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**The Role of Behavior in the Ecology and Interaction
of Underyearling Coho Salmon (*Oncorhynchus kisutch*)
and Steelhead Trout (*Salmo gairdneri*)^{1,2}**

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ABSTRACT

Two similar salmonids, coho and steelhead, cohabit many coastal rivers of British Columbia. Field collections reveal that the distributions of underyearling coho and steelhead are similar along the length of these streams. However, the micro-distribution of the two species is different. In spring and summer, when population densities are high, coho occupy pools, trout occupy riffles. In autumn and winter, when numbers are lower, both species inhabit the pools. Nilsson (1956) stated that segregation (such as that shown by coho and trout in spring and summer) may be indicative of competition resulting from similar ecological demands. To test this hypothesis the distribution and behavior of coho and steelhead were compared in a stream aquarium at different seasons with gradients of light, cover, depth or depth/velocity, and in experimental riffles and pools. Distributions and preferences of the two species in the experimental environments were most similar in spring and summer, the seasons when segregation occurred in nature, and least similar in autumn and winter, the seasons when the two species occurred together in nature. Spring and summer segregation in the streams is probably the result of interaction which occurs because of similarities in the environmental demands of the species and which is accentuated by dense populations and high levels of aggressiveness. The species do not segregate in streams in winter because certain ecological demands are different, numbers are lower, and levels of aggressiveness are low. When the two species were together in the experimental riffle and pool environment, trout were aggressive and defended areas in riffles but not in pools; coho were aggressive in pools but less inclined to defend space in the riffles. These differences in behavior probably account for the distribution of trout and coho in natural riffles and pools.

The data support the basic contention of Nilsson (1956) and illustrate the role of behavior in segregation produced by competition for space.

INTRODUCTION

TWO SIMILAR species of salmonids occur together in many of the coastal streams of British Columbia. These fish, coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*), resemble each other in several respects. Both coho and steelhead are anadromous. Young coho remain in the streams where they hatch for 1 or 2 years, steelhead may remain in the stream up to 3 years. In addition, they are similar in size and morphology. On the basis of present concepts, they are potential competitors.³

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²Based on a thesis submitted in conformity with the requirements for the degree of Doctor of Philosophy at the University of British Columbia.

³The meaning of competition, when used in this paper is, "The demand, at the same time, of more than one organism for the same resources of the environment in excess of immediate supply" (Milne 1961). The meaning of niche is as given in DeBach and Sundby (1963).

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Young coho and steelhead coexist along the lengths of streams, but within each stream they occur in different microhabitats. Their ecology is given more fully in the text. To introduce the problem, it is sufficient to note that microhabitat segregation is pronounced in the spring when population densities are high and breaks down during fall and winter when population levels are low.

Nilsson (1956) developed valuable concepts which may provide an explanation for the separation of coho and trout during spring and early summer. He postulates that allopatric populations of closely allied species, or species having similar ecological demands, utilize the full range of their ecological potentials under conditions of intense intraspecific competition. Intense interspecific competition in sympatric populations of similar or closely related species forces each species to compete only at its "ecological optimum," i.e. under those conditions to which it is best adapted or where it has some competitive advantage. It is this tendency of species to utilize only their ecological optima that results in segregation during rigorous interspecific interaction.

On the basis of Nilsson's ideas it seems likely that certain environmental requirements and aspects of behavior of young trout and coho may be more similar in spring and early summer than during fall and winter. Accordingly there are two objectives to this study. The first is to obtain and present data from the field study outlining in some detail the period and nature of interspecific segregation. The second objective is to compare, under partially controlled conditions, the environmental responses, preferences, and behavior of young coho and trout, and to determine if segregation occurs when these are most similar. Essentially this involves testing Nilsson's ideas (Nilsson, 1956, 1963) under controlled conditions. If the species are segregated at that period when requirements are similar, attempts will be made to ascertain the role of behavior in this interaction. Newman (1956), Lindroth (1955a), Kalleberg (1958), and Nilsson (1963) have shown how behavior enters into interspecific competition. It is not clear, however, what type of behavioral mechanism functions to give one species an advantage over the second species in one situation and for this advantage to be reversed in another situation.

The research is described in two sections; the first deals with studies under field conditions, the second deals with studies in a partially controlled environment. Methods and Results are within each section.

FIELD STUDY

DESCRIPTION OF STUDY AREA

Three rivers in the lower Fraser valley of southwestern British Columbia were studied (see insets of the Chilliwack, Alouette, and Salmon Rivers in Fig. 1).

CHILLIWACK RIVER

The Chilliwack River rises in the Cascade Range in Washington and drains north into Chilliwack Lake (elevation 620 m), thence it flows west

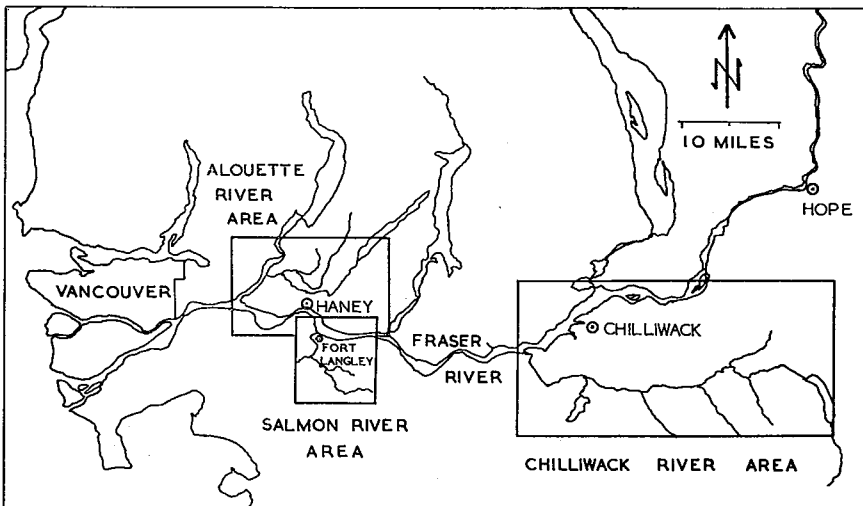


FIG. 1. Lower Fraser valley area in southwestern British Columbia showing Alouette, Chilliwack, and Salmon River systems.

into the Fraser River. Figure 2 shows the portion of the river studied and station locations.

The river runs through a deep valley in a stable rock channel from Chilliwack Lake to the region at V-28 (Fig. 2). Large areas of the upper river are covered with extensive log jams (Fig. 3,A). In the middle stretches of the river (V-28 to V-13), the channel bottom is less stable and large log jams are absent (Fig. 3,B). Several large tributaries (Slesse, Foley, Chipmunk, and Tamihi Creeks) enter this stretch of the river. The discharge of these tributaries fluctuates considerably, hence, below V-13 the channel is braided and much

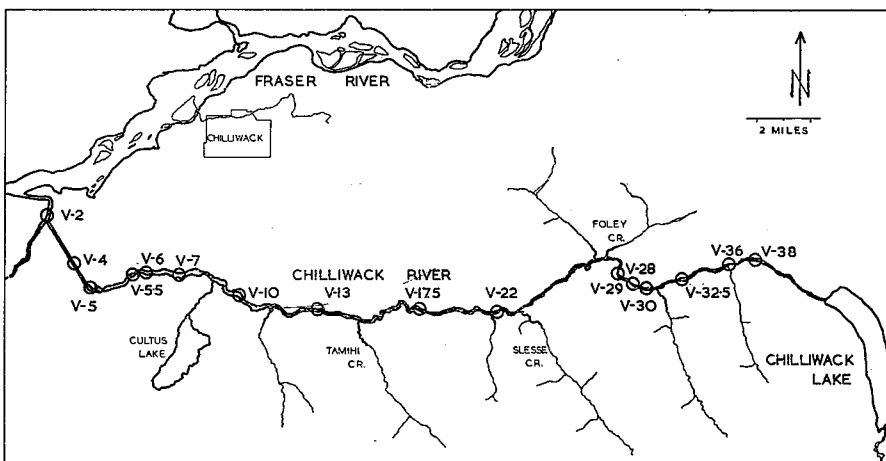


FIG. 2. Chilliwack River and location of stations.

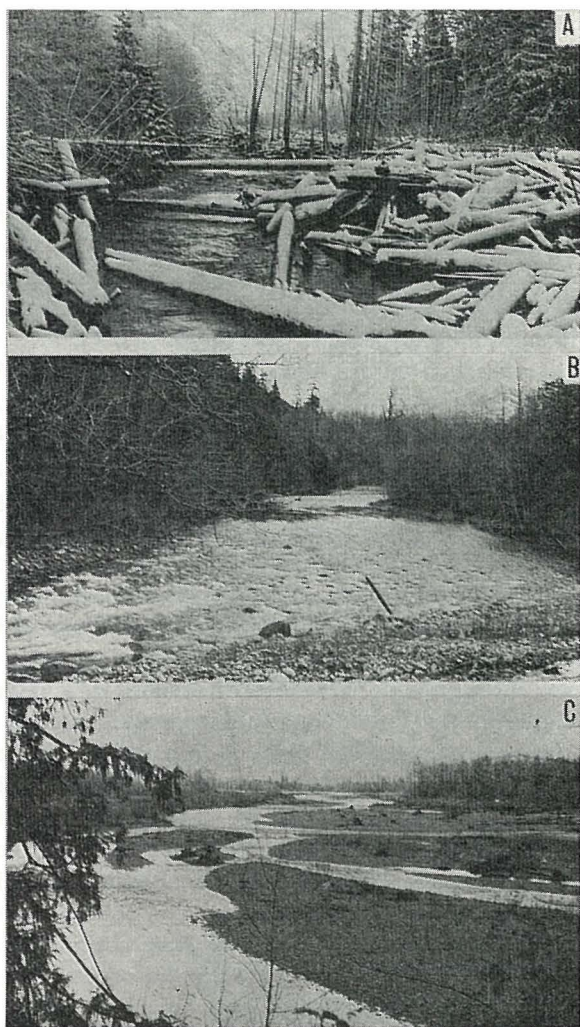


FIG. 3. A. Upper Chilliwack River in area of large log jams, V-36 to V-38. B. Chilliwack River in the region of V-17.5. C. Chilliwack River at V-5.5 and V-6. Note braided channel and unstable gravel bars.

of the bottom is unstable (Fig. 3,C). There is one log jam near V-5. The lowermost region of the river travels across flat terrain and the bottom is composed of unstable sand and gravel. Much of the channel is modified and dyked (see V-5 to V-2, Fig. 2).

The Chilliwack River drains an area of 1250 km². Between 1958 and 1962, highest flows occurred during two periods each year. In the first peak in May or June mean monthly flows ranged from 105 to 184 m³/sec. In the second peak, October to January, mean monthly flows ranged from 62 to 96

m³/sec (data from the Water Resources Division of the Department of Northern Affairs and National Resources).

During 1960, 1961, and 1962, mean monthly water temperatures ranged from a low of 2 C in January to a high of 13 C in August. (Details of temperature and discharge in the Chilliwack, Alouette, and Salmon Rivers are recorded in the thesis upon which this publication is based.)

ALOUETTE RIVER

The South Alouette River originates at the west end of Alouette Lake. It drains west into the Pitt River, a tributary of the Fraser. Figure 4 shows stations along the portion of the river which was studied.

The upper river (A-16 to A-9) runs down a shallow valley through big pools and stretches strewn with large boulders (Fig. 5,A). The stream bottom is relatively stable in most areas above A-9. From A-9 to below A-6 the river passes through flat terrain in a channel with an unstable rock and gravel bottom. In this region the river bed has been modified considerably to prevent flooding (Fig. 5,B). Lower sections of the Alouette (A-3 to A-0) lie in meadowland (Fig. 5,C). The stream bottom is composed of fine gravel, sand, and mud. Log jams are absent along the full length of the river.

The Alouette River drains an area of 205 km². During 1960, 1961, and 1962, highest mean monthly flows, 5.2–9.8 m³/sec, occurred in January. Lowest discharges occurred in July and August and ranged from 0.2 to 0.4 m³/sec. Although mean monthly discharges in winter are quite low, the Alouette River occasionally freshets violently, changing from flows of 2–3 to 112 m³/sec over a period of 5 or 6 days (data from Water Resources Division of Department of Northern Affairs and National Resources).

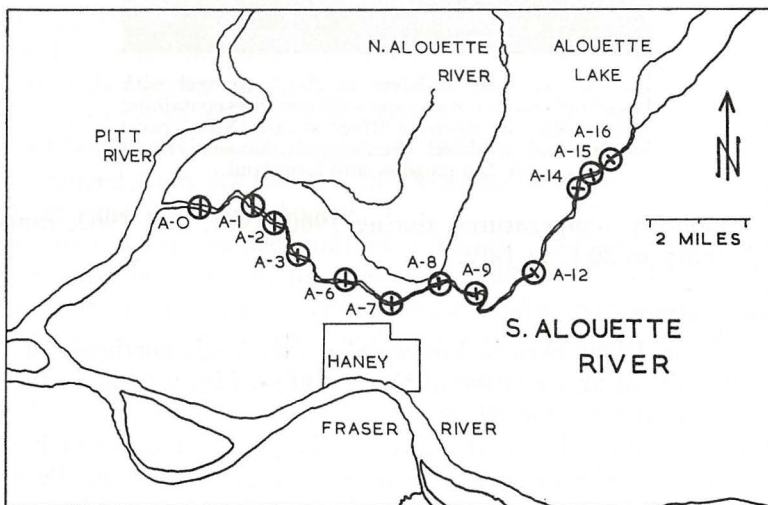


FIG. 4. Alouette River and location of stations.

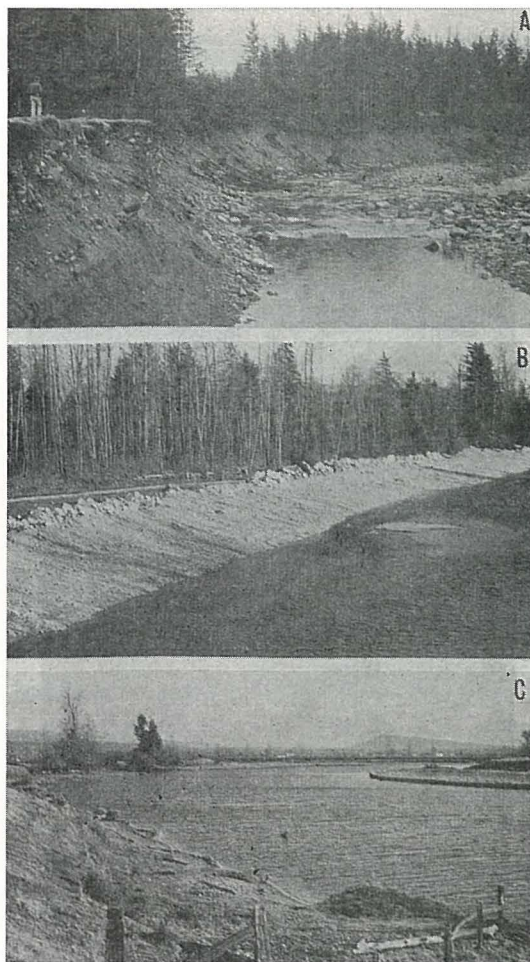


FIG. 5. A. Alouette River at A-12, channel with large boulders on bottom and with stretches containing large pools. B. Alouette River at A-7. Note gravel bottom and modified channel. C. Alouette River at A-2 in meadow and farm land.

Mean monthly temperatures, during 1960, 1961, and 1962, ranged from 2.8 C in January to 20 C in July.

SALMON RIVER

The Salmon River rises in low wooded farmland, northeast of Langley, British Columbia, at an elevation of about 100 m. Figure 6 shows the location of stations along the Salmon River.

The upper tributaries of the river lie in small valleys and have stable channels (see S-12 to S-19, and S-10 to S-18, Fig. 6). The middle section of the river lies in almost flat surroundings in a sand and gravel bed (Fig. 7,A). Below S-6 the river meanders through meadows in a mud and sand channel.

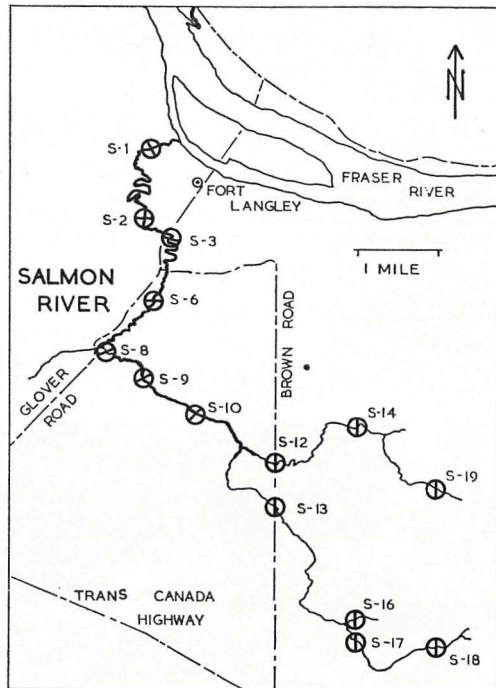


FIG. 6. Salmon River showing location of stations.

The overall character of the flow is gentle, with much of the river consisting of ripples and pools lying in well-wooded areas (Fig. 7,B).

The Salmon River drains an area of 83 km². Mean monthly flows (based on Water Resources Division data) reach a peak between November and February. In 1960, 1961, and 1962, mean monthly flows ranged from 0.23 m³/sec in July and August to 5.9 m³/sec in January and February. During winter, large short-term fluctuations in discharge occur, e.g. from 0.85 m³/sec on January 23 to 8.32 m³/sec on January 25, 1960.

In the Salmon River, during 1960, 1961, and 1962, mean monthly temperatures ranged from 3.2 to 3.8 C in December and January, and from 12.9 to 15.5 C in June, July, and August.

The three rivers studied contain a variety of types of habitat. These habitats ranged from small, low-elevation tributaries with gentle flows, to large, rapid, and turbulent rivers. Bottom conditions in each stream vary from unstable sand and gravel to stable gravel or boulders. In the field work dealt with in the next section, fish collections were made over the full range of conditions described for the three streams.

MATERIALS AND METHODS

Young coho salmon and steelhead trout were studied in three lower mainland rivers of British Columbia, the Chilliwack River (Fig. 2), the Alouette

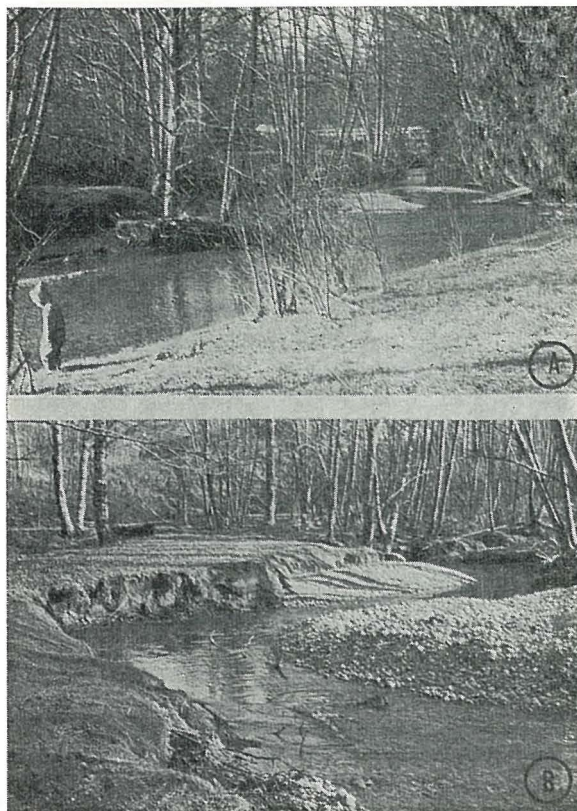


FIG. 7. A. Salmon River at S-9. B. Riffle and pool areas at S-14.

River (Fig. 4), and the Salmon River (Fig. 6). Twelve to 16 stations per river were visited about once a month from November 1959 to March 1962.

A routine collection procedure was followed if conditions permitted. Fish were always collected by seining in the Salmon River and wherever possible in the larger rivers. In addition C.I.L. "Prima Cord," a detonating fuse, and electrical blasting caps were used to collect fish among the large boulders and under log jams. The explosive was detonated in the stream above a set seine net and the fish drifted into the seine; the blast area (usually small) was searched.

Records, kept on a standard data sheet and a sketch map for each station, included number of fish collected and approximate area of stream bottom sampled. Temperatures were taken by Weksler temperature recorders. Stream velocities were calculated from the rate of movement of floating objects. Turbidity and bottom composition were recorded on a rough quantitative basis. In addition, distribution data based on collections were supplemented with a series of diving observations in the Chilliwack River. In each diving census the number, behavior, and distribution of fish were recorded in three

standard census strips on the stream margin at V-28 and V-30. Each strip was 67 m (200 ft) long and about 1 m wide.

RESULTS

LONGITUDINAL DISTRIBUTION IN STREAMS

Highest densities of young steelhead trout and coho in the Chilliwack occurred in the upper reaches of the river (Fig. 8). High densities recorded in Fig. 8 (V-29 to V-38) were not necessarily representative of the entire upper river. However the type of habitat where highest numbers were recorded (large log jams) was characteristic of the upper part of the Chilliwack. In this region, the river bed was more stable and offered better shelter to fish. For this reason numbers of fish at stations V-22, V-28, and V-30 (Fig. 8), where log jams were absent, were higher than those at comparable locations (V-17.5, V-13, and V-10) in the lower half of the river (Fig. 8). In the downstream portions of the Chilliwack (below V-10) where the bottom was unstable and the channel was braided, numbers of both species were lowest. The relative numbers of trout and coho and the general distribution pattern were the same in winter as in the period from March to September (Fig. 8). At most stations, coho were more abundant than steelhead. During the early summer young coho were captured further downstream than steelhead; but aside from this the two species were distributed in a similar fashion along the length of the river.

In the Alouette River, greatest concentrations of coho and steelhead occurred at stations A-9, A-12, A-14, and A-15 (Fig. 9), all of which are characterized by a cover of heavy boulders (Fig. 5,A). Below A-9 in areas with mud, sand, or unstable gravel bottom (Fig. 5,B and C), densities were low

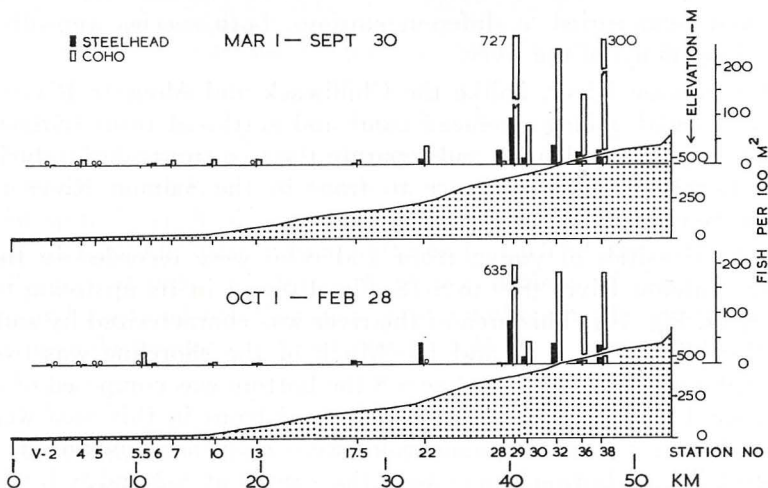


FIG. 8. Density and distribution of young coho and steelhead in the Chilliwack River (data combined for period from November 1959 to March 1962).

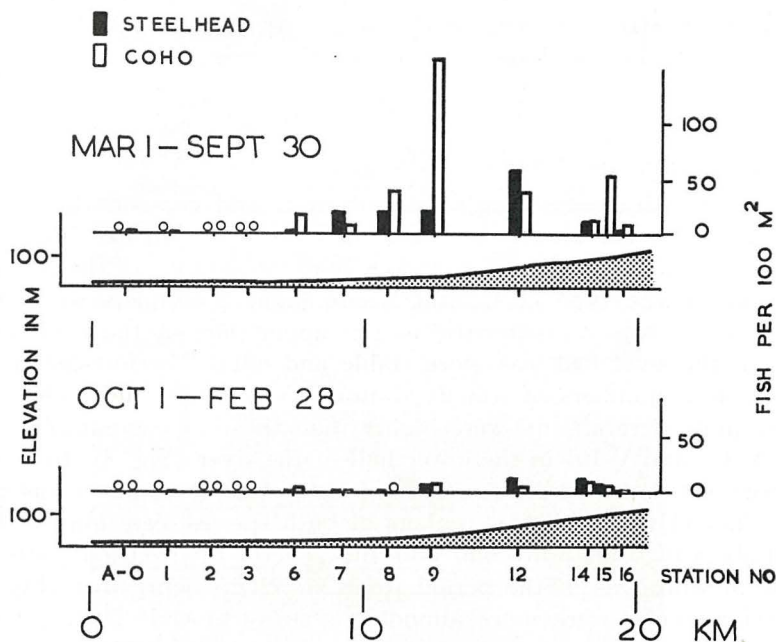


FIG. 9. Density and distribution of young coho and steelhead in the South Alouette River (data combined November 1959 to March 1962).

(Fig. 9). During the winter, density of both species was reduced to a low level, probably due to violent winter freshets which scoured the river periodically. In the period March 1 to September 30, coho fry were distributed further downstream than steelhead. Figure 9 shows that, although relative numbers of trout and coho varied at different stations, both species were distributed together along much of the river.

In the Salmon River, unlike the Chilliwack and Alouette Rivers, young coho occurred with young steelhead trout and cutthroat trout (*Salmo clarki*). It was not possible to identify and separate the two trout species during their first few months of life. Reference to trout in the Salmon River therefore includes some cutthroat as well as steelhead.

Highest densities of young trout and coho were recorded in the upper part of the Salmon River (S-9 to S-18, Fig. 10) and in its upstream tributary (S-12 to S-19, Fig. 10). This area of the river was characterized by small pools and gentle riffles (Fig. 7, A and B). Much of the shoreline was overgrown and covered with fallen trees. Below S-8 the bottom was composed of unstable gravel or sand and mud; numbers of coho and trout in this area were lower (Fig. 10). In early summer young coho were distributed down the Salmon River into the mud bottom portions of the stream at S-2 and S-3. Coho densities were higher than trout at all stations, but both species occurred together over most of the length of the stream (Fig. 10).

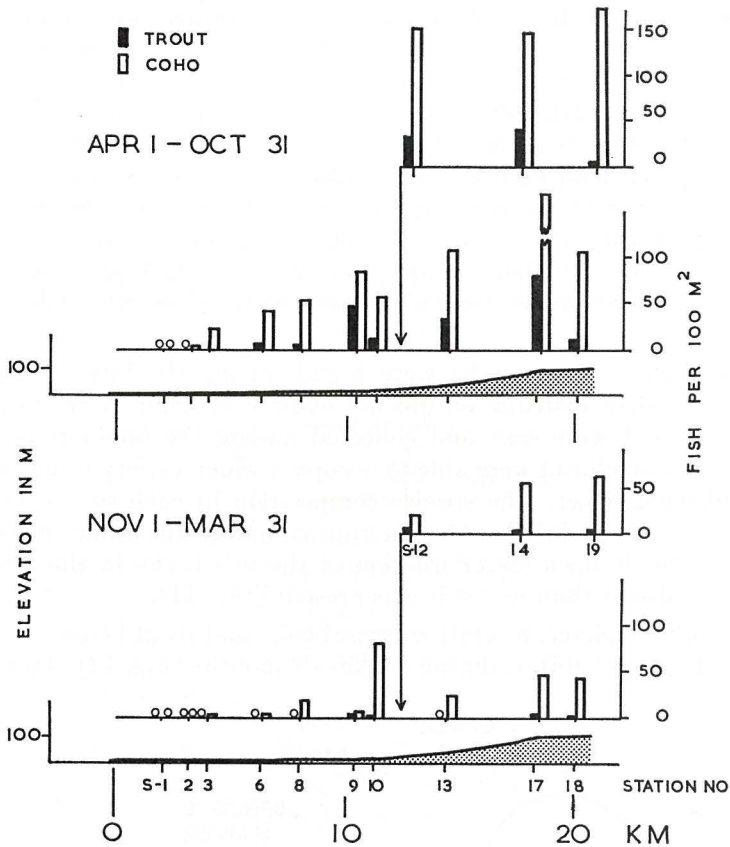


FIG. 10. Density and distribution of young trout and coho in the Salmon River (data combined November 1959 to March 1962). Broken bar in upper part of Figure represents 466 coho.

A variety of types of physical habitat was studied within each of the three rivers. Furthermore, size, bottom, and flow conditions differed considerably among the streams. Methods of sampling were not the same in all rivers. In spite of such differences in habitat and sampling the two species exhibited comparable distribution patterns in each of the three rivers (Fig. 8-10). Trout and coho cohabited the lower sections of the streams in low numbers and occurred together in highest numbers in the more stable environments near the headwaters or headwater lakes.

MICROHABITATS OF UNDERYEARLING COHO AND TROUT

In the Chilliwack and Salmon Rivers, young coho and trout exhibited seasonal changes in choice of microhabitat. In the Alouette River it was not clear whether or not changes in choice of microhabitat occurred at different seasons.

Recently-emerged trout and coho in the Chilliwack occupied three types of microhabitat: shallow water in small bays at the stream margin, small shallow riffles, and small crevices about the inshore portions of log jams and large boulders. The distribution changed during summer and early fall. By late fall most coho were located under log jams or under overhanging banks and boulders; steelhead occupied the rocky areas of the stream margin and the log jams. Figure 11 shows the density of steelhead and coho in relation to log jam cover during 3 seasons. A pronounced seasonal reduction in density occurred in areas where heavy log cover was absent. During winter those fish utilizing areas where log cover was absent were found only under or among the boulders.

In cases where young coho were found among the large stones at the stream margin, their distribution did not extend far from shore. Young trout on the other hand were seen and collected among the boulders as much as 8 m from shore. Steelhead were able to occupy a wider variety of microhabitats in the Chilliwack River. The species composition in each of the two microhabitats distinguished in Fig. 11 was approximately the same at all seasons but steelhead made up a larger fraction of the fish taken in the areas where log cover was absent than where it was present (Fig. 11).

In the Salmon River, recently-emerged coho and trout became segregated, with regard to microhabitat, during the first 2 months (Fig. 12). Trout density

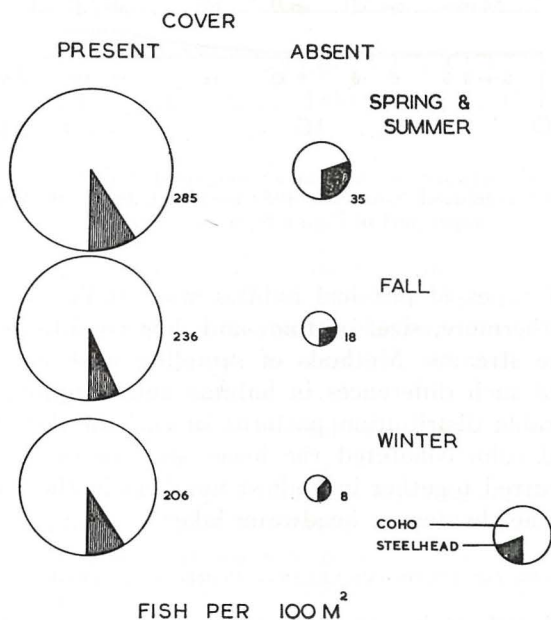


FIG. 11. Densities of young coho and steelhead in areas where cover (log jams) is present compared to areas where cover is absent. Data from the Chilliwack River, November 1959 to March 1962.

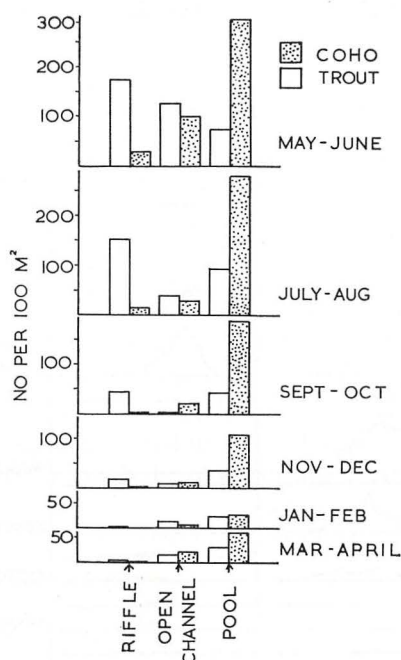


FIG. 12. Densities of young trout and coho in three types of stream habitat, riffle, open channel, and pool, during six periods of the year. Data from the Salmon River, November 1959 to March 1962.

was highest in the riffles and lower in the open channel habitats and pools throughout May–August. In this period coho densities were highest in the pools and lowest in the riffles. The density of fish decreased through the first 10 months (Fig. 12). In the fall and winter, when numbers of fish were lowest, the degree of habitat segregation was reduced. By January and February coho and trout exhibited the same pattern of microhabitat distribution (Fig. 12).

SIZE RELATIONSHIPS OF FISH IN THE SALMON RIVER

Coho began to emerge in late March, while the first trout emerged in early June. Because of this difference in hatching time, coho were larger than trout in June and July (Fig. 13). This size discrepancy decreased during late summer and autumn until, by winter, the size ranges were alike (Fig. 13). Virtually all coho migrated out of the Salmon River in May and June, at age of about 14 months. Trout remained in the river 2 years or more. Winter samples of trout could be separated into underyearling and "1 year plus" fish using length frequency plots of all trout (Fig. 14). Fish over 85 mm were designated as 1 year or more in age.

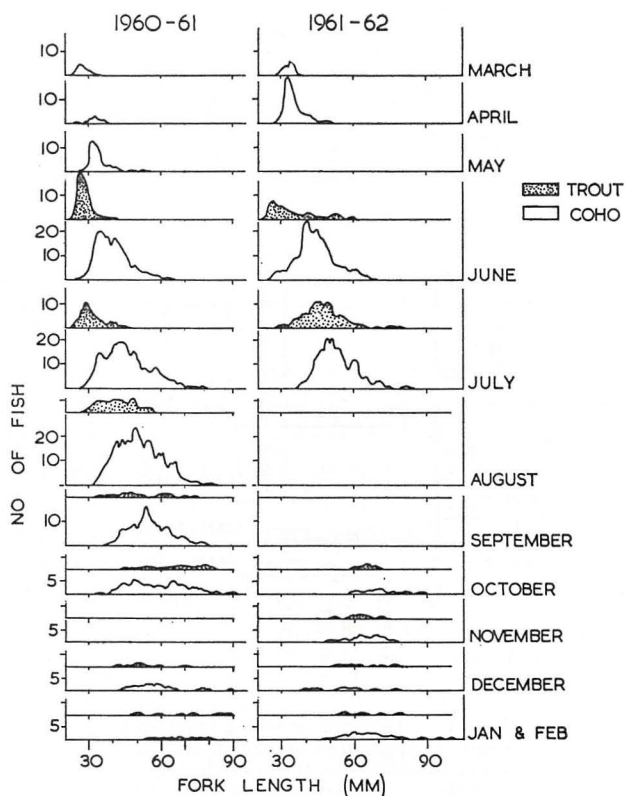


FIG. 13. Size relationships of underyearling trout and coho in the Salmon River. Smoothed curves are based on moving averages of three, data before smoothing was plotted in 1-mm length intervals.

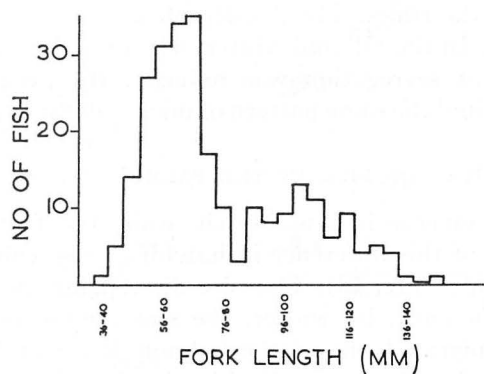


FIG. 14. Length frequencies of two or more year-classes of trout in the Salmon River. Data are lumped, October to February inclusive, for 3 winters.

SUMMARY AND COMMENTS

Field data show that trout and coho occur together along the lengths of the three streams. They are, however, found in different microhabitats within the streams. The differences in microhabitat distribution are most distinct in the small stream, the Salmon River, where trout and coho are segregated in riffles and pools in spring and summer, but to a large degree occur together in pools in winter.

This case, where segregation occurs at one season but not at another, provides a good situation where Nilsson's (1956) concepts may be tested. However, fish are difficult to observe and environmental conditions cannot be controlled in the natural stream habitat. For this reason the investigation was brought into the laboratory where fish could be studied in a stream aquarium; the second part of this paper describes the experimental facilities and the methods of comparing the distribution and behavior of the two species. Field results are discussed in the light of experimental data.

STUDY UNDER CONTROLLED CONDITIONS

MATERIALS AND METHODS

HOLDING CONDITIONS AND FISH

The experimental study was conducted between October 1962 and December 1963 in the Puntledge Park Hatchery at Courtenay, British Columbia.

The coho salmon were obtained from Little River, a small stream near Comox; the steelhead were from Big Qualicum River near Parksville. All fish were captured with seine nets. Fish used in the first series of observations (November 1, 1962, to February 20, 1963) were captured during October 15–22, 1962. Coho used in experiments between April 19 and October 9, 1963, were seined April 11–23, 1963. Trout used in work from June 9 to October 9, 1963, were obtained May 25, 1963. Size range and mean fork lengths of samples of fish, measured at several intervals during the work, are given in Appendix I.

All fish were held in running water in painted plywood troughs, 40 cm wide and 220 cm long. The troughs were housed in black plastic chambers and illuminated with fluorescent lights.

Fish used in spring and fall experiments were held at a 12-hr day length (see Appendices II and III), those used in winter experiments were held at a 12-hr day — subsequently reduced to 8 hr (see Appendix IV).

Water used in holding troughs and stream aquarium came from the City of Courtenay mains. Water temperature increased during spring and early summer, declined gradually during autumn and dropped to 0.5 C or less in winter (Fig. 15). Stream aquarium temperature in Fig. 15 will be referred to later in the text. The sharp rise and 3-day temperature peak, December 3–6 (Fig. 15), occurred when a break in the city water main forced the use of an alternate supply.

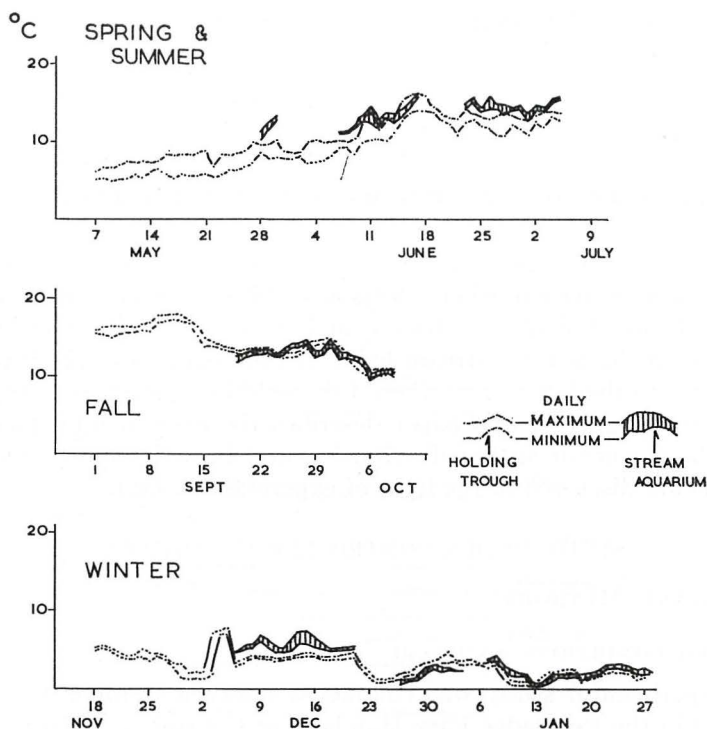


FIG. 15. Temperature maxima and minima (daily) in the stream aquarium during seasons in which the study was made (solid lines). Breaks in the line indicate that no experiments were in progress. Dotted lines represent temperature maxima and minima in holding troughs plotted for 2 weeks or more previous to experiments.

Fish in the troughs were fed a diet (by weight) 21% liver, 65% drained canned salmon, 8% brewer's yeast, 6% pablum, and salt (about 1 teaspoonful for 300 g of food). This food mixture was ground into a paste, frozen for storage, and fed in the form of frozen scrapings. Fish were fed once daily and remained healthy throughout the study.

DESCRIPTION OF STREAM AQUARIUM

The stream aquarium was designed to represent a short section of a small stream. Dimensions of the unit are 6.3 m long, 2 m high, and 1.2 m wide with an observation area 5 m long and 0.7 m deep (Fig. 16).

Most of the aquarium is made of 1-inch (2.5-cm) plywood supported in a framework of 2-inch \times $\frac{1}{4}$ -inch (5.1 \times 0.6-cm) angle iron. The windows are $\frac{5}{8}$ -inch (1.6-cm) plate glass. Construction of the axial-flow pump required a strong, nontoxic, rust-resistant material. This portion of the aquarium was therefore made of $\frac{1}{8}$ -inch (0.3-cm) welded mild steel lined with $\frac{1}{8}$ -inch (0.3-cm) fiber-glass reinforced plastic.

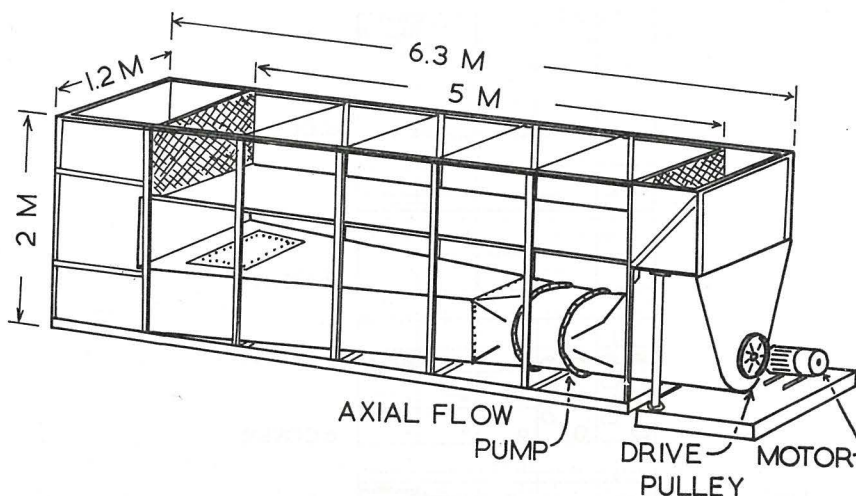


FIG. 16. Experimental stream aquarium. Details of the drive mechanism are not shown.

Current in the stream aquarium could be maintained at the desired velocity with a variable-speed-drive mechanism. Water level was adjusted with an inlet hose and a series of drain pipes. Water was circulated from the pumps along the tapered duct at the bottom of the unit, up at the end opposite the motor, and along the observation flume back to the pump.

The apparatus was lighted from overhead by parallel fluorescent lights running the full length of the observation flume.

An observation gallery of black polyethylene sheeting paralleled each side of the tank. Adjustable horizontal slits in the plastic facing the aquarium permitted observation from the darkened galleries without disturbing the fish.

DESCRIPTION OF EXPERIMENTAL ENVIRONMENTS

Behavior and distribution of fish were compared in a control environment, in four different environmental gradients, and in a riffle-pool environment. The following is a description of these arrangements and some of the conditions associated with them.

Figure 17 shows lateral aspects and plan views of control and four gradients. In the *control situation* (Fig. 17,a) the water depth (28–29 cm), bottom gravel (3–6 cm), velocity (22–24 cm/sec), and lighting conditions were uniform along the length of the observation flume.

The *light gradient* (Fig. 17,b) was produced with a series of 10 plexiglass sheets. The first sheet was clear, the remaining nine sheets were coated with progressively more black paint. Light intensity in the gradient was measured with a "Photovolt" model 514 M photometer. Table I shows the average light intensity (lux) along the observation flume. Bottom condition, depth, and velocity were the same as in the control.

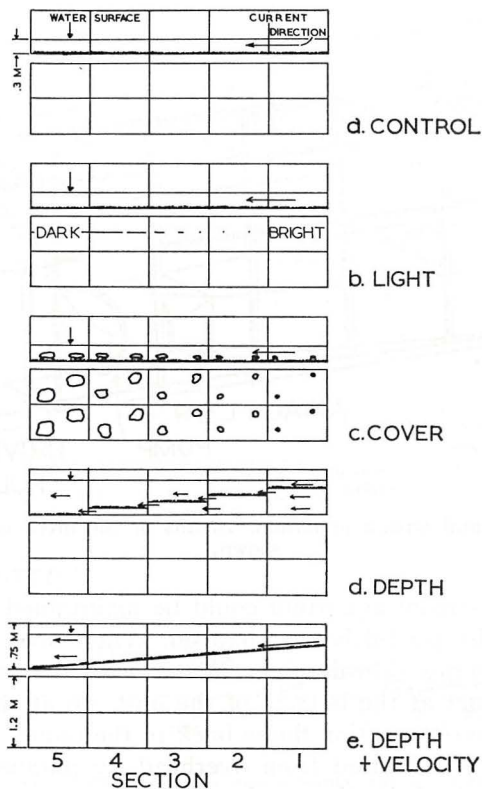


FIG. 17. Lateral and plan views of control arrangement and light, cover, depth, and depth and velocity gradients. Light and control conditions appear similar except for graded filters used to produce light gradient.

TABLE I. Average light intensity over the length of the observation flume. Photo cell readings taken on the bottom with no water in the aquarium.

5		4		3		2		1		Section
4.75	4.25	3.75	3.25	2.75	2.25	1.75	1.25	0.75	0.25	(Meters from upstream end)
2.60	10.8	23.8	48.6	85.3	157.7	189.0	201.9	375.8	281.0	(Lux) ^a

^aMean of three readings across the aquarium.

The *cover gradient* consisted of five groups of stones (Fig. 17,c). Stones were elevated above small depressions in the gravel so that each had a 4- to 6-cm cavity under it. The size of stones in each section varied somewhat as given in Table II.

To produce the *depth gradient* four sheets of plywood were arranged step-wise in sections 1, 2, 3, and 4 (Fig. 17,d). Screens between the leading and

TABLE II. Dimensions of stones used in cover gradient.

	Section				
	5	4	3	2	1
Range in:					
Length (cm)	22-30	15-17	13-15	10-14	7-12
Width (cm)	18-24	12-14	10-11	7-8	5-6
Thickness (cm)	4-6	4-7	2-4	2-5	2-4

trailing edges of the steps kept fish above them, but allowed an even flow of water so that velocities were near constant at all depths (Fig. 18). The bottom was covered with the same gravel used in the control. Illumination was slightly higher in the upstream section where the floor panels were elevated closer to the light source.

The *depth-plus-velocity gradient* was produced by means of a sloping false floor (Fig. 17, e). It was not possible to vary velocity along the length of the observation flume without altering depth or width. Details of velocity profiles in horizontal and sagittal planes are shown in Fig. 19. The bottom was covered with the same gravel used in the control. Light intensity on the raised upstream end of the false floor was slightly higher than on the downstream end.

Figure 20 represents the *riffle and pool environment*. This arrangement caused the current to exhibit complex flow patterns which are described briefly below:

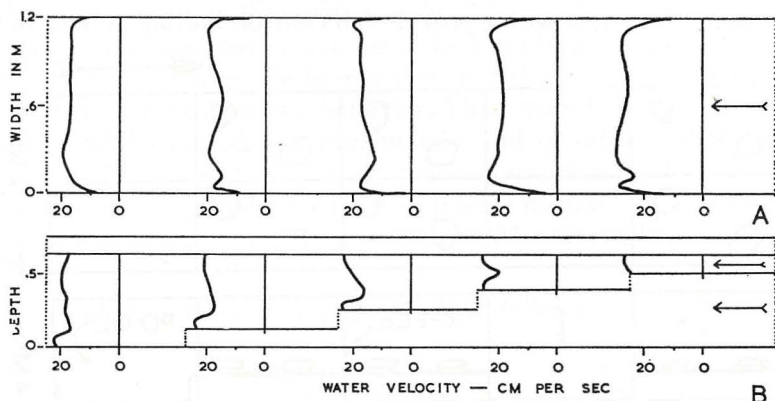


FIG. 18. Velocity profile in horizontal and sagittal planes in depth gradient. Upper figure shows velocities 10 cm above bottom, except in section 1, right end, where profile is drawn for position 5 cm above bottom. Lower figure shows conditions in sagittal plane (two center readings averaged). Arrows indicate direction of current, dotted lines represent screens.

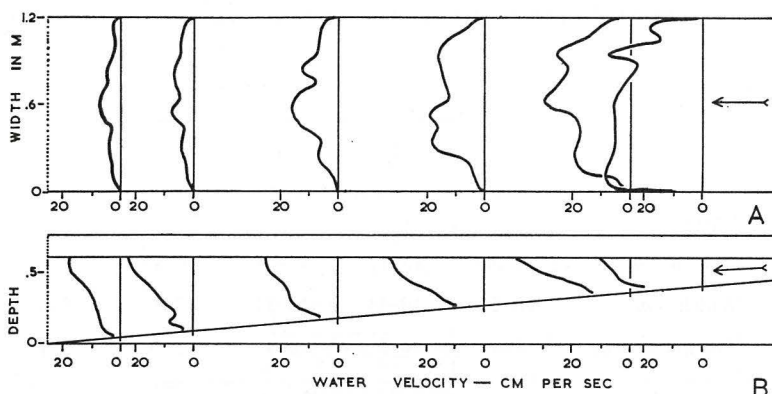


FIG. 19. Velocity profile in depth and velocity gradient. Upper figure shows velocities 10 cm above bottom. Lower shows velocities in sagittal plane (two center readings averaged). Arrows indicate direction of flow, dotted lines represent screens.

Pool in section 1, upper 30 cm of water current flows downstream at about 20 cm/sec. In lower 10–12 cm current circulates upstream along the bottom at 4–5 cm/sec.

Pool in section 4, velocity at the surface 28–30 cm/sec, at 20 cm depth about 10 cm/sec and at the bottom, current near 5 cm/sec circulating upstream.

Riffles in sections 2, 3, and 5, current 28–30 cm/sec at the surface and 20 cm/sec along the bottom.

Temperature in the aquarium (Fig. 15) was governed by seasonal changes in the temperature of the water supply, conditions within the building, and energy input from the pump. Tank temperature could usually be lowered by adding fresh water. It could be raised slightly by cutting the input of new water and hence allowing the propeller to heat that already in the aquarium. These measures did not however provide full control. During periods of freshet,

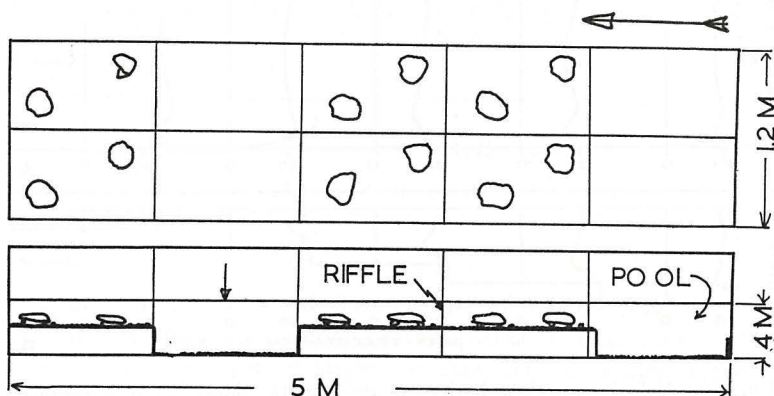


FIG. 20. Horizontal (upper) and lateral views of experimental riffle and pool environment. Horizontal arrow indicates direction of current. Vertical arrow indicates water surface.

the water source became turbid and consequently new water could not be run into the aquarium. If the air temperature in the building was high during such freshets the aquarium temperature rose. If it was low the aquarium temperature fell (see October 5 and 6, November 9, 10, and 11, 1962, and January 8-10, 12-13, 1963, Fig. 15).

Temperatures within the aquarium deviated somewhat from those of the holding troughs early in the winter but approximated them later (Fig. 15). During the spring and summer experiments, water in the stream aquarium ranged from 10 to 16 C and was generally warmer than that in the holding ponds. In the autumn, temperatures in the stream aquarium followed holding trough temperatures and fluctuated from 9.4 to 14.6 C.

Figure 15 shows that stream tank temperatures fluctuated seasonally and daily. They corresponded to those of the holding troughs but were generally higher.

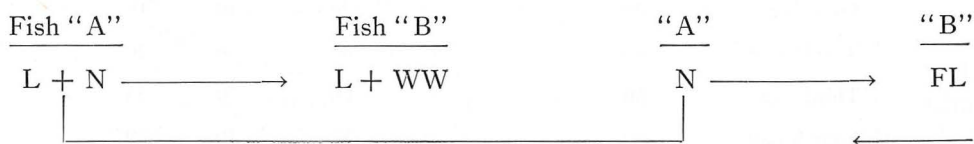
EXPERIMENTAL PROCEDURE

Day length was maintained at 12 hr (0600–1800 hr) in all experiments. This photoperiod was not consistent with that of the holding troughs during the winter. It was necessary however to use a 12-hr day in order to give the fish a 2-hr period of adjustment after the lights came on since the subsequent 10-hr observation period was necessary to obtain adequate records on distribution and behavior.

In all experiments fish were handled, fed, and observed as consistently as possible. In each experiment, 40 fish were placed in still water between 2000 and 2200 hr. At 0800 hr the following day, the current was started at 14 cm/sec and raised in two steps to 23 cm/sec in control, light, and cover gradient. During the first day numbers of fish in each section were recorded at $\frac{1}{2}$ - or 1-hr intervals. During the second day positions of all 40 fish were plotted 12–16 times on outline maps of the stream bottom.

Behavior was recorded in a series of 10-min observations along the length of the tank. A preliminary study revealed that the two species exhibited comparable components of agonistic behavior. These were coded so that a sequence of events could be recorded approximately and quantified. The following is a list of behavior elements and their code letters; details of behavior will be described later: L — lateral display, F — frontal display, N — nip, C — chase, WW — wig-wag display, TN — threat nip, IM — intention movement, and Fl — flight.

A protocol for a behavioral sequence is as follows:



In this series of events fish "A" displays in lateral posture then nips "B." Fish "B" displays lateral posture then exhibits a wig-wag display, "A" nips "B" again and "B" flees. The arrow under "FL" indicates the direction of flight.

Fish, fed twice daily in the stream aquarium, were given 8–10 cc of brine shrimp frozen into a block of ice. The food was placed above the screen in the upstream end of the tank where it melted during a period of 20–60 min. Many of the brine shrimp released kept circulating in the current for several hours, thus evoking feeding over a prolonged period. Immediately after feeding fish tended to shift about and temporarily take up new positions. Because of this, observations on behavior were not made until 30 min or more after feeding began.

The procedure followed in studying fish in the riffle-pool arrangement was slightly different from that used with the gradients. Coho and steelhead were studied separately in two series and then observed in combination in a third series. Table III gives numbers and species of fish used and the time schedule followed during the three series of experiments.

To begin each series 20 fish were placed in still water in the aquarium at about 2000 hr. The following day the current was started and increased stepwise to the desired velocity by 0900 hr. On each succeeding day, until the fourth, an additional lot of fish was added at 0800 hr. Feeding and recording of distribution and behavior were as previously described.

Experiments on fish in the riffle-pool arrangement were conducted in July and November 1963 with underyearling fish. Experiments in the control and gradients were done in the spring, fall, and winter. Appendices II–IV give details of gradient experiments.

SCOPE OF THE RESULTS

Experiments were conducted so that seasonal changes in behavior and distribution could be observed in each species and so that differences between

TABLE III. Number and species of fish used in experiments in riffle and pool environment. In Series 1 coho (C) were used alone, in Series 2, steelhead (S) were used alone, and in Series 3 the two species were combined.

	Series 1		Series 2		Series 3	
	C	No. of S	C	No. of S	C	No. of S
First day	20	—	—	20	10	10
Second day	40	—	—	40	20	20
Third day	60	—	—	60	30	30
Fourth day	80	—	—	80	40	40

species could be recorded. Seasonal and species comparisons were made on groups of one species of fish at a time. The interaction of the two species was studied in summer and winter conditions in certain experimental arrangements.

Distributional data are based on groups of animals. If individuals had been tested singly, the preferred positions may have been different from those inferred from the distribution of a group. The maximum number at a particular point in a gradient may not always represent the preferred position. In spite of this limitation, however, groups of fish were used because field data are based on the behavior of animals in groups.

Temperatures in the holding troughs and stream aquarium varied at different seasons. These temperatures also fluctuated within each season (Fig. 15). The day length at which fish were held was shorter during winter than during spring and autumn. The effects of variations in these conditions could not be fully evaluated, but physical conditions such as bottom configuration, bottom gravel, depth, water velocity, and light conditions were duplicated in all cases; hence the environment was partially but not fully controlled.

RESULTS

REPLICATION OF EXPERIMENTS

Certain experiments were replicated during the winter and the spring-summer series. Observations on the distribution of coho in the control environment were made twice in April and repeated in June 1963 (Fig. 21). Experiments with each species in the control, the cover gradient, and depth gradient were replicated under winter conditions (Fig. 21 and 22). In general, the duplicate distribution patterns were similar (Fig. 21 and 22). Differences between species were consistent in repeated experiments in the control and cover gradient during the winter series (Fig. 21). Repeated observations in the depth gradient produced similar distribution patterns for each species but the differences between coho and trout in the depth gradient were not consistent (Fig. 22). Although repeated experiments in the depth gradients did not give distributions that were identical, they did reveal that each species exhibited characteristic patterns. In the control and cover gradient, trout were distributed in a skewed "U"-shaped pattern, coho in a sigmoid pattern, usually with highest means in the first two sections of the tank (Fig. 21).

SEASONAL CHANGES IN DISTRIBUTION

Comparison of the data obtained during the three seasonal series of experiments indicates that numbers of fish were more uniform along the length of the tank in spring and summer than in fall or winter (Fig. 21 and 22). The greatest differences in sectional averages occurred in fall or winter. Such large variations in the average number of fish per section were a result of the tendency of many individuals to congregate in one portion of the tank during fall or winter conditions. In spring both species were distributed over the whole bottom area of the aquarium.

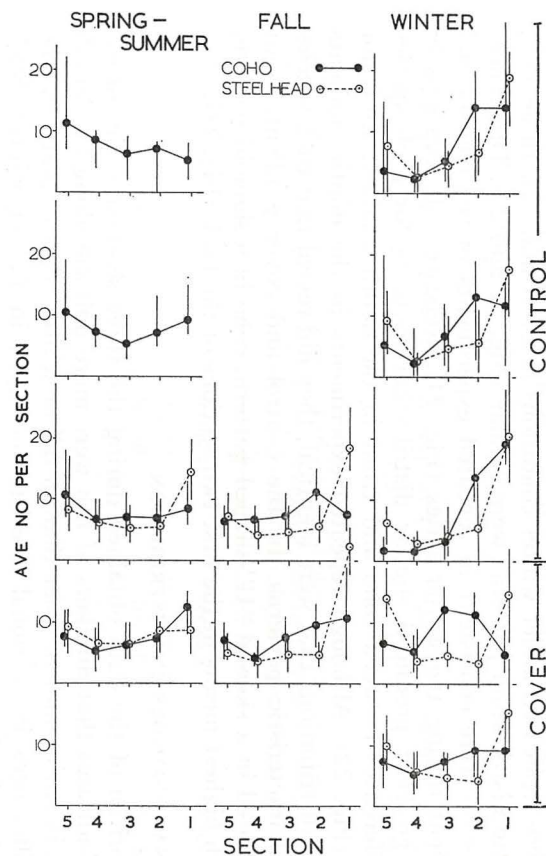


FIG. 21. (Left) Distributions of coho and steelhead in "control" and "cover" gradients, described in text, during 3 seasons. Dots and circles represent mean number of fish per section over a 1-day period (10-15 observations). Vertical lines indicate range. Section 1 represents the upstream end of the aquarium.

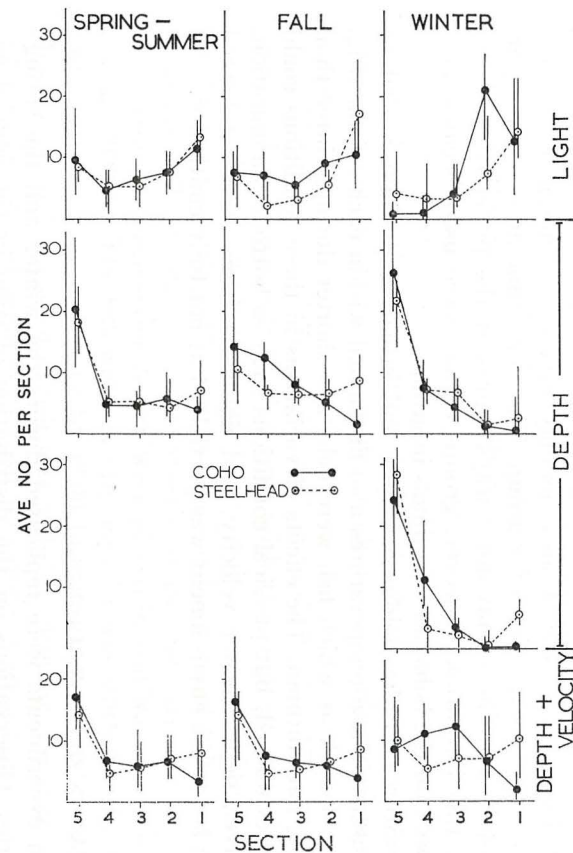


FIG. 22. (Right) Distributions of coho and steelhead in "light," "depth," and "depth and velocity" gradients, as described in text, during 3 seasons. Circles and dots represent mean number of fish per section (10-15 observations). Vertical lines represent range. Section 1 represents the upstream end of the aquarium.

Young coho were scattered in the spring and early summer but in autumn and winter they tended to form aggregates, with some social organization, near the upstream end of the aquarium in the control and the cover and light gradients (Fig. 21 and 22). In the depth gradient the seasonal trend exhibited by coho was a shift to the deepest section of the tank during winter.

In spring and early summer young steelhead were distributed along the tank in a fashion similar to the coho. In fall and winter many trout were active, i.e. moving about in the control, as well as the cover and light gradients (Appendices III and IV). These fish were usually moving and searching about the screen in section 1. The apparent seasonal shift into the upstream region of the aquarium is indicative of wandering and searching in the upstream end, rather than a preference for it. The numbers of stable steelhead positions in the upstream section was usually half, or less, of the numbers shown in Fig. 21 and 22 in the control, depth gradient, and light gradient. Considering this movement, it appears that steelhead which are not roaming assume a more scattered distribution than coho along the tank in the control and the light gradient. Activity accounts for the apparent seasonal shift of fish into section 1 in the cover gradient. However, the high numbers of fish in section 5 represents a preference for positions under or around the large stones. Steelhead, like coho, show a strong winter preference for the deepest section of the depth gradient. Trout exhibited no seasonal change in distribution in the depth-plus-velocity gradient (Fig. 22).

COMPARISON OF SPECIES IN GRADIENTS

In experiments conducted under spring and summer conditions, the distributions of coho and steelhead were similar in each of the five experimental conditions (Fig. 21 and 22). However, in autumn and winter experiments, the distribution differences between the species were greater. Environmental preferences, as inferred from experimental distributions, were most similar in spring and early summer, the season in which segregation was most pronounced in the Salmon River. Distributions and inferred preferences were divergent during fall and winter (Fig. 21 and 22), the seasons in which populations overlapped most in the Salmon River (see Fig. 12). During the season when laboratory distributions are similar the two species meet and interact in the natural stream environment. In the seasons when experimental distributions are different, the two species are most compatible in the natural stream environment. Different environmental responses in the laboratory (i.e. response to cover, Fig. 23, 24) are indicative of the mechanisms that allow the two species to coexist in close proximity in fall and winter.

In the cover and depth gradients young fish utilized stones and pool space in a similar fashion in spring and summer but not in winter. Coho, 6-8 weeks old, scattered among the stones which formed the cover gradation (Fig. 23). During spring about one-third (126 of a total of 412) of the positions taken by coho were immediately downstream from stones. Many positions recorded were among the stones. In winter, 126 of 390 positions occupied

were immediately downstream from the stones. Fish were, however, recorded at fewer positions among the rocks (Fig. 23) in the winter. Those that were not in the shelter of stones were at positions at the sides of the tank.

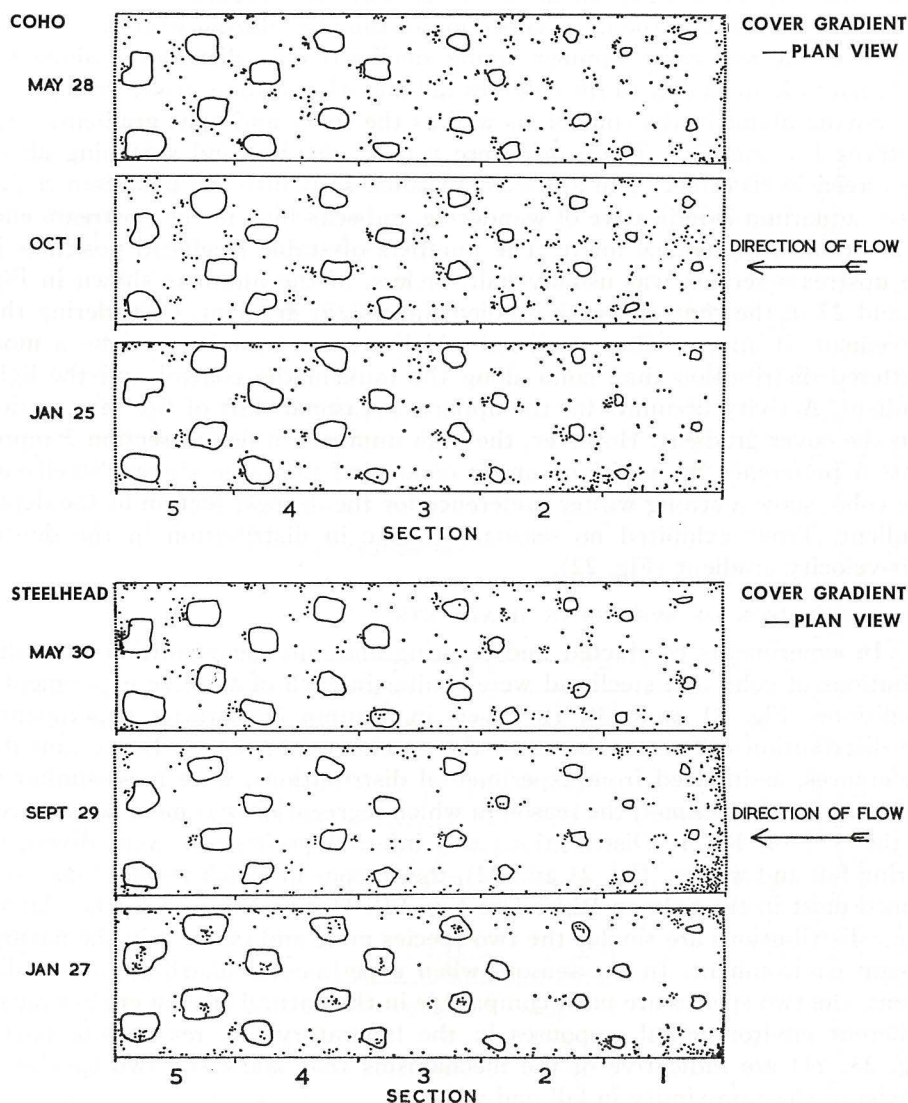


FIG. 23. (Top) Distribution of coho in cover gradient during 3 seasons. Locations of 40 fish during 10 combined observations are given. Groups of dots represent same fish occupying same location repeatedly, or different fish in same location repeatedly, in this and succeeding figures of this type. Points within the stone outlines represent fish under stones. Dotted lines represent screens at ends of aquarium in this figure and succeeding figures of this type.

FIG. 24. (Bottom) Distribution of steelhead in cover gradient during 3 seasons. Locations of 40 fish during 10 combined observations are given. Points within the stone outlines represent fish under stones.

Steelhead, 3-5 weeks old, distributed themselves in the same pattern as the 6-8-week coho (Fig. 24). During spring, one-third of the steelhead positions were immediately downstream from stones. As in the case of coho, the other positions were scattered among the stones, and none was under them (Fig. 24). During the fall, a large number of young trout was active and remained in the upstream end of the aquarium (Fig. 24). One-sixth of the positions recorded were immediately downstream from stones; only six positions were under them (Fig. 24). In winter one-fourth of the positions recorded were under stones and approximately one-eighth were downstream from them (Fig. 24).

It is evident that the distributions observed in the spring condition would result in a high degree of contact between species if together in a cover gradient. However, in winter the tendency of trout to hide under stones would, to a degree, isolate them from coho which do not do so (Fig. 23 and 24).

A second instance of trout and coho using the same space in a different manner, in winter, occurred in the depth gradient. Table IV shows that in June there is a significant difference in the numbers of young coho and trout in the upper and lower halves of sections 4 and 5 (chi square tests). Segregation is, however, more pronounced during winter. This increase in segregation is primarily due to a change in the behavior of steelhead. In summer conditions, about one-third of the steelhead were off the bottom where they would be in contact with coho if the species were mixed. In the winter most steelhead were spread over the bottom in the deep section. On the other hand most coho were distributed at the edges near the bottom or in loose aggregations up each side of the deepest section. Individuals of both species defended areas along the downstream edge of each depth zone. A large amount of intraspecific fighting occurred in these areas. When the two species were placed together during summer in equal numbers the amount of intraspecific and interspecific aggression was high (Table V). During winter when trout and coho were placed in the depth gradient together they were segregated spatially as already described. Intraspecific and interspecific aggression were lower than under summer conditions (Table V). Interspecific fighting was not disproportionately lower as expected on the basis of spatial segregation. However practically all inter-

TABLE IV. Numbers of coho (C) and steelhead (S) in upper and lower halves of sections 4 and 5 in the depth gradients in early summer and winter (June and January).

	June		January	
	C	S	C	S
Upper half	124	75	168	24
Lower half	103	145	161	281

TABLE V. Aggressive contests per fish per hundred minutes during June and January 1963. Symbols are as follows: C = coho; S = steelhead; C.C = coho attacking coho; C.S = coho attacking steelhead; S.S = steelhead attacking steelhead; and S.C = steelhead attacking coho.

Date	Fish		Number of contests				Observation
	C	S	C.C	C.S	S.S	S.C	
							<i>min</i>
June 28	20	20	12.7	6.1	6.3	1.3	90
January 17	20	20	4.4	1.3	2.4	0.9	90

specific contests occurred at the downstream edges of depth zones in sections 3 and 4. Few aggressive contests were recorded between the coho, in aggregations at the side of the deep section, and trout, on the bottom.

DESCRIPTION OF AGONISTIC BEHAVIOR

Young coho and steelhead display using a number of similar postures and movements. These displays and movements are listed in Materials and Methods. Before any classification and quantification of the behavior components are attempted, it is essential to understand the basis of the classification. Each of the different components appears in a variety of forms which appear to be related to the intensity of the behavior. In the following description of behavior, each component is described and the variability indicated. It is acknowledged that this type of fish behavior could be classified on a more refined scale by quantifying intensity or duration of components. Such was not feasible in this study because of the number of fish that were observed and the rapidity of the action.

Lateral display was described by Fabricius (1953) and Kalleberg (1958). This varied from a simple erection of the dorsal fin, lasting 1 or 2 sec, to a prolonged erection of dorsal and paired fins and a lowering of the basihyal apparatus for 10 or 15 sec. The dorsal line of the body was either straight or slightly recurved. The criterion for a lateral display was the erected dorsal fin and the line of the back. Figure 25,A shows characteristic lateral posture of 10-month-old coho, Fig. 25,B shows lateral posture of 8-month-old trout. Figures 25,C and 26,A illustrate lateral displays in 2-month-old coho. Lateral displays were similar for the two species, although the display was usually more obvious in coho which possess large median fins with long, colored edges (Fig. 25,C and 26,A).

The frontal display, described by Fabricius (1953) and Kalleberg (1958), varied from a posture in which the back was slightly arched, the dorsal fin compressed, and the basihyal extended for 1 or 2 sec (Fig. 25,B and 26,B), to a posture in which the back was strongly arched, the dorsal fully compressed, and the basihyal well extended for longer (unmeasured) periods.

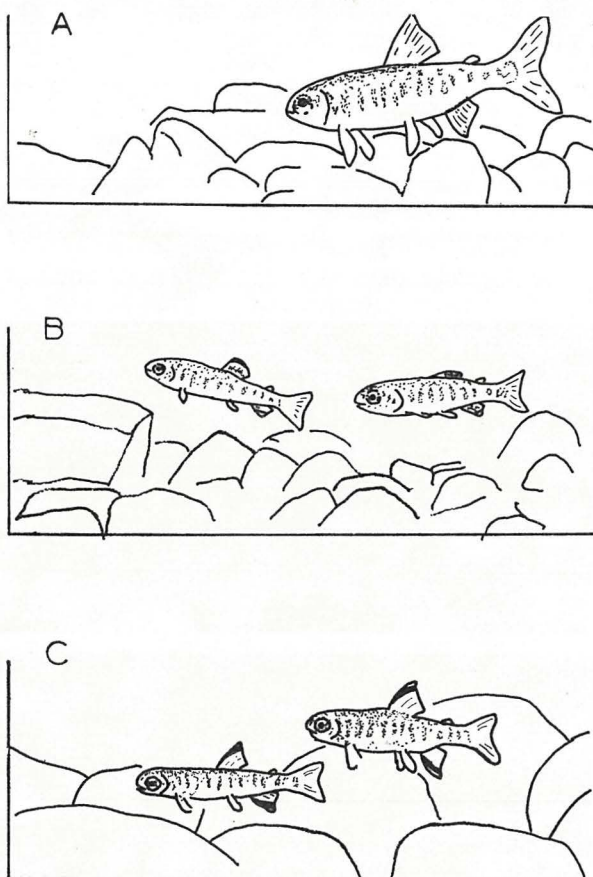


FIG. 25. A. Coho, about 10 months old, in lateral threat posture. B. Steelhead, about 8 months old, in lateral posture (see fish on the left). Fish on the right in frontal threat posture of low intensity. C. Coho about 2 months old, in lateral threat posture. (All figures are traced from photographs.)

In the wig-wag display fish adopted a lateral posture, usually with median and paired fins well extended, and swam with accentuated lateral movements with the head down and the body at a 20–30° angle from horizontal (Fig. 26,B and C). In this display the amount of fin erection varied. The angle of body inclination and the amplitude of swimming movement was low in displays that were of short duration. In wig-wag displays (inferred to be of high intensity) the fins were erected fully, the angle of inclination was steep (near 30°) and lateral movements were accentuated. The criterion for a wig-wag display was the erected fins, the inclined posture, and accentuated swimming movements. As in the case of the lateral display, the wig-wag was more striking in coho than trout because of differences in fin shape and color.

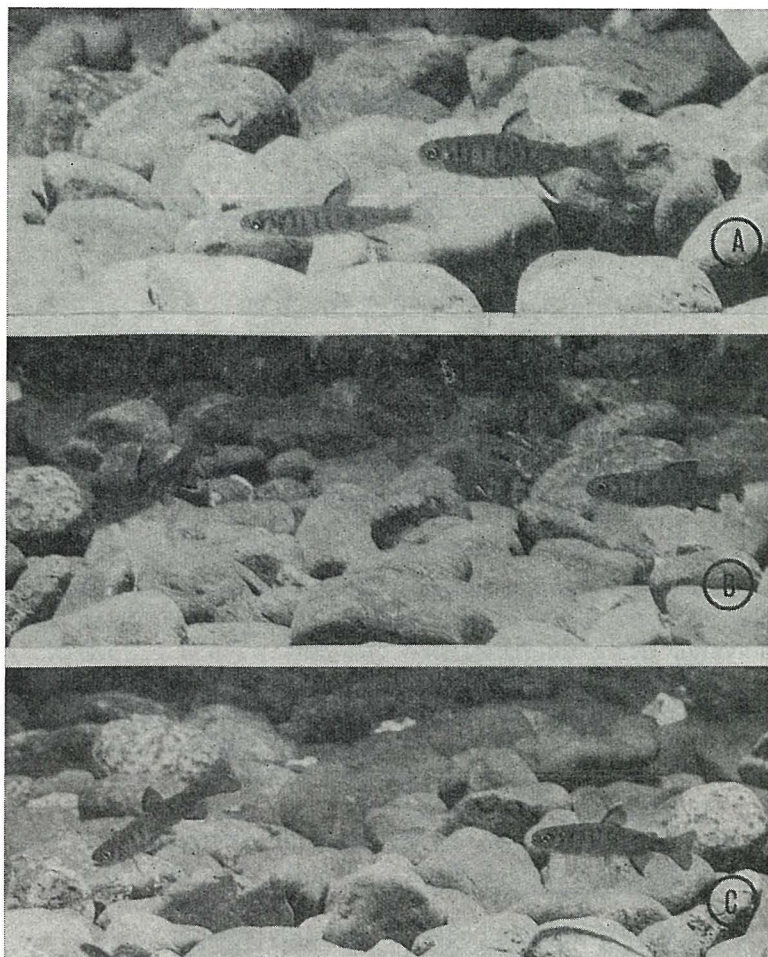


FIG. 26. A. Coho, about 2 months old, in lateral threat posture. B. Coho, about 2 months old, in frontal threat posture of low intensity (right). Coho, about 2 months old, in wig-wag posture (left). C. Coho, about 2 months old, in wig-wag (left) and lateral threat posture (right).

Chasing involved chase and flight. If one fish darted after another and pursued it past the point from which it fled it was designated as chasing. Pursuits ranged from slow short excursions of 20 or 30 cm to long chases of 2 or 3 m.

Nips were those bites in which there appeared to be a definite contact. In some instances fish only "mouthed" the individual attacked. In other cases the bites were so hard that the animals seemed to be briefly stuck together.

Threat nips were nips which were aimed at other fish. Such bites appeared to be inhibited and hence missed contact by as much as 20 or 30 cm. In some cases a fish swam a short distance and nipped in the direction of another.

In other situations they turned their heads and nipped in the direction of a neighbouring fish.

Intention movements were responses in which a fish only turned its head quickly toward another or made a short lunge at it. No threat nip was involved. These movements, which were brief, varied as described and were often difficult to distinguish from nonsocial behavior and threat nips.

An example of an aggressive bout involving several of the described aggressive components was given in the Materials and Methods section. Some contests were short and involved only two or three behavioral components, others were long and involved series of bites and displays interspersed among each other and reciprocated between individuals.

ANALYSIS OF BEHAVIOR

By recording bouts in terms of individual behavior components it was possible to examine the rate of occurrence of various aggressive components as well as complete contests. The breakdown of agonistic behavior into all its components made it possible to compare quality and quantity of aggressiveness in different seasons and species.

Figure 27 represents behavioral repertoires of coho and steelhead during 3 seasons. Details of observation time are given in Table VI. The diagrams in the figure show only the rate of occurrence of each component, they do not show how these may be related to each other during aggression. There are three main points illustrated in Fig. 27. First, the repertoires of the two species differ at all seasons. Second, within each species the amount of aggressive behavior decreases seasonally from spring to winter. Third, the quality of behavior exhibited by each species changes seasonally.

The most obvious species differences were the relatively strong nipping and chasing components of the trout as opposed to strong wig-wag, threat nip, and intention-movement components of coho. The lateral display, which often preceded the wig-wag, was stronger in the coho than in the steelhead during spring and autumn (Fig. 27).

Level of aggressive behavior among coho was high in spring, summer, and fall but decreased during winter. Among trout aggressiveness decreased progressively from spring to autumn and winter.

During spring and winter lateral displays, nipping and chasing were frequent in both species. Nipping and chasing components were very strong in the steelhead (Fig. 27) during spring and summer. Behavior composition of the two species was most similar in the spring; by autumn it had diverged. By winter the lateral display components were greatly reduced and equalled by threat nips and wig-wag elements in the coho. The most evident seasonal change in the steelhead configuration was the reduction of the chase component.

A higher frequency of elaborate displays and noncontact behavior was evident in the coho. The main behavior elements of the trout were lateral displays, biting, and chasing. Hartman (1963) showed that young brown trout (*Salmo trutta* Linn.) displayed frequently, but nipped less at low water velocities (8-9 cm/sec). At higher velocities (18-19 cm/sec and 28-30 cm/sec)

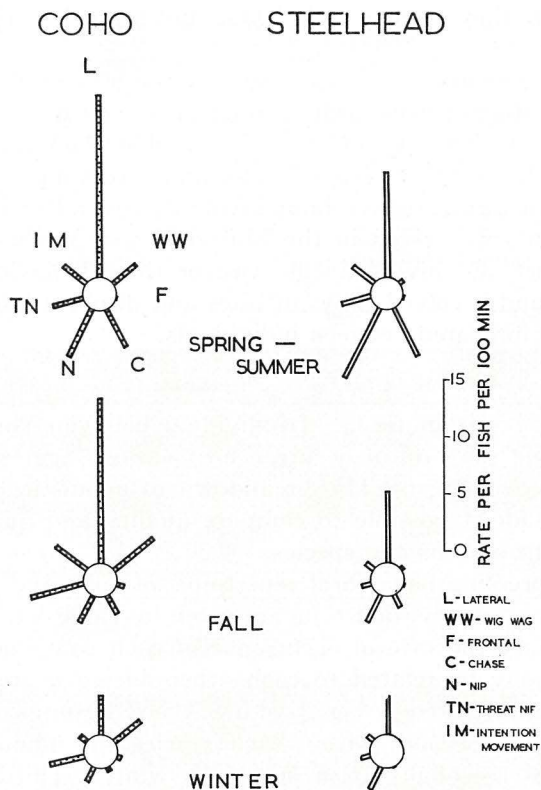


FIG. 27. Rate of occurrence of individual components in the agonistic behavior of young coho and steelhead. Data are based on combined observations of fish in the five experimental arrangements used. See text for description of behavior components.

they nipped relatively more and displayed less. The mechanical difficulty of holding position in the current with median and paired fins extended appeared to be the main reason that agonistic behavior took on a different character at higher water velocities. A comparison of behavior patterns of coho and steel-

TABLE VI. Minutes of observation of coho and steelhead in control and four experimental arrangements during spring, fall, and winter.

Coho	Steelhead	Season
750	410	Spring
390	440	Fall
890	720	Winter

head with brown trout suggests that steelhead behavior, involving primarily lateral displays, nips, and chases, is more adapted to rheocrene conditions than the behavior of coho which involves more wig-wag displays and less nipping. Results of field and laboratory studies also suggest that the differences in behavior of coho and steelhead are related to their ecology.

DISTRIBUTION IN RIFFLES AND POOL HABITAT

The major difference in distribution of trout and coho in the field was related to riffle and pool habitats. In the stream aquarium certain behavior features of each species appeared adaptive to particular current conditions and an attempt was made in the laboratory analyses to determine whether there were behavior characteristics which conferred advantages on trout in riffles and coho in pools.

Distributions in riffle and pool habitats (Fig. 28 and 29) indicate that both species preferred pools or that some environmental regulation of behavior allowed more individuals to remain in the pools. Both trout and coho had similar distributions in the riffle and pool habitats when the species were separate. Steelhead, however, were more numerous in the riffle areas (Fig.

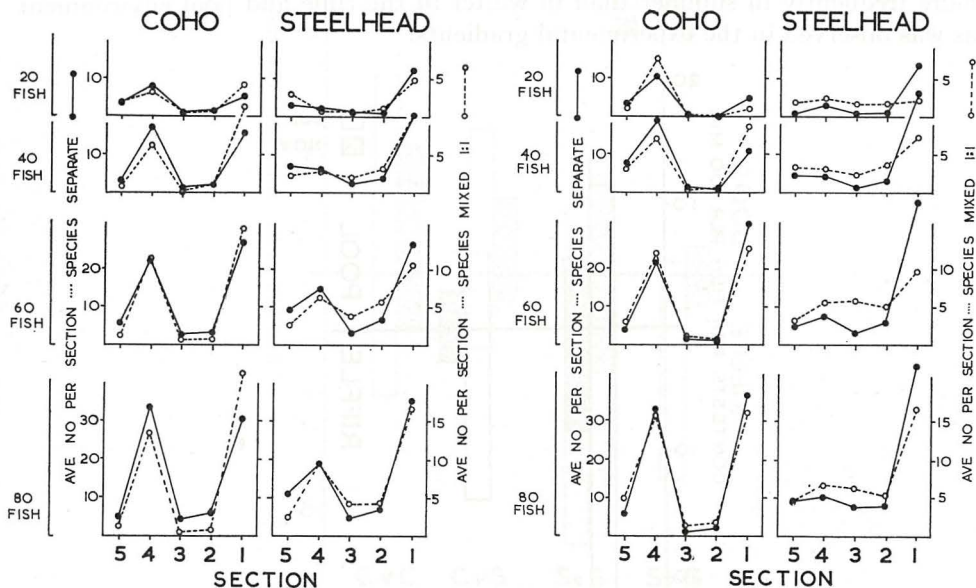


FIG. 28. (Left) Distribution of coho and steelhead at four different densities in riffle and pool environment (July). Solid dots represent the average number of fish per section, species separate. Circles and broken lines indicate the average number of fish per section, species mixed. Scale for the points for species mixed is half that for species separate.

FIG. 29. (Right) Distribution of coho and steelhead at four different densities in riffle and pool environment (November). Solid dots represent the average number of fish per section, species separate. Circles and broken lines indicate the average number per section, species mixed. Scale for the points for species mixed is half that for species separate.

28 and 29). When coho and steelhead were mixed in July experiments, density of steelhead was reduced (in relation to the situation where the species was alone) in six out of eight cases in the pool habitat, and increased in eight out of 12 instances in the riffle habitat. Coho density was reduced (in relation to the situation where the species was alone) in nine out of 12 cases in the riffles and increased in five out of eight instances in pools. Upon mixing, coho densities increased in the pools and decreased in the riffles, and steelhead densities changed in the opposite direction in more cases than expected by chance ($P < .05$, chi-square test). During winter the effects of interspecific mixing were not clear (Fig. 29). In experiments where the species were mixed, steelhead densities decreased in the pool in section 1, and increased in the three riffle sections in all but one instance. However, density of steelhead in mixed groups was higher in the pool in section 4 also. Changes in relative density of coho showed no consistent relation to those of steelhead as occurred in July (Fig. 28).

AGGRESSIVE BEHAVIOR IN RIFFLES AND POOLS

Levels of aggressiveness were higher in riffle habitat than in the pool habitat when the species were separate (Fig. 30). An exception to this was the case of steelhead under winter conditions. Fighting and displaying occurred more frequently in summer than in winter in the riffle and pool environment as was observed in the experimental gradients.

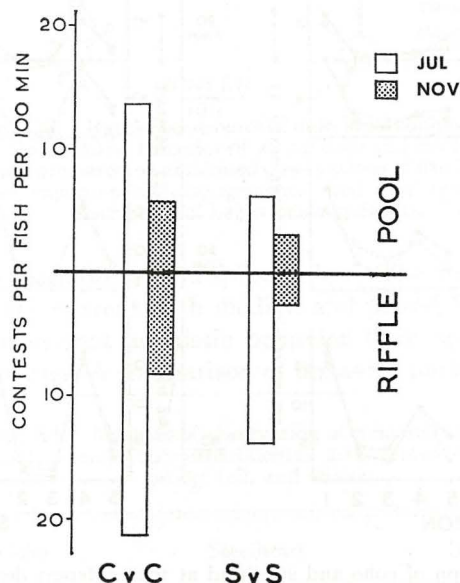


FIG. 30. Rate of aggressive behavior in riffle and pool habitats during July and November. Data based on observations made with species separate. C vs C indicates coho attacking coho and S vs S indicates steelhead attacking steelhead. Coho observed 390 min in July and 340 min in November; steelhead observed 380 min in each period.

Interspecific mixing revealed an environmental effect on behavior which may in a large degree explain why trout maintained themselves in the riffle sections of the aquarium and actually reduced utilization of this space by coho. Figure 31 shows that coho displayed a high level of interspecific and intraspecific aggressiveness within pools. Aggressiveness of trout was correspondingly low in the pools (Fig. 31). (Chi-square values indicate that differences in rates of aggressiveness of trout and coho in riffles and pools during July are significant $P > .01$.) In the riffle habitat of the aquarium coho were not particularly combative; steelhead on the other hand were aggressive (Fig. 31). In addition to being more aggressive, steelhead tended to defend temporary territories. A comparison of Fig. 30 and 31 indicates that mixing the two species in a riffle and pool environment had the effect of reducing the level of coho aggressiveness in riffles and increasing it in pools. The degree of aggressiveness of steelhead in riffles was increased in mixed groups. In mixed groups steelhead fighting was more frequent in the pools in November than in July; such was not the case when the species were separate (Fig. 30 and 31).

High rates of aggressive behavior in the riffles (species unmixed) resulted in low densities of fish in such areas. Behavior differences, which were related

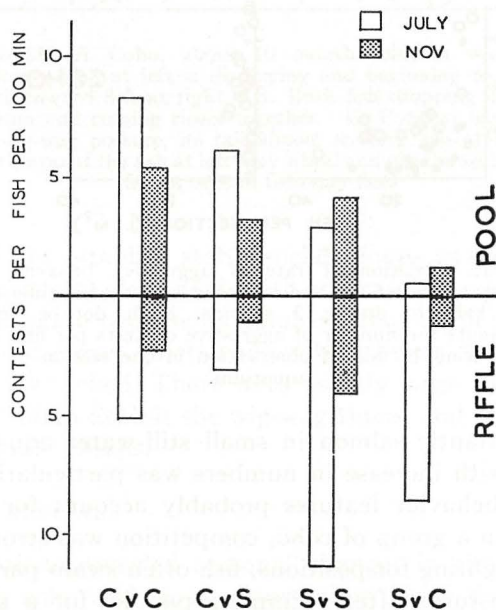


FIG. 31. Rate of aggressive behavior in riffle and pool habitat during July and November. Data based on experiments in which species were mixed in equal numbers and observed 270 min in July and 250 min in November. Meaning of symbols as follows: C vs C = coho attacking coho; C vs S = coho attacking steelhead; S vs S = steelhead attacking steelhead; S vs C = steelhead attacking coho.

to the environment, accounted for the strict density regulation in riffles. Strong current induces more distinct territorial tendencies as has previously been demonstrated (Kalleberg, 1958). In addition the presence of reference objects induces fish to establish and defend territories (Hartman, 1963). In the riffle sections current was fast and there were reference objects, i.e. large stones. Agonistic activities in these areas were easily induced, hence in Fig. 32 rates of aggression were high at low densities. High densities of fish did not occur because increased fighting led to displacement of fish.

In the pools, however, aggression decreased with an increase in fish density (Fig. 32). Keenleyside and Yamamoto (1962) demonstrated almost the

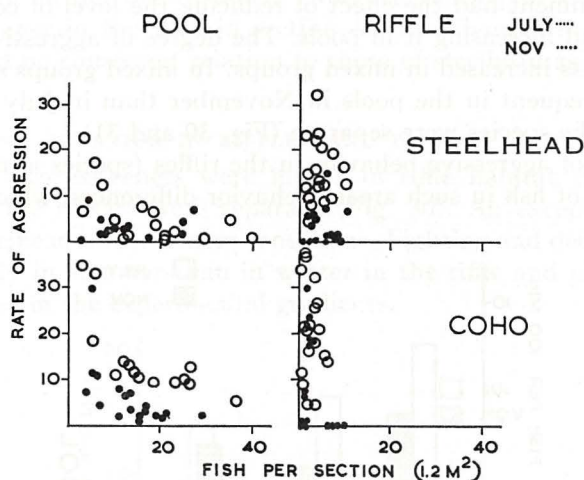


FIG. 32. Relation of rate of aggressive behavior to density of fish. Coho and steelhead compared in riffle and pool habitats during 2 seasons. Each dot or circle represents the number of aggressive contests per fish 100 min during 10 min of observation in one section of the aquarium.

same effect with Atlantic salmon in small still-water aquaria. Reduction in rate of aggression with increase in numbers was particularly evident in coho (Fig. 32). Certain behavior features probably account for this phenomenon in groups of coho. In a group of coho, competition was strongest for positions near the front. In fighting for positions, fish often swam parallel to each other in lateral threat posture. After swimming parallel for a short distance one fish, usually the dominant individual, darted ahead of the second and performed a wig-wag display in which it dropped backward downstream toward the second fish (Fig. 33,A-C). In many cases the upstream fish ended by literally brushing its opponent back with its tail (Fig. 33,C). If the displaced fish remained behind the victor, little more fighting occurred. The wig-wag threat was closely associated with the formation of stable social groups with one to three dominants at the front and several subordinates behind them.

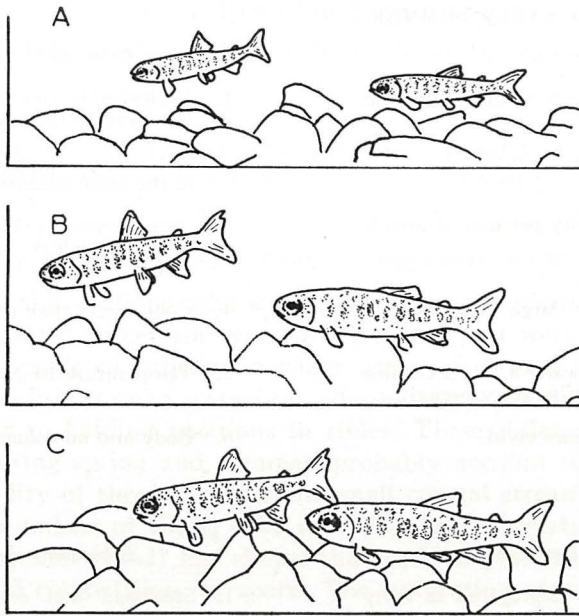


FIG. 33. A. Coho, about 10 months old, in wig-wag posture. Fish at left is displaying and beginning to drop back toward fish at right. B. Both fish dropping downstream and coming closer together. C. Coho at left still in wig-wag posture, its tail almost striking fish at right. At this point the fish at left may wheel and nip the second fish or second fish may flee.

Steelhead did not establish stable social groups as did coho. In July observations, aggressiveness decreased with increase in numbers of steelhead. Such a change took place because as numbers went up many steelhead settled to the bottom and became quiet while others began to roam about. These fish were not often attacked. There were usually large, potentially dominant trout; they did not often exhibit the wig-wag threat and did not hold the front positions in any stable groups.

SUMMARY OF RESULTS

Field observations revealed seasonal changes in the distributional relationships of young coho and trout. Concomitant with these were changes in water temperature, and population density. Laboratory experiments pointed to features of environmental and social behavior which were related to changes occurring in nature. Field and laboratory results are summarized below as an introduction to the Discussion. Field observations apply particularly to the Salmon River.

SPRING AND EARLY SUMMER

Field observations

1. Species largely segregated in different microhabitats.
2. Coho in pools, trout in riffles.
3. Population density per unit of area is high.
4. Coho relatively large compared to trout.
5. Temperature of water 8.3–17.2 C (time corresponds to laboratory period).
6. Body and fin colors vivid.

Laboratory observations

1. Both species have similar distributions in experimental gradients.
2. Both utilize space in pools and cover in the same manner.
3. Both species exhibit high level of aggression which involves much biting and chasing.
4. Coho larger than trout.
5. Temperature 10–16 C.
6. Body and fin colors vivid.

FALL

Field observations

1. Species partially segregated in early fall, coming together more in late fall.
2. Coho in pools, trout density about even in riffles and pools.
3. Population reduced in pools, reduced more in riffles.
4. Trout size range approximating that of coho.
5. Temperature of water 7.2–12.5 C.

Laboratory observations

1. Steelhead and coho have different distributions in experimental gradients.
2. Species utilize space and cover in about the same manner.
3. Coho aggression high, but less biting and chasing is exhibited. Steelhead aggression lower than in spring, relatively less chasing.
4. Temperature 9–14.5 C.
5. Body and fin colors less vivid.

WINTER

Field observations

1. Species exhibit no microhabitat segregation.
2. Highest density of both species in the pools.
3. Population density reduced further in pools, very low in riffles.
4. Trout size range approximating that of cohos.
5. Temperature of water 0.3–7 C.

Laboratory observations

1. Species have different distributions in experimental gradients.
2. They utilize space in pools and around cover in different manners.
3. Aggression very low in both species. Coho display components are strong, very little biting and chasing. Steelhead show only two components strongly: simple displays and biting.
4. Temperature 0.5–7.5 C.
5. Body and fin colors less vivid than in spring and fall.

DISCUSSION

An animal's behavior is adapted to its environment, as is its morphology and physiology. Accordingly, there are both environmental and social responses of coho and trout which relate to their ecology. Certain aspects of the ecology and behavior of coho and trout will be considered before entering the main body of the discussion, which will deal more directly with interspecific interaction.

BEHAVIOR OF STEELHEAD AND COHO IN RELATION TO THEIR ECOLOGY

Under natural conditions coho were most frequently distributed in groups which were restricted to certain types of habitat. Trout were more scattered and appeared capable of utilizing a wider array of stream habitats. Under experimental conditions coho were best adapted to maintaining positions in pools, and trout to holding positions in riffles. These differences, which are most evident during spring and summer, probably account for differences in population stability of the two species in small coastal streams. During May and June large numbers of young coho were displaced downstream in the Salmon River. Chapman (1962) has shown that such displacement is the result of aggression and competition for space. The emigration of young coho from streams occurred at a season when levels of aggression were highest and when behavior was least ritualized.

Downstream displacement of trout did not occur even though density and rate of aggression were high. Kalleberg (1958) showed that territory size decreased with increased population density of Atlantic salmon fry. Trout in the Salmon River may accommodate for changes in numbers by changing territory size. Coho, which are restricted to pools, may displace surplus individuals out of the pools. Experimental data indicated that such individuals would be unable to maintain positions against trout in the riffles. As a result coho, pushed out of pools, would move downstream to unused pool space or be displaced completely. The direction of retreat following combat may be important in a consideration of the matter of downstream displacement. Retreating trout in the experimental stream aquarium tended to move upstream or laterally. Figure 34 shows that about 25% of the coho retreats were lateral and 30% were upstream. However, the largest single percentage (about 45) of retreats was downstream. These differences are consistent with differences in amount of downstream displacement and with the type of aggressive behavior exhibited by coho and trout.

During winter, coho are usually found in dense groups. The tendency to form such groups is usually reflected in the winter distributions (Fig. 21 and 22). In winter no downstream emigration occurred in the Salmon River. Laboratory studies revealed several behavioral phenomena which would facilitate stability of groups in restricted areas of the stream during the winter. Levels of aggressiveness were lower in both species. The amount of biting and chasing was low in proportion to noncontact aggressiveness. The wig-wag display occurred frequently in laboratory conditions and was exhibited

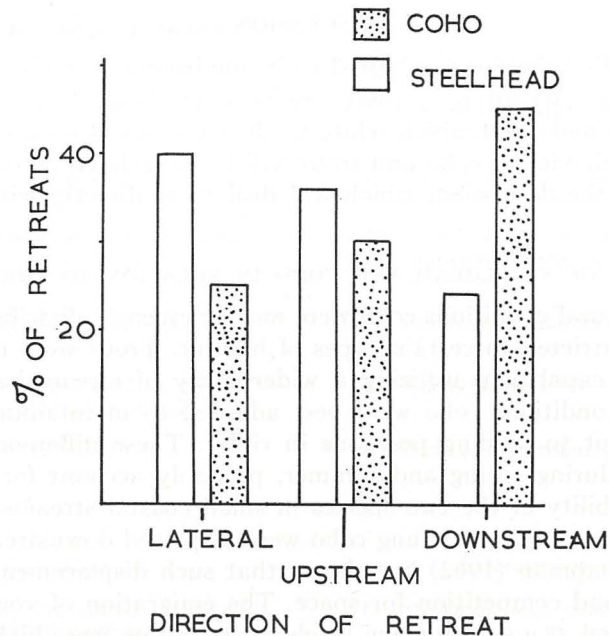


FIG. 34. Direction of retreat of coho and steelhead following intraspecific aggressive contests (based on 248 contests among steelhead and 458 among coho).

in contests for position near the front of a group. Fish which were displaced by others using the wig-wag threat were pushed back into the group of subordinates but were not driven entirely out of the group.

During winter, trout did not occur in tight groups as did coho. Behavior components (threat nips and wig-wag displays) which were evident in the group behavior of coho were exhibited infrequently in laboratory groups of trout.

Hiding behavior shown by trout under winter conditions has adaptive value in protecting them from "scouring" and predation. Coastal rivers of British Columbia are frequently subject to freshets, hence, hiding behavior, either in log jams or under stones, is advantageous in maintaining position. Lindroth (1955b) has shown that mergansers can take a heavy toll on trout parr populations. Lindroth and Bergström (1959) demonstrated that mergansers could easily see fish in open water and chase them tenaciously. The birds even searched actively under the stones for the trout parr. It may be assumed that fish in positions under large stones would gain considerable protection from such predation. In most cases hiding trout in the Chilliwack River were under rocks 20-40 cm in diameter. Many hiding fish were found well down among the stones rather than near the surface. The habit of seeking shelter is important in the ecology of young steelhead because it offers protection from winter freshets and from predation to many fish which are distributed along the stream margins in otherwise unprotected locations.

The foregoing comments have pointed out some differences in the behavior and ecology of the two species. Although trout occupy a wider variety of stream habitats than coho (particularly in the largest stream) the two species overlap to a large degree in space utilization.

INTERACTION OF YOUNG STEELHEAD AND COHO

Segregation of natural populations of young coho and trout occurred at the season in which experiments indicated great similarity of environmental preferences. Separation in the wild was least pronounced during winter months, when experiments indicated differences in preferences. These two observations considered together support the belief that interspecific competition may be manifested in segregated resource use as suggested by Nilsson (1956, 1963). Interaction, which occurred in spring and summer because both species had similar demands, was accentuated by three factors. Population densities (in the stream) were highest in spring and summer (Fig. 12). Levels of aggressiveness (laboratory) were highest early in the year (Fig. 27). In addition to this the aggressiveness shown involved much biting and chasing. Size differences may have contributed to the effect of segregation. Coho in the Salmon River were larger than the trout in spring and summer (Fig. 13) and could have displaced them from pools.

In direct opposition to the above situation, winter populations of coho and trout coexisted to a large extent in the pools. Three main factors contributed to this interspecific compatibility. First, spatial distribution and preferences of the two species in the stream aquarium were different in winter. Second, stream population densities were lower in winter (Fig. 12). Third, levels of aggressiveness were lower in winter (Fig. 27). These three factors must contribute substantially to the winter coexistence of coho and trout.

There is an apparent paradox in the fact that wild populations of both trout and coho occupy pools at a season when experiments indicate differences in preferences. It should be pointed out, therefore, that both species showed a preference for the deepest section of the depth gradient, which was comparable to a pool (Fig. 22). However, trout and coho utilized this pool space differently; coho formed groups in open water above bottom, and trout scattered across the bottom. In the cover gradient trout occupied space under stones but coho occupied space beside the stones or downstream from them (Fig. 23 and 24). In a stream during the winter both species may make a demand on pool space. However, small but important differences in the use of space and cover, such as those described, permit coexistence of both species in a pool within a few inches of each other. As already stated, such coexistence would be facilitated because levels of aggressiveness in both species are low during winter.

The previous discussion explains some of the reasons why coho and trout segregate spatially in spring and summer but occur together in winter. However one important question still remains. How do these two species remain in equilibrium in the two distinctive natural microhabitats, riffles, and pools?

To gain better understanding of this problem it may be valuable to consider the effect of environment on the behavior of young brown trout. Hartman (1963) showed that young brown trout could be induced to take up and defend positions if presented with simple visual reference points. If the structural complexity of these reference points was increased, the rate of occupancy was increased. Kalleberg (1958) showed that defence of territories by young brown trout and salmon was initiated by running water. Territorial behavior of young brown trout was released by certain stimuli, the effect of which could be reinforced by others. The behavior of choosing and defending territories appears to be a reactive type of behavior which is governed by a complex of environmental stimuli. Presumably young steelhead in the riffle environment received more stimuli which elicited aggressive behavior and territory defence, than they received in the pools. The responses of young coho to various stimuli were different, hence, they were more strongly motivated to defend space in pools and less so in riffles. Such a differential response to environmental conditions is indicated by the differences in aggressiveness in riffle and pool habitats (Fig. 31). Segregation in the Salmon River is probably maintained because of differences in motivational states of trout and coho in the three microhabitats of the stream. If it were not for this differential aggressiveness, coho displaced from pools would be able to eliminate the smaller trout from the riffles, thus shifting the balance, in the whole stream, in favor of one species.

In concluding the comments on the ecological relationship of these two species it is emphasized that changes in social behavior account, in a large way, for the seasonal change in severity of interaction. Differences in aggressiveness in riffle and pool environments account for the segregation and the equilibrium of coho and trout in the two microhabitats.

COMMENTS ON CONCEPTS OF COMPETITION

A number of investigators have reported instances in which competition or interaction between species is manifested in segregation (Beauchamp and Ullyott, 1932; Macan, 1961; Connell, 1961). Segregation produced by competition among fish has been recorded by Nilsson (1955, 1958, 1960, 1963). Miura (1962) reviewed several cases in which it occurred in competing species of Japanese fish. Lindroth (1955), Kalleberg (1958), and Saunders and Gee (1964) deal with segregation of competing species of stream-dwelling salmonids. In most of the preceding cases each species has a slight morphological, physiological, or behavioral advantage over the other in some part of the environment. It is considered necessary to emphasize that similar, competing species segregate and come into equilibrium in nature since many laboratory investigations on competition, carried out in homogeneous controlled environments, would indicate otherwise (reviews by Crombie, 1947; DeBach and Sundby, 1963). Grinnell (1904), Gause (1934), and DeBach and Sundby (1963) have indicated that species having the same niche cannot occur together without one eliminating the other. DeBach and Sundby (1963) have

recorded a case in which one species of *Aphytis* eliminates another and is subsequently displaced by a third species. They suggest that the displacement mentioned above illustrates "the competitive displacement hypothesis," i.e. species with identical ecological niches cannot coexist long in the same habitat. Because of the way the hypothesis has been stated and because of the variations in its interpretation, the competitive displacement concept has been controversial (Hardin, 1960; Cole, 1960; Patten, 1961; Van Valen, 1960; McIntosh, 1961). The concept might have been more acceptable if it had stated that in sympatric populations of similar species the level of competitive interaction will increase with the degree of ecological and behavioral similarity. This does not lead to the difficulty of discussing different species with *identical* niches, although it does still leave the problem of quantifying ecological and behavioral similarity. It is impossible to say how such interaction will be manifest, because competition in the natural environment may alter the numbers, the growth rate, or the niche of an animal in a particular habitat. Temperate freshwater fish are in general unspecialized and flexible (Larkin, 1956) and hence can alter their niche, as young trout and coho are presumed to do. This, on the other hand, may not be true of fish in the old freshwater environments studied by Fryer (1959).

Highly specialized animals such as the parasitic wasps (DeBach and Sundby, 1963) may be virtually incapable of occupying an altered niche; thus elimination of one species is the necessary outcome of competition when no additional factors control the numbers of both competing species. It is reasonable to assume that the amount of specialization as well as the degree of similarity of species will determine the effects of competition. These effects may involve displacement in space, displacement or segregation in food habits, separation in some gradient of environmental conditions, changes in growth rates, or the complete elimination of one species. Species interaction need not be manifested in one type of end result only.

In the field of ecology, hypotheses can be postulated more easily than they can be tested. The present research adds support for the concepts advanced by Nilsson (1956, 1963). In doing so it has emphasized the role of behavior in the interaction of species and has shown how animal behavior may enter into certain problems in population biology.

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APPENDIX I. Mean fork length and range of samples of fish used in experiments, October 30, 1962, to November 23, 1963.

Date preserved or measured	Period when used	Species ^a	Mean fork length	Range	Sample size
			mm	mm	
Oct. 19-20, 1962	Nov. 1, 1962 to Feb. 20, 1963	C	58.3	40-95	13 ^b
		S	50.9	38-72	20 ^b
Jan. 10, 1963	"	C	68.6	52-97	73
	"	S	60.7	50-75	40
Jan. 19, 1963	"	C	66.2	47-88	40
	"	S	61.7	47-76	40
Apr. 25, 1963	"	C	67.5	51-99	56 ^b
	"	S	59.3	49-67	40 ^b
May 1, 1963	May 7 to	C	37.9	35-42	15 ^b
May 25, 1963	Nov. 23, 1963	S	33.5	26-42	22 ^b
June 8, 1963	"	C	43.4	40-47	16 ^b
June 12, 1963	"	S	39.7	29-49	62 ^b
July 19, 1963	"	C	52.1	38-64	65
	"	S	42.7	35-56	64
Sept. 2, 1963	"	C	66.4	50-89	60
"	"	S	56.2	39-80	74
Oct. 8, 1963	"	C	73.1	52-104	65
"	"	S	72.7	54-102	36
Nov. 23, 1963	"	C	76.7	62-93	30 ^b
"	"	S	73.2	47-112	35 ^b

^aC = coho; S = steelhead.

^bMeasurements made on preserved material.

APPENDIX II. Details of spring and early summer experiments comparing behavior and distribution of coho and steelhead.

Date and year	Arrangement in aquarium	Species (40 fish)	Temperature range (C)	Day length in holding pond	Average number moving
1963					
April 19-21	Control	Coho	6.5-8.3	12	1.8
" 21-23	"	"	8.5-9.2	12	2.7
June 7-9	"	"	11.7-12.0	12	3.9
" 9-11	"	Steelhead	14.0-14.3	12	6.0
May 26-28	Cover	Coho	10.0-11.2	12	3.7
" 28-30	"	Steelhead	13.0-13.3	12	2.2
June 11-13	Light	Coho	13.0-13.5	12	4.1
" 13-15	"	Steelhead	13.4-14.0	12	1.9
June 22-24	Depth	Steelhead	15.2-15.6	12	4.8
" 24-26	"	Coho	14.0-15.9	12	4.1
June 30-July 2	Depth and velocity	Steelhead	14.0-14.5	12	9.8
July 2-4	" "	Coho	14.9-15.4	12	8.4
April 28-30	Cover	"	7.1-7.5	12	2.5
" 24-26	"	"	7.1-8.4	12	1.1
June 16-18	Depth	"	15.0-16.0	12	3.5

APPENDIX III. Details of fall experiments comparing behavior and distribution of young steelhead and coho.

Date and year	Arrangement in aquarium	Species (40 fish)	Temperature range (C)	Day length in holding pond	Average number moving
1963					
Sept. 19-21	Control	Steelhead	12.7-13.3	12	7.9
" 21-23	"	Coho	13.2-13.4	12	3.0
" 27-29	Cover	Steelhead	12.3-13.1	12	11.5
" 29-Oct. 1	"	Coho	14.2-14.5	12	2.6
" 23-25	Light	"	12.7-13.5	12	3.5
" 25-27	"	Steelhead	13.6-14.2	12	11.6
Oct. 1-3	Depth	Coho	12.5-13.0	12	3.9
" 3-5	"	Steelhead	11.6-12.1	12	7.2
" 5-7	Depth and velocity	Coho	10.1-10.6	12	6.2
" 7-9	" "	Steelhead	10.8-11.0	12	7.5

APPENDIX IV. Details of winter experiments comparing distribution and behavior of young steelhead and coho.

Date and year	Arrangement in aquarium	Species (40 fish)	Temperature range (C)	Day length in holding pond	Average number moving
1962-63					
Nov. 5-7	Control	Coho	6.9-7.1	12	8.7
" 19-21	"	"	7.2-7.8	9	6.3
Dec. 4-6	"	"	4.7-4.9	8	-
Nov. 11-13	"	Steelhead	7.0-7.1	12	18.3
" 17-19	"	"	6.2-7.2	12	17.7
Dec. 6-8	"	"	5.2-5.7	8	19.7
Nov. 30-Dec. 2	Light	Coho	2.7-3.2	9	2.2
Dec. 2-4	"	Steelhead	3.1-4.0	9	7.4
" 17-19	Depth and velocity	Coho	5.0-5.3	8	5.0
" 19-21	"	Steelhead	5.3-5.6	8	10.6
Jan. 19-21	Cover	Coho	2.0-2.4	8	1.1
" 23-25	"	"	2.4-2.8	8	2.1
" 21-23	"	Steelhead	3.0-3.1	8	7.0
" 25-27	"	"	2.8-2.8	8	8.1
" 8-10	Depth	Coho	1.7-2.5	8	2.3
" 12-14	"	"	0.5-1.0	8	0.6
" 6-8	"	Steelhead	3.9-4.4	8	0.7
" 10-12	"	"	0.8-1.0	8	0.9