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OF JUVENILE COHO SALMON (ONCORHYNCHUS KISUTCH)  
AND STEELHEAD TROUT (SALMO GAIIRDNERI).

University of Washington, Ph.D., 1974  
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SPATIAL REQUIREMENTS AND BEHAVIORAL INTERACTIONS OF  
JUVENILE COHO SALMON (*ONCORHYNCHUS KISUTCH*) AND  
STEELHEAD TROUT (*SALMO GAIRDNERI*)

By

BRIAN JAMES ALLEE

A thesis submitted in partial fulfillment

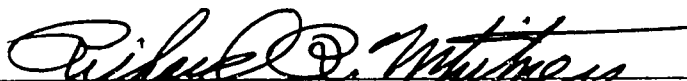
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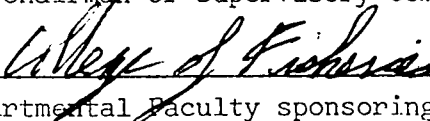
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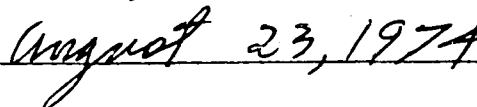
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UNIVERSITY OF WASHINGTON

Date: July 31, 1974

We have carefully read the dissertation entitled Spatial requirements and behavioral interactions of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*) submitted by Brian J. Allee in partial fulfillment of the requirements of the degree of Doctor of Philosophy and recommend its acceptance. In support of this recommendation we present the following joint statement of evaluation to be filed with the dissertation.

Mr. Allee has answered some significant questions about the coexistence in streams of juvenile coho salmon and steelhead trout. These questions are of practical importance to management agencies responsible for stocking streams with the two species, and of basic scientific interest as they relate to understanding adaptations for survival evolved by two species seemingly occupying the same space at the same time.

His work is a logical extension of recent work reported in the literature. He had clarified some ambiguities that remained, and has answered the next series of questions raised by that work. He devised an experimental stream system which included a feature not provided in previous studies--namely, a means for fish to leave the system as a way of competition for food and space.

Management agency procedures can alter a number of the factors that might affect the responses of the two species. For example, coho normally spawn first and the juveniles therefore appear first in the stream ahead of steelhead. Mr. Allee experimentally reversed the sequence, placing steelhead first to see if this would alter the outcome of the competitive interactions. He investigated the effects of differences in fish size and differences in season on the outcome. He studied the effects of introducing hatchery fish into systems where wild fish were already present.

His observations of behavioral interactions of the two species are particularly interesting. It is surprising to learn that where they occur together, coho juveniles will nip steelhead and each other, but steelhead, while they are just as active in nipping each other, rarely or never nip coho.

We find that he has imaginatively devised experiments and answered significant questions relating to the survival of these two important fish species.

DISSERTATION READING COMMITTEE:

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Doctoral Dissertation

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I would like to express my appreciation to the faculty of the College of Fisheries for providing the research station and facilities at Big Beef Creek. The opportunity to study there represented a unique and worthwhile experience.

Finally, I would like to dedicate this dissertation to my wife who has provided unfailing support and inspiration to me throughout this endeavor.

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## GENERAL INTRODUCTION

Coho salmon and steelhead trout are two closely-related salmonid species, both of which reside in freshwater for extended periods (a year or more) (Neave, 1958). They are reported to be sympatric from California to British Columbia (Burns, 1971; Fraser, 1969; Hartman, 1965; Johnston, 1967; and Peterson, 1966). These two species have been viewed as potential competitors, because, as Larkin (1956) states, freshwater stream environments are structurally simple and provide little opportunity for specialization. One mechanism which promotes the coexistence of sympatric fish species has been termed interactive segregation by Brian (1956) and has been discussed by Nilsson (1967). This mechanism promotes habitat selection and thereby reduces competition. Hartman (1965) has postulated that this process is a seasonal one for coho salmon and steelhead trout in British Columbia streams, with strong habitat selection occurring in spring and summer as a result of interspecific agonistic behavior differentially directed by steelhead against coho in riffles and by coho against steelhead in pools. Other workers studying sympatric populations of coho and chinook salmon (Lister and Genoe, 1970) and chinook salmon and steelhead trout (Everest, 1969) have emphasized the role of differences in emergence times and size specific habitat responses and have de-emphasized the role of agonistic behavioral interactions in the segregation process. Moreover, these workers have postulated that their respective populations have evolved genotypic responses to habitat and are at the end point of interactive segregation, termed selective segregation (Brian, 1956). Another study of coho salmon and steelhead trout ecology

was conducted by Fraser (1966) at Robertson spawning channel in British Columbia. Fraser concluded that coho and steelhead had evolved species-specific differences in growth rate and survival and also, by virtue of their different spawning time and consequent emergence time, they utilized the available habitat differently. Moreover, his observations on feeding behavior indicated that vertical separation was occurring among coho and steelhead. This corroborates two independent food-habit studies which suggested vertical stratification of these species based upon food items they selected (Johnston, 1967; Peterson, 1966). Fraser (1969) speculated that, both in terms of prior residence and size, coho were at an ecological advantage over steelhead because of their earlier emergence, just as Mason and Chapman (1965) concluded that early emergent coho were at an advantage over later-emerging coho in terms of their ability to secure territories.

The present study sought to contribute to the knowledge of coho salmon and steelhead trout by observing these species in a natural stream system located in western Washington, and in an experimental stream system where some control over parameters affecting these populations could be made. This represents an extension of and departure from both Hartman's (1965) and Fraser's (1969) work by providing long-term documentation of these sympatric populations in an environment which more closely simulates the natural environment, specifically in terms of (1) omission of artificial feeding, (2) provision of volitional residence, and (3) extended periods of experimental stream residence.

Since the experimental stream system is by definition an artificial structuring of aquatic habitats, it is necessary to consider the question

of experimental artifact. I see this question best approached by assuming that habitat simulation of the real stream environment is distributed along a continuum. At one end is the real stream habitat; at the other a laboratory aquarium system under uniform controlled conditions. The more recent stream aquarium concept, as developed by Chapman (1952) and modified by Mason (1966) and further modified in this study, would be found somewhere in between those extremes. The significant aspect of my system is that the fish had the option of leaving the system just as they would in a natural stream. This requirement would seem to be a necessity when attempting to extrapolate results back to the wild environment.

There are three major sections in this thesis. The first part is a description of coho and steelhead behavior in the natural stream. The second and third parts are descriptions of studies in the experimental stream designed to assess the role of prior residence and size on the social behavior and population ecology of coho salmon and steelhead trout.

The competitive advantage of prior residence has been described by Chapman (1962) for juvenile coho salmon and by Braddock (1949) for Platyocilus maculatus. Mason's (1966) work with juvenile coho indicated that the ecological advantage of prior residence is essentially an earlier feeding opportunity which would result in a size advantage. In terms of the application to multiple species interactions, Fraser (1968) speculates that coho having an earlier emergence than steelhead might be provided with an advantage. Griffith (1972), studying brook trout and cutthroat trout, specifically designed experiments within stream channels

to test the effects of prior residence. Brook trout, when they were prior residents, were not at a competitive advantage over cutthroat trout, whereas, cutthroat trout, when they were prior residents, had an advantage over brook trout.

Size of fish has been reported (Chapman, 1962) as being important in determining the outcome of intraspecific agonistic interactions within coho salmon populations. Newman's (1956) work with both rainbow and brook trout in mixed and separate populations showed that larger size conveyed an advantage in terms of social dominance. Certainly, with regard to sympatric populations of coho salmon and steelhead trout, the coho juveniles are larger in size than steelhead by virtue of their earlier emergence. Mason and Chapman (1965) in discussing coho salmon have stated that early emergent fry had an advantage over later emerging fry--that is, earlier-emerging fry were larger on the average and there were more of them in the final resident population than later-emerging fry.

## PART 1. DESCRIPTION OF COHO AND STEELHEAD BEHAVIOR IN THE NATURAL STREAM

### Description of the Natural Stream

Big Beef Creek is located on the west side of the Kitsap Peninsula and drains into Hood Canal in Western Washington (Fig. 1). A small estuary which empties completely at certain tidal levels lies at the mouth of Big Beef Creek. Lake William Symington, an artificial impoundment built in 1966, is located 6.4 km upstream from the mouth. Upstream from this lake the stream extends for another 8 km. The upper portion of the stream is low in gradient (0.2% slope) and composed of alternating sections of beaver ponds and slow-flowing runs with few riffle areas. For a distance of 3.2 km downstream from the lake the stream is characterized by narrow canyons where the gradient is swift (1.0%) (Cederholm, 1972). The remaining 6.4 km of stream are characterized by approximately 75% pool and 25% riffle, with an average gradient of approximately 0.8%. Riparian vegetation is composed of cedar (Thuja plicata), alder (Alnus oregona), vine maple (Acer circivatum), and broad leaf maple (Acer macrophyllum).

A number of salmonid species are indigenous to Big Beef Creek, as are some other fishes. These include, in order of decreasing abundance, coho salmon (Oncorhynchus kisutch), chum salmon (Oncorhynchus keta), steelhead trout (Salmo gairdneri), and sea-run cutthroat trout (Salmo clarki). Other indigenous species include sculpin (Cottus sp.), three-spine stickleback (Gasterosteus aculeatus), speckled dace (Rhinichthys osculus), Pacific lamprey (Entosphenous tridentatus), river lamprey

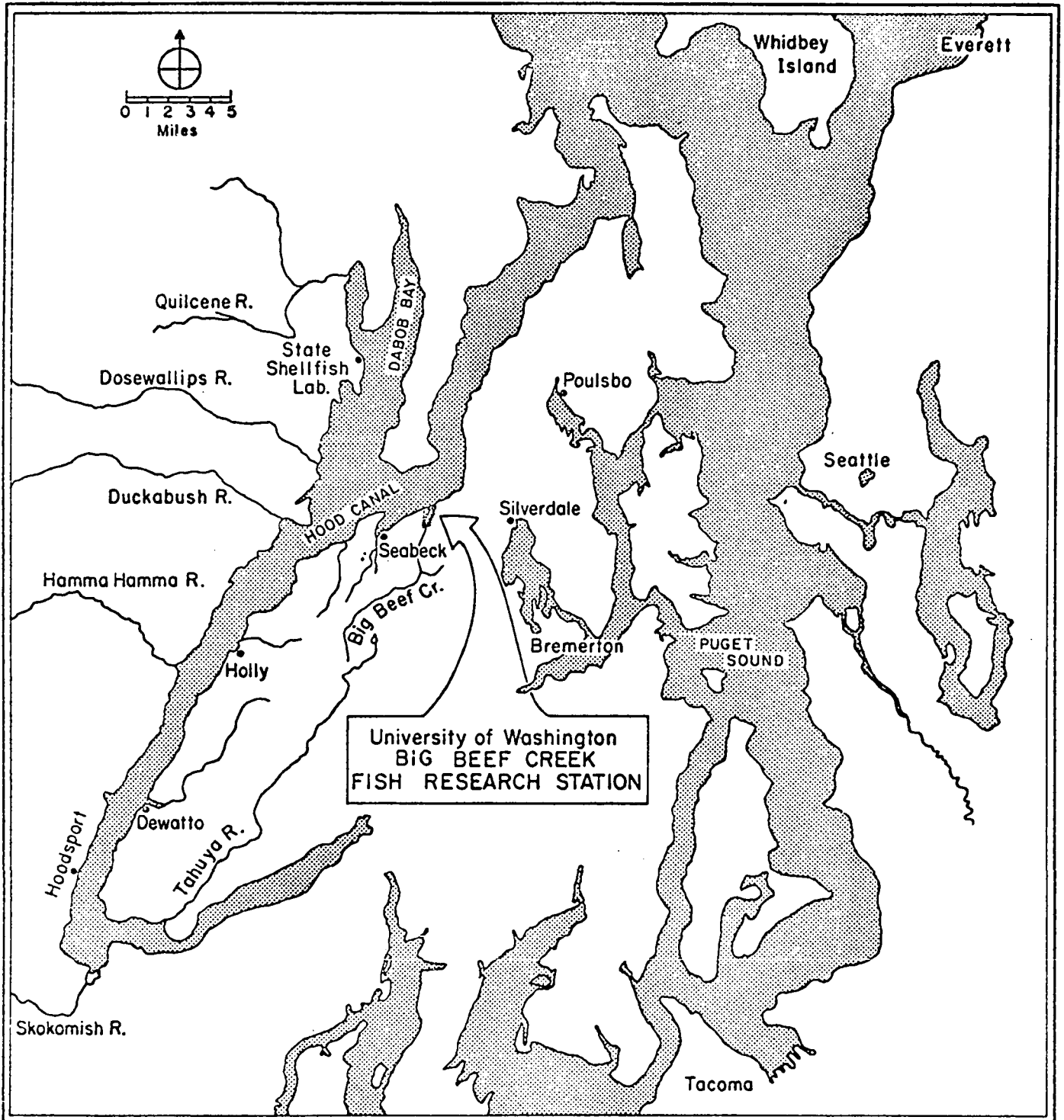


Fig. 1. Geographical location of Big Beef Creek in western Washington.

(Lampetra ayresi), and creek lamprey (Lampetra planeri). Yellow perch (Perca flavescens) have been introduced to this stream system.

#### Methods

Observations on seasonal distribution and abundance of coho and steelhead juveniles were made by diving with wet suit and snorkel into the stream. Areas to be observed were approached from a downstream position to minimize disturbance to the fish which were generally oriented upstream. Distributions in shallow riffles were determined by looking upstream into the riffle from a deeper area below. Diving observations took place over a three-year period from 1967 to 1970.

Habitats described in the stream include riffle, pool, and run, or open channel. These habitats are described on the basis of relative terms. A riffle is an area of fast velocity and shallow, rather than deep cross-section. A pool is characterized by slow velocity and shallow areas on the stream margins and a deeper center channel. A run is a transitional area lying between riffles and pools and intermediate in depth and velocity.

Stream temperature records were obtained from a Honeywell chart recorder which continuously documented temperatures on a seven-day cycle. Stream discharge records were available from a continuous water level station operated by the United States Geological Survey (U.S.G.S.), located 1.6 km from the mouth of Big Beef Creek.

Seining in the study pools of Big Beef Creek was carried out with a 4.6 x 1.8 m seine. When catch per unit effort declined to the point where three consecutive catches of zero fish were obtained in a given

study pool, it was assumed that the total population of coho and steelhead had been enumerated. Estimates of adult escapement were made by the Petersen mark-recovery method and by spawning ground surveys prior to 1970. After 1970, adult fish were enumerated at adult trapping facilities at the mouth of Big Beef Creek.

## Results

### Age and Abundance of Coho and Steelhead

Coho salmon spawn in November and December in Big Beef Creek. The adult run has been enumerated since 1966. It has ranged between 3,000 and 5,000 fish. Fry emerged primarily in the month of March. The fry generally spent 14 months in freshwater before migrating to sea. The coho smolts during 1966 and 1967 were found to be mainly 1 year of age (Williams, 1970). Only about 6% were age 2 fish in 1966 compared to 12% in 1967 (Williams, 1970). The maximum abundance of seaward migrants generally occurred in the first part of May (Williams, 1970). Numbers of downstream migrants have been estimated since 1967. The estimates ranged from 26,556 to 64,803.

Spawning migrations of steelhead trout began in December and extended to March. Adult trapping operations in 1969 and 1970 indicated that approximately 100-200 steelhead adults entered Big Beef Creek each year. Most steelhead fry emerged from the gravel during the months of May and June. These fish generally remained in freshwater for 2 years before migrating to sea (Briggs, 1953; Taft and Shapovalov, 1945). No specific age determination studies have been made on steelhead in this stream, but at the time of smolt migration in April and May there were only two

size classes of steelhead present, namely, under-yearlings and seaward migrants (smolts). Further, comparing the approximate average length of coho smolts (120 mm) and the average length of steelhead (175 mm), it is apparent that this difference in size could be achieved in one more season of growth. Therefore, I concluded that steelhead seaward migrants spent at least two years in Big Beef Creek. The number of downstream migrating steelhead smolts has been estimated since 1967. The estimates ranged from 1,000 to 2,000 fish. Thus, the steelhead population only represented approximately 3% of the combined coho-steelhead smolt production for Big Beef Creek. In Minter Creek the steelhead population ranged from 2.2 to 4.2% of the total smolt production from 1936 to 1953 (Salo and Bayliff, 1958). This lower Puget Sound stream has a similar smolt production to Big Beef Creek, and has comparable hydrological characteristics.

#### Seasonal Distribution of Coho and Steelhead

Observations made by diving in Big Beef Creek indicated both spatial and temporal differences in distribution of coho and steelhead. In the latter part of March, presmolts of both age 1 coho and age 1+ steelhead were found in large schools within the deepest part of pools, while age 1 steelhead were found predominantly in the fast-flowing riffle areas.

Due to the earlier spawning of adults, emergent coho fry preceded steelhead fry by approximately 2 to 2 1/2 months. Fry emergence for coho salmon generally occurred about March 15. The vast majority of these coho fry were found in the shallow areas along the stream margins.

Densities per unit area were very high during this period, and territorial behavior occupied a major part of their activity.

Steelhead fry emerged from the gravel in Big Beef Creek, on the average, by May 15. These fish were found to be distributed along the shallow stream margins. Population densities during this time were high, and territorial behavior was very highly developed. In general, at this time, three size classes of steelhead were present, representing fish of age 0, age 1, and age 1+. Two size classes of coho were present, representing age 0 and age 1 year.

The first change in this spring distributional pattern was directly related to termination of the smolt migration. When the coho and steelhead smolts were no longer present in the pools, age 0 coho fry left the margins and moved into the pool habitat proper. As the spring smolt migration proceeded, stream temperatures gradually warmed. As an example, stream temperatures during 1966 and 1967 showed a range of 47.4 F to 56.7 F (Table 1). Similarly, stream discharge from water-year 1970 showed a decreasing trend starting in March (38.7 cfs) (Table 2).

The second major change in distributional pattern occurred after the smolt migration with the advent of summer. At this time there were two size classes of steelhead present in the stream and one general size class of coho. These presumably represented age 0 steelhead, age 1 steelhead, and age 0 coho.

Age 0 coho fry generally moved into the pools in the main flow. They distributed themselves primarily within the top half of the water column vertically. Their organization was that of a loose aggregation

Table 1. Monthly maximum, minimum, and mean temperatures recorded from lower Big Beef Creek June 1966 - June 1967, Williams (M.S. 1970).

Month	Mean maximum	Mean	Mean minimum
June	60.3	56.7	53.1
July	61.2	57.4	53.7
August	61.9	57.8	53.7
September	57.9	54.9	51.9
October	50.9	49.2	47.4
November	45.2	44.5	43.8
December	43.5	43.0	42.6
January	40.6	40.2	39.8
February	42.3	41.3	40.3
March	45.0	43.6	42.1
April	49.7	47.4	45.0
May	55.4	52.1	48.8

Table 2. Monthly maximum, minimum and mean discharge recorded from U.S.G.S. station 1.6 kms from mouth of Big Beef Creek October 1967-September 1970

Month	Minimum	Mean	Maximum
October	7.0	10.6	21
November	9.0	19.9	54
December	10	96.5	318
January	29	117	259
February	33	63.1	158
March	22	46.9	103
April	20	38.7	133
May	11	14.2	20
June	4.8	7.0	10
July	3.5	4.3	5.8
August	2.6	3.4	4.2
September	3.2	4.2	5.8

where hierarchial behavior was the dominant behavior pattern. Orientation of the fish in this habitat was positively rheotactic. Some age 0 coho were also present in runs between riffles and pools. Age steelhead fry were also present in these areas.

The majority of age 0 steelhead were present in shallow areas of the stream, including both fast velocity and slow velocity areas. They were present in riffles, along the sloping sides of pools where the depth was less than in the main flow, and in transitional areas between pools and riffles. Within pools they were distributed along the bottom close to the substrate. Here they did not exhibit any directional rheotaxis, as they would within a riffle. Instead an appetitive behavior predominated in which fish actively searched on top of and among the rock substrate for food organisms. These fish exhibited territorial behavior, presumably based upon site orientation related to the substrate.

In contrast to age 0 steelhead, steelhead yearlings spending their second summer in the stream were found in the deep pools where cover was available, and also in areas with fast velocity where the average depth of a riffle deepened to form a pool. These areas were often turbulent and provided cover by scattering light. Their feeding positions within pools were at the most upstream point and at a depth which was less than the average pool depth. Generally, they were found in the bottom half of the water column closely associated with the substrate, exhibiting positive rheotaxis. This period was characterized by high water temperatures and low stream discharge.

Early fall distribution was similar to that during summer. By late fall increased discharge and lowered temperature necessitated a change

in the distribution. Those age 0 steelhead that were present in the riffle areas moved into the pools so that both age classes of steelhead were present in pools as well as the age 0 coho. Presence of both species within pools was related to the timing of the first discharge of large magnitude in late fall or early winter. After this time, no fish could be seen anywhere within the stream. The only age 0 coho and steelhead observed were under roots of one stump within a large pool, and these were few in number.

Conventional methods of seining and electrofishing were unsuccessful in capturing fish during this period. Therefore, on February 5, 1969 dynamite was used (Table 3). Two riffles and two pools were sampled with 50% ditching dynamite. Fish were only captured from the pool environments, two age 0 coho from one pool, and one age 0 steelhead and one age 1+ steelhead from the other.

#### Winter Outmigration

During the winter season and coincident with the first major freshet of the year, the outmigration of stream salmonids in Big Beef Creek began (Fig. 2). These age 0 coho and steelhead were caught in an inclined plane trap on a flow diversion from the main stream. This diversion channel is used for the operation of a spawning channel and as such maintains a stable flow regime. The numbers of fish caught during any time period represent a sample of the population migrating downstream.

Data presented in Fig. 2 are intended to indicate seasonal trends in downstream migration from January 1968 to December 1970. These data are not necessarily comparable from year to year, due to alteration in

Table 3. Winter collection of coho salmon and steelhead trout in Big Beef Creek - February 1969

	Age 0 coho	Age 0 steelhead	Age 1+ steelhead	Depth cm.	Location of blast
Pool 3400					
Number	2			122	Near undercut bank
Length	90 mm				
	65 mm				
Riffle 3350					
Number	0	0	0	20.3	Middle of riffle
Pool 3550					
Number		1	1	122	Middle of pool
Length		90 mm	119 mm		
Riffle 3750					
Number	0	0	0	12.7	Middle of riffle

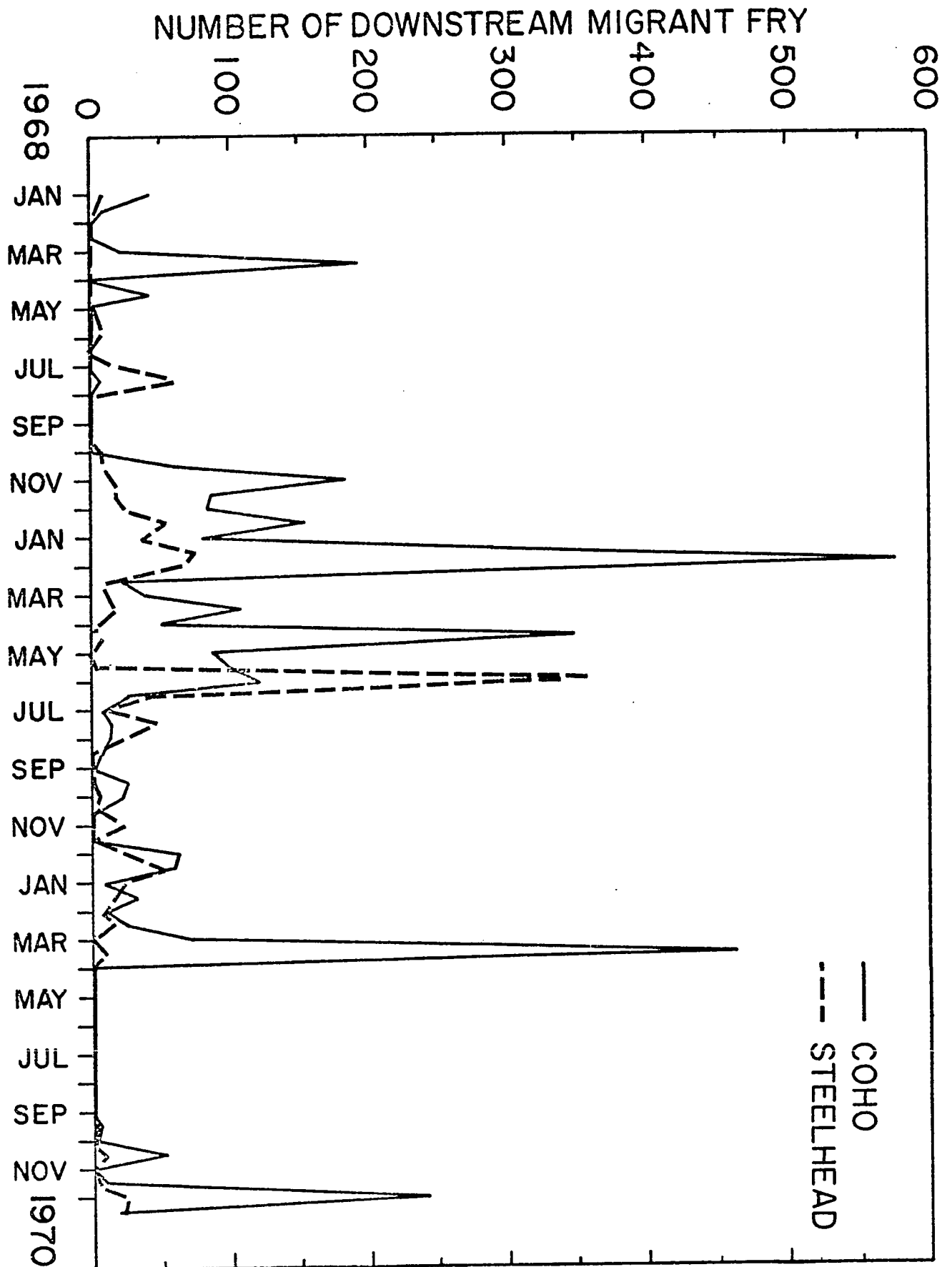


Fig. 2. Seasonal downstream migration of age 0 coho salmon and steelhead trout, January 1968 - December 1970.

stream channel hydrological characteristics immediately downstream of the intake structure, and alteration in discharge into the spawning channel diversion from year to year. Data collected from September 1968 to July 1969 are felt to be most consistent and reliable. Probably a minimum estimate of the total number of fish migrating downstream can be obtained by determining the proportion of discharge being diverted for spawning channel purposes from the total stream discharge. If this is done, using discharge figures for water-year 1970 (Table 2) and average spawning channel discharges, the proportion of the total streamflow taken is roughly 75% in November, 15% in December and January, and 23% in February. It is then possible to estimate the total out-migration, using the major peak in mid-February 1969 (Table 2) as an example. Given that the 770 coho migrants represented 23% of the out-migrants going down the channel, there was an estimated total population of 3,378 out-migrant coho at this time. In a similar way the major age 0 steelhead peak in February 1969 for the total stream can be estimated as 322. If these values are viewed relative to the total smolt production it can be shown that the out-migration during February alone represents from 5.2% to 12.7% of the range in coho smolt production, and 21.5% to 32.2% of the range in steelhead smolt production in Big Beef Creek.

For comparative purposes, the peak in numbers during the spring downstream movement of postemergent fry can be analyzed in a similar way (Fig. 2). The peak in the coho population occurred on May 1, when 346 fish were trapped. The steelhead fry peaked on June 15 at 358 fish. Since the flow in the main stream was dropping during this period, the

spawning channel diversion was taking an average of approximately one-half of the total discharge. Thus, assuming 50% of the fish were migrating in the main stream, and 50% of the fish were migrating in the diversion, the estimated number of total out-migrant coho and steelhead fry would be 692 and 716, respectively. Based upon these seasonal estimates of out-migration, which are admittedly subject to error, it can be seen that winter out-migration of coho and steelhead under-yearlings could have an impact upon stream production.

#### Home Pool Behavior

Experiments to ascertain the degree to which pool-dwelling salmonids exhibit a localized residential behavior were conducted in July 1969 in three stream pools, and in September 1970 in two of the same three study pools. Fish were seined from the study pools and marked. Recapture of fish from study pools was accomplished by seining, and fish in areas upstream and downstream from the study sites were examined by underwater observation (snorkeling). Data for age 0 coho indicate that at least 61.3% of those marked were present again either 4 or 10 days later (Table 4). Of those not present in the "home" pool, the largest percentage were accounted for only 10 feet away (upstream). One coho each from two different pools migrated upstream 800 to 600 feet, respectively.

Steelhead show habits similar to coho. If fish were captured at all they were either still within the same pool or they could all be accounted for within 10 ft upstream of the study pools. Of the total steelhead population originally marked in 1970, 85% to 88% were accounted for within 10 ft of the study pools. Numbers of age 1+ steelhead in the study pools were low, but 42 to 75% of them during 1969, and 50 to 73% in 1970, remained in or within 10 ft of the same pool.

Table 4. Mark-recapture data for coho salmon and steelhead trout in study pools in Big Beef Creek - July 1969 and September 1970

	Age 0 coho	% found	Age 0 steelhead	% found	Age 1+ steelhead	% found
JULY 1969						
MARKED IN POOL 3400						
Initial number	62		72		4	
Number 10 days later:						
Pool 3400	38	61	29	40	2	50
Pool 3410	8	74	11	55	1	75
Pool 4200	1	76				
JULY 1969						
MARKED IN POOL 3500						
Initial number	95		73		9	
Number 10 days later:						
Pool 3500	75	79	23	31	4	44
Pool 3510	1	80	1	33		
Pool 3800					1	55
Pool 4200	1	81				
JULY 1969						
MARKED IN POOL 4000						
Initial number	192		47		12	
Number 10 days later:						
Pool 4000	134	70	20	42	5	42
SEPTEMBER 1970						
MARKED IN POOL 3400						
Initial number	52		43		6	
Number 4 days later:						
Pool 3400	32	61	28	65	3	50
Pool 3410	9	79	10	88		
Pool 3500	2	83				
SEPTEMBER 1970						
MARKED IN POOL 3500						
Initial number	100		61		15	
Number 4 days later:						
Pool 3500	72	72	48	79	10	67
Pool 3510	16	88	4	85	1	73

When both years and pools are combined, differences between age 0 coho, age 0 steelhead, and age 1+ steelhead are minimized. That is, of the original population marked, 77% of the coho were accounted for, as compared to 70% for both the age 0 and age 1+ steelhead. This suggests that a pool population is rather stable in its composition.

### Spatial Requirements

Density. During the month of July, 1969, the spatial requirements of under-yearling coho and steelhead and over-yearling steelhead were determined in three study pools. These requirements, and with similar data taken in 1970 during the month of September, are shown in Table 5. Physical dimensions of the study pools are presented in Table 6. Densities of age 0 coho and age 0 steelhead are similar in the two years even though sampling dates between years were approximately two months apart and fish average sizes were different. In pool 3400 there were 2.30 coho/m<sup>2</sup> in 1969 and 2.31 coho/m<sup>2</sup> in 1970 while in pool 3500 there were 3.01 coho/m<sup>2</sup> in 1969 and 3.54 coho/m<sup>2</sup> in 1970 (Table 5). Age 0 steelhead density in pool 3400 was 2.62 steelhead/m<sup>2</sup> in 1969 and 2.40 steelhead/m<sup>2</sup> in 1970 compared to 2.38 steelhead/m<sup>2</sup> in 1969 and 2.18 steelhead/m<sup>2</sup> in 1970 in pool 3500.

Comparison of pool sizes from 1969 to 1970 indicates a diminution of actual physical space in 1970 (Table 6). Total numbers of coho and age 0 steelhead correspondingly went down in 1970, so that density figures for 1969 and 1970 in pools 3400 and 3500 were similar in the two years. A compensatory relationship between physical space and the number of coho and age 0 steelhead is apparent.

Table 5. Population characteristics of the resident population of coho salmon and steelhead trout in study pools in Big Beef Creek - July 1969 and September 1970

	Pool 3400		Pool 3500		Pool 4000	
	Age 0 coho	Age 1+ st	Age 0 coho	Age 1+ st	Age 0 coho	Age 1+ st
JULY 18, 1969						
Population number	64	73	105	82	218	71
Mean length	53.8	40.4	52.2	37.6	50.0	43.2
Mean weight	1.75	0.64	1.57	0.48	1.76	0.80
Total biomass	112.20	46.50	164.80	39.80	380.10	52.10
Percent of total	58.7	24.3	58.5	14.1	71.5	9.8
Density No/M <sup>2</sup>	2.30	2.62	3.05	2.38	3.13	1.02
Biomass Gms/M <sup>2</sup>	4.02	1.67	4.79	1.16	5.45	0.75
SEPTEMBER 16, 1970						
Population number	53	55	102	63	17	
Mean length	73.4	59.3	76.5	60.0	123.5	
Mean weight	3.80	2.45	4.11	2.52	9.87	
Total biomass	201.22	134.75	419.65	159.04	167.78	
Percent of total	51.3	34.3	56.2	21.3	22.5	
Density No/M <sup>2</sup>	2.31	2.40	3.54	2.18	0.59	
Biomass Gms/M <sup>2</sup>	8.78	5.88	14.56	5.52	5.82	

Table 6. Area and discharge data for study pools in Big Beef Creek - July 1969 and September 1970

	Area (M <sup>2</sup> )	Discharge (M <sup>3</sup> /Min)
7/18/69		
Pool 3400	27.87	7.14
Pool 3500	34.37	7.14
Pool 4000	69.68	7.14
9/16/70		
Pool 3400	22.92	5.95
Pool 3500	28.82	5.95

Differences between coho and age 0 steelhead are apparent if densities of fish per available space within years are observed. On the 1969 and 1970 sampling dates age 0 steelhead densities decreased with increasing pool size while coho densities increased.

The density of age 1+ steelhead increased as area of pool increased within 1969 and 1970. That is, in 1969, 0.14 steelhead/m<sup>2</sup> were present in pool 3400 and 0.29 steelhead/m<sup>2</sup> in pool 3500 while in 1970, 0.35 steelhead/m<sup>2</sup> were present in pool 3400 and 0.59 steelhead/m<sup>2</sup> in pool 3500. The larger pool 4000 in 1969 showed an intermediate density of 0.44 steelhead/m<sup>2</sup>.

Combining both species and all the age groups shows that in pool 3400 total densities in 1969 and 1970 were precisely the same, 5.06 fish/m<sup>2</sup>. In pool 3500 total densities were slightly higher (6.31 fish/m<sup>2</sup>) in 1970 than in 1969 (5.72 fish/m<sup>2</sup>). Pool 4000 yielded a density of 4.32 fish/m<sup>2</sup> in 1969, the lowest density of the three study pools. Based upon the previous discussion, the diminution in total density is explained by the fact that age 0 steelhead did not correspondingly increase with an increase in total area.

Biomass. Biomass has been calculated in Table 5 in two ways: total biomass present in the study pools, and relative biomass as a function of stream area. This represents another method of expressing carrying capacity, aside from absolute number, or relative number, as discussed in the preceding section.

Table 5 shows the percentage of the total fish biomass that consists of any one species and age class. Age 0 coho in pool 3400 for 1969 and 1970 made up 58.7 and 51.3% of the biomass, respectively, while in pool 3500 they made up 58.5% in 1969 and 56.2% in 1970. In pool 4000, with

the larger surface area, 71.5% of the total biomass was represented by coho in 1969. Age 0 steelhead in both years represented a smaller percentage of the total as pool size increased.

The value of expressing biomass as  $\text{gm}/\text{m}^2$  lies in the fact that areas of varying size may be compared within years and between years. If this is done, data from Table 5 indicate that a much greater biomass was elaborated by all species and age classes in 1970 than in 1969. This increase was apparent despite a decrease in area within pools 3400 and 3500 in 1970. Within each year apparent similarities in density, expressed as number of fish/ $\text{m}^2$ , disappeared when  $\text{gm}/\text{m}^2$  are taken into account. In pool 3400 in 1969, coho and steelhead relative numbers were 2.30 coho/ $\text{m}^2$  and 2.62 steelhead/ $\text{m}^2$ , respectively, while relative biomass estimates were 4.02  $\text{gm}/\text{m}^2$  for coho and 1.67  $\text{gm}/\text{m}^2$  for steelhead. The large numbers of age 0 steelhead in pool 3500 in 1969 gave higher numbers/ $\text{m}^2$  than age 1+ steelhead, 2.38 steelhead/ $\text{m}^2$  and 0.29 steelhead/ $\text{m}^2$ , respectively. However, when expressed as  $\text{gm}/\text{m}^2$ , the reverse was true as there were only 1.16  $\text{gm}/\text{m}^2$  of age 0 steelhead compared to 2.24  $\text{gm}/\text{m}^2$  of age 1+ steelhead.

### Discussion

#### Stream Seasonal Distribution Patterns of Coho and Steelhead

Postemergent coho fry were present in Big Beef Creek earlier than steelhead. However, utilization of habitat types overlapped in late spring and summer. Both coho and steelhead juveniles were found in pools. Diving observations indicated that coho were in the top of the water column and steelhead in the bottom. These observations on vertical

separation are supported by two independent food habit studies on coho and steelhead juveniles, one in British Columbia (Peterson, 1966), the second in Washington State (Johnston, 1967). Another study on spatial requirements of coho and steelhead in British Columbia (Fraser, 1969) showed the same relationship.

Hartman (1965), working with sympatric coho and steelhead populations in British Columbia, found coho juveniles in spring and summer in pools only and steelhead juveniles in riffles only. These specific and separate distributional patterns were hypothesized as being another verification of selective segregation. This mechanism has been postulated by Nilsson (1967) as explaining coexistence of closely related sympatric species of fish. Interactive segregation is the precursor of selective segregation and is exhibited among populations which have more recently come into contact with each other. Several recent studies with sympatric salmonid species have supported the concepts of selective segregation: Everest (1969) dealing with chinook salmon and steelhead juveniles in Idaho streams, and Lister and Genoe (1970) working with sympatric species of chinook salmon and coho salmon in Big Qualicum River, British Columbia.

Observations in Big Beef Creek during spring and summer showed that both species were present in transitional areas of habitat between riffles and pools, termed runs where depth and velocity were intermediate between riffles and pools. Within shallow fast riffles, steelhead were present alone. This evidence, then, seems contradictory in Hartman's work and creates the impression that coexistence in Big Beef Creek may be more recent and therefore would represent an example of interactive segregation.

In late fall and winter, both species occurred together in pools. This has been reported also in British Columbia by Hartman (1965). After the first series of freshets in late fall, and when stream temperature lowered, fish in Big Beef Creek exhibited what has been termed winter hiding behavior (Hartman, 1965). This same behavior has been shown to be temperature-dependent in Idaho streams (Chapman and Bjornn, 1969). There are two aspects of winter hiding behavior. One is the phenomenon of winter out-migration, toward the sea, and the other is actual hiding, either by burrowing in the substrate or by moving under stumps, undercut banks, log jams, etc. Hartman (1965) in his field studies observed no out-migration. Studies in Idaho on chinook salmon and steelhead trout documented downstream movement by both species (Edmundson, 1968; Everest, 1969). There seems to be a sequence of events with respect to winter hiding behavior. The first manifestation of this behavior is the downstream migration of coho and steelhead juveniles which is coincident with the first major series of winter freshets and, I speculate, a function of it. This behavior has not been reported previously in any of the Pacific coastal states from British Columbia to Oregon (Narver, personal communication; Hall, personal communication; Hartman, 1965; Salo, personal communication). I suspect that winter hydrological conditions are similar in these areas, if not worse than Hood Canal, Washington, so that what I observed in Big Beef Creek may represent a special circumstance. However, at Big Beef Creek, it represented from 5.2 to 12.3% of the coho smolt production and 21.5 to 32.2% of the steelhead smolt production. The annual smolt enumeration program is operated from the same trapping facility. In spring when the

total discharge of the main river is lower, a higher percentage of smolts is trapped than one would expect during the winter high discharge period. If anything, my estimates of winter out-migration are probably low. It seems that winter out-migration would be adaptive if winter hiding areas are limited in supply, as suggested by Chapman (1966). Streams which enter estuaries within Hood Canal can offer a temporary refuge over violent winter stream conditions. Salinity would not represent a barrier, since Hood Canal salinity ranges between 18-25 ppm, and the estuary proper would be less than this.

The other aspect of winter hiding behavior has to do with securing areas out of major current flow. This behavior has been reported to be illicited as water temperatures go down in fall and winter (Chapman and Bjornn, 1969). Chinook and steelhead juveniles in Idaho were observed to bury themselves in the gravel (Edmundson, 1968; Everest, 1969). Due to streambed instability during this season, the adaptive value of this behavior is questionable, in my opinion. I searched for fish in the substrate during the winter while diving and found none in the areas sampled. Fish were seen under roots and stumps in small numbers. Dynamite was used on one occasion to attempt to capture over-wintering salmonids. The only fish captured were in pools. Two coho were obtained from pool 3400 which, during summer low flow, had 141 individual salmonids present.

If winter hiding places are in limited supply, and downstream winter emigration is a result of lack of available spaces for refuge, then this may be a factor operating additively with a food-space complex

during summer to limit stream production (Chapman, 1966). Certainly the availability of winter hiding places would seem to be directly proportional to the degree of stability of the stream. Therefore, salmonids in streams which were geologically young and dynamic, or in streams under the influence of land use activities, might be expected to show winter emigration to a greater extent than those in stable streams.

That populations of salmonids show some degree of permanence of residence and stability within pools and are not randomly associated with an area of space has been shown in Big Beef Creek. The evidence showed that 77% of the coho and 70% of the two age groups of steelhead remained within their home pool. This supports the contention that there is directional site specific behavior similar to but different from the strict territoriality found in riffle environments. Edmundson (1968) has described territorial behavior in summer and winter for chinook salmon and steelhead trout juveniles in Idaho streams as well. Numerous other studies on brook trout (Shetter, 1937), brown trout (Schuck, 1945), cutthroat trout (Miller, 1957), and Atlantic salmon (Saunders and Gee, 1964) have reported on some degree of permanent association with a home area during their stream life history.

Data collected from the same two study pools in Big Beef Creek over two years during summer low flow suggest that, while densities in terms of relative numbers of fish per unit of stream area were quite similar, biomass elaborated was at least two times greater in 1970 than 1969. Fish were larger in 1970 by virtue of growth between the July sampling date and the September one, but stream discharge was lower in 1970 and available pool space was less. These physical parameters should predict

a lowered carrying capacity as Smoker's (1955) predictions of smolt production versus stream flows would indicate. Chapman (1966) has postulated a food-space complex as regulating populations of salmonids in streams, and this would therefore lead to the conclusion that a greater abundance of food may have been available during the 1970 season. It is also possible that differential recruitment of fry occurred in 1969 and 1970, and Big Beef Creek was below carrying capacity in 1969. This was suggested by Burns (1971), working in California streams where carrying capacity varied from year to year and was attributed to differential fry recruitment. The natural stream environment represents a complex of physical and biological parameters which are difficult to isolate and not possible to control for intensive study. Therefore, I developed an experimental stream system which would attempt to simulate the wild environment and yet allow manipulation of relevant biological parameters. This is described in the next section.

PART 2. ROLE OF PRIOR RESIDENCE ON THE SOCIAL BEHAVIOR AND  
POPULATION ECOLOGY OF COHO SALMON AND STEELHEAD TROUT  
IN THE EXPERIMENTAL STREAM SYSTEM

Description of the Experimental Stream

In designing the experimental stream, my purpose was to develop a natural system that would encompass the three factors discussed in the Introduction. I wanted an experimental system that would provide volitional residence, natural feeding, and be capable of maintaining fish for extended periods. In order to provide replication of experimental results, I designed two separate and parallel stream systems.

Each of these systems had at their upstream end a large major pool habitat connected to a stream channel habitat (Fig. 3). The pool habitats were 4.6 m in diameter and 0.8 m in depth, with a surface area of 53.9 m<sup>2</sup>. Four 30.5 cm windows were located equidistantly around the circumference of the pools. The bottom of each pool was covered with 5 cm of graded gravel, varying from 1.6 cm to 32 cm in diameter. Water flowed out of the pools into head troughs which supplied water to the stream channels. These stream channels were situated in parallel with an area between them for an observer. Their design was modified after the one developed by Chapman (1962) and Mason (1966). The channels were 4.6 m long, 0.9 m wide, and 0.6 m high, with a surface area of 4.2 m<sup>2</sup>. Four windows, 91.0 cm long and 30.0 cm high were situated along the inside wall of the stream channels. When the channels were divided into riffle and pool microhabitats, the first two upstream sections were riffle and the last two were pools. Riffles were created by adding greater amounts of graded gravel (1.6 cm to 3.2 cm in diameter) to those sections. Within

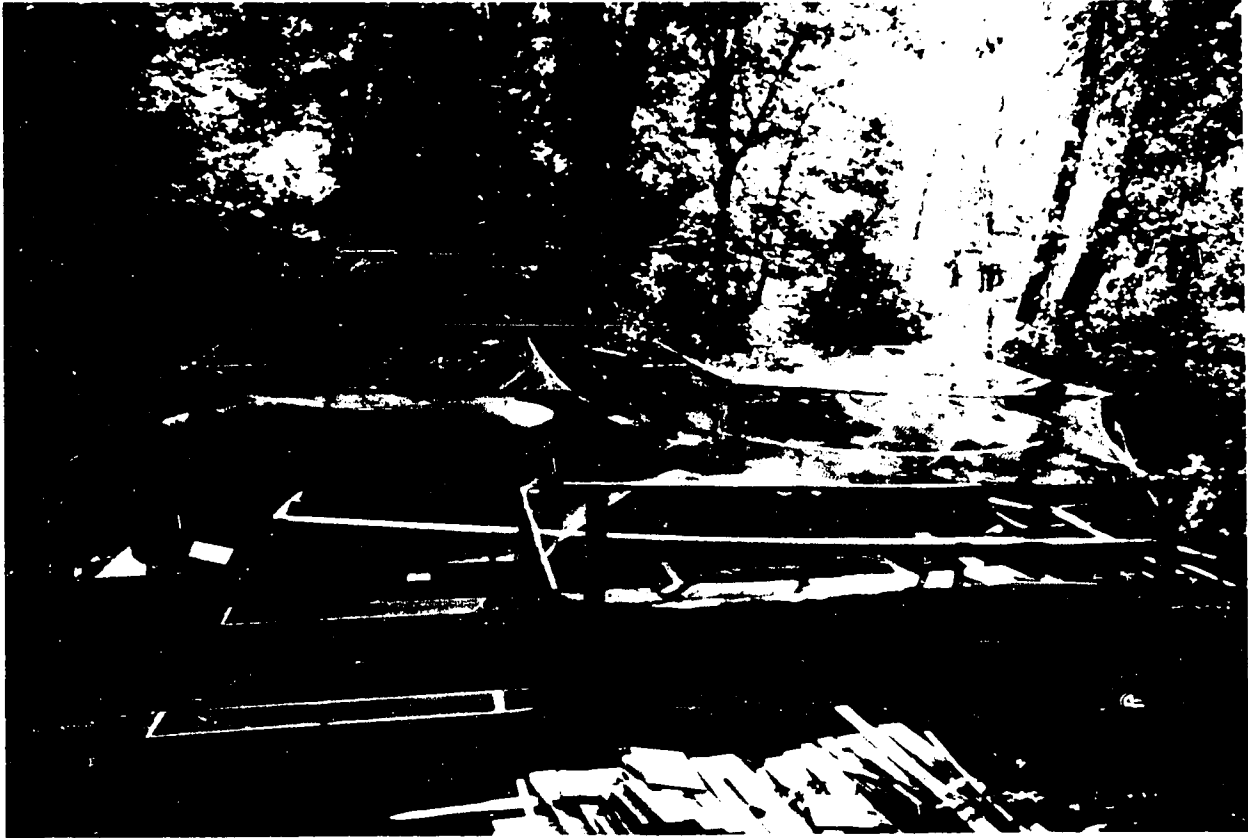


Fig. 3. Paired experimental stream system with central observation station.

each channel, the depth of the water in the riffles varied from 6.5 to 11.3 cm, while that in the pools varied from 29.3 to 35.4 cm. Velocities over the riffle ranged from 2.1 to 13.6 cm/sec., and those on the surface of the pool ranged between 0.8 and 5.4 cm/sec. A screened trough was located at the outflow of each channel. The total discharge from each system was 247.2 l/min. Water was obtained from an intake dam located on a spring. A four-inch plastic pipe delivered the water to the stream system 48.8 m from the intake facility. Two valves regulated the flow so as to provide equal flow to each stream system. During each experiment, thermographic records were kept on a daily basis, and their mean values ranged from 8.3 C to 11.3 C.

#### Evaluation of the Experimental System

Food Supply. In order to establish that the experimental stream system received comparable natural food, plankton nets were placed at the inlet of systems 1 and 2 and at the inlet of stream channels 1 and 2. Both sampling sites were monitored at dawn, mid-day, dusk, and midnight every two weeks for varying lengths of time. Samples taken at the inlet of systems 1 and 2 (i.e., before the water entered the large pools) were taken during the fall of 1969. Samples taken at the inlet of the stream channels were taken during the summer of 1970. All samples were taken while experiments were in progress.

There was a difference in the abundance of organisms in the invertebrate drift of the inlet of systems 1 and 2 over the entire sampling period; there were 1,194 in system 1 and 1,402 in system 2 ( $\chi^2 = 16.6$   $P < .05$ ). However, the significant difference in numbers

occurred primarily in the last sampling period, December 11, 1969 (Fig. 4). The most abundant taxon was larval Tendipedidae which were slightly more abundant in system 2 than in system 1 ( $\chi^2 = 4.4$   $P < .05$ ) (Fig. 5).

There was a definite temporal pattern in drift abundance during the fall sampling period (Fig. 6). Similar trends were seen for drift entering pool 1 and pool 2. Peak abundance occurred between sunset and midnight, while the period of lowest abundance was between sunrise and sunset. Of the drift entering pool 2, a secondary peak of abundance very close magnitude to the first occurred during the period from midnight to sunrise. This same period in pool 1 yielded a lower number of organisms than the corresponding period from mid-day to sunset. In general then, during this fall-winter sampling period, the numerical abundance of invertebrate drift was greatest from sunset to midnight.

Monitoring of the drift abundance coming into the stream channel portion, the lower part of the system, indicated that an equal quantity was entering stream channel 1 and channel 2 during the summer sampling period. The total number of organisms enumerated per 15-min sample for the sampling dates was 478 in channel 1 and 468 in channel 2. The most abundant component numerically in the drift was Tendipedidae followed by Ephemeroptera and Plecoptera (Fig. 7). Figure 8 illustrates the temporal pattern of drift abundance. The period of lowest abundance was found between sunrise and mid-day, while the highest abundance occurred between sunset and midnight. The period from midnight to sunrise was the next highest in abundance.

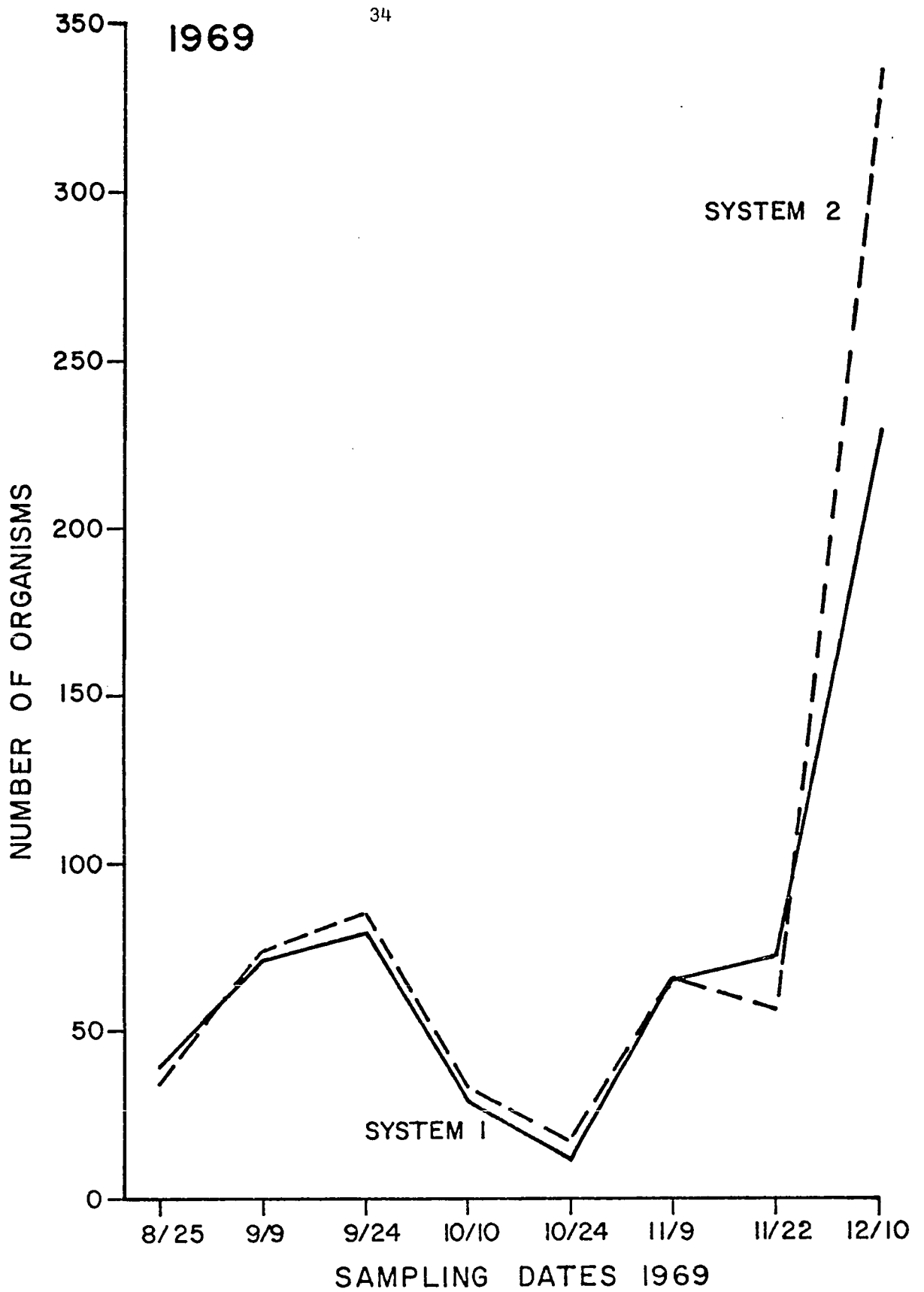


Fig. 4. Abundance of drifting invertebrates taken from the inlet of systems 1 and 2 by sampling dates, September 1969 - December 1969.

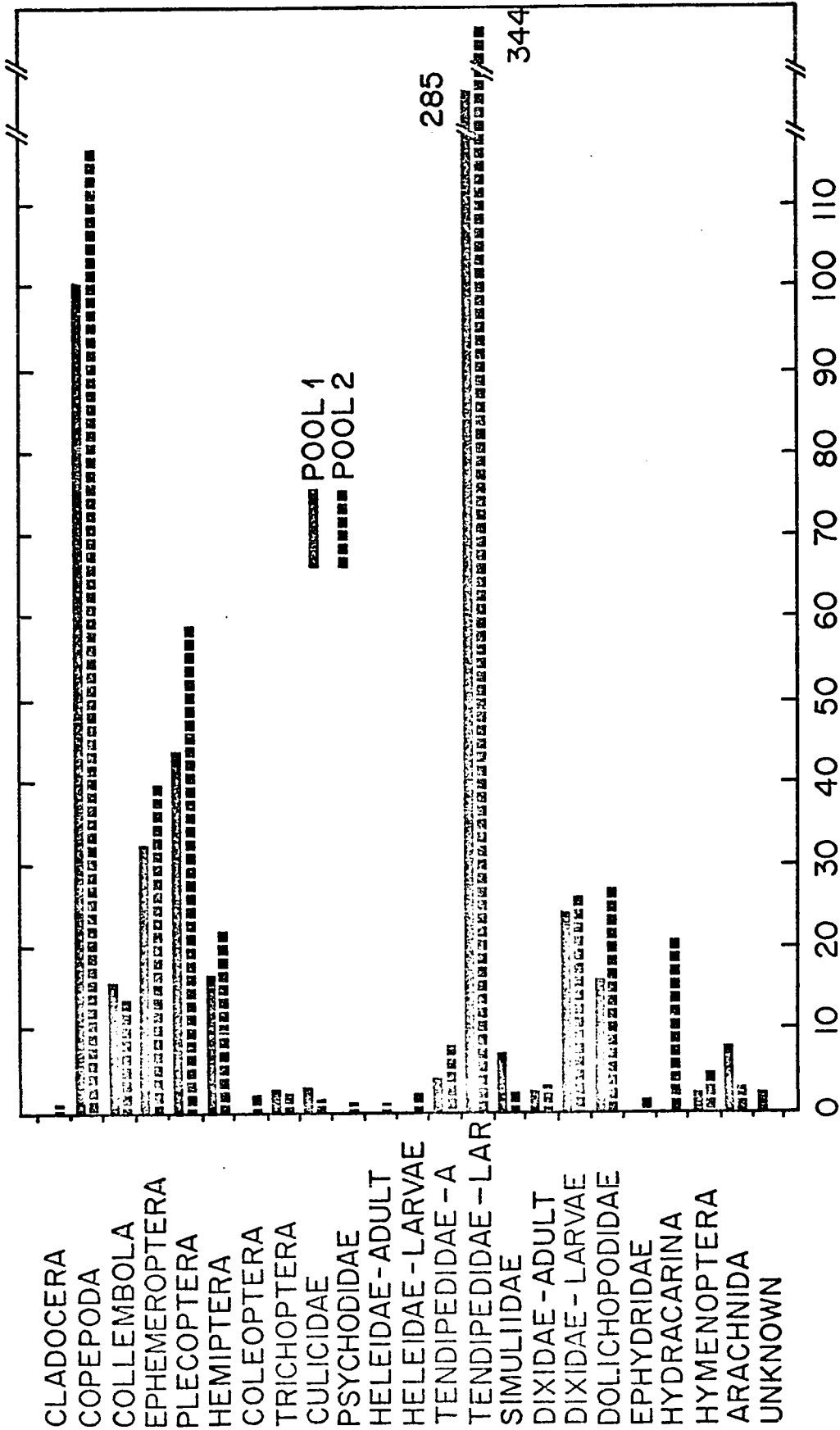


Fig. 5. Numerical abundance of major taxa in the invertebrate drift taken from the inlet of systems 1 and 2, September 1969-December 1969.

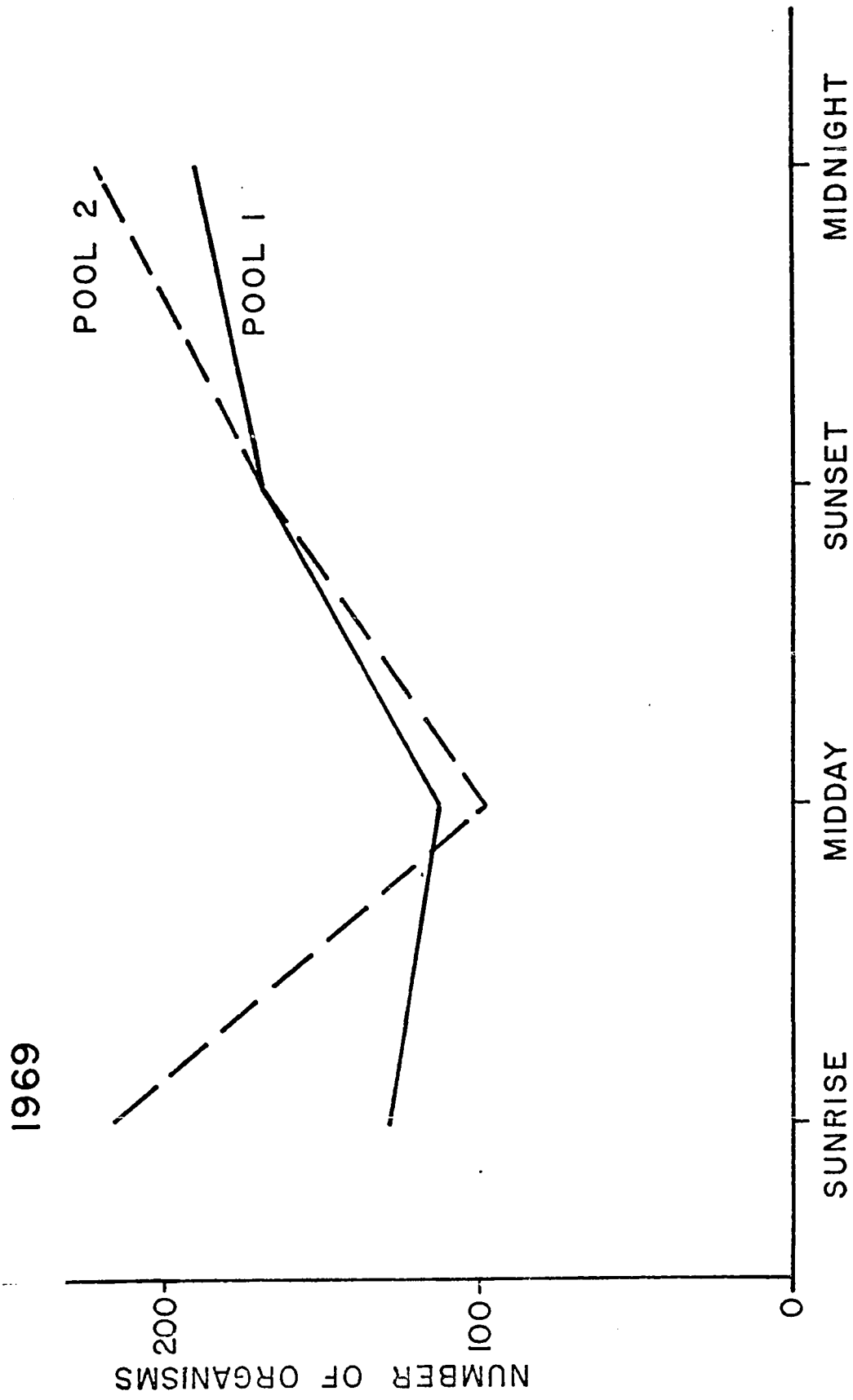


Fig. 6. Diel periodicity of invertebrate drift from the inlet of systems 1 and 2, September 1969 - December 1969.

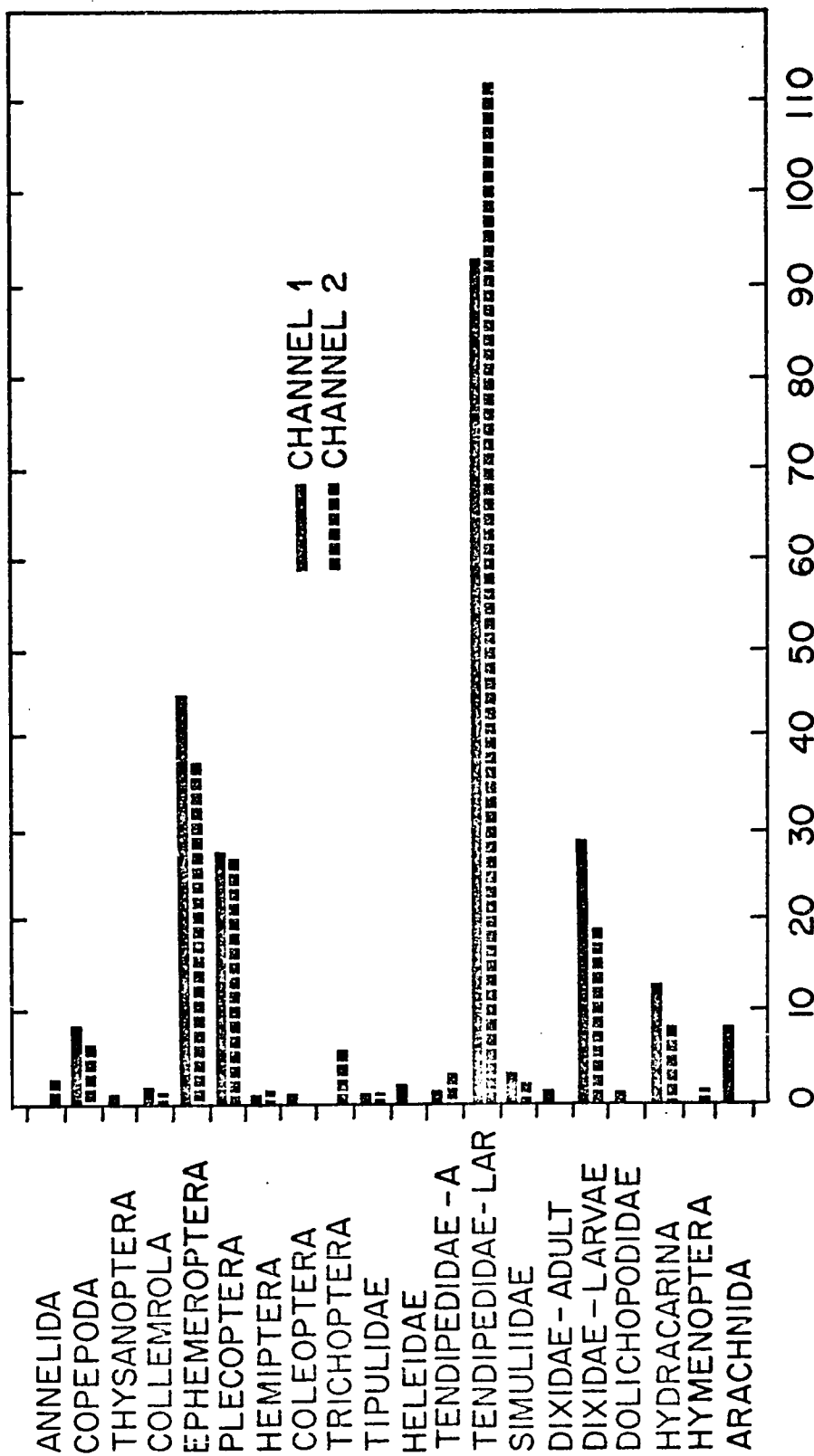


Fig. 7. Numerical abundance of major taxa in the invertebrate drift taken from the inlet of stream channel 1 and 2, September 1969 - December 1969.

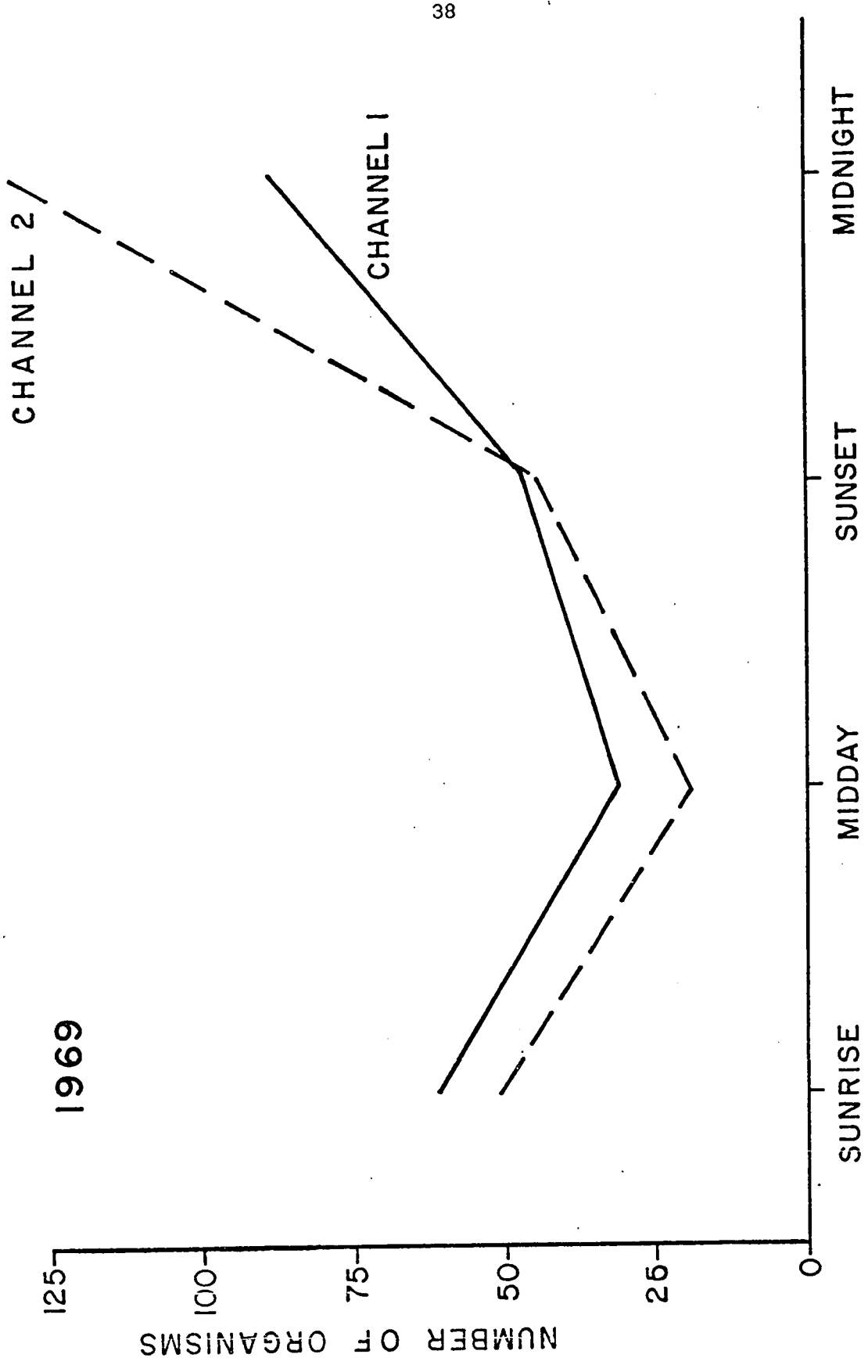


Fig. 8. Diel periodicity of invertebrate drift from the inlet of stream channel 1 and 2, September 1969 - December 1969.

Effects of Handling. In order to determine the effect of handling and to investigate the replicate nature of the experimental pool system, two techniques of introducing fish into a barren environment were tried. One technique most closely approximated the natural system in a stream. That is, emergence from the gravel and subsequent development of residential behavior. The other was planting postemergent fry by hand into a barren pool environment with the resultant development of residence. On March 9, 1968, 2,400 coho alevins were planted in gravel troughs located above experimental pool 2. These fish began to emigrate on March 29, 1968, and a total of 777 coho fry emigrated during the 42-day duration of the experiment. The total number of residents present at the end of the experiment, April 10, 1968, was 144. Those fish which emigrated from pool 2 were introduced into pool 1 on March 14, 1968, which was until then without fish. A total of 540 coho fry were planted, and 27 days later on April 10, 1968, 146 coho were left. There was no significant difference between the final population present in pool 1 or pool 2, in spite of the very different planting procedures used. If handling of fish caused them to behaviorally react in an abnormal manner, one would expect to find a significant difference in the number of final residents.

In experiment No. 4, March 31, 1970-June 1, 1970, during each of the three emigration periods the temporal pattern of emigration was monitored. Figure 9 illustrates this pattern in the first emigration period, March 31 to April 14, and shows that while there were differences in abundance of emigrants the peak always occurred after dusk and before midnight for both species in both systems. Given this relationship the

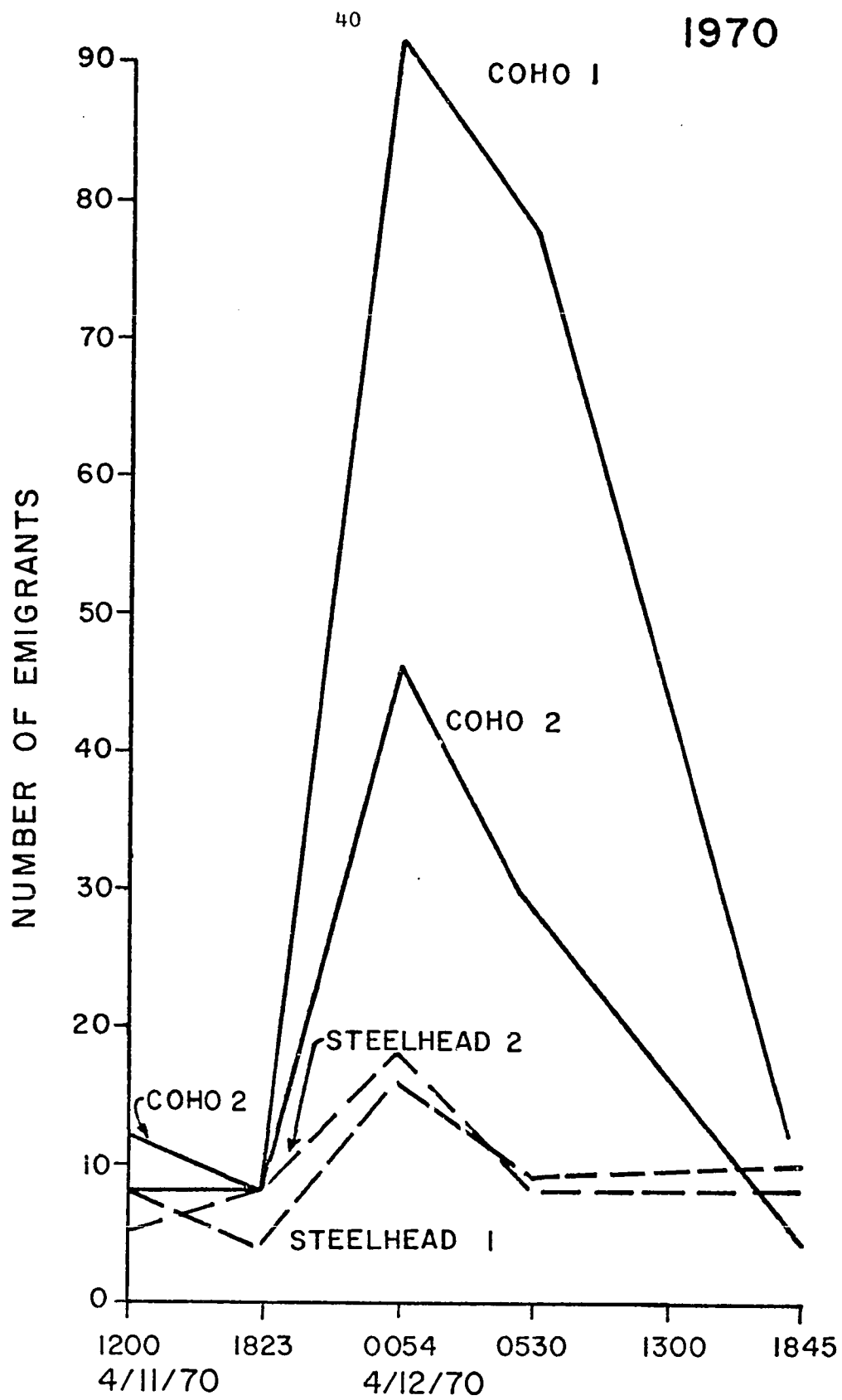


Fig. 9. Diel periodicity of coho salmon and steelhead trout emigration from the experimental stream system 1, March 31 - April 14, 1970.

number of emigrants was sampled hourly after sunset during the second emigration period April 15 to May 16. The first peak of abundance of emigrants occurred generally some time prior to sunset (1915 hours) and after early morning. But since no specific hour of abundance can be indicated the major emigration could have occurred anytime during this period. The main period of intensive sampling, hourly after sunset, indicated a major peak of abundance of emigrants between the hours of 2015 and 2115 for both species in both systems (Figs. 10 and 11). This peak of abundance was observed on the first day and at the same time on the second day. Another small peak of abundance which occurred during 0015 and 0830 hours was also evidenced (Figs. 10 and 11). During the third emigration period, May 17 to June 1, where steelhead were the principal emigrants, the major peak of abundance occurred between 2100 and 0100 hours (Fig. 12). A secondary peak of abundance occurred between 0900 and 1530 hours. However, this period of time was also associated with high turbidities due to heavy precipitation.

Based upon the pattern of diel emigration illustrated by these four figures it appears that the peak of emigration occurred after sunset and before midnight, probably initiated approximately one hour after dusk.

Moreover, if fish were seriously stressed upon initial introduction into the system, they would be assumed to exhibit a random type emigration response and not a directional behavioral pattern. The figures (Figs. 10, 11, and 12) on diel periodicity of emigrating coho and steelhead after introduction into the experimental stream system indicated that emigration of fish that were recently introduced occurred principally

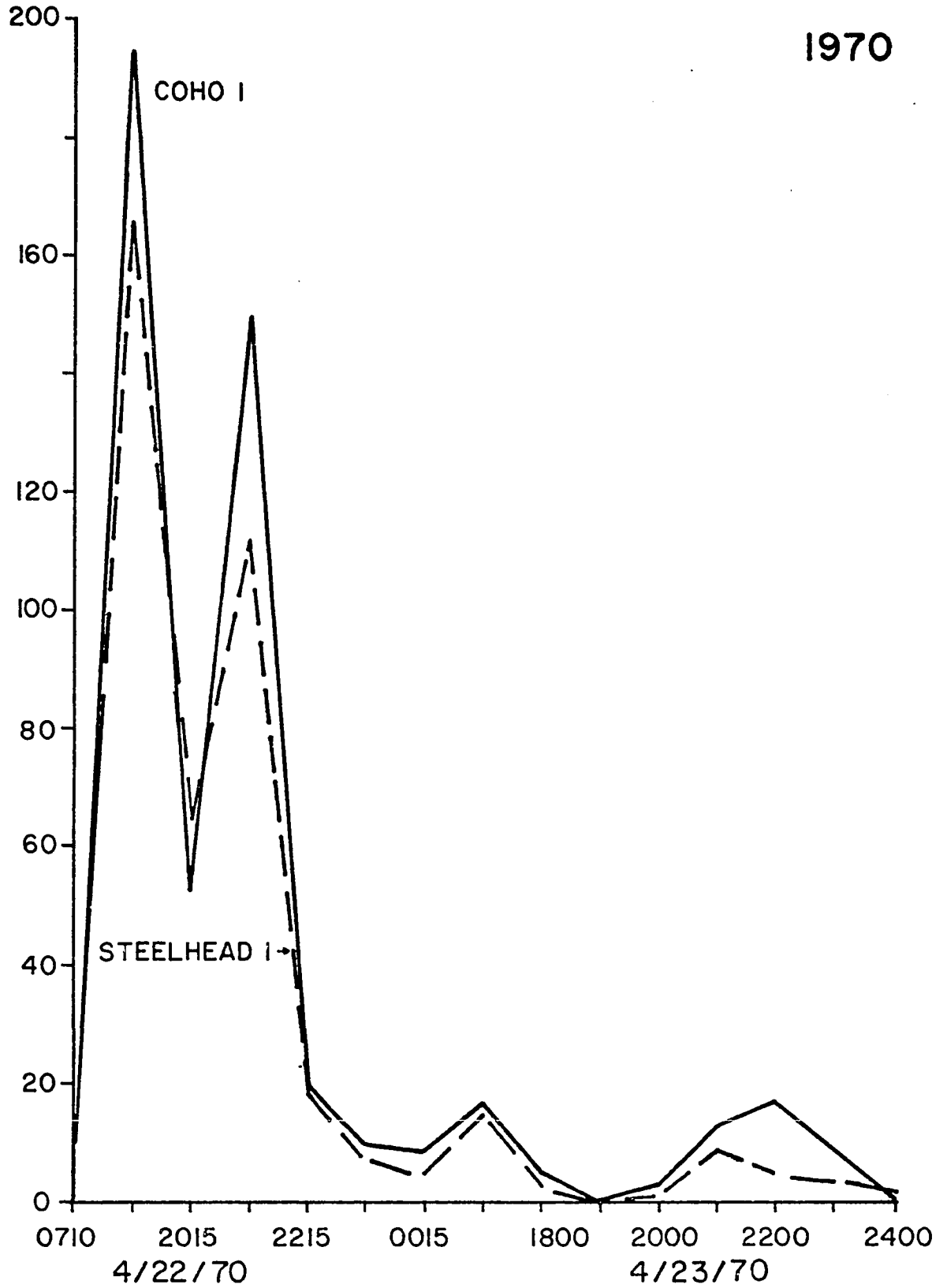


Fig. 10. Diel periodicity of coho salmon and steelhead trout emigration from experimental stream system 1, April 15 - May 16, 1970.

1970

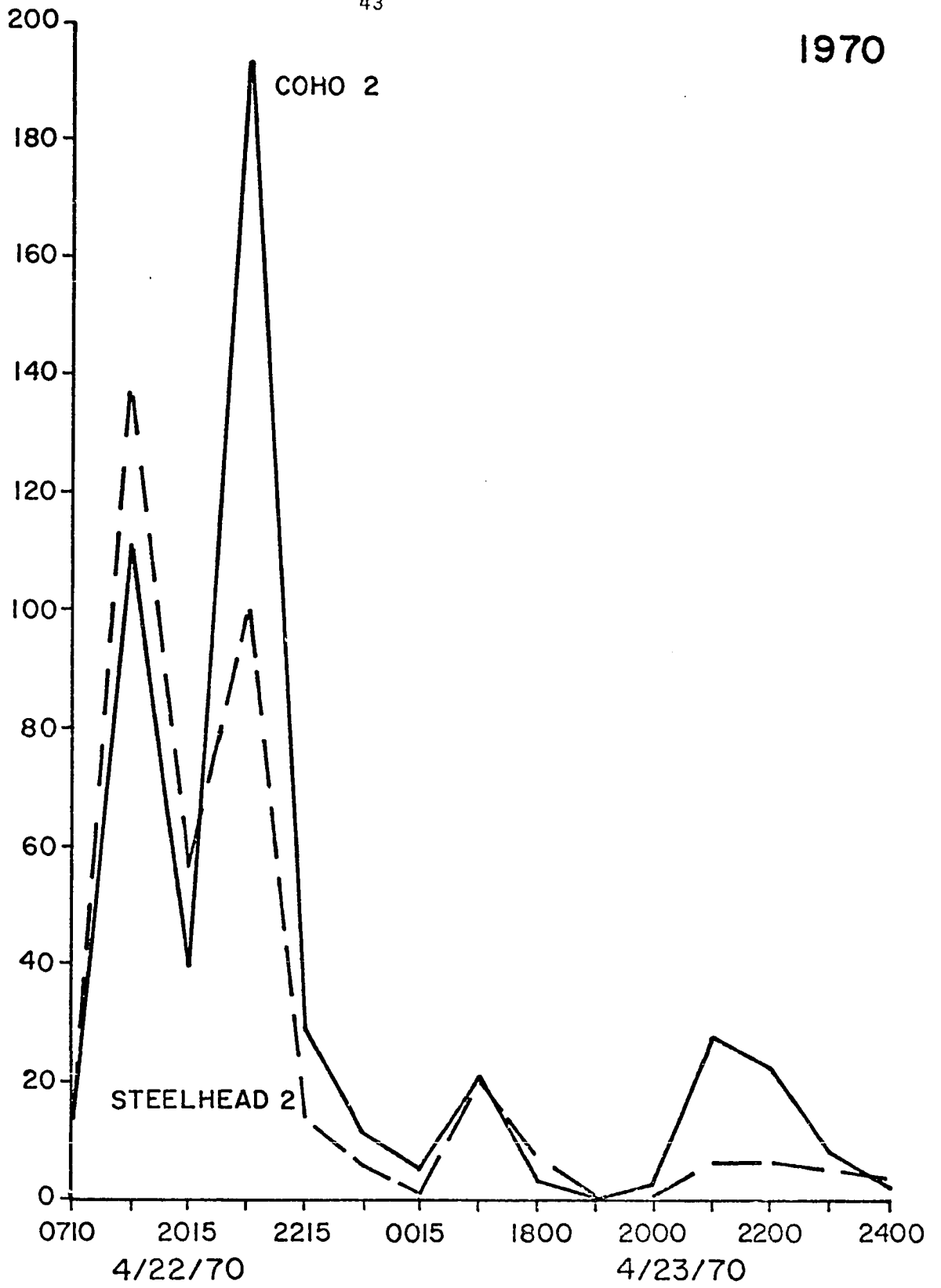


Fig. 11. Diel periodicity of coho salmon and steelhead trout emigration from experimental stream system 2, April 15 - May 16, 1970.

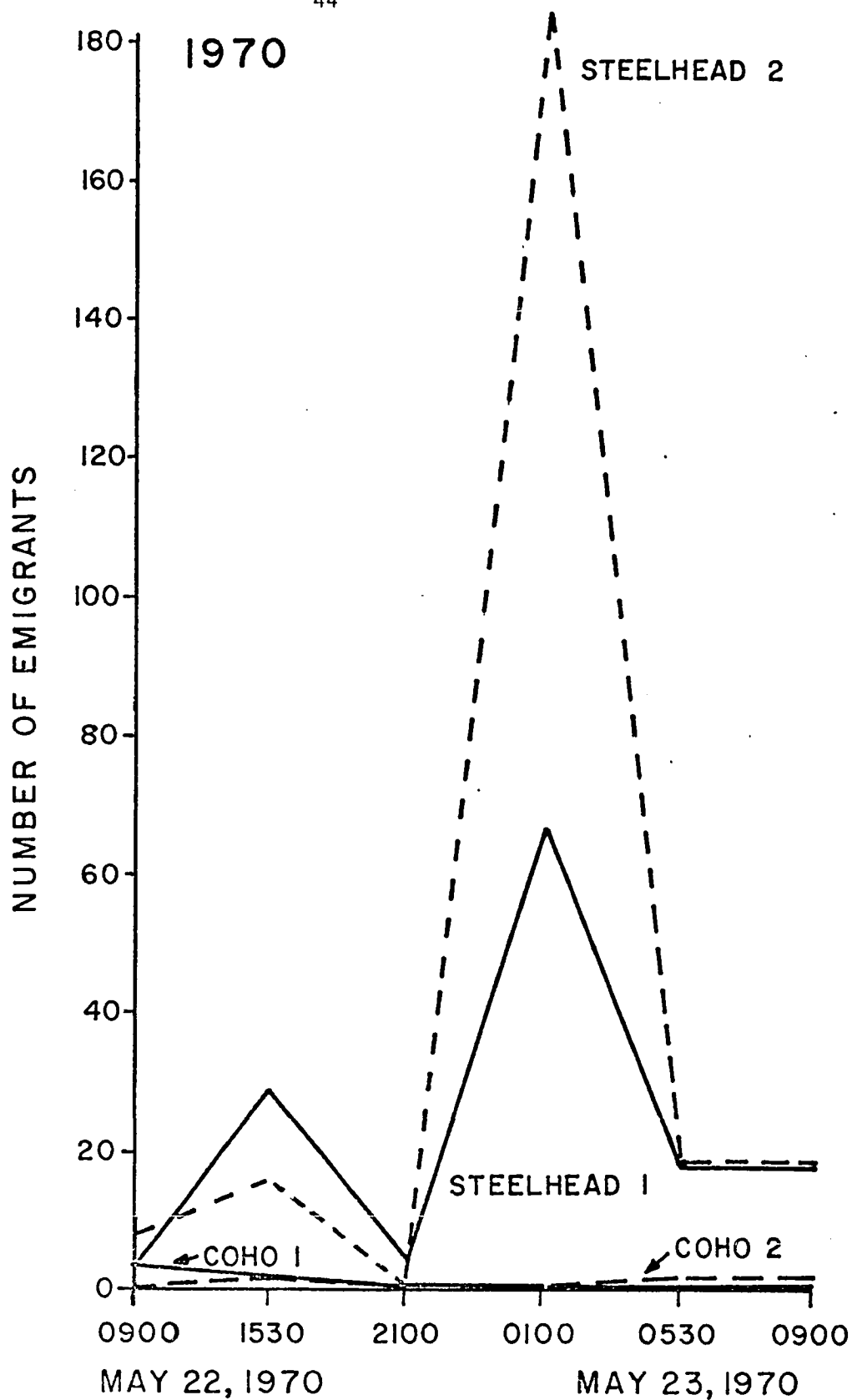


Fig. 12. Diel periodicity of coho salmon and steelhead trout emigration from the experimental stream system 2, May 17 - June 1, 1970.

under cover of darkness. I believe that a fish which was seriously affected by handling or artificiality of environment would not show such a directional response and certainly not one that would be the same between system 1 and 2. Furthermore, the fact that they became residents, maintained and defended territories, and fed normally indicated general adaptability and sense of opportunism that a fish can employ. The fact that fish will maintain residence when introduced into a barren stream environment was first shown by Chapman (1962) in both natural and experimental stream channels.

Replicate Nature of the Experimental System. On March 11, 1969, 1,152 coho fry were introduced into pool 1. They were forced to remain in this environment for 12 days before being allowed to migrate throughout the system. On March 25, 1969, after the system had been open two days, an additional 419 coho fry were added. After 27 days the experiment was terminated (April 7, 1969) at which time 284 coho comprised the resident population. Total biomass was 105.08 gm, and the average fish length was 38.0 mm.

On March 27, 1969, 1,100 coho fry were introduced into pool 2, and they were denied the ability to emigrate for 3 days. After 11 days, the final population numbered 290 at an average length of 37.1 mm and a total biomass of 107.01 gm. No significant difference in terms of final resident number per pool was found. It is also apparent that the total amount of biomass supported by the two experimental pools was very similar. Therefore, I conclude that different length of retention of fry in the pools before emigration was allowed did not affect the final resident populations of either pool 1 or pool 2.

### Experimental Methods

Each experiment was begun with a barren experimental stream. Fish were introduced into the major pool habitat and confined there by screening the outlet for 48 hours. The first group of fish to emigrate from the system after the initial period of acclimatization was subsequently returned to the pool habitat. Thereafter, fish were free to leave the entire system so that volitional residence was maintained. Fish could not migrate upstream from the stream channel habitat to the pool habitat.

Presumably, the final population within the habitat types of the stream system was a manifestation of habitat preference of each species and a balance between space available and abundance of available food. Food and space are inter-related to the extent that if food availability is high, density of fish occupying that space will be high, and vice versa (Chapman, 1966). That is, fish will tolerate larger numbers of other fish if food is readily available. Thus, an equilibrium state was achieved in the final resident population.

The emigrant trapping facility was sampled daily, and all fish were counted and sampled for length and weight. At the termination of each experiment, flow was interrupted and all fish were seined and netted from each major habitat type, pool, and stream channel. These fish were counted and sampled for length and weight.

No artificial feeding regime was imposed upon the fish within the experimental stream. Only natural drift-borne and benthic invertebrates were available as potential food items.

Observations of behavior were carried out from a darkened central observation area between the two stream channels. Observations on

horizontal distribution refer to the relative incidence of fish in either riffle or pool microhabitat during observation periods taken at random times throughout the day. Vertical distribution is defined as the relative incidence of one species being in the top half of the window at the pool microhabitat versus those in the bottom half of the window. Agonistic behavior is specifically defined as overt action in which a fish may charge one of its own species, or that of another species, with mouth open, and bite or make contact. This act is expressed as a "nip" and was described for coho salmon by Hoar (1951). The total number of nips observed during five minutes of observation time was documented for both intraspecific encounters (within species) and interspecific encounters (between species). These observations were taken at random times throughout the day during the course of an experiment.

All fish used in the experiments were either artificially spawned and incubated in the laboratory or were seined from Big Beef Creek as fry. Hatchery fish used were obtained either from Minter Creek Hatchery (coho) or Chambers Creek Hatchery (steelhead).

Both instantaneous growth and annual survival rates (Ricker, 1958) were computed for each species so that differences in length of residence for each species could be taken into account. Growth and survival can then be compared. Due to the nature of the experiment fish were only sampled for length and weight at the beginning and end of the experiment. Therefore, these rates must be qualified since they only represent two data points. The purpose of these computations is only for a comparison of gross trends in growth and survival for each species and not to precisely reflect short-term changes.

EXPERIMENT NO. 1. SIMULATION OF THE NATURAL EMERGENCE PATTERN  
WITH POSTEMERGENT COHO FRY AS PRIOR RESIDENTS  
IN THE EXPERIMENTAL STREAM SYSTEM

Procedures

In order to most closely approach the temporal pattern of fry emergence in the natural stream environment, postemergent coho fry were introduced into the barren experimental stream first. Postemergent steelhead fry were introduced 22 days later into this same environment now occupied by the coho. Both species were incubated in the laboratory and were the progeny of wild Big Beef Creek stock.

During this experiment, the stream channel was composed of a series of two upstream riffles, followed by two downstream pools, such that the stream channel was divided equally on an area basis into riffle and pool microhabitats. Mean riffle depths in channel 1 ranged from 8.6 to 11.3 cm, while those in channel 2 ranged from 8.9 to 10.7 cm. Mean riffle velocities ranged from 2.1 to 5.5 cm/sec in channel 1 to 1.8 to 4.7 cm/sec in channel 2. Within the pool microhabitat of channel 1, mean depths ranged from 31.0 to 31.3 cm, while those in channel 2 measured 30.3 to 30.4 cm. Mean surface velocities varied from 0.8 to 1.8 cm/sec in channel 1, compared with 0.3 to 1.3 cm/sec in channel 2. Mean bottom velocities were less than 0.2 cm/sec in channel 1 and less than 0.13 cm/sec in channel 2. The temperature during the course of the experiment varied from 9.5 to 13.3 C, with a mean value of 11.0 C.

## Results

### Characteristics of the Resident Population

Final Number. An initial population of 800 coho was introduced into system 1 and the same number in system 2, followed 22 days later by the introduction of 1,000 steelhead fry into each system. After a period of 95 days of residence for coho and 74 days for steelhead, more coho than steelhead occupied the pool environment in each system

$$(\chi_{P_1}^2 = 42.4 \text{ P} < .05, \chi_{P_2}^2 = 13.8 \text{ P} < .05).$$

Considerably more coho and steelhead were found in the pool habitat than in the stream channel habitat (Table 7). The final population of coho in pool 1 was greater than in pool 2 ( $\chi^2 = 11.5 \text{ P} < .05$ ). Pools 1 and 2 supported an equal number of steelhead ( $\chi^2 = 1 \text{ P} > .05$ ).

The final population of coho and steelhead in both channels was essentially equivalent ( $\chi_1^2$  coho and st. = 2.6,  $\text{P} > .05$ ,  $\chi_2^2$  coho and st. = 0.2,  $\text{P} > .05$ ,  $\chi_1^2$  and 2 coho = 0.3,  $\text{P} > .05$ ,  $\chi_1^2$  and 2 st. = 0.4  $\text{P} > .05$ ).

Biomass. The initial total biomass of both species was similar in system 1 and system 2 (Table 7). Final biomass, considering the entire experimental stream as one production unit, was also similar, 142.80 gm in system 1 and 134.50 gm in system 2. In pool 1 there were 126.80 gm of fish, and in pool 2 122.65 gm. Pool 1 supported a slightly greater coho biomass (88.25 gm) than pool 2 (79.20 gm), whereas pool 2 supported a slightly larger steelhead biomass (43.45 gm) compared to 38.55 gm in pool 1. Coho contributed approximately 69% of the biomass in pool 1 and

Table 7. Population characteristics of the resident population of coho salmon and steelhead trout in the experimental stream system - May 1969-August 1969  
 [coho were planted May 16 and steelhead June 1]

	Pool 1		Channel 1		Pool 2		Channel 2	
	Coho	Steelhead	Coho	Steelhead	Coho	Steelhead	Coho	Steelhead
Initial population number	800	1000			800	1000		
Final population number	129	57	5	14	80	52	7	11
Number of emigrants	482	745			551	774		
Percent emigration	54.77	68.98			62.61	71.67		
Initial mean length (mm)	33.4	32.4			33.4	32.2		
Final mean length	39.8	40.8	51.4	40.1	45.9	43.6	41.1	41.9
Instantaneous growth rate	0.682	1.201	1.677	1.110	1.237	1.498	0.807	1.291
Initial mean weight (gms)	0.27	0.24			0.26	0.24		
Final mean weight	0.68	0.68	1.18	0.72	0.99	0.83	0.81	0.73
Instantaneous growth rate	3.675	5.459	5.797	5.795	5.143	6.515	4.348	5.794
Survival	0.395	0.340			0.445	0.301		
Final total biomass	88.25	38.55	5.90	10.10	79.20	43.45	5.65	6.20
Percent of total	69.60	30.40	36.87	63.13	64.57	35.43	47.68	52.32
Initial density No/M <sup>2</sup>	14.85	18.57			14.85	18.57		
Final density No/M <sup>2</sup>	2.39	1.06	1.20	3.36	1.48	0.96	1.68	2.63
Initial biomass Gms/M <sup>2</sup>	3.95	4.39			3.91	4.44		
Final biomass Gms/M <sup>2</sup>	1.64	0.72	1.42	2.43	1.47	0.81	1.35	1.92

64% in pool 2. The steelhead, therefore, contributed roughly one-third of the biomass in both pools.

In the stream channels, steelhead contributed about 63% of the total biomass in stream channel 1 and 52% in channel 2. While steelhead were somewhat smaller in channel 1 they were also more abundant and thus produced more total biomass. The total coho biomass was approximately the same in channels 1 and 2.

Because the total biomass supported in both experimental systems was essentially the same, it is felt that this testifies to their replicate nature, given similar initial populations and a similar stocking regime.

Density. Density may be defined as number/unit space, or biomass/unit space, and in either case is assumed to express something about the spatial preferences of fish in a particular habitat type. Just as with absolute number and absolute biomass, the capacity of an environment or habitat type to support a given species may be better reflected in relative biomass or gm/unit space.

In pool 2, there were fewer coho/m<sup>2</sup> than in channel 2, but a greater weight (gm/m<sup>2</sup>) of coho was supported in the pool habitat (Table 7). Whether expressed as gm/m<sup>2</sup> or number/m<sup>2</sup>, more steelhead were supported in a channel habitat composed of 50% pool and 50% riffle than in a strictly pool habitat.

Growth. The initial lengths of coho and steelhead in systems 1 and 2 were essentially the same (Table 7). Coho average weights of 0.27 gm and 0.26 gm for pools 1 and 2, respectively, were somewhat heavier than steelhead at 0.24 gm each. The final resident population in pool 1 was

composed of coho and steelhead of equal size, contrary to pool 2 where coho were larger in both length and weight.

Instantaneous growth rates for length and weight of steelhead fry in pools 1 and 2 were higher than companion coho fry (Table 7). Coho and steelhead had better rates of growth for length and weight in pool 2 than in pool 1 (Table 7). Steelhead in pool 2 showed the highest growth rate of any fish in either habitat type (Table 7).

In the stream channel environment, coho in channel 1 were the largest fish in length (51.4 mm) and weight (1.18 gm) of either species in the pool or riffle environment. Both species in channel 2 were smaller than their companion pool 2 population. Steelhead in channel 1 were roughly the same size as pool 1 coho and steelhead, and were similar in size to channel 2 steelhead.

Growth rates for length and weight were higher for fish in channel 1 than pool 1 except for channel 1 steelhead length which was almost equal to pool 1 steelhead length. Comparable growth rates were lower for length and weight for fish in channel 2 than their companions in pool 2. Channel 1 coho grew faster than channel 2 coho, while channel 1 steelhead showed no difference in growth rate for weight from channel 2 steelhead.

Survival. Instantaneous survival rates were calculated for both species. Survivors were defined as those fish still present at the termination of the experiment plus the number of emigrants minus the original number introduced. Since length of residence varied with species, this method of expressing mortality was considered to be the most illustrative.

Survival rates for coho in system 1 and system 2 were 0.395 and 0.445, respectively. Those for steelhead were 0.34 and 0.301, respectively (Table 7). In both experimental systems, steelhead survival rate was lower than coho. System 2 coho survived better than system 1 coho, while the reverse was true for steelhead.

#### Behavioral Characteristics in Experimental Stream

Emigration. The total number of emigrants from system 1 was 482 coho and 745 steelhead, whereas system 2 had 551 coho and 774 steelhead (Table 7). There was no significant difference between the numbers of steelhead emigrating from either system ( $\chi^2 = .56, P > .05$ ). The total number of coho emigrants from systems 1 and 2 was just statistically different, but for practical purposes showed no difference ( $\chi^2 = 4.6, P < .05$ ).

The number of steelhead emigrants in system 1 was significantly larger than coho emigrants ( $\chi^2 = 46.2, P < .05$ ). Small differences in number of coho and steelhead emigrants in system 2 ( $\chi^2 = 4.5, P < .05$ ) would seem to reflect variability in the systems rather than real experimental differences. Figure 13 shows the cumulative emigration for both species in both systems. This figure illustrates the fact that the initially high emigration rate for coho in system 2 accounts for differences in final density of coho between pools 1 and 2.

A higher percentage of steelhead than coho emigrated in both systems (Table 7). Prior to the introduction of steelhead, 65.3% (315) of the coho in system 1, and 73.1% (403) of the coho in system 2 emigrated. This represents a significant difference between coho emigrants from

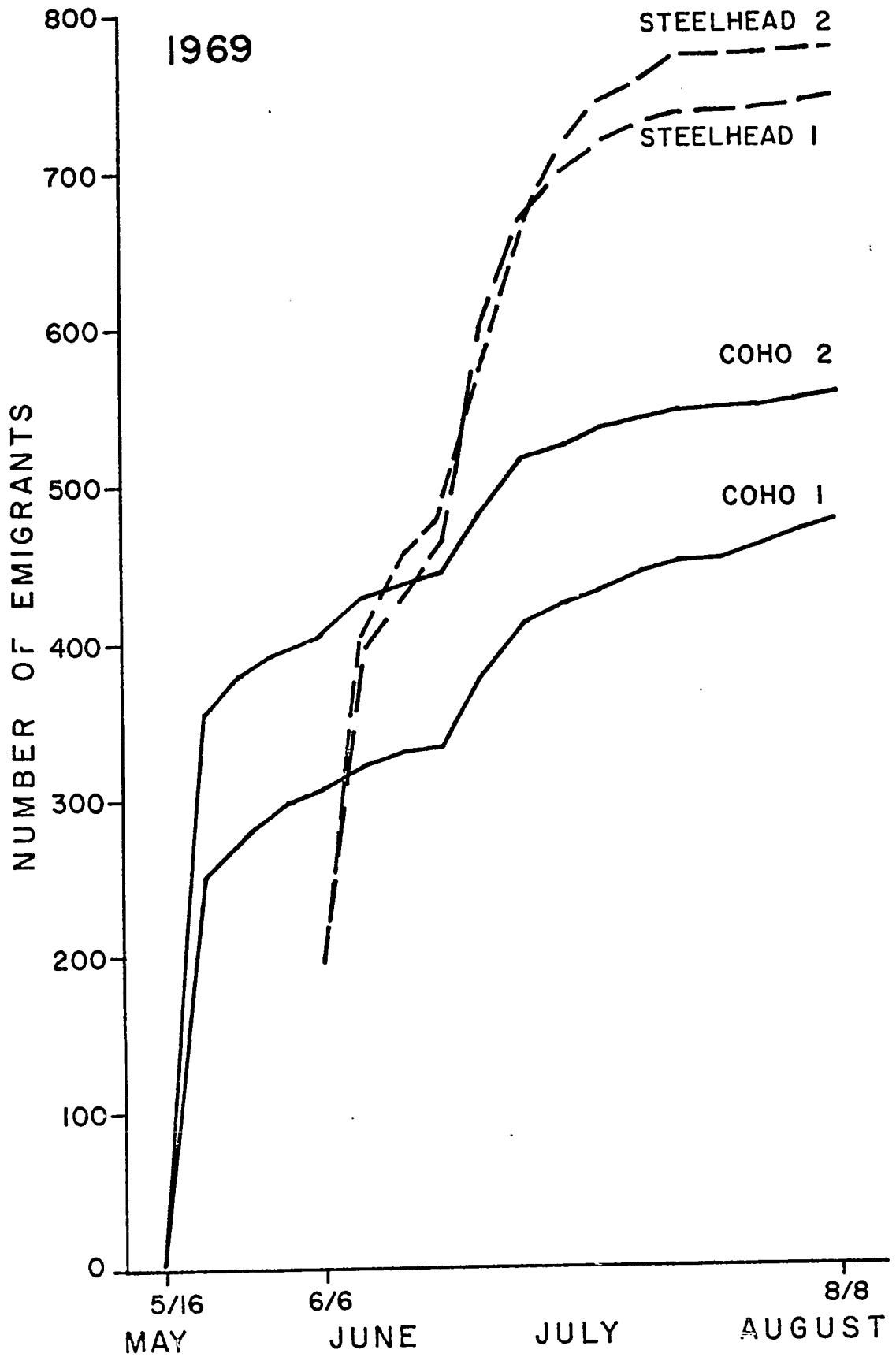


Fig. 13. Cumulative emigration of coho salmon and steelhead trout from the experimental stream system, May 1969 - August 1969.

systems 1 and 2 ( $\chi^2 = 10.8$ ,  $P < .05$ ). During the 74-day period after steelhead were introduced, 745 steelhead and 167 coho emigrated in system 1, while 774 steelhead and 148 coho emigrated in system 2. There was no significant difference between numbers of coho emigrants in either system after steelhead were introduced ( $\chi^2 = 1.1$ ,  $P > .05$ ).

Horizontal Distribution. Fish observed occupying feeding territories within the stream channel were categorized as being present in either riffle or pool habitat. As described before, the stream channels were 50% pool and 50% riffle on an area basis. Table 7 indicates the numbers of fish initially planted and numbers present in the final population of each habitat type. Within either stream channel environment, coho and steelhead were observed to be essentially equally distributed in pool or riffle microhabitats (Table 8). However, it was necessary to take into account the difference in initial number planted by species in order to compare the expected frequency of occupancy of microhabitats. When results for both stream channels were combined, differences in distribution suggested that steelhead were more abundant relative to coho in both riffles and pools than would have been expected on the basis of the numbers introduced.

$$(\chi_R^2 = 5.7, P < .05; \chi_P^2 = 4.5, P < .05).$$

Vertical Distribution. Both species were categorized as being within the top or bottom half of the water column. Table 9 indicates that in channel 1 significantly greater numbers of steelhead were present in the bottom half of the water column than the top half ( $\chi^2 = 7.2$ ,  $P < .05$ ).

Table 8. Horizontal distribution of coho salmon and steelhead trout in the experimental stream channel May 1969-August 1969

	Channel 1		Channel 2	
	Coho	Steelhead	Coho	Steelhead
Riffle	74	112	31	67
Pool	81	111	29	69

Table 9. Vertical distribution of coho salmon and steelhead trout in the pool microhabitat of the experimental stream channel - May 1969-August 1969

	Channel 1		Channel 2	
	Surface	Bottom	Surface	Bottom
Coho	52	34	31	15
Steelhead	31	56	41	56

More coho were present in the top half of the pool than the bottom, but not quite a statistically significant number ( $\chi^2 = 3.8, P > .05$ ). In channel 2, however, there were more significantly more coho in the top half of the pool ( $\chi^2 = 5.4, P < .05$ ). Steelhead in channel 2 were more numerous in the bottom half but there was no statistically significant difference between top and bottom ( $\chi^2 = 2.3, P > .05$ ). When the data were combined for channels 1 and 2, more coho were found in the top half of the water column while more steelhead were in the bottom half ( $\chi^2$  coho = 8.8,  $P < .05$ ,  $\chi^2$  st. = 8.6,  $P < .05$ ).

Agonistic Behavior. Intraspecific and interspecific agonistic behavior was documented within the two stream channel microhabitats and is presented in Table 10 as total nips observed in 190 minutes of observation. The hypothesis being tested is that no differences exist in the frequencies of agonistic behavior either intraspecifically or interspecifically. This outcome would be expected if the agonistic behavior of coho and steelhead were random in nature; therefore, any series of behavioral events that are directional would be observed as a significant deviation from the expected value. Expected values were calculated based on the fact that unequal numbers of coho and steelhead were present in the stream channel microhabitats.

Within the riffle microhabitat in channel 1, steelhead nipped other steelhead significantly more often than expected. In fact, steelhead were not observed to nip coho at all

( $\chi^2$  st. x st. = 46.1  $P < .05$ ,  $\chi^2$  st. x coho = 75  $P > .05$ ).

Coho nipped coho more frequently than expected, while coho nipped steelhead about as frequently as would be expected if nipping were random

Table 10. Total numbers of intraspecific and interspecific nips observed among coho salmon and steelhead trout in the experimental stream channel - May 1969-August 1969 [Observation time 190 minutes.]

Riffle	Channel 1			Channel 2		
	CxC	SxS	SxC	CxC	SxS	SxC
Observed	96	138	0	24	90	0
Expected	72	78	75	32.2	56.5	42.6
$\chi^2$	6.3	46.1	1.1	2.1	19.9	71.7
			128.5			
Pool						
Observed	18	24	0	6	12	0
Expected	10.4	20.2	14.5	6.5	5.3	5.8
$\chi^2$	6.8	0.9	5.0	0.0	8.5	14.3
			27.2			
Riffle						
Coho number		198			180	
Steelhead number		<u>204</u>			<u>246</u>	
		402			426	
Pool						
Coho number		60			54	
Steelhead number		<u>84</u>			<u>48</u>	
		144			102	

( $\chi^2$  coho x coho = 6.3 P<.05,  $\chi^2$  coho x st. = 1.1 P>.05).

Frequencies of nipping in the pool microhabitat of channel 1 were also higher than expected for coho against coho and significantly lower for coho against steelhead

( $\chi^2$  coho x coho = 6.8 P<.05,  $\chi^2$  coho x st. = 5.0 P<.05).

Steelhead in pool 1 again did not nip coho, while steelhead nipped steelhead as frequently as expected by chance

( $\chi^2$  st. x coho = 14.5 P<.05,  $\chi^2$  st. x st. = .9 P>.05).

Similar results were observed in channel 2 within the riffle microhabitat where steelhead nipped steelhead more frequently and steelhead nipped coho not at all

( $\chi^2$  st. x st. = 19.9 P<.05,  $\chi^2$  st. x coho = 42.6 P<.05).

Coho more frequently nipped steelhead than coho nipped coho in this riffle microhabitat ( $\chi^2$  coho x st. = 7.1 P<.05,  $\chi^2$  coho x coho = 2.1 P>.05). In the pool microhabitat again there were no steelhead-coho encounters, while higher frequencies of steelhead nipping steelhead were apparent

( $\chi^2$  st. x coho = 5.8 P<.05,  $\chi^2$  st. x st. = 8.5 P<.05).

In general, the largest deviations from random behavior were that steelhead did not nip coho at all in any microhabitats, and steelhead nipped steelhead very frequently in the riffle microhabitats.

Comparing the frequency of occurrence of the four behavioral categories between the riffle and pool microhabitats one concludes that coho-initiated nips against steelhead occurred more frequently in riffles than pools in channel 1. However, the other categories occurred with roughly equal frequencies in either microhabitat type.

EXPERIMENT NO. 2. A COMPARISON OF THE NATURAL AND REVERSED EMERGENCE PATTERN WITH POSTEMERGENT COHO AND STEELHEAD FRY AS PRIOR RESIDENTS

Procedures

On May 11, 1968, 800 laboratory-incubated, postemergent steelhead fry, the progeny of wild Big Beef Creek stock, were introduced into experimental stream system 1. On June 18, 1968, 38 days later, 700 naturally-reared coho seined from Big Beef Creek were introduced into system 1 with the now resident population of steelhead. This planting procedure was reversed in experimental stream system 2. That is, on May 15, 1968, 700 laboratory incubated, postemergent coho fry, the progeny of wild Big Beef Creek stock, were introduced. A subsequent introduction of 800 naturally-reared steelhead seined from Big Beef Creek was made on June 15, 1968, 31 days after the original coho population. Following this initial planting of steelhead, a second and final introduction of 800 laboratory-incubated, postemergent steelhead (Big Beef Creek stock) was made on July 2, 1968.

The habitat structure of the stream channel was uniformly one complete riffle in this experiment. The depths in stream channel 1 ranged from 9.4 to 10.3 cm, while those in stream channel 2 ranged from 9.4 to 12.7 cm. Velocities generated on each riffle extended from 2.5 to 7.1 cm/sec in stream channel 2. The temperature extended from 9.3 to 12.5 C, with a mean value of 10.6 C.

ResultsCharacteristics of the Resident Population

Final Number. In spite of the difference in order of stocking and initial numbers of coho and steelhead there was no difference in the final number of coho in pool 1 (119) and pool 2 (105) ( $\chi^2$  coho = 0.9  $P > .05$ ). In a similar way, no significant difference was found in number of steelhead in pool 1 (22) and pool 2 (39) ( $\chi^2 = 0.2$   $P > .05$ ). More coho were present in the pools than steelhead, even when steelhead had established prior residence (pool 1) ( $\chi^2_1 = 86.0$   $P < .05$ ,  $\chi^2_2 = 192.0$   $P < .05$ ).

Within the riffle habitat type, which was uniform in this experiment, the final number of coho in channel 1 was the same as channel 2. The number of steelhead was also the same in channels 1 and 2

( $\chi^2$  coho 1 and 2 = 1.6,  $P > .05$ ,  $\chi^2$  st. 1 and 2 = .93,  $P > .05$ ).

When differing initial numbers of both coho and steelhead are considered, the same proportion of coho and steelhead remained within each channel

( $\chi^2$  coho and st.<sub>1</sub> = .002,  $P > .05$ ,  $\chi^2$  coho and st.<sub>2</sub> = .37,  $P > .05$ ).

Biomass. The initial biomass of the fish varied and the population which was introduced into the system first was smaller in size and therefore lower in total biomass than the second population (Table 11). However great the initial differences, the final biomass supported in system 1 was similar to 2, being 216.4 gm and 229.6 gm, respectively. The difference between the two systems was attributed to a larger biomass of coho in pool 2, being 135.13 gm compared to 124.24 gm in pool 1, and

Table 11. Population characteristics of the resident population of coho salmon and steelhead trout in the experimental stream system - May 1968-August 1968  
 [In system 1 steelhead were introduced first (May 11) and coho later (July 18). In system 2 coho were introduced first and steelhead later.]

	Pool 1		Channel 1		Pool 2		Channel 2	
	Coho	Steelhead	Coho	Steelhead	Coho	Steelhead	Coho	Steelhead
Initial population number	700	800			700	800		
Final population number	119	22	8	9	105	39	14	26
Number of emigrants	480	489			546	1311		
Percent emigration	68.57	61.12			78.00	81.94		
Initial mean length (mm)	48.2	27.6			36.5	41.5		
Final mean length	46.5	59.1	59.5	56.2	48.9	49.8	47.7	46.5
Instantaneous growth rate	-0.185	2.625	1.086	2.452	1.026	0.912	0.939	0.399
Initial mean weight (gms)	1.22	0.15			0.32	0.39		
Final mean weight	1.04	2.42	2.37	2.20	1.29	1.35	1.17	0.97
Instantaneous growth rate	-0.823	9.476	3.423	9.147	4.848	6.208	4.505	3.204
Survival	0.482	0.242			0.852	0.477		
Final total biomass	124.24	53.33	18.99	19.85	135.13	52.84	16.38	25.27
Percent of total	69.97	30.03	48.89	51.11	71.89	28.11	39.33	60.67
Initial density No/M <sup>2</sup>	13.00	14.85			13.00	14.85		
Final density No/M <sup>2</sup>	2.21	0.41	1.92	2.16	1.95	0.72	3.35	6.23
Initial biomass Gms/M <sup>2</sup>	15.86	2.30			4.21	5.79		
Final biomass Gms/M <sup>2</sup>	2.31	0.99	4.56	4.77	2.51	0.98	3.92	6.05

also a greater biomass of steelhead in channel 2, 25.27 gm compared to 19.85 gm in channel 1.

Coho contributed about 70% of the biomass in both pools. The pool habitat appeared to support somewhat more coho biomass if the fish were larger in size and smaller in number and present in the system before steelhead were introduced. Steelhead showed a similar response in that a smaller number of larger individuals was present in pool 1 compared to pool 2 in which coho were the prior residents. However, steelhead biomass was equal in pool 1 and pool 2, being 53.33 gm and 52.84 gm, respectively.

Within the riffle habitat in this experiment, the total biomass supported in channel 1 was 38.84 gm, while the total in channel 2 was 41.65 gm. Channel 1 supported essentially an equivalent biomass of coho, 18.99 gm, and steelhead, 19.85 gm or 49 to 51% respectively. Channel 2 supported a larger biomass of steelhead (25.27 gm) than coho (16.38 gm). Steelhead in this case represented 60.7% of the biomass.

Density. Within the major pool habitat more coho (number/m<sup>2</sup>) were supported per unit space than steelhead (Table 11). However, in the stream channels more steelhead were supported. More coho and steelhead were supported in riffles than in pools, with the exception of coho in pool 1 and channel 1, where they were nearly equal. However, expressing density as weight per unit space, gm/m<sup>2</sup>, provides an even clearer understanding of the relationship. On that basis, the stream channel riffles supported more individual combined and species biomass per unit space than pools. For example, in system 1, 3.30 gm/m<sup>2</sup> of coho and steelhead

were supported while  $9.33 \text{ gm/m}^2$  were supported in channel 1. Similarly,  $3.49 \text{ gm/m}^2$  of combined coho and steelhead were supported in pool 2 compared with  $9.97 \text{ gm/m}^2$  in channel 2.

Growth. Species given the advantage of prior residence were larger in length and weight in final populations within pools (Table 11). Within the stream channel (riffle) this was true for steelhead but not for coho. However, instantaneous growth rates, by compensating for time of residence, allowed for a clearer interpretation and supported the contention that prior residents, regardless of species, had better growth in both pools and riffles (Table 11). Giving the steelhead prior residence gave a more striking demonstration of this fact than for coho. Comparing stream channels with pools indicated that larger coho were found in channel 1 than in pool 1, and they therefore showed greater growth rates, while somewhat smaller steelhead were found in channel 1 than in pool 1. System 2 found both smaller steelhead and coho in channel 2 than in pool 2, with growth rate paralleling this trend.

Survival. Instantaneous survival rates are shown in Table 11. The coho population in system 2 which had the advantage of prior residence showed the highest survival rate. In contrast, the prior resident steelhead population in pool 1 showed the lowest survival rate of all. However, this lower rate could reflect a size-dependent phenomenon since the fish were considerably smaller than the other groups of fish (Table 11). The two populations of coho in system 1 and steelhead in system 2, which were introduced after resident populations had been established, showed roughly the same rate, .482 and .477, respectively.

### Behavioral Characteristics in Experimental System

Emigration. A cumulative graph of the number of emigrants as a function of time is represented in Fig. 14. The total percentage of emigration by species and system was 68.6% coho and 61.1% steelhead in system 1 versus 78.0% coho and 81.9% steelhead in system 2. In each case, the total percentage emigration was higher for the species which were introduced into an environment that was previously occupied.

The total number of coho emigrants in system 1 (480) and system 2 (546) was the same ( $\chi^2 = 4,2 P > .05$ ). Differences between total steelhead emigrants, however, were large and seem to substantiate the statement above that emigration was higher for species introduced into an occupied environment ( $\chi^2 = 30.8 P < .05$ ). In this connection, it is especially useful to compare number of emigrants of the prior resident before and after introduction of the second species.

In system 1, 84.9% of the steelhead originally present emigrated before coho were planted; therefore, only 15.1% emigrated after. To be precise, only 74 steelhead emigrated after coho were introduced compared to 480 coho. This is obviously a significant difference.

In system 2, 85.7% of the coho emigrated before the introduction of steelhead, while only 14.3% emigrated after. Numerically, 78 total coho left after steelhead were introduced into system 1 compared with 1,311 steelhead emigrants. When the emigration period for steelhead is broken down even further, it can be seen that 600 steelhead (75% of the first plant) emigrated before the second planting, while only 30 coho emigrated. After the second steelhead plant, 711 steelhead emigrated versus 48 coho.

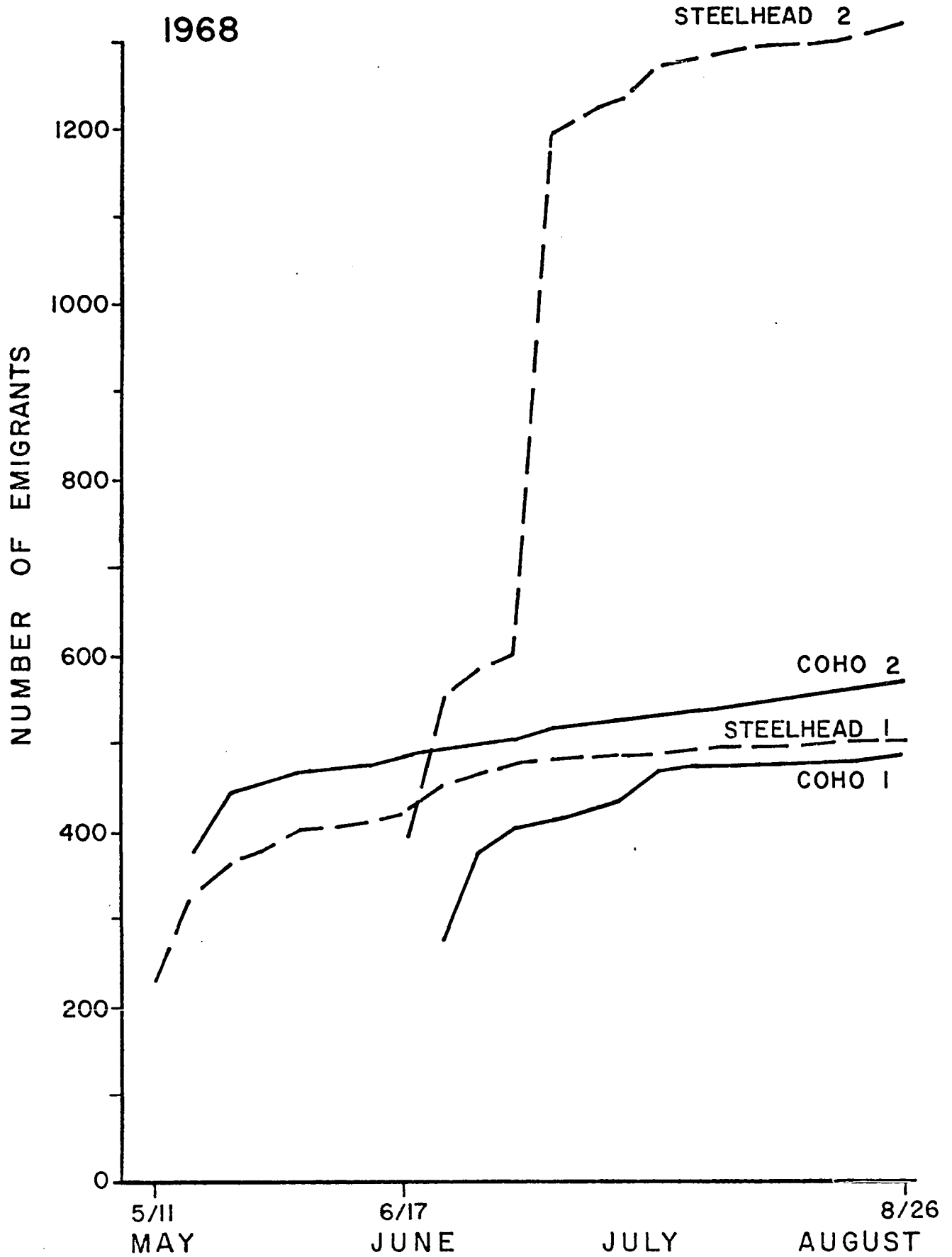


Fig. 14. Cumulative emigration of coho salmon and steelhead trout from the experimental stream system, May 1968 - August 1968.

The differences are quite obviously significant and point out that the majority of emigration on the part of the resident population occurred before planting of the introduced population. A final comparison shows that the two prior resident populations reacted similarly, in terms of the number of emigrants leaving after introduction of the other species, 78 coho left pool 2, and 74 steelhead left pool 1 ( $\chi^2 = 1.3$   $P > .05$ ).

Horizontal Distribution. The total number of steelhead observed in channel 1 was significantly higher (325) prior to the introduction of coho than after (182) ( $\chi^2 = 40.4$   $P < .05$ ) (Table 12). In contrast, the number of coho in channel 2 did not differ before (240) or after (262) the introduction of steelhead.

Table 12. Horizontal distribution of coho salmon and steelhead trout before and after the introduction of the second species in the experimental stream channel - May 1968-August 1968

	Channel 1		Channel 2
	Before		
Steelhead number	325	Coho number	240
	After		
Coho number	405	Coho number	262
Steelhead number	182	Steelhead number	470

Fewer steelhead took up prior residence in channel 1 (182) than did coho in channel 2 (262) ( $\chi^2 = 5.1$ ,  $P < .05$ ). However, the greatest differences were found between the numbers of the introduced population, coho in

channel 1 (405) and steelhead in channel 2 (470). Taking into account the different numbers planted these differences indicated that more coho than expected were present in channel 1 and less steelhead in channel 2 ( $\chi^2 = 104.5$   $P < .05$ ). These data suggest that resident steelhead were reduced in number in the stream channel after the introduction of coho, while resident coho in channel 2 were not reduced to the same extent upon the introduction of steelhead.

Vertical Distribution. Since the stream channel habitat was composed of riffles of comparatively shallow depth, vertical stratification of fish was not a consideration. Therefore, observations were made within the pool habitat.

Analysis of the two prior resident populations when they were alone showed that steelhead in pool 1 were equally as numerous in the top half of the water column as the bottom half ( $\chi^2 = .2$   $P > .05$ ) (Table 13).

Table 13. Vertical distribution of coho salmon and steelhead trout before and after the introduction of the second species in the pool microhabitat of the experimental stream channel - May 1968 - August 1968.

	Pool 1		Pool 2	
	Coho	Steelhead	Coho	Steelhead
Before				
Upper half		35	112	
Lower half		39	70	
After				
Upper half	117	8	117	34
Lower half	63	51	74	112

However, after the introduction of coho into pool 1, steelhead changed their behavior so that they were more prevalent on the bottom than the top ( $\chi^2 = 31.4$   $P < .05$ ). Coho in that pool were found to be more numerous in the top half of the water column ( $\chi^2 = 16.2$   $P < .05$ ). In pool 2 where coho were present alone prior to the introduction of steelhead, there were more coho in the top half of the water column than in the bottom ( $\chi^2 = 9.7$   $P < .05$ ). After the introduction of steelhead into pool 2, coho were unchanged in their preference for the top half of the water column ( $\chi^2 = 9.6$   $P < .05$ ). Steelhead were more numerous in the bottom half of the water column ( $\chi^2 = 41.6$   $P < .05$ ). Therefore, the data indicate a noticeable change in distribution for steelhead after the introduction of coho in pool 1. They changed from random distribution to a preference for the bottom. On the other hand, the introduced population of steelhead in pool 2 had no effect on the coho distribution.

Agonistic Behavior. Results of intraspecific and interspecific agonistic interaction within the stream channels before and after introduction of the second species are presented in Table 14. These data indicate that steelhead alone are more apt to nip each other than are coho alone ( $\chi^2 = 99.8$   $P < .05$ ). Nipping for both coho and steelhead was more frequent prior to the presence of the other species ( $\chi^2_c = 29.8$   $P < .05$ ,  $\chi^2_s = 217.8$ ,  $P < .05$ ). Within channel 1, after coho had been introduced into the stream system, all four behavioral categories differed significantly from what would be expected if nipping were randomly directed. The strikingly high frequency with which steelhead nipped steelhead, even in the presence of coho, was the most significant deviation from

Table 14. Total numbers of intraspecific and interspecific nips observed among coho salmon and steelhead trout in the experimental stream channel - May 1968-August 1968 [Observation time 200 minutes.]

	Channel 1			Channel 2			$\chi^2$	
	CxC	SxS	CxS	SxC	CxC	SxS		CxS
BEFORE								
5/11/68 - 6/18/68								
Observed		195			45			
Expected		117.6			122.4			99.8
AFTER								
6/18/68 - 8/26/68								
Observed	207	137	182	15	75	267	230	0
Expected	288.3	37.9	108.2	108.2	78.4	219.6	131.6	131.6
$\chi^2$	22.9	259.1	50.1	80.3	.15	10.2	73.6	131.6
					412.4			215.5
Total number of fish								
BEFORE								
Coho						43		
Steelhead								
AFTER								
Coho		387						195
Steelhead		142						330

random behavior of all ( $\chi^2 = 259.1, P < .05$ ). In contrast was the very low frequency of steelhead nipping coho ( $\chi^2 = 80.3, P < .05$ ). Coho, on the other hand, responded to steelhead by a high frequency of nipping ( $\chi^2 = 50.1, P < .05$ ). Coho nipping coho was correspondingly lower than expected ( $\chi^2 = 22.9, P < .05$ ).

Within channel 2 where coho were the prior residents, the data suggest that coho were nipping steelhead more frequently than coho

$$(\chi^2_{\text{coho x st.}} = 73.6 P < .05, \chi^2_{\text{coho x coho}} = .15 P > .05).$$

The reverse was true for steelhead which evidenced no interspecific aggression against coho but did frequently nip each other

$$(\chi^2_{\text{st. x coho}} = 131.6 P < .05, \chi^2_{\text{st. x st.}} = 0.2 P < .05).$$

In summary, steelhead when prior residents were more inclined to nip each other than when not. Whether or not they were prior residents, they did not to any extent nip coho. Coho, when prior residents, were equally as likely to engage in interspecific aggression with newly introduced steelhead as when they, themselves, were introduced in the presence of steelhead. But they were more apt to nip each other when they were prior residents than when they were the recently introduced species.

Feeding Behavior. Documentation of the number of times each species initiated a feeding thrust directed at either the surface or the bottom is shown in Table 15. Coho in both channels showed a significantly greater number of feeding movements on the water surface than on the bottom

$$(\chi^2_1 = 62.6 P < .05, \chi^2_2 = 49.8 P < .05).$$

Table 15. Feeding movements directed toward the surface and bottom by coho salmon and steelhead trout in the pool microhabitat of the experimental stream channel - May 1968-August 1968

	Channel 1		$\chi^2$	Channel 2		$\chi^2$
	Surface	Bottom		Surface	Bottom	
Coho number	104	17	62.6	94	19	49.8
Steelhead number	17	120	77.4	33	188	108.6

In contrast, steelhead in both channels fed significantly more on the bottom substrate than on the water surface

$$(\chi_1^2 = 77.4 \text{ } P < .05, \chi_2^2 = 108.6 \text{ } P < .05).$$

Since vertical stratification of fish is not a factor in a uniform riffle habitat such as was present in this experiment, the results strongly suggest directional feeding behavior.

EXPERIMENT NO. 3. A COMPARISON OF THE NATURAL AND REVERSED EMERGENCE  
PATTERN WITH SUMMER UNDER-YEARLING COHO AND STEELHEAD  
AS PRIOR RESIDENTS

Procedures

This experiment was designed such that each species had the advantage of larger size when introduced into the system with fish of the other species that had established prior residence in a barren environment. On August 16, 1969, 561 steelhead were introduced into system 1 and 750 coho were introduced into system 2. September 26, 1969, 42 days later, a similar planting of fish was made, 500 coho into system 1 and 475 steelhead into system 2. These fish were all seined from Big Beef Creek and were larger in size than those which were first stocked into the experimental stream.

During this experiment the stream channel was composed of a series of two upstream riffles, followed by two downstream pools, such that the stream channel was divided equally on an area basis into riffle and pool microhabitats. Riffle depths in channel 1 ranged from 8.6 to 11.3 cm, while those in channel 2 ranged from 8.9 to 10.7 cm. Velocities ranged from 2.1 to 5.5 cm/sec in channel 1 and 1.8 to 4.7 cm/sec in channel 2. Within the pool microhabitat of channel 1, depths ranged from 31.0 to 31.3 cm, while those in channel 2 measured 30.3 to 30.4 cm. Surface velocities varied from 0.8 to 1.8 cm/sec in channel 1 compared with 0.3 to 1.3 cm/sec in channel 2. Bottom velocities were less than 0.2 cm/sec and less than 0.03 cm/sec. The water temperature during the course of the experiment varied from 5.5 to 14.4 C with a mean value of 9.4 C.

## Results

### Characteristics of the Resident Population

Final Number. After 122 days of residence for the prior residents and 80 days of residence for the recently introduced species, the final resident numbers were 96 coho and 11 steelhead in pool 1, and 77 coho and 53 steelhead in pool 2 (Table 16). Coho that were prior residents in pool 2 were after steelhead were added, significantly less numerous than coho in pool 1 where steelhead were already present ( $\chi^2 = 17.3 P < .05$ ). This same relationship held for steelhead. There were fewer prior resident steelhead in pool 1 than introduced steelhead in pool 2 ( $\chi^2 = 35.0 P < .05$ ). Prior resident steelhead were significantly less abundant in pool 1 than introduced coho, while in pool 2 there was no difference between coho and steelhead numbers

$$(\chi_1^2 = 77.9 P < .05, \chi_2^2 = 2 P > .05).$$

Within the stream channel environment, which was 50% pool and 50% riffle on an area basis, the number of final resident coho and steelhead in channel 1 were equivalent ( $\chi^2 = .04 P < .05$ ). In channel 2 the prior resident coho were significantly less numerous than the introduced steelhead ( $\chi^2 = 9.3 P < .05$ ). The introduced steelhead were more numerous in channel 2 than resident in channel 1 ( $\chi^2 = 15.9, P < .05$ ). No significant differences were found between numbers of prior resident coho in channel 1 and introduced coho in channel 2 ( $\chi^2 = 1.5 P < .05$ ). Prior resident steelhead appear to be reduced in numbers by introduced coho, but introduced steelhead seem to have no similar advantage.

Biomass. Final total biomass supported in pool 1 was 272.9 gm and in pool 2, 308 gm (Table 16). The percentage of this total biomass contributed by coho was 88% in pool 1 and 51% in pool 2. Steelhead contributed 12% in pool 1 and 49% in pool 2. In both cases, the prior resident species contributed less to total biomass than their companion species which were introduced.

In the stream channel environment, the coho population in each channel achieved approximately the same biomass, 21.0 gm in channel 1 and 28.7 gm in channel 2. The comparative biomass achieved by the steelhead population in each channel was quite different, being approximately four times greater in channel 2 (75.75 gm) than in channel 1 (19.40 gm). The percentage contribution in channel 1 was 52% coho and 48% steelhead, while that in channel 2 was 27.5% coho and 72.5% steelhead.

Density. In this experiment the prior resident steelhead population was present in pool 1 at very low densities, both in terms of numbers and weight. This is contrasted with a higher density of steelhead in pool 2.

In pool 2, a nearly equal density by weight of coho and steelhead was supported, while in the stream channel steelhead were present in greater densities by weight and number than coho. In both systems 1 and 2 the stream channel habitat, which had equal areas of pool and riffle microhabitats, supported greater densities by weight than the deeper pool habitats. Both coho and steelhead were found in higher densities as introduced populations than as residents.

Table 16. Population characteristics of the resident population of coho salmon and steelhead trout in the experimental stream system - August 1969-December 1969  
 [In system 1 steelhead were introduced August 16 and coho September 26. In system 2 coho were introduced first followed by steelhead.]

	Pool 1		Channel 1		Pool 2		Channel 2	
	Coho	Steelhead	Coho	Steelhead	Coho	Steelhead	Coho	Steelhead
Initial population number	500	561			750	475		
Final population number	96	11	5	5	77	53	14	24
Number of emigrants	349	471			579	349		
Percent emigration	69.80	83.96			77.20	73.47		
Initial mean length (mm)	60.0	50.7			49.9	59.3		
Final mean length	64.3	65.7	74.8	72.0	60.2	68.3	58.8	68.1
Instantaneous growth rate	0.316	0.776	1.007	1.067	0.562	0.645	0.491	0.632
Initial mean weight (gms)	2.40	1.21			1.65	2.57		
Final mean weight	2.51	2.94	4.20	3.80	2.04	2.84	2.05	3.16
Instantaneous growth rate	0.205	2.658	2.555	3.426	0.635	0.456	0.650	0.944
Survival	0.6188	0.6570			0.8781	0.6065		
Final total biomass	240.60	32.30	21.00	19.40	157.45	150.55	28.70	75.75
Percent of total	88.16	11.84	51.98	48.02	51.12	48.88	27.48	72.52
Initial density No/M <sup>2</sup>	9.28	10.42			13.92	8.82		
Final density No/M <sup>2</sup>	1.78	0.20	1.20	1.20	1.85	1.27	3.35	5.75
Initial biomass Gms/M <sup>2</sup>	22.28	12.65			22.98	22.67		
Final biomass Gms/M <sup>2</sup>	4.47	0.60	5.04	4.65	2.92	2.79	6.87	18.15

Growth. The prior resident steelhead population exhibited greater instantaneous rates of growth in both length and weight in either pool or stream channel environment than the introduced coho population (Table 16). Higher growth rates were obtained by both coho and steelhead in stream channel 1 compared to pool 1. In fact, prior resident steelhead in channel 1 showed that the highest instantaneous growth rate (3.426) of both systems 1 and 2 in either habitat type.

In system 2 the prior resident coho population showed a greater instantaneous growth rate in weight than the introduced steelhead in the pool environment and nearly equivalent to steelhead in the stream channel environment. Steelhead, on the other hand, showed greater instantaneous rates of increase in weight in the stream channel than in the pool habitat. Comparing channels 1 and 2 it can be seen that both steelhead and coho had significantly higher instantaneous rates of growth in channel 1, which is also associated with the fact that there were fewer of each species in channel 1.

Survival. Instantaneous survival rates for coho and steelhead are shown in Table 16. The recently introduced fish in each system, coho in 1 and steelhead in 2, had very comparable survival rates, 0.619 and 0.606, respectively, which were lower than the prior residents in each case. The survival rate for prior resident coho in system 2 was significantly higher (0.878) than that for prior resident steelhead in system 1 (0.657). The initial sizes of the prior resident coho and steelhead populations were quite similar. These differences were probably not size-related, but species-specific in nature.

### Behavioral Characteristics in Experimental Stream

Emigration. The total number of emigrants is given in Table 16 and illustrated graphically in Fig. 15 as cumulative numbers over time. In system 1 more steelhead (471) emigrated than coho (349) ( $\chi^2 = 6.8 P < .05$ ). The number of coho and steelhead emigrants within system 2 (579) and (349), respectively, were not significantly different ( $\chi^2 = .5 P > .05$ ). The total numbers of emigrants of prior resident coho in system 2 and prior resident steelhead in system 1 were the same ( $\chi^2 = 1.8 P > .05$ ). The total numbers of emigrants of introduced coho in system 1 and steelhead in system 2 were also not significantly different. After the introduction of coho, 30.8% of the steelhead in system 1 emigrated, or 145 steelhead compared to 349 coho. In system 2, 26.4% of the coho emigrated after steelhead were added; i.e., 150 coho to 349 steelhead. The graph indicates that the rate of emigration of prior resident fish was not materially affected by the introduced species.

Horizontal Distribution. Within channel 1, after the introduction of coho, the abundance of prior resident steelhead dropped significantly in both the riffle and pool microhabitats ( $\chi_r^2 = 7.2 P > .05$ ,  $\chi_p^2 = 144.0 P < .05$ ). A similar diminution of abundance was shown in riffle and pool microhabitats for coho prior residents in channel 2 after the introduction of steelhead ( $\chi_r^2 = 33.4 P < .05$ ,  $\chi_p^2 = 10.0 P < .05$ ). Prior resident steelhead in channel 1 and coho in channel 2 were obviously more abundant in the pool microhabitat than in the riffle microhabitat (Table 17). After the introduction of the second species, the prior resident steelhead in channel 1 were equally as abundant in the riffle as in the pool microhabitat, while coho in channel 2

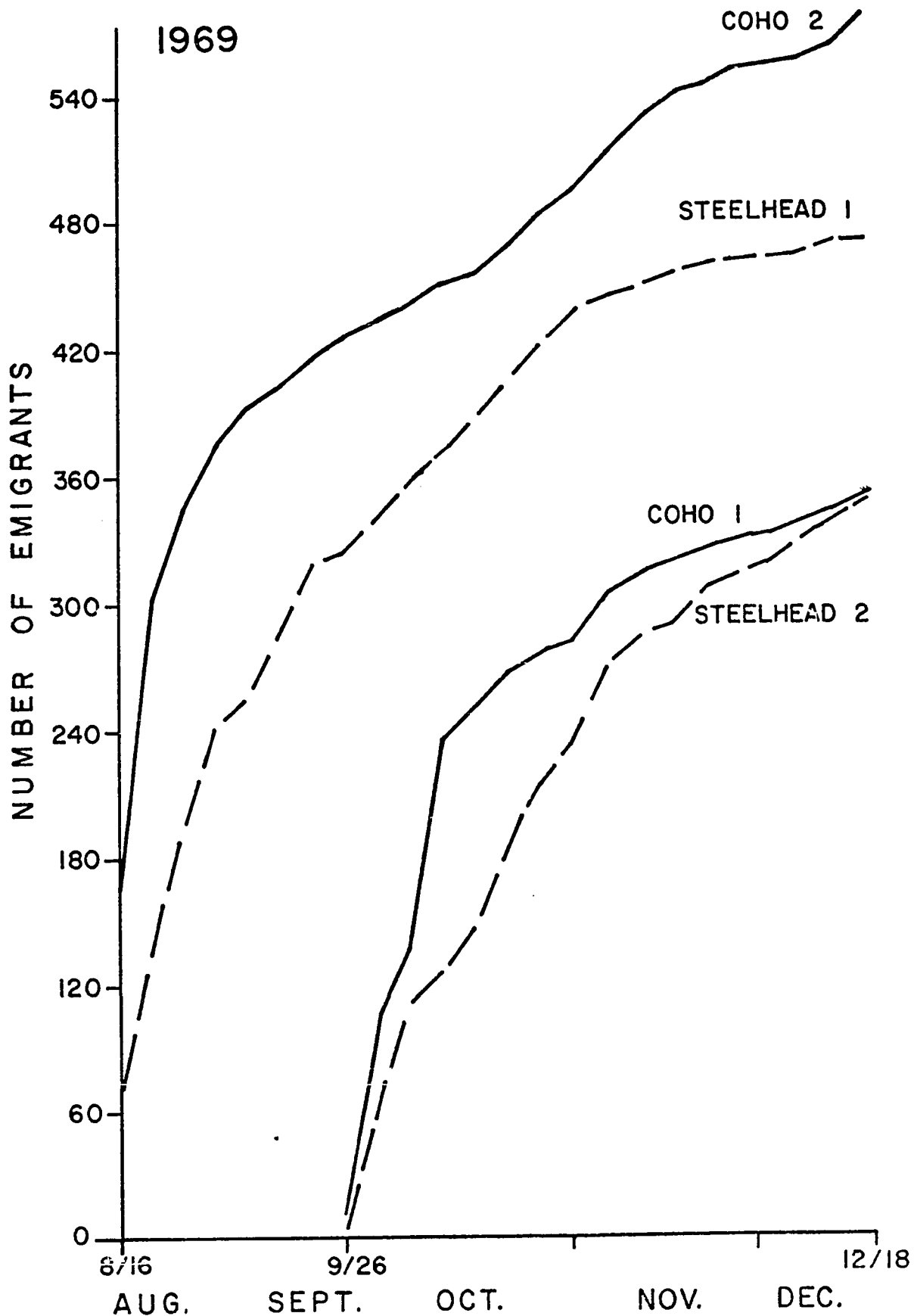


Fig. 15. Cumulative emigration of coho salmon and steelhead trout from the experimental stream system, August 1969 - December 1969.

Table 17. Horizontal distribution of coho salmon and steelhead trout before and after the introduction of the second species in the experimental stream channel - August 1969-December 1969

	Channel 1		Channel 2	
	Riffle	Pool	Riffle	Pool
Before				
Coho			160	526
Steelhead	188	442		
After introduction				
Coho	50	345	72	428
Steelhead	123	142	167	893

were still much more prevalent in the pool microhabitat. The two introduced populations, coho in channel 1 and steelhead in channel 2, were also significantly more abundant in the pool microhabitat than riffle. In summary, prior resident steelhead in channel 1 changed their horizontal distribution pattern from predominantly in pools to equally distributed between riffles and pools after the introduction of coho. No such change occurred with prior resident coho in channel 2 upon the introduction of steelhead.

Vertical Distribution. Vertical distribution of fish observed in the pool microhabitat of channels 1 and 2 is shown in Table 18. Both prior resident coho and steelhead in channels 1 and 2, respectively, were more prevalent in the top half of the water column than on the bottom ( $\chi^2_{st.} = 90.4$   $P < .05$ ,  $\chi^2_{coho} = 78.8$   $P < .05$ ). After the introduction of the steelhead the prior resident coho in channel 2 were more prevalent in the bottom as were the introduced steelhead

$$(\chi^2_{coho} = 5.8 \text{ } P < .05, \chi^2_{st.} = 451.6 \text{ } P < .05).$$

Table 18. Vertical distribution of coho salmon and steelhead trout in the pool microhabitat of the experimental stream channel - August 1969 - December 1969

	Channel 1		Channel 2	
	Top	Bottom	Top	Bottom
Before				
Coho number			385	175
Steelhead number	343	135		
After				
Coho number	159	202	193	243
Steelhead number	94	53	129	764

Prior resident steelhead in channel 1 did not change after coho were introduced and were more frequently observed in the top half of the water column, while coho were associated more with the bottom half

$$(\chi^2_{st.} = 11.4 P < .05, \chi^2_{coho} = 5.1 P < .05).$$

This represents a difference from the vertical stratification in the spring and summer where steelhead were present on the bottom and coho were present on the surface in Experiments Nos. 1 and 2 previously described.

Agonistic Behavior. Frequencies of intraspecific and interspecific agonistic behavior are presented in Table 19. When prior resident steelhead were alone in channel 1 there were significant differences in the frequency of intraspecific steelhead nipping in the riffle and pool microhabitats. They nipped more frequently in riffles than pools ( $\chi^2 = 26.4 P < .05$ ). The reverse was true for prior resident coho in channel 2. Coho nipped each other in pools more frequently than in riffles ( $\chi^2 = 19.9 P < .05$ ).

Table 19. Total numbers of intraspecific and interspecific nips observed among coho salmon and steelhead trout in the experimental stream channel -- August 1969-December 1969

	Channel 1			Channel 2			$\chi^2$		
	CxC	SxS	CxS	SxC	CxC	SxS		CxS	SxC
BEFORE									
Observation time: 200 minutes									
Riffle									
Observed		310			115		18.3		15.9
Expected		243.3			166.5				
Pool									
Observed		485			705		8.1		4.0
Expected		551.7			653.5		26.4		19.9
$\chi^2$									
AFTER									
Observation time: 360 minutes									
Riffle									
Observed	108	192	244	40	46	198		42	
Expected	61.8	266.3	127.9	127.9	47	153.5		84.7	
$\chi^2$	34.5	21.1	105.6	60.4	0.2	12.9	221.6	21.5	34.6
Pool									
Observed	115	26	63	53	73	102		86	
Expected	120.3	25.6	55.5	55.5	23.9	152.4		60.3	
$\chi^2$	0.2	0.01	1.0	0.1	1.3	17.7	1.3	10.9	139.3

Table 19. Total numbers of intraspecific and interspecific nips observed among coho salmon and steelhead trout in the experimental stream channel. August 1969-December 1969 (continued)

	Channel 1		Channel 2	
	Riffle	Pool	Riffle	Pool
BEFORE				
Coho			255	1000
Steelhead	320	725		
AFTER				
Coho	164	650	239	752
Steelhead	340	300	433	1897

After the introduction of coho in system 1, large differences in intraspecific and interspecific behavior were observed in the riffle microhabitat but not in the pool microhabitat ( $\chi^2_r = 221.6$   $P < .05$ ,  $\chi^2_p = 1.3$   $P < .05$ ). Within the riffles the most significant difference observed was the high frequency of interspecific coho-steelhead nipping. Steelhead-initiated interspecific nipping was significantly infrequent, even though they were more abundant numerically than coho. Steelhead nipped steelhead less frequently than coho nipped in this riffle microhabitat. Thus prior resident steelhead were generally less aggressive intraspecifically and interspecifically in the presence of coho. Agonistic behavior in riffles in channel 1 contrasted sharply with that evidenced in pools. Here intraspecific and interspecific aggression by coho and steelhead were about as frequent as their relative abundance would predict they would be ( $\chi^2 = 1.3$   $P > .05$ ).

Agonistic behavior in the riffle microhabitat of channel 2 after the introduction of steelhead was characterized by a high frequency of intraspecific steelhead nipping and low interspecific steelhead-initiated aggression against coho ( $\chi^2 = 34.6$   $P < .05$ ). Frequencies of intraspecific and interspecific coho-initiated agonistic behavior were not significantly greater than would be expected on a random basis in the riffle microhabitat. Within the pool microhabitat all behavioral categories were significantly different than expected ( $\chi^2 = 139.3$   $P < .05$ ). Coho intraspecific aggression was more frequent while steelhead intraspecific aggression was less frequent than expected. In stark contrast to channel 1, steelhead nipped coho more actively than expected while coho

were less active interspecifically. In general, when coho and steelhead were members of the introduced population they were more apt to initiate interspecific agonistic activity in either microhabitat than when they were prior residents.

Feeding Behavior. The numbers of fish observed to initiate feeding forays to the surface or at the substrate within the pool microhabitats in the stream channels are recorded in Table 20. These data indicate a significantly greater number of coho were feeding on the surface than on the bottom in both pool microhabitats

$$(\chi_1^2 = 48.0 P < .05, \chi_2^2 = 73.6 P < .05).$$

Steelhead, on the other hand, were feeding equally frequently on the top and on the substrate in both stream channels

$$(\chi_1^2 = 1.0 P > .05, \chi_2^2 = 3.6 P > .05).$$

Table 20. Feeding movements toward the surface and bottom by coho salmon and steelhead trout in the pool microhabitat of the experimental stream channel - August 1969 - December 1969

	Channel 1		Channel 2	
	Surface	Bottom	Surface	Bottom
Coho	71	9	84	3
Steelhead	43	34	32	49

Summary and Discussion

Both Chapman (1962) and Mason (1969), working with coho salmon only, have suggested that prior resident coho will ultimately be larger and will more successfully defend their territories against later-emerging coho fry. Based upon these studies it has been hypothesized that coho salmon have an ecological advantage over steelhead trout by virtue of the former's prior stream residence (Fraser, 1968). There have been no previous studies specifically designed to investigate the effects, if any, of prior residence among coho salmon and steelhead trout. The experiments in this section of my study were designed to investigate the effects by comparing the natural emergence sequence with one which has been reversed.

In the natural stream, coho salmon are prior residents by approximately two months in the early spring. This sequence of emergence was duplicated in the experimental stream system during the spring and summer. Reversal of this natural emergence sequence was also tried during the spring-summer period and during the fall-winter period.

In no case did prior residence provide either species with exclusive habitat occupancy. Coexistence was always the outcome. Species specific habitat selection seemed to be a more important determiner of final population structure than prior residence. In the spring-summer experiments, for example, the final number of coho was about the same whether they were the first resident or the introduced species. The same was true for steelhead.

During the fall-winter season prior resident coho and steelhead were less numerous than their introduced counterparts in the pool habitat. Within the stream channel habitat when steelhead were prior residents no differences in numbers of coho and steelhead final residents were found. Coho prior residents, however, were less numerous than steelhead. Therefore, the principal difference between summer and fall was that in the fall coho contributed less to the final population in the pool habitat when they were prior residents and more in the stream channel when they were the introduced species. This same trend was observed in terms of the biomass supported by each species within each habitat.

Regardless of season, coho prior residents exhibited the best survival. Steelhead prior residents showed their lowest survival in the spring-summer season. Better growth (instantaneous growth rate) was experienced by both coho and steelhead when they were prior residents, irrespective of season. A look at emigration behavior puts this information into perspective. In all experiments the majority of emigration occurred prior to the introduction of the second species. This is to be expected when fish are added to the system in excess of carrying capacity. The salient point is that growth and survival appear to be species specific phenomena more than the result of competitive interaction.

When coho were prior residents in both systems in the first experiment, a higher percentage of the steelhead emigrated than coho. When steelhead were prior residents, they had equal numbers of emigrants compared to introduced coho. This differential response suggests that in the spring-summer season coho derive greater advantages from prior residence than do steelhead. In contrast, prior resident coho in the

fall-winter season exhibited equivalent numbers of emigrants to introduced steelhead while prior resident steelhead emigrated to a larger extent than coho which were introduced last. Since the majority of emigration by prior resident steelhead occurred before coho were introduced, I suspect that these differences in emigration rates are a function of less dispersal on the part of both introduced species with the onset of winter.

An interesting contrast in distribution of fish within the stream systems was evident between the spring-summer and fall-winter season. Within the riffle microhabitat in the spring prior resident steelhead were reduced in numbers after coho were introduced and there was no similar change in numbers of prior resident coho when steelhead were introduced. During the fall-winter season both prior resident coho and steelhead became less abundant in the riffle and pool microhabitats after the introduction of the second species. Similarly, in terms of vertical stratification steelhead were evenly distributed in the pool habitat before the introduction of coho and were found only on the bottom afterward. No similar distributional change occurred for coho as they were distributed near the surface both before and after steelhead were introduced. In the fall-winter experiment coho and steelhead were distributed at the surface when alone. After coho were introduced, steelhead continued to be associated with the surface. After steelhead were introduced, the prior resident coho preferred the bottom. These changes in distribution indicate that coho have a greater potential negative effect upon steelhead in the spring than do steelhead upon coho.

Agonistic behavior during the spring-summer experiment where coho were the prior residents may be summarized as being largely intraspecific in nature by both coho and steelhead regardless of microhabitat type. The major exception was within the riffle microhabitat of system 2 where prior resident coho exhibited frequent aggression toward steelhead. Virtually no steelhead aggression toward coho was observed.

In the second experiment, also in the spring, prior residence conveyed no aggressive advantage to steelhead in terms of initiating nipping behavior toward coho. They rarely did so. Intraspecific aggression among steelhead was high regardless of whether they were introduced or prior residents. Coho, on the other hand, were equally likely to initiate interspecific aggression against steelhead, whether they were prior residents or the introduced species.

In contrast, in the fall-winter experiment steelhead actively initiated interspecific aggression against coho when steelhead were members of an introduced population in the pool microhabitat. However, when steelhead were prior residents, steelhead-initiated interspecific aggression was infrequent even though they were more abundant numerically than coho. Prior resident coho were less aggressive interspecifically toward steelhead than when they were among the introduced population. In general, frequent interspecific aggression by either coho or steelhead was exhibited only when they were the introduced species and not prior residents.

In conclusion, prior residence did not appear to confer upon its possessor unilateral advantages in terms of interspecific competition in the experimental stream systems. A more significant factor appears to be differences among species in habitat preference.

PART 3. EFFECTS OF SIZE ON THE SOCIAL BEHAVIOR AND POPULATION  
ECOLOGY OF COHO SALMON AND STEELHEAD TROUT IN THE  
EXPERIMENTAL STREAM SYSTEM

Experimental Methods

The methods used were the same as those described under experimental methods in Part 2.

EXPERIMENT NO. 4 RESULTS OF STOCKING LARGER SIZE POSTEMERGENT  
COHO FRY SIMULTANEOUSLY WITH POSTEMERGENT  
STEELHEAD FRY

Procedures

Steelhead alevins were obtained from the Chambers Creek Hatchery and incubated at Big Beef Creek until yolk sac absorption. Coho eggs were taken from wild Big Beef Creek stock and incubated at Big Beef Creek. The rate of development was manipulated through temperature adjustments so that both species would reach yolk sac absorption at the same time. Hence, fry of steelhead and coho in the postemergent stage were simultaneously stocked into both experimental stream systems on March 31, 1970, at an initial level of 859 steelhead and 860 coho.

On April 15, 1970, a second simultaneous plant of 450 steelhead and 450 coho was made into each system with the minor exception that 449 coho were planted in system 1. The third and final plant consisted of 650 incubator-reared steelhead fry, the progeny of Big Beef Creek stock which were planted into each system on May 17, 1970. The coho fry were larger than companion steelhead in every case. The objective was to fully saturate the system with steelhead which were presumed to have a size disadvantage.

The habitat of the stream channel was composed of a series of two upstream riffles followed by two downstream pools, such that the stream channel was divided equally on an area basis into riffle and pool microhabitats. Riffle depths in channel 1 ranged from 6.5 to 8.2 cm, while those in channel 2 ranged from 7.5 to 9.4 cm. Velocities generated on each riffle microhabitat extended from 7.5 to 13.6 cm/sec in channel 1

to 6.2 to 13.5 cm/sec in channel 2. Within the pool microhabitat of channel 1 depths extended from 29.4 to 35.4 cm, while those in channel 2 extended from 27.7 to 33.5 cm. Surface velocities varied from 3.1 to 5.4 cm/sec in channel 1 compared to 1.6 to 4.5 cm/sec in channel 2. Bottom velocities were less than 0.6 cm/sec in channel 2. The temperature during the course of the experiment varied from 7.2 to 11.6 C with a mean value of 9.0 C.

## Results

### Characteristics of the Resident Population

Final Number. On June 1, 1970, the experiment was brought to an involuntary conclusion by vandalism. A window was broken in each pool habitat causing the majority of water to run out this new exit instead of downstream and into the stream channels. It is, therefore, a possibility that fish escaped and were not enumerated. While no fish were found on the ground in the immediate vicinity of pool 1 there were three coho and one steelhead on the ground near pool 2. The premature termination of the experiment occurred 17 days after the third planting of steelhead in pool 1 and pool 2. Due to this short period of time the steelhead population may not have reached a point where emigration rates had decreased and density of the steelhead had reached an equilibrium with available space and food in the stream system. However, it appears from Fig. 16 that emigration had begun to level off. The resulting numbers of steelhead among the final population have to be interpreted with some caution.

No significant difference was found between the numbers of final resident coho in pool 1 (160) compared to pool 2 (133) ( $\chi^2 = 2.4$   $P > .05$ ) (Table 21). Steelhead final residents were more numerous in pool 1 (321) than in pool 2 (186) ( $\chi^2 = 36.0$   $P < .05$ ). Coho were less abundant in pool 1 than companion steelhead while no difference was found for these species in pool 2 ( $\chi^2 = 9.0$   $P < .05$ ,  $\chi^2 = 0.3$   $P > .05$ ).

Within the stream channel environment coho were no more numerous than steelhead in channel 1 or channel 2 ( $\chi^2 = 0.3$   $P > .05$ ). Coho in channel 1 were as abundant as coho in channel 2, while steelhead were marginally greater in abundance in channel 2 than in channel 1 ( $\chi^2_C = 2.4$   $P > .05$ ,  $\chi^2_S = 4.0$   $P < .05$ ).

Biomass. Initial biomass totaled for each species in each system was essentially the same, 383.98 gm of coho, 361.02 gm of steelhead in system 1 and 373.80 gm of coho, 356.92 gm of steelhead in system 2. Differences in biomass in the final resident population for each species and in each habitat type cannot, therefore, be attributed to initial differences.

Final biomass in pool 1 was 190.08 gm while 117.87 gm were supported in pool 2. It is apparent that more total biomass was supported in pool 1 and also greater biomass of both coho and steelhead individually were supported in pool 1 compared to pool 2 (Table 21). Further, coho and steelhead final biomass was roughly equivalent in pool 1 in contrast with pool 2 where more coho biomass than steelhead was supported.

Within the stream channels coho biomass was greater than steelhead in channel 1 and approximately the same in channel 2. Channel 1 supported

Table 21. Population characteristics of the resident population of coho salmon and steelhead trout in the experimental stream system - March 1970 - June 1970

	Pool 1		Channel 1		Pool 2		Channel 2	
	Coho	Steelhead	Coho	Steelhead	Coho	Steelhead	Coho	Steelhead
Initial population number								
3/31/70	860	859			859	860		
4/15/70	449	450			450	450		
5/17/70		650				650		
Final population number	160	321	21	27	133	186	18	44
Total % emigration	68.8	46.1			53.4	50.4		
Initial mean length(mm)								
3/31/70	34.2	29.6			34.2	29.2		
4/15/70	35.2	30.0			35.1	29.7		
5/17/70		31.0				31.1		
Final mean length	40.1	33.7	37.7	33.2	38.8	33.5	38.4	33.0
Initial mean weight(gms)								
3/31/70	0.31	0.17			0.30	0.16		
4/15/70	0.26	0.17			0.26	0.17		
5/17/70		0.22				0.22		
Final mean weight	0.61	0.29	0.54	0.28	0.52	0.26	0.58	0.26
Mortality	104	244			91	305		
Final total biomass	97.77	92.31	11.40	7.49	68.79	49.08	10.42	11.41
Percent of total	51.44	48.56	60.35	39.65	58.36	41.64	47.73	52.27
Initial density								
3/31/70 No/M <sup>2</sup>	15.97	15.95			15.97	15.95		
4/15/70 No/M <sup>2</sup>	8.34	8.35			8.35	8.35		
5/17/70 No/M <sup>2</sup>		12.07				12.07		
Final density No/M <sup>2</sup>	2.97	5.96	5.04	6.48	2.47	3.45	4.31	10.54
Initial biomass								
3/31/70 Gms/M <sup>2</sup>	4.92	2.65			4.76	2.62		
4/15/70 Gms/M <sup>2</sup>	2.21	1.41			2.18	1.39		
5/17/70 Gms/M <sup>2</sup>		2.63				2.61		
Final biomass Gms/M <sup>2</sup>	1.81	1.71	2.74	1.80	1.28	0.91	2.50	2.73

less steelhead final biomass than channel 2 while coho biomass was nearly equal between channel 1 and 2. On a percentage basis 51.4% of the biomass supported in pool 1 was contributed by coho and 58.4% in pool 2. Steelhead contributed 48.6% and 41.6%, respectively. Of the total biomass supported in channel 1, 60.3% was contributed by coho compared to 47.7% in channel 2. Steelhead contributed 39.6% in channel 1 and 52.3% in channel 2.

Density. The stream channel habitat supported greater densities of both coho and steelhead than the pool habitat (Table 21). Similar densities of coho and steelhead,  $1.81 \text{ gm/m}^2$  compared to  $1.71 \text{ gm/m}^2$  were supported in the pool habitat while coho were present at a greater density than steelhead,  $2.74 \text{ gm/m}^2$  compared to  $1.80 \text{ gm/m}^2$  in the stream channel in system 1. The initial and final larger size (length and weight) of coho seemed to be an advantage in terms of higher densities ( $\text{gm/m}^2$ ) achieved in the stream channel habitat but of no particular consequence in the pool habitat of system 1. This is contrasted with the greater density ( $1.28 \text{ gm/m}^2$ ) of coho than steelhead supported in the pool habitat ( $0.91 \text{ gm/m}^2$ ) and the lesser density of coho ( $2.50 \text{ gm/m}^2$ ) compared to steelhead ( $2.73 \text{ gm/m}^2$ ) in the stream channel habitat of system 2.

Growth. The initial average weight of the two coho populations stocked into system 1 and 2 ranged from 0.26 to 0.31 gm while the three steelhead populations stocked ranged from 0.16 to 0.22 gm. Therefore, coho had an initial size advantage. In final weight coho were at least twice as large as steelhead in either habitat type, pool or stream

channel. Coho and steelhead both attained larger size (weight) in pool 1 than in pool 2 while they were roughly equivalent in average weight in channel 1 and 2.

Mortality. Unspecified mortalities that were not directly enumerated and were not accounted for have been calculated for system 1 and 2. These mortalities could result from predation, diseases, parasites, stress or losses over screens. Within system 1 there were 104 coho and 244 steelhead compared to 91 coho and 305 steelhead in system 2 which were unaccounted for mortalities. No significant differences between coho in system 1 and coho in system 2 were found but steelhead had a significantly greater mortality in system 2 than in system 1

$$(\chi_c^2 = 0.9 >.05, \chi_s^2 = 6.8 <.05,$$

Steelhead mortalities in both systems 1 and 2 were significantly larger than coho ( $\chi_1^2 = 14.8 P<.05$ ,  $\chi_2^2 = 47.8 P<.05$ ). The higher steelhead mortality may explain the disparity in final number of steelhead in pool 1 and 2.

Mortalities were also enumerated daily in the liveboxes and were especially evident for a period following the stocking of a new population into the experimental stream systems (Table 22). The total enumerated mortalities were 123 coho and 464 steelhead in system 1 compared to 368 coho and 447 steelhead in system 2. Steelhead mortalities were again significantly higher than companion coho in both system 1 and system 2 ( $\chi_1^2 = 88.7, P<.05$ ,  $\chi_2^2 = 9.0, P<.05$ ). There were more coho mortalities in system 2 than in system 1 ( $\chi_c^2 = 122.2 P<.05$ ). Steelhead

Table 22. Emigration and mortality schedule for coho salmon and steelhead trout in the experimental stream system March 1970-June 1970

	System 1		System	
	Coho	Steelhead	Coho	Steelhead
1st emigration period				
4/12-4/17				
Number introduced	860	859	859	860
Number of mortalities	111	441	343	405
Number of emigrants	331	91	183	103
Percent emigration	44.2	21.8	35.5	22.6
2nd emigration period				
4/18-5/17 Steelhead				
4/18-5/31 Coho				
Number of residents	418	327	333	352
Number introduced	449	450	450	450
Number of mortalities	12	18	25	26
Number of emigrants	570	455	517	417
Percent emigration	66.7	59.9	68.2	53.7
3rd emigration period				
5/18-5/31				
Number of residents	285	304	241	359
Number introduced		650		650
Number of mortalities		5		16
Number of emigrants		357		467
Percent emigration		37.6		47.0

mortalities were the same in both systems ( $\chi^2 = 0.2$   $P > .05$ ). In general, steelhead mortality was higher than coho and as described above this may be a function of size. As stated before, an integration of emigration loss and loss to mortality, unaccounted and accounted for, will provide a better understanding of the differences in numbers in the final resident population.

### Behavioral Characteristics in Experimental Stream

Emigration. A graph of the cumulative number of emigrants as a function of time illustrates different responses of two populations of the same species in a similar environment (Fig. 16). The total percentage emigration was 68.8% for coho and 46.1% for steelhead in system 1, and 53.4% for coho and 50.4% for steelhead in system 2 (Table 21). This higher percentage figure for coho in system 1 represents a significant difference from the coho in system 2 ( $\chi^2 = 25.2, P < .05$ ). Within system 1 the coho, even though they were larger in length and weight, exhibited a higher number of total emigrants than did steelhead, while in system 2 differences between coho and steelhead total emigrants were not apparent ( $\chi_1^2 = 74.3 P < .05, \chi_2^2 = 1.5 P > .05$ ). Similarly, no differences were found between the total number of steelhead emigrants from system 1 or 2 ( $\chi^2 = 3.8 P > .05$ ).

A better understanding of the emigration response is afforded by a more detailed examination of emigrant number following the two introductions of coho and three introductions of steelhead (Table 22). This table separates the total number of enumerated mortalities and emigrants between new introductions of fish. From the data presented in the section on mortality it can be seen that mortality and emigration are compensatory. That is, coho in system 2 had a significantly higher number of mortalities than coho in system 1, but the number of coho emigrants from system 2 was significantly lower than system 1. Within system 1 the steelhead population had a significantly larger number of mortalities than coho, while the total number of coho emigrants was

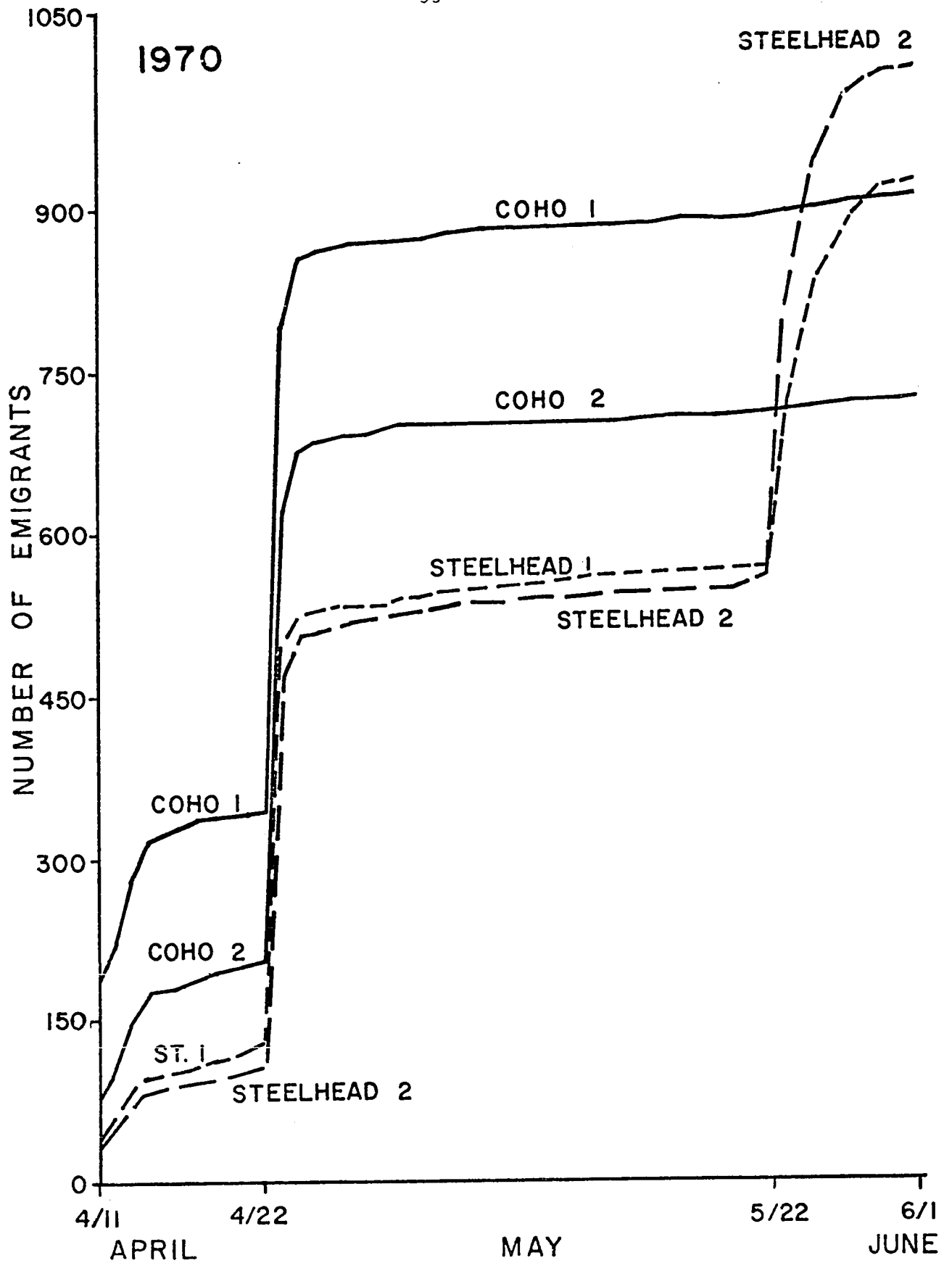


Fig. 16. Cumulative emigration of coho salmon and steelhead trout from the experimental stream system, March 1970 - June 1970.

higher than for steelhead. Viewed in this manner the unaccounted for mortalities would explain the differences in final number of resident fish. The single salient point from that discussion was that there was a significantly higher mortality of steelhead in system 2. This then explains the lower number of final steelhead residents in system 2.

Horizontal Distribution. More coho were present in the pool microhabitat of both stream channels than in the riffles

$$(\chi_1^2 = 47.4 P < .05, \chi_2^2 = 62.0 P < .05) \text{ (Table 23).}$$

Table 23. Horizontal distribution of coho salmon and steelhead trout in the experimental stream channel March 1970-June 1970

	Channel 1		Channel 2	
	Coho	Steelhead	Coho	Steelhead
Riffle	164	86	88	124
Pool	312	72	228	126

Steelhead were equally prevalent in riffle or pool microhabitats in both stream channels ( $\chi_1^2 = 1.2 P > .05$ ). Within microhabitats coho were more abundant in pools than steelhead in both channel 1 and 2

$$(\chi_1^2 = 272.2 P < .05, \chi_2^2 = 87.8 P < .05).$$

Steelhead were as abundant as coho in the riffle microhabitat of channel 2, but less numerous than coho in stream channel 1

$$(\chi_1^2 = 68.3, P < .05, \chi_2^2 = 0.2, P > .05).$$

Agonistic Behavior. Agonistic behavior in the riffle microhabitat of channel 1 was characterized by a high level of intraspecific steelhead nipping and a very low level of steelhead-initiated interspecific nipping (Table 24,  $\chi^2_{st. \times st.} = 38.9$   $P < .05$ ,  $\chi^2_{st. \times coho} = 68.2$   $P < .05$ ). Intraspecific and interspecific coho-initiated nipping were as frequent as would be expected on a random basis ( $\chi^2_{coho \times coho} = 1.3$ ,  $P > .05$ ). Similar random agonistic behavior was exhibited in the pool microhabitat of channel 1 for intraspecific and interspecific coho nipping

$$(\chi^2_{coho \times coho} = 3.4, P > .05, \chi^2_{coho \times st.} = 0.1, P > .05).$$

Steelhead intraspecific and interspecific aggression were not observed at all which was significantly different than would be expected

$$(\chi^2_{st. \times st.} = 23.1, P < .05, \chi^2_{st. \times coho} = 18.7, P < .05).$$

In channel 2 there was a high degree of coho-initiated nipping of steelhead as well as a low frequency of intraspecific aggression on the part of coho

$$(\chi^2_{coho \times coho} = 20.3, P < .05, \chi^2_{coho \times st.} = 77.0, P < .05).$$

Steelhead showed the reverse trend with high intraspecific aggression and low interspecific aggression

$$(\chi^2_{st. \times st.} = 20.7, P < .05, \chi^2_{st. \times coho} = 81.0, P < .05).$$

In the pool microhabitat as in channel 1 steelhead intraspecific and interspecific nipping were not evident whereas coho exhibited high frequencies of intraspecific and interspecific nipping

Table 24. Total numbers of intraspecific and interspecific nips observed among coho salmon and steelhead trout in the experimental stream channel - March 1970-June 1970  
 [Observation time 125 minutes.]

Rifle	Channel 1			Channel 2		
	CxC	SxS	SxC	CxC	SxS	SxC
Observed	135	130	15	38	126	0
Expected	122.5	75.7	95.9	77.8	84.2	81.0
$\chi^2$	1.3	38.9	2.1	20.3	20.7	81.0
			68.2	110.5	77.0	199.0
Pool						
Observed	174	0	17	75	0	33
Expected	151.3	23.1	18.7	51.4	10.4	23.1
$\chi^2$	3.4	23.1	0.1	10.8	10.4	4.2
			18.7	45.3	4.2	23.1
						48.5
Total numbers of fish						
Rifle						
Coho		175			147	
Steelhead		135			151	
Pool						
Coho		224			174	
Steelhead		25			75	

( $\chi^2_{\text{coho x coho}} = 10.8, P < .05, \chi^2_{\text{st. x st.}} = 10.4, P < .05,$

$\chi^2_{\text{coho x st.}} = 4.2, P < .05, \chi^2_{\text{st. x coho}} = 23.1, P < .05$ ).

In summary, coho-initiated interspecific aggression was more frequently observed than steelhead-initiated interspecific aggression in both microhabitats. High frequencies of steelhead intraspecific aggression were evidenced in both riffle microhabitats and not apparent at all in pool microhabitats. Intraspecific coho aggression was high in the pool microhabitat of channel 2 but not in the pool microhabitat of channel 1.

EXPERIMENT NO. 5. RESULTS OF STOCKING EQUAL SIZE AND SMALLER SIZE  
STEELHEAD FRY SIMULTANEOUSLY WITH NATURALLY-  
REARED COHO FRY

Procedures

Both steelhead and coho were simultaneously planted into the experimental stream system. On June 26, 1970, 300 coho were introduced into each of the systems while 679 steelhead were introduced into system 1 and 600 into system 2. All these fish were seined from Big Beef Creek except for the steelhead in system 2. The steelhead in system 2 were obtained from Chambers Creek Hatchery as fry.

The habitat of the stream channel was composed of a series of two upstream riffles followed by two downstream pools, such that the stream channel was divided equally on an area basis into riffle and pool microhabitats. Riffle depths in channel 1 ranged from 6.5 to 8.2 cm, while those in channel 2 ranged from 7.5 to 9.4 cm. Velocities generated on each riffle microhabitat extended from 7.5 to 13.6 cm/sec in channel 1 to 6.2 to 13.5 cm/sec in channel 2. Within the pool microhabitat of channel 1 depths extended from 29.4 to 35.4 cm, while those in channel 2 extended from 27.7 to 33.5 cm. Surface velocities varied from 3.1 to 5.4 cm/sec in channel 1 compared with 1.6 to 4.5 cm/sec in channel 2. Bottom velocities were less than 0.2 cm/sec in channel 1 and less than 0.6 cm/sec in channel 2. The temperature during the course of the experiment varied from 9.4 to 12.8 C with a mean value of 11.3 C.

ResultsCharacteristics of the Resident Population

Final Number. The initial number of steelhead stocked into both systems was twice that of coho (Table 25). The final resident population was composed of 65 coho and 44 steelhead in pool 1 and 79 coho and 43 steelhead in system 2. Comparing pool 1 to pool 2 no differences were found in the number of either coho or steelhead in spite of the fact that steelhead and coho in system 2 were the same size and steelhead in system 2 were twice as large as steelhead in system 1

$$(\chi_{\text{coho}}^2 = 1.4 \text{ P}>.05, \chi_{\text{st.}}^2 = 0.02 \text{ P}>.05).$$

Within the pool habitat of both systems more coho were present in the final population than steelhead

$$(\chi_1^2 = 45.5 \text{ P}<.05, \chi_2^2 = 54.4 \text{ P}<.05).$$

There were 8 coho and 9 steelhead in channel 1 and essentially the same, 8 coho and 10 steelhead, in channel 2. Within the stream channel habitat coho and steelhead numbers were not significantly different

$$(\chi_1^2 = 2.2 \text{ P}>.05, \chi_2^2 = 1.0 \text{ P}>.05)$$

The final number of steelhead supported was the same whether they were the same size as coho or half the size of coho.

Biomass. Initial biomass of coho and steelhead was approximately equal in system 1, but in system 2, steelhead biomass was about twice that of coho (Table 25). At the conclusion of the experiment the total biomass of both species was essentially the same for both systems. That is, in

Table 25. Population characteristics of the resident population of coho salmon and steelhead trout in the experimental stream system June 1970-August 1970

	Pool 1		Channel 1		Pool 2		Channel 2	
	Coho	St	Coho	St	Coho	St	Coho	St
Initial population number	300	679			300	600		
Final population number	65	44	8	9	79	43	8	10
Number of emigrants	193	471			195	524		
Percent emigration	64.33	69.37			65.00	87.33		
Initial mean length	42.7	35.0			41.4	43.7		
Final mean length	47.2	38.7	52.0	42.8	41.7	45.9	47.2	52.1
Instantaneous growth rate	0.611	0.613	1.201	1.314	0.044	0.299	0.799	1.072
Initial mean weight	0.78	0.33			0.66	0.65		
Final mean weight	1.20	0.57	1.48	0.79	0.90	0.78	1.13	1.29
Instantaneous growth rate	2.588	3.372	3.825	5.380	1.847	1.098	3.242	4.142
Survival	0.9516	0.2671			0.9516	0.8270		
Final total biomass	78.12	25.17	11.81	7.16	61.00	33.69	9.04	12.95
% of total biomass	75.6	24.4	62.3	37.7	67.8	32.2	41.1	58.9
Initial density NO/M <sup>2</sup>	5.57	12.61			5.57	11.14		
Final density NO/M <sup>2</sup>	3.96	2.68	1.92	2.16	4.81	2.62	1.92	2.39
Initial biomass GMS/M <sup>2</sup>	4.37	4.15			3.70	7.69		
Final biomass GMS/M <sup>2</sup>	1.45	0.47	2.84	1.72	1.32	0.62	2.16	3.10

pool 1 and pool 2 there were 103.29 gm and 104.69 gm, respectively, while in stream channel 1 and 2 there were 18.98 gm and 21.69 gm.

In terms of the relative contribution by each species 75.6% of the biomass in pool 1 was composed of coho compared to 67.8% in pool 2. The steelhead biomass in pool 1 was 24.4% and in pool 2 was 32.2%. Since the total biomass in pool 1 and 2 was the same, the greater contribution on the part of steelhead in pool 2 was by virtue of their initial larger size.

The final biomass in the stream channel environment serves to emphasize the results in the pools. More steelhead biomass (12.95 gm) was supported in channel 2 than channel 1 (7.16 gm). Coho contributed less biomass in channel 2 (9.04 gm) than in channel 1 (11.81 gm). Presumably, the larger initial size of steelhead was also responsible for these observed differences in biomass.

Density. There were more fish per square meter in the pool habitat than in the stream channel habitat (Table 25). Specifically, there were 3.96 coho/m<sup>2</sup>, 2.68 steelhead/m<sup>2</sup> in pool 1 and 1.92 coho/m<sup>2</sup> and 2.16 steelhead/m<sup>2</sup> in channel 1 compared to 4.81 coho/m<sup>2</sup> and 2.62 steelhead/m<sup>2</sup> in pool 2 and 1.92 coho/m<sup>2</sup> and 2.39 steelhead/m<sup>2</sup> in channel 2. However, when density is expressed as gm/m<sup>2</sup> it was evident that more coho and steelhead were supported in the stream channel than in the pools (Table 25). In the pool habitat the densities of coho, 1.45 gm/m<sup>2</sup> in pool 1 and 1.32 gm/m<sup>2</sup> in pool 2, were greater than steelhead, 0.47 gm/m<sup>2</sup> of steelhead in pool 1 and 0.62 gm/m<sup>2</sup> in pool 2. However, the density of the larger steelhead (gm/m<sup>2</sup>) in pool 2 was higher than in pool 1, while coho densities (gm/m<sup>2</sup>) were correspondingly lower in pool 2 than in pool 1.

Coho in channel 1 were present at greater densities than steelhead but in channel 2 densities were higher for steelhead. This again may be a reflection of the larger average weight of steelhead initially stocked in system 2.

Growth. Instantaneous growth rates were calculated and are shown in Table 25. Generally, instantaneous rates of growth for both length and weight were higher in the stream channel habitat than in the pool habitat for both coho and steelhead. Within the pool 1 habitat, where coho were twice as large in average weight, steelhead exhibited a higher instantaneous rate of growth in weight. In pool 2, where average weight of coho and steelhead were closer but with coho slightly larger, the instantaneous growth rate was greater for coho than for steelhead.

Within the stream channel 1 habitat coho again were twice as large in weight as steelhead but had lower instantaneous rates of growth than steelhead. Coho in channel 2 were somewhat smaller in average weight than steelhead and also had a lower instantaneous rate of growth than steelhead. Smaller steelhead in channel 1 exhibited a higher instantaneous growth rate than larger steelhead in channel 2.

Survival. Instantaneous survival rates are shown in Table 25. Survival rates for coho in both systems were the same (0.952) while steelhead rates were different. Perhaps due to their smaller initial size, steelhead in system 1 showed a significantly lower survival rate (0.267) than the larger steelhead in system 2 (0.827). Even though coho and steelhead initially were approximately equal in size and weight in system 2 the instantaneous survival rate was lower for steelhead than for coho.

Behavioral Characteristics in the Experimental Stream

Emigration. A graph of cumulative number of emigrants over time is presented in Figs. 17 and 18. Comparing stream systems, 64.3% of the coho and 69.4% of the steelhead emigrated in system 1, while 65% of the coho and 87.3% of the steelhead emigrated in system 2. The numbers of coho emigrants leaving system 1 and 2 were similar, but steelhead were not ( $\chi^2_{\text{coho}} = .01 P > .05$ ,  $\chi^2_{\text{st.}} = 13.2 P < .05$ ). The larger steelhead in system 2 emigrated at a higher rate than those in system 1. Based upon initial differences in numbers introduced, coho and steelhead in system 1 exhibited similar numbers of emigrants ( $\chi^2_1 = 0.7 P > .05$ ). However, in system 2 where coho and steelhead were approximately the same size, the number of steelhead emigrants was significantly greater than coho ( $\chi^2 = 12.3 P < .05$ ). Therefore, since the number of coho emigrants in each system was so similar it appears that coho in terms of emigration rates were not influenced by the size of the steelhead. Also, the number of steelhead emigrants in system 1, compared to system 2 steelhead can be explained as a compensation for the lower survival for these fish. A population experiencing a lower survival rate would be expected to have fewer emigrants.

Horizontal Distribution. Both coho and steelhead in channel 1 were more frequently observed in the pool microhabitat than in the riffle microhabitat ( $\chi^2_{\text{coho}} = 6.5 P < .05$ ,  $\chi^2_{\text{st.}} = 6.5 P < .05$ ) (Table 26). In channel 2 more coho and steelhead were also observed in pools than in riffles,

$$(\chi^2_{\text{coho}} = 6.8 P < .05, \chi^2_{\text{st.}} = 80.1 P < .05).$$

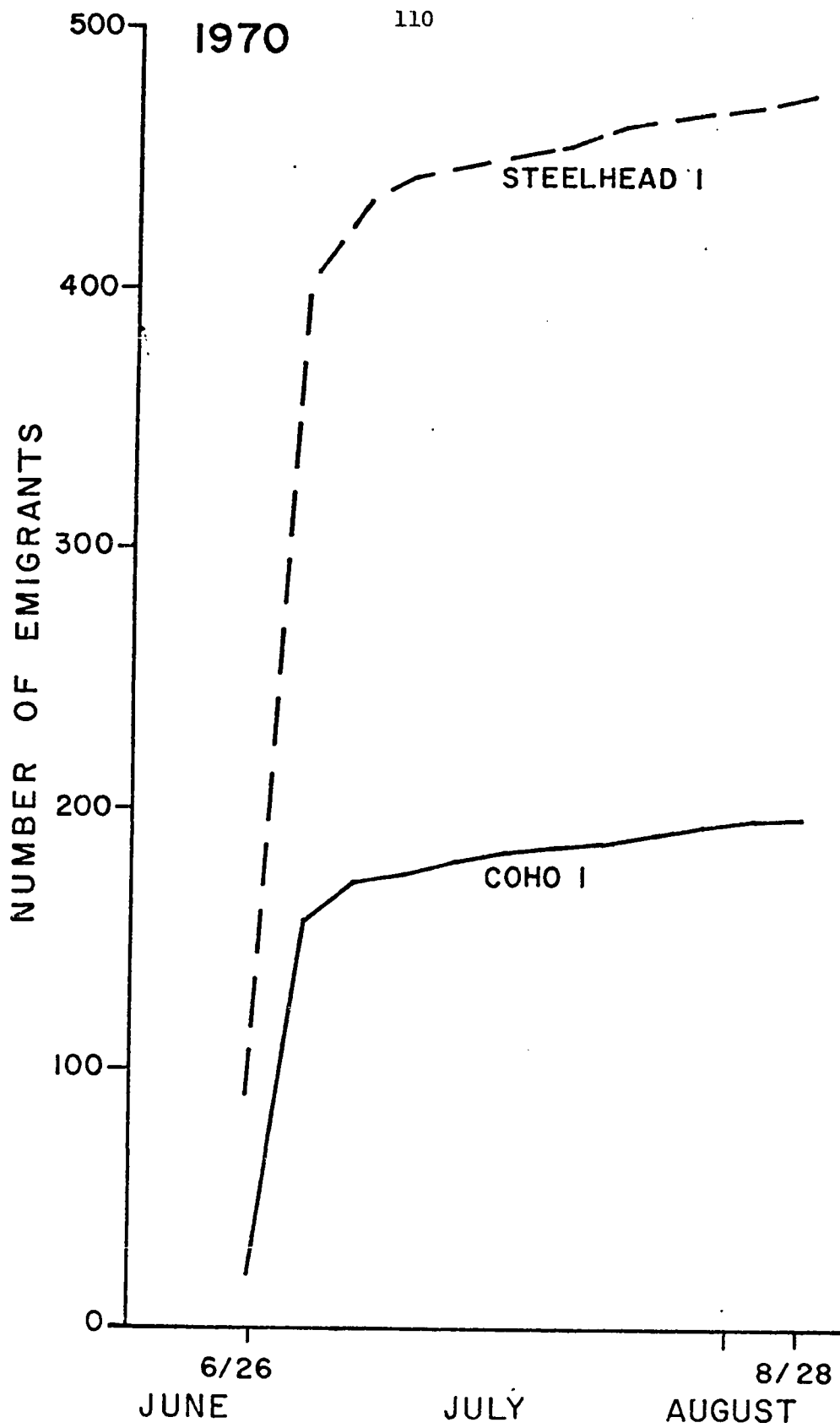


Fig. 17. Cumulative emigration of coho salmon and steelhead trout from experimental stream system 1, June 1970 - August 1970.

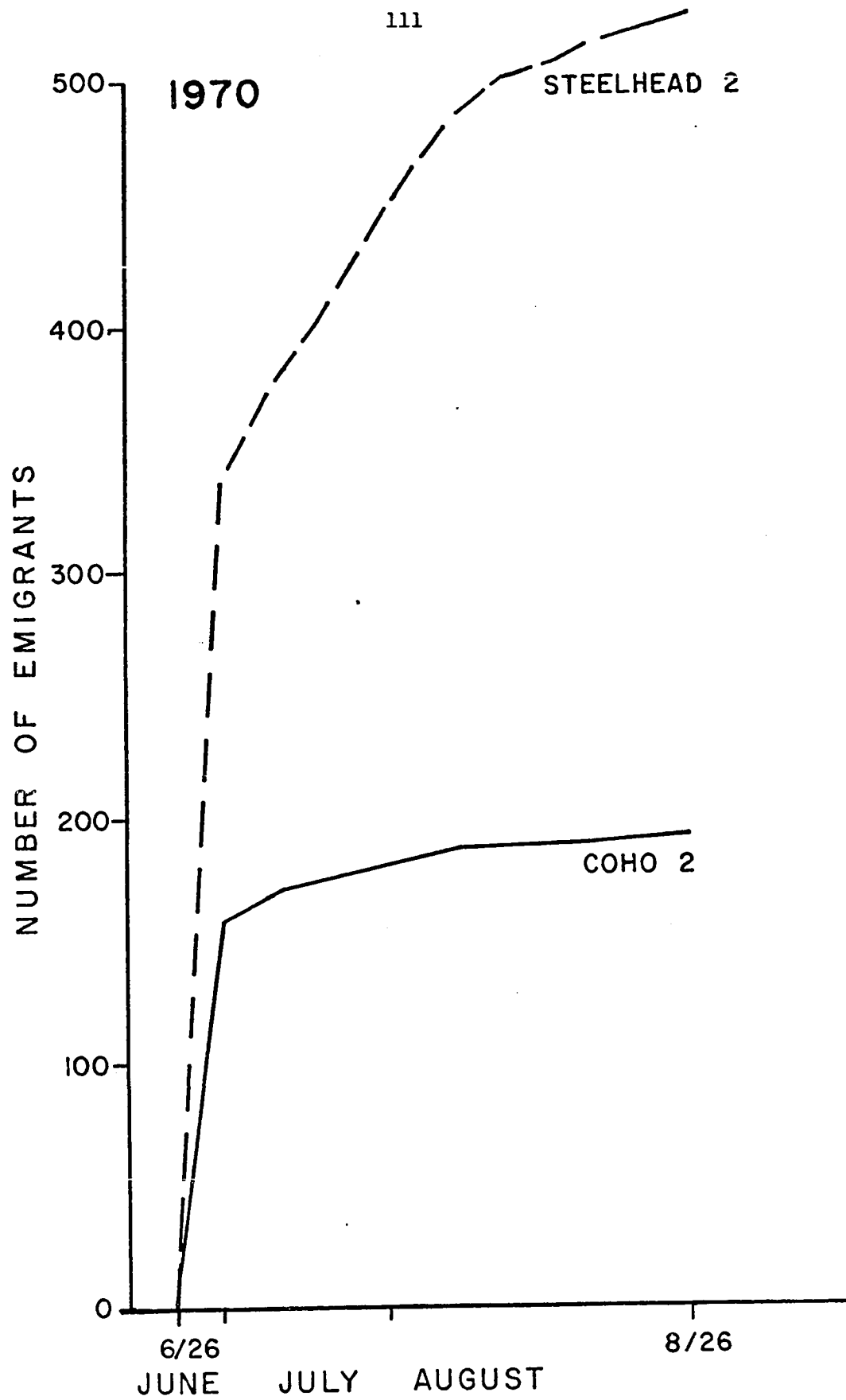


Fig. 18. Cumulative emigration of coho salmon and steelhead trout from experimental stream system 2, June 1970 - August 1970.

Table 26. Horizontal distribution of coho salmon and steelhead trout in the experimental stream channel June 1970-August 1970

	Channel 1		Channel 2	
	Coho	Steelhead	Coho	Steelhead
Riffle	46	46	49	49
Pool	74	76	67	186

While use of the microhabitats by steelhead was similar, numbers of steelhead in the pool microhabitat of channel 2 were greater than twice those in channel 1.

Vertical Distribution. Coho were found to be more frequently observed in the top half of the water column in both channel 1 and 2 (Table 27)

Table 27. Vertical distribution of coho salmon and steelhead trout in the pool microhabitat of the experimental stream channel June 1970-August 1970

	Channel 1		Channel 2	
	Surface	Bottom	Surface	Bottom
Coho	57	14	60	7
Steelhead	25	52	99	96

$$(\chi_1^2 = 26.0 P < .05, \chi_2^2 = 42.0 P < .05).$$

Steelhead were more often observed in the bottom half of the pool microhabitat in channel 1 ( $\chi^2 = 20.4, P < .05$ ) which corresponds to previous

experiments using wild steelhead. Steelhead in channel 2 were observed to be evenly distributed vertically, ( $\chi^2 = 0.05$ ,  $P > .05$ ). The steelhead in channel 2 were of hatchery origin and not native to Big Beef Creek as were steelhead in system 1.

Agonistic Behavior. Counts of steelhead and coho nips in riffle and pool microhabitats are presented in Table 28. Generally, more significant deviations from an expected distribution of the four categories were found in the riffle microhabitat than in the pool microhabitat of channel 1 ( $\chi_r^2 = 119.2$ ,  $P < .05$ ;  $\chi_p^2 = 12.7$ ,  $P < .05$ ).

Within the riffle microhabitat the very high levels of coho-initiated interspecific nipping can be contrasted with the complete absence of steelhead-initiated interspecific nipping in return. Steelhead nipping of steelhead was more frequently observed than would be expected, while coho nipping coho was less.

Agonistic behavior in the pool microhabitat of channel 1 was characterized again by the absence of steelhead-initiated interspecific nipping. Steelhead intraspecific nipping and coho-initiated interspecific nipping were about as frequent as would be expected if behavior was occurring randomly.

In stream channel 2 the total deviations from expected values in the four behavioral categories were statistically significant in both riffle and pool microhabitats ( $\chi_r^2 = 109.4$ ,  $P < .05$ ;  $\chi_p^2 = 49.9$ ,  $P < .05$ ). Within the riffle microhabitat the frequency of coho-initiated interspecific nipping was very high, and steelhead-initiated interspecific nipping was nonexistent. Coho intraspecific nipping was lower in

Table 23. Total number of intraspecific and interspecific nips observed among coho salmon and steelhead trout in the experimental stream channel - June 1970-August 1970  
 [Observation time 210 minutes.]

Riffle	Channel 1			Channel 2					
	CxC	SxS	CxS	SxC	CxC	SxS	CxS	SxC	
Observed	33	51	87	0	24	72	96	0	
Expected	59.5	29.1	41.7	41.7	43.3	57.6	47.4	47.4	
$\chi^2$	11.8	16.5	49.2	41.7	8.6	3.6	49.8	47.4	
Number of coho	81			60			60		
Number of steelhead	57			72			72		
Pool									
Observed	15	9	9	0	21	198	60	30	
Expected	9.4	7.2	8.2	8.2	66.4	242.5	52.5	52.5	
$\chi^2$	3.3	0.4	0.8	8.2	31.0	8.2	1.1	9.6	
Number of coho	48			51			51		
Number of steelhead	42			186			186		

frequency than would be expected while steelhead intraspecific nipping was higher in frequency. The greatest degree of difference from the expected frequency in the pool microhabitat was the very low frequency of coho intraspecific nipping compared with a high level of steelhead intraspecific nipping. In this pool steelhead-initiated interspecific nipping was at least documented, but it was at lower frequencies than expected if nipping were randomly directed. Coho-initiated interspecific nipping was as frequent as would be expected if occurring in a random manner. Size of steelhead in the stream channels generally did not alter the response of coho, since the trends of highly frequent initiated interspecific nipping in the riffle microhabitat were the same in channels 1 and 2 as were frequencies in the pool microhabitat. The steelhead in channel 2 were also more frequently nipping each other in the pool microhabitat than those in channel 1. Moreover, steelhead in the riffle microhabitat of channel 1 were more apt to nip each other than in channel 2.

EXPERIMENT NO. 6. RESULTS OF STOCKING LARGER SIZE HATCHERY-  
REARED COHO AND STEELHEAD INTO SYSTEMS WITH  
SMALLER PRIOR RESIDENT NATURALLY-REARED  
COHO AND STEELHEAD

Procedures

The initial population introduced into system 1 and system 2 consisted of a simultaneous plant of 200 coho and 200 steelhead on September 29, 1968. These fish were naturally reared and seined from Big Beef Creek. On October 22, 1968, 25 days later, another simultaneous planting of hatchery-reared steelhead and coho, 200 fish each, was introduced into both systems. The steelhead were Chambers Creek Hatchery stock and the coho were Minter Creek Hatchery stock.

The habitat structure of the stream channel was uniformly one complete riffle in this experiment. The depth in stream channel 1 ranged from 9.4 to 10.3 cm, while in stream channel 2 it ranged from 9.4 to 12.7 cm. Velocities generated on each riffle extended from 4.9 to 13.3 cm/sec in stream channel 1, 2.5 to 7.1 cm/sec in stream channel 2. The temperature in this experiment extended from 2.0 to 11.5 C with a mean value of 8.3 C.

Results

Characteristics of the Resident Population

Final Number. The final resident population after 112 days was composed predominantly of the hatchery coho and steelhead. The final numbers of hatchery fish in pool 1 were 195 coho and 99 steelhead compared to only 19 wild coho and 14 wild steelhead. In pool 2 there were

172 hatchery coho and 94 steelhead compared to 15 wild coho and 30 wild steelhead. In every case, pool or riffle habitat, differences between the numbers of hatchery and wild fish were statistically significant, hatchery fish being more numerous (Table 29). Within the pool habitat hatchery coho were more numerous than hatchery steelhead

$$(\chi_1^2 = 31.4, P < .05; \chi_2^2 = 22.8, P < .05).$$

Comparing wild fish, numbers of coho and steelhead were not different in pool 1, but steelhead were more prevalent than coho in pool 2

$$(\chi_1^2 = 0.8, P < .05, \chi_2^2 = 22.8, P < .05).$$

Within the stream channel habitats no coho of either hatchery or wild origin were among the final residents. Hatchery steelhead were more abundant than their wild counterparts in either channel 1 or channel 2 ( $\chi_1^2 = 17.8, P < .05$ ). Numbers of fish in either channel were similar, with 34 hatchery and 7 wild steelhead in channel 1 and 39 hatchery and 7 wild steelhead in channel 2 ( $\chi_H^2 = 0.3, P > .05$ ).

In summary, hatchery coho and steelhead were more abundant in the final population than their wild counterparts in both pool 1 and pool 2 habitats. Coho, either hatchery or wild origin, were not present in the stream channels, and hatchery steelhead were more abundant there than wild steelhead.

Biomass. The total biomass of the final resident population in pool 1 including hatchery and wild fish of both species was 2010.82 gm compared to 2082.67 gm in pool 2 (Tables 30 and 31). Of this total 5.7% and 7.8% were contributed by wild fish of both species in pools 1 and 2, respectively. In pool 1 there were 1034.8 gm of coho and 861.99 gm of

Table 29. Number of final resident coho salmon and steelhead trout of hatchery and wild origin in the experimental pool and the stream channel with chi square analysis September 1968-January 1969

Species and Origin Pool	Number		$X^2$	Statistically Significant at 5% level
	System 1	System 2		
HC1-HC2	195	176	1.5	No
HS1-HS2	99	94	0.1	No
HC1-HS1	195	99	31.4	Yes
HC2-HS2	176	94	22.8	Yes
WC1-WC2	19	15	0.5	No
WS1-WS2	14	30	5.8	Yes
WC1-WS1	19	14	0.8	No
WC2-WS2	15	30	5.0	Yes
HC1-WC1	195	19	144.8	Yes
HS1-WS1	14	99	64.0	Yes
HC2-HC2	175	15	131.8	Yes
HS2-WS1	94	30	33.0	Yes
Stream Channel				
HS1-HS2	34	39	0.3	No
WS1-WS2	7	7	0	No
HS1-WS1	34	7	17.8	Yes
HS2-WS2	39	7	22.6	Yes

Table 30. Characteristics of the resident population of wild origin coho salmon and steelhead trout in the experimental stream September 1968-January 1969

	Pool 1		Channel 1		Pool 2		Channel 2	
	Coho	Steelhead	Coho	Steelhead	Coho	Steelhead	Coho	Steelhead
Initial population number	200	200	200	200	200	200	200	200
Final population number	19	14	0	7	15	30	0	7
Number of emigrants	167	156			163	132		
Percent emigration	83.50	78.00			81.50	66.00		
Initial mean length	68.2	56.4			68.2	56.4		
Final mean length	69.6	69.0	--	69.4	70.8	70.3		67.7
Instantaneous growth rate	0.063	0.624	--	0.682	0.115	0.682	--	0.601
Initial mean length	3.26	2.11	--		3.26	2.11	--	
Final mean weight	3.41	3.57	--	3.62	3.42	3.72	--	3.42
Instantaneous growth rate	0.139	1.628	--	1.775	0.148	1.755	--	1.556
Survival	0.8106	0.5827			0.6977	0.5412		
Final total biomass	64.79	49.97	--	25.33	51.37	111.48	--	23.94
Percent of total	56.46	43.54		100.00	31.54	68.46		100.00
Initial density NO/M <sup>2</sup>	3.71	3.71			3.71	3.71		
Final density NO/M <sup>2</sup>	0.35	0.26	--	1.68	0.28	0.56	--	1.68
Initial biomass GMS/M <sup>2</sup>	12.11	7.83			12.11	7.83		
Final biomass GMS/M <sup>2</sup>	1.20	0.93	--	6.08	0.95	2.07	--	5.73

Table 31. Characteristics of the resident population of hatchery origin coho salmon and steelhead trout in the experimental stream system September 1968-January 1969

	Pool 1		Channel 1		Pool 2		Channel 2	
	Coho	Steelhead	Coho	Steelhead	Coho	Steelhead	Coho	Steelhead
Initial population number	200	200	200	200	200	200	0	39
Final population number	195	99	0	34	172	94	0	39
Number of emigrants	8	64			28	67		
Percent emigration	4.00	32.00			14.00	33.50		
Initial mean length	86.2	113.9			94.2	116.0		
Final mean length	88.2	113.4	--	118.0	97.3	116.1	--	118.0
Instantaneous growth rate	0.092	-0.014	--	0.157	0.130	0.003	--	0.074
Initial mean weight	5.10	8.76			5.92	9.00		
Final mean weight	5.30	8.71	--	9.23	6.24	9.01	--	9.24
Instantaneous growth rate	0.154	-0.023		0.227	0.211	0.005		0.114
Survival	1.000	0.9418			1.000	1.000		
Final total biomass	1034.08	861.99	--	313.84	1072.69	847.13	--	315.28
Percent of total	54.54	45.46	--	100.00	55.87	44.13	--	100.00
Initial density NO/M <sup>2</sup>	3.71	3.71			3.71	3.71		
Final density NO/M <sup>2</sup>	3.62	1.82	--	8.17	3.19	1.74	--	9.34
Initial biomass GMS/M <sup>2</sup>	18.94	21.97			21.97	33.43		
Final biomass GMS/M <sup>2</sup>	19.20	16.00	--	75.39	19.92	15.73	--	86.33

steelhead compared to 1072.09 gm of coho and 847.13 gm of steelhead in pool 2. More wild coho biomass, 64.79 gm, was supported in pool 1 than wild steelhead, 49.97 gm, where in pool 2 there was more wild steelhead biomass, 111.48 gm, than wild coho biomass, 51.37 gm.

Within the stream channel habitat (100% riffle) the total biomass of hatchery and wild steelhead was 339.17 gm in channel 1 and 339.22 gm in channel 2. Wild steelhead contributed 8.1% and 7.6% of the total biomass in pool 1 and pool 2, respectively. In channel 1 there were 313.84 gm of hatchery steelhead and 25.33 gm of wild steelhead compared to 315.28 gm of hatchery steelhead and 23.94 gm of wild steelhead in channel 2.

Density. Densities, whether expressed as number/m<sup>2</sup> or gm/m<sup>2</sup> reflect the same trends as absolute numbers and biomass, that is they show by a considerable magnitude (Tables 30 and 31) the density of both hatchery coho and steelhead was greater than wild coho and steelhead in the pool habitat. However, the significant point that a relative measure of numbers and biomass such as density brings out is that the stream channel supported a greater density, numbers/m<sup>2</sup> or gm/m<sup>2</sup> than the pool. In this experiment the stream channel was 100% riffle and in terms of gm/m<sup>2</sup> it supported 75.39 gm/m<sup>2</sup> of hatchery steelhead in channel 1 and 23.94 gm/m<sup>2</sup> in channel 2. The density of hatchery steelhead in channel 1 was 4.7 times that in pool 1, whereas in channel 2, 5.5 times the density was obtained. Wild steelhead density in channel 1 was 6.5 times that in pool 1 and in channel 2, 218 times that in pool 2.

Growth. Instantaneous growth rates for length and weight have been computed for both hatchery and wild fish and are shown in Tables 30 and 31. Prior resident steelhead which were initially smaller in length and weight than companion coho showed a significantly better growth in length and weight than coho prior residents in both pool habitats. Wild steelhead growth rate was slightly higher in channel 1 than in pool 1 and slightly lower in channel 2 than in pool 2.

Hatchery coho exhibited higher instantaneous growth rates than hatchery steelhead in both pools 1 and 2. Within channels 1 and 2 steelhead growth rates were higher for both length and weight than steelhead in pools 1 and 2. Comparisons of instantaneous growth rates between hatchery and wild fish indicated that wild steelhead had higher rates in both pool and stream channel habitat than did hatchery steelhead, while wild coho had somewhat slower rates of growth than hatchery coho in the pool environment. However, based upon the shape of the growth curve this comparison in instantaneous rates of growth between small and large fish is probably not valid since it reflects different points on the curve. Specifically, the average weight of hatchery coho was 5.30 gm and 6.24 gm in pools 1 and 2, respectively, while wild coho were 3.41 gm and 3.42 gm, respectively. Hatchery steelhead were 8.71 gm and 9.00 gm in average weight in pools 1 and 2, respectively. In channels 1 and 2 hatchery steelhead average weight was 9.23 gm and 9.24 gm, respectively, compared to 3.62 gm and 3.42 gm for wild steelhead, respectively.

Survival. Annual instantaneous survival rates have been calculated for both wild and hatchery stocks and are presented in Tables 30 and 31.

Survival rates for the prior resident wild stocks were appreciably lower than those for the more recently introduced hatchery stocks. Hatchery coho in both pools and hatchery steelhead in system 2 had no mortality at all, while steelhead in system 1 had a survival of 0.9418. Wild coho had significantly higher survival rates than companion wild steelhead in both systems.

#### Behavioral Characteristics in the Experimental Stream

Emigration. Out of the total number of wild coho and steelhead introduced into both systems, 82.5% of the coho and 72% of the steelhead emigrated from the system (Fig. 19). There was no difference between the number of coho emigrants in either system or of steelhead in either system

$$(\chi^2_{\text{coho}} = 0.05, P > .05, \chi^2_{\text{st.}} = 2.0 P > .05).$$

The number of coho emigrants was not significantly different from the number of steelhead emigrants in either system 1 or system 2

$$(\chi^2_1 = 0.2, P > .05; \chi^2_2 = 3.2, P > 0.5).$$

The results with wild fish are in sharp contrast to that found for hatchery fish. While the hatchery-reared fish were introduced into the system after the wild fish, only 4.0% of the hatchery coho and 32.0% of the hatchery steelhead emigrated in system 1 compared to 14.0% of the hatchery coho and 33.5% of the hatchery steelhead in system 2 (Fig. 20). Significantly more coho emigrated from system 2, but the number of steelhead emigrants was similar in system 1 and 2

$$(\chi^2_{\text{coho}} = 11.0, P < .05, \chi^2_{\text{st.}} = 0.1 P > .05).$$

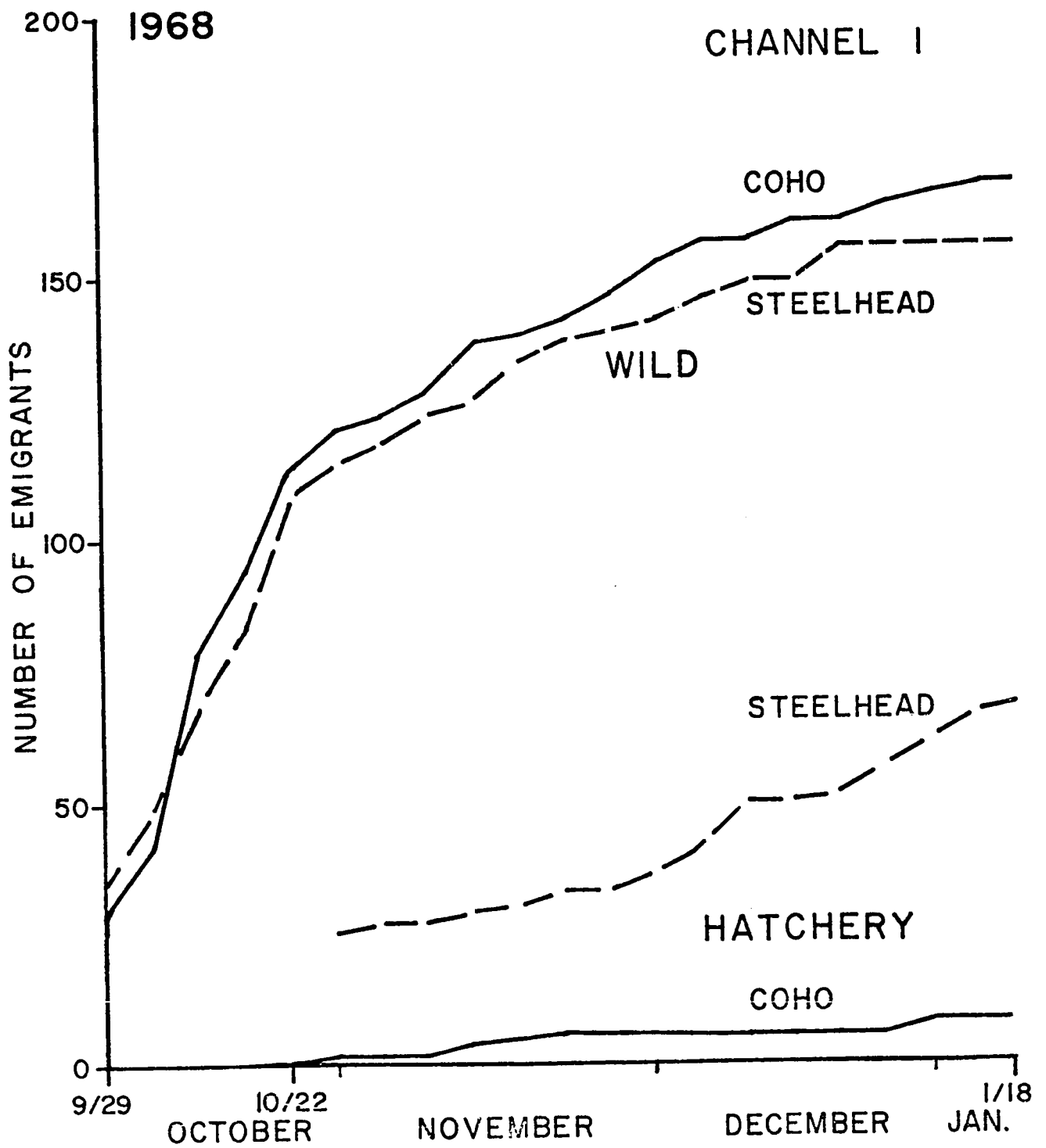


Fig. 19. Cumulative emigration of wild origin and hatchery origin coho salmon and steelhead trout from experimental stream system 1, September 1968 - January 1969.

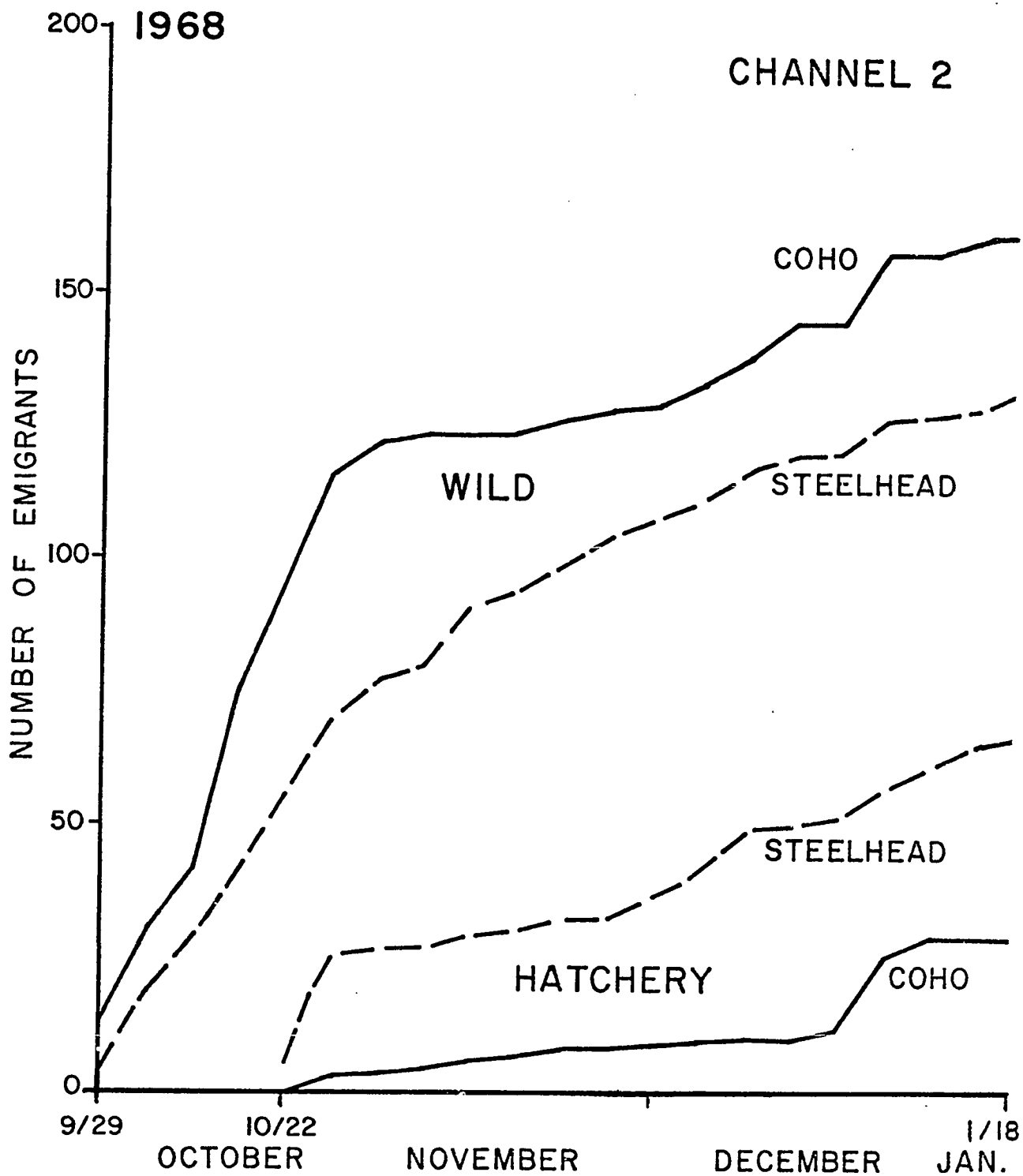


Fig. 20. Cumulative emigration of wild origin and hatchery origin coho salmon and steelhead trout from experimental stream system 2, September 1968 - January 1969.

Steelhead emigrated to a greater extent than coho in both system 1 and 2

$$(\chi_{\text{coho}}^2 = 11.0, P < .05, \chi_2^2 = 16.0, P < .05).$$

Generally, larger numbers of wild coho and steelhead emigrated from system 1 and 2 than hatchery coho and steelhead (Tables 30 and 31).

Table 32 shows the number of wild coho and steelhead emigrating after the introduction of hatchery fish and the percentage of the total emigrants these numbers represent. These data indicate that 43.7% and 40.5% of the wild coho emigrated after the introduction of hatchery fish in system 1 and 2, respectively. During this same time 47.4% and 57.6% of the wild steelhead in system 1 and 2, respectively, emigrated. A greater number of wild coho than hatchery coho emigrated in both systems

$$(\chi_1^2 = 72.6, P < .05, \chi_2^2 = 15.4, P < .05).$$

However, the number of hatchery steelhead and wild steelhead emigrating after the introduction of hatchery fish in both systems was not statistically different

$$(\chi_1^2 = 0.8, P > .05; \chi_2^2 = 0.6, P > .05).$$

Table 32. Emigration of hatchery origin and wild origin coho salmon and steelhead trout after introduction of hatchery origin coho salmon and steelhead trout

	Pool 1				Pool 2			
	Wild Coho	St	Hatchery Coho	St	Wild Coho	St	Hatchery Coho	St
Number of emigrants	73	74	8	64	66	76	28	67
Percent of total emigrants	43.7	47.4			40.5	57.6		

Horizontal Distribution. Wild steelhead were more abundant than wild coho in both riffle microhabitats prior to the introduction of hatchery fish

$$(\chi_1^2 = 73.0, P < .05; \chi_2^2 = 4.5, P < .05) \text{ (Table 33).}$$

After the introduction of hatchery fish, wild steelhead were also more abundant than wild coho

$$(\chi_1^2 = 73.0, P < .05; \chi_2^2 = 33.2, P < .05).$$

Hatchery steelhead were significantly more abundant than hatchery coho in both riffle microhabitats

$$(\chi_1^2 = 618.8, P < .05, \chi_2^2 = 490.4, P < .05).$$

In the riffle microhabitat steelhead of wild and hatchery origin maintained greater abundance than coho.

Table 33. Horizontal distribution of wild origin coho salmon and steelhead trout before and after the introduction of hatchery origin coho salmon and steelhead trout in the experimental stream channel September 1968-January 1969

	Coho	Wild Steelhead	Coho	Hatchery Steelhead
Before				
Channel 1	85	161		
Channel 2	74	102		
After				
Channel 1	92	250	12	654
Channel 2	60	142	14	531

Agonistic Behavior. Prior to the introduction of hatchery fish agonistic behavior among wild fish was characterized in channel 1 by high frequencies of intraspecific steelhead nipping and high frequencies of coho-initiated interspecific nipping (Table 34)

$$(\chi^2_{st. \times st.} = 10.0, P < .05, \chi^2_{coho \times st.} = 6.5, P < .05).$$

Steelhead-initiated interspecific nipping was absent while intraspecific coho nipping was as frequent as would be expected on a random basis

$$(\chi^2_{st. \times coho} = 26.8, P < .05; \chi^2_{coho \times coho} = 0.3, P > .05).$$

The single most frequent agonistic activity in channel 2 was intraspecific steelhead nipping ( $\chi^2_{st. \times st.} = 370.0, P < .05$ ). Both interspecific coho- and steelhead-initiated nipping were significantly less frequent than expected with the difference in steelhead interspecific nipping being of greater magnitude

$$(\chi^2_{coho \times st.} = 10.0, P < .05, \chi^2_{st. \times coho} = 26.7, P < .05).$$

Intraspecific coho nipping also occurred at lower frequencies than expected ( $\chi^2 = 10.7, P < .05$ ).

In general, in the riffle microhabitats before hatchery fish were introduced, steelhead intraspecific aggression occurred at high frequencies, while steelhead-initiated interspecific aggression was very low in frequency. Coho actively nipped steelhead in channel 1 but not to any extent in channel 2, and coho less frequently nipped themselves.

Subsequent to the introduction of hatchery fish most frequencies of agonistic behavior were low but similarly distributed, so that observations in channel 1 and channel 2 were combined. Within the general

Table 34. Total numbers of intraspecific and interspecific nips observed among wild and hatchery origin coho salmon and steelhead trout in the experimental stream channel September 1968-January 1969 - Observation time 200 minutes

	Channel 1			Channel 2				
	CxC	SxS	CxS	SxC	CxC	SxS	CxS	SxC
Before								
Observation time: 200 minutes								
9/29/68 - 10/22/68:								
Observed	20	50	40	0	66	120	27	13
Expected	22.4	32.1	26.8	26.8	98.5	24.6	49.3	49.3
$\chi^2$	0.3	10.0	6.5	26.8	10.7	370.0	10.0	26.7
								417.5
After								
Observation Time: 200 minutes								
10/23/68 - 1/18/69:								
WxW observed	17	7	3	17				
expected	3.4	12.4	6.5	6.5				
$\chi^2$	5.4	2.3	1.9	16.9				26.5
WxH observed	0	7	0	0				
expected	1.0	43.9	23.1	1.8				
$\chi^2$	1.0	31.0	23.1	1.8				56.9
HxH observed	0	242	0	14				
expected	0.3	154.9	6.5	6.5				
$\chi^2$	0.3	49.0	6.5	8.6				64.4
HxW observed	0	27	0	11				
expected	1.0	43.9	1.8	23.1				
$\chi^2$	1.0	6.5	1.8	6.3				15.6

category of wild fish nipping wild fish, high frequencies of intraspecific coho nipping and steelhead-initiated interspecific nipping were observed

$$(\chi^2_{\text{coho x coho}} = 3.4, P > .05; \chi^2_{\text{st. x coho}} = 16.9, P < .05).$$

Both steelhead intraspecific nipping and coho-initiated interspecific nipping were equally as frequent as would be expected on a random basis

$$(\chi^2_{\text{st. x st.}} = 31.0, P < .05).$$

The occurrence of agonistic activity among hatchery fish was exclusively evidenced by hatchery steelhead. Both intraspecific steelhead nipping and steelhead-initiated interspecific nipping were more frequent than expected

$$(\chi^2_{\text{st. x st.}} = 49.0, P < .05, \chi^2_{\text{st. x coho}} = 8.6, P > .05).$$

Hatchery fish nipping wild fish was also a phenomenon that was not recorded at all for coho intraspecific nipping and coho-initiated interspecific nipping. Both steelhead intraspecific nipping and interspecific steelhead-initiated nipping were recorded but occurred at frequencies which were significantly lower than expected on a random basis

$$(\chi^2_{\text{st. x st.}} = 6.5, P < .05; \chi^2_{\text{st. x coho}} = 6.3, P < .05).$$

In general, agonistic activity between hatchery and wild fish was of no significance. Between hatchery fish, steelhead exhibited a high level of intraspecific and interspecific aggression. Among wild fish, high levels of interspecific steelhead-initiated aggression and intraspecific coho aggression were evidenced.

Summary and Discussion

It is clear that an initial size advantage for coho does not lead to a simple exclusion of steelhead. In the first experiment where postemergent coho and steelhead fry were stocked simultaneously into the experimental stream system the coho fry were twice as large as the steelhead initially. This larger size of the coho provided them with no greater contribution in terms of numbers or biomass in the final population of either habitat type. In fact, in pool 1 coho were fewer in number than steelhead in the final population, while in pool 2 they were equal in abundance and in final biomass were greater than steelhead. No differences by species were exhibited in the stream channel habitat. In the final population coho were twice as large as steelhead. Coho also exhibited higher survival than steelhead.

The purpose of the second experiment was to determine whether there was any effect of varying the steelhead size. In this experiment steelhead in system 2 were equally as large as coho initially while steelhead in system 1 were approximately one-half as large as coho. The final number of coho and steelhead was the same in both systems. The number of coho was not affected by steelhead size. In contrast, the data on biomass supported within the pool habitat suggest that larger size conveyed an advantage to steelhead, because steelhead made up a higher percentage of that biomass in pool 2 (32.2%) than in pool 1 (24.4%). This trend was more strongly shown in the stream channel habitat for both numbers and biomass. That is, more steelhead biomass was supported in channel 2 where steelhead and coho were the same size than in channel 1

where steelhead were half the size of coho. Also, coho biomass was less than steelhead biomass in channel 2 and greater than steelhead in channel 1 where steelhead were smaller to begin with. The greater combined biomass in stream channel 2 cannot be attributed to a larger quantity of available food since drifting invertebrate food supply was sampled on a 24-hr basis and found to be essentially equivalent in each stream channel.

Larger steelhead exhibited higher instantaneous survival than smaller steelhead but lower survival than coho.

In the third experiment, the effect of introducing larger size hatchery coho and steelhead into populations of prior resident wild coho and steelhead of smaller size was tested. In the initial populations of wild fish the coho were larger than the steelhead. In the introduced hatchery fish the steelhead were larger than the coho.

The composition of the final resident population after 122 days was predominantly of hatchery coho and steelhead in terms of numbers and biomass supported. More hatchery coho than steelhead were present in the pool habitat. Of the original prior resident, wild population, coho and steelhead were equally abundant in pool 1 and steelhead were more numerous in pool 2. Within the stream channels, which were 100% riffle, the final resident population was composed solely of steelhead, with hatchery steelhead being more numerous than wild steelhead. The smaller wild population represented a rather negligible proportion of the total biomass supported in the experimental stream, being 5.7-7.8% in pools 1 and 2, respectively and 8.1-7.6% in riffles 1 and 2, respectively. The more significant consideration is the inordinately high density ( $\text{gm/m}^2$ )

that the hatchery coho and steelhead accounted for in either habitat type. In this connection the density of hatchery steelhead in the stream channel's riffle microhabitat was 4.7 and 5.5 times greater than pools 1 and 2, respectively. If these densities of hatchery fish are compared to densities of wild fish during a similar season in the 1969 experiment on effects of prior residence, it can be seen that densities of hatchery coho were from 4.3 to 6.8 times greater than wild coho in pools 1 and 2, respectively, while hatchery steelhead were 26.7 to 5.6 times greater than wild steelhead in pools 1 and 2, respectively. Within the stream channel habitat which was 100% riffle in the hatchery fish experiment and 50% riffle and 50% pool in the 1969 wild fish experiment the densities were 16.2 to 4.8 times greater for hatchery steelhead than wild steelhead in channels 1 and 2, respectively. This difference in density between wild fish and hatchery fish seems to be a direct contradiction to the bioenergetics of territory size and must be of poor adaptive value for hatchery fish in nature. This point will be expanded upon in a later discussion.

Another rather significant point is the specific habitat preference expressed by both hatchery and wild coho. There was no representation of coho in the final population of the riffle habitat and very few hatchery coho ever emigrated from the pool habitat.

Emigration behavior is probably a result of many factors within and between populations of two species. It may be a reflection of interspecific density adjustments whereby numbers of subordinate species are forced to leave a habitat. If viewed in this manner we would have expected more steelhead to emigrate in the first experiment where coho

were larger than steelhead. In fact, coho exhibited a greater number of emigrants than steelhead in system 1 and an equal number of emigrants to steelhead in system 2.

Coho in the second experiment did not show any different emigration behavior whether steelhead were equal in size or smaller. However, larger steelhead had greater numbers of emigrants than smaller steelhead. This difference in response may be due in part to a compensation for lower survival among the smaller steelhead or due to a larger spatial requirement for larger fish.

When larger size hatchery fish were stocked into the stream systems which already were occupied by wild fish the hatchery fish emigrated to a limited extent. Only 4.0 and 14.0% of the coho emigrated from systems 1 and 2, respectively, and 32.0 and 33.5% of the steelhead from systems 1 and 2, respectively.

After the larger hatchery fish were introduced into the stream system more wild coho than hatchery coho emigrated, while no differences were observed between wild and hatchery steelhead. The inclination of hatchery fish to stay in the system is probably not the result of their social dominance. Their higher densities, poorer growth rates, and lower condition factors suggest the reverse. I speculate that the lack of dispersion and higher densities are disadvantageous and due to an adaptation to the hatchery rearing environment. The high densities experienced by fish in the hatchery would tend to exert a selective pressure such that those fish which could not adapt to crowding would be eliminated. Therefore, these fish do not disperse but remain in loose aggregates.

The direct observation of agonistic behavior in the first experiment indicated that the larger coho initiated more nipping against steelhead than did steelhead against coho regardless of habitat type. Coho-initiated interspecific nipping was just as intense whether the steelhead were equal in size or smaller than the coho in the second experiment. There was no steelhead-initiated nipping of coho in return. Therefore, size of coho does not seem to be important in terms of attainment of social dominance in the stream channel environment.

Agonistic interactions between larger coho and steelhead of hatchery origin and smaller, wild coho and steelhead were practically nonexistent. Evidence of hatchery steelhead nipping wild steelhead, hatchery steelhead nipping wild coho, and wild steelhead nipping hatchery steelhead were observed but all occurred at frequencies lower than expected by chance. Other studies confirm that most intense interactions occur between individuals of the same size (Chapman, 1962; Newman, 1956). Before hatchery fish were introduced into the stream system, wild coho were more actively nipping wild steelhead while steelhead were most actively nipping other steelhead. This might suggest that coho were somehow inhibited interspecifically by the introduction of hatchery fish while steelhead were not. In contrast, steelhead were more active intraspecifically prior to the introduction of hatchery fish while coho were more active after their introduction.

In conclusion, analysis of agonistic behavior suggests that juvenile coho salmon are dominant over steelhead trout, regardless of size. It does not appear that larger sized hatchery fish were socially dominant over their wild counterparts. It would not appear to me to be justifiable to conclude from comparisons of agonistic behavior that coho will

force out steelhead regardless of size or that social dominance will have an overriding effect upon the composition of the ultimate population. In fact, species specific habitat preferences and intraspecific effects seem to play a greater role in the final species composition of experimental populations than do the direct interactions between species.

## GENERAL DISCUSSION

The purpose of the general discussion is to integrate the results of the natural stream studies and the experimental stream studies and to attempt to generalize on the outcome and determine what the implications are for management. One approach was to look at a stepwise regression to identify factors which had an effect on the abundance and habitat preference of coho and steelhead. At the outset we were attempting to describe the best measures of abundance, distribution and the factors affecting them.

### Carrying Capacity

In an effort to determine the best method of expressing carrying capacity in the major habitat types of pool and stream channel both the number and the total weight of fish per unit of space (area or volume) were analyzed by measuring the degree of relationship that these variables have to each other. All the data from Big Beef Creek and the experimental stream system were lumped together for this correlation. The results of this analysis are shown in Table 35. The highest correlation coefficients were found for the relationship between coho number and area of the stream section,  $r = .74$ , and coho number and volume of the section,  $r = .79$ . There was no significant difference between these two values, and therefore, since area is a much easier measurement to obtain it would be a more useful definition of carrying capacity. The correlation coefficients of steelhead number against area,  $.56$ , and volume,  $.67$ , were somewhat lower than those for coho, but they were significant at the 1% level. Acknowledging that the relationship with volume has a

better correlation than area it was nevertheless decided to use number of steelhead per unit area as an expression of carrying capacity for purposes of consistency with coho and ease of measurement. Chapman's (1964) work in three small streams in Oregon indicated that production of coho was best correlated with stream area. Burns (1971), also studying coho and steelhead, found that absolute biomass best correlated with stream surface area.

Table 35. Correlation coefficients for stream area, volume, and absolute number and biomass of coho salmon and steelhead trout for both Big Beef Creek and the experimental stream system

Dependent variable	Independent variable	R
Coho number	Area	0.74**
Coho number	Volume	0.79**
Steelhead number	Area	0.56**
Steelhead number	Volume	0.67**

\*\* Significant at 1% level.

#### Habitat Segregation

Regardless of planting regime, coho were more abundant than steelhead in pools during all three spring-summer experiments (1968, 1969, and 1970). Coho contributed 64-76% of the biomass supported in the pool habitat during this same season for all three years, with steelhead contributing the remaining 24-36%. The only exception to this was the experiment that was terminated by accident in June 1970, which resulted in fewer coho than steelhead in pool 1 but equal numbers in pool 2. I don't think this experiment lasted long enough to invalidate the results

of all the other experiments. Even so, coho in this experiment contributed 51-58% of the biomass supported within the pool habitat.

In the fall experiments coho were not as selective in their habitat choice. During the summer-fall experiment of 1969 with under-yearling coho and steelhead fry, there were more coho than steelhead in the final resident population in pool 1, while no significant differences were found in pool 2. The experiment in the fall and winter of 1968 found hatchery coho final residents being more numerous than steelhead, but wild coho were equally as numerous as steelhead in pool 1 and less than steelhead in pool 2. Coho contributed 51-88% to the final biomass during 1969 and 31-36% for wild coho and 54-56% for hatchery coho in 1968.

Irrespective of seasonal preferences coho in the pool habitat always contributed a minimum of 51% of the biomass supported in the final population with the exception of the one wild coho population in pool 2 during the winter of 1968. Comparing this to the natural stream in Big Beef Creek during the summer of 1969 and 1970, age 0 coho contributed from 51-59% of the total biomass in the two pools in the creek, while age 0 steelhead contributed 14-34%, and the remaining 14-27% was represented by age 1+ steelhead. These numbers are close to those in the experimental systems if 1+ steelhead are omitted. This serves to indicate the greater complexity of the natural environment. The contribution to the total biomass of the natural stream pool habitat by under-yearling coho and steelhead was less than in the experimental stream system where age 1+ steelhead were not included.

When the stream channel habitat was all riffle, coho whether of hatchery or wild origin were not present among the final residents in the winter. In contrast, during the summer no significant differences in the number of coho and steelhead in the final resident population were found. Specifically, in summer, steelhead made up 51-61% of the biomass supported in the riffle habitat.

When the stream channels were divided equally in area into pools and riffles, irrespective of season, no significant differences were seen in numbers of coho or steelhead in the final resident population. In terms of biomass supported, steelhead contributed from 38-63% in the spring-summer season and 48-73% in the fall-winter experiment of 1969.

Therefore, in general, spatial overlap by coho and steelhead occurred in the stream channel and pool habitats in all experiments except in the winter of 1968 when the habitat was 100% riffle and both wild and hatchery steelhead were the final residents. Moreover, simple competitive exclusion in either habitat type was not evidenced.

Within each habitat type stepwise multiple regression analyses were used to determine those parameters which most successfully predicted final carrying capacity of both coho and steelhead. Parameters that were used in multiple regression had been chosen by the degree of correlation each exhibited under single regression analysis with final carrying capacity for coho or steelhead. Accepting the number of fish per area as the "best" expression of carrying capacity the relative role of various parameters effecting this final carrying capacity was determined in the experimental stream system where some control of environmental

variability was possible. In the pool habitat for all experiments the best predictor of coho number/m<sup>2</sup> was steelhead number/m<sup>2</sup>, which accounts for 60.8% of the observed variability (Table 36). By including the initial coho number/m<sup>2</sup>, into the equation an additional 22.7% of the variability was accounted for which together with the initial steelhead number/m<sup>2</sup>, at 6.9%, accounts for 90.47% of the total observed variability. The fact that a positive regression of coho carrying capacity on carrying capacity of steelhead resulted would imply the possibility of coexistence or at least suggest that steelhead did not have a depressing effect on coho.

Table 36. Results of stepwise multiple regression analysis for carrying capacity of coho in the experimental pool

Dependent variable	Independent variable	F	R <sup>2</sup>	R
Coho NO/M <sup>2</sup>	Steelhead NO/M <sup>2</sup>	27.96**	.61	.78
	Coho initial NO/M <sup>2</sup>	43.11**	.83	.91
	Steelhead initial NO/M <sup>2</sup>	50.64**	.90	.95
	Coho percent emigrants	36.35**	.91	.95
	Steelhead wt/m <sup>2</sup>	27.44**	.91	.95
	Steelhead initial wt/m <sup>2</sup>	21.53**	.91	.95
	Coho initial wt/m <sup>2</sup>	17.10**	.91	.95

\*\* Significant at 1% level.

A similar analysis was applied to the final carrying capacity for steelhead in the pool habitat. The ability of the pool habitat to support coho is the best predictor of steelhead carrying capacity and accounts for 92.4% of the observed variability (Table 37). The other

six variables only account for an additional 3.7% of the variability. Again, for the range of densities that were used in the experiments if the environment would support coho it would support steelhead. This sort of relationship is not one that would result if competition were severe in the pool habitat.

Table 37. Results of stepwise multiple regression analysis for carrying capacity of steelhead in the experimental pools

Dependent variable	Independent variable	F	R <sup>2</sup>	R
Steelhead NO/M <sup>2</sup>	Coho NO/M <sup>2</sup>	13.43**	.92	.96
	Coho initial MO/M <sup>2</sup>	67.58**	.93	.96
	Coho wt/m <sup>2</sup>	42.36**	.93	.97
	Steelhead initial NO/m <sup>2</sup>	34.21**	.94	.97
	Coho initial wt/m <sup>2</sup>	33.02**	.96	.98
	Steelhead % emigrants	25.07**	.96	.98

\*\*Significant at 1% level.

Where both pool and riffle microhabitat types were present an effort was made to determine what environmental parameters influenced coho and steelhead habitat preference by running a stepwise multiple regression. Two of the differences between these habitats were their velocity and depth. The only other significant factor was the presence of the other species.

Depth explained 57.5% of the variability in observed coho density and 52.3% of the variability in steelhead observed density (Table 38). For both coho and steelhead the knowledge of the observed density of the other species added little to the explanation of the variation in the

Table 38. Results of stepwise multiple regression analysis for the observed density of coho and steelhead trout in experimental stream channel

Dependent variable	Independent variable	F	R <sup>2</sup>	R
Observed coho number/M <sup>2</sup>	Depth	52.79**	.57	.76
	Steelhead number/M <sup>2</sup>	1.47	.59	.77
	Velocity	0.37	.59	.77
Observed steelhead number/M <sup>2</sup>	Depth	42.83**	.52	.72
	Steelhead number/M <sup>2</sup>	1.47	.54	.73
	Velocity	0.19	.54	.74

\*\*Significant at the 1% level.

dependent variable and even less was explained by knowing the velocity. Since the regression was positive for depth it suggests that over the range in depths (4.2 cm to 35.4 cm) in the stream channel more fish were found when pools were deepest. Within the range of depths described for the stream channel habitat, production levels for both coho and steelhead were found to be comparable to those within the pool habitat. In fact, a compilation of salmonid production data from Big Beef Creek, the experimental stream system and three streams within the Alsea River system on the Oregon Coast (Chapman, 1962) suggests that the stream channel habitat was capable of producing equivalent or a higher biomass per unit area than the pool habitats (Table 39). If the data from the stream channel which again ranges in depth from only 4.2 cm to 35.4 cm can be extrapolated to the natural stream then these areas are sources of production which may equal that from the larger and more conspicuous

Table 39. Numerical and weight densities from Big Beef Creek and the experimental stream system

	Pool		Stream channel		Date
	No/M <sup>2</sup>	Gms/M <sup>2</sup>	No/M <sup>2</sup>	Gms/M <sup>2</sup>	
	<u>Experimental stream</u>				
Coho	1.48-2.39	1.47-1.64	1.20-1.68	1.35-1.42	8/26/69
Steelhead	0.96-1.06	0.72-0.81	2.63-3.36	1.92-2.43	
Coho	1.95-2.21	2.31-2.51	1.92-3.35	3.92-4.56	8/26/68
Steelhead	0.41-0.72	0.98-0.99	2.16-6.23	4.77-6.05	
Coho	2.47-2.97	1.28-1.81	4.31-5.04	2.50-2.74	6/2/70
Steelhead	3.45-5.96	0.91-1.71	6.48-10.54	1.80-2.73	
Coho	3.96-4.81	1.32-1.45	1.92-1.92	2.16-2.84	8/26/70
Steelhead	2.62-2.68	0.47-0.62	2.16-2.39	1.72-3.10	
Coho	1.78-1.85	2.92-4.47	1.20-3.35	5.04-6.87	12/15/69
Steelhead	0.20-1.27	0.60-2.79	1.20-5.75	4.65-18.15	
Coho wild	0.28-0.35	0.95-1.20			1/25/69
Steelhead	0.26-0.56	0.93-2.07	1.68-1.68	5.73-6.08	
Coho hatchery	3.19-3.62	19.20-19.92			
Steelhead	1.74-1.84	15.73-16.00	8.17-9.34	75.39-86.33	
	<u>Big Beef Creek</u>				
Coho	2.30-3.13	4.02-5.45			7/18/69
Steelhead	1.02-2.62	0.75-1.67			
Coho	2.31-3.54	8.78-14.56			9/16/70
Steelhead	2.18-2.40	5.52-5.88			
	<u>Alsea River</u>				
	<u>Deer Creek</u>				
Coho		2.3-3.1			8/59-8/62
		2.0-4.0			12/59-12/62
	<u>Flynn Creek</u>				
Coho		2.1-3.0			8/59-8/62
		2.0-4.5			12/59-12/62
	<u>Needle Branch</u>				
Coho		1.6-3.9			8/59-8/62
		1.8-2.8			12/59-12/62

pools. Being sources of production they are also areas of spatial overlap for coho and steelhead. These areas do not fit into the model of discrete habitat segregation as suggested by Hartman (1965) wherein coho stream production comes from pools and steelhead production comes from riffles.

In addition to horizontal habitat segregation, vertical stratification was observed in the pool microhabitat of the stream channel and in the pool habitat. Coho were distributed near the surface while steelhead were near the bottom in spring and summer in both the stream channel pool microhabitat and the pool habitat. The one exception was with hatchery origin steelhead during the summer 1970 experiment in which they showed no particular preference for surface or bottom. This behavioral preference appeared to change in the only winter experiment (1969) applicable when coho preferred the bottom and steelhead in each channel chose the surface and bottom respectively. This type of seasonal change in distribution was observed in the main stream and reported in British Columbia by Hartman (1965).

Feeding behavior further substantiates vertical stratification in a pool habitat. During the spring-summer experiment of 1968, steelhead were observed to be feeding predominantly upon the substrate while coho were feeding on surface or drift borne food items. This observation was mented in the major pool habitat and can be compared with observations during the fall-winter experiment in 1969 in the pool microhabitat in the stream channel. Coho were feeding on the surface while steelhead were feeding with equal frequency on the surface and on the substrate. Apparently no seasonal change in feeding behavior was seen for coho, but

steelhead were not exhibiting differential preferences in the winter season. Both studies on food habits of coho and steelhead have suggested vertical stratification based upon the incidence of terrestrial borne insects in coho stomachs and only benthic forms in steelhead (Johnston, 1967; Peterson, 1966).

Qualitative observations of steelhead feeding behavior between the natural stream and the experimental stream suggests that steelhead were acting something like "benthic grazers" as they made feeding thrusts on the surface of the substrate and would mouth or bite the material and spit it out. Coho did not show this behavior as obviously as steelhead did. This behavior was also reported by Frazer (1969). I speculate that steelhead have evolved and adapted to a distribution pattern in riffles where a benthic feeding behavior would have high survival value. This behavior would probably have come under genetic control being of high survival value and as such become a highly stereotyped and stylized behavior. Population pressures to expand from the riffle habitat have caused this species to become more widely distributed, but the behavioral feeding pattern has remained the same whether in riffle, open channel or pool habitats.

#### Competition

Perhaps the most productive way to discuss competition is to proceed from the viewpoint of evolutionary biology. That is, large numbers of fry are generally produced in every generation as well as great amounts of genetic variability. Natural selection then acts upon the population to eliminate extremes. Therefore, evidence of competition should be

present in every generation regardless of temporal differences in fry emergence or differential growth rates among some members of the population. Interspecific competition, however, would be minimized or eliminated by natural selection over time since it represents a wastage of energy and time. Ecological divergence in the form of habitat segregation would be an adaptive trait and would tend to evolve as a function of time of sympatry and of the selective disadvantage of interspecific competition.

As previously discussed, the idea that habitat segregation results from competition has been described by Brian (1956) and has been applied to fish species by Nilsson (1967). The evolutionary end point of this process is termed selective segregation whereas the intermediary phase is termed interactive segregation. Everest's (1969) work on the habitat segregation of juvenile chinook and steelhead in Idaho streams has been described in the introductory section as an example of selection segregation. Hartman's (1965) study showing that coho salmon occupy pools in spring and summer while steelhead occupy riffles has been described as an example of interactive segregation. Nilsson (1967) has suggested that coho and steelhead in British Columbia streams are an example of interactive segregation because when held separately in an experimental apparatus they had similar demands. Furthermore, habitat segregation was achieved by steelhead being more aggressive than coho in riffles and coho being more aggressive than steelhead in pools.

In the present study exclusive habitat segregation in the natural stream is observed for steelhead in riffles and for coho in the surface

areas of pools. In the experimental stream vertical stratification by species of the pool habitat was observed but the only exclusive occupancy of the riffle environment was observed during a fall-winter experiment. Only steelhead both of hatchery and wild origin were the final residents of the riffle habitat in this experiment. In terms of agonistic behavior coho salmon were socially dominant in both habitat types except for the aforementioned fall-winter experiment where hatchery and wild steelhead were more aggressive than coho.

Perhaps the disparity between Hartman's study and the present one has to do with time of sympatry of these two populations. Presumably, one would expect to find greater development of ecological divergence or habitat segregation in areas of longer sympatry. On the other hand, if we visualize habitat type as arrayed on a continuum of values from fast velocity, shallow riffles to slow velocity, deep pools we can find an operational solution. If one speculates that the ecological optima for steelhead are fast riffles and for coho are deep pools then both populations should have these phenotypic members in proportion to the severity of competition and the advantages to be gained by avoidance of competitive interaction. Presumably, then, genetic control over habitat selection would be strong in a population which had evolved in sympatry for quite some time and would thus be exhibiting selective segregation. However, competition would still be occurring in every generation even in this case by variants in the population. This interaction would probably be most obvious in the habitats within the stream where spatial overlap by fish species occurred, e.g., intermediate zones between riffles or pools called runs or open channels. Theoretically, those

individuals who were surplus to the riffle populations and pool populations and those weaker individuals forced to emigrate from the preferred areas due to density adjustments as the space available in the stream decreases would be the major participants in competitive interactions.

I suggest that the experimental stream channel environment in the present study represents those intermediate areas within the stream between riffles and pools. Something about competition can be deduced from a study of this environment. From the earlier discussion on microhabitat segregation it was found that both coho and steelhead densities were directly proportional to depth in the stream channel. It was also found that the carrying capacity of a stream for one species is positively related to the carrying capacity for the other species. Therefore coho and steelhead do not appear to have a negative impact upon each other. Furthermore, the fact that the final resident populations were generally equivalent numerically or in absolute biomass irrespective of prior residence or the individual average size of the introduced population suggests that intraspecific effects are greater than interspecific ones.

In terms of indirect measures of competition an important insight into the relative role of intra and interspecific density adjustments was gained in the present study by an analysis of the emigration rates of coho and steelhead prior residents. From this analysis I would speculate that intraspecific species effects are greater than interspecific ones so that coexistence is maintained in this manner.

MacFadden and Cooper (1964) suggest that population regulation in stream resident salmonids is effected mainly through changes in numbers

rather than through changes in growth. In the present study growth rate and survival appear to be largely species specific which agrees with Fraser's (1968) work on juvenile coho and steelhead. However, density adjustments were mediated through emigration in the present study in contrast to growth depression and decreased survival in Fraser's study.

The direct observation of competition can be achieved by observing interspecific territorial aggression (Orlans and Collier, 1963). Within the constraints of the experimental apparatus in this study, coho were dominant interspecifically in riffle and pool microhabitats over all season when wild stocks were used. The only exception was the fall-winter experiment of 1968 where wild interspecific steelhead and hatchery interspecific steelhead aggression toward wild and hatchery coho, was higher than coho interspecific aggression in return.

However, while steelhead were not exhibiting interspecific aggression toward coho generally they were directing it toward themselves so that intraspecific effects appear to have a greater impact on the steelhead population than interspecific ones. Even when steelhead were equal in size to coho the same lack of interspecific aggression was observed so that based upon the experimental results in this study size does not appear to be a consideration. It is not difficult to see that this behavioral avoidance of interspecific encounters would be advantageous in the context of energy expended versus energy gained. One might speculate that steelhead are more rigid in their behavioral responses as a result of greater genetic control and therefore behaviorally more highly evolved than coho. Everest (1969) suggests in his work with juvenile chinook and steelhead in Idaho streams that steelhead have more

rigid requirements than chinook in terms of habitat preference. Moreover, it is generally presumed that coho are an extremely resilient species in terms of their response to habitat change, and as such, seem to be more flexible and under less genetic control in terms of habitat selection.

It is probable that the populations which were observed in the experimental stream channel were fractions, possibly phenotypes, of the main population of Big Beef Creek which represent those variant groups in every population that are continually expanding their niche requirements. This procedure is an evolutionary process by which certain phenotypic variants in the population are found in all habitat types available. It would appear that those populations which became so specialized as to occur only in pools (coho) and only in riffles (steelhead) would be poorly adapted. Larkin (1956) states that freshwater temperate environments offer little opportunity for specialization and tend to support species which have wide tolerance of habitat type. Therefore, it seems reasonable to expect overlap in habitat requirements with coho in riffles and open channels or runs and steelhead in pools and open channels as well.

This study, as well as others, Fraser (1969), Johnston (1967), Peterson (1966), have shown that vertical separation of habitat occurs, even as in this study, in microhabitats that are only 30 cm deep. I speculate that coho and steelhead populations in Big Beef Creek have evolved differences in preferences for macrohabitat and microhabitats via competition in the past to the extent that selective segregation has produced phenotypes which innately respond to habitat gradients. However,

other phenotypes in the population are essentially invading other habitat types and are visual manifestations of the process of competition. As such, interspecific agonistic behavior is evidenced in these habitat types which by virtue of their depth and velocity are intermediate. However, these habitats are numerous in the stream environment and as the results in the experimental stream have pointed out, are productive units in themselves.

#### Management Implications

An ecological dilemma exists in the management of anadromous salmonid stocks in a number of Pacific coastal states, where the responsibility for species are divided according to whether a species contributes predominantly to a commercial fishery or a sport fishery. In light of the magnitude of the present day recreational fishing industry this division appears to be even more arbitrary than it was originally. As such, man's intervention into the structure of freshwater communities for management purposes has the potential to be damaging. This is especially true in the area of artificial propagation of salmonid species and their consequent stocking in freshwater streams for enhancement or other management purposes. Since no overall administrative or management entity directs or dictates the goals of these separate agencies it is possible for single species resource management to develop. One of particular concern is the magnitude of the stocking program in river or stream systems where species with extended freshwater residence reside. Spatial and temporal differences in spawning and emergence as well as habitat preference are mechanisms which have evolved to promote coexistence

of salmonids. These mechanisms can be broken down both genetically and by the sheer weight of numbers under the artificial stocking of one species without regard for the other. Under a standard smolt release program two impacts might be felt upon the stream salmonid population. One deals with the more subtle and long-term impact of surviving adults returning to spawn and their resultant fry superimposing their numbers upon the existing stream population. That is, to say, under natural conditions the ratio of abundance of individual species within the physical habitat types available will attain some level of equilibrium given long periods of sympatry and this balance can be upset to establish some new equilibrium between species that would favor the stocked species. The other impact is primarily the lack of adaptive behavior by hatchery-reared fish and secondarily the immediate effect of planted smolts upon the indigenous fish within the watershed system. This effect is one for which the present study can provide some useful information. Generally, within the experimental stream system if given the ability to emigrate, prior residence or large size did not prove to be competitive advantage for that species in all habitat types. This was because intraspecific effects were greater than interspecific ones. However, when fish which were reared under hatchery conditions were planted where naturally reared fish were prior residents, the hatchery fish appeared to crowd out the wild fish. It seems likely that lack of dispersion or emigration on the part of hatchery reared fish was the primary reason for their greater contribution to the final resident population. This behavior resulted in relatively higher population densities than wild fish which presumably had balanced spatial requirements upon food avail-

ability. These greater densities could represent a negative impact by interference. These hatchery fish as a result showed poorer growth. Moreover, observations on agonistic behavior did not suggest competitive advantage for hatchery fish over wild fish, because very low intensity interactions were observed. However, the high frequency of intraspecific interactions of hatchery steelhead compared to wild steelhead did seem to suggest that aggression was of high intensity within the hatchery fish.

It does appear that hatchery fish and wild fish behavior in this experiment were different, and I speculate that hatchery fish behavior in the experimental stream system would be of poor adaptive value in the natural stream environment. This agrees with a growing number of studies on comparative behavior of hatchery reared and wild reared fish. Fenderson, et al. (1968) and Fenderson and Carpenter (1971) have studied the comparative behavior of hatchery and wild Atlantic salmon and have concluded that hatchery fish are more aggressive than wild fish even to the point that aggression interferes with feeding activity. Moyle (1969) studying brook trout found similar results in terms of hatchery fish exhibiting higher nipping rates than wild fish. Differences in dispersion rates between hatchery and wild fish were not observed in rainbow trout and brown trout of wild and domestic origin in an experimental stream system (Jenkins, 1971).

Whether or not these changes in behavior are due to genetic differences as suggested by Vincent (1960) in brook trout or due to learned behavior in the crowded hatchery environment for Atlantic salmon as

suggested by Fenderson et al. (1968) has not been determined. However, in another experiment during the summer of 1970 I used hatchery reared steelhead fry which had only spent a short time in the hatchery environment before being transferred to the experimental stream system. These steelhead exhibited similar behavior to the wild steelhead except for vertical stratification in the stream channel. Therefore, I suggest that length of residence in the hatchery environment was the critical factor determining behavioral modification of these hatchery fish.

It may be stated that a smolt release program, due to its timing, precludes long periods of freshwater residence so that negative impacts within the stream are probably minimal. These same problems of competitive interaction may exist in the estuarine environment where spatial requirements and energy expenditure must be balanced against food availability. Reimer's (1971) work with fall chinook in an Oregon coastal stream showed that the estuary has a definite carrying capacity, and that those fish which successfully rear there as opposed to stream rearing contribute more abundantly to the adult return.

Quite obviously, enhancement programs are required and significantly contribute to both commercial and sport fisheries. However, a need for a unified, coordinated approach balancing the magnitude of single species stockings with some understanding of the optimum species composition in the stream to be stocked is needed. With steelhead and coho it might be useful to know the relative proportions in the stream of the pool run and riffle microhabitats preferred by coho and steelhead respectively so that levels of production for each stream may be indexed, catalogued, and used in management decision making.

I would also recommend an extension of the experimental stream approach to small natural streams where control over stocking density and planting sequence could be exercised. Furthermore, an attempt should be made to compare stocks of both coho and steelhead which have never come into contact with one another (allopatry) versus those which have similar distribution in range (sympatry). These studies would help to elucidate the mechanism of coexistence and help to predict the fate of stocking either species in streams for enhancement purposes.

#### LITERATURE CITED

- Braddock, J. C. 1945. Some aspects of the dominance-subordination relationship in the fish (Platycoecilus maculatus). *Physiol. Zool.* 18:176-195.
- Brian, M. V. 1956. Segregation of species of the ant genus Myrmica. *J. Anim. Ecol.* 25:319-337.
- Briggs, J. C. 1953. The behavior and reproduction of salmonid fishes in a small coastal stream. *Calif. Dep. Fish Game, Fish. Bull. No.* 94, 62 pp.
- Brown, W. L., J., and E. O. Wilson. 1956. Character displacement. *Syst. Zool.* 5:49-64.
- Burns, J. W. 1971. The carrying capacity for juvenile salmonids in some northern California streams. *Calif. Fish Game* 57(1):44-57.
- Cederholm, C. J. 1972. The short-term physical and biological effects of stream channelization at Big Beef Creek, Kitsap County, Washington. M.S. Thesis, Univ. Washington, Seattle. 91 pp.
- Chapman, D. W. 1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. *J. Fish. Res. Bd. Canada* 19(6):1047-1080.
- Chapman, D. W. 1965. Net production of juvenile coho salmon in three Oregon streams. *Trans. Amer. Fish. Soc.* 94(1):40-52.
- Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. *Amer. Natur.* 100:345-357.
- Chapman, D. W., and T. C. Bjornn. 1969. Distribution of salmon and trout in streams, with special reference to food and feeding. Pages 153-176 *in* T. G. Northcote, ed. *Salmon and Trout in Streams*. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver, B.C.
- Edmundson, E. H. 1968. Permanence of station in juvenile chinook salmon and steelhead trout. M.S. Thesis, Univ. Idaho, Moscow. 35 pp.
- Everest, F. H. 1969. Habitat selection and spatial interaction of juvenile chinook salmon and steelhead trout in two Idaho streams. Ph.D. Thesis, Univ. Idaho, Moscow. 77 pp.
- Fenderson, O. C., W. H. Everhart, and K. M. Muth. 1968. Comparative agonistic and feeding behavior of hatchery-reared and wild salmon in aquaria. *J. Fish. Res. Bd. Canada* 25(1):1-14.

- Fenderson, O. C., and M. R. Carpenter. 1971. Effects of crowding on the behavior of juvenile hatchery and wild landlocked Atlantic salmon. *Animal Behav.* 19:439-447.
- Frasier, F. J. 1969. Population density effects on survival and growth of juvenile coho salmon and steelhead trout in experimental stream-channels. Pages 253-266 *in* T. G. Northcote, ed. *Salmon and Trout in Streams*. Univ. British Columbia, Vancouver, B.C.
- Griffith, J. S., Jr. 1972. Comparative behavior and habitat utilization of brook trout (Salvelinus fontinalis) and cutthroat trout (Salmo clarki) in small streams in northern Idaho. *J. Fish. Res. Bd. Canada* 29:265-273.
- Hardin, G. 1960. The competitive exclusion principle. *Science* 131(3409):1292-1297.
- Harper, J. L. et al. 1961. The evolution of ecology of closely related species living in the same area. *Evolution* 15:209-227.
- Hartman, G. F. 1965. The role of behavior in the ecology and interaction of underyearling coho salmon (Oncorhynchus kisutch) and steelhead trout (Salmo gairdneri). *J. Fish. Res. Bd. Canada* 22:1035-1081.
- Hoar, W. S. 1951. The behavior of chum, pink, and coho salmon in relation to their seaward migration. *J. Fish. Res. Bd. Canada* 8:241-263.
- Jenkins, T. M., Jr. 1971. Role of social behavior in dispersal of introduced rainbow trout (Salmo gairdneri). *J. Fish. Res. Bd. Canada* 28(8):1019-1027.
- Johnston, J. M. 1967. Food and feeding habits of juvenile coho salmon and steelhead trout in Worthy Creek, Washington. M.S. Thesis, Univ. Washington, Seattle. 77 pp.
- Larkin, P. A. 1956. Interspecific competition and population control in freshwater fish. *J. Fish. Res. Bd. Canada* 13(3):327-342.
- Lister, D. E., and H. S. Genoe. 1970. Stream habitat utilization by cohabitating underyearlings of chinook (Oncorhynchus tshawytscha) and coho (Oncorhynchus kisutch) salmon in the Big Qualicum River, British Columbia. *J. Fish. Res. Bd. Canada* 27:1215-1224.
- McFadden, J. T., and E. L. Cooper. 1964. Population dynamics of brown trout in different environments. *Physiol. Zool.* 37(4):355-363.

- Mason, J. C. 1966. Behavioral ecology of juvenile coho salmon (O. kisutch) in stream aquaria with particular reference to competition and aggressive behavior. Ph.D. Thesis, Oregon State Univ., Corvallis. 195 pp.
- Mason, J. C., and D. W. Chapman. 1965. Significance of early emergence, environmental rearing capacity, and behavioral ecology of juvenile coho salmon in stream channels. J. Fish. Res. Bd. Canada 22:173-190.
- Miller, R. B. 1958. The role of competition in the mortality of hatchery trout. J. Fish. Res. Bd. Canada 15:27-45.
- Moyle, P. B. 1969. Comparative behavior of young brook trout of domestic and wild origin. Progr. Fish-Cult. 31(1):51-56
- Neave, F. 1958. The origin and speciation of Oncorhynchus. Trans. Royal Soc. Canada 52(3):25-39.
- Newman, M. A. 1956. Social behavior and interspecific competition in two trout species. Physiol. Zool. 29(1):64-81.
- Nilsson, N.-A. 1955. Studies on the feeding habits of trout and char in north Swedish lakes. Rep. Inst. Freshwater Res. Drottningholm 36:163-225.
- Nilsson, N.-A. 1956. Seasonal fluctuations in the food segregation of trout, char and whitefish in 14 North-Swedish lakes. Rep. Inst. Freshwater Res. Drottningholm 41:185-205.
- Nilsson, N.-A. 1963. Interaction between trout and char in Scandinavia. Trans. Amer. Fish. Soc. 92:276-285.
- Nilsson, N.-A. 1965. Food segregation between salmonid species in North Sweden. Rep. Inst. Freshwater Res. Drottningholm 46:58-78.
- Nilsson, N.-A. 1967. Interactive segregation between fish species. Pages 295-313 in S. D. Gerking, ed. The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford and Edinburgh.
- Orians, G. H., and G. Collier. 1963. Competition and blackbird social system. Evolution 17:449-459.
- Peterson, G. R. 1966. The relationship of invertebrate drift abundance to the standing crop of benthic organisms in a small stream. M.S. Thesis, Univ. British Columbia, Vancouver, B.C. 39 pp.

- Reimers, P. E. 1971. The length of residence of juvenile fall chinook salmon in Sixes River, Oregon. Ph.D. Thesis, Oregon State Univ., Corvallis. 99 pp.
- Ricker, W. E. 1958. Handbook of computations for biological statistics of fish populations. Fish. Res. Bd. Canada Bull. No. 119. 300 pp.
- Salo, E. O., and W. H. Bayliff. 1958. Artificial and natural production of silver salmon, Oncorhynchus kisutch, at Minter Creek, Washington. Wash. Dep. Fish. Res. Bull. No. 4. 75 pp.
- Saunders, R. L., and J. H. Gee. 1964. Movements of young Atlantic salmon in a small stream. J. Fish. Res. Bd. Canada 21(1):27-36.
- Schuck, H. 1943. Survival, population density, growth and movement of the wild brown trout in Crystal Creek. Trans. Amer. Fish. Soc. 73:209-230.
- Shapovalov, L., and A. C. Taft. 1954. Th life histories of the steelhead rainbow trout (Salmo gairdneri gairdneri) and silver salmon (Oncorhynchus kisutch) with special reference to Waddell Creek, California, and recommendations concerning their management. Calif. Dep. Fish Game, Fish. Bull. No. 98. 375 pp.
- Shetter, D. S. 1937. Migration, growth rate, and population density of brook trout in the north branch of the Au Sable, Michigan. Trans. Amer. Fish. Soc. 66:203-210.
- Smoker, W. A. 1955. Effects of streamflow on silver salmon production in western Washington. Ph.D. Thesis, Univ. Washington, Seattle.
- Vincent, R. E. 1960. Some influences of domestication upon three stocks of brook trout (Salvelinus fontinalis Mitchill). Trans. Amer. Fish. Soc. 89:35-52.
- Williams, K. 1970. Some ecological investigations of Big Beef Creek, 1966-67. Unpubl. MS. 72 pp.