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Effect of Cover and Social Structure on Position Choice by Brown Trout (Salmo trutta) in a Stream.

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Ray J. White
Major professor

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EFFECT OF COVER AND SOCIAL STRUCTURE ON POSITION CHOICE BY BROWN TROUT (*SALMO TRUTTA*) IN A STREAM

By

Charles Eugene Bassett

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ABSTRACT

EFFECT OF COVER AND SOCIAL STRUCTURE
ON POSITION CHOICE BY BROWN TROUT
(*SALMO TRUTTA*) IN A STREAM

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Position choice by adult wild brown trout was observed in controlled-flow stream channels during the summers of 1975 and 1976. In 1975, groups of 25-30-cm (TL) trout were offered pairs of cover types. Occupation of a specific type represented a choice between known stimuli. The response to overhead cover was primarily visual rather than tactile. Response was strengthened by reducing the amount of light reflected from the stream bed beneath cover. Visual response was the same to a landmark on the stream bed as to one which was 15 cm above the stream bed. Lateral visual concealment is an important function of opaque vertical surfaces.

In 1976, groups composed of small (23-28 cm FL) and large (35-41 cm FL) trout were observed from elevated blinds. One large (25 x 122 cm) and one small (25 x 61 cm) opaque overhead cover was provided for each group. Small trout avoided using cover with some large trout. Low current velocity beneath cover seemed preferable to large cover size, even for large trout. The trout avoided feeding in direct sunlight and in the fastest currents. Large trout fed closer to the channel walls than small trout.

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INTRODUCTION

The brown trout (Salmo trutta) is popular among stream fishermen. It tolerates higher water temperatures than the native brook trout and therefore provides fishing in streams that become too warm for brook trout. Several studies have demonstrated the brown trout's ability to maintain populations where other trout are severely depleted by heavy fishing pressure (Thorpe et al., 1947; Shetter, 1950; Cooper, 1952; Lemmien et al., 1957; Marshall and MacCrimmon, 1970). The brown trout is particularly difficult to catch because it hides beneath log jams, undercut banks, ledges, and other types of cover during the day (Butler and Hawthorne, 1968; Brynildson et al., 1973). Abundance of yearling and older brown trout has been strongly correlated with amount of hiding cover in streams (Lewis, 1969; Wesche, 1976; Enk, 1977).

Fishery managers have taken advantage of the brown trout's association with cover by building artificial cover in streams to increase carrying capacity. Results have generally been favorable. White (1975) reviewed evaluations of artificial cover addition on 6 streams containing brown trout for which several years of population measurements were available. In every case, abundance of brown trout or mixed populations of brown and brook trout increased, sometimes dramatically, following cover addition. The greatest benefits accrued to the largest size classes.

Cover requirements of adult brown trout are not clearly understood. Fishery managers have had to rely largely on intuition gained from fishing experience to guide decisions on the design and placement of artificial cover in streams. Consequently, most cover devices have been built to simulate undercut banks, and log jams, often at great expense (White and Brynildson, 1967; White, 1975), without knowledge of the specific physical characteristics that make such areas attractive. Manipulation of cover changes other aspects of brown trout living space as well. Changes in streamflow patterns and the availability of gravel after cover addition changes the availability of feeding and spawning microhabitat (Hunt, 1969).

Recently the fisheries literature has provided some information to aid in improving living space for stream salmonids. These studies indicate that position choice reflects responses to phototactic, thigmotactic, and rheotactic stimuli. Characteristics of the food supply and the social environment are also very important. A brief review of the influence of these factors follows.

Light is an important regulator of the activity of brown trout. Peak locomotory activity of wild age-II+ brown trout occurred during darkness and was independent of food availability (Chaston, 1968). Reversing the light conditions so that the dark period occurred at what was previously the light period reversed the response so that activity was still greatest during the dark period. Brown trout avoid incident light by using shade produced by objects above or below the water surface (Hartman, 1963; Butler and Hawthorne, 1968; Baldes and Vincent, 1969; Jenkins, 1969; DeVore, 1975). Large brown trout, in particular, avoid bright light and generally remain inactive during the day. Immature and mature brown trout show an attraction to dark backgrounds (Hartman, 1963; Ritter and MacCrimmon, 1973). Rainbow trout show the same response (MacCrimmon and Kwain, 1966; Kwain and MacCrimmon, 1967). The relative importance of incident and reflected light has not been studied.

A strong thigmotactic response has also been attributed to brown trout in flowing water. This response has been confounded with response to reduced current velocity close to solid objects in most studies, e.g. Hartman (1963) and Baldes and Vincent (1969). Clearer evidence for thigmotaxis has been found. Brown trout used overhead cover devices with clear plastic streamers fastened under both sides significantly more than covers without streamers (DeVore, 1975). Clear streamers presumably offered very little resistence to the current and little or no visual stimulus. Serchuk (1976) concluded that movements of adult brown trout along the walls of a pumped-storage resevoir demonstrated thigomotaxis as they were not affected by changes in light level or current velocity.

Current velocity may exceed the importance of other physical factors in determining position choice by brown trout in streams as it is the dominant factor determining energy expenditure (Vincent, 1969). Response to current velocity in this study is considered separately from response to cover, but in the stream the two usually cannot be separated. Objects below the water surface that provide shade and thigmotactic stimuli also usually create pockets of low current velocity. Adult brown trout tolerate a wide range in current velocity but seem to prefer velocities less than 15 cm/s (Baldes and Vincent, 1969; Wesche, 1976).

Food availability obviously is important in determining the suitability of streams for trout production. Feeding on drifting food from a more-or-less fixed station is characteristics of stream-dwelling salmonids. This permits maximum food intake with minimum energy expenditure (Allen, 1969a). Wild brown trout about 24 cm long in stream aquaria fed at the depth of maximum prey density and preferred the largest familiar items available (Ringler, 1975). In the natural stream environment, prey density and size are determined by streamflow patterns and velocity. Fast currents carry more food items per unit of time (Elliot, 1967) and larger items (Chapman and Bjornn, 1969) past feeding stations than do slow currents. The pattern of flow concentrates food in areas characterized as principal lines of drift. Brown and rainbow trout choose feeding stations in relatively slow currents overlain by these principal lines of drift (Jenkins, 1969). Drift food supply and its influence on position choice cannot be divorced from streamflow characteristics.

Temporal patterns of position choice by brown trout in streams may be influenced by the diel periodically of invertebrate drift (Elliot, 1970). But lack of correlation between drift availability and stomach contents in some cases (Warren et al., 1964; Chaston, 1969), indicates that reliance on drift is not complete. Bottom foraging and feeding on fish seems to be the primary sustenance for brown trout larger than about 40 cm long (Jenkins, 1969; Waters, 1972).

The social environment affects position choice of trout by influencing the expression of territoriality. Territoriality is a characteristic of most stream-dwelling salmonids (Allen, 1969b). Two types of social organization have been described for brown trout: territorial mosaics, and hierarchies. A territorial mosaic is where the stream bed is divided into many adjoining defended areas. This pattern is typical among juveniles (Kalleberg, 1958; Hartman, 1963). Each trout is consistently dominant only within its own fixed territory. Qualifications for mosaic formation seem to be uniformity in body size, physical homogeniety of the environment, and lack of movements (Jenkins, 1969).

Hierarchies tend to form in groups of trout containing a mixture of body sizes in a heterogeneous environment. Social rank is related to body size and individual agressiveness, but not to geographic location (Jenkins, 1969), i.e. social rank does not change after trout move to a new position. The highest ranking trout occupies the most upstream position under cover (Butler and Hawthorne, 1968; Butler, 1975) and at feeding areas in the open (Jenkins, 1969). The upstream position seems to have feeding advantage. Subordinates may move to better positions vacated by dominants but always yield these positions when the dominant returns.

In territorial mosaics and in hierarchies a space or "social force field" (McBride, 1964) surrounding the trout is defended. The area immediately upstream from the fish is defended most persistently (Butler, 1975). The size of the social force field depends on the motivation of the fish and the physical characteristics of the stream channel. The social force field is smaller when trout use cover than when they feed (Butler, 1975). Streambed features that provide visual isolation from competitors also reduce space requirements (Kalleberg, 1958; Hartman, 1963). Large trout defend more space than small trout (Allen, 1969b).

General objectives of this study are:

(1) To define characteristics of high quality hiding cover for adult brown trout.

(2) To describe the daily activity of two sizes of adult brown trout, with particular attention to the importance of cover use.

(3) To investigate the relative importance of the physical characteristics of cover and social rank on choice of feeding and cover positions.

Specific hypotheses concerning cover use are:

(1) The response to overhead cover is visual rather than tactile.

(2) Trout respond to light reflected from the stream bed beneath overhead cover.

(3) Visual isolation is an important function of cover offering lateral vertical surfaces.

(4) Lateral vertical surfaces are preferred if they have a distinct visual landmark low rather than high in the water column.

(5) Large (older) adult trout use cover more than small (younger) adult trout.

(6) Socially dominant trout feed closer to overhead cover than subordinates.

(7) Socially dominant trout use the largest overhead cover available.

(8) Socially dominant trout prevent subordinates from using overhead cover.

(9) Trout feed on the side of the stream channel with overhead cover.

FACILITIES

The study was conducted at the Field Office of the Michigan Department of Natural Resources in Grayling, Michigan during the summers of 1975 and 1976. The site was formerly a hatchery; raceways served as controlled-flow stream channels. Water was supplied to the channels from the East Branch of the AuSable River. The East Branch supports a mixed population of brown, brook, and rainbow trout with brown trout the predominant species. Daily ranges in water temperature during 1975 and 1976 parts of this study are presented in Appendix Tables A1 and A2. The physical characteristics of the experimental environment and the methods employed differed between years so they will be described separately.

METHODS - 1975

Two channels, 3.4 m wide and 61 m long, were used for the experiments in 1975 (Figure 1). Each channel was divided into two 27-m sections. Substrate in each channel ranged from one-inch diameter gravel at the upstream end to sand at the downstream end. The channel sides were concrete slab that sloped approximatley 100° to the water surface. Gravel sloped against the walls eliminated the toe of the wall as lateral cover (Figure 2).

Prior to the beginning of the experiments, the substrate in each channel was raked and smoothed to create a uniform cross-section throughout. Average depths and current velocities are presented in Table 1. Discharge measured at the midpoint of each section with a pygmy Gurley current meter was 0.158 cms in channel A and 0.144 cms in channel B. Constant discharge was maintained throughout the study by regulating the level of the head pool above the channels. Current deflectors placed just below the entry sluices to each channel dispersed flow evenly in the channel cross-section (Figure 1).

Table 1. Discharge and mean cross-sectional depth and current velocity in each channel section in 1975.

	Mean depth (cm)	Mean velocity (cm/s)	Discharge (cms)
A1	18.9	24.9	0.158
A2	23.1	21.9	0.158
B1	22.9	19.8	0.144
B2	22.5	20.4	0.144

Figure 1. - Controlled flow channels used in 1975 with positions of current deflectors and screen barriers.

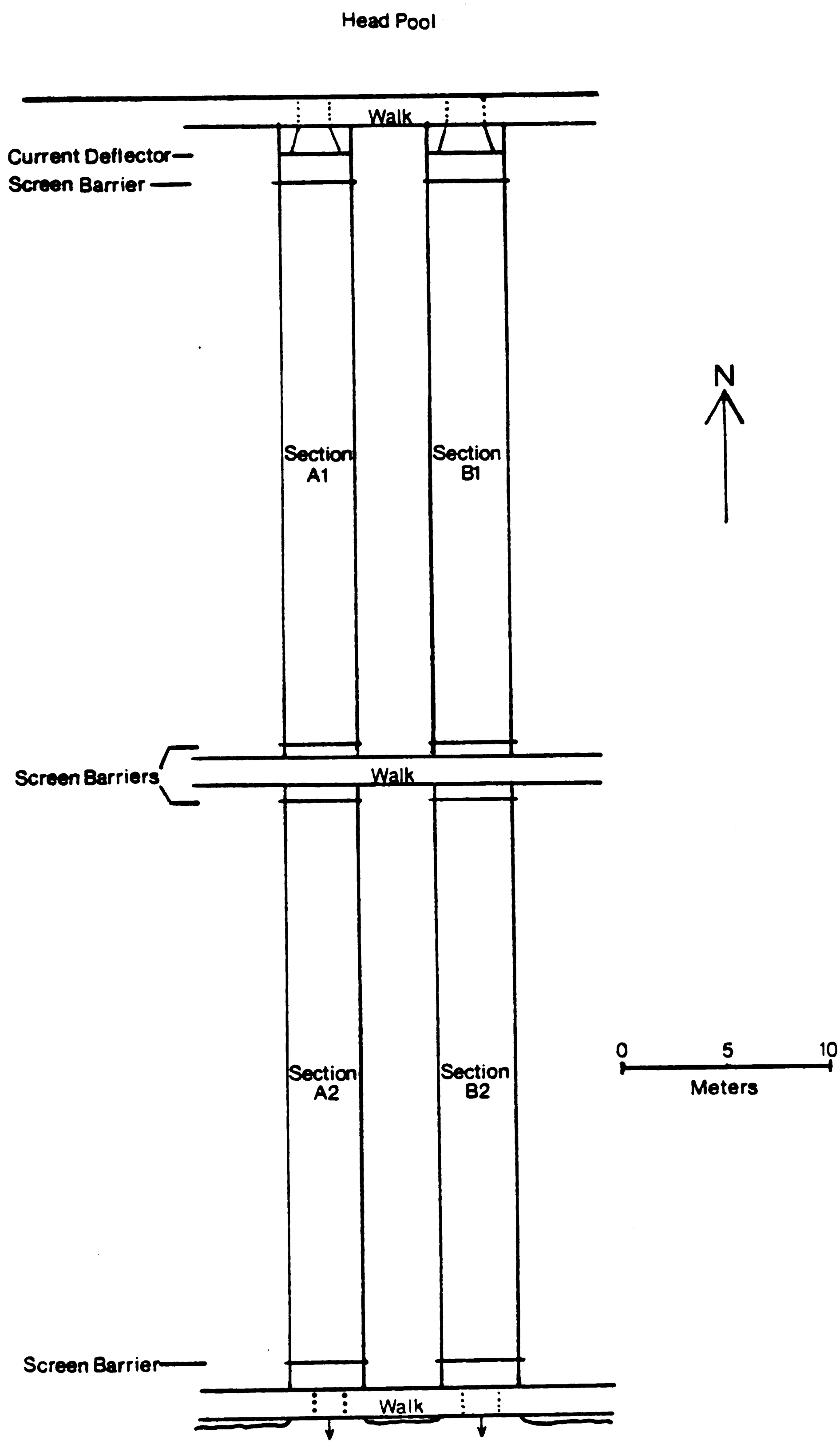

Head Pool
Walk
Current Deflector
Screen Barrier
N
Section A1
Section B1
Screen Barriers
Walk
Section A2
Section B2
0
5
10
Meters
Screen Barrier
Walk

Figure 1

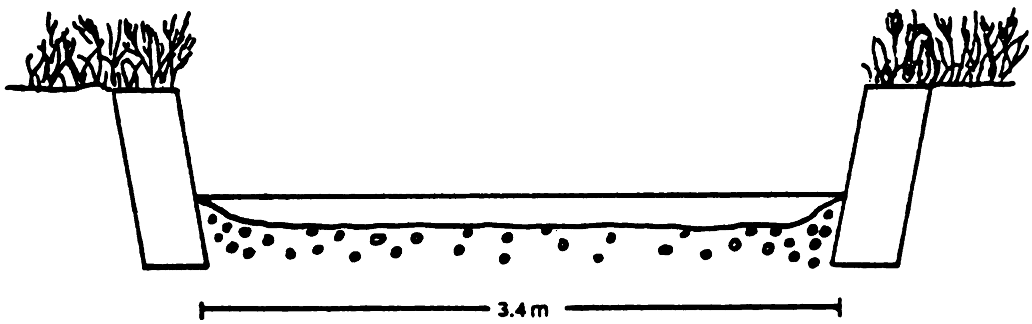


Figure 2. - Cross-sectional view of a channel showing gravel sloped against the walls.

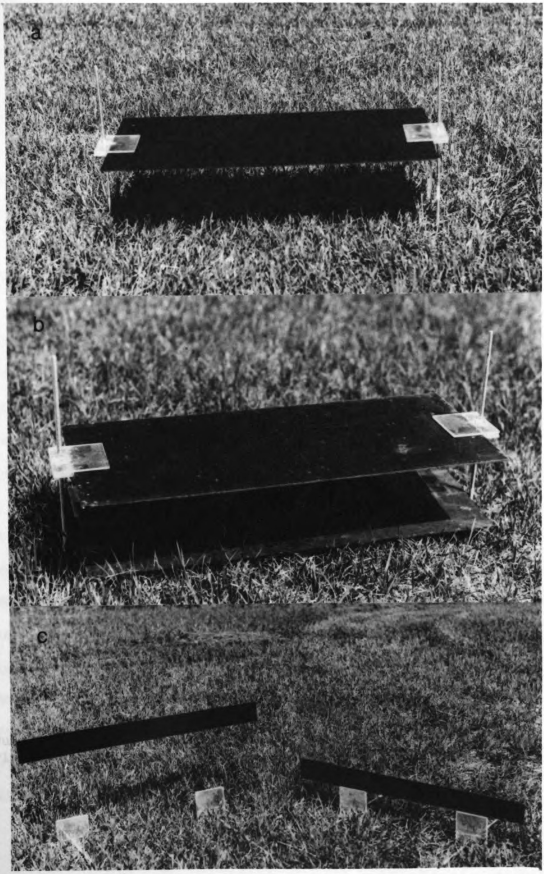
Screens with one-inch mesh blocked the head and foot of each section. The screens were cleaned daily to prevent buildup of debris that would have created an irregular pattern of flow, which in turn, might have influenced position choice of the trout.

Trout responses to overhead and lateral cover devices were tested. Overhead cover consisted of 25 × 61-cm plates of single-strength (1.6 mm) glass supported by plexiglas holders mounted on 6-mm-diameter threaded, galvanized rods (Figure 3a). These cover devices were thinner than those used by DeVore (1975) which he found had very minor influence on current velocity under the cover. Lateral cover consisted of glass plates supported in a vertical position by the plexiglas holders and rods which were buried horizontally just below the surface of the stream bed (Figure 3c).

Five pairs of evenly-spaced cover devices were placed in each section, each pair representing two cover options. Within each pair the devices were randomly assigned to the right or left side of the channel, 1 m from the wall (Figure 4). Three experiments were conducted with 3 different pairs of cover types. Experiments 2 and 3 were repeated with two groups of trout.

The subjects of the experiments were 25-30-cm (TL) wild brown trout. Two groups of 20 trout were used. Group I was captured in the AuSable River mainstream about 8 km east of Grayling using a boat-mounted 250 volt D.C. electro-fishing unit. Group II was captured with a backpack shocking unit in the East Branch of the AuSable River about 2 km above the DNR Field Office. Following capture, the trout were held for 5-7 days in a channel lacking overhead cover, but in

Figure 3. - Cover devices used in 1975. (a) Opaque overhead cover the same size as the transparent devices used in experiment 1. (b) Overhead opaque cover with "dark" substrate. (c) "High"- and "low"-stripe lateral cover devices. Both were buried to the level of the base of the low stripe.


a
b
c

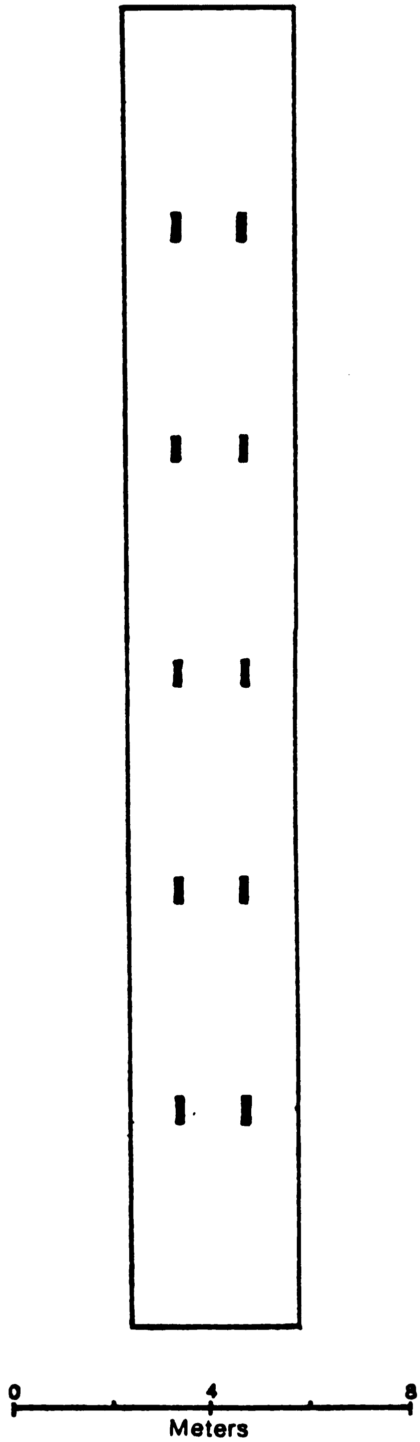


Figure 4. - Location of cover devices in one channel section in 1975. Placement was identical in all 4 sections.

which they had access to the walls. The holding period permitted some recovery from the effects, if any, of electro-fishing.

Five trout from each group were randomly assigned to each of the 4 channel sections. Each group was given 3 days to acclimate to the cover options available. Three to 5 days of observation followed. Then the trout were seined from the channels and transferred back into the holding area where they were confined for 18-24 h in a 3.7 × 1.2-m net enclosure while the next set of cover devices was installed. The entire procedure was repeated for later experiments. The first experiment with Group II was proceeded by a 10-day acclimation period because high, turbid water prevented observations according to the original schedule. Reassignment of trout to channel sections between experiments reduced the chance that prior social experience and familiarity with the section would influence choice of cover devices.

Observations were made 4 times daily at 1000 h, 1200 h, 1400 h, and 1600 h (EDT). A mirror fastened to the end of a 2-m pole permitted viewing trout under cover. The mirror and pole did not seem to disturb the trout. The observer approached the channels in a crouched position from downstream and facing into the sun when possible to avoid frightening trout with a moving shadow. Tall grasses bordering the channels also concealed the observer. Trout rarely fled when approached, even though they seemed to be aware of the observers presence. Trout that moved were recorded as having the pre-movement position.

Experiment 1

The choice was between transparent, overhead glass plates suspended 10 cm ("low") or 15 cm ("high") above the stream bed. This was tested only with Group I.

Experiment 2

The choice was between opaque, overhead glass plates with "dark" or "light" substrate beneath. Glass plates painted black were suspended 10 cm above the stream bed. A glass plate the same size as the overhead plate, either painted black or left transparent, was placed on the stream bed directly under each overhead plate (Figure 3b). The painted plates were positioned with the unpainted side up.

Experiment 3

The choice was between lateral glass plates with a 5-cm wide black stripe at the stream bed ("low") or 15 cm above the stream bed ("high") (Figure 3c). The plates were vertical and parallel to stream flow.

Use of overhead cover was defined as occupation of a position where any part of the trout's body was under cover. Use of lateral cover was defined two ways: (1) visual use - occupation of a position between a cover device and the wall or between a cover device and the longitudinal centerline of the channel, but not in direct contact with the cover device. Use of positions more than one body length upstream or downstream from a cover device was not considered use; and (2) tactile use - direct contact with any cover device.

Statistics

As individual trout could not be reliably identified, observations of the trout in each section were combined for a group total representing (the number of trout per section) × (number of observation periods/day) × (number of days observed). A flood midway through the study resulted in loss of trout and a change in the number of observation days per experiment, so the total number of sightings/group/experiment was not constant. Predators or vandals also removed some trout.

Cover preference was of primary interest in each experiment. The 3 options available to each trout - use of one of the cover types provided, or the other type, or no cover, were not independent, as use of one precluded use of any other. Data was therefore expressed as a derived variable (% of sightings at one cover type minus % sightings at the other cover type). Preference was determined by placing a confidence interval on the mean difference from all of the observation days combined. When the confidence interval did not include zero, the null hypothesis of "no preference" was rejected.

Use of derived variables may result in non-normal distributions and great repetition of some values due to the higher probability of occurrence of some percentages than others (Sokal and Rohlf, 1969). Great repetition of percentages did occur in some sets of data. Tests for non-normality and heterogeneous variance were applied prior to testing hypotheses. Non-normality and heterogeneous variance as determined by the Shapiro-Wilk W-test and the F-max test, respectively, were corrected with the arc-sine transformation (Gill, In press).

Several days of unusually high and turbid water created circumstances suspected of causing substantial differences in responses to cover between the two groups. Group differences in total cover use and cover preference were tested with a one-way analysis of variance. The effect of mean cross-sectional current velocity on sectional differences in response to cover was tested with a correlation analysis. Degrees of freedom in analysis of variance and correlations were derived from (number of days the experiment was repeated) × (number of channel sections).

RESULTS - 1975

Experiment 1

Trout did not prefer either the high or the low transparent overhead covers ($p < 0.5$; Table 2). Mean cross-sectional velocity at the channel section midpoint was negatively, but weakly correlated with total cover use ($r = -0.449$, $p < 0.05$).

Experiment 2

Trout in both groups preferred overhead cover with black substrate to overhead cover with light substrate ($p < 0.01$; Table 3). Total cover use was significantly lower for trout in Group II ($p < 0.05$). Less total cover use by Group II trout may be related to the fact that the water was turbid during the second experiment. Mean sectional current velocity was not correlated with total cover use ($p < 0.5$).

Experiment 3

Trout in both groups did not show visual preference for either the low- or high-stripe lateral cover devices ($p < 0.5$; Table 4). Tactile use of lateral cover was significantly greater for the low-stripe device ($p < 0.001$). Total cover use, visual and tactile, both types of devices, was negatively, but weakly correlated with mean sectional current velocity ($r = -0.440$, $p < 0.05$).

Positions close to the channel walls were used much more than positions permitting trout to touch lateral cover devices (Appendix

Table 2. - Number of sightings of trout under low (10 cm) or high (15 cm) transparent overhead cover devices, or not under cover. Tested only with Group I.

Day	Under low transparent cover	Under high transparent cover	Not under cover
		Section A1	
1	1	1	18
2	0	0	20
3	0	0	20
4	1	2	17
		Section A2	
1	8	1	11
2	5	4	11
3	4	4	12
4	4	4	12
		Section B1	
1	8	8	6
2	5	4	16
3	4	6	8
4	4	6	13
		Section B2	
1	4	1	15
2	0	1	19
3	4	0	16
4	1	1	18
Total	43	43	154

Table 3. - Number of sightings of trout under opaque overhead cover devices with dark substrate or light substrate, or not using cover. All other devices were 10 cm above the stream bed.

Group	Day	Under cover with dark substrate	Under cover with light[a] substrate	Not under cover
		Section A1		
I	1	8	11	1
	2	11	9	0
	3	11	9	0
II	1	5	3	12
	2	8	4	8
	3	8	4	8
	4	4	3	8
		Section A2		
I	1	6	11	3
	2	12	7	1
	3	11	7	2
II	1	7	12	1
	2	8	11	1
	3	8	9	3
	4	10	5	0
		Section B1		
I	1	11	2	3
	2	15	1	0
	3	12	3	1
II	1	3	2	15
	2	4	5	11
	3	10	4	6
	4	11	3	1
		Section B2		
I	1	7	5	8
	2	13	3	4
	3	12	7	1
II	1	5	8	7
	2	9	6	5
	3	7	9	4
	4	6	6	3
Total		242	169	117

[a]Transparent glass plates permitted light stream bed to show through.

Table 4. - Number of sightings of trout responding visually or tactually to lateral cover devices with low (at the stream bed) or high (15 cm above the streambed) dark stripe, or not responding visually or tactually. See text for definitions of "visual" and "tactile" responses.

Group	Day	Type of response				None
		Visual		Tactile		
		Low-stripe	High-stripe	Low-stripe	High-stripe	
		Section A1				
I	1	1	1	0	0	18
	2	1	4	0	0	15
	3	0	4	4	0	12
II	1	0	0	0	0	20
	2	2	0	0	0	18
	3	1	1	0	0	13
	4	4	1	0	0	15
	5	1	1	0	0	18
		Section A2				
I	1	1	6	2	1	10
	2	1	4	2	1	12
	3	1	3	0	3	13
II	1	0	2	7	0	11
	2	1	2	4	1	12
	3	2	2	3	1	7
	4	5	8	3	0	4
	5	3	3	6	0	8
		Section B1				
I	1	0	1	4	3	12
	2	1	4	0	0	15
	3	0	0	2	1	17
II	1	2	1	0	0	9
	2	1	0	5	0	6
	3	0	0	1	0	8
	4	1	2	0	0	9
	5	2	1	0	0	9

Table 4. (cont'd.)

			Section B2			
I	1	1	0	5	4	10
	2	1	0	4	2	13
	3	1	1	4	0	14
II	1	4	6	0	0	6
	2	1	4	1	0	10
	3	3	5	0	0	4
	4	3	6	0	0	7
	5	3	4	0	0	9
Total		48	77	57	17	364

Figures B1 and B2). Use of positions on the sloped gravel or at the base of the sloped gravel accounted for 54% of all sightings. Tactile use of low- and high-stripe cover devices accounted for only 13% of all sightings.

METHODS - 1976

The experiments were run in two concrete channels, 3.7 m wide and 45 m long. Each channel was divided into two 15.4-m sections separated by a 4-m buffer zone (Figure 5). Substrate in each channel was gravel. Channel walls were vertical 1.2 m high. Gravel sloped against the walls eliminated them as sources of lateral tactile stimuli.

Precautions taken in 1975 to create nearly uniform depth, current velocity and channel cross-section within each section, as well as to remove uncontrollable sources of cover were followed in 1976. Mean depth was slightly greater and mean current velocity slightly lower in the downstream sections (Appendix Figures B3-B6). Discharge was maintained at about 0.181 cms in channel A and 0.156 cms in channel B for the duration of the experiments. A low dam at the head of each channel dispersed flow evenly across the channel cross-section. Screens with one-inch mesh blocked the head and foot of each section. Screens were cleaned daily.

A small (25 × 61 cm) and a large (25 × 122 cm) black glass overhead cover was provided in each section. Large cover consisted of two small covers placed end to end (Figure 6). Both sizes of cover were supported 10 cm above the stream bed. One cover was placed 5 m downstream from the upper screen, the other was placed 5 m upstream from the lower screen. Both covers were placed the same

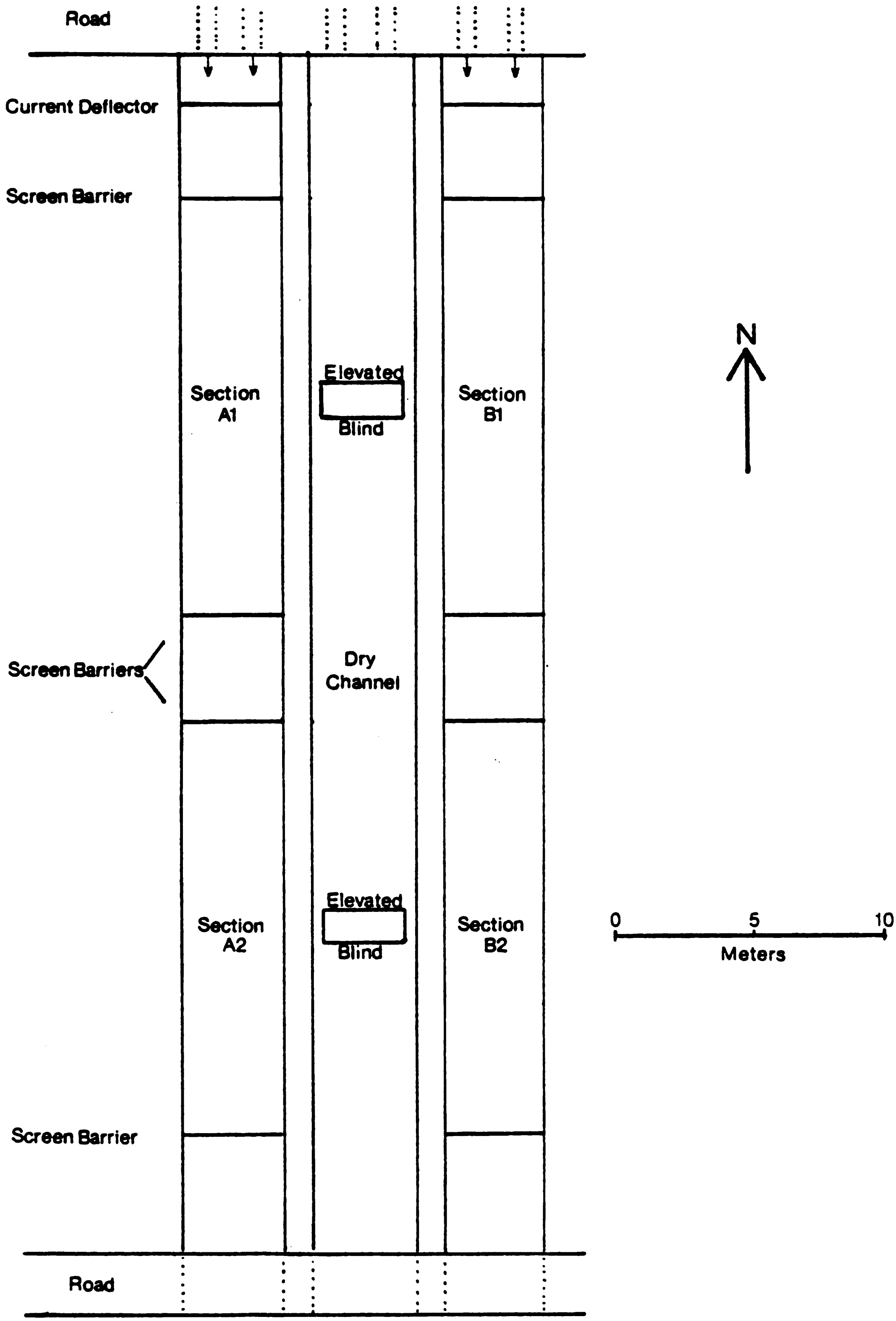


Figure 5. - Controlled flow channels used in 1976 with positions of current deflectors, screen barriers, and elevated blinds.

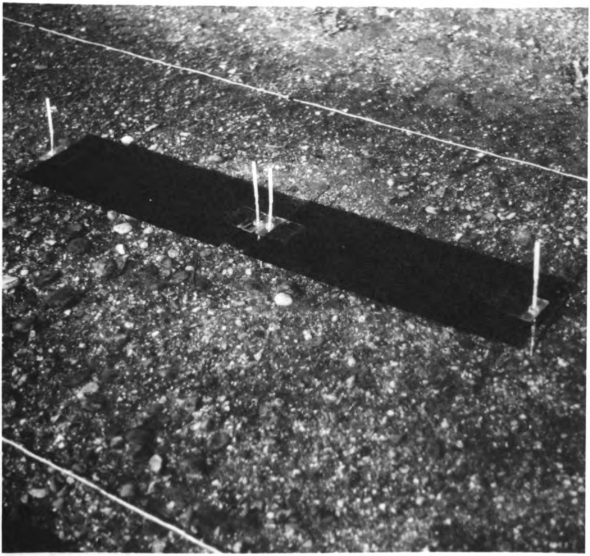


Figure 6. - Large overhead cover.

distance from the wall. Three cover positions were tested in each section: 0.5 m from the west wall; mid-channel, and 0.5 m from the east wall. Within a section, each position was tested for 3 weeks with a different group of trout. Covers 0.5 m from the walls did not extend over the sloped gravel. Cover positions were not the same in all sections during any single 3-week experiment (Figure 7).

Six "feeding references" were placed in each channel section before observing trout Groups II and III in an attempt to provide low velocity feeding stations not immediately adjacent to the channel walls. The references were 5.0 × 7.5-cm black plexiglas plates supported vertically from the substrate perpendicular to the direction of flow (Figure 8a). They were placed at longitudinal transects 1.5, 2.5, and 3.5, and at the latitudinal transects 1 m upstream from the upstream edge of each cover for Group II, and 1 m downstream from the downstream edge of each cover for Group III (Figure 7).

Use of feeding references was defined as feeding within 0.25 m of the reference, for at least 15 sec. Reduced current velocity farther than about 0.25 m upstream or downstream from references could not be detected with a pgymy Gurley current meter (Figure 8b, c). An unconfined rainbow trout approximately 30 cm long in the East Branch of the AuSable River frequently fed just downstream from a branch stub protruding above the stream bed that was less than one-half the size of the plexiglas references provided in the channels. Therefore, I assumed that the references were large enough to provide sufficient velocity buffer to attract even the largest trout used.

Figure 7. - Location of overhead covers and feeding references (·) during each 3-week experiment.

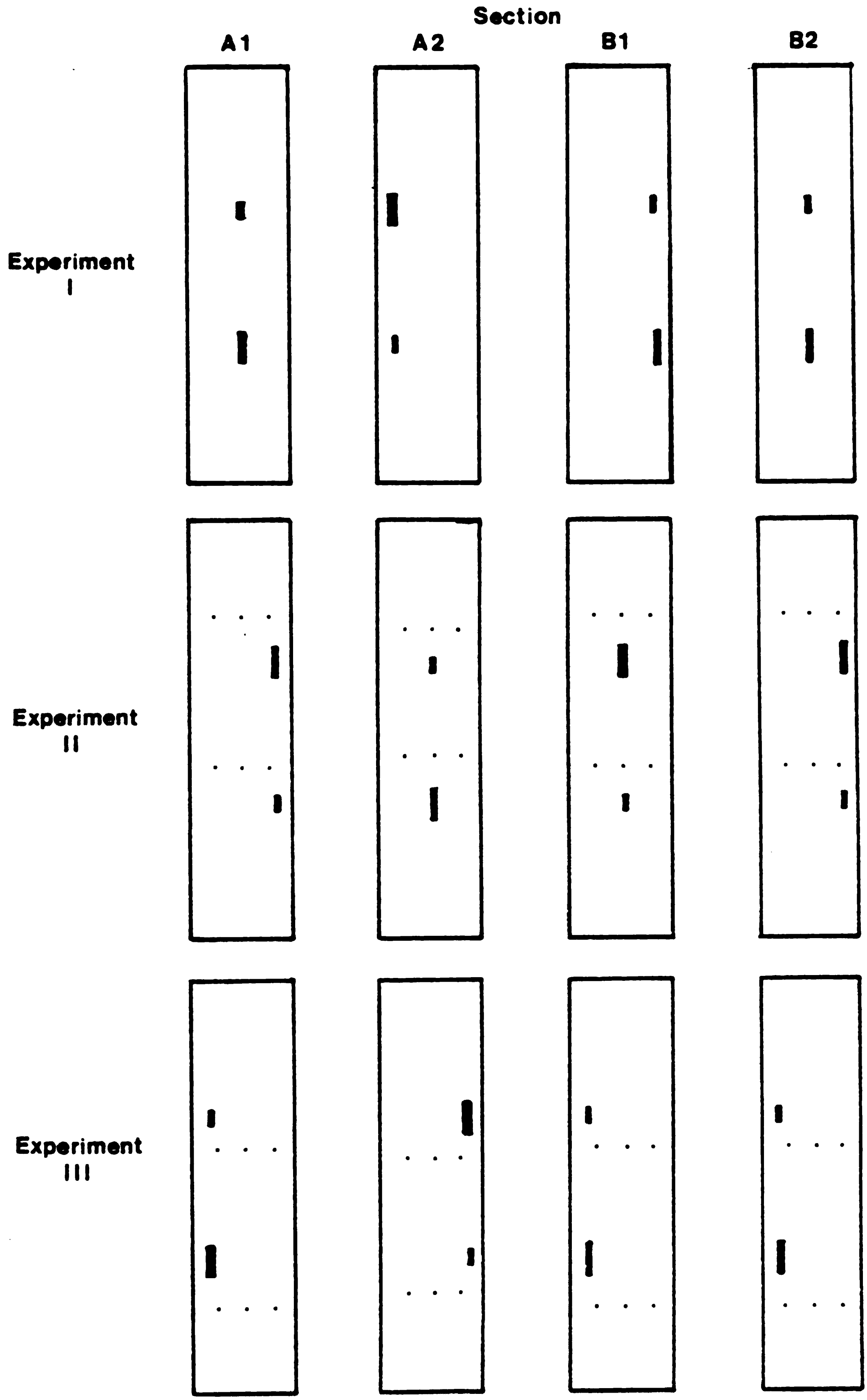

Section
A1
A2
B1
B2
Experiment I
Experiment II
Experiment III

Figure 7

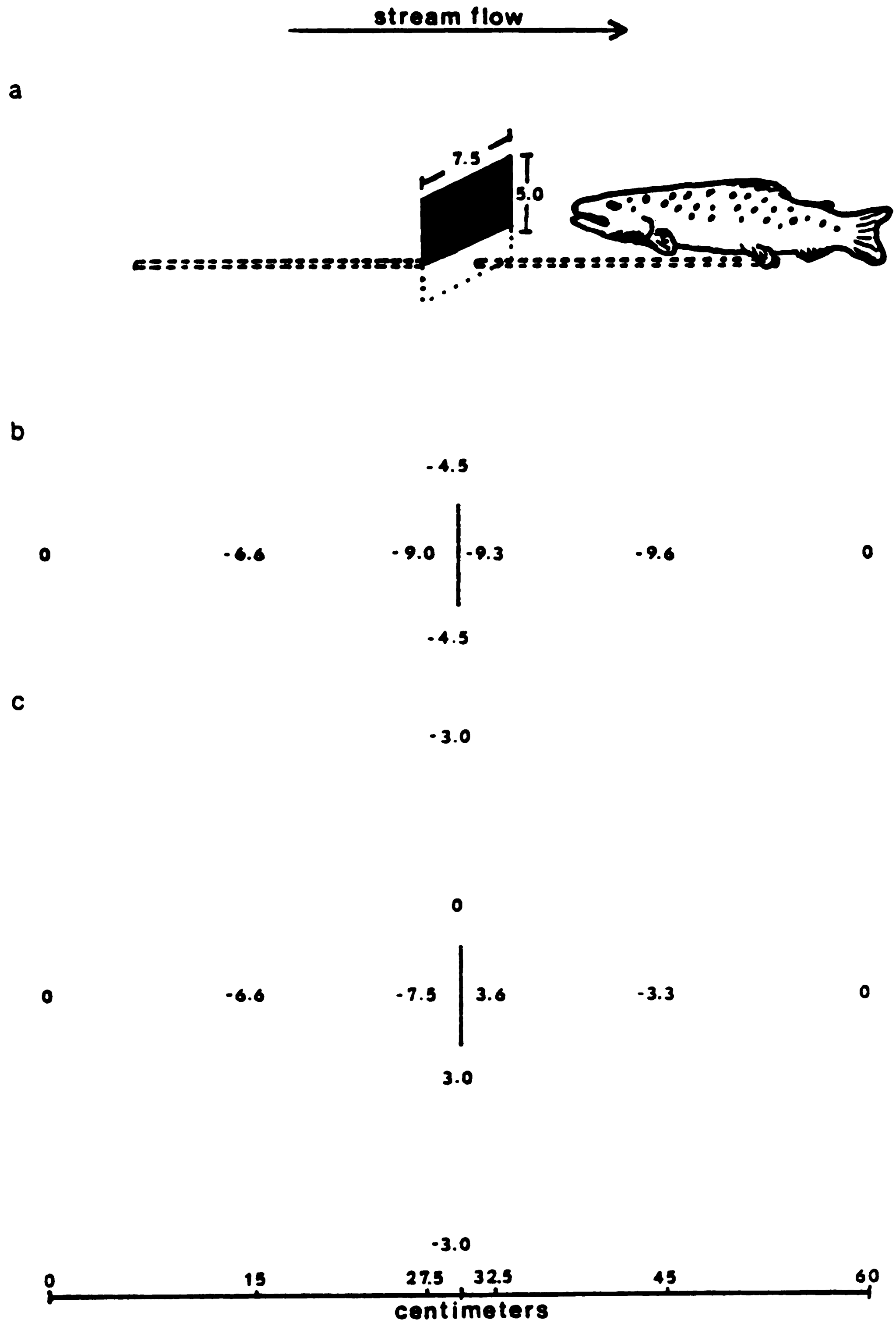


Figure 8. - (a) A feeding reference. Only the shaded part was above the stream bed. Top view of current velocity around a feeding reference (b) 2.5 cm and (c) 5 cm above the stream bed. Numbers indicate the mean difference (cm/s) from background velocity at 3 references.

Three groups of 16 wild brown trout were observed. Each group consisted of 8 small (23-28 cm FL) and 8 large (35-41 cm FL) trout (Appendix Table A3). All were captured by electro-fishing in the North Branch of the AuSable River near Lovells, Michigan. Trout were transported to the study site in an aerated tank. Following anaesthetization with tricaine methane sulfonate (MS-222), each trout was weighed, measured, and given a distinctive cold-brand (Everest and Edmondson, 1967) just under the dorsal fin on both sides of the body to allow individual identification. Two large and two small trout were randomly assigned to each channel section. Time from capture to transplantation in the channels did not exceed 6 h.

Each group was given 10-14 days of acclimation. This was followed by 5-10 days of observation. At the end of each experiment all trout were weighed and measured, then sacrificed to determine sex and to examine stomach contents. Trout were sacrificed at 0800 h and 2000 h (EDT) to compare day and night food consumption. I assumed that food in the digestive tract anterior to the junction of the pyloric cacae and small intestine indicated consumption during the previous 12 h. Organisms were identified to order and their volume measured by water displacement in a 10-ml graduated cylinder.

One 24 h drift net sample was gathered during the acclimation period for each of the 3 groups. The entire cross-section of each channel was sampled simultaneously. Nets were emptied at 6-h intervals and organisms were identified to order and measured volumemetrically as above. This provided a rough estimate of the relative availability of drift food in each channel.

Trout were viewed from elevated blinds. The floor of each blind was 5 m above water level. Each blind was placed so that the channel section on either side could be viewed. The high channel walls and enclosed ladder leading up into the blinds assured approach without detection by the trout (Figure 9).

Observations were made at irregular times. Both average length of observation periods and total observation time varied between channel sections and groups. I attempted to observe each section at least once during every daylight hour, but observations were concentrated during the morning hours when the trout were most active. Observations were lumped into 3 time categories: (1) morning - pre-sunrise to 4 h after sunrise, (2) evening - the 4 h preceding sunset and post-sunset, and (3) midday - all other hours. Low light level prohibited observations more than one-half hour before sunrise or after sunset.

Trout activity was classified as: (1) agonistic, (2) cover use, (3) feeding, and (4) miscellaneous. Time to the nearest 16 sec, and movement to the nearest 0.25 m were recorded for each activity for each trout in a section. Numbers painted at 0.5-m intervals on the channel walls and two white cords equally spaced and running the length of each section provided a grid for identifying positions of the trout.

At the beginning of an observation session, each visible trout was identified, using 7 × 50 binoculars with polarizing filters. Activity type, position, and time were recorded vocally on tape.

Figure 9. - Side view of the downstream observation blind showing the enclosed ladder and high channel walls. A window faces the channel on both sides of the blind.

Trout using cover were not visible unless very close to the edge of a cover device. Individuals that remained under cover for the entire observation session were recorded as using cover, but their position could not be specified. As trout moved, the time and new position and the new activity, if it changed, were recorded. All tape-recorded information was transcribed onto data sheets for analysis. Distance moved was determined by measuring distance between coordinates on scale drawings of the channel sections.

Over 60 h of observation time were accumulated (Appendix Table A4). Percent of total observation time in each time period was: morning--45%, midday--31%, evening--24%. Mean length of observation sessions was 21.3 min.

<u>Activity Definitions</u>

Cover Use: Time spent with any part of the trout's body directly under cover, provided no feeding activity occurred, was considered cover use. Movement associated with cover use was measured from the last position held in the open not clearly associated with one of the other 3 activity categories. Movement associated with other activities was defined similarly.

Feeding: Feeding time was that spent in positions from which drift or benthic prey were consumed at least once during 15 min of observation. Continuous swimming time which was interrupted at least once during 5 min to consume prey was also recorded as feeding time. Occasionally, occupation of a position not under cover for periods longer than 15 min without food consumption was recorded as feeding time if that individual fed from that position during a subsequent observation session. I expected that trout would not occupy the shallow open water unless motivated to feed. Time under cover was considered feeding time beginning with the occurrence of a foray from cover to intercept drift food or benthos. Feeding time was defined as ending 15 min after the last observed foray from cover. Time spent under cover following movement from a feeding position in the open was considered cover use time if no more feeding activity occurred within one minute. Movement from cover to a position where food was consumed was recorded as feeding movement.

Agonistic: Time involved in competitive interactions constituted agonism. Social rank determinations were based on the outcome of one-on-one agonistic bouts in which one of the interacting individuals was displaced from a feeding or cover position. Displacement was assumed to indicate inferior social status.

Miscellaneous: Time and movement involved in activities not included in the definitions of cover use, feeding, and agonistic behavior were lumped into the miscellaneous category.

<u>Light Intensity Beneath Cover</u>

After completing the outdoor experiments with trout, I measured light intensity beneath opaque covers indoors under a constant light source (Table 5)[1]. Doubling the width of covers used in this study to 50 cm, without changing cover length, reduced light intensity 3-fold. Doubling cover length to 122 cm, without changing width, did not measurably reduce light intensity beneath the device. Light intensity

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[1]Weston Model 856 RB selenium photovoltic cell and Keithley Instruments Model 150 B microvolt ammeter.

Table 5. - Light intensity under overhead cover devices of various sizes and heights above the stream bed. Measurements were made indoors under a constant light source.

Cover dimensions (cm)		Cover height (cm)	Light intensity under middle of cover (ft-c ± 6%)
25	61[ab]	10	0.0916
25	61[a]	15	0.2916
50	61	10	0.0332
25	122[b] (5 cm gap, see Figure 12)	10	0.0916 (measured beneath middle of upstream half)
30	30[c]	30	3.8076
61	61[c]	30	1.2416
91	91[c]	30	0.7332
		Incident light -	15.0808

[a]Cover sizes and heights used by DeVore (1975).

[b]Cover sizes and heights used in this study.

[c]Cover sizes and heights used by Butler and Hawthorne (1968).

beneath low cover (10 cm above the stream bed) was 1/3 that under high (15 cm) cover. Beneath large square (91 × 91 cm) cover, light intensity was 5-fold lower than beneath small square (30 × 30 cm) cover.

Statistics

Two factors were expected to have major influence on position choice by brown trout: social rank and time of day. A third factor, replicate (a group of trout in a channel section within one of the 3-week experiments) was of secondary interest as a random influence. The effect of each of these factors on trout behavior was evaluated with a 3-factor analysis of variance (ANOVA) adapted for use on sets of data with unequal replication between factor levels[2].

Daily records of the percent of total time and movement spent in each activity, and the rates of movement (cm/s) associated with each activity were used to calculate the mean percent of time and movement and the mean rate of movement for each trout. These means were the data points used in the ANOVA. Use of mean values in treatment combination cells precluded distinguishing variance due to the 3-way interaction of social rank, time of day, and replicate from random error variance. It was also impossible to estimate the component of variance contributed by the random factor, for the same reason. Three-way interaction variance was assumed to be zero. Degrees of freedom were derived from (number of social ranks) × (number of times of day) × (number of replicates). Social rank and time of

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[2]SPSS computer program, Michigan State University Computer Center.

day were considered fixed factors, replicate was considered a random factor. Calculation of F-values is summarized in Table 6.

An assumption of ANOVA is that residual errors are distributed independently (Sokal and Rohlf, 1969). Random assignment of trout to sections was an attempt to minimize non-independence. But randomization cannot correct for the effects of social factors operating within newly formed groups of trout. Follow-the-leader behavior would tend to reduce the range in behavior between trout in a replicate from what it would have been had each trout been observed in isolation (independently). Conversely, avoidance of dominants would tend to inflate the range in behavior. Either situation weakens the validity of the usual F-test of significance. Lack of independence is inherent in data from groups of animals. Results of ANOVA must be interpreted with this in mind.

All data sets were tested for normality and homogeneous variance prior to hypothesis testing. The Kruskal-Wallis non-parametric one-way ANOVA was applied to sets of data that did not meet these assumptions. Contrasts between factor level means were done with Tukey's w-procedure where replication was not badly unbalanced and variance was homogeneous, or with Scheffé's procedure where replication was badly unblanced and/or variance was heterogeneous. The Student's t-test was also used to contrast two means where variance was homogeneous (Gill, In press). One and two-factor ANOVA and simple regression were applied as needed.

Vandals removed several trout during acclimation periods so there were only 6 replicates with 4 trout during the observation days.

Table 6. - Derivation of F-values for 3-factor ANOVA with two fixed (F) and one random (R) factor, and unbalanced replication. MS = mean square.

	Source of Variation	Degrees of freedom	F-value[a]
A	Social rank (F)	3	MS_A/MS_{AC}
B	Time of day (F)	2	MS_B/MS_{BC}
C	Replicate (R)	5	MS_C/MS_E
AB	Social rank × Time of day	6	MS_{AB}/MS_E
AC	Social rank × Replicate	13	MS_{AC}/MS_E
BC	Time of day × Replicate	9	MS_{BC}/MS_E
E	Residual error[b]	14	

[a]From Gill, (In press).

[b]Cannot be distinguished from 3-way interaction (ABC).

Replicates with fewer than 4 trout were considered separate from these replicates as the social environments were not comparable. Hereafter, replicates will be designated by experiment (Roman numeral) and channel section.

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Precent of total cumulative observation time and movement in each activity category was (see Appendix Tables A5 and A6):

Activity	% Time	% Movement
Agonistic	0.9	39.5
Cover use	54.6	13.0
Feeding	34.8	44.6
Miscellaneous	9.7	2.9

Cover use time was actually greater than indicated here as time spent feeding under cover was put in the feeding category. Correcting for this, percent of time spent in cover use was 63.0%. The importance of miscellaneous activity is inflated, as 83% was contributed by only 4 trout. Movement in each activity was not proportional to time. Agonism involved much movement.

Replicates from which vandals had removed some trout were observed infrequently, as they provided less information on social interactions. Except where stated otherwise, results apply only to replicates with 4 trout.

Agonistic Behavior

Agonism usually consisted of an agonistic act by the initiator and one by the receiver. Agonistic acts included various types of agressive approaches, counter-approaches, direct attacks and submissive withdrawals. The sum of agonistic acts associated with one conflict period constituted an agonistic bout.

Three general types of one-on-one agonistic bouts were observed: approach-withdrawal, approach-counter-approach-withdrawal, and direct attack-withdrawal.

Approach-withdrawal: This type of agonistic bout was by far the most common. The initiator swam rapidly, either upstream or downstream, toward the receiver or drifted slowly downstream tail-first toward the receiver, resulting in withdrawal of the receiver without physical contact. The initiator often took up the position from which the receiver had been displaced, but occasionally returned to the previously occupied position or to a new position. The initiator often chased the receiver several meters from the site of the initial conflict following a head-first approach. Those receivers approached tail-first were chased much less frequently following displacement. Tail-first approaches were made exclusively by large trout. Regardless of the type of approach, subordinate receivers usually began flight while the initiator was still 1-2 m away.

Rarely, an initiator apparently terminated an approach before the would-be receiver responded. In those cases the initiator was always subordinate to the receiver.

Approach-counter approach-withdrawal: This type of bout occurred only 3 times. Following an approach by the initiator, the receiver either withdrew a short distance and then returned to displace the initiator, or did not withdraw at all and began chasing the initiator

while still one or more meters away. All counter approaches occurred following high-speed entry of cover by the initiator. Whether the intent of the entering individual was agonistic or cover-seeking in nature was questionable but the response of the cover occupant was clearly agonistic. These were the only occasions observed when rank-1 and rank-2 trout were displaced by subordinates. It seems likely that the initial exit from cover was in response to the sudden appearance of a disrupting or frightening stimulus in confined quarters rather than avoidance of a specific individual.

Direct attack-withdrawal: Direct attacks involved nips and head-first bumps to the body and fins of the receiver. This was observed only in replicate IIIB2. The receiver was an injured trout that was larger than the initiator. These bouts often began as the approach-withdrawal type but became more violent when the receiver withdrew to a corner of the channel section. Twice the receiver pressed sideways against the lower screen in a head-down position, exhausted, following repeated attacks.

On several occasions one or more trout followed or circled another, or swam slowly side by side. At least one of the large trout was always involved. These activities were also included in the agonistic category even though there was no apparent initiator or receiver, and displacement was not apparent.

Lateral threat displays, wigwag displays and other agonistic acts described for salmonids by several authors (Newman, 1956; Kalleberg, 1958; Jenkins, 1969) were not observed. The blinds were too far from the trout to permit viewing the more subtle agonistic acts that may have occurred.

A total of 187 bouts were observed (Appendix Tables A7, A8 and A9). One-hundred and sixty-five of these occurred in the 6 replicates with 4 trout. In these replicates, rank-3 trout were involved in the greatest number of bouts (96) and rank-4 in the fewest (70). Ranks 1 and 2 were both involved in 82 bouts.

More conflicts occurred between trout differing by only one social rank than between trout differing by two or three ranks (Table 7). Aggressiveness was greatest during feeding periods. More bouts resulted in displacement from feeding positions than in displacement from cover (Table 8). This occurred even though less time was spent feeding (32.36%) than using cover (65.74%).

Table 7. - Number of one-on-one agonistic bouts between pairs of socials ranks in replicates with 4 trout.

	Ranks of interacting trout						
	1+2	1+3	1+4	2+3	2+4	3+4	Total
Number of bouts	34	29	19	32	16	35	165
Percent of total	20.61	17.58	11.52	19.39	9.70	21.21	100.01

The social hierarchy was very stable in all replicates. Dominants lost only 2.14% of all bouts. Body weight was the primary determinant of social rank (Appendix Table A3). Rank 2 in replicate IIA1 weighed 15% more than rank 1 but clearly lost the single bout observed. No injury was apparent, but failure to feed and use cover in addition to the agonistic loss suggests that behavior had been

Table 8. - The number of agonistic bouts in which trout were displaced from cover or feeding stations in replicates with 4 trout.

Replicate	Trout displaced from Cover	Trout displaced from Feeding station[a]	Total
IA2	5	5	10
IIA1	8	6	14
IIA2	13	18	31
IIB1	4	34	38
IIB2	15	7	22
IIIA1	29	21	50
Total	74	91	165

[a]Includes feeding from cover.

affected by capture and handling. This trout was excluded from statistical analyses. Rank 2 in replicate IIIB2 was badly bruised by vandals. It weighed 28% more than rank 1 but lost all 11 of its bouts. It, too, did not feed and was excluded from statistical analyses. The effect of sex on social rank could not be determined due to the masking affect of body weight.

Mean percent of observation session time devoted to agonism increased from rank 1 to rank 3, but rank 4 spent less time in agonism than ranks 2 and 3 (Appendix Table A10). Differences between ranks were nearly significant during the morning ($p = 0.1$) but not during midday or evening sessions. A significantly greater portion of time was spent in agonism during the morning than during midday or evening ($p < 0.01$). Replicates did not differ significantly ($p < 0.1$).

Mean percent of observation session movement devoted to agonism was nearly the same during each time of day (Appendix Table A11). Social ranks also did not differ significantly ($p < 0.5$). But during midday and evening, rank 1 devoted a significantly greater portion of total movement to agonism than ranks 2, 3, and 4 considered together ($p < 0.001$). During these two time periods, most movement of rank 1 was associated with agonism. Replicates did not differ significantly ($p < 0.5$). Mean rate of movement (cm/s) in agonism was greatest for small trout (Appendix Table A12) but differences between ranks were not significant ($p < 0.5$). Times of day ($p < 0.5$) and replicates ($p < 0.5$) did not differ significantly.

The presence of dominants seemed to inhibit agonism among low-ranking trout. The intensity and duration of agonistic bouts was greater among small trout in replicates lacking large trout than in replicates where two large trout were present. This is reflected in time and movement (Table 9).

Table 9. - Mean percent of observation session time and movement, and mean rate of movement in agonism by small trout in replicates with two large trout and with no large trout.

	Number of replicates	% Time	% Movement	Rate of movement (cm/s)
Two large trout	6	0.60	20.61	14.88
No large trout	2	3.26	58.93	44.27

Cover Use

The highest ranking trout using cover always occupied the most upstream position. Usually the tip of the snout was just downstream from the leading edge of the cover. Subordinates moved to the upstream position following exit of higher ranking trout. As dominants entered cover, subordinates moved to the lower end of the cover or moved to the other cover. If a dominant entered cover occupied by two or more subordinates, the lowest ranking trout was most likely to move to the other cover. Occasionally trout displaced from cover remained in the open and began feeding rather than moving to the other cover.

Most agonistic bouts associated with cover use occurred as trout entered an occupied cover. If a bout did not occur immediately, the occupants usually coexisted for the duration of the session.

Trout were much less aggressive when using cover than when feeding. Chases originating from cover were shorter than those associated with displacement from feeding positions. All ranks used both covers in their section and seemed to displace subordinates just as readily from their preferred cover as from their non-preferred cover. Trout rarely moved from cover to chase approaching subordinates, even when subordinates approached from upstream. This contrasted sharply with behavior at feeding stations where trout that approached dominants closely from the side or upstream were usually chased.

Mean percent of observation session time spent under cover was highest for rank-1 trout (Appendix Table A13). Rank 1 used cover significantly more than ranks 3 ($p < 0.01$) and 4 ($p < 0.01$), but did not differ from rank 2 ($p < 0.4$). Cover use was greatest for all ranks during midday. Mean midday cover use was significantly greater ($p < 0.01$) than morning use but was not significantly different than evening use. Ranks 1 and 2 usually remained under cover well into the evening, but ranks 3 and 4 often left cover to feed once the channel was mostly shaded.

Rank 2 in replicate IIA1 and rank 4 in replicate IIIA1 were excluded from statistical analyses. Both spent most of their time in a small area around coordinates 1.25, 12 (Appendix Figure B3) where substrate irregularities reduced current velocity and produced surface turbulence that may have been responded to as overhead cover. Occupation of that position could have been related to motivation to feed or motivation to use cover.

Cover use was significantly greater in replicate IIB2 than in replicates IA2 ($p < 0.05$) and IIA2 ($p < 0.01$). Use in replicate IIA1 was significantly greater than in IIA2 ($p < 0.05$). Mean replicate cover use time was not significantly correlated with either mean sectional current velocity ($p < 0.5$) or depth ($p < 0.5$).

Mean percent of observation session movement (Appendix Table A14) associated with cover use was significantly lower during the evening than during morning ($p < 0.05$) and midday ($p < 0.05$). Differences between social ranks and replicates were not significant ($p < 0.5$). Differences in rate of movement (cm/s) (Appendix Table A15) also were not significant between social ranks ($p < 0.5$), times of day ($p < 0.5$) and replicates ($p < 0.5$).

Preferred Cover

Total time spent by trout at each cover in its section reflected responses to other trout as well as responses to the physical characteristics of the cover. I assumed that subordinates would occasionally not use their preferred cover due to avoidance of dominants under cover. Only time spent at each cover when dominants did not occupy _either_ cover, i.e., when "free choice" was possible, was used to determine individual preference. This included time spent feeding under cover, as there seemed to be no reason for the cover preferred for feeding to be different than the cover preferred when not feeding. Rank 1 always had free choice by definition. Free choice occurred less frequently proceeding from ranks 2 to 4, so that preference could not be determined for most of these trout.

Preferred cover was defined as the cover at which a trout spent at least 66% of its total "free-choice" cover use time. A preference judgement was based on the results of at least 3 observation sessions, and at least 20 min of total observation time. Preference was determined for 8 rank-1 trout, 3 rank-2 trout, and one rank-4 trout (Table 10). Rank-2 and rank-4 trout preferred the same cover as rank 1 in their section. Hereafter, "preferred" will refer to the cover preferred by rank 1.

Cover size did not strongly influence preference. Five of 8 rank-1 trout preferred small cover (Table 10). Relative current velocity seemed to be the most important stimulus involved in cover choice. Depth had no apparent influence on cover choice. Five rank-1 trout preferred the cover with the slowest current velocity beneath. Only two preferred the cover with the highest current velocity. One of these was a large cover and one was a small cover. In the remaining replicate where current velocity was the same under both covers, the large one was preferred.

Size of cover clearly influenced patterns of association between trout. Coexistence between rank 1 and one subordinate was most frequent under the preferred cover regardless of its size except in replicate IIA1 (Table 11). But in replicates where large cover was preferred, its use by rank 1 and one subordinate was proportionally greater than use of small cover by rank 1 and one subordinate in replicates where small cover was preferred. Ninety-one percent (n = 43 observations) of all multiple occupancies occurred under large cover in replicates where large cover was preferred. In replicates

Table 10. - Current velocity and depth at large and small covers in each replicate. "Free-choice" time and number of observation sessions spent under cover by each social rank indicates preference* as described in the text.

	Cover characteristics			"Free-choice"[a] events							
				Rank 1		Rank 2		Rank 3		Rank 4	
Replicate	Size[b] and position	Velocity[c] (cm/s)	Depth (cm)	no. obs.	Time (min)	no. obs.	Time (min)	no. obs.	Time (min)	no. obs.	Time (min)
					Group I						
IA1	S*	18.9	27.5	2*	54.0*	0	0	0	0		
	L	24.0	27.5	2	8.0	0	0	0	0		
IA2	L*	27.0	26.25	3*	42.5*	2	41.5*	0	0	0	0
	S	20.4	22.5	0	0	1	7.5	1	1.0	0	0
IB1	S*	23.4	21.25	4*	33.75*	0	0				
	L	18.0	20.0	3	6.0	0	0				
IB2	S	23.1	26.25	0	0	0	0				
	L	18.9	28.75	1	0.5	0	0				
					Group II						
IIA1	L	23.4	22.5	5	46.0	0	0	0	0	0	0
	S*	19.5	20.0	17*	300.5*	0	0	0	0	0	0
IIA2	S	24.0	28.75	2	6.25	0	0	1	5.5	0	0
	L*	18.0	30.0	17*	200.50*	2	4.0	1	9.0	5	29.0*
IIB1	L	28.2	25.0	4	17.75	3	13.75	3	5.5	0	0
	S*	23.4	25.0	8*	52.0*	9	66.5*	2	6.0	1	10.25
IIB2	L	18.0	26.25	1	14.0	0	0	0	0	0	0
	S*	15.0	25.0	4*	53.0*	0	0	0	0	0	0

Table 10 (cont'd.)

					Group III						
IIIA1	S	22.5	23.75	6	115.25	1	5.0	1	1.25	0	0
	L*	22.5	25.0	8*	225.25*	2	18.5*	1	1.0	0	0
IIIA2	L	22.5	27.5	1	39.0						
	S	18.9	20.0	2	34.0						
IIIB1[d]											
IIIB2	S	18.0	26.25	3	36.0	0	0				
	L	16.5	25.0	4	50.25	1	2.0				

[a]"Free choice" was when dominants did not use either cover.

[b]S - small, upstream L - large, upstream
L - large, downstream S - small, downstream

[c]Velocity measured under the middle of cover, 5 cm above the stream bed.

[d]All trout were removed from this replicate by vandals.

Table 11. - Time (min) and number of observation sessions spent under cover by each social rank alone and in all possible combinations with other ranks during sessions when positions of all 4 trout were known. Preferred covers indicated by an asterisk.

Rank of	Large cover												Small cover											
cover	Replicate												Replicate											
	IA2*		IIA1		IIA2*		IIB1		IIB2		IIIA1*		IA2		IIA1*		IIA2		IIB1*		IIB2*		IIIA1	
users	no.	min	no.	min	no.	min	no.	min	no.	min	no.	min	no.	min	no.	min	no.	min	no.	min	no.	min	no.	min
1	2	22.5	1	3.5	4	28.75	2	4.75	1	4.5	6	43.25	0	0	6	66.0	2	6.25	2	17.5	1	15.25	3	64.5
2	1	9.74	0	0	0	0	4	17.75	1	7.0	2	48.75	1	7.5	0	0	1	1.0	6	56.5	0	0	3	45.0
3	1	3.5	6	62.5	2	19.75	6	63.5	1	13.0	2	43.0	2	16.75	1	3.5	0	0	4	18.0	0	0	4	20.75
4	1	3.0	0	0	3	23	2	19.5	1	1.0	0	0	1	10.0	3	16.25	3	44.75	0	0	0	0	0	0
1+2	1	4.0	0	0	5	90.25	2	13.5	0	0	2	0.75	0	0	0	0	0	0	6	23.5	3	29.5	1	23.75
1+3	0	0	4	20.5	0	0	0	0	1	7.25	5	143.0	0	0	0	0	0	0	1	1.5	0	0	0	0
1+4	1	16.0	1	3.75	4	35.25	0	0	0	0	0	0	0	0	3	27.25	0	0	0	0	0	0	0	0
2+3	1	25.0	0	0	1	0.25	1	3.5	0	0	2	36.5	2	24.75	0	0	0	0	2	3.5	0	0	0	0
2+4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	7.0	0	0
3+4	1	3.5	4	30.75	0	0	1	4.25	1	22.5	0	0	0	0	1	3.0	0	0	0	0	0	0	0	0
1+2+3	0	0	0	0	1	18.25	0	0	0	0	1	4.0	0	0	0	0	0	0	2	7.75	0	0	1	3.0
1+2+4	0	0	0	0	2	10.25	0	0	0	0	0	0	0	0	0	0	0	0	1	16.0	0	0	0	0
1+3+4	0	0	0	0	0	0	0	0	1	1.25	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2+3+4	1	1.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1+2+3+4	0	0	0	0	1	8.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	10	88.75	16	121.0	23	234.25	18	126.75	7	56.5	20	319.25	6	59.0	14	116.0	6	52.0	24	144.25	5	51.75	12	157.0

where small cover was preferred, only 56% (n = 36 observations) of all multiple occupancies occurred under small cover. The extra space under large cover permitted more trout to coexist.

Failure to coexist with a dominant under cover could be the result of: (1) displacement immediately following an agonistic bout, (2) learned avoidance following several agonistic bouts in the more distant past, and (3) preference for cover not used by the dominant.[3] An evaluation of the effect of (2) on cover use was attempted by determining the extent to which trout took advantage of opportunities to avoid dominants under cover. Time spent under the non-preferred cover was expressed as a percentage of the total potential time available to use the non-preferred cover when only the preferred cover was occupied by dominants (Table 12). Time spent under the preferred cover when dominants occupied only the non-preferred cover was ignored as occupation of the preferred cover by a subordinate may have reflected preference for that cover rather than avoidance of a dominant. Data were too limited to permit evaluation of relations between specific pairs of ranks. The data in Table 12 therefore indicate avoidance of all dominants simultaneously.

Avoidance of dominants under cover increased from rank 2 to rank 4. Variability between replicates was so great, however, that differences between ranks were not significant overall ($p < 0.2$). Much of this variability was related to the size of the preferred

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[3]All trout were assumed to prefer the same cover but even rank-1 trout occasionally used the "non-preferred" cover.

Table 12. - Time available to use the "non-preferred"[a] cover when dominants were using only the "preferred" cover. Percent utilization indicates the extent to which ranks 2, 3, and 4 took advantage of opportunities to avoid dominants under cover. This only includes sessions when positions of all 4 trout were known.

		Rank					
		2		3		4	
Replicate	Size of preferred cover	Time (min)	% utilization	Time (min)	% utilization	Time (min)	% utilization
IA2	large	28.75	83	40.5	35	15.0	87
IIA1	small	b	b	108.0	94	16.5	100
IIA2	large	69.0	0	30.0	0	96.5	46
IIB1	small	68.75	7	70.75	85	15.5	100
IIB2	small	31.5	21	34.5	100	2.0	0[c]
IIIA1	large	72.0	51	171.75	24	b	
Mean			32.4		56.3		83.2

[a]"Non-preferred" cover is the cover used least by rank-1 trout.

[b]These trout did not use cover.

[c]Non included in the mean.

cover in the section. Ranks 3 and 4, considered together, avoided dominants significantly less ($p < 0.01$) in replicates where large cover was preferred than in replicates where small cover was preferred. However, cover size did not influence the degree of avoidance of rank 1 by rank 2: these two ranks coexisted as well under small cover as under large cover.

A separate analysis also indicated that relative social rank influenced trout association under cover. Observed frequencies of associations under cover by specific combinations of social ranks were compared with the frequencies that would be expected if associations were solely by chance. Use of large cover was considered separately from use of small cover as large and small covers were not equally attractive, i.e., the probability of using large cover differed from the probability of using small cover (Appendix Table A16). Ranks 1 and 2 used cover more frequently than subordinates and were therefore expected to coexist under cover by change more frequently than combinations including ranks 3 and 4. This was taken into account by calculating the probability of using cover separately for each social rank and then using these values to derive expected frequencies. Expected frequencies are derived in Table 13. They provide a measure of relative expectations of coexistence under cover. Time spent under cover and frequency of cover use were highly correlated ($r = 0.913$, $p < 0.05$).

Observed use of large cover by combinations of two or more social ranks was almost significantly different than expected ($p < 0.1$). Observed use of small cover was not significantly different than

Table 13. - Observed frequencies and derivation of expected frequencies of using small and large covers for combinations of social ranks.

Rank of cover users	Obs. freq.	Probability of[a] using cover together	Adj.[b] prob.	Exp.[c] freq.	Chi square value	Significance level
		Large cover				
1+2	10	0.26	0.104	4.784	5.687	
1+3	10	0.351	0.14	6.44	1.967	
1+4	6	0.3	0.12	5.52	0.042	
2+3	5	0.286	0.114	5.244	0.011	
2+4	0	0.244	0.098	4.508	4.507	$p < 0.1$
3+4	8	0.33	0.132	6.072	0.613	
1+2+3	2	0.162	0.065	2.99	0.328	
1+2+4	2	0.138	0.055	2.53	0.111	
1+3+4	1	0.187	0.075	3.45	1.739	
2+3+4	1	0.152	0.061	2.806	1.162	
1+2+3+4	1	0.086	0.034	1.564	0.199	
		Small cover				
1+2	10	0.184	0.207	4.968	5.097	
1+3	1	0.104	0.117	2.808	1.164	
1+4	3	0.102	0.115	2.76	0.022	
2+3	4	0.128	0.144	3.456	0.087	
2+4	1	0.126	0.142	3.408	1.702	$p < 0.3$
3+4	1	0.071	0.078	1.872	0.406	
1+2+3	3	0.050	0.056	1.344	2.039	
1+2+4	1	0.049	0.055	1.32	0.079	
1+3+4	0	0.028	0.031	0.744	0.739	
2+3+4	0	0.034	0.038	0.912	0.91	
1+2+3+4	0	0.013	0.015	0.36	0.361	

[a]Probability of using cover together is the product of the probabilities that each social rank used cover alone (Appendix Table A16).

[b]Sum of adjusted probabilities within a cover size category equals 1.

[c]Expected frequency is the product of the adjusted probability and the sum of observed frequencies (large cover = 46; small cover = 23).

expected ($p < 0.3$). However, it should be noted that a large portion of the total chi-square value was contributed by the rank-1-and-2 combination (Table 13). Rank 2 used cover with rank 1 more than expected regardless of cover size. Rank 4 used cover with rank 2 less than expected regardless of cover size. All other combinations were relatively as frequent as expected.

To summarize this section, cover use patterns were influenced by social rank, cover size, and probably by current velocity under cover. Individual choice of cover was determined at least as much by current velocity beneath as by cover size. Low current velocity seemed preferable to large size. Attractiveness of cover in regard to current velocity and other unmeasured physical features in the vicinity of cover was not sufficient to fully compensate for space limitations imposed by small cover size. Large cover received at least as much total use as small cover even in replicates where small cover was preferred. Much of the heavy use of large cover in replicates where small cover was preferred was due to avoidance of rank 1 by ranks 3 and 4 and by avoidance of rank 2 by rank 4. Trout differing by only one rank co-existed nearly as well under small cover as under large cover.

Cover Use and Feeding

There was a tendency for some trout to feed on the side of the channel with cover (Table 14). But, ANOVA on the difference between the percent of time spent feeding on the west and the east sides of the channel showed that differences between replicates with different cover locations were not significant ($p < 0.5$). Time spent

Table 14. - Location of feeding stations used by each social rank and location of overhead covers in replicates with 4 trout. Percent of total feeding time spent on the west and east sides of the channel and in the middle of the channel shown. Time spent feeding from cover is not included.

		Cover location								
		West			Middle			East		
		Feeding location			Feeding location			Feeding location		
Rank	Time of day	West	Middle[a]	East	West	Middle[a]	East	West	Middle[a]	East
		Group I, Section A2			Group II, Section A2			Group II, Section A1		
1	Morning	0	0	100.0	72.0	0	28.0			
	Midday									
	Evening				97.0	0	3.0			
2	Morning	100.0	0	0	9.5	0	90.5			
	Midday	82.0	0	18.0	0	0	100.0			
	Evening	100.0	0	0	100.0	0	0			
3	Morning	0	0	100.0	7.0	3.0	90.0			
	Midday				0	5.0	95.0			
	Evening	80.0	5.0	15.0	3.0	9.0	88.0	85.0	0	15.0
4	Morning	92.0	0	8.0	79.0	3.0	18.0	24.0	67.0	9.0
	Midday	100.0	0	0				0	0	100.0
	Evening	96.0	0	4	100.0	0	0	33.0	67.0	0
		Group III, Section A1			Group II, Section B1			Group II, Section B2		
1	Morning	0	0	100.0	100.0	0	0	0	0	100.0
	Midday	0	0	100.0						
	Evening	100.0	0	0						
2	Morning	1.0	0	99.0	94.0	6.0	0	16.0	0	84.0
	Midday	19.0	0	81.0						
	Evening	100.0	0	0						

Table 14 (cont'd.)

3	Morning	44.0	54.0	2.0	0	14.0	86.0	96.0	4.0	0
	Midday	0	100.0	0	0	78.0	22.0			
	Evening	72.0	0	28.0	0	11.0	89.0	94.0	0	6.0
4	Morning				23.0	41.0	36.0	0	7.0	93.0
	Midday				6.0	37.0	57.0			
	Evening				56.0	0	44.0	0	0	100.0
Mean		54.8	8.8	36.4	41.5	11.5	47.0	34.8	14.5	50.7
SD		44.9	26.0	44.7	43.8	20.6	39.6	40.9	27.8	47.5

[a]Trout were considered feeding in the middle of the channel only if the feeding station was on longitude 2.5.

feeding under cover was not included in the calculations, as this would have biased results in favor of the side of the channel with cover.

Large trout did not feed closer to cover than small trout (Figure 10; Appendix Table A17). Distance between the feeding station and the nearest cover, weighted by the percent of feeding time spent at the station did not differ significantly between ranks, ($p < 0.1$) or times of day ($p < 0.5$).

Mean percent of feeding time spent under cover was significantly less ($p < 0.05$) for rank 4 than for ranks 1, 2, and 3 considered together (Appendix Table A18). Rank 4 may have been particularly "afraid" to feed under cover used by dominants. But, low-ranking trout commonly fed from the lower end of cover when dominants occupied the upstream end of cover without agonistic conflict. Mean percent of feeding time spent under cover was highest during midday for all ranks, but extremely high individual variability nullified statistical differences between times of day ($p < 0.5$). Differences between replicates were nearly significant ($p < 0.1$).

Feeding

Types of Feeding Behavior

Three types of feeding behavior were observed. By far the most common type was drift feeding from a more-or-less fixed station. Short vertical and lateral forays to intercept surface and sub-surface drift food organisms were followed immediately by return to the station. Movements greater than 1 m from the station rarely occurred except to capture unusually large items that were artificially

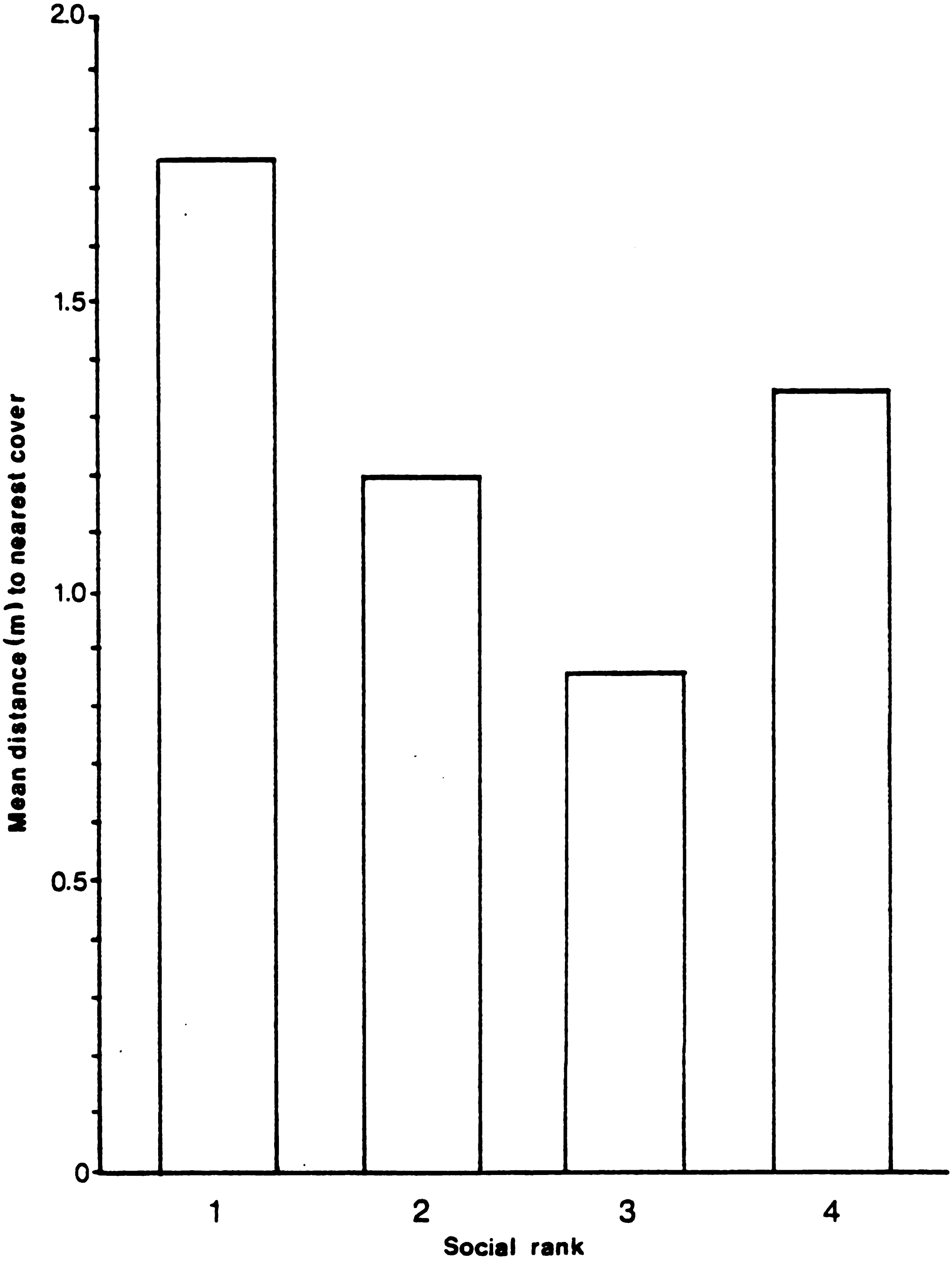

Figure 10. - Mean distance to the nearest cover from feeding stations used by each social rank in replicates with 4 trout. Distance weighted by the percent of feeding time spent at each station. Cover feeding stations are not included.

introduced. Constant swimming maintained the trouts' body in a stationary position above the stream bed. Less often, trout remained on the stream bed between forays. This occurred most among large trout and when food was not abundant.

Drift feeding while cruising about the channel was the second most common type of feeding behavior. It consisted of upstream swimming interrupted at irregular intervals by short vertical or lateral movements to consume drifting food. This occurred most often as trout moved between feeding stations during times when drift food was very abundant. When drift food was scarce, movement between feeding stations occurred without feeding.

Feeding on benthos was the least observed type of feeding behavior. Trout feeding on benthos cruised slowly about the channel showing little affinity to particular areas. The stream bed was bitten repeatedly, followed by conspicuous jaw movements and gill flaring to void detritus and fine sediment. Much of the stomach contents of these trout consisted of fine gravel and organic matter.

The assumption that trout would use positions not under cover only when motivated to feed was supported by almost all observations. The only exceptions were rank 2 in replicate IIA1 and rank 4 in replicate IIIA1 which exhibited abnormal behavior by rarely or never using cover and rank 2 in replicate IIIB2 which was injured.

Drift Food Supply

The volume of drift food entering both channels during 6-h drift net sampling periods was twice as great at night as during the day (Figure 11; Appendix Tables A19 and A20). Peak volume of drift occurred during the first half of the night (2000-0200 h). Daytime volumes were similar for both 6-h periods (0800-1400 h and 1400-2000 h).

Drift volume was over twice as great in channel A as in channel B on all 3 sampling days. Mean volume per food item in channel A was slightly greater than in channel B (Appendix Tables A19 and A20). Drift volume was about the same on the first two sampling days, but lower on the last day in both channels (Figure 11).

Caddisfly (Tricoptera) larvae and pupae (especially *Brachycentrus*) and aquatic isopods (*Asellus*) were the most common drift food organisms comprising 34.9% and 30.6%, respectively, of total drift net volume summed over the 3 sampling dates in both channels (Appendix Table A19). Fish (9.6%) and mayfly (Ephemeroptera) nymphs (7.0%) were the third and fourth largest groups represented. Fish were rare numerically, however (0.4%). The tiny mayfly *Tricorythodes* was extremely abundant on the last two sampling dates but drift net mesh size was too large (1.5mm) to retain most of them. The availability of this potential food source, as well as any others of similar or smaller size was underestimated.

Composition of the drift did not differ much between channels or sampling dates, with the notable exception of mayfly nymphs which increased in volume from 2% to 5%, to 19% of the total on the first, second, and third sampling dates, respectively. Diel composition was quite constant overall, though the absolute and relative contribution of ants (Hymenoptera) was greatest during mid-day.

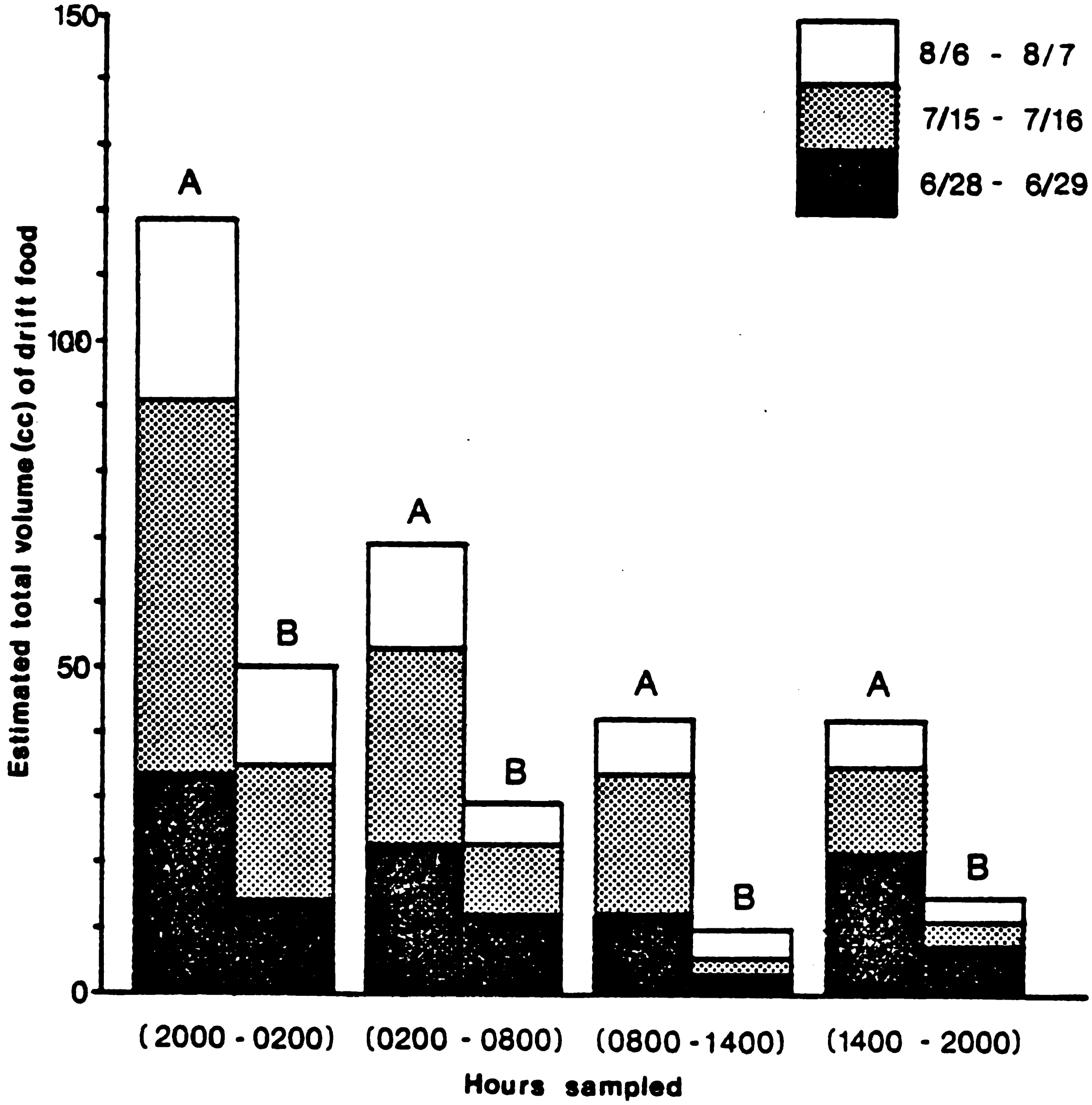

Figure 11. - Estimated total volume of drift food organisms that entered channels A and B on each sampling day. Volumes were estimated from subsamples equal to 5% of the total volume of organisms collected.

Drift Food Utilization

Trout consumed drift food roughly in proportion to its diel availability. Mean volume of food in the stomachs of large and small trout examined in the morning (0800 h) was over twice that in stomachs examined in the evening (2000 h) (Figure 12; Appendix Table A21). Morning and evening means were not significantly different within the large size group ($p < 0.2$), but were nearly significant within the small size group ($p < 0.1$). Mean volume of food in stomachs of small trout was over twice that in stomachs of large trout. Differences were significant in both the morning ($p < 0.05$) and the evening ($p < 0.02$).

Data were not sufficient to permit a statistical comparison of food consumption in channel A with consumption in channel B. There were no apparent differences despite the large measured difference in drift food availability. Perhaps much of the food consumed originated in the channels, rather than drifting in from upstream.

Isopods and adult mayflies composed a greater portion of stomach content volumes than of drift net volumes (Table 15). Caddisfly larvae and pupae were not as well represented in stomachs as in drift nets. As mentioned above, large mesh size was probably responsible for the low capture rate of mayfly adults.

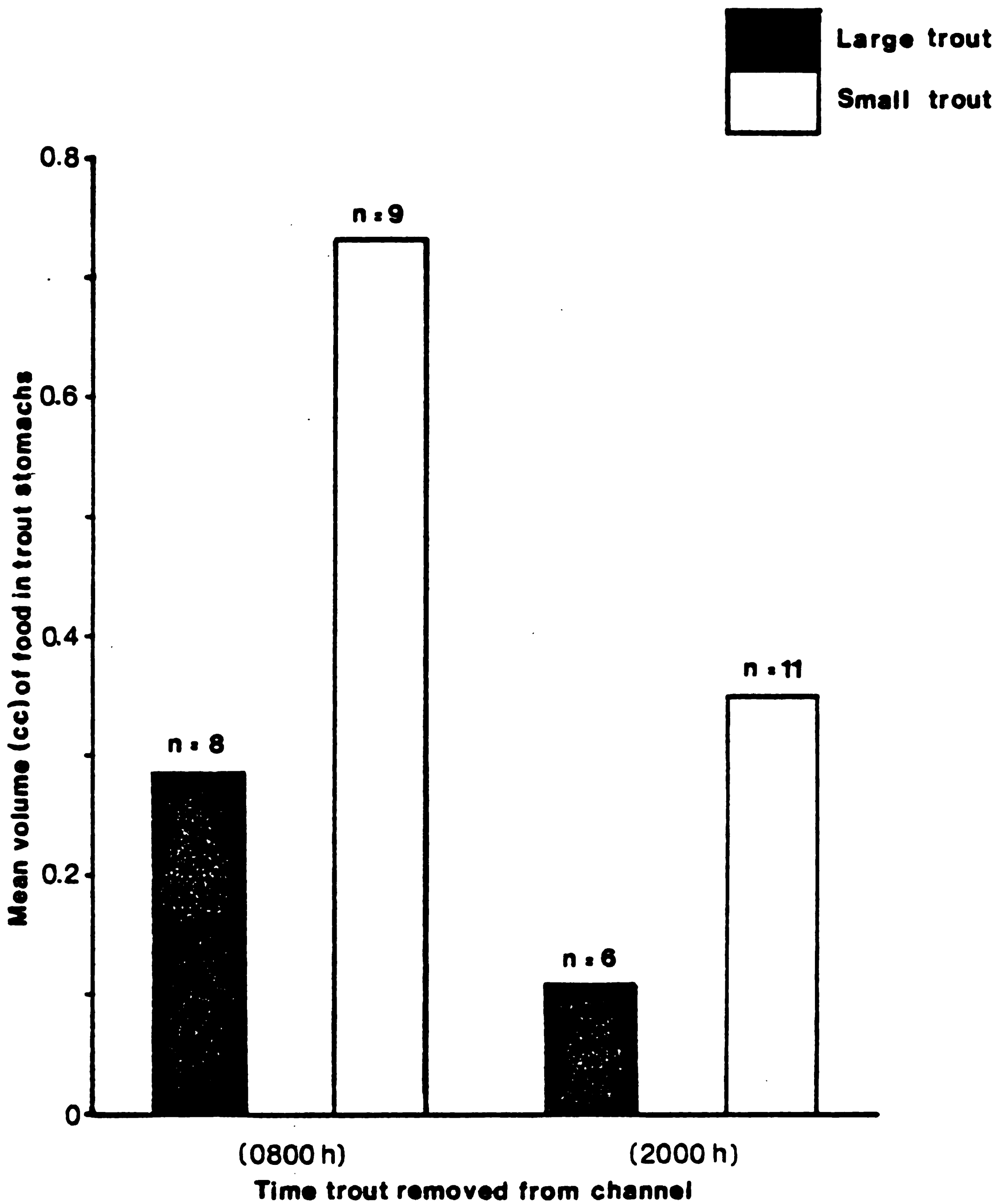

Figure 12. - Mean volume (cc) of food in the stomachs of large and small trout removed from the channels at 0800 h and 2000 h (EDT). n = number of stomachs checked.

Table 15. - Mean percent of the volume (cc) of trout stomach contents and drift net contents as isopods, mayflies, and caddisflies. Miscellaneous items were not included in the total volume.

	Isopods (All instars)	Mayflies (Adults)	Mayflies (Nymphs)	Caddisflies (Larvae and pupae)
Stomachs	56.8	9.3	0.9	6.7
Drift nets	31.0	2.3	7.2	36.1

Small trout as a group relied more heavily on isopods than large trout. Discounting miscellaneous items, isopods were the largest constituent by volume of stomach contents in 75% of the small trout, but is only 36% of the large trout (Appendix Table A21). Caddisfly larvae and pupae, mayfly adults, adult beetles, (Coleoptera), or snail and clams (Mollusca) constituted the major portion of the stomach contents in other trout.

The mean volume of individual food items was similar for large ($\bar{x}$ = 0.0064 cc) and small trout ($\bar{x}$ = 0.0090 cc). Means do not include items in the miscellaneous category for which numbers could not be reliably determined. Mean volume of individual food items was somewhat lower in Group-II trout ($\bar{x}$ = 0.0088 cc) than in either Group-I ($\bar{x}$ = 0.0190 cc) or -III, ($\bar{x}$ = 0.0111 cc) trout due largely to the predominance of Tricorythodes mayflies on the examination date for Group II. Mean volume of individual food items consumed at night ($\bar{x}$ = 0.0171 cc) was nearly twice that of daytime food ($\bar{x}$ = 0.0091 cc).

The assumption that food in the digestive tract anterior to the junction of the pyloric cacae and small intestine was a reliable indicator of consumption during the previous 12 h was supported by examination of stomachs from individuals that were known to have fed near the beginning of the 12-h period. In trout whose stomach contents were checked at 2000 h Tricorythodes mayflies that were consumed between 0800 h and 1000 h were concentrated in the lower stomach and pyloric cacae: few had moved into the intestine. All major food items were of similar size and digestability so that the importance of specific types should not have been biased by this method of analysis.

Additional support for this assumption comes from calculations of the rate of gastic evacuation for brown trout based on data presented by Elliot (1972) for 20-30-cm (TL) brown trout that were fed a variety of aquatic organisms similar in size to most of the foods available in this study. Mean water temperature during the 12 h preceding the time that stomachs were examined gave estimated times for complete gastic evacuation ranging from 10 h during the daylight period for Group I, to 15 h during the same period for Group III. The overall mean was 13.2 h. Elliot found that rates of gastric evacuation were not significantly different for different sized food organisms of the same taxon, for different sized meals, for mixed or multiple meals, or for different sized trout within the size range tested. His equations are therefore readily applicable in this study.

Food supply in the channels was not adequate to meet the energy demands of most trout, especially the large ones. Mean weight loss over 3-week experiment periods was 8.5% for large trout and 3.7% for small trout (Appendix Table A3). Mean weight losses among large trout were 11.5%, 7.7%, and 6.5% for Groups I, II, and III, respectively. Corresponding losses among small trout were 6.0%, 1.7%, and 3.2%.

Mean group weight losses did not parallel trends in drift net food volume. Among the 3 groups, weight loss among Group-II trout was intermediate despite the occurrence of the highest drift food availability during that period. Of course, this assumes that drift samples accurately indicated drift food availability throughout the experiment. Volume of benthic food organisms in the channels was not determined but presumably it increased, over the course of the experiments. Stream bed disturbances during initial channel preparation undoubtedly destroyed some of the initial standing crop which was probably replaced through immigration (Waters, 1972). This may explain why weight losses were conspicuously greater among Group-I trout than in those following.

Of the more important drift food items only Tricorythodes nymphs should have decreased substantially in abundance over the study period as ecdysis to the adult stage occurred daily throughout the last two experiments. Emergences of various caddisflies and Baetis mayflies occurred late in experiment III, but these were too late and too minor to have significantly reduced the availability of benthos or drift food in the channels.

Feeding Time and Movement

Mean percent of observation session time spent feeding increased from rank-1 to rank-4 trout (Appendix Table A22). Rank 1 fed significantly less than ranks 3 ($p < 0.01$) and 4 ($p < 0.01$) but did not differ significantly from rank 2 ($p < 0.2$). The greatest differences were during midday and evening when small trout commonly fed for short periods but large trout usually stayed under cover and did not feed.

Most feeding occurred during the morning at the peak of the Tricorythodes mayfly emergence and imago fall. Mean percent of time spent feeding was significantly greater during the morning than during midday ($p < 0.01$) and evening ($p < 0.05$). The midday mean was nearly significantly less ($p < 0.1$) than the evening mean. Small trout (ranks 3 and 4) fed about as much during the evening, once the channels were fully shaded, as during the morning. But large trout usually did not begin feeding until 10-20 min after sunset when light level became too low to permit individual identification.

On several evenings after sunset, small and large trout left cover to feed within a 5-min period. There was not a sudden change in light level that might have caused such a sudden change in behavior. The opposite behavior, i.e., sudden termination of feeding as light level increased before sunrise, was not observed. But pre-sunrise observations were not made as often as post-sunset observations so that similar behavior may have occurred. Drift food abundance was not monitored frequently enough to permit comparisons of food availability at comparable light levels in the morning and evening but visual inspection of the water surface with binoculars indicated no sudden change in food availability after sunset or before sunrise.

These observations suggest that there is a light threshold intensity below which cover is not required. However, that the abundant Tricorythodes mayflies released feeding behavior until late morning, even on sunny days, indicates that the typical negative response to high light intensity shown by adult brown trout is modified when food is abundant. The daily pattern of feeding activity is summarized in Table 16.

Table 16. - Summary of daily feeding activity by brown trout in this study.

Time period	Description of feeding activity
Dawn to beginning of *Tricorythodes* emergence.	Sporadic feeding by all trout.
During *Tricorythodes* emergence and imago fall.	Peak feeding by all trout.
End of *Tricorythodes* activity to sunset.	Sporadic feeding, mainly by small trout.
After sunset to dusk.	All trout feeding.

There were large differences between some replicates in percent of time spent feeding (Appendix Table A22). Significantly more feeding occurred in replicate IIIA2 than in replicate IIB2 ($p < 0.05$). Replicates IA2 and IIB2 also differed significantly ($p < 0.05$), and the mean difference between replicates IIB1 and IIB2 was nearly significant ($p < 0.1$). The source of differences between replicates was not differences in drift food availability. As shown above, drift food was twice as abundant in channel A as in channel B in experiment II. But mean percent of time spent feeding in replicate IIA1 was less than in replicate IIB1. In fact, all social ranks in every time period in replicate IIB1 spent proportionately more time feeding than their social counterparts in replicate IIA1. All ranks in replicate IIB2 fed less, on the average, than counterparts in other replicates. Each trout in a replicate was a fairly reliable indicator of the behavior expressed by other trout in its replicate. If one trout fed more than average for its social rank, then the same was often true of the other trout in its replicate.

Differences in feeding activity between replicates were strikingly apparent during the morning Tricorythodes activity. Visual inspection indicates that availability of Tricorythodes was similar in all channel sections. Yet on most mornings all 4 trout in replicates IIA2 and IIB1 fed heavily, while no trout or only the small ones fed in replicates IIA1 and IIB2. The same occurred in experiment I: feeding activity was consistently greater in section A2 than in section AI. Sectional differences in depth and current velocity did not correspond to differences in feeding activity. It seems likely that social factors determined behavior within replicates. This applies to cover use patterns as well.

As presented earlier, small trout in replicates without large trout were more active agonistically than small trout in replicates with large trout. This was not true of feeding activity. Mean percent of time spent feeding by small trout was 43.7% and 37.2% in replicates with and without large trout, respectively.

Mean percent of observation session movement devoted to feeding increased from rank-1 to rank-4 trout (Appendix Table A23). Mean percent of movement in feeding was roughly proportional to mean percent of time, spent feeding. Rank 1 differed significantly from rank 3 ($p < 0.05$) and rank 4 ($p < 0.01$) but did not differ from rank 2 ($p < 0.2$). Differences between times of day were not significant ($p < 0.25$). Replicates differed significantly overall ($p < 0.01$) but contrasts between means were not significant. This statistical result occurred because the sum of variation between all replicates was quite large but differences between any two replicates were relatively small; also the Scheffé procedure is quite weak in detecting mean differences (Dr. J.L. Gill, Statistician, Dept. Dairy Science, Michigan State University, pers. comm.).

Rate of movement (cm/s) during feeding was greatest during the morning and least during midday (Appendix Table A24). The midday and morning means differed significantly ($p < 0.05$). Fewer feeding station changes per unit of feeding time (Table 17) rather than fewer and/or shorter movements per feeding station (Table 18) was the reason for less midday movement. The number of minutes spent per feeding station during midday was significantly greater than during the morning ($p = 0.005$) (Table 17). Large trout (ranks 1 and 2) changed feeding stations less frequently than small trout (ranks 3 and 4) but these mean differences were not significant ($p < 0.5$). Rate of movement was significantly greater in replicate IIB2 than in all other replicates considered together ($p < 0.05$). This may reflect the fact that mean current velocity in section B2 was slower than in the other sections. Trout could swim against the current with less energy expenditure and thereby increase the effective availability of food.

To summarize, feeding activity was greatest at night and during the morning when drift food was most abundant. Small trout spent more time feeding than large trout and consumed more food than large trout. Absolute rate of movement associated with feeding was similar for all trout. High food availability resulted in more frequent changes in feeding stations for all trout. This appeared to be the result of more frequent agonism. There were considerable

Table 17. - Mean time (min) spent per feeding station by each social rank during morning, midday, and evening in replicates with 4 trout. This includes time spent feeding from cover.

	Morning				Midday				Evening				Replicate	
	Rank				Rank				Rank					
Replicate	1	2	3	4	1	2	3	4	1	2	3	4	Mean	SD
IA2	15.5	13.33	18.0	8.17		12.08	13.5	14.5		12.0	9.64	9.93	12.66	2.96
IIA1	24.0	a	16.45	8.36		a	33.75	16.0	22.0	a	9.0	17.33	18.36	8.28
IIA2	10.52	9.63	9.72	7.13	15.5	18.5	9.15	16.56	12.67	19.0	11.55	10.19	12.51	3.93
IIB1	10.56	5.5	7.13	3.8		20.0	9.8	11.5			4.71	10.13	9.24	4.9
IIB2	6.75	7.91	8.75	9.75							9.4	15.0	9.59	2.86
IIIA1	8.19	18.38	13.98	a	28.63	21.4	23.33	a	11.0	26.5	11.75	a	18.13	7.29

	Rank	
	Mean	SD
1	15.02	7.01
2	15.35	6.22
3	12.92	6.96
4	11.31	4.01

	Time of day	
	Mean	SD
Morning	10.98	4.93
Midday	17.61	6.92
Evening	13.05	5.39

[a] Abnormal behavior.

Table 18. - Mean distance (m) moved per feeding station by each social rank during morning, midday, and evening in replicates with 4 trout. This includes movement associated with feeding from cover.

	Morning				Midday				Evening				Replicate	
	Rank				Rank				Rank					
Replicate	1	2	3	4	1	2	3	4	1	2	3	4	Mean	SD
IA2	7.75	1.42	0.88	3.25		1.58	3.88	6.85		0.75	3.5	3.43	3.33	2.39
IIA1	2.25	a	4.25	3.8		a	5.25	0	1.0	a	9.75	5.33	3.95	3.03
IIA2	7.48	4.75	5.36	4.7	4.00	1.0	1.18	2.0	1.42	11.25	1.85	1.5	3.97	3.1
IIB1	3.56	4.31	6.52	4.11		4.0	1.05	3.13			3.43	1.25	3.48	1.64
IIB2	8.38	9.84	5.75	6.45							6.0	0.25	6.11	3.28
IIIA1	6.44	7.09	11.23	a	8.25	9.25	13.33	a	8.0	5.63	3.6	a	8.09	2.93

Rank	Mean	SD
1	5.32	2.92
2	5.07	3.63
3	5.12	3.54
4	3.29	2.13

Time of day	Mean	SD
Morning	5.43	2.59
Midday	4.32	3.71
Evening	4.00	3.26

[a] Abnormal behavior.

differences in feeding behavior between individuals and between replicates. Differences between replicates were not strongly related to relative food abundance or physical characteristics unique to particular sections. Social factors seemed to be responsible for differences between replicates.

Characteristics of Feeding Stations

Mean current velocity at feeding stations, measured 5 cm above the stream bed was 20.3 cm/s (Table 19). Mean depth at feeding stations was 24.4 cm (Table 20). Velocity and depth readings for individual trout at each feeding station were weighted by the percent of total feeding time spent at that station. Mean current velocity at feeding stations was approximately equal to mean sectional current velocity. Mean depth at feeding stations was about 2.5 cm deeper than mean sectional depth. Feeding station current velocity averaged lowest in section B2 which had the lowest mean current velocity. The greatest mean depth at feeding stations was in section A2 which had the greatest mean depth.

Social ranks did not differ significantly in mean current velocity ($p < 0.5$; Table 19) or depth ($p < 0.5$; Table 20) at feeding stations. However, rank-1 trout on the average used feeding stations with slightly lower current velocity and less depth than ranks 2, 3, and 4. There was not a significant difference in either current velocity or depth at stations used at different times of day ($p < 0.5$).

In calculating mean current velocity at feeding stations, 6.10 cm/s was subtracted from the velocities shown in Appendix Figures B3-B6 for stations within 0.25 m of feeding references. This value

Table 19. - Mean current velocity (cm/s) at feeding stations used by each social rank during morning, midday, and evening in replicates with 4 trout. This includes cover feeding stations. Current velocity is weighted by the percent of total feeding time spent at each station.

	Morning				Midday				Evening				Replicate	
	Rank				Rand				Rank					
Replicate	1	2	3	4	1	2	3	4	1	2	3	4	Mean	SD
IA2	19.5	24.6	23.4	21.0		25.8	20.4	22.5		21.0	21.0	17.7	21.7	2.4
IIA1	22.5	[a]	23.4	22.8		[a]	23.4	25.5	22.5	[a]	23.4	21.3	23.1	1.2
IIA2	18.0	18.3	18.3	18.6	18.0	18.0	19.2	21.3	17.4	22.5	18.6	16.5	18.7	1.6
IIB1	15.3	20.7	20.1	20.4		23.4	26.7	15.9			22.8	18.3	20.4	3.6
IIB2	15.6	16.2	15.6	16.8							19.5	18.0	16.9	1.5
IIIA1	21.3	14.4	21.9	[a]	17.1	14.4	18.9	[a]	25.5	24.6	23.1	[a]	20.1	4.2

Rank	Mean	SD
1	19.2	3.3
2	20.4	3.9
3	21.3	2.7
4	19.8	2.7

Time of day	Mean	SD
Morning	19.5	3.0
Midday	20.7	3.9
Evening	20.7	2.7

[a] Abnormal behavior.

Table 20. - Mean water depth (cm) at feeding stations used by each social rank during morning, midday, and evening in replicates with 4 trout. This includes cover feeding stations. Both weighted by percent of total feeding time spent at each station.

	Morning				Midday				Evening				Replicate	
	Rank				Rank				Rank					
Replicate	1	2	3	4	1	2	3	4	1	2	3	4	Mean	SD
IA2	18.7	26.2	25.0	27.2		24.2	22.5	24.5		25.5	26.7	25.2	24.6	2.5
IIA1	21.2	a	22.5	23.2		a	22.5	25.0	21.2	a	23.0	25.5	23.0	1.6
IIA2	28.7	21.5	26.0	26.7	30.0	25.0	23.7	29.5	25.7	26.2	26.5	24.7	26.2	2.4
IIB1	12.7	24.7	22.7	23.2		25.0	24.5	21.5			24.2	22.0	22.3	3.8
IIB2	22.5	21.2	22.2	26.7							26.2	25.0	24.0	2.3
IIIA1	23.5	21.2	24.7	a	13.7	19.0	27.5	a	26.2	23.7	25.7	a	22.8	4.3

Rank	Mean	SD
1	22.2	5.5
2	23.7	2.2
3	24.5	1.7
4	25.0	2.0

Time of day	Mean	SD
Morning	22.7	4.0
Midday	23.0	4.7
Evening	24.5	2.2

[a] Abnormal behavior.

approximates the reduction in current velocity experienced by trout feeding within 0.25 m of a reference (Figure 8).

Most trout avoided the highest current velocities in their section. The observed percent of feeding time spent by each trout at stations with current velocities higher than 19.5 cm/s or 24.0 cm/s was compared with the expected percent of feeding time spent at those stations with a chi-square analysis (Table 21). Expected values were based on the hypothesis that use of a particular range of current velocities would be proportional to the area of the channel section in that velocity range if trout had no velocity preference. The values 19.5 cm/s and 24.0 cm/s correspond to contours on the sectional current velocity maps (Appendix Figures B3-B6).

Use of feeding stations with current velocities exceeding 19.5 cm/s was significantly less than expected in replicates IIA2, IIB1, IIB2, and IIIA1 ($p < 0.001$ for all). Use of stations with current velocities greater than 24.0 cm/s was significantly less than expected in replicate IIA1 ($p < 0.001$). Mean current velocity, was higher in section A1 than in sections A2 and B2.

Rank 1 avoided high current velocities more consistently than all subordinate ranks. Use of feeding stations with velocities greater than 19.5 cm/s was significantly less than expected for rank 1 (Table 21). While rank 1 did not differ significantly from subordinates on an absolute scale (Table 19) it may have had a slight energetic advantage relative to the small range in velocities available for feeding stations.

Table 21. - Observed and expected percent of feeding time spent at current velocities greater than 19.5 and 24.0 cm/s in replicates with 4 trout. Expected values equal percent of section area in which velocities exceed 19.5 and 24.0 cm/s (Appendix Figures B3-B6). This includes cover feeding stations.

Replicate	Velocity[d] greater than (cm/s)	Percent of feeding time: Observed Rank 1	Observed Rank 2	Observed Rank 3	Observed Rank 4	Expected All ranks	Chi-square value
IA2	19.5	0	74	62	56	46	b
	24.0	0	38	28	21	8	b
IIA1	19.5	100	a	100	86	76	b
	24.0	0	a	0	31	35	68.96[c]
IIA2	19.5	14	36	41	23	46	34.47[c]
	24.0	0	0	3	0	8	25.13[c]
IIB1	19.5	5	69	67	48	67	62.70[c]
	24.0	3	1	47	7	36	82.28[c]
IIB2	19.5	0	0	0	4	37	176.35[c]
	24.0	0	0	0	0	2	b
IIIA1	19.5	45	23	65	a	76	49.19[c]
	24.0	18	11	20	a	35	31.15[c]

[a] Abnormal behavior.

[b] Not significant.

[c] Significantly less than expected ($p < 0.001$).

[d] Measured 5 cm above the stream bed.

The attractiveness of overhead cover or unmeasured features of the stream bed under cover encouraged some trout to feed at stations with relatively high current velocity. The preferred cover (large) in replicate IA2 was frequently used as a feeding station. Current velocity under this cover was 27.43 cm/s. Throughout the study trout rarely fed at stations in the open with such a high velocity. Mean current velocity at feeding stations was higher for trout in replicate IA2 than in replicate IIA2. Use of the preferred cover as a feeding station in replicate IA2 was partially responsible for the difference between replicates. Replicate IA2 also lacked feeding references which were present in replicate IIA2. Feeding references provided additional low velocity feeding stations in replicate IIA2.

Use of feeding references was highly variable between replicates (Table 22). Over 37% of total cumulative feeding time was spent at feeding references in replicate IIB1, 10% in replicates IIA2 and IIB2, and only 1% and 4%, respectively, in replicates IIA1 and IIIA1. Relatively high current velocity in section B1 may have made the references particularly attractive there but this explanation is not consistent with the observation that use of references was very light in section A1 which had a similarly high mean current velocity.

Percent of feeding time spent at feeding references increased from rank-1 to rank-3 trout. Use of references by rank 4 was lower than use by ranks 2 and 3 (Table 22). Feeding references provided current velocities in mid-channel comparable to velocities along the

Table 22. - Time (min) spent at feeding references by each social rank in replicates with 4 trout. Replicate IA2 did not have feeding references. Percent of total feeding time at references in parentheses.

Replicate	Rank 1		Rank 2		Rank 3		Rank 4		Replicate totals	
IIA1	0	(0)	a	a	0	(0)	4.0	(2.5)	4.0	(1.18)
IIA2	0	(0)	29.0	(13.18)	71.5	(21.68)	0	(0)	100.5	(10.44)
IIB1	5.0	(3.64)	21.5	(30.94)	80.5	(45.54)	140.5	(50.0)	247.5	(37.37)
IIB2	0	(0)	1.0	(1.61)	29.0	(29.82)	0	(0)	30.0	(10.44)
IIIA1	9.5	(9.41)	21.5	(5.12)	16.5	(5.63)	0	(0)	47.5)	(3.89)

[a] Abnormal behavior.

walls but this rarely induced large trout to feed away from the walls. That large trout did occasionally use feeding references, however, indicates that the size of the area of reduced current velocity created by a reference was sufficient to accomodate a large trout.

Cover location may have influenced choice of feeding references. Use of mid-channel references was by far the greatest in replicate IIB1 which was the only replicate among the 5 that held 4 trout that had mid-channel cover (Table 22). Without replication this is only speculative.

Large trout showed a strong attraction to the channel walls. Ranks 1 and 2 fed significantly ($p < 0.01$) closer to the channel walls than ranks 3 and 4 (Figure 13; Appendix Table A25). Distance from the nearest wall to each feeding station was weighted by the percent of total feeding time spent there.

Feeding activity was greatest on the shaded side of the channels (Table 23). ANOVA was performed on the difference between the percent of feeding time spent on the west and east sides of each section. Zero difference indicates no preference. A positive value indicated preference for the west side while a negative value indicated preference for the east side of the channel. The evening mean was positive and significantly different than the midday ($p < 0.005$) and morning ($p < 0.005$) means which were negative. Social ranks did not differ significantly ($p < 0.5$) but differences between replicates were nearly significant ($p < 0.1$). Preference for the east side of the channel during midday as well as during the morning reflects the fact that most feeding during midday occurred early in the period while the area along the east wall was still shaded.

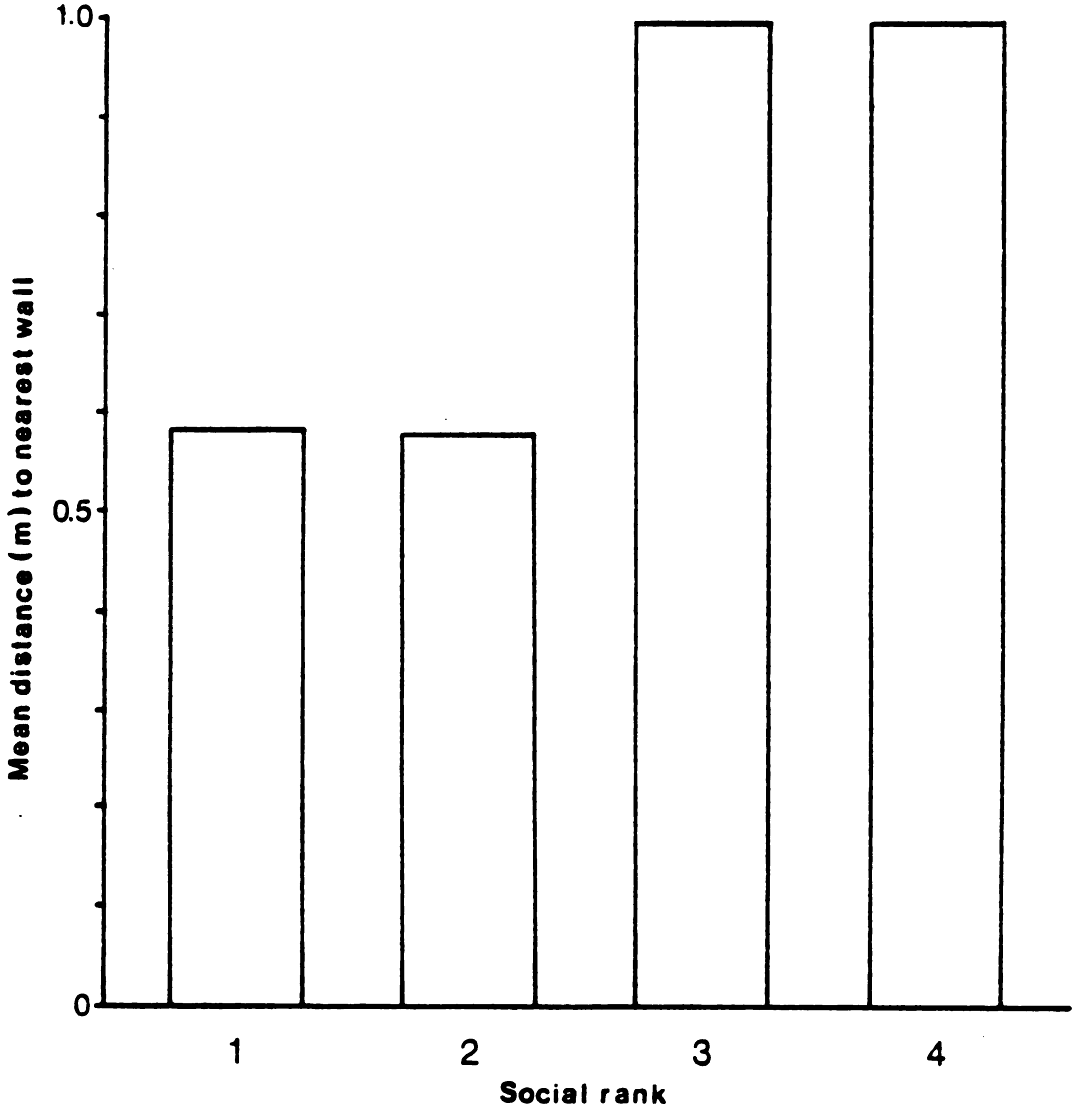

Figure 13. - Mean distance to the nearest wall from feeding stations used by each social rank in replicates with 4 trout. Distance weighted by the percent of total feeding time spent at each station. Cover stations are not included.

Table 23. - Location of feeding stations used by each social rank and location of shade in replicates with 4 trout. Percent of feeding time spent on the west and east sides of the channel and in the middle of the channel shown. Parentheses indicate the shaded side. Time spent feeding from cover is not included.

		Morning			Midday			Evening		
		Side of channel			Side of channel			Side of channel		
Replicate	Rank	West	Middle[a]	(East)	West	Middle[a]	(East)[b]	(West)	Middle[a]	East
IA2	1	0	0	100						
	2	100	0	0	82	0	18	100	0	0
	3	0	0	100	0	0	0	80	5	15
	4	92	0	8	100	0	0	96	0	4
IIA1	1									
	2									
	3							85	0	15
	4	24	67	9	0	0	100	33	67	0
IIA2	1	72	0	28				97	0	3
	2	9	0	91	0	0	100	100	0	0
	3	7	3	90	0	5	95	3	9	88
	4	79	3	18				100	0	0
IIB1	1	100	0	0						
	2	94	6	0						
	3	0	14	86	0	78	22	0	11	89
	4	23	41	36	6	37	57	56	0	44
IIB2	1	0	0	100						
	2	16	0	84						
	3	96	4	0				94	0	6
	4	0	7	93				0	0	100

Table 23 (cont'd.)

IIIA1	1	0	0	100	0	0	100	100	0	0
	2	1	0	99	19	0	81	100	0	0
	3	44	54	2	0	100	0	72	0	28
Mean		38	10	52	21	22	57	70	6	24

[a]Focal point of feeding station on longitude 2.5 (see Appendix Figures B3-B6).

[b]Most midday feeding occurred when the area along the east wall was still shaded.

Note that values reported for percent of feeding time spent on each side of a channel do not exactly correspond to the percent of feeding time spent in the shade. That is, at certain times of the day the "shaded" side of the channel was only partially shaded. The tendency for some trout to frequently dart into sunlit water from shaded feeding stations and the general high mobility associated with feeding would have made attempts to exactly quantify time spent in the shade very difficult. This does not invalidate this analysis however, as trout rarely fed in direct sunlight when shade was available. "Feeding on the shaded side of the channel" and "feeding in the shade" are synonymous for practical purposes. During later afternoon and early morning when more than half of the channel was shaded it was possible for trout to feed on the "unshaded" side of the channel when in fact they were feeding in the shade. This was most often true of small trout which often fed just inside the shadow edge. Therefore, small trout actually spent more time feeding in the shade than indicated in Table 23. Large trout fed close to the walls even when the entire channel was shaded. During the evening, trout seemed to avoid the sunlit east wall even when the water at the base of the wall was shaded.

Competition for feeding stations was not severe. Trout occasionally moved to stations vacated by dominants but generally each trout spent most of its feeding time in a characteristic position, or set of positions, that was different from the positions that other trout used the most. These characteristic positions were used even when dominants were not feeding. The only notable exception to this was in replicate IIB1 where ranks 3 and 4 competed strongly for two feeding references.

Most feeding activity occurred in the lower 2/3 of the sections. Only about 11% of total feeding time was spent in the upper 1/3 of the sections that held 4 trout. The reason for this was probably that current velocity was highest in the upper 1/3 of the sections. Trout also may have avoided feeding where overhead cover was not in sight. Two trout were very unusual in that they spent almost all of their time in the upper 1/3 of section A1. Rank 4 in replicate IIIA1 spent 97% of its feeding time in this area near coordinates 1.25, 12 (Appendix Figure B3). Rank 2 in replicate IIA1 apparently did not feed but spent nearly 100% of its total observation time in the same area. This area was attractive because a few pieces of large gravel located immediately upstream produced a pocket of relatively low current velocity (15.24 cm/s) and surface turbulence which, in effect, provided some overhead cover. The effects of the gravel were not noticed until current velocity was measured at the end of the last experiment.

To summarize this section, current velocity and light level strongly influenced choice of feeding positions. Current velocities over section means were avoided. All trout favored positions in the shade. The location of overhead cover had little, if any, influence on choice of feeding positions (see "Cover Use and Feeding" section). Large trout showed a strong attraction to the channel walls. Competition for feeding positions was generally weak so that social rank had little influence on choice of feeding positions.

Size of Trout and Size of Food

It was surprising that large trout which experienced severe weight losses, and therefore must have been hungry, ate less than small trout. Even during periods when as many as 10 to 15 spent *Tricorythodes* mayflies drifted past a feeding station per minute rank-1 trout in replicates IIA1 and IIB1 often ate fewer than one per minute while small trout ate nearly every mayfly that drifted near their station. Rank-2 trout in these replicates fed more actively, though usually not with such intensity as the small trout.

Large brown trout in streams rely heavily on crayfish, fish, and other large food items (Brynildson et al, 1973; C.E. Bassett, pers. obs.). To test the hypothesis that large trout in the experimental channels were not feeding as much as small trout because large food items were scarce I artifically introduced grasshoppers averaging 3 cm in length to replicate IIIA1 during 7 observation sessions. Grasshoppers were directed to the desired position in the channels from the observation blind by blowing them through a plastic soda straw.

Thirty-one grasshoppers were introduced to the channel (Appendix Table A26). Thirteen were consumed by large trout, 16 by small trout. Both large and small trout feeding in the open never refused a grasshopper, sometimes moving 2-3 m from their feeding stations to intercept one. Seven grasshoppers were consumed by large trout that had not indicated feeding activity during the preceding several minutes and were under cover. On two other occasions large trout under cover moved toward a grasshopper but did not eat it.

During a morning feeding session rank 1 twice moved from cover to consume a grasshopper and then moved to a shaded feeding position near the east wall for about 1 min before returning to cover. Grasshoppers introduced during midday and evening did not induce rank 1 to move to a feeding station in the open, though small trout did this occasionally.

Large trout fed on grasshoppers while ignoring small, naturally-occurring food items. Ninety-seven percent of the stomach contents by volume of rank 1 checked over 12 h after the last feeding test consisted of grasshopper remains (Appendix Table A21). Nineteen percent of the stomach contents of rank 2 consisted of grasshopper remains. That stomachs were checked in the early morning immediately following the heaviest feeding period (2000 - 0800 h) indicates that large trout ignored most small food items that were naturally available. These results suggest that large trout would have eaten more food if large food items had been available.

Miscellaneous

Three types of activity were included in the miscellaneous category: (1) pressing sideways against channel walls or screens, (2) occupation of a stationary position in the open, and (3) swimming about the channel that was not associated with feeding or agonistic activity.

Current action along the channel walls, particularly near screens, caused the gravel to slump in some spots, giving trout access to the walls. This situation was quickly corrected when it occurred, so that miscellaneous time was minimal.

Only two trout pressed sideways against screens. Rank 2 in replicate IIIA1 did this for 15 sec on the morning of the first observation day. No stimulus that might have caused this fright response was apparent. Covers had been destroyed by vandals 3 days earlier, causing all of the trout to press against the screens or each other. Covers were replaced the following day, and within 24 h all trout once again used cover. Rank 2 was the only trout to re-exhibit the fright response after observation sessions began, and only on this single occasion.

Rank 2 in replicate IIIB2 had been injured by vandals. It spent 72% of its observation time pressed against the lower screen, the walls, or small rocks along the walls. This behavior was largely associated with avoidance of rank 1, especially during and following violent attacks. Rank 2 successfully used cover only when rank 1 also used cover. Attempts by rank 2 to occupy either cover when rank 1 was feeding inevitably resulted in an agonistic bout with forced return to a wall or screen.

As mentioned earlier, 2 trout rarely or never used cover and spent a large portion of their observation time in a small area. Rank 2 in replicate IIA1 spent over 99% of its observation time in a single position, and never indicated feeding activity. Physical appearance was normal. All of this time was assigned to the miscellaneous category. Rank 4 in replicate IIIA1 presented a special problem in that it spent over 92% of its observation time in an area that served as a feeding station and as cover, due to the presense of surface turbulence. Motivation to use cover could not be reliably separated from motivation to feed necessitating use of the miscellaneous category. Times when food consumption was actually observed were recorded as feeding time, but since these data were not directly comparable to feeding data for other trout they were omitted from statistical analyses.

All miscellaneous movement was in the form of continuous swimming about the channel. This movement may have been associated with "surveillance" of the food supply as it occurred when other trout were feeding . But as motivation to feed was not clearly the cause of this movement it was assigned to the miscellaneous category.

Social Rank Summary and Energy Use

Time and movement in each activity category is summarized by social rank in Table 24. Rank 1 and rank 4 were on opposite ends of the behavioral spectrum. Rank-1 trout used cover more and fed less often than subordinates. To determine if dominance was an advantage, energy output was estimated for each social rank from swimming speeds and time spent in each activity. Energy gained in food consumption could not be validly compared among ranks as the absence of large food items put large trout at a disadvantage. Large trout could not capture enough small food items to compensate for the energy required to capture them. Even large trout that fed heavily on *Tricorythodes* mayflies lost as much weight as large trout that rarely fed. Dominance could be an advantage in the experimental environment only if it permitted trout to conserve energy by swimming less than subordinates.

Table 24. - Summary of the mean percent of observation session time and movement and mean rate of movement in each activity by social rank in replicates with 4 trout. Means with different superscripts are significantly different ($p < 0.05$).

	Activity	Rank 1	Rank 2	Rank 3	Rank 4	Mean
Mean % time	Agonistic	0.26^{a}	0.65^{a}	0.75^{a}	0.53^{a}	0.55
	Cover use[c]	81.63^{a}	69.12^{ab}	54.26^{b}	54.93^{b}	64.98
	Feeding[d]	15.09^{a}	29.97^{ab}	43.47^{b}	44.04^{b}	33.14
	Miscellaneous[e]	2.98	1.41	1.81	0.03	1.56
	Total	99.96	101.15	100.29	99.59	
Mean % movement	Agonistic	37.71^{a}	23.82^{a}	24.01^{a}	18.66^{a}	25.8
	Cover use[c]	21.6^{a}	22.0^{a}	14.82^{a}	12.98^{a}	17.62
	Feeding[d]	40.86^{a}	52.63^{ab}	62.66^{b}	70.03^{b}	56.54
	Miscellaneous[e]	1.5	0	0	0.3	0.45
	Total	101.67	98.45	101.49	101.97	
Mean rate of movement (cm/s)	Agonistic	31.35^{a}	29.19^{a}	26.55^{a}	30.09^{a}	29.29
	Cover use[c]	0.15^{a}	0.55^{a}	0.57^{a}	1.52^{a}	0.72
	Feeding[d]	0.77^{a}	0.8^{a}	0.8^{a}	0.95^{a}	0.84
	Miscellaneous	6.86	0	0	16.57	5.86

[c]Does not include feeding under cover.

[d]Includes feeding under cover.

[e]Miscellaneous items were not tested statistically.

Oxygen consumption provides an indirect measure of energy expenditure in calories. The precise relation between calories and oxygen consumed depends on the type of fuel metabolized. Most trout lost weight so that stored corbohydrate (liver glycogen) and fat were probably important sources of energy (Hill, 1976). Overall, diet was similar for each social rank. It has been assumed that the fuel metabolized was the same for all trout and that relative oxygen consumption provides a good approximation of relative energy expenditure among social ranks.

The relationship between swimming speed and oxygen consumption for brown trout in this study (Table 25) was estimated from rainbow trout data reported by Rao (1968). Beamish (1964) examined the relationship between standard metabolism and weight for adult brown trout but did not provide data on the influence of swimming speed on oxygen consumption. The similarity between brown and rainbow trout in phylogeny and body shape suggests a similar metabolism--swimming speed relationship for the two species. Rao's rainbow trout differed from the brown trout in this study in that they were smaller (54-135 g) and of domestic origin.

Table 25. - Relationship between metabolic rate ($Y = mgO_2/h$) and swimming speed ($X = cm/s$) for each social rank plotted from equations relating metabolic rate and body weight (g) at several swimming speeds for rainbow trout (Rao, 1968). Standard metabolism occurs when swimming speed is zero.

Rank	Mean weight (g)	Regression equation	Standard metabolism (mgO_2/h)
1	547.5	$\log Y = 1.6353+0.0098X$	43.18
2	473.6	$\log Y = 1.5869+0.0097X$	38.63
3	227.3	$\log Y = 1.3415+0.0089X$	21.96
4	145.6	$\log Y = 1.1926+0.0085X$	15.58

Extrapolating from immature to mature fish might lead to errors in the calculated difference in energy expenditure between social ranks. This is based on the observation by Brett (1965) that the slope of the regression line relating standard oxygen consumption to body weight is shallower for sockeye salmon in juvenile size classes than for adults. At routine and active levels of metabolism the relationship was the same for juveniles and adults. The regression equation relating oxygen consumption to swimming speed would assume a steeper slope than it should to properly reflect the relationship for adult fish only. If this is true for rainbow trout, the differences between social ranks in relative energy expenditure ($mgO_2/kg/h$) above standard metabolism (Table 26) are slightly high.

Extrapolating from domestic to wild fish probably does not introduce serious error to estimates of energy expenditure. The relationship between swimming speed and oxygen consumption is nearly identical for wild and hatchery rainbow trout (79-398 g) at water temperatures within the range prevailing in this study (Dickson and Kramer, 1971). Oxygen consumption estimates are based on a water temperature of 15 C which is close to the average temperature of the water in 1976 (Appendix Table A2).

Energy expenditure was estimated by the product (mean percent of time spent in an activity category) x (mean rate of oxygen consumption associated with that activity). The latter was derived from the swimming speed--oxygen consumption relationship (Table 25). Most feeding involved constant swimming to maintain a stationary position in the current. To account for this source of energy use, mean current velocity in the channels (20.73 cm/s) was added to swimming speeds in the feeding category. No corrections were necessary in the other categories as upstream swimming was as common as downstream swimming.

Rank-1 trout expended less energy in excess of maintenance requirements than any other social rank (Table 26) when oxygen consumption is expressed in terms of body weight ($mgO_2/kg/h$). Rank-4 trout expended the most energy. Even without compensating for differences in body weight, rank 1 used less energy above standard metabolism than ranks 2 and 3.

The important question is whether these differences in energy use reflect differences between ranks in the availability of preferred food or rather are a direct result of social status. Most of the difference between ranks occurred in the feeding category. Total energy use ($mgO_2/kg/h$) above standard metabolism was roughly proportional to percent of time spent feeding. Percent of time spent

Table 26. - Estimated energy use (mgO_2/h and $mgO_2/kg/h$) above standard metabolism (Table 25) for each social rank values were derived from time spent in each activity, mean swimming speed associated with each activity (Table 24), and equations relating metabolism to swimming speed (Table 25).

		Metabolism			
Rank	Activity	mgO_2/h	Above standard mgO_2/h	$mgO_2/kg/h$	Above standard $mgO_2/kg/h$
1	Agonistic	0.23	0.12	0.42 (0.48)	0.22 (2.67)
	Cover use	35.37	0.12	64.6 (74.18)	0.22 (2.67)
	Feeding	10.59	4.07	19.34 (22.21)	7.43 (90.06)
	Miscellaneous	1.5	0.21	2.73 (3.13)	0.38 (4.61)
	Total	47.69	4.52	87.02	8.25
2	Agonistic	0.49	0.23	1.03 (1.06)	0.49 (2.96)
	Cover use	27.03	0.32	57.07 (58.46)	0.68 (4.11)
	Feeding	18.72	7.29	39.53 (40.49)	15.39 (92.93)
	Miscellaneous	0	0	0 (0)	0 (0)
	Total	46.24	7.84	97.63	16.56
3	Agonistic	0.28	0.12	1.23 (1.03)	0.53 (2.17)
	Cover use	12.05	0.14	53.01 (44.35)	0.62 (2.54)
	Feeding	14.84	5.29	65.29 (54.62)	23.27 (95.29)
	Miscellaneous	0	0	0 (0)	0 (0)
	Total	27.17	5.55	119.53	24.42
4	Agonistic	0.15	0.07	1.03 (0.77)	0.48 (1.78)
	Cover use	8.83	0.23	60.65 (45.33)	1.58 (5.85)
	Feeding	10.49	3.63	72.05 (53.85)	24.93 (92.26)
	Miscellaneous	0.01	0.005	0.07 (0.05)	0.03 (0.11)
	Total	19.48	3.935	133.8	27.02

feeding by large trout, in particular, may reflect the scarcity of large food items. The agonistic and cover use categories are better indicators of the effect of social status. Rank 1 used conspicuously less energy in agonism than all subordinates, even though it was involved in at least as many bouts as ranks 2 and 4 (Table 7). Rank 1 also used conspicuously less energy in cover use than all subordinates. This could partially reflect the small amount of time rank 1 spent feeding as movements from feeding stations to cover were included in the cover use category. But, energy expended in cover use by rank 1, and other trout, was not proportional to the percent of time spent feeding as would have occurred if movements from feeding stations to cover were the only source of energy loss associated with cover use. The fact that rank 1 was the only rank not subject to displacement from cover probably permitted less energy use. Much of the movement between covers may have been the result of unseen agonism. The results of this analysis suggest that dominance permitted rank-1 trout to use less energy than subordinates.

Energy use estimates demonstrate clearly that the primary source of daytime energy loss for stream-dwelling trout is feeding. Overall energy use above standard metabolism in feeding was 92.6% of total energy use (Table 26). By limiting the amount of time spent feeding, large trout conserved a substantial amount of energy. Agonism was by far the most energy-consuming activity per unit of time spent, but it occurred too infrequently to be an important source of energy loss. Cover use was the least energy-consuming activity. All ranks devoted about the same portion of total energy use ($mgO_2/kg/h$) above standard metabolism to each activity.

Time of Day Summary

Time of day influenced behavior (Table 27) via changes in light intensity and drift food abundance. Cover was used most during midday when light level was highest. Most feeding occurred during the morning when drift food was most abundant. Agonism was also most frequent and intense during the morning as intense feeding then led to more total movement and greater aggressiveness. The portion of total movement devoted to feeding was greatest in the evening. Movement associated with cover use was minimal at this time. Trout often did not leave cover to feed until late evening and once in the open, they usually stayed there. At low light levels there is apparently little need for cover.

Replicate Summary

There were significant differences between replicates in percent of time spent using cover and feeding, and in the rate of movement associated with feeding (Table 28). Trout in replicate IIB2 used cover more, fed less, and moved more when feeding than trout in all other replicates. Current velocity was lower in section B2 than in all other sections and this might have encouraged greater movement when feeding. If a threshold density of food drifting past a feeding station were required to release feeding behavior as has been observed for brown trout (Ringler, 1975), then slow current velocity might have resulted in that threshold being reached less often, with less feeding as a consequence. However, this probably is not the explanation here as feeding activity seemed to be independent of drift food density in replicate IIB2. Cover use has been observed to decrease at reduced

Table 27. - Summary of the mean percent of observation session time and movement, and mean rate of movement in each activity by time of day in replicates with 4 trout. Means with different superscripts are significantly different ($p < 0.05$).

	Activity	Morning	Midday	Evening
Mean	Agonistic	1.06[a]	0.36[a]	0.2 [a]
%	Cover use[c]	53.92[b]	75.58[a]	66.39[ab]
time	Feeding[d]	45.05[a]	22.06[b]	32.98[ab]
	Miscellaneous[e]	1.12	1.67	1.82
	Total	101.15	99.67	101.39
Mean	Agonistic	25.85[a]	31.98[a]	20.64[a]
%	Cover use[c]	23.35[a]	22.87[a]	5.1[b]
Movement	Feeding[d]	51.39[a]	44.96[a]	73.38[a]
	Miscellaneous[e]	0.8	0.41	0
	Total	101.4	100.22	99.12
Mean	Agonistic	31.61[a]	26.52[a]	24.53[a]
rate of	Cover use[c]	0.6 [a]	0.79[a]	0.17[a]
movement	Feeding[d]	1.25[a]	0.41[b]	0.64[ab]
(cm/s)	Miscellaneous[e]	2.05	0.27	0

[c]Does not include feeding from cover.

[d]Includes feeding from cover.

[e]Miscellaneous items were not tested statistically.

Table 28. - Summary of the mean percent of observation session time and movement, and mean rate of movement in each activity by replicates with 4 trout. Means with different superscript are significantly different ($p < 0.05$).

	Activity	Replicate IA2	IIA1	IIA2	IIB1	IIB2	IIIA1
Mean	Agonistic	0.66^{a}	0.24^{a}	0.43^{a}	0.52^{a}	0.29^{a}	1.21^{a}
%	Cover use[d]	59.06^{bc}	74.47^{ab}	47.97^{c}	63.26^{abc}	81.89^{a}	67.78^{abc}
time	Feeding[e]	38.13^{ab}	25.2	49.8^{a}	35.18^{abc}	15.85^{c}	30.02^{abc}
	Miscellaneous[f]	1.67	0.09	0.93	1.19	4.3	0.4
	Total	99.52	100.0	99.13	100.15	102.33	99.41
Mean	Agonistic	27.85^{a}	25.73^{a}	31.49^{a}	14.62^{a}	20.87^{a}	31.62^{a}
%	Cover use[d]	23.82^{a}	15.02^{a}	8.47^{a}	21.23^{a}	16.55^{a}	21.05^{a}
movement	Feeding[e]	51.17^{a}	60.16^{a}	56.26^{a}	65.51^{a}	64.82^{a}	44.27^{a}
	Miscellaneous[f]	0	1.48	0	0	0.71	0.68
	Total	102.94	102.39	96.32	101.36	102.95	97.62
Mean	Agonistic	18.25^{a}	41.59^{a}	28.27^{a}	32.25^{a}	26.18^{a}	28.42^{a}
rate of	Cover use[d]	1.25^{a}	0.15^{a}	0.78^{a}	0.29^{a}	0.97^{a}	0.32^{a}
movement	Feeding[e]	0.5^{b}	0.62^{b}	0.6^{b}	0.76^{b}	2.18^{a}	0.85^{b}
(cm/s)	Miscellaneous[f]	0	1.9	0	0	1.66	0.38

[d] Does not include feeding from cover.

[e] Includes feeding from cover.

[f] Miscellaneous items were not tested statistically.

current velocities (Hartman, 1963). This has been explained as a reaction to reduced stress at lower current velocities. But this also contrasts with behavior in replicate IIB2 where cover use was the greatest observed despite the lowest current velocity among the 4 sections. Social factors seem to be responsible for differences between replicates.

DISCUSSION--1975 AND 1976

Introduction

The results are of value only to the extent that they reflect brown trout behavior in the wild. Simplification of the environment was essential in this study to determine the causation of behavior, but attempts were made to minimize unnatural sources of stress and to permit ample time for acclimation to the test environment. Human disturbances were kept to a minimum, though total extent of such disturbances were uncertain, as uninvited visitors could enter the study area. Occasional human disturbances had no doubt been experienced by all trout in their natural streams which are heavily fished. Most physiological effects of handling and anethesia with MS-222 disappear within a few hours (Wedemeyer, 1970; Houston, et al., 1971). Trout that showed highly unusual behavior were not included in statistical analyses (rank 2, replicate IIA1; rank 4, replicate IIIA1).

Trout densities in the study channels were higher than the average densities in northern Michigan streams, but were within the range of natural densities. Density per total area of water surface in the experimental stream was about 10.7 g/m^2 in 1975 and 23.3 g/m^2 in 1976. Trout density, (brook and brown), in the North Branch of the AuSable River from which the 1976 test trout were captured averages about 11.4 g/m^2 (1972-1976), and density of brown trout in the size classes used in this study averages 4.3 g/m^2 (William Buc, Fish

Habitat Biologist, Michigan DNR, pers. comm.). Density within the area of stream suitable as living space may be much higher than density expressed in terms of total water surface area. Allen (1969b) calculated that the average density of several species of stream salmonids over a wide size range was 1.7 g/m^2 surface area, but was 25.5 g/m^2 in living area ("territories"). Electro-fishing (AuSable and Pigeon Rivers, Michigan, C.E. Bassett, pers. obs.) and snorkling observations (DeVore, 1975) confirm that trout densities in the experimental channels were not higher than can occur naturally in the wild.

Weight losses during 1976 indicated that food availability was lower than in the native stream. Conflicting evidence in the literature makes it difficult to assess the effects of low food abundance on time spent feeding. Low food abundance may decrease time spent feeding if the threshold food density required to release feeding is reached less often (Ringler, 1975). Conversely, low food abundance may increase time spent feeding as hunger increases (Ware, 1972). This would also tend to increase agonism as trout are most aggressive when they feed. Results of the feeding experiment indicate that large trout would have eaten more had larger food items been available. However, other investigators have found that large brown trout fed infrequently during daylight in natural environments where availability of large food items was presumably very good (Butler and Hawthorne, 1968; Jenkins, 1969). I infer that the difference between large and small trout in percent of time spent feeding in this study mainly reflects inherent characteristics of these size classes and is not an artifact of the limited food supply.

Statistics

The F-test of significance in ANOVA assumes that test animals behave independently from each other (Sokal and Rohlf, 1969). Trout in groups do not behave independently--there was evidence for follow-the-leader behavior and avoidance behavior in this study. To the statistician, this is a problem as variance due to inherent characteristics of each trout and variance due to interactions between trout cannot be separated and quantified. Consequently, the alpha level of significance that corresponds to the assumption that trout behave independently cannot be determined. But the significance level obtained in ANOVA still reflects what actually occurred in the population sampled--this is the prime concern to the ethologist and biologist. Speculation as to how the significance level might have differed had trout been observed in isolation is relevant here only because trout population densities may be so low in some streams that social interaction is infrequent during the non-breeding season.

Indirect evidence for follow-the-leader behavior was strongest during feeding periods. Differences between social ranks in percent of time spent feeding, therefore, may actually be more significant than the alpha level indicates. Avoidance of dominant trout was associated with cover use but probably had little effect on the percent of time that each trout spent under cover. Avoidance of dominants under cover apparently determined which cover some trout used, but not the percent of time spent under cover. Trout were never excluded from both covers simultaneously in replicates included in statistical analyses.

In all activity categories, differences between rank-1 and rank-4 trout in percent of total movement and rate of movement were probably inflated by avoidance behavior. There was not clear evidence that the response of trout to each other within an activity category differed between times of day. Differences between times of day presumably would have been significant at the alpha levels obtained even if each trout had been observed in isolation.

Replicate was considered a random factor in ANOVA as there was no reason a priori to expect large differences in trout behavior between replicates. The physical environment was similar in each channel section. Usually the component of variance contributed by a random factor is estimated and expressed as a fraction of total variance. Mean differences between levels of a random factor are not normally contrasted as the difference cannot be attributed to a particular variable. The significance of mean differences between replicates was tested here for two reasons: (1) use of mean values in treatment combination cells precluded estimation of the random component of variance, and (2) consistent differences between group behavior (4 trout) in some replicates suggested that differences in the social environment caused those differences.

Activity Budget

This study agrees with earlier reports that adult brown trout spend most of their time under cover during daylight (Butler and Hawthorne, 1968; Brynildson et al., 1973; DeVore, 1975). This is especially true of trout larger than 35 cm (TL). Cover use, per se, involved almost no energy expenditure over maintenance demands.

Feeding was the second most time-consuming activity of trout in this study. It accounted for over 90% of the total estimated daytime energy expenditure. Over 90% of the energy loss involved with feeding resulted from maintaining a stationary position in the current (Table 26). Availability of low velocity feeding stations clearly could influence growth of stream salmonids.

Agonism composed less than 1% of the time budget of all trout, and only 2-4% of total energy expenditure. It was the most energy-demanding activity per unit of time spent, however, so a samll increase in agonism could produce a large increase in energy expenditure. Factors that disrupt social stability could lead to more agonism and poorer trout growth. One such factor might be frequent stocking.

Large trout expended only about 1/3 as much energy ($mgO_2/kg/h$) above maintenance demands as did small trout (Table 26). Large trout conserved energy by feeding only when drift food was very abundant or when large food items were provided artificially. In an environment where food items were too small to compensate for the energy required to capture and consume them and emigration to better areas was impossible, remaining motionless under protective cover was the best strategy for survival. The food supply was nearly sufficient for small trout. It was to their advantage to feed more often than large trout.

Social Structure

This study also agrees with earlier reports that social hierarchies are well-developed among adult stream salmonids (Newman, 1956; Jenkins, 1969; Butler, 1975). Each trout defended a space surrounding itself rather than a fixed geographic area. This "social force field" (McBride, 1964) was defended successfully only against smaller individuals so that a social hierarchy developed. Social rank decreased from the largest to the smallest trout. The social force field was largest during feeding periods and smallest during cover use.

Social hierarchies among fishes have been described as based on either "nip-dominance" or "nip-right" relationships (Braddock, 1945; Greenberg, 1947; Mryberg, 1972). In the nip-right hierarchy, dominants deliver attacks but are never attacked by lower ranked fish. In the nip-dominance society, dominants deliver more attacks than they receive from lower ranked individuals, but the outcome of a particular bout is not strictly predictable.

Brown trout in this study demonstrated a nip-right hierarchy. Subordinates displaced higher ranked trout but this occurred only 4 times and probably resulted from mistaken identity. A high level of social stability has also been reported for other populations of adult stream salmonids (Newman, 1956; Jenkins, 1969). Apparent dominance reversals, (i.e. fish "losing" bouts to previously subordinate fish) have been attributed to unsettled dominance early in hierarchy formation, partial territory, and mistaken identity (Greenberg, 1947). The 10-14-day acclimation period should have permitted stabilization of social interactions. Social hierarchies of brown trout have been observed to stabilize within 5 days (Jenkins, 1969). Partial territory involves defense of a <u>single</u> geographic area against all subordinates (Greenberg, 1947). A partial territory holder frequently resists dominants so that determination of social rank can be difficult. Dominants that are persistent eventually displace partial territory holders. Persistent defense of a single area did not occur in this study. Each social rank typically moved between a few favored positions which were readily yielded to dominants.

Mistaken identity of low-ranking trout by dominants seems to be the most likely cause of apparent dominance reversals in this study. Rank-1 trout exited from cover as rank-2 trout darted under the same cover on 3 occasions. However, rank 1 returned to cover and displaced rank 2 to the lower end of the cover almost immediately in each case. Once, rank 2 left cover as rank 3 entered. In this case rank 2 moved to the other cover and remained there. These were the only times observed where higher ranking fish were displaced by subordinates.

The explanation for mistaken identity seems to be that in each case the approach to cover was very rapid. Rapid approach was also characteristic of trout about to attack subordinates. A conditioning experiment demonstrated that fish respond to behavior type, e.g. dominant or submissive, in addition to other physical aspects of individual appearance (McDonald et al., 1968). Even the highest ranked trout in each replicate had probably experienced dominants in their native stream and would have been conditioned to submit to dominant behavior. Thus, a subordinate motivated to use cover could be mistaken for an attacking dominant if it acted like one. If this hypothesis is correct, then all 4 cases of reversed dominance may be considered "accidents". The social structure of brown trout then conforms to the strict definition of a "nip-right" hierarchy.

Social structure reflects the distribution of required resources in the environment. Where resources are clumped in a few areas, competition for them favors hierarchy formation. Brown trout competed for feeding positions at some feeding references but the nearly uniform distribution of drift food and current velocity minimized competition for feeding stations. Most agonism associated with feeding was more the result of a general increase in movement and aggressiveness associated with feeding rather than defense of a favored station. Conversely, competition for the upstream position under cover was very apparent and probably was the basis for hierarchy formation.

Trout tended to avoid some dominants under cover. Rank-4 trout, in particular, seemed to avoid dominants under small cover when that was possible (Tables 11, 12 and 13). In the wild, where emigration is possible, avoidance may influence the number and size of trout that inhabit an area of stream. This could be tested. On the other hand, subordinates were frequently "tolerated" by dominants under cover, especially under large cover. Several times, rank-1 trout permitted small trout to feed from the lower end of their cover without agonism. Overall, coexistence was a more prominent aspect of cover use behavior than avoidance. A small area of cover will accommodate many more trout than the same sized area of feeding habitat.

Reduction of aggression is commonly held to be the primary function of social hierarchies (Rowell, 1974). Brown trout in this study directed most aggressiveness towards fish ranked only one level lower. This has been observed in other fish populations as well (Greenberg, 1947; Newman, 1956; Jenkins, 1969; Mryberg, 1972) and represents a reduction in aggression over the condition immediately following formation of a new group where aggression is directed with equal intensity towards all other fish (Jenkins, 1969). Small trout learn to avoid agonistic bouts by remaining downstream and distant from larger trout. Subordinate brown trout often yielded positions to approaching dominants before the dominant approached close enough to initiate a chase.

The presence of dominants seems to inhibit the aggressiveness of low ranking hierarchy members towards their own subordinates. Agonistic bouts between small trout in replicates lacking large trout were more frequent and more intense than bouts between small trout in replicates with two large trout (Table 9). Jenkins (1969), cited two cases where removal of a dominant was followed by increased aggressiveness by the highest ranking trout that remained. Social hierarchies appear to reduce agonistic activity among brown trout by reducing the aggressiveness of trout toward dominants and subordinates.

This discussion so far has centered on the results of repulsive forces between trout. Attractive forces were also apparent in this study. This was shown in the tendency for stressed trout to aggregate in fright huddles and in other forms of synchronous behavior. Synchronous behavior provided evidence for social facilitation which is the tendency for the performance of a pattern of instinctive behavior by one animal to act as a releaser for the same behavior in another (Thorpe, 1963). The stimulus "dominant feeding" was not essential to elicit feeding in lower ranking trout but seemed to encourage it. Small trout in replicates where large trout usually fed during the morning (IA2, IIA2, IIB1) fed more during that period than small trout in replicates where dominants rarely fed at that time (Appendix Table A22).

Advantages of Dominance

Dominance confers the right to occupy the most upstream position under cover. An advantage of this position might be first opportunity to consume drift food--especially large food items. Butler (1975) reported that dominant trout feeding under the upstream end of cover fed primarily on large food items, while subordinates feeding farther downstream consumed small items. Dominant trout observed by Jenkins (1969) fed at the most upstream position in favored feeding lanes. These fish frequently had the highest volume of drift food in their stomachs, but occasional extreme values among lower ranking trout prevented detecting any statistically significant differences.

Dominance seems to have permitted rank-1 trout in this study to use less energy in cover use and agonism than subordinates (Table 26). Rank 1 was the only rank not subject to displacement by other trout. Rank-1 trout also used less energy in agonism than subordinates. This occurred even though rank 1 was involved in at least as many bouts as ranks 2 and 4. Subordinates may have yielded positions to rank 1 more readily than to lower ranking dominants.

The feeding positions held by dominant trout in Jenkins' (1969) study were closer to cover than subordinates' positions. This would seem to have obvious survival value. But ranks 1 and 2 in this study did not feed closer to overhead cover than subordinates. Position of overhead cover seemed to have very little influence on choice of feeding positions by most trout. Of much greater influence were the channel walls. Large trout fed half as far from the walls as from overhead cover. Small trout fed about the same distance from the walls as from overhead cover (Figures 10 and 13).

Differences between Jenkins' study stream and the stream used in this study may explain the conflicting results. In Jenkins' complex natural environment, response to relative current velocity and spatial patterns of drift food abundance could have easily been confounded with response to cover. Overhead cover, prominent lateral surfaces, and favored feeding stations in Jenkins' stream were mostly near the outside of meander bends. Flow resistance of the streambank at meander bends produces low velocity stations. Principle lines of drift occur close to the low velocity areas here. Dominant trout may have defended these positions due to the combination of low current velocity and high drift food abundance, not because they were close to cover per se.

In this study, cover did not produce a velocity buffer and principal lines of drift did not exist. Choice of feeding stations was potentially based on proximity to overhead cover and lateral surfaces, which could be clearly distinguished from each other. I conclude that dominance does not imply feeding close to overhead cover. The advantages of dominants' positions cannot be determined without simultaneous consideration of all factors that potentially influence survival and growth.

Lateral Surfaces

Large brown trout fed about half as far, on the average, from the channel walls as did small trout (Figure 13). Small trout occasionally moved to wall positions vacated by large trout, but more often entirely different mid-channel positions were used. I infer from the lack of competition between large and small trout for wall feeding positions that large trout have a greater behavioral need for lateral surfaces than small trout. There was very little evidence that use of feeding positions close to the walls by large trout reflected stronger preference for low-velocities or for shade than small trout. Greater use of wall positions by large trout than by small trout suggests that thigmotaxis becomes better developed as brown trout age but the mechanisms involved are not clear from this study. Greater use of wall positions by large brown trout could also reflect more experience with predators. Alexander (1976) reported that a substantial portion of the brown trout population in the North Branch of the AuSable River, Michigan in an area just upstream from the source of the brown trout used in 1976 was removed by avian predators. Close association with the streambank may provide large trout with a good source of large terrestial food items, as well as protection from predators.

The relative amounts of visual use of low- and high-stripe lateral devices in 1975 was considered to indicate the importance of the visual proximity of a distinct landmark to the stream bed. Results indicate that a visual reference 15 cm above the stream bed is just as attractive to brown trout as the same-sized reference on the stream bed. "Tactile" use of lateral cover devices was considered to indicate the importance of lateral visual concealment. Only trout pressed sideways against the low-stripe devices were visually isolated from their surroundings.

Preference for the low-stripe devices (tactile use) indicates that visual isolation is an important function of lateral surfaces to adult brown trout. Size of the visual stimulus offered by lateral cover also determines its attractiveness to brown trout. Use of positions close to the channel wall was over 3 times as great as use of positions that permitted trout to press sideways against lateral cover devices (Appendix Figures B1 and B2). This occurred even though direct contact with the walls was not possible. The large visual stimulus offered by the walls was apparently more attractive than the small visual and tactile stimuli offered by lateral cover devices.

Tactile stimuli were most important to trout that were stressed. Prior to acclimation, trout pressed sideways against screens or other trout in fright huddles rather than using the shade of overhead cover. In experiments with only lateral cover devices, frightened trout pressed against other trout rather than the lateral cover devices. This was surprising, as the tactile and visual stimulus offered by the low-stripe devices seemed comparable to that offered by the bodies of other trout. Attractive forces between brown trout become very strong in stress situations.

<u>Light</u>

Light intensity affected brown trout position choice very strongly in this study. Trout avoided direct sunlight by using positions shaded by overhead cover or by the channel walls. Several trout fed on the east side of the channel in the morning and on the west side in the evening to stay in the shade. Rank 1 in replicate IIB2 left cover to feed only before sunrise and on a cloudy morning. Several large and small trout consistently did not begin intense evening feeding until after sunset. This was not visibly associated with a sudden increase in the abundance of surface drift food. In a preliminary experiment, fine organic sediment deposited on the stream bed during the day was commonly swept away in several well-defined areas at night. This was clearly the result of trout activity and suggests that cover is not used as such when light level is low, though it may still serve as a landmark for orientation. Less use of opaque overhead cover by trout when water was turbid (1975) may have been the result of less light penetration and, therefore, less need for shade.

The response to overhead cover is largely a response to relative light level. DeVore (1975) suggested that brown trout preference for opaque overhead cover "low", rather than "high" in the water column was related to its closer overhead visual proximity to the trout's stream bed position. Failure to prefer transparent overhead plates low in the water column in this study confirms that the response to overhead cover is primarily visual rather than tactile. But an alternative interpretation of DeVore's results is that preference for low covers was related to the lower light level underneath them (Table 5). This was indicated in this study by preference for overhead cover with dark rather than light substrate. Dark substrates reflect less light than light substrates, and result in lower light intensity under the cover. Stewart (1970) concluded that use of overhead cover by wild rainbow trout was related to light level underneath. Use of overhead cover increased with increasing structure size, decreasing structure height above the substrate, and decreasing percent holes punched into the structure. Dominant brook, brown, and rainbow trout observed by Butler and Hawthorne (1968) preferred square overhead cover that was large (91 x 91 cm) or medium-sized (61 x 61 cm) rather than small (30 x 30 cm). A large (40.2 cm TL) brown trout used the shade of large and medium-sized overhead covers 80.6% of the time when located in the shade, but only 4.0% of the time when in direct sunlight. Clearly the response here was to relative light level rather than to size of overhead cover.

Brown trout in this study did not prefer large (long) overhead cover to small (short) overhead cover. This might seem to contradict the results just cited (Butler and Hawthorne, 1968), but might be explained by the relationship between cover shape and light intensity beneath cover. Light intensity beneath long (25 x 122 cm) cover in this study was the same as that beneath short (25 x 61 cm) cover (Table 5). Therefore, both types of cover were equally attractive to trout in terms of light intensity beneath the covers. In contrast, Butler and Hawthorne (1968) observed a strong preference by brook, brown, and rainbow trout for large (91 x 91 cm) and medium (61 x 61 cm) square covers rather than small square (30 x 30 cm) cover. Light intensity was lower under the larger covers (Table 5), probably accounting for the consistent preference by their trout for larger covers. A consistent preference for large cover by brown trout in this study would have been expected had the choice been between a wide (50 cm) and a narrow (25 cm) cover of the same length (61 cm). Light intensity is much lower beneath wide than narrow covers 61 cm long (Table 5). A study in progress is to investigate in more detail the influence of cover shape on light level and brown trout preference (J.C. Gruber, in preparation).

Somewhat confusing is the observation by DeVore (1975) that brown trout showed no preference when offered opaque overhead covers with either clear or dark plastic streamers along both sides. Dark streamers presumably lowered the light level under cover and would have been expected to increase its attractiveness. Dark streamers also obstructed lateral vision. DeVore suggested that obstruction of lateral vision could be an undesirable feature of cover because it might inhibit detection of food and predators. But brown trout in the wild frequently use positions where tree roots, and the stream bank obstruct lateral vision on one or both sides (E. Branch AuSable River, Pigeon River, Michigan; Stony Kill, New York, C.E. Bassett, pers. obs.). Lateral concealment from predators would seem to be a very desirable feature of cover even if it does obstruct vision. Brown trout in both parts of this study showed a strong attraction to lateral surfaces. Trout usually responded to drift food while it was still well upstream from their position. Lateral obstruction of vision, therefore, should not inhibit food detection. Perhaps the lateral tactile reference offered by DeVore's streamers was so attractive that the reduction in light intensity produced by dark streamers was relatively insignificant. The majority of the evidence indicates that the primary function of overhead cover for brown trout is concealment from high light intensity. This in turn provides protection from predators.

Current Velocity

The experimental environment in both parts of this study was designed to minimize the influence of current velocity on position choice. Mean current velocity at feeding positions was nearly the same for all social ranks. Velocities greater than sectional means were avoided (range of means 20.4-24.3 cm/s). Correlations between percent of trout using cover devices and mean sectional current velocity in 1975 were very weak or absent.

Conversely, choice of cover in 1976 seemed to be influenced by current velocity. Only two of 8 rank-1 trout preferred cover with the highest current velocity underneath. Lacking large differences in light intensity under cover the trout may have been particularly sensitive to small differences in current velocity on the order of 3-9 cm/s.

Minor irregularities in stream bed topography under cover also could have influenced cover choice. Trout in both years consistently used positions beside or immediately downstream from pieces of twig or stones protruding less than 2.5 cm above the stream bed. Use of shallow depressions in the stream bed was common in 1975 in the absence of overhead cover. Similar behavior has been observed among brown trout in other studies (Jenkins, 1969; DeVore, 1975). In 1976 two rank-1 trout preferred overhead cover with the highest current velocity. This may have reflected attraction to stream bed irregularities too minor to affect velocity measurements with a pygmy Gurley meter.

Application to Stream Management

This study and the review of literature in the introduction indicates that proper cover microhabitat for adult brown trout in streams has the following characteristics:

(1) Low current velocity. Observations by Wesche (1976) indicate that velocities near zero are preferred.

(2) Low light intensity. Except when drift food was very abundant, trout spent most of their time from sunrise to sunset under cover. Light intensity approaching nighttime levels seems to be preferred; that is, the darker it is under cover, the better.

(3) Overhead surfaces close to the stream bed. Distance between overhead cover and the stream bed should just exceed the body depth of the largest trout likely to use the cover.

(4) Lateral surfaces at the stream bed. This provides visual concealment from predators and competitors and offers tactile reference.

(5) Placement close to principal lines of drift. This minimizes energy use in movement between cover and feeding stations and minimizes exposure to predators.

Characteristics of proper feeding microhabitat for adult brown trout in streams are:

(1) Low current velocity closely adjacent to a principal line of drift.

(2) Shade from direct sunlight.

(3) Nearness to the stream bank or other extensive lateral surface. This is especially important for trout over 30 cm long.

The influence of cover location on choice of feeding positions probably depends on size of stream. In the confined channels of this study, trout could not move more than about 6 m from overhead cover, and there was no tendency for trout to feed very close to cover. Prominent channel walls and extensive shade during times of peak feeding activity offered sufficient security. I infer that in small streams where shade from bank vegetation is usually abundant and where trout are never far from the stream banks, utilization of potential feeding stations is not often limited by location of overhead cover. Cover location probably has more influence on choice of feeding stations in wide streams where a relatively large portion of the channel is sunlit for much of the day. The shade offered by overhead cover along the banks in large streams represents much of the total available shade for feeding. Low-ranking trout that could not defend available feeding stations close to cover would have to either expose themselves to predators in the sunlit water or not feed at all until shaded stations became available. Either situation would limit trout biomass. Creation of additional overhead cover in the middle of large streams should encourage better utilization of the food supply by offering additional shaded feeding stations, provided current velocity and drift food abundance were also suitable at these locations.

Habitat manipulations that produce a deeper, narrower channel may be especially successful (Hunt, 1971; White, 1975) because drift food supply is concentrated, cover and all potential feeding stations are brought closer together, a greater portion of the channel is shaded, and the stream bank becomes relatively more prominent. These factors encourage maximum food intake with minimum energy expenditure and minimize exposure to predators.

Carrying capacity of cover is apparently related to its length. Trout coexist indefinitely under cover as long as subordinates remain slightly downstream from dominants. This study suggests that an approximation to cover capacity might be that each trout requires a length of cover equal to its body length. Therefore 6 linear meters of overhead cover could support 20 30-cm trout. Electrofishing observations in the AuSable River system indicate that this is a reasonable figure. Increasing cover width tends to make cover more attractive by reducing light level, but probably does not increase the number of trout that can coexist under it unless more lateral visual concealment is provided (Kalleberg, 1958; Hartman, 1963).

Chapman (1966) suggested that stream salmonid populations are limited by the spatial demands of feeding and that cover is not as important. This is consistent with the results of this study. Space requirements of feeding trout in 1976 were roughly 6.5 m^2 or about 2.5 linear meters of channel length per trout. This estimate is based on the distance at which trout reacted aggressively toward subordinates during periods of peak food abundance. Small trout seemed to have about the same feeding space requirements as large trout. Six linear meters of feeding habitat would support 2 or 3 trout compared to 20 trout of the same size for the same length of overhead cover. Wide streams might have two or more principal lines of drift which would permit a few more trout to feed in this length of stream. Streams where drift food abundance is higher than in the channels used in this study also might support a few more trout per unit length of feeding habitat as feeding space requirements are apparently reduced where food is very abundant (Mason and Chapman, 1965). But, it is readily apparent that creating more cover space can increase stream carrying capacity (numerical abundance of trout) during the summer only to a limit imposed by the availability of space suitable for feeding. The fact that abundance of brown and brook trout is closely related to amount of cover in streams (Boussu, 1954; Lewis, 1969; White, 1975; Enk, 1977), where studied, does not contradict this. Rather, it shows that there is often not enough cover to support the number of trout that could fully utilize the available feeding habitat.

The suggestion by DeVore (1975) that creation of large covers near good feeding habitat might cause over-utilization of the food supply seems unlikely, at least over a long period. Large covers might initially attract more trout than the adjacent feeding habitat could support. But agonism would disperse low-ranking trout into areas where food abundance was insufficient to meet growth or maintenance demands--or into areas readily accessible to predators (Ondera, 1962; Symons, 1968). These conditions would cause emigration and mortality that would tend to bring the population back into equilibrium with the availability of high quality feeding habitat. The problem of too many trout for the available feeding habitat would persist only if the population in the stream as a whole were so unstable that immigrants continued to replace trout lost via emigration and mortality. Frequent over-stocking might cause this.

Stream habitat manipulation involves consideration of all constituents of trout living space including cover, feeding, and spawning microhabitats. Attempts to increase the availability of one type of microhabitat must not result in a shortage of another type. Stream morphology and the spatial distribution of required microhabitats can probably be manipulated to encourage more efficient utilization of stream resources by trout. Position choice results from responses to a few simple physical stimuli, but social factors can modify these responses. Social factors have the most influence where limited availability of essential microhabitat leads to strong competition.

Further study is needed to determine the influence of the social environment on spatial demands of wild trout. It may be possible to modify hierarchy size or the body size composition of hierarchy members to minimize energy wastage in agonism and to encourage more efficient use of the food supply. This might be achieved with special fishing regulations and habitat manipulation.

Living space requirements at night also deserve much study. Indirect evidence in this study suggests that brown trout do not use cover at night. This needs to be verified. Two other questions must be answered:

(1) Will brown trout feed farther from cover (overhead and lateral) at night than during the day?

(2) Are feeding space requirements smaller at night than during the day? This is especially of interest for adult brown trout as they are nocturnal feeders.

If the answer to these questions is "yes", then distribution of cover in the channel cross-section does not potentially limit use of feeding microhabitat as much as daytime observations have suggested. Winter living-space requirements of adult stream trout also must be defined before habitat can be managed comprehensively. The primary function of instream structure that provides concealment from direct sunlight during the summer seems to be protection from severe winter ice and floods on some streams (Ondera, 1962; Hartman, 1963; Hunt, 1969; Bustard and Narver, 1975).

SUMMARY

Daytime position choice by wild, adult brown trout was observed in controlled-flow stream channels during the summers of 1975 and 1976. In 1975 25-30-cm (TL) trout in groups of 5, with 4 groups tested simultaneously, were offered pairs of cover types. Occupation of a specific type represented a choice between known stimuli.

The response to overhead cover was primarily visual rather than tactile. In contrast to previously demonstrated preference for opaque overhead cover 10 cm rather than 15 cm above the stream bed, the trout showed no preference when offered transparent overhead cover devices 10 cm and 15 cm above the stream bed. The trout responded to light reflected from the stream bed beneath opaque overhead cover. Cover with dark stream bed beneath was preferred to cover with light stream bed beneath ($p < 0.01$).

Visual isolation is an important function of lateral vertical surfaces. The trout preferred to press sideways against lateral cover devices with a 5-cm-wide black stripe on the stream bed rather than devices with the stripe raised 15 cm above the stream bed ($p < 0.001$). Trout that were not pressed against lateral devices showed no preference; this indicated that the visual reference offered by the stripe on the stream bed was no more attractive as a landmark than the stripe above the stream bed.

In 1976, 6 groups (replicates) consisting of 2 small (23-28 cm FL) and 2 large (35-41 cm FL) trout were observed from elevated blinds. Five other groups of 1-3 trout were also observed. One small (25 x 61 cm) and one large (25 x 122 cm) opaque overhead cover was provided for each group. The trout developed a strong social hierarchy. Heavier trout held higher rank. Each trout defended a space around itself which moved as the trout moved rather than defending a fixed area of stream bed. Space upstream from the trout was defended more persistently than space downstream from the trout. Feeding trout defended much more space (about 6.5 m^2) than trout using cover (about 1 m^2).

The function of the social hierarchy appeared to be reduction of aggressiveness towards subordinates and dominants. Agonism between small trout in the absence of large trout was more frequent and intense than when large trout were present. In groups of 2 large and 2 small trout, most aggressiveness was directed toward trout of the next lowest rank.

Rank-1 trout used cover more than rank-3 and -4 trout ($p < 0.01$) and fed less than rank-3 and -4 trout ($p < 0.01$). Estimated total energy use ($mgO_2/kg/h$) above standard metabolism was lowest for rank-1 trout (8.25) and highest for rank-4 trout (27.02). This appeared to be related to relative social status. Superior status permitted rank-1 trout to use less energy in agonism and in movement between covers. Feeding accounted for 92.6% of the total estimated energy use by all trout combined. Over 90% of this was expended in maintaining a stationary position in the current. Agonism was the most energy-consuming activity per unit of active time.

Cover use patterns were influenced by current velocity beneath cover, by cover size, and by social rank. Individual cover preference was based at least as much on current velocity beneath cover as on cover size. Five of 8 rank-1 trout preferred the cover with the lowest current velocity beneath; 2 preferred the cover with the fastest current velocity beneath. Only 3 rank-1 trout preferred the largest cover available. Light intensity was the same under the large and small covers because the covers were of equal width.

Social rank strongly influenced choice of cover because competition for the upstream position under cover was strong and the area of cover was small. Subordinates preferred the same cover as rank-1 trout, but they often did not express that preference due to avoidance of dominants. The attractiveness of low current velocity beneath cover did not compensate for space limitations imposed by small cover size. Large cover received at least as much total use as small cover even in replicates where small cover was preferred. Much of the heavy use of large cover in replicates where small cover was preferred was due to avoidance of rank-1 trout by rank-3 and -4 trout and avoidance of rank-2 trout by rank-4 trout. Rank-3 and -4 trout considered together avoided dominants more in replicates where small cover was preferred than in replicates where large cover was preferred ($p < 0.01$). Trout differing by only one social rank coexisted about as often under small cover as under large cover.

Current velocity and light level strongly influenced choice of feeding positions. The trout avoided feeding at stations where current velocity exceeded the channel section mean ($p < 0.001$; range

of means 20.4-24.3 cm/s). Mean current velocity and depth at feeding stations was nearly the same for all social ranks. All social ranks fed more on the shaded side of the channel than on the sunlit side of the channel ($p < 0.005$). High-ranking trout did not feed closer to overhead cover than subordinates. But rank-1 and -2 trout fed closer to the channel walls than rank-3 and -4 trout ($p < 0.01$). Large trout rarely used mid-channel feeding stations with current velocities comparable to wall-side stations, and small trout usually did not move to wall-side stations vacated by dominants.

The trout spent less time per feeding station during the morning when surface drift food was most abundant than during midday and evening ($p = 0.005$). This resulted from more agonism during the morning than during midday and evening ($p < 0.01$). The nearly uniform distribution of current velocity and drift food in the channels (in contrast to more concentrated distribution in natural streams) minimized competition for feeding stations. Consequently, social rank had only minor influence on choice of feeding stations.

This study and a review of the literature indicated that the characteristics of proper cover microhabitat for adult brown trout in streams are: (1) low current velocity, (2) low light intensity, (3) overhead surfaces close to the stream bed, (4) lateral surfaces at the stream bed, and (5) placement close to principal lines of drift.

Characteristics of proper feeding microhabitat for adult brown trout are: (1) low current velocity, (2) shade from direct sunlight, and (3) nearness to extensive lateral surfaces.

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APPENDICES

APPENDIX A

TABLES

Table A1. - Daily maximum and minimum water temperatures for the East Branch of the AuSable River at the DNR Grayling Field Office during summer 1975.

Date[a]	Temperature C High	Temperature C Low	Date	Temperature C High	Temperature C Low
8/11	17.6	12.9	8/27	16.2	13.4
12	17.6	14.2	28	13.4	11.5
13	18.8	16.2	29	12.9	11.8
14	17.6	14.3	30	12.9	12.9
15	17.9	14.0	31	12.9	12.3
16	18.5	14.0	9/ 1	14.0	12.9
17	18.5	15.1	2	14.0	12.4
18	16.0	12.6	3	10.4	9.0
19	14.0	11.8	4	12.0	9.5
20	12.9	11.5	5	12.9	10.0
21	14.0	12.3	6	13.4	11.8
22	14.0	12.9	7	11.8	10.6
23	12.3	11.5	8	11.5	10.4
24	15.1	12.3	9	11.5	8.4
25	17.0	14.8	10	11.8	9.0
26	17.0	14.6	11	12.9	11.5
			12	11.8	9.2

[a]Water temperature was not measured during the first 7 days of the study (8/4 - 8/10).

Table A2. - Daily maximum and minimum water temperatures for the East Branch of the AuSable River at the DNR Grayling Field Office during summer 1976.

	Temperature C			Temperature C	
Date	High	Low	Date	High	Low
6/22	18.2	14.6	7/24	19.9	15.7
23	19.0	16.0	25	18.8	15.1
24	16.2	14.8	26	18.5	15.7
25	19.3	14.6	27	20.4	16.0
26	19.6	15.1	28	15.7	15.1
27	19.3	15.1	29	18.5	14.3
28	16.2	14.8	30	19.0	15.1
29	15.4	14.3	31	18.5	15.7
30	14.6	13.4	8/ 1	16.2	13.4
7/ 1	16.0	12.3	2	17.1	12.3
2	15.7	13.1	3	16.5	13.2
3	18.5	13.4	4	15.7	13.2
4	18.8	14.0	5	14.8	14.0
5	19.9	14.6	6	16.2	12.3
6	19.6	14.8	7	16.2	11.8
7	16.8	16.0	8	17.1	12.3
8	18.8	13.4	9	17.9	13.4
9	18.5	14.3	10	16.0	14.0
10	20.2	16.0	11	18.2	14.0
11	21.8	17.9	12	20.2	16.8
12	19.3	15.4	13	18.8	16.8
13	17.9	13.4	14	15.7	15.1
14	20.4	14.8	15	15.1	11.8
15	20.2	16.2	16	16.0	11.2
16	17.6	16.2	17	16.8	11.8
17	17.4	13.2	18	17.1	12.6
18	17.9	13.2	19	19.6	15.1
19	18.5	14.8	20	20.2	16.2
20	17.6	16.2	21	20.2	16.2
21	18.2	13.7	22	19.6	15.4
22	19.0	14.3	23	19.0	14.8
23	20.2	16.2	24	18.2	14.0
			25	16.8	14.0

Table A3. - Sex, social rank, and the weight and fork length of brown trout in each replicate at the beginning and end of each 3-week experiment.

	Weight (g)		Fork length (mm)			Social
Replicate	Begin	End	Begin	End	Sex	rank
IA1	640	560	392	392	M	1
	550	480	380	380	F	2
	228	210	268	268	F	3
IA2	465	440	350	350	F	1
	418	354	339	339	F	2
	228	215	276	276	M	3
	124	126	229	229	M	4
IB1	242	223	267	267	F	1
	166	153	249	249	M	2
IB2	172	158	258	258	Immature	a
	141	133	234	234	M	a
IIA1	535	485	357	357	M	2[b]
	455	430	359	359	F	1
	264	253	290	290	M	3
	120	119	228	228	F	4
IIA2	620	590	388	388	M	1
	565	530	382	382	F	2
	187	187	255	255	F	3
	153	140	238	238	M	4
IIB1	600	y50	389	389	F	1
	440	410	359	359	M	2
	242	240	288	288	F	3
	190	192	263	263	F	4
IIB2	610	555	386	386	M	1
	550	495	359	359	F	2
	181	180	245	245	M	3
	153	140	238	238	M	4
IIIA1	535	485	348	348	M	1
	395	380	340	340	M	2
	190	188	260	260	M	3
	137	134	234	234	F	4
IIIA2	200	176	262	262	M	
IIIB2	284	213	276	276	M	2[c]
	153	156	241	241	M	1

[a]No agonistic bouts observed, rank could not be determined.

[b]Abnormal behavior but no injury was apparent.

[c]Injured.

Table A4. - Time and number of observation sessions devoted to each replicate during morning, midday, and evening.

Replicate[a]	Morning Time (min)	Morning No obs.	Midday Time (min)	Midday No obs.	Evening Time (min)	Evening No obs.	Total Time (min)	Total No obs.	Mean length of observations (min)
IA1	69.5	4	56.5	5	46.0	4	172.0	13	13.23
IA2	62.0	4	109.0	5	90.0	4	261.0	13	20.08
IB1	34.5	3	52.0	3	21.0	3	107.5	9	11.94
IB2	30.0	3	33.0	3	21.0	3	84.0	9	9.33
IIA1	188.0	9	122.0	7	91.0	6	401.0	22	18.23
IIA2	224.5	9	120.5	7	90.0	5	435.0	21	20.71
IIB1	185.0	9	152.0	7	82.5	6	419.5	22	19.07
IIB2	197.0	9	91.0	6	66.0	5	354.0	20	17.70
IIIA1	399.0	7	268.0	6	182.0	5	849.0	18	47.17
IIIA2	118.0	4	42.0	2	81.0	4	241.0	10	24.10
IIIB2	111.0	4	75.0	4	93.0	4	279.0	12	23.25
Total	1618.5	65	1121.0	55	863.5	49	3603.0	169	21.32

[a]All trout in IIIB1 were removed by vandals.

Table A5. - Time trout spent in each activity during morning, midday, and evening. Values are cumulative over all social ranks and replicates.

	Time							
	Morning		Midday		Evening		Totals	
Activity	Min	%	Min	%	Min	%	Min	%
Agonistic	76.0	1.33	20.5	0.53	17.0	0.59	113.5	0.91
Cover use[a]	2585.25	45.33	2528.75	64.85	1716.25	59.22	6829.25	54.64 (63.0[b])
Feeding[b]	2528.75	44.34	898.5	23.04	918.0	31.7	4345.25	34.77
Miscellaneous	513.25	9.0	451.5	11.58	246.0	8.49	1210.75	9.69
Totals	5703.25	100.0	3899.25	100.0	2896.25	100.0	12498.75	100.01

[a]Does not include feeding from cover.

[b]Includes feeding from cover.

Table A6. - Movement trout devoted to each activity during morning, midday, and evening. Values are cumulative over all social ranks and replicates.

	Movement							
	Morning		Midday		Evening		Totals	
Activity	m	%	m	%	m	%	m	%
Agonistic	1146.75	39.3	356.0	41.75	217.5	37.15	1720.25	39.49
Cover use[a]	281.75	13.08	148.5	17.41	36.0	6.15	566.25	13.0
Feeding[b]	1295.0	44.38	317.25	37.2	332.0	56.7	1944.25	44.63
Miscellaneous	94.75	3.25	31.0	3.64	0	0	125.75	2.89
Totals	2918.25	100.01	852.75	100.0	585.5	100.0	4356.5	100.01

[a]Does not include feeding from cover.

[b]Includes feeding from cover.

Table A7. - Number of one-on-one agonistic bouts won and lost by each social rank in replicates with two small trout.

Social rank of loser	Replicate	Social rank of winner 1	2	Total number of losses
	IB1		0	
1	IB2		a	0
	IIIB2		0	
	IB1	8		
2	IB2	a		19
	IIIB2	11		
Total number of wins		19	0	19

[a]No bouts observed.

Table A8. - Number of one-on-one agonistic bouts won and lost by each social rank in the replicate with two large and one small trout.

Social rank of loser	Replicate	Social rank of winner 1	2	3	Total number of losses
1	IA1		0	0	0
2	IA1	1		0	1
3	IA1	1	1		2
Total number of wins		2	1	0	3

Table A9. - Number of one-on-one agonistic bouts won and lost by each social rank in replicates with two large and two small trout.

Social rank of loser	Replicate	Social rank of winner 1	2	3	4	Total number of losses
	IA2		0	0	0	
	IIA1		0	0	0	
1	IIA2		2	0	0	3
	IIB1		0	0	0	
	IIB2		0	0	0	
	IIIA1		1	0	0	
	IA2	2		0	0	
	IIA1	1		0	0	
2	IIA2	5		0	0	32
	IIB1	8		0	0	
	IIB2	2		0	0	
	IIIA1	13		1	0	
	IA2	0	3		0	
	IIA1	5	0		0	
3	IIA2	5	4		0	60
	IIB1	4	3		0	
	IIB2	0	3		0	
	IIIA1	15	18		0	
	IA2	0	2	3		
	IIA1	4	0	4		
4	IIA2	10	3	2		70
	IIB1	2	4	17		
	IIB2	3	6	8		
	IIIA1	0	1	1		
Total number of wins		79	50	36	0	165

Table A10. - Mean percent of observation session time spent in agonism by each social rank during morning, midday, and evening in replicates with 4 trout.

	Morning				Midday				Evening				Replicate	
	Rank				Rank				Rank					
Replicate	1	2	3	4	1	2	3	4	1	2	3	4	Mean	SD
IA2	0	0.37	1.39	0.35	0.95	0.95	0.62	1.39	0	0.14	0.89	0.89	0.66	0.49
IIA1	0.22	a	0.94	0.57	0.2	a	0.2	0	0	a	0	0	0.24	0.32
IIA2	0.51	1.0	0.26	0.26	0.6	0.56	0.21	0.42	0.4	0.4	0.26	0.26	0.43	0.22
IIB1	0.59	1.89	1.88	1.51	0	0	0	0	0	0	0.14	0.28	0.52	0.77
IIB2	0.19	0.36	0.92	1.96	0	0	0	0	0	0	0	0	0.29	0.59
IIIA1	0.39	3.89	3.98	a	0.11	0.25	1.39	a	0.45	0	0.45	a	1.21	1.59

Rank	Mean	SD
1	0.26	0.28
2	0.65	1.03
3	0.75	0.98
4	0.53	0.63

Time of day	Mean	SD
Morning	1.06	1.1
Midday	0.36	0.45
Evening	0.2	0.28

[a] Abnormal behavior.

Table All. - Mean percent of observation session movement spent in agonism by each social rank during morning, midday, and evening in replicates with 4 trout.

	Morning				Midday				Evening					
	Rank				Rank				Rank				Replicate	
Replicate	1	2	3	4	1	2	3	4	1	2	3	4	Mean	SD
IA2	0	21.99	21.26	29.41	65.38	14.91	49.49	35.77	0	25.0	19.55	23.61	27.85	17.49
IIA1	5.81	a	44.15	15.25	100.0	a	40.63	0	0	a	0	0	25.73	34.98
IIA2	18.37	24.49	32.65	30.72	75.0	48.48	2.73	11.46	50.0	50.0	16.67	17.31	31.49	20.76
IIB1	15.35	29.78	39.03	28.05	0	0	0	0	0	0	0	19.36	14.62	15.35
IIB2	12.2	24.23	57.07	31.74	0	0	0	0	0	0	0	0	20.87	21.84
IIIA1	30.37	29.31	27.66	a	22.16	17.71	27.89	a	100.0	0	29.44	a	31.62	27.39

	Rank			Time of day	
	Mean	SD		Mean	SD
1	37.71	36.23	Morning	25.86	12.4
2	23.82	15.42	Midday	31.98	29.68
3	24.01	18.74	Evening	20.64	26.38
4	18.66	12.74			

[a]Abnormal behavior.

Table A12. - Mean rate of movement (cm/s) associated with agonism for each social rank during morning, midday, and evening in replicates with 4 trout.

	Morning				Midday				Evening				Replicate	
	Rank				Rank				Rank					
Replicate	1	2	3	4	1	2	3	4	1	2	3	4	Mean	SD
IA2	0	19.84	7.04	32.0	6.8	6.8	4.69	15.76	0	3.2	34.4	51.68	18.25	16.32
IIA1	26.88	a	14.86	29.25	53.76	a	83.2	0	0	a	0	0	41.59	27.21
IIA2	67.14	64.32	38.59	44.32	5.55	14.4	12.8	4.16	30.4	30.4	12.8	14.4	28.27	21.63
IIB1	24.32	24.19	49.52	30.98	0	0	0	0	0	0	0	38.4	32.25	11.94
IIB2	31.04	20.16	26.11	27.41	0	0	0	0	0	0	0	0	26.18	4.52
IIIA1	20.59	22.67	21.49	a	49.6	76.8	10.48	a	14.4	24.96	14.8	a	28.42	26.35

	Rank			Time of day	
	Mean	SD		Mean	SD
1	30.04	19.59	Morning	30.61	14.97
2	27.98	22.66	Midday	26.52	28.75
3	25.44	21.84	Evening	24.53	14.1
4	28.84	14.37			

[a]Abnormal behavior.

Table A13. - Mean percent of observation session time spent under cover by each social rank in replicates with 4 trout. Time spent feeding from cover is not included.

	Morning				Midday				Evening				Replicate	
	Rank				Rank				Rank					
Replicate	1	2	3	4	1	2	3	4	1	2	3	4	Mean	SD
IA2	76.91	44.45	48.61	64.48	79.05	72.97	72.12	37.29	100.0	65.23	18.61	29.05	59.06	23.66
IIA1	87.82	a	57.71	53.75	99.8	a	78.57	85.71	83.33	a	66.67	56.86	74.47	16.29
IIA2	24.58	14.75	22.53	46.21	85.11	85.53	23.32	42.67	59.6	73.6	43.86	53.89	47.97	24.44
IIB1	27.65	66.44	52.6	10.0	100.0	85.71	46.53	56.56	100.0	100.0	55.55	58.05	63.26	28.91
IIB2	92.78	98.21	62.39	49.37	100.0	100.0	100.0	100.0	80.0	80.0	40.0	80.0	81.89	21.11
IIA1	95.11	42.99	43.94	a	84.9	46.83	80.04	a	92.68	60.0	63.56	a	67.78	20.95

Rank	Mean	SD	Time of day	Mean	SD
1	81.63	22.83	Morning	53.92	25.25
2	69.11	24.35	Midday	75.58	23.32
3	54.26	21.33	Evening	66.39	22.24
4	53.93	22.32			

[A] Abnormal behavior.

Table A14. - Mean percent of observation session movement associated wtih cover use by each social rank during morning, midday, and evening in replicates with 4 trout. Movement associated with feeding from cover is not included.

	Morning				Midday				Evening				Replicate	
	Rank				Rank				Rank					
Replicate	1	2	3	4	1	2	3	4	1	2	3	4	Mean	SD
IA2	27.03	31.14	12.08	26.98	34.62	60.38	15.82	12.60	0	0	29.32	13.19	23.92	16.02
IIA1	64.16	a	20.24	35.77	0	a	0	0	0	a	0	0	15.02	23.91
IIA2	3.45	18.54	0.39	4.99	0	31.82	20.23	10.0	0	0	8.62	3.57	8.47	10.13
IIB1	26.42	34.12	21.13	8.33	0	0	34.09	24.13	0	0	13.33	8.33	21.23	10.43
IIB2	66.67	9.37	2.38	20.87	0	0	0	0	0	0	0	0	16.55	25.81
IIIA1	41.03	23.3	15.36	a	17.37	33.39	48.65	a	0	0	10.36	a	21.05	17.19

	Rank			Time of day	
	Mean	SD		Mean	SD
1	21.6	24.36	Morning	23.35	17.7
2	22.0	18.85	Midday	22.87	17.84
3	14.82	13.5	Evening	5.10	8.03
4	12.98	10.97			

[a] Abnormal behavior.

Table A15. - Mean rate of movement (cm/s) associated with cover use by each social rank during morning, midday, and evening in replicates with 4 trout. Movement associated with feeding from cover is not included.

	Morning				Midday				Evening					
	Rank				Rank				Rank				Replicate	
Replicate	1	2	3	4	1	2	3	4	1	2	3	4	Mean	SD
IA2	0	2.0	0.11	0.18	0.05	0.34	1.18	7.65	0	0	1.02	2.53	1.25	2.19
IIA1	0.42	a	0.37	0.59	0	a	0	0	0	a	0	0	0.15	0.24
IIA2	0.34	2.82	0.14	0.06	0	1.28	4.61	0.03	0	0	0.08	0.02	0.78	1.47
IIB1	1.17	0.5	0.88	0.27	0	0	0.16	0.27	0	0	0.16	0.05	0.29	0.38
IIB2	0.16	0.19	0.08	11.2	0	0	0	0	0	0	0	0	0.97	3.22
IIIA1	0.06	0.24	0.78	a	0.48	0.58	0.77	a	0	0	0	a	0.32	0.33

Rank			Time of day		
	Mean	SD		Mean	SD
1	0.15	0.3	Morning	0.6	0.76
2	0.55	0.85	Midday	0.79	1.83
3	0.57	1.08	Evening	0.17	0.57
4	1.52	3.34			

[a]Abnormal behavior.

Table A16. - Number of observation sessions in which each social rank used large cover, small cover, and no cover, and the probability of using small and large covers in replicates with 4 trout. Sessions in which each rank used cover alone and in all possible combinations with other ranks are included in sums.

Rank	Large cover	Small cover and no cover	Sum	Probability of using large cover	Small cover	Large cover and no cover	Sum	Probability using of small cover
1	48	37	85	0.565	32	53	85	0.386
2	29	34	63	0.46	30	33	63	0.476
3	46	28	74	0.622	20	54	74	0.27
4	26	23	49	0.531	13	36	49	0.265

Table A17. - Mean distance (m) to the nearest cover from feeding stations used by each social rank during morning, midday, and evening in replicates with 4 trout. Distance weighted by percent of total feeding time spent at each station. Cover feeding stations are included.

	Morning				Midday				Evening					
	Rank				Rank				Rank				Replicate	
Replicate	1	2	3	4	1	2	3	4	1	2	3	4	Mean	SD
IA2	2.63	0.24	1.41	1.94	0	0.47	0	0.78	0	2.0	1.73	22.8	1.35	0.92
IIA1	0	a	0	0.87	0	a	0	0.38	0	a	0.14	0.69	0.27	0.35
IIA2	1.19	1.46	1.01	1.41	0	1.13	1.31	0	2.88	1.68	1.32	2.13	1.29	0.79
IIB1	1.94	1.04	1.64	1.64	0	0.3	1.71	0	0	0	0.95	2.16	1.26	0.74
IIB2	4.7	0.47	1.38	1.11	0	0	0	0	0	0	0.83	1.68	1.69	1.53
IIIA1	2.0	3.63	0.66	a	2.78	2.07	1.13	a	1.13	0.39	0.84	a	1.63	1.08

Rank	Mean	SD	Time of day	Mean	SD
1	1.75	1.48	Morning	1.47	1.11
2	1.21	1.03	Midday	0.80	0.87
3	0.86	0.59	Evening	1.34	0.81
4	1.34	0.71			

[a] Abnormal behavior.

Table A18. - Mean percent of feeding time spent feeding from cover by each social rank during morning, midday, and evening in replicates with 4 trout.

	Morning				Midday				Evening				Replicate	
	Rank				Rank				Rank					
Replicate	1	2	3	4	1	2	3	4	1	2	3	4	Mean	SD
IA2	0	83	53	0		66	100	23		0	9	0	33.4	38.7
IIA1	100	a	100	42		a	100	0	100		85	42	71.1	38.3
IIA2	56	0	1	12	100	0	100	0	0	0	0	0	22.4	39.6
IIB1	5	39	10	9		100	81	0			60	0	33.8	38.1
IIB2	59	29	40	25							66	0	36.5	24.1
IIIA1	15	10	37	a	0	28	2	a	0	30	32	a	17.1	14.9

Rank			Time of day		
	Mean	SD		Mean	SD
1	43.5	44.6	Morning	32.9	31.5
2	32.1	34.4	Midday	46.7	45.9
3	45.6	38.2	Evening	24.9	33.9
4	18.1	28.2			

[a] Abnormal behavior.

Table A19. - Number and volume (cc) of organisms in subsamples of drift net contents on each sampling day. Subsamples equal 5% of the total drift net contents.

	Nets set - 6/28, 2000h (EDT)															
	Time nets emptied															
	0200 h				0800 h				1400 h				2000 h			
	Channel				Channel				Channel				Channel			
	A		B		A		B		A		B		A		B	
Taxon	No.	Vol.	No.	Vol.	No.	Vol.	No.	Vol.	No.	Vol.	No.	Vol.	No.	Vol.	No.	Vol.
Isopoda	87	0.2	26	0.375	42	0.425	17	0.2	35	0.2	15	0.1	27	0.2	10	0.1
Amphipoda	2	0.025	6	0.025+	0	0	0	0	1	+	0	0	0	0	0	0
Hemiptera	5	0.025+	4	++	2	++	1	+	0	0	0	0	2	+	3	+
Coleoptera																
Adults	1	+	2	++	0	0	2	+	0	0	0	0	0	0	0	0
Immatures	3	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Osteichthyes	0	0	1	0.1	0	0	2	0.25	0	0	0	0	0	0	0	0
Homoptera	0	0	0	0	0	0	0	0	0	0	1	+	0	0	0	0
Hymenoptera	0	0	2	+	0	0	3	0.25	1	+	3	+	9	0.025	0	0
Mollusca	1	+	0	0	0	0	0	0	0	0	1	+	0	0	0	0
Ephemeroptera																
Adults	2	0.025+	1	+	1	+	3	+	0	0	5	0.025	1	+	3	+
Nymphs	9	0.05+	4	0.025+	4	0.025	1	+	2	+	0	0	4	0.025	0	0
Tricoptera																
Adults	3	0.05	2	0.025	0	0	0	0	0	0	0	0	0	0	0	0
Immatures	46	0.65	4	0.05+	32	0.7	4	0.075	17	0.35	1	0.025	24	0.825	6	0.2

Table A19 (cont'd.)

Diptera																
Adults	0	0	0	0	0	0	1	0.025	0	0	0	0	0	0	1	+
Immature	0	0	0	0	0	0	0	0	1	+	1	+	0	0	0	0
Miscellaneous	0	0	1	0.025	1	+	0	0	0	0	0	0	0	0	5	0.05
Nets set - 7/15, 1400 h (EDT)																
Isopoda	99	0.85	20	0.2	48	0.5	12	0.1	28	0.225	2	+	23	0.4	1	+
Amphipoda	2	+	38	0.375	7	0.1	9	0.15	0	0	0	0	1	+	1	+
Hemiptera	33	0.075	4	+	5	+	2	+	0	0	2	+	2	+	9	0.025
Coleoptera																
Adults	10	++	14	0.025	2	+	1	+	0	0	4	+	2	+	1	++
Immatures	2	++	0	0	3	+	0	0	0	0	0	0	3	+	0	0
Osteichthyes	0	0	0	0	1	0.2	0	0	0	0	0	0	0	0	0	0
Homoptera	0	0	3	+	0	0	0	0	3	+	0	0	0	+	0	0
Hymenoptera	1	+	24	0.025	1	+	13	0.025	2	+	4	+	1	+	23	0.075
Mollusca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	+
Ephemeroptera																
Adults	1	0.05	1	0.2	0	0	0	0	2	+	0	0	0	0	4	+
Nymphs	29	0.075	16	0.025	45	0.1	18	0.05	13	0.05	8	0.025	5	0.025	7	+
Tricoptera																
Adults	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Immatures	77	1.65	9	0.175	19	0.5	2	0.025	20	0.5	0	0	7	0.175	3	0.025

Table A19 (cont'd.)

Diptera																
Adults	6	0.025+	4	0.025	1	+	1	+	0	0	2	0.05	1	+	0	0
Immatures	8	++	3	+	5	+	7	0.025	5	+	2	+	3	+	5	+
Miscellaneous	4	0.025	0	0	0	0	1	0.15	1	0.3	0	0	0	0	0	0
Nets set - 8/6, 0800 h (EDT)																
Isopoda	35	0.2	3	0.025	55	0.425	7	0.05	13	0.1	1	+	15	0.1	0	0
Amphipoda	2	0.05	2	0.05	3	0.05	3	0.075	0	0	0	0	0	0	0	0
Hemiptera	2	+	0	0	0	0	1	+	1	+	2	+	3	+	6	0.025
Coleoptera																
Adults	1	+	1	+	0	0	3	+	0	0	0	0	0	0	0	0
Immatures	0	0	0	0	2	0.025	0	0	1	+	0	0	1	+	1	+
Osteichthyes	1	0.75	3	0.5	0	0	0	0	0	0	0	0	0	0	0	0
Homoptera	1	+	0	0	0	0	0	0	1	+	2	+	1	+	3	+
Hymenoptera	0	0	16	0.05	0	0	9	0.025	0	0	20	0.025	2	+	14	0.025
Mollusca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ephemeroptera																
Adults	0	0	0	0	0	0	0	0	1	+	3	+	5	+	5	+
Nymphs	40	0.175	24	0.05	43	0.2	43	0.125	12	0.05	15	0.1	14	0.05	22	0.05
Tricoptera																
Adults	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Immatures	10	0.125	4	0.05	8	0.1	1	+	7	0.2	0	0	5	0.1	1	+

Table A19 (cont'd.)

Diptera																
Adults	2	+	3	+	0	0	0	0	2	+	0	0	1	+	8	0.025
Immatures	2	+	4	+	3	+	1	+	2	+	3	+	2	+	5	+
Miscellaneous	5	0.025	5	0.025	2	+	0	0	0	0	4	0.05	4	0.025	3	+

+Not measurable, but considered equal to 0.0083 cc.

Table A20. - Total estimated number and volume (cc) of organisms collected in drift nets on each sampling day.

Time nets emptied (EDT)		Channel A		Channel B	
		Number	Volume	Number	Volume
6/29	0200 h	3180	34.332	1060	13.666
	0800 h[a]	1640	23.664	680	11.832
	1400 h	1140	11.832	540	3.5
	2000 h	1340	21.832	560	7.5
7/16	0200 h	5440	36.5	1100	21.5
	0800 h	2740	29.0	2720	11.0
	1400 h	1480	22.0	1320	2.0
7/15	2000 h	1020	13.332	480	3.666
8/7	0200 h	2020	27.166	1300	15.5
	0800 h	2320	16.332	1360	6.166
8/6	1400 h	800	8.0	1000	4.166
	2000 h	1060	6.5	1360	3.332

[a]The 95% confidence intervals on this sample were ±15% numbers, and ±23% volumes. Confidence intervals were not determined for other estimates.

Table A21. - Number and volume (cc) of organisms in stomachs of trout in each group in the morning (0800 h) and evening (2000 h). Ranks 1 and 2 are large trout, ranks 3 and 4 are small trout (Appendix Table A3).

Channel	Section	Rank	Isopoda		Ephemeroptera Adults		Ephemeroptera Nymphs		Tricoptera Adults		Tricoptera Immat.		Hemiptera		Coleoptera		Hymenoptera		Amphipoda		Mollusca		Orthoptera		Misc.[c]	Total	
			No.	Vol.	No.	Vol.	No.	Vol.	No.	Vol.	No.	Vol.	No.	Vol.	No.	Vol.	No.	Vol.	No.	Vol.	No.	Vol.	No.	Vol.	Vol.	No.	Vol.
													Group I - 0800 h														
A	1	1	2	0.05	0	0	0	0	0	0	2	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0.05	4	0.2
A	1	2	2	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	2	0.10
A	1	3	13	0.2	0	0	0	0	0	0	10	0.3	0	0	0	0	0	0	0	0	0	0	0	0	0.05	23	0.65
B	1	1	100	1.3	0	0	1	0.05	1	0.025	1	0.025	2	0.05	1	0.025	0	0	0	0	0	0	0	0	0.2	104	1.675
B	1	2	60	0.45	0	0	0	0	0	0	0	0	2	0.05	0	0	0	0	0	0	0	0	0	0	0.1	62	0.6
													Group I - 2000 h														
A	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.025	0	0.025
A	2	2	1	0.025	0	0	0	0	0	0	0	0	2	0.025	0	0	0	0	0	0	0	0	0	0	0	3	0.05
A	2	3	10	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.05	0	0	0.3	11	0.55
A	2	4	6	0.05	0	0	0	0	0	0	0	0	5	0.05	4	0.025	0	0	0	0	0	0	0	0	0.2	14	0.375
B	2	a	11	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.15	11	0.1
B	2	a	9	0.1	0	0	0	0	0	0	0	0	2	0.025	0	0	0	0	0	0	0	0	0	0	0.025	11	0.125

Table A21 (cont'd.)

												Group II - 0800 h														
B	1	1	0	0	5	0.025	0	0	0	0	5	0.1	0	0	3	0.4	0	0	0	0	0	0	0	0	0	13	0.525
B	1	2	30	0.25	11	0.025	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.25	41	0.525
B	1	3	19	0.15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.05	0	0	0.25	20	0.45
B	1	4	23	0.35	1	+	0	0	0	0	1	0.025	0	0	0	0	0	0	0	0	0	0	0	0	0	25	0.383
B	2	1	3	0.025	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	4	0.133
B	2	2	3	0.025	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.05	3	0.075
B	2	3	53	0.55	13	0.025	0	0	2	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.45	68	1.125
B	2	4	20	0.15	3	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.45	23	0.608
												Group II - 2000 h														
A	1	1	0	0	0	0	0	0	0	0	6	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	b	0.1
A	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A	1	3	22	0.125	0	0	0	0	0	0	0	0	1	0.025	0	0	0	0	0	0	3	0.2	0	0	0	19	0.375
A	1	4	18	0.15	0	0	0	0	0	0	0	0	1	0.025	0	0	0	0	0	0	0	0	0	0	0.2	26	0.35
A	2	1	0	0	100	0.15	1	+	0	0	0	0	0	0	3	0.1	0	0	0	0	0	0	0	0	0.05	104	0.308
A	2	2	0	0	110	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	110	0.2
A	2	3	12	0.1	125	0.25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.05	0	0	0.25	138	0.65
A	2	4	29	0.2	110	0.2	0	0	0	0	0	0	2	0.025	2	0.05	0	0	0	0	1	+	0	0	0	144	0.583

Table A21 (cont'd.)

Group III - 0800 h																											
A	1	1	1	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.3	0	3	0.308
A	1	2	8	0.05	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	+	7	0.225	1	0.15	0.35	18	0.983
A	1	3	60	0.55	0	0	1	+	0	0	0	0	0	0	0	0	0	0	13	0.1	7	0.3	0	0	0.2	80	1.15
A	1	4	21	0.225	0	0	1	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	22	0.333
Group III - 2000 h																											
A	2		2	0.025	1	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.333
B	2	1	0	0	0	0	1	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.55	3	0.567
B	2[b]	2	2	+	0	0	1	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

[a] Social rank could not be determined.

[b] Injured.

[c] Number of miscellaneous items could not be determined.

[+] Not measurable, but assumed to equal 0.0083 cc.

Table A22. - Mean percent of observation session time spent feeding by each social rank during morning, midday, and evening in replicates with 4 trout. This includes time spent feeding from cover.

	Morning				Midday				Evening					
	Rank				Rank				Rank				Replicate	
Replicate	1	2	3	4	1	2	3	4	1	2	3	4	Mean	SD
IA2	22.5	54.74	50.0	34.89	0	25.69	24.76	60.85	0	34.26	80.14	69.69	38.13	25.59
IIA1	11.11	a	41.22	45.68	0	a	21.23	14.29	16.67	a	33.33	43.14	25.2	16.22
IIA2	63.8	86.61	76.15	47.75	14.29	13.91	76.47	56.91	40.0	20.0	55.88	45.84	49.8	24.49
IIB1	71.55	31.67	47.77	88.19	0	14.29	39.09	43.44	0	0	44.44	41.67	35.18	28.06
IIB2	7.04	29.35	25.58	48.2	0	0	0	0	0	0	60.0	20.0	15.85	21.05
IIIA1	4.56	50.47	52.17	a	13.24	48.61	18.3	a	6.88	40.0	35.97	a	30.02	19.34

Rank	Mean	SD	Time of day	Mean	SD
1	15.09	21.82	Morning	45.05	23.4
2	29.97	23.94	Midday	22.06	22.78
3	43.47	21.61	Evening	32.98	23.97
4	44.04	21.69			

[a]Abnormal behavior.

Table A23. - Mean percent of observation session movement devoted to feeding by each social rank during morning, midday, and evening in replicates with 4 trout. This includes movement associated with feeding from cover.

	Morning				Midday				Evening					
	Rank				Rank				Rank				Replicate	
Replicate	1	2	3	4	1	2	3	4	1	2	3	4	Mean	SD
IA2	83.78	46.88	66.67	43.61	0	24.71	35.67	70.5	0	75.0	51.13	64.93	51.17	24.63
IIA1	16.67	a	52.28	52.99	0	a	59.38		100.0	a	100.0	100.0	60.16	38.52
IIA2	78.59	59.29	67.27	56.26	25.0	22.73	77.04	76.25	40.0	20.0	74.71	79.12	56.36	23.36
IIB1	54.95	36.09	36.23	63.62	0	100.0	52.73	88.57	0	0	86.67	70.7	65.51	22.90
IIB2	21.13	58.45	65.47	43.89	0	0	0	0	0	0	100.0	100.0	64.82	31.19
IIIA1	21.56	48.64	56.22	a	23.59	39.72	23.46	a	25.0	100.0	60.21	a	44.27	25.72

	Rank			Time of day	
	Mean	SD		Mean	SD
1	37.71	32.04	Morning	51.39	17.48
2	52.63	27.46	Midday	44.96	30.81
3	62.66	21.1	Evening	73.38	26.83
4	70.03	18.69			

[a] Abnormal behavior.

Table A24. - Mean rate of movement (cm/s) associated with feeding by each social rank during morning, midday, and evening in replicates with 4 trout. This includes movement associated with feeding from cover.

	Morning				Midday				Evening					
	Rank				Rank				Rank				Replicate	
Replicate	1	2	3	4	1	2	3	4	1	2	3	4	Mean	SD
IA2	0.84	0.2	0.08	0.58	0	0.72	0.27	0.85	0	0.1	0.67	0.65	0.5	0.3
IIA1	0.15	a	0.42	1.0	0	a	0.37	0	0.08	a	2.32	0.53	0.62	0.77
IIA2	0.97	0.89	1.15	1.32	0.43	0.08	0.25	0.22	0.5	0.37	0.45	0.58	0.6	0.39
IIB1	0.65	1.79	1.24	0.73	0	0.33	0.15	0.45	0	0	0.92	0.58	0.76	0.5
IIB2	1.75	3.46	1.57	5.26	0	0	0	0	0	0	1.0	0.03	2.18	1.88
IIIA1	1.32	0.68	1.39	a	0.48	0.73	0.9	a	1.22	0.33	0.6	a	0.85	0.38

Rank			Time of day		
	Mean	SD		Mean	SD
1	0.76	0.51	Morning	1.25	1.15
1	0.81	0.96	Midday	0.41	0.28
2	0.81	0.59	Evening	0.64	0.54
3	0.92	1.3			

[a]Abnormal behavior.

Table A25. - Mean distance (m) to the nearest wall from feeding stations used by each social rank during morning, midday, and evening in replicates with 4 trout. Distance weighted by percent of total feeding time at each station. Cover feeding stations are not included.

	Morning				Midday				Evening					
	Rank				Rank				Rank				Replicate	
Replicate	1	2	3	4	1	2	3	4	1	2	3	4	Mean	SD
IA2	0.38	0.57	0.57	1.05	0	0.57	0	0.57	0	0.57	0.8	0.69	0.64	0.19
IIA1	0	a	0	1.86	0	a	0	1.13	0	a	1.32	1.82	1.53	0.37
IIA2	0.59	0.56	0.66	0.65	0	0.57	0.6	0	0.57	0.57	0.78	0.57	0.61	0.07
IIB1	0.39	0.66	0.77	1.16	0	0	1.59	1.1	0	0	0.9	0.57	0.89	0.38
IIB2	0.57	0.27	0.62	0.99	0	0	0	0	0	0	0.57	1.13	0.69	0.31
IIIA1	0.57	0.44	1.5	a	0.41	0.41	1.89	a	1.13	1.13	1.5	a	1.0	0.56

Rank	Mean	SD	Time of day	Mean	SD
1	0.58	0.24	Morning	0.74	0.39
2	0.57	0.21	Midday	0.88	0.52
3	1.0	0.45	Evening	0.91	0.39
4	1.02	0.43			

[a] Abnormal behavior.

Table A26. - Schedule of artificial feeding and response of large trout in replicate IIIA1 to grasshoppers. Positions that grasshoppers landed in the channel are indicated by coordinates (longitude, latitude, see Appendix Figure B3).

Date	Time (h EDT)	Position grasshopper landed	Response of large trout
8/22	0835	1.5, 7	
	0836	2 , 7	None. Both large trout under unknown cover.
	0839	2 , 7	
	0945	2 , 12	Rank 1 under large cover (1.5, 5), none. Rank 2 moved from feeding station at 3.75, 1 to eat grasshopper at 2, 1.
	0946	2 , 12	Rank 1 moved from large cover to eat grasshopper at 2, 10, then moved to feeding station in shade at 3.5, 6 for two minutes, followed by return to large cover. Rank 2 under unknown cover - none.
	0959	3.5, 8	Rank 1 under known cover, none. Rank 2 feeding at 3.5, 6, ate grasshopper there.
	1006	2 , 7	Rank 1 moved from large cover to eat grasshopper at 2, 5, then moved again to feeding station at 3.5, 6 for one minute before returning to large cover.
	1420	1.5, 7	None. Rank 1 under small cover, rank 2 under large cover.
	1421	1.5, 11	Rank 1 none. Rank 2 moved from large cover to eat grasshopper and immediately returned to cover.
	1426	1.5, 7	None, both trout under covers indicated above.
	1427	2.25,7	Rank 1 moved to edge of small cover but did not eat grasshopper. Rank 2 under large cover, none.
	1428	1.5, 7	
	1432	2.25,7	None. Both large trout under covers indicated above.
	1434	2 , 7	
	1435	2 , 7	

Table A26 (cont'd.)

	1436	2 , 11	Rank 1 under small cover, none. Rank 2 momentarily left large cover to eat grasshopper.
8/23	1000	1.25,7	
	1001	1.5, 7	None. Rank 1 under unknown cover. Rank
	1005	1.75,7	2 under small cover.
	1007	1.25,7	
	1751	1.5, 7	Rank 1 briefly left large cover to inspect grasshopper but did not eat it. Rank 2 under unknown cover.
	1752	1.5, 7	
	1753	1.5, 10	None. Rank 1 under large cover, rank 2
	1754	1.25,13	under unknown cover.
	1800	1.75,8	Rank 1 briefly left large cover to eat grasshopper.
8/24	1557	2.25,7	
	1601	1.75,7	Rank 1 under unknown cover. Rank 2
	1605	2 , 7	feeding at 1.5, 1 ate all 4 grasshoppers.
	1607	1.25,11.5	
	1932	1.75,7.5	Rank 1 under large cover, none. Rank 2 moved from small cover to eat grass-hopper then returned to small cover.
	1934	1.75,7.5	Rank 1 briefly left large cover to eat hopper. Rank 2 under small cover, none.

APPENDIX B

FIGURES

Figure B1. - Location of trout sightings for Group I in test of lateral cover devices. L = low-stripe device, H = high-stripe device. Drawn to scale.

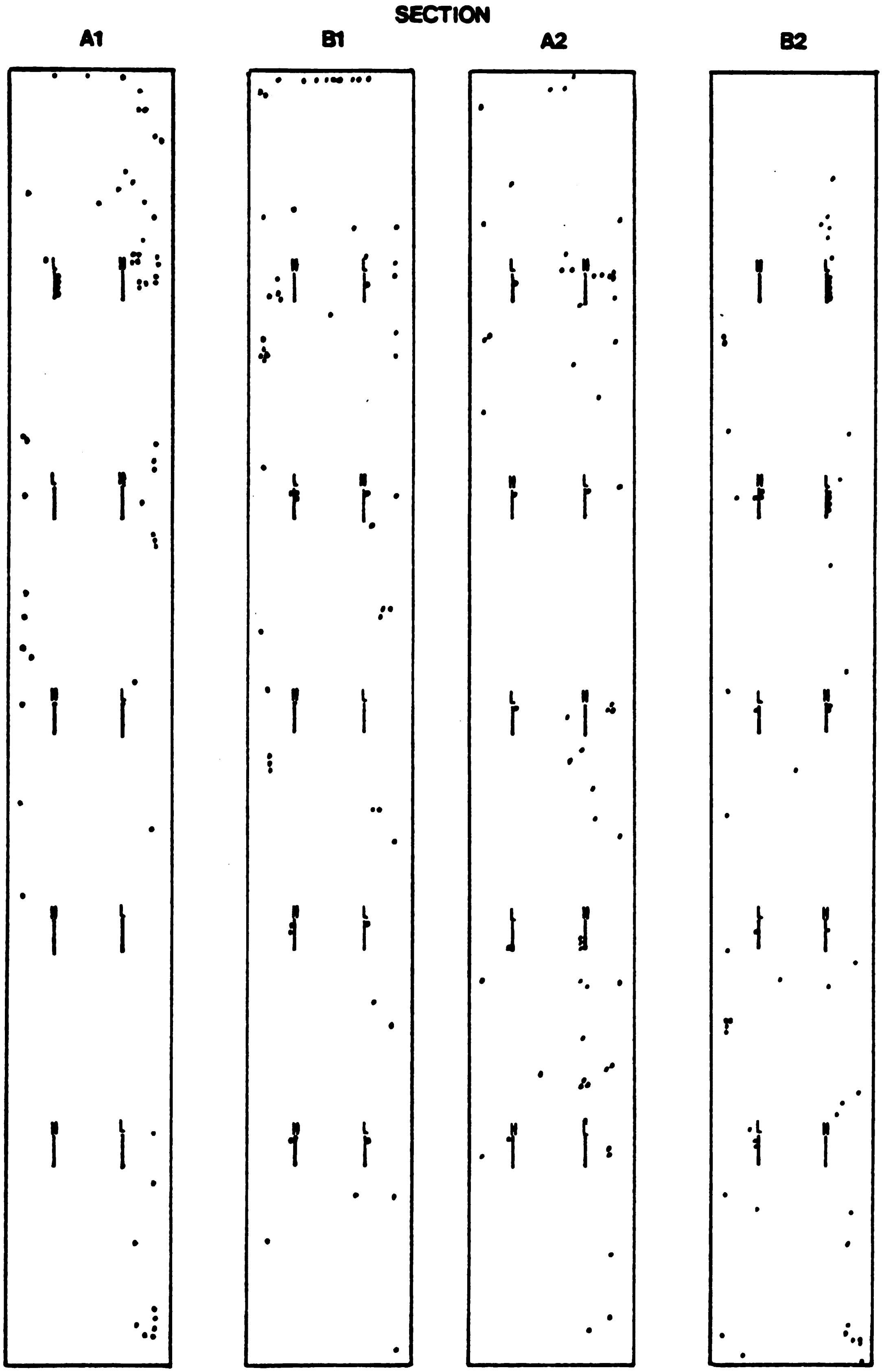


Figure B1

Figure B2. - Location of trout sightings for Group II in test of lateral cover devices. L = low-stripe device, H = high-stripe device. Drawn to scale.

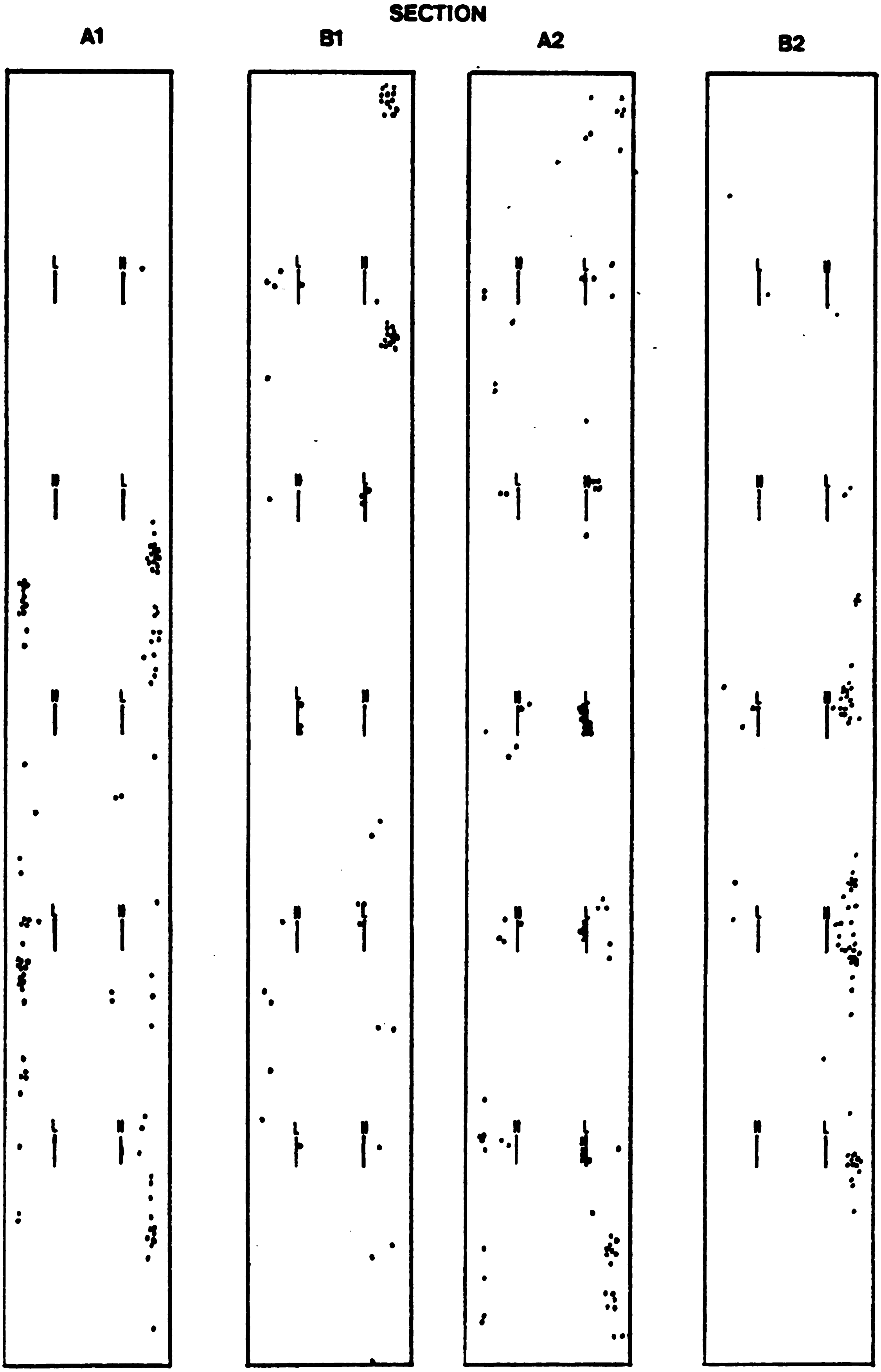


Figure B2

Figure B3. - Depth (cm) and current velocity (cm/s) in section A1. Numbers along the horizontal and vertical axes refer to coordinates used to identify trout positions. Distance between numbers on the vertical axis is 1 m. Mean depth-21.1 cm, mean velocity-21.9 cm/s. Velocity was measured 5 cm above the stream bed.

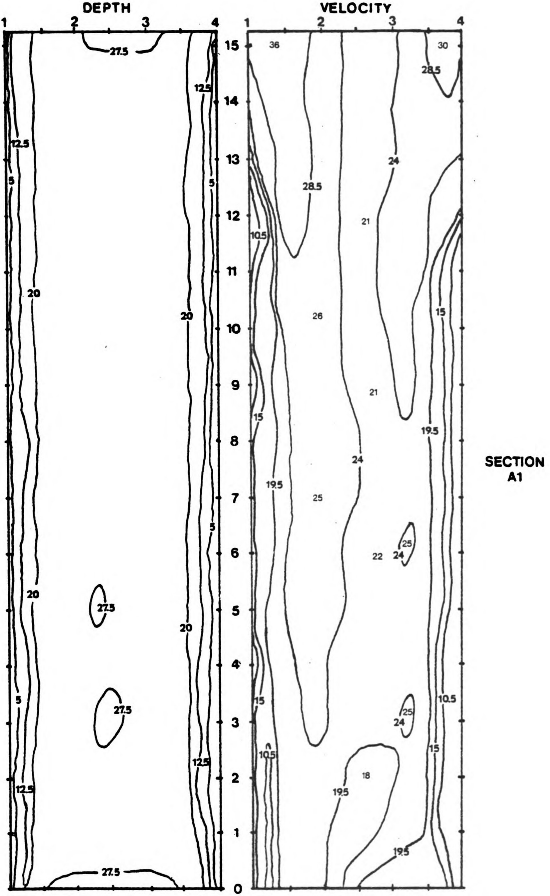

DEPTH
VELOCITY
1
2
3
4
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
27.5
12.5
5
20
36
30
28.5
24
21
10.5
26
15
19.5
25
22
18
SECTION
A1

Figure B3

Figure B4. - Depth (cm) and current velocity (cm/s) in section A2. Numbers along horizontal and vertical axes refer to coordinates used to identify trout positions. Distance between numbers on the vertical axis is 1 m. Mean depth-23.5 cm, mean velocity-20.7 cm/s. Velocity was measured 5 cm above the stream bed.

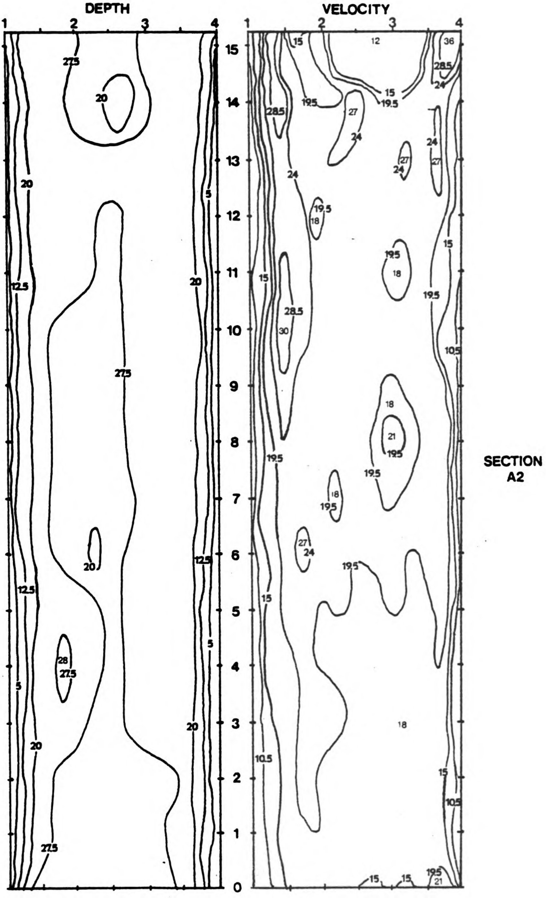


Figure B4

Figure B5. - Depth (cm) and current velocity (cm/s) in section B1. Numbers along the horizontal and vertical axes refer to coordinates used to identify trout positions. Distance between numbers on the vertical axis is 1 m. Mean depth-19.2 cm, mean velocity-21.6 cm/s. Velocity was measured 5 cm above the stream bed.

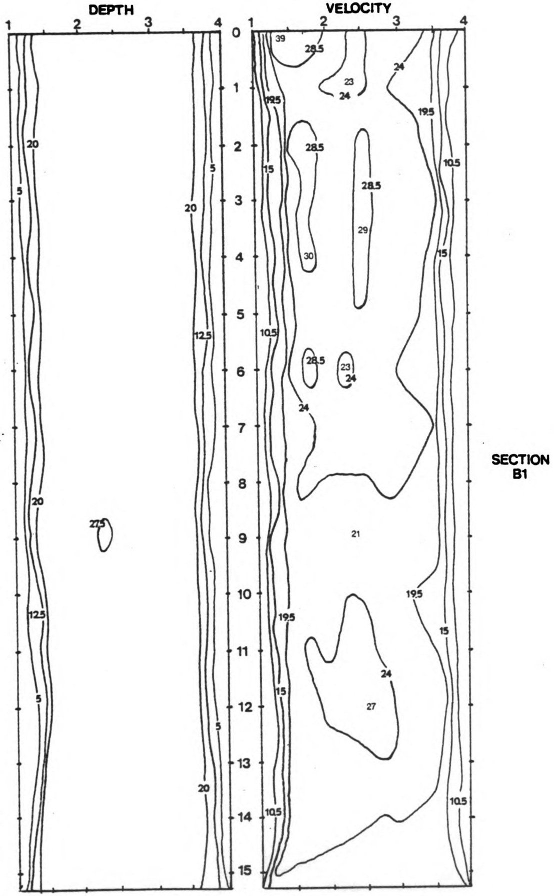
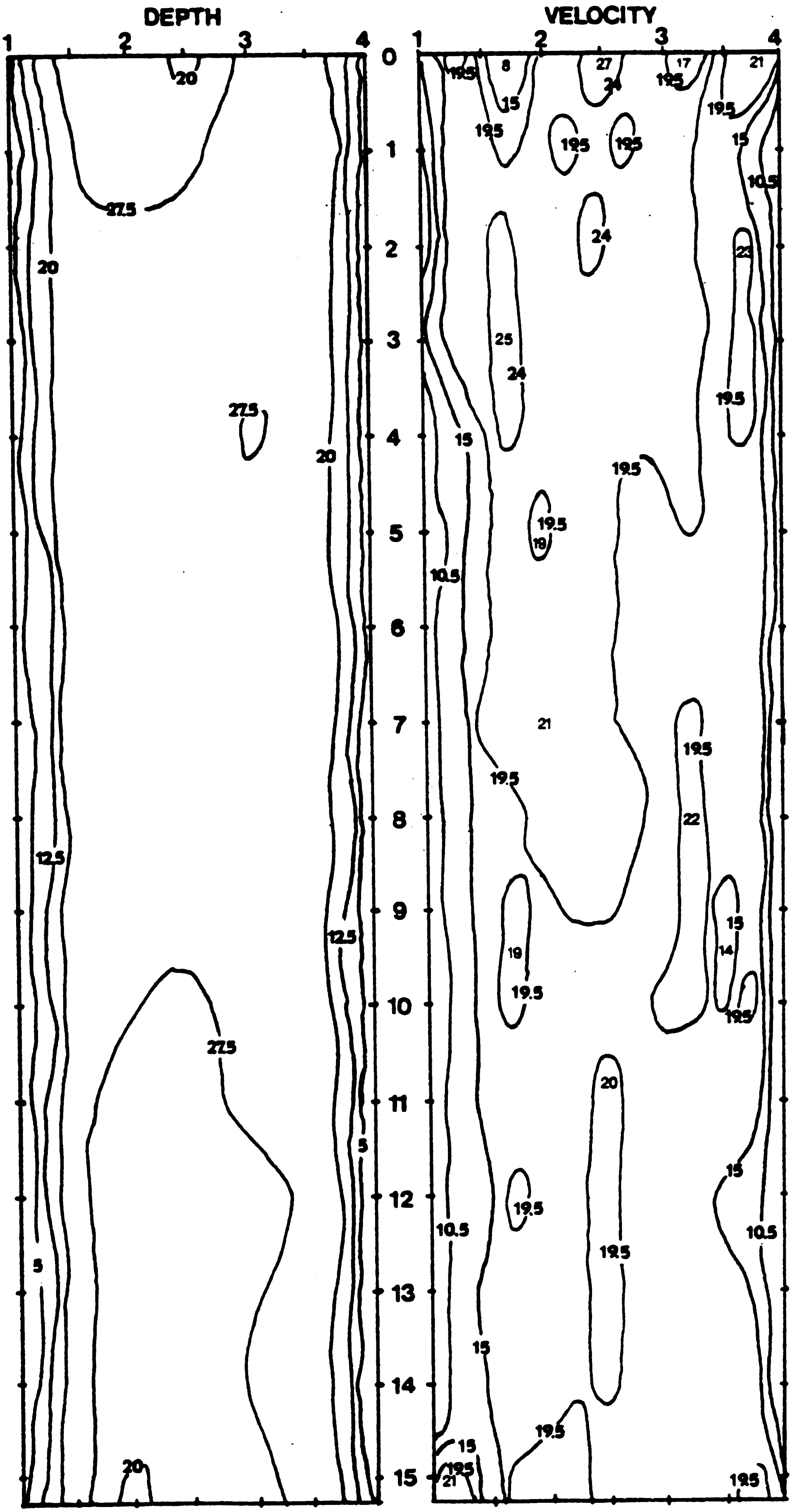


Figure B5

Figure B6. - Depth (cm) and current velocity (cm/s) in section B2. Numbers along the horizontal and vertical axes refer to coordinates used to identify trout positions. Distance between numbers on the vertical axis is 1 m. Mean depth-22.6 cm, mean velocity-17.4 cm/s. Velocity was measured 5 cm above the stream bed.



SECTION
B2

Figure B6