SOME FEATURES OF COHO SALMON, *ONCORHYNCHUS KISUTCH*, FRY EMERGING FROM SIMULATED REDDS AND CONCURRENT CHANGES IN PHOTOBEHAVIOR

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ABSTRACT

The emergence of sibling coho fry from simulated redds lasted 20-23 days during which 97-98% of the fry emerged. Average size of emerging fry increased with time but the largest fry emerged during the peak of emergence. No clear preference was shown for nocturnal or daylight emergence but the latter increased with time. Fry showed a positive current response, 69-82% moving upstream following emergence. Most fry emerged when yolk reserve was reduced to less than 10% of total dry weight. Later-emerging fry did not have lower yolk reserves, but fry moving downstream had slightly more yolk reserve than did fry moving upstream. Fry which were captured shortly after emergence had fed actively but had not yet filled their air bladders. Chironomids composed 70% of their diet.

Photoresponse of sibling fry denied the redd experience was studied in light-dark choice boxes with reference to the timing of emergence of fry from the simulated redds. The pronounced photonegative behavior of the denied fry was suddenly lessened at time of emergence but remained photonegative. Weakening of the negative photoresponse was not the outcome of starvation or recent light experience, and was not modified by repeated testing. Retention of the photonegative response is referred to hiding behavior and use of the gravel bed as a refuge.

The anadromous female Pacific salmon, *Oncorhynchus*, usually buries her eggs in several adjacent pockets in streambed or lakeshore materials and these egg pockets collectively constitute a redd. The eggs hatch after several months and the larvae may spend several weeks or months using up their extensive yolk stores prior to emerging from the redd area into open water.

Mortality during this extended period of subterranean life may be considerable (Royce 1959) and probably routinely exceeds 70% for most species of salmonids in natural habitats. Adaption to suboptimal conditions includes physiologic and behavioral responses in the embryo and larva which were reviewed, especially for sockeye salmon, *O. nerka*, by Bams (1969).

Because destructive influences on the egg and alevin stages are amenable to amelioration through manipulation of substrate structure and flow regime, spawning channels pioneered by Wickett (1952) at Nile Creek have become a major component of salmon enhancement strategy. Despite these advances, we have yet to define optimal redd conditions, biotic and abiotic, which maximize preemergence survival of any

salmonid. Furthermore, fry surviving to emergence may face extended ecological consequences of suboptimal conditions in the redd which alter timing of, or size at, emergence (Mason and Chapman 1965; Mason 1969). Neither can we yet define for the emerging fry physiologic and behavioral states which optimize survival in open waters. Thus, premature emergence, implying underdevelopment and reduced ability to respond adaptively is not referrable to a defined state of normality.

Alevins of *Oncorhynchus*, as are those of *Salmo* and *Salvelinus* (White 1915; Stuart 1953; Woodhead 1957), are initially negatively phototactic and respond to light by hiding (Hoar 1958). They become positively phototactic and rheotactic as emerged fry, orientation to current preceding the shift from negative to positive phototaxis (Dill 1969) as in *Salmo* (Grey 1929a; Stuart 1953) but the timing of this photobehavioral change in relation to emergence and remaining yolk reserve remains unknown in *Oncorhynchus* and disagreement has arisen as to its timing in *Salmo* (Woodhead 1957). Histophysiological studies by Ali (1959) showed that only emerged fry and older stages of *Oncorhynchus* are capable of full retinomotor responses; however, partially developed responses have obvious survival value.

In this paper, some features of sibling coho fry

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emerging from simulated stream redds are described. Light and current responses; length, weight, and condition; remaining yolk reserves at emergence; and changes in photoresponse were investigated. The possible effects on photoresponse of repeated testing, previous exposure to light, and feeding experience were also examined.

MATERIALS AND METHODS

Emergence from Simulated Redds

The emergence of coho salmon fry of known parentage (two males × one female) from four simulated redds was investigated in two pairs of wooden channels (Figure 1) located outdoors. Each channel was divided into three equal-sized compartments, and to simulate a redd, each center compartment was filled to a depth of 27 cm with stream pebbles 2-5 cm in diameter. A standpipe terminating at its lower end in a 10 cm × 10 cm platform on 10 cm stilts so as to enclose a chamber of 100 cm³ volume was buried in each redd at this time. In each redd the gravel surface was entirely underwater, but a shallow median depression served to concentrate the surface flow issuing through the V-notch openings.

The frames of the inner partitions were covered with a double layer of fine plastic screen to allow for circulation through the redds. Water flow through each channel was 12 liters/min, about 30% of which passed through the redds.

Ten days after hatching, 150 alevins from eggs incubated and hatched in standard baskets and previously unexposed to light were introduced into each redd at night via its standpipe and allowed to emerge spontaneously. Each standpipe was cleared of fry 1 h after stocking the redd by
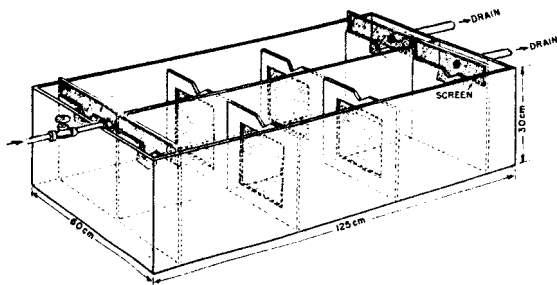

FIGURE 1.—Compartmentalized wooden channels. Center compartments contained the simulated redds. Dotted areas signify screens.

inserting a wire rod capped with rubber stoppers at either end and leaving the rod in place. Emerged fry could enter either the upstream or downstream compartments by way of the V-notch openings and were collected there daily at dawn and dusk.

Emerging fry were anesthetized with MS-222,[2] fork length was measured to the nearest 0.1 mm using a dissecting microscope, weight determined to the nearest 0.1 mg on a Mettler Grammamatic balance after blotting, and the fry then preserved in 5% Formalin. For each redd, samples of 20 fry were extracted from each quartile of the emerging population (total of 80 fry per redd) divided between fry moving upstream or downstream following emergence. Yolk reserve at emergence was determined by dissecting out the yolk material, drying both yolk and fry to constant weight at 80°C, and expressing yolk reserve as a percentage of total dry weight.

The resulting data were processed by regression and analysis of variance techniques to expose possible correlations between length, weight, condition (K) and yolk reserve with time, directional movement in current, and emergence during the daylight or darkness.

Photoresponse Tests

Ten days after hatching, sibling alevins from the same experimental stock as those used for the emergence study but denied the redd experience were separated into five groups of 50 fish each and held indoors in wire baskets except during testing. Two groups were held in complete darkness. One of these groups was tested frequently (dark experimental, DE); the other was tested once then not retested until 15 days later (dark control, DC). The three remaining groups were held in baskets partly exposed to daylight of about 200 ft-candles peak intensity from an adjacent window and were given three different treatments. One group was tested frequently (light experimental, LE); one was tested once then not retested until 15 days later (light control, LC). The remaining group was not tested until the 18th day and, in contrast to the other groups, was fed frozen ground beef liver three times daily from day 9 onward (light control plus food).

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[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Photoresponse tests were conducted in four choice boxes placed in an uncompartmentalized replicate of the emergence channels and located adjacent to them. The choice boxes were constructed of fine plastic screen on a wire framework (Figure 2) and divided equally into two compartments by a vertical partition that allowed a passage height of 1.5 cm beneath it. Both hinged top and the partition were made of black polyethylene sheeting. The wooden channel was covered with the same material, except in the areas taken up by the boxes, so that the compartments not covered by the hinged tops received most of the illumination in the boxes. Each box presented a choice between sharply contrasting light conditions rather than between "light" and "no light," because some light leaked under the partitions. A series of mirrors was mounted 1 m above the water surface, allowing observation from a blind.

Water flow in the channel was 10 liters/min and velocity less than 10 cm/min. Water depth in the choice boxes was 10 cm providing an air space of 3 cm between the water surface and the ceiling of the covered compartment. Average fish density was set so as to allow about twice as much water volume and 2.4 times as much bottom area as in the holding baskets. Temperature of the w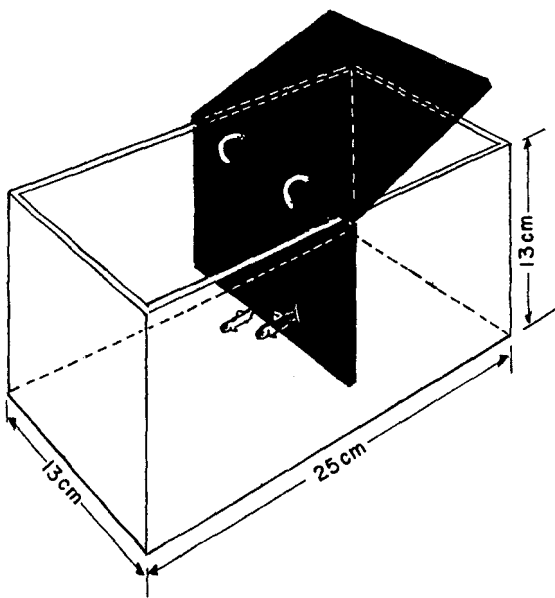ater supply (stream) ranged from 7.8° to 11.7°C during the experimental period. Light intensities at the exposed water surface ranged from 700 to 4,000 ft-candles during photoresponse tests.

The procedure for a photoresponse test was as follows. The appropriate group of fry was transferred to the test site in a covered pail, 40 fry were netted out and 10 fry put in each of the four choice boxes with the lids in an upright position. The lids were then closed in a common direction, and the remaining fry were returned to their holding basket. In the choice boxes, all fry swam into the dark compartments when the lids were dropped. After 30 min, the number of fry observed in the light compartments were recorded every 10 min for 40 min (5 observations in each of 4 compartments = 20 observations). A fish was considered to be in a light compartment when its head was visible. The lids were then reversed and, after 10 min, five additional observations were made at 10-min intervals. Thus, for each test, 40 counts were recorded on 40 fry, which spent 2 h in the choice boxes per test and about 10 min in the transfer process. The photoresponse tests were initiated 1 day before fry began emerging from the simulated redds and continued until the 22nd day of emergence. Length and weight measurements were taken for all fry groups on the following day. Data were tested for homogeneity using chi-square. There was no significant difference ($P<0.01$) between the first and second runs of five observations each made in individual choice boxes, χ^2 values ranging from 0.0 to 2.8 in 132 pairs of runs. Similarly, the data from individual choice boxes proved homogeneous within each test in 29 of the 33 tests performed ($P<0.01$) χ^2 values ranging from 1.1 to 7.8 with 3 degrees of freedom. The remaining four tests contained heterogeneous data, χ^2 values ranging from 14.7 to 36.5 and were excluded from further analysis. With homogeneity assured within most tests, the data within tests were pooled and processed.

RESULTS

Emergence from the Simulated Redds

Fry began emerging 25 days after hatching and 15 days following introduction to the redds. Emergence proceeded for 20-23 days during which 97-98% of the fry emerged. All four redds showed a similar pattern of emergence, peaking at the same time, 74 to 94% of the fry emerging during the median 10 days (Figure 3).
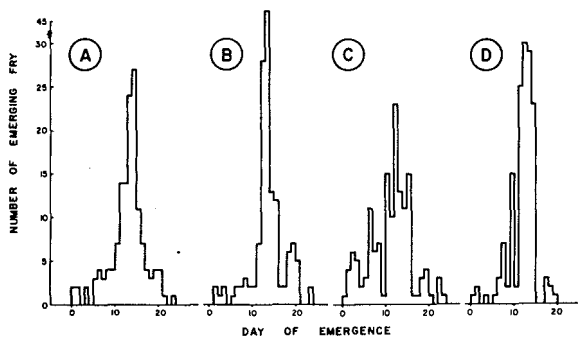

FIGURE 2.—Light-dark choice box showing the reversible opaque lid.

FIGURE 3.—Timing of coho salmon fry emergence from the simulated redds.

The average size of fry increased significantly ($P<0.01$) as emergence proceeded but the largest fry emerged during the peak of emergence from day 10 to day 15 (Figure 4).

More fry emerged at night than during the day in redds 2 and 3 (57% and 60%, respectively), but more fry emerged during the day in redd 1 (Table 1). No preference was shown by fry in redd 4 which emerged in equal numbers. Dividing the data into two time intervals, days 1 through 11, and days 12 through 24, revealed that emergence during the day increased some 30% in all four redds in the latter period.

Emerging fry showed a strong positive current response, the majority (69-82%) moving upstream subsequent to emergence, upstream movement increasing but slightly as emergence proceeded.

There were no significant differences in average length and weight ($P<0.01$) of fry moving upstream or downstream following emergence, but fry emerging during the day were, on the average, larger than those emerging at night (Table 1), significantly so in two redds (redd 3, $P<0.05$;
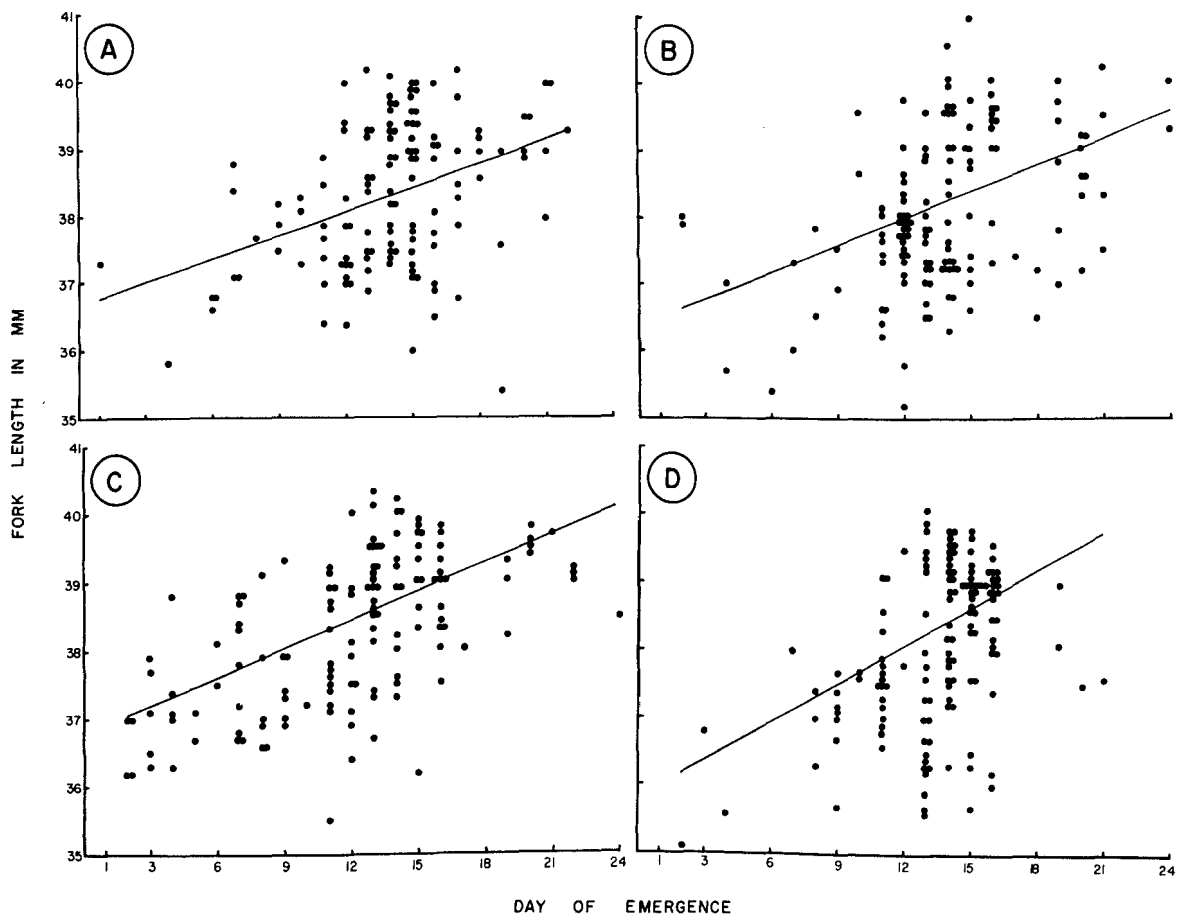

FIGURE 4.—Size of coho salmon fry at emergence including the regression lines.

TABLE 1. — Average lengths of sibling coho fry emerging from four simulated redds, stratified as to night and day timing and direction of movement. Values in parentheses are percentages.

Redd		Upstream movement	Downstream movement	Night emergence	Day emergence
1	Number of fry	94(69.1)	42(30.9)	53(39.0)	83(61.0)
	Mean fork length (mm) ± SE	38.39 ± 0.11	38.12 ± 0.18	38.13 ± 0.18	0.15 ± 0.15
2	Number of fry	115(80.4)	28(19.6)	82(57.3)	61(42.7)
	Mean fork length (mm) ± SE	38.08 ± 0.11	37.91 ± 0.21	38.00 ± 0.12	38.11 ± 0.15
3	Number of fry	113(79.0)	30(21.0)	86(60.1)	57(39.9)
	Mean fork length (mm) ± SE	38.25 ± 0.11	38.48 ± 0.18	38.14 ± 0.11	38.54 ± 0.15
4	Number of fry	116(82.3)	25(17.7)	70(49.6)	71(50.4)
	Mean fork length (mm) ± SE	38.10 ± 0.11	38.00 ± 0.38	37.68 ± 0.15	38.48 ± 0.13
Total emerging fry		438(77.8)	125(22.2)	291(51.7)	272(48.3)
Pooled mean fork length (mm)		38.19	38.14	38.12	38.38

redd 4, $P<0.01$). This is the outcome of the tendencies for both increased emergence during the day and increased size at emergence as time progressed.

Of the 584 fry that emerged from the simulated redds, 14 rather small fry emerged 5 or more days prior to the onset of general emergence. Twelve of these fry emerged at night and went downstream. They, and seven additional fry which also moved downstream and were designated as cripples due to truncated vertebral columns, were deleted from the analyses.

Most fry emerged when their yolk reserve was reduced to less than 10% of total dry weight (Figure 5), average reserve being 5-7% of total dry weight. The three rather high points (days 9-10) for fry moving downstream represent small samples whose means were inflated by premature fry. Yolk reserve in these samples was either less than 8% or ranged between 26 and 60% for individual fry. The large standard errors shown in Figure 5 are all associated with mean values inflated by premature fry. Yolk reserve did not diminish with time, indicating that the majority of fry were in a similar nutritional state at emergence. Although there were no significant differences in length and weight between fry moving up or downstream, fry moving downstream had more yolk reserve (9.2%) than did fry moving upstream (7.4%), this difference being significant at the 1% level. Similarly, in 13 of 16 possible pairs of samples from the four redds, the downstream fry contained more yolk reserve.

To discover if fry were feeding within a short time of emergence, the digestive tracts of 75 fry emerging from redds 1 and 2 were examined. These fry were representative with regard to night or day emergence and upstream or downstream movement following emergence, throughout the period of emergence. No dietary differences were found in the 74 fry that had fed shortly before their capture. As both stomach and intestine contained food particles, fry emerging at night probably fed that night or during the preceding hours of daylight while in the redd. Chironomids constituted nearly 65% of their diet (Table 2), mites and Collembola made up 17%, and together these three items were consumed by 83% of the fry.

At time of capture in the upstream and downstream compartments, no fry had yet reached neutral buoyancy although some had partially filled air bladders.
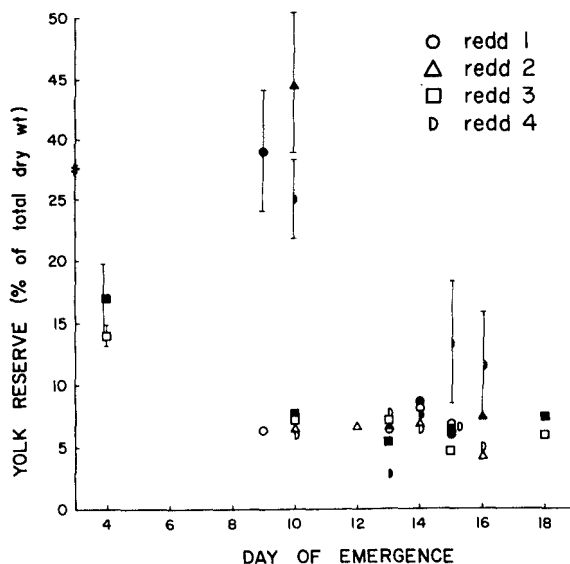

FIGURE 5.—Yolk reserve of coho salmon fry at emergence. Solid symbols indicate downstream movement following emergence; open symbols indicate upstream movement. Vertical bars indicate ±2 SE. For the remaining points, the range in SE was 0.1-1.0, and 90% ranged from 0.1 to 0.6.

171

TABLE 2. — Diet of 75 coho salmon fry emerging from two of four simulated redds supplied with river water.

Food item	Number of items	% of total items	% incidence
Chironomidae:			
Larvae	43	34.4	32.0
Pupae	20	16.0	21.4
Imagines	16	12.8	14.7
Total	79	63.2	68.1
Hydracarina	17	13.6	2.7
Collembola	13	10.4	12.0
Ephemeroptera nymphs	5	4.0	6.7
Arachnida	4	3.2	5.3
Trichoptera larvae	2	1.6	2.7
Plecoptera nymphs	1	0.8	1.3
Coleoptera imagines	1	0.8	1.3
Hymenoptera	1	0.8	1.3
Plant fragments	2	1.6	2.7

Concurrent Changes in Photoresponse

Photoresponse testing of fry denied the redd experience began on day 1, 1 day before their counterparts in the simulated redds began emerging. Their photoresponse remained essentially negative throughout the time period when, normally, they would have emerged. Until the eighth day of emergence (day 9), less than 3% of the denied fry were seen in the light compartments (Figure 6) and they remained strongly photonegative although nearly 13% of their sibs had emerged from the redds. By day 12, the collective negative photoresponse had weakened considerably, and nearly 15% of the denied fry were recorded then in the light compartments. By the 16th day of emergence, when 90% of their sibs had emerged, the percent of the fry recorded in the light compartments reached a plateau. From day 17 onward, 20-30% of the fry were seen in the light compartments (15 of 19 tests), but the response was more variable during the last day of

testing, two of the tests (LC and DC) providing heterogeneous data. Interaction stemming from territorial behavior was the most likely source of variability, the light compartments being sporadically defended by single fry attempting to drive the others away.

Despite a decidedly negative photoresponse during the first 10 tests (Figure 6, Table 3), in 8 of these tests more fry held in darkness between tests were recorded in the light compartments than were those exposed to illumination between tests ($P<0.01$). Because there was no significant difference attributable to light history in subsequent tests, novelty due to limited light experience may have stimulated exploratory behavior during testing in fry held in darkness between tests. When tested on days 15 and 17, the control
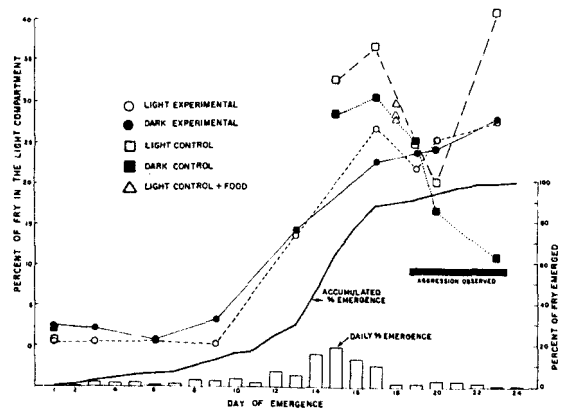

FIGURE 6.—Change in photoresponse of coho salmon fry held in baskets between tests. The histogram depicts the concurrent rate of emergence of 584 sibling fry from the four simulated redds.

TABLE 3. — Fry sightings in the light compartment of each of four choice boxes containing 10 fry during photoresponse tests, expressed as a percentage of possible sightings (400/test). Bracketed values are standard errors.

Day	Light experimental (LE)	Dark experimental (DE)	Light control (LC)	Dark control (DC)	Light control plus food (LC+F)
1	0.3(0.3)	2.5(0.6)	0.5(0.3)	1.8(0.5)	
3	0.3(0.6)	2.0(0.8)			
6	0.3(0.1)	0.5(0.3)			
9	0.0	3.0(0.8)			
13	13.3(1.6)	13.8(1.5)			
15			32.2(2.4)	28.0(2.3)	
˙17	26.3(1.8)	22.3(1.9)	36.3(2.9)	30.0(2.3)	
18					26.8(2.8)
					¹29.3(2.9)
					26.5(2.3)
19	21.5(1.8)	23.3(1.9)	24.3(2.0)	24.8(1.4)	
²20	25.0(1.6)	23.8(1.9)	19.8(1.6)	¹16.3(1.9)	
23	27.0(1.8)	27.5(2.3)	¹41.0(3.6)	¹10.8(1.3)	

¹Heterogeneous data.
²Fed in previous evening and 1 h prior to testing.

groups LC and DC showed higher counts ($P<0.01$) than did their experimental counterparts LE and DE tested on day 17 (Table 3). Nonsignificant differences in subsequent tests suggested that frequency of testing may have depressed the magnitude of photoresponse change.

Fry receiving supplemental food (LC+F) made scores similar to DC and LE groups ($P<0.01$) when tested on day 18, but lack of homogeneity in the data from one of the three tests performed precluded further evaluation.

Light history and recent feeding did not significantly affect response level when the four previously unfed groups were tested on day 20 ($t = 1.3$ with 158 df, $P<0.020$).

Differences in average length among the four unfed groups of fry 1 day after the last tests were not significant (Table 4, $F = 0.33$ with 3, 96 df) but fish in the LE and DE groups weighed significantly more and therefore had higher K values. Their heavier weight is attributed to feeding on natural drift foods available only in the choice boxes. The control group given supplemental food from day 9 onward were significantly longer than the other four groups of fry in average length ($F = 11.4$ with 4, 122 df, $P<0.01$) and weighed considerably more.

TABLE 4. — Average lengths, weights, and condition factors (K) of samples of 25 coho fry used in the photoresponse experiment, measured 1 day after final testing.

Treatment	Fork length (mm) SE	Live weight (mg)	K^1
Light experimental	38.38 ± 0.23	442.2	0.783
Dark experimental	38.29 ± 0.21	432.4	0.771
Light control	38.33 ± 0.19	391.6	0.695
Dark control	38.17 ± 0.23	399.6	0.719
Light control with food supplement	39.60 ± 0.24	473.6	0.763

$^1K = W \times 10^5/L^3$ where W is weight in milligrams and L is length in millimeters.

The average length of fry emerging from the redds (Table 1) did not differ significantly from that of the unfed siblings used in the photoresponse tests (Table 4). However, the emerging fry weighed somewhat less than fry of the experimental groups but more than those of the control groups ($\overline{X} = 425.7$ mg) and were in similar condition to the experimental groups ($K = 0.766$).

DISCUSSION

Emergence from these simulated redds involved several differences from that reported by Koski (1966) for natural redds of coho salmon.

Fry from individual natural redds took from 10 to 47 days ($\overline{X} = 35$ days) to complete emergence which peaked 8-10 days after first emergence, and size of fry decreased as emergence proceeded. In the simulated redds, duration of emergence was 20-23 days peaking at 12-13 days and size increased with time although yolk reserve remained nearly constant. The physical structure of the natural redd, particularly the proportion of smaller particle sizes, restricted permeability and impeded emergence. Low permeability reduced size of fry and increased mortality, later-emerging fry and those failing to emerge that were excavated from redds were emaciated, weight loss indicating exhaustion of yolk prior to emergence.

As yolk reserves remained fairly constant throughout emergence from the simulated redds, the larger, later-emerging fry probably developed from larger eggs. Koski (1966) found that large female spawners produced large fry at emergence, but large size of progeny did not alleviate physical hindrance to emergence, typifying the majority of redds, leading to decreasing size of fry as emergence progressed.

The strong upstream response shown by fry emerging from the simulated redds is characteristic of coho fry emerging in natural streams. Apart from counteracting downstream transport, upstream movement provides for the seeding of upstream rearing areas unavailable to, or not used by, spawners. The small but significant difference in yolk reserve between fry moving upstream or downstream may reflect, rather than a minor difference in swimming ability, behavioral differences associated with rising aggression, onset of territoriality, and commencement of feeding on the invertebrate drift.

The lack of preference for nocturnal emergence is in contrast to findings for sockeye salmon; pink salmon, *O. gorbuscha*; and chum salmon, *O. keta*, fry which emerge primarily at night (Neave 1955; Heard 1964). But like these other species, the coho salmon fry retained a photonegative response at emergence of potential survival value, e.g. escape from predators. Stuart (1953) also reported that fry of brown trout, *Salmo trutta*, remained photonegative during their ascent in simulated redds, even upon reaching positions only 1 or 2 inches from the gravel surface. For several days after emerging, fry of coho salmon and cutthroat trout, *S. clarki*, will bolt back into the gravel bed when disturbed (pers. obs.) and

similar observations led Neave (1955) to comment that migrating chum and pink salmon fry, failing to reach the ocean in a single night, hide during the day and resume migration at nightfall. Hiding behavior disappears in coho salmon fry at time of complete yolk absorption but is retained for several days at high light intensities (Hoar 1958); this suggests a threshold intensity for the avoidance response which increases as the alevin stage proceeds.

Concurrence between change in numbers of fry observed in the choice chambers, a collective response, and the accumulated number of emergent sibs could reflect either a sudden shift in photoresponse of individual fry or gradual erosion of the negative response occurring simultaneously in all fry. The sudden shift alternative is best supported by three patterns of behavior noted in the choice chambers. Individual fry were observed to spend considerable time in the light compartment upon entering it, alternately swimming about slowly and remaining locally quiescent. Positions were commonly adopted with the head projecting into the light compartment (Figure 1), or entrance, and departure was rapid, irrespective of the presence or absence there of other fry until the last few days of testing when aggression was observed (Figure 6).

Despite near depletion of vitellus at time of emergence, the shift in photoresponse did not appear to be due to starvation because the response was not altered significantly by feeding. This is of interest as Smith (1952) reported marked metabolic changes in rainbow trout, *S. gairdneri*, alevins a few days prior to emergence, suggesting that these physiological events signified the onset of starvation. The change in photobehavior appears to be an ontogenetic behavioral change normally associated with emergence from the redd rather than one instigated by nutritional deficiency, premature feeding, or light experience. It remains unclear as to whether or under what conditions such stimuli can modify this change significantly; however, under hatchery conditions, Harvey (1966) found that sockeye salmon fry took food 2 wk after hatching but that emergence of fry from a simulated redd coincided with complete yolk absorption some 3 wk later. Heard (1964) noted that most emerging sockeye salmon fry trapped from natural redds in an Alaskan stream contained little or no yolk, remained photonegative, and emerged primarily during hours of darkness.

The timing of the photoresponse change relative to emergence and yolk reserves may vary within common limits for most stream salmonids and differences may reflect species-specific adaptions of value to fishery biologists. As in the fry emerging from the simulated redds, the yolk reserve of coho salmon fry emerging from natural redds averaged 7% (unpubl. data). Stuart (1953) observed a definite change in photoresponse of *S. trutta* when yolk neared depletion, and the photoresponse change was employed by Gray (1929b) to denote the conclusion of incubation when measuring the effect of temperature on alevin size at time of yolk depletion. Woodhead (1957) disagreed with Stuart as to the timing of the photoresponse change in *S. trutta*, and asserted that it occurred coincident with maximum activity of the alevin 15 days after hatching when yolk reserve constituted 70% of the dry weight of the fry. This considerable difference in timing remains unresolved.

Denying the photoresponse fry streambed experience during the last few weeks of the alevin stage had no apparent effect on the final size of the fry, probably due to their advanced stage of development prior to application of treatment differences. Marr (1963, 1965) has shown that developmental efficiency is reduced by exposure to natural light or lack of substrate contour which stimulate locomotor activity at the expense of growth. However, marked effects on locomotor activity were only measurable until development was 75-80% complete. The weight disparity between experimental and control groups of fry (Table 4) which was the outcome of weight loss or reduced weight gain is presumed to be an outcome of reduced feeding opportunity.

In summary, the present results show that coho salmon fry underwent a definite shift (sudden or otherwise) from a strong to a weak negative photoresponse. This shift was accompanied by a positive response to water current leading to preferred movement upstream. The emerging fry was an actively feeding animal yet to fill, or in the process of filling, its air bladder, fed in the gravel prior to emergence, and emerged when average yolk reserves declined to 7% of total dry weight. In contrast to fry emerging from natural redds (Koski 1966), later-emerging fry were larger than those emerging earlier and may have derived from larger eggs. Because first-emerging fry held ecological advantage over later-emerging fry in stream aquaria (Mason and Chapman

1965), the timing of emergence and environmental conditions which modify it and the ecological state of fry at emergence should be fruitful considerations in future research.

ACKNOWLEDGMENTS

LITERATURE CITED

ALI, M. A.
1959. The ocular structure, retinomotor and photobehavioral responses of juvenile Pacific salmon. Can. J. Zool. 37:965-996.

BAMS, R. A.
1969. Adaptations of sockeye salmon associated with incubation in stream gravels. In T. G. Northcote (editor), Salmon and trout in streams, p. 71-87. H. R. MacMillan Lectures in Fisheries. Univ. British Columbia, Vancouver, B.C.

DILL, L. M.
1969. The sub-gravel behavior of Pacific salmon larvae. In T. G. Northcote (editor), Salmon and trout in streams, p. 89-99. H. R. MacMillan Lectures in Fisheries. Univ. British Columbia, Vancouver, B.C.

GRAY, J.
1929a. The growth of fish. II. The growth-rate of the embryo of Salmo fario. J. Exp. Biol. 6:110-124.
1929b. The growth of fish. III. The effect of temperature on the development of the eggs of Salmo fario. J. Exp. Biol. 6:125-130.

HARVEY, H. H.
1966. Commencement of feeding in the sockeye salmon (Oncorhynchus nerka). Verh. Int. Ver. Theor. Angew. Limnol. 16:1044-1055.

HEARD, W. R.
1964. Phototactic behaviour of emerging sockeye salmon fry. Anim. Behav. 12:382-388.

HOAR, W. S.
1958. The evolution of migratory behaviour among juvenile salmon of the genus Oncorhynchus. J. Fish. Res. Board Can. 15:391-428.

KOSKI, K. V.
1966. The survival of coho salmon (Oncorhynchus kisutch) from egg deposition to emergence in three Oregon coastal streams. M.S. Thesis, Oregon State Univ., Corvallis, 84 p.

MARR, D. H. A.
1963. The influence of surface contour on the behaviour of trout alevins S. trutta L. Anim. Behav. 11:412.
1965. Factors affecting the growth of salmon alevins and their survival and growth during the fry stage. Assoc. River Auth. Yearb., 1965:1-9.

MASON, J. C.
1969. Hypoxial stress prior to emergence and competition among coho salmon fry. J. Fish. Res. Board Can. 26:63-91.

MASON, J. C., AND D. W. CHAPMAN.
1965. Significance of early emergence, environmental rearing capacity, and behavioral ecology of juvenile coho salmon in stream channels. J. Fish. Res. Board Can. 22:173-190.

NEAVE, F.
1955. Notes on the seaward migration of pink and chum salmon fry. J. Fish. Res. Board Can. 12:369-374.

ROYCE, W. F.
1959. On the possibilities of improving salmon spawning areas. Trans. North Am. Wildl. Conf. 24:356-366.

SMITH, S.
1952. Studies in the development of the rainbow trout (Salmo irrideus). II. The metabolism of carbohydrates and fats. J. Exp. Biol. 29:650-666.

STUART, T. A.
1953. Spawning migration, reproduction and younger stages of loch trout (Salmo trutta L.). Freshwater Salmon Fish. Res. 5:1-39.

WHITE, G. M.
1915. The behaviour of brook trout embryos from the time of hatching to the absorption of the yolk sac. J. Anim. Behav. 5:44-60.

WICKETT, W. P.
1952. Production of chum and pink salmon in a controlled stream. Prog. Rep. Pac. Coast Stn., Fish. Res. Board Can. 93:7-9.

WOODHEAD, P. M. J.
1957. Reactions of salmonid larvae to light. J. Exp. Biol. 34:402-416.