# Comparison of Coastal Cutthroat Trout Populations in Allopatry and Those Sympatric with Coho Salmon and Sculpins in Several Small Coastal Streams on Vancouver Island, B.C.

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October 1977

## Fisheries & Marine Service Manuscript Report No. 1434

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Fisheries and Marine Service
Manuscript Report 1434

October 1977

# COMPARISON OF COASTAL CUTTHROAT TROUT POPULATIONS IN ALLOPATRY AND THOSE SYMPATRIC WITH COHO SALMON AND SCULPINS IN SEVERAL SMALL COASTAL STREAMS ON VANCOUVER ISLAND, B.C.

by

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Cat. no. Fs 97-4/1434 ISSN 0701-7618

## ABSTRACT

Glova, G. J., and J. C. Mason. 1977. Comparison of coastal cutthroat trout populations in allopatry and those sympatric with coho salmon and sculpins in several small coastal streams on Vancouver Island, B.C. Fish. Mar. Serv. MS Rep. 1434: 35 p.

Biomass density and growth of summer stocks of coastal cutthroat trout populations above (allopatric) and those below barrier falls sympatric with coho salmon and sculpins were compared in six small coastal streams on Vancouver Island, B.C.

Range in mean fish biomass densities in allopatric trout populations was 1-6 $g/m^2$ ($G\bar{X} = 2.2\ g/m^2$), whereas sympatric populations of coho, trout, and sculpins combined was 2-9 $g/m^2$ ($G\bar{X} = 5.1\ g/m^2$), with trout contributing less than 1 $g/m^2$ in all habitats. Biomass density of allopatric trout populations approximated that of the combined populations of sympatric trout and coho.

Mean body size for grouped age classes and summer growth of age 0 trout were significantly less in sympatric than in allopatric trout populations.

In stream simulator studies, microhabitat use and aggressive behavior were similar for both trout types when tested separately, other than that sympatric trout defended riffle territories more vigorously, responded to the feeding cycle with greater synchrony, and used components of aggressive display hydromechanically more suited to fast water habitats, than did allopatric trout.

Key words: Allopatric, sympatric, population(s), biomass density, barrier waterfall, microdistribution, aggression, segregation, limiting factor(s), management.

## RÉSUMÉ

Glova, G. J., and J. C. Mason. 1977. Comparison of coastal cutthroat trout populations in allopatry and those sympatric with coho salmon and sculpins in several small coastal streams on Vancouver Island, B.C. Fish. Mar. Serv. MS Rep. 1434: 35 p.

La biomasse et la croissance estivales de populations de truites fardées allopatriques établies en amont de chutes de barrage ont été comparées à celles de truites fardées sympatriques cohabitant avec des saumons coho et des chabots en aval, dans six petits cours d'eau côtiers de l'Île Vancouver.

En moyenne, la biomasse des truites allopatriques a varié entre 1 et 6 g/m$^2$ ($G\bar{X}$ = 2, 2 g/m$^2$), tandis que celle des truites, des saumons et des chabots sympatriques se situait globalement entre 2 et 9 g/m$^2$ ($G\bar{X}$ = 5, 1 g/m$^2$), les truites ne comptant que pour moins de 1 g/m$^2$ dans tous les habitats. La biomasse des truites allopatriques s'approchait de celle des saumons et de celle des truites sympatriques, combinées.

La taille moyenne des truites, selon les classes d'âge, et la croissance estivale des truitelles de l'année ont été sensiblement plus faibles chez les populations sympatriques que chez les populations allopatriques.

Des expériences menées séparément dans des cours d'eau simulés ont montré que les deux sortes de truites manifestent une agressivité identique et occupent les mêmes microhabitats. Toutefois, comparativement aux truites allopatriques, les truites sympatriques défendent les territoires en eau peu profonde avec plus de vigueur, s'adaptent mieux au cycle alimentaire et, exécutent des mouvements d'agression, mieux adaptés du point de vue hydromécanique aux eaux rapides.

# INTRODUCTION

Patterns of microhabitat use between populations of sympatric juvenile coho salmon and coastal cutthroat trout have been investigated in several small coastal streams (Glova and Mason 1976a; 1976b). Their pattern of spatial segregation followed that hypothesized by Nilsson (1967) for sympatric fishes in general, and paralleled Hartman's (1965) findings for populations of sympatric juvenile coho and steelhead. To elucidate in greater detail than was possible in natural populations, patterns and mechanisms of interactions for food and space between these two salmonids in general, were investigated for experimental populations in stream simulator studies (Glova and Mason 1977a; 1977b).

In the present study we explored possible differences in biomass density of summer stocks and growth of coastal cutthroat trout populations in several small coastal streams for those above (allopatric) and below (sympatric) barrier falls, to further substantiate our assessment of the ecological influence of populations of coho on trout. Feeding and microhabitat responses of these two trout population types were also investigated in stream simulator studies to ascertain possible adaptive behavioral adjustment in trout to sympatry with coho. As gene flow across a barrier falls is downstream only, allopatric cutthroat trout above a barrier falls are not likely to possess adaptations comparable to those of their sympatric conspecifics. Populations of rainbow trout (<u>Salmo</u> <u>gairdneri</u>) separated by a barrier falls in British Columbia have been reported to differ behaviorally (Northcote 1969) and also differ meristically and biochemically (Northcote et al. 1970).

The difficulty in studying interaction between sympatric populations of coho and cutthroat trout in streams is compounded by the presence of sculpins, either <u>Cottus</u> <u>aleuticus</u> or <u>C</u>. <u>asper</u> or both. Behaviorally, sculpins appear to interact little with salmonids in streams, but their high biomass dimensions (Glova and Mason 1976b; Mason and Machidori 1976) warranted consideration of their possible influence on trout populations in this study, but were inseparable from that of coho, other than by inference, and limited to general consideration of resource partitioning.

# METHODS

## A. NATURAL POPULATIONS OF FISH

Fish population densities were estimated in six small coastal streams on Vancouver Island, B.C. (Fig. 1), during the late summer period of low streamflows. Ayum, Bush and Holland creeks contained sympatric populations of coho salmon, coastal cutthroat trout and sculpins, primarily <u>Cottus</u> <u>aleuticus</u>. The extent of fish upstream movements in each of the three streams are delimited to approximately 2 km above high tide by a waterfall: Holland has a vertical falls dropping nearly 30 m into a large deep pool below; Bush and Ayum falls consist of sequential cascades into minor pools, dropping a total height of about 10 m.

Bings, French and Shawnigan creeks upstream of their falls contained allopatric (stream resident) cutthroat trout populations, plus minor populations of the three-spined stickleback, _Gasterosteus aculeatus_, in Bings Creek and of the coastrange sculpin, _Cottus aleuticus_, in Shawnigan Creek. Coho have not been reported to occur upstream of the falls in these three streams. In Bings and French creeks, the falls are situated several km from sea, consisting of sequential cascades into pools, dropping a total height of at least 5 m. In Shawnigan Creek, a vertical falls situated near the mouth drops more than 30 m into a pool below. In Shawnigan, the trout population sampled was that in the inlet stream to the lake. Physically, the six streams were fairly similar with watershed areas ranging from 15.9-31.6 $km^2$, average gradients in the mid-regions from 0.9-1.3% and minimum summer discharge from 1.2-3.5 $m^3$/min. Streambed materials in Holland and in Ayum differed slightly from the other four streams in that they contained less gravel and more rubble, boulders and bedrock formations. Further, Holland lacks a natural upper estuary due to a large culvert and spillway underlying the Island Highway/Railroad overpass, but this structure presents no barrier to upstream movements of fish during high tide.

Each stream was sampled progressively in an upstream direction in habitat sections of fairly uniform velocity, selected if the local physiography appeared to allow isolation of its resident fish. At least five of each of the pool, glide and riffle habitats in the mid-length of each 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-Roote Laboratories, Mark $V^3$), both intensively and systematically in successive runs until catches declined to zero or the occasional fish. Population estimates thus obtained were assumed to approximate absolute numbers. The stunned fish were collected with dip nets and held in plastic buckets 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 stop nets were removed.

Fish biomass estimates in each of the three habitat types were computed from linear regressions of the form $\bar{Y} = \bar{A}X^b$, using the measured mean fork length ($\bar{X}$) and calculated mean wet weight ($\bar{Y}$) by species for each stream. These equations were 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.

Homogeneity of variance in samples within habitat types for each of the fish populations was confirmed by Bartlett's Test (Sokal and Rohlf 1969). One-way analysis of variance and regression relations were used to determine the statistical significance of a series of hypotheses generated to test the possibility of specific differences in length, weight and biomass parameters between sympatric and allopatric cutthroat trout populations and their streams.

## B. EXPERIMENTAL POPULATIONS IN THE STREAM SIMULATOR

The two trout types tested in a stream simulator were obtained from separate streams: sympatric cutthroat trout (F.L. range 35-53 mm) were from Craigflower Creek; allopatric cutthroat trout (F.L. range 35-60 mm) were from Shawnigan Creek (inlet).

The collecting and holding of the fish, the stream simulator, and the routine experimental procedures applied were as previously described (Glova and Mason 1977a). The experiments were conducted during the period June-August.

Each trout type was tested separately in two replicates, to test the null hypothesis that there was no observable difference between their rates and quality of aggressive behaviors and their microhabitat use when exposed to several levels of (1) feeding activity, and (2) water velocity.

# RESULTS

## A. NATURAL POPULATIONS OF FISH

Statistics for the fish populations and related stream physical parameters are shown for each of the six streams by habitat type in Tables 1-6. Bush and Holland creeks were sampled for two consecutive years, and the remaining four streams for one year. General physiographic and hydrological characteristics were reasonably similar between allopatric and sympatric stream types, although the pools were slightly deeper but not larger in area in the latter type. However, trout standing crops (both numbers or biomass per unit area) were consistently different between sympatric and allopatric populations. We tested a number of hypotheses to elucidate the possible ecological basis for the disparity between these two types of cutthroat trout populations. Estimates of fish biomass (g/m$^2$) rather than density (numbers of fish/m$^2$) were used as they showed a more meaningful measure of levels of stream carrying capacity, due to the broad range in size of fish present in most populations.

Six hypotheses were tested as detailed below:

### Hypothesis 1

There is no difference in total fish biomass density between populations containing allopatric and sympatric cutthroat trout (includes nonsalmonid species).

The null hypothesis was rejected in part: density of fish biomass was significantly ($P < 0.001$) less in the allopatric than in the sympatric populations in two out of the three cases tested. Unlike in Bings, mean biomass density for all habitat types combined in either Shawnigan and French creeks averaged 1.2 and 1.9 g/m$^2$, being up to threefold less than that in Ayum, Bush and Holland creeks, which ranged from an average 4.5-5.4 g/m$^2$. Other small coastal streams on Vancouver Island with similar sympatric species composition have been reported to support higher densities on the east coast north of the present study locations (Mason and Machidori 1976; 7-10 $g/m^2$) but similar values on the west coast (Andersen and Narver 1975; 2-5 $g/m^2$). Biomass density in Bings was of intermediate value (3.4 $g/m^2$) and largely attributable to its higher carrying capacity in pools than that in French and Shawnigan creeks. In both allopatric and sympatric populations, fish biomass was consistently highest in pools and lowest in riffles. Linear regression plots of biomass by habitat type for each stream showed considerably steeper slopes and higher intercepts for the sympatric than the allopatric populations in all cases, although that of Bush and Holland was nonsignificantly ($P > 0.05$) different from that of Bings Creek (Fig. 2). However, certain of these comparisons are tempered by the relatively broad confidence limits on the means. In particular, both Bings and Ayum showed rather extensive limits in fish biomass between pools, ranging from 3.1-14.0 $g/m^2$ and from 2.6-21.3 $g/m^2$, respectively, with the deeper pools supporting more fish. Variability in fish biomass in sympatric populations was considerably greater for sculpins than for salmonids.

Sculpins was the major contributor to fish biomass in each of the three sympatric streams. Their biomass dimensions in these simple fish communities often exceeded that of coho and trout combined, as represented by their peak 83% of the fish biomass in riffles in Holland 1975. Sculpin biomass has been reported to range from 50-80% in other small coastal streams on Vancouver Island (Mason and Machidori 1976). Unlike for coho and for trout, the relative biomass for sculpins in linear regressions was more or less constant between habitat types in Bush and Holland creeks at about 55 and 68% (Fig. 3). However, in Ayum, a stream with an unusually high utilization of riffle space by salmonids, relative biomass of sculpins ranged from 64% in pools to 25% in riffles. Relative biomass of coho made up 14-50% in Bush, 20-42% in Holland, and 23-37% in Ayum, being generally lowest in riffles and highest in pools, but reversed in Ayum.

### Hypothesis 2

There is no difference in biomass density between populations of sympatric coho and cutthroat trout combined and that of allopatric cutthroat trout (excludes nonsalmonid species).

Data variability within both types of salmonid population gave no clear-cut rejection or acceptance of this hypothesis. However, in two out of the three cases, trout biomass in the allopatric streams was comparable to, or greater than, that of the salmonid biomass in each of the three sympatric streams. Analysis of variance indicated that trout biomass levels in French and Bings creeks (allopatric) were nonsignificantly ($P > 0.05$) different from that of coho and trout combined in each of the three sympatric streams, excepting for the significantly ($P < 0.01$) higher average mean 3.5 $g/m^2$ in Bings compared to the 1.5 $g/m^2$ in Holland. Salmonid biomass levels in Shawnigan was significantly ($P < 0.01$) less than those in both Bush and Ayum but comparable to that in Holland. Unlike in Bings and French, Shawnigan supported relatively few age 1+ trout (see Tables 1-3) and also contained a minor population of sculpins which made up 20% of the fish biomass in glides.

Regression plots of salmonid biomass by habitat type were reasonably similar for five out of the six streams sampled (Fig. 2a, c), with their slopes ranging from -0.2 to -0.9 and their intercepts from 1.6-4.3. Outstandingly different ($P < 0.01$) was that of Bings, which supported mean trout biomass levels in pools some twofold higher than that of sympatric coho and trout combined in each of the three streams. Pool carrying capacity was particularly high in Bings compared to that of French and Shawnigan, with age 1+ trout making up a mean 34% in the former and 24% and 6% in the latter two streams.

## Hypothesis 3

There is no difference in biomass density between allopatric and sympatric cutthroat trout populations.

As the feeding and spatial niches of both coho and sculpins overlap considerably with that of cutthroat trout (Glova and Mason 1976b; Mason and Machidori 1976), levels of trout biomass may be lower in sympatric than in allopatric populations. Pooling the data for each of the three habitat types within streams, trout biomass was consistently less for the sympatric than for the allopatric populations, although not significantly so for all three streams. A maximum sevenfold difference occurred between populations in Holland and Bings. Holland supported a particularly dense population of sculpins in all habitats, with the larger ones in the slower, deeper waters and the juveniles in the faster, shallower areas. Trout average mean biomass levels ranged from 0.5-0.9 g/m$^2$ in the sympatric populations and from 1.1-3.5 g/m$^2$ in the allopatric populations. The differences in trout biomass levels between these two population types was significant ($P < 0.05$) in two of the three cases, the exception being Shawnigan Creek, which supported only about 1 g/m$^2$ in all habitats. In general, trout biomass in sympatric populations did not exceed 1 g/m$^2$ and was up to tenfold less than those in allopatric populations in pools.

## Hypothesis 4

Levels of trout biomass do not differ between habitat types within sympatric and allopatric cutthroat trout populations.

Both the relative abundance and biomass of sympatric populations of coho and cutthroat trout have been documented to differ between habitat types, being higher for coho in pools and for trout in riffles (Glova and Mason 1976b). However, none of the six streams when tested separately showed rejection of the null hypothesis at $P < 0.05$. The difference in trout biomass between habitat types was in fact more pronounced in allopatric than in sympatric cases. In both Bings and French creeks, trout biomass in pools was approximately double that in riffles, but only slightly so in Shawnigan Creek (Tables 1-3). In contrast, trout biomass in sympatric populations was similar in all habitat types (Fig. 2b). Riffles did not consistently support higher biomass levels of trout than did pools (Tables 4-6), as one might expect as an outcome of habitat segregation. The explanation for this being that fish carrying capacity in riffles was generally less than half of that in pools, which masked patterns of segregation on an absolute scale.

## Hypothesis 5

There is no difference in mean body size of cutthroat trout within habitat types between allopatric and sympatric populations.

As sympatric cutthroat trout, coho and sculpins are potential competitors for food (Mason and Machidori 1976) and space (Glova and Mason 1976b), their growth may differ from populations in allopatry. Differential capacity for growth from an evolutionary standpoint and age structure differences between these two trout population types could conceivably result in slower growth in allopatry and thus affect this hypothesis. Pooling the data of all age-classes within habitats for the three populations in each of the two types, trout fork length was significantly ($P < 0.01$) larger in allopatry than in sympatry in each of the three habitats. Average fork length of allopatric trout in pools, glides and riffles was 70.5, 62.4, and 55.5 mm (Tables 1-3), whereas sympatric trout was 55.2, 48.0, and 47.9 mm, respectively (Tables 4-6). Comparisons of the means showed a maximum 20% size difference between populations in pools and a minimum 14% in riffles. A peak 30 mm difference in trout mean body size occurred between populations in Bings and Holland creeks in pools.

Differences in mean body size of trout were also apparent within population types. Among the three allopatric trout populations, Shawnigan contained the least number of age 1+ trout, with regression analysis showing significantly ($P < 0.05$) lower slope and intercept of mean fork length than that of Bings and French (Fig. 4). Among the sympatric trout populations, Ayum supported the greatest number of age 1+ trout, with mean fork length slope and intercept being significantly ($P < 0.05$) higher than those in Bush and Holland (Fig. 4). However, these observations are tempered by the relatively broad confidence limits about the means, particularly those in Ayum in pools due to the wide range in size of fish and small number of samples. Unlike Ayum and the three streams containing allopatric populations, mean size of trout in Bush and Holland was approximately the same in all habitats. This may suggest a considerable movement of trout between habitats.

## Hypothesis 6

There is no difference in growth of age 0 cutthroat between allopatric and sympatric populations.

The effects of coho social dominance and of possible interspecific competition for food, might show slower growth for cutthroat trout fy in sympatric than in allopatric populations as found for experimental populations in the laboratory (Glova and Mason 1976c). Pooling the data for age 0 trout within habitat types for the allopatric and for the sympatric populations clearly demonstrated a rejection of the null hypothesis. The average mean fork lengths of trout fry were significantly ($P < 0.001$) larger in allopatric than in sympatric populations by approximately 27% in pools and glides, and 15% in riffles. Further, regression plots of trout fry mean fork length in relation to habitat (Fig. 5) showed the slopes differed slightly between population types: in allopatry, trout were slightly larger in pools than in riffles; in sympatry, they were of common size in all habitats. Best growth for trout fry in allopatry occurred in French Creek, whereas in sympatry in Ayum Creek.

## B. EXPERIMENTAL POPULATIONS OF FISH

### Microdistribution

In the stream simulator, both allopatric and sympatric trout had similar microdistributions. Pooling all the data with respect to body size and feed-periods, either population type showed comparable densities in riffle and pool habitats (Table 7). Expressed on a percent basis, at the low test velocity approximately 40% of the fish occupied riffles and 60% pools. By doubling the water velocity, riffle occupancy decreased in favour of pools by some 26%. In five-way factorial analysis of variance only habitat interacted significantly ($P < 0.01$) with fish size for both population types. Simulated food supply and water velocity showed no significant interaction with fish microhabitat use. The relative microdistributions for both population types (see Glova and Mason 1977a for sympatric trout) indicated that (1) size of fish was the most important factor, and (2) simulated food supply was of secondary importance, and (3) acceleration of the water velocity was of least importance in summer.

Relative size largely determined priority of access 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 undersized fish at the bottom and in undercut areas.

Similarly, the simulated food supply stimulated comparable feeding responses in both types of trout. During feed periods, many actively penetrated into riffles and either established transient feeding territories superimposed on territories of resident trout, or displaced 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 shifts between habitat types in food exploitation was statistically significant ($P > 0.05$), however.

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 trouts, 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. Unlike in the simulator, in natural streams exploitation of drifting foods by fish with territories in undercut areas of pools may be better due to greater convergent flow at meanders.

## Aggressive behavior

Both trouts socialized using the signal set previously described by Glova and Mason (1977a). Qualitative analysis of individual components of their aggressive behaviors expressed on a percent basis of the pooled data (Fig. 6, bottom) show the following points. Firstly, the most frequently used behavioral elements in both trouts was that 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. Secondly, allopatric trout chased and threat-nipped less, but used lateral threat, circling and biting more than did sympatric trout. Lateral threat encounters between closely matched individuals in either of the two trout types, often led to prolonged bouts of circling, butting and biting usually near the bottom of pools, and occasionally to exhaustion (see Glova and Mason 1977a).

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 observations totalling 2400 min for each. However, 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. 6, top) than in allopatric trout; their aggression being highest in both riffles and pools when food was present, although significant ($P < 0.05$) only in the latter. Aggression levels in 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 (Table 8). 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.

# DISCUSSION

## FOOD AND SPACE AS LIMITING FACTORS ON PRODUCTION

From the sizeable discrepancy in biomass density between sympatric and allopatric populations of cutthroat trout, one may postulate that interspecific interaction may be limiting sympatric populations, although overall fish production may be greater in multi-species streams. Mean total fish biomass levels in the sympatric populations ranged from about 2-9 g/m$^2$

($G\bar{X}$ = 5.1 g/m$^2$), being lowest in riffles and highest in pools, with trout almost exclusively contributing less than 1 g/m$^2$ in all habitat types (7-39%). In allopatric populations, however, mean biomass density of trout ranged from about 1-6 g/m$^2$ ($G\bar{X}$ = 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 increase in stock size 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 then for salmon. In the case of anadromous cutthroat trout, they emerge into a stream environment which may already be filled to near-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. Our studies indicate that cohabiting populations of these two salmonids have broadly overlapping microdistributions with coho exerting social dominance over trout. Interaction with coho largely restricts trout to riffle areas made disproportionately low in abundance relative to pool-like conditions during the summer-early fall period by low streamflows. Habitat segregation may be lessened further as summer temperatures increase, disadvantageously to trout, as coho more frequently penetrate riffle areas as temperatures rise (Glova and Mason 1977a). In consequence, we suggest that availability of living space for sympatric trout populations may be seriously curtailed by coho during the seasons of best growth, which may in part explain the low biomass levels of trout in sympatric streams. Thus, trout populations in smaller streams probably remain unlimited by direct competition for food with coho, despite their relatively broad overlap in diets (Glova and Mason 1974; Mason and Machidori 1976). The preponderance of sympatric trout are found in the food-producing riffle areas and their more diverse feeding behavior would seem to support this contention.

Sculpins are abundant in all habitat types in streams and often achieve biomass levels greater than that of sympatric coho and trout combined. Numerous studies 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% (LeCren 1965; Mann 1971; Petrosky and Waters 1975; Glova and Mason 1976b; Mason and Machidori 1976).

If sculpins have any negative impact on production of stream salmonids, we suggest that food, rather than space considerations are involved. Their benthic, and cryptic habits minimize interaction with salmonids through vertical separation in most stream habitats other than stream edges. Sculpin and salmonid microdistributions showed no evidence of interaction in Bush and Holland creeks, but salmonids may have influenced reduced sculpin abundance in riffles of Ayum Creek. Sculpin microdistribution appears to be more the outcome of intraspecific 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 appears 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 reduce the availability of drift to coho in pools, with trout in riffles remaining little affected, due to their more flexible foraging strategies than those of coho.

Due to the presence of coho as a third-species variable, the possible significance of sculpins as a competitor for food with salmonids remains indiscernable in the present study. Range in biomass levels of allopatric trout populations (1.0-5.6 g/m$^2$) approximated those of sympatric trout and coho combined (0.4-4.2 g/m$^2$). Based on experimental evidence that trout have a similar but broader ecological niche than do coho (Glova and Mason 1977a; 1977b), trout biomass in allopatry ought to be comparable to 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 in total fish biomass in sympatric populations (2.0-9.0 g/m$^2$) than those in allopatric trout populations (1.0-5.6 g/m$^2$) may reflect 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 testing than those available to date (see Mason and Machidori 1976).

## IMPLICATIONS FOR TROUT MANAGEMENT

The behavioral similarity of allopatric and sympatric trout may reflect a general environmental similarity above and below barrier falls. Interaction with coho salmon has not exerted any apparent evolutionary changes in feeding behavior and in microhabitat responses. 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 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 would no doubt induce appropriate shifts in feeding and microhabitat responses to coho social dominance in pools and other slow water habitats. Assuming, as occurs in natural sympatry, that coho and trout populations above a barrier falls would effectively segregate into pools and riffles, respectively, we might expect trout biomass levels above barrier falls to decline to below 1 g/m$^2$, or approximately halved. Low summer flows disproportionately reduce riffle areas relative to pools, and thus further extend space limitations on sympatric trout brought about by 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 small coastal streams under experimental conditions before its acceptance as an effective enhancement strategy can be recommended.

## ACKNOWLEDGEMENTS

This work was jointly supported by Federal and Provincial Fisheries Agencies. We thank R. C. Thomas, D. W. Narver, and G. E. Reid of the B.C. Fish and Wildlife Branch for their interest and financial assistance; B. Bartlett, G. Bates, A. Campbell, S. Donaldson, J. Elford, S. Glova, B. Hughes, P. Naysmith, D. Straughn, and D. Sutherland for their field assistance in this study. G. J. Glova was in part assisted by a National Research Council of Canada Scholarship.

## REFERENCES

Andersen, B. C., and D. W. Narver. 1975. Fish populations of Carnation Creek and other Barkley Sound streams - 1974: Data Record and Progress Report. Fish. Res. Board Can. MS Rep. 1351: 73 p.

Andreasson, S. 1971. Feeding habits of a sculpin (Cottus gobio L. Pisces) population. Inst. Freshwater Res. Drottningholm Ann. Rep. 51: 5-30.

Brocksen, R. W., G. E. Davis, and C. E. Warren. 1968. Competition, food consumption and production of sculpins and trout in laboratory stream communities. J. Wildl. Manage. 32 (1): 51-75.

Glova, G. J., and J. C. Mason. 1974. Interactive ecology of juvenile salmon and trout in streams. I. Progress during 1973. Fish. Res. Board Can. MS Rep. 1300: 35 p.

1976a. Interactive ecology of juvenile salmon and trout in streams. II. Progress during 1974. Fish. Res. Board Can. MS Rep. 1391: 24 p.

1976b. Interactive ecology of juvenile salmon and trout in streams. Progress during 1975. Fish. Res. Board Can. MS Rep. 1400: 38 p.

1976c. Comparative effects of temperature and photoperiod on laboratory growth of underyearling coho salmon and coastal cutthroat trout. Fish. Res. Board Can. MS Rep. 1414: 50 p.

1977a. Interactions for food and space between sympatric populations of underyearling coho salmon and coastal cutthroat trout in a stream simulator in summer. Fish. Mar. Serv. MS Rep. (In press) 36 p.

1977b. Interactions for food and space between sympatric populations of underyearling coho salmon and coastal cutthroat trout in a stream simulator during winter and spring. Fish. Mar. Serv. MS Rep. (In press) 31 p.

Hartman, G. F. 1965. The role of behavior in the ecology and interaction of underyearling coho salmon (Oncorhynchus kisutch) and steelhead trout (Salmo gairdneri). J. Fish. Res. Board Can. 22: 1035-1081.

LeCren, E. D. 1965. Some factors regulating the size of populations of freshwater fish. Mitt. Int. Ver. Theor. Angew. Limnol. 13: 88-105.

Mann, R. H. K. 1971. The populations, growth and production of fish in four small streams in southern England. J. Anim. Ecol. 40: 155-190.

Mason, J. C. 1975. Seaward movement of juvenile fishes, including lunar periodicity in the movement of coho salmon (Oncorhynchus kisutch) fry. J. Fish. Res. Board Can. 32(12): 2542-2547.

1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. J. Wildl. Manage. 40(4): 775-788.

Mason, J. C., and S. Machidori. 1976. Populations of sympatric sculpins, Cottus aleuticus and Cottus asper, in four adjacent salmon-producing streams on Vancouver Island, B.C. Fish. Bull. 74(1): 131-141.

Moyle, P. B. 1977. In defense of sculpins. Fisheries 2(1): 20-23.

Nilsson, N. A. 1967. Interactive segregation between fish species, p. 295-313. In S. D. Gerking [ed.] The Biological Basis of Freshwater Fish Production. Blackwell Sci. Publ. Oxford and Edinburgh.

Northcote, T. G. 1969. Patterns and mechanisms in the lakeward migratory behavior of juvenile trout, p. 181-204. In T. G. Northcote [ed.] Salmon and Trout in Streams. H. R. MacMillan Lectures in Fisheries, Univ. of British Columbia, Vancouver, B.C.

Northcote, T. G., S. N. Williscroft, and H. Tsuyuki. 1970. Meristic and lactate dehydrogenase genotype differences in stream populations of rainbow trout below and above a waterfall. J. Fish. Res. Board Can. 27(11): 1987-1995.

Petrosky, C. E., and T. F. Waters. 1975. Annual production by the slimy sculpin population of a small Minnesota trout stream. Am. Fish. Soc. 104(2): 237-244.

Sokal, R. R., and F. J. Rohlf. 1969. BIOMETRY - The principles and practice of statistics in biological research. Freeman and Company. 776 p.

Table 1. Summary of statistics for fish populations and related stream physical parameters in Bush Creek, September-October 1974 and 1975.

| | | | | Total fish | | | | | | | Trout | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | % Biomass | | | | | | | | | Age 0 (mm) | | All ages combined (mm) |
| | Area $m^2$ | Water depth cm | Vel. cm/s | N | N/$m^2$ | g/$m^2$ | Trout | Coho | Sculpins | | N | N/$m^2$ | g/$m^2$ | % age 0 | % ≥ age 1+ | Mean F.L. ± S.E. | Range | Mean F.L. ± S.E. |
| | | | | | | | | | | **POOLS** | | | | | | | | |
| | | | | | | | | | | 1974 | | | | | | | | |
| | 27 | 40 | 6.7 | 192 | 7.1 | 7.4 | 10.7 | 72.0 | 17.3 | | 14 | 0.5 | 0.8 | 79 | 21 | 55.1 ± 0.93 | 43-52 | 55.7 ± 1.02 |
| | 29 | 14 | 9.5 | 211 | 7.1 | 8.6 | 8.5 | 58.9 | 32.6 | | 17 | 0.6 | 0.7 | 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 |
| $\bar{X}$, Σ | 32 | 22 | 7.4 | 861 | 5.8 | 7.2 | 7.2 | 49.5 | 43.7 | | 52 | 0.4 | 0.5 | 91 | 9 | 46.2 ± 0.84 | 32-55 | 46.6 ± 0.86 |
| | | | | | | | | | | 1975 | | | | | | | | |
| | 37 | 36 | 5.4 | 190 | 5.0 | 9.2 | 3.7 | 26.4 | 69.9 | | 8 | 0.2 | 0.3 | 75 | 25 | 48.1 ± 1.56 | 37-64 | 57.3 ± 6.56 |
| | 23 | 15 | 5.0 | 159 | 6.6 | 10.0 | 9.2 | 29.8 | 61.0 | | 12 | 0.5 | 0.9 | 83 | 17 | 45.1 ± 0.99 | 35-55 | 59.8 ± 6.99 |
| | 59 | 40 | 3.8 | 218 | 3.7 | 5.8 | 18.3 | 33.1 | 48.6 | | 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 |
| $\bar{X}$, Σ | 45 | 38 | 4.4 | 861 | 4.2 | 6.6 | 10.4 | 30.8 | 58.8 | | 78 | 0.3 | 0.6 | 82 | 18 | 47.5 ± 1.18 | 33-64 | 58.4 ± 6.38 |

**Table I (cont'd)**

| | | | | Total fish | | | | | | Trout | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | % Biomass | | | | | | | | Age 0 (mm) | | All ages combined (mm) |
| | Area m² | Water 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. ± S.E. | Range | Mean F.L. ± S.E. |
| | | | | | | | | | GLIDES | | | | | | | | |
| | | | | | | | | | 1974 | | | | | | | | |
| | 29 | 11 | 10.3 | 229 | 7.7 | 10.1 | 5.7 | 24.5 | 69.8 | 11 | 0.4 | 0.6 | 100 | - | 41.8 ± 1.30 | 33-50 | 41.8 ± 1.30 |
| | 43 | 12 | 16.4 | 237 | 5.5 | 6.9 | 9.2 | 40.4 | 50.4 | 22 | 0.5 | 0.6 | 86 | 14 | 52.1 ± 1.06 | 40-55 | 53.0 ± 3.50 |
| | 24 | 12 | 16.1 | 80 | 3.4 | 4.9 | 5.5 | 13.2 | 81.3 | 6 | 0.3 | 0.3 | 85 | 15 | 49.8 ± 0.78 | 42-55 | 50.2 ± 1.20 |
| | 27 | 14 | 15.9 | 81 | 3.0 | 3.4 | 13.7 | 49.3 | 37.0 | 12 | 0.4 | 0.5 | 100 | - | 49.4 ± 0.42 | 39-55 | 49.4 ± 0.42 |
| | 36 | 12 | 9.2 | 136 | 3.8 | 4.7 | 7.2 | 42.5 | 50.3 | 11 | 0.3 | 0.3 | 91 | 9 | 50.1 ± 0.56 | 38-54 | 53.0 ± 1.71 |
| $\bar{X}$, 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 ± 0.82 | 33-55 | 49.5 ± 1.63 |
| | | | | | | | | | 1975 | | | | | | | | |
| | 21 | 17 | 10.1 | 161 | 7.6 | 13.1 | 9.8 | 32.7 | 57.5 | 11 | 0.5 | 1.3 | 62 | 38 | 49.9 ± 1.78 | 33-59 | 66.2 ± 7.78 |
| | 37 | 10 | 14.9 | 116 | 3.1 | 4.3 | 6.7 | 22.6 | 70.7 | 9 | 0.2 | 0.3 | 78 | 22 | 43.9 ± 1.57 | 37-54 | 51.8 ± 5.57 |
| | 25 | 13 | 11.2 | 79 | 3.1 | 3.3 | 8.8 | 37.9 | 53.3 | 10 | 0.4 | 0.3 | 100 | - | 44.0 ± 1.45 | 38-52 | 44.0 ± 1.45 |
| | 33 | 9 | 8.3 | 127 | 3.8 | 4.1 | 7.8 | 32.2 | 60.0 | 14 | 0.4 | 0.3 | 100 | - | 44.2 ± 1.79 | 36-60 | 44.2 ± 1.79 |
| | 32 | 10 | 8.9 | 97 | 2.9 | 3.5 | 10.3 | 40.0 | 49.7 | 12 | 0.4 | 0.3 | 100 | - | 45.8 ± 1.84 | 38-57 | 45.8 ± 1.84 |
| $\bar{X}$, Σ | 30 | 12 | 10.7 | 580 | 4.1 | 5.7 | 8.7 | 33.1 | 58.2 | 56 | 0.4 | 0.5 | 88 | 12 | 45.6 ± 1.69 | 33-60 | 50.4 ± 3.69 |

Table 1 (cont'd)

| | | | | Total fish | | | | | | Trout | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | % Biomass | | | | | | | | Age 0 (mm) | | All ages combined (mm) |
| | Area m$^2$ | Water depth cm | Vel. cm/s | N | N/m$^2$ | g/m$^2$ | Trout | Coho | Sculpins | N | N/m$^2$ | g/m$^2$ | % age 0 | % ≥ age 1+ | Mean F.L. ± S.E. | Range | Mean F.L. ± S.E. |
| | | | | | | | | | **RIFFLES** | | | | | | | | |
| | | | | | | | | | 1974 | | | | | | | | |
| | 18 | 7 | 50.0 | 84 | 4.5 | 5.0 | 43.9 | 21.2 | 34.9 | 34 | 1.8 | 2.2 | 94 | 6 | 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 | 30 | 1.0 | 1.6 | 100 | - | 41.7 ± 0.90 | 32-52 | 41.7 ± 0.90 |
| | 7 | 13 | 29.4 | 44 | 5.7 | 6.8 | 25.8 | 23.0 | 51.2 | 13 | 1.7 | 1.8 | 85 | 15 | 49.1 ± 1.70 | 34-55 | 55.6 ± 5.45 |
| | 28 | 11 | 29.4 | 39 | 1.4 | 1.6 | 9.6 | 50.4 | 40.0 | 4 | 0.1 | 0.2 | 100 | - | 50.0 ± 1.44 | 42-54 | 50.0 ± 1.44 |
| | 29 | 12 | 25.0 | 89 | 3.1 | 3.7 | 15.3 | 34.2 | 51.5 | 16 | 0.6 | 0.6 | 100 | - | 48.7 ± 0.50 | 40-71 | 48.7 ± 0.50 |
| $\bar{X}$. Σ | 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 |
| | | | | | | | | | 1975 | | | | | | | | |
| | 26 | 8 | 35.7 | 61 | 2.3 | 2.9 | 14.1 | 5.5 | 80.4 | 11 | 0.4 | 0.4 | 100 | - | 48.0 ± 2.08 | 31-56 | 48.0 ± 2.08 |
| | 31 | 9 | 43.5 | 64 | 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 ± 12.50 |
| | 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 |
| $\bar{X}$. Σ | 33 | 9 | 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 |

Table 2. Summary of statistics for fish populations and related stream physical parameters in Holland Creek, September-October 1974 and 1975.

| | | | | Total fish | | | | | | Trout | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | % Biomass | | | | | | | | Age 0 (mm) | | All ages combined (mm) |
| | Area m² | Water 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. ± S.E. | Range | Mean F.L. ± S.E. |
| | | | | | | | | | 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 ± 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 ± 1.41 |
| | 30 | 38 | 7.8 | 74 | 2.4 | 5.4 | 5.1 | 26.5 | 68.4 | 6 | 0.2 | 0.3 | 100 | - | 43.7 ± 2.50 | 35-50 | 43.7 ± 2.50 |
| | 24 | 25 | 6.2 | 57 | 2.3 | 5.2 | 10.0 | 19.6 | 70.4 | 7 | 0.3 | 0.5 | 100 | - | 40.0 ± 2.42 | 31-50 | 40.0 ± 2.42 |
| | 21 | 33 | 8.3 | 65 | 3.0 | 7.2 | 6.4 | 16.6 | 77.0 | 6 | 0.3 | 0.5 | 100 | - | 41.0 ± 1.30 | 35-43 | 41.0 ± 1.30 |
| $\bar{X}$, Σ | 23 | 34 | 7.6 | 343 | 2.9 | 6.5 | 8.8 | 20.1 | 71.1 | 39 | 0.4 | 0.6 | 100 | - | 41.1 ± 1.79 | 31-51 | 41.1 ± 1.79 |
| | | | | | | | | | 1975 | | | | | | | | |
| | 22 | - | 18.5 | 69 | 2.8 | 5.5 | 1.6 | 28.4 | 70.0 | 5 | 0.2 | 0.1 | 100 | - | 37.6 ± 1.50 | 34-38 | 37.6 ± 1.50 |
| | 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 ± 0.00 | - | 103.6 ± 19.99 |
| | 45 | 35 | 7.8 | 121 | 2.6 | 6.9 | 3.5 | 22.6 | 78.9 | 3 | 0.1 | 0.2 | 100 | - | 37.5 ± 1.20 | 36-39 | 37.5 ± 1.20 |
| | 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 | 49.7 ± 9.73 |
| $\bar{X}$, 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 ± 1.04 | 34-44 | 53.2 ± 6.72 |

Table 2 (cont'd)

| | | | | Total fish | | | | | | Trout | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Biomass | | | | | | | | Age 0 (mm) | | All ages combined (mm) |
| | Area $m^2$ | Water depth cm | Vel. cm/s | N | N/$m^2$ | g/$m^2$ | Trout | Coho | Sculpins | N | N/$m^2$ | g/$m^2$ | % age 0 | % ≥ age 1+ | Mean F.L. ± S.E. | Range | Mean F.L. ± S.E. |
| GLIDES | | | | | | | | | | | | | | | | | |
| 1974 | | | | | | | | | | | | | | | | | |
| | 20 | - | 10.1 | 50 | 2.5 | 3.3 | 21.1 | 39.1 | 39.8 | 7 | 0.4 | 0.7 | 100 | - | 38.6 ± 1.10 | 34-42 | 38.6 ± 1.10 |
| | 21 | 16 | 7.7 | 76 | 3.5 | 4.6 | 31.1 | 33.2 | 35.7 | 14 | 0.6 | 1.4 | 87 | 13 | 37.2 ± 1.20 | 29-43 | 38.2 ± 0.64 |
| | 31 | 24 | 35.7 | 86 | 2.7 | 4.0 | 9.5 | 35.3 | 55.2 | 7 | 0.2 | 0.4 | 100 | - | 40.4 ± 1.71 | 33-45 | 40.4 ± 1.71 |
| | 24 | 33 | 20.0 | 83 | 3.4 | 4.6 | 13.3 | 44.3 | 42.4 | 6 | 0.2 | 0.6 | 100 | - | 34.3 ± 2.23 | 33-46 | 34.3 ± 2.23 |
| | 16 | 35 | 18.0 | 61 | 3.6 | 5.0 | 15.5 | 47.5 | 37.0 | 5 | 0.3 | 0.8 | 100 | - | 35.4 ± 2.30 | 30-43 | 35.4 ± 2.30 |
| $\overline{X}$, Σ | 22 | 27 | 18.3 | 356 | 3.1 | 4.3 | 18.1 | 42.0 | 39.9 | 39 | 0.3 | 0.8 | 97 | 3 | 37.2 ± 1.71 | 29-46 | 37.4 ± 1.60 |
| 1975 | | | | | | | | | | | | | | | | | |
| | 59 | - | 18.9 | 69 | 1.2 | 1.9 | 3.2 | 26.7 | 70.1 | 7 | 0.1 | 0.1 | 100 | - | 38.3 ± 0.64 | 35-40 | 38.3 ± 0.64 |
| | 42 | 23 | 21.3 | 114 | 2.7 | 5.9 | 2.4 | 22.5 | 75.1 | 9 | 0.2 | 0.1 | 100 | - | 41.9 ± 2.40 | 34-59 | 41.9 ± 2.40 |
| | 50 | 16 | 12.2 | 125 | 2.5 | 4.5 | 4.2 | 16.4 | 79.4 | 18 | 0.4 | 0.2 | 66 | 34 | 38.8 ± 0.66 | 36-43 | 38.8 ± 0.66 |
| | 32 | 20 | 13.9 | 82 | 2.6 | 4.2 | 6.2 | 22.9 | 70.9 | 11 | 0.3 | 0.3 | 80 | 20 | 38.2 ± 1.04 | 33-43 | 44.2 ± 6.04 |
| | 64 | 14 | 13.0 | 138 | 2.2 | 2.9 | 2.4 | 30.3 | 67.3 | 8 | 0.1 | 0.1 | 100 | - | 39.8 ± 1.29 | 33-43 | 39.9 ± 1.29 |
| $\overline{X}$, Σ | 49 | 18 | 15.9 | 528 | 2.2 | 3.9 | 3.6 | 23.8 | 72.6 | 53 | 0.2 | 0.2 | 89 | 11 | 39.4 ± 1.21 | 33-59 | 40.6 ± 2.21 |

Table 2 (cont'd)

| | | | | Total fish | | | | | | Trout | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | % Biomass | | | | | | | | Age 0 (mm) | | All ages combined (mm) |
| | Area m$^2$ | Water depth cm | Vel. cm/s | N | N/m$^2$ | g/m$^2$ | Trout | Coho | Sculpins | N | N/m$^2$ | g/m$^2$ | % age 0 | % ≥ age 1+ | Mean F.L. ± S.E. | Range | Mean F.L. ± S.E. |
| RIFFLES | | | | | | | | | | | | | | | | | |
| 1974 | | | | | | | | | | | | | | | | | |
| | 22 | 9 | 36.6 | 50 | 2.2 | 3.5 | 11.4 | 23.6 | 65.0 | 6 | 0.3 | 0.4 | 67 | 33 | 56.0 ± 2.50 | 34-45 | 57.0 ± 2.56 |
| | 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 |
| | 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 |
| | 13 | 5 | 40.0 | 29 | 2.1 | 3.0 | 28.9 | 24.8 | 46.3 | 7 | 0.5 | 0.9 | 100 | - | 40.4 ± 1.43 | 34-45 | 40.4 ± 1.43 |
| | 24 | 22 | 40.5 | 39 | 1.6 | 2.3 | 26.5 | 20.2 | 53.3 | 11 | 0.4 | 0.6 | 100 | - | 43.5 ± 1.70 | 35-50 | 43.5 ± 1.70 |
| $\bar{X}$, 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 ± 1.65 | 32-51 | 44.9 ± 1.66 |
| 1975 | | | | | | | | | | | | | | | | | |
| | 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 ± 2.54 |
| | 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 |
| | 51 | 13 | 40.5 | 40 | 1.1 | 1.3 | 18.5 | 7.7 | 73.8 | 12 | 0.2 | 0.2 | 92 | 8 | 40.3 ± 1.58 | 34-53 | 48.8 ± 8.58 |
| | 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 |
| | 37 | 6 | 44.1 | 103 | 2.8 | 1.9 | 16.8 | 1.6 | 81.6 | 16 | 0.4 | 0.3 | 100 | - | 43.6 ± 1.46 | 34-56 | 43.6 ± 1.46 |
| $\bar{X}$, Σ | 35 | 12 | 41.5 | 270 | 1.9 | 2.8 | 10.2 | 6.8 | 83.0 | 47 | 0.1 | 0.2 | 98 | - | 41.6 ± 1.74 | 34-56 | 43.3 ± 3.14 |

Table 3. Summary of statistics for fish populations and related stream physical parameters in Ayum Creek, October 1975.

| | | | | Total fish | | | | | | Trout | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | % Biomass | | | | | | | | Age 0 (mm) | | All ages combined (mm) |
| | Area m² | Water 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. ± S.E. | Range | Mean F.L. ± S.E. |
| POOLS | | | | | | | | | | | | | | | | | |
| | 60 | 55 | 6.2 | 208 | 3.5 | 21.3 | 0.7 | 11.9 | 87.4 | 7 | 0.1 | 0.1 | 100 | - | 51.7 ± 1.87 | 45-57 | 51.7 ± 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 ± 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 ± 1.47 | 42-55 | 73.0 ± 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 ± 0.50 | 41-47 | 99.9 ± 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 ± 0.48 | 49-51 | 49.8 ± 0.48 |
| $\bar{X}$, $\Sigma$ | 40 | 41 | 5.6 | 417 | 1.9 | 9.0 | 12.9 | 23.2 | 63.9 | 29 | 0.1 | 0.9 | 69 | 31 | 49.9 ± 1.08 | 41-57 | 76.5 ± 13.36 |
| 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 ± 1.23 | 43-65 | 69.5 ± 8.23 |
| | 36 | 19 | 17.3 | 84 | 2.3 | 5.7 | 25.3 | 49.4 | 25.3 | 30 | 0.8 | 1.4 | 90 | 10 | 51.4 ± 0.93 | 37-66 | 57.8 ± 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 ± 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 |
| $\bar{X}$, $\Sigma$ | 53 | 19 | 18.8 | 435 | 1.7 | 5.1 | 19.8 | 37.3 | 42.9 | 125 | 0.5 | 1.0 | 83 | 17 | 51.1 ± 1.12 | 37-76 | 62.2 ± 6.12 |
| RIFFLES | | | | | | | | | | | | | | | | | |
| | 29 | 13 | 46.9 | 39 | 1.4 | 2.6 | 48.1 | 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 | 28 | 1.0 | 1.2 | 45.0 | 31.7 | 23.3 | 15 | 0.5 | 0.5 | 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 |
| $\bar{X}$, $\Sigma$ | 56 | 15 | 31.4 | 238 | 1.0 | 2.0 | 38.5 | 35.7 | 25.8 | 115 | 0.5 | 0.7 | 98 | 2 | 52.2 ± 1.90 | 37-82 | 53.4 ± 2.89 |

Table 4. 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.

| | | | | Total fish | | | | | Trout | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | % Biomass | | | | Age 0 (mm) | | All ages combined (mm) |
| | Area m² | Water depth cm | Vel. cm/s | N | N/m² | g/m² | Trout | Others | % age 0 | % ≥ age 1+ | Mean F.L. ± S.E. | Range | Mean F.L. ± S.E. |
| POOLS | | | | | | | | | | | | | |
| | 57 | 22 | - | 17 | 0.3 | 2.2 | 100 | - | 18 | 82 | 60.0 ± 1.53 | 63-68 | 94.0 ± 4.24 |
| | 71 | 29 | 6.2 | 43 | 0.6 | 1.4 | 100 | - | 95 | 5 | 60.6 ± 1.16 | 50-84 | 64.3 ± 2.78 |
| | 68 | 32 | 7.8 | 25 | 0.4 | 1.9 | 100 | - | 76 | 24 | 66.5 ± 1.54 | 51-75 | 83.2 ± 6.65 |
| | 66 | 26 | 10.0 | 41 | 0.6 | 1.8 | 100 | - | 88 | 12 | 63.5 ± 1.21 | 47-76 | 69.2 ± 2.90 |
| | 52 | 22 | 10.0 | 33 | 0.6 | 1.7 | 100 | - | 94 | 6 | 64.3 ± 1.26 | 53-80 | 67.1 ± 2.66 |
| | 22 | 53 | 3.3 | 51 | 2.3 | 6.0 | 100 | - | 78 | 22 | 52.9 ± 1.88 | 36-71 | 66.9 ± 4.41 |
| $\bar{X}$, Σ | 56 | 31 | 7.5 | 210 | 0.8 | 2.5 | 100 | - | 75 | 25 | 62.3 ± 1.43 | 36-84 | 74.1 ± 3.94 |
| GLIDES | | | | | | | | | | | | | |
| | 51 | 11 | - | 8 | 0.2 | 1.3 | 100 | - | 25 | 75 | 61.5 ± 5.51 | 56-67 | 97.6 ± 12.14 |
| | 55 | 14 | 22.2 | 15 | 0.3 | 0.8 | 100 | - | 93 | 7 | 64.3 ± 1.73 | 55-73 | 68.9 ± 4.89 |
| | 67 | 19 | 14.9 | 31 | 0.5 | 1.3 | 100 | - | 93 | 7 | 64.0 ± 1.52 | 51-80 | 69.1 ± 3.86 |
| | 53 | 13 | 19.2 | 105 | 2.0 | 2.3 | 100 | - | 96 | 4 | 48.6 ± 0.86 | 29-67 | 50.6 ± 1.31 |
| | 43 | 21 | 18.9 | 37 | 0.9 | 3.0 | 100 | - | 81 | 19 | 59.8 ± 1.34 | 49-75 | 73.0 ± 5.09 |
| $\bar{X}$, Σ | 54 | 16 | 18.8 | 196 | 0.8 | 1.7 | 100 | - | 78 | 22 | 59.6 ± 2.16 | 29-80 | 71.8 ± 3.03 |
| RIFFLES | | | | | | | | | | | | | |
| | 32 | 11 | 33.0 | 15 | 0.5 | 0.9 | 100 | - | 100 | - | 60.3 ± 2.57 | 45-77 | 60.3 ± 2.57 |
| | 11 | 13 | 40.0 | 9 | 0.8 | 1.2 | 100 | - | 90 | 10 | 52.4 ± 4.00 | 36-68 | 55.8 ± 4.90 |
| | 17 | 8 | 40.0 | 23 | 1.3 | 1.6 | 100 | - | 100 | - | 46.0 ± 1.28 | 36-60 | 46.0 ± 1.28 |
| | 20 | 11 | 36.0 | 14 | 0.7 | 1.2 | 100 | - | 100 | - | 57.7 ± 2.12 | 49-71 | 57.7 ± 2.12 |
| $\bar{X}$, Σ | 20 | 11 | 37.3 | 61 | 0.8 | 1.2 | 100 | - | 98 | 2 | 54.1 ± 2.50 | 36-77 | 54.9 ± 2.72 |

Table 5. Summary of statistics for the resident fish populations and related stream physical parameters upstream of the barrier falls in Bings Creek, October 1976.

| | | | | | | | | | Trout | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Total fish | | | | | | | | | | Age 0 (mm) | | All ages combined (mm) |
| | | | | | | | % Biomass | | | | | | | | | |
| | Area $m^2$ | Water depth cm | Vel. cm/s | N | $N/m^2$ | $g/m^2$ | Trout | Stbk[a] | N | $N/m^2$ | $g/m^2$ | % age 0 | % ≥ age 1+ | Mean F.L. ± S.E. | Range | Mean F.L. ± S.E. |
| 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 ± 4.84 |
| | 38 | 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 |
| | 53 | 50 | 3.2 | 113 | 2.2 | 14.0 | 97.6 | 2.4 | 96 | 1.8 | 13.7 | 44 | 56 | 63.2 ± 1.72 | 49-88 | 94.4 ± 3.89 |
| $\bar{X}$, Σ | 46 | 36 | 6.1 | 355 | 1.4 | 5.6 | 95.8 | 4.2 | 324 | 1.2 | 5.4 | 66 | 34 | 59.3 ± 1.52 | 45-88 | 76.9 ± 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 | 62.6 ± 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 |
| $\bar{X}$, Σ | 50 | 18 | 18.4 | 246 | 1.1 | 2.6 | 97.5 | 2.5 | 238 | 1.1 | 2.6 | 85 | 15 | 58.9 ± 0.86 | 47-83 | 64.5 ± 2.08 |
| RIFFLES | | | | | | | | | | | | | | | | |
| | 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 | 55.1 ± 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 |
| $\bar{X}$, Σ | 27 | 11 | 30.6 | 119 | 1.3 | 2.1 | 100 | - | 119 | 1.3 | 2.1 | 91 | 9 | 56.3 ± 1.18 | 41-73 | 60.5 ± 3.33 |

[a] Denotes stickleback.

Table 6. Summary of statistics for the resident fish populations and related stream physical parameters in Shawnigan Creek (inlet), October 1975.

| | | | | Total fish | | | | | Trout | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Biomass | | | | | | | Age 0 (mm) | | All ages combined (mm) |
| | Area $m^2$ | Water depth cm | Vel. cm/s | N | N/$m^2$ | g/$m^2$ | Trout | Sculpins | N | N/$m^2$ | g/$m^2$ | % age 0 | % ≥ age 1+ | Mean F.L. ± S.E. | Range | Mean F.L. ± S.E. |
| | | | | | | | | 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 ± 5.28 |
| | 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 ± 1.24 |
| | 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 ± 3.17 |
| | 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 ± 2.31 |
| | 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 ± 2.17 |
| | 97 | 16 | 3.8 | 80 | 0.8 | 1.5 | 89.7 | 10.3 | 76 | 0.8 | 1.3 | 95 | 5 | 50.3 ± 1.24 | 39-71 | 57.2 ± 2.24 |
| $\bar{X}$, Σ | 71 | 31 | 3.7 | 292 | 0.7 | 1.4 | 89.5 | 10.5 | 269 | 0.6 | 1.2 | 94 | 6 | 56.7 ± 1.40 | 39-98 | 60.5 ± 2.74 |
| | | | | | | | | GLIDES | | | | | | | | |
| | 44 | 10 | 9.6 | 27 | 0.6 | 0.6 | 100 | - | 27 | 0.6 | 0.6 | 100 | - | 48.7 ± 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 ± 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 ± 1.77 | 39-72 | - |
| | 34 | 5 | 16.6 | 16 | 0.5 | 0.6 | 80 | 20 | 14 | 0.4 | 0.4 | 100 | - | 49.6 ± 1.70 | 39-61 | - |
| $\bar{X}$, Σ | 39 | 13 | 13.0 | 175 | 0.9 | 1.3 | 91.9 | 8.1 | 170 | 0.8 | 1.0 | 100 | - | 50.8 ± 1.35 | 38-98 | - |
| | | | | | | | | RIFFLES | | | | | | | | |
| | 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 | - |
| $\bar{X}$, Σ | 25 | 9 | 25.6 | 87 | 0.8 | 1.0 | 96.7 | 3.3 | 83 | 0.8 | 0.9 | 100 | - | 51.1 ± 1.79 | 38-76 | - |

Table 7. Overall mean numbers of allopatric and sympatric cutthroat trout fry in the riffle and pool habitats at two test velocities in the stream simulator. Cover in riffles refers to area beneath rocks; in pools to undercut areas.

| | Low velocity | | High velocity | |
|---|---|---|---|---|
| | Mean ± S.E. | Fish using cover (% of total) | Mean ± S.E. | Fish using cover (% of total) |
| Allopatric | | | | |
| Riffle | 7.7 ± 0.38 | 2.0 | 5.7 ± 0.48 | 4.2 |
| Pool | 11.5 ± 0.42 | 7.3 | 13.6 ± 0.84 | 13.0 |
| Sympatric | | | | |
| Riffle | 7.4 ± 0.43 | 0.0 | 5.7 ± 0.42 | 0.0 |
| Pool | 11.5 ± 0.36 | 10.1 | 13.5 ± 0.74 | 10.5 |

Table 8. Mean rate of aggressive encounters per fish per 100 min for allopatric and for sympatric cutthroat trout in the stream simulator in relation to the feed cycle for the low (no brackets) and high (brackets) test velocity. Increase in aggression at increasing velocity is indicated as +; the reverse as -.

| | Riffle | | | | Pool | | | |
|---|---|---|---|---|---|---|---|---|
| | Pre- | During- | Post-feed | Av. mean | Pre- | During | Post-feed | Av. mean |
| Allopatric | (30.8) | (32.5) | (25.2) | (29.5) | (87.7) | (53.4) | (27.9) | (56.3) |
| | 49.4 | 45.7 | 44.5 | 46.5 | 37.7 | 51.4 | 33.6 | 40.9 |
| | -18.6 | -13.2 | -19.3 | -17.0 | +50.0 | +2.0 | -5.7 | +15.4 |
| Sympatric | (22.9) | (41.8) | (31.9) | (32.2) | (24.4) | (50.6) | (30.8) | (35.3) |
| | 38.6 | 53.9 | 37.8 | 43.4 | 32.7 | 64.2 | 39.9 | 45.6 |
| | -15.7 | -12.1 | -5.9 | -11.2 | -8.3 | -13.6 | -9.1 | -10.3 |

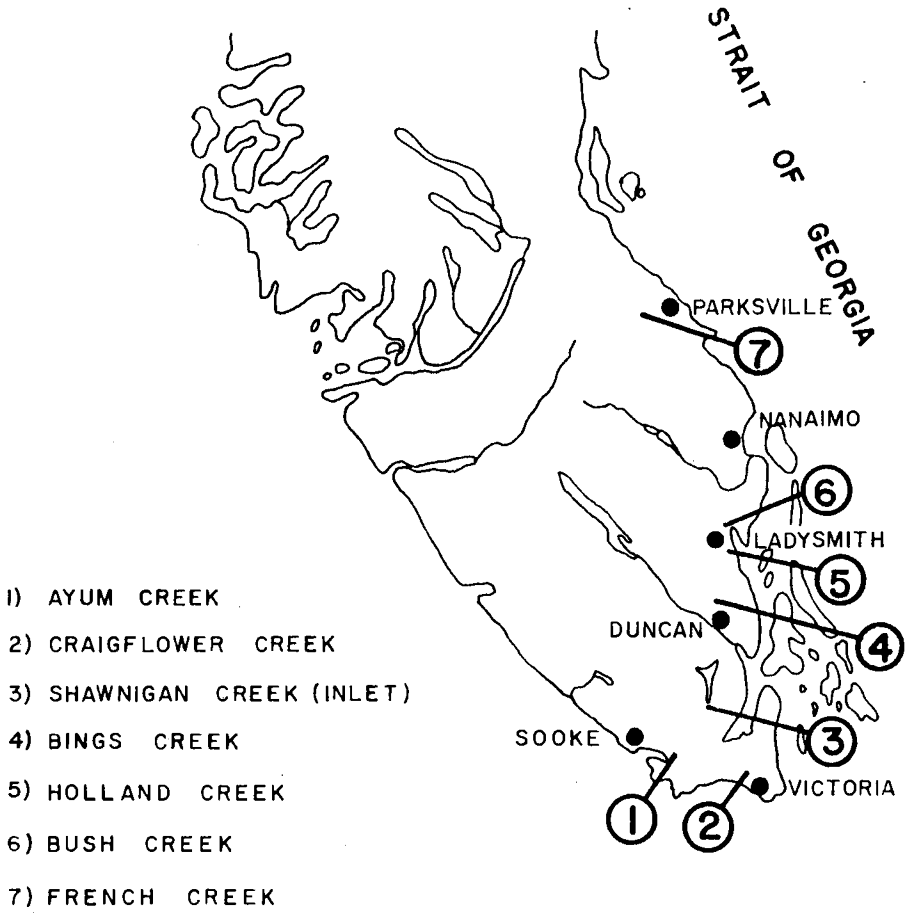

Fig. 1. **Partial map** of southern Vancouver Island showing general locations of study streams.

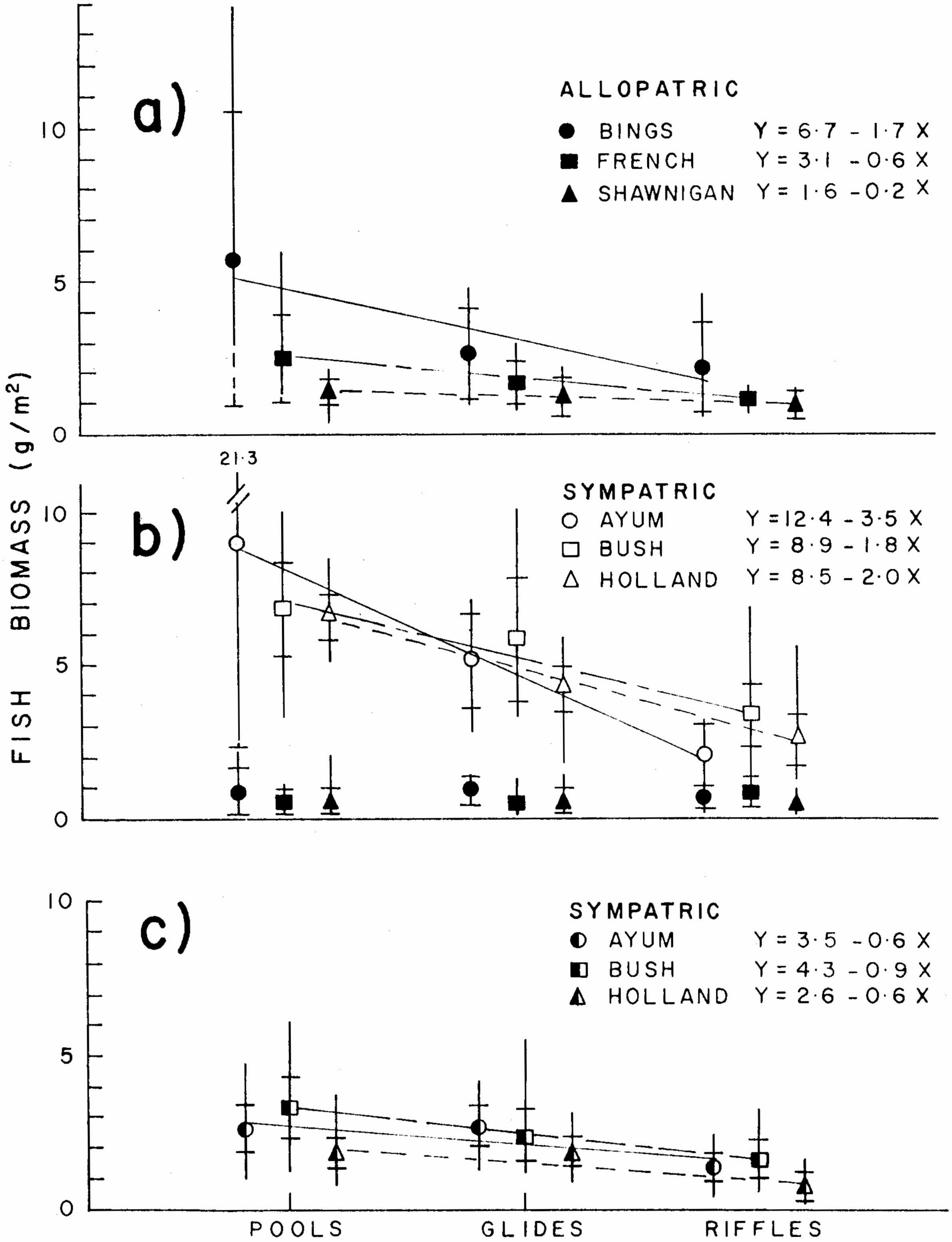

Fig. 2. Linear regression of fish biomass by stream habitat type of: (a) allopatric trout only, (b) sympatric total fish (open); trout only (solid), and (c) sympatric coho and trout combined. Symbols are means ± 95% confidence limits; vertical lines are range.

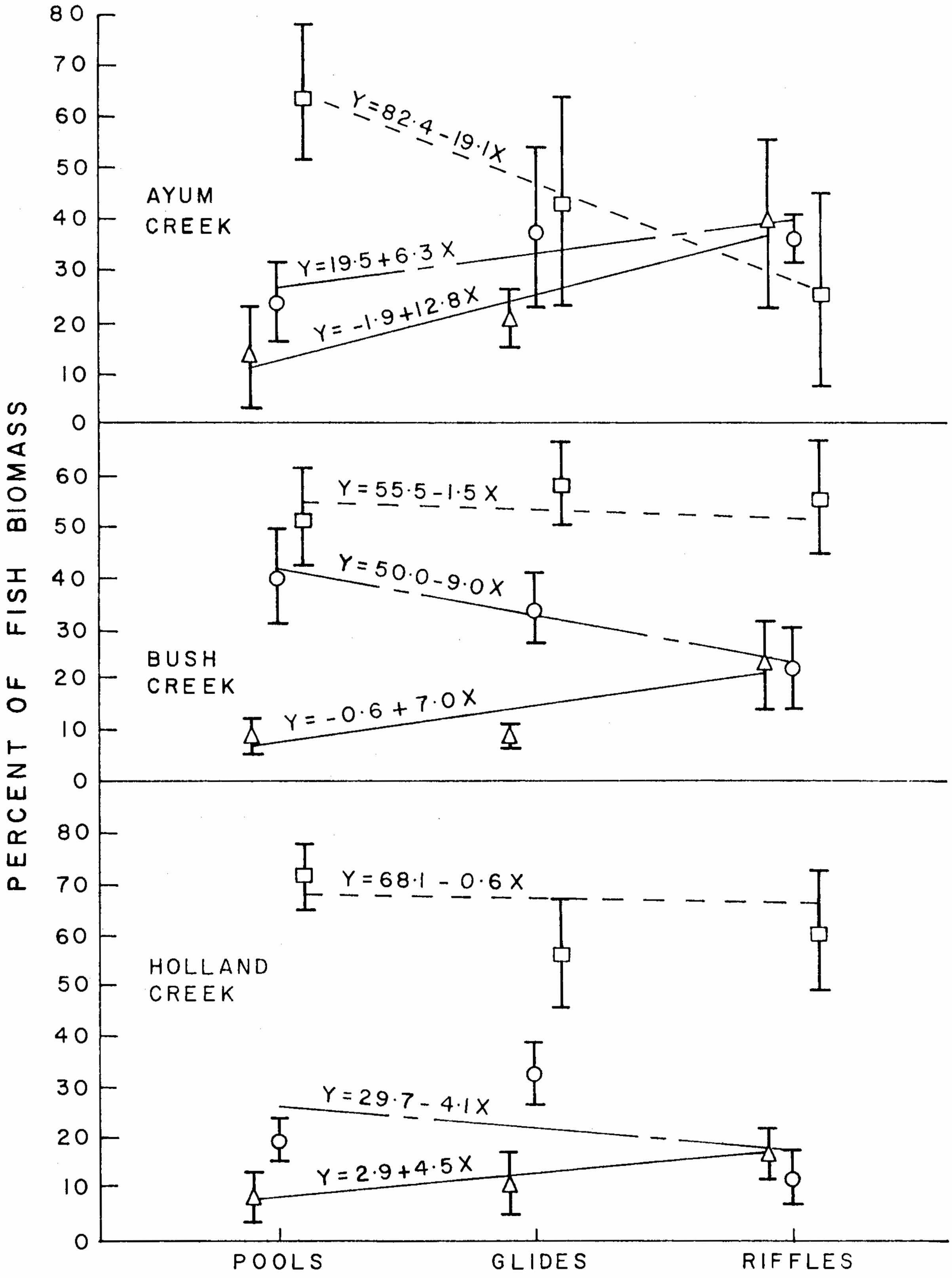

Fig. 3. Linear regressions of relative biomass by habitat in each of the three sympatric streams with coho, 0; trout, Δ ; sculpins, ◻ . Symbols are means ± 95 confidence limits.

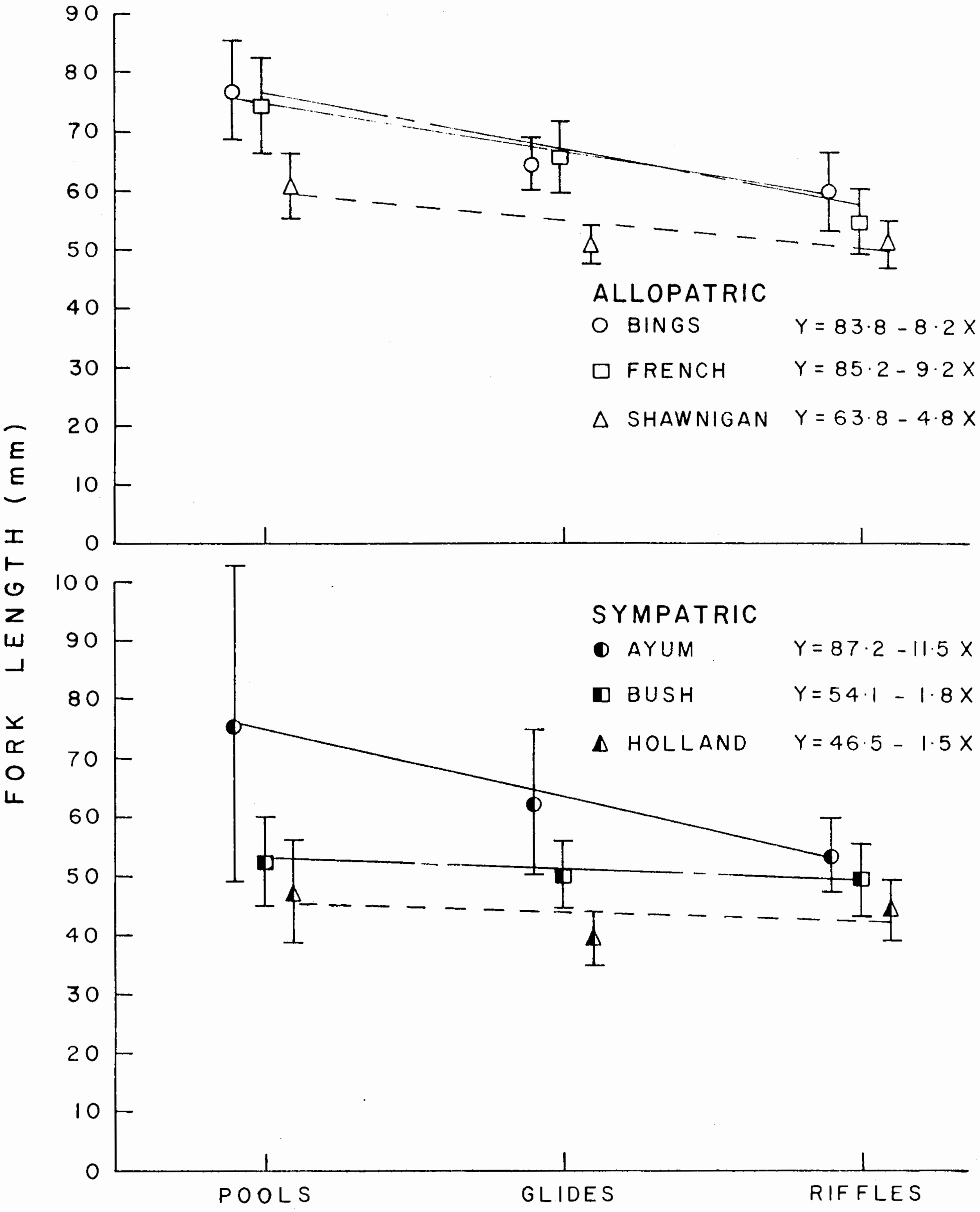

Fig. 4. Regressions of cutthroat trout mean fork length ± 95 confidence limits by habitat type in each of the three allopatric and sympatric populations.

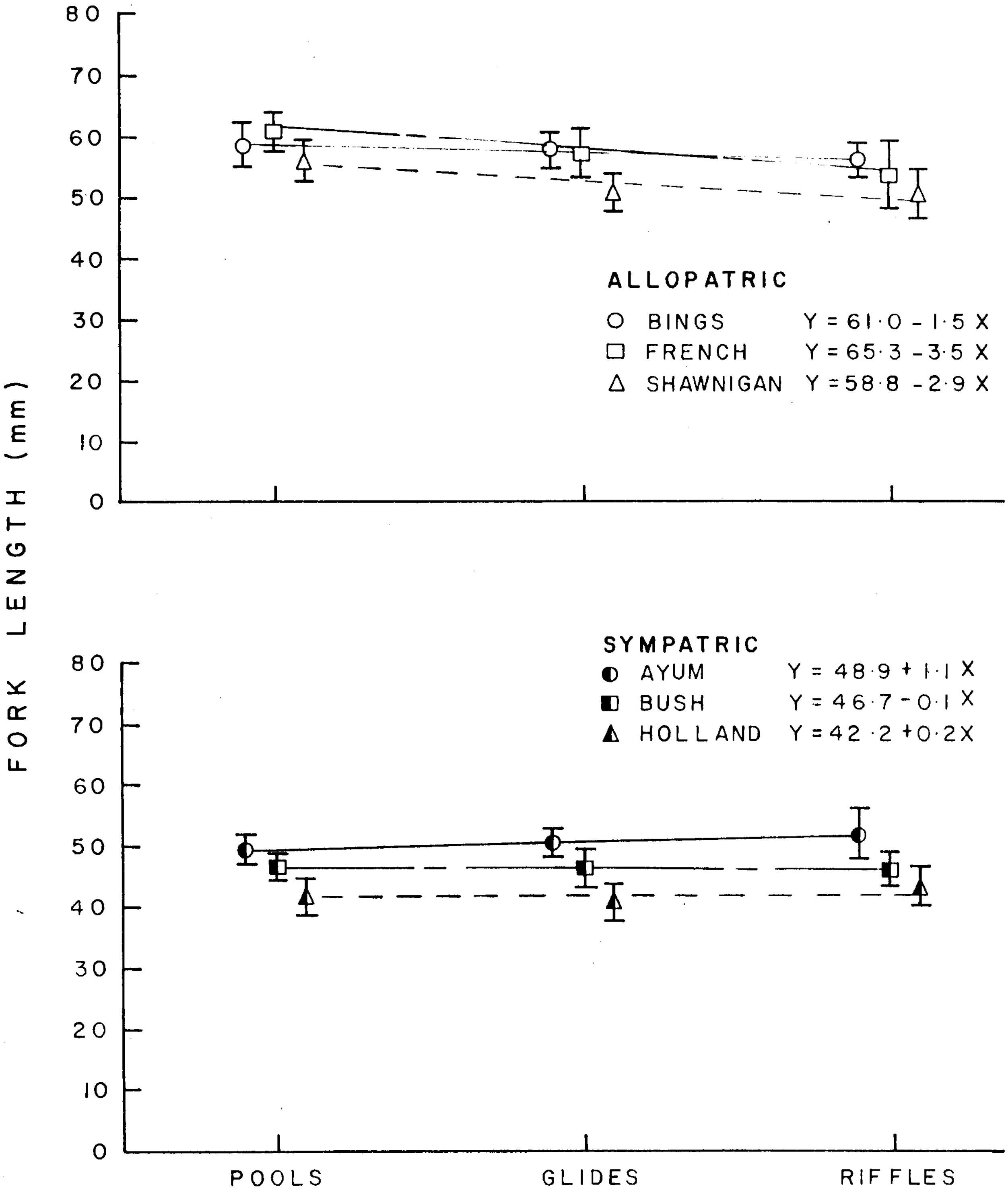

Fig. 5. Regressions of underyearling cutthroat trout mean fork length ± 95% confidence limits by habitat type in each of the three allopatric and sympatric populations.

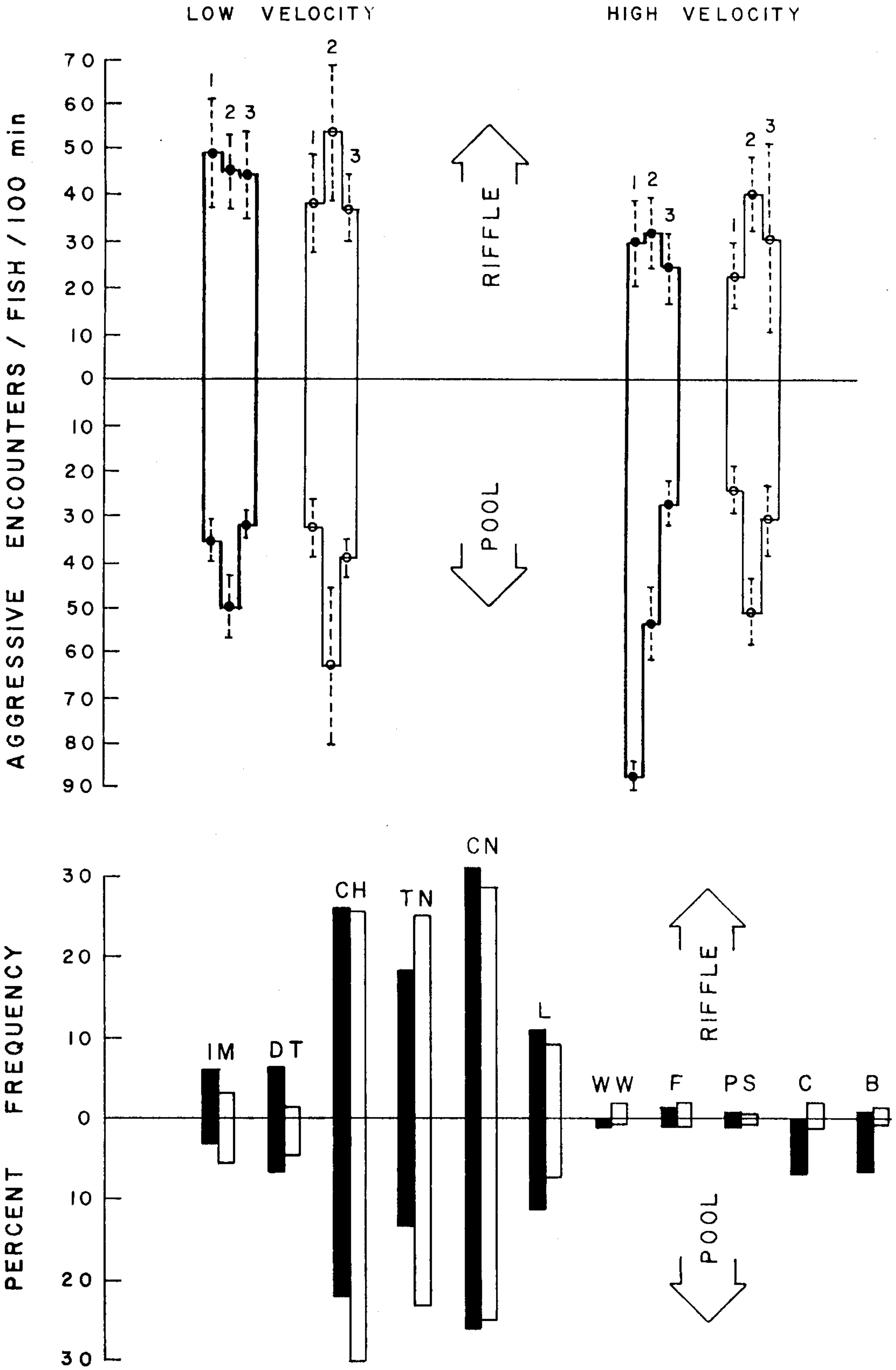

Fig. 6. Upper: mean rates of aggression ± S.E. in allopatric (heavy line) and sympatric (light line) cutthroat trout in relation to the feeding cycle (1, pre-; 2, during-; 3, post-feed period) in the riffle and pool environment. Lower: relative frequency of the components of aggression for allopatric (solid) and sympatric (open) cutthroat trout. Symbols are: IM intention movement; DT drive toward; CH chase; TN threat nip; CN contact nip; L lateral display; WW wig-wag display; PS parallel swimming; C circling; B biting.