FACTORS DETERMINING PRODUCTION OF COHO SALMON, *ONCORHYNCHUS KISUTCH*, IN THREE OREGON STREAMS

by

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FACTORS DETERMINING PRODUCTION OF COHO SALMON, *ONCORHYNCHUS KISUTCH*, IN THREE OREGON STREAMS

INTRODUCTION

General

This investigation, which was conducted in the Alsea Basin of Oregon from July, 1958, to March, 1961, was designed to measure production of coho salmon, *Oncorhynchus kisutch* (Walbaum), in terms of tissue elaborated in successive time intervals during the period of residence of coho in fresh water, and to determine some of the factors influencing this production. The study of fish production was part of a larger project which had the objective of determining the effects of two types of logging upon the aquatic resources of small coastal watersheds in Oregon. This logging-aquatic resources study was, in turn, part of a river basin investigation initiated in July, 1957, by the Oregon State Natural Resources Committee at the request of the state legislature. On July 1, 1959, this basin study was transferred to Oregon State College. The objective of the study was to learn how to obtain maximum resource productivity of a river basin. The Alsea River Basin (Figure 1) was chosen for this study, and several projects were undertaken by participators in the Natural Resources Committee as phases of the basin study. These projects included a soil-vegetation survey, a water resources inventory, a small-impoundment study, and a logging-aquatic resources study.

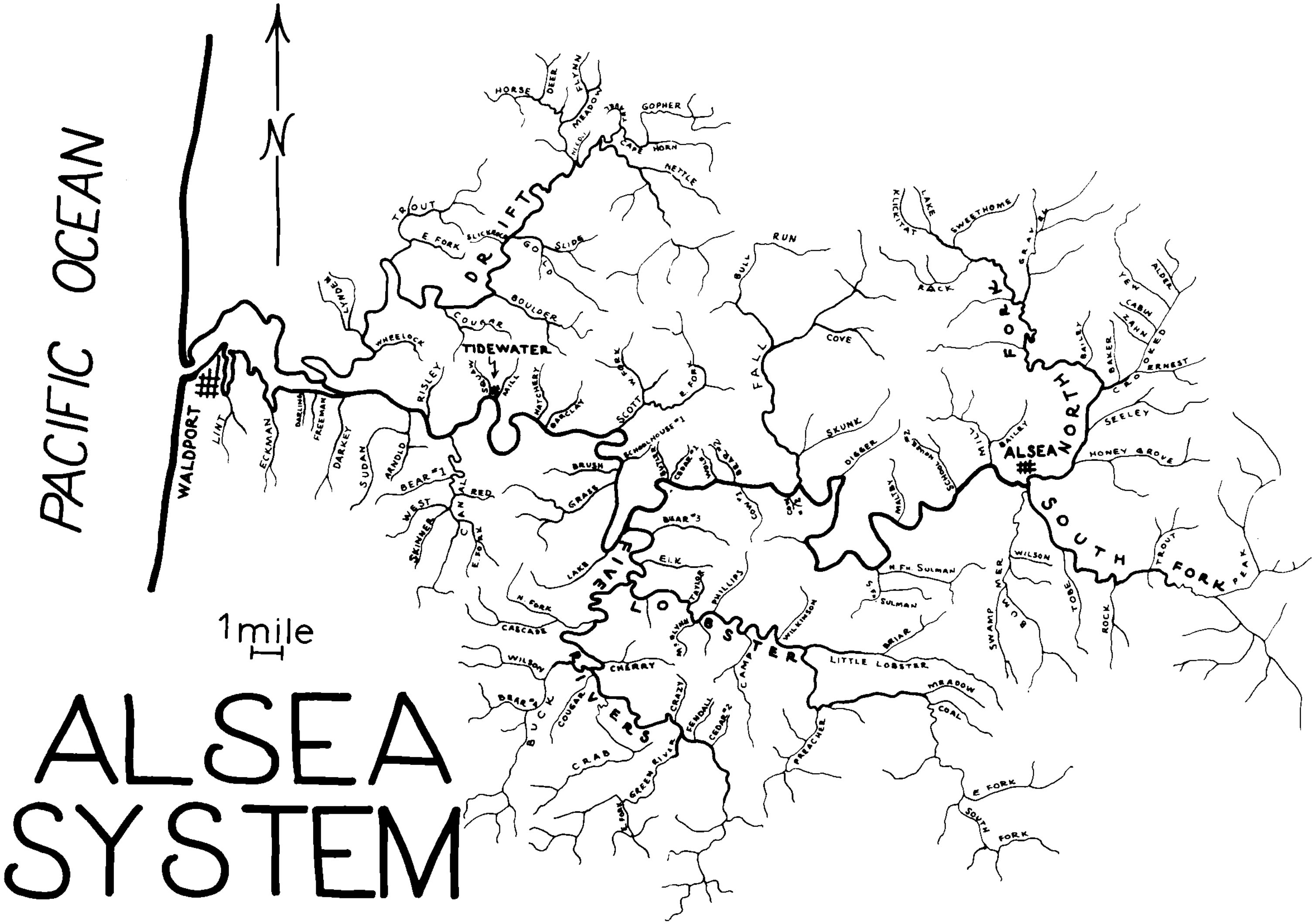
ALSEA SYSTEM
PACIFIC OCEAN
N
1 mile
WALDPORT
TIDEWATER
ALSEA
DRIFT
FALL
FIVE RIVERS
LOBSTER
NORTH FORK
SOUTH FORK
HORSE
DEER
FLYNN
MEADOW
GOPHER
CAPE HORN
NETTLE
TROUT
E. FORK
SLICKROCK
GOLD
SLIDE
BOULDER
COUGAR
LYNDEN
WHEELOCK
RISLEY
MILL
HATCHERY
BARCLAY
SCOTT
N. FORK
E. FORK
BULL RUN
COVE
SKUNK
DIGGER
KLICKITAT
LAKE
SWEETHOME
RACK
GRAY
YEW
ALDER
CABIN
ZAHN
BAILEY
BAKER
CROOKED
ERNEST
SEELEY
HONEY GROVE
LINT
ECKMAN
DARLING
FREEMAN
DARKEY
SUDAN
ARNOLD
BEAR #1
WEST
CANAL
RED
SKINNER
E. FORK
BRUSH
GRASS
SCHOOLHOUSE #1
CEDAR #1
BEAR #2
BEAR #3
ELK
LAKE
TAYLOR
PHILLIPS
McCLYAN
N. FORK
CASCADE
WILSON
BEAR #4
BUCK
COUGAR
CHERRY
CRAB
GREEN RIVER
CRAZY
FENDALL
CEDAR #2
CAMP
WILKINSON
N. FK. SULMAN
S. FK. SULMAN
BEAR
LITTLE LOBSTER
MEADOW
COAL
PREACHER
E. FORK
SOUTH FORK
MALTBY
SCHOOLHOUSE #2
SWAMP
BUMMER
WILSON
TOBE
ROCK
TROUT
PEAK

Figure 1

The logging-aquatic resources investigation was designed to study the effects of timber harvest upon stream runoff, water quality, and biology. Three watersheds were chosen within the Alsea River Basin. These uncut drainages were to be evaluated for six or seven years before logging took place. After this "calibration" period, timber on one drainage was to be clear-cut, timber on another was to be cut with a harvest method such as staggered-setting logging, and cover on the third was to be left undisturbed as a control area. Post-logging study was to continue for a time sufficient for evaluation of the changes caused by timber harvest.

Physical factors to be investigated on the three streams were soil characteristics, stream runoff patterns and quantity, water temperature regimes, suspended-sediment loads, and chemical water quality. Biological studies included vegetation of the watersheds, algal production, insect food habits, the role of organic material of terrestrial origin in the stream food web, survival of salmonid embryos during the incubation period, and production of salmonids.

Production as defined by Ivlev (25, p. 98-120) is the elaboration in a given time of new tissue in a given group or population of organisms, regardless of the fate of this tissue. Production in this sense can be estimated from knowledge of the cohort size and growth rate of the animals considered, in this case the coho salmon. Mortality influences production insofar as it changes cohort size and growth rate.

The general approach taken here to study coho production was to evaluate production, then to investigate some of the factors strongly influencing standing crop and growth rate of coho in the waters studied. An investigation of mortality causes would be a logical step in a study of reasons for standing crop changes. However, a perhaps more important cause of standing crop decrease suggested itself when it was learned that young coho moved out of the study streams throughout the year prior to smolt migration. This "drift" downstream of young fish appears to occur in most Pacific Coast streams for which data are available, as will be discussed in a later section. Knowledge that "drift" existed, and behavior work done by Hoar (21, p. 241-263), Kalleberg (27, p. 55-98), and others, indicated that the downstream movement of young coho (resulting in a decrease in standing crop) might be caused at least partly by social behavior in the coho population. Therefore, this area of study was selected as an interesting and important one. Causes of mortality were left for later study.

The small coastal streams of Oregon in which coho grow to smolt size are frequently heavily shaded and are apparently poor in aquatic primary producers. Thus, a question arose as to the energy sources of organisms utilized by coho for maintenance, growth, and hence production. The relative importance of aquatic and terrestrial plants as fixers of energy utilized in the aquatic environment became a matter of considerable interest when Demory (15), studying the streams used in the logging-aquatic resources project, learned that a substantial portion of the coho diet consisted of insects of terrestrial origin. Further, he learned that two insect forms important in the coho diet utilized substantial amounts of organic detritus of terrestrial origin as an energy source rather than algal material alone.

Demory was able to work on three aquatic insect groups that made up to 10 to 20 per cent of the aquatic part of the coho diet. It seemed worthwhile to supplement his effort with study of as many additional aquatic insect groups as possible, insofar as these groups were important to the coho. In this way, an attempt could be made to arrive at a preliminary estimate of the relative amounts of energy from the terrestrial and aquatic environments utilized in the coho food web. In short, the question to be answered was: What is the principal means of energy fixation leading to coho maintenance and growth?

In summary, then, this paper will deal principally with production of coho salmon in three small streams, the social behavior of coho as one mechanism regulating standing crop (and thus production), and the energy sources of organisms used by coho salmon in maintenance and production.

These topics make up three sections of the paper. Another section, the first, deals in detail with the physical characteristics of the three study streams. A brief and general description of the streams and their watersheds is included below, before the main body of the paper, as a means of orientation.

Description of Area

The three streams selected for study were Deer Creek, Flynn Creek, and Needle Branch, in Lincoln County, about 10 miles south of Toledo, Oregon (Figure 2). Deer Creek is a tributary of Horse Creek, a tributary of Drift Creek. Flynn Creek is a tributary of Meadow Creek, a tributary of Horse Creek. Needle Branch is a tributary of Drift Creek, entering the latter stream about 200 feet above the Horse Creek-Drift Creek confluence. Drift Creek enters Alsea Bay about four miles east of Waldport. The waters of the bay join the Pacific Ocean about one mile west of Waldport. The estuary is open to the sea at all times of year.

The study streams are described in some detail in the next section, but first a general summary of their features would be helpful. All three streams have extremely variable flows. Low flows range from less than one cubic foot per second (c.f.s.) in the summer, while high flows range from 15 to 76 c.f.s., depending on the stream. The Deer Creek drainage area is the largest, about 815 acres; the Flynn Creek drainage area is about 550 acres; Needle Branch drains about 230 acres. Elevations of the

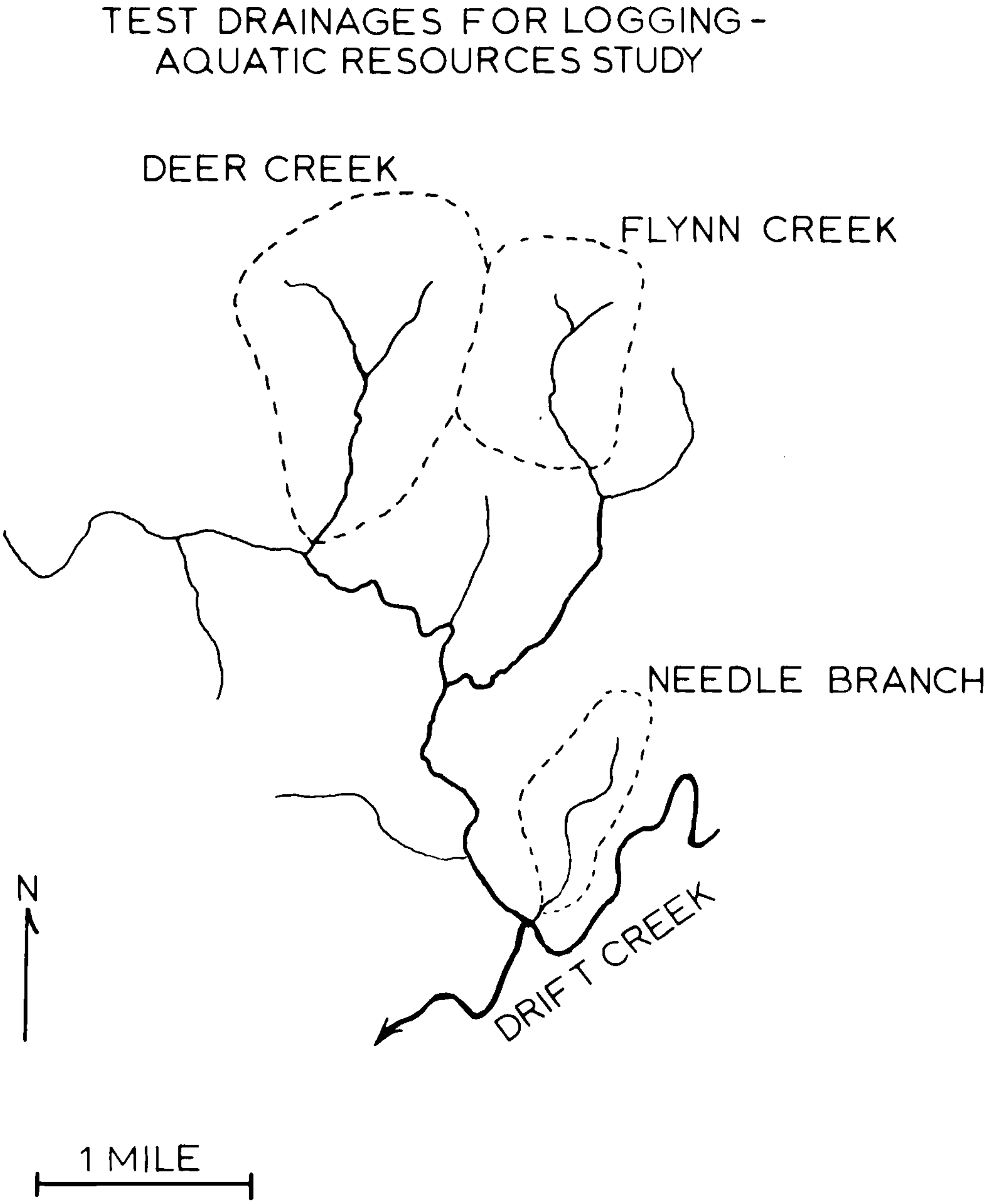
TEST DRAINAGES FOR LOGGING-
AQUATIC RESOURCES STUDY
DEER CREEK
FLYNN CREEK
NEEDLE BRANCH
DRIFT CREEK
N
1 MILE

Figure 2

streams at stream gage sites are 600 feet at Deer Creek, 685 at Flynn Creek, and 460 feet at Needle Branch. The streams flow over riffles with gravel bottoms and pools with silt bottoms, some stretches having rubble bottoms. They are densely shaded over most of their length. Areas open to direct sunlight are rare. The shade is a result of a heavy streamside overstory of deciduous vegetation and also conifers where these are close to the stream.

The following fishes are known to occur in all three streams: coho salmon, coastal cutthroat trout, *Salmo clarki clarki*, Richardson; *Cottus perplexus*, Gilbert and Evermann; steelhead trout, *Salmo gairdnerii gairdnerii*, Richardson; Pacific lamprey, *Entosphenus tridentatus* (Gairdner); and brook lamprey, *Lampetra planeri* (Bloch). Steelhead trout occur in Flynn Creek and Needle Branch as occasional juveniles only, but adult steelhead spawn in Deer Creek and the young develop and grow there.

STREAM CHARACTERISTICS

Methods for Determining Stream Characteristics

The following stream and drainage characteristics were inventoried or described: streamflow, rainfall, vegetation, water temperature, suspended-sediment loads, total light incidence, water chemistry, and physical characteristics of the streams such as total surface area. Physical characteristics of each stream were obtained by means of measurements and qualitative estimates in August and include total low water area, area of spawning gravel, length and area in pool, length and area in riffle, mean depth, mean high water stream area and area of gravel. The stream length was measured in 25, 50, and occasionally 100 foot sections. Width and depth were taken at the ends of sections. Gravel areas and lengths of pool and riffle were estimated by consideration of the entire length of each section.

Surface area for each stream was estimated only in that area available to coho salmon. In all three cases, the live stream areas above the uppermost points available to salmon were quite small, probably less than five per cent of the inhabited areas. While errors were obviously inherent in the survey methods used, the estimates were probably no more than 10 per cent higher or lower than the true values. Perhaps the most arbitrary estimates were those of gravel area. Spawning gravel was considered to be a bottom area larger than nine square feet that contained particles larger than sand, but no particles larger than four inches in largest dimension. Admittedly, gravel particles over four inches, and others possibly as small as sand, would be utilized by salmon, especially in years of high spawning density. It was believed that the arbitrary definition of spawning gravel would include over 90 per cent of the usable spawning area.

Stream gage heights were recorded at standard U. S. Geological Survey gaging stations above V-notch weirs. Water flow was determined from gage heights by means of calibration curves. Water temperatures were recorded continuously at the stream gages. Suspended sediment samples were usually taken at least daily during periods of stream fluctuation, but were taken only weekly in stable periods such as in midsummer. These samples were analyzed and correlated with stream flow to obtain stage-discharge relationships. The U. S. Geological Survey performed these computations. Rainfall was recorded continuously on weighing rain recorders of the standard U. S. Weather Bureau type. Light incidence was recorded with pyrheliometers, which record light energy in gram calories. Water samples for chemical analysis were collected by the Oregon State Sanitary Authority and standard methods of analysis were used. Analyses usually included pH, dissolved oxygen, sulfite, chloride, phosphate, ammonia nitrogen, total solids, suspended solids, dissolved solids, turbidity, color, alkalinity, hardness, and sodium.

As the physical characteristics of the streams were inventoried, permanent markers were placed on each 100 foot "station" to facilitate random or systematic sampling procedures in various aspects of the stream studies. When station numbers are mentioned in the text, these refer to the number of feet upstream from the stream gaging weir on each stream.

Where possible, data on stream characteristics were tabulated or graphed for the period of stream residence of the 1959 year class of coho. This period extended from February, 1959, to June, 1960.

Results of Stream Characteristics Determinations

The habitable areas for coho salmon in the three study streams at low water in 1959 were as follows: Deer Creek--51,140 square feet (4,753 square meters); Flynn Creek--26,454 square feet (2,459 square meters); Needle Branch--9,616 square feet (893 square meters). Table 1 gives these and the gravel, pool, and riffle areas in the coho rearing areas.

Low water estimates are probably fairly accurate, but the high water area values were estimated during summer and are only approximations. Stream elevation decrease in the areas inhabited by coho salmon above the fish traps were: Deer Creek, 200 feet; Flynn Creek, 175 feet; Needle Branch, 150 feet. Drop per 100 feet was about 2.8 feet on Deer Creek, 3.9 feet on Flynn Creek, and 5.5 feet on Needle Branch.

Table 1. Physical characteristics of streams during residence of 1959 year class of coho.

	Deer Creek		Flynn Creek		Needle Branch	
	U.S.	Metric	U.S.	Metric	U.S.	Metric
Low Water						
Total area	51,140 ft^2	4,753 m^2	26,454 ft^2	2,459 m^2	9,616 ft^2	893 m^2
Total gravel area	16,587 ft^2	1,541 m^2	6,758 ft^2	628 m^2	4,215 ft^2	392 m^2
Per cent gravel	32.4 %	32.4 %	25.5 %	25.5 %	43.8 %	43.8 %
Total pool area	30,931 ft^2	2,875 m^2	13,701 ft^2	1,273 m^2	5,810 ft^2	540 m^2
Total riffle area	20,209 ft^2	1,878 m^2	12,753 ft^2	1,185 m^2	3,806 ft^2	353 m^2
Mean depth	4.0 in.	.102 m	4.14 in.	.105 m	2.34 in.	.060 m
High Water						
Total area	109,348 ft^2	10,162 m^2	45,606 ft^2	4,238 m^2	16,700 ft^2	1,551 m^2
Total gravel area	79,129 ft^2	7,351 m^2	10,927 ft^2	1,015 m^2	7,655 ft^2	711 m^2
Per cent gravel	72.4 %	72.4 %	24.0 %	24.0 %	45.8 %	45.8 %

Stream flows for the period February 1, 1959, to June 30, 1960, are shown in Figures 3 and 4, and in Appendix 1. Deer Creek extremes were 0.5 and 68 c.f.s.; Flynn Creek extremes were 0.2 and 42 c.f.s.; Needle Branch extremes were 0.1 and 14 c.f.s. Mean flows in July and August, respectively, were 1.01 and 0.56 c.f.s. on Deer Creek, 0.65 and 0.30 c.f.s. on Flynn Creek, and 0.15 and 0.10 c.f.s. on Needle Branch.

The reason for the great variability in streamflow on the study streams can be seen in Figure 5 and Appendix 2, which show rainfall for the period from February 1, 1959, to June 1, 1960. Figure 5 shows rainfall for Deer Creek only. Precipitation on the other two streams shows a similar pattern, but total fall for the year July 1, 1959, to June 30, 1960, varied among the three streams: Deer Creek, 98.83 inches; Flynn Creek, 91.76 inches; Needle Branch, 101.50 inches. Distance between gages is shown in Appendix 2.

Temperatures of the three streams (Figure 6) show a remarkable lack of extreme fluctuation. Maxima and minima for the period February, 1959, to June 1, 1960, in degrees Fahrenheit were: Deer Creek, 58 and 40; Flynn Creek, 58 and 39; Needle Branch, 58 and 37. Mean low values during the salmonid embryo incubation period, December, 1958, through May, 1959, were 47 degrees on all three streams. During this incubation period, extreme values were 54 and 42 degrees on Deer Creek, 52 and 42 on Flynn Creek, 51 and 41 on Needle Branch. Of course, these

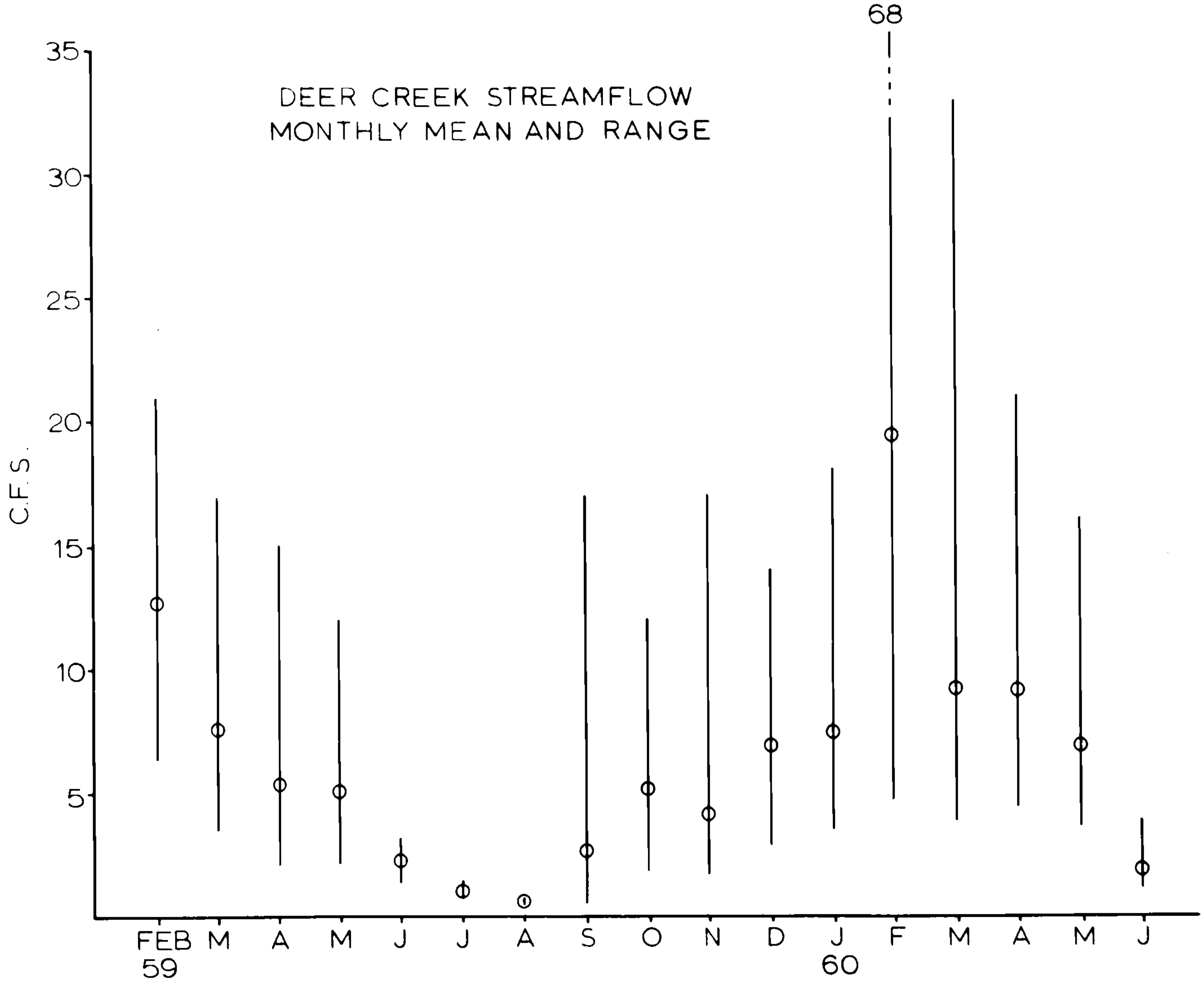
DEER CREEK STREAMFLOW
MONTHLY MEAN AND RANGE
C.F.S.
35
30
25
20
15
10
5
68
FEB 59
M
A
M
J
J
A
S
O
N
D
J 60
F
M
A
M
J

Figure 3

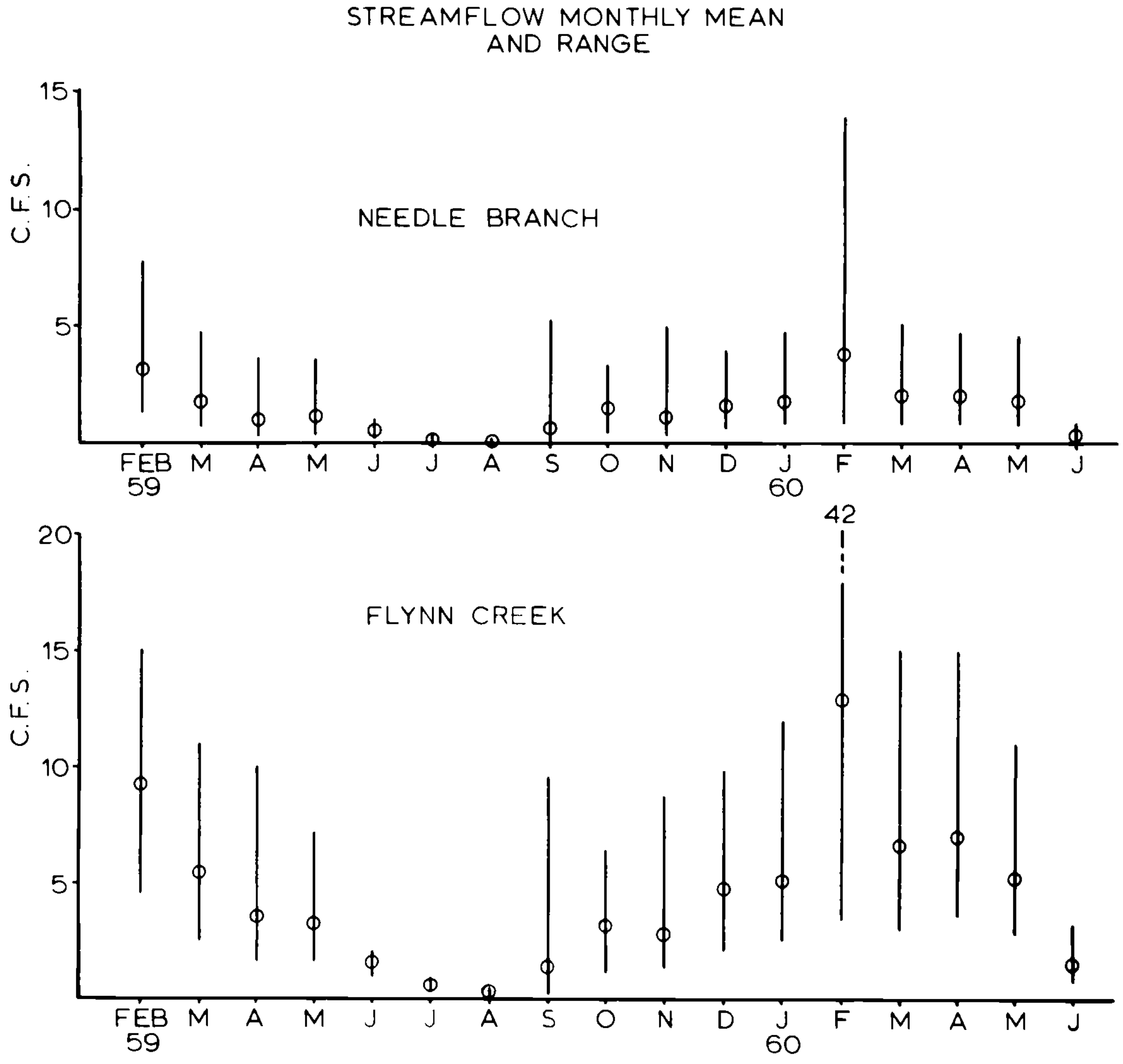
STREAMFLOW MONTHLY MEAN
AND RANGE
NEEDLE BRANCH
C.F.S.
15
10
5
FEB
59
M
A
M
J
J
A
S
O
N
D
J
60
F
M
A
M
J
42
FLYNN CREEK
C.F.S.
20
15
10
5
FEB
59
M
A
M
J
J
A
S
O
N
D
J
60
F
M
A
M
J

Figure 4

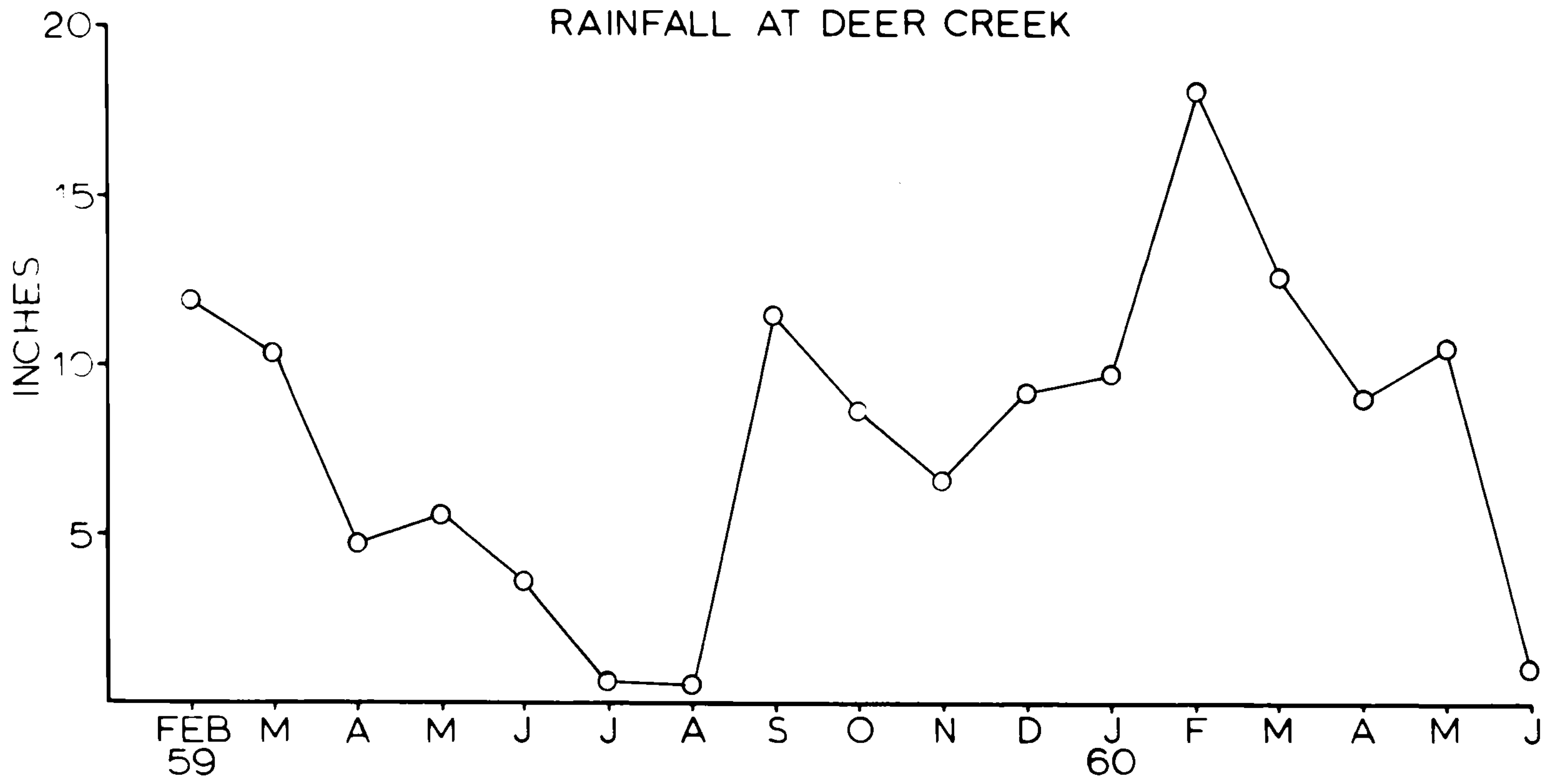
RAINFALL AT DEER CREEK
20
15
10
5
INCHES
FEB
59
M
A
M
J
J
A
S
O
N
D
J
60
F
M
A
M
J

Figure 5

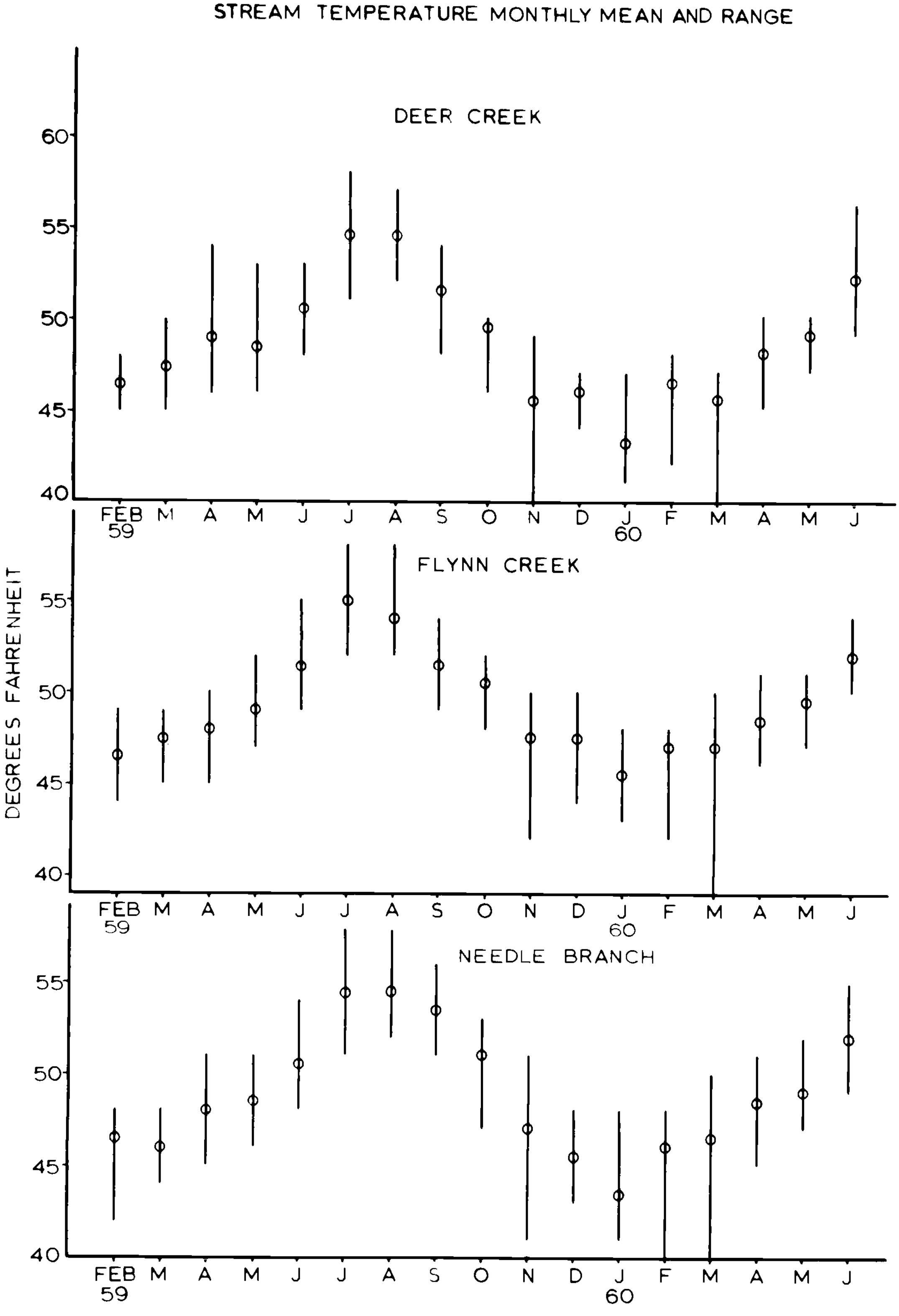
STREAM TEMPERATURE MONTHLY MEAN AND RANGE
DEER CREEK
FLYNN CREEK
NEEDLE BRANCH
DEGREES FAHRENHEIT
60
55
50
45
40
FEB 59
M
A
M
J
J
A
S
O
N
D
J 60
F
M
A
M
J

Figure 6

were surface water temperatures, and it is likely that intragravel water was slightly less variable in temperature.

Suspended sediment loads borne by the three streams are shown in Figures 7 and 8, and Appendix 3. Maximum values for the period of record were: Deer Creek, 104 ppm and 19 tons per day; Flynn Creek, 82 ppm and 11 tons per day; Needle Branch, 72 ppm and 2.2 tons per day. Minimum values were approximately 0 ppm and, of course, zero tonnage borne. The maxima occurred on about January 8, 1959. Even in periods of maximum sediment load, the streams were relatively clear and greenish. The streams rarely appeared muddy. This might be expected, except in extreme freshets, since the drainages are undisturbed. Needle Branch has a small patch of cut over land on its headwaters, but the cutting occurred several years previous to the beginning of the study, and the area appears to be well stabilized with vegetation.

Chemical water quality data obtained from the study streams are shown in Table 2. Concentrations in parts per million of total phosphates were greatest in late fall. This period is the time of maximum leaf fall and the early part of the period when adult coho salmon carcasses are decomposing. At this time, winter flows have not yet flushed much of the decaying plant and animal matter downstream.

Needle Branch tended to have a lower pH (laboratory), lower alkalinity, and lower hardness than the two larger streams. The

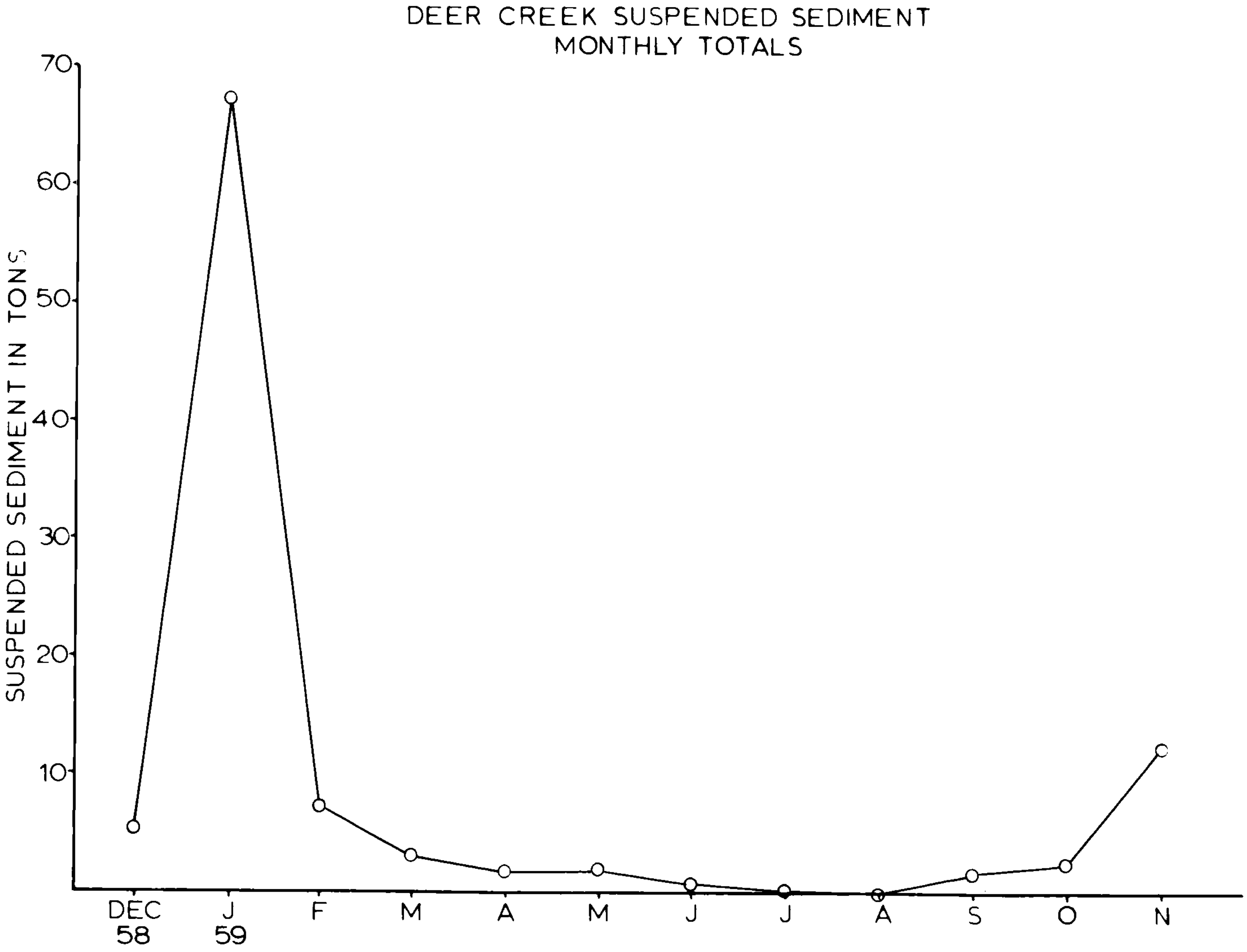
DEER CREEK SUSPENDED SEDIMENT
MONTHLY TOTALS
SUSPENDED SEDIMENT IN TONS
70
60
50
40
30
20
10
DEC 58
J 59
F
M
A
M
J
J
A
S
O
N

Figure 7

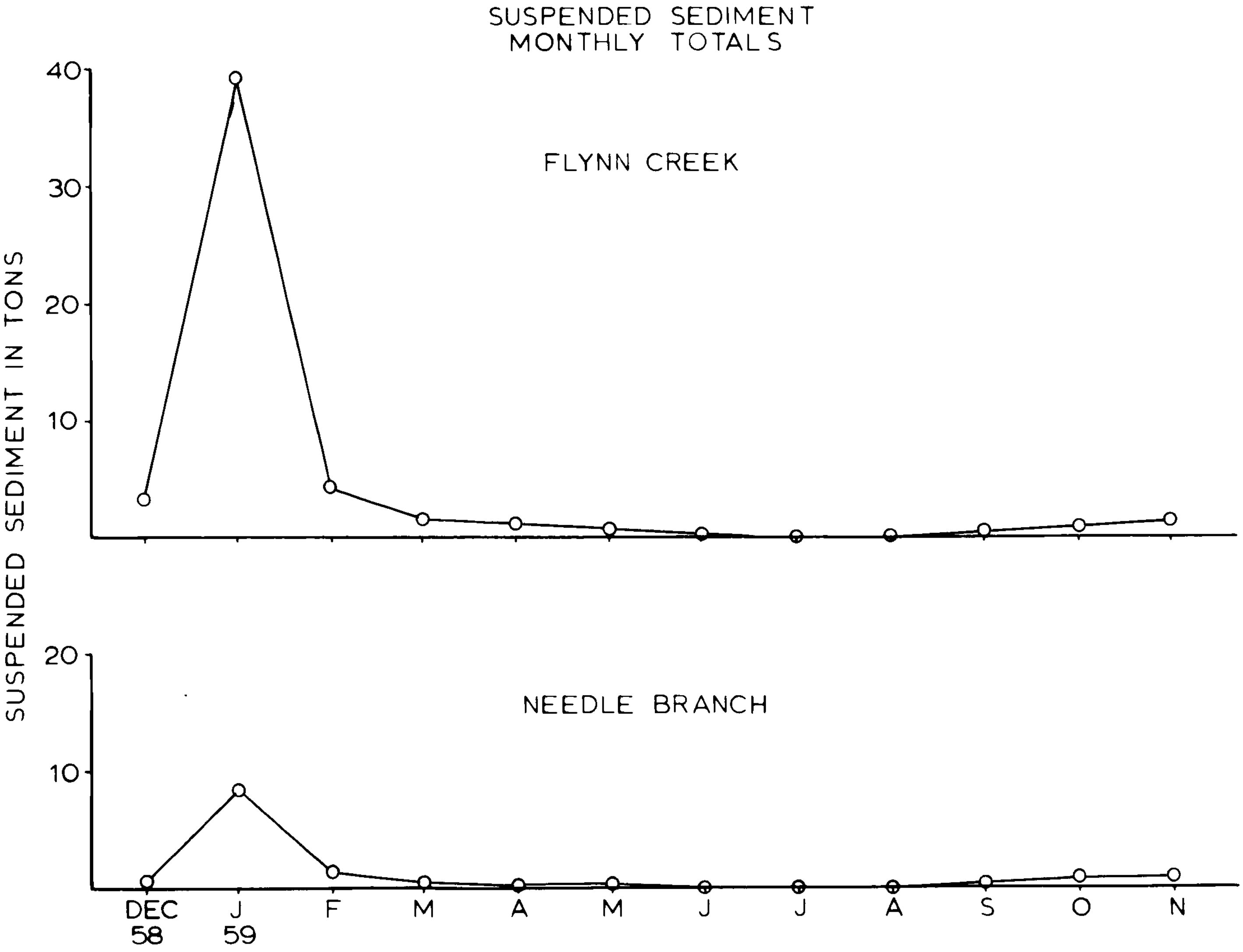
SUSPENDED SEDIMENT
MONTHLY TOTALS
SUSPENDED SEDIMENT IN TONS
FLYNN CREEK
40
30
20
10
NEEDLE BRANCH
20
10
DEC 58
J 59
F
M
A
M
J
J
A
S
O
N

Figure 8

Table 2ue, 1960.

Date and stream	Turbidity	Color	pH (lab)	Alkalinity as $CaCO_3$ - ppm	Hardness as $CaCO_3$ - ppm	Sodium (Na^+) - ppm
10/15/58						
Deer	2	14	6.45	13	14.1	5.5
Flynn	7	10	6.19	1	14.2	6.0
Needle	2	17	5.81	8	12.0	5.5
11/12/58						
Deer	7.5	31	6.8	21.0	21.4	4.2
Flynn	5.0	23	6.85	21.0	23.4	5.3
Needle	7.5	32	6.75	20.0	20.4	4.3
1/21/59						
Deer	0.3	5	6.80	9.0	11.2	5.1
Flynn						
Needle	1.5	6	6.40	8.0	8.1	4.5
8/10/59						
Deer	< 1	4	6.08	11.2	11.6	5.7
Flynn	< 1	4	6.25	9.5	13.0	5.5
Needle	< 1	4	5.90	9.2	10.8	4.8
11/10/59						
Deer	4	10	6.27	9.7	15.2	5.5
Flynn	4	4	6.13	8.4	14.4	5.4
Needle	5	7	6.00	8.0	14.2	5.0
4/21/60						
Deer	5	20	6.59	7.4	13.6	6.9
Flynn	5	15	6.60	7.0	18.0	5.2
Needle	5	15	6.50	8.0	10.8	4.1
6/14/60						
Deer	4	5	6.81	7.0	28.1	5.9
Flynn	5	5	6.73	10.3	15.4	5.1
Needle	4	7	6.66	9.2	9.7	5.1

slightly greater acidity may have been due to relatively greater content of decomposing leaf material per unit of water-covered area.

Although necessarily qualitative, a description of the streams as habitat for algal and insect forms is appropriate here. One of the most important factors governing algal production is light availability. As has already been mentioned, the study streams are densely shaded. The extent of this shading may be expressed in general terms. In conditions where moisture tends to be plentiful, as along the bottom land adjoining the study streams, the vegetation, if undisturbed, forms a complete canopy. This canopy consists mostly of red alder, Alnus rubra Bong, on about the middle half of Deer Creek and on small parts of Flynn Creek and Needle Branch. The understory vegetation in these areas is relatively sparse, but shading is nevertheless dense. In almost all other stream portions, the canopy is at a low level, consisting of salmonberry, Rubus spectabilis (Pursh); vine maple, Acer circinatum (Pursh); and red berry elder, Sambucus callicarpa (Greene); skunk cabbage, Lysichitum americanum Hulten and St. John; and thimble berry, Rubus parviflorus (Nutt). Other minor species also cause shading. Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco is the dominant coniferous tree form, and the forest canopy of this species shades the stream in some areas and decreases the length of time each day when direct sunlight could reach the streams. The heavy low growth of salmonberry and vine maple along the streams makes it impossible for one to walk upright in much of the stream bed. Many areas can be approached for sampling work only on hands and knees.

This dense shading profoundly influences algal distribution and variety. The only member of the Chlorophyta frequently apparent in the study streams is *Protoderma viride* Kutz, and this form seems to appear in the better lighted areas. The most abundant algal group is probably the Bacillariophycae, the most frequently observed genera being *Navicula*, *Gomphonema*, *Amphora*, *Cocconeis*, and *Pinnularia*. An abundant genus of the Cyanophyta is *Chamaesiphon*, with *Oscillatoria* and *Entophysalis rivularis* Kutz also present. *Chamaesiphon* and diatoms are the only ubiquitous algal forms in shady conditions. Under very dense shade, no algal forms are to be found except, perhaps, scattered diatoms. Areas producing much algae (*Chamaesiphon* and diatoms) are almost entirely confined to gravelly or rocky riffles and those shallow pools with a gravel or rubble substrate. Sand, silt, and very fine unstable gravels appear to support little algae but may provide a substrate for some diatoms during stable streamflow periods. Aquatic liverworts and mosses are found fairly frequently on stable substrata, usually in areas having large gravel or rubble. Genera identified are *Chiloscyphus*, *Riccardia*, *Scapania*, and *Eurhynchium*.

Insects also appear to be confined largely to the stable substrata, except for some cranefly larvae (Tipulidae) and bloodworms (Tendipedinae). The insect genera most frequently appearing in the productive riffle and stable pool areas are *Paraleptophlebia*, *Baetis*, *Cynigmula*, *Epeorus* (=*Iron* and *Ironodes*), and *Ephemerella*, all Ephemeroptera; *Acroneuria*, *Alloperla*, and *Kathroperla*, all Plecoptera; subfamilies Hydrobaeninae and Pelopiinae of Tendipedidae (Chironomidae); *Micrasema*, *Lepidostoma*, and Limnephilidae, members of the order Trichoptera. Elmidae larvae and adults appear fairly frequently in bottom samples. Genera identified are *Optioservus*, *Narpus*, and *Lara*. Other insect forms appear in samples rather infrequently. *Oxytrema silicula* (Gould), a snail, is extremely abundant, and may well be the most important herbivore present in terms of energy exchange.

The heavy growth of streamside vegetation has a profound effect upon energy entering the stream ecosystem, apart from a reduction in incident light, in that many terrestrial insect forms, as well as plant materials, fall from this vegetation into the streams.

In summary, the productive areas for both algal and insect forms appear to be riffles where stable gravel or rubble forms the substrate. Unstable substrata are not productive. In the stable areas, riffles are more productive than pools, as evidenced by an apparently higher standing crop of algae and insects.

This last statement is based on subjective observations of algae and on qualitative insect sampling done during collections for insect food habit studies.

As Table 1 indicates, riffle areas make up about half the total low water stream area on Needle Branch and Flynn Creek, and about two-fifths of the total Deer Creek area. Flynn Creek and Needle Branch gradients and general appearance change little throughout their length, but this is not true for Deer Creek, which has two distinct sections, a "canyon" and a "meadow." The former extends from about 400 feet to 1800 feet above the fish trap. The stream drops rapidly in the canyon, has steep, brushy slopes on either side, and no spawning gravel. Overhead cover is lighter in the canyon than above and below it. At 1800 feet above the fish trap, the canyon opens out into a meadow, where light incidence is less than in the canyon because of a heavy red-alder overstory, spawning gravel is fairly abundant, and gradient is less. There is no spawning gravel on Deer Creek below the meadow. In its meadow reaches, Deer Creek is similar to Flynn Creek and Needle Branch except that the overhead cover is largely alder rather than salmonberry.

Light incidence, as recorded on a pyrheliometer in an open meadow at Needle Branch, is shown in Figure 9. Data cover one year, August, 1959, to August, 1960. Mean daily light energy, calculated for each month, ranged from a low of about 100 gram calories per square centimeter in December to about 585 g.cal.

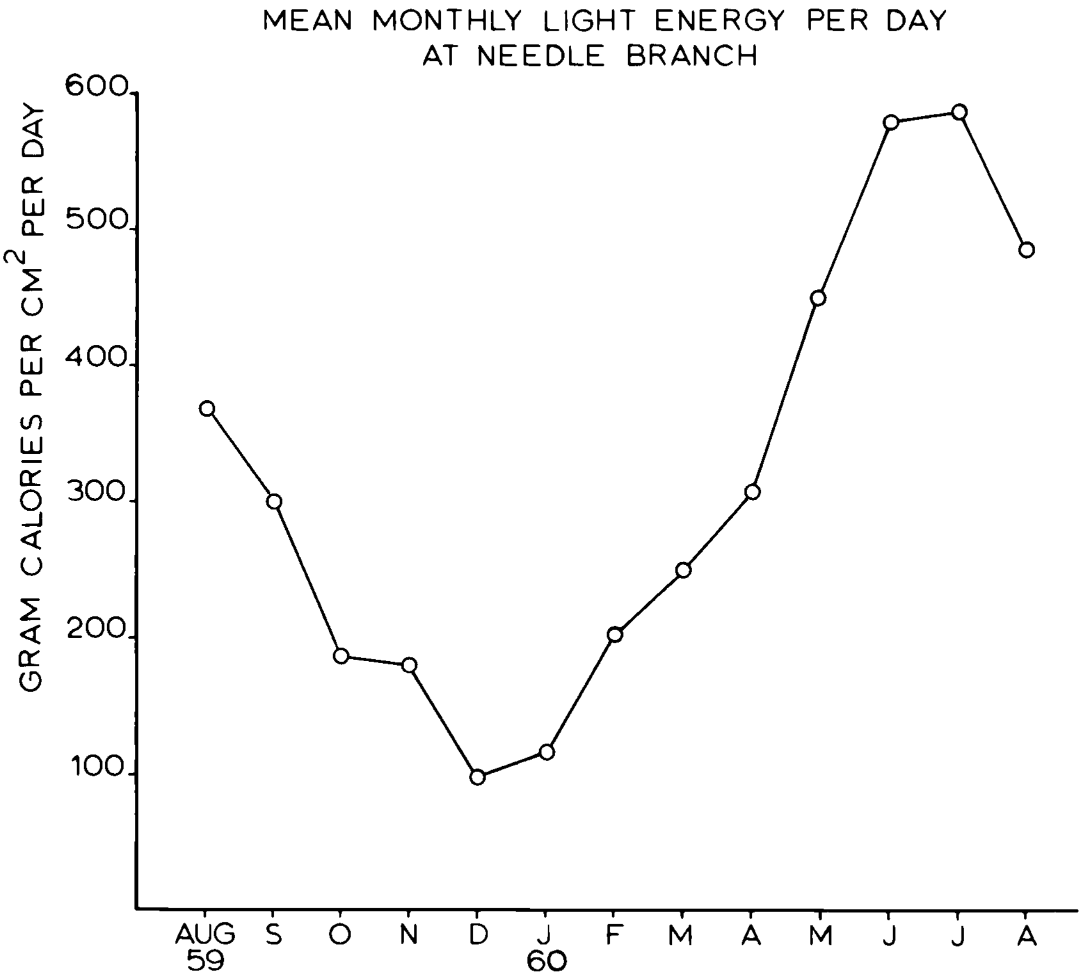
MEAN MONTHLY LIGHT ENERGY PER DAY
AT NEEDLE BRANCH
GRAM CALORIES PER CM^2 PER DAY
600
500
400
300
200
100
AUG
59
S
O
N
D
J
60
F
M
A
M
J
J
A

Figure 9

per sq. cm. in July. These data indicate seasonal fluctuations in light availability in the open, but conditions beneath the forest canopy on the three streams were greatly different. Table 3 shows relationships among pyrheliometer and light meter readings in the open, light meter readings under the canopy (at the same time of day and same area on the stream for each sample), and cloud cover. All data are for Needle Branch.

Table 3. Light energy and light incidence as recorded in an open meadow and under the forest canopy at Needle Branch.

	Open meadow		Under canopy[3]	Weather	
Date	Pyrheliometer[1]	Light[2] meter	Light meter[2]	Cloud cover	Light
Nov. 6, 1959	.50	2660	280	part cloudy	diffuse
Nov. 13, 1959	.75	3375	79	none	direct
Dec. 21, 1959	.15	475	125	cloudy	diffuse
Dec. 23, 1959	.18	375	131	cloudy	diffuse
Apr. 30, 1960	.91	1950	345	cloudy	diffuse
June 17, 1960	1.00	700	90	cloudy	diffuse
July 20, 1960	1.30	3950	47	none	direct

[1] Gram calories per square centimeter per minute.
[2] Foot candles.
[3] Stations 325-425.

As Park (36, p. 208-209) has shown for sub-canopy light incidence in hardwood stands near Chicago, light availability under the forest canopy is greater (at a given time of day and cloud condition) in mid-winter than in summer, because the deciduous trees are barren of leaves in winter. This situation would not hold for coniferous forest canopies. Further, light incidence at a given time of day under the forest canopy is greater when the sky is cloudy and the light diffuse than when the sky is clear and the light direct, even though light incidence in the open is greater on clear days. This is caused largely by differences in reflective loss of light from the overstory under diffuse and direct light conditions. Sampling for November 6 and 13, 1959, June 17 and July 20, 1960, show the difference between diffuse and direct light conditions. Table 4 shows paired observations of light availability for two days in winter of 1959 at the same stations on Needle Branch at midday. The deciduous canopy was largely gone in November, and gone entirely in December. Considerable overhead cover nevertheless existed due to branches and the influence of conifers to the south of the stream. Reflection from these apparently caused lower light levels to exist on November 13 even though light was direct. Obviously pyrheliometer readings in the open are of little value in making direct estimates of light availability under the forest canopy. Rather it might be surmised that pyrheliometer data could be used in an inverse manner, so that low readings indicate relatively high light availability at stream level.

Table 4. Light incidence beneath the forest canopy along Needle Branch under two weather conditions.

Station	November 13, 1959 1245-1325 Clear sky-pyrheliometer at .70 g.cal./cm^2/min. Foot candles[1]	December 21, 1959 1200-1300 Cloudy sky-pyrheliometer at .16 g.cal./cm^2/min. Foot candles[1]
100	145	300
200	160	275
300	125	225
400	105	250
500	60	120
700	30	75
800	35	160
900	30	155
1000	45	165
1100	30	150
1200	40	150
1300	30	185

[1] Readings taken with photoelectric cell one foot above stream surface at mid-stream.

The argument might be extended to say that winter is the period of greatest algal production because more cloudy days occur then and the canopy is then at its least density. This may in fact be true. Preliminary algal production work indicates that algal production in the period 10 a.m. to 1 p.m. is greater in December and April than in mid-summer. This statement is based on light-dark stirred aquarium tests with benthic flora, largely Chamaesiphon sp. and diatoms. Many factors, such as changes in day length, turbidity, water depth, current and molar action, make firm conclusions impossible at this time. General observation of algae standing crop and insect food habits indicates that late winter is probably the period of greatest productivity.

COHO PRODUCTION

Methods for Coho Production Study

Two papers concerned in part or wholly with fish production and soundly based in theory and technique are those by Allen (2, p. 168-177) and Ricker and Foerster (46, p. 173-211). The former worker measured fish production in a New Zealand stream, obtaining rates which he estimated had 50 per cent confidence limits. These rather wide-spread limits were caused by sampling error in the estimation of standing crop at particular times in the resident trout stock.

Ricker and Foerster were more fortunate in regard to securing an accurate measure of standing crop at some time of the year, a measure essential to production estimation. At Cultus Lake, British Columbia, where these authors worked, virtually all sockeye salmon, Oncorhynchus nerka (Walbaum), leave the lake at the end of a one-year period of residence. Another, less accurate measure of standing crop could be obtained in the case of the sockeye by estimating the quantity of eggs deposited and of young emerging from the gravel. There is a small residual population of sockeye that must also be considered in production estimates, but since these residents migrate out of the lake as two-year-old fish, they can be counted then for back-calculated estimates of number.

The situation at Cultus Lake is similar to that in the streams studied in this paper in that the coho salmon period of fresh water residence is generally one year. However, the coho move out of the streams throughout the year, and standing crop estimates were made by the mark and recovery method with recoveries from fish traps at the lower ends of the stream sections studied.

Yearly coho production, as used in this work, is the total elaboration of coho salmon tissue by a year class from emergence until migration of the bulk of these fish as yearlings. This is production as defined generally by Ivlev (25, p. 98-120), and net production by the formulas and definition of Neese and Dugdale (35, p. 426) and others. The time length for which production is calculated may vary from year to year, depending upon times of emergence and downstream migration.

"Effective yield" of coho salmon of a given year class is defined as the weight or number of yearling (age 1/) migrants moving downstream in a given year from November of one year through June of the next. Total yield is the entire outmovement of coho of a given year class, from emergence through smolt migration.

Ricker and Foerster (46, p. 176) state that the data necessary for computation of fish production are the standing crop present at some time during the year, the rates of growth at successive short periods during the year, and the rates of mortality during these same short periods. These data were used by Ricker and Foerster to compute production by two-week intervals.

As Allen (2, p. 169-173) points out, the excellent production information provided by Ricker and Foerster is derived somewhat laboriously by use of calculations, and the same production data could have been secured graphically more easily. Allen (2, p. 170-172) did this for a New Zealand trout stream. Neese and Dugdale (35, p. 429) determined production graphically for insect larvae by plotting standing crop in numbers at particular times on the ordinate, and mean individual weight at the same times on the abscissa. A planimeter may then be used to determine the areas under the production curve for particular time intervals, and hence production for those intervals.

The graphic method of production calculation was chosen for use in this coho work because it is simple, convenient, and shows production in a manner easy to interpret. The data necessary for production calculation with the graphic method are: standing crops in numbers at several times during the year and growth rates of coho over the period of fresh water residence.

The rates of growth of coho salmon for different periods were established by periodic sampling of each stream. Needle Branch and Flynn Creek were not sampled in the winter period. Spring, summer, and fall samples established the slope of the growth curve for coho in these streams, and Deer Creek data were used to establish points of inflection and deflection in late fall and early spring, respectively, on the curves. Confidence limits for mean lengths were calculated for all samples by means of formulas described in most statistical texts (28, p. 146).

Selectivity of netting and growth differences by area will be discussed later. A more intangible error could have resulted from the rather frequent disturbance of the stream bottom by sampling for mortality determination, insect food habit studies (15), stream surveying, and by other work. This periodic disturbance could possibly have increased growth rate and production to some extent by making normally unavailable insect forms available to the coho. It is obvious that the effects of periodic disturbance would be difficult or impossible to evaluate. It is considered that these effects were not a serious source of bias. Any error introduced should tend to have the same effect from year to year.

Capture of fish for marking was done with a small one-man net on a metal frame. Occasionally, a portable direct current electro-sampler was used. Coho fins were removed with clippers, usually without the aid of anesthetic compounds. All linear measurements taken from juvenile fish were made to the nearest millimeter. All weight determinations were made to the nearest twenty milligrams on a portable balance. No fish were released after marking and measuring until they were physically active and apparently in good condition.

An effort was made to capture fish for marking from a wide variety of areas. All fish sampled were released at the point of capture. Coho marking was done throughout the year in Deer Creek. Measurements and markings on Flynn Creek and Needle Branch were largely confined to the low water flow period of spring, summer, and early fall. These data were taken to establish the general slope of the growth and mortality curves. Deer Creek data characteristics were then used to complete the Flynn Creek and Needle Branch curves for the period between early fall and migration time.

At migration, all smolts were checked for marks, and samples were measured and weighed. Downstream traps were checked daily during the migration period. Traps are shown in Figures 10-13. All adult fish moving upstream, and nearly all juveniles moving downstream were forced to enter these traps and thus a total count of upstream migrants and a near-total count of downstream migrants could be made. Any coho fry moving downstream from emergence through November 1 is called a "nomad" in this paper. Juveniles moving downstream after November 1 are called migrants or smolts.

Since the 1960 smolt migration contained some age 2/ coho from the 1958 year class, these were separated before computation of mean lengths for trap-caught migrants. Care was taken to exclude 1958 year class fish also from residual coho mean

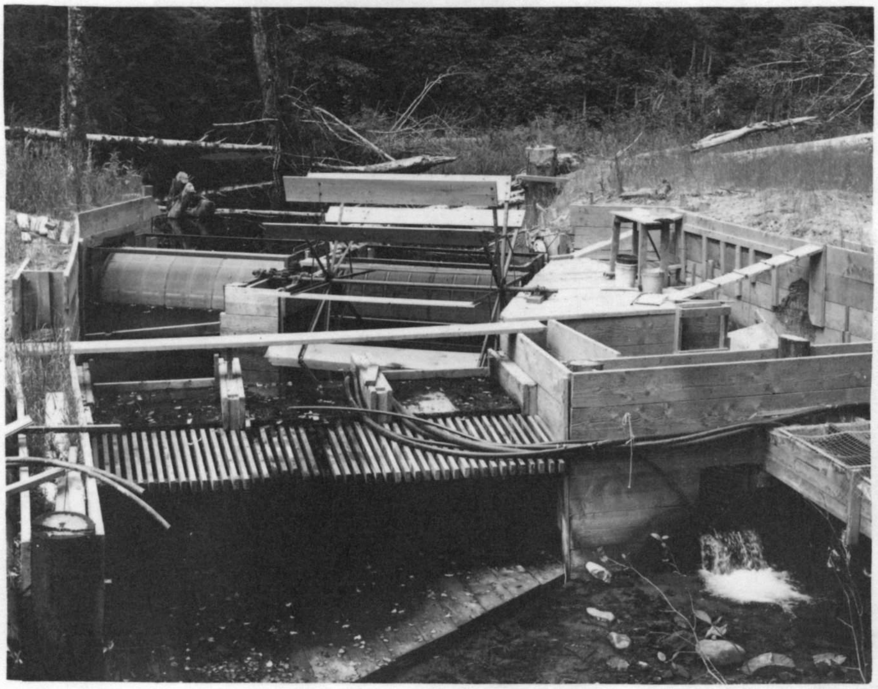

Figure 10

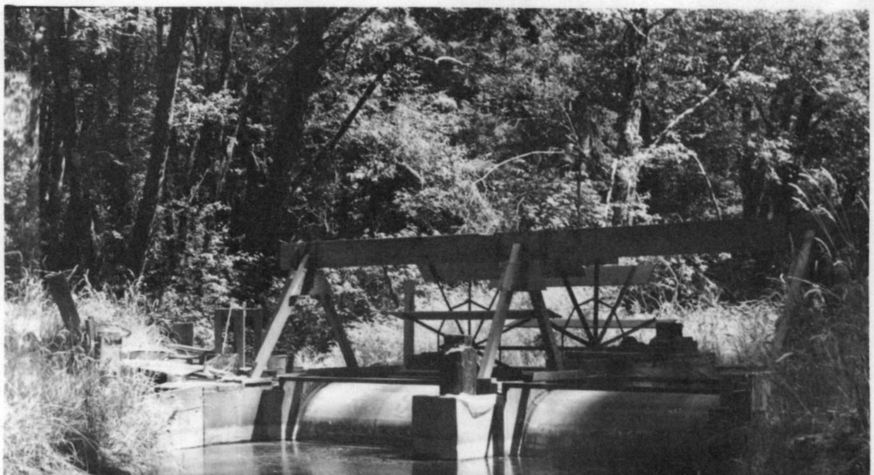

Figure 11

Figure 12

Figure 13

length calculations.

The coho marking conducted on all three streams was done at several periods through the year (Appendix 4). Five different fin markings; left ventral, right ventral, both ventral, anal, and half-dorsal, were used on fish from Deer Creek. Portions of the caudal fin were also clipped in marking done shortly before smolting occurred. Marks were not used during the winter period on Flynn Creek and Needle Branch. The fins removed were considered to be the least important ones. This decision was based upon observations of swimming fish in aquaria. Pectoral and dorsal fins appeared to be extremely important, and were therefore not removed except in the case of the half-dorsal mark.

Wales and German (61, p. 98-99) found single ventral fin marks to have no effect upon growth of Castle Lake eastern brook trout, Salvelinus fontinalis Mitchill. The effect of fin removal upon growth was checked in 1959-60. There was no significant difference in the lengths of marked and unmarked coho salmon trapped during the smolt migration. This being the case, any mortality resulting from fin removal would have to be due to handling loss directly, disease or parasite infection at the point of amputation, or to a decreased ability to escape from predators. The first possible cause was unlikely. All fish released were held until they were apparently in good condition, and one group of marked fish held overnight in a live cage suffered no mortality. Fish marked and used in behavior work, described later, were observed over periods of up to three weeks, and no ill effects due to marking were noted. No evidence was found of disease or parasitism at amputation points when subsequent growth checks were made. If any mortality resulted from fin removal, it seems likely that most of it occurred through decreased escape ability.

Anal fin marks were used on each stream, but the results from this mark were discarded because of evidence of bias due to differential mortality. Standing crop estimates based on anal fin marks were higher for each stream than crop estimates secured from ventral marks, even though anal marks were used later in the year than the ventral ones. Since recruitment could not have occurred any time after emergence, the higher crop estimates meant either that anal fin-marks caused lower survival or that relatively too many ventral marks were recovered. The former situation was more likely. The only anal fin marks used in calculations were those sampled on Needle Branch soon after marking, before much differential mortality could have occurred.

The count of coho smolts in the spring migration probably is very nearly an absolute one. Passage of fish through leaks past trap screens was believed to have occurred only at Deer and Flynn Creeks, and all fish escaping in this way were probably age 0/. This leakage is estimated for Deer Creek in the section on results of production study. Some "ride over" of coho occurred at Deer Creek trap in January, 1960, and also is estimated later. No fish were known to escape past Needle Branch trap from October, 1959, to June 1, but some passage could have occurred in January during about two days of high water.

The expression for estimated population size is $\hat{N} = \frac{M(C+1)}{R+1}$ (47, p. 84) where $\hat{N}$ = estimated population size at time T,

M = number marked at T,

C = total fish recaptured at downstream traps,

R = marked fish recaptured at traps.

It was assumed that C, the catch of all coho moving through downstream traps after time T, could not vary since it was the entire year class less the few members remaining in the stream for another winter. For all but three crop estimates, confidence limits for crop size were calculated using the approach of Cochran (12, p. 117), and using a binomial estimate of the error of R. The standard error of the crop estimates was:

$$\sqrt{\frac{M\,[M - R]\,[C+1]^2}{(R+1)^3}}$$

Confidence limits were found by multiplying this standard error by the appropriate "t" values corresponding to the number of degrees of freedom of R, the recovery of marked fish.

Where the catch of fish moving down after mark time T was low in proportion to the coho remaining for another winter, confidence limits were set by employing the Poisson distribution as used by Ricker (44, p. 349-353). These limits were conservative, and were used for the last crop estimate on each stream for the 1959 year class. Since an appreciable proportion of the population at this time became residual, the total fish recaptured at the traps did not include the entire population. The estimated population size ($\hat{N}$) at time T was plotted against time, and a cohort size (standing crop) curve was placed by eye.

A bias in production data was caused by the failure of the traps to catch and hold very small juvenile fish moving upstream. Once any juvenile fish was passed downstream, it could not return upstream as a juvenile nor could coho reared below the trap pass upstream, since the traps were complete blocks to juvenile up-migration. This source of error was checked on Needle Branch in 1960-61 by installing a fine-mesh trap inside the adult traps.

Most scale reading was done with a binocular microscope. All scale samples were dry-mounted on glass slides. Juvenile scale samples were mounted without cleaning.

Results of Coho Production Study

Growth in Length: Growth curves for the 1959 year class of coho are shown in Figures 14, 15, and 16. Solid lines show the growth in length of juvenile coho (residuals) in the stream above downstream trapping facilities. Dotted lines show changes in

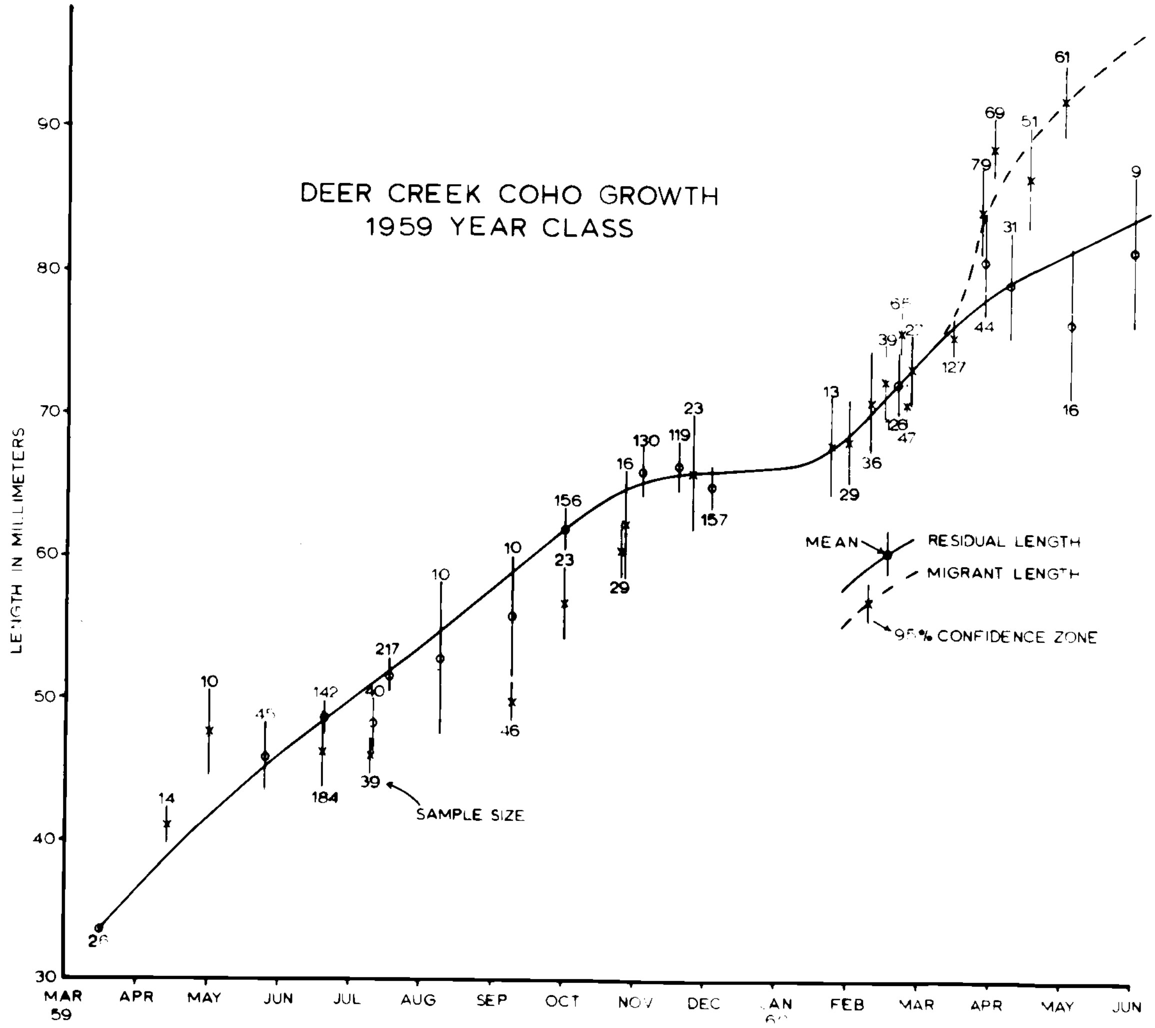
DEER CREEK COHO GROWTH
1959 YEAR CLASS
LENGTH IN MILLIMETERS
30
40
50
60
70
80
90
MAR 59
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN 60
FEB
MAR
APR
MAY
JUN
MEAN
RESIDUAL LENGTH
MIGRANT LENGTH
95% CONFIDENCE ZONE
SAMPLE SIZE
26
14
10
45
142
184
40
39
217
10
10
46
156
23
16
29
130
119
23
157
13
29
36
39
65
27
26
47
127
79
69
44
51
31
61
16
9

Figure 14

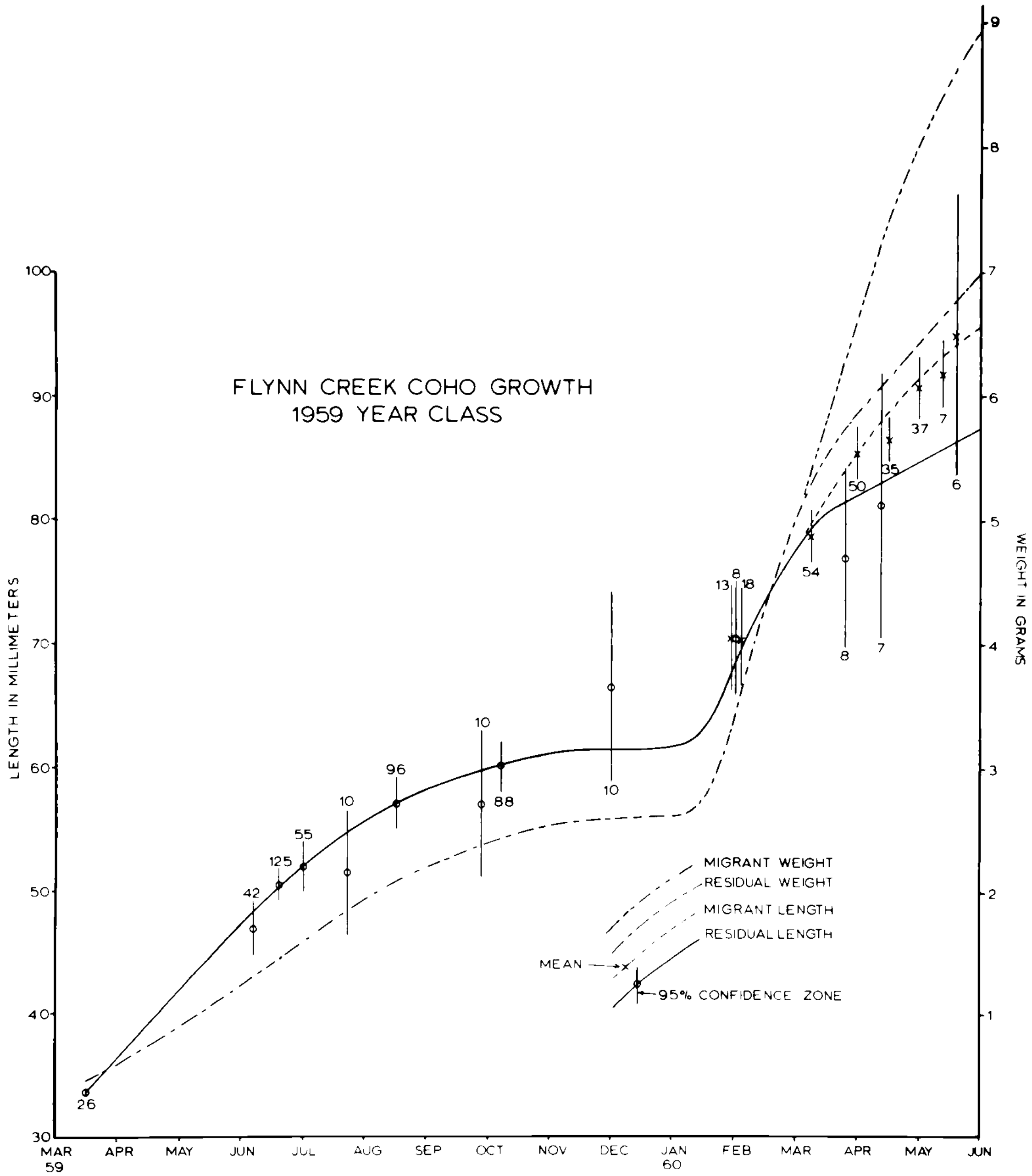
FLYNN CREEK COHO GROWTH
1959 YEAR CLASS
LENGTH IN MILLIMETERS
WEIGHT IN GRAMS
30
40
50
60
70
80
90
100
1
2
3
4
5
6
7
8
9
MAR 59
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN 60
FEB
MAR
APR
MAY
JUN
26
42
125
55
10
96
10
88
10
10
13
8
18
54
8
50
7
35
37
7
6
MIGRANT WEIGHT
RESIDUAL WEIGHT
MIGRANT LENGTH
RESIDUAL LENGTH
MEAN
95% CONFIDENCE ZONE

Figure 15

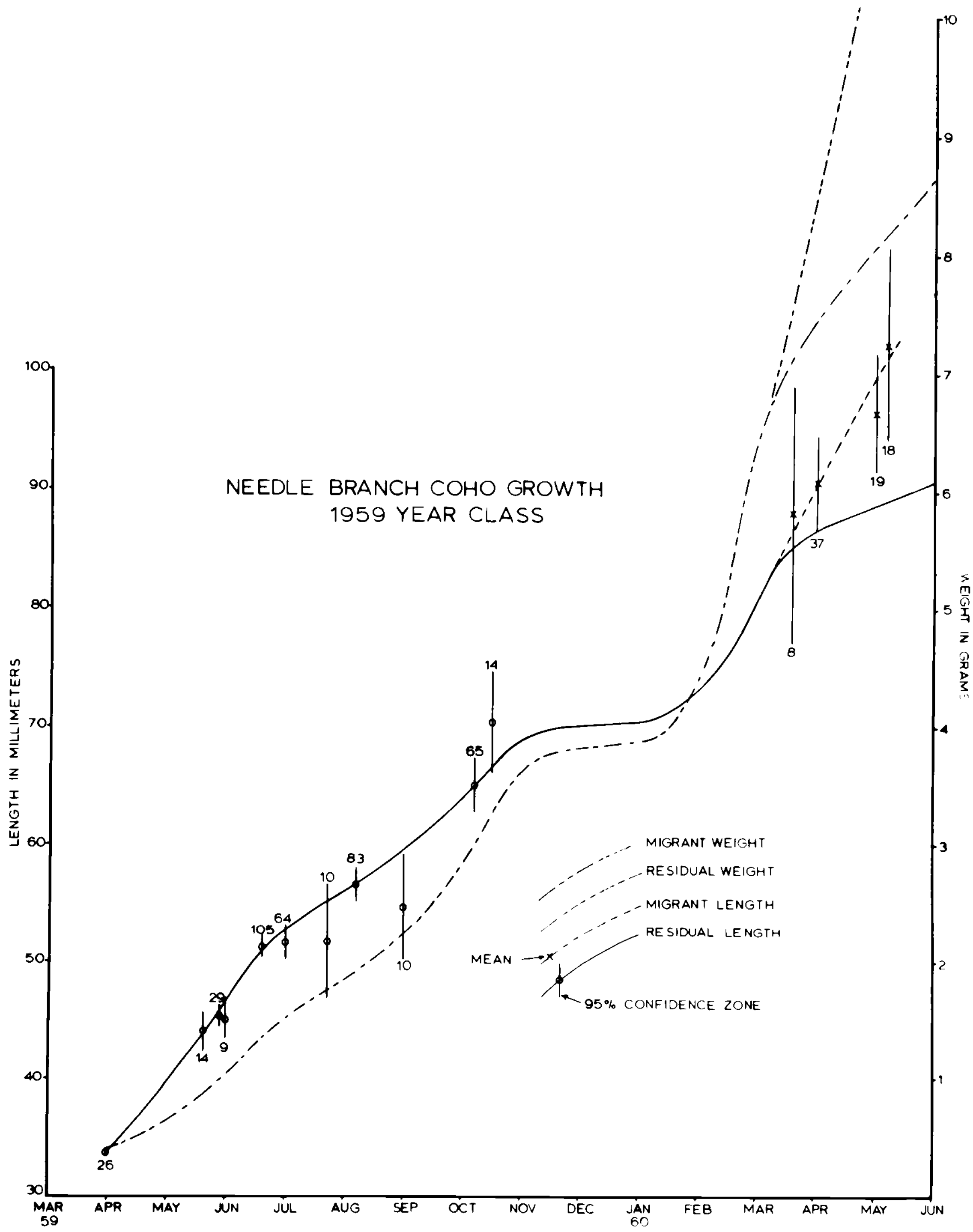
NEEDLE BRANCH COHO GROWTH
1959 YEAR CLASS
LENGTH IN MILLIMETERS
WEIGHT IN GRAMS
30
40
50
60
70
80
90
100
1
2
3
4
5
6
7
8
9
10
MAR 59
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN 60
FEB
MAR
APR
MAY
JUN
26
14
29
9
105
64
10
83
10
65
14
8
37
19
18
MIGRANT WEIGHT
RESIDUAL WEIGHT
MIGRANT LENGTH
RESIDUAL LENGTH
MEAN
95% CONFIDENCE ZONE

Figure 16

mean lengths of coho (nomads and migrants) taken in downstream traps (Appendix 7-8).

Growth data on Deer Creek show a separation in the residual and migrant mean lengths during two periods: early June through early November, 1959, when trapped fish were consistently smaller than residual fish; and mid-March through the end of the smolt migration, when residual fish were consistently smaller than migrants. Data on trapped fish in summer are not available on Flynn Creek and Needle Branch, since adequate downstream traps were not operated until early October on these streams.

When samples of residual and nomadic Deer Creek coho of the 1959 year class were measured within two weeks of each other in summer, the hypothesis that the mean lengths were equal was tested. Table 5 shows the results. In all cases the residual fish were larger than the nomads with significance levels as shown. The greater mean length of smolts as compared to residuals after mid-March is attributed to the tendency for the larger fish in the coho population to smolt and migrate, while the small, slow-growing members of the year class sometimes fail to smolt (46, p. 177-178) and (51, p. 88) and tend to remain in the stream until the succeeding spring.

The disparity between the lengths of nomads and residuals from early June to early November on Deer Creek is attributed largely to aggressive behavior of juvenile coho. This will be discussed in a later section on behavior.

Table 5. Comparisons of mean lengths of residual and migrant coho, 1959 year class, Deer and Flynn Creeks.

Date	Type	Mean length mm	Sample size	Difference mm	t	P*
6/15-6/20/59	Nomad	47.42	184	1.38	1.95	.10
6/18/59	Residual	48.80	142			
7/8-7/10/59	Nomad	46.07	39	2.18	1.92	.10
7/8/59	Residual	48.25	40			
6/15-7/10/59	Nomad	47.18	223	1.50	2.45	.02
6/18-7/8/59	Residual	48.68	182			
9/8/59	Nomad	50.00	46	6.00	3.03	.01
9/8/59	Residual	56.00	10			
10/26/59	Nomad	62.44	16	3.67	1.84	.10
11/3/59	Residual	66.11	130			
3/26/60	Migrant	85.02	81	4.18	1.77	.10
3/28/60	Residual	80.84	44			
4/15/60	Migrant	87.89	54	8.54	3.47	.01
4/8/60	Residual	79.35	31			
5/1/60	Migrant	93.93	67	17.24	6.11	.01
5/4/60	Residual	76.69	16			
		Flynn Creek				
4/1/60	Migrant	87.11	54	10.11	3.04	.01
3/17-4/4/60	Residual	77.00	8			
4/15/60	Migrant	89.32	41	8.04	1.75	.10
4/11/60	Residual	81.28	7			

*Significance level

Confidence limits for the means of lengths were calculated for all samples and are shown in Figures 14-16, and in Appendix 10-12. The "growth" curve for residual fish is affected, of course, by the fact that migrant fish vary in length from residual fish in the two time intervals mentioned earlier. Some of the change in mean length of residuals is caused by the loss downstream of fish smaller than residuals in summer, 1959, and larger than residuals in spring, 1960. Since the number of migrants from June to November was small (Appendix 7), the error thus introduced in the growth curve of residuals was slight. The effect on residual "growth" after March 15, 1960, however, was great. If mean lengths of residual samples on Deer Creek after March 15 were followed exactly in placing the growth curve, a negative growth would result. This, of course, would be an artifact, since individual residual fish apparently do grow during this period, and certainly could not lose length. Consideration of this fact led to a placement of the growth curve that would indicate the length of residuals reached about 100 mm by February of the next year. This was about the size of several smolt coho (in the spring migrations of 1959 and 1960) which had two annuli on scales, indicating that they were residuals. The lower anchor point for the residual length curve after March 12, 1960, was set at about the point where the trap and residual growth curves diverged.

Growth curves of residual fish for Flynn Creek and Needle Branch were sloped away from the migrant length curves, largely on the basis of evidence from Deer Creek, since it was assumed that generally similar situations would exist on both the former streams. Some evidence from two small Flynn Creek residual samples indicated that this assumption was reasonable. Table 6 shows comparisons of two sets of residual and migrant length samples in late March and early April on Flynn Creek. Resident fish were smaller in this period than the trapped fish, with probabilities as shown.

Table 6. Comparisons of mean lengths of residual and migrant coho, 1959 year class, Flynn Creek.

Date	Type	Mean length mm	Sample size	Difference mm	t	P*
4/14-4/16/60	Migrant	86.57	35	5.29	1.18	.30
4/11/60	Residual	81.28	7			
3/3-4/2/60	Migrant	85.60	50	8.60	2.63	.05
3/17-4/4/60	Residual	77.00	8			

*Significance level

Resident samples were not procured during spring on Needle Branch because of sampling difficulties. The residual growth curve was deflected at the same time and on about the same angle as the one for Deer Creek fish.

The lower anchor point used for all three growth curves was based on a 26-fish sample of fry taken just prior to the time of emergence, during embryonic-survival work conducted on Deer Creek by Coble (11, p. 1-37). Emergence times on Deer Creek and Needle Branch were estimated by adding 90 days to the time of peak upstream movement of adult coho females. Appendix 6 is a graph showing upstream movement of females on the two streams for which data were available. Data were complete on Needle

Branch, but the Deer Creek trap was out of order from about January 8 to February 6. It is believed that almost all coho movement took place before the trap washed out. Observation of spawning areas showed little activity during the trap failure. Appendix 6 shows movement of 1959-60 adults, and indicates that about one-third of the females moving upstream did so during the late January period. However, stream flow was unusual in the 1959-60 winter, with no major freshet occurring until January, a factor conducive to late migration of adults. Good freshets occurred in November and December the previous winter, 1958-59, a factor contributing to early migration of adults.

Needle Branch coho growth rate decreased definitely in July and August and then increased in late September. The summer decrease in growth is considered to be caused partly by low stream flow (Figure 4). Needle Branch was the only one of the three streams studied that became a series of disconnected pools in summer over most of its length, with little or no water flowing over the riffles. Flow was perceptible, reaching a low level of less than 0.1 c.f.s. at the stream gaging weir, but water tended to flow through the riffle gravel rather than over it. Since winter growth data are not available, the Needle Branch growth curve shape in this period was estimated from Deer Creek data.

A series of tests was made to determine if growth differences existed between marked and unmarked fish. These are shown in Table 7. The results of six tests are somewhat at

Table 7. Difference between mean lengths of marked and unmarked coho, 1959 year class, Deer Creek.

Date	Type	Mean length mm	Sample size	Difference mm	t	P*
7/16/59 (Netted)	Unmarked Marked	51.78 49.79	219 33	+ 1.99	1.72	.10
11/3/59 (Netted)	Unmarked Marked	67.42 63.55	43 22	+ 3.87	1.65	.20
11/18/59 (Netted)	Unmarked Marked	66.72 66.10	78 41	- .62	- .32	.80
12/2/59 (Netted)	Unmarked Marked	65.03 65.24	116 41	- .21	- .11	.95
2/21/60 (Netted)	Unmarked Marked	74.01 66.81	99 27	+ 7.20	3.21	.01
3/14/60 (Trapped)	Unmarked Marked before January 1	75.47 76.98	86 42	- 1.51	1.04	.30

*Significance level

variance. Samples obtained at two times, July 16, 1959, and February 21, 1960, indicated that marked fish were significantly smaller than unmarked ones ($P \leq .10$), but samples at four other times showed no significant differences between marked and unmarked fish. The most reliable test was made on marked versus unmarked fish during the seaward migration. The March 14 samples taken at the trap show no significant difference between marked and unmarked fish.

The differences between mean sizes of fish in different areas of the same stream at the same time were tested and the results are shown in Table 8. On October 1, 1959, 50 coho taken from the canyon area on Deer Creek were significantly longer (P = .05) than 106 fish taken in the meadow area above the canyon. The difference was 3.6 mm. On November 18, 1959, 68 canyon resident coho were 2.7 mm longer than 51 meadow resident coho. The significance level was .20 in the latter test. There does appear to be a real difference between fish taken in the canyon and in the meadow. However, in the absence of data on the proportion of the total population residing in each of these areas, length sampling was conducted throughout the length of the stream, with greatest emphasis on the above-canyon area. The growth curve for Deer Creek would not be altered materially even if all sampling were conducted in the same area with attendant bias.

Table 8. Comparison of mean lengths of residual coho in different areas, 1959 year class, Deer Creek.

Stream	Date	Station and area	Mean length mm	Sample size	Difference mm	t	P*
Deer	10/1/59	0 - 1500 Canyon	64.60	50	3.60	2.28	.05
		>1500 Meadow	61.00	106			
Deer	11/18/59	0 - 1500 Canyon	67.66	68	2.70	1.52	.20
		>1500 Meadow	64.96	51			

*Significance level.

Growth in Weight: Prediction equations for estimation of weight from length were calculated from samples of 161 coho on Deer Creek, 141 on Flynn Creek, and 73 on Needle Branch. Lengths and weights were converted to logarithms and a log-log linear regression of weight on length was calculated. Part of these calculations are shown in Appendix 5. The equations for each stream are as follows:

Deer Creek: $\log W_L = -2.15313 + 3.10027 \log L$

Flynn Creek: $\log W_L = -1.73726 + 2.87644 \log L$

Needle Branch: $\log W_L = -2.23255 + 3.15081 \log L$

Where W = weight at a given length,

L = length.

These regression lines are shown in Figure 17. Regression coefficients (Appendix 5) are significantly different ($P = .05$, F value = 6.208) for fish from the three streams, indicating that body shape on each of the streams was slightly different. Thus, in the general equation (in arithmetic terms) for weight and length, $W = a\,L^b$, where a and b are constants, the b value varies; being 3.10 for Deer Creek, 3.15 for Needle Branch, and 2.88 for Flynn Creek. The differences were considered sufficient to warrant prediction of weight for fish from each stream separately, rather than using a composite sample.

Weight curves, plotted from length curves after calculation of a number of weights at given lengths and times, are shown for each stream in Figures 15, 16, and 18. Weight-growth curves are,

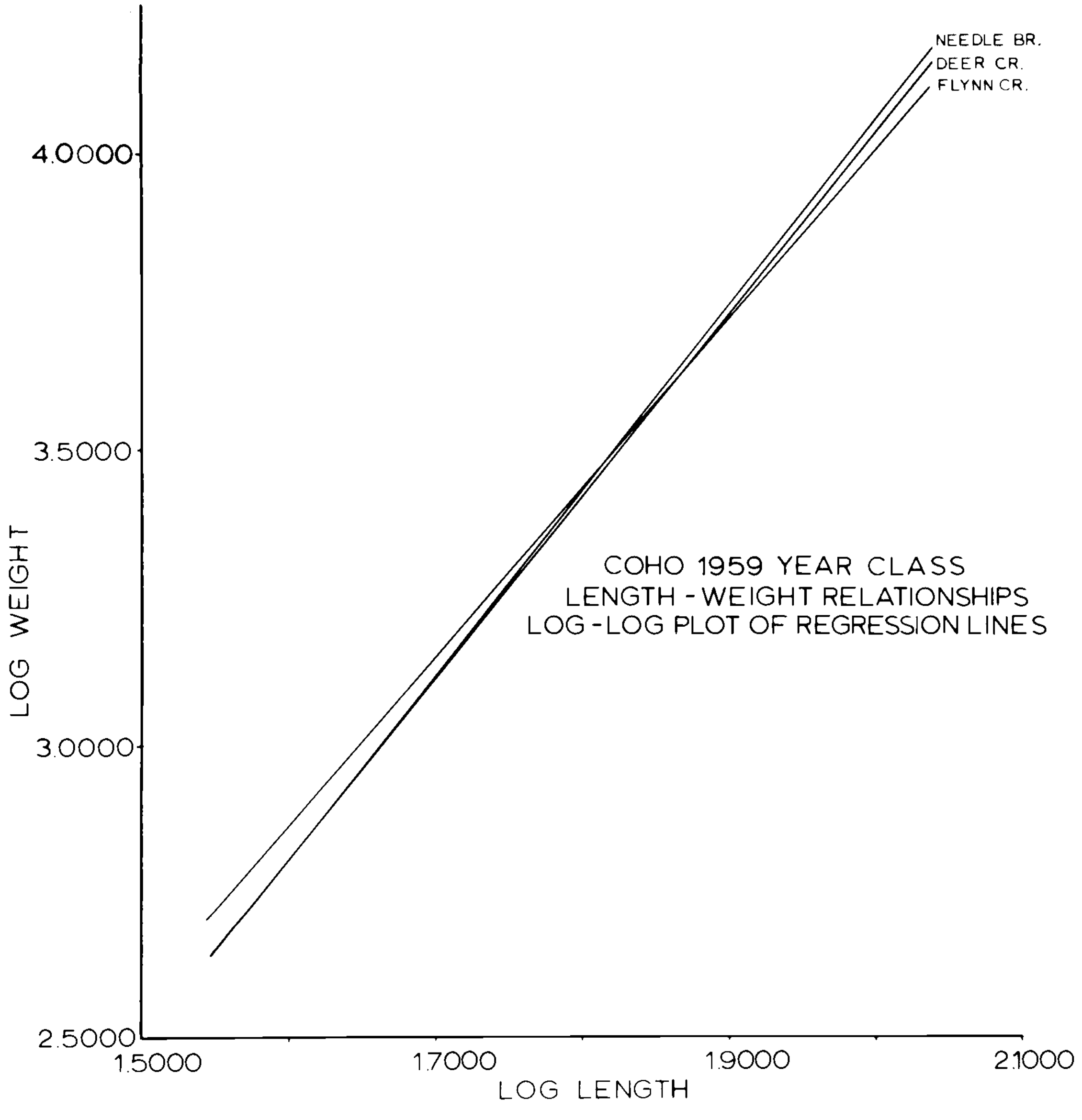
NEEDLE BR.
DEER CR.
FLYNN CR.
COHO 1959 YEAR CLASS
LENGTH - WEIGHT RELATIONSHIPS
LOG - LOG PLOT OF REGRESSION LINES
LOG WEIGHT
4.0000
3.5000
3.0000
2.5000
1.5000
1.7000
1.9000
2.1000
LOG LENGTH

Figure 17

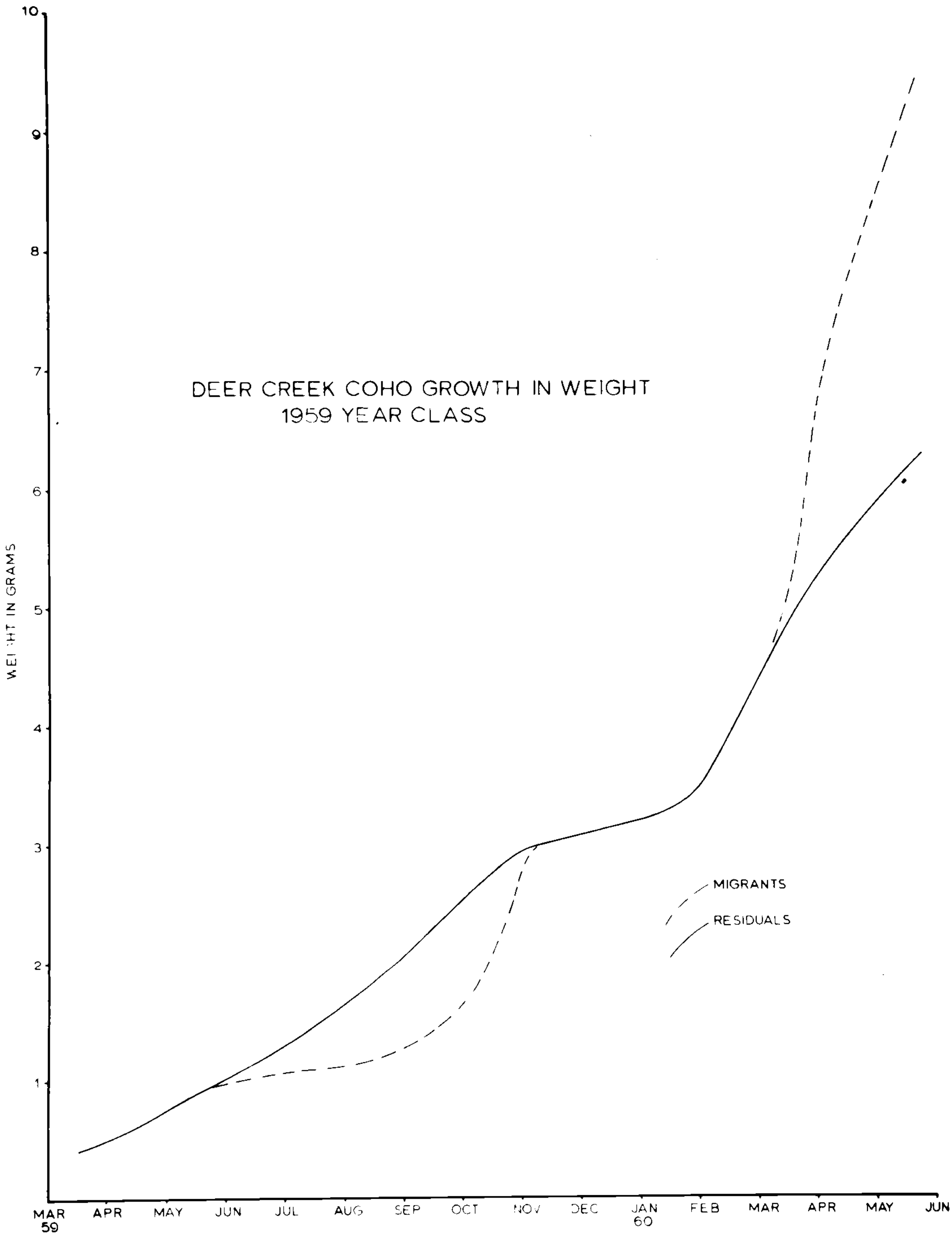
DEER CREEK COHO GROWTH IN WEIGHT
1959 YEAR CLASS
WEIGHT IN GRAMS
10
9
8
7
6
5
4
3
2
1
MAR 59
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN 60
FEB
MAR
APR
MAY
JUN
MIGRANTS
RESIDUALS

Figure 18

of course, dependent upon length-growth curves for their shape.

Standing Crop: As indicated in an earlier section, the standing crop of coho was estimated at several times during the year on each stream. Appendix 4 and Figures 19-21 show the estimated coho population size at each sampling time on each stream. Confidence limits for the point estimates are also tabulated in the appendix and shown in the figures.

The curves for population size were placed by eye. The population sizes at emergence time were set approximately by projecting a straight line prolongation of the survivorship curve to estimated emergence time. A rough check on the accuracy of this procedure can be found by multiplying potential egg deposition by an arbitrary figure of .65, to give survival from egg potential to emergence. Briggs (6, p. 47) gives 74 per cent as mean survival (to emergence) of eggs already deposited. An egg loss of 9 per cent is arbitrarily set here. Coble (11, p. 19) and Shapovalov and Taft (51, p. 69) estimate survivals of 62 and 65 per cent, respectively, in good environmental conditions in the gravel. Assuming that coho usually utilize "good" gravel, and that egg survival under experimental conditions might be somewhat lower than usual due to handling procedures, the figure of 65 per cent is probably fairly satisfactory.

Fecundity of coho was estimated from Shapovalov and Taft (51, p. 60) where number of eggs equals $0.01153 \times L^{2.9403}$, with L being fork length in centimeters. A total potential egg

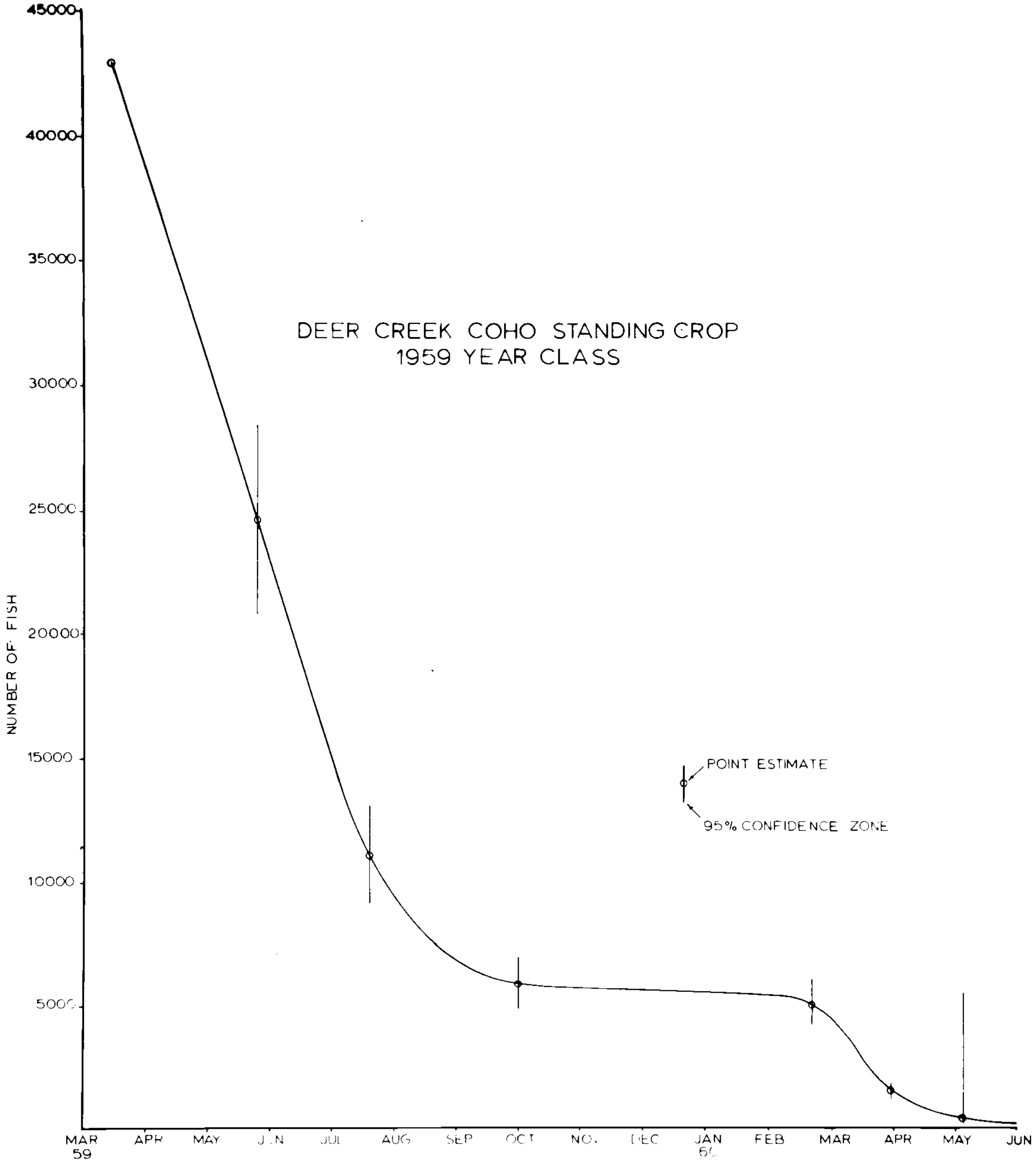
DEER CREEK COHO STANDING CROP
1959 YEAR CLASS
NUMBER OF FISH
45000
40000
35000
30000
25000
20000
15000
10000
5000
POINT ESTIMATE
95% CONFIDENCE ZONE
MAR 59
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN 60
FEB
MAR
APR
MAY
JUN

Figure 19

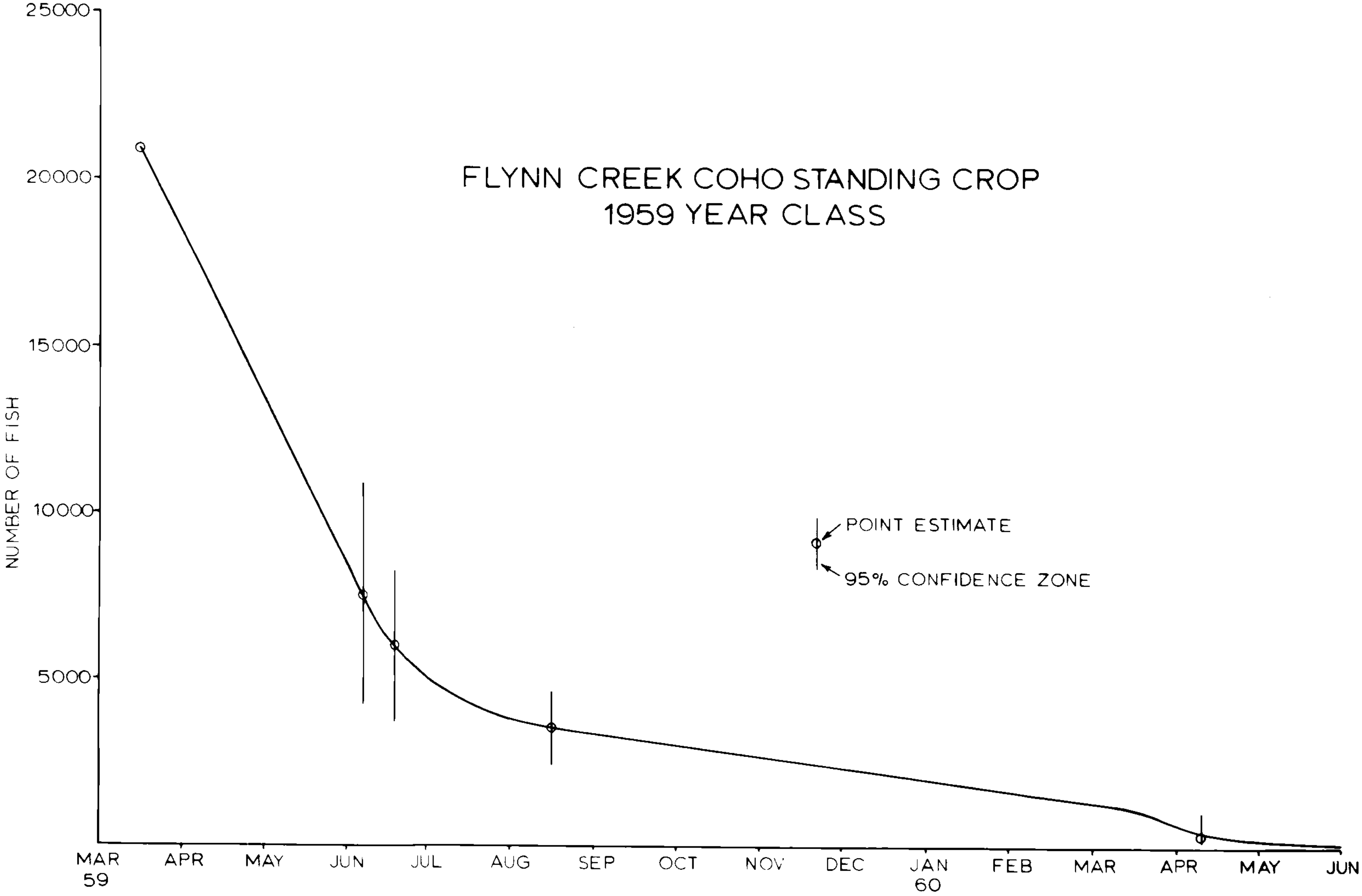
FLYNN CREEK COHO STANDING CROP
1959 YEAR CLASS
NUMBER OF FISH
25000
20000
15000
10000
5000
POINT ESTIMATE
95% CONFIDENCE ZONE
MAR
59
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
60
FEB
MAR
APR
MAY
JUN

Figure 20

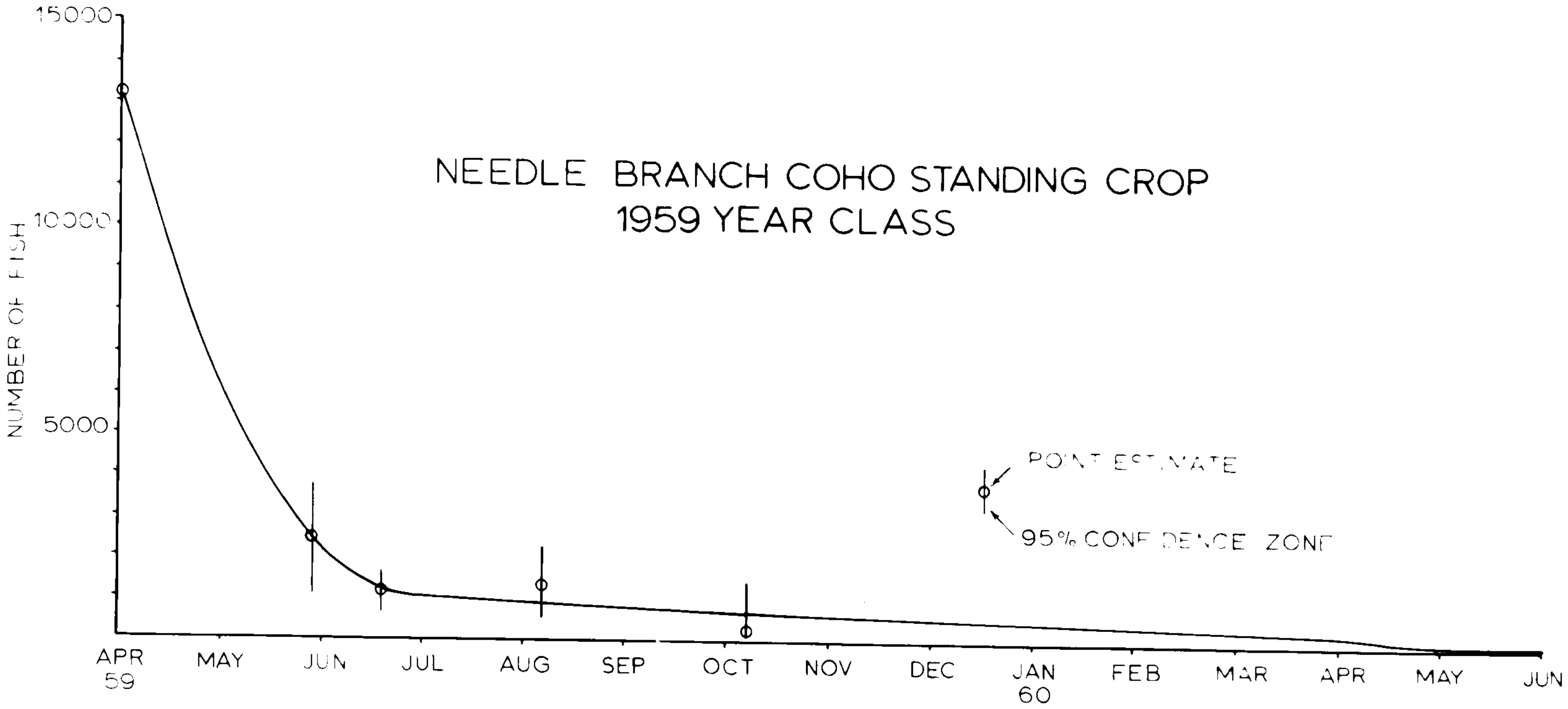
NEEDLE BRANCH COHO STANDING CROP
1959 YEAR CLASS
NUMBER OF FISH
15000
10000
5000
POINT ESTIMATE
95% CONFIDENCE ZONE
APR 59
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN 60
FEB
MAR
APR
MAY
JUN

Figure 21

deposition of about 64,000 was estimated for Deer Creek and 20,300 for Needle Branch. Multiplying these figures by .65 yields figures for survival to emergence of 42,000 for Deer Creek and 13,200 for Needle Branch. The former figure is quite close to the figure of 43,000 determined by projecting the Deer Creek survivorship curve back from May 25, 1959, to March, 1959.

The shape of the Needle Branch standing crop curve is not well defined on May 27, 1959, so no prolongation of the curve was attempted. Estimated survival from deposition was used as an anchor point.

For Flynn Creek, no data on potential deposition are available, hence the standing crop curve was prolonged to 20,900 on March 15. The shape of the survivorship curve on about June 1, 1959, was well defined, and the prolongation is probably not too erroneous.

Production: Production was obtained by determining the area under given portions of a curve plotted from data on standing crop and mean individual weight of residual coho at particular times.

Production curves for each stream, as plotted in this manner, are shown in Figures 22-24. As indicated earlier, production of the year class is the total area under each of the curves. This area, expressed as weight of tissue produced, was 48.97 kg. (107.97 lb.) on Deer Creek, 22.01 kg. (48.53 lb.) on Flynn Creek, and 7.31 kg. (16.09 lb.) on Needle Branch.

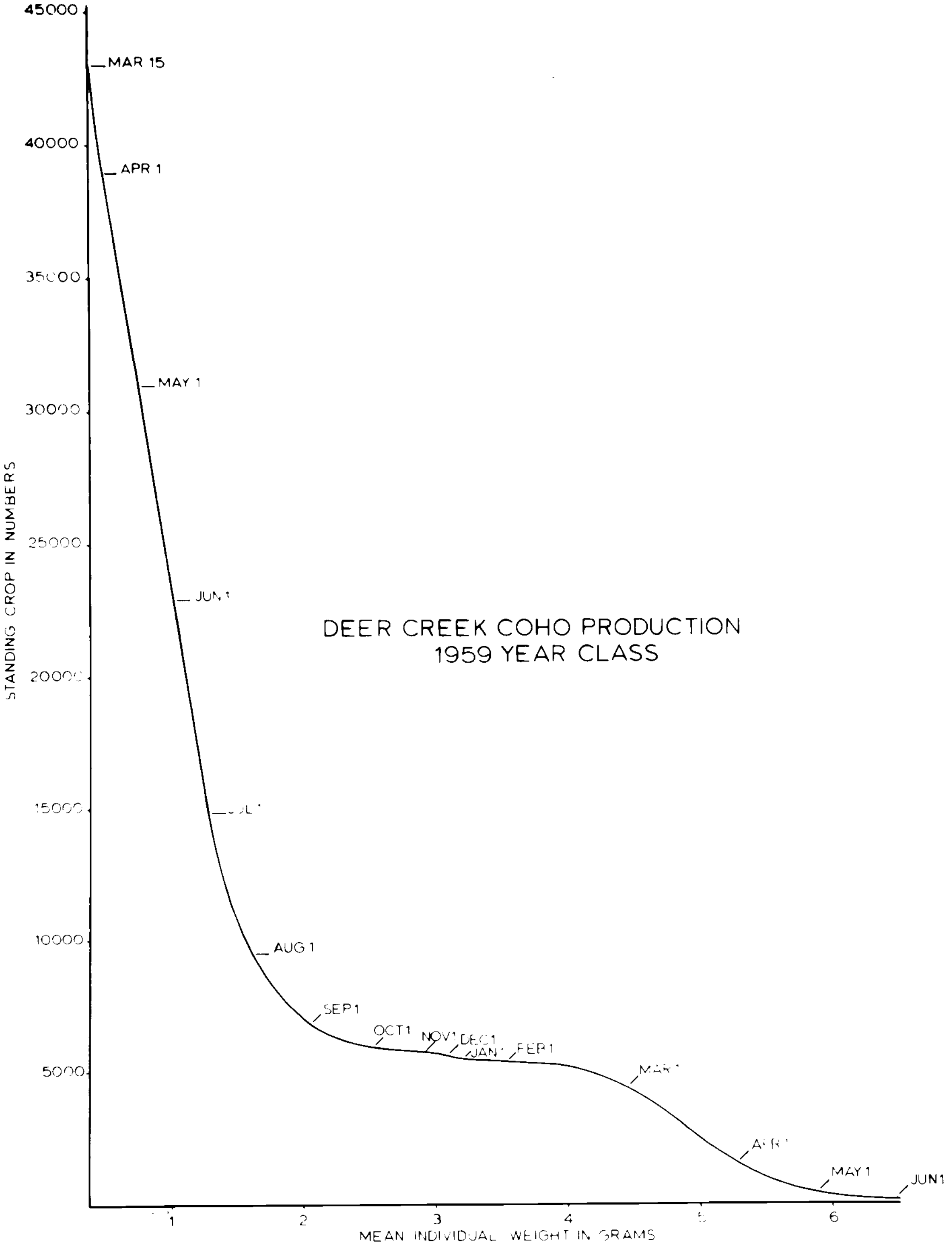
DEER CREEK COHO PRODUCTION
1959 YEAR CLASS
STANDING CROP IN NUMBERS
MEAN INDIVIDUAL WEIGHT IN GRAMS
45000
40000
35000
30000
25000
20000
15000
10000
5000
1
2
3
4
5
6
MAR 15
APR 1
MAY 1
JUN 1
JUL 1
AUG 1
SEP 1
OCT 1
NOV 1
DEC 1
JAN 1
FEB 1
MAR 1
APR 1
MAY 1
JUN 1

Figure 22

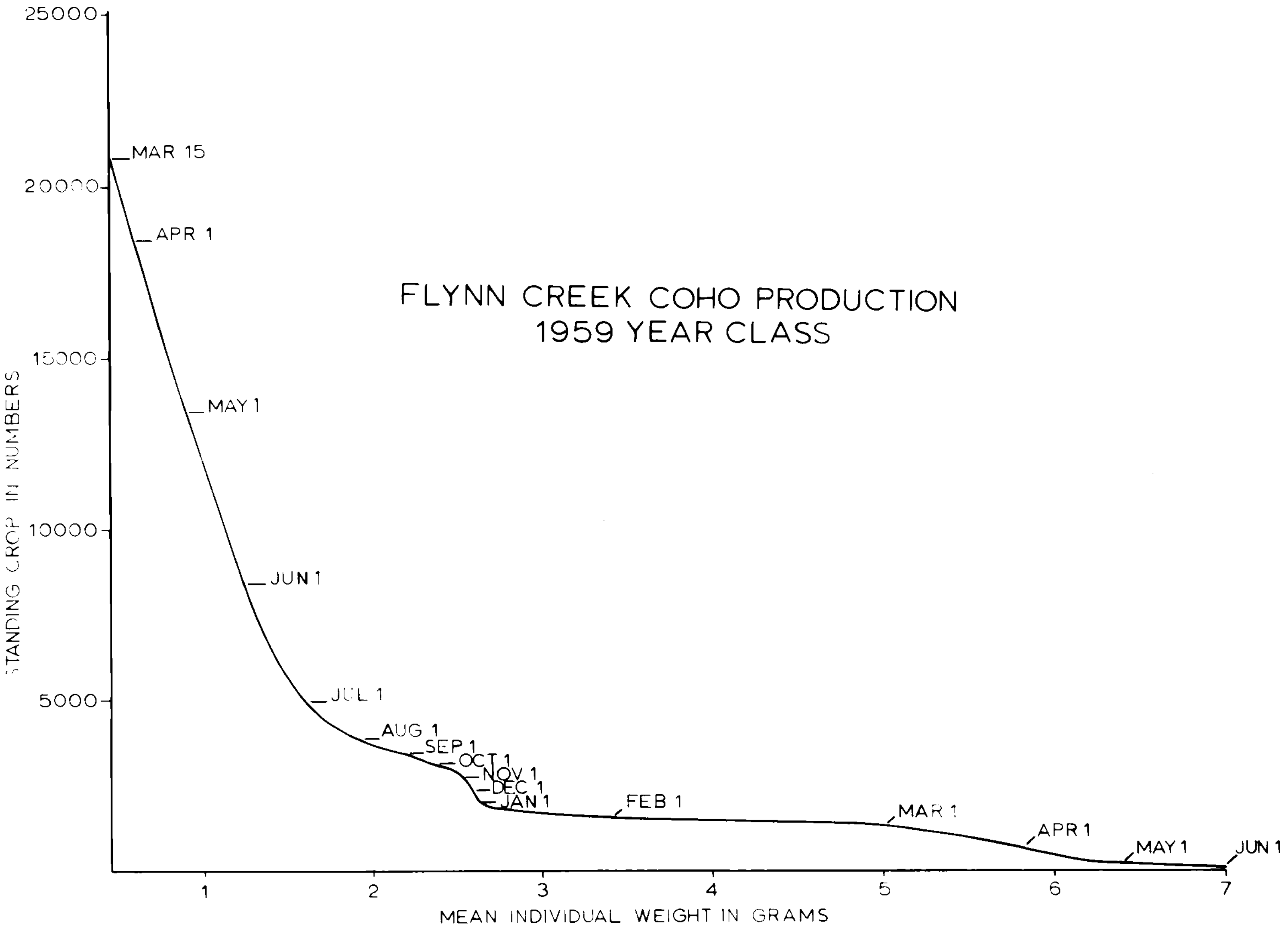
FLYNN CREEK COHO PRODUCTION
1959 YEAR CLASS
STANDING CROP IN NUMBERS
25000
20000
15000
10000
5000
MEAN INDIVIDUAL WEIGHT IN GRAMS
1
2
3
4
5
6
7
MAR 15
APR 1
MAY 1
JUN 1
JUL 1
AUG 1
SEP 1
OCT 1
NOV 1
DEC 1
JAN 1
FEB 1
MAR 1
APR 1
MAY 1
JUN 1

Figure 23

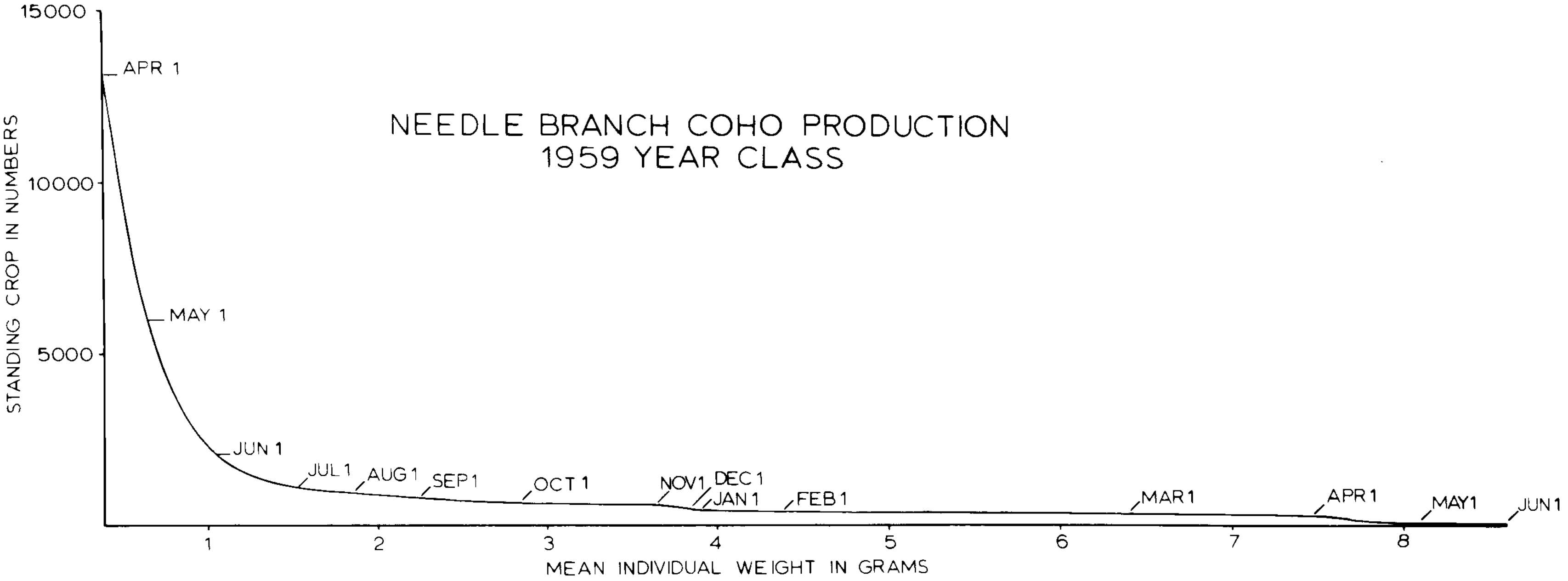
NEEDLE BRANCH COHO PRODUCTION
1959 YEAR CLASS
STANDING CROP IN NUMBERS
15000
10000
5000
MEAN INDIVIDUAL WEIGHT IN GRAMS
1
2
3
4
5
6
7
8
APR 1
MAY 1
JUN 1
JUL 1
AUG 1
SEP 1
OCT 1
NOV 1
DEC 1
JAN 1
FEB 1
MAR 1
APR 1
MAY 1
JUN 1

Figure 24

Figures 25-27 show production totals by two-week periods throughout the year. Results will be mentioned first in general terms for all streams. As can be seen from Figures 25-27, production per fortnight was highest soon after emergence, then dropped rapidly to a low in mid-winter. Production picked up sharply in late winter and early spring in the pre-smolt period, then dropped rapidly after the smolt migration.

The rapid drop in production after about April 15 was due to rapid decrease in standing crop (Figures 19-21) rather than to a slow growth rate (Figures 14-16). The decrease in crop is attributed partly to downstream-migration of fry (Appendix 7), but mostly to mortality in the post-emergence period.

Lower growth rates during winter, in conjunction with mortality, caused a low production period. Rapid growth after the winter period caused a very rapid increase in production during late January, February, and early March, 1960. Production fell rapidly in March when standing crop decreased due to migration.

Certain aspects of production are worth mentioning for each stream separately. One of these is the extreme dip in production (Figure 27) on Needle Branch in June, July, August, and September. This is attributed to a decrease in growth rate caused indirectly by low flow and "pooling" of Needle Branch at extreme low flow.

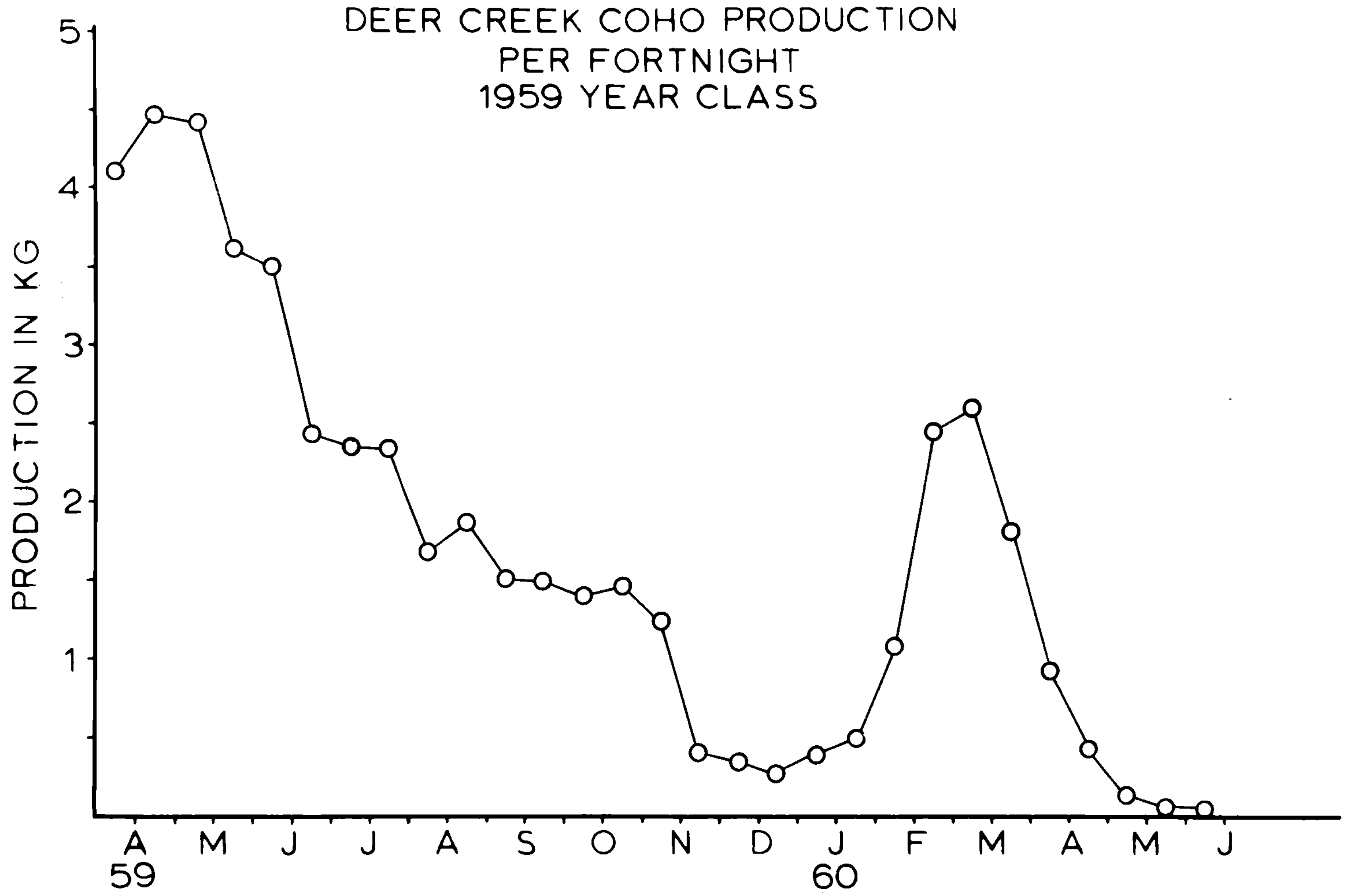
DEER CREEK COHO PRODUCTION
PER FORTNIGHT
1959 YEAR CLASS
PRODUCTION IN KG
5
4
3
2
1
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
59
60

Figure 25

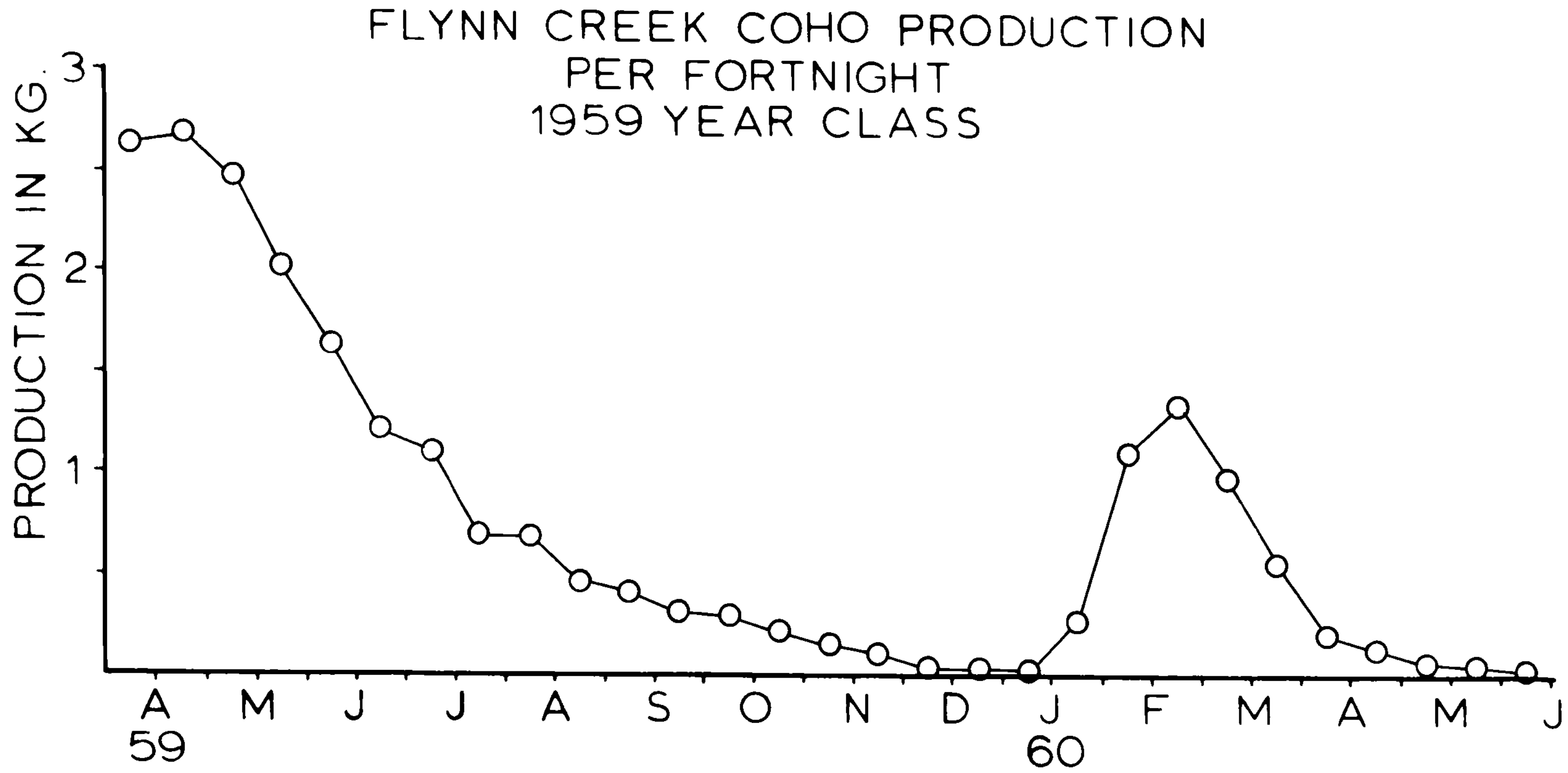
FLYNN CREEK COHO PRODUCTION
PER FORTNIGHT
1959 YEAR CLASS
PRODUCTION IN KG.
3
2
1
A
59
M
J
J
A
S
O
N
D
J
60
F
M
A
M
J

Figure 26

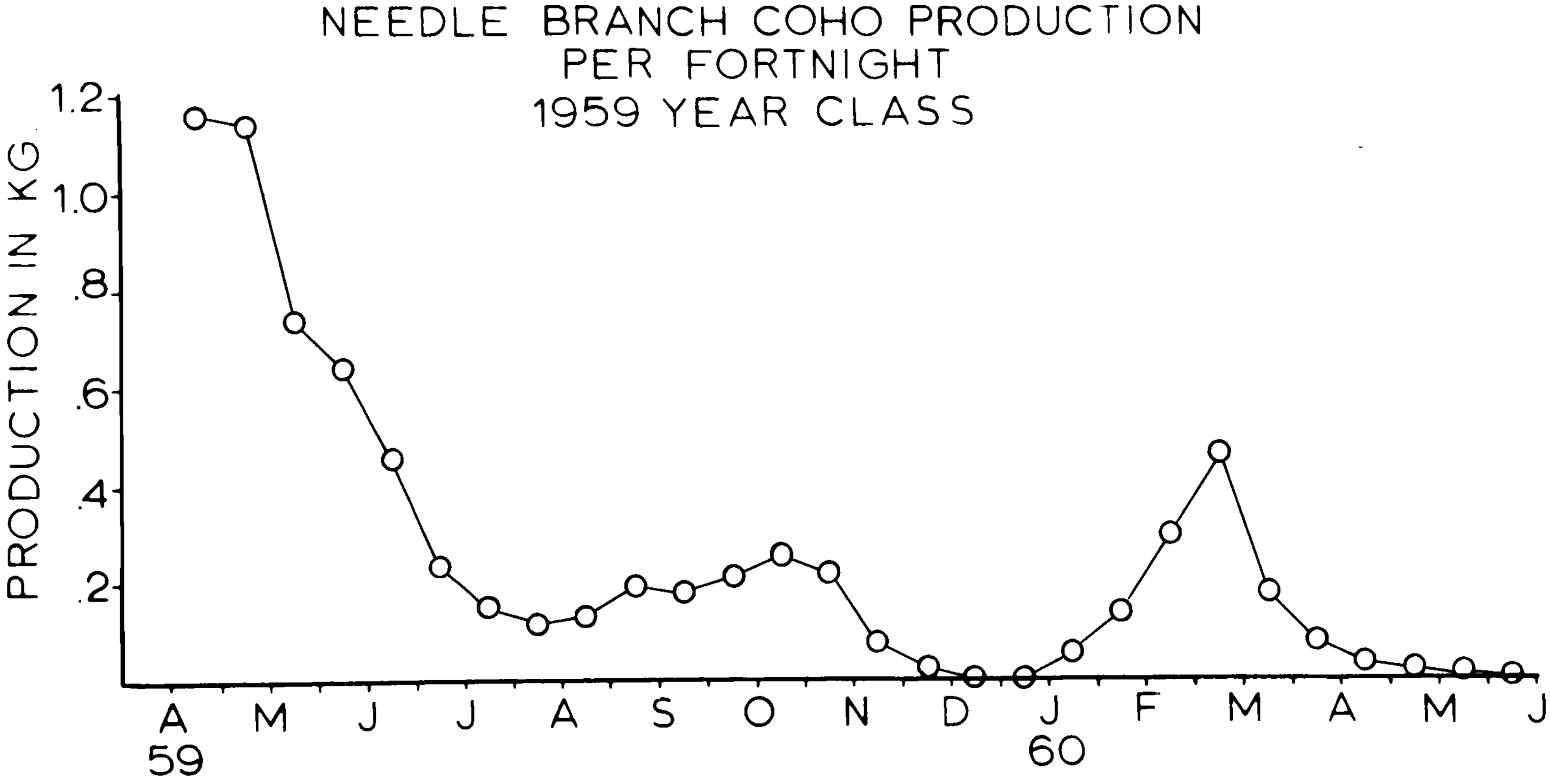
NEEDLE BRANCH COHO PRODUCTION
PER FORTNIGHT
1959 YEAR CLASS
PRODUCTION IN KG
1.2
1.0
.8
.6
.4
.2
A
59
M
J
J
A
S
O
N
D
J
60
F
M
A
M
J

Figure 27

Table 9 shows production per unit of stream area, pool area, riffle area, high-water gravel area, and low-water gravel area. Comparison of data for each stream shows similarity in total production per unit of total area: 10.30 gm/m^2 on Deer Creek, 8.95 gm/m^2 on Flynn Creek, and 8.19 gm/m^2 on Needle Branch.

Table 9. Coho production per unit areas for all streams, 1959 year class, March, 1959 - June, 1960.

	Deer Creek	Flynn Creek	Needle Branch
Total production	48.97 kg.	22.01 kg.	7.31 kg.
Production per unit of total area	10.3 gm/m^2	8.95 gm/m^2	9.18 gm/m^2
Production per unit of pool area	17.03 gm/m^2	17.29 gm/m^2	15.59 gm/m^2
Production per unit of riffle area	26.07 gm/m^2	18.57 gm/m^2	17.25 gm/m^2
Production per unit of gravel area	6.66 gm/m^2	21.68 gm/m^2	10.28 gm/m^2

Needle Branch production was about 20 per cent lower per unit of total area than Deer Creek production. This is possibly due to the pooling of the stream and concomitant decrease in growth rate. If the semi-monthly production total line for Needle Branch were altered to extend directly from May to October, in a shape roughly characteristic of Deer Creek, the total production figure would then be about 9.1 kg., or about 10 gm/m^2, a figure approaching Deer Creek production per unit area more closely than the actual Needle Branch production total per unit area. Flynn Creek extreme low flow was 0.2 c.f.s., twice that of Needle Branch. The flow on the former stream remained low for a shorter period than was the case on Needle Branch as Figure 4 shows. This might explain why Flynn Creek production per fortnight did not dip as sharply as did production in Needle Branch.

Production per unit of riffle area was calculated at 26.07 gm/m^2 on Deer Creek, 18.57 gm/m^2 on Flynn Creek, and 17.25 gm/m^2 on Needle Branch. Production per unit of pool area was: Deer Creek - 17.03 gm/m^2, Flynn Creek - 17.29 gm/m^2, and Needle Branch - 15.59 gm/m^2. Close agreement of these pool area unit production figures suggests a living space mechanism, such as territoriality or foraging space.

Accuracy of Production Data: The 95 per cent confidence limits shown for population estimates (Figures 19-21 and Appendix 4) range from ± 15.5 per cent to ± 21 per cent on Deer Creek, ± 31 per cent to ± 44 per cent on Flynn Creek, and ± 44 per cent to ± 62 per cent on Needle Branch. These percentages are ratios of 95 per cent confidence zones to estimated population size. Not included are the final crop estimates on each stream which were set with Poisson limits, and which had very wide confidence zones due to small numbers of fish marked and recorded, and the emergence crop estimates for which no estimates of error are available. The Poisson-set confidence limits played little part when the standing crop curves were placed by eye.

The 95 per cent confidence zones for mean lengths, shown in Figures 14-16 and Appendix 10-12, considering only those samples used in setting growth curves, ranged from ± 2.6 per cent to ± 5.2 per cent of the mean value on Deer Creek; ± 2.6 per cent to ± 13.2 per cent on Flynn Creek; and ± 1.9 per cent to ± 16 per cent on Needle Branch. Error apart from these values probably was introduced in placement of growth curves by eye, and in conversion of lengths to weights.

A reasonable estimate of the accuracy of growth (in weight) data would be ± 7 per cent on Deer Creek, and ± 15 per cent on Flynn Creek and Needle Branch. The lack of adequate growth data in late winter and early spring on the latter two streams is responsible for the wider limits.

When the accuracy of crop and growth data are considered together, a very rough estimate of overall accuracy of production data can be made. The estimated value for production on Deer Creek probably lies within ± 25 per cent of the true value; on Flynn Creek, ± 50 per cent; and on Needle Branch, ± 60 per cent. These figures probably overestimate the error. It should not be said that the accuracy estimates are made at the 95 per cent confidence level because of the uncertainty arising from error in placement of the growth curves, particularly in the period shortly after emergence of coho.

Yield: Total yield of coho was calculated for the entire period from emergence through migration on Deer Creek, and "effective yield" from November 7, 1959, through migration was calculated for all streams. Appendix 13-15 show the effective yields. Effective yield of smolts per 100 m^2 was 67 on Deer Creek, 52 on Flynn Creek, and 22 on Needle Branch, including 1958 year class residuals. Total yield for Deer Creek for the period February 23, 1959, to June 1, 1960, is shown in Appendix 13. This yield, corrected for all losses, was 8,030 coho, or 24.572 kg. Effective yield (Appendix 13) was 3,042 fish, or 20.059 kg.

Corrections shown in Appendix 13-15 for addition to the total known trap catches were necessary for several reasons. Fish were removed from the population for stomach sampling by Demory (15) and by trap kill. Lengths of these fish were known and weights were calculated from the length-weight regression equations.

Several corrections for Deer Creek total yield were necessary. Predation by cutthroat trout in the trap extended from emergence of coho through early June, 1960 (Appendix 9). About 188 cutthroat were trapped in this period. Some probably took no coho, others took as many as 13. It was assumed that this predation occurred in the trap. The mean loss per cutthroat was estimated to be 5 coho, giving a total loss of 950 coho. Since these fish were probably the smaller migrants, a mean weight of .5 grams was assigned to each coho lost, giving a total weight loss of 470 gm. During high flow in mid-January (Figure 3), coho were observed riding over the revolving screens. On the basis of short observation periods, the loss was estimated to be 100 fish having a mean weight of 3.35 gm. (taken from Figure 18). The total weight loss was thus about 335 gm.

The revolving screens on Deer Creek were known to pass some fish, since small fry were seen between the screens and the dam. In 1960, this loss was tested by placement of an inclined-plane trap on the overflow dam. Table 10 shows the overflow trap catch, total trap catch, and per cent of water strained by the overflow trap, for four periods in 1960. The best estimate of this loss was obtained in the period May 6 to May 19, when all overflow water was strained. Twenty-one cutthroat in the main downstream trap were assumed to have taken about 105 coho fry, and these were added to the downstream trap catch for the period, giving a total down catch of about 420 fish. A correction factor for the 1959 leakage of coho fry is then .2 times the total down catch, including predation losses. The figures for loss between emergence and June 21, 1959, is .2 (2601), or 520 fry.

Effective yields on Flynn Creek and Needle Branch are shown in Appendix 14 and 15. Yield on the former stream was 1157 fish or 7.191 kg. On Needle Branch, yield was 193 fish, or 1.766 kg.

Table 10. Portable trap catch of coho fry at trap dam below revolving screens, Deer Creek, 1960.

Period	Overflow catch	Overflow water strained	Main trap catch
4/20-5/6	52	33%	81
5/6-5/19	76	100%	420*
5/19-5/27	24	33%	161
5/27-5/31	6	100%	102

*Estimated predator take of 105 coho included.

Effective yields in numbers per unit area are shown in Appendix 13-15. Yield of smolts per 100 m^2 was 64 on Deer Creek, 48 on Flynn Creek and 21 on Needle Branch, excluding 1958 year class residuals.

Analysis of scale samples taken from five fish each week at the downstream traps during the 1960 smolt migration indicated that four per cent of 122 Deer Creek smolts, four per cent of 50 Needle Branch smolts, and ten per cent of 71 Flynn Creek smolts were apparently age 2/ fish, or 1958 year class. It was therefore necessary to apply correction factors to the trap catches to remove these fish from the yield calculations for the 1959 year class. The age 2/ fish were also separated in calculation of mean size or trap-caught coho in the spring migration as well as in calculation of residual mean length. In short, the 1958 year class was separated entirely from the 1959 class in standing crop, length, production, and yield calculations.

Fate of Production: With the estimates made for Deer Creek, it is possible to prepare a balance sheet showing the fate of coho tissue produced. Table 11 shows this balance for Deer Creek. About half the production of the 1959 year class was lost as mortality.

Table 11. Fate of Deer Creek coho production, 1959 year class, emergence to June 1, 1960.

Yield	24,572 gm.
Residual stock[1]	1,500
Mortality	22,896
Total production of year class . . .	48,968 gm.

[1] 200 fish x 7.5 gm. (Figures 18-19)

Estimation of mortality is possible, beginning at two points on the standing crop curve. One of these is the estimated survival from deposition, found by prolongation of the standing crop curve to April 1, 1959; the other is the first standing crop estimate in 1959, on May 25. Appendix 16 shows the survival calculations. Estimated survival to May 4, 1960, is 19 per cent from estimated emergence and 33 per cent from May 25, 1959, or mortality of 81 and 67 per cent respectively.

Neave (34, p. 10) shows an average efficiency of 22.8 per cent for coho spawning on two small tributaries of the Cowichan River, as calculated from counts of fry leaving the streams (as a proportion of potential egg deposition). Complement of this efficiency figure would be a mortality of about 77 per cent.

The part played by smolts in the spring following egg deposition is not clear in this paper.

Mortality data for Deer Creek are taken from Appendix 16, calculated from an anchor point of 42,500, the estimated emergence of the 1959 year class. Fish moving out of the stream are excluded from the computation so that the mortality data applies to residuals only. Mortality rates would probably be higher if nomads had remained in the stream, and would certainly be higher if nomad mortality could be considered as part of the mortality loss for the year class. Movement of nomads amounted to about 4800 fish from emergence to early November, 1959. Assuming these fish suffered at least the same rate of mortality as residuals after May 25, 1959, about 70 per cent of the nomads, or 3360 fish, would have suffered mortality by the next May 4. Thus overall survival (from emergence to smolting) of the 1959 year class for Deer Creek would be estimated at about 12 per cent instead of the 19 per cent figure determined without consideration of nomadic coho mortality.

Relationship between survivorship and instantaneous mortality rate (47, p. 24) is shown for Deer Creek coho in Figure 28. Instantaneous mortality rate reaches its greatest level in mid-June, decreases gradually to near zero in winter, and rises again slightly in spring. This latter increase might be ascribed to predator activity as water levels drop and smolt coho move downstream on the seaward migration. Movement through the

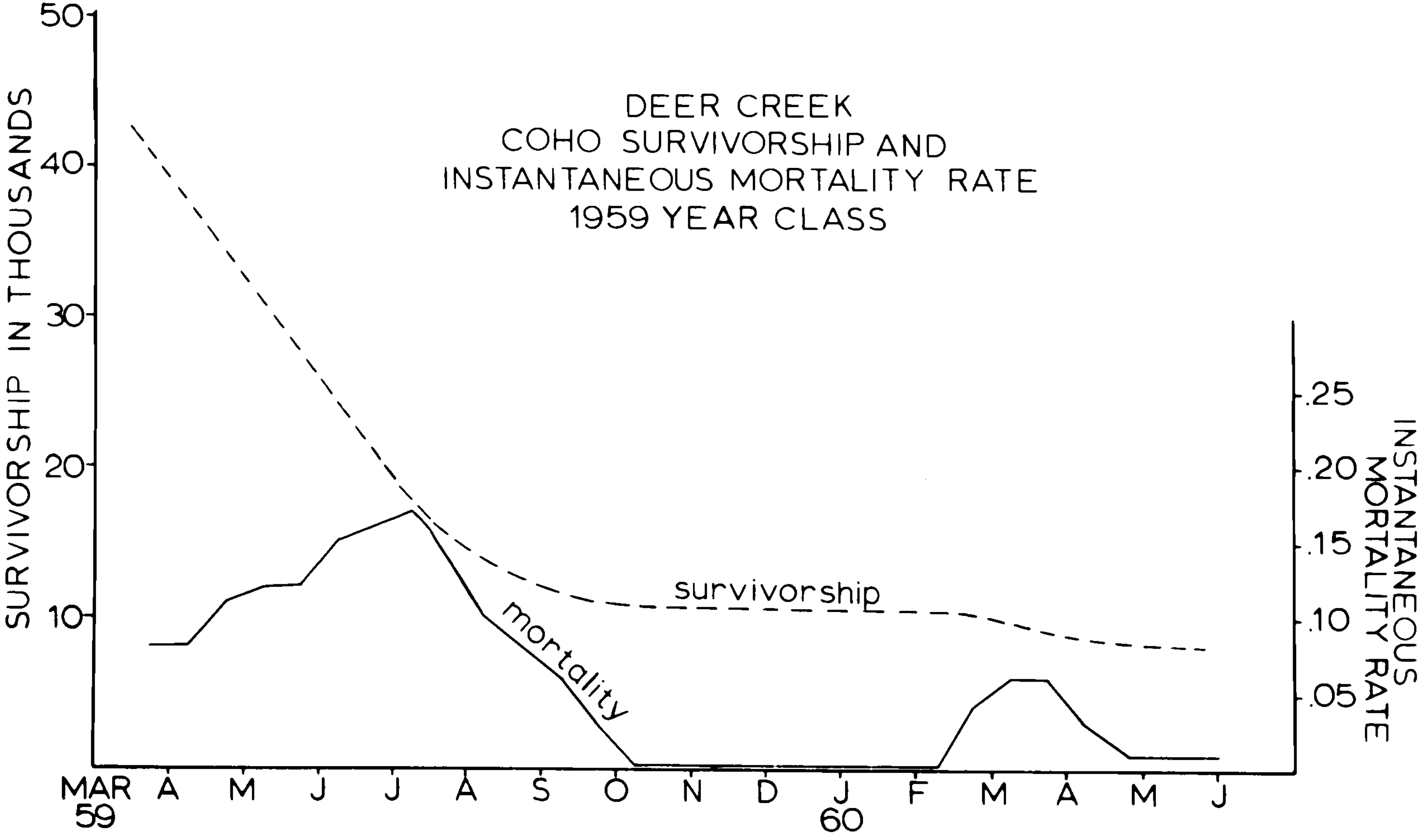
DEER CREEK
COHO SURVIVORSHIP AND
INSTANTANEOUS MORTALITY RATE
1959 YEAR CLASS
SURVIVORSHIP IN THOUSANDS
50
40
30
20
10
INSTANTANEOUS MORTALITY RATE
.25
.20
.15
.10
.05
survivorship
mortality
MAR 59
A
M
J
J
A
S
O
N
D
J 60
F
M
A
M
J

Figure 28

downstream trap has been removed from consideration in the survivorship curve, so that the instantaneous mortality rate applies to coho above the trap only.

The relationships among growth, mortality, standing crop in numbers, production and biomass are shown for Deer Creek in Figure 29. Biomass, or the total weight of fish present at a particular time, is seen to have two maxima; one in the first spring of life of the year class, and another in the next spring, just prior to out-migration of smolts.

Relationship of growth, monthly production, and standing crop is shown for Flynn Creek and Needle Branch in Figures 30 and 31.

Summary of Production Results: The following conclusions regarding production statistics for the coho 1959 year class in three streams are presented as a summary, to facilitate connection of this work with that on behavior and energy transfer.

1. A large movement downstream of coho fry occurred in the study streams from April through June, 1959. Small numbers of fry moved downstream in summer and early fall. The smolt migration occurred largely from January through May of the year following emergence.

2. Migrant coho fry were smaller than residual coho in spring, summer, and early fall. From November to March, migrant smolts were about the same size as residual coho. From March to June, migrant smolts were larger than residual yearling coho.

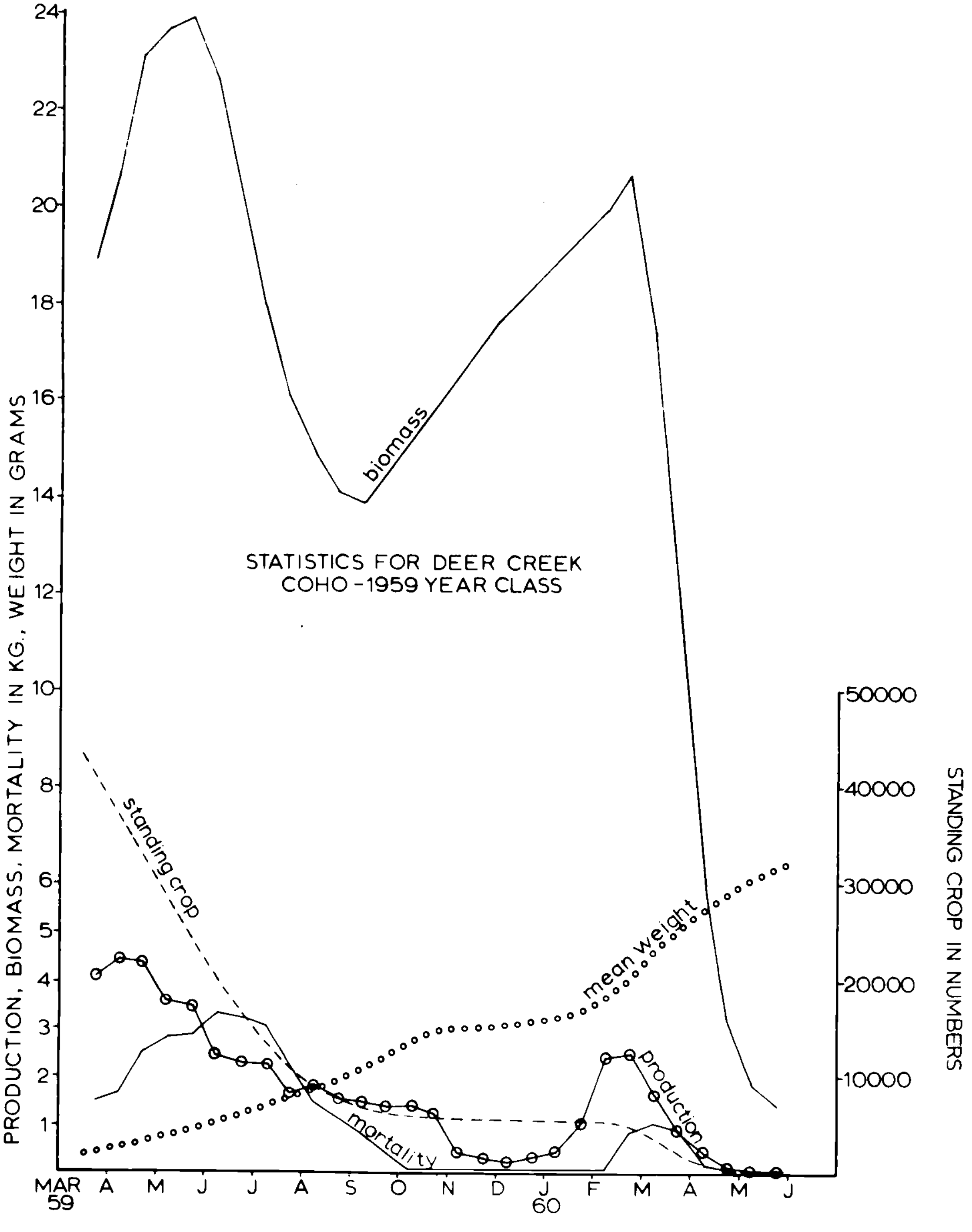
STATISTICS FOR DEER CREEK
COHO -1959 YEAR CLASS
PRODUCTION, BIOMASS, MORTALITY IN KG., WEIGHT IN GRAMS
STANDING CROP IN NUMBERS
biomass
standing crop
mean weight
production
mortality
24
22
20
18
16
14
12
10
8
6
5
4
3
2
1
50000
40000
30000
20000
10000
MAR 59
A
M
J
J
A
S
O
N
D
J 60
F
M
A
M
J

Figure 29

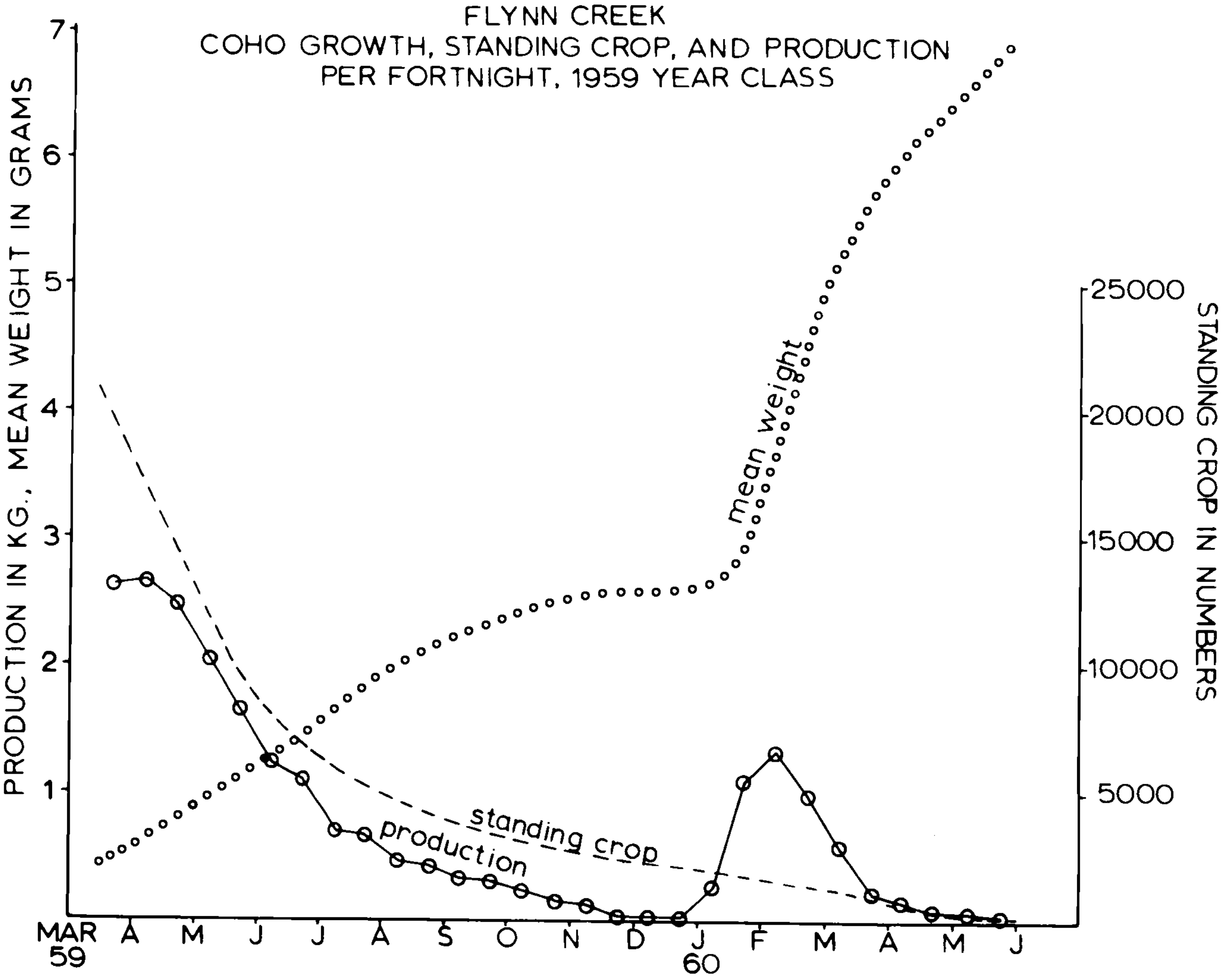
FLYNN CREEK
COHO GROWTH, STANDING CROP, AND PRODUCTION
PER FORTNIGHT, 1959 YEAR CLASS
PRODUCTION IN KG., MEAN WEIGHT IN GRAMS
7
6
5
4
3
2
1
STANDING CROP IN NUMBERS
25000
20000
15000
10000
5000
mean weight
standing crop
production
MAR
59
A
M
J
J
A
S
O
N
D
J
60
F
M
A
M
J

Figure 30

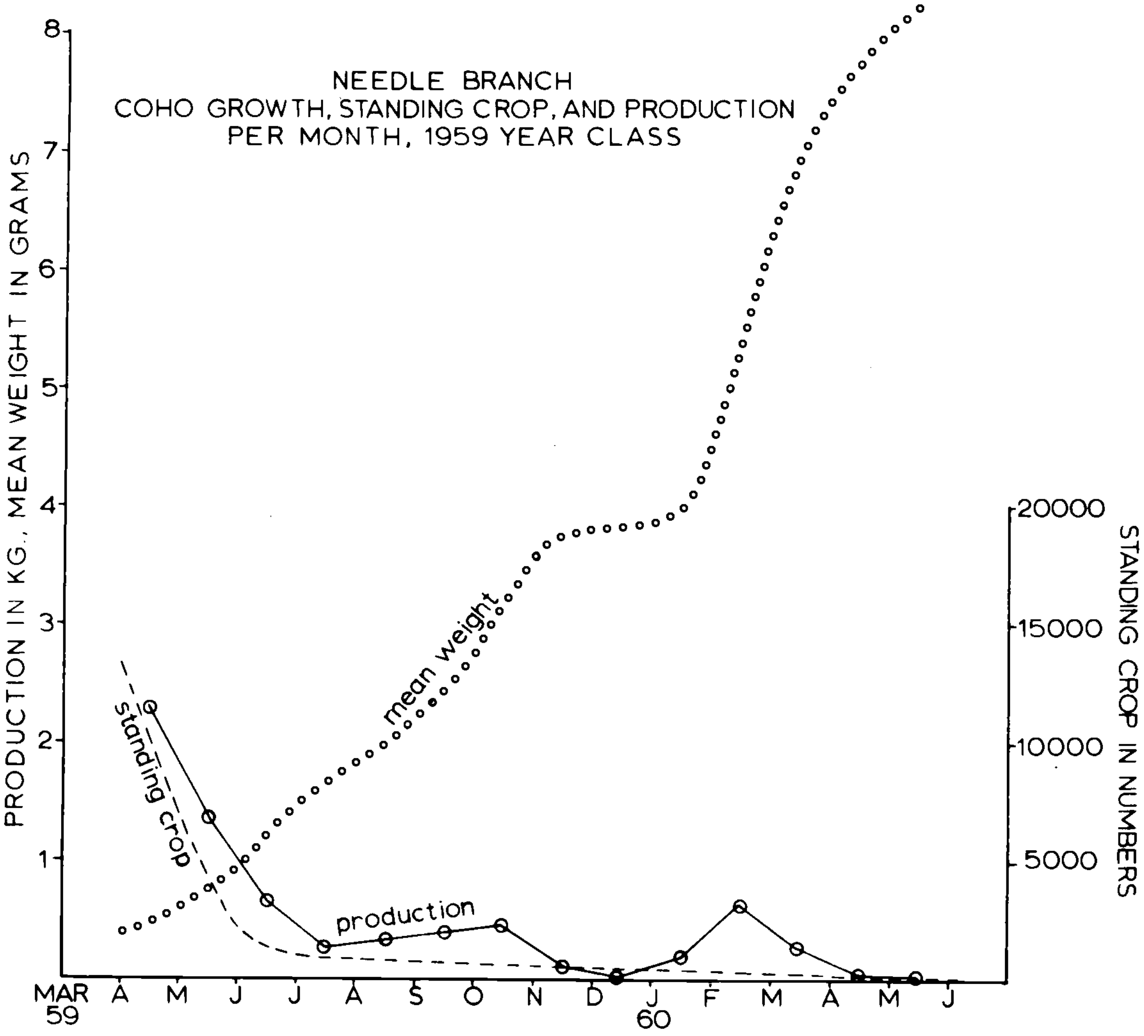
NEEDLE BRANCH
COHO GROWTH, STANDING CROP, AND PRODUCTION
PER MONTH, 1959 YEAR CLASS
PRODUCTION IN KG., MEAN WEIGHT IN GRAMS
8
7
6
5
4
3
2
1
STANDING CROP IN NUMBERS
20000
15000
10000
5000
mean weight
standing crop
production
MAR 59
A
M
J
J
A
S
O
N
D
J 60
F
M
A
M
J

Figure 31

3. Growth rate of coho decreased sharply from November 15 to January 15.

4. Growth rates of coho in the three streams were not greatly different.

5. Standing crop, in numbers of coho, decreased rapidly from emergence of fry to July, then decreased slowly until migration of yearling smolts.

6. Production per fortnight showed two peaks; one soon after fry emergence, and another shortly prior to migration of smolts. Biomass showed the same peaks.

7. Coho production on Needle Branch showed an obvious decrease in mid-summer, probably due to low flow.

8. Coho production per unit of pool area was nearly the same on all streams, ranging from about 15.6 gm/m^2 on Needle Branch to 17 gm/m^2 on Deer Creek. Production data per unit of total area and riffle area showed greater differences among the three streams.

9. Yields of smolts per 100 square meters of stream area were: Deer Creek - 64 smolts, Flynn Creek - 48 smolts, Needle Branch - 21 smolts.

10. About 50 per cent of the total coho tissue (in weight) produced in Deer Creek suffered mortality.

11. Estimated total mortality (in numbers) of Deer Creek coho, from emergence to completion of smolt migration in May the next year, was about 88 per cent.

COHO BEHAVIOR

This section deals with the causes of downstream "drift" of coho fry and fingerlings in the period from emergence through November. Fry movement could be attributed to one or more possible factors: displacement by current, innate tendency to migrate (apart from movement forced by aggression), random shifts in position, or aggression (such as territorial behavior) within the fry population. The principal hypothesis tested was that the downstream drift of age 0/ coho, or nomads, was caused by aggressive behavior of coho in the stream area above downstream trapping facilities.

Methods for Behavior Study

Two techniques were used to test the principal hypothesis. The first was the placement of nomads in artificial stream sections, both test and control, constructed in observation troughs and operated from April to September, 1960. Test sections contained a resident group of coho while control sections were barren of resident fish. The second was placement of nomads in a controlled natural stream area or stream from which resident coho had been removed or were absent. Both methods tested the idea that the nomads would cease movement downstream if given adequate living space. Nomadic coho should not remain in trough channels or in controlled natural areas if their movement was due to current displacement or innate tendency to migrate. Random movement will be discussed later.

Artificial Channels: Three troughs (Figures 32 and 33) were constructed at the downstream side of the Deer Creek fish trap. The first (left-hand) trough, called trough A, was eight feet long, 34 inches wide, and 18 inches deep. The upstream 10 inches of the trough was a "forebay", into which the incoming water was spilled. Fine-mesh nylon and metal screens separated this forebay from the artificial pools below. The trough below the screens was longitudinally partitioned into two channels, each 17 inches wide. The outlet of each of the channels was a V-notched board over which water spilled into a trap constructed so escape of any fish entering it from upstream was impossible. Fish could easily leave the channels by going over the notched board into the traps. Outflowing water then spilled about two feet to the stream bed. The walls and bottom of this trough were wood, covered with black polyethylene sheeting.

The second (center) trough, called trough B, was eight feet long, 28 inches wide, 18 inches deep, and the walls were glass. Clear polyethylene sheeting was used to waterproof the trough bottom and ends. This trough was divided into two 14-inch channels by a solid wood partition. The third trough (right-hand), called trough C, was 6 feet 8 inches long, 30 inches wide, 12 inches deep, had glass walls, and was partitioned into two equal channels part of the time only.

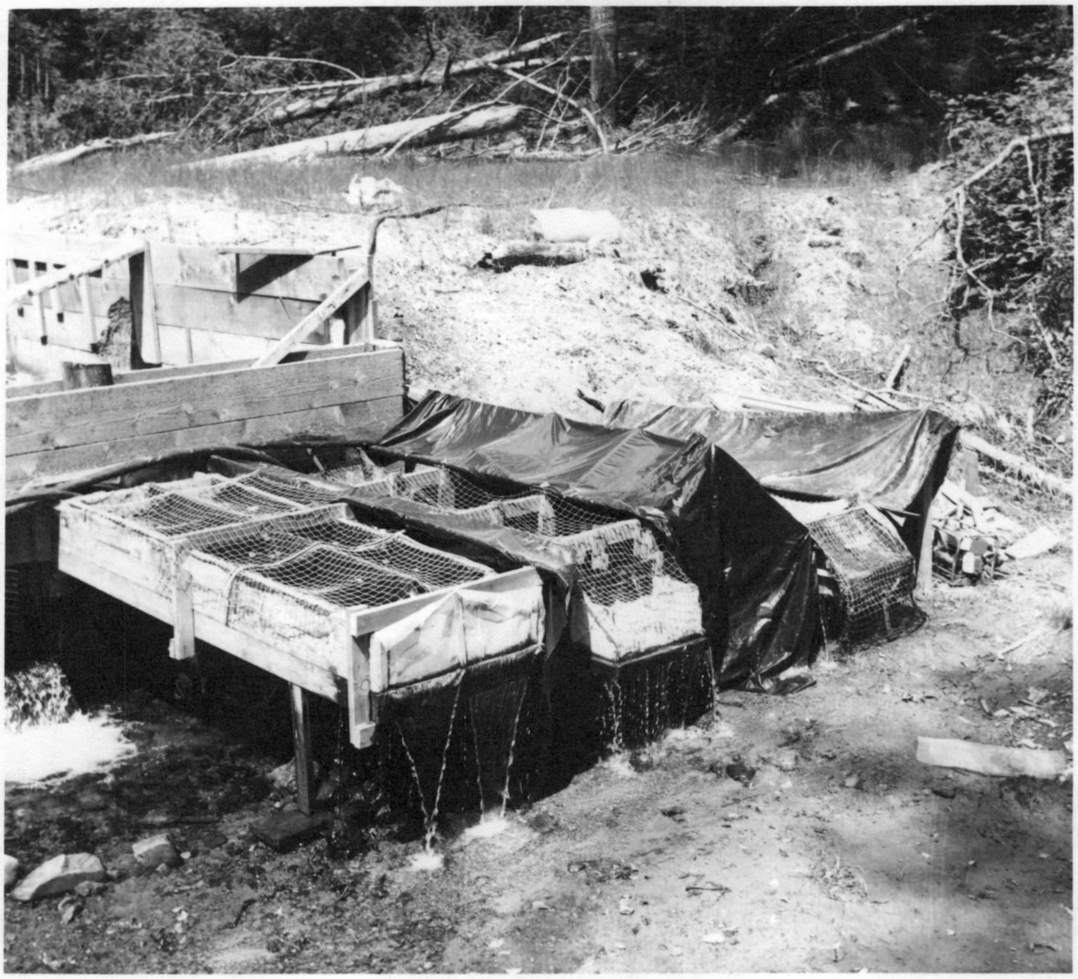

Figure 32

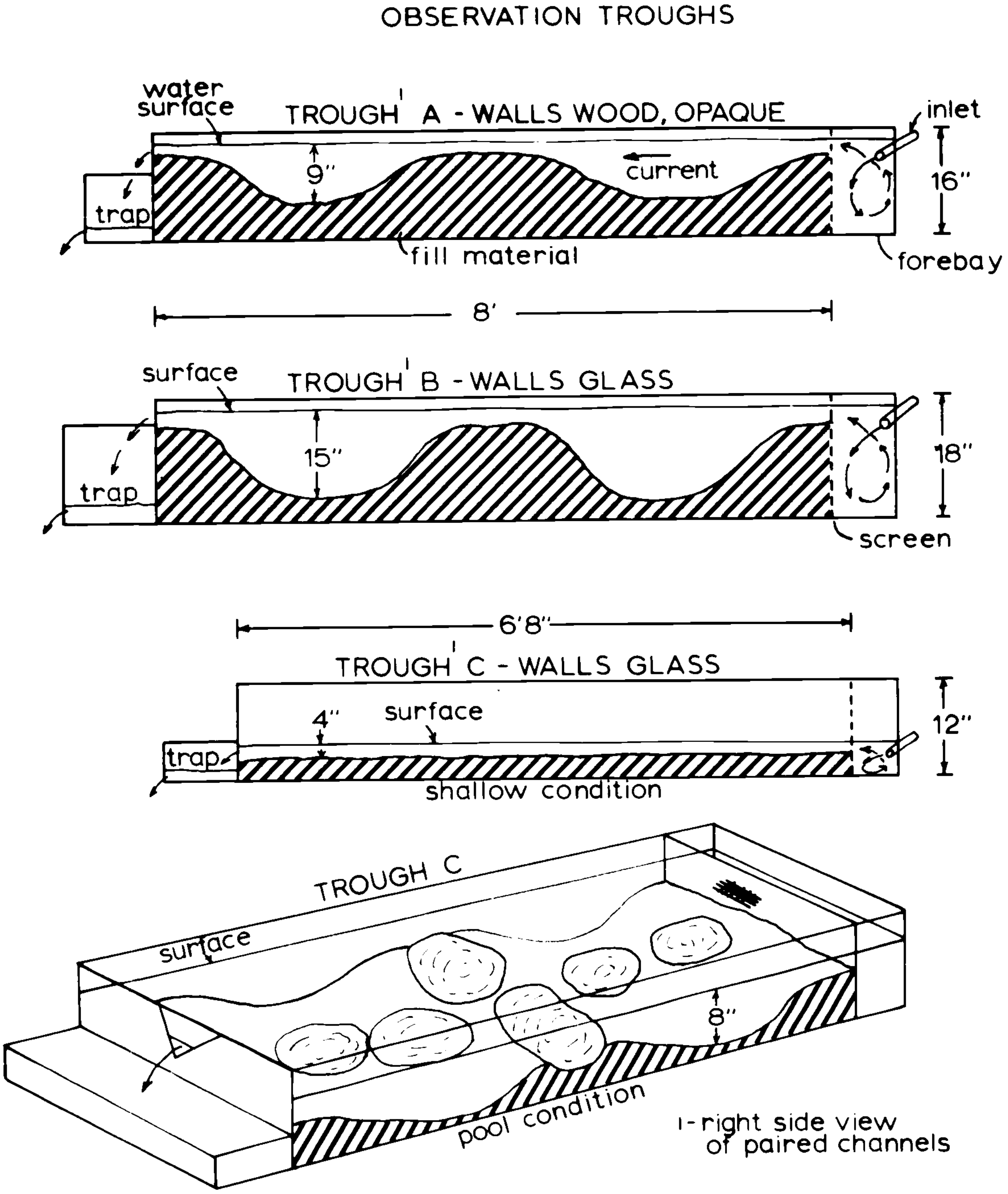
OBSERVATION TROUGHS
water surface
TROUGH¹ A - WALLS WOOD, OPAQUE
inlet
9"
current
16"
trap
fill material
forebay
8'
surface
TROUGH¹ B - WALLS GLASS
15"
18"
trap
screen
6'8"
TROUGH¹ C - WALLS GLASS
4"
surface
12"
trap
shallow condition
TROUGH C
surface
8"
pool condition
1-right side view
of paired channels

Figure 33

Water was provided for all troughs by siphoning through 1.5 to 2 inch plastic pipe from above the dam at the fish trap. When stream flow dropped to summer levels, this water was supplemented by a siphon from 250 feet upstream.

Flow through each trough was controlled by siphon pipe diameter and head difference between troughs and source water. Flow through each all-wood A trough channel was about 2.8 gallons per minute; through the glass-walled B channels it was 4 g.p.m.; and through the right-hand glass-walled trough C it was 4 g.p.m. These flows decreased slightly as streamflow dropped in late spring.

The bottoms of the A and B channels were built up by addition of natural stream bottom rocks, sand, and silt so that each channel had two pools and three relatively shallow riffles. Figure 33 shows a side view sketch of these channels. Invertebrate forms were present in the material placed in the troughs, but additional mayfly and midge larvae were added before fish were placed in the troughs. An abundant algal growth, consisting largely of *Oscillatoria* sp., became established in the A and B channels soon after the troughs were constructed.

The bottom of trough C was at first only a single layer of rocks having diameters less than about four inches, and the trough was divided into two channels, each about three inches deep. Later the trough was changed into a single pool with large rocks breaking up the pool into four areas, as in Figure 33.

Twine netting having 1.5 inch mesh was placed over all troughs to prevent birds from preying upon experimental fish, and to provide fish with some cover. Troughs B and C had benches on either side, and black polyethylene canopies over the benches minimized disturbance by observers. These canopies extended down back of the observers so that experimental fish looked out upon a dark area. Light was unobstructed above troughs except for shade from the protective netting.

No coho could pass the screening between forebays and observation troughs. Any coho placed in the trough channels had to live in the channels, die there, or pass downstream.

During part of the work with artificial stream channels, the fish were fed. Adult brine shrimp, *Artemia* sp., were frozen in one-gram lots in ice cubes and used according to a feeding schedule. The food cubes were placed at the upper end of each channel in wire baskets placed in the water. As the cubes melted, the brine shrimp drifted downstream. Experimental coho, 35 to 65 mm, fed avidly upon these shrimp. More food was fed than could be consumed at each feeding. Fish were fed twice daily early in the work, then once daily as it became evident that this was adequate.

Nomads for artificial channel experiments were obtained from the Deer Creek downstream trap, and were then measured and marked. Marks consisted of removal of a portion of one of the ventral fins or a notch in the caudal, anal, or dorsal fins. Fish were selected randomly if more than the number required were in the trap. After being held in plastic buckets for 15 minutes, the coho were placed in the channels at the upstream ends.

In initial experiments, the capacities of troughs A and B were determined by means of introductions of nomads into barren channels, followed by additional introductions into the channels after "resident" coho had become established. When capacities of trough channels had been determined approximately, groups of three to five coho were placed at the same time in each channel of trough B. In one channel, the test channel, a resident group of coho established itself. These fish formed the resident population to which new nomads were added. In the other channel, designated as a control, all coho were removed before new groups of coho were introduced. In other words, one introduced group of coho was added to a group of resident fish in the test channel while another introduced group was added simultaneously to the barren control channel. The test and control channels were essentially alike except that the test channel contained a resident group of coho.

In some experiments the resident coho were removed from the test channel, measured, and in all respects handled in the same manner as nomads to be introduced. Observation of subsequent behavior patterns and test results revealed no difference between results of tests conducted in this manner and those in which the resident group was not handled.

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

Controlled Stream Section: A 60-foot controlled stream section was formed by screens, with the upstream end of the section located about 100 yards below Deer Creek trap. A downstream trap was placed at the lower end of the section. Appendix 17 shows a sketch of the stream section. A by-pass was constructed so that migrating fish could move around the controlled section, either up or downstream.

All resident coho were removed from the controlled section before experimental fish were added. A direct current electrosampler was used to remove the resident stock. Trout taken in this operation were measured and returned to the controlled section. Coho removed were released in the by-pass. The controlled section was operated from early July to mid-September, 1960.

Nomads were secured in the downstream trap at Deer Creek, were then measured and marked with a single ventral fin amputation, and released after 15 minutes just below the upper control screen. These fish had to live in the controlled section, die there, or pass into the downstream trap at the lower end of the section.

There were about 420 square feet (39 m^2) of stream area in the section, of which about 83 per cent was one inch or greater in depth. The controlled section was not unlike many other Deer Creek stream areas in general appearance.

Transfer of Coho to Barren Stream: Since one adult female coho was "gilled" and lost on the barrier below the Needle Branch trap, and since only one other adult female and several males passed above the trap, a transfer of 1627 Flynn Creek nomads was made to Needle Branch in the period April 16 to May 6, 1960, to compensate for the loss of the female killed. The transfer provided a further test of the idea that nomads would become residents if living space were available. The transfer, four miles by road, was made in a ten-gallon milk can, and only one fish died in the process. The transferred coho were released in small lots through the area available to coho on Needle Branch. No coho fry were present in Needle Branch at time of fry transfer.

Observation of Coho Behavior: Observations of agressive behavior among coho in residence in natural areas were made on Deer Creek and Needle Branch. The total numbers of observed nips were recorded. These observations were made on areas of known size for given time intervals, usually ten or twenty minutes. The areas used for observation were not randomly chosen, but were selected for the visibility they afforded. An effort was made to watch shallow as well as deep areas.

Observation of behavior was made while nomadic coho were in the artificial channels described earlier. For the most part, these were qualitative, but some counts of nips were recorded. In making these counts, the observer usually listed the pair of fish involved, where individual fish could be identified. Care was taken to avoid sudden movements that might startle the experimental fish, but the coho in glass-walled aquaria usually ignored all movement outside the troughs below the level of the water. Any movement above the troughs severely frightened the fish.

Where growth percentages in periods of time are used, these were calculated as the ratio of change in length to initial length, multiplied by 100.

Results of Behavior Study

Description of Behavior Patterns: The social behavior patterns of coho salmon were observed in artificial stream channels and natural stream areas. The behavior noted included lateral display and parallel swimming (27, p. 76), dominance posturing (26, p. 107) or threat (54, p. 149-150), nipping (21, p. 242), chasing or driving (54, p. 149 and 18, p. 273), flight, hiding, fighting (54, p. 150 and 36, p. 67), submission (36, p. 67 and 4, p. 178), territorial defense (27, p. 78-80), displacement activities (57, p. 57-58), and formation of hierarchies (18, p. 178-179). All of these activities except hiding, fighting, displacement, and hierarchy formation were observed in the stream coho population as well as in aquaria.

Lateral display in the coho consists of erected dorsal and anal fins and an open mouth. The white-edged dorsal and anal fins were most obvious in displays. The body sometimes quivers during display, and may be tilted to one side if the object of the threat is above or below it, being maintained roughly perpendicular to the line of sight to the object of the threat. Pectoral fins are sometimes spread in display. Figure 34 shows a coho in lateral threat toward a fish lying near the bottom of the aquarium. Kalleberg (27, p. 76) describes lateral threat in Atlantic salmon parr, Salmo salar Linnaeus, as a similar display, except that the mouth is rarely open and the gill cover complex is at least partly raised.

Lateral display was seen during the period of hierarchy establishment in aquaria, during territorial defense in aquaria and stream, and sometimes during the course of hierarchical dominance activities in the aquaria. Lateral threat may be a mutual vigorous display between a pair of coho, and sometimes results in parallel swimming (27, p. 79-80), in which a pair of coho travel parallel for a distance of from a few inches to perhaps two feet. These fish usually swim three or four inches apart.

Dominance posturing, or threat, in the coho is apparently quite similar to that of the Kamloops trout, Salmo gairdnerii

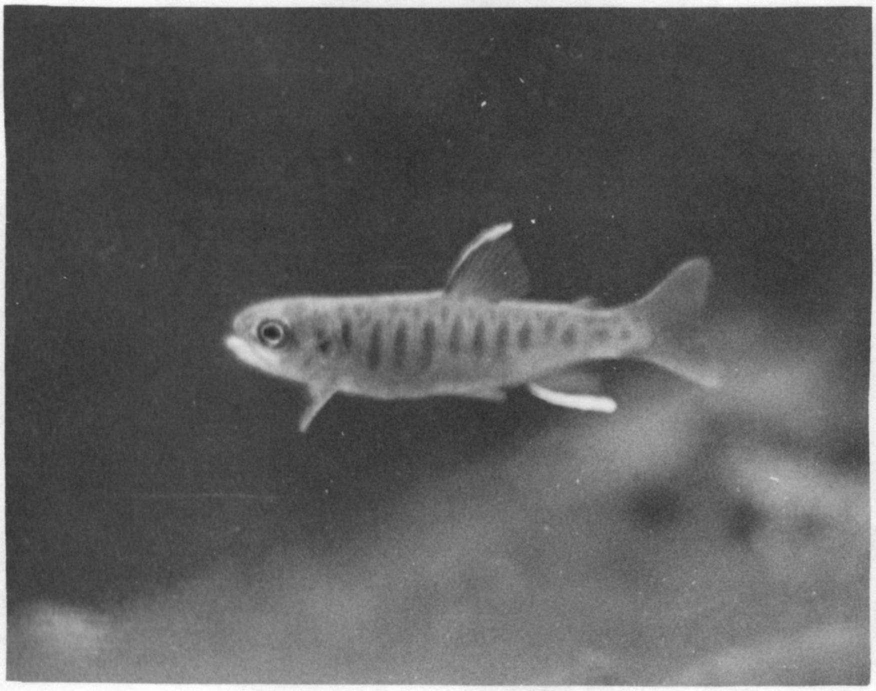

Figure 34

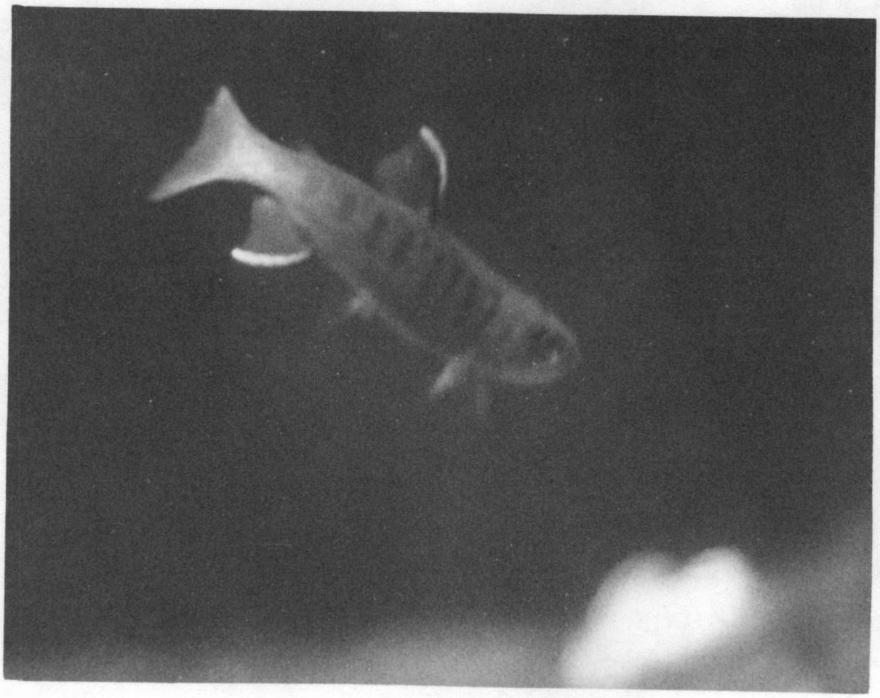

Figure 35

kamloops (Jordan), (54, p. 149-150). The dorsal, anal, and usually the pectoral fins are erected, the mouth is partly open, the caudal portion of the body is twisted until it makes an angle with the anterior part, the angle alternating from side to side. The threatening fish may swim in this posture or may remain in one spot. In either case the head may be either up or down, so that the body is at angles ranging from about 30 to 90 degrees from the horizontal position. Swimming is jerky, and the fish usually turns back after moving a few inches and either repeats this threat or makes a lateral threat. Figure 35 shows the dominance posture or threat. The latter term is used by Stringer and Hoar (54, p. 149) and will be used here to describe the posturing activity in preference to the "dominance posturing" of Jones and Ball (26, p. 107). Threat was seen very frequently in aquaria when social hierarchies were being established, and in the stream and aquaria during territorial defense. It can have either defensive or offensive character.

Nipping in coho (Figure 36) has been described by Hoar (21, p. 242) as the activity "in which the fish makes a quick darting movement toward, and bites usually close to the base of, another fish's tail." Hoar states that the action does not involve any actual contact between fish for only the water near the attacked fish is "bitten." While the nipping coho usually does not actually bite the attacked fish, some especially violent encounters during a contest for dominance in aquaria

Figure 37

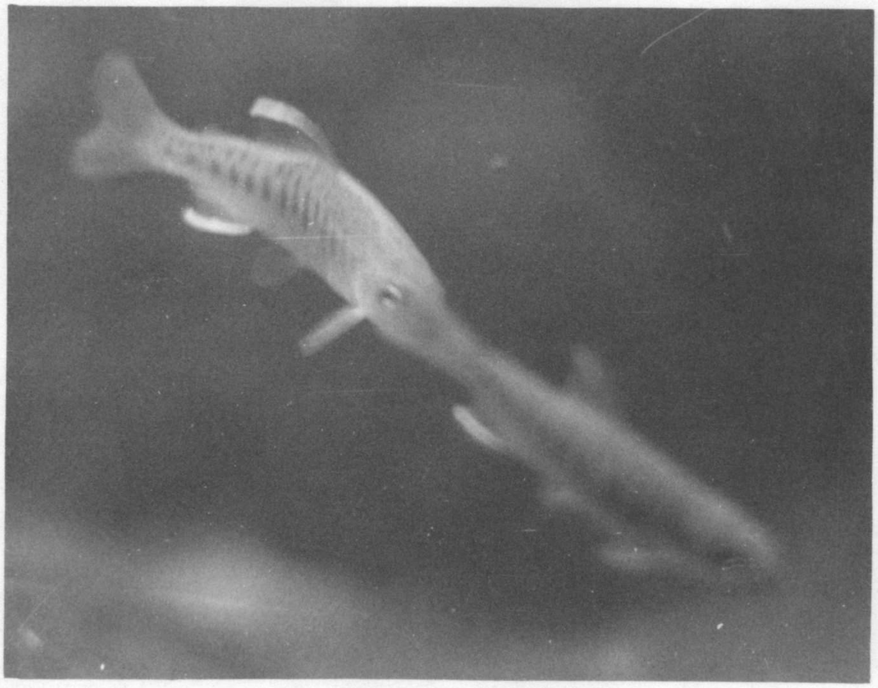

Figure 36

appeared to include physical contact. Nipping, after the initial contest for dominance, usually became ritualized.

Frontal threat, including convex dorsal profile, lowered dorsal fin, extension of all other fins, open mouth, and dilation of a "gular pouch" as described for Atlantic salmon by Kalleberg (27, p. 73-74) was not seen in the coho. Kalleberg believed Hoar's description of coho nipping indicated a simplified frontal threat, a darting approach usually followed by a threat bite. The closest thing to the "frontal threat" seen in aquaria was repeated positioning of one coho about four inches from the flank of another, followed by a darting attack and apparent bite or bump in the caudal region of the attacked fish. The attacked fish nipped in return, then the process was repeated. Delay between nips might be several minutes or only a few seconds, and the threatening fish remained perpendicular to the flank of the opponent. This activity was seen only once.

Fighting, as described by Stringer and Hoar (54, p. 150) for the Kamloops trout, and by Newman (36, p. 66-67) for rainbow and eastern brook trout, was seen in the behavior of coho in aquaria during establishment of dominance-subordination relationships. Fights involved two fish swimming in a close circle, repeatedly attacking (nipping) each other. These fights were usually of short duration and dominance was quickly established. Circling and nipping usually alternated with threats. On many occasions, dominance was established by threats only, especially when opponents were disparate in size.

Submission without flight in the coho, as in the case of eastern brook trout and rainbow trout (36, p. 67), involves lowering of all fins (Figure 37), particularly the dorsal, often a collapsing of the caudal fin, and sinking toward the bottom. Sometimes a darkening of the body is noted, particularly along the sides between parr marks. The submissive fish often settles to rest on the aquarium bottom. Submission without flight could not be noted in the natural streams. Submission was also indicated in the aquarium coho by drifting downstream away from the threatening or dominant fish. Fins were generally lowered in this type of submission. Submission by flight was frequently seen, especially after dominance relationships were well established. Subordinate fish were often driven rapidly about the aquaria until they found a hiding place. In this case, the fins were erect as the subordinate coho darted about in apparent panic. Less extensive flight, better called retreat, was noted in intruders being threatened by a territorial fish. Flight in this case usually was brief, lasting only until the intruder was out of the territory.

Displacement activities (57, p. 57-58) were frequently observed. Displacement occurs, according to Baerends (3, p. 247), when there is (1) a conflict between incompatible instincts, such as aggression and flight; (2) when external stimulation necessary for the completion of the activity either does not turn up, or suddenly ceases (as when, at the beginning of a fight, the opponent suddenly flees). Displacement is a result of internal conflict. It was seen in coho when a subordinate fish was repeatedly nipped by other fish. The subordinate fish being unable to, or afraid to, nip an individual in return, apparently transferred the aggressive urge to tufts of algae or particles on the bottom, viciously mouthing these and spitting them out. Displacement also was evidenced by dominant fish when a chased subordinate suddenly disappeared, hiding under a rock. The aggressor was repeatedly seen to pick up algal tufts and spit them out.

Territorial defense in streams, other than that occurring in reproductive behavior, has been noted for several salmonids including brown trout, <u>Salmo trutta</u> Linnaeus (30, p. 113-115 and 27, p. 61-68), Atlantic salmon (27, p. 61-68), rainbow trout (54, p. 149-151 and 36, p. 64-81), eastern brook trout (36, p. 64-81), and coho salmon (21, p. 253-256). Territory is defined as a defended area by Noble (37, p. 267), implying aggression against intruders.

Territorial defense was observed in the aquaria and in the stream. In defending a territory, the resident threatens intruders with lateral threat, nipping, or combination of these. The territory is defended against all intruders.

"Partial territory," noted by Greenberg (18, p. 272-273) for the green sunfish, <u>Lepomis cyanellus</u> Rafinesque, was also seen in the coho. This situation occurs when a subordinate fish in a hierarchy defends an area against all but the individual or individuals above in the hierarchy. Defense of the partial territory is the same toward all but the dominant fish as that described for complete territory defense.

Stable hierarchies have been described in stream-dwelling salmonids by Newman (36, p. 64-81) for rainbow and eastern brook trout. Hierarchies have been shown to exist in several other kinds of fishes, such as the green sunfish (18, p. 271-274), and Platypoecilus (4, p. 178-180). Stringer and Hoar (54, p. 151) noted no well-organized peck order or nip-right among Kamloops trout.

Fairly stable hierarchies were frequently observed in coho groups within artificial stream channels. When less than five fish were present in aquaria, these hierarchies could be ascertained and observed over periods of up to two weeks. Hierarchies were usually of the "nip-right" type (4, p. 178), in which one fish would nip another without being nipped in return.

When three to five nomadic 0/ age coho were placed in a channel (glass-walled) previously empty of fish, they at first were quite light in color and tended to spread dorsal and anal fins for a few seconds. After about a minute, one or two fish might swim about the upper pool, where they were introduced, appearing to examine the area. After a few contacts against the trough glass wall, the fish usually made no effort to pass through it. The other, less inquisitive, fish usually settled to the bottom of the channel and remained there.

After five to ten minutes, one or two fish, usually the inquisitive ones, might wander into the lower pool, sometimes returning to the upper one soon after. The first sign of aggression usually appeared 5 to 15 minutes after the fish were introduced. Color of all fish was usually darker by this time. Initial aggression was usually a threat. Sometimes the single threat was sufficient to establish a dominance-subordination relationship between a contact pair, especially if the aggressive fish was much larger than the object of the threat. The dominated individual usually sank submissively toward the bottom or drifted downstream a short distance. Usually the initial threat was made by fish other than the smallest in the group introduced to the trough. The smallest coho sometimes was unmolested by the larger fish until a day or more had passed, and during this period the nip-right was usually established among the larger fish. The smallest fish usually took up inconspicuous stations downstream from the larger coho.

If the fish placed in the control channel were close to the same size, sometimes the two largest fish set up territories, one in each pool. Other smaller fish were forced to take up partial territories or shuttle from one territorial fish to another, being hipped or chased upon entering each territory.

The area at the extreme head of the upper pool, the "riffle" between pools, and the extreme tail of the channel were areas where subordinate fish usually remained. As long as the subordinates remained close to the bottom out of sight, the dominants paid them little heed. As soon as a subordinate rose to feed, he was nipped or chased. If a co-dominant carried his chase into the other dominant's territory, he was threatened or nipped by the defending territory holder.

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

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

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

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

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

Noble (38, p. 118) points out that in Xiphophorus, either a single newcomer, if sufficiently large, or a group of new fish will produce a revolution in the resident hierarchy. In the latter case each fish fights for itself against residents and introduced individuals. While the dominant resident usually remains the despot, a fish from either group may rise to second place in the order. No such rapid revolution was seen in the artificial stream channels, where resident fish held a distinct advantage, but enforced confinement, where fish could not leave the channels, might have eventually produced the "revolution."

Braddock (5, p. 164) shows that prior residence in an area confers upon an individual Platypoecilus a greater potential for dominance than it would otherwise have. Braddock indicates that this effect is most important in initial contacts between individuals, and that if the intruder is larger than the resident, size may prevail in the contact. Braddock's words could well be applied to coho salmon, except that the prior resident always prevailed in artificial stream channels. The introduction of intruders larger than the resident despot tended to prolong the conflict between the pair.

Behavior in Troughs: Table 12 summarizes pertinent results obtained in artificial stream channels. These results should be elaborated to some extent, and will be discussed in the order shown in the table.

Trough A--Opaque Walls: The introductions of nomads in these paired channels were to determine roughly the capacity of the troughs to hold coho. After about one month, April 15 to May 19, 1960, during which 12 nomadic coho were placed in one channel and 18 in the other, it was found that from four to seven coho fry, 35-45 mm, would hold in each channel.

Trough B--Glass Walls: Early in May, tests were begun in these channels in order to observe coho behavior. Work with the A troughs had indicated that five to ten coho fry probably would be maximum stocking for trough B channels. From May 11 to

Table 12. Summary of pertinent information derived in artificial stream channels, 1960.

Trough	Dates	Coho introduced								Purpose and Methods	Summary
		Control channel				Test channel					
		In	Resident[1]	Out	Proportion remaining[2]	In	Resident[1]	Out	Proportion remaining[2]		
A	4/15-5/18	12	0	8		18	0	11		To secure estimate of trough capacity.	Capacity of each channel was four to seven coho fry, 35-45 mm.
	5/18-5/19					5	7	5			
B	5/11-5/14	5	0	1		5	0	2	.60	To observe behavior patterns, establish trough capacity.	Largest nomad in introduced groups became dominant. Nip-right established by size. New fish at disadvantage in contacts with residents. Behavior seen included nipping, chasing, flight, hiding, fighting, lateral display, threat, parallel swimming, submission, territoriality, displacement, and hierarchy formation. Channel capacity was three to six coho, 38-46 mm.
	5/14-5/18					5	3	2	.60		
	5/18-5/20				.80	5	6	5	.00		
	5/20-5/27	5	0	0	1.00	5	5	2	.60	To determine tendency of nomads to cease movement if living space was provided. Test channel had residents present while control channel was barren when new nomads were introduced. To determine if feeding would hold more fish in channels. Brine shrimp fed June 6-July 9.	Prior residents had advantage. Despot soon established dominance over new fish. Control fish placed in barren channel established hierarchy by size. Aggression less frequent in control. Despot in test channel established dominance over newly-introduced nomads larger than himself. Control fish tended to remain in trough while test fish usually left trough. Growth of dominant fish superior to that of subordinated, May 11 - June 1. Feeding failed to increase number of coho remaining in channels.
	5/27-6/1	4	0	2	.50	4	8	3	.25		
	6/1-6/13	4	0	2	.50	4	5	4	.00		
	6/13-6/16	5	0	3	.40	5	4	3	.40		

(continued)

Table 12 continued.

	Coho introduced									
	Control channel				Test channel					
Dates	In	Resident[1]	Out	Proportion remaining[2]	In	Resident[1]	Out	Proportion remaining[2]	Purpose and Methods	Summary
B 6/16-6/25	12	0	9	.25	12	0	12	.00	To determine if larger fish tended to leave channels and smaller ones to remain. Both channels barren at time of each introduction. Test fish grouped as large nomads, control fish grouped as small.	Larger fish tended to be restless and to leave channel, while smaller ones tended to stay. Aggression was more frequent in group of small fish. Only two fish over 50 mm ever remained in either channel for a week or more in any period. Trough capacity one to three coho, 41-57 mm.
6/25-7/1	5	0	3	.40	3	0	2	.33		
7/1-7/17	5	0	2	.60	4	0	2	.50		
8/18-9/7	4	0	3	.25	4	0	3	.25	To determine if group of coho of nearly same length would exhibit more aggression than group of varied sizes. Fish seined from stream.	Aggression more frequent in test group of near-homogeneous sizes. Largest fish in each group became dominant and remained in channels until September 7. Fish as large as 71 mm remained in channels. Trough capacity one coho, 51-71 mm.
9/7-9/13	4	0	3	.25	4	0	3	.25		

[1] Number of fish in trough just prior to introduction of new group.

[2] Proportion of latest introduction remaining in trough at ending date.

20 it was established that each channel would hold three to six coho, 38-46 mm in length. The behavior patterns described earlier in this paper were first seen in this period.

From May 20 to June 16, four separate experiments were conducted in the B channels. A resident group had become established in the test channel by May 20, and was allowed to remain there. In each experiment a group of nomads was taken from the Deer Creek downstream trap and placed in the test channel. At the same time an equal number of coho (usually four or five) was placed in the barren control channel.

As Table 12 shows, most of the coho placed in the test channel left within a few days, while more of the coho remained in the control channel. In the test channel, prior residents had the advantage in contacts with newcomers. The resident despot in the test channel quickly dominated all newcomers, forcing them into areas downstream from his feeding station. Aggression was less frequent in the control channel, in terms of nips per fish per unit of time, than in the test channel. Table 13 shows the number of nips given and received by four control channel fish in one hour, shortly after the fish were placed in the channel on June 1.

Table 13. Nipping in control channel 1215-1415, June 1, 1960.

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

Mean nips given per fish per 10 minutes = .25

Table 14 shows nipping in the test channel in the same time interval.

Table 14. Nipping in B test channel 1220-1420, June 1, 1960.

Aggressor	Nip recipients									
(mm)	52 mm	48	42-41[1]		41-40[1]	39	53	50	42	40
52 [2]	--			19		2	10	4	8	18
48 [2]		--		3		10	1	3	12	45
42-41 [2]			--		3	1 11				8
41-40					--					
39						--			1	9
53	10						--			
50								--	1	
42									--	
40										--

Mean nips per fish per 10 minutes = 1.6

[1] Separation of 42-41 and 41-40 impossible at times. Nips recorded at these times are listed between columns.

[2] As measured later, on June 13.

Nipping was recorded in the test channel on June 13, 1960, for 2.5 hours following introduction of a new group of nomads. The nips recorded are shown in Table 15. The despot in the channel did most of the nipping, and only the largest newly-introduced nomad contested for dominance. This large nomad was dominated by the resident despot and left the channel within 24 hours.

Table 15. Nipping in B test channel 1130-1400, June 13, 1960.

Aggressor (mm)	Nip recipients									Total nipping
	Old residents				Introduced nomads					
	52 mm	42	41	41[1]	60	49	48	46	40	
52	--	8	6		3	40	3	5	16	81
42	2	--				3			2	7
41			--			7	1		4	12
41				--						0
60	5	1			--				1	7
49						--				0
48							--			0
46								--		0
40									--	0

Mean nips given per fish per 10 minutes = 0.8

[1] Hiding

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

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

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

Dominant fish tended to grow more rapidly than subordinate coho. Table 16 shows growth of dominant and subordinate fish that were introduced into the channels at the same times. Growth was determined after the time intervals shown in the table, and is expressed in terms of percentage increase in length.

Table 16. Growth of dominant and subordinate coho in B channels

Channel and time period	Initial length (mm)	Final length (mm)	Percent growth
Control channel May 11 - May 20			
Dominant	46	47	2.2
Subordinate	41	41	0.0
	39	44	0.0
Control channel June 1 - June 13			
Dominant	53	56	5.6
Subordinate	42	44	4.8
Test channel May 11 - June 13			
Dominant	45	52	15.0
Subordinate	41	43	5.0
Subordinate	39	41	7.0

In mid-June, the resident despot in the test channel left the channel. This fish, present from May 11 to June 15, was 52 mm long and had shown increasing aggressiveness and displacement activities in the week preceding his departure. A 65 mm nomad left the control channel on June 16, three days after being placed in the trough. This fish was dominant in the left channel. For these two coho, the channels seemed to be inadequate in some way. Food was abundant, but perhaps the space was inadequate after these large coho reached some critical size or state. Aggression certainly was not responsible for causing the movement of these dominants.

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

Subsequent experiments with groups of coho separated by size indicated that smaller fish would tend to hold in the troughs better than larger coho. Table 17 shows growth of dominant and subordinate coho. Dominant fish grew more rapidly. Feeding ended on July 9.

Table 17. Growth of dominant and subordinate coho in B channels

Channel and time period	Initial length (mm)	Final length (mm)	Percent growth
Control channel June 21 - June 25			
Dominant	43	46	7.0
Subordinate	43	44	2.4
Control channel June 25 - July 1			
Dominant	44	46	5.0
Sub-dominant	42	43	2.5

Several experiments were conducted in the C channels from June 14 to 25, to determine if speed of current would affect aggressiveness in introduced nomads.

The flow through the channels was fairly rapid and the water only three inches deep. Territories seemed to be organized rapidly and recognizably in this shallow, faster water, and size appeared to play a part in location of the territories. Larger nomads tended to locate feeding stations furthest upstream. Due to operational difficulties, nothing beyond these general observations was learned in the shallow C channels.

On June 25, the partition between the C channels was removed and the bottom arranged to form a single pool with four areas separated by large rocks. This pool was constructed with the aim of providing a more spacious area for holding larger nomads than would remain in the B channels.

Five nomads, 47-54 mm in length, were placed in the C pool on July 1. All these fish left the pool within two days. The C pool was inadequate for this group in some way, as evidenced by the fact that in another group, taken from the Deer Creek downstream trap the same day and placed in the B control channel, two out of four fish remained in the channel for a two-week test period. On July 3, five coho, 40-48 mm, were placed in the pool. A 48 mm coho became dominant, nipping and chasing subordinates over the entire pool almost constantly. Three weeks after introduction, the dominant fish left the trough at a length of 55 mm. During his last week in the channel, this fish was extremely aggressive and restless, seeming to seek the two remaining subordinates to nip and chase. This could be termed "appetitive" behavior (14, p. 91).

From August 18 to September 13, two experiments, summarized in Table 12, were conducted to determine if a group of coho of nearly the same size would exhibit more aggression than a group of fish of disparate lengths. Table 18 shows nipping frequency in the groups introduced to the channels on August 18. The coho used after August 18 were resident fish seined from a natural stream area.

Table 18. Nipping in B channels on August 18, 1960.

Left channel 60 minutes					Right channel 89 minutes				
	Nip recipients					Nip recipients			
Aggressor (mm)	58 mm	55	53	51	Aggressor (mm)	58 mm	58	58	57
58	--	1	4	4	58	--	7	12	9
55		--		1	58	3[1]	--	4[3]	6
53		3	--	7	58	2[2]	3[2]	--	8
51				--	57				--

Total = 20 nips
Nips per 10 minutes = 3.3

Total = 54 nips
Nips per 10 minutes = 6.1

[1] At 2 hours
[2] At 20 hours
[3] At 24 hours

Table 19 shows nipping frequency in the groups introduced on September 7. Observations were made periodically from September 7 to 9. Aggression was more frequent among coho of near-equal lengths than among coho of disparate lengths. In both of the last experiments shown in Table 12, all fish but the dominant coho left the channel.

Table 19. Nipping in B channels, September 7-9, 1960.

Left channel 65 minutes					Right channel 90 minutes				
	Nip recipients					Nip recipients			
Aggressor (mm)	62 mm	62	60	59	Aggressor (mm)	71 mm	69	65	65
62	--	15	9	4	71	--		2	
62		--			69	1		1	
60	2		--	1	65				
59				--	65				

Total = 31 nips
Nips per 10 minutes = 4.7

Total = 4 nips
Nips per 10 minutes = .4

It should also be noted that in the last two experiments, using "resident" coho, fish as large as 71 mm remained in the channels, whereas large nomads tended to leave in earlier experiments. The reason for this is unclear at this time. It could be that nomads, having once shown a propensity for movement, would do so with less stimulation than that required for movement of "resident" coho placed in the channels. The possibility also remains that an innate tendency to migrate acted upon the larger introduced nomads.

Observation of Coho in Natural Stream Areas: Behavior of resident coho salmon in natural stream areas was observed at several times during the summer and fall of 1960. Table 20

Table 20. Frequency of coho nipping in natural stream areas, 1960.

Stream	Station	Date	Time	Area observed sq.ft.	Mean depth in.	Bottom	Coho present	Area per fish sq.ft.	Nips or near nips	Nips per fish per 10 minutes
Deer Cr.	-150	8/1	1150-1200	25	8	rubble	5	5.0	2	0.4
Deer Cr.	005	8/1	1415-1425	16	6	sand	8	2.0	24	3.0
Deer Cr.	040	8/1	1430-1440	36	5	gravel	6	6.0	17	2.8
Deer Cr.	120	8/1	1450-1500	16	12	silt-sand	5	3.2	12	2.4
Deer Cr.	-125	8/7	1520-1530	12	4	silt-sand	6	2.0	10	1.7
Deer Cr.	-125	8/7	1535-1545	16	12	rubble	10-12	1.4	17	1.5
Deer Cr.	1100	7/23	1135-1145	25	12	silt-sand	12-15	1.9	42	3.2
Deer Cr.	1100	7/23	1200-1210	12	6	rubble	5	2.4	9	1.8
Needle Br.	150	7/27	1515-1530	15	4	gravel	4	3.7	7	1.2
Deer Cr.	4250	9/9	0926-0946	16	4	gravel	4	4.0	4	0.5
Deer Cr.	3900	9/9	1015-1035	16	6	gravel	3	5.3	4	0.7
Deer Cr.	2500	9/9	1045-1055	25	10	gravel-silt	5-6	4.5	14	2.0
Deer Cr.	2480	9/9	1105-1125	16	4	gravel	4	4.0	3	0.4
Deer Cr.	6500	9/13	1220-1240	20	3	gravel	5-6	3.6	18	1.6
Deer Cr.	6180	9/13	1255-1305	24	3	gravel-silt	8	3.0	33	4.1
Deer Cr.	2600	9/13	1410-1420	24	8	gravel-silt	6-8	3.4	20	2.9
Deer Cr.	3710	9/29	1005-1025	16	5	gravel	5	3.2	15	1.5
Deer Cr.	4050	9/29	1045-1105	15	13	gravel-silt	3-5	3.7	6	0.7
Deer Cr.	4125	9/29	1110-1120	30	5	gravel-silt	11-15	2.3	34	2.6

Mean area per fish = 3.4
Mean area per fish in depths less than 8" = 3.3
Mean area per fish in depths over 8" = 3.5
Mean nips per fish per 10 minutes = 1.8
Mean nips per fish in depths less than 8" = 1.9
Mean nips per fish in depths over 8" = 1.7

shows the results of these observations. Mean area of stream occupied per fish was calculated, and this ranged from 1.4 to 6 square feet per coho, with a mean of 3.5. Confidence limits for the mean, at the 95 per cent level, were 2.8 and 4.2 square feet. Mean number of nips recorded per fish per 10 minutes was 1.9, ranging from 0.4 to 4.1. Confidence limits at the 95 per cent level were 1.3 and 2.5.

The number of nips expressed on the basis of depth is also of interest. Behavior in water less than eight inches deep (11 instances) was compared to behavior in water over eight inches deep (8 instances). No significant difference could be shown between nipping or area per fish in shallow and deep areas.

Observations in natural stream areas were made primarily to determine roughly the extent of nipping. The most significant point was that nipping was frequent and probably continuous. The comparison of deep and shallow areas to test differences in area and nipping per fish are not regarded as conclusive, since activity in water over about 18 inches deep could not be observed properly. Comparison of activity in pools 20-50 inches deep with that in pools less than 8 inches deep might reveal some information of interest.

Figures 14-16 and 39-40 show that downstream-migrant coho became equal in length to residual fish by about November 6 in 1959 and by mid-November in 1960. This period coincided with rise in stream flow due to the first fall rains. Presumably, living space would become more plentiful as water flow increased.

Early in the winters of 1959 and 1960, as has been noted, the coho salmon changed their place of residence or stations from open, relatively shallow water to deeper pools. They apparently preferred locations with heavy overhead cover. On December 13, 1960, a group of Deer Creek coho was observed with the aid of a water glass. About ten coho were observed for about 20 minutes over a bottom area of about two square feet. No sign of aggression was noted in this group. All fish held positions close to the bottom, feeding on drifting material. Several fish were only two or three inches apart. The area occupied per fish was about 0.2 square feet. At the same location on August 1, the area per fish had been about 3.2 square feet and the nips seen per fish over 10 minutes had averaged 2.4.

On December 20, another group of seven coho lying close to the bottom in a sheltered area was observed. These fish were congregated over a bottom area of about two square feet. The bottom area per fish was about 0.3 square feet and no nipping was seen in 15 minutes of observation. Three other coho were seen feeding in separate locations about two feet apart. No aggression was seen among these fish.

General observations made during two winters regarding the locations preferred by coho indicated that the young fish preferred deep water to shallow (or preferred slower current), and tended to congregate in areas sheltered by overhead cover. Coho smolt aggregation noted by Hoar (21, p. 256-259) was associated with a preference for cover. Cover and slow current preferences may well have caused the aggregation of coho observed in the study streams. However, a lessening of aggressive behavior must have occurred, for the dense groupings seen in the streams were never observed in the spring, summer and fall months (of the first year of life) when aggressive behavior was strong and frequent.

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

Controlled Stream Section Trials: On July 13, 1960, the 39 square meter controlled stream section was electro-sampled and 34 coho were removed. Mean length of these fish was 53 mm. The trout and cottids which were shocked were replaced in the section. Beginning July 13, the following nomads, taken from the Deer Creek downstream trap, were placed in the uppermost pool of the section on the dates shown:

Date	Nomads added
July 13, 1960	55 mm
July 14, 1960	40
	39
July 17, 1960	43
	42
July 20, 1960	47
	45
July 23, 1960	42
July 25, 1960	55
	53
July 31, 1960	57
	41
August 31, 1960	41

All nomads were marked by removal of one ventral fin. The absence of a resident coho stock when nomads were introduced and the presence of a trap at the outlet and a barrier screen at the upper end of the section were the principal ways in which this section differed from an uncontrolled section.

On July 17, a hole was cut by water under the upstream screen barrier. The hole was repaired and five unmarked coho that had entered the section were removed by electro-sampling on July 19. One marked coho, 42 mm in length, was killed in the process. At the time of shocking, five marked fish should have been in the section. Four of these were seen and identified, leaving the one fish unaccounted for. The largest marked coho, 55 mm, was present.

No marked fish left the controlled section by August 20, five weeks after introductions began. On August 22-23, a hole was present in the downstream trap, and some coho could have left the section without being counted.

Another period of possible interchange of marked and unmarked fish occurred on August 22 and 23, when the outlet trap was pushed out of place for several hours each day by a small freshet.

On September 7, 1960, the section was sampled with an electro-sampler to remove all coho. The following marked fish were found, accounting for 8 out of 12 introduced coho that should have been present:

63 mm
61
59
57
54
52
47
40

The four fish not found could have been shocked but lost under debris, could have suffered mortality in the section, or could have moved out of the section during the two periods of possible leakage.

All the marked fish recovered were found in the pool where they were released, in spite of the fact that two pools were available below the uppermost one (Appendix 17). This probably indicated that population density never became sufficiently high in the upper pool to cause fish to move into lower pools. During the test period, three cutthroat, 93 to 122 mm, and one 77 mm cottid were taken in the outlet trap, indicating that the trap would catch and hold fish moving downstream. Mesh of the down trap was sufficiently fine to hold the 0/ age coho if they had moved.

Transfer of Fry to Barren Area: A total of 1627 nomadic Flynn Creek coho was transferrred to Needle Branch in the period April 16 to May 6, 1960. By May 31, a total of 139 coho had moved out of Needle Branch. Two hundred and four of the transferred coho had been marked with an anal fin removal. Decreased survival due to this mark might be expected (see section on standing crop estimation methods), but should not be a serious bias in the first month after marking.

Nine anal fin marks were recovered by May 31 in the downstream trap. The proportion of marked fish in the trap was therefore about eight per cent. The proportion in the population of transferred fish at time of marking was about 12.5 per cent. The lower ratio in the trap could have been due either to differential mortality of marked coho or to recruitment of fry from spawning of the single adult female that was passed upstream. If the marked fish behaved in a manner similar to unmarked ones, and if mortality was not differential for anal fin-marked fish, the proportion of transferred coho leaving Needle Branch about one month after transfer was approximately four per cent. If there was differential mortality, the nine marks recovered represented about 14 marked fish that should have moved, or a total out-movement of less than seven per cent of the transferred coho. The total number of trapped coho fry up to May 31, or 130 fish, was eight per cent of the total transfer of 1627 fish, a proportion that checks well with the seven per cent maximum movement calculated from anal fin-marked coho.

In sampling 117 coho on Needle Branch on July 6, 1960, two months after the Flynn Creek coho were transferred, seven anal marks were recovered. Proportion of marked fish at this sampling was thus six per cent, indicating that at least some of the transferred coho were alive and doing well. Mean length of the anal fin-marked fish on July 6 was 56.3 mm, while the mean length of the 110 unmarked coho was about 49 mm.

Figure 38 shows a histogram of lengths of the Needle Branch coho sampled on July 6, 1960. If important recruitment of naturally spawned fry had occurred, of necessity after the transfer of Flynn Creek coho at a mean length of about 39 mm, there should be bimodality on the histogram with modes about 5 mm or more apart. There is no clear indication of such bimodality on the histogram.

Neither is bimodality evident in the May 18 sample of 124 coho (Figure 38). Dark points mark the location on the histogram of anal fin-marked fish sampled. The tendency for these fish to lie on the right (high) side of the distribution is of interest. Anal-marked fish were selected as randomly as possible from the fish to be transferred from Flynn Creek and, if any bias

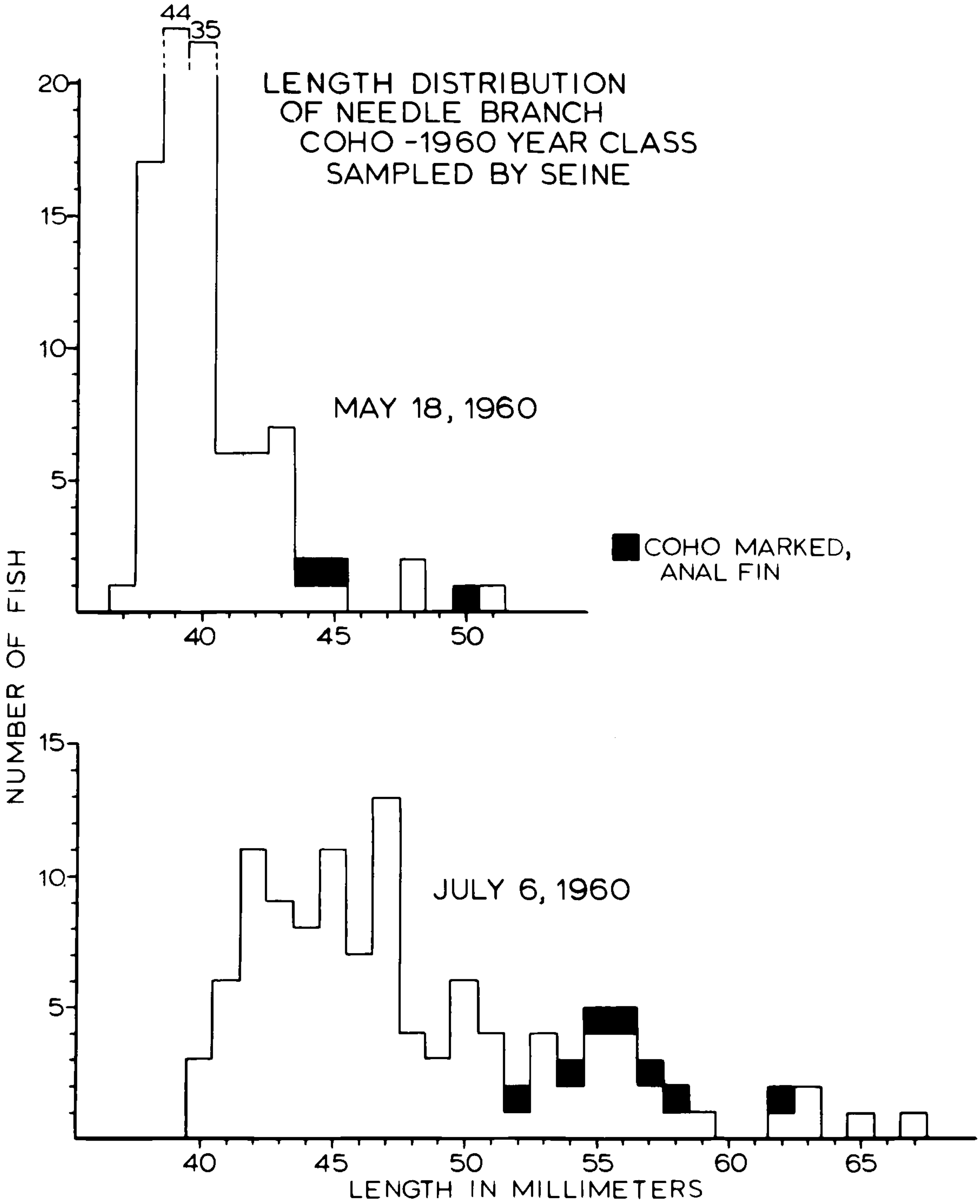
LENGTH DISTRIBUTION
OF NEEDLE BRANCH
COHO -1960 YEAR CLASS
SAMPLED BY SEINE
44
35
20
15
10
5
MAY 18, 1960
40
45
50
■ COHO MARKED, ANAL FIN
NUMBER OF FISH
15
10
5
JULY 6, 1960
40
45
50
55
60
65
LENGTH IN MILLIMETERS

Figure 38

resulted in size of fish selected for marking, it should have been in the direction of smaller fish, since the fish to be marked were caught by hand from buckets of three or four hundred coho, and one might expect larger coho to best evade capture. Mean length of 50 fish selected for marking on April 15 was 39.06 mm, while mean length of 43 unmarked fish transferred on May 2 was 39.58.

The number of fish transferred is shown by date below:

April 15 - 509 (included 200 marked fish)
April 23 - 35
May 2 - 444 (included 4 marked fish)
May 6 - 639
1,627

The disparity in size of anal-marked and unmarked coho on July 6 could have been partly due to a better start for these fish early in the transfer series, or to mortality among marked fish that tended to take small marked fish preferentially.

In summary, then, the majority of the 1,627 transferred nomadic Flynn Creek coho stayed in Needle Branch after transfer. The stream was barren of naturally spawned coho at the time of transfer of at least the first 500 fish. Less than eight per cent of 204 fish marked in the initial transfer moved out of Needle Branch, and many transferred fish were alive and growing well after two months in the stream.

An additional 62 coho fry moved out of Needle Branch from May 31 to August 7, making a total out-movement of about 12.5 per cent of the 1,627 transferred coho, assuming no recruitment of naturally spawned fry.

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

Figure 14 shows "growth" curves for nomadic and residual coho of the 1959 year class on Deer Creek, and Figures 39-41 show the same information for the 1960 year class on all three streams. Tables 5 and 21 for the 1959 and 1960 year classes, respectively, show the results of comparisons of mean lengths of residual and nomadic coho. Pairs of samples considered were taken at the same times. In all pairs of samples on Deer and Flynn Creeks (these included all available data taken at suitably similar times) taken from shortly after emergence to early fall, the nomadic coho were smaller in mean length (P values .10 to .01). These differences are all the more remarkable in that samples of residual fish almost certainly included some coho that would soon become nomadic. If these fish could somehow have been removed from the residual samples, the

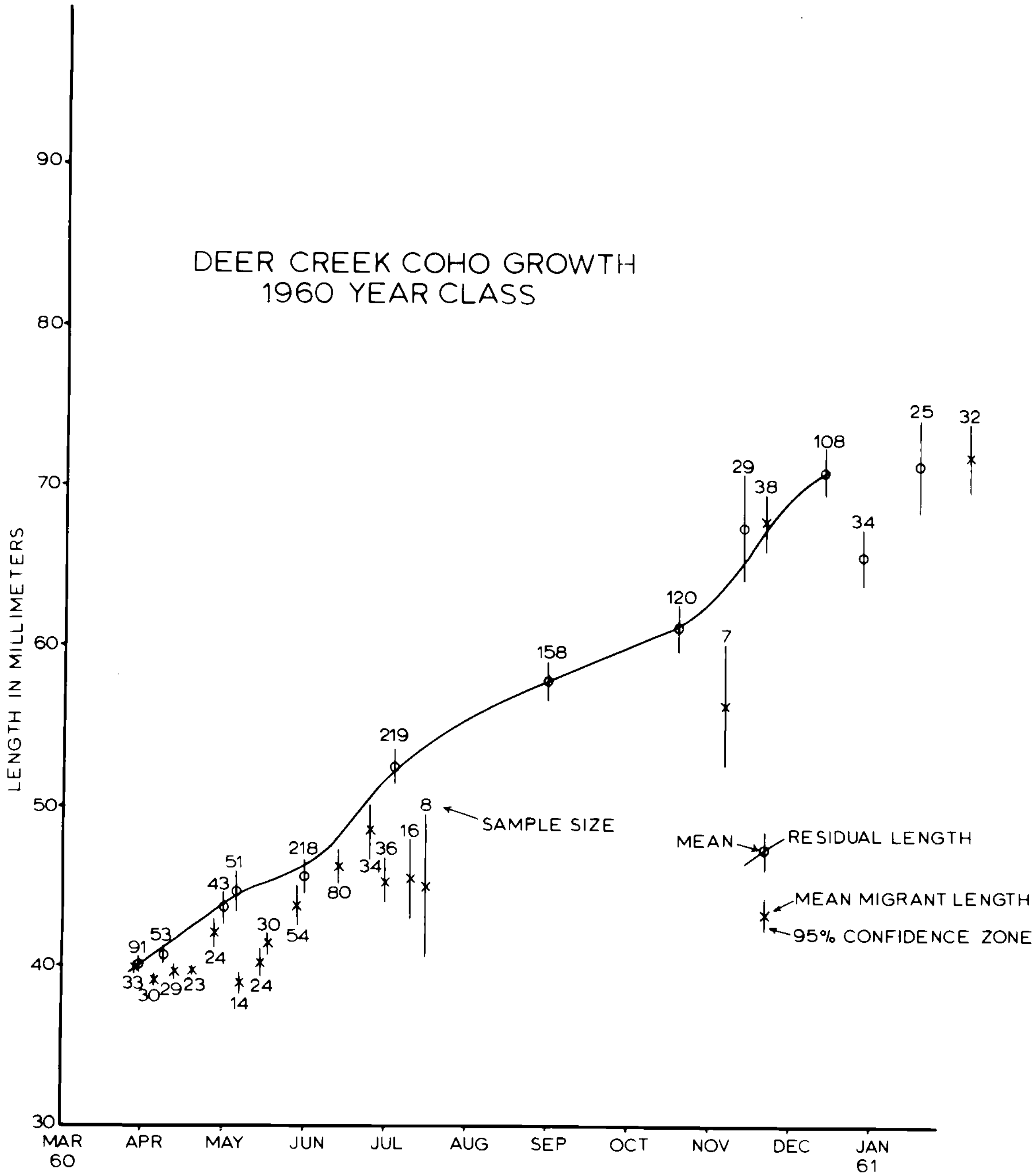
DEER CREEK COHO GROWTH
1960 YEAR CLASS
LENGTH IN MILLIMETERS
30
40
50
60
70
80
90
MAR 60
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN 61
91
53
33
30
29
23
43
51
24
14
24
30
54
218
80
219
34
36
16
8
158
120
7
29
38
108
34
25
32
SAMPLE SIZE
MEAN
RESIDUAL LENGTH
MEAN MIGRANT LENGTH
95% CONFIDENCE ZONE

Figure 39

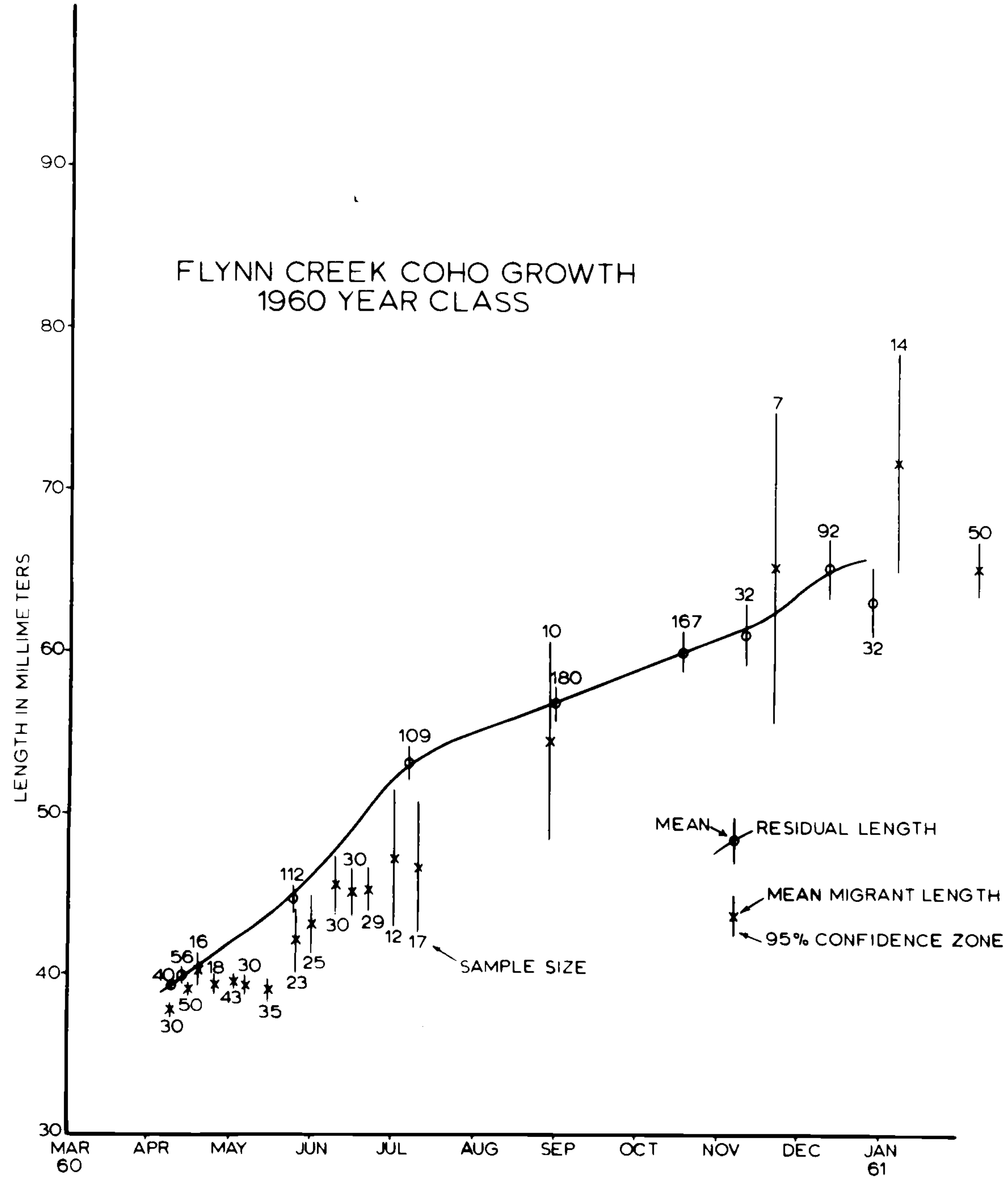
FLYNN CREEK COHO GROWTH
1960 YEAR CLASS
LENGTH IN MILLIMETERS
90
80
70
60
50
40
30
MAR 60
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN 61
40
56
16
18
30
30
50
43
35
112
23
25
30
30
29
12
17
109
10
180
167
32
7
92
32
14
50
SAMPLE SIZE
MEAN
RESIDUAL LENGTH
MEAN MIGRANT LENGTH
95% CONFIDENCE ZONE

Figure 40

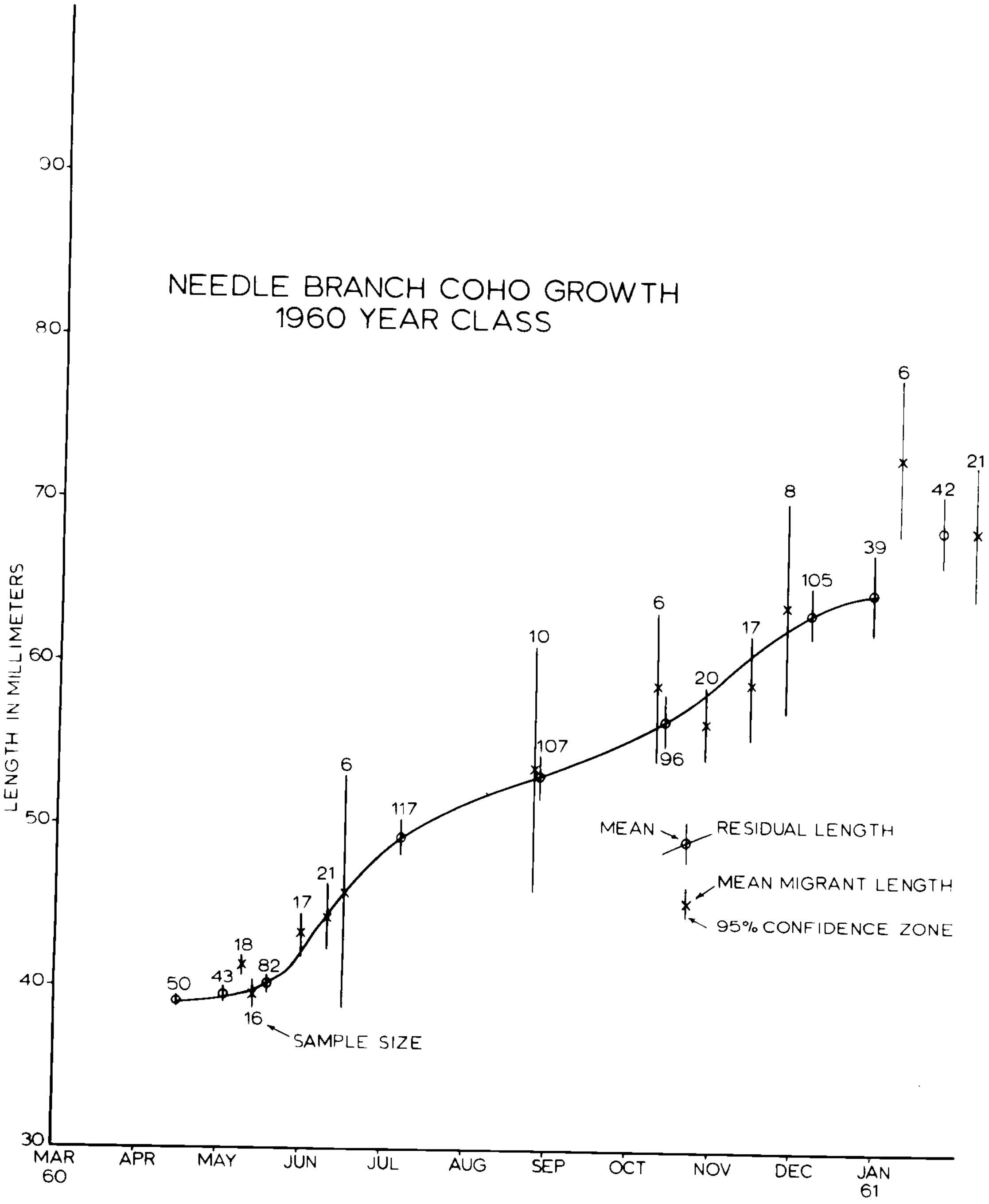
NEEDLE BRANCH COHO GROWTH
1960 YEAR CLASS
LENGTH IN MILLIMETERS
30
40
50
60
70
80
90
MAR 60
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN 61
50
43
18
82
16
SAMPLE SIZE
17
21
6
117
10
107
6
96
20
17
8
105
39
6
42
21
MEAN
RESIDUAL LENGTH
MEAN MIGRANT LENGTH
95% CONFIDENCE ZONE

Figure 41

Table 21. Comparison of mean lengths of nomadic and residual coho sampled at same time, 1960.

Date-Stream	Type	Mean length mm	Sample size	Difference mm	t	P*
4/4 - Deer	Nomad	39.17	30	.98	3.34	.01
3/28 - Deer	Residual	40.15	91			
4/26 - Deer	Nomad	42.08	24	1.57	2.18	.05
4/30 - Deer	Residual	43.65	43			
5/6 - Deer	Nomad	38.86	14	5.89	8.39	.01
5/4 - Deer	Residual	44.73	51			
5/24-31-Deer	Nomad	43.89	54	1.77	2.10	.05
5/30 - Deer	Residual	45.66	218			
7/5-11-Deer	Nomad	45.50	16	7.09	5.49	.01
7/3 - Deer	Residual	52.59	219			
11/21-Deer	Migrant	67.81	38	-.43	-.23	.90
11/14-Deer	Residual	67.38	29			
4/8 - Flynn	Nomad	37.87	30	1.43	4.72	.01
4/9 - Flynn	Residual	39.30	40			
4/14 - Flynn	Nomad	38.47	15	1.48	2.69	.01
4/13 - Flynn	Residual	39.95	56			
5/23 - Flynn	Nomad	42.17	23	2.51	2.37	.02
5/23 - Flynn	Residual	44.68	112			
7/3-14-Flynn	Nomad	46.71	17	6.39	3.16	.01
7/6-8-Flynn	Residual	53.10	109			

* Significance level

disparity between nomads and residuals would have been greater. As Figures 14, 39, 40, and Tables 5 and 21 show, at some time in the fall the coho moving downstream become equal in mean size to residuals. In early spring the migrants become larger than the residual fish. Needle Branch data for the 1960 year class are shown in Figure 41, but nomad and residual coho lengths are not compared statistically. The beginning of growth of these fry seemed to have been delayed by transfer from Flynn Creek, and confused by the several groups of fish introduced over a three-week interval.

The possible error introduced in results showing movement of nomads by failure of traps to take upstream migrants was checked at Needle Branch in 1960. A fine-mesh trap was installed inside the upstream trap used to take adults. From June 1 to November 1, 1960, 12 0/ age coho were caught in this trap. A total of 208 0/ age coho passed downstream from May 1 to November 1, 1960. Distribution of the juvenile movement is shown in Table 22.

Table 22. Monthly distribution of coho fry movement at Needle Branch trap, May-November, 1960.

	Downstream	Upstream
May	128	No trapping
June	52	1
July	8	3
August	12	7
September	0	1
October	8	0
	208	12

It appears that coho fry moving downstream in late spring usually do not return upstream, and that movement is not equal in both directions, at least in Needle Branch.

An upstream trap for juveniles was operated in Deer Creek adult trap during September. No coho were taken in this trap.

Summary of Pertinent Behavior Results: The following points are presented for two reasons: first, as evidence for the hypothesis that downstream drift of coho fry was caused by aggressive behavior of coho in the stream; second, as evidence that coho salmon have definite social behavior patterns.

1. Behavior noted repeatedly in artificial stream channels included lateral display, parallel swimming, threat, nipping, chasing, flight, hiding, fighting, submission, territorial defense, displacement activities, and formation of hierarchies.

2. Nomadic coho placed in artificial stream channels barren of fish formed social hierarchies and tended to remain in the channels.

3. Nomads added to existing "resident" groups in artificial channels were dominated by the resident dominant fish and tended to leave the channels.

4. Nomadic coho fry moving downstream through fish traps at a given time in the springs of 1960 and 1961 were consistently smaller than coho resident in natural stream areas at the same given time.

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

6. Dominant fish grew more rapidly than subordinate fish.

7. Aggression observed in natural stream areas was frequent, probably continuous, and consisted of territoriality, partial territoriality, nipping, threatening, and chasing. Hierarchies could not be positively observed in stream areas.

8. Nomads taken from one stream and transferred to another stream barren of resident stock remained in the latter stream.

9. Nomads transferred to a 39 square meter controlled stream section barren of resident coho remained there, taking up residence in the pool where they were released. Population density in this pool apparently never became great enough to force fish into two lower pools in the controlled section.

ENERGY PATHWAYS

One important aspect of coho production is the path by which energy from incident sunlight reaches the coho population. The proportions of the energy for maintenance and growth of coho salmon which are derived from terrestrial and aquatic autotrophic plants are of considerable ecological interest. Only preliminary studies of a rather qualitative nature were possible.

Food habits of coho salmon were investigated by Demory (15) to determine what insect forms were important in the diet throughout the year of stream residence undergone by the fish. He also studied the food habits of some of the insects utilized by the fish. This information, which is summarized below, was then used as groundwork for further investigation of aquatic insect food habits. Insect guts were examined throughout one year to determine the proportion of aquatic and terrestrial plant materials ingested.

Methods for Evaluating Energy Sources

Procedures followed in insect stomach examination were much the same as those used by Demory. Aquatic insects were collected at randomly selected stations on Deer Creek and Needle Branch. Insects were placed in plastic vials which were cooled in ice water to reduce the metabolic rates of animals. Some insect samples were preserved in 70 per cent ethanol immediately after sampling. Stomachs of the insects were examined within six hours of collection time. Preserved stomachs were examined within 72 hours of collection to minimize chlorophyll leaching from green plant material within the guts.

Samples were collected with a fine mesh cloth net capable of holding insects as small as one millimeter in length. Care was taken to prevent samples from being collected from a spot known to have been disturbed previously. About one square foot of bottom was agitated and the net swept upstream along the bottom to pick up the sample. Areas for sampling were selected by use of 100-foot station markers and random number tables. At each sampling point, a pre-determined distance above or below the 100-foot stations, the specific spot to be sampled was chosen by random selection of center, left, or right one-third of the stream. Samples were taken at the middle of the one-third section chosen. Twenty samples on Deer Creek and ten on Needle Branch were taken each sampling day.

Three insects of a given type were examined from each sample if they were available. The animal to be examined was measured, then decapitated on a microscope slide and the thoracic gut contents forced out on the slide. Further dissection was necessary in the case of some of the larger insects to reach the gut. Gut contents were then mounted in water beneath a cover slip and examined under a compound microscope. Usual magnification was 537 power, with occasional use of 125 power.

An arbitrary estimate was then made of the proportion of gut contents made up by algal forms. Aquatic mosses were included in this proportion. The complementary proportion was classed either as detritus or as leaf material when the latter was recognizable. Identification of algal genera was made in some cases. The arbitrary nature of the algal proportion estimate leaves the data subject to error. An estimate of 25 per cent might refer to a true percentage of algae as low as 10 or as high as 50 per cent. This estimate was checked by calculating percentages of given insects containing algae at each sampling time to determine if trends in feeding were accurately reflected by the arbitrary estimates.

The detritus classification is open to question in that it may have included dead algal material. If much dead algal material were present in the detritus, however, diatom frustules would have been much more in evidence. Diatoms were to be found abundantly intermingled in any benthic algal population, and should be present and recognizable in dead algal material as well, since the frustules retain their form for long periods after the cell protoplasm is dead (52, p. 442-443). Frustules were scarce in what was called "detritus." As Erichsen (16, p. 162) indicated in his work, grit is usually mixed with detritus in insect stomachs. Grit was absent in stomachs containing recognizable leaf fragments, and usually was absent from stomachs containing predominantly algae.

Some error was possible when detritus or algae was observed in the gut of an insect form known to be carnivorous. This plant material could have come from the stomachs of prey organisms not noted.

Since Demory's study of the food of coho is so important to the present work, it is worthwhile to discuss briefly the methods he employed.

A total of 272 coho stomachs was analyzed for the three streams: 112 from Deer Creek, 116 from Flynn Creek, and 44 from Needle Branch. Individual samples from the latter stream were frequently small, resulting in large sampling error, and no fish were taken in some winter months. The small coho population size on Needle Branch precluded adequate sampling.

Coho for stomach samples were taken at least monthly, usually twice monthly, over a wide area of the streams, thus avoiding some error due to conditions in a localized area. Because of weighing difficulties with small groups of organisms from one coho, stomach samples for each day were lumped. Thus no estimate of variance can be made or confidence limits set for each sample.

The anterior half of the stomach was removed from the fish, the identifiable contents were separated into taxonomic groupings and these were dried for 24 hours at 60-70° F. Groups were then weighed to the nearest 0.1 mg on an analytical balance. The proportion of the total identified material made up by each group was then calculated for each month. Data for particular months included from one to three samples of five fish. At least one sample was taken in each month.

All percentages calculated for the annual diet of coho are means of monthly diet data. This method, used to express importance to coho of given forms, ignores daily ration changes that occur as coho grow, changes in coho population size, and varying digestibility and caloric value of insect forms. In the absence of data on these factors, it will be assumed that all taxonomic groups contributed equal amounts of energy per unit weight.

Results of Energy Transfer Study

Fish Feeding Habits: Analysis of fish food habits throughout the year was a necessary foundation for estimation of energy sources for coho production and it provided directly an estimate of the proportion of coho food made up by terrestrial insects.

Results obtained in coho food habit studies by Demory (15) are summarized in Appendix 19. Insects of terrestrial origin made up 34 per cent of the coho diet on Deer Creek, 31 per cent on Flynn Creek, and 30 per cent on Needle Branch.

Insects of aquatic origin, including aquatic adults, made up 62 per cent of the coho diet on Deer Creek, 61 per cent on Flynn Creek, and 31 per cent on Needle Branch. Items from uncertain habitats made up about 4 per cent on Deer Creek, 8 per cent on Flynn Creek, and 39 per cent on Needle Branch.

Most of the forms from uncertain habitats in Needle Branch were believed to be terrestrial, and the proportional contributions were probably about 32 per cent aquatic, 60 per cent terrestrial, and 8 per cent of uncertain origin. The data thus indicate that terrestrial insects were roughly twice as important there in the coho diet as in either of the two other streams. Adequate sampling on Needle Branch was limited to the spring, summer, and early fall of 1959. In Deer and Flynn Creeks, aquatic insects became important in the coho diet in the winter and in the early spring of 1960 before smolt migration. Absence of Needle Branch samples in this period may have been in part responsible for the lower percentage of aquatic forms in the data on that stream. Demory (15) compared food habit data from the three streams in the months May-September, when sampling was adequate on all streams, and found the following proportions of the coho diet made up by terrestrial insects: Deer Creek - 21 per cent, Flynn Creek - 29 per cent, and Needle Branch - 40 per cent.

About one-third of the coho diet for one year in the study streams was apparently of terrestrial origin. The remaining portion, consisting largely of aquatic insects, was classed by taxonomic group.

Insect Food Habits: The procedure to be followed here will be to show all available results on aquatic insect food habit studies, then to use life history and food habit information from the literature to arrive at estimates of the amounts of energy obtained from different sources by insects not actually studied.

Estimates of amounts of energy from different sources used by insects have been made only for Deer Creek. Coho stomach sampling was inadequate on Needle Branch and insects were not sampled on Flynn Creek. Insect stomach sampling data from Needle Branch will be used for comparison with Deer Creek data.

The first column of Table 25, taken from Demory (15), summarizes the proportional occurrence of aquatic insect larvae and adults in Deer Creek coho stomachs throughout one year. Purely aquatic forms and aquatic adults have been lumped in this table so that any percentage of the aquatic total is a percentage of all aquatic insects identified. This table shows that midge larvae (Tendipedidae) were by far the most important single group in Deer Creek samples, about 25 per cent of the total. It is believed that nearly all of the midge larvae taken by coho belonged to the sub-family Hydrobaeninae. This is also the tendipedid group taken most frequently in insect sampling work.

Demory's insect gut content analysis showed that 377 Hydrobaeninae larvae had a mean algal content of about 12 per cent on Deer Creek. On Needle Branch, 255 Hydrobaeninae stomachs had a mean algal content of 14 per cent. The proportion of the diet complementary to algae was made up by detritus, believed to be terrestrial plant material.

Table 25 indicates that *Baetis* sp. made up 2.2 per cent of the coho diet on Deer Creek. Demory examined stomachs of 405 *Baetis* larvae from Deer Creek and found a mean algal content of 74 per cent. He found that 220 *Baetis* larvae from Needle Branch contained 60 per cent algae. Detritus made up the complementary portion of the stomach contents.

Paraleptophlebia sp. made up 4.5 per cent of the Deer Creek coho aquatic insect diet. Demory examined 536 stomachs of *Paraleptophlebia* larvae from Deer Creek and found a mean algal content of 6 per cent. He also found that in 371 Needle Branch *Paraleptophlebia* stomachs, algae made up a mean of 5 per cent. Animals of this genus were primarily detritus feeders.

Stomachs of twenty-one taxonomic groups of insects were examined in the present work. These were: *Simulium* sp., *Dixa* sp., *Ephemerella* sp., *Cynigmula* sp., *Epeorus* sp., *Limnephilidae*, Hydropsychidae, Psychomyiidae, *Rhyacophila* sp., *Glossosoma* sp., *Lepidostoma* sp., Philopotamidae, *Micrasema* sp., *Alloperla* sp., *Acroneuria californica* (Banks), *A. pacifica* Banks, *Kathroperla perdita* Banks, *Nemoura* sp., *Peltoperla brevis* Banks, *Optioservus quadrimaculatus* (Horn), and Elmidae.

The frequency with which stomachs of a particular form were examined was determined by the abundance of that form in bottom samples. For some groups, only one individual was taken. For other groups, over 100 insects were examined in samples well distributed through the year.

Tables 23 and 24 show the mean estimated percentages of algae, number of organisms, and size range of organisms examined at each sampling time. An arithmetic mean (of algae percentage) of the sample means is shown for each herbivorous group. This was the mean to be used in estimating contribution of terrestrial energy to insect groups, and was rounded to the nearest five per cent.

As mentioned previously, the arbitrary nature of the algae percentage estimates could promote errors. Erichsen (16, p. 159-174) analysed insect food habit data by calculating the percentage of insects, in a given sample, that contained a particular food. In this method there is little error possible, for an insect stomach either contains an item of food or it does not. This type of calculation was made for Cynigmula sp., a form present in quantity in sampling in Deer Creek at several times. Figure 42 shows the trends in arbitrarily-estimated algal percentage of the insects containing algae. The trends shown by each type of percentage are similar, demonstrating that the arbitrarily-estimated algal percentages are true indicators of changes in feeding habits. The arbitrarily-set percentages are not precise estimators of the true proportion of algae at any one sampling time, but are valid as trend indicators, and should provide a rough idea of the relative importance of algae in the insect diet.

Table 23. Mean percentage[1] of algae found in insect stomachs, Deer Creek, May, 1960 - March, 1961.

Taxonomic group	5/13[2]	6/9	7/21	8/23	10/3	10/24	12/1	1/17	2/28	Mean of sample means
Ephemerella sp.			75-2(6)						40-5(3-6)	60%
Cynigmula sp.	58-15(2-6)	71-11(2-5)	53-6(3-11)	26-7(1-4)	9-10(2-10)	15-9(3-8)	19-39(1-7)	63-63(1-8)	20-46(2-6)	40%
Epeorus sp.	78-5(1-5)	80-3(2-12)				5-1(3)	13-5(2-5)	80-5(2-10)	63-5(3-7)	55%
Peltoperla brevis	75-1(2)				75-1(3)			100-1(4)	100-1(5)	90%
Nemoura sp.					0-3(2-3)	0-4(2-3)	0-7(5-7)			0%
Kathroperla perdita	66-3(1-8)			5-2(7-9)						35%
Alloperla sp.[3]	An-1(3)	An-5(2-6)	An-3(4-5)	An-4 0-1 (2-6)	An-1(6)	An-4 0-5 (4-5)	An-1(6)		An-1(4)	Predaceous
Acroneuria californica	An-1 100-1 (7-14)		An-3(13-14)	An-1(15)	An-1(3)	0-1(6)	An-1(5)	An-6 100-1 (12-14)		Predaceous
A. pacifica				An-2(2-4)		An-1(3)		An-2(4-8)		Predaceous
Rhyacophila sp.	An-1(10)	An-1 95-3 (3-11)	An-1(5)		5-2(8-11)	0-2(6-9)				Predaceous
Glossosoma sp.									95-11(3-7)	95%
Psychomyiidae							An-1 100/1 (4-5)			Predaceous
Hydropsychidae							100-1(6)			100%
Limnephilidae, wood case					0-1(4)	0-6(3-19)	95-1(5)	0-1(3)		25%
Limnephilidae, stone case	95-4(1-5)	96-4(1-6)	84-5(3-6)	62-7(2-6)		58-3(5-6)	29-6(2-15)	100-3(2-5)	88-4(2-8)	75%
Lepidostoma sp.			0-2(3-5)	36-21(1-7)	0-17(2-7)	0-21(3-11)	0-1(4)			5%
Micrasema sp.	100-2(2-3)	100-1(3)			64-5(1-3)		100-5(2-4)	90-9(3-5)	100-10(2-6)	90%
Optioservus quadrimaculatus[4]			62-2(2)	70-4(2-8)						65%
Elmidae[5]	100-2(2-4)	95-2(4)	100-1(2)	75-4(2-7)	90-1(6)					90%
Simulium sp.		35-4(3-6)	7-3(2-5)	20-2(3-5)	0-1(3)	0-2(4)	1-7(3-7)	2-8(4-5)	3-2(3-6)	10%
Dixa sp.					4-4(4-6)					5%

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[1] Complement is detritus percentage.

[2] First figure is percentage of algae, second figure is number of stomachs examined, and third set of figures is range in length of animals.

[3] "An" - Animal matter.

[4] Adults.

[5] Larvae.

Table 24. Mean percentage[1] of algae found in insect stomachs, Needle Branch, May, 1960 - March, 1961.

Taxonomic group	5/14[2]	6/10	7/10	8/23	10/4	12/3	1/20	2/28	Mean of sample means
Cynigmula sp.	37-6(2-5)	50-2(3-4)	80-1(4)	19-5(2-3)	3-2(3)	7-18(1-3)	50-28(2-5)	51-23(2-6)	35%
Epeorus sp.	90-1(3)				0-2(6-8)		3-3(4-5)	5-2(3-4)	25%
Peltoperla brevis					0-1(3)	0-1(3)			0%
Nemoura sp.						0-6(4-5)		0-3(3-6)	0%
Kathroperla perdita	42-5(3-4)		0-2(5-8)	0-2(5-8)		0-1(4)	0-5(4-5)	0-1(4)	5%
Alloperla sp.[3]	An-1(3)	An-3 0-1(1-7)	An-5(3-9)	An-3(5-7)	An-2(3-5)	An-3 0-1(3-7)	An-3 50-2(3-9)	0-2(4)	Predaceous
Acroneuria californica	An-3(4-10)		An-2(4-9)	An-5(3-16)	An-2(4-5)	An-3(3-16)	An-2 0-1(2-12)		Predaceous
Rhyacophila sp.		80-1(6)	An-4 75-1(5-6)						Predaceous
Glossosoma sp.								100-2(6)	100%
Philopotamidae							75-1(6)		75%
Hydropsychidae								0-1(12)	0%
Limnephilidae, wood case						0-3(5-15)		100-1(4)	50%
Limnephilidae, stone case	64-4(2-5)	77-4(3-5)		26-3(3-5)	18-5(2-13)	0-1(2)	100-1(6)	98-6(3-7)	55%
Lepidostoma sp.			0-2(4-7)	1-7(2-4)	0-10(4-6)		0-4(2-3)	17-6(3-6)	5%
Micrasema sp.	94-4(2-4)	33-3(2-4)						100-3(3-5)	75%
Optioservus quadrimaculatus[4]						0-1(2)			0%
Elmidae[5]	100-1(6)								100%
Simulium sp.						0-2(3)	0-2(3-5)	9-5(4-6)	5%

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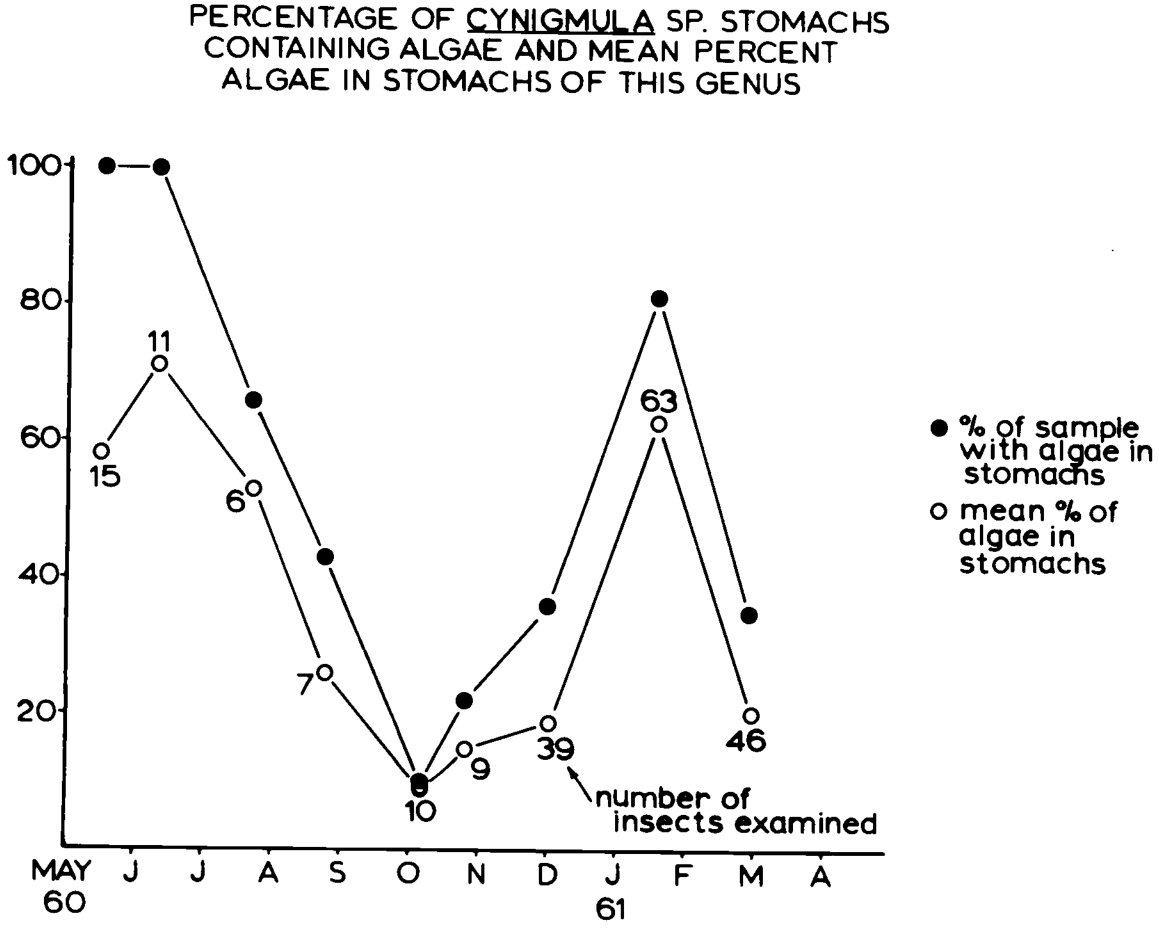
[1] Complement is detritus percentage.

[2] First figure is percentage of algae, second is number of stomachs examined, and third set of figures is range in length of animals.

[3] "An" - Animal matter.

[4] Adults.

[5] Larvae.



PERCENTAGE OF CYNIGMULA SP. STOMACHS CONTAINING ALGAE AND MEAN PERCENT ALGAE IN STOMACHS OF THIS GENUS

Figure 42

The insects examined will be discussed in the general taxonomic order in which they appear in Table 23. Some of the data obtained are usable in arriving at an estimate of the energy source for coho production, and some are not usable because of small sample size, varied feeding habits, or lack of specific identification in coho stomachs samples.

Ephemerella sp.: Seven *Ephemerella* sp. larvae taken from Deer Creek contained 60 per cent algae. The algae forms taken were diatoms and *Batrachospermum sp.*

Cynigmula sp.: Mean algal content of 206 stomachs of larvae of this genus was 40 per cent. Eighty-five *Cynigmula sp.* stomachs in Needle Branch samples held 35 per cent algae. This algae was almost exclusively diatoms, including these genera: *Navicula*, *Gomphonema*, *Pinnularia*, and *Cocconeis*. This is one of the few insect genera that ingests considerable amounts of grit along with diatoms. *Cynigmula sp.* is the most abundant and ubiquitous heptageniid in the study streams, and is believed to make up most of the "Heptageniidae" seen by Demory in coho stomach samples.

Epeorus sp.: Twenty-four larvae of this genus from Deer Creek contained 55 per cent algae, largely diatoms. Eight larvae from Needle Branch contained 25 per cent algae.

Peltoperla brevis: Four larvae from Deer Creek contained 90 per cent algae, and two larvae from Needle Branch contained detritus only.

Nemoura sp.: Fourteen larvae from Deer Creek, and nine from Needle Branch contained no algae. The larvae examined usually contained leaf material.

Kathroperla perdita: Five larvae from Deer Creek contained 35 per cent algae, and 16 larvae from Needle Branch held five per cent algae. Leaf fragments were the usual food of the larvae examined.

Alloperla sp.: Twenty-two Alloperla larvae were examined in Deer Creek samples, and twenty of these were found to contain animal parts. Needle Branch Alloperla sp. were also predaceous. This Plecoptera genus was one of several whose food habits were examined. If food habits of all the stoneflies found in the study streams had been similar, the source of energy for "miscellaneous Plecoptera" could have been estimated. The genera were found to differ greatly in their food habits.

Acroneuria californica and A. pacifica: Nymphs of these species were found to be predaceous.

Rhyacophila sp.: Ten larvae of this genus were examined. All but one contained animal parts. This genus is one of several Trichoptera groups examined in the hope that food habits might vary little among groups, so that the energy source of the miscellaneous Trichoptera listed in Table 25 could be determined. This was a false hope, for the groups varied widely in their food habits.

Glossosoma sp.: Eleven Deer Creek larvae of this genus contained 95 per cent algae. Two larvae from Needle Branch contained 100 per cent algae. These samples were all taken in late February, 1961, so no data are available on year-long feeding habits.

Philopotamidae: One larva of this family from Needle Branch contained 75 per cent algae.

Psychomyiidae: Only two larvae of this family were taken in samples from Deer Creek. One larva contained animal parts, the other had been feeding on diatoms. No estimate of energy source can be made for predaceous forms.

Hydropsychidae: One larva of this family from Deer Creek contained diatoms entirely, and one from Needle Branch contained detritus only.

Limnephilidae: Thirty-six stone-cased limnephilids from Deer Creek contained 75 per cent algae, including diatoms, Chamaesiphon sp., Entophysalis rivularis, and Protoderma sp. Nine wood-cased limnephilids contained 25 per cent algae. Data for stone-cased forms will be used in Table 25, where energy sources are summarized. Although Demory (15) did not separate wood-cased from stone-cased limnephilids, he frequently found stone particles in coho stomachs that contained larvae of this family. Needle Branch stone-cased and wood-cased Limnephilidae contained about 50 per cent algae.

Lepidostoma sp.: Sixty-one Deer Creek *Lepidostoma* larvae contained 5 per cent algae, and 29 larvae from Needle Branch also contained 5 per cent algae. This genus feeds almost exclusively on leaves.

Micrasema sp.: Thirty-two larvae of this genus from Deer Creek held 90 per cent aquatic plant material, largely in the form of mosses and liverworts. *Eurhynchium sp.* appeared frequently in stomachs. Ten *Micrasema* from Needle Branch contained 75 per cent aquatic plant material.

Optioservus quadrimaculatus: Six Deer Creek adults of this elmid species contained 65 per cent algae, and one adult from Needle Branch contained detritus only.

Elmidae: Ten larvae from Deer Creek contained 90 per cent algae, and one Needle Branch larva held 100 per cent algae. Even in mid-summer, when other algae feeders such as *Cynigmula sp.* began feeding largely on detritus, elmid larvae continued to feed on algae.

Dixa sp.: Only four larvae of this genus in Deer Creek were examined. They contained a mean of five per cent algae, entirely diatoms. The remainder of the stomach contents was detritus. Insects of this genus have been said to feed on organisms in the surface film (63, p. 401). Dixids occur along the downstream margins of rocks or floating branches (63, p. 401).

Simulium sp.: Twenty-nine simuliids taken from Deer Creek contained 10 per cent algae, indicating that this genus feeds primarily on detritus. Needle Branch simuliid stomachs contained 5 per cent algae. *Simulium* sp. is morphologically adapted to strain the current for drifting food particles. Stomachs of this genus contained a conglomerate of amorphous detritus, some leaf fragments, and a few diatoms. The diatoms present could have been strained from the current or taken off the rocks to which members of this genus are usually attached.

Some of the insect groups listed in Table 25 were not taken in the course of insect food habit studies. In order to arrive at an estimate of energy source, it will be necessary to use some published information on feeding habits and life history of these forms. The division of energy sources is stated as follows: Autochthonous - that which originated within the water of the stream environment; Allochthonous - that which originated elsewhere. The latter includes forms from potholes and other wet spots on the terrestrial environment, a necessary consideration when dealing with mosquitos and other forms requiring still water. All aquatic animals not actually studied in insect food habit work will be dealt with as they appear in Table 25.

Annelida: Annelids found in coho stomachs were believed to be primarily oligochaetes originating in muddy areas. Oligochaetes were occasionally found in bottom samples taken from a muddy substrate. This habitat preference indicates a detritus feeding habit, and the ingested material probably consists of animal as well as plant material. Pennak (43, p. 280) states that oligochaetes feed by ingesting quantities of the substrate and digesting the organic component as it passes through the alimentary canal.

Gammaridae: Pennak (43, p. 436) states that amphipods in general are omnivorous, general scavengers. Hence no estimate of energy can be made.

Baetidae: These organisms were identified by Demory by head characteristics only and could not be separated to generic groups. Baetid mayflies are primarily herbivorous, but the forms seen in coho stomachs may have been algal or detritus feeders.

Heptageniidae: *Cynigmula* sp. is the most abundant heptageniid genus in the study streams, and occasional members of *Epeorus* sp. also appear in bottom samples. It is believed that most of the forms identified in stomach analysis by head characteristics as in the family *Heptageniidae* were *Cynigmula* sp. Data on food habits of this form are shown in an earlier section.

Miscellaneous Ephemeroptera, Plecoptera and Trichoptera: No detailed identification was possible, hence no estimate of energy source can be made for these groups.

Corixidae: Usinger (58, p. 190) and Griffith (19, p. 290-292) indicate that Corixidae may feed on algae, protozoans or rotifers. Hungerford (23, p. 248-249) shows that Corixidae are largely herbivorous, feeding on algae and taking some oligochaetes along with the plant material. No corixids were taken in bottom samples, and no estimate can be made of the energy source utilized.

Dytiscidae: This family is entirely predaceous. No data are available on prey in the study streams or on preferred substrata. No estimate can be made of the energy source utilized.

Heteroceridae: This is not a true aquatic beetle family, but the larvae do live in littoral zones and presumably the adult organisms taken by coho in Deer Creek fell or were washed into the water. Source of energy utilized by this group would be outside the streams.

Tipulidae: Larvae of this group are found in the study streams buried in mud or sand. Larvae identified have belonged to the genus Hexatoma. The habitat of the larvae probably indicates a detritus feeding habit.

Culicidae: Adults of the subfamily Culicinae appeared occasionally in coho stomachs, but larvae did not. This tends to confirm the opinion that mosquito larvae are not found in the study streams proper; a conclusion based on observation of the stream. Mosquito larvae are usually herbivorous, according to Pennak (43, p. 643). Adults are predaceous. In any case, the energy uptake by mosquitoes can be attributed to sources outside the stream, since the mosquito habitat is not in the stream environment.

Heleidae: Some members of Heleidae are herbivorous, and some carnivorous. Absence of adequate detail on the specific forms taken by coho makes it impossible to determine the energy source in this family.

Bezzia: *Bezzia* sp. larvae are predaceous, according to Thompson (56, p. 77). An estimate of energy source cannot be made.

Tabanidae: Wirth and Stone (63, p. 443) state that the larvae of Tabanidae are all predaceous on soft-bodied invertebrates. Tabanidae larvae occur in the study streams and occasionally are taken by coho. The larvae are relatively soft-bodied and would tend to be found in quiet water areas. Their prey in these areas would probably consist of detritus-feeding forms such as false cranefly larvae, Liriopeidae, cranefly larvae, Tipulidae, and perhaps oligochaetes. Larvae probably also occur in still pools outside the stream. Adult female tabanids are predaceous, but males may be nectar or pollen feeders (63, p. 443). The energy utilized by tabanids almost certainly is originally derived from sources outside the stream.

Dolichopodidae: The larvae taken by coho in Deer Creek cannot be identified in detail. This entire group is predaceous (63, p. 449). The known aquatic larvae generally seem to live in muddy areas, a habitat preference that would indicate detritus-feeding prey.

Empididae: Wirth and Stone (63, p. 457-459) state that adults of this family are predaceous on smaller animals, and that adults of one genus, Wiedemannia, have been seen dragging simuliid larvae from the edge of swift streams in the Sierra Nevada of California. Vaillant (59, p. 187) shows that simuliid larvae in Algeria are the prey of one empidid genus, Hermerodromia. Larvae may live in moist spots and two subfamilies are known to have aquatic larvae. No larvae of this family have been found in the study streams or in coho stomachs. It will be assumed that adult Empididae found in the coho stomachs derived their energy from outside the streams. If simuliid larvae formed a major part of the diet of the empidid adults found in coho, this energy source was derived largely from detritus, since simuliids feed primarily on drifting detritus, as shown earlier.

Miscellaneous Diptera larvae: In the absence of detailed identification, nothing can be said about the energy utilized by this group.

Gastropoda: No estimate of energy source can be made because no detailed identification data are available. The only abundant snail in the study streams, Oxytrema silicula, is herbivorous, feeding on material of terrestrial as well as aquatic origin.

Table 25 summarizes the proportion of the coho diet made up by various aquatic prey and the estimated proportion of

Table 25. Estimated energy sources for coho production on Deer Creek.

Group	% of coho aquatic diet	% of source energy allochthonous	% of coho energy from aquatic insects		
			allochthonous	autochthonous	Not accounted for
Annelida	11.4	80-100[1]	10.3	1.1	
Gammaridae	1.0				1.0
Baetidae	5.5				5.5
Baetis	2.2	26[2]	.6	1.6	
Paraleptophlebia	4.5	95[2]	4.3	.2	
Ephemerella	1.0	40[3]	.4	.6	
Heptageniidae	3.7	60[3]	2.2	1.5	
Epeorus	.9	45[3]	.4	.5	
Miscellaneous Ephemeroptera	4.7				4.7
Miscellaneous Plecoptera	6.4				6.4
Corixidae	.4				.4
Psychomyiidae	4.1	predaceous[3]			4.1
Limnephilidae	1.9	25[3]	.5	1.4	
Miscellaneous Trichoptera	6.7				6.7
Dytiscidae	.4				.4
Elmidae	1.0	10[3]	.1	.9	
Heteroceridae	.7	80-100[1]	.6	.1	
Tipulidae	.4	80-100[1]	.4		
Culicinae	.5	100[1]	.5		
Dixidae	2.7	95[3]	2.6	.1	
Simulidae	4.8	90[3]	4.3	.5	
Tendipedidae larvae, pupae	24.6	88[2]	21.6	3.2	
Tendipedidae adults	1.6	88[2]	1.4	.2	
Heleidae	.2				.2
Bezzia	.4				.4
Tabanidae	1.3	100[1]	1.3		
Dolichopodidae	.4	80-100[1]	.4		
Empididae	.5	100[1]	.5		
Miscellaneous Diptera	5.6				5.6
Gastropoda	.4				.4
Fish eggs	.2				.2
Total percentage of aquatic animals energy in each category			52 %	12 %	36 %
Proportion of total coho energy intake in each category . . . . (0.62 x total percentage of animal energy in category)			32 %	7 %	26 %[4]

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[1] Literature sources
[2] Demory (15)
[3] Result of present work
[4] Includes insects from uncertain habitats (4% of coho diet)

allochthonous energy used by prey organisms. In the case of such forms as Tipulidae, the estimates, based on life history information from the literature, are 80-100 per cent allochthonous. The range given was to allow for possible inclusion of some algal detritus in the diet.

Table 25, the summary of energy sources for Deer Creek coho production, shows that roughly half of the aquatic insect portion of the coho diet represented energy that originally had been fixed by autotrophic producers outside the stream ecosystem. About twelve per cent of the aquatic insect energy entering coho was estimated to be derived originally from autotrophs in the stream, and 36 per cent of the energy entering coho could not be established as being of terrestrial or stream origin. Reasons for failure to estimate origin of 36 per cent of the aquatic insect diet were: lack of detailed identification data, predatory or omnivorous feeding habits of some forms, or lack of reference material on life histories and feeding habits.

Sixty-two per cent of the coho diet was made up by aquatic insects. Multiplying this figure by 0.52, the estimated allochthonous proportion of the energy intake of the aquatic insects found in coho, yields a figure of 32 per cent, a figure referring to the estimated allochthonous energy contributed to coho by aquatic insects.

As has been mentioned previously, 34 per cent of the dry weight of insects found in Deer Creek coho stomachs was made up by terrestrial insects. Addition of this percentage and the 32 per cent figure estimated by study of the aquatic insect portion of the coho diet results in a total of 66 per cent. This latter figure is an estimate of the amount of allochthonous energy used by coho for production.

Some of the energy, 26 per cent, used by coho was not accounted for in Table 25. Even if this 26 per cent were entirely assigned to autochthonous sources, the allochthonous energy estimate of 66 per cent for coho would not be reduced. In fact, some of the 22 per cent would be allochthonous, a factor increasing the allochthonous energy for coho production to more than 66 per cent.

It seems safe to state here that over half the energy used in coho production was derived originally from terrestrial energy fixers.

Summary of Energy Pathway Results: The following summary is presented as evidence that terrestrial energy sources contribute materially to the study stream ecosystem, particularly to the production of coho salmon. The summary also facilitates connection of this phase of the study with work on behavior and production. The summary deals with Deer Creek coho energy sources only.

1. About 34 per cent of the annual diet of coho salmon (based on dry weight of fish stomach contents) was made up by terrestrial insect forms.

2. About 62 per cent of the annual diet of Deer Creek coho consisted of aquatic insects.

3. About 4 per cent of the Deer Creek coho diet could not be attributed to terrestrial or aquatic groupings.

4. Analysis of aquatic insect food habits indicated that about 52 per cent of the food ingested by coho salmon prey was of allochthonous origin, 12 per cent was autochthonous, and 36 per cent could not be assigned to allochthonous or autochthonous energy sources.

5. Application of aquatic insect food habit data to the data on coho food habits indicated that 66 per cent of the total energy intake of coho salmon was derived from allochthonous sources, either directly as terrestrial insects or indirectly as aquatic insects that fed upon terrestrial detritus.

6. Seven per cent of the coho total energy intake was attributed to autochthonous sources.

7. About 26 per cent of the coho total energy intake could not be established as of autochthonous or allochthonous origin.

DISCUSSION

It has been shown by indirect evidence that aggressive behavior of coho is one factor causing the spring downstream movement of coho fry. It appears probable that this factor, perhaps in combination with other density-regulatory factors, would cause the number of smolts leaving a given stream to remain relatively constant from year to year. Since the present work contains no data on yearly production or yield variation, the literature concerning coho yield was reviewed.

Hunter (24, p. 871) shows the total number of coho salmon smolts migrating from Hooknose Creek, on Port John Bay, King Island, British Columbia, from 1948 through 1957 (Table 26).

Table 26. Hooknose Creek coho migration, 1948-1957.

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

* Unpublished data of the Fishery Research Board of Canada (9)

The relatively small amount of fluctuation in smolt numbers from year to year suggests some type of regulatory mechanism operating in freshwater. The number of out-migrant smolts bears no relationship to the number of adult females in the parent run, or to the out-migration of siblings as fry. In the same time interval, the total number of pink salmon, *Oncorhynchus gorbuscha* (Walbaum), and chum salmon fry, *O. keta* (Walbaum), passing through the Hooknose Creek trap ranged from 98,524 to 1,409,225 (24, p. 857) with great fluctuations from year to year, particularly in the case of the pink salmon. The period of residence undergone in Hooknose Creek by the coho appears to be a stabilizing influence upon the number of out-migrants.

Salo and Bayliff (50) show data from Washington for Minter Creek smolt migrations for several years. Data shown in Table 27 are for those years when no hatchery-reared fish were placed in the stream above Minter Creek trap. Footnotes indicate that age 2/ coho are included in some of the smolt counts and not in others. In spite of the uncertainty resulting from this, it appears that the count of wild smolts migrating from Minter Creek does not fluctuate greatly from year to year.

Two other research facilities have been used to secure coho data over the past several years. One of these is a weir on Gnat Creek, tributary to the lower Columbia, operated by the Oregon Fish Commission. Data from this station are not available for reference. A trap on Spring Creek, tributary to the Wilson River near Tillamook, Oregon, was operated by the Oregon Fish Commission from December, 1949, to August, 1958. Some data secured there (41, p. 9) are shown in Table 28.

Table 27. Minter Creek coho migrations, 1938-1949.

Smolt brood	Females in parent run	Sibling fry[5]	Smolts (1+)
1938	967	52,000	35,452 [1,2]
1940	1,393	211,136	32,085 [3]
1942	786	60,000	31,893 [2]
1943	906	?	23,117 [2,4]
1944	500	101,000	30,408 [2,4]
1946	500	24,614	41,848 [1]
1949	114	920	27,691 [4]

[1] Includes some 2+ fish of 1937 brood released after hatchery rearing.

[2] Number of age 2+ fish of this brood not known.

[3] Includes 6,829 age 2+ wild fish and some age 2+ fish of hatchery origin.

[4] Includes some wild age 2+ fish of previous brood year, number unknown.

[5] From unpublished data, Washington Department of Fisheries (39).

Table 28. Spring Creek coho migrations, 1948-1952.

Adult brood year	Females passed upstream	Resulting juveniles	
		Fry out	Smolts out
1948[1]	11	1701	1055
1949[1]	24	1594	1228
1950	35	2498	1947
1951	54	9377	1209
1952	12	4662	1887

[1] Values may be minimal due to high water.

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

Data on downstream movement of 0/ age coho are available for Minter, Spring, and Hooknose creeks. Data secured at Hooknose Creek, Table 26, indicate that a large movement of 0/ age coho does occur there. Mode of the movement generally occurred in late April or May in the 12 years of record (9). Operation of the Hooknose Creek weir ceased in early June in most years, hence no data are available for the summer movement, if any, of 0/ age coho.

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

Spring Creek coho fry movements occur largely in spring, and their magnitude in the years of record (Table 28) bears no particular relationship to the parent runs or to the sibling smolt migrations.

Minter Creek data (39), shown in Table 29, suggest that fry movement is related to parent egg potential, but some of these same data, Table 27, show that the smolt migration bears no relationship to parent egg potential or sibling fry movement. All fry moving downstream into the Minter Creek trap were placed back upstream. Examination of Salo and Bayliff's (50) Table 19, their appendix, and unpublished data of the Washington Department of Fisheries in Table 29 of the present

Table 29. Minter Creek coho downstream migrants, 1937-1957.

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

work, indicates that a relatively greater total fresh water mortality occurs in years of large egg deposition and large fry migration.

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

Smoker (53, p. 5-12) examined coho salmon yield to the commercial fishery in the Puget Sound area in relation to total stream runoff in year of stream residence for given year classes. He obtained a strong positive correlation. The two most logical effects of greater streamflow upon coho production would be in increasing the effective spawning areas for adults and in providing greater living space for juveniles.

Neave (34, p. 11) shows a lower availability of coho to sportsmen fishing Cowichan Bay, B. C., for year classes which experienced low summer flows in their juvenile stages in the Cowichan River. McKernan, Johnson, and Hodges (33, p. 440) show a significant correlation between annual coho salmon catches in Oregon near the Siletz River and summer low flows of that river two years previously. A similar test on data from the Coquille River area showed no significance. Wickett (62, p. 89) shows two low counts of coho leaving Nile Creek, B. C., associated with two years of low summer rainfall in a four-year interval from 1946-1949.

The results of these investigations tend to show that more water provides more fish, but cannot separate the mechanism involved, be it associated with predation, disease, territoriality, food supply, or combinations of these.

Effective yields, or smolt yields, in the study streams in the year 1959-60 were 4.3 g/m^2 in Deer Creek, 2.9 g/m^2 in Flynn Creek, and 2.0 g/m^2 in Needle Branch. These yields are the population statistics most comparable to yield per unit area of other bodies of water in terms of harvest by seine, yield to a fishery, or yield determined by draining and poisoning waters involved.

In unpublished work on two artificial streamside rearing ponds for coho, located in the Alsea River basin, Chapman (10, p. 3) determined yield of coho smolts by draining and poisoning the ponds after the fish had reared from fry stage for one year, 1958-1959. This yield is the same statistic as "effective yield" from the study streams. One of the ponds, 0.9 acres in size, was a naturally-fertilized one built on a dairy barnyard; the other pond, 2.0 acres, covered a brushy area not used formerly for agriculture. Yield in the fertile pond was 7 g/m^2. Yield in the more "natural" pond area was 2.4 g/m^2. It is interesting to note that the yield of the latter standing water area was close to that obtained in the three study streams. Survivals in the ponds were high; 60 per cent in the fertile pond, 27 per cent in the larger pond, and the smolts were about 50 per cent larger than those migrating out of the study streams.

Although effective yield does not vary greatly from year to year on a given stream as indicated by reports in the literature, production could fluctuate relatively more widely. This fluctuation could occur, for example, as a result of fluctuations in amount of egg deposition. Ricker and Foerster (46, p. 189) show great variability in sockeye production in Cultus Lake, but their data are taken from a lake environment and a schooling species.

Malikova (31, p. 241-245) shows some values for the chemical composition of Salmo salar. Moisture was about 75 per cent of the live fish weight. Of the dry weight, about 71 per cent was protein, 15 per cent was fat, and one per cent was carbohydrate. Hawk and Bergheim (20, p. 799) state that protein contains 4.1 kilocalories per gram, fat - 9.3 k Cal. and carbohydrate - 4.1 k Cal. Assuming that coho salmon and S. salar are ecologically and anatomically similar species, and using the data shown above, one can estimate the calorific value per unit weight of coho tissue and use these data to assist in making a comparison with carnivore production in other waters.

Live tissue of coho can be estimated to be 17.7 per cent protein, 3.8 per cent fat, and 0.2 per cent carbohydrate. Therefore, one gram of live coho tissue contains 730 calories as protein, 350 cal. as fat, and 82 cal. as carbohydrate, or a total of 1.162 k Cal. per gram. Thus Deer Creek 1959 year class coho production represented in the neighborhood of 57,000 kilocalories.

Net 1959 year class production per square meter of stream was then about 11 k Cal. for the year April, 1959 to March, 1960. Net production on the other two streams was as follows: 10 k Cal./m^2/yr. on Flynn Creek, and 9 k Cal./m^2/yr. on Needle Branch. Cutthroat trout and cottid production are ignored here of course, as are production data for the few 1958 year class coho present in the year considered.

Odum (40, p. 61-62) shows a dominant carnivore production of 6 k Cal./m^2/yr. for a Florida spring. Lindeman (29, p. 406) estimates a carnivore net productivity of 13 k Cal./m^2/yr. in a senescent lake.

Allen (2, p. 188) shows a mean annual brown trout production per square meter of about 51 grams, or roughly 59 k Cal. This net carnivore production in a New Zealand stream was much higher per unit area than coho production in the study streams and offers an interesting comparison. The Horokiwi stream, Allen's study area, is much larger and less shaded than the streams studied in the present work. Terrestrial insects amounted to only 5 per cent of the annual food of brown trout (2, p. 142). Phosphate levels and carbonate hardness were greater in the New Zealand stream as shown in Table 2 and Allen (2, p. 35).

Available facts indicated that the New Zealand stream was much more productive than the streams studied in the present work, in terms of energy flow. Some of the difference can be attributed to exclusion of cutthroat trout from calculation of production per square meter in the study streams.

Since growth rates on the three study streams were not greatly different for the 1959 year class, population size was the factor which must have caused variation in production data. It has been shown that production per unit of pool area was nearly equal on the three streams. This means essentially that the numbers of fish present per unit of pool area through the year were similar in the three streams. This suggests that living or forage space is a factor important to coho production. Riffle area, as a food-producing substrate, must be important also, but any differences in food produced on different riffle areas on the three streams would tend to be masked by terrestrial and adult aquatic insect contributions to coho diet.

Coho production and biomass maxima occurred at two times during the year of residence of the 1959 year class; in the spring following emergence of the year class and the next spring just prior to seaward migration. These spring peaks are all the more definite if other resident coho year classes are considered. In April, 1959, for instance, there were fish of the 1958 and 1959 year classes present in the study streams, both classes producing at high rates. If data for at least two years were computed, the spring peaks in production for all coho would be greater than is the case for one year class alone.

These seasonal peaks in production coincide with peaks in percentage of aquatic insects found in coho stomachs (15) and with peaks in estimated proportion of algae in stomachs of aquatic insects (15) (Figures 43 and 44). It is probable that the following network of events is involved in the spring maxima in coho production: Water area, light incidence, water temperature, and bottom stability are together generally most favorable to algae and insect production and high standing crop.

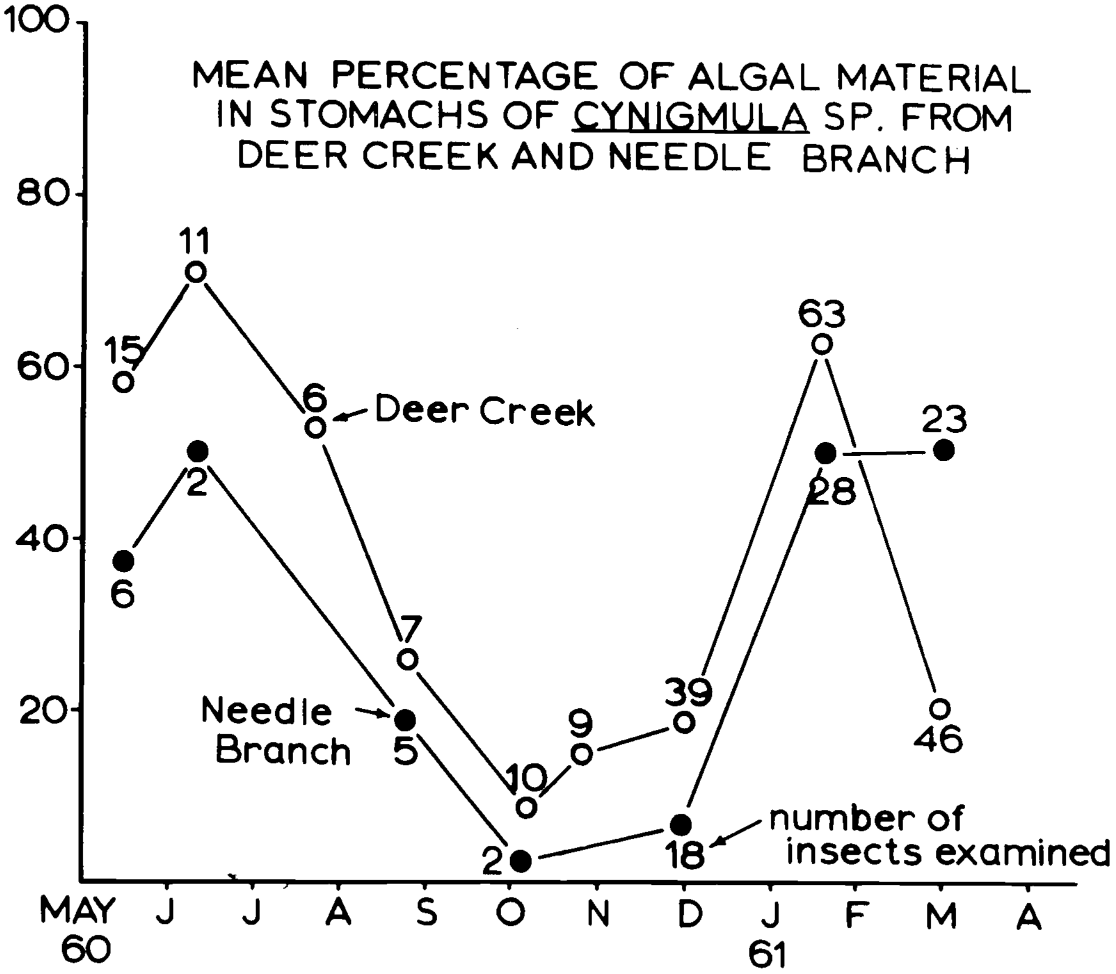
MEAN PERCENTAGE OF ALGAL MATERIAL IN STOMACHS OF CYNIGMULA SP. FROM DEER CREEK AND NEEDLE BRANCH
100
80
60
40
20
15
11
6
7
10
9
39
63
46
Deer Creek
6
2
5
2
18
28
23
Needle Branch
number of insects examined
MAY 60
J
J
A
S
O
N
D
J 61
F
M
A

Figure 43

MEAN PERCENTAGE OF ALGAL MATERIAL IN STOMACHS OF LIMNEPHILIDAE FROM DEER CREEK AND NEEDLE BRANCH

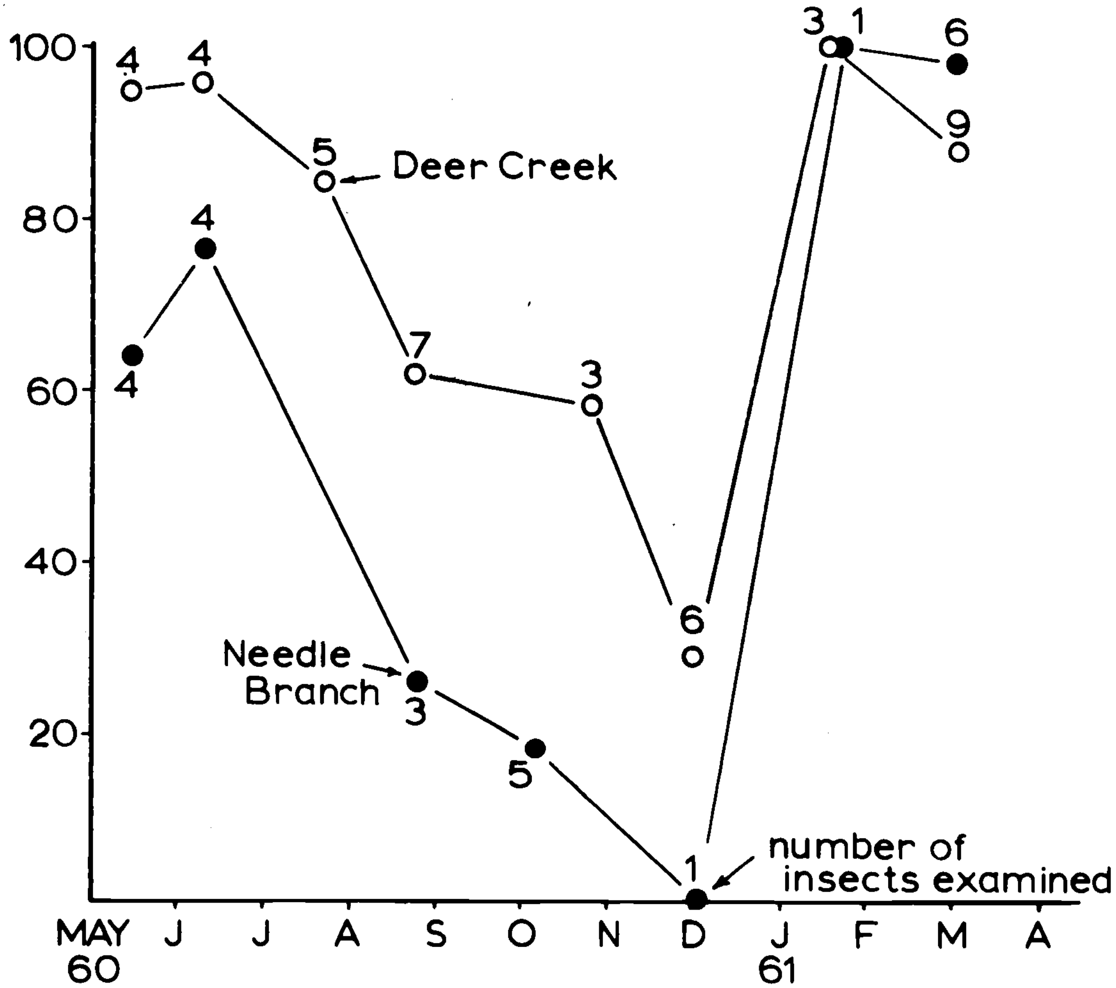

Figure 44

The energy content of detritus is high. Coho are spread over a large water area in spring, the yearlings taking advantage of faster, deeper water while fry use the eddies and slow, shallow stream sections. A high standing crop of insects is available for coho cropping, and water velocities are such that many nymphs could be washed off as seston. Many aquatic insects emerge and become available to drift-feeding coho at this time of year.

Low production levels in summer and fall occur at times when the percentage of aquatic food in the coho diet decreases (15), stream water areas are decreased, and the number of coho is reduced. The bottom surface available for insect production, and the stream surface on which terrestrial insects may fall are low. Algae production has been depressed, in part by low light availability, and terrestrial detritus material has not yet been replenished by fall of deciduous tree leaves. Detritus remaining from the previous fall is low in nutrient content, being mostly cellulose, after leaching and bacterial action have proceeded for several months.

Winter coho production probably is low, in spite of heavy leaf infall and greater water area, because the area covered by water has not yet had time to produce a crop of aquatic insects, and stream water velocities fluctuate rather violently. Production may also be reduced, as indicated by growth rate reduction, because metabolic rates of coho are reduced by low water temperatures or because coho may require more energy for maintenance in this rapid-flow period.

The contribution of terrestrial insects to the annual coho diet on the study streams, a contribution ranging from 30 to 34 per cent, indicates the importance of drift-feeding to coho. Observations in artificial streams and natural stream areas show that drift-feeding on aquatic forms was also important. This drift-feeding habit is probably closely related to the aggressive behavior of coho salmon, as Kalleberg (27, p. 82) suggests for Atlantic salmon, and as mentioned earlier.

Some indication that space is more important than short-term food increases is afforded by the feeding experiment outlined in the behavior section of this paper. Capacity of artificial stream channels to hold coho was unaltered by provision of food in excess.

As was mentioned earlier, downstream movement of coho fry in the study streams could have been caused by one or more of these factors: displacement by current, innate tendency to migrate (apart from desire for movement enforced by aggression), random shifts in position, or aggression (such as territorial behavior) within the fry population.

Displacement by current is an attractive explanation for fry movement since this would explain the disparity in size of residual and nomadic fry, the latter being smaller and presumably less able to hold position in the current. However, as

Figures 14 and 39-40 show, the size differences are slight, and should not be sufficient in themselves to explain nomad movement, particularly when some of the fry that move are larger than some of the fry that remain in the stream. Furthermore, current speeds decrease from April through June while mean size of fish increases, making inability to hold in the current an unlikely possibility.

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

Hoar (22, p. 441) points out that coho fry actively defend territories during the day, then settle to the bottom and become inactive at night, a behavior characteristic that leads to permanent residence in the stream. This type of settling behavior was noted in artificial stream channels and in natural stream areas as well. In both areas, fry tended to be on or close to the stream bottom in hours of darkness. Feeding activity commenced in artificial channels with the first increase in light level at dawn.

Settling behavior at night is not conducive to displacement by current. Activity at night, on the other hand, would be conducive to displacement, as Hoar (22, p. 443) indicates. Appendix 18 illustrates preference of coho fry for night movement. This preference was marked in March and April, less so in May.

Activity at night or a failure to settle and hold close to the bottom evidently leads to nomad movement. The facts summarized at the end of the behavior section suggest that movement would cease if the fish were placed in a suitable environment free of a resident population of coho. This, in turn, lends support to the suggestion that failure to hold position, either in daylight or at night, is due largely to the presence of other fish. If fry are forced by aggression into locations unsuited for settling and holding, displacement by current may play a part in causing movement.

Kalleberg (27, p. 82) states that territoriality in Atlantic salmon and brown trout is a characteristic evolved as a food supply mechanism. This also is a logical explanation for the aggressiveness of coho, a fish which depends strongly upon drift food on the surface and in the mid-water. However, a similar Darwinian explanation could be offered involving pathological organisms and predation. Aggressiveness could act as a population spreader, decreasing probability of disease, parasite-caused mortality, or predation.

It has been shown that nomadic coho will cease movement if offered an environment free of other coho. It has not been shown directly that aggression caused the out-migration of all, or even any, nomads. Circumstantial evidence does indicate that some, or perhaps most, of the spring, summer, and fall movement of coho fry was due to aggression. The smaller size of nomads, as compared to residuals, fits in well with artificial stream channel observations in which small coho were seen to be subordinate to large ones, to have poorer opportunities for feeding and growth, and to leave artificial channels after aggression by larger fish.

The tendency of coho to aggregate in the winter and decrease aggression helps explain the cessation of downstream movement of small nomads in early winter. Groups of fish moving after this time tended to be the same mean length as residuals, or larger, and probably were the vanguard of the smolt migration that began in January.

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

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

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

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

Allee (1, p. 195) and Collias (13, p. 84-88) present evidence that a dominant position within a group is correlated with greater individual survival potential. Noble (38, p. 115) reported that dominant individuals in a group of Xiphophorus sp. lost less weight during periods of starvation than did subordinates, that larger and heavier fishes occupied positions of greater dominance, and that prior residence was an advantage in contacts with newcomers. Braddock (5, p. 163-166) reported similar results for Platypoecilus sp.

Aggression seems to be sufficient to account for part of the considerable range in size of coho at a given time. As indicated by artificial stream work, growth of dominant fishes is greater than that of subordinates. Some of the variability in size stems from varying emergence times and varying sizes at emergence of fish emerging at the same time. The rather remote possibility of a feedback mechanism of growth control also exists, Rose (48, p. 188-199). Brown (7, p. 375) suggests that growth of small Salmo trutta may be inhibited by the mere presence of larger individuals or by increased production of adrenocorticotropin due to stress (stress being caused by the presence of larger individuals).

For the sake of discussion it is worthwhile to use available primary production data to estimate total possible autochthonous energy that could have been available for top carnivore production. In studies of algal production in Needle

Branch, production of oxygen was measured on seven days by means of light-dark tests in stirred aquaria placed in the stream bed. Tests were conducted on two square feet of gravel and rubble having visible growth of Chamaesiphon sp. and diatoms. This growth was the most abundant seen anywhere on the study streams, and the strata chosen probably constituted maximum-production areas. Tests were conducted in November, December, April, June, and July. Highest production was measured in winter and spring.

Mean oxygen production measured in this period was 3.1 mg.O_2 per square foot per hour. This figure was obtained at mid-day. Assuming this maximum rate occurred on all 9,616 square feet of Needle Branch for all 4,380 hours of daylight for one year, a total of 130 kg. O_2 could have been produced. This is based on the photosynthetic equation discussed by Ryther (49, p. 73). At a photosynthetic quotient of 1.25 (49, p. 76), 23 kg. of carbon per year could have been fixed from CO_2 in Needle Branch by autotrophic algae. Assuming that respiration used up 45 per cent of this gross production (32, p. 349), net production could have been 13 kg. C.

Assuming all 13 kg. C was assimilated by herbivorous insects, and 25 per cent stored as growth (55, p. 298), the herbivores could have had a net production of 3.2 kg. C if they fed on algae alone. If all of this insect production were ingested by salmonids, and growth efficiency of these fish were the same as brown trout, roughly 20 per cent according to Brown (7, p. 386), then maximum net production of salmon and trout would have been about 0.6 kg. or 1.3 lb. C.

Live teleost tissue is about 10 per cent carbon (60, p. 495), so that a maximum of 6 kg. or 13 lb. of salmonid flesh would have been produced by the salmon and trout population in one year, if aquatic energy sources alone were used. These series of assumptions are on the high side in regard to estimation of the possible contribution of algae to consumer production. It therefore seems impossible that the coho, cutthroat trout, and cottid populations could have been supported by aquatic plant energy fixers alone. Cottids and small carnivores like Acroneuria californica take herbivores that might otherwise be available for coho and cutthroat. Coho production alone amounted to about 16 pounds in Needle Branch for about one year.

In order for 49 kg. of Deer Creek coho flesh to be produced, in the neighborhood of 250 kg. of animal tissue must have been assimilated by coho if coho growth efficiencies are similar to those of brown trout (7, p. 386). Since about a third of the annual coho diet consisted of terrestrial insects, roughly 80 kg. or 180 pounds of terrestrial forms and 170 kg. or 370 pounds of aquatic insects were assimilated by the 1959 year class of coho while the fish were in the stream.

As suggested earlier, the assumptions and methods used to determine energy sources for coho production are subject to possible error. In spite of this, gross relationships existed between coho salmon and the original autotrophic plant energy fixers. It is obvious from the data secured by Demory (15), and the present work, that terrestrial plants supply most of the energy eventually used by coho salmon for maintenance and growth in the three study streams.

To a certain extent, the division of aquatic energy into allochthonous and autochthonous types is artificial. The terrestrial environment and stream ecosystem are inextricably related. An example of this relationship can be found in the fact that trace minerals required for aquatic autotrophic production are leached from decayed organic material in the soil and carried in groundwater into the stream. Mosses found in the splash-zone along stream margins become submerged in periods of high streamflow, and might be considered aquatic plants in any case. The possibility that some of the blue-green algae genera found in the study streams are facultative heterotrophic forms could mean an even closer dependence of algae upon the terrestrial environment than is now recognized.

The data available for Cynigmula sp. (Figure 43) and for stone-cased Limnephilidae (Figure 44) indicate a seasonal change in percentage of algae consumed. Demory (15) shows a similar change for Baetis sp.

Observations of the study streams indicate that peak abundance of algae occurs in late winter and early spring, coinciding with absence of a deciduous leaf canopy and increase of day length. Butcher (8, p. 269-271) shows a seasonal change in algae in calcareous streams in England. Summer was found to be the period of maximum algae production. The English streams studied were relatively exposed to light.

Wissmeyer (64, p. 682) shows a suggestion of a seasonal change in the food of *Cloëon* sp. in cold European brooks. Ten *Cloëon* sp. nymphs contained 8-30 per cent detritus on August 11, 1922, and six nymphs taken October 22, 1922, contained 45-92 per cent detritus.

It appears that some of the insect groups in the study streams change food preference seasonally or that availabilities of algae and detritus change. Both factors together could also cause the observed phenomenon. The changes in quantities of terrestrial detritus and algae observed in the streams were so striking that they appeared sufficient to explain the seasonal changes in food habits of insects.

Factors other than food type availability or food preference of insects might cause seasonal or even diel changes in food habits. Behavior is one of these factors. Demory (15) showed that the negatively-phototropic *Paraleptophlebia* sp. fed to some extent on algae at night and in daylight in areas under deep cover, but took mostly detritus in periods of greater light intensity.

Diel changes in insect food habits could have influenced insect food habit data secured in the present work. This possible source of error in results was checked in Needle Branch insect sampling on one occasion. Samples were secured at midnight and at mid-day in the same 24-hour period. No difference in algal content could be detected in the two sets of samples.

A consideration of energy source for coho production has led to some interesting relationships. One of these was indicated by Demory (15) when he showed feeding habits from May through September of coho on three streams. Fish stomach sampling intensity was about equal in all streams in this period, as indicated earlier.

Deer Creek coho stomachs in this period contained 21 per cent terrestrial organisms, Flynn Creek coho contained 29 per cent terrestrial insects, and Needle Branch coho contained 40 per cent terrestrial animals.

There is no reason to think that this relative relationship would change greatly if a full year of data were available on all streams. Flynn Creek data for a year show a terrestrial insect contribution to the coho diet about equal to that occurring in Deer Creek. The limited data available for a full year on Needle Branch coho diet indicate that terrestrial forms were more important to coho in this stream than in the other two.

It is likely that the Flynn Creek and Needle Branch coho populations would show a dependence upon terrestrial energy sources at least equal to that in Deer Creek. Application of insect energy source estimates for Deer Creek to the forms taken by coho on Flynn Creek results in an estimated terrestrial energy contribution to coho of well over 50 per cent.

Figures 43 and 44 indicate that Needle Branch aquatic insects may ingest a greater proportion of detritus than is the case for Deer Creek nymphs. This fact and the limited data showing a greater proportion of terrestrial insects in Needle Branch coho stomachs suggest that dependence of Needle Branch coho upon the terrestrial environment may be even greater than is the case in the other two streams. Heavy overhead cover and summer pooling conditions would tend to limit algae and aquatic insect production in low flow periods, so the contribution of terrestrial energy may have been a result of low aquatic energy availability.

Inductively, one may come to the suggestion that the wider a coastal stream becomes, as it flows seaward, the less dense overhead cover will be and the less important terrestrial insects will be in the diet of coho, or probably of other salmonids as well. It seems likely that the importance of terrestrial detritus to the diet of aquatic insects would also decrease as the stream becomes larger.

SUMMARY

1. A study of coho salmon production was conducted from July, 1958, to March, 1961, in three small Oregon coastal streams. Factors investigated included production in terms of tissue elaborated by time period, coho behavior as a factor affecting coho population size, and energy transfer as a factor affecting coho growth. Production studies involved the 1959 coho year class.

2. Downstream migration of coho fry began soon after fry emergence in spring. A large movement occurred in the late spring, lesser numbers of fry moved in the summer and fall, and the smolt migration took place from late winter through May of the year following emergence of fry from the gravel.

3. Migrant coho fry were smaller than residual coho in spring, summer, and early fall. From November to March, migrant smolts were about the same size as residual coho. From March to June, migrant smolts were larger than residual yearling coho.

4. Growth rates of coho decreased sharply from November 15 to January 15, and rates of growth through the year were similar in the three streams.

5. Standing crop, in numbers of coho, decreased rapidly from emergence of fry to July, then decreased slowly until migration of yearling smolts.

6. Production per fortnight showed two peaks; one soon

after fry emergence, and another shortly prior to migration of smolts. Biomass showed the same peaks.

7. Coho production in the smallest stream showed an obvious decrease in mid-summer, probably due to low flow.

8. Coho production per unit of pool area for about 14 months was nearly the same on all three streams, ranging from about 15.6 gm/m^2 to 17.0 gm/m^2. This suggests that living space is a factor important to coho production. Production data per unit of total area and riffle area showed much greater differences among the three streams.

9. Yields of 1959 year class smolts per 100 square meters were: Deer Creek - 64 smolts, Flynn Creek - 48 smolts, Needle Branch - 21 smolts.

10. About 50 per cent of the total 1959 year class coho tissue (in weight) produced in Deer Creek suffered mortality.

11. Estimated total mortality (in numbers) of Deer Creek 1959 year class coho, from emergence to completion of smolt migration in May the next year, was about 88 per cent.

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

13. Nomadic coho (those migrating downstream from time of fry emergence through late fall) placed in artificial stream

channels barren of fish formed hierarchies and tended to remain in the channels rather than migrating on downstream through the unscreened channel outlets.

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

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

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

17. Feeding of coho with brine shrimp, in quantities in excess of requirements, did not alter capacity of artificial stream channels to hold nomadic coho.

18. Aggression observed in natural stream areas was frequent, probably continuous, and consisted of territoriality, partial territoriality, nipping, threatening, and chasing. Hierarchies could not be positively observed in stream areas.

19. Nomads taken from one stream and transferred to another stream barren of resident stock remained in the latter stream.

20. Nomads transferred to a 39 square meter controlled stream section barren of resident coho remained there, taking up residence in the pool where they were released. Population density in this pool apparently never became great enough to force fish into two lower pools in the controlled section.

21. It was concluded that aggressive behavior of juvenile coho is one important factor governing population density in the stream environment, and hence is one factor determining production of coho.

22. About 34 per cent of the annual diet of coho salmon (based on dry weight of fish stomach contents) was made up by terrestrial insect forms.

23. About 62 per cent of the annual diet of Deer Creek coho consisted of aquatic insects.

24. About 4 per cent of the Deer Creek coho diet could not be attributed to terrestrial or aquatic groupings.

25. Analysis of aquatic insect food habits indicated that about 52 per cent of the food ingested by coho salmon prey was detritus of allochthonous origin, 12 per cent was autochthonous material in the form of algae, and 36 per cent could not be assigned to allochthonous or authochthonous energy sources.

26. Application of aquatic insect food habit data to the data on coho food habits indicated that 66 per cent of the total energy intake leading to coho salmon production was derived from allochthonous sources, either directly as

terrestrial insects or indirectly as aquatic insects that fed upon terrestrial detritus.

27. Seven per cent of the coho total energy intake was attributed to autochthonous sources.

28. About 26 per cent of the coho total energy intake could not be established as of autochthonous or allochthonous origin.

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APPENDIX

Appendix 1. Streary, 1959 to June, 1960.

	191960 FeJan.	Feb.	Mar.	Apr.	May	June
Mean Flow						
Deer Creek	12.7.30	19.3	9.03	9.08	6.90	1.94
Flynn Creek	9.5.26	13.0	6.66	7.01	5.26	1.58
Needle Branch	3.1.93	3.93	2.12	2.11	1.93	0.40
Maximum Flow						
Deer Creek	21.8.0	68.0	23.0	21.0	16.0	3.8
Flynn Creek	15.2.0	42.0	15.0	15.0	11.0	3.2
Needle Branch	7.4.8	14.0	5.2	4.8	4.6	0.9
Minimum Flow						
Deer Creek	6.3.5	4.7	3.8	4.4	3.6	1.1
Flynn Creek	4.2.6	3.5	3.1	3.7	2.9	0.8
Needle Branch	1.0.8	0.9	0.8	0.9	0.8	0.2

Appendix 2. Rainfall by month at three streams,[1] February, 1959-June, 1960.

	Deer Creek (inches)	Flynn Creek (inches)	Needle Branch (inches)
1959			
February	12.00	10.46	12.17
March	10.47	9.82	11.33
April	4.83[2]	4.70	4.95
May	5.70[2]	5.22	6.30
June	3.62[2]	3.37	3.90
July	0.65	0.69	0.78
August	0.60	0.56	0.52
September	11.49	11.26	13.12
October	8.73	7.77	9.43
November	6.59	5.95	6.96
December	9.26	8.16	8.95
1960			
January	9.81	10.29	11.00
February	18.16	15.07	17.71
March	12.77	12.77	13.65
April	9.04	8.32	9.24
May	10.53	9.84	9.19
June	1.20	1.08	.95
Total (July, 1959 to June, 1960)	98.83	91.76	101.50

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[1] Distances between gages:
Deer-Flynn = 1.31 mi.;
Flynn-Needle = 1.69 mi.;
Needle-Deer = 2.06 mi.

[2] Mean of record for Flynn Creek and Needle Branch

Appendix 3. Suspended sediment loads in three streams, December, 1958, to November, 1959.

	Mean ppm range	Tons per day range	Total tonnage
December, 1958			
Deer Creek	0-16	0-0.7	5.3
Flynn Creek	1-10	<.05-0.4	3.2
Needle Branch	1-9	<.05-1.0	.8
January, 1959			
Deer Creek	0-104	0-19.0	67.3
Flynn Creek	4-82	< .1-11.0	39.1
Needle Branch	1-72	<.05-2.2	8.5
February			
Deer Creek	1-27	< .05-1.5	7.2
Flynn Creek	2-12	< .05-0.4	4.3
Needle Branch	0-14	0-0.3	1.3
March			
Deer Creek	0-9	0-0.3	3.1
Flynn Creek	1-7	<.05-0.1	1.4
Needle Branch	0-10	0-0.1	0.5
April			
Deer Creek	1-12	< .05-0.3	1.8
Flynn Creek	1-9	< .05-0.1	1.1
Needle Branch	0-4	0- .05	0.2
May			
Deer Creek	1-8	< .05-0.3	2.0
Flynn Creek	1-7	< .05-0.1	0.8
Needle Branch	0-11	0-0.1	0.3
June			
Deer Creek	1-8	<.05-0.1	0.8
Flynn Creek	1-6	.05	0.2
Needle Branch	0-2	0- <.05	0.0
July			
Deer Creek	1-4	0- <.05	0.1
Flynn Creek	0-4	0- <.05	0.0
Needle Branch	0	0	0

(continued)

Appendix 3 continued.

	Mean ppm range	Tons per day range	Total tonnage
August, 1959			
Deer Creek	1-6	0- <.05	0.1
Flynn Creek	0-4	0- <.05	0.0
Needle Branch	0-2	0- <.05	0.0
September			
Deer Creek	1-21	<.05-1.0	1.7
Flynn Creek	0-13	0-0.3	0.6
Needle Branch	0-21	0-0.3	0.4
October			
Deer Creek	0-11	0-0.3	2.5
Flynn Creek	0-6	0-0.1	1.0
Needle Branch	0-6	0- <.05	1.0
November[1]			
Deer Creek	0-68	<.05-5.0	12.3
Flynn Creek	0-12	<.05-0.3	1.5
Needle Branch	0-17	0- <.05	1.0

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[1] Preliminary estimate.

Appendix 4. Statistics for estimation of standing crop in numbers.

Date	Fin mark	Number marked	Marks recovered at trap	Total catch	Estimated population at marking time	Standard error of population estimate	95 % Confidence limits	
							Lower	Upper
DEER CR.								
5/25/59	LV	656	127	4,798	24,595	1,950	20,773	28,417
7/17/59	RV	315	86	3,064	11,097	1,012	9,114	13,080
10/1/59	BV	133	66	2,969	5,896	519	4,879	6,913
2/21/60	1/2 Dors.-Ad.	102	53	2,699	5,100	476	4,148	6,052
4/1/60	Top 1/2 caud.	55	34	951	1,494	152	1,184	1,804
5/4/60	Lower 1/2 caud.	9	2	116	351	---[1]	104	3,462
FLYNN CR.								
6/5/59	LV	114	18	1,262	7,578	1,585	4,234	10,922
6/18/59	RV	127	23	1,134	6,006	1,103	3,723	8,289
8/15/59	BV	92	28	1,120	3,556	546	2,437	4,675
4/10/60	Top 1/2 caud.	7	6	318	319	---[1]	171	1,014
NEEDLE BR.								
5/27/59	LV	113	13	301	2,438	610	1,108	3,768
6/17/59	RV	86	17	241	1,156	242	643	1,669
8/5/59	BV	68	10	222	1,379	380	520	2,238
10/5/59	Anal	43	3[2]	18	204	---[1]	108	1,433

[1] Limits set with Poisson distribution.

[2] Netted in area not sampled in marking. Recoveries made within three weeks of marking.

Appendix 5. Calculations for prediction of coho weights from lengths. Length and weight in logarithms.

Deer Creek

Number of coho sampled	161
SSx	2.547590
SP	7.898210
SSy	25.178600
b	3.100267

Log weight = -2.15313 + 3.10027 log length

Flynn Creek

Number of coho sampled	141
SSx	1.749100
SP	5.031180
SSy	15.403650
b	2.876440

Log weight = -1.73726 + 2.87644 log length

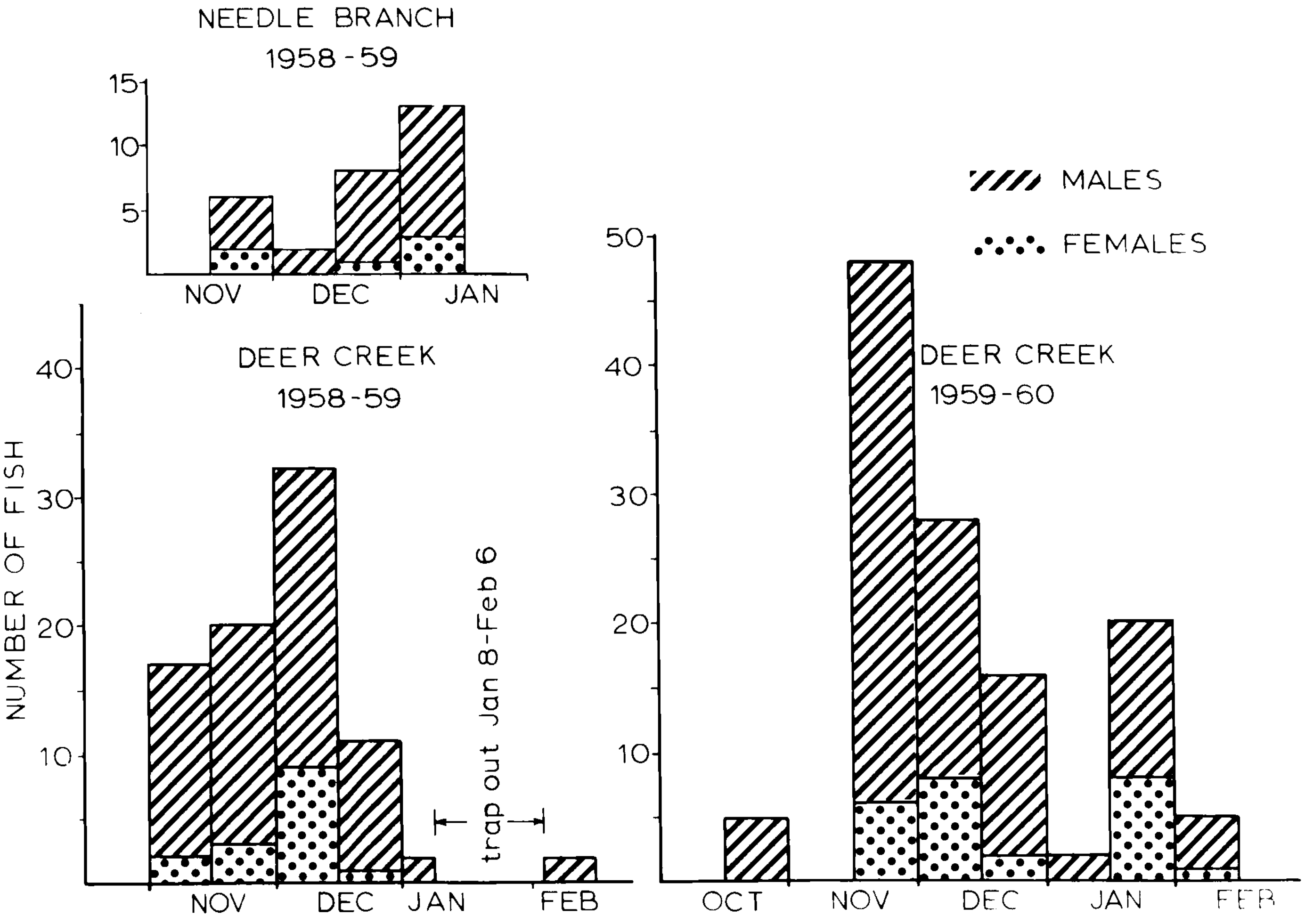
Needle Branch

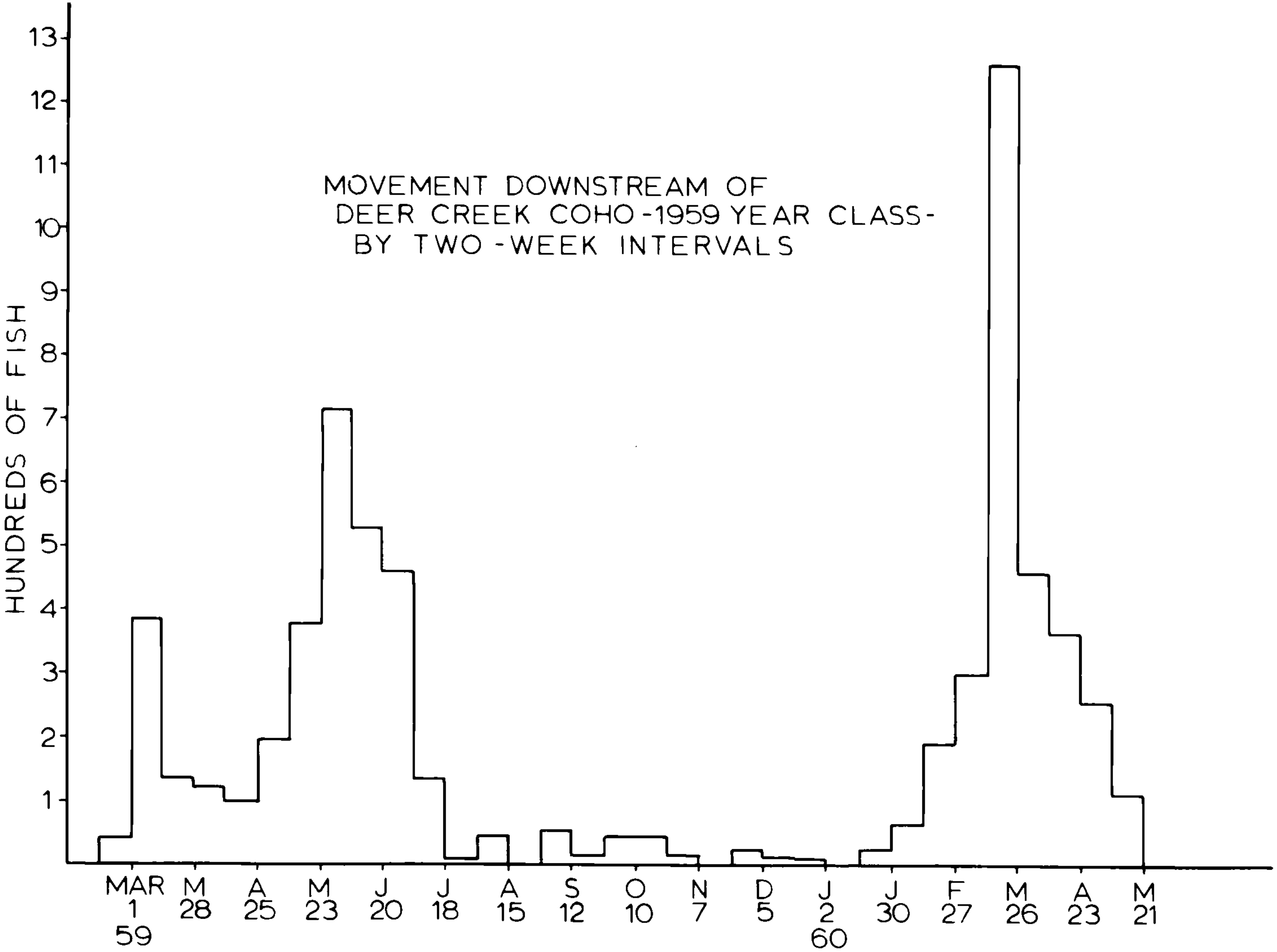
Number of coho sampled	73
SSx	0.456610
SP	1.438690
SSy	4.697454
b	3.150810

Log weight = -2.23255 + 3.15081 log length

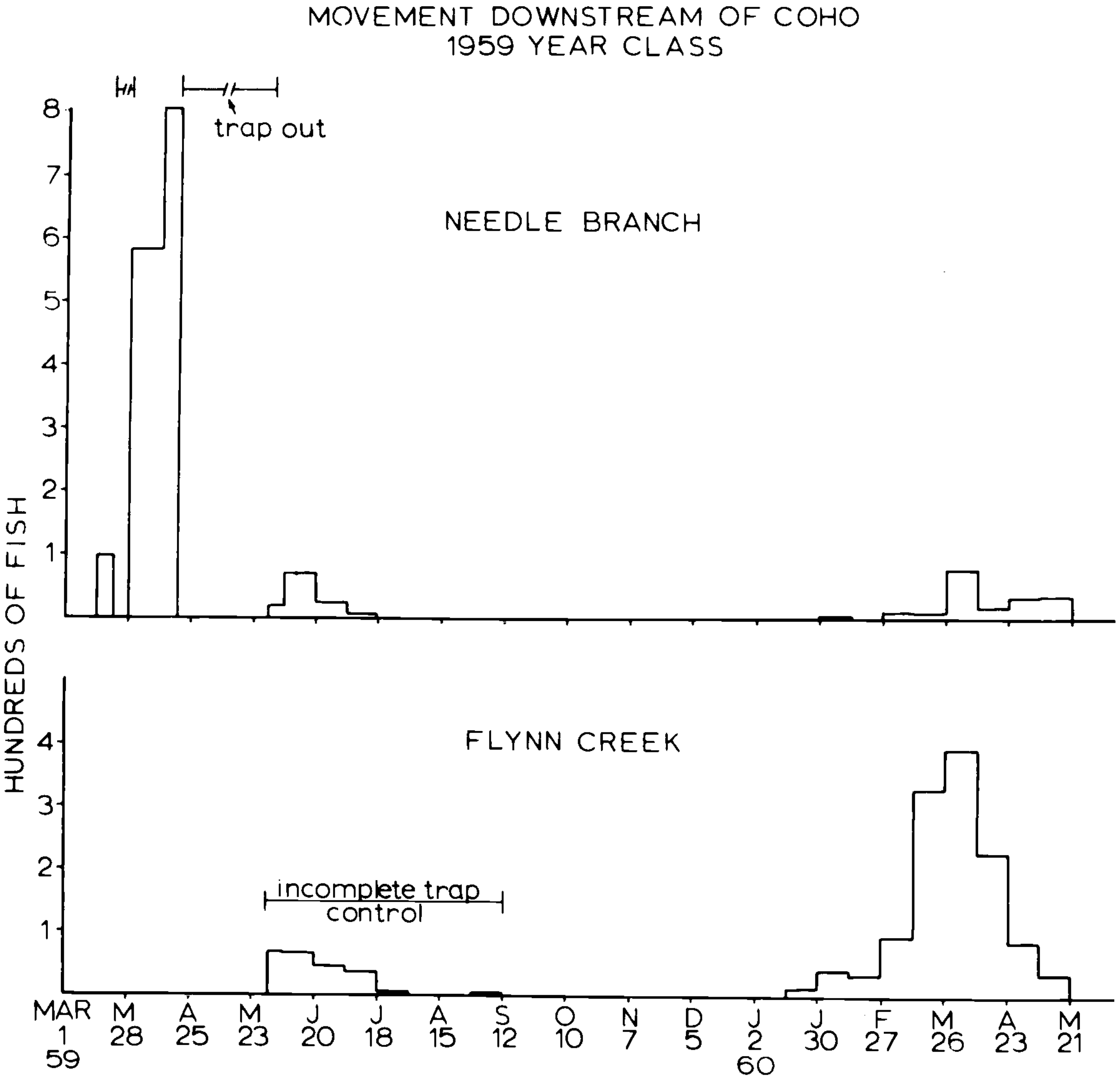
Appendix 6

UPSTREAM MOVEMENT OF ADULT COHO




MOVEMENT DOWNSTREAM OF DEER CREEK COHO - 1959 YEAR CLASS - BY TWO - WEEK INTERVALS

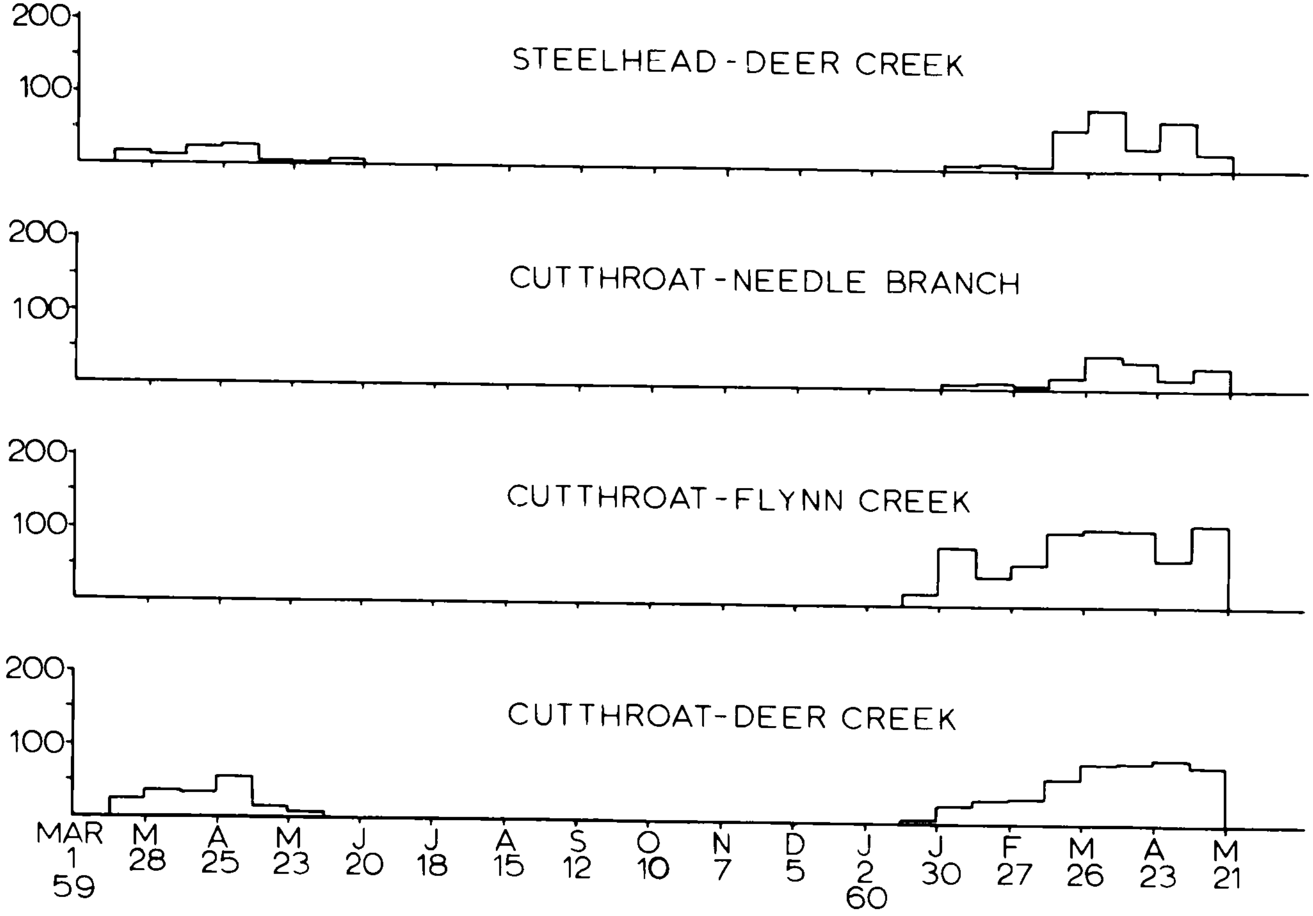
Appendix 7


MOVEMENT DOWNSTREAM OF COHO
1959 YEAR CLASS
trap out
NEEDLE BRANCH
FLYNN CREEK
incomplete trap control
HUNDREDS OF FISH
8
7
6
5
4
3
2
1
4
3
2
1
MAR 1 59
M 28
A 25
M 23
J 20
J 18
A 15
S 12
O 10
N 7
D 5
J 2 60
J 30
F 27
M 26
A 23
M 21

Appendix 8

Appendix 9

DOWNSTREAM
MOVEMENT OF TROUT
PER FORTNIGHT



Appendix 10. Confidence limits for mean lengths of coho, 1959 year class, Deer Creek, March 1959-June, 1960.

Date-Type	Mean length mm	Sample size	Variance	Half of 95% confidence zone	Limits	
					L	U
3/1-emergence	33.62	26	.52	.29	33.33	33.91
4/13-migrant	41.14	14	6.00	1.40	39.74	42.87
4/29-migrant	47.70	10	17.77	3.01	44.69	50.71
5/25-residual	46.04	45	64.09	2.40	43.64	48.44
6/18-migrant	47.42	184	29.89	2.51	44.91	49.93
6/18-residual	48.80	142	48.12	1.13	47.67	49.93
7/9-migrant	46.08	39	14.82	1.27	44.81	47.35
7/8-residual	48.25	40	35.72	1.92	46.33	50.17
7/16-residual	51.78	217	78.81	1.18	50.60	52.96
8/8-migrant	53.00	10	56.67	5.38	47.62	58.38
9/8-residual	56.00	10	34.67	4.21	51.79	60.21
9/8-migrant	50.00	46	22.20	1.39	48.61	51.39
10/1-migrant	57.10	23	30.20	2.36	54.74	59.46
10/1-residual	62.10	156	86.23	1.47	60.63	63.57
10/23-migrant	60.69	29	26.46	1.97	58.72	62.66
10/24-migrant	61.46	35	35.09	2.04	59.42	63.50
10/26-migrant	62.44	16	50.67	3.79	58.65	66.23
11/3-residual	66.11	130	100.22	1.74	64.37	67.85
11/18-residual	66.50	119	95.25	1.76	64.74	68.26
11/24-migrant	66.13	23	86.86	4.02	62.11	70.15
12/2-residual	65.08	157	97.50	1.56	63.52	66.64

(continued)

Appendix 10 continued.

Date-Type	Mean length mm	Sample size	Variance	Half of 95% confidence zone	Limits	
					L	U
1/22-migrant	68.00	13	33.17	3.49	64.51	71.49
1/31-migrant	68.38	29	61.28	2.97	65.41	71.05
2/9-migrant	71.14	36	110.34	3.57	67.57	74.71
2/15-migrant	72.62	39	62.18	2.57	70.05	75.19
2/21-migrant	76.02	65	37.30	1.50	74.52	77.52
2/21-residual	72.47	126	148.12	2.14	70.33	74.61
2/24-migrant	71.02	47	24.41	1.46	69.56	72.48
2/26-migrant	73.37	27	40.46	2.50	70.87	75.87
3/13-migrant	75.72	127	58.46	1.32	74.40	74.04
3/26-migrant	84.47	79	172.12	2.94	81.53	87.41
3/28-residual	80.84	44	144.67	3.66	77.18	84.50
4/1-migrant	88.90	69	70.53	2.02	86.88	90.92
4/8-residual	79.35	31	104.37	3.73	75.62	83.08
4/15-migrant	86.82	51	135.00	3.48	83.34	90.30
5/1-migrant	92.26	61	97.80	2.52	89.74	94.78
5/4-residual	76.69	16	98.63	5.28	71.41	81.97
5/30-residual	81.78	9	47.75	5.30	76.48	87.08

Appendix 11. Confidence limits for mean lengths of coho, 1959 year class, Flynn Creek, June, 1959-June, 1960.

Date-Type	Mean length mm	Sample size	Vari-ance	Half of 95% confidence zone	Limits	
					L	U
6/5-residual	47.14	42	52.44	2.26	44.88	49.40
6/18-residual	50.61	125	54.23	1.31	49.30	51.92
7/1-residual	52.05	55	55.83	2.02	50.03	54.07
7/22-residual	51.50	10	52.67	5.18	46.32	56.68
8/15-residual	57.21	96	110.46	2.14	55.07	59.35
9/22-residual	57.10	10	67.89	5.88	51.22	62.98
10/6-residual	60.09	88	102.77	2.06	58.03	62.15
12/1-residual	66.66	10	114.67	7.67	58.99	74.33
2/1-residual	70.63	8	30.29	4.61	66.02	75.24
2/1-migrant	70.69	13	49.75	4.27	66.42	74.96
2/5-migrant	70.72	18	61.29	3.90	66.82	74.62
3/7-migrant	78.80	54	63.74	2.18	76.62	80.98
3/28-residual	77.00	8	76.29	7.31	69.69	84.31
4/1-migrant	85.60	50	57.51	2.16	83.44	87.76
4/11-residual	81.28	7	133.50	10.68	70.60	91.96
4/15-migrant	86.57	35	30.79	1.92	84.65	88.49
5/1-migrant	90.80	37	56.44	2.51	88.29	93.31
5/12-migrant	91.86	7	91.86	2.74	89.12	94.60
5/18-migrant	95.00	6	95.00	11.39	83.61	106.39

Appendix 12. Confidence limits for mean lengths of coho, 1959 year class, Needle Branch, May, 1959-June, 1960.

Date-Type	Mean length mm	Sample size	Vari-ance	Half of 95% confidence zone	Limits	
					L	U
5/20-residual	43.93	14	8.38	1.66	42.27	45.59
5/27-residual	45.31	29	6.64	.98	44.33	46.29
5/27-residual	45.00	9	5.55	1.78	43.22	46.78
6/17-residual	51.21	105	23.68	.92	50.29	52.13
7/1-residual	51.61	64	35.00	1.48	50.13	53.09
7/22-residual	51.70	10	47.56	4.93	46.77	56.63
8/5-residual	56.59	83	45.98	1.42	55.17	58.01
9/1-residual	54.70	10	40.22	4.52	50.18	59.22
10/5-residual	65.14	65	86.50	2.30	62.84	67.44
10/15-residual	70.40	14	54.38	4.26	66.14	74.66
3/18-trap	88.12	8	173.28	10.83	77.29	98.95
3/30-trap	90.78	37	73.36	4.04	86.74	94.82
4/28-trap	96.74	19	45.33	5.02	91.72	101.76
5/7-trap	102.56	18	69.06	8.10	94.46	110.66

Appendix 13. Yield of coho in weight and numbers, 1959 year class, Deer Creek.

Period	Weight (gm.)	Number	Fate
2/23/59 to 6/1/60	24,645	6,435	Trap catch
	335	100	Screen rideover
	470	940	Predation in trap
	260	97	Escape around trap
	241	520	Killed for stomach samples
	146	65	Trap kill
	26,097	8,157	Grand total yield
	-1,525	-127	Less 1958 year class migrants
	24,572	8,030	Corrected grand total yield, 1959 year class

- -

11/7/59 to 6/1/60	20,994	3,013	Trap catch
	335	100	Screen rideover
	92	14	Trap kill
	163	42	Killed for stomach samples
	21,584	3,169	Grand total effective yield
	-1,525	-127	Less 1958 year class migrants
	20,059	3,042	Corrected grand total effective yield, 1959 year class

- -

Yield per unit area

67[1] effective smolts per 100 square meters.
64[2] effective smolts per 100 square meters.

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[1] Includes 1958 year class residuals.

[2] Excludes 1958 year class residuals.

Appendix 14. Yield of coho in weight and numbers, 1959 year class, Flynn Creek.

Period	Weight (gm.)	Number	Fate
11/7/59	8,306	1,243	Trap catch
to	120	26	Killed for stomach samples
6/1/60	83	12	Trap kill
	8,491	1,281	Grand total effective yield
	-1,300	-124	Less 1958 year class migrants
	7,191	1,157	Corrected grand total effective yield

Yield per unit area

52[1] effective smolts per 100 square meters.
48[2] effective smolts per 100 square meters.

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[1] Includes 1958 year class residuals.

[2] Excludes 1958 year class residuals.

Appendix 15. Effective yield of coho in weight and numbers, 1959 year class, Needle Branch.

Period	Weight (gm.)	Number	Fate
11/7/59	1,835	186	Trap catch
to	45	12	Killed for stomach samples
6/1/60	12	2	Trap kill
	1,892	200	Grand total effective yield
	-126	-7	Less 1958 year class migrants
	1,766	193	Corrected grand total effective yield

Yield per unit area

22[1] effective smolts per 100 square meters.
21[2] effective smolts per 100 square meters.

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[1] Includes 1958 year class residuals.

[2] Excludes 1958 year class residuals.

Appendix 16. Coho mortality and survival, 1958 year class, Deer Creek, calculated from estimated population size at emergence and at first crop estimate on May 25, 1959.

Calculated emergence,[1] 3/15/59	42,500 coho
Residual stock, 6/1/60	-200
	42,300
Total corrected yield 2/23/59-6/1/60	-8,030
Mortality	34,270
Per cent mortality, emergence to 6/1/60 . . .	81%

Calculated stock, 5/25/59	24,595
Escape past trap	520
Trap predation	940
Trap catch	1,356
	27,411
Per cent survival from emergence	65%

Calculated stock, 7/17/59	11,097
Escape past trap	520
Trap kill	51
Trap predation	940
Killed for stomach samples	29
Trap catch	3,192
	15,829
Per cent survival from emergence	37%
Per cent survival from 5/25/59	65%

Calculated stock, 10/1/59	5,896
Escape past trap	520
Trap kill	51
Trap predation	940
Killed for stomach samples	55
Trap catch	3,310
	10,772
Per cent survival from emergence	25%
Per cent survival from 5/25/59	44%

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[1] Based on potential deposition, multiplied by .65

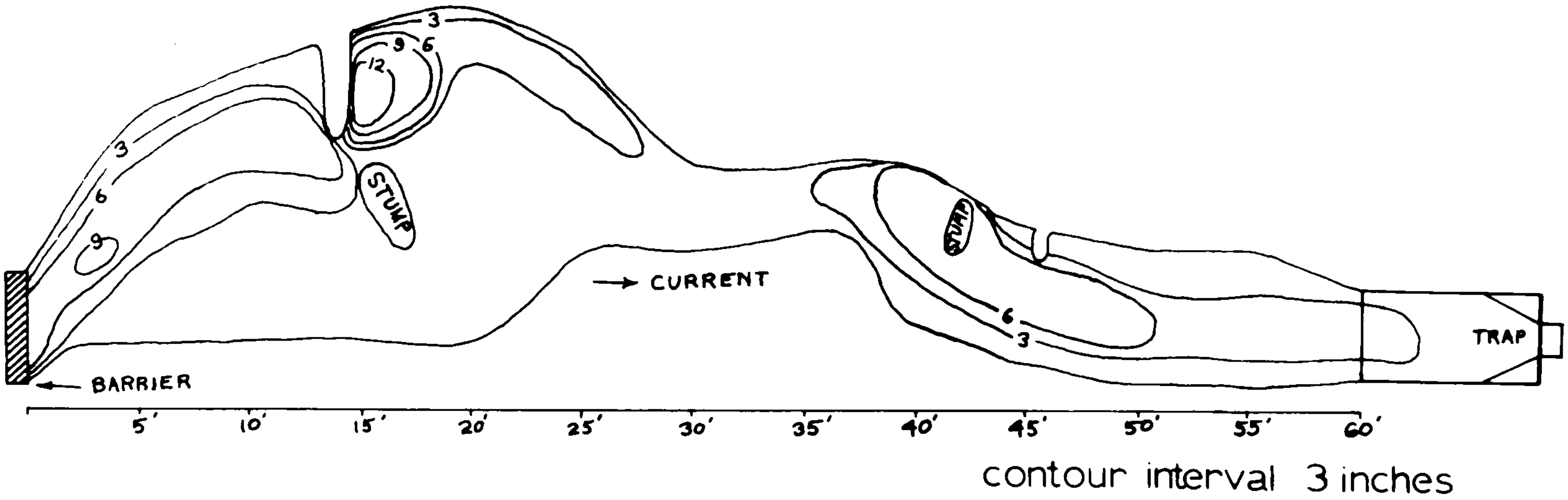
Appendix 16 continued.

Calculated stock, 2/21/60	5,100 coho
Escape past trap	520
Screen rideover	100
Trap kill	54
Trap predation	940
Killed for stomach samples	80
Trap catch	3,617
	10,411
Per cent survival from emergence	25%
Per cent survival from 5/25/59	42%

Calculated stock, 4/1/60	1,494
Escape past trap	520
Screen rideover	100
Trap kill	58
Trap predation	940
Killed for stomach samples	90
Trap catch	5,513
	8,715
Per cent survival from emergence	21%
Per cent survival from 5/25/59	35%

Calculated stock, 5/4/60	351
Escape past trap	520
Screen rideover	100
Trap kill	65
Trap predation	940
Killed for stomach samples	92
Trap catch	6,242
	8,310
Per cent survival from emergence	19%
Per cent survival from 5/25/59	33%

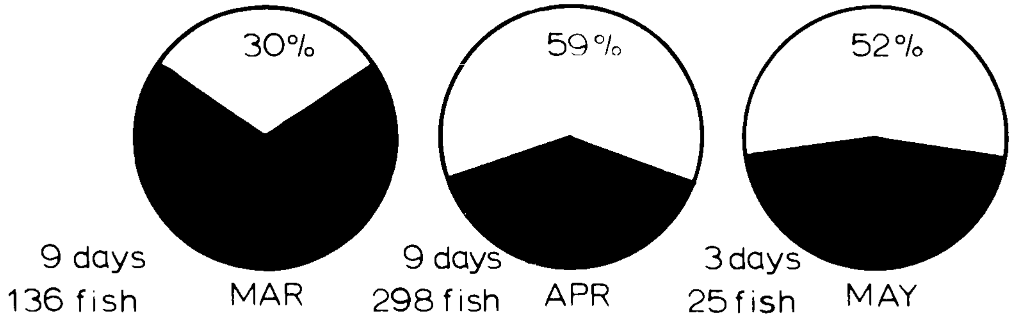
SKETCH OF CONTROLLED SECTION ON DEER CREEK



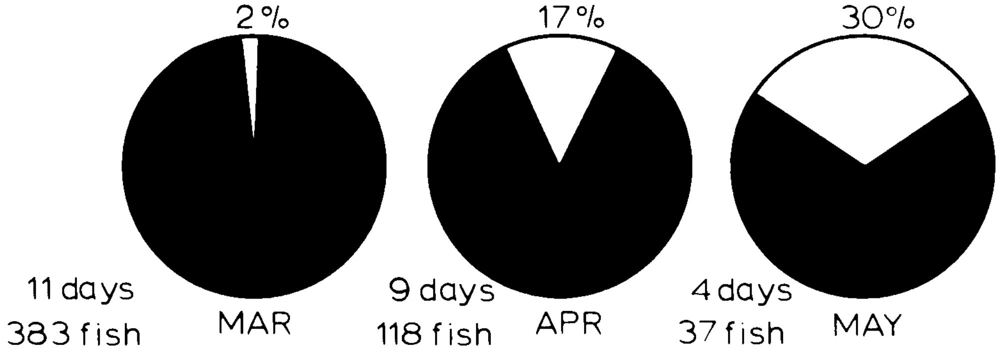
Appendix 17

DAYLIGHT - DARK MOVEMENT
DEER CREEK-1959

COHO SMOLTS
1958 YEAR CLASS



COHO FRY
1959 YEAR CLASS



Appendix 18

APPENDIX 19. Summary data of food items, based on dry weights, found in fish stomachs and arranged by habitat origin, Deer Creek, May 25, 1959 to April 22, 1960.

Food items	Aquatic items				Aquatic aerial items				Terrestrial items				Items of uncertain habitats				Total		
	Wt. in mg.	% of total wt.	% wt. of aquatic items	% wt. of food group	Wt. in mg.	% of total wt.	% wt. of aerial items	% wt. of food group	Wt. in mg.	% of total wt.	% wt. of terrestrial items	% wt. of food group	Wt. in mg.	% of total wt.	% wt. of items of uncertain habitats	% wt. of food group	Wt. in mg.	% of total wt.	% wt. of food group
ANNELIDA	0.68	7.1	12.6	100.0															
TOTALS	0.68	7.1	12.6	100.0													0.68	7.1	100.0
ISOPODA									0.03	0.3	0.9	100.0							
TOTALS									0.03	0.3	0.9	100.0					0.03	0.3	100.0
GAMMARIDAE	0.06	0.6	1.1	100.0															
TOTALS	0.06	0.6	1.1	100.0													0.06	0.6	100.0
CHILOPODA									0.02	0.2	0.6	100.0							
TOTALS									0.02	0.2	0.6	100.0					0.02	0.2	100.0
DIPLOPODA									0.26	2.7	7.9	100.0							
TOTALS									0.26	2.7	7.9	100.0					0.26	2.7	100.0
COLLEMBOLA									0.34	3.5	10.4	100.0							
TOTALS									0.34	3.5	10.4	100.0					0.34	3.5	100.0
EPHEMEROPTERA																			
Heptageniidae	0.22	2.3	4.1	16.4															
Epeorus nymphs	0.05	0.5	1.0	3.7															
Baetidae	0.33	3.4	6.1	24.6															
Baetis nymphs	0.13	1.4	2.4	9.7															
Paraleptophlebia nymphs	0.27	2.8	5.0	20.1															
Ephemerella nymphs	0.06	0.6	1.1	4.5															
Misc. Ephemeroptera	0.28	2.9	5.2	20.9															
TOTALS	1.34	14.0	24.9	99.9													1.34	14.0	99.9
PLECOPTERA	0.31	3.2	5.7	81.6	0.07	0.8	12.5	18.4											
TOTALS	0.31	3.2	5.7	81.6	0.07	0.8	12.5	18.4									0.38	4.0	100.0
HOMOPTERA and HEMIPTERA																			
Aphididae									0.08	0.8	2.4	72.7							
Corixidae	0.02	0.2	0.4	18.2															
Misc. Homoptera and Hemiptera													0.01	0.1	2.7	9.1			
TOTALS	0.02	0.2	0.4	18.2					0.08	0.8	2.4	72.7	0.01	0.1	2.7	9.1	0.11	1.1	100.0
TRICHOPTERA																			
Psychomyiidae	0.04	0.4	0.7	5.3	0.21	2.2	37.5	27.6											
Limnephilidae	0.11	1.1	2.1	14.5															
Misc. Trichoptera	0.40	4.2	7.4	52.6															
TOTALS	0.55	5.7	10.2	72.4	0.21	2.2	37.5	27.6									0.76	7.9	100.0
LEPIDOPTERA									0.05	0.5	1.5	100.0							
TOTALS									0.05	0.5	1.5	100.0					0.05	0.5	100.0
HYMENOPTERA													0.04	0.4	10.8	100.0			
TOTALS													0.04	0.4	10.8	100.0	0.04	0.4	100.0
COLEOPTERA																			
Dytiscidae	0.02	0.2	0.4	2.2															
Staphylinidae									0.20	2.1	6.1	22.7							
Elmidae	0.06	0.6	1.1	6.9															
Chrysomelidae									0.55	5.7	16.8	62.5							
Heteroceridae									0.04	0.4	7.1	4.5							
Misc. Coleoptera													0.01	0.1	2.7	1.1			
TOTALS	0.08	0.8	1.5	9.1					0.75	7.8	22.9	85.2	0.01	0.1	2.7	1.1	0.88	9.2	99.9
DIPTERA																			
Tipulidae	0.02	0.2	0.4	0.5															
Culicidae					0.03	0.3	5.4	0.7											
Dixidae	0.16	1.7	3.0	3.9															
Simuliidae	0.28	2.9	5.2	6.8															
Tendipedidae	1.47	15.3	27.2	35.7	0.10	1.0	17.8	2.4											
Heleidae	0.01	0.1	0.2	0.2															
Bezzia larvae	0.02	0.2	0.4	0.5															
Tabanidae					0.08	0.8	14.3	1.9											
Dolichopodidae	0.02	0.2	0.4	0.5															
Empididae					0.03	0.3	5.4	0.7											
Misc. Diptera	0.34	3.5	6.2	8.2					1.25	13.0	38.1	30.3	0.31	3.2	83.8	7.5			
TOTALS	2.32	24.2	43.0	56.3	0.24	2.5	42.9	5.8	1.25	13.0	38.1	30.3	0.31	3.2	83.8	7.5	4.12	42.9	99.9
ARACHNIDA									0.50	5.2	15.2	100.0							
TOTALS									0.50	5.2	15.2	100.0					0.50	5.2	100.0
GASTROPODA	0.02	0.2	0.4	100.0															
TOTALS	0.02	0.2	0.4	100.0													0.02	0.2	100.0
FISH EGGS	0.01	0.1	0.2	100.0															
TOTALS	0.01	0.1	0.2	100.0													0.01	0.1	100.0
CATEGORY TOTALS	5.39	56.1	100.0	—	0.56	5.8	100.0	—	3.28	34.2	99.9	—	0.37	3.9	100.0	—	9.60	100.0	—
TOTAL WEIGHT																	9.60	—	—