

AN ABSTRACT OF THE THESIS OF

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Title: STREAM HABITAT UTILIZATION AND BEHAVIOR OF SYMPATRIC AND ALLOPATRIC WILD CUTTHROAT TROUT (*SALMO CLARKI*) AND HATCHERY COHO SALMON (*ONCORHYNCHUS KISUTCH*)

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The behavior and stream habitat utilization of juvenile hatchery-reared coho salmon (*Oncorhynchus kisutch*) and wild cutthroat trout (*Salmo clarki*) were examined to assess the nature of interactions between the species potentially resulting from introductions of hatchery coho salmon in streams. Habitat utilization was monitored in Mill Creek, Polk Co., Oregon by manipulating the composition of fish within three study sections to include either allopatric or sympatric populations of hatchery coho salmon and wild cutthroat trout. In allopatry, coho salmon and cutthroat trout selected feeding microhabitat that was similar in physical characteristics and exhibited extensive dietary overlap. When the two species occurred in sympatry, feeding microhabitat used by coho salmon was altered, however, that of cutthroat trout was comparable to allopatric cutthroat trout. No discernable differences in dietary composition between allopatric and sympatric fish were detected. While allopatric cutthroat trout always gained mass, allopatric coho salmon

always lost mass. Stomach fullness indices were higher for allopatric cutthroat trout than allopatric coho salmon. Sympatric cutthroat trout had comparable or greater gains of mass, indices of stomach fullness, and hepatic glycogen reserves relative to allopatric cutthroat trout. Conversely, sympatric coho salmon had greater losses of mass, reduced hepatic glycogen reserves, and apparently lower indices of stomach fullness than allopatric salmon.

Behavioral observations made through the use of an in-stream viewing chamber in Berry Creek, Benton Co., Oregon, indicated that in allopatry populations of hatchery coho salmon and wild cutthroat trout were structured as linear dominance hierarchies that were organized by quantitatively and qualitatively similar aggressive interactions. In sympatry, however, cutthroat trout were more aggressive and socially dominant to coho salmon. The shift in use of micro-habitat and reduction in habitat utilization effectiveness of hatchery coho salmon in the presence of cutthroat trout can, thus, be interpreted to occur as a result of interference competition mediated through interspecific aggression.

Stream Habitat Utilization and Behavior of Sympatric
and Allopatric Wild Cutthroat Trout (*Salmo clarki*)
and Hatchery Coho Salmon (*Oncorhynchus kisutch*)

by

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Stream Habitat Utilization and Behavior of Sympatric
and Allopatric Wild Cutthroat Trout (*Salmo clarki*)
and Hatchery Coho Salmon (*Oncorhynchus kisutch*)

INTRODUCTION

Hatchery-reared anadromous salmonids can undergo extended stream residence after release (Wagner et al. 1963, Reimers and Lueffel 1967, Feldman 1974, Reimers and Concannon 1977, Lorz and McPherson 1976, Bjornn et al. 1978, Hart et al. 1981). Since wild salmonids commonly reside in systems that receive introductions of hatchery fish, it is important to know what interactions occur among hatchery-released salmonids and wild, resident salmonids and how these interactions may influence their habitat utilization.

In Oregon most coho salmon (*Oncorhynchus kisutch*) production originates from hatchery propagation (Scarnecchia 1978), a process that involves releasing large numbers of juvenile fish into river systems. Cutthroat trout (*Salmo clarki clarki*) often occur in systems that receive introductions of hatchery coho salmon (Scott and Crossman 1973). Glova (1978) showed extensive habitat overlap among populations of wild cutthroat trout and wild coho salmon. He further demonstrated that in sympatry wild coho salmon were socially dominant and more aggressive than wild cutthroat trout, and that coho salmon apparently excluded cutthroat trout from mutually preferred feeding microhabitat. Moreover, there is evidence that hatchery salmonids may be more aggressive than wild counterparts (Fenderson and Carpenter 1967, Fenderson et al. 1968, Moyle 1969, Bieber 1977). Thus, introductions of hatchery coho salmon may adversely affect wild cutthroat trout populations by interfering with cutthroat

trout habitat use. Conversely, Miller (1958) showed that survival of hatchery-reared rainbow trout (*Salmo gairdneri*) that were introduced into streams that supported wild cutthroat trout could be less than 50 percent. He attributed mortality of hatchery fish to competition for food and space with resident cutthroat trout. Therefore, it is also possible that resident cutthroat trout may adversely affect hatchery coho salmon.

To clarify the nature of instream interactions between hatchery-reared coho salmon and wild cutthroat trout, I designed a study to examine habitat utilization by these species. My objectives were to: 1) compare coho salmon and cutthroat trout feeding microhabitat, 2) compare the relative effectiveness of stream habitat utilization by each species, 3) determine how the association of the fishes may affect their utilization of stream habitat and effectiveness of habitat use, and 4) compare behavioral components that may influence habitat utilization.

To meet the first three objectives I manipulated the composition of a salmonid community to include allopatric and sympatric populations of coho salmon and cutthroat trout. Among experimental populations I compared feeding microhabitat in terms of feeding distribution and dietary composition, and habitat utilization effectiveness. I defined habitat utilization effectiveness as the relative degree that each species used stream habitat for energy accumulation, a measure of fitness in fish (Li and Brocksen 1977, Werner and Hall 1976). Energy accumulation is best measured by changes in biomass or growth. However, due to seasonal limitations of resources in streams (Chapman

1966), growth in stream-dwelling salmonids can be below empirically detectable levels (Warren et al. 1964, Allen 1969, Averett 1969). A more sensitive indicator of energetic status is hepatic glycogen. In teleosts, hepatic glycogen levels correlate well with total energetic status; liver glycogen levels progressively increase with net anabolism and decrease as energetic demands exceed energetic inputs (Hochachka 1961, Kamra 1966, Swallow and Fleming 1970, Heidinger and Crawford 1977, Bulow et al. 1978, Milne et al. 1979, Moon and Johnston 1980). Hence, I used levels of hepatic glycogen reserves in conjunction with changes in mass as a relative index of habitat utilization effectiveness.

To gain understanding of the nature of behavioral mechanisms that may affect habitat utilization, I examined behavioral components of social structure of wild cutthroat trout and hatchery coho salmon and how social behavior was influenced by the association of these species. These behavioral observations comprised a second set of experiments in which detailed observations of agonistic behavior of allopatric and sympatric populations were made in a natural stream equipped with a viewing chamber.

MATERIALS AND METHODS

Coho salmon, obtained from Sandy State Fish Hatchery, Oregon, were held at Smith Farm, Oregon State University's fish rearing facility, until needed for experimentation. Fish were kept in 350 l circular tanks with a water exchange rate of approximately 4 l/min and at a density of approximately 8 g/l. At Smith Farm coho salmon were fed to repletion daily with Abernathy dry pellets. Cutthroat trout were obtained as needed from tributaries of Mill Creek for stream habitat utilization studies or Berry Creek and Soap Creek for behavioral observations by electroshocking (Coffelt model BP-3 backpack electroshocker). Prior to experimental introductions, all fish were held instream at experimental sites in live cages for at least 7 days. Fish were held at densities of 1.8 g/l (Mill Creek) and 3.5 g/l (Berry Creek) and fed to repletion daily, cutthroat trout with earthworms (*Lumbricus* sp.) and coho salmon with Abernathy pellets.

Stream Habitat Utilization

To compare stream habitat utilization of cutthroat trout and coho salmon, I stocked 14 cutthroat trout, 14 coho salmon, or 14 cutthroat trout and 14 coho salmon into three separate stream sections of Mill Creek. Mill Creek (Polk Co, Oregon) is a third order coast range stream of the Willamette drainage. Elevation of the study site was approximately 250 m. Pacific lamprey (*Entosphenus tridentatus*), cutthroat trout, and several species of sculpins (*Cottus* sp.) resided in the study sections. Approximately 8 km downstream, coho salmon, rainbow trout, squawfish (*Ptychocheilus oregonensis*), redbottom shiners

(*Richardsonius balteatus*), speckled dace (*Rhinichthys osculus*), and largescale suckers (*Catostomus macrocheilus*) also occurred. Each experimental section consisted of a pool and riffle bordered up- and downstream by runs. To prevent fish passage, I anchored block seines (1.5 cm mesh) across the bordering runs. Seins were cleared of debris daily. I selected the stream sections so that each contained similar biomasses of resident cutthroat trout (Appendix I). These resident fish were removed prior to experimental stocking by means of an underwater fish immobilizer (Everest 1978). Each species was stocked at approximately 50 percent of the former resident biomass of cutthroat trout. Therefore, the biomass of allopatric sections (sections that received cutthroat trout or coho salmon) was approximately half of the biomass of former resident cutthroat trout, and the biomass of the sympatric section (the section that received cutthroat trout and coho salmon) replaced the former biomass of resident cutthroat trout (Appendix I). This stocking protocol was adopted because it: 1) minimized intraspecific competition and, thus, allowed habitat preferences of each species to be assessed clearly, and 2) held intraspecific competition constant while allowing interspecific competition to vary (see Werner and Hall 1976, 1977). Because size may be an important factor influencing the outcome of competitive interactions among salmonids (Chapman 1962, Jenkins 1969, Symons 1971), the stocked fish were selected to be similar in size, and mean weights of stocked populations of each species were comparable (Appendix II). All stocked fish were anesthetized (MS-222, 50 mg/l), weighed to the nearest 0.1 g, and uniquely cold branded (Everest and Edmudson

1967) approximately 1 hr prior to release.

Fish were allowed to reside in the sections for 14 days (23 June to 7 July) and then removed with the underwater fish immobilizer. Within 1 to 5 min of removal from the stream, fish were reweighed and dissected for stomach and liver samples. Individual stomachs were placed in vials, transported on dry ice, and frozen. Entire livers were placed in pre-weighed 15-ml capped test tubes that contained 2.0 ml of 30 percent KOH.

In an attempt to compensate for potential confounding effects due to variation in habitat quality among stream sections, I replicated the experiment from 15 to 29 July, but randomized which stream sections received which species of fish (Appendix I). During the study, stream temperature averaged 10.5 °C and 15.0 °C and streamflow averaged 385 l/sec and 225 l/sec for replicates I and II, respectively.

To determine feeding distribution I used daily skindiving observations to assess feeding positions of stocked fish during the 14-day experimental periods. I defined feeding positions as areas of the stream channel where I observed fish take food or display feeding behavior. Feeding positions were marked with color coded sinkers, and the use of these sites was confirmed by repeated observations of fish in marked positions. After removal of the fish I measured the distance of sinkers from upstream nets of respective stream sections. After completing both replicated I assessed stream depth and current profiles of each section by averaging three depth and velocity readings (taken at 0.6 of total stream depth with a Marsh-McBerney model 201 electronic flow meter) recorded every 2 m of length within

each section from up- to downstream nets. Feeding distribution of each species was expressed in relation to stream depth-velocity profiles.

Dietary composition was determined by analyzing stomach contents. Food contents were removed from partially frozen stomachs and weighed to the nearest 0.1 mg. I enumerated all contents of each stomach according to 23 taxa of prey and measured prey items to the nearest 0.1 mm using a dissecting scope equipped with an ocular micrometer. I expressed prey composition in terms of average percent dry weight, with dry weights of prey determined from appropriate length-weight regressions (Beaver and Baldwin 1975; Cummins, unpubl. data).

Habitat utilization effectiveness was measured in terms of changes in mass, hepatic glycogen reserves, and stomach fullness. Stomach fullness served as a relative index of food consumption and was determined by dividing the weight of food items contained in a given stomach by the final weight of the associated fish. Changes in mass were determined by computing the difference in weight of stocked versus recovered fish less any weight due to stomach contents. To determine hepatic glycogen levels, glycogen was precipitated from entire livers (Good et al. 1933) and the resulting glucose was assayed using a phenol-sulfuric acid colorimetric method (Montgomery 1957) with modifications to accommodate entire livers. Recovery of commercially purified oyster glycogen (Sigma Chemical Co.) that corresponded to levels occurring in experimental fish averaged 98 ± 2 percent (95 percent CI) with this assay.

Statistical analyses involved parametric procedures when

assumptions could be met; nonparametric procedures were used otherwise (Sokal and Rohlf 1969, Zar 1974). Specific tests are outlined in the results section. A minimum of 10 fish from each treatment (14 fish/treatment) was recovered. For replicates I and II, respectively, 91 percent and 88 percent of the recaptures occurred on day 14, with the other recaptures occurring on day 15. Within respective experimental groups data on diet and energetic parameters of fish recaptured on day 15 were usually within 1 standard deviation, and always within the range of values for fish recaptured on day 14. Hence, I included data from all recaptured fish in subsequent analyses. The fate of fish unaccounted for was unknown, but may be explained by predation or concealment in the stream.

Behavioral Observations

Behavioral observations were conducted at Berry Creek (Benton Co., Oregon), a second order woodland stream of the Willamette drainage approximately 16 km northwest of Corvallis. Flow was controlled in a 500 m section (Warren et al. 1964). Throughout the study water flow through the study section was 56.6 l/sec and stream temperature averaged 8 °C and remained within a range of 2 °C. In the 500 m section a steel reinforced concrete booth with two 1.3-m laminated glass windows permitted observation of 2.4 m of pool and 2.4 m of riffle along the streambed. Area of the observation section was 29.4 m². To confine fish to the observation section, screens (1.3 cm mesh hardware cloth) were placed at up- and downstream boundaries of the viewing glass. To facilitate

viewing of fish, 3 open-sided, plywood boxes (30 x 15 x 15 cm) were placed against the glass in the stream pool.

From 29 April through 27 May, I conducted three experiments to assess social behaviors of coho salmon and cutthroat trout. Experiments corresponded to: 1) 4 cutthroat trout observed in allopatry, 2) 4 coho salmon observed in allopatry, and 3) 4 coho salmon and 4 cutthroat trout observed in sympatry. To compensate for influences of size on outcomes of agonistic encounters (Chapman 1962, Henderson and Chiszar 1977), I restricted the size range of simultaneously stocked fish to less than 3 g (Appendix III). Fish were uniquely identified while under anesthesia (MS-222, 50 mg/l) by attaching a colored dangler tag (Howett Plastics Co.) to a loop of vinyl thread inserted beneath the pterygiophores of the dorsal fin. Following the day of introduction, fish were observed 2 hr/day for 14 days. I recorded: 1) occurrences of aggressive initiations (an offensive act exhibited by a fish that elicited an agonistic bout between itself and another fish), 2) fish distribution, and 3) the presence of feeding behavior. Only aggressive acts that caused submissive behavior (e.g., fleeing or fright posture) were recorded to allow distinctions of winners and losers in all bouts. Aggressive initiations were recorded as: 1) display, 2) nip, 3) chase, and 4) charge (Kalleberg 1958, Chapman 1962, Keenleyside and Yamamoto 1962). All aggressive initiations that were qualitatively ambiguous or did not conform to these categories were placed in a category referred to as "other".

Based on frequencies of aggressive initiations, in each

experiment, fish were ranked according to dominance order (Brown 1975). Frequencies of aggressive initiations of individual species in sympatric and allopatric associations were compared with χ^2 analysis (Sokal and Rohlf 1969).

RESULTS

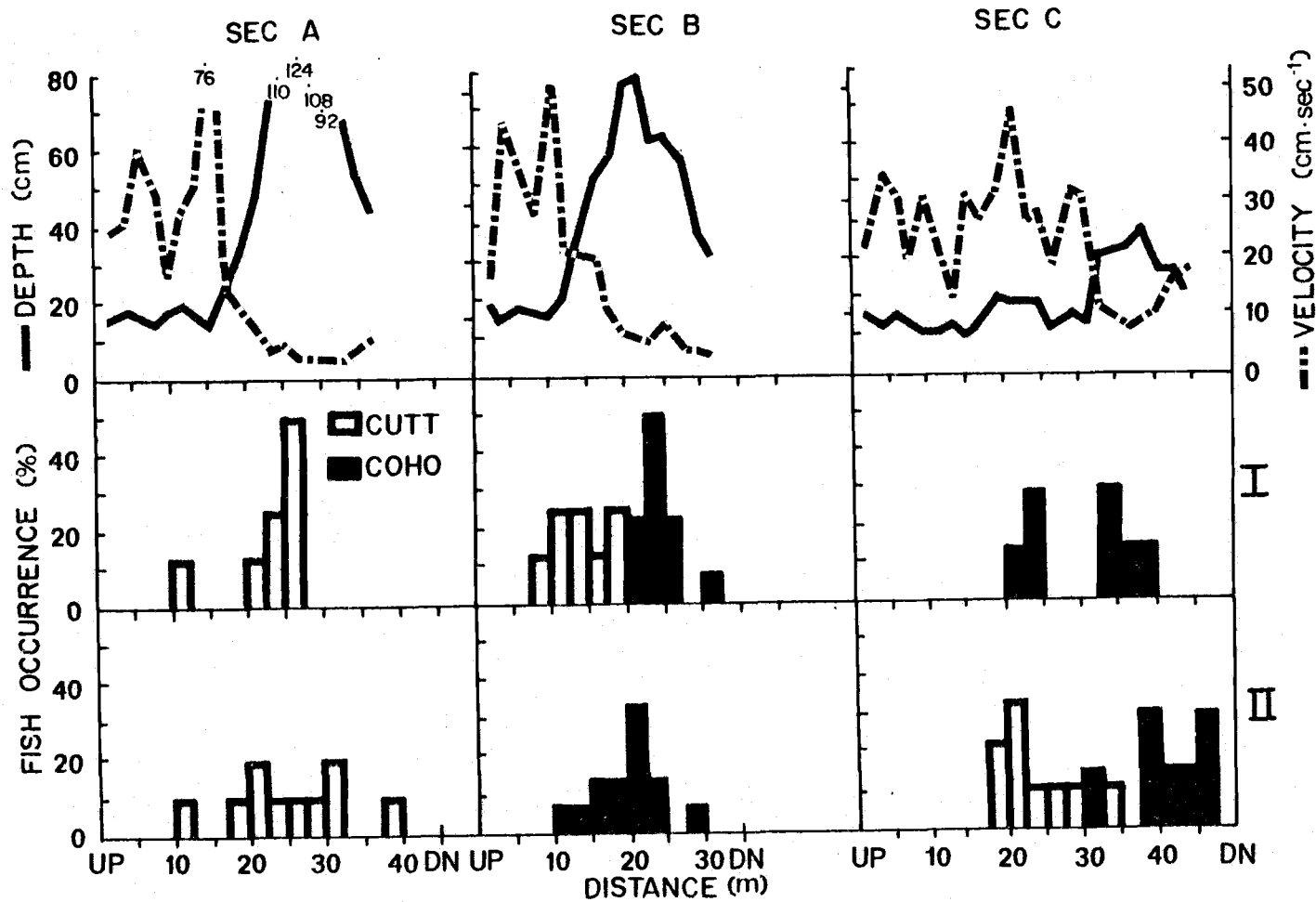
Stream Habitat Utilization

Feeding Distribution - Feeding positions of cutthroat trout were apparently unaffected by the presence of coho salmon. However, coho salmon occupied different feeding positions in the presence than in the absence of cutthroat trout (Figure 1). In both replicates allopatric fish tended to feed in areas of close proximity to maximum water depth and highest current velocity within the sections. These feeding areas corresponded to upper reaches of pools. In upper pools fish appeared to occupy loosely defined territories with all individuals maintaining a discrete area of the stream bottom. During periods of experimentation I observed resident cutthroat trout outside the experimental sections feeding in areas of similar physical characteristics and also arranged in loosely defined territories.

In sympatry, cutthroat trout also fed in upper pools. Coho salmon occurred downstream in slower, deeper water (Figure 1). As in allopatry, individual cutthroat trout appeared to occupy territories. Coho salmon did not appear to maintain discrete stream portions; they tended to occur in shifting aggregates that appeared to be hierarchical in nature in that no discrete portion of the stream channel was maintained by a given individual fish and agonistic confrontations occurred as individuals shifted positions or approached food items.

To compare feeding distribution of allopatric and sympatric fish I expressed feeding positions of individual cutthroat trout and

Figure 1. Feeding distribution of cutthroat trout and coho salmon in relation to stream depth and velocity. Fish occurrence is expressed as percentage of all individuals of a given species in a given stream section (denoted as A, B, and C). UP and DN are upstream and downstream boundaries of stream sections. I and II are experimental replicates.

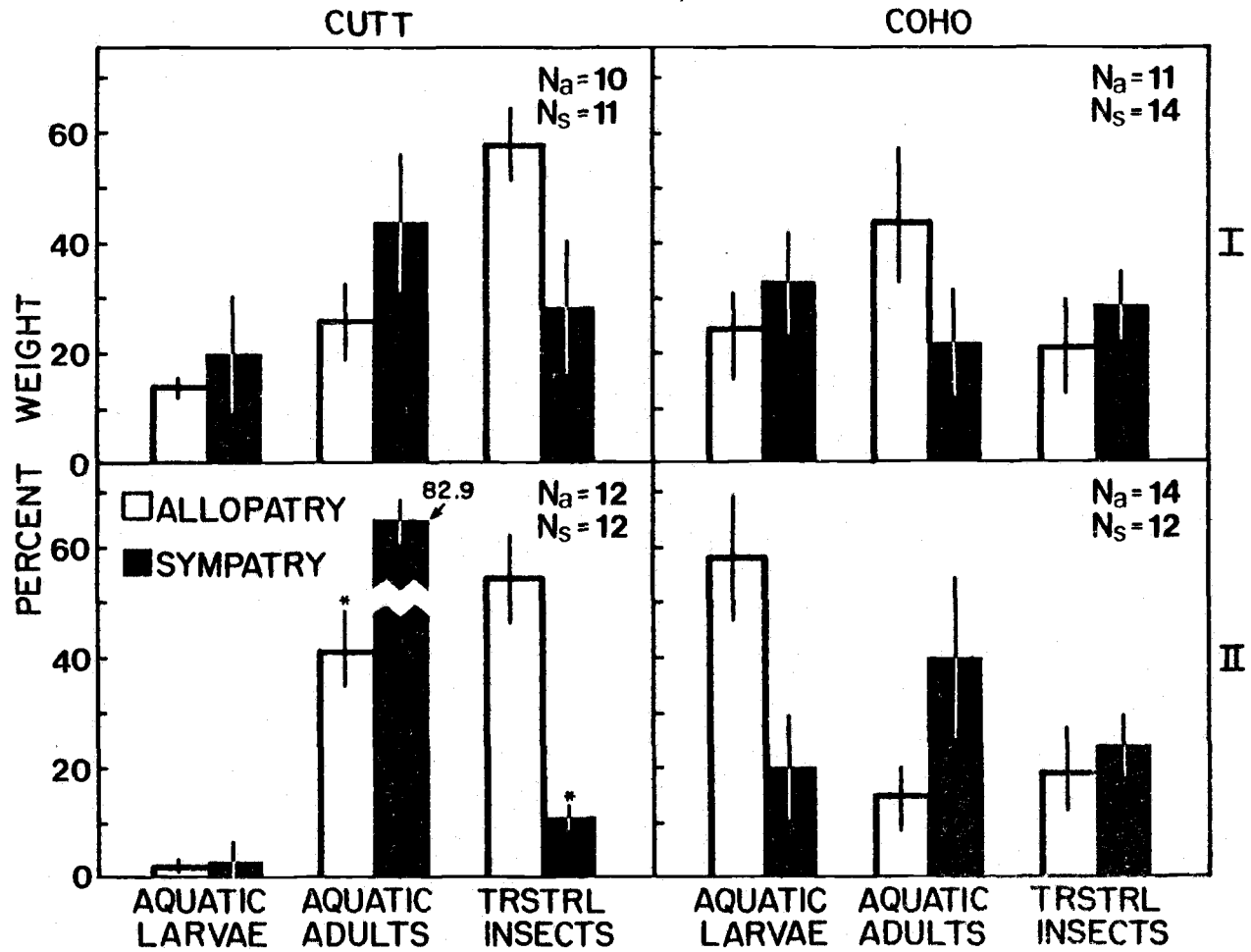


coho salmon as distance from highest available water velocities of respective stream sections and compared these distances with a nonparametric Mann-Whitney U-test. I first tested for differences between each of the four pairs of replicates (e.g., sympatric cutthroat trout: cutthroat trout in section B versus cutthroat trout in section C, Figure 1) and found all replicates to be homogeneous ($p > 0.05$). Hence, I pooled replicates and tested for differences between allopatric and sympatric groups of each species. Test results indicated that although no differences occurred between feeding distributions of allopatric and sympatric cutthroat trout ($p > 0.05$), feeding distributions of allopatric and sympatric coho salmon differed significantly ($p < 0.001$).

Dietary Composition - Dietary composition of cutthroat trout and coho salmon was expressed as three prey types that corresponded to groups of insects that required different foraging behavior for use by the fish. The insect groups were: 1) aquatic larvae, prey associated with the stream substrate and mid-water drift (Hynes 1970, Merritt and Cummins 1978); 2) aquatic adults, prey associated with mid-water and surface drift (Hynes 1970); and 3) terrestrial invertebrates, prey associated predominately with surface drift (pers. observation).

Generally prey types utilized by cutthroat trout and coho salmon were highly variable and strongly overlapped between the two species (Figure 2). In replicate II, allopatric and sympatric cutthroat trout showed significant differences in proportions of aquatic adult and terrestrial prey types used ($p < 0.05$, Student's

Figure 2. Dietary composition of cutthroat trout and coho salmon. Values expressed as mean percent weight \pm 1 standard error. Prey groups are explained in text. I and II are experimental replicates; * denotes significant differences between allopatric and sympatric groups by species with $\alpha = 0.05$; and N_a and N_s refer to the number of allopatric and sympatric fish examined, respectively.

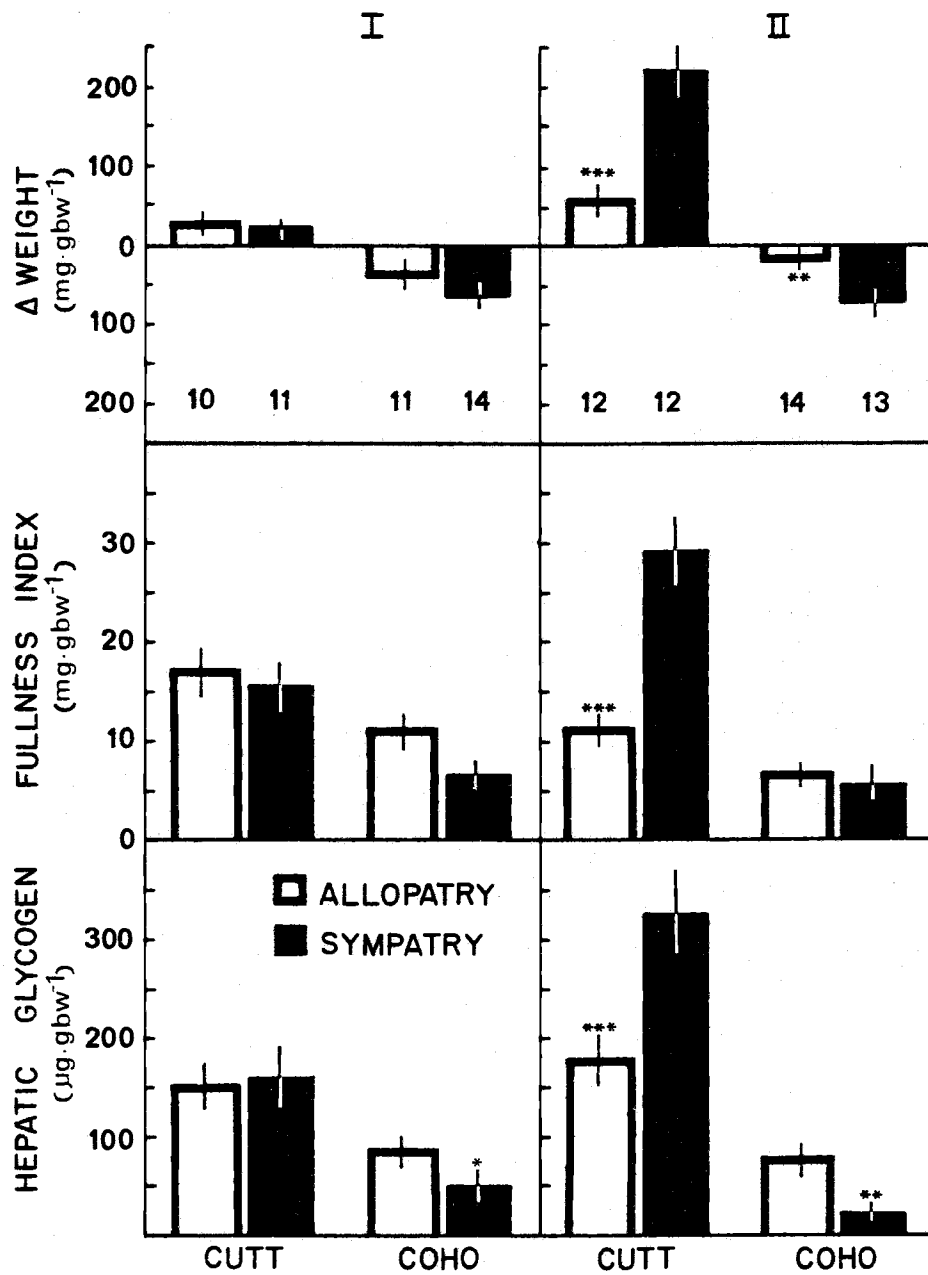


t-test with arc sin transformed values). There were no other differences in prey type utilization among treatments in allopatric and sympatric associations. To compare dietary overlap between coho salmon and cutthroat trout, I computed percent overlap indices according to Pianka (1973). Overlap indices were high among both sympatric and allopatric fish. For sympatric fish, percent overlap was 89 percent and 86 percent in replicates I and II, respectively; among allopatric fish percent overlap was 75 percent and 41 percent in respective replicates.

Energetic Parameters - Energetic parameters indicated that effectiveness of stream habitat utilization was greater for cutthroat trout than for coho salmon. Furthermore, habitat utilization effectiveness of cutthroat trout appeared not to be influenced by coho salmon; however, habitat utilization effectiveness of coho salmon was reduced by cutthroat trout.

In both replicates cutthroat trout gained and coho salmon lost mass. Mass gains of cutthroat trout were not reduced by the presence of coho salmon, yet, coho salmon, in sympatry with cutthroat trout, always lost more mass than allopatric coho salmon (Figure 3). In replicate I, gains in mass for sympatric and allopatric cutthroat trout were comparable; both groups gained an average of 30 mg/g of initial mass ($p > 0.05$, Student's t-test). In replicate II, sympatric cutthroat trout gained nearly three times more mass than allopatric cutthroat trout (60 mg/g versus 235 mg/g of initial body mass, $p < 0.001$, Student's t-test). Mean losses of mass by sympatric coho salmon were approximately two and four times the losses of allopatric

Figure 3. Changes in wet weight (weight change in mg/g initial body weight), stomach fullness (mg of stomach contents/g final weight), and hepatic glycogen (μg of liver glycogen/g final body weight) of allopatric and sympatric populations of cutthroat trout and coho salmon. I and II are experimental replicates; numbers at bottom of upper graph are sample sizes for each treatment and numbers of fish recaptured and * indicates differences between allopatric and sympatric treatments (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).



coho salmon in replicates I and II, respectively (Figure 3). Differences between allopatric and sympatric coho salmon were significant in replicate II ($p < 0.01$, Student's t-test).

Stomach fullness, a relative index of food consumption, was greater for cutthroat trout than for coho salmon regardless of the species association (Figure 3). Fullness indices of cutthroat trout groups in replicate I were comparable ($p > 0.05$, Student's t-test). In replicate II sympatric cutthroat trout had a mean fullness index approximately three times the index of allopatric cutthroat trout ($p < 0.001$, Student's t-test). For coho salmon, stomach fullness appeared higher in allopatric fish than sympatric fish in both replicates. Differences, however, were not statistically significant.

Levels of hepatic glycogen were higher in cutthroat trout than coho salmon. Relative to allopatric groups of each species, levels of hepatic glycogen were reduced in sympatric coho salmon but not sympatric cutthroat trout (Figure 3). Comparable levels of hepatic glycogen occurred for both replicate I cutthroat trout groups ($p > 0.05$, Student's t-test). In replicate II, hepatic glycogen content of sympatric cutthroat trout was significantly higher than that of allopatric cutthroat trout ($p < 0.05$, Student's t-test). Allopatric coho salmon had levels of hepatic glycogen approximately two- and threefold higher than levels occurring for sympatric coho salmon in replicates I and II, respectively. These differences were statistically significant (replicate I, $p < 0.05$, Student's t-test; replicate II, $p < 0.01$, Student's t-test).

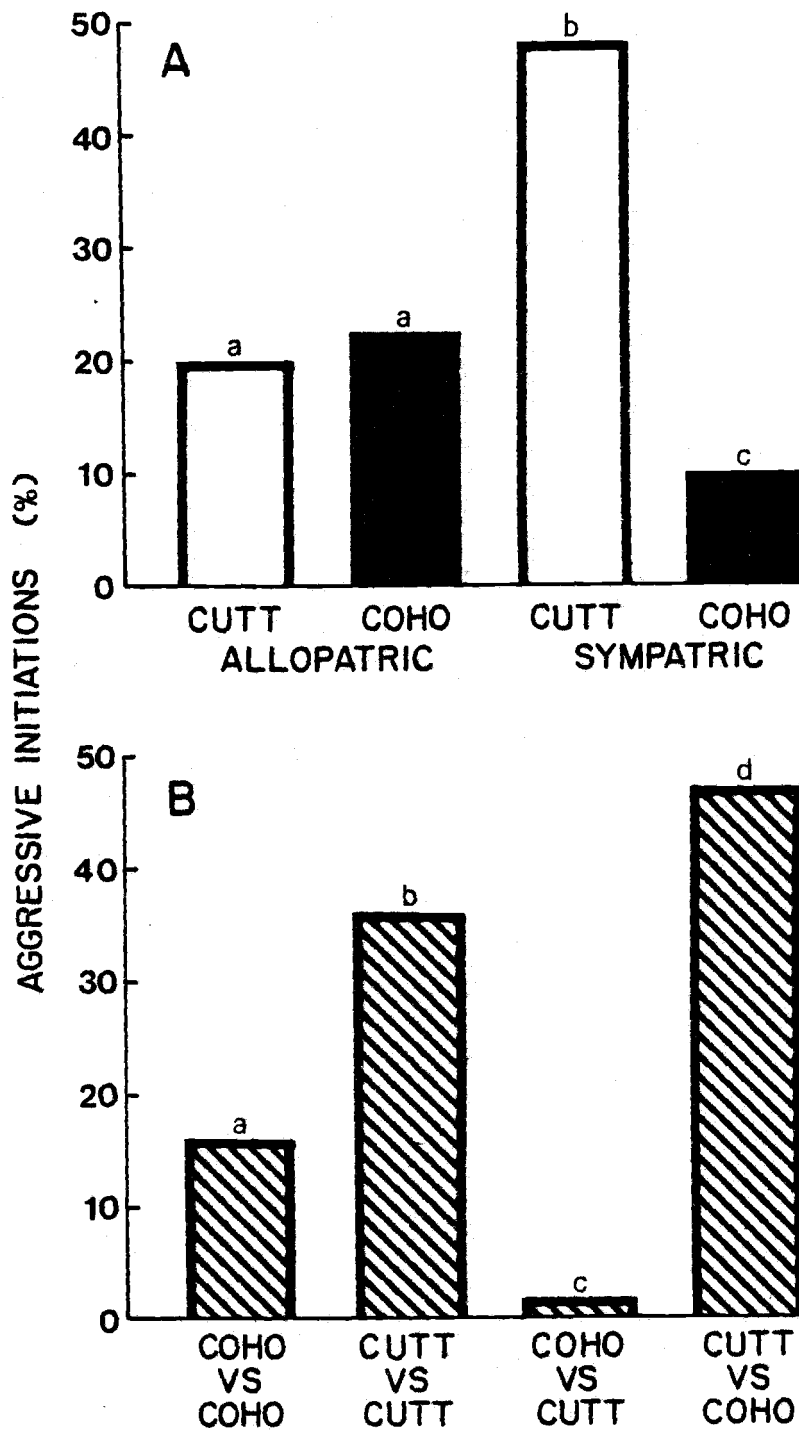
To assess the energetic status of experimental versus

non-experimental fish, I compared levels of hepatic glycogen of: 1) native cutthroat trout of Mill Creek and experimental cutthroat trout, and 2) coho salmon at the Smith Farm rearing facility and experimental coho salmon. Hepatic glycogen levels were: Mill Creek cutthroat, $127.8 \mu\text{g/g} \pm 18.6$ (SE); Smith Farm coho salmon, $233.4 \mu\text{g/g} \pm 44.2$ (SE). Hepatic glycogen levels of all experimental groups of cutthroat trout (cf. Figure 4) were comparable, if not greater, than those of resident cutthroat trout of Mill Creek ($p > 0.05$, ANOVA, Newman-Keuls). Alternatively, relative to coho salmon maintained under hatchery conditions, hepatic glycogen levels were reduced by approximately two and five times for allopatric and sympatric coho salmon, respectively ($p < 0.001$, ANOVA, Newman-Keuls; cf. Figure 4).

Behavioral Observations

Levels of Aggression - Aggressive activity occurred at comparable levels among allopatric populations of cutthroat trout and coho salmon. When both species occurred together, aggressive activity of coho salmon was suppressed and largely restricted to intraspecific exchanges, whereas, cutthroat trout increased their aggressive activity by becoming aggressive towards coho salmon. Frequencies of aggressive initiations were nearly equal in allopatric assemblages of coho salmon and cutthroat trout ($p > 0.05$). However, relative to allopatric fish, a significantly higher frequency of aggressive initiations was observed among sympatric cutthroat trout ($p < 0.001$), and a significantly lower frequency of aggressive initiations was observed

Figure 4. (A) Frequency of aggressive initiations of coho salmon and cutthroat trout in allopatry and sympatry. Data are expressed as percentage of total aggressive initiations observed. Groups indicated by different letters are significantly different from all others ($p < 0.001$). (B) Frequency of intraspecific and interspecific aggressive initiations of sympatric coho salmon and cutthroat trout. Data are expressed as percentage of total sympatric aggressive initiations observed. Groups indicated by different letters are significantly different at $p < 0.001$ except in the case of b versus d where $p < 0.05$.

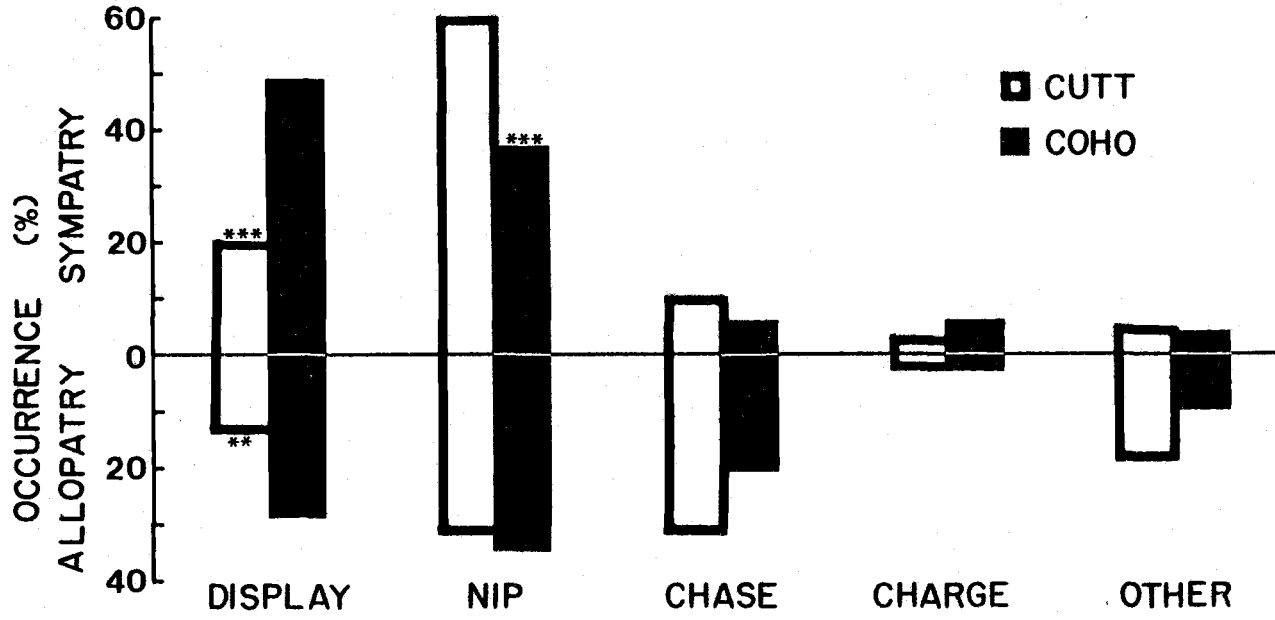


among sympatric coho salmon ($p < 0.001$, Figure 4A).

Based on frequencies of inter- and intraspecific aggressive initiations by sympatric fish (Figure 4B), cutthroat trout initiated most aggression ($p < 0.001$), with more cutthroat trout aggression directed toward coho salmon than other cutthroat trout ($p < 0.05$). Alternatively, aggressive initiations of coho salmon were almost entirely intraspecific; the difference in interspecific versus intraspecific aggressive initiations of coho salmon was highly significant ($p < 0.001$).

Aggressive Repertoire - Cutthroat trout and coho salmon communicated through similar behavioral repertoires in allopatry and in sympatry, but frequencies of various aggressive initiation components differed between species (Figure 5). In allopatry, all categorized components of aggressive initiations were used by cutthroat trout and coho salmon. With the exception that displaying was more frequent for coho salmon ($p < 0.01$), aggressive initiations as categorized occurred at statistically comparable frequencies. Nipping was the most frequent aggressive initiation for both species. In sympatry both species also used all categorized components of aggressive initiations. Categories other than nipping and displaying accounted for only a minor proportion of their aggressive repertoires, consisting of approximately 16 percent and 19 percent of the aggressive initiations of coho salmon and cutthroat trout, respectively. Significant differences occurred in frequencies of displaying and nipping between species, with displaying being significantly greater for coho salmon ($p < 0.001$) and nipping significantly greater for cutthroat trout ($p < 0.001$).

Figure 5. Frequencies of aggressive initiations of coho salmon and cutthroat trout in sympatry and allopatry. Aggressive initiations are categorized, and data within each category represent percent of total aggressive initiations of each species in either sympatry or allopatry; *** indicates categories significantly different at $p < 0.001$ and ** indicates categories significantly different at $p < 0.01$.



Keenleyside and Yamamoto (1962) found nipping was most commonly initiated by dominant individuals and directed towards subordinates, while displaying was more prevalent among fish of equal social status. Because sympatric cutthroat trout directed most aggressive initiations toward coho salmon, and coho salmon, in contrast, directed almost all aggression toward conspecifics, differences that I observed in frequencies of displaying and nipping between the species may reflect cutthroat trout dominance and coho salmon subordination.

Social Structure - Assemblages of allopatric cutthroat trout and coho salmon were organized in linear dominance hierarchies (Murchison 1935, Table 1). For both species the top ranking, or alpha, individual initiated most aggressive acts and received the fewest. Beta ranked individuals also initiated more aggressive acts than they received, but not to the degree of alpha fish. Similar social structures have been reported for laboratory populations of green sunfish (*Lepomis cyanellus*, Greenberg 1947), and brook trout (*Salvelinus fontinalis*) and rainbow trout (Newman 1956). While movement of subordinate fish was restricted, alpha individuals had free reign of the entire stream section. For both coho salmon and cutthroat trout, alpha individuals chose to occupy the upper reach of the pool where they commonly engaged in feeding activity and continually prevented others from feeding. Most aggression occurred within the first 7 days of observation. Thus, social structure was established early and remained stable.

Among sympatric fish, cutthroat trout occupied the first four

Table 1. Dominance matrices for allopatric and sympatric cutthroat trout and coho salmon. T1-T4 and S1-S4 refer to individual cutthroat trout and coho salmon, respectively. Column order represents dominance ranking of individuals with respective dominant individuals in the left hand column of each matrix. N is the total number of aggressive initiations observed for each respective assemblage.

 Allopatric Cutthroat Trout

	Initiator	Recipient				Total Initiations	Total Receipts
		T1	T2	T3	T4		
	T1		16	23	18	57	6
	T2	6		20	14	40	18
	T3	0	1		2	3	44
	T4	0	1	1		2	34
N=102							

 Allopatric Coho Salmon

	Initiator	Recipient				Total Initiations	Total Receipts
		S1	S2	S3	S4		
	S1		8	46	22	76	5
	S2	4		10	9	23	8
	S3	1	0		15	16	58
	S4	0	0	2		2	46
N=117							

 Sympatric Cutthroat trout and Coho Salmon

	Initiator	Recipient								Total Initiations	Total Receipts
		T1	T2	T3	T4	S1	S2	S3	S4		
	T1		3	10	17	8	16	9	23	86	4
	T2	3		20	31	15	7	18	25	119	10
	T3	0	4		17	5	4	0	5	35	31
	T4	0	3	0		0	4	2	0	9	66
	S1	0	0	1	0		11	0	5	17	37
	S2	1	0	0	0	6		6	5	18	50
	S3	0	0	0	0	3	2		2	8	37
	S4	0	0	0	1	0	6	2		8	65
N=300											

social positions of the eight-fish association. While, as in allopatry, sympatric cutthroat trout formed a linear dominance hierarchy, sympatric coho salmon did not organize in an observable linear relationship (Table 1). Thus, cutthroat trout apparently altered social structure of coho salmon. As in allopatry, the alpha individual had free reign of the stream channel and selected the upper reach of the pool for feeding. However, unlike in allopatry, the second-ranked fish initiated most of the aggressive acts. The temporal distribution of aggressive initiations was sporadic and showed no discernable pattern over the 14-day observation period.

DISCUSSION

In allopatry hatchery coho salmon and wild cutthroat trout by selecting upper pools as feeding sites and consuming the same prey items, showed extensive microhabitat overlap. Both coho salmon and cutthroat trout may have selected upper pools because these stream areas offered optimal feeding habitat. High velocity riffles that provided maximal abundances of drifting prey organisms (Everest and Chapman 1972, Wankowski and Thorpe 1979) were readily accessible but excessive energy expenditure due to maintaining position in these high velocity riffle areas was probably avoided. A preference for pool habitat was also observed for wild cutthroat trout by Glova (1978) and Griffith (1972); for wild coho salmon by Hartman (1965), Stein et al. (1972), Allee (1974), and Glova (1978); and for hatchery coho salmon by Allee (1974). Because allopatric cutthroat trout always gained and allopatric coho salmon always lost mass, cutthroat trout appeared more effective at utilizing upper pool microhabitat than coho salmon. Higher stomach fullness indices of allopatric cutthroat trout compared to allopatric coho salmon indicated that differences in habitat utilization effectiveness were probably related to differences in abilities to procure food. Differences in habitat utilization effectiveness have also been observed among species guilds of congeneric sunfish (Centrarchidae) (Werner and Hall 1979).

Relative to allopatric fish, sympatric cutthroat trout used the same feeding microhabitat and exhibited comparable or greater habitat utilization effectiveness, whereas, sympatric coho salmon exhibited a shift in feeding microhabitat and a reduction in

habitat utilization effectiveness. Thus, it appears that cutthroat trout reduced habitat utilization effectiveness of coho salmon by displacing coho salmon from preferred feeding sites to downstream portions of pools. In downstream portions of pools coho salmon possibly encountered reduced food availability due to reduced insect drift and, hence, experienced relatively low food consumption. Results of behavioral experiments in which cutthroat trout, through higher levels of aggressive activity, were socially dominant to coho salmon and able to disrupt coho salmon social structure, support my belief that this shift in feeding microhabitat of coho salmon was a consequence of interspecific agonistic behavior. Thus, the outcome of the interactions between these species is an example of interspecific interference competition (Miller 1967). In natural communities of fish interspecific interference competition commonly results in interactive segregation among the associated species (Nilsson 1956). Flexible behaviors of subordinate species may enable subordinates to use alternative microhabitat (referred to as competitive refuges by Case and Gilpin 1974), and consequently allow stable coexistence among members of the community. Studies documenting interactive segregation in fish communities include Hartman (1965), Nilsson (1965), Werner et al. (1977), Glova (1978), Hixon (1980), and Larson (1980). In the present study, however, due to 1) the relatively low degree of environmental diversity available to smolt-sized coho salmon and cutthroat trout in streams (see Larkin 1956 and Chapman and Bjornn 1969), and 2) the high degree of morphological and behavioral similarity between the two genera (see Scott and Crossman 1973).

and Glova 1978), competitive refuges may not be available to sympatric coho salmon, and hence, interactive segregation may not operate effectively. Therefore, the excessive weight loss and energetic depletion of hatchery coho salmon in sympatry with cutthroat that I observed would be expected. Likely, the coho salmon were forced to occupy areas of the stream that potentially offered lowest relative food availability for drift-feeding fish (Everest and Chapman 1972, Wankowski and Thorpe 1979). Although I did not detect mortality of sympatric coho salmon, the relatively short experimental interval (14 days) may have been insufficient to allow depletion of energy reserves to reach lethal levels. It is possible that under conditions of routine hatchery release, if seaward migration does not occur rapidly, interspecific competition with wild cutthroat trout may result in mortality of hatchery coho salmon. Alternatively, resident cutthroat trout are apparently not adversely affected by introductions of hatchery coho salmon. These speculations should be considered in accordance with the experimental design, in which equal numbers of equal sized cutthroat trout and coho salmon were compared. Under conditions of routine hatchery practices, numbers of coho salmon greatly outnumber cutthroat trout and significant size discrepancies may exist between the two species. Therefore, interactions under these conditions deserve further research.

In interpreting results of this study potentially confounding factors must be considered. Notable, at Mill Creek I assumed that habitat quality was comparable among the three stream sections. Yet, in replicate II, cutthroat trout in section C consumed different

prey and exhibited greater habitat utilization effectiveness than cutthroat trout in section A, an indication of higher habitat quality in section C. Nevertheless, coho salmon that resided in section C with cutthroat trout had the lowest habitat utilization effectiveness recorded. Thus, it appeared that interspecific interactions between coho salmon and cutthroat trout were consistent even with a degree of environmental variation.

Another potentially confounding factor relates to the physiological state of the experimental coho salmon. Prior to migration coho salmon undergo smoltification, a process that supposedly involves a physiological preadaptation to allow seaward migration and marine residence (Hoar 1976, Folmar and Dickhoff 1980). Increases in gill $\text{Na}^+/\text{K}^+\text{ATPase}$ activity and absence of parr-marks have been used as indicators of smoltification (Vanstone and Markert 1968, Zaugg and McClain 1972). In routine hatchery releases coho salmon that are most likely to display extended stream residence are either fish that have not yet undergone smoltification, or fish that have been released after smoltification and have reverted to presmoltification conditions. Hence, it may be argued that if experimental coho salmon were undergoing smoltification results of this study do not simulate conditions of extended residence by hatchery-released fish. I assumed the experimental coho salmon were past the stage of smoltification because: 1) ATPase activity in coho salmon from Sandy Fish Hatchery (the source of the experimental fish) returns to presmoltification levels by early May (Zaugg, unpubl. data) and my experiments occurred in June and July, and 2) the experimental coho

salmon exhibited parr-marks. Therefore, I believe the experimental coho salmon behaved as would hatchery-released coho salmon that exhibit extended stream residence.

Because my results differ from those of Glova (1978) who found that wild cutthroat trout are socially subordinate to wild coho salmon and that wild coho salmon are apparently more effective at feeding on drift than wild cutthroat, it appears that hatchery coho salmon may be behaviorally different than their wild counterparts. Recently Reisenbichler and McIntyre (1977) and Hjort (1980) showed phenotypic differences between hatchery-reared and wild salmonid stocks. Due to the artificial nature of hatchery rearing programs it is possible that behavioral modifications occur in hatchery coho salmon that may impair their ability to optimally perform in the presence of other species under natural stream situations.

In summary, feeding microhabitat used by wild cutthroat trout and hatchery coho salmon overlapped extensively. However, cutthroat trout were more effective at utilizing this microhabitat than coho salmon. When the two fishes occurred sympatrically, feeding microhabitat used by coho salmon was altered, whereas that of cutthroat trout was unchanged. Relative to allopatric fish, a reduction in stream habitat utilization effectiveness occurred for coho salmon but not cutthroat trout. The shift in feeding microhabitat and reduction of habitat utilization effectiveness of sympatric coho salmon may have occurred as a result of interference competition with cutthroat trout mediated through interspecific aggression.

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APPENDICES

Appendix I. Physiographic comparison of experimental stream sections (A, B, and C), number and biomass of resident cutthroat trout, and composition and biomass of introduced experimental fish. I and II refer to experimental replicates.

	Sections		
	A	B	C
Area (m ²)	258	215	485 ^a
Volume (m ³)	138	89	81
Number of resident cutthroat trout (>10g)	19	18	12
Biomass of resident cutthroat trout (g)	638.9	694.1	615.9
Biomass of coho salmon in replicate I (g)	-	392.4	380.2
Biomass of cutthroat trout in replicate I (g)	365.8	374.4	-
Biomass of coho salmon in replicate II (g)	-	396.3	411.1
Biomass of cutthroat trout in replicate II (g)	406.8	-	368.9

^aDue to features in channel morphology the upper net in section C was placed further upstream than nets of other sections and thus, the section had larger total area than the other sections. The additional area was composed of a shallow high velocity reffle that was unsuitable for use by fish of the size of the experimental fish.

Appendix II. Fork lengths and weights of fish stocked into the experimental sections of Mill Creek. Values are expressed as means \pm 95 percent confidence intervals with ranges below each value in parentheses. N=14 for all groups. I and II refer to replicates I and II, respectively.

Date	Group	Fork Length (cm)	Wet Weight (g)
6 June	Allopatric Coho I	14.0 \pm 0.4 (13.0-15.0)	27.2 \pm 2.2 (21.7-35.5)
6 June	Allopatric Cutthroat I	13.9 \pm 0.4 (12.5-15.0)	26.1 \pm 2.2 (19.1-31.9)
6 June	Sympatric Coho I	14.2 \pm 0.4 (13.5-15.5)	28.1 \pm 2.1 (19.0-35.8)
6 June	Sympatric Cutthroat I	14.4 \pm 0.5 (12.5-16.0)	28.9 \pm 2.9 (19.0-35.8)
17 July	Allopatric Coho II	14.2 \pm 0.3 (13.0-14.5)	28.3 \pm 1.7 (24.1-36.0)
17 July	Allopatric Cutthroat II	14.1 \pm 0.3 (13.0-14.5)	29.1 \pm 1.5 (24.5-33.2)
17 July	Sympatric Coho II	14.6 \pm 0.4 (13.5-15.0)	29.4 \pm 1.4 (24.6-33.6)
17 July	Sympatric Cutthroat II	14.0 \pm 0.4 (13.5-16.0)	26.3 \pm 1.7 (23.7-34.3)

Appendix III. Fork lengths and weights of fish used in behavioral observation experiments at Berry Creek. N=4 for all groups.

Lengths and weights are expressed as means \pm 95 percent confidence intervals with ranges below each value in parentheses.

Date	Group	Fork Length (cm)	Wet Weight (g)
29 April	Allopatric Cutthroat	12.0 \pm 0.4 (11.6-12.5)	18.4 \pm 1.2 (17.0-19.7)
13 May	Allopatric Coho	12.8 \pm 0.4 (12.2-13.0)	20.5 \pm 1.7 (19.0-22.0)
27 May	Sympatric Cutthroat	13.1 \pm 0.5 (12.5-13.5)	21.8 \pm 0.6 (21.0-22.3)
27 May	Sympatric Coho	13.2 \pm 0.7 (12.5-13.5)	21.7 \pm 1.6 (19.5-22.8)