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Title BEHAVIORAL ECOLOGY OF JUVENILE COHO SALMON (O.

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COMPETITION AND AGGRESSIVE BEHAVIOR.

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The behavioral ecology of juvenile coho salmon, with particular reference to competition and aggressive behavior, was studied in stream aquaria. Series of riffle and pool environments and volitional residence were employed to simulate the natural environment.

In populations of fry allowed to emerge from simulated redds, individuals which emerged first enjoyed ecological advantages over later-emerging fry. First-emerging fry were larger at a given time and had a greater tendency to remain in the stream aquaria than later-emerging fry, suggesting that they had "settler's rights" to the available environment and (or) better feeding opportunity. Distribution and social stability are related to competition and aggression. A behavior pattern

termed "fright huddling" is described and related to aggression. Environmental rearing capacity is discussed in terms of living space and food availability.

Post-emergence competitive relations in the stream aquaria of fry that were initially exposed to physiological stress (lowered oxygen level) during development revealed that these relations were a direct reflection of stress history. Initial size disparities induced by developmental stress were amplified with time, and fry enduring the most severe developmental stress showed the lowest residence tendency. Emigrants placed in a vacant, replicate system remained there, grew rapidly, and were as large, or larger, than their counterparts that did not emigrate. At termination, size of former emigrants reflected enhanced feeding opportunity through lowered competition for food and space in the replicate system. Competition was referred more precisely to stress history by standardizing growth and migration performance in terms of indices of ecological stress and net production. These results are compared with the growth of replicate fry fed to "excess" under hatchery conditions. Initial disparities in size were not amplified with time in the latter. This replicate population was subsequently exposed to the same experimental procedure in the stream aquaria where their performance substantiated the previous findings. The over-all results are discussed in terms of ecological significance,

particularly competition for food and space and the importance of a size-related social order. The adequacy of the stream aquaria with reference to the natural environment and the implications of volitional residence are considered.

The significance of aggression as an instrument implementing social relations and the pattern of food and space distribution was explored in small groups of fish. Coho fry are capable of complex behavioral interaction involving threat display and territoriality at time of emergence. Interest in external feeding is associated with the amount of unspent yolk reserve and intensity of aggressive behavior. The hunger drive is probably related to onset of aggression. A direct relationship was found between feeding opportunity and aggression. The stimulation to feed may involve summation features since intensity of aggression continued to increase following food consumption and remained at a high level for several hours.

Juvenile coho in small groups exhibit nip-dominance organization, individuals of high social rank dealing out most of the aggression but receiving the least in return. In despotic hierarchies, the despots grew, all subordinates lost weight, and death was associated with low social rank. Despots fed to satiation and prevented subordinates from feeding in the presence of excess food. By increasing social complexity without changing density, mortality was prevented and weight loss and

social stability were reduced. Dispensation of aggression was more equitably shared and subordinates displayed partial territoriality.

Threat display is considered with regard to its behavioral context. The influence of the physical environment and social relations on the frequency of threat display is examined. Intensity of aggression is negatively correlated with frequency of threat display.

Daily cycles of activity and aggression are described and related to dawn and dusk and competition for feeding opportunity in the riffles. Nocturnal activity and feeding opportunity are considered. Behavior during the winter months is characterized by inactivity and avoidance of currents, increased sensitivity to light and cover, and near-absence of aggression. Feeding and aggression re-appear in early spring and allow renewed growth prior to the parr-smolt transformation.

Yearling smolts exposed to estuarine salinities retained their aggressive behavior and formed size-related, despotic hierarchies. The possibility of reversing behavioral shifts associated with seaward migration is considered.

BEHAVIORAL ECOLOGY OF JUVENILE COHO SALMON (<u>O</u>. <u>KISUTCH</u>)
IN STREAM AQUARIA WITH PARTICULAR REFERENCE TO
COMPETITION AND AGGRESSIVE BEHAVIOR

by

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GENERAL INTRODUCTION

In the present work, the potential value of stream aquaria for studying the behavioral ecology of stream fishes is explored with the aim of contributing to the development of more adequate concepts regarding the natural regulation of stream fish populations, especially those of salmonid species.

The stream aquarium approach used here advances a meaningful compromise between the natural stream with the uncontrollable physical variability deriving primarily from fluctuations in flow and attendant biological complexity, and the obvious artificiality of the simple laboratory environment. This approach allows opportunity to manipulate quantitatively major environmental features and to discipline such manipulation by permitting volitional residence, whereby the experimental animals can express dissatisfaction or migrational tendencies by leaving the system.

There is an underlying theme woven throughout the following series of experiments that were pursued under a variety of conditions: the social relations of juvenile coho salmon - and probably most stream-dwelling salmonids - are of major importance in their ecology. These social relations are the outcome of aggressive behavior that is keyed to competition through the use of aggression to resolve the problems

attending distribution of limited food and space resources within the population.

I hope that the present findings will stimulate a more fundamental and ecological emphasis in fishery research pertaining to the management of salmonid species whose life histories entail periods of extended residence in streams.

BEHAVIORAL ECOLOGY OF JUVENILE COHO SALMON (O. KISUTCH) IN STREAM AQUARIA WITH PARTICULAR REFERENCE TO COMPETITION AND AGGRESSIVE BEHAVIOR

SIGNIFICANCE OF EARLY EMERGENCE, ENVIRONMENTAL REARING CAPACITY, AND ASSOCIATED BEHAVIOR

INTRODUCTION

The fry of stream-dwelling salmonids must migrate out of the gravel in which they were deposited as fertilized eggs. Little is known of this initial migratory phase of the general life history in terms of the mortality attributable to it, or of behavioral mechanisms in fry that may account for it. Possible delay of migration, either by the individual fry or by the redd population to which it belongs, and the ecological significance of such delay have received scant attention. Similarly, the question of trophic relations, onset of feeding behavior, and the host of possible circumstances capable of influencing intra-gravel movement and migration have been little investigated.

That the rate of emergence and length of the emergence period may vary considerably in both natural redds and in laboratory facsimilies is well known. Apart from the factors responsible for the nature of emergence from the gravel, the ecological significance of a particular position on the emergence time scale is presently unknown for both the individual fry or its population.

First-emerging coho salmon fry (Oncorhynchus kisutch) move downstream in small numbers soon after emergence. Whether this movement is due to an innate migratory urge or to displacement by the current is unknown but Chapman (1962) has reported that this "drift"

occurs despite an apparent abundance of suitable living space at the stream margins.

Chapman (1962) has shown that aggressive behavior is an important concomitant of downstream movement of coho fry prior to the smolt migration. Aggression in juvenile coho is associated with intra-specific competition for food and space. The present experiment is the first of a series reported here concerning the behavioral ecology of juvenile coho salmon. The primary objectives were to evaluate possible significance of early emergence, to establish when aggression and territoriality develop in newly emerged coho fry, and to attempt measurement of the relative roles of pool and riffle environments, in terms of rearing capacity, for the juveniles of this species. The study extended from February to early July 1963.

DESCRIPTION OF THE APPARATUS

Two glass-fronted wooden stream aquaria, 6.6 meters long and 0.9 meters in both width and height, located at the Alsea Trout Hatchery (Oregon State Game Commission) on the North Fork of the Alsea River in Western Oregon, were used for the study (Figure 1). These stream aquaria were positioned side by side with approximately 1.5 m between them to facilitate construction of a median observation enclosure. Rapid observation of both systems with minimal disturbance could be made from a central bench.

Figure 1. Paired stream aquaria. Walls facing the central observation
chamber are glass.

The water supply was tapped from the main line entering the hatchery from a collection system located some 400 meters upstream at a concrete dam across the river. The flow was directed into each system through aluminum irrigation pipe and controlled by separate valves. Out-flow from each system passed through an inclined-plane trapping facility into a V-notch 90-degree weir forebay. Both weirs were calibrated so that identical flows could be maintained in both systems and a constant flow of 12.4 liters per second was passed through each stream aquarium.

In each aquarium, an alternating series of riffles and pools was constructed of plywood. The left system contained three riffles and three pools, each 1.2 m in length, while the right system was composed of two riffles, each 2.4 m in length (Figure 2). Thus, the two aquaria differed in the relative amounts of each bottom type present, the left system containing 50 percent more pool area but 25 percent less riffle area than did the right system.

The flooring was constructed to allow 13 cm of water depth over the riffle boards and 46 cm over the pool boards. Both riffles and pools were overlain with graded gravel between 2.5-5.1 cm in greatest diameter. At the constant flow rate of 12.4 liters per second the average riffle velocities ranged from 24 to 27 cm per second.
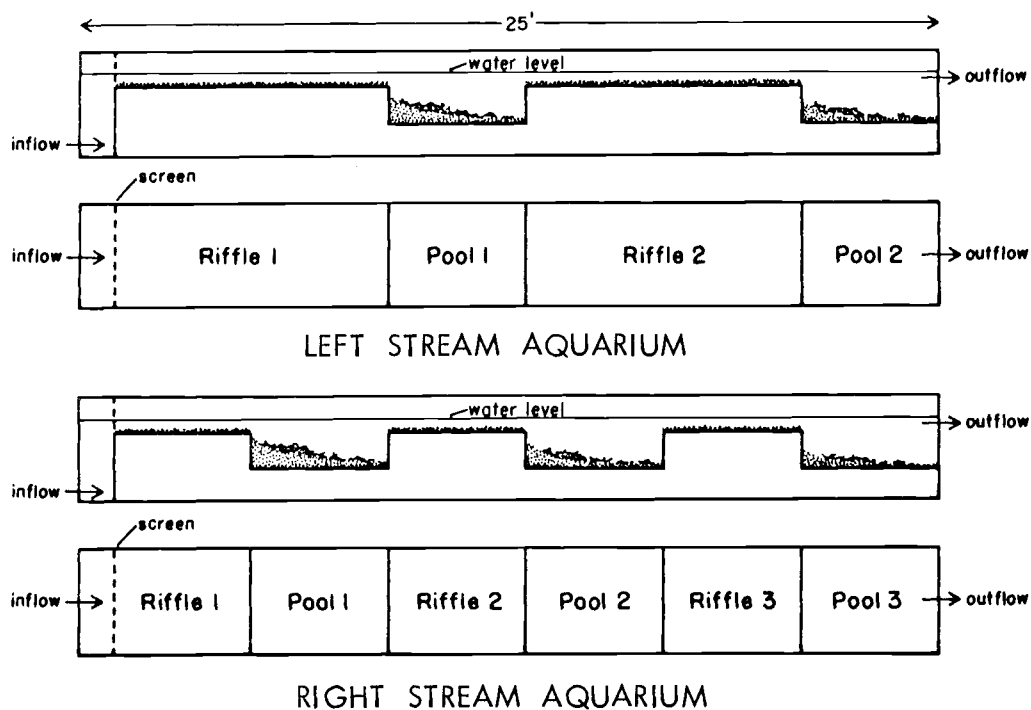
Figure 2. Diagrams showing the side and top aspects of each stream aquarium as they were used for the early emergence experiment.

The upstream end of each stream aquarium was screened so that resident fish were able to leave the system only by passing out through wall slots in the downstream end of the aquarium into the inclined-plane trap.

During the experimental period, mean maximum and minimum weekly temperatures based on daily records ranged from $7.3-14.4^{\circ}$ C and from $6.1-12.4^{\circ}$ C, respectively.

METHODS

Fertilized eggs from Fall Creek Salmon Hatchery (Oregon Fish Commission), two males X one female, were incubated in standard hatchery baskets in laboratory facilities at Oregon State University until well into the sac fry stage. On February 22, 1963, the sac fry were transported to the stream aquaria and 300 fry were installed in each system within a nontoxic plastic screen container. A 15 cm layer of gravel was carefully placed over the fish in the containers so that to escape the container, the fry had to migrate up through the layer of gravel. One of the containers was suspended in the first pool of each system against the far wooden wall. Emergence from the gravel into the pool simulated the natural environmental experience of coho fry except that the initial post-emergence period was spent in pools rather than among the spawning rubble of the natural stream bed.

The first 25 fish to emerge in the left system and the first 46 fish in the right system were fin-clipped for future identification by removal of the right pelvic fin. Fry leaving the stream aquaria entered the traps, were measured for total length, and released into the Alsea River. Residence was maintained strictly on a voluntary basis to approximate as closely as possible behavior in the natural stream environment. Juvenile coho behavior was observed for a period of some four months prior to termination of the experiment in early July.

RESULTS

Initiation of Aggression and Territoriality

The first fry emerged on March 7, in the left aquarium, and in the right aquarium between March 7-10. By March 15, the emergence was well underway in both systems and the first fry were taken in the traps. On March 13, about 40 fry were observed feeding vigorously in the first pool of the right system. No aggression was detected in this group during a 10-minute observation period, but 6 nips were recorded among some 50 fry in this pool during a similar period 2 days later. On the latter date the first fry were seen feeding actively on the riffle areas in the right aquarium, however, they were few in number, the majority remaining in the pools.

By March 19, fry in the left stream aquarium had invaded the riffles and were present in large numbers in the first riffle, well-scattered and exhibiting frequent aggression in the form of threat, nipping, and short drives and chases involving adjacent individuals. Little sign of aggression was observed in the pools at this time. Similar observations were recorded on March 26.

On March 29, when freshet conditions in the main stream turned the water quite turbid, much food was present in the drift, and the fry were actively feeding throughout both systems. Aggressive behavior was frequent in the riffle areas when the fish could be seen. Variably turbid water conditions prevailed during the first week of April but territorial behavior in the riffles was frequent when observation was possible. Riffle-invading fry pursued a characteristically zig-zag course up through the riffle as they entered specific territories and were driven from them by their aggressive owners. Unless a vacant area could be found or unless territorial fish were successfully displaced, such invaders would turn and flee downstream into the pool.

Aggressive behavior in these fry began within one week of emergence from the gravel. At this time, the invasion of riffle areas coincided with the appearance of aggressive interactions amongst coho fry in the pools. Within ten days after appearance of emergent fry, large numbers had invaded the shallow riffle areas, occupying and

defending feeding territories. When aggressive behavior was intitially observed in the pool, it consisted of simple nipping and chasing but aggression in the riffles four days later entailed threat, nipping, driving, and chasing amongst adjacent individuals. Aggression in the riffles was particularly directed toward fry that were invading the riffle areas and, by doing so, trespassing in territories defended by resident coho.

Characteristics of Aggressive Behavior

Nipping, chasing, flight, fighting, territorial defense, redirected aggression, dominance posturing, lateral display, and parallel swimming, behavior patterns discussed by Chapman (1962), were commonly seen in the stream aquaria. Formation of hierarchies could not be confirmed due to the large numbers of coho present in the pools but the general size-dominance relationship usually determined the outcome of social interactions between individuals. Neither hiding nor submission was observed. The largeness and uniformity of the environment may have discouraged hiding and submission may be an artifact induced by the close confines of small aquaria wherein adequate escape opportunities are not provided.

To furnish some basis for interpreting the significance of aggressive behavior, nip intensity was recorded in the pools and riffles. As previously indicated, the first signs of aggressive behavior were

observed within one week of first emergence on March 7 (Table 1).

A trend toward increasing aggression may be seen. When the data

were pooled within the two time intervals, March 13-May 4 and

May 11-May 30, and subjected to a t-test, the resulting mean

aggression levels in the later period were significantly higher (P< .05).

The rise in level of aggression paralleled the rate of egress from both

systems and rising water temperature. When aggression level was

plotted against the daily rate of outmigration during the seven-day

period bracketing the day whereon aggression was measured, there

appeared to be a positive correlation between these two variables but

the relationship was not statistically significant. The correlation

between aggression and temperature level was a positive and significant

one (P< .05).

The levels of aggression in riffle and pool environments are not

strictly comparable since the relative intensity of interaction does not

appear to be equal in both areas. Riffle interactions are more violent,

involve higher degrees of locomotor activity due to the additional

current velocity, and more often culminate in a chase —> near-contact

nip or chase —> contact nip than do pool interactions. The latter

involve less active chasing and nipping except in the case of prolonged

territorial disputes. In addition, pool interactions are associated with

more circling, parallel swimming, and low level dominance posturing.

TABLE 1.   CHANGES IN LEVEL OF AGGRESSION DURING THE EARLY EMERGENCE EXPERIMENT

Date	No. of Fish In Channels	Observed	No. of 10 min. Observation Periods	Observation Time Limits	Level of Aggression (nips/fish/10 min.)		
					Mean	Range	95% Confid. Limits
March 13	55	30	1	0915–0925	0.0		
15	60	50	1	1316–1326	0.12		
April 18	210	105	3	0900–0930	0.53	0.08–1.33	0.0–2.21
May 4	287	235	10	0900–1100	0.78	0.0–2.00	0.33–1.24
11	281	110	10	1010–1200	2.64	0.0–5.00	1.44–3.84
20	241	93	10	1000–1150	7.85	0.0–21.00	3.20–12.50
30	155	60	4	1015–1120	4.67	4.0–6.00	1.09–8.24

Juvenile coho exhibit intense fighting behavior that appears to be associated primarily with attempts to set up or maintain territories in pools. Rapid circling and severe nipping attempts concentrated at the caudal region typify this behavior. Whereas fighting was commonly seen in the stream aquaria during the spring, frequence of fighting declined as the season progressed until in May, when the coho averaged about 45-48 mm in total length, fighting was quite rare. The last fight observed took place on May 11, between two small coho and pertained to a territorial dispute. The average length of the 16 coho in this pool was 45.6 mm on May 1.

The Fright Huddle

When juvenile coho were badly frightened, either purposefully by the observer, or due to natural events such as the overflight of birds or foraging of water ouzels (Cinclus mexicanus) in the riffles, a predictable sequence of events was initiated. Coho occupying territories in the riffles fled rapidly into their "home" pool, and assumed a quiescent position on or near the bottom and adjacent to the glass wall. If the disturbing influence was extended to the pool, all fish moved into close contact with one another near the bottom of the pool, forming a close grouping. This fright behavior is best described as huddling and the consequent grouping is termed the "fright huddle". It has also been elicited in a smaller stream aquarium containing groups of 10 to 20 coho.

Physical contact both with the bottom and with adjacent individuals, rapid respiratory movements, complete lack of aggression, and maintenance of position by slight fin movements characterized this group-behavioral reaction in the pools. Breakup of the huddle commenced when a few individuals at the periphery made short drives to and from the huddle, usually toward the surface, and engaged in short-term and low intensity aggressive behavior directed at close companions. The huddle slowly expanded and reached dimensions two to three times that of its original size before an appreciable number of coho ventured from it.

By the time the huddle had lost its identity as a close grouping of fish, the more aggressive coho were actively feeding and behaved as they did prior to the disturbance. Smaller coho which usually left the huddle first were also first to re-invade the riffles but their territorial opportunities were terminated by the larger fish when they began feeding again.

Huddling behavior was elicited in riffle conditions of rapid flow and shallow water by carefully introducing groups of coho from a container. The great majority of fish moved to the glass wall and maintained position in the current, forming an elongated but compact grouping that preserved its identity for 10-20 minutes before any aggression returned. The few fish not joining the huddle swam rapidly

downstream into the pool. Breakup of the riffle huddle was signified by
a "stringing out" in a downstream direction, precipitated when the up-
stream members of the group initiated low intensity dominance posturing
which increased in vigor, accompanied by driving and nipping at
nearby companions.

The fright reaction involved contact with the substrate and
adjacent individuals and, in rapid flow, maintenance of position
against the current. Low level fright reaction of coho feeding in the
riffles when disturbed resulted in their fleeing into the pools.

Social Habit, Territoriality, and Social Stability

To measure the stability of the distribution in the stream aquaria,
the changes in location of individual fish were recorded. Fin clips and
differences in coloration, fin shape, body size, and behavior made it
possible to identify individual fry.

Over the period of a week, the fish in the right aquarium were
closely observed for individual characteristics. Of the 60 coho living in
the system, 10 fin-clipped coho and 3 unmarked coho were selected for
further study. These 13 fish could be recognized with complete relia-
bility within the population. They were healthy, active fish that
reflected the range in size encountered in the population and gave no
indication that they were in any way abnormal or aberrant in behavior. The
coho were closely observed during the daylight hours on three days,

June 23, 25, and 27. The position and general activity of each fish was recorded at least once per hour and far more often during early morning and later evening.

Position changes averaged one per fish per 24 hours of aggregate observation time. One individual never moved and five moved only once. Ten of 13 coho showed definite constancy of preference for one pool or one riffle. Travel in the system was confined to a pair of adjacent pool-riffle units. Larger coho (seven fish of 80-90 mm) chose positions along the walls in the uppermost pool and riffle and tended to remain there. None were seen in the second riffle or pool. Smaller coho (six fish of 70-75 mm) spent their riffle time in riffle 2 but their pool time in pool 1, wandered in position more than the larger fish while in the riffle, and tended to take a central position in pool 1. Even though well-distributed along riffle 2, they were never seen in pool 2.

Individual coho tended to develop habitual patterns of living within the system. These patterns fell into two general categories involving primary association either with a particular riffle or pool, at least during the daylight hours. Both categories were strongly identified with territoriality. Coho preferring riffle association fled into the pools when frightened.

Distribution in the Stream Aquaria

The coho fry emerged from the gravel into the uppermost pool of each stream aquarium. Their post-emergence distribution involved an initial radiation in both upstream and downstream directions (Table 2). Main movement out of pool 1 took place between March 15-19 and was in a downstream direction in the left system but in an upstream direction in the right system. The possibility exists than an inequality in flow created this discrepancy as the channels were not calibrated at this time. But the impetus for distribution throughout the systems is taken to be the rapid accumulation of fry in the uppermost pools.

Although a few fry passed out of both aquaria during the first week, their numbers were but a small fraction of the resident populations. Rate of emigration increased following March 19, remaining high until March 26, in the left system and April 3, in the right system (Figure 3), indicating an initial large-scale numerical adjustment of the post-emergence populations. The pattern of outmigration is supported by the population estimates plotted in Figure 4. Resident populations stopped increasing following the main wave of emergence, coincident with the rapid decline in rate of outmigration at the end of March. The April 2 and April 10 estimates in the right aquarium are considered to be poor ones.

TABLE 2. NUMBERS OF COHO AND THEIR DISTRIBUTION IN THE STREAM AQUARIA, MARCH 13 to JUNE 27, 1963.

		March				April				May		June
		13	15	19	26	3	11	18	28	18	31	27
Left System												
Riffle	1	0	0	3	19	16	5	13	14	11	6	5
	2	0	0	1	11	8	2	7	9	6	5	3
	3	0	0	0	4	9	3	6	6	4	3	2
Pool	1	) 15	10	27	60	75	70	76	70	55	31	20
	2	)	14	40	40	25	41	40	28	23	11	3
	3	0	0	1	20	20	25	15	11	12	3	3
Sum		15	24	72	154	153	146	137	138	111	59	36
Right System												
Riffle	1	0	4	39	50	35	19	25	25	35	20	16
	2	0	2	3	15	21	13	13	16	14	11	7
Pool	1	40	30	50	70	60	80	110	100	75	45	31
	2	0	0	19	35	23	25	25	20	13	6	4
Sum		40	36	111	170	139	137	173	161	137	82	58
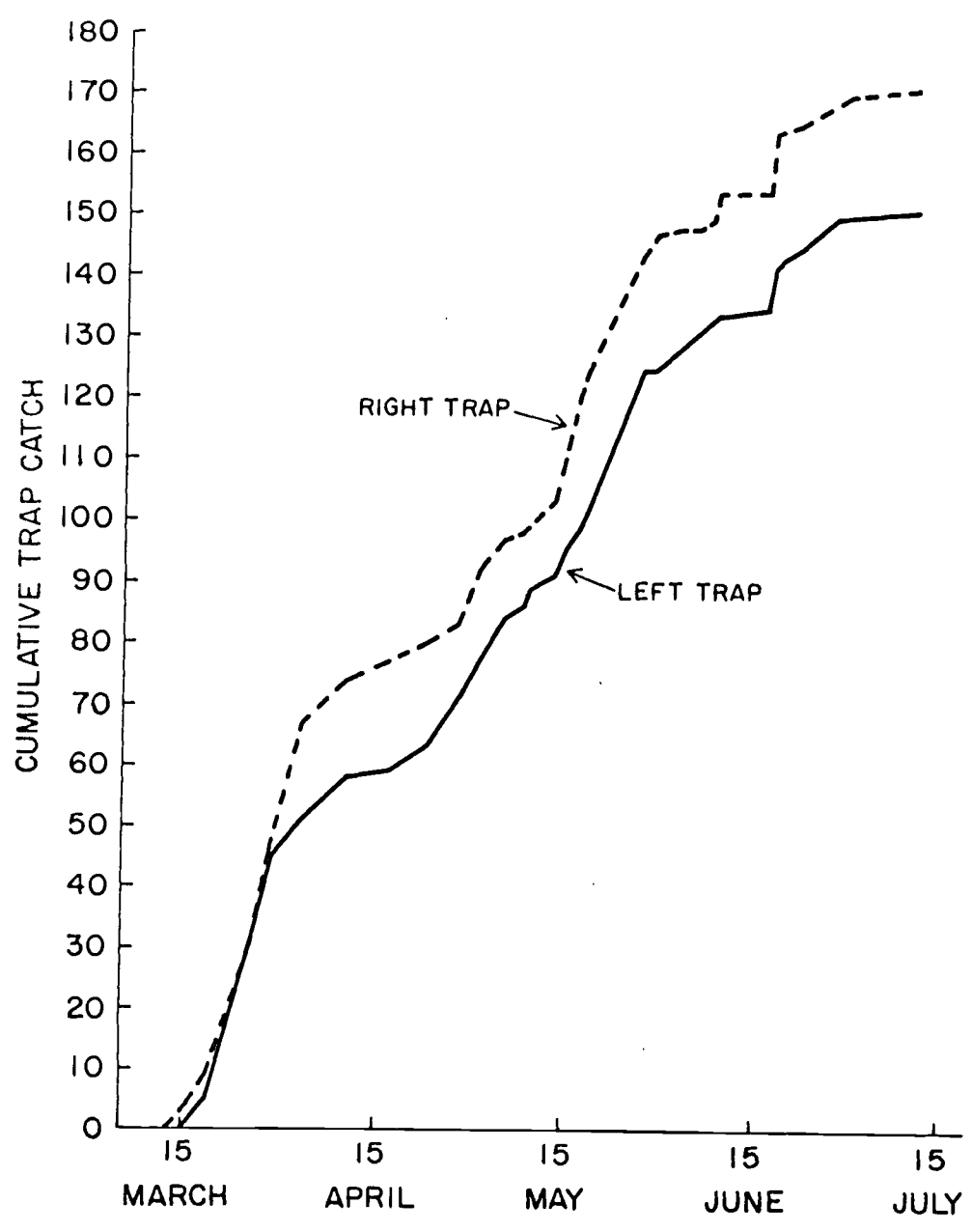
Figure 3. Cumulative trap catch at the outlet of each stream aquarium, March 13-July 10, 1963.
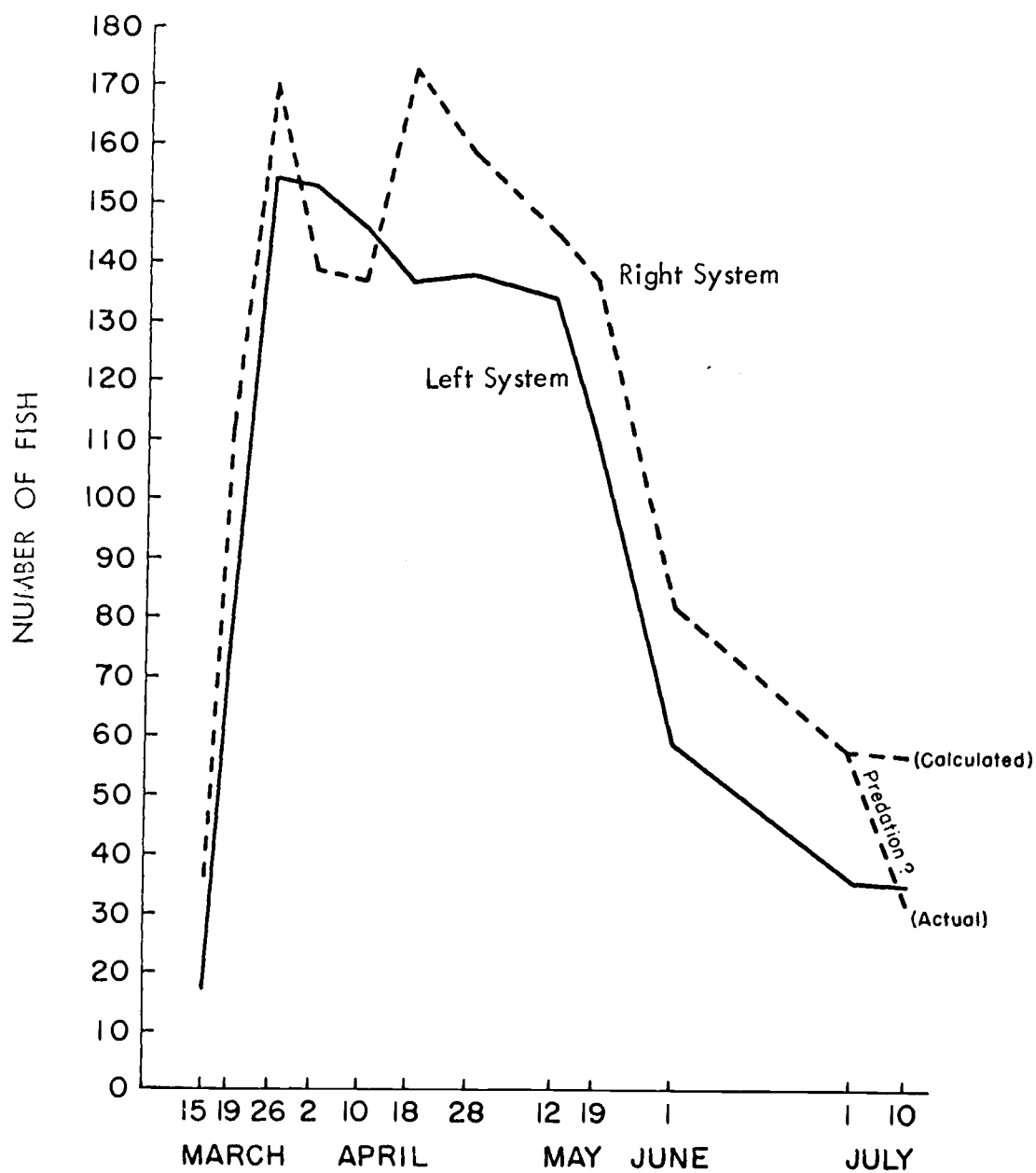
Figure 4. Estimated number of coho in each stream aquarium, based on visual counts, March 15–July 10, 1963.

A relatively fixed pattern of distribution persisted throughout the experiment. The fry were concentrated toward the upstream ends of both stream aquaria (Table 2). The extent to which this occurred and the accompanying degree of variability in numbers of fry occupying each environmental unit is depicted by Figure 5. These plots are based on hourly fry counts in each pool and riffle from sunrise to sunset.

This density gradient was associated with a gradient in size of individual fry. Due to the possibility of adversely affecting behavior, the two populations were not sampled extensively. However, the coho in the pools were sampled on May 1 and the resulting data are compiled in Table 3. In both systems the greatest average lengths were found in the first pools and were significantly different (P< .05) from those of the second pools. The mean length in pool 1 of the left system was significantly greater than that of the third pool at the 10 percent level. The high mean length reported for the sample of eight fish taken from the latter pool is due to the influence of two large coho (50 mm and 53 mm). The remaining six fish fell within the range of 43-45 mm.

TABLE 3. MEAN LENGTH IN MILLIMETERS FOR COHO SAMPLED FROM
THE POOLS ON MAY 1, 1963, AND SOME RELATED STATISTICS

	Left Aquarium Pools			Right Aquarium Pools	
	1	2	3	1	2
Sample size	39	17	8	52	16
Sample mean	48.03	43.76	46.25	48.02	45.63
Standard error	0.49	0.55	1.20	0.44	0.77
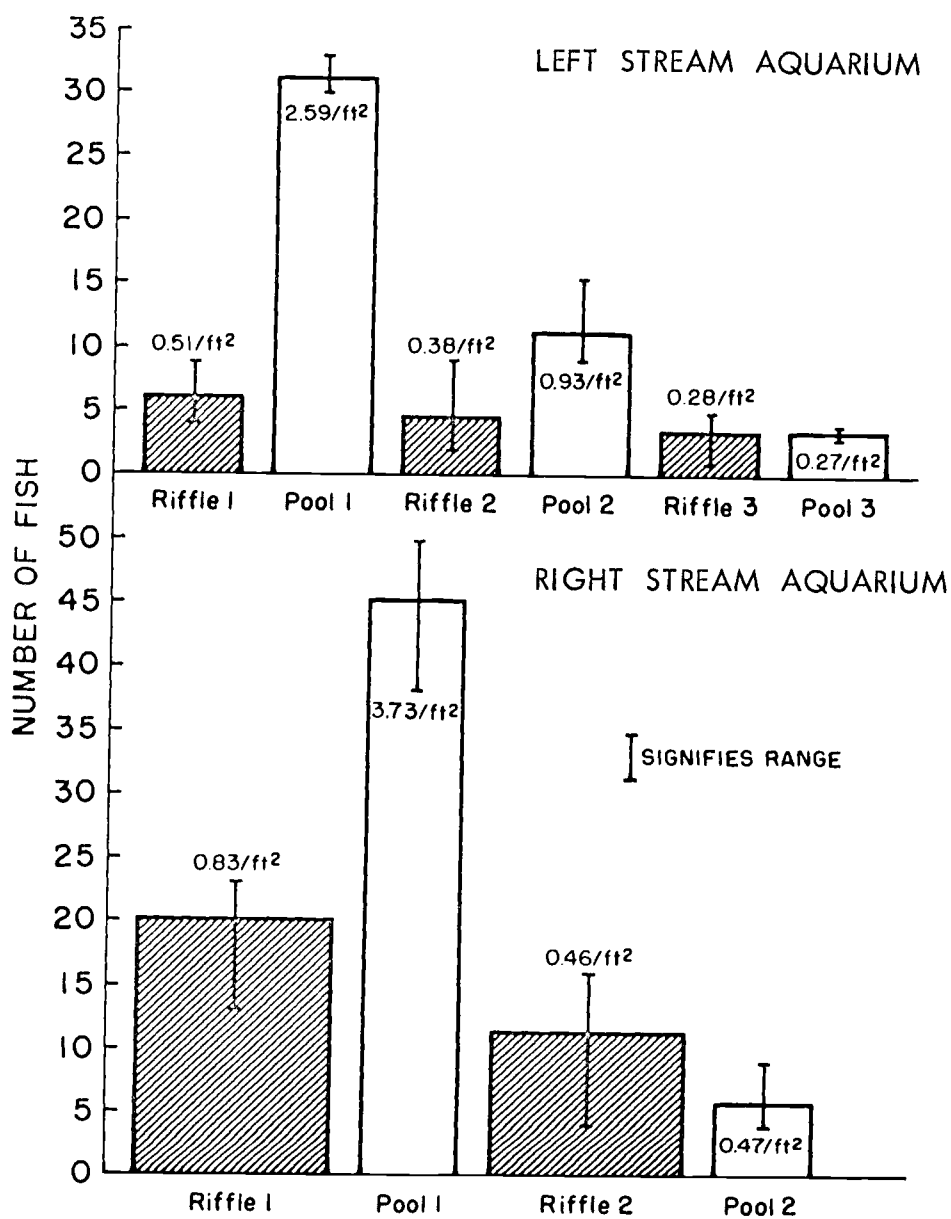
Figure 5. Mean density of coho observed in each environmental unit, March 13-June 27, 1963, together with the range in counts.

TABLE 4. THE AVERAGE LENGTH OF MARKED AND UNMARKED COHO
IN THE TRAP CATCHES; EARLY EMERGENCE EXPERIMENT.

Date	Stream Aquarium	Unmarked		Marked		Sign of Difference
		No. of Coho	Length(mm)	No. of Coho	Length(mm)	
March 15	R	1	38.0	2	38.0	0
19	L	4	38.0	1	39.0	+
26	L	23	38.9	3	40.6	+
29	R	14	40.0	1	42.0	+
April 6	L	2	42.0	1	47.0	+
18	L	1	43.0	1	46.0	+
28	L	6	42.5	1	47.0	+
May 5	L	6	47.5	1	47.0	−
	R	2	49.0	1	52.0	+
27	L	23	62.3	1	66.0	+
	R	19	54.9	2	64.3	+
June 8	R	4	65.0	1	69.0	+
17	L	6	60.6	2	79.0	+
	R	6	67.7	4	65.8	−
July 9	R	1	68.0	2	87.0	+

Fate of First-Emerging Fry

The first fry to emerge from the gravel were marked by removal of the right pelvic fin. The fate of these marked coho was followed in the trap catches, in the population samples, through behavioral observation, and by their contribution to the final populations upon termination of the experiment.

Marked fish emigrated in small numbers from both stream aquaria throughout the experiment as shown by Table 4. In the majority of trap records pertaining to marked fish (12 of 14 cases) these fish exceeded the average length of the unmarked trapped fish. A sign test (Li, 1957) indicated that the difference was significant at the one percent level.

On the average, marked coho were larger than unmarked coho on May 1, in the right system, and in both systems upon termination of the experiment (Table 5). The differences between the average lengths of fin-clipped and unmarked fish were all significant at the five percent level and were amplified as growth progressed.

Marked coho were seldom observed in the second and third pools in the left aquarium and none was seen in the second (last) pool in the right aquarium, although emigrants obviously passed through this pool in order to enter the trap. Thus, distribution correlated with the general size gradient in horizontal distribution previously discussed.

TABLE 5. DIFFERENCES BETWEEN AVERAGE LENGTHS (mm) OF MARKED
AND UNMARKED COHO, EARLY EMERGENCE EXPERIMENT

	Left Stream Aquarium		Right Stream Aquarium	
	Marked	Unmarked	Marked	Unmarked
May 1				
Sample size	Only one marked coho was taken in this sample		12	34
Sample mean			50.67	47.09
Standard Error			1.08	0.44
July 10				
Sample size	5	30	8	24
Sample mean	84.25	76.48	84.86	77.47
Standard error	0.99	1.52	2.87	1.42

The experiment was terminated on June 10, due to an unidentified disturbance of the population in the right stream aquarium between June 30 and July 1. A routine check on July 2 revealed that 16 fish had entered the trap and 16 were concentrated in the last pool. Twenty-five coho were missing. No fish were found upstream from the last pool and none moved back upstream during the following four days although the trapped fish were released into the last pool. Three fish entered the trap during this time. During the next four days the general behavior of the population remained quite abnormal, the fish being highly sensitive to stimulation. Very low numbers of coho occupied the riffles. There was no sign of interference in the left system and all fish were accounted for upon termination. Although the left system was unaffected, avian predation in the right system was suspected.

Due to the loss in the right aquarium, the number of fish that would probably have been present was calculated by subtracting the accumulated trap catches since the last population estimate (June 27) from that estimate: 58 - 1 = 57 coho; in the left system the number was 36 - 1 = 35 coho. The revised biomass values were calculated using the mean weights for both terminal populations in case mortality in the right population was exerted primarily on the smaller fish. Less than a 20 gram difference resulted (Table 6).

TABLE 6. FINAL POPULATION STATISTICS FOR THE EARLY EMERGENCE
EXPERIMENT, JULY 10, 1963.

	Left Stream Aquarium	Right Stream Aquarium	
		Actual	Revised
Number	35	32	57
Biomass(gm)	166.3	160.3	270.8^a-290.1^b
Mean length(mm)			
Unmarked fish	76.48	77.47	
Marked fish	84.25	84.86	
All fish	77.59	79.32	
Mean weight(gm)			
Unmarked fish	4.48	4.46	
Marked fish	6.36	6.67	
All fish	4.75	5.09	

[a] based on mean weight of coho in the left system.

[b] based on mean weight of coho remaining in the right system.

First-emerging fry marked by fin removal initially composed 8.3 and 15.3 percent of the total fry emerging into the left and right systems, respectively. These marked fry showed a stronger tendency to remain in the aquaria than did later-emerging fry, composing 14.3 and 25.0 percent of the terminal populations. Discounting the possibility of weight differences between early and later-emerging fry, the marked coho also increased their importance in terms of biomass, composing 14.8 and 32.3 percent of the terminal population biomass in the left and right system, respectively.

Of the 300 sac fry put in each system, 212 and 234 fish, respectively, in the left and right aquaria, can be reliably accounted for. Two dead fry were found in each container upon completion of emergence. Undetected emigration during the March-early April freshet period, avian predation and, less probably, cannibalism among the fry, are the most reasonable major causes of loss.

There was little difference in size of fish in the two systems on July 10, but biomass in the right aquarium was greater (Table 6), suggesting that the right stream aquarium received a greater share of the organic drift due to the hydraulic conditions in the incoming water supply system. This hypothesis was tested by sampling the drift entering both aquaria with plankton nets. The result of a 24-hour series of samples taken every 3 hours with 1/2-hour intervals (7 pairs of

samples) revealed this to be the case. The right system received 36.7
percent more total settled volume of drift material and 36.4 percent
more volume in potential fish food organisms. Available food level
may be a primary factor among those determining the rearing capacity
of these semi-natural systems. In view of the distribution pattern
of fish in the aquaria, and the associated behavioral aspects involving
competition, this finding should not be surprising.

DISCUSSION

The coho fry first to emerge from the gravel enjoyed an eco-
logical advantage over the fry emerging subsequently. Several factors
could be involved in producing such an ecological advantage. Genetic
superiority in such terms as constitutional vitality, greater growth
potential, and above-average aggression levels may well be operating.
I doubt that an ecological advantage was enjoyed by a portion of the
embryos during development since incubation proceeded at oxygen
saturation levels and normal temperature. The eggs were of above-average
size and produced large and vigorous sac fry that spent two to three
weeks in the gravel prior to emergence. Genetic and environmental
interactions would be difficult to evaluate within the framework of the
experimental design. Koski (1966) found that size of coho fry emerging
from natural redds decreased as emergence proceeded.

Assuming no important relationship between state of health and time of emergence from the gravel, there arises the distinct possibility that first-emerging fry have "settler's rights" to the available environment and (or) the feeding opportunity to create or maintain a size gap between themselves and the later fry. Very small differences in size were found by Chapman(1962) to determine the outcome of aggressive interaction between coho fry, with the larger fish gaining dominance. Furthermore, level of aggression was found to be higher among groups of coho of uniform size than among groups of disparate size. Similar observations were reported by Newman(1956) for mixed and homogeneous groups of rainbow and brook trout.

I postulate that social stability is positively related to growth depensation in single age-class populations and that the complexity of size structure typical of multi-age-class populations may promote social stability.

Ecological advantage in juvenile coho is expressed through the medium of behavioral dominance dictating feeding opportunity for subordinate coho of lesser size. Other factors such as production of adrenocorticotropin due to socially instigated physiological"stress" as reported in brown trout (Salmo trutta) by Brown (1957) may well be involved. Coho fry are cannibalistic and this propensity in underyearling smallmouth bass (Micropterus dolomieui) was reported by Langlois (1936) to result in a high degree of growth depensation.

The numerical and size distribution of coho throughout the stream aquaria are almost certainly associated with feeding opportunity and food availability levels, competition, and behavioral dominance through aggessive behavior. The populations depended almost entirely on the organic drift carried by the incoming water supply but were able to supplement their diet to a small degree by surface feeding on adult insects. Insects produced within the systems are considered to have been of minor consequence in the diet.

The significant positive correlation between level of aggression and water temperature may be an indirect result of increased locomotor activity and demands for food, cover, and space. Gradual increases in temperature are probably not a direct cause of increased aggressive activity.

A positive correlation between level of aggression and rate of emigration from the stream aquaria would suggest that population adjustments in these systems are mediated by intensity of aggressive behavior. Factors encompassing the food-space-shelter complex are no doubt of primary importance in population adjustments and related to aggressive behavior in juvenile coho. The role of aggression in hierarchical and territorial behavior has received considerable attention as a mechanism by which food and space are distributed within fish populations (Allee et al, 1948; Collias, 1944; Hartman, 1965; Kalleberg, 1958; Kawanabe, 1958; Magnuson, 1962; Newman, 1956; Noble and

Borne, 1938; Yamagishi, 1962).

Increased aggression following the introduction of food has been reported for several salmonids including brown trout and Atlantic salmon (S. salar) (Kalleberg, 1955); S. salar (Keenleyside and Yamamoto, 1962); rainbow trout (S. gairdneri) and brook trout (Salvelinus fontinalis) (Newman, 1956); Dolly Varden (Salvelinus malma), cutthroat trout (Salmo clarki) , and coho (Newman, 1960). Aggression was found to more than triple during the late evening when coho were feeding at the water surface on ovipositing adult insects. A similar rise in aggression and feeding activity during the later evening was observed in rainbow and brook trout in Sagehen Creek by Newman (1956).

Kalleberg (1958) suggested that non-reproductive territoriality has been developed in stream-dwelling salmonids as a mechanism to assure adequate food distribution. Coho have substituted conventional competition for space for direct competition for food but this substitution is by no means complete. Direct competition involving both surface and sub-surface feeding was commonly observed in the pools and may be chiefly associated with a flexible hierarchical organization.

Social stability may be an outcome of spatial fixation, these factors varying in positive relation to one another. The spatial fixation shown by juvenile coho supports the hypothesis that social stability is an important outcome of aggression in fish populations exhibiting

hierarchical and (or) territorial organization. The larger individuals were dominant within the stream systems. Strong fixation to territories was reported by Kalleberg (1958) for juvenile Atlantic salmon.

All available evidence indicates that the right system yielded considerably more coho than did the left one, both in terms of numbers (63 percent) and biomass (78 percent). Random influences do not seem to have played an important role since population trends are quite similar in both systems. I suspect that the dissimilar yields are, at least partly, a reflection of dissimilar levels of food availability.

A study of coho production in three small streams indicated that production was more strongly correlated with the available pool area in late summer than with either riffle area or total stream area (Chapman, 1965). If the carrying capacity of the environment is determined primarily by the spatial demands of the fish, the left system should have held the most coho. It contained 50 percent more pool area and 20 percent more volume than did the right system. Therefore, spatial demands per se cannot be invoked in explanation.

The precise relationships between spatial requirements, aggression, and food availability remain to be worked out. The present results conflict somewhat with those of Chapman (1962) who reported that artificially high food level had no effect on the holding capacity of small, stream aquaria. Perhaps short-term, high levels of feeding are not effective since they do not adequately simulate the natural drift.

The question of what constitutes "environmental capacity to produce coho" is not a simple one and is closely associated with the problem of interpreting volitional residence in the present experiment. Some rather large coho left the systems, and the marked emigrants were generally larger than the average coho entering the traps. Other factors appear to be important in determining residency besides size, aggressive behavior, and their relation to food availability. Chapman (1962) suggested that one possible explanation for emigrant coho larger than many resident fish is an insufficiency of suitable living areas for larger fish in the natural environment. These results emphasize that the ecological interpretation of behavioral studies wherein volitional residence is denied, demands considerable caution.

SUMMARY

1. Two large stream aquaria containing a series of riffles and pools
   are described. Experimental populations of juvenile coho salmon
   were allowed volitional residence in these systems and could
   leave by moving downstream into traps. These populations emerged
   from a simulated redd environment and were subsequently studied
   for four months.

2. Aggressive behavior in these fry was initiated within one week of
   first emergence from the gravel and, within 10 days, coho occupied
   and defended feeding territories well-distributed on the riffles.
   Initial aggression consisted of nipping and chasing but within two
   weeks of emergence aggression also involved threat display.
   Fighting gradually declined with time, becoming quite rare when
   total length reached 45-48 millimeters in early May.

3. A behavior pattern termed "fright huddling" is described that is
   characterized by lack of aggression, physical contact with the bottom
   and with near individuals, and stationary position in both riffle and
   pool environments. Expansion and eventual breakup of the huddle
   occurs as aggressive behavior returns.

4. Individual coho are prone to develop habitual patterns of living
   within the system, involving primary association with a particular

riffle or pool during daylight hours. These patterns are strongly linked with territoriality but the pools form the basic security orientation for all fish in the system.

5. A relatively fixed pattern of distribution persisted throughout the experiment whereby the fry concentrated toward the upstream ends of both aquaria. The numerical gradient was associated with a size gradient, larger fish being farthest upstream.

6. First-emerging fry enjoyed ecological advantages over fry which emerged later. The former fry were larger at a given time and had a greater tendency to remain in the stream aquaria, suggesting the possibility that they have "settler's rights" to the available environment and (or) better feeding opportunity.

7. There was little difference between the two populations in final size of resident fish but the right system held more fish: 35 to 57 coho. The greater biomass in the right system is possibly explained by the fact that this population received more drift organisms of potential value as fish food.

8. The results are discussed with reference to environmental rearing capacity and volitional residence.

THE INFLUENCE OF EMBRYONIC STRESS ON THE
POST-EMERGENCE COMPETITIVE RELATIONS OF FRY

INTRODUCTION

In general, only a small part of the eggs deposited in gravels

by Pacific salmon survive to become emerging fry. Less than ten

percent of the eggs deposited by chum (Oncorhynchus keta), pink

(O. gorbuscha), and sockeye salmon (O. nerka) in streams of British

Columbia and Alaska usually leave the redds as free-swimming fry

(Royce, 1959). Coho salmon tend to spawn in more stable environments

than do pink or chum salmon, and may undergo less mortality in the

gravel but, by termination of the extended freshwater life, only one to

two percent pass seaward as smolts (Neave and Wickett, 1953). In

a recent study, Koski (1966) determined that mean survival to emergence

was 27 percent for coho fry emerging from natural redds in three small

streams.

Conditions within the gravel beds are frequently inimical to high

survival. The oxygen supply to eggs and fry, as determined by the inter-

relationships between gravel permeability, apparent water velocity, and

dissolved oxygen concentration is associated with survival (Wickett,

1954, 1958, 1962; Cooper, 1956; Gangmark and Bakkala, 1960; Phillips

and Campbell, 1961; Coble, 1961; McNeil, 1962a; Ziebell and Mills,

1963; McNeil and Ahnell, 1964). In addition, these interrelationships

are further complicated by spatial and temporal variation (Wickett,
1954; McNeil, 1962b; and others).

The oxygen requirements of salmonid embryos and fry have under-
gone much laboratory investigation (Lindroth, 1942; Hayes, Wilmot,
and Livingstone, 1951; Nikiforov, 1952; Alderdice, Wickett and Brett,
1958; Garside, 1959; Silver, Warren and Doudoroff, 1963; Shumway,
Warren and Doudoroff, 1964; Brannon, 1965). The interplay between
dissolved oxygen concentration and water velocity to determine the
actual supply of oxygen available to the embryo has been elucidated
by Wickett, 1954 and 1962; Silver et al., 1963; and Shumway et al.,
1964. Evidence presented in the latter two papers suggested that the
growth of embryos was restricted at saturation oxygen tensions and
high water velocities. Daykin (1965) used mass transfer theory to pro-
vide a theoretical basis for the dissolved oxygen requirements of fish
eggs relative to water velocity and clarified this relationship consider-
ably.

Decreased oxygen availability induces respiratory stress ultim-
ately leading to developmental abnormalities and embryo mortality when
the compensatory ability of the embryo to reduce its metabolism is ex-
ceeded. Hatching delay, premature hatching, and lengthening of the
hatching period are also induced by lowered oxygen supply. Embryo
size at hatching is decreased and may be accompanied by general de-
bility depending on the degree of stress applied.

In terms of population biology, the survivors of such stressful circumstances are of questionable ecological significance as they must yet migrate successfully out of the gravel and compete with more fortunate fry. In the previous experiment, first-emerging coho fry were ecological dominants in stream aquaria populations. These fry grew more rapidly and were more prone to remain in residence than fry which emerged later, thus suggesting enhancement of their potential reproductive role. Their developmental history prior to emergence suggested no differential oxygen stress, although, within the framework of the experimental design, the success of first-emergents could not be assigned to physiological or psychological factors, nor could the significance of genetic-environmental interaction be weighed.

As oxygen supply has been identified as a primary component of environmental stress operating during the pre-emergence phase of the life history, the relationship between respiratory stress during embryonic development and its possible reflections in terms of post-emergence competitive relations among salmonid fry was examined in detail. Coho salmon eggs were incubated at three levels of dissolved oxygen tension (11, 5, and 3 milligrams per liter) and a common water velocity in an apparatus specifically designed for this type of experiment. Water temperature was increased to compensate for developmental delay, allowing the production of fry attaining the behavioral and physiological

state of emergence simultaneously. The performance of these groups

of fry was recorded under simulated natural conditions in the stream

aquaria previously described and in a holding tank where the fish

were artificially fed. In the stream aquaria, the behavior of the fry

was examined to clarify their ecological performance in terms of

volitional residence, distribution patterns, aggressive behavior,

growth, and net production.

DESCRIPTION OF THE APPARATUS

Incubation Apparatus

A simple and reliable apparatus allowing the production of fry

subjected to various levels of physiological stress induced by lowered

oxygen concentration was developed. The apparatus is illustrated by

the photograph in Figure 6 and in the schematic diagram in Figure 7.

Incoming water enters aerated, constant-head reservoirs (19 liter

Nalgene containers) where desired temperatures are maintained by 2000-

watt stainless steel immersion heaters coupled with thermoregulator

and relay units.

Temperature-regulated water from the reservoirs enters stripping

columns, except when oxygen-saturated water is desired, where dis-

solved oxygen level is controlled by scrubbing with nitrogen gas. The

water is then passed through ball-displacement flowmeters to the embryo

containers.

Figure 6. Front view of the incubation apparatus.
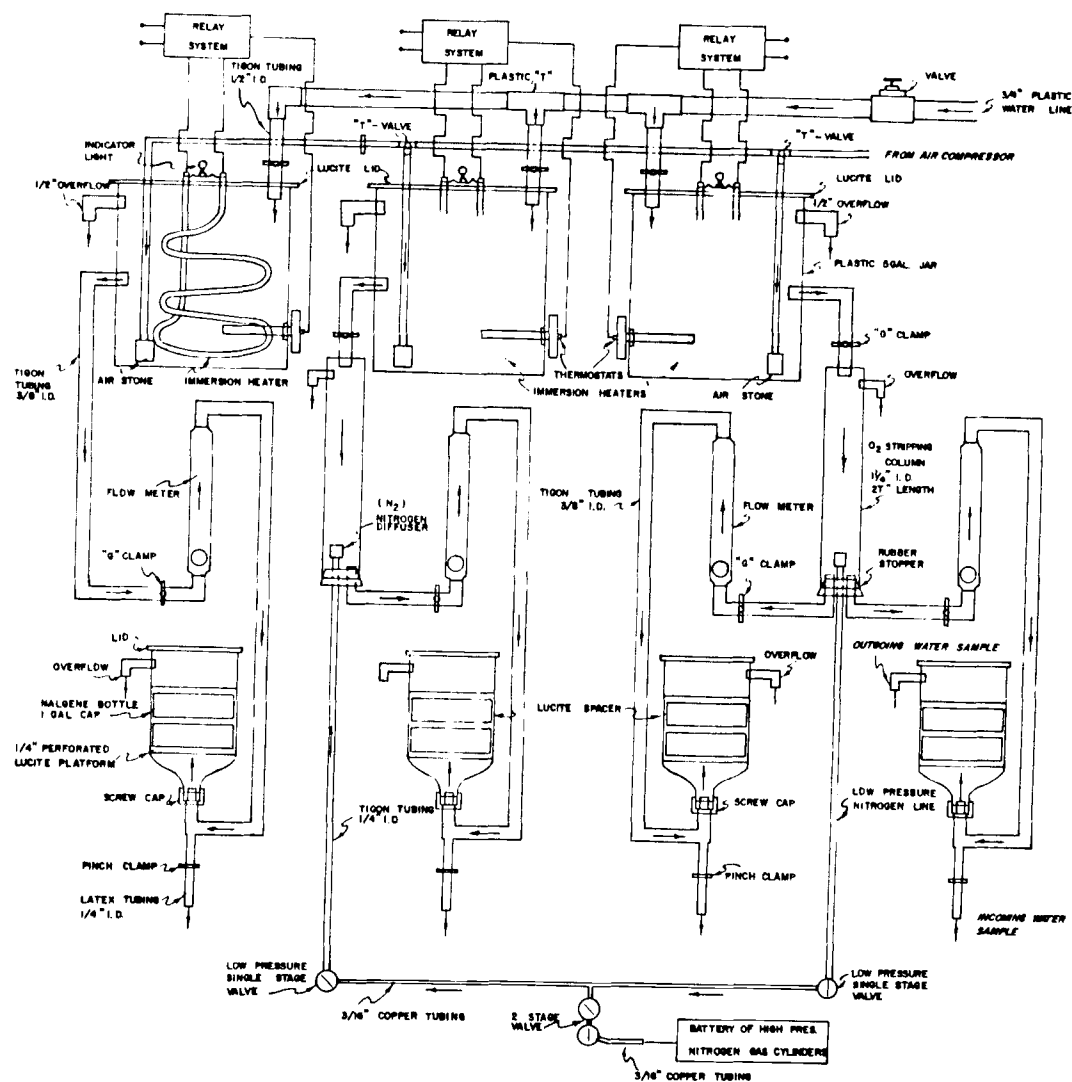
Figure 7. Schematic diagram of the incubation apparatus.

Raschig rings were removed from the stripping columns as less nitrogen was then required to obtain the same oxygen concentrations. The rings increased coalescence of the nitrogen bubbles, thus decreasing the efficiency of stripping action by reducing bubble surface area.

A cut-away diagram of the embryo container is shown in Figure 8. The container is an inverted, 3.8 liter Nalgene bottle with the bottom removed. Platforms for the eggs or fry are 64 mm thick Lucite discs perforated with 400 apertures per plate (porosity of 19 percent). The lowest platform rests on heat-produced indentations in the exterior wall of the container. Two Lucite spacers, 6.4 mm thick and 6.4 cm high, separate the three platforms.

Each platform has a single layer capacity of 200 coho salmon eggs or 400 steelhead trout eggs. Two layers of eggs on the middle platform alone allow rapid detection and removal of dead eggs and fry. When dead eggs or fry need not be removed, capacity can be tripled by using all three platforms. The top platform can be used as a screening lid when fry are maintained to the advance stage, or the outlet may be screened and is readily accessible for cleaning without disturbing eggs on the uppermost platform.

The screw-cap allows easy reverse-flushing of the container without disturbing the eggs when siltation is a problem. Water samples

OVERFLOW

1/4" LUCITE PLATE
5 ¾" DIAMETER

3/16" LUCITE SPACER

etc.

etc.

2 ½"

APERTURE
1/8" DIAMETER

etc.

NALGENE BOTTLE
I GAL. CAP.

RUBBER STOPPER

BOTTLE CAP

PLASTIC REDUCER

TIGON TUBING 3/8" DIAMETER

GLASS "Y"

*INCOMING
WATER*

O₂ SAMPLING POINT
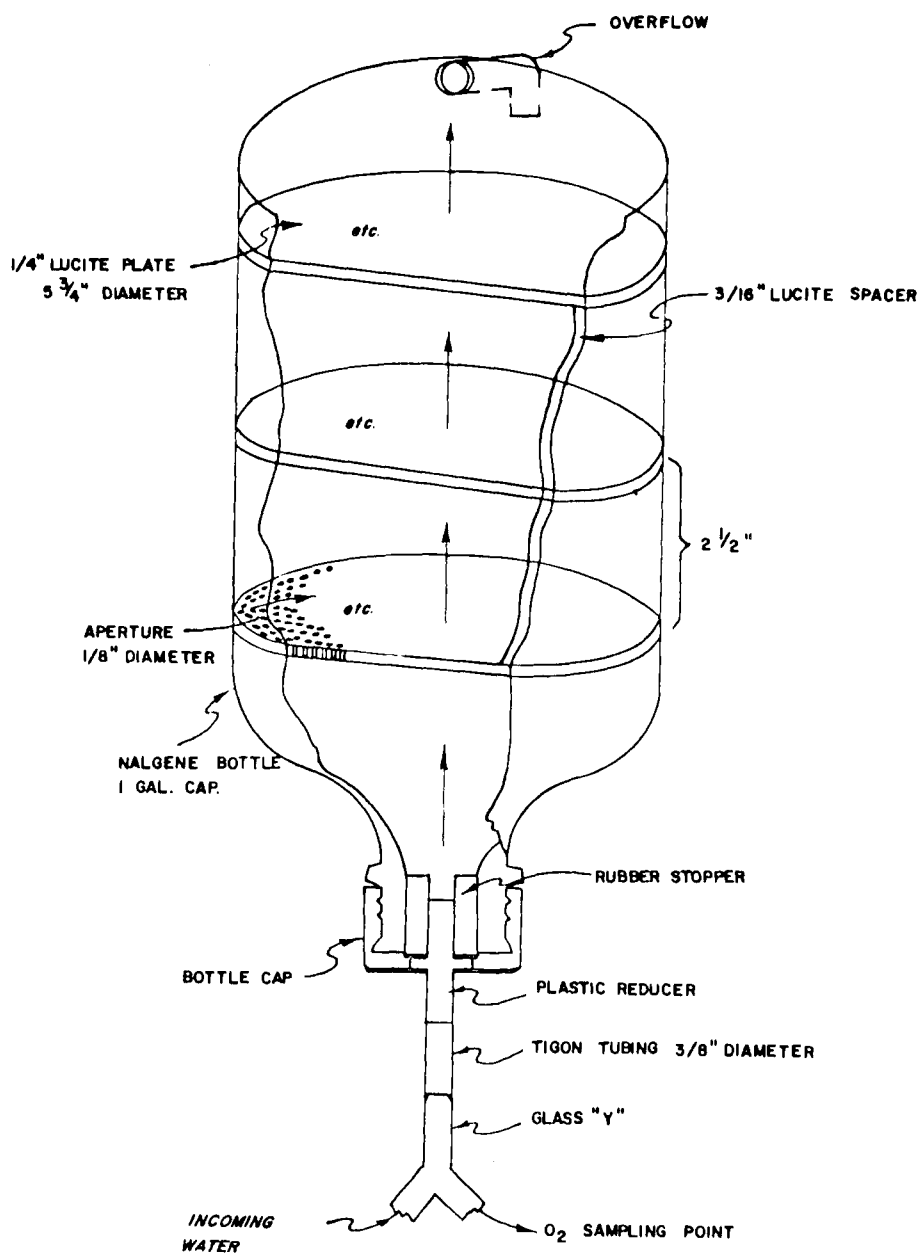
Figure 8. Cut-away diagram of the embryo container.

for the determination of dissolved oxygen content are taken from the 1 cm

latex tubing outlet shown with the pinch clamp attached in Figure 7, and

consist of the water in the bottle neck and beneath the first platform.

Samples of outgoing water are siphoned above the uppermost platform.

All other tubing and fittings are of non-toxic Tygon, rubber, and glass.

Stream Aquaria

The stream aquaria were described in detail in the previous

experiment but subsequent modifications justify further description.

The gravity flow system was replaced by a low-head, high capacity

electrically-powered pump in conjunction with a 3.8 cubic meter,

constant-head reservoir. Intake pipes to the stream aquaria issue

from the base of the reservoir on opposite sides and water flow into the

aquaria is controlled by butterfly valves.

Both aquaria were divided into four environmental units con-

sisting of alternating riffles and pools (Figure 9). Water flow into

the stream aquaria was held constant at 12.4 liters/second and water

depth in the riffles set at 13 cm resulting in velocities of 24 to 27

cm/second.

To discourage avian predators and provide some overhead

cover, both stream aquaria were equipped with collapsible wood

frames covered with fine monofilament herring gillnetting. The net-

ting was overlaid with pieces of black plastic sheeting cut into six
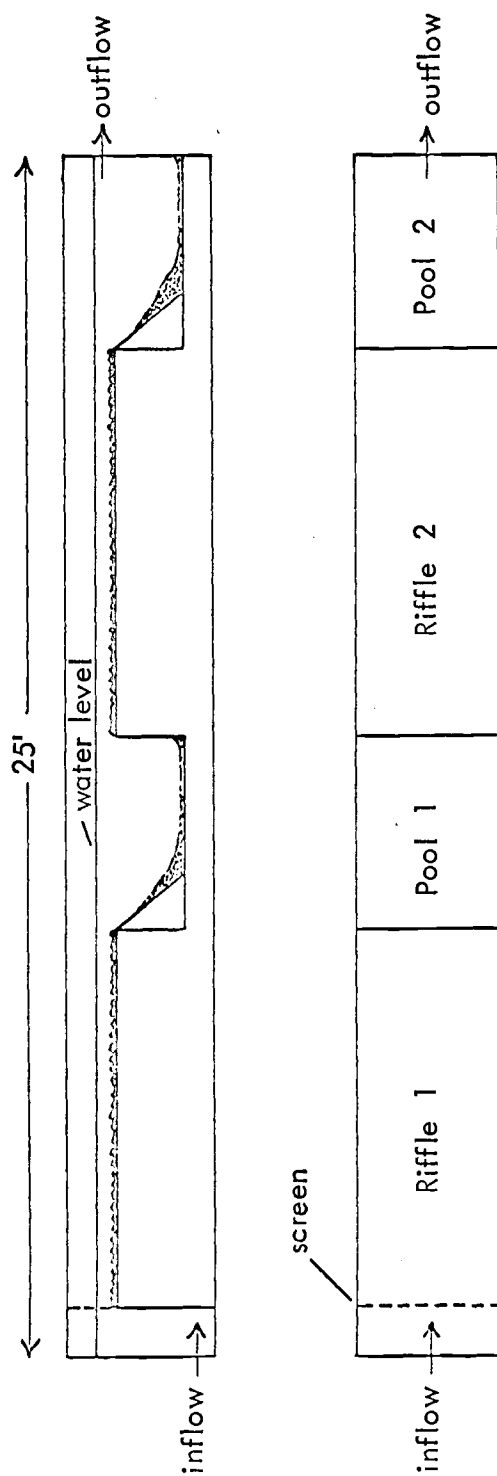
Figure 9. Diagrams showing the side and top aspects of each stream aquarium as they were used for the embryonic stress experiment.

irregular geometric forms and fastened to the netting in an alternating

series so that pairs of figures were no closer than about 1.2 m on

the diagonal and 2.4 m in an upstream-downstream direction. In the

pools, single rectangular strips were fastened at each pool side to

simulate undercut banks. About 25 percent of the overhead area was

covered by plastic in this way.

Holding Tank

Fry were subjected to an artificial feeding regime in a circular

aluminum tank of 860 liters capacity. Flow into the tank was con-

trolled at 38 liters/minute, allowing an exchange rate of 4.4 percent/

minute. An exchange rate of 60.4 percent/minute, or approximately

14 times greater than that in the holding tank was maintained in the

stream aquaria.

Maximum and minimum mean weekly temperatures based on

daily records ranged from 9.1 to 16.8° C and from 7.1 to 13.7° C,

respectively.

METHODS

Incubation History of Eggs and Fry

Fertilized eggs from Fall Creek adults (two males X one female)

were incubated in standard hatchery baskets at the Fall Creek Salmon

Hatchery for fifteen days. They were then transported to the Alsea

Trout Hatchery and installed in the incubation apparatus - 400 eggs

per embryo container, in two layers on the middle platform. Test

conditions were approached gradually over the following 24 hours.

Dead eggs were not removed for the first ten days, but were removed

daily thereafter.

The compensatory increases in water temperature necessary

to overcome the developmental delay due to respiratory stress

accompanying lowered oxygen availability to the embryos incubated

at 5 and 3 mg/liter were calculated from unpublished data of Phillips[1].

The corresponding temperature increases for incubation to yolk ab-

sorption at 5 and 3 mg/liter were calculated by converting the expected

delay in days into temperature units. Slight temperature adjustments

were made during the last two weeks of incubation to rectify the

small difference in state of yolk absorption between the three groups.

Two days after complete hatching, samples of 25 fry were

removed and various size and weight measurements taken. The incu-

bation phase was terminated upon yolk absorption and the fry were

removed to holding baskets. Samples of 30 fry each were then taken

for growth measurements.

[1]Phillips, Robert W., Division of Wildlife Research, Oregon
State Game Commission.

Marking the Fry

Samples of 250 fry from each incubation treatment were separated from the survivors. The saturation fry were marked for future identification by removing the right pelvic fin (RV), using corneal surgical scissors and a dissecting microscope. The left pelvic fin (LV) was removed from the 5 mg/liter fry and the 3 mg/liter fry were not marked. All three groups of fry were anesthetized using tricaine methanesulfonate (M.S. 222-Sandoz), the 3 mg/liter fry being subjected to the same handling procedure as the other two fry groups except for actual removal of the fin.

Following one day of recuperation, two lots of 110 fry each were removed from each of the three groups. Of these, one lot from each treatment (330 fry) was transferred to the left stream aquarium (population I) and the remaining 330 fry were put in the holding tank (population II).

Feeding the Fry

In the holding tank, fry were fed ground beef liver and fry meal at hourly intervals during the day for the first week, five times per day during the subsequent two weeks, and three times per day during the last three weeks of the test period. The fry in the stream aquaria relied entirely upon natural stream foods for nourishment.

In the Stream Aquaria

Daily outmigration records were kept of the fork length (to the nearest 0.1 mm), live weight (to the nearest 0.1 mg), and mark of individual fry. After a one hour holding period to allow recovery from the anesthetic, outmigrants from the left stream aquarium were transferred to the right one. Outmigrants from the right system were similarly processed but released into the Alsea River following recovery.

Distribution patterns were recorded weekly from dawn to dusk at hourly intervals or more frequently. Counts were made in both stream aquaria by pool and riffle and by treatment (mark). Aggressive behavior was recorded similarly, using a systematic time schedule.

After six weeks, population I was removed from the stream aquaria and fork length, weight, and mark recorded for all resident fry. Population II in the holding tank was treated likewise, given one day for recovery, and transferred to the left stream aquarium. The performance of population II in the stream aquaria provided partial replication of the competitive experience.

RESULTS

Performance in the Incubation Apparatus

There were slight fluctuations in water flow, temperature, and dissolved oxygen concentration that could have been reduced further

by using a filtered water supply (Table 7). Developmental delay amounted

to 66 and 168 compensatory temperature units, respectively, for the 5

and 3 mg/liter fry.

Survival of both embryos and fry was directly related to the

degree of stress applied, highest mortalities being associated with

the lowest oxygen tension (Table 8). Most of the mortality occurred

prior to hatching although, at 3 mg/liter, successful hatching was

followed by high mortality of fry, reaching 29 and 36 percent of the

total mortality.

Discounting daily hatching rates of less than five fry, the

spread of the hatching period was least at saturation oxygen tension,

being seven, eight, and ten days, respectively, for the three treatments

(Figure 10). The highest peak of daily hatching rate also occurred

in the saturation group, reaching 135 fry/day.

Size of fry following hatching was greatly reduced at the lowered

oxygen levels as measured in terms of length, volume, and dry weight

(Table 9). Differences in mean length were highly significant $(P_{.01})$.

Volumetric and dry weight relationships indicate a considerably loss

in yolk conversion efficiency at 3 mg/liter. The 5 mg/liter dry weighed

twice as much as the 3 mg/liter fry yet they retained nearly as much

yolk reserve as did the latter fry. The size difference between the

5 mg/liter fry and the saturation fry was only partly due to reduction

TABLE 7. OPERATING LEVELS OF WATER FLOW, OXYGEN CONCENTRA-
TION, AND TEMPERATURE DURING DEVELOPMENT OF COHO
EGGS IN THE INCUBATION APPARATUS, JANUARY 31 TO APRIL
16, 1964. BASED ON DAILY MEASUREMENTS.

Environmental Factor	Treatment		
	Saturation	5 mg/l	3 mg/l
Mean flow rate (ml/min)	518.4[a]	517.0	518.8
range	430-530	449-569	449-550
standard error	6.5	5.5	4.5
Mean dissolved oxygen concentration (mg/liter)	11.45	5.14	3.12
range	11.2-12.5	4.3-6.0	2.6-4.0
standard error	0.11	0.02	0.04
Mean temperature (°C)	8.84	9.56	10.68
range	7.3-9.4	8.8-11.1	10.0-11.7
standard error	0.06	0.06	0.01

[a]equivalent to an apparent velocity of 223 cm/hour, based on cc
flow/hour/cm^2 of cross-sectional area, including both solids
and voids. Actual velocity at the plate pores was about 1180
cm/hour, based on a porosity of 0.19 (19 percent of the plate
area was composed of pores). The mean actual velocity past
the eggs lies between these two values, probably at about one-
half of the pore velocity.

TABLE 8. COHO SALMON EMBRYO AND FRY MORTALITIES IN THE
INCUBATION APPARATUS. VALUES IN PARENTHESES ARE
PERCENTAGES.

Mean Oxygen Concentration (mg/l)	Number of eggs	Embryo Mortality	Fry Mortality	Total Mortality
11.45	429	65 (15.2)	9 (2.1)	74 (17.2)
5.14	405	85 (21.0)	7 (1.7)	92 (22.7)
3.12				
(a)	399	107 (26.8)	61 (15.3)	168 (42.1)
(b)	396	111 (28.0)	46 (11.6)	157 (39.7)

Note: Fry mortality in a hatchery basket control group was one percent,
therefore some mortality in the apparatus may have been due to
handling. The comparatively high fry mortality at 3.12 mg/liter
is taken to be due primarily to environmental stress other than
that due to handling. Unfortunately, egg mortality in the hatchery
basket control group was not recorded.
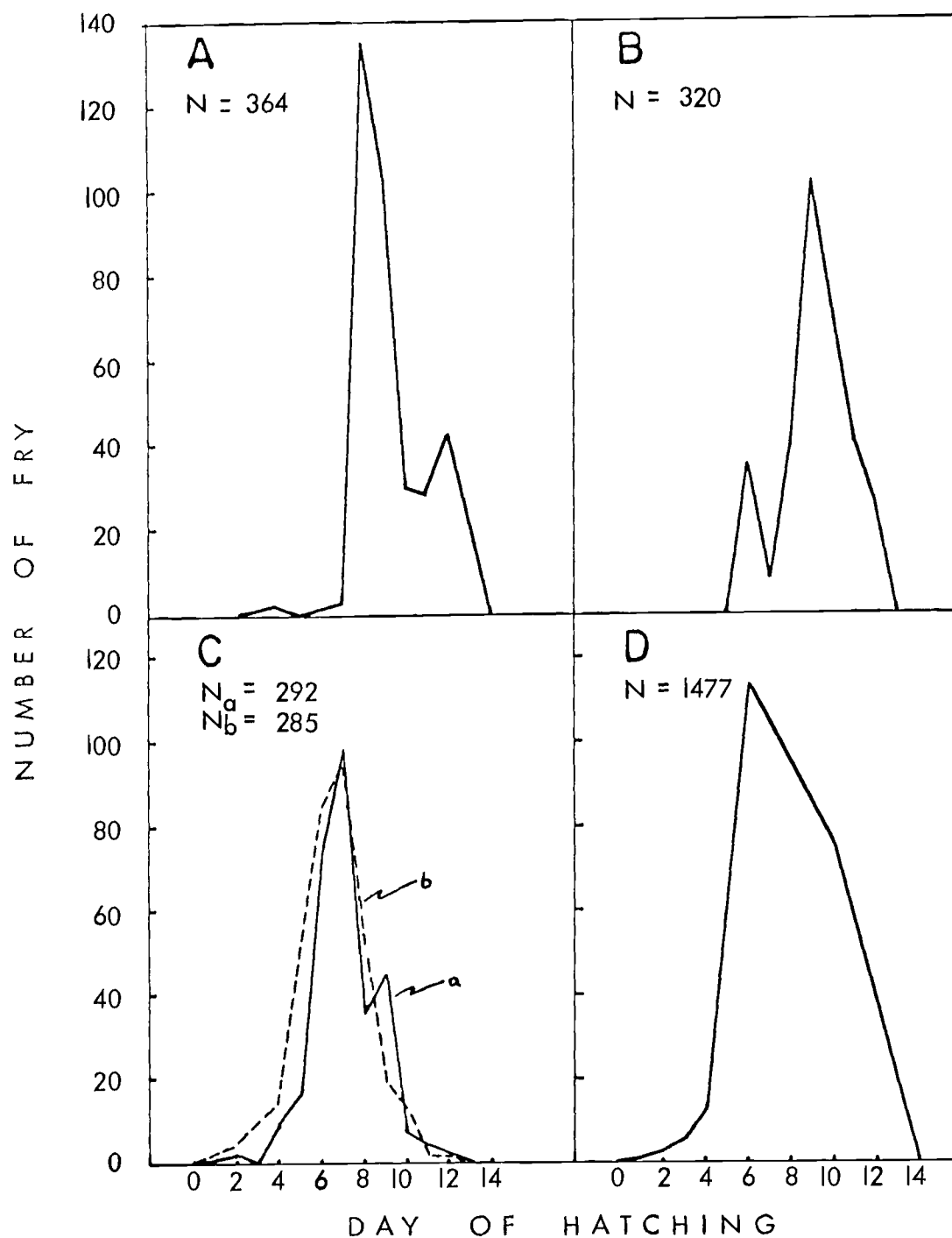
Figure 10. The temporal pattern of hatching. In the incubation apparatus: A - 11.45mg O_2/liter, B - 5.14mg/liter, C - 3.12mg/liter with 2 replicates. D - hatchery basket group at river temperature - hatching began 18 days later than in experimental groups.

TABLE 9. GROWTH STATISTICS AT HATCHING FOR COHO SALMON FRY DEVELOPING AT THREE CONCENTRATIONS OF DISSOLVED OXYGEN. BASED ON SAMPLES OF 25 FRY TAKEN TWO DAYS AFTER COMPLETE HATCHING. VALUES IN PARENTHESES ARE PERCENTAGES.

Fry at Hatching	Dissolved Oxygen Concentration		
	Saturation	5 mg/liter	3 mg/liter
Mean length (mm)	28.12	25.42	22.88
range	24.7 – 29.7	24.6 – 27.1	19.7 – 24.1
standard error	0.27	0.20	0.21
Embryo mean volume (cc)	0.177 (43.0)	0.079 (29.2)	0.49 (20.5)
Yolk mean volume	0.115 (57.0)	0.192 (70.8)	0.190 (79.5)
Total mean volume[a]	0.272 (100)	0.271 (100)	0.239 (100)
Embryo mean dry weight (mg)	14.7 (17.4)	10.1 (10.8)	5.3 (5.9)
Yolk mean dry weight	69.9 (82.6)	83.1 (89.2)	84.8 (94.1)
Total mean dry weight	84.6 (100)	93.2 (100)	90.1 (100)

[a]Mean volume of eggs just prior to hatching was 0.287 cc. Therefore, about 5 percent of egg volume is lost upon hatching at saturation oxygen levels. The 3 mg/liter fry hatched from eggs that lost 16.7 percent of volume.

in yolk conversion efficiency in the former group. Both yolk and total

weights of the 5 mg/liter fry were greater than those of the saturation

fry although the 5 mg/liter fry weighed less than the saturation fry.

Apparently, potential growth to yolk absorption of the 5 mg/liter

fry remained high as a consequence of lowered energy expenditure up

to the time of hatching accompanying reduced conversion of yolk

supply.

Upon absorption of the yolk supply, group differences in

mean length all remained highly significant $(P_{.01})$ although the relative

size difference between the saturation and 5 mg/liter fry had become

markedly reduced (Table 10). The 3 mg/liter fry were much smaller,

there being nearly 5 mm difference in body length between them and

the saturation fry. Comparative length-weight relations expressed as

"K" values revealed that the NM (3 mg/liter) coho were in the best

condition and the RV (saturation) fry in the worst, although the difference

between the RV and LV (5 mg/liter) fry was not great. Yolk conversion

efficiency was high in all three groups of fry but highest for the saturation

fry.

Outmigration and Growth in the Stream Aquaria - Population I

Outmigration

After a five day familiarization period, the outlet screen was

removed from the left stream aquarium and daily outmigration recorded.

TABLE 10. GROWTH STATISTICS AT YOLK ABSORPTION FOR COHO FRY DEVELOPING AT THREE CONCENTRATIONS OF DISSOLVED OXYGEN BASED ON SAMPLES OF 30 FRY. VALUES IN PARENTHESES ARE PERCENTAGES.

Fry at Emergence	Dissolved Oxygen Concentration		
	Saturation	5 mg/liter	3 mg/liter
Mean length (mm)	37.77	37.02	33.11
range	36.0 – 39.7	35.8 – 38.6	30.8–34.7
standard error	0.18	0.14	0.21
Mean wet weight (mg)	436.0	417.4	326.9
Mean dry weight	81.0	79.4	76.0
Percent moisture loss	81.4	81.0	76.8
Dry weight loss[a]	3.6 (5.2)	13.8 (16.6)	14.1 (16.6)
Yolk conversion efficiency	0.948	0.834	0.834
Coefficient of condition (K)	0.809	0.823	0.901

[a] From hatching to time of yolk absorption. Values in parentheses are percentages of yolk dry weight at hatching.

Trends in outmigration were soon established for the three stress treatments and remained stable until May 19 when a sudden acceleration in the outmigration of RV coho took place (Figure 11). Sixteen RV fish left in three days then a new trend was established whereby outmigration consisted primarily of RV coho. The LV and NM fish were little affected, outmigration of LV fish increasing but slightly during the same three day period. The sudden increase in outmigration is attributed to reduction in flow resulting from an interruption in electrical service for two hours. During this time, the gravity flow system was used and provided about 20 percent of the normal flow.

A total of 113 coho entered the trap from the left aquarium and was transferred to the right aquarium. Few fish left this system (Figure 11) illustrating that the environmental needs of outmigrants from the left system were usually satisfied. Only three of eighty-seven (3.4 percent) coho, all NM fish, had left the right stream aquarium by May 21, when a similar increase in outmigration took place that predominantly involved RV and LV coho. These fish were probably from the same group which were disturbed by flow reduction in the left aquarium. A three day delay in its reflection in the right system suggests that flow reduction had not greatly disturbed resident coho here, and that the handling procedure accorded emigrants from the left system may have inhibited, or at least delayed, continued outmigration.
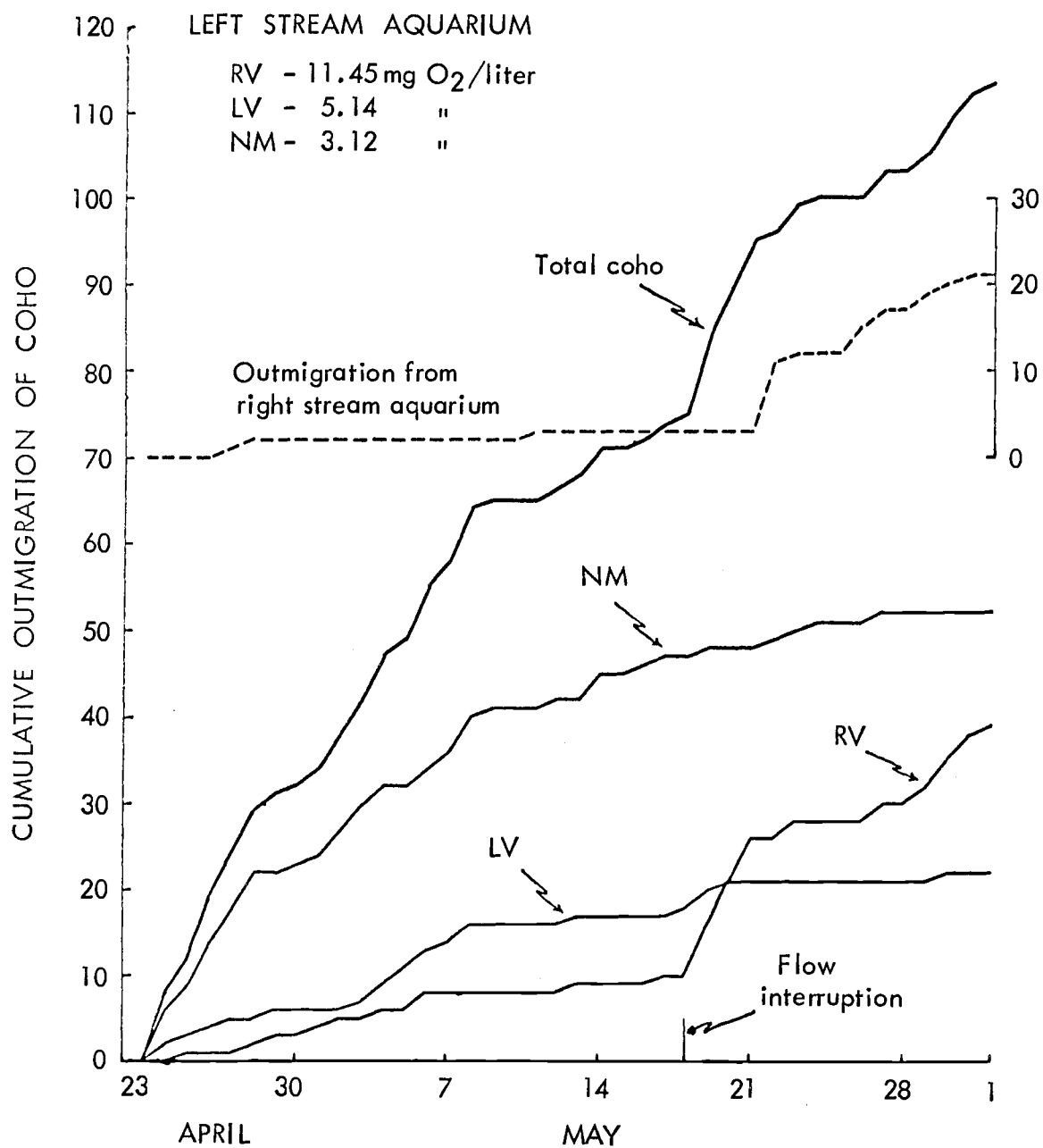
Figure 11. Outmigration from the stream aquaria - population I, April 23 to June 1, 1964.

The outmigrant biomass trends in the left system reflected the numerical trends and served to emphasize the effect of flow disturbance on the RV coho. These fish composed nearly 62 percent of the total biomass lost from the system.

Outlet traps were checked twice daily, usually at sunrise and sunset. More coho entered the traps during daylight hours than at night but, on an hourly basis, there was no significant difference. Fifty-eight percent of the outmigration took place during the day, and daylight hours constituted about 60 percent of the 24-hour cycle.

This phase of the experiment was cut short on June 2 due to complete cessation of flow for 20 minutes while repairs were made in the water collection system. When the flow ceased, many coho began searching behavior and swam downstream into pool 2. A large number of fish swam upstream and began jumping vigorously at the screens when flow was resumed. Fourteen coho fled into the left trap but none entered the right one. These trapped fish were put into pool 1 without delay. That evening, 11 coho were found in the left trap and 15 in the right one, prompting removal of population I from the stream aquaria, two weeks prematurely.

Terminal Population

The 213 fish remaining in the left stream aquarium amounted to 65 percent of their initial number (Table 11). There were more

TABLE 11. RESIDENCE, EMIGRATION AND GROWTH OF POPULATION I IN
THE LEFT STREAM AQUARIUM, APRIL 18 to JUNE 1, 1964.
VALUES IN PARENTHESES ARE PERCENTAGES.

	Fry Group		
	RV	LV	NM
Initial population	110	110	110
Total fish		330	
Terminal population	71 (33.3)	88 (41.3)	54 (25.4)
Total fish		213	
Number of emigrants	39 (34.5)	22 (19.5)	52 (46.0)
Total		113	
Number of missing fish	0	0	4
Initial mean length (mm)[a]	37.77	37.02	33.11
Standard error	0.18	0.14	0.21
Terminal mean length	64.73	60.63	48.02
Standard error	0.35	0.30	0.61
Percent increase	71.4	63.8	45.0
Initial mean weight (gm)	0.4360	0.4174	0.3269
Terminal mean weight	3.4636	2.7081	1.2012
Standard error	0.0686	0.0499	0.0565
Percent increase	694.4	548.8	267.5
Coefficient of condition (K) Initial	0.809	0.823	0.901
Terminal	1.277	1.215	1.085
Emigrant biomass (gm)	61.6	18.0	19.9
Net production (gm)	307.5	210.4	48.8

[a]Initial measurements were based on samples of 30 fry each. All fry
were weighed and measured at termination.

resident LV coho (41.3 percent) than RV coho (33.3 percent) and fewest

NM coho (25.4 percent). However, had the RV fish not responded as

they did to the interruption of flow, only about 14 RV fish would have

left the system and the terminal number of RV coho (96 fish) would

have been 40.3 percent in comparison to 32.0 percent for the LV

group. Four coho, all NM fish were unaccounted for and presumed

to be the victims of cannibalism.

The initial size differences among the three groups of fry were

considerably amplified in terms of both length and weight. The size

disparity between RV and LV coho increased from 0.75 mm to 4.10 mm,

the RV fish growing faster, in terms of relative percentage increase

in length and weight, than the other two groups. The significance

of this performance is considerably enhanced when one considers

that relative size increase is greater in smaller individuals under

conditions of equal nutrition. Condition factors (K) followed the same

ranking order as was obtained for size and weight. Relative to initial

values, the condition of the RV coho increased but that of the LV and

NM groups decreased.

In the right stream aquarium, the same rank order of size was

maintained although the disparities in size were greatly reduced

(Table 12). On the average, LV and NM coho were larger than those

remaining resident in the left system. Relative growth in length and

TABLE 12. RESIDENCE, EMIGRATION AND GROWTH OF POPULATION I
IN THE RIGHT STREAM AQUARIUM (LEFT STREAM AQUARIUM
EMIGRANTS), APRIL 18 TO JUNE 1, 1964. VALUES IN
PARENTHESES ARE PERCENTAGES.

	Fry Group		
	RV	LV	NM
Input population	39 (34.5)	22 (19.5)	52 (46.0)
Total fish		113	
Terminal population	21 (26.9)	17 (21.8)	40 (51.3)
Total fish		78	
Number of emigrants	18 (54.5)	5 (15.2)	10 (30.3)
Total		33	
Number of missing fish	0	0	2
Initial mean length (mm)[a]	37.77	37.02	33.11
Standard error	0.18	0.14	0.21
Terminal mean length	64.80	63.41	55.46
Standard error	0.60	1.02	0.66
Percent increase	71.6	71.3	67.5
Initial mean weight (gm)	0.4360	0.4174	0.3269
Terminal mean weight	3.4504	3.2949	2.0588
Standard error	0.1297	0.1779	0.8641
Percent increase	691.4	689.4	529.8
Coefficient of condition (K)			
Initial	0.809	0.823	0.901
Terminal	1.268	1.292	1.207
Input biomass (gm)	61.6037	18.0414	19.9395
Emigrant biomass	33.3	5.7	4.8
Net production (gm)	44.1	43.7	67.2

[a] Initial values are those for the left system. (Table 11).

weight were nearly equal for the RV and LV coho, the NM fish following

closely behind. Condition factors increased in all three groups,

LV and NM values being higher than in the left system, and the LV

fish were in better condition than were the RV coho in the left system.

Two fish, both NM coho, were missing and presumed to be the vic-

tims of cannibalism.

As these results strongly suggest a ranking response to

a limited food supply, the growth data were standardized, based

on the growth of the RV coho. A competitive stress index was cal-

culated where

$$\text{competitive stress index} = \frac{\text{RV percentage weight gain}}{\text{mark percentage weight gain}}$$

In these terms, the stress index in the left system was 1.27 for LV

coho and 2.60 for NM coho. In the right system, there was no

difference between RV and LV fish (1.00 in both cases) and the stress

index for NM coho was halved to 1.31.

The biomass relations of the three groups of coho were a

function of both numbers and growth in the two stream aquaria. Out-

flow of biomass from the left system remained fairly smooth until the

flow disturbance on May 21. Thereafter, it increased sharply and in-

volved primarily the RV fish, the total biomass loss being 99.6 grams.

Despite this loss, the terminal RV biomass slightly exceeded that of

the LV coho and composed nearly 45 percent (245.9 gm) of the total

terminal biomass in the left system. The NM coho made up only 11.8 percent of the sum total of nearly 550 grams.

In the right stream aquarium, most of the biomass outflow seemed to involve recent outmigrants from the left system responding to the flow distrubance and RV fish made up 76 percent of the 43.8 grams of biomass lost. The 210.8 grams of terminal biomass was composed of 34.4 percent RV coho, 26.6 percent LV coho, and 39.1 percent NM coho.

Net production in the systems was calculated for each group of fish by subtracting the initial or input biomass from the sum of the terminal and emigrant biomasses (Table 11 and Table 12). Net production is the total growth in the population and is, therefore, the outcome of growth rate, number of fish, and time in residence. Net production values are made slightly conservative by the loss of a few fish from each group of coho. Total net production amounted to 518.8 grams in the left system and 155.0 grams in the right one. Production was distributed as follows: RV coho - 50.0 and 28.5 percent, LV coho - 40.6 and 28.2 percent, and NM coho - 9.4 and 43.4 percent, respectively, in the left and right system.

A production index using NM production as a base, was derived to facilitate comparison where

$$\text{production index} = \frac{\text{mark percentage gain in biomass}}{\text{NM percentage gain in biomass,}}$$

and where

$$\text{percentage gain in biomass} = \frac{\text{net production in grams}}{\text{initial or input biomass in grams}} \times 100$$

for each group of fry. In the left system, the RV group elaborated four

times as much tissue as did the NM group, the production index being

3.98 for the RV and 3.37 for the LV coho. The situation was almost

reversed in the right system where NM production was nearly five

times that of the RV value, due to the large-scale outmigration of

NM fish from the left aquarium early in the experiment and greatly

enhanced growth shown by these outmigrants following transfer to the

right system. Here, the production index was 0.21 for the RV fish and

0.72 for the LV fish.

Growth of Population II in the Holding Tank

Due to an overflowing drain, a number of fry escaped into a

small holding pond. Forty-seven were recaptured on the same day

and nine were observed still at large. From their size, the latter

fry were most likely RV and LV fish. Four dead NM fry were removed

from the tank and the other 20 NM fry unaccounted for are assumed to

have escaped or been eaten by larger coho in the tank.

Fish reared in the holding tank (population II) and fed to "excess"

on a hatchery diet did not grow as large as their counterparts (population

I) in the stream aquaria, where RV and LV coho gained about twice as

much weight. Neither was there a significant difference among the

three groups of coho in percentage increase in length, the range being 34.6 to 36.1 percent (Table 13). This is in stark contrast to the situation in the stream aquaria where these values ranged from 71.4 (RV) to 45.0 (NM) percent.

Growth in length while in the tank suggested that competition for food was prevented by excess feeding. However, there was a gradient in percentage weight increase but one far weaker than that shown by population I in the left stream aquarium. Terminal mean weights were significantly different ($P_{<.025}$). Also, the condition of all three groups decreased in the holding tank.

The near-equal relative length increases for the groups of coho in the tank indicates that food competition occurred late in the experiment. Premature reduction in frequency of feeding apparently operated to the advantage of the larger fish. The competitive stress index was 1.15 for the LV coho and 1.45 for the NM fish, based on percentage weight increase.

Outmigration and Growth in the Stream Aquaria - Population II

Outmigration

Following recovery from handling, the surviving members of population II in the holding tank were put in the left stream aquarium. The downstream screen was removed to permit outmigration after a five day familiarization period.

TABLE 13. INITIAL[a] AND TERMINAL STATISTICS FOR POPULATION II MAINTAINED ON A HATCHERY DIET, APRIL 18 TO JUNE 1, 1964.

	Fry Group		
	RV	LV	NM
Initial population	110	110	110
Total fish		330	
Terminal population	107	103	86
Total fish		296	
Initial mean length (mm)	37.77	37.02	33.11
Standard error	0.18	0.14	0.21
Terminal mean length	51.39	49.84	44.89
Standard error	0.20	0.27	0.24
Percent increase	36.1	34.6	35.6
Initial mean weight (gm)	0.4360	0.4174	0.3269
Terminal mean weight	1.4007	1.2177	0.8262
Standard error	0.0846	0.0221	0.0015
Percent increase	221.3	191.7	152.7
Coefficient of condition (K)			
Initial	0.809	0.823	0.901
Terminal	1.032	·0.984	0.913

[a]Based on samples of 30 fish. All fish were weighed and measured at termination.

Extensive outmigration declined rapidly within three days to a low level that lasted for the rest of the experiment (Figure 12). During the first 5 days, 85 coho entered the left trap and were transferred to the right system. Only ten of these first occupants in the right system moved into the trap, and subsequent outmigration rate remained consistently low. Relative to their initial numbers, outmigration rate was highest for the NM coho and lowest for the RV coho. At termination, total emigrant numbers were equal (46 coho per group), being 49, 52, and 67 percent of initial numbers for the RV, LV, and NM coho, respectively.

Terminal Population

At termination, the left system was dominated numerically by the RV fish although the fate of 13 coho remains unknown (Table 14). The disproportionately high number of missing NM fish suggests cannibalism. In the right stream aquarium, four RV and three LV coho are thought to have escaped from the trap (Table 15).

Population II responded much in the same way in the stream aquaria as did population I. Initial size differences between the three groups of fry were considerably amplified despite their larger initial sizes when put in the stream systems. As in population I, emigrants were able to increase their growth rates in the right system and thus exceed the size of non-emigrant cohorts remaining in the left aquarium
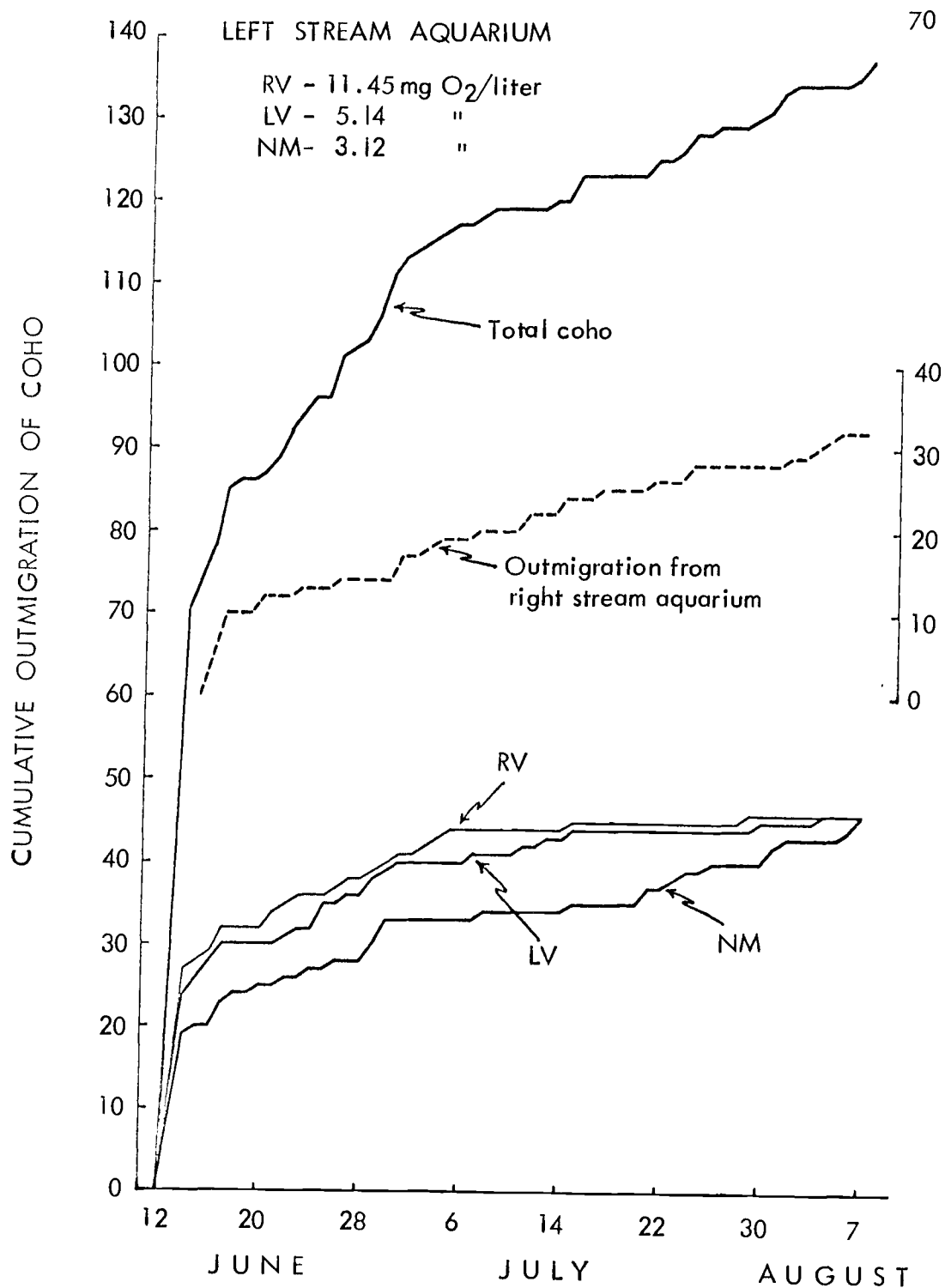
Figure 12. Outmigration from the stream aquaria - population II, June 12 to August 7, 1964.

TABLE 14. RESIDENCE, EMIGRATION AND GROWTH OF POPULATION II
IN THE LEFT STREAM AQUARIUM, JUNE 6 TO AUGUST 7, 1964.
VALUES IN PARENTHESES ARE PERCENTAGES. ALL FISH WERE
WEIGHED AND MEASURED.

	Fry Group		
	RV	LV	NM
Initial population	95 (37.7)	88 (34.9)	69 (27.4)
Total fish		252	
Terminal population	47 (46.5)	40 (39.6)	14 (13.9)
Total fish			
Number of emigrants	46	46	46
Total		138	
Number of missing fish	2	2	9
Initial mean length (mm)	51.73	50.15	44.84
Standard error	0.27	0.28	0.29
Terminal mean length	74.19	64.10	52.67
Standard error	1.51	1.22	1.07
Percent increase	43.4	27.8	17.5
Initial mean weight (gm)	1.4417	1.2400	0.8216
Standard error	0.0943	0.0214	0.0167
Terminal mean weight	4.9324	2.9209	1.5328
Standard error	0.3790	0.2381	0.0936
Percent increase	242.1	135.6	86.6
Coefficient of condition (K)			
Initial	1.042	0.983	0.911
Terminal	1.208	1.109	1.049
Emigrant biomass (gm)	78.2	75.7	50.1
Net production (gm)	173.0	83.4	14.9

TABLE 15. RESIDENCE, EMIGRATION AND GROWTH OF POPULATION II
IN THE RIGHT STREAM AQUARIUM (LEFT STREAM AQUARIUM
EMIGRANTS), JUNE 13 TO AUGUST 7, 1964. VALUES IN
PARENTHESES ARE PERCENTAGES. ALL FISH WERE WEIGHED
AND MEASURED.

	Fry Group		
	RV	LV	NM
Input population	45 (34.9)	41 (31.8)	43 (33.3)
Total fish		129	
Terminal population	28 (30.4)	30 (32.6)	33 (35.9)
Total fish		92	
Number of emigrants	14 (43.8)	8 (25.0)	10 (31.3)
Total		32	
Number of missing fish	4	3	0
Initial mean length (mm)[a]	51.73	50.15	44.84
Standard error	0.27	0.28	0.29
Terminal mean length	74.30	69.56	55.94
Standard error	1.73	1.64	0.69
Percent increase	43.6	38.7	24.8
Initial mean weight (gm)[a]	1.4417	1.2400	0.8216
Standard error	0.0943	0.0214	0.0167
Terminal mean weight	4.8717	3.9161	1.7765
Standard error	0.3981	0.3266	0.0784
Percent increase	237.9	215.8	116.2
Coefficient of condition (K)			
Initial	1.042	0.983	0.911
Terminal	1.188	1.164	1.105
Input biomass (gm)	76.6962	68.3797	46.0604
Emigrant biomass	26.6	15.4	14.0
Net production	81.5	64.5	26.5

[a] Initial values are those for the left system.

(Tables 14 and 15). Initial relative differences between the three groups of fry in length and weight were larger in population II than in population I, and were more extensively amplified with time.

Condition factors increased in all three groups of coho, were highest for the RV coho and lowest for the NM coho in both systems. They were lower than the corresponding values for population I, in part due to the initially lower values for population II when put in the left stream aquarium. As in population I, the LV and NM coho experienced more severe competitive stress in the left system than in the right one, the competitive stress index values being 1.79 (LV) and 2.80 (NM) as compared to 1.10 and 2.05 in the right system. However, greater stress was encountered in both stream aquaria by population II than by population I.

Emigrant biomass trends paralleled the numerical trends, reflecting the size differences among the three groups of fish, and amounting to 203.9 grams and 56.0 grams, respectively, for the left and right systems. Terminal biomass in the left aquarium (370.1 grams) was composed of 62.6 percent RV, 31.6 percent LV, and 5.8 percent NM coho. In the right system, RV coho accounted for 42.8 percent of the terminal biomass (307.6 grams), LV coho - 38.2 percent, and NM coho -19.1 percent.

Net production amounted to 271.3 grams in the left system and 172.5 grams in the right one. Production was distributed as follows: RV coho - 63.8 and 47.2 percent, LV coho - 30.7 and 37.4 percent, and NM coho - 5.5 and 15.4 percent, respectively, in the left and right systems. Production index values were 4.80 for the RV coho and 2.91 for LV coho in the left system, and 1.84 and 1.64 in the right one. More than five times as much tissue was elaborated in the left aquarium by population I than by population II but the production index values were very similar in both populations. In the right system, production index values were higher in population II than in population I, reflecting the more intense competitive stress in population II noted previously.

Distribution in the Stream Aquaria

General Distribution

As in the previous experiment, juvenile coho adopted a rather fixed distributional pattern in the stream aquaria, concentrating toward the upstream ends. In both populations I and II, the first riffles were dominated by the RV coho, which also dominated riffle 2 of the right system in population II. The majority of fish occupied pool 1 under all circumstances (Figures 13 and 14).

I hypothesized that no significant difference in distribution existed between the three groups of coho, and that, on the average
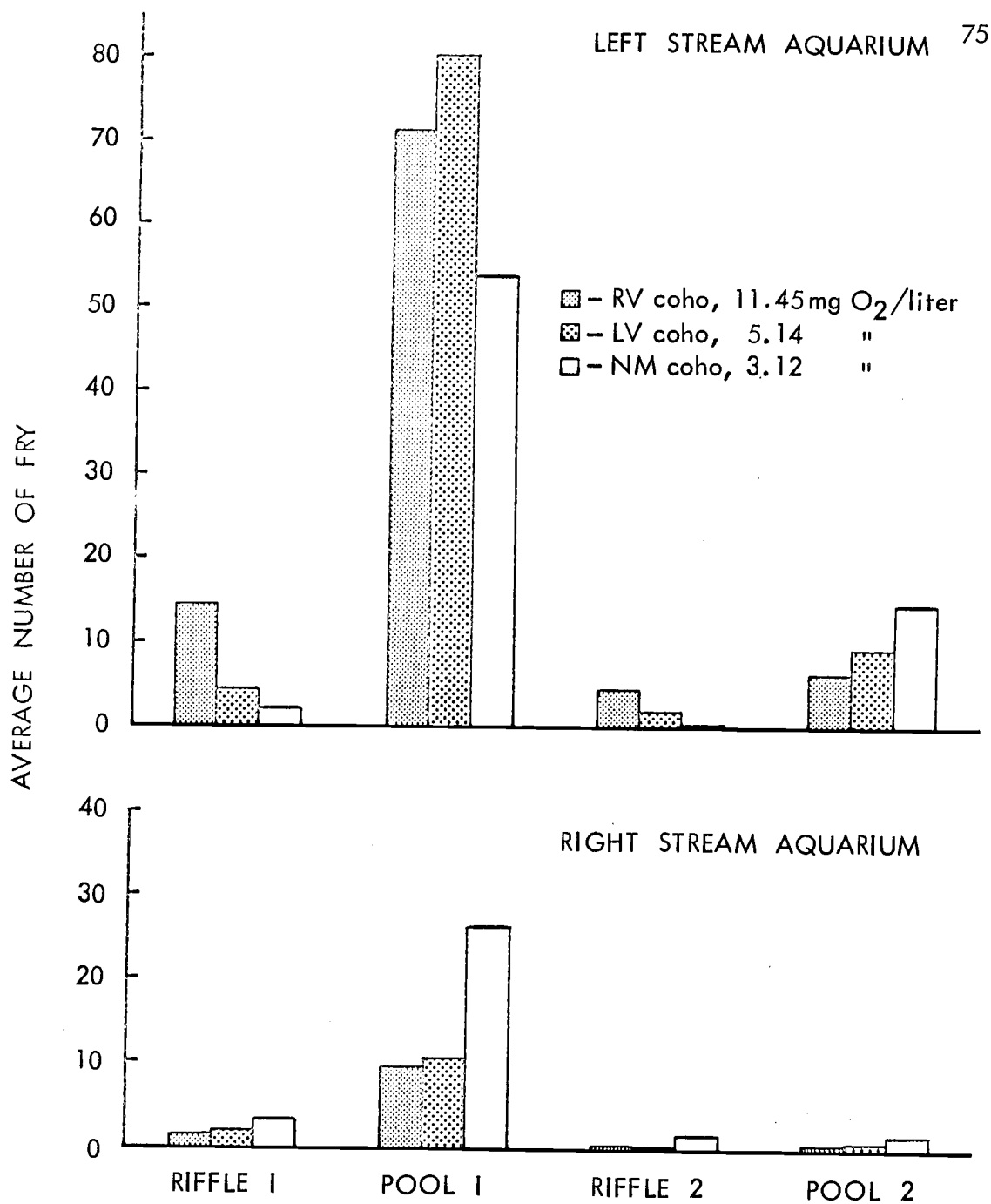
Figure 13. Mean density of coho in each pool and riffle, recorded by treatment, for population I between April 23 and May 31, 1964.
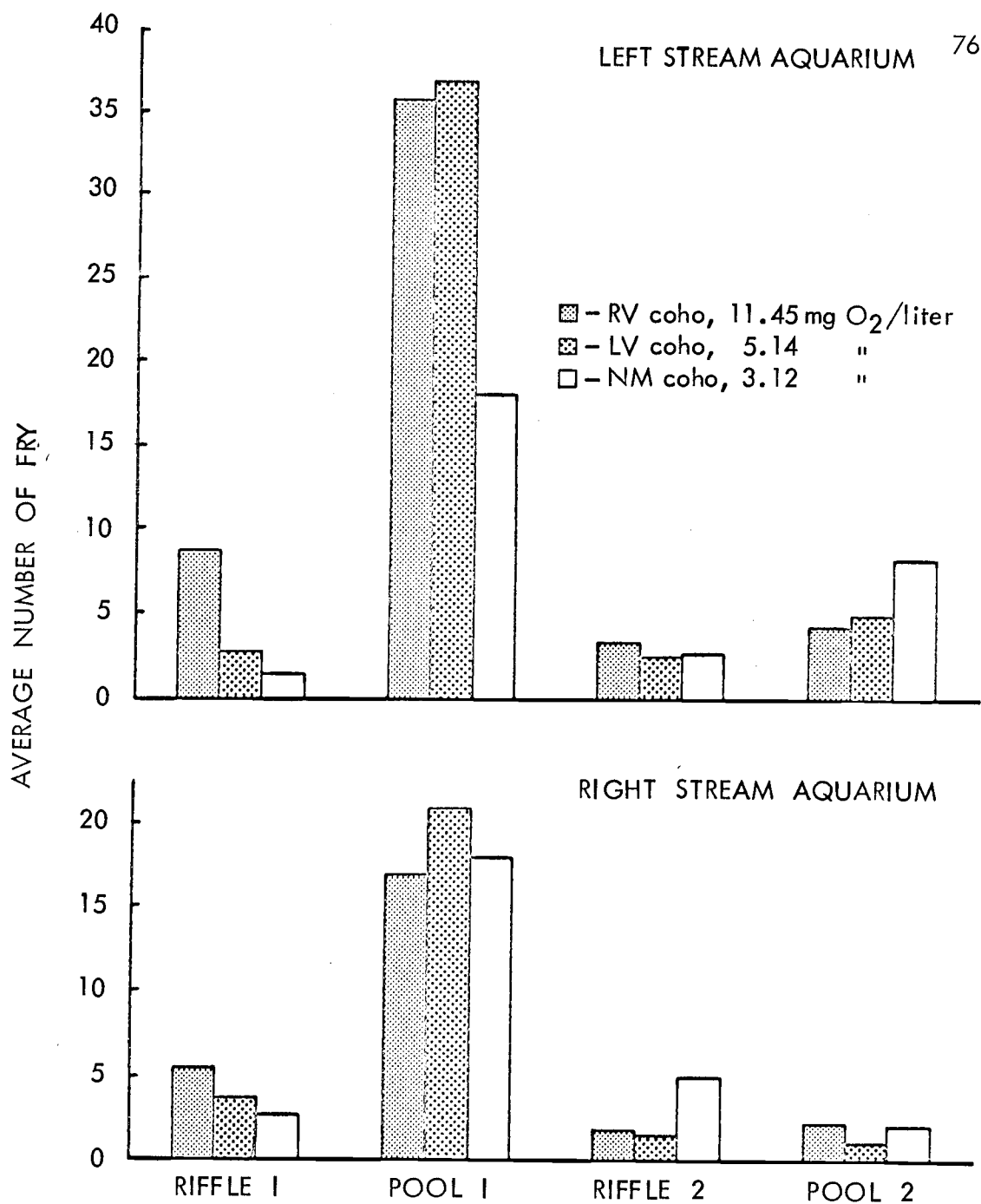
Figure 14. Mean density of coho in each pool and riffle, recorded by treatment, for population II between June 12 and July 28, 1964.

the three groups should be represented in any observed number of fish

in accordance with the total number of fish from each group present

in the system. The differences in distribution in three of the four

environmental units, based on hourly counts throughout the day, were

expressed as percentage deviations from the expected percentage

composition values for each group. Expected values were derived

from the initial population numbers and the outmigration records,

corrected for the unaccountable loss of fish in the systems by spread-

ing these losses over the appropriate periods of time. These per-

centage deviations for populations I and II are compiled in Appendices

1 and 2, and shown in Figures 15 and 16. In general, the weekly

deviations support the overall differences in density already noted

between the three groups of coho (Figures 13 and 14) and emphasize

the disproportional representation of the groups in various parts of

the stream aquaria.

Territorial and Hierarchical Organization

Coho set up and defended feeding territories, forming a

territorial mosaic in both riffles and pools. Territories were more

sharply defined in the riffles, where they were often accompanied by

higher intensity of aggression. Riffle-invading fish typically pursued

a zig-zag course as they advanced upstream, violating the ter-

ritorial boundaries of resident coho. Residents responded very
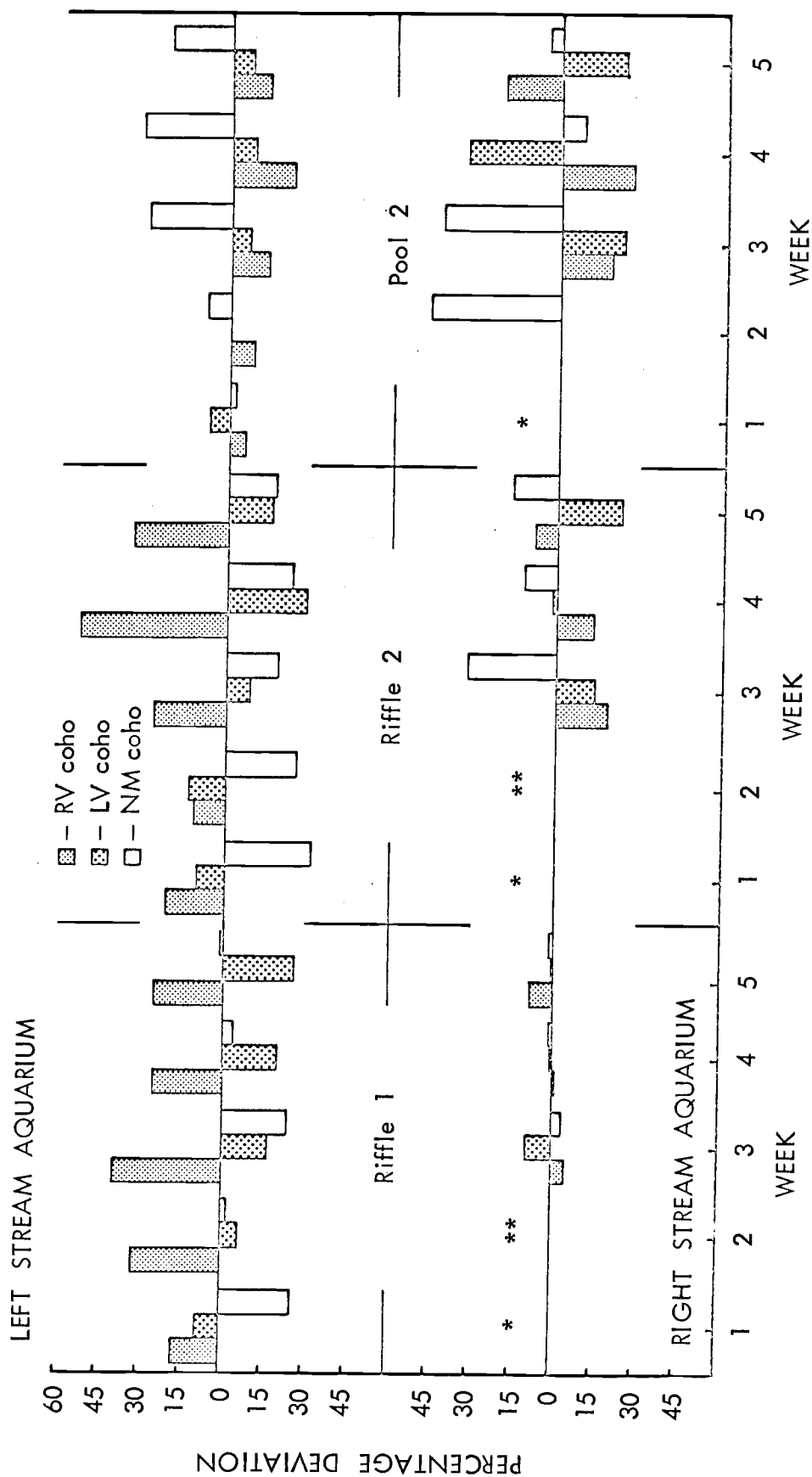
Figure 15. Percentage deviations from the expected percentage composition values for each of the three coho groups based on visual counts in the pools and riffles shown – population I, April 29 to May 26, 1964. Symbols as follows: * – all 27 coho residing in pool 1; ** – 45 of 46 coho residing in pool 1.
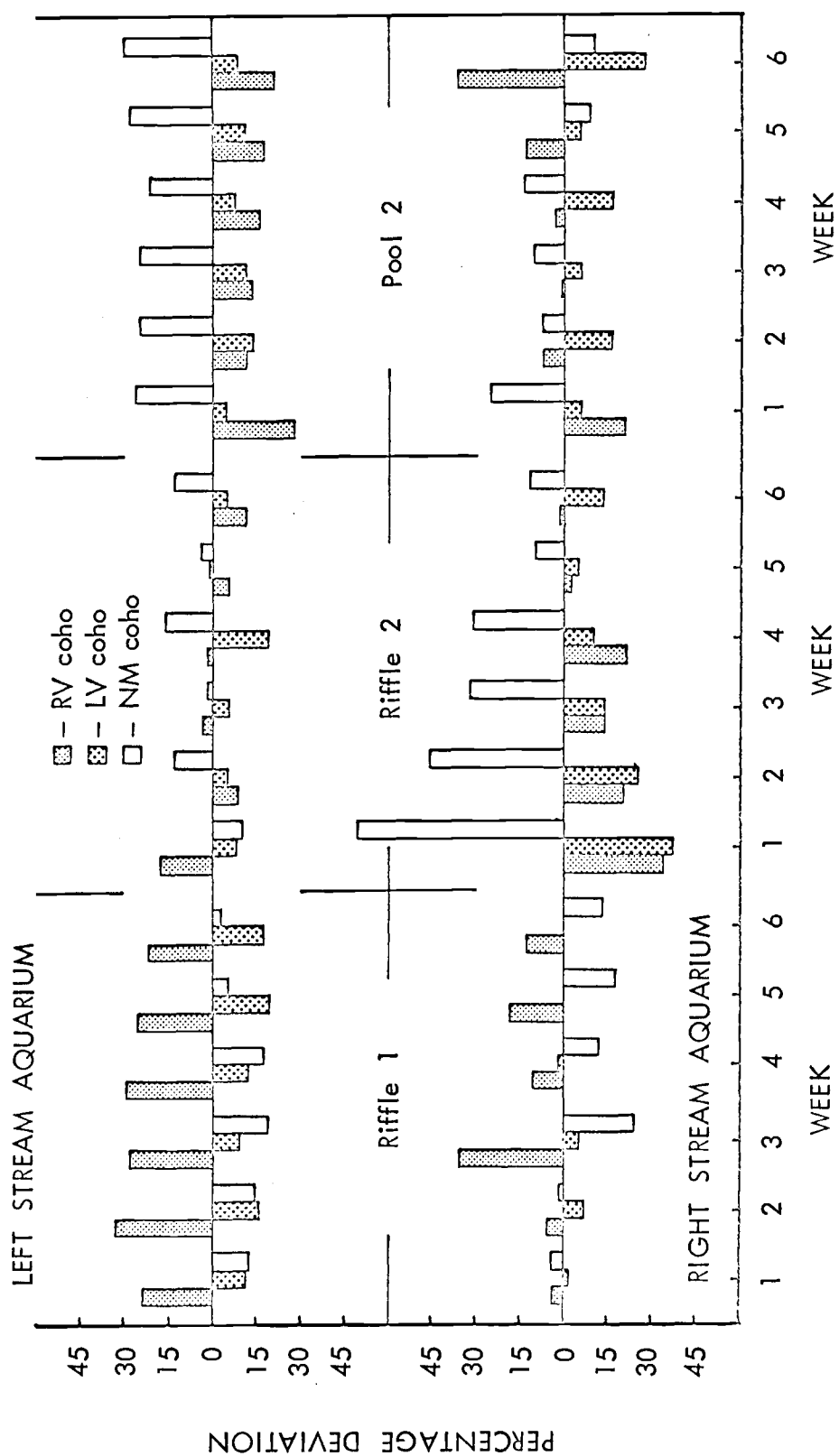
Figure 16. Percentage deviations from the expected percentage composition values for each of the three coho groups based on visual counts in the pool and riffles shown – population II, June 16 to July 28, 1964.

aggressively in attempting to drive out the invaders and were usually quite effective. Invading coho fled quickly downstream into the pool unless a resident could be displaced.

Fish in the riffles were nearly all territorial and defended an area surrounding the feeding station and strongly projected upstream, but only a fraction of the fish in the pools defended feeding territories, about 15 and 11 percent, respectively, in the left and right systems. A map of typical territorial relations in the pools is given in Figure 17. Of 11 territorial coho in pool 1 of the left system, 9 were RV fish and 2 were LV fish. In pool 2, 8 of 16 coho defended territories, 4 were RV fish and 4 were LV fish. No territories were held in either pool by NM coho. In pool 1 of the right stream aquarium, RV coho defended 5 of 7 territories, LV and NM fish each defending a territory. Nearly all of pool 2 was defended by a single, medium-sized RV coho although 3 NM coho were present. When patrolling, the dominant fish attempted to drive the NM fish upstream into riffle 2.

Size of pool territory varied but, in general, larger fish kept larger territories in both pools and riffles. Downstream territories were often larger in both riffles and pools yet defending fish were often smaller in size than upstream defenders. For these reasons, average values for size of territory in riffle 2 and pool 2 would be
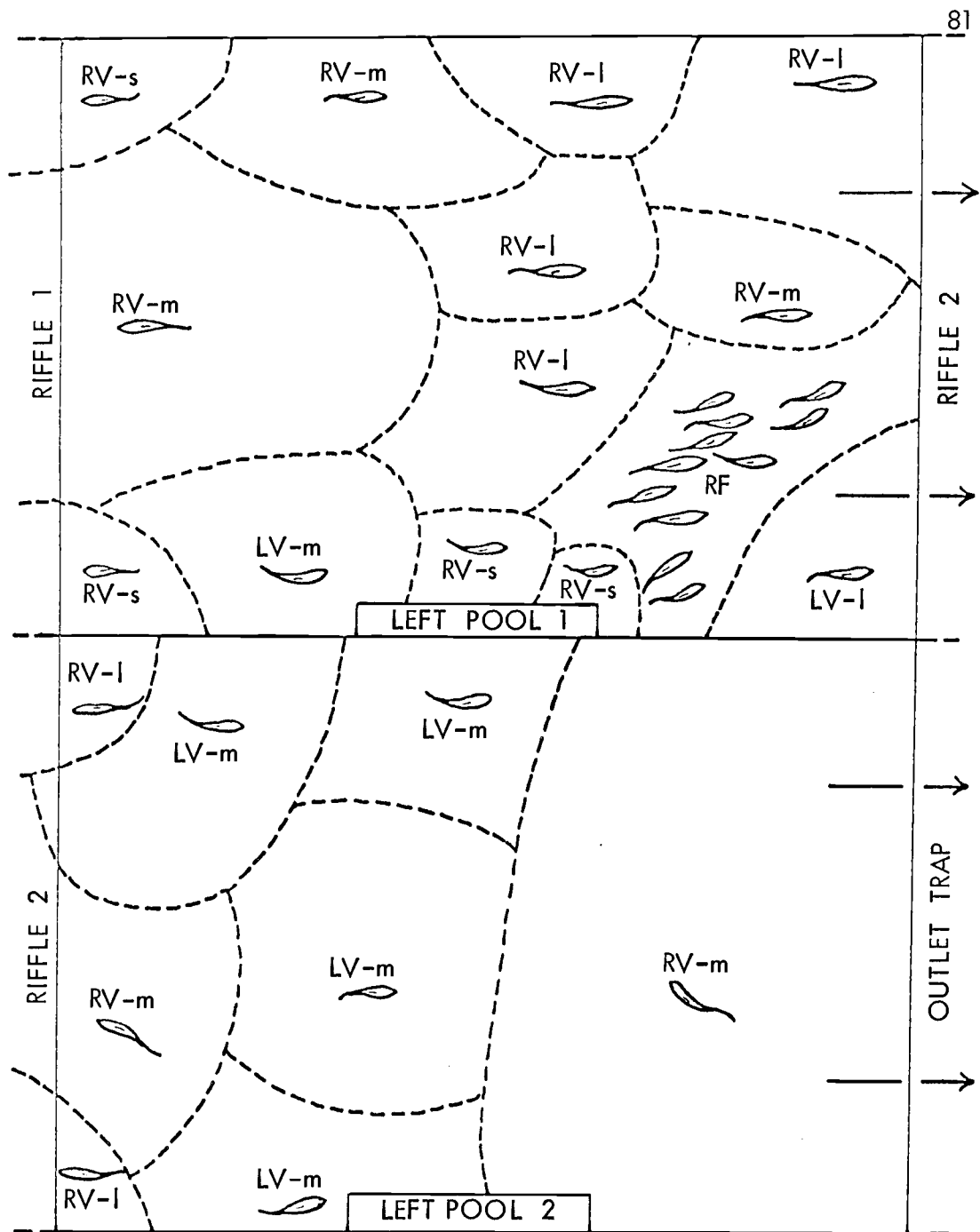
Figure 17. Pool territoriality in the left stream aquarium – population II on July 24, 1964. Broken arrows indicate the direction of the primary food current; l – large, m – medium, s – small, RF – resting fish.

misleading, but comparison of territory size in pool 1 and riffle 1 may be of value. Coho defended larger territories in the riffles than in the pools; 17.2 dm^2 and 10.1 dm^2, respectively, in the left . system; 22.3 dm^2 and 16.0 dm^2 in the right system. The larger mean size of coho in the right system may account for the larger territories. Population size and density, range in size of individual fish, and food availability may be factors of considerable importance in determining territorial behavior and size of territory.

Pool territoriality primarily involved orientation to the secondary food current depicted in Figure 18 (pool 2-side view) where coho on the bottom faced downstream as pictured in Figure 17. Most of the pool fish (70 percent) belonged to a close-knit, size-related hierarchy orienting to the primary food current flowing off the upstream riffle. This size hierarchy is diagrammatically re-presented by Figure 18 for pool 1 of the left aquarium but it was just as clearly expressed in pool 1 of the right system. In pool 2 of the left system, the hierarchy was recognizable but more loosely formed due to the lower number of coho present. The foremost fish in the hierarchy were large, aggressive individuals, size decreasing down-stream so that the trailing fish belonged predominantly to the NM group.
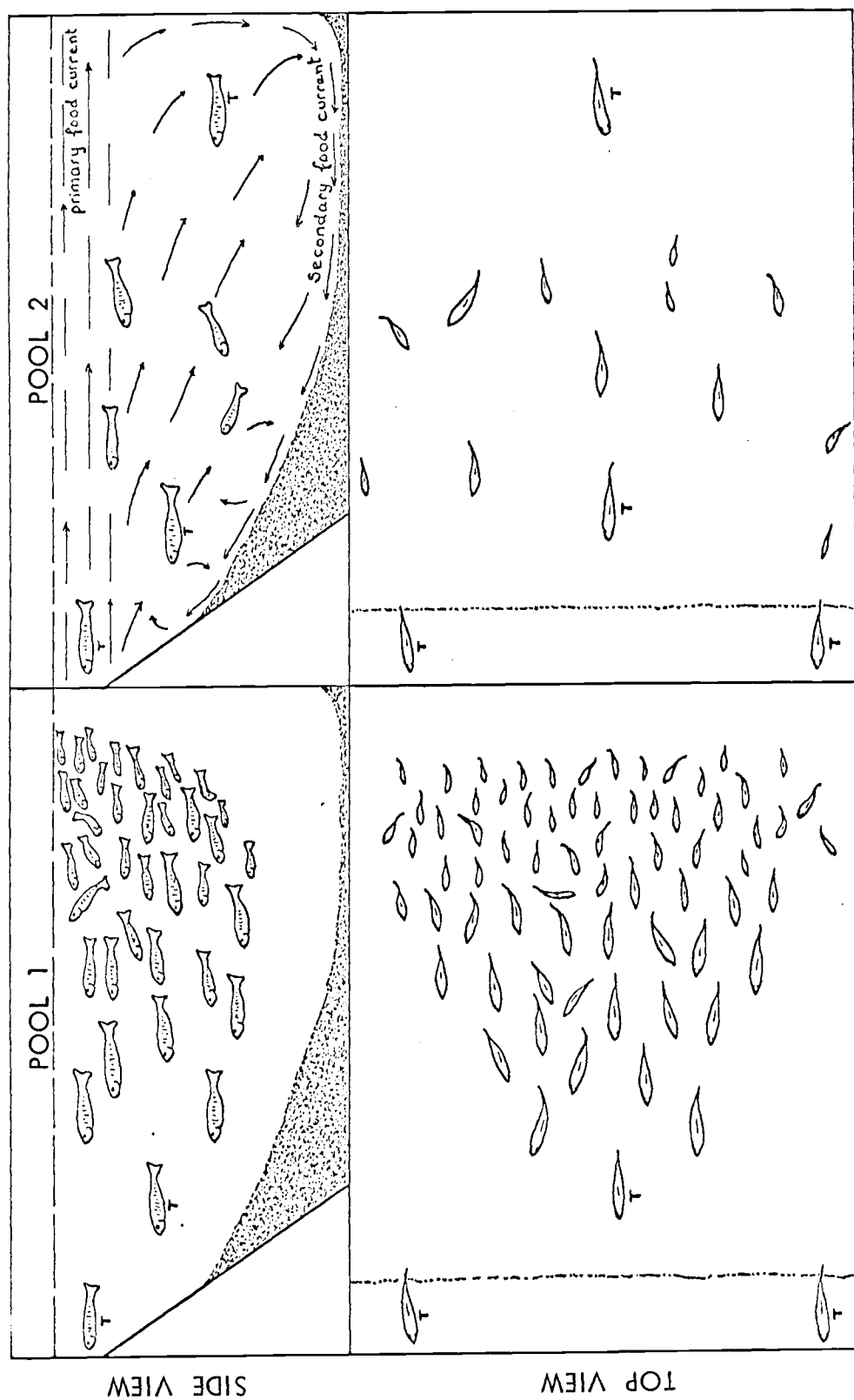
Figure 18. Size hierarchy formation in the left stream aquarium – population II. Reproduced from detailed pencil sketches and visual counts made between July 12 and July 16, 1964. T - territorial fish.

In addition to territorial and hierarchical social structuring in pool 1, a third group of coho could be identified constituting a close aggregation of large, non-territorial individuals which oriented in the secondary food current at the bottom of the pool (Figure 17). They were assigned the identity of "resting fish" since they exhibited very low aggression, little movement, and stayed close to each other. Of all such fish in pool 1 (110 coho in the pool) of the left aquarium, 5 were RV fish, 4 were LV fish, and 2 were NM fish. Most of these coho seemed to have distended digestive tracts.

Social organization in pool 1 of the left system was categorized and counts were made during morning and afternoon observations for five consecutive days. The graphic representations are partly derived from these data which are given in Table 16. RV coho dominated the positions at the riffle-pool margins and no NM fish were observed here. The RV fish also composed most of the fish in the front half of the pool, and were either territorial or dominant hierarchical individuals. The NM coho counted in the front half of the pool are considered to be wanderers as they were quickly chased off. The front portion of the hierarchy was dominated by LV coho (71 percent) while NM coho made up most of the fish in the rear portion (61 percent). Coho oriented in the secondary food current (territorial and resting fish) were predominantly RV and LV fish, the NM coho making up but ten percent of the fish in this category.

TABLE 16. DISTRIBUTION OF COHO BY MARK[a] WITHIN FIVE BEHAVIORAL CATEGORIES IN POOL 1, LEFT STREAM AQUARIUM. COMPILED FROM MORNING AND AFTERNOON COUNTS FOR FIVE CONSECUTIVE DAYS, JULY 12 to JULY 16, 1964.

Behavioral Category	RV Coho			LV Coho			NM Coho			Total Count
	No. of Coho	Range	% of Total	No. of Coho	Range	% of Total	No. of Coho	Range	% of Total	
Coho at the margin between pool 1 and riffle 1.	24	2-3	85.7	4	0-1	14.3	0	0	0	28
Occupants of the front half of the pool, including the runway.[b]	36	2-5	66.7	15	1-2	27.8	3	0-1	5.6	54
Front portion of the hierarchy in the primary food current in the pool	29	2-4	22.8	90	7-12	70.9	8	0-2	6.3	127
Rear portion of the hierarchy in the primary food current in the pool.	19	1-3	10.2	54	4-8	29.0	113	8-14	60.8	186
Coho in the secondary food current in the pool	93	6-14	60.4	42	2-6	27.3	19	1-4	12.3	154

[a]The percent contribution of the three groups of coho to the total population in the stream aquarium during the five day test period was as follows: RV coho, 41.4 percent; LV coho, 37.1 percent, NM coho, 21.6 percent. The total population was 116 fish, about 80 of which were in pool 1.

[b]The runway is the sloping approach board at the front end of the pool which leads up to the margin between the pool and the riffle ahead of it.

Aggressive Behavior in the Stream Aquaria

Intensity of aggressive behavior in both populations was measured

weekly in each riffle and pool (45 minutes of observation per unit)

according to a prescribed schedule. Individual and group intensities

of aggression based on the number of aggressive acts committed

during a 10 minute period are compiled in Appendices 3 and 4 and

presented graphically in Figures 19 and 20.

Coho were most aggressive in riffle 1 in population I, pop-

ulation II showing no significant differences among the pools and

riffles. In three of four cases (two populations in two systems),

total aggression was highest in pool 1, due partly to the very high

densities of fish in these pools. In the fourth case, total aggression

was highest in riffle 1 (Figure 19 - left system) and the second high-

est value was recorded in pool 2. In three of four cases, neither

population expressed downstream gradients in intensity of aggression,

the exception being population I in the right system which showed a

decreasing gradient downstream in intensity of aggression per coho

only.

Despite their low numbers, coho in pool 2 were quite aggres-

sive and, in two cases, were more aggressive than either pool 1

or riffle 2 fish. Unlike population I, population II showed a con-

sistently high intensity of aggression throughout both stream aquaria.
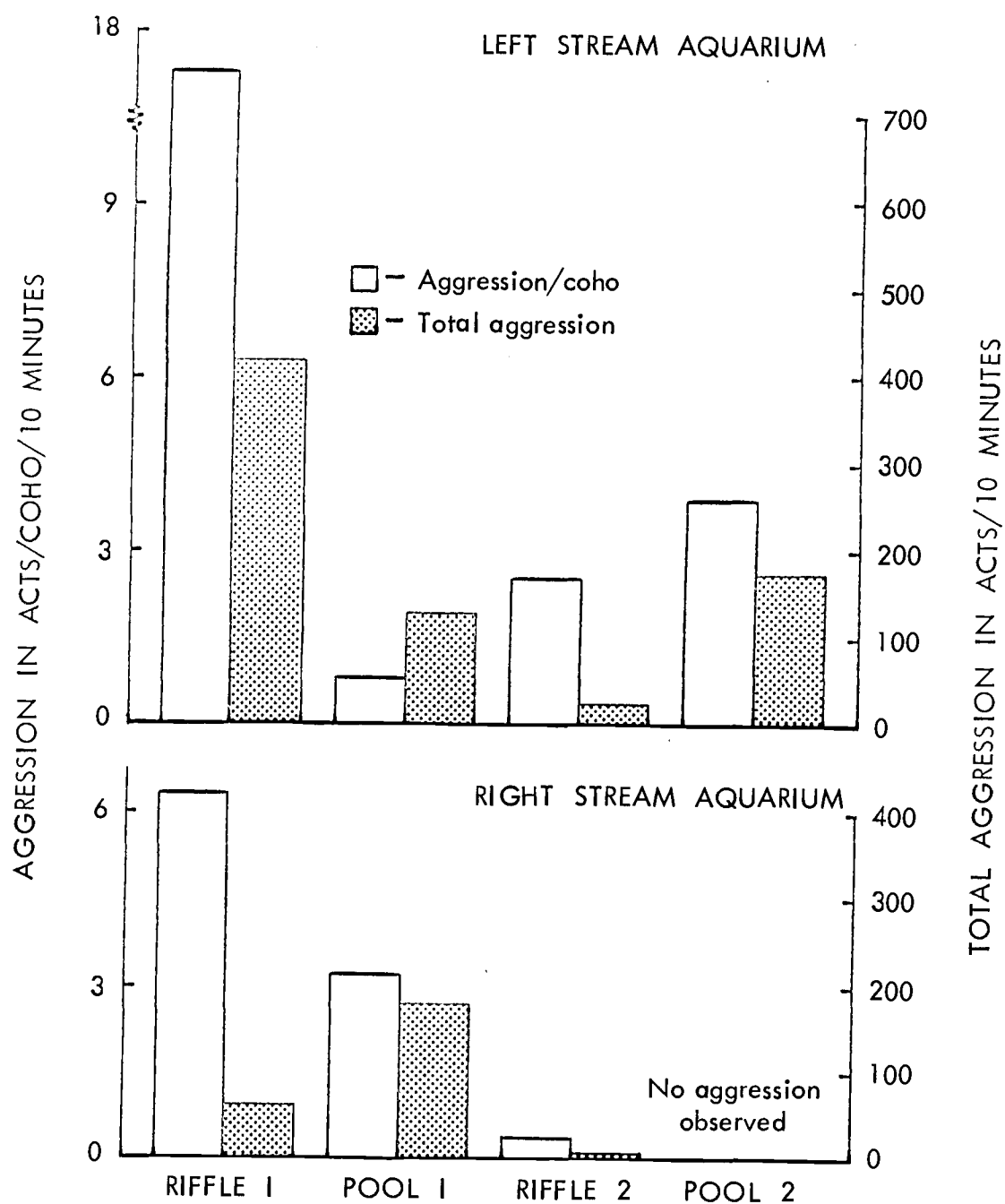
Figure 19. Mean intensities of aggression in population I, based on weekly observation periods. Total observation time was 25.5 hours.
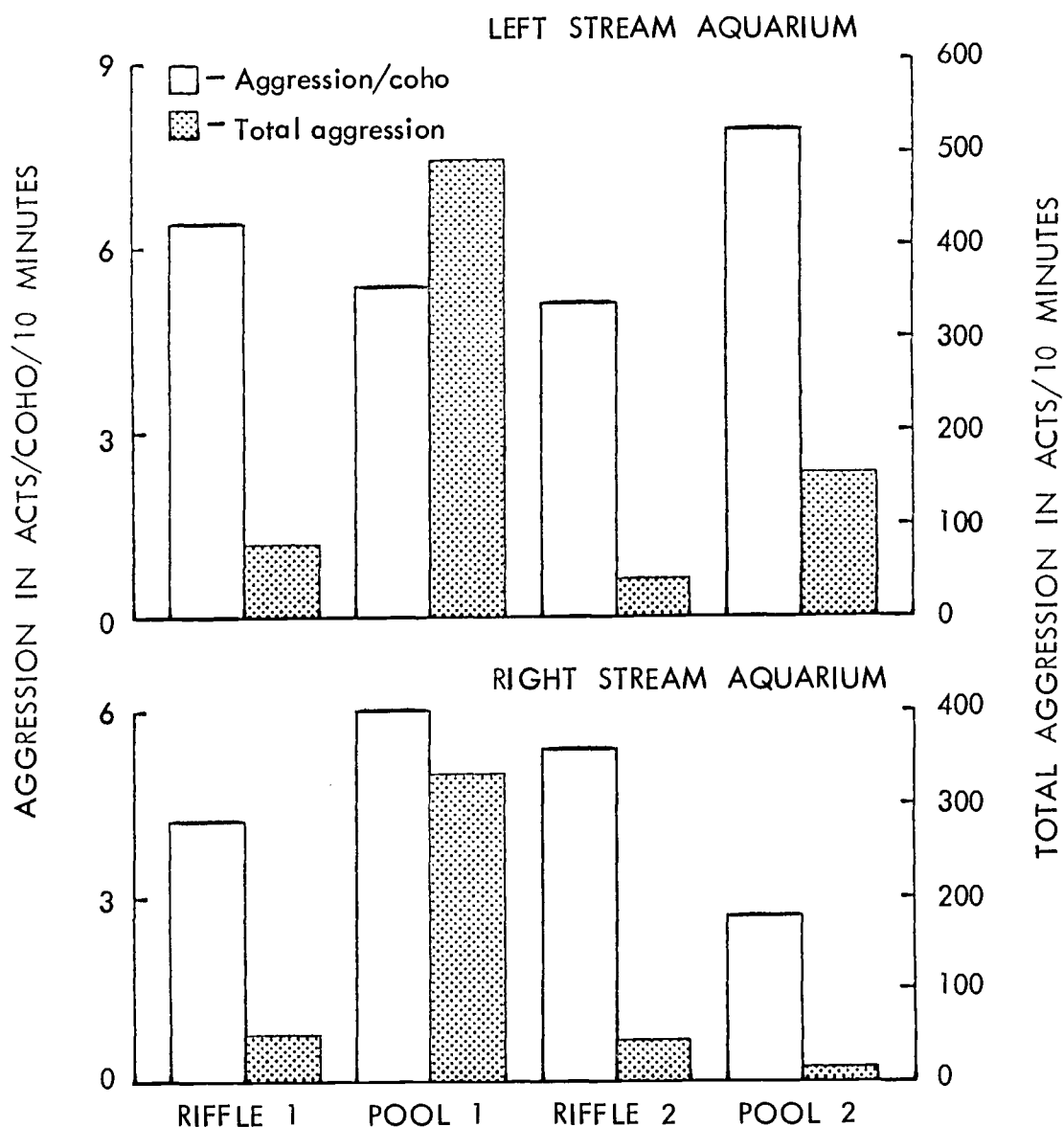
Figure 20. Mean intensities of aggression in population II, based on weekly observation periods. Total observation time was 36 hours.

Mean intensities of aggression were highest for population II (5.4

compared to 4.1 acts/coho/10 minutes for population I), the dif-

ference being not quite significant at the five percent level. In

both populations, differences between the left and right systems

were non-significant.

The single significant correlation found between intensity

of aggression, water temperature, and rate of emigration involved

water temperature and emigration in population I, where emigration

decreased with increased temperature ($b = 2.26$, $r = 0.95$, $F =$

23.2 with 1, 6 degrees of freedom, $P < .01$). The corresponding

regression for population II was negative but insignificant. A fluct-

uating food supply directly influencing intensity of aggression but

reflected in delayed emigration may be instrumental in beclouding

the interaction of these three variables. Precise control of these

factors is necessary if their interactions are to be adequately measured.

Behavioral interaction was recorded in five categories related

to a gradient in intensity of aggression (Table 17). Threat display

is considered to involve conflict between escape and attack (Tinbergen,

1952). The behavioral context of threat display in juvenile coho sub-

stantiates this analysis and threat is considered here to entail less

aggression than non-threat categories of aggressive behavior. The

latter appear to represent a fairly straightforward gradient of aggression

culminating in "nip contact."

TABLE 17. CATEGORIES OF AGGRESSIVE BEHAVIOR AND THEIR RELATIVE FREQUENCIES SHOWN BY COHO IN THE STREAM AQUARIA DURING THE SPRING AND SUMMER MONTHS – POPULATIONS I AND II.

Behavioral Category	Population I				Population II			
	RIFFLES		POOLS		RIFFLES		POOLS	
	Acts	%	Acts	%	Acts	%	Acts	%
Nip contact	47	9.0	24	12.8	27	4.6	32	5.5
Nip close	68	13.0	34	18.1	32	5.5	76	13.1
Nip toward	76	14.5	29	15.4	31	5.3	88	15.2
Drive toward	154	29.4	43	22.9	284	48.6	190	32.8
Sum	345	66.0	130	69.1	374	64.0	386	66.6
Threat display								
Horizontal	148	28.3	47	25.0	130	22.3	124	21.4
Head up	none		5	2.7	none		39	6.7
Head down	30	5.7	6	3.2	80	13.7	31	5.3
Sum	178	34.0	58	30.9	210	36.0	194	33.4
Total acts	523		188		584		580	
Mean intensity of aggression [a]	7.0		2.5		5.4		5.4	

[a] Acts/coho/10 minutes

Despite differences in mean intensity of aggression, the incidence of threat display remained rather stable in both populations. Mean threat values composed 32.6 (population I) and 33.9 (population II) percent of total behavior, based on weekly measurements. Differences between environments and populations were not statistically significant, however, incidence of threat was slightly higher in the riffles than in the pools for both populations (Table 17).

In both populations, the nip categories involving higher aggression were more frequent in the pools than in the riffles although their relative incidence is much lower in population II. Here, the incidence of "drive toward" was much higher, and threat slightly higher, in both pools and riffles, than in population I. Coho in population II were larger than those in population I while in the stream aquaria and were more aggressive.

Discussion

Embryos and fry exposed to saturation oxygen tension were larger at hatching and at time of emergence, and suffered lower mortality during development than embryos and fry of the same parents exposed to lower oxygen concentration and slightly higher temperatures. Due to the onset of branchial respiration, the hatching process is accompanied by considerable reduction in respiratory stress. Reduced respiratory stress in embryos of Salmo salar was reported by Hayes, Wilmot, and Livingstone (1951).

Reduced size of the 5 and 3 mg/liter fry is primarily the outcome of lowered oxygen availability, although the possibility of added stress induced by increased temperature cannot be discounted. Gray (1928a, 1928b) subjected the embryos of S. fario to 5, 10, and 16°C, concluding that the higher the temperature, the more rapid the growth and greater the decrease in size at hatching. However, Wood (1932) concluded that the relation between respiration and growth in embryos of this species remained unchanged over the normal temperature range. Above and below this range (about 3 to 12°C), respiration increased in proportion to growth and resulted in smaller fry at emergence.

In the left stream aquarium, competition for the limited food supply composed chiefly of incoming insect drift was clearly expressed in terms of growth rate, number of resident fish, and net production,

and reflected the degree of physiological stress imposed during develop-
ment. Saturation fry proved far superior to the 5 mg/liter fry even though
the latter fry were less than 1 millimeter smaller in mean length at time
of emergence. Length differences of one millimeter were behaviorally
significant in the aggressive interactions of coho fry in other experi-
ments, the larger fish usually gaining dominance. In both populations,
initial size differences were amplified with time, the NM coho bearing
the brunt of competition. In the holding tank, population II showed
slight amplification of size differences in terms of body weight, but
each group of fry increased its body length by 35 to 36 percent.

In both populations, emigrants transferred to the right system
took up residence there, signifying fulfillment of needs not met in the
left system. At termination, these emigrants were as large (RV coho)
or considerably larger (LV and NM coho) than their group cohorts re-
maining in the left system and showed similar or higher coefficients of
condition. Larger terminal size appears to be more the outcome of
higher growth rate due to feeding conditions enhanced by lowered
competition for food and space than of a size disparity between residents
and emigrants at time of emigration. Emigrants were probably smaller
than residents in the left stream aquarium, the difference in size being
greatest in the fry most stressed during early development.

As upstream movement elicits more aggression than does the reverse behavior, upstream emigration in the natural stream might involve large individuals concerned with needs only secondarily-related to food availability, such as suitable cover and water depth. Downstream emigrants are most likely to be ecological failures, smaller individuals distressed primarily by their inadequate food relations. Emigrants must displace residents equipped with a prior-residence competitive advantage as described in juvenile coho by Chapman (1962) and in _Platypoecilus maculatus_ by Braddock (1949). This is a rather dismal prospect for downstream emigrants of inferior social position and nutritional history.

The ecological advantage bestowed upon the larger fry reared at saturation oxygen tension is principally the outcome of social interaction whereby social dominance associated with size dictates the feeding relations among members of the population. Larger coho enjoyed better feeding opportunity than did smaller fish by defending the areas of highest food availability in the stream aquaria, the uppermost riffle and the anterior part of the pool immediately beneath it. The gradients in numbers and size of individual fish aptly reflected the central interest of the entire population with feeding opportunity, food availability being highest at the upstream ends of the aquaria.

Brown trout, rainbow trout, and eastern brook trout establish size hierarchies in aquaria (Brown, 1946; Stringer and Hoar, 1955; Newman, 1956). Hierarchical social structure has been described in several non-salmonid fishes (Allee, 1938; Noble and Borne, 1938; Noble, 1939; Collias, 1944; Braddock, 1945; Greenberg, 1947; Allee et al, 1948; Magnuson, 1962). Hierarchical organization is associated with size and aggressive behavior. The benefits of high social position in terms of higher survival, resistance to starvation and disease, better growth and reproductive opportunity have been variously pointed out by a number of workers (Allee, 1938; Noble and Borne, 1938; Noble, 1939; Collias, 1944; Barrow, 1955; Chapman, 1962; Magnuson, 1962; Yama-gishi, 1962).

Territorial and hierarchical organizational patterns associated with aggression have evolved throughout the animal kingdom as social conventions (Wynne-Edwards, 1962). In stream-living fishes, these patterns appear to solve the problem of food distribution. Juvenile coho in nursery streams rely chiefly on downstream invertebrate drift for nourishment, a food supply that is limited and spatially diluted. These features of the food supply have resulted in food-related, conventional-ized competition for space via territoriality. This species, and no doubt many other drift-reliant fish species, exhibits ecological flexibility through the formation of non-territorial hierarchies, a type

of social organization that is secondarily-related to space and adaptive in periods of abundant food supply.

Some factors must operate to set the upper limits on intensity of aggression. Visual isolation brought about by bottom configuration, aquatic plants, turbidity, and deposited water-borne debris would serve to this end and may be somewhat independent of food availability. Size of both reproductive and feeding territories can be reduced by such means (Fabricius, 1951; Fabricius and Gustafson, 1955; Forselius, 1957; Kalleberg, 1958) and is certainly associated with aggression. Increasing isolation under conditions of limited but dispersed food supply decreased the competitive advantage of dominant medaka (Oryzias latipes) held in small aquaria by Magnuson (1962). Emigration primarily by socially inferior, smaller coho appears to be strongly linked with food availability and, in later experiments, food was found to play an important role in setting the intensity of aggression in populations.

Intensity of aggression was also mediated by food satiation, shown particularly by large individuals in the population. Rising aggression accompanied rising motivation to feed. This relationship was most clearly seen in large, satiated "resting fish" in the pools. Returning motivation to feed could be quickly recognized in such individuals by their rising aggression toward adjacent fish which moved away in response. Within a few minutes, the aggressive coho moved

to the front of the pool, interacted aggressively with territorial fish in the primary food current, and ultimately invaded the upstream riffle. Thus, while intensity of aggression may be determined by food satiation in large, dominant coho of high social rank, it is controlled in part in smaller coho of low social rank by social inhibition involving fear of punishment by the social dominants in its vicinity.

These findings emphasize that survival to emergence marks the onset of a stream life primarily oriented to social relations, the ecological rewards being survival to reproduce, or, in anadromous species, to participate in the journey seaward. Among fry emerging from the natal gravels, size is of major importance in implementing the pattern of food distribution. Small fry are poor competitors and face almost certain death from predation, disease, or starvation (most likely, a combination of these) unless competitive stress can be relieved by emigration etc. Small size resulting from poor growth or insufficient time to grow no doubt increases the probability of predation since small fry spend more time within the predator-vulnerable size range (Ricker and Foerster, 1948; Neave and Wickett, 1953; Larkin, 1956).

The potential size of salmonid fry at emergence is determined by the quality and quantity of yolk reserves available as nourishment. Both temperature and dissolved oxygen supply are critical secondary

environmental factors capable of extensively reducing the potential size

of fry at emergence. The influence of temperature in this regard on nat-

ural populations of trout was pointed out by Hobbs (1953) who discussed

the possible interplay between maternal parent, egg size, time of spawn-

ing, and the ensuing water temperature regimen in tributary streams used

as spawning and rearing areas by lake populations of brown trout in

New Zealand. Possibly, social relations involving post-emergence com-

petition tended to amplify size variation originating from a complex

interaction of parental stock structure and spawning behavior, egg size,

genetic growth potential etc., and the physicochemical environment

during development.

Nikolskii (1962) suggested that, under favorable feeding conditions,

range in individual size remains small but that deterioration of food con-

ditions results in increased size variability. Within this frame of

reference, favorable feeding conditions must involve a non-limiting food

supply that becomes unfavorable when total population demands are not

met, increased size variation being the outcome of food competition.

Such a view of favorable feeding conditions may be appropriate for the

pond propagation of carp fingerlings. In more natural populations, part-

icularly those of stream-dwelling salmonids relying on the invertebrate

drift, a food supply that probably cannot be overexploited, food may be

nearly always limiting. Feeding conditions are first the concern

of the individual, then its population, and favorable feeding conditions are reserved for individuals best suited to represent the population through competition.

The competitive stress measured in this experiment was exerted chiefly through the size relations of fry exposed to different oxygen concentrations prior to emergence. Decreased size of fry through lowered growth efficiency may not be the only outcome of respiratory stress. Subtle differences in health or impairment of specific physiological functions may accompany reduction in size. But, if the present findings are based primarily on size relations in the population, one may tentatively assume that environmental factors leading to reduction in size of fry are most likely stressful and deleterious.

The influence of non-lethal respiratory stress incurred by embryos and fry in the redd is strongly projected into the social phase of the life history following emergence. Concern for dissolved oxygen standards set at some below-saturation concentration supposedly not harmful to salmonid populations when such standards are thought appropriate for upriver regions of first consideration as spawning and rearing areas is thus rendered rather suspect. In all probability, respiratory stress induced by lowered oxygen supply merely adds to an already stress-filled environment.

The competitive relations described here result from the organizational mechanics of the population as they take form through behavioral

response to the stream aquaria. Admittedly, this environment is an over-simplification of its natural stream counterpart; but the core of juvenile coho environment is well-represented despite the simplicity and stability of the systems. Predator-prey interaction is a major biological reality strongly attenuated in these aquaria. Cannibalism is thought to be of minor consequence. Emigration far outweighed any loss through predation that might be expected if an appropriate number of larger piscivorous fish were present in the systems. One might argue that the presence of such predators could result in large-scale emigration of the coho, but large populations of juvenile coho are commonplace in nursery streams supporting populations of cutthroat trout (S. clarki), and both species reside in the same environments.

Vertebrate predator-prey relations are typified by moments of terror punctuating long periods of near-indifferent behavior on the part of both parties. Coho rapidly overcome fright in natural streams and in the stream aquaria. Predator effectiveness would be high in the aquaria due to the lack of undercut banks and large debris in the pools. Introducing the environmental complexity of the natural streambed would serve merely to interject behavioral variability to the point where the underlying behavioral relationships described in this paper would have proved most difficult to perceive and measure. Response to avian pseudo-predatory harassment was conveniently provided by the flyover

antics of a male songsparrow which chose to include the experimental area within its reproductive territory. These activities commonly prompted the coho to flee into the pools.

I suspect that the most competent judges of the experimental facilities are the fish themselves. As volitional residents, they were not reluctant to express dissatisfaction by leaving the aquaria via the downstream traps. Resumption of residence by the majority of emigrants upon transfer to the alternate system is deemed sufficient proof that environmental dissatisfaction could be adequately relieved in the same environment associated with a smaller population of coho.

Summary

1. Following incubation and development in an apparatus designed to

    produce, simultaneously, emergent fry having known histories of

    embryonic stress, coho fry were allowed to compete in stream

    aquaria. Their performance was measured in terms of volitional

    residence, distribution patterns, growth, net production, and

    aggressive behavior. A replicate set of fry (population II) was

    kept on unrestricted rations in a hatchery tank.

2. Size of fry at time of hatching and at emergence reflected the

    degree of stress imposed on them, although the fry reared at

    5 mg/liter of oxygen (LV fry) nearly attained the size of the RV

    fry reared at saturation, being but 0.75 mm smaller in mean length

    and 18.6 mg lighter in mean weight at emergence. Fry reared at

    3 mg/liter (NM fry) were much smaller.

3. Outmigrants from population I in the left system were predominantly

    NM fry. Until an interruption in flow induced some of the large RV

    coho to emigrate, emigration reflected the degree of stress imposed

    during development. Emigrants from the left system were put in the

    right system, an unoccupied replicate environment. The majority

    of emigrants elected to become residents. On the average, emi-

    grants were probably smaller than residents at any one time during

    the experiment.

4. At termination, the left system contained more LV than RV fish and fewest NM fish. Had flow interruption not occurred, composition of the terminal population might have better reflected the degree of respiratory stress during early development. Initial size differences among the three groups of fry were amplified with time. Condition factor followed the same ranking order as did size and weight. The same ranking order of size was shown by emigrants from the left system that were put in the right system, but the size disparities were greatly reduced and condition factor increased.

5. An ecological stress index based on relative weight gain of the RV coho was 1.27 and 2.60 for the LV and NM coho, respectively, in the left system. In the right system, there was no difference between RV and LV fish and the stress index for NM fish was reduced to 1.31. There was also a rank order in net production that was a function of number of residents, time in residence, and rate of growth. A production index based on the NM coho was 4.72 and 3.37, respectively, for the RV and LV fish in the left system. In the right system, comparable values were 0.21 and 0.72, the NM fish gaining 5 times as much production as the RV fish.

6. In population II, fed to "excess" on a hatchery diet, there was no significant difference in relative percentage length increase among the three groups of fry while in the tank but these fish

gained only half as much weight as those feeding on natural drift foods in the stream aquaria. Population II was then put in the left stream aquarium and the same procedure followed as was applied to population I.

7. Outmigration followed the same trends seen in population I, being 49, 52, and 67 percent of the initial numbers of RV, LV, and NM coho, respectively. When put in the right system, most of the left system emigrants took up residence there. Initial size differences between the three groups of coho were amplified with time. As in population I, the LV and NM emigrants put in the right system exceeded the size of their group cohorts that elected to remain in the left system.

8. Both populations showed the numerical and size gradients in horizontal distribution reported in the previous experiment. Territorial and hierarchical organizational structure is described and social structure is related to stress history of the fish. The RV coho dominated the areas of highest feeding opportunity, namely, riffle 1, the margin between riffle 1 and pool 1, and the front half of pool 1. They also constituted most of the territorial fish in pool 1 and no territories were held by NM fish in the pools. The front portion of the large feeding hierarchy in pool 1 was dominated by LV coho while NM coho made up most of the fish in the rear portion.

9. No clear-cut upstream-downstream gradient in intensity of aggression was found but coho were usually most aggressive in riffle 1. Population II showed a consistently higher intensity of aggression throughout the systems than did population I, thus reinforcing the suggestion made regarding growth response that competition was more intense than in population I.

10. Exposure to respiratory stress during early development resulted in decreased size of fry at time of emergence. The degree of stress exposure was of profound ecological significance as successful competition for limited food and space resources appeared to be largely determined by a size-related social order that put smaller individuals at a serious disadvantage. The "naturalness" of the stream aquaria was evaluated and the core of juvenile coho environment was considered to be well-represented. The most competent judges of these systems were probably the fish themselves. Their dissatisfaction with the experimental conditions appeared to concern population density as related to fulfillment of food and space needs.

THE ROLE OF AGGRESSION IN SOCIAL RELATIONS

INTRODUCTION

The social relations of juvenile coho center about their patterns of organization, the territorial mosaic and the hierarchy. These patterns are typified by dominance-subordinance, size-related interactions that are nearly always settled in favor of the larger individual. Juvenile coho form rather stable hierarchies in small stream aquaria. Dominant individuals defend territories and grow more rapidly (Chapman, 1962).

To explore further the significance of aggression as an instrument implementing these social relations, several experiments were performed concerning aggressive behavior and ecological reward in a small stream aquarium. These experiments were designed to supplement behavioral observations of the large populations of considerable social complexity in the main stream aquaria. Particular attention was given to the distribution of aggression, food, and space under various conditions.

The small stream aquarium was a glass-fronted, wooden structure 2.4 m long, 46 cm in width and depth, and fitted with a downstream trap. An overhead bank of fluorescent lights was arranged to provide an intensity of 150 f-c in all experiments. Water temperature, flow and velocity relations, and specific modifications are described in their appropriate context.

AGGRESSIVE BEHAVIOR OF ADVANCED ALEVINS

Introduction

Salmonid fry undergo a drastic change in their surroundings upon emergence from the streambed. They are equipped for this transition with instinctive behavior patterns that insure adaptive response to major features of the open river. The social behavior of juvenile coho is essentially aggressive and is used to insure efficient distribution of limited resources. Advanced alevins were studied to provide more information on the timing and nature of aggression in young fry and possible relation to feeding.

Methods

The aquarium was modified to provide a uniform riffle with 10 cm of water over a substrate composed of pea-sized gravel. A flow rate of 15 liters/minute was maintained to give an average velocity of 0.5 cm/second through the system.

A population of 50 advanced alevins previously held in hatchery baskets was introduced into the riffle and observed for two weeks during the period of transition to feeding on natural drift foods. On March 25, 100 fry were put in the riffle, given 2 days to adjust, then the downstream screen was removed to allow volitional residence during the last test period.

Results and Discussion

Advanced alevins distributed themselves in the riffle according to degree of yolk absorption. The most advanced fry positioned themselves at the upstream end of the riffle (Figure 21). The fry were categorized according to three degrees of yolk absorption (advanced, intermediate, and least advanced). The first (upstream) and last (downstream) ten fry in the riffle were so classified during six hourly observations on each day of testing. The marked initial difference between the upstream and downstream fry was gradually attenuated with time but some difference still remained after ten days.

Upstream fry actively defended territories and were more aggressive than were downstream fry. With the exception of a few individuals, territoriality was seldom observed in the downstream fry until February 25. At that time, the fry were well-spaced throughout the riffle except for a small aggregation of 9-12 fry that tended to shift position in response to aggression elicited from surrounding territorial fry.

Intensity of aggression was highest at the upstream end of the riffle (Table 18). The mean intensity of aggression of the first and last five fry, 4.21 and 1.28 acts/coho/10 minutes, was significantly different at the 1 percent level.
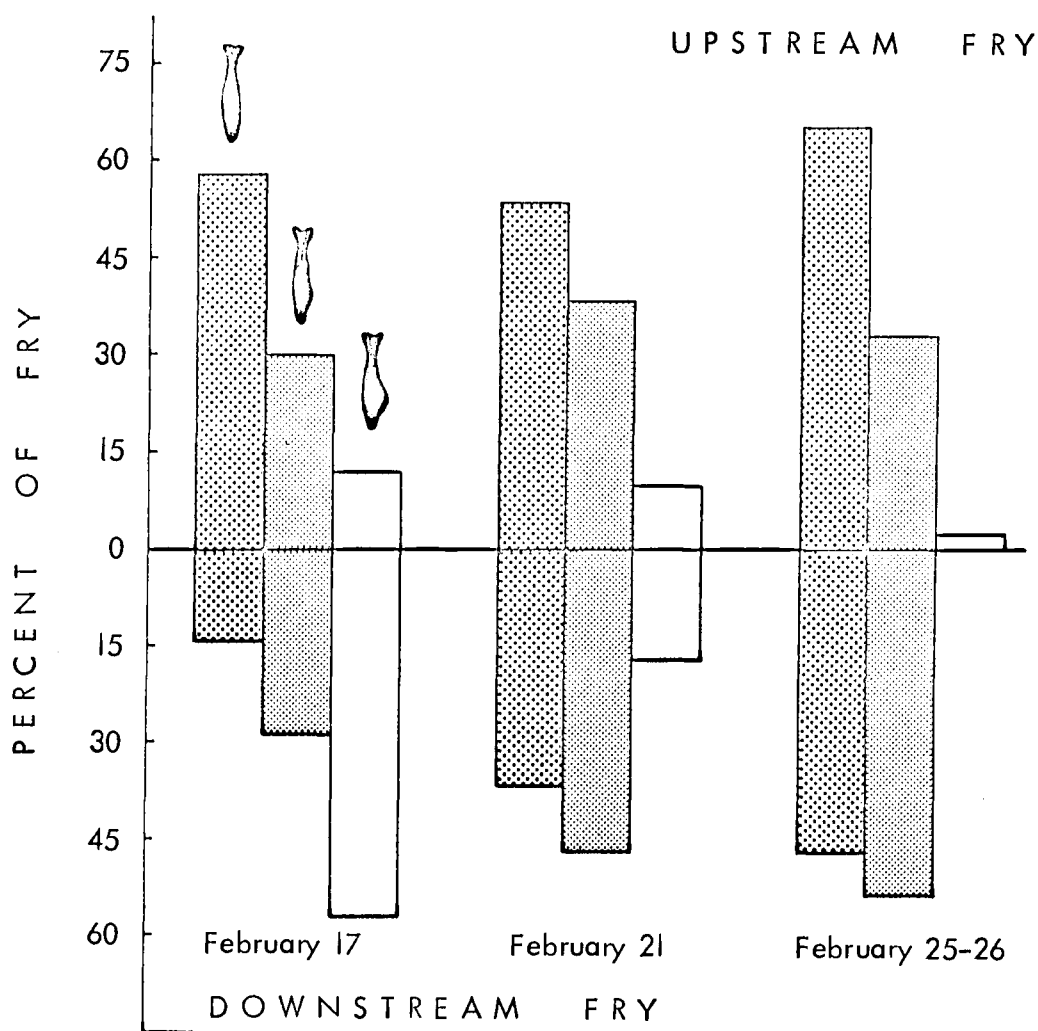
Figure 21. The upstream-downstream distribution pattern of coho fry in a small stream aquarium as related to the degree of yolk absorption. Based on 18 counts of the first and last 10 fry.

TABLE 18. POPULATION SIZE, OBSERVATION TIME, AND SOME
          BEHAVIORAL STATISTICS FOR ADVANCED COHO SAC FRY
          HELD IN A SMALL STREAM AQUARIUM DURING THE
          TRANSITION TO FEEDING ON NATURAL DRIFT FOODS.

	February 17	February 21	February 25-26	March 30 - April 2
Population size	50	50	50	82-62
Observation time (min)	180	60	120	180
Upstream Fry				
Total acts	220	169	221	541
Percent threat	19.1	33.7	42.5	38.4
Aggression level[a]	2.54	5.63	3.69	6.01
Mean		4.21		
Downstream Fry				
Total acts	60	52	68	165
Percent threat	15.0	13.5	38.2	33.9
Aggression level[a]	0.67	1.73	1.13	1.83
Mean		1.28		

[a]Intensity of aggression of the first or last five fry,
expressed as acts/coho/10 minutes.

To detect possible behavioral maturation in these fry during the transition period, their behavior was recorded in the categories described in Table 19 (the point-scoring scale was not used in this experiment). Non-threat behavior was recorded by body region - head, midbody, and tail. The threat displays are thought to involve both attack and escape tendencies, but the remaining categories chiefly involve aggressive, attack features and were defined to reflect a gradient in intensity of these features.

The relative frequencies of the non-threat categories remained fairly stable (Figure 22) although "drive toward" (Dto) decreased with time in both upstream and downstream fry. The frequency of threat behavior increased with time as shown by the insert histogram (upper) in Figure 22, and Table 18. Quality of threat also changed with time, being primarily horizontal threat in the first population. Combined head-up and head-down threat composed about 37 percent of the total threat in population two. Relative frequency of non-threat behavior directed at the tail region of the opponent fry stayed nearly constant but aggression directed at the head region increased primarily at the expense of declining attack on the midbody region as shown by the lower insert histogram in Figure 22.

Increased frequency of threat and declining attack on the midbody region suggest that the fry underwent a gradual increase in

TABLE 19. COMPONENTS OF AGGRESSIVE BEHAVIOR AND THEIR POINT
        SCORES

Symbol	Point Score	Description of Behavioral Component
Tho	0.5	Horizontal threat-equivalent to lateral threat display. Characterized by lowering of the basihyal apparatus, partially opened mouth and expanded opercles.
Thd	0.5	Head-down- threat - similar to lateral threat. Body axis may vary from a few degrees to about 80 degrees from the horizontal. Occurred in both riffle and pool environments and may be accompanied by slow undulations of the tail region.
Thu	0.5	Head-up threat - body axis reversed but otherwise equivalent to Thu. Seen only in pools under low velocity conditions.
Dto	2.0	Drive toward - movement toward adversary with the mouth closed. Action broken off usually by adversary moving away.
Nto	3.0	Nip toward - drive at adversary with the mouth open, followed by a nip made more than one head-length away from the other fish.
Ncl	4.0	Nip close - drive at adversary with the mouth open, followed by a nip made within one head length of the other fish .
Nco	5.0	Nip contact - drive at adversary with the mouth open, followed by a nip that appears to make contact.
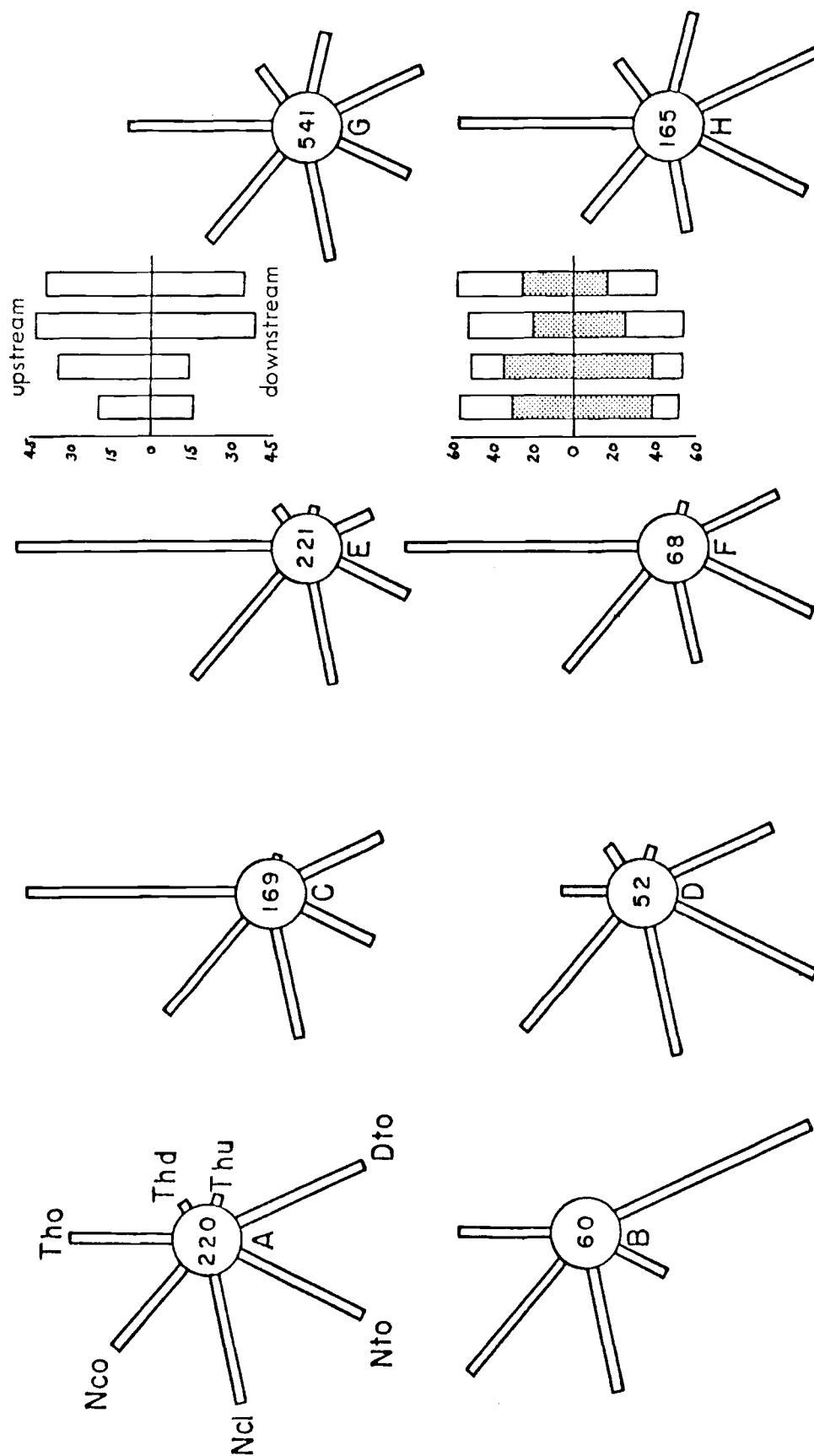
Figure 22. Categories of aggressive behavior and their percentage occurrence in advanced coho sac fry held in a small stream aquarium during the transition to drift feeding. See Table 18 for test dates. Encircled values indicate the number of acts recorded; top series – first five upstream fry, bottom series – last five downstream fry. The upper insert histogram shows the percentage of threat in behavior of upstream and downstream fry. The lower histogram shows the percentage of non-threat behavior directed at the head and mid-body regions by upstream and downstream fry – aggression directed at the mid-body is stippled.

social awareness involving recognition of size relations and the effectiveness of frontal and posterior attack tactics. Territorial behavior may discourage development of parallel feeding stations in adjacent fry, thus decreasing the probability of attack directed at the midbody region.

For about one week in the large stream aquaria, recently emerged fry remained in the pools where they were non-territorial and showed very little aggression. Thereafter, they invaded the riffles and vigorously defended feeding territories against intruders, showing the complete behavioral repertoire of older subyearlings and yearling coho. The delay in territoriality may well have been due to a reluctance to utilize the riffles (high water velocity) as long as food and space was non-limiting in the pools.

The present results indicate that, upon emergence, coho fry are capable of complex behavioral interaction including the complicated threat displays and show the urge to defend feeding territories. Initial interest in feeding is associated with amount of unspent yolk reserve, indicating that onset of aggressive behavior may be triggered by the hunger drive. The fry of brown trout and Atlantic salmon were found to be non-aggressive until they commenced feeding on natural drift foods (Kalleberg, 1958). Salmonid fry do not normally emerge from the stream-bed until the yolk reserve is nearly spent.

Nipping by the less-advanced fry consisted of a mouthing of the fins of adjacent fish rather than the typical quick nipping seen in more aggressive and actively feeding upstream fry. Young fry nipped indiscriminately at moving objects, whether in the drift or on the substrate, and they may be stimulated to snap at the moving fins of their companions for this reason. Probably, the nipping response is instinctively based, becoming overlain by an assemblage of conditioned responses acting to heighten discriminatory ability based primarily on optical stimulation.

The sudden appearance of small midges from the adjacent river provided an opportunity to observe perfection of feeding behavior in these fry. Insects captured by advanced fry were rejected, seized again, and the cycle repeated several times. Prey were often lost to other fry generally showing the same response, before being finally swallowed. Captured insects were rarely rejected and lost to neighboring fry on the next day. In the main stream aquaria, older fry rose to insect exuviae but seldom took them, especially in the pools where more inspection time was afforded them. Rejected items were usually sampled again further downstream by other fry, commonly several times during the few seconds of travel through the riffle.

INFLUENCE OF FOOD ON AGGRESSION

Introduction

As stated earlier, aggression following the introduction of food

has been reported for several salmonid species. The link between

aggression and feeding is no doubt of common occurrence in omnivorous

fishes and has been recorded for several non-salmonids including the

goldfish (Carassius auratus) by Spencer (1939), the darters Etheostoma

exile and E. flabellare (Winn, 1958), the medaka by Magnuson (1962),

and the cod (Gadus callarias) (Brawn, 1961). Aggressive behavior may

be food-linked also in herbivorous species. The Japanese "Ayu"

(Plecoglossus altivelis) exhibits non-reproductive territoriality in

mountain streams (Kawanabe, 1958).

When laboratory-held fishes must rely on an infrequent source

of food, the food regimen appears to play a vital role in the elicitation,

increase, and timing of aggressive behavior. Medaka lacked aggression

only when food was supplied in excess (Magnuson, 1962). Juvenile

Atlantic salmon were more aggressive when fed frequently than when fed

infrequently (Keenleyside and Yamamoto, 1962). Newman (1960) stated

that the aggression of rainbow and brook trout held in aquaria increased

following fulfillment of the hunger drive. He did not measure the in-

tensity of aggression until some time after feeding had ceased although

he observed little aggression during feeding. Similarly, aquarium-held cod showed no aggression during feeding but considerable aggression thereafter, more than occurred during feeding, and lasting for more than an hour (Brawn, 1961). Increased aggression and swimming activity may continue long after the food has been consumed, periods up to three hours being recorded for the goldfish by Spencer (1939).

These results could be interpreted in part as the outcome of social instability induced by scramble feeding. A temporary collapse of dominance-subordinance relations could demand a subsequent increase in aggression so that social stability could be re-established. Juvenile Atlantic salmon tolerated intrusion while actively feeding but vigorously defended their territories within three to four minutes after the food had been consumed, aggression remaining high for at least 45 minutes following feeding (Keenleyside and Yamamoto, 1962). However, a series of disturbance tests by these workers designed to promote violation of territories by subordinate fish suggested that increased aggression is not solely the result of spatial displacement.

In order to shed more light on the influence of feeding regimen on aggressive behavior in coho, the influence of food availability on the intensity and duration of increased aggression was examined.

Apparatus and Methods

The small stream aquarium was modified into a riffle-runway-pool environment, the respective lengths of each unit being 107 cm, 61 cm, and 61 cm. Water depth over a layer of pea-sized gravel was 10 cm in the riffle and 38 cm in the pool. Water flow was maintained at 40 to 45 liters/minute, giving a water velocity of 1.5 cm/second in the riffle. Water temperature ranged from 6.1 to 9.4°C during the experiment.

A population of nine wild underyearling coho was introduced to the system and allowed to adjust to the apparatus for five days. The fish were fed once daily at noon on brine shrimp (Artemia salina) from a feeding device emptying into the incoming water supply. The device was adjusted to deliver two to three times as much shrimp as the fish could consume during a two hour feeding period. The excess food left the system through the downstream outlet.

After the conditioning period, tests were conducted every other day (five tests in nine days). During each test, aggressive behavior was tape-recorded in 45 minute observation periods. Food or food odor was introduced during the first ten minutes of the "feeding" observation period. Recording time amounted to about 60 percent of the total test time.

Results

The introduction of food or food odor precipitated a rapid and extensive rise in aggression, which reached intensities three to four times those of pre-feed values (Figure 23). Food odor alone was nearly as effective in this respect as the highest concentration of food presented. Duration of increased aggression was the chief difference in aggressive behavior at the various levels of feeding. Although both food odor and low food concentration (tests B and C) increased aggression, the duration of intense aggression was short and intensity fell rapidly from peak values. At higher food concentrations (D and E), the level of aggression did not peak during the observation period that included feeding but continued to rise. The fish were more aggressive nearly two hours after feeding than during the observation period that included feeding. Moreover, at the highest food concentration (E), aggression remained high and far above pre-feed levels nearly four hours after feeding.

There was a close relationship between aggressive response to feeding and the amount of food fed (Figure 24). As aggression increased slightly during the second pre-feed observation period in tests D and E, the number of pre-feed aggressive acts was subtracted from the totals for all tests. The general relationship was little disturbed by so doing.
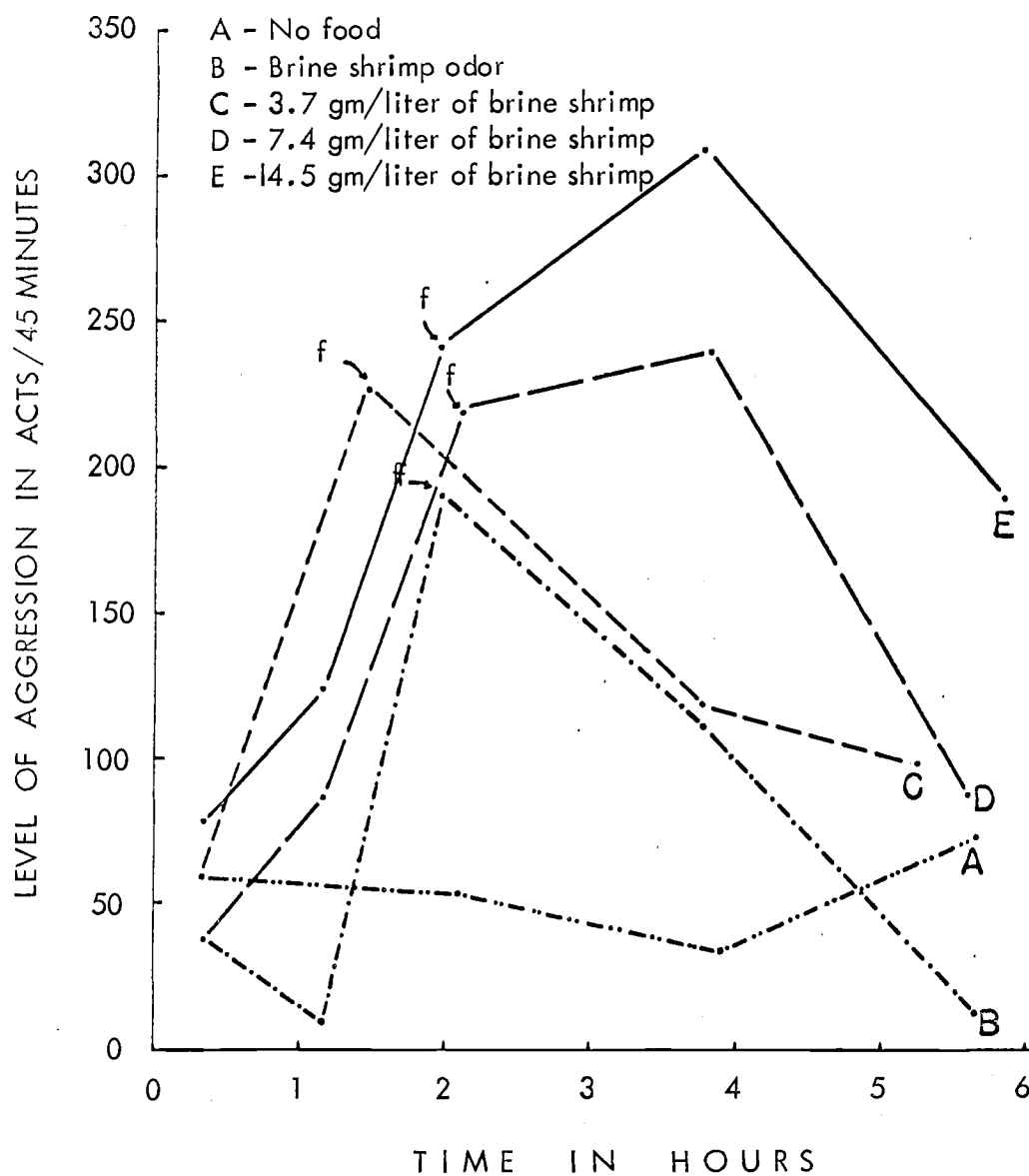
Figure 23. Influence of food concentration on the level of aggression in a small population of underyearling coho – nine fish in a riffle-pool environment. Each point represents 45 minutes of observation time – total of 17.3 hours, 58 percent of total experimental time. f – denotes the observation period wherein food was given.
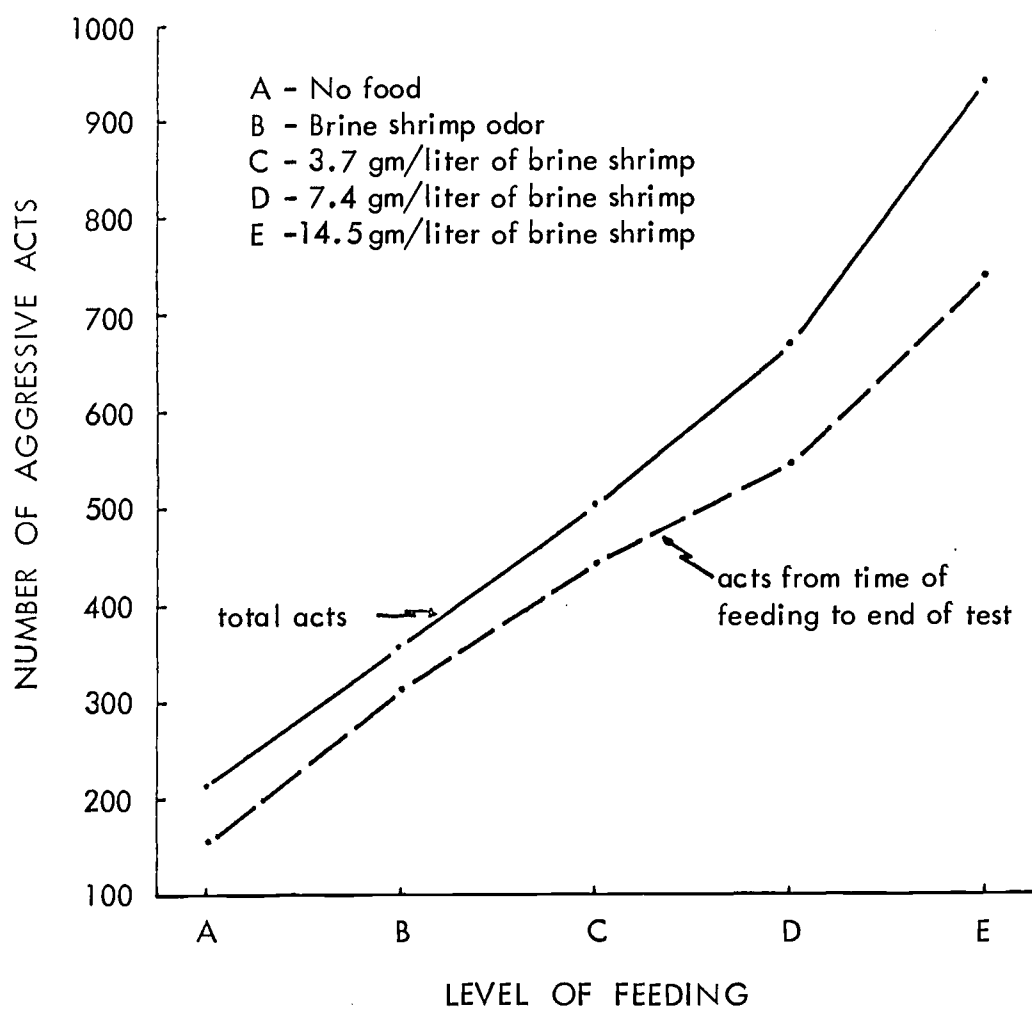
Figure 24. The influence of feeding regime on the intensity of aggression in a population of nine underyearling coho in a riffle-pool environment. Length of tests ranged from 315 to 345 minutes; each point represents nearly 60 percent of the test period.

The distribution of shrimp during feeding insured that individual fish were stimulated to move only short distances to capture food. Three of the nine coho established permanent territories. One fish defended the entire riffle, one defended the runway except for a four-to-five inch alley along the glass wall, and one defended the pool. Two of the other six fish tried to maintain partial territories at the runway-pool margin. The remaining four fish were usually found in certain positions on the runway against the glass wall and two of these coho attempted to defend small areas here at different times.

Subordinate coho were tolerated in the three permanent territories prior to feeding and were driven out inconsistently and without much vigor. When food was presented, the owners of these three territories drove out all subordinates and clashed with each other at the territorial boundaries. The two partial territories at the runway-pool margin disappeared as the primary territories were expanded. The link between feeding, aggression, and territoriality was clearly revealed.

Discussion

Sustained high aggression was not associated with length of time while feeding but rather with cumulative stimulation associated with feeding. The higher rates of food delivery within the fixed time interval gave more opportunity to view, seize, taste, and swallow the shrimp.

The connection between aggression and food may thus include summation features. The possibility of time-extended feeding opportunity cannot be ruled out entirely at the higher levels of feeding. However, few, if any, shrimp remained in the system for more than a few minutes after food introduction had ceased.

These fish were conditioned to a feeding regime characterized by a spatially diluted, steady delivery of excess food over an extended time period (two hours). Territorial relations were consistent and social stability was little disturbed by an artificially high, short-term delivery of food, and scramble feeding was inhibited. Scramble feeding may be a response conditioned by past experience with a limited food supply.

SOCIAL RANK, SURVIVAL, AND GROWTH

Introduction

The use of aggression by juvenile coho to implement the pattern of food and space distribution that was described previously was examined in small hierarchies under more rigorously controlled and observable conditions in the small stream aquarium.

Apparatus and Methods

In addition to the environment used for the last experiment, the aquarium was partitioned into equal-sized, flow-through compartments. These compartments were 30 or 60 cm long, 45 cm wide, and 38 cm deep. Flow rate was kept at three liters/minute in all experiments.

Populations of underyearling or yearling coho were maintained for two or more weeks in the aquarium and their social relations recorded. Brine shrimp were introduced into each compartment through food tubes emptying into the incoming water current (Figure 26).

Results

Aggression and dominance-subordinance

Small groups of juvenile coho soon arranged themselves into hierarchies whereby a size-related dominance subordinance social order was maintained apparently through individual recognition. A
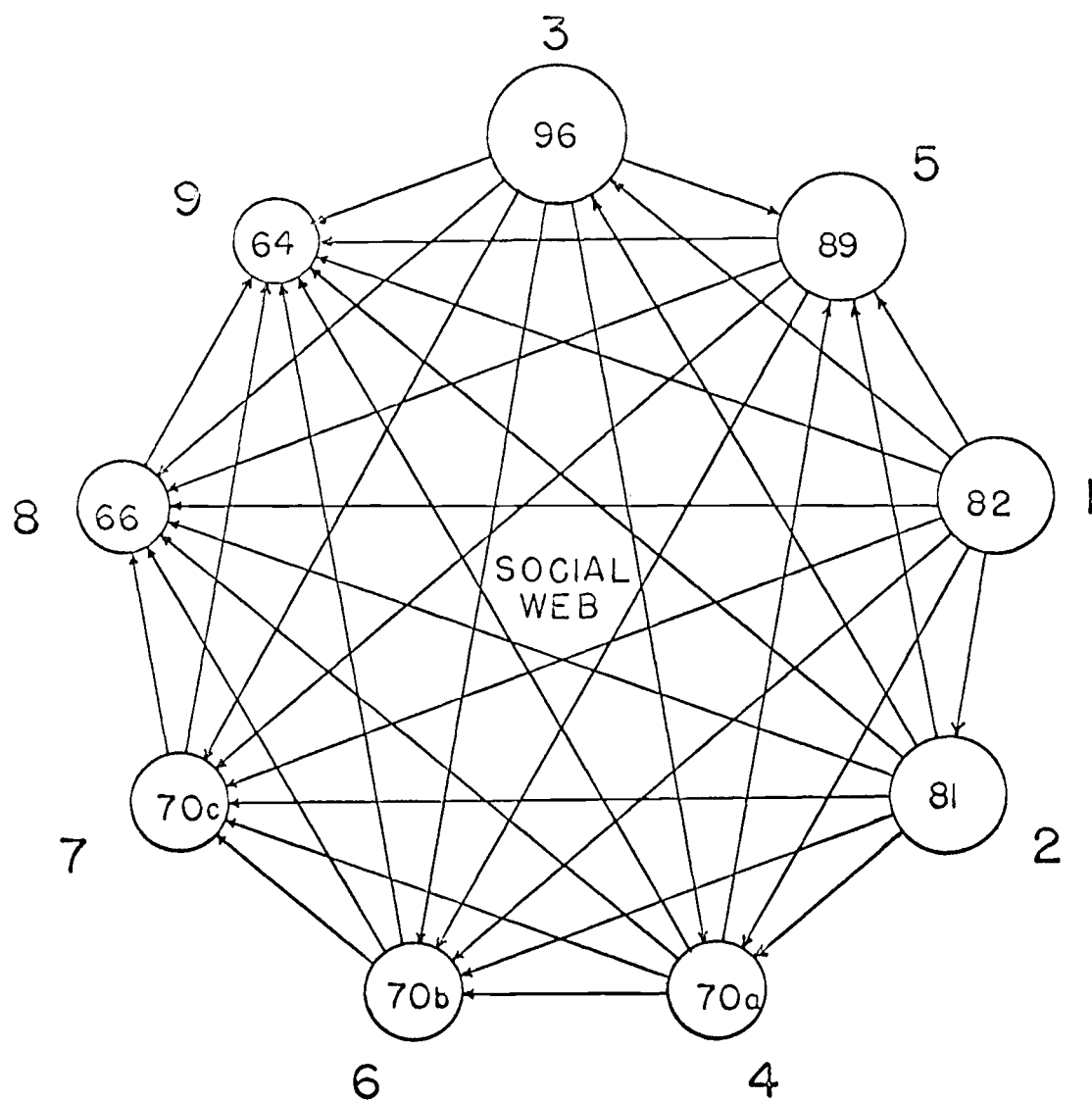
Figure 25. Dominance-subordinance relations in a small hierarchy of under-
yearling coho. Encircled values indicate length of fish in milli-
meters, large numerals indicate social rank, and arrows indicate
the direction of social dominance. Based on 26 hours of observ-
ation involving 6,598 aggression points.
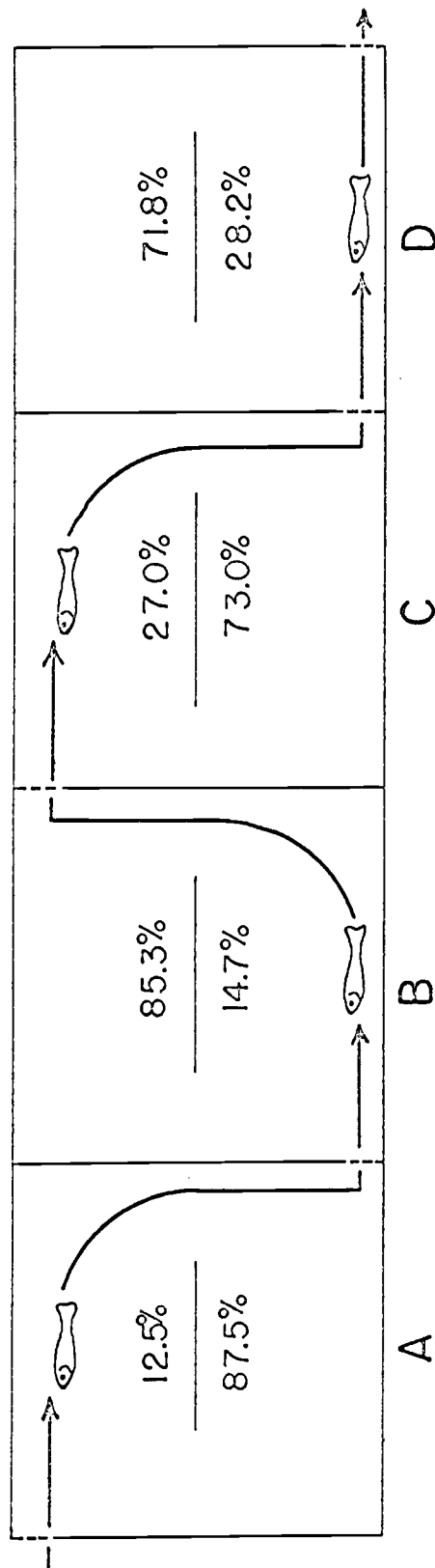
Figure 26.   The amount of time spent in the upper and lower half of each compartment by the despot in five-fish hierarchies, expressed as percentages.   Based on the number of sightings in the upper half of each compartment – position recorded every minute of the first twenty minutes of each hour for ten hours on two successive days (400 observations).   The despots are shown in their feeding position in the primary current.

social web for the population of nine underyearlings is illustrated in

Figure 25, based on the social interaction data compiled in Table 20

where interaction has been converted into social points (Table 19).

Only 2 of 72 possible pairs of interaction ($n^2 - n$) were not observed

in 26 hours of observation spread over 9 days (Table 20).

Rather than a nip-right hierarchy wherein aggression is directed

only at subordinate individuals, juvenile coho exhibited nip-dominance

organization. Social rank and the pattern of distribution of aggression

in terms of social points given and received by individual fish are com-

piled in Table 21. Social rank was determined from the number of pairs

in which a fish was subordinated by its partner. Within a pair, the

subordinate fish received more aggression from its partner than the

partner received in return. The dominance-subordinance pattern re-

vealed a straight-line hierarchy. There were no triangles.

In general, the higher the social rank, the larger the share

of total aggression given by the individual and the lower the amount of

aggression received. All fish participated actively in social inter-

action, the percentage values of total involvement ranging from 5.7

to 15.3 percent. When social involvement was expressed as the

quotient of aggression points given divided by points received (G/R),

the ranking order of quotients closely followed the social ranking order,

high values being associated with high social rank. The brunt of the

TABLE 20.   BREAKDOWN OF THE SOCIAL INTERACTION IN A HIERARCHY OF NINE UNDER-
YEARLING COHO (IDENTIFIED BY LENGTH) IN A SMALL STREAM AQUARIUM,
RECORDED AS AGGRESSION POINTS.   SEE TABLE 2 FOR DETAILS OF POINT
SCORING.

| | | | | | AGGRESSION POINTS GIVEN | | | | | |
Coho	95	89	82	81	70(a)	70(b)	70(c)	66	64	Sum
95	*	46-1/2	177	96	16	25	14-1/2	3	4	382
89	85	*	138	79	63	13-1/2	27-1/2	0	6-1/2	412-1/2
82	50-1/2	42-1/2	*	41-1/2	21-1/2	0	1	1/2	1	158-1/2
81	71-1/2	11	78-1/2	*	110	11-1/2	29-1/2	8	2-1/2	322-1/2
70(a)	48	18	163	120-1/2	*	59	77-1/2	5	2-1/2	428-1/2
70(b)	60	67	21	213	141	*	12-1/2	1-1/2	10	828
70(c)	152-1/2	46	59	156	378	144-1/2	*	3	2	704
66	209-1/2	51-1/2	343	442	374	322-1/2	172-1/2	*	31	1946
64	160	56	264	258-1/2	311	297	19	51-1/2	*	1417
Sum	837	338-1/2	1243-1/2	1406-1/2	1414-1/2	873	354	72-1/2	59-1/2	6599

AGGRESSION POINTS RECEIVED

TABLE 21. HIERARCHICAL SOCIAL RELATIONS AMONG NINE UNDERYEARLING COHO BASED ON AGGRESSION POINT SCORES.

Social Rank	Coho (length in mm)	Aggression Points Given	%	Aggression Points Rec'd	%	G/R	Total Involvem't	%
1	82	1243-1/2	18.8	158-1/2	2.4	7.9	1402	10.6
2	81	1406-1/2	21.3	322-1/2	4.9	4.2	1729	13.1
3	96	837	12.7	382	5.8	2.2	1219	9.2
4	70(a)	1414-1/2	21.5	428-1/2	6.5	3.4	1843	14.0
5	89	338-1/2	5.1	412-1/2	6.2	0.8	751	5.7
6	70(b)	873	13.2	828	12.5	1.1	1701	12.9
7	70(c)	354	5.4	704	10.7	0.5	1057	8.0
8	66	72-1/2	1.1	1946	29.5	0.4	2018-1/2	15.3
9	64	59-1/2	0.9	1417	21.5	0.4	1476-1/2	11.2
Total		6599	100.0	6599	100.0		13198	100.0

total aggression was born by the smaller fish of lowest social rank.

Coho 8 and 9 sustained 51 percent of the total aggression dispensed

within the hierarchy and from 49 to 71 percent originated from the

four coho of highest social rank.

Survival and Growth

Survival and growth in small populations of underyearlings and

yearlings were related to social rank. Social rank, survival, and growth

relations in four hierarchies of five underyearlings held in small compart-

ments are given in Table 22. The bottom area of 1350 cm^2 was purposely

made less than the space requirements of two territorial fish within the

range of size used. The result was that the most aggressive coho de-

fended the entire compartment as a territory and ruled as a despot.

In each hierarchy, one or two fish died during the experiment,

mortality occuring in two populations within the first week (Table 22).

Both large and small fish died but social rank was either the lowest

(fifth) or next lowest just prior to death. Social rank was size-related

and social rank among survivors remained stable. The ratios of

aggression points given and received (G:R) followed the order of social

ranking. Only the despots grew, and their weight increase was higher

during the second week (5.4 to 7.7 percent weight gain) despite the

presence of excess food. The despots were satiated at every feeding

and, on the average, dispensed 79 percent (59 to 99 percent) of the

TABLE 22. SOCIAL RANK, DISTRIBUTION OF AGGRESSION, SURVIVAL AND GROWTH IN HIERARCHIES OF FIVE UNDERYEARLING COHO. AGGRESSION WAS RECORDED THREE TIMES WEEKLY FOR A TOTAL OF THREE HOURS PER HIERARCHY.

Hierarchy/coho		Initial Values			Week One			Week Two		
		Length in mm	Weight in gm	Condition Factor (K)	%Weight Change	Social Rank	(G:R)	Total %Weight Change	Social Rank	(G:R)
I	1	60.0	2.007	0.929	died on day 6	4	1:28			
	2	57.5	1.847	0.972	+1.3	1	72:1	+7.7	1	59:2
	3	55.3	1.619	0.958	11.5	3	0:17	died on day 10	4	0:36
	4	55.0	1.548	0.930	6.0	2	28:14	7.9	2	38:27
	5	50.1	1.135	0.903	4.3	5	0:40	4.6	3	2:35
II	1	60.2	1.950	0.894	+3.3	1	84:3	+7.5	1	71:3
	2	58.3	1.936	0.977	5.4	2	12:19	9.8	2	21:10
	3	57.8	1.816	0.941	8.4	3	1:36	-9.0	3	4:26
	4	51.5	1.301	0.958	7.7	4	3:32	12.4	4	3:61
	5	49.1	0.973	0.822	died on day 4	5				
III	1	60.0	2.133	0.987	5.7	2	11:24	7.5	2	15:21
	2	57.4	1.859	0.983	6.6	4	1:28	10.7	3	15:24
	3	54.5	1.486	0.923	0.7	1	73:2	+7.1	1	71:2
	4	53.9	1.394	0.890	9.0	3	15:19	8.6	4	0:28
	5	48.2	1.018	0.909	6.4	5	1:27	died on day 14	5	0:26
IV	1	59.8	2.066	0.966	14.6	2	1:55	died on day 10	5	0:1
	2	56.3	1.767	0.990	+0.8	1	99:1	+5.4	1	99:0
	3	55.5	1.663	0.973	6.6	3	0:10	11.5	2	0:34
	4	52.6	1.315	0.903	9.0	4	0:31	7.3	3	1:36
	5	50.0	1.229	0.983	15.5	5	0:5	19.5	4	0:30

Note: Total aggression points for weeks one and two were as follows: Hierarchy I – 463 and 1140; Hierarchy II–794 and 399; Hierarchy III–392 and 597; Hierarchy IV–534 and 593. G:R is the ratio of aggression points given (G) and received (R) expressed as percentages.

total aggression recorded.

Population Size and Social Complexity

Compartment size was doubled by removing two of the inside partitions. Ten underyearlings of a range and distribution in size comparable to those of the previous hierarchies were put in each compartment. The general experimental procedure remained unchanged.

In both ten-fish hierarchies, the second largest coho became the despot although there was only a small length difference between the two largest fish. The dominant coho in hierarchy I defended the entire upper half of the compartment plus some 60 percent of the bottom area. In both groups, the largest subordinates established three to four partial territories that were spatially and temporally unstable.

No fish died in either hierarchy and the weight loss of subordinates was reduced for most coho (Table 23). Only the dominants grew but their percentage weight gains were somewhat lower than in the previous experiment. Initial condition factors were similar for the majority of fish.

There was a marked reduction in the relative share of aggression dealt out by the despots. These fish accounted for 29 and 48 percent of the total aggression recorded, 17 and 30 percent originating from the first subordinate coho. Social ranking was less stable than in the five-fish hierarchies but shifts in rank were not extensive and may reflect

TABLE 23. SOCIAL RANK, DISTRIBUTION OF AGGRESSION, AND GROWTH IN HIERARCHIES OF TEN UNDERYEARLING COHO. AGGRESSION WAS RECORDED THREE TIMES WEEKLY FOR A TOTAL OF SIX HOURS PER HIERARCHY.

Hierarchy/coho	Length in mm	Weight in gm	Condition Factor (K)	Week One %Weight Change	Week One Social Rank	Week One (G:R)	Week Two Total %Weight Change	Week Two Social Rank	Week Two (G:R)
1	59.7	2.293	1.078	4.1	8	3:16	6.7	7	5:21
2	59.6	2.304	1.088	1.1	1	30:4	+2.2	1	29:1
3	58.2	2.162	1.096	1.2	2	30:6	1.5	2	23:5
4	57.6	2.049	1.072	5.2	7	5:7	9.4	5	9:4
5	56.2	1.920	1.081	4.7	6	4:4	6.6	6	0:5
6	56.0	1.801	1.025	4.7	5	4:23	3.3a	3	17:2
7	54.0	1.723	1.094	2.5	3	11:5	1.7a	4	10:10
8	53.9	1.643	1.049	0.9	4	6:10	3.1	8	5:22
9	52.0	1.495	1.024	2.1	10	1:21	4.2	10	2:5
10	51.9	1.328	0.950	2.9	9	5:6	5.9	9	0:25
				Total aggression points = 1310			= 1700		
1	60.9	2.425	1.074	5.4	6	3:11	10.0	7	0:25
2	59.5	2.223	1.055	+0.7	1	35:1	+6.2	1	48:2
3	57.2	2.086	1.115	4.9	3	14:7	6.3	2	17:5
4	57.0	1.898	1.025	3.7	5	5:3	5.8	6	2:5
5	56.2	1.834	1.033	1.9	2	25:6	5.3	5	6:8
6	55.2	1.644	0.977	0.8	9	2:17	1.4	9	3:15
7	54.0	1.714	1.089	3.5	7	4:15	5.0	4	4:8
8	52.7	1.458	0.996	2.8	8	3:13	5.6	8	6:15
9	52.0	1.531	1.048	+0.6	4	9:10	2.5	3	12:10
10	51.0	1.358	1.024	10.0	10	0:17	14.8	10	2:8
				Total aggression points = 1549			= 1789		

a fish gained weight in week two.

insufficient observation time rather than actual rank changes.

Groups of four yearlings were held in the four compartments and fed sparingly on brine shrimp to assess effects of a limited food supply upon the social relations described above. These fish were considerably larger than the underyearlings, being 61 to 95 mm in length. In all four groups, the largest coho quickly became despotic. The despots consumed all the available food and their weight changes reflected food availability (Table 24). All subordinates survived but lost weight, and the severest loss was sustained by the smaller individuals. Any potential influence of condition factor on social relations was probably offset by the appreciable differences in size. Social rank paralleled rank in size within each hierarchy.

Despotism and Social Control

When not being fed, the despots in the hierarchies of five fish spent most of their time in the half of the compartment least affected by the current flow through the system (Figure 26). Subordinates were kept in the bottom half of the compartment, in the corners and along the sides, and away from the food-current entrance when it was located at the bottom of the compartment. Even when satiated in the presence of excess food, each despot attempted to deny feeding privileges to all subordinates and was highly aggressive following the presentation of food.

TABLE 24.   WEIGHT CHANGES IN HIERARCHIES OF FOUR YEARLING
            COHO KEPT ON RESTRICTED RATIONS FOR 37 DAYS,
            APRIL 18 to MAY 25, 1964.

Hierarchy/coho		Length in mm	Weight in gm	Condition Factor (K)	%Length Change	%Weight Change
		INITIAL FACTORS			TERMINAL VALUES	
I	1	95	8.82	1.029	+4.2	+7.1
	2	82	5.78	1.048	none	⁻6.8
	3	74	3.60	0.888	"	⁻16.7
	4	60	2.15	0.995	"	⁻15.6
II	1	93	7.98	0.992	+3.8	+15.8
	2	82	5.78	1.048	none	⁻7.4
	3	71	3.73	1.042	"	⁻19.0
	4	61	2.13	0.938	"	⁻22.1
III	1	90	7.25	0.995	none	⁻4.4
	2	81	4.95	0.931	"	- 8.1
	3	70	3.58	1.044	"	-10.1
	4	66	2.68	0.932	"	-13.4
IV	1	90	7.85	1.077	none	- 7.3
	2	76	4.42	1.007	"	-15.6
	3	70	3.58	1.044	"	-10.6
	4	66	2.88	1.002	"	-21.5

Note: all fish in III and IV lost weight.

Mortality, extensive weight loss, distribution of aggression, and the psycho-physiological state of subordinates indicate a strong degree of social control by the despot in hierarchies of both underyearling and yearling coho despite an abundance of food.

The despot's aggression could be inhibited by feeding houseflies of sufficient size as to prevent rapid consumption yet small enough that the despot's interest did not wane, to the point of rejection and variable behavior toward the fly. A short description of the test procedure is as follows: a fly of suitable size was introduced at the water surface after aggressive interaction had been tape-recorded for 20 minutes. Aggression was recorded until the fly was consumed (feeding period), and for a subsequent 10-minute period. Time from seizure to swallowing was variable and the despot swam about holding the fly securely in its jaws from eight to fifteen minutes before swallowing the insect. The results of four tests in the four underyearling hierarchies are depicted in Figure 27.

Most of the aggression was dispensed by the despot during the pre-feeding period. Aggression directed at the despot was seen in only one hierarchy and then composed only a minor fraction of subordinate aggression. Most of the latter aggression was distributed among the subordinates. The despot became markedly less aggressive while preoccupied with the fly. The first subordinate coho became very
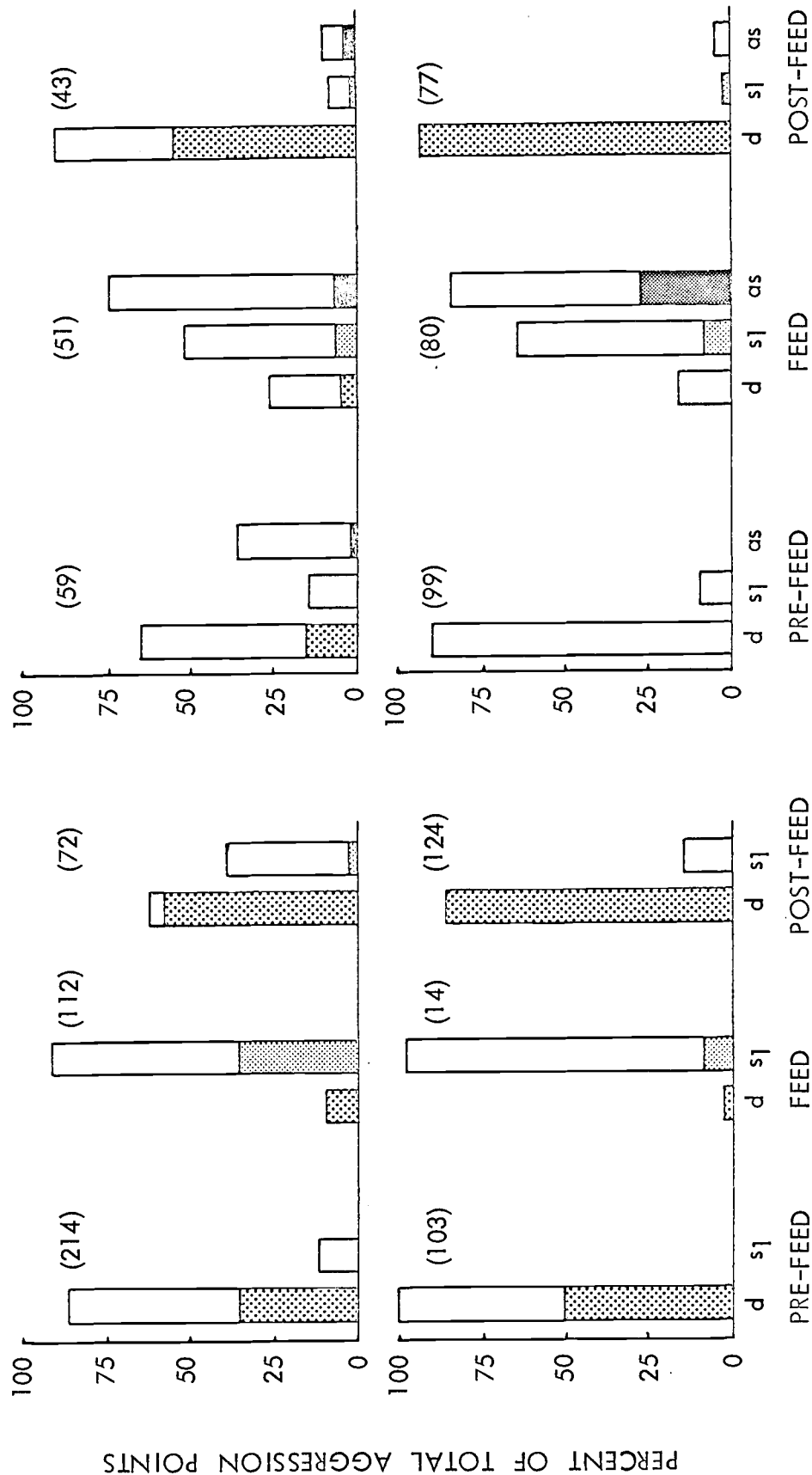
Figure 27. Inhibition of the despot's social control, role of subordinate-1, and recovery of social control by the despot in four hierarchies of five underyearling coho each. Symbols as follows: d – despot, s] – first subordinate, as – all subordinates. ▦ – given to s] by the despot, ▨ – given to the despot by s], ▩ – given to the despot by all subordinates, ( ) – total aggression points given in the hierarchy.

PERCENT OF TOTAL AGGRESSION POINTS

137

aggressive and the other subordinates showed some aggression in two

of the four hierarchies (upper and lower right histograms in Figure 27).

Only the despot and first subordinate were aggressive in hierarchies I

and II (upper and lower left histograms). After swallowing the fly, the

despot again became highly aggressive while subordinate aggression

decreased drastically. The despot rapidly regained social control of

the hierarchy.

The significance of these events is made clearer when the shifts

in distribution of aggression are examined further. Although the first

subordinate fish (s_1) experienced a variable amount of the despot's

aggression prior to feeding, it received most of the aggression during

the post-feeding period when the despot was regaining social control.

In hierarchies III and IV (two right-hand histograms in Figure 27) more

than one subordinate displayed aggression during the feeding period,

and directed some aggression at the inhibited despot. The despot

responded aggressively but at a low level, and directed its aggression

at several subordinates. Little or no aggression was directed at the

despot during pre-feeding and post-feeding periods.

During these tests, aggression levels within each hierarchy

fell within the following ranges: 6.0 - 7.9; 2.1 - 4.3; 4.1 - 10.7;

and 4.8 - 7.3 acts/coho/10 minutes. No trends between periods were

discernable. Possibly, the precise temporal relations of aggression

during the feeding and post-feeding periods remained undetected due to the recording procedure.

Discussion

As in other vertebrates, hierarchical social organization in fishes may involve strong precedence features applied to the distribution of available resources. When resources are limited, high social rank insures better access to food and space and results in superior growth. Higher survival and resistance to disease and starvation are logical outcomes of better access to food and space. The rigorous social control exerted by despotic individuals emphasizes the role of territoriality in competition among juvenile coho. The link between food and space as vital resources is clearly shown by the efforts of despots to deny feeding privileges to subordinates when satiated and in the presence of excess food. But the ecological significance of this behavior remains unclear since the role of conditioning to artificial feeding regimes is yet to be assessed. However, inhibition of feeding by subordinates when dominant individuals are able to defend a localized food source by including the source within their territories was reported by MacPhee (1961), Magnuson (1962), Chapman (1962), and Yamagishi (1962).

Increased aggression of despots in the presence of food did not appear to result from loss of social control. Very subtle changes in

the behavior of quiescent subordinates may have gone undetected by the observer. The slightest attempts of subordinates to feed incurred severe punishment from the despot. Subordinate coho stayed in corners and along the sides of the compartment on the bottom. They displayed very submissive postures, e.g., resting in a head-up or head-down position with collapsed fins and showing very dark coloration. Starving subordinates watched brine shrimp passing within a few centimeters of their positions but rarely moved to seize them. When shrimp passed close to the mouth of such a fish, the shrimp was sometimes snapped up. Such feeding was usually followed by an obvious shrinking down into the substrate.

Despite the high degree of social control exerted by despots in small groups of fish, the response of subordinates to their inhibited despot suggests that the seeds of revolution were ever-present. Subordinates were quick to demand proof of superiority, indicating the constant competitive pressure for satisfaction of needs when available resources are limited. These results cannot be construed to mean that social conditioning was not an effective tool at the disposal of the despot. Despots discouraged subordinates from feeding by actively patrolling the territory and punishing subordinates. One would think that motivation to feed would be rather strong in starving individuals. Probably, despotic social relations do not occur in nature to the degree

noted in these experiments, which were designed purposefully to elicit despotism in a simplified environment.

THREAT DISPLAY AND SOCIAL RELATIONS

Description of Display

The threat displays of salmon and trout consist of rather stylized postures in which various parts of the body, particularly the fins that may be highly colored, are used to create conspicuous effects of signal value to other members of the species. Threat displays have been interpreted as behavior patterns involving conflict between attack and escape tendencies (Tinbergen, 1952; Lorenz, 1964).

Intensity of aggression appears to play a role in these displays. The frontal threat is highly aggressive, of short duration, and most frequently seen just prior to attack in brown trout and juvenile Atlantic salmon (Kalleberg, 1958; Kennleyside and Yamamoto, 1962). Lateral threat in these species is of much longer duration than frontal threat and is probably more defensive in character since mutually aggressive juvenile Atlantic salmon employ lateral threat more frequently than frontal threat in such encounters (Keenleyside and Yamamoto, 1962). Lateral threat in juvenile coho is of variable duration, lasting from a few seconds to a minute or more.

Juvenile coho, both underyearlings and yearlings, were not seen to use the frontal threat display described by Kalleberg (1958). Under the variety of experimental conditions in the present work, threat display consisted entirely of lateral threat. Hartman(1965) reported frontal

threat in juvenile coho but in rather low incidence. Threat display in populations of underyearlings in the main stream aquaria consisted mostly of horizontal display, the latter accounting for 21.4 to 28.3 percent of the behavior recorded (Table 17). Threat with the head held either up or down was of much lower incidence. When approached from the downstream direction, territorial coho on the riffles either slowly elevated the tail as they assumed the threat posture or maintained the fully-developed display while in the horizontal plane and drifted downstream tail-first toward the intruder. In either case, the encounter was usually terminated by the territory-holder swinging across the current, approaching head-first, and chasing out the intruder, often with a nip action. From photographic analysis, it was determined that the body axis commonly reached a 45 degree angle to the horizontal and may exceed 50 degrees at water velocities from 18 to 23 cm/second.

The intruding coho usually responded to the defender's threat posture by adopting the horizontal display. Continued advancement or maintenance of position by the intruder when the defender had taken the head-down posture induced the latter to undulate the caudal region in a slow, rhythmic fashion. These undulations no doubt enhanced the intimidating value of the display and appeared to be related to rising aggression in the defender. The steepness of the body axis and intensity of caudal undulation both increased, and the jaws widened

when the intruder failed to heed the initial posturing, and when the drive at the intruder took place, the attack was often quite violent.

Caudal undulations accompanying lateral threat with the head pointed downward have been described also for juvenile brown trout and Atlantic salmon held under high velocity conditions (Kalleberg, 1958). This posturing was termed "wig-wag display" by Hartman (1965). The fighting behavior of spawning brown trout includes a threat posture assumed with the head held up and the body axis at about 45 degrees to the horizontal. This display has been called "dominance posturing" by Jones and Ball (1954). Undulation of the caudal region accompanying head-up and head-down threat, the body axis reaching 90 degrees from the horizontal, was described for the Kamloops trout by Stringer and Hoar (1955). Juvenile coho in the pools of the main stream aquaria displayed both head-up and head-down threat with caudal undulations, the body axis reaching 70 to 80 degrees from the horizontal plane. Head-up threat was not seen in the riffles (Table 17). These various data indicate that lateral threat display is similar in members of Oncorhynchus and Salmo, and that water velocity and depth may modify threat behavior significantly. Present observations suggest that the undulatory movements are more exaggerated and spasmodic in pools than are those accompanying head-down threat in the riffles.

Threat display in juvenile coho is modified by intensity of

aggression also. During the feeding experiment previously described,

feeding rate directly influenced intensity and duration of aggression,

aggression increasing with higher feeding rate. When plotted against

total aggression, percentage threat display fell rapidly with increased

aggression (Figure 28). The temporal change in threat frequency for

both moderate and high feeding levels is shown in Figure 29. Threat

fell more steeply at the higher feeding level although the overall change

for both feeding levels was not great. Incidence of threat when no

food or food odor alone was given showed no such change. Possibly,

the low intensity of aggression in these tests introduced variability in

otherwise weak trends. However, at the low feeding level, percentage

of threat decreased strongly upon introduction of food from an initial

value of 19 percent and stayed below 5 percent for the remainder of

the test.

Display and Social Stability

The fight pattern of juvenile coho contains a gradient of

aggressive interactions ranging from non-contact intimidations by use

of threat displays to intensive contact bites that result in loss of

scales and shredded fins. When strange fish are brought together

in groups, fighting interspersed with frequent and intense threat
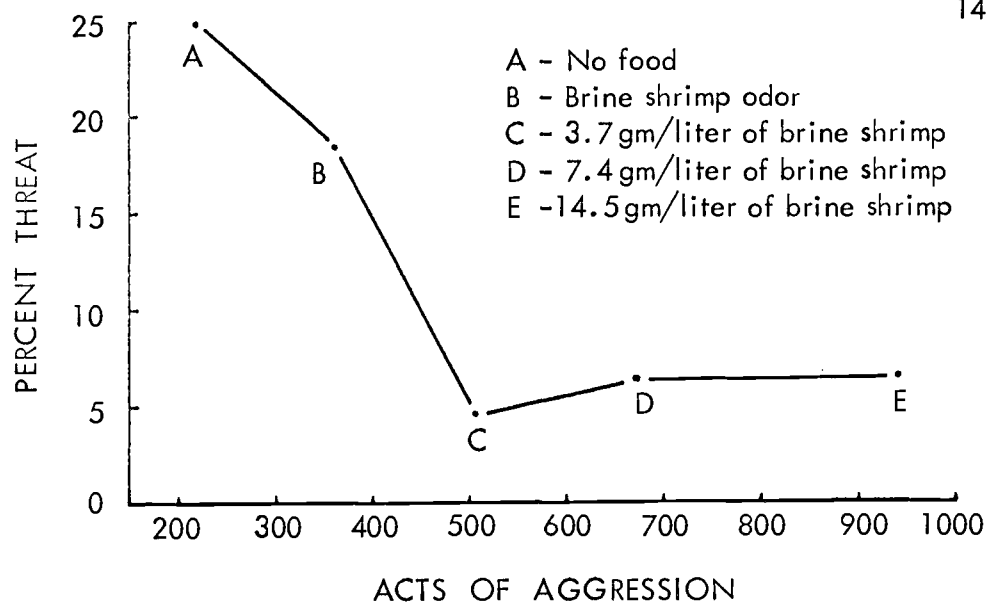
Figure 28. The reduction of threat components in the behavior of underyearling coho with rise in aggression.
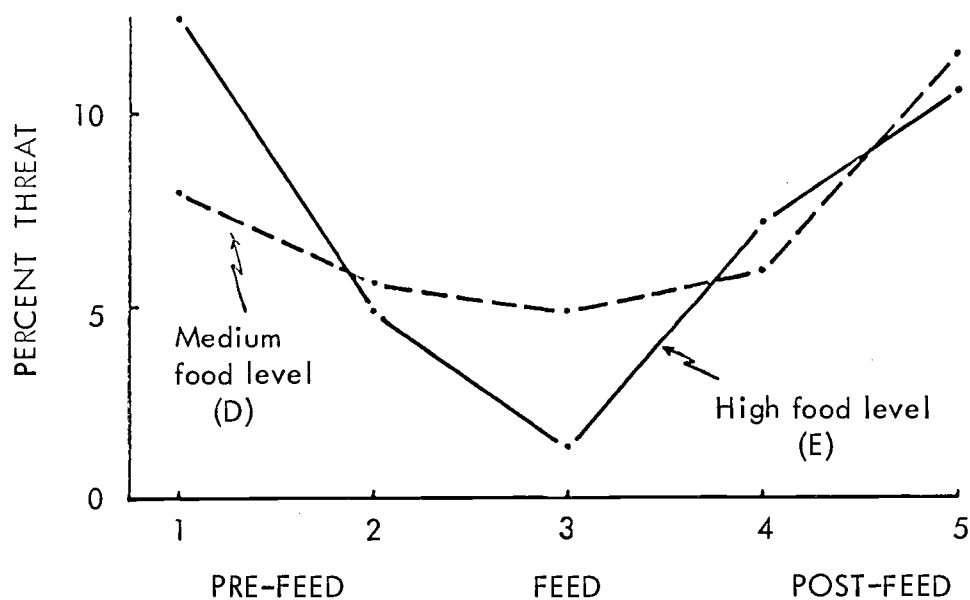
Figure 29. The temporal reduction of threat components in the behavior of underyearling coho at two levels of feeding (during five observation periods – see Figure 23).

display proceeds until a hierarchy is formed. The number of territories depends on population density and availability of bottom area. Social relations become fairly stabilized after formation of the hierarchy and the amount of threat display decreases. Reduced threat display could be the outcome of mutual recognition in small groups of fish. Mutual recognition could thus contribute to stability of the social order by lowering arousal of conflict between attack and escape tendencies during confrontations. The importance of mutual recognition in this regard in large populations containing as many as 50 to 75 fish is rather doubtful. However, the distribution patterns of coho in the main stream aquaria indicate that spatial location is related to size of the individual. This structuring of size in space may promote social stability in large populations.

Little threat display was seen in despotic hierarchies. Threat accounted for less than 15 percent (average of 6 percent) of the behavior recorded (Table 25). Doubling size of population from five to ten fish without changing density did not modify the frequency of threat despite the increased social complexity. Frequency of threat was higher in the main stream aquaria containing large populations of underyearlings. Threat ranged from 30.9 to 36.0 percent of total behavior recorded and was remarkably stable throughout the experiments (Table 17). Comparison of the two populations revealed no

TABLE 25. FREQUENCY OF THREAT BEHAVIOR AND INTENSITY OF AGGRESSION IN HIERARCHIES OF UNDERYEARLING COHO. OBSERVATION TIME WAS 3 HOURS FOR EACH OF THE 5 and 10-FISH HIERARCHIES, AND 3 HOURS 5 MINUTES FOR THE 9-FISH HIERARCHY.

	Total Acts	Percent Threat	Intensity of Aggression (acts/coho/10 min)
Hierarchies of 5 fish			
August 13-27, 1964	472	3.6	5.2
11.1-16.8°C.	409	14.9	4.5
mean = 13.8°C.	366	7.1	4.1
	309	0.6	3.4
		mean = 6.8	mean = 4.3
Hierarchies of 10 fish			
September 7-21, 1964	1212	7.1	6.7
11.1-12.7°C.	1170	5.5	6.5
mean = 11.8°C.		mean = 6.3	mean = 6.6
Hierarchy of 9 fish			
November 15-17, 1964	271	6.3	1.7
6.7-7.2°C.			
mean = 6.9°C.			

Note: population density ranged from 270-338 cm^2/coho in the 5 and 10-fish hierarchies, and was 1170 cm^2/coho in the 9-fish hierarchy.

significant differences in threat behavior although incidence of threat was slightly higher in the riffles than in the pools in both populations. The incidence of threat display in these large populations was rather low in view of the degree of social complexity involved.

Reduced use of threat with increased stability of the social order in coho is substantiated by the work of Stringer and Hoar (1955) on rainbow trout. These authors reported that the behavior of aquarium-held populations consisted mainly of nipping. Calculations made from their data show that threat made up only seven percent of total behavior recorded during eight hours of observation. Chapman (1962) reported that threat was very frequently seen in aquarium-held coho when hierarchies were being established. Further evidence is provided from data on juvenile Atlantic salmon studied by Keenleyside and Yamamoto (1962), who showed that encounters between two aggressive fish involved a low percentage of charge, nip, and chase components and a high incidence of threat - about 53 percent. In encounters between an aggressive fish and a non-aggressive fish, threat incidence was reduced to about 24 percent, but charge, nip, and chase components nearly doubled in frequency.

The incidence of threat display in the present experiments is in contrast to values reported for juvenile coho by Hartman (1965). Calculations made from his Figure 27 indicate that in populations of

40 fish, mean incidence of threat ranged from about 55 to 65 percent

at comparable water velocities. Higher frequency of threat may have

been the outcome of unstable social relations during his short-term

experiments. Behavioral differences may also be induced by differences

in history of confinement prior to testing. Aggressiveness of juvenile

Atlantic salmon was greatly modified by time in captivity and holding

facility (Keenleyside and Yamamoto, 1962). Fish held in the test aquaria

prior to testing were considerably more aggressive than fish held in

circular holding tanks but with previous experience in the test aquaria.

The latter group were less aggressive than fish only recently confined

in these tanks and having no experience in the test aquaria. In addition

to adjustment to the apparatus, methodology in behavioral studies of

social groups of animals must take into account sufficient opportunity

for psycho-social adjustments among animals that are previously

strangers to one another.

SUMMARY

1. To supplement behavioral observations made in the large stream

 aquaria, the significance of aggression as an instrument imple-

 menting social relations was explored further in several experi-

 ments conducted in a small stream aquarium allowing more

 adequate control of some important environmental factors.

2. Advanced alevins distributed themselves in a riffle environment

 in accordance with their degree of yolk absorption. The up-

 stream area was dominated by the well-developed individuals.

 These upstream fry defended territories and showed much higher

 aggression than did less-advanced, downstream fish. The

 quality of aggression changed with time (behavioral maturation)

 but coho fry are capable of complex behavioral interaction in-

 volving threat displays and territoriality at time of emergence

 from the gravel. Delay in the appearance of aggression noted in

 a previous experiment (first emergence experiment) may have been

 the result of delayed competition through initially unlimited food

 and space. Onset of interest in feeding is associated with the

 amount of unspent yolk reserve, and the hunger drive appears to

 be related to the onset of aggression.

3. The connection between feeding and aggression was explored in

a pool-and-riffle environment containing wild underyearlings conditioned to feed on _Artemia salina_. A direct relationship was found between feeding opportunity and aggression. The stimulation to feed may involve summation features since aggression continued to increase after feeding stimulus was removed but decreased rapidly when little food or food odor only was presented. A ceiling on intensity of aggression was reached from pre-feeding norms regardless of the amount of food given or if food odor alone was given. Presentation of food resulted in increased aggression and disappearance of partial territories. Territorial fish displayed reduced tolerance of boundary violations and expanded their territories to include space previously occupied by subordinates. The link between aggression, feeding, and territoriality was clearly revealed.

4. The use of aggression to implement the pattern of food distribution in the main stream aquaria was examined more closely in small hierarchies. A size-related dominance-subordinance social order was found that is apparently based on individual recognition. Juvenile coho in small groups exhibited nip-dominance organization, individuals of high social rank dispensing most of the aggression but receiving the least in return.

5. In despotic hierarchies, the despot claimed all or nearly all of the available environment as its territory, death was associated with low social rank, and all fish except the despot lost weight.

The despots gained weight, fed to satiation, and prevented sub-ordinates from feeding even when more food was present than the hierarchy could consume. Increasing the social complexity of hierarchies by doubling size of groups without changing density resulted in no mortality, reduced weight loss by subordinates, and possibly lessened stability in social ranking. In addition, there was a marked reduction in the relative amount of aggression dealt out by the despot and the high-ranking subordinates defended three to four partial territories characterized by spatial and temporal instability.

6. Threat display in juvenile coho is described in some detail and with regard to its behavioral context. The influence of physical environmental factors and social relations, particularly social stability, on threat display is examined by drawing together relevant data from the present work and from the literature. Intensity of aggression was inversely correlated with frequency of threat display.

DAILY AND SEASONAL CHANGES IN BEHAVIOR

INTRODUCTION

In addition to marked seasonal changes in activity, fishes often show rhythmic activity of a diel nature. Such daily patterns may involve relocation through shore-oriented migration in lake populations as reported by Spoor and Schloemer (1939), Carlander and Cleary (1949), Hasler and Bardach (1949), and Hasler and Villemonte (1953). They may also be an integral part of the reproductive cycle (Lorz and Northcote, 1965). That freshwater fishes may undergo diel vertical movements similar to those found in marine species has been documented by several workers (Johnson, 1961; McNaught and Hasler, 1961; Northcote et al., 1964).

Many of these daily cycles probably involve patterns of feeding activity characteristic of the species and its particular ecological circumstances. Peaks of activity during the diel cycle show temporal differences between species (Clausen, 1933, 1936; Spencer, 1939; Higginbotham, 1947) and temporal relations differ in multi-species populations (Hart, 1931). Feeding and, or, activity rhythms may be associated with dawn and dusk (Oliphan, 1957; Alabaster and Robertson, 1961; Darnell and Meierotto, 1961; Swift, 1962, 1964).

The large populations of underyearling coho in the stream aquaria presented the opportunity to determine whether or not their daily behavior

contained rhythmic elements, and to consider the possible significance of light and water temperature on behavioral rhythms. General observations were also made on behavior during the winter and the following spring, and on behavior associated with smolting. The aggressive behavior of yearling smolts was studied in flow-through aquaria with regard to the transition to esturarine salinities.

HORIZONTAL DISTRIBUTION ON THE RIFFLES

Significant diel changes in density of fish were apparent only for riffle 1 in both stream aquaria, the numerical changes involving passage of coho to and from pool 1. Five daily cycles of density relations on riffle 1 are depicted in Figure 30. The sampling dates, represented by the sequence A through E, and associated weather data are given in Table 26. In the sequence A-E, the daily trend consisted of high densities during the pre-sunrise and post-sunset periods that are separated by a fairly consistent low density during most of the daylight hours. This cycle occurred regardless of weather conditions and water temperature regime, the weakest and strongest cycles (C and E) obtaining during the identical weather conditions and similar course of temperature. The density cycle did not appear to be keyed to water temperature as a primary directive factor since the cycle was well-defined on June 30 (B) when associated with a very shallow daily pulse
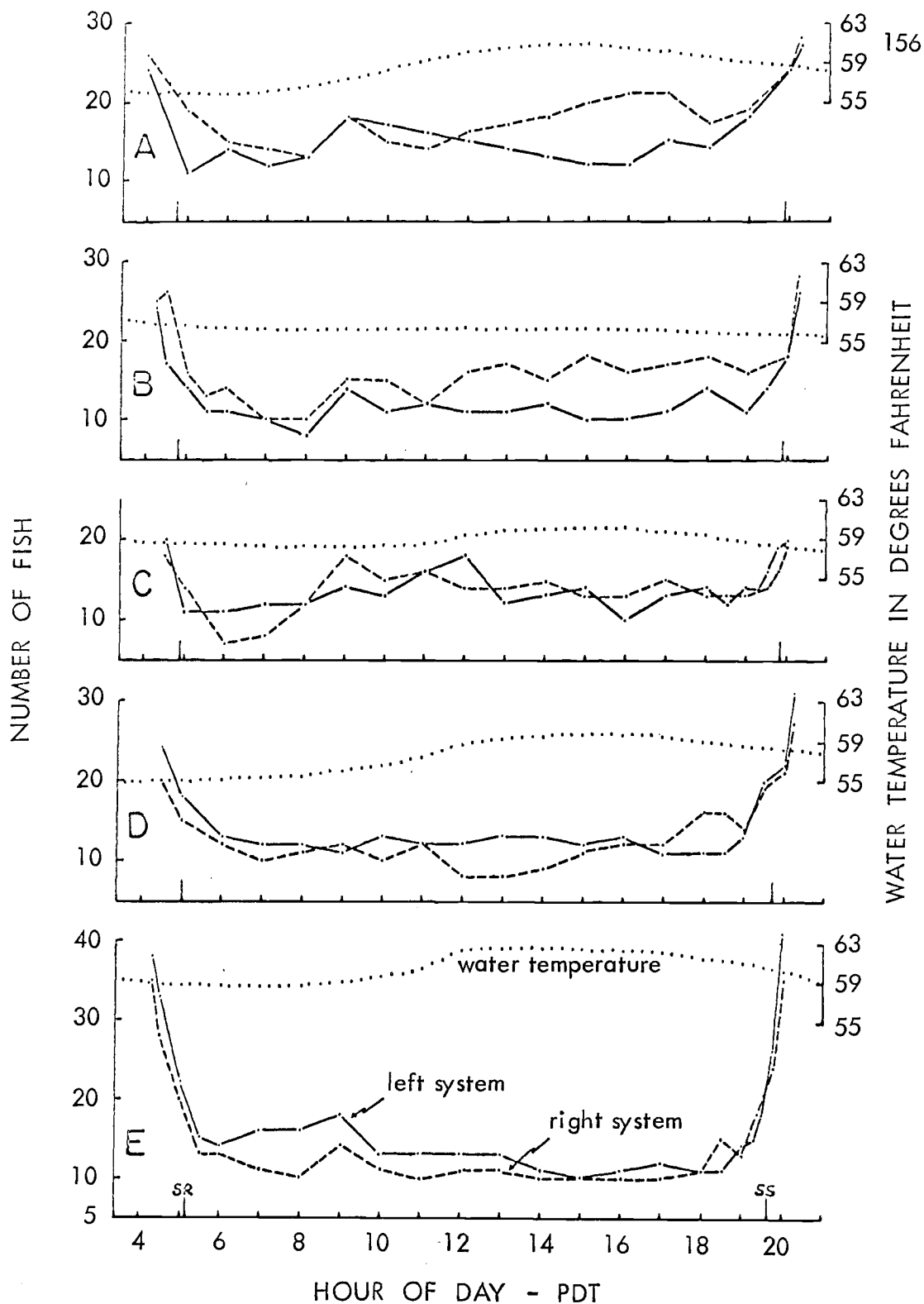
Figure 30. Daily cycle of density change in riffle 1 in both stream aquaria. SR – sunrise, SS – sunset.

TABLE 26. GENERAL WEATHER CONDITIONS ON DAYS WHEN ACTIVITY CYCLES WERE RECORDED FOR POPULATION II (EMBRYONIC STRESS EXPERIMENT).

	Date	Weather Conditions
A	June 23	Solid overcast all day.
B	June 30	Solid overcast until noon when the sun broke through. Clouds gave way to a nearly clear sky by late afternoon.
C	July 7	Cloudless and warm.
D	July 15	Light rain until 0800 hours with partial clearing and occasional sun until 1300 hours, followed by a solid overcast for the rest of the day.
E	July 28	Cloudless and warm.

in temperature.

The density of coho in riffle 1 decreased due to growth-related expansion of space needs by territorial fish, the greater decrease in density taking place in the right system (Table 27).

VERTICAL DISTRIBUTION IN THE POOLS

Each pool was divided optically into three strata of similar thickness by fastening pairs of horizontal nylon cords to both front and rear walls. The water surface was used as the upper limit of the surface stratum. Vertical distribution of fish was recorded by counting the number of fish in the surface and bottom strata throughout the day (Figures 31 and 32). The records for pool 2 are similar but more variable due to the small number of coho present there.

No daily trends in vertical distribution were discernable in either system but significant trends in magnitude of counts, based on hourly counts from 6:00 AM to 7:00 PM, were apparent over the five week period (Table 27). In the left system, the number of fish in the bottom stratum increased slightly but steadily from week to week while surface stratum counts decreased sharply (Figure 31). In the right system, surface stratum counts were initially quite low and increased steadily so that, during the last week, surface counts were nearly equal in both systems (Figure 32).

TABLE 27. CHANGES IN THE DISTRIBUTION OF POPULATION II
(EMBRYONIC STRESS EXPERIMENT) IN THE STREAM
AQUARIA. MEAN DENSITIES ARE BASED ON HOURLY
COUNTS FROM 0600 TO 1900 HOURS.

	June		July		
	23	30	7	15	28
Riffle 1					
Left stream aquarium	14.2	11.2	13.2	12.6	13.2
Right stream aquarium	16.9	14.9	13.2	11.0	10.9
Distribution in pool 1					
Left surface stratum	45.7	30.9	29.4	24.0	24.6
Left bottom stratum	6.6	10.8	11.1	13.9	13.9
Right surface stratum	6.1	18.1	13.5	18.8	25.8
Right bottom stratum	17.0	15.0	23.5	16.1	18.5
Secondary feeding current					
left	10.7	13.1	13.2	15.9	21.2
right	22.4	19.1	30.3	24.6	25.4
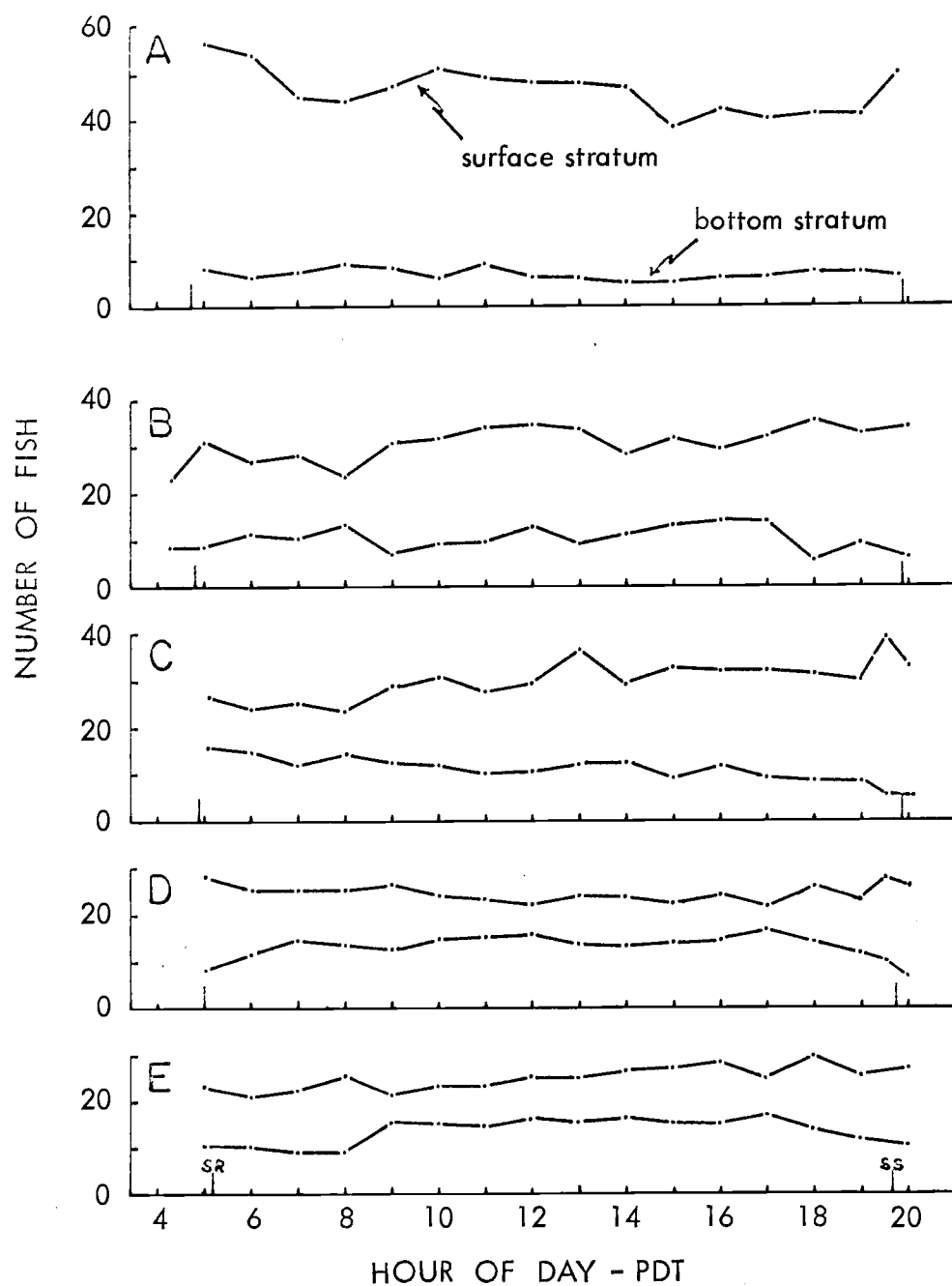
Figure 31.   Daily record of changes in vertical distribution of fish in pool 1 of the left stream aquarium.
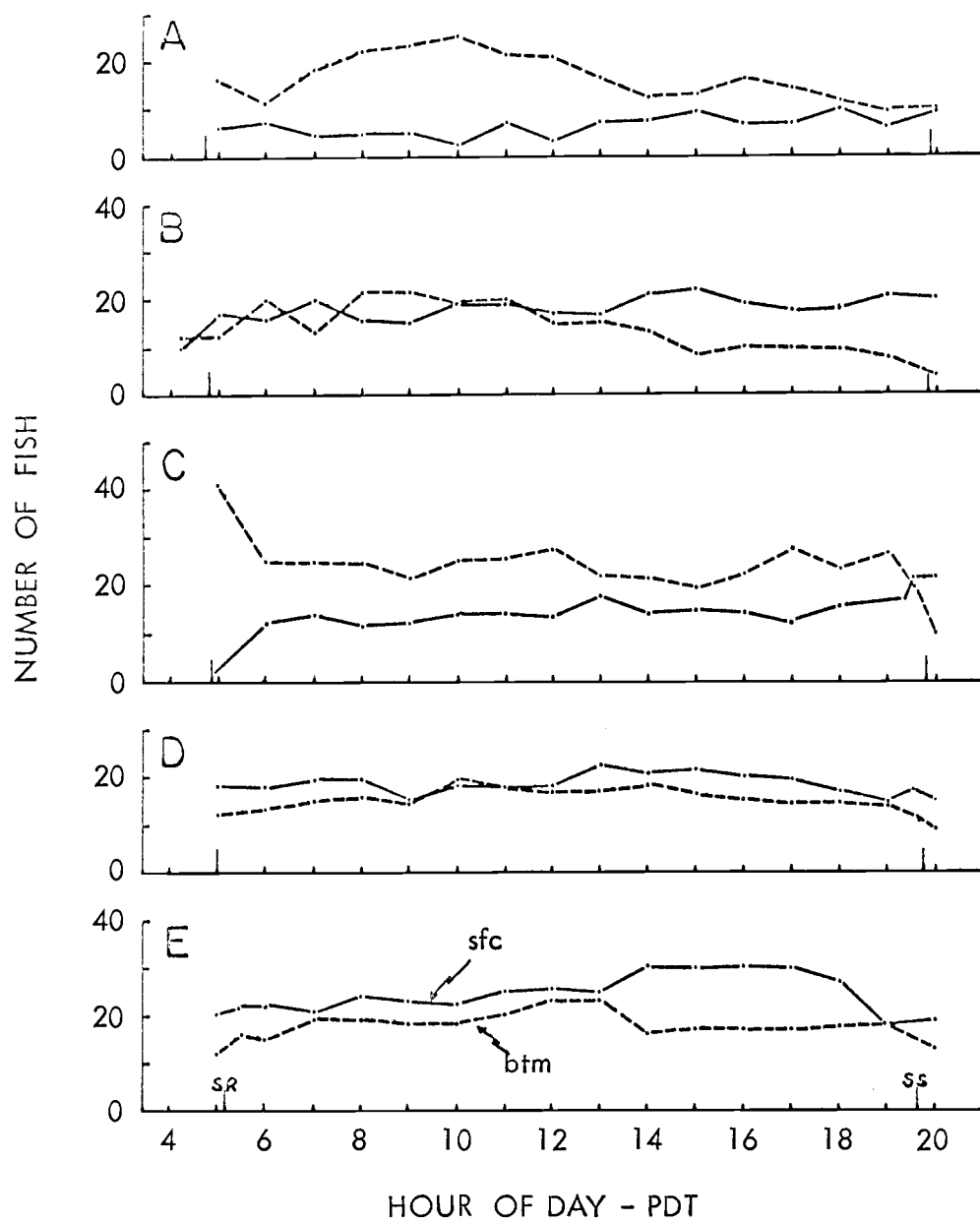
Figure 32. Daily record of changes in vertical distribution of fish in pool 1 of the right stream aquarium. sfc – surface stratum, btm – bottom stratum.

Fish present in the secondary food current in pool 1 (upstream return current that flows along the bottom of the pool) were identified by their orientation downstream. There was no apparent daily cycle in the number of fish thus positioned but counts did tend to increase slightly following sunrise and to decrease to a similar degree just prior to sunset (Figure 33). Numerical trends from week to week were recognizable only in the left system where the number of fish increased gradually from an initially low level. The number of fish present in the secondary food current showed no significant changes in the right system (Table 27).

DAILY CYCLE OF AGGRESSION

Intensity of aggression and frequency of invasion-retreat activity were measured from dawn to dusk to determine if the daily cycle of density change in riffle 1 involved competition for territorial rights in the riffle. Invasion-retreat activity was recorded at the pool-riffle margin as the number of coho that invaded or fled from the riffle during 15 minute observation periods throughout the day. Aggressive behavior was measured as the number of aggressive acts committed by individual fish observed for 30 seconds during 15 minute observation periods.

The dawn and dusk peaks in density of fish in riffle 1 were
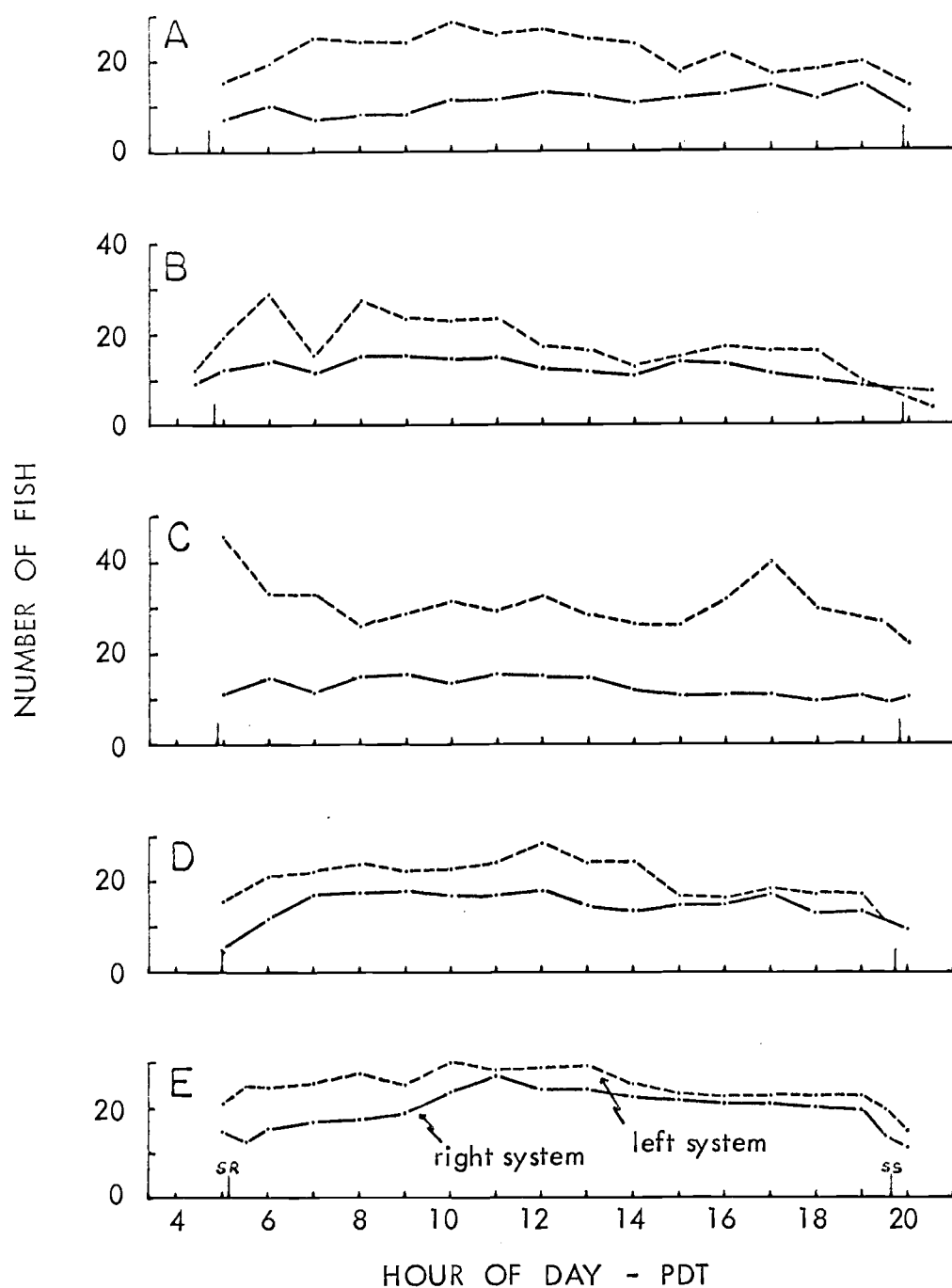
Figure 33. Daily record of changes in the number of fish in the
secondary food current in pool 1 of both stream aquaria.

accompanied by increased aggression and frequent attempts by riffle-invading coho from pool 1 to remain in the riffle and compete for food and space with territory-holders. The synchrony of these cycles (Figures 34 and 35) follows the daily rhythm indicated in Figure 30. Aggressive behavior showed a similar daily rhythm in the front half of pool 1 (Figure 34) and appeared to involve primarily the riffle-invaders.

NOCTURNAL BEHAVIOR

Coho in the stream aquaria were observed to feed actively at very low light levels. The possibility that marked changes in their distribution might accompany nocturnal behavior was investigated by observing population II (embryonic stress experiment) with an infra-red viewing apparatus[2]. Also, drop screens were used to isolate riffle 1 from pool 1 during the night.

Unfortunately, the penetrating power of the infra-red viewer was limited to the detection of fish located within four inches of the glass wall. Hourly counts were made in both stream aquaria during two successive daylight cycles of the total number of fish present on each riffle and the number present within the four inch margin along the glass. The number of fish in this margin was counted with the infra-red viewer during the intervening hours of darkness.

[2]Detectirscope (Model 5500C) - Varo, Inc.
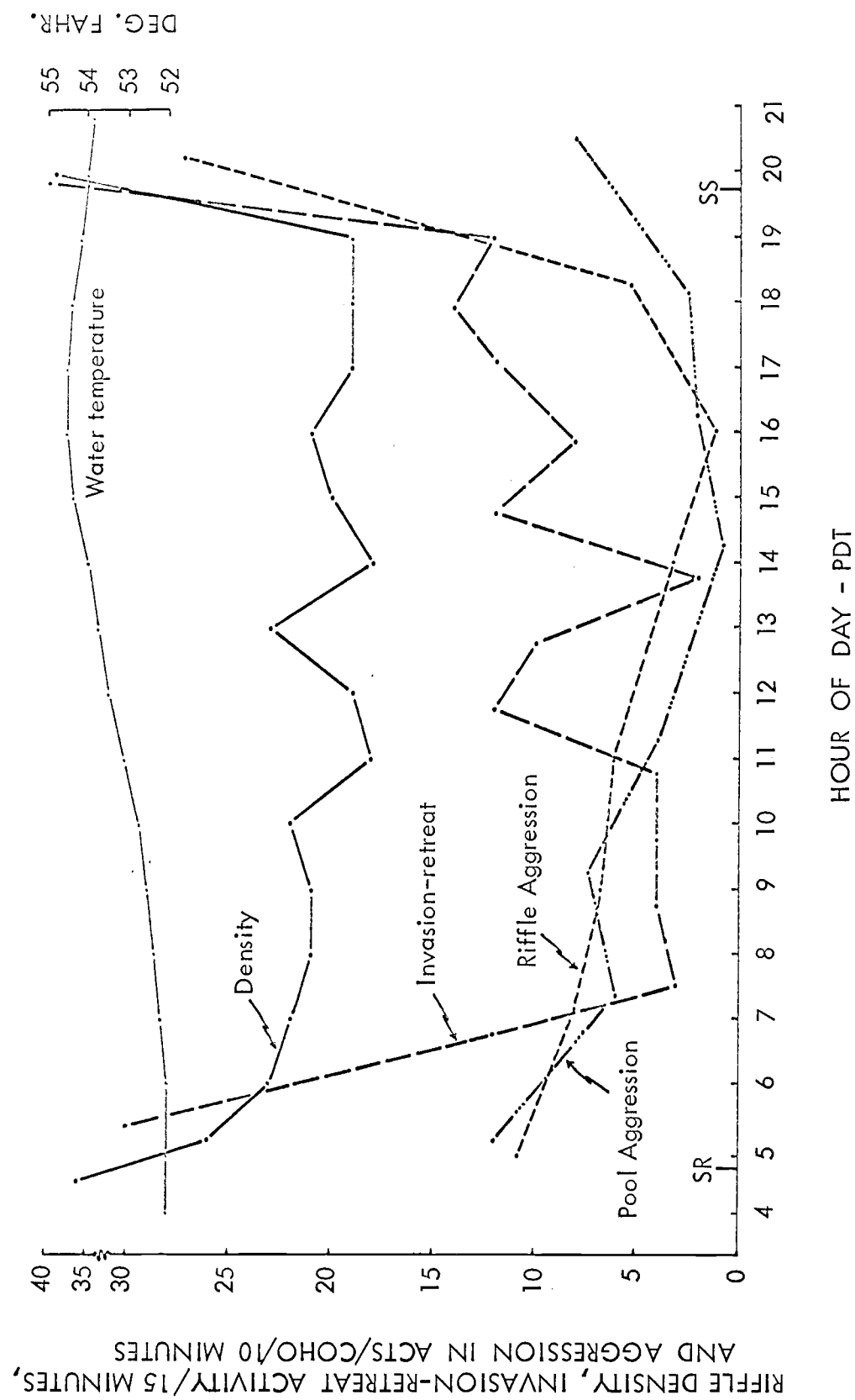
Figure 34. Daily cycle of activity associated with riffle 1 and pool 1, left stream aquarium on May 31, 1964.
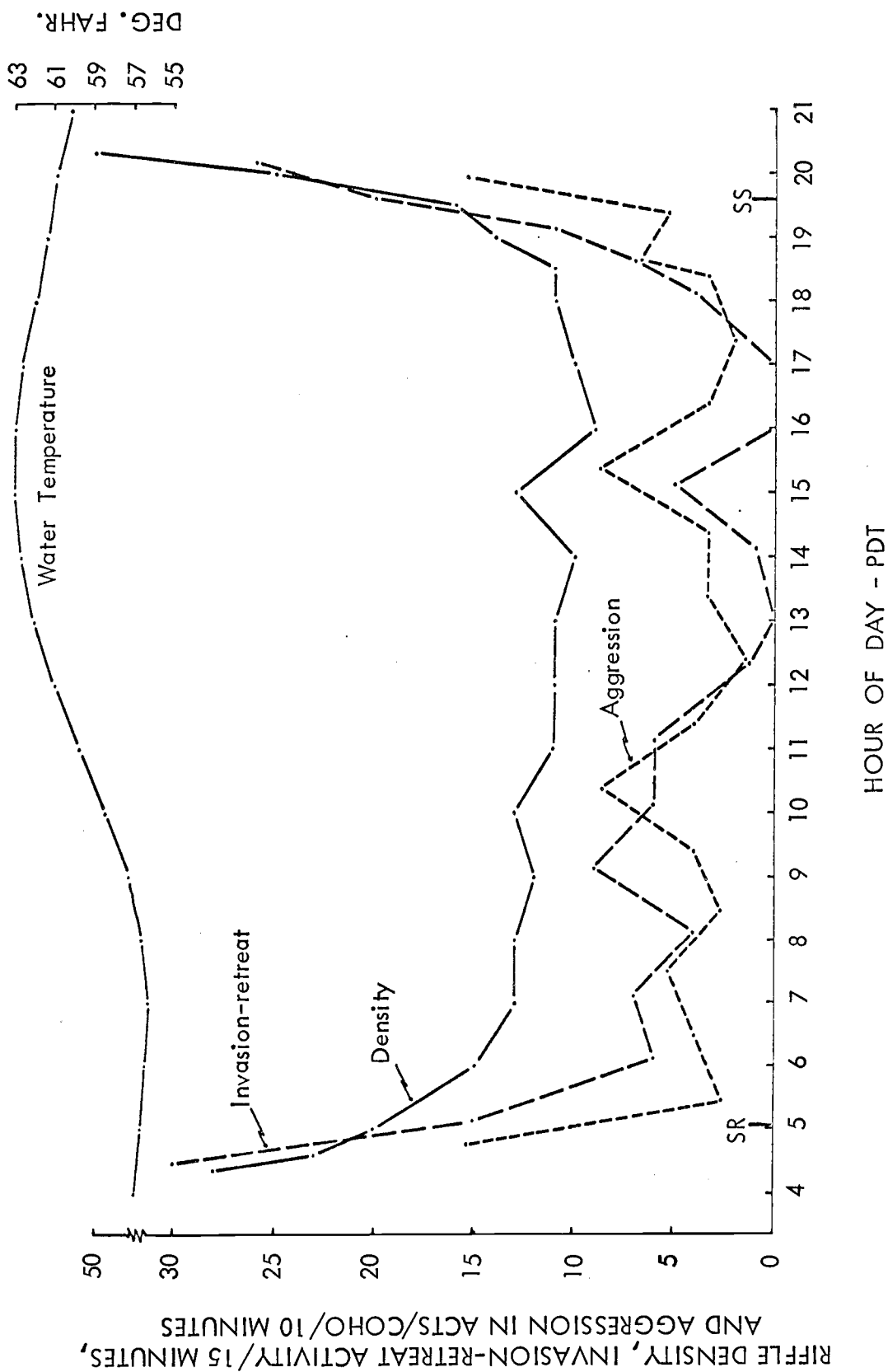
Figure 35. Daily cycle of activity associated with riffle 1, left stream aquarium on July 24, 1964.

The only significant differences between mean counts for each riffle were those between night and day margin counts (Table 28). Day counts were not significantly different from one day to the other. With one exception, night margin counts were significantly higher than day counts at the one percent level. Riffle 2 of the left system showed no difference between night and day counts.

Additional data on the nocturnal behavior of these populations was secured upon termination of the experiment. Sliding screen partitions that isolated riffle 1 from pool 1 were dropped into position at 1:00 AM, and the coho thus trapped were removed at daylight. The screen in the right system malfunctioned and the several seconds of delay did not justify continuation of the procedure.

In the left system, more than twice as many coho were found in riffle 1 at night than during the day but the relative proportion of each coho group was very similar to the corresponding daylight values (Table 29). Thus, the disproportionate use of riffle 1, which was dominated by the larger fish (RV) during the day was unchanged by nocturnal behavior despite the doubling of density in the riffle. Comparison of the night and day population in pool 1 revealed that the increased number of fish in riffle 1 at night came primarily from pool 1. Furthermore, the fish on the riffle at night were larger on the average than their group cohorts remaining in pool 1 at night. These differences

TABLE 28. MEAN DENSITY OF COHO IN THE RIFFLES OF BOTH STREAM AQUARIA, JULY 22 AND 23, 1964, BASED ON HOURLY COUNTS. NIGHT MARGIN COUNTS WERE MADE WITH INFRA-RED APPARATUS. VALUES IN PARENTHESES ARE STANDARD ERRORS OF THE MEANS.

Observation Period	Margin Count		Total Count	
	Left	Right	Left	Right
Day One – 14 counts				
riffle 1	3.4 (0.36)	3.4 (0.22)	14.2 (0.45)	11.6 (0.16)
riffle 2	2.2 (0.16)	2.1 (0.13)	8.3 (0.25)	7.6 (0.42)
Night – 9 counts				
riffle 1	6.7 (0.33)	7.8 (0.33)		
riffle 2	2.1 (0.04)	3.6 (0.24)		
Day Two – 14 counts				
riffle 1	4.1 (0.27)	3.6 (0.27)	13.7 (0.20)	12.6 (1.50)
riffle 2	2.1 (0.22)	2.0 (0.10)	7.1 (0.37)	5.9 (0.44)

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TABLE 29. DIEL CHANGES IN THE SPATIAL DISTRIBUTION OF COHO IN THE LEFT STREAM AQUARIUM (POPULATION II – EMBRYONIC STRESS EXPERIMENT). VALUE IN PARENTHESES ARE PERCENTAGES.

Coho Group	Fry Group			Total
	RV	LV	NM	
Day population in riffle 1[a]				
Mean number of coho	8.8 (64.8)	2.8 (20.4)	2.0 (14.8)	13.5 (100.0)
standard error	0.41	0.28	0.26	0.57
Night population in riffle 1[b]				
Number of coho	21 (63.8)	8 (24.2)	4 (12.1)	33 (100.0)
Mean length in mm.	77.4	66.0	56.2	
standard error	2.56	1.87	2.55	
Day population in pool 1[c]				
Mean number of coho	33.2 (42.0)	37.3 (47.2)	8.5 (10.8)	79 (100.0)
Night population in pool 1[b]				
Number of coho	26 (38.2)	32 (47.1)	10 (14.7)	68 (100.0)
Mean length in mm.	71.6	62.5	51.3	
standard error	0.53	1.45	0.83	

[a] July 27, 1964 – based on 15 hourly counts.
[b] August 7, 1964 – terminal population, determined by drop screens.
[c] Calculated values based on counts made in the other three environmental units and on total population estimates from trap records.

were all significant at the five percent level, and the data support the inference of increased riffle occupancy at night suggested by observations made with the infra-red viewer.

WINTER-SPRING BEHAVIOR OF YEARLINGS

A thorough study of over-wintering behavior was rendered impossible by flow fluctuations that necessitated a major overhaul of the water supply system to the stream aquaria. However, some general observations were made during February and March, when the lowest water temperatures were recorded, monthly mean temperatures being $6.2^{\circ}C.$ (5.0 to $7.8^{\circ}C.$) and $6.9^{\circ}C.$ (5.6 to $8.6^{\circ}C.$), respectively.

A population of 58 yearling coho having a mean fork length of 71.7 mm (58 to 94 mm) was installed in the right stream aquarium on February 9, 1964. During the subsequent two weeks, only one small fish (60 mm) moved into the downstream trap. This fish was dead upon recovery from the trap. All but seven coho stayed in pool 1. Fish in both pools remained quiescent, near the bottom in close proximity to each other, and rarely displayed aggression. No fish were seen in the riffles until March 5 when 8 small-to-medium-sized coho invaded the riffles after overhead cover was provided.

From March 7 to 16, a total of 12 large fish entered the trap and were transferred to the vacant left system after receiving small, individualized fin marks. All fish moved out within three days of transfer

although the coloration changes indicating the onset of the parr-smolt transformation were not detected and all fish showed the patterns of parr coloration. By April 15 when the experiment was ended, 35 of the original 58 fish remained in the right system, and 3 of the 23 fish removed from the trap were dead. Smolt coloration was not seen in members of the terminal population or in the persistent outmigrants.

Significant feeding activity was first seen in early March and, by late March, considerable aggression was observed throughout the system. Intensity of aggression was measured during 6 hours of observation on April 1, 2, and 3, and ranged from 2.0 to 2.6 acts/ coho/10 minutes in the riffles. Fish in the pools were not aggressive.

The terminal population contained some large coho, the 5 largest fish (101 to 114 mm) being 9 to 15 percent larger than the largest 5 fish in the initial population.

AGGRESSION AND SMOLTIFICATION

Rising aggression and the onset of territorial behavior in the spring accompanies renewal of growth in yearling coho prior to the smolt transformation. Considerable behavioral modification attends this preparation for a saltwater existence. In contrast to underyearlings, coho smolts are easily disturbed, show lessened territoriality and aggression, prefer to aggregate and hide during the daylight hours, and

respond to low light levels by rising to the surface and actively swimming about (Hoar, 1951, 1954, 1958; Hoar et al., 1958).

As the social behavior of smolts exposed to estuarine conditions has received little attention, behavioral changes associated with smolting, particularly the influence of exposure to sea water on aggression and territoriality, were explored in small groups of smolts held in aquaria. Populations of 5 smolts were maintained in 83 liter aquaria, and the water was recirculated at a rate of 5 liters/minute with centrifugal pumps. Light intensity was set at 300 f-c and followed the natural photoperiod. Fish were fed twice daily on brine shrimp, and the water was changed every three days.

Yearling smolts reared at the Alsea Hatchery retained their aggression in 44 and 87 percent solutions of natural sea water (Table 30). Mean aggression values for the three groups differed significantly from each other only in fresh water (phase I). Intensity of aggression increased upon exposure to these salinities, and the increases were significant at the one percent level. The control group remaining in fresh water showed no significant change during the experiment. Low initial intensities of aggression in the two experimental groups may have been the outcome of unresolved hierarchical relations.

Yearing smolts captured while migrating downstream in the Sandy River retained their aggressive behavior in sea water also (Table 31),

TABLE 30. AGGRESSIVE BEHAVIOR OF YEARLING COHO SMOLTS (ALSEA HATCHERY FISH) EXPOSED TO THREE SALINITIES, MAY 25 TO JUNE 13, 1964. TOTAL OBSERVATION TIME WAS NINE HOURS. MEAN MINIMUM AND MAXIMUM WATER TEMPERATURES WERE 12.6 AND 13.5°C. VALUES IN PARENTHESES ARE RANGES.

Test Phase	Control Group	Experimental Groups	
		1	2
Range in length (mm)	87-117	98-122	96-116
I - Fresh water, days 1-7			
Tests on days 2, 3, 4			
Test periods (20 minute)	4	4	4
Total aggressive acts	248 (34-100)	98 (2-56)	143 (5-72)
Mean acts/coho/10 minutes ± SE	6.2 ± 1.73	2.5 ± 1.14	3.6 ± 1.74
II - Sea water, 15°/oo, days 8-12			
Tests on days 9, 10, 11			
Test periods (20 minute)	3	3	3
Total aggressive acts	180 (43-75)	141 (35-59)	136 (39-54)
Mean acts/coho/10 minutes ± SE	6.0 ± 0.97	4.6 ± 0.89	4.5 ± 1.40
III - Sea water, 30°/oo, days 13-20			
Tests on days 16, 21			
Test periods (20 minute)	2	2	2
Total aggressive acts	137 (46-91)	176 (82-94)	180 (76-104)
Mean acts/coho/10 minutes ±	6.9 ± 2.24	8.8 ± 1.89	9.0 ± 1.39

TABLE 31. AGGRESSIVE BEHAVIOR OF YEARLING COHO SMOLTS (SANDY RIVER MIGRANTS) EXPOSED TO FRESH WATER AND 30°/oo SALINITY, JUNE 14 TO JULY 13, 1964. TOTAL OBSERVATION TIME WAS 24 HOURS. MEAN MINIMUM AND MAXIMUM WATER TEMPERATURES WERE 12.6 AND 14.9°C. VALUES IN PARENTHESES ARE RANGES.

Test Phase	Control Group	Experimental Groups	
		1	2
Range in length (mm)	91–120	89–118	94–114
I – Fresh water, days 1–4			
Tests on days 2, 3, 4			
Test periods (20 minute)	12	12	12
Total aggressive acts	572 (30–174)	386 (34–87)	440 (13–114)
Mean acts/coho/10 minutes ± SE	4.8 ± 0.93	3.2 ± 0.35	3.7 ± 0.75
II – Sea water, 30°/oo, days 5–30			
Tests on days 7, 18, 30			
Test periods (20 minute)	12	12	12
Total aggressive acts	480 (29–125)	466 (32–137)	520 (29–109)
Mean acts/coho/10 minutes ± SE	4.0 ± 0.55	3.9 ± 0.70	4.3 ± 0.44

Note: The smallest or second smallest fish in all three groups died during phase II.

These fish were exposed to a sudden increase in salinity to $30^O/oo$ and held at this salinity for more than 3 weeks. There were no significant differences in intensity of aggression throughout the experiment.

In both experiments, a size-related hierarchical system of dominance-subordinance was established and the most dominant individual endeavored to defend most of the aquarium. The dominant smolt regained social control of the group within ten minutes after water changes, dealt out most of the punishment, consumed most of the food, and prevented nearly all of the subordinates from feeding. Removal of the dominant resulted in the ascendance of the first subordinate to the position of despot. Successive removal of the most dominant fish revealed individuals that were potentially aggressive but were being socially inhibited by the presence of the dominant. Contests took place when only two fish remained in the aquaria, indicating that all individuals probably would have defended territories had enough space been available.

DISCUSSION

Rhythmic and Nocturnal Behavior

The diel rhythm of behavior seemed to be most closely related to the rapid change in light intensity at dawn and dusk, especially when illumination was less than 150 f-c. The water temperature

usually approached the daily minimum at dawn and had fallen from the daily maximum to an intermediate value by dusk. The behavioral rhythm was well-defined when the daily temperature cycle was hardly recognizable.

Swift (1962) described a diurnal activity cycle in brown trout held in cages on the bed of Lake Windermere. This cycle involved a sharp rise in activity at dawn after nocturnal inactivity, and the increased activity lasted until dusk when it fell rapidly. Neither the water temperature nor the sight or smell of food was responsible for the rhythm since fish held under artificial feeding regimes showed the same diurnal activity pattern (Swift, 1964). A diurnal activity cycle in artificially fed roach (Rutilus rutilus), bream (Abramis brama) and perch (Perca fluviatilis) was reported by Alabaster and Robertson (1961). Evidence was provided that discounted the primary influence of temperature and dissolved oxygen concentration, and these authors concluded that the activity cycle was probably keyed to the diurnal light cycle.

The density cycle shown by juvenile coho is undoubtedly indicative of a feeding rhythm and not merely the outcome of lowered visibility at dawn and dusk modifying territoriality. The density changes were initiated at light levels adequate for full photopic vision (Ali, 1959) and were accompanied by increased aggression. Increased aggression was induced by riffle-invaders that disrupted the fairly well-defined territorial relations existing during most of the day. These peaks in activity

do not detract from the fact that, throughout the day, the great majority

of fish were primarily concerned with the organic drift passing through

the stream aquaria.

The fish often fed actively during the night. On moonless

nights, fish flashing toward the surface were commonly seen. Brett

(1957) reported that rate of _Daphnia_ consumption by underyearling coho

underwent no significant reduction until light intensity fell to 10^{-4} ft-c.

Nocturnal feeding was more readily seen under moonlight conditions.

Fish rose toward the surface when feeding in the riffles, and apparently

detected food items against the night sky light. They chased drift

items 40-50 cm downstream, perhaps after missing them in the first

attempt or detecting them too late to employ a direct, head-on encounter.

These fish then returned to their feeding stations.

Fish were seldom aggressive at night. Under a full moon,

aggression was infrequently seen and consisted of simple nipping among

individuals in close proximity to one another. Nocturnal feeding occurred

below the cone threshold of 10^{-1} ft-c (Ali, 1959) and the quality of

scotopic vision may discourage aggression.

These data lend little support to the hypotheses advanced by

Hoar that trout are habituated to sleep during the hours of darkness (1942)

or that juvenile coho show a lessened tendency to inhabit fast waters

and are quiet at night (1951, 1958), responses that would appear to be

adaptive with respect to downstream displacement. Rather, the higher

retinal cone sensitivity of coho fry (threshold of 10^{-1} ft-c as compared

to 1 ft-c in pink and chum fry) reported by Ali (1959) suggests the

possibility that this difference is of adaptive value in the exploitation

of the organic drift cycle in streams (Muller, 1963; Waters, 1962,

1965) during the extended freshwater life history. Investigation of

the retinal photo-mechanics and photo-behavior of chinook salmon fry

(O. tshawytscha), an ecologically-similar and territorial species, may

shed further light on this point.

The hydraulic conditions in the stream aquaria may be sufficiently stable to allow riffle occupancy at night and habituation to specific

patterns of turbulence as non-visual, spatial reference features. Regardless, the presence of large numbers of fish in the riffles at light

intensities insufficient for visual feeding remains an enigma. Fishes

do not show simple responses to light even in aquaria. The light

response of minnows (Phoxinus phoxinus) could be reversed by the

presence or absence of suitable cover (Jones, 1956). Without cover,

these fishes were active during the day and quiet at night. When

cover was provided, they remained inactive during the day and were

very active at dawn and dusk. Woodhead (1956) found that hunger and

sexual maturation altered the reactions of the adult fish to light.

Aggressive Behavior in Smolts

Retention of aggression by smolts during several weeks of ex-

posure to high salinities suggests that aggression has little direct

connection with the parr-smolt transformation or the environmental

cues instigating downstream movement to the sea. Reduction in

aggressive and territorial behavior was reported by Hoar (1951) but

he did not find that aggression between fry and smolt operated as a

possible causative mechanism in the smolt outmigration. Fry usually

nipped other fry while smolts nipped both fry and other smolts. The

present results do not indicate that aggression in smolts is reduced

by exposure to estuarine salinities. In fact, aggression increased in

hatchery smolts exposed to high salinities while the freshwater controls

showed no significant change in aggression (Table 30).

These experiments were conducted under conditions that might

tend to stimulate retention of territorial and aggressive behavior patterns:

conditioning to a temporally-limited food supply, crowding, and non-

volitional residence. In the natural environment, the shift in light,

cover, and depth responses of the smolt may inhibit both territoriality

and aggression. Heightened sensitivity to stimulation is characteristic

of smolts. That this sensitivity may be reversed is indicated by the

behavior of smolts in aquaria, fish that were captured while moving down

to the sea.

SUMMARY

1. Populations of juvenile coho in the large stream aquaria were observed to determine if their daily behavior contained rhythmic elements of ecological interest. General observations were made of behavior during the winter and following spring, and associated with smolting. Aggression of yearling smolts was studied in continuous-flow aquaria with regard to the transition to estuarine salinities.

2. There was a two to four-fold increase in density of underyearlings in riffle 1 associated with dawn and dusk below a light intensity of 45 m-c. This density cycle was not visibly influenced by general weather conditions during the day and bore no apparent relation to the daily cycle of water temperature. This density cycle was related to competition for food and space in riffle 1 and was synchronous with cycles in intensity of aggression and frequency of riffle invasion attempts by coho from pool 1.

3. Inferential data provided by observations made with an infra-red viewer and actual counts obtained by trapping coho at night revealed that nearly twice as many fish occupied riffle 1 at night than during the day. The pattern of disproportionate numerical dominance of the riffles by larger coho obtaining during daylight hours remained unmodified in the night population. Feeding

commonly occurred at night, even under moonless conditions, and appeared to involve both photopic and scotopic visual systems. Nocturnal feeding may be an adaption to the diel cycle in organic drift.

4. Behavior during the winter months was characterized by inactivity and avoidance of current, increased sensitivity to light and cover, and near-absence of aggression. Outmigration started in early March and fish showing persistent outmigration still retained parr coloration. Significant feeding accompanied by aggression was observed in early March and resulted in renewed growth. The terminal population in mid-April contained some large fish but no fish showed signs of coloration changes usually associated with smolting.

5. Yearling smolts of Alsea Hatchery stock increased their aggression in $15^{o}/oo$ and $30^{o}/oo$ dilutions of natural sea water. They formed size-related despotic hierarchies as do underyearlings and pre-smolt yearlings. Actively-migrating smolts from the Sandy River showing full smolt coloration were exposed suddenly to $30^{o}/oo$ salinity and exhibited comparable behavior. Successive removal of the dominant smolt indicated that all smolts probably would have expressed territoriality if sufficient space had been available. These results suggest that behavioral shifts associated with seaward movement may be reversed by appropriate environmental manipulation.

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APPENDICES

APPENDIX 1. DEVIATIONS FROM THE EXPECTED PERCENTAGE COMPOSITION VALUES FOR EACH OF THE THREE COHO GROUPS OF POPULATION I, (EMBRYONIC STRESS EXPERIMENT) BASED ON HOURLY COUNTS, APRIL 29 TO MAY 26, 1964

Unit and Date	No. of Hourly Counts	LEFT STREAM AQUARIUM						No. of Hourly Counts	RIGHT STREAM AQUARIUM					
		RV		LV		NM			RV		LV		NM	
Riffle One														
April 29	1	+17.2	12[a]	+ 8.8	10[a]	-26.6	1[a]	1	All 24 coho residing in Pool One					
May 4	5	+32.6	98	- 6.1	44	-26.5	2	5	34 of 35 coho residing in Pool One					
12	7	+39.6	147	-16.4	39	-23.1	3	7	- 5.3	6	+ 8.7	14	- 3.5	24
20	8	+24.4	71	-20.3	20	- 4.1	23	11	- 0.9	22	+ 0.2	18	+ 0.7	54
26	9	+25.1	108	-25.8	22	+ 0.3	38	9	+ 8.5	21	+ 0.2	26	+ 1.1	29
Sum	30		436		135		67	33		49		58		107
Riffle Two														
April 29	1	+20.6	5	+ 9.7	4	-31.0	0	1	All 24 coho residing in Pool One					
May 4	5	+11.9	20	+13.6	21	-25.5	1	5	34 of 35 coho residing in Pool One					
12	7	+26.9	30	- 7.7	14	-18.3	3	7	-18.5	0	-14.0	1	+32.4	10
20	8	+52.8	30	-28.8	3	-24.0	0	11	-13.4	1	+ 1.5	2	+11.9	5
26	9	+33.5	53	-16.7	17	-17.1	4	9	+ 8.5	7	-23.4	0	+15.8	8
Sum	30		138		59		8	33		8		3		33
Pool Two														
April 29	1	- 0.6	9	+ 7.2	13	- 2.0	9	1	All 24 coho residing in Pool One					
May 4	5	- 8.7	48	- 0.0	64	+ 8.8	64	5	One of 35 coho residing here					
12	7	-14.1	40	- 6.8	50	+29.1	90	7	-18.5	0	-23.1	0	+43.3	28
20	12	-23.0	53	- 8.6	101	+31.6	193	11	-25.9	0	+33.6	0	- 7.7	6
26	9	-14.8	38	- 7.2	58	+21.6	81	8	+20.6	6	-23.4	8	+ 4.2	9
Sum	34		188		286		437	33		6		8		43

[a] Number of coho counted.

APPENDIX 2. DEVIATIONS FROM THE EXPECTED PERCENTAGE COMPOSITION VALUES FOR EACH OF THE THREE COHO GROUPS OF POPULATION II, BASED ON HOURLY COUNTS, JUNE 12 TO JULY 28, 1964.

Unit and Date	No. of Hourly Counts	LEFT STREAM AQUARIUM						RIGHT STREAM AQUARIUM					
		RV		LV		NM		RV		LV		NM	
Riffle One													
June 16	8	+23.9	77[a]	-11.5	28[a]	-12.3	19[a]	+ 3.3	19[a]	- 0.4	23[a]	+ 3.8	21[a]
23	14	+32.8	128	-15.5	39	-13.9	23	+ 5.7	72	- 6.8	47	+ 1.0	61
30	10	+28.0	83	- 9.2	32	-18.7	5	+35.1	88	- 5.9	36	-23.8	13
July 7	14	+29.5	124	-12.2	44	-17.4	10	+10.2	75	+ 1.6	60	-11.7	39
15	14	+25.1	117	-19.5	31	- 5.7	28	+18.0	78	- 0.2	53	-17.8	27
28	15	+21.2	130	-17.8	39	- 3.4	28	+12.9	64	- 0.1	51	-12.8	31
Sum	75		659		213		113		396		270		192
Riffle Two													
June 16	8	+17.9	37	- 8.3	17	- 9.4	12	-33.8	0	-36.9	0	+70.8	16
23	14	- 8.5	43	- 5.2	45	+13.7	58	-20.6	18	-25.3	10	+45.7	103
30	10	+ 3.7	40	- 5.6	27	+ 1.8	22	-13.6	15	-13.6	18	+32.7	64
July 7	14	+ 2.2	50	-18.6	22	+16.0	46	-21.3	15	- 9.6	30	+31.0	84
15	14	- 5.4	49	+ 1.1	52	+ 4.1	35	- 1.7	33	- 4.0	33	+ 9.7	45
28	15	-10.0	35	- 3.7	35	+13.7	29	+ 0.9	46	-12.9	29	+12.0	60
Sum	75		254		198		202		127		120		372
Pool Two													
June 16	8	-27.6	26	- 4.1	49	+26.4	88	-20.2	3	- 5.0	7	+25.3	12
23	14	-11.3	47	-13.8	39	+25.0	40	+ 7.1	29	-15.8	12	+ 8.5	29
30	10	-13.4	54	-11.2	48	+24.5	92	+ 0.1	26	- 5.5	24	+10.5	39
July 7	14	-15.3	76	- 6.7	92	+21.9	137	+ 3.2	27	-16.2	13	+14.6	38
15	14	-17.3	68	-10.9	74	+28.0	140	+13.2	37	- 4.8	24	- 8.4	22
28	15	-21.2	56	- 8.8	71	+30.0	115	+36.9	41	-27.0	3	- 9.8	13
Sum			327		373		612		163		83		153

[a] Number of coho counted.

APPENDIX 3. INTENSITY OF AGGRESSION IN POPULATION I IN THE LARGE STREAM AQUARIA, BASED ON 45 MINUTE OBSERVATION PERIODS FOR EACH RIFFLE AND POOL. TOTAL OBSERVATION TIME WAS 25.5 HOURS.

Date and Aquarium	RIFFLE ONE		RIFFLE TWO		POOL ONE		POOL TWO		Weighted Mean
	Aggression per Coho[a]	No. of Coho	Aggression per Coho	No. of Coho	Aggression per Coho	No. of Coho	Aggression per Coho	No. of Coho	Aggression per Coho
LEFT AQUARIUM									
April 29	6.7	70	1.5	18	1.1	143	1.6	52	2.6
May 6	15.3	55	2.9	14	0.2	127	1.3	65	3.8
13	21.8	30	4.0	9	0.9	156	7.1	50	4.8
21	5.6	16	2.2	6	0.9	164	7.1	33	2.2
27	2.9	15	3.1	8	1.1	164	4.5	27	1.7
weighted mean	11.3		2.6		0.9		3.9		3.1
RIGHT AQUARIUM									
May 1					0.2	30			0.2
7					4.9	51			4.9
14	4.7	8	0.0	2	4.9	57	0.0	1	4.7
21	5.8	9	0.0	0	0.5	79	0.0	1	1.0
28	8.0	12	1.1	5	5.6	60	0.0	1	5.6
weighted mean	6.4		0.8		3.3		0.0		3.5

[a] in acts/coho/10 minutes.

APPENDIX 4. INTENSITY OF AGGRESSION IN POPULATION II IN THE LARGE STREAM AQUARIA, BASED ON 45 MINUTE OBSERVATION PERIODS FOR EACH RIFFLE AND POOL. TOTAL OBSERVATION TIME WAS 36 HOURS.

Date and Aquarium	RIFFLE ONE		RIFFLE TWO		POOL ONE		POOL TWO		Weighted mean
	Aggression per Coho[a]	No. of Coho	Aggression per Coho	No. of Coho	Aggression per Coho	No. of Coho	Aggression per Coho	No. of Coho	Aggression per Coho
LEFT AQUARIUM									
June 24	2.9	12	3.3	13	5.1	124	10.2	18	5.4
July 1	4.9	11	7.3	8	4.4	96	7.8	21	5.2
8	10.0	10	4.4	8	6.0	94	8.2	21	6.6
16	8.7	15	6.4	8	8.4	85	9.3	21	8.5
22	6.7	14	7.1	6	3.1	85	6.9	21	4.3
29	5.3	12	2.9	6	4.2	87	4.2	17	4.3
weighted mean	6.4		5.1		5.2		7.8		5.7
RIGHT AQUARIUM									
June 25	4.7	12	1.3	12	5.8	17	0.4	4	3.8
July 2	2.7	11	1.3	9	4.9	58	2.7	11	4.0
9	3.3	17	9.6	12	7.6	59	2.9	7	6.7
17	10.0	10	3.1	5	9.1	70	1.3	4	8.5
23	2.7	10	11.8	6	5.3	66	6.0	4	5.5
30	3.1	12	6.2	8	2.9	63	2.4	2	3.2
weighted mean	4.3		5.4		6.0		2.7		5.5

[a] in acts/coho/10 minutes.