Interactions for Food and Space Between Sympatric Populations of Juvenile Coho Salmon and Coastal Cutthroat Trout in a Stream Simulator During Winter and Spring

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INTERACTIONS FOR FOOD AND SPACE BETWEEN SYMPATRIC POPULATIONS OF JUVENILE COHO SALMON AND COASTAL CUTTHROAT TROUT IN A STREAM SIMULATOR DURING WINTER AND SPRING

by

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ABSTRACT

Glova, G. J., and J. C. Mason. 1977. 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. 1429: 31 p.

Interactions for food and space between sympatric populations of underyearling coho salmon and coastal cutthroat trout were investigated in a stream simulator during winter and spring.

Temperature was the main determinant of coho and trout microhabitat use in winter. At 3 C, both species almost exclusively occupied pools, whether in allopatry or in sympatry. At 5 C, minor segregation was evident, with species relative abundance in riffles being higher for trout and in pools for coho. Factorial analyses of variance indicated temperature, size of fish, water velocity and simulated food supply were ranked (high to low) as affecting microdistribution.

Coho and cutthroat trout fry communicated using the same signal set as in summer with chases, nips and lateral displays comprising more than 80% of their total aggressive activity. Non-contact behaviors were more frequently used by coho; nipping was more frequently used by trout. Both salmonids were most aggressive when food was present, irrespective of temperature. However, levels of aggressiveness differed with temperature and space: at 3 C, aggression was low and neither species defended riffles; at 5 C, aggression was higher and both species actively defended riffles during feeding.

Patterns of species microhabitat use and behavioral interactions in spring were similar to, but more pronounced than those in winter at 5 C.

Stream management strategy should take into account the importance of providing adequate winter cover appropriate to the different age-classes in sympatric populations of coho salmon and coastal cutthroat trout.

Key words: Interaction, aggression, microdistribution, temperature, allopatry, sympatry.

RÉSUMÉ

Glova, G. J., and J. C. Mason. 1977. 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. 1429: 31 p.

Les auteurs ont simulé un cours d'eau, en hiver et au printemps, pour étudier les interactions reliées à la nourriture et à l'espace entre des populations sympatriques de saumons coho et de truites fardées de moins d'un an.

La température était le principal facteur déterminant l'utilisation du microhabitat par les deux espèces en hiver. À 3° C, en sympatrie ou en allopatrie, les deux espèces occupaient exclusivement les trous d'eau. À 5° C, une ségrégation mineure était évidente, la truite étant relativement plus abondante dans les rapides et le saumon coho, dans les trous d'eau. Les analyses factorielles de la variance ont indiqué que la température, la taille du poisson, la vitesse de l'eau et l'apport de nourriture influaient dans cet ordre sur la microrépartition.

Les alevins des deux espèces utilisaient pour communiquer les mêmes signaux qu'en été, les poursuites, les morsures et les présentations latérales représentant plus de 80 % de toutes leurs activités d'agression. Les attitudes de menace (sans contact physique) étaient plus fréquentes chez le saumon, et la morsure était utilisée plus fréquemment par la truite. Quelle que fût la température, les deux salmonidés étaient plus agressifs en présence de nourriture. Toutefois, le niveau d'agressivité variait avec la température et l'espace: à 3° C, l'agressivité était faible, et ni l'une ni l'autre espèce ne défendait les rapides; à 5° C, l'agressivité était plus grande, et les deux espèces défendaient les rapides en présence de nourriture.

Au printemps, les modes d'utilisation du microhabitat par les espèces et les interactions de comportement étaient semblables mais plus accentués qu'en hiver à 5° C.

Les aménageurs de cours d'eau devraient tenir compte de l'importance d'assurer un abri pour l'hiver adéquat et approprié aux différentes classes d'âges dans les populations sympatriques de saumons cohos et de truites fardées.

Mots clés: Interaction, agressivité, microrépartition, température, allopatrie sympatrie.

INTRODUCTION

This is the last of a series of six reports from our study on the interaction between sympatric populations of juvenile coho salmon and coastal cutthroat trout. Here we explore the interactions for food and space between these two salmonids in a stream simulator during mid-winter and early spring. In accordance with Hartman (1965), sympatric stream populations of coho and steelhead trout are least likely to segregate in winter, the season when their overall densities and levels of aggressiveness are both relatively low and certain species environmental demands might be different, such as their degree of association with the stream bottom. The applicability of Hartman's findings to sympatric populations of coho and coastal cutthroat trout in general was investigated in this study.

Previously we have hypothesized that stream water temperature and velocity are the key abiotic factors operating in the summer-early fall segregation process between juvenile populations of coho salmon and coastal cutthroat trout -- an evolutionary outcome possibly related to the common occurrence of longitudinal gradients of these two variables in streams. Similarly in winter, although interaction between them may be lessened, their utilization of specific cover-types in streams appear to be strongly influenced by seasonal thermal and hydrological extremes. As temperature and/or velocity approach extreme levels in winter, salmonids associate more closely with specific cover requirements, whose availability may in fact limit overwinter survival (Mason 1976; Bustard and Narver 1975a). In streams with restricted overwintering cover, coho and trout may well compete for such places, although not necessarily in an interactive context but rather through mere physical occupancy of specific sites. More exacting information on the possible overlap in the overwintering requirements between these two cohabiting salmonids is vital to fisheries management in British Columbia, particularly since in specific streams smolt production may be enhanced through manipulation of appropriate environmental factors determining species effective cover requirements.

The null hypothesis tested in the winter and spring period was the same as that tested in the summer experimental series (Glova and Mason 1977): that juvenile coho salmon and anadromous coastal cutthroat trout show no observable difference in their behavior as measured by rate and quality of aggressive activities, and extent of microhabitat use when tested under several levels of 1) feeding activity, and 2) water velocity. The critical temperature and/or velocity thresholds inducing cover-seeking behavior in these two stream-dwelling salmonids was also investigated.

METHODS

Test fish were taken from sympatric populations of coho salmon and coastal cutthroat trout in two small coastal streams situated at the south end of Vancouver Island, B.C.: winter fish (fork length ranges: coho 45-94 mm; trout 43-96 mm) were from Ayum Creek; spring fish (coho 48-98 mm; trout 45-107 mm) were from Craigflower Creek. (See Glova and Mason 1976 for stream locations.) The collecting and holding of the fish, the test facility used, and the routine experimental procedures applied were as described in the summer test series (Glova and Mason 1977), excepting the following: 1) winter fish were bulk-collected in advance in late November and held in the laboratory under conditions described below in order to avoid possible difficulty in obtaining adequate numbers of fish under high flows at a later date, 2) average freshet velocities as measured in the riffles was increased from 43.1-50.7 cm/s (see Table 1), compensating for the larger body size of fish in the winter and spring experiments from those used in summer, and 3) both allopatric and sympatric tests in spring were not replicated due to time limitations imposed by season.

The winter fish-holding facilities provided at the Pacific Biological Station, Nanaimo, B.C. consisted of a bank of twelve 60 × 60 × 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-, medium- and large-sized individuals per tank. They were fed chopped fresh-frozen euphausiids at least once every 2 days. The selected fish in each of the experiments were transferred in fry cans at their acclimated test temperature, direct to the test facility at the University of Victoria on the initial day of each test.

The winter experiments were conducted at 3.0 and 5.0 ± 0.5 C during December 2-January 27, 1976; the spring experiments were conducted at 7.5 ± 0.5 C during March 15-April 21, 1975. Test temperatures paralleled those in home streams in each season. The experiments conducted and their pertinent fish length data are given in chronological order in Appendix Table 1.

RESULTS

I. IN WINTER

A. General

When first placed into the simulator both salmonids invariably moved immediately to the bottom of the pools. A gradual active spacing-out of the fish through mechanisms of territoriality and social dominance was limited and restricted to specific sites. Compared to the summer test period (Glova and Mason 1977), breadth of microhabitat use, general mobility and aggressive activity in winter was relatively low. This subdued behavioral state in winter served to reduce the variance between replicates. By the end of day 2, fish were habituated to the test facility, both feeding and microhabitat responses thereafter were fairly constant.

Mortality in all experiments was low, not exceeding 5%. All losses involved small fish pinned against the downstream screen during periods of high velocity at night. As smaller fish are less capable swimmers than larger fish (Glova and McInerney 1977), they were more susceptible to dislocation downstream. Both salmonids showed temporary upstream movement when the water velocity was incrementally accelerated from the low to the high test level which, in nature, would counteract downstream displacement during fresheting in streams.

B. Comparison of species microdistribution patterns

Temperature was the major determinant of breadth of microhabitat use in winter. At 3 C both coho and trout fry failed to utilize riffles to any great extent, but remained in pools, particularly in areas under cover and lowest relative water movement. There was no obvious species interactive effect on the utilization of space *per se* in the riffle and pool environment, although the total numbers of fish in pools was slightly higher in sympatry than in allopatry. Mixing the species had the effect of increasing the carrying capacity slightly in pools. Pooling the data with respect to body size and feed-periods, 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 (Table 2). However, mean numbers of coho in pools were slightly higher than for trout, ranging from 19.6-20.0 and from 18.0-19.2, respectively. On a percent basis, 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. Accelerating the velocity had virtually no effect on the coho's overall pattern of microdistribution.

Elevating the test temperature to 5 C increased breadth in microhabitat use by both species, but slightly more so for trout. When pooling the data there was a definite increase, although not statistically significant for coho at the high test velocity, in the mean numbers of fish in riffles (Table 2). 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.

Six-way factorial analyses of variance were computed on the block of winter data in an effort to determine the level of statistical significance in the possible combinations of interactions between each of the test variables (Table 3). In the analyses, highest levels of order of interactions that are significant overrule those at lower levels of order, involving wholly or in part the same test variables. Overall, habitat type was the common denominator in all significant ($P < 0.01$) interactions occurring in both intra- and interspecific cases. Relative difference in the quality of cover in riffles and pools were probably the chief determinants of microhabitat use, interrelated to a number of other factors. For example, in pools, the use of cover by both coho and trout decreased with decreasing size of fish, decreasing water velocity, increasing water temperature and when food was drifting in the system. The same response patterns to cover prevailed in riffles excepting that use increased with decreasing body size. In all second-order levels of interaction with habitat types as by species mean percent-frequency plots (Fig. 1), temperature appeared to be the primary factor controlling utilization of space in winter. Relative size of fish, acceleration of the water velocity within limits and a restricted food supply were of lesser importance, ranked in that order.

Relatively small differences in temperature induced evident responses in the fish. In the sympatric trials at 3 and 5 C, there was a significant ($P < 0.01$) interaction between temperature, habitat type, velocity and species. Over the 2 C rise in temperature both species showed an increased utilization of riffles, particularly when feeding. However, coho showed a greater sensitivity to the changes in water velocity than did trout, their invasion of riffles being generally of a shorter duration and more closely related to the actual feeding periods.

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 adequate overhead cover in pools. Cover response also differed slightly between species, being more pronounced in trout than in coho in both riffles and pools. In allopatry, the percentages 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 cover-carrying capacity in pools was increased slightly 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%.

Both coho and trout fry showed reduced feeding response at 3 C. Accordingly, the imposed cycle of food availability had minimal impact on species microdistribution patterns, both in allopatry and sympatry. However, the 2° increase in temperature (3-5 C) altered behavioral responses to food and space appreciably. At 3 C, neither species was inclined to exploit the food supply in riffles but preferred to remain in cover sites, primarily in pools. At 5 C, the feeding response exceeded that for cover, particularly in coho, and fish were more inclined to exploit the food supply in riffles. However, none of these behavioral differences showed any significant interactions between feed periods and patterns of space utilization over the different test conditions (Table 3). Interspecific differences in strategies to exploiting the food supply appeared to be greater in the most rigorous winter tests. Trout showed greater capacity to feed in riffles than did coho under critically low temperature and high velocity conditions, 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.

C. Comparison of species aggressive behaviors

Coho and cutthroat trout socially communicated in winter using the signal set described in the summer test period (Glova and Mason 1977). As in summer the most frequently used components of aggression in winter when tested at 3 C were that of lateral displays, nips and chases; together these comprised more than 80% of the total aggressive acts for each species. Unlike in summer, activity was relatively low in the winter test conditions, which probably explains the proportional reduction in frequency of chases and an increase in threat nips and displays (see Fig. 3, bottom). Intraspecifically, in pools, lateral displays and threat nips combined made up almost 60% of the total offensive encounters for both coho and trout. Interspecifically, the pattern of offensive aggressive activity in pools was similar to the above, excepting that lateral displays were less for coho and threat nips were less for trout. Such changes in aggressive behavior might be related in part to age of fish and season, as well as temperature (Hartman 1966). In riffles, aggressive activity was too low to warrant qualitative behavioral analysis.

The winter test conditions showed marked but similar environmental effects on both coho and cutthroat trout patterns of aggressive behavior. Neither salmonid showed any inclination to defend riffle space at 3 C, irrespective of the test conditions, with the exception that trout occasionally interacted for cover sites beneath rocks. In both allopatry and sympatry, at either test velocity, coho and trout interacted only in pools. In general, aggression was low for both species but pulsed in synchrony with the feeding cycle (Fig. 2, 3). 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 post-feed periods. However, coho maintained a higher level of aggression in post-feed periods than did trout, but significant ($P < 0.01$) only intraspecifically.

Mean levels of aggression in relation to the feeding cycle differed markedly between species, although their ranges did overlap (Fig. 4). When mixed, unlike trout, coho total offensive 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 size-related 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.

Mixing the species showed no interactive effect on their levels of aggression. Overall, total aggressive encounters for either species in sympatry was proportionately halved of that in allopatry, being 6409 and 3410 for coho and 3892 and 1988 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 (Fig. 2, 3). When mixed with coho, trout were less inclined to defend feeding stations but tended to remain more in areas of cover. Accordingly, coho directed a near twofold greater amount of their total offensive activity against conspecifics than against trout, with total encounters amounting to 2243 and 1167, respectively. Trout total offensive activity was more evenly distributed with a total of 944 encounters against conspecifics and 1044 against coho.

Accelerating 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. 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. 3). Trout aggression intraspecifically was unaffected by the acceleration of the water 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. 5). Both species at 5 C actively defended riffles at least during feeding. With this relatively small rise in temperature, cover response decreased while that for 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° 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 C was in general similar to that at 3 C, 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 offensive 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.

II. IN SPRING

Species patterns of microhabitat use and aggressive behaviors in spring were similar to those in winter at 5 C, for both allopatric and sympatric tests. Utilization of riffles and levels of aggression were slightly higher for both species in the spring test series and was probably more related to the 2.5° rise in temperature than to season. However, as these experiments were not replicated, they are precluded from further analysis here.

DISCUSSION

SPECIES ENVIRONMENTAL RESPONSES IN RELATION TO THEIR WINTER ECOLOGY

Unlike in summer, in winter, quality of space rather than food, appears to be of greater importance to juvenile coho salmon and cutthroat trout in small streams. Low water temperatures and high stream flows create sufficiently adverse conditions that fish exploit areas of shelter and rest, more so than food. Its adaptive significance may be manifested in reducing both downstream displacement and predation, during a period of lowered metabolism, reduced food requirements and poor swimming ability by fish. Quality and quantity of such space may be the regulatory factor in overwintering stream salmonid populations and the simulator findings must be interpreted with caution. Cover in the simulator was intentionally kept simple to facilitate observation of the fish. Fluctuating, adverse conditions in natural environments may be tempered by greater spatial complexity available to fish.

In general the present findings concur with those reported by Hartman (1965) in his investigation of the interaction between underyearlings of coho and steelhead trout populations tested in a similar riffle and pool environment. Underyearlings of sympatric populations of coho salmon and coastal cutthroat trout when tested together in winter, did not distinctly segregate as in summer (Glova and Mason 1977), but rather coexisted in pools. Their need for cover and deeper water was illustrated by their more frequent use of the undercut areas in pools. Smaller-sized trout, however, were able to utilize cover in both riffles and pools but preferred the latter. Similar cover preferences for the different size-classes of these two salmonids has been demonstrated experimentally under semi-natural conditions (Bustard and Narver 1975b). Space in pools was partioned vertically more along a size-related than on a species basis: larger fish of either species remained predominantly in midwater, with coho nearer to the surface than trout; smaller fish of either species were commonest along the bottom. The greater compatibility between coho and trout in winter permits more overlap in their overwintering, than in their summer spatial niches. Crowding and possible interspecific competition in preferred pool space is more likely to occur between the smaller-sized individuals as these make up a greater percentage of the total numbers of populations. This may explain at least in part why age 0 trout more commonly utilize cover in riffles when in sympatry with coho salmon.

Coho and cutthroat trout interact minimally over space <u>per se</u> in winter. Typically, rates of interaction were positively related to temperature but inversely to velocity. Hartman (1966) observed similar behavioral responses to temperature in juvenile coho and steelhead. However, food drifting in the system at periods of dawn and dusk in the present study markedly elevated species levels of interaction in pools, but with minor dispersal only 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). In summary, the present findings indicate that species levels of aggressiveness and scope in microhabitat use were more strongly influenced by change in temperature than that of water velocity. The pronounced species responses obtained in going from 3-5 C than from a doubling of the water velocity from 15-30 cm/s, suggests that temperature differences are more critical at the lower end of the temperature scale. The importance of low winter temperature as a factor controlling microdistributions of juvenile coho and steelhead in streams has been sufficiently demonstrated by Bustard and Narver (1975a). As both thermal and hydrological conditions in streams are commonly severe in winter, and the availability of drifting foods may be sparse, we infer from the present findings that socially, 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.

MANIPULATION OF WINTER COVER -- AN ENHANCEMENT STRATEGY

Winter carrying capacity of some salmonid-producing streams may be limited by the level of appropriate cover available to fish (Mason 1976; Bustard and Narver 1975a).

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. In an intensive but unquantified electrofishing survey in six Vancouver Island small coastal streams during winter, age 0 trout were 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 (e.g. Fig. 6). They were almost never present in whitewater areas lacking such cover types. 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 compounded by broad overlap and diversity in cover types used: coho utilize a variety of cover types both within and outside main streams (Bustard and Narver 1975a), trout remain mostly in the former; common sites to both are the deeper waters containing upturned or undercut root masses (e.g. Fig. 7) and log accumulations particularly those 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 possibilities both within (e.g. Fig. 8) and outside (e.g. Fig. 9) the main stream wherever feasible, taking advantage of existing hydrological and physiographical features and naturally occurring architectural components of cover -- an approach which may reduce installation and maintenance costs and increase utilization of such sites by fish.

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Table 1. Mean water velocity and depth in each of the riffles and pools. Each value is based on a total of 12 specifically located measurements. Both surface and bottom velocities were taken approximately 1 in from their respective interfaces. Values in b) in riffles were taken immediately upstream of rocks.

		Low velocity (cm/s)			High velocity (cm/s)			Water depth (cm)
		Surface	Bottom	Shallow edge	Surface	Bottom	Shallow edge	
		a) Without rocks in riffles						
Riffles	R1	24.4 ± 0.0	16.2 ± 0.0	<8	47.5 ± 0.0	27.7 ± 0.0	25.6 ± 0.26	13.7 ± 0.3
	R2	25.6 ± 0.0	16.6 ± 0.0	<8	53.9 ± 0.0	40.5 ± 0.0	20.4 ± 0.14	12.6 ± 0.3
		25.0 ± 0.0	16.4 ± 0.0	<8	50.7 ± 0.0	34.1 ± 0.0	23.0 ± 0.20	13.2 ± 0.3
Pools	P1	16.2 ± 0.0	<8	<8	46.6 ± 0.0	-	<8	45.7 ± 3.7
	P2	16.5 ± 0.0	<8	<8	50.9 ± 0.1	-	<8	45.4 ± 3.1
		16.4 ± 0.0	<8	<8	48.8 ± 0.1	-	<8	45.6 ± 3.4
		b) With rocks in riffles						
Riffles	R1	9.1 ± 0.0	12.2 ± 0.0	<8	15.2 ± 0.0	22.9 ± 0.0	<8	13.7 ± 0.3
	R2	9.1 ± 0.0	14.3 ± 0.0	<8	19.2 ± 0.0	26.8 ± 0.0	<8	12.6 ± 0.3
		9.1 ± 0.0	13.3 ± 0.0	<8	17.2 ± 0.0	24.9 ± 0.0	<8	13.2 ± 0.3
Pools	P1	16.0 ± 0.0	<8	<8	14.3 ± 0.0	-	<8	45.7 ± 3.7
	P2	16.2 ± 0.0	<8	<8	20.5 ± 0.0	-	<8	45.4 ± 3.1
		16.1 ± 0.0	<8	<8	17.4 ± 0.0	-	<8	45.6 ± 3.4

Table 2. Overall mean numbers of coho and trout fry in the riffle and pool habitats in winter at the two test velocities. The numbers of fish shown in sympatry are doubled that of the actual values in order to equalize the numerical scale with that in allopatry.

		Low velocity		High velocity	
		Mean ± S.E.	Fish using cover (% of total)	Mean ± S.E.	Fish using cover (% of total)
		a) <u>Tested at 3 C</u>			
<u>Allopatry</u>					
Coho	Riffle	0.5 ± 0.1	4.4	0.4 ± 0.1	11.5
	Pool	19.7 ± 0.6	30.9	19.6 ± 0.8	39.3
Trout	Riffle	2.3 ± 0.2	69.2	2.0 ± 0.2	54.8
	Pool	18.0 ± 0.6	49.2	18.0 ± 0.7	51.2
<u>Sympatry</u>					
Coho	Riffle	0.2 ± 0.0	0.0	0.2 ± 0.0	0.0
	Pool	20.0 ± 0.3	41.6	20.0 ± 0.2	47.5
Trout	Riffle	1.3 ± 0.1	48.9	0.6 ± 0.1	28.3
	Pool	19.0 ± 0.5	72.4	19.2 ± 0.4	69.8
		b) <u>Tested at 5 C</u>			
<u>Sympatry</u>					
Coho	Riffle	4.0 ± 0.3	0.0	2.2 ± 0.3	0.0
	Pool	15.2 ± 0.4	15.7	18.4 ± 0.4	23.4
Trout	Riffle	5.5 ± 0.3	42.4	5.0 ± 0.3	28.1
	Pool	15.2 ± 0.4	54.4	15.0 ± 0.6	63.7

Table 3. Comparison of F-values ($P < 0.01$ underlined) from factorial analyses of variance of the coho and trout test series in winter. Both allopatric and sympatric trials were tested between and within species. Test variables are H, habitat; Z, size; F, feed-period; V, velocity; T, temperature; S/E, species/experiment type.

		Between species		Within species	
Variables	dF	Allopatry	Sympatry	Coho	Trout
H	7	293.69	311.29	364.24	242.43
Z	2	1.74	8.67	1.72	6.52
H Z	14	31.03	28.83	38.63	19.04
F	2	0.14	2.01	0.08	0.78
H F	14	3.67	7.90	6.35	4.02
Z F	4	0.06	0.63	0.07	0.05
H Z F	28	0.23	1.87	0.83	0.47
S/E	1	6.45	2.49	1.48	9.14
H S/E	7	10.44	81.53	6.02	19.88
Z S/E	2	2.05	0.45	0.91	0.59
H Z S/E	14	7.52	3.93	6.51	2.25
F S/E	2	0.01	0.95	0.06	0.29
H F S/E	14	0.34	1.23	0.31	0.80
Z F S/E	4	0.03	0.43	0.07	0.15
H Z F S/E	28	0.20	1.23	0.46	0.65
T	1		6.13		
H T	7		36.33		
Z T	2		0.24		
H Z T	14		5.29		
F T	2		0.33		
H F T	14		1.40		
Z F T	4		0.41		
H Z F T	28		0.79		
S T	1		1.18		
H S T	7		6.48		
Z S T	2		0.02		
H Z S T	14		2.63		
F S T	2		0.04		
H F S T	14		1.21		
Z F S T	4		0.20		
H Z F S T	28		1.09		
V	1	1.15	6.26	2.17	0.82
H V	7	18.44	21.72	24.91	19.36
Z V	2	0.55	0.10	0.53	0.52
H Z V	14	1.77	1.97	1.23	3.22
F V	2	0.41	0.47	0.09	0.32
H F V	14	0.59	1.21	0.74	0.31
Z F V	4	0.13	0.34	0.15	0.27
H Z F V	28	0.19	0.33	0.27	0.39
V S/E	1	0.0	0.95	0.16	0.01
H V S/E	7	0.65	10.84	3.65	3.61
Z V S/E	2	0.06	0.64	0.06	0.05

Table 3 (cont'd)

		Between species		Within species	
Variables	dF	Allopatry	Sympatry	Coho	Trout
H Z V S/E	14	1.82	1.73	2.50	2.08
F V S/E	2	0.07	0.54	0.07	0.07
H F V S/E	14	0.41	0.58	0.15	0.49
Z F V S/E	4	0.24	0.34	0.09	0.06
H Z F V S/E	28	0.24	0.58	0.37	0.20
T V	1		0.87		
H T V	7		1.14		
Z T V	2		0.32		
H Z T V	14		2.49		
F T V	2		0.15		
H F T V	14		0.36		
Z F T V	4		0.20		
H Z F T V	28		0.60		
S T V	1		0.19		
H S T V	7		5.61		
Z S T V	2		0.65		
H Z S T V	14		1.31		
F S T V	2		0.63		
H F S T V	14		0.60		
Z F S T V	4		0.08		
H Z F S T V	28		0.43		
Error	576/288				

Table 4. Mean rate of aggressive encounters per fish per 100 min in each of the allopatric tests in winter at pre-, during- and post-feed periods tested at a low (no brackets) and a high (brackets) water velocity at 3 C. Increase in aggression at increasing velocity indicated as +, reverse as -.

	Riffle				Pool			
	Pre-	During-	Post-feed	Av. mean	Pre-	During-	Post-feed	Av. mean
a) Coho	(0)	(0)	(0)	(0)	(20.0)	(54.4)	(27.6)	(34.0)
	0	0	0	0	13.0	45.6	33.3	30.6
					+7.0	+8.8	-5.7	+3.4
b) Trout	(1.0)	(0)	(0)	(0.3)	(9.9)	(39.1)	(16.6)	(21.9)
	0.5	1.3	0	0.6	12.4	41.9	18.0	24.1
	+0.5	-1.3		-0.3	-2.5	-2.8	-1.4	-2.2

Table 5. Mean rate of aggressive encounters per fish per 100 min in each of the sympatric tests in winter at pre-, during-, and post-feed periods tested at a low (no brackets) and a high (brackets) water velocity at 3 and 5 C. Increase in aggression at increasing velocity are indicated as +, reverse as -.

	Riffle				Pool			
	Pre-	During-	Post-feed	Av. mean	Pre-	During-	Post-feed	Av. mean
				a) Tested at 3 C				
Coho-coho	(0)	(0)	(0)	(0)	(9.1)	(33.4)	(15.1)	(19.2)
	0	0	0	0	4.5	44.3	20.0	22.9
					+4.6	-10.9	-4.9	-3.7
Coho-trout	(0)	(0)	(0)	(0)	(4.0)	(17.5)	(9.2)	(10.2)
	0	0	0	0	3.1	31.2	9.9	14.8
					+0.9	-13.7	-0.7	-4.6
Trout-trout	(0)	(0)	(0)	(0)	(4.7)	(16.8)	(7.5)	(9.7)
	0	0	0	0	2.4	17.0	7.3	8.9
					+2.3	-0.2	+0.2	+0.8
Trout-coho	(0)	(0)	(0)	(0)	(2.9)	(30.2)	(7.2)	(13.4)
	0	0	0	0	3.5	17.4	5.6	8.9
					-0.6	+12.8	+1.6	+4.5
				b) Tested at 5 C				
Coho-coho	(0)	(8.6)	(0)	(2.9)	(15.9)	(21.6)	(13.2)	(16.9)
	4.6	34.4	19.0	19.3	24.8	52.9	29.1	35.6
	-4.6	-25.8	-19.0	-16.4	-8.9	-31.3	-15.9	-18.7

Table 5 (cont'd)

	Riffle				Pool			
	Pre-	During-	Post-feed	Av. mean	Pre-	During-	Post-feed	Av. mean
Coho-trout	(0)	(14.0)	(0)	(4.7)	(18.5)	(11.5)	(16.0)	(15.3)
	4.4	33.0	13.8	17.1	9.9	33.6	13.6	19.0
	-4.4	-19.0	-13.8	-12.4	+8.6	-22.1	+2.4	-3.7
Trout-trout	(1.7)	(9.0)	(10.8)	(7.1)	(16.7)	(24.1)	(17.4)	(19.4)
	2.1	32.3	3.5	12.6	10.9	29.7	14.3	18.3
	-0.4	-23.3	+7.3	-5.5	-5.8	-5.6	+3.1	+1.1
Trout-coho	(0)	(23.7)	(0)	(7.9)	(12.4)	(20.1)	(18.9)	(17.1)
	1.3	35.8	3.6	13.6	8.7	30.5	22.2	20.5
	-1.3	-12.1	-3.6	-5.7	+3.7	-10.4	-3.3	-3.4

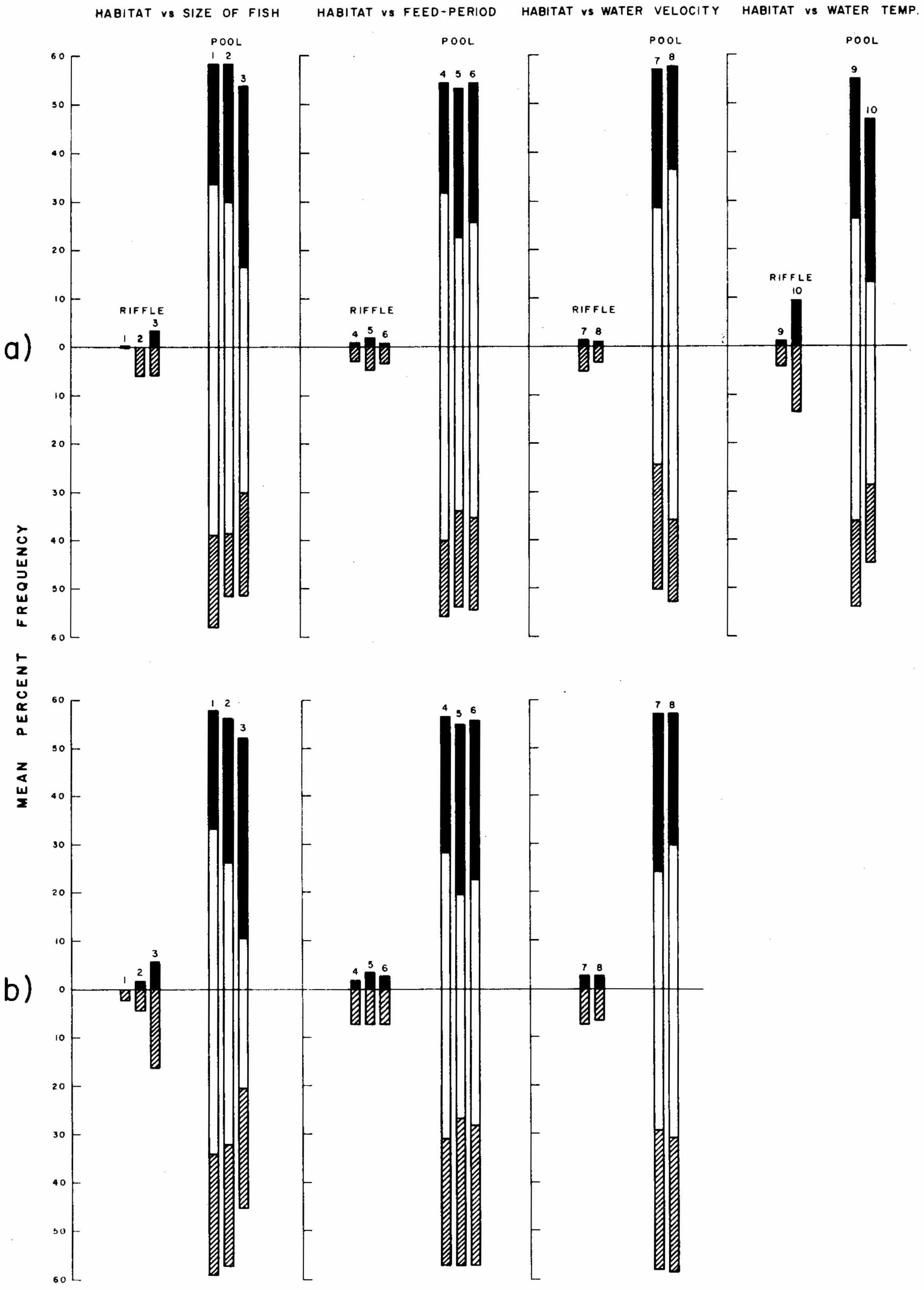

Fig. 1. Mean percent frequency plots of coho (solid) and cutthroat trout (hatched) in riffles and pools in relation to size of fish (1, large; 2, medium; 3, small-sized individuals), feed-period (4, pre-; 5, during-; 6, post-feed), water velocity (7, low; 8, high) and water temperature (9, at 3 C; 10, at 5 C) in a) sympatric and b) allopatric tests. Open portion of bars refer to undercut areas in pools.

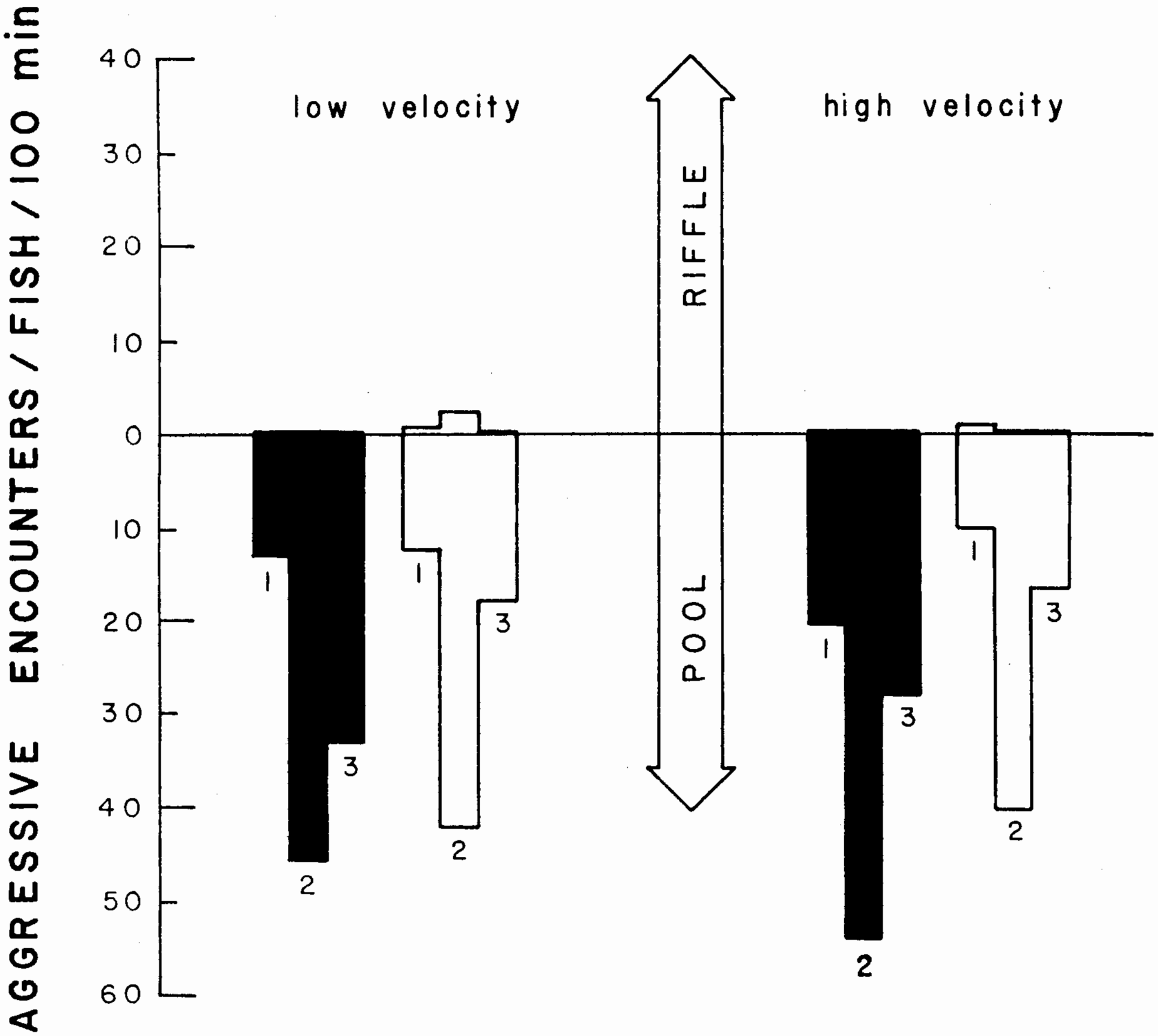

Fig. 2. Mean rate of aggression in allopatric coho (solid) and cutthroat trout (open) in relation to the feeding cycle (1, pre-; 2, during-; 3, post-feed period) in the riffle and pool test environment.

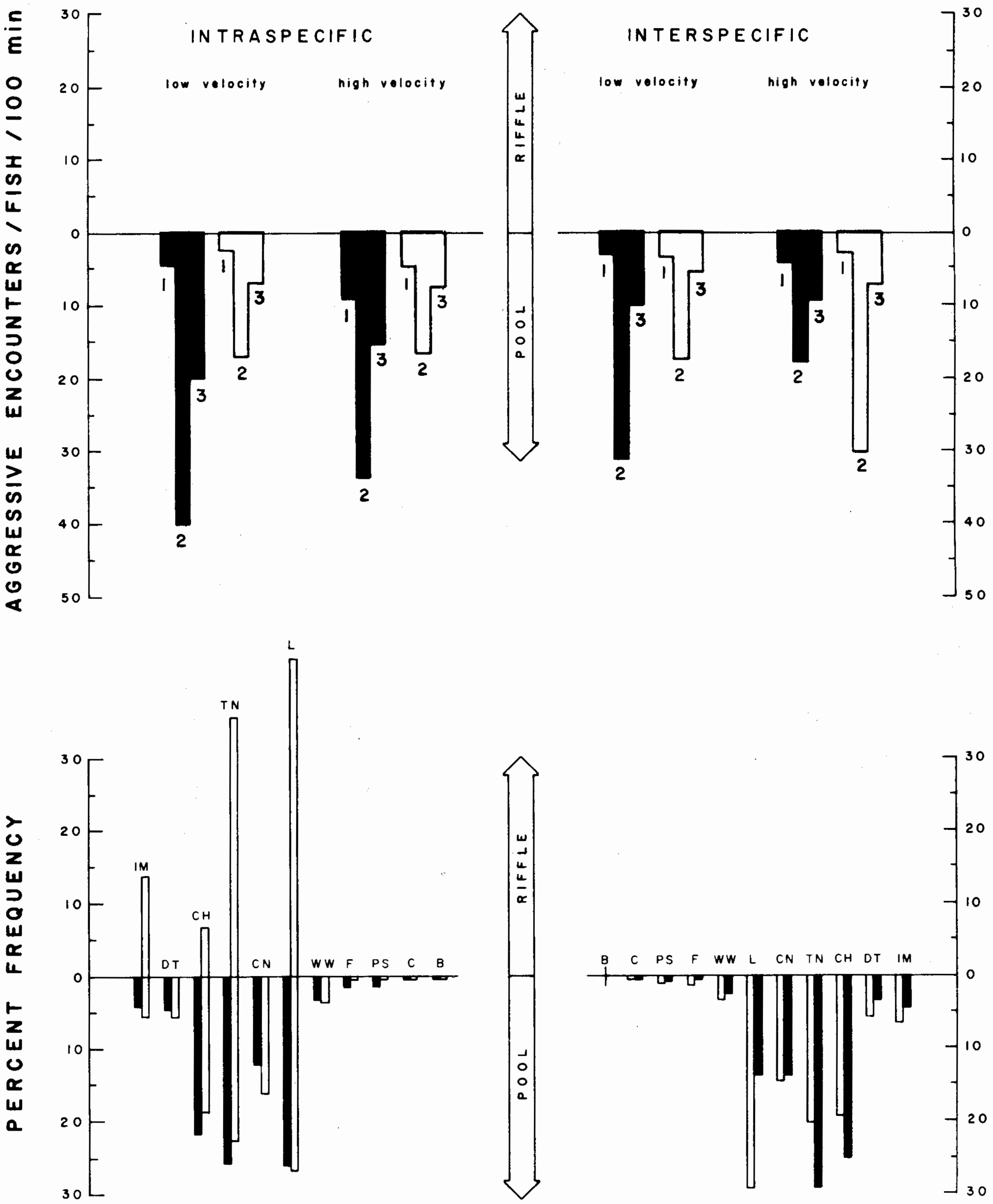

Fig. 3. Upper: mean rates of agression in sympatric coho (solid) and trout (open) in the riffle and pool environment at 3 C. Numbers relate to the feed cycle as in Fig. 2. Lower: relative frequency of the components of aggression in intra- and interspecific cases for coho (solid) and trout (open). Symbols are: IM intention movement; DT drive toward; CH chase; TN threat nip; CN contact nip; L lateral; WW wig-wag; F frontal; PS parallel swimming; C circling; B biting.

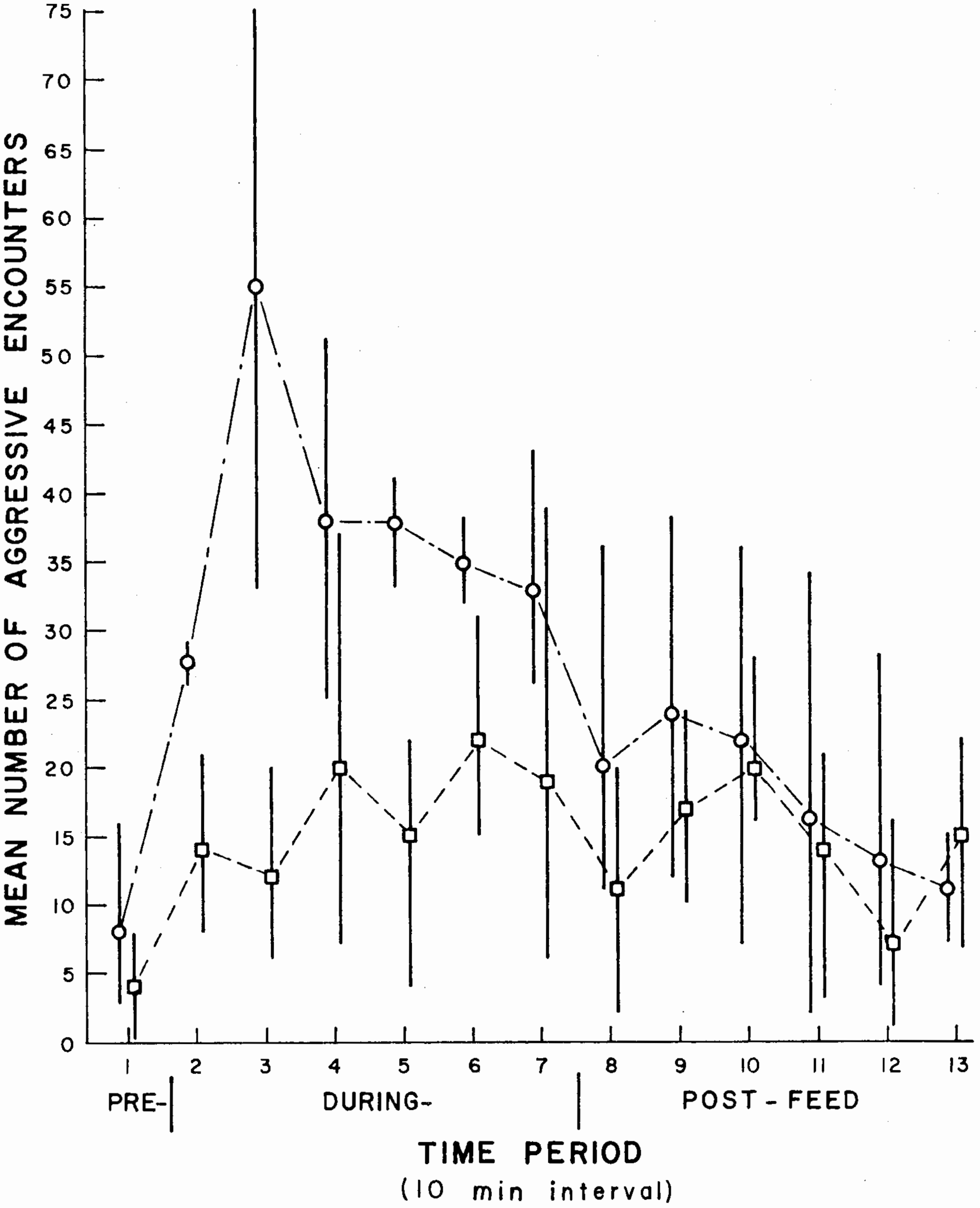

Fig. 4. Rate of aggression (number per fish per 100 min) for coho (circle) and cutthroat trout (square) in pools in relation to the feed cycle for the high test velocity at 5 C. Duration of each observation period is 5 min at successive 10 min intervals. Vertical lines indicate range.

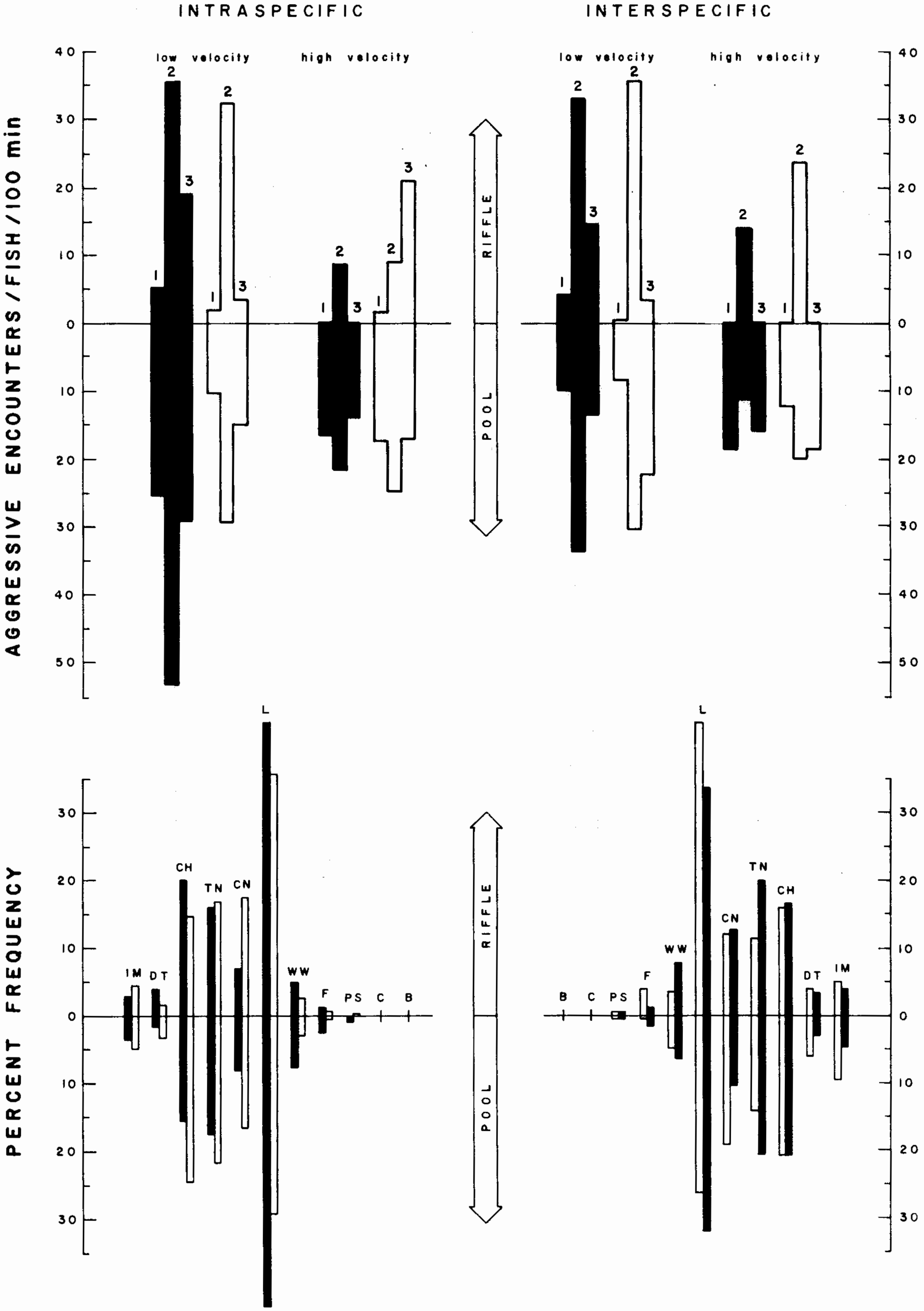

Fig. 5. Upper: mean rates of aggression in sympatric coho (solid) and trout (open) in the riffle and pool environment tested at 5 C. Lower: relative frequency of the components of aggression in intra- and interspecific cases for coho (solid) and trout (open). Symbols are as in Fig. 3.

Fig. 6. Upper Ayum Creek showing abundance of large boulders and thick shrub growth along streambank typifying age 0 trout winter habitat. Arrows: white indicate key cover sites used by fish; black, direction of stream flow.

Fig. 7. Lower Bush Creek showing extensive undercutting of large cedar root mass at abrupt meander serving as excellent overhead cover to both coho and age 1+ trout. Arrows as in Fig. 6.

Fig. 8. Lower Stocking Creek at a pronounced meander showing a potentially favorable site for improvement of cover in the mainstream (white arrow) acceptable to both coho and age 1+ trout. A semi-natural complex might consist of sections of clay tile sewer pipe or other similar dense structures, intermixed with accumulations of logs, debris and/or root masses. Note point bar formation at lower right. Black arrows indicate direction of stream flow.

Fig. 9. Lower Holland Creek showing a flooded sidepool (white arrow), a primary site for development of shelter and rest areas to coho during winter.

Appendix Table 1. Summary of experiments conducted in the stream simulator in winter and spring, 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)
	a) Winter				
Tested at 3 C					
Allopatry	Dec. 2-18, 1975	50.5 ± 0.60	45-55	47.7 ± 0.55	43-53
		66.9 ± 0.45	65-70	59.9 ± 0.86	56-67
		77.7 ± 0.49	76-79	73.8 ± 1.56	71-81
Sympatry	Dec. 18-25	55.8 ± 0.58	52-58	53.9 ± 0.48	51-57
		68.6 ± 0.87	65-72	65.4 ± 1.36	61-71
		83.7 ± 1.33	81-85	82.7 ± 0.88	81-84
Allopatry	Dec. 25-Jan. 8, 1976	58.1 ± 0.48	51-60	53.4 ± 0.56	50-58
		72.9 ± 0.41	70-75	63.0 ± 0.62	60-67
		88.7 ± 0.61	86-90	76.8 ± 1.08	74-80
Sympatry	Jan. 8-14	60.1 ± 0.40	57-62	57.3 ± 0.54	54-61
		70.1 ± 0.70	69-74	70.0 ± 0.44	68-71
		90.7 ± 3.33	84-94	92.0 ± 3.05	86-96
Tested at 5 C					
Sympatry	Jan. 14-21	56.0 ± 0.83	51-60	55.1 ± 0.60	51-59
		67.3 ± 0.81	64-70	65.9 ± 1.08	62-70
		83.3 ± 3.18	77-87	81.3 ± 3.18	75-85
Sympatry	Jan. 21-27	57.4 ± 0.47	55-60	55.9 ± 0.54	53-59
		66.4 ± 0.65	64-69	64.7 ± 0.99	63-69
		80.3 ± 1.20	78-82	81.0 ± 1.53	78-83
	b) Spring				
Tested at 7.5 C					
Allopatry	Mar. 15-Apr. 5, 1975	86.4 ± 1.10	81-91	98.8 ± 2.57	85-107
		67.4 ± 0.68	63-73	73.6 ± 0.82	69-78
		51.6 ± 0.45	48-55	59.0 ± 1.29	45-65
Sympatry	Apr. 7-21	95.2 ± 0.86	93-98	100.8 ± 0.49	100-102
		76.4 ± 0.72	73-80	76.5 ± 0.96	73-81
		55.5 ± 0.87	49-60	61.7 ± 2.25	47-64