THE ROLE OF BEHAVIOR IN THE INTERACTION

OF UNDERYEARLING COHO AND STEELHEAD

(ONCORHYNCHUS KISUTCH AND SALMO GAIRDNERII)

by

GORDON F. HARTMAN

B.A., The University of British Columbia, 1954

M.A., The University of British Columbia, 1956

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Department of ___Zoology_____

The University of British Columbia,
Vancouver 8, Canada

Date ___May 29, 1964_____

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 microhabitat 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 is produced by ecological similarities of the species and accentuated by dense populations and inherently high levels of aggressiveness. The species do not segregate in streams in winter because certain ecological demands are different, numbers are lower and inherent 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.

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INTRODUCTION

Two similar species of salmonids occur together in
many of the coastal streams of British Columbia. These fish
- coho salmon (<u>Oncorhynchus kisutch</u>) and steelhead trout (<u>Salmo
gairdnerii</u>) - resemble each other in morphology, behavior and
early life history. On the basis of present concepts, they
are potential competitors.[1]

Young coho and steelhead coexist along the lengths of
streams but occur in different microhabitats; their ecology is
given more fully in the text. To introduce the problem, it is
sufficient to note that segregation is pronounced in the spring
and breaks down during fall and winter.

Nilsson (1956) has 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 intra-specific
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

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[1] The 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 <u>niche</u> is as given in De Bach and
Sundby (1963).

utilize only their ecological optima that results in segregation during rigorous interspecific interaction.

On the basis of this concept one might ask if the requirements and behavior of young trout and coho are similar in spring and early summer but different during fall and winter.

There are three 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 conditions are most similar. Essentially this involves testing Nilsson's ideas (Nilsson, 1956 and 1963) under controlled conditions. If the species are segregated at that period when requirements are similar, the third objective will be 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 "species A" an advantage in one situation and "speciesB" an advantage in another.

Part I.   FIELD STUDY

DESCRIPTION OF STUDY AREA

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

A. 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 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
rocky 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).   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. 4).   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 of the bottom
is unstable (Fig. 5).   There is one log jam near V-5.   The
lowermost region of the river travels across flat terrain; 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 1,250 km^2.
Mean monthly flows, 1958 to 1962, in Appendix I are based on
data from Water Resources Papers 128 and 131, and on unpublished
data from the Water Resources Division of the Department of

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

4.

Fig. 2. Chilliwack River and locations of stations.

Fig.3.   Upper Chilliwack River in area of
large log jams, V-36 to V-38.

Fig.4.   Chilliwack River in the region of
V-17.5.

Fig.5. Chilliwack River at V-5.5 and V-6.
Note braided channel and unstable
gravel bars.

Northern Affairs and Natural Resources. Highest monthly flows
occur during two periods - May to July and October to January.
Over and above seasonal changes, discharge fluctuates sharply
during periods of one or two days.

Mean monthly temperatures and ranges in the Chilliwack
River, near V-13, are presented in Appendix II.

B. 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 6 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. 7A). 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. 7B). Lower sections of
the Alouette (A-3 to A-0) lie in meadowland (Fig.8). 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 km^2. Appendix
I shows mean monthly flows from 1958 through 1962. Records for
1958 and 1959 represent spillage over the dam on the outlet of
Alouette Lake (data from B.C. Hydro and Power Authority). These
volumes do not accurately represent the flow in the river.
Several small tributaries in combination with ground seepage
prevent the river from drying up, hence flows are never zero as

Fig.6. Alouette River and locations of stations.

A

B

Fig.7A.   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.

Fig.8.   Alouette River at A-2 in meadow
          and farm land.

indicated in Appendix I. Discharge from April 1960 to April 1962 was obtained from Water Resources Paper No.131 and unpublished information from the Water Resources Division. These data were recorded near the town of Haney and therefore represent the true flow of the Alouette River. Highest mean monthly discharges occur during December and January. Periodic spill of excess water at the dam on Alouette Lake during heavy rains, results in sharp fluctuations of flow and damage to the river fauna.

Appendix III contains mean monthly temperatures and ranges (Alouette River) recorded near A-9.

C. Salmon River

The Salmon River rises in low wooded farmland, northeast of Langley, British Columbia, at an elevation of about 100 m. Figure 9 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.9). The middle section of the river lies in almost flat surroundings in a sand and gravel bed (Fig. 10A). Below S-6 the river meanders through meadows in a mud and sand channel. The overall character of the flow is gentle, with much of the river consisting of ripples and pools lying in well wooded areas (Fig. 10B).

The Salmon River drains an area of 83 km^2. Mean monthly flows (Appendix I, based on Water Resources Division data), reveal a peak run-off between November and February. During winter large short term fluctuations in discharge occur,

Fig.9. Salmon River showing locations of stations.

A

B

Fig.10A.   Salmon River at S-9.

B.   Riffle and pool areas
at S-14.

e.g. from 0.85 m^3 on January 23 to 8.32 m^3 on January 25, 1960.

Appendix IV contains mean monthly temperatures and ranges (Salmon River) recorded at S-9.

The three rivers studied contain a variety of types of habitat. These habitats range 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.

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 River (Fig. 6) and the Salmon
River (Fig. 9). 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 (Fig.11) and the fish drifted into the
seine; the blast area (usually small) was searched (Fig.11).

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 constant temperature recorders. Stream
velocities were calculated from the rate of movement of floating
objects. Turbidity and bottom composition were recorded on a
crude 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 one meter wide.

Fig.11.   Collection of fish with detonating fuse.

(See small explosion left foreground,
upper photograph)

R E S U L T S

A. Early Life History of Coho and Trout

1. Longitudinal distribution in streams

Highest densities of young trout and coho in the Chilliwack occurred in the upper reaches of the river (Fig.12). High densities recorded in Fig. 12, (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. 12), 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 (See Fig. 12). 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 was the same in winter as in the period from March to September (Fig. 12). At most stations, coho were more abundant than steelhead. During the early summer, young coho were captured further downstream than steelhead; aside from this, however, the two species were distributed in a similar fashion along the length of the river.

In the Alouette River, greatest concentrations of coho and trout occurred at stations A-9, A-12, A-14 and A-15, (Fig.13), all of which are characterized by a cover of heavy boulders (Fig. 7A). Below A-9 in areas with mud, sand or unstable gravel bottom, (Fig. 7B and Fig.8), densities were low (Fig. 13). During

Fig.12. Density and distribution of young coho and steelhead in the Chilliwack River. (Data combined for period from November 1959 to March 1962).

Fig.13. Density and distribution of young coho
and steelhead in the South Alouette
River. (Data combined November 1959
to March 1962).

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 13 shows that, although relative numbers of trout and coho varied at different stations, both species were distributed together along much of the river.

Highest densities of young trout and coho were recorded in the upper part of the Salmon River, (S-9 to S-18) and in its upstream tributary, (S-12 to S-19, Fig.14). This area of the river was characterized by small pools and gentle riffles (Fig. 10). 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. 14). 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 were more dense than trout at all stations, however both species occurred together over most of the length of the stream (Fig. 14).

A variety of types of physical habitat were studied within each of the three rivers. Furthermore size, bottom and flow conditions differed considerably between 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.12, 13, and 14). 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 head-waters or

Fig.14. Density and distribution of young
         trout and coho in the Salmon River.
         (Data combined November 1959 to
          March 1962).

head-water lakes.

2. 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, in late fall, occupied the rocky areas of the stream margin and the log jams. Figure 15 shows the density of steelhead and coho in relation to log jam cover during three 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. The steelhead was able to occupy a wider variety of microhabitats in the Chilliwack river. The species composition in the two microhabitats distinguished in Figure 15 was approximately the same at all seasons.

Fig. 15. 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.

In the Salmon River recently emerged coho and trout became segregated, with regard to microhabitat, during the first two months (Fig. 16). Trout density was highest in the riffles and lower in the open channel habitats and pools throughout May, June, July and 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. 16). 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. 16).

3. 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. 17). This size discrepancy decreased during late summer and autumn until, by winter, the size ranges were alike (Fig.17). Virtually all coho migrated out of the Salmon River in May and June, at age of about 14 months. Trout remained in the river two years or more. Winter samples of trout (Fig. 18) could be separated into underyearling and "one year plus" fish using length frequency plots of all trout (Fig. 18). Fish over 85 mm were designated as one year or more in age.

4. 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

Fig.16. 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.

Fig.17. 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 one mm length intervals.

Fig.18. Length frequencies of two or more year
classes of trout in the Salmon River.
Data are lumped, October to February,
inclusive, for three winters.

stream, the Salmon River, where the two species 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.

Part II. EXPERIMENTAL STUDY

MATERIALS AND METHODS

1. 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 between October 15 and 22, 1962. Coho used in experiments between April 19 and October 9, 1963 were seined April 11 to 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 V.

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 VI and VII; those used in winter experiments were held at a 12 hr day - subsequently reduced to 8 hr (see Appendix VIII).

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 5°C or less in winter (Fig.19).
Stream aquarium temperature in Fig.19 will be referred to later
in the text. The sharp rise and two-day temperature peak
(Fig.19) occurred when a break in the city water main forced
the use of an alternate supply.

Fish in the troughs were fed a diet 21% by weight
liver, 65% drained canned salmon, 8% brewer's yeast, 6% pablum
and salt (ca. one teaspoonful for 300 gr. 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.

2. 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 (Fig.20). The observation flume
is 5 m long, 12 m wide and .7 m deep.

Most of the aquarium is made of 1" (2.5 cm) plywood
supported in a 2" x ¼" (5.1 x 0.6 cm) angle iron frame (Fig.20).
The windows are of 5/8" (1.6 cm) plate glass. Construction of
the axial flow pump required a strong, non-toxic rust-resistant
material. This portion of the aquarium was therefore made of
1/8" (0.3 cm) welded mild steel lined with 1/8" (0.3 cm) fiber-
glass reinforced plastic.

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

Fig.19. Temperature maxima and minima (daily) in the
stream aquarium during three 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 two weeks or more previous to experiments.

6.3 M

5 M

1.2 M

2 M

AXIAL FLOW
PUMP

DRIVE
PULLEY

MOTOR

Fig.20. Experimental stream aquarium. Details of the
drive mechanism are not shown.

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.

3. 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 21 shows lateral aspects and plan views of control and four gradients. In the control situation (Fig.21a) the depth (28 to 29 cm), bottom gravel (3 to 6 cm), velocity (22 to 24 cm/sec) and lighting conditions were uniform along the length of the observation flume.

The light gradient (Fig. 21b) was produced with a series of 10 plexiglass sheets. The first sheet was clear, the remaining 9 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.

The cover gradient consisted of five groups of stones (Fig. 21c). Stones were elevated above small depressions in the

Fig.21. Lateral and plan views of control arrange-
ment 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 1. Average light intensity (Lux) over the length of the observation flume. Three readings, across the tank, were averaged for each figure. Readings were taken on the bottom with no water in the aquarium. Section 1 is at the upstream end of the tank.

Meters from Upstream End of Tank

4.75	4.25	3.75	3.25	2.75	2.25	1.75	1.25	.75	.25
2.60	10.8	23.8	48.6	85.3	157.7	189.0	201.9	375.8	281.0 (Lux)

Table II. Dimensions of stones (in cm)
used in cover gradient.

	S E C T I O N				
	5	4	3	2	1
Range in:					
Length	22-30	15-17	13-15	10-14	7-12
Width	18-24	12-14	10-11	7-8	5-6
Thickness	4-6	4-7	2-4	2-5	2-4

Fig.22. Velocity profile in horizontal and saggital 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 saggital plane (two center readings average). Arrows indicate direction of current, dotted lines represent screens.

Fig.23. Velocity profile in depth and velocity gradient. Upper figure shows velocities 10 cm above bottom. Lower shows velocity in saggital plane (two center readings averaged), Arrows indicate direction of flow, dotted lines represent screens.

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. 21d).

Screens between the leading and 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. 22). The

bottom was covered with the same gravel used in the control.

Illumination was slightly higher in the upstream end where

the floor panels were elevated closer to the light source.

The depth + velocity gradient was produced by means

of a sloping false floor (Fig. 21d). It was not possible to

vary velocity along the length of the observation flume without

altering depth or width. Details of velocity profiles in

horixontal and sagittal planes are shown in Fig. 23. 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 the downstream lend.

Figure 24 represents the riffle and pool environment.

This arrengement caused the current to exhibit complex flow

patterns which are described briefly below:

Pool in Section 1, upper 30 cm of water current flows

downstream at about 20 cm/sec. In lower 10 to 12 cm current

circulates upstream along the bottom at 4 to 5 cm/sec.

Riffles in Sections 2, 3 and 5, current 28 to 30 cm/

sec at the surface and 20 cm/sec along the bottom.

Temperature in the aquarium (Fig. 19) was governed by

seasonal changes in the temperature of the water supply,

Fig.24. Horizontal (upper) and lateral views of experimental
         riffle and pool environment. Horizontal arrow indicates
         direction of current. Vertical arrow indicates water
         surface.

conditions within the building and energy input from the pump. Tank temperature could usually be lowered by adding more new 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, 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 would rise. If it were low the aquarium temperature would fall (see October 5 and 6, November 9, 10 and 11, 1962 and January 8, 9, 10, 12 and 13, 1963, Fig. 19).

Temperatures within the aquarium deviated somewhat from those of the holding troughs early in the winter but approximated them later (Fig. 19). 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 19 shows that stream tank temperatures fluctuated seasonally and daily. They corresponded to those of the holding troughs but were generally higher.

4. Experimental procedure

Day length was maintained at 12 hr (06.00 to 18.00 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. Current was started and adjusted over the same time period. In each experiment, 40 fish were placed in still water between 20.00 and 22.00 hr. At 08.00 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 half or one hour intervals. During the second day positions of all 40 fish were plotted 12 to 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:

Fish "A"	Fish "B"	"A"	"B"
L + N ⟶	L + WW	N ⟶	Fl

In this series of events fish "A" displays in lateral posture

than 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 to 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 to 60 min. Many of the brine shrimp released kept circulating in the current for several hours, thus evoking feeding over a prolonged period.

The procedure followed in studying fish in the riffle-pool arrangement was slightly different than 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 of fish was placed in still water in the aquarium at about 20.00 hr. The following day the current was started and increased stepwise to the desired velocity by 09.00 hr. On each succeeding day, until the fourth, an additional lot of fish was added at 08.00 hr. Feeding and recordings 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 VI to VIII give details of gradient experiments.

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 No. of		Series 2 No. of		Series 3 No. of	
	C	S	C	S	C	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

5. 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 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 to 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. 19). 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. However, 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

1. 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. 25). Experiments with each species in the control, the cover gradient and depth gradient were replicated under winter conditions (Fig. 25 and 26). In general, the duplicate distribution patterns were similar (Figs. 25 and 26). Differences between species were consistent in repeated experiments in the control and cover gradient during the winter series (Fig. 25). 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. 26). 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. 25).

2. 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 (Figs. 25 and 26). The greatest differences in sectional averages occurred in fall or winter. Such large variations in the average number of fish per section

Fig.25. Distributions of coho and steelhead in "control" and "cover" gradients, described in text, during three seasons. Dots and circles represent mean number of fish per section over a one day period (10-15 observations). Vertical lines indicate range. Section 1 represents the upstream end of the aquarium.

Fig.26. Distributions of coho and steelhead in "light", "depth" and "depth and velocity" gradients, as described in text, during three 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.

were a result of the tendency of many individuals to congregate in one portion of the tank under fall or winter conditions. In spring both species scattered across the bottom of the tank as well as along its full length.

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 (Figs.25 and 26). 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 scattered and distributed along the tank in a similar fashion 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 VII and VIII). 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 Figures 25 and 26 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 + velocity
gradient (Fig. 26).

3. 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 (Figs. 25 and
26). 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 (Figs. 25 and 26), the seasons in which
populations overlapped most in the Salmon River (see Fig.16).
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 more compatible in the natural stream
environment. Different environmental responses in the
laboratory, (i.e. response to cover and depth, Figs. 27, 28,
31 and 32), are indicative of the mechanisms that allow the two
soecies 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 to 8 weeks old, scattered among the

stones which formed the cover gradation (Fig. 27). 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. 27) in the winter. Those that were not in the
shelter of stones were at positions at the sides of the tank.

Steelhead, 3 to 5 weeks old, distributed themselves
in the same pattern as the 6 to 8 week coho (Fig. 28). 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. 28). During the fall, a large number of young
trout were active and remained in the upstream end of the
aquarium (Fig. 28). One sixth of the positions recorded were
immediately downstream from stones, only six positions were
under them (Fig. 28). In winter one-fourth of the positions
recorded were under stones and approximately one-eighth were
downstream from them (Fig. 28).

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
However, in winter the tendency of trout to hide under stones
would, to a degree, isolate them from coho which do not do so
(Figs. 27 and 28).

A second case of trout and coho using the same space
in a different manner, in winter, occurs in the depth gradient.

Fig.27. Distribution of coho in cover gradient during three 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 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.

STEELHEAD — COVER GRADIENT — PLAN VIEW

MAY 30

SEPT 29

DIRECTION OF FLOW

JAN 27

SECTION 5 4 3 2 1

Fig.28. Distribution of steelhead in cover gradient during three seasons.
Locations of 40 fish during 10 combined observations are given.
Points within the stone outlines represent fish under stones.

Figures 29 and 30 show that the horizontal distributions of coho and steelhead are similar in spring, but different in winter. 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. Vertical distribution of both species (Figs. 31 and 32) considered in conjunction with horizontal distributions (Figs. 29 and 30) show that 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 (Fig. 33) 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 (Fig. 34) 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 interspecific 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.

Table IV. Numbers of coho (C) and steelhead (S)
in upper and lower halves of sections
4 and 5 in the depth gradient 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

Fig.29. Distribution of coho in depth gradient during three seasons. Locations
of 40 fish during 10 combined observations are given. Rows of points
at section boundaries represent fish occupying positions along the
edges of the depth zones.

Fig.30. Distribution of steelhead in depth gradient during three seasons.
Locations of 40 fish during 10 combined observations are given.
Rows of points at section boundaries represent fish occupying
positions along edges of depth zones.

COHO
JUNE 26

OCT 3

JAN 10

DEPTH GRADIENT
—LATERAL VIEW

DIRECTION OF FLOW

5   4   3   2   1.

SECTION

Fig.31. Distribution of coho, lateral view, in depth
gradient during three seasons. Locations of
40 fish in 10 combined observations are given.

Fig.32. Distribution of steelhead, lateral view, in depth
gradient during three seasons. Locations of 40
fish in 10 combined observations are given.

JUNE 28   DEPTH GRADIENT
                                                  —PLAN VIEW
   COHO

   STEELHEAD

   COHO   —LATERAL VIEW

   STEELHEAD   DIRECTION OF FLOW
                                                      ←   ←

        5   4   3   2   1
                      SECTION

   Fig.33. Relationship of coho and steelhead combined in depth
            gradient during summer conditions. Locations of 20
            coho plus 20 steelhead in 10 combined observations
            are given.

Fig.34. Relationship of coho and steelhead combined in depth
gradient during winter conditions. Locations of 20
coho plus 20 steelhead in 10 combined observations
are given.

Table V. Aggressive contests per fish per 100
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	N u m b e r o f						
	Fish		C o n t e s t s				Minutes
	C	S	C·C	C·S	S·S	S·C	Observation
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

4. Description of agonistic behavior

Young coho and steelhead display using a number of
similar postures and movements. These displays and movements
are listed in the "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 one or two seconds to a prolonged erection
of dorsal, and paired fins and a lowering of the basihyal
apparatus for 10 or 15 seconds (Fig.35). 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. 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. 35C).

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 one or two seconds (Fig. 36A), to a posture in which

Fig.35A. Coho, ca 10 months old, in lateral threat posture.

B. Steelhead, ca 8 months old, in lateral posture (see fish on the left). Fish on the right in frontal threat posture of low intensity.

C. Coho, ca 2 months old, in lateral threat posture.

Fig.36A. Coho, ca 2 months old, in frontal threat posture of
low intensity (right). Coho, ca 2 months old, in wig
wag posture (left).

B. Coho, ca 2 months old, in wig wag (left) and lateral
threat posture (right).

the back was strongly arched, the dorsal fully compressed and the basihyal well extended for longer (unmeasured) periods.

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 to 30 degree angle from horizontal (Fig. 36B). 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 degrees) 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.

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 (Fig. 37). 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

Fig.37. Nipping in the pair of fish on the left. Picture taken a
fraction of a second before the front fish was nipped.
Second pair of fish (right side) in characteristic lateral
postures.

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 non-social 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.

5. Analysis of behavior

By recording bouts in terms of individual behavior components it was possible to examine the rate of occurrence of individual 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 38 represents behavior repertoires of coho and steelhead during three 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 Figure 38. First, the repertoires of the two species differ at all seasons. Second,

Fig.38. 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.

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

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.38).

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

During spring and summer lateral displays, nipping and chasing were frequent in both species. Nipping and chasing components were very strong in the steelhead (Fig.38), 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 non-contact 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 to 9 cm/sec). At higher velocities (18 to 19 cm/sec and

28-30 cm/sec) 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 steelhead 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 suggest that the
differences in behavior of coho and steelhead are related to
their ecology.

6. Distribution in riffle and pool habitat

The major difference in distribution of trout and
coho in the field was related to riffle and pool habitats. In
the laboratory 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 (Figs. 39 and
40) 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 (Figs. 39 and 40). When coho and steelhead were
mixed in July experiments, density of steelhead was reduced

Fig.39. 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,
(see Fig.24 for details of riffle and
pool environment).

Fig.40. 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,
         (see Fig.24 for details of riffle-pool
         environment).

COHO   STEELHEAD

SECTION

(in relation to the situation where the species was alone) in 6 out of 8 cases in the pool habitat, and increased in 8 out of 12 instances in the riffle habitat. Coho density was reduced (in relation to the situation where the species was alone) in 9 out of 12 cases in the riffles and increased in 5 out of 8 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. 40). 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. 39).

7. Aggressive behavior in riffles and pools

Levels of aggressiveness were higher in riffle habitat than in the pool conditions when the species were separate (Fig. 41). 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.

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 42

Fig.41. Rate of aggressive behavior in riffle and
pool habitats during July and November.
Data based on observations made with species
separate. C v C indicates coho attacking
coho, and S v S indicates steelhead attacking
steelhead. Coho observed 390 minutes in July
and 340 minutes in November, steelhead
observed 380 minutes in each period.

Fig.42. Rates 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 minutes in July and 250 minutes in November. Meaning of symbols as follows: C v C - coho attacking coho, C v S - coho attacking steelhead, S v S - steelhead attacking steelhead and S v C - steelhead attacking coho.

shows that coho displayed a high level of interspecific and
intraspecific aggressiveness within pools. Aggressiveness of
trout was correspondingly low in the pools (Fig. 42). (Chi-
square values indicate that differences in rates of aggressiveness
of trout and coho in riffles and pools is significant. $P < .01$).
In the riffle habitat of the aquarium coho were not combative,
steelhead on the other hand were particularly aggressive
(Fig. 42). In addition to being more aggressive, steelhead
tended to defend temporary territories. A comparison of Figures
41 and 42 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 (see Figs. 41 and 42).

High rates of aggressive behavior in the riffles
(species unmixed) resulted in low densities of fish in such
areas. Behavior differences, which were related 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 Figure 43 rates of aggression were high at
low densities. High densities of fish did not occur because

Fig.43. Relation of rate of aggressive behavior to
density of fish. Coho and steelhead compared
in riffle and pool habitats during two seasons.
Each dot or circle represents 10 minutes of
observation in one section of the aquarium.
(Data obtained with species separate).

increased fighting led to displacements of fish.

In the pools however aggressiveness decreased with an increase in fish density (Fig. 43). Keenleyside and Yamamoto (1962) demonstrated almost the 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. 43). 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 (Figs. 44A, B and C). In many cases the upstream fish ended by literally brushing its opponent back with its tail (Fig. 44C). 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 as illustrated in Figure 45.

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

Fig.44A. Coho, ca 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.

Fig.45. Small group of 8 coho with one dominant (second
from right) and seven subordinates. Small fish
occasionally avoided attack by remaining still
and resting down among the stones, see foreground.

and did not hold the front positions in any stable groups.

<u>8. Summary of results</u>

Field observations revealed seasonal changes in the distribution 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 briefly below as an introduction to the Discussion. Field observations apply particularly to the Salmon River.

1. SPRING AND EARLY SUMMER

<u>Field observations</u>   <u>Laboratory observations</u>

1. Species largely segregated in different micro-habitats.

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 period corresponds to laboratory period).

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. Temperature 10° to 16°C.

5. Body and fin colors vivid.

'2.   FALL

Field observation	Laboratory observation
1. Species partially segregated in early fall, coming together more in late fall.	1. Steelhead and coho have different distributions in experimental gradients.
2. Coho in pools, trout density about even in riffles and pools.	2. Species utilize space and cover in about the same manner.
3. Population reduced in pools, reduced more in riffles.	3. Coho aggression high, but less biting and chasing is exhibited. Steelhead aggression lower than in spring, relatively less chasing.
4. Trout size range approximating that of coho.	4. Temperature 9° to 14.5°C.
5. Temperature of water 7.2° to 12.5°C.	5. Body and fin colors less vivid.

3.   WINTER

1. Species exhibit no microhabitat segregation.	1. Species have different distributions in experimental gradients.
2. Highest density of both species in the pools.	2. They utilize space in pools and around cover in different manners.
3. Population density reduced further in pools, very low in riffles.	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. Trout size range approximating that of cohos.	4. Temperature 0.5° to 7.5°C.
5. Temperature of water 0.3° to 7°C.	5. Body and fin colors less vivid than in spring and fall.

DISCUSSION

An animal's behavior is adapted to its environment just 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 now be considered before entering the main body of the discussion, which will deal more directly with interspecific interaction.

A. 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 condition 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. Coho on the other hand moved downstream or laterally, (Fig. 46). 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 (Figs. 25 and 26). 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 non-contact aggressiveness. The wig wag display occurred frequently in laboratory conditions and was exhibited 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.

Fig.46. Direction of retreat of coho and steelhead
following intraspecific aggressive contests
(based on 248 contests, among steelhead and
458 among coho).

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 chased 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 to 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. The relationship of similar species such

as the trout and coho making demands on the same resource leads
to a fundamental interest in eco-biology.

B. Interaction of Young Steelhead and Coho

Segregation of natural populations of young coho and
trout occurred at the season in which experiments indicated
greatest 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 (Nilsson 1956, 1963). Interaction, which occurred
in spring and summer because both species had similar demands,
was accentuated by three factors. Population densities were
highest in spring and summer (Fig. 16). Levels of aggressiveness
were highest early in the year (Fig. 38). In addition to this
the aggressiveness shown involved much biting and chasing. Size
differences may have contributed to the effect of segregation.
Coho were larger than the trout in spring and summer (Fig. 17)
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
compatability. 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. 16). Third, levels of aggressiveness were lower
in winter (Fig. 38). 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. 26). However trout and coho utilized this pool space differently, coho formed groups in open water above bottom, and trout scattered across the bottom (Figs. 31 and 32). In the cover gradient trout occupied space under stones but coho occupied space beside the stones or downstream from them (Figs. 27 and 28). 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, could 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 the 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. 42). Segregation in the Salmon River is probably maintained because of differences in motivational states of trout and coho in the three micro-habitats 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.

C. Comments on Concepts of Competition

A number of investigators have reported instances in which competition or interaction between species is manifested in segregation (see Beauchamp and Ullyott, 1932; Macan, 1961; and Connell, 1961). Segregation produced by competition among fish has been recorded by Nilsson (1955, 1958, 1960 and 1963). Muira (1962) reviewed several cases in which it occurred in competing species of Japanese fish. Lindroth (1955a), 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 necessary to point out 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; de Bach and Sundby, 1963). Grinnell (1904), Gause (1934) and De Bach and Sundby (1963) have indicated that species having the same niche cannot occur together without one eliminating the other. De Bach 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 s*i*mpatric 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 <u>identical</u> 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 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
(De Bach 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 often be postulated much more easily than they can be tested. The present research does not demonstrate that the concepts put forward by Nilsson (1956 and 1963) apply in all cases, although it does demonstrate that such concepts provide a valuable framework for interpreting certain situations in nature and in the laboratory. Moreover the work provides further support for the concept that species tend to be segregated in their use of a particular resource when it is in short supply. In addition, the study has emphasized the role of behavior in the ecological relationships of the two species and demonstrated a strong behavioral basis for the marked segregation which they show.

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Appendix I. Mean monthly discharge in M^3 per second, for the Chilliwack River at Vedder
Crossing, the Alouette River at 14th Street bridge and for the Salmon River
at Springbrook Road bridge (1958 to 1962).

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Chilliwack R.												
1958	56.9	52.1	40.5	46.7	130.5	103.9	45.3	25.4	34.2	65.4	70.8	95.7
1959	70.5	32.3	32.8	72.2	91.4	135.5	110.4	43.5	68.8	74.2	82.7	48.9
1960	22.7	37.6	22.2	47.3	65.4	105.3	73.9	35.1	28.0	36.8	56.3	62.0
1961	73.9	75.0	47.0	55.2	81.4	183.7	95.4	57.7	27.8	49.8	45.6	44.2
1962	88.9	70.5	22.9	57.6	-	-	-	-	-	-	-	-
Alouette R.												
1958	7.9	0.0	0.0	0.0	0.0	0.3	3.7	0.0	0.0	0.0	2.0	1.4
1959	0.6	0.0	0.0	0.0	0.0	0.0	10.5	2.2	2.2	0.0	0.0	0.0
1960	-	-	-	2.3	1.7	1.1	0.4	0.6	0.7	1.9	2.4	2.1
1961	9.8	5.2	3.1	1.6	1.3	0.6	0.4	0.3	0.4	2.1	3.5	7.0
1962	5.2	2.2	1.1	1.5	-	-	-	-	-	-	-	-
Salmon R.												
1958	-	-	-	-	-	-	*.28	*.23	*.40	-	-	-
1959	-	-	-	-	-	-	*.14	*.38	*.31	-	±1.64	-
1960	5.10	3.20	1.40	1.40	1.40	.50	.28	.23	.27	1.50	2.70	3.14
1961	4.67	5.97	3.70	1.47	1.27	.33	.33	.25	.21	.86	1.67	3.40
1962	3.51	1.98	1.50	1.61	1.34	.54	.24	.29	.33	.94	3.26	3.93

1958-59 Alouette River data from B.C. Hydro & Power Authority - see text.
* Misc. single readings Water Resources Division.
± Average of two estimates by author.

Appendix II. Maximum, minimum and mean monthly temperature ($^{\circ}$C) of the Chilliwack River. (*mean based on less than 20 days data, **mean based on less than 10 days data).

| | 1960 | | | 1961 | | | 1962 | | |
	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
January	5.9	-2.0	2.8	6.0	2.0	4.2	3.7	-1.0	2.0
February	6.0	-2.0	4.2*	5.2	3.0	4.1*	5.0	-1.0	2.3**
March	8.0	-1.0	4.3	6.0	2.0	3.6*	7.5	-0.5	3.0
April	10.1	4.3	6.2	8.8	2.5	5.9	11.5	2.0	6.2
May	10.3	5.9	7.5*	10.6	4.5	6.9	11.7	5.5	8.1
June	12.0	5.8	8.6	12.2	6.5	9.3			
July	17.0	8.4	12.4	15.8	8.2	11.9			
August	17.5	10.0	13.0	16.0	9.0	13.0			
September	13.8	9.0	11.2	-	-	-			
October	12.1	6.6	9.1	10.0	5.5	7.5*			
November	8.1	4.5	6.2	4.1	-1.0	2.4*			
December	6.0	3.4	4.8	4.0	0.0	2.2			

Appendix III. Maximum, minimum and mean monthly temperature ($^{\circ}$C) of the Alouette River.
(*mean based on less than 20 days data, **based on less than 10 days data).

	1 9 6 0			1 9 6 1			1 9 6 2		
	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
January				6.4	0.7	4.2*	6.5	0.0	2.8
February				7.2	1.7	5.4*	7.4	4.2	6.1*
March				10.3	5.0	6.3*	10.6	1.5	5.5
April				11.1	5.0	8.4*	13.4	5.2	8.9
May				20.5	6.1	12.0	15.0	6.9	10.5
June	23.4	10.5	15.2*	25.0	11.2	17.8*	20.6	9.6	14.3
July	27.8	12.8	20.8*	27.1	13.1	20.1			
August	27.8	12.2	15.6*	23.8	12.1	18.0**			
September	13.7	10.0	11.3**	15.0	11.1	13.2**			
October	11.6	6.6	9.1	15.0	3.4	10.2**			
November	8.8	2.1	5.3	5.5	4.5	5.2**			
December	6.1	0.0	2.5	5.0	3.0	4.0**			

Appendix IV. Maximum, minimum and mean monthly temperature (°C) of the Salmon River.

	1 9 6 0			1 9 6 1			1 9 6 2		
	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
January				7.2	0.6	3.7	6.4	0.0	3.2
February				7.8	3.6	5.5	9.2	-0.5	5.4
March				10.3	3.1	6.8	10.3	0.3	5.0
April	11.7	5.0	8.1	11.7	5.9	8.7	14.7	5.9	9.5
May	11.7	7.2	9.0	15.3	8.6	11.2	14.2	7.3	10.6
June	13.4	8.6	10.8	17.5	11.4	14.0	17.8	9.5	12.9
July	16.4	10.0	13.0	20.3	10.0	15.5			
August	17.0	9.2	12.1	18.4	10.0	15.2			
September	13.1	8.9	11.2	15.9	8.6	11.7			
October	12.0	7.2	9.5	12.2	5.6	8.7			
November	9.2	3.9	6.4	8.4	2.8	5.3			
December	7.6	0.6	3.8	6.7	1.1	3.7			

Appendix V. Mean fork length and range of samples of fish used in experiments, October 30,
1962 to November 23, 1963. (* – measurements made on preserved material).
Coho – C, Steelhead – S.

Date preserved or measured	Period when used	Species	Mean Fork L. in mm.	Range in mm.	Sample Size.	
Oct. 19-20, 1962	Nov.1, 1962-Feb.20,1963	C	58.3	40-95	13	*
	" " " "	S	50.9	38-72	20	*
Jan. 10, 1963	" " " "	C	68.6	52-97	73	
	" " " "	S	60.7	50-75	40	
Jan. 19, "	" " " "	C	66.2	47-88	40	
	" " " "	S	61.7	47-76	40	
April 25, "	" " " "	C	67.5	51-99	57	*
	" " " "	S	59.3	49-67	40	*
May 1, 1963	May 7 to Nov.23, 1963	C	37.9	35-42	15	*
May 25, "	" " "	S	33.5	26-42	22	*
June 8, "	" " "	C	43.4	40-47	16	*
June 12, "	" " "	S	39.7	29-49	62	*
July 19, "	" " "	C	52.1	38-64	65	
" "	" " "	S	42.7	35-56	64	
Sept. 2, "	" " "	C	66.4	50-89	60	
" "	" " "	S	56.2	39-80	74	
Oct. 8, "	" " "	C	73.1	52-104	65	
" "	" " "	S	72.7	54-102	36	
Nov. 23, 1963	" " "	C	76.7	62-93	30	*
" "	" " "	S	73.2	47-112	35	*

Appendix VI. 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 & Velocity	Steelhead	14.0-14.5	12	9.8
July 2-4	" "	Coho	14.9-15.4	12	8.4
April 28-30	Cover	Coho	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 VII. 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
Sept. 27-29	Cover	Steelhead	12.3-13.1	12	11.5
Sept. 29-Oct. 1	"	Coho	14.2-14.5	12	2.6
Sept. 23-25	Light	Coho	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
Oct. 5-7	Depth & Velocity	Coho	10.1-10.6	12	6.2
" 7-9	" "	Steelhead	10.8-11.0	12	7.5

Appendix VIII. 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	Cay Length in Holding Pond	Average number moving
1962-1963					
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	Control	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	Light	Steelhead	3.1-4.0	9	7.4
Dec.17-19	Depth & Velocity	Coho	5.0-5.3	8	5.0
Dec.19-21	Depth & Velocity	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
Jan.21-23	Cover	Steelhead	3.0-3.1	8	7.0
" 25-27	"	"	2.8-2.8	8	8.1
Jan. 8-10	Depth	Coho	1.7-2.5	8	2.3
" 12-14	"	"	0.5-1.0	8	0.6
Jan. 6-8	Depth	Steelhead	3.9-4.4	8	0.7
" 10-12	"	"	0.8-1.0	8	0.9