SUMMER ECOLOGY AND BEHAVIOR OF THE GRAYLING OF McMANUS CREEK ALASKA

A THESIS

Presented to the Faculty of the
University of Alaska in Partial Fulfillment
of the Requirements
for the Degree of
MASTER OF SCIENCE

By
Gian L. Vascotto, B.S.
College, Alaska
May 1970

SUMMER ECOLOGY AND

BEHAVIOR OF THE GRAYLING

OF McMANUS CREEK

ALASKA

APPROVED:

George C. West

Judith S. Weeden

James E. Morrow

Chairman

Samuel J. Harbo

Department Head

APPROVED: Brina Kessel DATE: 20 August 69

Dean of the College of Biological
Sciences and Renewable Resources

Vice President for Research
and Advanced Study

ABSTRACT

A study of the summer ecology and behavior of the Arctic Grayling was undertaken on the summer population of McManus Creek, Alaska.

An effort to determine the distribution and the patterns of the fish's movements in the stream was made.

The grayling spent the summer months in pools where they established feeding territories. Within each feeding territory a feeding range, where all feeding activities took place, was found.

In each pool a hierarchial ordering based on a dominant subordinate relationship existed. This hierarchy was established and maintained by a series of displays.

The grayling of McManus Creek were found to feed solely on the surface and at mid-depth. The food items consisted both of flying insects and aquatic insects, the latter making up the largest portion of their diet. It appeared that the fish relied primarily upon benthic drift for nutrition. Being visual feeders, the fish were unable to utilize the large numbers of organisms known to drift during periods of high and muddy water.

ACKNOWLEDGEMENTS

Research on McManus Creek, Alaska, was financed by grants from the Institute of Water Resources Research of the University of Alaska to Dr. James E. Morrow, Professor of Zoology, Department of Biological Sciences.

I would like to express my appreciation to Dr. Morrow, Chairman of my Committee, for his help and guidance throughout the study and for his critical reading of the manuscript. Mrs. Judith S. Weeden, Lecturer in Zoology, Department of Biological Sciences, and Dr. George C. West, Professor of Zoophysiology, Institute of Arctic Biology, critically read the manuscript. Thanks also are due Dr. L. Gerard Swartz, Associate Professor of Zoology, Department of Biological Sciences, who identified a sample of Nematomorphs. Mr. Lynn Boddie, graduate student in fisheries biology, and Mr. Paul J. Frey of the Alaska Water Laboratory contributed to some valuable discussions.

TABLE OF CONTENTS

PAGE

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES

INTRODUCTION

The Arctic Grayling *Thymallus arcticus* (Pallas), is one of the most important game fishes of interior Alaska. Little is known about the life history, ecology and behavior of this species. A survey of the summer movements, distribution, feeding habits and behavior of the grayling made in an interior Alaska, non-glacial stream exposed new facts which could form a base for future studies. The Arctic Grayling is distributed in the Arctic watersheds from the Ob River in Russia east to the Churchill River on Hudson Bay, Athabaska and Churchill drainages in Alberta, and established artificially in a few of the North Saskatchewan river systems (Carl, Clemens, and Lindsey, 1959).

Some grayling survived the last glaciation south of the ice sheet in Michigan where they became extinct in the 1930's, and in the upper Missouri drainage of Montana. Cutting of the forest, and the subsequent scouring of the bottom by the logs decimated the spawning areas, and the stocking of rainbow trout apparently contributed to the extinction of the Michigan grayling (Vincent, 1962).

Thymallus arcticus may reach a length of 20 to 24 inches and weigh from 2 to 5 pounds. It has a very dark back and purplish-gray sides varying in darkness. The belly is whitish with gray blotches. A yellow stripe runs along the ventral side from the pelvic fins to the pectoral fins in adults. The large dorsal fin is long and high, its base longer than the depth of the body. It is dark gray to black and blue in color, punctuated with pink and azure spots and deep blue cross-rows, often bordered with red and yellow. The pelvic fins, abdominal in position, are crossed by three pink stripes. The head is brownish in color, with large eyes, and a small terminal mouth.

Brown (1938b), Leonard (1938), Miller (1946), and Schallock (1965), published notes on the food habits of the fish. They showed that the grayling's diet is made up almost entirely of small insects and aquatic larvae. They suggest that the diet is limited by their small mouth, weak teeth, and cold water habitat.

The Arctic Grayling's habitat has not been extensively studied. In Alaska, the fish is described as inhabiting most of the fast clear streams of the Yukon basin (Evermann and Goldsborough, 1906). In the winter grayling are also reported from the glacier-fed streams which during this season run clear. The grayling are also common in lakes, where some of the largest specimens have been reported. In lakes they favor the mouths of streams and the outlets of the lakes.

Spawning has been observed in Montana (Brown 1938, Nelson 1952, and Tryon 1947) where it is reported to take place between March 15, and June 1 at temperatures below 10° C. The Alaska spawning dates given by Warner (1958) and Reed (1964) are from May 20 to June 25. Wojcik (1955) reports finding ripe individuals between May 13 and June 16. The spawning act is described in detail by Brown (1938a) and Reed (1964). Tryon (1947) and Ward (1951) describe them as polygamous non-nest builders.

The fish produce from 2000 to 4000 eggs, amber in color owing to the presence of oil drops which render them semi-buoyant; their adhesive nature enables them to become coated with stirred-up sand so that they will sink to the bottom (Brown, 1938a). Warner (1958) did not find the eggs adhesive, and reported considerable numbers being washed downstream.

Incubation is complete after two weeks and varies with the temperature of the water. Fry begin feeding on plankton at about the fourth day (Brown and Buck, 1939).

The European species has been studied much more thoroughly, especially in terms of management, and substantial ethological and ecological data have been gathered by Degteva (1965), Egorov (1956), Fabricius and Gustafson (1955), Kafanova (1965), Peterson (1968), Sommani (1953), Starmach (1956), and Svetovidov (1936).

DESCRIPTION OF STUDY AREA

The study was conducted along 18 miles of McManus Creek from its origin near Twelvemile Summit, altitude 3150 feet, to a diversion dam at mile 68, Steese Highway, altitude 1450 feet. The area is located between 146°00' to 146°25' West Longitude and 65°17' to 65°25' North Latitude (Figs. 1 and 2) in interior Alaska.

McManus Creek is a youthful, rapid runoff stream, having a narrow V-shaped valley and a steep gradient. The gradient drops 400 feet per mile at the headwaters and 50 feet per mile at the junction with Faith Creek, resulting in a grade of 7.7% and 0.9% respectively (Schallock, 1965).

Thirteen small tributaries enter the stream in a trellis pattern, the major ones being Montana Creek, Idaho Creek, Smith Creek, and Faith Creek. Of the four, Faith Creek is the largest and nearly doubles the volume of McManus (Fig. 1).

Half a mile below the junction of Faith Creek and McManus Creek (Fig. 1), the flow is interrupted by a dam built to divert water into a man-made ditch (Davidson Ditch) for hydroelectric use. This dam delineated the lower limit of the study area.

Due to the presence of boulders, the coarseness of the bottom, and the steepness of the gradient, the waters are constantly being churned, resulting in excellent aeration.

Figure 1. Map showing McManus Creek, the 43 pools studied, and the three sections of stream. Reproduced from U.S.G.S. Alaska Map, Circle (B-5).

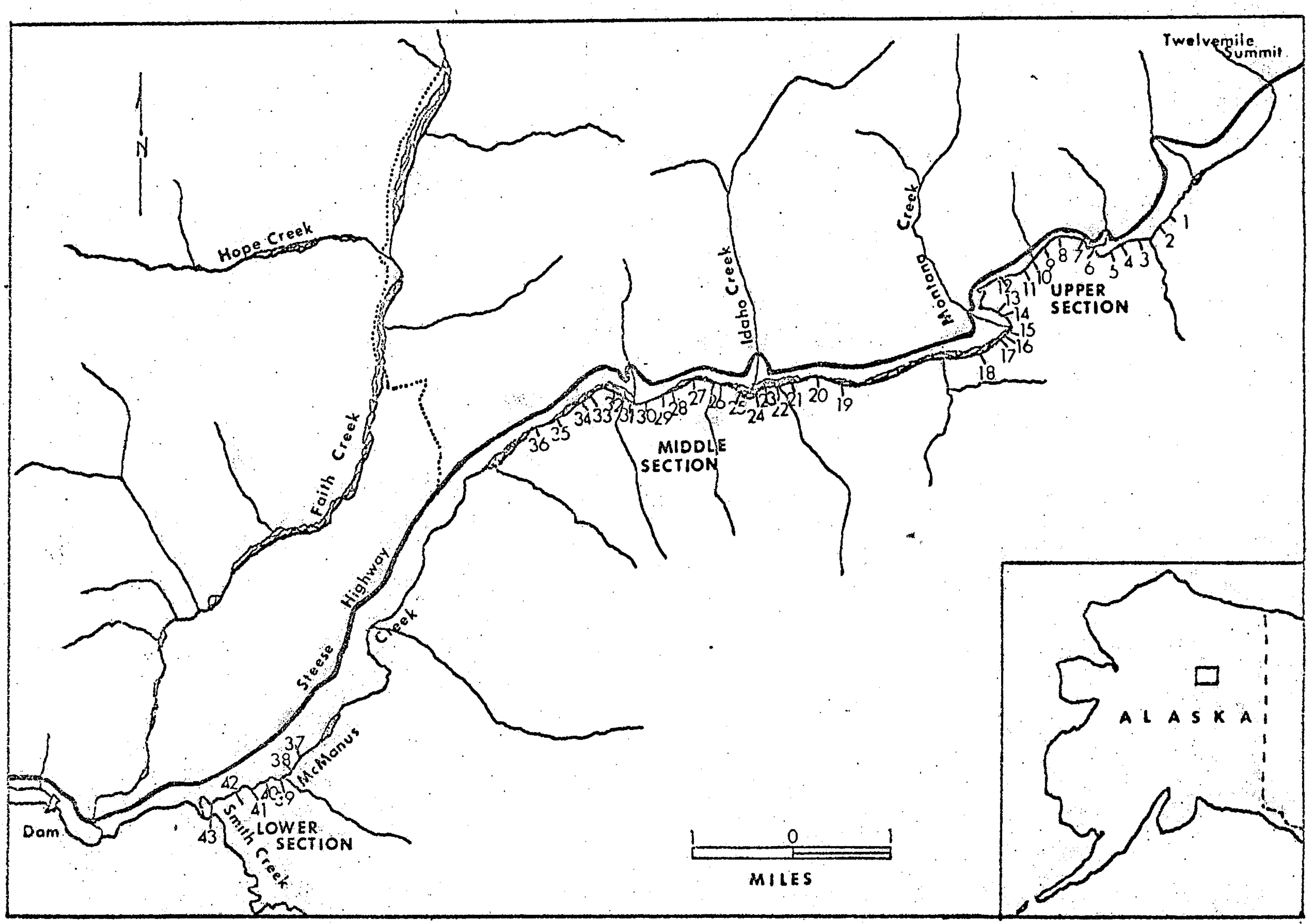
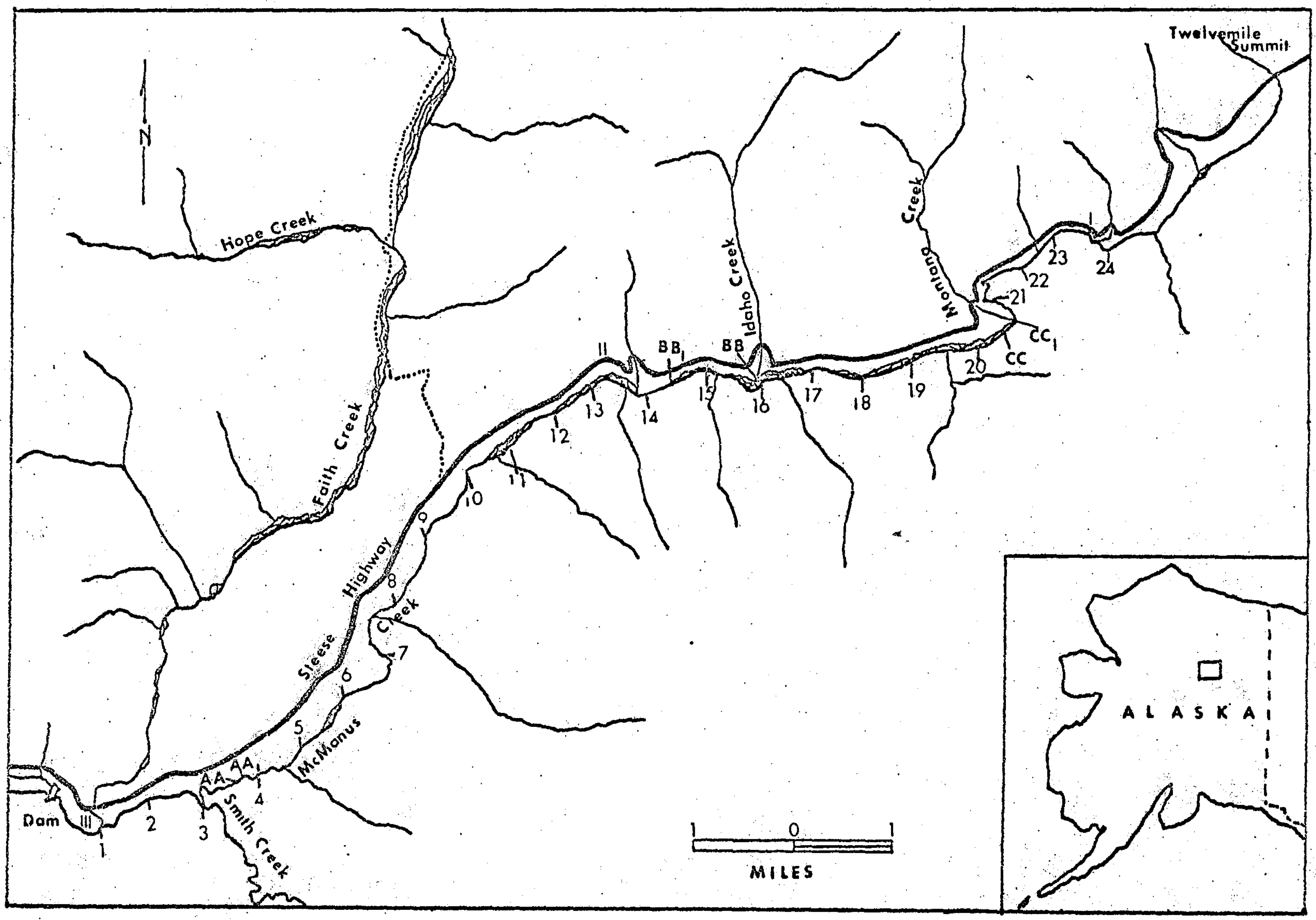

Twelvemile Summit
N
Hope Creek
Faith Creek
Steese Highway
Creek
Idaho Creek
Montana Creek
UPPER SECTION
MIDDLE SECTION
LOWER SECTION
McManus
Smith Creek
Dam
1 0 1
MILES
ALASKA

Figure 2. Map showing McManus Creek, the 24 seining sections, and the six observation pools. Reproduced from U.S.G.S. Alaska Map, Circle (B-5).


Twelvemile Summit
N
Hope Creek
Faith Creek
Idaho Creek
Montana Creek
Steese Highway
Creek
McManus
Smith Creek
Dam
III
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
AA
AA1
BB
BB1
CC
CC1
1 0 1
MILES
ALASKA

The water is exceptionally clear. Human pollution is nil since there are no mining operations or inhabitants in the drainage except at mile 82 of the Steese Highway where a seasonal highway camp is located.

The character of the stream remains relatively constant from two miles from the stream's origin to the junction with Montana Creek. Cascading riffles are predominant, intermixed with small pockets of slower water lying either by the undercut banks or below boulders in the middle of the stream. Most of the "pools" are 12 to 24 inches deep and less than 30 feet long; often there are water chutes where the water deepens, resulting in stretches of slow water near the bottom. Deeper pools are present at the junctions of the various creeks.

Below the mouth of Montana Creek (Fig. 1), the gradient decreases noticeably and the creek takes on a braided appearance. Larger stretches of quiet water are present, the pools are larger and deeper with small sweepers commonly trailing in the water (Table I, Appendix I). Typically, the side of the pool away from the undercut bank consists of a rubble or gravel bar which is submerged during the spring.

In the last five miles there are long stretches of quiet, deep water. The surface is commonly shadowed by trees. The banks are high and rubble bars are rare. Deep holes are present on the outside of bends, with many uprooted trees lodged on the banks. Some of these holes reach a depth of over five feet, and the quiet waters extend for hundreds of feet. The water looks much darker, apparently from the organic matter deposited on the bottom by the relatively weak current.

THE HABITAT, SEASONAL MOVEMENTS, AND ABUNDANCE OF GRAYLING

MATERIALS AND METHODS

In order to determine the type of habitat utilized by the grayling in McManus Creek, 43 pools known to contain grayling were described in detail.

The size of each pool was estimated by the investigator after having measured by tape five pools, which showed that the estimated size showed an error of less than 15%. The depth, whenever possible, was measured by walking into the stream and reading the maximum depth on hip boots which had been marked off at six inch intervals. Where the pools were too deep, the depth was estimated.

The bottom composition of each pool was determined by a visual estimation. All rocks larger than 10 inches in diameter were considered boulders; all rocks between 1 and 10 inches as rubble; and any rocks between approximately 3/16 and 1 inch as gravel. Everything smaller was considered as sand.

Daily air temperatures for the area were obtained by means of a PTC Model 615 dry stylus thermograph, located at the junction of Faith and McManus Creeks. The instrument was wrapped in a plastic bag, placed inside a can nailed to a spruce tree five feet above the ground, and away from direct sunlight.

The water temperatures were taken by means of a centigrade laboratory thermometer in the riffles above each pool. The thermometer was completely immersed and lodged between rocks for five minutes.

At three stations marked I, II, and III on Figure 2, 250 ml water samples were collected in airtight glass bottles, placed in a closed box, and kept below 56°F. Later the contents were mixed in a Waring Blender and turbidity readings taken on a Hellige Turbidimeter. The pH was measured at the the three stations using Brom-Thymol Blue and a Hach colorimeter model DR-1599 B.

Stream velocities were obtained with an immersible Kahl Scientific Instrument Co. water flow meter. The measurements were taken from randomly selected pools in each of the 24 stations at mid-depth, in feet per second except where stated otherwise.

In order to determine the population of the stream and the presence of seasonal movements, tagging operations were conducted throughout the summer of 1966 and 1967. The stream was divided into 24 stations (Fig. 2). The fish were captured with 1/8 and 1/4 inch mesh 20 foot drag seines, and by hook and line. Each individual was anesthetized, fork length was measured, the weight determined with Chatillon spring scales, and for later studies scales were removed from the right side of the fish, just below the dorsal fin.

A monel peduncle tag was affixed and the fish released. The fish were released in the same section where they were captured, but not necessarily in the same pool.

At the pools marked AA, BB, CC, and DD (Fig. 1), 21 fish were tagged with color coded spaghetti tags for quick identification. Using the four color rings--yellow, red, blue, and green--and alternating their order, 21 different combinations were obtained.

RESULTS

Early summer

No data were obtained during the spring months. The ice began to break up in the creek between May 20 and May 25, 1967; but the investigator did not reach the area until June 4.

From June 12 to June 20, 1967, and from June 16 to June 24, 1968, grayling were seen attempting to surmount the diversion dam. Fishermen had reported seeing fish jump prior to these dates. For descriptions of the jumping see Schallock (1965). Between 2145 and 2300 on June 13, 1967, ten fish were counted trying to negotiate the dam; of these, only two were successful. At this time there was a drop of 4.5 to 5.0 feet between the lip of the dam and the stream.

Between June 10 and June 20, 1967, the creek was seined from station 24 to station 6 (Fig. 1) to determine the fish population present. The water was high, swift, and carrying a considerable silt load. The banks consisted mostly of packed snow and ice up to 10 feet thick, and in portions the ice nearly blocked the stream.

During the ten-day seining operation, only one grayling was captured, this being a 120 mm parr taken on June 12 (Fig. 3). The fish was found under brush protruding from the bank of a backwater pool. The pool was 27 feet long,

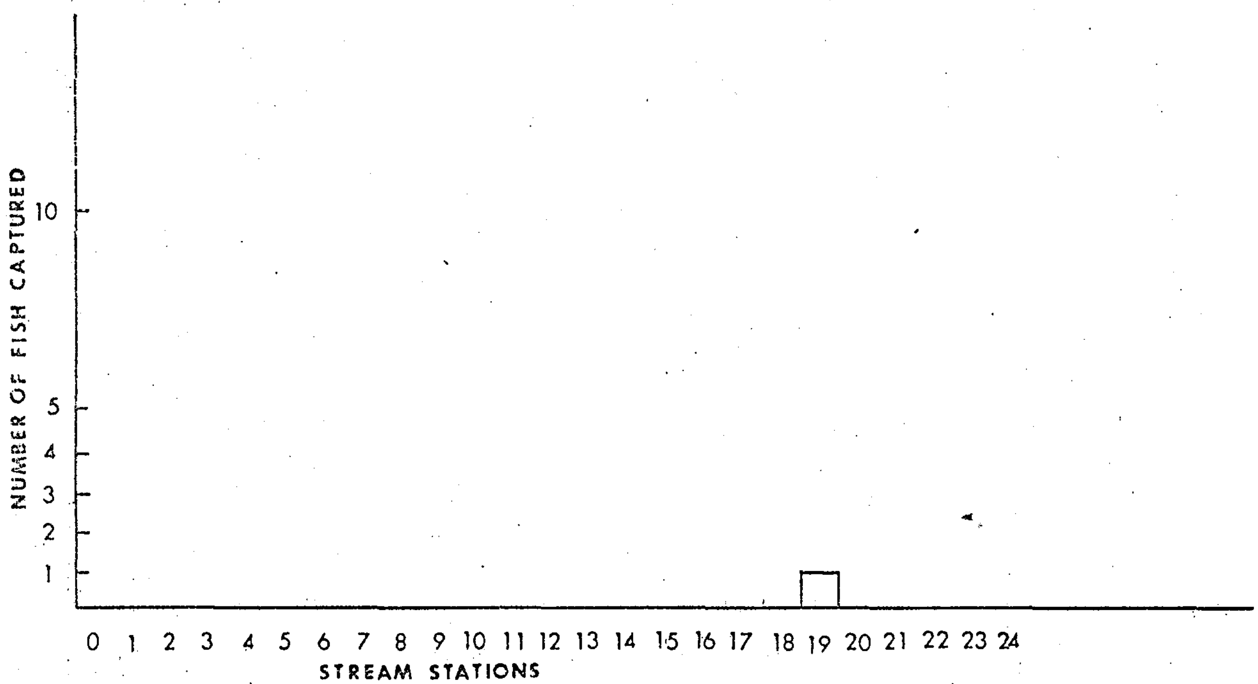


Figure 3. Distribution of fish in early summer, as determined by seining from station 24 to station 6.

6 feet wide, and 3 feet deep, located approximately 100 yards below station 19. Ice was present along the edges, and the bottom was sand-covered. The water temperature was 4^{o} C, and the velocity within the pool was zero feet per second. The current in the main channel was measured at 3.5 fps at center, and 1.7 fps at one third of the distance from the bank.

In the same operation two parr approximately 150 mm long were seen between stations 22 and 14. In both cases the parr was scurrying under the ice in rapid current. A third fish approximately 250 mm long was seen moving upstream in the main channel in a current of 6 fps.

In the very shallow riffles, between rocks at the lower end of rubble bars, large numbers of grayling alevins under 40 mm long were found. They appeared to be basking in micro-pools about three inches in depth. In these pools the alevins moved together in school-like fashion. They rested close to the bottom, but if frightened they exhibited avoidance reactions by either moving out into faster water or hiding under the rocks. The water in these micro-pools reached temperatures up to 10^{o} C during the day but dropped to 4^{o} and 5^{o} C at night.

Mid summer

The creek was seined from station 24 to 0, between June 28 and July 15. By the latter date the water level at Faith and McManus had dropped 16 inches and the turbidity had dropped to 4 parts per million of suspended matter. The velocity at the point where the first parr had been captured was, at this time, down to 1.7 fps.

On June 26, nine grayling were collected between stations 3 and 5, and all were found in the faster stretches. Two were seen attempting to surmount riffles and were immediately caught. Three were captured near the banks, where the water was two to three feet deep and very swift (3.5 fps). The remaining four were taken from a deep sandy pool, six feet long and six feet wide and more than four feet deep, both upstream and downstream from which the water was extremely fast and turbulent. Six of the nine fish had ragged tails and dorsal fins.

Observations of the grayling's behavior were made at two pools. These were both twenty feet long, four to five feet deep and on the north banks. Dead spruce trees were jutting into the current. On June 26 the pools held 20 to 25 parr, all under 180 mm in length. Occasionally large fish were seen moving upstream into the pool and disappearing under the sweeper. They came singly and in groups of two or three. In that same afternoon, three individuals were seen leaving the pool, heading upstream.

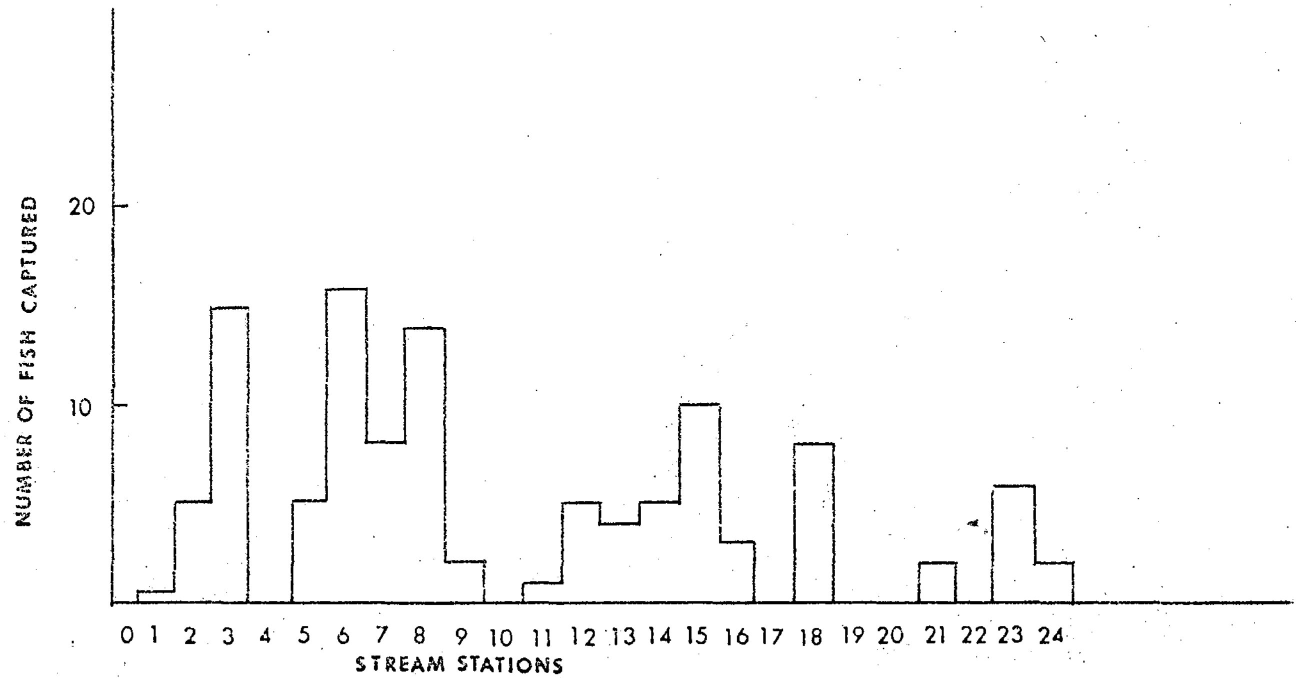


Figure 4. Distribution of fish in mid-summer, as determined by seining from station 24 to station 0.

The seining operations from June 28 to July 15 indicated that the fish were distributed evenly through the length of the stream (Fig. 4). The seining began at station 24 and worked downstream. On the 28th, the maximum water temperature was 5° C and by the end of the seining operations the temperature reached a high of 13° C. Ice was present along stretches of the banks until July 10.

Late summer

Between August 25 and September 5, 1966, McManus was seined by graduate students Lynn Boddie and Marshall Danby. Using the same stations but a smaller mesh seine, the results indicated that the bulk of the fish were occupying the upper half of the stream (Fig. 5). Although no seining was conducted in 1968, a distribution similar to Figure 6 was evident from my observations.

Fall

The data available for periods after September 5 are scanty; in 1968, observations were made at three pools, one in station 22, one in station 18, and one in station 1, on September 1 and 14. In the pools of stations 18 and 22 the fish were still present and in larger concentrations than at any previous time. On August 20, grayling parr were attempting repeatedly to jump over the spillways of the culverts where McManus' tributaries are crossed by the Steese Highway They were unsuccessful, since a drop of six feet was present.

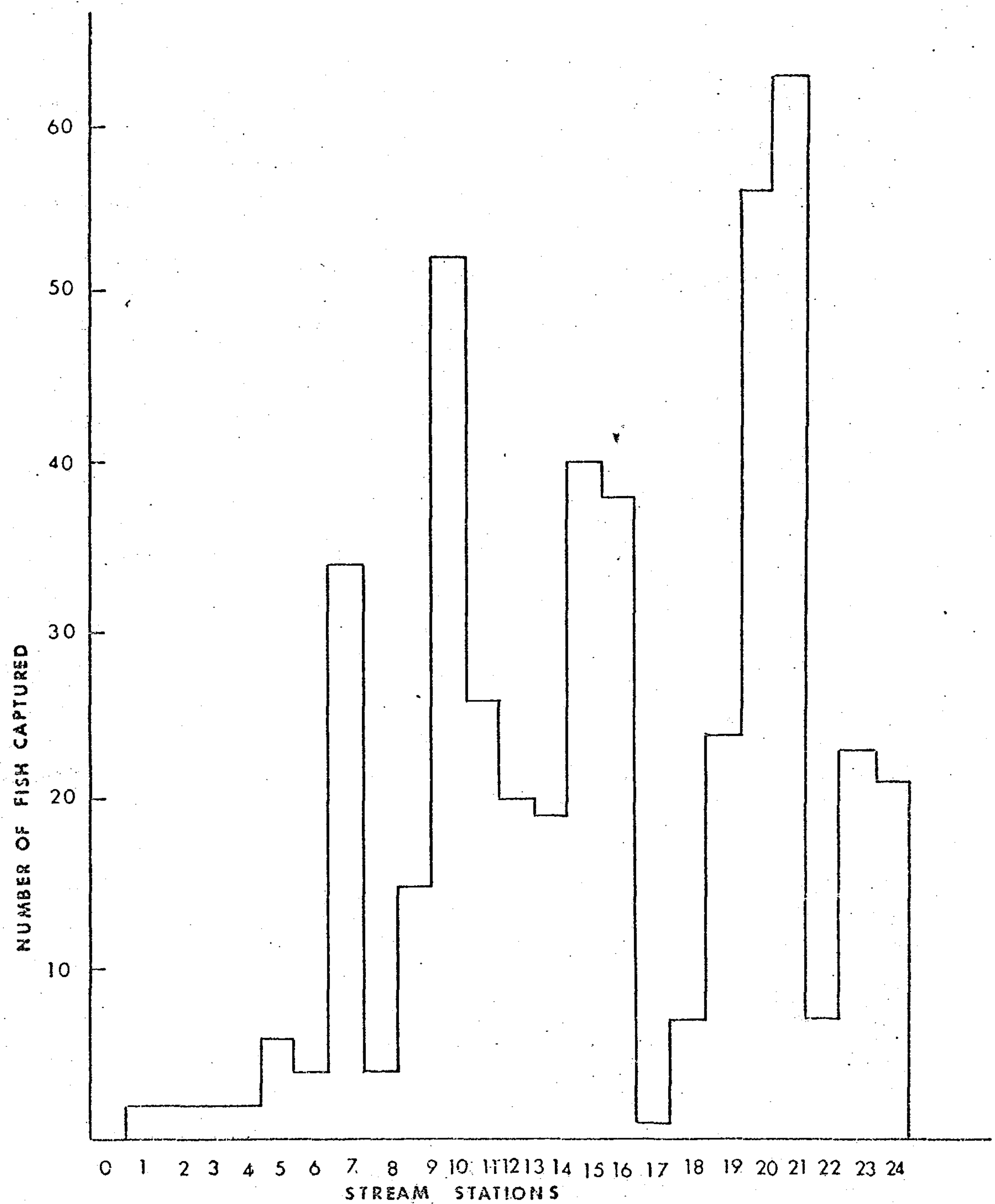


Figure 5. Distribution of fish in late summer, as determined by seining from station 1 to station 24.

<u>Tagging results</u>

In the summer of 1966, 354 fish were tagged and 144 fin-clipped in McManus Creek. At the time of tagging, the crew had estimated that at least 75% of the fish with fork lengths greater than 180 mm had been captured due to the low water and high visibility (Lynn Boddie, personal communication). Such conditions would have increased the efficiency of the seine by allowing the workers to see the fish.

Between September 28 and September 30, 1966, 18 fish which had been tagged on August 28, 1966 were recaptured by a fisherman (Fig. 6). Over the one month between tagging and recapture, the fish exhibited a random upstream-downstream movement.

During the summer of 1967, in two seining operations, 105 fish were tagged and 59 fin-clipped. During the same operation, 10 fish tagged in 1966, and 17 others with scars from lost tags were recaptured. Of the fish tagged in 1966 2.8% were recaptured still bearing tags, and 7.5% bearing either tags or tag scars. Four tagged fish were recaptured below the dam.

During 1968, only five tagged fish were recaptured from the previous years. One of these had been tagged in 1966, the others in 1967. Two of them were taken below the dam. None were found with tag scars.

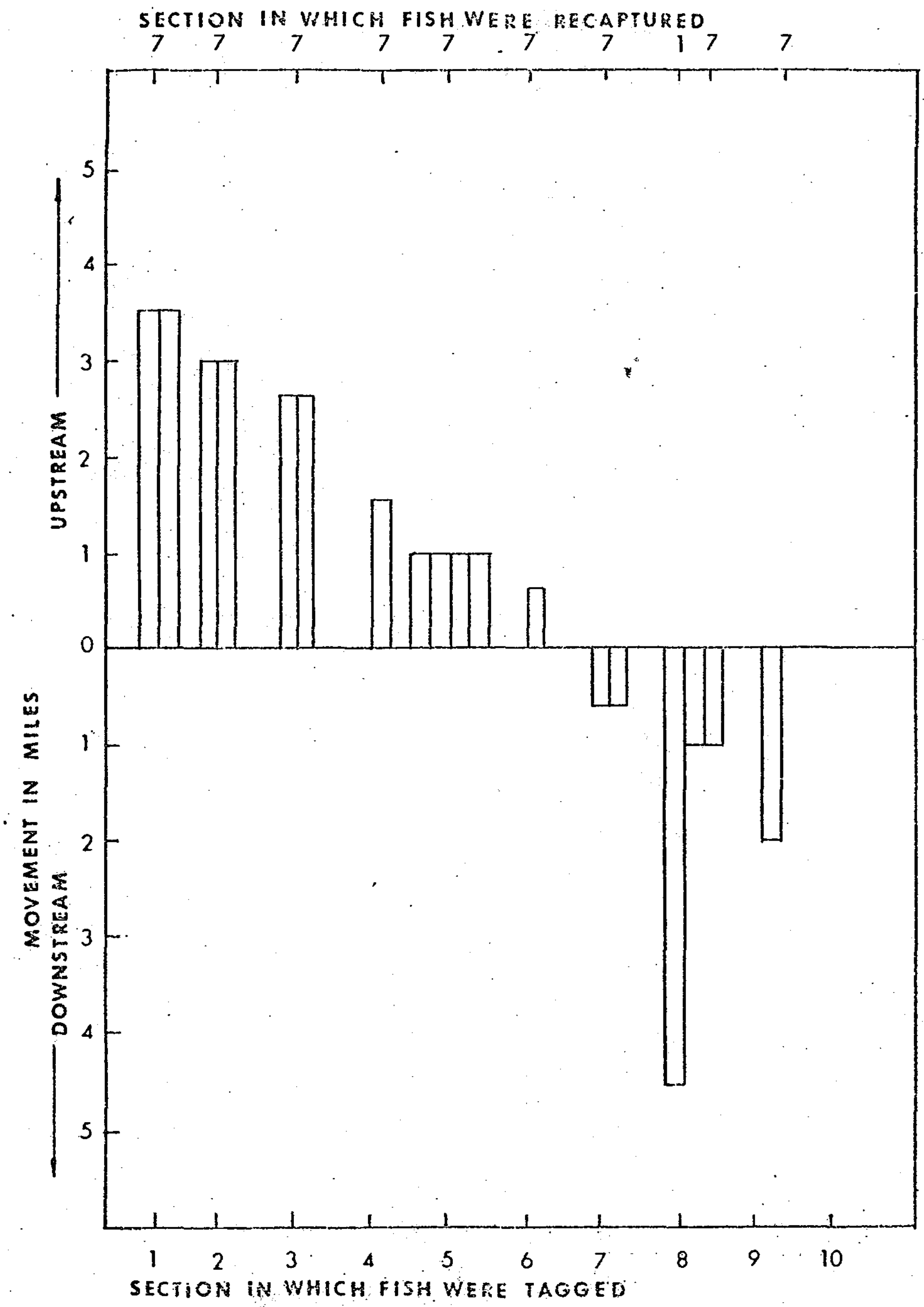


Figure 6. Results of the recapture of 18 fish, tagged August 28, 1966, and recovered September 28-30, 1966.

Of the fish with colored tags, four from pool AA vanished in the first week of July. Three of these were recovered in the third week of August between pools BB and CC. The fourth one disappeared and is presumed to have been captured by fishermen. The fate of some of the remaining 17 will be discussed later.

Characteristics of pools in which the grayling were found

A sample of 43 pools was studied intensively to describe the type of habitat utilized by the fish. Of these, 18 pools were selected from the upper portion, 18 from the middle and 17 from the lower section of stream (Fig. 1).

The lengths of the pools varied from six feet to 150 feet, the average being 35 feet. The data obtained were tabulated in Table I, Appendix I, and the mean values per section for pool lengths, depths, surface area and estimate of plant cover are shown in Table II, Appendix I. The data on plant cover were converted to frequency of occurrence per section, and then to frequency of occurrence for the entire study area. The results of the evaluation of the bottom composition, water velocities, and surface are tabulated in Tables III and IV, Appendix I.

DISCUSSION

The seining data indicate that, even allowing for loss of effectiveness of the seine due to the high and murky water, few fish were present in McManus Creek up to mid June. All those seen or captured were small and probably survived the winter in one of the deeper pools.

The presence of fry in the stream from June 12 to June 20, 1967, and the absence of mature individuals at this time, appear to indicate that the grayling which are reported to spawn in late May and early June (Nelson 1954, Reed 1964), had spawned in the stream at least two weeks earlier, and then had migrated back downstream. Such a movement would appear to agree with Reed (1964), Warner (1956), and Ward (1951) who indicate that spawning grayling from lakes move up into the creeks in May or early June, and then move back downstream within one or two weeks.

In McManus Creek the grayling apparently move upstream to spawn as soon as the ice goes out. Once spent they move back downstream. A few weeks later, another group ready to spawn moves up and this is the population which inhabits the stream during the summer. This second group would be the fish in spawning condition which were captured below the diversion dam as late as June 20. Reed (1964), in describing grayling streams of the Tanana drainage, mentions that some grayling remained in the stream after spawning; this does not seem to be the case with the grayling responsible for the mid-June fry in McManus Creek, but would apply to the later migrants.

Another possibility would be that some grayling may spawn in the fall, with the fertilized eggs remaining in the gravel over the winter. Unfortunately no ripe individuals have been seen by the investigator or other workers from the Alaska Department of Fish and Game in the fall. Fishermen from other drainages, notably the Salcha River, maintain that they have caught ripe individuals in late August.

Schallock (1965) indicates that the young of the year vanish from the stream by August. This was not the case in 1966, 1967, or 1968. Both young of the year and one year old fish remained common throughout the summer. However, they did change their habits considerably, since in June and July they were commonly found in shallow pools formed by rubble bars. By August they were found in the deeper pools, where they stayed close to the brush and were camouflaged with the bottom. Their presence was shown during the tagging operations in 1966, when 95 fish under 180 mm were fin-clipped between stations 17 and 24 and countless ones under 95 mm were released, all after August 25. Similar results were obtained in 1967.

It appears that most of the summer population of the stream comes from below the dam. The evidence for this can be seen in Figures 4 and 5, which show that in the early part of June the stream is nearly devoid of fish, but is well populated by July 1. Further evidence to support the above idea is given by data from the recapture of grayling marked the previous year. Even if only 50% of the taggable fish had been tagged in 1966, the complete absence of fin-clipped recaptures in 1967, and the low recapture, 7.5%, of previously tagged fish strongly implies an almost complete turnover in population. The presence of previously tagged fish below the diversion dam, 18.8% of the total recaptures, where they were captured and seen attempting to jump, leads to speculation that emigration in fall or winter does take place. It should be noted that recaptured fish showed that the tag had severely damaged the fish's peduncular region. A marked swelling and open wound was present on all recaptures, even though the tag had been inserted the previous year. It appeared that the swimming was hampered, and such a wound could have severely affected the ability of the fish to negotiate the dam. The sharp decline in number of fish captured in 1967 (165), opposed to 498 in 1966, may be a reflection of the damage caused by the tags either by keeping fish from surmounting the dam, or by increasing the mortality of the individuals.

An upstream spring or early summer migration is evident in McManus Creek. This migration conforms to the data available from other localities, Brown (1938a) in Montana; Degteva (1965) in Russia; Leach (1923) and Vincent (1962) in Michigan; and Warner (1956) in Alaska. However the migration in this area differs from the others in that here the fish do not return immediately downstream to a lake after spawning, and that the McManus grayling do not move en masse, but either singly or in groups of two or three. This may be due to the presence of the diversion dam which disrupts the movement of the fish as a group, or due to the high latitude, which results in virtually continuous daylight during mid and late June. Other authors report observing the migration of the fish only after sundown.

The pools occupied in early summer are those found in the deepest and slowest portion of the stream, which also contains the largest pools. These characteristics are found in the lower section of the stream (Tables II, III, IV, Appendix I).

This investigator believes that the lowest section of the stream serves as a stopping-over area where the grayling stop on their migration, waiting the subsidence of the water. The depth, combined with the slow current makes these pools ideal during the spring runoff. As the water and the current continue to slacken, smaller and smaller fish are able to make the journey. Such a movement would be difficult earlier because just above the lower section the character of the stream is such that there is a complete absence of protected pools, resulting in turbulent and very strong currents.

By the end of June, the fish were found to be still moving upstream, although by then individuals had already reached the uppermost portion. The fish in the lower section were still moving. This was observed visually, and was verified by color tagging four fish in the first week of July. The rapid changes in distribution of fish in the stream seen in Figures 4 and 5 took approximately one week. In July the upstream movement appeared slower than it had been in late June. At this time only a few smaller individuals were seen moving upstream.

By the last week of July of both 1967 and 1968, large grayling had virtually disappeared from the lower section, but considerable numbers of fish under 160 mm in length were still present.

Once the fish reach the upper or middle sections of the stream they tend to settle down in individual pools where they remain for the rest of the summer. Marked individuals have been observed living in the same pools for as much as five weeks, but these will be discussed in a later section. During mid-summer the distribution is uniform throughout the stream (Fig. 4), with the largest individuals concentrated in the upper half.

The habitat in which the individuals settle down for the summer consists of clear water of 0-4 ppm turbidity and 97 to 100% oxygen saturation.

The fish in the upper reaches stay near the bottom by day, and leave the pools as darkness approaches. I was unable to see what happened once they left the observed pools in the evening. I suspect that a random movement upstream and downstream takes place, which would explain the random distribution shown by Figure 6.

In the lower Chatanika River grayling were reported moving upstream as late as the last week of September, when 850+ grayling were counted at a weir maintained by the Alaska Department of Fish and Game. These fish were accompanying a school of whitefish (Gene Roguski, personal communication).

No data were obtained beyond September 15, but reports from fishermen indicate a downstream movement at the end of the month, when fish were being taken in pools between stations 0 and 1, an area where they had been absent in both spring and summer. At this time, the water was too low for the grayling to be able to jump over the dam, and the only place they could have come from was upstream.

Other data that might indicate a late fall or winter downstream migration are the capture of six tagged grayling below the dam in the spring, coupled with reports of fishermen taking many tagged fish at the dam in early June.

The summer movements described above appear to follow closely those observed by Shetter (1937) while working with brook trout in Michigan. There, the brook trout remained in their pools through the summer, and migrated 3/4 of a mile upstream on the average in autumn. During the winter there was a downstream migration of the bulk of the population for as far as 18 miles. This was followed by a return to the tagging locality on the following year.

The grayling of McManus Creek differed from the trout studied by Shetter only in that their period of stability in a pool did not last through June, July, August and early September, but only through late July and August.

DISTRIBUTION, TERRITORIALITY, AND SOCIAL HIERARCHY OF THE GRAYLING WITHIN THE POOLS

MATERIALS AND METHODS

In the summer of 1968 six pools were selected for extensive studies. Two were selected from each of the main sections previously described. The selections were based on the following criteria:

a) pools which were representative of the section in which they were located.

b) ease of access.

c) pools allowing observation even during periods of relatively high water.

d) availability of observation posts which would not alarm the fish.

The pools were designated as AA, AA_1, BB, BB_1, CC, and CC_1 (Fig. 1). Pools AA, AA_1, and CC were visited weekly or more often after having been established; pool BB was visited biweekly. Pools BB_1 and CC_1 were visited three times, once each in July, August, and September.

Pools AA and CC were under observation from June 25 to September 14, from 0700 to 0200 on the days of observation; the rest were observed from July 22 to September 2.

On each visit the observer approached with caution and sat in a position allowing clear view of the pool, while still having a brushy barrier present as camouflage. From fifteen minutes to one half hour was allowed for the fish to adjust to the observer. Visual observations of the distribution of the fish, both vertical and horizontal, were made, activities that the fish were engaged in were described either in written form or on tape, and whenever possible Super 8 movie films of the activities were taken. At hourly intervals water temperatures were taken.

The physical characteristics of the six observation pools are tabulated in Table 1. In Figures 8 to 12 the character of the pools and the distribution of the fish within each are illustrated.

To determine the areas occupied by individual fish in pools AA and CC, the fish's movements over a ten-minute period were plotted. This was done by scaling a paper into 1 inch equals 1 foot sections, and tracing all movements as they occurred during that period of time.

The horizontal distribution of the fish was determined visually from above the surface of the water. The vertical distribution was determined with the aid of a glass bottom bucket.

TABLE I. CHARACTERISTICS OF SIX OBSERVED POOLS

POOL NO.	DATE STUDIED	MAX. LENGTH (m)	MAX. WIDTH (m)	MAX. DEPTH (m)	RATIO OF BOTTOM COMPOSITION % Rubble	% Gravel	% Sand	NO. OF FISH PRESENT	SIZES OF FISH PRESENT (in mm)
AA	6/25-7/23	2.05	1.10	0.70	0	80	20	8	75 to 185
AA_1	6/25-7/23	12.50	6.00	1.80	0	10	90	3	75 to 200
BB	7/22-9/2	9.00	3.00	1.35	50	50	0	15+	120 to 350
BB_1	7/22-9/2	45.00	6.00	1.80	100	0	0	10+	100 to 380
CC	7/16-9/16	7.50	3.00	0.90	30	60	10	12	125 to 250
CC_1	7/16-9/16	9.00	3.00	0.90	10	80	10	8-10	120 to 230

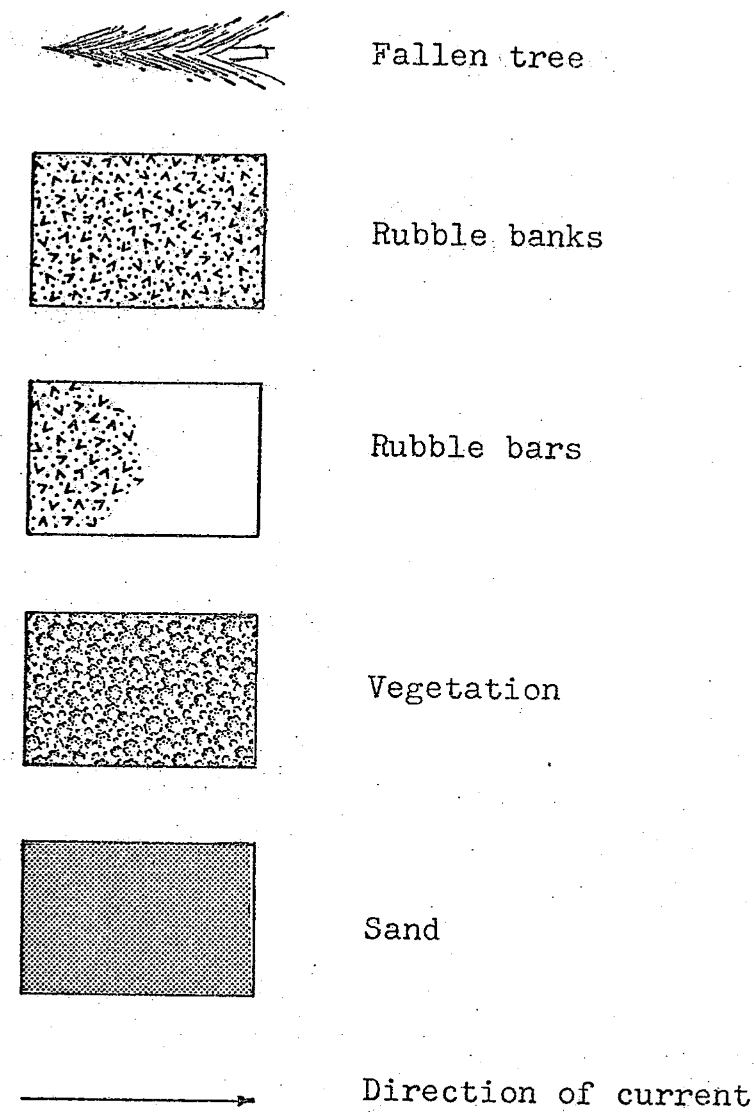
RESULTS

Horizontal and vertical distribution of the fish

In the six pools studied, and most of the other 37 pools observed, the larger fish occupied positions close to the bottom (Fig. 12), and the smaller ones were distributed in the mid-depths. In the same pools the largest members were found in the most forward positions in relation to the current (Figs. 7, 8, 9, 10, and 11), and the smaller ones trailed behind. When a pool was observed in cross section, it was found that the largest fish occupied the deepest portion of the pool, often corresponding to the center, with smaller fish on either side, and the fish becoming progressively smaller as one neared the shore.

The generalizations stated above held true whether the pools had a population of parr, adults, or a mixture of the two. The latter was the most common combination found.

The nature of McManus Creek is such that the deepest portion of each pool usually is to be found immediately below the upstream riffle. In this part of the pool the current is swiftest, and the only rocks deposited are of rubble and boulder size. Due to the uneven bottom, the large fish occupy positions immediately behind large rocks, where the current is not as strong. Measurements taken



Key to the following five figures.

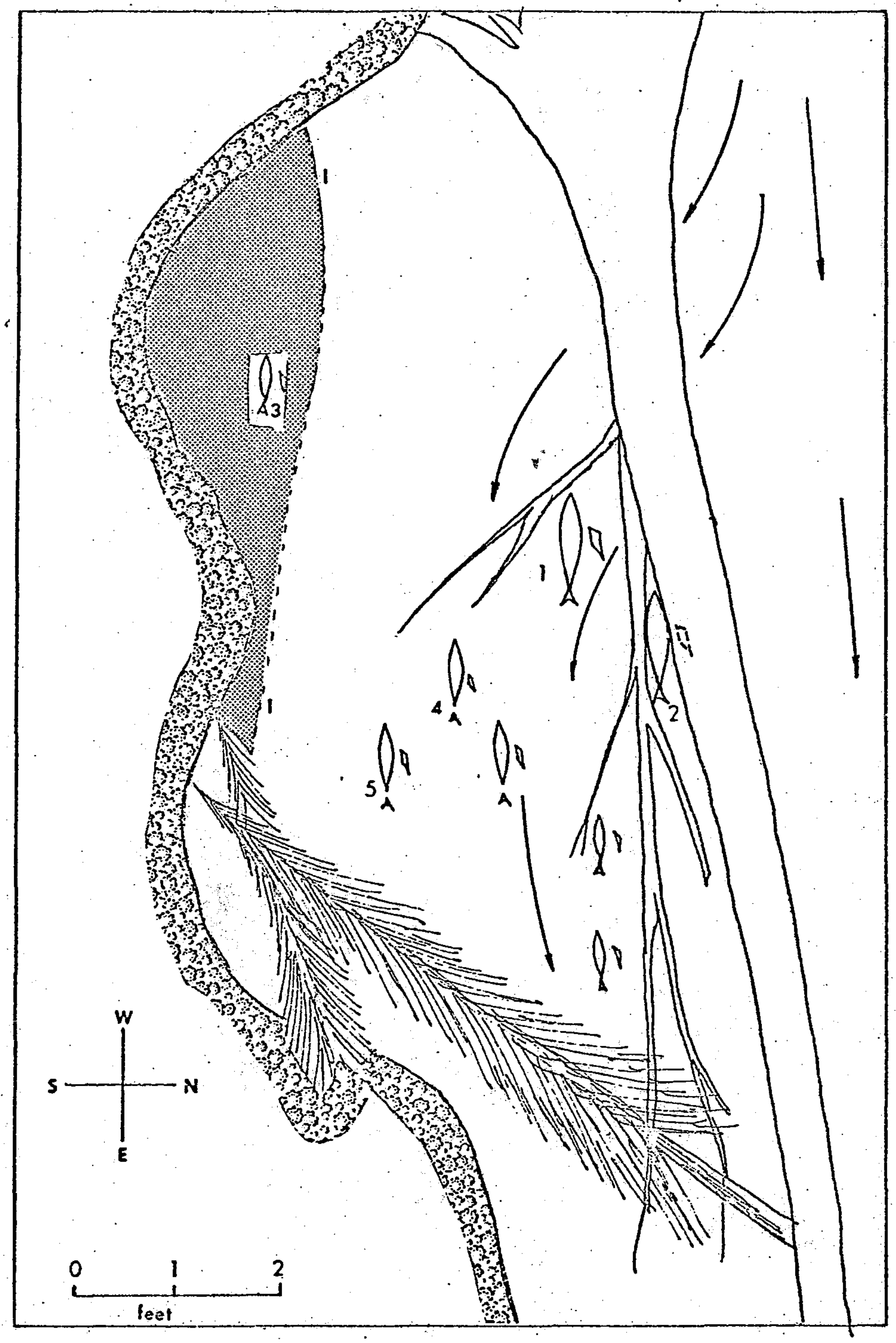


Figure 7. Pool AA.

Viewed from above and looking upstream.

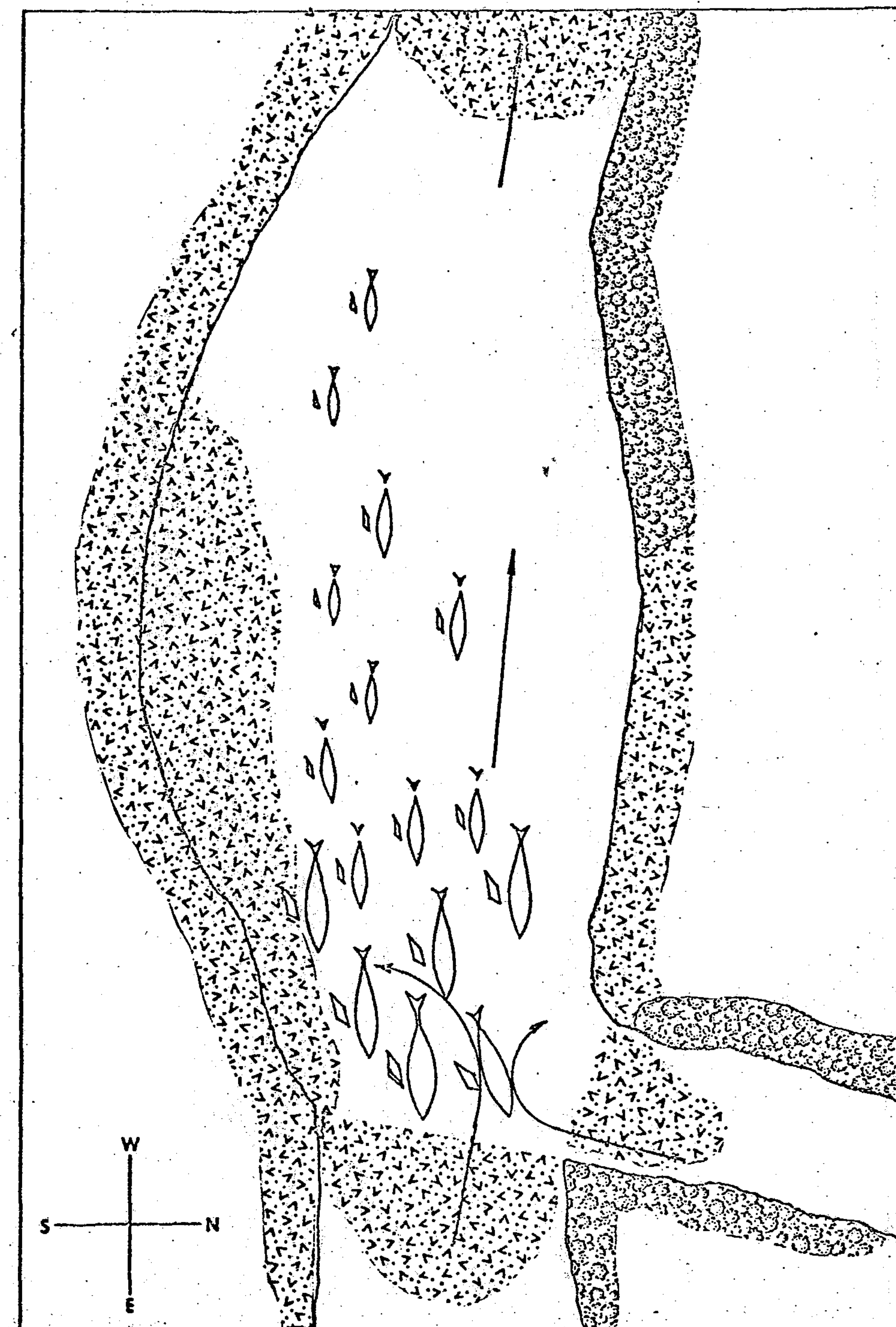


Figure 8. POOL BB.

Viewed from above and looking downstream.

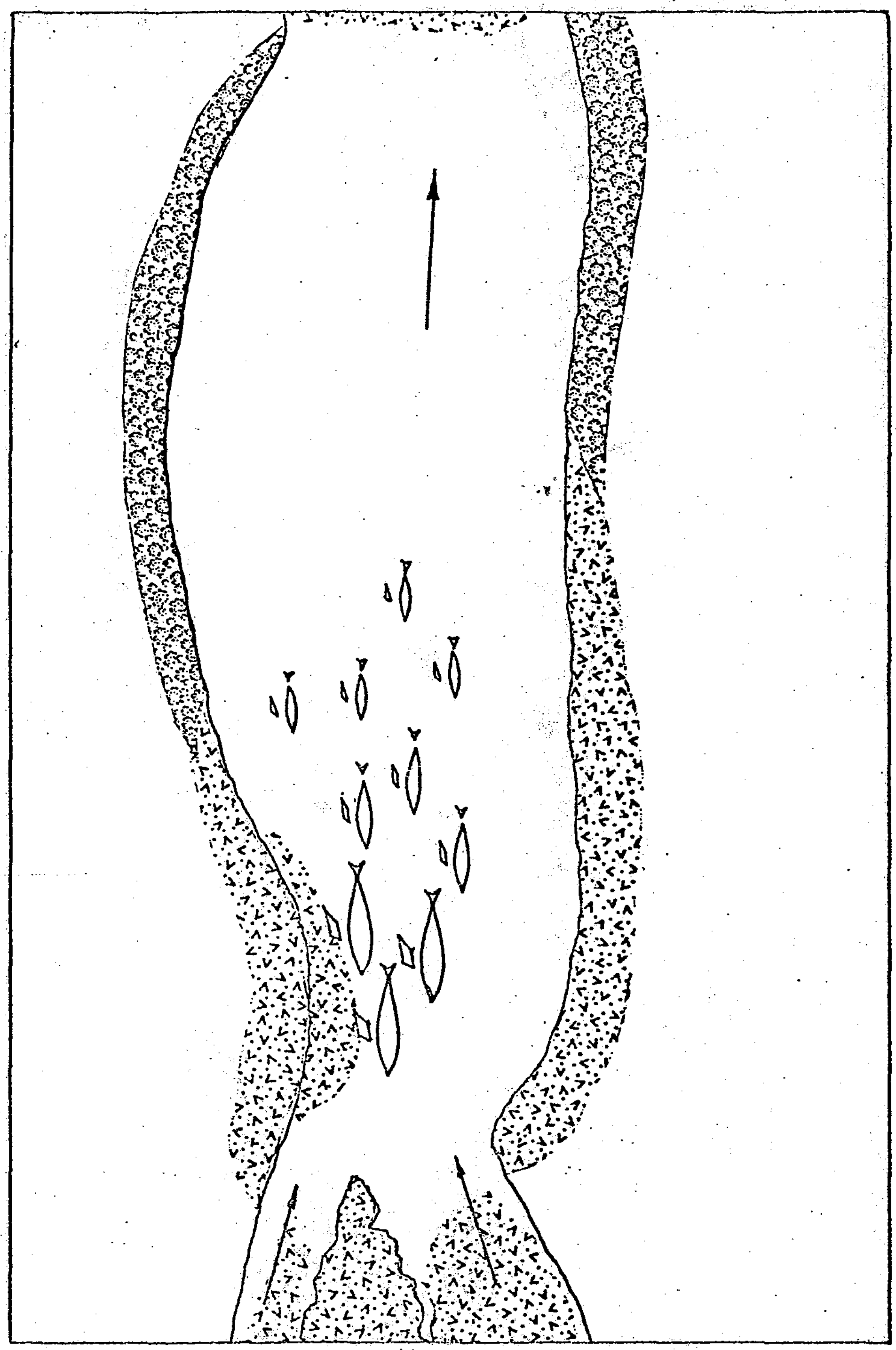


Figure 9. POOL BB_1.
Viewed from above and looking downstream.

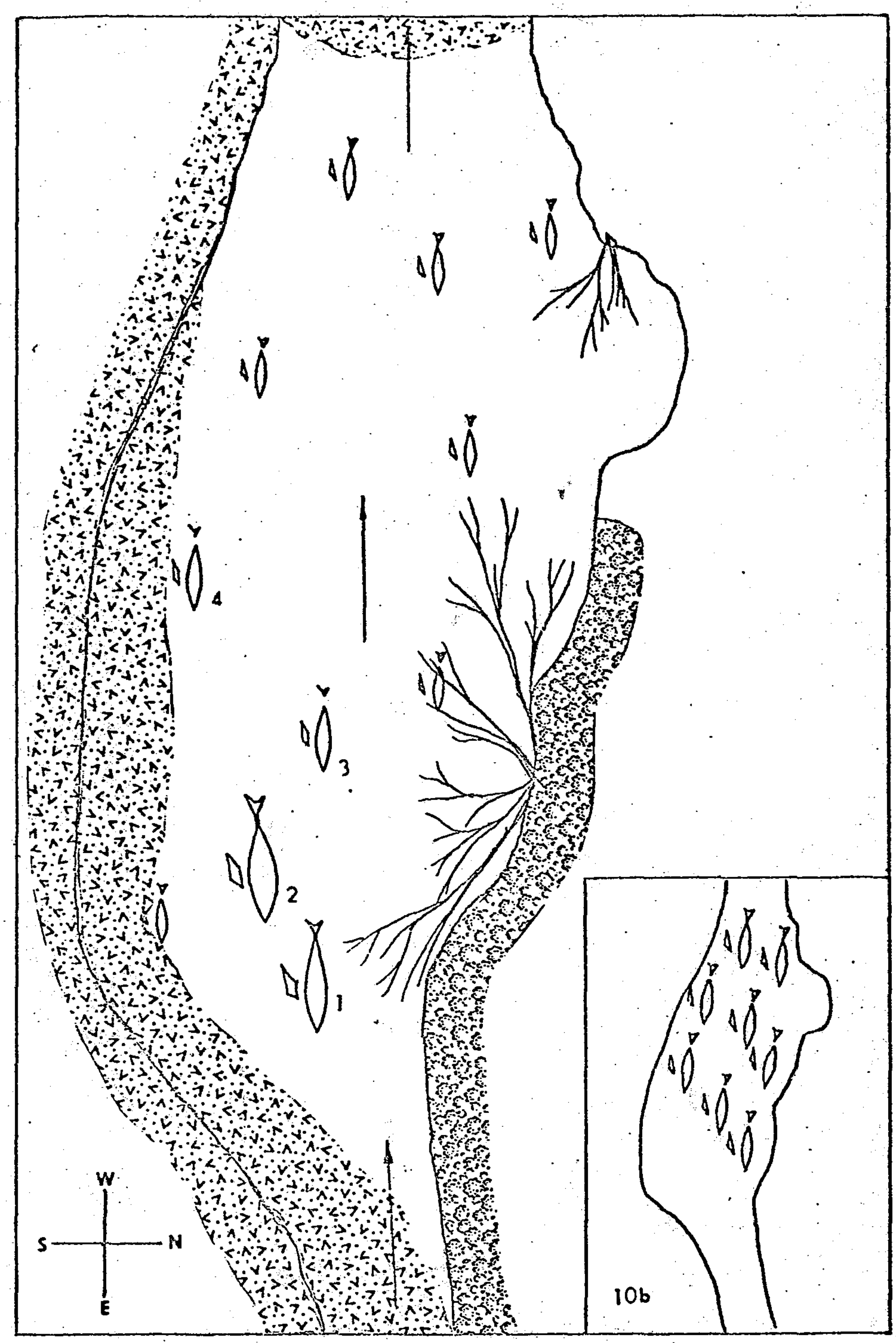


Figure 10. POOL BB.
Viewed from above and looking downstream.

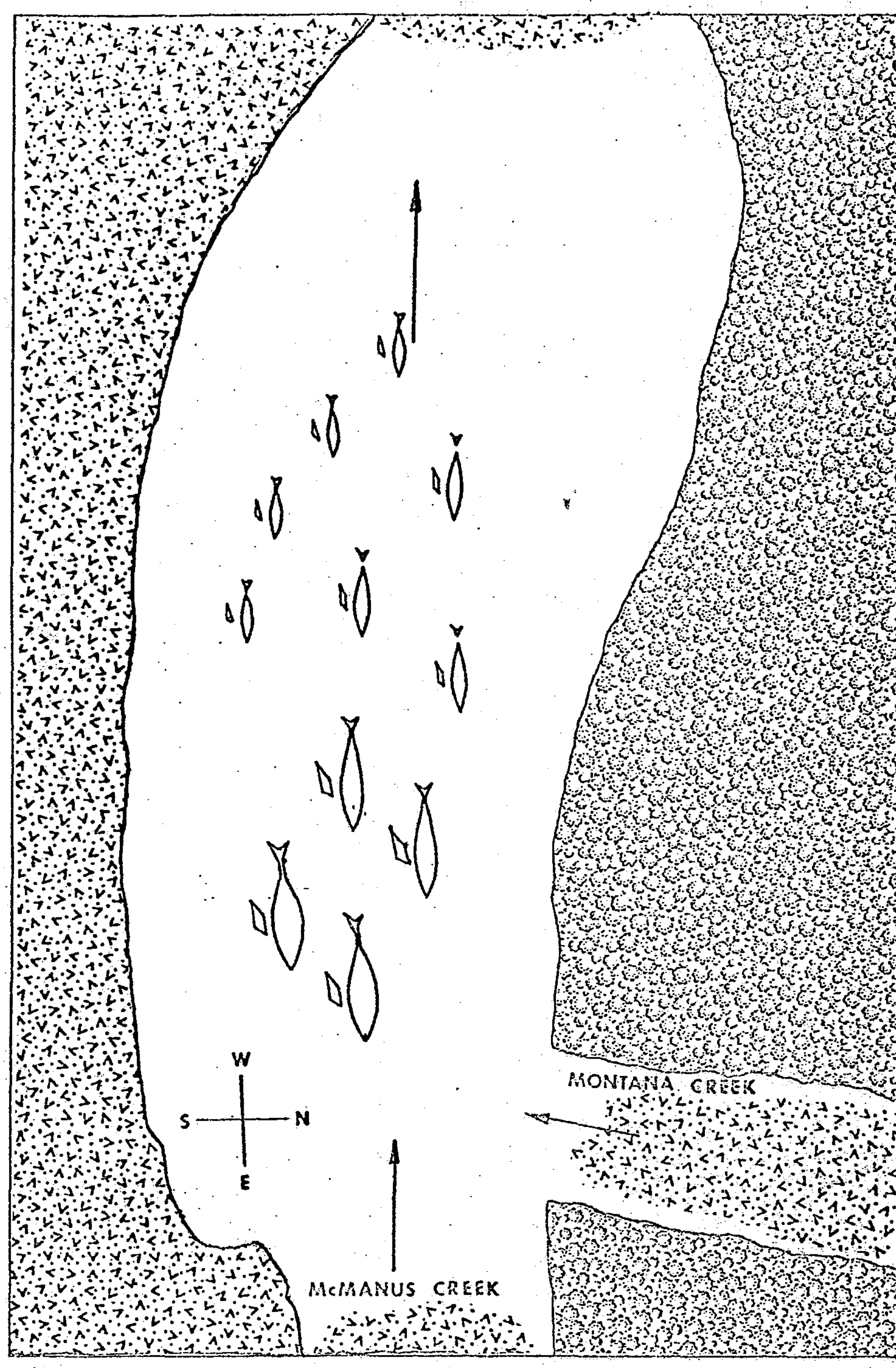
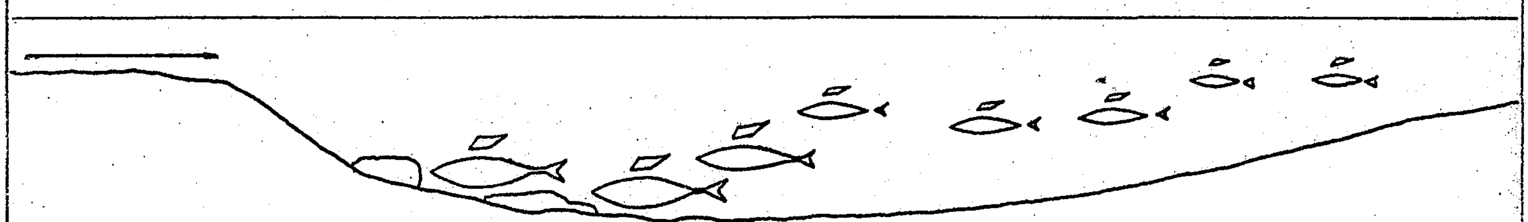


Figure 11. Pool CC_1.
Viewed from above and looking downstream.

Figure 12. Vertical distribution of grayling in a pool.



Longitudinal view.

in the summer of 1967 indicated that the velocity near the bottom, at the head of the pool, was similar to the velocity at mid-depth further back in the pools, where most of the parr were found.

Exceptions to the distribution stated above occurred:

a) among adult fish which had been previously tagged.

b) in long narrow pools in turbulent stretches of stream.

c) in standing pools with little or no current.

d) in all the pools observed after September 2.

Adults carrying peduncle tags were seen in three cases, and one of these was in pool CC, where it was observed from June 25 to July 28. In all three cases the tagged fish were the largest fish in the pool, and yet occupied a position behind a slightly smaller fish. The physical appearance of the tagged fish was poor. Aside from the swollen peduncle and tail, their bellies were withdrawn. The index of condition for two of the fish was determined by using the equation (Lagler, 1956):

$$K = \frac{W}{L^3}$$

K = index of condition
W = weight in grams
L = length in millimeters

K for the two tagged fish was 56.7×10^{-7} and 58.9×10^{-7}, as compared to 109.2×10^{-7} for healthy fish of the same size, collected in the same area and during the same week.

In the situation involving narrow pools in turbulent stretches of stream, the horizontal distribution also varied from the norm. These pools occurred primarily in the upper portions of the stream. In these the larger fish were typically found in the deepest portion of the pool, which usually corresponded to a location half-way down the length of the pool. The parr were located both ahead and behind the larger fish (Fig. 13).

The lack of typical distribution was also observed in the pool below the diversion dam (Fig. 14), in pool AA_1, and at the junction of Homestake and Charity Creeks at the headwaters of Faith Creek. All three of these pools were characterized by large size, deep water, and lack of a strong current.

The pool below the diversion dam (Fig. 14) was the deepest point in the drainage. When the water level dropped in late June, the pool had a considerable portion of standing water. As soon as the water dropped and the current diminished, the fish, which previously had been lying close to the bottom, began milling around in schools. The movement of the schools was in a counter-clockwise

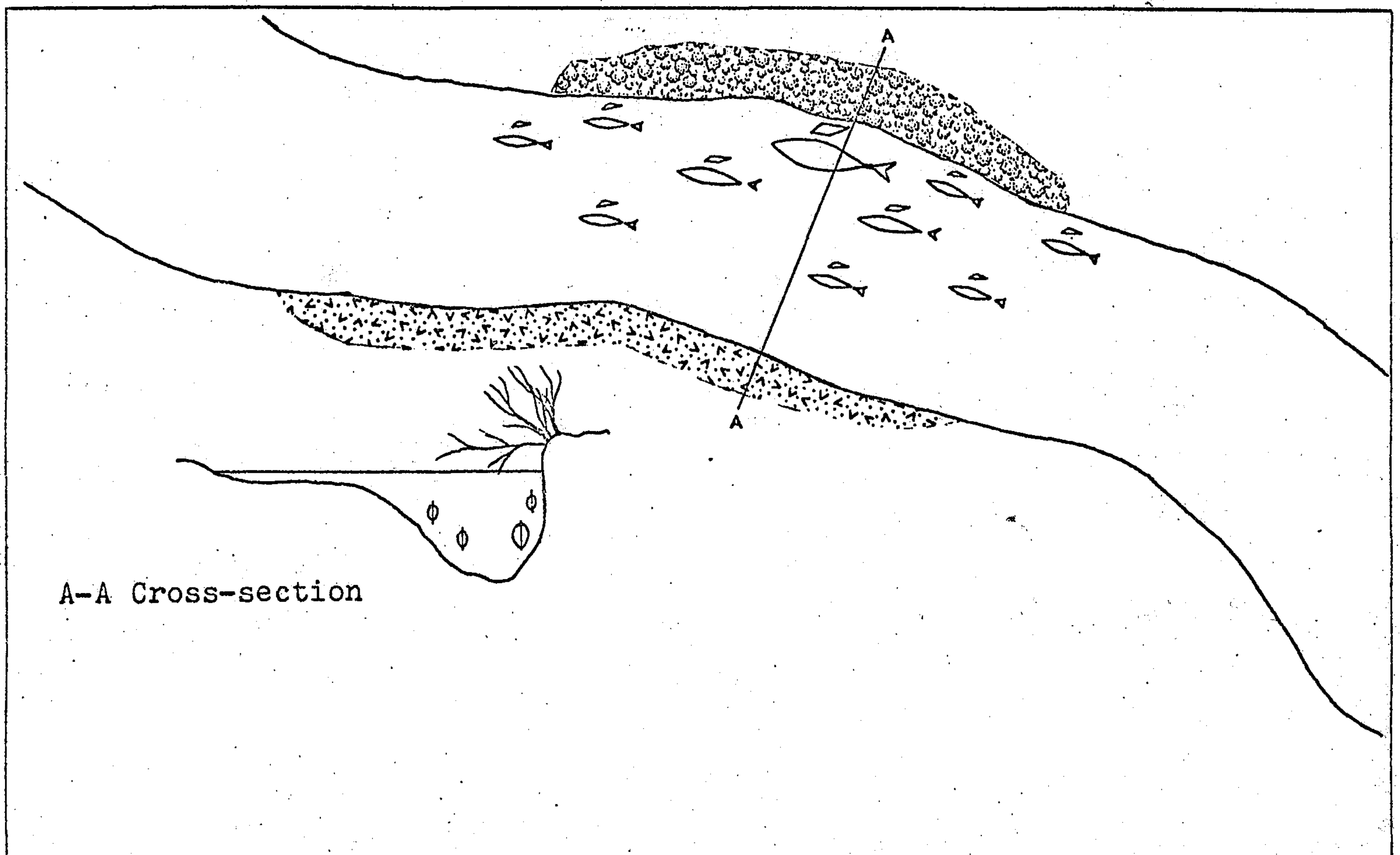


Figure 13. Distribution of fish in narrow pools.

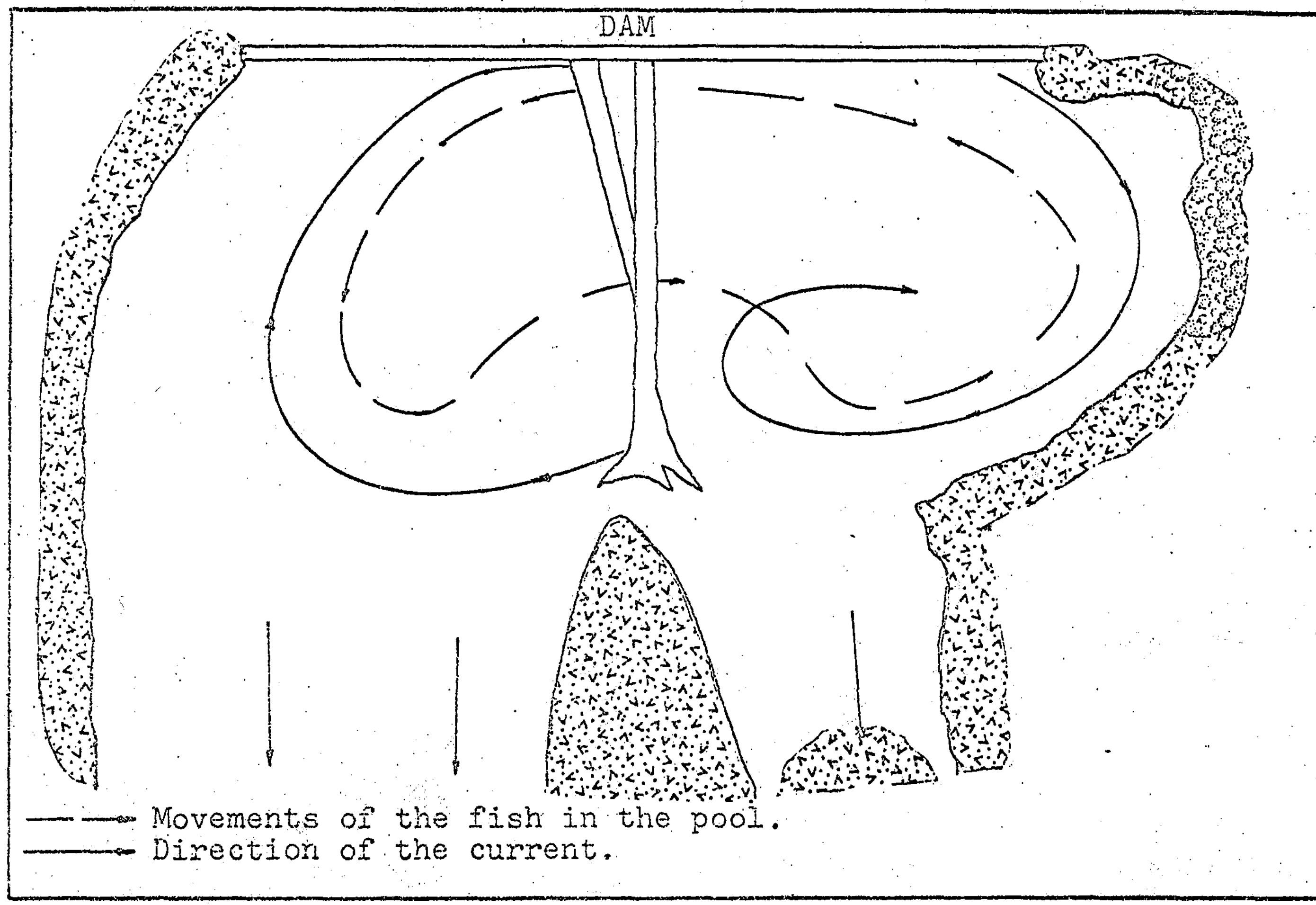


Figure 14. Movements of fish in the pool below the dam. Solid lines indicate motion of the water, the dashed line shows movement of the fish.

direction, the direction of travel was counter to that of the slight clockwise current present. The schools had the larger fish in the forefront and center of the mass, with smaller ones at the periphery and trailing behind. In early July, when schools of round whitefish (*Coregonus cylindraceus*) entered the pool, the grayling joined these schools and moved together as a group.

Pool AA_1, the only one of the three pools that was within the study area, was also a large pool with very slow current. Here the fish were wandering in a figure eight pattern.

The best illustration of the conditions under which the breakdown of the horizontal distribution occurred was the pool at the junction of Homestake and Charity Creeks. Up until July 20, this pool was approximately 30 feet long and 12 feet wide. The distribution of 11 fish inhabiting it followed closely the pattern illustrated in Figure 11 for CC_1. After July 20 a reservoir was created by an earthen dam constructed 50 meters below the pool. After the dam was built a reservoir approximately $1\frac{1}{2}$ meters deep and inundating an area about 50 meters by 30 meters resulted. As the water began to rise, the fish left their previous positions and began moving around the pool in a school for the remainder of the summer. Because of the continuous movement of the school, the large size of the reservoir, and the lack of a suitable vantage point, observations of the ordering of the school could not be made. One thing was apparent however, the number of individuals in the school was constantly increasing throughout the summer. Whether the additions came through the discharge pipes, or moved down from the two tributaries was not determined.

On September 14, pools AA, AA_1, CC, and CC_1 were observed for the last time. AA and AA_1 were devoid of fish, CC and CC_1 still contained fish, but the composition had changed. Both pools contained only adult fish, and the horizontal distribution appeared random, with all of the fish staying close to the bottom. Evidences of changes in composition first became apparent on September 2, when both in CC and BB, fish which had been color tagged on July 22 started disappearing for the first time in 42 days.

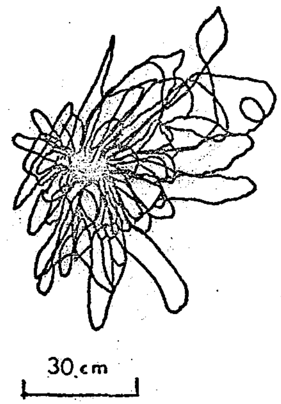
Feeding range and feeding center

Using Burt's (1943) definition of home range as "the area, usually around a home site, over which the animal normally travels in search of food," then the grayling observed from June 20 to September 2 can be said to have a home range. However, this range will be referred to as a feeding range since all movements considered here were feeding movements. All of the fish wandered from a range center, but they always began their movements from it and returned to it.

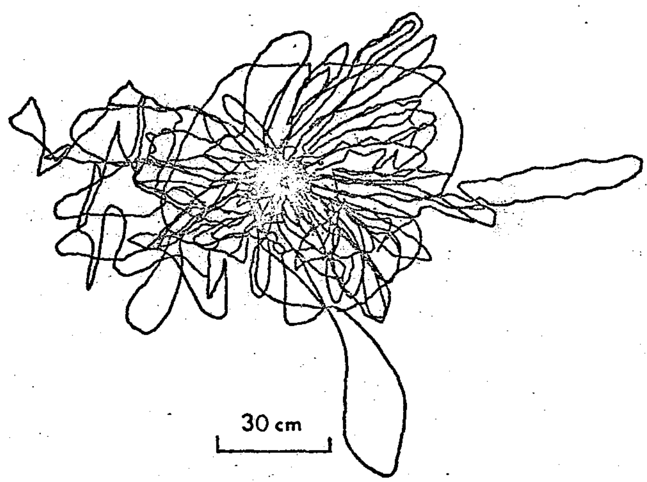
The presence of the feeding range and feeding center is illustrated in Figure 15. These are two tracings of the movements of two fish, Figure 15a of fish #1 in pool AA, and Figure 15b of parr #4 in pool CC, over a ten-minute period. Eighteen such tracings were made in pools AA and CC. Of the 18, only 8 included only feeding movements, and these latter ones were the only ones that could be used in relation to feeding ranges. The distances traveled are tabulated in Table II. From the table it was calculated that the larger fish seldom moved more than 60 cm in any one direction in search of food, only 6.8% of the movements exceeded 70 cm, and 4.8% were greater than one meter. The parr, however, designated as Group B in Table II, had on the average larger home ranges, as 15.9% of all movements exceeded 70 cm, but only 5.2% exceeded one meter.

The range centers of individual fish were very definite; individuals could often be recognized by their association with a pebble no larger than four centimeters in diameter. After excursions away from the range center the fish would return and occupy exactly the same spot.

These sites were semi-permanent, that is they remained



a) Movements of dominant fish in pool AA.



b) Movements of fish #4 in pool CC.

Figure 15. Tracings of the movements of two fish over ten minute periods.

TABLE II. MOVEMENTS OF GRAYLING OVER TEN-MINUTE PERIODS

GROUP A	DATE	POOL NO.	TOTAL FORWARD	0-30 cm	30-60 cm	60-90 cm	90+ cm	TOTAL BACKWARD	0-30 cm	30-60 cm	60-90 cm	90+ cm
	7-9	BB_1	5	4	0	0	1	44	16	12	0	0
	7-16	CC	7	5	1	0	0	38	28	8	0	2
	7-23	CC	9	4	4	1	0	42	16	20	2	4
Mathematical mean for Group A			7.00	4.25	1.66	0.33	0.33	41.33	15.00	7.66	0.66	2.00
GROUP B												
	7-9	BB_1	23	7	14	2	0	52	32	18	0	2
	7-9	AA	14	3	3	4	4	45	21	17	7	0
	7-16	CC	27	6	15	6	0	41	25	7	4	5
	7-16	AA	31	17	6	6	2	48	30	18	0	0
	7-23	CC	30	19	6	2	3	35	20	7	6	2
Mathematical mean for Group B			25.00	10.4	8.8	4.0	1.8	44.2	25.6	13.4	3.4	1.80

the same throughout the summer for as long as the composition of the fish in the pool did not change. If a fish was removed from a pool the rest of the fish behind him would move up and occupy different feeding ranges.

Territories and Hierarchies

The individual grayling in the pools exhibited restricted movements over a small area, their feeding range. An area slightly larger than the feeding range was defended against other members of the species whenever the latter entered it, thus exhibiting definite territoriality.

The first time that the pools were visited on June 25 the territories had already been established and the procedure that the fish had used in distributing themselves was not seen. However, due to the fishes' peculiar fright behavior, some insight on how the original spatial distribution might have taken place can be gained.

Whenever the pools were disturbed, either by someone walking along the bank or seining, the fish scurried at first to the deepest portion of the pool and if the disturbance persisted they moved to the downstream end of the pool. Slowly, after the disturbance subsided, the smaller parr moved to the head of the pool in the vicinity of the position formerly held by the largest fishes. These parr would return mostly in small groups of similar size, the groups of the smallest fish coming first, until approximately 15 minutes later when the largest fish returned. As these groups returned to the head of the pool, each returning individual began a display with its closest neighbor which had already settled in the area, seemingly trying to displace the latter and usually succeeding. Each fish did not display with every fish smaller than itself, but only with the one or two slightly smaller than itself, and only to regain the position held in the pool before the disturbance. As a fish was displaced it moved downstream in the pool, and as it did so, so did every other smaller fish behind it, maintaining fixed distances between the members of the group. For pool CC (Fig. 10) the distances between fish were:

Fish #1 and #2 - approximately 25 cm
Fish #2 and #3 - approximately 25 cm
Fish #3 and #4 - approximately 50 to 60 cm

In pool AA (Fig. 7) dealing with smaller fish, the distances between fish were as follows:

Fish #1 and #2 - 40 cm
Fish #3, #4, and #5 - 20 to 25 cm
Smallest fish - 8 to 15 cm

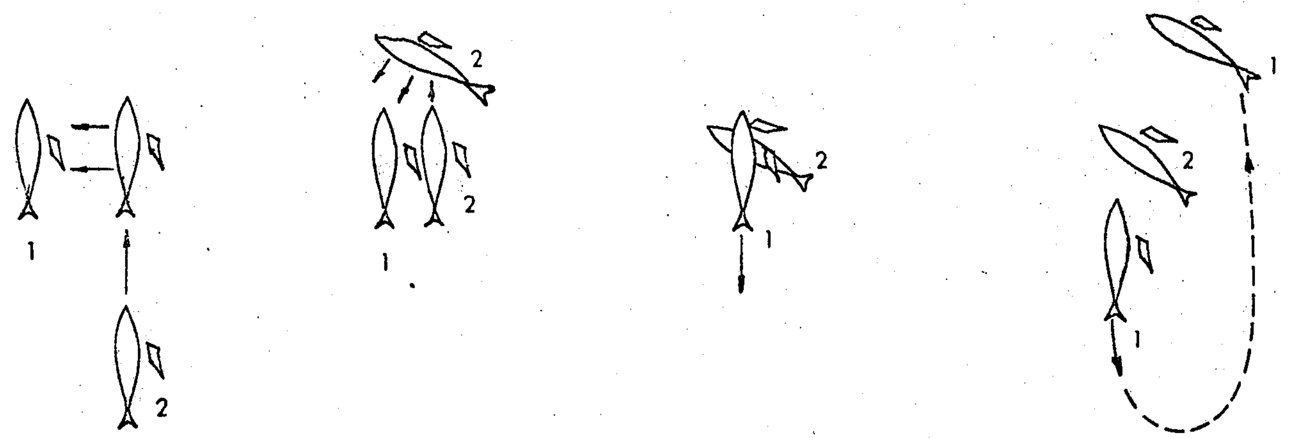
After the pools were disturbed the returning fish began to display with each other. These displays, which are called challenge displays, were always initiated in the same manner.

1. This began with the "invader" moving up to the "defender" until parallel with him.
2. Both fish then lay very still with dorsal fins folded across their back.
3. Then slowly the invader would begin drifting toward the other until their bodies were less than one centimeter apart.
4. Then one, usually the invader, moved forward until 14 or 15 cm away and assumed an arched position so that the inside of the arch was presented to the head of the other fish.
5. In this position the arched fish, the invader, moved backwards and as it neared the defender, the invader began sinking until beneath the defender.
6. Once beneath, it began rising in the water column and as the two fish drew close, the defender would begin drifting backwards (Fig. 16).

At this point one of two things would happen:

1. The retreating fish kept on retreating until it was out of the area.
2. The retreating fish moved around the rising fish until parallel and then the pattern of events was repeated with the protagonists reversing their role.

Figure 16. Steps in establishing dominance in a set.
a. Invader approaches dominant defender.
b. and c. Invader displays and sinks below defender.
d. Defender begins display.



(a) (b) (c) (d)

#1- defender
#2- invader

The display as described above happened quickly, and was observed in its entirety only five times when conditions allowed the use of a glass bottom bucket. Many similar displays had been seen from the surface, but, due to the turbulence and surface reflection, some of the details were missed. Thirty-seven observations made from above the surface all share a striking similarity to the display described above. However, it should be noted that the description above is one of the most complete seen. In most cases the dominance between fish was determined by step 3. The most intense displays occurred among parr 150 to 200 mm long. Among the largest fish the displays very seldom reached step 3, usually terminating at step 2. In pool CC I never saw a display between fishes #1 and #2 go beyond step 1, as fish #2, which was wearing a peduncle tag, was prompt in retreating. The tag-bearing fish, although larger, was found occupying a less dominant position, moved less than any other fish, was frightened more easily than any other, and recovered from fright much slower, so that it always was the last fish to return. The great majority of displays in my notes appear as follows:

July 13, Pool CC, 1700

"Involving fishes #3 and #4. The two fish moved until parallel to each other, then the aggressor moved forward five inches and assumed a scimitar stance, and began drifting toward the defender, the latter drifted back with the current and left the territory. . ."

In all of the pools, if the lead fish moved either forward or backward, the rest of the fish responded by doing the same as a group. The critical distance that the lead fish had to move before the rest of the group followed was not determined. Nine times in pool AA, and five times in pool CC the lead fish rushed up to the riffles and spent several minutes there. Slowly the fish occupying #2 position moved up until they occupied the spot previously occupied by #1. On #1's return the fish did not move back to their old places until #1 displayed mildly with #2, at which time all of the fish moved back to their old positions.

In pool CC it first became apparent that the positions occupied by #1 and #2 were, for the same reason, favored by the other fish in the pool. Whenever one of the two moved out of the pool, their exact positions were taken over by fishes #3 and #4. This type of behavior was especially well demonstrated in this pool when fish #2 vanished, apparently taken by a fisherman on July 28. Upon his disappearance fishes #3 and #4 moved up to #2's position. There a series of interactions in the form of displays between the two fish took place, until #4 remained and #3 moved approximately 30 cm back. A week later a fish approximately 250 mm in length had moved into the pool and occupied exactly the same spot previously held by #2, and #3 and #4 moved back to their former positions.

Similar behavior had been exhibited in several of the pools used for the collection of fish. In these, within 24 hours of the removal of the larger fish, the inhabitants had reorganized themselves by moving up and occupying the exact spot of the removed fish.

Once the territories were established, the fish still occasionally interacted, as smaller fish appeared to be constantly attempting to move forward in the pools. Competition for position was especially keen among parr occupying the middle of the ordering, and considerable energy was expended in maintaining and defending the position in the pool against fishes of similar sizes.

The larger individuals were especially tolerant of fish much smaller than themselves to be present ahead of them. Thus, in pool AA_1 there was a parr, #3, which occupied a position upstream and north of fish #1 (Fig. 7). This situation was allowed as long as #3 did not move toward the center of the current. Whenever #3 moved across line I-I (Fig. 7), which denoted the end of a sand bar, he was subject to attack by #1. If #3 moved too far back he was promptly attacked by #4. In pool CC there was a fish approximately 130 mm long between fishes #1 and #2, but off to the south. This fish was not allowed to come toward the center by #2, but otherwise was not molested except by #'s 3 and 4 who regularly tried to chase the fish out of the area at least once per observation period. In the "chases", #3 or #4 would rush toward the smaller fish, which fled to the head of the pool only to return slowly a few minutes later.

During the defense of territories by the various fish, the following types of displays took place:

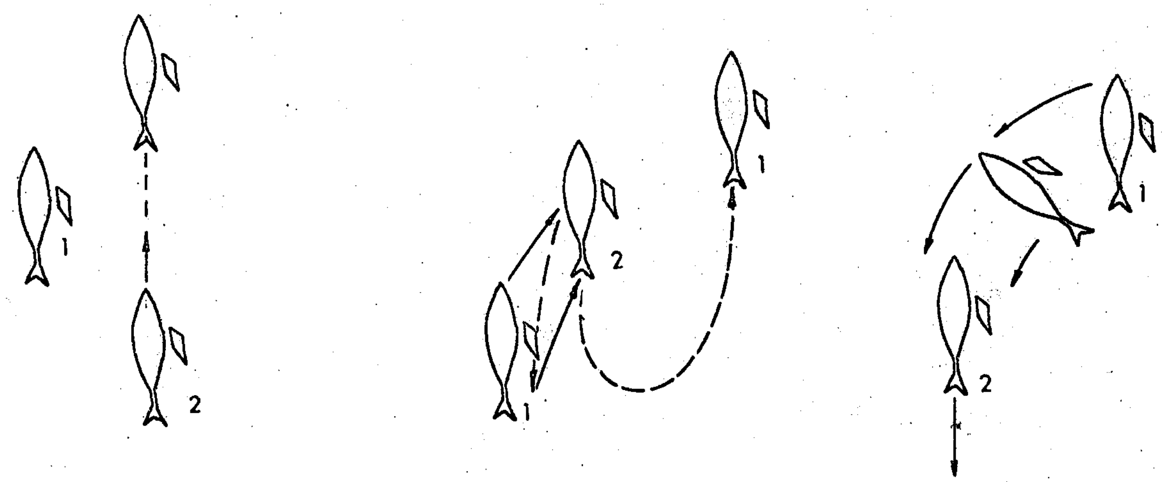
The invading fish would move to a position ahead of a larger fish, the latter would make quick rushes to the invader's flanks, when 5 or 6 cm apart, and 4 to 5 cm upstream of the invader. Then the defender would slide or drift backward toward the other fish at a position 30° to the current. Most of the time, 33 out of 42 observed displays, the invader would drift backwards as the defender got to within 3 cm of the invader's snout (Fig. 17).

Two variations of the above display have been observed. In one the defender simply rushed up to the invader's side and the latter quickly left the area, swimming with the current and the defender in pursuit. Actual contact was never made.

In the second variation, the invader did not leave the forward position when rushed, but moved instead to one side of the pool. This behavior was observed only five times. Each time, as the invader moved toward the side of the pool, the defender returned to his usual position. A few seconds later, the defender followed with a new rush as before, to which the invader responded by moving to some other position or by going back to the lower end of the pool. After the

Figure 17. Steps in territorial defense.

a. Invader assumes dominant position.
b. Defender rushes invader.
c. Defender displays to invader.



(a) (b) (c)

second charge, as happened in three of the five situations, the defender would rush and pursue the intruder, harrassing him continuously until he left the territory. Of the three incidents, twice the invader left the territory on the third rush and once on the first rush.

Fish of similar size seldom interacted, and the few times that they did, each individual returned to its range center after very mild displays.

On July 16 I recorded a defense of an area by more than one fish. This was the first time that I had observed this, but similar behavior was later observed twice at pool CC. In the incident at pool AA, fish #5 moved next to #4 and was promptly rushed by #4. #5 seemingly ignored #4 and moved to a position between #1 and #4. Both #1 and #4 rushed #5's flanks, stopping approximately 1 cm from actual contact. After #1 and #4 joined the melee, #5 swam back to its original position.

Figure 18 shows the movement of #4 after another larger fish moved to a position approximately 60 cm ahead of #4. Note the increase in area covered during the ten minutes, and the four dashes toward the intruder, which are labeled I,II,III, and IV. These were of decreasing intensity and took place only during the first two minutes of intrusion.

In the fall the hierarchial ordering appears to break down completely (Fig. 10b). On September 16, the breaking down of the hierarchy was very noticeable at pool CC, where

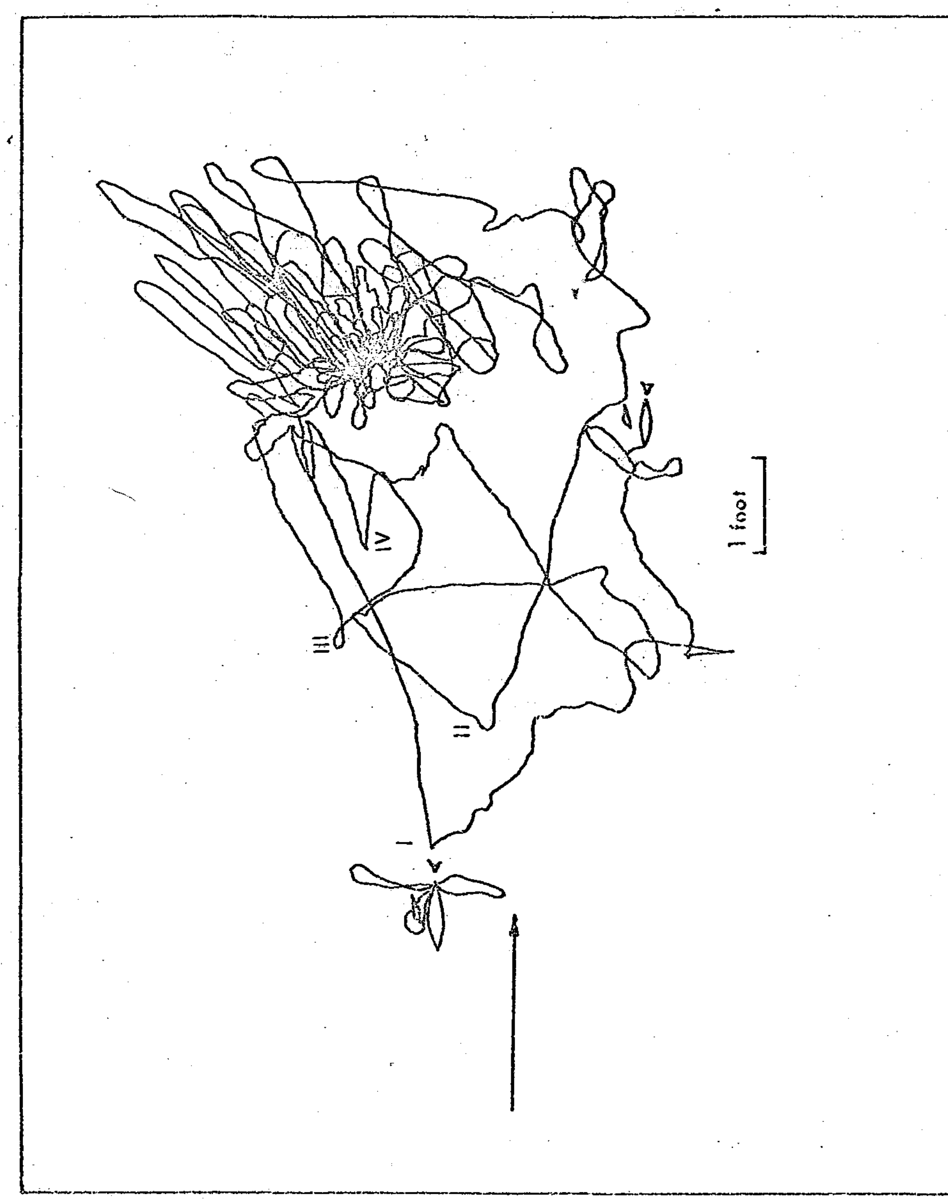


Figure 18. Movements of fish in territorial defense. Arrow indicates direction of current. See text for discussion.

adults and sub-adults were intermixed horizontally, and all occupied positions close to the bottom. No displays of any type were noted over a seven hour period, although twice smaller grayling moved rapidly back in the pool upon the approach of their counterparts.

DISCUSSION

In the distribution of living organisms it is found that many animals tend to aggregate, mostly for mutual benefit (Allee et al., 1949). These aggregations, particularly among vertebrates, are brought about primarily through three major principles of behavior--territoriality, hierarchy, and home range. Most animals display just one of these principles, but subtle traces of the other two can often be found.

Although many kinds of territoriality are recognized (Allee et al., 1949, p. 412), the most commonly described is the mating territory, in which the nest is defended against all intruders by one or both members of an established pair. In fishes this was first described by Noble and Curtis (1939) in the cychlid *Hemichromis bimaculatus*, and in the poeciliid *Xiphophorus helleri* by Noble (1939).

Territoriality in non-spawning individuals has been described by Greenberg (1947) among immature and adult green sunfish (*Lepomis cyanellus*). In this species the territories established were defended by the residents against subordinates but not against dominant individuals.

The concept of home range in fishes has been used by Gerking (1950, 1953) in discussing the stability of fish populations in streams, and later by Newman (1956) in the study of interspecific competition between two trout.

Although all of the studies mentioned above use Burt's

(1943) definition of home range, none of the works on fish used the definition as the authors had defined it. Gerking (1950, 1953) and Newman (1956) when discussing the home range and home areas of salmonids, interpreted the home range as being the pools in which the fish had been tagged. Some of their pools were in excess of 300 feet long. When discussing movements in an out of the home range the authors interpreted it as meaning movement from pool to pool, and this was tested by the tag and recapture method. However, Miller (1957) showed that the home pool was more than a home range for some trout, because some trout were born, grew, reproduced and died within one pool, and different parts of the pool were used for different life processes. Further studies might indicate that the home range in the pools, using Burt's definition, might be considerably smaller than previously thought.

The present study is unique in that a home pool was observed as a unit, and its inhabitants were observed individually and in relation to each other under natural conditions. The data indicate that the Arctic Grayling in McManus Creek during the summer indeed have true home ranges as defined by Burt (1943). In these "home ranges", which here are discussed as feeding ranges, there is a range center where most of the time is spent, and from which all forays, whether feeding or otherwise, begin and end. These feeding ranges varied little with the size of the fish, although parr appeared to make slightly longer feeding forays than adults.

Gerking (1953) defined defense of territory as "the aggressive response of an animal for the protection of an area from invasion." Following the above definition, then, the arctic grayling in the stream do exhibit territorial defense.

The territory defended by these fish tended to be slightly larger on the upstream side than the feeding range, and only the area ahead of the fish was defended. The territorial defense movements differed from feeding movements in that they were more intensive (i.e., quicker movements), and often covered a distance twice as long as the feeding movements.

In the defense of territory the grayling followed through what appeared to be a ritualistic display. They bent their body in a scimitar shape while drifting toward their opponent. A similar display is described for *Platypoecilus maculatus* by Braddock (1945), who interprets the bent body as a challenge movement.

Fabricius and Gustafson (1955) briefly described the aggressive behavior of the European grayling *Thymallus thymallus*. *T. thymallus* apparently is much more aggressive, its activities involving considerable physical contact and resulting in nipping at each other's tails and flanks. Aggressive behavior also involved violent vibrations of the body and erection of the dorsal fin, none of which occurred in McManus Creek during the period studied. The dorsal fin of the arctic grayling is larger than the ones on the European species, and the musculature controlling the movements of the dorsal rays, as revealed by dissection, appears poorly developed. This, coupled with the creek's fast and turbulent current, would make the use of the dorsal fin as a display organ disadvantageous. Due to its size, it would offer, when extended, a considerable surface area for the current to act upon. Hence, gains obtained by using such an organ for displays would probably be offset by the energy utilized in fighting the current. Perhaps the fish in the slower Alaskan streams and lakes may employ the dorsal fin to a larger extent. The lack of utilization of such an obvious organ as the large fin of the arctic grayling presents a puzzle. Its size and coloration would lead one to speculate that it would have great adaptive value in the life of the grayling, and yet none was found. It is unfortunate that the spawning behavior of the fish was not observed, because possibly the answer to the fin's significance might be found there.

When the fish established their distribution in the pools, it was found that the distribution was attained through a series of aggressive displays, in which one fish became the dominant and occupied the forward position in the pool. In each set of displays a set of dominant-subordinate relationships were formed. The subordinate fish expressed his submission by backing off slowly 5 to 10 cm, and then fleeing with the current and re-establishing a feeding or territorial center 25 to 50 cm downstream.

The establishment of sets of dominant-subordinate relationships automatically resulted in the establishment of a hierarchy. This hierarchy was not a true straight line hierarchy, since many of the smaller fish were allowed between and around more dominant fish (Fig. 19). It resembled more closely a pseudo-straight line hierarchy where the positions of one or more individuals were undetermined. The undetermined individuals consisted primarily of the smallest occupants of the pools which were often allowed in positions close to members several times larger than themselves. A hypothetical hierarchial ordering of the fishes of a pool is shown in Figure 19.

Fishes setting up territories in a stream are faced with environmental factors much different from pond-living fishes or fishes held in tanks. The primary difference is the presence of a strong current. Most lotic organisms, and fishes are no exception, exhibit rheotaxis (Fraenkel and Gunn, 1961). That is, the fish turn so as to face the current and spend most of their time and considerable energy swimming just strongly enough to keep their location in the stream. Rheotaxis was brilliantly demonstrated by Lyons' experiments in 1904 which are summarized in Fraenkel and Gunn (1961). His fish, whenever placed in standing water, displayed milling behavior, while in running water or simulated running water they always

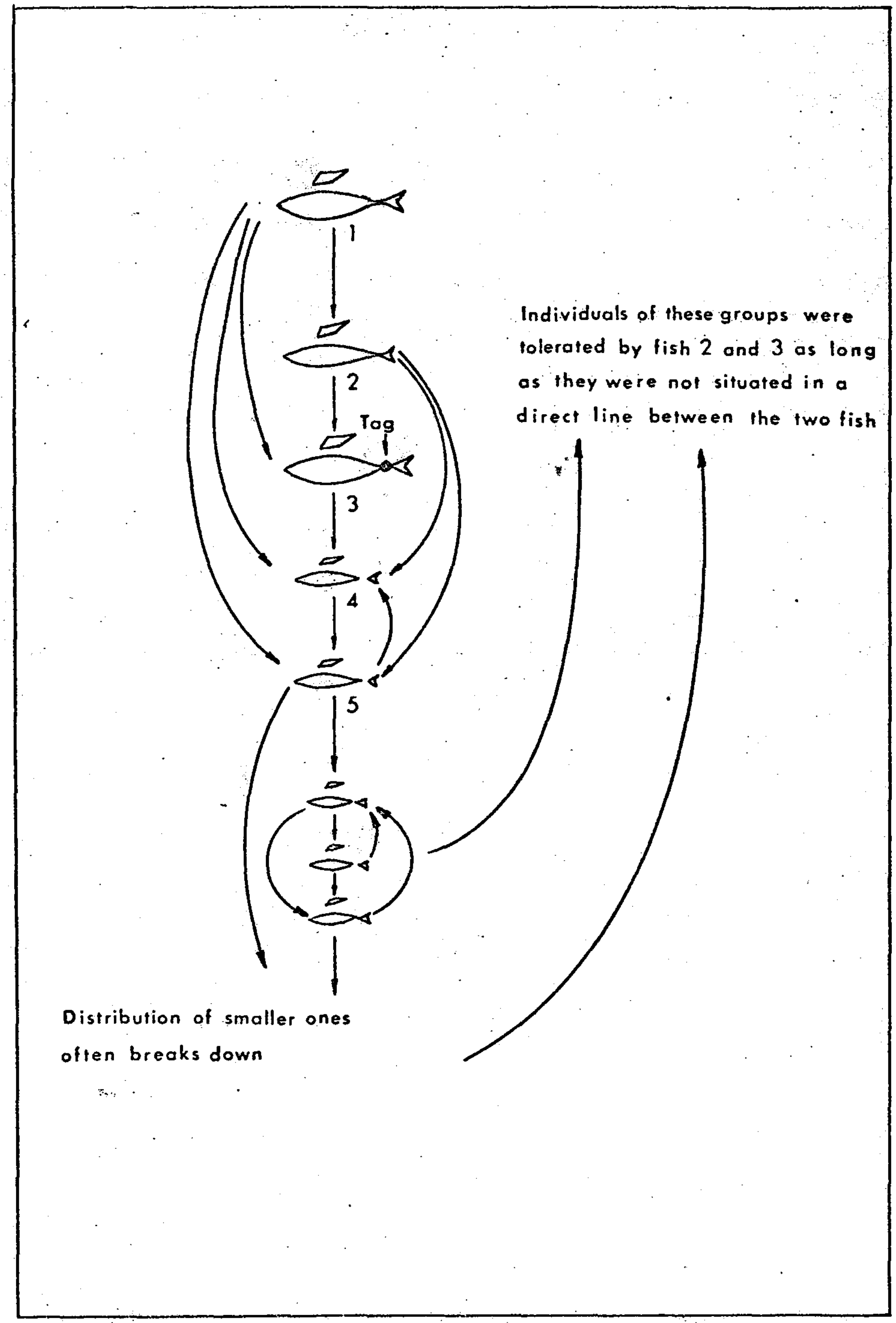


Figure 19. Hypothetical hierarchial ordering of fish.

oriented themselves against the current. Grayling displayed this also. Specimens removed from the Chena River in October 1968 and placed in standing tanks oriented themselves at random, and when disturbed exhibited milling reactions. The same fishes moved to a Living Stream tank immediately oriented themselves facing the current and remained in this position for the month that they were held. Increasing or slowing the current did not affect their orientation. In the field, such observations were complemented when the grayling in the reservoir at Homestake and Charity Creeks broke up their pool ordering as soon as the water in the reservoir began rising and the current all but disappeared. It is interesting to note that schools formed in standing pools, such as the one below the diversion dam, show a similar within-school distribution as the distribution of the fish in the pool, the primary difference being that the distance between the fishes was much reduced. That is, the largest fish are found in the front and center of the schools, and the smaller ones occupy the outside and rear.

Due to the grayling's rheotactic orientation and their feeding habits (see section on feeding behavior), the grayling's territories differ in shape from other territories described for fishes inhabiting lentic waters. In the grayling's territories the center was located at the downstream portion of the guarded area. All of the defense movements take place upstream or to the side of this position. If one looks at the distribution of the fish and the shape of their territories within a hypothetical pool, the result would be sets of semi-lunar territories, one behind the other, broken down into smaller but more numerous such territories as one moves downstream (Fig. 20). I suspect that if more stream inhabiting fishes were closely observed in their natural habitats, similar within-pool distribution and possible hierarchies would be found.

Greenberg (1947), Gerking (1953) and Newman (1956) describe the hierarchies displayed by the fish that they studied as a nip-right ordering. The dominant fish in nip-right hierarchies asserted their dominance by nipping the flanks of subordinates. The more dominant individual was noted, by Greenberg (1947) and Braddock (1945), to be nipping more frequently than the others. Within the framework of their fishes' hierarchies there was a steady downward progression in the amount of nipping done by fishes occupying the several ranks. In grayling the nip-right type of hierarchy was not present, since physical contact between displaying individuals was never made. Contrary to what Greenberg and Braddock observed in their studies, with the grayling there was an upward progression in the number of displays occurring by the fishes occupying the several ranks. Thus, the more dominant fishes very seldom displayed. Seemingly,

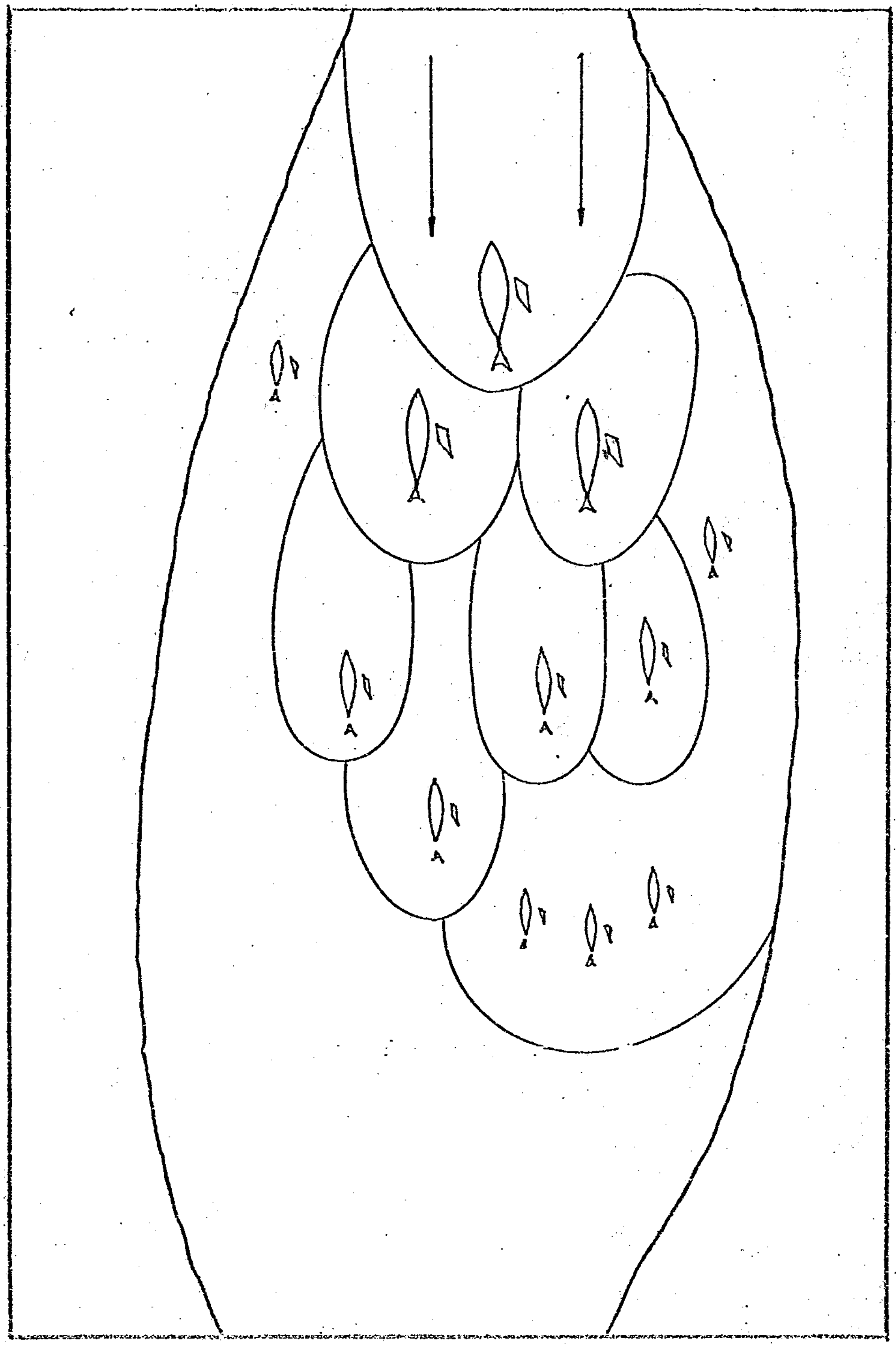


Figure 20. Hypothetical distribution within a pool. Elliptical lines indicate approximate boundaries of defended territory.

the size of the dominant individuals was enough to inhibit any challenge motivation from subordinate members of the pool.

The displays observed during the formation of the distribution appeared to indicate that dominance was achieved primarily by the more aggressive and biologically better fit member of the pair, which usually was the larger member. This explains the secondary position occupied by the tagged fishes, even though they were the largest fishes in the pools. Hoar (1953) found tagged coho smolts (Oncorhynchus kisutch) also occupying subordinate ranks and in poor condition. He attributed this to their being kept from feeding by the healthier individuals.

The breaking down of the hierarchy of the grayling in the fall appears similar to situations described by Hoar (1953). He found that coho smolts were characterized by aggressive behavior during the seasons when they occupied particular locations. The smolts lost their aggressiveness during periods nearing migration time. The grayling lost their aggressiveness, and thus disrupted the hierarchies in the pools in September. This was a period when considerable movement was taking place, as shown by the complete changes in composition in the pools.

FOOD HABITS

METHODS OF STUDY

Grayling were collected weekly in the upper and middle sections of the stream from July 1 to September 16, 1968, for determination of food habits. During each collection period, the relative abundance of food organisms present in the stream was determined by collecting the benthic organisms present in three square feet of riffles by means of a standard square foot Surber net. No attempts were made to determine the abundance of terrestrial or pool-inhabiting benthic organisms.

The organisms collected were preserved in 70% ethyl alcohol and later identified, counted, and sorted into the various taxonomic groups (Table 1, Appendix II). Their abundance for each half of the month was determined (Figs. 21 and 22).

A total of 68 stomachs was collected, none of which was totally empty. The fish were taken by hook and line, and it appeared that no regurgitation of food took place. While the fish were fresh, their stomachs were removed and placed in vials containing 70% ethyl alcohol.

In the laboratory each stomach was treated as a unit. The contents were removed and the total volume determined. Then the contents were sorted under a dissecting microscope into various taxonomic groups. The numbers present from each

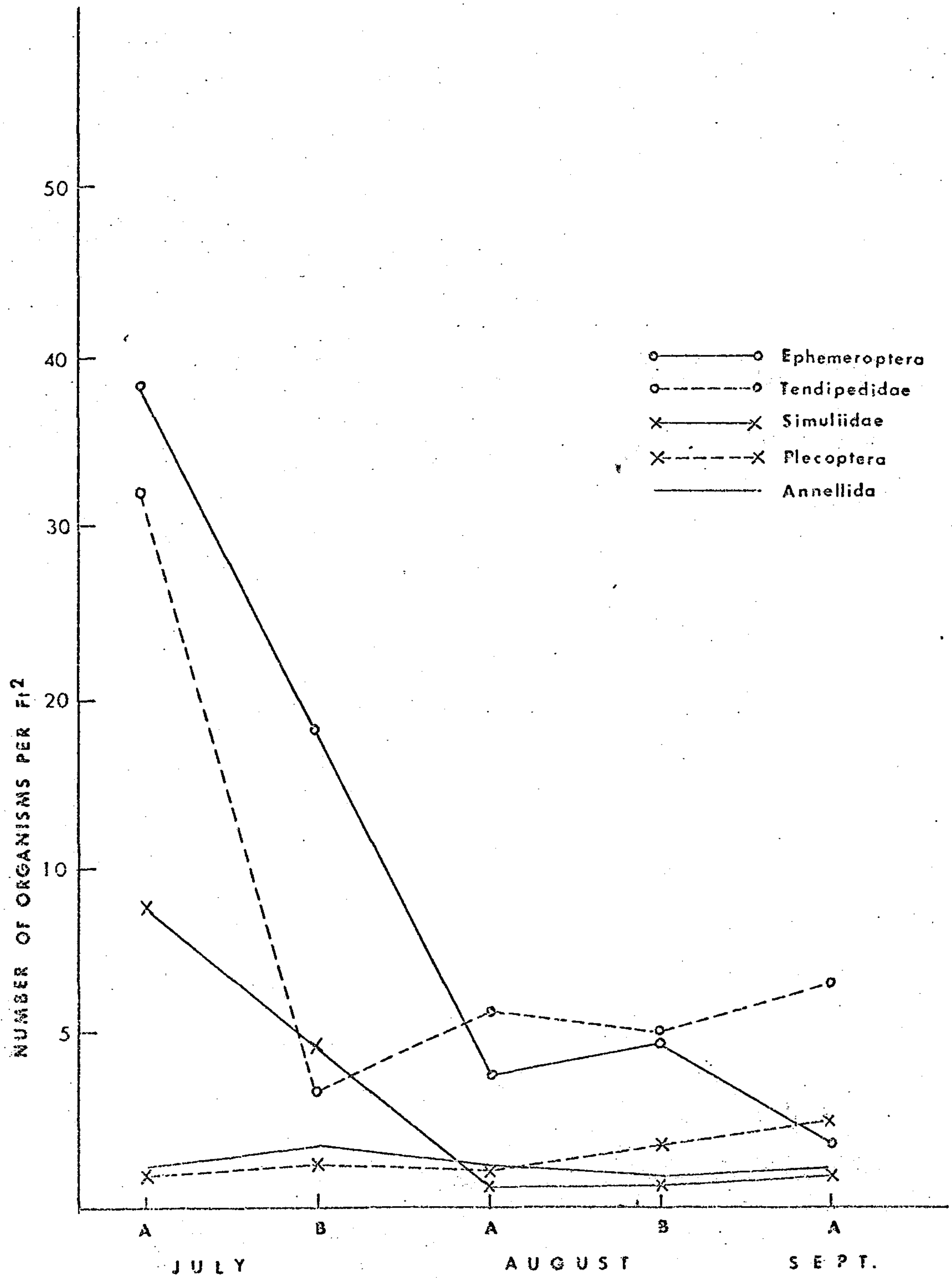


Figure 21. Absolute abundance of organisms in the stream. A = first half, B = second half of each month.

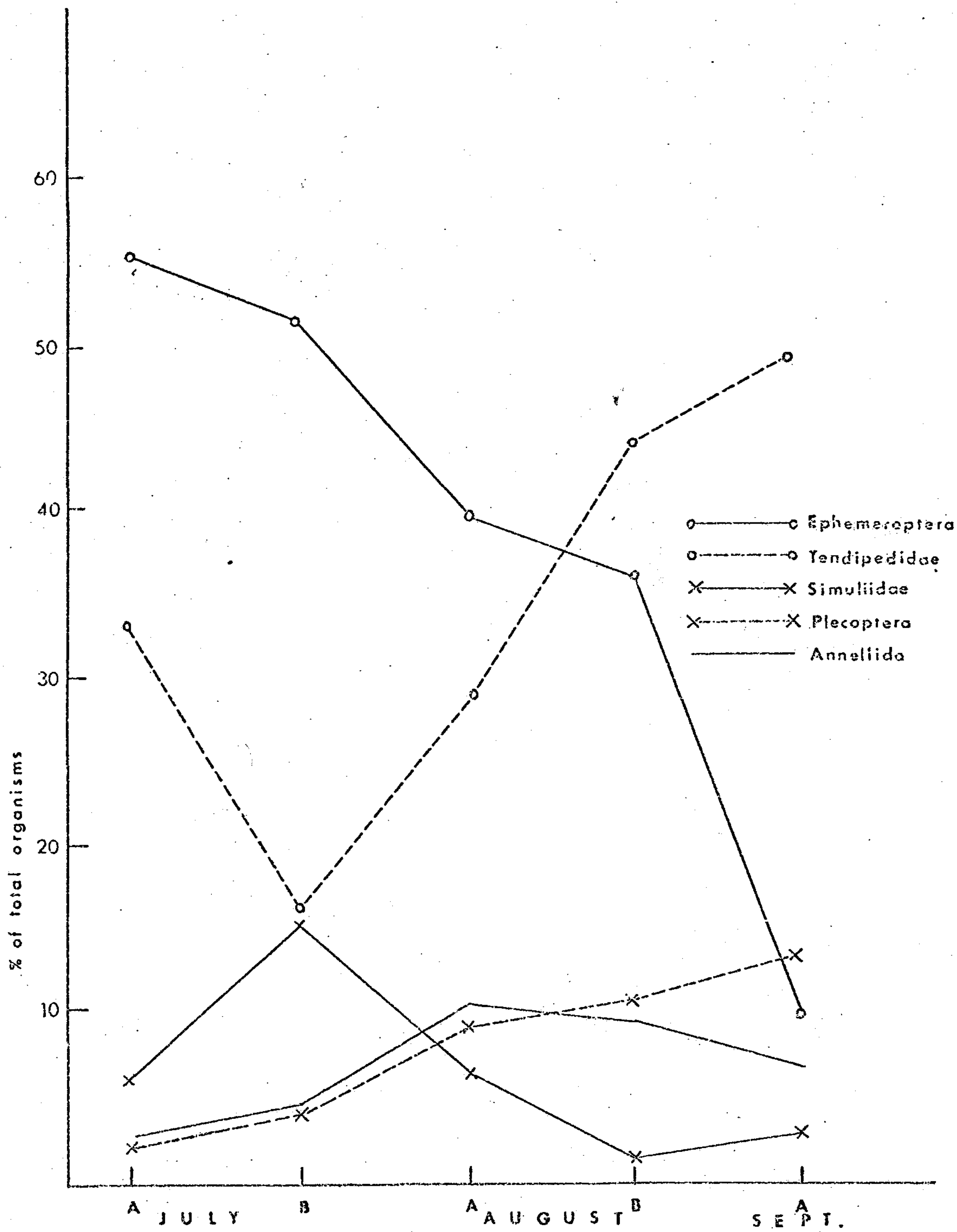


Figure 22. Relative abundance of organisms in the stream. A = first half, B = second half of each month.

group and the volumes were determined. Volumes were determined by water displacement using a calibrated centrifuge tube. For small items the 0.2 ml marks were used and estimations were made. For food items too small to be measured, only their presence was recorded.

The frequency of occurrence, volumetric method, and numerical method of analyzing stomach contents were all employed because it was felt that one method alone would not give a true estimate of the importance of the food items. Consideration of only the numbers of the various food items will not give a good picture of the importance because of the large differences in size of individuals. Volumetric measurements are biased in favor of larger items because they take longer to digest. Frequencies, on the other hand, tend to be biased in favor of smaller items (Windell, 1968).

From the three methods of stomach analysis, an attempt to determine the relative importance of the aquatic organisms utilized by the fish as food items for the summer was made. On standard graph paper the frequency of occurrence was plotted on the Y axis, on the positive X axis the mean percent of organisms per stomach was plotted, and on the negative X axis the mean percent volume was plotted by breaking down the total volume of the recognizable food items so that they occupied a segment equivalent in length to the segments of the other two axis. In this manner, for each food item a triangular area was enclosed, and the ratios of the areas formed by these triangles were used as relative indices of importance (Fig. 29).

RESULTS

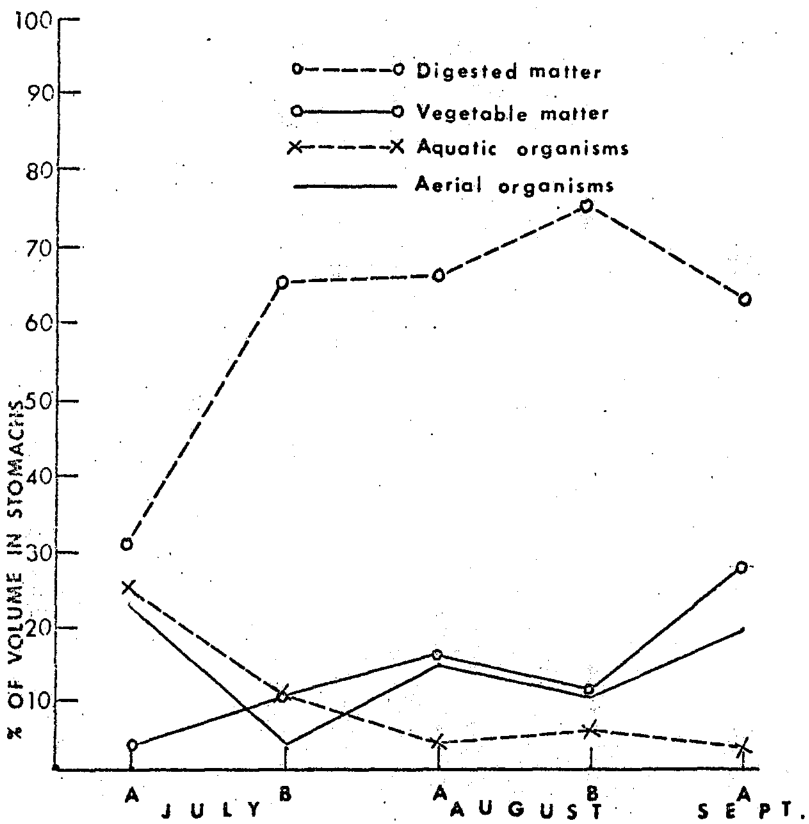
Utilization of the food in the habitat

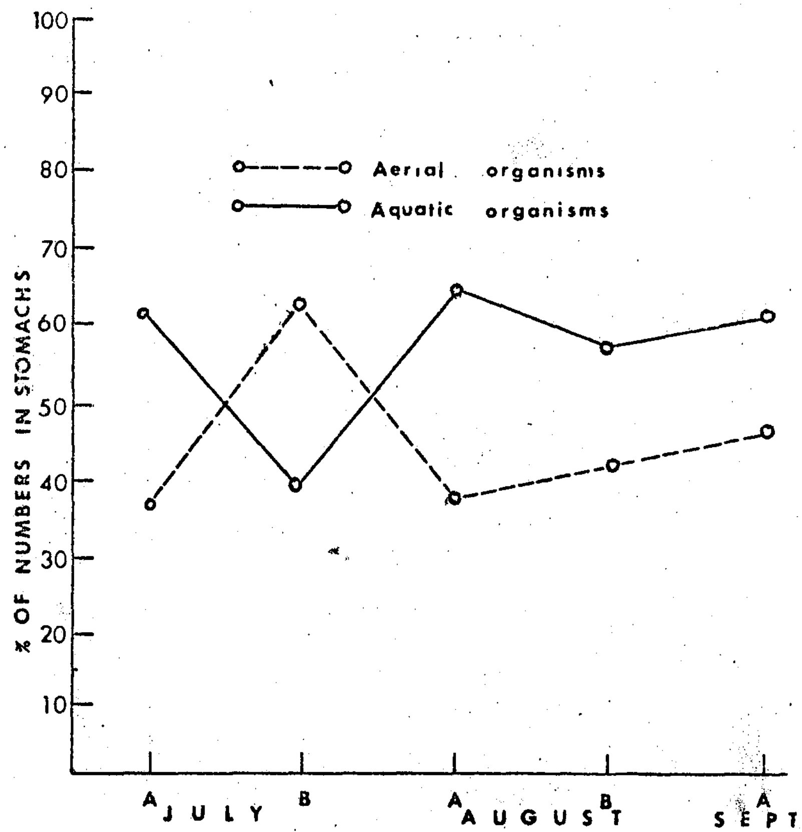
With the exception of the last two weeks of July, which corresponded to the warmest two weeks of the summer, aquatic organisms constituted a higher percentage both numerically and volumetrically of the diet of the fish than aerial insects (Fig. 23). The aquatic organisms made up a greater percentage of the diet in August and early September, even though the number of aquatic organisms available ~~were~~ was at ~~their~~ its highest in early July, at which time the average number of insects per square foot was more than twice as great as at any other time during the summer (Table I, Appendix 2).

Ephemeroptera - Mayfly larvae were the most numerous organisms in the riffles during July and the first half of August. Their relative importance declined as the summer progressed, falling sharply in the first two weeks of September, when they made up only 12% of the organisms present (Fig. 22).

In the stomachs ~~these~~ mayflies were found only as larvae, appearing in nearly 30% of the stomachs collected. Their peak of occurrence in the stomachs was in early July, corresponding to the peak of abundance in the stream. At this time, in the stomachs, they made up only 6% of the total number of organisms present, but, even so, numerically they

Figure 23. Volumetric and numerical distribution of food organisms. A = first half, B = second half of each month.


100
90
80
70
60
50
40
30
20
10
% OF VOLUME IN STOMACHS
Digested matter
Vegetable matter
Aquatic organisms
Aerial organisms
A
JULY
B
A
AUGUST
B
A
SEPT.


100
90
80
70
60
50
40
30
20
10
% OF NUMBERS IN STOMACHS
Aerial organisms
Aquatic organisms
A
JULY
B
A
AUGUST
B
A
SEPT.

were second in importance. As the summer progressed, their abundance in the stomachs declined, and by September they had completely disappeared. Volumetrically ~~the importance of~~ the recognizable mayflies in the stomachs had nearly vanished by the second week of July (Fig. 25).

Plecoptera - Stone flies larvae appeared in small numbers in the stream in July, when less than one individual per square foot was found, but they increased slowly, reaching a maximum in the last samples collected in September. At that time, they made up more than 15% of the total number of organisms present, and had a frequency of 3.4 individuals per square foot.

In the stomachs, they were the third most abundant aquatic food item in early July and early August, when they made up nearly 11% of the total organisms present. They decreased steadily through late August, disappearing entirely by September 16th.

Volumetrically they were the most significant food items found in early July, a time when their presence in the stream was at its lowest. In September, when they were at their maximum abundance in the stream, they did not occur in the stomachs. Stone flies were the only insects found in the stomachs in significant numbers both as larvae and adults. Since the adults found in the stomachs had the wings fully extended and the body completely sclerotized, it appears

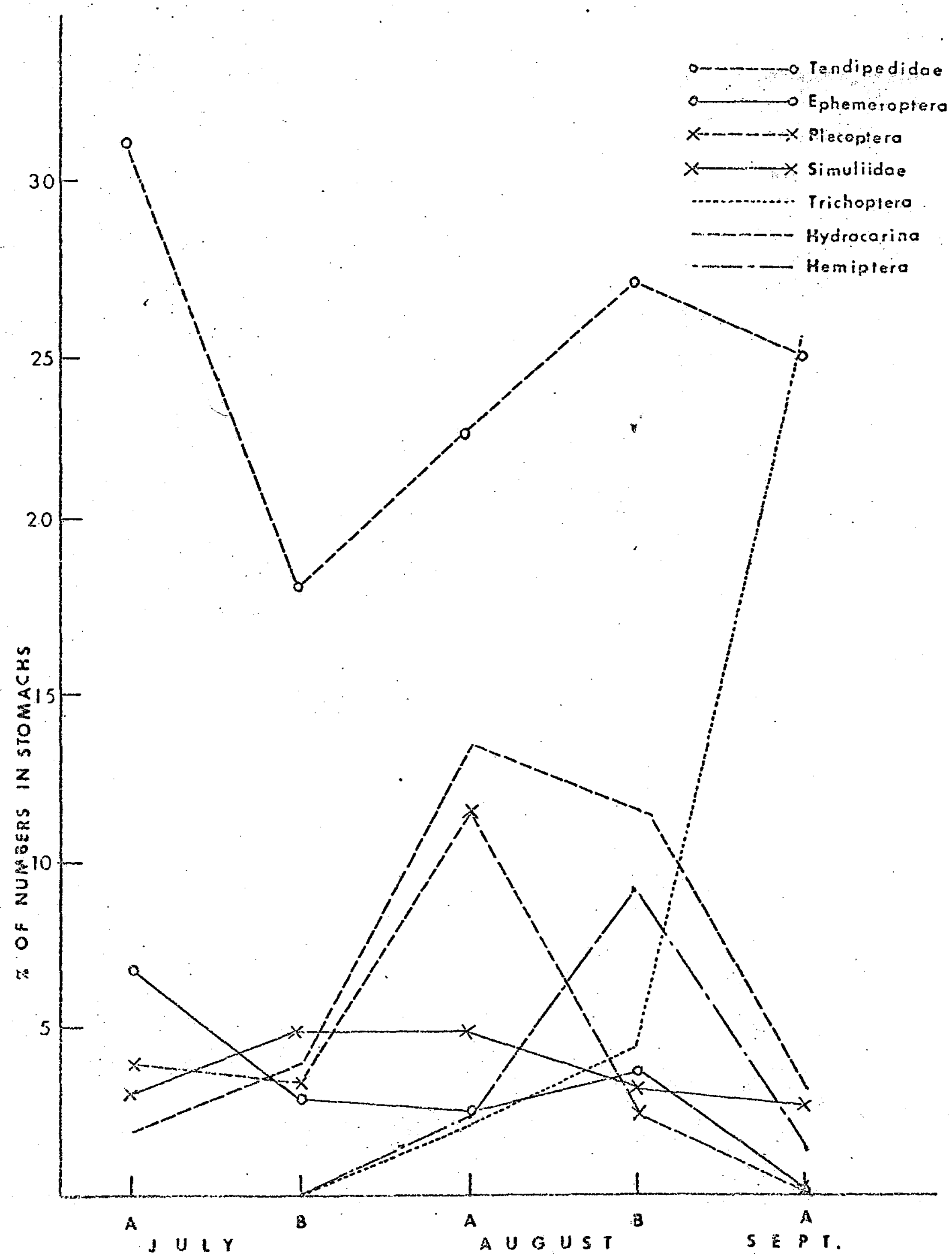


Figure 24. Numerical abundance of aquatic organisms in the stomachs. A = first half, B = second half of each month.

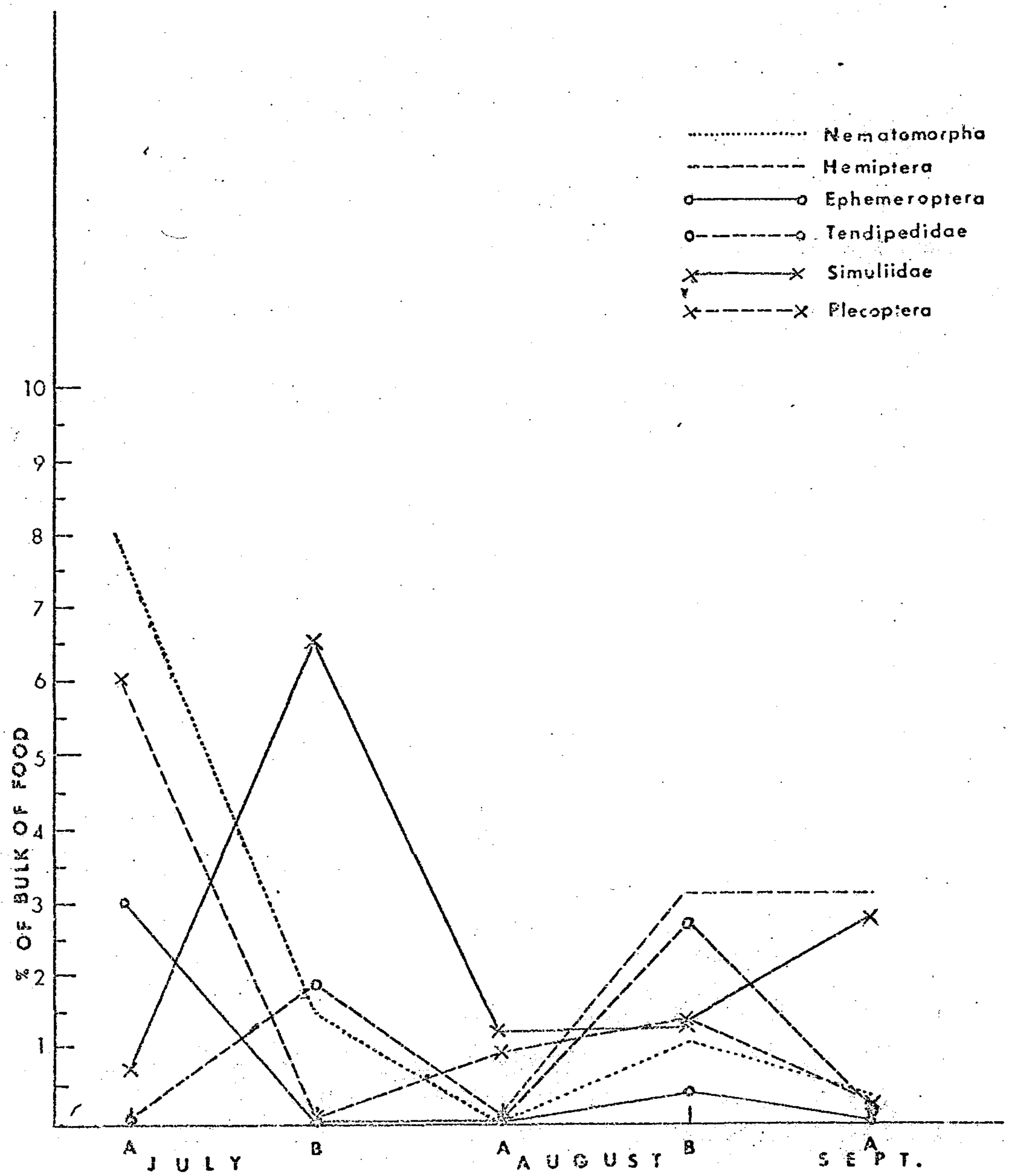


Figure 25. Volumetric abundance of aquatic organisms in the stomachs. A = first half, B = second half of each month.

probable that the insects when taken by the fish were hovering over the water. Thus they were included among the aerial insects.

Trichoptera - ~~The~~ Caddisfly larvae were absent during the summer in the stream's riffles. However, large numbers of individuals could be seen moving in the pools. They began to be found in the fish stomachs in early August, reaching a maximum in September when numerically they were as important as the Tendipedidae, which were the most abundant organisms (Figs. 21 and 22). Volumetrically they became significant during the latter part of August, and then declined slowly through September as did most of the other organisms.

Diptera - The only aquatic dipterans collected in measurable amounts were members of the families Tendipedidae, Simuliidae, and Tipulidae.

Tendipedidae - Midge flies were the second most abundant organisms found in the stream in July and early August, but became the most numerous during late August and September. Their low point in relative abundance occurred in late July, then began climbing steadily (Fig. 25), reaching their maximum abundance at the last sampling date.

In the stomachs they were the most numerous single organisms found. Their ups and downs followed closely the variation of the population of the stream, the one exception being September. At this time, while the stream population increased, the abundance in the stomachs declined. It should be noted that, although the relative abundance in the stream changed, the absolute numbers of organisms remained rather constant (Table I, Appendix II).

Due to the midges' small size, their volumetric values were not as high as one would expect from the numbers present. The high volumetric values for late July and late August are not necessarily correlated to the numbers present, but rather to the size of the individuals; during sorting of the late July and late August samples it was found that the individuals were considerably larger.

Tendipedidae were very common in the drift samples collected between 2000 and 0200 from August 1 to the 15th, at times making up as much as 93% of the organisms collected. In each drift sample these organisms were found encased in a jelly-like substance and entwined in filamentous algae. No organisms were found in the drift samples collected on September 2 and 16 (Table III).

Simuliidae - The black flies appeared in large numbers in the stream in mid-July, at which time they were found attached by the thousands to the rocks of the riffles, appearing as a black carpet. After emergence of adults in August, the numbers in the stream decreased markedly.

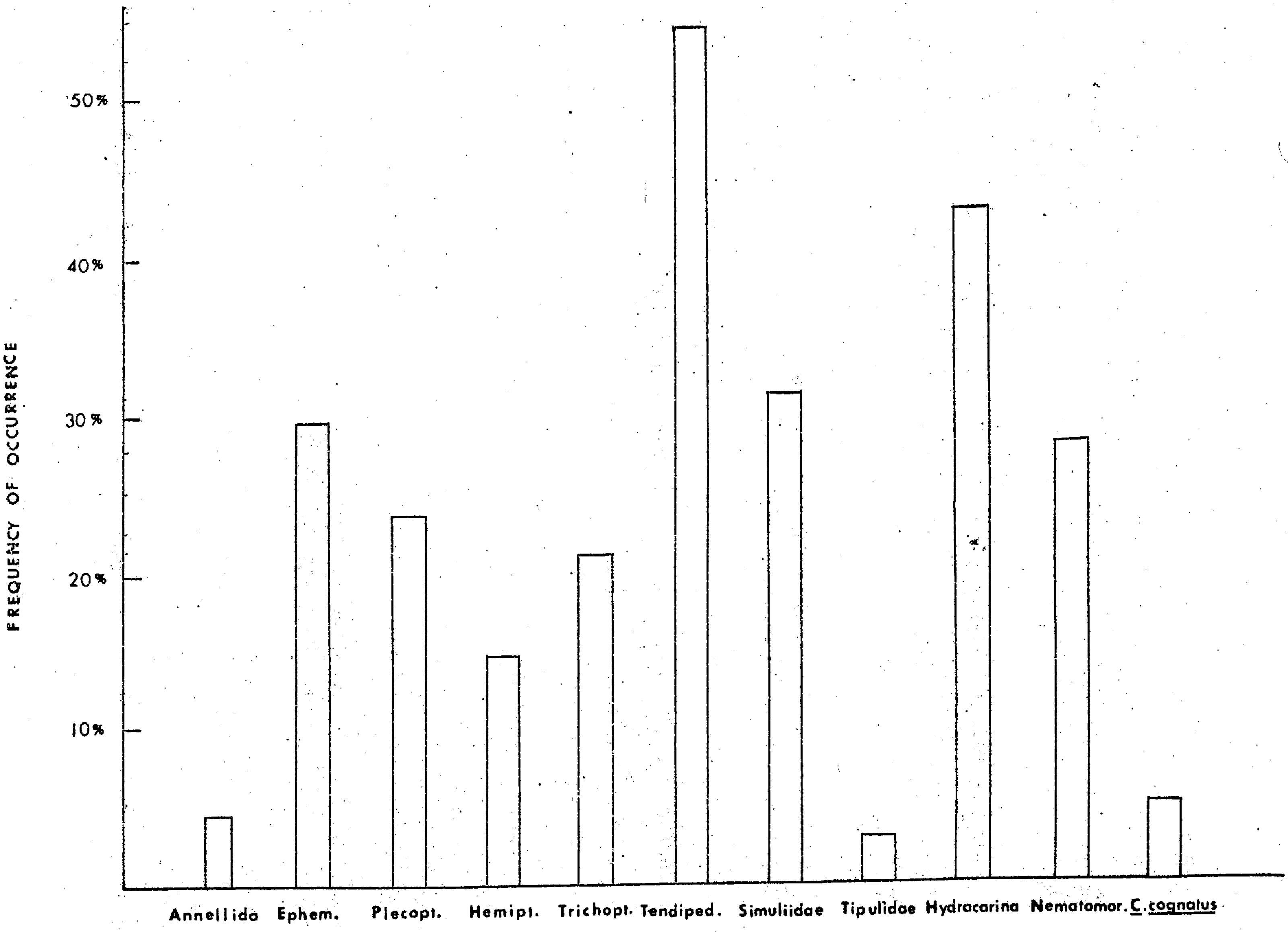
In the stomachs these organisms' abundance followed closely the changes in population. When the Simuliids reached their peak in the stream in mid-July, they also became the most important aquatic food items volumetrically.

Tipulidae - The crane flies were not as common as the other previously mentioned organisms either in the stream or in the stomachs, occurring in only 2.9% of the latter (Fig. 26). They were found singly, contributing little to the bulk or to the percentage of total numbers in the stomach, consequently they are interpreted as being incidental food items. Their scarcity in the samples may be due to their habits of living underneath rocks and in crevices.

Hemiptera - The order Hemiptera was represented only by members of the family Corixidae. These water boatmen were never found or seen in the stream, but did occur in 14.7% of the stomachs, and contributed considerably to the bulk in late August and September, a time when the absolute number of organisms in the stream was decreasing. Volumetrically, at this late time, the Hemiptera became the most important food item.

Acarina - Water mites (Hydracarina) were never collected in the stream, however they were numerous in nearly half of the stomachs. The species collected were anatomically adapted for swimming, having long oar-like appendages. At least four free living species were represented, but none showed signs of being digested.

Figure 26. Frequency of occurrence of aquatic organisms in the stomachs.


FREQUENCY OF OCCURRENCE
50%
40%
30%
20%
10%
Annellida
Ephem.
Plecopt.
Hemipt.
Trichopt.
Tendiped.
Simuliidae
Tipulidae
Hydracarina
Nematomor.
C. cognatus

Annellida - Segmented worms were moderately abundant in the stream, reaching a maximum abundance of 10% of total organisms in the stream in early August, and then diminishing slowly. They were found in interstices between and under rocks, which might explain their absence from the fish stomáchs. They occurred in only 4.4% of the stomachs, and always singly.

Nematomorpha - 27.9% of the stomachs contained large numbers of long, thin, brownish worms, a sample of which were identified as Nematomorpha of the genus *Gordius* or *Paragordius*.

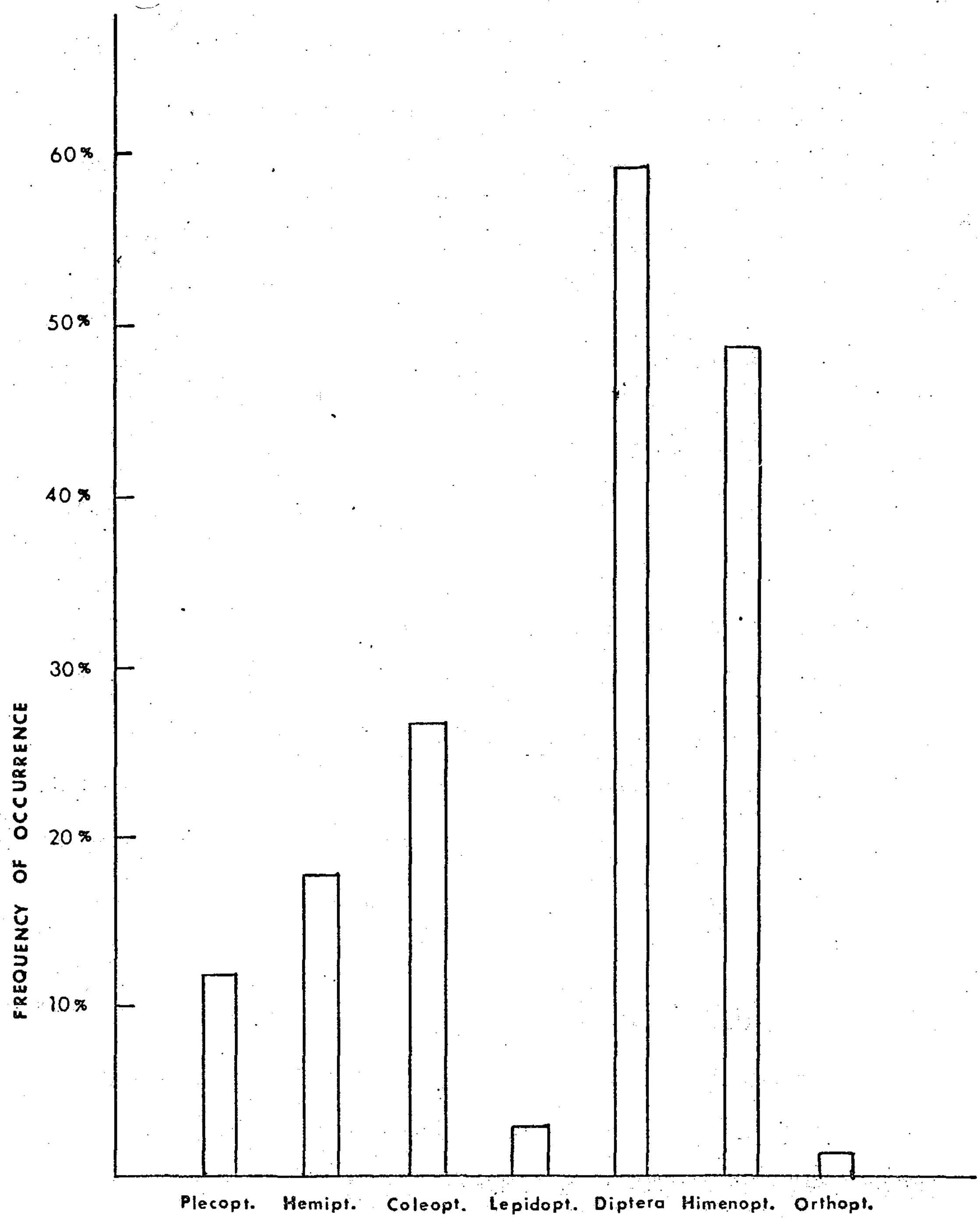
The highest incidence of occurrence took place in early July, when they were found in 87.5% of the stomachs. By late July the incidence dropped to 75.0%, by mid-August down to 12.5%, and by September down to 9.0%. During July not only was the frequency of occurrence high, but the number in which the worms occurred and the bulk which they occupied made them the most important single item in the stomach.

Aerial organisms

As previously mentioned, the terrestrial insects made up an important part of the grayling's diet in the early part of the summer.

During rainy periods, flying insects were conspicuously absent from the stomachs, and by September were nearly non-existent.

Figure 27. Frequency of occurrence of aerial organisms in the stomachs.


FREQUENCY OF OCCURRENCE
60%
50%
40%
30%
20%
10%
Plecopt.
Hemipt.
Coleopt.
Lepidopt.
Diptera
Himenopt.
Orthopt.

The main orders represented in the stomachs were the Hemiptera, Coleoptera, Plecoptera, Diptera, and Hymenoptera.

Hemiptera occurred in 17.6% of the stomachs (Fig. 27), and were represented primarily by leaf hoppers, family Cicadellidae, which presumably dropped in the water from the banks. These organisms were also present in some of the drift samples.

Coleopterans were found in 26.5% of the stomachs. These occurrences were primarily from fish collected in July, with a few individual remains scattered through August.

Diptera and Hymenoptera were the most frequently occurring terrestrial orders, the former being found in 58.8% and the latter in 48.5% of the stomachs. Diptera were represented mainly by the families Culicidae, Tendipedidae, Tipulidae, and Simuliidae. No attempts were made at quantitatively breaking down the aerial dipterans into families.

The Hymenoptera were represented primarily by the Vespidae, Ichneumonidae, Apiidae, and Formicidae. Members of at least three species of ants were significant, especially in July and early August when they were swarming.

DISCUSSION

The stream grayling is primarily a surface and mid-depth feeder. Thus, an understanding of benthic drift is pertinent in discussing their food habits.

Not until recently has the importance of drifting benthic organisms been realized in measuring the productivity of streams. Muller (1954) found that drifting organisms made up a significant portion of the diet of trout. Waters (1961) noted that the total daily drift over an area was many times larger than the standing crop on that area. This could indicate that a fish can be somewhat independent of the productivity of the area occupied, and could rely instead on upstream production.

The occurrences of benthic drifts in streams have been described by Muller (1963) as being primarily due to behavioral changes in activity on the part of the organisms involved. Typically the drifts occur at low magnitude during the day, with high peaks at night (Muller, 1963, Waters, 1962). However, recent studies have shown that a considerable variation in times of drift can occur even between related species located in different areas. Waters (1962) found Simulium drifting at a constant rate through the day in the midwest, Pearson and Franklin (1968) found that Simulium exhibited two daily high peaks of drifting, at 1600 and 0200, in the western United States. The drift samples collected on McManus Creek were too few to allow the determination of drifting times, but they did show that total drift decreased markedly as fall approached, nearing zero by September (Table III).

The relative importance of the aquatic organisms found in the grayling stomachs (Fig. 28) follow closely the abundance of organisms in the drift samples, more so than the abundance on the stream bottom. It is interesting to note the large difference between the abundance of organisms found on the stream bottom, and in the drift samples (Table III, Fig. 22). For example, mayfly larvae and midges were very close in stream bottom abundance during August. However, in the drift samples midges were more than 10 times as abundant as mayflies, a ratio which is also displayed in the relative importance of organisms (Fig. 28).

In attempting to find a way of measuring the relative importance of the food items, no single satisfactory method could be found, since each and every one appeared to be biased toward certain organisms. By plotting the frequency of occurrence, numerical abundance, and volumetric abundance in the manner previously described (Fig. 29), I felt that the bias introduced by one method would offset the bias introduced by the other. Thus the bias introduced by the volumetric measurements favoring the larger organisms would be offset by the axis on numerical importance which favors smaller organisms. The results obtained should give a more realistic

TABLE III. RESULTS FROM ANALYSIS OF DRIFT SAMPLES

DATE (1968)	TIME	ANN.	EPH.	PLEC.	HEMIP. *	TRICH.	TEND.	HYDRO.	TIPU.	*C. COGNAT*.
8-3	1200									
	2400	--	1	5	4	--	220	4	--	--
8-6	1800	--	3	3	--	1	65	--	1	2
	2200	--	13	4	--	--	133	--	2	--
8-14	1500	--	--	--	--	--	1	--	--	--
	1800	--	1	--	--	--	14	1	--	--
	2300	--	--	2	--	--	13	--	--	--
8-21	1400	--	--	1	--	--	21	--	--	--
9-2	0800	--	--	--	--	--	2	--	--	--
	1200	--	--	1	--	--	3	--	--	--
	1600	--	--	--	--	--	--	--	--	--
9-16	1000	--	--	--	--	--	--	--	--	--
	1200	--	--	--	--	--	--	--	--	--
	1600	--	--	--	--	--	--	--	--	--
	1800	--	--	--	--	--	--	--	--	--

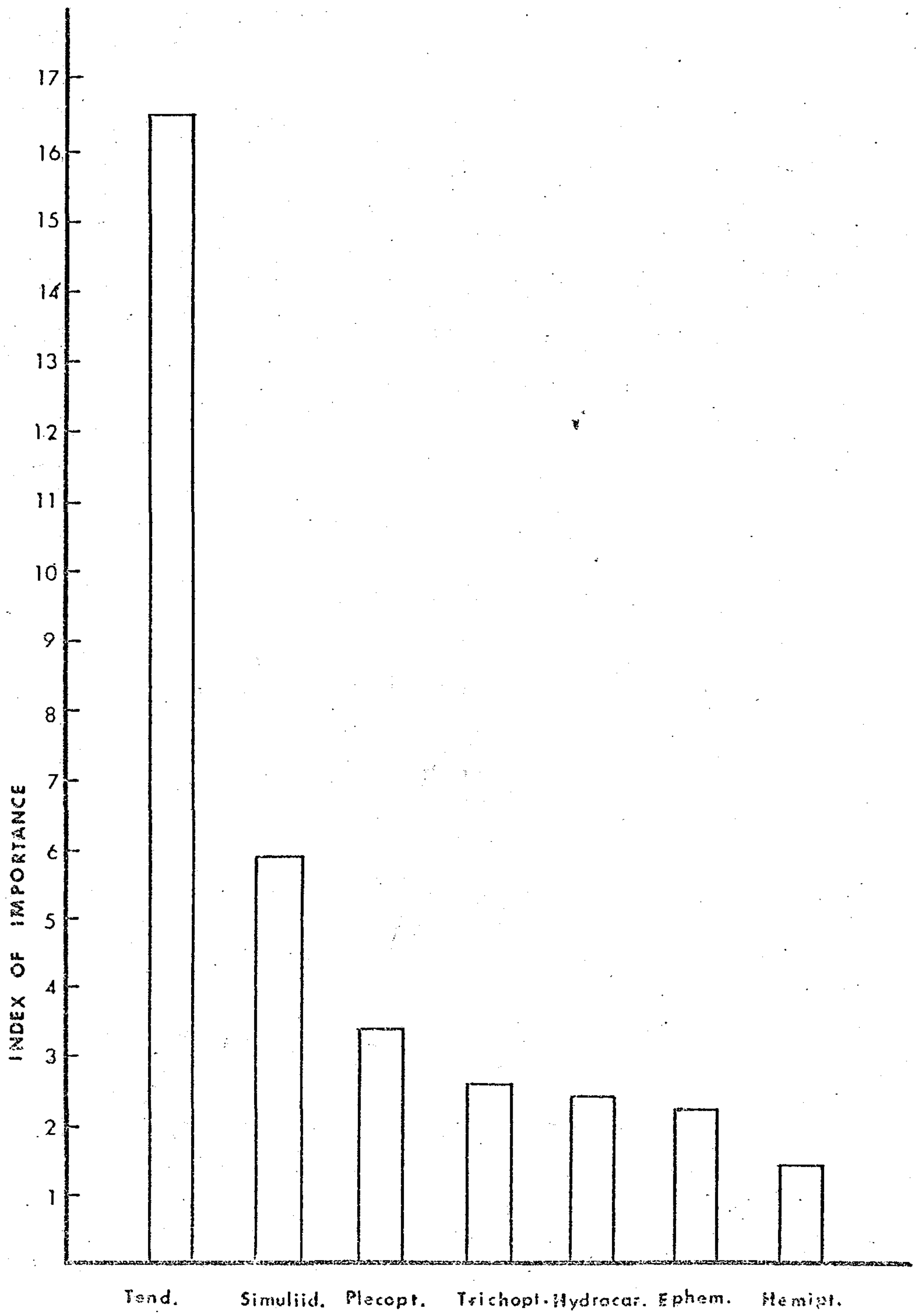


Figure 28. Relative importance of food organisms in the grayling stomachs according to the triangular area assessment method. See text and Fig. 29.

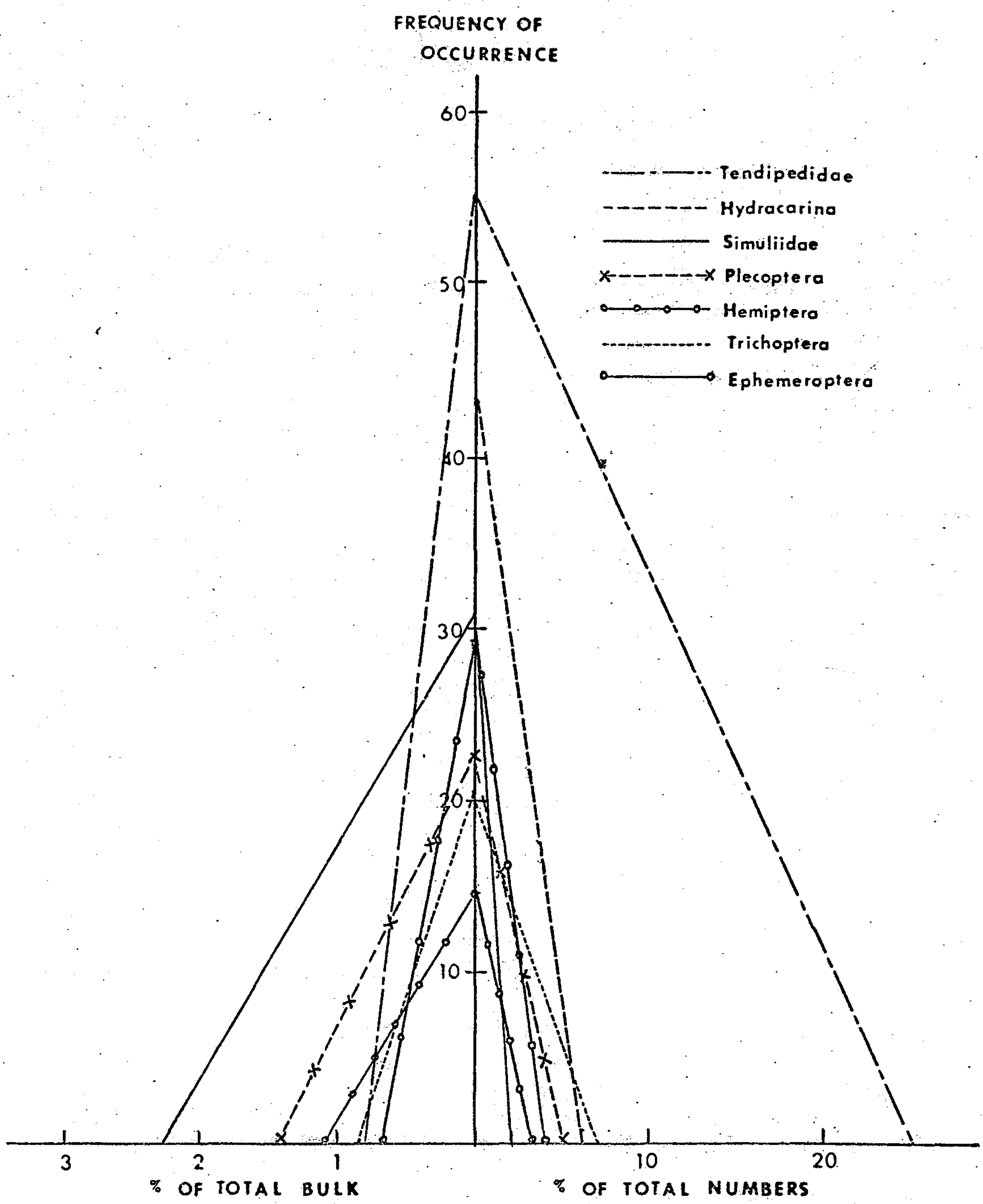


Figure 29. Triangles obtained by plotting frequency, numerical values, and volumetric values.

picture of the role of the various food items. The results obtained by this method agree closely with the results obtained from the drift samples, and the latter I feel are good indices of the food available to the grayling.

The Tendipedidae and Simuliidae were the most important aquatic food items utilized. Tendipedidae were also the most common items in the drift samples, and for the last half of the summer were the most numerous benthic organisms in the stream. Their frequency of occurrence in the drift can best be accounted for by their habits. Tendipedids occurred primarily in close association with algae and organic debris and when these drifted the midges were carried along. Anderson and Lehmkuhl (1968) found a similar situation in a woodland stream. Because of the midges' habits of living in the stream's organic litter rather than attached to rocks like the simuliids, five times as many midges than simuliids were present in the drift samples. The conspicuous absence of simuliids in the drift samples from McManus Creek is perplexing, especially so since they were occurring both in the stomachs and in the Surber samples in limited amounts. Perhaps the simuliids displayed periodic drifts which did not correspond to any of the times sampled. It should also be noted that the first drift samples were collected at the time of the simuliid population low.

Mayflies and stoneflies were restricted to secondary positions of importance as food items. The Ephemeroptera for most of the summer were the most numerous organisms in the stream, but occurred in low numbers both in the drift samples and in the stomachs. This I do not believe to be an indication of selectivity by the fish, but rather to be due to the drifting habits of the organisms. Some mayflies drift readily, but others do not. Anderson and Lehmkuhl (1968) found that of 8 species of Ephemeroptera present in their study area only two contributed to the drift. The others remained firmly attached to the substrate even during high water periods.

The stoneflies turned out to be more important to the fishes than the mayflies. Even though the latter were much more numberous in the stream, in the drift samples they occurred in equal numbers. Such data lead one to speculate that, to the stream inhabiting grayling, the benthic organisms present in the drift are the only important ones as aquatic sources of food.

The low occurrence of segmented worms in the stomachs can be attributed to their habits. The worms were always found in interstices between rocks and never in the drift.

The Trichoptera larvae were never numerous in the riffles but were common in the pools. As food items they did not become important until September, a time when the occurrence of the summer aquatic food in the stream declined sharply. The manner which the caddisflies were fed upon was not observed. However, the lack of drifting fauna and the observed sluggishness of the fish at this time of the year allow for some speculation. The fish in the fall spent much of their time close to the bottom. It is conceivable that at that time, due to the unavailability of summer food, they switched to feeding on the slow moving organisms inhabiting the substrate of pools, in this case the caddisfly larvae. I think that the caddisfly cases are also responsible for the increase in occurrence of sticks and stones in the stomachs collected in late August and September, as illustrated in Figures 23 and 24.

The hairworms (Nematomorpha) present a problem because their role in the stomach is not known. No mention of their occurrence in grayling stomachs was found in the literature. They may have been food items, but they were never seen or collected in the stream. Pennak (1953) and Morgan (1930) describe them as free living, but spending part of their life cycle as parasites in other organisms, primarily insects. No mention of hairworms being parasitic on fish was found. It appears likely that the nematomorphs entered the fish via some of the insects eaten which had been parasitized. Since some of the hairworms showed signs of having been partly digested they were included as food items.

The water mites (Hydracarina) are known to occupy the quiet pools, where they crawl about the substrate and brush

(Pennak, 1953; Morgan, 1930; and Baker and Wharton, 1952). They are not known to swim in rapid current. Apparently those mites eaten by the fish had been swept out of the pools by the current. Although these organisms had a high frequency of occurrence in the stomachs, volumetrically they were insignificant because of their minute size.

The importance of the aerial insects should not be overlooked, as they accounted for at least 40% of the total organisms eaten and in the early part of the summer accounted for as much as 65% of the total. Volumetrically their importance was gone by August. By September aerial insects were scarce in the environment. Those seen were mostly adult forms of aquatic Diptera.

From the data collected, one can conclude that during the summer the arctic grayling is totally dependent on drifting organisms and flying insects. As fall approaches the fish become more dependent on the benthic drift. Due to the low benthic productivity of sub-arctic streams, the fish do not show selectivity in choosing their food. This follows Ivlev's (1961) findings that, as the availability of food decreases in the environment, the selectivity of the fish decreases accordingly.

FEEDING BEHAVIOR

In the section on territoriality and social hierarchies feeding movements were discussed in relation to the area occupied by the fish, the feeding range. In this section the movements concerned with the actual taking of food will be discussed.

METHOD OF STUDY

Observations of feeding behavior were gathered by means of films, sketches, and with the aid of a glass bottom bucket. Movements about the home center were sketched over ten minute periods on papers marked off in foot intervals. In order to determine if learning took place, various items were dropped in the pools and attempts to ingest the items were observed. These items included crushed mosquitoes, hookless flies attached to 4 lb test nylon line, and spruce needles. In order to determine the feeding periods of the fish two methods were employed. One consisted of testing the catchability of fish at different times of the day. The other consisted of counting the number of rises seen in a pool over a set time.

The pool directly below the diversion dam, which Schallock (1965) estimated as containing over 2000 fish, was used for the catchability study. From June 24 until

September 10, every Sunday, when possible, the pool was fished for five minutes every hour with a brown hackle dry fly to test for surface feeding, and for five minutes with a No. 1 weighted Mepps spinner to test for underwater feeding. The number of fish captured and those seen attempting to take the lures were noted.

It became apparent by mid-July that grayling were capable of recognizing unpalatable food items if presented often enough. This was feared to be introducing some bias in the catchability study. This would be especially true toward the end of the day, resulting from the fish recognizing the lures and avoiding them, even if still feeding. Another index was sought which would not disturb the fish. The method used was to count the number of rises occurring over a five minute period in a pool having a relatively stable population. For this, pool CC was used.

In discussing the feeding behavior I have arbitrarily divided the fish into three main categories; Group A consisted of fish over 23 cm in length, Group B consisted of fish between 15 and 23 cm in length, Group C consisted of fish under 15 cm in length. The reason for dividing the fish into these groups was that there appeared to be different behavioral feeding patterns among fish of different size. It would not have been feasible to catch and measure each fish in the pools without risking the possibility of changing the fish's future behavior, so the lengths were estimated from above the surface of the water.

RESULTS

Group A

These large fish occupied the deepest portions of the pools, staying close to the bottom. Observations with the glass bottom bucket indicated that these fish, even though appearing motionless from the surface of the water, were in reality constantly moving from side to side as if buffeted by the current. Actually, however, much of this movement was caused by the fish turning to face drifting particles of debris.

Through observations, it was found that most of the movement of the fish involved the taking and investigating of food items, the only exceptions to this being the movements connected with territorial establishment and defense.

Three diagrams were made of group A's movements over ten-minute periods. Counts of the number of dashes made by the grayling showed that 21.9% of all recorded movements were forward movements. Of these, 57.1% were under 30 cm from the territorial center, and only 19.0% extended for over 60 cm. Of the backward movements, which accounted for 78.1% of all noted, 64.2% were less than 30 cm in extent, and only 5.7% extended for more than 60 cm (Table II). All of these represent feeding movements. Defensive movements were purposely omitted.

The movements mentioned were primarily dashes made from the home center to investigate possible food items drifting downstream. Each outward dash was followed by a return to the feeding center by a different route. Occasionally several items were investigated before a return to the home center was made.

These larger fish occupied positions at the head of the pools, and seldom investigated food items ahead of them, but instead turned to face the oncoming object head on. If the object was at mid-depth, a short dash was made as the item passed by, and the item engulfed.

For food items that were approaching close to or floating on the surface of the water, the fishes turned upward so as to keep a constant angle with the food. In so doing he rose slowly and drifted slightly backwards. The fish kept on rising until the food was directly overhead. With a quick lunge and swirling motion the food was taken into one corner of the mouth. As the swirl continued the fish dove while also moving downstream, making a lateral loop before returning to his home center (Fig. 30). When large numbers of objects were floating down, the fish often stayed in the mid-depths, and actually moved forward to intercept and investigate the particles.

A characteristic of the larger fish was the deliberateness of their movements in taking food. They rose slowly,

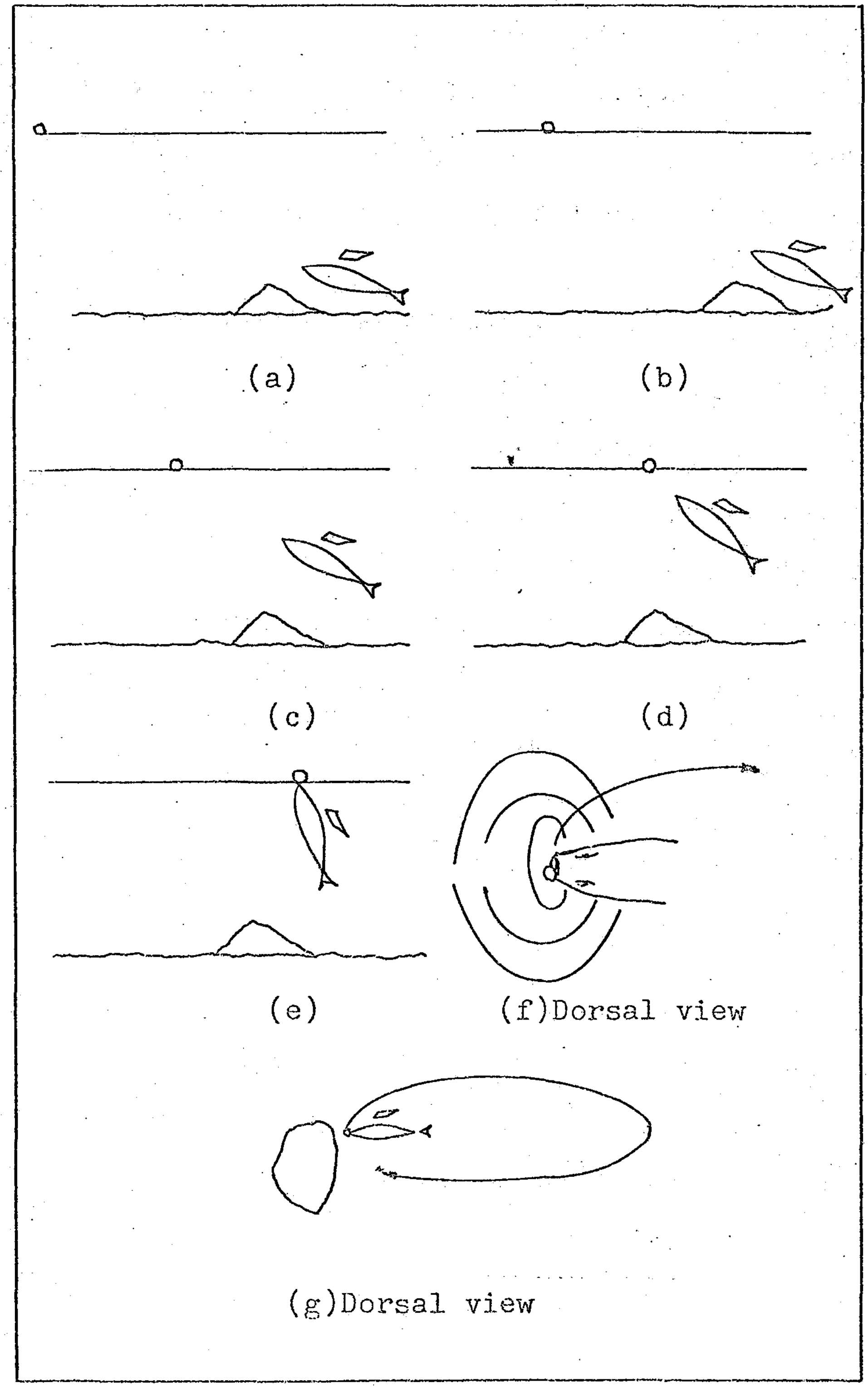


Figure 30. Feeding movements by group A.
See text for detailed explanation.

took their food slowly, barely breaking the surface or exposing very little of their back, and sinking down slightly faster than they rose. At no time, over a two summer period, did I see an adult grayling clearing the water while attempting to take an insect.

Crushed mosquitoes, hookless artificial flies, and spruce needles were dropped in the pools. The grayling refused to rise or make investigational movements when the spruce needles were dropped. However, they rose and took the dry flies which they mouthed and dropped several times before allowing them to drift backwards to where other fish took them. Usually these larger fish rose to no more than two casts. After a two hour interval the fish rose only to the first cast. When mosquitoes were dropped the fish rose readily to them. However, many drifted past the first fish and were taken by others.

<u>Group B</u>

Observations with the glass bottom bucket indicated that the fish of Group B were in continuous motion, much more so than Group A. Five diagrams of the activity of Group B over a ten minute period indicate that there was a 58.1% increase in activity over Group A. Also, while the ratio of forward to backward dashes among the larger fish was approximately 1:6, those of Group B changed to 1:2 ratio, indicating a noticeable increase in forward movements (Table II).

When dropping artificial flies in pool AA, the following results were experienced: #1 took the first four flies, #2 took 8, while #3 took the remaining 3. It should be noted here that the first four were taken by #1, and then he refused to take the remaining 11, although on the 7th, 8th, and 9th he did rise close to the fly and then sank back. The 12th, 14th and 15th were taken by #3.

With the spruce needles, #1 came up and took the first four, #2 took the 5th, 6th, 7th, 8th, 9th, 11th, and 12th; and #3 took the 10th, 13th, 14th and 15th. In each case the spruce needle was taken under, mouthed, released, mouthed again, released, and often mouthed several times. After the last mouthing, the needle was allowed to float downstream where it was picked up by other fish. Apparently spruce needles were not edible. A week later the same experiment was attempted with the spruce needles but all of the fish refused to touch them.

The manner in which the food was taken by this group also varied from group A. Although the rise and backward drift was common among this size group, it was executed much more quickly.

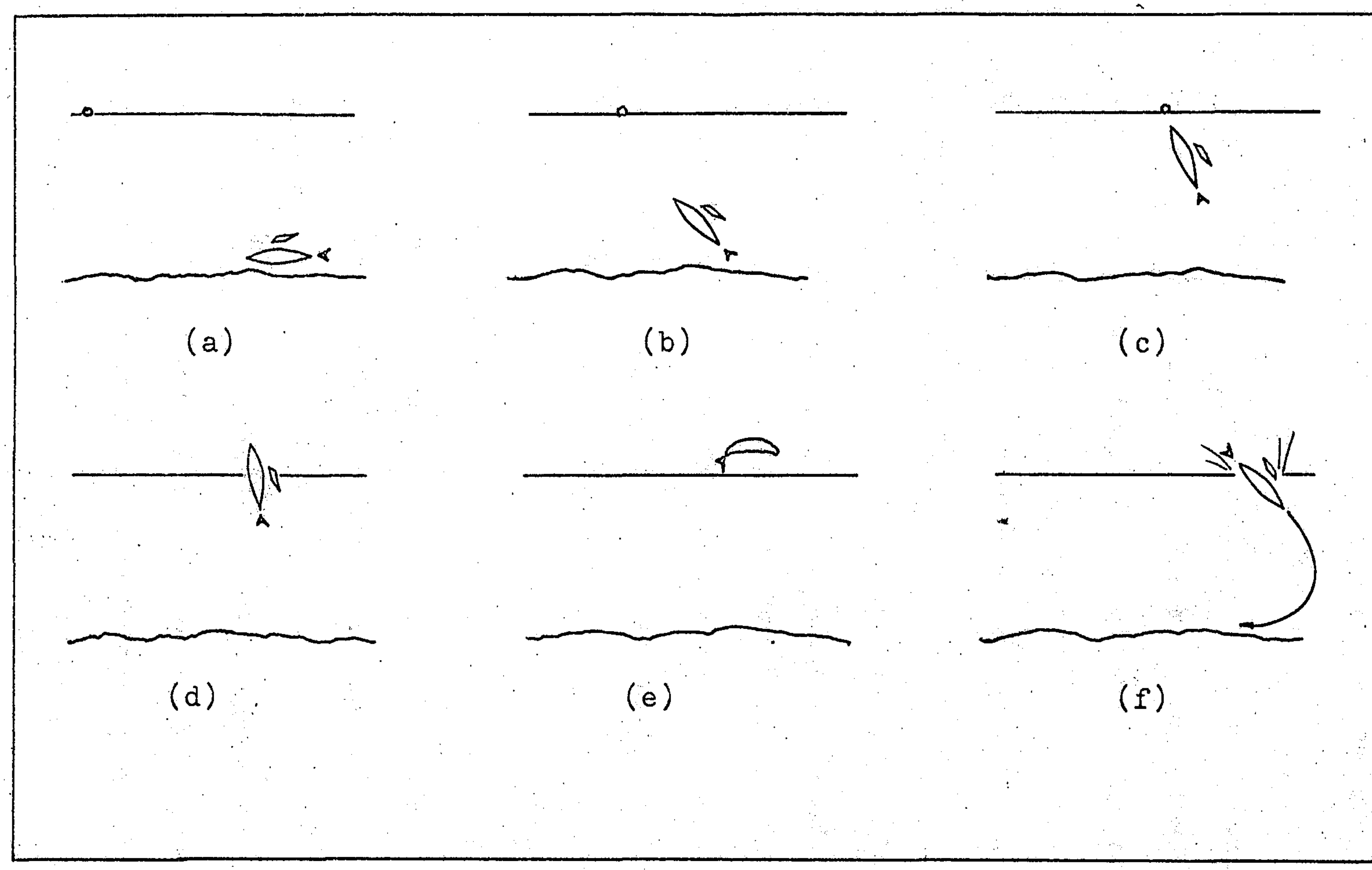
In pools such as CC, where the #3 position appeared to be often in dispute, the food was often taken by quick forward dashes. When the food was taken in this manner, the fish would move upward and forward quickly, take the food in on one side of the mouth, and in so doing expose nearly half of the body above the surface. While still moving forward, the fish would dive to the bottom and then return to the feeding center.

Jumping clear of the water, as the food passed overhead, was common in fast current and where considerable competition existed among parr. In these cases the fish would rise rapidly, at approximately a 110° angle to the bottom, grasp the item and clear the water, bending the body in mid-air with the head usually facing downstream, and diving quickly for the bottom (Fig. 31). This type of behavior was especially common on very bright days.

A third type of feeding displayed by this group was one in which the parr would clear the water, strike the food item, causing it to sink, and then pick it up on the way to the bottom. This type was found to occur both ahead of and behind the fish's station in the pool. This behavior was common in the evenings, but occasionally it was also noted at other times of the day, and no conclusive reason for its occurrence was determined. While this type of behavior was in progress in a pool, all of the parr feeding at the time were employing the same method.

Parr feeding at night were found to exhibit the deliberate rising exhibited by adults. They did not emerge from the water, but barely dimpled the surface as they ingested the food item.

Figure 31. Feeding movements by group B.


(a)
(b)
(c)
(d)
(e)
(f)

Group C

These smallest fish were observed primarily at pools AA and CC. Although they were distributed primarily at the posterior end of the pools, individuals were occasionally found in other portions as well. This group appeared much more active than the other two, but no diagrams for them were formulated. The backward and forward dashes appeared equal in intensity, as the fish chased everything that moved with the current or against it.

Territoriality among these fish did not appear to be as marked as among larger fish. This was especially true in pools where fish of all sizes were present. In these pools the young fish were found only a few inches apart and competing for food items which escaped the larger fish. As an item drifted downstream two or three fish would dash forward toward it, and the first one to reach the item would mouth it. If palatable it was ingested. If not it was rechewed several times and spat out. Eventually it was allowed to float backward to where the other fish repeated the same feeding movements.

These young fish consistently broke the surface while feeding, often leaping clear of the water. They were the only fish which were regularly seen chasing flying insects which were up to six inches above the surface, leaping and taking them in mid-air. In one incident, a four-inch fish was seen to chase a flying cranefly for eight feet, jumping out of the water four times in the process and capturing the insect on the last leap.

During the chasing of food items close to the surface, the small grayling often infringed on the territory of larger fish. In this type of relationship, territoriality appeared to break down for a few seconds or for the duration of the chase. The intruders were not chased out of the territories and returned by themselves to their respective areas.

Young of the year, during the time that they spent in the very shallow pools, were not seen feeding. Brown (1938) and Sommani (1953) mentioned that the fingerlings in hatcheries were feeding on plankton, and perhaps this is the case in the stream also.

Feeding intensities

In late June the water was high, turbulent and slightly murky. No fish could be taken with the dry fly. However, the spinner fished deep and slow during the day consistently caught fish. For the first two weeks of July, fish could be taken at a constant rate at all hours of the day with the weighted spinner. With the dry fly, fish were taken only between 1000 and 1800, reaching a maximum at 1600 (Table 1 Appendix III).

For the last half of July the number of fish taken by both methods remained constant from 0600 to 2200.

Through August the fishing success steadily declined. By dry fly, fish were taken only between 1200 and 1900. With the spinner, fish were caught only between 1000 and 1800, and at this time the spinner's effectiveness was much poorer than with dry flies.

In September the catchability of the fish dropped to the interval between 1100 and 1400 on both the dry flies and the spinner.

By counting the number of rises per five minute period in pool CC, the following results were obtained. The lowest surface feeding intensity in July was noted through early morning up to mid-day, increasing slowly as evening approached, the maximum occurring between 2200 and 0200. Once the sun rose over the horizon the fish stopped feeding almost completely. During the maximum intensity of rises, the intensity per five minute period was approximately twice the intensity value for mid-day (Table I, Appendix II).

In August the maximum number of rises appeared again between 2200 and 0200. The difference from the previous month lay primarily in that the rise intensity between noon and midnight increased seven fold, and the midnight maximum was three times the July maximum (Table II, Appendix III).

Data obtained on September 16 indicated that the feeding periods had changed from the previous months. From 0630 to 1030 no rises occurred. From 1100 to 1500, surface feeding became noticeable but not to the extent seen in the previous months. By 1500 all activity had ceased except for occasional rises. After 1800 it became too dark for observation.

During the early evening of September 16, between 1630 and 1800, a mild emergence of mayflies was in progress over the pool, but this event failed to increase the intensity of rises.

Observations were made on July 3 and August 2, which were rainy days. Visibility was poor due to murkiness, but the fish could still be discerned lying close to the bottom. They did not appear to be feeding. Attempts at counting rises failed because if any rises were taking place they could not be separated from dimples caused by the rain. Fishing on rainy days proved to be an arduous task, as flies had to be passed over a fish repeatedly in order to persuade it to strike.

DISCUSSION

The data gathered, sketches, films, and observations, all point to the grayling as being primarily a mid-depth and surface feeder. No evidence of active searching on the bottom was obtained, and the data from 68 stomach contents support this.

The grayling is also a visual feeder. As an item is sighted, by moving from side to side the fish is able to bring the item into the narrow cone ahead of his snout where binocular vision is possible (Curtis, 1949). Once both eyes are fixed on the object, better estimation of distance is possible, and the whole animal moves so that the food item remains within the small cone at a constant angle to the body.

The larger fish, being more deliberate in their movement, are more efficient in taking food items from the surface of the water. Since there is no competition from fish ahead of him, the larger fish can sight an object, and have enough time to intercept it at the food's shortest distance from the feeding center.

The higher intensity of movement showed by the smaller fish appears to be due to the more intense competition with which they are faced. This also explains the difference in the ratio of forward to backward dashes shown by Group A as compared to Group B. The former have no competition ahead or to the side of them, so they can wait until the food is very close before rising in the water column. The smaller fish on the other hand, inhabit areas where competition for each food item is steep. The only food items reaching the posterior of the pools are those which pass by the larger fish. This results in the parr actually chasing food items as soon as they are sighted.

The disparity in availability of food between the upstream and downstream portions of the pool raises some questions as to the validity of drawing conclusions on learning from the experiments where the different items (hookless flies, mosquitoes, and spruce needles) were dropped in the pools. It is true that the smaller fish appeared slower at recognizing inedible food. But is it that they are slower in recognizing the item, or is it that the competition and scarcity of food force them to snap at anything that is drifting by? I suspect the latter to be the case.

The abandon with which the parr attack the food items may also be due to increased competition. In pool AA, for example, the largest fish were approximately 185 mm long, and these behaved like the fish of Group A in pool CC, which contained fishes of all sizes. Thus it would appear that the positions occupied in the pool, rather than the size of the fish, determines the type of feeding behavior exhibited.

As shown in Tables I and II (Appendix III) the feeding periods change as the summer progresses. During the end of June, when the water was high and murky, fish could be taken during most of the day, but only close to the bottom. As the summer progressed the fish could be taken much more readily on the surface than near the bottom for most of the day, with the peaks in feeding intensities switching from mid-afternoon to midnight. In August the intensity of the midnight feeding activities increased drastically, until the midnight illumination dropped to less than 10 foot candles in mid August. By September feeding at night stopped completely, and the feeding activity took place only during a short period at mid-day. At lower latitudes Hoar (1953) found that trout also did not feed at night.

From July 16 to September 2, the data from the catchability (Table I Appendix III) and the rise experiments (Table II, Appendix III) do not seem to agree. Since they were taken from areas having different characteristics, one a pool with much standing water, the other a running pool, this might account for the differences. I tend to accept the rise count data more readily because it was collected from a pool typical of the stream, and because the fish were not disturbed in any manner during the counts.

During September the feeding period became restricted to the time between 1100 and 1400, but during this period the fish fed intensively. However, the fish needed considerable motivation before beginning to feed. The feeding activity increased in intensity only after one fish reinforced or motivated another. That is, when one fish began to rise over another, the latter did not move until the first fish had risen several times, after which the second fish rose slowly. After two or three such rises it began to be more active, and other fish in the pool soon followed suit. Similar behavior was observed in other drainages as late as mid-October. In the cases mentioned above, it appeared as if the food was not the stimulus releasing the feeding activity in the fish, but rather the sight of other fish feeding.

During rainy days the feeding activities appeared to be nil. These observations are supported by the analysis of eight stomachs collected on rainy days, and comparing the bulk contained with the stomachs of fishes of similar sizes collected on sunny days (Table IV). In most cases the total volumes of the stomachs collected on rainy days were 1/3 to 1/4 the value of the sunny days total, and among the stomachs collected on rainy days 78 to 100% of the contents were a partly digested mass indicating that no recent feeding had taken place. The stoppage of feeding I attribute to the

TABLE IV. STOMACH CONTENTS ON RAINY DAYS AS CONTRASTED TO SUNNY DAYS.

RAINY DAYS			SUNNY DAYS		
Date Collected	Length of Fish	Vol. of Stomach Contents (in ml)	Date Collected	Length of Fish	Vol. of Stomach Contents (in ml)
8/5/68	208	0.35	7/22/68	218	1.18
	240	0.40		243	2.28
	180	0.23		173	0.60
	170	0.22			
	170	0.37			
	147	0.10		147	0.48
	140	0.23		138	0.45

inability of the fish to see the food items drifting down due to the roiled water. Anderson and Lehmkuhl (1968) found that, during periods of high water and rain, the amount of drift in a stream increased from five to ten times the sunny day's normal. This indicates that the grayling are unable to utilize a substantial food source available during periods of heavy rain. This tends to support the hypothesis that the grayling is a visual feeder.

The result of the distribution and orientation of the fish in the pools was that they were distributed so as to best utilize the food which was being transported into the pool by the current.

The fish's food habits and feeding behavior both indicate that they are primarily mid-depth and surface feeders. What is even more important, the bulk of their diet is made up of benthic drift. This benthic drift dependency is an interesting adaptation, as it allows fish inhabiting low production streams to utilize food produced in other areas. Thus in McManus Creek most of the stream consisted of riffles, which are areas of very high benthic productivity (Morgan, 1930).

The fish amassed in the pools were able to utilize large areas of production upstream from them (i.e., all of the areas between pools). The relatively small sizes of the pools, coupled with the infrequency of pools in the stream, and territoriality which may limit the number of fish in the stream, allow for survival of the population in the unproductive stream.

The within-pool distribution allows for the largest fish to utilize the incoming food supply at its fullest. Since they occupy the portion of the pool where the water enters in greatest volume, it appears likely that they are able to utilize a considerable number of organisms in the drift. By staying close to the bottom they conserve energy since the current is considerably slower there. Because of their size, it is conceivable that their needed daily ration is larger than that of the smaller individuals, and by occupying the upstream position they are able to satisfy this. The result of the distribution of the fish is that the fish needing smaller rations occupy positions where the food made available is lower.

What appears to take place in the grayling pools is that feeding territories are set up in a hierarchial fashion by means of dominant subordinate relationships. The result is that by means of behavioral displays a distribution is achieved satisfying the nutritive needs of the individuals involved, and a maximum utilization of the resource is attained. A secondary benefit of such a distribution is that it helps in maintaining a healthy stock of fish. The fish in better condition, by means of displays are able to gain a territory where their nutritive needs can be satisfied. Weak individuals, such as the tagged fishes, are relegated to positions where their daily rations are smaller than their needs. The result of this is a poorly conditioned animal which may not be able to survive the long winter, a time when the benthic fauna is drastically reduced.

SUMMARY

1. Tagging and recapture of Arctic Grayling in McManus Creek during the summers of 1967 and 1968 indicated that an upstream migration takes place through the summer.

2. A diversion dam located below the junction of Faith and McManus Creeks was found not to be a complete barrier to fish migrating upstream during the spring, but may act as a barrier during the summer.

3. The grayling were found to distribute themselves in the summer pools according to size, the largest ones occupying the uppermost portions of the pools, and the smallest ones the periphery.

4. Each fish in a pool had a feeding range with a range center from which all of his activities began. Since the area was defended by aggressive displays the area defended was considered a feeding territory.

5. Each individual's position in the pool was obtained by behavioral displays between sets of individuals until one emerged as the dominant fish and the other as the subordinate. In this manner a pseudo-straight line hierarchy was formed.

6. In the fall the fish began moving out of the pools and the hierarchies dissolved.

7. Sixty-eight stomachs were analyzed and from this data and visual observation it was determined that the grayling is primarily a surface and mid-depth feeder.

8. Benthic drift and flying insects were found to be the most important organisms eaten. In June and early July flying insects were the most important food items, and the rest of the time benthic drift was the important food source.

9. In order to determine the relative importance of various food items their frequency of occurrence, numerical abundance, and volumetric abundance were plotted so that a triangular area was enclosed. The ratio of the various areas was used as an index of relative importance.

10. Behavioral observations appeared to indicate that the grayling is a visual feeder. Stomachs collected at times when the water was roiled substantiated this.

11. Adults and parr exhibited different feeding behavioral patterns. The former fed in a deliberate manner; the latter instead fed quickly, often jumping clear of the water while taking the food.

12. The maximum feeding intensity periods of the grayling show several variations. In August the peak was at midnight, and in September the feeding period was limited from 1100 to 1400.

13. It is postulated that the feeding territories established during the summer ultimately result in the best utilization of space for fish having the feeding habits displayed by the grayling.

LITERATURE CITED

Allee, W. C., A. E. Emerson, O. Park, and K. F. Schmidt. 1949. Principles of animal ecology. Saunders, Philadelphia and London. 837 p.

Anderson, N. H., and D. M. Lehmkuhl. 1968. Catastrophic drift of insects in a woodland stream. Ecology 49: 198-206.

Baker, E. W., and G. W. Wharton. 1959. An introduction to Acarology. The MacMillan Company, New York. 465 p.

Braddock, J. C. 1945. Some aspects of the dominance-subordination relationship in the fish Platypoecilus maculatus. Physiol. Zool., 48:176-195.

Brown, C. J. D. 1938a. Observations on the life-history and breeding habits of the Montana grayling. Copeia, 1938:132-136.

______. 1938b. The feeding habits of the Montana grayling (Thymallus montanus). Jour. Wdlf. Mgt., 2:135-145.

Brown, C. J. D., and C. Buck, Jr. 1939. When do trout and grayling fry begin to take food? Jour. Wdlf. Mgt., 3: 134-140.

Burt, W. H. 1943. Territoriality and home range concept as applied to mammals. Jour. Mammal., 24:346-352.

Carl, G. C., W. A. Clemens, and C. C. Lindsey. 1959. The freshwater fishes of British Columbia. British Columbia Provincial Museum, Dept. Education, Handbook No. 5. 192 p.

Curtis, B. 1949. The life story of the fish: his morals and manners. Dover Publications, Inc., New York. 284 p.

Degteva, G. K. 1965. Materialy po biologii khariusa ozera Chistogo. Tikhookeanskoga Nauch-Issled Rybn Khoz Okeanogr., 59:224-226. (Original not seen. From Bios. Abs., 48:52885.)

Egorov, A. G. 1956. Mechenie Khariusa na r Angare. Voprosy Ikhthiol., 1956(6):121. (Original not seen. From Bios. Abs., 32:25980.)

Evermann, B. W., and E. L. Goldsborough. 1906. The fishes of Alaska. Bull. U. S. Bur. Fish., 12:219-376.

Fabricius, Eric, and Karl-Jacob Gustafson. 1955. Observations on the spawning behavior of the grayling, Thymallus thymallus (L). Rept. Inst. Freshwater Res., Drottningholm, 36:75-103.

Frankel, G. S., and D. L. Gunn. 1961. The orientation of animals. Dover Publications, Inc., New York. 376 p.

Gerking, S. D. 1950. Stability of a stream fish population. Jour. Wdlf. Mgt., 14:194-202.

______. 1953. Evidence for the concepts of home range and territory in stream fishes. Ecology, 34:347-365.

Greenberg, B. 1947. Some relations between territory, social hierarchy and leadership in the green sunfish (Lepomis cyanellus). Physiol. Zool., 20:269-299.

Hoar, W. S. 1953. Control and timing of fish migration. Biol. Rev., 38:437-452.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. (Translated from Russian by the Yale University Press, New Haven. 302 p.)

Kafanova, V. V. 1965. K izncheniyu khariusa ozera Nizhnee Kulagash-Bazhi (bassein r. Chylyshmana). IZV Ataiskogo Otd Geogr Obshchest SSSR, 5:165. (Original not seen. From Bios. Abs., 98:16208.)

Lagler, K. F. 1956. Freshwater fishery biology. Wm. C. Brown Company, Dubuque, Iowa. 421 p.

Leach, G. C. 1923. Artificial propagation of whitefish, grayling, and lake trout. Bur. Fish. Doc. No. 949. 39 p.

Leonard, J. W. 1938. Feeding habits of the Montana grayling (Thymallus montanus Milnes) in Ford Lake, Michigan. Trans. Am. Fish. Soc., 68:188-195.

Miller, R. B. 1946. Notes on the arctic grayling from Great Bear Lake. Copeia, 1946(4):227-236.

______. 1957. Permanence and size of home territory in stream-dwelling cutthroat trout. J. Fish. Res. Bd. Can., 15:27-45.

Morgan, A. H. 1930. Field book of ponds and streams. G. P. Putnam's Sons, New York. 448 p.

Muller, K. 1954. Investigations of organic drift in north Swedish streams. Rept. Inst. Freshwater Res., Drottningholm., 35:133-148.

______. 1963. Diurnal rhythm in "organic" drift of Gammarus pulex. Nature, 198:806-807.

Nelson, P. H. 1954. Life history and management of the American grayling in Montana. Jour. Wdlf. Mgt., 18: 324-342.

Newman, M. A. 1956. Social behavior and interspecific competition in two trout species. Physiol. Zool., 29: 64-81.

Noble, G. K. 1939. The experimental animal from the naturalist's point of view. Amer. Naturalist, 73: 113-126.

Noble, G. K., and B. Curtis. 1939. The social behavior of the jewel fish, Hemichromis bimaculatus. Bull. Amer. Mus. Nat. Hist., 76:11-76.

Pearson, W. D., and D. R. Franklin. 1968. Some factors affecting drift rates of Baetis and Simuliidae in a large river. Ecology, 49:76-81.

Pennak, R. W. 1953. Fresh water invertebrates of the United States. The Ronald Press Company, New York. 769 p.

Peterson, H. H. 1968. The grayling Thymallus thymallus (L), of the Sundsvall Bay Area. Rep. Inst. Freshwater Res., Drottningholm, 48:36-56.

Reed, R. J. 1964. Life history and migration patterns of arctic grayling, Thymallus arcticus (Pallas), in the Tanana river drainage of Alaska. Research Report No. 2. Alaska Dept. of Fish and Game.

Schallock, E. W. 1965. Investigations dealing with probable grayling movement in relationship to water development projects. Unpublished M.S. thesis, University of Alaska. 117 p.

Shetter, D. S. 1937. Migration, growth rate, and population density of brook trout in the north branch of the Au Sable, Michigan. Trans. Amer. Fish. Soc., 66: 203-210.

Sommani, E. 1953. Esperimenti di allevamento artificiale del temolo (Th. thymallus L.). Boll. Pesca Piscic. Idrobiol., 47-57.

Starmach, K. 1956. Rybacka i biologiczna charakterystyka rzek. Polskve Arch. Hydrobiol., 3:307-332. (Original not seen. From Bios. Abs., 33:8897.)

Svetovidov, A. 1936. Grayling, genus Thymallus Cuvier, of Europe and Asia. Travaux de l'Institut Zoologique de l'Academie des Sciences de l'URSS, 3:183-301.

Tryon, C. A. 1947. The Montana grayling. Prog. Fish. Cult., 9:136-143.

Vincent, R. E. 1962. Biogeographical and ecological factors contributing to the decline of Arctic grayling, Thymallus arcticus Pallas, in Michigan and Montana. Dissert. Abst., 23:3059-3060.

Ward, J. C. 1951. The breeding biology of the Arctic grayling in the southern Athabaskan Drainage. Unpubl. M. S. thesis, University of Alberta.

Waters, T. F. 1961. Standing crop and drift of stream bottom organisms. Ecology, 42:532-537.

______. 1962. Diurnal periodicity in the drift of stream invertebrates. Ecology, 43:316-320.

Windell, J. T. 1968. Food analysis and rate of digestion, p. 197-203. In W. E. Ricker, Methods for assessment of fish production in fresh waters. Blackwell Scientific Publications, Oxford and Edinburgh.

Wojcik, F. J. 1955. Life history and management of the grayling in interior Alaska. Unpublished M.S. thesis, University of Alaska. 54 p.

APPENDIX I

TABLE I. SUMMARY OF PHYSICAL CHARACTERISTICS OF THE POOLS OF MC MANUS CREEK.

POOL	SECTION OF STRM. (Location of Pool)	SURFACE AREA OF POOL (meas. in ft.^{2})	MAX. DEPTH OF POOLS (in feet)	TYPES OF BANKS SURROUNDING THE POOLS			BOTTOM COMPOSITION OF THE POOLS		
				Brush pres. (both banks)	Brush pres. (one bank)	Both Banks barren	% Rubble	% Gravel	% Sand
1	Upper	240	1.5	--	X	--	100	0	0
2	"	35	2.0	--	--	X	100	0	0
3	"	400	1.5	--	--	X	50	50	0
4	"	150	2.5	--	--	X	100	0	0
5	"	200	1.5	--	X	--	100	0	0
6	"	140	2.0	--	X	--	100	0	0
7	"	24	2.0	--	--	--	100	0	0
8	"	180	2.0	X	--	--	100	0	0
9	"	198	4.0	--	--	--	100	0	0
10	"	270	3.0	--	--	X	10	80	10
11	"	280	3.0	--	X	--	75	5	20
12	"	75	1.0	X	--	--	100	0	0
13	"	180	5.0	--	X	--	10	15	75
14	"	300	3.0	--	--	X	75	20	5

APPENDIX I

TABLE I. Continued.

15	"	450	3.0	--	X	--	50	35	15
16	"	216	2.5	X	--	--	50	50	0
17	"	77	3.0	--	X	--	100	0	0
18	"	120	1.5	--	X	--	100	0	0
19	Middle	275	2.0	--	X	--	70	25	5
20	"	24	1.0	--	--	X	50	50	0
21	"	280	3.0	--	X	--	50	50	0
22	"	150	3.0	X	--	--	85	15	0
23	"	480	4.0	--	--	X	100	0	0
24	"	350	2.5	--	X	--	60	30	10
25	"	275	3.0	--	X	--	80	10	10
26	"	350	3.0	--	X	--	60	40	0
27	"	270	3.5	--	X	--	85	15	0
28	"	220	1.5	X	--	--	100	0	0
29	"	525	4.0	--	X	--	95	0	5
30	"	800	2.0	--	X	--	95	5	0

APPENDIX I

TABLE I. Continued.

31	"	297	3.0	--	X	--	30	50	20
32	"	300	4.0	--	X	--	75	15	10
33	"	450	5.0	--	X	--	50	25	25
34	"	4500	5.0	--	X	--	70	20	10
35	"	2250	4.0	X	--	--	60	30	10
36	"	105	4.0	X	--	--	75	20	5
37	Lower	220	2.0	--	X	--	100	0	0
38	"	200	3.5	--	X	--	50	25	25
39	"	525	5.0	--	X	--	10	0	90
40	"	600	5.0	--	X	--	10	35	55
41	"	1500	1.5	--	X	--	33	33	33
42	"	1000	5.0	--	--	X	75	15	10
43	"	1000	4.5	--	--	X	50	40	10

APPENDIX I

TABLE II. SUMMARY OF PHYSICAL DESCRIPTIONS OF POOLS ALONG MC MANUS CREEK.

SECTION	POOL NO.	POOL LENGTH (arithmetic mean in ft.)	DEPTH (arithmetic mean in feet)	SURFACE AREA	BANK TYPES		
					No Vegetation	Vegetation on 1 bank	Vegetation on both
Upper	18	25.1	2.44	194.4	31.2%	50.0%	18.7%
Middle	18	38.8	2.97	661.2	11.1%	72.2%	16.6%
Lower	6	51.0	3.79	720.7	28.6%	71.4%	-0-

APPENDIX I

TABLE III. SUMMARY OF BOTTOM COMPOSITION OF POOLS ALONG MC MANUS CREEK.

	RUBBLE			GRAVEL			SAND		
	% of Bottom of pools covered by rubble	% of Bottom of sections covered by rubble	Freq. of occurrence in section	% of Bottom of pools covered by gravel	% of Bottom of section covered by gravel	Freq. of occurrence in section	% of Bottom of pools covered by sand	% of Bottom of sections covered by sand	Freq. of occurrence in section
UPPER SECTION	77.6%	77.6%	100%	36.4%	15.0%	41.2%	25.0%	7.3%	29.4%
MIDDLE SECTION	71.6%	71.6%	100%	26.6%	22.2%	83.3%	11.1%	5.5%	50.0%
LOWER SECTION	46.8%	46.8%	100%	29.0%	20.8%	71.4%	37.1%	31.8%	85.8%

APPENDIX I

TABLE IV. SUMMARY OF THE WATER VELOCITIES PRESENT IN THE POOLS ALONG McMANUS CREEK.

	Frequency of Occurrence of Water Velocities			Frequency of Occurrence of Combinations of Water Velocities					
SECTION WHERE POOLS OCCURRED	FAST	MED.	SLOW	FAST ONLY	FAST MED.& SLOW	MED. & FAST	MED. & SLOW	MEDIUM ONLY	SLOW ONLY
UPPER SEC. (18 pools)	61.1%	66.6%	38.8%	16.6%	11.1%	27.7%	11.1%	16.6%	16.6%
MIDDLE SEC. (18 pools)	61.1%	83.3%	44.4%	11.1%	16.6%	33.3%	22.2%	11.1%	5.5%
LOWER SEC. (6 pools)	16.6%	50.0%	83.3%	-0-	16.6%	-0-	33.3%	16.6%	33.3%

APPENDIX II

TABLE I. RESULTS OF ANALYSIS OF SURBER SAMPLES

DATE COL-LECTED (1968)	ANNELL.	EPHEM.	TRICH.	PLECOPT.	SIMUL.	RHAG.	TEND.	TIPU.	C. COG.	TOTAL ORGAN-ISMS
7/7	--	4	--	1	--	--	--	--	--	5
"	10	75	--	3	11	3	51	--	--	153
"	3	89	1	1	11	2	52	--	--	159
"	3	53	--	--	6	1	45	--	--	108
"	--	36	--	--	14	--	1	--	--	51
7/8	3	153	--	6	89	--	242	--	--	493
"	4	97	--	--	55	1	51	3	--	211
7/20	1	30	--	3	26	--	10	1	--	71
7/22	--	32	--	1	3	--	9	1	--	46
"	14	34	--	3	--	--	7	--	--	58
"	2	43	--	--	7	--	4	--	--	56
"	8	77	--	10	34	--	21	2	--	147
8/5	4	26	1	7	6	--	29	2	--	75
"	2	7	--	1	1	--	3	1	--	15
"	4	11	1	2	1	--	9	--	1	29
"	7	21	--	2	2	--	43	1	--	77
8/12	12	7	--	1	--	--	12	1	1	34
"	--	6	--	1	--	--	3	--	--	10
"	--	16	2	4	--	--	12	--	--	34
"	--	12	--	5	1	--	19	--	1	41
8/18	3	18	--	7	2	--	24	--	--	54
"	2	11	--	4	1	--	5	--	--	23
9/2	--	1	--	3	--	--	9	4	--	17
9/14	8	10	--	12	5	1	30	2	--	68

APPENDIX III

TABLE I. CATCHABILITY OF FISH AT DIFFERENT TIMES OF THE DAY

DATE	TIME	DRY FLIES	WEIGHTED SPINNERS
6/24/68	1000	1	1
	1100	0	1
	1200	0	2
	1500	0	2
	1600	0	2
	1800	0	1
	2100	0	0
7/7/68	0800	0	0
	1000	0	0
	1200	1	2
	1400	2	1
	1500	0	0
	1600	0	1
	1700	0	2
	1800	0	0
	1900	0	0
	2200	0	1
	2300	1	1
	2400	0	0
7/8/68	0100	0	0
7/15/68	1500	0	1
	1600	1	0
	1700	2	3
	1800	11	3
7/21/68	1000	1	2
	1200	2	1
	1400	3	2
	1500	3	1
	1600	4	2
	1700	0	2
	1900	1	1
7/28/68	0600	0	1
	0700	2	1
	0900	3	3
	1000	3	2
	1700	3	2
	1800	3	2
	2200	2	1
	2300	2	0
	2400	0	0
7/29/68	0200	0	0
8/10/68	0800	0	0
	1000	0	1
	1200	2	1
	1400	3	2
	1500	0	2
	1600	1	1
	1700	2	1
	1800	1	1
	1900	1	0
	2000	0	0
8/24/68	0800	0	0
	1000	0	1
	1200	1	0
	1600	1	1
	1800	1	0
	2200	0	0
9/2/68	0800	0	0
	1000	0	0
	1200	2	1
	1400	1	2
	1600	0	0
	2400	0	0
9/14/68	1000	0	0
	1100	2	1
	1300	1	2
	1400	0	3
	1500	0	0

APPENDIX III

TABLE II. RISE COUNTS AT POOL CC.

DATE	TIME	AVERAGE NO. OF RISES/ 5 MINUTE PERIOD
7/16/68	1200	2.4
	1400	2.2
	1500	2.0
	1600	3.4
	2200	6.6
	2300	9.0
	2400	7.8
7/17/68	0100	6.5
	0200	-0-
7/28/68	0900	2.4
	1200	3.0
	1400	3.2
	1500	3.4
	1900	4.5
	2400	8.5
7/29/68	0100	6.0
	0200	2.2
8/3/68	0900	3.4
	1200	6.0
	1500	11.8
	2000	20.0
	2200	21.1
8/21/68	0900	2.4
	1100	4.5
	1300	6.0
	1600	12.0
	2200	27.4
	2400	28.2
	0200	6.5
9/2/68	0600	-0-
	1000	-0-
	1200	2.4
	1400	4.0
	1500	1.8
	1700	0.2
	1800	0.2
	1900	-0-