Interactions for Food and Space Between Sympatric Populations of Underyearling Coho Salmon and Coastal Cutthroat Trout in a Stream Simulator During Summer

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INTERACTIONS FOR FOOD AND SPACE BETWEEN SYMPATRIC POPULATIONS OF UNDERYEARLING COHO SALMON AND COASTAL CUTTHROAT TROUT IN A STREAM SIMULATOR DURING SUMMER

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 summer. Fish. Mar. Serv. MS Rep. 1428: 36 p.

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

In sympatry, partitioning of space was rapid and similar to that in nature, in that coho numerically dominated pools and trout dominated riffles. In allopatry, their microhabitat use was similar, in that 60-75% of either species occupied pools. Factorial analyses of variance indicated that size of fish, simulated food supply and water velocity were ranked (high to low) as affecting microdistribution.

Coho and cutthroat trout fry communicated using an array of similar body postures and movements, 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. Species levels of aggressiveness were similar in allopatry, but differed between habitat types in sympatry, coho being more inclined to defend pools and trout riffles.

Stream management strategy should take into account the importance of maintaining habitat diversification in streams supporting sympatric populations of coho salmon and cutthroat trout.

Key words: Interaction, Microdistribution, Allopatry, Sympatry, Strategy.

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 summer. Fish. Mar. Serv. MS Rep. 1428: 36 p.

Les auteurs ont simulé un cours d'eau, durant l'été, pour étudier les interactions, liées à la lutte pour la nourriture et l'espace, entre des populations sympatriques de saumons coho et de truites fardées de moins d'un an.

Em sympatrie, la répartition spatiale s'est faite rapidement et de façon identique à ce qu'on observe dans la nature: les saumoneaux dominaient en nombre dans les trous d'eau; les truitelles dans les partires peu profondes. En allopatrie, le microhabitat était le même, chaque espèce préférant les trous d'eau dans une proportion de 60 à 75 %. Les analyses factorielles de la variance ont montré que que la taille du poisson, l'apport de nourriture simulé et la vitesse du courant influaient dans cet ordre sur la microdistribution.

Les deux espèces comminiquaient entre elles au moyen d'attitudes et de mouvements semblables. Leur agressivité prenait, dans plus de 80 % des cas, le forme de morsures, de poursuites, et de déplacements latéraux. La plupart du temps, ces deux dernières formes de comportement, était le fait des saumoneaux tandis que le plus souvent, les truitelles avaient tendance à mordre. C'est en présence de nourriture que les salmonidés ont été le plus agressifs. En allopatrie, les deux espèces étaient également agressives pour la défense de l'espace, mais en sympatrie, les saumoneaux avaient tendance à défendre leurs trous d'eau et les truitelles les parties peu profondes.

Les aménageurs de cours d'eau devraient tenir compte de l'importance de la diversité des habitats dans les cours d'eau qui abritent des populations sympatriques de saumons coho et de truites fardées.

Mots-cles: Interaction, Microdistribution, Allopatrie, Sympatrie, Plan d'amenagement.

INTRODUCTION

During the summer period of low stream flows, sympatric populations of juvenile coho salmon and coastal cutthroat trout spatially segregated to a varying degree into a consistent pattern in a number of small coastal streams on Vancouver Island, B.C. (Glova and Mason 1976a, 1976b, 1974). In accordance with Hartman (1966), cohabiting stream populations of *Oncorhynchus* and *Salmo* are most likely to segregate during summer, the season when their densities and levels of aggressiveness are both relatively high and certain environmental demands might be similar. Segregation undoubtedly attenuates interspecific competition for resources in general, and possibly for food in particular. Some advantages of segregation likely involve higher species overall growth, survival, and smolt yields to sea than might be achieved in the unsegregated state.

The ecological differences separating coho from sympatric coastal cutthroat trout in nursery streams appear to be relatively small. Both salmonids show flexible feeding (Mason and Machidori 1976; Glova and Mason 1974) and habitat responses (Glova and Mason 1976a), trout possibly more so than coho. Whether the trout's greater behavioral flexibility reflects more primitive state or a more recent evolutionary adaptation remains a moot point. However, it does appear to compensate for their social subdominance attributable to their later time of emergence, and smaller size at emergence. Such life history differences inevitably result in inequitable partitioning of resources, particularly that of space, advantageously to first arrivals. Pool-like conditions generally typify most stream regions during periods of low flow, and coho show competitive advantages over trout, particularly under these conditions (Glova and Mason 1976).

Understanding and interpretation of the ecological relations between juvenile coho and cutthroat trout associated with their behaviors and particularly applicable to management strategy are not possible in natural streams. Investigation of species behavioral mechanisms and environmental responses requires detailed behavioral observation and experimental manipulation of specific biological and ecological factors under, at best, semi-controlled conditions. To this end we employed a stream simulator as other workers have often done in attempts to better their understanding of the interactions between two salmonid species (Griffiths 1972; Hartman 1965b; Kalleberg 1958). Essentially, all experiments were designed to test the null hypothesis 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. This experimentation was intended to clarify our understanding of competitive relations between these two species in streams but to especially separate their interactions for food and space.

METHODS

A. THE TEST FACILITY

The stream simulator used was that described by Hartman (1965a), presently located at the University of Victoria, B.C. Overall dimensions and construction are shown in Fig. 1a, the maximum volume of the experimental area being 5 m long × 1.2 m wide × 0.75 m deep. The only two modifications made to the basic facility involved replacing the up- and downstream nylon screens with stainless steel mesh (2.54 × 2.54 × 0.64 mm) and installation of incandescent lighting (12, 25W bulbs) with rheostat control under the ceiling-suspended fluorescent fixtures used by Hartman (1965b). One layer of "Albanene" transparent paper running the full length and width of the lighting system was fastened to the underside to provide a more diffused light source. Artificial light intensity was uniform over the length of the test facility, averaging 250 Lux measured with a "Photovolt" model 210 photometer. Natural photoperiod was provided through a bank of high windows running the full length and directly opposite the experimental section. Water temperature was maintained to within ±0.5 C by a refrigeration unit situated at the upstream end of the test facility. On-off control of water circulation from the simulator through the refrigeration system was maintained by a thermoregulator and solenoid hookup to the recirculating pump, plus a series of gate valves which were manually operated. Water which had passed through the refrigeration system re-entered the simulator in the downstream well, being thoroughly mixed in the return flume by the drive propellor.

The water supply was from the City of Victoria, dechlorinated by facilities at the University of Victoria. Incoming water to the simulator was via a 3-cm PVC line, with ball-valve control, situated above the water surface and running the full width in the upstream well, with numerous fine jets directed downstream. Water volume in the simulator was continuously renewed with a turnover cycle of 2 days. Water depth was held constant with an adjustable standpipe arrangement in the upstream well with overflow draining into a floor sump.

The experimental section consisted of four equal units providing a duplicate pair of riffle-pool sequences starting from the upstream end (Fig. 1b, c). The foundation for the stream-bottom profile was of 3/4-in fir plywood prefabricated structures, glued and nailed, coated with "Rustoleum" paint, and assembled on-site. Running the full length of the right side (facing upstream) of the experimental section was the support for the stream edge, made of plywood 0.4 m wide with a 1 in 4 rise towards the right sidewall. The underside of this edge in both pools was covered with a wood lath, then mottled with a "Rustoleum" paint of earthen tones, followed by two coats of a mixture of fiberglass resin, asbestos powder, and fine sand to simulate texture of undercut bank materials. The outside surface of the glazing in the undercut area was covered with heavy brown paper, coated with a mottled pattern of earth-colored paints. All seams between plywood structures and walls of the experimental section were made fish-proof with narrow wood trim and caulking expansion sealant.

The substrate materials used were representative of those in streams: boulders 30 cm and over, rubble 8-29 cm, gravel 0.5-7 cm, sand less than 0.5 cm, and inorganic silt. All materials were taken from a stream, excepting the gravel and sand which were obtained from a commercial gravel quarry. The substrate compositions of each of the four microhabitat types in the simulator were arranged to resemble those in streams (Fig. 1b, c): riffles contained rubble in a staggered pattern with each slightly elevated over a shallow depression in the streambed; pools contained boulders and gravel filled in with fines and inorganic silt deposits at the head; undercut bank- and stream-edge areas contained a mixture of gravel and sand with few rubble in the latter in riffle areas. The base substrates on vertical and sloped surfaces were embedded in an earthen-colored mixture of fiberglass resin and asbestos powder holding them permanently in place. A 5 in Ø × 4 ft long log taken from a stream was obliquely positioned in each pool (see Fig. 1) as further cover for fish. Two similar logs were also placed longitudinally over the steel frame superstructure of each pool as overhead cover.

A darkened observation corridor of black polyethylene from floor to ceiling was provided on the left side (facing upstream) of the simulator. Horizontal slits in the plastic on the simulator side, along with a wood platform of full length and profile of that of the stream bottom, permitted full observation into the experimental section without disturbing fish.

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

B. THE FISH

Coho and cutthroat trout fry of sympatric origin were obtained from Craigflower Creek, a small coastal stream in Saanich, B.C. They were collected with a D.C. fish shocker and/or pole seine, transferred to the laboratory in fry cans, and held at a 12-h day length in fresh water in aerated, 50-gal tanks at temperatures similar to those in streams at time of collecting. In all cases, the fish were collected on the initial day of each experiment. Surplus fish, along with those used in the experiments, were returned to the stream upon completion of each test.

C. EXPERIMENTAL PROCEDURE

In the laboratory the selected fish were individually measured (fork length) and damp weighed under mild anaesthetic (2-phenoxyethanol). Each test required 40 fish comprised of large, medium, and small size-classes, each numerically proportional (6, 14, and 20 animals, respectively) to that in the wild populations. In tests with coho and cutthroat mixed (in sympatry) the number of fish of each species in each of the three size-classes was half of that when the species were tested separately (in allopatry) in order to keep density constant. All tests were duplicated. Appendix Table 1 gives the experimental conditions, including fish length and weight change data for each of the experiments conducted during the period June 2-September 16, 1975.

The fish were given a minimum of 2-h recovery time from the effects of the anaesthetic and handling, in well aerated water in a 20-gal dark plastic container with a cover. They were then released in the center of the test facility between 1600 and 1800 h under the available natural light in still water at 13.0 ± 0.5 C followed by initiation of the low water velocity (see Table 1) 1 h after their introduction. Each experiment lasted 1 wk. The fish were given 2 days habituation time to the test facility. Thereafter, observations were made at the low test velocity for a period of 2 1/2 days, followed by the high test velocity in the remaining 2 1/2 days, which was incrementally stepped up over a 3-h period.

Specific morphological and hydrological limitations of the simulator made it impossible to attain surface velocities in the pools comparable to those often found in streams. Despite the more than threefold greater depth in the pools than in the riffles in the simulator, the lack of both widening-out at the pools and gravity flow resulted in higher surface velocities in this habitat than those usually found in streams (Table 1). Under low-flow conditions in streams, pool-riffle near surface velocity ratios are generally around 1:5 (Glova and Mason 1976a). Rocks in the riffles created complex patterns of turbulent flow, with velocities immediately upstream being about twice as high near the bottom than that near the surface, due to the clearance provided beneath as cover for fish.

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

The timing of the routine daily observations on the positions and aggressive interactions of the fish was governed by the imposed feeding cycle: pre-feed period when no food was drifting in the system; during-feed period begun 15 min after initiation of release of drifting foods; post-feed period begun 30 min after the release of any drifting food was stopped. The observation schedule was repeated in the morning and late afternoon, usually extending from 0800-2200 h daily. The approximate horizontal and vertical (upper, mid, and lower) positions, size-class and species of each fish were recorded on outline maps of the stream bottom at each observation period. The aggressive behavior of all the fish in each of the four riffle and pool sections was recorded for a period of 10 min, each section chosen randomly. The behavioral components of aggressive encounters (both intra- and inter-specific) were coded and quantitatively recorded on a bank of four multiple key laboratory count denominators. Pilot studies of their interspecific interactions indicated that behavioral components of both species could be similarly coded, although differences were apparent in certain behaviors which will be discussed later. In experiments with coho and trout mixed, four possible types of interactions were recorded: coho-coho, coho-trout,

trout-trout, trout-coho. The behavioral elements that were recorded which appeared to best describe their interactions, elicited either singly or in a sequence of events, is described later. These were decoded onto standardized data sheets following completion of each observation period.

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

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

D. PROCESSING OF DATA

Microdistribution data was statistically tested by factorial analysis of variance. Interactions between all possible combinations of the test variables was investigated in each analysis, the maximum number of variables consisting of habitat type, fish size, feed period, water velocity, water temperature,and species tested. To standardize the numbers of fish in each of the three size-classes in a given habitat, each observation was expressed as a percent of the total fish of each size-class, yielding mean percent values in the actual computations. Statistical analysis was applied to determine if the difference was significant in 1) between species when tested in allopatry; 2) between species when tested in sympatry; and 3) within species between allopatric and sympatric tests.

For behavioral analysis, species individual components of aggression in each observation were summed and divided by the number of fish observed in order to standardize fish density. This provided a comparative measure of species rates of agression. Size of fish was not considered in the analyses, such data being available for allopatric but not sympatric trials, due to the lack of recording equipment necessary to include size in the latter tests. Student-t and chi-square tests were used wherever applicable.

RESULTS AND DISCUSSION

A. GENERAL

Partitioning of the available space in the stream simulator between coho and cutthroat trout fry in summer was rather rapid and similar in pattern to that observed in nature. There was a gradual spacing-out from their initial aggregations in pools with trout invariably showing stronger upstream responses than did coho, particularly the smaller individuals. Data collected during the 2-day habituation period showed a significant ($P < 0.001$) interaction in factorial analysis of variance between habitat type and size of fish between the initial 2 days and the following 2 days in typical experiments. Initially there was considerable shifting about in establishment of territories and dominance hierarchies. Thereafter, partitioning of space was relatively stable over time but patterns of social interactions were dynamic and different between species (Fig. 2). Unlike coho, trout initially showed a somewhat ubiquitous behavior in exploitation of food and space, actively defending both riffles and pools. However, coho aggressiveness markedly increased in subsequent days and trout decreased, the former establishing social control, showing obvious priorities in choice of space and feeding opportunities in both riffles and pools under the low flow conditions. Feeding territories in riffles were almost always immediately upstream of rocks. Overall mean levels of aggression may have been slightly higher for trout and lower for coho if the first 2 days of each experiment had been included in our routine observations. As this was generally a period of instability in the process of partitioning between the species, our observations made during the first 2 days throughout the experimental series were precluded from further analyses.

Probably the single most important variable in the test series was the time lag between replicate experiments. However, simultaneous replicate testing was not possible in the apparatus. So as to spread possible time effects evenly, a total of 4 wk lapsed between replicates. With increasing size and/or maturation, certain behaviors and environmental responses of the fish may have changed, particularly from those in the early fry stages, and more so for trout due to their later timing of emergence. Factorial analyses of variance indicated that significant ($P < 0.001$) differences between replicates were invariably that of interaction between habitat type and size of fish. Differences in their mean body size between replicates were restricted but unavoidable due to rapid growth in summer (see Appendix Table 1). Moreover, the variance in microdistributions tended to be magnified in our computations as observed values were converted to percent of fish in each size-class to standardize actual numerical discrepancies relating to size in the experimental design.

B. COMPARISON OF SPECIES MICRODISTRIBUTION PATTERNS

Microdistributions of coho and trout fry in sympatry, but not allopatry, showed distinct interspecific differences, resembling those found in nature. Pooling all the data with respect to body size and feed periods, the grand means of species numbers per habitat type in sympatry were significantly ($P < 0.01$) different at both low- and high test velocities (Table 2). Through interactive segregation, the numbers of coho in pools were about doubled that of trout, the reverse occurred in riffles. In allopatry, species numbers were similar within habitat types with differences ranging only from 1-6%. Expressed on a percent basis (Fig. 3), at the low test velocity approximately 40% of either species occupied riffles and 60% pools; an almost doubling of the velocity reduced their occupancy in riffles and increased it in pools by about 15%. Similarly, in sympatry under low flow, riffle-pool percent ratios were about 23:77 for coho and 62:38 for trout. At high flow, trout occupancy decreased in riffles and increased in pools by approximately 12%, while that of coho was essentially unaffected in both replicates.

Factorial analyses of variance were conducted in an effort to determine the statistical significance of each of the test variables in coho and trout microdistributions (Table 3). Of the possible combinations of interactions between all of the five test variables, only that of habitat type interacted significantly ($P < 0.01$) with species and fish size in all statistical tests, excepting in the allopatric tests between species. When given the choice, the microhabitat demands of these two salmonids were very similar for given size-classes. Comparisons of their relative microdistributions in sympatry for second-order levels of interaction with habitat type (Fig. 4) indicate that 1) size of fish was the most important factor, 2) simulated food supply was of secondary importance, and 3) acceleration of water velocity was of least importance in summer.

Relative size largely determined either salmonids priority of access to food and space. Fish strategically positioned in riffles and at the heads of pools had competitive feeding advantages over individuals in other areas in the simulator. In both coho and trout the pattern of habitat segregation into pools and riffles was further modified by size effects. For both species mean percent frequencies of fish in riffles were higher for the larger than for the small-sized individuals, the reverse occurred in pools. The bottom and undercut areas of pools were common refuge sites for undersized fish, actively contained there by larger, socially dominant fish, resulting in infrequent feeding opportunities for small fish. Overall size effects on fish microdistribution patterns in allopatry were similar but of lesser magnitude than in sympatry.

The simulated food supply influenced spatial partitioning and revealed certain interspecific differences in exploitation strategies when tested together. Unlike trout, coho microdistribution showed a more obvious association to the food supply; during feed periods many actively penetrated into riffles and either established transient feeding territories superimposed on trout, or displaced some into pools. In post-feed periods there was typically an influx of coho back into the pools, causing a net out-movement of trout back into riffles. However, in allopatry, both species showed similar microhabitat responses while exploiting the food supply as did coho in sympatry. However, none of these shifts between habitat types in food exploitation were significant ($P > 0.01$). Furthermore, neither species microdistribution differed significantly ($P > 0.01$) when tested in sympatry with- (pre-feed periods only) and without food in the system, suggesting there was no inherent bias in the design of drift simulation. Vertically, the prevailing spatial pattern during feeding on the simulated drift involved coho above and trout nearer to the bottom (see Fig. 5a), which may have important implications in partitioning of the food supply in natural streams.

An almost doubling of the water velocity (see Table 1) did not seriously alter the fishes' overall microdistribution patterns: in allopatry coho occupancy in riffles was reduced by 31%, trout by 23%; in sympatry, unlike trout, coho occupancy in riffles actually increased slightly, probably in response to increased levels of aggression in pools under the accelerated velocity conditions (see Fig. 7). Unlike trout, small subordinate coho did not move close to cover and frequently were actively chased out of pools by larger fish, particularly in post-feed periods.

Submerged areas of cover beneath rocks in riffles and undercut banks in pools were not heavily utilized by either coho and cutthroat fry in summer. Smaller fish were the more frequent users of cover sites, often in escape from aggressive encounters. In both salmonids, sites offering maximization of food-getting rather than overhead cover were generally more directly associated with territories of dominant fish. In riffles, coho were never found, and trout were rarely found, in areas under cover. In pools, utilization of undercut areas ranged from 2.4-8.2% for coho and 10.1-19.7% for trout, both species showing slightly higher utilization during periods of accelerated flow and also when tested in sympatry (see Table 2; Fig. 4). Unlike in the simulator, in natural streams exploitation of drifting foods by fish with territories in undercut areas may be better due to greater convergent flow at meanders.

C. COMPARISON OF SPECIES' AGGRESSIVE BEHAVIORS

Coho and cutthroat trout fry communicated using an array of similar body postures and movements previously described by other workers for stream-dwelling Salmonidae: lateral and frontal threat displays (Fabricius 1953; Kalleberg 1958); intention movement, chasing, threat and contact nips, and wig-wag threat display (Hartman 1965b; Mason 1969); parallel-swimming, circling and biting (Mason 1969). Of these, only the lateral threat display showed apparent differences between species. Firstly, duration of intra-specific displays was quantitatively found to be generally longer in trout (1 to about 120 s) than in coho (1 to about 15 s), the former often simultaneously involving either singly or in sequence, parallel swimming, circling, intense nipping and biting of the peduncle region. Secondly, cutthroat trout possess a brightly orange-coloured hyoid slash which is exposed when the basihyal apparatus is lowered in bouts of high intensity lateral threat aggression (see Fig. 5b), and is accompanied by rapid quivering of the caudal region. Its adaptive significance is uncertain but it appears to function as an auxiliary intraspecific communication signal between contesting fish. Size and colour intensity of the hyoid slash may be important also. Intraspecific lateral threat encounters between closely matched trout often led to prolonged bouts of butting and biting usually near the bottom of pools, occasionally to a state of physical exhaustion. In an extreme case, a total of 530 aggressive acts over a period of 12 min, mostly intense nipping and biting, was exchanged between two trout in a territorial dispute. In contrast, interspecific lateral threat encounters rarely exceeded 10 s, even in cases where the fish were closely matched.

Qualitative analysis of individual components of aggressive behavior expressed on a percent basis of the pooled data show the following points (see Fig. 7, bottom). Firstly, the most frequently used behavioral elements in both coho and cutthroat trout was that of chases, nips, and lateral displays, comprising more than 80% of their total aggressive activity. Secondly, the more elaborate threat displays and non-contact behaviors were more frequently used by coho as opposed to the predominant nipping behavior by trout. Nipping activity made up 45% of a total 11,088 aggressive encounters for trout and 33% of a total 15,257 encounters for coho. Neither species showed obvious differences in frequencies of displaying and nondisplaying forms of aggressive activity between the riffle and pool environments when tested under the low and high velocity conditions, as reported by Hartman (1963) for young brown trout.

Habitat had greater effects on species levels of aggressiveness in sympatry than in allopatry. In allopatry, overall levels of aggression in either salmonid were similar ($P > 0.05$) between pools and riffles, although both species were socially less active in riffles at high velocities (Fig. 6). Over a possible maximum period of pooled observations of 2400 min, coho offensive activity amounted to 3225 and 2022 aggressive acts, and 2326 and 2054 for trout in pools and riffles, respectively. In sympatry, intraspecific aggression in coho was significantly ($P < 0.01$) higher in pools than in riffles, the pattern being reversed in trout but significant ($P < 0.01$) only under the low test velocity conditions. Pooling the data for both test velocities, intraspecific offensive activity was 2152 and 515 for coho, and 242 and 703 for trout, in pools and riffles, respectively. However, differences in interspecific offensive activity between pool and riffle environments was non-significant in either species (coho 677 and 477; trout 435 and 618). Mixing the two species in a riffle and pool environment had the overall effect of reducing coho aggressiveness in riffles and trout in pools. In total, coho aggressive activity was some 30% higher than that of trout.

Rate of aggression in both salmonids showed a definite relation to the feeding cycle, in both allopatry and sympatry (Fig. 6, 7). Typically, mean levels of aggressiveness peaked in both riffle and pool environments when food was drifting in the system. However, chi-square tests were not significant in all cases. In allopatry, only the aggressiveness of trout in pools rose significantly ($P < 0.01$) in relation to feeding at both test velocities. In sympatry, interspecific levels of aggression for both coho and trout showed a significant ($P < 0.01$) increase when feeding in pools. In riffles, rate of coho intra- and interspecific aggression peaked significantly ($P < 0.01$) when feeding for both test velocities; trout aggressiveness increased significantly ($P < 0.01$) only against coho for the accelerated velocity conditions. With the onset of feeding, aggressiveness was more rapidly elevated in coho than in trout, the former actively penetrated riffles, exerting social control and largely displaced trout from the better feeding territories. Unlike in riffles, in pools trout appeared to be less rigorous competitors against coho, as suggested by the latter's significantly ($P < 0.01$) higher offensive activity against members of their own species than against trout at both test velocities.

The near twofold acceleration of the water velocity did not appreciably effect species levels of aggression. In both allopatry and sympatry,velocity effects on fish aggression were similar (Tables 4, 5): in riffles, level of aggression in both species decreased, although non-significant ($P > 0.05$); in pools, aggressiveness in coho but not trout, increased significantly ($P < 0.05$) when the velocity was accelerated, paralleling results reported for Atlantic salmon (Kalleberg 1958).

D. SPECIES RELATIVE DENSITY EFFECTS

Typically, sympatric populations of juvenile coho salmon and trout in streams spatially segregate to a varying degree into pools and riffles, respectively, during the seasons of best growth. The degree of overlap in microhabitat use between populations of these salmonids may in part reflect species relative density effects. The possibility of greater intraspecific competition for food and space under relatively high population density may force species to exploit breadth of niche. We tested this possibility for coho salmon and cutthroat trout in the stream simulator at 14 C, looking specifically at patterns of microhabitat partitioning and rates of aggressive activity. See Appendix Table 1 for the relative numbers and size of fish used in each experiment.

Habitat segregation was less distinct when species relative densities were grossly different from 1:1. In the 1:3. coho:trout density situation, trout overlapped considerably with coho in pools, in the reverse experiment, coho overlapped with trout in riffles more so than in 1:1 situations (Fig. 8, bottom).

Rates of intraspecific aggression in either species were similar, being positively proportional to their relative density and probably served to increase dispersal between habitats (Fig. 8). Intraspecific aggression increased at least threefold for the relatively high density test in either species. Coho and trout differed markedly in level of interspecific aggressions accompanying density change. Unlike trout, coho upheld social control at both high and low densities, their offensive activity being at least 6 times higher in the case where trout were high rather than low in numbers. In coho, but not in trout, rate of interspecific offensive activity related to probability of encounter.

GENERAL DISCUSSION

Juvenile coho salmon and coastal cutthroat trout are potential competitors for food and space during the summer season of low stream flows. Segregation, either selective (Brian 1956) or interactive (Nilsson 1967) is one means by which competition between species might be attenuated. Our laboratory findings confirm field observations, that when in sympatry coho and cutthroat trout socially interact which maintains their segregation within pools and riffles, the degree of overlap depending on relative and absolute densities of populations. Hartman (1965b) reported segregation in summer between coho and steelhead trout in a riffle and pool test environment. These findings illustrate convergent microhabitat demands of underyearling coho and steelhead and cutthroat trouts in summer, with pools being their preferred space. The intriguing question can be raised, as to what happens spatially when populations of all three species occur in sympatry? We speculate that coho would maintain social control in pools and that the trouts would partition the available riffle habitat longitudinally, overlap being greatest in the mid-region of the system: steelhead in the deeper, lower reaches; cutthroat in the shallower, upper reaches, small tributaries being common. Such distribution patterns for sympatric populations of steelhead and cutthroat have been reported to occur in numerous southwestern British Columbia streams (Hartman and Gill 1968). Cutthroat trout are probably socially subdominant to steelhead and exploiters of the more marginal habitats in streams, but their behavioral relationships require appropriate study under simulator conditions.

Considering our overall laboratory findings, we accept the null hypothesis in part. There appears to be no difference in the patterns of microhabitat use and feeding between sympatric populations of coho salmon and coastal cutthroat trout fry when the species are tested separately. Given the choice both species show similar spatial demands and responses to exploiting a simulated food supply. When the species are mixed their patterns of environmental exploitation differ, with the available food and space partitioned through mechanisms of social interaction. Concerning species levels of aggressiveness, we reject the null hypothesis only in cases when the species are mixed, with coho being significantly more aggressive than trout. Socially, coho dominate trout, often when the latter has up to about a 10% size advantage. In a riffle and pool environment coho are more likely to take a greater share of a limited drifting food supply than would trout when in sympatry. The more frequent occurrence of slight increases in coho body weight than in trout (see Appendix Table 1) may be considered as further evidence of the former's competitive advantages in feeding on drift. However, the duration of each of the experiments was too short to result in any conclusive differential effects on species growth. Interestingly enough, Symons (1976) found no differences in growth between juvenile Atlantic salmon, an aggressive and specialized feeder of drift, and that of three coarse fish species tested simultaneously in sympatry in a stream simulator, fed a limited daily ration of drifting live and dead foods. Actual size differences between the species used in his experiments may have confounded possible competitive feeding interactions given a range in size of prey.

The findings of the present study point to the importance of maintaining adequate habitat diversification in streams when managing for sympatric populations of salmon and trout. Its lack may favour one species over the other. Typically, hydrological conditions of summer low stream flows offer competitive advantages to salmon over trout, despite the broader spatial and feeding niches of the latter. Certain velocity and substrate-oriented instream engineering (Parkinson and Slaney 1975) implemented in specific streams would encourage habitat segregation between sympatric salmon and trout populations, simultaneously improve their food supply, and probably enhance their production.

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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 measurements systematically located. 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	Surface	Bottom	
		a) Without rocks in riffles				
Riffles	R1	24.4	16.2	40.4	23.5	13.7
	R2	25.6	16.6	45.8	34.4	12.6
		25.0	16.4	43.1	29.0	13.2
Pools	P1	16.2	< 8	39.6	-	45.7
	P2	16.5	< 8	43.3	-	45.4
		16.4	< 8	41.5	-	45.6
		b) With rocks in riffles				
Riffles	R1	9.1	12.2	12.9	19.4	13.7
	R2	9.1	14.3	16.3	22.8	12.6
		9.1	13.3	14.6	21.1	13.2
Pools	P1	16.0	< 8	12.2	-	45.7
	P2	16.2	< 8	17.4	-	45.4
		16.1	< 8	14.8	-	45.6

Table 2. Overall mean numbers of coho and trout fry in the riffle and pool habitats in summer at the two test velocities. The number of fish shown in sympatry are doubled that of the actual values in order to equalize species density in allopatry. Cover in riffles refers to under rocks; in pools, to undercut areas.

		Low velocity		High velocity	
		Mean number of fish ±S.E.	% of fish in cover	Mean number of fish ±S.E.	% of fish in cover
		a) Allopatry			
Coho	Riffle	7.3 ± 0.55	0.0	5.1 ± 0.34	0.0
	Pool	11.8 ± 0.51	2.4	14.4 ± 0.38	4.8
Trout	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
		b) Sympatry			
Coho	Riffle	4.6 ± 0.23	0.0	4.7 ± 0.31	0.0
	Pool	15.1 ± 0.32	7.3	13.8 ± 0.45	8.2
Trout	Riffle	10.8 ± 0.22	1.5	9.0 ± 0.31	0.0
	Pool	6.3 ± 0.23	11.9	8.9 ± 0.47	19.7

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

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

Table 4. Mean rate of aggressive encounters per fish per 100 min in allopatry 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
a) Coho	(27.3)	(41.7)	(27.6)	(32.2)	(56.4)	(48.8)	(39.0)	(48.1)
	42.5	49.1	46.9	46.2	48.3	44.4	48.2	47.0
	-15.2	-7.4	-19.3	-14.0	8.1	+4.4	9.2	+1.1
b) Trout	(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

Table 5. Mean rate of aggressive encounters per fish per 100 min in sympatry 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 -. C, coho; T, trout in aggressive encounters.

	Riffle				Pool			
	Pre-	During-	Post-feed	Av. Mean	Pre-	During-	Post-feed	Av. mean
C-C	(3.5)	(23.3)	(14.4)	(13.7)	(46.6)	(44.5)	(57.1)	(49.4)
	11.3	27.9	16.9	18.7	42.1	44.0	35.8	40.7
	-7.8	-4.6	-2.5	-5.0	+4.5	+0.5	+21.3	+8.7
C-T	(2.5)	(23.0)	(5.6)	(10.3)	(12.0)	(33.3)	(18.5)	(21.3)
	9.3	34.1	17.5	20.3	6.4	16.7	11.7	11.6
	-6.8	-11.1	-11.9	-10.0	+5.6	+16.6	+6.8	+9.7
T-T	(9.4)	(7.8)	(6.5)	(7.9)	(6.4)	(13.8)	(5.9)	(8.7)
	16.0	25.3	22.3	21.2	8.1	8.9	7.3	8.1
	-6.6	-17.5	-15.8	-13.3	-1.7	+4.9	-1.4	+0.6
T-C	(8.3)	(26.1)	(7.6)	(14.0)	(14.7)	(32.7)	(7.6)	(18.3)
	10.0	22.8	15.4	16.1	23.7	20.7	13.8	19.4
	-1.7	+3.3	-7.8	-2.1	-9.0	+12.0	-6.2	-1.1

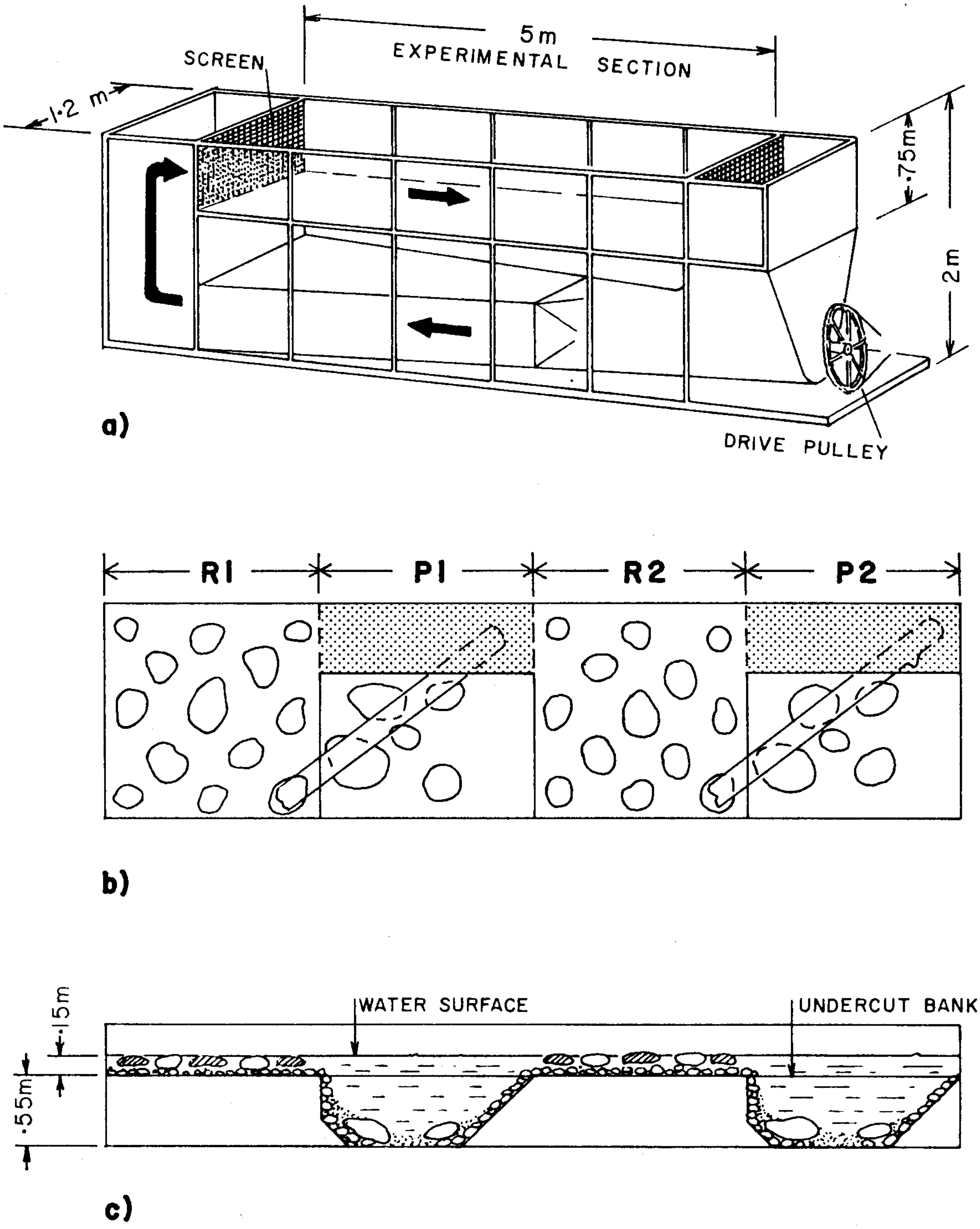

Fig. 1. a) Schematic of stream simulator (after Hartman 1965) with heavy arrows indicating direction of stream flow; b) plan view of the experimental section showing outline of rocks, logs, and undercut bank (stippled), riffles - R1, R2; pools - P1, P2; c) side view showing physiographic profile of the experimental section.

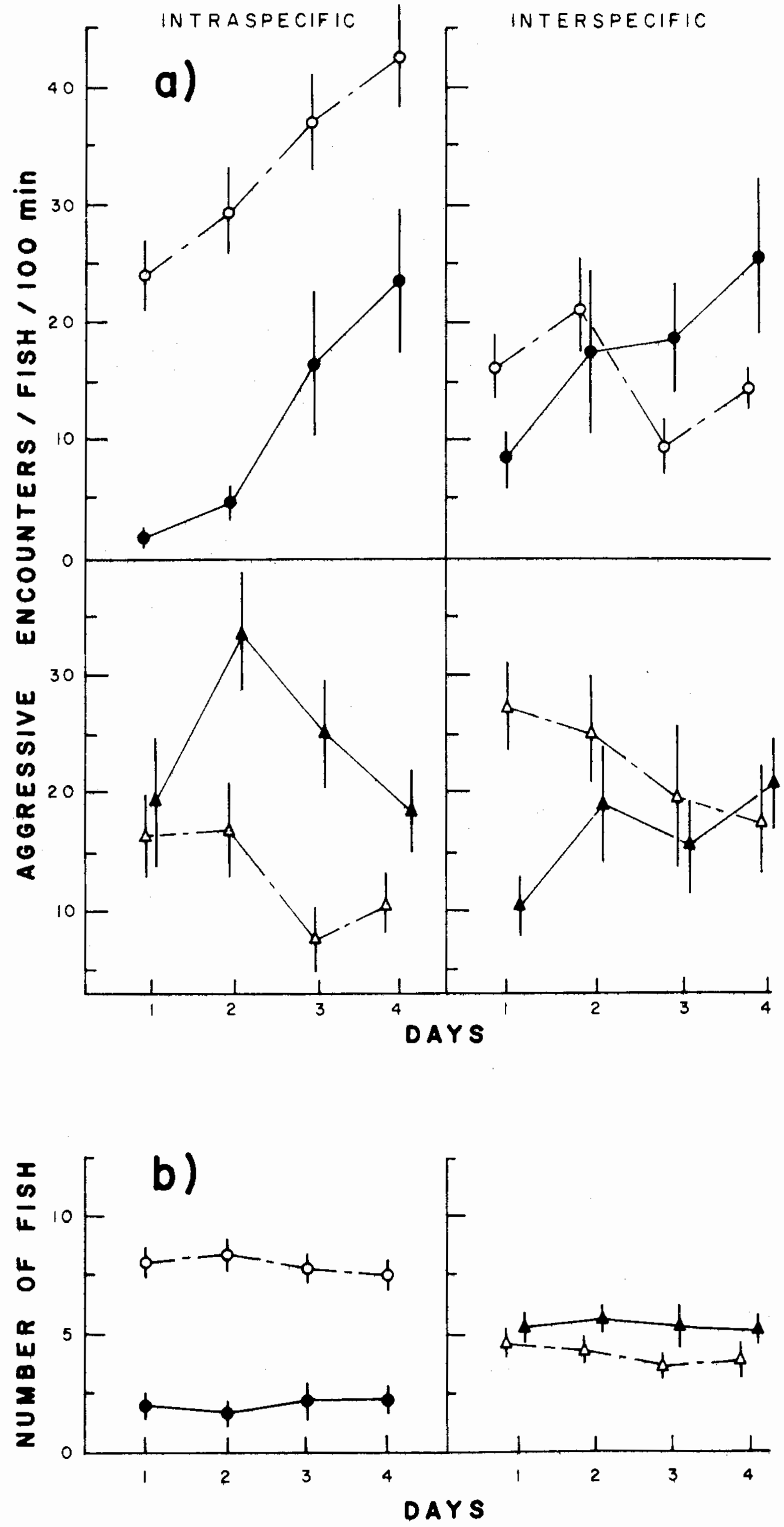

Fig. 2. Rate of aggressive encounters a) and fish microhabitat use b), for coho (circles) and cutthroat trout (triangles) in pools (open) and riffles (closed) during their initial 4 days in the stream simulator. Symbols are means ± one standard error.

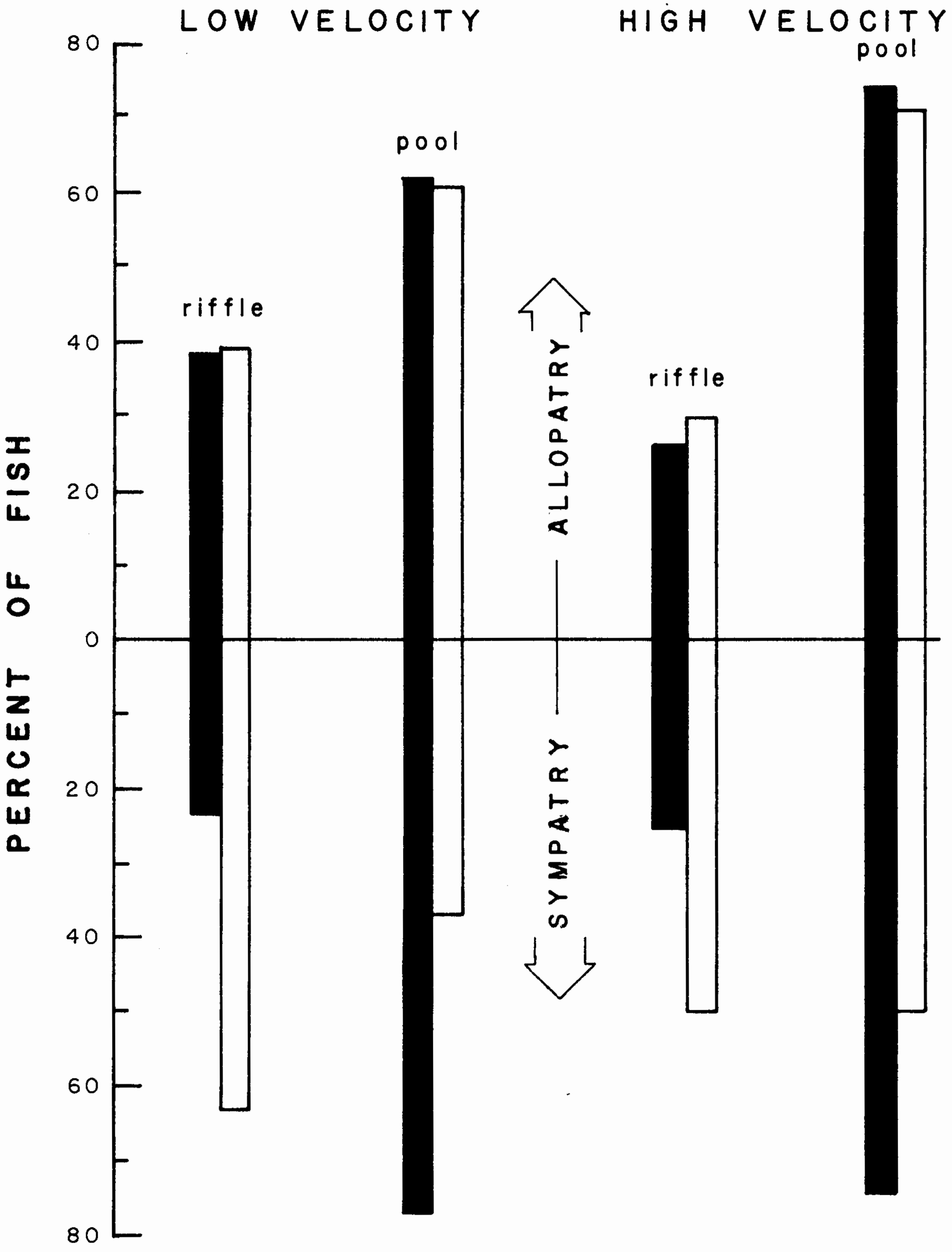

Fig. 3. Mean percent of coho (solid) and cutthroat trout (open) in riffles and pools for the low and high test velocity in both allopatry and sympatry.

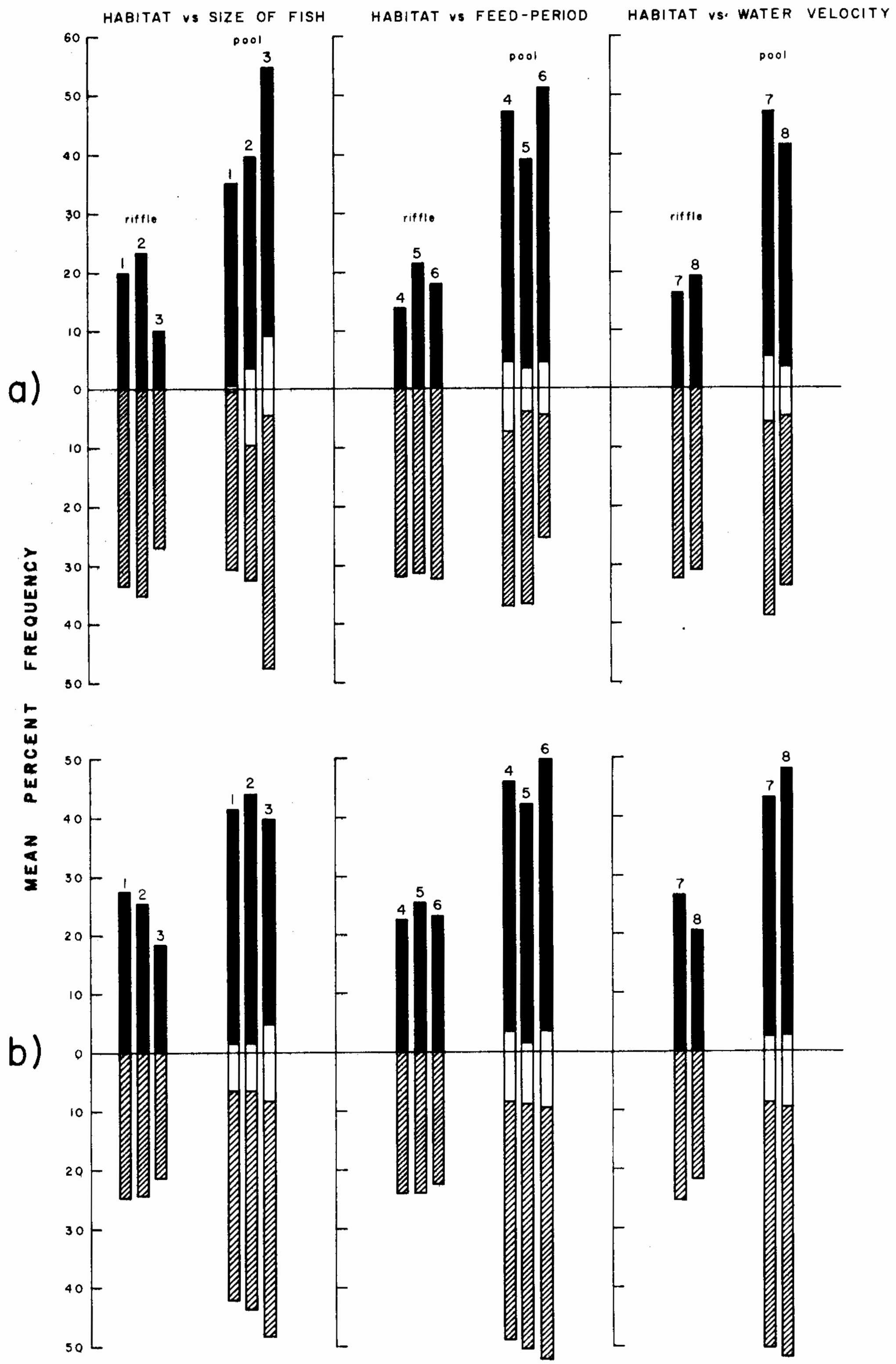

Fig. 4. Mean percent frequency plots of coho (solid) and cutthroat trout (hatched) in riffles and pools in relation to size of fish (1, large; 2, medium; 3, small-sized individuals), feed-period (4, pre-; 5, during-; 6, post-feed) and test velocity (7, low; 8, high) in a) sympatry and b) allopatry. Open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

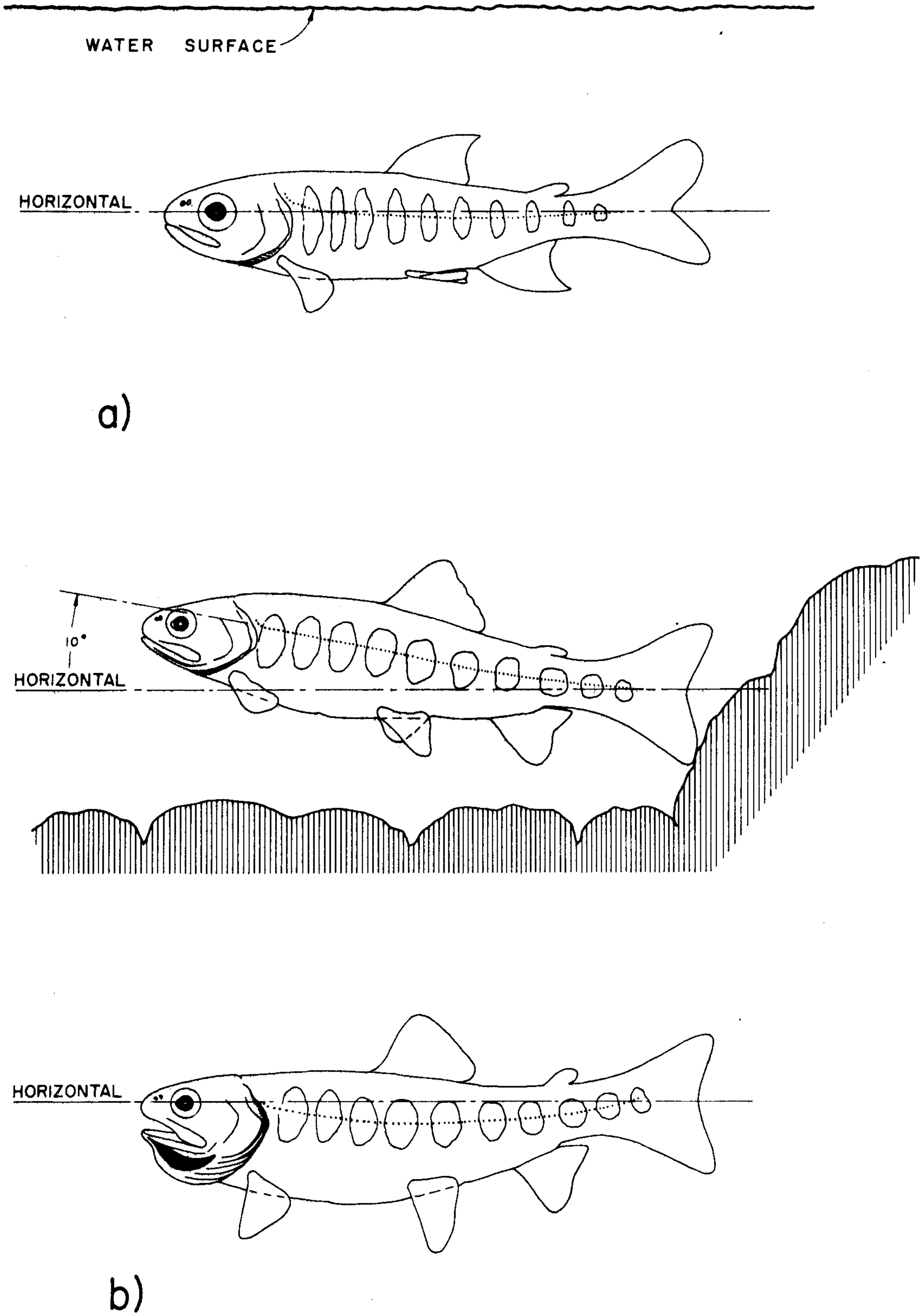

Fig. 5. a) Common pattern of body alignment and vertical partitioning in streams between coho (upper), a more specialized feeder of drifting food and cutthroat trout (lower), a more generalized feeder of both drifting and bottom foods; b) cutthroat trout in high intensity lateral threat posture showing pronounced lowering and flaring-out of the basihyal apparatus, exposing the brightly colored hyoid slash(solid). Body axis is slightly recurved, dorsal and all ventral fins are fully extended.

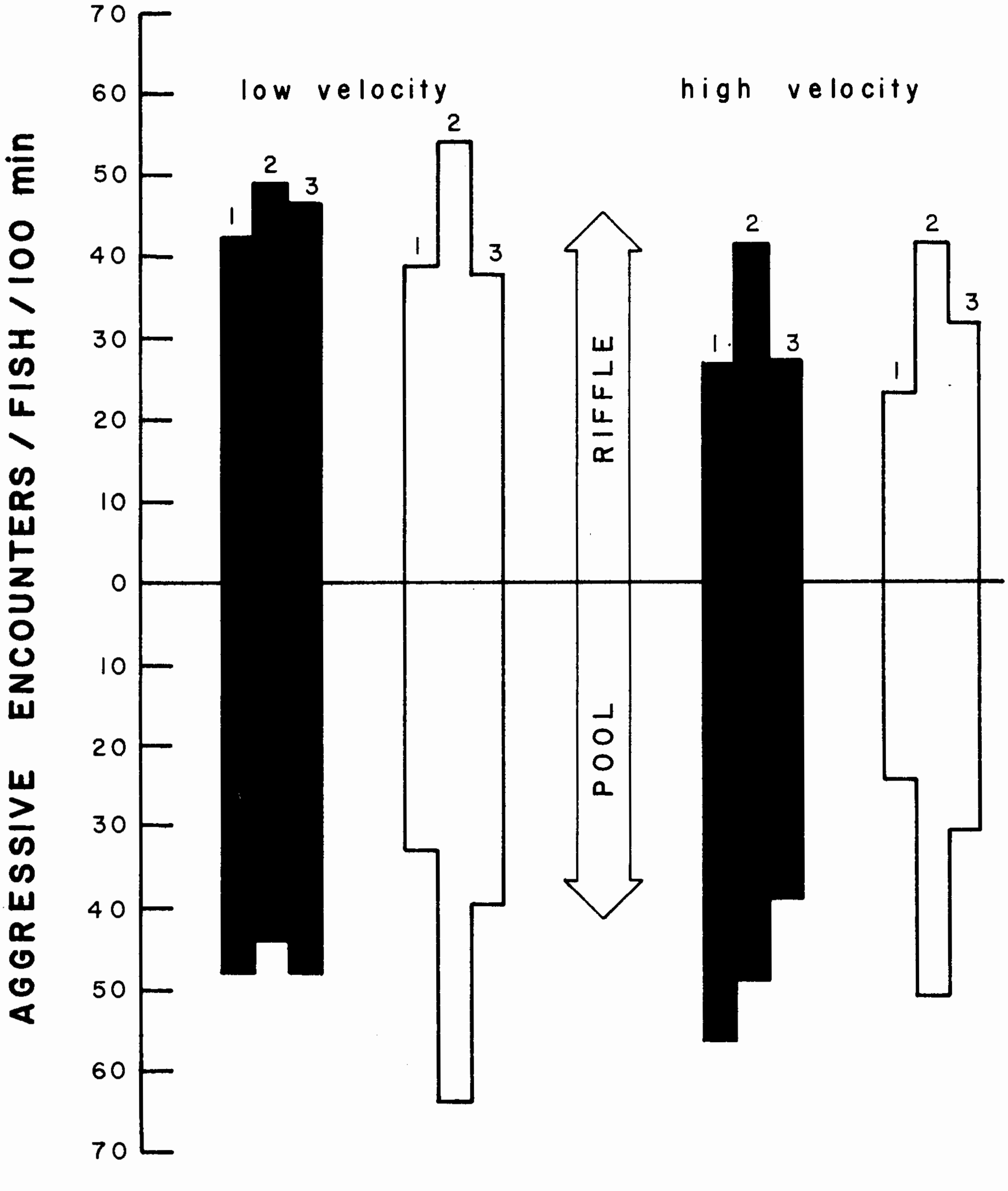

Fig. 6. Mean rate of aggression in allopatric coho (solid) and cutthroat trout (open) in relation to the feeding cycle (1, pre-; 2, during-; 3, postfeed period) in the riffle and pool test environment.

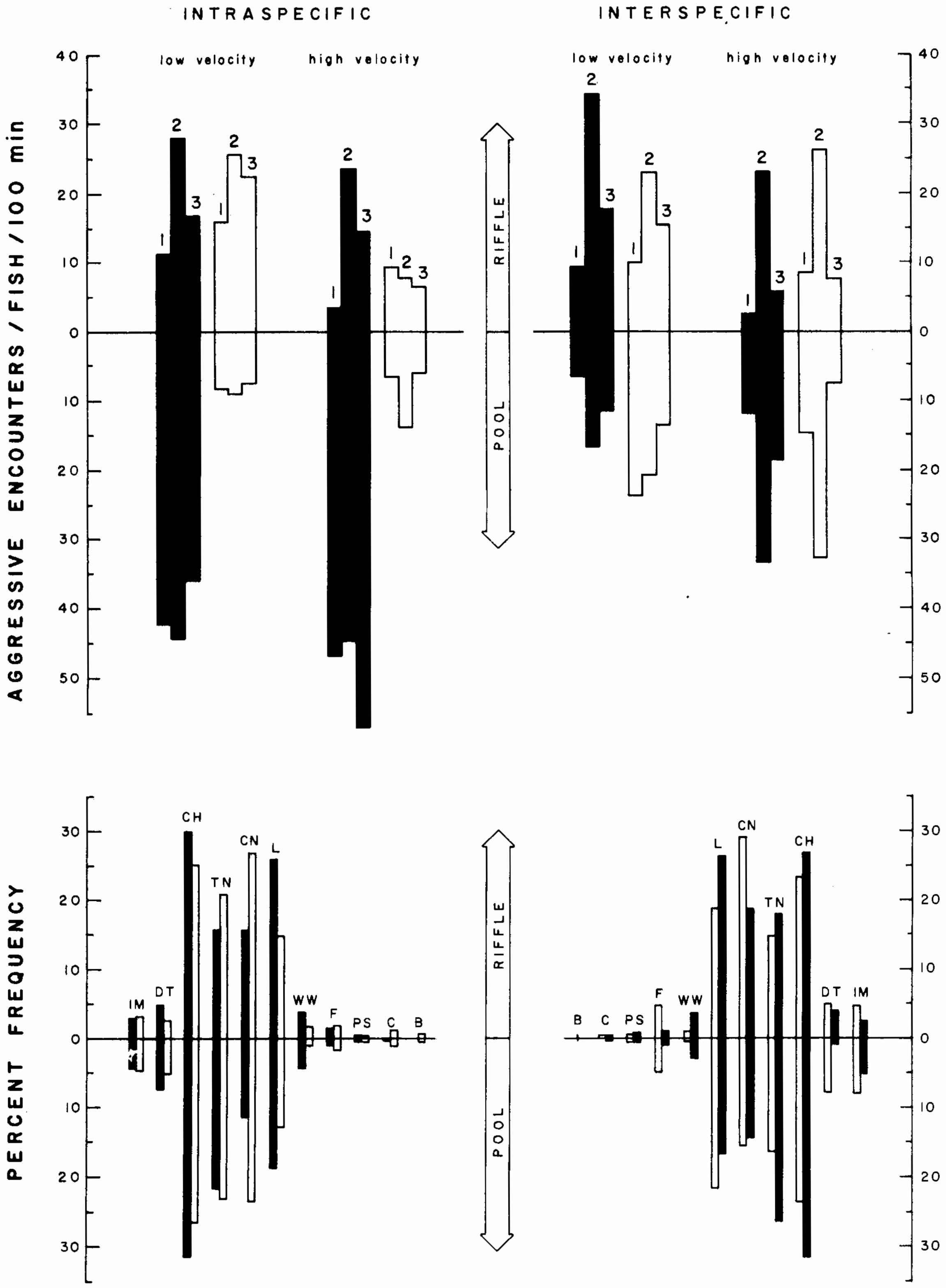

Fig. 7. Upper: mean rates of aggression in sympatric coho (solid) and cutthroat trout (open) in riffles and pools. Numbers relate to the feed cycle as in Fig. 6. Lower: relative frequency of the components of aggression in intra- and interspecific cases for coho (total 12,197 and 3,060) and trout (total 8,786 and 2,302). Symbols are: IM intention movement; DT drive toward; CH chase; TN threat nip; CN contact nip; L lateral display; WW wig-wag display; F frontal display; PS parallel swimming; C circling; B biting.

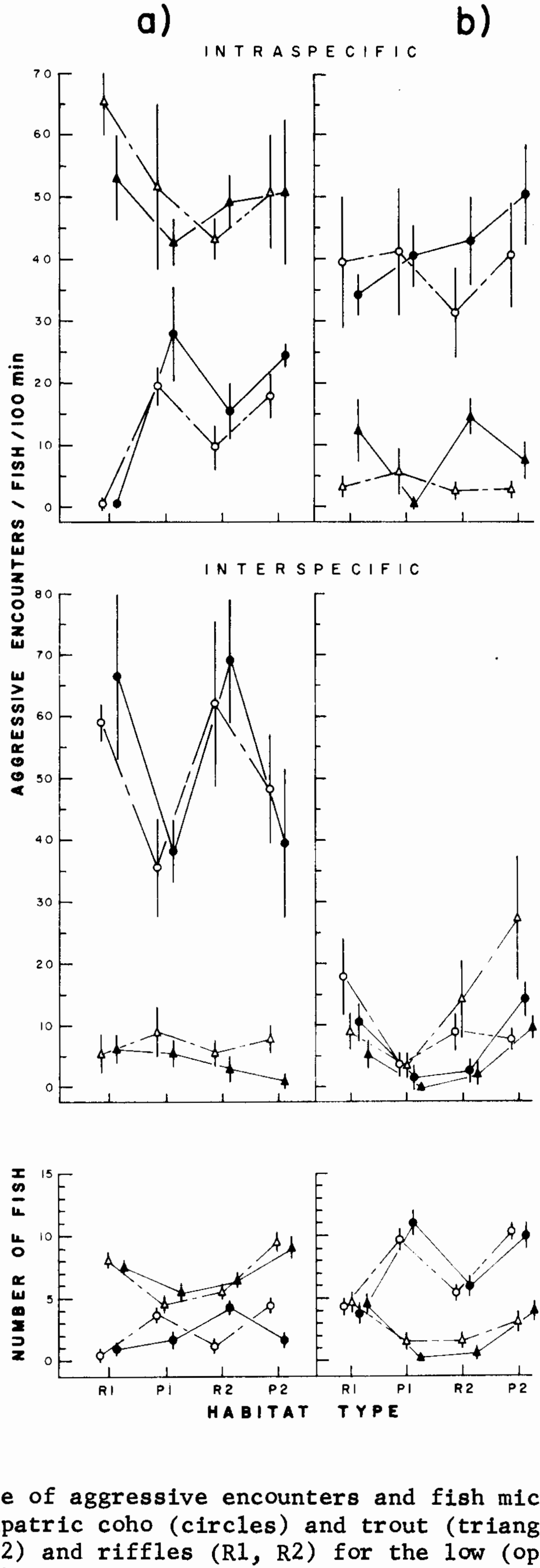

Fig. 8. Rate of aggressive encounters and fish microhabitat use for sympatric coho (circles) and trout (triangles) in pools (P1, P2) and riffles (R1, R2) for the low (open) and high (closed) water velocity at two different species relative densities: a) 10 coho, 30 trout; b) 30 coho, 10 trout. Symbols are means ± one standard error.

Appendix Table 1. Summary of experimental conditions in summer, including the fish length and weight change data in each of the three size-classes used for each experiment.

		Coho			Trout		
Experiment	Time period	Mean F.L. ±S.E. (mm)	F.L. range (mm)	% Δwt	Mean F.L. ±S.E. (mm)	F.L. range (mm)	% Δwt
		a) Main experiments					
Allopatry (1)	Jun. 2-16	36.3 ± 0.19	35-38	+15.5	37.3 ± 0.38	35-40	+12.8
		40.2 ± 0.26	39-42	+16.0	40.7 ± 0.40	39-43	+14.3
		47.0 ± 1.29	43-53	+21.8	48.7 ± 1.74	43-53	+15.8
Sympatry (1)	Jun. 16-23	38.0 ± 0.26	37-39	+7.7	37.3 ± 0.43	34-39	-3.8
		44.4 ± 0.20	44-45	+8.9	44.1 ± 0.74	40-46	+3.6
		53.7 ± 0.88	52-55	+14.5	54.3 ± 1.67	51-56	+3.6
Allopatry (2)	Jul. 7-22	38.8 ± 0.27	37-41	+3.8	38.7 ± 0.33	35-41	+28.1
		48.1 ± 0.40	45-50	+6.2	44.3 ± 0.28	43-46	+12.2
		57.7 ± 1.20	53-60	+12.7	51.6 ± 0.62	49-53	+8.5
Sympatry (2)	Jul. 22-28	38.6 ± 0.22	38-40	+4.1	38.6 ± 0.22	37-39	+7.7
		46.7 ± 0.42	45-48	+8.0	45.8 ± 0.74	43-48	+4.2
		56.3 ± 1.20	54-58	+6.8	55.3 ± 2.68	50-59	+6.0
		b) No food in system					
Sympatry (1)	Aug. 11-18	41.7 ± 0.27	40-43	-9.1	41.2 ± 0.49	39-44	-13.1
		51.3 ± 0.64	49-53	-15.1	50.6 ± 0.42	50-53	-13.3
		61.2 ± 0.44	61-62	-9.6	61.5 ± 1.32	59-64	-9.7
Sympatry (2)	Aug. 18-24	40.6 ± 0.40	39-43	-4.1	39.7 ± 0.56	37-42	-6.2
		51.7 ± 0.52	50-53	-6.0	48.0 ± 1.38	43-53	-5.7
		63.7 ± 0.88	62-65	-4.5	65.7 ± 2.03	62-69	-7.1

Appendix Table 1 (cont'd)

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