# Aggressive Behavior in Juvenile Coho Salmon as a Cause of Emigration[1]

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## ABSTRACT

Large numbers of coho fry (called nomads) move downstream from shortly after emergence through early fall. These fry are smaller than residual coho. Study of behavior showed coho to be aggressive and territorial or hierarchical. Nomadic coho placed in stream aquaria barren of resident fish tended to remain in the aquaria rather than continuing downstream movement, while nomads added to resident groups of coho were dominated by the resident dominant fish and tended to leave the channels. Hierarchies were organized on the basis of fish size, with larger fry having better growth opportunities. Feeding of coho in excess of requirements did not alter holding capacity of stream aquaria. Aggression observed in natural stream areas was frequent, probably virtually continuous. Nomads transferred to natural stream areas barren of other coho remained there, while nomads added to resident populations tended to move downstream. It was concluded that aggressive behavior is one important factor causing downstream movement of coho fry.

## INTRODUCTION

THIS PAPER reports a study of aggression in coho salmon (*Oncorhynchus kisutch*), showing that downstream movement of coho fry is an important result of aggressive behavior.

Several workers have recorded extensive emigrations or downstream movements of coho fry in the spring subsequent to the emergence of fish from the spawning gravel (Salo and Bayliff, 1958; Oregon Fish Commission, 1958; Chapman *et al.*, 1961; and unpublished studies at the Fisheries Research Board of Canada Biological Station, Nanaimo, B.C.). The downstream movements of fry usually begin soon after emergence and continue through early summer. This downstream fry migration, coupled with the concepts of behavior developed by several workers, suggested that the aggressive behavior of certain dominant individuals in the coho population was one stimulus leading to the observed downstream migration.

Aggressive behavior has been found to be a significant mechanism of intraspecific competition and is regarded as a factor important in the ecology and sociology of natural animal populations (Collias, 1944). Territoriality in stream-dwelling salmonids, apart from reproductive behavior, has been suggested to be a characteristic evolved as a function to assure adequate food supply (Kalleberg, 1958) and a factor promoting wide distribution of the fish in streams (Hoar, 1951).

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Aggressive behavior of eastern brook trout (*Salvelinus fontinalis*) and rainbow trout (*Salmo gairdneri*) has been shown by Newman (1956), who observed formation of social hierarchies as well as territoriality. Kalleberg (1958) showed that brown trout (*Salmo trutta*) and Atlantic salmon (*S. salar*) were strongly territorial. These species developed a mosaic of territories in aquaria. Increase in population density beyond saturation caused some individual territories to completely disappear rather than adjusting by the compression of the living area of less aggressive fish. Hoar (1951) reported territorial behavior in coho

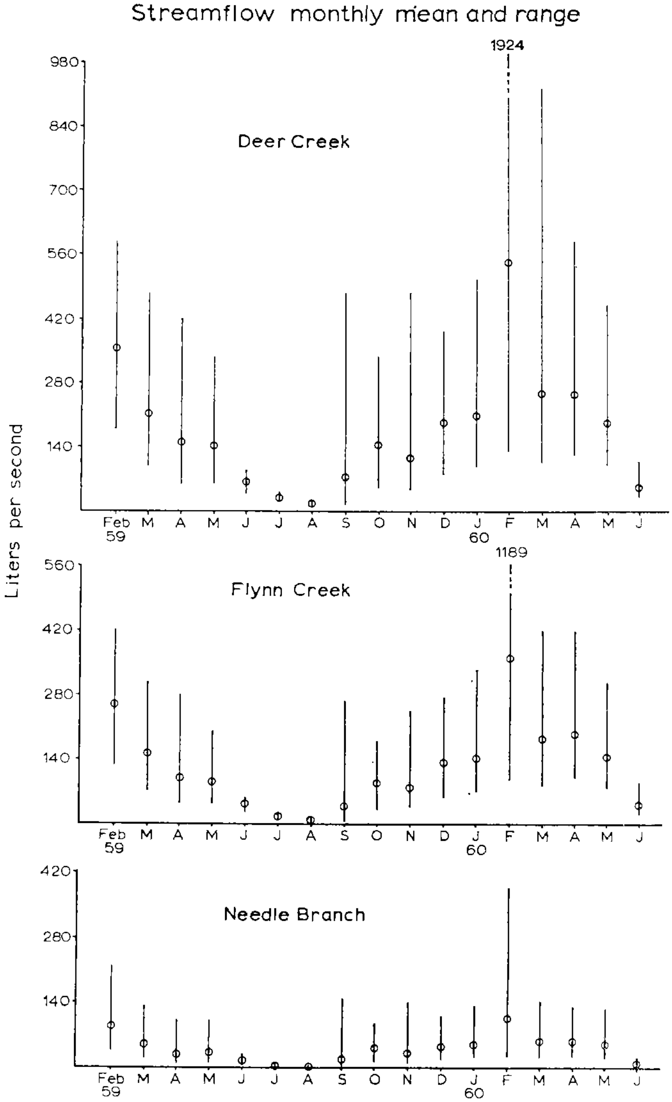
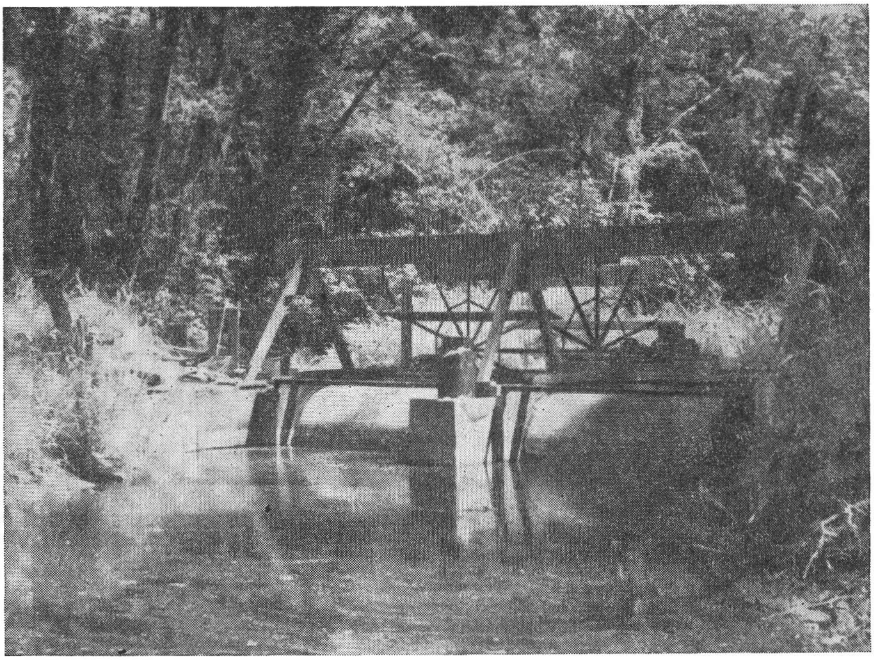


FIG. 1. Streamflow monthly mean and range in liters per second, February, 1959 to July, 1960.



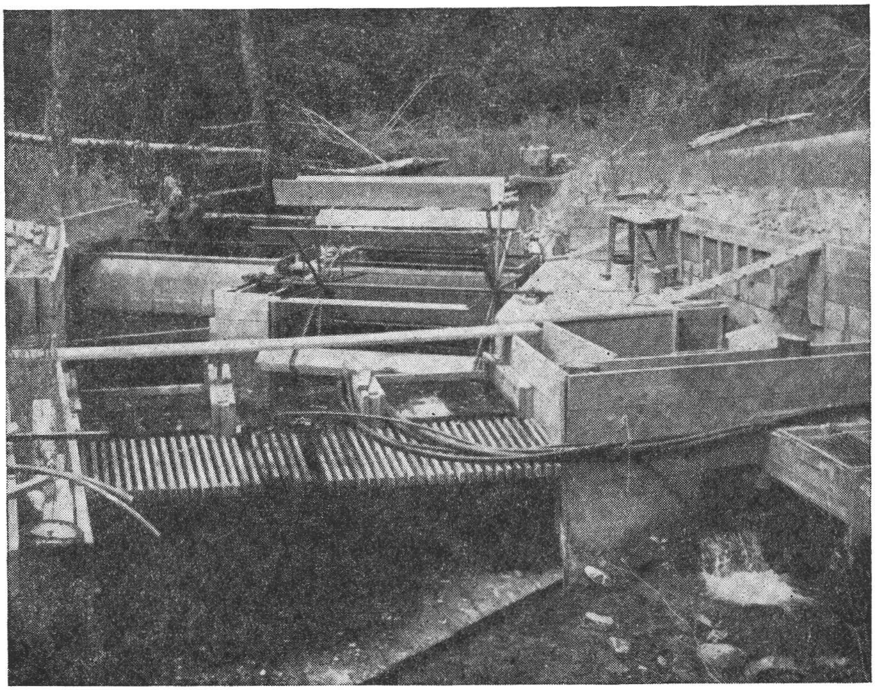


FIG. 2. *Above:* upstream view of the traps used at Flynn Creek; *below:* downstream view of the traps at Deer Creek.

salmon fry, stating that coho fry maintain definite positions relative to certain objects in their environment, and tend to remain in slower flows and to be quiet at night. Hoar felt that these traits prevent downstream displacement of fry.

Downstream movement of fry can, of course, be attributed to one or more possible factors: displacement by current, innate tendency to migrate (apart from movement enforced by aggression), random shifts in position, or aggression (such as territorial behavior) within the fry population. The principal hypothesis tested in this paper was that the downstream drift of coho fry was caused primarily by aggressive behavior of residual coho. Work was conducted from April, 1960, to November, 1961.

## DESCRIPTION OF STUDY AREA

Most of the research reported here was conducted on three tributaries (Deer Creek, Flynn Creek and Needle Branch) of Drift Creek, the latter stream draining into Alsea Bay near Waldport on the Oregon coast. The streams are about 4.0 km, or less, apart, and their seasonal changes in biotic and physical characteristics are parallel. The three streams are described in another paper (Chapman *et al.*, 1961). Figure 1 shows stream flow in each stream, demonstrating that great seasonal variability in flow occurs.

Salmonid fishes present in the streams are coho salmon, coastal cutthroat trout (*Salmo clarki clarki*), and steelhead trout (*S. gairdneri*). Coho salmon are

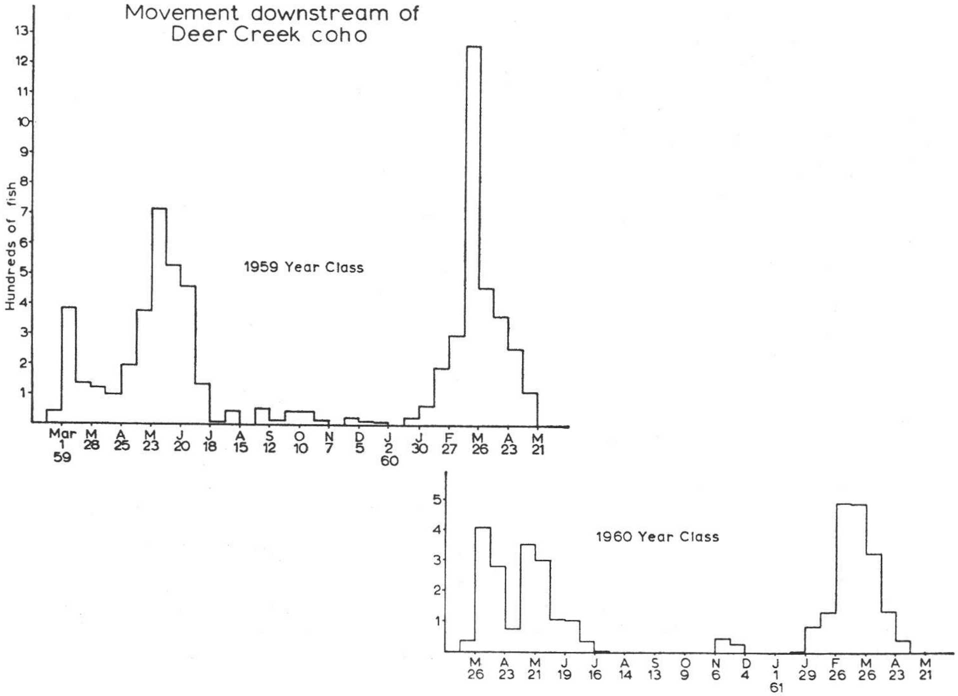


FIG. 3. Downstream movement of juvenile coho salmon in Deer Creek, 1959 and 1960 year-classes.

the most abundant of the three species. Data on upstream and downstream movements were collected by means of fish traps on the three streams. The trap used on Deer Creek is shown in Fig. 2. Virtually all fish moving upstream and downstream are taken in the traps. Available data on downstream movements of coho are shown in Fig. 3 and 4 in order to give some idea of the importance of the downstream drift of fry in the first few months of life. Coho fry moving through downstream traps from time of emergence through October are termed "nomads" in this paper. Coho moving downstream after October are called migrants or smolts.

## METHODS

The means used to test the principal hypothesis were of necessity indirect. Nomads were placed in artificial stream sections, both test and control, constructed in observation troughs, and observations were made of their behavior and interaction with coho resident in the sections. Test sections contained a resident group of coho while control sections were barren of resident fish.

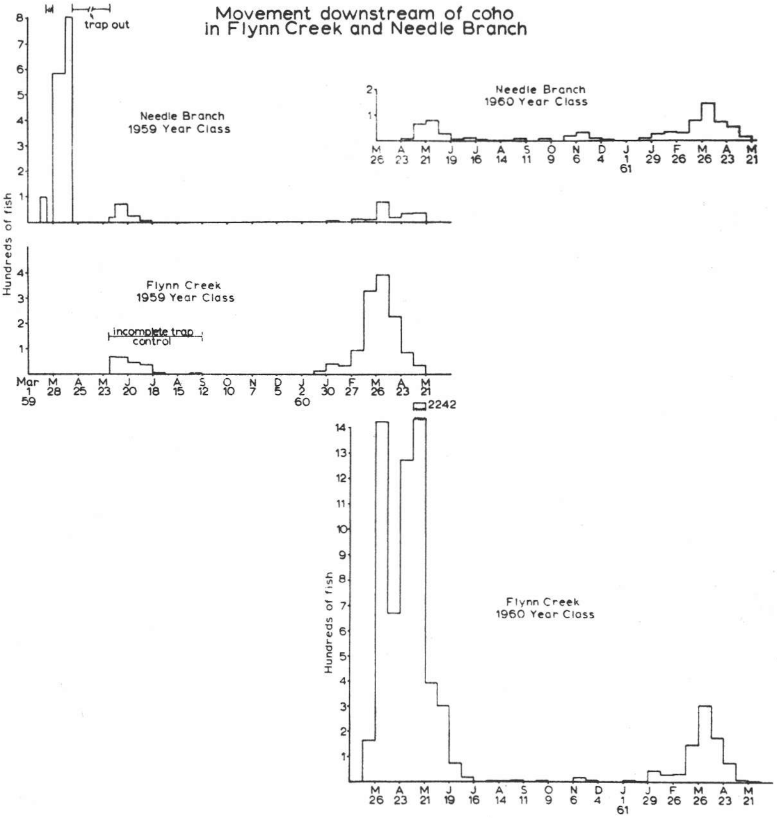


FIG. 4. Downstream movement of juvenile coho salmon in Flynn Creek and Needle Branch, 1959 and 1960 year-classes.

Nomads were also placed in a controlled natural stream area or stream from which resident coho had been removed. Both methods tested the theory that nomads would cease movement downstream if given adequate living space. Nomadic coho should not remain in observation channels or in controlled natural areas if their movement was due to their displacement by strong water current or innate tendency to migrate. In addition to the two experimental methods of testing the hypothesis, supporting evidence was gathered through the observation of coho behavior and sampling of growth of nomadic and residual coho fry in the study streams.

### ARTIFICIAL CHANNELS AT DEER CREEK

Two troughs (Fig. 5 and 6), each consisting of paired channels, were constructed at the downstream end of the Deer Creek fish trap. Water for troughs was passed through plastic pipe leading from the pool above the fish trap dam to the trough forebays. Flow through each A channel was about 10.6 liters per minute; through each B channel it was 15 l/min in 1960 and 95 l/min in 1961.

The bottoms of all 4 channels were built up by addition of natural stream bottom materials so that each channel in 1960 had 2 pools and 3 shallow areas or riffles. Invertebrate forms were present in the material placed in the troughs,

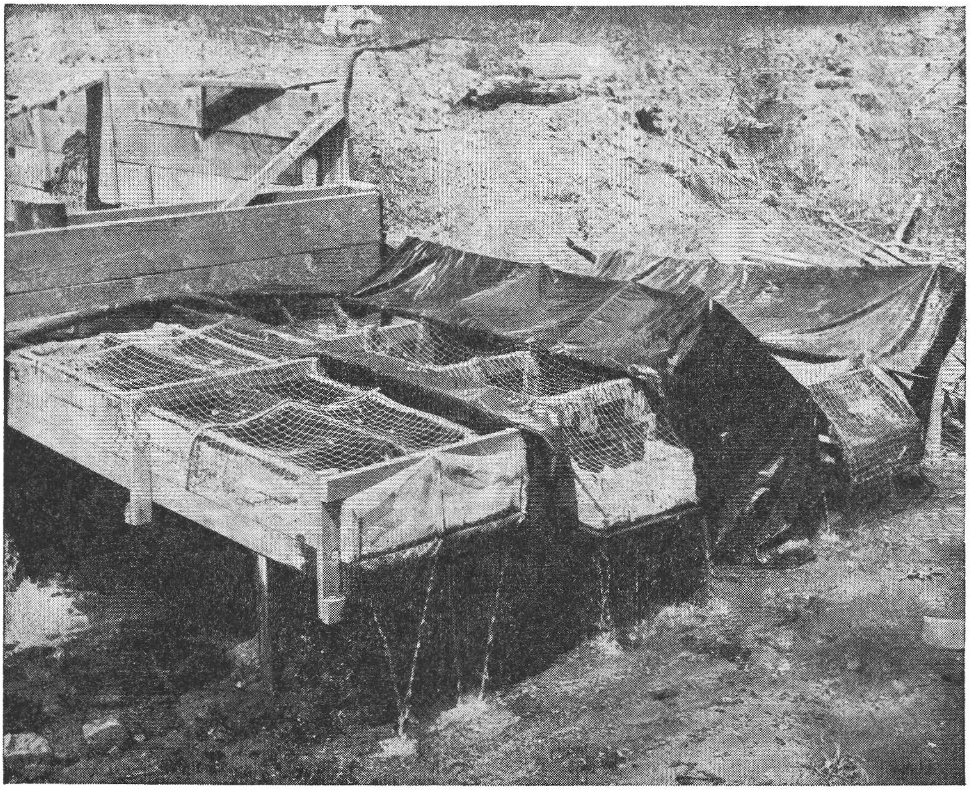


FIG. 5. Artificial stream channels at Deer Creek used for study of coho behavior.

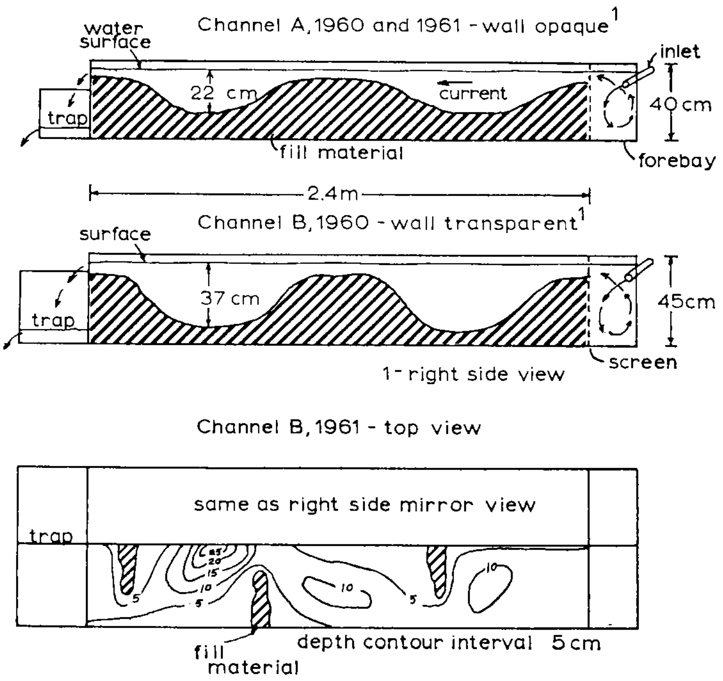


FIG. 6. Schematic drawing of artificial channels at Deer Creek.

and additional insect larvae were added before fish were placed in the troughs to help insure an adequate supply of insect forms used by coho (Demory, MS, 1961). An abundant algal growth, largely *Oscillatoria* sp., became established soon after the troughs were constructed. In 1961 the channels were altered so that 3 shallow pools and 3 riffles were created (Fig. 6) in each channel. Water was maintained in the A and B channels through the winter of 1960–61 so that an invertebrate population was established and present during 1961 experiments.

Twine netting having a mesh of 38 mm from knot to knot was placed over all 4 channels to prevent birds from preying on experimental fish, and to provide some cover. Benches were placed at the sides of the B channels, and black polyethylene canopies or tents were placed over benches so that fish looked out upon a dark area.

No coho could pass the screening between forebays and observation channels. Any coho placed in the channels had to live there, die there, or pass downstream into inclined plane traps from which they could not escape.

During part of the 1960 studies with troughs A and B, the fish were fed. Adult brine shrimp, *Artemia* sp., were frozen in 1-gram lots in ice cubes and used according to a feeding schedule. The quantity of food fed was determined from coho growth data obtained by personnel of the Fish and Game Management Department at Oregon State University. These data indicated that maximum growth of coho was induced by a ration of about 150 mg (wet weight) of amphipods daily per gram of fish tissue. Therefore a daily ration of about 300 mg of brine shrimp per gram of fish tissue was fed to assure an excess of available food. The food cubes were placed at the upper end of each channel in wire baskets placed in the water. As the cubes melted, the shrimps drifted downstream. Experimental coho, 35 to 65 mm, fed avidly upon these shrimps. Fish were fed twice daily early in the work, then once daily as it became evident that this was adequate.

Nomads for artificial channel experiments were obtained from the Deer Creek downstream trap, and measured and marked by a notch in one of the fins. Fish for experimental use were selected randomly if more than the number required were in the trap. After being held in plastic buckets for 15 minutes to permit recovery from handling, the coho were placed in the channels at the upstream ends.

In initial experiments the capacities of A and B channels were determined by means of introductions of nomads into barren channels. When capacities had been determined approximately, groups of 3 to 5 coho were placed at the same time in each channel. One group of nomads was added to a resident group of coho in the test channel while another introduced group was added simultaneously to the barren control channel.

In the test channel a resident group of coho was established, and these fish formed the population to which new nomads were added. In the second channel, designated as a control, all coho were removed before new groups of fish were introduced. The test and control channels were essentially alike except that the test channel contained a resident group of coho.

In several experiments the resident coho were removed from the test channel, measured (fork lengths), and in all respects handled in the same manner as nomads to be introduced. Observation of subsequent behavior patterns and test results revealed no difference between behavior of resident coho handled in this manner and those not handled at all.

In some experiments late in August and September, 1960, resident coho seined from a stream area were used, since no nomads were available at that time.

### ARTIFICIAL CHANNELS AT OAK CREEK

A pair of artificial stream channels was constructed at Oak Creek, 5 miles west of Oregon State University, for long-term study of coho behavior. The paired channels are shown in Fig. 7.

The bottom of the channels was built up with gravel and sand to the level of the window bottoms, and the final surface layer at that level was flat, smooth, and composed of rock particles about 3 mm in diameter.

Flow in each channel varied from a maximum of 227 l/min to a minimum of 114 l/min, depending on the head of water in the source stream. Depth in the channels decreased as stream flow decreased, from 51 mm to a minimum of 25 mm.

The channels were exactly alike in all possible respects: depth, bottom type, current, total flow, overhead cover, and surroundings. All channel wood parts were painted a dull brown to simulate soil coloration. Tents were constructed

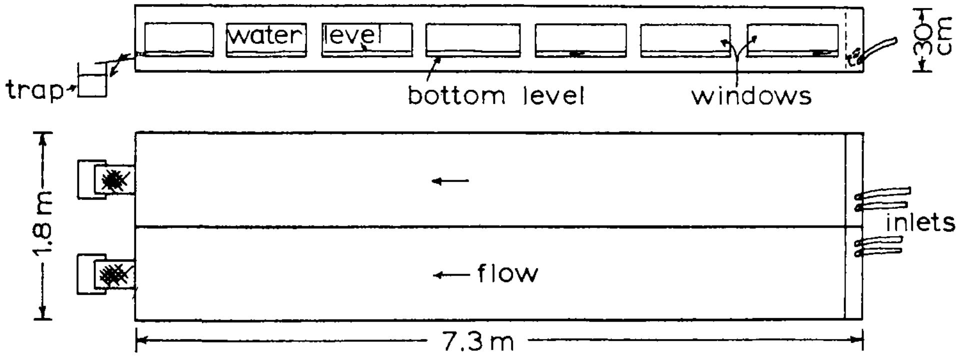


FIG. 7. Schematic drawing of artificial channels at Oak Creek.

on the sides of the channels so that experimental fish looked out upon a dark area beyond the channel windows. The tents also hid movements of observers.

Fish placed in the channels had free access to the exit orifices and could leave the channels at will, but could not return. Nomads used in the Oak Creek channels were transferred there from the downstream migrant trap at Deer Creek.

Fish in both channels were fed once each day with brine shrimps in the same manner as described for the Deer Creek observation channels. Daily ration was 300 mg of brine shrimps per gram of coho tissue.

## CONTROLLED STREAM SECTION

A controlled stream section (Fig. 8) 18 m in length was formed by screens in Deer Creek, with the upstream end of the section about 91 m below Deer Creek trap. A downstream trap was placed at the lower end of the stream section and a by-pass constructed so that migrating fish could move around the controlled section, either up or downstream.

All resident coho were removed from the controlled section by electrofishing before experimental fish were added. Trout and cottids taken in this operation were returned to the controlled section, which was operated from early July to mid September, 1960.

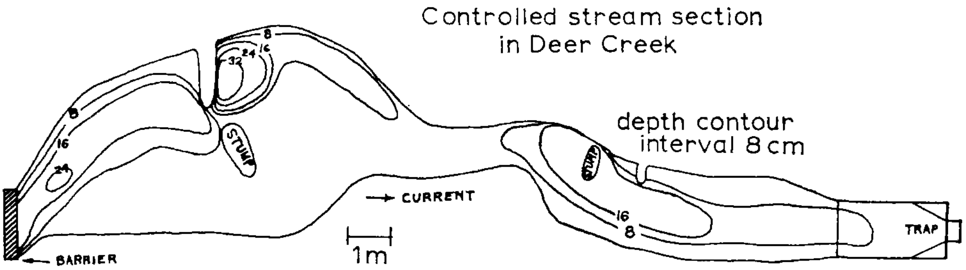


FIG. 8. Controlled stream section in Deer Creek.

Nomads were secured in the downstream trap at Deer Creek, then marked and handled as in artificial channel work. These fish could live in the controlled section, die there, or pass downstream into the trap at the end of the section.

There were about 39 m$^2$ of stream area in the section, of which about 83% was 25 mm or greater in depth. The controlled section was not unlike many other Deer Creek stream areas in general appearance.

### TRANSFER OF FRY TO BARREN STREAM

A transfer of 1627 coho nomads from Flynn Creek to Needle Branch was made from April 16 to May 6, 1960. No coho fry were present in Needle Branch at the time of this fry transfer because of failure of the adult coho run of the previous fall. The transfer provided a further test of the idea that nomads would become residents if living space were available. The transferred coho were released in small lots through the available stream area on Needle Branch.

A transfer of 1577 coho nomads from Flynn Creek to Needle Branch was made from April 19 to May 4, 1961. Coho fry were present naturally in Needle Branch at time of transfer. The coho were released as they were in the previous year. The object of this release was to determine if the natural population already present in Needle Branch would result in a smaller proportion of the introduced nomads becoming resident than had been the case in 1960.

### OBSERVATION OF COHO BEHAVIOR

Observations of aggressive behavior among coho resident in natural stream areas were made on Deer Creek. The total numbers of observed nips were recorded. These observations were made on areas of known size for given time intervals, usually 10 or 20 minutes. The areas used for observation were not randomly chosen, but were selected for the visibility they afforded. An effort was made to watch deep as well as shallow areas.

In addition, observations of behavior were made while nomadic coho were in the artificial channels described earlier. For the most part these were qualitative, but some counts of nips were recorded. Care was taken to avoid sudden movements that might startle the experimental fish, but coho in the glass-walled channels usually ignored all movement outside the channels below the level of the water surface. Any movement above the water obviously frightened the fish.

### GROWTH OF COHO

Comparisons were made of growth of dominant and subordinate coho in artificial channels in several time intervals, measured as fork length. Where growth percentages in periods of time are used, these were calculated as the ratio of change in length to initial length, multiplied by 100.

Comparisons were made of mean size of nomadic and residual coho at given times. Residual fish were sampled by seining and direct-current electrofishing throughout the stream length available to coho. Nomads for length measurements were obtained from downstream traps.

## RESULTS

### DESCRIPTION OF BEHAVIOR PATTERNS

The social behavior patterns of coho salmon were observed in artificial stream channels and natural stream areas. The behavior and resultant phenomena noted included lateral display and parallel swimming (Kalleberg, 1958), dominance posturing (Jones and Ball, 1954) or threat (Stringer and Hoar, 1955), nipping (Hoar, 1951), chasing or driving (Stringer and Hoar, 1955; Greenberg, 1947), flight, hiding, fighting (Stringer and Hoar, 1955; Newman, 1956), submission (Newman, 1956; Braddock, 1945), territorial defense (Kalleberg, 1958), redirected aggression, and formation of hierarchies (Greenberg, 1947). All of these activities except hiding, fighting, redirected aggression and hierarchy formation were observed in the stream coho population as well as in aquaria.

Lateral display (Fig. 9) in the coho is similar to that described by Kalleberg (1958) for Atlantic salmon, consisting of erected dorsal and anal fins and an open mouth. The white-edged dorsal and anal fins were most obvious in displays.

Lateral display was seen during the period of hierarchy establishment in aquaria, during territorial defense in aquaria and stream, and sometimes during the course of hierarchical dominance activities in the aquaria. Lateral threat may be a mutual vigorous display between a pair of coho, and sometimes results in parallel swimming (Kalleberg, 1958). It appears to be of defensive character.

Dominance posturing, or threat, (Fig. 10) in the coho is apparently quite similar to that of the Kamloops trout, *Salmo gairdnerii kamloops* (Stringer and Hoar, 1955). Threat was seen very frequently in aquaria when social hierarchies were being established, and in the stream and aquaria during territorial defense. It can have either defensive or offensive character.

Nipping in coho (Fig. 11) has been described by Hoar (1951). Nipping, after the initial contest for dominance, usually was incomplete, with little actual body contact.

Fighting, as described by Stringer and Hoar (1955) for the Kamloops trout, and by Newman (1956) for rainbow and eastern brook trout, was seen in the behavior of coho in aquaria during establishment of dominance–subordination relationships.

Submission without flight in the coho (Fig. 12) is similar to that observed in eastern brook trout and rainbow trout (Newman, 1956). Submission by flight was frequently seen, especially after dominance relationships were well established. Subordinate fish were often driven rapidly about the aquaria until they found a hiding place.

Redirected aggression was frequently evidenced by aggressive dominant fish when a chased subordinate suddenly disappeared by hiding under a rock. The aggressor repeatedly was seen to pick up algal tufts and spit them out. Subordinate fish, when repeatedly nipped by aggressive coho, apparently were unable to, or afraid to, nip in return and apparently transferred the aggressive urge to tufts of algae or particles on the bottom, viciously mouthing and ejecting them. Redirected aggression does not fit definitions of displacement activities given by Baerends (1957) and by Tinbergen and van Iersel (1947).

Territorial defense in streams, other than that occurring in reproductive behavior, has been noted for several salmonids including brown trout (Lindroth, 1955, Kalleberg, 1958), Atlantic salmon (Kalleberg, 1958), rainbow trout (Stringer and Hoar, 1955, Newman, 1956), eastern brook trout (Newman, 1956), and coho salmon (Hoar, 1951). Territory is defined as a defended area by Noble (1939), implying aggression against intruders.

Territorial defense was observed in the aquaria and in the stream. Partial territoriality, noted by Greenberg (1947) for the green sunfish, *Lepomis cyanellus*, was also seen in the coho. Defense of the partial territory is the same, toward all but the dominant fish, as that described by other workers for complete territory defense.

Stable hierarchies have been described in stream-dwelling salmonids by Newman (1956) for rainbow and eastern brook trout. Hierarchies have been shown to exist in several other kinds of fishes, such as the green sunfish (Greenberg, 1947), and *Platypoecilus* (Braddock, 1945). Stringer and Hoar (1955) noted no well-organized peck order or nip-right among Kamloops trout.

Fairly stable hierarchies were frequently observed in coho groups within artificial stream channels. When less than 5 fish were present in aquaria, these hierarchies could be ascertained and observed over periods of up to 2 weeks. Hierarchies were usually of the "nip-right" type (Braddock, 1945), in which one fish would nip another without being nipped in return.

The first sign of aggression or agonistic activity in groups of 3 to 5 coho introduced to a channel previously empty of fish usually appeared 5 to 15 minutes after nomads were placed in the observation channel. Initial action was usually a threat. Sometimes the single threat was sufficient to establish a dominance–subordination relationship between a contact pair, especially if the displaying fish was much larger than the object of the threat. The dominated individual usually sank submissively toward the bottom or drifted downstream a short distance.

If the fish placed in the control channel were close to the same size, sometimes the 2 largest fish set up territories, 1 in each pool. Other smaller fish were forced to take up partial territories or shuttle from one territorial fish to another, being nipped or chased upon entering each territory. The area at the extreme head of the upper pool, the "riffle" between pools, and the extreme tail of the channel were areas where subordinate fish usually remained. As long as the subordinates remained close to the bottom out of sight, the dominants paid them little heed. As soon as a subordinate rose to feed, he was nipped or chased. If a co-dominant carried his chase into the other dominant's territory, he was threatened or nipped by the defending territory holder.

Usually, nip-rights rather than territories were established with subordinate fish either shifting position frequently or occupying partial territories. In most observed groups, the first three fish in the nip-right could be easily identified. Relationships among the subordinate fish were usually obscured by the activities of the dominant fish.

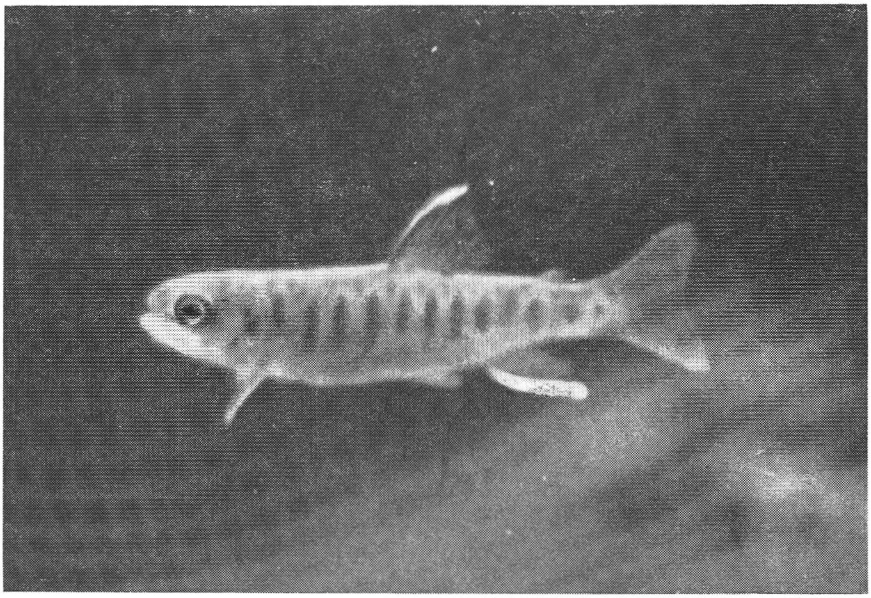


FIG. 9. Lateral threat.

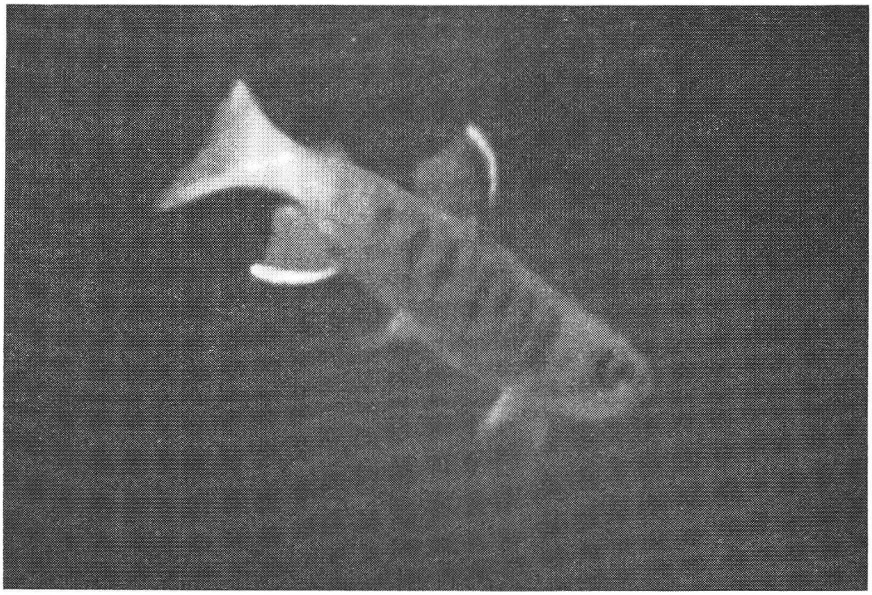


FIG. 10. Threat.

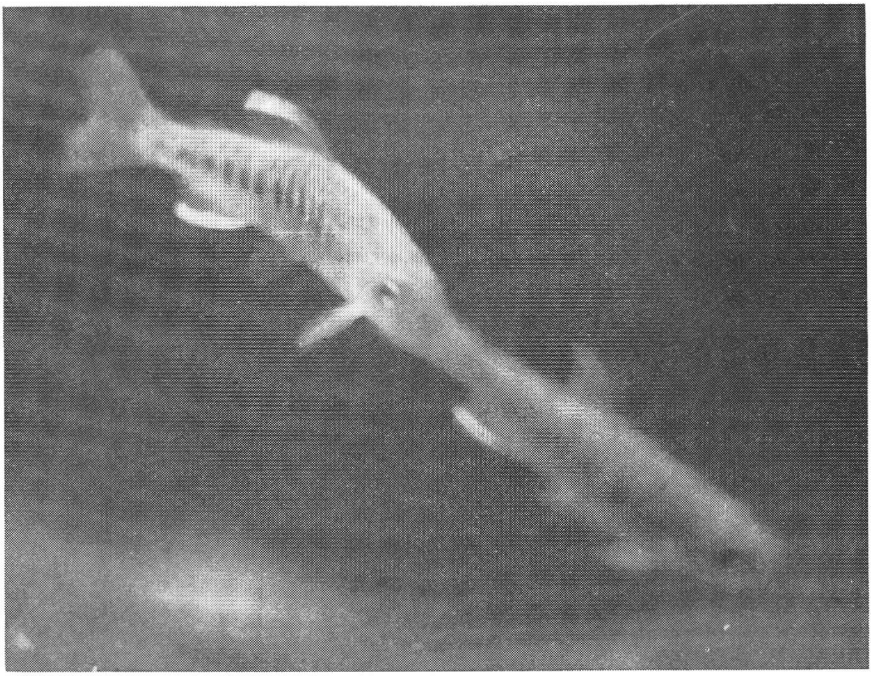


FIG. 11. Nipping.

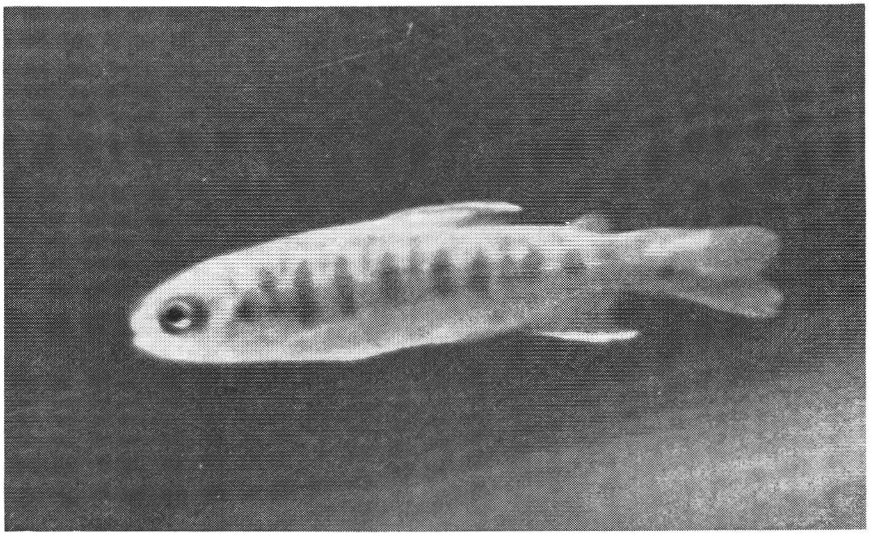


FIG. 12. Submission.

When a group of nomadic coho was added to a channel already containing a resident population, the new fish were usually threatened by the despot in the established hierarchy. If all the new fish were smaller than the despot, they were dominated and forced to submit, either dropping to the bottom or downstream. This domination usually took place in less than an hour.

If some of the new fish were the same size as, or larger than, the residents, a period of up to 4 hours might pass before the resident despot dominated the new fish. But the important observation is that the despot did dominate the introduced fish, even though the latter was larger. Never did a large introduced coho, say 50–60 mm long, dominate the resident despot (45–55 mm). The largest new fish in each introduced group usually passed out of the channel within 24 hours after being dominated by the resident despot. The smaller introduced fish might be dominated by the despot and perhaps by the subordinates, then in a day or two work part way up the hierarchy by dominating resident fish smaller than themselves.

Size was the principal factor governing hierarchy arrangement in all cases observed except as discussed above. Prior residence appeared to govern hierarchy initially, but after a day size again became important.

Often the introduced fish were harassed strongly by the despot and one or more subordinates. On several occasions the submissive introduced fish were seen to be chased out of the trough outlets by aggressive residents.

Noble (1939) points out that in *Xiphophorus*, either a single newcomer if sufficiently large, or a group of new fish, will produce a revolution in the resident hierarchy. In the latter case each fish fights for itself against residents and introduced individuals. While the dominant resident usually remains the despot, a fish from either group may rise to second place in the order. No such rapid revolution was seen in the artificial stream channels, where resident fish held a distinct advantage, but enforced confinement, where fish could not leave the channels, might have eventually produced the "revolution".

Braddock (1949) shows that prior residence in an area confers upon an individual *Platypoecilus* a greater potential for dominance than it would otherwise have. Braddock indicates that this effect is most important in initial contacts between individuals, and that if the intruder is larger than the resident, size may prevail in the contact. Braddock's observations could well be applied to coho salmon, except that the prior resident always prevailed in artificial stream channels. The introduction of intruders larger than the resident despot tended to prolong the conflict between the pair.

### BEHAVIOR IN ARTIFICIAL CHANNELS AT DEER CREEK

Capacity of the channels to hold coho was estimated in the period April 15 to May 19, 1960. From 4 to 7 coho, 35–45 mm, were found to remain in the A channels 1 month after introduction. Capacity of the B channels was found to be 3 to 6 coho.

From May 20 to June 16, 1960, 4 experiments were conducted in the B channels to test whether the nomads added to a barren channel would tend to remain there more readily than those added to a resident population. Table I shows proportions of introduced nomads remaining in the test and control channels. In 3 of the 4 experiments, a greater proportion of the control fish remained.

In 1961 all experiments in A and B channels had as their objective to determine whether nomads would cease movement if adequate living space was provided. From April 21 to May 31, four tests were carried out in the A channels. In all cases a greater proportion of introduced nomads tended to leave the channels where resident coho were already present than left the barren channels.

Flow patterns and bottom configuration in the B channels were altered considerably in 1961. Figure 6 shows the changes made in the bottoms of the channels. Flow was about 6 times greater than it had been in 1960, ranging from 95 to 76 l/min. Five experiments were conducted, and in 4 of these the fish tended to leave the test channel more readily than they did the control channel.

Table I shows details of a sign test (Li, 1957) of the equality of proportions of introduced coho groups remaining in the control and test channels in all suitable experiments in 1960 and 1961. The analysis indicated that the proportion of introduced nomads that remained in the test channels was significantly smaller (at the 1% significance level) than the proportion of nomads remaining in the control channels. In other words, such a difference could have occurred by chance with a probability of 1 in 100.

TABLE I. Test of behavior in A and B channels to determine if nomads added to a resident population had greater tendency to leave their channel than did nomads added to a barren channel. Equal numbers of coho (3 to 5) were placed in each channel at the start of the replication. The test channel had a resident group of coho present.

| | Observed proportions remaining | | |
|---|---|---|---|
| Replications | Control | Test | Sign of difference |
| B – May 20–May 27, 1960 | 1.00 | 0.60 | – |
| B – May 27–June 1 | 0.50 | 0.25 | – |
| B – June 1–June 13 | 0.50 | 0.00 | – |
| B – June 13–June 16 | 0.40 | 0.40 | . . . |
| B – Apr. 6–Apr. 21, 1961 | 0.40 | 0.60 | + |
| B – Apr. 21–Apr. 24 | 1.00 | 0.33 | – |
| B – May 19–May 26 | 0.66 | 0.33 | – |
| B – May 26–May 31 | 0.33 | 0.00 | – |
| B – May 31–June 10 | 0.33 | 0.00 | – |
| A – Apr. 21–Apr. 29 | 0.66 | 0.33 | – |
| A – Apr. 29–May 10 | 0.33 | 0.00 | – |
| A – May 10–May 19 | 1.00 | 0.33 | – |
| A – May 19–May 31 | 0.33 | 0.00 | – |

Number of replications = 12 (omitting B – June 13, 1960).
Hypothetical frequency of negative signs = 6.
$\chi^2 = 8.33$ with 1 d.f. (significant at 1% level).

There appeared to be a tendency for fewer coho to become resident in the test channel in 1961 than had been the case in 1960. The increase in water velocity may have reduced the areas usable as stations and territories. Bottom contours were altered considerably, however, and this may have been responsible for any change in capacity of the channels.

Kalleberg (1958) showed that reduction in water velocity tended to cause territorial Atlantic salmon and brown trout to rise away from contact with the stream bottom and move about the aquarium observation channel. It may be that low-velocity pool environments are more conducive to hierarchy formation than to territoriality, while faster flows elicit greater territoriality. The environments utilized by coho in the study streams are of both slow and fast current types, but the former flow condition is more frequently the case in the period June to October because of low streamflow.

Aggression was less frequent in the control channel than in the test channel during experiments in 1960. Tables II and III show nipping counts in each channel during one experiment.

From June 6 to July 9, both test and control fish were fed daily with brine shrimps to determine if more coho could be held in the troughs by an abundant food supply. When food was introduced each day, all coho usually gorged themselves, then continued to catch and spit out the shrimps. Aggression usually ceased in both channels during feeding, but began again when food ceased to drift downstream.

TABLE II. Nipping in control channel, 12:15–14:15 hours, June 1, 1960. Mean nips given per fish per 10 minutes = 0.25.

| | 53 mm | 46 mm | 45 mm | 42 mm |
|---|---|---|---|---|
| Nips given | 8 | 7 | 0 | 0 |
| Nips received | 0 | 2 | 10 | 3 |

TABLE III. Nipping in B test channel 12:20–14:20 hours, June 1, 1960.

| Lengths of aggressor (*mm*) | Nip recipients (length in *mm*) Residents | | | | | Nomads added | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 52[c] | 48[c] | 41[c] | 40[c] | 39[c] | 53 | 50 | 42 | 40 |
| 52 | – | 0 | 19[a] | ... | 2 | 10 | 4 | 8 | 18 |
| 48 | 0 | – | 3[a] | ... | 10 | 1 | 3 | 12 | 45 |
| 41 | 0 | 0 | – | 3 | 11[b] | 0 | 0 | 0 | 8[b] |
| 40 | 0 | 0 | 0 | – | ... | 0 | 0 | 0 | ... |
| 39 | 0 | 0 | 0 | 0 | – | 0 | 0 | 1 | 9 |
| 53 | 10 | 0 | 0 | 0 | 0 | – | 0 | 0 | 0 |
| 50 | 0 | 0 | 0 | 0 | 0 | 0 | – | 1 | 0 |
| 42 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | – | 0 |
| 40 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | – |

[a] Some of these nips may have been directed at the resident 40 mm fish. At times the 41 and 40 mm fish could not be distinguished.

[b] Some of these nips may have been made by the resident 40 mm fish.

[c] These resident coho lengths were obtained on June 13, while the nomads were measured on June 1 before they were added to the channel.

Feeding failed to increase the capacity of the troughs to hold coho. Before feeding began, capacity of the channels ranged from 2 to 4 fish one week after introduction of a given group of nomads. After food in excess was supplied, the channel capacities ranged from 1 to 4 fish one week after introduction of a given group of nomads.

Hierarchies were organized in the control channel soon after nomads were introduced. Dominance order in these hierarchies was organized on the basis of size, with the largest coho becoming dominant.

Dominant fish tended to grow more rapidly than subordinate coho. Table IV shows growth of dominant and subordinate fish introduced into the channels at the same time. Growth was determined after the time intervals shown in the table.

TABLE IV. Growth of dominant (D) and subordinate (S) coho in B channels.

| Channel and time period | | Initial length | Final length | Growth |
|---|---|---|---|---|
| | | *mm* | *mm* | % |
| *Control channel* | | | | |
| May 11–May 20 | D | 46 | 47 | 2.2 |
| | S | 41 | 41 | 0.0 |
| | S | 39 | 39 | 0.0 |
| May 20–June 25 | D | 43 | 46 | 7.0 |
| | S | 43 | 44 | 2.4 |
| June 1–June 13 | D | 53 | 56 | 5.6 |
| | S | 42 | 44 | 4.8 |
| June 25–July 1 | D | 44 | 46 | 5.0 |
| | S | 42 | 43 | 2.5 |
| *Test channel* | | | | |
| May 11–June 13 | D | 45 | 52 | 15.0 |
| | S | 41 | 43 | 5.0 |
| | S | 39 | 41 | 7.0 |

From June 16 to July 17, 1960, a series of 3 experiments was conducted to determine if groups of nomads separated by size would react differently in the troughs. Both B channels were cleared of fish and 12 nomads, 39–43 mm, were placed in the control channel and 12 fish, 41–55 mm, were placed in the test channel. Both groups were fed brine shrimps daily. All of the large coho left the test channel within 5 days, but four of the small fish remained in the control channel after 5 days. The largest two of these fish set up territories between which the smaller coho were chased and harassed. One dominant coho occupied the upstream half of the channel while the downstream coho had a partial territory in the lower half of the channel. The latter fish was submissive to the dominant coho, but defended his territory against all subordinates. In the control channel, 26 nips were counted in 25 minutes of observation just after the 12 fish were introduced to the channel. In the test channel, 13 nips were counted in the 45 minutes just after the fish were introduced. Nine days after the start of the experiment, 3 of the small nomads were still in the control channel.

The 2 territorial coho and 1 subordinate remained. Subsequent experiments with groups of coho separated by size indicated that smaller fish would remain in the troughs more readily than larger coho.

From August 18 to September 13, 1960, two experiments were conducted to determine if a group of coho of nearly the same size would exhibit more aggression than a group of fish of disparate lengths. Table V shows nipping frequency in the groups introduced to the channels on August 18. The coho used at this time were resident fish seined from a natural stream area. Aggression was more frequent in the group of coho of near equal size than in the group of disparate size.

TABLE V. Nipping in B channels on August 18, 1960. Fish in right channel were nearly equal in length while those in left channel were disparate in length.

| Left channel 60 minutes | | | | | Right channel 89 minutes | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Aggressor (*mm*) | 58 | 55 | 53 | 51 | Aggressor (*mm*) | 58 | 58 | 58 | 57 |
| 58 | – | 1 | 4 | 4 | 58 | – | 7 | 12 | 9 |
| 55 | 0 | – | 0 | 1 | 58 | 3 | – | 4 | 6 |
| 53 | 0 | 3 | – | 7 | 58 | 2 | 3 | – | 8 |
| 51 | 0 | 0 | 0 | – | 57 | 0 | 0 | 0 | – |
| Total = 20 nips<br>Nips per 10 minutes = 3.3 | | | | | Total = 54 nips<br>Nips per 10 minutes = 6.1 | | | | |

Table VI shows nipping frequency in the groups introduced on September 7. Observations were made periodically from September 7 to 9. Aggression was more frequent among coho of near-equal lengths than among coho of disparate lengths. In both of the experiments from August 18 to September 13, all fish but the dominant coho left the channel.

## BEHAVIOR IN ARTIFICIAL CHANNELS AT OAK CREEK

On May 10, 1961, 294 coho fry were taken from the downstream trap at Deer Creek and transported to Oak Creek, near Corvallis. These fish were placed in the artificial channels: 194 in the right channel, 100 in the left. The fry were fed soon after being placed in the channels and daily thereafter. Mean size of the fry on May 10 was 40 mm.

By May 12, 40 fry had moved out of the left channel and 99 had left the right channel. A few fish each week left the channels in the next month. On June 17 all remaining coho were netted from the channels, counted, and measured. Exactly 23 coho were found in each channel. Coho mean lengths were as follows: 49.6 mm in the left channel and 48.6 mm in the right channel. The 1 mm difference between means was not significant at the 5% level.

Calculated density of coho in each channel was 2.9/m$^2$ on June 17. In the week before June 17, 10 coho moved out of the right channel and at least 3 departed the left channel. After all coho were counted and measured, they were returned to the channels and the water level was raised 46 cm, so that both

TABLE VI. Nipping in B channels, September 7–9, 1960. Fish in left channel were of similar lengths while those in right channel were disparate in length.

| Left channel, 65 minutes | | | | | Right channel, 90 minutes | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Nip recipients | | | | | Nip recipients | | | |
| Aggressor (*mm*) | 62 | 62 | 60 | 59 | Aggressor (*mm*) | 71 | 69 | 65 | 65 |
| 62 | – | 15 | 9 | 4 | 71 | – | 0 | 2 | 0 |
| 62 | 0 | – | 0 | 0 | 69 | 1 | – | 1 | 0 |
| 60 | 2 | 0 | – | 1 | 65 | 0 | 0 | – | 0 |
| 59 | 0 | 0 | 0 | – | 65 | 0 | 0 | 0 | – |
| Total = 31 nips<br>Nips per 10 minutes = 4.7 | | | | | Total = 4 nips<br>Nips per 10 minutes = 0.4 | | | | |

channels were essentially pools. No food was placed in the channels after June 17. No coho left the channels in the following 4 months.

The results of the experiment at Oak Creek indicated that presence of artificial food in excess of the coho daily ration had no apparent influence upon density of fish in the channels. More than twice as much food was placed in the right channel as in the left, yet the coho density was the same in each channel at conclusion of the experiment.

Cessation of all coho movement out of the channels following an increase in water depth, and hence space, suggests that limited living space was the factor causing downstream movement. Other factors may have brought about some of the initial heavy downstream movement following placement of coho in the channels on May 10.

## BEHAVIOR IN NATURAL STREAM AREAS

Behavior of resident coho salmon in natural stream areas was observed at several times during the summer and fall of 1960. Table VII shows the results

TABLE VII. Frequency of coho nipping in natural stream areas on Deer Creek, 1960.

| Station | Date | | Time | Area observed | Mean depth | Bottom | Coho present | Fish per m² | Nips per fish per 10 min. |
|---|---|---|---|---|---|---|---|---|---|
| | *month* | *day* | *hours* | *m²* | *cm* | | *no.* | *no.* | *no.* |
| -150 | 8 | 1 | 1150–1200 | 2.3 | 20 | rubble | 5 | 2 | 0.4 |
| 005 | 8 | 1 | 1415–1425 | 1.5 | 15 | sand | 8 | 5 | 3.0 |
| 040 | 8 | 1 | 1430–1440 | 3.3 | 13 | gravel | 6 | 2 | 2.8 |
| 120 | 8 | 1 | 1450–1500 | 1.5 | 30 | silt-sand | 5 | 3 | 2.4 |
| -125 | 8 | 7 | 1520–1530 | 1.1 | 10 | silt-sand | 6 | 5 | 1.7 |
| -125 | 8 | 7 | 1535–1545 | 1.5 | 30 | rubble | 10–12 | 7 | 1.5 |
| 1100 | 7 | 23 | 1135–1145 | 2.3 | 30 | silt-sand | 12–15 | 6 | 3.2 |
| 1100 | 7 | 23 | 1200–1210 | 1.1 | 15 | rubble | 5 | 4 | 1.8 |
| 4250 | 9 | 9 | 0926–0946 | 1.5 | 10 | gravel | 4 | 3 | 0.5 |
| 3900 | 9 | 9 | 1015–1035 | 1.5 | 15 | gravel | 3 | 2 | 0.7 |
| 2500 | 9 | 9 | 1045–1055 | 2.3 | 25 | gravel-silt | 5–6 | 2 | 2.0 |
| 2480 | 9 | 9 | 1105–1125 | 1.5 | 10 | gravel | 4 | 2 | 0.4 |
| 6500 | 9 | 13 | 1220–1240 | 1.9 | 8 | gravel | 5–6 | 3 | 1.6 |
| 6180 | 9 | 13 | 1255–1305 | 2.2 | 8 | gravel-silt | 8 | 3 | 4.1 |
| 2600 | 9 | 13 | 1410–1420 | 2.2 | 20 | gravel-silt | 6–8 | 3 | 2.9 |
| 3710 | 9 | 29 | 1005–1025 | 1.5 | 13 | gravel | 5 | 3 | 1.5 |
| 4050 | 9 | 29 | 1045–1105 | 1.4 | 33 | gravel-silt | 3–5 | 3 | 0.7 |
| 4125 | 9 | 29 | 1110–1120 | 2.8 | 13 | gravel-silt | 11–15 | 4 | 2.6 |

of these observations. Mean density of fish was calculated, and this ranged from 2 to 7 coho per m$^2$, with a mean of 3. Mean number of nips recorded per fish per 10 minutes was 1.9, ranging from 0.4 to 4.1.

The number of nips relative to depth of water is also of interest. Behavior in water less than 20 cm deep (11 instances) was compared to behavior in water over 20 cm deep (7 instances). No significant difference could be shown between nipping or area occupied per fish in shallow and deep areas.

Observations in natural stream areas were made primarily to estimate the extent of nipping. The most significant point was that nipping was frequent and probably nearly continuous. The comparison of deep and shallow areas to test differences in area and nipping per fish are not regarded as conclusive, since activity in water over about 46 cm deep could not be observed properly.

Figures 13–17 show that downstream-migrant coho became equal in length to residual fish by about November 6 in 1959 and by mid-November in 1960. This period coincided with rise in streamflow due to the first fall rains. Presumably, living space would become more plentiful as water flow increased.

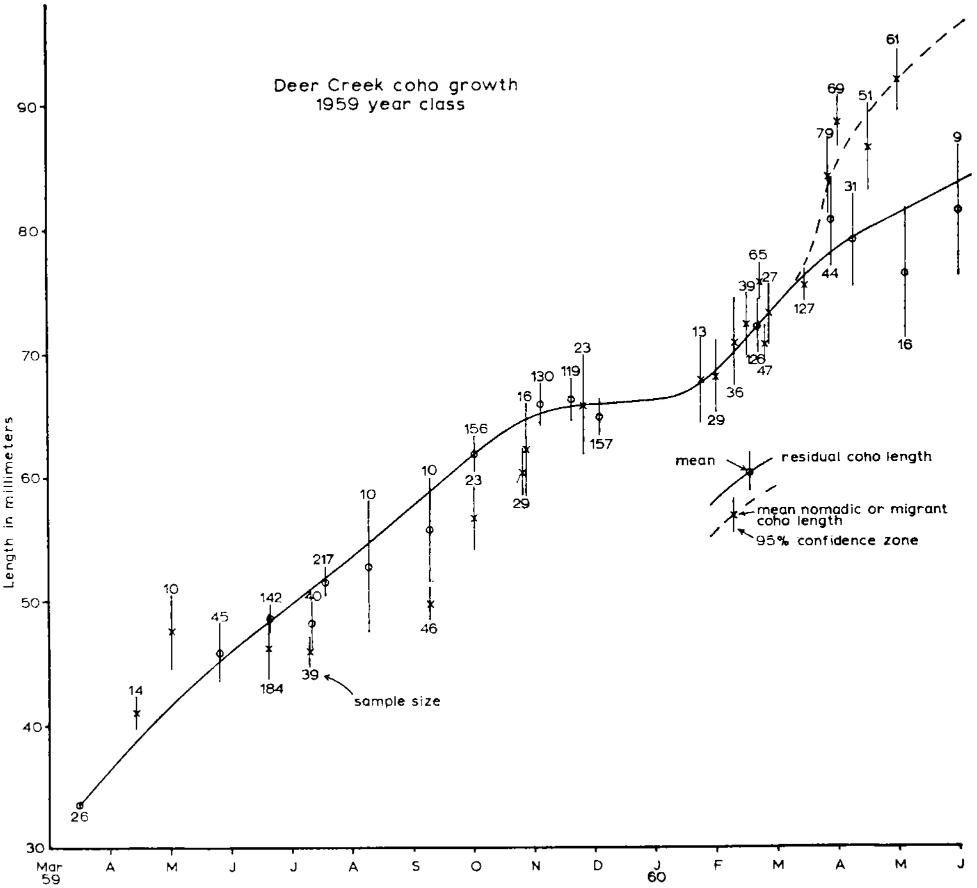


FIG. 13. Growth of juvenile coho in Deer Creek, 1959 year-class

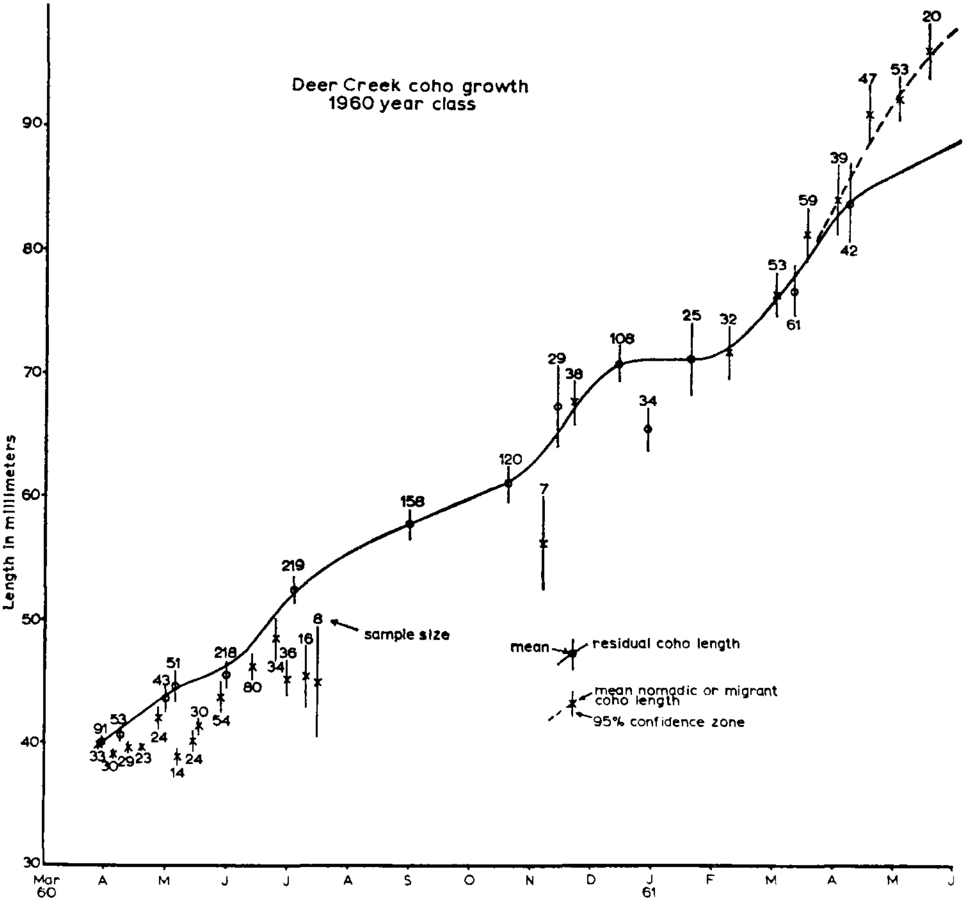


FIG. 14. Growth of juvenile coho in Deer Creek, 1960 year-class.

Early in the winters of 1959 and 1960, the coho salmon changed their place of residence or stations from open, relatively shallow water to deeper pools. They apparently preferred locations with heavy overhead cover. On December 13, 1960, a group of Deer Creek coho was observed with the aid of a water glass. About 10 coho were observed for 20 minutes over a bottom area of about 0.18 $m^2$. No sign of aggression was noted in this group. All fish held positions close to the bottom, feeding on drifting material. Several fish were only 5 to 8 cm apart. The calculated number of coho per square meter was 54. At the same location on August 1, the fish per unit area had been about 3.2 per $m^2$ and the nips seen per fish over 10 minutes had averaged 2.4.

On December 20, another group of 7 coho lying close to the bottom in a sheltered area was observed. These fish were congregated over a bottom area of about 0.18 $m^2$. The density of coho was about 38/$m^2$ and no nipping was seen in 15 minutes of observation. Three other coho were seen feeding in separate locations about 60 cm apart. No aggression was seen among these fish.

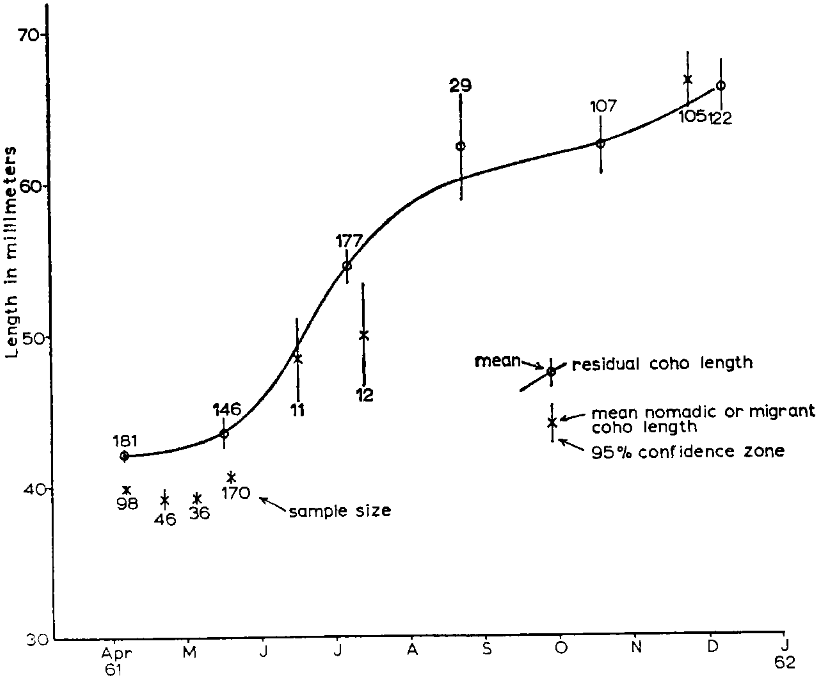


FIG. 15. Growth of juvenile coho in Deer Creek, 1961 year-class.

General observations made during two winters regarding the locations preferred by coho indicated that the young fish preferred deep water to shallow (or preferred slower current), and tended to congregate in areas sheltered by overhead cover. Coho smolt aggregation noted by Hoar (1951) was associated with a preference for cover. Cover and slow current preferences may well have caused the aggregation of coho observed in the study streams. However, a lessening of aggressive behavior must have occurred, for the dense groupings seen in the streams were never observed in the spring, summer and fall months (of the first year of life) when aggressive behavior was a frequent occurrence.

The tendency of coho to aggregate, or a lessening of aggressive behavior, could have been responsible for the cessation of downstream movement of fry smaller than residual fish in early winter.

## BEHAVIOR IN CONTROLLED STREAM SECTION

On July 13, 1960, the 39 $m^2$ controlled stream section was electro-sampled and 34 coho were removed. Mean fork length of these fish was 53 mm. Beginning July 13, nomads from the Deer Creek downstream trap were placed in the uppermost pool of the section as follows: July 13, 55 mm; July 14, 39 and 40 mm; July 17, 42 and 43 mm; July 20, 45 and 47 mm; July 23, 42 mm; July 25, 53 and 55 mm; July 31, 41 and 57 mm; August 31, 41 mm.

All nomads were marked by removal of one ventral fin. The absence of a resident coho stock when nomads were introduced and the presence of a trap

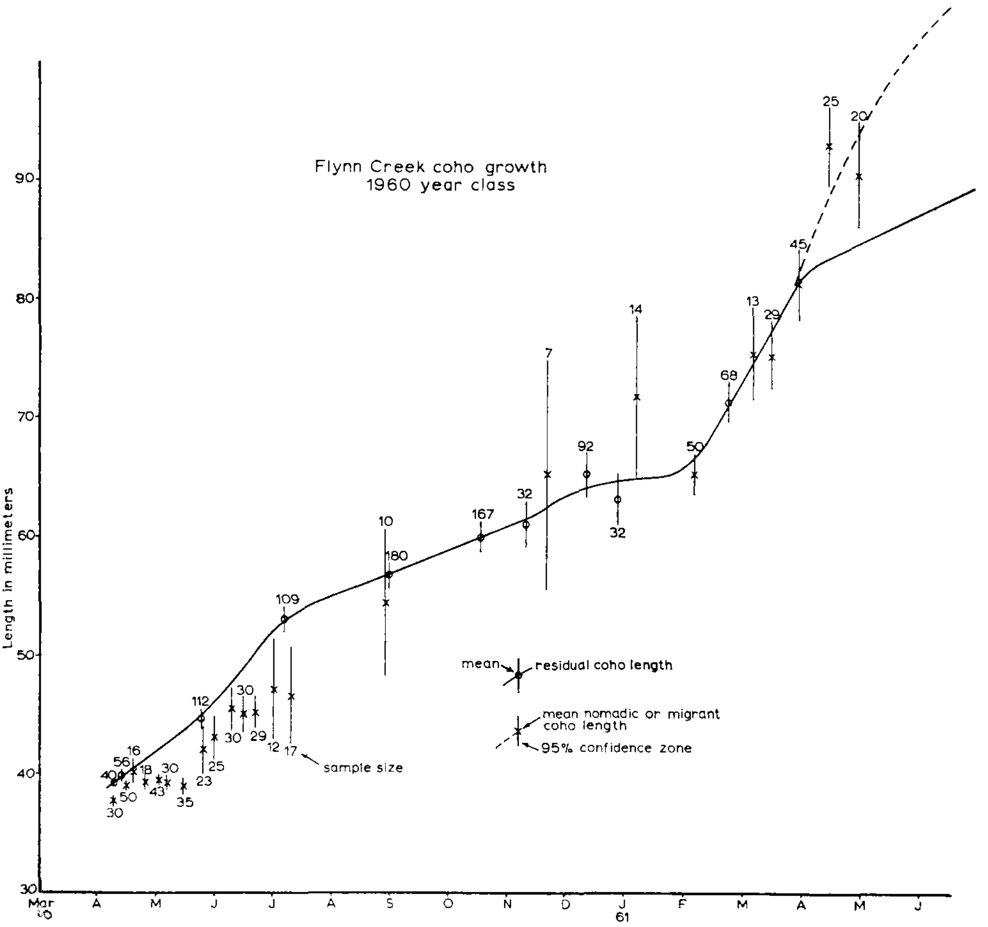


FIG. 16. Growth of juvenile coho in Flynn Creek, 1960 year-class.

at the outlet and a barrier screen at the upper end of the section were the principal ways in which this section differed from an uncontrolled section.

On September 7, 1960, the section was electro-sampled to remove all coho. Eight marked fish were found, out of 12 introduced coho that should have been present; their lengths were 63, 61, 59, 57, 54, 52, 47 and 40 mm. The 4 fish not found could have been shocked but lost under debris, could have suffered mortality in the section, or could have moved out of the section during two brief periods of possible leakage.

All the marked fish recovered were found in the pool where they were released, in spite of the fact that two pools were available below the uppermost one (Fig. 8). This probably indicated that population density never became sufficiently high in the upper pool to cause fish to move into lower pools. If all 12 introduced nomads had remained in the upper pool, coho density there would have been only about 1 fish per m$^2$, less than half the mean density shown in Table VII. During the test period, 3 cutthroat trout, 93 to 122 mm, and

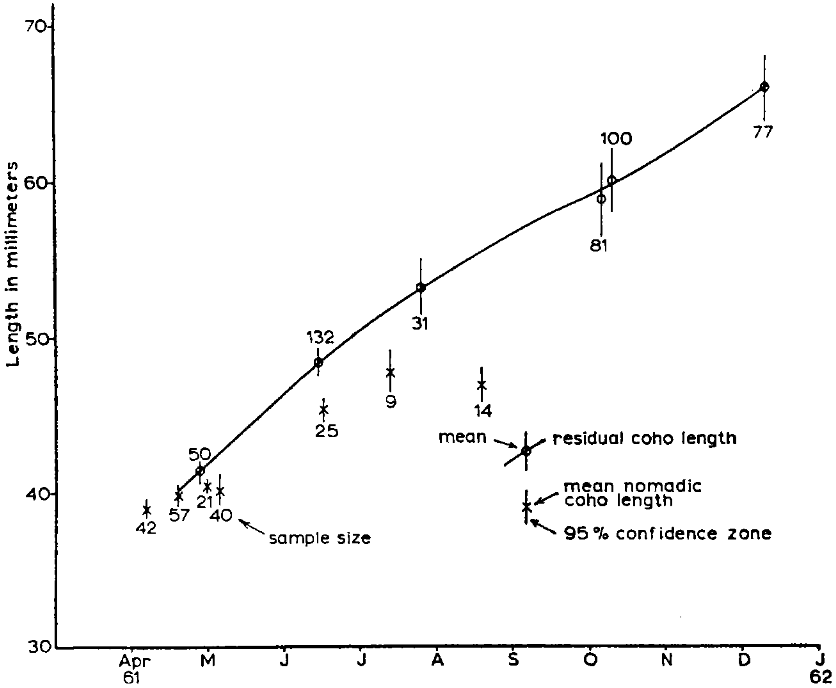


FIG. 17. Growth of juvenile coho in Flynn Creek, 1961 year-class.

one 77-mm cottid were taken in the outlet trap, indicating that the trap would catch and hold fish moving downstream. Mesh of the trap was sufficiently fine to hold the coho fry if they had moved.

### TRANSFER OF FRY TO AREA BARREN OF RESIDENT STOCK

Of the 1627 nomads transferred from Flynn Creek to Needle Branch from April 16 to May 6, 1960, about 4% moved through the downstream trap in the 1 month following their transfer. It should be noted that the stream was barren of naturally-spawned coho fry at time of the transfer.

Of the 1577 nomads transferred from Flynn Creek to Needle Branch from April 19 to May 4, 1961, about 27% moved through the downstream trap in the 1 month following their transfer. Naturally recruited fry were present in Needle Branch when the Flynn Creek nomads were released in Needle Branch. These results again indicated that introduced nomads would tend to remain in a stream area barren of resident stock, and tend to leave if resident stock were present.

### GROWTH AND MOVEMENT OF NOMADS

Observations of dominance–subordination relationships in artificial stream channels indicated that slight differences in length of individual fish in contact pairs were sufficient to bring about subordination of smaller fish. Differences as slight as 1 mm were found to be important. For this reason, the "growth" curves for nomadic and residual coho of the same year class should be examined carefully.

Figures 13, 14 and 15 show "growth" curves for nomadic and residual coho of the 1959, 1960 and 1961 year classes on Deer Creek, and Figures 16 and 17 show the same information for the 1960 and 1961 year classes on Flynn Creek. Table VIII for the 1959–1961 year classes shows the results of comparisons of mean lengths of residual and nomadic coho. Pairs of samples considered were taken at the same time. In all pairs of samples on Deer and Flynn Creeks (these included all available data taken at suitably similar times) taken from shortly after emergence in spring to early fall, the nomadic coho were smaller in mean length (P values 0.10 to 0.01). These differences are all the more remarkable in that samples of residual fish almost certainly included some coho

TABLE VIII. Comparisons of mean lengths (L) of residual and nomadic or migrant coho, year-classes 1959–1961, in Deer and Flynn Creeks. The last column, P, is the upper limit of the range in which the significance level of the length difference lies.

| Nomads or migrants | | | Residuals | | | Diff. in length | *t* | Max. P |
|---|---|---|---|---|---|---|---|---|
| Date | No. | L | Date | No. | L | | | |
| | | *mm* | | | *mm* | *mm* | | |
| *Deer Creek*—**1959** *year-class* | | | | | | | | |
| Jun 15–20/59 | 184 | 47.42 | Jun 18/59 | 142 | 48.80 | 1.38 | 1.95 | 0.10 |
| Jul 8–10/59 | 39 | 46.07 | Jul 8/59 | 40 | 48.25 | 2.18 | 1.92 | 0.10 |
| Jun 15–Jul 10/59 | 223 | 47.18 | Jun 18–Jul 8/59 | 182 | 48.68 | 1.50 | 2.45 | 0.02 |
| Sep 8/59 | 46 | 50.00 | Sep 8/59 | 10 | 56.00 | 6.00 | 3.03 | 0.01 |
| Oct 26/59 | 16 | 62.44 | Nov 3/59 | 130 | 66.11 | 3.67 | 1.84 | 0.10 |
| Mar 26/60 | 81 | 85.02 | Mar 28/60 | 44 | 80.84 | 4.18 | 1.77 | 0.10 |
| Apr 15/60 | 54 | 87.89 | Apr 8/60 | 31 | 79.35 | 8.54 | 3.47 | 0.01 |
| May 1/60 | 67 | 93.93 | May 4/60 | 16 | 76.69 | 17.24 | 6.11 | 0.01 |
| *Flynn Creek*—**1959** *year-class* | | | | | | | | |
| Apr 1/60 | 54 | 87.11 | Mar 17–Apr 4/60 | 8 | 77.00 | 10.11 | 3.04 | 0.01 |
| Apr 15/60 | 41 | 89.32 | Apr 11/60 | 7 | 81.28 | 8.04 | 1.75 | 0.10 |
| *Deer Creek*—**1960** *year-class* | | | | | | | | |
| Apr 4/60 | 30 | 39.17 | Mar 28/60 | 91 | 40.15 | 0.98 | 3.34 | 0.01 |
| Apr 26/60 | 24 | 42.08 | Apr 30/60 | 43 | 43.65 | 1.57 | 2.18 | 0.05 |
| May 6/60 | 14 | 38.86 | May 4/60 | 51 | 44.73 | 5.89 | 8.39 | 0.01 |
| May 24–31/60 | 54 | 43.89 | May 30/60 | 218 | 45.66 | 1.77 | 2.10 | 0.05 |
| Jul 5–11/60 | 16 | 45.50 | Jul 3/60 | 219 | 52.59 | 7.09 | 5.49 | 0.01 |
| Nov 21/60 | 38 | 67.81 | Nov 14/60 | 29 | 67.38 | −0.43 | −0.23 | 0.90 |
| *Flynn Creek*—**1960** *year-class* | | | | | | | | |
| Apr 8/60 | 30 | 37.87 | Apr 9/60 | 40 | 39.30 | 1.43 | 4.72 | 0.01 |
| Apr 14/60 | 15 | 38.47 | Apr 13/60 | 56 | 39.95 | 1.48 | 2.69 | 0.01 |
| May 23/60 | 23 | 42.17 | May 23/60 | 112 | 44.68 | 2.51 | 2.37 | 0.02 |
| Jul 3–14/60 | 17 | 46.71 | Jul 6–8/60 | 109 | 53.10 | 6.39 | 3.16 | 0.01 |
| *Deer Creek*—**1961** *year-class* | | | | | | | | |
| Apr 4–8/61 | 98 | 39.79 | Apr 4–6/61 | 181 | 42.05 | 2.26 | 8.07 | 0.01 |
| May 16–19/61 | 170 | 40.68 | May 16/61 | 146 | 43.54 | 2.86 | 6.35 | 0.01 |
| Jul 7–14/61 | 12 | 50.00 | Jul 5/61 | 177 | 54.56 | 4.56 | 2.75 | 0.01 |
| Nov 23–27/61 | 105 | 66.60 | Dtc 7/61 | 122 | 66.15 | −0.45 | −0.36 | 0.80 |
| *Flynn Creek*—**1961** *year-class* | | | | | | | | |
| Apr 28–29/61 | 21 | 40.52 | Apr 27/61 | 50 | 41.34 | 0.82 | 1.78 | 0.10 |
| Jun 16/61 | 25 | 45.44 | Jun 14/61 | 132 | 48.52 | 3.08 | 4.89 | 0.01 |
| Aug 18/61 | 14 | 46.93 | Jul 25/61 | 31 | 53.32 | 6.39 | 6.08 | 0.01 |

that would soon become nomadic. If these fish could somehow have been removed from the residual samples, the disparity between nomads and residuals would have been greater. As the available data show, at some time in the fall the coho moving downstream become equal in mean size to residuals. In early spring the migrants become larger than the residual fish.

Needle Branch data were not used because of artificiality in growth data introduced by transfer of Flynn Creek nomads.

Earlier in this paper it was pointed out that random movement might explain the downstream drift of coho fry. If this were so, there should have been a rather considerable upstream movement of fry. Huntsman (1945) reported movements of Atlantic salmon parr downstream and upstream.

Table IX shows the catch of downstream and upstream traps during periods when juvenile upstream traps were operated. Obviously there is very little movement upstream of fry, and the nomads passing downstream apparently do not return upstream to any important extent.

TABLE IX. Monthly distribution of coho fry movement at traps.

| Trap | Period | Downstream | Upstream |
|---|---|---|---|
| Needle Branch | May, 1960 | 128 | No trapping |
| | June | 52 | 1 |
| | July | 8 | 3 |
| | August | 12 | 7 |
| | September | 0 | 1 |
| | October | 8 | 0 |
| Needle Branch | April, 1961 | 249 | 1 |
| | May | 368 | 0 |
| | June | 27 | 0 |
| | July | 10 | 3 |
| | August | 1 | 5 |
| | September | 3 | 1 |
| | October | 0 | 1 |
| Deer Creek | September, 1960 | 0 | 0 |
| | June, 1961 | 123 | 0 |
| | July | 22 | 6 |
| | August | 4 | 0 |
| | September | 4 | 0 |
| | October | 4 | 0 |
| Flynn Creek | June, 1961 | 171 | No trapping |
| | July | 23 | 1 |
| | August | 23 | Trap defective |
| | September | 4 | 0 |

## DISCUSSION

Study of coho behavior in artificial stream channels and natural stream areas has demonstrated that aggressive behavior among coho is frequent, in fact nearly continuous in the period from emergence of fry until fall. Experiments conducted in artificial stream channels, in a controlled-stream section, and in a natural stream show that nomadic coho will tend to cease downstream movement if offered an environment with sufficient space free of resident coho.

Nomadic coho are smaller on the average than coho that do not move downstream. Size governs position in social hierarchies and outcome of contacts between coho, with larger coho having the advantage.

The foregoing facts indicate that aggressive behavior is one factor causing the spring downstream movement of coho fry. It appears probable that this factor, perhaps in combination with other density–regulatory factors, would tend to cause the density of resident coho per unit area to remain rather constant each year. If this is the case, then the yield of coho migrants, or smolts, should not fluctuate very greatly from year to year, although streamflow differences might cause some fluctuations.

Since data on yearly coho smolt yield from Deer Creek, Flynn Creek and Needle Branch are incomplete, data obtained by others should be reviewed. Hunter (1959) shows total numbers of coho smolts leaving Hooknose Creek on King Island, British Columbia, from 1948 through 1957 (Table X).

TABLE X. Hooknose Creek coho migrations, 1948–1957, Data from Hunter (1959) and unpublished records of the Fisheries Research Board of Canada.

| Smolt migration year | Smolt numbers | Females in parent run | Sibling fry migration |
|---|---|---|---|
| 1948 | 7,959 | ... | ... |
| 1949 | 3,550 | 221 | 2100 |
| 1950 | 2,982 | 198 | 22031 |
| 1951 | 4,389 | 277 | 20512 |
| 1952 | 3,620 | 71 | 8155 |
| 1953 | 4,034 | 29 | 5062 |
| 1954 | 5,987 | 228 | 29417 |
| 1955 | 6,756 | 72 | 15767 |
| 1956 | 4,508 | 162 | 7779 |
| 1957 | 6,074 | 229 | 32220 |

The number of smolts in a given year bears no evident relationship to the number of adult females in the parent run or to the drift of sibling fry. In the same time interval, the total number of pink salmon, *Oncorhynchus gorbuscha*, and chum salmon fry, *O. keta*, passing out of Hooknose Creek, ranged from 98,524 to 1,409,225 (Hunter, 1959), with great fluctuations from year to year, particularly in the case of pink salmon. Of course, these species leave fresh water soon after emerging from the spawning gravel. The 1-year period of residence undergone in Hooknose Creek by the coho appears to be a stabilizing influence upon the number of smolts.

Salo and Bayliff (1958) show data from Washington for Minter Creek smolt migrations for several years. Data shown in Table XI are for those years when no hatchery-reared fish were placed in the stream above Minter Creek trap. Footnotes indicate that age 2/ coho are included in some of the smolt counts and not in the others. In spite of the uncertainty resulting from this, it appears that the total number of wild smolts migrating from Minter Creek does not fluctuate greatly from year to year.

TABLE XI. Minter Creek coho downstream fry and smolt migrations, 1938–1949. Data on fry movement from unpublished data of the Washington Department of Fisheries.

| Smolt brood | Females in parent run | Sibling fry | Smolts (1+) |
|---|---|---|---|
| 1938 | 967 | 52,000 | 35,452[a,b] |
| 1940 | 1,393 | 211,136 | 32,085[c] |
| 1942 | 786 | 60,000 | 31,893[b] |
| 1943 | 906 | ? | 23,117[b,d] |
| 1944 | 500 | 101,000 | 30,408[b,d] |
| 1946 | 500 | 24,614 | 41,848[d] |
| 1949 | 114 | 920 | 27,691[d] |

[a] Includes some 2+ fish of 1937 brood released after hatchery rearing.
[b] Number of age 2+ fish of this brood not known.
[c] Includes 6829 age 2+ wild fish and some age 2+ fish of hatchery origin.
[d] Includes some wild age 2+ fish of previous brood year, number unknown.

Two other research facilities have been used to secure coho data over the past several years. One of these is a weir on Gnat Creek, tributary to the lower Columbia, operated by the Oregon Fish Commission. Data from this station are not available for reference. A trap on Spring Creek, tributary to the Wilson River near Tillamook, Oregon, was operated by the Oregon Fish Commission from December, 1949 to August, 1958. Some data secured there (Oregon Fish Commission, 1958) are shown in Table XII.

TABLE XII. Spring Creek coho migrations, 1948–1952.

| Adult brood year | Females passed upstream | Resulting juveniles | |
|---|---|---|---|
| | | Fry out | Smolts out |
| 1948 | 11[a] | 1701 | 1055 |
| 1949 | 24[a] | 1594 | 1228 |
| 1950 | 35 | 2498 | 1947 |
| 1951 | 54 | 9377 | 1209 |
| 1952 | 12 | 4662 | 1887 |

[a] These figures may be minimal due to high water.

Broods after 1952 were affected by passage of controlled numbers of females, and are not considered here. The smolt migration in the years of record tended to be relatively constant.

Data on downstream movement of 0/ age coho are available for Minter, Spring, and Hooknose creeks. Data secured at Hooknose Creek, Table X, indicate that a large movement of 0/ age coho does occur there. Mode of the movement generally occurred in late April or May in the 12 years of record. Operation of the Hooknose Creek weir ceased in early June in most years, hence no data are available for the summer movement, if any, of 0/ age coho.

Gnat Creek coho fry movements apparently are similar in timing to those on other streams for which data are available. Three peaks in yearly juvenile downstream movement are known (Oregon Fish Commission, verbal communication): in spring (age 0/), November (age 0/), and the following spring (age 1/).

Spring Creek coho fry movements occur largely in spring, and their magnitude in the years of record (Table XII) bears no particular relationship to the parent runs or to the sibling smolt migrations.

Minter Creek data shown in Table XIII (unpublished data of Washington Department of Fisheries), suggest that fry movement is related to parent egg potential, but some of these same data, Table XI, show that the smolt migration bears no relationship to parent egg potential or sibling fry movement. All fry moving downstream into the Minter Creek trap were placed back upstream. Examination of Salo and Bayliff's (1958) tables, their appendix, and the data of our Table XIII, indicates that a relatively greater total fresh water mortality occurs in years of large egg deposition and large fry migration.

TABLE XIII. Minter Creek coho fry movement downstream, 1937–1957, and parent egg potential.

| Brood year | Parent egg potential | Fry movement |
|---|---|---|
| 1937 | ? | 23,000 |
| 1938 | ? | 52,000 |
| 1939 | none | none |
| 1940 | 4,577,398 | 211,130 |
| 1941 | none | none |
| 1942 | 1,873,038 | 60,000 |
| 1943 | 2,092,860 | ? |
| 1944 | 1,376,500 | 101,000 |
| 1945 | none | none |
| 1946 | 1,097,000 | 24,614 |
| 1947 | none | none |
| 1948 | 186,200 | 805 |
| 1949 | 287,864 | 920 |
| 1950 | none | none |
| 1951 | 1,086,684 | 86,800 |
| 1952 | 1,929,186 | 105,000 |
| 1953 | 1,150,413 | 34,672 |
| 1954 | 812,500 | 32,334 |
| 1955 | 396,000 | 821 |
| 1956 | 603,000 | 4,374 |
| 1957 | 650,000 | 8,319 |

All available evidence indicates that the year of stream residence undergone by coho tends to stabilize the fluctuations caused by varying parent egg potential, producing a smolt yield of relatively uniform magnitude from year to year, in a given stream.

Smoker (1953) examined coho salmon yield to the commercial fishery in the Puget Sound area in relation to total stream runoff in year of stream residence for given year-classes. He obtained a strong positive correlation. The two most logical effects of greater streamflow upon coho production would be in increasing the effective spawning areas for adults and in providing greater living space for juveniles.

Neave (1949) shows a lower availability of coho to sportsmen fishing Cowichan Bay, B.C., for year-classes which experienced low summer flows in their juvenile stages in the Cowichan River. McKernan *et al.* (1950) show a significant correlation between annual coho salmon catches in Oregon near the

Siletz River and summer low flows of that river 2 years previously. A similar test on data from the Coquille River area showed no significance. Wickett (1951) shows 2 low counts of coho leaving Nile Creek, B.C., associated with 2 years of low summer rainfall in a 4-year interval from 1946 to 1949.

The results of these investigations tend to show that yield of smolt cohoes is positively correlated with summer streamflows, but they do not define the mechanism involved, be it associated with predation, disease, territoriality, food supply, or combinations of these.

As mentioned earlier, downstream drift of coho fry could be due to one or more of the following factors (in addition to aggression in the fry population): displacement by current, innate tendency to migrate, or random shifts in position. The latter possibility has already been shown to be unlikely.

Displacement by current is an attractive explanation for fry movement since this would explain the disparity in size of residual and nomadic fry, the latter being smaller and perhaps less able to hold position in the current. However, as Fig. 13–17 show, the size differences are slight, and should not be sufficient in themselves to explain nomad movement, particularly when some of the fry that move are larger than some of the fry that remain in the stream. Furthermore, current speeds decrease from April through June while mean size of fish increases, making inability to hold in the current an unlikely possibility.

It is likely that a part of the spring downstream emigration of coho fry, probably the portion of the movement that occurs soon after emergence of fry, is due to current displacement or to an innate migration urge, for a few fry (from the first emerging groups of coho) are known to move downstream soon after emergence. This drift occurs in spite of the apparent abundance of quiet marginal water area for living space. The very early arrivals at the downstream traps are 37–39 mm in length.

Hoar (1953) points out that coho fry actively defend territories during the day, then settle to the bottom and become inactive at night, a behavior characteristic that leads to permanent residence in the stream. This type of settling behavior was noted in artificial stream channels and in natural stream areas as well. In both areas, fry tended to be on or close to the stream bottom in hours of darkness. Feeding activity commenced in artificial channels with the first increase in light level at dawn.

Settling behavior at night is not conducive to displacement by current. Activity at night, on the other hand, would be conducive to displacement, as Hoar (1953) indicates. Figure 18 illustrates preference of coho fry for night movement. Data were obtained by Deer Creek trap checks at dawn, dusk, midnight and noon. This preference was marked in March and April, less so in May. Activity at night or a failure to settle and hold close to the bottom evidently leads to nomad movement.

The work summarized in this paper indicates that downstream movement would cease if the drifting fish were placed in a suitable environment free of a resident population of coho. This, in turn, suggests that failure to hold position, either in daylight or at night, is due largely to the presence of other fish. If

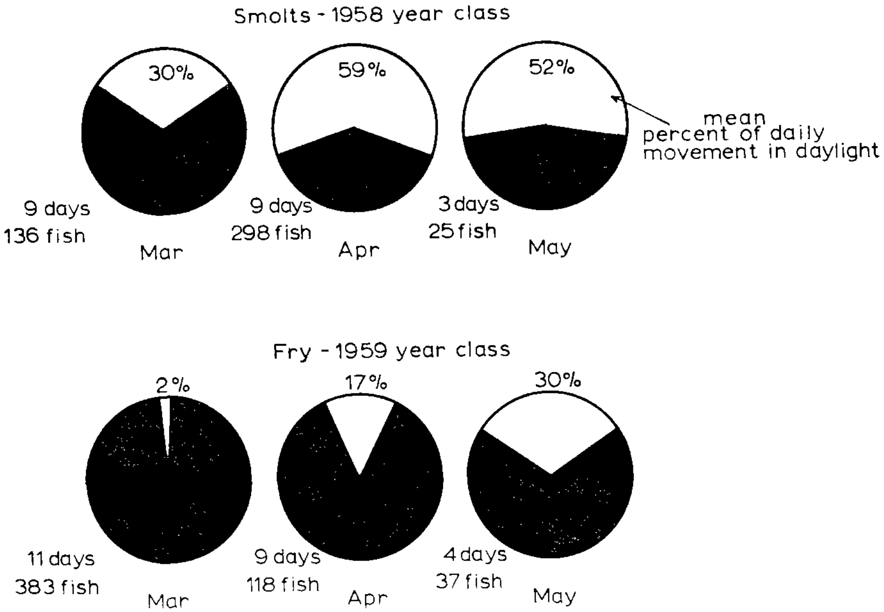


FIG. 18. Downstream movement of juvenile coho in Deer Creek during daylight and darkness, 1959.

fry are forced by aggression into locations unsuited for settling and holding, displacement by current should play a part in causing downstream drift.

Kalleberg (1958) states that territoriality in Atlantic salmon and brown trout is a characteristic evolved as a food supply mechanism. This also is a logical explanation for the aggressiveness of coho, a fish which depends strongly upon drift food on the surface and in the mid-water. However, a similar Darwinian explanation could be offered involving pathological organisms and predation. Aggressiveness could act as a population spreader, decreasing probability of disease, parasite-caused mortality, or predation.

Allee (1938) and Collias (1944) present evidence that a dominant position within a group is correlated with greater individual survival potential. Noble (1939) reported that dominant individuals in a group of *Xiphophorus* sp. lost less weight during periods of starvation than did subordinates, that larger and heavier fishes occupied positions of greater dominance, and that prior residence was an advantage in contacts with newcomers. Braddock (1949) reported similar results for *Platypoecilus* sp.

Aggression seems to be sufficient to account for part of the considerable range in size of cohoes at a given time. As indicated by artificial stream studies reported here, growth of dominant fishes is greater than that of subordinates. Some of the variability in size stems from varying emergence times and varying sizes at emergence of fish emerging at the same time. The rather remote possibility of a feedback mechanism of growth control also exists (Rose, 1960). Brown (1957) suggests that growth of small *Salmo trutta* may be inhibited by the mere presence of larger individuals or by increased production of adrenocorticotropin due to stress (stress being caused by the presence of larger individuals).

It is suggested that aggressiveness of coho is one factor tending to stabilize numbers of smolts yielded by unit areas, operating as a population spreader. The spread of coho populations after emergence, as streamflow decreases and growth proceeds, should assure adequate food supply for the aggressive members of the population, may help reduce transmittal of pathological organisms, and should insure better survival of aggressive coho. These aggressive fish should have better growth opportunity and pass out of the predation-vulnerable small size classes most rapidly.

At first glance, one might find an anomaly in the explanation of aggression as a food supply mechanism and the fact that experimental provision of excess food did not decrease aggression or alter capacity of artificial stream channels for coho. However, it is probable that aggression is a relatively inflexible innate characteristic that can be little altered by temporary changes in food availability.

Another anomaly appears to exist in the fact that some nomads are larger than many residual coho, and should therefore have been able to dominate smaller fish and obtain adequate living space. However, space for a 40-mm coho may not be adequate for a 50-mm fish, nor do the areas occupied by various size groups appear to be similar in physical characteristics. Then, too, some of the movement of large nomads may be due to an innate "desire" to migrate.

The selective advantages gained by coho through aggression are obvious. Probably there is a limit maximizing profitable aggression at a level compatible with maximum growth and survival. Further extension of fish beyond this maximum should result in over-expenditure of energy for maintenance at the expense of growth (Ivlev, 1945) and hence survival probability (Ricker and Foerster, 1948).

Theoretically, a coho stream rich in drift food should have a native race of coho with smaller territorial requirements than would be the case in streams with low food availability. That such differences in food grade exist is almost certain. The environmental differences found in the range of coho salmon are very great (Shapovalov and Taft, 1954; Salo and Bayliff, 1958; Neave, 1949), and should be sufficient to cause large differences among streams in quantity of seston.

As pointed out earlier, the mechanism whereby increased water area yields more coho has not been isolated. The most likely possibilities, entirely apart from spawning area considerations and confined to living space, are decreases in disease and parasite-caused mortality, decreased predation, increased food supply, or increased area for territory-holding fish. It is probable that all these factors play a part in increasing coho smolt yield. It is suggested that the intense and continuous aggressive activity of coho plays an important role in survival.

## SUMMARY

1. A study of aggression in coho salmon was conducted from March, 1959 to October, 1961, in three small Oregon streams. The principal objective of the

study was to determine if emigration of coho fry, occurring from time of fry emergence to November of the first year of life, was caused by aggression in the coho population.

2. The study was made in artificial stream channels and natural stream areas. Glass-sided observation channels were used for part of the study.

3. Downstream movement of coho fry began soon after fry emergence in spring. A large movement took place in the late spring and lesser numbers of nomads moved downstream through the summer and fall. Upstream movement of fry was negligible.

4. Coho fry moving downstream from spring to early fall (these fry are called "nomads" here) were smaller than residual coho. From March to June, migrant smolts were larger than residual yearling coho.

5. Coho behavior patterns and phenomena noted repeatedly in artificial stream channel aquaria included lateral display, parallel swimming, threat, nipping, chasing, flight, hiding, fighting, submission, territorial defense, redirected aggression, and formation of hierarchies.

6. Nomads placed in artificial stream channels barren of fish formed hierarchies and tended to remain in the channels rather than migrating downstream through the unscreened channel outlets.

7. Nomads added to existing resident groups of coho in artificial channels were dominated by the resident dominant fish and tended to leave the channels.

8. Hierarchies and territories observed in artificial stream channels were organized on the basis of fish size, with smaller fish either leaving the channels or being continuously harassed. Small fish that remained in the channels were chased and nipped unless they remained still near the stream bottom or hid among bottom particles, either of the latter two situations resulting in inferior opportunities for feeding and growth.

9. Dominant coho grew more rapidly than subordinate fish in artificial channels.

10. Feeding of coho with brine shrimps, in quantities in excess of requirements, did not alter capacity of artificial stream channels for nomads.

11. Aggression observed in natural stream areas was frequent, probably continuous, and consisted of territoriality, partial territoriality, nipping, threatening, and chasing.

12. Nomads transferred to a 39 $m^2$ controlled stream section barren of other coho remained there, taking up residence in the pool where they were released.

13. Of 1627 nomads taken from one stream in 1960 and transferred to another stream barren of resident stock, about 4% moved down and out of the stream in 1 month following their transfer. Of 1577 nomads transferred in like manner in 1961, but added to an existing population, about 27% moved down and out of the stream in the month following transfer.

14. It was concluded that aggressive behavior is one factor causing the downstream movement of coho fry.

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