Competition among juveniles of coho salmon (<u>Oncorhynchus kisutch</u>),
brook trout (<u>Salvelinus fontinalis</u>), and brown trout (<u>Salmo trutta</u>)
for stream resources, with emphasis on Great Lakes tributaries.[1]

by

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Salmonids have been introduced throughout the world to habitats where they were not indigenous. During the last 30 years, Pacific salmon of the genus Oncorhynchus were successfully established in the Great Lakes and northwest Europe, and have been introduced at various times to waters of the Atlantic coast of North America. Fisheries biologists in each geographic area have expressed concern that the introduced salmon may have detrimental effects on established populations of brown trout (Salmo trutta), brook trout (Salvelinus fontinalis), and Atlantic salmon (Salmo salar) (Peck 1970, Taube 1975, Berg 1977, Gruenfeld 1977, Solomon 1979).

Since 1956, three Pacific salmon have been added to the fish community of the Laurentian Great Lakes. Pink salmon (Oncorhynchus gorbuscha) originating from releases in two Lake Superior tributaries near Thunder Bay, Ontario in 1956, have established self-sustaining populations in all five Great Lakes (Emergy 1981, Kewain and Lawrie 1981). Juveniles of coho salmon (O. kisutch) were introduced in two Lake Michigan streams and one Lake Superior stream in 1966, and juveniles of chinook salmon (O. tshawytscha) were released in similar locations in 1967 (Latta 1974). In Michigan, both species are now stocked annually in tributaries of Lakes Mighigan and Huron, and some Lake Superior streams. In the Great Lakes, many returning adult salmon stray to other tributaries, probably because the juveniles are released as advanced smolts and do not imprint on the stream (Peck 1970, W. McClay pers. comm.). Consequently, with continued introduction in Michigan and other states, coho and chinook salmon now use many suitable Great Lakes tributaries for spawning. Although most returning adult chinook and coho salmon originate from hatcheries, an estimated 10% are naturally reproduced (Patriarche 1980, Carl 1980).

The coho, chinook, and pink salmon that ascend Great Lakes tributaries, like the brook and brown trout residing in these streams, are fall spawners. The eggs hatch in late winter and young emerge from gravel redds in early

spring, but the three species of salmon spend different periods growing in nursery streams. Pink salmon migrate downstream to the lake soon after emergence. Chinook salmon leave Great Lakes tributaries after three to six months of growth, and coho salmon remain 12 to 15 months, smolting in the spring of the year following hatching.

Salmon and resident trout may interact in several ways in Great Lakes tributaries: (1) adult salmon and trout may compete directly for spawning sites or later spawners could dig up redds of earlier spawners (Avery 1974), (2) adult trout and salmon may prey on juveniles of either species, (3) spawning fish excavating redds decrease the invertebrate food supply for resident fish (Hildebrand 1971), and (4) individual trout that eat eggs of salmon can accumulate a significant body burden of pesticides (Merna 1979). In addition to these, 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 coexist with juvenile trout during their 12 to 15 months of residence in Great Lakes tributaries and may compete with them strongly.

The purpose of this research was to study competition among juveniles of coho salmon, brook trout and brown trout for resources in streams. 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 communities are studied, the effects of niche shifts are usually measured in terms of growth in weight, which is suspected to be a sensitive indicator of fitness (Werner and Hall 1976).

Salmonids in streams compete for two major classes of resources, food and space. These fish maintain and defend relatively fixed stream positions called focal points, and make short forays from them to catch drifting invertebrates (Kalleberg 1958). Thus, the food and space resources used by salmonids are related in streams because defending a specific position ensures a fish access to the food drifting nearby. In view of this relationship, Chapman (1966) proposed that competition for space had been substituted for direct competition for food among stream salmonids.

Moreover, because more invertebrate drift is delivered to stream positions close to swift currents, Fausch and White (1981) 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. Fausch (MS) confirmed that juvenile salmonids compete for advantageous positions that maximize net energy gain (energy from drift minus swimming cost), and also related the specific growth rate of individual fish to their potential net energy gain.

In this research, we measured niche shifts of juvenile stream salmonids both by comparing the stream positions fish occupied in sympatry and allopatry, and by comparing specific-growth-rate-vs.-net-energy-gain relationships when species were alone and together. Changes in these growth-vs.-resource relationships should provide information about the effects that niche shifts have on the energy available to fish when competitors are present and absent.

Measuring competition among 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 adult size, as do birds for instance, the size structure of a population has marked effects on competitive relationships where larger fish are dominant. Given the problem of size-structured populations, we focused

on two areas of research: determining the size structure of juvenile salmonid populations in Lake Michigan tributaries, and measuring the innate competitive ability of juvenile salmonids in laboratory stream experiments using fish of equal size.

In view of the aggressive nature of juvenile coho salmon reported by Hartman (1965) and Glova and Mason (1977), we suspected that coho juveniles were superior competitors and could exclude equal-sized juvenile brook and brown trout from advantageous positions in a stream aquarium. If this hypothesis proved correct, 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 age-0 trout.

METHODS

Natural Populations

To determine the size distribution for juveniles of coho salmon, brook trout, and brown trout in natural populations, we measured the timing of emergence, the size at emergence, and the relative growth of juvenile salmonids during their first summer of life in eight Lake Michigan tributaries (Fig. 1). We 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 (Fig. 1) 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 0-8 other fish species (Table 1).

Populations in the five coho nursery streams were sampled by the senior author approximately every three weeks from April to September 1979. Three streams without coho were added in July. On each sampling date fish were captured 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 (MS 222), weighed, measured, and returned to the stream. In early spring newly emerged trout and salmon were captured with a hand net in areas of low water velocity along stream margins. On two sampling dates in August and September, three 30-m hauls were made downstream with a 3-mm seine in Pine Creek to measure the possible bias caused by electrofishing.

Laboratory Competition Experiments

All laboratory competition experiments were conducted in a recirculating stream aquarium described in detail in Fausch and White (in press). The stream aquarium was constructed in two sine-generated meanders, the

natural pattern that streams tend to curve (Leopold and Langbein 1966), and included naturally shaped riffles and pools which produced the diversity of depths and flow that are important habitat characteristics for juvenile salmonids in lotic systems.

The channel, constructed of clear plexiglass, was 7.28m long, 30cm wide and 30cm deep, and during experiments was divided into replicate sections 3.64m long. The bed was formed of 2-3cm diameter gravel shaped to form riffles 5cm deep on average, and pools of 15cm maximum depth. Stream flow was generated by air-lift pumping (Fausch and White in press) and was adjusted during each experiment according to the swimming ability of fish to prevent them from congregating on the upstream riffle. Current velocities ranged from 20-30 cm/second over the riffles and ranged from nearly zero to about 20 cm/second in the pools. Four 10cm diameter rocks in each section provided flow refuges for fish.

All experiments were conducted at $15\pm0.5C$, and oxygen was 100% saturated throughout the stream due to air-lift pumping. Water was circulated through a biofilter (built according to Spotte 1979) to maintain optimum water chemistry. Ranges of chemical constituents in ppm (except for pH) measured at the beginning and end of each experiment were: $CaCO_3$ alkalinity 104-217, pH 8.09-8.53, NH_3-N .01-.05, NO_3-N 2.01-4.44.

Stream lighting was brightened and dimmed for about 30 minutes at the beginning and end of a 12-hr photoperiod. Light intensity at the water surface varied between 40-55 $\mu E/m^2/sec$ over 90% of the stream area and ranged from 25-55 $\mu E/m^2/sec$. Fish did not prefer areas of lower light intensity. Curtains enclosed the stream channel to conceal observers who could view fish through adjustable horizontal slits spaced 40-45cm along the channel.

We conducted three laboratory competition experiments to measure niche shifts of juvenile salmonids: brook trout vs. brown trout (experiment A), brook trout vs. coho salmon (B), and brown trout vs. coho salmon (C). To measure niche shifts we compared stream positions used by juvenile salmonids when groups of 14-20 fish (13-18 fish per m^2) were together in sympatry (7-10 fish of each species in each stream half), and when the same fish were separated in allopatry in the two halves. ~~During experiments B and C,~~ We also determined the specific growth rates of each species as a function of food resources and made some measurements of agonistic behavior. Much of the experimental procedure summarized below is described in detail in Fausch (MS).

All fish used in experiments were hatched from eggs of wild trout captured in Michigan streams and adult coho salmon returning from Lake Michigan. Eggs were hatched in an incubator and transferred to gravel beds in a stream holding tank to promote normal development and emergence. Fish were isolated from human disturbance and were exposed to photoperiods and temperatures identical to those during experiments. Because coho hatch and emerge at a larger size, brook and brown trout were fed more to grow all species to equal size.

Invertebrate drift in the stream aquarium was simulated by introducing a suspension of _Daphnia_ and water continuously into the riffle at the head end of each section. Fish were acclimated in allopatry to the stream aquarium and to feeding on drifting _Daphnia_ for periods from 5-13.5 days prior to experiments (Table 2). Prior to experiments A and B fish were acclimated for five days to the stream aquarium and food, except that in experiment B fish were acclimated to feeding on _Daphnia_ an additional two days.

For each experiment fish were selected to be as uniform in length and length distribution as possible, and varied only 6.5 mm or less when experiments began (Table 2). Fish were individually marked prior to experiments using combinations of five finclips; the tips of the dorsal, anal, adipose, and top and bottom lobes of the candal fins. Most fish received one to three finclips which did not affect their growth (Fausch MS) or interfere with behavioral signals. Fish were weighed (±0.01 g) and measured (fork length due to finclips, ±0.25 mm) immediately before and after the sympatry phase of each experiment and after allopatry. In each case fish were starved for 12 hours to ensure a standard level of gastric evacuation.

In experiments A and B fish of each species were randomly divided between stream sections for sympatry. Fish were grown for 10.5 days in sympatry, then weighed, measured, and isolated for 2 days in downstream traps under low light and flow conditions and fed a maintenance ration each day. The procedure was designed to minimize the effects of prior residence on the allopatric portions of experiments A and B, which lasted for 10 days (Table 2).

Brown trout and coho salmon in experiment C were treated similarly, except that a large group of each species was acclimated to the stream aquarium and food for 13.5 days. From this larger group of fish, 16 fish of nearly equal size were chosen for the sympatry portion of the experiment, and were sorted into a smaller and larger group to further equalize length and weight. Experiment C consisted of 9.5 days sympatry and 9 days allopatry with the 2-day isolation period between. During the three experiments, species were assigned alternately to upstream and downstream sections of the stream aquarium in allopatry to eliminate bias (Table 2).

The potential net energy gain or potential profit at the stream position held by each fish was determined each day during experiments. The procedure summarized below for determining potential profit is described in detail in Fausch (MS). Potential profit is defined as the energy available as drifting _Daphnia_ within the fish's feeding radius, minus the cost of swimming to maintain the position, both expressed as Cal/hr.

Drift energy available to fish was determined by sampling drift daily at five cross-sections along each stream half according to the procedure described in Fausch (MS). The rate of supply of drifting _Daphnia_ was found to be an increasing linear function of water velocity at each cross-section. The slopes of these drift-energy-vs.-water-velocity lines for the five cross-sections declined as a negative exponential function of distance from the food source at the upstream end of each stream half, mostly because fish ate the _Daphnia_, but also because some sank into the gravel and were not resuspended. Rates of drifting _Daphnia_ were converted from numbers to calories by first counting the number per gram dry weight, and Then determining the calories per gram dry weight using bomb calorimetry (Fausch MS).

Because positions of juvenile salmonids varied little after social hiearchies were established during each half of an experiment, the cost of swimming could be accurately determined from a daily measurement of focal point velocity for each fish, using equations given in Fausch (MS) that depend on fish weight, water temperature and swimming velocity. Similarly, the amount of drift available to each fish was determined daily by measuring the maximum water velocity with in a two-fork-length radius above and in front of its focal point. This maximum velocity was used to calculate the amount of drift passing through the portion of a fish's feeding radius in which it most frequently fed, employing the equations for the rate of drift

energy described above (cf. Fausch MS).

The daily protocal for each experiment may be summarized as follows. During the morning and afternoon of each day, half of the fish in each stream section were chosen randomly, and identified by their finclips, for measurement of positions. The positions of all fish to be measured were temporarily marked on the plexiglass stream wall and characteristics of the stream bed at each position were recorded to aid in future recognition, before any fish were disturbed. The curtains were then opened and the three characteristics of each fish position needed to calculate potential profit were measured: focal point water velocity, maximum water velocity within a two-fork-length radius above and in front of the focal point, and distance of the position from the upstream end of the stream section. Water velocities were measured either with midget Bentzel tubes (Everest 1967) or a hot-bead anemometer (LaBarbera and Vogel 1976). Drift was measured in random order at 11-1300 h each day, 3 hr after the photoperiod began at 0800 h EDT.

Specific or instantaneous growth rates were calculated for each fish during each half of experiments and plotted as a function of mean potential profit. Michaelis-Menten equations were fit to these relationships according to procedures in Fausch (MS).

During experiments B and C, agonistic behavior was measured by recording all agonistic acts initiated or received by individual fish during two minutes of observation. Fish were chosen randomly for behavioral observation every other day. Agonistic acts consisted of all nips, chases, and frontal threats, but lateral displays only when initiated. Because repeated observations of the same fish were not independent, I used McNemar's test (Gill 1978, p.83) to test differences in agonistic behavior among species in sympatry.

RESULTS

Natural Populations in Lake Michigan Tributaries

Juvenile coho salmon emerged from gravel redds earlier in the spring and were larger at emergence than juveniles of 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 similar rates in a sympatric population, and in two allopatric populations in streams close to each other.

In the three streams having both coho salmon and brown trout, Bigelow Creek, Pine Creek, and the Green River, coho salmon emerged earlier and were larger than brown trout through the first summer of life (Fig. 2). Sampling was not begun early enough in any of these streams to capture newly emerged coho. But in Sand Creek, where brook trout and coho salmon are sympatric, newly emerged coho averaged 34.9 mm (SE 0.51) in mid-April, which coincided with the size at emergence when coho salmon were raised in the laboratory stream. Newly emerged brown trout caught in mid-May were 28.6 mm (SE 0.61) in Pine Creek and 28.1 mm (SE 0.86) in the Green River, 6-7 mm smaller than coho salmon at emergence.

By extrapolating coho salmon growth in Pine Creek and the Green River back to the 35 mm emergence length, we estimate that coho emerged about three weeks earlier than brown trout in Pine Creek (Fig. 2A) and about two weeks earlier in the Green River (Fig. 2B). 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, a 10-16-mm and 0.5-2.0-g size advantage in Pine Creek (Fig. 2A), and a 10-20-mm and 0.5-4.0-g size advantage in the Green River (Fig. 2B).

We were concerned that our electrofishing might not capture a representative sample of coho salmon in Lake Michigan tributaries. However, for two dates in August and September, electrofishing in Pine Creek captured coho only 2.3 and 2.4 mm larger on average than three downstream seine hauls with a 3-mm seine. These non-significant differences (p > .30, p > .50 by t-test) indicated that electrofishing was a fairly unbiased method of sampling juvenile salmonids.

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 do coho salmon, and may often exclude brook trout from these stream reaches (Fausch and White 1981). Naturally reproduced brook trout and coho salmon were found in Sand Creek (Fig. 1), a marginal stream for salmonids due to low flow and warm temperatures in late summer. Adult brook trout were common, but three hours of electrofishing often produced less than 10 juvenile brook trout although several hundred juvenile coho salmon could be caught in the same period.

Coho salmon began emerging in mid-April at about 35 mm 34.9 mm (SE 0.51) in Sand Creek, while brook trout emerged two to three weeks later at 29.5 mm (SE 0.50) (Fig. 3A). 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 about 5.5-8.5 mm larger than brook trout at emergence in Lake Michigan tributaries. In Sand Creek coho maintained an 8-14-mm length advantage and a 0.5-3.0-g weight advantage over brook trout throughout the summer (Fig. 3A).

Brook and brown trout were of nearly equal size during their first summer of life in Egypt Creek, where they are sympatric, and in Spring-brook and Smith Creeks, two allopatric populations in streams close to each other (Fig 3B). Although brown trout were not captured in Egypt Creek until June, brook trout emerged at 29.5 mm (SE 1.05) and were *only* *(range: p > .30-.50 for all sampling dates)* 1-5 mm longer, and 0.5-1.0 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 in Love Creek grew larger than in other streams (Fig. 3C), probably because of favorable water temperatures and barnyard enrichment. Love Creek also held age-I and older brook trout of hatchery origin, but only one age-O wild brook trout was caught. Age-O coho equalled the lengths of the smallest age-I brook trout by June in 1979 *in this stream.*

Laboratory Competition Experiments

Coho salmon were clearly the dominant competitor when pitted against either brook trout or brown trout of equal size in the stream aquarium. Brook trout were also clearly dominant over brown trout of equal size. These conclusions result from comparison of relationships of specific growth rate as a function of potential profit, distribution of fish positions along the stream channel, and behavior of fish, in sympatry versus allopatry.

In all experiments, fish competed for positions that offered the highest potential for net energy gain (Fausch MS). Therefore, it is instructive to describe the distribution of resources *in the stream aquarium* before the results of competition experiments *are presented.*

The potential for net energy gain generally decreased with distance
from the food source in each stream section. Figure 4 *(after Fausch MS)* shows a contour
map of potential profit (cal/hr) for coho salmon in the upstream section
during the allopatry phase of experiment C. To construct this figure,
potential profit was determined for specific positions near the stream
bed from velocity measurements at three depths, using equations of
available drift energy and swimming cost *as functions of velocity,* as described in Fausch (MS).
These are conservative estimates for potential profit at fish positions
because fish could use small irregularities of the stream bed as refuges
to reduce swimming velocity, which would decrease swimming costs and
increase potential profit.

During most experiments water velocities on the upstream riffle were
greater than the maximum sustained swimming speed of the juvenile
salmonids, which prevented them from using positions there unless they
found some refuge from the high velocities. The dominant fish in each
section usually held a position downstream from the first large rock that
provided a current velocity refuge at the upstream end of the pool.
From this focal point, the dominant fish could make short forays from
the area of low water velocity at its focal point to forage on drifting
Daphnia concentrated in the region of high water velocity near the outer
wall. The com*b*ination of low focal point velocities close to regions of
high drift abundance made positions at the head of the pool the most
advantageous (Fausch MS) unless current velocity refuges providing low
focal point velocities were available on the upstream riffle.

Experiment A: Brook Trout vs. Brown Trout

All fish lost weight during the sympatry phase of this

experiment, probably because the net weight of Dapnia introduced as
drift each day was only 9% of the total net weight of fish in each
section (Table 2). Brett (1979, Fig 21) showed that specific growth
rates of sockeye salmon (Oncorhynchus nerka) fed marine zooplankton
were poor compared to growth when fed other commercial diets.
Moreover, the brook and brown trout were acclimated only five days to
the food and stream aquarium, and at about 70 mm were probably too
large to forage efficiently on drifting Daphnia.

During allopatry, two brook trout grew and another maintained
its weight, but the other 11 brook trout and all brown trout lost
weight, even though all fish should have been acclimated by this time.
Therefore, because growth was poor, we did not fit equations to the
specific-growth-rate-vs.-mean-potential-profit relationships for
comparison of sympatry to allopatry.

When all fish positions measured during sympatry are plotted as
a function of their distance from the upstream end of each section,
and compared to allopatry, brook trout are clearly the dominant
competitors (Fig. 5). In sympatry, the four fish holding positions
furthest upstream in each section were brook trout. These dominant
brook trout actively drove away all brown trout, forcing them to
subsist in less advantageous positions downstream. The hatched
portions of bars representing brook trout in Fig. 5 show the daily
positions of the one most dominant brook trout in each section during
the ten days of sympatry. In the upstream section the second fish
in the hierarchy held a position on the upstream riffle throughout
sympatry, and together with the most dominant, regularly defended the
area from 40-150 cm along the channel. In the downstream section,

no one brook trout held a position upstream of the most dominant

brook trout during more than one observation period. In neither

section did brown trout ever hold a position upstream of the dominant

brook trout on any given day.

Brook trout held positions that were significantly further

upstream than those of brown trout in both sections during sympatry:

The mean distances were 243 *172* cm vs. 289 *224* cm in the upstream section,

and 172 *243* cm vs. 224 *289* cm in the downstream section (p <.001 for both).

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 allopatry, brown trout shifted to more upstream positions

(mean distance 204 cm) when released from competition with brook

trout (Fig. 5). The dominant brown trout chased other fish from the

upstream 130 cm of the stream, which represented 36% of the total

364 cm section. Similarly, one dominant brook trout drove all others

downstream onto the lower riffle (mean distance 277 cm) during

allopatry. This very aggressive fish reserved 76% of the stream

section for itself, by alternately feeding from a position at 130 cm

and one at 260 cm from which it drove other fish downstream. The

few positions shown at 200 cm were brook trout that hid in stream bed

crevasses in shallow water on the bar at the inside of the meander

bend. The dominant brook trout tolerated fish using these positions

only if they were not visible from its positions in deeper water

of the main channel.

During this and subsequent experiments, brown trout that were

forced into positions in swift currents 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 also did this occasionally, and Atlantic salmon are reported to show this behavior as well (Kalleberg 1958, *Jones 1975,* Gibson 19 *61* 77). In contrast, coho salmon never rested on the bottom but swam continuously until exhausted, even in the fastest water if no velocity refuge was available.

This behavior by trout affected the potential profit estimates during all experiments. Whenever trout were seen resting on the stream bed during experiments A and B, they were assigned a daily potential profit of zero because we assumed they were not foraging. During experiment C, brown trout were assigned a focal point velocity of zero because we assumed that they required little energy to main- tain the position, but the maximum velocity was 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 the six most dominant trout of each species were dissected after the experiment, none were sexually mature.

Experiment B: Brook Trout vs. Coho Salmon

During sympatry with brook trout, the specific growth rates of

all coho salmon were positive or zero, but were unrelated to mean potential profit (Fig. 6A). Coho salmon may not have been sufficiently acclimated to the food or the stream aquarium during the five to seven days prior to sympatry, although all but four fish gained weight. Only one brook trout grew during sympatry, but brook trout specific growth rates were clearly less than coho salmon for similar mean potential profit. A Michaelis-Menten equation fit to these data is similar in shape and position to the brook trout curve for the allopatry phase of the experiment.

In allopatry, most coho salmon grew and converted potential profit to growth more efficiently than brook trout (Fig. 6B after Fausch MS). Only three brook trout maintained their weight or grew in allopatry. Moreover, brook trout required a higher threshold of potential profit (5.5 vs. 2.5 cal/hr) to grow than did coho salmon. Ten brook trout disappeared into the gravel in allopatry and were never recovered. All of these fish were healthy, but held unfavorable stream positions that had negative mean potential profits (range: -0.2 to -2.9 cal/hr) for the daily positions measured during allopatry before they disappeared. One coho salmon that disappeared on the last day of allopatry also had a negative mean potential profit of -1.3 cal/hr during allopatry.

The distribution of positions along the stream channel clearly shows that coho salmon dominated the advantageous upstream positions and drove most brook trout downstream (Fig. 7). In sympatry, most brook trout held positions in the downstream half of each section, while coho salmon held favorable positions in the pool. In the up-stream section, the only brook trout to maintain a moderately

profitable position and have a positive specific growth rate held a position at about 195 cm. Positions shown at 20-40 cm were held by five different brook trout on different days and the rest of the brook trout positions in the lower pool (170-270 cm) were in shallow water along the inside of the meander bend where potential profit was low. A number of brook trout burrowed in the gravel during sympatry and allopatry to escape competitors and unfavorable conditions, especially in areas of high velocity on the lower riffles (270-364 cm).

In the downstream section during sympatry, the largest brook trout was the dominant fish (Fig. 7) and actively competed with the largest coho for the most advantageous position. However, even though this fish held a profitable position (6.7 cal/hr mean potential profit) its specific growth rate was negative, which lies below the specific-growth-rate-vs.-potential-profit curve for brook trout in sympatry (Fig. 6A), probably because it spent excessive energy on agonistic behavior against coho. The brook trout positions shown at 20 cm in the downstream section were held by three different trout, and most of the fish in the lower pool held positions close to the stream bed in shallow water on the bar, similar to brook trout in the upstream section.

Positions held by coho salmon in sympatry were significantly further upstream than those held by brook trout. Mean distances were 151 for coho salmon vs. 229 cm for brook trout in the upstream section and 143 vs. 238 cm downstream ($p < .001$ for both). 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 were more persistent at maintaining their stream

positions despite vigorous agonistic bouts-- in short, coho could

eat and defend positions at the same time. In contrast, brook trout

were more easily intimidated, usually retreated downstream after a

few nips from a coho or larger brook trout, and often did not feed

for ~~one or more~~ several minutes after an agonistic bout. Moreover, brook

trout were observed to win agonistic bouts only against coho of smaller

size, and because coho quickly grew larger, most brook trout re-

treated further downstream as the sympatry phase progressed. Brook

trout agonistic behavior at this age appeared much less intense than

that of coho, and coho often did not react to behavioral displays

unless brook trout nipped them directly.

When records were compiled of the number of two-minute obser-

vation periods of individual fish where any agonism was observed,

brook trout showed significantly more agonism towards coho salmon

than among themselves during sympatry in the downstream section ($p < .05$)

but not the upstream section (Table 3). Brook trout initiated and

received agonistic acts about 1.5-5.0 times more frequently with coho

than among themselves. Coho salmon showed just the opposite pattern,

exhibiting agonism about 2-3 times more frequently among themselves than with

brook trout, a significantly greater amount ($p < .025$ for both sections).

Thus coho exhibited more agonistic behavior than brook trout during

sympatry, and the data 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 frequency of agonistic acts in allopatry are not comparable

to those in sympatry because in each section twice as many of either

species were present in allopatry as in sympatry. Therefore, it might

be expected that intraspecific agonism would be about twice as

frequent in allopatry as sympatry. However, in allopatry brook trout

interacted about 3-13 times more frequently than in sympatry, while

coho salmon interacted only slightly less frequently in allopatry than

sympatry (Table 3).

Experiment C: Brown Trout vs. Coho Salmon

Coho salmon were clearly the dominant competitor over brown

trout during this experiment, both in specific growth rate and

dominance of favorable positions in the stream aquarium. All coho

salmon grew during sympatry with brown trout, were more efficient at

growing on the food source than brown trout, and required a lower

threshold of potential profit for growth (1.0 vs. 7.5 cal/hr, Fig. 8A).

Conversely, all but one brown trout lost weight in sympatry. Of all

experiments, the relationships between specific growth rate and mean

potential profit for this one should be the most accurate, because all

brown trout and coho salmon were acclimated to the stream aquarium

and to feeding on drifting _Daphnia_ for 13.5 days in allopatry prior

to the sympatry phase (Table 2). Three brown trout from the upstream

section in sympatry died during the isolation period, but all held

positions affording low mean potential profits during sympatry

(-0.5, 1.0, and 2.1 cal/hr). A fourth brown trout in the same section

during sympatry was not found after allopatry, but also held a

position with negative mean potential profit of -3.6 cal/hr through-

out allopatry and was the most subordinate fish. These deaths

reduced the number of brown trout from 16 to 13 during allopatry and to 12 at the end of the experiment.

All coho salmon grew in allopatry (Fig. 8B), *after Fausch MS.* had a similar threshold of potential profit as they did in sympatry, and grew at similar specific rates for a given mean potential profit. In allopatry, coho again showed higher specific growth rates and required a lower threshold of potential profit than brown trout *(1.1 vs. 4.0 cal/hr)*.

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, 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 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 that held a typical position on the upper riffle throughout allopatry was excluded as an outlier. This fish maintained a focal point between the stones in the stream bed on the upper riffle, but was assigned high potential profits each day because of the swift currents overhead and the upstream position. However, the fish was able to capture only a small portion of the drift passing by, due to the swift currents and because the two most dominant coho held positions just upstream and downstream of its position and often attacked when it fed.

Coho salmon actively drove brown trout from the pool into poorer positions on the upper and lower riffles and into shallow water along the inside of the meander bends (Fig. 9). In the upstream section

during sympatry, one brown trout persistently maintained a position from 40-80 cm along the stream course within the range of vision of the dominant coho, but hid from view in front of the large rock shown in Fig. 4 at all times. Two other brown trout held transient positions in shallow water along the edges of the upper pool and riffle, far from the advantageous positions in the main part of the channel. The rest of the brown trout held relatively poor positions in shallow water along the bar in the lower pool and on the lower riffle.

Similarly, in the downstream section during sympatry, one brown trout held a position between stones in the stream bed at about 140 cm, concealed from view of the surrounding coho. Another brown trout remained lodged between gravel and the outside plexiglass stream wall at about 200 cm, and the rest of the brown trout held positions in shallow water along the bar in the lower pool, or in poor positions on the lower riffle.

Because some brown trout held poor positions in the upper riffle and pool in the upstream section during sympatry, mean distances were similar there (181 cm for coho vs. 191 cm for brown trout, $p >$ .25). In the downstream section, coho salmon positions were significantly further upstream than brown trout (149 vs. 260 cm, $p < .001$).

During allopatry coho salmon formed a typical aggregation in mid-pool (Fig. 9), although the dominant fish in this experiment usually occupied a position on the upper riffle. Brown trout used positions along the entire stream section but by the end of allopatry, one fish defended an area from 40-180 cm, which was 39% of the section, and the three most dominant brown trout controlled the stream from

40-270 cm, driving other fish into poor positions or into crevasses in the gravel. Dominant brown trout were similar to brook trout in that they reserved more space for themselves in allopatry than did coho salmon.

Brown trout were observed to win agonistic bouts only when coho were smaller, which was not often because fish were sorted into two groups of nearly equal size before sympatry. Moreover, most coho grew slightly larger than most brown trout in each section during sympatry because of their superior specific growth rate. Similarly to brook trout in experiment B, brown trout were observed to be less persistent than coho in maintaining stream positions in the face of agonism.

Brown trout initiated or received agonistic acts about 5-6 times more frequently with coho salmon than brown trout in the upstream section during sympatry (p < .025), but in the downstream section interacted with both species with about equal frequency (Table 3). Conversely, coho salmon interacted about 1.5-4.0 times more frequently among themselves than with brown trout in sympatry, which was a significant difference (upstream p < .10; downstream p < .01).

As in experiment C, the frequency of intraspecific agonism was expected to approximately double in allopatry due to the doubling of fish of the same species. However, brown trout showed agonism about 2-9 times more frequently among themselves when alone than when coho were present, especially during the acclimation period. Conversely, coho showed agonism about as frequently when alone as when brown trout were present. These trends in frequency of agonistic behavior are similar to those measured for brook trout vs. coho salmon in experiment B.

significance of the decreses in these curves, inspection of the original

data (Figs. 6 and 8) shows that the brown trout curve appears to have

changed most significantly from ~~sympatry~~ allo to ~~allopatry~~ sym, and the curve

for coho salmon changed little. The change in the brown trout curve

was due to an increase in the threshold value for potential profit from

4.0 to 7.5 cal/hr and a general flattening of the curve, which 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. Our

measurements of agonistic behavior show that brown trout were involved

in agonistic behavior no more frequently in sympatry than allopatry

(Table 3), refuting the first reason. We favor the second reason, and

observed that brown trout did not forage as efficiently during sympatry

because they were intimidated by coho.

The threshold of mean potential profit for brook trout also increased

from 5.5 cal/hr in allopatry to 7.7 cal/hr when sympatric with coho

salmon, which may be attributed to a similar behavioral mechanism.

However, we suspect that a more common effect of niche shifts 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

competing with coho salmon, because the average 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 for brown trout was increased significantly

between sympatry and allopatry (Table 2).

There are four main reasons that several plots of specific growth rate as a function of mean potential profit are variable, making the fitting of the Michaelis-Menten equation difficult. First, the acclimation period may have been inadequate. We increased acclimation periods from four to fourteen days during all experiments (cf. Fausch MS) with corresponding improvements in the data collected. These acclimation periods are significantly longer than those used during most other studies of salmonid competition. Second, although the specific growth ratio of fish can be accurately measured, determining the mean potential profit available at specific positions is difficult because drift is difficult to measure accurately, equations for swimming metabolism may not be accurate for small fish, and the energy spent on forays to catch drift and on agonism could not be determined. Third, relationships ideally would be fit to specific growth rates as a function of actual rations eaten, as is done with fish feeding trials. Fourth, Michaelis-Menten equations are difficult to fit when few individuals are growing close to the maximum specific rate, but the dominance hierarchy established by juvenile salmonids prevents more fish from growing faster (see discussion in Fausch MS).

The change in trout positions when released from competition with coho salmon provides a second convincing line of evidence that coho were the superior competitor (Figs. 7 and 9). Coho actively drove trout from advantageous positions in the stream aquarium, so trout held marginal positions and grew poorly as a result. In allopatry, both brook trout and brown trout shifted to use more favorable pool positions. These niche shifts resulted from direct interference competition by coho salmon through agonism against trout. Coho salmon easily forced brook

or brown trout from preferred positions and actually showed agonism more frequently within their own intraspecific hierarchy than against trout in sympatry. Conversely brook or brown trout spent more time fighting with coho than among themselves in sympatry (Table 3).

The combination of superior physiological potential and behavioral dominance gave coho the advantage in the stream aquarium. Thus, even when the larger trout in an experiment gained relatively advantageous positions when competing against the smaller coho, the coho quickly grew larger, and larger body size ensured their dominance.

In four Great Lake tributary streams where coho salmon and either brook or brown trout are sympatric, coho emerged earlier and were larger at emergence, giving them a 6-20-mm length advantage during their first summary of life (Figs. 2 and 3). This size advantage coupled with the superior competitive ability of coho demonstrated in the stream aquarium should give juvenile coho an overwhelming advantage over trout in Great Lakes tributaries if resources become scarce.

Only a few other investigators have studied interactions among juveniles of coho salmon and either brook or brown trout. Taube (1975) calculated population estimates of brown trout in two experimental sections of the Platte River, Michigan (one stream where coho were first introduced) before and after the salmon spawned there, and in a control section without salmon. He found a significant decrease in the numbers of age-0 brown trout in both experimental stream sections when age-0 coho were abundant, but concluded that the decrease had little long-term effect on each year class of trout because of their greater compensatory survival to older ages.

After eight years of sampling juvenile salmonid populations in
five Lake Superior tributaries, Stauffer (1977) concluded that numbers
of juvenile brook and brown trout were lower when age-0 coho were abundant,
although sample sizes of the trout were small compared to coho as we
found in Lake Michigan tributaries. Based on these data, Stauffer (1977)
suggested that juvenile coho may depress trout numbers. The negative
relationships between abundance of age-0 coho and trout from these two
field studies support our conclusions that juveniles of coho salmon are
superior competitors over those of brook and brown trout.

Gibson (1981) observed stream positions and measured agonistic
behavior of coho salmon, brook trout, and Atlantic salmon of about 100 mm
sympatric in an elliptical stream aquarium without cover. However,
brook trout averaged 9, 15, 15 and 25 mm longer than coho salmon in
four experiments, and in the last three experiments the smallest brook
trout was of equal or greater length than the largest coho. As a result,
brook trout dominated coho salmon and the most dominant fish in the last
three experiments were brook trout. Despite these size differences,
Gibson (1981) reports that an 86 mm coho was more dominant than 99 mm
brook trout in the 1st experiment. These data may indicate that brook
trout can dominate coho salmon of this size if the trout are more than
about 10-15% larger than the coho.

Gibson (1981) also found that coho salmon and brook trout preferred
the same microhabitat in the stream aquarium, that dominant fish tended
to prefer the upstream positions, that coho formed aggregations in
pools, and that brook trout sometimes used their pectoral fins to hold
themselves on the stream bed in fast water but that coho never did.
All of these observations coincided with our findings.

Competition and Resource Partitioning Among Stream Salmonids

Cases of interacting stream salmonids that have been investigated fall into two categories: species that evolved together and those that did not. For species that evolved together there appears to have been strong selection for mechanisms to partition resources, especially space, that is habitat or microhabitat, and the times at which different life history stages use these habitats. Space and time are two of the three major classes of resources for which animals are thought to compete (Schoener 1974). Food, the third resource class, is difficult for fish to partition in freshwater ecosystems (Finger 1982) because most fish are opportunistic and forage onfood sizes that may span several orders of magnitude (Werner 1977), and because the array of sizes of fish in a population feeds on a wide range of prey that vary greatly with time.

All of the studies we found of interactions between species of stream salmonids that evolved together involved juvenile fish, at least one of which was an anadromous species that used streams for spawning and rearing of juveniles only. Mechanisms whereby coevolved stream salmonids minimize competition usually involve differences in life history characteristics, such as the timing of spawning and emergence, the size of fry at emergence, and the length of fry residence in nursery streams.

Good examples of juvenile salmonids that partition stream resources are available from the Pacific Coast of North America where many species of Salmo, Salvelinus, and Oncorhynchus evolved and now occur in sympatry. For instance, fall-spawning coho salmon coexist with spring-spawning steelhead and cutthroat trout (Salmo clarki) in coastal streams of

British Columbia. Coho fry emerge from gravel redds in March, about the
time steelhead and cutthroat are spawning, which gives the coho up
to a 15-20-mm size advantage over trout fry during the first summer of
life. All three species prefer microhabitat in pools, but most steel-
head and cutthroat fry occupy positions in riffles during summer, apparently
being forced from pool positions by the salmon (Hartman 1965, Glova
and Mason 1977). Thus, segregation of coho salmon and either steelhead
or cutthroat trout occur both in time and space. The salmon and either
trout spawn during different seasons and the fry emerge several months
apart so that coho are significantly larger. As a result, the species
pairs also use different microhabitats because coho salmon are larger
and dominate the pools during summer, even though all species apparently
prefer pool microhabitat.

Both steelhead and cutthroat trout are spring spawners and similar
in ecology, but appear to segregate by spawning in different macrohabitat.
Steelhead typically use medium size rivers for spawning and rearing of
juveniles, whereas coastal cutthroat spawn in the small tributaries
(Hartman and Gill 1968, Nichols 1978). As a result, the two species are
reproductively isolated and the juveniles coexist over a relatively
narrow range of stream sizes.

Fall-spawning coho and Chinook salmon are also resported to spawn
in different but overlapping macrohabitats in an Oregon river (Stein
et al. 1972). Chinook primarily used larger river habitat for spawning
and smolted after about three months of stream residence, whereas coho
spawned mainly in smaller tributaries and remained in the stream for
at least one year, both similar to life histories in Great Lakes tributaries.
Distribution of coho and chinook fry overlapped during spring, and coho

were dominant over chinook of equal size in laboratory experiments. However, during summer when the main river temperature exceeded 20 C, coho were found only in cooler tributaries while chinook also used the main river due to their tolerance of higher water temperatures.

Conversely, Lister and Genoe (1970) found that chinook salmon spawned earlier, emerged earlier, and were larger at emergence and through the first summer of life than coho salmon (69 vs. 42mm in mid-June) in a British Columbia stream. As a result, chinook fry moved into faster and deeper water earlier than coho, a ~~movement~~ pattern common among juvenile salmonids and suspected to be a result of the greater food supply and cover afforded by the faster and deeper water (Chapman and Bjornn 1969, Everest and Chapman 1972). Therefore, in this case chinook and coho were largely segregated along gradients of depth and velocity until chinook ~~coho~~ smolted in June.

Thus, coho and chinook salmon, which both spawn during fall, appear to minimize competition by several mechanisms. These include use of different macrohabitat for spawning and rearing, or slightly different times of spawning and emergence, and different sizes at emergence which result in use of different microhabitat by fry. Moreover, chinook leave these nursery streams after about three months and eliminate further competition with coho fry.

Chinook salmon and steelhead trout that use tributaries of the Columbia River in the interior of the Pacific Northwest for spawning occupy similar habitat as fry, but they spawn at different seasons and steelhead remain in streams for three years before smolting whereas chinook smolt after one year. In Idaho tributaries of the Columbia River, Everest and Chapman (1972) found that these differences in spawning

season resulted in differences in size of 30 mm or more among
cohorts of both species that served to minimize their interaction for
microhabitat, because each cohort moved into progressively faster
and deeper water as they grew. Although lengths of age-1 chinook and
steelhead began to converge after about 12 months of stream residence,
chinook smolted after about 14-15 months, thus eliminating the
potential for interaction.

The length of stream residence of juvenile salmonids appears to be
a mechanism to minimize competition among other anachromous salmonids
as well. Pink and chum (O. keta) salmon leave nusery streams soon
after emergence, and sockeye fry move downstream to use lakes for
juvenile growth, so all three effectively eliminate competition with
other stream-dwelling juvenile salmonids.

In rivers along the Atlantic coasts of North America and Euorpe,
brook trout or brown trout coexist with Atlantic salmon. All three
species are fall spawners and there are both resident and anadromous
forms of brook or brown trout. All species use freshwater streams as
nursery habitat for a minimum of several years, and are expected to
prefer similar resources because of similar spawning and emergence of
fry.

Randall (1982) reports that brook trout are 2-4 mm smaller at
emergence than Atlantic salmon in New Brunswick streams, but the
trout emerge two to three weeks earlier than the salmon and maintain
a 10-15 mm size advantage through the first summer due to early
growth. Brook trout are found mainly in the pools during summer, and
Atlantic salmin in riffles (Gibson 1966). Atlantic salmon are more
agressive than brook trout, but do not displace trout of larger

size (Gibson 1973 in Randall 1982). Thus, despite reports that brook
trout use riffles as well as pools when salmon are not present (Gibson
1978), we suspect that both species prefer pools (see below for Atlantic
salmon, this study for brook trout) and that the brook trout, being
larger, are dominant and prevent Atlantic salmon from using the pools.

In England and Scandinavia, a similar situation occurs between
juvenile brown trout and Atlantic salmon, and brown trout are known to
be the dominant competitor (Kalleberg 1958, Lindroth 1955). Egglishaw
and Shackley (1977) report that brown trout and Atlantic salmon are
difficult to distinguish at emergence, but found that the trout emerged
about 2-3 weeks earlier than salmon. As a result, trout were 10-15 mm
longer than salmon through the first summer of life (Egglishaw and Shackley 1973) and would be expected
to be successful competitors due to size alone. Both species prefer
pools, but Atlantic salmon shift to use riffle microhabitat when brown
trout are present (Kennedy and Strange 1980) and are thought to be
better adapted to use areas of higher velocity because their larger
pectoral fins allow them to maintain positions in swift currents
(Jones 1975) as described in the Results section.

Thus with respect to coevolved stream salmonids, a number of
potential mechanisms combine to minimize competition among juvenile
stages in stream: 1) use of different macrohabitat for spawning and
rearing by two species, which may be selected for when species spawn
during the same season; 2) different spawning seasons and subsequently,
different times of fry emergence from gravel; 3) different sizes of fry
at emergence, which is usually related to egg size; 4) use of different
microhabitat by fry, which usually results from one species being
larger and dominant as juveniles, and excluding the other species from

preferred microhabitat, which is usually in pools; and 5) different periods of fry residence in streams, which minimizes the time during which species interact, or eliminates contact entirely if one species smolts or migrates soon after emergence. Therefore, although the controversy about the importance of competition in the coevolution of species and in shaping the structure of communities continues (Connell 1980, Schoener 1982), stream salmonids appear to have evolved ways to minimize competition for space during the same times. Some of the mechanisms are genetically fixed, such as spawning and emergence times and lengths of stream residence for juveniles, while others are *shifts in microhabitat use when competitors are present. However, when the latter,* plastic, such as shifts occur, the subordinate species are still able to profitable use resources available in the less preferred micro-habitat. For instance, Hartman (1965) reports that when juvenile coho salmon are present and dominate the preferred pool microhabitat, steelhead fry defend positions in riffles and are able to garner enough food to grow in these areas.

In contract to indigenous salmonid communities where competition for resources appears to be minimized, situations where non-native salmonids are introduced often result either in failure of the introduc-tion or displacement of the native salmonid by the introduced species. Investigations of interaction among stream salmonids that did not evolve together are relatively rare. However, the cases studied so far indicate that the similarity in life history attributes are *also* important, in shaping interaction during the first year of life.

Griffith (1972) measured microhabitat use by native cutthroat and brook trout in small Idaho streams where brook trout were introduced in the 1940's, and behavior of both species in a laboratory stream aquarium.

Because brook and cutthroat trout spawn in fall and spring respectively,
and cutthroat often not until June in high altitude streams, brook trout
emerged earlier and maintained a 20-mm size advantage through the first
summer. Juvenile brook trout dominated those of cutthroat trout in the
stream aquarium due to this size difference, even though the cutthroat
dominated brook trout when both were of equal sizes. In streams, age-0 cutthroat
chose positions in shallower water than age-0 brook trout due to their
size difference, which served to partially segregate the species
during their first summer of life. However, microhabitat of age-I and
-II trout overlapped substantially, while age-III brook and cutthroat
trout appeared to show subtle differences in use of pool microhabitat.

Brook trout introduced throughout the Rocky Mountains since the late
1800's have displaced native cutthroat from much of its original habitat
(Behnke 1979). The mechanisms responsible for displacement remain unclear,
but involve the species differences with regard to susceptibility to
angling (MacPhee 1966), tolerance to high stream gradient, age at
maturity and concommittant reproductive output, as well as interspecific
behavior.

Brook and brown trout also appear to be very similar species with
regard to life history and ecology, and are suspected to compete strongly
in waters of northeastern North America, where brook trout are native
and brown trout have been introduced (Fausch and White 1981). Both are
fall spawners, and both use pools and overhead cover extensively in
streams. Our research shows that young emerge and grow almost identically
in Michigan streams, and that brook trout dominated brown trout of
equal size in the stream aquarium. Both species preferred pools, but
brown trout, the subordinate species, were unable to shift to positions in

riffles and grow well, as steelhead and Atlantic salmon do in the presence
of dominant competitors (Hartman 1965, Kennedy and Strange 1980).
~~Two~~ _Thus_ brook and brown trout appear to have no mechanism to partition resources
and minimize competition.

The results of our laboratory experiments were surprising, because
we earlier reported that adult brown trout were able to exclude adult
brook trout from favorable positions in a Michigan stream (Fausch and
White 1981), and because brown trout have displaced brook trout from
much of the habitat they once occupied in North America. As with brook
and cutthroat trout, this displacement also involves differences
between the species in susceptibility to angling, to predation, and
preference for water temperature, stream gradient, and stream size
(cf. Fausch and White 1981). However, Kjellberg (1969) gives anecdotal
evidence that introduced brook trout dominate native brown trout in
small, cold headwater streams and lake systems in Sweden. Perhaps the
competitive ability of brook trout changes with temperature or size,
or because different populations of the two species are better adapted
to different environmental conditions.

The 6-20-mm size advantage of coho salmon over brook and brown
trout in Lake Michigan tributaries may lead to the partitioning of
depth and velocity microhabitat by these species. The implications this
has for competit_ve_ion interactions among these species in Great Lakes
tributaries will be discussed below.

Laboratory and Field Specific Growth Rates

One way to compare the suitability of the stream aquarium and
drifting Daphnia for growth of juvenile salmonids with conditions in

natural streams is to compare laboratory specific growth rates to those in the field for fish of equal size. We calculated relationships between mean specific growth rate (calculated using mean weights of fish on each sampling date) vs. mean weight for each species in all streams (Fig. 11). The negative exponential relationships show the average decrease in specific growth rate as mean weight increased through the summer. Although coho were always larger, all species grew at similar rates for equal weight. The three species grew at high specific rates after emergence in early spring, but declined to specific growth rates less than 0.010 per day during the first summer of life.

The highest laboratory specific growth rates for individual coho salmon, brook trout and brown trout grown in sympatry and allopatry are shown for comparison. The highest laboratory 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 (Fig. 11).

It is evident that brook and brown trout in the stream aquarium lacked some critical resource for growth, and food or cover are the most probable. Perhaps trout require a different food type than coho, or forage 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), blackfly (Simuliidae), and mayfly (Ephemeroptera) larvae in the Platte River, Michigan, which we suspect were carried to their positions in the drift. Dill et al. (1981) report that 40-50-mm coho salmon made 78% of feeding motions towards

drift during ~~Tues~~the day in a British Columbia stream, but that benthos

abundance was a better predictor of territory size. Chapman (1966)

proposed that salmonids, in general, cannot subsist on the benthos

living within their territory, and that benthos must move to be

detected by foraging salmonids. The senior author often observed

young salmon and trout feeding during the day, and found that they

primarily captured ~~any~~ particles of drift that fit in their mouths.

However, most small particles drifting in streams were detritus and were

rejected, so it appears that salmonids must learn to distinguish edible

from inedible particles in the drift. We suspect that the food types

required by juvenile coho and trout and their ability to feed on drift

are similar, and that these fish are opportunistic, feeding on the food

items that are available. Thus, a difference in food does not appear

to be the main reason that trout grew poorly in the laboratory stream.

The other critical resource that probably limited brook and brown

trout growth in the stream aquarium was cover. There was virtually

no cover affording concealment or visual isolation in the stream

aquarium other than the four rocks (see Fig. 4). During allopatry

dominant trout drove away all other trout that they could see, and

subordinate trout retreated into interstices of the gravel to hide.

The time and energy required for dominant trout to defend large areas

must have detracted from energy for growth.

The importance of cover that provides visual isolation for trout

has also been reported by other investigators. Kalleberg (1958)

noticed that more Atlantic salmon occupied the same area in a laboratory

stream when he placed larger rocks on the stream bed, and attributed

this to the visual isolation they afforded. 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 cleared out than in control streams.

In contrast, coho salmon apparently also use cover in pools during
summer (Hartman 1965) and especially winter (Bustard and Narver 1975),
but appear to be less closely associated with cover than trout. We
observed them to coexist in loose aggregation in pools far from cover
in Michigan streams, whereas trout were almost always directly associ-
ated with cover. In the stream aquarium coho always maintained a
three-dimensional aggregation in the pools, with the most dominant
fish at the head and successively subordinate fish spaced downstream
and above the more dominant ones. Hartman (1965) also observed
coho forming these aggregations in his stream aquarium.

The relationships between specific growth rate and potential
profit for these salmonids, and the need for visual isolation among
trout fits with the life history patterns evolved in these fish.
For instance, it is reasonable to suspect that natural selection would
favor larger coho smolts. Studies of returns of adult coho salmon
from hatchery smolt releases are complicated (cf. _Hager and Noble 1976,_ Bilton et al. 1982),
but generally reveal that larger smolts have a higher probability of
returning as adults (Dill et al. 1981). Thus, selection favoring
larger coho smolts should favor maximum growth rates during juvenile
stages, as Dill et al. (1981) suggested. The high specific growth
rates we measured in the stream aquarium for coho compared to those of
trout support this hypothesis. Moreover, we suspect that little
advantage would be conferred to coho juveniles reserving large areas
of the stream to ensure suitable cover or future food supply, since

coho usually leave streams after one year and $\land$ most of the energy for coho growth and reproduction comes from the ocean.

Conversely, it is clear that resident populations of brook and brown trout must extract enough energy from streams for growth and success-ful reproduction. Gaining this energy over the long term requires reserving a suitable position that provides an adequate food supply, but also one that affords cover to ensure concealment from competitors and predators, and refuge from high flows and winter ice. Therefore, in 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 in natural streams.

Interactions Among Juvenile Salmonids in Great Lakes Tributaries

Our results indicate that coho salmon have an overwhelming compe-titive advantage over brook and brown trout in Great Lakes tributaries, and most likely will be detrimental to resident trout populations. In addition to the advantage of size and dominance of favorable positions by coho, several other factors should contribute to their success in these streams. Coho produce many more young because of their larger size, and in all streams we studied they far outnumbered young trout. Where gravel in the stream bed is limited, we expect high incidence of superimposition of redds and reduction of benthos due to salmon spawning (cf. Hildebrand 1971), both of which would be more detrimental to resident trout than salmon. Salmon from the Great Lakes are known transfer pesticides to trout that eat salmon eggs (Merma 1979). This body burden of pesticides and the disease fostered by dying salmon may also be detrimental to trout.

Conversely, several other mechanisms may slightly ameliorate the competition among age-0 coho salmon, brook and brown trout. Because juvenile coho are larger on average, they move into faster and deeper water of the main channel earlier than brook or brown trout, so the majority of age-0 salmon and trout may partition stream microhabitat on the basis of depth and velocity due to the size difference. In many of the streams we sampled, age-0 coho did appear to use faster and deeper water than age-0 brook and brown trout, which were more closely associated with cover along the stream margins in early and mid-summer. However, age-I and older trout also occupied the main channel, and were often associated with cover provided by logs there. Therefore, if age-0 coho grow as large as the smallest age-I trout during their first summer of life, they may compete directly with these trout for space. Moreover, all trout and salmon of the same size probably exploit a common drift food resource. A second factor, visual isolation afforded by cover, may also be important to the existence of juvenile brook and brown trout in Great Lakes tributaries by reducing both intraspecific competition, and interspecific competition with coho salmon. In stream areas with little cover, age-0 coho may severely inhibit growth and survival of age-0 brook and brown trout.

In Great Lakes tributaries where food and space resources become limited, we suspect that resident brook and brown trout will subsist with difficulty in the face of competition and other interactions with coho salmon. If these resident populations of trout are valued, a more favorable management strategy might be a gradual shift to planting more chinook salmon smolts which use nursery streams for a shorter period, a strategy that Michigan appears to be pursuing (   ).

Alternatively, the technology is now available to render juvenile coho sterile by immersion in methyltestosterone at the egg and alevin stages (Hunter et al. 1982). This would virtually eliminate adult salmon from ascending streams to spawn, but might not be favored by stream salmon anglers.

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Table 1. Study sites in Lake Michigan tributaries

Stream	Stream order[a]	Salmonid species[b] (abundance[c])	Number of other fish species
1. Love Creek	1	BK[d](C) CO(A) S(A)	7
2. Springbrook Creek	2	BR(A)	3
3. Smith Creek	1	BK(A)	0
4. Sand Creek	1	BK(C) CO(A) S(A) BR[d](R)	8
5. Egypt Creek	3	BK(A) BR(A) CO(R)	4
6. Bigelow Creek	3	BR(C) CO(A) CH(A) S(A)	4
7. Pine Creek	2	BR(A) CO(A) CH(A) S(A)	2
8. Green River	2	BR(A) CO(A) BK(R) CH(A) S(A)	1

a. Determined from 1:24,000 maps according to Strahler's (1957) method.

b. BK - brook trout, BN - brown trout, CO - coho salmon, CH - chinook salmon, S - steelhead trout.

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

d. Introduced hatchery fish, and few or no age-0 fish captured.

Table 2. Design of Competition Experiment

Experiment	Section[a] in allopatry	No. of fish	Number of days			Mean initial length (mm FL)		Mean initial weight (g)		Food as percent of wet weight	
			Accli-mation	Sym-patry	Allo-patry	Sym-patry	Allo-patry	Sym-patry	Allo-patry	Sym-patry	Allo-patry
A. Brook Trout vs. Brown Trout											
Brown trout	U	14	5	10.5	10	69.7 (67.0-72.5)[b]	69.4	3.23 (2.84-3.72)	2.97	9	9
Brook trout	D	14	5	10.5	10	70.6 (68.0-72.5)	70.9	3.21 (2.87-3.36)	3.02	9	9
B. Brook trout vs. Coho Salmon											
Brook trout	U	20	5[c]	10.5	10	34.3 (31.0-37.5)	33.7	0.31 (0.20-0.42)	0.26	77	68
Coho Salmon	D	20	5[c]	10.5	10	34.5 (32.0-37.0)	35.1	0.28 (0.19-0.42)	0.32	63	68
C. Brown Trout vs. Coho Salmon											
Coho salmon	U	16	13.5	9.5	9	40.6 (39.0-42.5)	41.3	0.55 (0.43-0.65)	0.62	50	52
Brown trout	D	16[d]	13.5	9.5	9	41.3 (39.0-43.5)	41.0	0.56 (0.44-0.72)	0.50	50	80

Table 2. Design of Competition Experiment (cont.)

a. U = upstream half of stream aquarium, D = downstream half.

b. Ranges of initial lengths and weights.

c. Fish were acclimated to eating drifting _Daphnia_ for 7 days.

d. Three brown trout died between sympatry and allopatry.

All numbers and calc. checked against
data summaries. 3/10/83.

3

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

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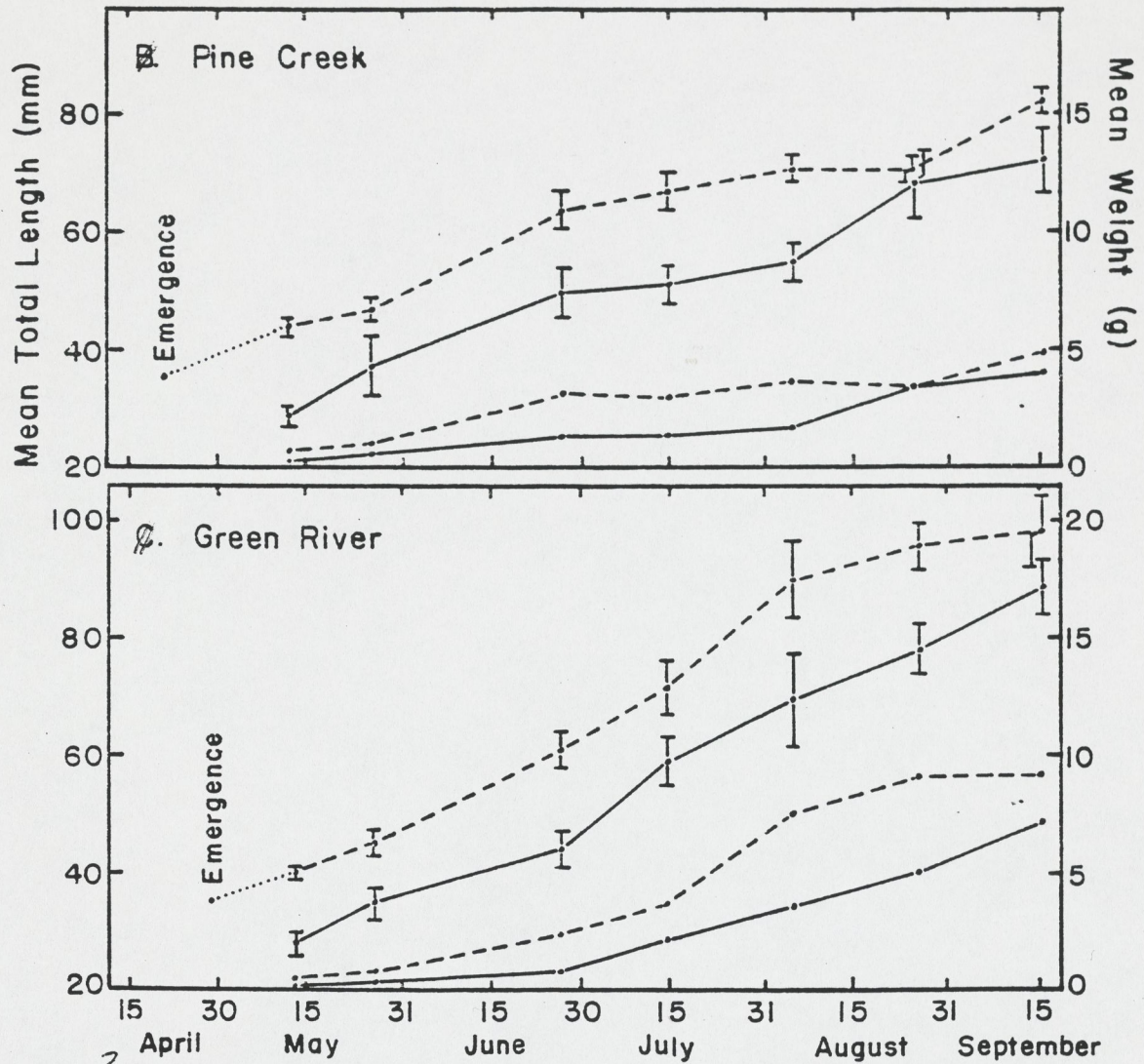
Figure 7.--Growth of juvenile coho salmon and brown trout in ~~three~~ Two
Lake Michigan tributaries during 1979. Top curves are body
length, bottom curves are weight. ~~A "*" denotes a sample
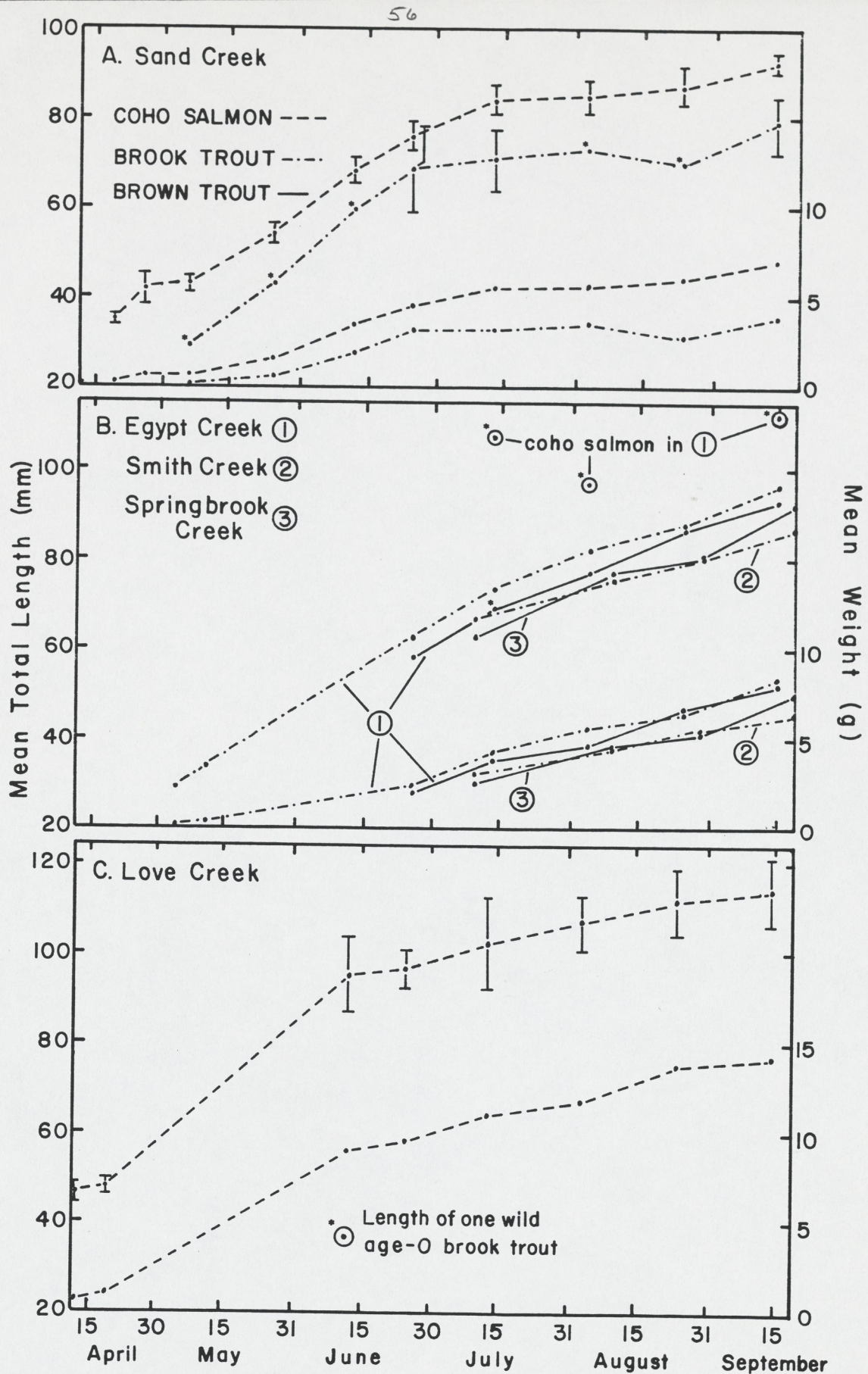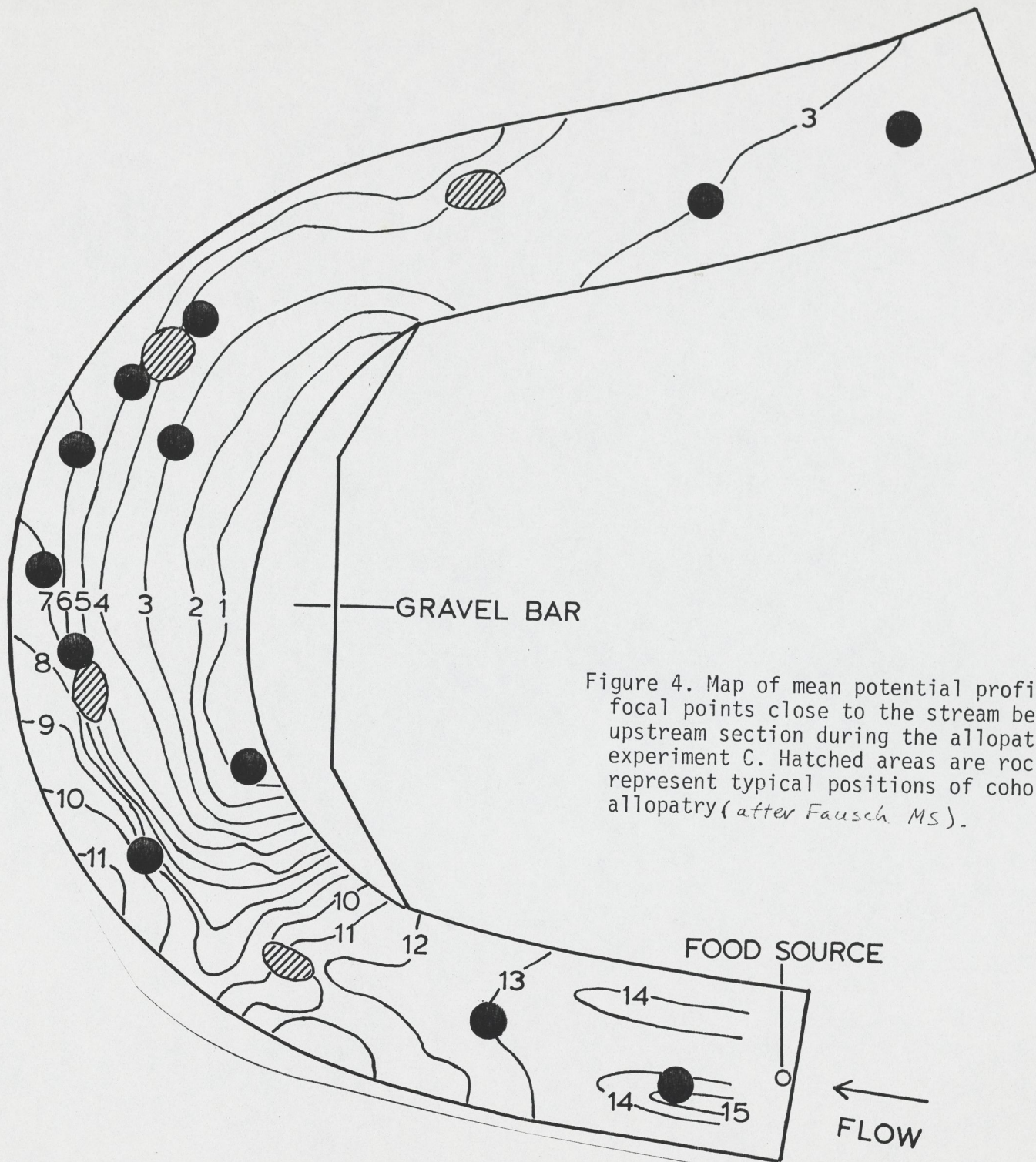of three fish or less, and~~ Bars show 95% confidence inter-
vals on each mean.

Figure 3. 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 mean weight.

Figure 4. Map of mean potential profit (cal/hr) at focal points close to the stream bed in the upstream section during the allopatry phase of experiment C. Hatched areas are rocks. Circles represent typical positions of coho salmon in allopatry (after Fausch MS).

GRAVEL BAR

FOOD SOURCE

FLOW
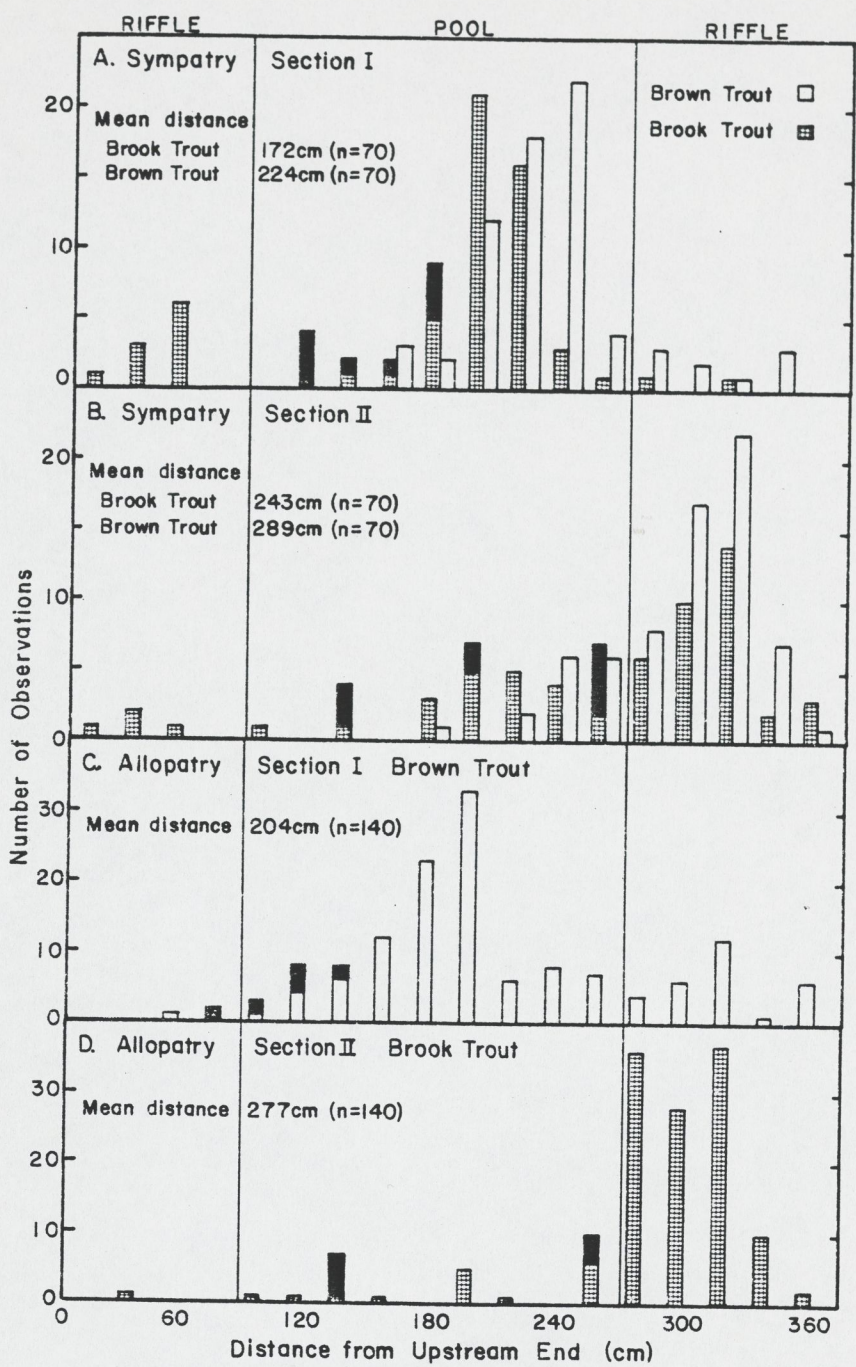
Figure 12.--Distribution of positions held by brook and brown trout
during sympatry (a and b) and allopatry (c and d).
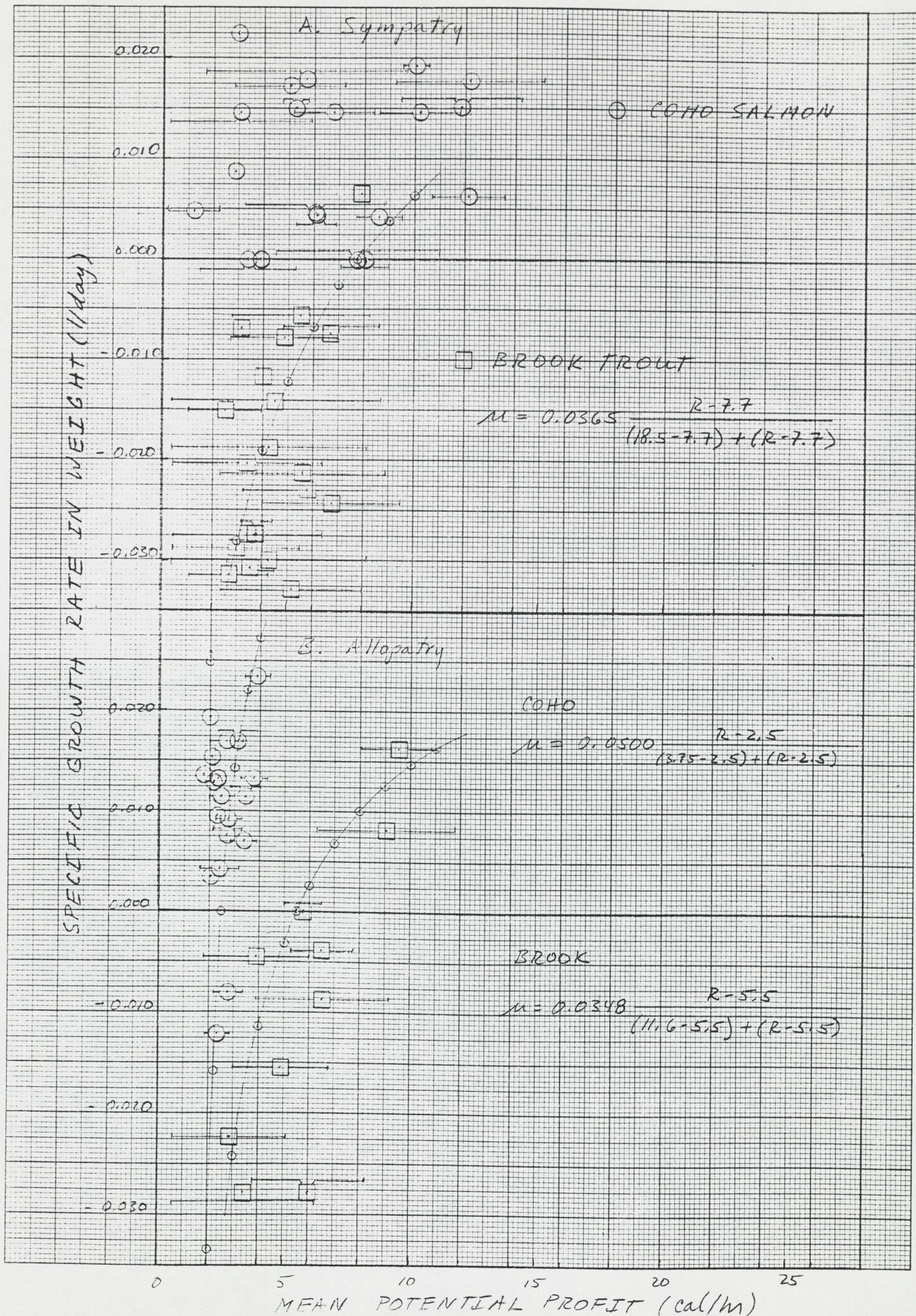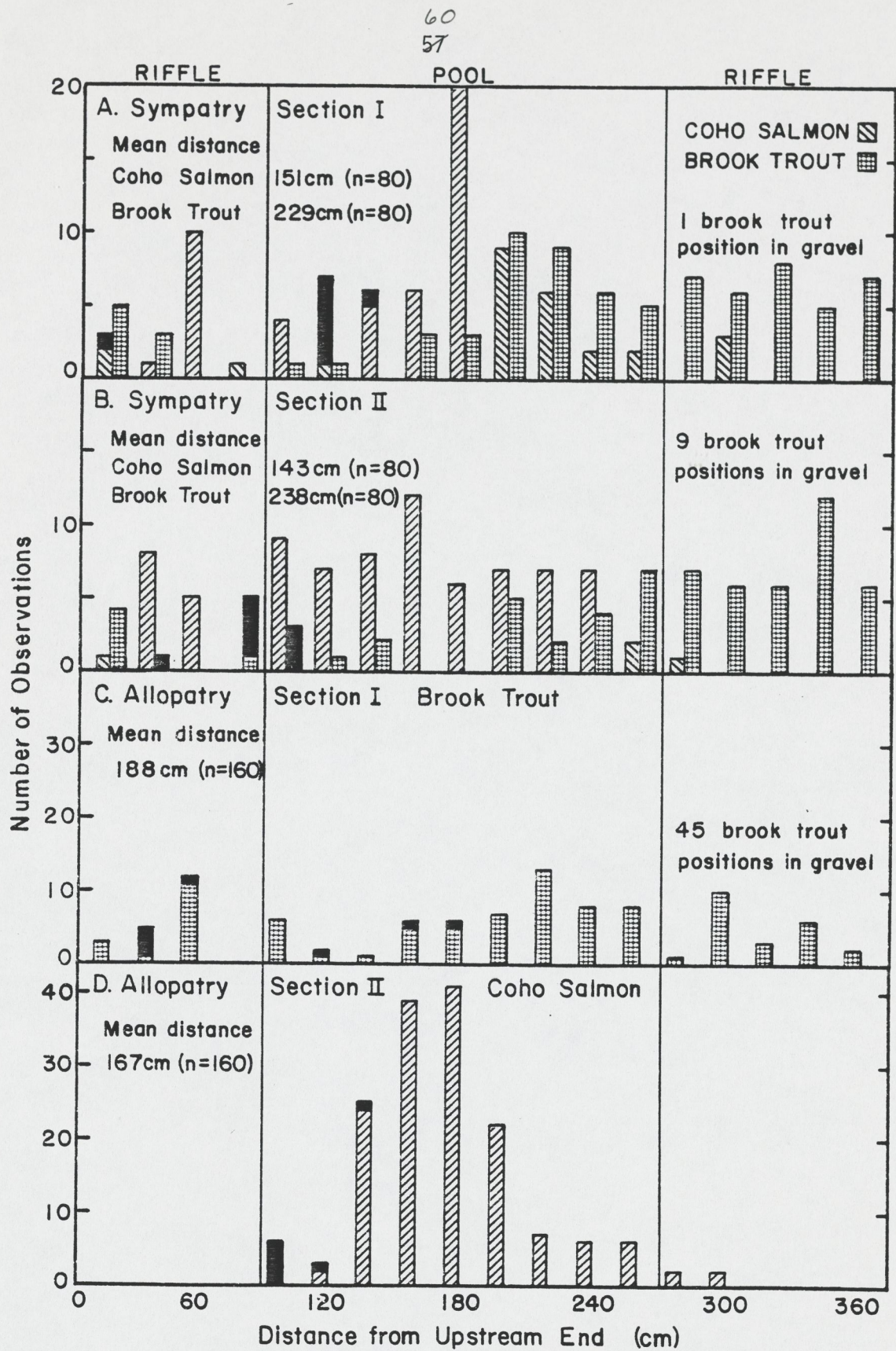Black portions of bars are positions of dominant fish.
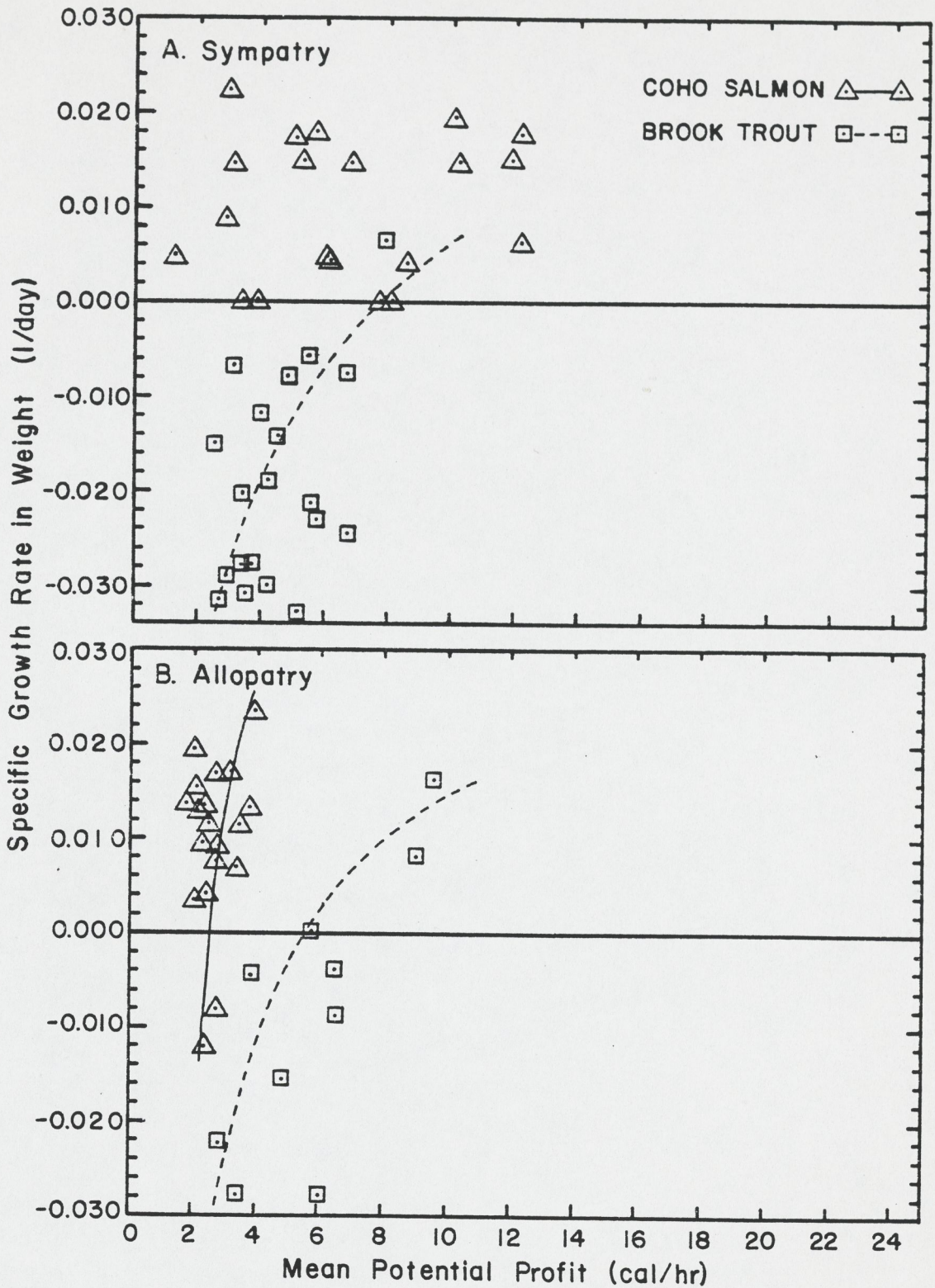
Figure 13.--Specific growth rate as a function of mean potential profit for brook trout and coho salmon in sympatry (a) and allopatry (b).

59a.

Experiment B - Brook vs. Coho

A. Sympatry

COHO SALMON

BROOK TROUT

$$\mu = 0.0365 \frac{R - 7.7}{(18.5 - 7.7) + (R - 7.7)}$$

B. Allopatry

COHO

$$\mu = 0.0500 \frac{R - 2.5}{(3.75 - 2.5) + (R - 2.5)}$$

BROOK

$$\mu = 0.0348 \frac{R - 5.5}{(11.6 - 5.5) + (R - 5.5)}$$

SPECIFIC GROWTH RATE IN WEIGHT (1/day)

0.020
0.010
0.000
-0.010
-0.020
-0.030

0.020
0.010
0.000
-0.010
-0.020
-0.030

0   5   10   15   20   25

MEAN POTENTIAL PROFIT (cal/m)

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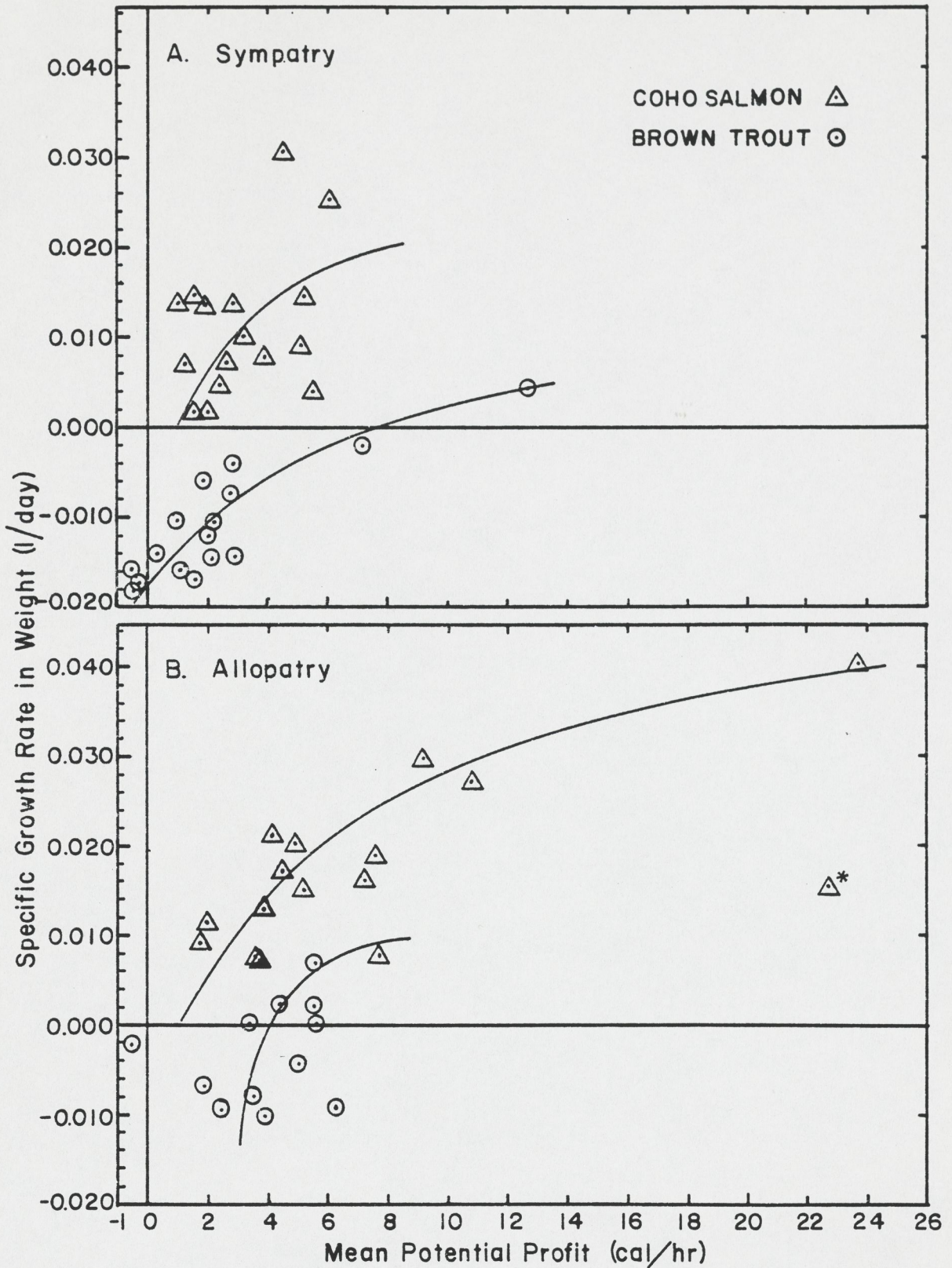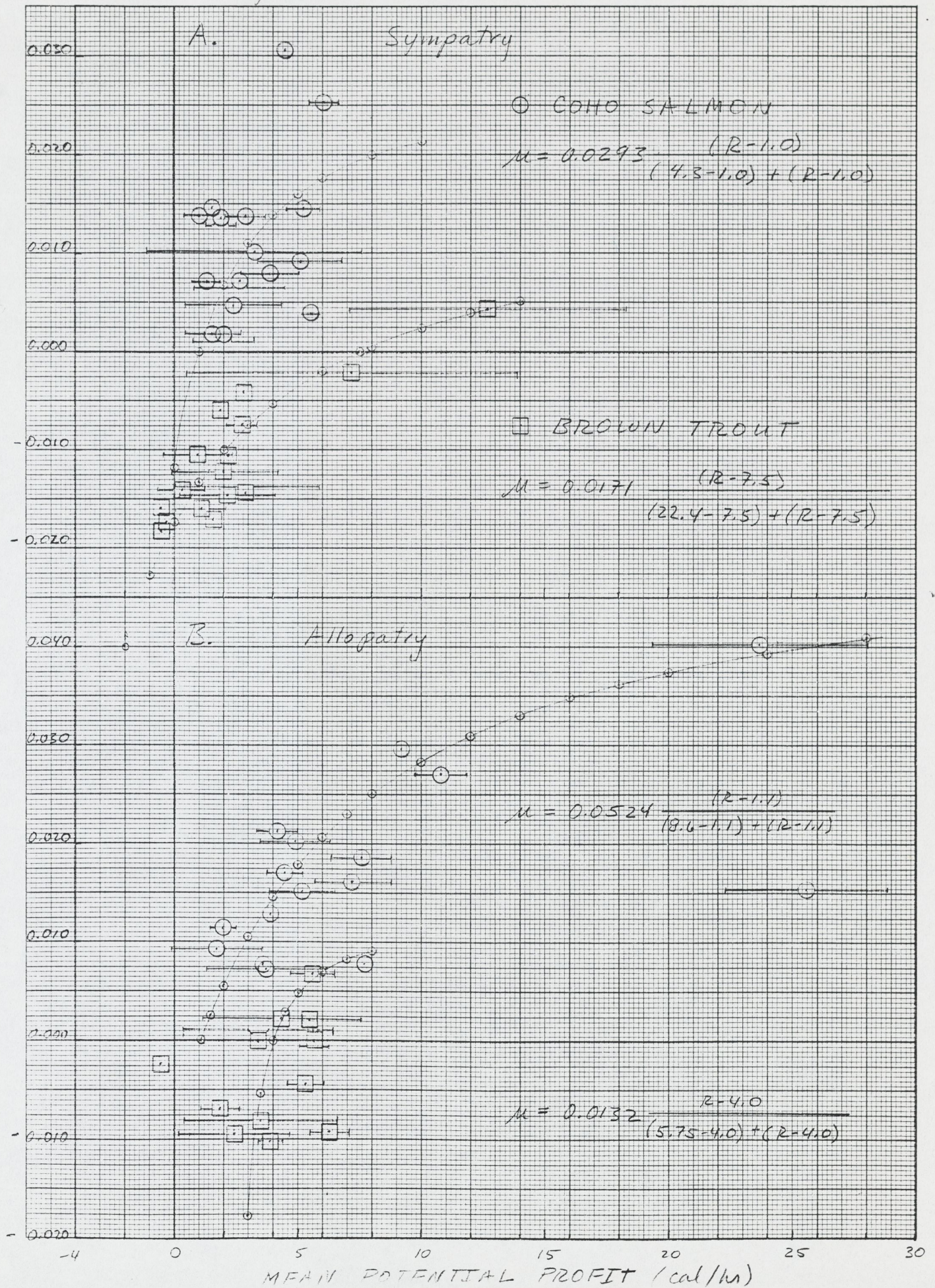
Figure 15.--Specific growth rate as a function of mean potential profit for brown trout and coho salmon in sympatry (a) and allopatry (b). One coho salmon in allopatry was excluded as an outlier (*).

Experiment C - Brown vs. Coho

A.   Sympatry

⊙ COHO SALMON

$$\mu = 0.0293 \frac{(R-1.0)}{(4.3-1.0)+(R-1.0)}$$

▢ BROWN TROUT

$$\mu = 0.0171 \frac{(R-7.5)}{(22.4-7.5)+(R-7.5)}$$

B.   Allopatry

$$\mu = 0.0524 \frac{(R-1.1)}{(8.6-1.1)+(R-1.1)}$$

$$\mu = 0.0132 \frac{R-4.0}{(5.75-4.0)+(R-4.0)}$$

(y-axis) SPECIFIC GROWTH RATE IN WEIGHT (1/day)
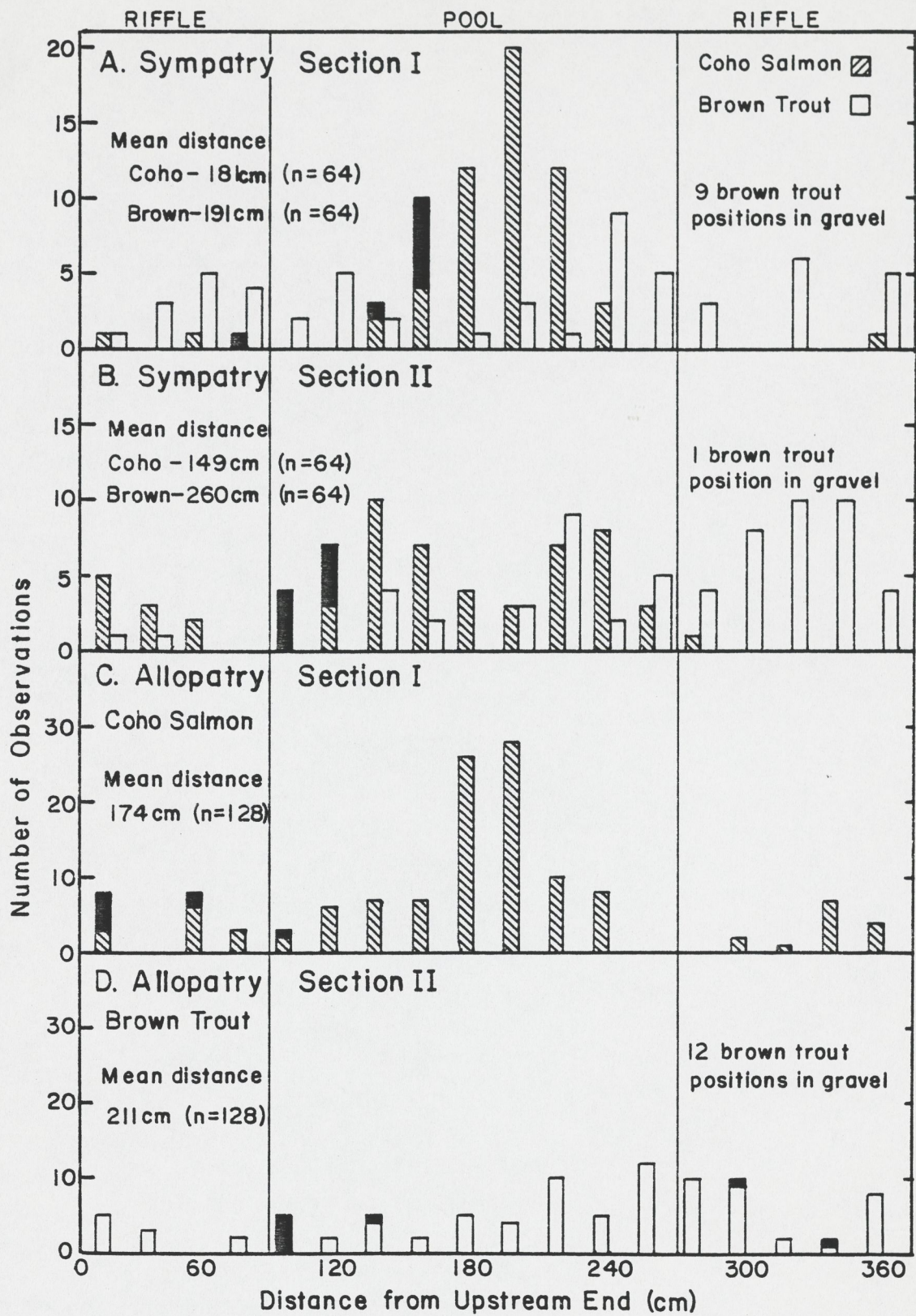
(x-axis) MEAN POTENTIAL PROFIT (cal/hr)

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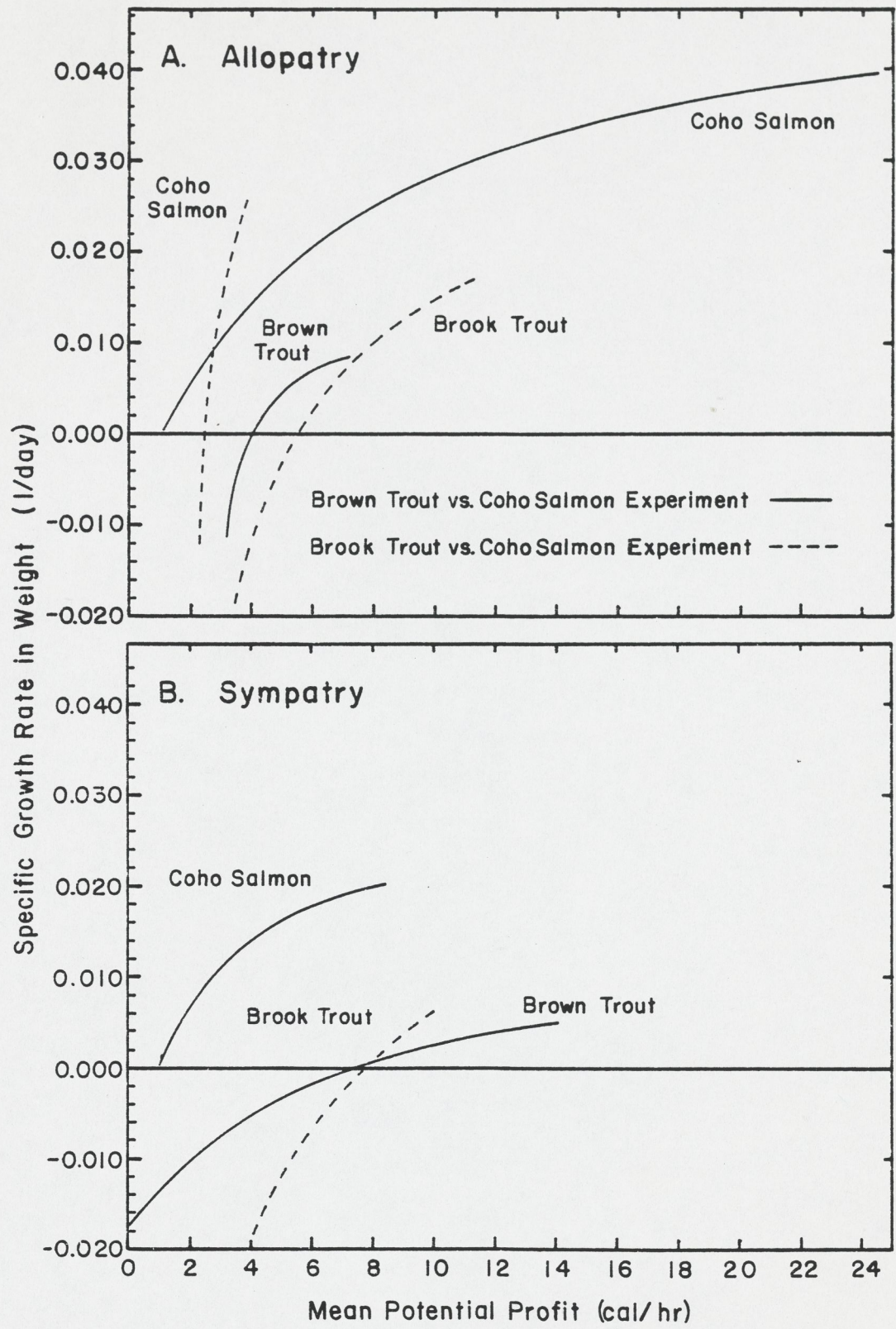
Figure 17.--General relationships between specific growth rate and
mean potential profit for coho salmon, brook and brown
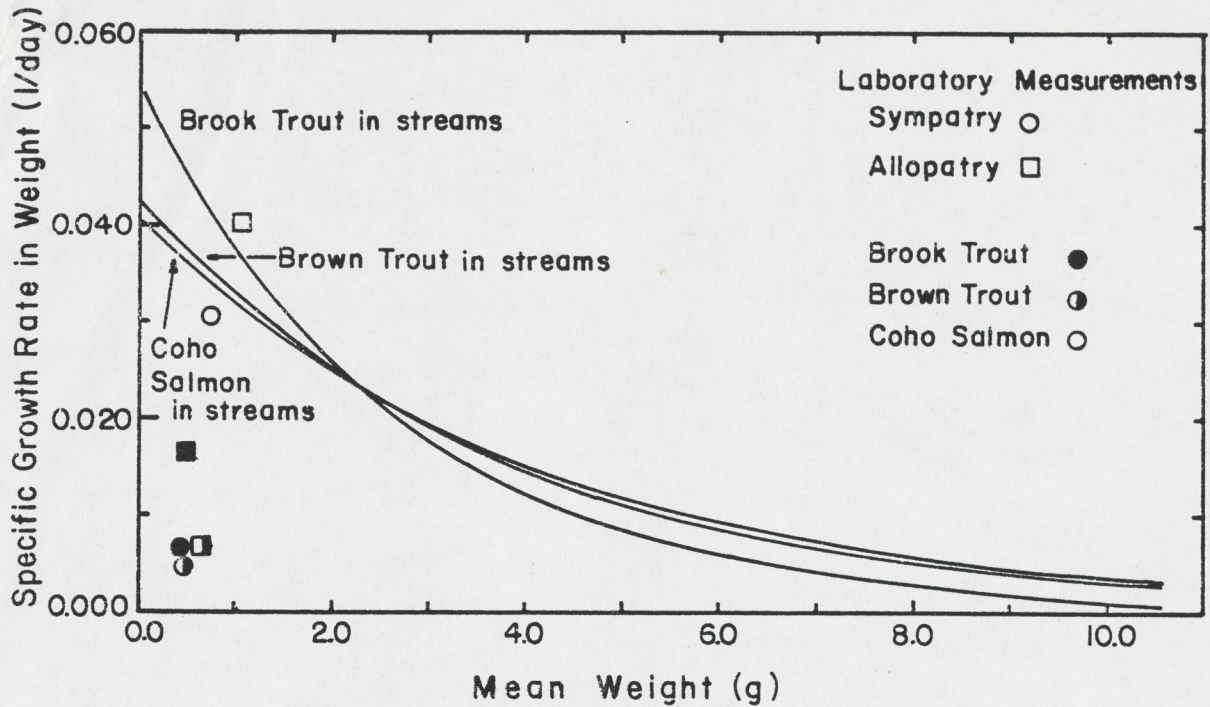trout in allopatry (a) and sympatry (b).

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.

2 - adult salmon prey on juveniles (not in
                                        streams)

39 - can't live only benthos - Cement Crk. Colo.
                            trout density
                            invert density

                        - Bachman
                          Spruce Crk
                          eat mostly
                          benthos

41 ?

43 methyltestosteron
   immersion;
   in feed