Behavior and microhabitat competition of brown trout and greenback cutthroat trout in an artificial stream
by Lizhu Wang

A thesis submitted in partial fulfillment of the requirements for the degree o f Master of Science 1 n Biological Science
Montana State University

Abstract:
Behavior and competition of yearling greenback cutthroat trout (Salmo clarki stomias) and brown trout (S. trutta) were tested in an indoor stream aquarium during June-September 1987 and January-May 1988. Brown trout were, more aggressive than equal-sized greenback cutthroat trout. Brown trout initiated 92% of 2050. attacks in four sympatric experiments. Attack involvement of cutthroat trout was significantly higher in sympatry than in allopatry, but that of brown trout was almost the same in sympatry as in allopatry. Brown trout showed better ability in competing for energetically profitable stream positions. Brown trout occupied 72% of the 207 pool positions in sympatry with equal-sized cutthroat trout. The distance of cutthroat trout from food source was significantly greater in sympatry than in allopatry, but that of brown trout was almost the same in sympatry as in allopatry. In sympatry, food-source distance of cutthroat trout was significantly greater than that of brown trout. Cutthroat trout lost more weight than brown trout in sympatry. Brown trout could outcompete greenback cutthroat trout that were 1.27 times longer and 1.69 times heavier. The behavior of greenback cutthroat trout was the same under two different light intensities and two different water velocities. However, slow current combined with dim light significantly increased attack frequency of brown trout.

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by

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citation, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

Behavior and competition of yearling greenback cutthroat trout (*Salmo clarki stomias*) and brown trout (*S. trutta*) were tested in an indoor stream aquarium during June-September 1987 and January-May 1988. Brown trout were more aggressive than equal-sized greenback cutthroat trout. Brown trout initiated 92% of 2050 attacks in four sympatric experiments. Attack involvement of cutthroat trout was significantly higher in sympatry than in allopatry, but that of brown trout was almost the same in sympatry as in allopatry. Brown trout showed better ability in competing for energetically profitable stream positions. Brown trout occupied 72% of the 207 pool positions in sympatry with equal-sized cutthroat trout. The distance of cutthroat trout from food source was significantly greater in sympatry than in allopatry, but that of brown trout was almost the same in sympatry as in allopatry. In sympatry, food-source distance of cutthroat trout was significantly greater than that of brown trout. Cutthroat trout lost more weight than brown trout in sympatry. Brown trout could outcompete greenback cutthroat trout that were 1.27 times longer and 1.69 times heavier. The behavior of greenback cutthroat trout was the same under two different light intensities and two different water volocities. However, slow current combined with dim light significantly increased attack frequency of brown trout.

INTRODUCTION

Indigenous cutthroat trout (*Salmo clarki*) have declined in abundance so drastically that many subspecies are extinct or nearly so (Behnke 1979). Behnke (1972) believed that at least 99% of the original populations of interior cutthroat trout have been lost in the last 100 years. One of the factors responsible in the decline is thought to be interspecific competition (Hanzel 1959; Behnke 1979; Liknes 1984).

The competition between cutthroat trout and some other salmonids, such as brook trout (Griffith 1972), steelhead (Hartman and Gill 1968), and rainbow trout (Nilsson 1981), as well as coho salmon (Glova 1984, 1986), and Dolly Varden (Andrusak and Northcote 1971; Schutz and Northcote 1972; Henderson and Northcote 1985; Hinder et al. 1988), has been well recorded. However, competition between cutthroat trout and brown trout (*S. trutta*) has not been carefully studied.

The autecologies of cutthroat trout and brown trout are well known, but not their synecology. They have similar food and habitat preferences (Miller 1957; Hartman and Gill 1968; Jenkins 1969; Brown 1971; Bustard and Narver 1975; Bachman 1984; Javorsky 1984; Scarnecchia and Bergersen 1986; Gatz et al. 1987). Therefore, interspecific competition probably happened when brown trout were first introduced into cutthroat trout streams, and may still be happening where these species are sympatric and food or habitat is in short supply.

When species with similar ecological requirements first mix together, particularly intense competition between them may ensue. Subsequently, one or both species may adapt morphologically, physiologically, or behaviorally to coexistence, or the competitively less successful species may die out locally or retreat to marginal habitats and no longer significantly overlap its competitor's spatial distribution or resource use (Nilsson 1967). Unlike the interactive segregation of cutthroat trout with Dolly Varden (Andrusak and Northcote 1971; Schutz and Northcote 1972; Hindar et al. 1988), and with coho salmon (Bustard and Narver 1975; Glova 1984, 1986), which are probably coevolutionary, interaction between cutthroat trout and brown trout, a result of recent artificial sympatry, would be expected to take the form of competitive exclusion.

The existence of competition between cutthroat and brown trout can be tested in an artificial stream, and various characteristics of the interaction could be examined. Trophic or habitat shift of one species when in the presence of another species is evidence for interspecific competition (Werner and Hall 1976). Overlap in resource use alone does not necessarily mean that two species are competing (Sale 1979), but resource overlap together with niche shift in sympatry is considered evidence of competition (Diamond 1978; Gatz et al. 1987). Therefore, the possibility of active displacement of cutthroat trout by brown trout and the behavioral advantage of one over the other could be evaluated by examining aggressive behavior and microhabitat use in allopatry and sympatry.

The broad objectives in this study were to determine whether interspecific competition exists between yearlings of greenback cutthroat trout (Salmo clarki stomias) and of brown trout, whether intraspecific competition exists within groups of these kinds of fish, and what may be the characteristics of such inter- and intraspecific competition. Specific objectives (if competition exists between these species) were to determine (1) the dominant species, (2) the role that body size may play in competition, (3) how the competition may be affected by light intensity, and (4) how the competition may be affected by water velocity.

MATERIALS AND METHODS

Experimental Animals

Yearling wild brown trout were obtained by electrofishing from Darlington Ditch, Gallatin County, Montana, in March and December 1987. Greenback cutthroat trout were obtained from the U.S. Fish and Wildlife Service's Fisheries Technology Center (BFTC) in Bozeman, where a brood stock of these fish is maintained. Female brood stock descended from females brought from Como Creek, Colorado, to Bozeman in 1977, but male gametes are brought each year from Hunters Creek, Colorado, both streams being in the South Platte River drainage.

The brown and cutthroat trout were raised separately in 2 2,000-liter flow-through circular tanks for 2 to 3 months under hatchery-operation conditions of lighting (primarily window light) and water temperature (12-15 C). Then they were held separately in a 1,000-liter flow-through tank, divided into sections by screens. Water temperature was held at 15 C. The photoperiod cycle was 12 hours light (0700-1900 h MDT) and 12 hours dark (1900-0700 h MDT). The tank was covered with screen to prevent fish from leaping out. The fish were fed Rangen trout pellets 2 to 3 times during each light period at a daily rate of 10% of the biomass of fish held in the tank.

The Stream Aquarium

The observations were made in an indoor stream aquarium at the BFTC. The aquarium was in the form of a hollow, rectangular "doughnut" circuit channel (Fig. 1) that was level (Fig. 2), that had cross-sectional dimensions of 60 cm wide and 40 cm deep (Fig. 3), and that had its current generated by an electric outboard motor. The long sides of the rectangle were screened at each end to form individual straight channels 4.5 m long (Fig. 1). The inner sides of the stream aquarium were plate glass, allowing unobstructed view above or below the water surface. The bottom and outside walls were plywood painted with black epoxy.

Inner volume of the channel circuit was about 3,172 liters. The "open water" (pools, riffles and traps) was about 1,336 liters, and the volume of gravel and interstitial water was about 1,593 liters.

The aquarium chamber that lay just downstream from the current-generating motor was designated as section I, the other chamber as section II. The downstream end of each section had a trap to catch fish that moved downstream (Fig. 1). The channel bed was gravel of 2-3 cm diameter. The bed surface was shaped to simulate riffles of 15-17 cm water depth and pools of 32 cm maximum water depth (Fig.

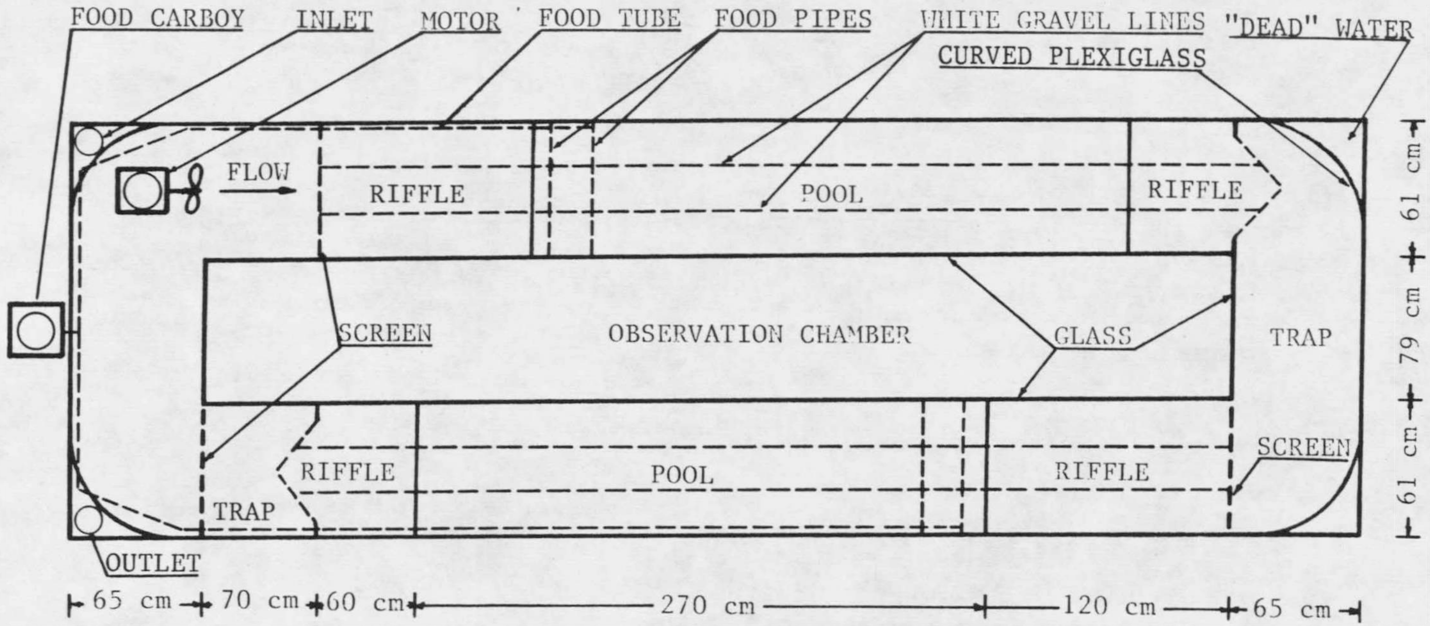

Figure 1. Top view of the stream aquarium.

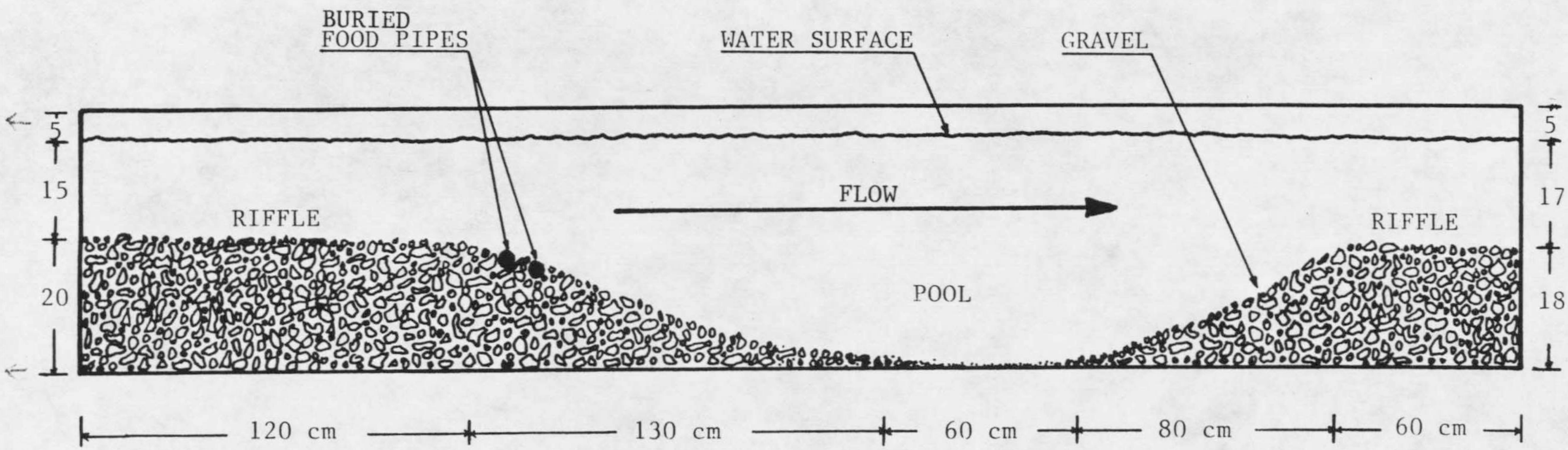

Figure 2. Side view of the aquarium to show the structure of riffles and pool.

2). The inner channel walls were marked at 10-cm intervals with bits of masking tape, attached to the outside surface of the glass and numbered from upstream downward.

Longitudinal lines of light-colored gravel in the bed demarcated 3 20-cm reference lanes. The vertical and horizontal markings along the bottom and inner wall of each section created 270 visual reference spaces of 10x10x20 cm, which were used to identify the positions of fish.

Water current was driven by the propeller of a 5-speed electric outboard boat motor (Sears, Roebuck and Co. "Gamefisher" Model 217-590290), located upstream from section I (Fig. 1). Water replacement rate was about 10 L/min, resulting in complete turnover about every 4 hours. During the experiments, only the first (lowest) and second speed of the propeller was used. The first motor speed generated streamflow discharge of 9.5 L/s and maximum water velocity of 20 cm/s (Table 1 and Fig. 4), as measured with a Montedoro-Whitney electromagnetic water velocity meter, model PVM-2A. The second motor speed generated discharge of 12.4 L/s and maximum water velocity of 27 cm/s (Table 1 and Fig. 5).

The aquarium was lit primarily by 20 40-w fluorescent

Table 1. Water velocity in the stream aquarium.

Depth below water surface (cm)	Upper riffle N	Upper riffle Maximum	Upper riffle Minimum	Upper riffle Mean	Pool N	Pool Maximum	Pool Minimum	Pool Mean	Lower riffle N	Lower riffle Maximum	Lower riffle Minimum	Lower riffle Mean
First motor speed												
Section I												
3	49	20	9	13.4	91	15	2	8.1	21	10	7	8.3
12	49	16	4	7.8	91	14	2	6.0	21	10	7	8.3
21		gr	gr	gr	84	9	1	4.4		gr	gr	gr
30		gr	gr	gr	35	5	0	2.9		gr	gr	gr
Section II												
3	49	16	6	9.5	91	14	0	6.4	21	13	6	9.2
12	49	16	5	10.3	91	11	0	6.7	21	14	6	9.2
21		gr	gr	gr	77	9	0	4.2		gr	gr	gr
30		gr	gr	gr	28	5	0	2.2		gr	gr	gr
Second motor speed												
Section I												
3	49	27	7	15.7	91	19	3	8.7	21	12	7	8.8
12	49	23	1	9.7	91	17	2	7.1	21	11	8	9.4
21		gr	gr	gr	84	10	0	4.7		gr	gr	gr
30		gr	gr	gr	35	6	0	2.6		gr	gr	gr
Section II												
3	49	17	5	11.4	91	14	0	7.6	21	15	8	10.8
12	49	19	6	11.9	91	15	0	8.0	21	16	8	11.7
21		gr	gr	gr	77	10	0	4.8		gr	gr	gr
30		gr	gr	gr	28	5	0	2.0		gr	gr	gr

gr = gravel

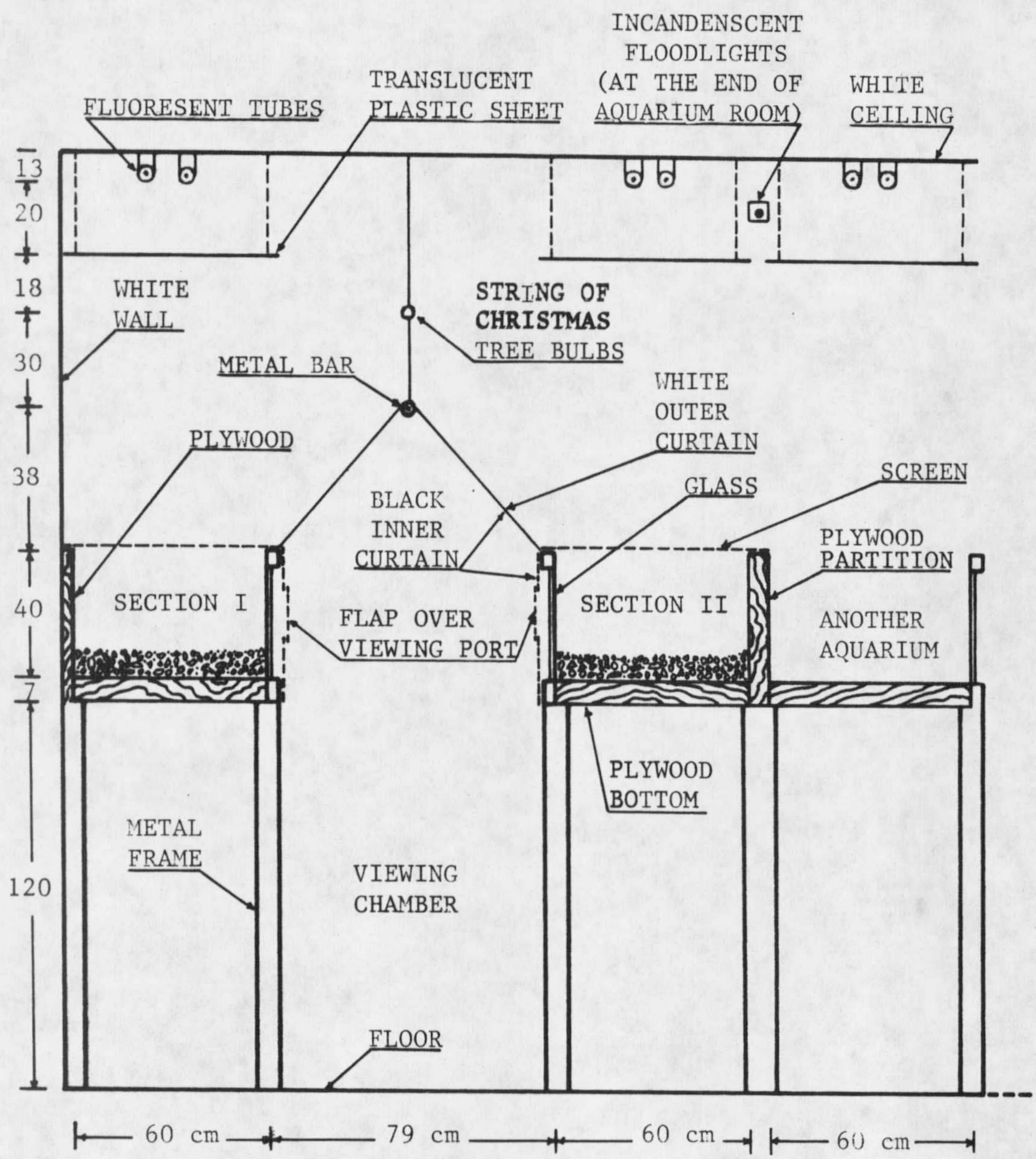

Figure 3. Cross-sectional view of the aquarium to show structures of lights and curtains.

tubes aligned in pairs above the channel (Fig. 3), creating an average light intensity of 14.9 $\mu E/m^2/s$ (range 8-21) at the water surface, as measured with a Li-Cor 1000 light meter. The light was diffused through translucent white plastic sheets 1.5-mm thick, hung 20 cm below the tubes and 90 cm above the water surface. A white ceiling above the fluorescent lamps reflected light downward. A timer was used to switch the fluorescent lights on and off and maintain the photoperiod of 12 hours light (0700-1900 h MDT) and 12 hours dark (1900-0700 h MDT). To simulate dawn or dusk before or after each period of fluorescent lighting, an automatic rheostat and timer were used to create a 30-minute period of gradual brightening or dimming of two 130-w incandescent floodlights, one at each end of the room, shined against the end walls, which reflected light throughout the ceiling area.

A horizontal metal bar was hung 80 cm below the ceiling and above the center of the viewing chamber to support curtains that extended diagonally from the metal bar to the top of the inner wall of each aquarium, and two other curtains hung vertically from the top curtains to the bottom of the aquarium glass (Fig. 3). The upper, diagonal curtains were composed of 2 layers of cloth, white cloth toward the lights and black cloth toward the viewing chamber. This provided a light environment above the water surface and darkness in the observation chamber. The vertical curtains were black and had rectangular (10-X-8-cm) viewing ports positioned below the water level at 50-cm intervals along the channel. The viewing ports were covered by black cloth shields when not in use.

Water temperature was held at 15 C (± 1 C) by adjusting cold and warm springwater intake valves. Dissolved oxygen was about 100% of saturation (7.8 mg/L at 15 C), as measured at the upstream and downstream ends of the aquarium circulation. Other aspects of water quality were well within the range of tolerance for trout (Appendix Table 15).

Feeding

During experiments, invertebrate drift was simulated by injection of a suspension of frozen brine shrimp that had been thawed in water. The brine shrimp suspension entered through pipes buried in the gravel at the upper end of each pool (Figs. 1 and 2) for 4-6 hours each day. A magnetic stirrer kept the brine shrimp in suspension in a 25-liter carboy that was 1 m above the aquarium, and the brine shrimp suspension flowed by gravity through 12-mm-diameter tubing to the feeding pipes. The tubes connecting the carboy with the feeding pipes were covered by gravel where they ran through the aquarium. The feeding pipes were glass with numerous holes for dispensing the suspension.

The food drift was measured in the presence of fish (3 brown and 3 cutthroat trout in each section) at 8 cross-sections (Figs. 18 and 19) with each net having a square opening 10 x 10 cm and a 5-cm-deep bag of 0.3-mm-mesh netting. Three nets were set once for 30 minutes across the 61-cm width of the channel with equal spacing between nets and at a distance below water surface that was 60% of water-column depth. This depth was chosen because it is generally the depth of mean water velocity (Work Group 1 on Surface Water 1980: 1-28). The collected food was washed into a dish and dried at 100 $\pm$ 5 C for more than 24 hours. The dried food was weighed on an electro-scale.

Food drift entered at the border between the upstream riffle and pool in each aquarium section. Therefore, food drift was highest (about 5 mg/h) at the upstream end of the pools and lowest (about 0.5 mg/h) at the downstream part of the upstream riffles (Figs. 4 and 5).

Measurement of Fish

Before each experiment and at the conclusion of some experiments fork length of each fish was measured to the nearest 0.2 millimeter after anesthesia. After length measurement and finclipping to individually mark each

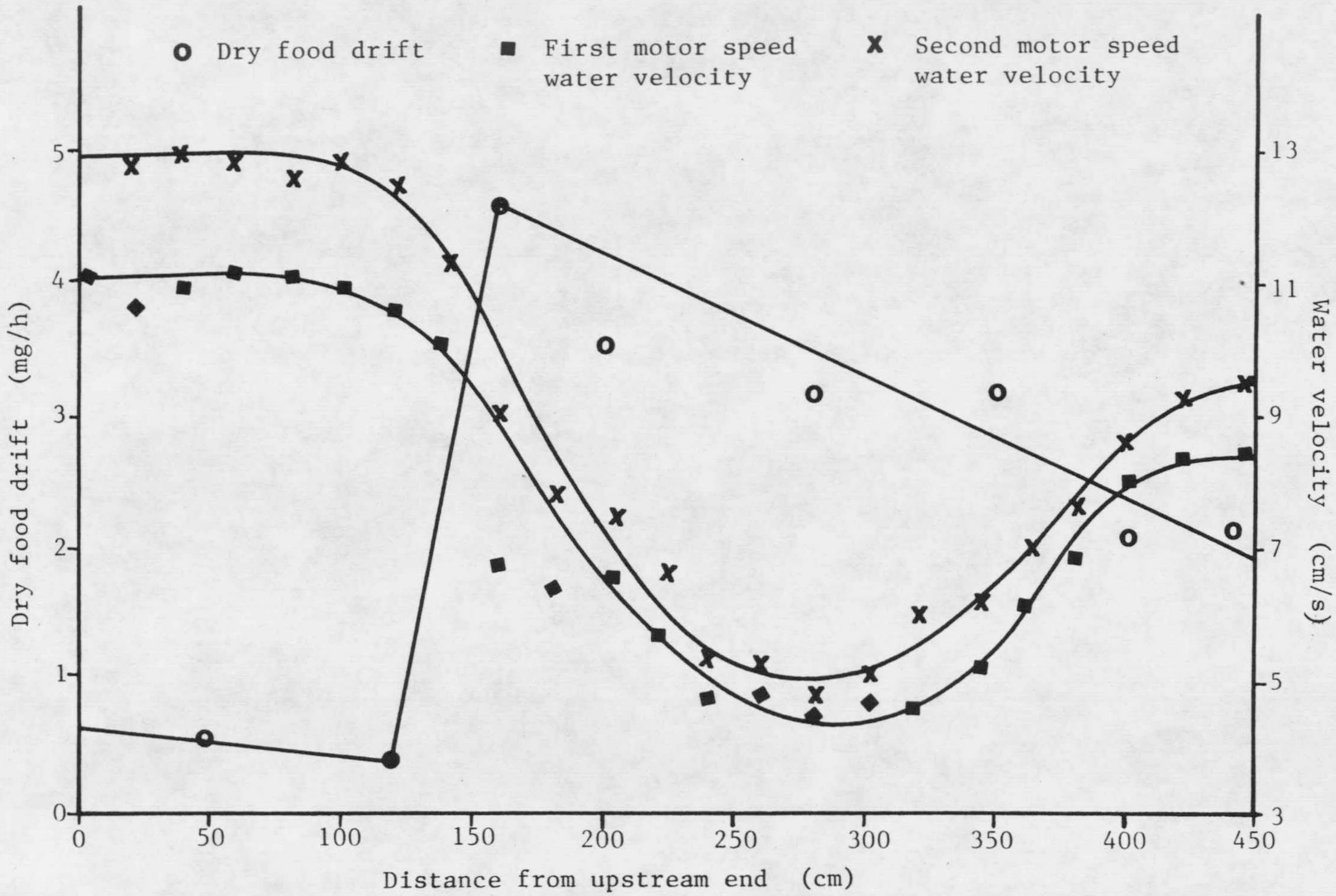

Figure 4. Distribution of food drift and water velocity in section I of the artificial stream (curves fitted by eye).

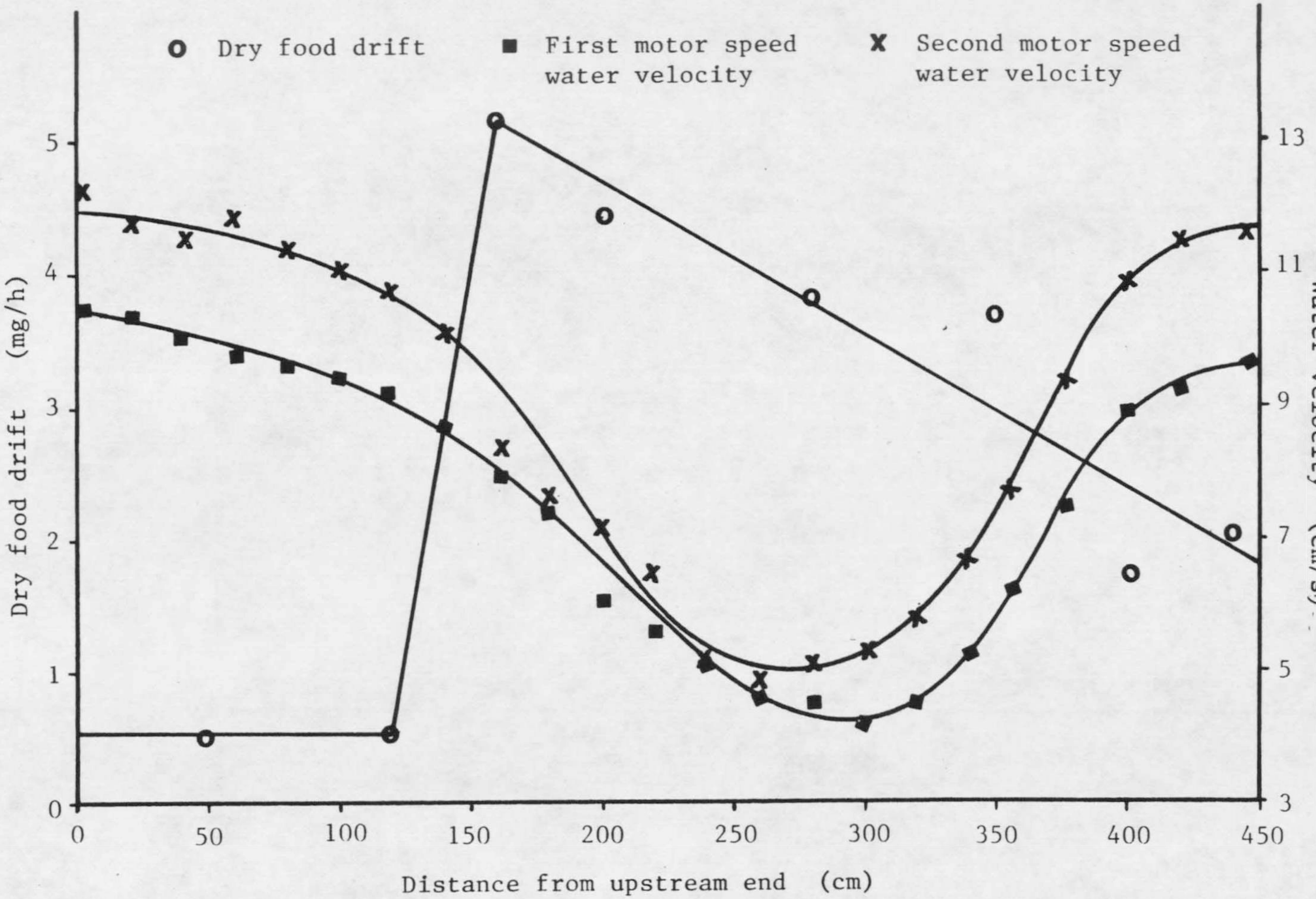

Figure 5. Distribution of food drift and water velocity in section II of the artificial stream (curves fitted by eye).

fish, the fish were rolled 4 times on a paper towel and weighed in a 1-liter glass beaker on an electro-scales. Correction for weight of the beaker and the water in the beaker was automatically made by the scales.

Experimental Design

Determination of Fish Population Density

Two tests (July 3-28, 1987) were conducted to determine the amount of fish (equilibrium density) to be held in the aquarium during experiments. Ten cutthroat trout averaging 144 mm fork length (range 138-149 mm) and 32.6 g body weight (range 27.3-34.2 g) were put in section I, and 10 brown trout averaging 141 mm fork length (range 137-149 mm) and 33.0 g (range 26.4-34.8 g) were put in section II. These fish had been marked for individual identification by finclipping. During 5 days' acclimation, the fish were confined to the aquarium sections by blocking the openings of the downstream traps. On day 6, the trap entrances were uncovered. Thereafter, fish that entered traps were recorded and returned to the channel from which they had come at 1600 h each day. If a fish entered a trap 3 times, it was removed from the experiment. After 5 days with the trap open, the remaining cutthroat trout were moved from section I to section II, and the remaining brown trout were moved from section II to section I. After a 3-day acclimation, during which trap entrances were blocked, I began to record the fish in the trap again. Five or 6 remained in the sections when the population had been reduced such that no third-entry event occurred for 4 consecutive days. Therefore, 5 or 6 fish were used per section during the behavioral experiments.

Interactions between Fish of Equal Size

Competition and behavioral differences between brown and cutthroat trout were measured in allopatry and sympatry. Fish were selected to be as uniform as possible in length and weight. After assignment to aquarium sections, the fish were acclimated for 5 days to aquarium conditions, including the food supply. Overt behaviors (Table 2) and the sites occupied by fish for more than 1 minute during an observation period were recorded. Current was generated at the faster (second) motor speed (Table 1).

Allopatry experiments. Six cutthroat trout averaging 145.6 mm fork length (range 137-150 mm) and 27.45 g (range 26.03-29.12 g) were put in section I, and 6 brown trout averaging 145.0 mm in fork length (range 140-150 mm) and 27.55 g (range 26.21-28.98 g) were put in section II. After the 5-day acclimation, the fish were observed, and the sites they occupied were recorded at about 0900h and

Table 2. Fish behaviors observed during the experiments.

Behavior	Description
Approach	One fish swims directly toward another at slow to moderate speed. (1) Tail-first approach: approaching fish drifts backward toward another fish (Jenkins 1969). (2) Intentional movement: approaching fish swims toward another fish and stops short of it (Wolfe 1978).
Frontal display	Head of one fish presented to another; back arched higher than head and tail; dorsal fin contracted and pectoral fins expanded (Hartman 1965).
Lateral display	Side of one fish presented to another; back arched and lower than head and tail; fin expansion of displaying fish variable, but often all fins maximally extended. Sometimes result is parallel swimming with fish swimming forward or backward slowly, side by side (Hartman 1965; Jenkins 1969).
Wigwag display	One fish swims away from another fish with an exaggerated, undulating motion; body held at 20- to 30-degree angle to the horizontal, with head down and tail up, or head up and tail down; all fins of displaying fish expanded (Jenkins 1969; Wolfe 1978; Hartman 1965).
Direct attacks	One fish bites another; nips directed to any area of target fish (Jenkins 1969).
Appeasement	Fish being approached by a much stronger fish drops motionless to bottom or rises to surface of water instead of swimming away (Jenkins 1969).
Cruise	Swimming by dominant fish around its territory to drive away other fish.

Table 3. Initial lengths and weights of fish used in equal-sized allopatric experiments.

Experiment and date	Brown Trout Fork length (mm)	Brown Trout Weight (g)	Cutthroat Trout Fork length (mm)	Cutthroat Trout Weight (g)
	Section I		Section II	
1 Feb. 1-8, 1988	141	26.78	148	27.86
	146	28.19	149	28.02
	140	26.21	141	26.39
	146	27.31	148	27.31
	146	27.86	137	26.03
	150	28.97	150	29.12
	Section II		Section I	
2 Feb. 9-16 1988	146	28.37	141	26.21
	145	27.66	138	26.01
	142	26.32	149	28.09
	141	26.49	142	26.19
	150	28.65	150	29.09
	146	27.43	148	27.35
	Section I		Section II	
3 Aug. 4-11 1987	153	35.85	154	36.19
	146	32.48	151	35.71
	135	24.92	143	29.51
	151	37.76	144	25.65
	142	28.71	148	32.87
	Section II		Section I	
4 Aug. 23-30 1987	139	25.35	141	28.12
	142	30.54	147	32.19
	141	30.88	143	32.12
	144	29.23	141	24.18
	145	32.48	136	23.87

Table 4. Initial lengths and weights of fish used in equal-sized sympatric experiments.

Experiment and date	Section	Brown Trout		Cutthroat trout	
		Fork length (mm)	Weight (g)	Fork length (mm)	Weight (g)
1	I	138	25.16	136	22.42
Jan. 14-		128	19.05	135	23.67
21, 1988		134	25.37	145	27.69
	II	131	20.17	134	24.14
		138	24.69	136	19.64
		143	27.47	146	27.83
2	I	129	21.94	134	25.21
Jan. 22-		127	22.06	128	22.36
29, 1988		131	24.24	127	22.01
	II	132	20.68	134	21.31
		133	20.93	133	20.43
		132	20.94	134	19.80
3	I	146	32.22	142	32.75
Feb. 17-		145	26.89	137	25.40
24, 1988		146	29.79	148	31.47
	II	149	35.54	148	34.91
		141	27.00	141	26.57
		140	27.76	150	35.87
4	I	146	36.40	144	29.44
Sept. 11-		148	37.03	149	37.57
18, 1987		144	29.23		
	II	149	33.74	149	36.02
		148	35.84	144	34.64

1500h each day for 3 days. The fish to be observed in each section were chosen randomly using Cochran and Cox's experimental design table (Neter et al. 1985). Each fish was observed for 30 minutes each day. The agonistic behaviors were observed and number of attacks were recorded.

After 3 days of observation, the trout in each section were replaced with a new group of the other species--cutthroat trout in section II and brown trout in section I. The same acclimation and observation procedures as in the previous tests were followed. These experiments were done twice with 6 fish and twice with 5 fish for each species (Table 3). Therefore, 22 fish of each species were observed, and 6 site locations (1 at the beginning and 1 at the end of each of the 3 daily observation periods) and 3 30-minute observations were recorded for each fish.

Sympatry experiments. Four groups of cutthroat trout, averaging 141 mm fork length (range 127-150 mm) and 27.63 g (range 19.64-37.57 g), and 4 groups of brown trout averaging 139 mm (range 127-149 mm) and 27.14 g (range 19.05-35.84 g) were chosen separately (6 fish of each species in each of the first 3 groups and 5 fish of each species in the fourth group). Three fish of each species in the first group were randomly distributed to section I and section II. After 5 days' acclimation, the same observations and position measurements as in the allopatry experiments were made for 3 days, then the fish in the channel were replaced by 6 new fish from the second group of each species. The experiment was repeated on the second group and on a third group of fish. A fourth and a fifth group of fish were tested in the same way as were groups 1 to 3, except that 5 fish of each species were used, 2 of them in one section, and 3 in the other (Table 4).

In 32 days of sympatry experiments, 23 fish of each species were observed. Six observations of site occupation and 3 30-minute behavior observations were recorded for each fish.

Interactions Between Fish of Unequal Size

All fish for the unequal-size test were acclimated in another channel similar to that used in the tests in the same room for 12 days before starting the tests. Water velocity and light intensity were the same as in the experiments with equal-sized fish.

Ten cutthroat trout, ranging from 108 to 180 mm fork length and from 11.21 to 54.54 g in weight were selected to form 5 pairs of fish, with each pair being composed of fish having approximately equal size, and 4 brown trout of almost uniform size (146-149 mm fork length and 32.22-

Table 5. Initial lengths and weights of fish used in tests with unequal-sized fish.

Experiment and date	Pair number by size rank	Species	Section I		Section II	
			Fork length (mm)	Weight (g)	Fork length (mm)	Weight (g)
1	1	cutthroat[a]	180	54.54	185	57.22
Feb. 25–	2	cutthroat[a]	158	38.09	160	39.63
29, 1988	3	cutthroat[a]	150	32.86	152	35.94
	4	brown[b]	146	32.22	149	35.45
	5	cutthroat[a]	125	19.15	138	22.75
	6	cutthroat[a]	108	11.21	103	10.55
2	1	cutthroat	185	57.22	180	54.54
Feb. 29–	2	cutthroat	160	39.63	158	38.09
Mar. 5,	3	cutthroat	152	35.94	150	32.86
1988	4	brown	146	36.98	147	35.22
	5	cutthroat	138	22.75	125	19.15
	6	cutthroat	103	10.55	108	11.21
3	1	cutthroat	183	54.87	180	58.32
Mar. 6–	2	cutthroat	163	48.01	164	40.35
13, 1988	3	brown	150	41.82	154	39.63
	4	cutthroat	152	40.06	153	36.01
	5	cutthroat	125	19.32	134	22.04
	6	cutthroat	118	11.71	105	10.84

a These same pairs of fish were used in experiment 2 but with sections reversed.

b Different brown trout were used in all experiments.

36.98 g weight) were chosen as experimental animals (Table 5). After the traps were blocked, 1 fish from each pair of cutthroat and 1 brown trout were put in section I and the other cutthroat and 1 brown trout in section II. The two extra brown trout were put in the blocked trap to acclimate for future use.

Eighteen hours later, fish behavior was observed, and number of attacks between the largest cutthroat trout and the brown trout in each section were recorded for 3 30-minute periods each day. On day 4 of the experiment, the position of each fish was recorded 3 times (0900, 1200, 1500 h), after which the brown trout were removed from both sections. After 18 hours, the sites occupied by cutthroat trout were recorded at 0900, 1200, and 1500 h.

After all the observations, the cutthroat trout in section I and II were switched, and the 2 brown trout in the trap were put into section I and II. After 42 hours of acclimation, the number of attacks between the largest cutthroat trout and brown trout were recorded for 3 30-minute periods (0900-0930, 1200-2130, and 1500-1530 h) each day for 3 days. On day 5 of the experiment, sites of occupation were recorded at 0900, 1200, and 1500 h. The brown trout were then removed from the channel, and after an 18-hour wait, the position of cutthroat trout were recorded at 0900, 1200, and 1500 h. Then all fish were removed from the channel.

Five more pairs of cutthroat trout in the 105-183-mm range of fork length and 10.84-58.23 g weight, and 1 pair of brown trout (150-154 mm and 39.62-41.82 g--Table 6) were chosen. One fish from each pair was put in section I and the other in section II. After 2 days of acclimation, the number of attacks between the largest cutthroat trout and the brown trout were recorded 3 times a day. On day 7, sites of occupation were recorded 3 times (0900, 1200, 1500 h), after which the brown trout were removed from the channel. Eighteen hours later, the positions of cutthroat trout were recorded at 0900, 1200, and 1500 h.

Among the 6 runs of the experiment, the average length of the largest cutthroat trout was 1.23 times (range 1.17 to 1.27) that of the brown trout, and the average weight of the largest cutthroat trout was 1.53 times (range 1.31 to 1.69) that of the brown trout. The average length of the second largest cutthroat trout was 1.08 times that of the brown trout (range 1.06 to 1.09), and the average weight of the second largest cutthroat trout was 1.10 times that the of brown trout (range 1.02 to 1.18, Table 5).

Interactions Between Equal-sized Fish in Different Combinations of Light Regimen and Water Current

Allopatry experiments. Five brown trout averaging 145 mm fork length (range 135-152 mm) and 31.90 g (range 28.71-37.76 g) were acclimated in section I, and 5 cutthroat trout averaging 148 mm (range 143-154 mm) and 31.99 g (range 25.56-36.19 g) were acclimated in section II. The stream aquarium was lit by the fluorescent lights described above, and the flow was generated by the first motor speed, which produced a discharge of 9.5 L/s and water velocities ranging from 0 to 20 cm/s (Table 1).

After 5 days of acclimation, sites of occupation were recorded twice a day for 3 days. Two fish were randomly chosen for 30-minute observation of agonistic behavior in each section each day.

On the third observation day, after completing all observations, the motor was changed to the second speed, which produced a discharge of 12.4 L/s and velocities of 0 to 27 cm/s (Table 1). After 42 hours of acclimation, the above observations were repeated.

After this second period of observations, a new nighttime light intensity was instituted. Instead of no nighttime lighting (other than minimal light leakage from outside the aquarium room), 35 red Cilvestry miniature Christmas tree bulbs, strung 75 cm above the water surface were turned on at night. After a 50-hour acclimation, a third period of nighttime observations (between 2100h and 0100h) was conducted in the same way as during periods 1 and 2.

After these observations, water current was restored to the original discharge of 9.5 L/s. After a 44-hour acclimation, a fourth series of nighttime observations was made. After all 4 periods of observations were done, the fish were removed and weighed again.

The 4 experiments described above were then repeated with new fish, but the cutthroat trout were put in section I and the brown trout in section II.

Sympatry experiments. Three brown trout, averaging 146 mm fork length and 34.22 g, and 2 cutthroat trout averaging 147 mm and 33.51 g were put in section I. Two brown trout, averaging 148 mm and 34.79 g, and 3 cutthroat trout, averaging 147 mm and 35.02 g were put in section II. After a 5-day acclimation at 10.5 cm/s water velocity and fluorescent light, the experiments were conducted exactly as in allopatry. The sympatry experiment was not done twice because the 2-section experiment was a repetition.

RESULTS

Qualitative Observations of Agonistic Behavior

Seven agonistic activities (Table 2) were identified during this study. These activities were commonly expressed by brown trout and cutthroat trout in both inter- and intraspecific interactions.

When first introduced into the aquarium, whether as single- or mixed-species groups, the trout would rest motionless on the bottom, would be exceedingly sensitive to movement of other fish or of the observer, and would be easily caused to dash wildly about. For brown trout, this initial phase of high sensitivity lasted about 10 to to 30 minutes; for cutthroat trout, 3 to 15 minutes. After this phase of resting and high sensitivity, they would begin swimming about the tank, up the sides, and into the corners as though trying to escape. An hour to a day later, this activity was replaced by aggressive social interaction.

The first social interaction between 2 fish in an aquarium group would typically consist of reciprocal threat displays and fighting, resulting in dominance of 1 fish over the other. The aggressive displays were essentially the same in both species, but some were more elaborately developed in 1 species and some in the other.

Approach (Table 2) was the essential way in which cutthroat trout reacted to each other in intraspecific bouts. Cutthroat trout, in competing for social dominance, usually made approaches instead of direct attacks. Brown trout, however, often attacked directly to win the competitive bouts. The main displays were frontal and lateral displays. Wigwag displays were done only by brown trout, and they did them in both intra- and interspecific bouts. In most appeasement displays of cutthroat trout, the subordinate fish would rise to the surface of water and remain there motionless, whereas the brown trout appeasement display was a sinking to the bottom followed by motionlessness. Cruise behavior was basically the same in both species, but brown trout undertook it more often than cutthroat trout did.

Competition Between Equal-sized Fish Under Constant Current and Single Light Regimen

Because food was introduced at the upper end of each pool (Fig. 2) and current was slow in the pools (Figs. 4 and 5), greatest energetic advantage would exist at the upper ends of pools, and the advantage would decrease downstream from that area. Fish of both species preferred the sites offering greatest energetic advantage (Fig. 6). Sites in upstream riffles were least preferred by both species (Fig. 6). Therefore, the distribution of occupied sites and the distance between occupied sites and the food source provided evidence for determining the dominant competitor.

In sympatry, the dominant brown trout maintained positions upstream of cutthroat trout in the pool and drove many of them into downstream and upstream riffles (Fig. 6c). Brown trout were more concentrated in pools than were cutthroat trout. Among the 108 observations of brown trout, 81% were in pools, and 19% were in downstream riffles. Only 28% of sites held by cutthroat trout were in pools, 36% were in downstream riffles, and 36% were in upstream riffles.

In allopatry, cutthroat trout occupied pools more than riffles (Fig. 6a). Of 72 observations, 57% were in pools, and 43% were in riffles. The proportion of sites on downstream riffles (35%) was almost the same as in sympatry, whereas that on upstream riffles (18%) was much less than in sympatry. On the other hand, the proportion of brown trout sites in pools was greater in sympatry than in allopatry (Figs. 6c and 6b), 87% in contrast to 65%. Brown trout occupation of upstream riffles increased from none in sympatry to 24% in allopatry, and occupation of downstream riffles decreased from 19% in sympatry to 11% in allopatry.

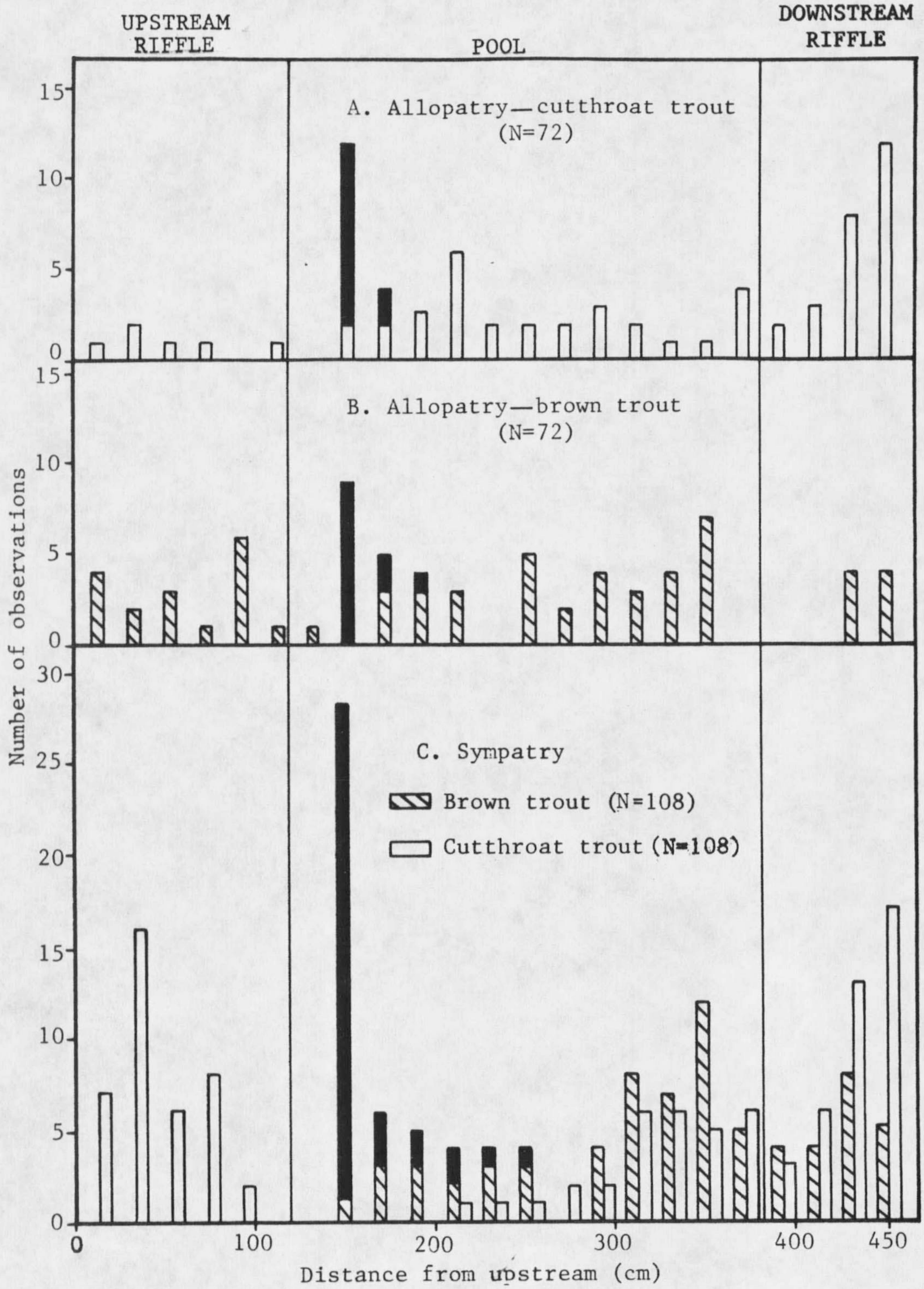

Figure 6. Distribution of observed site occupations by equal-sized cutthroat and brown trout in allopatry and sympatry. Black portion of bars are positions of the dominant fish.

In the 8 sympatry experiments, the 8 fish holding the sites farthest upstream in pools were brown trout. Each of these dominant brown trout controlled the upper 2/3 of its pool and drove all cutthroat trout and other brown trout into the downstream 1/3 of the pool or into riffles. Some cutthroat trout were driven into upstream riffles.

Another way of regarding much the same situation is in terms of distance from the place where food entered the channel (food-source distance). In sympatry, cutthroat trout were significantly farther from the food source than were brown trout (314 vs. 141 cm, $p<0.001$), but in allopatry, mean food-source distances of the 2 species were not significantly different (195 vs. 204 cm, Fig. 7). Mean food-source distance of cutthroat trout in sympatry was significantly greater than that in allopatry, 314 vs. 195 cm ($p<0.001$), but for brown trout, sympatric food-source distance was not significantly different from the distance in allopatry, 141 vs. 204 cm (Fig. 7).

In measurements of number of attacks, cutthroat trout were involved in (initiated or received) significantly more attacks per unit time during sympatry than during allopatry, 26 vs. 6/h/fish ($p<0.001$), but for brown trout, there was no significant difference in the sympatric and allopatric attack involvement rate, 36 vs. 30/h/fish (Fig.

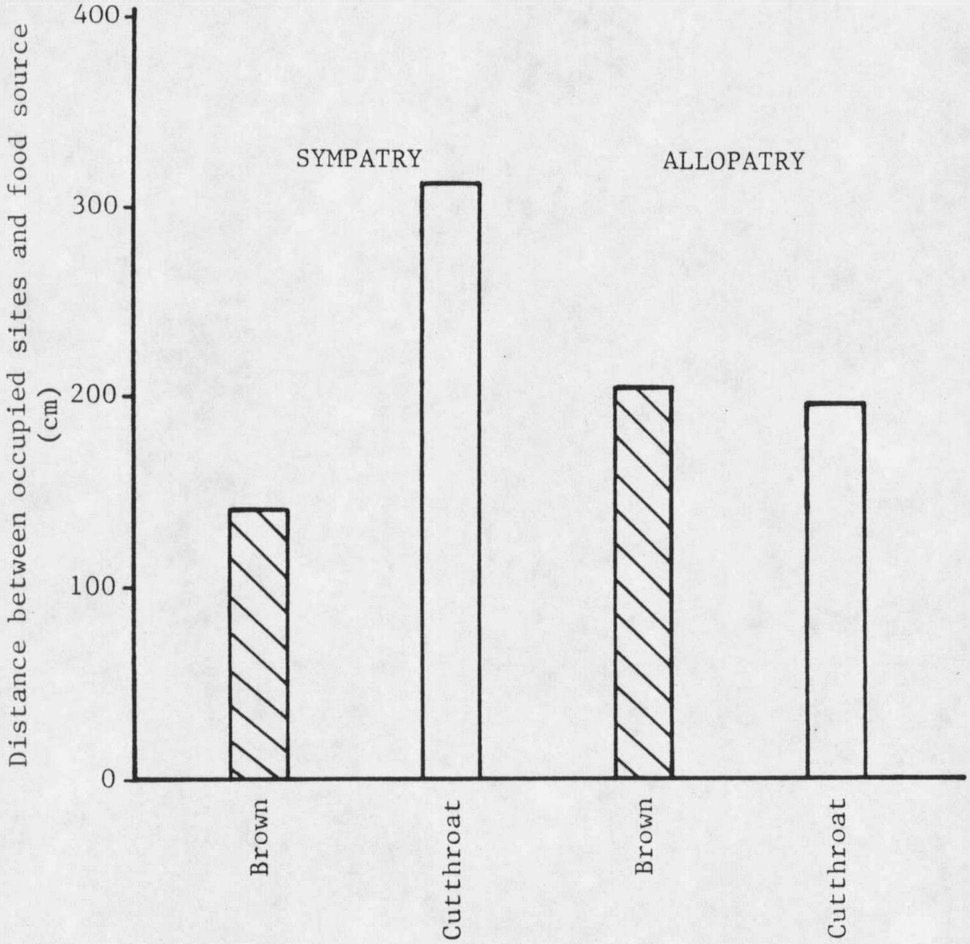

Figure 7. Food-source distance of brown and cutthroat trout in sympatry and allopatry.

8). Brown and cutthroat trout had essentially the same attack involvement rate during sympatry (36 vs. 28/h/fish). During allopatry, brown trout were involved in significantly more attacks than cutthroat trout were (30 vs. 6/h/fish, Fig. 8).

In all 8 sympatric tests, cutthroat trout had significantly more attack interactions with brown trout than among themselves (62 vs. 6 attacks/h/fish, $p<0.001$). Brown trout interacted significantly more often with cutthroat trout than among themselves (62 vs. 28 attacks/h/fish, $p<0.001$). The intraspecific interaction of brown trout was significantly more intense than that of cutthroat trout (28 vs. 6 attacks/h/fish, $p<0.001$).

During the 4 runs of 8 sympatry experiments (74 observations on 46 fish), brown trout initiated 92% of the 2,224 attacks (Tables 6, 7, 8, and 9). The number of attacks initiated by brown trout was 11.5 times that of cutthroat trout (Table 10).

Competition Between Unequal-sized Fish Under Constant Current and Single Light Regimen

In the previous 8 sympatry experiments with fish of equal size, all of the most dominant fish were brown trout. This experiment was conducted to test competition of brown trout with cutthroat trout that were larger than

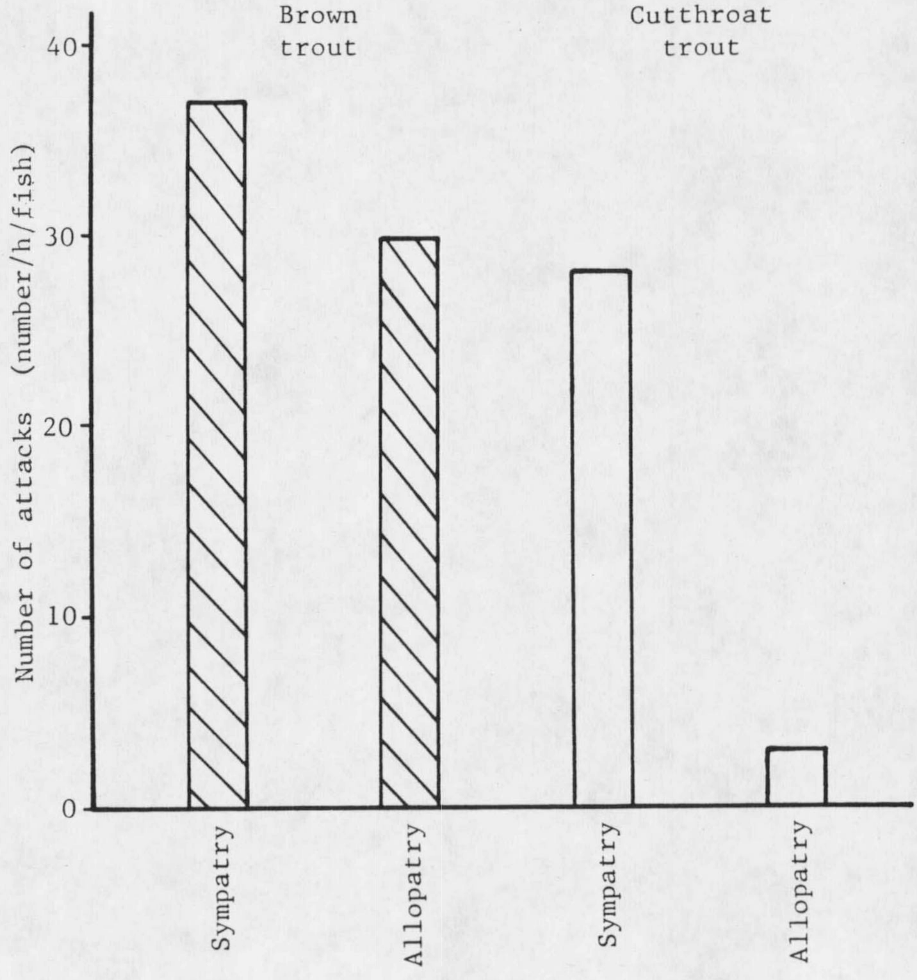

Figure 8. Attack involvement rates of brown and cutthroat trout in sympatry and allopatry.

Table 6. Initiating and receiving fish in attacks between equal-sized brown and cutthroat trout in constant current and and single light regimen--Experiment 1.

Initiator	Receiver: Brown trout 1*	2	3	7	8	9	Cutthroat trout 4	5	6	10	11	12	Total initiations
Brown trout													
Group 1													
1*	-	5	11	-	-	-	28	9	14	-	-	-	67
2	11	-	14	-	-	-	15	19	15	-	-	-	74
3	0	5	-	-	-	-	29	20	25	-	-	-	79
Group 2													
7	-	-	-	-	0	0	-	-	-	27	14	14	55
8	-	-	-	25	-	6	-	-	-	22	2	33	88
9	-	-	-	26	21	-	-	-	-	42	4	83	176
Cutthroat trout													
Group 1													
4	0	0	0	-	-	-	-	6	1	-	-	-	7
5	0	0	0	-	-	-	0	-	0	-	-	-	0
6	0	0	2	-	-	-	13	20	-	-	-	-	35
Group 2													
10	-	-	-	0	0	0	-	-	-	-	4	3	7
11	-	-	-	0	0	0	-	-	-	0	-	0	0
12	-	-	-	0	0	0	-	-	-	15	10	-	25
Total receptions	11	10	27	51	21	6	85	74	55	106	34	133	613

* Individual identification number of the fish

Table 7. Initiating and receiving fish in attacks between equal-sized brown and cutthroat trout in constant current and single light regimen--Experiment 2.

	Receiver												
	Brown trout						Cutthroat trout						Total
Initiator	4*	5	6	7	8	9	1	2	3	10	11	12	initiations
Brown trout													
Group 1													
4*	-	48	10	-	-	-	33	16	16	-	-	-	123
5	0	-	9	-	-	-	22	8	1	-	-	-	40
6	0	2	-	-	-	-	19	25	4	-	-	-	50
Group 2													
7	-	-	-	-	0	0	-	-	-	8	20	6	34
8	-	-	-	9	-	50	-	-	-	62	12	15	148
9	-	-	-	8	0	-	-	-	-	30	6	4	48
Cutthroat trout													
Group 1													
1	0	0	0	-	-	-	-	13	6	-	-	-	19
2	0	0	0	-	-	-	0	-	2	-	-	-	2
3	0	0	0	-	-	-	0	0	-	-	-	-	0
Group 2													
10	-	-	-	2	0	0	-	-	-	-	5	7	14
11	-	-	-	0	0	0	-	-	-	0	-	0	0
12	-	-	-	2	0	0	-	-	-	0	2	-	4
Total receptions	0	50	19	21	0	50	74	62	29	100	45	32	482

* Individual identification number of the fish.

Table 8. Initiating and receiving fish in attacks between equal-sized brown and cutthroat trout in constant current and single light regimen--Experiment 3.

	Receiver												
	Brown trout						Cutthroat trout						Total
Initiator	1*	2	3	7	8	9	4	5	6	10	11	12	initiations
Brown trout													
Group 1													
1*	-	40	47	-	-	-	22	29	35	-	-	-	173
2	11	-	0	-	-	-	4	13	2	-	-	-	30
3	10	10	-	-	-	-	10	11	10	-	-	-	51
Group 2													
7	-	-	-	-	25	89	-	-	-	64	16	39	233
8	-	-	-	0	-	0	-	-	-	0	3	3	6
9	-	-	-	0	26	-	-	-	-	44	9	25	104
Cutthroat trout													
Group 1													
4	0	0	0	-	-	-	-	0	1	-	-	-	1
5	0	0	0	-	-	-	0	-	0	-	-	-	0
6	0	0	0	-	-	-	0	0	-	-	-	-	0
Group 2													
10	-	-	-	0	7	3	-	-	-	-	4	1	15
11	-	-	-	0	0	0	-	-	-	0	-	0	0
12	-	-	-	0	2	0	-	-	-	0	4	-	6
Total receptions	21	50	47	0	60	92	36	53	48	108	36	68	619

* Individual identification number of the fish.

Table 9. Initiating and receiving fish in attacks between equal-sized brown and cutthroat trout in different combination of light regimen and water current experiment.

Initiator	Receiver: Brown Trout 3*	4	5	9	10	Cutthroat trout 1	2	6	7	8	Total initiations
Brown trout											
Group 1											
3*	-	43	27	-	-	73	79	-	-	-	222
4	0	-	3	-	-	14	4	-	-	-	21
5	0	23	-	-	-	15	16	-	-	-	54
Group 2											
9	-	-	-	-	2	-	-	15	9	9	35
10	-	-	-	43	-	-	-	37	42	18	140
Cutthroat trout											
Group 1											
1	0	5	9	-	-	-	20	-	-	-	34
2	0	0	0	-	-	0	-	-	-	-	0
Group 2											
6	-	-	-	1	0	-	-	-	0	0	1
7	-	-	-	0	0	-	-	0	-	0	0
8	-	-	-	2	1	-	-	0	0	-	3
Total receptions	0	71	39	46	3	102	119	52	51	27	510

* Individual identification number of the fish.

Table 10. Attacks among equal-sized brown and cutthroat trout in constant current and single light regimen experiment.

Species	Number of observation hours	Number of fish observed	Attacks Initiated No.	%	CT:BT*	Attacks Involved in No.	%	CT:BT
Sympatry I								
CT	9	6	74	12		285	46	
BT	9	6	539	88		328	54	
Total	18	12	613		1:7.3			1:1.5
Sympatry II								
CT	9	6	39	8		198	41	
BT	9	6	443	92		284	59	
Total	18	12	482		1:11.4	482		1:1.4
Sympatry III								
CT	9	6	23	4		260	42	
BT	9	6	594	96		359	58	
Total	18	12	619		1:24.0	619		1:1.4
Sympatry IV								
CT	10	5	36	7		204	40	
BT	10	5	474	93		306	60	
Total	20	10	510		1:13.2	510		1:1.5
All sympatry								
CT	37	23	174	8		947	43	
BT	37	23	2,050	92		1,277	57	
Grand total	74	46	2,224		1:11.5	2,224		1:1.3

* CT = Cutthroat trout, BT = Brown trout

themselves.

Interactions between small brown trout and relatively larger cutthroat trout were basically the same as for equal-sized fish, but the brown trout had greater difficulty defending their territories. Smaller cutthroat trout would be allowed to feed in a brown trout territory temporarily, but cutthroat trout of the same or larger size as the brown trout would never be allowed to do this. Sites occupied by brown trout were generally farther downstream than those of the most dominant brown trout in the equal-size experiments. Brown trout used wigwag displays more often than in the equal-size experiments, and spent most of their time upstream of the largest cutthroat trout instead of making cruise displays. The number of attacks initiated by the largest cutthroat trout was almost the same as that by brown trout (Table 11).

In the 56 hours of observations on the largest cutthroat trout and brown trout, the most attacks were observed 18 to 22 hours after the fish were put into the aquarium. From then on, attack frequency declined for about 90 hours, after which it remained constant (Fig. 9).

In 18 observations on 6 equal-sized brown trout and 90 observations on 30 unequal-sized cutthroat trout in the sympatry, the positions held by brown trout were between 140 and 340 cm from the upstream end of the aquarium

Table 11. Initiation and receiving fish in attacks of the largest cutthroat and brown trout in experiment with fish of uneqal size.

Initiator	Receiver: Brown Trout 1	2	3	4	5	6	Cutthroat trout 7	8	9	10	11	12	Average initiations
Brown trout													
1							7,7,5*						6.3
2								9,8,3					6.7
3									9,13, 3, 4, 6, 3				6.3
4										8,8, 4,2, 1,3			4.3
5											8,9, 11,5, 5,5,7, 4,5,8		6.7
6												8,7, 7,3, 5,7, 7,6, 6,2	5.8
Cutthroat trout													
7	4,3, 6												4.3
8		7,5, 5											5.7
9			7,9, 6,6, 5,3										6.0
10				14,7, 5,4, 5,4									6.5
11					11,7, 8,6, 5,8, 3,5, 6,5								6.4
12						10,5, 9,5, 7,3, 6,3, 4,5							5.7
Average receptions	4.3	5.7	6.0	6.5	6.4	5.7	6.3	6.7	6.3	4.3	6.7	5.8	

* Each number represents number of attacks during a 30-minute observation.

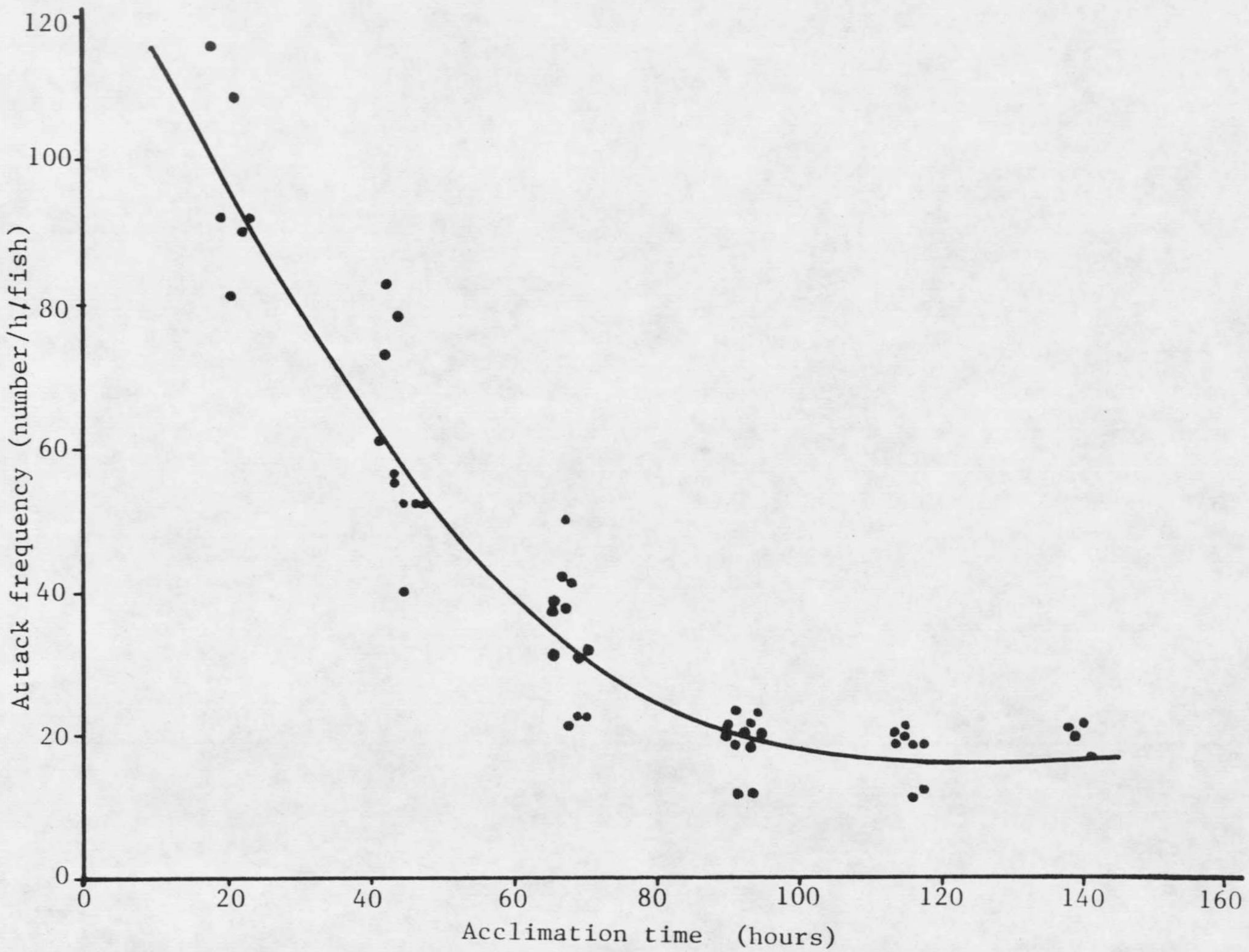

Figure 9. Relationship of acclimation time and number of attacks between the largest cutthroat and brown trout in different size fish experiment. Curve fitted by eye.

section, of which 67% were between 180 and 280 cm, the upper-middle part of the pool. Brown trout never occupied the upstream or downstream riffles. The sites held by the largest cutthroat trout were between 240 and 440 cm below the upstream end. Of these, 67% were at 320 to 380 cm, which was in the downstream part of the pool, and 22% were in the downstream riffle. The sites occupied by brown trout were significantly further upstream than that of the largest cutthroat trout (Fig. 10, $p<0.001$).

In 90 observations on 30 unequal-sized (103-185 cm in fork length) cutthroat trout in allopatry, after releasing competition from brown trout, the positions held by the largest fish were 140-300 cm from the upstream end of the aquarium, among which 78% were 140-220 cm (the upstream part of the pool). The largest cutthroat trout was never seen on upstream or downstream riffles. In allopatry, the largest cutthroat trout were distributed significantly farther upstream in the pool than they were in sympatry (Fig. 10a,b, $p<0.001$), as well as being farther upstream than were brown trout in sympatry (Fig. 10a,b, $p<0.001$).

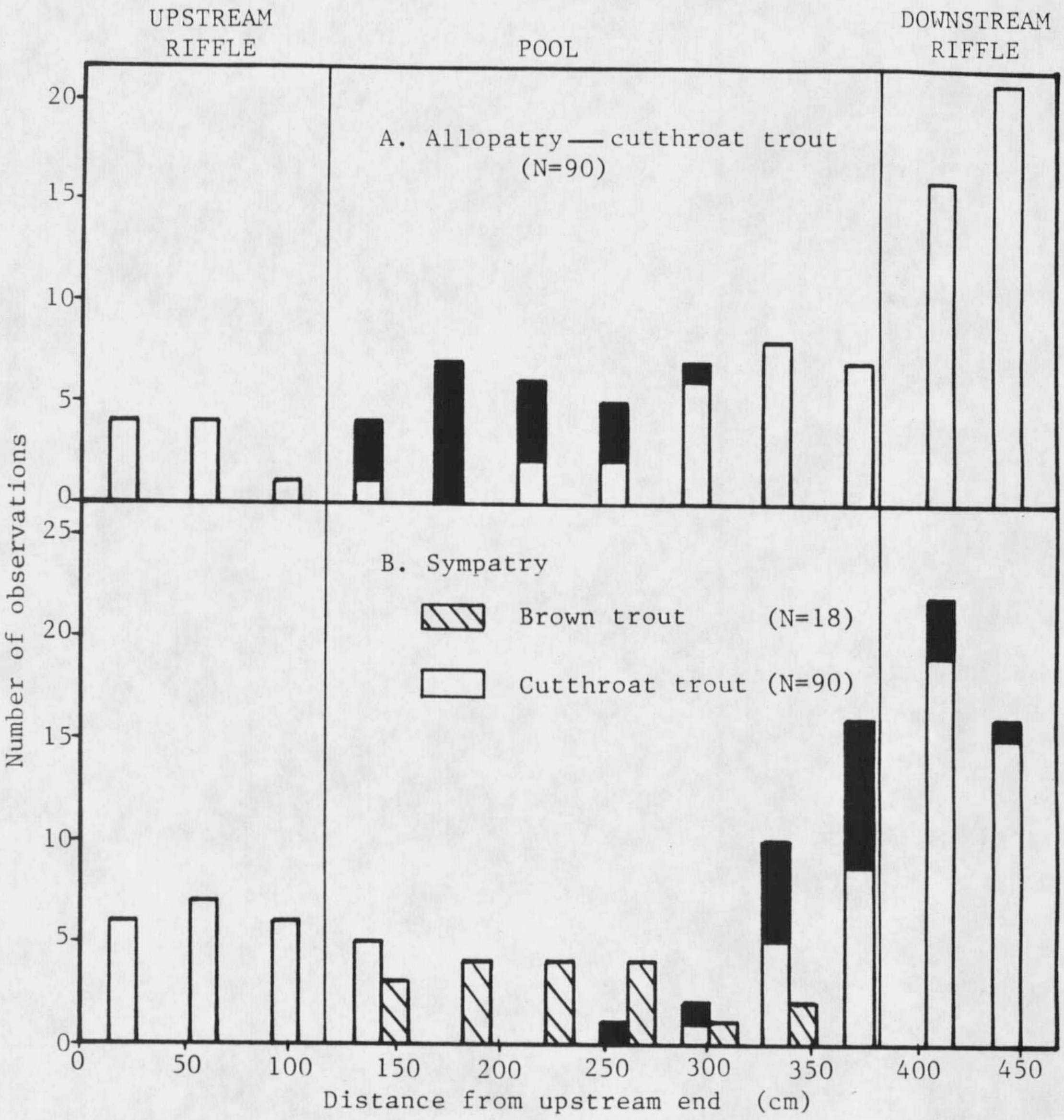

Figure 10. Distribution of positions held by different size cutthroat trout with brown trout (B) and without brown trout (A). Black portions of bars are positions of the largest cutthroat trout.

Competition Between Equal-sized Fish Under Different Combinations of Light Regimen and Water Current

Results of Competition

During sympatry (120 observations on 10 fish of each species under different light intensity regimens and water velocities), 54% of the sites occupied by brown trout were in pool areas (91% of these in the upstream part of the pool), 43% were in downstream riffles, and only 3% were in upstream riffles. In contrast with brown trout, only 23% of cutthroat trout positions were in pools (89% of them in downstream area of pools), 68% in upstream riffles, and 9% in downstream riffles (Fig. 11c).

Without interspecific competition, the proportion of cutthroat trout positions in upstream riffles decreased from 68% (sympatry) to 6% (allopatry). The proportion of occurrence in pools increased from 23% in sympatry to 52% in allopatry. In the downstream riffle, the proportion went from 9% to 42% (Fig. 11a,c). Brown trout showed just the opposite pattern, reducing their downstream riffle occupation from 43% in sympatry to 25% in allopatry, increasing their upstream riffle occupations from 3% to 17%, and increasing their pool occupancy from 54% to 68% (Fig. 11b,c).

During the two 17-day experiments, all fish lost

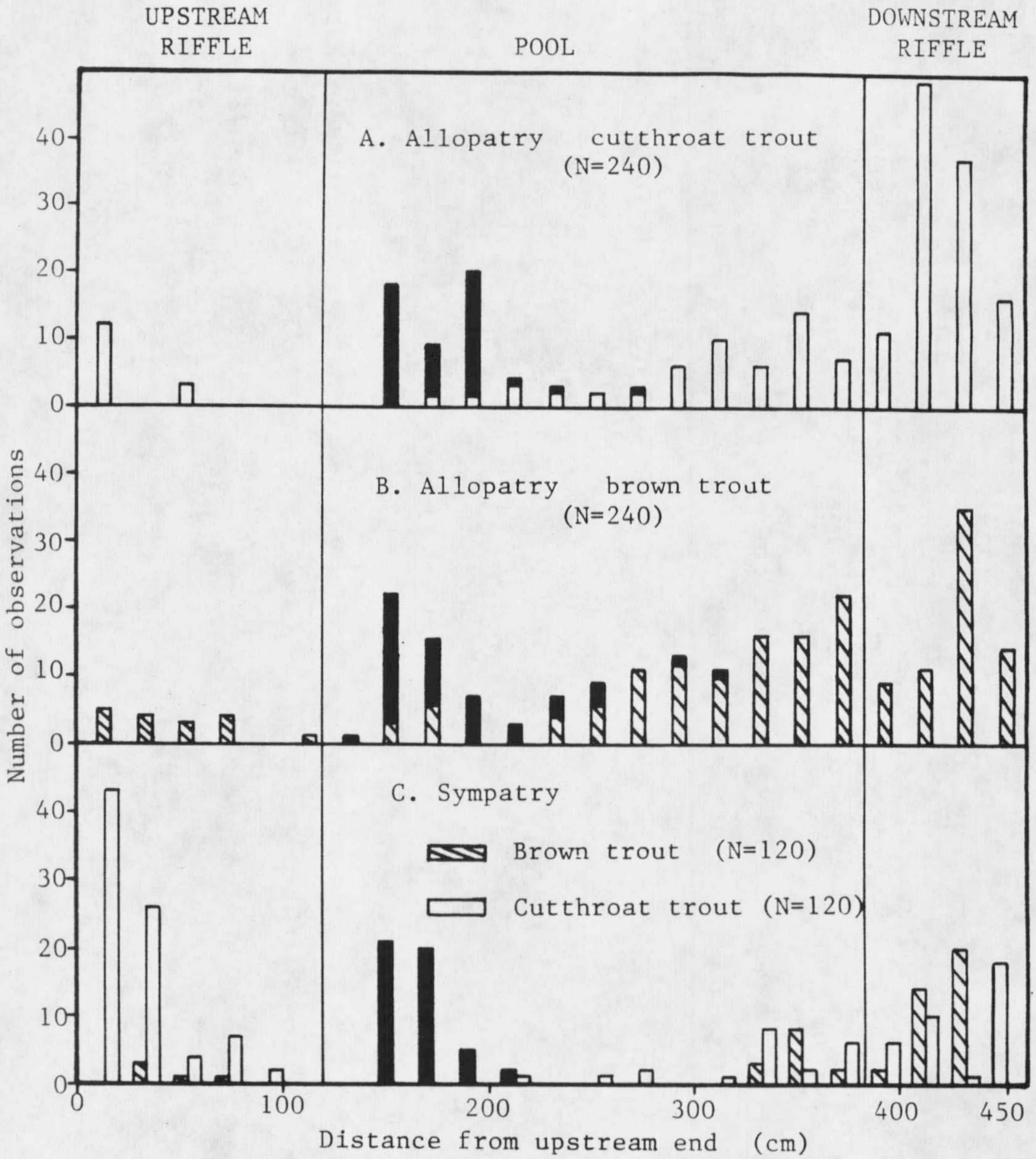

Figure 11. Numbers of observations of sites occupied by cutthroat and brown trout during allopatry and sympatry under different combinations of light regimen and water current. Black portions of bars are positions of the dominant fish (all brown trout in C).

weight in both sympatry and allopatry. In allopatry, weight loss was slower for cutthroat trout than for brown trout (5.51% vs. 6.08%). But in sympatry, cutthroat trout lost weight significantly faster than brown trout ($p<0.005$) and significantly more than in allopatry ($P<0.001$--Fig. 12). Brown trout lost slightly more weight in sympatry than in allopatry (7.97% vs. 6.08%).

In sympatry, brown trout attacks were constantly more numerous than those by cutthroat trout under each condition of light and current tested (Fig. 13), however, the differences in attack frequency were not statistically significant ($P>0.05$). In allopatry, attack frequency of brown trout was significantly higher than that of cutthroat trout under all light and current conditions tested (Fig. 14). Brown trout did not have any significant difference between sympatric and allopatric attack frequency in any of the light and current conditions tested (Fig. 15), but for cutthroat trout, attack frequency in sympatry was significantly higher than that in allopatry under each set of light and current conditions except the bright-light/fast-current test (Fig. 16).

In sympatry, brown trout were significantly closer to the food source than were cutthroat trout under each set of light and current conditions (Fig. 17b). In allopatry,

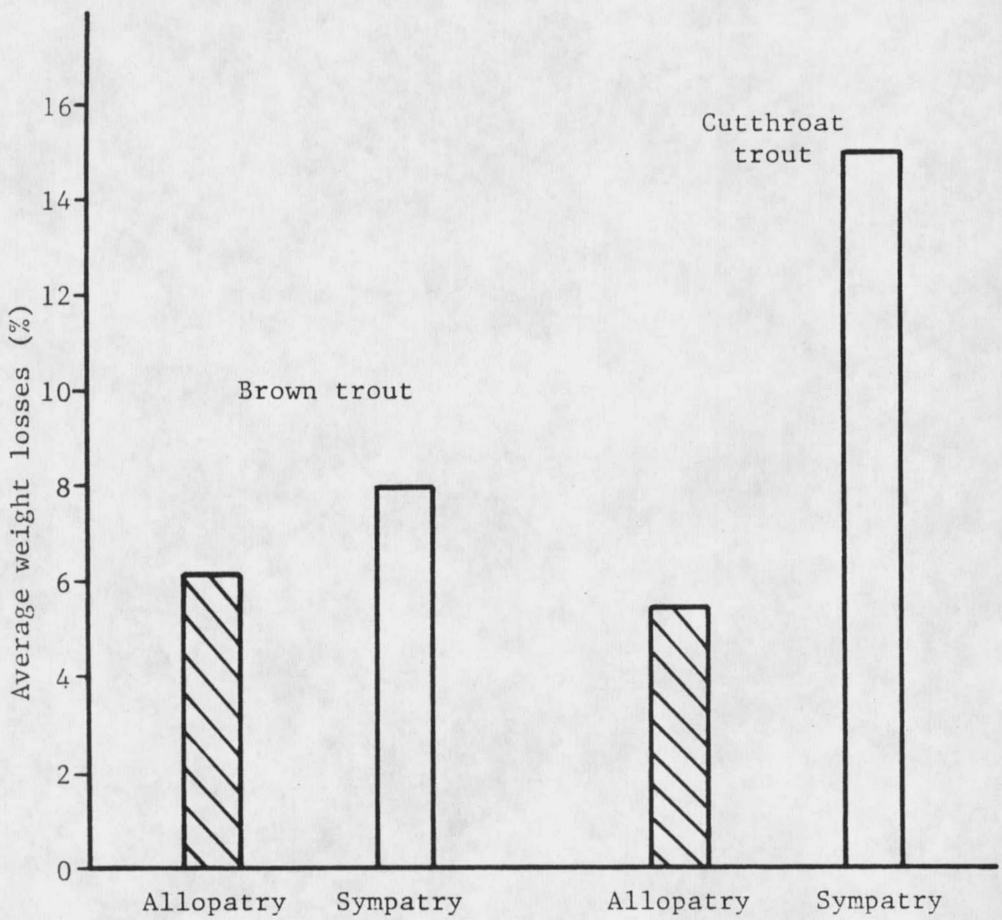

Figure 12. Weight losses of brown and cutthroat trout in sympatry and allopatry.

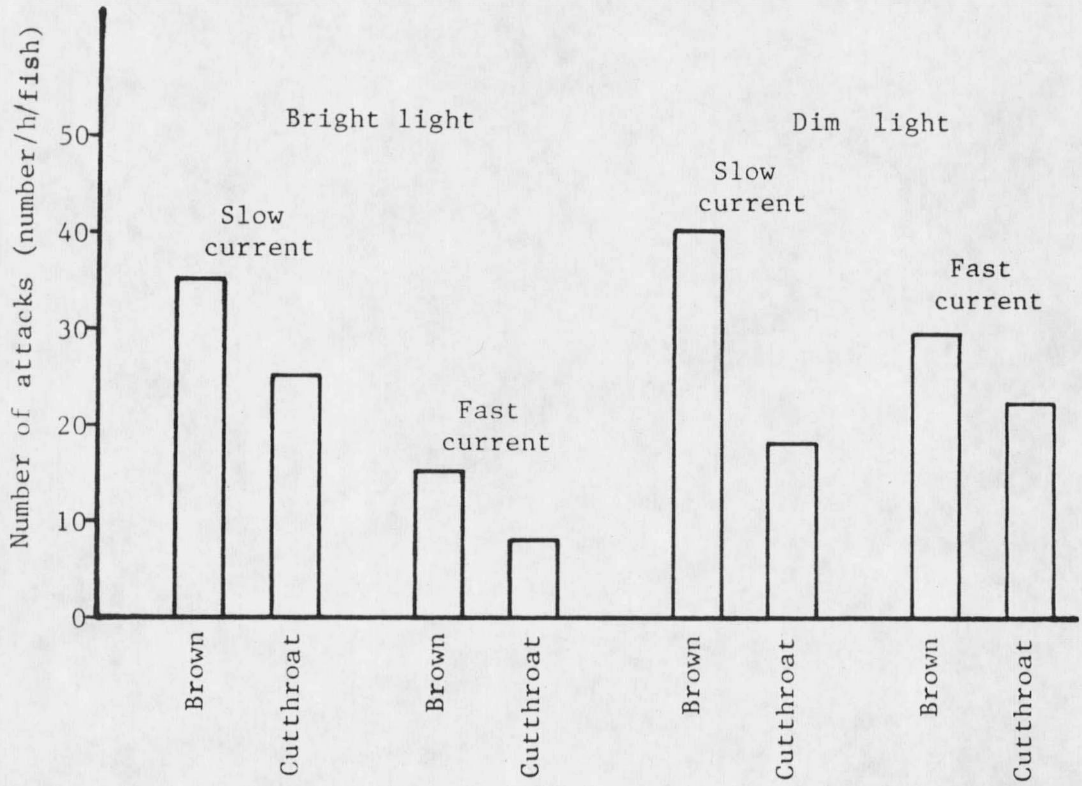

Figure 13. Sympatric frequency of attack involvement for brown and cutthroat trout under different conditions of light (Tables 22 and 23) and current (Tables 20 and 21).

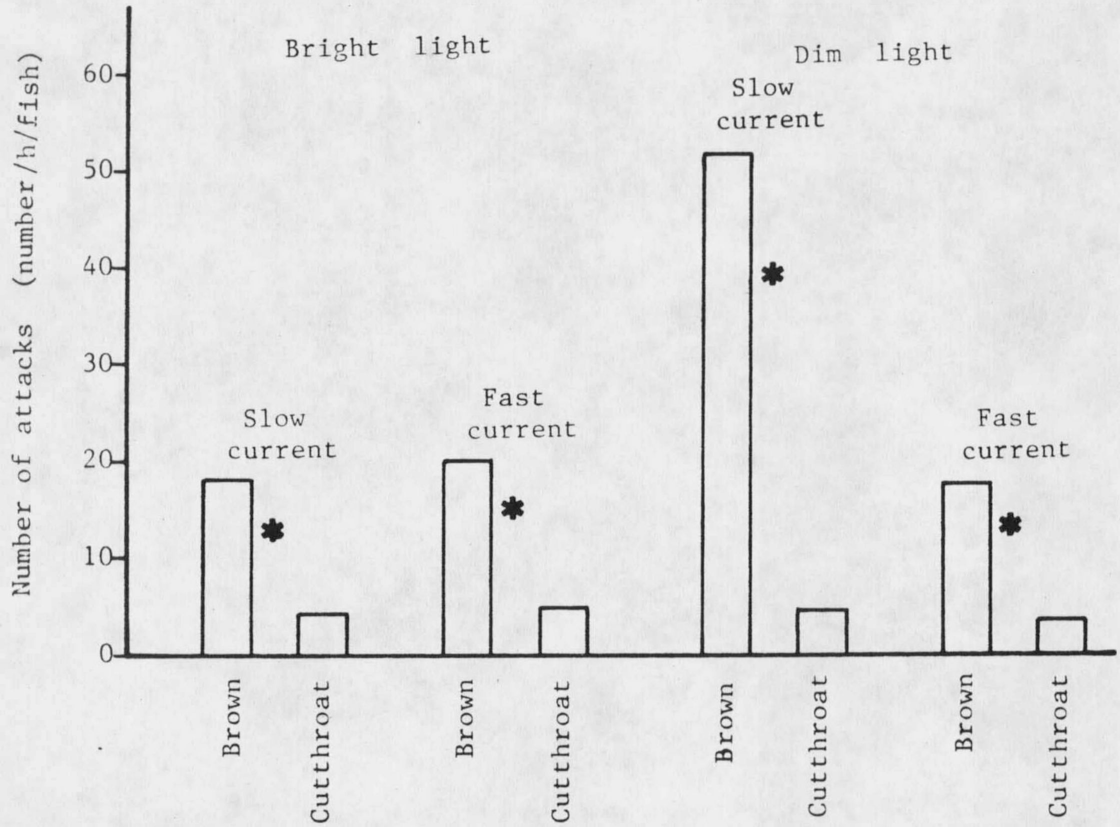

Figure 14. Allopatric frequency of attack involvement for brown and cutthroat trout under different conditions of light (Tables 22 and 23) and current (Tables 20 and 21). *=Paired T-test is significant, $P<0.05$.

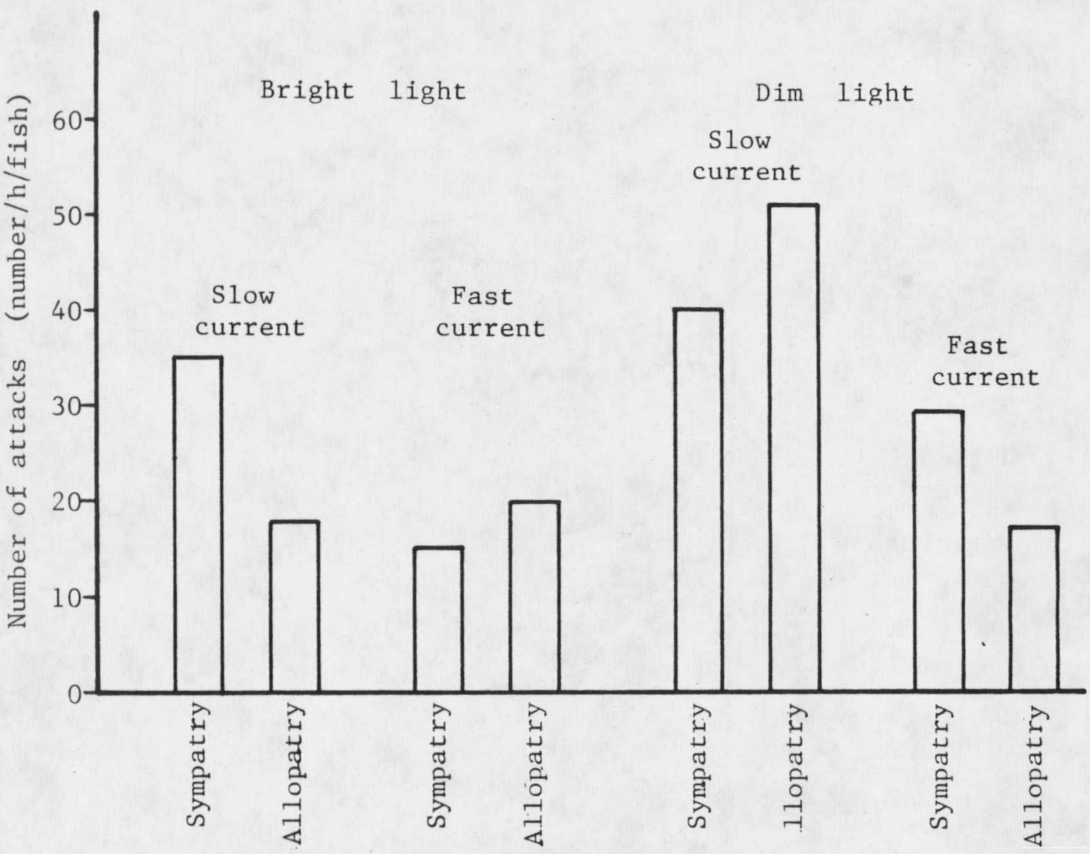

Figure 15. Attack involvement of brown trout in sympatry and allopatry.

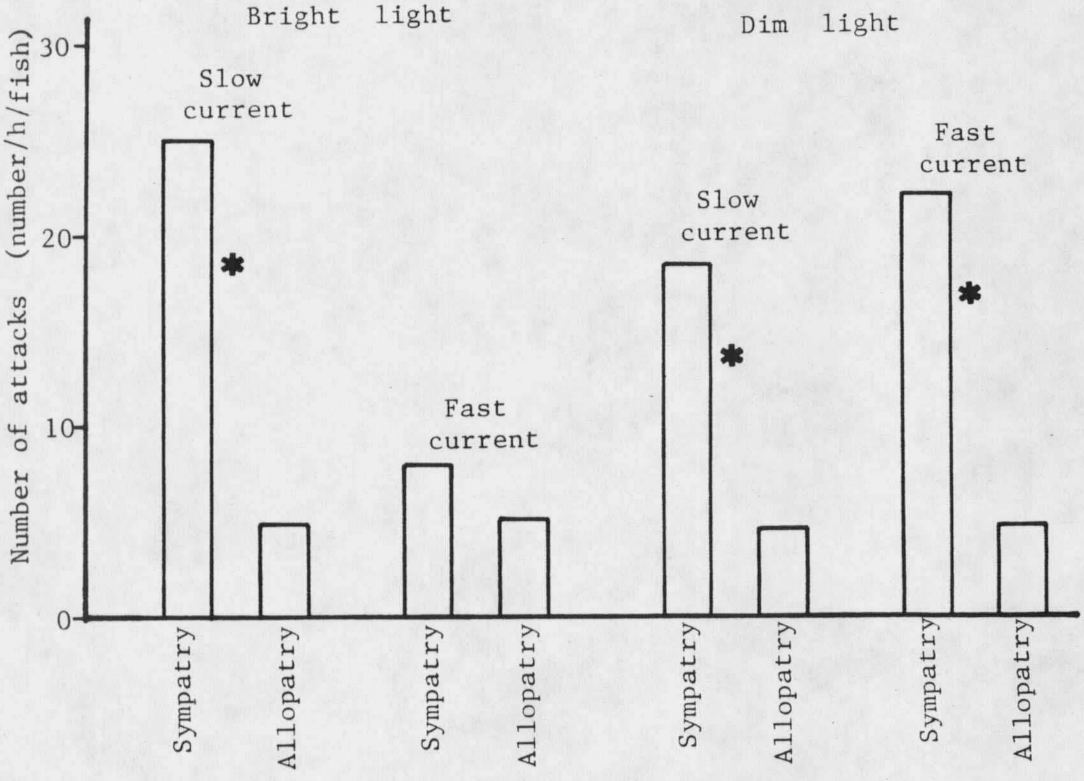

Figure 16. Attack involvement of cutthroat trout in sympatry and allopatry (* T-test is significant, $P<0.05$).

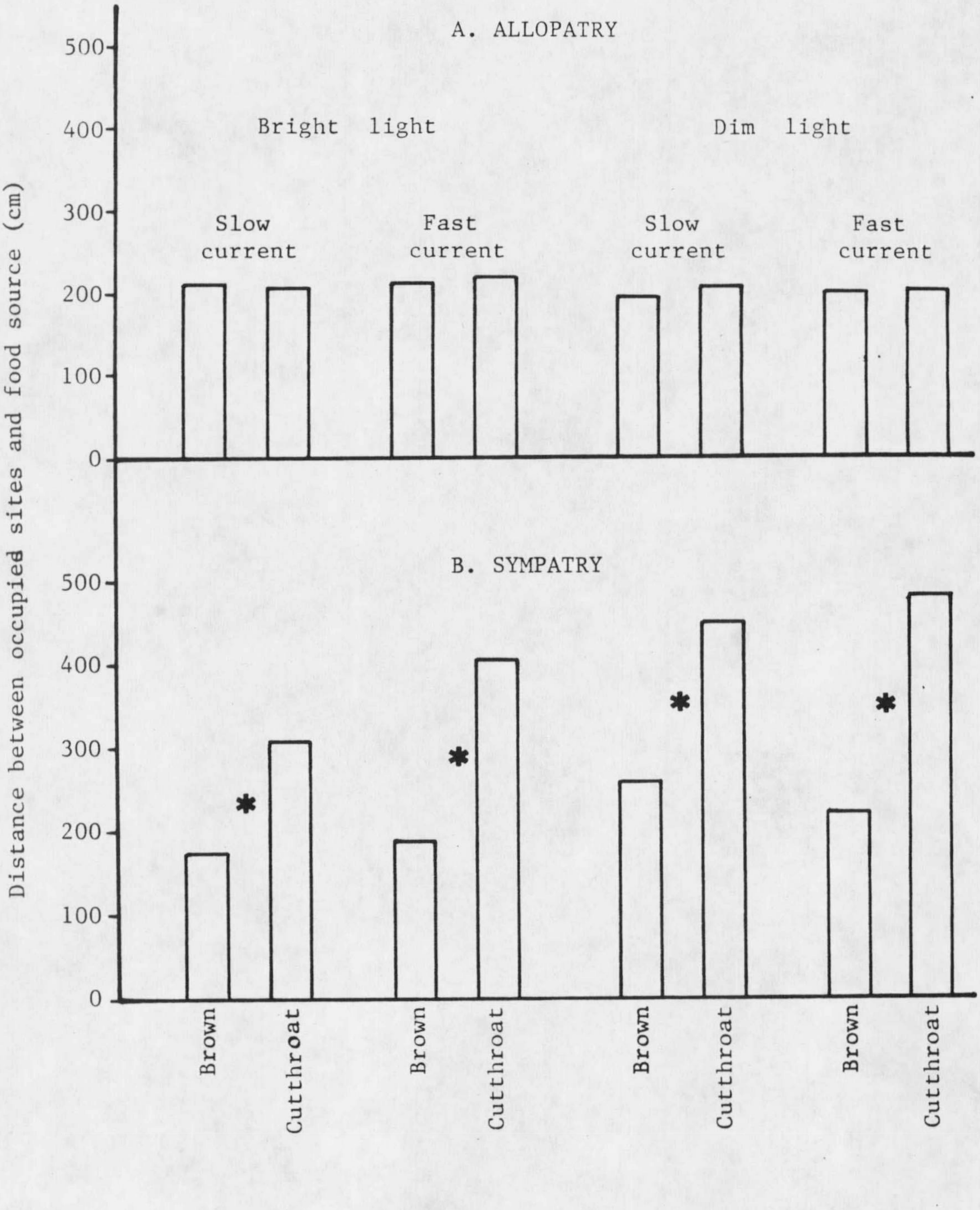

Figure 17. Mean distance between sites of occupation and food source for brown and cutthroat trout in sympatry and allopatry (* paired T-test significant, P<0.05).

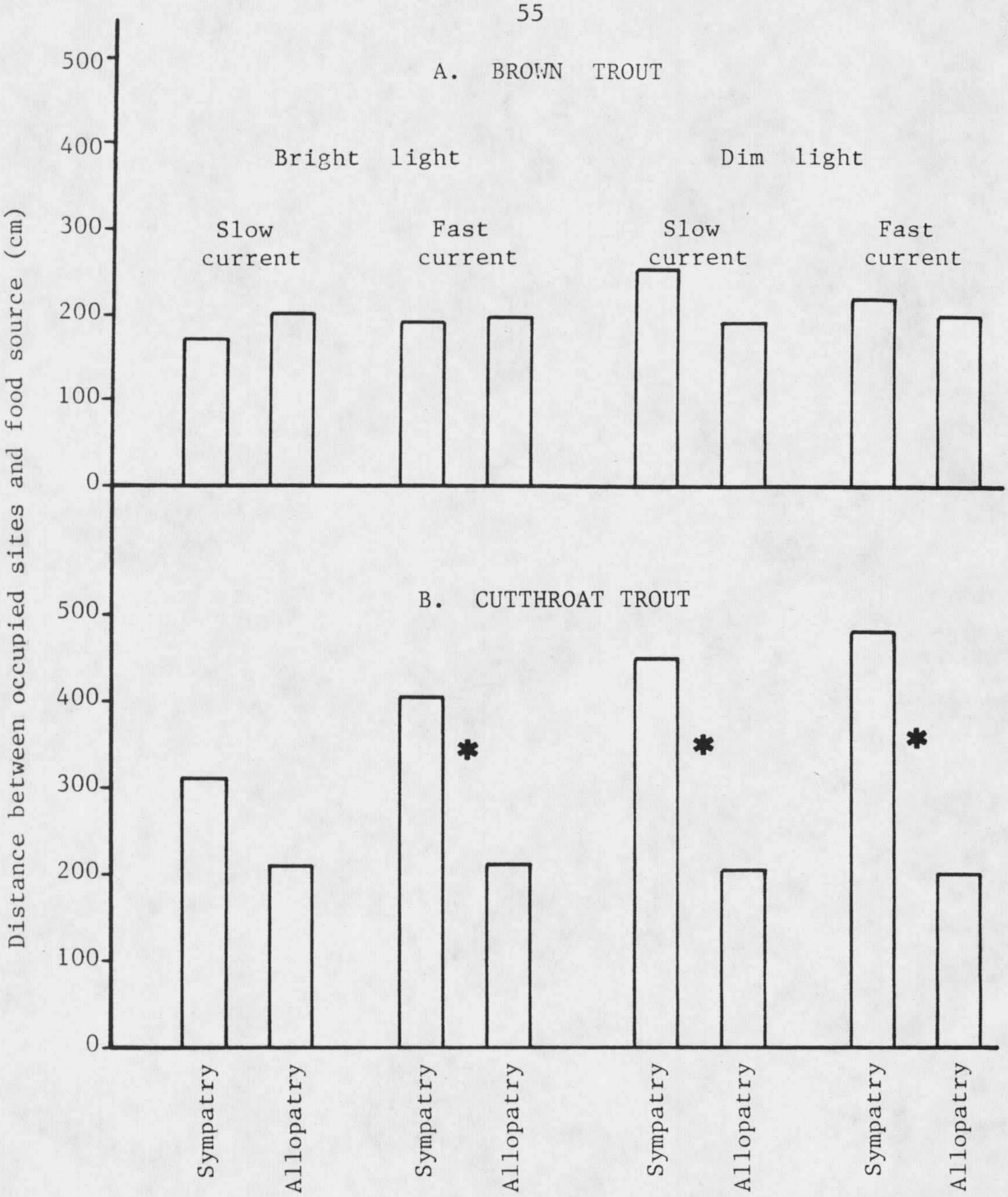

Figure 18. Distance between sites of occupation and food source for brown and cutthroat trout in sympatry and allopatry (* T-test is significant, P<0.05).

mean distance to food source was almost the same for brown trout as for cutthroat trout under each set of light and current conditions (Fig. 17a). Mean distance to food source was about the same for brown trout in allopatry and sympatry under each set of light and current conditions (Fig. 18a). However, for cutthroat trout, mean distance to food source in sympatry was significantly greater than in allopatry in each set of conditions except bright light and slow current (Fig. 18b).

Results of changes in light and current on fishbehavior.

Light intensity and water velocity, within the range tested (Appendix Tables 20-23), had no significant effect on attack frequency of cutthroat trout in either allopatry or sympatry (Tables 12, 12 and 13). However, brown trout in allopatry under slow current attacked significantly more often in dim than in bright light ($p<0.03$ in paired T-test, Table 12), and in dim light, they attacked significantly more often in slow than in fast current ($p<0.05$, Table 13). Both water velocity and light intensity significantly affected attack frequency of brown trout (Table 14), and these two factors had strong interaction ($p=0.0106$ in multi-factor ANOVA).

Light intensity and water velocity within the ranges studied had no significant effect on the food-source

Table 12. Paired T-test analysis of effects of light intensity on attacks and food-source distance of brown and cutthroat trout.

Trout species	Relative level of current	Attacks/h at relative light level: Bright	Dim	P-value	Food-source distance (cm) at relative light level: Bright	Dim	P-value
Allopatry (N=10)							
Cut-throat	slow	4.8	4.8	1.000	209	209	1.000
	fast	5.4	4.5	0.758	215	200	0.198
Brown	slow	18.3	51.6	0.026*	201	190	0.611
	fast	20.4	16.8	0.573	199	200	0.939
Sympatry (N=5)							
Cut-throat	slow	25.2	18.4	0.475	301	402	0.015*
	fast	8.0	22.4	0.184	402	483	0.093
Brown	slow	35.2	40.4	0.721	176	257	0.300
	fast	11.2	29.6	0.198	188	223	0.264

* Significant, $P<0.05$

Table 13. Paired T-test analysis of effects of water velocity on attacks and food-source distance of brown and cutthroat trout.

Trout species	Relative level of light	Attacks/h at relative current level: Slow	Fast	P-value	Food-source distance (cm) at relative current level: Slow	Fast	P-value
Allopatry (N=10)							
Cut-throat	bright	4.8	5.4	0.820	209	215	0.731
	dim	4.8	4.5	0.879	209	200	0.565
Brown	bright	18.3	20.4	0.406	201	199	0.911
	dim	51.6	16.8	0.004*	190	200	0.637
Sympatry (N=5)							
Cut-throat	bright	25.2	8.0	0.069	301	402	0.019*
	dim	18.4	22.4	0.665	449	483	0.531
Brown	bright	35.2	11.2	0.135	176	188	0.366
	dim	40.4	29.6	0.600	257	223	0.679

* Significant, $P<0.05$.

Table 14. Multi-factor ANOVA results of effects of light intensity and water velocity on attacks and food-source distance of brown and cutthroat trout.

Trout species	Relative level of light and current	Number of attacks (No./h)	P-value	Food-source distance (cm)	P-value
Allopatry (N=10)					
Cutthroat	fast	5.0		209	
	slow	4.8	0.950	208	0.976
	bright	4.7		205	
	dim	5.1	0.849	212	0.817
Brown	fast	18.6		200	
	slow	35.0	0.022*	196	0.885
	bright	19.4		195	
	dim	34.2	0.036*	200	0.868
Sympatry (N=5)					
Cutthroat	fast	21.8		443	
	slow	15.2	0.306	375	0.098
	bright	16.6		352	
	dim	20.4	0.557	466	0.009*
Brown	fast	37.8		217	
	slow	22.4	0.184	206	0.868
	bright	25.2		182	
	dim	35.0	0.396	240	0.415

* Significant, $P<0.05$.

distance of brown trout (Tables 12, 13 and 14). Distance to food source for cutthroat trout in sympatry and slow current was significantly greater in dim light than in bright light (p=0.0155 in paired T-test, Table 12), and in bright light it was significantly greater in fast than in slow current (p=0.0199, Table 13). However, multi-factor ANOVA showed that only light intensity had significant effect on food-source distance of cutthroat trout in sympatry (p=0.0095, Table 14). Food-source distance of cutthroat trout in allopatry was not affected by the variation of light intensity and water velocity within the range studied.

DISCUSSION

Competition for Profitable Position

The most profitable sites for a salmonid in a natural stream or an artificial aquarium are those with lowest velocity, closest to the swiftest current (hence richest food source), where a fish can minimize the energy expended on swimming and maximize energy gained from its environment (Fausch and White 1981). According to this, the positions that should be preferred by fish in the artificial stream of our experiments are, in order, the pools, the downstream riffles, and the upstream riffles (Figs. 4 and 5). This is because positions closest to the upstream ends of pools, where food entered had access to the most drifting food (Figs 4 and 5) in combination with relatively slow current (Table 1 and Figs. 4, 5). Fish that held these positions had the greatest proportion of initiation in agonistic encounters and the lowest rate of weight loss (Fig. 19).

Brown trout were clearly superior competitors over cutthroat trout during the experiments. In sympatry, brown trout held positions significantly closer to the food source and in slower current than cutthroat trout. From the pattern of profitable position distribution along the stream (Figs. 4 and 5), I infer that the sites

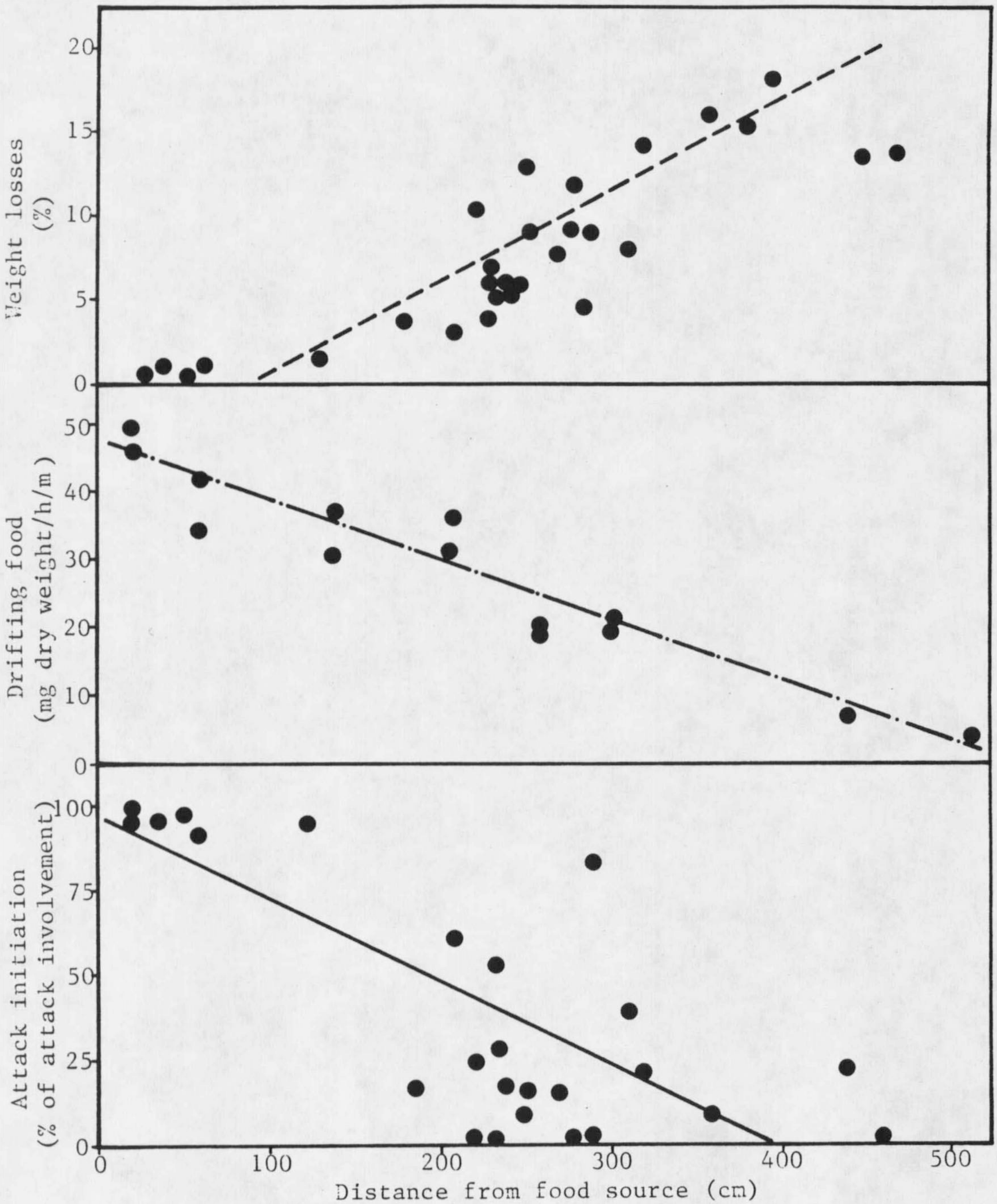

Figure 19. **Relationship between attack-initiation rates, food-drift rates, weight-loss rates, and distances from food source for fish (brown and cutthroat trout combined) in the artificial stream.** The data are combined from both aquarium sections.

occupied by most brown trout were more profitable than those of most cutthroat trout (Figs. 6c, 10b and 11c). In absence of brown trout, cutthroat trout shifted to a wider range of positions, including more profitable ones near upper end of pools (Figs. 6a, 10a and 11a). These changes in site occupation were directly due to interference competition. Brown trout overtly drove cutthroat trout from profitable pool positions, so that the cutthroat trout were forced to occupy unprofitable parts of the channel and lost more weight than brown trout did (Fig 12). In contrast to cutthroat trout, mean positions of brown trout did not change significantly between sympatry and allopatry. Increased occupation of upstream riffles by brown trout in allopatry was due to the increased level of competition involved in having 6 brown trout together in the same section, rather than 3 brown and 3 cutthroat trout, as was the case in sympatry. Because of the increased competition among allopatric brown trout, some of them occupied upstream riffles. Therefore, the intraspecific dominance hierarchy of brown trout had the greatest effect on the site occupation of both species, and interference competition from cutthroat trout had little effect. The weight loss rates of brown trout changed little from sympatry to allopatry, but the weight loss rates of cutthroat trout were significantly higher in sympatry than in allopatry (Fig 12), lending further support to my conclusion.

Although nobody has previously reported studies of interactions between brown and cutthroat trout, some investigators have studied interactions between cutthroat trout and salmonids other than brown trout. Through both field and laboratory studies, Griffith (1972) found that yearling or older brook trout did not displace equal-sized cutthroat trout, but that in streams, underyearling brook trout had size advantage and consistently dominated the underyearling cutthroat trout with which they normally lived. As a result, the two species used different microhabitats, particularly with respect to water depth, and this minimized interaction. Schutz and Northcote (1972) found that Dolly Varden (Salvelinus malma) fed more successfully on benthic prey and cutthroat trout on surface prey. They suggested that this feeding difference may be inherent, and that the benthic-vs-surface habitat segregation is largely selective rather than interactive. In comparing 17 allopatric and 10 sympatric lake populations of rainbow and cutthroat trout, Nilsson (1981) found that the spatial distribution of the two species differed between allopatry and sympatry and that rainbow trout were far more aggressive both intra- and interspecifically than cutthroat trout in aquarium experiments. In a study of interaction between juvenile coho salmon and coastal cutthroat trout, which are naturally sympatric, Glova (1986) concluded that the highly aggressive and socially dominant coho salmon was an effective interference competitor against cutthroat trout in pools and other slow-water habitats. Conversely, the equally aggressive but socially subdominant cutthroat trout appeared to exert a similar interference against coho in riffles and other fast-water habitats. The mechanism of segregation between coho salmon and cutthroat trout was clearly the interactive type that Nilsson (1981) had described.

My results reveal that juvenile brown trout can displace not only equal-sized cutthroat trout but also those of somewhat larger size. Although I do not have field evidence, and the tests of competition between fish of unequal size were only conducted on a few brown trout, it appears that brown trout dominate cutthroat trout because of inherent competitive ability, not size advantage. That salmonids of one species can be dominated by smaller salmonids of another species was also seen by Gibson (1981), who observed that an 86-mm coho salmon dominated brook trout of 99-mm and 102-mm.

General Aggressive Ability in Sympatry

Brown trout were much more aggressive than cutthroat trout in the experiments with fish of equal size. Of 2,224 attacks, 92% were initiated by brown trout (Table 9). Cutthroat trout had significantly more fights in sympatry than in allopatry (Figs. 8 and 16). Number of attacks of brown trout were essentially the same in sympatry and allopatry (Figs. 8 and 15). The difference between brown and cutthroat trout in attack frequency during sympatry was small (Figs. 8 and 13). The interaction between brown and cutthroat trout resembled that between coho salmon and brown or brook trout (Fausch and White 1981) and between rainbow and cutthroat trout (Nilsson and Northcote 1981). It differed from the interaction between brook and cutthroat trout (Griffith 1972), or between brook and rainbow trout (Newman 1965; Wolfe 1978), in which individuals of two species aggressively responded to each other much as though they were of the same species (Newman 1965). In my tests with fish of unequal size, there were approximately equal attack-initiation rates of brown trout and of the cutthroat trout that were larger than they, although the displacement ability of brown trout was greater, as had been the case in the equal-size experiments.

Details of Agonism

Brown trout were not only consistently more aggressive in general than were cutthroat trout, they also differed in details of aggressive encounters. In both allopatry and sympatry with fish of equal size, dominant brown trout attacked their cohorts with rapid rushes or biting. Cutthroat trout appeared to be calmer, and their attacks were slower and more deliberate. This is in agreement with Nilsson's observations (1981). In the equal-size tests, the dominants of both brown and cutthroat trout cruised about occasionally to defend their territory and never allowed subdominant fish to stay anywhere upstream between them and food source. This is consistent with Butler and Hawthorne's (1968) report that large brown trout frequently tolerate smaller trout downstream of them, but never upstream. In the unequal-size tests, however, with 1 midsized brown trout among 5 different size cutthroat trout, the brown trout consistently stayed some distance upstream of the largest cutthroat trout instead of cruising, and allowed smaller cutthroat trout to feed upstream from them temporarily (Fig. 10). This may have been because the brown trout were not able to completely defend their territories when they had to spend most of their time and energy fighting with a larger cutthroat trout.

The cutthroat trout, like brook trout (Wolfe 1978), did not perform the wigwag display described for coho salmon and steelhead trout (Hartman 1965), for brown and rainbow trout (Jenkins 1969), and for rainbow trout (Wolfe 1978). Brown trout performed the wigwag display in equal-size sympatry and allopatry tests as the result of intraspecific interactions. However, in the unequal-size tests, the wigwag display of brown trout resulted from interaction with cutthroat trout and occurred much more in unequal-size tests than in equal-size tests. Wigwag display in my experiments seems to be not only a locomotory adaptation to compensate for fin erection (Jenkins 1969) or simply one fish swimming away from another fish in a rushed manner (Wolfe 1978), but also a threatening behavior. In my equal-size tests, the wigwag display of brown trout was performed by subordinate fish while they were swimming rapidly away from dominant fish. In the unequal-size tests, brown trout wigwagged as a threatening behavior. When the largest cutthroat trout slowly approached brown trout, the brown trout often wigwagged to threaten the cutthroat trout instead of running away or re-attacking the cutthroat trout. Sometimes the wigwagging display lasted as long as 1 minute. The display would end by 1 fish or both slowly swimming away. This behavior also occurred at the beginning of the equal-size tests before social hierarchies were established, but then the wigwag display was often accompanied by a quick swimming away.

Effects of Light and Current on Competition

Differences in water velocity and in light intensity significantly affected the agonistic behavior of brown trout. In allopatry, brown trout made many more attacks in dim than in bright light, and in slow than in fast current. Changes in light intensity and water velocity significantly affected neither the aggressive behavior of brown trout in sympatry nor that of cutthroat trout in sympatry or allopatry. Therefore, dim light and slow current may increase aggressive behavior of brown trout but not cutthroat trout. In studying interaction of rainbow and brook trout, Newman (1956) found that the greatest activity occurred toward evening, after which the fish left their daytime positions and moved out of view. Hoar (1942) found that Sagehen Creek trout were quite inactive during daytime. These findings agree with our results for brown trout.

Light intensities and water velocities tested did not affect the ability of brown and cutthroat trout to feed and to occupy profitable positions in allopatry. However, cutthroat trout in sympatry occupied sites significantly farther from the food source in dim than in bright light, and in fast than in slow current. The distance from food source in allopatry did not show any significant change under different light intensity and water velocity. Schutz and Northcote (1972) found that Dolly Varden were more successful than cutthroat trout in capturing benthic prey in dim light. Also, the visual irradiance threshold and saturation irradiance threshold were higher for cutthroat trout than for Dolly Varden (Henderson and Northcote 1985). Fausch and White (1981) found that brown and brook trout occupied resting positions during the day and assumed that large trout fed mainly during late evening when large stream insects emerged. Chapman (1966) briefly discussed the importance of visual stimulation to feeding salmonids and noted that bottom organisms must move to be attacked. Schutz and Northcote (1972) commented that this generalization may hold true for cutthroat trout but is less likely to apply to Dolly Varden. These previous findings are consistent with our results that in slow current and dim light brown trout occupied more profitable sites than cutthroat trout do.

That cutthroat trout in sympatry were farther from food source in dim than in bright light is clearly due to the more aggressive activities of brown trout in dim than in bright light. However, it is not clear why sympatric cutthroat are farther from food source in fast current than in slow current. It may be because fast current brings more food to downstream positions, and cutthroat trout do not have to occupy such close positions as in slow current to get the same amount of food, even though brown trout reduced their aggressive activities in fast current.

Ability of Greenback Cutthroat Trout to Coexist with Brown Trout

Associated with coexistence of ecologically similar species are (1) interspecific aggression, (2) ability of the subordinate species to use some feature of the habitat that provides escape from the dominant species, and (3) temporal variation in intensity of competition (J. H. Brown 1971; Linzey 1984; Hindar et al. 1988). The interspecific aggressive ability of cutthroat trout is generally weak compared to rainbow trout (Nilsson 1981), coho salmon (Glova 1984, 1986), and char (Andrusak and Northcote 1971; Hindar et al. 1988). However, cutthroat trout are stronger competitors than brook trout of equal size (Griffith 1972). In most cases, cutthroat trout minimize chances for interaction with the dominant species by using different microhabitats (Nilsson 1981; Glova 1986; Hindar et al. 1988). Competitive intensity of cutthroat trout with other fishes varies daily (Andrew 1985) and seasonally (Glova 1986), as well as on an evolutionary time scale (Schutz and Northcote 1972). These variations provide evidence that cutthroat trout may be able to coexist as subordinates with dominant species, such as steelhead trout (Hartman and Gill 1968), rainbow trout (Nilsson 1981), coho salmon (Glova 1984,1986), and char (Hinder et al. 1988).

There are few studies on coexistence of cutthroat trout with brown trout. Hanzel (1960) reported brown trout in 14.7% of the 943 Montana cutthroat trout streams that he surveyed in 1957 and 1958. Liknes (1984) reported brown trout in 7.7% of the 655 cutthroat trout streams in most of the same area. In contrast, brook trout were found in 45% and rainbow trout in 47% of the cutthroat trout streams in Montana in 1957-1958 (Hanzel 1960), and in recent years, brook trout inhabited 50% and rainbow trout 32% of the streams containing cutthroat trout (Liknes 1984). I have found no report about habitat or trophic shift of cutthroat trout when released from brown trout competition in natural streams, although cutthroat trout have showed dietary and spatial segregation with coho salmon (Glova 1984, 1986), Dolly Varden (Andrusak and Northcote 1971; Hinder et al. 1988), rainbow trout (Nilsson 1981), brook trout (Griffith 1972).

Brown trout have similar habitat to the aforementioned species that coexist with cutthroat trout. However, the brown trout is such a strong competitor that cutthroat trout might hardly get a chance to develop coexistent food and space segregation. An extreme result of interaction between two species is the complete displacement of one species through the invasion or introduction of the other (Nilsson 1967). The displacement can involve either the extinction of the defeated species or the persistence of the defeated species in only marginal habitats. I suspect that the displacement of cutthroat trout by brown trout belongs to the latter type because present cutthroat trout distribution is mainly in headwater streams and overlaps only slightly with brown trout distribution (Hanzel 1960, Liknes 1984).

The competitive ability of a species is developed during evolution. The formation of new species proceeds by adaptation to the abiotic and biotic conditions of the geographical zone in which they became established. Nikolsky (1963) maintained that species with similar geographical origins are adapted to each other, and that species from complex biotic environments have developed intensive protective, predatory, and competitive abilities during their evolution. If species that originated in complex biotic environment are mixed with species that originated in a simple biotic environment, the former generally become dominant (Nikolsky 1963). Species evolved in simple biotic environments have less protective, predative, and competitive ability, but they can adapt to marginal environments in which the other species have difficulty competing (Nikolsky 1963). The strong competitive ability of brown trout with rainbow trout (Gate et al. 1987), brook trout (Fausch and White 1981), and other North American species (Nilsson 1967) may be due to its European environmental origination. The dietary and spatial segregation of cutthroat trout from other native North American salmonids, such as Dolly Varden, steelhead trout, rainbow trout, and coho salmon in the aforementioned studies, and the fact that cutthroat trout competed poorly with brown trout in this study, support this idea. The habitat shift by cutthroat trout from pools in allopatry to riffles in sympatry in this and other studies (Glova 1986), does not appear to be due to less efficient resource exploitation in pools than competitors, but rather to social subdominance. Cutthroat trout in allopatry appear as capable as coho salmon in feeding and using cover in pools (Glova 1986), and in riffles, they might be considered a more efficient exploiter of resources because they can use both bottom and drifting foods (Glova 1984).

The present headwater-restricted distribution of cutthroat trout (Hanzel 1960, Liknes 1984) may be due to their simple biotic environmental origination. The cutthroat trout strains that now remain are adapted to habitats in which it is relatively unprofitable energetically for potential competitors to live. The cost for their competitors to maintain social dominance over cutthroat trout in headwaters may exceed the benefits they derive from such habitats. Supporting this hypothesis are (1) the evidence that aggressiveness and social dominance over cutthroat trout benefited coho salmon in pools and other slow-water habitats, while benefiting cutthroat trout in riffle and other fast-water habitats (Glova 1986), and (2) the theory that species with simple biotic environmental origin have weak competitive ability and strong adaptive ability to marginal environments (Nikolsky 1963).

Caveat

The cutthroat trout used in this experiment, although from gametes of wild stock, are hatchery-reared fish. They may differ in survival ability from wild cutthroat trout in natural streams (Miller 1952,1954; Bachman 1984). However, Bachman (1984) found that hatchery brown trout moved more frequently, engaged in more agonistic encounters than wild brown trout, and won as many contests as they lost. Miller (1952) reported that the difference in mortality of hatchery-reared and wild cutthroat trout was due to the wild fish's residence. There was no evidence to suggest different competitive ability between wild and hatchery-reared fish. Therefore, I suspect that there is no important effect on our experiment using hatchery-reared or wild cutthroat trout.

I suspect that I did not provide enough food or that fish density was higher than natural population. Although the density was determined by feeding experiments, almost all fish lost weight in the behavioral experiments. That the fish fought more than in other studies also may be associated with food shortage in my study. Not having provided enough food, i.e., having created a food-limited environment, may not have adversely affected the experimental results because food limitation sometimes exists in natural streams. If fish density was too high, it may have created an intensified intra- and inter-specific competitive situation resembling that of natural streams, and therefore it may not have led to false conclusions. The frequency of agonistic encounters makes it difficult to quantitatively estimate net energy gain of fish because the fish spent much energy interacting with each other rather than spending most of their energy on feeding. Furthermore, the dominant fish in each group not only fed at their preferred sites, but also fed as they cruised to defend their territories. These make it improper to use the model developed by Fausch and White (1986) to quantitatively estimate profitable positions, but the principle is applicable.

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APPENDIX

Table 15. Chemical conditions of the water in the quarium*.

Chemical parameters	Warm spring	Cold spring
Phosphorus		
Ortho	0.01 mg/l	<0.01 mg/l
Total	0.08 mg/l	
Iron		
Ferrous	<0.025 ppm	<0.025 ppm
Ferric	<0.025 ppm	<0.025 ppm
Total	<0.025 ppm	<0.025 ppm
Manganese (Total)	0.002 ppm	0.001 ppm
Sodium (Total)	4.260 ppm	1.410 ppm
Calcium (Total)	54.8 ppm	50.1 ppm
Magnesium (Total)	22.7 ppm	20.0 ppm
Potassium (Total)	1.40 ppm	0.77 ppm
Copper (Total)	0.003 ppm	0.003 ppm
Zinc (Total)	<0.001 ppm	<0.001 ppm
Silicon	8.0 mg/l	3.0 mg/l
Alkalinity		
Bicarbonate	208.8 mg/l	181.3 mg/l
Total (as $CaCo_2$)	171.2 mg/l	148.6 mg/l
Hardness	230 mg/l	207 mg/l
Ammonia nitrogen	<0.005 mg/l	<0.005 mg/l
Nitrite	<0.010 mg/l	<0.010 mg/l
Nitrate	0.050 mg/l	0.050 mg/l
Sulfate	80 mg/l	30 mg/l
Chloride	0.190 mg/l	0.230 mg/l
Total dissolved solids	263.7 mg/l	192.9 mg/l
Resistance (ohms)	448 µmhos/cm	385 µmhos/cm
pH	7.7	7.6
Non filterable solids	0.6 mg/l	1.9 mg/l
Fluoride	0.47 ppm	0.23 ppm

* The data are from the Bozeman Fisheries Technology Center

Table 16. Attacks and food-source distance of brown and cutthroat trout in allopatric tests during June-September, 1987.

	Bright light				Dim light			
	Slow current		Fast current		Slow current		Fast current	
Identification number	Attack (No./h)	Food-source distance (cm)	Attack (No./h)	Food-source distance (cm)	Attack (No./h)	Food-source distance (cm)	Attack (No./h)	Food-source distance (cm)
				Brown trout				
1	18	463	15	297	54	165	21	283
2	21	242	9	236	33	163	15	241
3	24	264	33	227	57	283	9	221
4	9	73	15	26	111	0	54	46
5	18	272	27	231	117	242	21	192
6	0	293	9	305	18	284	0	236
7	24	153	30	148	36	225	3	204
8	33	89	36	37	60	37	21	83
9	9	165	0	291	30	260	9	208
10	27	215	30	191	0	245	15	289
Mean	18.3	201	20.4	199	51.6	190	16.8	200
				Cutthroat trout				
1	3	225	0	278	0	329	0	257
2	0	223	0	312	0	333	9	283
3	27	68	18	15	3	5	0	5
4	0	135	9	241	0	287	0	255
5	0	267	3	273	6	260	15	273
6	6	261	24	227	24	158	15	180
7	0	287	0	283	6	185	0	264
8	9	50	0	51	3	43	3	50
9	0	259	0	188	0	270	3	232
10	3	280	0	280	6	215	0	205
Mean	4.8	209	5.4	214	4.8	208	4.5	200

Table 17. Attacks and food-source distance of brown and cutthroat trout in sympatric tests during June-September, 1987.

	Bright light				Dim light			
	Slow current		Fast current		Slow current		Fast current	
Identification number	Attack (No./h)	Food-source distance (cm)	Attack (No./h)	Food-source distance (cm)	Attack (No./h)	Food-source distance (cm)	Attack (No./h)	Food-source distance (cm)
				Brown trout				
3	84	3	12	3	66	22	48	33
4	22	290	32	289	24	313	38	393
5	0	301	0	304	14	248	48	256
9	28	245	18	302	80	320	2	383
10	42	43	14	42	18	380	12	50
Mean	35.2	176	15.2	188	40.0	256	29.6	223
				Cutthroat trout				
1	24	273	16	360	22	506	44	655
2	44	497	4	492	48	366	30	521
6	24	278	6	422	16	469	26	406
7	22	220	8	387	4	489	10	416
8	12	236	6	351	2	416	2	419
Mean	25.2	301	8.0	402	18.4	449	22.4	483

Table 18. Attacks and food-source distance of brown and cutthroat trout in sympatric tests during January-May, 1988.

		Brown trout		Cutthroat trout	
Experiment	Section	Average attacks (No./h, N=3)	Average food-source distance (cm, N=6)	Average attacks (No/h, N=3)	Average food-source distance (cm, N=6)
1	I	31	47	31	201
		29	197	27	283
		29	243	33	295
	II	46	20	18	230
		35	127	37	252
		47	237	43	337
2	I	58	30	24	228
		23	176	22	302
		16	247	13	483
	II	55	2	44	150
		26	70	21	318
		19	192	15	364
3	I	49	5	28	507
		28	197	36	526
		33	246	30	540
	II	65	7	42	227
		54	142	35	294
		31	165	22	330
4	I	84	3	22	220
		42	43	12	236
		28	245		
	II	22	290	24	273
		0	301	24	278
				44	497
Mean		36.9	141	28.1	310

Table 19. Attacks and food-source distance of brown and cutthroat trout in allopatric tests during January-may, 1988.

Experiment	Section	Brown trout: Average attacks (No./h, N=3)	Brown trout: Average food-source distance (cm, N=6)	Cutthroat trout: Average attacks (No./h, N=30	Cutthroat trout: Average food-source distance (cm, N=6)
1	I	59	7	11	9
		16	48	5	205
		34	173	1	233
		50	340	7	248
		19	405	9	278
		52	459	7	340
	II	69	14	15	12
		54	173	8	60
		35	177	8	141
		21	215	8	203
		30	218	2	233
		35	257	0	243
2	I	9	73	9	50
		18	272	3	280
		9	165	0	223
		27	215	3	255
		0	293	0	287
	II	33	89	27	68
		24	153	0	135
		21	242	0	259
		18	243	6	261
		24	264	0	267
Mean		29.9	204	5.9	195

Table 20. The distribution of water velocity generated by the first motor speed in the artificial stream (cm/s).

Distance from upstream end (cm)	Distance from inside wall (cm)													
	Section I							Section II						
	2	10	20	30	40	50	58	2	10	20	30	40	50	58
	3 cm from water surface													
5	17	19	11	11	13	12	10	5	16	14	12	12	9	6
25	17	18	15	15	16	15	12	5	15	15	15	11	9	2
45	19	15	17	14	14	11	12	11	14	13	12	10	7	3
65	20	18	12	15	12	9	8	11	15	13	11	9	6	3
85	15	18	12	11	13	12	9	13	13	14	12	9	7	5
105	16	16	13	12	11	14	10	13	14	14	11	8	6	6
125	15	16	12	11	12	10	9	13	15	12	10	7	6	5
145	15	15	11	11	12	9	14	12	14	13	11	7	5	4
165	15	13	10	8	10	6	10	11	11	11	8	8	5	3
185	9	10	8	8	7	8	7	12	12	13	13	4	5	3
205	13	11	9	8	8	7	9	12	13	9	7	6	5	3
225	13	8	6	7	5	10	5	10	12	6	3	4	1	1
245	8	7	7	5	6	7	6	11	11	9	7	3	1	1
265	9	8	6	6	6	8	7	9	13	9	5	4	2	1
285	7	8	6	5	2	6	6	9	9	7	5	1	0	0
305	8	9	5	5	3	5	5	9	11	7	3	1	1	0
325	6	6	4	5	5	5	3	10	12	6	3	3	0	1
345	7	8	5	5	4	4	3	9	11	7	4	2	2	1
365	8	6	7	7	6	6	7	9	12	8	4	3	3	3
385	8	8	8	7	6	8	8	10	12	10	6	5	4	5
405	10	8	8	8	8	7	8	11	13	10	9	6	6	7
425	10	8	9	8	9	8	7	10	12	11	8	8	8	7
440	8	10	8	8	9	10	7	11	12	10	9	9	8	6
	12 cm from water surface													
5	8	19	6	9	9	1	1	15	16	15	14	11	11	7
25	13	7	7	1	1	5	5	11	15	12	12	10	10	5
45	16	9	4	4	2	6	6	10	13	13	13	10	9	5
65	12	12	7	6	5	8	6	12	13	10	12	10	8	5
85	14	13	7	7	6	10	7	10	13	10	11	9	7	5
105	10	16	10	5	5	5	10	11	10	11	10	10	7	5
125	11	13	8	5	6	9	11	13	12	11	10	8	7	6
145	11	13	4	6	3	9	8	9	11	10	9	7	5	3
165	12	10	4	5	7	5	6	10	11	9	9	7	5	5

Table 20. Continued

Distance from upstream end (cm)	Distance from inside wall (cm) Section I							Section II						
	2	10	20	30	40	50	58	2	10	20	30	40	50	58
185	9	12	6	5	5	5	9	12	12	10	7	6	2	1
205	14	11	5	5	4	4	7	11	11	11	6	4	2	2
225	7	7	3	3	3	6	5	11	11	10	7	4	1	1
245	9	6	4	0	4	8	7	10	12	11	7	4	1	1
265	7	6	6	2	3	6	5	11	11	8	5	4	0	1
285	9	5	4	3	3	5	3	11	12	8	8	2	1	2
305	9	5	3	4	4	7	6	10	11	8	4	3	0	0
325	4	7	5	4	3	3	6	8	10	8	4	3	1	1
345	6	7	6	4	3	5	5	8	11	9	4	3	2	2
365	8	7	6	5	5	6	4	10	12	12	7	4	4	3
385	6	8	8	8	7	7	6	9	12	11	8	6	6	5
405	8	10	9	8	7	8	7	11	14	11	9	8	6	10
425	8	10	9	9	8	8	6	12	12	10	8	7	6	8
440	7	9	10	9	10	8	8	8	10	11	9	8	8	7
							21 cm from water surface							
165	2	4	4	0	3	3	3	2	3	2	2	2	1	1
185	2	7	1	2	3	3	3	3	3	3	3	1	1	0
205	6	6	4	0	1	2	6	7	6	6	5	2	0	0
225	6	9	5	2	3	3	5	7	8	7	5	1	1	1
245	8	7	2	2	4	6	6	7	6	6	5	0	0	0
265	9	6	3	2	4	2	3	7	9	6	3	2	2	0
285	9	6	6	1	4	5	3	8	9	7	3	2	1	0
305	5	4	5	3	2	4	3	8	8	6	5	2	2	0
325	5	6	6	5	5	6	4	8	9	7	5	4	2	0
345	4	6	5	5	5	3	5	8	7	7	7	4	3	1
365	5	7	6	6	5	6	4	6	9	8	6	5	4	3
385	5	8	7	6	5	5	3	7	9	9	7	6	4	2
							30 cm from water surface							
235	4	2	0	1	1	2	2	3	3	3	1	1	1	1
255	2	5	3	3	0	0	0	4	4	2	2	1	1	0
275	5	5	3	1	3	4	2	4	5	4	1	1	1	1
395	3	8	6	2	4	3	5	3	3	4	3	4	1	0
315	3	2	3	3	2	3	2							

Table 21. The distribution of water velocity generated by the second motor speed in the artificial stream (cm/s).

Distance from upstream end (cm)	Distance from inside wall (cm)													
	Section I							Section II						
	2	10	20	30	40	50	58	2	10	20	30	40	50	58
	3 cm from water surface													
5	17	23	20	24	15	8	7	6	15	14	12	11	9	6
25	27	24	17	23	15	15	15	7	16	15	15	11	5	6
45	23	23	18	15	15	16	15	13	15	15	13	10	6	6
65	18	15	20	14	12	13	11	15	17	16	14	11	8	7
85	17	14	17	12	11	11	12	17	16	15	12	8	7	7
105	21	14	16	14	12	12	14	15	17	15	11	8	9	5
125	14	19	14	13	12	13	16	15	16	15	13	8	8	7
145	14	16	12	11	11	12	13	14	16	15	11	8	7	6
165	19	13	11	11	8	11	11	13	14	12	9	8	6	4
185	18	14	12	10	9	10	10	13	14	12	10	7	5	3
205	18	15	10	9	8	9	7	13	14	11	7	6	4	3
225	15	9	7	7	8	8	7	13	14	12	8	4	2	1
245	13	8	7	7	8	7	6	13	14	12	7	3	1	0
265	7	11	5	5	6	7	6	12	14	10	5	1	1	0
285	10	9	7	7	4	3	10	11	12	10	3	3	1	0
305	12	5	4	5	4	8	6	12	12	8	6	2	1	1
325	11	10	6	5	4	8	7	10	14	8	5	2	1	1
345	8	7	6	6	6	5	6	11	11	9	5	3	2	2
365	10	8	8	8	6	6	4	12	13	11	11	5	4	3
385	12	8	10	8	7	5	6	12	15	13	7	6	6	6
405	9	9	9	8	7	9	8	12	15	11	9	7	9	8
425	9	12	9	10	8	9	7	12	14	15	10	10	9	9
440	8	10	9	9	9	9	9	11	15	13	10	10	11	8
	12 cm from water surface													
5	12	23	6	8	13	5	2	18	19	18	17	14	12	9
25	11	7	3	1	3	10	5	15	17	15	15	13	11	6
45	17	12	8	7	4	8	5	10	13	15	15	11	10	7
65	15	16	9	4	6	9	15	13	14	14	14	11	10	7
85	15	15	11	10	6	10	9	14	14	12	12	10	9	6
105	12	16	11	8	7	10	14	14	14	12	11	10	8	6
125	15	16	10	8	7	12	10	12	13	12	12	10	6	6
145	15	15	8	6	8	10	7	12	13	12	11	9	7	4

Table 21. Continued

Distance from upstream end (cm)	Distance from inside wall (cm)														
	Section I							Section II						
	2	10	20	30	40	50	58	2	10	20	30	40	50	58
165	17	17	9	8	6	10	5	12	12	10	8	6	9	2
185	9	12	8	4	4	8	8	13	14	13	9	7	4	1
205	15	10	5	3	7	7	9	12	14	14	11	7	1	1
225	11	10	6	5	3	8	5	14	13	12	9	3	2	0
245	9	6	5	5	3	5	7	14	12	11	7	5	2	1
265	8	8	5	3	3	5	6	13	13	10	7	4	2	1
285	7	9	2	3	3	4	6	13	13	11	5	3	1	0
305	7	10	4	2	4	9	7	12	12	10	6	3	2	1
325	6	8	5	5	4	4	7	12	13	11	6	4	1	1
345	8	9	5	4	4	7	8	11	12	11	9	5	4	2
365	9	8	7	6	6	8	5	11	12	11	9	7	5	4
385	8	10	8	7	9	10	7	12	15	13	10	8	7	6
405	9	10	9	9	9	9	8	13	16	14	12	11	8	8
425	9	10	9	10	10	9	8	12	16	13	12	10	10	9
440	9	9	10	10	10	11	10	12	15	14	13	11	9	8
21 cm from water surface														
165	3	1	0	0	2	1	2	1	2	4	3	1	0	0
185	4	6	1	0	1	3	4	7	7	7	5	3	1	0
205	10	7	1	1	2	7	3	8	6	6	4	2	1	1
225	7	6	4	4	1	5	7	8	10	8	5	1	1	1
245	11	7	3	3	4	1	7	10	10	8	5	1	2	0
265	12	6	3	2	3	6	6	9	9	7	4	1	0	1
285	8	4	2	1	4	6	4	10	9	7	4	1	2	1
305	7	7	6	2	6	5	3	9	10	8	4	1	0	0
325	9	8	6	4	5	4	4	10	10	7	6	4	2	0
345	7	7	7	4	3	5	5	7	10	10	7	5	3	2
365	7	8	8	7	6	5	5	8	10	9	6	6	4	4
30 cm from water surface														
235	1	1	0	0	0	0	2	0	3	4	2	0	0	0
255	2	4	4	0	2	0	0	3	4	4	2	1	0	0
275	4	3	5	2	2	2	3	4	4	4	2	0	0	0
295	4	5	3	2	3	4	3	4	5	4	2	2	1	0
315	5	6	5	3	3	3	5							

Table 22. The distribution of light intensity lit by "bright" light in the artificial stream ($\mu E/m^2/s$).

Distance from up-stream end (cm)	Distance from inside wall (cm)									
	Section I					Section II				
	2	16	30	44	58	2	16	30	44	58
5	12	10	12	12	9	11	13	13	11	9
25	14	16	15	13	11	11	13	13	11	9
45	14	17	15	14	11	12	15	14	12	10
65	15	17	17	15	11	14	16	15	13	10
85	16	17	16	14	13	15	18	17	15	11
105	15	17	16	15	12	15	18	17	15	12
125	16	17	17	14	11	15	18	16	14	11
145	15	18	17	15	12	16	20	18	16	12
165	14	16	17	14	11	15	20	19	17	14
185	14	18	16	14	11	16	19	19	17	14
205	15	18	17	15	11	17	20	20	17	13
225	13	18	16	14	10	17	20	18	17	14
245	14	18	16	14	10	18	20	19	18	14
265	15	17	17	16	11	17	21	19	17	14
285	14	16	16	15	12	19	21	19	16	15
305	14	17	16	15	11	19	21	19	17	15
325	14	16	16	15	11	18	20	19	18	14
345	14	16	17	15	11	18	20	19	18	14
365	12	17	16	15	10	19	20	18	18	14
385	12	14	13	11	10	18	20	19	18	13
405	10	10	10	9	8	17	20	18	15	12
425	11	11	9	9	8	15	18	17	14	12
440	10	11	9	9	8	15	16	17	13	12

Table 23. The distribution of light intensity lit "dim" light in the artificial stream (x 10^{-3} $\mu E/m^2/s$).

Distance from upstream end (cm)	Distance from inside wall (cm)									
	Section I					Section II				
	2	16	30	44	58	2	16	30	44	58
5	25	27	32	39	28	34	46	45	33	27
25	30	32	34	42	33	35	47	46	39	32
45	27	36	34	43	30	32	48	44	37	29
65	38	37	39	42	36	36	46	44	35	31
85	41	39	41	46	32	36	46	42	33	35
105	36	42	39	44	31	36	47	44	35	32
125	32	46	36	41	33	39	43	42	35	33
145	29	43	39	46	37	34	46	43	36	33
165	32	43	44	45	32	32	43	44	35	34
185	39	41	40	46	33	33	45	44	36	35
205	39	42	43	41	38	36	46	45	38	34
225	38	42	42	41	37	35	46	43	37	32
245	36	41	42	39	35	34	45	42	36	30
265	36	39	38	42	33	36	49	44	37	31
285	38	46	42	41	38	38	47	46	39	35
305	41	45	41	39	32	33	45	41	38	36
325	39	46	43	41	31	33	46	42	39	35
345	36	47	42	41	33	35	45	41	42	33
365	36	45	43	39	32	30	42	44	40	28
385	39	42	40	39	36	30	44	41	43	29
405	38	40	46	37	30	31	40	39	38	26
425	37	40	45	37	33	28	41	38	39	28
440	28	36	39	40	37	27	39	39	38	28

Table 24. Weight change of fish used in experiments on interaction between equal-sized fish.

Identification number	Brown trout			Cutthroat trout		
	Start (g)	End (g)	Changes (%)	Start (g)	End (g)	Changes (%)
			Allopatric experiments			
1	35.85	33.50	6.6	36.19	31.78	12.2
2	32.48	29.00	10.7	35.71	32.37	9.4
3	24.92	21.61	13.3	29.51	29.44	0.2
4	37.76	37.31	1.2	25.61	24.59	4.1
5	28.71	26.92	6.2	32.87	30.69	6.6
6	25.35	14.40	4.8	28.12	27.38	2.6
7	30.54	29.15	3.6	32.19	29.39	8.7
8	30.80	30.45	1.4	32.12	31.98	0.4
9	29.23	27.18	7.0	24.18	22.98	5.1
10	32.48	30.40	6.0	23.18	22.48	5.8
Mean	30.81	28.99	6.1	29.97	28.31	5.5
			Sympatric experiments			
1	36.40	34.04	6.9	29.44	26.06	13.0
2	37.04	32.32	14.6	37.57	32.65	13.1
3	29.23	26.78	9.2	36.02	29.45	18.2
4	33.74	31.35	7.6	34.64	29.92	15.8
5	35.84	35.27	1.6	34.39	29.59	16.2
Mean	34.45	31.95	8.0	34.41	29.53	15.3