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COMPETITION AMONG JUVENILES OF COHO SALMON,  
BROOK AND BROWN TROUT FOR RESOURCES IN STREAMS

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Kurt D. Fausch

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Major professor

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COMPETITION AMONG JUVENILES OF COHO SALMON, BROOK  
AND BROWN TROUT FOR RESOURCES IN STREAMS

By

Kurt Daniel Fausch

A DISSERTATION

Submitted to  
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ABSTRACT

COMPETITION AMONG JUVENILES OF COHO SALMON, BROOK  
AND BROWN TROUT FOR RESOURCES IN STREAMS

By

Kurt Daniel Fausch

9/17/77  
Coho salmon (Oncorhynchus kisutch) were introduced to the Great Lakes in 1966. Naturally reproduced juvenile coho may have detrimental effects on juveniles of resident brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta) in Great Lakes tributaries. I investigated the timing of fry emergence, their size at emergence, and the growth of the three species during their first summer of life in eight Lake Michigan tributaries. In a laboratory stream aquarium, the competitive relationships between pairs of the three species were studied by measuring niche shifts of the subordinate species to more advantageous stream positions after release from competition with the dominant species. I also developed and tested a model of specific growth rate as a function of "potential profit" at stream positions. Potential profit was a measure of the energy potentially available from the invertebrate drift at a fish's position in the stream, minus the cost of swimming to maintain that position.

In Lake Michigan tributaries coho salmon emerged 2-3 weeks earlier and were 6-8 mm longer than either brook or brown trout at

emergence. On average, coho were larger than brook or brown trout in all streams, maintaining a 6-20-mm length advantage and a 0.5-4.0-g weight advantage through their first summer of life. In laboratory experiments, coho salmon dominated brook or brown trout of equal size, and brook trout dominated equal-sized brown trout. Coho salmon grew at higher specific rates than either brook or brown trout at all levels of potential profit, and ceased growing at a lower threshold of potential profit than the trout.

These results indicate that age-0 brook and brown trout could not gain advantageous stream positions in the face of competition from age-0 coho salmon even if the coho were of equal size. In streams where they occur together, juveniles of coho are larger than those of brook and brown trout, which gives the coho an even greater competitive advantage. Instream cover that affords visual isolation may somewhat ameliorate the competitive disadvantage of brook and brown trout in Great Lakes tributaries where coho salmon reproduce.

To my grandfathers:

Christian David Fausch

Ralph Clark Smythe

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## TABLE OF CONTENTS

	Page
LIST OF TABLES. . . . .	vii
LIST OF FIGURES . . . . .	viii
INTRODUCTION . . . . .	1
METHODS . . . . .	5
Sampling Natural Populations . . . . .	5
Stream Aquarium. . . . .	8
The Model of Growth as a Function of Net Energy Gain . . . . .	15
Specific Growth Rate . . . . .	15
Net Energy Gain. . . . .	17
The Relationship Between Specific Growth Rate and Potential Profit . . . . .	22
Experiments on Potential Profit vs. Specific Growth Rate . . . . .	25
1. Initial Measurements and Acclimation . . . . .	25
2. Measuring Characteristics of Fish Positions . . . . .	28
3. Measuring Food and Drift Energy . . . . .	29
Experiments to Measure Competition . . . . .	31
Experiment on Brook Trout vs. Brown Trout . . . . .	31
1. Initial Measurements and Acclimation . . . . .	31
2. Measuring Characteristics of Fish Positions . . . . .	32
3. Measuring Food and Drift Energy . . . . .	32
Experiment on Brook Trout vs. Coho Salmon . . . . .	33
1. Initial Measurements and Acclimation . . . . .	33
2. Measuring Characteristics of Fish Positions . . . . .	33
3. Measuring Food and Drift Energy . . . . .	34
Experiment on Brown Trout vs. Coho Salmon . . . . .	35
1. Initial Measurements and Acclimation . . . . .	35
2. Measuring Characteristics of Fish Positions . . . . .	35
3. Measuring Food and Drift Energy . . . . .	35
RESULTS AND DISCUSSION . . . . .	37
Natural Populations in Lake Michigan Tributaries. . . . .	37
Sympatry Between Coho Salmon and Brown Trout . . . . .	37
Sympatry Between Coho Salmon and Brook Trout . . . . .	39
Brook and Brown Trout in Sympatry and Allopatry . . . . .	40
Coho Salmon in Allopatry. . . . .	40

	Page
Specific Growth Rate as a Function of Potential Profit .	42
Competition Experiments . . . . .	50
Brook Trout vs. Brown Trout . . . . .	50
Brook Trout vs. Coho Salmon . . . . .	55
Brown Trout vs. Coho Salmon . . . . .	61
General Stream Positions and Behavior. . . . .	65
Significance of Competition Experiments . . . . .	66
Relationships Between Specific Growth Rate and Potential Profit . . . . .	70
Laboratory and Field Specific Growth Rates . . . . .	73
Interactions Among Juvenile Salmonids in Great Lake Tributaries . . . . .	79
CONCLUSIONS . . . . .	81
LITERATURE CITED . . . . .	83
APPENDIX . . . . .	87

## LIST OF TABLES

Table	Page
1. Study sites in Lake Michigan tributaries. . . . .	7
2. Design of experiments . . . . .	27
3. Relationships between slopes of drift-energy-vs.-water-velocity regressions and distance downstream from the food source . . . . .	46
4. Parameters for Michaelis-Menten relationships of specific growth rate as a function of potential profit for juvenile salmonids . . . . .	49
5. Summary of agonistic behavior among trout and coho salmon. Percents of all two-minute observations where any agonism was observed are shown, with actual numbers of observations where agonism was observed in parentheses . . . . .	60
A1. Chemical characteristics of water in the stream aquarium at the beginning and end of each experiment.	87
A2. Mean dry weight and percent ash of frozen <u>Daphnia</u> fed per 3 h and per day during each experiment. SEM are shown in parentheses . . . . .	88
A3. Mean length and weight of juvenile salmonids in eight Lake Michigan tributaries during 1979. Sample size and half-widths of 95% confidence intervals are shown for each date. . . . .	89



## LIST OF FIGURES

Figure	Page
1. Lake Michigan tributaries where natural populations of juvenile salmonids were sampled. Perpendicular lines were upstream barriers to fish migration in major rivers during 1979. . . . .	6
2. Plan view of stream aquarium . . . . .	9
3. The stream aquarium. The plastic diffuser panels and the food carboy for the downstream section appear near the top of the photograph. . . . .	11
4. Water depth (cm) in Section I (upstream). Depths were measured at sampling points shown . . . . .	12
5. Water depth (cm) in Section II (downstream). Depths were measured at sampling points shown . . . . .	13
6. a. Hypothetical regressions of energy from drifting <u>Daphnia</u> as a function of water velocity for five distances downstream from the food source. . . b. Hypothetical decrease in slopes of drift-energy-vs.-water-velocity regressions as a function of downstream distance . . . . . c. Hypothetical relationship between specific growth rate and a critical resource for an organism (see text). . . . .	19
7. Growth of juvenile coho salmon and brown trout in three Lake Michigan tributaries during 1979. Top curves are body length, bottom curves are weight. A "*" denotes a sample of three fish or less, and bars show 95% confidence intervals on each mean. . . . .	38
8. Growth of juvenile coho salmon, brook and brown trout in five Lake Michigan tributaries during 1979. Top curves are body length, bottom curves are weight. A "*" denotes a sample of three fish or less, and bars show 95% confidence intervals on each mean. . . . .	41

Figure		Page
9.	Specific growth rate of coho salmon (a) and brown trout (b) in allopatry as a function of mean potential profit at fish positions. One outlier (*) was excluded from the brown trout relationship (see text). . . . .	43
10.	a. Relationships between water velocity and drift energy at five distances from the upper end of Section I during the allopatry phase of the brown-trout-vs.-coho-salmon experiment . . . b. Slope of the drift-vs.-velocity relationship as a function of distance from upper ends of Sections I and II during the same experiment. Bars show 95% confidence intervals for slopes, transformed to natural logs. . . . .	45
11.	Specific growth rate as a function of mean potential profit for brook and brown trout in sympatry (a) and allopatry (b). One brown trout in allopatry was excluded as an outlier (*). . . . .	51
12.	Distribution of positions held by brook and brown trout during sympatry (a and b) and allopatry (c and d). Black portions of bars are positions of dominant fish . . . . .	53
13.	Specific growth rate as a function of mean potential profit for brook trout and coho salmon in sympatry (a) and allopatry (b) . . . . .	56
14.	Distribution of positions held by brook trout and coho salmon during sympatry (a and b) and allopatry (c and d). Black portions of bars are positions of dominant fish . . . . .	57
15.	Specific growth rate as a function of mean potential profit for brown trout and coho salmon in sympatry (a) and allopatry (b). One coho salmon in allopatry was excluded as an outlier (*) . . . . .	62
16.	Distribution of positions held by brown trout and coho salmon during sympatry (a and b) and allopatry (c and d). Black portions of bars are positions of dominant fish . . . . .	64
17.	General relationships between specific growth rate and mean potential profit for coho salmon, brook and brown trout in allopatry (a) and sympatry (b). . .	71

Figure	Page
18. Specific growth rate of juvenile salmonids in eight Lake Michigan tributaries as a function of mean weight. Dashed lines are negative exponential equations fit to all data for each species. . . . .	74
19. Comparison of salmonid specific growth rates as a function of mean weight in Lake Michigan tributaries with the highest rates for individual fish in laboratory experiments . . . . .	75
A1a. Water velocities (cm/sec) in Section I (upstream) 2.5 cm below water surface. Water velocities were measured at points shown . . . . .	90
A1b. Water velocities (cm/sec) in Section I 7.5 cm below water surface. Water velocities were measured at points shown . . . . .	91
A1c. Water velocities (cm/sec) in Section I 12.5 cm below water surface. Water velocities were measured at points shown. . . . .	92
A2a. Water velocities (cm/sec) in Section II (downstream) 2.5 cm below water surface. Water velocities were measured at points shown . . . . .	93
A2b. Water velocities (cm/sec) in Section II 7.5 cm below water surface. Water velocities were measured at points shown . . . . .	94
A2c. Water velocities (cm/sec) in Section II 12.0 cm below water surface. Water velocities were measured at points shown . . . . .	95
A3. Light ( $\mu\text{E}/\text{m}^2/\text{sec}$ ) at surface of Section I. Light was measured 1 cm above water surface at sampling points shown. The positions of mercury vapor (open circles) and incandescent lamps (filled circles) are shown . .	96
A4. Light ( $\mu\text{E}/\text{m}^2/\text{sec}$ ) at surface of Section II. Light was measured 1 cm above water surface at sampling points shown. The positions of mercury vapor (open circles) and incandescent lamps (filled circles) are shown . .	97

## INTRODUCTION

Salmonids have been introduced throughout the world to habitats where they were not indigenous. During the last century, after many attempts, Pacific salmon of the genus Oncorhynchus were successfully established in the Great Lakes, and have recently been introduced to the Atlantic coast of North America and northwest Europe. Fishery biologists in each geographic area have expressed concern that the introduced salmon may have detrimental effects on established populations of Atlantic salmon (Salmo salar) and resident stream trout (Gruenfeld 1977, Solomon 1979, Taube 1975).

Since 1956, three salmon from the Pacific coast of North America have been added to the Great Lakes fish community. Pink salmon (Oncorhynchus gorbuscha) originating from releases in two Lake Superior tributaries near Thunder Bay, Ontario in 1956, have spread to all five Great Lakes (Emery 1981, Kwain and Lawrie 1981). Juveniles of coho salmon (O. kisutch) and chinook salmon (O. tshawytscha) were introduced in two Lake Michigan streams and one Lake Superior stream in 1966 and 1967 respectively (Latta 1974). Both species are now stocked annually in Michigan streams tributary to Lakes Michigan and Huron, and some Lake Superior tributaries. Many returning adult salmon stray to other tributaries, probably because the juveniles are planted as advanced smolts and do not imprint on the stream (Peck 1970). Consequently, with continued

introduction in Michigan and other states, coho and chinook salmon now use many suitable Great Lakes tributaries for spawning.

The coho, chinook and pink salmon that ascend Great Lakes tributaries, like the brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta) residing in these streams, are fall spawners that bury their eggs in gravel redds to incubate during the winter. The eggs hatch in late winter and young emerge from the gravel in early spring, but each species of salmon spends a different period growing in the nursery streams. Pink salmon migrate downstream to a lake or ocean soon after emergence. Chinook salmon leave tributaries in summer after three to six months of growth, and coho salmon remain 12 to 15 months, smolting in the spring of the year following hatching in Great Lakes streams.

These large salmon may affect resident trout in several ways: (1) adult salmon and trout may compete directly for spawning sites or later spawners could dig up redds of earlier spawners, (2) adult trout and salmon may prey on juveniles of either species, (3) spawning fish excavating redds decrease the invertebrate food supply (Hildebrand 1971), and (4) deteriorating salmon may spread diseases. However, the species interaction most likely to have long-term effects on resident trout populations is competition among juveniles of salmon and trout for food and space in nursery streams. Pink salmon juveniles do not remain in tributaries to compete with juvenile trout, and chinook salmon occupy them only for a few months, but coho salmon juveniles may compete strongly with juvenile trout during their 12 to 15 months of residence in Great Lakes tributaries.

The purpose of this research was to study competition among juveniles of coho salmon, brook and brown trout for resources in streams. Salmonids in streams compete for two major classes of resources, food and space. These fish defend territories, maintain relatively fixed positions called focal points within the territories, and make short forays from the focal point to catch drifting invertebrates (Kalleberg 1958). However, the food and space resources of salmonids are related in streams because more invertebrate drift is delivered to areas of the stream with swifter currents, so that defending a specific area ensures a fish access to the food drifting nearby. In view of these relationships, Chapman (1966) proposed that competition for space had been substituted for direct competition for food among stream salmonids. Fausch and White (1981) further proposed that salmonids should compete for positions in streams that maximize the potential for energy intake from the drift, while minimizing the energy cost of swimming--in essence, positions that maximize net energy gain.

The most direct way to measure the effects that two competing species have on each other is to measure niche shifts--that is, changes in resource use that affect survival, growth, physiology, or behavior--of one or both species when their competitor is removed (Connell 1975, Diamond 1978, Sale 1979). When fish are used in such experiments, the effects of niche shifts are usually measured in terms of growth in weight, which is presumed to be a sensitive indicator of fitness (Werner and Hall 1976). To measure the effects of competition for advantageous stream positions among juvenile salmonids,

I compared relationships of specific growth rate in weight for individual fish as a function of the net energy gain from drifting food at the fish's position in the stream. Changes in these growth-vs.-resource relationships when sympatry is compared to allopatry should provide information about the effects that niche shifts have on the energy available to fish when competitors are present and absent.

Measuring competition between fish in natural populations is complicated by variation in the size of individuals of the same age. Because fish do not grow to a uniform species specific adult size, as do birds for instance, the size structure of a population has marked effects on competitive relationships where larger fish are dominant. Therefore, I divided the research into two parts: (1) determining the size structure of juvenile salmonid populations in Lake Michigan tributaries, and (2) measuring the innate competitive ability of juvenile salmonids in laboratory experiments using fish of equal size.

In view of the aggressive nature of the coho salmon reported by Hartman (1965) and Glova and Mason (1977), my hypothesis was that juveniles of coho salmon are superior competitors and could exclude equal-sized juvenile brook and brown trout from advantageous positions in a stream aquarium. If this proved to be true, coho salmon might reduce resident brook and brown trout populations in Great Lakes tributaries, where juvenile coho were expected to have a slight size advantage over the age-0 trout.

## METHODS

### Sampling Natural Populations

To determine the size distribution of juveniles of coho salmon, brook and brown trout in natural populations, I measured the timing of emergence, the size at emergence, and the relative growth of juvenile salmonids during the first summer of life in eight Lake Michigan tributaries (Figure 1). I chose study streams to include all combinations of the three species in sympatry and allopatry. All streams are first-to-third-order tributaries of larger rivers draining into Lake Michigan, and support salmonids that are naturally reproduced except where noted in Table 1. Several streams also contained steelhead trout (Salmo gairdneri) and chinook salmon as well as a variety of other fishes (Table 1).

I sampled populations in the five coho nursery streams approximately every three weeks from April to September 1979. Three streams without coho were added in July. On each sampling date, I captured fish by electrofishing (1 ampere, 175 volts DC) a 100-400-m section of stream chosen to yield large numbers of fish. All fish captured were anesthetized (MS222), weighed ( $\pm 0.05$  g), measured ( $\pm 0.5$  mm TL), and returned to the stream.

In early spring, I captured newly emerged trout and salmon with a hand net in areas of low water velocity over silt flats along the stream margins. On two sampling dates in August and



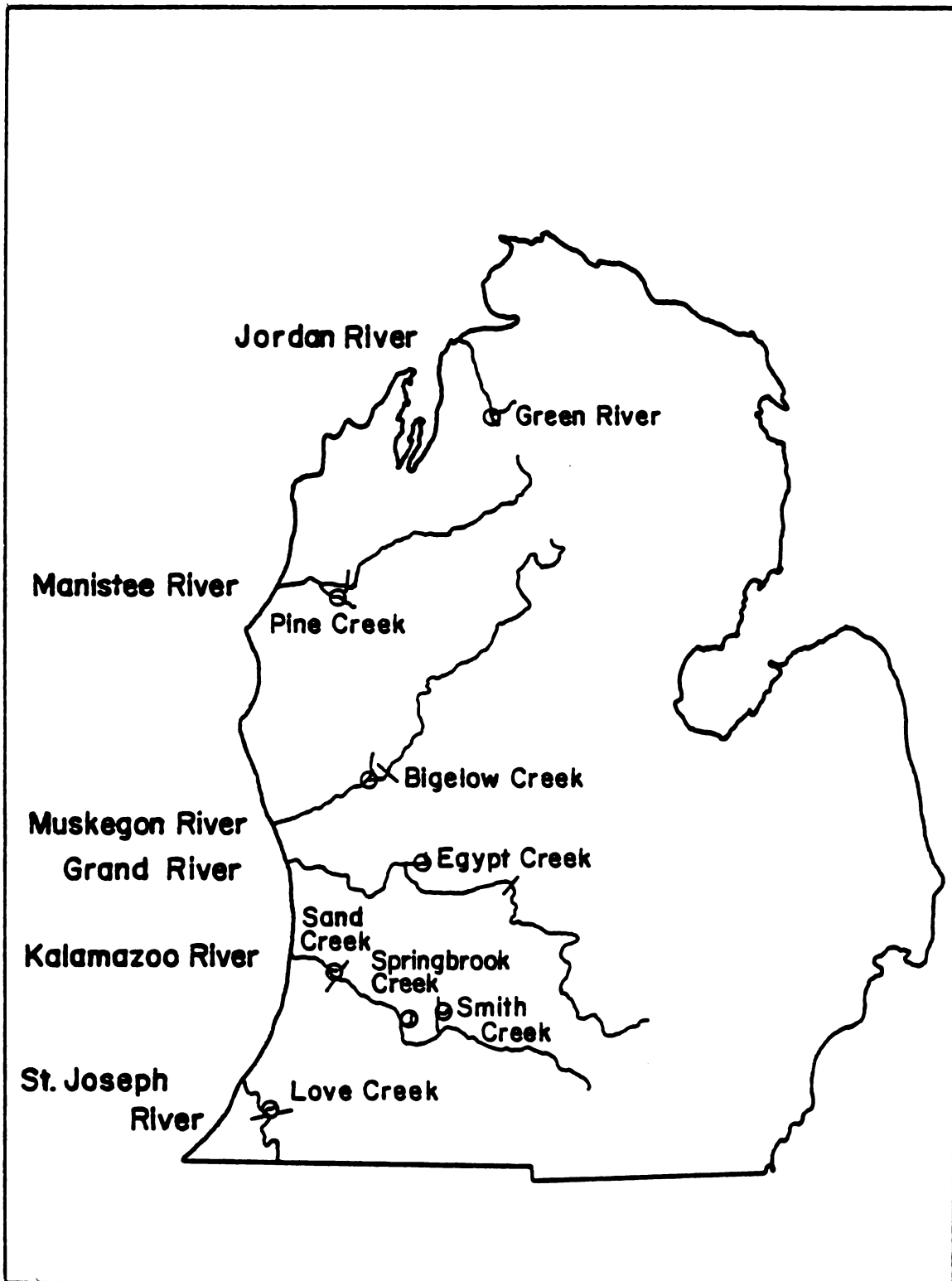


Figure 1.--Lake Michigan tributaries where natural populations of juvenile salmonids were sampled. Perpendicular lines were upstream barriers to fish migration in major rivers during 1979.

TABLE 1.--Study sites in Lake Michigan tributaries.

Stream	Location	Stream order <sup>a</sup>	Species presence and abundance				
			Salmonids <sup>b</sup>		Non-salmonids <sup>c</sup>		
			Trout	Salmon			
1. Love Creek	T6S,R17W,S17	1st	brook steelhead	C <sup>d</sup> A	coho A		1,2,3,4,5,6,7
2. Springbrook Creek	T1S,R10W,S18	2nd	brown	A			1,10,14
3. Smith Creek	T1S,R9W,S2	1st	brook	A			None
4. Sand Creek	T3N,R14W,S34	1st	brook brown steelhead	C <sup>d</sup> R <sup>d</sup> A	coho A		1,8,9,10,11,12,13,14
5. Egypt Creek	T7N,R10W,S4	3rd	brook brown	A A	coho R		4,14,16,17
6. Bigelow Creek	T12N,R12W,S20	3rd	brown steelhead	C A	coho chinook A	A A	2,9,14,15
7. Pine Creek	T21N,R14W,S6	2nd	brown steelhead	A A	coho chinook A	A A	3,13
8. Green River	T30N,R6W,S8	2nd	brown brook steelhead	A R A	coho chinook A	A A	13

a Strahler's modification of Horton (1945).

b A=abundant, 11 or more fish captured on each date sampled; C=common, 1-10 fish captured; R=rarely found.

c Non-salmonid species list:

1. Green sunfish (Lepomis cyanellus)
2. Rainbow darter (Etheostoma caeruleum)
3. Central mudminnow (Umbra limi)
4. Fathead minnow (Pimephales promelas)
5. Bluntnose minnow (Pimephales notatus)
6. Emerald shiner (Notropis atherinoides)
7. White sucker (Catostomus commersoni)
8. Burbot (Lota lota)
9. Bluegill sunfish (Lepomis macrochirus)
10. Longear sunfish (Lepomis megalotis)
11. Blacknose dace (Rhinichthys atratulus)
12. Creek chub (Semotilus atromaculatus)
13. Slimy sculpin (Cottus cognatus)
14. Mottled sculpin (Cottus bairdi)
15. Longnose dace (Rhinichthys cataractae)
16. Yellow perch (Perca flavescens)
17. Fantail darter (Etheostoma flabellare)

d Hatchery fish introduced, and few or no age-0 fish captured.

September I measured the bias in electrofishing in Pine Creek by making three 30-m hauls downstream with a 3-mm seine.

### Stream Aquarium

The recirculating stream aquarium (Figures 2 and 3) used for competition experiments in the laboratory, unlike most stream aquaria which are straight, circular, or ellipsoid, was constructed in a sine-generated curve, the pattern of meandering taken by natural streams (Leopold and Langbein 1966). The more natural riffle-pool ratio and the associated bottom contour simulated the stream habitat of juvenile salmonids more accurately than could be achieved with other channel shapes.

The channel shell, constructed of clear Plexiglass, was 7.28 m long, 30 cm wide and 30 cm deep, and had no slope. I divided the channel into two 3.64-m sections, the upstream section referred to as Section I, and the downstream Section II, and constructed a V-shaped trap at the downstream end of each section to retain fish passing downstream. The channel bed was formed of 2-3-cm diameter gravel, shaped to simulate the natural pattern of riffles and pools, which had 8 and 15 cm maximum water depth respectively (Figures 4 and 5). Flow began at an upstream header box and followed the meandering channel to a collector box. Return flow was through a 20-cm diameter PVC pipe beneath the channel.

Stream flow was generated by air-lift pumping (Spotte 1979) using a large air stone located in the return pipe below the header box. Discharge was controlled by an air-pressure regulator. The

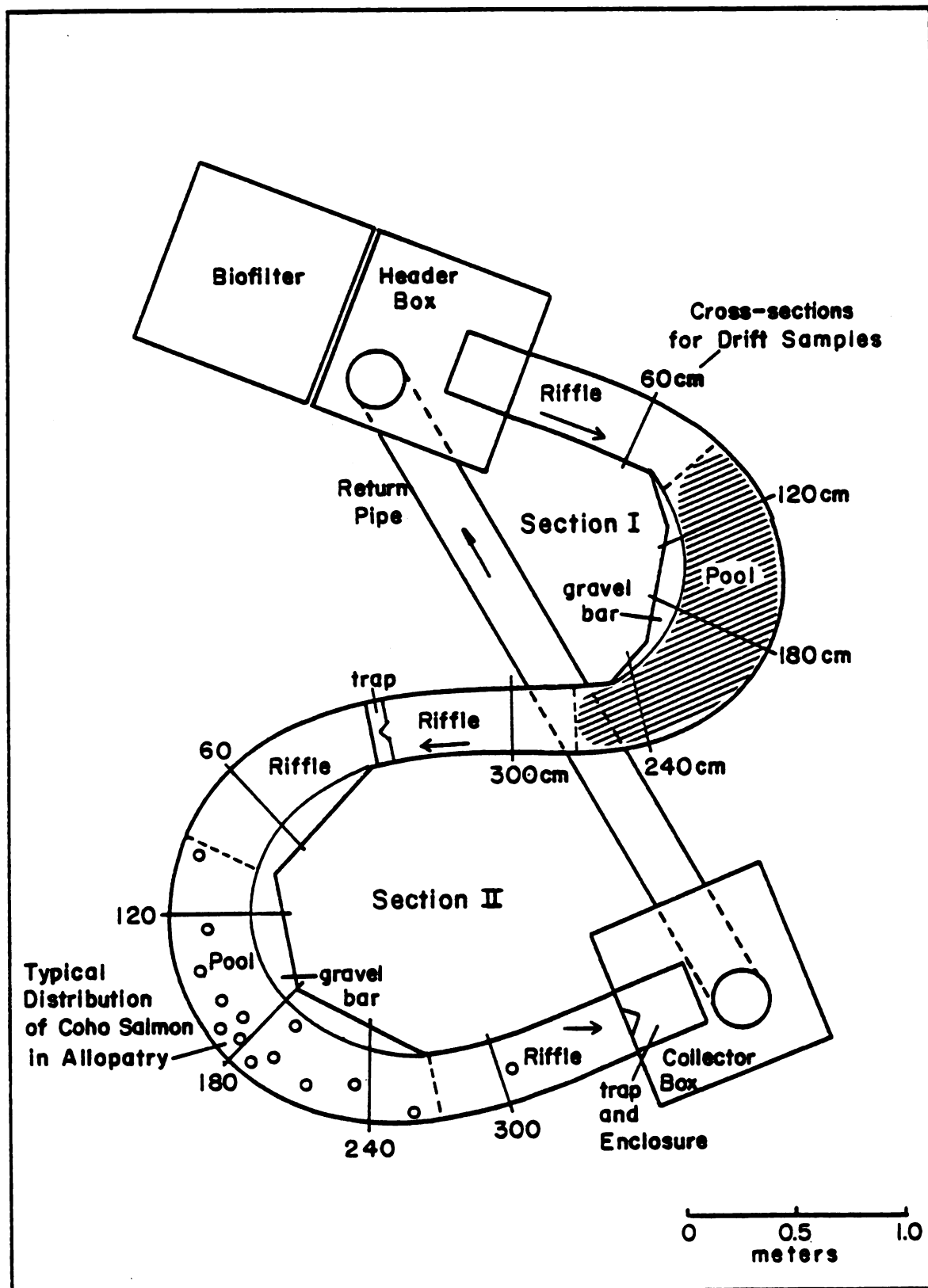


Figure 2.--Plan view of stream aquarium.

Figure 3.--The stream aquarium. The plastic diffuser panels and the food carboy for the downstream section appear near the top of the photograph.

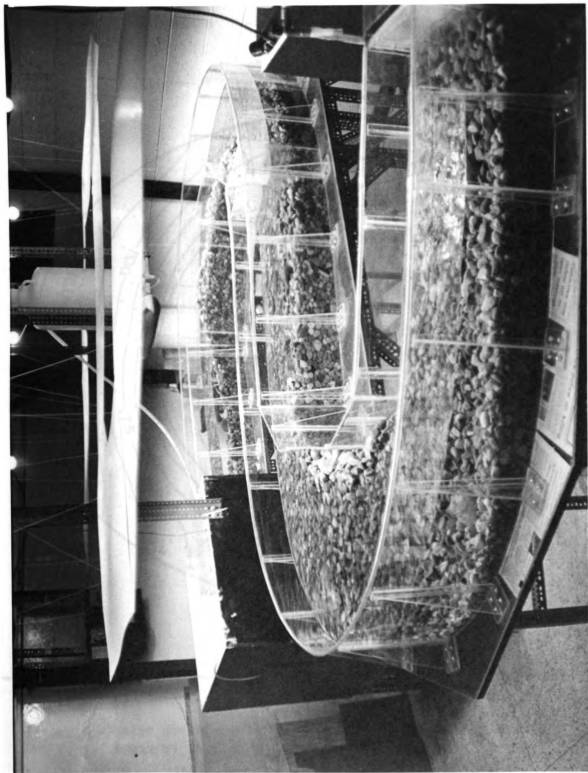


Figure 3.---The stream aquarium.

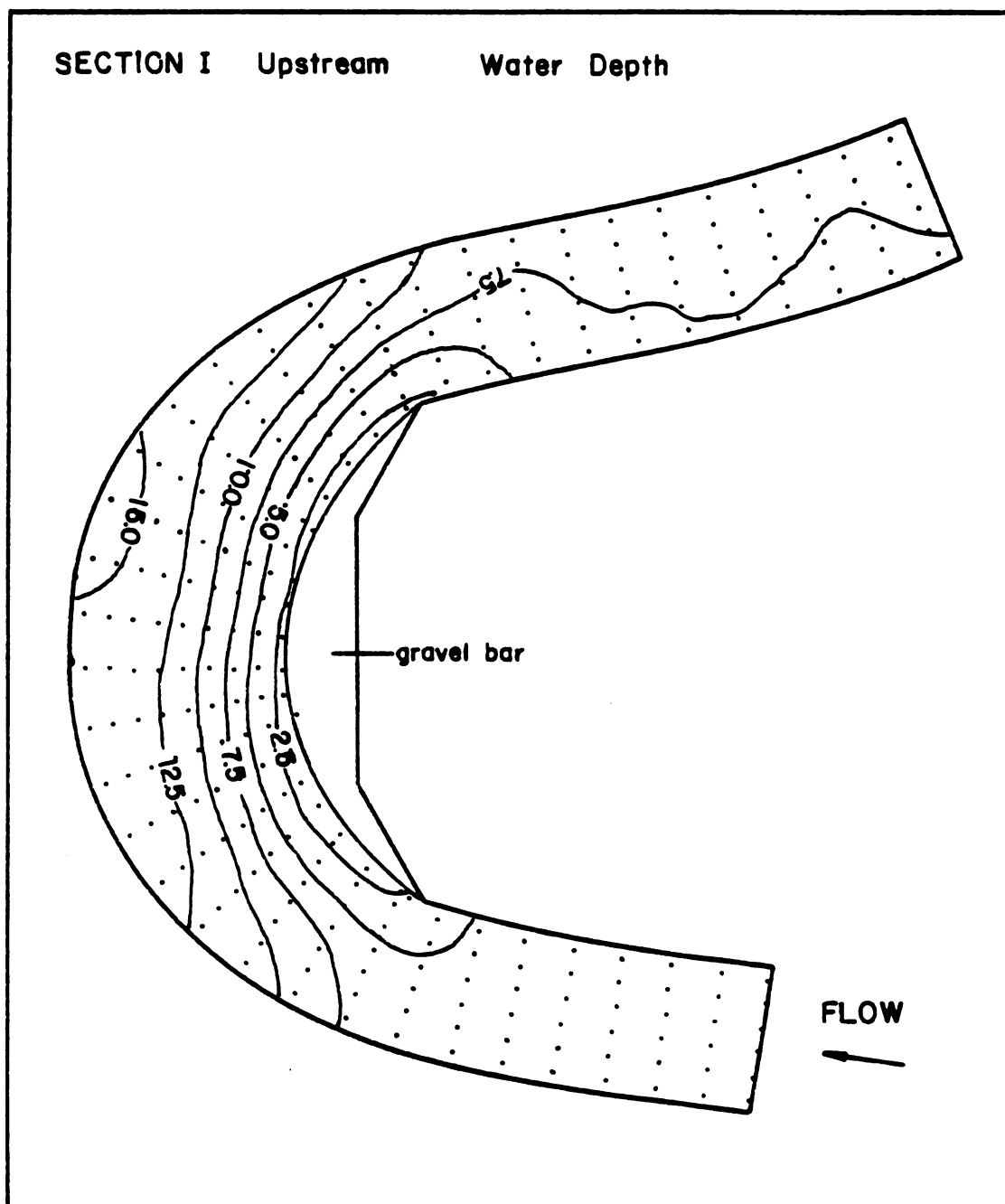


Figure 4.--Water depth (cm) in Section I (upstream). Depths were measured at sampling points shown.

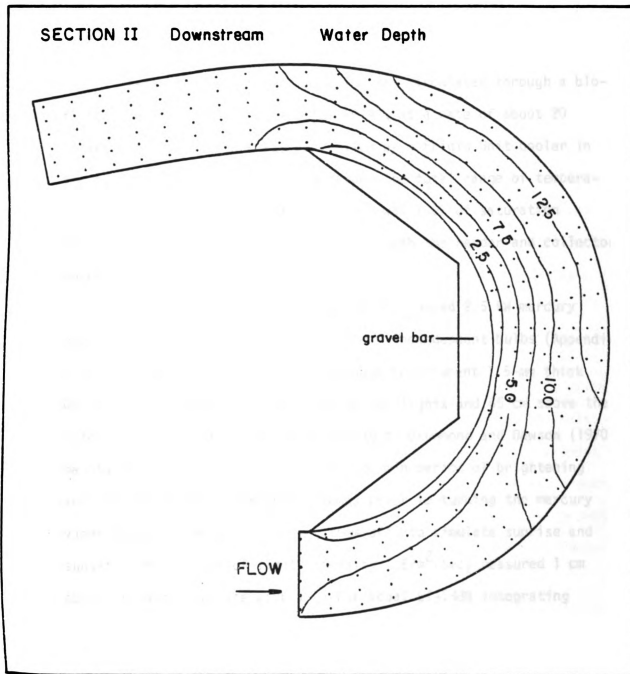


Figure 5.--Water depth (cm) in Section II (downstream). Depths were measured at sampling points shown.



velocity pattern at 50 psi, corresponding to a discharge of 0.00260 m<sup>3</sup>/sec (0.0919 cfs) is shown for three depths in Appendix Figures A1 and A2.

Water from the stream aquarium was circulated through a bio-filter, built according to Spotte (1979), at a rate of about 20 liters/min. Temperature was controlled by a Frigid Unit cooler in the biofilter, which effectively damped the total range of temperature oscillations to about 1 C. Oxygen was 100% of saturation (9.9 mg/liter at 15 C) when measured in both the header and collector boxes.

The stream was lit by five equally spaced 2.5 kW mercury vapor lamps and ten equally spaced 100 W incandescent bulbs (Appendix Figures A3 and A4), all diffused through translucent 1.5-mm thick white plastic sheets hung 50 cm below the lights and 65 cm above the water surface. A timer built according to Drummond and Dawson (1970) maintained a 12-h photoperiod with a 30-min period of brightening and dimming of the incandescent lamps prior to turning the mercury vapor lamps on and after turning them off, to simulate sunrise and sunset. The pattern of light intensity ( $\mu\text{E}/\text{m}^2/\text{sec}$ ) measured 1 cm above the water surface with a Li-Cor model LI-188B integrating photometer is shown in Appendix Figures A3 and A4.

A white false ceiling above the lamps reflected light downward, and curtains reaching from the false ceiling to the table on which the stream rested were lined with white cloth, all of which produced a uniformly lit environment. A flap extended perpendicularly from the curtain to the top of the stream wall, and below this

flap the curtain was lined with black cloth. The curtains had viewing slits positioned below the water level and spaced every 40–45 cm along the channel to allow an observer to watch fish while remaining concealed.

During the experiments, I simulated invertebrate drift by continuous introduction of a suspension of Daphnia in water at the head of each section for 12 h each day. Frozen Daphnia were thawed and kept in suspension in 27 liters of stream water in two carboys using airstones. The suspension drained through a 1.5-mm orifice in about 3 h, so that the carboys were refilled four times each day.

### The Model of Growth as a Function of Net Energy Gain

Growth in fish should be related to net energy gain. In this section I develop a model of specific growth rate as a function of net energy gain for stream salmonids. I first examine the reasons why specific growth rate is a valid measure of growth, then propose a method to measure net energy gain at salmonid positions in streams. Last, I attempt to show how the relationship between specific growth rate and net energy gain can be used to examine interspecific competition.

#### Specific Growth Rate

The rate of growth of an organism can be expressed simply as the change in weight per unit time, in familiar units such as grams per day. However, because the weights of individual organisms differ, growth rate is better expressed per gram of weight, by dividing by the mean weight of the individual during the growth period. This

quantity is called the specific growth rate ( $\mu$ ), with units of 1/day, and may be calculated as follows:

$$\mu = \frac{\frac{\Delta W}{\Delta t}}{\text{Mean } W} \quad (1)$$

where:  $W$  = weight (g)  
 $t$  = growth period (days)

This linear calculation of specific growth rate is adequate for growth over short periods. For longer periods between weight measurements, it may be more accurate to assume that the organism grows at an exponential rate given by:

$$W_t = W_o e^{\mu t} \quad (2)$$

where:  $W_t$  = final weight (g)  
 $W_o$  = initial weight (g)

The specific growth rate during the growth period ( $t$ ) is calculated by converting equation (2) to natural logs and solving for  $\mu$ :

$$\mu = \frac{\ln W_t - \ln W_o}{t} \quad (3)$$

Note that the growth rate at any time can be calculated from the weight of the organism:

$$W \cdot \mu = \text{growth rate (g/day)} \quad (4)$$

For my purposes, the specific growth rate (1/day) is a better measure of fish growth than the growth date (g/day) because it adjusts for small weight differences among individual fish.

### Net Energy Gain

Although the specific growth rate for juvenile salmonids can be calculated from initial and final weight measurements, calculating their exact net energy gain would require a complete energy budget for each individual. However, because these fish maintain relatively fixed focal points with respect to the stream bed, the potential for net energy gain or "potential profit" (P) at a given stream position can be estimated as the energy potentially available from the drifting food (D) minus the energy required for swimming to maintain the position (S), or:

$$P = D - S \quad (5)$$

where: P = potential profit (cal/hr)  
 D = potential drift energy (cal/hr)  
 S = swimming cost (cal/hr)

If the water velocity at the focal point can be measured, the cost of swimming at a fixed position is easily calculated, excluding the energy required for short forays to catch the drifting food. I used general metabolic equations for coho salmon and rainbow trout presented in Stewart (MS) to calculate the swimming cost in calories per hour given fish weight, water temperature, and swimming velocity. The following equations are for a water temperature of 15 C:

$$\text{Coho salmon:} \quad S = 0.9906 W^{0.784} e^{0.0186 V} \quad (6)$$

$$\text{Rainbow trout:} \quad S = 0.7007 W^{0.763} e^{0.0327 V} \quad (7)$$

where: S = swimming cost (cal/hr)  
 W = fish weight (g)  
 V = focal point water velocity (cm/sec)

During experiments in the stream aquarium, Daphnia were introduced only at the upstream end of each section. The amount of

drifting food decreased with downstream distance, primarily because fish ate it, but also because some Daphnia sank into the gravel. To determine the energy available to fish from drifting Daphnia, I needed to estimate the drift delivered to any point in the stream aquarium as a function of water velocity when fish were present. To do this, I first sampled drift and measured water velocity at various places in five cross-sections located at 60-cm intervals along each section (shown in Figure 2). For each cross-section, I then regressed the values of drift energy against the corresponding velocity measurements, forcing the equations through the origin:

$$E = a \cdot V \quad (8)$$

where:  $E$  = drift energy (cal/hr/cm<sup>2</sup>)  
 $a$  = slope of the relationship  
 $V$  = water velocity (cm/sec)

These regressions are shown hypothetically in Figure 6a.

Next, I calculated negative exponential functions to describe the decrease in the slopes of these drift-energy-vs.-water-velocity regressions as a function of distance downstream from the food input:

$$a = be^{-cX} \quad (9)$$

where:  $a$  = slope of drift-vs.-velocity regression  
 $X$  = distance from food source (cm)  
 $b$  and  $-c$  are fitted constants

An hypothetical curve is shown in Figure 6b. Using these two equations, the drift energy ( $E$ ) in calories per hour per square centimeter at any point in the vertical plane of the cross-section can be estimated if the distance downstream from the food source ( $X$ ) and the water velocity ( $V$ ) are known:

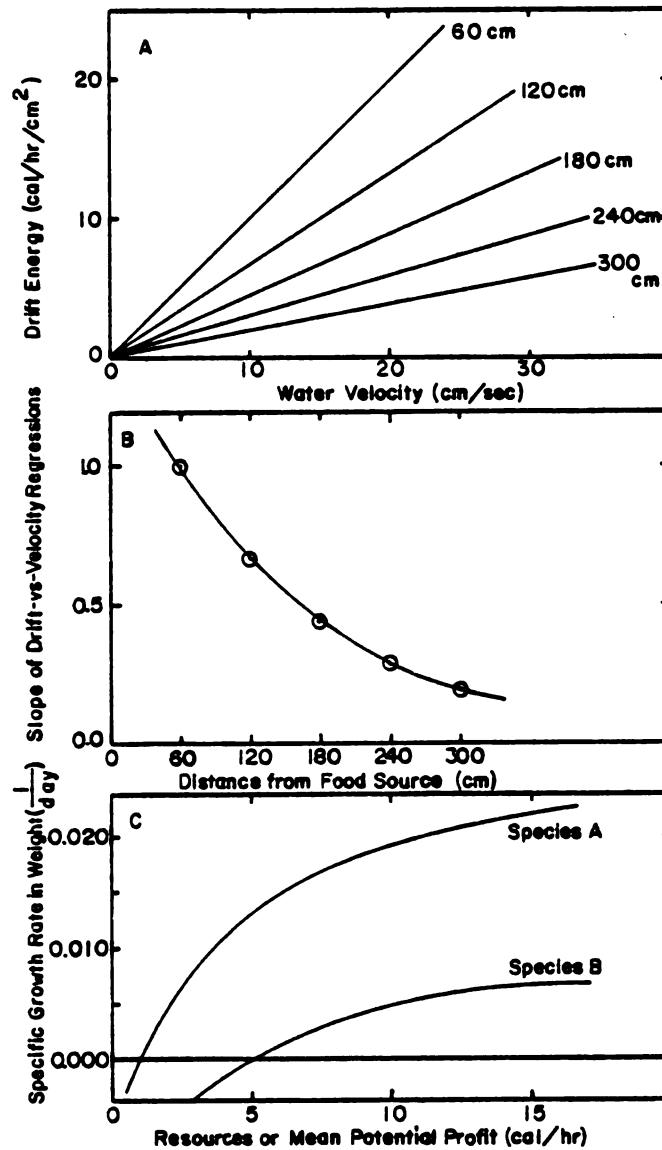


Figure 6.--a. Hypothetical regressions of energy from drifting *Daphnia* as a function of water velocity for five distances downstream from the food source.  
 b. Hypothetical decrease in slopes of drift-energy-vs.-water-velocity regressions as a function of downstream distance.  
 c. Hypothetical relationship between specific growth rate and a critical resource for an organism (see text).

$$E = be^{-CX} \cdot V \quad (10)$$

Given an estimate of food delivered to any point in the stream, I still needed to determine the drift energy available to each fish by assigning it a foraging area in the vertical plane. Coho salmon and brown trout I observed during a pilot study foraged mainly in the area of maximum velocity above and in front of their focal point, within a radius of about two fish lengths. For fish positions in the pools, this area of maximum velocity was near the outside wall of the stream bend where the water was deepest, shown in the depth and velocity profiles in Figures 4 and 5, and Appendix Figures A1 and A2. To estimate the drift energy passing through the fish's foraging area ( $D$  in equation (5)), I envisioned a semi-circle centered at the focal point and extending to a radius of two fish lengths (fork length), and assigned to each fish the drift energy passing through one quarter of this semicircle ( $1/8\pi r^2$ ) at a rate dictated by the maximum velocity measured within the two-fish-length radius:

$$D = 1/8\pi r^2 \cdot E \quad (11)$$

Substituting equation (8) for  $E$ , and using the maximum velocity within two fish lengths then gives:

$$D = 1/8\pi r^2 (a \cdot V) \quad (12)$$

where:  $D$  = potential drift energy (cal/hr)  
 $r$  = two-fish-length radius (cm)  
 $a$  = slope of drift-vs.-velocity relationship  
 $V$  = maximum water velocity within two fish lengths of the focal point (cm/sec)

Further substituting equation (9) for 'a' gives the potential drift energy as a function of downstream distance and the maximum water velocity within the two-fish-length radius:

$$D = 1/8\pi r^2 \cdot b e^{-cX} \cdot V \quad (13)$$

where:  $X$  = distance downstream from food source (cm)  
 $b$  and  $-c$  are fitted constants

During the laboratory experiments I measured the distances traveled from the focal point to capture drifting Daphnia for two coho salmon, and found the frequency of forays dropped sharply at distances greater than 1.5-2.0 fish lengths from the focal point. Wankowski (1981) found that the area of capture upstream of positions held by juvenile Atlantic salmon was fan shaped in the horizontal plane, and that the capture distance varied seasonally from 1.9 to 9.9 fish lengths. Although the area of capture for stream salmonids should be expected to vary with water velocity, particle size, hunger level, and fish species, it appears that my "two fish length" criterion may be a conservative estimate for the foraging area of juvenile salmonids.

In summary, to relate specific growth rate of stream salmonids to the net energy gain or "potential profit" at their stream positions, the following data were necessary, where S indicates that the data were used to calculate swimming cost (equations (6) and (7)), and D means that the data were used to calculate potential drift energy (equation (13)):



Measured for each fish each day:

1. Focal point velocity (S)
2. Maximum velocity within two fish lengths at the focal point (D)
3. Distance of fish position downstream from the food source (D)

Measured during each experiment:

1. Drift delivered as a function of downstream distance (D)
2. Individual fish weights (S)
3. Mean fish length (D)
4. Water temperature (S)

### The Relationship Between Specific Growth Rate and Potential Profit

Relating the specific growth rate of an organism to one or more critical resources that can be measured, has inherent advantages over density-dependent growth equations in the analysis of the growth of individual organisms or of populations. Such relationships define the growth rate of a population or of an individual in terms of a resource required for growth, instead of in terms of numbers of intraspecific or interspecific competitors as the familiar Verhulst-Pearl and Lotka-Volterra models do. The specific rate as a function of a critical resource often takes the form of the curves shown in Figure 6c, which can be described by an equation known variously as the Michaelis-Menten or Monod function:

$$\mu = \mu_{\max} \frac{R}{K_R + R} \quad (14)$$

where:  $\mu$  = specific growth rate  
 $\mu_{\max}$  = maximum specific growth rate  
 $R$  = resource  
 $K_R$  = resource level at  $\frac{1}{2} \mu_{\max}$  or half-saturation constant

When a threshold resource value at which no growth occurs is subtracted to transform the equation so that the curve passes through the origin, it takes the form:

$$\mu = \mu_{\max} \frac{(R - T)}{(K_R - T) + (R - T)} \quad (15)$$

where:  $T$  = resource threshold at which no growth occurs

Although this approach has most often been used in biological science to describe population growth of microorganisms, algae (Young and King 1980), or diatoms (Tilman 1981), a brief search of the literature (D. King, personal communication) revealed similar relationships for specific growth rates of two species of zooplankton grazing on phytoplankton (Lampert and Schober 1980), and for pelagic sockeye salmon juveniles eating zooplankton (Warren 1971, p. 260). In short, the relationship may be a general one for an organism whose specific growth rate can be measured in terms of one limiting resource at a time.

It is clear, however, that there are differences between relationships of specific growth rates of populations as a function of a resource, and the specific growth rates of individual organisms using a resource. Rates for populations include births, deaths and reproduction, whereas those for individuals describe only body growth.

If the curves of specific growth rate vs. a limiting resource are determined for two species, A and B, growing in allopatry, they can be used to make predictions about competitive relationships between the species for this resource. At high levels of resource  $R$ ,

Figure 6c shows that species A grows faster than species B, and is the superior competitor for resource R. As the individuals of species A and B deplete resource R, species B ceases growing at a higher resource level or threshold (T) than A, so that A is still the superior competitor at low resource levels.

These types of predictions, based solely on single-species relationships, may be appropriate for populations of microorganisms, algae and probably some invertebrates, but ignore the additional complex behavioral components of interspecific competition among individuals of higher invertebrates and vertebrates. For instance, if species B in Figure 6c tenaciously defends areas with high levels of resource R from species A, individuals of A may be excluded to areas where the resource is scarce, and grow at a lesser rate than species B. However, if A and B have access to equal amounts of resource R, and if body size is important to competitive dominance, species A would soon grow larger than B and be the superior competitor.

The critical resource for stream salmonids in terms of the model outlined above is the mean potential profit for individual fish at their positions in the stream, which should be related to their specific growth rates as shown in Figure 6c. Relationships of specific growth rate vs. potential profit for salmonids in allopatry integrate the effects of the basic physiology and intraspecific behavior on specific growth rate. These same relationships calculated for two species in sympatry integrate basic physiology and intraspecific behavior, but also interspecific behavior, and any

changes in intraspecific behavior due to the presence of another species. Therefore, comparing the relationships of specific growth rate vs. potential profit measured in sympatry with those in allopatry should indicate changes in behavior resulting from interspecific competition, and may reveal mechanisms to explain niche shifts.

#### Experiments on Potential Profit vs. Specific Growth Rate

I conducted two experiments in the stream aquarium to determine the relationship between potential profit and specific growth rate for coho salmon and for brown trout grown separately in allopatry. In each experiment, I measured position characteristics for each fish on each day to estimate the potential profit and related it to their specific growth rate over an 18-day period.

To help ensure that inferences from laboratory experiments would apply to natural populations in Great Lakes tributaries, all juvenile salmon and trout used were hatched from eggs of returning Lake Michigan coho salmon, or of wild trout from Michigan streams. After hatching, eggs were transferred from incubator trays to a gravel bed in a holding stream tank to promote normal fry development and emergence. Because coho hatch and emerge at a larger size, brook and brown trout were fed at a greater rate to grow all species to equal size.

##### 1. Initial Measurements and Acclimation

Twenty five coho salmon and brown trout were individually finclipped, using combinations of no more than four of the following five finclips on any one fish: tip of dorsal fin, tip of anal fin,

top caudal lobe, bottom caudal lobe, and adipose fin. Most of the fish were given one to three finclips, but one four-clip combination was used, and one fish had no finclips. Coho salmon averaged 54.1 mm in fork length (range 50.0-57.5 mm) and 1.59 g in weight (range 1.21-2.03 g). Brown trout averaged 52.4 mm (range 47.5-54.5 mm) and 1.40 g (range 0.99-1.63 g). I measured the fork lengths of fish during all laboratory experiments because the caudal finclips interfered with total length measurements.

Fish were acclimated to the stream aquarium and food for four days prior to the experiment (Table 2), during which the traps were blocked to prevent fish from leaving the sections. Coho salmon were placed in the upstream section and brown trout downstream in this experiment (Table 2). I opened the mouths of the traps at the downstream end of each section after the initial acclimation period to allow downstream migration. Fish entering a trap were returned to the head of the section, but if a fish entered a trap three times it was removed from the experiment. Of the original 25 fish of each species, 17 brown trout and 22 coho salmon remained in the channel at the end of the 18-day experiment.

Water velocity was adjusted to about 30 cm/sec on the upstream riffles to prevent all fish from occupying the upstream end of each section, a problem discovered during the pilot study. Streamflow discharge measured 40 cm from the upstream end of the upper section was  $.00179 \text{ m}^3/\text{sec}$  (0.0632 cfs). In all experiments, water temperature was maintained at  $15 \text{ C} \pm 1 \text{ C}$ . Chemical characteristics of the

TABLE 2.--Design of experiments.

Experiment	Section <sup>a</sup> in allopatry	Number of days		No. of fish	Mean initial length(mmFL)		Mean initial weight (g)		Food/fish ratio <sup>b</sup>				Stream discharge (m <sup>3</sup> /sec)
		Accli- mation	Sym- patry		Sym- patry	Allo- patry	Sym- patry	Allo- patry	g/day		percent		
									Sym- patry	Allo- patry	Sym- patry	Allo- patry	
1. Specific Growth Rate vs. Potential Profit													
Coho salmon	U	4	-	18	-	54.1	-	1.59	-	18.1	-	10	.00179
Brown trout	D	4	-	18	-	52.4	-	1.40	-	13.3	-	11	
2. Brook Trout vs. Brown Trout													
Brown trout	U	5	10.5	10	14	69.7	3.23	2.97	20.0	20.0	9	9	.00300
Brook trout	D	5	10.5	10	14	70.6	3.21	3.02	20.0	20.0	9	9	
3. Brook Trout vs. Coho Salmon													
Brook trout	U	5 <sup>c</sup>	10.5	10	20	34.3	0.31	0.26	21.0	21.0	77	68	.00198
Coho salmon	D	5 <sup>c</sup>	10.5	10	20	34.5	0.28	0.32	21.0	21.0	63	68	
4. Brown Trout vs. Coho Salmon													
Coho salmon	U	13.5	9.5	9	16	40.6	0.55	0.62	21.0	27.2	50	52	.00260
Brown trout	D	13.5	9.5	9	16 <sup>d</sup>	41.3	0.56	0.50	25.2	27.2	50	80	

a U=upstream, D=downstream.

b Wet weight of Daphnia fed per day expressed as percent of fish wet weight at end of experiment.

c Fish were acclimated to eating Daphnia for 7 days.

d Three brown trout died between sympatry and allopatry.

water were measured before and after each experiment (Appendix Table A1).

To measure growth, fish were starved prior to measurement for 12 h (2000 to 0800 h EDT) before and after each experiment to reach a standard level of gastric evacuation. I individually anesthetized (MS222), measured ( $\pm 0.5$  mm), and weighed ( $\pm 0.01$  g) each fish in a tared beaker of water after light blotting on a cloth towel. The specific growth rate for each fish was calculated on a per-day basis to the nearest 0.5 d.

## 2. Measuring Characteristics of Fish Positions

On each day of the experiment, I measured three position characteristics at the focal point of each fish to calculate potential profit: water velocity, the maximum water velocity within two fish lengths, and distance from the food source at the upstream end of the section. I used the mean initial length of all fish in each experiment to calculate the two-fish-length radius. Water velocities were measured to the nearest 0.5 cm/sec with midjet Bentzel current speed tubes built according to Everest (1967). I measured focal point velocities at the fish's head, and maximum velocities within two fish lengths of this point (100 cm). Distances of fish positions from the upstream end of each section were judged from marks at 5 cm intervals along the stream wall. When in doubt, the next distance upstream of the fish position was recorded.

The fish in each section were chosen randomly to be measured during the morning or afternoon each day. Because I wanted to

measure undisturbed positions of fish, during each measuring period I located all the randomly chosen fish in the stream before measuring their positions by looking through the viewing slits in the curtains, and marked their positions in the vertical plane on the stream wall with a wax pencil. To locate each fish position in the horizontal plane I recorded notes about a prominent feature of a specific stone directly below each fish. After all fish to be measured were located in a section, the curtains were parted and the position characteristics measured.

### 3. Measuring Food and Drift Energy

A relatively constant food-to-fish ratio was maintained by decreasing the amount of Daphnia introduced to each section as fish migrated out and were removed. Coho were fed 10% of their wet weight in thawed Daphnia (18.1 g/day at the end of the experiment) and brown trout 11% or 13.3 g/day at the experiment's end (Table 2). Mean dry weight of the ration for coho was 0.280 g/day (7.5% ash), and for brown trout was 0.172 g/day (8.7% ash) (Appendix Table A2). Fine-meshed screens removed all residual Daphnia at the end of each section, but they disturbed stream flow and were abandoned in subsequent experiments.

I usually measured drifting Daphnia at the five cross-sections shown in Figure 2 with 0.3-mm mesh drift nets measuring 5-by-5 cm at the mouth ( $25\text{ cm}^2$ ) with an 18-cm long bag. However during this experiment I sampled drift only at 60, 180 and 300 cm. I set blocks of four or five nets simultaneously in each cross-section for 120-min



periods, but measured drift at only one cross-section at a time in each section. After this experiment, drift was measured at the usual five distances without fish in each section to provide baseline data. Drift nets were difficult to place and retrieve without temporarily frightening fish away from their usual positions, but the fish became conditioned to this activity by the end of each experiment, and maintained normal positions during drift sampling.

After each drift sampling period, I removed the nets and measured the water velocity at the center and the edges of each net mouth along its horizontal midline. Water velocity profiles measured around net frames with and without nets showed that the netting caused an 8.6% (SE 2.18) reduction in flow on average. The Daphnia were washed out of the drift nets into a gridded petri dish and counted under 15X magnification. The thawed Daphnia were frequently broken when they reached the drift nets, so when counted, the pieces were tallied and equated to the largest Daphnia found, which measured about 2 mm. Smaller, unbroken Daphnia were similarly tallied.

Because some Daphnia were broken, I suspected that thawing them, mixing them in water, and drifting them downstream may have ruptured their bodies and reduced their caloric content to fish. To determine the caloric content of the drifting Daphnia, I first converted Daphnia counts to dry weight. I counted 10 samples of Daphnia that had been thawed in stream water, circulated with an airstone for 1.5 h to simulate treatment in the carboy, and strained in a drift net. I then dried them at 105 C for 24 h for dry weight measurement. Next, to convert dry weight to calories, I similarly

circulated, strained and dried samples of thawed Daphnia from which five replicates of known dry weight were taken. These were combusted in an adiabatic bomb calorimeter to calculate calories per gram dry weight.

### Experiments to Measure Competition

I conducted three experiments to measure competition between pairs of the three species of juvenile salmonids. For each experiment groups of fish were selected to be as uniform in length and length distribution as possible, and were acclimated to the stream aquarium and to foraging on drifting Daphnia. I measured specific growth rates, characteristics of fish positions, and behavior when equal numbers of each species were in sympatry in both stream sections, and later when the same fish were in allopatry in separate sections. Most experimental procedures were the same as during the experiment on potential profit vs. specific growth rate, except as described below.

#### Experiment on Brook Trout vs. Brown Trout

##### 1. Initial Measurements and Acclimation

Fourteen brook trout averaging 70.6 mm in fork length (range 68.0-72.5 mm) and 3.21 g in weight (range 2.87-3.36 g), and fourteen brown trout averaging 69.7 mm (67.0-72.5 mm) and 3.23 g (range 2.84-3.72 g) were acclimated in allopatry to the stream and to feeding on drifting Daphnia for five days (Table 2). I distributed fish of each species to sections randomly for the sympatry phase. I measured fish position characteristics for 10 days in sympatry, then separated the

fish for the 10-day allopatry phase, and made similar measurements. Between the sympatry and allopatry portions of the experiment, I removed fish from the stream sections and placed them in 30-cm square enclosures in the header and collector boxes under low light and water velocity, to reduce the effects of prior residence before measurements in allopatry began. During this two-day rest period, fish were fed a small amount of Daphnia to maintain their weight. To calculate specific growth rates, I measured fish length and weight on the morning before starting the sympatry phase of the experiment, the morning of the first rest day, and the morning after allopatry ended.

## 2. Measuring Characteristics of Fish Positions

I measured fish position characteristics as during the experiment on potential profit vs. specific growth rate, except that the two-fish-length radius was 140 mm during this experiment. Previously unmeasurable velocities less than 6 cm/sec were measured with a hot-bead thermistor flowmeter built according to LaBarbera and Vogel (1976). Because the meter probe tip was small, I also used this meter to measure all velocities around drift nets during this and all subsequent experiments. Stream discharge was adjusted to 0.00300 m<sup>3</sup>/sec (0.1059 cfs) which created velocities excluding most fish from the upstream riffles.

## 3. Measuring Food and Drift Energy

In each stream section, I fed fish 20.0 g of thawed Daphnia per day throughout the experiment. This represented 9% of fish wet

weight in sympatry and allopatry (Table 2), and averaged 0.331 g dry weight and 9.1% ash (Appendix Table A2). Drift was sampled for 30 min with blocks of four or five nets set at the five distances located at 60-cm intervals from the upstream end of each section when fish were present during sympatry and again in allopatry. All Daphnia captured were counted and the pieces equated to the largest Daphnia as during the experiment on potential profit vs. specific growth rate.

### Experiment on Brook Trout vs. Coho Salmon

#### 1. Initial Measurements and Acclimation

I acclimated 20 brook trout averaging 34.3 mm in fork length (range 31.0-37.5 mm) and 0.31 g in weight (range 0.20-0.42 g), and 20 coho salmon averaging 34.5 mm (range 32.0-37.0 mm) and 0.28 g (range 0.19-0.42 g) to feeding on drifting Daphnia for seven days and to the stream aquarium in sympatry for five of these days (Table 2). I assigned fish to sections randomly for the sympatry portion of the experiment, and measured the position of each fish for only eight of the ten days in sympatry and in allopatry, with the usual two day rest period between. I placed brook trout in the upstream section in allopatry, and coho salmon downstream. Stream discharge was  $0.00198 \text{ m}^3/\text{sec}$  (0.0699 cfs) and the two-fish-length radius was 70 mm.

#### 2. Measuring Characteristics of Fish Positions

Fish positions were measured as during the experiment on brook trout vs. brown trout. During this and the subsequent

experiment, I also measured agonistic behavior by recording all agonistic acts received or initiated by individual fish during two minutes of observation. I chose fish randomly so that each was measured every other day. Agonistic acts consisted of lateral displays (recorded only when initiated) and all nips, chases, and frontal threats. Because repeated observations of the same fish were not independent, I used McNemar's test (Gill 1978, p. 83) to test differences in agonistic interactions among species in sympatry.

### 3. Measuring Food and Drift Energy

Fish in each section were fed 21.0 g of thawed Daphnia per day throughout the experiment, representing 63-77% of their wet weight (Table 2) and averaging 0.294 g/day dry weight and 8.9% ash (Appendix Table A2). I improved the sampling and counting of drift during this and the subsequent experiment by using only two drift nets at a time in each cross-section and positioning them at least 50 mm apart to prevent the flow disturbance of one net from affecting the other. In total, eight 20-min samples were collected at each of the five cross-sections during sympatry and again in allopatry. In previous experiments, fish were observed to selectively capture the larger drifting Daphnia, so that only those less than about 0.5 mm in diameter reached the downstream end of each section. Therefore, to measure the drift available to each fish, instead of the total drift, I counted only Daphnia larger than 0.5 mm in mean diameter.

## Experiment on Brown Trout vs. Coho Salmon

### 1. Initial Measurements and Acclimation

I selected 16 brown trout averaging 41.3 mm in fork length (range 39.0-43.5 mm) and 0.56 g in weight (range 0.44-0.72 g), and 16 coho salmon averaging 40.6 mm (39.0-42.5 mm) and 0.55 g (range 0.43-0.65 g) from larger groups of fish acclimated in allopatry for 13.5 days in the two stream aquarium sections. Fish were acclimated to the stream aquarium and to feeding on drifting Daphnia for such a long period because those used in previous experiments were suspected of inadequate acclimation.

For the sympatry portion of the experiment, I sorted the fish of each species into two groups of eight fish each to further equalize length and weight, and placed the smaller fish in the upstream section and the larger fish downstream. I measured the position of each fish for eight of nine days in sympatry and again in allopatry, with the standard two-day rest period between. Coho salmon were upstream in allopatry and brown trout downstream. The discharge was adjusted to  $0.00260 \text{ m}^3/\text{sec}$  (0.0919 cfs) and the two-fish-length radius was 82 mm.

### 2. Measuring Characteristics of Fish Positions

Positions and behavior of individual fish were measured as during the brook-trout-vs.-coho-salmon experiment.

### 3. Measuring Food and Drift Energy

I fed fish in each section 50% of their wet weight in sympatry, which was 21.0 g thawed Daphnia per day (0.299 g/day dry

weight) in the upstream section and 25.2 g per day (0.419 g/day dry weight) downstream (Table 2 and Appendix Table A2). During the allopatry portion of the experiment, I increased the food in both sections to 27.2 g per day (0.418 g/day dry weight), which was 52% of wet weight of coho and 80% of brown trout wet weight. Percent ash ranged from 7.1 to 10.6 (Appendix Table A2). Drifting Daphnia were measured as during the experiment on brook trout vs. coho salmon.

## RESULTS AND DISCUSSION

### Natural Populations in Lake Michigan Tributaries

Juveniles of coho salmon emerged from gravel redds earlier in the spring and at a larger size than either brook or brown trout in four sympatric populations. Coho salmon maintained a 6-20-mm length advantage and a 0.5-4.0-g weight advantage over brook or brown trout during their first summer of life in the four streams. Brook and brown trout emerged at similar sizes and grew at about equal rates in a sympatric population, and in two allopatric populations in streams close to each other.

### Sympatry Between Coho Salmon and Brown Trout

In the three streams having both coho salmon and brown trout, Bigelow Creek, Pine Creek and the Green River, coho emerged earlier and were larger than brown trout through the first summer of life (Figure 7). Although no newly emerged coho were caught in these three streams, in another stream, Sand Creek, having brook trout and coho salmon, newly emerged coho averaged 35 mm in April, which coincided with the size at emergence when coho were raised in the laboratory. Newly emerged brown trout caught in mid-May were 28.5 mm in Pine Creek and 28 mm in the Green River, 6-7 mm smaller than coho salmon at emergence.



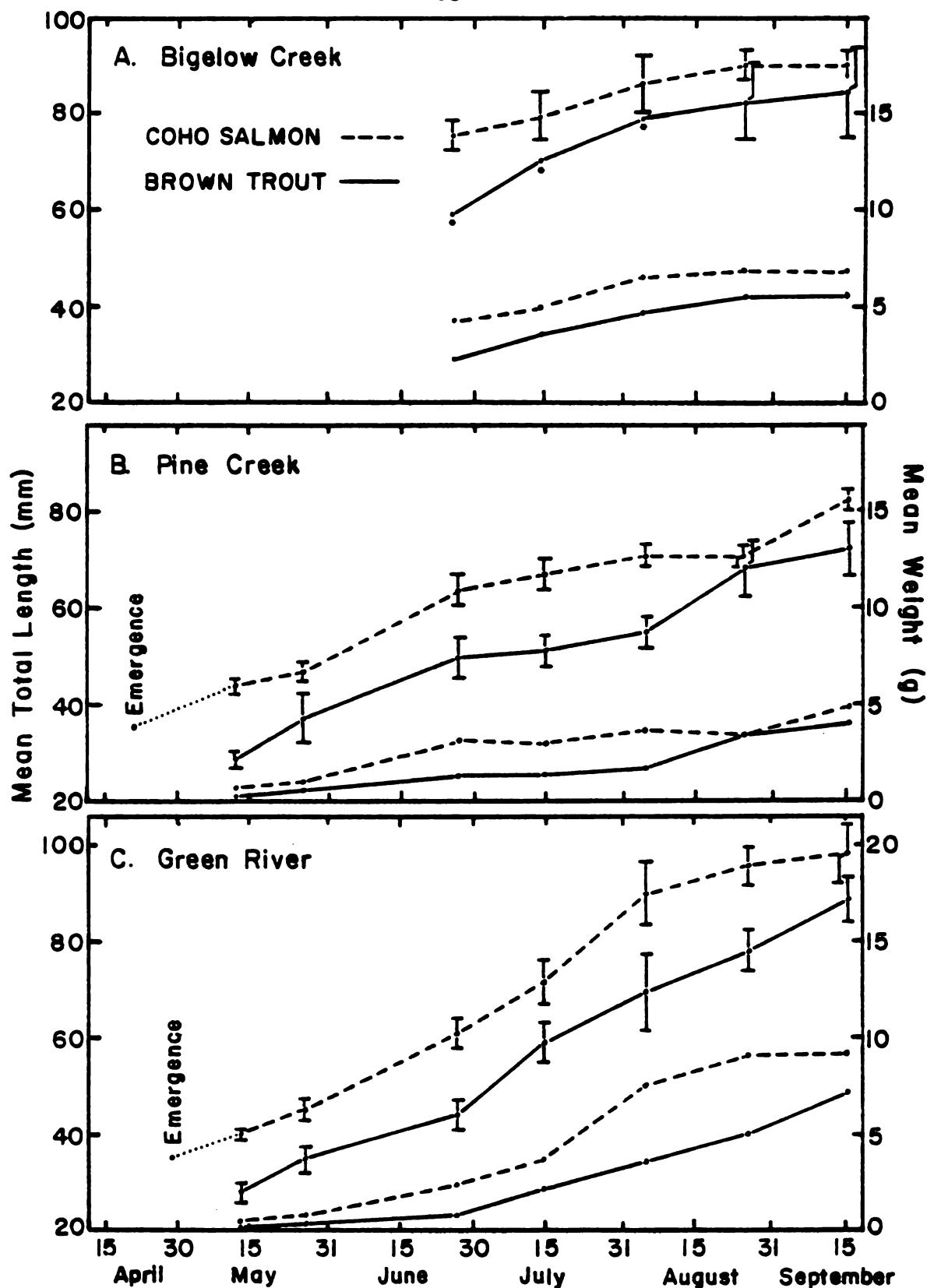


Figure 7.--Growth of juvenile coho salmon and brown trout in three Lake Michigan tributaries during 1979. Top curves are body length, bottom curves are weight. A "\*" denotes a sample of three fish or less, and bars show 95% confidence intervals on each mean.

By extrapolating coho salmon growth in Pine Creek and the Green River back to the 35-mm emergence length, I estimated that coho emerged about three weeks earlier than brown trout in Pine Creek (Figure 7b), and two weeks earlier in the Green River (Figure 7c). Earlier emergence and larger size at emergence gave coho salmon a 6-8-mm length advantage and a 1-2-g weight advantage over brown trout throughout the summer in Bigelow Creek (Figure 7a), a 10-16-mm and 0.5-2.0-g size advantage in Pine Creek (Figure 7b), and a 10-20-mm and 1.5-4.0-g size advantage in the Green River (Figure 7c). For two separate dates, a difference of only 2.3 and 2.4 mm was found between the mean lengths of coho salmon caught by electrofishing and by three seine hauls in Pine Creek ( $p > .30$ ,  $p > .50$ ), indicating that the electrofishing was a fairly unbiased method of sampling juvenile salmonids.

#### Sympatry Between Coho Salmon and Brook Trout

Sympatric populations of coho salmon and brook trout are difficult to find in Lake Michigan tributaries, probably because brown trout have access to the same streams as coho salmon, and may exclude brook trout (Fausch and White 1981) from these stream reaches. I found naturally-reproduced brook trout and coho salmon only in Sand Creek, a marginal stream for salmonids due to low flow and warm water temperatures in late summer. Although adult brook trout were common, three hours of electrofishing on each sampling date often produced less than 10 juveniles.

Coho salmon began emerging in mid-April in Sand Creek at 35 mm, while brook trout emerged two to three weeks later at 29.5 mm (Figure 8a). In early May, newly emerged coho were 35 mm and brook trout were 26.5 mm in Minnie Creek, a stream near Bigelow Creek that I sampled only once. Thus coho salmon are 5.5-8.5 mm larger than brook trout at emergence. In Sand Creek, coho maintained an 8-14-mm length advantage and a 2-3-g weight advantage over brook trout throughout the summer (Figure 8a).

#### Brook and Brown Trout in Sympatry and Allopatry

Brook and brown trout were of nearly equal size during their first summer of life in Egypt Creek, a sympatric population, and in Springbrook Creek and Smith Creek, two allopatric populations in streams close to each other (Figure 8b). Brook trout emerged at 29.5 mm in Egypt Creek, and were 1-5 mm longer and 0.5 g heavier than brown trout through the summer. On three separate sampling dates, one juvenile coho salmon was captured in Egypt Creek.

#### Coho Salmon in Allopatry

Coho salmon grew larger in Love Creek than in other streams (Figure 8c), probably because of enrichment from an agricultural watershed and favorable water temperatures. Love Creek also held age-I and older brook trout of hatchery origin, but only one age-0 wild brook trout was caught. Coho grew large enough by June to equal the lengths of the smallest of these age-I brook trout.

In summary, coho salmon were always larger than trout, while brook and brown trout were about of equal size when sympatric. The

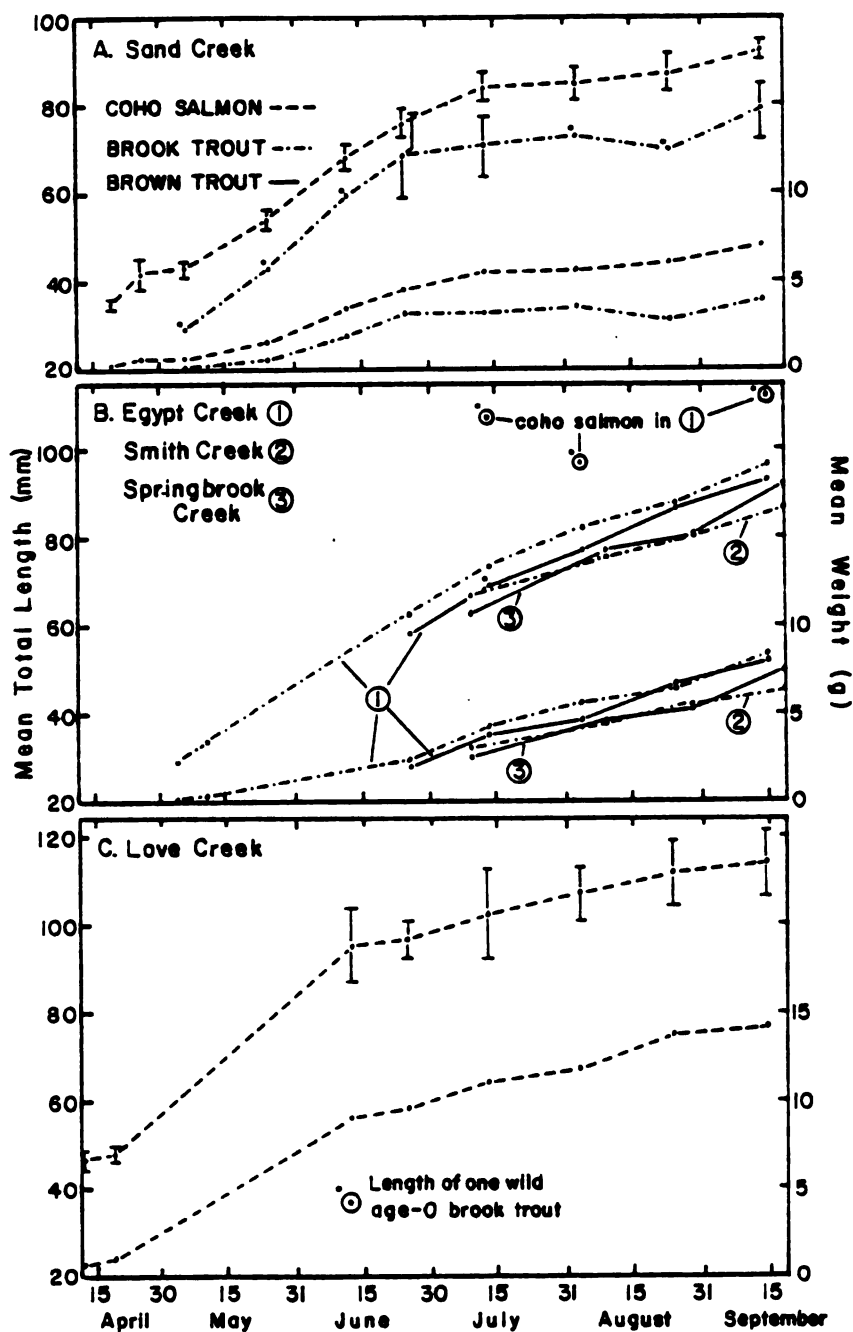


Figure 8.--Growth of juvenile coho salmon, brook and brown trout in five Lake Michigan tributaries during 1979. Top curves are body length, bottom curves are weight. A "\*" denotes a sample of three fish or less, and bars show 95% confidence intervals on each mean.

main determinants of the coho size advantage in each stream were emergence two to three weeks earlier and 6-8 mm longer than either brook or brown trout. Mean lengths and weights of fish from each stream on each sampling date are shown with 95 percent confidence intervals in Appendix Table A3.

#### Specific Growth Rate as a Function of Potential Profit

In the stream aquarium, the specific growth rates of coho salmon and brown trout grown in allopatry increased with mean potential profit at fish positions (Figure 9). Growth of coho approached a maximum rate at high potential profits, but only two brown trout grew and one was excluded as an outlier for reasons explained below. The relationships can be described by Michaelis-Menten or Monod functions (see equation (15)), where specific growth rate approaches some maximum as potential profit increases, but not enough data are available for brown trout at high potential profits to describe the function accurately. However, these results confirm that the specific growth rates of juvenile salmonids are related to energy constraints dictated by a fish's stream position. Studies of salmonid behavior show, in turn, that the stream position is determined by constraints within the social hierarchy (Jenkins 1969). Therefore, it is not surprising that the dominant coho salmon in this experiment held positions that had the highest potential for net energy gain (Figure 9a). Moreover, the next three coho in the dominance hierarchy held positions that provided successively lower potential profit. These patterns provide evidence to support the hypothesis

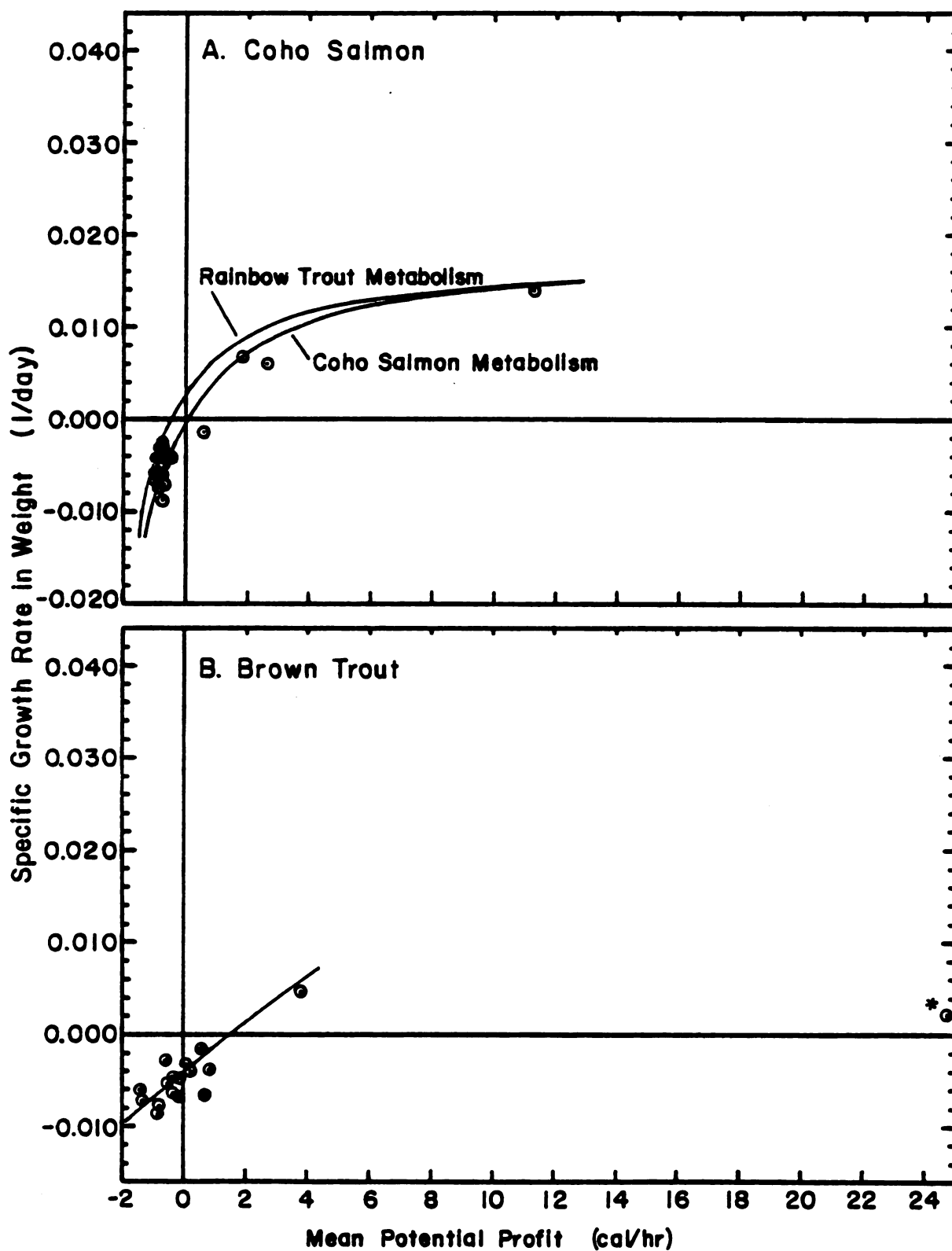


Figure 9.--Specific growth rate of coho salmon (a) and brown trout (b) in allopatry as a function of mean potential profit at fish positions. One outlier (\*) was excluded from the brown trout relationship (see text).

of Fausch and White (1981) that salmonids compete for stream positions that maximize net energy gain.

The relationship between potential drift energy and water velocity described in the Methods section (equations (8) through (13) and Figures 6a and 6b) generally held true for this and all subsequent experiments, especially at the three sampling points in the pools (120-240 cm downstream from the food source), but the drifting Daphnia were not uniformly distributed at the 60-cm distance. Drift was usually sampled during 1100-1300 h during each experiment, but a few samples from 0800-0900 h showed that fish captured a greater proportion of the drift early in the day. These early-morning samples and some others biased by equipment failure were not used.

The best drift-vs.-velocity relationships were achieved during the experiment of brown trout vs. coho salmon competition (Figure 10a). The decline in slopes of drift-vs.-velocity relationships with downstream distance for the two channel sections during the allopatry portion of this experiment were fit to negative exponential equations, shown in Figure 10b. Table 3 shows the slope-vs.-distance equations used to estimate potential drift energy for each experiment.

Relationships for drift without fish are only shown in Table 3 for the first experiment, because too few drift samples were taken without fish during subsequent experiments to allow accurate slope-vs.-distance curves to be fit. However, all samples showed that more drift was available without fish than when fish were present.

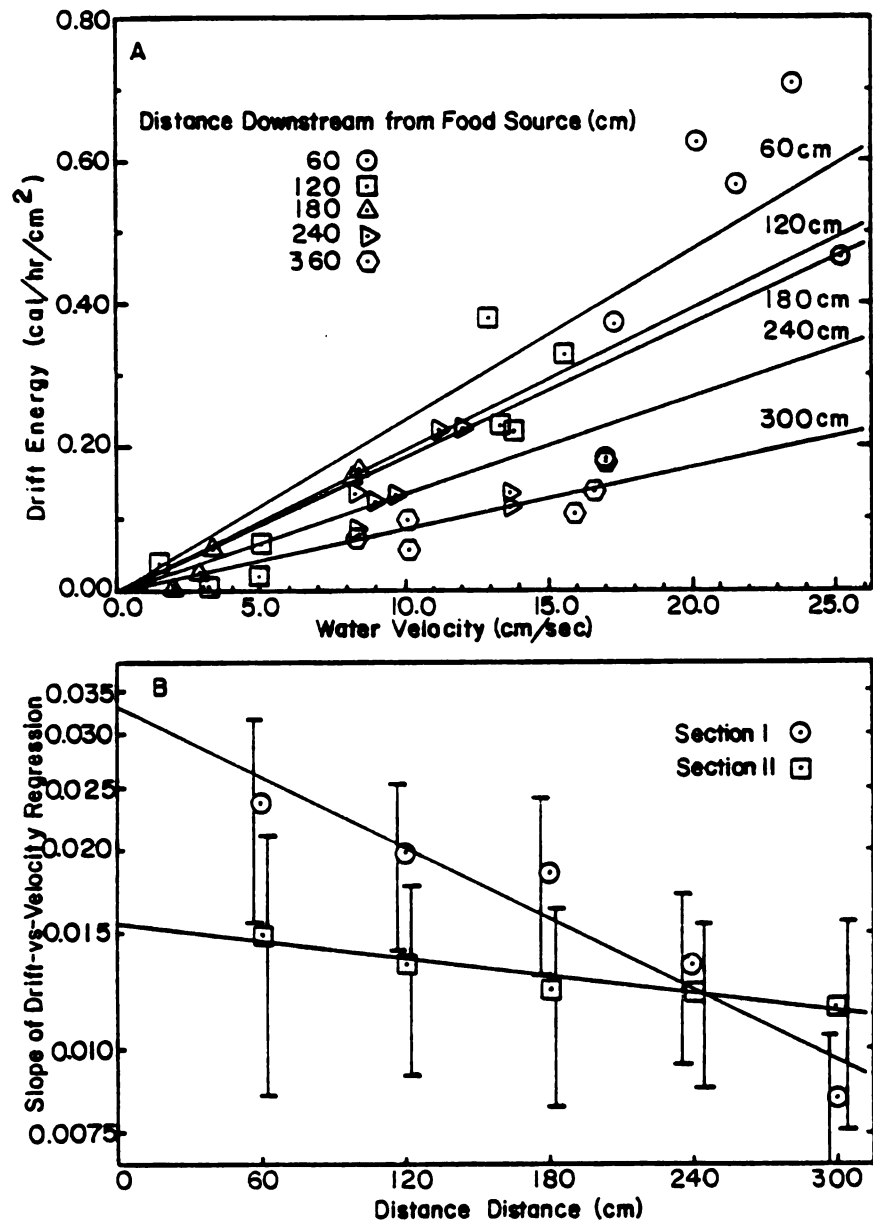


Figure 10.--a. Relationships between water velocity and drift energy at five distances from the upper end of Section I during the allopatry phase of the brown-trout-vs.-coho-salmon experiment.  
 b. Slope of the drift-vs.-velocity relationship as a function of distance from upper ends of Sections I and II during the same experiment. Bars show 95% confidence intervals for slopes, transformed to natural logs.



TABLE 3.--Relationships between slopes of drift-energy-vs.-water-velocity regressions and distance downstream from the food source.

Experiment	Stream section	Drift equation <sup>a</sup>
<b>1. <u>Profit vs. Growth</u></b>		
Coho salmon	Upstream	$S=0.1002 e^{-0.0236 D}$
Brown trout	Downstream	$S=0.0546 e^{-0.0207 D}$
Drift without fish	Upstream	$S=0.02572 e^{-0.002338 D}$
	Downstream	$S=0.02598 e^{-0.005103 D}$
<b>2. <u>Brook trout vs. Brown trout</u><sup>b</sup></b>		
Sympatry	Upstream	$S=0.05185 e^{-0.006076 D}$
	Downstream	$S=0.06237 e^{-0.007885 D}$
Allopatry		
Brown trout	Upstream	$S=0.01551 e^{-0.01190 D}$
Brook trout	Downstream	$S=0.02480 e^{-0.008060 D}$
<b>3. <u>Brook trout vs. Coho salmon</u></b>		
Sympatry	Upstream	$S=0.03501 e^{-0.0003560 D}$
	Downstream	$S=0.03004 e^{-0.002370 D}$
Allopatry		
Brook trout	Upstream	$S=0.03298 e^{-0.0007465 D}$
Coho Salmon	Downstream	$S=0.02458 e^{-0.003053 D}$
<b>4. <u>Brown trout vs. Coho salmon</u></b>		
Sympatry	Upstream	$S=0.02222 e^{-0.003185 D}$
	Downstream	$S=0.01645 e^{-0.003946 D}$
Allopatry		
Coho salmon	Upstream	$S=0.03304 e^{-0.004096 D}$
Brown trout	Downstream	$S=0.01539 e^{-0.001003 D}$

a Drift equation of general form:  $Slope = b \cdot e^{-c \cdot \text{Distance downstream(cm)}}$

b All drift equations for this experiment divided by four (see text).

When the potential profits at fish positions were calculated for each day, the cost of swimming reduced the potential energy from the drift by a relatively small amount, usually 10-25%. Therefore, it made little difference whether the equations for rainbow trout or coho salmon (equations (6) or (7)) were used to calculate the cost of swimming and potential profit. When both were used to calculate the mean potential profit for coho salmon (Figure 9a), the threshold values for the two relationships only differed by about 0.5 cal/hr. In subsequent experiments, the coho metabolic equation was always used to calculate the cost of swimming for coho, and the rainbow trout equation was used for the brook and brown trout.

During this experiment, only three coho salmon and two brown trout grew; the rest of the fish lost weight. However, fish were fed only 10-11% of their wet weight, and both species captured virtually all of the Daphnia introduced to their respective sections. In two-hour drift samples, less than three Daphnia were captured in each of four nets positioned 300 cm below the upper end of the brown trout section, and none were caught in the coho section at the 300-cm mark.

One brown trout held a position in a crevasse in the stream bed of the upper riffle (45-60 cm) for most of the experiment, and was assigned very high potential profits each day because the swift currents overhead (25-35 cm/sec) and the upstream position contributed to a high estimate for drift energy. However, due to the swift currents, this fish was able to capture only a small proportion of

the drift passing by, and so was excluded as an outlier from the relationship (Figure 9b).

In this and subsequent experiments, individual fish occasionally swam to other parts of the stream for short periods to use atypical positions. These outliers were detected from abnormally high or low potential profit values for one day relative to other days, and were excluded by the method of Grubbs and Beck (1972). When one, or rarely two, daily potential profit measurements were excluded for a fish, the mean profit was recalculated using the remaining measurements.

Although both coho salmon and brown trout were fed similar fractions of their wet weight, the relationships show that coho were more efficient in capturing this energy and converting it to growth (Figure 9). In addition, coho salmon began growing at a lower threshold of potential profit than did brown trout. The three parameters needed to calculate the Michaelis-Menten relationship (equation (15)): maximum specific growth rate ( $\mu_{\max}$ ), half-saturation constant ( $K_R$ ), and threshold value ( $T$ ), are shown in Table 4 for each experiment.

The results of these preliminary experiments on brown trout and coho salmon in allopatry may be used to predict which species would grow larger in sympatry if interspecific behavior were ignored. Thus, at equally profitable positions in the stream, coho would quickly grow larger than brown trout. I speculate that the larger size of coho might then confer advantages in interspecific agonistic bouts and allow coho to dominate advantageous stream positions.

TABLE 4.--Parameters for Michaelis-Menten relationships of specific growth rate as a function of potential profit for juvenile salmonids.

Experiment	Parameters in Michaelis-Menten equation		
	Maximum specific growth rate ( $\mu_{\max}$ )	Half-saturation constant ( $K_R$ )	Threshold potential profit (T)
<b>1. <u>Potential Profit vs. Growth Rate</u></b>			
Coho salmon			
Coho metabolism	0.0192	3.3	0.0
Rainbow metabolism	0.0180	1.9	-0.5
Brown trout	0.2590	99.8	1.5
<b>2. <u>Brook Trout vs. Brown Trout<sup>a</sup></u></b>			
Sympatry			
Brook trout			
Upstream Section	$\mu = -0.01049 + 0.000334 P$		
Downstream Section	$\mu = -0.01020 + 0.000495 P$		
Brown trout			
Upstream Section	$\mu = -0.00885 + 0.000108 P$		
Downstream Section	$\mu = -0.00983 + 0.000277 P$		
Allopatry			
Brook trout	0.0229	6.1	1.4
Brown trout	0.0162	13.0	2.0
<b>3. <u>Brook Trout vs. Coho Salmon</u></b>			
Sympatry			
Brook trout <sub>b</sub>	0.0365	18.5	7.7
Coho salmon <sup>b</sup>	no relationship was fit		
Allopatry			
Brook trout <sub>c</sub>	0.0348	11.6	5.5
Coho salmon <sup>c</sup>	0.0500	3.75	2.5
<b>4. <u>Brown Trout vs. Coho Salmon</u></b>			
Sympatry			
Brown trout	0.0171	22.4	7.5
Coho salmon	0.0293	4.3	1.0
Allopatry			
Brown trout	0.0132	5.75	4.0
Coho salmon	0.0524	8.6	1.1

a Linear regressions were fit because relationships were poor (see text).

b No relationship was fit because of inadequate acclimation (see text).

c Equation fit by inspection.

### Competition Experiments

Coho salmon were clearly the superior competitor when pitted against either brook trout or brown trout of equal size in the stream aquarium. Brook trout were dominant over brown trout of equal size. These conclusions are evident when the relationships of potential profit vs. specific growth rate, the downstream distances of fish positions, and the behavior of fish in sympatry are compared with those in allopatry.

#### Brook Trout vs. Brown Trout

All fish lost weight in sympatry (Figure 11a), but brook trout lost weight at a lesser rate than brown trout, when the stream sections are considered separately. The weight loss is not surprising, considering that fish were fed only 9% of their body weight per day (Table 2), were acclimated only five days to the food and the stream aquarium, and were probably too large to forage efficiently on drifting Daphnia. To adjust for the selectivity by trout for large Daphnia throughout this experiment, I reduced the potential drift energy relationships to 25% of their original values. Because the data for sympatry are variable, I simply fit straight lines to relate specific growth rate to mean potential profit (Figure 11a).

During allopatry, two brook trout grew, and another maintained its weight (Figure 11b), but all brown trout lost weight, even though all fish should have been acclimated by this time. One brown trout was excluded as an outlier, but did not occupy an atypical position. I conclude that in the stream aquarium, brook trout

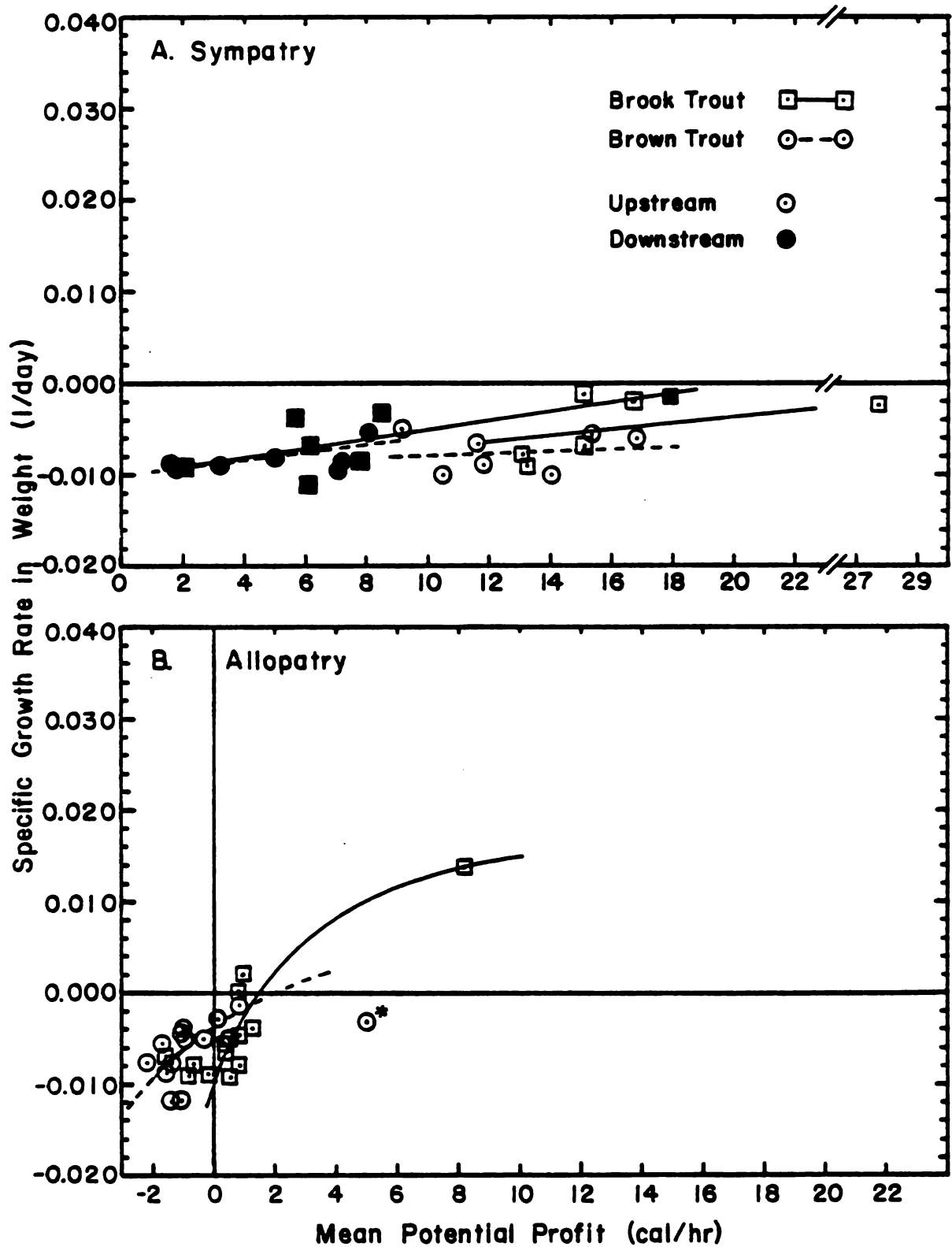


Figure 11.--Specific growth rate as a function of mean potential profit for brook and brown trout in sympatry (a) and allopatry (b). One brown trout in allopatry was excluded as an outlier (\*).

of this size were more efficient at foraging on drifting Daphnia and converting it to growth than were brown trout.

Because acclimation and feeding presented problems during this experiment, the distribution of downstream distances of fish positions, and qualitative behavioral observations provide better evidence that brook trout were the dominant competitor. In sympatry, the dominant brook trout maintained positions upstream of brown trout and actively drove them downstream in both sections (Figure 12a and 12b). The black portions of the bars representing brook trout show the positions of the dominant brook trout in each section during the ten days of sympatry. Brook trout held positions that were significantly further upstream than those of brown trout in both sections during sympatry: the mean distances were 243 cm vs. 289 cm in the upstream section ( $p < .001$ ) and 172 cm vs. 224 cm in the downstream section ( $p < .001$ ). The frequencies of fish positions in allopatry (Figures 12c and 12d) are shown at half scale for easy comparison with the sympatry distributions.

In allopatry, brown trout shifted to more upstream positions (mean distance 204 cm) when released from competition with brook trout (Figure 12c). The dominant brown trout chased other fish from the upstream 130 cm of stream, which was 36% of the total section. One dominant brook trout drove all others downstream onto the lower riffle (mean distance 277 cm) during allopatry (Figure 12d), reserving 76% of the stream section for itself.

In sympatry, the four fish holding positions furthest upstream in each section were brook trout. Two brook trout

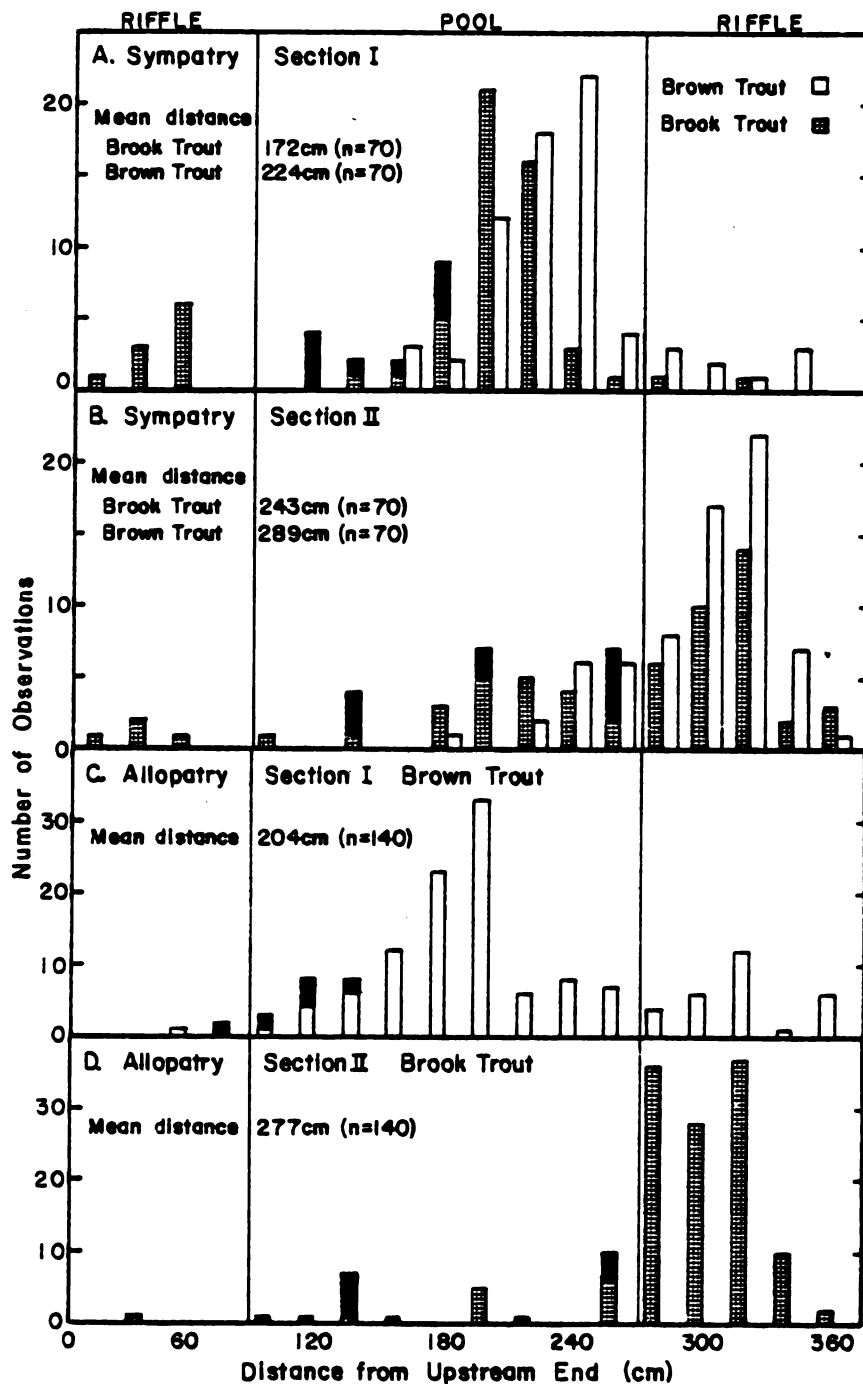


Figure 12.--Distribution of positions held by brook and brown trout during sympatry (a and b) and allopatry (c and d). Black portions of bars are positions of dominant fish.



controlled the area from 40-150 cm in Section I, and one brook trout in Section II drove all others downstream below 240 cm. There appeared to be no difference in the patterns of agonistic behavior of brook trout and brown trout, but brown trout were more easily intimidated by brook trout of equal or slightly larger size.

In this and subsequent experiments, brown trout that were forced into positions in fast water often applied the leading edges of their pectoral fins to the stream bed to hold themselves on the bottom with little energy expenditure. Brook trout were also observed doing this occasionally, and it is reported that Atlantic salmon use this technique (Gibson 1977, Kalleberg 1958). Coho salmon never rested on the bottom. Whenever trout were seen resting on the stream bed during the brook-vs.-brown and the brook-vs.-coho experiments, they were assigned a daily potential profit of zero because I assumed they were not foraging. During the brown-vs.-coho experiment, brown trout were assigned a focal point velocity of zero because I assumed that they required little energy to maintain the position, and were given a maximum velocity measured only to the distance from the focal point that they were observed to forage.

In natural populations, male brook trout can mature as early as age 0 and females as early as age I (Jensen 1971), but brown trout do not mature sexually until one or more years later for each sex (McFadden and Cooper 1964). Because the fish used in this experiment were hatched during January 1980 but were not used in the experiment until February 1981, I suspected that the dominant brook trout may

have been sexually mature males. However, when dominant brook and brown trout were dissected after the experiment, none were sexually mature.

#### Brook Trout vs. Coho Salmon

In sympatry with brook trout, the specific growth rates of all coho salmon were positive or zero, but were unrelated to mean potential profit (Figure 13a). It appears that coho were not sufficiently acclimated to the food or the stream aquarium, although all but four fish gained weight. Only one brook trout grew in sympatry, but the relationship between specific growth rate and potential profit is similar to that for fish grown in allopatry (Figures 13a and 13b).

In allopatry, most coho salmon grew, and converted potential profit to growth more efficiently than brook trout (Figure 13b). Only three brook trout maintained their weight or grew in allopatry. Moreover, brook trout required a higher threshold of potential profit to grow than did coho salmon (Figure 13b). Ten brook trout disappeared into the gravel during allopatry and were never recovered. All of these fish were healthy, but held unfavorable stream positions and had negative mean potential profits for the daily positions measured before they disappeared. One coho salmon disappeared on the last day of allopatry and was never found.

In sympatry, most brook trout held positions in the lower half of each stream section (Figures 14a and 14b), although one subordinate brook trout consistently occupied the upper riffle in

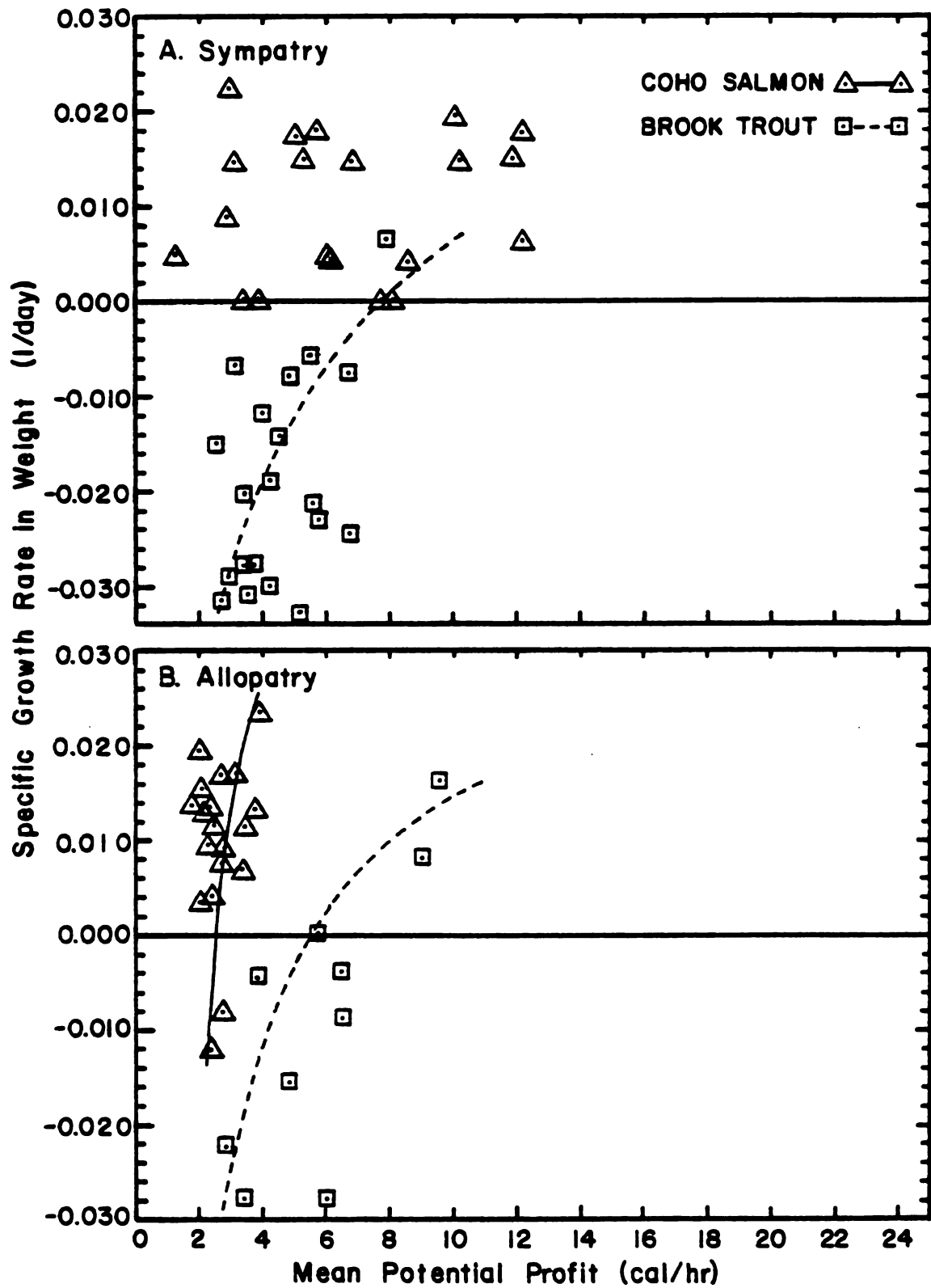


Figure 13.--Specific growth rate as a function of mean potential profit for brook trout and coho salmon in sympatry (a) and allopatry (b).

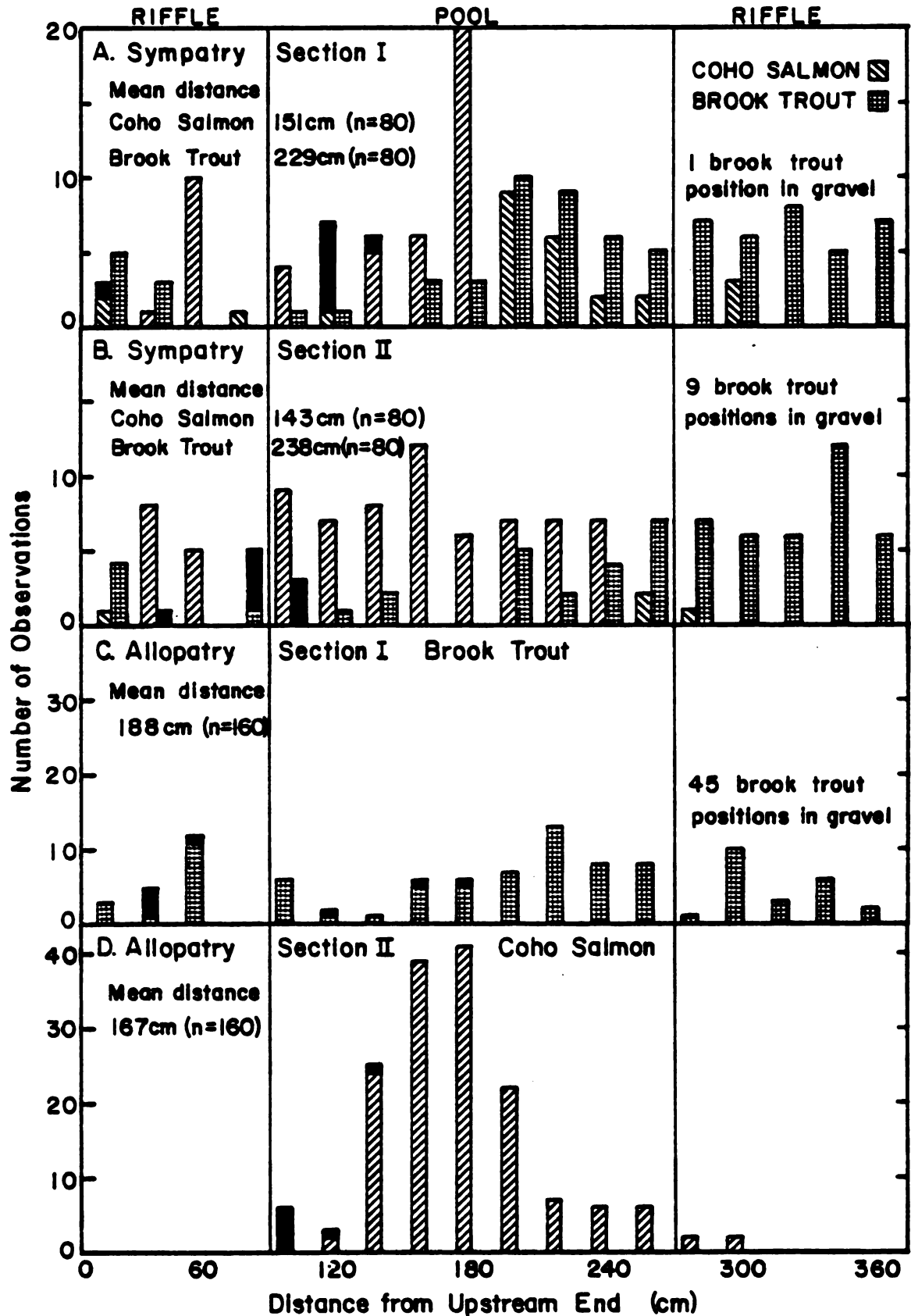


Figure 14.--Distribution of positions held by brook trout and coho salmon during sympatry (a and b) and allopatry (c and d). Black portions of bars are positions of dominant fish.

the upper section. In the downstream section, the largest brook trout was the dominant fish, shown as the black portion of the bars in Figure 14b, and competed with the largest coho for the most advantageous position at the head of the pool.

Positions held by coho salmon in sympatry were significantly further upstream than those held by brook trout in Section I (mean distances were 151 vs. 229 cm,  $p < .001$ ) and Section II (143 vs. 238 cm,  $p < .001$ ). A number of brook trout burrowed into the gravel in sympatry and allopatry to escape competitors (Figure 14).

In allopatry, brook trout shifted to positions more evenly distributed throughout the stream section (Figure 14c). The dominant fish occupied positions in the upper riffle and upper pool from 20-180 cm, and drove away other fish from upstream positions, apparently attempting to defend the upper 50% of the section. The dominant coho salmon held a position at the head of the characteristic aggregation at mid-pool (Figure 14d). This fish also drove away all other coho from upstream positions, but tolerated subordinate positions that were just downstream of its own.

In general behavioral observations, coho salmon were clearly the dominant competitor in sympatry. They appeared to be more efficient at foraging than brook trout, and more persistent at maintaining stream positions in the face of agonistic bouts--in short, coho could eat and defend positions at the same time. In contrast, brook trout often retreated downstream after a few nips from a coho or larger brook trout, and often did not feed for one or more minutes after

an agonistic bout. Brook trout also appeared to win agonistic bouts only against coho of smaller size.

In measurements of agonistic acts, brook trout interacted more often with coho salmon during sympatry than among themselves in Section II ( $p < .05$ ), but not in Section I. Brook trout initiated and received about 1.5-5.0 times more agonistic acts to and from coho than to and from themselves (Table 5). Coho salmon showed just the opposite pattern, initiating and receiving about 2-3 times more agonistic acts to and from brook trout than coho (Table 5), a significantly greater amount (Sections I and II, both  $p < .025$ ). These data indicate that, in sympatry, coho exhibited more agonistic behavior than brook trout, and reflect that not much agonism was required by coho to drive brook trout away. Conversely, brook trout spent more time and energy fighting with coho than among themselves in sympatry.

The measurements of agonistic acts in allopatry are not comparable to those in sympatry, because more than twice as many of either species were present in allopatry than in sympatry. Thus, it might be expected that agonistic acts would be about twice as frequent in allopatry than sympatry. However, in allopatry brook trout interacted about 3-13 times more frequently than in sympatry, while coho salmon interacted slightly less frequently in allopatry than in sympatry (Table 5).

TABLE 5.--Summary of agonistic behavior among trout and coho salmon. Percents of all two-minute observations where any agonism was observed are shown, with actual numbers of observations where agonism was observed in parentheses.

Experiment	Trout agonistic acts					Coho agonistic acts				
	From trout	To trout	From coho	To coho	n <sup>a</sup>	From coho	To coho	From trout	To trout	n <sup>a</sup>
<u>Brook trout vs. Coho salmon</u>										
Sympatry										
Section I	14 (5)	11 (4)	23 (8)	14 (5)	35 <sup>b</sup>	50 (18)	31 (11)	22 (8)	14 (5)	36
Section II	3 (1)	5 (2)	17 (7)	17 (7)	40 <sup>b</sup>	43 (19)	36 (16)	25 (11)	14 (6)	44
Allopatry	40 (20)	36 (18)			50 <sup>b</sup>	33 (26)	27 (21)			79 <sup>b</sup>
<u>Brown trout vs. Coho Salmon</u>										
Acclimation <sup>c</sup>	48 (12)	64 (16)			25 <sup>b</sup>	26 (9)	26 (9)			34
Sympatry										
Section I	3 (1)	0 (0)	18 (6)	15 (5)	33 <sup>b</sup>	27 (11)	33 (13)	13 (5)	20 (8)	40
Section II	10 (4)	7 (3)	10 (4)	5 (2)	40	33 (13)	27 (11)	10 (4)	7 (3)	40
Allopatry	17 (7)	24 (10)			42 <sup>b</sup>	39 (31)	36 (29)			80

a Number of two-minute observations.

b Fish hiding in gravel were excluded from totals.

c Data are from 6 days of pre-experiment allopatry.

### Brown Trout vs. Coho Salmon

All coho salmon grew when in sympatry with brown trout, were more efficient at growing on this food source than brown trout, and required a lower threshold of potential profit for growth (Figure 15a). All but one brown trout lost weight in sympatry. The relationships between specific growth rate and mean potential profit should be accurate for both sympatry and allopatry, because all brown trout and coho salmon were acclimated to the stream aquarium and to foraging on drifting Daphnia for 13.5 days in allopatry prior to this experiment (Table 2). Three brown trout died during the two-day rest period, and one was not found after allopatry, reducing the number from 16 to 13 during allopatry and to 12 at the end of the experiment.

All coho salmon grew in allopatry (Figure 15b), grew at similar specific rates for a given potential profit as they did in sympatry, and had a similar threshold of potential profit. In allopatry, coho again showed higher specific growth rates and a lower threshold than brown trout. Brown trout grew at higher rates in allopatry than in sympatry for a given level of potential profit, and had a lower threshold of potential profit for growth (Figure 15 and Table 4), although only five of twelve fish grew or maintained their weight. This change in brown trout growth rates after release from competition with coho salmon indicates that, in the presence of coho salmon, brown trout were either unable to forage on the available drifting Daphnia as efficiently, or were unable to convert as much energy to growth as when they were alone. One coho salmon



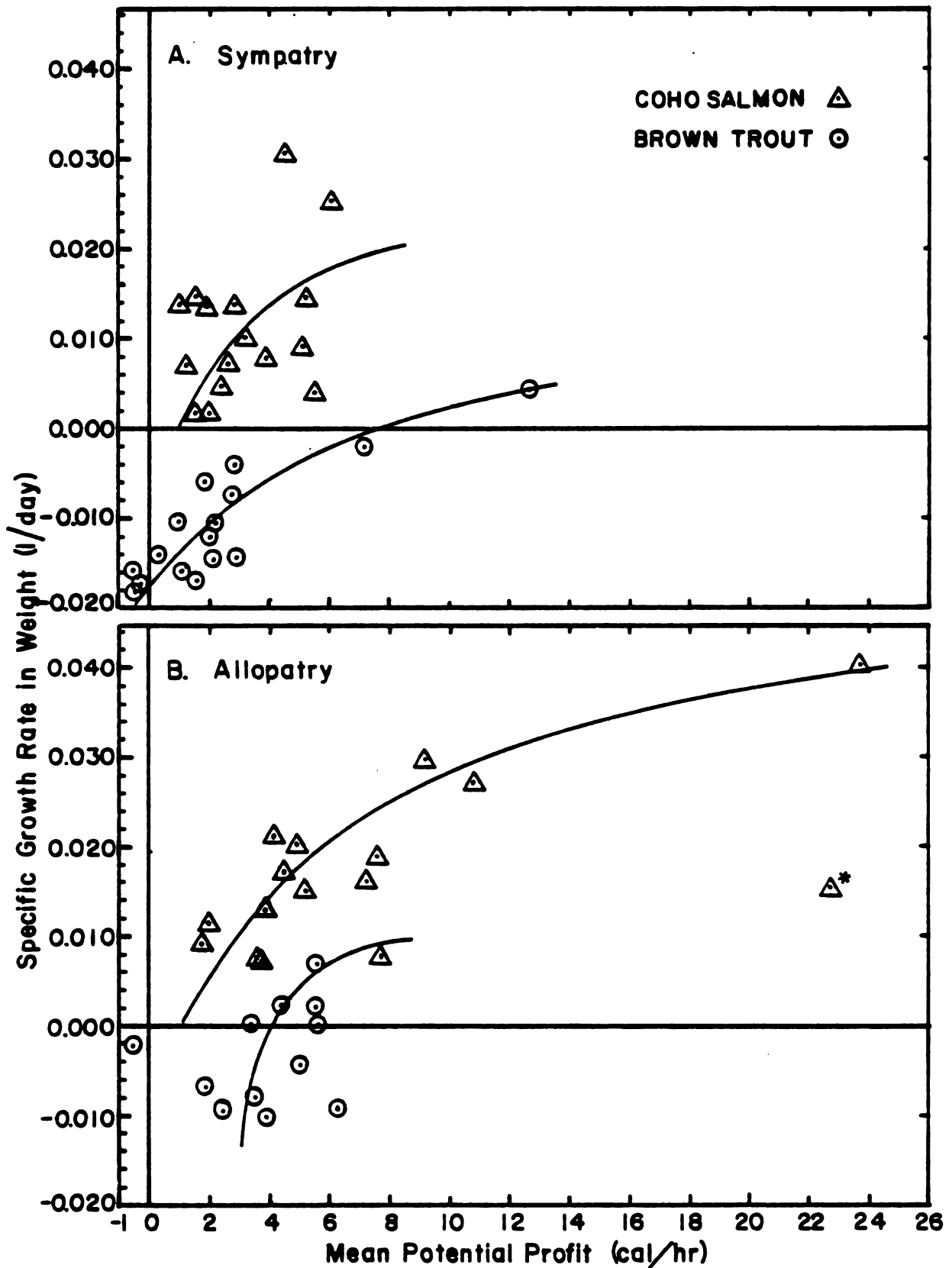


Figure 15.--Specific growth rate as a function of mean potential profit for brown trout and coho salmon in sympatry (a) and allopatry (b). One coho salmon in allopatry was excluded as an outlier (\*).

that held a position on the upper riffle during allopatry was excluded as an outlier for the same reasons given for a similar fish in the experiment of specific growth rate as a function of potential profit.

Coho actively drove brown trout from the pool onto the riffles in both sections during sympatry (Figures 16a and 16b). Most brown trout were forced into positions in the lower pool and the lower riffle, but two occupied the upper riffle in Section I, which caused the mean distances of coho and brown trout to be similar there (181 vs. 191 cm,  $p > .25$ ). In Section II, coho salmon positions were significantly further upstream than brown trout (149 vs. 260 cm,  $p < .001$ ), but one trout hid in a crevasse at 140-160 cm in the middle of the dominant coho's territory in the upper pool.

During allopatry, coho salmon showed the typical aggregation in mid-pool (Figure 16c), although the dominant fish in this experiment usually occupied a position on the upper riffle. Brown trout used positions along the entire stream section (Figure 16d), but by the end of the allopatry portion of the experiment, one fish defended the stream from 40-180 cm, which was 39% of the total 360-cm section, and three brown trout controlled the stream from 40-270 cm. Dominant brown trout were similar to brook trout in reserving more space for themselves in allopatry than did coho salmon.

Brown trout appeared to win agonistic bouts only when coho were smaller, which was not often because fish were sorted into two groups before sympatry and were all nearly equal in size. I also observed that brown trout were less persistent than coho in maintaining stream positions in the face of agonistic attacks. In

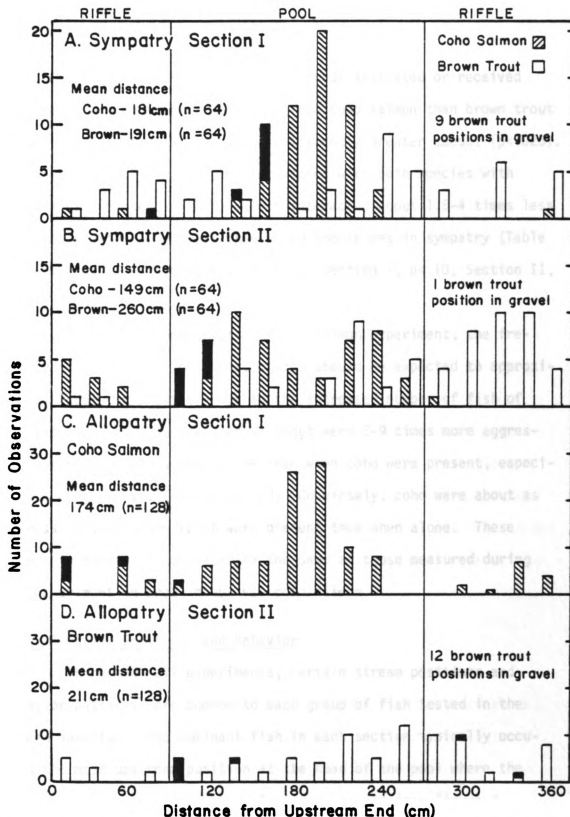


Figure 16.--Distribution of positions held by brown trout and coho salmon during sympatry (a and b) and allopatry (c and d). Black portions of bars are positions of dominant fish.

measurements of agonistic acts, brown trout initiated or received 5-6 times more agonistic acts to or from coho salmon than brown trout in Section I during sympatry, a significantly greater amount ( $p < .025$ ). But in Section II, brown trout interacted with both species with about equal frequency. Coho salmon interacted about 1.5-4 times less frequently with brown trout than among themselves in sympatry (Table 5), which was a significant difference (Section I,  $p < .10$ ; Section II,  $p < .01$ ).

As in the brook-trout-vs.-coho salmon experiment, the frequency of intraspecific agonistic acts should be expected to approximately double in allopatry due to the increased number of fish of the same species. However, brown trout were 2-9 times more aggressive among themselves when alone than when coho were present, especially during the acclimation period. Conversely, coho were about as aggressive when brown trout were present than when alone. These trends in agonistic behavior are the same as those measured during the experiment on brook trout vs. coho salmon.

#### General Stream Positions and Behavior

Throughout all experiments, certain stream positions and behavior patterns were common to each group of fish tested in the stream aquarium. The dominant fish in each section typically occupied the most upstream position at the head of the pool where the water became deeper and water velocity decreased (see Figure 2, Section II). This fish often held a position a few centimeters above the bottom about 10 cm from the outside stream wall, and

moved to faster and deeper water near this outside wall to catch drifting food.

The subordinate fish in each section were arrayed in a hierarchy downstream from the dominant, and were spaced closer to each other with each successively lower member in the hierarchy, with a group of fish positioned 180-220 cm from the upstream end. One subordinate fish often occupied a position behind a protruding stone on the upper riffle, if tolerated by the dominant who often attacked all other fish trying to gain upstream positions.

The more subordinate fish in the hierarchy used positions on the lower riffle or in shallow water along the bar in the pool. Among coho salmon, there was often one opportunistic subordinate fish that took a position in shallow water on the bar at the head of the pool, but swam 30-40 cm to the deep fast water next to the far wall to capture drifting food. Subordinate brook and brown trout often burrowed in the gravel, presumably to escape their competitors, but coho simply retreated to shallow, quiet water when intimidated, and were never seen to burrow into the gravel.

#### Significance of Competition Experiments

From the experiments of competition in the stream aquarium, I conclude that coho salmon were superior competitors over either brook or brown trout of equal size at all food levels, and when no visual concealment was available. Coho salmon drove trout from advantageous positions in the stream aquarium, which were those positions in the upstream portion of the pool. Coho also grew faster

at all levels of potential profit than trout, and continued to grow at a lower threshold of potential profit than trout. Therefore, even if brook or brown trout could have gained positions as profitable as those of coho, the coho would quickly have grown larger, and larger body size would soon have ensured their dominance over trout.

Only a few other investigators have studied interactions among juveniles of coho salmon and either brook or brown trout. Gibson (1977) measured agonistic behavior of coho salmon that were nearly smolt size ( $>120$  cm) and brook trout of equal size, in a stream aquarium devoid of cover. He found that brook trout displaced coho more often than vice versa. However, the smolt transformation may have reduced coho aggression, some brook trout may have been sexually mature, and the coho length distribution he reported appeared to be slightly smaller than that of trout. Although these results contradict my findings, Gibson (1977) did note that coho and brook trout both preferred positions in pools, that coho salmon tended to aggregate in the pool, and that coho attacked each other more frequently than they attacked trout in sympatry, all of which coincided with my findings.

Taube (1975) calculated population estimates of brown trout in two sections of the Platte River, Michigan, one of the original streams where coho salmon were introduced, before and after the salmon were allowed to spawn there. He found a significant decrease in the numbers of age-0 brown trout when salmon were present for both stream sections, but concluded that the decrease had little

long-term effect on this year class of trout because of their greater compensatory survival to older ages.

On the basis of eight years of juvenile salmonid population estimates in five Lake Superior tributaries, Stauffer (1977) concluded that numbers of juvenile brook and brown trout were lower when age-0 coho were abundant, and suggested that juvenile coho may depress trout numbers. The negative correlations between coho salmon and trout abundance from these two field studies support my conclusions that juveniles of coho salmon are superior competitors over those of brook and brown trout.

My stream aquarium studies also show that juvenile brook trout were superior competitors over equal-sized brown trout, gaining more of the advantageous upstream positions and actively displacing brown trout downstream. Kjellberg (1969) observed that brook trout excluded brown trout from small lake inlets in Sweden, and eventually crowded them out. He attributed this to competition for territories between juvenile brook and brown trout during their first summer of life, and stated that brook trout, in general, show considerably more aggressive territorial behavior than brown trout. However, on the basis of shifts in adult brook trout positions after brown trout were removed from a section of a Michigan stream, Fausch and White (1981) concluded that brown trout larger than 150 mm were superior competitors and excluded equal-sized brook trout from advantageous positions.

In contrast to the assemblages of exotic salmonids discussed above, studies of interactions among salmonids that evolved together

suggest that these species partition stream resources in several ways to avoid competition. Research on interactions between steelhead trout and coho salmon (Hartman 1965), cutthroat trout (Salmo clarki) and coho salmon (Glova and Mason 1977), and Atlantic salmon and brook trout (Gibson 1966) show that the former species of each set occupies the riffles and the latter the pools during the summer. This is often termed interactive segregation, meaning that the segregation occurs as a result of behavioral interactions, and is not genetically fixed. Consequently, one species often shifts to a different microhabitat if the other is removed.

Everest and Chapman (1972) propose that sympatric steelhead trout and chinook salmon avoid competition by different timing of fry emergence. Because the salmon are fall spawners and the young emerge earlier than the spring-spawning steelhead, the young salmon move from the stream margins into faster and deeper water before the steelhead young emerge. This mechanism is probably important to segregate all sympatric fall and spring spawning salmonids during the early part of their first summer of life, but by early fall, the size distributions of all salmonids are about equal (cf. Hartman 1965).

The measurements of agonistic behavior during the laboratory competition experiments reveal two main patterns during sympatry between coho salmon and brook or brown trout: (1) trout often fought with coho more frequently than among themselves, and (2) salmon always fought more frequently among themselves than with trout (Table 5). I suspect that this reflects that coho drove trout into



scattered, unfavorable positions by occasional attacks, but that once the trout were in unfavorable positions they interacted little with other trout. In contrast, coho always aggregated in the pools during both sympatry and allopatry, which probably resulted in higher frequency of agonism among coho than was directed towards trout.

The frequency of agonistic acts among brook or brown trout in allopatry should have been roughly double than in sympatry, but was often higher, especially during acclimation of brown trout. In each experiment, I observed that, after 9-10 days in allopatry, one dominant trout defended a large area in the upstream part of the pool where food was abundant, and that the three most dominant trout usually defended a majority of the stream area. These more dominant trout often travelled 50-75 cm to attack other trout. I suspect that brook and brown trout defended large territories because the stream aquarium offered no visual isolation other than that afforded by distance along the stream bend. In contrast, the majority of coho salmon remained closely aggregated in the pool during all allopatric experiments, and the dominant fish defended a moderate area of the stream, but tolerated subordinates within about 20 cm downstream.

#### Relationships Between Specific Growth Rate and Potential Profit

I chose the relationships between specific growth rate and potential profit, shown in Figure 17, as the best curves for juveniles of coho salmon, brook and brown trout on the basis of length of acclimation to the food and the stream aquarium, and accuracy of drift measurement. The relationships measured in allopatry account

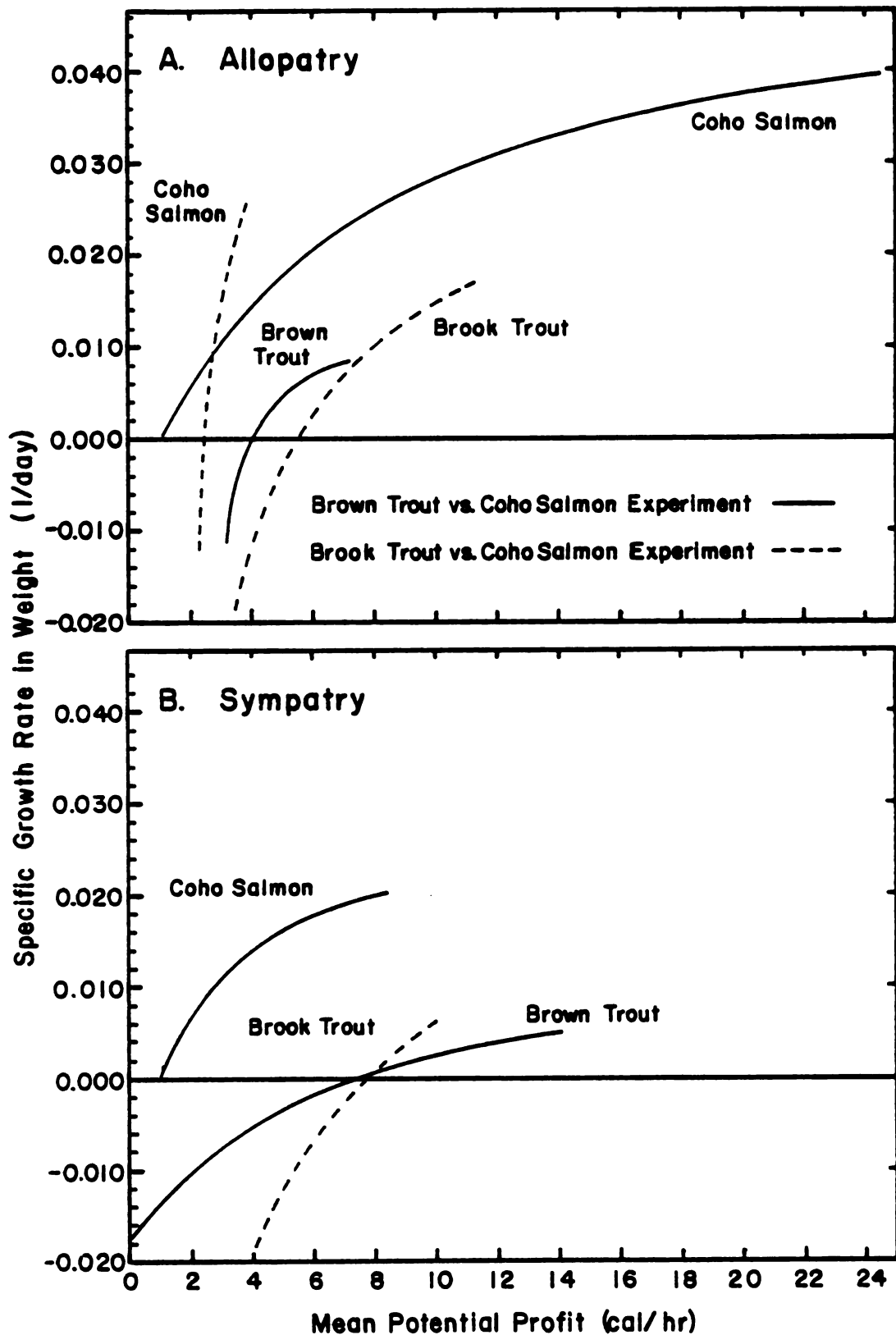


Figure 17.--General relationships between specific growth rate and mean potential profit for coho salmon, brook and brown trout in allopatry (a) and sympatry (b).

for differences in the basic physiology and intraspecific behavior among the three species. Those measured in sympatry account for interspecific behavior and any changes in intraspecific behavior due to sympatry, as well as basic physiology. Valid comparisons can only be made within each experiment, but the differences between sympatry and allopatry curves for a species should be caused mainly by interspecific competition.

When sympatry is compared to allopatry for each species within an experiment, the curves were lower in sympatry (Figure 17). Although no measure is available about the statistical significance of these decreases, inspection of the original data (Figures 13 and 15) shows that the brown trout curve appears to be the only one that clearly changed from allopatry to sympatry. This change was mainly due to an increase in the threshold value for potential profit of about 3.5 cal/hr. This general flattening of the brown trout curve, and the increase in the threshold potential profit may have occurred for two reasons: (1) brown trout spent more time and energy on agonism during sympatry than allopatry, or (2) brown trout foraged less efficiently on drifting Daphnia during sympatry than allopatry. Because the measurements of agonistic behavior (Table 5) generally refute the first reason, I suspect that brown trout may have been intimidated by coho, and did not forage as efficiently in sympatry as when alone.

I suspect that a more common effect of interspecific competition on these relationships would be to move individuals of the subordinate species to the left and down the curves, as a result of

their being forced into poorer positions. This appears to have occurred among brook trout when competing with coho salmon, because the average of mean potential profit for brook trout was significantly less during sympatry than allopatry ( $p < .05$ ), as was the average specific growth rate ( $p < .025$ ). This comparison cannot be made for the brown trout vs. coho salmon experiment because the food level was changed significantly between sympatry and allopatry (Table 2).

#### Laboratory and Field Specific Growth Rates

One way to compare the suitability of the stream aquarium and the drifting Daphnia for growth of juvenile salmonids, with the conditions in natural streams is to compare laboratory specific growth rates to those in the field for fish of equal size. The relationships between mean weight and specific growth rate for each species are shown for all streams in Figure 18. The dashed lines are negative exponential equations fit to all points to show the average decrease in growth rate as mean weight increases. Although coho are always larger (Figures 7 and 8), all species grew at similar rates for equal weight. The three species grew at high rates after emergence in early spring, but their specific growth rates decreased to less than 0.020 per day during the first summer of life (Figure 18).

The three negative exponential curves from Figure 18 are shown in Figure 19 along with the highest growth rates for individual coho salmon, brook and brown trout grown in sympatry and allopatry

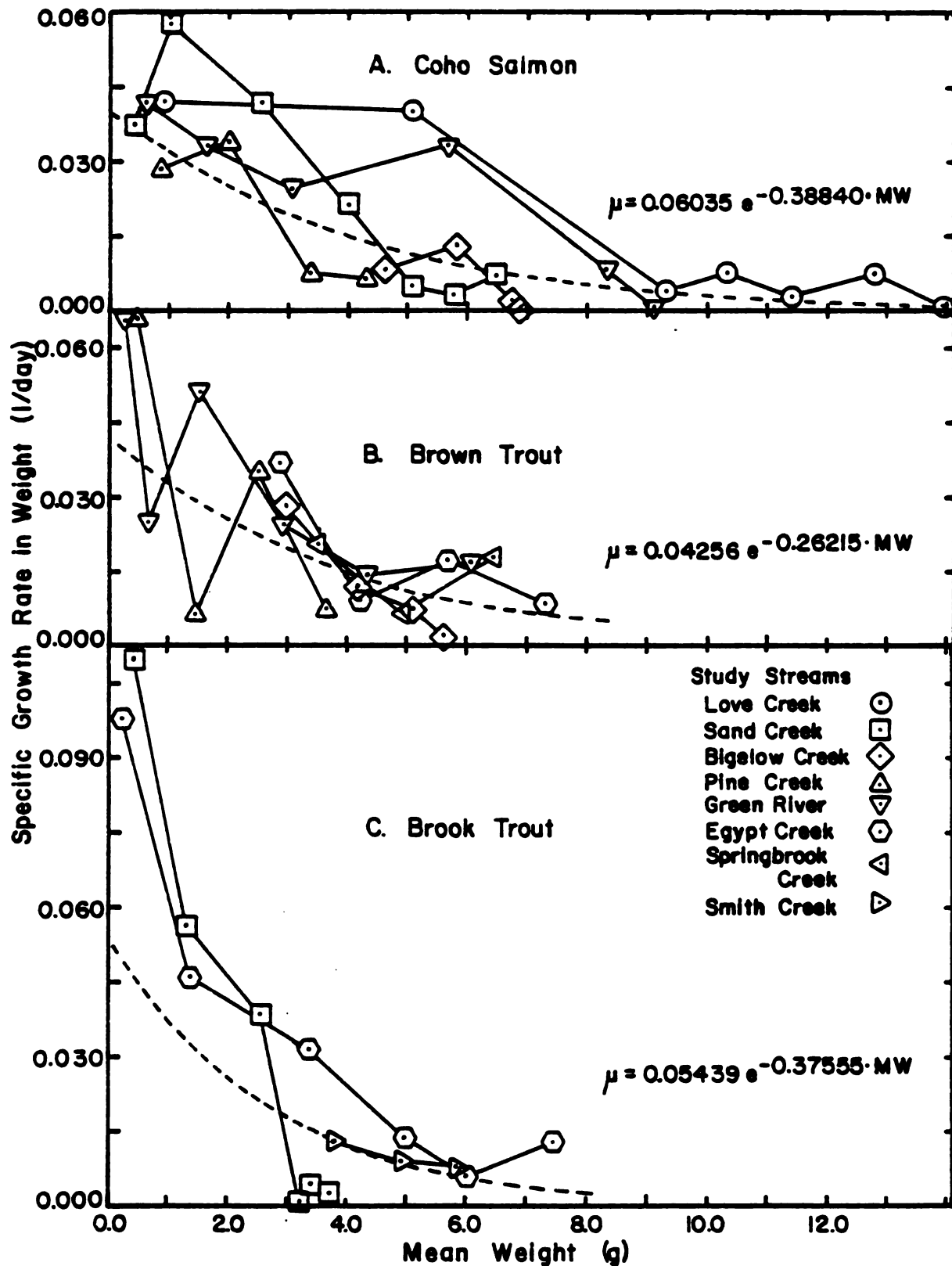


Figure 18.--Specific growth rate of juvenile salmonids in eight Lake Michigan tributaries as a function of mean weight. Dashed lines are negative exponential equations fit to all data for each species.

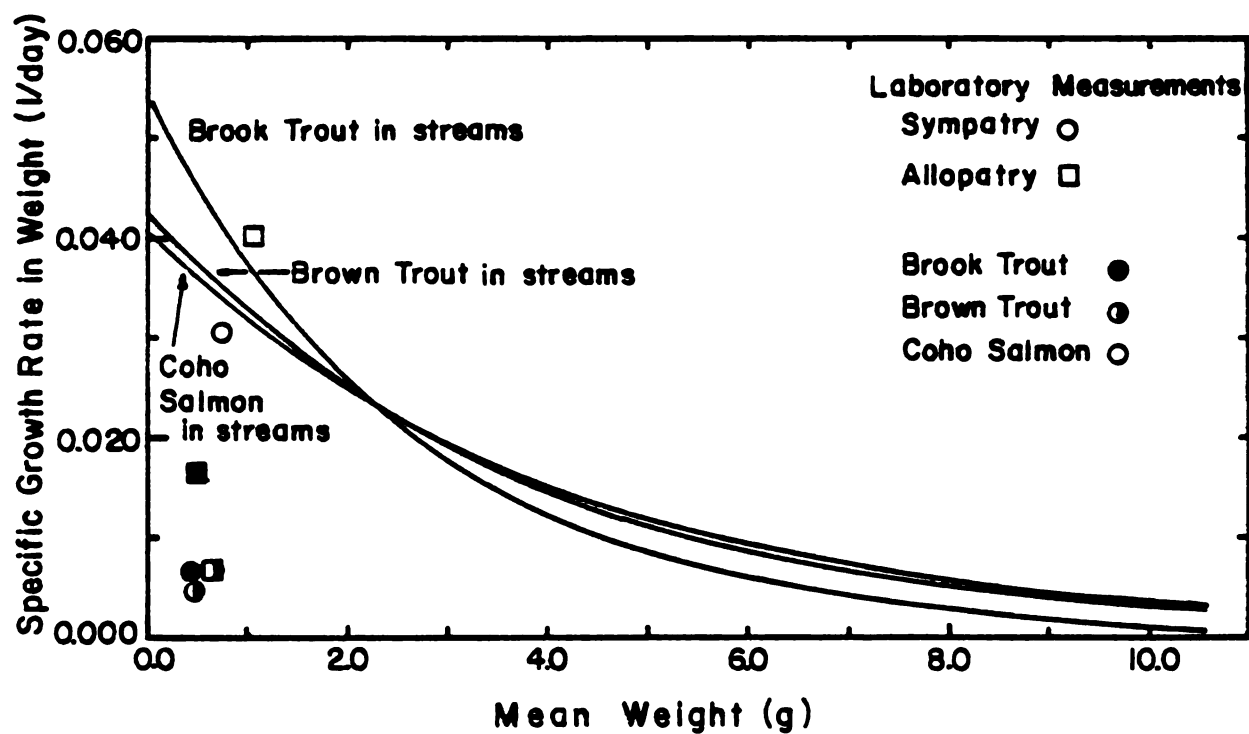


Figure 19.--Comparison of salmonid specific growth rates as a function of mean weight in Lake Michigan tributaries with the highest rates for individual fish in laboratory experiments.

in the stream aquarium. The highest laboratory specific growth rates for coho salmon are close to the field rates, indicating that conditions in the stream aquarium adequately simulated those in Great Lakes tributaries, at least for coho. However, the highest laboratory specific growth rates for trout fell far short of those measured in natural streams.

It is evident that brook and brown trout in the stream aquarium lacked some critical resource for growth; probably either food or cover. Trout may require a different food type, possibly foraging more on benthic invertebrates than those carried in the drift. However, Wagner (1975) found that age-0 brown trout and coho salmon foraged mainly on midge (Tendipedidae) and blackfly larvae (Simuliidae), which I suspect were carried to their positions in the drift. Moreover, Chapman (1966) proposed that salmonids, in general, can not subsist on the benthos living within their territory, and that benthos must move to be detected by foraging salmonids. But if juvenile brook and brown trout food requirements and ability to feed on drift are similar to those of coho, they should have grown at field rates in the stream aquarium, all other things being equal.

Another critical resource that probably limited brook and brown trout growth in the stream aquarium was cover. Within the confines of the stream sections, there was virtually no cover affording visual isolation, and during allopatry dominant trout drove away all other trout that they could see. The time and energy required

for dominant trout to defend large territories detracted from energy for growth. Mortensen (1977) found that natural mortality of age-0 brown trout, corrected for density-dependent mortality, was higher in Danish streams where weeds and wood debris were cleaned out than in control streams. In contrast, coho salmon were not oriented to cover in laboratory studies (Hoar 1958, Glova and Mason 1977) nor were they observed to use cover in the streams I sampled unless frightened, whereas brook and brown trout were most often associated with cover in these streams.

These relationships between specific growth rates and potential profit, and the need for visual isolation fit with what can be surmised about the evolution of these fishes. Neave (1958) presents evidence that the genus Oncorhynchus evolved from an ancestral anadromous Salmo. Coho salmon are considered to be the most primitive of the Oncorhynchus, but have a short stream residence compared to steelhead trout (Salmo gairdneri), which is thought to resemble the ancestral line from which the Pacific salmon developed (Neave 1958). Natural selection appears to have favored less stream residence and earlier smolting for the four more advanced salmon as well; pink and chum salmon (O. keta) smolt soon after emergence, chinook salmon smolt after a few months, and sockeye salmon smolt soon after emergence but have a more complex life history involving growth in a freshwater lake before ocean residence.

During the evolution of coho salmon, it is reasonable to suspect that natural selection would favor larger smolts. Studies



of the return of adults from hatchery smolt releases reveal that larger coho smolts produce both larger adult fish and a higher proportion of early returning male fish, called "jacks" (Bilton 1978, Hager and Noble 1976). The survival rate of smolts cannot be easily determined because the salmon returning are only those that escape the commercial fishery. Selection pressures favoring larger coho smolts should favor maximum growth rates during juvenile stages, much like those I measured in the stream aquarium. However, I suspect that little selective advantage would be conferred to coho juveniles reserving large areas of the stream to ensure suitable cover or a future food supply, because coho are not oriented to cover and most of the energy for coho growth and reproduction comes from the ocean.

Brook and brown trout evolved a life history of residence in streams of the northern hemisphere, and originally were generally Holarctic in distribution (MacCrimmon and Campbell 1969, MacCrimmon and Marshall 1968). Although the relationships between specific growth rate and potential profit measured in the laboratory evidently do not apply to natural streams, it is clear that these trout must extract enough energy from streams for growth and successful reproduction. To do this requires reserving enough space to provide an adequate food supply, but also a space that affords cover to ensure concealment from predators and competitors, and refuge from high streamflow and winter ice. Therefore, in the absence of cover, it is not surprising that brook and brown trout attempted to reserve

large areas of a stream aquarium and did not grow as fast as they did in natural streams.

#### Interactions Among Juvenile Salmonids in Great Lakes Tributaries

In Great Lakes tributaries, different ages and sizes of juvenile salmonids occupied different areas of the stream, according to my electrofishing and snorkeling observations. Coho salmon emerged earlier and were larger than brook or brown trout on average, although some equal-sized age-0 coho and trout were always present. Newly emerged trout occupied the silt flats in early spring and were often associated with cover afforded by wood debris or aquatic vegetation. Coho were found in shallow open areas after emergence, but quickly moved to faster and deeper water as they grew.

During the summer, brook and brown trout juveniles were still associated with cover, but had moved to the faster and deeper water at the edge of the main channel. Coho salmon were found in groups in the deeper water at the channel edge and in the main channel during this time of year. Thus age-0 coho salmon and brook and brown trout may partition space resources in streams and avoid direct competition for this resource, while both probably exploit a common invertebrate drift resource. Age-I and older trout also occupied the main channel and were often associated with cover provided by logs found there. Therefore, if coho juveniles grow as large as the smallest age-I trout during their first summer of life, they may compete directly with these trout for food and space, because both occupy the main stream channel.

Combining the results of the laboratory experiments, where lack of visual isolation probably reduced trout growth, and the field observations of cover use by juvenile trout, I further speculate that visual isolation provided by cover in natural streams may be important to the existence of juvenile brook and brown trout, especially when faced with competition from coho salmon. In stream areas with little cover, age-0 coho may severely inhibit the growth and survival of age-0 trout. In laboratory tests of interspecific competition among equal-sized fish, coho dominated brook and brown trout. In natural streams, coho will have an even greater competitive advantage because of their greater size. Moreover, juvenile salmon populations often far outnumber those of brook or brown trout because adult female salmon produce large numbers of eggs relative to smaller trout. With these considerations, I would expect juvenile coho salmon populations to thrive, and brook and brown trout populations to subsist with difficulty in Great Lakes tributaries where coho salmon reproduce.

## CONCLUSIONS

1. Juvenile coho salmon emerged 2-3 weeks earlier in the spring and were always 6-20-mm larger than either brook or brown trout when sympatric in Lake Michigan tributaries. Brook and brown trout emerged at similar times and grew at about equal rates in both sympatric and allopatric populations.
2. The specific growth rates of juvenile salmonids are predictable functions of the potential net energy gain or "potential profit" measured at their stream positions, and may be described by Michaelis-Menten or Monod equations. Dominant individuals held positions with the highest potential profit of any fish in the stream section, and grew at the highest specific rates. This supports the hypothesis that salmonids compete for stream positions that maximize net energy gain.
3. In laboratory tests of competition juvenile coho salmon dominated juvenile brook and brown trout, excluding them from advantageous positions in the stream aquarium. Coho salmon also grew more efficiently than either brook or brown trout in both sympatry and allopatry, and required a lower threshold of potential profit to maintain growth than did the trout.
4. Juveniles of brook trout dominated those of brown trout and excluded them from advantageous stream positions. During allopatry in each experiment, a few dominant trout always defended

large areas of the stream from subordinates, probably because of the lack of cover affording visual isolation in the stream aquarium.

5. In natural streams where age-0 coho are significantly larger than age-0 brook and brown trout on average, coho are expected to exclude brook and brown trout from profitable areas of the stream, and to thereby reduce their growth and survival. The competitive disadvantage of brook and brown trout may be reduced somewhat if coho and trout partition space resources in the stream along depth and velocity gradients, or if large amounts of cover affording visual isolation are present.

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## LITERATURE CITED

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## APPENDIX

TABLE A1.--Chemical characteristics of water in the stream aquarium at the beginning and end of each experiment.

Sample date	Water temp (C)	Concentration (mg/liter or ppm)						meq. <sup>a</sup> alka- linity	Free CO <sub>2</sub> (μmol/l)	Total inorganic carbon <sup>b</sup> (mmol/l)
		Alka- linity (CaCO <sub>3</sub> )	pH	Hard- ness (CaCO <sub>3</sub> )	NO <sub>3</sub> -N	NO <sub>2</sub> -N	NH <sub>3</sub> -N			
1. <u>Specific Growth Rate vs. Potential Profit</u>										
10/7/80	15	102	8.14	130	1.83	.21	.01	2.04	39.0	2.07
10/24/80	15	100	8.08	127	3.43	.01	.01	2.00	44.0	2.04
2. <u>Brook Trout vs. Brown Trout</u>										
2/11/81	15	217	8.09	245	2.21	.01	.02	4.34	93.2	4.41
3/4/81	15	207	8.26	235	3.30	.01	.05	4.14	59.9	4.17
3. <u>Brook Trout vs. Coho Salmon</u>										
5/12/81	14	128	8.34	140	2.98	.02	.01	2.56	30.7	2.57
6/4/81	15	117	8.12	140	4.44	-	.01	2.34	46.9	2.38
4. <u>Brown trout vs. Coho Salmon</u>										
6/22/81	15	108	8.24	120	2.01	.01	.01	2.16	32.7	2.18
7/13/81	15	104	8.53	125	2.56	-	.02	2.08	16.0	2.07

<sup>a</sup>meq. = milliequivalents.

<sup>b</sup>Calculated from equilibrium constants at 15C.

TABLE A2.--Mean dry weight and percent ash of frozen *Daphnia* fed per 3 h during each experiment. SEM are shown in parentheses

Experiment	Dry weight (g)	Ash-free dry weight (g)	Percent ash	n	Dry weight fed per day (g)
<b>1. <u>Growth vs. Profit</u><sup>a</sup></b>					
Coho salmon	0.070 (0.00309)	0.065 (0.00286)	7.5 (0.711)	5	0.280
Brown trout	0.043 (0.00430)	0.039 (0.00396)	8.7 (0.410)	5	0.172
<b>2. <u>Brook trout vs. Brown trout</u><sup>b</sup></b>					
Sympatry and Allopatry	0.0827 (0.00272)	0.0752 (0.00250)	9.1 (0.577)	13	0.331
<b>3. <u>Brook trout vs. Coho salmon</u><sup>b</sup></b>					
Sympatry	0.0681 (0.00373)	0.0625 (0.00339)	8.2 (0.158)	8	0.272
Allopatry	0.0786 (0.00224)	.0710 (0.00160)	9.5 (0.811)	9	0.314
<b>4. <u>Brown trout vs. Coho salmon</u><sup>b</sup></b>					
Sympatry Upstream	0.0748 (0.00837)	0.0669 (0.00733)	10.6 (0.850)	4	0.299
Downstream	0.1048 (0.00973)	0.0955 (0.00929)	9.0 (1.533)	4	0.419
Allopatry	0.1046 (0.00281)	0.0972 (0.00281)	7.1 (0.379)	8	0.418

a Weighed on balance accurate to  $\pm .001$  g.

b Weighed on balance accurate to  $\pm .0001$  g.

TABLE A3.--Mean length and weight of juvenile salmonids in eight Lake Michigan tributaries during 1979.  
Sample size and half-widths of 95% confidence intervals are shown for each date.

Date	Coho Salmon						Brown Trout						Brook Trout					
	Length (mm)	95% CI <sup>a</sup>	n	Weight (g)	95% CI <sup>a</sup>	n	Length (mm)	95% CI <sup>a</sup>	n	Weight (g)	95% CI <sup>a</sup>	n	Length (mm)	95% CI <sup>a</sup>	n	Weight (g)	95% CI <sup>a</sup>	n
<u>Love Creek</u>																		
4-12	46.5	2.2	6	0.77	0.17	6												
4-19	47.8	1.5	12	1.03	0.16	12												
6-12	95.4	8.4	14	9.08	2.27	14							37.0	b	1	0.35	b	1
6-25	96.7	4.3	14	9.60	1.17	13												
7-13	102.5	10.2	8	11.05	2.95	8												
8-03	107.3	5.9	10	11.78	1.91	10												
8-24	111.7	7.5	10	13.82	2.44	10												
9-14	114.0	7.6	9	14.10	2.48	9												
<u>Sand Creek</u>																		
4-19	34.9	1.3	7	0.29	0.09	7												
4-26	42.1	3.6	11	0.65	0.18	10							29.5	b	2	0.09	b	2
5-06	43.1	1.9	24	0.54	0.11	22							43.0	b	1	0.70	b	1
5-25	54.4	2.1	44	1.63	0.20	25							59.5	b	2	1.93	b	2
6-12	68.3	2.8	33	3.46	0.56	26	52.0	b	1	1.5	b	1	68.5	9.6	4	3.17	1.14	4
6-25	76.0	3.0	47	4.57	0.82	32							70.7	6.8	6	3.23	.79	6
7-13	84.0	3.0	29	5.66	0.59	29							73.0	b	3	3.53	b	3
8-03	84.9	3.4	24	5.57	0.77	24							69.7	b	3	2.87	b	3
8-24	87.3	4.2	20	5.97	0.91	20							78.4	6.6	9	3.91	.80	9
9-14	92.4	2.0	44	6.97	0.51	44												
<u>Egypt Creek</u>																		
5-04													29.5	2.5	8	0.15	.11	4
5-11													34.3	3.9	8	0.30	.15	7
6-26							58.3	13.3	4	1.95	1.46	4	62.7	5.1	12	2.42	.51	12
7-14	107.0	b	1	11.20	b	1	69.5	b	2	3.80	b	2	73.9	7.6	8	4.26	3.32	8
8-04	97.0	b	1	8.70	b	1	77.0	7.8	5	4.64	1.60	5	82.0	5.1	16	5.67	1.28	16
8-25							86.4	11.8	7	6.66	2.37	7	87.6	4.7	22	6.41	.94	22
9-15	112.0	b	1	11.10	b	1	93.2	4.2	6	7.97	1.29	6	96.5	6.2	20	8.43	1.79	20
<u>Bigelow Creek</u>																		
6-26	75.7	2.9	23	4.28	0.51	23	59.0	b	2	2.20	b	2						
7-14	79.5	4.9	8	4.99	1.12	8	70.5	b	2	3.65	b	2						
8-04	86.3	5.9	8	6.60	1.17	7	79.0	b	1	4.70	b	1						
8-25	90.3	3.2	16	6.89	0.78	16	82.7	7.9	4	5.50	1.73	4						
9-15	90.4	3.2	32	6.86	0.70	32	84.5	9.2	8	5.73	1.73	8						
<u>Pine Creek</u>																		
5-12	44.0	1.8	37	0.69	0.11	29	28.6	1.5	7	0.20	0.07	6						
5-26	46.8	1.9	66	1.03	0.28	26	37.3	5.3	7	0.50	0.21	7						
6-27	63.7	3.3	64	3.06	0.70	30	49.8	3.9	16	1.29	0.35	16						
7-15	67.0	3.4	55	2.95	0.55	40	50.9	3.1	18	1.30	0.25	18						
8-05	70.7	2.4	70	3.69	0.48	40	54.7	3.2	32	1.66	0.27	32						
8-25	70.7	2.1	69	3.30	0.33	69	68.1	5.7	22	3.35	0.95	22						
9-16	82.6	2.1	64	4.89	0.37	64	72.4	5.6	25	3.96	0.78	25						
<u>Green River</u>																		
5-13	39.8	0.9	29	0.48	0.09	15	28.1	1.9	10	0.16	0.04	10	26.0		2	0.11		2
5-27	45.2	2.2	21	0.86	0.15	21	35.1	2.8	11	0.40	0.12	11						
6-27	61.1	3.0	36	2.41	0.40	31	43.9	3.1	19	0.87	0.17	19						
7-15	71.5	4.4	20	3.75	0.69	20	59.2	4.4	12	2.21	0.52	12	63.0	b	1	2.50	b	1
8-05	90.1	6.7	12	7.57	1.84	12	69.5	7.7	11	3.66	1.04	11	64.0	b	1	2.30	b	1
8-26	95.7	4.0	29	9.08	1.23	29	78.2	4.3	25	4.99	0.75	25						
9-16	98.2	6.3	19	9.16	1.64	19	88.8	4.7	26	7.13	1.06	26	84.0	b	1	5.40	b	1
<u>Springbrook Creek</u>																		
7-10							62.7	2.9	21	2.48	0.34	21	66.7	7.5	16	3.04	0.98	16
8-09							76.8	3.7	30	4.59	0.64	30	75.6	5.7	30	4.50	0.98	30
8-29							80.9	4.0	28	5.24	0.78	28	80.4	5.6	33	5.37	1.07	33
9-19							92.0	4.4	30	7.64	1.12	30	86.7	5.6	36	6.32	1.11	36
<u>Smith Creek</u>																		

a Half-width of 95% confidence interval.

b Confidence intervals not shown for samples of three or fewer fish.

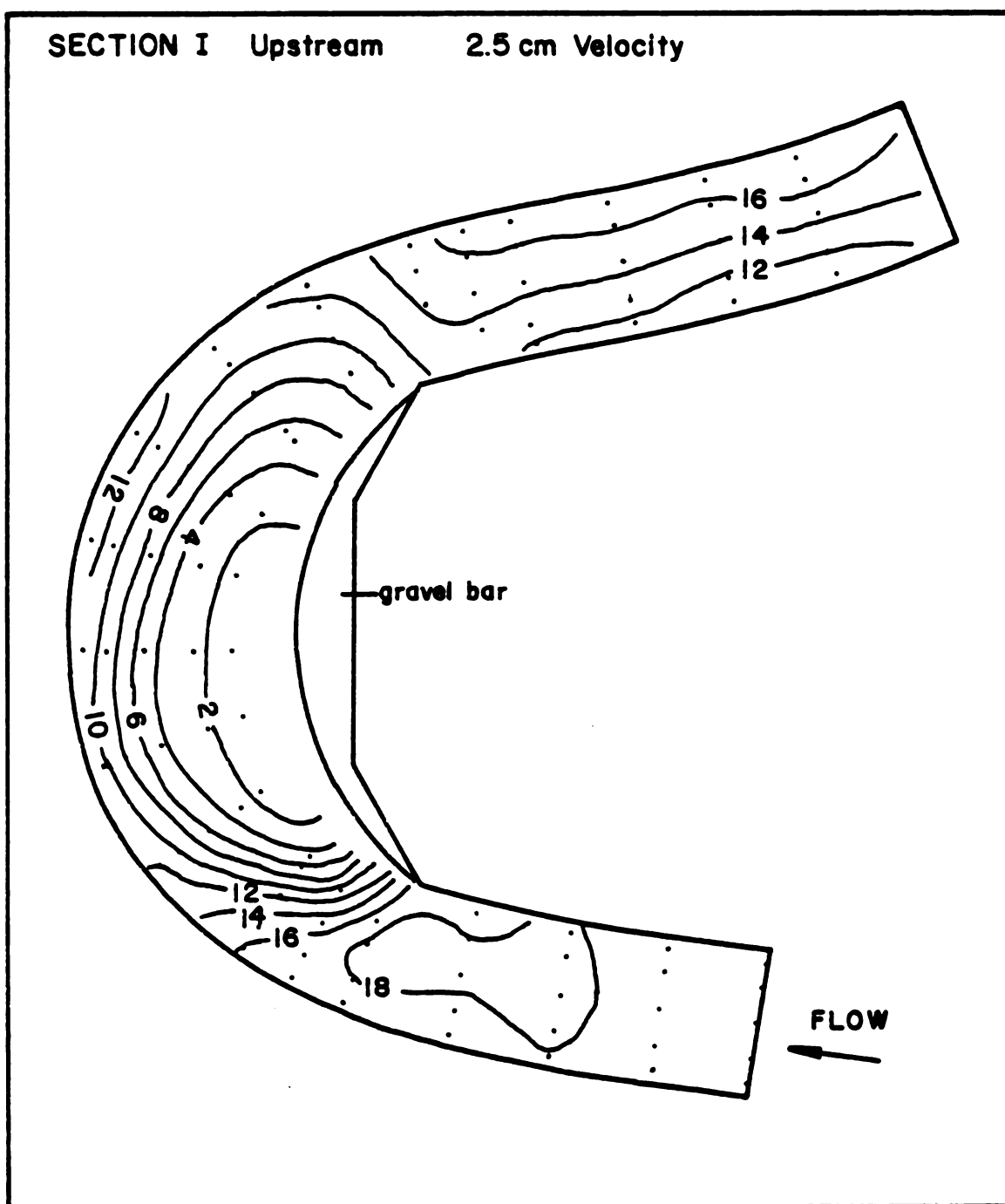


Figure 1a.--Water velocities (cm/sec) in Section I (upstream) 2.5 cm below water surface. Water velocities were measured at points shown.

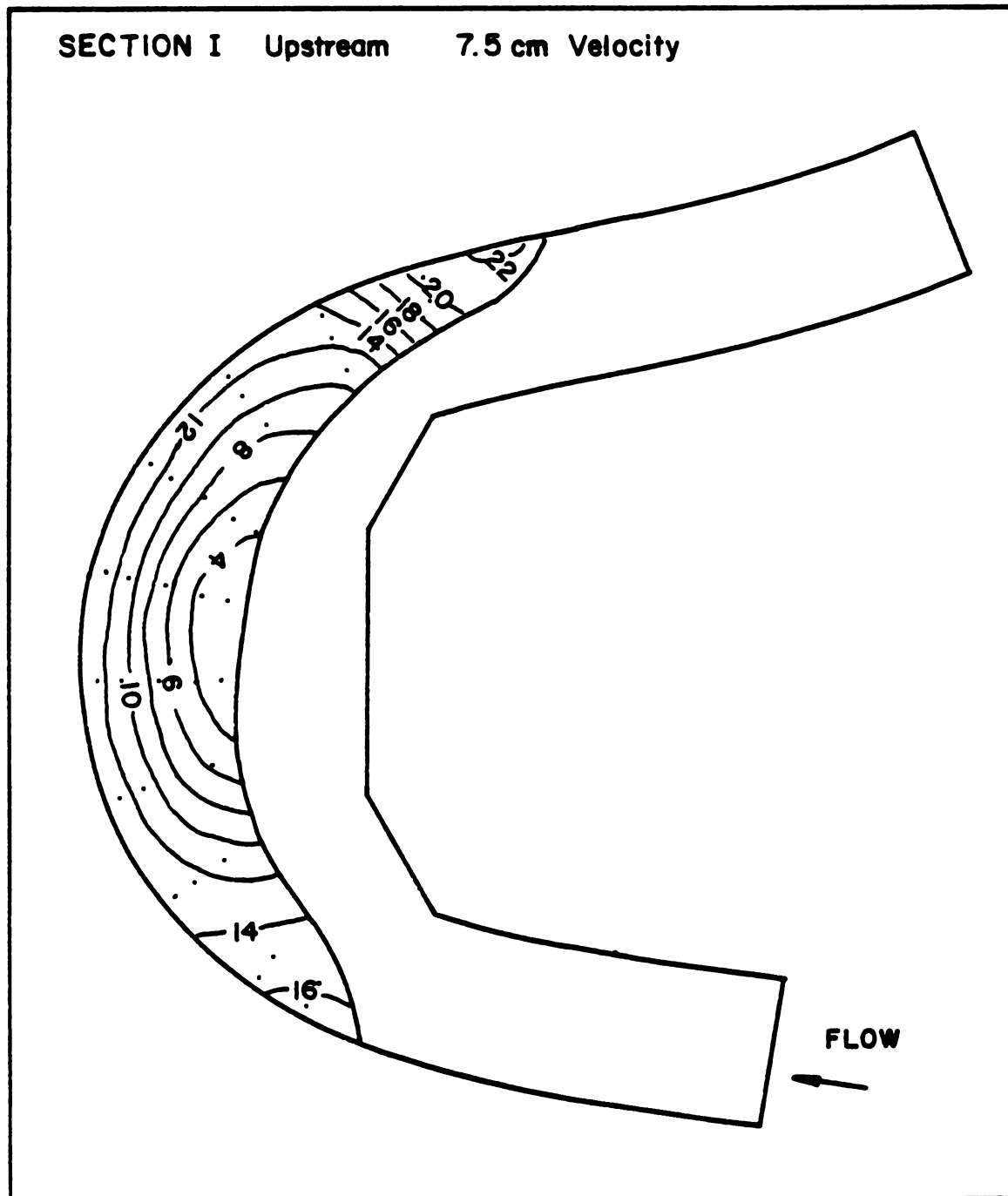


Figure Alb.--Water velocities (cm/sec) in Section I 7.5 cm below water surface. Water velocities were measured at points shown.



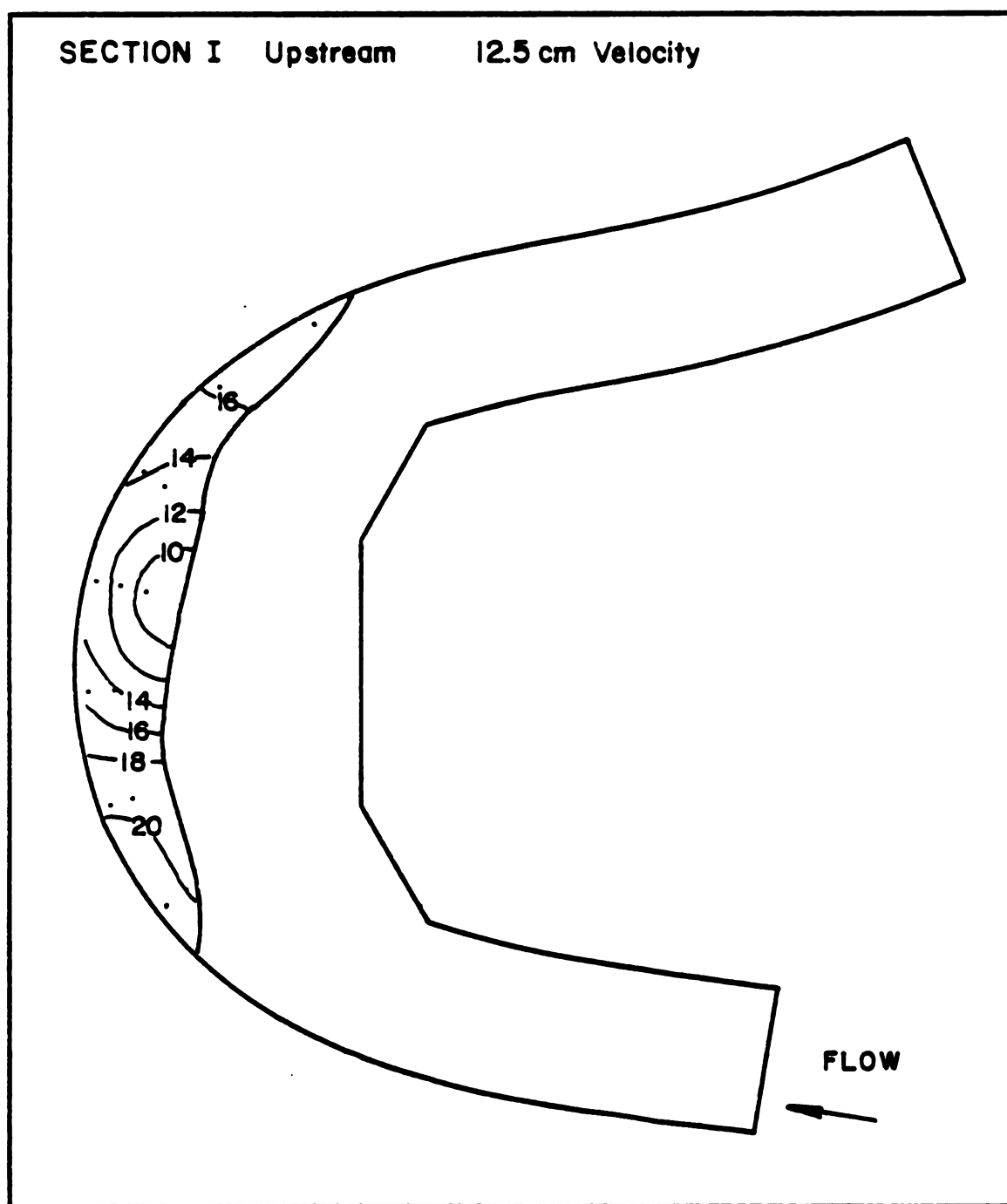


Figure A1c.--Water velocities (cm/sec) in Section I 12.5 cm below water surface. Water velocities were measured at points shown.

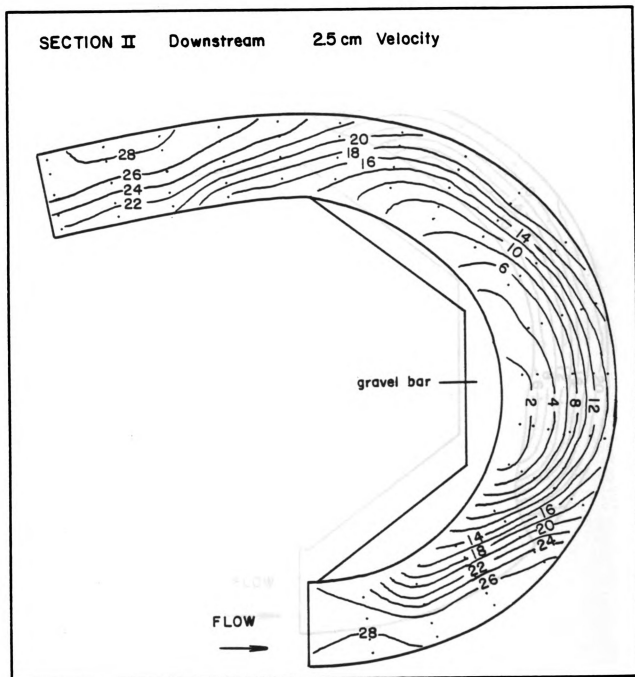


Figure A2a.--Water velocities (cm/sec) in Section II (downstream) 2.5 cm below water surface. Water velocities were measured at points shown.

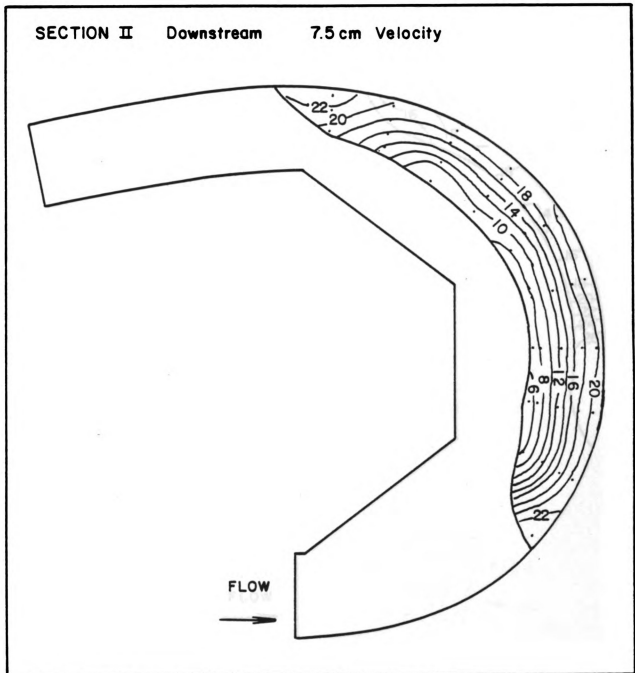


Figure A2b.--Water velocities (cm/sec) in Section II 7.5 cm below water surface. Water velocities were measured at points shown.

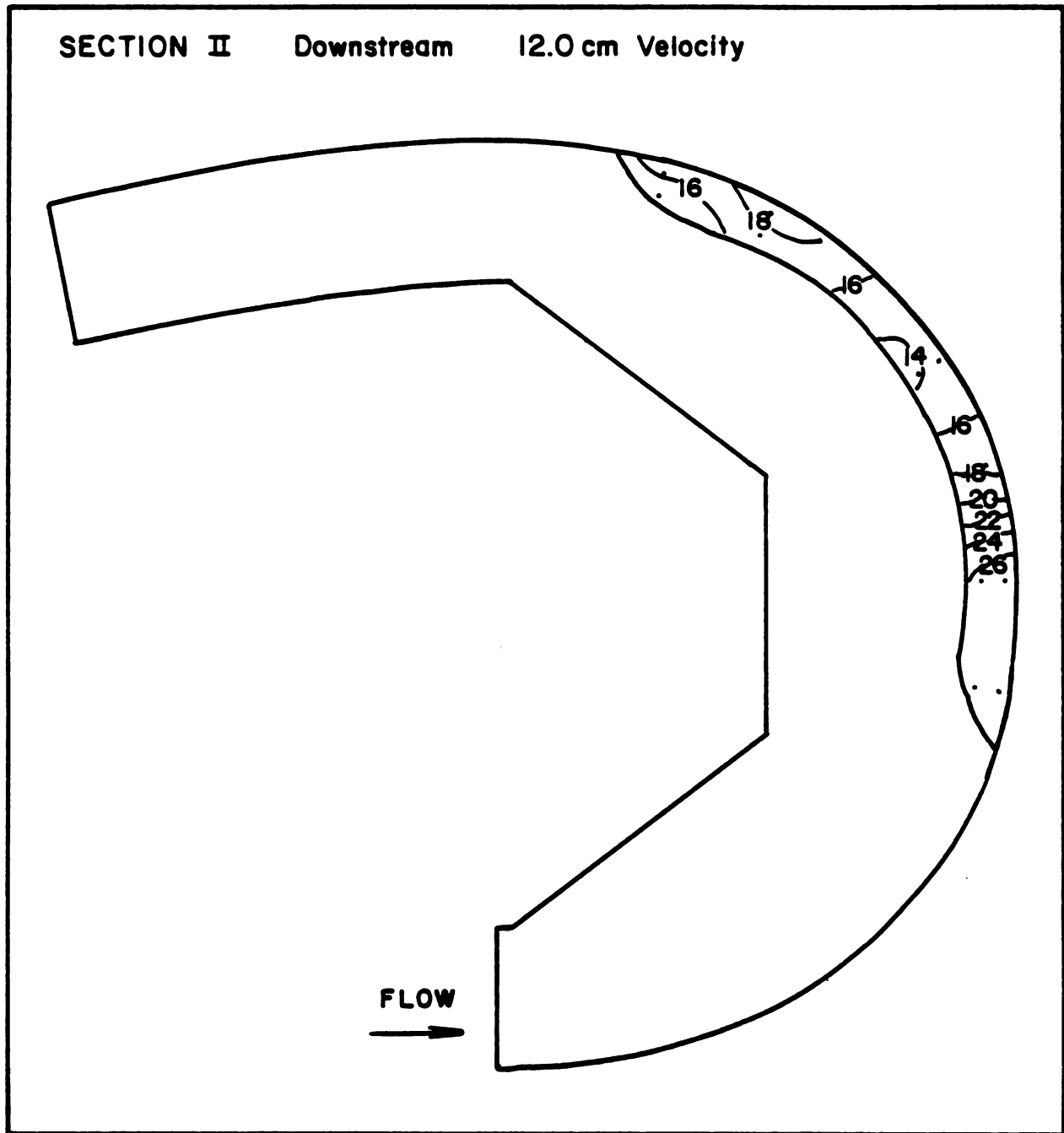


Figure A2c.--Water velocities (cm/sec) in Section II 12.0 cm below water surface. Water velocities were measured at points shown.

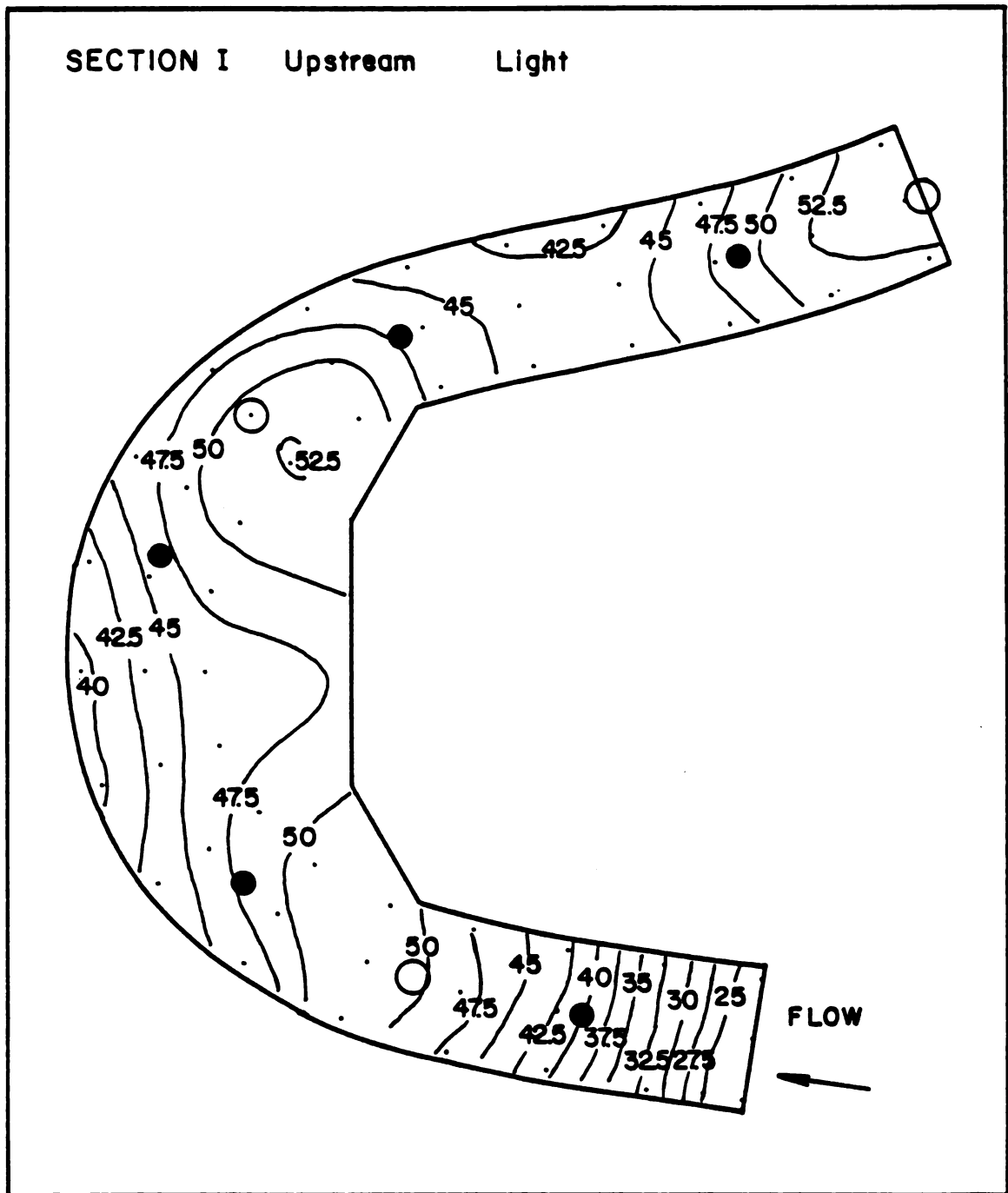


Figure A3.--Light ( $\mu\text{E}/\text{m}^2/\text{sec}$ ) at surface of Section I. Light was measured 1 cm above water surface at sampling point shown. The positions of mercury vapor (open circles) and incandescent lamps (filled circles) are shown.

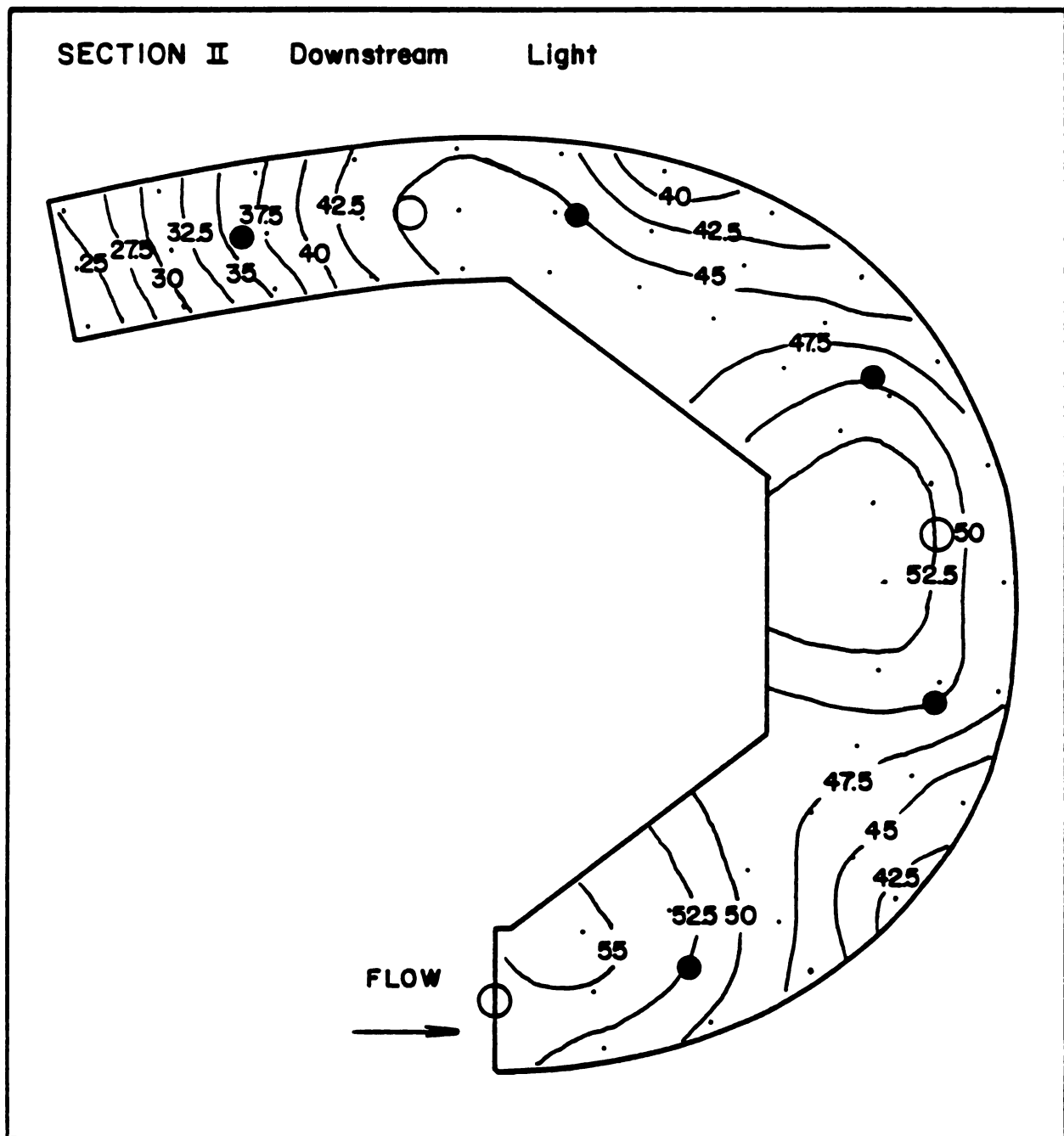


Figure 4.--Light ( $\mu\text{E}/\text{m}^2/\text{sec}$ ) at surface of Section II. Light was measured 1 cm above water surface at sampling points shown. The positions of mercury vapor (open circles) and incandescent lamps (filled circles) are shown.