PATTERN AND MECHANISM OF RESOURCE PARTITIONING BETWEEN STREAM POPULATIONS OF JUVENILE COHO SALMON (Oncorhynchus kisutch) AND COASTAL CUITHROAT TROUT (Salmo clarki clarki)

by

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ABSTRACT

Anadromous populations of juvenile coho and cutthroat frequently occur sympatrically in coastal streams of western North America. Their apparently similar external morphology and macrodistribution in streams suggest they might broadly overlap in resource use. This study examines resource partitioning between these two salmonids in streams and in laboratory experiments.

In small coastal streams, during late summer low flow, sympatric populations of juvenile coho and cutthroat were partially segregated in microhabitat use and diet. Abundance and biomass of coho were highest in low velocity microhabitats (pools, glides) whereas that of cutthroat were highest in riffles and lowest in pools. In all microhabitats examined, adult insects were more common in the diet of coho than cutthroat, whereas chironomid larvae and pupae showed the reverse pattern.

In laboratory stream experiments, partitioning of space between underyearling coho and cutthroat from sympatric populations was similar to that in streams. When tested together in summer at 12-14 ^OC, coho numerically dominated pools and trout dominated riffles. When tested separately, their microhabitat use was similar (60-75% of either species occupied pools). In winter, at 3 ^OC, both species showed strong preference for pools and overhead cover, whether tested separately or together.

In laboratory stream experiments, coho and cutthroat fry displayed a similar array of aggressive activity although non-contact aggression was more frequent in coho and nipping more frequent in cutthroat.

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Both salmonids were most aggressive when food was presented, regardless of season. When tested together in summer at 12-14 °C, intensity of aggression was high and cutthroat more actively defended territories in riffles and coho in pools; in winter at 3 °C, aggression was low and both species weakly defended pools. Microhabitat use and aggressive behavior of allopatric and sympatric cutthroat tested separately in the laboratory stream were similar, although sympatric trout defended riffle territories more vigorously, responded to the feeding cycle with greater synchrony, and used components of aggressive display apparently more suited to high water velocity habitats.

When fed <u>ad libitum</u> in the laboratory, underyearling coho grew faster than cutthroat in winter, irrespective of temperature range (5-15 °C) and photoperiod (8-16 h), whether tested separately or together; in summer, growth was similar for both species at the same test conditions as above. When cohabiting during summer in two coastal streams, underyearling cutthroat grew faster than coho, possibly because of greater behavioral diversity in feeding and microhabitat utilization, and lesser social dissipation of energy.

The data provide evidence of interactive segregation (Nilsson 1956) and illustrate the flexible behavior of these two salmonids, cutthroat slightly more so than coho, possibly due to subdominance. Behavioral flexibility may counteract heterogeneity and instability of stream environments, and may permit opportunistic exploitation of broadly overlapping niches when resources are plentiful.

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CHAPTER I. GENERAL INTRODUCTION

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Studies on resource partitioning between closely related or ecologically similar taxa have gained considerable momentum (see review by Schoener 1974) ever since Hutchinson (1959) posed his query: "- - why are there so many kinds of animals?" While Hutchinson's concept of the "ecological niche" stimulated renewed interest in the structure of communities and in species interaction, the foundation for such works had developed from an interplay of theoretical and experimental studies since the early 1900's. Joseph Grinnell (1904), an American naturalist, was the first to appreciate the concept that no two ecologically similar species could coexist indefinitely on a single resource. This concept was later acknowledged in the mathematical equations of competition by Lotka (1925) and Volterra (1926). During this era, experimental evidence supporting Grinnell's concept had been generated by several workers, although most notably by Gause (1934), a Russian biologist. Gause found that when two closely related species of Protozoa (Paramecium) were cultured on a single culture medium in the laboratory, one species was invariably eliminated in time by the other. More recent laboratory competition experiments by Park (1962) on the flour beetles Tribolium castaneum and T. confusum, have parallelled Gause's findings, although the species of beetle that persisted depended on the environmental conditions: castaneum prevailed in warm and moist conditions, while confusum did so in drier and cooler ones; both species, however, preferred warm, moist conditions.

The results of the earlier laboratory competition experiments led to the formulation of "Gause's principle" (Lack 1944) or the "competitive exclusion principle" (Hardin 1960), which both in essence reaffirmed Grinnell's concept that no two species can coexist indefinitely on the same limiting resource. Extension of this concept to natural communities rapidly gained popularity when scientists attempted to explain morphological and behavioral differences between species as a means to reducing competition for resources. Since then numerous studies have revealed ecological differences between seemingly similar species in sympatry (e.g. Hartley 1953; Betts 1955; MacArthur 1958). Thus, while some sympatric species may appear to closely resemble one another, no two are exactly alike, and if one looks hard enough one is likely to find some interspecific differences.

Juveniles of anadromous populations of coho salmon (<u>Oncorhynchus</u> <u>kisutch</u>) and coastal cutthroat trout (<u>Salmo clarki clarki</u>) frequently occur sympatrically in freshwater nursery areas throughout their natural geographic range. The nonanadromous forms of coastal cutthroat trout is also common and frequently occurs in allopatric populations that are isolated from salmon in lakes and streams inaccessible from the sea. Like other Pacific salmon species, coho spawn in the fall and in early winter, whereas cutthroat trout typically spawn in late winter - early spring (Hart 1973). Coho emerge earlier and are of a larger size at emergence than trout. The young of both species normally reside in freshwater for one or more years before going to sea. However, in some coho populations a large proportion of the young fry move seaward, if not to it (e.g. Chapman 1962; Andersen and Narver 1975; Mason 1976) and this is believed to be the result of

intraspecific competition for food and space (Mason and Chapman 1965).

In British Columbia and elsewhere in Western North America, small coastal streams are important nursery areas for juveniles of coho salmon and coastal cutthroat trout (Hart 1973). Their seemingly similar external morphology and ecological requirements suggest they may be potential competitors for resources in streams. Their coexistence may in large part depend on differences in their behavioral ecology as documented for sympatric populations of juvenile coho and steelhead trout (Hartman 1965b).

Resources between animal populations may be partitioned spatially into horizontal patches or vertical layers, or both (Cody 1968). The small stream environment provides the three major types of flowing water habitat--riffles, pools and glides or intermediate channels (Mundie 1974), in which resources may be partitioned horizontally between habitat types or vertically within the deeper water habitats. While the small stream environment may provide, a highly productive nursery area for young salmonids (Egglishaw 1967; LeCren 1969; Mundie 1969; Mason 1976), some may be of extreme temporal and spatial heterogeneity, susceptible to pronounced changes seasonally in hydrology, physiography (in unstable streambeds), thermal budget, and in the availability of cover and food organisms for fish. In response to environmental instability, stream salmonids have evolved flexible behaviors, permitting opportunistic exploitation of resources, as hypothesized by Larkin (1956) for freshwater fishes in general. Stream salmonids are usually not

characterized by occupying totally different habitats (e.g. Lister and Genoe 1970; Hartman 1965b), or eating distinctly different foods (Griffith 1974), as in taxonomically distant forms inhabiting relatively stable environments. Rather, stream salmonids are more likely to exploit broadly overlapping niches during periods when resources are plentiful, with a more apparent expression of niche differentiation during seasons when resources are scarce. Fish species in tropical stream communities have been reported to show such niche shifts between wet and dry seasons. Zaret and Rand (1971) found that during the dry season, the diets of eleven species of fish in a small stream in Central Panama overlapped less than during the wet season. Their findings suggest that when streamflow was reduced, food resources diminished, and the fish adopted more specialized feeding behavior, thereby avoiding intense competition. The tendency towards greater niche plasticity in species inhabiting fluctuating environments as opposed to those with greater niche specialization in more stable ones has been frequently demonstrated in the literature (e.g. Moldenke 1975; Heinrich 1976; Grant et al. 1976).

This study investigates pattern and mechanism of resource partitioning between juveniles of sympatric populations of coho salmon and coastal cutthroat trout in small streams on Vancouver Island, British Columbia. The general strategy adopted in this study was to first investigate the pattern of microhabitat use and the diets of sympatric populations of juvenile coho salmon and coastal cutthroat trout in three small coastal streams. I also investigated microhabitat use of allopatric cutthroat trout populations (upstream of a barrier falls) in three small

coastal streams to provide 1) an assessment of the spatial niche of cutthroat trout in the absence of coho, and 2) a comparison of population structure and biomass between allopatric (coho absent) and sympatric (coho present) populations of trout. The field studies also served to provide the basic framework from which to test pertinent hypotheses and to evaluate the results of laboratory experiments conducted on these two salmonids. For these experiments, a laboratory model of a stream section consisting of riffle and pool habitat was used, allowing observation of fish microdistribution and social behavior, and allowing environmental manipulation including that of the food supply. While a number of studies have documented behavioral and spatial interactions for various combinations of salmonid species (Lindroth 1955; Newman 1956; Kalleberg 1958; Hartman 1965b; Jenkins 1969; Lister and Genoe 1970; Everest and Chapman 1972; Griffith 1972), none of these have examined experimentally the role of the food supply in species interactions. Also, as dominance hierarchy in stream salmonids is size dependent (Jenkins 1969; Mason 1969), and since growth rate may be positively related to"competitive fitness" (Bagenal 1967; Hall et al. 1970), a series of laboratory growth experiments were conducted in this study to investigate the possibility of different seasonal patterns of growth for these two salmonids.

The possible importance of interspecific competition for resources in general, and for food in particular, between populations of these two salmonids was not investigated directly in this study. Competition as defined by Birch (1957), Andrewartha (1961) and Milne (1961) continues to remain a most elusive phenomenon to demonstrate, and

the stream environment is no exception. Competition for food between fish species in streams has been frequently inferred from apparent overlap in their diets (Hartly 1948, Maitland 1965; Straskraba et al. 1966; Mann and Orr 1969; Mason and Machidori 1976). However, experimental studies providing hard evidence of interspecific competition in nature are relatively few and do not include fishes, being namely those by Connell (1961) for barnacles, Grant (1972) and Redfield et al. (1977) for microtine rodents, Jaeger (1971, 1972) for salamanders, Haven (1973) for limpets and DeBenedictis (1974) for anuran tadpoles. Using the inferential definition of competition proposed by Maitland (1965), I compared biomass of allopatric and sympatric cutthroat trout populations to assess the probable importance of interspecific competition for resources in general in the sympatric fish communities. As food may be a limiting factor of juvenile salmonid production in small streams (Mason 1976), any additional similar species, or species feeding similarly, may reduce the biomass of a species through sharing of a limiting food supply.

CHAPTER II. NATURAL POPULATIONS OF SALMONID AND NONSALMONID FISHES IN THE STUDY STREAMS

INTRODUCTION

Pianka (1973) has emphasized that ecologically similar animal species partition resources in three basic ways: spatially, trophically and temporally. Schoener (1974) in his review of the subject presented evidence indicating that animal populations partition resources more often along dimensions of habitat rather than food and even less so by temporal means which may be manifested in the fact that the distribution of resources are often habitat specific (Werner and Hall 1977). The concept of interactive segregation as advanced by Nilsson (1956) is one means by which ecologically similar species might spatially partition the available resource spectrum and reduce interspecific competition. Basically, this concept states that under conditions of intense intraspecific competition, allopatric populations of species having similar ecological demands, tend to utilize the full range of their ecological potentials. Conversely, under conditions of intense interspecific competition, sympatric populations of species having similar ecological demands, tend to utilize those resources to which they are best adapted, or have some competitive advantage over the other. Among salmonid fishes, such segregation has been demonstrated to largely account for resource partitioning between stream populations of juvenile coho salmon and steelhead trout in coastal British Columbia (Hartman 1965b).

Accordingly, interactive segregation might also largely account for resource partitioning between stream populations of juvenile coho salmon and coastal cutthroat trout.

To initiate this study, I tested two null hypotheses using several small coastal streams on Vancouver Island, during the late summer period of low streamflow: 1) there is no difference in the pattern of microhabitat use and in the diets between juveniles of sympatric populations of coho salmon and coastal cutthroat trout; 2) there is no difference in the pattern of microhabitat use and in the biomass between sympatric (coho present) and allopatric (coho absent; upstream of barrier falls) populations of coastal cutthroat trout. I restricted sampling of fish populations to period of low flow, as this presumably is when salmonid-producing streams are at carrying capacity (Burns 1971) and segregation between salmonids is best defined. Allopatric populations of trout were unique to this study in that they served as a "control" in nature. Such populations provided the basis for investigation of the ecological potential of cutthroat trout in the absence of coho, a competitor species. I assumed that the microhabitat requirements of both trout types and that the physical conditions of their streams were similar.

Investigation of the ecological relations between sympatric populations of coho and cutthroat trout in small coastal streams is frequently faced with the problem of the presence of sculpins, either <u>Cottus aleuticus or C. asper</u>, or both. Sculpins are a common cohabitant with anadromous salmonids in reaches of such streams accessible from

the sea (Andersen and Narver 1975; Mason and Machidori 1976). These two groups of fish are distinctly different taxonomically (Hart 1973), but not necessarily so ecologically (Mason and Machidori 1976). The importance of the ecological role of sculpins in guilds of these fishes has been demonstrated by 1) their frequently higher biomass levels than those of sympatric salmon and trout combined (LeCren 1965; Mann 1971; Petrosky and Waters 1975; Mason and Machidori 1976), 2) the considerable overlap in their diets with those of salmonids (Dineen 1951; Andreasson 1971; Mason and Machidori 1976), and 3) by their negative effect on the production of cutthroat trout in laboratory streams, presumably through interspecific competition for food (Brocksen et al. 1968). Based on these premises, I surmised that the pattern of microhabitat use by stream salmonids is influenced, at least to some degree, by sculpin populations. In this study, sculpins were therefore given similar sampling effort as were coho and cutthroat trout. They have, however, been neglected in previous studies dealing specifically with the subject of interaction between stream salmonids.

DESCRIPTION OF STUDY STREAMS

Six small coastal streams on the east and south sides of Vancouver Island, B. C. were selected for study of their fish populations. Of these, Ayum, Bush and Holland creeks (Fig. 1) contained sympatric populations of coho salmon, coastal cutthroat trout and sculpins, primarily <u>Cottus aleuticus</u>. The extent of upstream movements by fishes in



Fig. 1. Plan view and stream gradient of each of the streams containing sympatric populations of coho, cutthroat trout and sculpins. Heavy solid line denotes section of stream sampled; dotted line, perimeter of watershed; hatched area, ocean; \mathbf{V} , barrier falls.

each of the three streams are restricted to approximately 2 km above high tide by a waterfall. The others, Bings, French and Shawnigan creeks (Fig. 2) upstream of their barrier falls contained allopatric (nonanadromous) populations of coastal cutthroat trout isolated from salmon. Also present were sparse populations of the three-spined stickleback, <u>Gasterosteus aculeatus</u>, in Bings Creek and of the coastrange sculpin, <u>Cottus aleuticus</u>, in Shawnigan Creek (from the lake below). Coho have not been reported to occur, and none were taken in this study, upstream of the falls in each of these three streams. In Bings and French creeks, the falls are situated several km from sea; in Shawnigan Creek, the fall is situated near the mouth. The length of the stream segments in which cutthroat trout were abundant was about 3 km in both Bings and Shawnigan creeks and about 6 km in French Creek.

Physically, the six streams are fairly similar, ranging in watershed area: from 17 to 31 km², average gradient from 1.0 to 4.5% and minimum summer discharge from 1.2 to 5.7 m³/min (Table 1). The forest stand in all is a mixture of second growth deciduous and coniferous species; the understory consists mainly of salal, sword fern, salmonberry, stinkcurrent and devil's club. Vegetation along the streambank is dense in most areas, mainly of salmonberry, stinkcurrent and alder. Pools are slightly deeper but not larger in area in the streams containing the sympatric populations of fish than in those containing the allopatric populations of cutthroat trout. Streambed materials in Holland and in Ayum appeared to contain less gravel and more rubble, boulders and bedrock formation than in the other four streams. Further, Holland lacks a natural upper estuary due to a large culvert and spillway under-



Fig. 2. Plan view and stream gradient of each of the three study streams containing allopatric populations of cutthroat trout. See Fig. 1 for caption details.

· · · ·			MINIMUM				`,
	WATERSHED AREA (km ²)	STREAM GRADIENT (%)	SUMMER DISCHARGE ^a (m ³ /min)	ME	AN AREA GLIDES	(m ²) RIFFLES	MEAN DEPTH (cm) POOLS
<u></u>			<u>, , , , , , , , , , , , , , , , , , , </u>	<u> </u>			
Bush Ho11and Ayum	23 31 17	1.3 2.6 4.5	1.2 1.2 3.5	39 27 40	31 36 53	28 27 56	30 36 41
Bings French Shawnigan	20 26 22	1.5 1.0 1.0	5.7 1.6 1.5	46 56 71	50 54 39	27 20 25	36 31 31
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Summary of some physical characteristics of the study streams. Table 1.

^a average weekly readings August 15-September 30 during study years

lying the Island Highway/Railroad overpass, but this structure presents no barrier to upstream movements of fish during high tide.

A complete annual cycle of both stream temperature and discharge is available only for Bings Creek (Fig. 3), with temperature being highest in July and August and discharge highest from November to January. These data are considered fairly representative in temporal pattern, although not necessarily in magnitude, of the other five study streams. In all streams, during the fall sampling period, the range in water temperature was from about 11 to 15 °C and in stream discharge from about 1-2 $m^3/$ min. Hydrochemical composition (major and minor ions) was monitored monthly over one complete annual cycle in Bush and Holland creeks (Appendix Tables 1, 2); peaks in total dissolved solids, nitrates, phosphates and other major ions occurred at the onset of heavy rains in the fall. These may be "fairly" representative in seasonal pattern, although not necessarily in magnitude, in the other four streams. Turbidity was not measured in any of the streams, the water being clear in all during the fall sampling period.

METHODS

A. POPULATION ESTIMATES

Sampling of fish for determination of population estimates took place in all streams approximately from mid August- end September. Bush and Holland creeks were sampled in three consecutive years from 1973 to 1975; the remaining four streams were sampled only one year



Fig. 3. Mean monthly temperature (Δ) and discharge (0) in Bings Creek; vertical lines represent range (data collected by Water Survey Canada: temperature 1961-1976; discharge 1976).

in 1975-76. The repeated sampling in Bush and Holland provided replication of the results in order to assess the variability between years for a portion of the fish populations studied. Burns (1971) found that variation between years in salmonid standing crops by natural means alone, was relatively high in several streams in northern California. I surmised that significant changes in species relative abundance between years should they occur, would result in differences in species pattern of microhabitat use.

Fish population estimates were determined by the removal method (Seber and LeCren 1967). For small streams and catches large relative to the total population, this method has proven satisfactory (Narver and Andersen 1974). Each stream was sampled progressively in an upstream direction in habitat sections of fairly uniform velocity, selected if the local physiography appeared suitable to isolate the inhabiting fish with stopnets. At least five of each of the pool, glide and riffle habitats in the mid-region of each study stream were sampled. Fine mesh minnow seines were stretched across the down- and upstream limits of each chosen section and held snug to the bottom with small rocks when necessary. The blocked off section was then electrofished with a 440-V DC fish shocker (Smith-Root Laboratories, Mark V) from the downstream end up, for a minimum of three successive runs, or until catches declined to zero or nearly so. This sampling technique was similar to that used by Egglishaw (1970) for stream salmonids in Scotland. The stunned fish were collected with dip nets and held in separate plastic buckets for each successive run until sampling was completed. All fish captured were anaesthetized in MS-222, fork length

and species identification recorded for each fish and scale samples taken from individuals obviously exceeding the length range of age 0+ fish. Upon complete recovery, the fish were returned to the section sampled and the stopnets were removed shortly after the fish had distributed themselves within the confined area.

Physical data gathered for each sampling site included stream velocity (pool < 8 cm/s; glide 8-20 cm/s; riffle > 20 cm/s), area sampled and water depth. In addition, substrate composition was also recorded in Bush and Holland creeks in 1973. Mean sampling areas in all streams ranged from 27-71 for pools, 31-54 for glides and 20-56 m² for riffles.

Fish biomass estimates in each of the three habitat types were computed from the measured mean fork length (X) and mean wet weight (Y) by species for each stream in the linear regression equation, $Y = AX^{b}$. The equation was for each population of fish, derived from length and weight determination of live samples of fish from each stream, held in the laboratory 1-2 days without food prior to measurement.

I determined the distribution and abundance of the fish populations in both Bush and Holland creeks from the mouth to the barrier falls in 1973, to establish if the populations were distributed uniformly or clumped. I surmised that their pattern of habitat segregation would be best defined in the zone of maximum overlap between populations, due to possible accentuation of interspecific competition for resources. Both streams were stratified longitudinally into lower-,

mid- and upper sections based on major changes in their stream bottom profiles and substrate compositions (Fig. 4). At least five of each of the pool, glide and riffle habitats in each of the three sections were sampled. Sampling was otherwise restricted to the mid-section of the study reaches in each of the six streams in subsequent years.

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B. DIETS OF SALMONID FRY

Underyearling coho and cutthroat trout were subsampled during routine sampling of a selected pool, glide and riffle habitat in the midsections of Bush and Holland creeks, 1973. The fish were preserved in 10% formalin for diet analysis. No regurgitation of food occurred during this process. In the laboratory, the stomach was extracted and placed in a labelled vial containing 10% formalin. The contents of the fore-stomach (Mundie 1971) were extracted and the identifiable food items were separated and counted into taxonomic categories with the aid of a binocular microscope.

C: GROWTH OF SALMONID FRY

Coho and cutthroat trout fry were seined biweekly from various habitat types in Bush and Holland creeks from 3 June - 27 September, 1974. They were anaesthetized in MS-222 and the species identification and fork length were recorded for each fish. Scale samples were taken from individuals in the upper size range of the fry to ensure no inclusions of age 1+ fish. Upon complete recovery, the fish were returned to the section sampled. Stream discharge was estimated for the same time intervals in both streams using midget-Bentzel pitot tubes (Everest 1967).

D. BREADTH AND OVERLAP IN RESOURCE USE

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I calculated breadth of microhabitat niche for sympatric coho, trout and sculpins in each of the three streams and breadth of food niche for coho and trout in Bush and Holland. I used Simpson's index of diversity as employed by MacArthur (1972):

$$B = \frac{1}{\frac{n}{\sum_{i=1}^{n} p_{i}^{2}}}$$

where in the present study, B is niche breadth and p_i represents the relative proportion of a species in the i^{th} habitat or relative consumption of the i^{th} food-type. Values of p were obtained from average density estimates or percentage composition by number of an item in their diet in the relation

$$p_i = \frac{d_i}{\sum_{i=1}^{d} d_i}$$

where d_i represents grams or numbers of fish per unit wetted-area of stream, or frequency of an item in the total diet of a species. Niche breadth can vary from unity to the number of habitats sampled, or the number of food categories eaten. For comparative purposes, breadth of microhabitat and of food niche were standardized by dividing by the three microhabitats (pools, glides, riffles), or by the number of food-types (see Fig. 14), respectively (range 0-1.0).

Overlap in microhabitat use and in diet between species pairs in the sympatric populations of fish were calculated from Pianka (1973):

$$0_{ij} = 0_{ji} = \frac{\sum (P_{ik} P_{jk})}{\sqrt{\sum P_{ik}^2 \sum P_{jk}^2}}$$

where in this study, $O_{ij} = O_{ji}$ = niche overlap between species i and species j (range 0 to 1.0); P_{ik} and P_{jk} are the proportions of the kth resource as used by ith and jth species. Overlap in microhabitat niche between species was calculated aby, both numerical and biomass estimates of fish. Confidence limits cannot be calculated for either of these indices, but rather, gross differences or marked similarities between species may be observed.

RESULTS

SYMPATRIC POPULATIONS

Juvenile salmonids and sculpins were not distributed uniformly over the length of the study reaches in Bush and Holland creeks, 1973 (Fig. 4). Combining the data of pools, glides and riffles within each of the three zones per stream, average mean abundance of salmonids was highest in the mid-zone of both streams. This was the area of maximum overlap in the longitudinal distribution of coho and trout. Sculpin abundance was also highest in the mid-zone in Holland, but in the lowerzone in Bush, the latter contained numerous young in shallow riffles and glides near the mouth. Pooling salmonid and sculpin densities, fish were about twice as abundant in Bush as in Holland, throughout the study reaches. My estimated abundances of sculpins are no doubt conservative, due to the difficulty in adequately sampling age 0+ fish, a problem





Fig. 4. Density of coho (solid), cutthroat trout (hatched) and sculpins (open) in the lower-, mid- and upper regions of Bush and Holland creeks, 1973. The data represent the average mean of pools, glides and riffles combined. Numbers are total fish sampled.
reported by others (Krohn 1967; Goodnight and Bjornn 1971).

The pattern of habitat segregation between coho and cutthroat trout was similar in lower-,mid- and upper zones in Bush and Holland creeks, 1973 (Figs. 5, 6, bottom). In both streams, coho made up a greater percentage of the salmonid biomass in pools (53.1 to 90.8%) than did trout (9.2 to 46.9%), while in riffles, trout dominated the biomass, particularly in Holland (63.4 to 88.0%); glides were areas of intermediate biomass for both species, with coho ranging from 51.8 to 80.8% and trout from 25.0 to 48.2%.

Total biomass of coho and cutthroat trout combined (Figs. 5, 6, top) was highest in pools and lowest in riffles in Holland Creek in all three zones; the same pattern occurred in Bush Creek in the lower zone but in mid- and upper zones, glides contained considerably higher salmonid biomass than did pools. In Bush, coho and trout in pools were of a smaller body size in the upper two-thirds than in the lower third of the study reach (Glova and Mason 1974).

Juveniles of coho and cutthroat trout showed a similar pattern of habitat segregation in Bush and Holland creeks during the late summer period of low streamflow from 1973-75 (Figs. 7, 8). Both relative abundance and biomass of coho were highest in the slower velocity habitats, while that of trout were highest in riffles and lowest in pools. Glides supported intermediate levels of abundance and biomass of both salmonids, excepting in Holland, 1974. Sculpins, consisting mainly of



Fig. 5. Absolute (upper) and relative (lower) biomass of coho (open) and cutthroat trout (hatched) in Bush Creek. The number of samples are indicated and those in parentheses indicate total number of fish sampled.



Fig. 6. Absolute (upper) and relative (lower) biomass of coho (open) and cutthroat trout (hatched) in Holland Creek. See Fig. 5 for details.



Fig. 7. Relative abundance of coho (solid), cutthroat trout (hatched) and sculpin (stippled) populations in Bush and Holland creeks, 1973-75.



Fig. 8. Relative biomass of coho (solid), cutthroat trout (hatched) and sculpin (stippled) population in Bush and Holland creeks, 1973-75.

of <u>Cottus aleuticus</u>, showed no distinct pattern of microhabitat use in either study stream. They were abundant in all habitat types. In Holland, and in all but a few cases in Bush, the relative abundance and biomass of sculpins surpassed that of coho and trout combined, in each of the three habitat types. Sculpin biomass has been reported to range from 50-80% in other salmonid-producing streams on the east coast of Vancouver Island (Mason and Machidori 1976).

In Holland, but not in Bush, major changes in fish standing crops occurred from 1973-75; cutthroat trout abundance and biomass declined significantly (P < 0.05) in 1974, while that of coho and sculpins increased, although nonsignificantly so (Glova and Mason 1976a). This altered the pattern of segregation between coho and trout slightly; relative abundance and biomass of coho increased in glides, while that of trout decreased, compared to that in 1973 (Figs. 7, 8).

I compared the pattern of segregation between sympatric cutthroat trout, coho and sculpins between streams, using the average means of the relative biomass of each species in Bush and Holland creeks from 1973-75 (Fig. 9). Trout biomass was consistently highest in riffles, intermediate in glides and lowest in pools, in all three streams. Coho biomass was higher in both pools and glides than in riffles, in both Bush and Holland; in Ayum Creek, however, the pattern was reversed, with a high 36% in riffles and a low 18.8% in pools. Sculpins showed no discernible pattern of microhabitat use in Bush and Holland, but in Ayum they were distinctly highest in pools and



Fig. 9. Mean relative biomass ±95 confidence limits of coho (solid), cutthroat trout (open) and sculpin (hatched)populations in Ayum, Bush and Holland creeks.

lowest in riffles, the opposite to that of salmonids. Sculpin distribution appeared to be more related to that of trout than that of coho. In cases in which trout population densities were relatively low, such as in Bush (1973-75 inclusive) and in Holland (1974 and 1975) creeks, sculpins in riffles comprised an average high of 59.3% as opposed to a low 11.0% in Ayum Creek, 1975, which contained an abundance of trout. Sculpins live almost entirely on the stream bottom, often beneath rocks, particularly the smaller individuals. I frequently observed trout fry chase and nip young sculpins that emerged from beneath rocks in shallow glide and riffle areas. Sculpin emergence from beneath rocks was crepuscular and may serve to minimize agonistic interactions with trout during the day.

Total biomass of salmonids and sculpins combined showed a negative linear relation with stream water velocity (Fig. 10a). The negative relationship Y = 7.801-0.137X (Y, biomass; X, velocity) was significantly correlated at P<0.01 with Pearson's correlation coefficient being -0.922. Fish biomass was highest at lowest water velocities and areas with water velocities exceeding about 60 cm/s are likely to contain fewcle or no fish. By the same analysis, mean fish biomass and pool depth showed no correlation (P>0.05), although biomass was generally higher in the deeper pools. Both depth and velocity were reported to be important factors affecting the production of juvenile coho in artificial rearing channels (Ruggles 1966).

I postulated that individuals of juvenile coho and cutthroat trout compete for space at the head of pools to attain priority in



Fig. 10. Relation between a) fish biomass (coho, trout and sculpins) and stream water velocity, and b) salmonid biomass (coho and trout) and pool surface area in Ayum (\blacktriangle), Bush (\bigstar) and Holland (\triangle) creeks.

exploitation of invertebrate drift. Salmonid biomass-per-unit space would therefore, be higher in small pools than in large ones due to relatively low densities of fish toward the downstream ends in the latter. All applicable data were pooled and a logarithmic transformation applied in linear regression analysis. The negative relationship log $Y = 1.506-0.729 \log X$ (Y, biomass; X, pool area) was significantly correlated at P<0.01 and salmonid biomass ranged from 1.1 to 6.0 g/m², in pools of 100 and 10 m², respectively (Fig. 10b). This phenomenon may account in part for the variability in salmonid biomass between pools (Appendix, Tables 3-5).

Standardized breadth of microhabitat use for sympatric coho, trout and sculpins is shown for each of the three streams (Table 2). Breadth of microhabitat use, either by biomass or numerical densities, was consistently higher for trout than for coho over the 3-yr period in Bush and Holland and for the single year in Ayum. For sculpins, breadth of microhabitat niche was similar to that of trout in Bush and Holland, but substantially less than that of either sälmonid in Ayum. These findings may reflect the ideas of Morse (1974) and Wilson (1975), who postulated that socially subordinate species usually have a broader niche than do dominant ones. Although unquantified, my many casual observations in the field suggested cutthroat trout fry are socially subdominant to coho fry, whereas sculpins, at least young-of-year, are subdominant to both.

Microhabitat use by coho, cutthroat trout and sculpins over-

Table 2. Standardized breadth of microhabitat use for populations of (a) sympatric cutthroat trout, coho and sculpins and (b) allopatric cutthroat trout. Values derived from fish biomass are unbracketed; those from numerical density are bracketed.

a) sympatric

	Bush	Holland	Ayum	Average
Trout Coho Sculpins	0.87(0.90) 0.78(0.77) 0.94(0.96)	0.91(0.95) 0.74(0.71) 0.85(0.97)	0.98(0.85) 0.87(0.91) 0.63(0.64)	0.92(0.90) 0.80(0.80) 0.81(0.86)
		b) <u>al</u> lc	patric	

	French	Bings	Shawnigan	Average
Trout	0.92(1.0)	0.84(1.0)	0.99(0.98)	0.92(0.99)

lapped extensively in each of the three streams (Table 3). The analysis consistently showed that whether by biomass or numerical density, spatial overlap was less between coho and trout than it was for either salmonid with sculpins, in both Bush and Holland over the 3-yr period of study. Coho and trout segregated into slow and fast velocity habitats, respectively, whereas sculpins were abundant in all habitats. In Ayum, the pattern of interspecific overlap in microhabitat use was different from that in Bush and Holland creeks; coho broadly overlapped with trout and to some extent also with sculpins, whereas trout and sculpins overlapped least, particularly in faster velocity water.

COMPARISON OF ALLOPATRIC AND SYMPATRIC POPULATIONS

Statistics of the fish populations and some related stream physical parameters are summarized for each of the six streams by habitat type (Appendix, Tables 3-8). Here, allopatric populations are those of cutthroat trout upstream of the barrier falls in Bings, French and Shawnigan creeks; sympatric populations are those of cohabiting coho, cutthroat trout and sculpins in Bush, Holland and Ayum creeks. I compared the pattern of microhabitat use of these two population types, using estimates of biomass (g/m^2) rather than density (numbers of fish/m²), as they were more meaningful with the broad range in size of fish present. I examined statistical significance of these by parametric one-way analysis of variance, or by the Kruskal-Wallis nonparametric statistic (Siegel 1956) in cases where Bartlett's test (Sokal and Rolf 1969) indicated lack of homogeneity of variance.

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Table 3. Overlap in microhabitat use between cutthroat trout (T), coho (C) and sculpins (S) for (a) by year in Bush and Holland and (b) by stream, using mean values in Bush and Holland creeks. Values above the diagonal are calculated from fish biomass, those below the diagonal from numerical density.

1973			1974		1975			
BUSH CREEK								
<u>T</u>	<u>C</u>	<u>S</u>	<u>T</u>	<u>C</u>	<u>S</u>	<u>T</u>	<u><u>C</u></u>	<u>s</u>
1.0 0.48 0.93	0.78 1.0 0.77	0.92 0.82 1.0	1.0 0.55 0.67	0.73 1.0 0.94	0.76 0.96 1.0	1.0 0.76 0.67	0.82 1.0 0.92	0.97 0.92 1.0
HOLLAND CREEK								
1.0 0.64 0.91	0.67 1.0 0.90	0.91 0.92 1.0	1.0 0.83 0.98	0.88 1.0 0.91	0.88 0.83 1.0	1.0 0.67 0.95	0.71 1.0 0.87	0.95 0.89 1.0
	Bush		Ē	lo11and			Ayum	
1.0 0.60 0.76	0.78 1.0 0.88	0.89 0.90 1.0	1.0 0.72 0.95	0.75 1.0 0.90	0.91 0.88 1.0	1.0 0.83 0.48	0.94 1.0 0.85	0.48 0.87 1.0
		$\begin{array}{cccc} \underline{T} & \underline{C} \\ 1.0 & 0.78 \\ 0.48 & 1.0 \\ 0.93 & 0.77 \end{array}$ $\begin{array}{c} 1.0 & 0.67 \\ 0.64 & 1.0 \\ 0.91 & 0.90 \end{array}$ $\begin{array}{c} \underline{Bush} \\ 1.0 & 0.78 \\ 0.60 & 1.0 \\ 0.76 & 0.88 \end{array}$	$ \begin{array}{ccccccccccccccccccccccccccccccccccc$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$				

The distribution of the biomass of allopatric cutthroat trout by habitat type, resembled that of sympatric coho, trout and sculpins combined (Fig. 11a, b). In both population types, fish biomass was consistently highest in pools, intermediate in glides and lowest in riffles in all six streams, However, the total biomass of the populations in sympatry were significantly (P < 0.05) higher than those in allopatry, excepting in Bings Creek. Pooling the data of all habitat types by stream, average mean biomass in Shawnigan and French creeks was only 1.2 and 1.9 g/m², respectively; those in Ayum, Bush and Holland ranged from 4.5 to 5.4 g/m². Sculpins comprised a major portion of the fish biomass in each of these three streams (Appendix, Tables 3-5). Other small coastal streams on Vancouver Island with a similar sympatric species composition as in the present study, have been reported to support similar fish biomass on the west coast (Andersen and Narver 1975), but higher on the east coast, some 100 km north of the present study location (Mason and Machidori 1976).

The distribution of the biomass of cutthroat trout by habitat type was markedly different between allopatric and sympatric populations (Fig. 11a, c). Biomass of allopatric trout wass some two-fold higher in pools than in riffles in Bings and French creeks, although less so in Shawnigan Creek; conversely, biomass of sympatric trout was similar between habitat types in all three streams and did not exceed 1 g/m². Riffles did not support higher biomass of sympatric trout than did pools, as one might expect as an outcome of their segregation from coho. Pooling the data for each of the three habitat types within each of the six streams, trout biomass was significantly (P<0.05) less for the sympatric



Fig. 11. Mean biomass ±95% confidence limits in pools (1), glides (2) and riffles (3) of a) allopatric populations of cutthroat trout, b) sympatric populations of coho, cutthroat trout and sculpins combined, and c) sympatric populations of coho (solid) and cutthroat trout (open).

(range 0.5 to 0.9 g/m²) than for the allopatric (range 1.1 to 3.5 g/m²) populations, in all but Shawnigan Creek (1 g/m²). However, the biomass of coho and trout combined in Ayum and Bush creeks was not significantly different (P<0.05) from that of the trout in Bings and French creeks.

Habitat segregation between coho and cutthroat trout showed a size-related pattern. Size frequency histograms by habitat type (Fig. 12) indicated that pools and glides most often contained a broader range in size of fish than did riffles, for both salmonids in Bush, Holland and Ayum creeks. This pattern was more pronounced in trout than in coho populations due to higher frequency of age 0+ fish in the latter. Thus, coho and trout coexisting in pools were more widely separated by size (more than one age class of trout), whereas in riffles they were more closely matched (mostly age 0). Sculpins showed a similar pattern of size distribution between habitat types as did salmonids. Considering all three species, the coexistence of all age-classes within pools suggests that size segregation within habitat types may be more possible in the deeper water environments. Pooling all age-classes within species for all three streams in one-way analysis of variance, only trout showed a significant $(P < 0.05)^*$ difference in mean fork length (mm) between habitat types (table below).

	Pools	<u>Glides</u>	<u>Riffles</u>	<u>F-ratio</u>
Coho	51.9	51.4	50.6	0.11
Trout	64.0	51.0	49.1	4.74*
Sculpins	69.5	65.9	62.0	0.43



Fig. 12. Histograms of fork length frequency of the sympatric populations of coho, cutthroat trout and sculpins by habitat type in Bush, Holland and Ayum creeks, 1975.

Size frequency distribution by habitat for allopatric trout (Fig. 13) resembled those of sympatric salmonid and sculpin populations. In Bings, French and Shawnigan creeks, trout range in fork length was broadest in pools and narrowest in riffles; pools contained trout of all age classes whereas riffles were restricted mostly to age 0+ individuals.

In conclusion, microhabitat niche of allopatric trout was broader than that of sympatric trout when compared by numbers; by biomass they were roughly the same (see Table 2). Allopatric trout were about equally distributed between habitat types, whereas sympatric trout were more common in riffles than in pools. The restricted microhabitat use by sympatric trout may in large part reflect coho social dominance in the slower velocity habitats.

DIETS OF SYMPATRIC COHO AND TROUT FRY

Segregation was not clearly evident in the diets between sympatric populations coff coho and cutthroat trout in streams (Fig. 14). The food items eaten appeared to largely reflect food availability and fish microdistribution, in contrast to the more selective diet reported for hatchery juvenile rainbow trout in an experimental stream (Bisson 1978). Chironomid larvae and pupae were numerically the most important food items in both coho (43.9-66.4%) and trout (66.5-80.7% in all habitat types in Bush Creek. Mundie (1969) reported a comparable diet for coho fry in a small stream on Vancouver Island, similar in many respects to that of Bush Creek. In Holland, food habits of both salmonids were more variable: chironomid larvae and pupae made up from 32.3-37.7% in trout and from 5.7-26.4% in coho;



Fig. 13. Histograms of fork length frequency of the allopatric populations of cutthroat trout by habitat type in Bings (1976), French (1976), and Shawnigan (1975) creeks.



Fig. 14. Diet analysis of underyearling coho and cutthroat trout in Bush and Holland creeks, August, 1973, in pools (open), glides (hatched) and riffles (solid).

other benthic forms of importance to both salmonids were trichopteran and other dipteran larvae. Plecopteran and ephemeropteran nymphs were relatively unimportant in the diets of either coho or trout in Holland.

Aerial foods, particularly dipteran and hemipteran forms were more common in the diet of coho than in trout in both streams (Fig. 14), suggesting greater surface feeding by coho. In both streams, however, coho sampled in riffles contained more chironomids and less aerial foods than those sampled in pools; this may suggest they forage more on bottom and mid-water sources of food at higher water velocities. Trout showed no such difference between riffle and pool habitats. Coho social dominance in pools (Hartman 1965b) may have reduced the opportunities for trout to feed at the surface.

Breadth of diet for coho and cutthroat trout in Bush Creek was similar, irrespective of habitat type, but not in Holland Creek (Table 4). In Bush, although both salmonids foraged on a variety of food taxa, chironomid larvae constituted a high percentage of their total diets, resulting in a relatively narrow food niche for either species. In Holland, breadth of diet was greater for coho than for trout in all habitats, but particularly in pools, due to the higher contribution of aerial foods in the diet of the former. In general, trout ate a wider array of food items with less variation between taxa in the faster velocity habitats, the reverse being true for coho whose dietary breadth increased in pools.

Table 4. Standardized breadth of diet for sympatric populations of coho and cutthroat trout for 14 food taxa in two streams, August-September, 1973.

	Sample size	Pools	Glides	<u>Riffles</u>	Average			
Bush Creek								
Trout Coho	30 29	0.21 0.29	0.19 0.17	0.16 0.12	0.19 0.19			
Holland Creek								
Trout Coho	25 25	0.33 0.67	0.48 0.54	0.41 0.51	0.41 0.57			

Table 5. Overlap in diet between sympatric populations of coho and cutthroat trout by habitat type in two streams, August-September, 1973.

	Pools	Glides	Riffles	Average	
Bush Creek Holland Creek	0.89 0.41	0.98 0.67	1.0 0.90	0.96 0.66	

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Diets of coho and trout overlapped considerably, but more so in Bush than in Holland (Table 5). In both streams, interspecific overlap in diet was lowest in pools and highest in riffles, ranging from 0.89-1.0 in Bush and from 0.41-0.90 in Holland. In riffles, the stomachs of both salmonids contained predominantly benthic foods (e.g. chironomid larvae, pupae), whereas in pools, trout contained more benthic and coho more aerial foods (Fig. 14).

GROWTH OF SYMPATRIC COHO AND TROUT

Summer growth of salmonid underyearlings was higher for trout than for coho in both Bush and Holland creeks, 1974 (Figs. 15, 16). In Bush, mean fork length of trout sampled from all habitat types in late June, was about 10 mm less than that of coho; by late September, although the range in fork length was much greater for coho than for trout, mean length of both species was approximately 47 mm. Similarly, in Holland, trout mean fork length was about 10 mm less than that of coho in late June; by late September coho mean fork length was about 51 mm and trout about 45 mm. The growth (inclength) of trout was similar in both streams; however, in Holland Creek, trout initially were slightly smaller than, and coho grew slightly faster than their conspecifics in Bush Creek. These differences appear to account for the pattern of interspecific growth between these two streams. Throughout this three-month period, streamflow was similar and remained consistently low in both streams.



Fig. 15. Mean fork length ± 2 S.E. (horizontal lines) of underyearling coho (*) and cutthroat trout (\triangle) in Bush Creek, 1974. Vertical lines are size ranges: \Box , denotes stream discharge.



Fig. 16. Mean fork length of underyearling coho and cutthroat trout and stream discharge in Holland Creek, 1974. See Fig. 15 for details.

DISCUSSION

RESOURCE PARTITIONING

Habitat is an important dimension of resource partitioning among animal populations in general (Schoener 1974). Resources are usually not distributed independently of habitat type, but rather the two are often highly correlated (Werner and Hall 1977). The present findings indicate that habitat is the major means of resource partitioning between sympatric populations of juvenile coho salmon and coastal cutthroat trout in small streams. During summer, although they overlap considerably, populations of these two salmonids spatially segregate in a pattern similar to that reported for sympatric coho and steelhead trout in larger coastal streams of British Columbia (Hartman 1965b). Both Hartman's and my study show that coho dominate in pools, while steelhead trout and cutthroat trout dominate in riffles. Glides or open channels are generally areas of greatest interspecific overlap, with the degree of overlap depending in part, on relative and absolute densities of populations. Krebs and Wingate (1976) also noted that the habitat use by species of small mammal communities in the Kluane region, Yukon, changed from year to year with their relative abundance; as population density increased, they moved into more habitat types resulting in greater interspecific overlap. Resource partitioning predominantly by means of habitat segregation has been documented for other combinations of sympatric salmonids both in streams (Lister and Genoe 1970; Everest and Chapman 1972; Griffith 1972) and in lakes (Andrusak and Northcote 1971), and for centrarchids in lakes

(Werner et al. 1977), and for cyprinids in a stream (Mendelson 1975).

Habitat segregation presumably attenuates interspecific competition for resources in general and possibly for food in particular, as shown by Nilsson (1963) for lake dwelling populations of char (Salvelinus alpinus) and trout (Salmo trutta) in Sweden. Like many stream salmonids, coho and cutthroat trout appear to lack marked or effective interspecific differentiation in their morphology that would allow distinct trophic separation. Their diets show broad overlap within habitat types in this study and elsewhere (Mason and Machidori 1976). Thus food resources appear to be divided between these two salmonids primarily through partitioning of the available stream space as found in brook trout and cutthroat trout in some Idaho streams (Griffith 1972). However, their diets within habitat types (this study) suggest that coho might be a more specialized feeder of drifting foods and cutthroat trout a more generalized feeder of both benthic and drifting foods. Such interspecific behavioral differences, however, may not be effective in shallow water habitats due to the lack of adequate vertical separation between species. In other aquatic habitats, partitioning of food resources is commonly along a combination of resource dimensions rather than a single resource axis, as demonstrated for numerous sympatric species, notable examples being those for intertidal starfishes (Menge and Menge 1974), marine inshore percid fishes (Bray and Ebeling 1975) and lake-dwelling centrarchid fishes (Werner et al. 1977).

Some authors (Morse 1974; Wilson 1975) are of the opinion that

subdominant species usually have a broader niche than do socially dominant ones. The possibility of greater niche plasticity among socially subdominant species may be a manifestation of their difficulty in obtaining an adequate share of available resources. The ability of subdominant species to shift to habitats providing optimal foraging yield during periods of superabundant resources, allows them to exploit opportunistically resources from which they are excluded at other times by the socially dominant species. I found that cutthroat trout consistently occupied a broader microhabitat niche than coho in each of the three sympatric streams. In addition to utilizing the faster velocity habitats, smaller cutthroat trout commonly inhabited shallow waters of stream margins and small side channels (unpublished data). This study and previous studies (Hartman and Gill 1968; Hall and Lantz 1969; Griffith 1972; Mason and Machidori 1976) suggest that cutthroat trout may utilize a variety of microhabitat types, ranging widely in water velocity, depth and temperature, and in available cover. Niche breadth of this species appears to assure maintenance of population in highly fluctuating environments. However, breadth of food niche for cutthroat trout did not exceed that for coho in two of my study streams, paralleling results by others (Mason and Machidori 1976). Werner and Hall (1977) also found that the bluegill sunfish occupies a broader microhabitat niche, but lesser food niche, than the socially dominant green sunfish in ponds and lakes.

Populations of allopatric cutthroat trout utilized pools more

so than riffles, possibly due to the absence of coho. I speculate this reflects species behavioral diversity in habitat response to environmental instability, rather than that of genetically based behavioral differences between populations of trout above and below a barrier falls, due to downstream gene flow across such barriers. Habitat shift by cutthroat trout from pools into riffles when in sympatry with coho corroborate the interactive segregation concept advanced by Nilsson (1956), and parallel his findings for lake populations of trout and char in Sweden (1960, 1963). Nilsson ascribes niche shift in the more plastic, sub-dominant char, to both exploitation and interference competition by the more territorial and aggressive trout. Coho may exert a similar behavioral influence on cutthroat trout in pools and other low velocity habitats.

The influence of sculpins on the pattern of microhabitat use by salmonids was not documented in this study. Spatially, they overlapped extensively with salmonids and were abundant in all habitat types, although their absolute biomass was generally highest in pools due to the preponderance there of large individual sculpins. Sculpins showed no consistent use of microhabitat relative to salmonids between the three study streams; in Bush and Holland creeks their biomass was high in all habitat types, whereas in Ayum Creek it was highest in pools and lowest in riffles. Sculpin breadth of microhabitat niche was slightly less than that of trout in Holland and Ayum, possibly due to the preponderance of recruits and mature sculpins, respectively. However, the extensive dietary overlap of trout and sculpins (Mason and Machidori 1976) suggest they may be competitors in small streams for a common food

resource - the benthic invertebrate community, as these workers pointed out.

LIMITING FACTORS: FOOD OR SPACE?

Based on the difference in biomass between sympatric and allopatric populations of cutthroat trout, I postulate that interspecific interaction may be limiting sympatric populations of trout, although total fish production may be greater in multi-species streams. Mean total fish biomass levels in the sympatric populations ranged from about 2-9 g/m² ($av. = 5.1 g/m^2$), being lowest in riffles and highest in pools, with trout almost exclusively contributing less than 1 g/m² in all habitat types. In allopatric populations, however, mean biomass density of trout ranged from about 1-6 g/m² ($av. = 2.2 g/m^2$) being lowest in riffles and highest in pools. In populations isolated from coho salmon and sculpins, cutthroat trout had up to a tenfold higher biomass in some cases. As to which of the two species, coho or sculpins, may have a more negative impact on cutthroat trout biomass levels in streams remains unknown. In this context it is important to consider whether sympatric trout populations might be food or space limited.

Stream production of juvenile coho during summer has been shown to be limited by food rather than space (Mason 1976). These findings may not be applicable to salmon-trout-sculpin communities, particularly for trout populations due to their much later time of emergence than salmon. In the case of anadromous cutthroat trout, they

emerge into a stream environment that may already be filled to carrying capacity by coho fry, considering the high rates of coho fry emigration and instream mortality (Mason 1975), and loss of rearing habitat with receding streamflows in summer. Trout are largely restricted to riffle areas during summer-early fall, the habitat that is usually low in abundance relative to pools during this period of low streamflow. I surmise that habitat segregation may be lessened further as summer temperatures increase, disadvantageously to trout, as coho use of riffles may increase due to their higher swimming performance in warmer water (Glova and McInerney 1977). Thus, the availability of living space for sympatric trout populations may be reduced considerably by coho during the seasons of best growth, which may in part explain the low biomass levels of trout in sympatric streams. On the eother hand, trout populations in small streams may be little affected by direct competition for food with coho, despite their relatively broad overlap in diets, as the trout are found predominantly in the food-producing riffle areas.

Sculpins are abundant in all habitat types in streams and often achieve biomass levels much greater than that of sympatric coho and trout combined. Numerous studies, including the present one, have converged on the generalization that sculpin biomass levels are both higher and more variable than those of salmonids, with ranges extending from 25-90% of total fish biomass in any one stream (LeCren 1965; Mann 1971; Petrosky and Waters 1975; Mason and Machidori 1976). If sculpins have any negative impact on production of stream salmonids, I suggest that food, rather than space is involved. Their benthic and cryptic habits (hiding beneath rocks) appear to minimize interaction with salmonids through vertical

separation in most stream habitats, a possible exception being that of stream edges. Sculpin distribution showed no consistent evidence of spatial segregation with salmonids in Bush and Holland creeks, but salmonids may have reduced sculpin abundance in riffles of Ayum Creek. In general, sculpins appear to be distributed in a pattern more related to intra - than interspecific interaction, with larger individuals most common in deeper, slower velocity areas and juveniles in shallower, faster velocity habitats. While sculpin predation on stream salmonid fry populations appear to be of minor importance (see review by Moyle 1977), that of possible competition for food may not, and has been frequently suggested by numerous authors (Brocksen et al. 1968; Andreassen 1971; Mason and Machidori 1976). Conceivably, under high population densities and low invertebrate production, sculpins might significantly reduce the availability of food for salmonids.

The possible significance of sculpins as a competitor for food with salmonids was not documented in this study. Range in mean biomass levels of allopatric trout populations $(1.0-5.6 \text{ g/m}^2)$ approximated those of sympatric trout and coho combined $(0.4-4.2 \text{ g/m}^2)$. Based on my field evidence that cutthroat trout have a similar but broader ecological niche than do coho, trout biomass in allopatry ought to be about the same as the summed biomass of trout and coho in sympatry, all other factors being equal. Further, assuming stream carrying capacity for salmonids to be similar above and below the barrier falls, these biomass comparisons may suggest that sculpin spatial and feeding niches overlap little with those of salmonids. The significantly higher ranges of mean fish

biomass in sympatric populations $(2.0-9.0 \text{ g/m}^2)$ than those in allopatric trout populations $(1.0-5.6 \text{ g/m}^2)$ may reflect higher productivity in downstream reaches, and/or more efficient use of the stream environment, through sculpin exploitation of a niche not utilized by salmonids. The ecological role of sculpins in these simple fish communities awaits further definition under more rigorous experimental conditions than those available presently.

CHAPTER III. LABORATORY STUDIES OF STREAM POPULATIONS OF UNDERYEARLING COHO SALMON AND COASTAL CUTTHROAT TROUT

INTRODUCTION

My field investigations showed that during the late summer period of low streamflows, sympatric populations of coho salmon and cutthroat trout broadly overlapped in diet but segregated into habitats of relatively slow and fast water velocity, respectively, with the pattern of separation depending in large part, on absolute and relative densities of their populations. Hartman (1965b) reported similar seasonal segregation between sympatric populations of coho and steelhead trout, which he experimentally demonstrated to be of the interactive type (Nilsson 1956), occurring in summer but not in winter. Such segregation may attenuate interspecific competition for resources in general, and possibly for food in particular, during the season of relatively high population density. Distinct spatial segregation but broadly overlapping diets have also been reported for ecologically similar nonsalmonid fishes in streams (Gee and Northcote 1963; Gibbons and Gee 1972). Some advantages of segregation likely involve higher species overall growth and survival, and in the case of anadromous salmonids, higher smolt yields to sea.

In this study, laboratory populations of underyearling coho and cutthroat trout of natural sympatric origin were tested in a stream simulator to elucidate in detail, not possible in nature, pattern and mechanism of partitioning of food and space during summer and winter. Depending on season, I tested the null hypothesis that there was no observable statistical difference between their pattern of microdistribution and of intensity of aggression when exposed to different levels of 1) feeding activity, 2) water velocity, 3) water temperature and 4) relative density of species. Possible adaptive behavioral adjustment in cutthroat trout, if any, to living with coho, was also investigated by comparing trout microhabitat use and aggression for fish of sympatric (downstream of barrier falls) and allopatric (upstream of barrier falls) origin from two small coastal streams.

METHODS

A. THE TEST FACILITY

The stream simulator used was the one described by Hartman (1965a), now located at the University of Victoria, B. C.. Overall dimensions and construction are shown in Fig. 17a, the volume of the actual experimental section being 5m long x 1.2m wide x 0.75m deep. Two modifications made to the basic facility involved replacing the up- and downstream nylon screens with stainless steel mesh ($2.54 \times 2.54 \times 0.64 \text{ mm}$) and installation of incandescent lighting (12, 25W bulbs) with rheostat control under the ceiling-suspended fluorescent fixtures used by Hartman (1965b). Artificial light intensity was roughly uniform over the length of the test facility, averaging 250 Lux along the centreline (range 235-









Fig. 17. a) Schematic of stream simulator (after Hartman 1965a) with heavy arrows indicating direction of stream flow; b) plan view of the experimental section showing outline of rocks, logs, and undercut bank (stippled); riffles - R1, R2; pools - P1, P2; c) side view showing physiographic profile of the experimental section.

57.0
260 Lux) measured with a "Photovolt" model 210 photometer. Natural photoperiod was provided through a bank of high windows running the full length and directly opposite the experimental section. Water temperature was maintained to within ± 0.5 °C by a refrigeration unit situated at the upstream end of the test facility. On-off control of water circulation from the simulator through the refrigeration system was maintained by a thermoregulator and solenoid hookup to the recirculating pump, plus a series of gate valves which were manually operated. Water that had passed through the refrigeration system re-entered the simulator in the downstream well, being thoroughly mixed in the return flume by the drive propellor before entering the experimental section.

The water supply was from the City of Victoria, dechlorinated by facilities at the University of Victoria. Incoming water to the simulator was via a 3-cm PVC line, with ball-valve control, situated above the water surface and running the full width in the upstream well, with fine jets at 2.5 cm on centre directed downstream. Water in the simulator was continuously renewed with a turnover cycle of 2 days.

The experimental section consisted of four equal units providing a duplicate pair of riffle-pool sequences starting from the upstream end (Fig. 17b, c). The foundation for the stream-bottom profile was of fir plywood prefabricated components, assembled on-site. Running the full length of the right side (facing upstream) of the experimental section was the stream edge, 0.4m wide with a 1 in 4 rise. The underside of this edge in both pools was covered with a wood lath, and then mottled

with an earthen colored mixture of fiberglass resin and sand to simulate texture of undercut bank materials. The outside surface of the glazing panels in the undercut area of pools was covered with mottle-patterned heavy brown paper. All seams between plywood structures and walls of the experimental section were made fish-proof with narrow wood trim and caulking expansion sealant.

The substrates of the experimental section consisted of boulders (30 cm and over), rubble (8-29 cm), gravel, sand and inorganic silt. The size composition, and distribution of substrates in each of the four microhabitat types in the simulator were arranged in a manner resembling those in the study streams (Fig. 17b, c): riffles contained rubble in a staggered pattern, with each of the rocks slightly elevated over a shallow depression in the streambed; pools contained boulders and gravel filled in with fines and inorganic silt deposits at the head; undercut bank- and stream-edge areas contained a mixture of gravel and sand, with few rubble in the latter areas in riffles. The substrates on sloped surfaces were held permanently in place with an earthen-colored fiberglass resin. A log about 0.15m \emptyset x 1.2m long taken from a stream was obliquely positioned in each pool (see Fig. 17b) as further cover for Two similar logs were also placed longitudinally over the steel fish. frame superstructure of each pool as overhead cover.

A darkened observation corridor of black polyethylene from floor to ceiling was provided on the left side (facing upstream) of the simulator. Horizontal slits in the plastic on the simulator side, along with a wood platform of full length and profile of that of the stream bottom, permitted

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observation into the experimental section without disturbing fish.

A food-dispensing apparatus, one for each riffle, was located in the refrigeration bath of the test facility, providing controlled simulation of drifting food. Each unit consisted of a 10-l plastic container, with a water submersible centrifugal-type pump (capacity $45-\ell$ /min) on the bottom, partially submerged in the refrigeration bath. Openings near the bottom of the container covered with fly-screening provided an upwelling of incoming water, keeping food in suspension. The flows of both pumps were equalized (ball valve and flowmeter) and separately connected to a 1.9-cm PVC pipe buried in the gravel across the upstream end of each of the two riffles; suspended food was released into the stream via fine exit jets directed obliquely upwards and downstream. Positioned above each plastic container in the refrigeration bath was a 500-ml glass beaker with electric agitator and with microcontrol (glass flowmeter and diaphragm valve hook-up) of incoming water supply. Food placed into the beaker was released into the stream via the exit jets at a rate dependent on the rate of water overflow from the beaker.

B. THE FISH

Coho and cutthroat trout fry of sympatric origin were from two small coastal streams situated at the south end of Vancouver Island (see Fig. 1): summer fish were from Craigflower Creek (F.L. range, 35-69 mm); winter fish were from Ayum Creek (F.L. range, 43-96 mm). They were

collected with a D.C. fish shocker and/or pole seine, and transferred to the laboratory in fry cans. The summer fish were collected on the initial day of each experiment. The winter fish were bulk-collected in advance in late November to avoid possible difficulty in obtaining adequate numbers of fish in freshets of streams later on.

The winter fish were held in laboratory facilities at the Pacific Biological Station, Nanaimo, B. C.. These consisted of a bank of twelve 60 x 60 x 30 cm clear plexiglass tanks with painted plywood covers and a black plastic shroud over the front side to minimize disturbing the fish. Incoming fresh water from an overhead mixing manifold was at about 2*l*/min, maintaining temperatures within 3-5 °C. Photoperiod was natural through a north-facing window with no artificial lighting provided. Several 15-cm long half-sections of 9-cm diam PVC pipe were scattered on the bottom of each tank as cover for fish. The two species were held separately from one another, primarily to reduce handling time when selecting fish, each grouped into small- (F.L. range 47-60 mm), medium-(66-72 mm), and large-sized (76-96 mm) individuals per tank. They were fed chopped fresh-frozen euphausiids at least once every 2 days.

C. EXPERIMENTAL PROCEDURE

In the laboratory the selected fish were individually measured (fork length) and damp weighed under mild anaesthetic (2-phenoxyethanol). Each test required 40 fish comprised of individuals of the large, medium, and small size-classes (6, 14, and 20 animals, respectively), as summarized in the Appendix (Tables 9, 10). The relative density of each

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of the three size-classes was approximately proportional to that of the wild sympatric populations of coho and trout in the three study streams. In tests with coho and trout mixed (in sympatry), the number of fish of each species in each of the three size-classes was half of that when the species were tested separately (in allopatry) in order to keep density constant. The selected fish in each of the winter experiments were transferred in fry cans at their acclimated test temperature, directly to the test facility at the University of Victoria on the initial day of each test. All tests were duplicated. The experimental conditions, in both the summer and winter tests including weight change data for each of the summer experiments, are shown in the Appendix (Tables 9, 10).

The fish were given a minimum of 2-h recovery time from the effects of the anaesthetic and handling, in well aerated water in a 90- ℓ dark plastic container with a cover. They were then released in the centre of the test facility between 1600 and 1800 h under the available natural light in still water, followed by initiation of the low water velocity (25 cm/s) 1^{ch} after their introduction. Each experiment lasted 1 wk. The fish were given 2 days habituation time to the test facility. Thereafter, observations were made at the low test velocity for a period of 2 1/2 days, followed in the remaining 2 1/2 days by the high test velocity, that was incrementally stepped upcover a 3-h period.

Both the water temperature and the high water velocity levels differed between the two test seasons: summer fish were tested during the period June 2-September 16 at 13.0 ± 0.5 °C and a high velocity averaging 43.1 cm/s in riffles; winter fish were tested during the period December 2-

January 27 at both 3 and 5±0.5 °C and a high velocity averaging 50.7 cm/s in riffles. The increase in velocity was intended to allow for the larger body size of the winter fish, compared to those used in summer. Absolute velocity at specific sites within each habitat are summarized in previous reports (Glova and Mason 1977a, 1977b).

Fish were fed twice daily a ration consisting of chopped freshfrozen euphausiids, amounting to 5% of their body weight. The food was released as simulated drift in streams by the apparatus described earlier. Day length was natural with the artificial lighting superimposed from about 0800-2000 h in summer and 0800-1700 h in winter.

The timing of the routine daily observations on the positions and aggressive interactions of the fish was governed by the imposed feeding cycle: pre-feed period when no food was drifting in the system; during-feed period began 15 min after initiation of release of drifting foods; post-feed period began 30 min after the release of any drifting food was stopped. The observation schedule was repeated in the morning and late afternoon, usually extending from 0800- dusk daily. The approximate horizontal and vertical (upper, mid and lower thirds) positions, size-class and species of each fish were recorded on outline maps of the stream bottom at each observation period. The aggressive behavior of all the fish in each of the riffle and pool sections was recorded for a period of 10 min, with each of the four sections chosen randomly. The behavioral components of aggressive encounters (both intraand interspecific) of coho and of trout was similarly coded, and quantitatively recorded on a bank of four multiple key laboratory count

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denominators. The behavioral categories recognized in this study are described later. In experiments with coho and trout mixed, four possible types of interaction were recorded: coho-coho, coho-trout, trout-trout, trout-coho. These were elicited either singly or in a sequence of behavioral events. At the end of each observation period, the information was decoded onto standardized data sheets.

Fish mortality in any one experiment rarely exceeded 5% and most often involved small individuals pinned against the downstream screen at night, particularly during the test period of freshet conditions. Mortalities were accounted for at the beginning of each day, the observations at all times reflecting the mean responses of the surviving fish. Dead fish were removed from the downstream screen during night hours to avoid disturbing the fish unduly.

At the end of each experiment the tank was drained with most fish retreating into the pools. They were dipnetted out and anaesthetized for determination of fork length and weight.

D. PROCESSING OF DATA

The microdistributions of coho and of trout in the stream simulator were tested statistically by factorial analysis of variance. Interaction between test variables was investigated in each analysis, the maximum number of variables consisting of habitat type, fish size, feed period, water velocity, water temperature, and species tested. To standardize the numbers of fish in each of the three size-classes in a

given habitat, each observation was expressed as a percent of the total fish of each size-class. The data were then transformed by the arcsine transformation (Sokal and Rohlf 1969). Statistical analysis was applied to determine if the difference in microdistribution was significant 1) between species when tested in allopatry, 2) between species when tested in sympatry, and 3) within species between allopatric and sympatric tests.

For behavioral analysis, species individual components of aggression in each observation were summed and divided by the number of fish observed in order to standardize fish density. This provided a comparative measure of species rates of aggression. Size of fish was not considered in the analyses, such data being available for allopatric but not sympatric trials, due to the lack of recording equipment necessary to include size in the latter tests. The data were statistically tested by student-t and chi-square tests wherever applicable. The Mann-Whitney U-test (Sokal and Rohlf 1969) was used in cases of nonparametric analysis.

RESULTS

I. COHO AND TROUT OF SYMPATRIC ORIGIN

General

In summer, partitioning of the available space in the stream simulator between coho and cutthroat trout fry was rather rapid and similar in pattern to that observed in nature. During the first day the fish showed a gradual spacing-out from their initial aggregations in pools. Trout usually showed a stronger tendency to move upstream than did coho, particularly the smaller individuals. However, both salmonids

moved temporarily upstream when the water velocity was incrementally accelerated from the low to the high test level. This, in nature, would seem to counteract downstream displacement during periods of high velocities and fluctuating flows in streams.

In winter, an active spacing-out of the fish through territoriality and social dominance, as in summer, was largely limited to feeding period and restricted to low velocity sites for both salmonids. In nonfeeding periods both species tended to aggregate in the areas of pools with overhead cover and minimal water velocity. Compared to the summer tests, their breadth of microhabitat use, general mobility and social interactions in winter were low. The scope of these activities was highly influenced by water temperature and velocity. In winter, near-freezing water temperatures and high velocities in the simulator restricted their exploitation of food and living space almost exclusively to slow water areas, which may in part, reflect their lowered metabolism and poorer swimming ability at low temperature.

Within the first two days of any one experiment, fish of either species frequently shifted position within habitat types. Such activity represented the period when individual territories and dominance hierarchies were unstable, and was more noticeable in summer than in winter. Pattern of habitat partitioning between species changed little after the first two days, whereas that of their social interactions did, particularly in summer (Fig. 18). Unlike coho, trout initially actively defended both riffles and pools. Subsequently, aggressiveness markedly increased in coho

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Fig. 18. Summer aggression (a), and microdistribution (b), of coho (circles) and cutthroat trout (triangles) in pools (open) and riffles (closed) during their initial 4 days in the stream simulator. Symbols are means \pm S.E.

and decreased in trout, with coho establishing social dominance and showing obvious priorities in choice of space and feeding opportunities in both riffles and pools, at least under the low flow conditions. By the end of the fourth day in each of the experiments, the social structure within each of the riffle and pool habitats was relatively stable. Jenkins (1969) reported stable social structure between individuals of juvenile populations of brown trout and rainbow trout in streams.

Mean levels of aggression may have been slightly higher for trout and lower for coho if the first 2 days of each experiment had been included in routine observations (Fig. 18). As this was generally a period of instability in the process of resource partitioning between the species, observations made during the first 2 days throughout the experimental series in both summer and winter, were precluded from further analyses.

Simultaneous replicate testing was not possible in the apparatus used. In order to spread possible time effects evenly, a total of 3 wk lapsed between replicates. With increasing size and/or maturation, certain behaviors and environmental responses of the fish may have changed. Factorial analysis of variance indicated that significant (P < 0.01) differences between replicates for either species were invariably that of interaction between habitat type and size of fish. Differences in their mean body size between replicates were restricted but unavoidable in summer, due to rapid growth.

6.8:

MICRODISTRIBUTION

Summer

The summer microdistributions of coho and cutthroat trout fry tested in sympatry, but not allopatry, showed distinct interspecific differences. Examples of cumulative plots of their actual positions in the stream simulator for both allopatric and sympatric trials are shown in Fig. 19. Pooling all the data with respect to body size and feed periods (Table 6), the grand means of species numbers per habitat type in sympatry were significantly (t-test, P < 0.01) different at both lowand high test velocities. Through interactive segregation, under low velocity, the numbers of coho in pools were about double that of trout, while the reverse occurred in riffles. Under high velocity, their pattern of segregation was similar, but interspecific differences were less pronounced, primarily due to the trout's reduced use of riffles (Table 6). In allopatry, species numbers were similar withinbhabitat types with differences ranging only from 1-6%.

Expressed on a percent basis (Fig. 20a), in allopatry, at the low test velocity approximately 40% of either species occupied riffles and 60% pools; an almost doubling of the velocity reduced their occupancy in riffles and increased it in pools by about 15%. Similarly, in sympatry under low flow, riffle-pool percent ratios were about 23:77 for coho and 62:38 for trout. At high flow, trout occupancy decreased in riffles and increased in pools by approximately 12%, while that of coho was essentially unaffected in both replicates.



Fig. 19. Cumulative plots of the summer microdistribution (one replicate only) of coho and cutthroat trout during the pre-feed periods in a) allopatry and b) sympatry. The percent number of fish per habitat is shown for each species. The open circles indicate position of fish above the undercut bank (i.e. floodbank area). See Fig. 17 for details of the experimental section.

Table 6. Mean number of coho and cutthroat trout fry in the riffle and pool habitats in summer at the two test velocities. The number of fish shown in sympatry are doubled that of the actual values in order to equalize density with that in allopatry. Cover in riffles refers to under rocks; in pools, to undercut areas.

		Low velo	ocity	High veloci	ty
		Mean ± S.E.	% number of fish using cover	Mean ± S.E.	% number of fish using cover
			Allopat	ry	
Coho	Riffle Pool	7.3 ± 0.55 11.8 ± 0.51	0.0 2.4	5.1 ± 0.34 14.4 ± 0.38	0.0 4.8
Trout	Riffle Pool	7.4 ± 0.43 11.5 ± 0.36	0.0 10.1	5.7 ± 0.42 13.5 ± 0.74	0.0 10.5
			Sympatr	<u>y</u>	
Coho	Riffle Pool	4.6 ± 0.23 15.1 ± 0.32	0.0 7.3	4.7 ± 0.31 13.8 ± 0.45	0.0 8.2
Trout	Riffle Pool	$\begin{array}{c} 10.8 \pm 0.22 \\ 6.3 \pm 0.23 \end{array}$	1.511.9	9.0 ± 0.31 8.9 ± 0.47	0.0 19.7



Fig. 20. Relative microdistribution of coho (solid) and cutthroat trout (open) in allopatry and in sympatry in a) summer and b) winter.

Submerged areas of cover beneath rocks in riffles and undercut banks in pools were not heavily utilized by either coho and cutthroat fry in summer (Table 6). Smaller fish were the more frequent users of cover sites, often in escape from aggressive encounters. In both salmonids, sites offering maximization of food-getting rather than overhead cover were generally more directly associated with territories of dominant fish. In riffles, coho were never found, and trout were rarely found, in areas under cover. In pools, utilization of undercut areas ranged from 2.4-8.2% for coho and 10.1-19.7% for trout, both species showing slightly higher utilization during periods of accelerated flow and also when tested in sympatry (Table 6). Unlike in the simulator, in natural streams exploitation of drifting foods by fish with territories in undercut areas may be higher due to greater convergent flow at meanders.

Factorial analyses of variance were conducted to determine statistical significance of each of the test variables in coho and trout microdistributions. The results of these are summarized in Table 7. Of the possible combinations of interactions between all of the five test variables, only that of habitat type interacted significantly (P < 0.01) with species and with size of fish in all statistical tests, excepting in the allopatric tests between species. When tested separately, the microhabitat demands of these two salmonids were very similar for given sizeclasses. Comparisons of their relative microdistributions in sympatry for second-order levels of interaction with habitat type (Fig. 21) indicate that 1) size of fish was the most important factor, 2) food supply was of intermediate importance, and 3) acceleration of water velocity was of least importance in summer.

Table 7. Comparison of F-values (P<0.01 underlined) from factorial
analyses of variance of the coho and cutthroat trout test series in
summer. Both allopatric and sympatric trials were tested between and
within species. Test variables are H, habitat; Z, size; F, feed-period;
V, velocity; S, species; E, experiment type (allopatry or sympatry).

		Between s	pecies	Within species	
Variables	dF	Allopatry	Sympatry	Coho	Trout
Н	7	102.78	79.88	131.65	50.69
Z	2	3.32	2.33	2.10	2.60
ΗZ	14	0.73	9.26	10.30	9.30
F	2	0.79	0.06	0.85	1.02
ΗF	14	0.39	0.65	1.29	0.28
ZF	4	1.50	1.49	0.13	0.16
HZF	28	0.67	0.50	0.72	0.74
S/E	1	2.67	3.87	6.47	0.71
H S/E	7	0.09	26.62	9.71	8.27
Z S/E	2	0.42	0.75	1.34	1.20
H Z S/E	14	0.31	2.63	2.37	2.20
F S/E	2	0.38	0.21	0.06	0.56
H F S/E	14	0.30	1.00	0.56	0.27
Z F S/E	4	0.38	0.44	0.74	0.54
H Z F S/E	28	0.42	0.66	0.45	0.40
V	1	0.46	2.25	0.53	0.75
ΗV	7	0.99	1.16	2.23	0.85
ZV	2	0.06	2.80	1.43	1.68
ΗΖV	14	0.31	1.32	0.99	0.94
FV	2	0.09	0.27	0.16	0.13
HFV	14	0.30	0.38	0.49	0.27
ZFV	4	0.34	0.45	0,27	0.38
HZFV	28	0.08	0.48	0.31	0.40
V S/E	1	0.02	0.44	0.05	0.22
H V S/E	7	0.64	0.72	2.41	1.14
Z V S/E	2	0.70	1.56	0.44	1.10
H Z V S/E	14	0.84	1.18	0.79	0.80
F V S/E	2	0.05	0.09	0.02	0.24
HFVS/E	14	0.28	0.58	0.29	0.22
Z F V S/E	4	0.20	0.39	0.52	0.40
HZFVS/E	28	0.38	0.44	0.41	0.42
Error	288/96				



Fig. 21. Relative microdistribution of coho (solid) and cutthroat trout (hatched) in summer in a) sympatry and b) allopatry in relation to size of fish (1, large; 2, medium; 3, small), feed-period (4, pre-; 5, during-; 6, post-feed) and test velocity (7, low; 8, high). Open portion of bars refer to fish in undercut areas in pools.

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Relative size of fish largely determined their priority of access to food and space. Fish in riffles and at the heads of pools had feeding advantages over individuals in other areas as they were nearer to the incoming food source. In both coho and trout the pattern of habitat segregation into pools and riffles was influenced by size effects. For both species mean percent frequencies of fish in riffles were higher for the larger than for the small-sized individuals, the reverse occurring in pools (Fig. 21). Size effects on fish microdistribution pattern in allopatry were generally similar, but of lesser magnitude than in sympatry. Further, their vertical distribution in pools differed between size-classes. There was a significantly (P < 0.05)higher number of small than of medium-large size fish for both species in the lower level of pools in both allopatric and sympatric trials, excepting in the latter case for trout (Table 8). The bottom and undercut areas of pools were common refuge sites for small fish, actively contained there by larger, socially dominant individuals.

The food supply influenced pattern of microdistribution and revealed certain interspecific differences in strategies of food exploitation. In sympatry, unlike trout, coho microdistribution showed a more pronounced association to the food supply: during feeding periods the numbers of coho in riffles increased (Fig. 21a) with many establishing transient territories superimposed on trout from above (Fig. 22a); in post-feeding periods there was a net return of coho from riffles into the pools. However, when pooled together, these movements between habitat types were generally nonsignificant (P > 0.05). In allopatry, both species

Table 8. Vertical microdistribution of coho and cutthroat trout by size class (S, small; M, medium; L, large) in pools, combining the data of pre-, during- and post-feeding periods in summer at both test velocities. Differences (* P < 0.05) in the data between upper and lower levels were tested by factorial analysis of variance (2 X 2 design with a minimum of 25 observations per cell). The mean number of fish shown in sympatry are twice that of the actual values in order to equalize density with that in allopatry.

	Coho				Trout		
	Upper	Mid	Lower	Upper	Mid	Lower	
			Allop	atry			
S M & L	3.3* 1.7	3.7 4.5	8.0* 2.2	1.3* 0.9	3.1 6.4	8.3* 2.8	
			Sympa	try			
S M & L	1.4* 1.2	6.6 7.2	6.6* 4.8	1.8 0.9	2.4 2.8	1.8 1.4	



Fig. 22. a) Common pattern of body alignment and vertical positioning of coho (upper) and cutthroat trout (lower) in the stream simulator; b) cutthroat trout in high intensity lateral threat posture.

showed similar microhabitat responses while exploiting the food supply as they did in sympatry (Fig. 21b).

Feeding also affected fish microdistribution longitudinally within habitat types. In allopatry, during-feeding, medium-large size coho were present in significantly (P < 0.05) higher numbers than were small fish in the upstream half of riffles (Table 9). Trout showed a similar pattern, although one not statistically significant. In sympatry, similar size effects occurred during-feeding but trout were more numerous than were coho in the upstream half of riffles (Table 10). Analysis of the microdistribution plots in allopatric and sympatric trials indicated that feeding territories of both salmonids in riffles were most commonly situated upstream of rocks and least so alongside them (Table 11).

An almost doubling of the water velocity did not significantly alter either species overall microdistribution pattern (Fig. 21): in allopatry coho occupancy in riffles was reduced by 31%, trout by 23%; in sympatry, unlike trout, coho occupancy in riffles actually increased slightly, probably in response to increased levels of aggression in pools under the accelerated velocity conditions. Unlike trout, small subordinate coho did not associate closely with bottom cover and frequently were actively chased out of pools by larger fish, particularly during post-feed periods.

Winter

The winter microdistributions of coho and cutthroat trout fry at 3 ^oC were fairly similar in both allopatric and sympatric tests, as

Table 9. Horizontal microdistribution (mean \pm S.E.) of coho and cutthroat trout in allopatry by size class (see Table 8) in the upstream and downstream halves in riffles and pools (upper third of water column) during-feeding period in summer. The differences between size classes were tested by student t-distribution; P < 0.05 is underlined.

	Riffle segment					Pool s	egment	,
i	Jpstream	Down	stream		Upst	ream	Downs	tream
S	MĘL	. S	MĘL		S	M&L	S	M&L
				<u>Coho</u>				
<u>1.3±</u>	.2 4.2±.5	0.4±.1	1.5±.3	1.	2±.3	1.5±.1	2.1±.4	0.8±.2
			·· , •	Trout				
1.5±.	.3 2.3±.3	1.5±.2	1.3±.1	0.	8±.1	0.8±.2	0.8±.2	0.5±.2

Table 10. Horizontal microdistribution (mean \pm S.E.) of sympatric coho (C) and cutthroat trout (T) for all size classes combined, in the upstream and downstream halves in riffles and in pools (upper third of water column) during-feeding period in summer; P < 0.05 is underlined.

	Riffle s	segment			Pool segment		
Upst	ream	Downs	tream	Upst	ream	Downs	stream
C	Т	C .	T	C	Т	С	Т
			·	1			
			Rep.	licate I			
<u>2.7±.3</u>	3.2±.2	1.2±.3	1.6±.3	1.6±.3	0.9±.2	0.7±.2	0.7±.2
			Rep	licate 2			
<u>1.8±.3</u>	3.0±.2	0.6±.1	2.3±.1	0.5±.1	1.0±.2	0.6±.2	0.8±.2
2.3	3.2	0.9	2.0	1.1	1.0	0.7	0.8

	Coho			Trout	
UPS	DNS	ALS	UPS	DNS	ALS
		<u>Allopa</u>	atry		
79.0	12.6	8.4	60.4	22.9	16.7
		Sympat	cry		
72.1	19.2	8.7	58.8	31.5	9.7

Table 11. Percent number of coho and cutthroat trout with respect to their position to rocks in riffles (UPS, upstream of; DNS, downstream of, and ALS, alongside of rocks) during-feeding period in summer.

shown by examples of cumulative plots of their actual positions (Fig. 23). There was no obvious species interactive effect on their distribution in the riffle-pool space, other than that total number of fish in pools was slightly higher in sympatry than in allopatry, and that trout were more numerous than coho in undercut areas in pools when tested together. Mixing the species had the effect of slightly increasing the number of fish in pools. Pooling the data with respect to body size and feedperiods (Table 12), the grand means of species numbers per habitat type showed no significant (t-test, P>0.05) interspecific differences in both allopatry and sympatry at either test velocity. Mean numbers of coho in pools were slightly higher than those of trout, ranging from 19.6-20.0 and from 18.0-19.2, respectively. On a percent basis (Fig. 20b), more than 98% of the coho occupied pools whereas trout ranged from 88-97%, being highest under the accelerated velocity conditions when the species were mixed. Increased velocity had virtually no effect on the coho's overall pattern of microdistribution.

Six-way factorial analyses of variance were computed on the block of winter data to determine statistical significance of interactions between the test variables. The results of these are summarized in Table 13. Overall, habitat type interacted significantly (P < 0.01) with all test variables in either intra- or interspecific cases, excepting that of feed-period. Relative differences in the quality of cover between riffles and pools (i.e. under rocks or within undercut bank areas, respectively) were probably the main determinants of fish microhabitat use in winter, which appeared to be interrelated to a number of other factors. In pools, the use of cover by both coho and trout decreased



Fig. 23. Cumulative plots of the winter microdistribution (of one replicate only) of coho and cutthroat trout at 3 $^{\rm OC}$ during the pre-feed periods in a) allopatry and b) sympatry. See Fig. 19 for caption details.

		Low velo	city		High velo	city
		Moon + S E	% number of fish using	Mean	+ S E	% number of fish using
	<u></u>				- U.L.	
			Tested at	<u>3 °C</u>		
A11opat	ry					
Coho	Riffle Pool	0.5 ± 0.1 19.7 ± 0.6	4.4 30.9	0.4 19.6	± 0.1 ± 0.8	11.5 39.3
Trout	Riffle Pool	2.3 ± 0.2 18.0 ± 0.6	69.2 49.2	2.0 18.0	± 0.2 ± 0.7	54.8 51.2
Sympatr	Y					
Coho	Riffle Pool	0.2 ± 0.0 20.0 ± 0.3	0.0 41.6	0.2 20.0	± 0.0 ± 0.2	0.0 47.5
Trout	Riffle Pool	1.3 ± 0.1 19.0 ± 0.5	48.9 72.4	0.6 19.2	± 0.1 ± 0.4	28.3 69.8
		. • • .	Tested at	5 °C		
Sympatr	Y					
Coho	Riffle Pool	4.0 ± 0.3 15.2 ± 0.4	0.0 15.7	2.2 18.4	± 0.3 ± 0.4	0.0 23.4
Trout	Riffle Pool	5.5 ± 0.3 15.2 ± 0.4	42.4 54.4	5.0 15.0	± 0.3 ± 0.6	28.1 63.7

Table 12. Mean number of coho and cutthroat trout fry in the riffle and pool habitats in winter at the two test velocities. The number of fish shown in sympatry are doubled those of the actual values in order to equalize density with those in allopatry.

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Table 13. Comparison of F-values (P < 0.01 underlined) from factorial analyses of variance of the coho and cutthroat trout test series in winter. Both allopatric and sympatric trials were tested between and within species. Test variables are H, habitat; Z, size, F, feedperiod, V, velocity; T, temperature; S, species; E, experiment type (allopatry or sympatry).

	• • • • • •	Between s	pecies	Within s	pecies
Variables	dF	Allopatry	Sympatry	Coho	Trout
Н	7	293.69	311.29	364.24	242.43
Z	2	1.74	8.67	1.72	6.52
ни	14	31.03	28.83	38.63	19.04
	2	0.14	2.01	0.08	0.78
	14	3.67	7.90	6.35	4.02
	4	0.06	0.63	0.07	0.05
	28	0.23	1.87	0.83	0.47
о/ E H	$\frac{1}{7}$	0.45	2.49	1.48	9.14
7 S/F	2	2 05	81.55	0.02	19.88
H Z S/E	1/	2.05	0.45	0.91	0.59
F S/E	2	$\frac{7.32}{0.01}$	<u>3.95</u> 0.05	$\frac{0.51}{0.06}$	4.25
H F S/E	14	0.01	1 23	0.00	0.29
Z F S/E	4	0.03	0 43	0.01	0.00
HZFS/E	28	0.20	1.23	0.07	0.15
Τ .	1		6.13	0.10	0.05
НТ	7		36.33		
ΖT	2		0.24		
НΖТ	14		5.29		
F T	2		0.33		
HFT	14		1.40		
ZFT	4		0.41		
H L F I	28		0.79		
5 I U C T	1		1.18		
П З І 7 С Т.	/		6.48		
431 [°] H7ST	ے 14		0.02		
FST	14		2.03		
HFST	14		0.04		
ZFST	4		1.21		
HZFST	28		1 09		
V	$\tilde{1}$	1.15	6.26	2 17	0 82
ΗV	- 7	18.44	21.72	24 91	10 36
ΖV	2	0.55	0.10	0.53	0 52
ΗΖV	14	1.77	1.97	1.23	3.22
F V	2	0.41	0.47	0.09	0.32

Table 13 (cont'd)

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	Between s	species	Within species	
dF	Allopatry	Sympatry	Coho	Trout
$\begin{array}{c} \mathbf{d}^{\mathbf{r}} \\ 14 \\ 4 \\ 28 \\ 1 \\ 7 \\ 2 \\ 14 \\ 2 \\ 14 \\ 4 \\ 28 \\ 1 \\ 7 \\ 2 \\ 14 \\ 4 \\ 28 \\ 1 \\ 7 \\ 2 \\ 14 \\ 4 \\ 28 \\ 1 \\ 7 \\ 2 \\ 14 \\ 4 \\ 28 \\ 1 \\ 7 \\ 2 \\ 14 \\ 4 \\ 28 \\ 1 \\ 7 \\ 2 \\ 14 \\ 4 \\ 28 \\ 1 \\ 7 \\ 2 \\ 14 \\ 4 \\ 28 \\ 1 \\ 7 \\ 2 \\ 14 \\ 2 \\ 14 \\ 2 \\ 14 \\ 2 \\ 14 \\ 2 \\ 14 \\ 2 \\ 2 \\ 14 \\ 2 \\ 2 \\ 14 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ $	0.59 0.13 0.19 0.0 0.65 0.06 1.82 0.07 0.14 0.24 0.24	$\begin{array}{c} 1.21\\ 0.34\\ 0.33\\ 0.95\\ 10.84\\ 0.64\\ 1.73\\ 0.54\\ 0.58\\ 0.34\\ 0.58\\ 0.34\\ 0.58\\ 0.34\\ 0.58\\ 0.34\\ 0.58\\ 0.34\\ 0.58\\ 0.34\\ 0.58\\ 0.34\\ 0.58\\ 0.34\\ 0.58\\ 0.34\\ 0.58\\ 0.34\\ 0.58\\ 0.34\\ 0.58\\ 0.65\\ 1.31\\ 0.65\\ 1.31\\ 0.63\\ 0.60\\ 0.08\\ 0.47\\ \end{array}$	0.74 0.15 0.27 0.16 <u>3.65</u> 0.06 2.50 0.07 0.15 0.09 0.37	0.31 0.27 0.39 0.01 <u>3.61</u> 0.05 2.08 0.07 0.49 0.06 0.20
	dF 14 4 28 1 7 2 14 14 2 14 14 2 14 14 14 14 14 14 14 14 14 14	$\begin{array}{c cccc} & & & & & & \\ \hline & & & & \\ \hline \hline & & \\ \hline \hline & & \\ \hline & & \\ \hline \hline \\ \hline & & \\ \hline \hline \hline \\ \hline \hline \hline \\ \hline \hline \hline \hline \\ \hline \hline$	dF Allopatry Sympatry 14 0.59 1.21 4 0.13 0.34 28 0.19 0.33 1 0.0 0.95 7 0.65 10.84 2 0.06 0.64 14 1.82 1.73 2 0.07 0.54 14 0.14 0.58 4 0.24 0.34 28 0.24 0.34 28 0.24 0.58 1 0.87 7 1.14 2.49 2 2 0.15 14 4 0.20 28 0.60 1 0.19 7 5.61 2 2 0.65 14 1 0.19 7 2 0.63 14 4 0.60 4 4 0.60 43	dF Allopatry Sympatry Coho 14 0.59 1.21 0.74 4 0.13 0.34 0.15 28 0.19 0.33 0.27 1 0.0 0.95 0.16 7 0.65 10.84 3.65 2 0.06 0.64 0.06 14 1.82 1.73 2.50 2 0.07 0.54 0.07 14 0.14 0.58 0.15 4 0.24 0.34 0.09 28 0.24 0.58 0.37 1 0.87 0.32 14 2.49 2 0.15 14 0.20 28 0.60 1 0.19 7 5.61 2 0.65 14 1.31 2 0.63 0.43

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with decreasing size of fish, decreasing water velocity, increasing water temperature and when food was drifting in the system (Fig. 24). The use of cover in riffles (under rocks) was almost exclusively by that of small and medium size trout. Comparisons of the relative microdistributions of coho and trout in sympatry for second-order levels of interaction (Fig. 24a) indicated that temperature was the primary factor controlling salmonid use of space in winter. Relative size of fish, increased water velocity within limits and the food supply were of lesser importance, ranked in that order.

Témperature was the major determinant of coho and trout breadth of microhabitat niche in winter. A relatively small elevation in temperature resulted in pronounced differences in fish microdistribution (Table 12; Fig. 24a). At 3 °C both coho and trout fry did not utilize riffles to any great extent but remained in pools under cover. At 5 °C their use of riffles increased (P < 0.05) in all tests excepting that by coho at the high velocity. With the 2 °C rise in water temperature, mean numbers of fish in riffles increased by about 20% for coho and 15% for trout under low flow conditions; riffle:pool percent ratios of the means were about 21:79 for coho and 27:73 for trout. At high flow, coho occupancy decreased in riffles by approximately 10% relative to that at low flow, whereas that of trout essentially remained unchanged. Interspecifically, mean numbers of fish per habitat type differed significantly (P < 0.05) only at the high velocity conditions, with numbers of trout in riffles being more than twice as high as for coho.

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Priority of access to food and space was largely determined by an individual's relative body size. For both salmonids size of fish interacted significantly (P < 0.01) and similarly with habitat type in both allopatry and sympatry. The larger-sized coho and trout were rarely found in riffles but preferred the deeper water with overhead cover in pools (Fig. 24). Cover response also differed slightly between species, being more pronounced in trout than in coho in both riffles and pools (Table 12). In allopatry, the percentage of coho using cover in riffles and pools, respectively, ranged from 4.4-11.5 and from 30.9-39.3, whereas that of trout ranged from 54.8-69.2 and from 49.2-51.2. Within the depressions beneath each of the rocks in riffles, there was almost never more than one fish per rock. In sympatry, the use of cover increased slightly in pools but not in riffles. When the species were mixed, coho use of cover in pools ranged from 41.6-47.5% and trout from 69.8-72.4%.

The microdistribution of both coho and trout in pools differed significantly (P<0.05) with size of fish and with vertical strata in both allopatric and sympatric trials (Table 14). In the lower third of pools, small fish were more numerous than were medium and large size individuals. Also, fish of all size-classes were most abundant in the lower two-thirds of pools. Their relative abundance in these lower strata depended on water velocity. From the low to the high test velocity, the numbers of both species for all three size-classes increased significantly (P<0.05) in the lower third of pools.

Both coho and trout fry showed a reduced feeding response at 3 °C.

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Table 14. Vertical microdistribution of coho and cutthroat trout by size class (see Table 8) in pools, combining the data of pre-, duringand post-feeding periods in winter. Differences in the means between all upper and lower levels by size class were significant (P < 0.05) when tested by factorial analysis of variance. The mean number of fish shown in sympatry are twice those of the actual values in order to equalize density with those in allopatry.

		Coho				Trout	
	Upper	Mid	Lower		Upper	Mid	Lower
			r) <u>A</u>	llopatry			
			<u>1</u>	ow velocity	<u>/</u>		
S M & L Total	$\begin{array}{r} 0.5 \\ 0.1 \\ \hline 0.6 \end{array}$	8.8 $\underline{13.1}$ $\underline{21.9}$	9.6 6.8 16.4		$0.7 \\ 0.1 \\ 0.8$	9.7 $\frac{13.0}{22.7}$	4.5 6.5 11.0
			h	igh velocit	ty		
S M & L Total	$\begin{array}{c} 0.0 \\ \underline{0.1} \\ \hline 0.1 \end{array}$	$\begin{array}{r} 4.3 \\ \underline{11.8} \\ 16.1 \end{array}$	14.7 $\underline{8.0}$ 22.7		$0.4 \\ 0.1 \\ 0.5$	5.5 9.6 15.1	$\frac{11.1}{9.5}$ $\frac{20.6}{20}$
			ि <u>ः</u>	Sympatry			
			<u>1</u>	ow velocity	7		
S M & L Total	$\begin{array}{c} 0.9 \\ \underline{0.0} \\ 0.9 \end{array}$	7.0 13.4 20.4	$\begin{array}{r} 12.6 \\ \underline{5.7} \\ 18.3 \end{array}$		$0.3 \\ 0.1 \\ 0.4$	$ \begin{array}{r} 15.0 \\ \underline{14.3} \\ \overline{29.3} \end{array} $	8.8 5.3 14.1
			h	igh velocit	ty		
S M & L Total	$\begin{array}{c} 0.0\\ \underline{0.0}\\ 0.0\\ \hline 0.0 \end{array}$	4.4 12.4 16.8	$\begin{array}{r} 15.4\\ \underline{7.4}\\ \underline{22.8}\end{array}$		0.0 <u>0.0</u> <u>0.0</u>	$8.1 \\ \frac{11.6}{19.7}$	10.5 7.9 18.4

Accordingly, the imposed cycle of food availability had minimal impact on species microdistribution patterns, both in allopatry and sympatry. However, a 2 $^{\circ}$ increase in temperature (3 to 5 $^{\circ}$ C) altered behavioral responses to food and space appreciably. At 3 $^{\circ}$ C, neither species exploited the food supply in riffles but remained primarily in pools. At 5 $^{\circ}$ C, the relative abundance of fish in riffles was higher (Fig. 24), primarily due to their movement into this habitat during feeding period. However, none of these behavioral differences showed any significant interactions between feed periods and patterns of space utilization when tested by factorial analysis of variance. Under critically low temperature and high velocity conditions, trout appear better adapted to feed in riffles than do coho possibly due to hydromechanical advantages gained by their closer association with the stream bottom. Coho feeding in riffles under severe physical conditions consisted of short-term invasion of choice feeding sites.

During winter freshets, stream salmonids may experience a net downstream displacement. To counteract this phenomenon, fish may instinctively move upstream. I compared the numbers of coho and trout in the upstream- and in the downstream halves of the experimental section for tests conducted at 3 $^{\circ}$ C (Table 15). The numbers of fish for both species for all three size-classes, increased significantly (P<0.05) in the upstream half when the velocity was increased, in both allopatric and sympatric trials. In addition, the small fish of both species were more abundant in the upstream half than were the medium and large fish combined. In nature, such longitudinal distribution may permit a size segregation, with smaller fish in upstream reaches and larger fish in

Table 15. Horizontal microdistribution (mean \pm S.E.) of coho and cutthroat trout by size class (see Table 8) in the upstream half (R1 + P1) and the downstream half (R2 + P2) during-feeding period in winter. The number in sympatry are twice that of the actual values to equalize density with that in allopatry.

	Upstre	am half			Downstre	eam half	
Co	ho	Trout		C	oho	Tr	out
S	M&L	S	MĘL	S	M&L	S	MĘL
			Allopat	cry			
			low vel	locity			
11.0±0.4	8.1±0.7	12.2±0.3	10.9±0.4	8.4±0.4	13.1±0.3	7.6±0.4	11.4±0.5
			high ve	elocity			
16.5±0.5	11.3±0.6	15.5±0.4	13.7±0.5	3.1±0.4	8.7±0.7	4.4±0.4	6.3±0.5
		.•	Sympat:	ry			
			low ve	locity			
10.4±0.3	8.8±0.2	5.6±0.3	6.6±0.2	9.6±0.3	11.0±0.2	14.4±0.3	10.9±0.5
			high v	elocity			
16.5±0.2	9.0±0.2	14.6±0.3	13.4±0.2	3.5±0.2	11.2±0.2	5.5±0.3	9.2±0.5
						,	
downstream reaches.

AGGRESSIVE BEHAVIOR

General

Coho and cutthroat trout fry used similar body postures and movements in social interactions, as previously described by other workers for stream-dwelling Salmonidae; lateral and frontal threat displays (Fabricius 1953; Kalleberg 1958; Chapman 1962); intention movement, chasing, threat and contact nips, and wig-wag threat display (Hartman 1965b; Mason 1969); parallel-swimming, circling and biting (Mason 1969). Of these, only the lateral threat display showed apparent differences between species. Firstly, duration of intraspecific displays was generally longer in trout than in coho and frequently involved either singly or in sequence, parallel swimming, circling, intense nipping and biting of the opponent's peduncular region. Secondly, cutthroat trout possess a bright orange-colored hyoid slash, which is exposed when the basihyal apparatus is lowered in bouts of high intensity lateral threat aggression (see Fig. 22b), and is accompanied by rapid quivering of the caudal region. Its adaptive significance is uncertain but it appears to function as an intraspecific signal between contesting fish. Size and color intensity of the hyoid slash may also be important. Particularly in summer, intraspecific lateral threats between closely matched trout often led to prolonged bouts of butting and biting usually near the bottom of pools, occasionally to a state of physical exhaustion. In an extreme case, a total of 530 aggressive acts over a period of 12 min, mostly intense nipping and biting, was exchanged between two trout in a territorial dispute. In

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contrast, interspecific lateral threat encounters were brief even in cases when the fish were closely matched.

Individual components of aggressive behavior were expressed on a percent basis of the pooled data for either species (see Fig. 26-27, bottom). In both summer and winter, the most frequently used components of aggression by both coho and cutthroat trout were those of chase, nip and lateral display; together these comprised more than 80% of the total aggressive acts for each species. In summer, the more elaborate threat displays and non-contact behaviors were more frequently used by coho as opposed to the predominant nipping behavior by trout. Of their total aggressive acts, nipping activity made up 45% for trout and 33% for coho. Neither species showed obvious differences in frequencies of display and non-display forms of aggressive activity between the riffle and pool environments when tested under the low and high velocity conditions. Hartman (1963) reported that young brown trout used less display than non-display forms of aggression when in faster water. In winter, fish activity was relatively low and confined almost entirely to pools. Accordingly, they showed a proportional reduction in relative frequency of chases and an increase in threat nips and displays compared to those in summer. Lateral displays and threat nips combined made up almost 60% of the total aggressive encounters for both coho and trout.

Rate of aggressive activity in both coho and trout was roughly proportional to body size at either test velocity (Table 16). Aggression was least for small fish and highest for large fish, the differences ranging from three to psix fold in magnitude. During high water velocity,

Table 16. Mean level of aggression (number of encounters per fish per 100 min) of coho and cutthroat trout in allopatry by size class (see Table 8) of fish in pools in winter at 3 °C, combining the data for pre-, during- and post-feeding periods. P1 and P2 as in Fig. 17.

	Coho			Trout		
	S	М	L	S	М	L
			Low veloci	ity_		
P1 P2 Average	$\begin{array}{c} 6\\ \underline{11}\\ \underline{8.5} \end{array}$	31 <u>21</u> 26	57 <u>47</u> 52	22 <u>10</u> 16	45 <u>37</u> 41	49 54 52
			High velo	city		
P1 P2 Average	8 <u>8</u> 8	19 <u>29</u> 24	50 <u>47</u> 49	$\frac{13}{13}$	31 <u>39</u> <u>35</u>	81 <u>63</u> 72

large trout were considerably more aggressive in the upstream pool, which may be a response to counteract downstream displacement in streams.

Summer

Habitat had greater effects on species levels of aggressiveness in sympatry than in allopatry (see Figs. 25, 26). Mixing the two species in a riffle and pool environment had the overall effect of reducing coho aggressiveness in riffles and trout in pools. In sympatry, intraspecific aggression in coho was significantly (P<0.01) higher in pools than in riffles, the pattern being reversed in trout but significant (P < 0.01) only under the low test velocity conditions. When the data were pooled for both test velocities (total observation period 2400 min), intraspecific aggressive activity in pools and riffles, respectively, was 2152 and 515 for coho, and 242 and 703 for trout. However, their interspecific aggression between pool and riffle environments was similar for either species totalling 677 and 477 for coho, and 435 and 618 encounters for trout. In total, coho aggressive activity was some 30% higher than that of trout. In allopatry, at low velocity overall levels of aggression in either salmonid were similar between pools and riffles; at high velocity both species were socially less active in riffles than in pools. Their aggressive activity in pools and riffles, respectively, amounted to 3225 and 2022 encounters for coho, and 2326 and 2054 for trout.

Rate of aggression in both salmonids showed a definite relation to the feeding cycle, in both allopatry and sympatry (Figs. 25, 26). Typically, mean levels of aggressiveness peaked in both riffle and pool environments when food was drifting in the system. However, chi-square



Fig. 25. Mean aggression \pm S.E. of allopatric coho (solid) and cutthroat trout (open) in a) summer and b) winter (3 °C) in relation to the feeding cycle (1, pre-; 2, during-; 3, post-feed period) and water velocity.

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Fig. 26. Upper: Mean summer aggression of sympatric coho (solid) and cutthroat trout (open) in riffles and pools. Numbers relate to the feed cycle as in Fig. 25. Lower: Relative frequency of the components of aggression in intra- and interspecific cases for coho (solid) and trout (open). Symbols are: IM, intention movement; DT, drive toward; CH, chase; TN, threat nip; CN, contact nip; L, lateral display, WW, wig-wag display; F, frontal display; PS, parallel swimming; C, circling; B, biting.



tests were not significant in all cases, when combining the data of both replicates. In allopatry, only the aggressiveness of trout in pools rose significantly (P < 0.01) in relation to feeding at both test velocities (Fig. 25a). In sympatry, interspecific levels of aggression for both coho and trout showed a significant (P < 0.01) increase when feeding in pools only at high velocity (Fig. 26, upper). In riffles, rate of coho intra- and interspecific aggression peaked significantly (P < 0.01) when feeding at both test velocities; trout aggressiveness increased significantly (P < 0.01) only against coho for the high velocity conditions. With the onset of feeding, aggressiveness was more rapidly elevated in coho than in trout; coho actively penetrated riffles, exerting social dominance and largely displaced trout from the better feeding territories. Unlike in riffles, in pools trout appeared to be less vigorous competitors against coho, as suggested by the latter's significantly (P < 0.01) higher aggressive activity against members of their own species than against trout at both test velocities.

The nearly twofold acceleration of water velocity did not appreciably affect species levels of aggression. In both allopatry and sympatry, velocity effects on fish aggression were similar in riffles, as level of aggression in both species decreased although non-significantly (P>0.05); in pools, aggressiveness in coho but not trout, increased significantly (P<0.05) when the velocity was accelerated, paralleling results reported for Atlantic salmon (Kalleberg 1958).

Winter

The winter test conditions showed marked but similar

environmental effects on both coho and cutthroat trout patterns of aggressive behavior. Neither salmonid defended riffle space at 3 °C, irrespective of the test conditions, with the exception that trout occasionally interacted for cover sites beneath rocks. Mixing the species showed no interactive effect on their levels of aggression. Overall, total aggressive encounters for each species in sympatry was proportionately halved of that in allopatry with respect to actual fish densities used, being 3410 and 6409 for coho and 1988 and 3892 for trout. However, rate of aggressive activity differed significantly (P < 0.05)between species in sympatry but not in allopatry, but only during periods when food was drifting in the system. When mixed with coho, trout defended feeding stations less and usually remained more in areas of cover. Accordingly, coho directed a near two-fold greater amount of their total aggressive activity against conspecifics than against trout, with total encounters amounting to 2243 and 1167, respectively. Trout total aggressive activity was more evenly distributed with a total of 944 encounters against conspecifics and 1044 against coho.

As in summer, in winter, rate of aggression in both salmonids showed a definite relation to the feeding cycle in both allopatry (Fig. 25b) and sympatry (Fig. 27). In general, aggression was low for both species but pulsed in synchrony with the feeding cycle. Despite the rigorous test conditions, fish actively competed for food in pools as portrayed by their significant (P < 0.01) increase in rate of aggression when food was drifting in the system. Typically, aggression in both species was lowest in pre-, highest in during-, and intermediate in



Fig. 27. Aggression of sympatric coho and cutthroat trout in winter at 3 °C (upper) and relative frequency of the components of aggression (lower). Symbols as in Fig. 26.

post-feed periods. However, coho maintained a higher level of aggression in post-feed periods than did trout, but significantly (P < 0.01) only intraspecifically.

Aggressive response in pools in relation to the feeding cycle differed markedly between species (Fig. 28). When mixed, unlike trout, coho total aggressive activity showed a rapid initial increase, reaching peak levels shortly after initiation of the simulated drift. Trout response to food was slower and less intense, with peak levels of aggressiveness being less than half of that for coho and lagging behind by some 15 min. Coho feeding strategy showed obvious advantages over that of trout. Their@more rapid response gave them priority to choice sites, permitting a greater take of the limited food supply. The overall effect of increased aggressiveness in both species when feeding, tended to disrupt aggregations in the preferred cover sites and led to a sizerelated longitudinal and vertical partitioning of open pool space, with only slight increase in numbers in riffles. Typically, the larger fish were positioned near the head and in the upper level of the pools, with coho most often in front of and above trout.

Increasing the water velocity had insignificant (P>0.05) effects on species levels of aggressiveness at 3 °C in both allopatric and sympatric trials, as fish remained predominantly in pools close to cover. With a doubling of the water velocity, rates of aggression in coho, but not trout, decreased slightly for both intra- and interspecific cases, particularly in the latter (Fig. 27, upper). Trout aggression intraspecifically, was unaffected by the acceleration of the water



Fig. 28. Winter aggression (mean number of encounters per fish per 100 min) of coho (0) and cutthroat trout (\Box) in pools in relation to the feed cycle for the high test velocity at 5 °C. Duration of each observation period was 5 min at each successive 10 min intervals. Vertical lines indicate range.

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velocity but increased considerably interspecifically when food was drifting in the system. The latter was mostly the response of highly territorial and aggressively active large-sized trout during feeding.

Behavioral interactions increased when water temperature was elevated by 2 °C (Fig. 29, upper). Both species at 5 °C actively defended riffles at least during feeding. With this relatively small rise in temperature, their use of cover decreased while that of feeding increased. Total aggressive activity in both pools and riffles combined, increased by 14% for coho and 50% for trout in response to the 2 $^{\circ}$ increase in temperature. However, levels of aggression did not differ significantly between species for any of the test conditions, excepting a significantly (P < 0.01) higher rate of intraspecific aggression for coho than for trout in pools at the low test velocity. At least in pools, species patterns of aggressiveness to the various test conditions at 5 ^oC was in general similar to that at 3 ^oC, but more pronounced. Coho but not trout, showed a significant (P < 0.05) decline in both intra- and interspecific rates of aggression under the accelerated velocity conditions in riffles, as well as pools. Under the low velocity conditions, in pools but not riffles, coho directed a significantly (P < 0.05) greater portion of their aggressive activity against conspecifics than against trout, respectively, totalling to 2184 and 1059 encounters. Trout offensive activity was more evenly distributed within and between species in both riffles and pools.



Fig. 29. Aggression of sympatric coho and cutthroat trout in winter at 5 °C (upper) and relative frequency of the components of aggression (lower). Symbols as in Fig. 26.

RELATIVE DENSITY OF SPECIES

Sympatric populations of juvenile coho salmon and cutthroat trout in streams spatially segregate into pools and riffles, respectively, during the seasons of rapid growth. The degree of overlap in microhabitat use between populations of these salmonids may in part reflect species relative density effects. The possibility of greater intraspecific competition for food and space under relatively high population density may force a species to exploit a broader microhabitat niche. I tested this possibility for summer fry of coho salmon and cutthroat trout in the stream simulator at 14 °C, looking specifically at patterns of microhabitat use and rates of aggressive activity (see Appendix, Table 9, for the relative numbers and size of fish used in each experiment).

Habitat segregation was less distinct when species relative densities were grossly different from 1:1. In the 1:3 coho:trout density situation, trout overlapped considerably with coho in pools, in the reverse experiment, coho overlapped with trout in riffles more so than in 1:1 situations (Fig. 30, bottom).

Rates of intraspecific aggression in either species were similar, being positively proportional to their relative density and probably served to increase dispersal between habitats (Fig. 30). Intraspecific aggression increased at least three-fold for the relatively high density test in either species. Coho and trout differed markedly in level of interspecific aggressions accompanying density changes.

10.8



Fig. 30. Mean ±S.E. of aggression and of microdistribution of sympatric coho (circles) and trout (triangles) in summer in pools (P1, P2) and riffles (R1, R2) for the low (open) and high (closed) water velocity at two different species relative densities: a) 10 coho, 30 trout; b) 30 coho, 10 trout.

Unlike trout, coho upheld social dominance at both high and low densities, and their aggressive activity was at least 6 times higher in the case in which trout was high rather than low in numbers. In coho, but not in trout, rate of interspecific aggressive activity was related to probability of encounter.

II. COMPARISON OF ALLOPATRIC AND SYMPATRIC TROUT TYPES

Comparisons were made of the summer microdistribution and aggression of allopatric and sympatric cutthroat trout population types when tested in the stream simulator. Trout of allopatric origin (F.L. range 35-60 mm) living isolated from coho were from the area upstream of the barrier falls in Shawnigan Creek (inlet); trout of sympatric origin (F.L. range 35-53 mm) living together with coho were from Craigflower Creek. I postulated that the microhabitat niche and mode of feeding of these two populations might differ, due to the influence of coho in one and not the other.

Each trout type was tested separately in two replicates, using the routine experimental procedures previously described to test the null hypothesis: There was no observable difference between their rates and quality of aggressive behaviors and their microhabitat use when exposed to routine levels of (1) feeding activity, and (2) water velocity, as described earlier.

Microdistribution

Allopatric and sympatric trout population types showed similar

microdistributions in the stream simulator. Pooling the data with respect to body size and feed-periods, either population type showed similar densities in riffle and pool habitats (Table 17). At the low test velocity approximately 40% of the fish occupied riffles and 60% pools; with an almost doubling of the velocity, their riffle occupancy decreased in favour of pools by some 25%. In five-way factorial analysis of variance only habitat interacted significantly (P<0.01) with fish size for both population types. The simulated food supply and water velocity showed no significant interaction with fish microhabitat use. The relative microdistributions for both trout population types indicated that (1) size of fish was the most important factor, (2) simulated food supply was of secondary importance, and (3) acceleration of the water velocity was of least importance in summer.

Relative size seemed to determine priority of paccess to food and space for both types of trout. Trout positioned in riffles and at the heads of pools had feeding advantages over individuals in other areas of the simulator. For both population types, mean percent frequencies of fish in riffles were slightly higher, although nonsignificantly so (P > 0.05), for the larger than for the small-sized trout, whereas in pools there was a preponderance of small fish at the bottom and in undercut areas.

Similarly, the food supply stimulated comparable feeding responses in both types of trout. During feeding periods, many actively penetrated into riffles and either established transient feeding territories superimposed on territories of resident trout, or displaced

Table 17. Mean number of cutthroat trout fry of allopatric and of sympatric origin, tested separately in the riffle and pool habitats in summer at the two test velocities. Cover in riffles refer to areas beneath rocks; in pools to undercut areas.

	Low ve	locity	High veloc	ity
	Mean ± S.E.	<pre>% number of fish using cover</pre>	Mean ± S.E.	% number of fish using cover
		Allopa	tric	
Riffle Pool	7.7±0.38 11.5±0.42	2.0 7.3	5.7±0.48 13.6±0.84	4.2 13.0
		Sympat:	ric	
Riffle Pool	7.4±0.43 11.5±0.36	0.0 10.1	5.7±0.42 13.5±0.74	0.0 10.5

some residents into pools. In post-feed periods there was typically an influx of transient riffle-dwellers back into pools, causing a net out-movement of previously displaced trout back into riffles. None of these movements between habitat types in food exploitation were statistically significant (P > 0.05) when pooled in each experiment.

Submerged areas of cover beneath rocks in riffles and undercut banks in pools were seldom used by either trout type. Small fish were the most frequent users of cover, often to escape aggression from larger fish. In both allopatric and sympatric trout, sites most opportune for feeding rather than for cover were more directly associated with territories of dominant fish. In riffles, utilization of cover was rare, not exceeding 4%. In pools, the use of cover was slightly higher and similar for both trouts, ranging from 7-13% with the higher levels of use occurring during periods of high velocity (Table 17).

Aggressive behavior

Allopatric and sympatric trout types used the same signal set of social interactions described earlier. The most frequently used behavioral elements were those of chases, nips and lateral displays, which comprised about 85% of their total aggressive activity in riffles, with the same in pools for sympatric trout but slightly less for allopatric trout (Fig. 31). However, allopatric trout chased and threatnipped less, but used lateral threat, circling and biting more than did sympatric trout. Total aggressive activity in both the riffle and pool environments combined was similar for both trouts, amounting to 4298 acts for allopatric and 4380 acts for sympatric trout over a period of



Fig. 31. Upper: summer aggression (mean \pm S.E.) of cutthroat trout of allopatric (heavy line) and of sympatric (light line) origin in riffles and pools, tested separately in the stream simulator. Lower: relative frequency of the components of aggression for trout of allopatric (solid) and sympatric (open) origin. Symbols are as in Fig. 25, 26.

observation totalling 2400 min for each. Habitat had similar but greater effects on levels of aggression in allopatric than in sympatric trout: total aggression for allopatric trout between pools and riffles differed significantly (P<0.05) from those expected being 2602 and 1696, but not for sympatric trout, being 2326 and 2054. In pools, total aggression was about 12% higher for allopatric than for sympatric trout, whereas in riffles total aggression was about 21% higher for sympatric than for allopatric trout.

Rates of aggression in sympatric trout showed a more definite relation to the feeding cycle (Fig. 31, upper) than in allopatric trout. Aggression of sympatric trout was highest in both riffles and pools when food was present, although significant (P < 0.05) only in the latter. Aggression of allopatric trout was inconsistent in relation to the feeding cycle, peaking as often when food was present as when food was absent. Aggression decreased for both types of trout when water velocity was increased, except for the significant (P < 0.05) increase by allopatric trout in pools. However, the latter may not be representative of the population per se, as the data include an atypical case of intensive and extended aggression between two closely matched individuals. For either of the two trout types, the total number of aggressive acts was considerably less in both riffles and pools during the high test velocity, with a maximum threefold reduction for sympatric trout in riffles.

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DISCUSSION

BEHAVIORAL ECOLOGY OF COHO AND CUTTHROAT TROUT

Juvenile coho salmon and coastal cutthroat trout are potential competitors for food and space during the summer season of low stream flows. Segregation, either selective (Brian 1956) or interactive (Nilsson 1956), is one means by which competition between species might be attenuated. My laboratory findings confirm field observations. Sympatric coho and cutthroat trout segregate into pools and riffles through social interaction, the degree of overlap depending on relative and absolute densities of population. These findings parallel the pattern and mechansm of segregation between sympatric populations of juvenile coho and steelhead in spring and summer (Hartman 1965b). Segregation appears to be primarily the outcome of interspecific differences in behavior. When together, the socially dominant coho more frequently defend pools, whereas trout more frequently defend riffles. In addition, habitat shift by either cutthroat or steelhead trout from pools (their preferred space) into riffles, when in sympatry with coho, may illustrate exploitation and/or interference competition by coho, a phenomena that has been demonstrated for sympatric populations of salmonids (Nilsson 1960; 1963; Andrusak and Northcote 1971) and of centrarchids (Werner and Hall 1977). In a competitive context, coho may feed more efficiently in pools and trout in riffles. Quantitative evidence for this is lacking, but the more frequent occurrence of slightly higher growth for coho than trout in the stream simulation experiments in summer, suggest that coho may have taken a greater share

of the food supply than did trout (see Appendix Table 9).

Underyearlings in sympatric populations of coho salmon and coastal cutthroat trout did not segregate distinctly in winter as in summer, but rather coexisted in pools. Sympatric coho and steelhead trout have also been found to remain in the unsegregated state in pools in winter (Hartman 1965b). Both Hartman's and my findings suggest that relatively low level of aggression and slight interspecific differences in their microhabitat demands in winter are important factors in the coexistence of coho and trout in pools. In particular, trout associate more closely with bottom cover than do coho in pools. In streams, however, this appears to be the niche of older trout: age 1+ rather than age 0+ trout are the more common cohabitants with coho in pools; age 0+ trout are more frequently found near the edge in the shallower, faster waters, containing an abundance of both instream and overhead cover (Glova and Mason 1977b). The apparent lack of segregation between coho and trout in the stream simulator in winter may reflect the age 0+ trout's occupancy of a vacant niche, otherwise occupied by their age 1+ conspecifics in nature. In the simulator, age 0+ trout were behaviorally flexible, and utilized cover in both riffles and pools, but "preferred" the latter.

Unlike in summer, in winter, quality of space rather than food supply appears to be of greater importance to juvenile coho salmon and cutthroat trout in small streams. Sufficient cover may be a key requirement for salmonid residency in streams in winter (Bjornn 1971; Bustard and Narver 1975a; Mason 1976). In the stream simulator, the need for cover and deeper water in winter of both coho and cutthroat trout was illustrated by their predominant use of the undercut areas in pools. Such knowledge of seasonal spatial preferences by stream salmonids has been known for some time. Some three centuries ago, Isaak Walton (1676) said of brown trout to his good friend Charles Cotton, while fishing in one of his favorite trout streams in England: "- - - and you are to take notice, that the fish lies or swims nearer the bottom, and in deeper water, in winter than in summer; and also nearer the bottom in any cold day, and then gets nearest the lee side of the water".

It has been shown experimentally that both coho and trout prefer areas of cover rather than areas of no-cover when tested under semi-natural conditions (Bustard and Narver 1975b). Low water temperatures and high stream flows in winter create sufficiently adverse conditions that fish tend to exploit areas of shelter and rest. Possible adaptive significance of this behavior could involve reduction of downstream displacement and predation (Hartman 1965b) during a period of lowered metabolism, reduced food requirements and poor swimming ability. Quality and quantity of cover may be the regulatory factor in overwintering stream salmonid populations as suggested by Mason (1976) for juvenile coho. While adverse conditions in natural environments may be tempered by greater spatial complexity, cover in the simulator was intentionally kept simple to facilitate observation of the fish. My laboratory findings, however, agree with those of natural populations of sympatric coho and cutthroat trout.

Coho and cutthroat trout interact minimally over space per se in winter. Typically, rates of interaction were positively related to

temperature but inversely to velocity. Hartman (1966) observed similar responses to temperature in juvenile coho and steelhead. Food drifting in the system at periods of dawn and dusk in the present study markedly elevated species levels of interaction in pools, but elicited only minor dispersal from their preferred winter habitat. Intense interaction was typically short term, and waned rapidly to relatively low levels in post-feed periods, paralleling results reported for Atlantic salmon (Keenleyside and Yamamoto 1962). Level of aggression and scope in microhabitat use for both coho and cutthroat trout were more strongly influenced by change in temperature than that of water velocity. The pronounced species responses obtained in raising the temperature from 3 to 5 °C, relative to that arising from a doubling of the water velocity from 25-50 cm/s, suggest that minor differences in temperature at the lower end of the temperature scale can be of significant ecological importance. The role of low winter temperature as a factor controlling microdistribution of juvenile coho and steelhead in streams was demonstrated by Bustard and Narver (1975a). As both thermal and hydrological conditions in streams are commonly severe in winter, and drifting foods may be sparse, I infer from the present findings that wild sympatric populations of coho and cutthroat trout interact minimally during winter, despite their similar microhabitat demands. However, in streams with restricted overwintering cover they may compete for preferred spaces through mere physical occupancy of specific sites.

Factors affecting the microdistribution of coho and cutthroat trout in the stream simulator differed seasonally in rank of their importance. In summer, size of fish, the simulated food supply and

acceleration of the water velocity within limits, were ranked in decreasing order of importance as affecting fish microdistribution. In winter, temperature appeared to be the primary factor controlling utilization of space; relative size of fish, acceleration of the water velocity within the imposed limits and the food supply were of lesser importance, ranked in that order. Size-related differences in use of space minimize potential for social interactions, both intra- and interspecific (Everest and Chapman 1972). In summer, space in the stream simulator was partitioned longitudinally in riffles and both longitudinally and vertically in pools, with the larger fish being more common at the upstream half in each habitat type. In winter, partitioning of space was vertical and confined to pools, with both species aggregated in the lower two-thirds and small fish being more common on the bottom.

Laboratory studies (this and Hartman 1965b) have shown that the riffle environment is a refuge from interspecific competition for underyearlings of either cutthroat or steelhead trout in summer when tested in sympatry with coho salmon. Behavioral differences between these salmonids appear to account for resource partitioning in streams. In contrast, genetically-based differences rather than interspecific interaction appear to account for resource partitioning between sympatric populations of coho and chinook (Lister and Genoe 1970; Stein et al. 1972) and of steelhead and chinook (Everest and Chapman 1972) in streams. Populations of coho, cutthroat and steelhead trout occurring sympatrically, are common in coastal streams in British Columbia. I speculate that for such

populations coho would maintain social dominance in pools and that the trout would partition the available riffle habitats longitudinally, overlap being greatest in the mid-region of the system: steelhead in the deeper, lower reaches; cutthroat in the shallower, upper reaches, small tributaries being common. Such distribution patterns for sympatric populations of steelhead and cutthroat have been reported to occur in numerous southwestern British Columbia streams (Hartman and Gill 1968). Exploitation by cutthroat trout of the more marginal habitats in streams also containing steelhead suggest the former are likely to be socially subdominant.

IMPLICATIONS FOR MANAGEMENT OF STREAM SALMONIDS

Habitat diversification

The findings of the present study point to the importance of maintaining adequate habitat diversity in streams in summer when managing for sympatric populations of salmon and trout. Low habitat diversity may favour one species over the other. During this season streams typically have reduced riffle/pool ratios and elevated streamwater temperatures, conditions which tend to minimize effective spatial segregation between salmon and trout. Low summer stream-flows offer competitive advantages to salmon over trout, despite the broader spatial and feeding niches of the latter. The cutthroat trout is a polytypic species potentially capable of survival over a relatively broad range in stream water temperatures and velocities (Hall and Lantz 1969; Glova and Mason 1977c). Juvenile coho salmon are considered equally flexible to a variety of stream conditions but make restricted

use of higher velocity habitats, particularly at lower temperatures. When such habitat is sparse, coho may socially control access to marginal stream space and trout survival may be reduced. Certain velocity and substrate-oriented instream engineering (Parkinson and Slaney 1975) implemented in specific streams would encourage habitat segregation between sympatric salmon and trout populations, simultaneously improve their food supply, and probably enhance their production and smolt yield to sea.

Winter cover

Winter carrying capacity of some salmonid-producing streams may be limited by the level of appropriate cover available to fish (BustardSand Narver 1975a;Mason 1976). The findings of the present study emphasize the importance of cover to stream salmonids at temperatures below 3 °C, a range that is common in streams of coastal British Columbia during winter.

Streams managed for production of sympatric populations of coho salmon and coastal cutthroat trout should provide sufficient optimal cover types appropriate to age 0+ trout and also to coho and age 1+ trout. Age 0+ trout are most frequently found near the edge in the shallower, faster waters, containing an abundance of large boulders and thick, low, overhanging shrubs at the streambank. They are almost never present in whitewater areas lacking such cover types (Glova and Mason 1977b). Enhancement of age 0 trout may be most effectively achieved by manipulating both instream and overhead cover, particularly those of the larger substrates and streambank vegetation (see Parkinson and Slaney 1975). Analysis of overwintering requirements of coho and age 1+ trout is confounded by broad overlap and diversity in cover types used: coho utilize a variety of cover types in both main channel and side channel habitats (Bustard and Narver 1975a), whereas trout remain mostly in main channel areas. Sites common to both species are the deeper waters containing upturned or undercut root masses and log accumulations at meanders. Trout, but not coho, are also found in close association with large boulders. Strategies to improve winter cover for these salmonids should consider the entire river course and include existing hydrological and physiographical features (sidepools, side channel, backwaters at meanders, etc.) Such an approach may well reduce installation and maintenance costs and increase utilization of existing sites by fish.

Superimposition of coho on trout

The behavioral similarity of allopatric and sympatric trout types, may reflect a general environmental similarity above and below barrier falls. Within the populations investigated in this study, interaction with coho salmon has not produced any "apparent" evolutionary changes in feeding behavior and microhabitat responses of trout. However, sympatric trout defended riffle territories more vigorously, showed a more synchronous response to the feeding cycle, and used aggressive display components more suited hydromechanically to faster velocity habitats than did allopatric trout. These differences could be interpreted as adaptive responses to sympatry with coho. Any evolutionary changes in sympatric trout populations attributable to their interaction with coho would face dilution from downstream gene flow from allopatric populations above barrier falls. Until the magnitude of downstream

displacement from isolated trout populations, relative to size of the sympatric receiver population has been documented, especially as instigated by severe winter freshets, the potential importance of this genetic dilution factor will remain unknown.

In contrived sympatry such as that which would be produced from superimposition of hatchery-reared coho fry on wild allopatric trout populations, the interactive outcome may not differ appreciably from that for natural sympatry. The polytypic nature of trout populations in general (Trojnar and Behnke 1974) would no doubt induce appropriate shifts in feeding and microhabitat responses to allow for coho social dominance in pools and other low velocity habitats. Assuming that coho and trout populations brought together in an unnatural sympatry above a barrier falls, would segregate into pools and riffles, respectively, as in natural sympatry, we might expect the biomass levels of such trout populations to decline to below 1 g/m^2 , or be approximately halved. Low summer flows disproportionately reduce riffle areas relative to pools, and thus further extend space limitations to trout sympatric with coho, through habitat segregation. The present results suggest that superimposition on wild cutthroat trout stocks of cultured coho fry surplus to hatchery needs requires additional testing in coastal streams under a variety of experimental conditions before recommendations can be made as to the suitability of such stocking as a strategy to enhance salmon stocks consistent with conservation of sympatric populations of trout.

Escapement control

Stocks of anadromous cutthroat trout are a potentially valuable recreational resource (Giger 1972; Johnston and Mercer 1976). Enhancement of natural production of cutthroat trout smolts for stream populations sympatric with coho salmon are likely to be limited by the trout's socially subdominant role in allocation of stream resources. Coho escapement could be controlled in selected sympatric streams particularly productive of cutthroat trout. Since coho spawn in the fall and cutthroat trout spawn in the spring, partial or complete exclusion of coho in specific streams by escapement control is feasible, using temporary stream barriers. Comparison of biomass density of allopatric and sympatric trout populations in this study, suggest that the above management strategy would encourage the behaviorally flexible trout to approach production levels similar to those of sympatric coho and trout combined. The exclusion of sculpins in such streams also merits consideration in the context discussed by Mason and Machidori (1976).

CHAPTER IV. LABORATORY GROWTH OF UNDERYEARLING COHO SALMON AND COASTAL CUTTHROAT TROUT

INTRODUCTION

Relative body size plays an important role in competitive interactions between stream salmonids (Hartman 1965b; Mason 1965; Jenkins 1969). Larger individuals by way of social dominance have access to sites providing locally superior feeding and shelter conditions, which in turn may better their probability of survival compared to that of smaller fish. Size-related competitive advantages may therefore be associated with accelerated growth. In the case of two closely related and ecologically similar species living sympatrically, the pattern of interspecific growth may be clearly dominated by one of the species or the growth rates of both species may be similar. Social dominance is one factor that may influence the rate of growth of sympatric populations, particularly in situations where food shortages occur.

Stream populations of cutthroat trout fry face marked size disadvantages in partitioning of resources with coho salmon. Size disparity between these two salmonids is assured each generation by the trout's later emergence, and smaller size at emergence. Reduction in interspecific size differences would increase the trout's competitive ability and provide them a more equitable share of the available resources. In Bush and Holland creeks I observed that fry of cutthroat trout grew faster than fry of coho (see Figs. 15, 16). Faster growth for trout may have accrued from behavioral (e.g. lesser social dissipation of energy, greater food intake) and physiological (e.g. higher food conversion efficiency) strategies, or both.

Laboratory growth studies were conducted to investigate the possibility of differences in pattern of growth between these two salmonids that might be of consequence in their interspecific social interactions and partitioning of stream resources. In addition, my many casual observations of their distribution and abundance in larger streams (coho being more common in the lower, warmer reaches; trout in the upper, cooler reaches), suggested coho may "do better" in warmer water, while trout may Edo better" in colder water. I tested the null hypothesis that there was no statistical difference in growth and body condition (Brown 1957) between underyearlings of coho and cutthroat trout for a seasonally representative range of combinations of temperature and photoperiod. Photoperiod was included in the design of the test space, as several works give evidence to suggest it has important underlying interactions with temperature on growth of fish (Brown 1957; Gross et al. 1965; Huh et al. 1976) and on fish movements in streams (Northcote 1958). Hierarchical and density effects on growth were also investigated to a limited degree as these phenomena have important impact on relative growth in laboratory studies (e.g. Brown 1946, juvenile brown trout).

METHODS

A. THE FACILITIES

Facilities at the Pacific Biological Station, Nanaimo, B. C. were used. A total of nine troughs, each 2.42 x 0.89 x 0.14 m, were partitioned lengthwise into three identical compartments constructed entirely of 1-cm thick polyviny1ch1oride (PVC). Each compartment was further subdivided across with removable nylon fly screens into two equal experimental cells (total of 54 cells in all) each 1.09 x 0.29 x 0.14 m, and a small outflow chamber at the downstream end. These were placed on Dexion 225 steel angle frame and plywood shelving arranged to provide a 3 x 3 factor space having a total of nine test combinations of temperature (rows) and photoperiod (columns) (Fig. 32). Each cell was equipped with a removable clear plexiglass cover with a 10-cm diam Nalgene feeding funnel at the upstream end, an airstone, and a 15-cm halfsection of 9-cm diam PVC pipe, placed centrally on the tank bottom as cover. A movable shroud of black drapery and black polyethylene sheeting was placed over the entry side of each of the three stacks to provide access and complete photoperiod isolation to each stack.

Test temperatures of 5, 10 and 15 °C were manually maintained to within ± 0.5 °C in all but the summer 5 °C level (+1 °C) by manipulating ball valves controlling the delivery of chilled, normal and heated fresh water from header tanks (each 0.91 x 0.46 x 0.44 m) to three mixing manifolds. Water temperatures in each manifold were continuously



Fig. 32. Details of the test facility used in laboratory growth experiments: a) diagrammatic representation of the 9 test combinations of temperature and photoperiod including the 3-diagonal test points (along broken line) and 2 points tested in sympatry in winter (\Rightarrow), b) cross-section of the entire test facility and c) plan detail of one test point unit.
monitored by Taylor manual recorders. The inflow to each cell from the respective manifolds was held at about 2 ℓ/\min (renewal rate once/ 45 min) and the water level constant at 0.13 m with a standpipe in the outflow chamber.

Test photoperiods of 8, 12 and 16 hr light at an intensity of 1 lux were obtained through time-switch control of incandescent overhead lights in each test space. The facility provided a maximum of nine test combinations of temperature and photoperiod with three replicates per point for each of the two species tested (Fig. 32a).

B. THE FISH

Comparable growth studies were done during both summer and winter; summer fish were early fry (coho: FL 42.9±1.3, range 38-55 mm; trout: FL 44.2±1.2, range 38-51 mm) from Craigflower Creek and winter fish were advanced fry (coho: FE 56.7±1.1, range 51-62 mm; trout: FL 56.4±1.4, range 48-63 mm) from Holland and Bush creeks (see Fig. 1 for stream locations). Their mean initial weights ranged from 0.7-0.8 g in summer and from 1.7-2.0 g in winter. They were collected with a D.C. fish shocker and pole seine, transferred to the laboratory, and held in fresh water at the respective ambient stream-water temperatures at time of collecting.

C. EXPERIMENTAL PROCEDURE

In the laboratory all individuals were measured and damp weighed

under mild anaesthetic (2-phenoxyethanol) and simultaneously sorted into 1-mm fork-length classes. Ten fish of each species for each experimental cell (0.25 fish/ ℓ were then dipnetted from tanks containing individual length class in systematic order to equalize mean sizes over the entire test space (see Appendix Glova and Mason 1976c). Each species was assigned alternate cells in the test facility to account for any possible biases inherent in the apparatus. They were then acclimated to their respective test temperatures at the rate of 1 °C change/day under natural photoperiod. When acclimation was completed in all cells, test temperatures and photoperiods were then imposed for the duration of the experiments. As a precautionary measure against possible diseases, all fish were initially exposed to 1:4000 formalin solution for 20 min.

The summer experiment lasted from 17 June to 8 September, 1975. Growth rates for both coho and trout in allopatry were determined at all nine test points in the factor space (see Fig. 32a) with three replicates/ point. The fish were individually measured to the nearest mm in fork length but batch damp-weighed (10 fish of each species/cell) to the nearest 0.1 g at each 3-wk interval. Fish mortalities that occurred during the first week of the experimental period were replaced with comparable-sized fish to account for the relatively high initial losses in some tests.

The winter experiment lasted from 16 December, 1974 to 27 February, 1975. Growth rates in allopatry were determined at all nine test points in the factor space for coho, but for trout only the diagonal points (see Fig. 32a) were done due to the difficulty in obtaining the

necessary numbers of winter fry. Growth in sympatry, five fish of each species per cell, was also determined at test points 5C--12-hr light and 10C--16-hr light (see Fig. 32a). At the end of the first month, the fish were individually measured to the nearest mm in fork length and to the nearest 0.01 g damp-weight while under mild anaesthetic. Subsequent measurements were done at each 2-wk interval. As in the summer experiment, the fish were starved for 24 hr prior to being measured. Mortalities in the initial week were replaced with comparablesized fish.

The fish were hand-fed twice daily at regular hours with chopped fresh-frozen zooplankton consisting almost entirely of <u>Euphausia</u> <u>pacifica</u>. This diet was chosen over commercial feeds in the light of favourable reports on growth and stimulation of appetite in the supplementary feeding of juvenile salmonids in streams by Mason (1976). Each quantum ration was deposited in the feeding funnel fixed in the plexiglass cover of each cell, washed down with water. Daily rations were determined on a wet-weight basis and were related to test temperatures: 15 °C level received 8%, 10 °C level received 5% and the 5 °C level received 2.5% of the mean body weight of 10 fish. These rations were slightly in excess of those required for maximum growth at each of the three test temperatures and were adjusted accordingly following each measurement period to account for growth. As part of routine maintenance, all cells were cleaned free of wastes every 3 days.

RESULTS

MORTALITY AND GROWTH

Fish losses appeared to be primarily of behavioral rather than physiological origin, regardless of season. Mortality of either species was mostly the outcome of caudal infections from Saprolegnia sp., which appeared to be initiated by the aggressive nipping of fish. Total mortality in the summer and winter period, respectively, amounted to 8.1% and 10.7% for coho, and 5.2% and 35.5% for trout. In both species most mortalities involved fish that were about 20% less than the mean fork length in any given test group. The much greater percent loss of trout than coho in winter, may be due in part to the bias in testing trout at the diagonal points only of the test space. Chi-square tests for goodness of fit indicated fish losses in most cases were significantly $(P \le 0.01)$ higher than those expected at the higher temperatures and longer photoperiods. Both salmonids were approximately three times as aggressive at 15 than at 5 °C. Presumably, subdominant fish exposed to combinations of higher temperature and longer photoperiod were subjected to greater social stress, which may have increased their susceptibility to infectious diseases.

Mean growth rates for both coho and trout were calculated for each of the test points at the end of each time interval, according to Brown (1957).

 $G = \frac{\log_e Y_T - \log_e Y_t}{T} \times 100,$

where G designates specific rate of growth expressed as percent change in weight of fish per day; Y_T , Y_t represents weight of fish at end and beginning of each time interval, respectively, and T is the time interval between measurements in days. The measure of specific growth was useful in comparing growth of fish of different sizes in the summer and winter experiments. The results are summarized graphically in threedimensional plots only for those experiments in which all points of the factor space were tested (Fig. 33).

Summer growth of allopatric coho and cutthroat trout fry were fairly similar (Fig. 33). Typically, they grew faster at combinations of higher temperature and longer photoperiod. An exception was the initial reverse response to photoperiod at 15 °C for coho, which is suspect of being of behavioral rather than physiological origin. Shorter day length may have lessened stress imposed by the test facility and/or by social interactions, resulting in better growth. Outstanding were the more rapid and more pronounced effects of temperature than those of photoperiod on growth of both salmonids. By the end of the first three weeks, their growth was an approximate two-four fold higher at 15 than at 5 °C, irrespective of photoperiod. Definite trends in photoperiod effects were delayed until after the initial six weeks.

Four-way factorial analysis of variance indicated that the interaction between temperature and photoperiod in summer was insignificant (P>0.05), although photoperiod effects appeared earlier and were more influential at higher temperatures. The only significant



Fig. 33. Mean $\pm 95\%$ confidence limits (three replicates) of specific growth rates of coho and cutthroat trout fry tested separately for the 9 test combinations of temperature and photoperiod. The growth rates are chronologically shown: in summer at each 3-wk intervals (a-d); in winter at 4-wk after initial time (a) and at each subsequent 2-wk intervals (b-d).

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(P < 0.01) interaction was that between temperature, time and species: growth rates decreased over time, at a faster rate at higher temperatures and differently between species. From the beginning to the end of the experiment maximum growth decreased from 3.4 to 1.2%/day in coho, and from 2.2 to 1.4%/day in trout. Deceleration of growth was probably related to increasing size and/or age of fish and parallels findings by Brown (1946) and Laarman (1969). Final acceleration of summer growth for both coho and trout was highest at 15 °C--16-hr-light and lowest at 5 °C--8-hr-light.

Winter growth of allopatric coho and cutthroat trout fry, for the diagonal points of the test space, were similar in pattern but differed strikingly in magnitude (Table 18). As in summer, growth of sooth species was strongly accelerated by temperature compared to that of photoperiod, but coho grew almost twice as fast as trout. Final optimum conditions for acceleration of coho growth coincided at test combinations that were seasonally in phase, being best at those of lower temperature and shorter photoperiod (Fig. 33). Photoperiod seasonally out of phase in winter inhibited coho growth at low temperatures. Minimum growth for coho at the 15 °C level in the final stage was largely attributable to the negative effects of smoltification on growth (Wagner 1974). As in summer, in winter the interactive effects between temperature and photoperiod on growth were not significant (P > 0.05), whereas those of temperature and time were significant (P < 0.01); both salmonids showed a near twofold decrease between their initial and final maximum rate of growth.

Table 18. Coho and cutthroat trout fry mean rate of growth \pm 95 confidence limits for a 3 X 3 temperature and photoperiod test space.

Temperature (C)	Photoperiod (hr of light)	Growth (% / day)			
		Allopatry		Sympatry	
		Coho	Trout	CCoho	Trout
		a) <u>In</u>	summer		
5 5 10 10 10 10 15 15 15	8 12 16 8 12 16 8 12 16 16	$\begin{array}{c} 0.85 \pm 0.24 \\ 0.94 \pm 0.06 \\ 1.10 \pm 0.13 \\ 1.48 \pm 0.31 \\ 1.59 \pm 0.09 \\ 1.59 \pm 0.12 \\ 1.84 \pm 0.60 \\ 4.80 \pm 0.43 \\ 1.69 \pm 0.39 \end{array}$	$\begin{array}{c} 0.80 \pm 0.14 \\ 0.71 \pm 0.10 \\ 0.92 \pm 0.07 \\ 1.06 \pm 0.17 \\ 1.33 \pm 0.20 \\ 1.36 \pm 0.20 \\ 1.34 \pm 0.27 \\ 1.66 \pm 0.26 \\ 1.69 \pm 0.20 \end{array}$		
		b) <u>In</u>	winter		
5 5 5 10	8 12 16 8	1.12±1.02 1.09±1.92 0.85±0.97 2.00±1.54	0.65±0.22	1.19±0.17	0.57±0.06
10 10 15 15 15	12 16 8 12 16	1.86±1.84 1.85±1.38 2.00±3.01 2.17±3.58 1.90±2.89	1.26±0.29	1.94±0.45	1.14±0.18
T2		1.90±2.89	1.49±0.29		

In both summer and winter, the average rate of growth of coho and cutthroat trout was lowest at 5 °, intermediate at 10 ° and highest at 15 °C (Table 18). In summer and winter, respectively, daily acceleration of growth for coho in allopatry ranged from 0.85-1.84% and from 0.85-2.17%; those for trout ranged from 0.80-1.69% and from 0.65-1.49%. Overall, photoperiod effects were some three-fourfold less influential than those of temperature, regardless of season. Considering both salmonids, average photoperiod effects on growth acceleration ranged from 0.17-0.26%/day, whereas those of temperature ranged from 0.75-1.04%/day. Sympatrically, daily growth rates for the experimental period in winter were slightly more for coho and less for trout than their respective growth in allopatry (Table 18). Ranking of growth in sympatric trials also remained unchanged with coho growing about twice as fast as trout at both the 5 and 10 °C test combinations.

CONDITION FACTOR

Patterns of summer condition factor over the test space resembled those of specific growth (Fig. 34). In both species fish were in better condition at test combinations of higher temperature and longer photoperiod, with maximum condition at 15 $^{\circ}$ C and 16-hr light. More pronounced in coho than in trout was a second peak in body condition at 10 $^{\circ}$ C and 8-hr light which probably reflects the influence of short photoperiod on fish social interactions. Aggression was particularly high in coho and interaction with photoperiod on condition factor is suspected.



Fig. 34. Mean condition factor of coho and cutthroat trout fry tested separately for the 9 test combinations of temperature and photoperiod. Initial fish condition is shown at a). Subsequent time intervals (b-e) are as in Fig. 33 (a-d).

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Changes in condition over time we're consistently positive in both salmonids but considerably higher in coho. Final average condition factor over the test space was 1.162 for coho and 0.967 for trout, their initial differences in condition being negligible. Ultimately, condition factor ranged from 1.08 to 1.25 in coho and from 0.87 to 1.06 in trout, being minimal in both cases at the low temperature combinations.

Condition factorooficoho and trout in summer was analysed by four-way factorial analysis of variance. Like growth rate, salmonid condition showed a highly significant difference between species (P < 0.01) and pronounced effects of both temperature and time (P < 0.01) on condition factor relative to those of photoperiod (P > 0.05). Temperature interactions with both time and photoperiod were also significant (P < 0.01) due to condition factor increasing more rapidly at the higher test combinations. Variance in condition factor over the entire test space was approximately two times greater in coho than in trout, but in both cases variances increased with time and at increasing temperature and photoperiod.

In winter, coho in allopatry were initially in slightly better condition than were trout and this difference was magnified approximately twofoldd within the first 6 wk; average condition factor for coho increased from 1.050 to 1.172; for trout from 0.956 to 1.022. Coho condition factor increased significantly at rising temperature (P<0.01) and at shortening photoperiod (P<0.01), showing a maximum at 15 °C and below 16-hr light. This coincided with the onset of smoltification of the

larger fish and parallels the decrease in condition factor reported by Wagner (1974) in steelhead trout. As trout in allopatry were tested only at the diagonal points of the test space, temperature and photoperiod effects could not be separated. Trout condition factor was lowest at 5 °C and 8-hr light.

Comparisons of coho and trout condition factors in sympatry were limited to trials at 5 °C--12-hr light and at 10 °C--16-hr light. Condition of both species was slightly less in sympatry than in allopatry, but interspecific differences were similar in both experimental groups; coho were in much better body condition than were trout.

HIERARCHICAL EFFECTS ON GROWTH

Relative size within each trial was probably the most important factor influencing the growth of individual fish. Although the range in size of the test fish was initially restricted, a maximum range of 17 mm was unavoidable in some trials due to the large numbers of fish needed. Size disparity probably accelerated establishment of size-dependent social hierarchies and an individual's growth rate presumably was largely determined by its rank.

In all allopatric trials, the larger fish consistently grew faster than the smaller ones during both summer and winter. By length, mean summer growth of the largest fish (presumably the social dominant) in allopatry was similar for coho and trout as exemplified in trials at the diagonal points of the test space (Fig. 35). However, in winter the



Fig. 35. Growth comparisons by length of the largest coho (\bullet), the largest cutthroat trout (\blacktriangle) and the group mean of coho (\circ) and of cutthroat trout (\bigtriangleup) fry, in allopatry, at each of the three diagonal points of the test space in summer and winter.

largest coho in any one trial grew more rapidly than did trout particularly at 10 and 15 °C, at which coho increase in length doubled that obtained by trout. For both species in most trials, the final differences in size between the largest fish and the mean size of all test fish per trial was about double that of their initial size difference in both the summer and winter experiments.

In sympatry, the absolute gain in weight of the largest fish in both species was approximately twofoldi less than that in allopatry for the same test conditions. However, ranking of interspecific growth in sympatry remained unchanged from that in allopatry, with coho growing faster than trout at both 5 and 10 $^{\circ}$ C (Fig. 36). In most trials, the final mean weight of the largest trout was less than that of the smallest coho, although their initial weights were comparable. The prevailing hierarchical growth pattern in sympatry was coho at the top and trout at the bottom.

DENSITY EFFECTS ON WINTER GROWTH

In winter, densities of stream populations of juvenile salmonids in specific habitat sites (log jams at meanders, undercut root mats of trees, backwaters, etc.) may be relatively high (Hartman 1965b, Bustard and Narver 1975a, Glova and Mason 1977b). Under such conditions growth of fish may be lessened, particularly through greater competition for a limited winter food supply. I tested the null hypothesis that there is no difference in winter growth of coho and cutthroat trout fry





both in allopatry and in sympatry at low, medium and high density levels (14, 7 and 3.5 ℓ living space per fish, respectively), fed a minimum food ration. Daily feeding rates were well below optimum and consisted of chopped fresh-frozen euphausiids at 2.0% of their wet body weight. Three replicates per each treatment were done in the period 30 January-19 March, 1975, in clear plexiglass tanks (58 x 48 x 20 cm), each partitioned into three compartments with flowthrough screens for allopatric and sympatric trials. Water temperature was maintained at 10 °C and photoperiod at 12-hr light. Mean starting weights ranged from 3.1-3.8 g for coho and from 2.8-3.5 g for trout.

Their daily weight gain showed a density-dependent relationship; relative growth in both species was approximately two-fold greater at low than at high densities in both allopatric and sympatric trials (Table 19). Lessened growth at higher densities may have resulted from an increase in their maintenance requirements primarily in response to greater social dissipation of energy. Species aggressive interactions were not quantified but were noted to be intense duringfeeding periods; these appear to have had the greatest influence on growth at the medium density level, in which both species gained approximately 15% less weight in sympatry than in allopatry. Further, when fed a minimum food supply, weight gained by trout was generally higher than that of coho, particularly at the higher density levels in sympatry. During feeding, coho became highly aggressive while trout were more inclined to scramble for food.

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Table 19. Mean winter growth of coho and cutthroat trout fry at three different densities, fed a submaintenance ration for seven weeks: C, coho; T, trout.

per fish	% weight gain ± S.E.		
	Allopatry	Sympatry	
3.5	C 24.5 ± 12.2 T 39.1 ± 7.5	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	
7	C 56.1 ± 14.8 T 55.7 ± 7.1	41.4 ± 13.6 40.2 ± 5.7	
14	C 59.6 ± 18.7 T 52.6 ± 5.1	64.7 ± 47.5 74.3 ± 3.2	

DISCUSSION

TEMPERATURE AND PHOTOPERIOD EFFECTS ON GROWTH

Growth of underyearling coho salmon and coastal cutthroat trout over the range of test combinations of temperature and photoperiod, was similar in pattern but not in magnitude. Coho grew faster than trout in most of the test combinations, but particularly at those above 5 °C. The higher growth rates observed for coho may reflect the summation effects of a number of underlying physiological and behavioral interspecific differences. Possible differences in food consumption rates may have been an important factor. Cutthroat trout fry in general show a much slower conditioning response to artificial environments than do coho. As maintenance requirements are positively related to temperature up to a certain limit (Brown 1957), initially, food intake by trout might have been below that required for maximum growth, particularly at the higher temperatures. Further, better growth by coho might also be coupled to a higher food conversion efficiency than in trout. No data are available forfurther qualify this statement. Also a reduction in swimming activity at rising temperatures has been suggested to compensate for increases in basal metabolism (Kelso 1972; Brown 1946), keeping energy budgets in check. However, in this study, a lesser energy expenditure for coho than for trout in the test facility is doubted due to the more intense aggressive activity of the former. Aggression in coho was found to be at least. threefold higher than in trout at all three test temperatures (Glova and Mason 1976c). Thus, social dissipation of energy through aggressive activity alone would seem to be higher for coho than for trout. However, trout might have dissipated more energy than coho through general stress imposed by the test facility.

Temperature effects on growth of coho and cutthroat trout fry were far more pronounced and more rapid than those of static photoperiods during summer and winter. Within a minimum period of 3 wk, I obtained maximum temperature acceleration of specific growth rates, which were at least twofolds higher at 15 than at 5 °C. The relative effects of temperature and photoperiod in this study agree with those of Huh et al. (1976) for age 0+ walleye, Stizostedium vitreum, one of the few comparable experiments in the literature. Clarke^b recently obtained a similaripattern oferelativeleffects of temperature and photoperiod on growth of coho fry in spring, but higher growth rates than those of the present study. I obtained average growth rates for coho of 0.96, 1.55 and 1.78%/day for 12 wk at 5, 10 and 15 °C. respectively, in summer. Clarke obtained growth rates of 1.85, 2.58 and 3.01%/day for 13 wk at 8, 11.5 and 15 °C. Both of these experiments used fish of comparable initial weights (0.6-0.8 g) but differed in other respects; Clarke used a diet of Oregon Moist Pellet, large tanks with circular flow and dynamic photoperiod (similar to that of natural photoperiod but accelerated in time), whereas I used a diet of zooplankton, small tanks with thru flow and static photoperiod. In my experiments, tank size, shape and flow pattern may have permitted important behavioral influences on growth.

Clarke, C. Letter dated 24 August, 1977. Pacific Biological Station, Nanaimo, B. C.

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Unlike the direct effects of temperature on metabolic activity (Fry and Hart 1948; Brown 1946; Schaeperclaus 1933), photoperiod regulation has been postulated to act indirectly on fishes via the endocrine system (Saunders and Henderson 1970; Gross et al. 1965; Hoar 1957), thus requiring longer exposure time for measurable effects to occur. The rate of photoperiod response in this study was temperaturerelated, being more rapid at the higher temperatures. Minimum exposure time for definite trends in photoperiod effects on patterns of salmonid growth was about 8 wk. Gross et al. (1965) obtained more marked photoperiod effects on growth in 2- to 4-yr-old green sunfish within 6 wk, but their experimental temperatures went to a high of 25.5 °C. These authors suggest that dynamic photoperiod, rather than static, might obtain more pronounced stimulative or inhibitive effects on growth. In my study, prior acclimation to test photoperiods might have accelerated and possibly magnified the photoperiod effects.

My findings demonstrate definite shifts in the optimum conditions for coho growth, and possibly the same for trout, between the summer and winter periods. In summer, optimum conditions for growth occurred at combinations of high temperatures -- longer photoperiods, whereas in winter there was a shift toward combinations of intermediate temperatures -- shorter photoperiods. Such shifts in growth responses parallel those of seasonal growth cycles of fish in north temperate regions. Further evaluation requires consideration of the possible influence of prior temperature-photoperiod history on the experimental fish. The summer stock had prior exposure to both naturally increasing water temperature and daylength; the winter stock had prior exposure to

reverse conditions. The observed stimulative and inhibitive effects of longer photoperiod on growth in the summer and winter periods, respectively, suggest prior phototropic exposure may be an important consideration in growth studies, as suggested by Phillips (1969). I conclude, at least for static photoperiods, that growth rate is likely to be less for fish exposed to photoperiods seasonally out of the phase, all other factors being equal. The precise role of photoperiod as it may affect growth remains unknown, but activation of the pituitary gland via light manipulation (Pickford and Atz 1957), and occurrence of specific growth hormone in fish pituitary gland (Hoar 1957) have been demonstrated, and shown to vary seasonally in quantity in accord with higher growth rates in spring and summer (Swift and Pickford 1962). Photoperiod control of growth hormone production may in part regulate protein and/or fat synthesis in fish as speculated by Gross et al. (1965).

ECOLOGICAL IMPLICATIONS

Growth comparisons between underyearling coho salmon and coastal cutthroat trout in the laboratory differed from those observed in natural sympatric populations in small streams. In the laboratory, when tested separately and fed an excess ration, coho grew faster than trout at most of the temperature/photoperiod test combinations. In streams, growth of trout appears to be less affected by being sympatric than is coho. Despite possible interspecific competitive disadvantages to trout, associated with their later emergence, and smaller body size at emergence, growth of trout was higher, than that of coho (Glova and Mason 1974, 1976b). Better growth by trout in streams, may at least in part, be due to their greater behavioral diversity in feeding and microhabitat use, permitting greater potential exploitation of foods than by coho. For example, the trout's ability to forage on both drift and benthos (Mason and Machidori 1976) offers an obvious feeding advantage when the food supply is limited. Further, this study and other studies (Chapman 1962; Mason and Chapman 1965) have shown that coho fry are highly aggressive. The dissipation of energy in social interactions in my two study streams@might have been considerably higher by coho than by trout, depressing the growth of the former. Such interspecific differences may have assisted in closing the size gap between the young-of-the-year among populations of these two salmonids.

CHAPTER V. GENERAL DISCUSSION AND CONCLUSIONS

The niche of juvenile coho salmon and of coastal cutthroat trout in small streams broadly overlap. These two salmonids are generalized exploiters of stream resources, trout slightly more so than coho, possibly due to their social subdominance in interspecific competitive interactions. The behaviorally flexible feeding and microhabitat responses of these salmonids, may in large part, be manifested in the instability and heterogeneity, both spatially (diversity of habitat) and temporally (within the same space), of small streams in general. Sanders (1968) suggested that in severe and unpredictable environments, species adaptations are primarily in response to the physical environment, resulting in broadly overlapping niche development. On the other hand, in benign and predictable environments, adaptations are primarily to other organisms, yielding narrowly overlapping niches of populations. It is commonly accepted that generalists are favored in fluctuating environments, while specialists are favored in stable ones (Schoener 1969).

The small stream environment seems to offer few discrete spatial and trophic choices to fish -- they are either riffle- or pooldwellers, feeding on drift or benthos, or both. Accordingly, the niches of sympatric species broadly overlap. This study and others (Andersen and Narver, 1975; Mason and Machidori 1976) have adequately documented that fish biomass in small coastal streams of British Columbia is typically dominated by two salmonid species (a drift feeder, and a drift

and benthic feeder) and sculpins (benthic feeder). The food niche of the more generalized salmonid (the drift and benthic feeder) broadly overlaps with those of its cohabitants as shown by Mason and Machidori (1976).

In small streams, competition between fish species may reduce fish diversity through lack of opportunities for niche specialization. Menge and Sutherland (1976) suggest that competition may be the dominant organizing interaction in trophically simple communities, whereas predation may be dominant in trophically complex ones. During the late summer period of low streamflows, competition between species continues to remain an elusive phenomenon to demonstrate experimentally on the basis of accepted concepts (Birch 1957, Milne 1961). Its presence in nature, however, may be implicated by, for example, the frequently low condition factor for salmonids (Glova and Mason 1976a), the substantial increase in coho growth and survival with supplementary feeding in streams (Mason 1976), and by the up to ten-fold higher biomass for allopatric than for sympatric populations of cutthroat trout (Glova and Mason 1977c).

Habitat segregation between stream populations of coho and cutthroat trout during the seasons of rapid growth presumably functions to reduce interspecific competition for resources. Competition is seen to be of the exploitative or interference type (Brian 1956; Case and Gilpin 1974). Segregation may stem from interference when one species learns from experience that resources are less easily secured in habitats frequented by the other species, or of the offensive nature of the other species (e.g. aggression) odor). For example, Randall (1978)

reported that although sympatric populations of Microtus montanus and M. longicaudus in eastern Washington rarely showed strong aggressive encounters, the latter tended to be excluded from its preferred grass habitat by its greater propensity to withdraw from the larger and socially dominant, montanus. Alternatively, segregation may occur when one species is more efficient than another in exploitation of a specific resource (e.g. food, space) as illustrated for example, by Nilsson (1967) for salmonids and by Heinrich (1976) for social insects. Of these two types of competition, I consider the exploitative strategy to be of lesser importance in the segregation process between sympatric populations of coho and cutthroat trout. Habitat shift, by trout from their preferred pool space to riffles when in sympatry with coho, do not appear to be due to their lesser efficiency than coho in resource exploitation in pools, but rather to social subdominance. Trout in allopatry appear equally adept as coho in feeding and in utilizing cover in pools. In riffles, however, trout might be considered a more efficient exploitor of resources than coho, as reflected in their ability to utilize both passive and active foraging, and to also use submerged cover. Coho use of riffles involves short-term exploitation of food resources more limited by decreasing water temperature and increasing velocity than in the case of trout.

Matual agonistic interference between coho and cutthroat trout in this study appears in large part to account for partitioning of resources (e.g. food, habitat), as documented by Hartman (1965b) for fry of sympatric coho and steelhead trout. The highly aggressive and

socially dominant coho is an effective interference competitor against either trout species in pools and other slow-water habitats. Conversely, the equally aggressive but socially subdominant cutthroat and steelhead trout appear to exert a similar interference against coho in riffles and other fast-water habitats. These reciprocal outcomes of interspecific interaction render unprofitable utilization of resources in habitats in which the other species has adaptive competitive advantages. Hydromechanically, the predominant aggressive behaviors and relative body positioning with respect to the streambed for trout (nipping, positioning nearer to streambed) are more suited to faster velocity habitats, whereas those for coho (threat displays, positioning nearer to water surface) are more suited to slower velocity habitats. Additionally, species rates of aggression differ within habitat types, coho being more inclined to defend pools and trout to defend riffles when in sympatry. Werner and Hall (1977) concluded that agonstic interference largely accounts for habitat segregation between sympatric populations of centrarchids in lakes and ponds.

Southwood (1977) in a thorough review on the subject of ecological strategies in nature, concluded that each arises from the evolutionary "trade-offs" of costs versus benefits in the process of adaptation to habitats. Interference between sympatric coho and cutthroat trout, may in part, be energetically governed; i.e. trout may be restricted to microhabitats in which interference is energetically unprofitable to coho. The cost of maintaining social dominance over trout in fast-water and marginal stream habitats may exceed the benefits (food, shelter) to coho. Structurally complex environments (e.g. riffles)

might also decrease the foraging efficiency of a predator as shown for juvenile rainbow trout (Ware 1972). In this context, pools might permit more efficient feeding by coho and by salmonids in general, than do riffles. As invertebrate drift comprises a major portion of the diet of juvenile coho (Mundie 1969, 1971), the more complex array of submerged cover and of higher velocities in riffles than in pools, might reduce their foraging efficiency on drift. Moreover, Case and Gilpin (1974) emphasize that if the interference competitor is to be able to dominate or exclude the exploitation competitor, it must do so in those habitats in which the carrying capacity is highest for populations of both species. This argument is consistent with my findings; coho socially minimize the cutthroat trout's use of pools, the habitat in which salmonid carrying capacity is typically some threefold higher than in riffles.

In streams, the pool environment appears to be the most predictable of habitats for rearing of fish. The species having priority of access to stream resources, will in all probability, maximize its competitive fitness in pool habitats. The earlier emerging and socially dominant coho are competitively oriented to habitats (e.g. pools, glides) at the rich end of the resource gradient, while the later emerging and socially subdominant trout are so at the impoverished end (submarginal rearing habitats). Coho is a "sit-and-wait" predator on invertebrate drift in pools, and may face food shortages due to diel patterns of drift abundance (Waters 1969; Mundie 1971) and low drift rates during summer minimum streamflows. Cutthroat trout is a more generalized "searching" predator, capable of cropping the drift and grazing the benthos in both

fast and slow water habitats. The greater breadth of food and microhabitat niche of trout than of coho may allow them greater opportunism in exploitation of resources. Heinrich (1976) suggested that the optimal foraging strategy for any species will ultimately be tested during times of lowest, not highest resource availability. In streams, this occurs during the summer period of low streamflow, the season when densities, metabolism and food requirements of fish populations may all be high relative to the available food supply. Under such conditions, fish in riffles may show more rapid growth than those in pools. Food shortages for salmonids in some streams is seen to be wrought through summer low flows as was emphasized more than a decade ago by Roderick Haig-Brown (1964) -- "stability of flow, especially enough flow in the summer months, is probably the most critical factor, since the young fish spend a full year or more feeding in a stream before migrating to sea; a very low summer flow will mean losses through starvation".

Predation and cannibalism, although not investigated in this study, may significantly influence the pattern of segregation between stream populations of juvenile salmonids. Lindstrom (1962) emphasized that the differential ability of fish to avoid predators in different situations, may reinforce segregation of sympatric prey species. In stream simulator studies, young salmonid fry are readily consumed by adult sculpins (Patten 1977) and by presmolt salmonids (Glova, unpublished data); both predators are commonest in sites of deeper water with adequate cover in natural streams. Both Patten's and my work identified relative body size and learned avoidance behavior as important factors counteracting predation. The possibility that size-related patterns of micro-

habitat use of coho and of cutthroat trout fry in streams, may in part, represent a predator avoidance behavior cannot be precluded in this study. Habitat segregation, while due to the outcome of social interactions in the stream simulator, might in nature be reinforced through size selective predation. Unlike coho, the smaller and more generalized trout may find the shallower water habitats an effective refuge from possible predators as well as one from the socially dominant coho in pools. Symons and Heland (1978) found that in some Atlantic salmon (<u>Salmo salar</u>) populations of New Brunswick, age 1+ fish (fork length > 10 cm) reduced the number of underyearlings in the deeper riffle habitats, by chasing them, and occasionally by catching and eating them. Bohlin (1977) showed a similar size segregation for a population of juvenile sea trout (<u>Salmo trutta</u>) in a closed area of a small stream, with the larger age 1+ fish being most common in deeper water areas and age 0+ fish in shallow, smooth-bottom riffles.

In summary, juveniles of coho salmon and coastal cutthroat trout are viewed as generalized exploiters of stream resources, possibly in response to spatial and temporal heterogeneity and unpredictability of small stream environments in general. Accordingly, sympatric populations of these two salmonids show broad overlap in resource use. Partitioning of resources is predominantly through physical habitat rather than trophic dimensions, and varies seasonally. Overlap in microhabitat use is least during the late summer period of low streamflow when coho concentrate in pools and trout in riffles, the season when water temperatures are warm and populations of these salmonids are typified by elevated levels of metabolism, food requirement, aggression and density.

Conversely, overlap in microhabitat use is greatest during the winter period of high streamflow and cold water temperatures, with both salmonids seeking cover predominantly in pools, the season when populations show reversed levels to the above phenomena in summer. Allopatrically, both species prefer pools irrespective of season. While a number of mechanisms may contribute to their segregation seasonally, that of mutual agonistic interference within habitat types appears to be most important. Laboratory growth of coho surpasses that of trout, regardless of season and of temperature/photoperiod conditions. In nature, the reverse pattern of interspecific growth in summer might be attributable to higher social dissipation of energy and to lesser food availability for coho in pools than for trout in riffles. Comparison of body size and biomass of allopatric and sympatric cutthroat trout populations suggest that populations of the latter type might be resourcelimited through interspecific competition from coho or sculpins, or both.

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		0	N	D	J	F	М	A	М	J	J	A	S	0	
Mdd	Chlorides Calcium Magnesium Sodium Potassium Diss. Iron T.D.S. Sulphates	210.0 97.0 3.4 0.1 523.4 27.0	3.6 2.1 0.4 1.7 0.1 - 28.2 4.1	1.9 1.8 0.4 1.6 0.2 0.1 37.5 2.8	13.6 5.6 1.0 5.6 0.1 0.1 59.0 5.1	6.8 2.9 0.3 3.0 0.1 0.1 32.7 4.8	4.2 2.3 0.5 2.2 0.1 0.1 37.4 5.8	4.2 3.1 0.2 2.8 0.2 0.1 31.9 7.0	9.6 4.8 0.9 6.2 0.2 0.1 49.7 7.4	12.8 5.8 1.0 5.8 0.2 0.1 53.0 3.0	31.8 - - 0.1 21.2 3.0	33.6 16.5 3.5 18.0 0.4 0.1 - 3.2	63.5 20.0 3.2 23.0 0.6 0.1 210.3 5.6	57.8 25.0 4.3 22.0 0.2 0.1 228.3 4.8	
g-at/L	Nitrates Phosphates Ammonia Silicates	11.2 0.8 7.1 107.9	8.9 0.3 0.5 30.0	7.6 0.2 0.5 34.1	9.2 0.2 1.8 142.6	5.2 0.1 0.6 95.0	3.1 0.4 0.3 71.1	1.5 0.1 0.1 75.0	0.3 0.1 0.3 107.9	3.6 0.2 0.3 87.6	- - 0.6 -	10.6 0.1 0.1 111.2	10.0 0.1 200.9	1.1 0.2 0.4 203.4	

Appendix Table 1. Monthly water chemistry of Bush Creek over a 1-yr period, 1973-74

	0	N	D	J	F	M	A	М	J	J	A	S	0
Chlorides Calcium Magnesium Sodium Potassium Diss. Iron T.D.S. Sulphates	40.0 9.1 1.3 8.0 0.3 0.1 99.5 7.0	2.6 2.0 0.4 1.1 0.1 - 13.7 4.1	$1.5 \\ 1.3 \\ 0.3 \\ 0.9 \\ 0.1 \\ 0.1 \\ 28.1 \\ 2.7$	5.4 3.8 0.6 2.6 0.2 0.1 40.6 5.2	2.2 2.2 0.4 1.1 0.1 0.1 24.0 4.3	2.0 1.8 0.4 1.2 0.1 0.1 28.7 5.2	1.62.00.11.20.20.121.56.8	$\begin{array}{c} 3.0 \\ 2.3 \\ 0.4 \\ 1.6 \\ 0.1 \\ 0.1 \\ 24.5 \\ 6.8 \end{array}$	$\begin{array}{c} 3.0 \\ 2.4 \\ 0.4 \\ 1.6 \\ 0.1 \\ 0.1 \\ 22.9 \\ 2.6 \end{array}$	13.2 - - 0.1 15.1 1.8	37.8 16.5 3.2 11.5 0.5 0.1 - 4.3	31.5 14.0 2.2 11.0 0.5 0.1 136.7 7.4	36.2 19.5 3.4 14.5 1.0 0.1 164.8 5.7
Nitrates Phosphates Ammonia Silicates	11.1 0.9 5.9 112.9	9.4 0.3 0.3 22.8	4.1 0.2 0.3 14.1	7.1 0.1 1.2 110.6	4.2 0.1 0.4 69.0	2.4 0.3 0.2 52.4	0.6 0.1 0.1 74.5	0.3 0.1 0.1 93.1	$1.0 \\ 0.1 \\ 0.3 \\ 36.6$	- 0.1	0.1 0.1 101.0	13.0 0.1 175.4	11.9 0.1 1.1 96.3

	÷			-		•									Tr	out		
						Т	otal fisi	h									••	All ages combined
		Water	;					% Biom	155							- Age Ο (π	m)	(mm)
	Area m ²	depth cm	Vel. cm/s	N	N/m²	g/m²	Trout	Coho	Sculpins		N	N/m²	g/m²	·% age 0	%≥. age 1+	Mean F.L. <u>+</u> S.E.	Range	Mean F.L. <u>+</u> S.E.
			·															
										POOLS								•
						÷		•		<u>1974</u>								
	27	40	6 7	192	71	74	10.7	72 0	173		14	0.5	0.8	70	21	45 1 + 0 03	13-52	55 7 1 1 0
	29	14	9.5	211	7.1	8.6	8.5	58.9	32.6		17	0.6	0.0	100	-	44.6 ± 1.02	32-49	44.6 ± 1.02
	57	19	8.9	183	3.2	4.3	4.2	38.4	57.4		8	0.1	0.2	100	· _	44.6 + 0.82	36-55	44.6 + 0.82
	24	18	7.1	174	7.3	9.5	2.2	44.8	55.0		4	0.2	0.2	.75	25	45.3 + 1.03	40-50	47.0 + 1.05
	22	21	5.0	101	4.5	6.2	10.5	33.3	56.2		9	0.4	0.7	100	-	41.3 ± 0.40	35-46	41.3 ± 0.40
x , _z	32	22	7.4	861	5.8	7.2	7.2	49.5	43.7		52	0.4	0.5	91	9	46.2 <u>+</u> 0.84	32-55	46.6 <u>+</u> 0.86
								, , , , , , , , , , , , , , , , , , ,	· · · ·							· .		
	۰.					-				1975								
	37	36	54	190	5.0	92	37	÷ 26 ≟	69 9		8	0.2	0.3	75	25	69 1 1 1 56	27 64	573,654
	23	15	5.0	159	6.6	10.0	9.2	29.8	61 0		12	0.2	0.0	83	25	40.1 ± 1.00	35-55	5984690
	59	· 40	3.8	218	3.7	5.8	18.3	33.1	48.6	1.11	28	0.5	1.1	79	21	46.5 ± 1.09	33-63	64.2 + 8.09
	54	54	4.5	123	2.3	3.3	13.0	25.2	61.8		18	0.3	0.4	89	11	47.8 + 0.96	38-64	53.0 + 3.96
	53	47	3.5	171	3.2	4.8	7.7	39.6	52.7		12	0.2	0.4	85	15	49.8 ± 1.30	38-61	57.9 ± 6.30
Χ, Σ	45	38	4.4	861	4.2	6.5	10.4	30.8	58.8		78	0.3	0.6	82	18	47.5 + 1.18	33-64	58.4 + 6.38

Table 3. Summary of statistics for fish populations and related stream physical parameters in Bush Creek, September-October 1974 and 1975.

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						· .									Tre	out		
						То	tal fís	h								Age 0 (m	m)	All ages combined (mm)
	Area	Water depth	Vel.	N	. N/m²	g/m ²	Trout	7 Biom Coho	Sculpins		N	N/m ²	g/m ²	% age 0	%≥ age l+	Mean F.L. + S.E.	Range	Mean F.L. + S.E.
											·	· .						
	•									<u>GL1DE5</u> <u>1974</u>	5					·		•
	29 43 24 27 36	11 12 12 14 12	10.3 16.4 16.1 15.9 9.2	229 237 80 81 136	7.7 5.5 3.4 3.0 3.8	10.1 6.9 4.9 3.4 4.7	5.7 9.2 5.5 13.7 7.2	24.5 40.4 13.2 49.3 42.5	69.8 50.4 81.3 37.0 50.3		11 22 6 12 11	0.4 0.5 0.3 0.4 0.3	0.6 0.6 0.3 0.5 0.3	100 86 85 100 91	- 14 15 - 9.	$\begin{array}{r} 41.8 \pm 1.30 \\ 52.1 \pm 1.06 \\ 49.8 \pm 0.78 \\ 49.4 \pm 0.42 \\ 50.1 \pm 0.56 \end{array}$	33-50 40-55 42-55 39-55 38-54	$\begin{array}{r} 41.8 \pm 1.30 \\ 53.0 \pm 3.50 \\ 50.2 \pm 1.20 \\ 49.4 \pm 0.42 \\ 53.0 \pm 1.7 \end{array}$
x . Σ	32	12	13.6	763	4.7	6.0	8.3	.34.0	57.8	•	62	0.4	0.5	92	8	48.6 <u>+</u> 0.82	33-55	49.5 <u>+</u> 1.6
			<u> </u>	·			, ,,			1975				··· ·		· · ·		
	21 37 25 33 32	17 10 13 9 10	10.1 14.9 11.2 8.3 8.9	161 116 79 127 97	7.6 3.1 3.1 3.8 2.9	13.1 4.3 3.3 4.1 3.5	9.8 6.7 8.8 7.8 10.3	32.7 22.6 37.9 32.2 40.0	57.5 70.7 53.3 60.0 49.7		11 9 10 14 12	0.5 0.2 0.4 0.4 0.4	1.3 0.3 0.3 0.3 0.3	62 78 100 100 100	38 22 - -	$\begin{array}{r} 49.9 \pm 1.78 \\ 43.9 \pm 1.57 \\ 44.0 \pm 1.45 \\ 44.2 \pm 1.79 \\ 45.8 \pm 1.84 \end{array}$	33-59 37-54 38-52 36-60 38-57	$\begin{array}{r} 66.2 \pm 7.7 \\ 51.8 \pm 5.5 \\ 44.0 \pm 1.4 \\ 44.2 \pm 1.7 \\ 45.8 \pm 1.8 \end{array}$
x . z	30	12	10.7	580	4.1	5.7	8.7	33.1	58.2		56	0.4	0.5	88	12	45.6 <u>+</u> 1.69	33-60	50.4 <u>+</u> 3.6
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Table 3 (cont'd)

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						Tot	al fish:											All age combine	s
		Water	,					% Biomas	ري م					*	، ۱	Age U (m	(u		
	Area m ²	depth cm	Vel. cm/s	N	N/m ²	g/m²	Trout	Coho	Sculpins	I	N	2 ^ω	/m² ag	د 0 د د 0	∕⊱ ≥ lge I+	Mean F.L. + S.E.	Range	Mean F. + S.E	
		·	•						:										
									. - 1	RIFFLES									
								•		1974									
	18	7	50.0	84	4.5	5.0	43.9	21.2	34.9		34 .1	∞.	2.2	94	9	45.5 ± 1.00	31-54	49.7 ±	1.68
	29	10	37.0	79	2.7	3.2	51.3	23.8	24.9	* 1	30 1	0.	1.6	100	•	41.7 ± 0.90	32-52	41.7 ±	0.90
	7	13	29.4	77	5.7	6.8	25.8	23.0	51.2		[]	.7	1.8	85	15	49.1 ± 1.70	34-55	55.6±	5.45
	28	= :	29.4	39	1.4	1.6	9.6	50.4	40.0	-	- - - - -		0.2	001	1	50.0 ± 1.44	42-54 60 71	50.0+	1.44
	67	71	0.02	69	۲.۲	۲.۲	c.ci	34.2	c.1c	. 1	0	0.	0.0	00	•	40.1 ± 0.00	40-11	+1 /.0+	00.0
х.	22	11	34.2	335	3.5	4.1	29.2	30.5	40.5		97 1	0.	1.3	96	4	47.0 ± 1.11	31-71	49.1 +	1.99
				-															1
										1975		•							
	26	ø	35.7	19	2.3	2.9	14.1	5.5	80.4		11 0	. .	0.4	001		48.0.+ 2.08	31-56	48.0+	2.08
	31	6	43.5	7 9	2.0	2.6	18.1	13.1	68.8		18 0	.6	0.5	100	,	45.4 ± 1.09	37-57	45.4 +	1.09
	55	10	28.6	96	1.7.	2.3	16.5	13.5	70.0		12 0	.2	0.4	75	25	41.6 ± 1.50	36-53	59.6 <u>+</u> 1	2.50
	27	11	22.7	70	2.6	2:3	20.4	17.4	62.2		18 0	. 7	0.5	100	•	43.4 ± 1.38	36-55	43.4 +	1.38
	28	7	37.0	88	3.1	3.5	12.6	18.9	68.5	·	14 0	.5	0.4	100	•	46.9 ± 1.79	37-60	46.9 +	1.79
<u>х</u> . <i>Е</i>	33	6	33.5	379	2.3	2.7 .	16.3	13.7	70.0		73 0	.5	0.4	95	5	45.1 ± 1.57	31-60	48.7 ±	3.77
										1									

		<u>.</u>	•												Tı	rout		
	·					To	tal fist	1 ·								Age O (m	m)	All ages combined (mm)
	Area	Water depth	Vel.					% Bioma					()	%	% ≥	Mean F.L.	Dance	Mean F.L.
	m ²	cm	cm/s	N	N/m²	g/m²	Trout	Coho	Sculpins		N	N/m²	g/m²	age O	age i+	<u>+</u> S.E.	Kange	<u>+ 5.E.</u>
												. *		. 1				
										POOLS								
										1974								
	24	⁽⁻ 39	6.1	89	3.6	7.5	10.9	24.3	64.8		10	0.4	.0.8	100.	-	38.6 <u>+</u> 1.30	33-46	38.6 ± 1.30
	18	33	9.8	58	3.2	7.0	11.7	13.6	74.7		10	0.6	0.8	100	-	42.4 ± 1.41	37-51	42.4 ± 1.43
	30	38	7.8	74	2.4	5.4	5.1	26.5	68.4 70.4		6 7	0.2	0.3	100	-	43.7 ± 2.30 40.0 ± 2.42	31-50	40.0 + 2.42
	24 21	25 33	6.2 8.3	57 65	2.3	5.2 7.2	6.4	19.6	77.0		· 6	0.3	0.5	100	-	41.0 ± 1.30	35-43	41.0 ± 1.30
Χ. Σ	23	34	7.6	343	2.9	6.5	8.8	20.1	71.1		39	. 0.4	0.6	100	-	41.1 <u>+</u> 1.79	31 - 51	41.1 <u>+</u> 1.7
																	•	
										<u>1975</u>								
	22	_	18.5	69	28	55	1.6	28.4	70.0		5	0.2	0.1	100	- '	37.6 + 1.50	34-38	37.6 <u>+</u> 1.5
	14	· -	12.7	57	3.2	6.0	1.3	22.2	76.5		3	0.2	0.1	100		37.7 ± 1.20	36-40	37.7 ± 1.20
	16	36	12.1	65	2.7	8.0	26.8	20.4	52.8		5	0.2	2.1	21	79	40.0 <u>+</u> 0.00	-	103.6 ± 19.9
	45	35	7.8	121	2.6	6.9	3.5	22.6	78.9		3	0.1	0.2	100	-	37.5 <u>+</u> 1.20	36-39	37.5 ± 1.2
	56	39	7.3	167	3.0	8.5	1.4	9.0	89.6		6	0.1	0.1	83	17	40.0 + 1.30	36-44	<u>49.7 ± 9.7</u>
 x. Σ	31	37	11.7	479	2.9	. 7.0	6.9	20.5	72.6		22	0.2	0.5	81	19	38.7 <u>+</u> 1.04	34-44	53.2 <u>+</u> 6.7

Table 4. Summary of statistics for fish populations and related stream physical parameters in Holland Creek, September-October 1974 and 1975.

-	ages ined		F.L. E.			1.10	1.71	2.23	1.60		0.64	0.66	6.04 1.29	2.21	
	All é combi		Mean + S.			38.6 38.2 +	+++ + 0 - 7	34.3 + 35.4 +	37.4 ±		38.3 + 41.9 +	38.8 +	44.2 + 39.9 +	40.6 ±	
	-		Range			34-42 29-43	33-45	33-46 30-43	29-46		35-40 34-59	36-43	33-43 33-43	33-59	
out		Age U (m	Mean F.L. ± S.E.			38.6 ± 1.10 37.2 ± 1.20	40.4 + 1.71	34.3 ± 2.23 35.4 ± 2.30	37.2 ± 1.71		38.3 ± 0.64 41 9 ± 2 40	38.8 + 0.66	38.2 ± 1.04 39.8 ± 1.29	39.4 ± 1.21	e e
Tro			% ≧ age 1+			- 1	1	1 1	e ,		• •	34	20	11	
			パ age O		,	100 87	100	100	67		100	66	80 100	89	
			g/m²			0.7	0.4	0.6	0.8		1.0	0.2	$0.3 \\ 0.1$	0.2	
	• .		N/m²			0.4 0.6	0.2	0.3	0,3		0.1	0.4	0.3 0.1	0.2	
			N	TIDES	1974	14	6	o v	39	1975	7 0	18	11 8	53	
		S	Sculpins		I	39.8 35.7	55.2	42.4	39.9		70.1	79.4	70.9 67.3	72.6	
		7, Biomas	Coho			39.1 33.2	35.3	44. 3 47.5	42.0		26.7	16.4	22.9 30.3	23.,8	
	tal fish		Trout			21.1	9.5	13.3	18.1		7 5 7 7	4.2	6.2 2.4	3.6	
	Tot		g/m ^z .			3.3	4.0	4.6 5.0	4.3		1.9	4.5	4.2 2.9	3.9	
			sm/m²			2.5 3.5	2.7	3.6 3.6	3.1		1.2	2.5	2.2	2.2	
			2			50 76	86	83 61	, 356		69 114	125	82 138	528	
			.Vel. cm/s			10.1	35.7	20.0 18.0	18.3		18.9	12.2	13.9 13.0	15.9	
	·	Water	depth cm			- 4	24	35 35	27		- 66	16	20 14	18	
			Area m ²		·	20	31	24 16	22		59 42	50	32 64	49	
	· ·				•				<u>x</u> , τ					11 .×.	

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Table 4 (cont'd)

Table 4 (cont'd)

$ \begin{array}{c c c c c c c c c c c c c c c c c c c $										÷					•	Tr	out		
$\begin{array}{c c c c c c c c c c c c c c c c c c c $						·	T	otal fisl	h 								Age () (1	(ann	All ages combined
$\begin{array}{c c c c c c c c c c c c c c c c c c c $			Water						% Biom	ass					-,				
$\frac{\text{RIFFLES}}{1974}$ $\frac{22}{20} = 9 - 36.6 - 50 - 2.2 - 3.5 - 11.4 - 23.6 - 65.0 - 2.0 - 10 - 1.7 - 3.7 - 4.1 - 92.2 - 1 - 0.1 - 0.1 - 0.1 - 0.0 - 45.0 \pm 0.00 - 32.45 - 45.0 \pm 0.0 - 40.4 \pm 1.43 - 32.45 - 40.4 \pm 1.4 - 24 - 22 - 40.5 - 39 - 1.6 - 2.3 - 26.5 - 20.2 - 53.3 - 11 - 0.4 - 0.6 - 100 43.5 \pm 1.70 - 35.50 - 43.5 \pm 1.7$		Area m²	depth cm	Vel. cm/s	N	N/m²	g/m²	Trout	Coho	Sculpins		N	N/m²	g/m²	% age 0	%≥ age l+	Mean F.L. <u>+</u> S.E.	Range	Mean F.L: <u>+</u> S.E.
$\frac{\text{RIFFLES}}{1974}$ $\frac{22}{22} \begin{array}{c} 9 \\ 36.6 \\ 50 \\ 20 \\ 11 \\ 40.7 \\ 20 \\ 11 \\ 40.7 \\ 20 \\ 11 \\ 40.7 \\ 20 \\ 11 \\ 40.7 \\ 20 \\ 11 \\ 40.7 \\ 20 \\ 11 \\ 40.7 \\ 20 \\ 11 \\ 40.7 \\ 20 \\ 11 \\ 40.7 \\ 20 \\ 11 \\ 40.7 \\ 20 \\ 12 \\ 13 \\ 5 \\ 41.2 \\ 21 \\ 10 \\ 24 \\ 22 \\ 40.5 \\ 39 \\ 1.6 \\ 2.3 \\ 26 \\ 5 \\ 20.2 \\ 40.5 \\ 39 \\ 1.6 \\ 2.3 \\ 26.5 \\ 20.2 \\ 53.3 \\ 11 \\ 7 \\ 5 \\ 11 \\ 39.8 \\ 159 \\ 1.7 \\ 2.5 \\ 23. \\ 15 \\ 15 \\ 13 \\ 40.5 \\ 40 \\ 10 \\ 1.7 \\ 2.5 \\ 23. \\ 15 \\ 11 \\ 34.0.5 \\ 40 \\ 1.7 \\ 23 \\ 15 \\ 37 \\ 6 \\ 44.1 \\ 103 \\ 2.8 \\ 1.9 \\ 1.6 \\ 2.9 \\ 1.7 \\ 2.5 \\ 23. \\ 15 \\ 37 \\ 6 \\ 44.1 \\ 103 \\ 2.8 \\ 1.9 \\ 16.8 \\ 1.6 \\ 81.6 \\ 1.6 \\ 81.6 \\ 1.6 \\ 81.6 \\ 1.6 \\ 81.6 \\ 1.7 \\ 7 \\ 7 \\ 1.7 \\ $. •											-			
$\frac{1974}{22}$ $\frac{22}{20} 9 36.6 50 2.2 3.5 11.4 23.6 65.0 \\ 20 11 40.7 20 1.0 1.7 3.7 4.1 92.2 \\ 13 6 41.2 21 1.6 2.2 46.7 13.9 39.4 \\ 24 22 40.5 39 1.6 2.3 26.5 20.2 53.3 \\ \overline{\chi}, \ \overline{\chi} 18 11 39.8 159 1.7 2.5 23.4 17.4 59.2 \\ 15 15 38.5 50 3.1 5.6 2.9 10.5 86.6 \\ 47 12 48.3 43 0.9 1.4 8.6 7.1 84.3 \\ 23 15 40.5 40 1.1 1.3 18.5 7.7 73.8 \\ 23 15 36.1 34 1.4 3.9 4.6 7.2 88.2 \\ 37 6 44.1 103 2.8 1.9 16.8 1.6 81.6 \\ \overline{\chi}, \ \overline{\chi} 35 12 41.5 270 1.9 2.8 10.2 6.8 83.0 \\ \overline{\chi}, \ \overline{\chi} 35 12 41.5 270 1.9 2.8 10.2 6.8 83.0 \\ \overline{\chi}, \ \overline{\chi} 35 12 41.5 270 1.9 2.8 10.2 6.8 83.0 \\ \overline{\chi}, \ \overline{\chi} 35 12 41.5 270 1.9 2.8 10.2 6.8 83.0 \\ \overline{\chi}, \ \overline{\chi} 35 12 41.5 270 1.9 2.8 10.2 6.8 83.0 \\ \overline{\chi}, \ \overline{\chi} 35 12 41.5 270 1.9 2.8 10.2 6.8 83.0 \\ \overline{\chi}, \ \overline{\chi} 35 12 41.5 270 1.9 2.8 10.2 6.8 83.0 \\ \overline{\chi}, \ \overline{\chi} 0.1 0.2 98 - 41.6 \pm 1.74 34-56 43.3 \pm 3.$											RIFFLE	S							
$\begin{array}{cccccccccccccccccccccccccccccccccccc$								• •			<u>1974</u>								
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		22	9	36.6	50	2.2	3.5	11.4	23.6	65.0		6	0.3	0.4	67	.33	56.0 <u>+</u> 2.50	34-45	57.0 <u>+</u> 2.56
$ \frac{13}{13} \begin{array}{c} 6 \\ 112 \\ 13 \\ 24 \\ 22 \\ 22 \\ 40.5 \\ 39 \\ 1.6 \\ 22 \\ 22 \\ 40.5 \\ 39 \\ 1.6 \\ 2.3 \\ 26.5 \\ 20.2 \\ 2.1 \\ 3.0 \\ 28.9 \\ 24.8 \\ 26.5 \\ 20.2 \\ 53.3 \\ \hline \overline{X}, \overline{\Sigma} 18 \\ 11 \\ 39.8 \\ 159 \\ 1.7 \\ 2.5 \\ 23.4 \\ 17 \\ 2.5 \\ 23.4 \\ 17.4 \\ 59.2 \\ \hline \overline{X}, \overline{\Sigma} 18 \\ 11 \\ 39.8 \\ 159 \\ 1.7 \\ 2.5 \\ 23.4 \\ 17.4 \\ 59.2 \\ \hline \hline \overline{X}, \overline{\Sigma} 18 \\ 11 \\ 39.8 \\ 159 \\ 1.7 \\ 2.5 \\ 23.4 \\ 17.4 \\ 59.2 \\ \hline \hline \overline{X}, \overline{\Sigma} 18 \\ 11 \\ 39.8 \\ 159 \\ 1.7 \\ 2.5 \\ 23.4 \\ 17.4 \\ 59.2 \\ \hline \hline \overline{X}, \overline{\Sigma} 18 \\ 11 \\ 39.8 \\ 159 \\ 1.7 \\ 2.5 \\ 23.4 \\ 17.4 \\ 59.2 \\ \hline \hline \overline{X}, \overline{\Sigma} 18 \\ 11 \\ 39.8 \\ 159 \\ 1.7 \\ 2.5 \\ 23.4 \\ 17.4 \\ 59.2 \\ \hline \hline \overline{X}, \overline{\Sigma} 18 \\ 11 \\ 39.8 \\ 159 \\ 1.7 \\ 2.5 \\ 23.4 \\ 17.4 \\ 59.2 \\ \hline \hline \overline{X}, \overline{\Sigma} 18 \\ 11 \\ 39.8 \\ 159 \\ 1.7 \\ 2.5 \\ 23.4 \\ 17.4 \\ 59.2 \\ \hline \hline \overline{X}, \overline{\Sigma} 35 \\ 12 \\ 41.5 \\ 270 \\ 1.9 \\ 2.8 \\ 10.2 \\ 6.8 \\ 83.0 \\ \hline \hline \overline{X}, \overline{\Sigma} 35 \\ 12 \\ 41.5 \\ 270 \\ 1.9 \\ 2.8 \\ 10.2 \\ 6.8 \\ 83.0 \\ \hline \hline \overline{X}, \overline{\Sigma} 35 \\ 12 \\ 41.5 \\ 270 \\ 1.9 \\ 2.8 \\ 10.2 \\ 6.8 \\ 83.0 \\ \hline \hline \overline{X}, \overline{\Sigma} 35 \\ 12 \\ 41.5 \\ 270 \\ 1.9 \\ 2.8 \\ 10.2 \\ 6.8 \\ 83.0 \\ \hline \hline \overline{X}, \overline{\Sigma} 35 \\ 12 \\ 41.5 \\ 270 \\ 1.9 \\ 2.8 \\ 10.2 \\ 6.8 \\ 83.0 \\ \hline \hline \overline{X}, \overline{\Sigma} 35 \\ 12 \\ 41.5 \\ 270 \\ 1.9 \\ 2.8 \\ 10.2 \\ 6.8 \\ 83.0 \\ \hline \hline \hline \overline{X}, \overline{\Sigma} 35 \\ 12 \\ \hline \hline \overline{X}, \overline{\Sigma} 35 \\ \hline \hline \overline{X}, \overline{\Sigma} 35 \\ 12 \\ \hline \overline{X}, \overline{\Sigma} 35 \\ 12 \\ \hline \overline{X}, \overline{\Sigma} 35 \\ 12 \\ \hline \overline{X}, \overline{\Sigma} 19 \\ \overline{X}, \overline{\Sigma} 19 \\ \overline{X}, \overline{\Sigma} 19 \\ \overline{X}, \overline{\Sigma} 10 \\ X$		20	11	40.7	20	1.0	1.7	3.7	4.1	92.2		. 1	0.1	0.1	100	-	45.0 ± 0.00	32-45	45.0 ± 0.00
$\frac{13}{24} \begin{array}{c} 22 40.5 29 2.1 3.0 28.9 24.8 46.3 \\ 24 22 40.5 39 1.6 2.3 26.5 20.2 53.3 \\ \hline \overline{x}, \ \overline{\Sigma} 18 11 39.8 159 1.7 2.5 23.4 17.4 59.2 \\ \hline \overline{x}, \ \overline{\Sigma} 18 11 39.8 159 1.7 2.5 23.4 17.4 59.2 \\ \hline 15 15 38.5 50 3.1 5.6 2.9 10.5 86.6 \\ 47 12 48.3 43 0.9 1.4 8.6 7.1 84.3 \\ \hline 51 13 40.5 40 1.1 1.3 18.5 7.7 73.8 \\ \hline 13 40.5 40 1.1 1.3 18.5 7.7 73.8 \\ \hline 12 37 6 44.1 103 2.8 1.9 16.8 1.6 81.6 \\ \hline \overline{x}, \ \overline{\Sigma} 35 12 41.5 270 1.9 2.8 10.2 6.8 83.0 \\ \hline \overline{x}, \ \overline{\chi} 35 12 41.5 270 1.9 2.8 10.2 6.8 83.0 \\ \hline \end{array} \begin{array}{c} 7 0.5 0.9 100 - 40.4 \pm 1.43 34-43 40.4 \pm 1.43 43-43 \pm 1.44 40.6 \pm 1.44 43.5 \pm 1.44 44.9 \pm 1.44$		13	· 6	41.2	21	1.6	2.2	46.7	13.9	39.4		7	0.5	1.0	100	-	38.7 ± 2.61	32-51	38.7 ± 2.61
$ \frac{\overline{x, r}}{\overline{x, r}} \frac{18}{11} \frac{11}{39.8} \frac{159}{1.7} \frac{1.7}{2.5} \frac{23.4}{23.4} \frac{17.4}{17.4} \frac{59.2}{59.2} $ $ \frac{1975}{32 \ 0.4 \ 0.6 \ 93 \ 7 \ 44.7 \pm 1.65 \ 32-51 \ 44.9 \pm 1.7 \ 44.$		13 24	22	40.0 40.5	29 39	2.1	3.0 2.3	28.9	24.8	46.3 53.3		11	0.5	0.9	100	-	40.4 ± 1.43 43.5 ± 1.70	34-45 35-50	40.4 ± 1.43 43.5 ± 1.70
$\frac{1975}{15}$ $\begin{array}{cccccccccccccccccccccccccccccccccccc$	<u></u> <i>x</i> , Σ	18	11	39.8	159	1.7	2.5	23.4	17.4	59.2		32	0.4	0.6	93	7	44.7 <u>+</u> 1.65	32-51	44.9 <u>+</u> 1.66
$\frac{1975}{15}$ $\begin{array}{cccccccccccccccccccccccccccccccccccc$,		
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$											1975								
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		15	15	38.5	50	3.1	5.6	2.9	10.5	86.6		5	0.3	0.2	100	-	38.4 + 2.54	34-48	38.4 <u>+</u> 2.54
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		47	12	48.3	43	0.9	1.4	8.6	7.1	84.3		8	0.2	0.1	100	-	42.6 + 1.94	36-53	42.6 ± 1.94
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		51	13	40.5	40	1.1	1.3	18.5	7.7	73.8		12	0.2	0.2	92	8	40.3 <u>+</u> 1.58	34-53	48.8 <u>+</u> 8.58
$\frac{37}{\overline{X}, \Sigma} \begin{array}{cccccccccccccccccccccccccccccccccccc$		23	- 15	36.1	34	1.4	3.9	4.6	7.2	88.2		6	0.3	0.2	100	-	43.3 ± 1.20	41-48	43.3 ± 1.20
\overline{X} , Σ 35 12 41.5 270 1.9 2.8 10.2 6.8 83.0 47 0.1 0.2 98 - 41.6 \pm 1.74 34-56 43.3 \pm 3.		. 37	. 6	44.1	103	2.8	1.9	16.8	1.6	81.6	_	16	0.4	0.3	100	- `	43.6 <u>+</u> 1.46	34-56	43.6 + 1.46
	Χ, Σ	35	12	41.5	2 70	1.9	2.8	10.2	6.8	83.0	_	47	0.1	0.2	98	-	41.6 <u>+</u> 1.74	34 - 56	43.3 <u>+</u> 3.14

															Tr	out		
						To	tal fist	l								Age 0 (m	m)	All ages combined (mm)
	Area	Water depth	Vel.					% Bioma	ass	×.		11/2	- 1-2	· ¾	% ≥	Mean F.L.	Bango	Mean F.L.
	m ²	cm	cm/s	N	N/m²	g/m²	Trout	Coho	Sculpins		N	N/m∼	g/m~	age U	age 1+	<u>+</u> S.E.	Kange	<u><u> </u></u>
																		· ·
									•	POOLS				•				
	60	55	6.2	208	3.5	21.3	0.7	11.9	87.4		7	0.1	0.1	100	-	51.7 <u>+</u> 1.87	45-57	51.7 <u>+</u> 1.87
	21	37	5.1	41	2.0	9.7	22.7	26.6	50.7		4	0.2	2.2	25	75	57.0 <u>+</u> 0.00		108.3 ± 20.50
	45	44 .	4.7	53	1.2	4.6	10.1	20.4	69.5		6	0.1	0.5	84	16	46.6 <u>+</u> 1.47	42-55	73.0 <u>+</u> 26.47
	41	44	3.8	84	2.0	6.8	25.3	21.3	53.4		8	0.2	1.7	38	62	44.7 <u>+</u> 0.50	41-47	99.9 <u>+</u> 17.50
	29	24	8.1	31	1.1	2.6	5.7	35.6	58.7		4	0.1	0.2	100	-	49.8 <u>+</u> 0.48	49-51	<u>49.8 +</u> 0.48
<u></u> π, Σ	40	41	5,6	417	1.9	9.0	12.9	23.2	63.9		29	0.1	0.9	69	31	49.9 <u>+</u> 1.08	41-57	76.5 <u>+</u> 13.36
				. <u></u>		•	•											
	•			• •						GLIDES								
	52	20	20.0	117	2,3	4.9	25.0	50.3	24.7		21	0.4	1.2	81	19	54.1 <u>+</u> 1.23	43-65	69.5 <u>+</u> 8.23
	36	19	17.3	84	2.3	-5.7	25.3	49.4	25.3		30	0.8	ľ.4	90	10	51.4 <u>+</u> 0.93	37-66	57.8 <u>+</u> 3.93
	75	25	19.5	115	1.5	5.0	20.9	31.4	47.7		39	0.5.	1.1	82	18	51.9 + 0.98	41-76	61.1 <u>+</u> 3.98
	37	17	19.5	50	1.3	7.2	9.8	9.2	81.0		- 8	0.2	0.7	63	· 37	47.2 + 1.19	38-57	71.8 + 13.19
	63	14	17.5	69	1.1	· 2.9	17.9	46.3	35.8		27	0.4	0.5	100	-	50.9 ± 1.25	39-66	50.9 ± 1.25
x , z	53	19	18.8	435	1.7	5.1	19.8	37.3	42.9		125	0.5	1.0	83	17	51.1 <u>+</u> 1.12	37-76	62.2 <u>+</u> 6.12
																	· .	
										RIFFLE	<u>s</u> .							
	29	13	46.9	39	1.4	2.6	48.İ	35.9	16.0		20	. 0.7	. 1.3	95	5	55.4 + 1.10	40-82	58.9 + 4.10
	61	15	41 2	106	1.6	3.2	37.7	43.0	19.3		48	0.8	1.2	96	4	52.8 + 0.66	42-78	55.4 + 2.66
	29	19	21 2	23	0.8	2.7	7.9	29.7	62.4		5	0.2	0.2	100	-	52.0 + 5.17	37-64	52.4 + 5.17
	28	13	23.8	29	10	1 2	45 0	31 7	23 3		15	0.5	05	100	-	48.4 + 1.64	39-62	48.4 + 1.64
	131	12	23.9	42	0.3	0.5	54.0	38.0	8.0		27	0.2	0.3	100	-	52.2 ± 0.89	44-62	52.2 ± 0.89
<u></u> Σ, Σ	56	15 ·	31.4	238	1.0	2.0	38.5	35.7	25.8		115	0.5	0.7	98	2	52.2 <u>+</u> 1.90	3 7- 82	.53.4 <u>+</u> 2.89

Table 5. Summary of statistics for fish populations and related stream physical parameters in Ayum Creek, October 1975.

	,						<u></u>	· ·				. Trout		
	,					Total í	lish				· · · · ·	Age 0 (m		All ages combined (mm)
		Water	•				% Bi	omass		2	% >	Mean F I	· · · · · ·	Mean F.L.
	Area m ²	depth cm	Vel. cm/s	N	N/m²	g/m²	Trout	Others		age O	age l+	<u>+</u> S.E.	Range	<u>+</u> S.E.
									POOLS	• *		· .	•	
	57 71 68 66 52 22	22 29 32 26 22 53	6.2 7.8 10.0 10.0 3.3	17 43 25 41 33 51	0.3 0.6 0.4 0.6 0.6 2.3	2.2 1.4 1.9 1.8 1.7 6.0	100 100 100 100 100 100	- - - -		18 95 76 88 94 78	82 5 24 12 6 22	$\begin{array}{r} 60.0 \pm 1.53 \\ 60.6 \pm 1.16 \\ 66.5 \pm 1.54 \\ 63.5 \pm 1.21 \\ 64.3 \pm 1.26 \\ 52.9 \pm 1.88 \end{array}$	63-68 50-84 51-75 47-76 53-80 36-71	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$
<u></u> Σ, Σ	56	31	7.5	210	0.8	2.5	100	_ ·		75	25	62.3 <u>+</u> 1.43	36-84	74.1 ± 3.94
						,			GLIDES					
	. 51 55 67 53 43	11 14 19 13 21	22.2 14.9 19.2 18.9	8 15 31 105 37	0.2 0.3 0.5 2.0 0.9	1.3 0.8 1.3 2.3 3.0	100 100 100 100 100		· .	25 93 93 96 81	75 7 7 4 19	$\begin{array}{c} 61.5 + 5.51 \\ 64.3 + 1.73 \\ 64.0 + 1.52 \\ 48.6 + 0.86 \\ 59.8 + 1.34 \end{array}$	56-67 55-73 51-80 29-67 49-75	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$
<u></u> . Σ	54	16	18.8	196	0.8	1.7	100			78	22	59.6 <u>+</u> 2.16	29-80	71.8 + 3.03
,			· · ·					· · ·	RIFFLES		· ·		x	· .
	32 11 17 20	11 13 8 11	33.0 40.0 40.0 36.0	15 9 23 14	0.5 0.8 1.3 0.7	0.9 1.2 1.6 1.2	100 100 100 100	-		100 90 100 100	10	$\begin{array}{r} 60.3 \pm 2.57 \\ 52.4 \pm 4.00 \\ 46.0 \pm 1.28 \\ 57.7 \pm 2.12 \end{array}$	45- 77 36-68 36-60 49-71	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$
<u></u> , Σ	20	11	37.3	61	0.8	1.2	100			98	2	54.1 <u>+</u> 2.50	36- 77	, 54.9 <u>+</u> 2, 72
									•					

Table 6 · Summary of statistics for the resident population of cutthroat trout and related stream physical parameters upstream of the barrier falls in French Creek, September 1976.

														Tro	ut		
•				<u> </u>		Total f	fish								Age O (m	um)	All ages combined (mm)
	Area	Water depth	Vel.	N	N /m2	a /m²	% Bi	Sthin		N	N /m 2	~ /=3	×.	% ≥	Mean F.L.		Mean F.L.
			cm/s			g/m		SCDK.		N	N/m~	g/m ⁻³	age U	age 1+	<u>+ 5.E.</u>	Range	<u>+ S.E.</u>
																	•
							•		POOLS			÷					
	41	33	6.4	32	0.8	3.1	97.4	2.6		31	0.8	. 3.0	68	32	59.2 + 1.03	50-70	76.0 + 4.99
	76	35	9.6	61	0.8	3.6	100	-		61	0.8	3.6	64	. 36	59.5 + 2.08	48-70	79.6 + 4.14
	39	40	5.0	42	1.1	3.3	97.8	2.2		41	1.0	3.2	78	22	57.6 ± 0.92	48-71	70.3 ± 4.12
	28	30	8.6	37	1.3	5.7	100	-		37	1.3	5.7	54	46 ·	58.2 ± 2.39	46-72	78.7 <u>+</u> 4.84
	52	28	4.0	70	1.9	4.0	82.0	18.0		58	1.6	3.3	90	10	57.8 ± 1.00	45-75	62.2 ± 2.03
			J ,2	11.2	2.2	1,4.0	97.0	2.4		90	1.8	13./	44		53.2 ± 1.72	49-88	94.4 <u>+</u> 3.89
Χ, Σ	46	36	6.1	355	1.4	5.6	95.8	4.2		324	1.2	5.4	66 .	34 ·	59.3 <u>+</u> 1.52	45-88	76.9 <u>+</u> 4.00
			•										• •				
							•		GLIDES					· .			
	64	14	17.2	33	0.5	1.2	100	-		33	0.5	1.2	88	12	59.1 ± 0.83	51-73	64.0 + 2.45
-	49	18	13.3	26	0.5	1.1	92.7	7.3		23	0.5	1.0	.83	17	58.7 + 1.02	51-67	62.5 + 2.06
	29	25	14.9	60	2.1	4.8	97.3	2.7		58	2.0	4.7	78	22	54.5 + 0.69	47-69	64.1 + 2.26
	61	19	23.8	58	1.0	2.1	98.0	2.0		56	0.9	2.0	89	11	59.0 + 0.92	47 - 72	63.0 + 1.81
	49	16	22.7	69	1.4	4.0	99.3	0.7		68	1.4	4.0	86	14	63.0 ± 0.84	53 - 83	68.7 ± 1.84
Χ , Σ	50	18	18.4	246	1.1	2.6	97.5	2.5	·	238	1.1	2.6	85	15	58.9 <u>+</u> 0.86	47 - 83	64.5 <u>+</u> 2.08
															· · · · · · · · · · · · · · · · · · ·		
	•								RIFFLES	<u> </u>					•	· · · ·	
	53	10	29.4	13、	0.3	0.6	100	-		13	0'3	0.6	92	8	61.2 ± 0.95	55-67	63 7 + 2 10
	14 .	14	20.8	47	3.3	4.9	100	-		47	3.3	4.9	94	6	52.8 ± 1.00	45-73	551 ± 1.67
	23	10	40.0	14	0.6	1.4	100	-		14	0.6	1.4	86	14	52.4 + 1.23	45-63	63.9 + 8.50
	20	9	29.4	21	1.1	1.7	100	-		21	1.1	1.7	. 90	10	54.3 + 1.65	41-68	57.0 + 2.41
	25	13	33.3	24	1.0	2.1	100	-		24	1.0	2.1	92 .	8	60.6 ± 1.08	51-69	63.0 ± 1.99
x , Σ	27	11	30.6	119	1.3	2.1	100	-	-	119	1.3	2.1	91	9	56.3 <u>+</u> 1.18	41-73	60.5 <u>+</u> 3.33
	*Denete	a atialil	a b a a la					4	•				•			······	

Table 7. Summary of statistics for the resident fish populations and related stream physical parameters upstream of the barrier falls in Bings Creek, October 1976.

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Table 8. Summary of statistics for the resident fish populations and related stream physical parameters in Shawnigan Creek (inlet), October 1975.

										,				Tro	out		
					· .	Total	fish							• <u>.</u>	Age O (n	m)	All ages combined (mm)
	Area	Water	Vel				Х. В	iomass					1.	%_≥	Mean F.L.	<u></u>	Mean F.L.
	m ²	cm	cm/s	N	N/m²	g/m²	Trout	Sculpins		N	N/m²	g/m²	age O	age 1+	<u>+</u> S.E.	Range	<u>+</u> S.E.
		<u></u>															
					· · ·				POOLS								
	63	32	3.9	15	0.2	0.6	96.4	3.6		13	0.2	0.5	92	8	61.4 ± 2.28	49-95	62.2 + 5.2
	45	42	3.4	34	0.8	2.0	78.0	22.0		30	0.7	1.6	100	-	63.9 ± 1.24	50-78	63.9 ± 1.2
	82	54	4.8	49	0.6	1.2	100	-		49	0.6	1.2	90	10	54.1 ± 1.17	42-74	60.8 ± 3.1
	70	22	2.5	58	0.8	1.7	82.6	17.4		48	0.7	1.4	94	6	58.3 ± 1.31	42-92	61.4 ± 2.3
	71	22	. 3.5	56	0.8	1.4	90.0	10.0		53	0.8	1.3	96	4	52.3 ± 1.17	39-98	57.4 ± 2.1
	97	16	3.8	80	0.8	1.5	89.7	10.3		76	0.8	1.3	95		50.3 ± 1.24	39-71	57.2 + 2.2
<u></u> x, Σ	71	31	3.7	292	0.7	1.4	89.5	10.5	•	269	0.6	1.2	94	6	56.7 <u>+</u> 1.40	39-98	60.5 <u>+</u> 2.7
									GLIDES				_				· . ·
	44	.10	9.6	2.7	0.6	0.6	100	-		27	0.6	0.6	100	-	48.7 <u>+</u> 0.81	42-59.	-
	53	23	9.9	77	1.4	2.3	79.5	20.5		74	1.4	1.8	100	· -	52.8 <u>+</u> 1.04	38-98	-
	40	11	14.9	32	0.8	0.9	100	-		32	0.8	0.9	100	-	51.0 ± 1.41	38-71	-
	22	16	13.8	23	1.0	1.2	100 ·			23	1.0	1.2	100.	-	51.7 <u>+</u> 1.77	39- 72	-
	34	5	16.6	16	0.5	0.6	80	20		14	0.4	0.4	100	-	49.6 <u>+</u> 1.70	39-61	-
Χ.Σ	39	13.	13.0	175	0.9	1.3	91.9	8.1		170	0.8	1.0	100	-	50.8 <u>+</u> 1.35	38-98	-
						· · .											
								•	RIFFLES					۰.			
	19	· 8	32.3	8.	0.4	0.5	100	-		8	0.4	0.5	100	. .	52.1 + 2.68	42-67	
	45	15	18.6	30	0.7	1.4	95.6	4.4		28	0.6	1.3	100		61.4 + 1.54	47-76	-
•	37	7	24.4	28	1.5	1.5	88	12		26	1.4	1.3	100	-	47.2 + 1.15	38-57	-
	14	12	18.2	12	0.8	0.8	100			12	0.8	0.8	100	-	48.7 + 1.92	38-62	-
	10	5	34.5	9	0.8	0.7	100		•	9	0.8	0.8	100		45.9 ± 1.66	38-52	· -
x . Σ	-25	9	25.6	87	0.8	1.0	96.7	3.3		83	0.8	0.9	100	-	51.1 <u>+</u> 1.79	38 - 76	-

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	Time period		Coho		Trout			
Experiment		Mean F.L. ±S.E.(mm)	F.L.range (mm)	%∆wt	Mean F.L. ±S.E.(mm)	F.L.range (mm)	% ∆wt	
		`æ`	Main expe	riments				
Allopatry (1)	Jun. 2-16	36.3 ± 0.19 40.2 ± 0.26 47.0 ± 1.29	35.38 39-42 43-53	+15.5 +16.0 +21.8	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	35-40 39-43 43-53	+12.8 +14.3 +15.8	
Sympatry (1)	Jun.16-23	38.0 ± 0.26 44.4 ± 0.20 53.7 ± 0.88	37-39 44-45 52-55	+ 7.7 + 8.9 +14.5	37.3 ± 0.43 44.1 ± 0.74 54.3 ± 1.67	34-39 40-46 51-56	- 3.8 + 3.6 + 3.6	
Allopatry (2)	Ju1. 7-22	$\begin{array}{r} 38.8 \pm 0.27 \\ 48.1 \pm 0.40 \\ 57.7 \pm 1.20 \end{array}$	37-41 45-50 53-60	+ 3.8 + 6.2 +12.7	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	35-41 43-46 49-53	+28.1 +12.2 + 8.5	
Sympatry (2)	Ju1.22-28	38.6 ± 0.22 46.7 ± 0.42 56.3 ± 1.20	38-40 45-48 54-58	+ 4.1 + 8.0 + 6.8	38.6 ± 0.22 45.8 ± 0.74 55.3 ± 2.68	37-39 43-48 50-59	+ 7.7 + 4.2 + 6.0	
			No food i	n system				
Sympatry (1)	Aug.11-18	$\begin{array}{r} 41.7 \pm 0.27 \\ 51.3 \pm 0.64 \\ 61.2 \pm 0.44 \end{array}$	40-43 49-53 61-62	- 9.1 -15.1 - 9.6	$\begin{array}{rrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrrr$	39-44 50-53 59-64	-13.1 -13.3 - 9.7	
Sympatry (2)	Aug.18-24	40.6 ± 0.40 51.7 ± 0.52 63.7 ± 0.88	39-43 50-53 62-65	- 4.1 - 6.0 - 4.5	39.7 ± 0.56 48.0 ± 1.38 65.7 ± 2.03	37-42 43-53 62-69	- 6.2 - 5.7 - 7.1	

Appendix Table 9. Summary of experiments conducted in the stream simulator in summer, showing fish fork length and range, and weight change data in each of the three size-classes.

Appendix Table 9 (cont'd)

			Coho	,		Trout		
Experiment	Time period	Mean F.L. ±S.E.(mm)	F.L.range (mm)	% ∆wt	Mean F.L. ±S.E.(mm)	F.L.range (mm)	e %∆wt	
		د. 	Initial 2	days of te	est period			
Sympatry	Aug.27-Sep.1	42.2 ± 0.30 49.4 ± 0.90 60.7 ± 0.33	41-43 47-54 60-61		40.7 ± 0.68 50.4 ± 0.72 58.0 ± 0.58	38-45 47-53 57-59		
		c_{c}	Relative d	ensity				
Total coho: 1 Total trout:	Sep. 1-7 -0 30	$\begin{array}{rrrr} 42.0 \ \pm \ 0.00 \\ 46.0 \ \pm \ 0.00 \\ 51.5 \ \pm \ 0.50 \end{array}$	42 46 51-52	- 3.5 + 1.9 - 5.7	39.5 ± 0.23 43.9 ± 0.46 50.2 ± 0.58	37-41 42-46 49-52	- 7.9 - 1.2 + 4.2	
Total coho: 3 Total trout:	Sep. 7-16 30 10	$\begin{array}{r} 42.9 \pm 0.47 \\ 50.1 \pm 0.53 \\ 58.2 \pm 0.20 \end{array}$	40-46 47-53 58-59	- 4.3 - 2.7 + 1.8	$\begin{array}{r} 43.6 \pm 1.03 \\ 50.7 \pm 1.76 \\ 57.5 \pm 0.50 \end{array}$	40-46 48-54 57-58	-11.7 - 8.8 -12.8	

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Appendix Table 10. Summary of experiments conducted in the stream simulator in winter showing fish fork length and range in each of the three size-classes.

		Coho		Trout			
		Mean ± S.E. (mm)	Range (mm)	Mean ± S.E. (mm)	Range (mm)		
		<u>Winter</u>					
Tested at :	3 °C						
Allopatry	Dec.2-18, 1975	50.5 ± 0.60 66.9 ± 0.45 77.7 ± 0.49	45-55 65-70 76-79	47.7 ± 0.55 59.9 ± 0.86 73.8 ± 1.56	43-53 56 - 67 71-81		
Sympatry	Dec.18-25	55.8 ± 0.58 68.6 ± 0.87 83.7 ± 1.33	52-58 65-72 81-85	53.9 ± 0.48 65.4 ± 1.36 82.7 ± 0.88	51-57 61-71 81-84		
Allopatry	Dec.25-Jan.8	58.1 ± 0.48 72.9 ± 0.41 88.7 ± 0.61	51-60 70-75 86-90	53.4 ± 0.56 63.0 ± 0.62 76.8 ± 1.08	50-58 60-67 74-80		
Sympatry	Jan.8-14	$\begin{array}{r} 60.1 \pm 0.40 \\ 70.1 \pm 0.70 \\ 90.7 \pm 3.33 \end{array}$	57-62 69-74 84-94	57.3 ± 0.54 70.0 ± 0.44 92.0 ± 3.05	54-61 68-71 86-96		
Tested at S	5 °C						
Sympatry	Jan.14-21	56.0 ± 0.83 67.3 ± 0.81 83.3 ± 3.18	51-60 64-70 77-87	55.1 ± 0.60 65.9 ± 1.08 81.3 ± 3.18	51-59 62-70 75-85		
Sympatry	Jan.21-27	57.4 ± 0.47 66.4 ± 0.65 80.3 ± 1.20	55-60 64-69 78-82	55.9 ± 0.54 64.7 ± 0.99 81.0 ± 1.53	53-59 63-69 78-83		

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