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Title: POPULATION DYNAMICS OF THE COHO SALMON AND ITS RESPONSE TO LOGGING IN THREE COASTAL STREAMS

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Dr. James Hall

This study examines the ecology and dynamics of coho salmon (*Oncorhynchus kisutch*) in environments experimentally altered by logging. The objective was to evaluate processes that stabilize or regulate the populations.

Two small watersheds in Oregon's Coast Range were logged in 1966, one clear-cut, the other patch-cut. A third adjacent watershed was left uncut as a control. The influence of these treatments on the biology of the coho was assessed. Attention was concentrated on populations of the six year classes 1963 to 1968.

The natural variability of streamflow-related conditions influencing both the magnitude and pattern of coho recruitment each year was increased in the logged watersheds. Peak flow during storms increased; intragravel dissolved oxygen levels decreased in the stream draining the clear-cut watershed. These changes, however, were apparently within the range of variation that the coho naturally experience. Increased stream temperatures and mortalities, due to the logging effects, altered the post-recruitment life conditions of the coho in that stream but did not significantly affect the final smolt yield.

The nocturnal behavior of recently emerged fry leads to recruitment along the stream length. Fry tend to emerge en masse from the redds at night, and large numbers proceed immediately to disperse downstream. This migration continues for several successive nights, beginning each night soon after dark. Evidence is presented indicating that fry emigration is primarily a dispersal mechanism that distributes fry from redd sites to nursery areas. It is hypothesized that the series of events leading from fry dispersal to be quiescent behavior at night, characteristic of resident fry, is a developmental sequence involving the physiology and maturity of the fry, modified by agonistic activity.

Adjustments in coho population size were largely accomplished by fall, resulting in stable and characteristic population levels in each stream. A stable smolt yield was a further result. These adjustments are accomplished through high mortality during the months of the first spring and summer. This mortality is likely density dependent and related to the territorial and agonistic behavior of the fish.

Growth, biomass, and net production varied greatly during each year. Seasonal changes in growth rate resulted in seasonal variations in biomass that were in contrast to the stabilized trends of population number. The pattern of net production rate was also largely determined by the seasonal growth pattern, and like biomass, did not show a tendency to stabilize with time. It averaged 5 g/m^2 among the three streams for the period June 1 to April 15.

The coho populations seem naturally regulated most importantly with respect to number. The patterns of biomass and rate of net production may be understood as an interaction of seasonally variable growth rate with stabilizing population numbers.

This study has shown that coho streams normally produce characteristic levels of smolt yield in spite of large natural variations in fry input and conditions for growth. The range of environmental variation for which this result holds may include short-term changes due to logging. However a normal population response to such a severe alteration as occurred on Needle Branch is very likely conditional upon a program that at least includes vigorous stream clearance, the restriction of additional mortality to early summer, when population adjustments are far from complete, and the encouragement of streamside revegetation. A streamside buffer strip of trees is an effective way of protecting aquatic resources.

Population Dynamics of the Coho Salmon and its Response to Logging in Three Coastal Streams

by

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POPULATION DYNAMICS OF THE COHO SALMON AND ITS RESPONSE TO LOGGING IN THREE COASTAL STREAMS

INTRODUCTION

Among Pacific salmon the coho (Oncorhynchus kisutch Walbaum) characteristically spawns and completes the freshwater phase of its life history in the many small streams bordering the subarctic North Pacific. The portions of these streams constituting the spawning and nursery grounds of the coho are frequently the drainages of small watersheds. They are often only a few miles in length, and normally may have a complement of only a few dozen adult spawners. The combined output of thousands of such watersheds supports the commercial and sport fisheries for coho salmon.

The small size of the streams draining these watersheds, coupled with the high rainfall of the region, give rise to relatively large changes in stream conditions during the course of a season. There may be sudden freshets that cause scouring, erosion, and shifting of gravel bars. In cold, dry winters stream flows may drop low and freezing may occur. During the summer, flows may again be greatly reduced, and in areas not protected by shade, water temperatures may rise steeply.

Sudden freshets, characteristic of small mountain streams, while introducing short-term and often drastic variations in stream conditions, also work to maintain stability in the long run. The flushing action of abrupt rises in discharge tends to keep the channels clear of obstructions and to wash out local and temporary accumulations of silt and debris. Such are some of the physical characteristics of typical coho streams to which the species is adapted.

Conditions arising from man-made disturbances are also part of this environment. Coastal coho streams are not normally suited for hydroelectric plants or required for irrigation diversions, so obstructions to smolt or adult migrations are usually not a problem. However the spawning and nursery grounds of coho frequently lie in regions of commercial timber, and logging operations may affect the freshwater habitat of the species. Not only may the coho be subject to the effects of watershed alteration through logging, but they may also suffer mortality from direct, physical contact with men, machines, and logs during the timber harvesting operations.

In 1957 a project was initiated in Oregon to study the effects of logging on coho salmon resources. This project, the Alsea Watershed Study, involved three adjacent watersheds in the upper drainage basin of Drift Creek, a tributary of the Alsea River in Oregon's Coast Range. One watershed was to be clear-cut, another patch-cut, and the third left unlogged as a control. The effects of these environmental modifications were to be monitored for at least 7 years. The history and development of this project, including many of the effects observed to date, have been reported in detail by Chapman et al. (1961) and Hall and Lantz (1969).

Coho salmon studies on the project began in 1959. There followed a careful study of these populations up through 1966, the year of the timber harvest, in order to establish both the nature of coho biology before logging and the natural variability of the system. Post-logging studies on coho ecology have continued to the present time. The results of the studies up through 1962-63 have been reported by Chapman (1961, 1962, 1965). Other work completed under the auspices of the project includes studies on primary productivity, aquatic entomology, the cutthroat trout (*Salmo clarki*), and the reticulate sculpin (*Cottus perplexus*). This paper will report on the biology of the coho salmon and the effects of logging on the populations. Results through 1962 will be reviewed and newer knowledge gained to date given.

Description of the Study Area

The three study streams lie in Oregon's Coast Range (Figure 1). Deer Creek drains the largest watershed, with an area of 304 hectares. Flynn Creek drains 203 hectares; Needle Branch has the smallest drainage, of 71 hectares. These small streams enter Drift Creek, a tributary of the Alsea River. The study streams are located 16 km from the Oregon coast and are about 40 river km from the sea. The study watersheds lie between 140 and 490 meters above sea level.

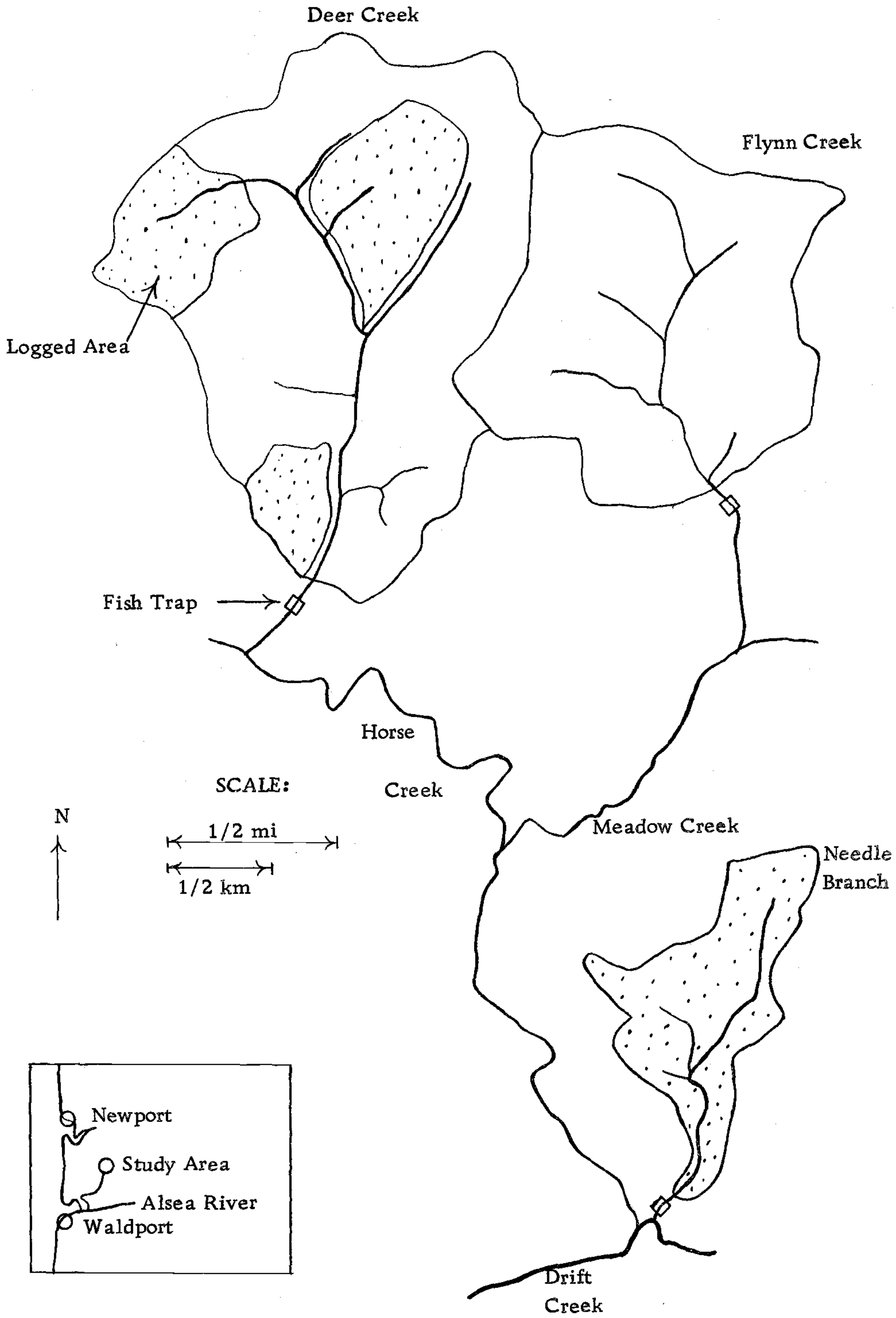


Figure 1. The three watersheds of the Drift Creek study.

They have average slopes between 34 and 40 percent. I will often refer to these three streams as the Drift Creek study streams.

The climate of the area is Pacific maritime. Annual precipitation has varied between 208 to 292 cm with a mean of 244 cm. Most of the precipitation occurs as rain from October through March. These storms bring on the large, characteristic freshets of the fall, winter, and early spring months. During winter there may be some snow and ice along stream margins. Air temperatures range from about -7° C in winter to 32° C in summer.

Corliss and Dyrness (1965) give a detailed description of the soil and vegetational characteristics of the area. Forests of Douglas-fir predominate with an understory of vine maple, sword fern, and salal. Salmonberry and red alder are found, particularly along the stream bottoms. The stream substrate is sandstone.

Besides coho salmon there are populations of the coastal cutthroat trout, the reticulate sculpin, and two species of lampreys (_Lampetra_ _tridentata_ and _L._ _richardsoni_) in the study streams. Lowry (1965, 1966) has described the biology of these cutthroat and Krohn (1968) that of the sculpin. A few steelhead trout (_Salmo_ _gairdneri_) are sometimes seen in the streams. They apparently spawn only in Deer Creek.

Other animals found in and around the streams include beaver, muskrat, mink, raccoon, Columbian blacktailed deer, and Roosevelt elk.

The belted kingfisher and the great blue heron, both predatory on small fish, are frequently seen.

Plan and Execution of the Study

Logging in the three watersheds was according to the following plan. Flynn Creek was designated the control or non-logged watershed. Deer Creek was patch-cut, i.e. clear-cut in three isolated units, approximately 30% of the timber being harvested. A narrow section of timber was left alongside the stream as a buffer strip. The Needle Branch watershed was completely clear-cut.

Construction of logging access roads occurred in 1965. Logging of the timber occurred during 1966. On Needle Branch, completely logged with no protective buffer strip, considerable debris in the form of branches, twigs, leaves, and bark collected in the stream. The larger debris was removed from the stream in September, 1966. This was a very important step in the rehabilitation of the stream. In October of the same year the watershed was burned to remove the slash and to prepare the area for reseeding.

The effects of these environmental modifications, especially as have occurred in Needle Branch, are documented by Hall and Lantz (1969). Deer Creek, with its protective buffer strip, was little affected. The changes in Needle Branch include increases in sedimentation, decreases in dissolved oxygen (both in the stream waters and within the gravel of the stream bed), and increases in stream temperature. These effects as they have influenced the coho populations will be discussed throughout this paper.

An Overall View of Coho Populations in the Study Streams, 1959-69

There are two general features of these coho populations that are revealed in the relationship between input of spawning females and output of their progeny as smolts (Table 1). First, there are large differences in the numbers of spawning females occurring in each stream from year to year. These differences are magnified through variations in fecundity and survival to fry emergence so that differences in fry input are even greater (Table 1). Second, and in contrast, the numbers of smolts vary relatively little between years. There were no obvious changes in the output of smolts in the post-logging years, 1966-1968, due to logging. There was a significant decrease in smolt output for the 1969 year class in Needle Branch. But because there were also similar decreases in Flynn Creek, the unlogged watershed, for both the 1968 and 1969 year classes, the Needle Branch decrease cannot be clearly ascribed to logging. The significance of these recent decreases in output is not yet clear.

Another view of this same set of data is obtained by studying the survival relationships involved. Survival (emergent fry to smolts) is

Table 1. Summary of population statistics for coho salmon - Alsea Watershed study streams 1959-1969 year classes.

	Deer Creek				Flynn Creek				Needle Branch			
Year class[a]	Spawning females[b]	Emergent fry[c]	Emigrant fry[d]	Smolts[e]	Spawning females	Emergent fry	Emigrant fry	Smolts	Spawning females	Emergent fry	Emigrant fry	Smolts[g]
1959	f	f	f	3,175	f	f	f	1,248	f	f	f	194
1960	24	17,212	2,076	1,915	10	4,190	7,225	890	3[h]		202	484
1961	18	14,874	3,290	2,237	19	9,368	10,527	627	2	1,275	1,916	242
1962	30	26,610	6,651	2,795	55	26,303	30,002	1,413	14	8,040	12,200	630
1963	18	14,874	4,415	2,073	2	986	65	566	4	2,634	6,192	308
1964	29	23,964	7,417	2,371	20	8,379	6,497	770	15	9,562	14,008	166
1965	49	39,153	8,823	1,809	10	4,486	3,162	663	28	17,849	23,113	300
1966	26	20,775	2,611	2,252	12	5,561	2,764	969	25	15,937	16,578	327
1967	55	48,452	12,533	2,460	55	26,303	28,820	622	18	11,853	5,567	276
1968	23	17,122	6,651	1,856	9	3,904	3,358	442	16	10,200	3,672	409
1969	39	26,904	8,288	1,377	19	7,397	5,219	207	17	9,405	7,204	199

a) Year-class refers to season of fry emergence
b) Corrected for stray females that did not stay in stream
c) Estimated from mean fecundity and survival to emergence data (see text)
d) Fry migrating from immediately after emergence until July of the same year
e) Fingerlings migrating November through July
f) Data incomplete or unavailable
g) Data for 1961-1965 year classes from incomplete trapping (downtrap out November 1 to February 1). Numbers adjusted upwards by 10% based on percentage migration at Deer Creek and Flynn Creek for same period.
h) None of these females spawned successfully, and 1,627 fry from Flynn Creek were released into Needle Branch, which was barren, from April 16 to May 6, 1960.

seen to be a decreasing function of fry input. (Figure 2). The latter is the product of numbers of females, the mean fecundity per female, and the mean survival in the redds (eggs spawned to emergent fry).

Fecundity was not estimated directly from the females in the study streams because the removal of even a few of the spawning females would have seriously affected the populations. Instead the fecundity is based on a length-fecundity regression derived by Koski (1966) for the nearby stock at the Fall Creek Salmon Hatchery. The survival from egg deposition to fry emergence is from data of the Oregon Game Commission. A nylon fry trap (Phillips, 1966) was placed over marked redds enabling the emergent fry to be trapped and enumerated. Lantz (1967) gives a table of survivals calculated from these data. The variability is great, with the 1964-66 survivals in Deer, Flynn, and Needle creeks ranging from 0% to 78%, 0% to 48%, and 0% to 82% respectively. The post-logging, 1967 survivals ranged from 14% to 62%, 28% to 60%, and 0% to 41% for these same three streams. The overall mean survivals, 1964 to 1967, weighted by the numbers of samples, were 34.7%, 19.5%, and 27.1% for Deer, Flynn, and Needle streams respectively. These are the survival values used to estimate emergence. A check on the validity of using these mean values was obtained by using the ranges as given in Lantz's table to estimate the variance (Snedecor, 1956) of the survivals within each year. The significance of each year's mean survival was then

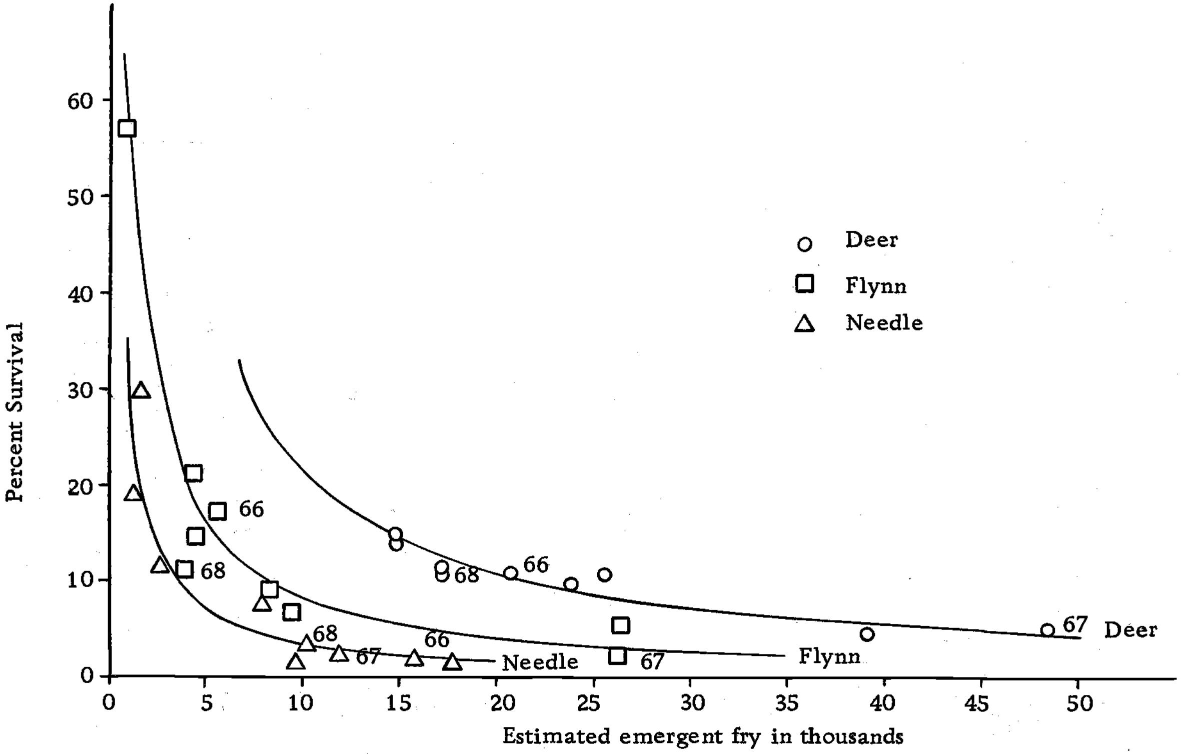


Figure 2. Relationship between survival (emergent fry to smolts) and fry input. Data include year classes 1960-1968, with post-logging year classes identified.

compared to the overall mean survival (t-tests). None of the differences was significant, implying that mean survival did not differ between years in each stream.

The survivals from 1960-1968 closely follow the regression curve for each stream (Figure 2). This closeness of fit is the significant feature of the graph. The regression curve in each case is contrived from the interdependence of the dependent and the "independent" variables, and is an equilateral hyperbola of the form:

$$y = c/x$$

where y is survival, from emergent fry to smolts, x is the number of emergent fry, a random variable, and c is the average or expected number of fry, a constant for each stream. The hyperbolic relationship has been discussed by Watt (1968), who cautioned that the population density series, N_{t+1}/N_t, when plotted against N_t yields a spurious correlation even when density dependent relationships do not exist. However Green (1968) has shown that survival ratios must be independent of N_t in cases where the model, $N_{t+1}/N_t = e^r$, holds and that such regression analyses are valid. In the present case the closeness of fit to the hyperbola is due to the relatively small changes in year-to-year smolt output from each stream, implying a continuous reduction of the large and random differences in input. This relative constancy of smolt output has persisted through pre and post-logging years until 1968. Points for the post-logging years, 1966-68, are so labeled on the graph.

Survivals calculated in this analysis are not very reliable. The effects of emigrant fry (Table 1) are not taken into account. Substantial errors can be expected in the estimates of emergent fry, stemming from the great variability of survival in redds and the small spawning populations involved. Calculated survivals greater than 20% are very likely excessive. Nevertheless the analysis is of interest; the closeness of fit of the survival points to the hyperbola suggests that natural processes are regulating the populations.

The fact that coho output has varied little in spite of the effects of logging means that the problem of timber and coho has to be redefined somewhat. The question is not so much how logging affects coho, but rather how coho populations are able to withstand environmental changes. To better evaluate this question all phases in the freshwater life history of the coho should be examined. This is the approach taken in this paper.

THE STREAM ENVIRONMENT IN THE STUDY AREA AND ITS ALTERATION BY LOGGING

Streamflow

Large fluctuations in stream discharge are characteristic of small streams in regions of high rainfall. The erratic shape of the winter hydrograph record represents a series of small floods following each rainstorm, e.g. that of Deer Creek (Figure 5, p. 24). The other two streams have similar shaped hydrographs but with lesser discharges, Needle Branch having the smallest flows.

The successive peaks in the hydrograph rise precipitously. The shape of the rising portion of each peak and final level reached depend upon the duration, intensity, and pattern of the rainfall. The declining portion of the curve, or recession, tends to be characteristic for a watershed. The curve declines relatively slowly, the discharge being powered by a decreasing head. Its shape is essentially dependent upon the physical features of the drainage basin alone (Linsley, Kohler, and Paulhus, 1949). In the Drift Creek study streams the recession curves are practically the same, the major differences being that each continues toward lower levels of base flow in Deer, Flynn, and Needle creeks, in that order.

Logging may affect watershed discharge in at least two ways: (1) Increased debris in the streams may alter channel flow characteristics through damming effects and by otherwise slowing water movement. (2) Removal of vegetation from a watershed reduces its water storage capability during water input periods and allows more ground water input during summer base flow conditions, when the transpiration effects of vegetation are important. Channel effects of logging were reduced in Needle Branch by the stream clearance program after the logging operation. In Deer Creek the buffer strip protected the stream. Vegetational effects caused significant increases in peak discharge at the stream outlet of Needle Branch (Figure 3). The effect in the patch-logged Deer Creek watershed was barely noticeable, at least in the discharge measurements at the stream outlet. Increased discharges similar to those of Needle Branch did occur in tributaries of the cut-over sections of Deer Creek (Harper, 1969; Hsieh, 1970).

The abrupt rises in stream discharge associated with each rainstorm introduce a weather-controlled variability in stream characteristics. These hydraulic pulses tend to clear debris from the channel and also rework the channel course to some extent. The major effects are seen within the channel bed, where a shifting of gravel bars, flow patterns, and pool shapes takes place. After each rainstorm one can see many examples of new and bare gravel expanses that have shifted downstream. The velocity gradients associated with these peak discharges impose special problems in movement and residence on the fish inhabiting such streams.

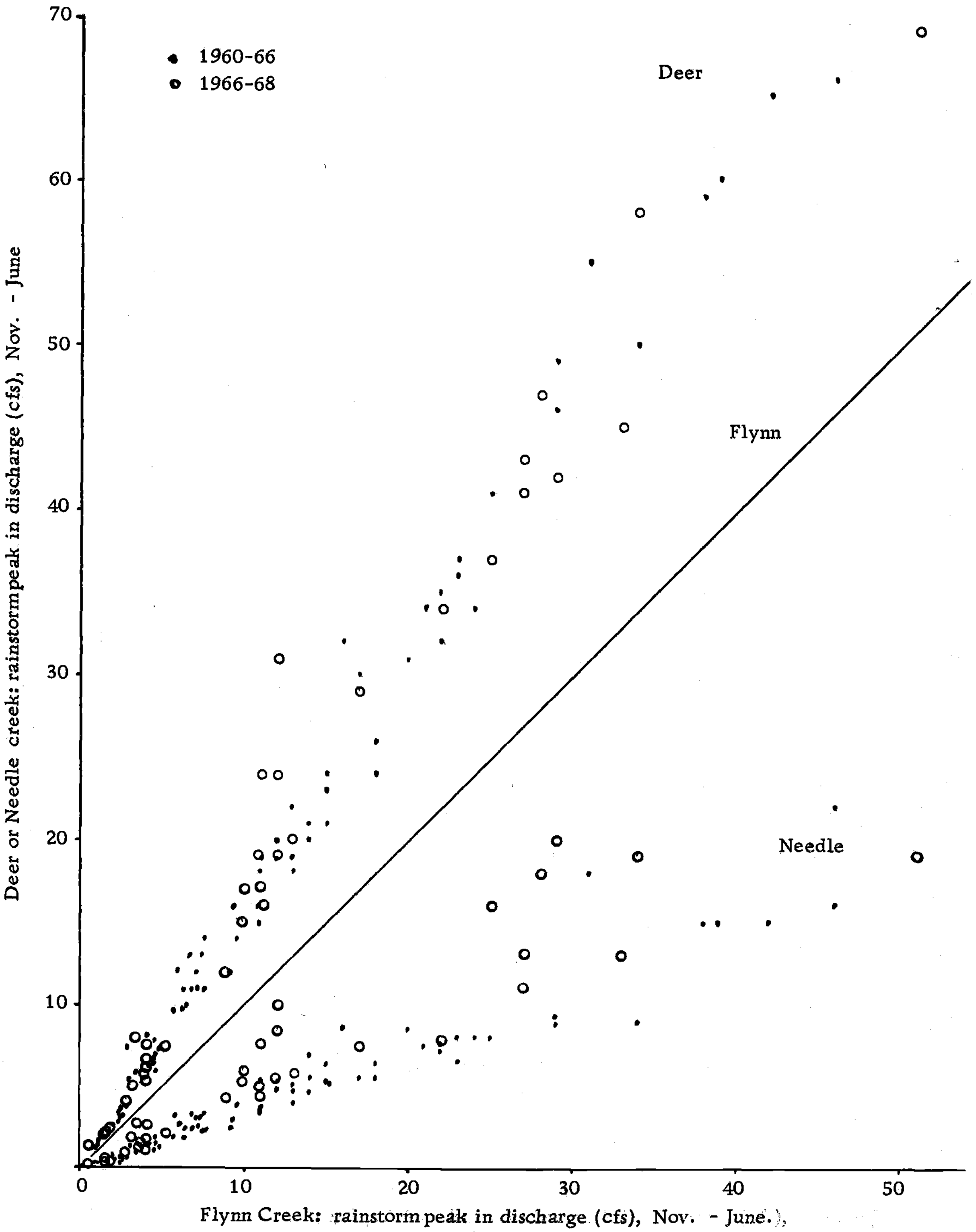


Figure 3. Relationship between peak discharge for an individual storm in Deer or Needle creeks and Flynn Creek (control stream) before (•) and after (o) logging. Data from U. S. Geological Survey.

Temperature

The smaller a stream the more closely it follows atmospheric temperature processes. During cooling phases such as at night and during the winter, water temperatures follow the declining air temperatures. The temperature to which a stream will ultimately cool is limited by the ambient air temperature. Winter temperatures in the study streams generally have ranged between 6 and 9° C. Air temperatures at the same time can dip below freezing. Insolation is the major source of heat during warming phases.

After logging in 1966 summer warming was accelerated strikingly (Figure 4), especially in Needle Branch, then exposed to direct solar radiation. A maximum daily temperature of 30° C occurred there in 1967. Details of the daily temperature cycle under those conditions can be found in Brown and Krygier (1970). The highest mean temperatures occurred in 1967 (Figure 4). The main reason for this one-year temperature lag in Needle Branch was that debris from the logging provided some shade to the stream during the first summer. After logging the highest temperatures tended to occur in July rather than in August, as is normally the case. This may have been due to the more direct effect of insolation on the stream temperatures.

Nocturnal cooling processes were capable of reducing high diurnal temperatures to near normal levels before the start of the next

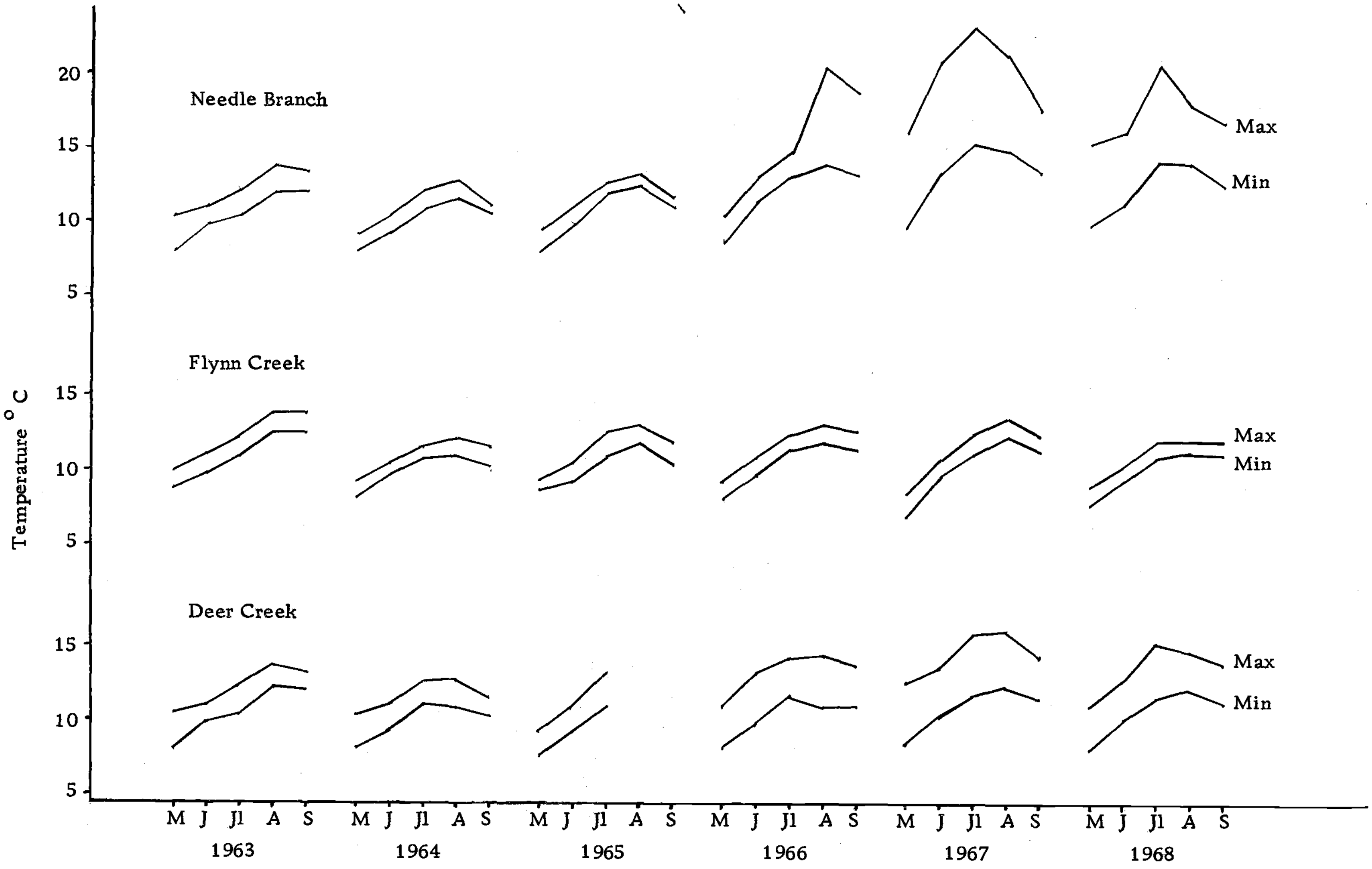


Figure 4. Mean monthly maximum and minimum daily temeratures, May through September, 1963-1968, for Deer, Flynn, and Needle creeks. Data from U. S. Geological Survey.

day's heating. Mean minimum temperatures just before dawn increased only about 2° in the post-logging years. The rates of temperature increase during the day were therefore large in Needle Branch.

Possible effects of both higher mean temperatures and high rates of temperature increase on coho populations will be discussed later. Whatever the effects they influenced only a few year classes of coho. By 1969 regrowth of vegetation along the margins of Needle Branch was providing sufficient shade to moderate the spectacular temperature increases seen from 1966 to 1968 (Brown and Krygier, 1970).

Oxygen

Dissolved oxygen in small streams is typically at or just below saturation, particularly so when such streams are shallow and turbulent, or have extensive riffle areas. Oxygen levels within the gravel substrate of the streams decrease with depth and depend upon the rate of exchange between intragravel and surface waters as well as rates of oxygen utilization within the gravel. Vaux (1968) has shown that surface water trajectories tend to enter gravel riffles on the upstream faces and leave on the downstream faces following curvilinear upward paths, thus renewing the intragravel oxygen supply.

After logging in 1966 significant decreases in both surface and intragravel oxygen levels occurred in Needle Branch, but not in Deer

Creek (Hall and Lantz, 1969). During the spring and summer following the logging, oxygen levels in surface waters decreased enough to cause coho mortality in some sections of the stream. The oxygen decline in the stream was mostly due to debris, which reduced the flow and aeration of the water and increased the oxygen demand through decomposition. The high stream temperatures aggravated the oxygen decline. With stream clearance and the coming of the fall freshets, surface water oxygen returned to normal.

When oxygen levels in surface waters decrease, intragravel levels must also drop. Intragravel oxygen fell about 3 mg/liter but unlike the surface water oxygen, remained at below normal levels for at least three winters following logging. Increased sedimentation over and within the gravel, reducing its permeability, was one probable cause. Another likely cause was increased deposition and subsequent decomposition of organic material in the gravel. The distribution of organic and inorganic sediments in natural stream gravels must be varied, reflecting the complexities of stream flow patterns. Thus Ringler (1969) was not able to show that the reduced intragravel oxygen in Needle Branch was accompanied by significant increases in deposited organic sediments over that in the other two streams. However he suggested that decomposition of organic debris was a cause of the decline in dissolved oxygen.

Spawning female coho, in the process of digging redds, effect a cleaning of the spawning gravel. Since this activity occurs during higher levels of stream flow, sediments may be washed out to a large degree as suggested by Ringler (1969). Such cleaning in salmon redds has been described by McNeil and Ahnell (1964) and Cooper (1965). This is an example of how both biological and physical processes may work in conjunction to return a disturbed stream back to normal conditions.

Other Dissolved Materials

Chemical characteristics of the study streams have been described by Chapman (1961, 1965). Small but significant increases in nutrients, especially phosphates and nitrates, have since occurred in the discharge of the logged watersheds (unpublished data, Pacific Northwest Water Laboratory).

Likens et al. (1970) reported a much larger increase in chemical constituents in an eastern deciduous watershed on which all the vegetation was clear-cut but not removed. The high rate of nutrient loss they observed was due to effects from the felled timber and slash and to herbicide treatments of the watershed that blocked the vegetational effect on uptake and storage of nutrients. The authors point out that nutrients are normally well conserved in an ecosystem, primarily in the biological compartment. The effects of nutrient loss from a watershed are not known, but long term and far reaching consequences might occur due to decreases in the basic primary productivity of the ecosystem. This should be an important consideration in decisions on timber harvesting.

Summary

The typical coho habitat, a small mountain stream, is seen as a highly variable environment, which under normal, forested conditions is largely under the influence of weather patterns. Perhaps the most variable components of that environment are stream discharges and intragravel dissolved oxygen. The adaptive significance of ecological patterns in the coho life history and the environmental influences on their biology, including that of logging, will now be discussed. It will be seen that large variations in biological input occur normally and that the species is able to reduce these variations to within the environmental capacity of the system.

THE INPUT OF COHO INTO THE STREAMS

The Spawning Migration

Adult coho ascend into the Drift Creek study streams to spawn, primarily from November through January. The arrival of spawners coincides with the period of high water in the streams. During that time the fish appear in small groups, usually two or three per day. Approximately 80% of the combined daily runs to all three streams are composed of nine or less individuals, or about three or less per stream. Male fish outnumber the females by a ratio of about four to one. Some of the males are jacks, precocious males that have spent only one growing season at sea.

Relationship to Stream Discharge

That the coho enter the streams from the sea with the coming of the rains is well known among sport fishermen. The factors governing this relationship are not so well understood, however. The first effects upon the coho must take place in the estuary. But the farther the spawning streams from the estuary the less clear will be the relationship between cause and effect. Both estuarine coho and those that have "holed up" in the stream while enroute to their spawning grounds will be influenced by migratory cues so that time and distance factors complicate understanding. Gribanov (1948), in studies of Kamchatkan coho, stated that the fish enter the bays from the sea, following the gradient of lowering salinities. They then enter the streams during the rising tide and journey upstream at rates of 11-18 km/day. At that rate the Oregon coho would take from 2 to 3 days to reach the study streams. They appear to enter the traps at the mouths of these streams at night, perhaps in the early morning hours. Movement upstream may have occurred mainly during daylight hours, however, as has been observed in the Cowichan River (Neave, 1943) and at Waddell Creek (Shapovalov and Taft, 1954).

The arrival sequence of coho (Figure 5) clearly shows that the spawning runs are associated with times of peak stream discharge. The fish arrive during days of both rising and falling water, but the mode of occurrences is centered at the time of peak discharge (Figure 6). The skewness of that histogram is due to the fact that there are many more days of declining flows than rising flows. Successive peaks in the adult runs, perhaps representative of individual cohorts of spawners, are even more closely associated with times of peak stream discharge (Figure 6).

The fact that adult movement occurs during both rising and falling streamflows has made analysis of the factors involved difficult. Shapovalov and Taft (1954) also noted that coho in Waddell Creek moved upstream during both rising and falling streamflows, but movement ceased during the time of peak flood. The above authors, as well as

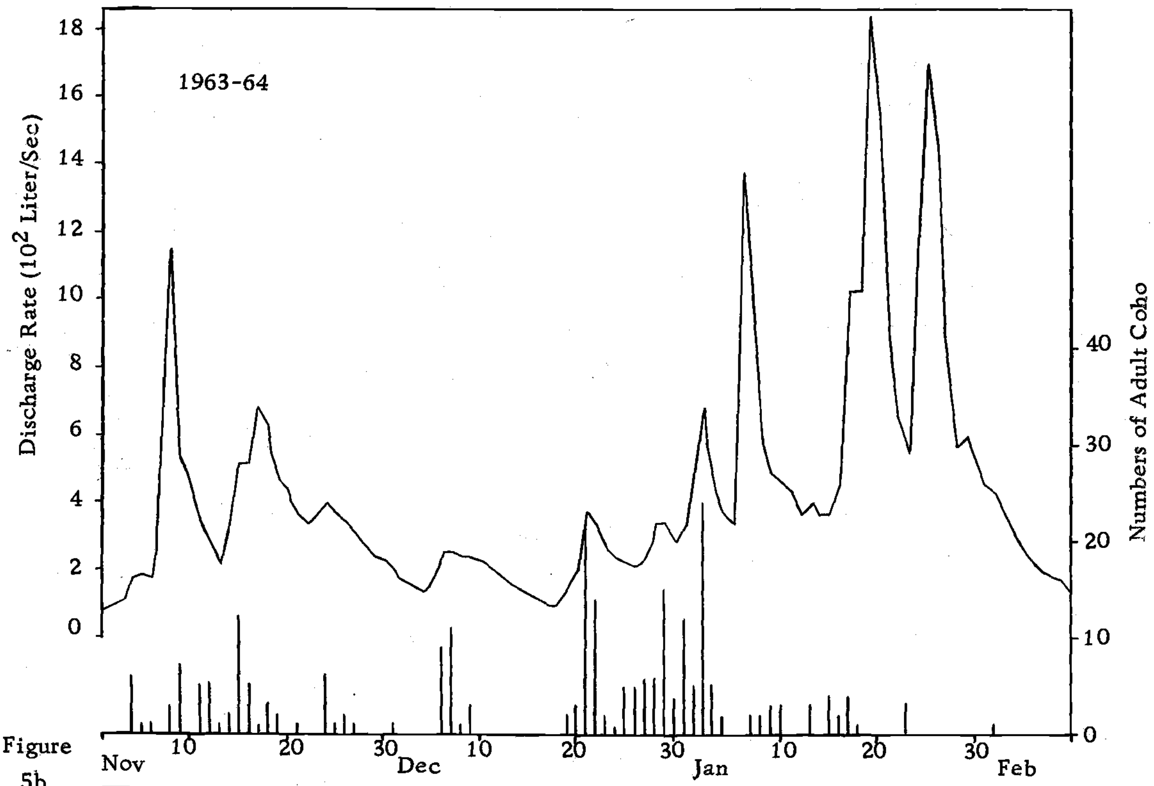


Figure 5b

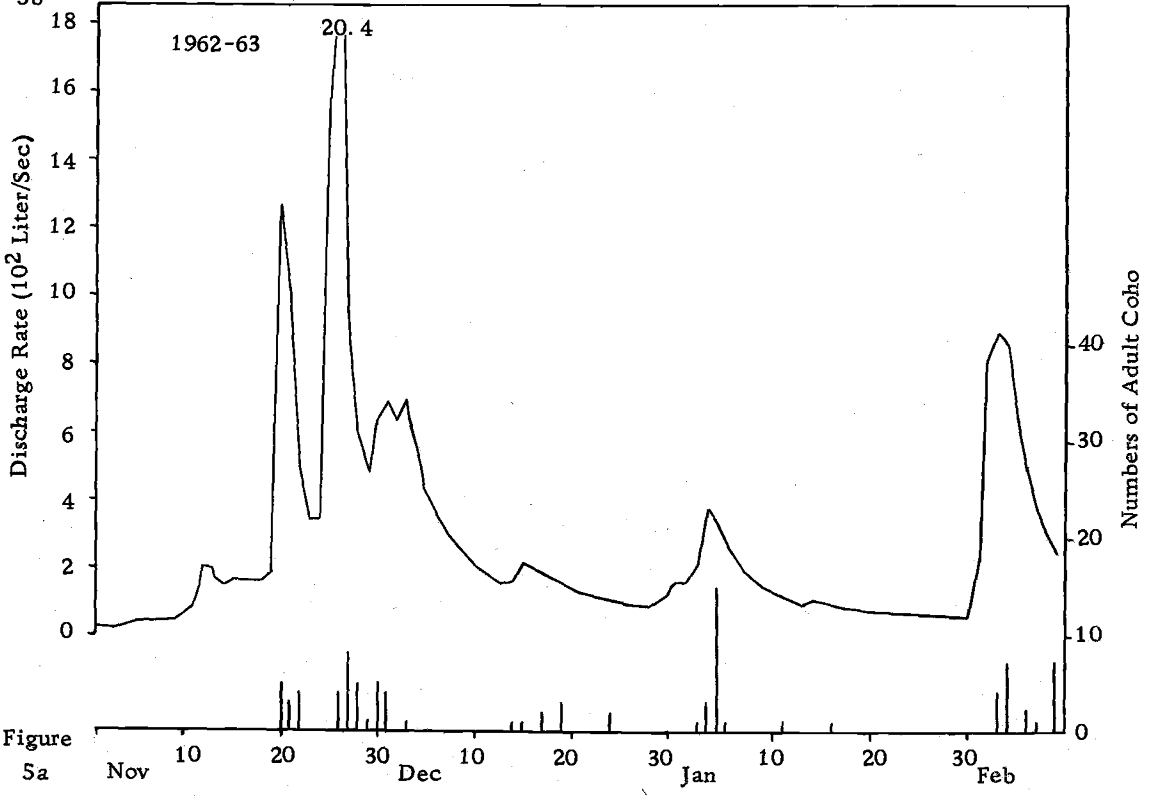


Figure 5a

Figure 5a, b. Stream discharge (Deer Creek hydrograph) and combined adult migration to the three creeks during the main spawning period.

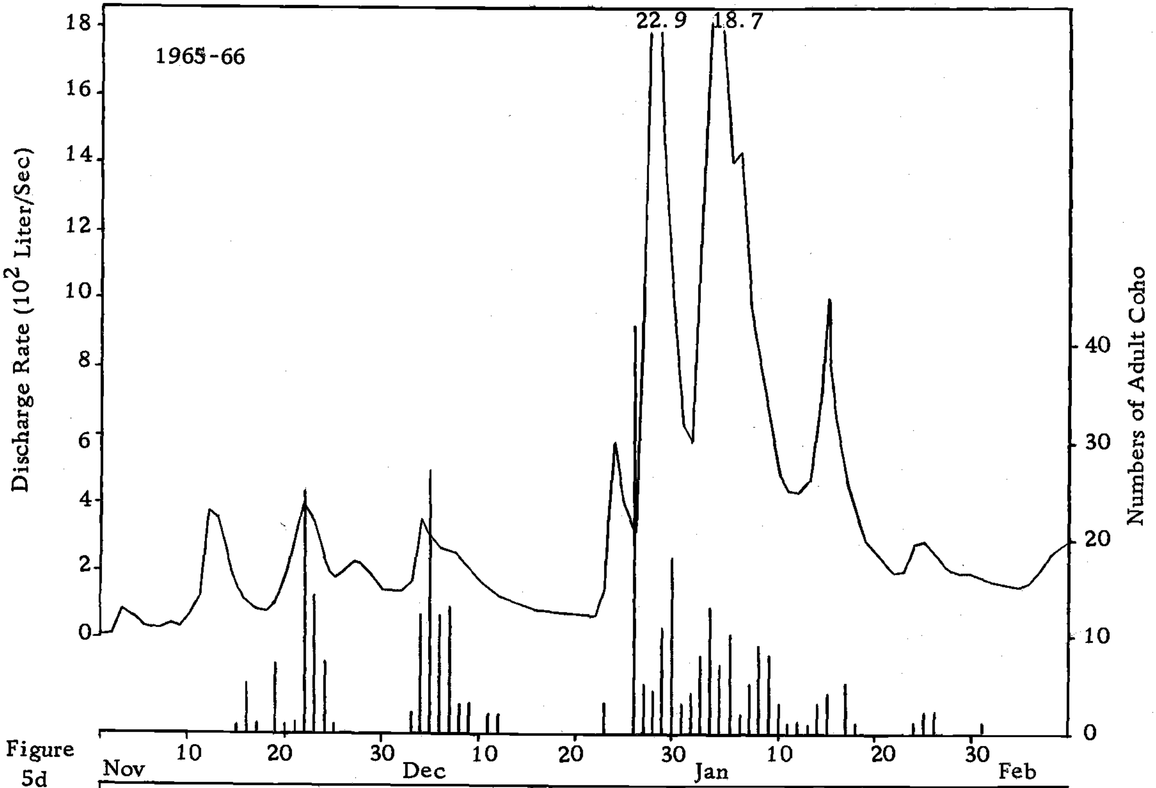


Figure 5d

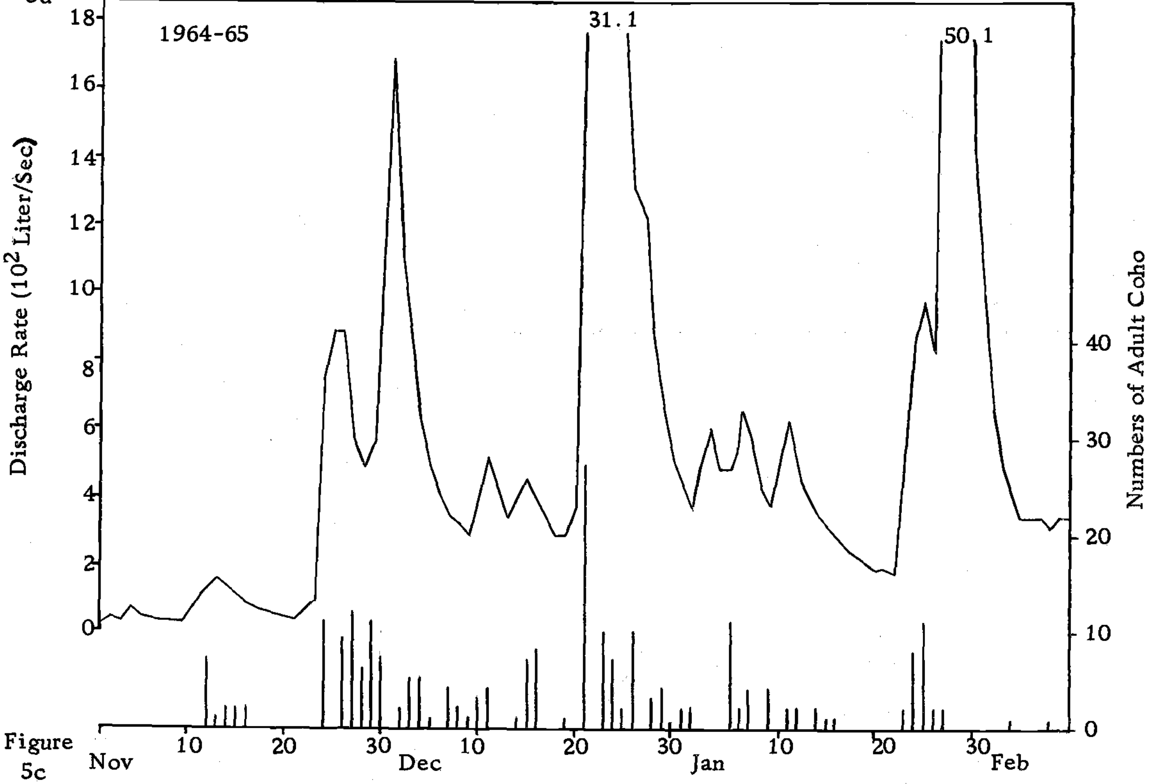


Figure 5c

Figure 5c, d. Stream discharge (Deer Creek hydrograph) and the combined adult migration to the three creeks during the main spawning period.

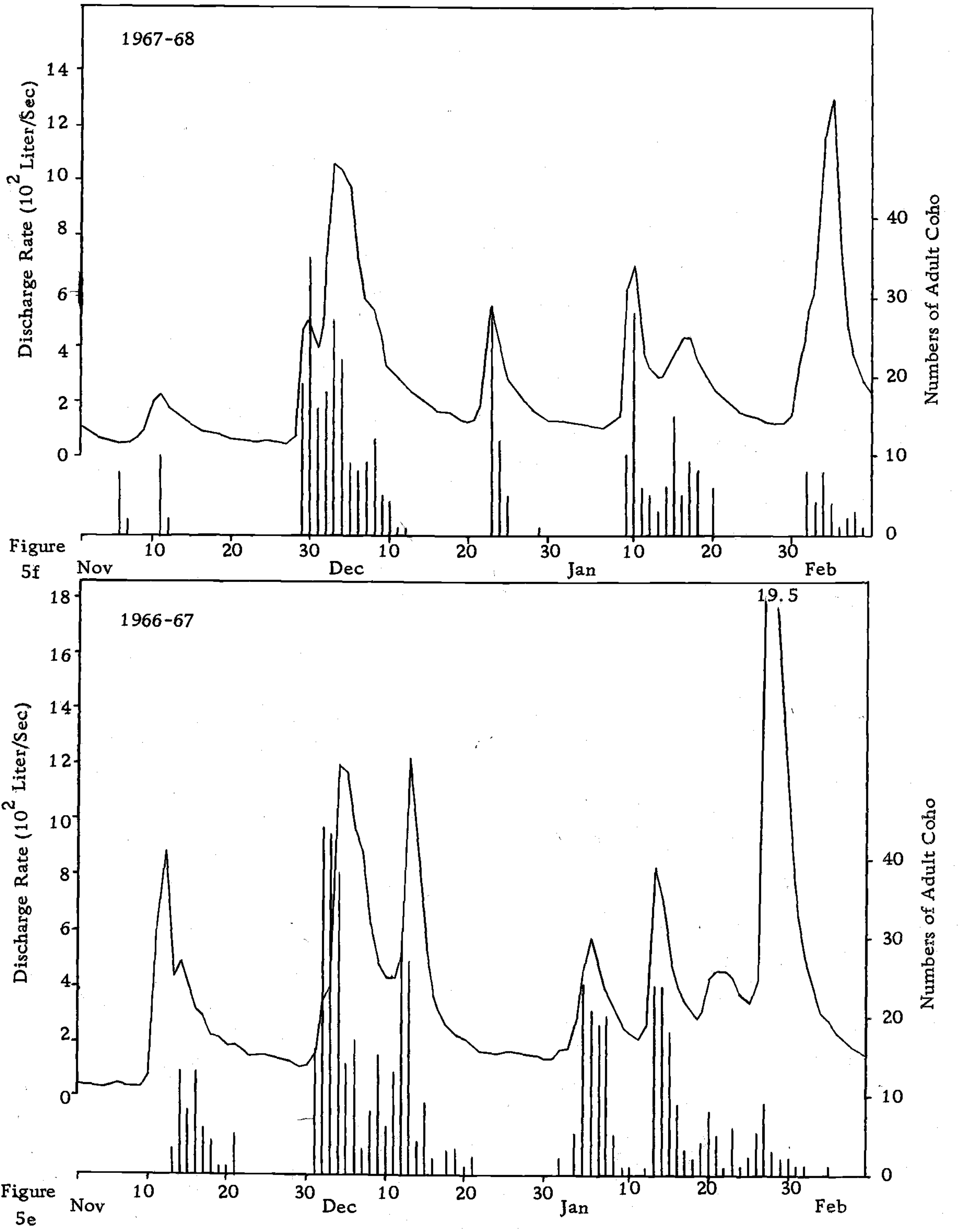


Figure 5f

Figure 5e

Figure 5e, f. Stream discharge (Deer Creek hydrograph) and combined adult migration to the three creeks during the main spawning period.

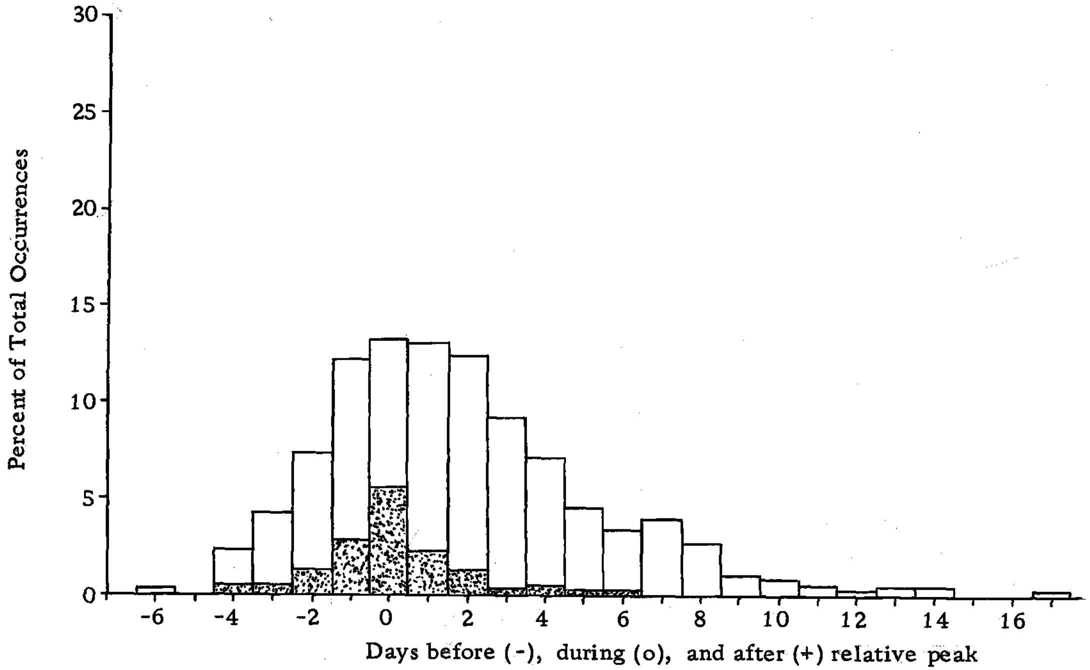


Figure 6. Percent occurrence of adult coho with respect to each peak in streamflow, all streams combined, 1960-69. Shaded portion represents percent occurrence of those fish making up each peak in adult runs.

Chapman (1941) and Neave (1943), could not decide on the factors influencing the movement.

Because spawning adults tend to arrive during peaks in stream discharge, I attempted to show quantitatively how the numbers of adults arriving were related to streamflow conditions (Figure 7). The percentage of the total run during a season (all streams combined) represented by each "cohort" of adults was plotted on a field of increases in stream discharge and base discharge levels (Deer Creek hydrograph). I reasoned that the percentage of adults arriving in the period from the start of a rise in the hydrograph to 3 days after adequately encompassed each separate "cohort."

At lower levels of average flow (base discharge) any increase in stream discharge during the spawning season usually resulted in relatively large numbers of coho arriving at the study streams (Figure 7). With higher average flows the size of the runs tended to be smaller, except perhaps when high rates of increasing flows occurred. Thus adult coho seem stimulated to enter the streams and begin their spawning journey at any time in the season when increased stream discharge occurs. Whenever stream discharge rates fall to low levels, the fish are unable or are not induced to migrate, so that a "pooling up" may result as they await the next rise in stream flow. When it occurs, even small increases in discharge will cause the fish to resume or start their migration. The likelihood of large runs appearing at the

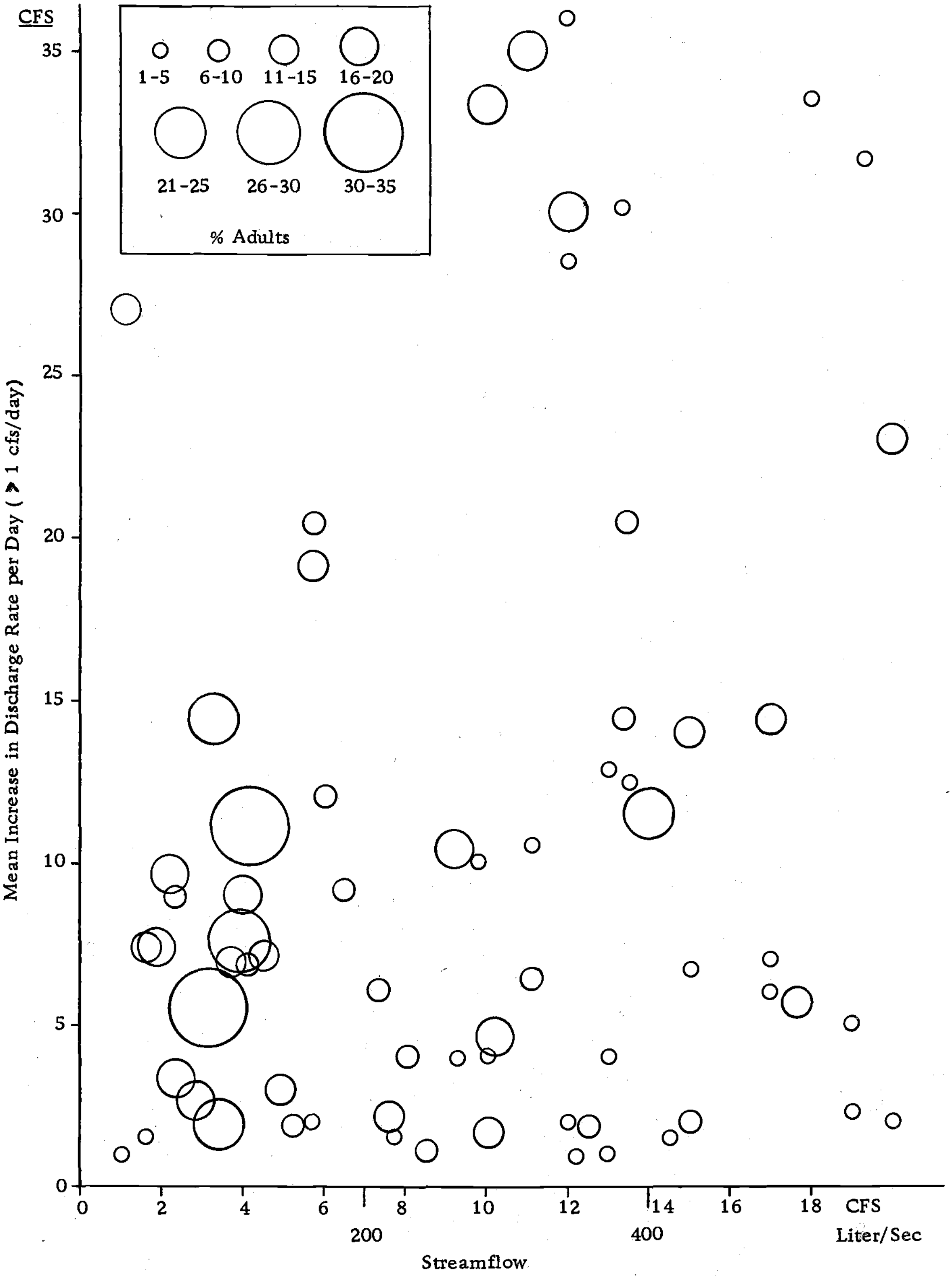


Figure 7. Percent of total adults in each year's run (all streams combined), arriving from start of each peak in stream discharge to three days after, according to increases in stream flow and flow level just prior to the increase. 1959-69.

traps after a period of low flows is therefore increased. Even though migration of adult coho may be initiated by rising streamflows, the fish apparently continue their movement after the peak in discharge has passed. Most of the fish spawning in the three streams arrive during rising stream discharge. In five out of the eight seasons, 1960-61 to 1967-68, significantly more fish (χ^2 test) arrived during rising flows then falling. There were two seasons in which more fish arrived during falling flows and one season in which the difference between numbers arriving with respect to streamflow was not significant (Table 2). Thus the arrival times of the individual fish at the spawning grounds may be quite variable with respect to streamflow.

Part of the effect of stream discharge may be purely mechanical. One may expect that a minimum flow level in the streams must be maintained for efficient upstream swimming, but that the fish are capable of continuing their journey at relatively high levels of discharge.

Once the fish are at the spawning grounds, construction of redds by females is aided by fast streamflow. Observations of spawning activity suggest that the main function of female "digging" behavior is to direct and augment the existing current into the gravel so that excavation is possible.

Size Composition

The mean lengths of jack, male, and female adult coho have been

Table 2. Total numbers of adult coho arriving at the study streams during each season with respect to rising or falling streamflows, and the significance of the differences.

Season	Number Adult Coho	Percentage arriving with respect to streamflow[a] Rising	Falling	χ^2
1960-61	227	66.0	34.0	22.84**
1961-62	312	57.5	42.5	6.48*
1962-63	89	36.0	64.0	6.47*
1963-64	252	57.1	42.9	4.84*
1964-65	238	49.7	50.3	0.004
1965-66	316	35.6	64.4	24.95**
1966-67	578	56.1	43.9	8.21**
1967-68	386	60.6	39.4	16.89**

a) Fish arriving during day of peak discharge are considered to have arrived during a rising stream discharge.

approximately 40, 63, and 70 cm respectively (Appendix A-1). Females almost always average larger than males, although some males are often larger than any female. This situation is in contrast to that reported by Shapovalov and Taft (1954), who found that the males averaged 1 or 2 cm longer than the females. Godfrey (1965), in his summary of the life history of the species, also stated that males were larger than females. I considered jack coho to be those males less than 47 cm long. There is usually a break in the length frequency histograms in this range, so separation of these precocious 2-year-old males was seldom a problem. Inspection of scales indicated some overlap among jacks and the 3-year-old males in the range 40 to 50 cm, but there were about as many 3-year-olds less than 47 cm as there were jacks larger than or equal to 47 cm. There did not appear to be any trend in the sizes of jacks, males, or females during the course of the season, as has been seen e.g. at Minter Creek, Washington (Salo and Bayliff, 1958).

Sex Ratio

Males outnumber females in the spawning runs, the male:female ratios (Appendix A-2) being about 4:1 for each stream. If jacks are excluded, the ratio is about 3:1. Not all male fish can be considered spawners, for they do not all remain on the spawning grounds. There is, in fact, a rather steady emigration of males back out of the study streams throughout the spawning season. At the beginning of the season most of these fish are jack males, but later jack and 3-year-old males emigrate in about the same proportion as upon arrival. A few females also drift down from the spawning areas, but they are mostly spent spawners. Emigrating males may be temporary strays. A correction was therefore applied to derive a more realistic ratio. Jacks were excluded, along with those male emigrants that had stayed on the spawning grounds less than 5 days. This procedure assumes that such males, constituting about 50% of the emigrants, had not spawned. Even when this correction to male numbers is employed, males outnumber females in these study streams by about 2:1 (Table A-2). Gribanov (1948) also reported excess males over females on Kamchatka spawning grounds, and he attributed it to the longer male survival after spawning. He reported an equal ratio in the escapement. In contrast, Shapovalov and Taft (1954) observed an excess of females over males in Waddell Creek when the jacks were excluded. The ratio was in favor of males when the jacks of the same brood year were included so that the overall male to female ratio was 1:1. On the other hand Willis (1962) found a 1:1 sex ratio among adult coho exclusive of jacks in Gnat Creek, Oregon.

In the Drift Creek study streams, males outnumber females at the time of first appearance at the traps so that differential stream mortality cannot explain the uneven ratio. Since unspawned males do emigrate from the streams, there may be a certain amount of wandering of unattached fish seeking mates in the vicinity of their natal streams. This would contribute to the excess of males. However male fish passing through the traps are marked as they arrive, and most of the males entering during the season are unmarked. Therefore if a wandering of males is the cause of the disproportion, the contribution must be mainly from other than the study streams. This implies either that other coho tributaries on Drift Creek are at times short of males or that somehow the entire drainage has an excess male population. Small streams such as are involved in this study may be swamped by a small percentage of wandering or straying males from large runs in the main river nearby or from larger adjacent streams. Such an effect has been described by Lindsey, Northcote, and Hartman (1959) in an analysis of percentage homing and straying of rainbow trout in two spawning streams.

Because there still remains an excess of males after corrections for wandering males and jacks are applied, it is worthwhile to check for differential mortality among the sexes as a cause. The sex ratio in juveniles and smolts is 1:1 (unpublished data, Oregon Game Commission). Since some of these smolts are marked for population estimates (to be discussed later), tests for equivalence in the ratio of marks among the adult males and females are possible. If it is assumed that male and female smolts possess equal proportions of marks, then the proportion of marks in the returning males and females should also be equal unless the male population is being diluted by males originating from other streams. Otherwise differential mortality must be the cause of the disproportionate sex ratios.

The ratio of marked to unmarked fish was not significantly different (χ^2 tests) between males and females in each stream and in the combined data of all three streams (Table 3). The implication is that there exists a differential mortality against females at sea, perhaps due to a difference in habits. In view of the small proportion of marks in the adult population and the small total run of adults each season, these estimates of the true mark ratio may be very imprecise. The above result should therefore be taken with caution. Further speculation on the cause of the disproportionate sex ratio in the Drift Creek study streams must await additional information on sex ratios in other tributaries of the system, or in the overall escapement population.

Spawning and Redd Survival

Location

Stream surveys for location of spawning redds have been conducted since the start of the project. Distances were measured in feet upstream or downstream from the weir; however they are reported in meters throughout this paper. Since 1963 greater efforts have been

Table 3. Chi-square contingency tests for independence of mark ratio between sexes of adults.

Stream	Inclusive Seasons	Males Number Marked	Males Total	Females Number Marked	Females Total	$\chi^2(1)$
Deer	1964-65 1968-69	28	718	6	193	0.090
Flynn	1965-66 1968-69	23	365	6	97	0.002
Needle	1966-67 1968-69	9	174	1	53	0.407
All	1964-69	60	1257	13	343	1.815

made to attempt the location of all spawning females. In the last few years these attempts have been facilitated by the use of radio transmitter tags, which are attached to females as they pass through the traps. The combined available data from these surveys show that there are some sections of stream that are favored for spawning, although practically all areas with suitable gravel have had redds in one season or another (Figure 8). Each stream seems to have a lower and an upper favored area, most notably so in Deer Creek. Inasmuch as females often proceed directly to spawning locations in the upper sections of the streams, by-passing areas where spawning subsequently occurs that same season, the possibility exists that the fish may be able to home to specific areas of their natal streams.

Fecundity

The regression of fecundity $(\hat{Y})$ on length in cm (X) estimated from the nearby Fall Creek stock is: $\hat{Y} = -3184 + 78.1X$ (Koski, 1966). From his figure the 95% confidence interval of a predicted individual is $\hat{Y} \pm$ about 400 eggs. For an average female coho of 70 cm in the Drift Creek study streams, the relationship predicts a fecundity of about 2,300 eggs. This fecundity is somewhat lower than found in some other North American stocks. At Shashin Creek, Alaska it is about 2,900 eggs (Crone, 1968). Neave (1948) gives a fecundity of about 2,700 as an average for several British Columbia streams. In Scott Creek,

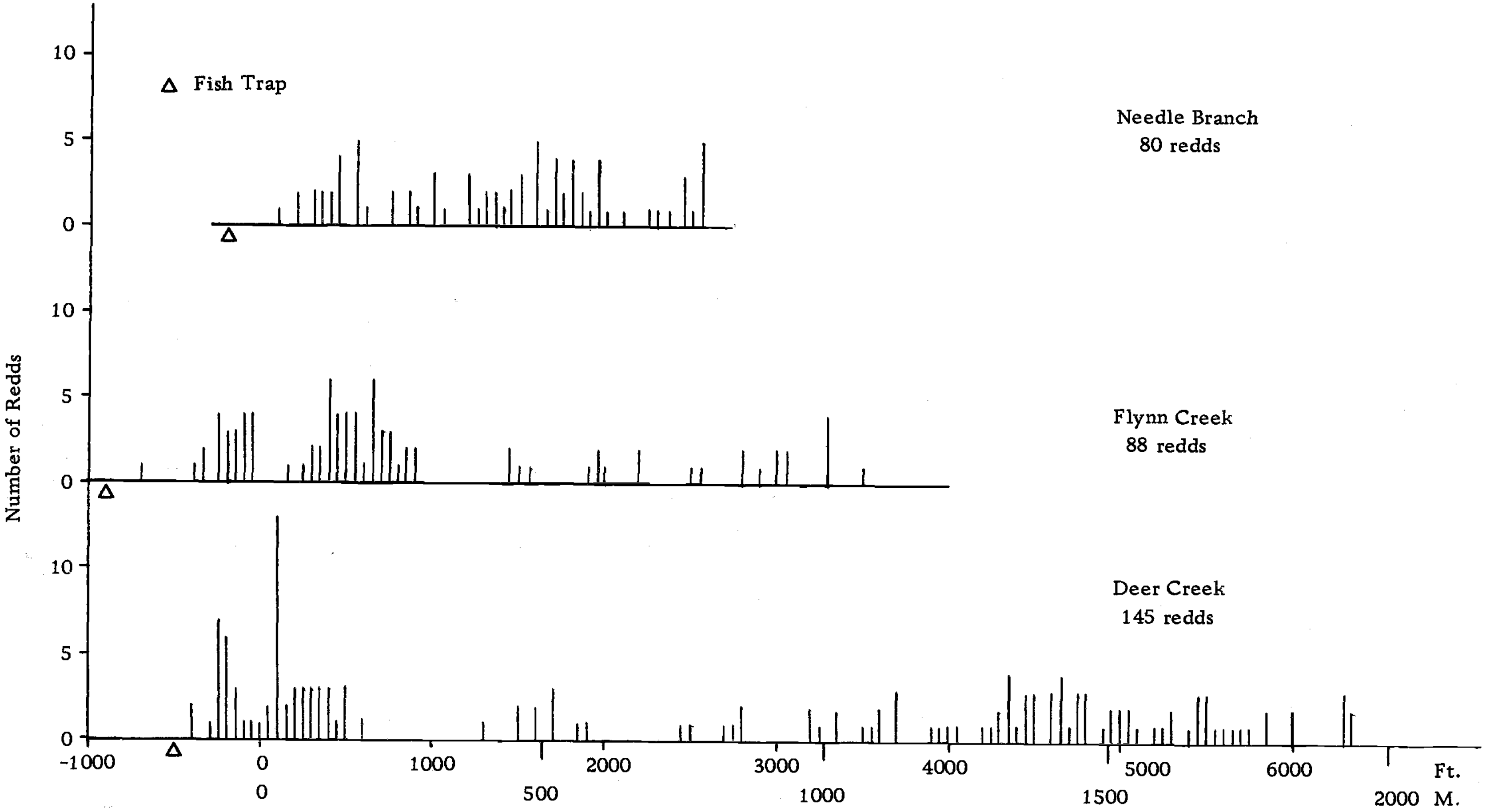


Figure 8. Distribution of coho redds along the length of study streams upstream from fish traps. Data from 1959-1970 combined. Distance origin is at weir.

California, Shapovalov and Taft (1954) show a fecundity of about 3000 for females 70 cm long. For the same sized females fecundities were about 3,000 eggs at Minter Creek, Washington (Salo and Bayliff, 1958) and 3,200 eggs at Gnat Creek, Oregon (Willis, 1962). Asian coho may have even higher fecundities. Gribanov (1948) gives mean fecundities for two Kamchatkan stocks as 4,350 and 4,883 with ranges from 2,800 to 7,600 eggs per female.

Survival Within Redds

Survival of eggs within redds is highly variable in the Drift Creek streams (p. 9). Survivals ranged from 0 to over 80% with a mean of approximately 30%. In general, mean intragravel survival from egg deposition to emergence must be low, and the range in survivals attests to a great variability in the hazards of that environment. This may stem largely from variability in the distribution of intragravel sedimentation and the resulting decreases in intragravel water exchange. The latter reduces the supplying of oxygen and the removal of metabolites from the redds (McNeil and Ahnell, 1964; Cooper, 1965). Increased sedimentation may also impede the physical emergence of fry from the redds (Koski, 1966). In the Cowichan River, Neave (1948) reported survivals from 11.8 to 40% with a mean of 22.8%. Shapovalov and Taft (1954), reviewing literature on survival to hatching, listed values ranging from 1 to 75%. They felt that under favorable conditions, primarily the absence of heavy silting, survival to emergence was high, between 65 and 85%.

Fry Emergence

In the Drift Creek study streams fry begin to emerge from the redds after about 100 days from the date of spawning, the time to emergence depending primarily upon water temperature. This emergence is primarily at night (Figure 9). Data were obtained by counting emerged fry caught in a redd trap approximately every 2 hours during the period of high emergence at night, and at longer intervals during the day. Because the numbers so counted were cumulatives of fish emerging between removals, the data were converted to average numbers per hour before plotting. The instantaneous emergence rate as a function of time is approximated by the smooth curve, drawn by eye, through the histograms. Although the data obtained are unnatural to the extent that the redd trap may influence emergence behavior, there is no reason to expect that the general features of fry emergence are not portrayed. These data represent only one or two days and nights in the emergence sequence of a particular redd, not necessarily the times of peak emergence for that redd.

Besides being primarily nocturnal another notable feature of emergence is the high rate during certain hours. The curves in the figure probably de-emphasize this aspect, but in Needle Branch (518 m)

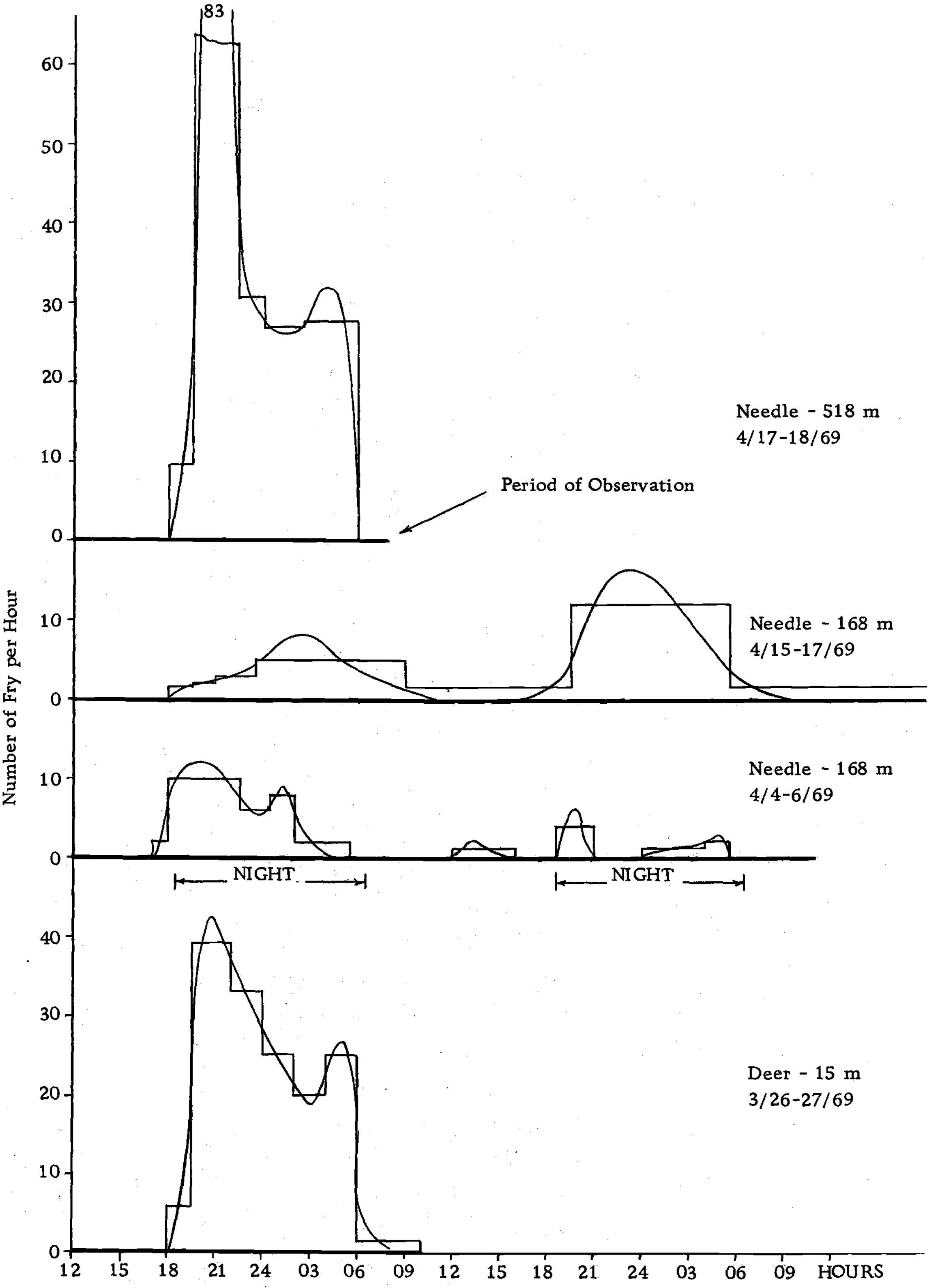
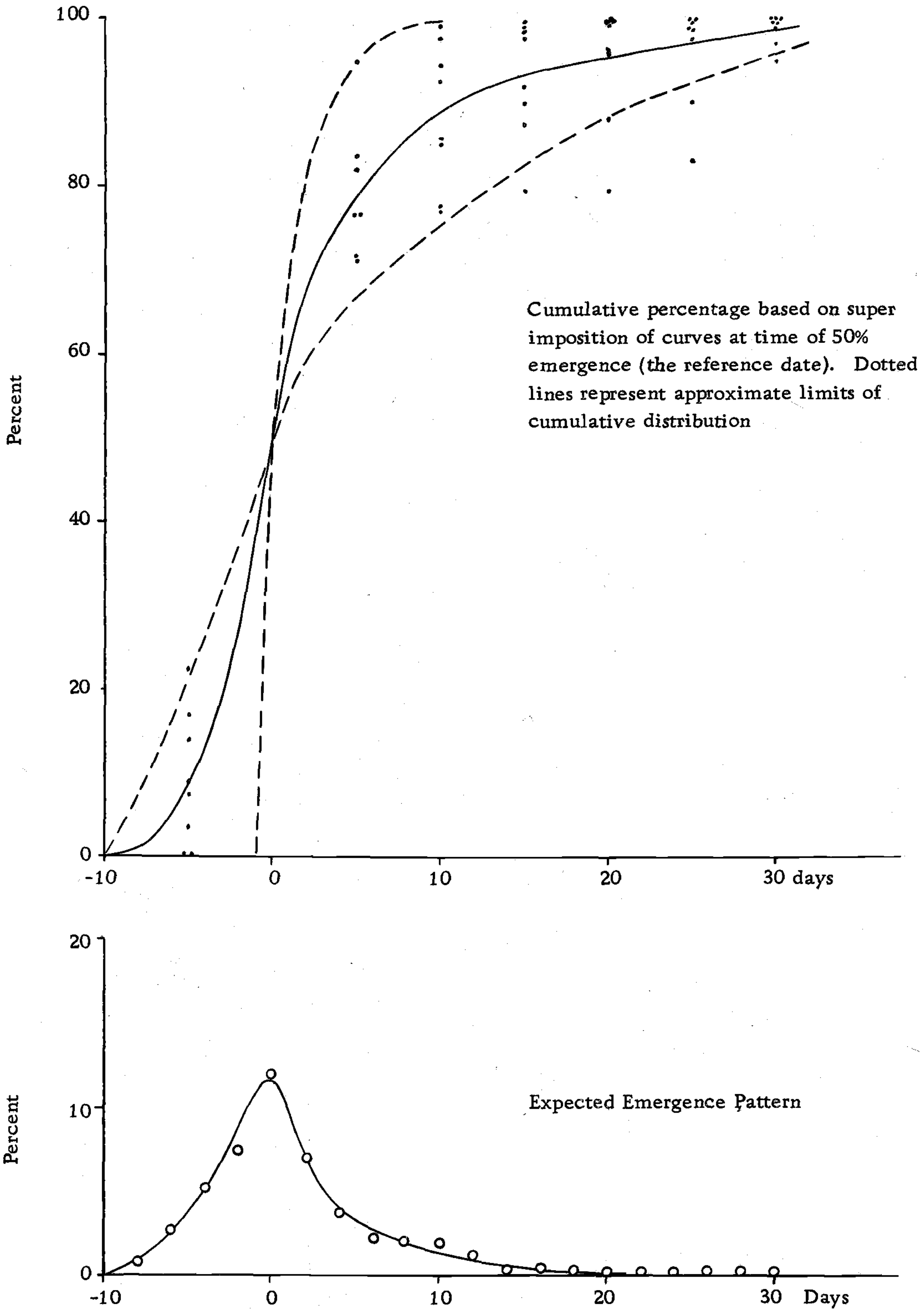


Figure 9. Emergence from redds: average number of fry per hour vs. time. The histograms are plotted as average rates of emergence over the period between observations. The instantaneous rate of emergence is approximated by the smooth curve.

more than 200 fry may have emerged during the span of an hour. The highest rate of emergence appears to characteristically occur a few hours after darkness. This peak of mass fry emergence in the early hours of the night is probably due to an accumulation of fry below the gravel surface during the day. These fry are photo-negative so are inhibited from emerging during daylight. As soon as night falls they penetrate the gravel surface, thus producing the primary emergence peak at about 2000 hours.

Experiments I have conducted on pre-emergent coho fry indicate that there are no appreciable differences in activity levels between night and day hours when the fry are continuously kept in darkness. In these experiments the fry were suspended in small bags of netting which in turn were attached to a kymograph. The results are probably valid at least for the larger fry, ready to emerge. Thus the evening peak emergence is most likely due to the inhibiting effects of daylight upon fish which would otherwise have emerged during the day. In a study of the intragravel behavior of sockeye fry,Bams (1969) found that the daily light cycle caused an accumulation of fry just beneath the gravel surface during daylight.

The total emergence from a given redd is a process that may last for over a month (Figure 10). Once begun, emergence increases rapidly to produce a characteristic and rather sharp peak in the total pattern. This peak may occur up to 10 days from the time the first



Cumulative percentage based on super imposition of curves at time of 50% emergence (the reference date). Dotted lines represent approximate limits of cumulative distribution

Expected Emergence Pattern

Figure 10. Sequence of total fry emergence from redds: mean percent vs. days. Data from Deer Creek, 1968 year class.

fry appear. After that the numbers of fry emerging per day decrease rapidly, but a low rate of emergence continues for weeks thereafter. There may be secondary emergence peaks during this post-peak phase. These may be associated with subsequent and different pockets of eggs deposited in the redd by the female, or perhaps to instances of superimposition by other females. The data in Figure 10 are from Oregon Game Commission records on eight redds that were trapped on Deer Creek in 1968. The mean cumulative percentage distribution (solid line, upper panel of figure) shows that 10 days after peak emergence, approximately 90% of the fry from a particular redd will have emerged. Although the general pattern of emergence is preserved in each redd, individual variations do occur. To give some idea of these variations the percentages from individual redds are plotted at 5 day intervals in the figure with dotted curves giving the approximate, limiting curve types encountered. From the mean, cumulative percentage pattern the expected emergence pattern was derived (lower panel, Figure 10).

Because emergence is such a drawn out process, commonly lasting over 30 days, the input of fry into a stream resulting from all the redds is nearly continuous during the spring emergence season (March through May). But the emergence peaks of individual redds, superposed to varying degree, may be expected to give an erratic pattern to total fry emergence in the stream. This pattern would in part be a function of the previous spawning sequence.

Summary and Discussion

Smith (1957) considered Pacific salmon primitive reproductively since they die after spawning. I prefer to consider the species highly adapted to their habitat and mode of life. If the precursor of Oncorhynchus was a trout-like ancestor of the genus Salmo, similar to the steelhead trout (Neave, 1958), then the post-spawning mortality feature should be considered a specialization associated with the development of the obligatory anadromous habit.

The general fluvial and drift-feeding habit of salmonids requires that their larvae be at an advanced stage when they first enter that environment. That salmonids spawn relatively large eggs is therefore not surprising. Rounsefell (1957) has shown that lacustrine salmonids, including the sockeye salmon (O. nerka), have smaller eggs than the fluvial anadromous Oncorhynchus species, and thus form a grouping distinct from the latter on this basis. The large and vulnerable eggs of the fluvial species are protected from dislodgement and injury by incubation within the gravel mass. New hazards faced there must be secondary to the main problem of successful incubation in a stream environment.

Adult coho arrive at the spawning grounds in a pattern associated with rises in streamflow. This is likely due to a necessity of higher water for the adults to successfully navigate to their spawning destinations and deposit their eggs within the gravel. The trip upstream from the estuary must be both hazardous and arduous, and so again it is not too surprising that Pacific salmon use their entire energy resources to make the journey only once. It seems that the enormous task of navigation, mating, and deposition of the large eggs is most efficiently financed by energy gathered at sea, and so heavy is its commitment to this task that death of the adult results. Necrotic changes in Pacific salmon associated with the mobilization of body resources for these reproductive activities have been described by Robertson and Wexler (1960) and Robertson, Wexler, and Miller (1961).

The reproductive conditions considered, it would seem a difficult feat for salmon to also maintain an iteroparous habit. Murphy (1968) stated that rainbow trout that survive after first spawning contribute only a small percentage to reproductive potential. Although it is easier to increase biotic potential through fecundity than through iteroparity (Cole, 1954), natural selection would generally favor the iteroparous mode in unpredictable environments where survival was uncertain (Murphy, 1968; Holgate, 1967). While their special anadromous habits favor semelparity, those Pacific salmon that spend a variable number of years at sea before returning to spawn may still be achieving some of the benefits of iteroparity.. Coho in the study streams, however, have a very regular ocean schedule; furthermore the great majority spend only one year in fresh water. Each coho stock would thus seem to have little insurance against the occurrence of a catastrophe on the spawning grounds during the season of their scheduled return. But the very protracted spawning run in any year, lasting in the extreme from October through February, may be considered a degree of iteroparity too, for the reproductive potential is guarded against disaster by being thinly spread over the long period. In comparison with other Pacific salmon the spawning season of the coho is relatively long. This might be interpreted to mean that conditions for successful spawning are similar each year in a stream, but within each year the timing of these conditions varies greatly and unpredictably.

The straying habit is another mechanism that helps to maintain coho populations. Should the small numbers of adults normally destined to spawn in a certain mountain stream fail to arrive for some reason, a few coho straying into that stream could establish a near normal population complement there.

After spawning,the coho eggs are left to incubate in the gravel for approximately 100 days, the exact period depending upon such variables as stream temperature and intragravel oxygen levels (Shumway, Warren, and Doudoroff, 1964). The former is the primary factor determining developmental rate. The fry emerge from the redds primarly at night and in large numbers. The varying degrees of coincidence of emergence peaks from the total redds present produce the erratic total emergence pattern.in a stream. This pattern, I believe, largely reflects the spawning pattern, which in turn depends upon those random weather events that initiate adult input and spawning.

In streams such as are involved in this study the numbers of spawning adults returning each year are normally small, and the between-year variations in numbers large (Appendix A-2). The 95% confidence intervals of the mean yearly number of returning adults, excluding jacks, are 107-187, 47-127, and 5-49 for the streams Deer, Flynn, and Needle respectively, assuming a normal distribution of the sizes of adult returns. If a change as large as 50% of the average yearly adult return had occurred as a result of logging, and if it be further assumed that the standard deviation of the runs remained the same after logging, then the new average would have to be maintained for periods of about 6, 16, and 48 years, for the three streams respectively, in order that the differences be statistically significant. This of course does not prevent one from speculating on short-term effects of logging on coho salmon should a series of two or three year's runs be unusually low (or high).

FRY DISPERSAL AND STREAM COLONIZATION

After emergence coho fry spread away and mostly downstream from the redds. I call this movement "dispersal" or "dispersion" because, like the analogous physical process of diffusion, it results in individuals being scattered or dispersed between the origin and some outer distance limit. The location of the mode of the distribution depends upon the "dispersiveness" of the system. Dispersive movement by definition is not goal oriented, in contrast to "migration." In the following discussion, however, the terms "migration" and "emigration" will often be used loosely to describe the downstream movement of fry.

The downstream migration of recently emerged fry probably occurs, at least to some degree, in all coho streams. In British Columbia it has been reported at Williams Creek (McDonald, 1960), in the Cowichan River (Neave, 1949), and at Nile and Hooknose Creeks (Hoar, 1951). At the latter streams fry move past the downstream traps by thousands and may subsequently be seen swimming in tidal areas and sometimes in brackish water (Hoar, 1968). Many thousands of fry have been observed emigrating directly into the estuary during spring and summer at Sashin Creek, Alaska (Crone, 1968). This may be the general case in smaller coastal streams. From inspection of 6,312 scales of British Columbia coho, Prichard (1940) decided that

0.4% had left the rivers to enter the sea as fry. In Kamchatka both Gribanov (1948) and Semko (1954) state that coho fry disperse throughout the river system, from near the river mouth to areas upstream from the spawning grounds. The latter author gives statistics of tens of thousands of coho fry emigrating each year from the Karymaisky Spring (a tributary) where the adults had spawned. Neave (1949), in discussing the Cowichan River populations, stated that in smaller tributaries a migration of fry to the river probably begins almost immediately after emergence and continues throughout the spring months.

In the Drift Creek study streams several thousand fry emigrate past the downstream traps each spring (Table 1). These migrants were first described by Chapman (1961), who called them "nomads." The fry output from Needle Branch frequently surpassed that of the other two streams. The average number of migrants per season was about 6,400 for Deer Creek and about 10,000 each for Flynn and Needle creeks. Average fry migration as a percentage of total estimated fry emergence (Table 1) was thus about 26% for Deer Creek and over 100% for both Flynn and Needle creeks. The large natural variations in survival within redds and the relatively small numbers of spawners involved are likely responsible for the latter result in Flynn and Needle creeks. Furthermore the trap on Needle Branch was inoperative during several years so that accurate counts of ascending females were not obtained. Average emigration probably exceeded 50% in those two streams.

Numbers of migrating fry appear to be directly proportional to numbers of emergent fry each year (Figure 11). Estimates of emergent fry can be obtained by multiplying numbers of spawning females by a constant incorporating average fecundity and redd survival. However for simplicity spawning females (X) were used as an index of fry emergence. Even in years of poor spawning escapement some fry are counted through the downstream traps. Thus it is reasonable to assume that any regression of numbers of emigrant fry on emergent fry must pass through the origin. Since there is a suggestion of upward curvature in the relationship, I investigated the form of the regression by attempting to fit a second degree polynomial to the data (Appendix A-3). For each stream the additional sum of squares due to X^2 was not significant. The linear regression coefficients given in the table describe the regressions plotted along with the data points in Figure 11. Although this analysis indicates that no more than a linear relationship exists between total fry migration and total fry emergence, curvilinearity cannot be entirely ruled out. This is realized when one considers that numbers of spawning females are only a crude index of numbers of subsequently emerging fry.

Many more fry, for a given number of females, are likely to emigrate from Needle and Flynn creeks than from Deer Creek, with the totals from Needle Branch being the largest (Figure 11). In this regard the main spawning areas (Figure 8) are nearest the downstream

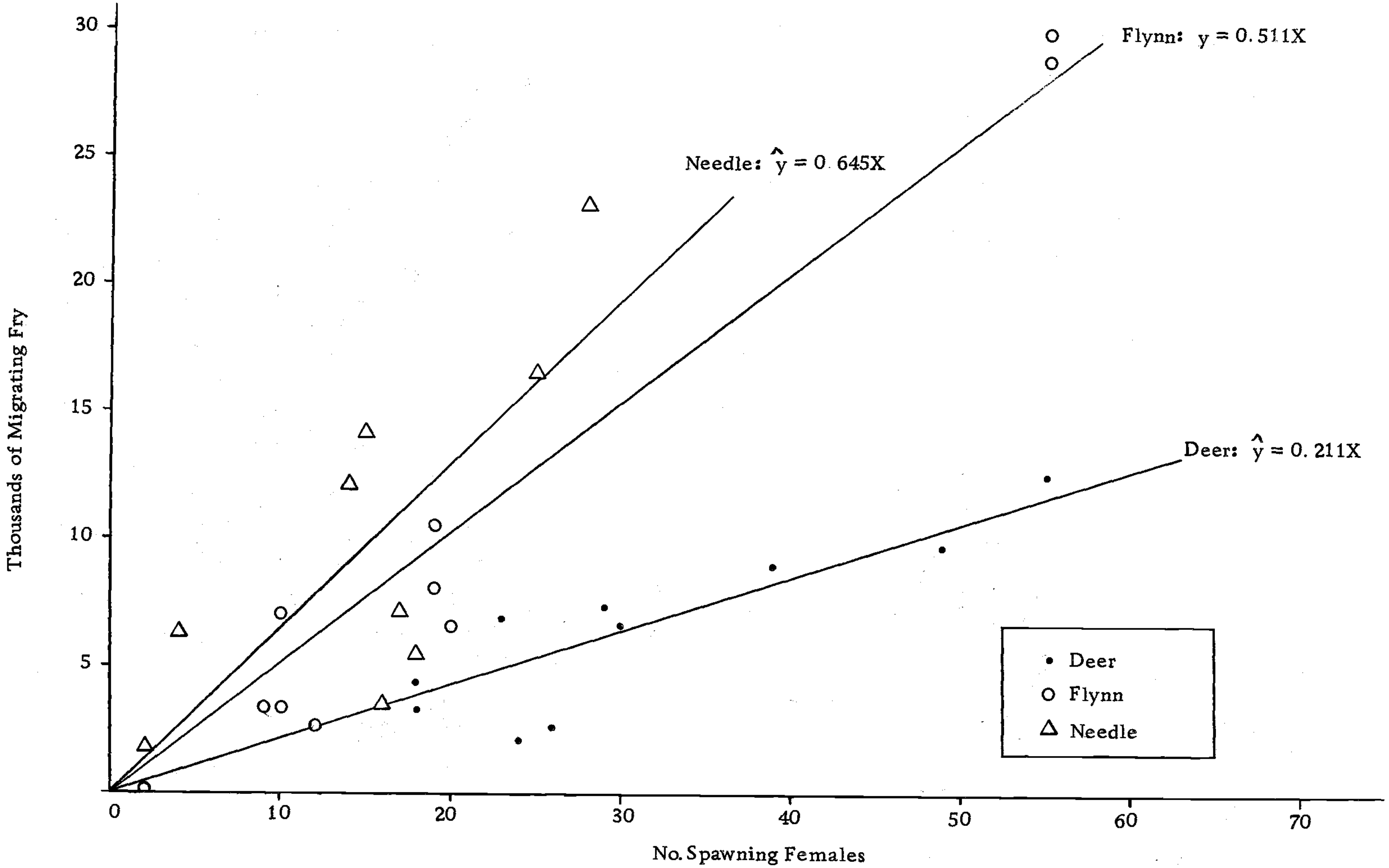


Figure 11. Relationship between numbers of migrating fry and spawning females (the latter an index of emergent fry). Data from each year, 1960-1969.

traps in Needle Branch and Flynn Creek, while in Deer Creek a considerable proportion of total spawning may occur almost a mile upstream from the trap. Daily fry emigration rates also tend to be higher in Needle Branch and Flynn Creek.

The actual numbers of coho fry emigrating from the study streams were even larger than given in Table 1, for there were always some fry that managed to escape enumeration. Some fry were able to bypass the trap by going through the screens on the main spillway. Traps installed in these spillways sampled fry to various degrees of efficiency. At times some of the main downstream traps were inoperative during periods of high water. Data on fry movement through the main spillways have been incorporated in the table whenever possible. Fry enumerations are from the beginning of fry emergence through July 31. The July counts very seldom exceeded 1% of the total movement for the period.

Fry emigration is usually negligible for the rest of the summer, with only a few individuals passing downstream from time to time during that period (Appendix A-4). This latter movement is best regarded as fingerling rather than fry emigration. The fingerling movement increases in the fall, declines, and then merges with the main smolt migration the next spring.

The Nature of Fry Movement

The Pattern in Time

The daily pattern of fry migration is highly erratic, with large fluctuations in intensity (Figure 12). The data are numbers of fry caught in the downstream traps between March 15 and June 4. Rates in excess of a thousand fry per day are not uncommon, particularly in Needle Branch, and often in Flynn Creek. Some of the migration peaks coincide with peaks in stream discharge (upper panel, Figure 12). Undoubtedly an augmentation of migration occurs whenever a particular fry movement happens to coincide with a spring freshet. Such coincidences in emigration and discharge peaks usually do not involve all three streams concurrently, even though each stream is experiencing peak discharges at the same time. Evidently stream conditions can influence fry migration only to the extent that such fry are available.

A notable feature of fry migration is the tendency for general periods of high daily migration to occur during similar times in each of the streams. A likely cause of this effect might be a tendency for periods of high fry emergence to occur within the same time intervals in the three streams. This could result from the fact that adult spawners tend to arrive concurrently, the spawning migration itself being markedly influenced by common weather and streamflow conditions. Once spawning has occurred, the time to fry emergence is

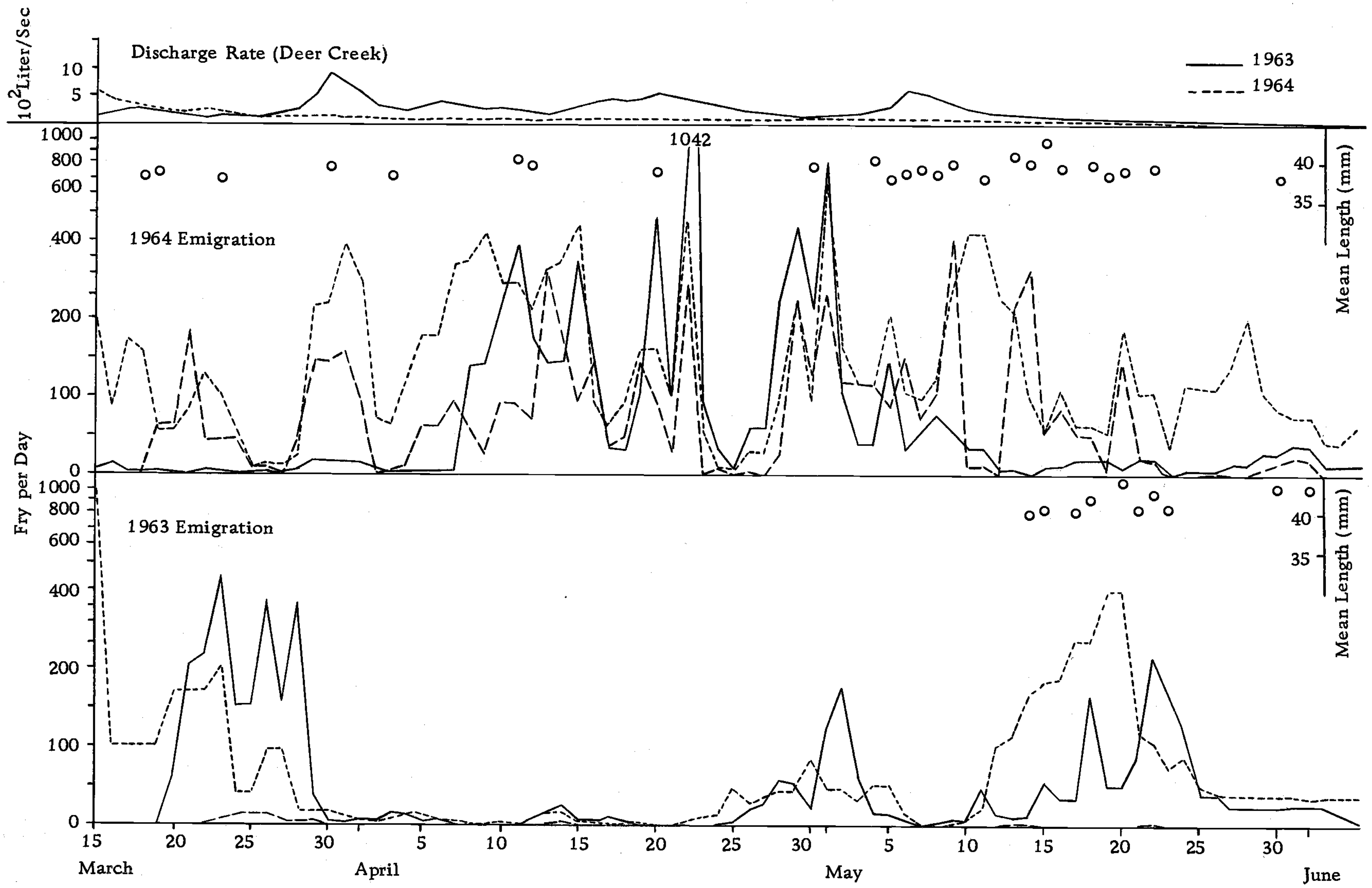


Figure 12a. Fry emigration record (Deer ———; Flynn - - - - - -; Needle · · · · · ·), stream discharge, and mean daily lengths (o). Spring 1963, 1964. Ordinate adjusted after 200.

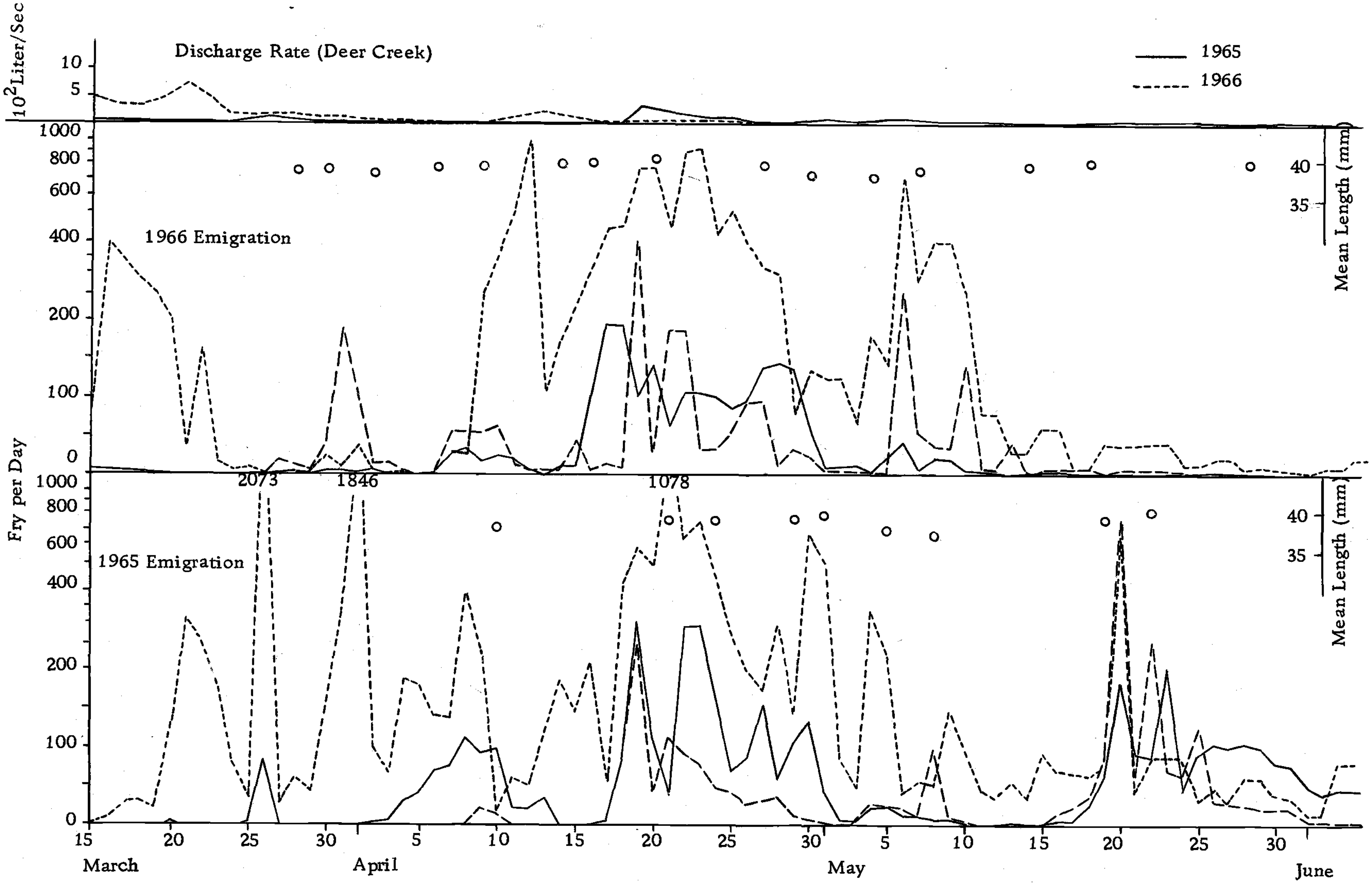


Figure 12b. Fry emigration record (Deer ———; Flynn ------; Needle ······), stream discharge, and mean daily lengths (o). Spring 1965, 1966. Ordinate adjusted after 200.

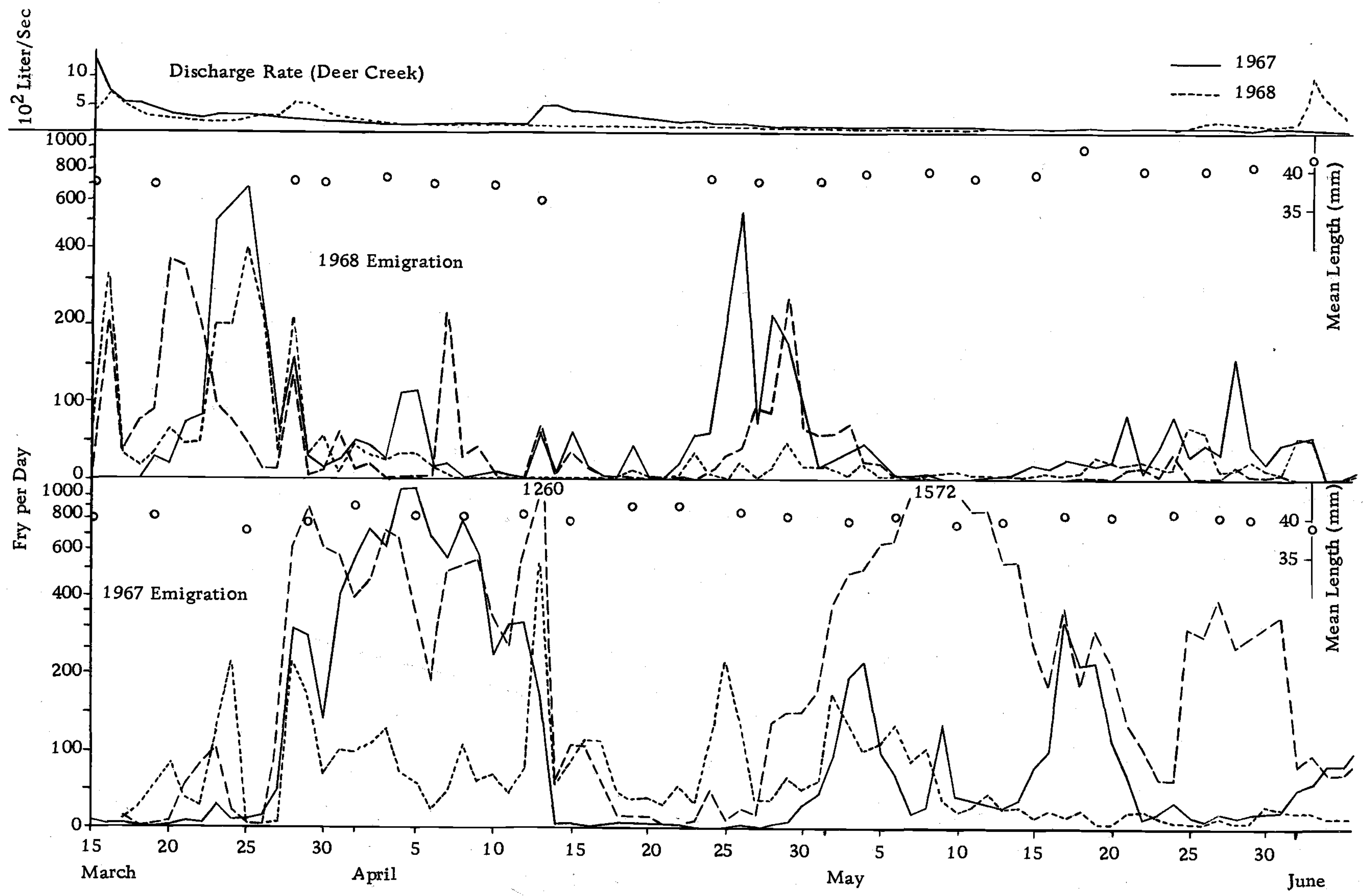


Figure 12c. Fry emigration record (Deer ———; Flynn -------; Needle ·······); stream discharge, and mean daily lengths (⊙). Spring 1967, 1968. Ordinate adjusted after 200.

controlled mostly by ambient temperature, which pattern also tends to be common to the three streams. Thus the effects of weather pattern seem manifested even as far as fry migration in the life history of the coho.

Relationship Between Fry Migration and Emergence

The above conclusion rests strongly upon the premise that migrating fry are in fact recently emerged fry. It is difficult to escape this conclusion, either after inspecting the records of fry migration or after the proper field observations. Fry usually begin to appear in the streams in March, and emergence continues through May and sometimes early June. Migrating fry usually begin appearing in the downstream traps in March. By June 1, when fry emergence is virtually complete, an average of 93.7, 86.9, and 91.3 percent of the total fry to be caught up through July 31 have passed through the traps on Deer, Flynn, and Needle creeks respectively. The additional numbers caught during July average only 0.9, 0.5, and 0.4 percent of the total respectively.

More direct evidence of the close association between fry emergence and emigration is shown by data from the 1969 year class in Needle Branch (Figure 13). Eight out of a possible 14 redds in that stream were trapped by the Oregon Game Commission that season. Fry migrating up to the first of April originated from other than the

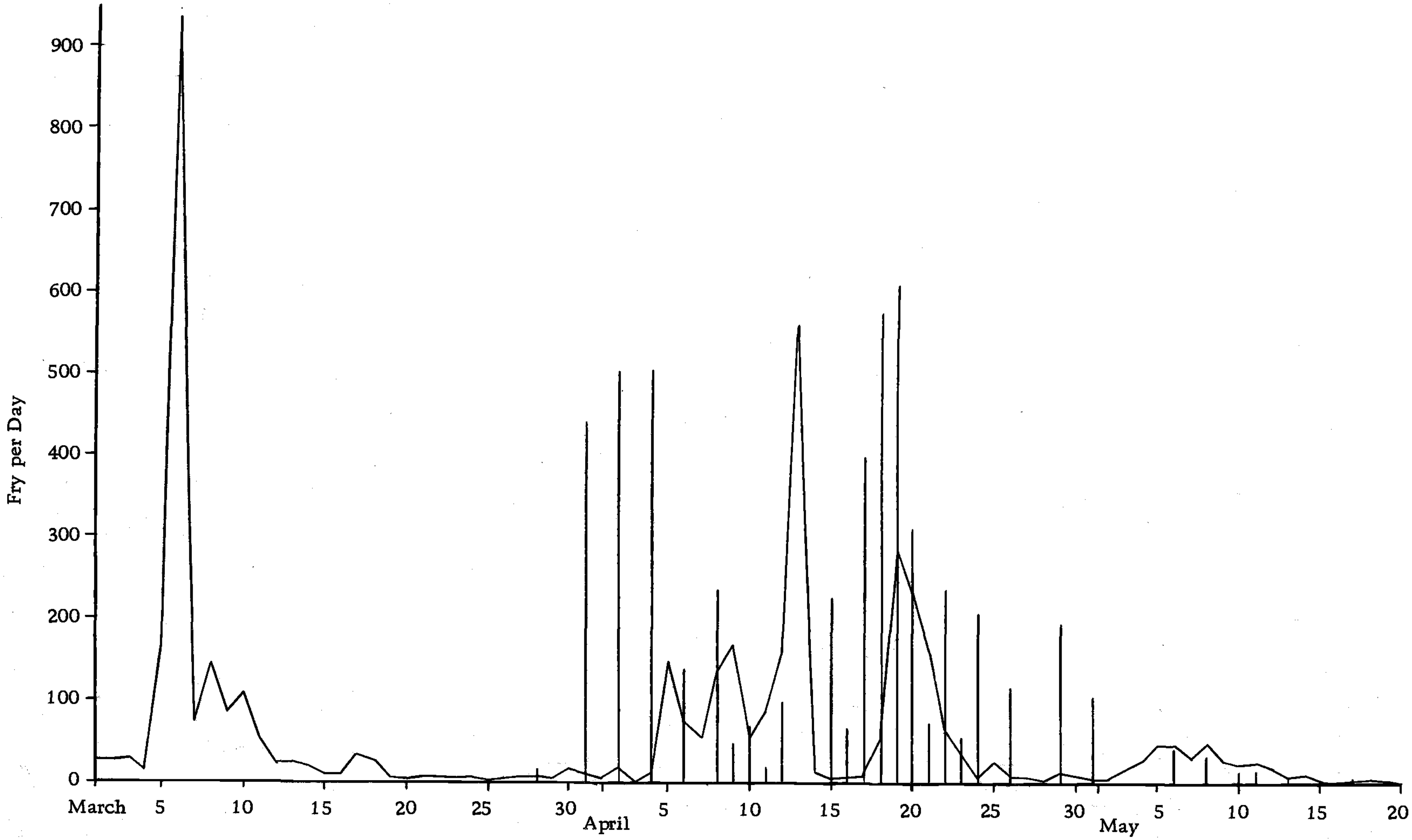


Figure 13. Relationship between fry emigrating past downstream trap (curve) and fry emerging from trapped redds (vertical bars). Needle Branch, 1969.

trapped redds. The first emergence from one of the latter occurred on March 28, following a 9-day period during which the migration rate was less than 10 fry per day. After that date the association between total daily releases from the trapped redds (verticals in figure) and the migration record at the downstream trap is apparent. During the period March 28 to April 15, the events of redd emergence appear to precede in time the catches in the downstream trap, but after the 15th, these two series of events are largely in phase. During both periods emergence from the redd at 168 m was an important contributor to the total fry input. But it is perhaps significant that in the former period the major contribution was from the redd at 778 m, while in the latter period it was from the redd at 518 m. The average distance between downstream trap and contributing redds may thus have an important bearing on the particular sequence of events observed at any downstream trap.

Length frequencies of fry caught in the downstream and in the redd traps also suggest the relationship between fry emergence and migration (Figure 14). The bottommost graph in each figure depicts the size distribution of emergent fry, representing data from 18, 15, and 20 trapped redds in Deer, Flynn, and Needle creeks, respectively (obtained by the Oregon Game Commission between 1965 and 1968). There is a close similarity between the length distributions of emergent fry and migrant fry. The lengths of fry migrating in a particular

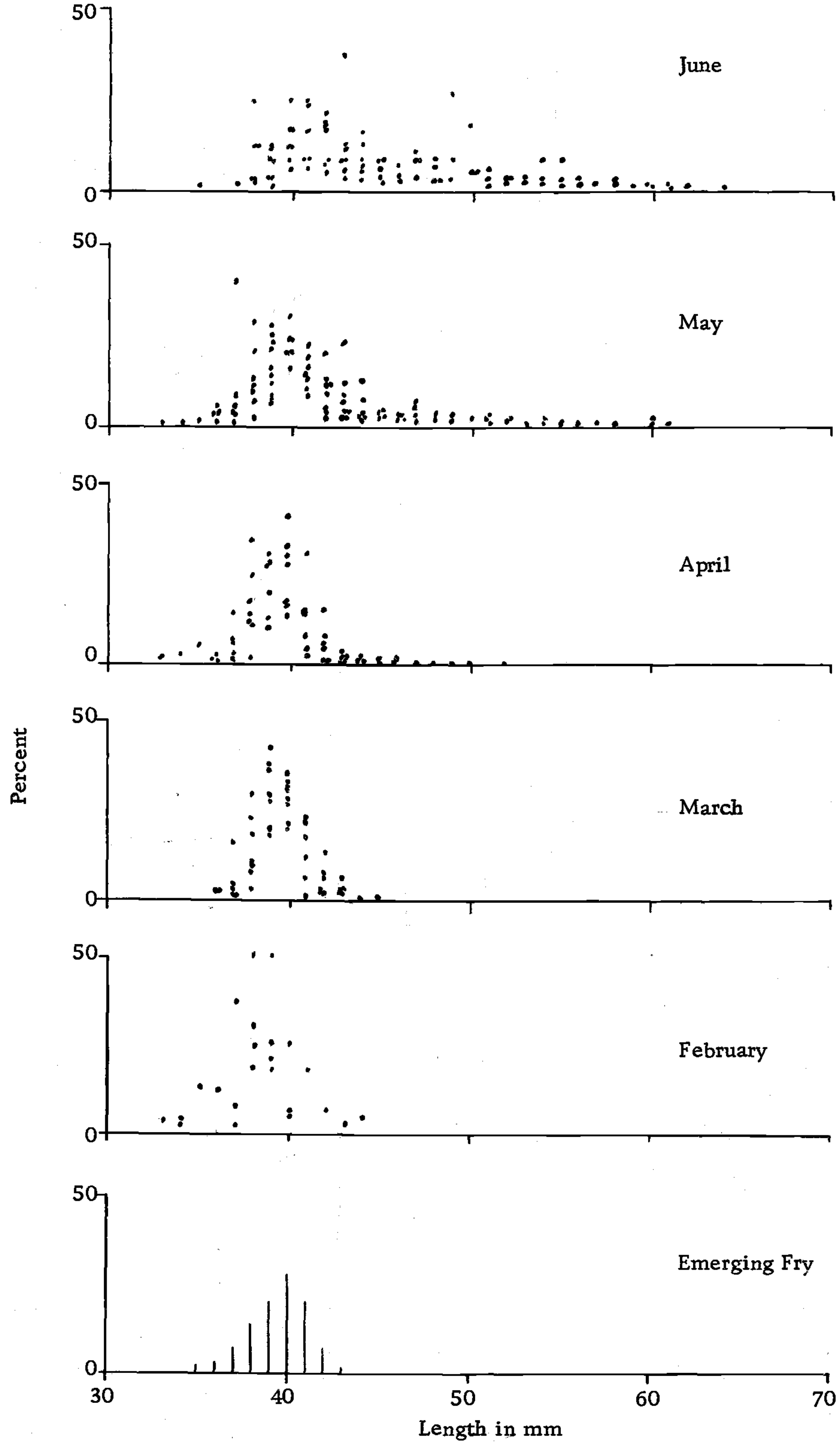


Figure 14a. Deer Creek: Percentages by length categories of total fry migrants during each month in years 1960-68 (dot graphs) and of fry emerging from trapped redds in years 1965-68 (bar graph).

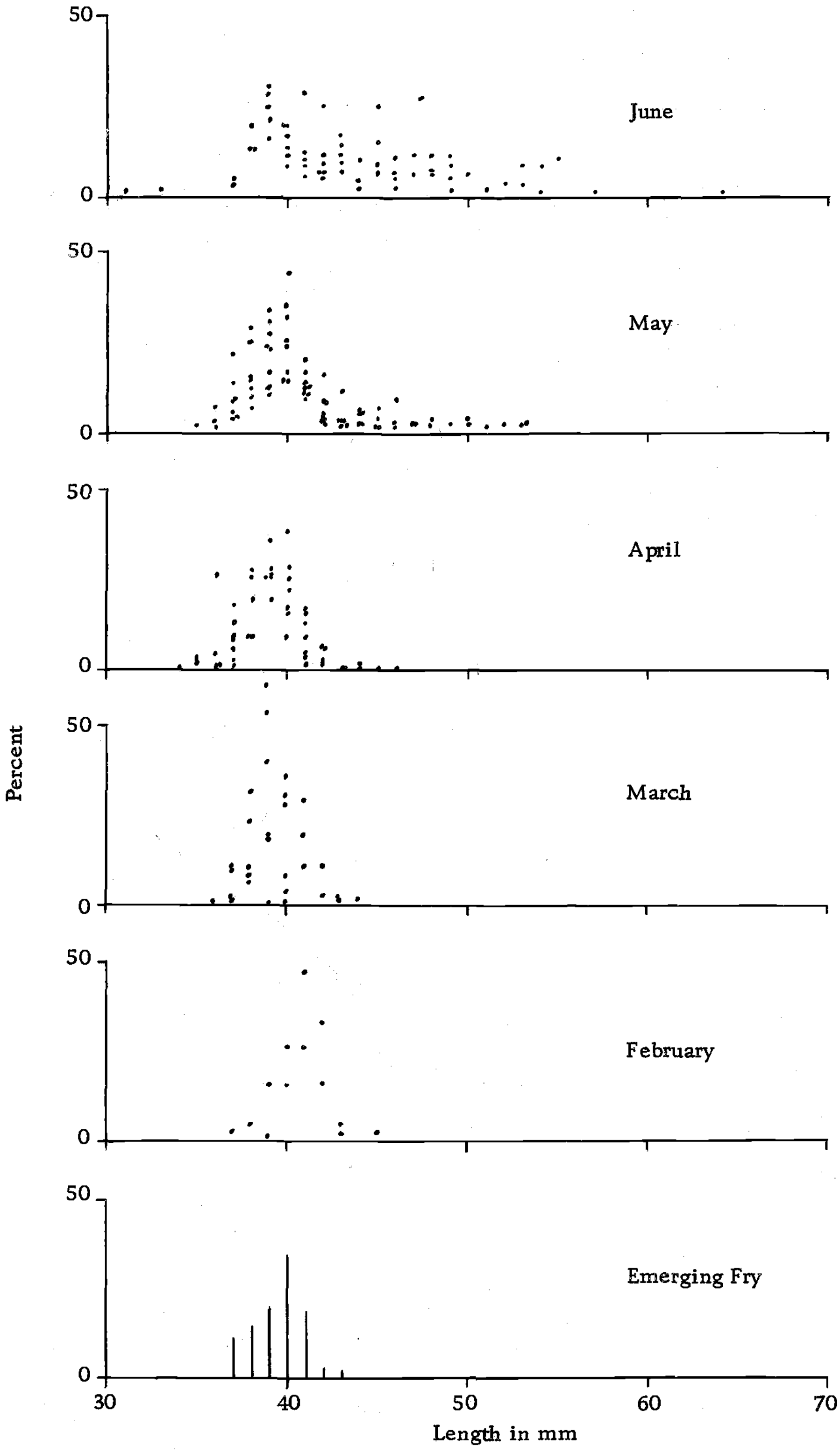


Figure 14b. Flynn Creek: Percentages by length categories of total fry migrants during each month in years 1960-68 (dot graphs) and of fry emerging from trapped redds in years 1965-68 (bar graph).

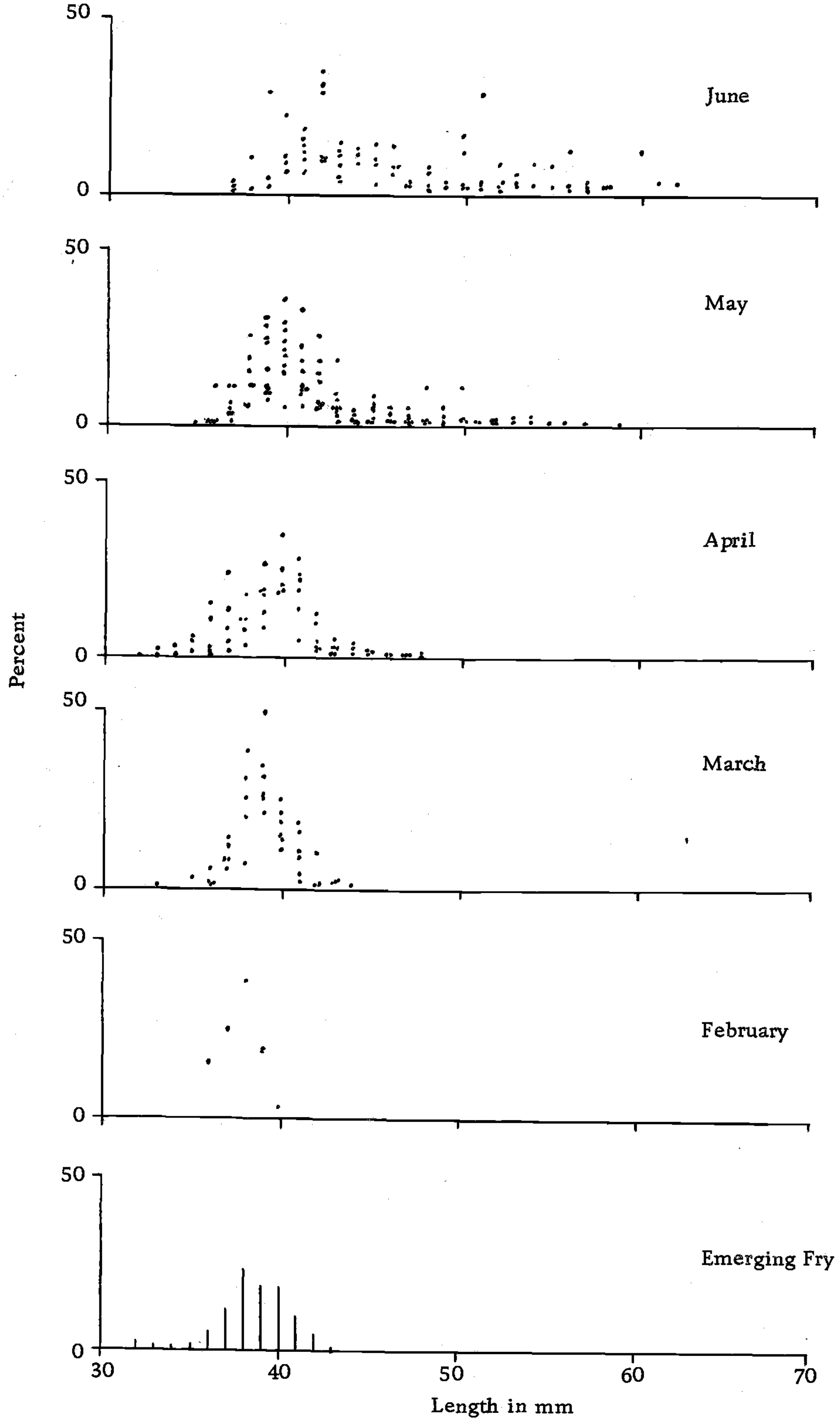


Figure 14c. Needle Branch: Percentages by length categories of total fry migrants during each month in years 1960-68 (dot graphs) and of fry emerging from trapped redds in years 1965-68 (bar graph).

month are more closely grouped than indicated in the figures because each distribution shown is a composite of the data from 1960 to 1968. The size distributions from individual redds seldom depart more than 2 mm from the mean, which is usually between 38 and 41 mm. In general, emergent fry and migrant fry average about 40 mm in length. Emergent fry from Needle Branch are somewhat smaller, averaging about 38 mm.

After May 1 an increasing proportion of the migrant fry are larger than the upper size limits of the emergent fry, reflecting growth by members of the population that had emerged earlier. But a mean daily length of about 40 mm persists with very little variation until June, when the average size begins to increase (Figure 12). This may be an indication of the importance of recently emerged fry as a component of fry migration. Although individuals exhibiting growth show up in May and June, and even April, it is not till June, when both emergence and migration are practically over, that such individuals become numerous enough to increase the mean daily lengths.

Marking of fry and their subsequent capture in the downstream traps enable direct measurements of the time individual fry may stay in the stream before emigrating. During several years of this study, fry were marked as early as April or May. These marked fry emigrated at a low and steadily declining rate up till about a month after marking. But their emigration history usually did not show the erratic pattern characteristic of total fry emigration. That pattern, especially when the catch per day is several hundred and certainly when it is greater than a thousand per day, must be composed largely of recently emerged fry, plus a steady and smaller component of older, displaced fry.

Patterns of Migration Within the Streams

The daily rates of fry migration shown in Figure 12 represent observations taken at a particular locality, the downstream trap in each of the study streams. They are therefore local rates of change. The observed local rates are in part due to particular sets of processes occurring upstream from the trap. These processes result from emergence, settling, or resumption of migration along the stream length; from physical, downstream advection of fry by the current; and from behavioral changes among the migrating individuals. In a subject known as the "theory of distribution of variables" (e.g. Sverdrup, Johnson, and Fleming, 1942) the proper interpretation of local rates of change (which may be considered the partial derivative in Euler's expansion of the individual derivative) is shown to require observations at several points along the path of movement. Furthermore such observations should be simultaneous, i.e. the data should be synoptic.

Observations of this kind were obtained on Needle Branch during the spring of 1969. Screens were placed diagonally across the stream at intervals of about 90 m, forming a complete barrier to fish movement. Small fish traps were placed at the downstream apex of the screen barrier and stream bank. All traps were inspected at as close to the same time as was possible. Fish caught in the traps were counted and released immediately below the trap to minimize alteration of the natural fry movement. These observations, to the extent that they are simultaneous and at intervals close enough to detect the major details of migration, constitute a series of synoptic pictures, or "snapshot" views, of the migration pattern along the length of the stream at different instants of time. The results of one such series of observations (April 4-7) are shown in Figure 15, presenting the simultaneous fry movement rate (fry/hr) at each trap station along the length of the stream, for each hourly interval during a period of 3 days. The figure is a three-dimensional, space-time portrayal of the fry migration pattern. Fry movement is downstream, i.e. right to left along the abscissa. Time progresses vertically along the ordinate. The movement rates represent the average interpolated number of fry caught in the hour previous to the time indicated.

At the time this series of observations was initiated, movement of fry into the study section (0-427 m) had probably been taking place for about a week, for migrating fry were being captured at the

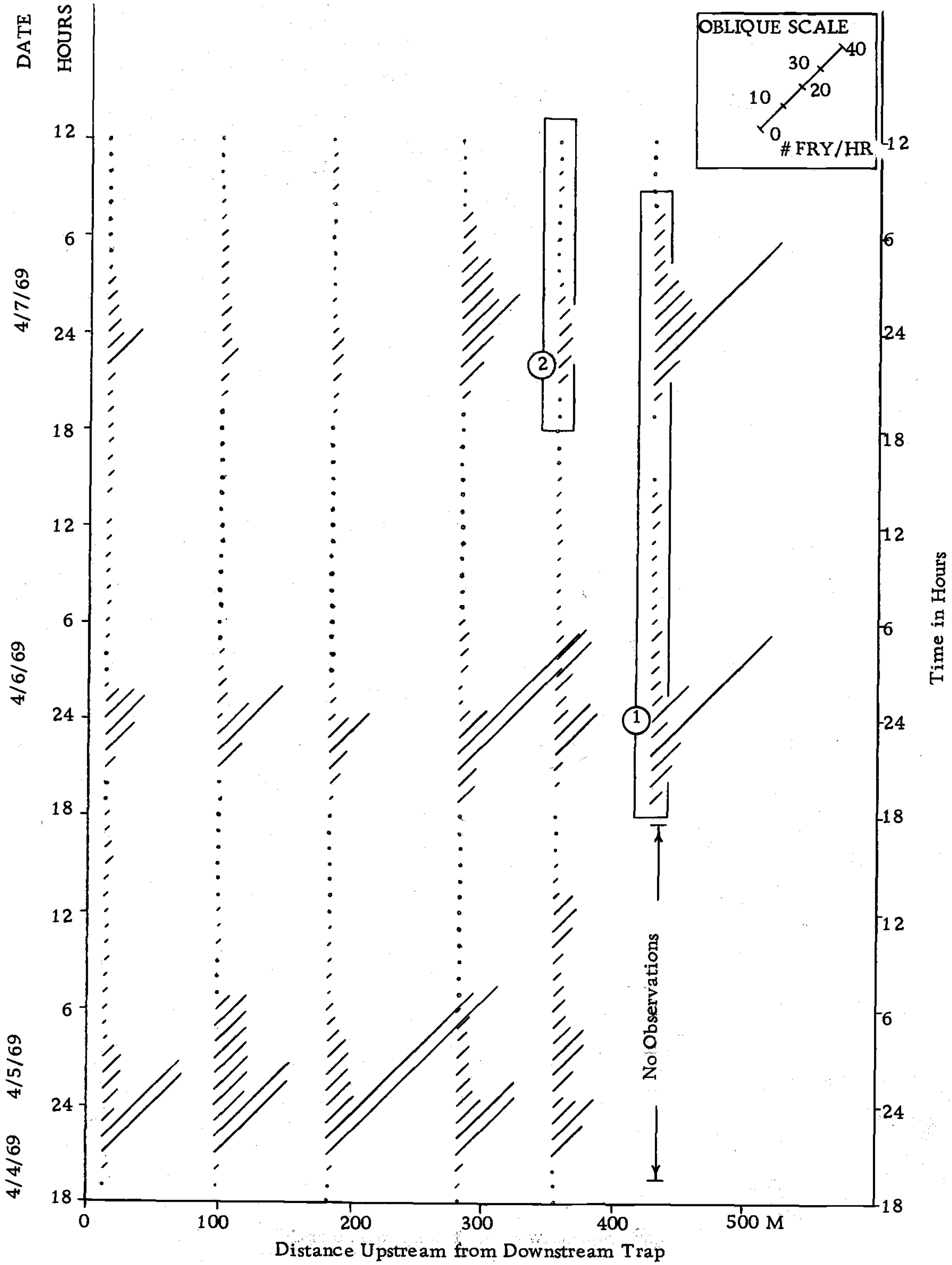


Figure 15. Synoptic space-time distribution of fry migration. Migration rates (obliques) plotted on field of time (4/4-7/69) and distance along stream. Rectangles and circles represent manipulated movements; see text. Data from Needle Branch.

downstream trap during that time (Figure 13). The main input had probably been from releases out of the trapped redds at 778 m and 168 m, these two being the only trapped redds then producing fry. There were other untrapped redds that had not been precisely located in the stream; they may also have been producing fry. However all such redds were probably located above the study section. Thus fry input into the section was primarily from redds located above the uppermost stream trap at 427 m. It follows that the fry movement rates observed were representative of fish that had already entered the section prior to the observation period plus the additional inputs, mostly from above the section, that occurred during the period.

The most notable feature of fry migration is the fact that it is primarily a nocturnal phenomena (Figure 15). Movement was usually well underway by 2000 hours. There was often a strong peak in migration between this time and 2200 hours, indicating a strong initial surge in movement associated with the onset of darkness. Such peaks were often greater than 60 fry/hr, and probably represented movement in excess of 100 occurring in a shorter length of time. There were other, usually smaller, movement peaks during the remainder of the night, probably representing secondary groups of migrating fish. After midnight, movement generally declined and was practically over by dawn, at about 0600 hours.

Viewed synoptically along the length of the study section of the stream (any histogram series parallel to the abscissa) fry movement appears to begin simultaneously along the total section of the stream upon nightfall; the movement continues till dawn. Migration seems to progress in a wavelike fashion, increasing in magnitude as its mode moves downstream. After the hours of peak movement, migration rates decrease along the stream until nearly all movement ceases at dawn. During this time the mode tends to continue moving downstream. These features are best seen during the first night of the migration study (Figure 15). Note that a peak in migration can occur at a locality without a similar peak occurring previously upstream, indicating that the migrating fry producing the peak were already present in that portion of the study section.

As part of this series of observations, experiments on fry movement were conducted by releasing groups of fry and blocking movements at certain localities in an attempt to identify the groups as they proceeded downstream. After the first night no fry were allowed to pass through the 427 m stream trap and after the second night, none were allowed past the 354 m trap. These manipulations are shown in Figure 15 as blocked off histograms. During the second night 200 fry were released at 2400 hours just below the 427 m trap. Three hours later a peak in the migration rate began to appear at the next trap downstream at 354 m, indicating the arrival and passage of a large portion of the

200 fry. On the third night 196 fry were released below the 354 m trap at about 2200 hours. The migration sequence at the next lower trap, at 280 m, had previously been increasing, indicating movement of fish already present in the intervening section. But after the peak rate at 2300 hours, movement remained relatively high until after 0300 hours. Again this was probably due to the arrival and passage of many of the 196 fry.

In each of these experiments, fish passing the trap next below the release point could have come only from fry groups already present in the intervening section or from the released group of fry. The latter appear recognizable as peaks in movement rate occurring at the next lower trap a few hours after release. Inspection of these rate histograms shows that in each case a period of about three hours was required for the main body of fry to travel the 73 m between release and capture points. These results may be seen in Figure 15, after midnight during the second and before midnight during the third night. It appears that fry are capable of travelling nearly 300 m during a night.

Perhaps the most interesting feature of fry migration brought out by these synoptic observations is the fact that the nocturnal migration, starting almost simultaneously for all groups along the stream, continues downstream each succeeding night. The numbers of fish so moving diminish all the while. The rapid increase in rate of movement, often independent of prior rate changes upstream or subsequent changes downstream, suggests that fry movement in general is composed of many loose aggregations of fish independently beginning migration at nightfall. The members of each group gradually settle out along the stream as the group progresses downstream on successive nights, thus attenuating the movement.

Another series of observations of the same type was taken during April 14-18, 1969. Unlike the previous series, however, fry movement was practically nil in the stream when these observations were started (Figure 13). No fry were captured in the downstream trap on the night of April 14 and only a few were caught in the other stream traps then. This situation prevailed until the night of April 17. Although some movement had been seen that afternoon at the 427 m trap, associated with a brief freshet, the first large numbers of fry began to enter that trap at 2100 hours (Figure 16). These fish were pale and appeared weak and flaccid. I believe they were newly emerged from some untrapped redd upstream. Earlier at 2000 hours a group of 45 fry obtained from the trapped redd at 229 m was released below the 427 m trap, and they too began to move through the section. The downstream progression with time of all these fry may be seen in Figure 16, where the solid arrows are drawn in to suggest the general trend and extent of movement. The progression of the peak associated with the 2100 hour input is particularly evident.

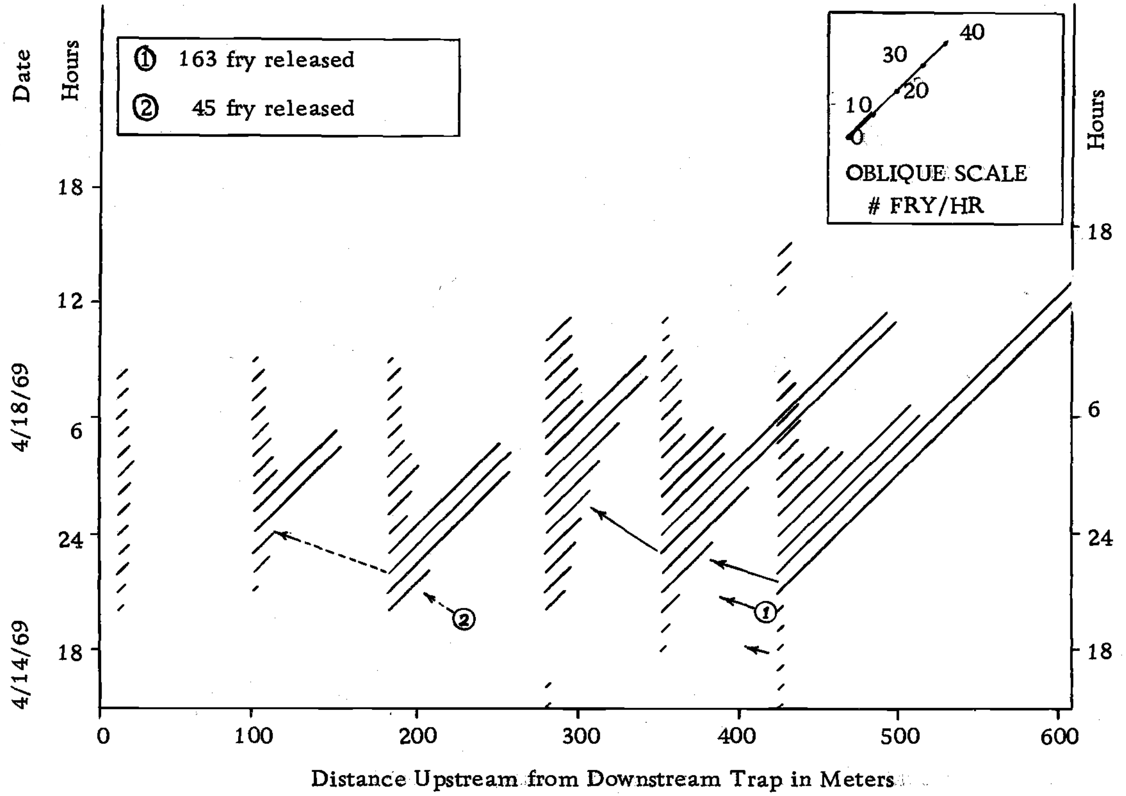


Figure 16. Synoptic space-time distribution of fry migration within Needle Branch 4/14-18/69. Arrows and encircled numbers refer to specific releases described in text.

Farther downstream in another experiment 163 newly emerged fry from the 229 m trapped redd were released just below that redd at 1930 hours. The downstream progression of these fish also is evident and is suggested by the dashed arrows.

These observations and experiments on the third night again demonstrate how newly emerged groups of fry move downstream. The peaks in movement rate may be evident for about 10 hours, and the average distances spanned,over 150 m. The movement peaks become more diffuse with time and distance downstream as individuals gradually settle out during each successive night.

At night migrating fry can be seen all along the length of the stream,usually in the shallows along the margins. The fry face upstream into the current, swimming gently. They appear to move downstream mostly by a process of losing headway against the current. However it is possible that much of the movement actually occurs in midstream where the fry are difficult to observe.

Some Streamside Experiments on Fry Migratory Behavior

Further observations on the details of fry migration that lead to the space-time pattern of movement were obtained in wooden tanks, alongside Deer Creek during the spring of 1969. These tanks (183 x 61 x 61 cm) were supplied with water via a flume from the pool above the downstream trap. Nine such tanks were constructed, two with glass windows. The lower third of each tank was sloped upwards with gravel so that the last 12 cm of the tank were only about 3 cm deep, simulating the beginning of a riffle. The water then flowed over a sill into a trap compartment. Water flow through the tank was about 1 liter/sec, depending upon stream flow.

Each tank was designed to simulate a natural pool into which migrating fry happen to enter. The simulated pool probably departed from a natural stream pool mainly in that there were no shallows along the sides and that the inflow was from a 15 cm opening rather than as a broad sheet of water. When migrant fry, caught in the downstream trap, were introduced into such a tank at night, most would emigrate by morning. This behavior clearly resembled the mass nocturnal movement of fry seen in the stream and is recognized as being part of the same phenomena.

Time of introduction greatly influenced the results. If the introduction was during the day, the number emigrating was only about 5 - 10% (Table 4). The percentage of migration at night was always greater than that of the day no matter what the input time, day or night. Moreover night migration of night-input fry was very much greater than that of day-input fry. The day migration of day-input fry averaged higher than the day migration of night-input fry. It was mainly the newly input fry that emigrated, and the closer migration was measured to a particular input time, the higher the percentage seen.

Table 4. Percentage emigration of fry from tanks according to day or night input rate and total input.

Input Time Input Rate Total Input			Day 60/3-4 hrs. 300				Day 25/3-4 hrs. 262			
			In	Cuml. In	Out	% Out	In	Cuml. In	Out	% Out
Successive Day or Night	1	D	60	60	3	5	25	25	0	0
		N		57	0	0		25	2	8
	2	D	240	297	20	6.7	100	123	6	4.9
		N		277	36	13		117	7	5.5
	3	D		241	8	33	137	247	10	4.5
		N		233	5	2.1		237	30	12.7
Weighted Mean		D				5.18				4.05
		N				7.24				10.29

Input Time Input Rate Total Input			Night 100 or 66 at one time 166				Night 25/2 hrs. 50			
			In	Cuml. In	Out	% Out	In	Cuml. In	Out	% Out
Successive Day or Night	1	D	--	--	--	--	--	--	--	--
		N	100	100	86	86	50	50	41	82
	2	D		14	1	7.1		9	0	0
		N	66	79	49	62		9	0	0
	3	D		30	1	3.3		9	0	0
		N		29	0	0		9	0	0
Weighted Mean		D				4.55				0
		N				64.90				60.3

In all cases it seemed that the longer the fry had in daylight hours to familiarize themselves with the tank, the less likely were they to emigrate that night. The actual rate of fry input and the magnitude of this input did not seem to have any consistent effect on emigration rate.

Because the age, or daylight hours of experience, seemed to be such an important factor in fry migration, it was desirable to continue such studies with fry that were truly inexperienced, i. e. fry taken immediately after emergence from a redd. For several days up until April 26 over a hundred fry per day had been passing through the Flynn Creek downstream trap. It was reasonable to believe that this relatively large migration was composed mainly of recently emerged fry. A series of experiments comparing the behavior of these "inexperienced" fry with "experienced" fry was conducted in the same streamside tanks. "Experienced" fry consisted of individuals caught during the day in the stream below the downstream trap on Deer Creek plus some fry left over and still residing in the experimental tanks.

The first tests on such fry revealed low nocturnal migration rates in both groups. One likely explanation was that bright moonlight conditions prevailed then. Since daylight seemed to enable fry to establish residence in a pool, I reasoned that moonlight might have a similar though lesser effect. To test this idea some of the tanks were blacked out against moonlight with black plastic. Nocturnal emigration rates were then measured in six parallel tanks in which moonlight, input time, and the degree of "experience" of the fry were the variables (Table 5). "Inexperienced" fry were definitely more prone to emigration, although if introduced during the day, such fry behaved similarly to "experienced" fry. Moonlight seemed to quite definitely depress emigration at night, suggesting that nocturnal movement is related to loss of visual reference to the stream substrate. The importance of day vs. night input time was again apparent, especially among the "inexperienced" fry. Even with the "experienced" group a few hours of daylight reduced nocturnal emigration (1845 vs. 2030 hours input time).

Further observations on the effect of the degree of "experience" of fry were obtained by introducing groups of fry into a tank and then reintroducing each night's emigrants the next morning. The emigration tendency of the same individuals was thus monitored over a period of time. The separate experiments were not all run for the same length of time, primarily because of conflicts with other, concurrent tank observations.

Emigration tended to decrease with each successive day and night (Figure 17a). The largest migration occurred on the night of fry input. Usually it was still substantial the following day, but by the second night emigration was often down to 10%. No consistent effects of input level or rate were apparent. After several days, percentage emigration rose to relatively high levels. These experiments

Table 5. Effects of "experience," time of input, and moonlight on fry emigration from tanks during the first night following introduction.

Type Fry	"Experienced"						"Inexperienced"		
Day or Night Input	Day		Night				Day	Night	
Time	1320	1325	1845	1845	2030	2030	1325	2030	2030
Fry Input	40	42	25	50[a]	25	38[a]	40	40	40
Moonlight	Yes	No	Yes	No	Yes	No	No	Yes	No
% Emigration	7.9	15	0	12	16	21.1	7.5	20	85

a) These two columns represent experiments conducted on the second night, and the numbers 50 and 38 include fry remaining from the two experiments represented by the third and fifth columns.

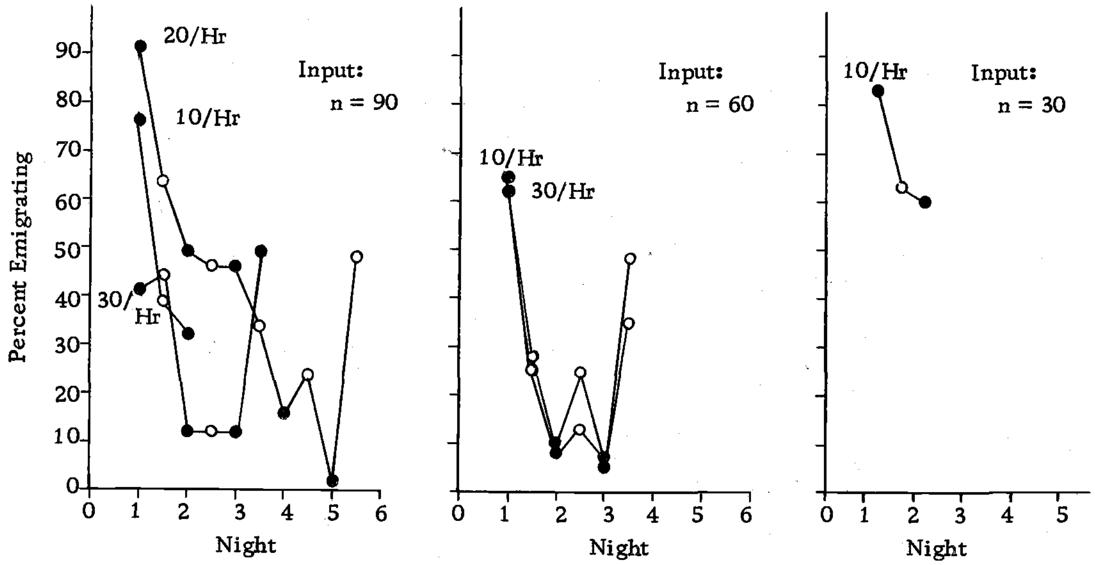


Figure 17a. Emigration trends for three initial input levels and rates. ● = night %; o = day %.

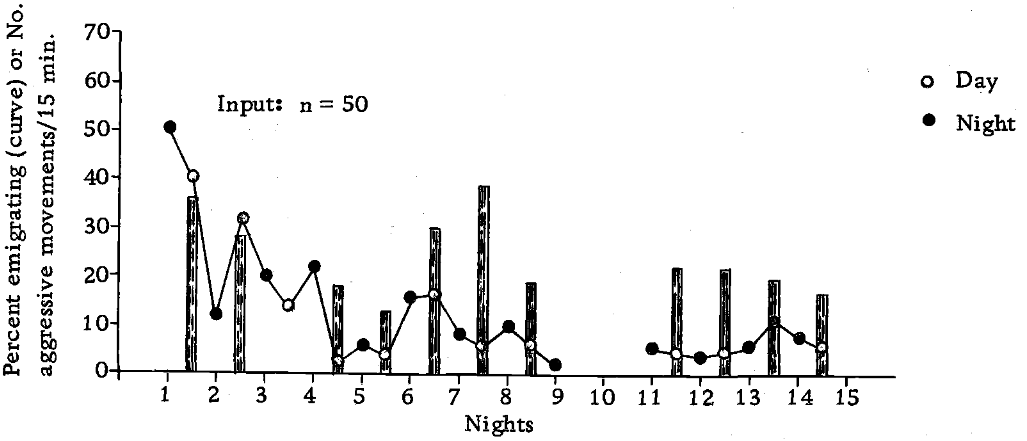


Figure 17b. Emigration trend and aggressive activity.

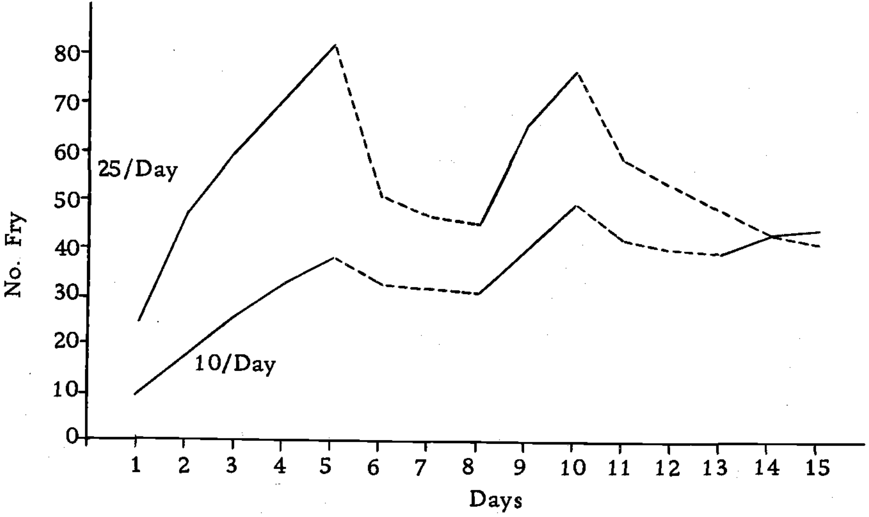


Figure 17c. Cumulative fry in troughs with volitional residence permitted. Days of input (2 rates) alternated with days of no input.

measuring percentage emigration of the same lot of fry as a function of time, suggest that as the fry mature and gain experience with the tank environment, their migration tendencies decrease. This further suggests that nocturnal migration is caused by an inability of fry to hold a position in the stream due to lack of time to develop a behavioral pattern that prevents displacement.

The continuing emigration and the final increased rates during the day suggest that intraspecific stresses were increasing within the tanks and bringing about a second cause of migration. The fish were not fed during these experiments so that they had to rely on natural drift into the tank. Fry that had initially settled and become resident may have been increasingly induced by competition for food and space to seek residence farther downstream. The well known territorial behavior of coho fry probably plays an important part in this process.

Measurements of aggressive activity (vertical bars, Figure 17b) among a group of 50 newly emerged fry obtained from a trapped redd show that this activity was associated with nocturnal emigration. The fry were introduced into a tank at night at 2200 hours and their emigration trend (line graph, Figure 17b) measured as before. Aggressive activity was measured by viewing the fry each evening at 1700 hours through the glass windows of the tank and counting the numbers of aggressive movements observed over a period of 15 minutes. The emigration trend declined erratically during the first 5 days, and the aggressive activity seemed to parallel the decline. The minor peak in daytime emigration on the second to the last day was associated with a rush of turbid water created when a beaver dam upstream was broken, again suggesting that reduced visual orientation promotes migration. It is interesting to note that on the morning after introduction (0800 hours) no aggressive movements were seen among the fry. They swam about the tank seemingly without preference to any particular locality. No dominant fry were noted. By afternoon aggressive activity was very obvious, and a few fry near the inflow were clearly the dominants.

In the streams, fry still migrating at dawn enter pools under conditions that permit visual orientation. These fish are then "day-input" fry. To see how the population in such a pool might build up through the addition of successive inputs of new fry each morning, an experiment was run in which fry were introduced at two rates, 25/day and 10/day, into two different tanks. Unfortunately the supply of fry from the downstream trap was ending at that time. As a result the experiment consisted of two fry input periods, lasting 5 and 2 days, each followed by 3-day periods without input. During the days of fry input the population in each tank increased, but at a decreasing rate due to emigration (Figure 17c). During periods without fry input the population size dropped rather slowly, except at high population levels. This suggests that adjustment of population density in a given pool is gradual in comparison with processes that build up the population density. The two curves (input rates: 10/day, 25/day) show some evidence of converging, indicating that eventually a steady state might have been reached at the carrying capacity of the tanks.

A final series of tank observations, begun on May 23, 1969, involved investigation of the resistance to emigration by resident fry (Table 6-A). Twenty fry, at least 2 weeks old and saved from one of the previous experiments, were introduced by day into Tank 1, already containing 24 resident fry of the same age. The introduced fry were marked for identification. I wanted to see if a greater emigration rate would characterize the introduced fry when both groups were the same age. The condition simulated was that in which previously resident fry, seeking improved habitats, enter a pool farther downstream that happened already to have a complement of resident fry. Another group of fry, also 2 weeks old and originating from the same group as the above 20, was introduced at the same time into Tank 2, empty of fry. This tank was altered somewhat by the addition of large rocks. Here I wished to see if experienced fry, by chance entering a new but empty pool, would be able to stay in that pool.

Both groups in Tank 1, the introduced and already resident fry, had similar, low emigration tendencies. None of the other group of fry, introduced into the empty tank, emigrated at all until freshet conditions occurred and increased the emigration in both tanks.

Table 6. Emigration trends (emigrants/day) of "Resident" type coho fry.

A. Daytime Introduction

Tank		1				2			Remarks
Group		Residents		Introduced		Residents	Introduced		
Introduction time		--		1000		--	1000		
No. Introduced		24		20		0	22		
Day or Night		D	N	D	N		D	N	
Successive day	1	1	1	1	1		0	0	
	2	0	0	0	1		0	0	
	3	0	0	0	0		0	0	
	4	0	0	0	0		0	0	
	5	0	0	0	0		0	0	
	6	0	1	0	2		0	1	Freshet
	7	3	3	2	2		4	0	Freshet
	8	0	0	0	0		1	0	
	9	0	0	0	0		1	0	

B. Nighttime introduction (tanks w/o fry at start)

Fry source		Pool below Deer Creek trap				Horse Creek			
Tank		1		2		3		4	
Introduction time		2200		2200		1830		2200	
No. Introduced		32		32		30		30	
Day or Night		D	N	D	N	D	N	D	N
Successive day	1	-	13	-	16[a]	-	0	-	4
	2	1	0	2	2	4	5	4	2
	3	0	6	1	3	0	0	0	0
	4	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	3	0
	7	1	0	0	0				

a) Returned these fry back into tank

If "experienced" fry are introduced during the night, the results are similar, but with somewhat higher emigration percentages the first night (Table 6-B). The fry for these night introductions were obtained from two sources: the pool below the Deer Creek trap and a pool in Horse Creek approximately 2 km below that trap. Except for the high emigration rate occurring the first night among the fry from Deer Creek, emigration was relatively low throughout.

In general these experiments show that fry that have already taken up residence in the streams are much less prone to further emigration than are "inexperienced," recently emerged fry. Furthermore the low emigration rates demonstrate that population adjustment through downstream movement is a gradual process.

During migration periods, fry can be seen at night swimming near the surface in the shallows. They are in exposed positions and definitely are not in hiding. In contrast, larger fry and fingerlings are seen at night at the bottoms of the deeper portions of the pools. During the day, of course, the fry are seen in surface or midwater positions, holding position and feeding in the current. In the two tanks provided with glass windows, resident fry could be observed at night too. These fry swam very slowly, and seemingly without regard to direction, in the quiet water immediately above the silt-covered bottom of the tank pool. During the daytime all fry were very actively darting about, feeding in the current or exploring the sides of the tank. Such observations suggest that the mechanism enabling newly emerged fry to initiate and maintain residence in a particular locality and to cease the successive nocturnal downstream movements, is the development of this bottom resting behavior at night.

Diel Changes in Fry Behavior

In the spring of 1970 facilities were set up at the Oak Creek Laboratory near Corvallis to enable observations of fry behavior within the water column. It was the aim of these observations to see how the transition from migratory to resident behavior took place in fry. Two small plexiglass aquaria (61 x 30 x 10 cm) were built. The narrow width of the aquaria was designed to permit viewing of the fry against the background of natural, nocturnal light levels alone. The forward half of each tank was filled with gravel to simulate a riffle bar with about 4 cm of water flowing over its surface. The rear half was the pool environment. Flow through the aquaria was about 0.2 liter/sec. The forward edge of the gravel bar was a perforated stainless steel plate that enabled water to flow directly into the gravel mass at all depth levels. The first series of observations began with the burial of eyed coho eggs 15 cm deep in the gravel.

The transition among successfully emerging fry from the intragravel to stream environment was quite dramatic. The fry repeatedly darted to the surface to gulp air, sometimes resting amongst the surface gravel momentarily. Their whole behavior pattern presented a picture of distress. They swam erratically and in a jerky fashion, their bodies at approximately 45° to the horizontal. As this awkward swimming continued, the fry were swept by the current into the pool section of the aquarium, where they were prevented from being washed through the outflow by a screen. In the pool they continued the jerky and angled darting at the surface. By the end of the first night hydrostatic equilibrium had been achieved, but the fry continued to swim in the surface current both day and night. They could be observed feeding on drift organisms and often snapping up and then rejecting inedible bits. Nipping behavior was common.

The fry continued dwelling in the surface current for about 6 days before some began to settle into the quiet water near the bottom at night. After 10 days nocturnal activity had decidedly decreased, although some fry continued to be active for another 2 weeks. There was some indication that when food was artifically supplied, an increase in the tendency to settle quietly at night occurred.

The possibility that feeding could affect nocturnal activity was investigated in a second series of observations where each aquarium was divided into two to make up a total of four separate tanks. A separate feeding schedule for each of the aquaria was then maintained as follows: once/day, once/2 days, once/4 days, and once/week. The food was a combination of commercial trout food and live mosquito larvae. Previously-hatched fry were kept in darkness until their yolk sacs were absorbed and then introduced at night over the gravel in each aquarium. Thus all the fry in this second observation series were the same age.

The bobbing, erratic swimming behavior was also observed in this series of observations. The fry were swept to the pool of each aquarium by the current almost immediately after introduction. They continued swimming jerkily there, their bodies angled to the surface; many were seen gulping air. When frightened, as by light from a flashlight, they dove into the gravel and silt at the bottom of the aquarium. As soon as the light was removed, the fry returned to the surface to resume their frantic activity. The next day the fry were observed swimming calmly and steadily in the current. They did not feed as did the fry of the first series, which were larger (about 39 mm vs. 34 mm) and perhaps more mature when they emerged from the gravel. Each night the fry resumed their intense activity, though no more air gulping was seen after the first night. Some fry were seen repeatedly darting from surface to bottom layers. The fry seemed to increase their activity as night approached.

After 10 days, when nocturnal activity had begun to taper off, the fry began to feed. By the twelfth night the fry were moving about slowly or holding in the current, as during daylight hours. However in the aquarium in which the fry were fed only once per week, an active exchange among individuals between top and mid-water layers continued.

By the seventeenth night after introduction nocturnal activity was definitely at a lower level than diurnal activity in all aquaria. The reduced activity of the fry fed only once per week was probably due to their weakening from the inadequate feeding. They had previously been observed trying to swim downstream past the outlet screen both during the day and night. Their prolonged, agitated swimming was thus probably escape behavior. In the other tanks, the fry, fed at more ample levels, rested or moved about slowly at night. Most stationed themselves just off the bottom or at other levels in the lee of the larger pebbles forming the upstream and downstream ends of the pools. Some fry remained swimming in the main current of the upper layer, but this swimming was steady as during the day.

It was difficult to tell quantitatively how the different feeding schedules affected the development of quiescent nocturnal behavior. The process was gradual but interspersed with much individual variation in activity. Fry swimming in the surface current layer were characteristic of both early and late stages. Those fry seen swimming adjacent to edges of the gravel bar may or may not have been resting, depending upon the strength of the current there. It was clear however that the fry being fed once per week continued their high nocturnal activity for about a week after the onset of feeding. In contrast the fry in the aquaria fed once per day and once per 2 days were definitely less active within 3 nights after the onset of feeding. Their behavior became very similar to the more purposeful swimming patterns seen during the day.

These observations suggest that the quiescent behavior of fry seen in tanks and stream pools at night is part of a developmental sequence. The behavior enables fry to hold their positions in fast flowing streams at night despite diminished visual cues for orientation. The development of nocturnal resting behavior is gradual. It may take several days before fry are sufficiently protected against displacement by this mechanism. The actual time may be intimately linked to the physiological development of the fry.

In the natural stream those fry that are unable to secure sufficient food for maintenance and growth probably fail to develop this behavioral adaptation, and therefore continue being displaced (or continue actively swimming) downstream each night. Whether sufficient food and space are available for each morning's new immigrants into a particular pool may depend largely upon the social organization of the coho fry already present (Chapman, 1962; Mason and Chapman, 1965). Each night's journey brings migrant fry into successively new stream sectors downstream. Each successive day would bring new opportunities for such fry to compete for a share of the available food and space and for further development and maturity of nocturnal resting behavior. I believe that when the latter is attained and the former adequate, migrating fry settle and become residents.

Dispersal and Colonization by Fry from an Individual Redd

A rare opportunity to check the conclusions drawn from the experiments and observations during 1969 and 1970 arose on Needle Branch in March 1970. That year only one female successfully spawned there. The redd was located with certainty at 778 m, and a nylon fry trap placed over it. Observations on dispersal and colonization by fry from this redd were planned because the age and origin of all fry in the stream could be known.

For such observations wire screen traps were again placed across the stream at the following distances downstream from the trapped redd: 107 m, 213 m, 320 m, 472 m, 632 m. The downstream trap provided a sixth trap in the series at 838 m from the redd. These traps were a modified version of the 1969 stream barriers and traps, previously described. Mr. Richard Severson of the Oregon Game Commission directed their design and installation. Emergent fry were marked and released at the redd site at night. Their subsequent dispersal downstream was monitored by observations at each of the traps in the series. As before, the fry caught at each trap were released immediately after counting so that their downstream journey could be continued. The releases were made in large batches simulating peak emergence conditions.

Movement Patterns

The first group consisted of 591 fry that had accumulated in the redd trap during the previous 2 nights. Most had emerged during the second night. On the evening of release (March 22) they were removed from the trap and their upper caudal fin notched. The fry were then released in one group just below the redd at 2200 hrs. Bright moonlight prevailed at that time and lasted for the rest of the night.

The fry began their downstream dispersal immediately upon release. After 1 hour small bands of 6-12 fry were seen in front of the first trap at 107 m. Fry could then be seen singly or in small groups all along the stream from that trap up to the redd. They were visible most often in the quiet water along the stream margins, facing into the current. Where the stream course curved, the fry were often in the shallows off the inside, convex bank where the point bar formed. These fry may have been "deposited" there by the current for much the same reasons that cause the accumulation of gravel in such locations.

The rapid dispersal of fry over the 107 m distance and the fact that many were holding in the weaker currents all along the interval, suggest that a more rapid core of movement existed. Such a core can be envisioned as the main body of fry moving downstream, with small groups separating off as it proceeds.

The rate of fry movement increased during the night and peaked just before dawn (Figure 18). The highest rate, at 0600 hrs, was 28 fry/hr, reflecting a relatively slow movement throughout. At that time the first fry were beginning to enter the 213 m trap. The next day fry could be seen holding and feeding in the current all along the stream section from the redd to the 213 m trap. Some fry continued to move downstream during the day from the uppermost section.

The next night, fry movement was well underway through the first two sections (0-107m, 107m-213m) by 2000 hrs. A few fry began to show up in the 320 m trap by 0400 hrs on this second night. Very little migration occurred on the third night, but a few fry did continue on downstream each night for the next 2 weeks. After the fifth night some fry from this original group passed through the 472 m trap.

The second group of fry was released on the third night (March 24) at 1900 hrs. Their caudal fins were bottom notched to distinguish them from the other fry. A total of 842 fry was released from the redd. There was bright moonlight after midnight.

The most notable feature of this group was their high rate of movement (Figure 18). Within 1 hour after release some of these fry were passing through the 107 m trap at the rate of 150/hr. A half-hour later some were at the 213 m trap, and 1 1/2 hours later a few

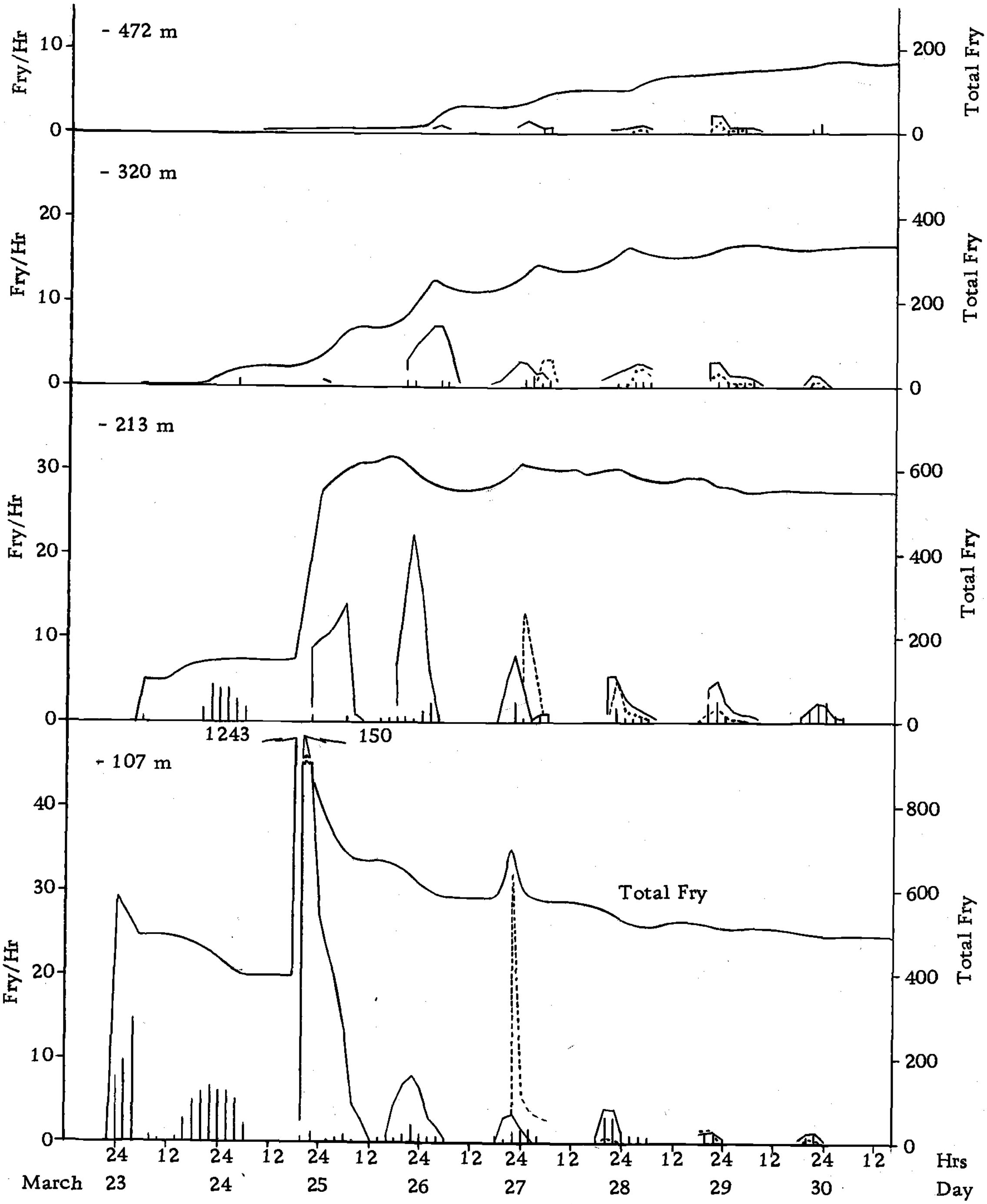


Figure 18. Movement rates and calculated total population size within each section at successive distances downstream from trapped redd at 778 m in Needle Branch. Fry from three releases: 591 at 2200 hrs, 3/22/70 (verticals); 842 at 1900 hrs, 3/24/70 (solid line); and 123 at 2025 hrs, 3/26/70 (dotted lines).

were at the 320 m trap. By the second night some were passing through the 472 m trap.

The third group of fry, 123 in all, was released on March 26 at 2025 hrs. These fry were not marked since they were the last group. They constituted the last major output from the redd. Bright moonlight prevailed after 0300 hrs on the night of release.

Movement rates were intermediate between those of the first and second groups, partly because of the fewer fish involved (Figure 18). Like the second group some travelled past the 320 m trap during their first night. The wavelike nature of their downstream movement was particularly evident during the first 2 nights following release.

Many fry must have entered the traps by actively swimming downstream along the screen barriers leading to the traps. The small bands of fry seen in front of the traps seemed always to face upstream, swimming rather vigorously. But they appeared to be losing ground against the current, and those fry that found themselves against a screen were frequently seen actively attempting to penetrate it. With their snouts against the screen they swam vigorously back and forth, apparently searching for an opening.

Discussion

The timing and distances involved in the migration of each group demonstrated again that fry resume their downstream movements on successive nights. This was particularly evident during the second night's migration of the second and third fry groups. Not only did those fry start entering the 213 m section at nearly the same time as fry were entering the 107 m section, but they entered the farther section in greater numbers.

The dispersal of the first group of fry was relatively slow with respect to numbers moving and distances travelled. On the first night movement increased to a dawn maximum at the 107 m trap, indicating a late arrival there of the main bulk of dispersing fry. These fry were essentially entering habitats devoid of competitors, there being no other redds in the stream. For the first 2 days and nights the only major source of competition for food and space was members of their own group. The main pattern of fry distribution was established during those first 2 nights, indicating rapid adjustment of population density. Fry that emigrated then from the first section (0-107 m) could not entirely have been responding to population stresses. For at the end of the second night the population level in that section was about 400 fish, but after introduction of the second group of fry on the third night, it increased about 1.7 times. Thereafter population levels decreased slowly, stabilizing at about 480 fish after 2 weeks. Similarly movement out of the second section (107 m - 213 m) on the second night and out of the third (213 m - 320 m) and fourth (320 m - 472 m) sections on subsequent nights occurred while population levels were rising in those sections. Emigration thus took place from stream sections not yet fully occupied with fish.

The migration pattern of the second group of fry was quite different from that of the first group. On the first night of introduction, movement rates decreased during the night to a dawn minimum at the 107 m trap. Dispersal was high in both numbers and distances travelled. Some fry migrated beyond 320 m the first night. The pattern of trap catches presented a picture of a fast-moving body of fry being preceded and followed by lesser numbers of faster and slower moving fish respectively. Emigration took place under conditions of increasing population levels in the second and third sections during the first night after release, and in the third and fourth sections on subsequent nights. Thus these fish too were not entirely responding to stresses stemming from population density. Emigration beyond 472 m, in spite of low population densities in the preceding section, makes this point clear.

Fry of the third group appeared to move downstream as fast as did those of the second group, but the pattern at the traps was slightly different. Individuals began passing through the 107 m trap about 2 hours after release and through the 213 m trap about 2 hours later. At each of these traps movement was high initially, with decreasing numbers appearing as the night went on. The main body of migrants seemed to move through the second stream section without reducing its average speed. Only at the 320 m trap did movement rates increase during the night, suggesting that the center of distribution had been left behind.

The fry of the third group were the first to exhibit approximate stability in numbers, with fry input tending to be balanced by output in each stream section. This stability occurred by the second night following introduction. Introduction of these fry into the first section had little effect on total population levels there. Declining population levels in that section thereafter resulted mainly from the continued movement of the first two fry groups. If emigration were primarily being caused by competition from the previously established fry in the stream sections, stability in the population of the third group should have occurred last.

Percentage migration increased with each new fry group introduced (Figure 19). This increased migration was true even for the first nights of fry introduction, probably before the fry had had a chance to feed and form territories to any extent. Such results might have been expected on the basis that each successive fry group faced greater competition from the increasing numbers of previously introduced fish. But no nocturnal mechanism that might produce such effects had been seen in previous observations and experiments.

Fry observed at night during the present dispersal study exhibited no noticeable agonistic behavior. In fact the small bands of fry that

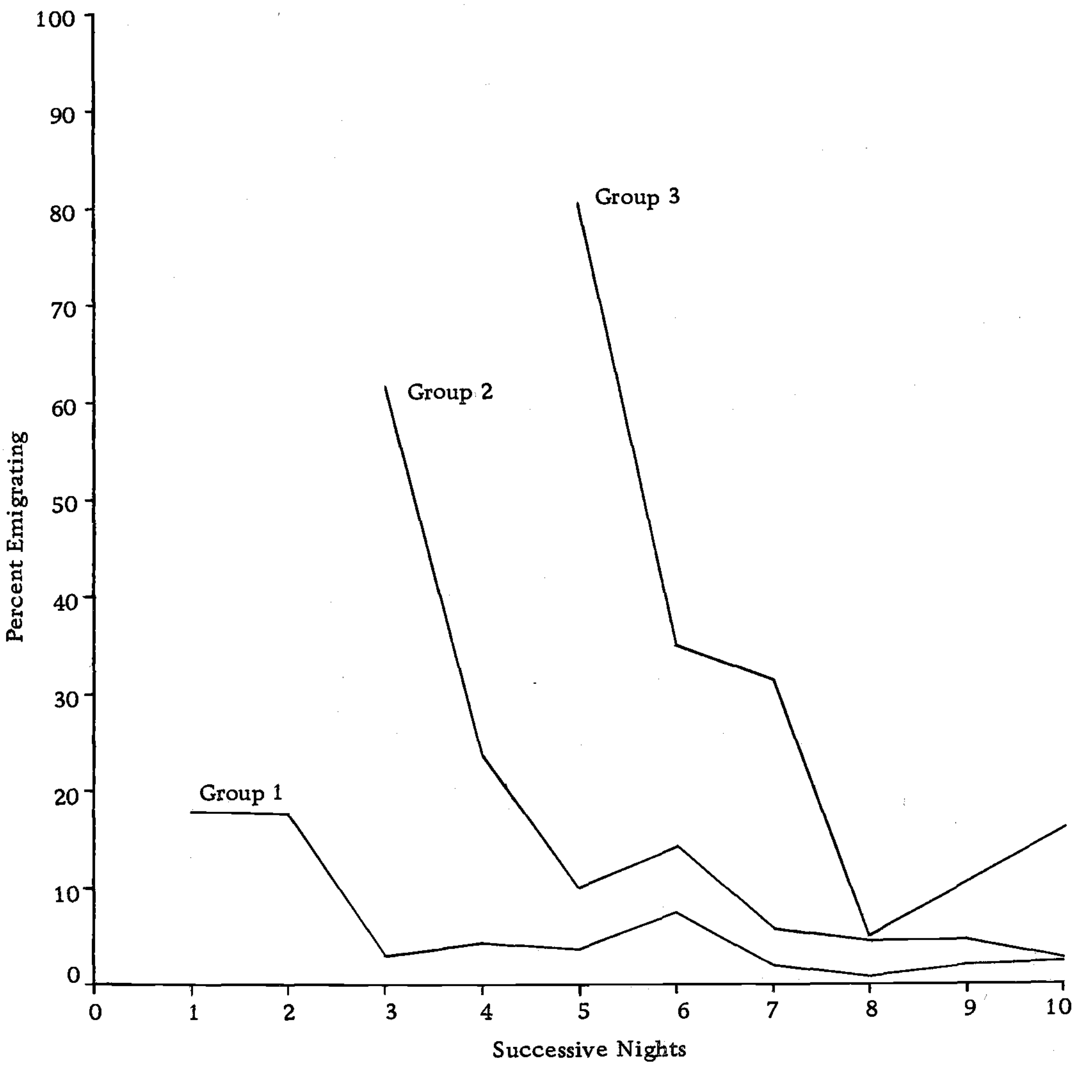


Figure 19. The trend of emigration from the first stream section (0 - 110 m) in each group of introduced fry. Percentage is based on numbers of fry of each group estimated to be within the section in Needle Branch.

seemed to be moving slowly downstream together suggested that mutual attraction rather than aggression was the characteristic behavior. Migrating fry from each newly introduced group contributed to the total migrants during a particular night. Yet the migration of each group seemed independent of the others, at least as could be detected in the pattern of trap captures (Figure 18). It is difficult to believe that the fast-moving fry of the second and third groups could have had enough time to significantly interact with resident fry, at least by the aggressive behavioral mode seen during the day. It is also difficult to believe that the fast-moving fry of these same two groups, migrating through the sparsely populated 213 m - 320 m and 320 m - 472 m sections, were reacting significantly to population stresses at all.

One might postulate that population stresses originating from within the groups of newly emerged fry themselves provided the stimuli for their migration. If this were accepted the second fry group (842 fish) should have had a higher percentage migration than did the smallest, third fry group (123 fish). But in fact the latter group exhibited the highest migration rate (80.5% vs. 61.4% during the first night).

One aspect of nocturnal fry behavior consistent with the observations is the effect of moonlight. Previously evidence was presented indicating that moonlight depresses the fry migration. The progressively later hour of moonrise during each of the nights of fry introduction could have produced the progressively increasing percentage migration.

In spite of the above reasoning, the idea of a density dependent control of fry migration remains attractive. Salmonid fry and juvenile migrations have been implied as a population regulating mechanism by several writers e.g. Kalleberg (1958), Onodera (1962), Hunt (1965), Johnson (1965), Le Cren (1965), and for coho salmon most notably by Chapman (1962, 1966), Mason and Chapman (1965), and Mason (1969). These latter authors have presented evidence for aggressive activity among coho fry being a cause of their downstream migration. The successively greater emigration rate of each of the three fry groups in the present study distributed the mode of each population farther downstream (Figure 20). This might be considered evidence for a displacement effect exerted by the preceding, resident group of fry. But notice that the main features of spatial distribution were established during the first night for the first two groups and by the second night for the last group (Figure 20). After the second night very little change in distribution occurred in any of the three groups. Even the patterns 11 days apart (March 28 - April 8, Figure 20) showed relatively little change, suggesting that once the fry settle, competitive displacement has little effect, at least at lower population densities.

If aggressive activity is a cause of the downstream fry migration, then it must occur and be effective at night and rather immediately

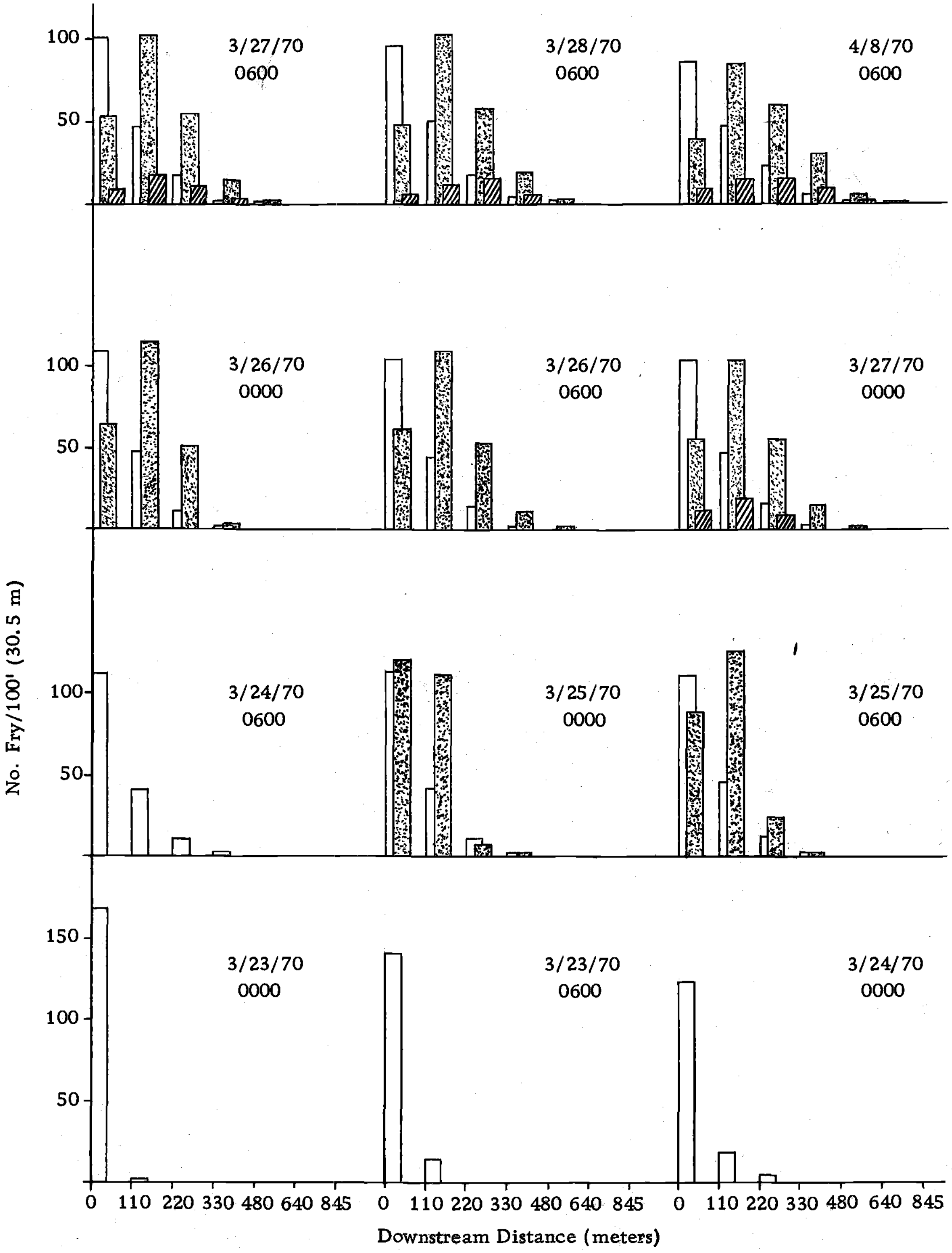


Figure 20. The distribution of three groups of fry within successive intervals downstream from release site during the period 3/23/70 - 4/8/70. Needle Branch, 1970. Numbers released:

☐ 591 at 2200, 3/22/70 ▩ 842 at 1900, 3/24/70 ▨ 123 at 2025, 3/26/70 after the fry emerge into the stream. No intraspecific activity that might lead to such effects was obvious in the nocturnal behavior observations conducted at Oak Creek. Nevertheless it could quite conceivably exist. Even on the darkest nights fry are probably able to see each other to some degree. Interactions may also occur as a result of fry sensing each other through their lateral line system or even by accidental touching encounters. It would seem obvious, however, that any nocturnal interactions among fry must be at least qualitatively different from those observed during the day.

The Ecology and Mechanism of Dispersal and Colonization

From the preceding discussion it should be clear that fry dispersal and colonization are part of the same process. As the waves of fry disperse downstream each night, small groups settle out along the way. These groups are the recruits, temporarily at least, to any particular stream section. The section is thus colonized by successive recruitment over a period of many nights during the season. Some of these fry originate directly from some upstream redd. Others have been in the stream several days. They continue to disperse each night because they have not yet found suitable habitats for colonization or are not yet capable of doing so. Each new day these fry find themselves in new localities with renewed opportunities to find and develop the conditions necessary for residence. The fry in any group do not disperse and evenly colonize the areas downstream from their point of origin. Depending upon their "dispersiveness" the center of their distribution may be at varying distances from the origin. "Dispersiveness" is probably a function of both a physiological and physical readiness to settle and the degree of intraspecific competition that the fry encounter. The latter probably takes place mostly during the day from interactions with prior residents and may be of importance as a population regulatory mechanism. It is by these processes of dispersal and settling, continuous over several days and nights, that fry from a given redd spread out and colonize the downstream areas.

It is important to note at this time the distinction between dispersal and competitive displacement. Upon emergence coho fry disperse, i.e. they become spread over large distances downstream from the redd without necessarily interacting with resident fry. After the first day some fry may be displaced from suitable sites within a particular pool through intraspecific competition, but their further downstream movement that night is not primarily a process of competitive displacement. The movement does not lead to a progressive and further filling of all available habitats with downstream distance on each successive night. Instead stream colonization seems accomplished by continuous recruitment along its length from a series of dispersing waves of fry. The combined dispersal patterns from redds scattered spatially and temporally can thus produce an overall patchy distribution of fry in the stream.

Many examples of fry dispersal can be seen in the stream observations described above, and some have already been pointed out. In each of these cases, groups of fry both moved past and settled in colonized and uncolonized stream sections alike. In none of these instances did previous movements through a stream section signify that no more colonists could be added.

The Ecological Importance of Fry Dispersal

The ecological principle behind coho fry dispersal must lie in the necessity of distributing potential colonists to areas downstream from the redds. Initially fry are concentrated at the discrete redd sites due to processes that promote mass emergence at night. These fry must be particularly vulnerable because they have not yet adjusted to the new environment. They are disoriented, not yet in hydrostatic equilibrium, and have difficulty in swimming. Their behavior resembles that of animals in distress, providing favorable stimuli to predators. Such predators may largely be fingerling coho and cutthroat trout. A mechanism that disperses these fry under cover of darkness would be advantageous to their survival. Furthermore, mass movement downstream provides additional protection. Any schooling, herding, or flocking behavior or potential prey essentially saturates a predator's time for processing this food on the less frequent occasions that it is encountered (Brock and Riffenburg, 1960; Holling, 1965). Thus the nocturnal, mass movement of fry is an efficient method of distributing and redistributing fry to suitable habitats in the stream. The importance of this function is appreciated when the relatively limited spawning sites are compared with the potential nursery areas in the stream, both in the vicinity of the redds and downstream from the major spawning areas.

Dispersal results in rather extensive downstream colonization. During the summer, resident juvenile coho may be found all along Horse and Meadow Creeks and for at least 8 km downstream in Drift Creek. Many of these fish undoubtedly originated from the study streams. Drift Creek is a large stream and represents a rather abrupt change in habitat. Most of the fry dispersing from Needle Branch enter that stream directly. That many such fry are successful in establishing residence in Drift Creek, at least within the first 200 m downstream, is shown by the occasional capture there of juveniles previously marked in Needle Branch.

The Role of Nocturnal Behavior

It is generally recognized that young coho are quiescent at night. Hoar (1951) and Smirnov (1960) both stated that coho fry rest quietly over the bottom, holding their positions against the current. Hoar (1958), in a comparative study of migratory behavior among juvenile Pacific salmon, noted that coho fry do not show the marked increase in activity at night characteristic of migrating pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), and sockeye (*O. nerka*) fry. These studies imply that the quiescent behavior enables coho fry to resist downstream displacement and to establish residence.

It is clear from the Drift Creek studies, however, that prior to assuming this behavioral pattern, coho fry are intensely active at night. Not only are many individuals to be found in the water column all during the first night of emergence, but for several nights thereafter. At first the behavior associated with obtaining air from the surface is the direct cause of displacement. Air gulping is characterized by darting, struggling motions toward the surface. The obvious vulnerability to downstream displacement of such newly emerged fry has been considered by other wirters as a cause of downstream dispersal. Kalleberg (1958) pointed out that this behavior, rather than aggressive activity, might be the cause of downstream movement of recently emerged, Atlantic salmon (Salmo salar) fry. Similar conclusions were reached by Bams (1969) in his studies of sockeye salmon alevins. An interesting series of related results was obtained by Thomas, Banks, and Greenland (1969). They found that a period of reduced swimming ability occurred in chinook salmon alevins (O. tshawytcha) shortly before complete yolk sac absorption. In their tests this period corresponded with the time of peak migration. They postulate that this reduced swimming ability is a cause of fry displacement.

It appears that dispersal of coho fry results largely from physical displacement by current acting upon the nocturnally active fish. Until they settle to the bottom these fry seem incapable of holding a position in the stream permanently. The speed of dispersal suggests that the movement involves a "core" of fry moving faster than the small bands of fry easily observed along the stream margins.

Observations in aquaria and streams also suggest that there may be a component of active downstream swimming involved. Where fry encountered screen barriers to their movement, many were observed actively trying to penetrate the screens in a downstream direction. Perhaps fry, upon being swept into stream localities where further movement is restricted, normally seek to escape such areas by downstream oriented activity.

By the end of the first night all the fry doubtless have managed to achieve hydrostatic equilibrium. There was certainly no evidence, in streams or aquaria, of erratic swimming behavior during the day. Nevertheless some fry continue to move on downstream on subsequent nights. These fry are still active within the water column at night, though they no longer angle jerkily toward the surface. It seems that their general nocturnal activity, even while at hydrostatic equilibrium, still enables the current to carry them downstream.

The arrival of each new dawn brings the end to that night's fry movement. This is probably due to the increased possibilities for visual orientation. During the day, fry may generally be seen swimming steadily in the current and feeding. If other fry are already resident in the pools that the new fry happen to settle into during the night, social interactions between the two groups result.

Kalleberg (1958) and Chapman (1962) both recognized the possibility that downstream movement of salmonid fry could occur exclusive of intraspecific, competitive activity. Hoar (1958) stated that coho fry may move downstream in large numbers after emergence, being displaced by the current to become widely distributed away from the redd sites. Coho fry migrations in Williams Creek, British Columbia, are described as occurring at night and stemming from displacement by the current when visual orientation is reduced (McDonald, 1960). In contrast Mason and Chapman (1965) found that coho fry emerging in artificial channels moved downstream in small numbers. The stream observations described in the present paper, however, suggest that this is not the usual case.

Nocturnal dispersal seems a fundamental characteristic of Oncorhynchus. Hoar's comparative study (1958) did not include the chinook, the most flexible member of the genus with regard to life history patterns, but nocturnally emerging chinook fry apparently disperse downstream through artificial channels even more strongly than do coho fry (P. E. Reimers., Oregon Fish Commission, pers. comm.). It is characteristic of the chinook that juveniles may reside in streams, rivers, or the sea. Evolution seems to have capitalized upon the dispersal process in two directions from the very generalized mode exhibited by the chinook. On the one hand specialization has occurred in sea or lake dwelling species to increase the efficiency of dispersal. Increased schooling and nocturnal activity, decreased aggressive and territorial behavior, and decreased propensity for hiding during daylight may be viewed as a generalized, graded series in specialization from the sockeye to the pink salmon "pelagic" species. On the other hand the coho has developed a capability to reduce dispersal and allow colonization of the upper stream areas. The relatively rapid acquisition of the behavior facilitating residence during dispersal from the redd site represents an abridgement of the generalized dispersal tendency.

The Idea of "Dispersiveness"

The result of downstream dispersal during the first night after emergence is that fry become distributed all along the stream from the redd to the point of farthest downstream travel. I believe that the center of distribution, perhaps corresponding to the possible "core" of movement, may be at any distance downstream within the interval. Its position would be determined by the "dispersiveness" of the fry.

This "dispersiveness" must be a function of current speed, turbulence, diminished visual cues, and the characteristics of the fry themselves. My studies suggest a developmental aspect to the latter, for it seemed that the onset of feeding enhanced the development of a nocturnal settling behavior. Settling at night into quiet and sheltered areas of a stream must be an important mechanism preventing further downstream dispersal. If the development of this new form of behavior is delayed due to stress or inability of the fry to obtain sufficient food and space requisites, dispersal continues. If this is true then it can be seen how the particular developmental condition of fry upon emergence, the inherent suitability of stream sections to provide the requirements of food and space, and competition with other fry for the latter all interact to control "dispersiveness." When and where the total physical and biological components of stream environment permit the development of the new nocturnal resting behavior, fry dispersal would cease. "Dispersiveness" may be considered the complement of the average degree of development toward this quiescent nocturnal behavior.

Intraspecific Interactions and Dispersal. It must largely be during the day that the newly emerged fry compete to become permanent residents. The particular stream location in which these fry find themselves after the night's dispersal may largely be happenstance, but whether or not they become resident there is probably not. Competition may occur between members of the new fry group itself or with prior resident fry. It has been shown that the latter fry have a competitive advantage over newcomers (Mason and Chapman, 1965). The evidence from my stream observations and experiments indicates that the process continues for several nights until all fry are suitably established. Each night sees a smaller number of unestablished fry continuing on downstream.

It is implied above that competitive displacement of fry is an indirect process. The fry do not seem to be driven from the pools by intraspecific competition. Rather it seems that competition results in some fry remaining unable to establish themselves through the proper behavioral activities that permit residence. These fry are therefore further dispersed downstream by the current at night. It is implied that the fry to be further dispersed are determined during the day, and that dispersal that night is largely a physical process, characterized by the "dispersiveness" of the fry.

"Dispersiveness" itself, however, also implies a biological, density dependent action. At the very beginning of this section the analogy between dispersal and diffusion processes was remarked upon. In both processes the movement rate of particles or individuals from any locality at any time is determined by the density gradients at hand there. Watt (1968) described a computer program simulating general biological dispersal based on just such principles. Beverton and Holt (1957) employed the one-dimensional diffusion equation, familiar in heat flow and gas diffusion problems, to study the offshore movement of plaice. They were able to show that this movement corresponded to the assumptions underlying the diffusion process, in which the "dispersiveness" was proportional to the mean velocity of the fish, considered on such a time scale that such movement was essentially random. Biologically such diffusion processes mean that individuals disperse in response to population pressures at any particular time and locality. The mechanism for such a response, operating at night, has not yet been seen among coho, but some possibilities were discussed above. The evidence so far is that while "dispersiveness" may have biological, density dependent components, the manner of dispersal is largely physical.

The possibility of random movement among coho fry as a cause of their downstream migration was discussed by Chapman (1962), who rejected the idea on the basis that such movements would result in considerable upstream movement of fry, which only occurs to a limited degree. His conclusion is invalid for cases where the current imparts a net downstream movement on the random motion, or where there may actually be a greater probability for downstream movement within the random regime.

Dispersal Capability. The capability of coho fry to disperse seems to be rather great. In the 1969 observations on Needle Branch I calculated some fry to travel about 300 m per night. The 1970 experiment there saw some individuals move 320 m per night. Some fry emerging from trapped redds in Deer Creek were also marked in 1969 to study downstream movement rates. A single fry from a redd 1830 m above the downstream trap arrived at the trap 8 nights after release, representing an average speed of about 230 m/night. From another redd 150 m above the trap 18.7% of those marked arrived the first night. From visual inspection of the stream it was obvious that the fry from the redd at 1830 m had made the extensive journey through considerable stretches of very sparsely populated, or even completely unpopulated stream. This again demonstrates the property of downstream movement called "dispersiveness."

The Interpretation of Fry Movement Rates

The mass downstream movement of coho fry from their spawning grounds each spring is one of the most dramatic aspects of the ecology of the species. The interpretation of the movement rates observed at any particular locality, such as at a trap site is therefore of considerable interest.

It is clear that the number of migrating fry counted at any trap facility does not represent the excess population from the stream area above the trap. It represents only the local rate of movement detected at that particular location. The particular set of upstream events determining any local rate is unique for every observation point and time. It follows that the downstream trap records in the Drift Creek study streams are partly a function of the location of those trap facilities. On any night when fry are migrating, there may be hundreds, even thousands, of fry on the move, only some of which will ever be seen at the downstream trap.

Fry counted at the downstream trap would represent an excess to the coho rearing capacity of upstream areas only if the fry were to fully occupy each stream section before any passed through. Under such conditions the entire stream section would eventually have its maximum complement. Any subsequent fry additions or fry competitively displaced would be excess and detected at the downstream trap. The particular location of the trap would not be critical so long as it was within fully occupied sections and below the point of initiation of fry movement.

Some fry are very likely actually displaced through competitive interactions from particular pools in the stream. They are then excess fry from those pools. However their subsequent downstream movement that night is a dispersal process rather than biological displacement. Detection of some of their numbers at the trap would not signify a saturation of living space upstream, but only that displacement had occurred in some upstream pool.

Fry dispersing downstream directly after emergence from a redd appear to be moving with little regard to existing population densities in the stream. Fry dispersing after spending at least 1 day in the stream may have been compelled to do so because of daytime aggressive activity by already resident fry. It is my belief, however, that these migrants continue to move primarily because of a failure to adequately develop the proper behavior that enables residence.

The Pattern of Stream Residence

During the process of stream colonization competitive displacement augments fry dispersal by forcing some of the newer fry to continue with their nocturnal migration. However, once residence is established, further downstream movement of those fry seems greatly curtailed. The vast majority of migration is over by the end of May. Approximately 90% of the total fry to be caught through the end of July have already passed through the downstream traps by that time.

It may be demonstrated in aquaria that aggressive activity continues among populations of fry or fingerlings during spring and throughout the summer. Since fry emigrating from such aquaria are generally the smaller or newer members, competitive displacement may be inferred. This displacement may partly reflect inadequacies in artificial channels with respect to space, refuges, and the probability of obtaining food. Such experiments have figured strongly in development of the hypothesis of aggressive activity as a population regulatory mechanism among coho juveniles (Chapman, 1962, 1966; Mason and Chapman, 1965; Mason, 1969).

In the streams aggressive activity among coho is also readily observed throughout the summer. Yet during this period almost no juvenile coho emigrate through the downstream traps. It appears that any displaced coho must move downstream only short distances if at all. They no longer display the dramatic nocturnal dispersal of the colonization phase. During the summer the juvenile coho are probably expanding their territories to meet their increasing needs for food and space. The considerable mortality that occurs then is an indication of the existence of population stresses. The fact that little emigration results in spite of the continued agonistic activity suggests that the phenomena of mass fry movement is associated primarily with initial distribution and colonization, rather than with population adjustment.

A demonstration of the spatial stability of juvenile coho is afforded by further history of the 1970 year class on Needle Branch. The downstream distribution of that population changed relatively little after the first 2 days following fry input (Figure 20).as inferred from the trap catches. A better picture of the actual spatial distribution of fry was obtained from sampling along the length of the stream (Figure 21). Samples were obtained both with electric shocker and by counting fry while slowly walking upstream. By June 20, this population, which had originated from the redd at 777 m, had spread slightly farther downstream from the April position, primarily in response to a series of spring freshets. Thereafter the spatial distribution of the coho remained stable through mid-August. Some of the original screen traps from the spring experiment were left in the stream throughout the summer. There was virtually no movement at all through these traps. However some fry did move upstream from the redd as far as the waterfall barrier at 808 m.

Further evidence of the spatial stability of resident coho is shown by the distribution pattern of juveniles of the 1968 year class marked for population estimates (Figure 22). These fish were marked in specific sections of each stream. Later, in the process of placing a new set of marks into the population, the percentages of marks among the fish from each 30.5 m stream section were obtained. In all three streams the late September samples showed that the early summer marks were still closely associated with the stream sections where originally applied. By mid-winter the marked fish had drifted downstream somewhat from their application sites. This is shown in the distributions of marks applied both in late September and early summer. From these results the summer growing period seems not

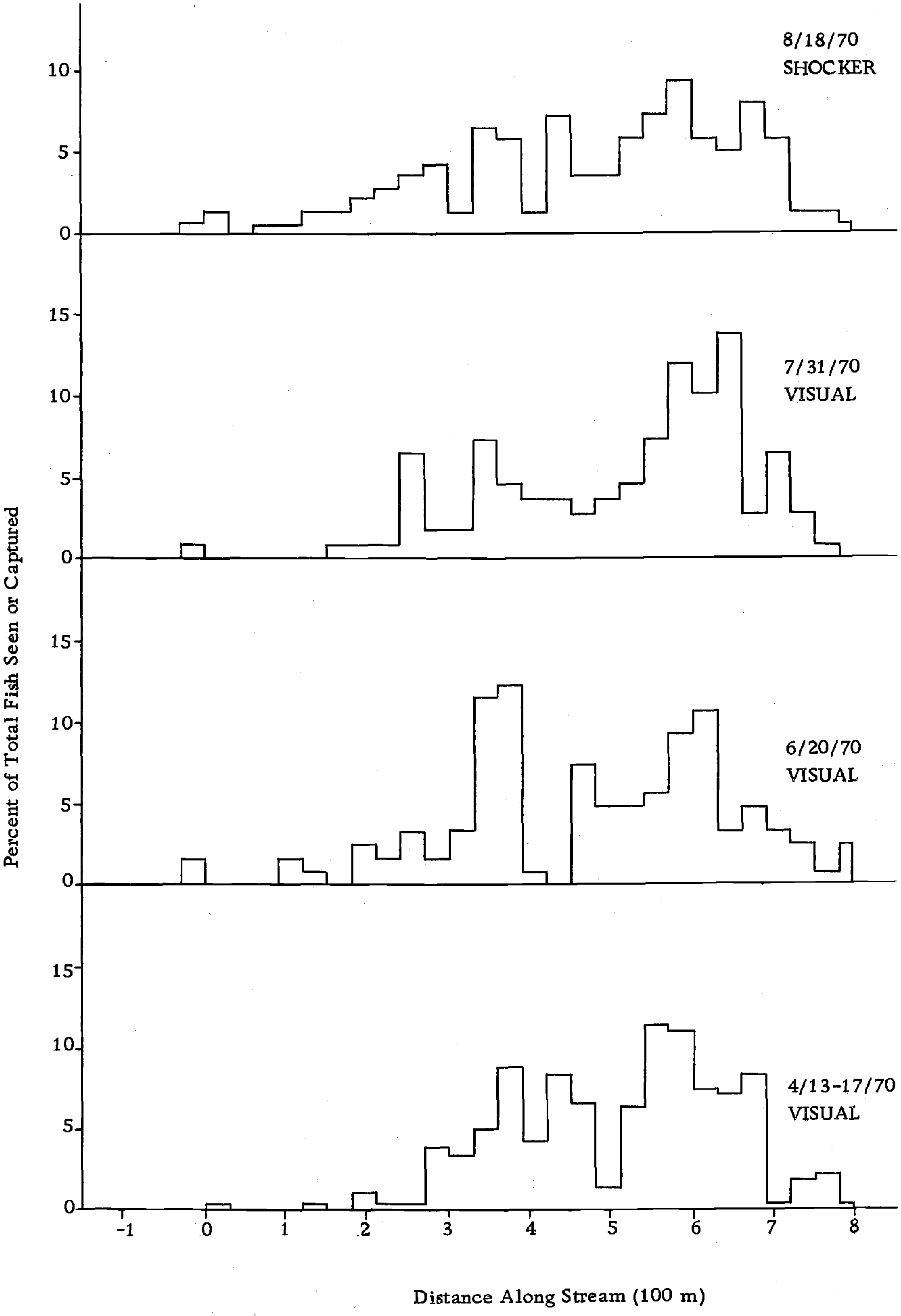


Figure 21. Summer distribution of the 1970 year class, Needle Branch, by visual and electric shocker census.

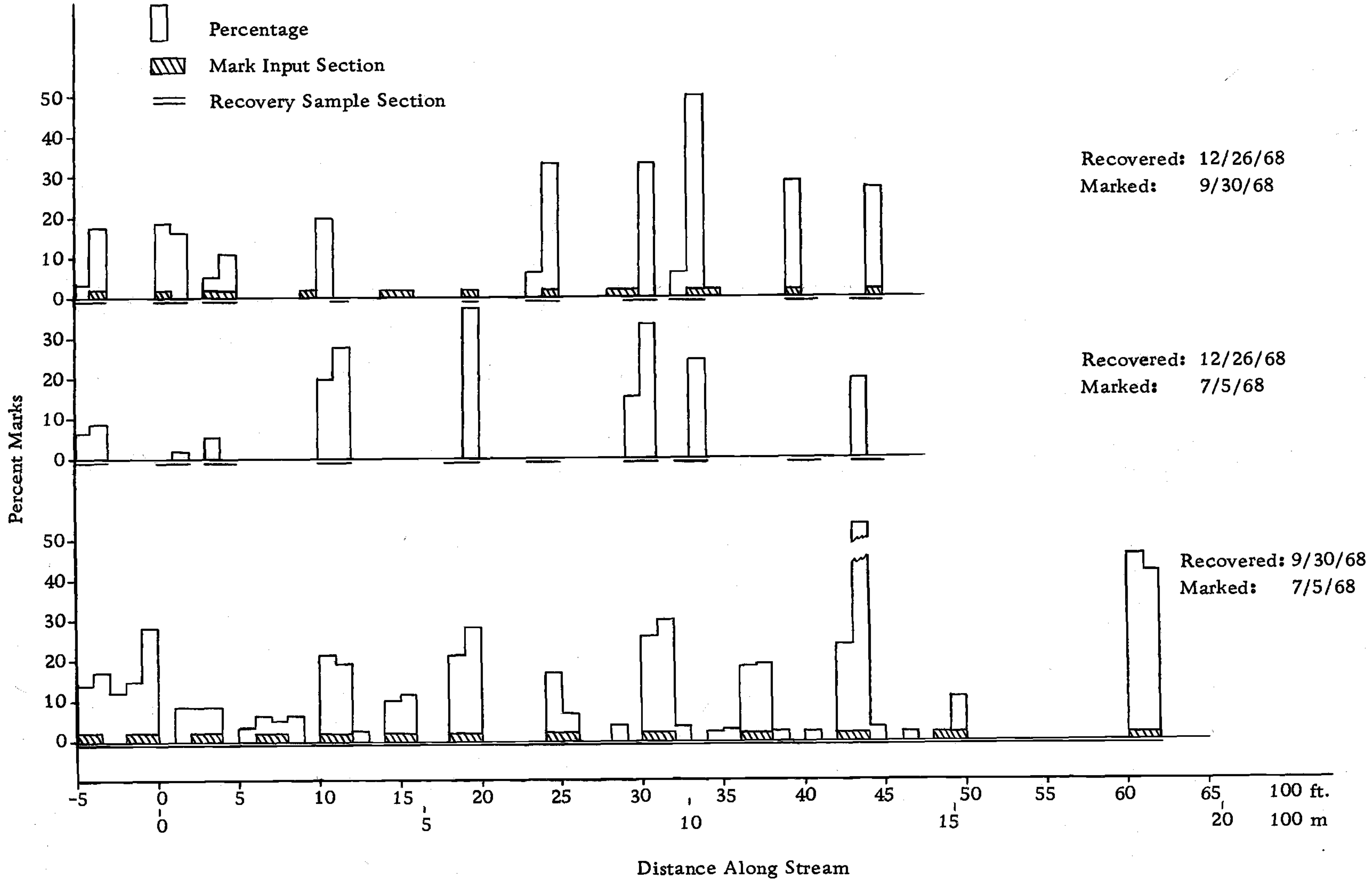


Figure 22a. Deer Creek, 1968 year class: Distribution of marked fish in various 100' (30.5 m) stream sections expressed as percentage of recaptures in sample from each section. Note tendency of marked fish to remain in sections where marks were applied.

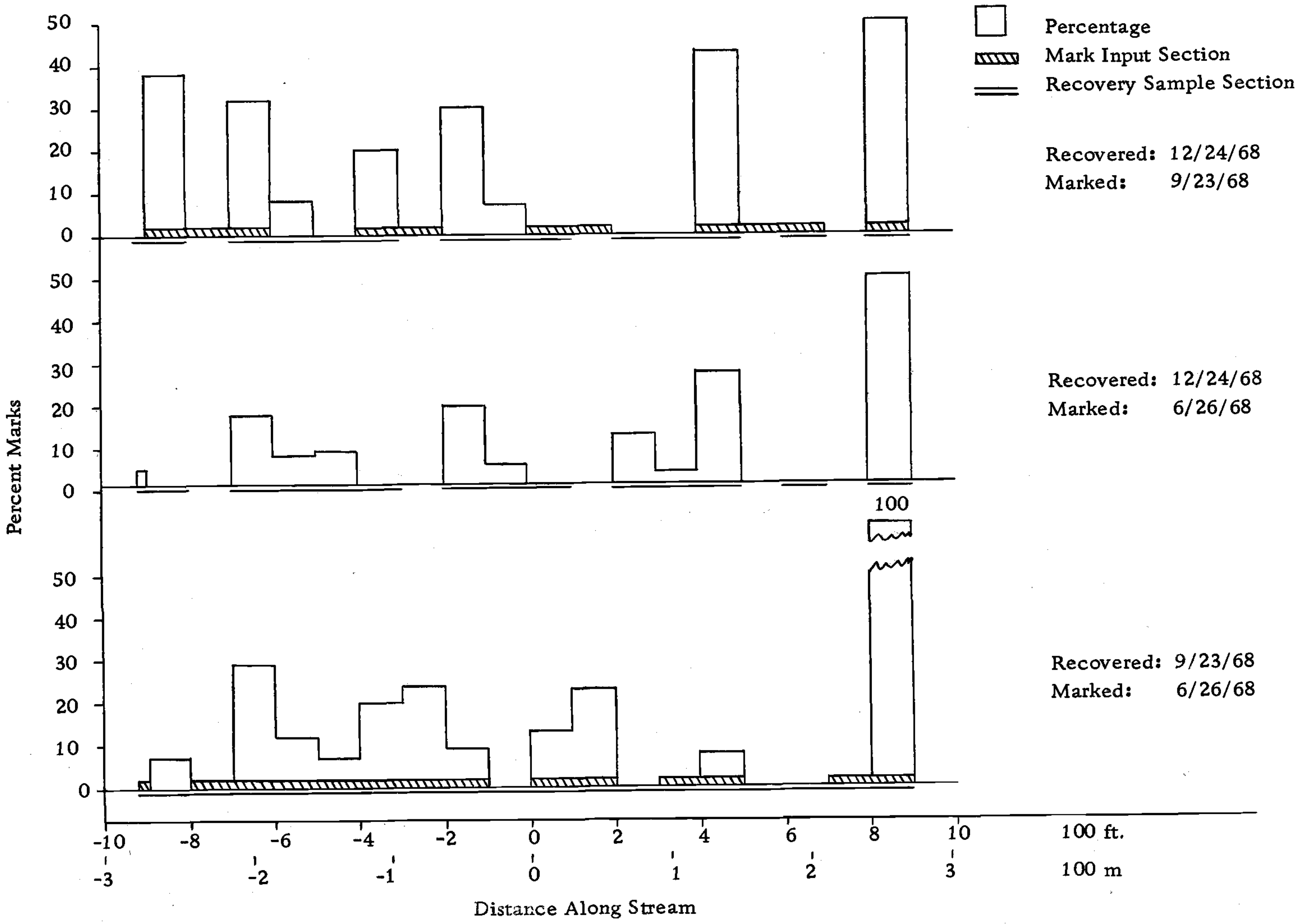


Figure 22b. Flynn Creek, 1968 year class: Distribution of marked fish in various 100' (30.5m) stream sections expressed as percentage of recaptures in sample from each section. Note tendency of marked fish to remain in sections where marks were applied.

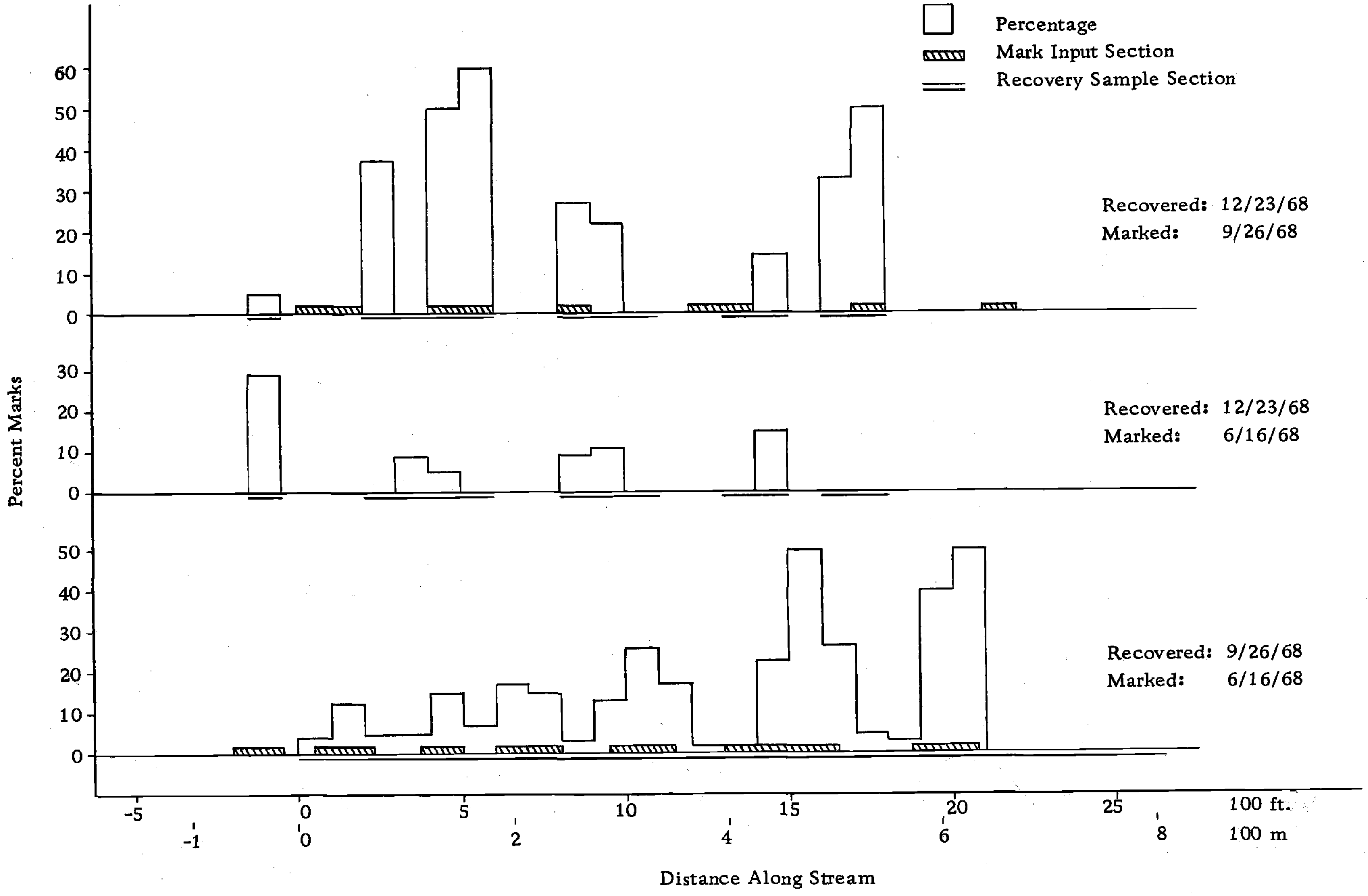


Figure 22c. Needle Branch, 1968 year class: Distribution of marked fish in various 100' stream sections expressed as percentage of recaptures in sample from each section Note tendency of marked fish to remain in sections where marks were applied.

attended by any large degree of downstream movement of juvenile coho, in spite of the ubiquity of aggressive activity displayed and the growth occurring then.

A General Scheme of Migratory Processes

The concept presented in this paper is that dispersal, colonization, and territorial behavior are continuous, overlapping, and sequential processes. Dispersal operates to efficiently distribute fry from the spawning areas to downstream colonization sites. The colonial or resident fry adopt a territorial behavior that both assists further dispersal and enables a more efficient utilization of their habitat site.

A general scheme demonstrating the processes that result in migrations of coho fry and fingerlings is presented in Figure 23. This scheme is an attempt to tie together the major aspects of coho behavior.

The Colonization Phase

During colonization the main processes are nocturnal dispersal and its gradation into nocturnal resting behavior (Figure 23). The former is initiated by nocturnal emergence and augmented by the initial disequilibria of the emerged fry and by stream velocity and turbulence. Moonlight inhibits dispersal as does daylight.

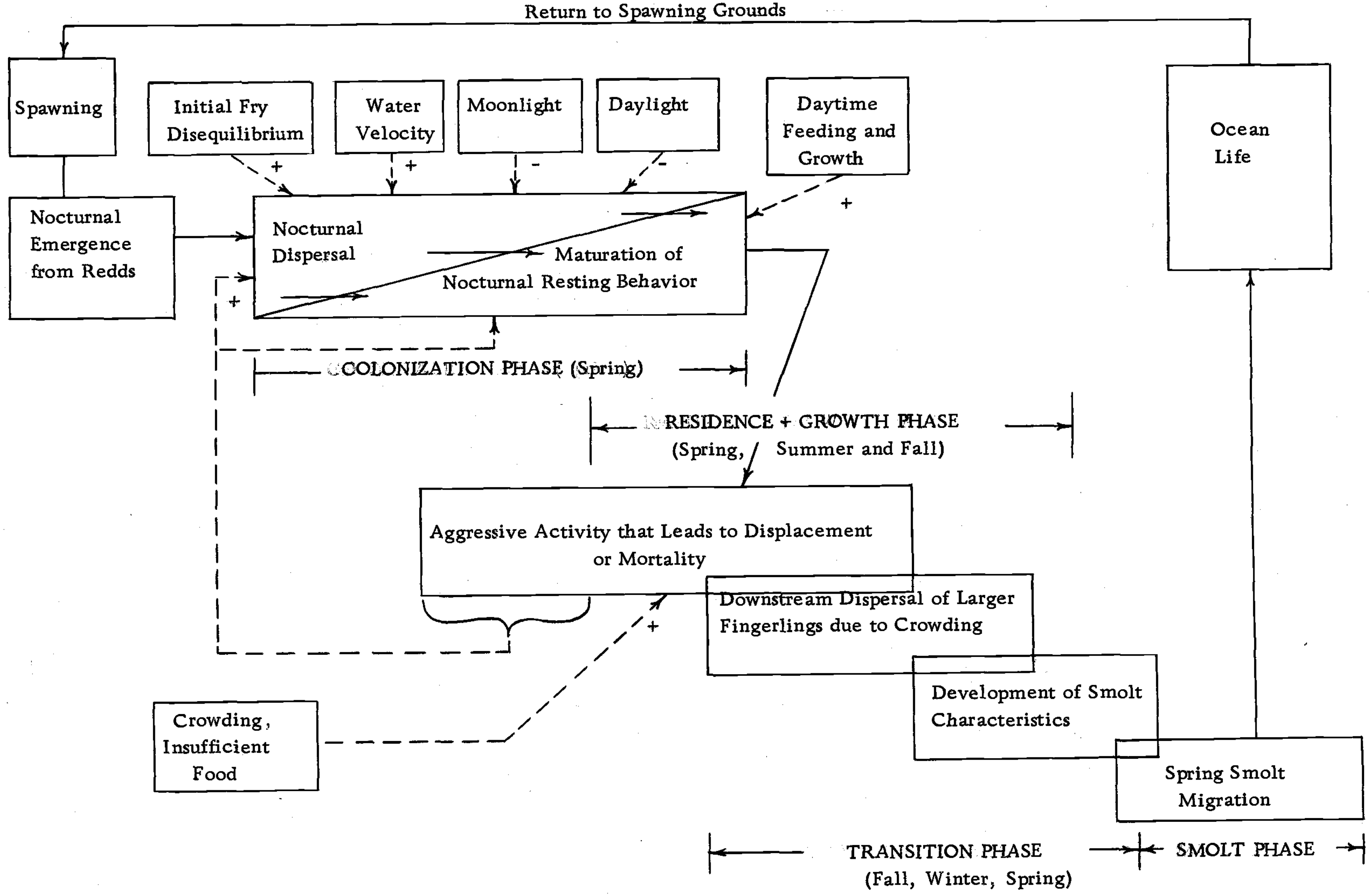


Figure 23. Scheme of migration processes during fry, fingerling, and smolt phases of coho salmon life history.

Nocturnal resting behavior, i.e. the seeking of sheltered spots near the bottoms of pools, is pictured as developing rather gradually over several days as a process of fry maturation. Maturation is a function both of the initial physiological condition of the fry and feeding and growth occurring during the day. Feeding opportunities are mediated through hierarchial social structures especially developed among resident fry. Intraspecific competition for food and space slows the maturation of resting behavior and results in the continuation of nocturnal dispersal.

The Residence and Growth Phase

The next phase in coho life history begins with the fry establishing themselves as residents in the stream (Figure 23). It is characterized by daytime aggressive activity and intraspecific competition for food and space. Since fry movement is not evidently a major feature resulting from the intraspecific competition, the major importance of agonistic, territorial behavior must lie in the regulating of mortality and growth processes.

The transition to the residence stage occurs during spring and early summer. A greater proportion of fry movement in early summer occurs during the day, reflecting the decline of nocturnal dispersal and the increasing importance of diurnal agonistic activity. Chapman (1962) has shown that the percentage of juvenile coho migrating during the day increased from 2% in March to 30% in May. Such migrating coho are also larger, as he has shown, indicating growth had occurred, but they remain smaller on the average than resident coho. When the fry become fully established as residents, the extensive migrations seen earlier largely cease.

Transition and Smolt Phases

As the season progresses and individual growth continues, some of the larger juvenile coho may be compelled to emigrate. This is a phenomenon commonly observed in artificial stream channels. Probably the best explanation is that larger coho may require more living space (Chapman, 1966). They thus outgrow the spatial resources of their home pools. The result is that the smaller, displaced coho grade into larger sized migrants toward the end of the growing season. The larger coho also tend to develop smolting behavior earlier. After the fall months, migrating juveniles tend to be larger than resident fish. Thus the movement of larger coho seeking less restricted habitats grades into the early movement of smolts during winter and spring. Finally the majority of the remaining coho leave as smolts in the spring, after spending a year in the streams.

Population Regulation, Dispersal, and Territoriality

The majority of fry movement occurs during spring associated with fry emergence and dispersal processes. If for each stream the total emigrating fry during spring are subtracted from the total estimated fry input, estimated net fry inputs are obtained (Table 7). These estimates are crude because the total estimated inputs cannot be obtained accurately. One result is that for Flynn Creek and Needle Branch, fry output often appears greater than fry input. Nevertheless if the positive estimates of net fry input are momentarily accepted, their year-to-year variability is so great that to believe the fry migrations serve a major purpose in regulating population size is difficult. The net input during a particular year often exceeds the estimated total input of another. If the fry migrations are regulatory, then it must also be postulated that year-to-year variability in stream carrying capacity for coho is also exceedingly great.

It is worthwhile at this time to return to Figure 11, where the relationship between numbers of migrating fry and spawning females (or estimated total fry input) was shown to be linear. This means that the greater the fry input, the greater would be the fry output through emigration, but also the greater would be the number of fry remaining in the streams. This does not describe a regulatory mechanism, although the effects of overcrowding are capable of being reduced, and, when total input is small, even prevented. In order for fry emigration to function in regulating population density, the relationship between fry input and fry output cannot be linear as indicated in Figure 11. Instead percentage emigration should increase with increasing fry

Table 7. Estimated net input of coho fry into streams (total estimated emergence - total spring fry emigration).

Year Class	Deer	Flynn	Needle
1963	12,456	940	a
1964	14,223	1,876	a
1965	28,347	a	a
1966	19,428	3,476	1,117
1967	39,583	a	7,168
1968	10,789	637	6,859
1969	18,341	2,386	2,245

a) Apparently greater fry output than input

input, i.e. the relationship should be curvilinear upwards. It appears then that fry emigration is an inefficient mechanism at best in the control of population size. The close association between fry emergence and emigration suggests further that the pattern of the latter may ultimately reflect the density independent weather factors that determine the initial pattern of spawning.

Population regulation instead must operate within the resident coho population, i.e. after the main dispersal and colonization phase is over. That the observed territorial and hierarchial behavior of coho are most important in this respect cannot be doubted. In general, social factors, e.g. history of prior residence or dominance, are of prime importance in the structuring of animal societies in habitats where competition for resources exists. This has been shown by Landau (1951 a, b). The structuring of coho society must not only have importance in the regulation of mortality and growth, but in the overall view it must also operate to increase the efficiency of growth and survival processes in the populations.

POPULATION HISTORY IN THE STUDY STREAMS

The spawning grounds in the Drift Creek study streams are important rearing areas for coho salmon. The stream sections above the downstream traps include the bulk of these spawning grounds. The downstream trap on each stream provides a convenient cutoff point in the study of populations that are never completely stable in space. The trap facilities also provide information on juvenile coho output from the stream sections above.

Distribution of the Coho Populations

Coho populations in the study streams are distributed both above and below the downstream traps. The extensive populations of coho below the traps on each stream are not specifically included in this study. Neither the extent of spawning there nor the distribution and survival of migrants into those sections is known with any degree of certainty.

The spatial distributions of coho of the 1968 year class are indicative of the patterns in population density to be expected above the traps. In each stream there was an upper and a lower distribution to the population, the latter distribution increasing steadily in density toward the traps (Figure 24). The dip in densities between these two groups coincided, in Deer and Flynn creeks, with stream sections of relatively steep gradient where a canyon is entered. In Needle Branch a section of relatively homogeneous, shallow, and unsheltered stream appeared responsible for the lower densities in the middle section of the stream.

These spatial distributions correspond to what might be expected from the general distributions of spawning areas (cf. Figure 8). The upper limit of coho distribution in each stream corresponded to the approximate position of the uppermost redd during that year. On Needle Branch this limit is a physical one due to the falls (at 808 m) that blocks off the upper portions of the stream. There was no successful spawning in Flynn Creek above the canyon section in 1968. Only residual fingerlings from the 1967 year class existed there.

The density distributions in each stream appeared to be relatively stable throughout the summer. However by December the pattern showed that a downstream shift in the populations had occurred. The early summer censuses (lower panels Figure 24) were in general agreement by both visual and electric shocker techniques.

The spatial distributions of fish species in the study streams reflect the ecology of the species. The other common salmonid in the streams is the coastal cutthroat trout. The distribution of 0-age trout is shown for September (middle panels Figure 24). These fish inhabit the upper reaches of each stream, where most of their spawning probably takes place. On Needle Branch such areas are completely blocked off to coho by the falls. The small trout definitely decreased in abundance as their populations intergraded downstream into those

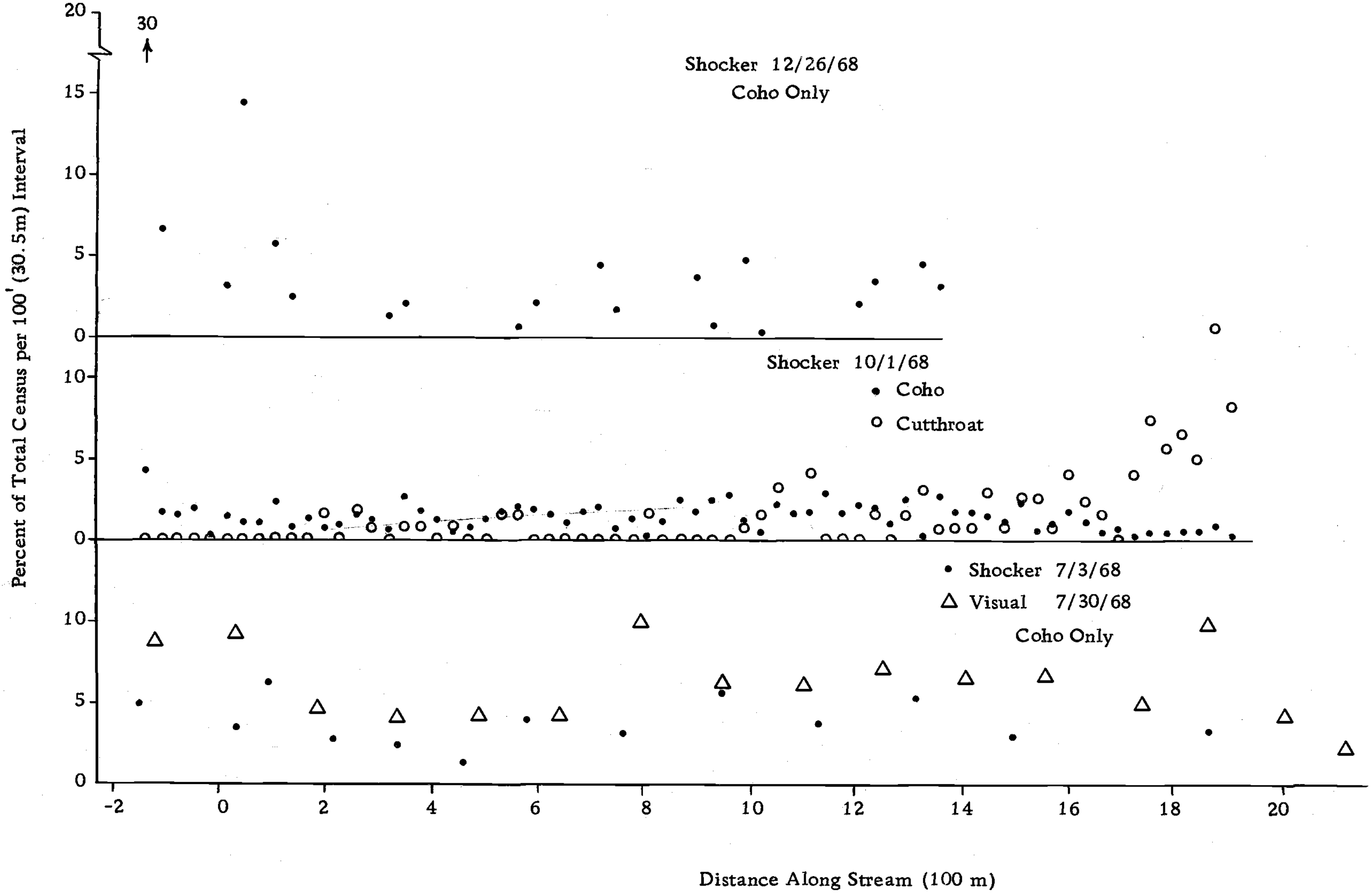


Figure 24a. Distribution of coho salmon and cutthroat trout in Deer Creek during 1968 determined from visual counts and electric shocker samples.

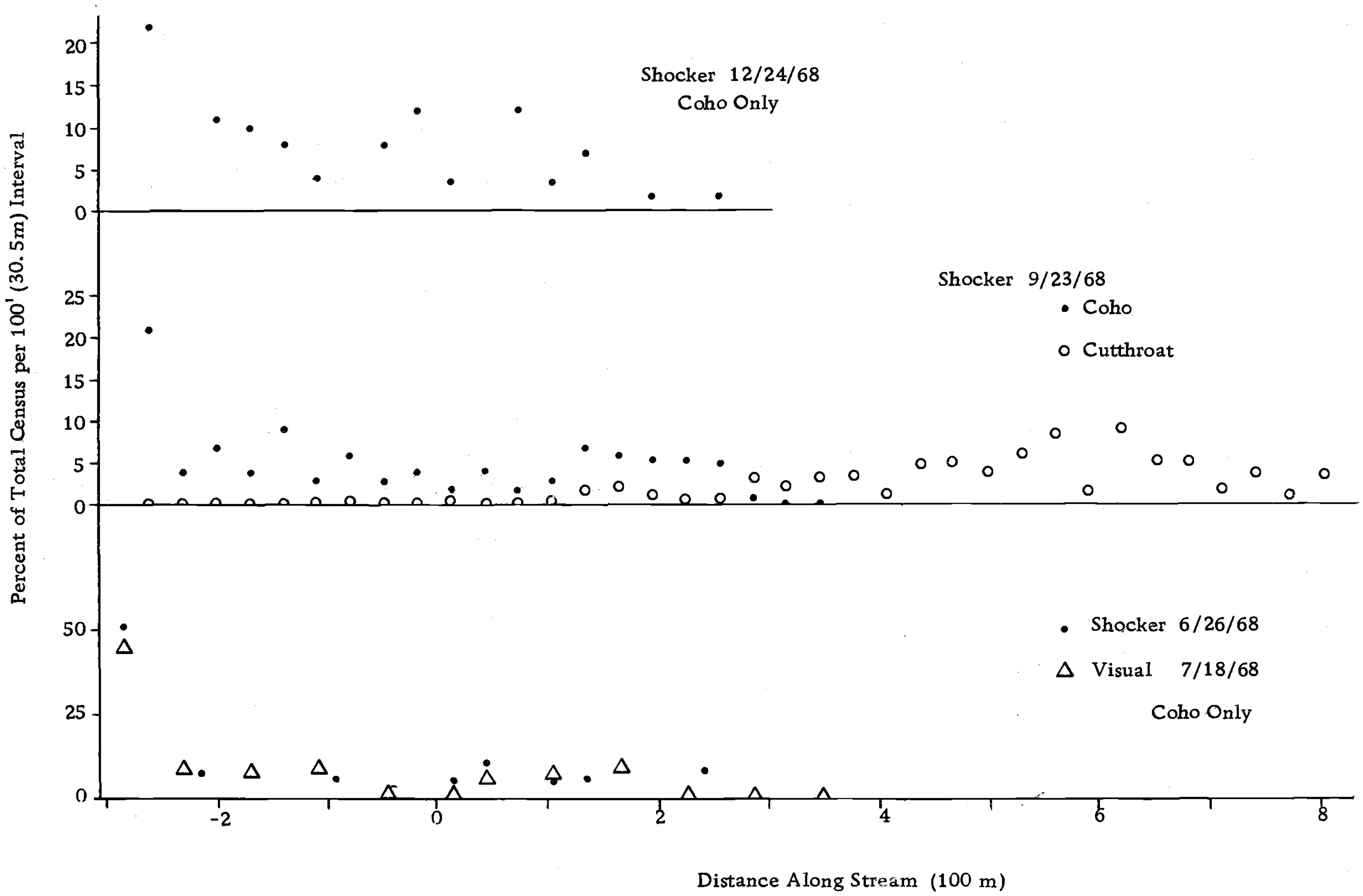


Figure 24b. Distribution of coho salmon and cutthroat trout in Flynn Creek during 1968 determined from visual counts and electric shocker samples.

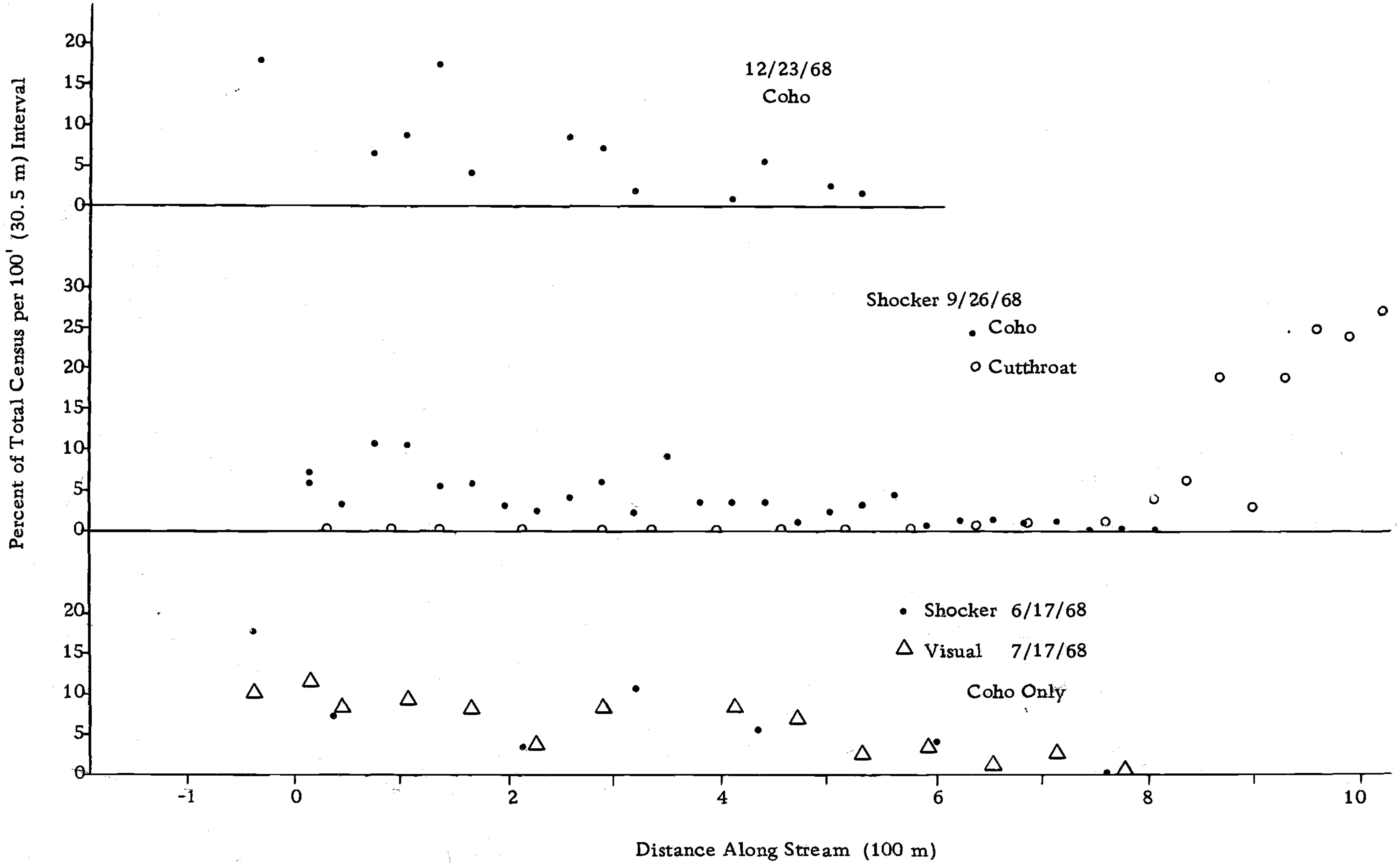


Figure 24c. Distribution of coho salmon and cutthroat trout in Needle Branch during 1968 determined from visual counts and electric shocker samples.

of the coho. This may be an effect of interspecific competition with the aggressive coho. In Deer and Flynn Creeks the trout fry were again abundant in the canyon sections, which are relatively unsuitable for coho. The O-age trout tend to increase in size with downstream distance. Like coho the trout apparently disperse downstream somewhat as they grow. In stream sections inhabited by coho, small trout are not found except occasionally in swifter riffle areas. They are largely restricted to the headwaters of the streams, above the coho populations. In contrast, yearling and older trout (and also sculpin) are relatively evenly distributed throughout the stream, including the sections inhabited by coho. Probably the cottids and larger trout do not compete extensively and directly with coho for the same food source. McIntyre (1970) found that large trout in Berry Creek, Oregon tended to spend more time in surface feeding than did coho, which fed largely on drift. In general, coho are largely pool dwellers, capitalizing on the tendency of food to accumulate there. On the other hand O-aged trout seem to prefer riffles and faster stream sections, as might be inferred from their more robust body construction.

The distribution of coho in the streams shows that their densities, unlike that of O-aged trout, does not decline with downstream distance (except locally) and with approach to the traps. Coho populations extend past the traps as a continuation of the pattern shown. Such populations must have originated to a considerable extent from spawning above the traps.

Population Estimates

Methods

The Petersen estimate was employed in this study to estimate population size. Principles of the method are outlined by Ricker (1958). Essentially the proportion of marks in the population should remain constant up through the time of sampling. The population estimate, N_t, applies to the time of marking.

The formula used for the point estimate is that of Bailey (1951) given by Ricker (1958) as:

$$\hat{N}=M(C+1)/(R+1)$$

relating $\hat{N}$ to the census sample or catch (C) and to the numbers of recaptured, marked fish (R). The 0.95 confidence limits of estimates were obtained using the criteria of Chapman (1948) as modified slightly by Davis (1964). Usually the binomial or Poisson approximations to the probability distributions of recovered marks were appropriate.

Operations leading to population estimates of coho involved the placing of marks in the population and subsequent inspection of smolts for the presence of those marks. Coho were marked by various fin-clip combinations. Usually from 4 to 6 separate markings were applied to the population. After 1967, only 3 sets of marks were applied: in June or July, September, and December. The coho were captured for marking by electric shocker and seine. An attempt was always made to return the marked fish to their original pools. The spring run of smolts, captured and inspected at the downstream traps, comprised the census sample. I estimate that the numbers of residual fingerlings, i.e. 1+ aged coho that would remain in the streams an additional year, are almost always less than 10% of the population. Therefore the smolt population as a census sample consists of practically all survivors of the year class under study. However the smolts pass through the traps over a period of about three months, during which time mortality occurs. If they are to provide an unbiased estimate of the population mark ratio, the marks must be thoroughly mixed within the population. The territorial nature of coho considered and the fact that marks were often applied by starting at the downstream trap and working upstream until a certain quota (usually about 300-500 fish) had been marked, random distribution of marks is not likely. I therefore considered it best to regard the smolt run as a series of separate samples for the mark ratio, with the total run comprising a weighted mean estimate. Larger runs were thus considered more likely to consist of fish originating from along the entire stream. With such a procedure it was necessary to reject some monthly "samples" prior to the main smolt run as being non-representative. The sample census (C) for each population estimate was therefore not always the same size for each mark type during a particular year.

Reliability

Bias in population estimates results from errors that are largely uncorrectable. They usually stem from violations of the model on which the estimate is based. The degree of departure from the conditions specified is usually unknown. Watt (1968) considered bias the main problem in measurements of populations.

In the study streams the main source of bias probably resulted from differential mortality between marked and unmarked fish. Other sources of error were not so important. The sample for marks involved practically the entire smolt population so is probably accurate. Recruitment to the population during the first spring can inflate population estimates then, but in most years the estimates did not apply to times earlier than June 1.

Perhaps the only way that bias can be detected and corrected is through independent methods of estimation. Each time new marks are applied to the population in the stream, the observed proportions of fish already marked can provide means for additional and independent Petersen-type estimates. Estimates based both on average mark ratios observed during the year and on ratios found during each marking operation were calculated for each mark type. In addition a method was used that makes use of the fact that recovered marks among the smolts afford estimates of survival for each mark type.

Such survivals, divided into the total of recovered marks that were applied earlier, provide estimates of the number of total marks present at the time of application. Combining this information with the observed ratios of total marks in the stream samples, estimates of the population size at the time of sampling can be obtained (Appendix A-5). The assumptions of the model are that mortality is constant within each time period for all marks regardless of when they were applied. Differential mortality between marked and unmarked fish does not bias the estimates in this model.

Estimates of population size by these additional methods (Table A-6) were generally much lower than those of the "regular" Petersen estimate, where the mark ratio was measured in the smolt population. At first glance this would seem to indicate a large upward bias in the "regular" estimates, perhaps due to differential mortality. However the fact that all the additional methods relied on stream sampling for the mark ratio leads me to believe that the relatively low estimates of population sizes thereby obtained stemmed from that common factor. The mark ratios sampled in the streams usually decreased with time and were usually higher than those found among smolts. From 1964 to 1968 14 of 16 mean ratios from Deer Creek, representing the different marks in different years, were significantly lower X^2 tests) among smolts than among stream fish. But of 11 of 17 and 17 of 18 such ratios that were lower from Flynn Creek and Needle

Branch respectively, only 9 and 6 of these respective ratios were significantly lower. Thus although the Deer Creek data seemed to reflect the effects of differential mortality, the results from the other two streams suggests an additional factor. The low values of all population estimates derived from stream ratios points to a common bias in these ratios. It probably stems from the territorial nature of the coho. Marked fish would not tend to disperse, and sampling effort might tend to be expended in the same stream localities time after time due to accessibility of these locations. The result would be a non-random sample for the mark ratio, with the same fish tending to be caught repeatedly. Thus some of the stream ratios were too high to be representative of the population, the population estimates being correspondingly too low. The tendency for stream and smolt mark ratios to differ decreasingly from Deer to Flynn to Needle creeks may be due to more complete sampling in smaller streams. I concluded that the "regular" Petersen estimate of population size, using the mark ratio measured among smolts, was the best of the methods available.

Results

The basic form of the coho population curves has been shown by Chapman (1965), who studied the year classes 1959 to 1962. In general the curves are J-shaped, showing high mortality in spring and summer.

A secondary period of decreasing population size occurs again during late winter. With these curves as models and mindful of the confidence limits, smooth curves were drawn through the Petersen estimates for the year classes 1963 to 1968 (Figure 25, Appendix A-7). The earliest points of the curves represent extensions of the trends in spring and sometimes go through point estimates (not shown) for times earlier than June 1. The estimated net fry input was also considered in drawing the early parts of the curves.

Chapman's (1965) curves start in mid-March at his "anchor point," the estimated total fry input for the season. While such a procedure is useful in producing estimates of survival trends during early life history, it should be recognized that the "anchor point" is qualitatively different from any of the point estimates. Due to fry emigration and mortality, at no point in time could the coho population size have been equivalent to the total of spring fry emergence. Caution should be exercised when estimating population trends between point estimates and such a "lumped" statistic. In reality the population histories should show a rise from zero abundance in February or early March, a peaking in April or May, followed by the general decline that is characteristic of summer.

The population curves of Figure 25 show that the major population size adjustments are usually accomplished by September. The size at which the coho populations began to stabilize tended to increase

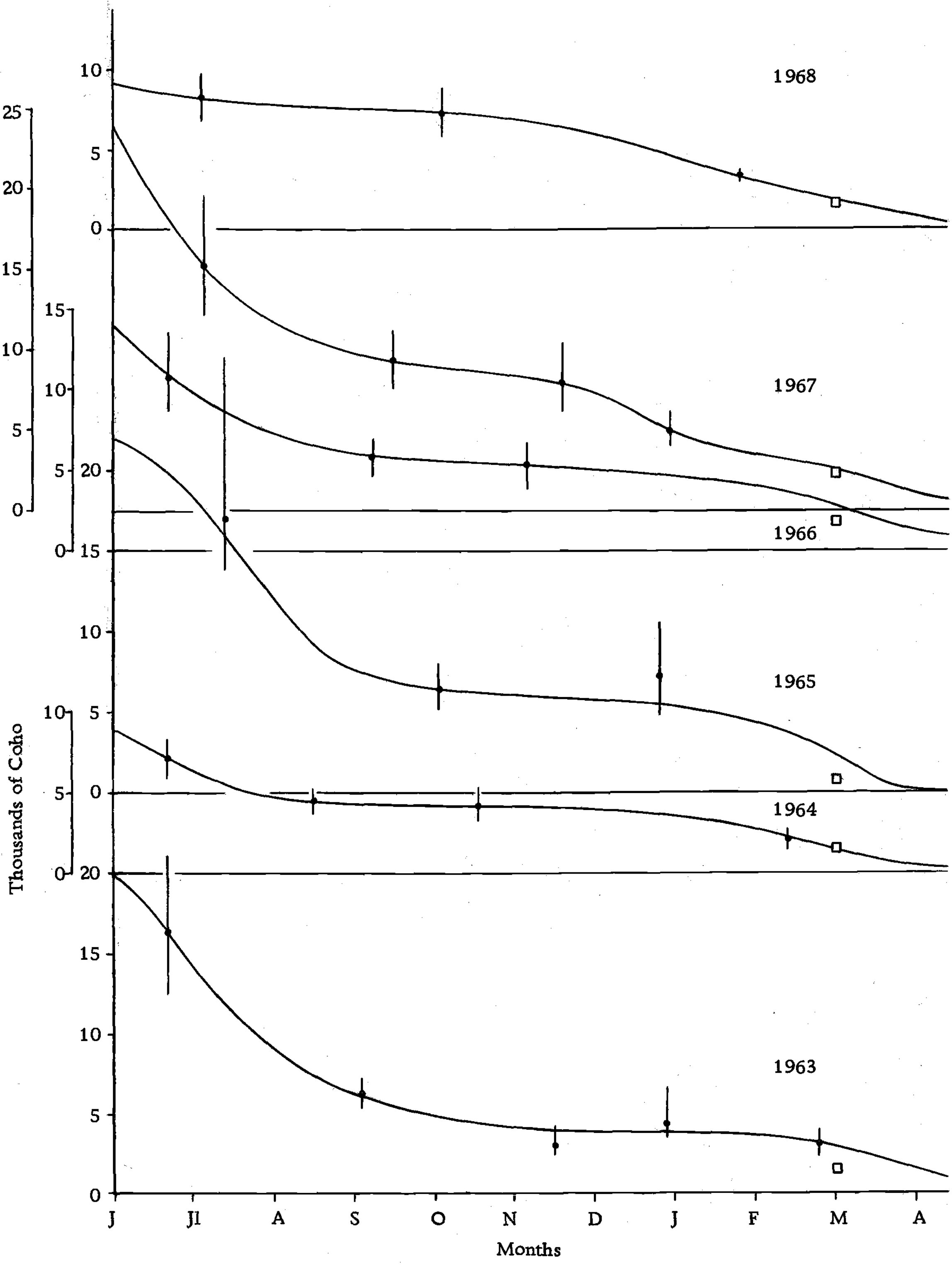


Figure 25a. Deer Creek: Coho population size by year class.

● Point estimate and 0.95 confidence limit

□ Minimum fingerlings present by March 1

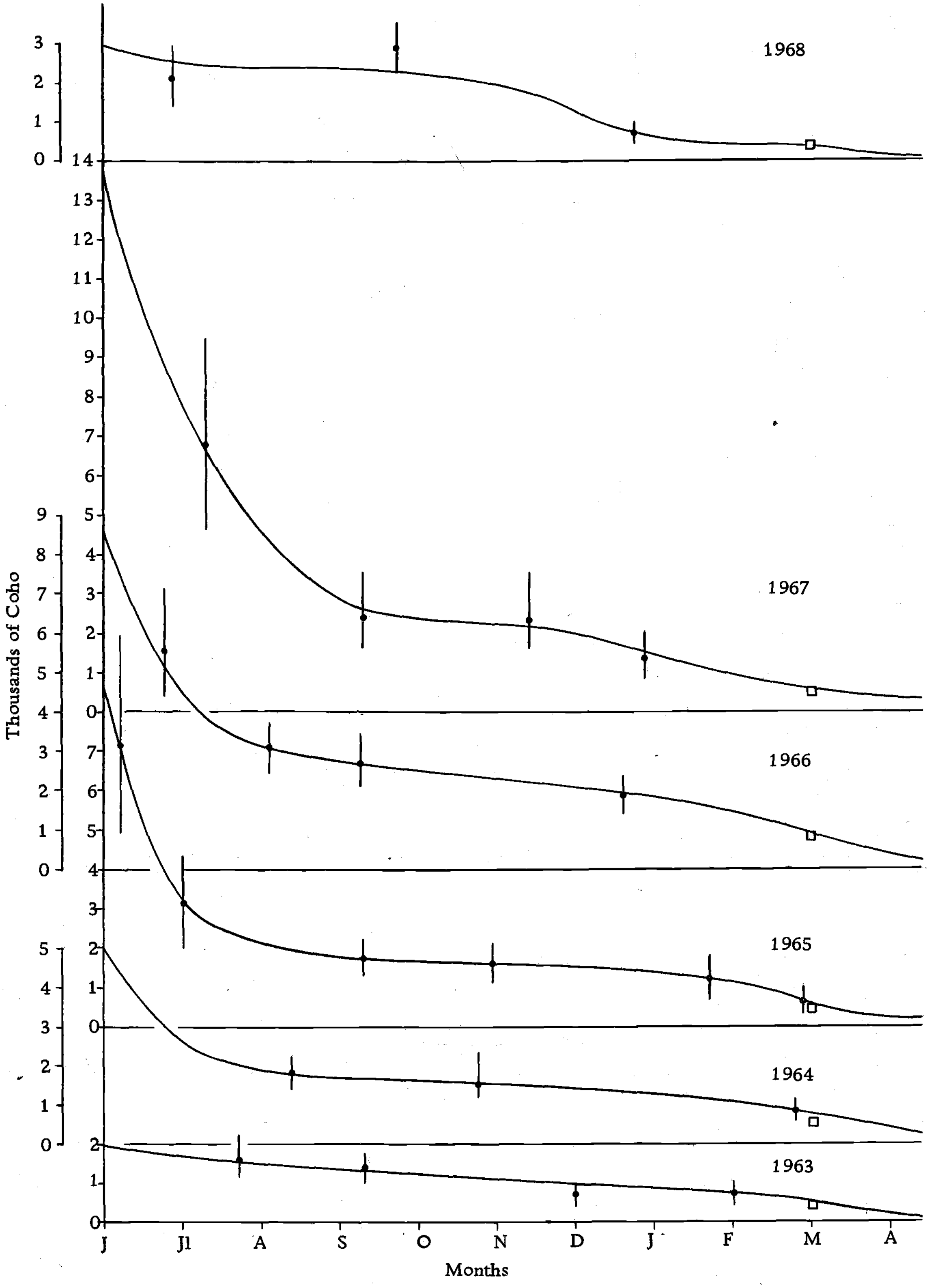


Figure 25b. Flynn Creek: Coho population size by year class. See legend, Figure 25a.

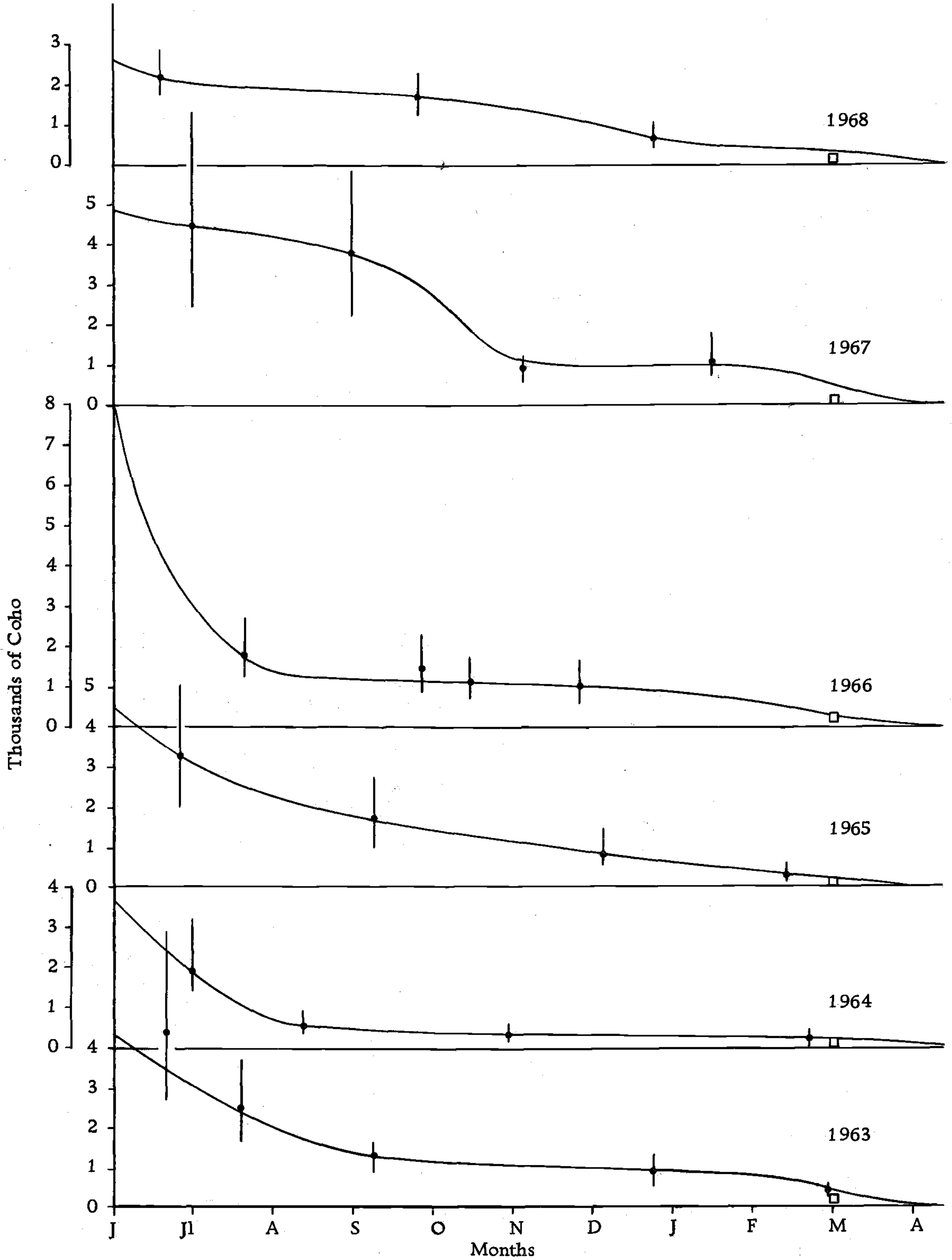


Figure 25c. Needle Branch: Coho population size by year class. See legend, Figure 25a.

from 1963 through 1968. This is best seen in the year-to-year trends in population size at the beginning of each month (Figure 26). This effect was especially noticeable in Deer and Flynn creeks. In Needle Branch the trend was modified in the 1967 year class, which initially approached stability at an anomalously high level in July. The population then decreased rapidly between September and November, remaining stable thereafter until the next spring. This decrease seems to have been the only effect on population size that could have been related to the logging that took place in 1966.

Survival and Mortality During the Residence Phase

Concepts and Methods

Relative survival of members of a population over a period of time is expressed as a proportion, N_{t+1}/N_t. It is often useful to think of this as the probability of survival of the initial population, N_t, over the period t to t+1. The assumption then is that each individual fish has the same probability of survival, independent of the fate and activities of other individuals. Obviously such an assumption is not entirely realistic, especially for coho.

Survival may more conveniently be discussed in terms of its complement, mortality. The usual mathematical description of a population that is changing under the effects of mortality is:

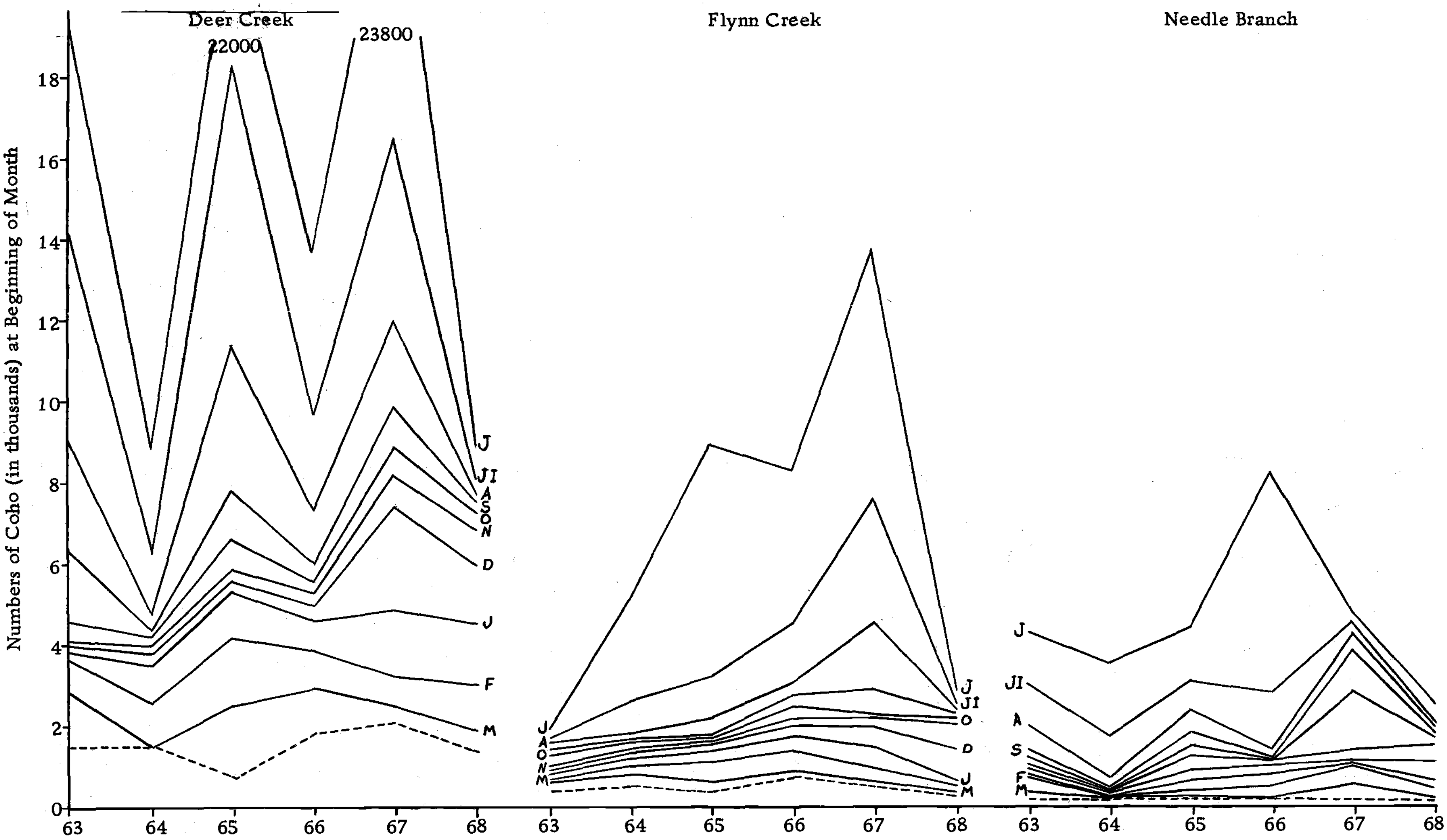


Figure 26. Monthly population trends, June through March, in successive year classes. Lower dashed curve is the total spring output of smolts (minimum present on March 1).

$$N_t = N_o e^{-f(t)t} \qquad (1)$$

where N_o is the initial population size. This equation reflects the tendency of animal populations to change geometrically in time. If the function, $f(t=\Delta t)$ is a constant, i, for any length of time, Δt, then the population will change exponentially during that time period. This period may be of any length, from less than a day to several years. Constancy implies that all instants of time within Δt are governed by $f(\Delta t)=i$, which is then called the instantaneous mortality parameter for that time period. If the population trend is characterized by a series of time intervals, each having separate i's, then the population curve will be made up of a series of exponential curves. In the limiting case when the time intervals themselves are instants, f(t) varies continuously with time and the population curve may take any shape depending on the value of the function f(t).

When f(t) is equivalent to the constant, i, over some interval, Δt, equation (1) becomes:

$$N_t = N_o e^{-it} \qquad (2)$$

which is the appropriate solution to the differential equation:

$$\frac{1}{N}\frac{dN}{dt} = -i \quad . \qquad (3)$$

Therefore the parameter, i, is the instantaneous probability of death in a population expressed in terms of the time unit of the period,

Δt, during which this death rate is assumed constant. It follows then that equation (2) is the model for such a population. Obviously instantaneous parameters should be specified by their appropriate time units. The exponential in equation (2) is equivalent to the discrete change (1 - a) over the same period, where a is the "annual" mortality rate.

In fishery work the curve of a population changing in time is often assumed as being composed of a series of stanzas, each a separate exponential curve. Unless the lengths of such stanzas are sufficiently short, the series of calculated instantaneous mortalities will describe unrealistic exponential curve segments that are concave beneath the curve empirically drawn from the data (Ricker, 1958). I shall assume that such an empirical curve, drawn with some understanding of the biology of the population and sources of error in its measurement, is correct as far as allowed by the data. Particularly when the population is decreasing rapidly, the time stanzas must be increasingly shortened in order that the calculated and empirical curves become suitably matched. The function $f(t)=i_{\Delta t}$ then approaches the continuously varying function, f(t). In the limit the population no longer changes exponentially, even during short time segments, and any assumption of equation (2) is purely for convenience.

The degree of correspondence between empirical and calculated curves is a measure of the accuracy of the calculated mortality rates in describing the former curve. Ultimately this accuracy is a function of the reliability of the empirical curve. The fact that the statistic, i, is referred to as being "instantaneous" refers only to the assumption of constancy of mortality rate within the time interval, Δt. It does not necessarily constitute a more accurate or more detailed description of mortality.

Since the population curves (Figure 25) are not exponentially decreasing curves, except perhaps locally in time, instantaneous mortality rates were calculated directly from the data described by the empirical curves. The instantaneous mortality rate, or probability of death at time t:

$$-i_t = \frac{1}{N}\frac{dN}{dt}, \tag{4}$$

where dN refers to the decrease in population numbers due to death during the infinitesimal time interval dt, may be suitably estimated by direct approximation of the value of the derivative dN/dt. If the time interval Δt is so chosen that the population curve within the interval is for all practical purposes linear, then $\Delta N/\Delta t \cong dN/dt$ at mid-interval and equation (4) becomes:

$$-i_t = \frac{1}{N_t}\frac{\Delta N}{\Delta t} \tag{5}$$

where N_t is either the value of N_t read midway within the interval Δt or its very near equivalent, $(N_t+N_{t+\Delta t})/2$. By this technique the instantaneous rate is estimated without any a priori assumptions regarding population change. The near linear aspects of the data are utilized in the approximation (5), but linearity is not thereby assumed. This method involves discrete calculations from values interpolated between observations, a procedure that may be considered irrational (Chapman, 1966). However I take the position that the empirical curve is the best estimate of average population trend and derived statistics that describe that curve, directly or indirectly, should be consistent with it. If care is taken to make Δt sufficiently small so that the calculated curve accurately portrays the empirical, the proportional change being measured will usually be small enough that the value of i is identical whether calculated from (5) or from the appropriate solution to (2). This results from the fact that an exponential change becomes nearly linear when the percentage change is small, i.e.:

$$\exp(\pm x) \cong 1 \pm x$$

when x is a small quantity.

Results

Instantaneous mortalities were calculated and the trends drawn for the period between June and March (Figure 27), approximately the time span between the recruitment and smolt emigration phases. The instantaneous mortality rate is given as percent dying per week, but it should be realized that this is merely how the rate, actually referring to an instant of time, is expressed. The absolute mortality rate in numbers dying per month is also shown in Figure 27. This

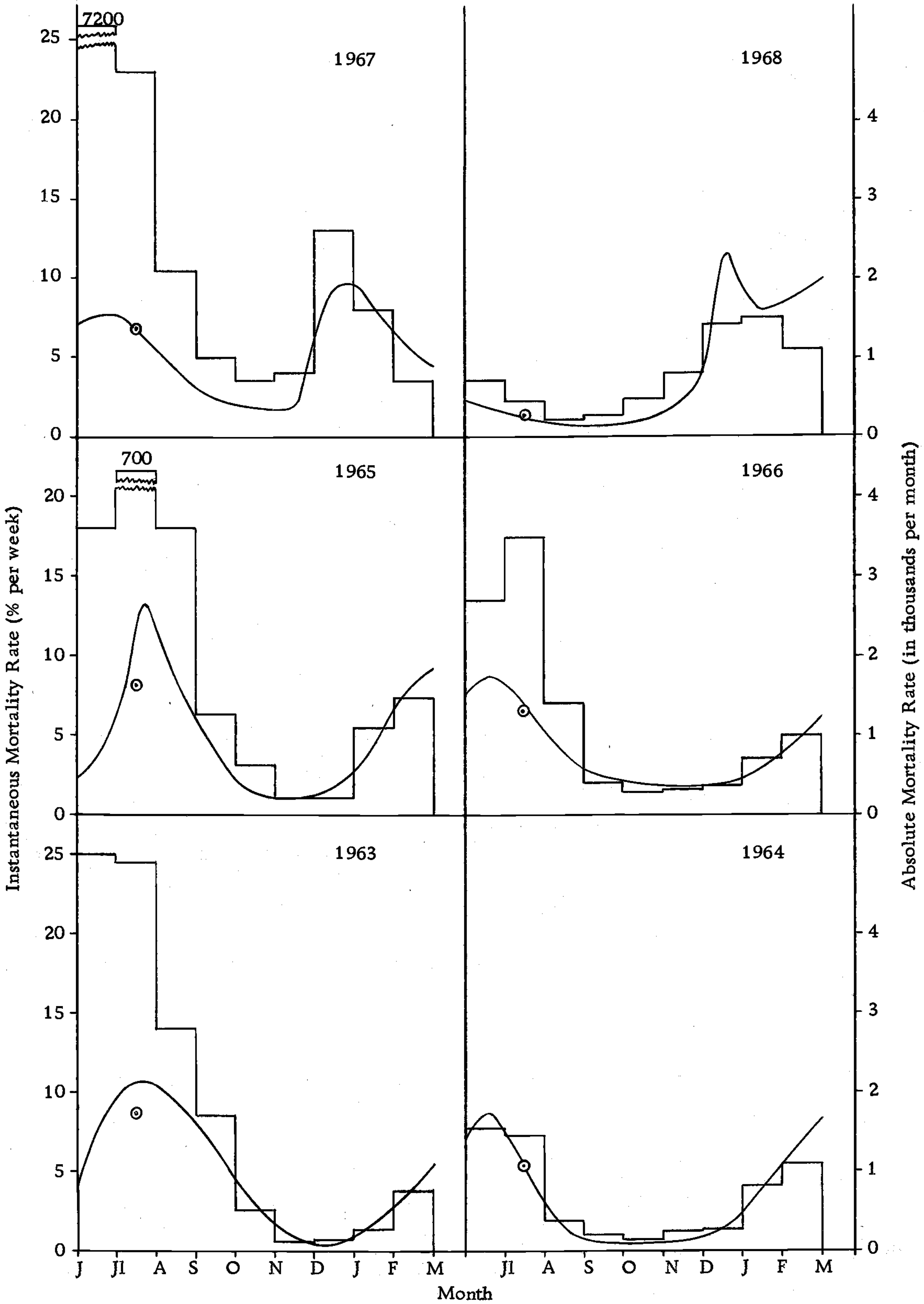


Figure 27a. Deer Creek: Instantaneous (curve) and absolute (histogram) mortality rates by year class. ⊙ = avg. "i", June - September.

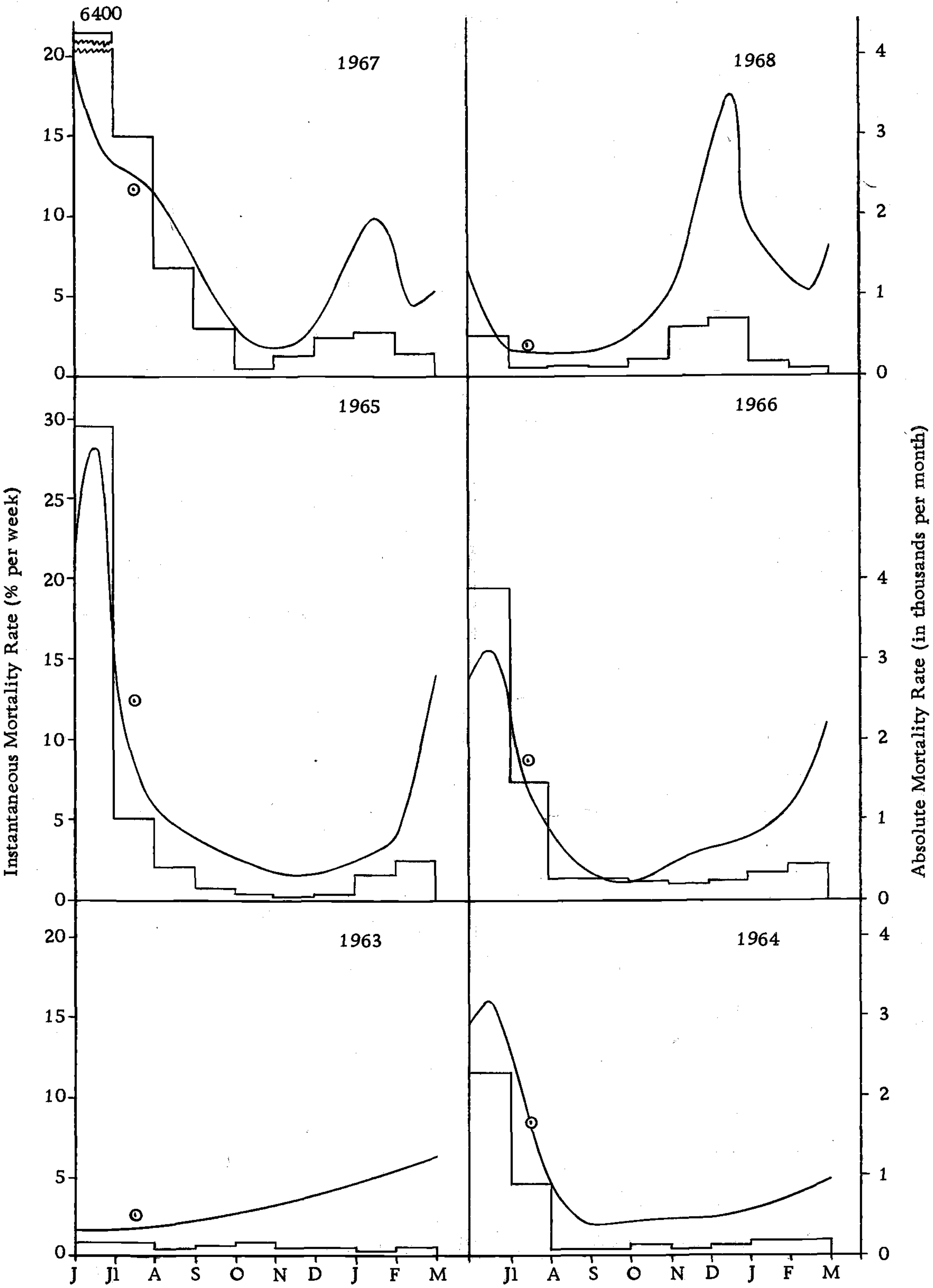


Figure 27b. Flynn Creek: Instantaneous (curve) and absolute (histogram) mortality rates by year class. ⊙ = avg. "i", June - September.

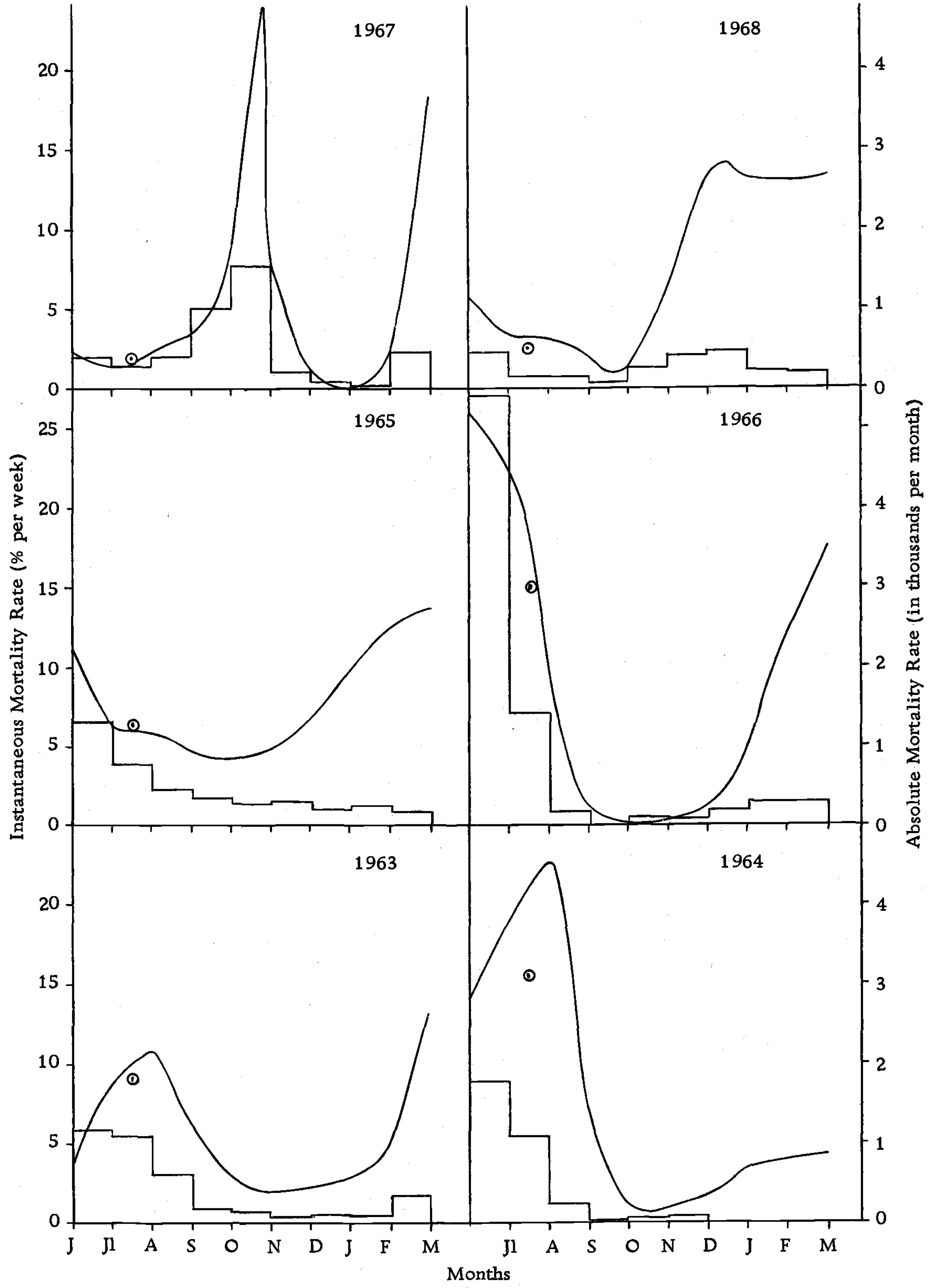


Figure 27c. Needle Branch: Instantaneous (curve) and absolute (histogram) mortality rates by year class. ⊙ = avg. "i", June - September.

rate is helpful in interpreting the timing and the impact of the relative rate processes operating on the populations.

The mortality curves for the 1963-1968 coho year classes in the Drift Creek study streams exhibit a characteristic form. There is generally a rise in instantaneous mortality from some intermediate value in June to a mid-summer peak. The rate then declines to low levels in the fall (usually less than 2%/week). After that, mortality increases slowly until late winter, when it begins to rise steeply. The 1967 and 1968 year classes in all streams, except Needle Branch in 1967, showed a secondary winter peak in instantaneous mortality. The exception reflects the anomalous population curve previously referred to with respect to the effects of logging.

Absolute mortalities (histograms in Figure 27) show the actual mortalities that give rise to the relative mortality curve. The high instantaneous mortalities of summer stem from the large number of deaths occurring then as the population curves drop down to the relatively stable levels of the fall months. There then follows a period of nearly constant and low numbers of deaths per unit time, giving rise to increasing relative mortality. After mid-winter, absolute mortality increases as the smolt migration gets under way. The instantaneous mortalities then show rapid increases that continue into the spring months. The mid-winter and earlier peaks in relative mortality of 1967 and 1968 were associated with periods of increased numbers of deaths that were superimposed on the general pattern of mortality.

Interpretation of the Instantaneous Mortality Curve

Unlike absolute mortality, trends in instantaneous mortality rate are not readily apparent from simple inspection of population size curves. Careful examination of the curves shown in Figures 25 and 27 is therefore worthwhile to properly interpret mortality rates.

It is somewhat surprising to see some of the instantaneous mortality curves rise to a peak during the summer. High initial mortalities declining throughout the summer are more to be expected. Chapman (1961) obtained a mortality curve for the 1959 year class in Deer Creek which similarly peaked in late summer. This led him to suggest that low summer streamflows were important in regulating coho population sizes.

Rising instantaneous mortality rates in early summer (Figures 25 and 27) appear when near constant numbers of death per unit time occur. From equation (4) or (5) one sees that this condition will give rise to increasing relative mortality because the ratio of a constant divided by a decreasing number series must increase. The point of inflection on the population curve, i.e. where the curvature changes and population size begins to decrease less rapidly, determines the approximate position of the peak in relative mortality rate. A great deal of freedom exists in the way curves may be drawn through three points. The greater the magnitude of the initial point relative to the others, the greater will be the tendency to draw a linearly decreasing curve with its inflection close to the second point. This will give rise to increasing relative mortality with a peak late in the season. Chapman's (1961, 1965) population curves start from a point in early spring equivalent to total estimated emergence, assuming 65% survival to emergence. This increased the tendency for rising instantaneous mortality with peaks after mid-summer. My curves (Figure 25) start from the estimated population size in June, the end of the recruitment season, and assume a survival to emergence of only about 30%. Thus the mortality rates of Figure 27 tend to peak before mid-summer. Obviously the shape of the peaked instantaneous mortality curve of summer is subjective and only partly determined by the distribution of data points. Furthermore it is apparent that consideration of relative mortality rates without also examining absolute mortality may be misleading with regard to the processes involved in population trends.

Although the population curves of Figure 25 were drawn with the fact in mind that each curve must start from zero near the end of February and maximize during the next three months, sources of error in mortality estimation remained. If data points on population size extended back into the recruitment phase, probably they would not describe the dome-shaped, true population curve. Such data points would be biased upwards because of dilution of the mark ratio through recruitment. Therefore population curves through data points within the recruitment phase would be too steep, causing inflated mortality estimates. Even if the true population curve were described, the recruitment effects responsible for the dome would bias the mortality estimates. In either case a peaked relative mortality curve during the summer would likely result. I partly avoided these problems by considering only the post-recruitment life history, after June 1. Nevertheless the effects on relative mortality of small changes in shape of empirically drawn population curves, especially important at the high population densities of early summer, remained a serious problem to objective description.

Effective Instantaneous Mortality, June - September. These difficulties suggest that an average or effective instantaneous mortality for the period June to September would best measure mortality rate then. Assuming therefore the model described by equation (2), where i is considered constant during Δt = June-September, instantaneous mortality rates were calculated for each stream for the year classes, 1963-68 (circled dots over July 15, Figure 27). The summer peaks in mortality rate (Figure 27) are therefore considered artifacts of the particular empirical curves of population size that were drawn as decreasing nearly linearly during that period. The averages of these effective instantaneous rates, June to September for the years 1963-

1968, were 5.7, 6.6, and 6.7%/week for Deer, Flynn, and Needle creeks respectively.

Seasonal Characteristics. The higher mortalities of summer occur as the populations adjust down to their levels of relative stability in the fall. The coho populations of 1963-1968 decreased by an average of 56% through summer mortality. Territoriality, aggression, and social structuring are important activities within the coho populations during this season. Such activity must be very important in mediating mortality processes. Intraspecific agonistic behavior in coho salmon probably measures and eliminates that portion of the population that is in excess of the stream's carrying capacity for the species. The hierarchial structuring of coho society ensures that the less fit individuals continue to be eliminated during adjustment. This kind of mortality operating on excess portions of populations is considered important among vertebrates, especially birds and mammals (Errington, 1946). It corresponds to Ricker's (1952) type C predation.

The cause of this mortality is difficult to assign. Predation by cutthroat trout and larger coho juveniles may be major factors. Lowry (1965), however, did not find evidence of heavy predation on coho by the cutthroat trout in these same streams. Small coho are occasionally seen in the process of being eaten or digested by cutthroat trout, coho smolts, and crayfish, but actual deaths are rarely observed. Even in carefully controlled experimental stream channels in British Columbia the specific causes of coho mortality could not be assigned (Fraser, 1969). The evidence from the present study indicates an instantaneous mortality rate of about 6%/week for the period, June to September. If 10,000 coho fry were in a 4,000 ft (1219 m) stream section, this would amount to an average of about 2 fish dying per 100 ft (30.5 m) interval per day. The chances of observing deaths are therefore slight.

After September the coho populations tend to decline at a slow and steady absolute rate until mid-winter. This results in a gradual increase in the instantaneous mortality rates for that period. The population curves suggest that a small and constant number of fish are dying per unit time interval. This condition would occur if a small and limited number of predators could take no more than a fixed number of prey per unit time. The predators' food handling capacity would essentially be swamped by their prey. This kind of predation corresponds to Ricker's (1952) type A predation. Elson (1962) has shown that kingfishers (*Megaceryle alcyon*) exhibited this kind of predation and were not important sources of mortality to Atlantic salmon. Perhaps in the Drift Creek streams a few predators, including the kingfisher, are relatively important in determining the mortality pattern between fall and winter.

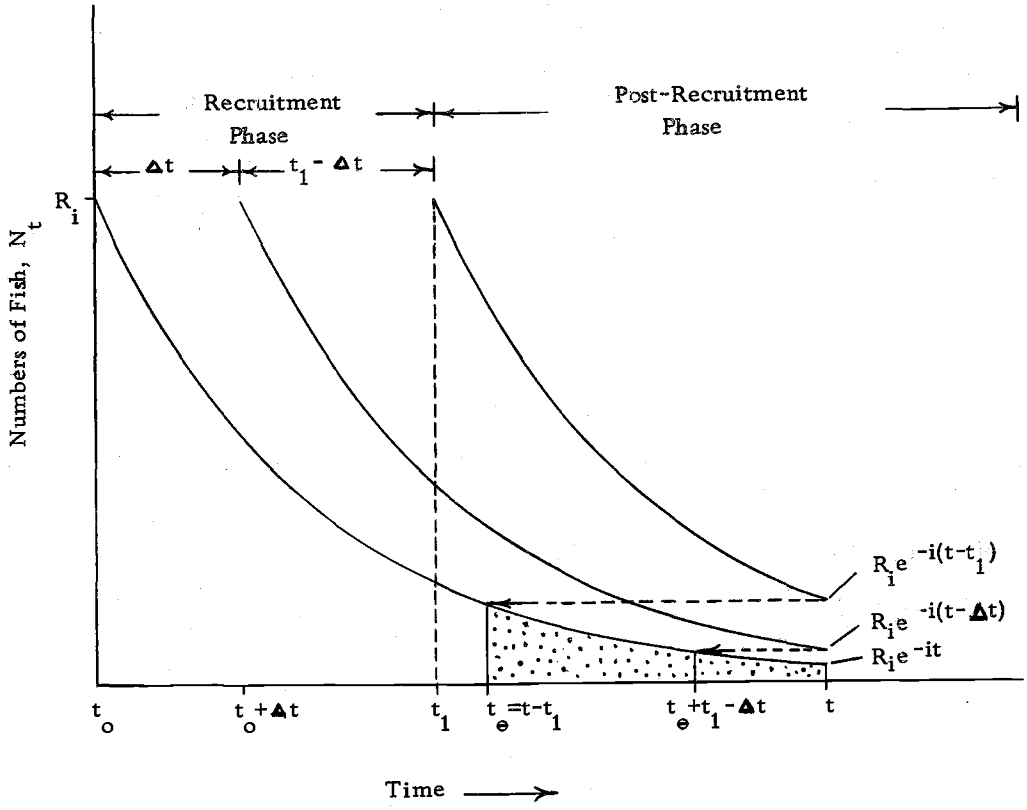
With the approach of spring, mortality rates increase again. These increases continue into the smolt migration phase, and are probably associated with increased vulnerability as the coho leave their accustomed places of residence. Mortality rates shown in Figure 27 for February are likely too high in many cases, being influenced by the dipping of the population curves in spring (Figure 25) that reflects mostly emigration rather than mortality. Chapman (1965) was able to set discrete drops, representing emigration, in some of his curves, thus producing a series of more gradual declines. Without more information on population size in the spring, it is difficult to separate the pattern of smolt emigration from mortality.

Survival and Mortality During the Recruitment or Colonization Phase

Methods

Mortality rates during the recruitment phase of coho life history cannot be estimated directly because both mortality and recruitment are occurring simultaneously over this 3 month period (March through May). Only if each recruited cohort of fry were to decline linearly with time over this period would it strictly be proper to lump the total net recruitment and consider it to have occurred in mid-season. Survivals could then be calculated by the usual methods.

A solution to the problem of estimating mortality under conditions of continuous recruitment may be approached through geometrical considerations and some simplifying assumptions. First assume that recruitment occurs continuously within the period t_o to t_1 and at a constant rate equal to $R/(t_1-t_o)$, where R is the total net recruitment, i.e. emergent minus emigrant fry from March through May. For a stream like Deer Creek, this would correspond to an average instantaneous recruitment rate equivalent to about 230 emergent fry/day. Coho fry do not emerge continuously from the gravel, so one may conveniently think of this constant rate as being equivalent to 230 fry emerging at discrete intervals, say at midnight of each day. Now assume furthermore that each cohort of fry, recruited throughout the March through May period, declines through natural mortality at an average or effective constant rate (instantaneous mortality rate) equal to i expressed in the same time units, i.e. the interval t_1-t_o. The recruitment rate, $R/(t_1-t_o)$ will henceforth be called R_i for simplicity, the i referring to its instantaneous nature. R_i may be considered the average number of fry recruited at each instant, expressed in terms of the standard time interval. Now the population size of the first cohort recruited at time $t_o=0$ will be equal to $R_i\exp(-it)$ at some later time t, where $t > t_1$, the end of the recruitment period (see Figure 28). Similarly the cohort recruited at the end of the recruitment phase will be reduced to $R_i\exp(-i(t-t_1))$ at time t. And the cohort recruited at



With continuous and constant rates of recruitment (R_i) and mortality (i), population size at time t (N_t) after the recruitment phase is:

$$N_t = \int_{t_e}^{t} R_i e^{-iT} dT$$

equivalent to the stippled portion under the lower curve.

Figure 28. Geometric interpretation of the relationship between population size, mortality, and an extended recruitment period.

some intermediate time $t_o+\Delta t$, where $t_o < (t_o+\Delta t) < t_1$, will be equal to $R_i\exp(-i(t-\Delta t))$ at time t. Now notice in Figure 28 that these three population sizes at time t may be transferred as equivalent ordinates of the lowermost curve for the times t, $t_\theta + (t_1-\Delta t)$, and t_θ for recruitment beginning at times t_o, $t_o+\Delta t$, and t_1. This is the well-known result that under steady state conditions of recruitment and mortality, the relative strengths of recruitment classes observed at time t are equally described by the historical record of any particular class of recruits observed at each successive recruitment interval. Under the conditions of continuous recruitment assumed one sees that the sum of all surviving cohorts recruited between t_o and t_1 and observed at time t will be equivalent to the area under the lower curve from t_θ to t. And since

$$R_i\exp(-i(t-t_1)) = R_i\exp(-it_\theta)$$

t_θ must be equal to $t-t_1$. Therefore the population size at time t, i.e. N_t, may be expressed

$$N_t = \int_{t-t_1}^{t} R_i e^{-iT}\,dT = \frac{R_i}{i}\left(e^{-i(t-t_1)} - e^{-it}\right). \qquad (6)$$

When $t_1 = 1$, R_i is simply designated R and the equation becomes

$$N_t = \frac{R}{i}\left(e^{-i(t-1)} - e^{-it}\right) \qquad (7)$$

the general relation between survivors and recruits.

A useful form of (7) is when $t=t_1=1$. Then

$$N_1 = \frac{R}{i}\left(1 - e^{-i}\right) = R\,\frac{a}{i} \tag{8}$$

where a is the "annual" mortality. If the ratio $N_1/R = a/i$ is known or estimated, the value of i may conveniently be found from Ricker's (1958) Appendix II where corresponding values of a/i and i are tabulated.

Equation (8) proves to be the same as that given by Ricker (1958) and Beverton (1954) for the number of surviving recruits at the end of a period of continuous recruitment under equilibrum conditions. Beverton's approach is nicely straightforward: Let recruitment R and mortality i both proceed at a constant rate over a given period t_o to $t_1 = 1$. The population process may then be described by the differential equation:

$$\frac{dN}{dt} = -iN_t + R \tag{9}$$

the appropriate solution for which is:

$$N_t = \frac{R}{i}\left(1 - e^{-it}\right). \tag{10}$$

At the end of the period when t=1, equation (10) becomes

$$N_1 = \frac{R}{i}\left(1 - e^{-i}\right) = R\,\frac{a}{i} \tag{11}$$

and is thus seen to be a special case of (7). For at any time t greater than t=1, when recruitment is over, population size is:

$$N_t = \frac{R}{i}\,ae^{-i(t-1)} \tag{12}$$

which is equivalent to equation (7).

Results and Conclusions

The ratio, a/i, was estimated by the ratio $\hat{N}_1/R$ where $\hat{N}_1$ is the estimated population size on June 1 (Figure 25) and R is the estimated net input of fry (Table 7). The corresponding instantaneous mortality rate i for the period March through May was then taken from Ricker's (1958) Appendix II. Unfortunately the necessary data were not very reliable, as inferred from the fact that the estimated population size in June was usually greater than the estimated net fry input in Flynn Creek and Needle Branch. I believe this is due to systematic bias in estimating fry emergence. On Deer Creek however the data appear reasonable for the year classes 1964 to 1968. The estimated instantaneous mortality rates during the recruitment phase of those year classes ranged from 3 to 8.7% per week. In 3 of the 5 year classes the rate for the recruitment period was greater than that of the summer phase. The average instantaneous mortality rate, 5.7%/week, was the same for both recruitment and the summer phases in Deer Creek (Table 8). For Flynn Creek and Needle Branch the best that can be said is that the $\hat{N}_1/R$ ratio was likely greater than 50%, i.e. i was less than 12.4%/week. These data suggest that instantaneous mortality is about the same over the period March to September, at least in Deer Creek. I believe it very likely that instantaneous mortality rates are at least equally high during both recruitment and summer phases in each stream, with i actually tending

Table 8. Instantaneous mortality rates, i(in % per week), during the recruitment phase (March - June) and the summer phase (June to September). Ratio of "annual" to instantaneous mortality (a/i) estimated by ratio of June population to net recruitment (N_1'/R).

Year Class	N_1/R = a/i during recruitment Deer	Flynn	Needle	i during summer Deer	Flynn	Needle
63	b	b	b	8.60	2.62	9.04
64	.618	b		5.38	8.36	15.50
65	.777	b		8.10	12.40	6.36
66	.711	b		6.46	8.69	15.00
67	.602	b	.676	6.84	11.70	1.89
68	.830	b	.364	1.38	1.93	2.55
Mean a/i	.708		7.50			
Mean i	5.72		$<$12.4	5.70	6.60	6.70

b) $N > R$

to decrease during the summer. The overall average survival has previously been shown to be 44% for the summer period from June to September. Assuming the same survival rate to be operating during the recruitment period from March to June, about 1-(.44) (.44) = .806 or about 80% of the recruits die by September.

Survival of Emigrant Fry

A considerable proportion of juvenile coho residing in stream areas below the downstream traps must have emigrated there from the upstream spawning areas during the spring dispersal period. Therefore to attempt an estimate of their overall stream survival, thereby obtaining an idea of their importance to the biological success of the coho stocks is of interest. Emergent fry in numbers approximately 25% of total emergence in Deer Creek and greater than 50% in Flynn and Needle creeks emigrate beyond the downstream traps each spring. The potential of these fish to be important components of year-class success is therefore great. Evidence considered in this paper would suggest that these coho represent a dispersal from the spawning areas to downstream habitats and therefore remain important to the stocks as a whole.

Methods

Estimates of survival among emigrant fry may be obtained through a very simple model that describes the temporal distribution of survival. Note that Deer Creek flows into the upper section of Horse Creek, and Flynn Creek into the upper section of Meadow Creek, which then joins Horse Creek (Figure 1). Needle Branch flows directly into Drift Creek, a large stream that is qualitatively different from the small Horse and Meadow creeks. Now assume that survival conditions for coho in those upper sections of Horse and Meadow Creeks are approximately the same and can be described by the common survival parameter s_s. This is the overall survival from fry emergence to the time of emigration as smolts. Further assume that when the smolts enter the ocean, they are subject to a common ocean survival, s_o, lasting until the survivors reappear as adults at the spawning grounds. The female spawners may be considered the true survivors of the female half of their year class, with little straying being involved. There is evidence that the male to female ratio in the fry and smolt populations is 50:50. The following linear equation can then be written for coho of a given year class:

$$0.5(S + Ms_s)s_o = F \qquad (13)$$

where: 0.5 refers to the 50:50 male to female ratio in the juveniles

S = numbers of smolts

M = numbers of emigrant fry

F = numbers of returning female spawners

s_s = common stream survival, a constant

s_o = common ocean survival, a constant.

Now writing separate equations for Deer and Flynn Creeks, the simplest system of two simultaneous equations in two unknowns is obtained:

$$\left[0.5(S + Ms_s)s_o = F\right]_{\text{Deer}}$$

$$\left[0.5(S + Ms_s)s_o = F\right]_{\text{Flynn}} \qquad (14)$$

for which solutions can easily be found (under the constraints that $s_s \geq 0$ and $s_o > 0$). Working with female fish only, i.e. 1/2 the numbers of smolts and emigrant fry, the expressions for s_s and s_o become:

$$s_o = \left(F_d - \frac{M_d}{M_f} F_f\right) \Big/ \left(S_d - \frac{M_d}{M_f} S_f\right)$$

$$s_s = \left(F_d - S_d s_o\right) \Big/ M_d s_o \qquad (15)$$

where the subscripts d and f refer to the streams Deer and Flynn.

Results and Conclusions

The data from the year classes 1960-1967 in Deer and Flynn Creeks were used in the analysis. Only 4 sets gave positive survival values, perhaps indicating that the relatively small numbers of returning females are importantly affected by local, short-term mortality factors. The average ocean survival (s_o) obtained was 4.01%. This compares with 3.11% ocean survival calculated directly from the adult female:smolt output ratio. This latter figure is already expected to be biased upward since smolts from populations below the traps are not considered. Therefore 3.11% ocean survival was taken as the better of the two estimates. The average stream survival (s_s) of the emigrant fry population came out to be 21.9%. This figure may be compared with estimates of survival in the resident populations above the downstream traps, calculated as the ratio of smolts to June 1 population size. For Deer and Flynn creeks those survivals average 15.6 and 14.0% respectively (data from Table 1 and Appendix A-8).

An estimate of stream survival for the Needle Branch emigrants was obtained by substituting the ocean survival, 3.11%, into the expression (13) written for that stream. The average stream survival (s_s) obtained was 7.65%. This figure is comparable to a mean survival of 7.3% in the resident population calculated as before.

The results of this exercise, utilizing a simple scheme of survival distributions, are consistent with the concept that emigrant fry are primarily dispersed, rather than competitively displaced. The latter implies a displacement to less suitable habitats downstream. Estimates of stream survival obtained through the model suggest that coho fry emigrating beyond the downstream traps in the spring suffer approximately the same mortality during the year as the populations that remain behind. I believe the emigrant fry are an important extension of the coho stocks beyond the spawning grounds.

Mortality and Population Regulation

The high mortality of the spring and summer periods is obviously the major factor reducing the large and variable initial population sizes of coho to the relatively stable levels observed the following spring. If mortality during the spring recruitment phase is similar to that of the summer phase, then the data would indicate that about 80% of the original recruits die by September. Any such high mortality, if continuous until the time of smolting, could in itself account for the great reduction in the disparities of initial year-class strengths observed. However the fact that this mortality occurs in the spring and summer when population size is greatest, the observation that population sizes are reduced to relatively stable levels by September, and the implication (Figure 2) that survival increases at lower population densities all suggest strongly a density dependent mode of action. This implies that the mortality schedule is a mechanism that operates to reduce excessive population sizes to within limits imposed by the stream's capacity to rear coho.

Beverton and Holt (1957) developed a population model in which the instantaneous mortality rate increased linearly with population density. A density independent factor was also a component of the mortality. Their model resulted in a converging of different initial population numbers such that the relative difference between the numbers continuously decreased. The greater was the importance of the density dependent component of mortality, the more recruitment to some later stage became independent of initial population size. The predicted results from their model are descriptive of the population trends observed in the Drift Creek study streams. One may expect therefore that the high initial mortalities observed during spring and summer there are similarly density dependent.

Relationships between average instantaneous mortality rate, June to September, and estimated population size in June indicate that this is the case (Figure 29). In Deer and Flynn creeks, at least, mortality rate increased positively with population size, hence is density dependent. The Needle Branch data suggest that density independent environmental factors may be relatively important.

There appears to be a curvature in the Deer and Flynn Creek data (Figure 29). Le Cren (1965) has shown for populations of *Salmo trutta*, which is territorial like the coho, that the curve of instantaneous mortality is a linear logarithmic function of population density. A similar relationship may hold in the study streams.

Although the data from Needle Branch are not very convincing, the mortalities in Deer and Flynn creeks are definitely density dependent. I believe that if more accurate data on early season population size were available, all the streams would demonstrate density dependent mortality. Mortalities are high during the early summer and

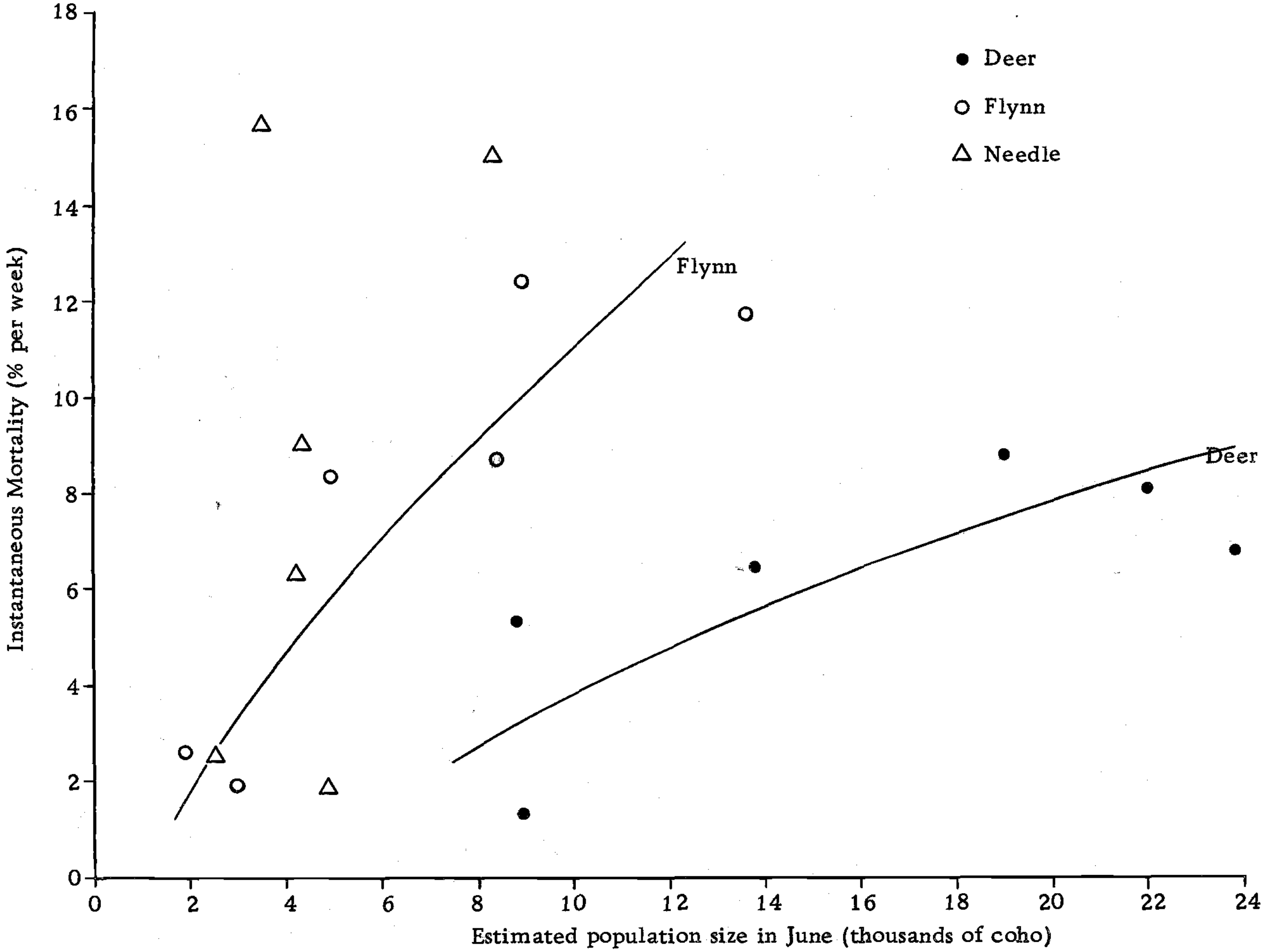


Figure 29. Relationship between instantaneous mortality rate during the period June to September and the population size in June; data from 1963-1968 year classes. Curves fitted by inspection.

during those months much intraspecific behavioral interaction occurs among the resident coho. Thus behavior may well be of major importance in the mortality processes that bring about the population regulation. The result is a relatively constant smolt output from widely varying initial year-class strengths.

Other Population Adjustments

Not all the population adjustment after the spring recruitment phase can be ascribed to mortality. Some of the population decline continues to result from emigration. Fingerlings can be expected to pass through the downstream traps during all months of the year. The numbers are least between mid-summer and mid-fall. A rather substantial emigration then occurs during the late fall and winter months (Appendix A-4. A small peak in emigration is thus produced, preceding the main smolt emigration to occur during the coming spring. The cause of the fall-winter emigration peak is not understood at this time. It was suggested in a previous section that after the summer growth period, some fish might emigrate because they find their territories no longer spatially adequate.

GROWTH AND RELATED POPULATION PROPERTIES AFFECTING YIELD

Growth and development are a necessity for the biological success or continued survival of any species. Growth in the coho populations, the related properties of biomass and production, and their relationships to yield are therefore of primary interest in this study, particularly with regard to watershed modification induced by logging in 1966.

Growth and Biomass

Methods

Data for growth studies were obtained from samples of coho taken in the study streams at various times during the year. Fork lengths of the fish in each sample were measured and smooth curves drawn through time plots of the mean lengths in each sample. The average length at emergence, as smolts, and the 95% conficence interval of each sample mean were considered in the construction of these growth curves. Confidence intervals were calculated from measures of standard deviation of lengths in each sample (Appendix A-9).

Conversion of lengths to weights provided data for estimating weight growth. The relationship between length (L) and weight (W) is expressed by the allometric formula $W=aL^b$, where a and b are constants. Linear regressions were fitted through the combined data of logarithms of length and weight for each year class, representing samples of individual lengths and weights taken at various times during the year to obtain estimates of the constants (Table 9). A plot of the weight-length regression on log paper yields a convenient method of estimating the weight corresponding to any given length, based on the best fit to the data.

Slopes (b) of the linear regressions of log weight on log length differed significantly (covariance tests) between years. Separate regressions for weight estimation were therefore used for each year class. The interaction between relationships of length and weight growth make it difficult to ascribe meaning to the annual differences in the derived constants, a and b, as Richards and Kavanaugh (1945) have pointed out.

Because of the non-linear weight-length relationship, mean weights will be underestimated if obtained by applying the allometric formula to mean lengths. Pienaar and Ricker (1968) have shown a convenient method of calculating unbiased mean weights. They show that the expected value of weight

$$E(w) = \int_{-\infty}^{\infty} ax^{b} f(x)dx \qquad (16)$$

where f(x) is the normal probability density function and x is length, may be calculated as

Table 9. Statistics for the relationship between length (L) in mm and weight (W) in grams of the form: $W = a L^b$.

	Deer		Flynn		Needle	
Year Class	a*	b	a*	b	a*	b
1963	13.26	2.95766	14.31	2.94556	5.59	3.16255
1964	5.04	3.18914	6.48	3.12736	22.97	2.85386
1965	42.64	2.69307	87.96	2.52285	249.23	2.25476
1966	59.24	2.64567	36.23	2.74794	8.05	3.07863
1967	122.33	2.39523	3.40	3.30250	6.23	3.11904
1968	16.30	2.90140	6.48	3.12869	12.06	2.97532

* Multiply these values by 10^{-6}.

$$E(W) = a(\bar{x}^b + a_1\bar{x}^{b-2}s^2 + a_2\bar{x}^{b-4}s^4 + a_3\bar{x}^{b-6}s^6 + \ldots) \qquad (17)$$

where a_1, a_2, and a_3 are constants and s is the standard deviation of lengths. The difference between E(W) and $a\left[E(x)\right]^b$ as a fraction of the latter (denoting the usual method of calculation) is

$$a_1 \frac{s^2}{\bar{x}^2} \; . \qquad (18)$$

Values of the constants a_1 and a_2 are given in a table as a function of b. The average b value in the Drift Creek study streams is about 2.9 (Table 9). For an average coho of about 50 mm in June and 85 mm in April the variances of length are approximately 42.2 and 81 respectively. Substituting these values into equation (18) and using $a_1 = 2.75$ from Pienaar and Ricker's table, the errors in weight estimates amount to 4.65% in early summer and 3.08% the following spring. The corresponding weight corrections are +0.064 and +0.202 grams. The weight estimates derived by conventional methods were therefore judged accurate enough for the purposes of this study.

Computations of growth in weight and biomass were made from the estimated trends in average weight and population size (Appendix A-8). Biomass was calculated simply as average size of the coho population times the average individual weight during a time period. Growth in weight (g) was expressed in relative terms as the proportional increase rate over the period Δt

$$g = \frac{1}{\bar{w}\Delta t} \; \frac{\Delta w}{\Delta t} \; .$$

Since $\Delta t=2$ weeks was approximately a linear interval for weight change, g estimates the instantaneous growth rate for the period:

$$g_{\Delta t} = \frac{1}{w}\frac{dw}{dt} .$$

Growth Rates

In general, relatively fast growth occurs in summer and again the next spring with slow growth between (Figure 30). Between June and the next April the average coho increases in length by about 45 mm. The second period of relatively fast growth may occur in mid-winter. The beginning of this period is much more variable than the ending of the summer growth period, which nearly always falls in September (indicated by bunching of monthly trend lines). Except for the growth rate of the 1963 year class in Flynn Creek (a very sparse population resulting from 2 spawning females), year-to-year trends in growth were similar in each stream, suggesting a common factor affecting the populations. This factor may be population size. It has already been mentioned that trends in spawning input, and hence initial population size, tend to be parallel among the three streams. If the population strengths in June (Figure 25) are compared with the mean lengths achieved through growth by September (Figure 30), an inverse relationship may be seen, at least in Deer and Flynn Creeks. The relationship is less clear in Needle Branch, suggesting again that environmental factors extrinsic to the populations are relatively important in that small stream.

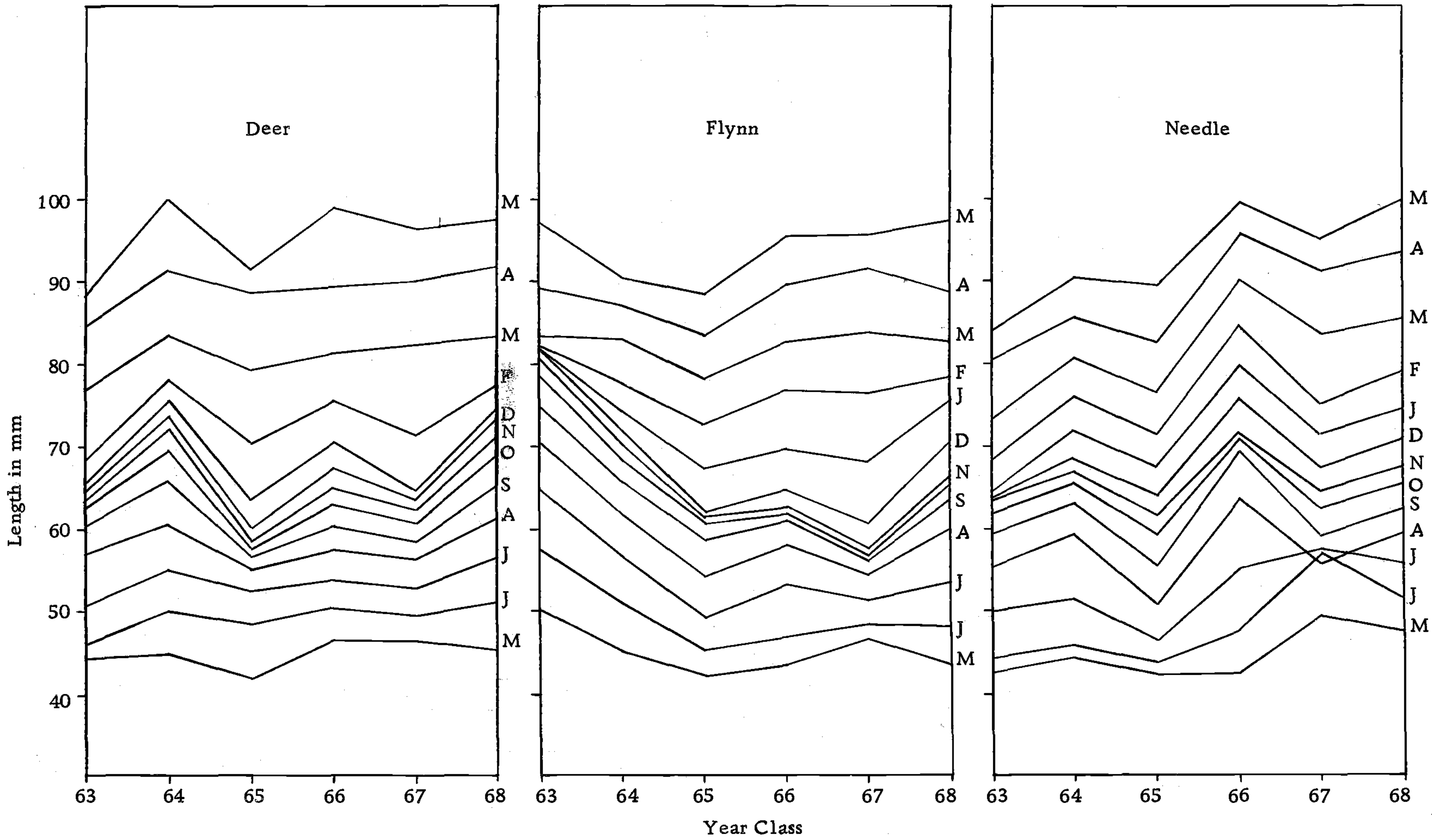


Figure 30. Growth in length of coho showing trends in average monthly lengths, May through May, for the 1963 through 1968 year classes.

Between-year differences in average length of the fish may be due in part to differences in average age of the fish. The average age is dependent upon the fry emergence pattern for each year. An apparent decrease in average length occurred during August 1967 in Needle Branch. This seemed partly to have resulted from greater mortality among the larger fish, associated with high stream temperatures in the unshaded stream.

Growth in weight, reflecting the condition of the fish, is another important aspect of developmental history. Relative rates of growth in weight (instantaneous growth rate, g) reflect the length data in that there is in general a summer and a spring period of relatively fast growth separated by a fall and winter period of slow growth (Figure 31). The instantaneous growth rate g is expressed as a percentage change in weight per two weeks and averaged about 10% of body weight per 2 weeks. During the period of slow growth g may approach zero. In the summer fast growth period g may exceed 20%. Values of g tend to decline steadily throughout the summer. In some cases the growth rate of the following spring exceeds that of the summer period. In general the overall level of relative growth rate did not change much from year to year and between streams. Note that the scale for g in Figure 31 does not change among streams whereas the scales for biomass and production rate do.

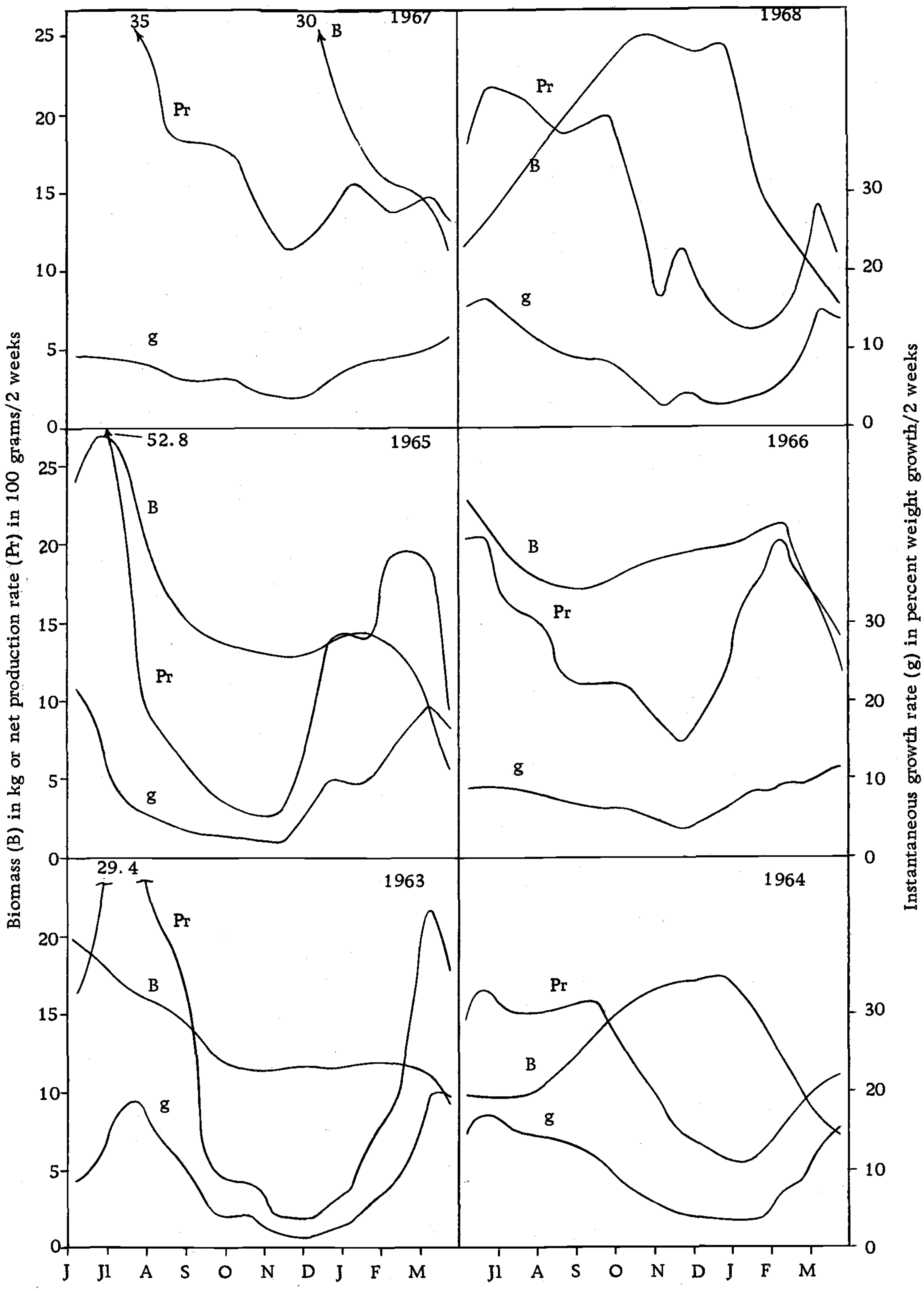


Figure 31a. Deer Creek: Instantaneous growth rate (g), biomass (B), and net production rate (Pr) by year class.

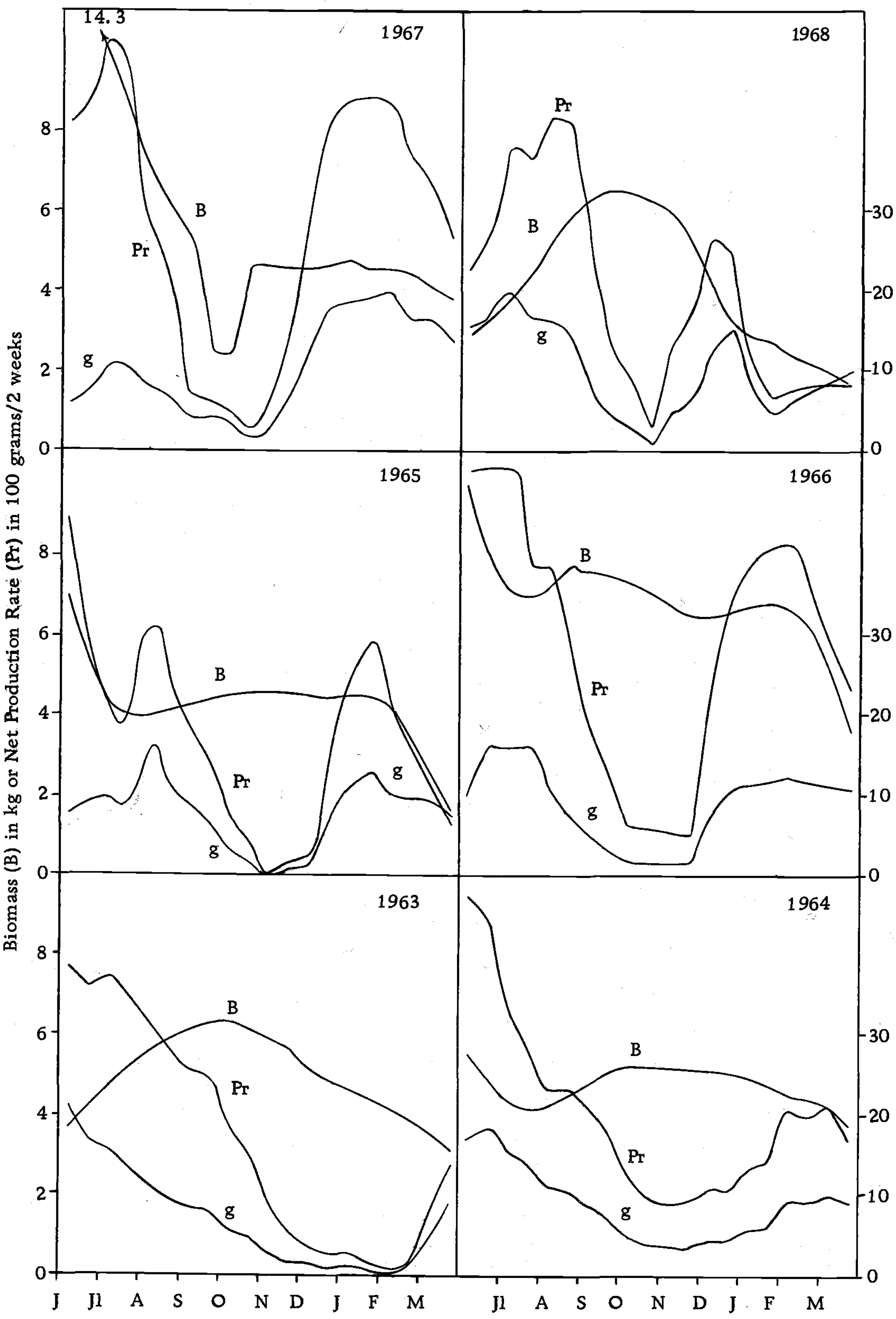


Figure 31b Flynn Creek: Instantaneous growth rate (g), biomass (B), and net production rate (Pr) by year class.

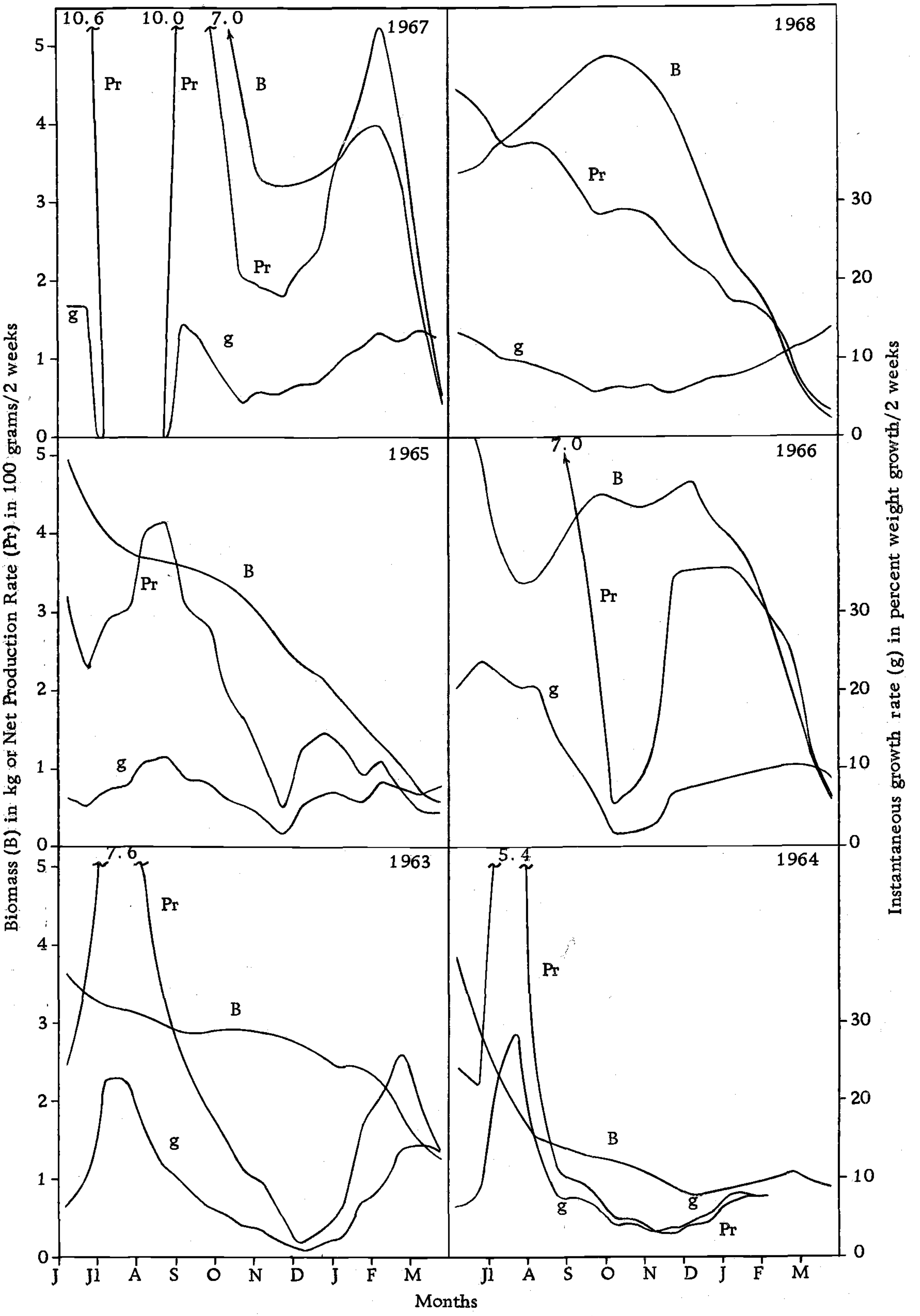


Figure 31c. Needle Branch: Instantaneous growth rate (g), biomass (B), and net production rate (Pr) by year class.

The seasonal distribution of g shows considerable variation from year to year although the general pattern is largely preserved. Most notable is the occurrence of substantial relative growth in late fall and early winter, particularly in the years 1965 to 1968. This winter growth may be associated with the onset of the turbulent streamflow conditions of winter, following the long period of declining flows of late summer and fall. The winter growth pattern usually merges into that of spring growth. The latter is associated with the onset of smolting.

Biomass Trends

The biomass of coho populations varies considerably from year to year (Figure 31), in marked contrast to the conservative pattern of population number (Figure 25). Both the average level of biomass and its seasonal pattern vary greatly. Of course a few grams difference in average weight can have a major effect on biomass, especially in the early summer when population size is large. In general, biomass decreases with decreasing population size during early summer. But as soon as the population size begins to stabilize in late summer, biomass will tend to increase. If growth rate is still high then, biomass may rise rapidly to form a dome-shaped curve. As the season of slow growth arrives, biomass again starts to decrease. In the spring, biomass tends to increase again in spite of the reduction in population size due to the emigration of smolts. This occurs because of the high growth rates in effect then. These relatively high growth rates of late winter and spring boost the biomass curve near the end of the season and thus often produce a curve that is relatively flat for a substantial portion of the year. Finally with the continued emigration of smolts the biomass curve drops off steeply.

Discussion

Seasonal Aspects. A major source of between year variation in total coho growth stems from seasonal modifications of the general growth pattern. These variations do not appear related to population size or biomass. They are probably related to weather and streamflow conditions that affect the production and availability of food. The occurrence of winter growth is most important as a source of this modification of the growth pattern. Growth in winter may proceed with greater efficiency than at other times of the year if food is available. Warren and Davis (1967) have presented data showing winter growth for cutthroat trout in aquaria that occurred at both higher rate and gross efficiency than during spring. Lower maintenance costs associated with the lower temperatures of winter were the probable cause. These differences in yearly growth pattern among the coho populations have important effects upon biomass and net production.

The great variability, seasonally and yearly, in the pattern and magnitude of coho biomass reflects a basic, non-compensatory aspect to growth rate. Coho salmon probably continuously adjust their territory sizes in accordance with food availability so that their growth rate tends to remain independent of the latter. This mechanism has been suggested by Mason and Chapman (1965). While the average growth realized during a season may be related inversely to the effects of population density on food availability and on the degree of intraspecific competition for this food, the territorial behavior of coho results in an incomplete growth compensation, allowing biomass to vary greatly from season to season. Particularly after population adjustment has occurred in the fall, the seasonal pattern of biomass reflects growth conditions determined by factors extrinsic to the population. Density independent growth rate may be typical in stable populations of territorial, stream dwelling salmonids (McFadden, 1969) and has been shown in populations of brook trout (McFadden, Alexander, and Shetter, 1967; Cooper, Boccardy, and Andersen, 1962) and in Atlantic salmon (Elson, 1962).

Although between-year variations may largely reflect variations in food availability to numerically regulated coho populations, it still seems self-defeating for a population not also to regulate its biomass. Biomass is probably a better index of biological load on an environment than is population number. With increasing biomass, total food consumption rate can be expected to eventually peak and then decrease as the consumption rate exceeds the food replacement rate (Warren and Davis, 1967). Since the food necessary for body maintenance increases with individual size, a fish population with unregulated biomass could severely tax its food resources.

In the Drift Creek study streams growth appears to proceed normally in spite of large variations in biomass. An intriguing possibility is that the hierarchial organization of coho social structure enables the population to increase its overall efficiency in obtaining energy from the stream. Perhaps the social organization results in a subdivision of the niche space according to individual size, aggressiveness, or physiology. Chapman (1962) noted that aggressive behavior among coho was reduced in populations made up of several size groupings. It is not at all unusual to find in late summer coho less than 50 mm long that appear to be in as robust condition as the members of the population greater than 70 mm long. These observations lend support to the idea that coho social organization is much more than a mechanism for continuously sifting out weaker members.

Effects of logging on growth. A conspicuous effect on growth following the logging of 1966 occurred during the summer of 1967 in Needle Branch (Figure 32). In July and August the coho there decreased in average size and weight (Figure 30), a development associated with the high stream temperatures occurring then due to the lack

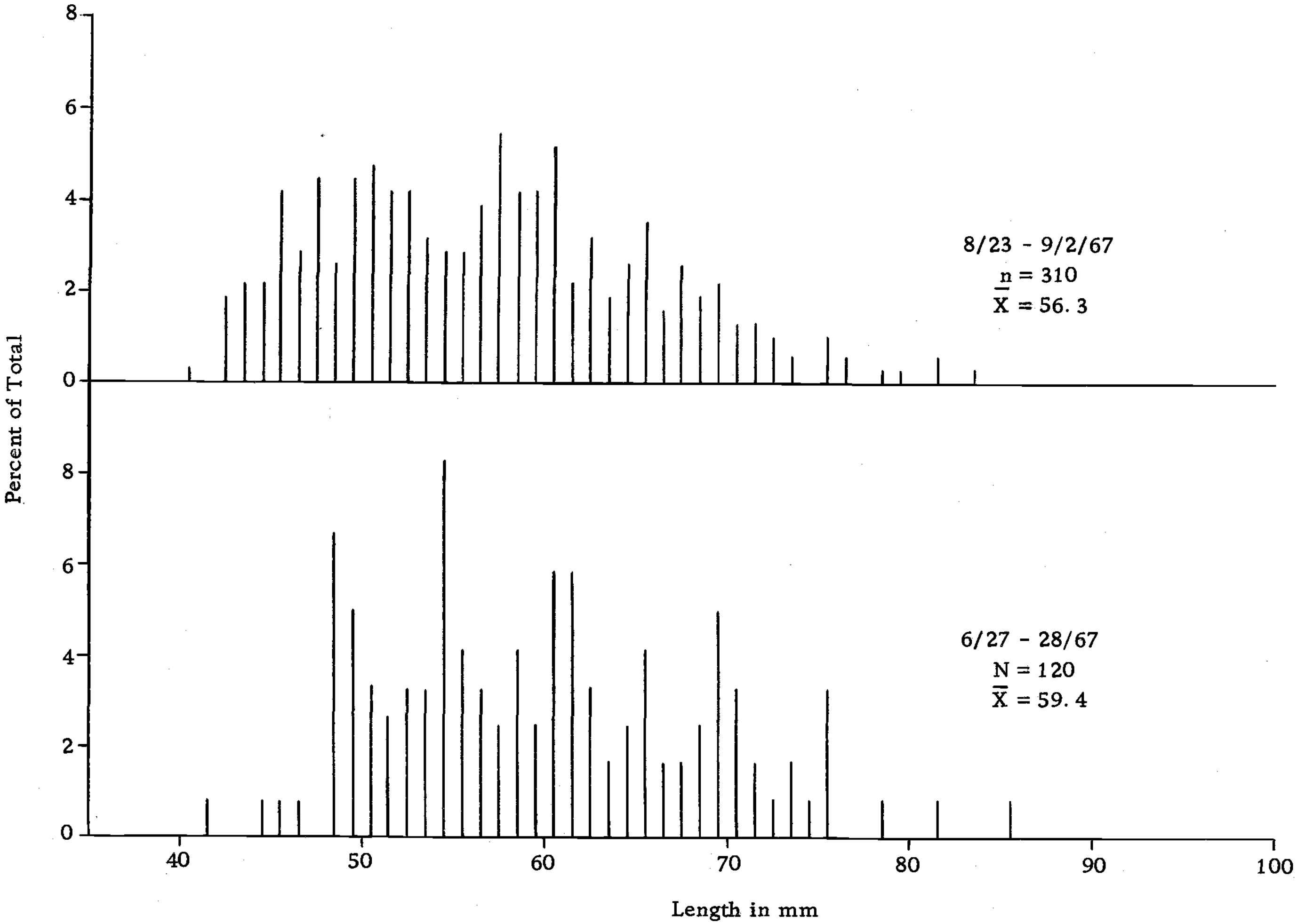


Figure 32. Length frequencies of coho sampled from Needle Branch during the summer of 1967, showing the decrease in average length and the change in relative frequency in the length distributions.

of shade (Figure 4). This loss in average weight was small and did not affect biomass very much at that time. The average size decreased from 59.4 mm in late June to 56.3 mm in September. The length frequencies for these dates (Figure 32) show that a qualitative change had occurred. Compared with the sample of June 27-28 the later August 23 - September 2 population sample had fewer fish larger than 70 mm and more fish less than 50 mm in size. The latter size group was poorly represented in the earlier sample, indicating that sampling error was partly responsible for the decrease in size.

The decrease in relative abundance of the larger coho may have been due to mortality brought on by loss of condition as metabolism and maintenance requirements rose with the abnormal stream temperature. If so, it must have occurred in spite of their increased opportunities for feeding resulting from their higher social standing (Carline, 1968). Perhaps the high mid-day temperatures curtailed feeding behavior enough to nullify this advantage.

Average condition factor (K) was lower for the 1967 year class in late summer (Table 10) than for similar periods in 1966 and 1968. The condition factor was calculated as:

$$K = \frac{W \times 10^5}{L^3}$$

where W = weight in g

L = length in mm.

Table 10. Condition factors (K) by mean length categories (designated by midpoint of 5 mm groups) for Needle Branch coho.

Length Category	Date 10/8/66	 9/19/67	 9/14/68
45		.937	1.034
50		1.209	1.052
55	1.214	.978	1.066
60	1.128	1.072	1.079
65	1.045	1.018	1.048
70	1.119	1.044	1.104
75	1.164	.993	1.094
80	1.169		1.131
85	1.014		
Mean K	1.1204	1.022	1.074
$s_{\bar{x}}$	.0179	.0293	.0050
n	43	57	94

This index is a fairly reliable measure of condition (Brown, 1957) because fish tend to grow isometrically for the most part, except during such times as smoltification and spawning. Strictly speaking the condition factor is valid only in comparing fish of the same age, sex, length, and time of sample (Rounsefell and Everhart, 1953). Nevertheless the evidence in the table indicates that the coho were in poorer condition than fish of approximately the same age in both the year before and after 1967, although the differences between mean condition factors were not statistically significant.

The coho in Needle Branch were subjected to a rapidly fluctuating temperature regime that summer. Daily stream temperatures during July rose to an average of 23° C. (Brown and Krygier, 1970). The minimum temperatures at dawn were about 14° C and the daily maxima occurred at about 1300 hrs. Diurnal temperature rises were therefore precipitous. Temperatures usually started to decrease after 1500 hrs.

The substantial survival shown (Figures 25c, 27c) by the coho in spite of the temperature stress may have been due to its transitory nature. Average maximum temperatures were below 25° C, the upper lethal limit for coho according to Brett (1952), although temperature maxima occasionally approached 30° C. It is possible moreover that the coho could find refuge from overly warm water deep in bank recesses, particularly if ground water inflow were substantial in such places. Although one might expect that the rapid daily rates of temperature increase would be particularly adverse to salmon, this might not be the case. Watt (1968), after reviewing recent literature on the effects of fluctuating temperatures on animal metabolism, concluded that the fluctuations themselves had no special effects other than through the different temperatures that these fluctuations caused the animals to experience.

The greater population size that existed in Needle Branch during the summer of 1967 made up for the effects of weight loss and mortality associated with the high summer temperatures. Smolt output the following spring was not significantly different from that of previous years. The sharp change in population abundance in the fall of that year (Figure 25) may have represented an adjustment to normal population levels after the larger than average densities of summer.

Net Production

Concepts and Methods

The total amount of matter and energy input into a population, in the form of food, that has ever resulted in growth during a period of time is the net production of the population for that period. An operational definition of net production (Pr) is therefore the summation of all growth increments over a period of time, regardless of the subsequent fate of each increment. This is the definition given by Ivlev (1945), Clarke (1946), and Ricker (1958).

From the definition of net production whereby the fate of the biomass formed is ignored, it is clear that net production is fundamentally the rate of energy flux into a population, as correctly pointed out by Macfadyen (1948) and Watt (1968). In fact only in the context of rate, rather than quantity, can net production have reality, as usually the greater portion of the amount calculated up to a given time no longer exists then. Net production is calculated using instantaneous rates of biomass increase as the unit measure, thus avoiding the difficulty of biomass loss through subsequent mortality and catabolism.

Macfadyen (1948) advocated use of the term, "productivity," to designate this production rate, but it appears not to have become accepted by fishery biologists, apparently because Ricker (1946) and Clarke, Edmondson, and Ricker (1946) preferred the term "production" and reserved "production rate" for the differential dPr/dt. Use in fisheries work of the term "production" in place of a word connoting a rate is probably unfortunate because of the confusion that can occur between meanings of production in the biological and in the everyday sense, the latter being synonymous with "yield." In this paper I will use the term "production rate" to mean the measure of production over a given time period, thus emphasizing the flux rate aspects of the concept.

As a measure of biological load, total food consumption, totality of growth, or of the importance of a population as a channel for energy flow in a particular community, net production rate is a potentially useful statistic. One of the best known production studies was conducted by Ricker and Foerster (1948). An increased yield of sockeye salmon smolts (*O. nerka*) had been observed in Cultus Lake, B. C. following predator control. By computing net production they were able to establish that this increase was due to improved survival rather than an increased net production due to removal of competitors. Another well-known study is that of Allen (1951) on brown trout (*S. trutta*) in a New Zealand stream. There are several other production studies of fish populations, and they have been carefully reviewed by Chapman (1967). An imaginative example of such studies is that of Hall (1963), who estimated net production in a lamprey (*Ichthyomyzon castaneus*) population and then used the measure as an indirect means of assessing the mortality on rainbow trout (*S. gairdneri*) due to the lamprey.

Studies of net production rate should be designed to clarify the nature of processes that determine growth, mortality, population size, and energetics. They should seek to make comparisons of populations of the same species under a variety of physical and biological conditions, or conversely of populations of different species under the same physical and biological conditions. Production studies of whole ecological groups at the same trophic level, e.g. all species of insectivorous fish in different combinations would be exceedingly interesting. In my opinion measures of production rate in single species populations isolated in space and time are of dubious value. It would do well to remember that while production rate may be revealing with respect to population ecology, the statistic can contain no more information than do its components, growth and population size. Backiel and Le Cren (1966) have expressed similar opinions with regard to production studies.

In the Drift Creek study, coho populations have been monitored since 1959 in the same three streams, before and after logging. Studies of net production are therefore both appropriate and interesting. Chapman (1965) has computed annual net production rates for the year classes 1959-1962 in each of the streams. He obtained an average rate of about 9 g/m^2 per year. I estimated production rate for the period June 1 to April 15, the time period during which most of the annual growth occurs.

The fundamental formula for net production rate (Pr) over the time interval T may be written

$$Pr = \int_T N_t \left(\frac{dw}{dt}\right)_t dt \qquad (19)$$

(e.g. Beverton and Holt, 1957) where N_t is the population size and w_t is the individual weight at time t. The function $N_t(dw/dt)_t$ is usually not known, except under theoretical conditions, so that the integral (19) cannot be found by direct mathematical calculation. However it may be approximated by

$$Pr = \sum_{T} \bar{N}_{\Delta t} \left(\frac{\Delta w}{\Delta t} \right) \qquad (20)$$

where Δt is some short time interval.

The theoretical computation of net production rate has been worked out by Ricker (1946), Clarke et al. (1946) and Allen (1949). These authors assume constant rates of instantaneous growth and mortality (or constant difference in rates) over the period of interest. Under such conditions they show that net production rate per unit time is

$$Pr_{\Delta t} = \bar{B}_{\Delta t} \cdot g_{\Delta t} \qquad (21)$$

where g is the constant instantaneous rate of individual weight growth, $\frac{1}{W}$ dw/dt, and $\bar{B}$ is the average biomass during Δt. This results from the fact that the summation over Δt of all instantaneous products, say $A_t B_t$, where A_t changes continuously and B_t is a constant expressed as $B/\Delta t$, is simply $(\bar{A}\ B)_{\Delta t}$. Thus all that is required to accurately calculate net production rate by equation (20) is to choose a time interval Δt such that the absolute growth rate $\Delta w/\Delta t$ is constant, i.e. Δw is linear. If Δt is so chosen that N_t also changes almost linearly, then $\bar{N}_{\Delta t}$ may be estimated by the simple arithmetic mean. Under these conditions Δw is usually small enough that

$$\frac{1}{\bar{w}_{\Delta t}} \frac{\Delta w}{\Delta t} \cong \frac{1}{w} \frac{dw}{dt} = g_{\Delta t} \text{ .}$$

The expression under the summation sign of equation (20), which may be written

$$Pr_{\Delta t} = (\overline{n\bar{w}})_{\Delta t} \cdot \frac{1}{\bar{w}_{\Delta t}} \frac{\Delta w}{\Delta t} \qquad (22)$$

is then seen to be practically equivalent to equation (21). The difference is that equation (21) assumes $\frac{1}{w}\frac{dw}{dt}$ constant while the expression from equation (20) merely makes use of approximately linear intervals of $\Delta w/\Delta t$. The simple formula (20), with Δt defining linear changes in N_t and Δw, was therefore used in this paper to calculate net production rate, the computations being done in tabular form. A time interval Δt of 2 weeks was found appropriate, with net production rate being simply

$$Pr = \bar{N} \Delta w \qquad (23)$$

for that interval.

Another way of calculating net production rate is by Allen's (1951) graphical method. The net production rate is simply the area under a curve of N_t vs. $\bar{w}$. Notice that this is merely another way of summing (23). A disadvantage of Allen's method is that the time scale is distorted graphically, necessitating a replotting of production rate against time in order to study the trends. Nevertheless it is a convenient method of obtaining the total net production rate over a period of time. The area under the curve may be found mechanically by planimeter or by approximate integration methods e.g. by "Weddle's rule," one of "Simpson's rules" based on Newton's interpolation formula (see e.g. Alger, 1957).

A frequent problem in calculations of net production rate involves periods of weight loss or "negative growth." Both from the definition of net production by Allen's method and expression (20), a period of weight loss would seem to involve a subtraction of net production, i.e. negative production." Chapman (1966, 1967, 1968) concluded that negative production should be subtracted from the summations of net production rate, thus constituting an exception to the definition that ultimate fate of biomass formed be ignored.

This development seems to have resulted from a confusion between net production as rate of energy flux and as biomass yield in the ordinary sense. At each instant of time the net production is the net gain of anabolic over catabolic processes in the population biomass. By definition, only these net gains figure in the calculations, for only they produce growth increments. Since only net gain is being measured, there is no need to account for the amount of the catabolic process occurring at the instant. The summation of all such gains over all instants of a time period constitutes a method whereby full account is taken of the gains regardless of whether any are catabolized or lost to mortality at any time subsequent to their formation. There are no losses as a function of time involved, for the integral deals only with instants of synthesis. This is why net production is fundamentally a measure of the rate of energy flow into a population and not the net change in weight in any sense. Because energy flows in only one direction through a biological system, by the laws of thermodynamics this energy cannot be subtracted once incorporated, however temporarily, into the population. Just as losses to catabolism do not negate net gains at the instant, so too losses by catabolism or mortality at some later time do not negate the fact of any previous gains or of energy flow. Catabolic weight loss by a population is therefore not "negative production" but simply "no production," no net gains having been made.

This reasoning does not deny the possibility that "negative production" may be a useful concept, but only states that it makes no sense within the context of net production rate. In this paper instances of population weight loss will be treated as zero net production.

The idea of a zero rate of net production brings up another problen of the net production statistic. For even if the average fish shows zero or "negative" growth, as long as some fish do show positive growth, the conclusion of zero net production constitutes a violation of its definition. Inspection of equations (19, 20, 21) reveals that use of mean growth rate in their calculation is valid only when all fish are showing some positive growth. Only then can the mean growth rate as used in these formulae produce unbiased estimates. Since this condition must frequently be violated in natural populations, it may point to a weakness in the statistic itself. When zero production is calculated it may be best to think of it as simply meaning that, on the average the population of fish was not growing, even though some fish were.

Results

Net production rates (Pr) for the period June 1 to April 15 were calculated for the year classes 1963-1968 in each stream (Figure 31). Smooth curves, drawn through each production rate increment representing a 2-week interval, depict the trend in net production rate. The data for these calculations are given in Appendix A-8. Production rate curves follow closely the pattern of growth rate. This results from the fact that population size is relatively stable.

The total net production rate, from June 1 to April 15, increased in all streams after 1965. A decline from the higher levels of 1966 and 1967 occurred in 1968 (Table 11). The means for this period were 29.0, 9.0 and 5.6 kg for Deer, Flynn, and Needle creeks respectively. Using the low water stream areas accessible to coho that are listed by Hall and Lantz (1969), this amounts to an average of 6.15, 3.37, and 5.30 g/m^2 of net production rate in the three respective streams.

Table 11. Net production for period June 1 to April 15 and smolt yield/net production for coho year classes 1963-1968. Data in grams.

Stream	Year Class	Net Production	Smolt Biomass	Yield / Production	Production / m²
Deer	1963	24864.8	13826.9	.556	
	1964	23516.7	21955.5	.934	
	1965	30062.3	13477.0	.448	
	1966	29082.7	19705.0	.678	
	1967	38096.4	21525.0	.565	
	1968	28648.6	14720.8	.514	
	Mean	29045.2	17535.0	.616	6.154
Flynn	1963	6990.6	4528.0	.648	
	1964	8252.0	5520.9	.669	
	1965	6742.1	4110.6	.611	
	1966	12053.7	8139.6	.675	
	1967	11878.0	6325.7	.532	
	1968	7888.7	3607.4	.457	
	Mean	8967.5	5372.0	.599	3.371
Needle	1963	4922.8	1872.2	.369	
	1964	2771.3	1215.1	.438	
	1965	3891.0	1569.0	.403	
	1966	8815.0	3270.0	.371	
	1967	8091.0	2208.0	.273	
	1968	5218.1	3093.7	.593	
	Mean	5618.2	2204.7	.408	5.300

Discussion

The total rate of net production varied greatly from year to year in each stream. Much of the variation was due to year-to-year differences in initial year-class strength, about one-third of the net production being produced in the period June 15 to August 15, when growth rate interacted with the still high, but rapidly declining, population number . But a considerable amount of the variation was due to changes in the seasonal pattern of growth. After September, population numbers are largely stabilized and seasonal growth variations, particularly those in winter, become important. The fractional contributions (Table 12) to total net production, according to five, 2-month periods, show the relative importance of different times of the year to production rate. The summer and early fall periods (6/15-8/15, 8/15-10/15) were the greatest contributors to net production rate, but after the low period of late fall (10/15-12/15), substantial contributions were made in the winter period (12/15-2/15). Winter net production rate averaged about 14% of the total and that period was one of the most variable in terms of production during the entire year. Thus winter growth rate, which often starts to rise in late fall, is an important component of net production.

Net production rate for the 1967 year class was high in all three streams primarily because of better than average year-class strength

Table 12. Fractional contribution to total net production (6/15 - 4/15) by each 2-month period.

Stream	Year Class	Summer 6/15 - 8/15	Early Fall 8/15 - 10/15	Late Fall 10/15 - 12/15	Winter 12/15 - 2/15	Spring 2/15 - 4/15
Deer	1963	.403	.159	.044	.091	.236
	1964	.266	.249	.144	.106	.172
	1965	.313	.070	.063	.203	.175
	1966	.230	.154	.118	.228	.201
	1967	.293	.190	.136	.150	.138
	1968	.292	.264	.144	.094	.143
	Mean	.300	.181	.108	.145	.178
Flynn	1963	.399	.277	.093	.019	.101
	1964	.310	.180	.093	.141	.161
	1965	.296	.192	.023	.271	.113
	1966	.334	.109	.064	.255	.154
	1967	.280	.073	.091	.291	.195
	1968	.361	.223	.151	.012	.081
	Mean	.330	.176	.085	.165	.134
Needle	1963	.462	.192	.055	.093	.148
	1964	.543	.119	.051	.095	.103
	1965	.316	.314	.114	.122	.052
	1966	.391	.148	.103	.151	.046
	1967	.186	.273	.098	.193	.087
	1968	.302	.241	.199	.135	.037
	Mean	.367	.214	.103	.132	.076

in June. Net production was also relatively high during the winter of that year in all streams.

In Needle Branch during 1967 the curve of population size did not continue to drop away rapidly after June as is normally the case. It decreased relatively slowly throughout the summer, finally dropping rapidly during the fall season. The resulting summer population numbers, though anomalously high, contributed relatively little to total net production rate (only 18.6%) because of an apparent drastic decrease in mean growth rate between June 15 and September 1 (Figure 31c). Instantaneous growth rate was initially high, about 22%/2 weeks in May. The favorable stream conditions reflected by this growth may have been responsible for the early leveling of the population curve in June. But by July, stream temperatures were fluctuating as high as 30° C and the previously discussed decrease in mean length of the coho resulted. There was then, by calculation, no net production during most of July and August, at least for the population of "average fish." In fact, however, some net production must have occurred, especially since the qualitative change in population structure (Figure 32) was at least partly responsible for the "negative" growth rate. The high rates of net production before and after this drop in growth rate, when population size was still large, together with the relatively high winter net production, still enabled the 1967 year class of Needle Branch to be better than average in net production rate. Growth rate recovered in September as stream temperatures trended back to normal.

The 1966 year classes in Needle and Flynn creeks were also above average in the rate of net production. Initial population size was relatively high that year in both streams too. Summer growth rate in Needle Branch was better than average, as it started out to be 1967. These better growth rates may partly have reflected decreases in the cutthroat trout population there in the post-logging years (Hall and Lantz, 1969). McIntyre (1970) has presented evidence that the presence of these trout can reduce net production in sympatric coho populations. Winter net production was also relatively high in 1966, as in fact it was in all years 1965-68 in all streams. Net production rates during 1963 and 1964 in all streams were lower than average. The relatively low net production during winter in those years seems partly responsible.

McFadden (1969), in a review of salmonid ecology, concluded that net production among stream-dwelling species is determined solely by population density rather than by growth, the latter being density independent. However once density dependent mortality has effected population adjustment to the relatively stable levels determined by the stream's carrying capacity, seasonal variations in growth rate contribute importantly both to the pattern and totality of net production, as seen in the present study. The mean fractional contribution of the winter period to the June to April net production was only about 14%, but it ranged up to 29.1% (Table 12).

Chapman (1965) found that the coho of the year classes 1959-62 in each of these same three streams averaged about 9 g/m^2 in annual net production. He cited the similarity in these estimates as evidence for regulation of net production. Net production for the period June 1 to June 1 was also presented. These latter data are comparable to my estimates of net production rate for the 1963-1968 year classes covering the period June 1 to April 15. This is because relatively little is contributed to net production after April. My values of mean net production rate per unit area are 6.2, 3.4, and 5.3 g/m^2 (Table 11) as compared with his 5.2, 5.0, and 4.2 g/m^2 for the streams Deer, Flynn, and Needle respectively. These latter values are of course substantially less than the mean of 9 g/m^2 computed from March to March because of exclusion of the spring months, when high population levels contributed greatly to total net production. Moreover that mean was based on a 65% redd survival, probably excessive.

The year classes 1966 and 1967 seem mostly responsible for the difference between pre-logging and post-logging periods. Net production rates were high in 1966 and 1967 in both Flynn Creek and Needle Branch. They were high in all years after 1964 in Deer Creek but especially so in 1967. If 1966 and 1967 are considered anomalous years and their values eliminated from calculations, mean net production rate was 26.8, 7.5, and 4.2 kg for Deer, Flynn, and Needle creeks respectively. Except for that of Flynn Creek, these values compare favorably with Chapman's 26, 13, and 4.2 kg for the same three streams respectively during the years 1959-62. Mean net production in Flynn Creek prior to 1963 was larger because of larger estimated population densities.

Changes in the rate of net production, like that of biomass, depended largely upon the seasonal pattern of growth. But unlike biomass, the rate of net production is not a measure of standing crop, hence the two are not comparable with respect to regulation. If a population of fish were operating on nearly the maximum of the food energy capable of being supplied by its environment, then possibly total net production rate would tend to be constant for similar such environments during similar years. But if the fish were feeding opportunistically on a wide variety of food as is characteristic of temperate, freshwater forms (Larkin, 1956, then their total food consumption would depend strongly upon the vagaries of coincidence in food availability and population density. Under such conditions one should not expect net production to be regulated in the sense that the energy flow it represents is continuously adjusted. However Chapman's conclusion (1965) that spatial needs and food supply are important determiners of the general level of net production in a salmon population must be essentially correct.

The Smolt Yield

The smolt yield, representing the final result of the population processes acting in the stream, has been shown to vary little even under the severe environmental alteration that occurred in 1966 on the Needle Branch watershed (Table 1). Evidence has been presented indicating that of all the processes: fry emigration, growth, net production, and mortality, the latter is the most important as a regulatory mechanism. Mortality works through the important intraspecific behavioral interactions characteristic of coho to reduce the variable initial input of fry to stable population densities, presumably within the limits of the stream's capacity to support coho. Thus the direct mortalities suffered by the Needle Branch coho during both logging and stream clearing activities merely claimed fish destined to die by natural mortality. The high subsequent stream temperatures that occurred in the summer of 1967 because of lack of protective shade caused both mortality and loss of weight, but again smolt output was not seriously affected. It seems that the coho, having evolved to meet the adversities of a variable environment, were able to adjust to the severe environmental conditions brought on by logging. This conclusion, however, should be tempered with the knowledge that the post-logging years 1966 and 1967 were apparently exceptionally productive years for coho in all streams (Table 11), and the fact that since 1969 spawning females and smolt output have been lower than average in Needle Branch. Continued monitoring of this stream will be required to complete the assessment of the effects of logging on the salmon population.

The ratio of smolt yield to total net production was relatively constant (Table 11). Mean values of the smolt biomass : net production ratio were 0.616, 0.599, and 0.408 for Deer, Flynn, and Needle creeks respectively. The relative constancy of the ratio reflects the tendency for stability in the populations after fall and the common element of growth in smolt biomass and measurements of net production rate.

The effect of population density in the regulation of smolt yield (Table 1) has been shown in Figure 2 but is better demonstrated using the June population estimates calculated in a previous section. Curves (Figure 33) can be drawn through plots of smolt numbers vs. June population size, considering the fact that each curve must approach the origin. Population regulation in the relationship is evident.

Most of the smolts spend two growing seasons at sea before returning to the study streams as spawners. Their ocean survival, based only upon the smolts counted at the downstream traps, is about 3%. Their arrival at the spawning grounds completes the cycle of the species.

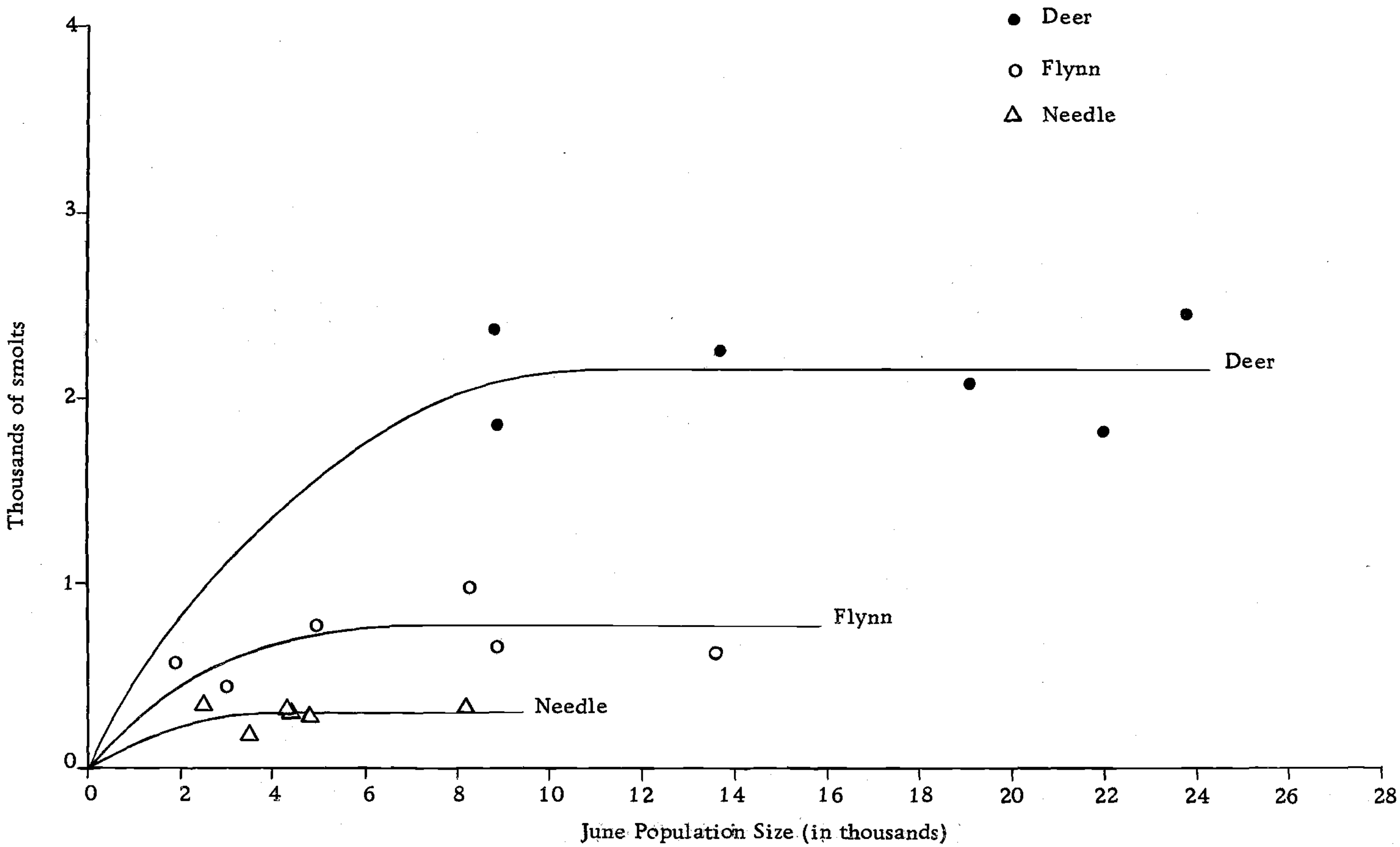


Figure 33. Relationships between coho smolt yield and population size in June of first spring, showing independence of smolt yield and initial population size. Curves fitted by inspection.

SUMMARY

The Alsea Watershed Study was designed to evaluate the effects of different patterns of timber cutting on aquatic resources. The three small streams involved, Deer, Flynn, and Needle in order of decreasing size, have each produced relatively constant numbers of coho salmon smolts each year since the study began in 1959. The logging operations of 1966 (patch logging on the Deer Creek watershed, complete clear-cutting on the Needle Branch watershed) did not significantly alter this result. Stabilizing factors in the ecology and dynamics of these coho populations (year classes 1963-68) are examined in this paper.

The spawning and nursery grounds of the coho are highly variable in streamflow and intragravel environment. The former directly influences the latter. Intragravel oxygen levels vary from area to area in the streams, reflecting the complexities of streamflow and sedimentation, and partly explain the varied survival rates of alevins within the redds (0 to 80%).

Changes due to logging occurred in streamflow, temperature, and oxygen characteristics after 1966. Peak flows increased significantly over pre-logging levels, particularly in Needle Branch, probably hastening recovery of that stream through the increased flushing action. Striking rises in diurnal temperature occurred in the completely

logged watershed (Needle Branch). A maximum stream temperature of 30° C was recorded in July 1967. Shade provided by the streamside buffer strip in the partly logged watershed (Deer Creek) largely protected it from similar temperature increases. Surface and intragravel oxygen levels decreased in Needle Branch after logging.

The size of the coho spawning escapement to each stream was highly variable from year to year (range: 18-55, 2-55, 1-28 females into Deer, Flynn, and Needle creeks respectively, 1959-69). Their arrival pattern partly reflected the winter weather pattern. The significance to coho ecology of this association lies both in the resulting protracted spawning and in the highly variable pattern of fry emergence.

Adults arrive at the study streams in the ratio of about 4 males per female. Females average larger than males in size. Spawning occurs wherever suitable gravel exists, although certain stream areas seem preferred.

Survival of alevins within the redds averaged only about 30%, but was highly variable. Fry emerge en masse from the gravel into the stream at night, primarily during the first hours of darkness. About 90% of the total emergence from a redd occurs within the first 10 days after initial emergence. The varied emergence schedule of individual redds, reflecting varied times of spawning, the varied survival of alevins, and their mass nocturnal emergence affect the pattern of fry input into each stream. Besides differing greatly between years, fry input thus becomes an erratic sequence of events within the period March through May of any given year..

Immediately upon emergence fry begin to disperse downstream from the redd site. This dispersal results in newly emerged fry being distributed relatively long distances downstream (up to 300 m per night) from the redd site. The erratic pattern of emigrating fry detected at the downstream trap on each stream seems primarily to reflect this nocturnal dispersal of recently emerged fry.

The mass downstream movement of fry starts simultaneously each night along the length of stream through which migration has been occurring. The fry continue dispersing during each successive night until all have settled and become resident. During the day the fry maintain position and feed in the current. Experiments and observations on these fry suggest that nocturnal migratory behavior is part of a developmental sequence beginning with the initial hydrostatic disequilibrium of the fry and ending in the quiescent resting behavior of resident fry at night. Until this last behavioral stage is reached, the nocturnally active fry are subject to displacement by the current. The transition to quiescent nocturnal behavior appears to be gradual, perhaps taking a week for some individuals. The process must depend upon the initial condition of the emerged fry and the degree of competition and food availability encountered during the day. Intraspecific competitive stress stemming from prior resident fry is viewed as an important augmenter of the dispersal process, delaying the acquisition of nocturnal resting behavior.

The ecological function of fry dispersal must be the distribution and redistribution of recently emerged fry away from the redd sites so that nursery areas of the stream may be more fully utilized. The nocturnal mass movement of these fry is an efficient mechanism accomplishing this dispersal. An overall scheme of migratory processes is presented to attempt an ecological synthesis of behavior from fry dispersal to smolt emigration.

Evidence is presented to suggest that fry migration is inefficient as a mechanism of population regulation. While the migration reduces the stresses of overpopulation, the emigration rate does not appear governed by the existing population densities. Approximately 90% of the total migration is over by June. Fry emergence is also ending then, an indication that distribution rather than population adjustment is the major function of the migration.

Coho territorial and agonistic activity, while important in the dispersal process, continue into the summer long after migration is over. This activity must be important in adjusting the populations to the stable levels occurring by fall that are characteristic of each stream. These adjustments occur largely through mortality, not migration.

Temporal patterns of coho population size are typically J-shaped, with greatest mortality occurring in spring and early summer. Calculations indicate that about 80% of each year's recruits die by September, the mortality rate probably being equally high during the spring recruitment phase and during early summer. Evidence is presented indicating that the mortality rates involved are density dependent and therefore regulatory in nature. Territorial and agonistic behavior among coho are thought to be most important in this respect. Population levels changed relatively little after September, thus producing the near constant smolt output each year from each stream. The natural ability of the coho populations to thus deal with the highly variable fry input each year apparently also extended to the detrimental effects of logging.

A simple model relating the temporal distribution of survival was used to obtain survival estimates of the emigrant fry population residing downstream of the traps. The resulting estimates of their total stream survival were such as to be consistent with the concept that emigrating fry are largely dispersing fry, not ecological rejects.

Growth among coho populations occurs largely during the summer and the following spring, just before the fish emigrate as smolts. The average coho increases in size by about 45 mm between June and the next April. A decrease in mean size occurred in the logged Needle Branch during the summer of 1967. It was associated with high stream temperatures occurring then in that unshaded stream. A change in population structure was involved, partly due to differential mortality affecting the larger coho.

Seasonal modifications of the general growth pattern are an important component of year-to-year variations in growth rate. In some years winter growth contributed significantly to total growth. Although coho from larger populations tended to be smaller at the end of the first growing season, this growth compensation did not prevent large fluctuations in biomass. Such fluctuations are a consequence of growth being affected by territorial behavior and seasonal environmental factors extrinsic to the populations.

Biomass decreases with the populations in spring and early summer and tends to increase after population stability has been achieved. It is often temporarily sustained the next spring by a balance between dropping population levels, due to smolt emigration, and increased growth rate. These changes are due to seasonal variations in growth rate acting upon relatively stable population levels and are not indicative of a mechanism operating to stabilize biomass.

A simple method of calculation was derived and used to obtain net production estimates for the period June 1 to April 15. They averaged 6.2, 3.4, and 5.3 g/m^2 in Deer, Flynn, and Needle Creeks respectively. Net production rates were higher than average for the post-logging year classes 1966 and 1967 in Flynn and Needle creeks and 1967 in Deer Creek. The seasonal patterns of net production rate, like those of biomass, are largely a response to time-dependent variations in growth rate.

These studies of the 1963-1968 coho year classes indicate that of all the processes: fry emigration, growth, net production, and mortality, the latter is the most important in regulating the populations. Numerical size therefore was the only feature of the populations that characteristically exhibited a pattern of increased stability with time. It accounted for the stability of the smolt yield, even during the post-logging years.

About 90% of the yearling coho emigrate in the spring as smolts. Mean values of the smolt biomass:net production ratio were 0.62, 0.60, and 0.41 for Deer, Flynn, and Needle creeks respectively. Evidence is presented showing that the smolt yield is largely independent of initial year-class strength in June, a consequence of population regulation via mortality. Ocean survival of these smolts is less than 3%.

This study has shown that coho streams normally produce characteristic levels of smolt yield in spite of large natural variations in fry input and conditions for growth. The range of environmental variation for which this result holds may include short-term changes due to logging. However a normal population response to such a severe alteration as occurred on Needle Branch is very likely conditional upon a program that at least includes vigorous stream clearance, the restriction of additional mortality to early summer, when population adjustments are far from complete, and the encouragement of streamside revegetation. A streamside buffer strip of trees is an effective way of protecting aquatic resources.

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Table A-1 Mean length (cm) and range (in parenthesis) of jack (J), male (M), and female (F) adult coho by year and stream.

	Deer Cr.			Flynn Cr.			Needle Br.		
Year	J	M	F	J	M	F	J	M	F
1959-1960	39.25	61.30	67.24	43.67	59.56	68.43	40.00	61.50	61.00
	(32-47)	(50-88)	(56-76)	(39-46)	(47-74)	(65-72)	(34-46)	(57-66)	(57-65)
1960-1961	41.36	61.72	70.65	38.63	64.16	74.25	38.77	62.67	71.80
	(31-46)	(48-86)	(60-81)	(34-44)	(48-82)	(65-84)	(36-46)	(55-75)	(66-80)
1961-1962	41.00	63.68	72.34	39.82	64.75	73.35		72.50	68.43
	(34-45)	(48-84)	(60-84)	(33-46)	(47-86)	(57-84)		(59-83)	(46-79)
1962-1963	41.30	63.80	70.90	38.00	63.50	74.50	37.67	75.00	71.50
	(35-46)	(50-88)	(57-82)	(32-43)	(51-77)	(70-79)	(34-41)	(74-76)	(69-76)
1963-1964	39.70	60.57	70.60	43.00	62.71	69.47	a		
	(33-46)	(49-83)	(62-80)	(40-46)	(52-74)	(62-80)			
1964-1965	42.12	63.42	69.90	44.00	63.04	71.40	a		
	(38-47)	(48-81)	(51-79)		(49-75)	(69-76)			
1965-1966	42.17	64.55	70.40	39.95	62.07	72.15	a		
	(37-46)	(48-83)	(63-78)	(34-48)	(49-79)	(64-78)			
1966-1967	41.67	65.75	73.40	38.78	63.71	72.89	39.17	62.23	72.00
	(36-47)	(48-83)	(55-84)	(29-46)	(48-82)	(47-80)	(33-46)	(52-79)	(63-79)
1967-1968	39.25	65.11	70.17	43.00	63.86	70.40	39.65	60.20	71.35
	(32-46)	(48-82)	(62-79)	(32-45)	(47-86)	(68-78)	(32-45)	(48-84)	(61-80)
1968-1969	41.78	60.37	67.41	43.00	57.36	67.60	41.89	58.91	67.24
	(33-46)	(48-78)	(51-76)	(37-46)	(48-80)	(54-77)	(34-47)	(48-72)	(56-73)
Mean	40.96	63.03	70.30	41.18	62.47	71.44	39.52	64.72	69.04

a) Upstream trap not operable; no data available.

Table A-2. Male (M) to female (F) ratios in returning adult coho by year and stream.

		Totals			Excluding Jacks		Adjusted for non-spawning adults [a]		
Stream	Year	M	F	M/F	M	M/F	M	F	M/F
Deer	1959-60	99	26	3.81	79	3.04	59	24	2.46
	60-61	73	18	4.06	51	2.83	41	18	2.28
	61-62	138	32	4.31	130	4.06	83	30	2.77
	62-63	53	18	2.94	43	2.39	24	18	1.33
	63-64	146	29	5.03	125	4.31	79	29	2.72
	64-65	156	49	3.18	148	3.02	102	49	2.08
	65-66	140	27	5.18	127	4.70	76	26	2.92
	66-67	223	57	3.56	214	3.75	163	55	2.96
	67-68	164	23	7.13	94	4.09	59	23	2.56
	68-69	162	40	4.05	144	3.60	118[b]	38[b]	3.11
	Mean			4.24		3.62			2.59
Flynn	1959-60	35	16	2.19	32	2.00	24	10	2.40
	60-61	82	20	4.10	55	2.75	41	19	2.16
	61-62	125	55	2.27	115	2.09	83	55	1.51
	62-63	9	2	4.50	6	3.00	5	2	2.50
	63-64	50	20	2.50	48	2.40	28	20	1.40
	64-65	25	10	2.50	24	2.40	15	10	1.50
	65-66	139	14	9.93	87	6.21	49	12	4.08
	66-67	175	55	3.18	158	2.87	103	55	1.87
	67-68	86	10	8.60	43	4.30	26	9	2.89
	68-69	87	20	4.35	81	4.05	56[b]	20[b]	2.80
	Mean			3.66		2.92			2.03
Needle	1959-60	9	4	2.25	4	1.00	2	3[e]	
	60-61	14	5	2.80	4	0.80	4	2	2.00
	61-62	8	14	0.57	8	0.57	8	14	0.57
	62-63	10	4	2.50	2	0.50	1	4	0.25
	63-64	c	c		c		c	c	
	64-65	c	c		c		c	c	
	65-66	c	c		c		c	c	
	66-67	70	19	3.68	59	3.10	35	18	1.94
	67-68	101	17	5.94	45	2.65	44	16	2.75
	68-69	77	17	4.53	69	4.06	47[b]	17[b]	2.76
	Mean			3.61[d]		3.26[d]			2.47[d]

a) Spawning males equal the numbers remaining above the traps plus 50% of those that pass back down (the percentage estimates the numbers that had remained upstream at least five days and had presumably spawned); females have been adjusted for known numbers of non-spawners.

b) Adjustment based on inspection at traps for unspawned adults among those moving downstream.

c) Trapping record incomplete during this period.

d) Because of incomplete trap records mean is based on the 1966-67 to 1968-69 data only.

e) None of these three fish appeared to have spawned.

Table A-3. Regression analysis of fry emigrants vs. spawning females (X).

A. Tests of significance of partial regression coefficients

Stream and years	Source of Variation	SS	D.F.	M.S.	F
Deer 1960-69	Total	101.6768	10		
	Regress. due to X and X^2	77.4675	2	38.7338	12.7997**
	Regress. due to X alone	76.6407	1	76.6407	25.3261**
	Additional due to X^2	.8268	1	.8268	.2732
	Residual	24.2093	8	3.0262	
Flynn 1960-69	Total	1012.7712	10		
	Regress due to X and X^2	986.4211	2	493.2106	149.7391**
	Regress. due to X alone	971.4738	1	971.4738	294.9401**
	Additional due to X^2	14.9471	1	14.9471	4.5380
	Residual	26.3501	8	3.2938	
Needle 1960-69	Total	385.5521	9		
	Regress. due to X and X^2	236.3831	2	118.1916	5.5463*
	Regress. due to X alone	220.5146	1	220.5146	10.3480*
	Additional due to X^2	15.8685	1	15.8685	.7447
	Residual	149.1690	7	21.3099	

B. Linear regression coefficients

Stream	Beta
Deer	0.2107
Flynn	0,5114
Needle	0.6452

Table A-4. Numbers of emigrant juvenile coho by month and year class.

Stream	Month	Year Class 1963	1964	1965	1966	1967	1968
Deer	J						
	F		22			28	18
	M	2080	399	91	295	1515	2548
	A	277	4867	3218	1944	7459	2090
	M	1658	1691	4978	201	2267	931
	J	298	359	500	154	1113	975
	Jl	92	29	25	14	106	89
	A	3	13	11	2	14	66
	S	5	0	-[a]	1	21	7
	O	2	0	-	0	11	4
	N	111	313	193	90	26	122
	D	30	142	334	32	84	103
	J	151	72	234	39	25	122
	F	218	330	336	305	249	126
	M	734	734	260	722	806	384
	A	609	626	342	709	1004	657
	M	220	149	129	349	263	337
	J		4	1	6	1	2
	Jl		0				1
	A		1				
Flynn	J						
	F		253			202	
	M	53	1028		269	6053	1827
	A	2	2396	1059	1643	7568	1050
	M	6	2548	1934	676	13724	443
	J	4	223	153	138	1106	34
	Jl	0	38	16	21	155	3
	A	0	11	0	4	12	2
	S	0	0	1	10	-[a]	0
	O	0	1	-[a]	3	-	1
	N	6	39	3	16	4	32
	D	97	20	15	67	11	25
	J	8	18	51	8	4	18
	F	23	123	148	79	36	29
	M	263	242	197	457	221	113
	A	131	287	209	225	272	184
	M	36	38	40	117	72	40
	J	2	2				
	Jl						
	A						

A-4. Continued.

Stream	Month	Year Class 1963	1964	1965	1966	1967	1968
Needle	J						
	F		747				
	M	2642	2548	4065	2227	1468	2608
	A	404	5306	14689	9661	2624	367
	M	2807	4912	3480	3343	1334	501
	J	329	478	810	1204	115	174
	Jl	9	12	63	143	4	22
	A	1	0	11	-[a]	12	12
	S	0	0	0	-	10	1
	O	0	0	4	-	44	52
	N	-[a]	-[a]	23	51	6	188
	D	-	-	-	13	39	59
	J	-	-	-	25	54	39
	F	29	27	70	52	47	10
	M	118	28	104	59	40	34
	A	87	78	59	76	70	49
	M	44	14	11	51	20	20
	J		3	1			
	Jl		1	1			
	A						

a) Dash indicates trap inoperable during month.

Table A-5. A. A model for population estimation in the presence of differential mortality.

		Population Model							Calculations			
		Marks Surviving by Time Period										
Time	Marks Applied	t_1	t_2	t_3	t_4	t_5	t_6[a]	Mark Survival to t_6	Estimated[b] Mark Survival to t_6	Mark[c] Ratio in Sample	Estimated[d] Total Marks Present	Estimated[e] Population at Time t
t_1	m_1	m_1	m_1s_1	$m_1s_1s_2$	$m_1s_1s_2s_3$	$m_1s_1s_2s_3s_4$	$m_1s_1s_2s_3s_4s_5$	$s_1s_2s_3s_4s_5$	$S_{1,6}$		O	
t_2	m_2		m_2	m_2s_2	$m_2s_2s_3$	$m_2s_2s_3s_4$	$m_2s_2s_3s_4s_5$	$s_2s_3s_4s_5$	$S_{2,6}$	R_2	M_2	N_2
t_3	m_3			m_3	m_3s_3	$m_3s_3s_4$	$m_3s_3s_4s_5$	$s_3s_4s_5$	$S_{3,6}$	R_3	M_3	N_3
t_4	m_4				m_4	m_4s_4	$m_4s_4s_5$	s_4s_5	$S_{4,6}$	R_4	M_4	N_4
t_5	m_5					m_5	n_5s_5	s_5	$S_{5,6}$	R_5	M_5	N_5

a) All marked fish of each type are captured at t_6 as smolts, enabling estimates of mark survival.

b) Estimated by the ratio of numbers of marked fish surviving as smolts ($m_is_i \cdots s_5$) to the number initially marked (m_i), e.g. $S_{1,6} = \frac{m_1s_1s_2s_3s_4s_5}{m_1}$ estimates $s_1s_2s_3s_4s_5$; $S_{2,6} = \frac{m_2s_2s_3s_4s_5}{m_2}$ estimates $s_2s_3s_4s_5$; etc.

c) The marked fish (all types combined)found in each stream sample, expressed as a fraction of the sample.

d) Estimated total marks present at time of marking; $M_2 = m_1s_1 \cdots s_5/S_{2,6}$; $M_3 = (m_1s_1 \cdots s_5 + m_2s_2 \cdots s_5)/S_{3,6}$;

$M_4 = (m_1s_1 \cdots s_5 + m_2s_2 \cdots s_5 + m_3s_3 \cdots s_5)/S_{4,6}$; etc.

e) Estimated population size at time t is: M_t/R_t.

Table A-5. Continued. B. Hypothetical example.

Populations					Calculations			
Time Period	# Marked	Total Marks Present at Beginning of Period. Survival = 0.5/period	Unmarked Fish Present at Beginning of Period. Survival = 0.6/period	Total Fish Present	Survival of Each Mark Type to Period 6	Mark Ratio in Stream Sample	Estimated Total Marks Present at Start of Period	Estimated Population Size at Time t
1	m_1=400	0	5000	5000	0.030	0	0	
2	m_2=300	200	2760	2960	0.063	0.068	200	2963
3	m_3=200	250	1476	1726	0.125	0.145	250	1726
4	m_4=100	225	766	991	0.250	0.227	225	991
5	m_5=80	163	400	563	0.500	0.290	162	560

Table A-6. Examples of population estimates of juvenile coho by various methods for the 1964 and 1965 year classes.

Date	N_t[a]	N_t[b]	N_t[c]	N_t[d]
		Deer Creek		
5/2/64	20345	5282	4486	--[f]
6/17-18/64	7316	3557	1587	1387
6/17/64	4642	2128	657	1401
10/17/64	4098	4346	2154	1997
2/13/65	2023	--[e]	--[e]	2034
5/22/65	24581	4592	2254	--[f]
7/12/65	19688	9125	3420	2090
10/2/65	6883	2813	1393	2522
12/23/65	7245	--[e]	--[e]	4921
		Flynn Creek		
4/26/64	10754	19010	9000	--[f]
8/2-13/64	1876	1370	570	2286
10/24/64	1752	3316	1816	1280
2/23/65	1104	--[e]	--[e]	1426
6/5/65	7436	2547	748	--[f]
7/1/65	3362	2855	--[g]	871
9/8-10/65	1882	866	563	--[g]
10/30/65	1621	2321	864	724
1/22/65	1212	1962	731	1540
2/26/66	605	--[e]	--[e]	585
		Needle Branch		
4/19/64	7260	7500	--[g]	--[f]
6/30/64	1906	1007	337	--[g]
8/11/64	619	412	195	277
10/31/64	367	300	100	224
2/20/65	214	--[e]	--[e]	372
4/24/65	14040	21429	--[g]	--[f]
6/24/65	3843	2000	--[g]	--[g]
9/7/65	2700	1415	961	--[g]
12/4/65	960	7000	186	664
2/12/66	354	--[e]	--[e]	278

a) Petersen estimate using mark ratio from the smolt population.

b) Petersen estimate using the mean ratio of each mark found in stream samples during the year.

Table A-6. Continued.

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c) Petersen estimate using the ratio of each mark found in the stream in the first recapture sample after marking.

d) Population size using estimates of mark survival and numbers of marks extant at the time of marking (Table A-5).

e) The method does not yield an estimate for the time of the last marking operation in the stream.

f) The method does not yield an estimate for the time of the first marking operation in the stream.

g) Data not available.

Table A-7. Estimates of coho population size derived from Petersen estimates using the mark ratio from the smolt population.

Deer Creek						
Mark Date	No. Marked	No. Recapt'd	Mark Ratio	N_t	0.95 Confidence Interval Lower	0.95 Confidence Interval Upper
5/4/63	331	73	0.041	8145		
6/18-20/63	500	62	.030	16429	12627	21114
7/17/63	501	64	.031	15955	12341	20534
9/3/63	559	182	.088	6323	5435	7211
11/6-23/63	111	65	.036	3433	2662	4350
12/28-31/63	118	45	.028	5010	3618	6660
2/22/64	110	61	.034	3147	2400	4039
5/2/64	412	46	0.020	20346		
6/17-18/64	498	157	.068	7316	6128	8320
8/17/64	300	149	.066	4642	3800	5184
10/17/64	113	63	.027	4098	3278	5272
2/13/65	56	50	.027	2023	1490	2605
5/22/65	450	31	0.021	24581	16613	34610
7/12/65	399	37	.023	19680	13788	26932
10/2/65	301	81	.046	6883	5192	8014
12/23/65	149	31	.020	7245	4896	10201
6/8/66	439	88	0.040	11054	8756	13478
8/1-3/66	400	76	.034	11439	9028	14357
9/9/66	300	113	.051	5897	4794	6897
11/5/66	127	53	.024	5270	3928	6731
5/20/67	500	44	0.018	27022	19529	36067
7/6/67	461	71	.030	15405	12090	19632
9/14-15/67	407	93	.043	10647	7635	11071
11/18/67	206	62	.026	7952	6112	10220
12/27/67	200	86	.040	5398	3988	5958
7/2-9/68	523	118	0.064	8139	6707	9571
9/30-10/3/68	427	108	0.058	7255	5919	8591
12/26-27/68	273	145	0.084	3235	3115	3355

Table A-7. Continued.

Flynn Creek

Mark Date	No. Marked	No. Recapt'd	Mark Ratio	N_t	0.95 Confidence Interval	
					Lower	Upper
4/13/63	103	24	0.043	2278	1454	3366
6/11-13/63	145	15	.027	5093	2852	8312
7/16, 26-27/63	141	44	.080	1733	1243	2223
9/10/63	151	59	.107	1392	1056	1728
11/30/63	51	35	.069	783	508	987
2/1/63	40	21	.560	787	442	1024
4/26/64	400	25	0.037	10754	6738	15070
8/12-13/64	252	98	.140	1876	1454	2118
10/24/64	126	52	.072	1752	1291	2247
2/23/65	69	38	.078	1104	641	1117
6/5/65	405	35	0.054	7436	5033	9959
7/1/65	157	28	.050	3362	2057	4290
9/8-10/65	168	58	.094	1882	1343	2183
10/30/65	130	52	.079	1621	1197	2045
1/22/66	51	24	.040	1212	772	1790
2/26/66	19	13	.029	605	324	1025
6/23/66	350	60	0.062	5548	4197	7074
8/3-4/66	284	85	.092	3167	2446	3674
9/7/66	200	67	.072	2844	2108	3404
12/19/66	140	65	.074	1875	1436	2351
5/27/67	450	13	0.028	18321	8618	24239
7/7-10/67	379	33	.054	6833	4670	9525
9/8-13/67	303	76	.133	2404	1796	2720
11/11/67	108	27	.044	2399	1572	3466
12/26/67	56	17	.040	1873	860	2006
6/25-28/68	166	34	0.078	2096	1456	2862
9/23-24/68	400	60	.136	2898	2286	3509
12/24/68	85	47	.115	726	538	944

Table A-7. Continued.

Needle Branch						
					0.95 Confidence Interval	
Mark Date	No. Marked	No. Recapt'd	Mark Ratio	N_t	Lower	Upper
5/18/63	327	7	0.025	11568	4868	23690
6/20/63	350	19	.075	4445	2667	6872
7/16, 23/63	250	27	.096	2527	1656	3651
9/5, 10/63	181	38	.135	1313	953	1547
11/23/63	30	10	.039	772	357	1248
12/23/63	78	23	.085	920	563	1305
2/29/64	68	40	.158	421	324	486
4/19/64	300	4	0.033	7260	2338	18623
6/30/64	301	23	.152	1906	1368	3168
8/11/64	113	26	.188	619	428	904
10/31/64	57	22	.161	367	248	543
2/20/65	19	6	.077	214	84	464
4/24/65	300	4	0.030	14040	3692	17971
6/24/65	312	18	.090	3843	2052	5030
9/7/65	150	12	.081	2700	1053	2713
12/4/65	98	24	.102	960	676	1442
2/12/66	26	17	.070	354	204	561
5/28/66	300	8	0.027	9933	4425	19400
7/19/66	200	31	.109	1862	1290	2667
9/28/66	100	17	.064	1656	908	2282
10/14/66	101	22	.087	1115	698	1675
11/25/66	100	21	.088	1091	674	1657
5/13/67	355	14	0.056	5940	3252	9891
6/27-28/67	260	15	.054	4501	2521	7346
8/23-9/2/67	316	15	.080	4957	2300	5782
11/4/67	188	50	.199	1021	729	1213
1/13/67	139	27	.117	1152	822	1782
6/14-21/68	316	61	0.145	2146	1775	2953
9/25, 27/68	246	60	.143	1698	1382	2299
12/23/68	79	27	.116	657	459	1000

Table A-8. Interpolated values of population size (N) and individual weight (W, in grams) at beginning of each two week interval (Δt) for use in calculating instantaneous growth rate ($\Delta W/\overline{W}$), biomass ($\overline{NW}$), and net production rate ($\overline{N}\Delta W$).

	Deer Creek											
	1963		1964		1965		1966		1967		1968	
Date	N	W	N	W	N	W	N	W	N	W	N	W
June 1	19100	1.03	8800	1.12	22000	1.02	13700	1.72	23800	1.72	8900	1.24
15	17200	1.12	7400	1.30	20250	1.27	11700	1.88	20100	1.88	8500	1.45
July 1	14000	1.25	6250	1.56	18300	1.51	9700	2.07	16500	2.07	8175	1.71
15	11275	1.48	5300	1.80	15200	1.66	8400	2.25	13900	2.25	7900	1.98
Aug 1	9000	1.77	4775	2.10	11400	1.77	7250	2.45	11900	2.45	7750	2.25
15	7600	2.03	4500	2.44	9200	1.85	6600	2.66	10700	2.66	7600	2.50
Sept 1	6300	2.30	4400	2.77	7775	1.96	6000	2.83	9900	2.83	7500	2.75
15	5250	2.50	4275	3.15	7075	2.00	5700	3.03	9400	3.03	7350	3.00
Oct 1	4575	2.59	4225	3.50	6575	2.10	5575	3.22	8925	3.22	7200	3.30
15	4275	2.70	4175	3.80	6200	2.13	5400	3.43	8575	3.43	7100	3.53
Nov 1	4075	2.81	4025	4.06	5950	2.21	5275	3.60	8200	3.60	6750	3.73
15	4025	2.87	3950	4.29	5750	2.23	5175	3.77	8000	3.77	6400	3.80
Dec 1	3950	2.92	3800	4.45	5600	2.31	5000	3.90	7400	3.90	5950	4.05
15	3900	2.97	3750	4.66	5500	2.46	4850	4.10	6300	4.10	5300	4.18
Jan 1	3800	3.05	3525	4.80	5250	2.72	4600	4.32	4850	4.32	4500	4.30
15	3725	3.15	3200	4.98	4850	3.00	4300	4.72	3800	4.72	3750	4.45
Feb 1	3550	3.36	2600	5.16	4200	3.30	3900	5.10	3200	5.10	3000	4.64
15	3275	3.60	2025	5.53	3500	3.80	3450	5.58	2725	5.58	2500	4.90
Mar 1	2800	4.05	1500	6.00	2575	4.45	2900	6.10	2500	6.10	1900	5.35
15	2150	4.92	1100	6.80	1300	5.42	2100	6.80	2000	6.80	1500	6.18
Apr 1	1300	5.95	900	7.90	600	6.42	1200	7.64	1200	7.64	900	7.10
15	300	6.67	700	9.26	300	7.45	700	8.75	600	8.75	500	7.94

Table A-8. Continued.

	Flynn Creek											
	1963		1964		1965		1966		1967		1968	
Date	N	W	N	W	N	W	N	W	N	W	N	W
June 1	1875	1.80	5000	1.18	8900	1.22	8310	1.28	13600	1.18	3000	1.00
15	1800	2.22	3600	1.40	5150	1.32	6125	1.42	9900	1.25	2700	1.16
July 1	1700	2.63	2650	1.68	3150	1.45	4450	1.67	7600	1.35	2525	1.37
15	1600	3.08	2100	1.96	2600	1.60	3500	1.96	6000	1.50	2450	1.67
Aug 1	1525	3.52	1825	2.24	2200	1.72	3050	2.30	4525	1.68	2400	1.97
15	1450	3.95	1750	2.50	2000	2.07	2850	2.56	3600	1.80	2325	2.32
Sept 1	1375	4.35	1700	2.77	1800	2.32	2750	2.76	2900	1.96	2300	2.67
15	1300	4.73	1625	3.02	1700	2.54	2600	2.90	2550	2.01	2225	2.89
Oct 1	1225	5.12	1600	3.25	1675	2.71	2475	3.00	2325	2.06	2175	3.01
15	1175	5.43	1525	3.41	1600	2.80	2375	3.05	2200	2.10	2025	3.10
Nov 1	1025	5.70	1450	3.54	1600	2.85	2225	3.10	2175	2.12	1975	3.13
15	1000	5.88	1400	3.67	1600	2.85	2125	3.15	2100	2.18	1750	3.27
Dec 1	900	5.99	1350	3.80	1600	2.87	2000	3.20	1950	2.34	1350	3.50
15	800	6.07	1275	3.96	1500	2.90	1900	3.43	1700	2.66	900	3.96
Jan 1	775	6.13	1200	4.13	1425	3.12	1750	3.80	1475	3.18	625	4.60
15	725	6.20	1100	4.36	1300	3.48	1600	4.26	1200	3.83	576	4.97
Feb 1	700	6.23	1000	4.63	1100	3.96	1400	4.80	950	4.64	475	5.22
15	625	6.25	850	5.07	900	4.40	1200	5.43	800	5.66	400	5.56
Mar 1	600	6.32	800	5.55	600	4.84	925	6.10	625	6.68	350	5.98
15	500	6.60	650	6.13	400	5.32	700	6.83	500	7.87	275	6.53
Apr 1	400	7.20	500	6.70	200	5.74	300	7.62	400	9.05	200	7.22
15	200	8.00	300	7.17	100	6.20	100	8.40	300	10,17	100	8.18

Table A-8. Continued.

	Needle Branch											
	1963		1964		1965		1966		1967		1968	
Date	N	W	N	W	N	W	N	W	N	W	N	W
June 1	4300	0.86	3500	1.21	4400	1.20	8200	0.98	4825	1.52	2500	1.31
15	3800	.92	2600	1.29	3600	1.28	4650	1.20	4600	1.80	2200	1.53
July 1	3100	1.02	1800	1.39	3100	1.35	2800	1.52	4500	2.13	2075	1.73
15	2475	1.28	1200	1.73	2700	1.45	1800	1.90	4350	2.05	2000	1.92
Aug 1	1950	1.60	700	2.30	2350	1.57	1400	2.33	4200	1.97	1900	2.10
15	1600	1.88	525	2.68	2100	1.75	1225	2.86	4075	1.90	1850	2.32
Sept 1	1375	2.10	475	2.90	1850	1.96	1200	3.31	3800	1.82	1800	2.50
15	1225	2.30	400	3.12	1625	2.14	1200	3.67	3425	2.10	1750	2.70
Oct 1	1200	2.46	375	3.32	1500	2.32	1175	3.90	2800	2.35	1700	2.86
15	1125	2.60	350	3.45	1325	2.47	1100	3.95	2100	2.52	1600	3.04
Nov 1	1075	2.70	300	3.59	1175	2.60	1075	4.02	1275	2.64	1450	3.23
15	1025	2.79	275	3.70	1025	2.70	1075	4.14	1150	2.80	1275	3.44
Dec 1	975	2.84	200	3.82	850	2.75	1050	4.48	1100	2.96	1075	3.64
15	925	2.86	200	4.00	800	2.90	950	4.82	1050	3.16	825	3.88
Jan 1	850	2.90	200	4.23	650	3.10	800	5.25	1000	3.40	600	4.17
15	800	2.97	200	4.57	525	3.32	650	5.74	1000	3.76	475	4.50
Feb 1	775	3.18	200	4.94	400	3.52	525	6.30	975	4.20	375	4.90
15	600	3.47	180	5.34	325	3.82	350	6.96	800	4.79	225	5.40
Mar 1	400	3.98	175	5.80	200	4.10	200	7.70	500	5.42	75	6.05
15	300	4.58	150	6.18	150	4.38	100	8.53	100	6.20	50	6.82
Apr 1	200	5.25	125	6.62	100	4.73	50	9.30	25	7.05	20	7.84
15	100	5.90	100	7.32	50	5.23	20	10.00	0	8.00	0	9.18

Table A-9. Mean lengths (mm) from stream (S) and downstream trap (T), and standard deviations of lengths (parentheses) by date and year class. Standard deviations were used as guides in drawing growth curves and were calculated only for resident fish and smolts.

Deer Creek

	1963			1964			1965			1966			1967			1968		
Month	Day	S	T	Day	S	T	Day	S	T	Day	S	T	Day	S	T	Day	S	T
F						37.8									39.5			37.7
M						38.7			39.8			39.2			40.0			39.1
A						39.7			38.6			38.8			40.7			38.7
M	4	44.4	42.3	2	42.8	40.5	22	43.0	39.4			38.0	20	48.3				
		(4.29)			(3.29)			(4.11)						(7.78)				
J	19	46.0	43.9	7	51.2	41.2			40.5	18	51.7							
		(6.28)			(6.27)						(6.74)							
Jl	17	51.6	45.7				12	47.7	57.1				6	50.8		2	54.0	
		(7.82)						(6.33)						(7.16)			(7.96)	
A				17	59.9					2	54.5							
					(7.05)						(6.81)							
S	3	58.8								9	60.0		14	57.7				
		(9.57)									(8.98)			(8.18)				
O				17	68.7		2	57.3								1	67.5	
					(7.43)			(8.27)									(9.06)	
N	20	62.9	63.2			70.1			61.8	5	65.2	62.8	18	62.3	60.6			71.4
		(10.30)				(6.82)			(8.25)		(9.18)	(8.39)		(8.41)	(7.82)			(8.83)
D	29	66.2				75.0	23	59.9	63.5			69.5	27	64.7	64.4	26	74.0	74.4
		(10.03)				(7.13)		(7.87)	(8.96)			(7.11)		(8.49)	(7.91)		(8.72)	(9.37)
J						73.4			65.2			72.2			63.5			77.6
						(6.38)			(8.25)			(7.02)			(5.23)			(8.82)
F	22	69.9	69.0	3	79.6	76.0			71.4			75.8			71.4			77.9
		(6.17)	(9.04)		(8.67)	(7.19)			(9.83)			(7.87)			(7.76)			(7.59)
M			77.2			83.4			78.9			81.0			82.5			83.4
			(9.86)			(7.55)			(11.08)			(8.20)			(9.26)			(8.23)
A			84.9			92.1			89.0			90.0			90.0			92.3
			(11.42)			(10.43)			(9.29)			(10.87)			(10.0)			(9.92)
M			88.6			100.1			93.0			99.0						96.7
			(9.01)			(8.88)			(7.69)			(9.64)						(8.82)

Table A-9. Continued.

Flynn Creek

	1963			1964			1965			1966			1967			1968		
Month	Day	S	T	Day	S	T	Day	S	T	Day	S	T	Day	S	T	Day	S	T
F				26	42.5 (3.62)	41.2									40.5			
M						39.5						39.2			40.1			38.5
A	13	42.0 (2.12)				39.8			36.4			39.8			40.7			37.7
M						39.6			38.6			39.4	27	45.0 (6.87)	39.6			
J	11-13	57.0 (5.93)					5	44.6 (5.28)	40.1	23	48.6 (5.18)				40.6	25-28	49.6 (6.96)	
Jl	26-27	65.2 (5.81)					1	46.5 (5.94)	42.3			41.0	7-10	50.4 (6.81)				
A				12-13	61.0 (8.13)					3-4	56.2 (7.14)							
S	10	72.1 (7.90)					8-10	57.8 (8.53)		7	60.4 (7.24)	47.5	8-13	55.8 (9.75)		23-24	64.9 (9.43)	
O				24	68.0 (7.34)		30	61.8 (7.91)										
N	30	81.0 (8.25)				69.7 (7.05)						61.8 (7.37)	11	57.3 (9.04)				64.9 (10.31)
D			82.0 (9.65)			72.9 (6.77)			60.0	19	65.2 (10.45)	65.0 (6.98)	26	62.9 (9.34)		24	73.8 (8.14)	71.6 (11.17)
J						74.8 (7.20)	22	69.0 (8.92)	68.3 (6.01)			71.8 (10.43)						75.7 (9.27)
F	1	82.0 (8.31)		23	75.4 (9.17)	78.6 (7.94)	26	73.3 (9.28)	72.1 (6.74)			77.4 (6.59)			76.4 (7.30)			78.4 (6.20)
M	21	85.13 (7.74)	83.0 (7.40)			84.0 (8.33)			78.0 (6.97)			82.0 (10.14)			82.6 (7.38)			83.6 (7.68)
A			89.0 (10.05)			87.0 (8.39)			84.0 (8.35)			88.3 (10.91)			91.9 (8.76)			88.6 (9.88)
M			97.0 (9.44)			89.0 (8.78)			87.0 (10.39)			96.0 (8.94)			94.5 (8.48)			98.5 (7.81)

Table A-9. Continued.

		Needle Branch																
		1963		1964			1965			1966			1967			1968		
Month	Day	S	T	Day	S	T	Day	S	T	Day	S	T	Day	S	T	Day	S	T
F						37.7												
M	18	43.0 (3.74)	41.0			38.5			39.3			39.0			38.7			38.8
A				19	44.0	39.2	24	41.2 (2.42)	39.5			38.8			40.8			39.8
M						41.4			39.2	28	44.4 (4.26)	40.5	13	49.2 (6.06)	40.6			40.4
J	20	44.8 (4.22)	43.0	30	47.5 (4.57)	51.0	24	44.4 (4.91)	42.1			48.2 (7.88)	27-28	59.0 (8.74)	45.4	14-21	52.2 (6.94)	44.8
Jl	16-23	50.9 (7.23)	46.2						44.8	19	56.6 (7.23)	51.7 (5.98)						47.7
A				11-13	58.5 (8.57)								30	55.9 (8.25)				49.1
S	5-10	58.3 (9.07)					7	54.2 (9.31)		28	70.3 (7.48)					25-27	63.5 (10.05)	55.0
O				31	66.3 (9.19)				52.0	14	70.7 (8.29)				54.9 (4.99)			61.4 (6.72)
N	23	63.5 (9.32)	65.5						49.0	25	74.1 (11.20)	70.6 (6.87)	4	63.7 (8.74)	54.8 (4.83)			65.8 (9.04)
D	23	63.9 (8.52)					4	63.1 (10.57)				76.9 (6.02)			68.5 (10.69)	23	73.5 (8.64)	69.4 (9.85)
J	29	69.8 (9.86)		9	71.2								13	68.6 (9.24)	72.2 (9.20)			73.1 (11.72)
F			69.6 (9.32)	20	77.3 (9.87)	81.1 (10.36)	12	73.0 (9.31)	70.6 (10.50)			84.5 (8.80)			77.3 (10.33)			73.5 (9.43)
M			73.0 (8.59)			79.6 (7.86)			74.4 (10.61)			90.0 (7.96)			83.5 (8.20)			86.4 (12.23)
A			80.6 (8.69)			85.7 (7.44)			83.7 (8.49)			96.0 (11.18)			91.8 (9.75)			93.3 (9.64)
M			83.8 (6.57)			89.8 (7.75)			87.9 (11.22)			99.0 (9.86)			93.6 (8.70)			80.2 (20.14)