatus in Wolfe Lake. Vertical axis indicates the percent composition of food in the guts using the point method of analysis.

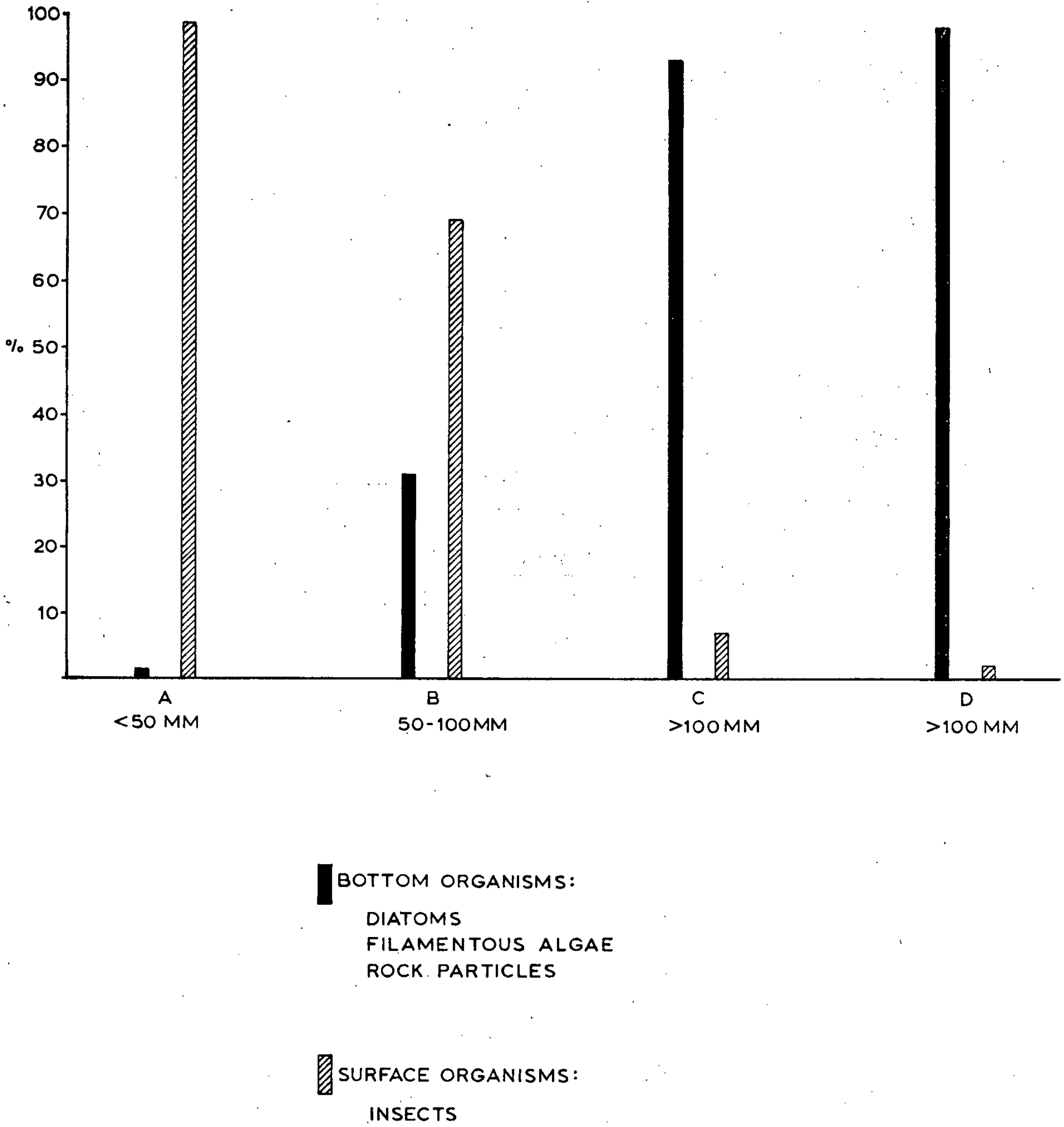


Figure 11. The diet of adult and juvenile A. alutaceus in the Okanogan River, August 4 - 6, (A, B, C), and of adults in the inlet stream of Wolfe Lake during the spawning period (D). Vertical axis indicates the percent composition of food using the point method of analysis.

Table I. The number of different items eaten by adults of a given species in Wolfe Lake which are not eaten by any other species compared to the number of items eaten which are also eaten by other species. Based on data of Tables III and IV. "S" indicates food items shared by more than one species. "U" indicates items eaten only by that species.

	A. alutaceus		*C. macrocheilus*		*M. caurinus*		Hybrid suckers	
	S	U	S	U	S	U	S	U
May	7	2	5	3	8	1	9	0
June	6	2	6	3	6	2	5	0
July	6	2	6	4	2	3	6	0

Table II. The average amount of food in the stomachs of adult *A. alutaceus* in Wolfe Lake, from May through July, and in the Okanogan River, August 4 - 6, 1965. Numbers indicate precent of total stomach capacity. n = sample size.

	May	June	July	August
	86.1	61.2	43.1	55.4
n =	42	60	77	44

Table III. The diet of A. alutaceus, hybrid suckers, C. macrocheilus and M. caurinus adults in Wolfe Lake. Numbers indicate percent composition of food items in the gut, using the occurrence method of analysis

	A. alutaceus			Hybrid suckers			C. macrocheilus			M. caurinus		
	May	June	July	May	June	July	May	June	July	May	June	July
Organic debris	21.3	27.0	22.9	23.8	29.4	22.2	42.8	36.6	28.6	9.7	25.0	
Diatoms	29.0	30.4	23.9	23.8	29.4	27.8	28.6	31.7	14.3	11.0	6.2	16.0
Filamentous algae	25.1	25.9	28.7	14.3	23.5	17.1			11.3			
Lemna	10.9	4.1	1.1							17.1	12.5	
Rock particles			1.6	4.8	5.9	11.1				1.2		
Insects	3.8	3.5	2.6	9.5		5.5		4.9	5.7	14.6	12.5	
Chironomid larvae	6.5	2.8	9.6	9.5		11.1		4.9	5.7	14.6		
Chironomid pupae	1.6	2.8	9.6									
Trichoptera larvae	0.6	1.2										
Ephemeroptera naiads	1.1										3.6	6.2
Crustacea					5.9		1.4	2.4	5.7			6.2
Copepods							8.6					
Chydorids				4.8			5.7	7.3	14.3			
Grammarids				4.8	5.9		4.3	2.4		26.8	25.0	4.0
Cladocera							7.1	7.3	5.7			[illegible]
Ostracods				4.8			1.4					
Daphnia						11.1		2.4	5.7			72.0
Fish eggs												4.0
Molluscs											6.2	4.0
Bryozoa									2.8			
Nostoc colonies										1.2		
Sample size	55	64	77	7	10	15	30	18	17	37	16	27

Table IV. The diet of A. alutaceus, Hybrid suckers, C. macrocheilus and M. caurinus adults in Wolfe Lake. Numbers indicate percent composition of food items in the guts using the point method of analysis

	A. alutaceus			Hybrid suckers			C. macrocheilus			M. caurinus		
	May	June	July	May	June	July	May	June	July	May	June	July
Organic debris	24.5	24.3	17.5	24.2	17.4	12.1	61.5	53.9	30.0	17.1	15.0	
Diatoms	32.1	34.8	22.5	32.8	39.4	35.6	13.9	16.0	14.8	7.1	2.0	1.7
Filamentous algae	27.1	28.0	33.2	18.0	22.9	10.1			2.0			
Lemna	9.3	4.3	0.2							9.4	19.0	
Rock particles			0.8	11.6	1.8	5.4				1.4		
Insects	0.9	3.0	2.0	3.9		10.1		3.3	3.7	20.1	11.0	
Chironomid larvae	3.8	2.9	11.3	3.9		6.7		4.9	2.0	10.0		
Chironomid pupae	0.4	2.0	12.4									
Trichoptera larvae	0.1	0.7										
Ephemeroptera naiads	1.7									3.6	3.0	
Crustacea					0.9		2.9	1.6	0.8		14.0	
Copepods							11.3					
Chydorids				0.8			3.2	9.8	23.9			
Gammarids				8.6	17.4		4.6	2.6		30.8	34.0	3.1
Cladocera							1.7	5.5	2.0			
Daphnia						20.1		1.3	12.3			93.8
Ostracods				6.2			0.5					
Fish eggs												0.3
Molluscs											2.0	1.5
Bryozoa									8.2			
Nostoc colonies												
Sample size	55	64	77	7	10	15	30	18	17	37	16	27

Table V. The diet of juvenile *A. alutaceus*, *M. caurinus* and *P. oregonense* and of both juvenile and adult *R. balteatus* in Wolfe Lake, June through July, 1965. Numbers indicate the percent composition of food in the guts, using the point method of analysis

	A. alutaceus		*M. caurinus*		*P. oregonense*		*R. batteatus*	
	June	July	June	July	July	July	June	July
Organic debris	14.2	27.5			3.5	3.0	3.3	4.0
Diatoms	4.4	18.2		2.5	3.3		4.0	2.7
Filamentous algae	1.6	9.9			1.1		1.0	
Insects	5.6	21.5	1.2	6.2	19.1	34.0	26.3	37.3
Chironomid larvae	65.2	15.5			42.9	25.0	7.3	
Chironomid pupae	6.8	5.1			8.8	8.0	14.3	
Trichoptera larvae					2.2			
Crustacea			18.1					
Copepods			9.4	6.2	4.2			
Chydorids		2.3	41.9	18.7	3.1	30.0	8.7	16.0
Cladocera				6.2				
Daphnia				57.5			30.0	16.0
Ostracods	2.2		29.4	2.5	9.7		1.7	13.3
Invertebrate eggs							3.3	10.7
Sample size	35	33	13	7	34	12	12	10

Table VI. The diet of *A. alutaceus* in the Okanogan River, August 4 - 6, 1965. Numbers indicate percent composition of food in the guts, using the point method of analysis.

	Fork length		
	50 mm	50 - 100 mm	100 mm
Diatoms	0.8	22.1	48.9
Filamentous algae	0.6	5.8	30.6
Rock particles		3.9	14.5
Insects	98.6	69.1	6.6
Sample size	19	11	49

The diet of adult *A. alutaceus* in the inlet stream of Wolfe Lake during the spawning period, 1965.

Diatoms	30.2
Filamentous algae	47.2
Rock particles	10.2
Insects	0.8
Organic debris	10.7
Lemna	0.8
Chironomid larvae	0.1
Sample size	13

to the environment. Because of this construction, digestive enzymes in the gut of Acrocheilus have ready access to the cell contents. That this occurs in Acrocheilus is evidenced by the fact that diatoms in the stomach usually contained their cell contents, while diatoms in the hindgut consisted only of empty frustules (shells). This diet is very similar to that of Tilapia esculenta, which feeds on planktonic filamentous algae and diatoms but digests only the diatoms (Fish, 1951).

The diatoms were virtually all of the Pennate group. Diatoms consumed by Acrocheilus were always associated with filamentous algae upon which they are epiphytic. This was not necessarily the case with diatoms eaten by other species.

"Organic debris" referred to in Tables III, IV, V, and VI, is a general term used to indicate a variety of material which could not be positively identified. It is thought, on the basis of microscopic examination, to consist to a large extent of unicellular algae, and protozoa, and to a lesser extent of oil droplets, cell contents of digested diatoms and bottom sediments. The bulk of it is probably epiphytic flora and fauna associated with filamentous algae. Its nutritive value is unknown.

"Insects" referred to in Tables III, IV, V, and VI, includes primarily adult winged forms which had been ground by the pharyngeal teeth to such an extent that they could not be further identified.

Lemna was apparently taken deliberately by both Acrocheilus and M. caurinus, however it did not undergo noticeable digestion in either species.

The diets of the species examined are shown in Figures 9, 10, and 11 and Tables III, IV, V, and VI. The importance of an item in terms of its percent contribution to the total food volume of the sum of all guts examined is given on the vertical axis. Figures 9, 10, and 11 are based on data obtained by the points method of analysis. Differences in the values obtained using the two methods of analysis are probably due either to small sample sizes in a few cases, or to difficulty in estimating relative volumes of many small organisms, especially when the organisms are intermingled. As Hynes (1950), Thompson (1959), and others have noted, no method of gut analysis is free from subjectivity. As the size of the gut decreases, the problems are compounded. Hynes also notes that as the sample size increases most of the different methods give comparable results.

In this study the two methods gave comparable results in most cases, at least in terms of relative abundance of the major items.

For future discussion certain comments can be made at this time about the food items.

Diatoms, organic debris, and filamentous algae if present in a species can be considered to have been taken as a single item. The first two items are almost never found separately, and algae if present is with the diatoms and debris. The remainder of the items show much more independence of each other.

It can be seen from Tables III and IV, that adult _A. alutaceus_, _C. macrocheilus_, _M. caurinus_ and hybrid suckers in many cases feed on the same items. The number of items eaten only by a single species is fairly low in all cases. _Acrocheilus_ "shares" all of its major food items (with one exception in July). Hybrid suckers "share" all items. It appears that their trophic specialization has been lost as a result of hybridization. _Acrocheilus_ does not show the tendency displayed by _C. macrocheilus_ and _M. caurinus_ to increase the number of unshared items as the summer progresses (Table I). _P. oregonense_ adults were excluded from the study since they are primarily piscivorous (Thompson, 1959). A few _Ptychocheilus_ stomachs examined at Wolfe Lake confirmed this.

Figure 10 and Table V shows the diet of juvenile _Acrocheilus_, _M. caurinus_, _P. oregonense_, and both juvenile and adult _R. balteatus_. Juvenile _C. macrocheilus_ were excluded because their diet is very similar to that of the adults (as determined by the examination of a few stomachs).

There is little selection of different food items by the different species (Table V). Nearly all items are shared. The major food items of young chiselmouths are often also the major food items of young P. oregonense and of all ages of R. balteatus.

The data from the river population were collected over a short (3 day) period and from only two locations. This introduces the possibility of having made the collection during a period of peak abundance of a particular food item, such as insects. However, small samples from other rivers suggest that the limited number of items found in the guts of Okanogan River fish is not atypical (Fig. 11, Table VI).

Adult chiselmouths caught in the inlet of Wolfe Lake during the spawning migration in June and July, 1965, also showed a narrowing of the diet, in spite of the fact that part of the sample was known to include fish which had fed in part in the lake (Fig. 11). The guts of some of these fish contained items found only in the lake.

It thus seems valid to conclude that in the Okanogan River, and perhaps in rivers in general, Acrocheilus has a much more restricted diet than it does in Wolfe Lake. It is noteworthy that the diets of young chiselmouths in both the river and the lake were similar, in that insects and Chironomids were more important food items than was plant material.

THE ABUNDANCE OF ACROCHEILUS RELATIVE TO PTYCHOCHEILUS IN RIVERS AND LAKES

Since there may be some interaction occuring between Acrocheilus and Ptychocheilus (because of the similarity in the diets of the juveniles and the spawning area of the adults), it is of interest to examine the relative density of the two species in the two kinds of environments (Table VII).

In Wolfe Lake, accurate counts of Acrocheilus and Ptychocheilus were not obtained, however it can safely be said that Ptychocheilus well outnumbers Acrocheilus.

Table VII. The ratio of A. alutaceus to P. oregonense in lakes and rivers

Location	A. alutaceus	P. oregonense
Vidette Lake, B. C.	122	23
Missezula Lake, B. C.	246	96
Yakima River, Wash. (Patten, 1960)	2000	4260
Okanogan River, Wash.	<10	70

In the lower Columbia River, Thompson (1959) shows that Acrocheilus is the most important cyprinid food item of Ptychocheilus.

On the basis of the above, and of data in Table VII, it is suggested that Acrocheilus , when in rivers, frequently outnumbers Ptychocheilus, while in lakes the reverse occurs.

DISCUSSION

In this discussion the disjunct distribution and local rarity of Acrocheilus will be examined in terms of certain ecological adaptations of the species.

The present distribution of the species can be explained as follows. After withdrawal of the Wisconsin ice sheet from British Columbia, Acrocheilus probably entered the Fraser drainage via the Okanogan River, in whose tributaries it is now most common in British Columbia. Access to the Fraser was possible via a temporary post-glacial lake which connected the Nicola and Similkameen watersheds. At a later date access was again possible via the Salmon River connecting the same lake to the Okanogan system. Further retreat of the ice sheet resulted in establishment of the present drainage of the Nicola basin into the Fraser system. At a later date, access to the Fraser again resulted from the drainage of a different lake situated in the Thompson basin and draining via the Salmon River into the Okanogan River. Again, further retreat of the ice exposed lower outlets to the Fraser system (Mathews, 1944).

Acrocheilus had continuous access to the Malheur system in Oregon via the Malheur River which emptied into the Columbia. Relatively recent volcanic activity blocked off this river and isolated the entire Malheur drainage (Snyder, 1908).

The distribution of Acrocheilus over its range can be correlated with the effects of glaciation. *Acrocheilus* is most abundant and widespread in warm streams with moderate current and a fairly rich bottom flora. This is in contrast to the so-called "typical trout stream", having a fast current and low temperature and productivity. As a result of recent glaciation in British Columbia, streams which favor *Acrocheilus* are rare and the trout type of stream predominates. In unglaciated mid-Washington and Oregon, slower, warmer streams are more common, and so is *Acrocheilus*. Although northern Washington, where *Acrocheilus* is common, was glaciated at the same time as British Columbia, the topography of the land is more like that of the unglaciated region to the south, probably because the duration of glaciation was less there than to the north.

While the chiselmouth does occur in lakes, this is not common according to the literature, and such populations are small relative to those of other cyprinids present. *Acrocheilus* seems to occur in lakes most often in British Columbia, probably as a result of the absence of suitable streams.

There are several reasons for believing that *Acrocheilus* is primarily adapted to a riverine as opposed to a lacustrine habitat. First, as has just been noted, *Acrocheilus* is most abundant in rivers, and river populations are denser than are lake populations.

The manner in which *Acrocheilus* feeds is clearly adapted to scraping Aufwuchs from a smooth substrate. Because of sedimentation in a lake there may be fewer suitable sites for the attachment of Aufwuchs. In contrast, river beds with current-swept bottoms often composed of stream-rounded smooth rocks provide a most suitable substrate both for the attachment of filamentous algae and for scraping by the cheselmouth.

In the large aquarium in the laboratory, a variety of different species of filamentous algae became established on the glass over an 18 month period, while no algae grew either on the mud or sand bottom.

Finally, an examination of the habitats of species with mouth modifications and diets similar to those of Acrocheilus supports the conclusion that a scraping mouth is especially adapted to a riverine habitat. The Eurasian Cyprinid genus Chondrostoma contains six species and several subspecies. All of these have a lower jaw which closely resembles that of Acrocheilus; in some cases, the similarity is striking. Berg (1948) lists the habitats of all species as riverine. G. V. Nikol'skii (pers. comm.) states that the diet of Chondrostoma is algae which is obtained by scraping from flat rocks in the stream bed.

A similar example is the Japanese salmonid, Plecoglossus. The mouth morphology of this fish is quite different from that of Acrocheilus, nevertheless it does have a blunt lower jaw which it uses to scrape algae from rocks. This fish also lives in rivers.

The habitats occupied by Acrocheilus in the lake and the river are very different. In the Okanogan River, Acrocheilus was widely distributed over the bottom, apparently in accordance with the distribution of food. In Wolfe Lake, as in most lakes, the food supply for a herbivorous fish is limited to a narrow photic zone around the margin of the lake. It is likely that within this area the amount of food available to Acrocheilus is limited by the amount of suitable substrate for the growth of algae and scraping by the fish. In Wolfe Lake, only sunken trees and branches appeared to provide such a substrate.

It is likely then, that a lake environment will support fewer chiselmouths than will a river environment of equal area. This will be further referred to when competition is considered.

If it is accepted that Acrocheilus is less well adapted to lakes than to rivers, this will provide a partial explanation for the unusual distribution and abundance of the species. First, if there are few suitable streams it will be uncommon. Secondly, when it occurs in lakes it will remain at a low density because less useable food is available than in rivers.

An additional mechanism by which Acrocheilus might be excluded from otherwise suitable environments is provided by the observation that the temperature required for spawning by Acrocheilus is higher than that required by the other local cyprinids. Although outlet temperatures of many lakes may reach 17°C, due to warming of surface waters, the outlet stream would be suitable for spawning only if it possessed certain characteristics such as a very slow current to allow the return of the fry to the lake.

The fact that the lake environment may provide fewer food resources for the chiselmouth suggests that intraspecific competition for food may be occurring in Wolfe Lake and possibly other lakes. As has been discussed previously, the chiselmouth is adapted to scraping algae from smooth, hard substrates. Since there are probably few such areas in Wolfe Lake, it is likely that the chiselmouths will be forced to compete for food in these areas. The fact that the diet of Acrocheilus in the lake is much more varied than in the river is good evidence that in the lake Acrocheilus is eating items other than those which it is best adapted to consume. In the absence of samples of species composition of potential food resources in the lake and river, it is impossible to state definitely in which environment a greater choice of items exists. However, there is no reason to assume a less varied flora and fauna in rivers than in lakes. Kendiegh (1961) gives data which indicate that a stream of the sort in which Acrocheilus occurs supported a more varied biota than did several different types of lake bottom. Nilsson (1957) found that Salmo trutta had a more varied diet in rivers than it did in lakes. Thus it is probable that the chiselmouth in Wolfe Lake is eating a varied diet out of necessity rather than choice. That food may be in short supply for the adult chiselmouth in Wolfe Lake is evidenced by the fact that as the summer progressed the diet became slightly more specialized. Nilsson (1960) found that seasonal specialization was characteristic of situations where food was limiting. This may also be related to the decrease in average fullness of the stomach of Acrocheilus from May to July, 1965 (Table II). Finally, competition for food may be the explanation for the reduced growth rate in Wolfe Lake compared with the growth rate in the Okanogan River. Chiselmouths from the Okanogan River also contained large fat deposits on the viscera, while fish of the same size, age and sex in Wolfe Lake only very rarely had such deposits.

A reduction in maximum size attained as a result of a reduced growth rate may reduce the fecundity of the fish (Peppar, 1965) thus resulting in one more potential factor limiting the population density in the lake.

The overlap in the diet of Acrocheilus and of the other species examined in Wolfe Lake, together with the fact that Acrocheilus seems to be feeding on items other than those it is primarily adapted to consume, suggest that interspecific competition for food may be occurring.

Larkin (1956), in a review of interspecific competition in freshwater fishes, concludes that freshwater fishes have a wide tolerance of habitats, and a flexibility of feeding habits and, because of this plasticity, species are in general able to share many resources. Fryer (1959) has since shown that in the tropics, freshwater fishes are usually very specialized. Thus Larkin's conclusion should be restricted to fishes in temperate regions only. Even in temperate areas, where there is interspecific overlap of diet for example, species have certain optima to which they are best adapted. When two similar species are sympatric and one or both is displaced from its optimal requirements, such things as a reduced growth rate or population density may result (Nilsson, 1958; Carlander, 1955).

Thus, while fishes often have broad diets and can tolerate some overlap, they are specialized to the extent that they can only show maximal growth rate and standing crop when they are not sympatric with other species having the same food or other requirements.

Before discussing competition involving _Acrocheilus_, competition among herbivores in general must be considered. Mayr (1963) states that generalized herbivores are not usually food limited. Instead, disease, and predation serve as controls of population size.

There are a number of reasons why this may not apply to _Acrocheilus_ when it occurs in lakes.

It has already been shown that the chiselmouth is specialized, both in terms of diet and method of feeding. Thus _Acrocheilus_ is not a generalized herbivore.

Diseased chiselmouths were never seen in the field, but it was noted previously that _Acrocheilus_ is extremely susceptable to disease following injury of any sort. It is unlikely though, that disease would hold all chiselmouth populations in British Columbia at the same low density at the same time and for so long.

The significance of predation as a mechanism regulating population density in lakes is an open question.

In the discussion of competition between _Acrocheilus_ and other species to follow, it must be remembered that in the absence of data concerning whether or not a given environmental resource is limited, all that can be done is to show why _Acrocheilus_ would be the species most critically affected if a resource such as food were to become limiting in the lake.

The only fish which would appear to be in direct competition with _Acrocheilus_ are the hybrid suckers. Due to the low numbers of these fish in the lake, they can not be considered serious competitors for the food of _Acrocheilus_. The similarity of diet of the two kinds of fish is probably related to the fact that the lower jaw of the hybrids has a scraping edge similar to that of the chiselmouth.

Although the diet of _C. macrocheilus_ partially overlaps that of

Acrocheilus, it is unlikely that these two species feed in the same microhabitat. This conclusion is based on the fact that while the major components of the diet were similar in the two species, minor components which were very likely consumed along with the major components, were different. Unlike Acrocheilus, C. macrocheilus probably feeds on soft substrates such as sediment and detritus deposits. While feeding on the same thing in different microhabitats does not necessarily prevent competition, it could in cases such as this where the ability of items such as filamentous algae and diatoms to disperse is low.

M. caurinus is primarily a crustacean feeder. At times, however, it feeds on the same items as Acrocheilus. As in the case of C. macrocheilus, M. caurinus probably feeds in a different microhabitat from that of Acrocheilus.

In summary, neither of the adults of the two more abundant species in Wolfe Lake are in direct competition with the chiselmouth. By feeding in different microhabitats on food items having a slow rate of dispersion, interspecific competition is avoided.

Miura (1961) and others (Nilsson, in LeCren and Holdgate, 1962), have noted that the diets of young fishes of different species often overlap. In Wolfe Lake this occurs with respect to the diets of Acrocheilus and Ptychocheilus, and to a lesser extent, R. balteatus of all ages. Unlike the adults, the juvenile chiselmouth has a similar diet in both Wolfe Lake and the Okanogan River. Since the diet of the young fish is not as specialized as that of the adult, the juvenile chiselmouth in the lake is probably not at the same competitive disadvantage as are the adults.

Mayr (1963) states that when other things are equal and two species occupy the same habitat, the species with the greater fecundity and life span will prevail. In rivers it appears that the greater potential of Ptychocheilus to increase (Cartwright, 1956) is not expressed. In lakes conditions are such that the relative density of the two species is reversed, and Ptychocheilus predominates. It is possible that the large population of juvenile squawfish limit the amount of food available to the young chiselmouths.

Reproduction of Acrocheilus and Ptychocheilus in Wolfe Lake may have been complicated by the rise in water level resulting from damming. Although both species spawn in a part of the stream uninfluenced by the rise in lake level, it is possible that one or both species formerly utilized a more downstream part of the creek or the lakeshore prior to flooding of these areas, since the squawfish is known to spawn on gravel beaches in some lakes (K. W. Stewart, pers. comm.). In any case, the occurrence of eggs of Acrocheilus and Ptychocheilus together indicates that the two species must spawn very close to each other at present. As in the case of competition between juveniles for food, the large numbers of Ptychocheilus may enable it to crown Acrocheilus from the most suitable parts of (d) X the spawning beds. While it is known that the two species also spawn in close proximity to each other in rivers, from the fact that hybrids between the two are known from rivers as well as lakes (Patten, 1960), it is noteworthy that the proportion of hybrids relative to chiselmouths in Patten's large sample was much lower than the same ratio in Wolfe and Missezula Lakes (K. W. Stewart, pers. comm.).

Laboratory observations indicate that the chiselmouth displays aggressive behavior towards individuals both of its own and other species. This may explain at least in part the fact that in the river Acrocheilus was spaced out and other species were rare. In the lake, all species were caught together although the adult chiselmouth did not seem to form any sort of school, suggesting that in both the lake and river the chiselmouth is not gregarious.

In the river, where food useable to Acrocheilus is abundant and other species are apparently at a lower density relative to the chiselmouth, it is possible, in view of laboratory observations, that Acrocheilus is territorial. This is the situation in the algae-eating ayu, Plecoglossus, already mentioned.

In lakes, on the other hand, food is present only in a limited zone around the edge of the lake. Within this zone, food useable to the chiselmouth is probably concentrated in certain areas such as on deadfalls and drowned trees. Other species are also present in abundance. If the chiselmouth behaves towards other species in the field as it does in the laboratory, then the lake environment may subject the fish to considerable stress. Individual chiselmouths will be constantly faced with maintaining distance or territory in the face of frequent interaction with individuals of other species, as well as individuals of their own species seeking what may be a limited food supply.

The environment in the lake may exemplify the classical example of the advantages and disadvantages of territoriality in different environments. In the river, the fish could achieve a net energy gain by defending an exclusive feeding area. In lakes, the "cost" of defence in terms of energy might exceed the energy gained from having an exclusive feeding area.

If the behavioral characteristics of the chiselmouth are not flexible enough to adapt to the lake environment by abandoning territorial behavior, then the fish may be subject to one more debilitating effect.

CONCLUSIONS

The biology of the chiselmouth suggests several possible explanations for the unusual distribution and abundance of the species.

The adaptation of Acrocheilus resulting from the specialized mouth, to a relatively warm, productive riverine habitat, together with the possibility of requiring a warmer temperature for reproduction than other sympatric cyprinids, may explain its limited occurrence in British Columbia's cooler, faster and less productive streams.

The single most important factor regulating population density of

Acrocheilus in Wolfe Lake, and perhaps in other British Columbia lakes, is probably intraspecific competition for food. This results from the fact that the lake presents a limited amount of substrate suitable for both the growth of food useable by *Acrocheilus* and for feeding by the method used by *Acrocheilus*.

Interspecific competition for food may occur between juvenile chiselmouths and squawfish, but since the availability of the food is not known a definite conclusion can not be made.

Interspecific competition for spawning sites by adult chiselmouths and squawfish may also occur.

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