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Title: PRODUCTION AND BEHAVIORAL INTERACTIONS OF SALMONIDS IN AN EXPERIMENTAL STREAM

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The behavior of two species of stream salmonids, juvenile coho salmon, Oncorhynchus kisutch (Walbaum) and cutthroat trout, Salmo clarki clarki Richardson, was studied in terms of the time spent by individual fish in carrying out various activities. Studies were conducted from June 1968, through May 1969, at Berry Creek, a small woodland stream located approximately ten miles north of Corvallis, Oregon. A 1500 foot section of the stream was brought under complete flow control for experimental purposes by a concrete diversion dam and a bypass channel. Water flow into the experimental section was controlled by a large gate valve at the dam. The lower part of the controlled section was divided into experimental sections that were separated by inclined-screen fish traps. The Berry Creek Experimental Stream Laboratory is maintained as a field research station by the Department of Fisheries and Wildlife, Oregon State University.

Behavioral observations were made from an observation booth located in an experimental section of Berry Creek. Time-budget analyses derived from observational data were used to evaluate the effects on production of the interaction between individual salmon stocked at different densities in separate stream sections and the interaction among populations comprising both species stocked separately and together at similar densities in different sections of the stream.

The growth rates of juvenile coho salmon stocked during June and July 1968, at different biomasses in five of the experimental sections generally declined with increases of salmon biomass. Downstream movement and mean percentages of time spent in agonistic behavior by individual salmon increased with increases in biomass.

Higher values of production and mean biomass were generally recorded for an experimental group comprising salmon and trout than for single species groups. Several of the trout on occasion occupied the riffle area of the observation section, whereas, coho salmon remained in the pool throughout the experiment. The use of the riffle area by the trout may have resulted in more efficient utilization of space and food and may explain, in part, the differences in production between the trout-salmon group and the single species group.

The growth and location in the stream section of an individual trout or salmon appeared to depend on the fish's position in the integrated social structure. Fish of high social position benefitted in terms of increased amounts of feeding time, decreased activity and decreased agonistic behavior as compared with fish of lower social position.

The effect of intraspecific interaction among salmon appeared to be greatest at those stocking densities which resulted in a decline of growth rate from the growth rates that were associated with the highest values of production. This interaction appeared to lead to a compromise between energy expenditures for agonistic behavior and efficient metabolism that resulted in stock densities between two and three grams/meter^2 of section area.

Production and Behavioral Interactions of Salmonids in an Experimental Stream

by

John Demaris McIntyre

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PRODUCTION AND BEHAVIORAL INTERACTIONS OF SALMONIDS IN AN EXPERIMENTAL STREAM

INTRODUCTION

This study concerns the influence of the behavioral interactions of stream dwelling salmonids on their production. The work was done at the Berry Creek Experimental Stream Laboratory, a field research station maintained by the Department of Fisheries and Wildlife, Oregon State University, from June 1968 through May 1969.

The production process has been defined as, "The total elaboration of new body substance in a stock in a unit of time, irrespective of whether or not it survives to the end of that time" (Ricker, 1958). Values of production are based upon measurement of the growth rate and the biomass of the stock. An understanding of the factors that influence growth and biomass is essential for rational management of valuable fish populations.

Many factors in the biological and physical environment of a fish create demands on the energy that it can obtain from its food. Growth occurs only when food energy is obtained in excess of these demands. Laboratory studies have provided useful information on the growth and bioenergetic relations of fish (Warren and Davis, 1967) but, there is a paucity of information on the kinds and levels of activity that fish must carry on in nature. It is known that various kinds of agonistic activities characterize salmonid behavior (Kalleberg, 1958; Chapman, 1962; Newman, 1956; and Hartman, 1965), however, little is known of the manner in which agonistic, feeding and other kinds of activities are related to the biomass of the stock, its growth and production.

Methods are not yet available for measuring in energy terms the various behavioral costs of fish in nature. In the experiments reported herein the behavior of two species of stream salmonids, juvenile coho salmon, Oncorhynchus kisutch (Walbaum) and cutthroat trout, Salmo clarki clarki Richardson, was studied in terms of the time spent by individual fish in carrying out various activities. Behavioral observations were made with an underwater observation facility located in one of the sections of the Berry Creek experimental stream. These observations provided a means of interpreting the effects of behavior on the production relationships of salmonids stocked under different experimental conditions in other sections of the stream. Time-budget analyses derived from observational data were used to evaluate the effects on production of the interaction between individual salmon stocked at different densities. These analyses were also used for comparisons of the effects on production of the interaction among populations comprising both species stocked separately and together at similar densities in different sections of the stream.

The use of time-budget analyses in studies of the behavior of the salmon and trout provides a basis for future studies of the energy relations of fish in nature. The utility of time-budget analyses has been demonstrated for two bird species (Orians, 1961).

METHODS AND MATERIALS

Experimental Facilities

Berry Creek is a small woodland stream located approximately ten miles north of Corvallis, Oregon. A 1500 foot section of the stream was brought under complete flow control for experimental purposes by a concrete diversion dam and a bypass channel. Water flow into the experimental section was controlled by a large regulating valve at the dam. The physical, chemical and general biological characteristics have been described in detail by Warren et al. (1964) and only a brief description of the facilities will be given here.

The lower part of the controlled section was divided into nine experimental sections which were numbered 0 through VIII proceeding downstream. Sections 0, I, IV, V and VI were used in this study (Table 1). Each section was separated from adjoining sections by inclined-screen fish traps constructed of eighth-inch mesh hardware cloth. The traps prevented upstream movement of the fish and provided for the collection in small live-boxes of fish that moved downstream.

Other facilities included two laboratory trailers and a large observation booth placed along one side of the stream in section 0 for studies of fish behavior. The booth (Figure 1), which was

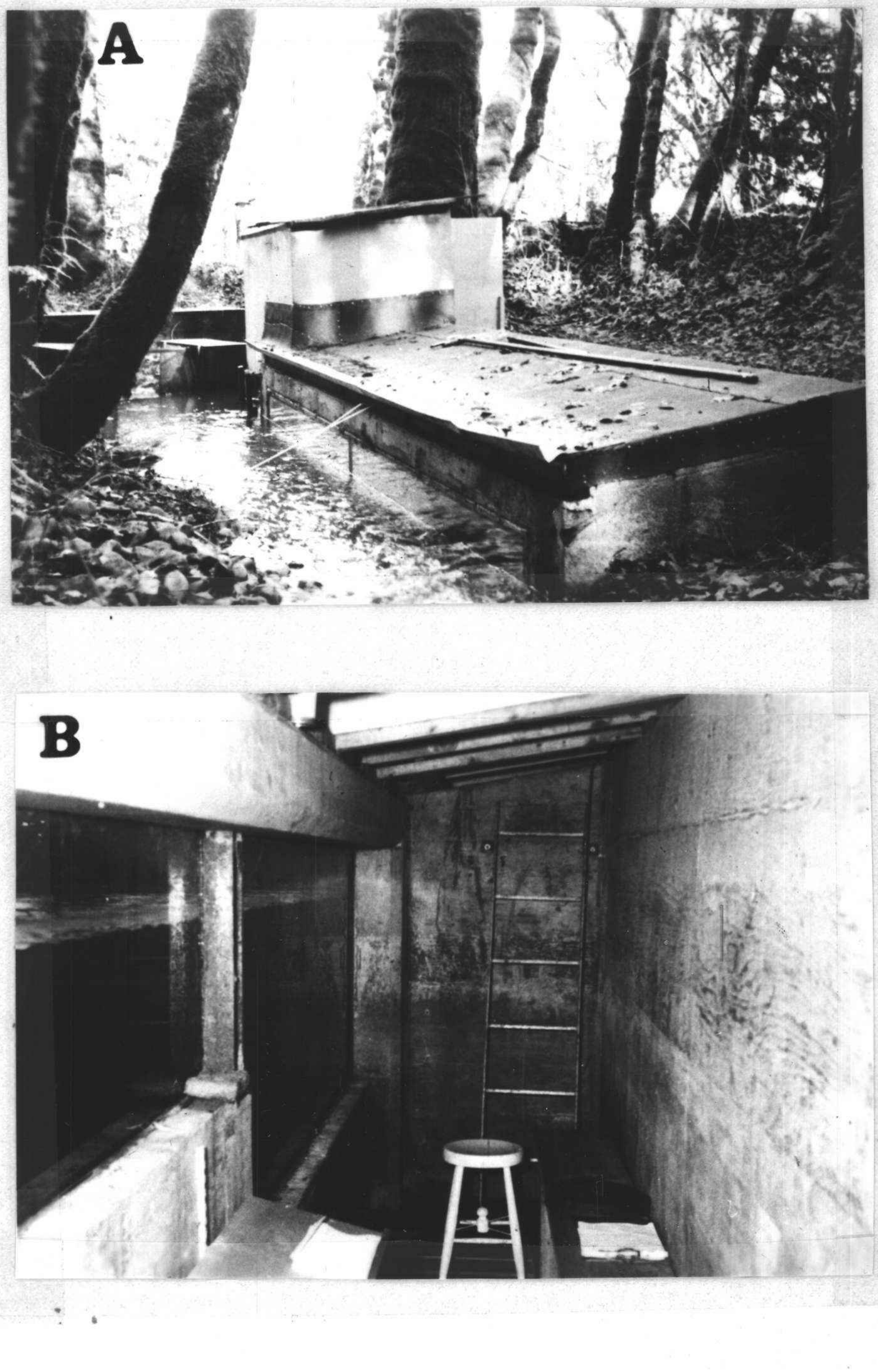

Figure 1. The observation booth in section 0 of Berry Creek; (A) exterior, and (B) interior.

constructed of steel reinforced concrete, is approximately 17 feet long, four feet wide and has two one-half inch laminated-glass windows that permit observation of eight feet of riffle and eight feet of pool along the streambed.

Table 1. Riffle, pool and total section areas, in square meters, for the experimental sections of Berry Creek used in this study, measured at a stream flow of approximately 1.8 cubic feet per second.

Section	Riffle	Pool	Total
0 (Observation section)	26.26	5.59	31.85
I	29.93	39.77	69.70
IV	41.81	44.94	86.75
V	25.42	41.79	67.21
VI	40.81	47.24	88.05

Stream flow (Figure 2) was recorded at a V-notch weir located at the downstream end of the study section. Stream temperatures were obtained with a maximum-minimum thermometer (Figure 3).

Experimental Fishes

The native cutthroat trout and juvenile coho salmon were seined as needed from Berry Creek or other nearby streams. Wet weights were obtained before they were stocked in experimental sections. Those placed in the observation section were usually tagged with color-coded vinyl pennant tags (3/16 by 3/32 inch). Tags were attached with a solid vinyl thread (diameter 0.019 inch) which was

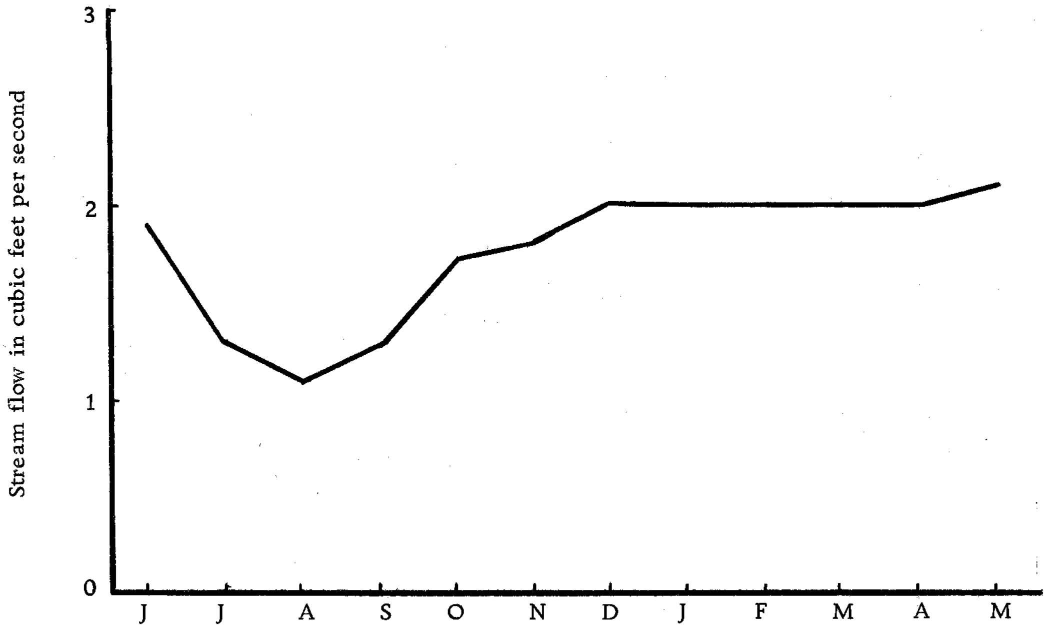

Figure 2. Monthly mean stream flows in the controlled section of Berry Creek from June 1968 through May 1969.

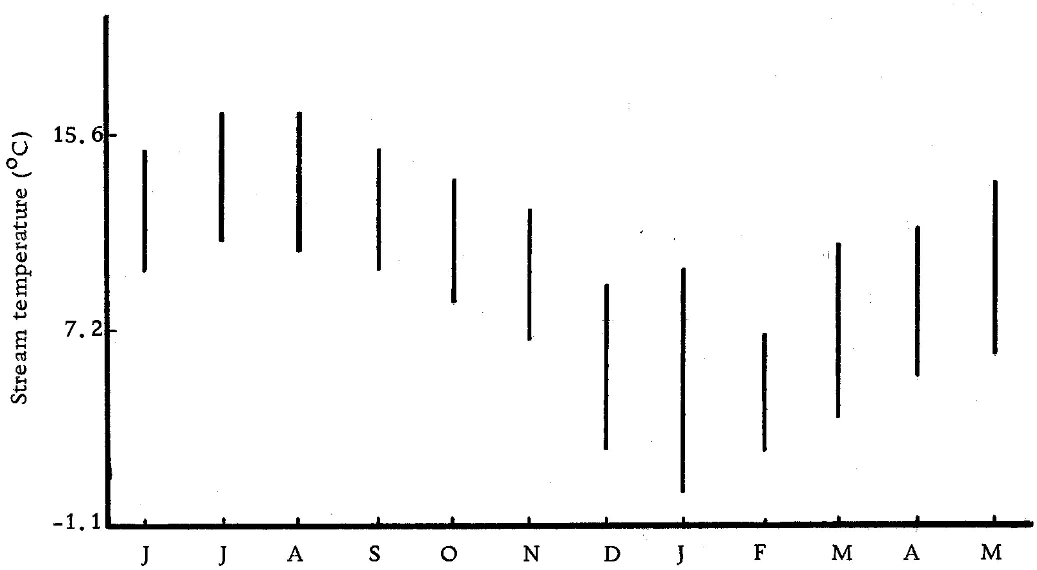

Figure 3. Monthly maximum and minimum stream temperatures in the controlled section of Berry Creek from June 1968 to May 1969.

inserted with a needle through the dorsal surface between the pterygiophores and the ends were then tied together. Pyle (1965) found no influence of similar tags on the growth of trout. During the present study it was periodically necessary to remove algae that grew on the tags and thread. The accumulation of algae on the tags resulted in the occasional loss of a tag.

At approximately monthly intervals the fish were seined from the stream sections for weighing. To facilitate handling, each fish was anesthetized with MS-222 (tricaine methane-sulfonate). Upon recovery from the narcotic, the fish were returned to their respective stream sections.

Changes in wet weights during a sampling interval were used to compute growth rates. The initial and terminal weights were used to estimate the mean biomass present in a section during a given sampling interval. The values of growth rate and mean biomass were used to compute production of the fish. In some experiments, production was estimated graphically based upon measurements of the numbers of fish and their mean individual weights according to the method described by Allen (1951). With the use of this method production is equivalent to the area under a curve relating mean individual weights of fish and numbers of survivors on any sampling date.

Behavior

Preliminary observations of trout or salmon in the observation section indicated that the fish usually maintained a relatively constant station in the stream. From these stations, most movements by a fish tended to be directed toward a food item or to be agonistic movements. These movements were generally followed by an immediate return by the fish to its original station. Other kinds of movements included a complete change of station which often resulted from an aggressive attack by a dominant fish. These characteristic types of movements were used as the basis for estimating the amounts of time expended by experimental fish in various kinds of activities.

Feeding movements were identified according to the location in the stream section in which the food item was encountered by the fish. The categories "drift-feeding," "surface-feeding" and "bottom-feeding" included the ingestion of any food item in suspension in the current, on the stream surface and on the bottom substrate, respectively. "Incomplete-feeding" included any apparent feeding movement toward an object which was not taken into the mouth. "Random-feeding" included general swimming activity which appeared to be associated with feeding. The latter was usually associated with small, subordinate fish that were unable to maintain a station because of their apparently low status in the social structure of the experimental population.

Agonistic movements were classified to four general categories: "chase," "flee," "threat," and "combination agonistic." The latter included any combination of agonistic movement that could not be readily separated into one of the other categories of agonistic behavior. Two other categories, "random-swimming" and "position-swimming," were used to classify, respectively, swimming movements not associated with feeding or agonistic behavior and swimming movements associated with the maintenance of a station in the current. Movements were not recorded until a fish actually left its station.

The time spent in various movements described above were recorded on magnetic tape with a portable recorder. When a fish under observation began to move, the voice command "start" was recorded and when the fish returned to its original position or a new position the voice command "stop" was recorded followed by identification of the specific movement category, such as "drift." The total time during which a particular fish was observed was measured with a stop-watch. The tape-recording for each observation period was later replayed and the elapsed time for each movement was measured with a stop-watch and recorded on prepared data sheets. These data were the basis of the time-budgets calculated for the experimental groups of fish. The total activity of the fish was divided into two general categories for time-budget analyses. "Activity" was used to represent the amount of time that fish spent in feeding movements, agonistic movements and random swimming movements. "Position-swimming" was used to represent the amount of time the fish spent "swimming in place" at a station in the stream.

This classification of behavior permitted examination of the influence of intraspecific and interspecific interaction on fish behavior and the relationship of behavior to growth.

Intraspecific Interaction

Studies were carried out to examine the influence of stocking density on fish growth and behavior. Different biomasses of juvenile coho salmon were stocked in five of the sections (Table 2) during a 25 day experiment in June and July, 1968. The weights of any salmon that moved from the sections and were collected in the downstream traps within the first three days of each experiment were subtracted from the initial biomass values. At the end of the experimental period, the salmon were seined from the stream sections and their weights were recorded for calculation of growth rates and mean biomass.

Time-budgets were calculated in studies of changes in the behavior of young coho associated with different stocking densities. Three separate groups of coho salmon, each having a different biomass, were stocked in the observation section during a 21-day period in August 1968 (Table 3). The fish in each group were held in the observation section for seven days before they were removed and weighed. The amounts of time spent in various activities was recorded during the last three days of each period. An attempt was made at each observation period to observe all of the salmon in the section. Separate observations were recorded for fish in the pool and on the riffle. All observations were made between 12 and 4 PM.

Table 2. Biomasses and mean weights of juvenile coho salmon stocked in experimental sections of Berry Creek in June 1968.

Section	0	I	IV	V	VI
Number stocked	67	142	106	158	49
Number after three days	38	102	86	148	45
Mean weight (grams)	2.13	1.53	1.86	1.85	2.02
Biomass (g/m^2)	2.54	2.24	1.84	4.40	1.03

Table 3. Numbers, mean weights and biomasses of three groups of salmon stocked in the observation section of Berry Creek for seven-day periods in August 1968.

Stocking date	14 Aug	21 Aug	23 Aug
Numbers stocked	11	23	39
Mean weight (grams)	3.18	2.72	3.33
Biomass (g/m^2)	1.05	1.88	3.90

Interspecific Interaction

Growth of three groups of salmon and trout was studied from September 1968 through May 1969. Forty-six coho salmon and 28 cutthroat trout were stocked in sections I and V, respectively (Table 4). A combined group of 54 coho salmon and 29 cutthroat trout was stocked in Section IV (Table 4). In a concurrent study, time-budget analyses were used to study the behavior of a group of six coho salmon (S1-S6) and six trout (T1-T6) in the observation section (Table 5).

Table 4. Numbers and mean weights of individual trout and salmon stocked in sections I, IV and V in September 1968.

Section	I		IV		V	
	no.	$\bar{w}$ (grams)	no.	$\bar{w}$ (grams)	no.	$\bar{w}$ (grams)
Salmon	46	4.44	54	4.50		
Trout						
small (0+)			20	4.20	19	3.44
large (I+)			9	15.80	9	16.25

Table 5. Weights of salmon and trout stocked in the observation section of Berry Creek in September 1968.

Salmon		Trout	
fish no.	weight (g)	fish no.	weight (g)
S1	3.75	T1	12.64
S2	4.22	T2	18.85
S3	5.09	T3	2.81
S4	4.75	T4	4.28
S5	4.40	T5	4.25
S6	5.13	T6	3.59

Before fish were stocked in the observation section for this experiment, an eighth-inch mesh hardware cloth screen was positioned across the riffle near the upstream end of the observation booth. Although this screen reduced the riffle area from 26.3 m^2 to 3.1 m^2, it restricted the use of the riffle area by fish to the area in view from the observation booth.

RESULTS AND INTERPRETATION

Intraspecific Interaction

The growth rates of salmon that were stocked at different densities in five experimental sections in June 1968 generally declined with increases of biomass (Figure 4). Coincidentally, the numbers of fish that moved from the sections into the downstream traps tended to increase with increases of salmon biomass, although this relationship was not well established.

Experiments with different biomasses of salmon in the observation section during August 1968, also indicated that downstream movement increased with increases of salmon biomass. At the two lowest biomasses (1.05 and 1.88 g/m^2) no fish moved into the downstream trap. However, at a salmon density of 3.90 g/m^2 eight salmon were recovered from the downstream trap. The numbers of salmon observed in the riffle area of the observation section also increased with increases of salmon biomass. The average numbers of salmon were 2.0, 2.0 and 5.2 at biomasses of 1.05, 1.88 and 3.90 g/m^2, respectively.

The percentages of time spent in activity (feeding, agonistic and random swimming movements) by fish in the pool and on the riffle of the observation section varied with salmon stocking density.

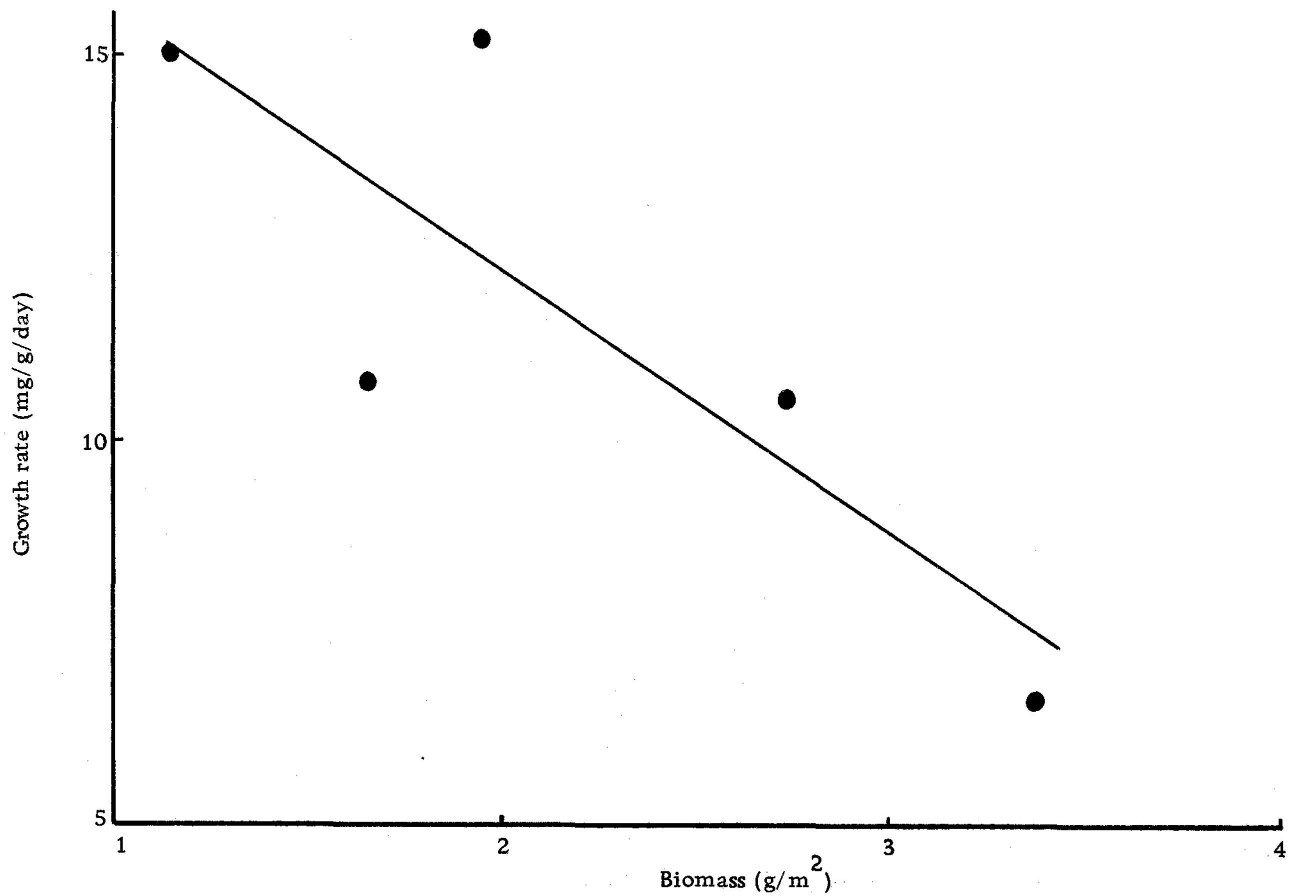

Figure 4. Relationship between salmon growth rate and biomass during June and July 1968.

Activity increased in the pool and decreased on the riffle with increases of salmon biomass (Table 6). The time spent in agonistic behavior by fish in the pool increased with increases of biomass (Table 7). Random swimming generally increased with increases of biomass in both the pool and the riffle. The time spend in feeding by the salmon in both the riffle and pool generally decreased with increases of stocking density.

Table 6. Total time observed and percentages of time spent in activity by three groups of salmon during August 1968.

Biomass (g/m^2)	Total time observed (seconds)		Percentage of time in activity	
	Pool	Riffle	Pool	Riffle
1.05	3253	190	15.9	11.8
1.88	4061	1020	18.0	1.9
3.90	5793	1889	20.7	6.6

Table 7. Percentages of time spent by three groups of salmon in various kinds of activity during August 1968.

Biomass	1.05 g/m^2		1.88 g/m^2		3.90 g/m^2	
Activity	Pool	Riffle	Pool	Riffle	Pool	Riffle
Agonistic						
chase	5.1	-	1.5	-	6.5	9.9
flee	6.1	-	1.3	-	2.1	12.5
threat	2.7	-	11.4	-	4.0	0.0
combination	0.0	-	4.6	-	18.2	0.0
total	13.9	-	18.8	-	30.8	22.4
Feeding						
surface	4.5	9.8	4.2	34.9	5.4	11.0
drift	26.4	58.2	15.4	13.8	8.5	20.3
bottom	0.2	2.7	0.0	4.2	0.4	0.6
incomplete	16.7	29.3	8.6	25.9	13.1	9.5
random	21.3	0.0	42.8	21.2	16.6	0.0
total	69.1	100.0	71.0	100.0	44.0	41.4
Random	17.0	0.0	10.2	0.0	25.2	36.2

Interspecific Interaction

In studies of the interaction between salmon and trout, comparisons were made of the values of production for groups of fish comprising salmon only, salmon and trout combined and trout only. The graphical method of Allen (1951) permits the fitting of smoothed curves to values of survivorship and of mean size plotted against time (A and B, Figures 5 through 10). The area under the production curves (C, Figures 5 through 10) for each group of fish is equivalent to the total production from September 1968 through May 1969, in grams (Table 8).

A "best" estimate was made of the shape of each survivorship curve during the initial sharp decline in numbers on the basis of numbers of fish that entered the downstream trap of each section. This procedure was also used to approximate the shapes of the survivorship curves for the young salmon that moved from sections I and IV (Figures 5 and 6) during April and May 1969. Estimates of salmon mean biomass during the period 7 April through 20 May were not included in Table 8 because of the rapid decrease in numbers of these fish in this period. Comparisons of production and biomass values between experimental groups were, therefore, limited to periods before 7 April 1969. The downstream movement of the salmon during the spring was associated with the seaward migration of this

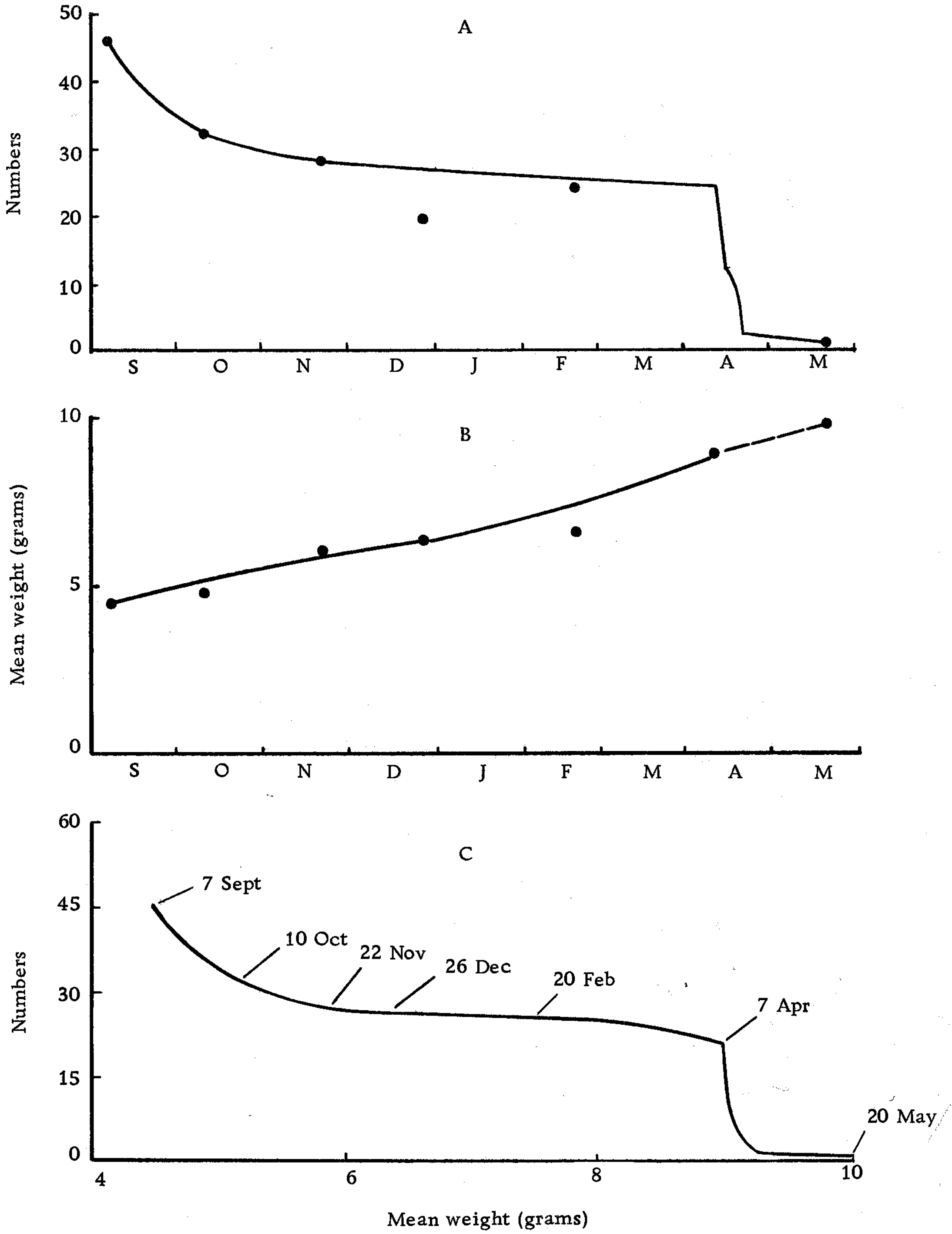

Figure 5. Numbers (A), mean weights (B) and production (C) of salmon in section I from September 1968 through May 1969.

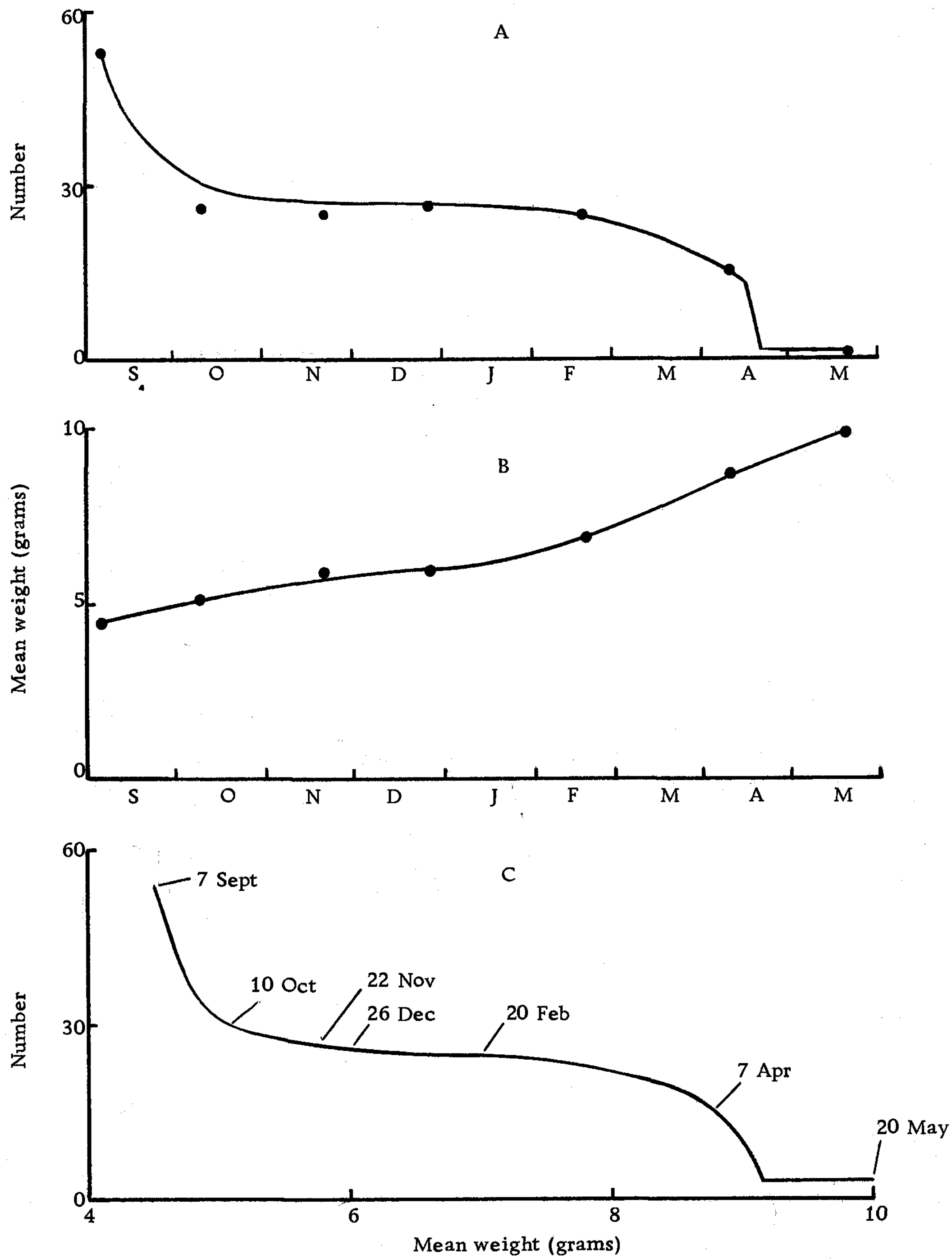

Figure 6. Numbers (A), mean weights (B) and production (C) of salmon in section IV from September 1968 through May 1969.

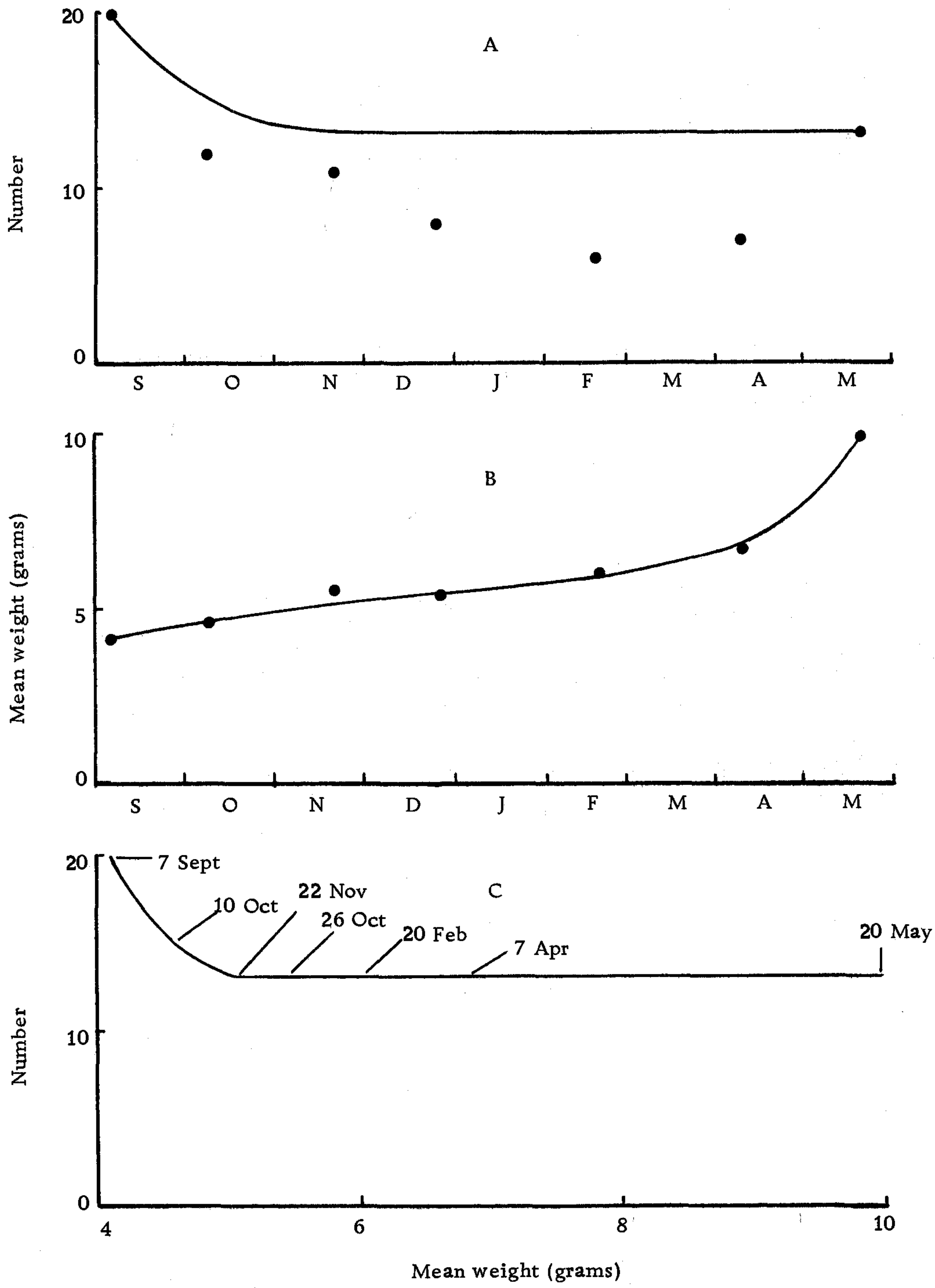

Figure 7. Numbers (A), mean weights (B) and production (C) of small trout (0+) in section IV from September 1968 through May 1969.

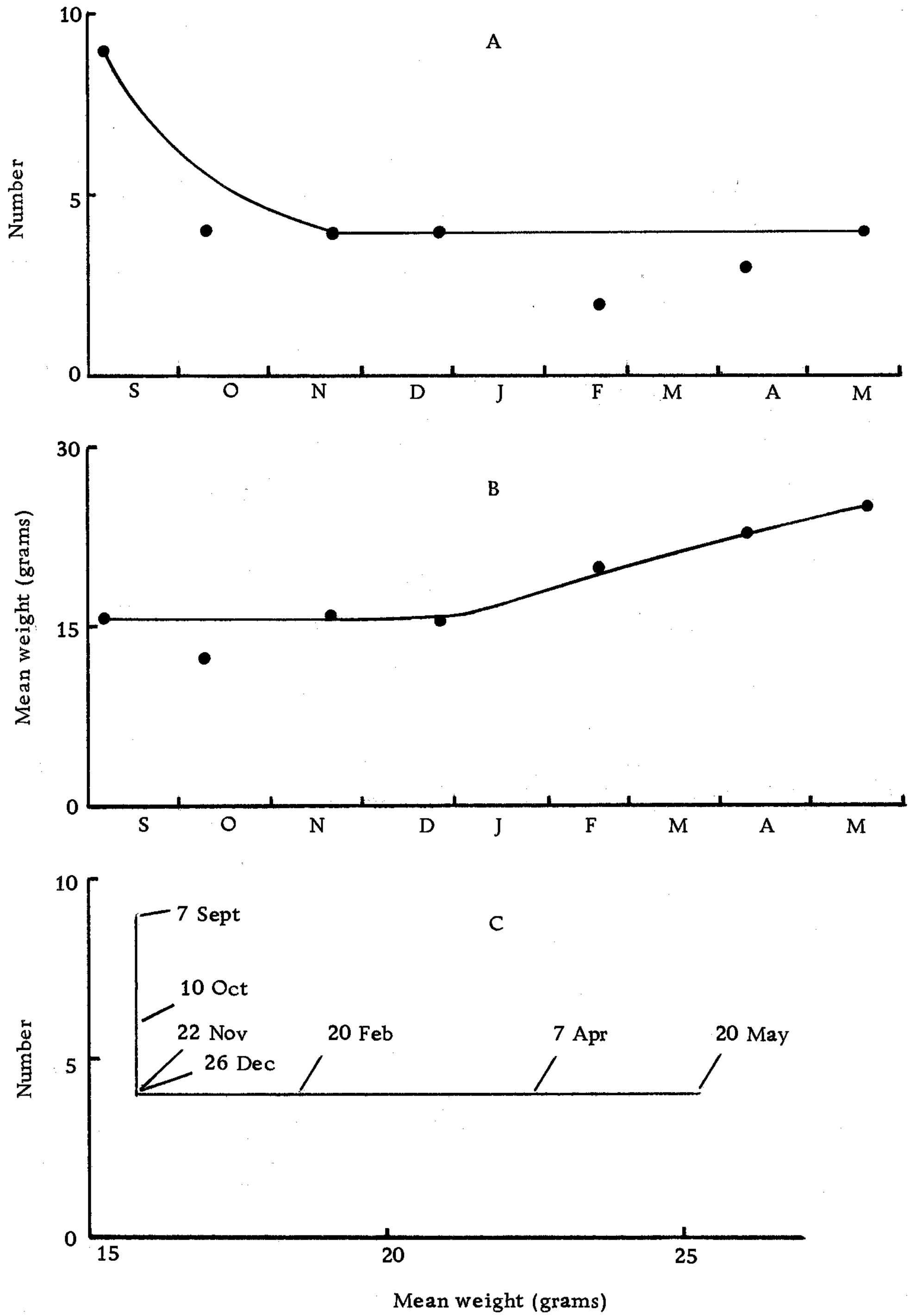

Figure 8. Numbers (A), mean weights (B) and production (C) of large trout (I+) in section IV from September 1968 through May 1969.

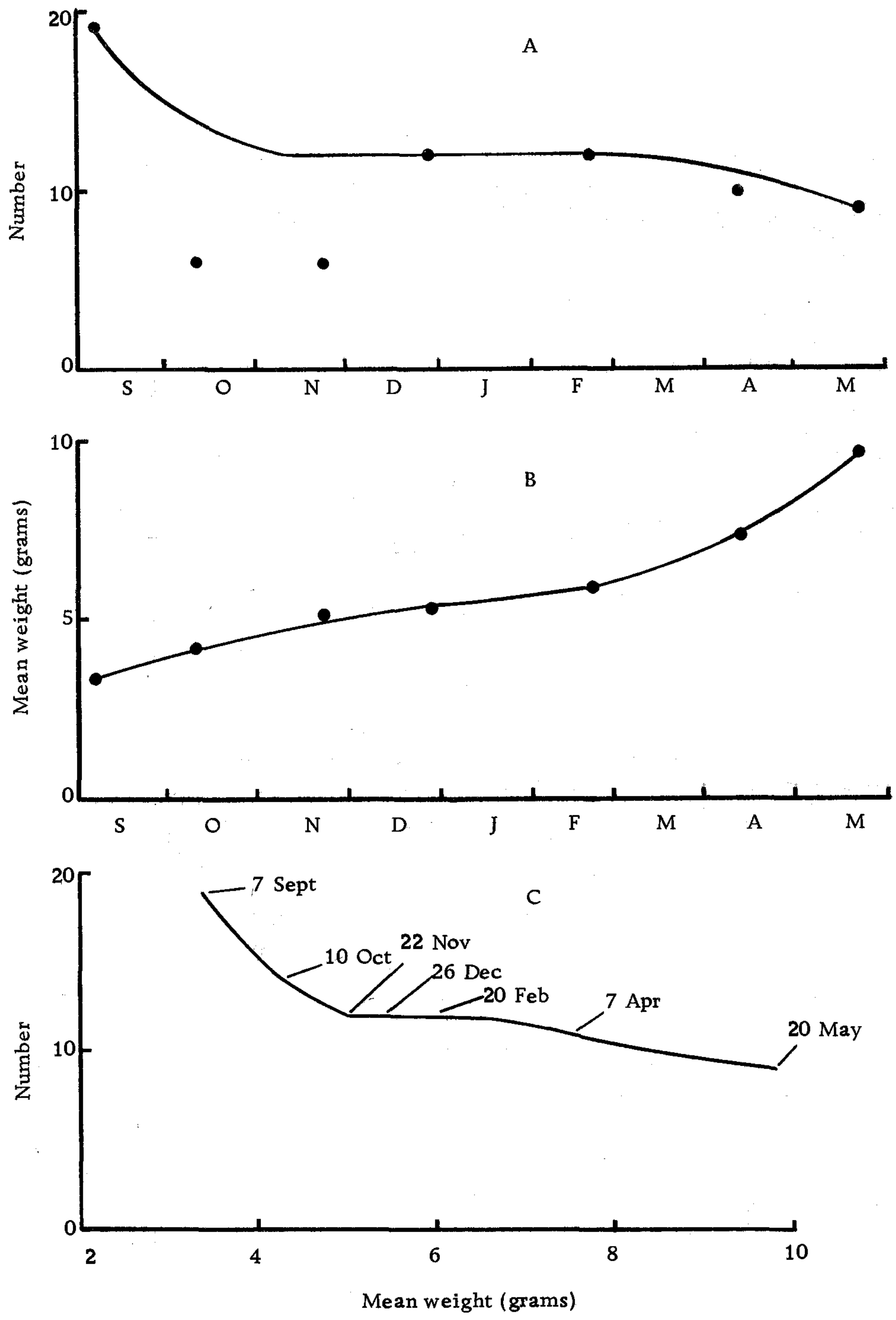

Figure 9. Numbers (A), mean weight (B) and production (C) of small trout (0+) in section V from September 1968 through May 1969.

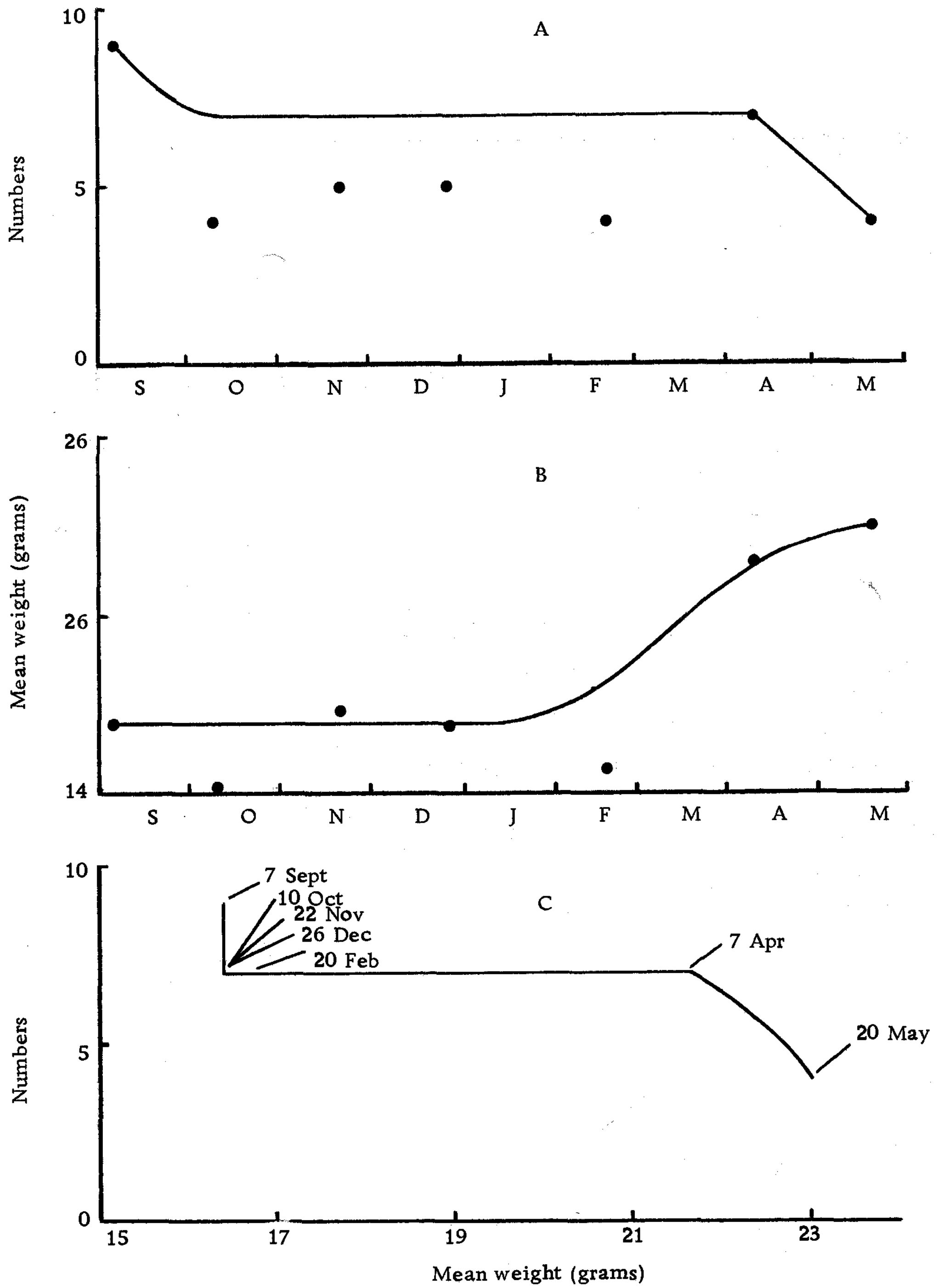

Figure 10. Number (A), mean weight (B) and production (C) of large trout (I+) in section V from September 1968 through May 1969.

Table 8. Values of production and mean biomass of salmon and trout from September 1968 through May 1969.

Section	Species	7 Sept. - 10 Oct.	10 Oct. - 22 Nov.	22 Nov. - 26 Dec.	26 Dec. - 20 Feb.	20 Feb. - 7 Apr.	7 Apr. - 20 May
				Production (g/m^2)			
I	salmon	0.4	0.3	0.2	0.3	0.5	0.0
IV	salmon	0.4	0.2	0.1	0.3	0.4	0.0
	small trout	0.1	0.1	0.1	0.1	0.1	0.5
	large trout	0.0	0.0	0.0	0.1	0.2	0.1
	Total	0.5	0.3	0.2	0.5	0.7	0.6
V	small trout	0.2	0.2	0.1	0.1	0.3	0.3
	large trout	0.0	0.0	0.0	0.0	0.5	0.1
	Total	0.2	0.2	0.1	0.1	0.8	0.4
				Mean Biomass (g/m^2)			
I	salmon	2.7	2.4	2.4	2.6	2.7	-
IV	salmon	2.0	1.7	1.7	1.9	1.7	-
	small trout	0.9	0.8	0.8	0.8	0.9	1.2
	large trout	1.3	0.9	0.7	0.8	0.9	1.1
	Total	4.2	3.4	3.2	3.5	3.5	
V	small trout	0.9	0.9	0.9	1.0	1.1	1.3
	large trout	2.0	1.7	1.7	1.7	2.0	1.8
	Total	2.9	2.6	2.6	2.7	3.1	3.1

anadromous species.

Production values for each experimental group generally decreased from the beginning of the experiment until November and December and then generally increased until the end of the experimental period. Higher values of production and mean biomass were generally recorded for the experimental group comprising salmon and trout than for either single species group (Table 8). The mean of the monthly biomass values of salmon only, of trout and salmon combined and of trout only during the period before 7 April were 2.6, 3.6 and 2.8 g/m^2, respectively. The sums of the monthly production values for the groups of salmon only, trout and salmon combined and trout only were 1.7, 2.2 and 1.4 g/m^2, respectively, for the period ending 7 April 1969. Low production values for the trout group probably were, in part, related to the high maintenance requirements of the large fish (age-group I+) in the trout group. Larger fish would require more food to maintain their body weight, thus a smaller proportion of their food energy would have been available for growth. This would also tend to reduce production values for the salmon-trout group. During the April-May time interval, production values for the trout were higher in section IV than in section V which contained trout only (Table 8). This increased production of trout in section IV probably resulted from the decrease in total fish biomass that occurred when the young salmon migrated from this section.

Comparison of production values between each single species group and the group containing both species indicated that there was some effect of interspecific interaction when the two species were together. The sum of the production values for trout during the five time intervals between 7 September 1968 and 7 April 1969, was 0.8 g/m^2 when associated with salmon and 1.4 g/m^2 when separate from salmon. Production values totaled over the five time intervals for salmon were 1.4 g/m^2 when associated with trout and 1.7 g/m^2 when separate from trout. These comparisons suggest that some overlap in environmental requirements may have limited the production of each species when together in the same stream section.

Percentages of time in activity, that represented amounts of time in specific kinds of movements (Table 9) were used in calculating seasonal time budgets for salmon (S1-S6), large trout (T1-T2) and small trout (T3-T6) in the observation section. Results of observations recorded for each group between 12 and 4 PM were combined to permit general comparison between the time budgets for the fall (September, October and November), winter (December, January and February) and spring (March, April and May) (Figure 11).

Coho salmon generally spent greater percentages of time in total activity than did small or large trout in each of the three seasons (Table 9). Percentages of time in activity for small trout, though generally higher than percentages of time in activity for large trout were generally lower than comparable percentages recorded for young salmon. Percentages of time in activity for salmon changed only by small amounts in each season. Amounts of activity for small trout decreased through fall and winter to relatively low values in spring. The results for trout indicated a general reduction in activity during the course of their first year of life.

Table 9. Percentages of time spent in activity (feeding, agonistic and random movements) by trout and salmon during different observation times in the fall, winter and spring, 1968-69.

Season	Observation period	small trout	large trout	salmon
fall	4- 8 AM	3.6	3.7	14.8
	8-12 AM	5.1	1.4	9.1
	12- 4 PM	8.9	2.3	9.6
	4- 8 PM	11.2	-	6.4
mean		7.2	2.4	9.9
winter	4- 8 AM	-	-	-
	8-12 AM	7.4	-	6.9
	12- 4 PM	4.3	-	11.6
	4- 8 PM	-	-	-
mean		5.8	-	9.2
spring	4- 8 AM	5.3	1.8	8.9
	8-12 AM	4.8	2.5	12.1
	12- 4 PM	6.0	8.7	9.8
	4- 8 PM	2.2	5.9	11.4
mean		4.5	4.7	10.5

The time in activity of the salmon and both age-groups of trout during the fall, winter and spring, 1968-69, is shown in Figure 11 as the sum of the percentages assigned to various categories of fish movement. Comparisons of the percentages of time spent by small trout, large trout and salmon in feeding movements during each season suggested that small trout and salmon depended largely on organisms drifting in the water current. Percentages of time spent by small trout and salmon in capturing organisms which fell on the stream surface decreased to low levels in the winter. Organisms on the stream surface appeared to be more important than aquatic drift for the large trout in spring. Considerable amounts of time were spent by the fish performing incomplete feeding movements in each season. These movements generally were in response to floating or drifting objects that were not taken into the mouth. The fish apparently did not obtain important amounts of food directly from the stream substrate.

Percentages of time spent in agonistic behavior during each season by small trout and salmon consisted largely of threat and combinations of agonistic movements. This was not true for salmon in the spring, however, when high percentages of time were spent in fleeing movements which corresponded to high percentages of time in chase movements by large trout.

Of the two large trout (T1 and T2, Table 5) stocked in

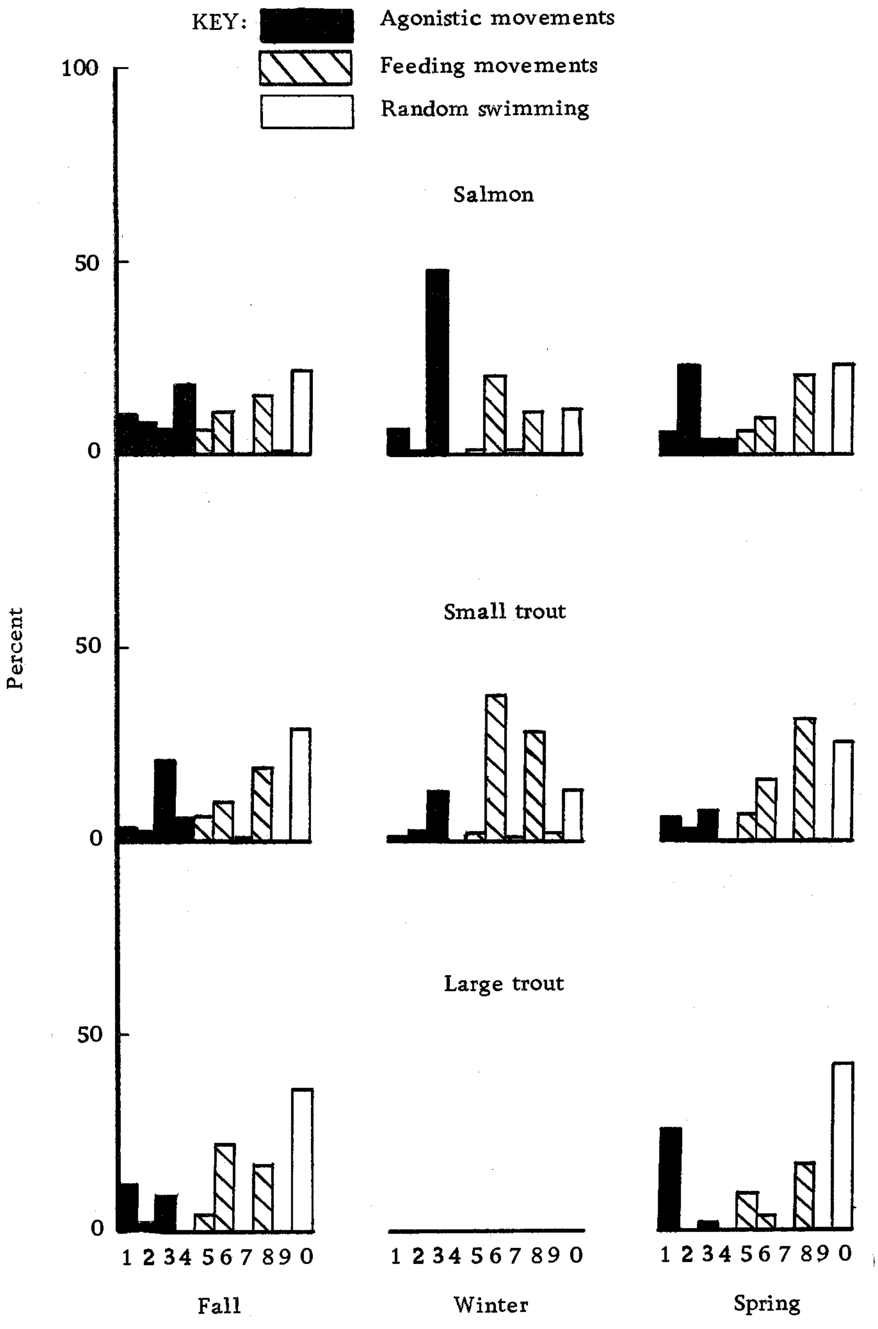

Figure 11. Percentages of time spent in specific activities by trout and salmon from 12 to 4 PM during fall, winter and spring, 1968-69. (1) chase, (2) flee, (3) threat, (4) combination agonistic, (5) surface, (6) drift, (7) bottom, (8) incomplete, (9) random, (0) random swimming.

September, only T2 was available for observation after November 1968. Near the end of November, T1 moved into the downstream trap of the observation section and was removed from the experimental population. T2 was not observed between 25 October and 5 March. This fish apparently remained beneath an undercut bank across the stream from the observation booth.

Comparison of time-budgets for trout and salmon between different times of the day during the fall (Figure 12) indicated that salmon spent the greatest proportion of feeding time in drift-feeding throughout the day. Between 4 AM and 4 PM, most feeding time by small trout was spent in drift-feeding; however, there was a tendency toward a high proportion of surface-feeding by these fish between 4 and 8 PM. Large trout spent the largest percentage of total feeding time in surface-feeding from 4 to 8 AM and in drift-feeding from 8 AM to 4 PM.

Percentages of time expended by trout in agonistic behavior increased during the fall from zero in the 4 to 8 AM time period to relatively high values for small trout in the 4 to 8 PM time period. Agonistic behavior was an important part of time expenditure by salmon from 4 AM to 4 PM but decreased to a relatively small proportion of activity time from 4 to 8 PM.

During the winter, time-budgets for small trout and salmon were obtained for the 8 to 12 AM and the 12 to 4 PM time periods

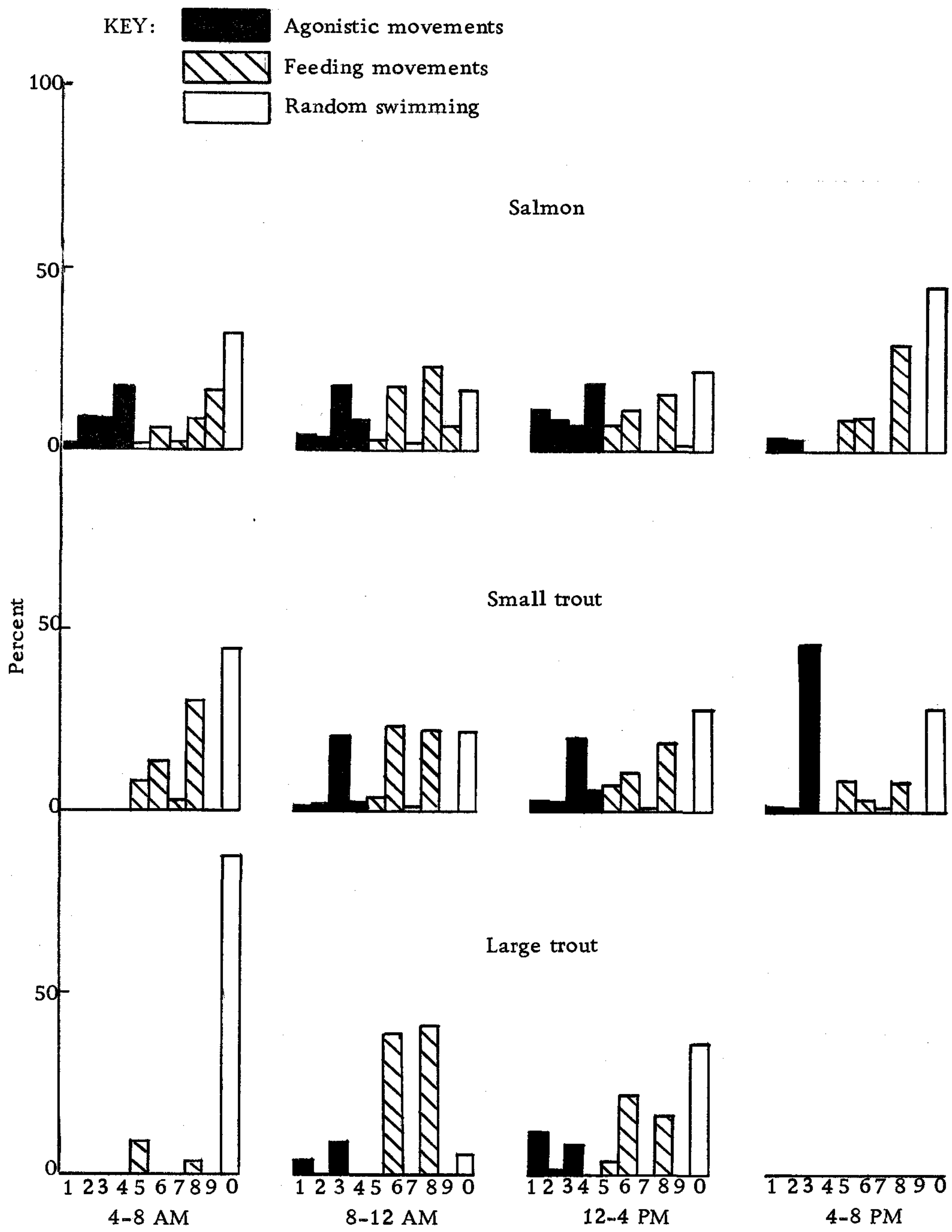

Figure 12. Percentages of time spent in specific activities by trout and salmon in four periods of the day during the fall, 1968. (1) chase, (2) flee, (3) threat, (4) combination agonistic, (5) surface, (6) drift, (7) bottom, (8) incomplete, (9) random, (0) random swimming.

(Figure 13). Feeding time by salmon and trout was largely associated with the aquatic drift. Small trout expended a greater proportion of time in activity in the morning than salmon (Table 9), however, the opposite was true in the afternoon. These differences appeared to be related to the proportions of time spent in threat displays (Figure 13).

During the spring (Figure 14) drift-feeding generally remained the most important feeding activity for small trout and salmon. Surface-feeding was most important for the single large trout (T2) that remained in the observation section except during the 4 to 8 AM time period. Results of these observations suggested that there was a tendency for decreased amounts of agonistic behavior by both species in the 4 to 8 AM and 4 to 8 PM time periods in the spring.

It was readily observed in these experiments that trout and salmon "understand" each other's repertoire of agonistic movements. This phenomenon has been observed among other salmonids (Hartman, 1965; Kalleberg, 1958; Newman, 1956; and Nilsson, 1965). The numbers of aggressive acts initiated by trout were approximately equally directed against trout and salmon in the fall, however, 70 percent of aggressive acts initiated by the salmon were directed against salmon and 30 percent were directed against trout (Table 10). Approximately two-thirds of the aggressive acts initiated by either trout or salmon during winter or spring were directed against salmon and

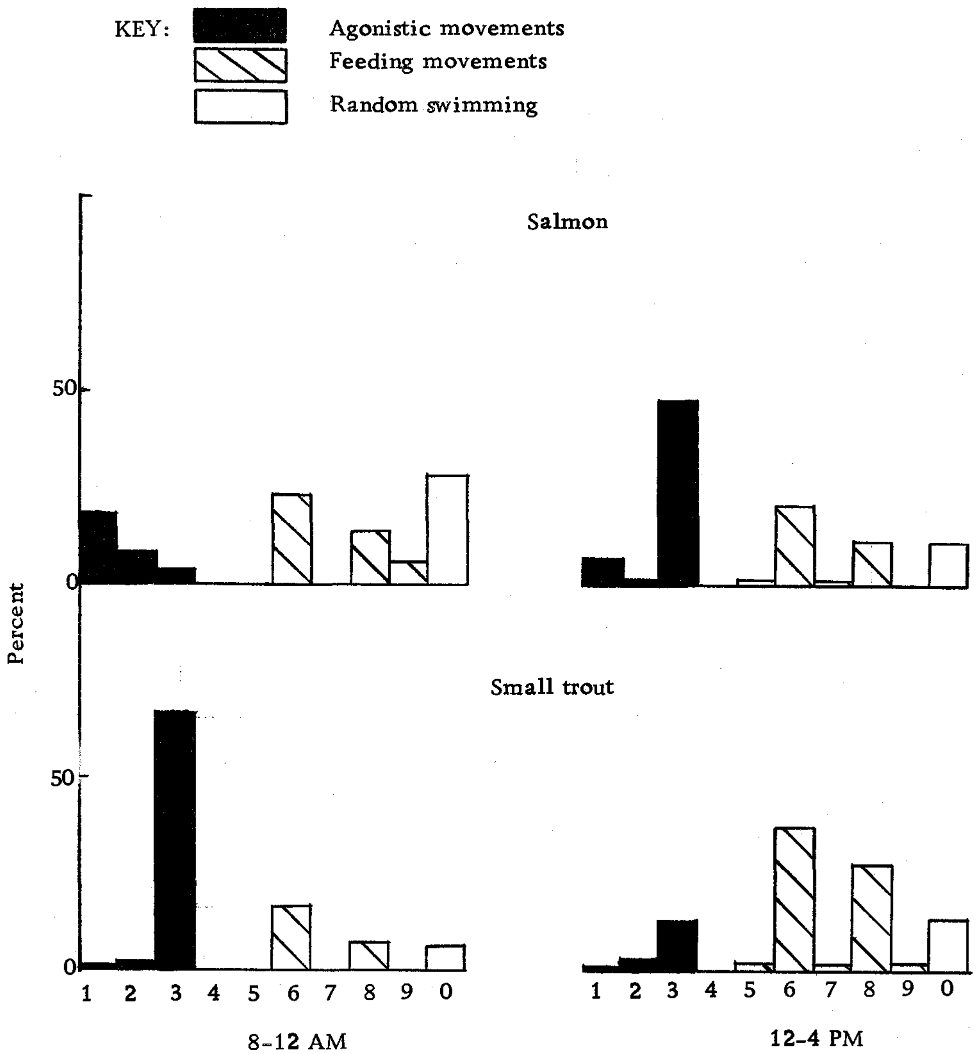

Figure 13. Percentages of time spent in specific activities by trout and salmon during two periods of the day in the winter, 1968-69. (1) chase, (2) flee, (3) threat, (4) combination agonistic, (5) surface, (6) drift, (7) bottom, (8) incomplete, (9) random, (0) random swimming.

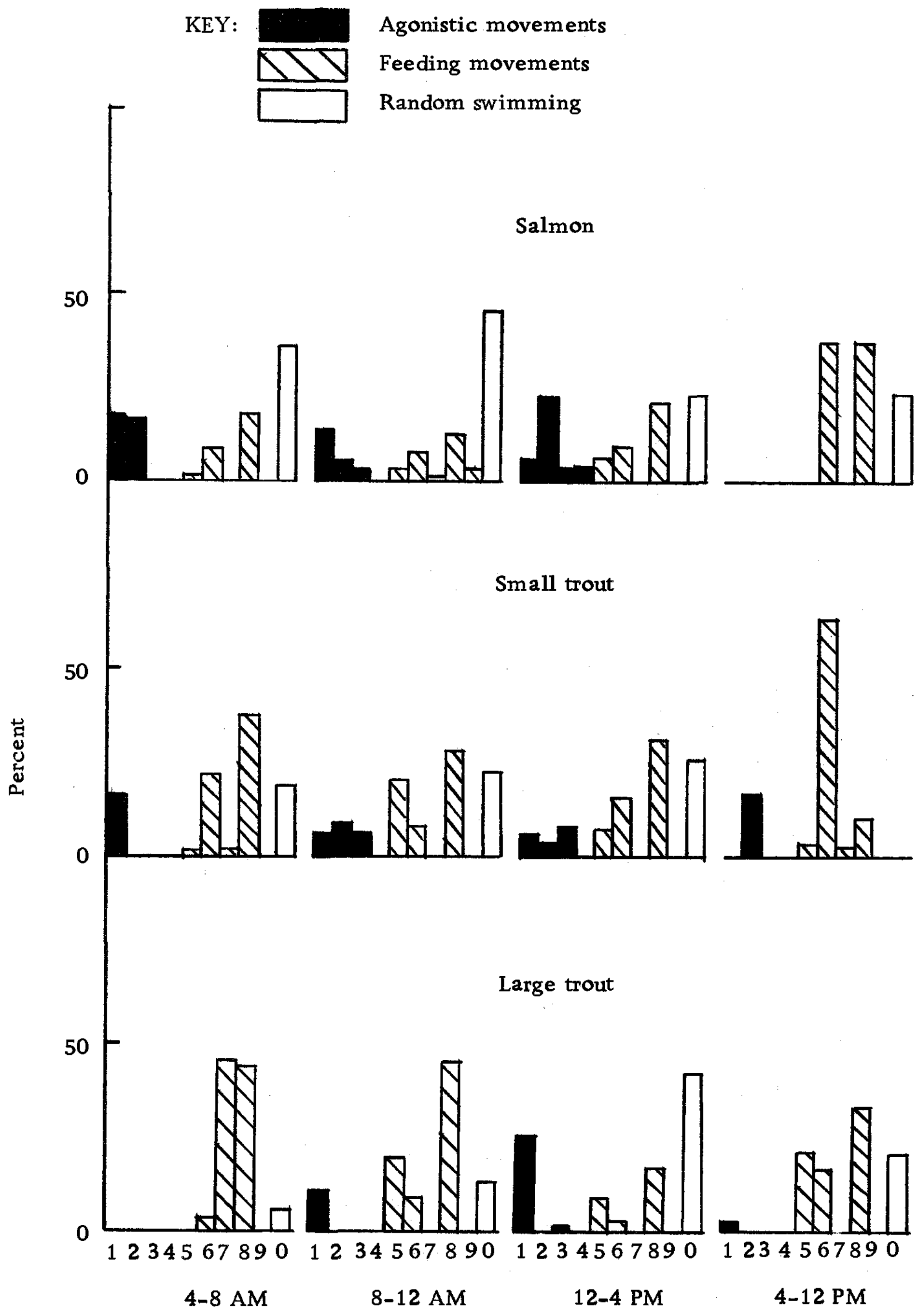

Figure 14. Percentages of time spent in specific activities by trout and salmon during four periods of the day in the spring, 1969. (1) chase, (2) flee, (3) threat, (4) combination agonistic, (5) surface, (6) drift, (7) bottom, (8) incomplete, (9) random, (0) random swimming.

approximately one-third of the acts initiated by either species was directed against trout. These results suggest that most aggressive acts initiated by either species were directed against salmon. However, the salmon frequented the pool and were in contact with the large trout which initiated but did not receive aggressive acts. In addition, the relative numbers of trout in the mixed population declined with the loss from the section of the large trout (T1). The subordination of the salmon probably was more apparent than real.

Table 10. Comparison of interspecific and intraspecific agonistic behavior between salmon and trout during fall, winter and spring, 1968-69.

	fall	winter	spring
Percentage of the total number of acts initiated by trout which were directed at salmon.	48	62	68
Percentage of the total number of acts initiated by trout which were directed at trout.	52	38	32
Percentage of the total number of acts initiated by salmon which were directed at salmon.	70	74	67
Percentage of the total number of acts initiated by salmon which were directed at trout.	30	26	33

Studies of the trout and salmon did not indicate any differences between the behavioral characteristics of the two species that would invalidate comparisons of individual fish on the basis of a common social structure. Time-budget values for individual trout (Figure 15)

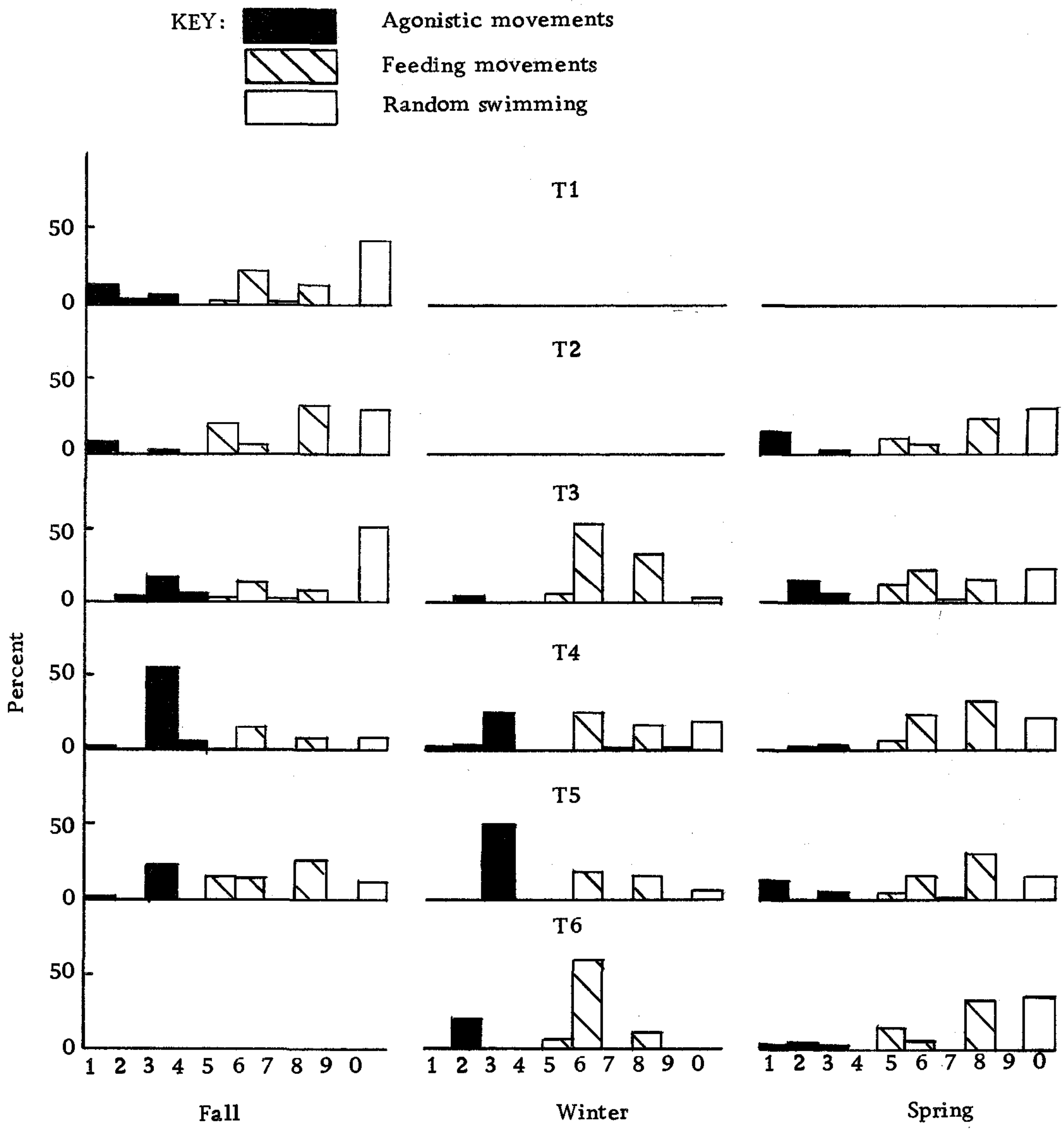

Figure 15. Percentages of time spent in specific activities by trout during the fall, winter and spring, 1968-69. (1) chase, (2) flee, (3) threat, (4) combination agonistic, (5) surface, (6) drift, (7) bottom, (8) incomplete, (9) random, (0) random swimming.

and salmon (Figure 16) were used in studies of social relationships.

To determine the approximate position in the social structure which was established among individuals of the experimental group, the number of aggressive acts initiated by each fish was divided by the total number of aggressive acts in which that fish was involved. These quotients ranged from 0 (complete subordination) to 1 (complete domination) (Table 11) and were used as an index of the social position of each fish relative to the other fish.

The absence of observations for large trout, turbid water conditions which resulted from persistent rainfall during the winter and early spring and the sharp decline in numbers of salmon during the spring, 1969, period caused the analysis to be limited to the more complete data recorded during the fall. Data on social positions, amounts of activity, and changes in weight recorded for each fish during the winter and spring are included in Appendix I and II.

Table 11. Social positions of trout and salmon during the fall, 1968.

Trout	Position	Salmon	Position
T_1	0.7	S_1	0.5
T_2	1.0	S_2	0.3
T_3	0.3	S_3	0.2
T_4	0.4	S_4	0.7
T_5	0.5	S_5	0.5
T_6	0.7	S_6	0.7

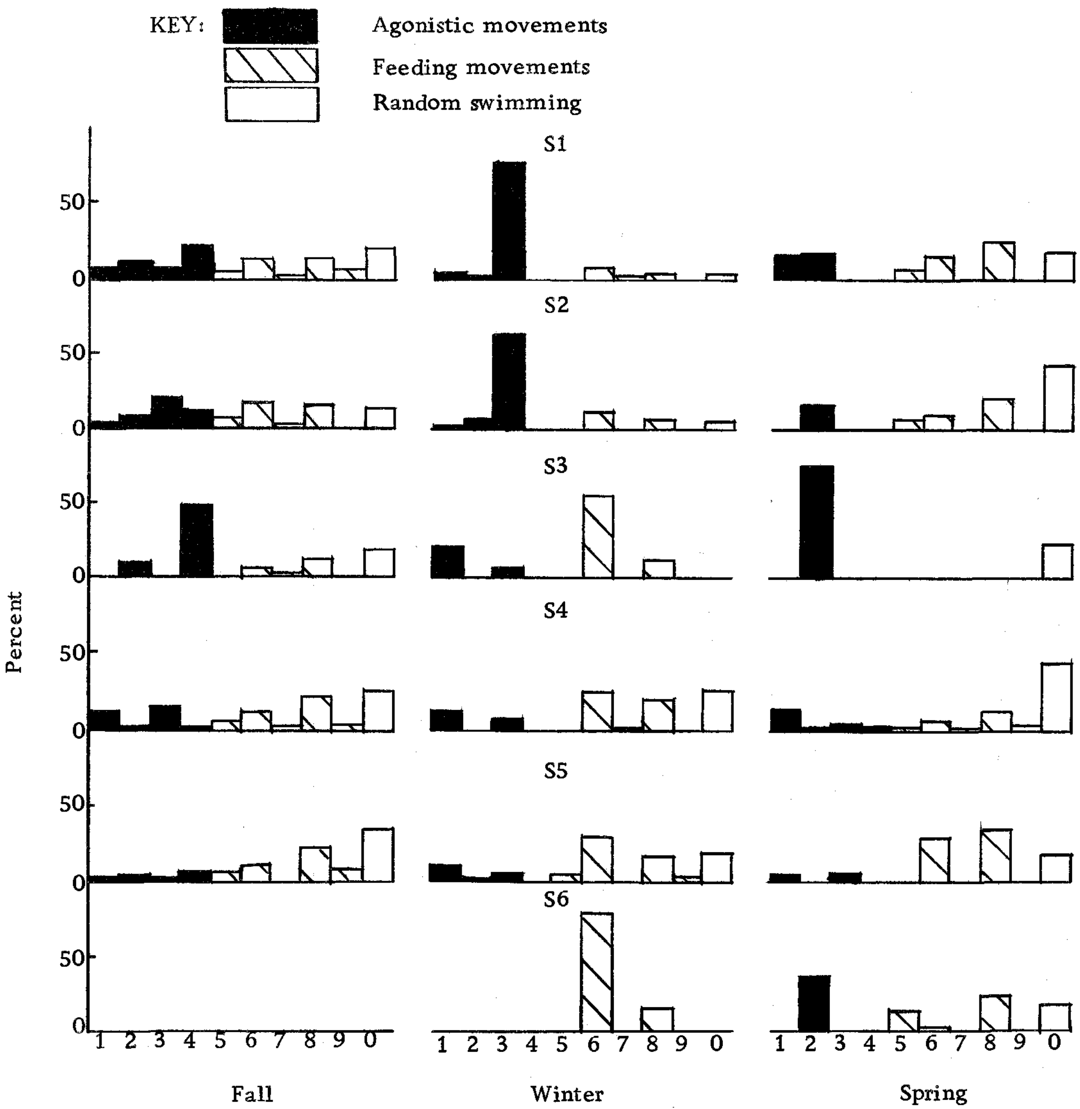

Figure 16. Percentages of time spent in specific activities by salmon during the fall, winter, and spring, 1968-69. (1) chase, (2) flee, (3) threat, (4) combination agonistic, (5) surface, (6) drift, (7) bottom, (8) incomplete, (9) random, (0) random swimming.

The social position of each fish was directly related to its weight (Table 5) at the beginning of the experimental period (Figure 17). High social position was advantageous to the fish in that changes in body weight were directly related to social position (Figure 18). A high social position was generally associated with low percentages of time spent in activity (Figure 19) and of this, high percentages of time in feeding activity (Figure 20). Associated with increased amounts of time in activity for fish in low social positions was a general trend toward increased percentages of time in agonistic behavior (Figure 21). Percentages of time in random swimming movements generally increased with increases of social position (Figure 22). This trend probably resulted from the freedom of fish in high social position to move throughout the experimental area as compared with subordinate fish which were subject to attack from fish of higher social position if they changed positions in the stream.

Records were made of the position in the stream section that individual salmon or trout occupied during each period. The position held by a fish was recorded on an outline drawing of the observation area as to one of several general areas, labeled A, B, C, D or E (Figure 23). The mean of social position index values recorded for fish observed in each area provided a basis for comparing the position the fish occupied in the stream with its social position. The fish of highest social status generally inhabited areas A and C

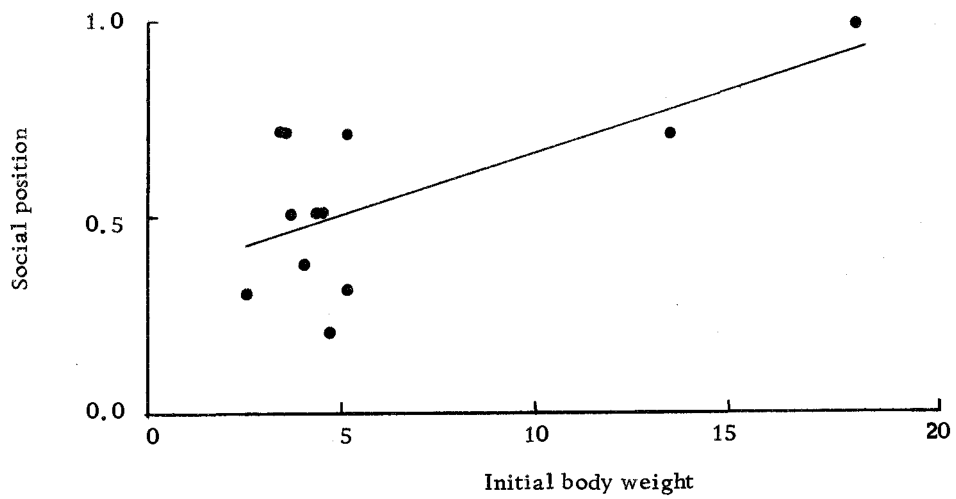

Figure 17. Relationship between social position and initial body weight for trout and salmon during the fall, 1968.

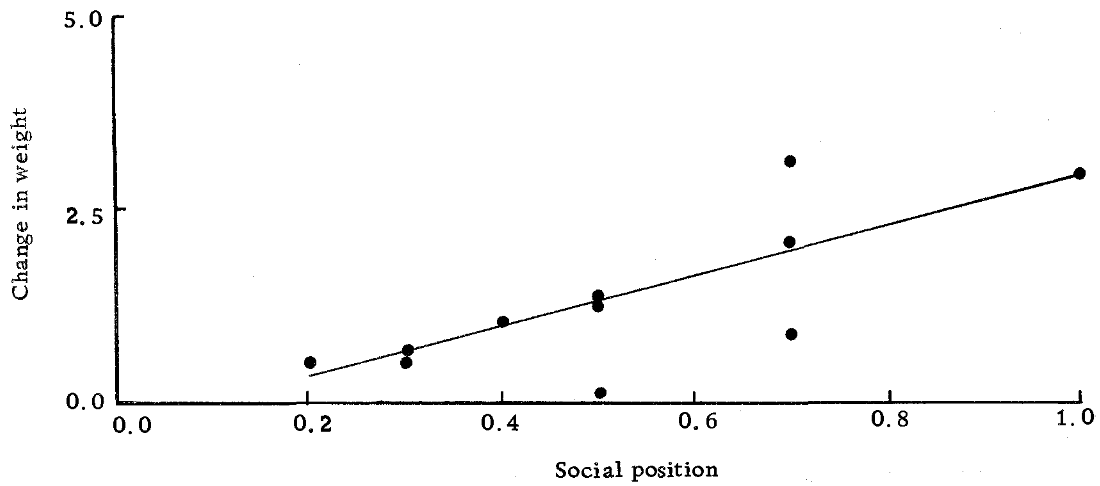

Figure 18. Relationship between the change in weight and social position for trout and salmon during the fall, 1968.

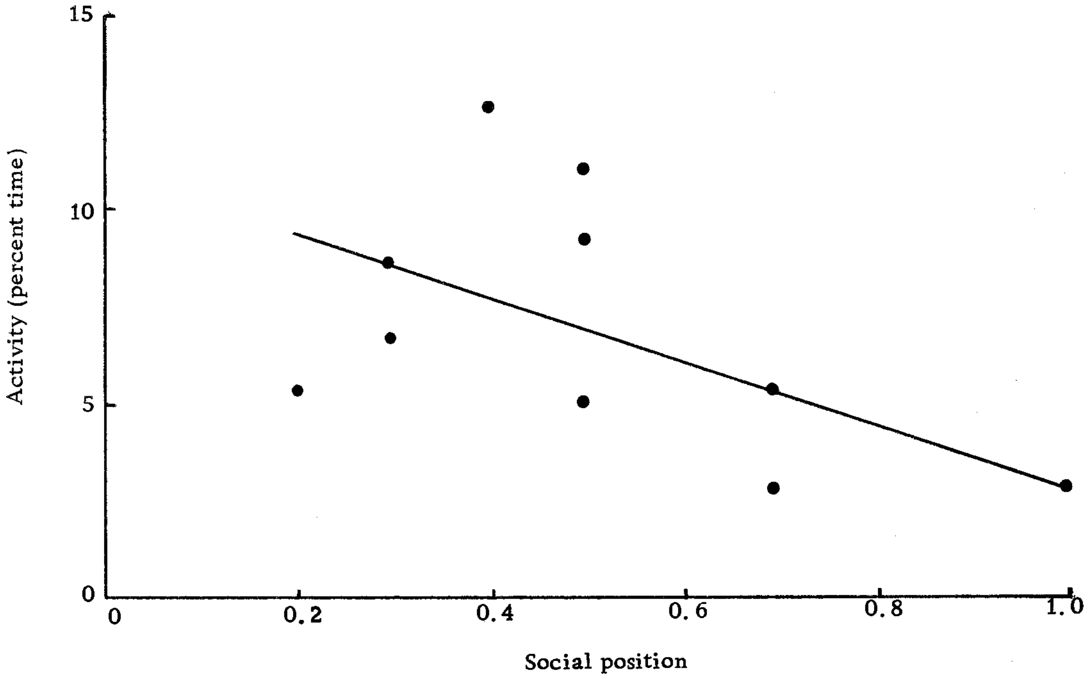

Figure 19. Relationship between the percentages of time in activity and social position for trout and salmon in the fall, 1968.

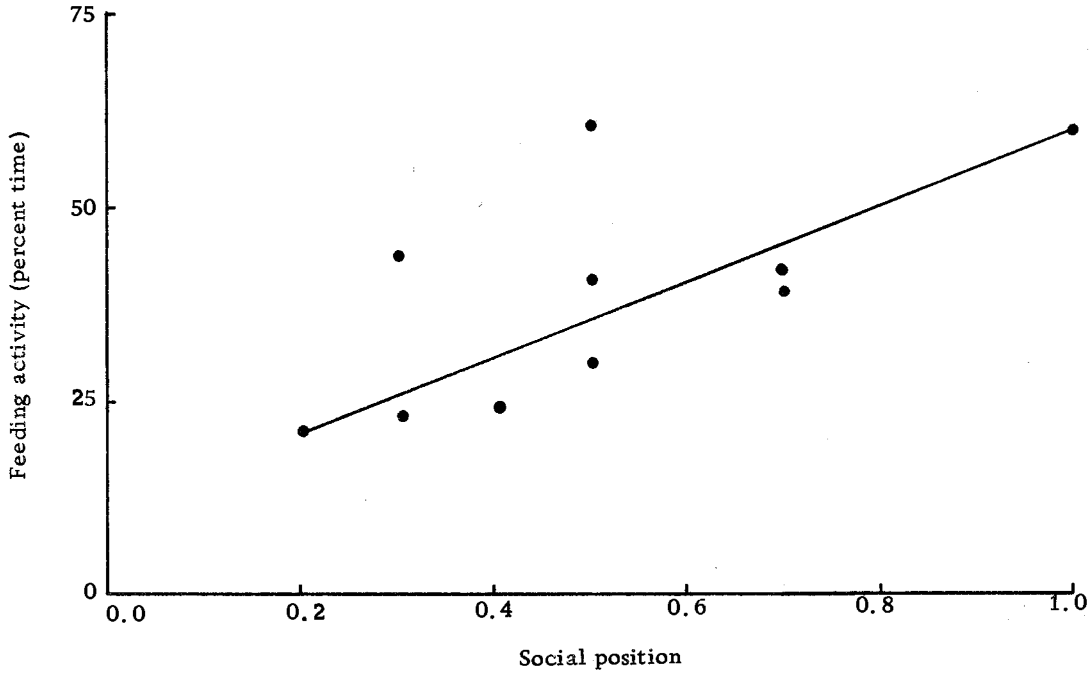

Figure 20. Relationship between percentages of time in feeding activity and social position for trout and salmon during the fall, 1968.

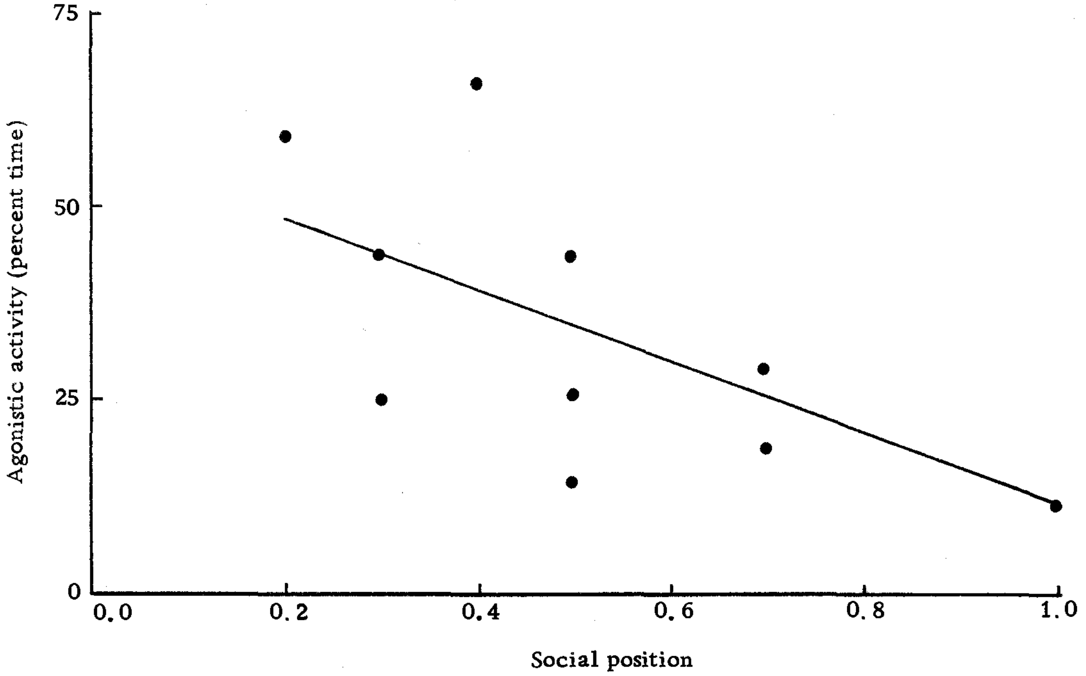

Figure 21. Relationship between the percentage of time in agonistic activity and social position for trout and salmon during the fall, 1968.

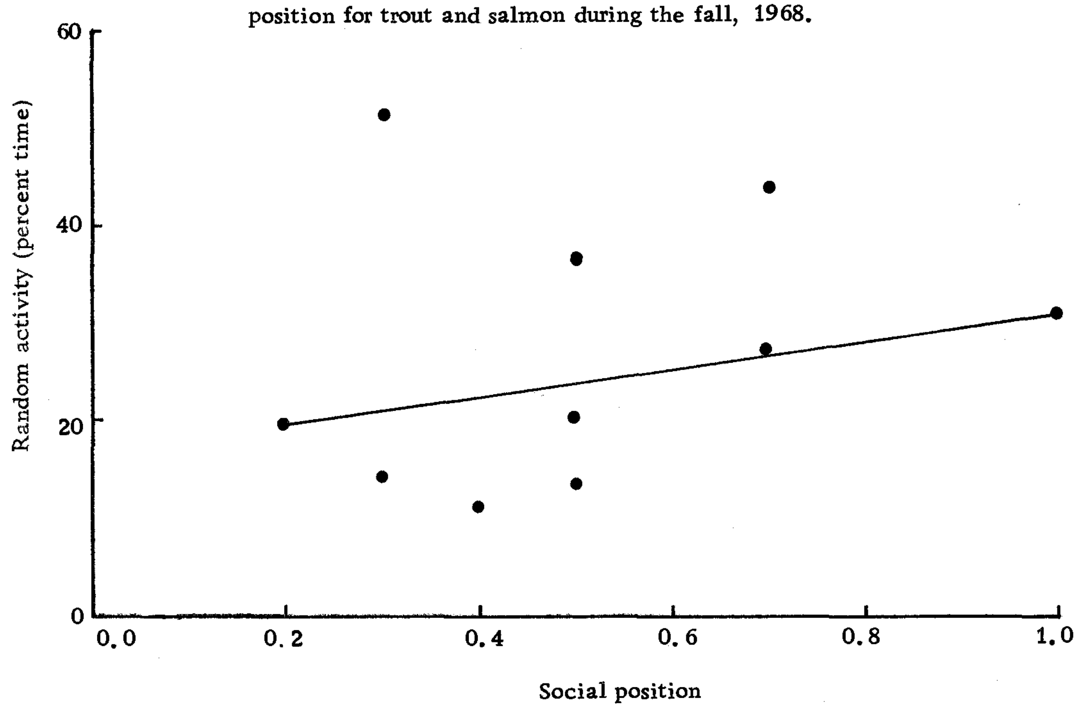

Figure 22. Relationship between the percentage of time in random swimming activity and social position for trout and salmon during the fall, 1968.

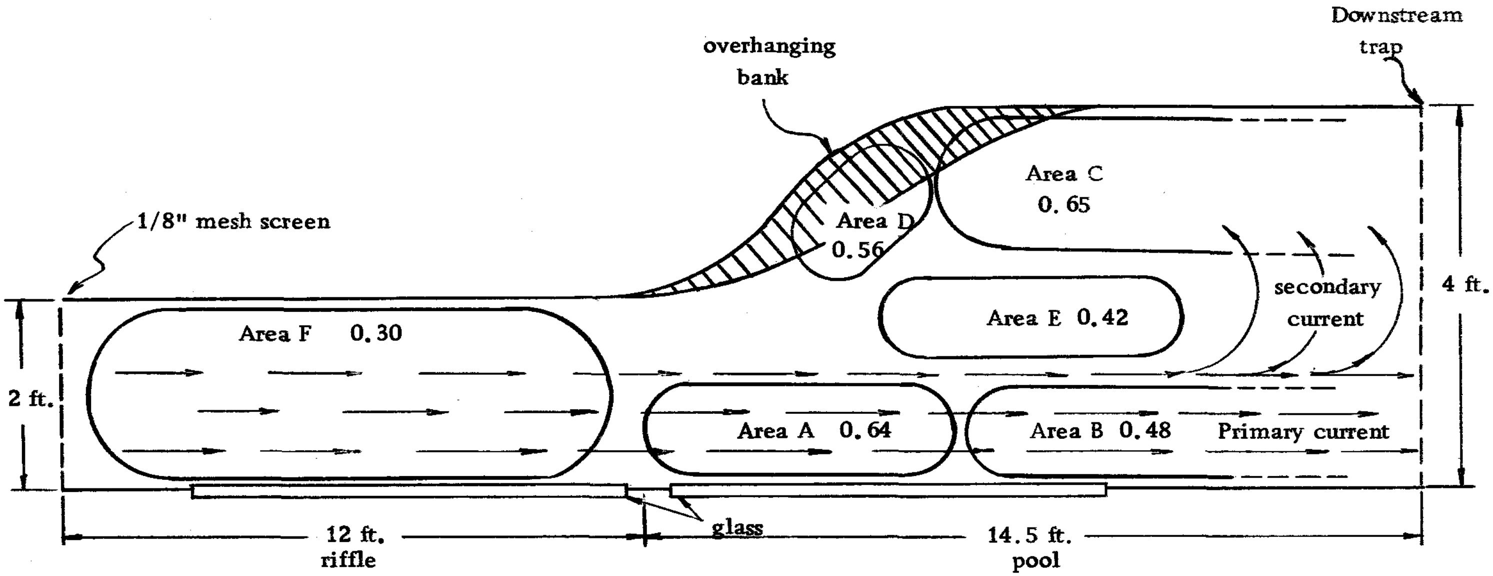

Figure 23. Diagrammatic representation of the observation section in surface view with areas usually frequented by experimental fish during the fall, 1968. Numbers represent mean social status of fish usually found in corresponding area.

(Figure 23). Area A provided fish with ready access to food organisms which entered the pool as drift. Stream flow created an eddy current in area C. Fish in area C probably received smaller amounts of food from the drift than did the fish in area A. However, area C provided cover and access to large amounts of pool surface area for feeding and appeared to be preferred by some of the dominant fish. Fish of intermediate social position tended to inhabit areas B and D usually downstream from dominant fish. Only fish of low social position inhabited the riffle area for extended periods of time.

Fish of intermediate social position appeared to spend higher percentages of time in drift-feeding than fish in high or low social positions. The largest trout (T2) held the highest social position and spent a large percentage of time in surface-feeding. Fish of low social position spent only small amounts of time in any type of feeding activity (Figure 20).

The growth of an individual trout or salmon appeared to depend on the fish's position in the integrated social structure. Fish of high social position benefitted in terms of increased amounts of feeding time, decreased activity and decreased agonistic behavior as compared with fish of lower social position.

There were no marked differences in behavior of the salmon and trout that can be used to explain the higher values of production for the combined species group than for the groups of salmon or trout. Several of the trout on occasion occupied the riffle area of the observation section (Table 12), whereas, coho salmon remained in the pool area throughout the experiment. The use of the riffle area by the trout may have resulted in more efficient utilization of space and food and may explain, in part, the differences in production between the trout-salmon group and the single species groups. Feeding positions maintained in the riffle would have allowed small trout to capture drifting food organisms that were available only on the riffle.

Table 12. Percentages of total time observed that individual trout occupied the riffle area during fall, winter and spring, 1968-69.

Trout no.	T_1	T_2	T_3	T_4	T_5	T_6
Season						
fall	-	-	54	-	-	-
winter	-	-	84	-	13	100
spring	-	.02	41	64	-	-

DISCUSSION

Studies of the intraspecific interactions of juvenile coho salmon permitted examination of the relationships of production, food consumption and behavior to the density of the experimental populations (Figure 24). The relationship between production and biomass for the several densities studied showed that maximum production values occurred at a biomass of approximately 2.2 g/m^2 (Figure 24, A) and that production declined at biomasses beyond this intermediate level. The explanation of this relationship of production to biomass lies not only with behavioral interaction but with limitations imposed by the food resource. Estimates were made of the amounts of food consumed by the fish based upon their growth rates and upon relationships established between the rates of growth and rates of food consumption of juvenile coho salmon kept in aquaria at the Oak Creek Fisheries Laboratory, Oregon State University (Carline, 1968). Estimates of total food consumption per square meter of stream section area were then made by multiplying food consumption rates times the product of mean biomass of salmon and the number of days in the experiment. At biomasses below approximately 2.2 g/m^2, the food resources were not fully utilized by the salmon (Figure 24, B). Total food consumption increased with increases of biomass up to a point and then remained constant with further increases in biomass.

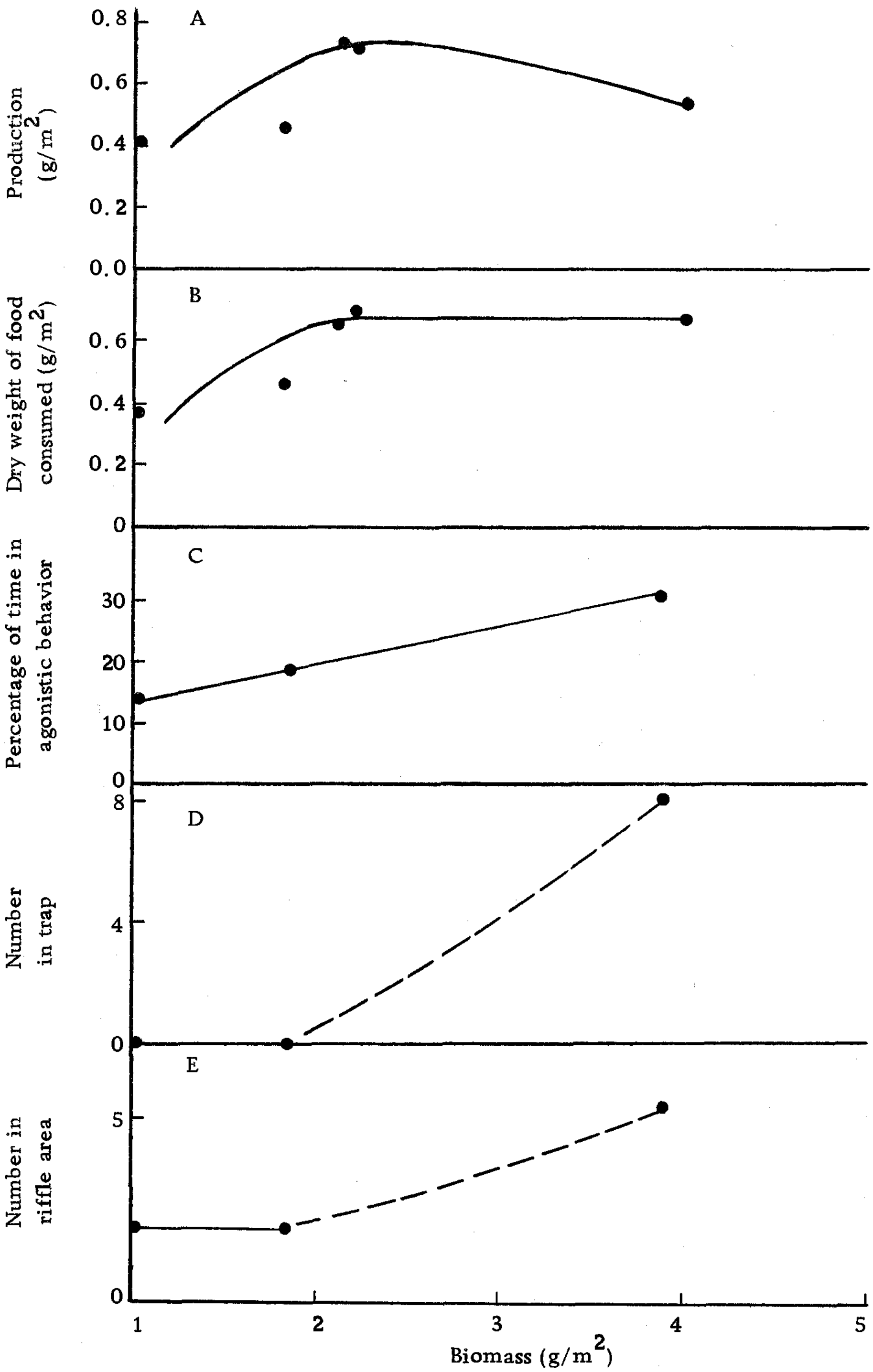

Figure 24. Relationships of salmon production (A) and food consumption (B) to salmon biomass in five sections of Berry Creek in June 1968. Relationships of salmon agonistic behavior (C), emigrants (D) and riffle utilization (E) to salmon biomass in the observation section during August 1968.

The constant food consumption values over a wide range of biomasses suggests that the salmon were unable to overexploit their food resource.

The percentages of time in agonistic behavior increased with increases of salmon density (Figure 24, C) and the amounts of food consumed by each fish necessarily decreased with increases of density. If aggressive activities require significant amounts of energy, then increasing aggressive costs and decreasing amounts of food consumption probably were incompatible for some of the salmon, leading to decreased production at the higher levels of biomass (Figure 24, A). Increases in the downstream movement (Figure 24, D) with increases in salmon biomass probably can be related to the reductions of food consumption and increased agonistic activities. The increase in the utilization of the riffle area with increases of biomass (Figure 24, E) probably resulted in increased utilization of the food resources of the section.

The energetic cost of aggressive activity by juvenile coho salmon was studied by Carline (1968). His results indicated that total activity costs were directly related to aggressive involvement of the salmon. Total activity costs increased greater than four-fold for salmon in high levels of aggressive involvement over salmon involved in the lowest levels of aggression. These results showed that at high salmon biomasses energy expenditures for aggressive activity became a significant part of the energy-budget of some salmon.

From the above considerations it appeared that, as stated by Chapman (1966), "There must be a compromise between space defended and efficient metabolism." It is suggested that this compromise would result in a biomass of between 2 and 3 g/m^2 in Berry Creek. Results obtained for salmon kept in section I from September 1968, through April 1969, indicated that the mean salmon biomass for this period was approximately 2.6 g/m^2 (Table 8). Values for the trout group and the salmon-trout group during the same period were 2.8 and 3.6 g/m^2, respectively. The higher biomasses maintained by the trout group and trout-salmon group may be explained, in part, by the greater use of the riffle area by the small trout than the salmon. Hartman (1965) found similar kinds of differences between juvenile coho salmon and steelhead trout in British Columbia. Juvenile steelhead were capable of utilizing a wider array of stream microhabitats and were more aggressive in riffle areas than were salmon, factors which helped to explain the general segregation of these species.

The severity of interaction between small cutthroat trout and juvenile coho salmon in Berry Creek was probably reduced because of the differences in general distribution within the stream section when both species were together. Although, these kinds of of differences were not evident between large trout and coho salmon, the tendency for large trout to spend greater percentages of time in surface-feeding and lower amounts of time in activity in winter than salmon probably moderated interactions between the largest trout and the salmon. Low levels of activity by large trout in winter probably reflected reduced amounts of available food.

The amounts of time spent in various activities by individual fish appeared to be related to the density of the experimental group and the social position of individual fish. Mean percentages of time spent in specific activities by the salmon-trout group ranged from 4.5 to 10.5 percent (Table 9). Determination of the energy demand for these activities relative to the total energy demands of trout and salmon in nature was beyond the scope of this investigation. As suggested earlier, energy expenditures for agonistic behavior may be important for some individuals, especially those of small body size and low social position.

Hartman (1965) reviewed the classical concepts of competition which led to "the competitive displacement hypothesis." He emphasized that sympatric species with similar requirements usually segregate and come into equilibrium in nature. This is contrary to concepts derived from studies of animals in homogeneous, controlled environments. He suggests that the concept of competitive displacement, ". . . might have been more acceptable if it had stated that in sympatric populations of similar species the level of competitive interaction will increase with the degree of ecological and behavioral similarity."

Interaction between sympatric groups of coho salmon and cutthroat trout at Berry Creek resulted in lower values of growth and biomass than for the single-species groups. The effect of the intraspecific interaction among salmon, as indicated by the behavioral observations, appeared to be greatest at those stocking densities which resulted in a decline of growth rate from the growth rates that were associated with the highest values of production (Figure 24). This indicated that there was some competitition for space among these salmonids.

The term "space" is not sufficiently restrictive to describe the spatial requirements of stream salmonids. These requirements are more appropriately described by the term "feeding space." Large trout often permitted small trout and salmon to maintain positions in their immediate vicinity. The large fish generally would not respond to the presence of a small fish unless the small fish was positioned upstream from him. Often, the large fish would not respond to the presence of a small fish positioned upstream unless the small fish made swift feeding movements toward the water surface or a drifting object. Small fish were less tolerant of these activities of subordinates. Tolerance of this sort probably tended to prevent large fish from expending excess amounts of food energy for agonistic behavior.

V. S. Ivlev, the late Russian ecologist who made outstanding contributions to the knowledge of the food and energy relations of aquatic animals summarized his views on the importance of food in the interactions between animals as follows:

> Endeavors to analyze possible forms of relations between animals convince one that the fight for food is of overwhelming importance among them, and that it occupies a predominant position among all forms of the struggle for existence. Without denying the part played by the struggle for the conditions of reproduction, etc., it is beyond doubt that all other forms of competitive relations, apart from food relations, have a particular and subordinate meaning. In addition, analysis of such subsidiary forms of the struggle for existence very often forces one to recognize that there, too, competition for food is ultimately the basic factor (Ivlev, 1961).

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APPENDICES

APPENDIX I. Social positions and changes in body weight by each experimental fish in the observation section during winter and spring. Final body weights for fish which left the experimental section were measured as each fish entered the downstream trap.

Fish no.	Winter		Spring	
	Social position	ΔW	Social position	ΔW
T_1	-	-	-	-
T_2	-	3.41	1.0	11.57
T_3	0.0	0.99	0.0	2.56
T_4	0.5	1.25	0.4	5.10
T_5	0.6	1.51	0.6	5.48
T_6	0.7	0.70	0.4	0.00
S_1	0.7	2.14	0.4	0.22
S_2	0.4	1.20	0.3	2.77
S_3	0.8	1.76	0.0	
S_4	0.5	1.59	0.7	1.24
S_5	0.3	2.70	0.6	2.44
S_6	0.0	0.76	0.0	2.56

APPENDIX II. The total time that each trout and salmon was observed during the fall, winter and spring and the total amounts of time each fish spent in various kinds of movements.

Fish	Time in movement (seconds)										Time observed (seconds)
	Chase	Flee	Threat	Combination agonistic	Surface	Drift	Bottom	Incomplete	Random feeding	Random swimming	
						Fall					
T_1	23.6	5.2	13.6	-	2.2	52.3	3.4	29.2	-	100.7	8187
T_2	22.7	-	1.2	-	47.3	13.8	-	77.4	-	69.8	8190
T_3	-	13.8	64.8	19.5	4.3	52.0	3.6	29.7	-	200.1	4575
T_4	10.9	9.4	262.4	28.2	-	75.5	-	38.7	-	45.9	3730
T_5	7.4	1.2	118.3	-	-	82.1	3.4	130.5	-	65.8	9840
T_6	-	-	-	-	-	-	-	-	-	-	-
S_1	47.4	93.3	44.9	193.4	29.0	103.6	3.9	125.8	55.7	178.4	7935
S_2	14.3	39.4	102.9	65.5	34.4	93.6	5.1	85.7	-	71.9	7636
S_3	-	21.2	2.3	110.2	-	17.0	1.5	31.7	-	43.6	4251
S_4	134.1	18.8	189.5	19.5	65.8	159.8	15.8	292.8	44.8	326.7	11430
S_5	13.9	26.7	16.2	29.4	37.3	68.1	-	148.0	57.3	225.0	6780
S_6	-		-	-	-	-	-	-	-	-	-
						Winter					
T_1	-	-	-	-	-	-	-	-	-	-	-
T_2	-	-	-	-	-	-	-	-	-	-	-
T_3	-	4.4	-	-	5.4	52.6	-	32.0	-	2.6	3720
T_4	2.4	4.4	47.6	-	-	49.8	1.2	35.0	5.5	39.3	3010
T_5	-	-	114.7	-	-	46.3	-	41.1	-	17.8	2835
T_6	-	3.8	-	-	1.1	10.9	-	2.2	-	-	780
S_1	17.4	2.5	282.3	-	-	33.7	2.0	14.3	-	14.8	1620
S_2	1.7	10.8	109.9	-	-	21.9	-	14.2	-	12.1	930
S_3	7.0	-	2.3	-	-	18.0	-	4.4	-	-	1020
S_4	37.1	-	22.0	-	-	73.1	4.6	57.2	-	75.6	3975
S_5	15.9	2.4	7.0	-	7.2	43.9	-	25.6	6.5	28.4	1250
S_6	-	-	-	-	-	11.4	-	2.4	-	-	360

(Continued)

APPENDIX II. (Continued)

Fish	Time in movement (seconds)										Time observed (seconds)
	Chase	Flee	Threat	Combination agonistic	Surface	Drift	Bottom	Incomplete	Random feeding	Random swimming	
						Spring					
T_1	-	-	-	-	-	-	-	-	-	-	-
T_2	129.5	-	5.6	-	102.6	60.6	14.8	190.6	-	247.1	12840
T_3	-	18.5	7.4	-	14.5	28.5	11.5	18.9	-	28.4	1740
T_4	-	4.0	6.2	-	10.9	31.7	-	43.7	-	28.4	4510
T_5	45.3	6.6	20.6	-	16.8	54.9	2.0	105.8	-	53.2	5340
T_6	4.2	4.9	3.7	-	17.3	7.5	-	38.3	-	30.8	1410
S_1	41.0	41.5	-	-	14.1	35.0	-	58.9	-	40.7	2985
S_2	-	25.5	-	-	10.9	14.7	-	29.9	-	61.9	1435
S_3	-	36.7	-	-	-	-	-	-	-	11.6	540
S_4	93.1	13.6	29.8	13.8	14.4	54.0	6.5	88.5	22.0	286.3	4050
S_5	2.2	-	2.4	-	-	11.8	-	14.5	-	7.5	435
S_6	-	16.3	-	-	6.2	0.5	-	10.6	-	7.9	1110