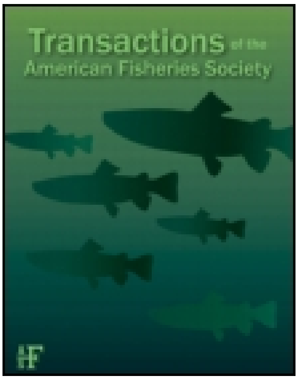

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Net Production of Juvenile Coho Salmon in Three Oregon Streams

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Net Production of Juvenile Coho Salmon in Three Oregon Streams

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ABSTRACT

Net production of juvenile coho salmon was estimated in three small streams in Oregon for 4 consecutive years. Annual net production of coho was greatly different in the 4 years, but production per unit area was similar among streams, averaging about 9 g/m² per year. No significant differences were found among streams in production per unit area for 14 months from emergence of fry one spring through seaward migration the next spring. For 4 years biomass averaged 5–12 g/m² shortly after emergence of fry, declining to 2–3 g/m² by July and remaining at about 2–4 g/m² until emigration of smolts in the following spring. In all years, mean production declined from 1.9–2.8 g/m² per month after emergence to 0.2–0.3 g/m² per month in winter, then increased to 0.5–0.6 g/m² per month prior to emigration. Monthly instantaneous growth rates were highest shortly after emergence of fry, declining until late winter, then increasing just before smolt emigration. The mean monthly instantaneous growth rate was about 0.19 for all streams and years. Yield of smolts as seaward emigrants ranged from 18 to 67 per 100 m². Net production was 1.5 to 3.0 times greater than yield as biomass of smolts. Net production of all fish in one stream containing coho, steelhead and cutthroat trout, and cottids was estimated to be 16 g/m² per year and compared with data from other waters. Relatively large freshets appeared to cause large downstream movements of juvenile coho. Downstream drift of postemergence fry and emigration of yearlings tended to bias estimates of growth and net production in the residual populations.

INTRODUCTION

This paper reports estimates of net production of juvenile coho salmon (*Oncorhynchus kisutch*) in three small streams. The investigation was undertaken to provide understanding of the relationships among biomass, growth, net production, and yield of coho, and was part of a larger study of the effects of logging on stream limnology.

The study was conducted from early 1959 through June 1963, in Deer Creek, Flynn Creek, and Needle Branch, which drain into Drift Creek, a tributary of Alsea Bay near Waldport, Oregon. The streams are less than 2.5 miles apart and have similar physical and biotic characteristics. The stream biota are described in detail by Chapman and Demory (1963). There is considerable seasonal fluctuation in streamflow but little seasonal variation in temperature (Figure 1). Annual rainfall in the study area is usually near 100 inches. The drainage areas are as follows: Deer Creek, 815 acres; Flynn Creek, 550 acres; and Needle Branch, 230 acres.

Levels of total dissolved solids, total phosphates, and nitrates are shown in Figures 2 and 3 for the period from January 1962 through February 1963. Most values of total dissolved solids in all three streams lay between 25 and 55 parts per million, with values for Needle Branch usually lowest. Most phosphate levels were between 0.010 and 0.035 ppm with levels lowest in Needle Branch. Nitrate content of water in Deer and Flynn Creeks fluctuated seasonally, with a minimum of about 0.40 ppm in midsummer and a high of about 1.70 ppm in midwinter. Nitrate in Needle Branch never exceeded 0.20 ppm. Mean water conductivity in micromhos per centimeter at 25° C for four dates was 46, 44, and 35 for Deer Creek, Flynn Creek, and Needle Branch, respectively (Table 1).

The salmonid species present in the streams, in order of abundance, are coho salmon, coastal cutthroat (*Salmo clarki clarki*), and rainbow trout (*S. gairdneri*) or steelhead. Other fishes include the Pacific lamprey (*Lampetra tridentata*), brook lamprey (*L. planeri*), and a cottid (*Cottus perplexus*). Rainbow trout occur in Flynn Creek and Needle Branch as occasional juveniles only, but both adults and juveniles utilize Deer Creek.

Coho in the study streams spawn in the period from November through February, most fry emerge from redds during the period 1 March to 15 May, and a large downstream movement of postemergence coho occurs in the period, through June. Seaward movement

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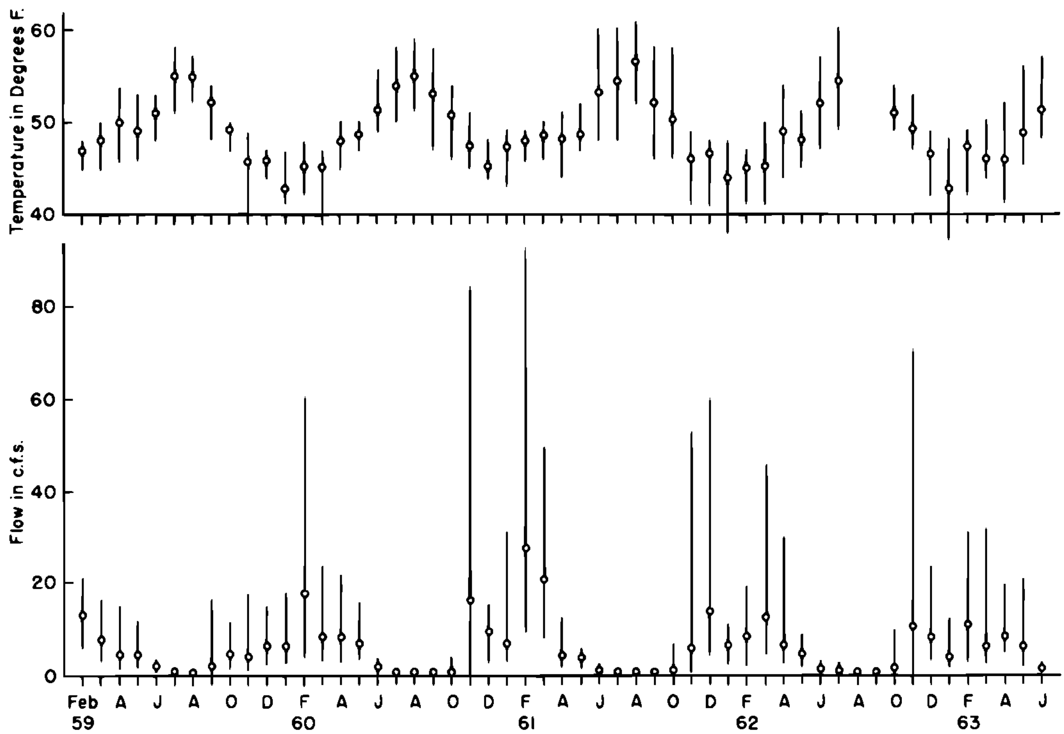

FIGURE 1.—Streamflow (ft³/sec) and temperature (°F) in Deer Creek.

of smolts occurs from early February through May of the year following emergence. A very small part of each year class has remained in the streams for two winters before moving seaward.

METHODS

The first two important papers concerning net production in fish populations were those of Ricker and Foerster (1948) and Allen (1951). Data necessary for computation of production are: Standing crop present at sometime during the year, rates of growth at successive short periods during the year, and rates of mortality in these same periods. Ricker and Foerster used these data to compute sockeye (*O. nerka*) production in Cultus Lake, British Columbia by 2-week intervals.

Allen points out that the method of computing production used by Ricker and Foerster is somewhat laborious, requiring calculation of many instantaneous growth and mortality rates, and that the same result can be obtained by graphic means. Allen determined production graphically for the brown trout (*S. trutta*) of Horokiwi Stream, and Neess and Dugdale (1959) used a similar method for estimating production of aquatic insect larvae. The graphic method entails plotting standing crop in numbers on an ordinate, and mean individual weight of animals on the abscissa. A planimeter may then be used to determine areas under the resulting production curve for particular time intervals. I used the graphic method of calculating production because it is simple, convenient, and requires no artificial division of data into short intervals. The data necessary for graphic estimation of production are: (1) standing crops in numbers at several times during the period of interest, and (2) growth in weight of animals during the same period.

Estimates of the size of coho populations were made by the Petersen single census method (Ricker, 1958). Fish were marked by different fin mutilations at several times during their stream life from shortly after emergence from the gravel as fry to seaward mi-

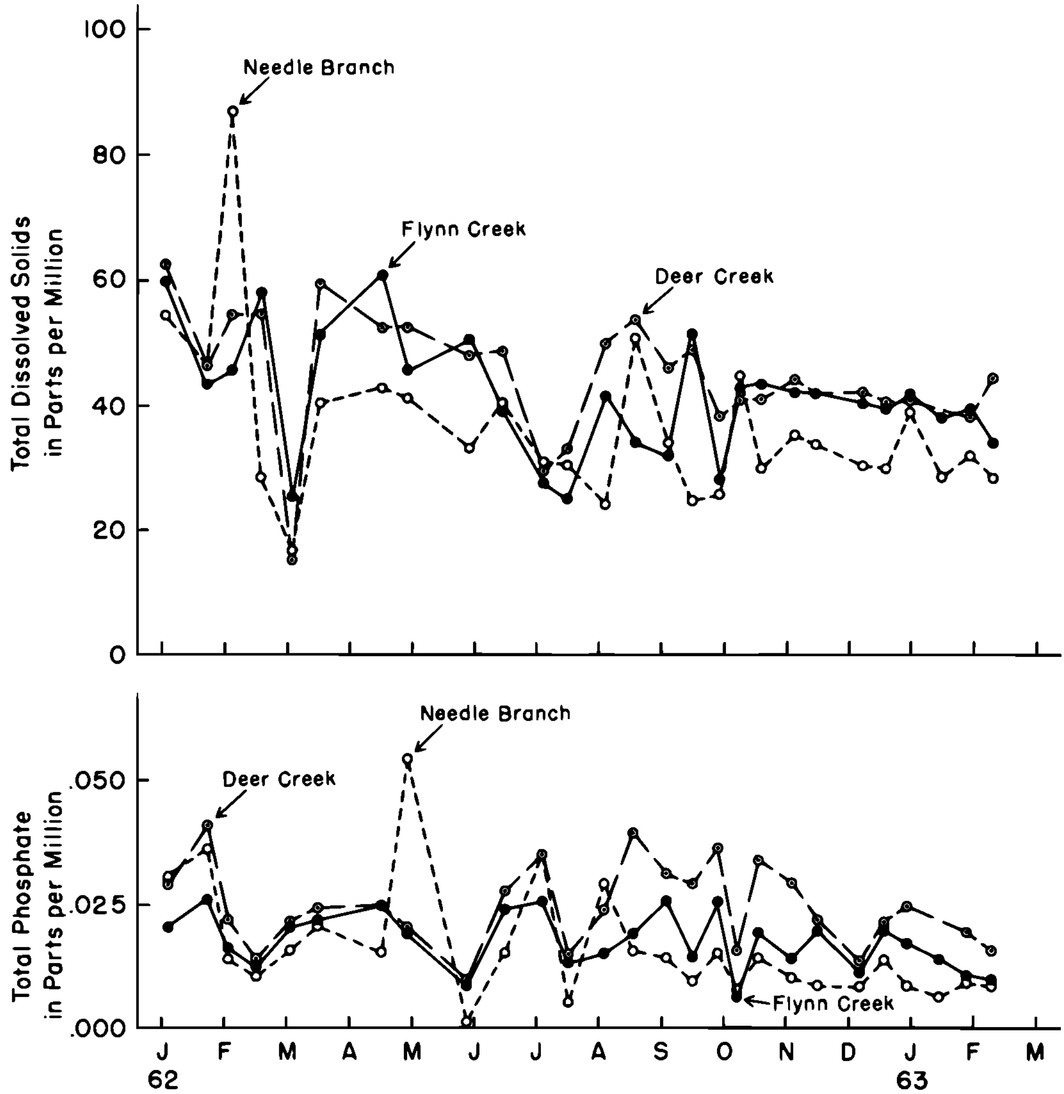

FIGURE 2.—Content of total dissolved solids and total phosphate as PO_4 (ppm) in water of Deer Creek, Flynn Creek, and Needle Branch.

gration as smolts in the following spring. Ratios of marked-to-unmarked coho were determined as the population left the streams in the seaward migration. Upstream and downstream traps (Figure 4) provided a means of capturing most of the smolts migrating downstream and all juveniles moving upstream. Movement upstream of young coho and trout was negligible. All fish passing through traps were passed over in the appropriate direction.

I usually captured fish for fin marking with a small seine hung on a metal frame, but used a direct-current portable electro sampler for a few samples. Studies of fin marking, such as that of Wales and German (1956), indicate that single ventral fin marks would be least likely to affect fish growth. Fins mutilated for population estimates, beginning with the mark used first after fry emergence, were left ventral, right ventral, both ventrals, ventral–adipose fin combinations, and half-dorsal–adipose. Notches of the caudal fin were used for the final mark prior to seaward movement.

TABLE 1.—*Water conductivity in micromhos per cm at 25° C in three study streams*

Date	Deer Creek	Flynn Creek	Needle Branch
21 April 1960	45	48	36
14 June 1960	35	33	26
17 November 1961	62	54	43
30 January 1962	42	42	34
Mean	46	44	35

There was no difference in growth of marked and unmarked smolts moving through downstream traps. Observation of marked animals up to 3 weeks in glass-walled channels or live-boxes indicated no ill effects due to marking. If mortality from marking occurred, it probably was due to decreased ability to escape from predators.

Standard errors of population estimates were calculated using the methods of Cochran (1953). When some smolts were not examined for marks, e.g., when some bypassed downstream traps during high water periods, standard errors were obtained using the Poisson distribution (Ricker, 1937).

I established rates of coho growth in length by periodically sampling each stream. Confidence limits for mean lengths were calculated for all samples by standard statistical methods. Length was converted to weight by use of a regression based on lengths and

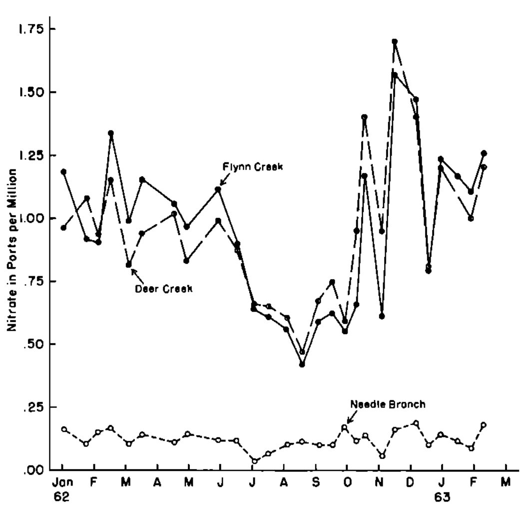

FIGURE 3.—Content of nitrate as NO_3 (ppm) in water of Deer Creek, Flynn Creek, and Needle Branch.

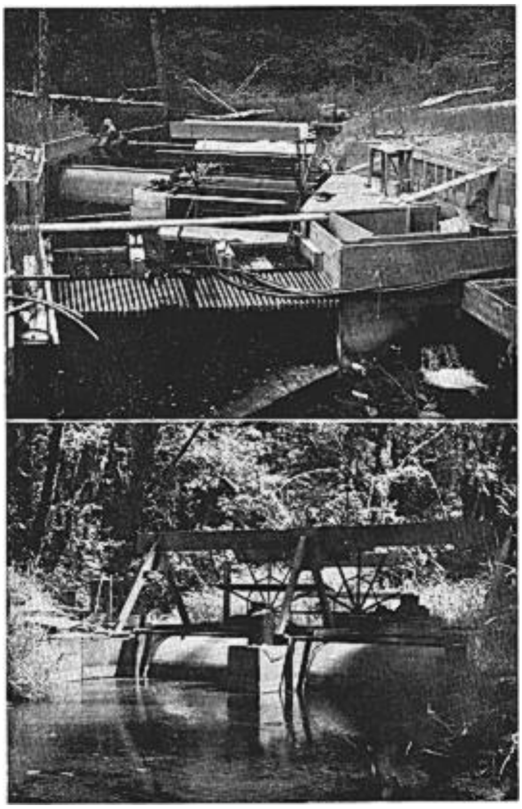

FIGURE 4.—Trap used to capture fish moving up- or downstream in Deer Creek.

weights of 161 juvenile coho from Deer Creek:

$$\log W = -2.15313 + 3.10027 \log L,$$
where W = weight in milligrams
L = length in millimeters.

One disadvantage of this conversion method is possible seasonal change in length–weight relationships as observed in a brook trout (*Salvelinus fontinalis*) population studied by McFadden (1961).

An effort was made to capture coho for marking and measurement from a wide variety of areas in the streams. All fish sampled were released at the point of capture. Marked fish recaptured in subsequent marking periods were released with mark unchanged. Coho spending two winters in the streams were eliminated from growth rate and population estimates by use of scale analysis and length frequencies.

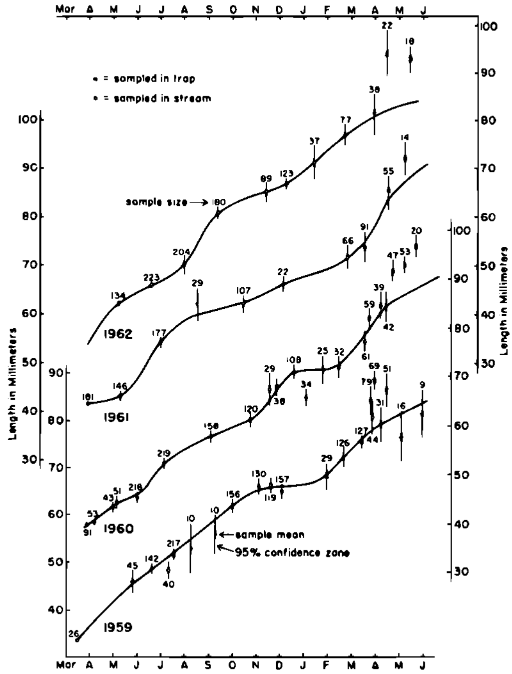

FIGURE 5.—Growth of coho in Deer Creek, four year classes.

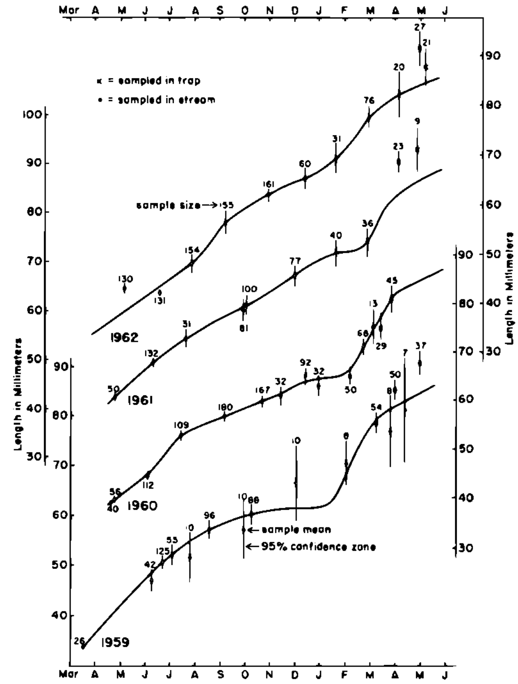

FIGURE 6.—Growth of coho in Flynn Creek, four year classes.

Curves for both survivorship and growth were placed by inspection, taking sample sizes and confidence limits into account. No confidence limits can be set for production estimates, largely because no statistical technique is available for computing standard errors.

The number of yearling coho moving through downstream traps is reported as yield. In some periods for up to 36 hours the downstream trap diversion screens in Deer Creek were inoperative because of high water. At these times the stream flowed completely over the screens and large movements of fish downstream could have occurred undetected. Such movement should not bias population estimates, since marked and unmarked fish can be expected to behave similarly.

Adult coho migrating upstream were trapped, counted, sexed, and measured to the nearest one-quarter inch. I estimated egg potential from the data of Shapovalov and Taft (1954).

Estimated total stream areas (measured at low water in August 1959) and pool areas (estimated at the same time) between fish traps and uppermost limits of stream accessible to coho are shown in Table 2.

TABLE 2.—*Stream and pool areas in square meters accessible to coho. Measured or estimated in August 1959*

Stream	Area	Year			
		1959	1960	1961	1962
Deer	Total area	4,753	4,753	4,720[1]	4,720
	Pool area	2,875	2,875	2,793[1]	2,793
Flynn	Total area	2,459	2,760[1]	2,657[1]	2,657
	Pool area	1,273	1,633[1]	1,563[1]	1,563
Needle Br.	Total area	926	1,114[1]	1,060[1]	1,060
	Pool area	561	747[1]	684[1]	684

[1] Correction from previous year to reflect changes in fish trap and stream gage pools due to construction or deposition of silt.

RESULTS

Data on growth, population size, and net production have been obtained for four year classes, 1959–62, and yields of smolts were determined for year classes 1958–62. Point estimates for mean length of coho at each sampling time, 95 per cent confidence limits, and sample sizes are shown in Figures 5, 6, and 7. Coho moving through downstream traps have

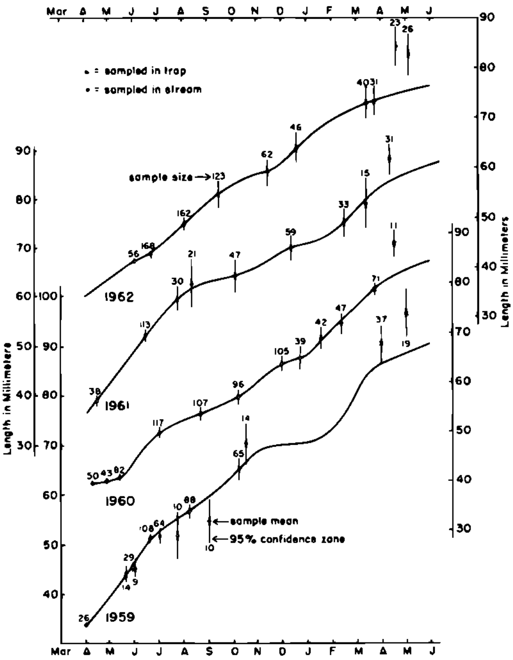

FIGURE 7.—Growth of coho in Needle Branch, four year classes.

been separated on the charts from coho sampled in the streams above the traps. A growth curve was placed through the series of points for mean lengths of coho remaining in the study stream. This procedure has obvious disadvantages (discussed later) which must be accepted if net production is to be estimated.

Figures 8 to 10 show data on standing crop in numbers. The graphs show point estimates for population size, 95 per cent confidence limits, and have on them a curve fitted by inspection. The first point on each curve, population size at time of emergence, is speculative. Briggs (1953), sampling stream gravels, gives 74 per cent as mean survival to emergence of coho embryos already deposited. Coble (1960) and Shapovalov and Taft (1954) estimate by experimentation that coho survivals from deposition to emergence of 62 and 65 per cent, respectively, occur in good environmental conditions. Assuming that coho normally use suitable gravel, and that experimental handling may have somewhat depressed survivals in the studies reported by the latter two papers, I multiplied potential egg deposition by 0.65 to obtain survival to emergence.

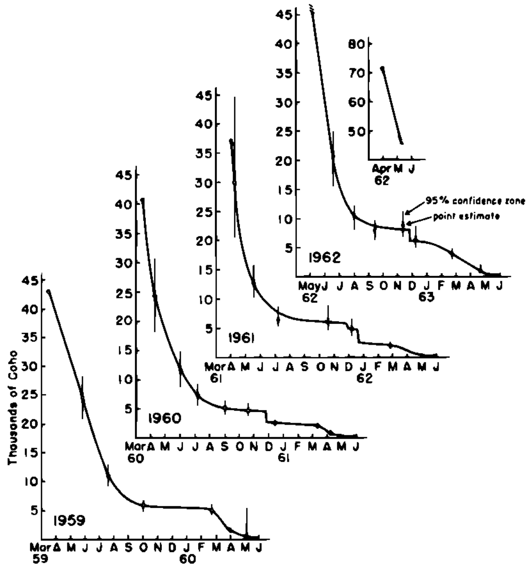

FIGURE 8.—Coho population size in Deer Creek, four year classes.

A rough check may be made on this speculation by prolongation backward of the survivorship curve from the first three population estimates to the mean emergence time.

Figures 8 to 10 indicate a sharp drop in coho population size following relatively large freshets in the winters of 1960–61 and 1961–62. These sharp declines were set in the survivorship curves on the basis of population estimates before and after the freshets and the fact that movements downstream of coho increased sharply just before the traps became inoperable in high water. In Table 3 I have listed, for each stream and year, the

TABLE 3.—*Streamflow data in ft³/sec by water year (1 October to 30 September)*

Stream	Year	Mean flow	Max. flow[1]	Peak flow[2]	Max. flow / peak flow	Date of maximum and peak flow
Deer Cr.	1960	5.83	61	65	0.94	9 Feb. 1960
	1961	7.73	94	113	0.83	24 Nov. 1960 (105 ft³/sec, 10 Feb. 1961)
	1962	5.54	60	79	0.76	22 Nov. 1961
	1963	5.58	72	105	0.69	25 Nov. 1962
Flynn Cr.	1960	4.14	39	43.6	0.89	Dates
	1961	5.36	59	73	0.81	same
	1962	3.82	39	47	0.83	as
	1963	3.97	48	70	0.69	for
Needle Br.	1960	1.38	18	20	0.90	Deer
	1961	1.70	24	33	0.74	Creek
	1962	1.23	18	30	0.60	
	1963	1.25	18	28	0.63	

[1] Maximum average flow for 24-hour day.
[2] Instantaneous peak flow.

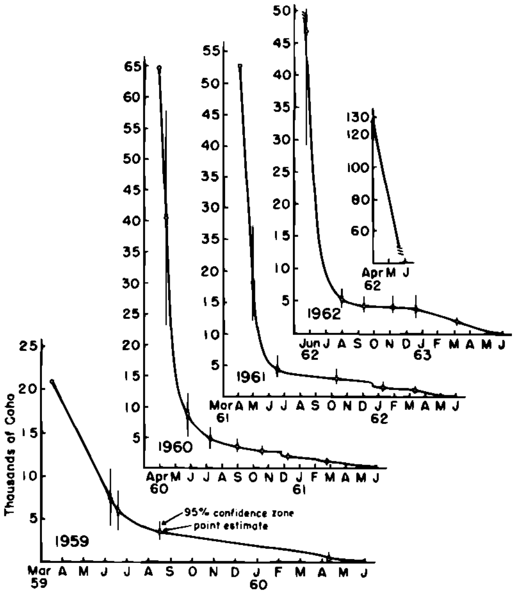

FIGURE 9.—Coho population size in Flynn Creek, four year classes.

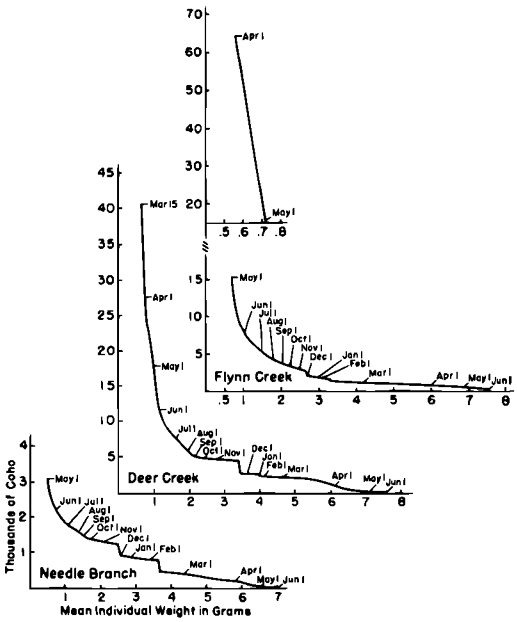

FIGURE 11.—Coho production curves for three streams, 1960 year class.

mean annual stream flow, maximal discharge for 24 hours, and daily instantaneous peak discharge in ft^3/sec. Ratios of maximal daily discharge to instantaneous peak discharge are also shown. The ratio was higher in 1960 than in all other years; 10.5 per cent higher in Deer Creek, 8.7 per cent in Flynn Creek, and 16.6 per cent in Needle Branch. A high ratio indicates a sudden rise and fall in the peak discharge. In 1960 there was no indication in survivorship data of emigration in periods of freshet condition. The data suggest that variable flows may stimulate or cause emigration, voluntary or not.

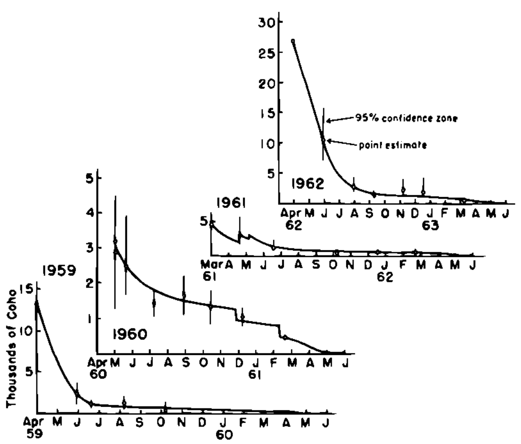

FIGURE 10.—Coho population size in Needle Branch, four year classes.

Figure 11 shows examples of production curves, and Table 5 and Figure 12 indicate the results of converting areas under the production curve to monthly net production. The length of the production year is from mean emergence of fry (15 March–1 April) to 1 June of the next year. Data in Table 4 are annual net production in kg, production per unit of total stream surface (area at low flow in August), and per unit of pool surface in g/m^2. I have also shown production for the period 1 June to 1 June to permit eliminating the somewhat speculative period from emergence to the first population estimate.

Annual net production for coho in the three streams was greatly different in given years, but coho production per unit area in the different streams was remarkably similar. The similarity is even more striking if data for the periods from 1 June to 1 June are compared. No significant differences ($P = 0.01$) were found among streams in production per

TABLE 4.—*Net production of the 1959, 1960, 1961, and 1962 year classes of coho in Deer and Flynn Creeks and Needle Branch*

Observation	Period	Deer Creek				Flynn Creek				Needle Branch			
		1959	1960	1961	1962	1959	1960	1961	1962	1959	1960	1961	1962
Total production (kg)	15 March–1 June	49	34	26	60	22	21	16	43	7	5	5	12
	1 June–1 June	29	20	20	35	9	12	11	20	4	4	3	6
Per unit stream area, g/m^2	15 March–1 June	10	7	5	13	9	8	6	16	8	5	5	11
	1 June–1 June	6	4	4	7	4	4	4	8	4	4	3	6
Per unit pool area, g/m^2	15 March–1 June	17	12	9	21	17	13	10	27	16	7	7	18
	1 June–1 June	10	7	7	13	7	7	7	13	7	5	4	9

unit area. But data on production per unit area must be qualified since estimates of area were based primarily on measurements made in 1959. Flows in August were less in 1960 and 1961 than in 1959 and 1962, so in the former 2 years production per unit area actually was higher than I have shown. This would tend to smooth annual estimates.

Successive year classes show fairly discrete periods of net production (Table 5). Production declined steadily from 1.9–2.8 g/m^2 in April, shortly after emergence, to about 0.2–0.3 g/m^2 per month in December and January. In February, just prior to emigration of smolts, net production increased to 0.5–0.6 g/m^2 per month (Figure 12). As in the case of the 1959 year class in Deer Creek (Table 5), production in the period of 1 April to 31 March would separate virtually completely the preceding and succeeding year classes, and for practical purposes would be equal to production of a year class from emergence through May of the next year. For all streams and year classes, production of a year class outside the period 1 April to 31 March averaged 6 per cent of production from emergence one year through May the next year.

Production of residual coho is relatively small. For example, residuals of the 1958 year class in Deer Creek produced only about 1 kg while the 1959 year class was producing 49 kg.

In Table 5 are shown estimates of biomass for the start of each month for four year classes of coho, and plotted in Figure 13 is monthly biomass, averaged over four year classes of coho for each stream. Biomass was relatively high, 5–12 g/m^2 shortly after emergence of fry, but declined to 2–3 g/m^2 by July, and remained relatively constant at 2–4 g/m^2 until the smolt migration in the following spring when it declined sharply during emigration.

Since I estimated net production graphically, instantaneous growth rates were not calculated as components of production, so I computed them from growth data and tabulated monthly instantaneous growth rates in Table 5. Plotted in Figure 14 are monthly instantaneous growth rates averaged over four year classes for each stream. The highest rates occurred in the first 2 months after the fry emerged. Instantaneous growth rates then declined until late winter, when they increased sharply. These seasonal changes had great effects on net production. In the period from July through the next March the trend of monthly net production followed the trend of the monthly instantaneous growth rates although biomass remained relatively stable.

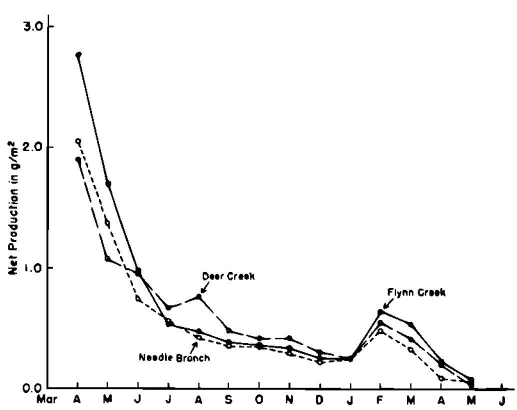

FIGURE 12.—Monthly net production of coho in three streams averaged over four year classes.

TABLE 5.—*Biomass (B) of coho in each stream, four year classes, expressed in g/m² at start of each month, net production (P) in g/m² for each calendar month, and monthly instantaneous growth rates (g)*

Stream and month	1959			1960			1961			1962		
	B	*g*	*P*	*B*	*g*	*P*	*B*	*g*	*P*	*B*	*g*	*P*
Deer Creek												
March	2.7		0.86[1]	5.5		1.36[1]	–		–	–		–
April	4.0	0.419	1.86	4.4	0.257	1.15	5.1	0.233	0.83	5.9	0.560	3.74
May	5.5	0.294	1.50	3.6	0.170	0.56	2.8	0.198	0.46	7.4	0.273	1.72
June	4.8	0.227	1.01	2.7	0.318	0.83	2.1	0.470	1.07	5.9	0.160	0.86
July	4.0	0.236	0.85	2.5	0.195	0.48	2.5	0.272	0.68	3.6	0.216	0.65
August	3.1	0.236	0.71	2.3	0.104	0.22	3.0	0.154	0.43	3.0	0.472	1.63
September	2.9	0.210	0.61	2.3	0.119	0.28	3.2	0.060	0.15	4.0	0.210	0.90
October	3.1	0.150	0.57	2.5	0.147	0.37	3.4	0.052	0.18	4.7	0.097	0.50
November	3.6	0.047	0.16	2.7	0.253	0.69	3.4	0.123	0.42	5.1	0.066	0.36
December	3.6	0.041	0.14	2.0	0.106	0.19	3.2	0.078	0.21	4.0	0.137	0.60
January	3.8	0.087	0.32	2.0	0.012	0.03	3.8	0.060	0.10	4.5	0.207	0.55
February	4.0	0.240	1.03	2.0	0.141	0.27	1.7	0.142	0.22	4.5	0.159	0.66
March	4.2	0.173	0.51	2.0	0.274	0.56	1.7	0.198	0.27	3.6	0.117	0.37
April	1.8	0.107	0.12	1.3	0.153	0.13	1.3	0.419	0.39	2.1	0.076	0.11
May	0.5	0.097	0.03	0.4	0.069	0.02	0.6	0.112	0.03	0.5	0.038	0.02
June	0.3	–	–	0.3	–	–	0.3	–	–	0.3	–	–
Flynn Creek												
March	3.8	–	1.07[1]	–	–	–	–	–	–	–	–	–
April	4.5	0.439	2.10	13.0	0.244	2.24	11.0	0.432	1.54	19.0	0.319	5.19
May	4.9	0.321	1.49	4.0	0.336	1.13	4.1	0.310	0.82	17.0	0.239	3.31
June	4.1	0.255	0.94	2.9	0.378	1.03	2.1	0.259	0.48	8.3	0.273	1.38
July	3.3	0.193	0.56	2.8	0.187	0.51	2.0	0.193	0.36	3.0	0.240	0.66
August	3.0	0.126	0.35	2.7	0.118	0.30	2.1	0.141	0.30	2.3	0.325	0.97
September	3.1	0.087	0.25	2.6	0.020	0.24	2.3	0.147	0.35	2.6	0.297	0.67
October	2.9	0.051	0.16	2.5	0.181	0.26	2.5	0.167	0.44	3.4	0.145	0.50
November	2.9	0.012	0.06	2.5	0.124	0.22	2.5	0.159	0.47	3.8	0.024	0.53
December	2.4	0.019	0.03	2.0	0.068	0.10	3.5	0.123	0.33	4.5	0.196	0.44
January	2.2	0.257	0.55	1.9	0.034	0.05	2.1	0.086	0.13	4.1	0.164	0.68
February	2.2	0.235	0.94	1.7	0.338	0.54	2.0	0.042	0.05	4.1	0.260	1.00
March	2.6	0.155	0.31	1.8	0.347	0.63	1.8	0.357	0.51	3.8	0.186	0.63
April	1.5	0.148	0.09	1.7	0.141	0.41	1.6	0.149	0.16	2.6	0.099	0.18
May	0.5	0.095	0.04	1.3	0.087	0.21	0.7	0.102	0.03	1.4	0.061	0.06
June	0.3	–	–	0.8	–	–	0.2	–	–	0.8	–	–
Needle Branch												
March	–	–	–	–	–	–	1.7	0.223	0.30	–	–	–
April	5.7	0.470	2.48	–	–	–	1.7	0.419	0.58	10.0	0.300	3.07
May	4.2	0.466	1.49	1.4	0.392	0.66	1.9	0.498	1.02	9.4	0.288	2.30
June	2.3	0.399	0.73	1.4	0.378	0.60	2.1	0.354	0.71	7.2	0.223	0.85
July	1.6	0.197	0.30	1.7	0.245	0.47	1.9	0.299	0.54	3.9	0.304	1.06
August	1.8	0.196	0.37	2.0	0.029	0.19	1.8	0.125	0.20	3.2	0.271	0.93
September	1.9	0.233	0.43	2.0	0.198	0.27	1.8	0.036	0.08	2.8	0.213	0.66
October	2.2	0.245	0.52	2.2	0.194	0.41	1.7	0.072	0.14	2.8	0.105	0.32
November	2.4	0.056	0.12	2.4	0.202	0.42	1.7	0.130	0.22	2.9	0.120	0.37
December	2.0	0.015	0.02	2.2	0.107	0.29	1.8	0.097	0.17	2.8	0.142	0.77
January	1.9	0.116	0.11	2.2	0.173	0.38	1.8	0.051	0.10	3.3	0.147	0.44
February	1.9	0.379	0.82	2.4	0.242	0.43	1.7	0.182	0.32	3.1	0.123	0.37
March	2.4	0.153	0.28	1.5	0.292	0.38	1.4	0.189	0.34	3.1	0.082	0.24
April	2.4	0.080	0.08	1.1	0.119	0.07	1.8	0.113	0.15	2.1	0.052	0.06
May	0.9	0.062	0.03	0.3	0.075	0.02	0.7	0.074	0.02	0.9	0.053	0.05
June	0.4	–	–	0.2	–	–	0.7	–	–	0.5	–	–

[1] Biomass on 15 March, net production 15–31 March.

Averaged over all streams and years, the ratio of monthly net production to biomass, or the mean monthly instantaneous growth rate, was about 0.19.

Rather large differences in recruitment of fry occur from year to year, especially in Flynn Creek and Needle Branch (Figures 9 and 10), due to variable numbers of spawning adult coho. Table 5 shows that net production from emergence of fry to 1 June varies greatly, primarily depending upon number of fish in the newly emerged year class.

Yields of coho smolts for all year classes studied are shown in Table 6. Placed on a basis of yield per 100 m² the smolt yield has averaged, by stream: Deer Creek, 50; Flynn Creek, 41; Needle Branch, 34. These yields substantially exceed the estimate of 20 smolts per 100 yd² made by Wickett (unpublished) for several streams in British Columbia.

Table 7 shows a comparison of net production and biomass of smolt yield for each year class, both on the basis of grams per square meter. Net production is on the average about 1.5 to 3 times greater than yield as biomass, suggesting the importance of obtaining production data for any quantitative consideration of trophic relationships in these streams. From Tables 5 and 7 it may be seen that yield of smolts in weight was often larger than bio-

TABLE 6.—*Yield in numbers of downstream-migrant yearling coho in three streams, 1 November to 1 June*

Year class	Deer Creek Total	Deer Creek Per 100 m²	Flynn Creek Total	Flynn Creek Per 100 m²	Needle Branch Total	Needle Branch Per 100 m²
1958	1,680[1]	36	No data		No data	
1959	3,169	67	1,281	52	200	22
1960	1,919[2]	40	872[2]	32	471	42
1961	2,298[2]	49	757	28	191[3]	18
1962	2,762	59	1,356	51	550[4]	52

[1] Trapping began 12 February. Figure estimated on basis of proportions of yield in other years in period 1 November to 12 February; 1,514 counted.

[2] Minimal due to movement of fish when traps were inoperable.

[3] Count minimal due to incomplete trapping.

[4] Estimated on basis of proportion of flow trapped; 447 counted.

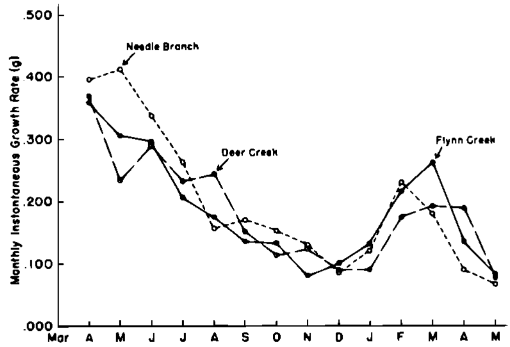

FIGURE 14.—Monthly instantaneous growth rates of coho in three streams, averaged over four year classes.

mass in February. This can be so because of net production in the spring.

DISCUSSION

Variations in survivorship among streams and years appear to have strong impact on net production. A demonstration of this is provided by the 1960 and 1961 year classes (Figure 8) when large freshets appeared to flush coho out of the study areas. Net production of the 1960 year class of coho in Deer Creek appeared to be much less than it might have been if no flushing took place. Although coho flushed downstream are lost to net production of fish in the study streams, they may very well contribute to net production of areas downstream.

Obviously the rapid decline in cohort size

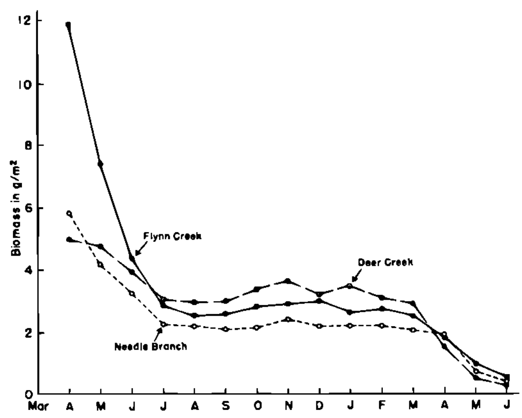

FIGURE 13.—Biomass of coho in three streams, averaged over four year classes.

from emergence of fry to early July has an important effect upon net production. This decline appears partially to be a result of a high rate of fry mortality. No cause has yet been assigned to this mortality. Predation by cutthroat trout has not been shown to be important by Lowry (unpublished). Sampling with alligator-forceps of about 171 stomachs from live cutthroat revealed that only occasional salmonid fry are taken even during a period of relatively high availability of coho fry (9 February to 12 June). On the basis of dry weight, about 10 per cent of the stomach contents was identified as juvenile salmonids.

Chapman (1962) discussed in detail the relationship between social behavior and emigration of coho fry. Magnitude of emigration of fry was positively related to density of fry after emergence. Emigration of fry was shown to be at least partially a result of social behavior.

Upstream movement of juvenile coho and trout has almost no effect on net production estimates. Chapman (1962) showed, for example, that from April through September 1961, only 10 juvenile coho passed upstream into the study area in Needle Branch while 658 emigrated downstream.

In addition to possible errors in growth calculations based on length alone, a problem similar to Lee's phenomenon exists in the growth curves. During emergence of coho fry, the fish emerging first appear to enjoy an ecological advantage. They may reach 45 to 50 mm before the last fry emerge at less

TABLE 7.—*Annual*[1] *net production of coho and yield of smolts as biomass, g/m²*

Year class	Deer Creek		Flynn Creek		Needle Branch	
	Prod.	Yield	Prod.	Yield	Prod.	Yield
1959	10.3	4.8	8.9	3.7	7.8	2.0
1960	7.1	3.6	7.9	2.9	4.6	3.3
1961	5.4	3.7	6.0	2.4	4.9	1.5
1962	12.7	5.6	16.2	3.7	11.5	3.9

[1] Period of production usually 14 months, from mean time of emergence to 1 June of following year.

than 35 mm. From emergence through June, a large emigration of coho fry takes place through downstream traps, and the emigrants are smaller on the average than cohorts remaining in the stream (Chapman, 1962). Growth estimates in the spring are therefore maximal. If mortalities such as predator consumption of coho fry act more heavily on the smaller coho, the overestimate of growth is even greater.

Beginning in January, the seaward-migrant coho are larger on the average than residual fish, and estimates of growth based on mean size of residuals are minimal. This is strikingly exemplified in April and May 1960 by coho of the 1959 year class in Deer Creek (Figure 5).

Estimates of net production are biased by the analogues of Lee's phenomenon, the direction of bias being the same as that in the growth estimates. The best estimates of growth would be those obtained from a sample of individually identifiable fish of sizes representative of the population. In the absence of such estimates, some interesting quirks can appear in estimates of production. If estimates of growth are obtained from a population losing large members through emigration, negative growth and negative production might be assumed while, in reality, residual members of the population continue to grow, tissue is elaborated, and positive production occurs. Negative production can only occur when the animals in the population actually lose weight, on the average. Immigration of large numbers of small fish such as newly recruited fry was noted by Lowry (unpublished) in cutthroat trout, and care would be necessary in this situation to prevent underestimation of growth and net production.

As would be expected, annual net production was greatly different among the three streams. Net production per unit area was not significantly different among streams, suggesting that such factors as spatial needs and (or) food supply are involved in regulating net production. Chapman (1962) suggested that spatial limitations act as density regulators in coho. Unpublished work by Mason and Chapman suggests that available food level may be a primary factor among those determining the holding–rearing capacity in artificial stream channels with controlled flow.

Demory (unpublished) reported on feeding habits of coho in the three study streams from May through September. Coho from Deer Creek contained 21 per cent terrestrial organisms (on dry weight basis); coho from Flynn Creek, a smaller stream, contained 29 per cent terrestrial animals; and coho from Needle Branch, the smallest and most densely shaded stream, contained 40 per cent terrestrial forms. Since net production per unit area has been only slightly lower each year in Needle Branch than in the other two streams, it may well be that yield to coho of prey per unit area is really determined, in part, by catchment of terrestrial insects per unit area, and that availability of aquatic insects per unit area is lower on Needle Branch than on the other streams. It may also be, of course, that spatial requirements regulate density below ceilings imposed by food supply in a given year, a notion supported by the fact that biomass of coho was lowest in Needle Branch (Figure 13), but instantaneous growth rate at least was equal to that on Deer and Flynn Creeks.

This suggestion implies that spatial requirements are either a function of some factor other than food supply such as minimization of mortality due to pathological agents or have been generally determined by years in which food supply was relatively low. It seems unlikely that spatial requirements set by years of low food supply are so rigid that they prevent utilization by coho of prey in a year when food is abundant.

As pointed out by John Mason (personal communication), food availability may mediate spatial requirements so that available food is channeled into a biomass size allow-

TABLE 8.—*Net production in selected waters, in g/m² per year*

Water	Species	Value	Reference
Reservoir, Oregon	Steelhead trout	5.3	Coche[1]
Eutrophic reservoir, Oregon	Chinook salmon	15.6	Higley, 1963[2]
Dystrophic lakes, Wisconsin and Michigan	Rainbow trout	1.9–8.4	Johnson and Hasler, 1954
New York lakes	Brook trout	3.3–6.5	Hatch and Webster, 1961
Cultus Lake, British Columbia	Sockeye salmon	5.9	Ricker and Foerster, 1948
Lawrence Creek, Wisconsin	Brook trout	18.1	McFadden, 1961[3]
Horokiwi Stream, New Zealand	Brown trout	54.7	Allen, 1951
Berry Creek, Oregon	Cutthroat trout and cottids	7–10	Warren et al., 1963
Deer Creek	Salmonids and cottids	16	

[1] Coche, Andre. Unpublished data, Oregon Game Commission, Corvallis, Oregon.
[2] Higley, Duane L. (1963). Food habits, growth, and production of juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in a eutrophic reservoir. Master's thesis, Oregon State University, Corvallis. 55 pp.
[3] I estimated net production from information on biomass and growth in the paper by McFadden.

ing maintenance of a near-optimum growth rate when growth can be accompanied by high utilization efficiency.

Both biomass and instantaneous growth rate (the latter largely a reflection of food supply) began at high levels early in the spring and declined subsequently, probably for closely associated reasons.

Positive relationships between total dissolved solids and various indicators of biological productivity of lakes have been noted by Northcote and Larkin (1956). McFadden and Cooper (1962) made an interesting comparison of six brown trout streams, attempting to correlate selected environmental and population statistics. They found a significant correlation ($P < 0.05$) between instantaneous growth rates of brown trout and water conductivity, the latter an index of water fertility. The correlation between conductivity and biomass of all fish species was high enough ($P < 0.25$) to suggest a positive relationship.

Estimates of biomass and annual net production of coho in Deer Creek, Flynn Creek, and Needle Branch indicate that the latter stream was probably least productive although no statistical significance is attached to the difference. Figures 2 and 3 and Table 1 show that levels of total dissolved solids, conductivity, total phosphates, and nitrates were all lowest in Needle Branch. Experimentation and further sampling are necessary to clarify and prove any existing relationship.

It is useful to compare data on net production obtained in the present study with results obtained in studies of salmonids in several waters. Analysis of cutthroat trout population statistics indicates that net production of cutthroat in Deer Creek in 1962 was about 4 g/m² per year (Lowry). Net production of the residual coho (1958 year class) remaining in Deer Creek a second year is calculated to be about 0.25 g/m² per year. Mean production of coho in Deer Creek over 4 years has been about 9 g/m² per year. Using available information on biomass and growth of steelhead and cottids, annual net production of steelhead is estimated as 1.5 g/m² per year and that of the cottids at 1.8 g/m² per year in Deer Creek. Adding estimates of net production for all species, I obtain a rough estimate for all net production of about 16 g/m² per year in Deer Creek. In Table 8 are listed data on net production obtained in several studies of waters containing salmonids.

Fragmentary data on chemical water quality of Lawrence Creek and Horokiwi Stream preclude a satisfactory analysis of factors causing differences among streams in productivity. Little would be gained by comparing in detail the physical–chemical–productivity relationships of the streams and lakes listed in Table 8. The data indicate that stream environments studied to date are relatively high producers of fish tissue. Estimates of production for all the waters listed in Table 8 are based on surface area; in lakes the water volume beneath a given surface area is greater than in streams, but in the latter a great volume of water passes over each square meter of substrate annually. Another way of stating this is that about 4,300 acre-feet of water were required to produce 76 kg of fish tissue in Deer Creek, while only about 278 acre-feet were needed to produce 1,150 kg of fish tissue in a eutrophic reservoir in central Oregon (Higley, see footnote 2, Table 8), the most productive of the standing waters listed in Table 8.

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