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REPRODUCTION BY ADFLUVIAL SALMONIDS IN SPAWN CREEK, CACHE COUNTY, UTAH

by

David R. Bernard

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Wildlife Science

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Logan, Utah

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David R. Bernard

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ABSTRACT

Reproduction by Adfluvial Salmonids in Spawn Creek, Cache County, Utah

by

David R. Bernard, Master of Science

Utah State University, 1976

Major Professor: Clair B. Stalnaker
Department: Wildlife Science

The migration and production of indigenous populations of brown, brook, and cutthroat trouts in Spawn Creek, Cache County, Utah, were studied in 1973 and 1974 to elucidate the role of this stream vis-a-vis the rest of the watershed. Spawn Creek and its watershed were described climatically, hydrologically, geologically, vegetatively, recreationally, and chemically. The prevalent, aquatic taxa of fauna and flora were also listed. The equipment and techniques used in the study to collect data, including a two-way fish trap and electro-fishing gear, were delineated. The collected data consisted of periodic estimates of mean weight and density stratified by year classes. These year classes were separated by length-frequency histograms, the length of individuals of known age, and the determination of age via counts of annuli on scales. This last method of aging was adjusted for the failure of cutthroat trout to form an annulus in their first year of life. The estimates of density were obtained through a modified form of the two-catch removal estimator. This estimator was designed to correct the estimates for emigration from the sampled area between the two sampling efforts. The biases in several unmodified multi-catch removal estimators vis-a-vis the populations of trout in Spawn Creek were discussed relative to the different, individual sizes of several year classes. Mathematical models to describe the time-dependent growth and density were constructed from the von Bertalanffy equation and the equation of depensatory mortality, respectively, by adding trigonometric components to each. The added constraints imposed by these components were discussed for models of both growth and density. These models were fitted to the appropriate, periodic estimates of growth and density to provide functions of these states vis-a-vis time. The calculation of production for each year class consisted of differentiating the appropriate model of growth, multiplying the resultant differential equation by the appropriate model of density, and integrating the product for various intervals of time. A numerical routine for integration was used when the solution of the integral of the aforementioned product was unattainable in closed form. The basic alogarithm of this routine was discussed. The periodic estimates from the data showed that several year classes such as the 1971 year class of cutthroat trout and the 1970 and 1971 year classes of brook trout, were numerically dominant in 1973 but not in 1974. When most of the individuals in the last two year classes died via senescence in 1974, the density and productive capacity of the brook trout population declined. This decline was a result of the failure of this taxa to produce new dominant year classes in 1973 and 1974. The periodic estimates from the data also showed that growth was similar in 1973 and 1974 except for the 0+ age group. The brown and cutthroat trouts of this age grew less in 1974 while the brook trout grew more.

Immigration occurred seasonally with the adult cutthroat trout migrating in the spring, and the juvenile cutthroat and brown trouts moving in the fall. No precedent for the fall emmigration of cutthroat juveniles was found in the literature. Emigration was a random affair save for the 0+ age group of cutthroat trout. Migration of brook trout was not significant. Production was greater in the growing season of 1973 than in 1974 for all species. During the year of trap operation only the 1974 year class of cutthroat trout and the 1970 year class of brown trout showed an increase in produced biomass. The failure of the brook trout to produce new dominant year classes was discussed and was attributed to the evacuation of beaver in Spawn Creek and the subsequent dilapidation of their ponds. The underestimation of the production of the 1974 year class of cutthroat trout and the probable causes for said error were discussed. The net emigration of juvenile cutthroat trout and the loss of produced biomass were tied together as a partial cause and effect. The failure of the net immigration of cutthroat trout adults to enhance the productive capacity of these year classes in this stream was attributed to reproductive activity and subsequent mortality of these individuals. This relationship along with the predominant emigration of cutthroat juveniles showed Spawn Creek vis-a-vis this species to be primarily a vehicle to enhance the reproduction of migrants exclusive to any other activity by this species. The relationship among migration, production, and reproduction of brown trout appeared as described above for the cutthroat trout, however, the small density of the population of this trout prevented any firm illation.

INTRODUCTION

Problem

The importance of fluvial streams to the reproduction of salmonids in lakes is well documented (Carlander, 1969). Cutthroat trout, Salmo clarki Richardson; rainbow trout, Salmo gairdneri Richardson; brown trout, Salmo trutta Linnaeus; and to a lesser extent brook trout, Salvelinus fontinalis (Mitchill), adults must leave the lentic environment in season and spawn in fluvial streams.

In the intermountain west a similar phenomenon has been recorded for certain salmonids in large, lotic systems where primary and secondary tributaries serve important functions in the reproductive life histories of indigenous species (Kiefling, 1972; Rankel, 1971). If these tributaries represent a significant portion of the spawning and brood habitat within the watershed, manipulation of their environment may increase the optimal harvest of the fishery when the birth rate is retarded by poor reproductive success. This yield might feasibly be increased by management practices that are directed towards an increase of the reproductive success in the tributaries. A comprehensive study on the reproductive history of the indigenous fishes could set the framework for the profering of management policies and schedules for the tributaries to increase harvestable, fishery yield throughout the entire watershed.

An investigation into the presence or absence of such a phenomenon in a large watershed would necessarily be logistically substantial. As a beginning in such an investigation Spawn Creek in the Wasatch National

Forest in northern Utah was chosen as the site for research into the aforementioned phenomenon.

Objectives

The objectives of the subsequent research were as follows:

1. To procure information on the growth, survivorship, and interstream migrations of fishes indigenous to Spawn Creek,

2. To calculate the production by these fishes,

3. To describe the intraspecific deviations in the growth and density of these populations, and

4. To compare the trends in the dynamics of production and migration of fishes with respect to their reproduction in Spawn Creek.

DESCRIPTION OF SPAWN CREEK

Spawn Creek is a spring-fed, secondary tributary of the Logan River, and is located approximately 24 km northeast of Logan, Utah (Figure 1). The average elevation of the drainage is 2,314 m (range: 1,814-2,749 m) with a 1,382 ha catchment basin. The stream is 3.8 km in length and averages 2.14 m in width. The gradient over the lower four-fifths of the stream is 58 m/km. Average discharge was 0.28 m^3/sec in 1974 (range: 0.17-0.42 m^3/sec); maximum discharge occurred during snowmelt in May and June with summer rainfall having only minor effects. Climatic conditions during the study were relatively severe with ambient air temperatures that ranged from 32.2 to -26.1 C. The water temperature at the main spring remained a constant 4.4 C while the temperature near the confluence reached a mean daily level of 12.2 C during the summer of 1974. Under the more extreme winter conditions, anchor ice formed in the lower stretches. Annual precipitation ranged from 50.8 cm (50 percent as snow) and 124.5 cm (78 percent as snow) of water at the lowest and the highest elevations respectively.

Williams (1948) showed that the Spawn Creek watershed is geologically composed of substrate from the Bloomington, Nounan, and Wasatch Formations. These groups are composed of calcareous, dolomitic, and conglomeratic parent materials respectively. Wasatch Conglomerate is the predominant group.

The vegetation that covers the watershed is generally differentiated via altitude. The lower elevations are vegetated with sagebrush (Artemesia sp.) and mixed grasses with intermittent aspen (Populus tremuloides)

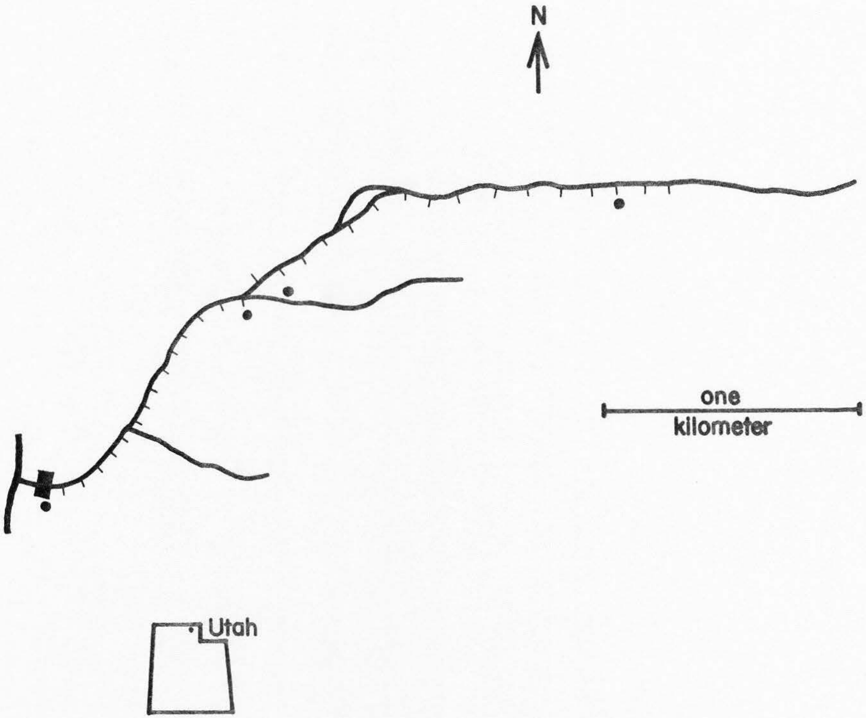

Figure 1. A map of the Spawn Creek study sections, trap, and chemical sampling stations ( )

groves; middle elevations are dominated by fir (*Pseudotsuga menziesii*), mountain mahogany (*Cerocarpus ledifolius*), and associated shrubs[1]; and the upper elevations are vegetated by spruce (*Picea engelmannii*) and their understory[1].

Since Spawn Creek is entirely contained within the boundaries of the Wasatch National Forest, the watershed has been managed via a multi-use philosophy. The entire basin has been grazed by domestic cattle and sheep. Logging has been intermittently conducted in the higher elevations. Extensive recreational activity occurs seasonally in various sections of the watershed.

Populations of beaver have made major alterations in the hydrology of the stream. The lower 3 km contain many beaver impoundments, all of which are abandoned although many still retain water. The rest of the stream does contain several active ponds.

The chemical composition of the water of Spawn Creek is typical of those streams that flow through this region. Table 1 is a list of the yearly means and ranges of several chemical constituents found in samples of water taken weekly from four stations (Figure 1).

The inputs of energy for Spawn Creek arise from both allochthonous and autochthonous sources. The first source is primarily composed of the silts from overland inflow and the leaf-fall of aspen, willow, and fir trees. The latter source is dominated by the vascular plants and the periphyton. The vascular component is dominated by *Amblystegium* sp., *Brachythecium* sp., *Carex* sp., *Fissidens* sp., *Marcantia* sp., and

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[1] Personal communication. Dr. Ted Daniels, Professor Emeritus, Department of Forest Science, Utah State University, Logan, Utah 84322. October 23, 1974.

Table 1. The means and ranges of the chemical constituents of water samples that were taken at Spawn Creek from December 12, 1973, to December 26, 1974.[1] Means were calculated by summing over stations and weeks to obtain yearly estimates

Constituents and Units	High	Mean	Low
pH	8.7	8.35[a]	6.6
Alkalinity (mg/l $CaCO_3$)	214	199.1	98
Hardness (mg/l $CaCO_3$)	232	203.9	106
Conductivity (μmhos/cm)	398	366.1	327
Inorganic Carbon (mg/l)	50	42.1	32
Soluble Organic Carbon (mg/l)	26	6.9	0
Particulate Organic Carbon (mg/l)	10	1.47	0
Suspended Solids (mg/l)	4.2	1.45	.1
Volatile Suspended Solids (mg/l)	10	.51	0
Ortho-Phosphate-P (μg/l)	18	7.23	0
Filtrate Total-P (μg/l)	85	14.01	0
Total Phosphorus (μg/l)	85	18.66	1
Ammonium (μg/l)	167	55.8	14
Nitrite + Nitrate-N (μg/l)	457	188.2	54
Calcium (mg/l $CaCO_3$)	149	118.9	61
Chloride (mg/l)	6	2.47	0
Potassium (mg/l)	1.5	.66	0
Sodium (mg/l)	6.6	4.01	2.1
Sulfate (mg/l)	26	6.0	3
Total Iron (μg/l)	69	18.7	1

[a] Mode.

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[1] Personal communication. Hal Runke, Graduate Research Assistant, Department of Civil and Environmental Engineering, Utah State University, Logan, Utah 84322. March 15, 1975.

Nasturium sp. The periphyton is composed largely of a diverse diatom flora with high concentrations of green and golden-brown algae, Cladophora sp., Hydrurus sp., and Ulothrix sp., in limited areas.

The community of primary consumers is composed largely of detritivores, a few grazers, and a complement of predators. The dominant taxa in numbers are Baetis sp. and Ephmerella sp. (Ephemeroptera) and Planarridae (Tricladia). Table 2 provides a more complete taxanomic list of the invertebrate community.

The indigenous fishes are cutthroat trout, rainbow trout, brown trout, and brook trout. The brown and brook trout populations, respectively, occupy the lower and the upper reaches of the stream as is typical in many intermountain rivers (Miller, 1966). The cutthroat trout population is ubiquitous. The brown and cutthroat trout populations have migratory components; the brook trout population does not. The rainbow trout population consists of a few migrants and is not reproductively sustained within the stream: supplemental introductions of hatchery stocks occur downstream in the Logan River watershed.

Table 2. List of the invertebrate taxa found in Spawn Creek in the summer of 1974[1] in benthic samples

Taxa	Abundance[a]	Taxa	Abundance
Arachnida		Hemiptera	
		Gerridae	
Acarina		*Gerris* sp.	2
Hydrachnidae			
Hydracarina sp.	3	Plecoptera	
		Chloroperlidae	
Insecta		*Alloperla* sp.	2
		Nemouridae	
Coleoptera		*Nemoura* sp.	2
Dytiscidae		Perlidae	
Agabus sp.	2	*Acroneuria* sp.	3
Elmidae	2	Perlodidae	
		Isoperla sp.	1
Diptera			
Ceratopogonidae	2	Trichoptera	
Chironomidae		Hydropsychidae	
Diamesia sp.	3	*Parapsyche* sp.	3
Ptychopteridae		Lepidostomatidae	
Ptychoptera sp.	2	*Lepidostoma* sp.	1
Simulidae		Limnephilidae	
Prosimulium sp.	2	*Hesperophylax* sp.	1
Stratiomyidae		*Oligophlebodes* sp.	1
Euparyphus sp.	2	Rhyacophilidae	
Tipulidae		*Glossosoma* sp.	3
Hexatoma sp.	2	*Rhyacophila* sp.	3
Tipula sp.	3	Psychomyiidae	
		Neureclipsis sp.	1
Ephemeroptera			
Baetidae		Oligochaeta	
Ameletus sp.	2	Plesiopora	
Baetis sp.	4	Tubificidae	3
Ephemerella sp.	4		
Paraleptophlebia sp.	3	Turbellaria	
Heptageniidae		Tricladia	
Cinygmula sp.	3	Planariidae	4
Rhithrogena sp.	3		

[a] 4 = abundant, 3 = moderately abundant, 2 = rare, 1 = extremely rare

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[1] Personal communication. Scott Reger, Graduate Research Assistant, Department of Wildlife Science, Utah State University, Logan, Utah 84322. March 15, 1975.

METHODS

Collection of Data

Spawn Creek was divided to facilitate the sampling effort. Study sections were 100 m long and ran contiguously for 2.4 km upstream from a two-way fish trap (Twedt and Bernard, 1976). Preliminary studies of the upper reaches of the stream and the larger tributaries showed that populations in those areas were virtually non-existant. The uppermost 0.8 km of stream were inaccessable to sampling and subsequently were not included in the study.

The fish trap was placed into operation on November 21, 1973, and was used to monitor movements of fish until November 20, 1974. The facility was checked at intervals dictated by migrational patterns and seasonal conditions. All captured fish were anesthetized with MS-222 and quinaldine (Schoettger and Steucke, 1970), measured in total length (TL), weighed if feasible (missing weights were later supplied from time and species specific length-weight regressions from pertinent field samples), sexed in season, and marked for later identification if appropriate. Large fish (>200 mm) were individually tagged with numbered Floy FD-67 anchor tags (Dell, 1968); small fish (199-100 mm) were fin clipped on the right pelvic; and fry and fingerlings below 100 mm were not marked. This marking regime was designed to mitigate the hazard of differential growth between tagged and untagged juveniles (Barclay, 1973; Carline and Brynildson, 1972) and the hazard of differential survival between clipped and whole fry and fingerlings (Coble, 1971; Nicola and Cordone, 1973). Fish were held until revived and then released in their previous direction of travel.

Fish populations were sampled monthly from April, 1973, to November, 1974 (Appendix). When estimates of both growth and density were needed, two consecutive samples were removed and replaced from all the sections in the study area. When only an estimate of growth was required, one sample was removed and replaced from several, randomly chosen sections. Since streams such as Spawn Creek can be quantitatively sampled with only electricity (Larsen, 1955), fish were captured with a 300 w AC back-pack generator with a variable-voltage DC pulsator; DC was used at all times to provide a galvanotaxic response and to reduce mortalities (Pratt, 1955; Taylor, Cole, and Sigler, 1957). All captured fish were anesthetized, measured, sexed, and weighed as were the trap samples. After July 24, 1973, all unmarked fish above 75 mm TL were cold-branded with individually identifiable numbers (Everest and Edmundson, 1967). All recaptures of marked individuals were noted. Scale samples were taken on all unbranded individuals except those of the 0+ age groups. These scales were taken from above the lateral line and below the anterior margin of the dorsal fin on brown and cutthroat trout (Lagler, 1956) and from the caudal peduncle from brook trout (Carlander, 1969). Fish were held until revived and then released at intervals along the section of stream from which they came.

Special field collections were made at various intervals throughout the study. Whenever electrofishing was conducted on the 100 m section upstream and adjacent to the trap, the facility was checked after the first catch to assess the number of fish that left this section between units of effort. Also, certain sections were sampled several times to provide data for a comparison of various multi-catch removal methods of population number estimation.

Analysis of Data

Time

Time in the following mathematical models was expressed in weeks that began on January 1, 1973, and sequentially progressed 98 hebdomadal periods to November 20, 1974.

When production was calculated for the 1973 and 1974 year classes, their times of emergence were calculated from relationships of egg development vis-a-vis water temperature from Embody (1934) and Merriman (1935). The mean, daily water temperature was transformed into a fraction of the total development; for instance, if a brown trout egg takes 95 days to develop from deposition to emergence when held at 5 C, one day at this temperature corresponds to 1/95 of the total development towards emergence. The fractions of development were added as the days passed from the week of the deposition of eggs until their sum reached unity. At this time the corresponding week was noted as the period of emergence. The week of deposition was chosen as the period when the maximal amount of spawning activity was noted for the adults of that species.

Separation of year classes

Since electrofishing is size-selective (Sullivan, 1956) and growth, survivorship, and recruitment may vary among age groups and species

(Ricker, 1958), all estimates and calculations were stratified by species and by year class.

Year classes within a species were separated by the discontinuities within length-frequency histograms, by the determination of age via counts of annuli on scales, and by the position in the length distribution of previously aged individuals. Because cutthroat trout in the Logan River and its tributaries do not form an annulus in their first year of life (Fleener, 1952), the ages of this species as determined by counts of annuli were adjusted accordingly. Although the scales taken from yearling cutthroat did show that some formed an annulus in their first winter, this proportion was small (3 out of 55 sampled) and was therefore ignored.

Cutthroat trout exhibit the above phenomenon in other waters as well. Brown and Bailey (1952) found a similar occurrence in Montana. The first few circuli are laid down in such a uniform fashion that the cessation and subsequent resumption of growth during the colder seasons do not visibly interrupt the pattern. Mallet (1961) found that up to 11 circuli could be laid down in the first year in the life of a cutthroat in the Middle Fork of the Salmon River before an annulus was created. Also, some populations even fail to form scales in their first year of life, such as the populations in Yellowstone Lake (Laasko and Cope, 1956).

Migration

The numbers and weights of emigrants and immigrants were obtained from data from the trap. Because rarely did enough fish migrate weekly to provide the means to directly separate the migrants into year classes by the forementioned methods, the boundaries between adjacent year classes as calculated from the regular samples of the upstream populations were used. The critical boundary in TL between every possible couplet of year classes was regressed vis-a-vis time. The least-squares fit was made via techniques outlined by Snedecor and Cochran (1967). The resultant linear models were interpolated to provide estimates of the boundaries for the separation of the weekly migrants into their appropriate year classes. The statistics for each of these models are listed in Table 3.

Ignorance of hydrologic conditions during the early months of the summer precluded adequate preparations for the extreme bed-load sedimentation that occurred in May and June, 1974. This bed-load movement stopped operation of the trap for 31 days (June 17 to July 18, 1974) until adjustments could be made. Because no knowledge of the migrational patterns for this period was available, attempts were not made to fill this gap in the data.

Inefficiencies in equipment prevented the adequate sampling in the trap of the 1974 cutthroat trout year class until 10 weeks past their emergence (the last week in June of that year). Since most studies have shown that cutthroat fry remain in their natal stream at least several months beyond emergence (Cope, 1957a; Kiefling, 1972; and Rankel, 1971), the migration during this period was assumed to be relatively nil. This assumption allowed the numbers of animals that migrated in this period to be estimated from the numbers of animals that migrated later. The weekly estimates of this latter group were fit to a normalized density function (Parton and Innis, 1972)

Table 3. List of the slopes, intercepts, and coefficients of determination that were derived through regressions of linear models of fish length on time. The dependent variables are the boundaries in mm TL between two, contiguous year classes of a species of trout; the independent variables are time in weeks from January 1, 1973. These models were calculated from boundaries that were based on data from periodic electro-fishing samples from the stream and were then used to separate the forementioned year classes in migrant populations that were captured at the trap between said electro-fishing samplings

Bounded year classes	Slope	Intercept	Coefficient of determination (r^2)
Brown trout			
1974–1973	1.023	–.411	.995
1973–1972	1.601	32.165	.849
1972–1971	1.054	132.387	.927
1971–	.814	206.141	.962
Cutthroat trout			
1974–1973	1.023	–25.411	.995
1973–1972	1.773	–12.991	.900
1972–1971	1.463	74.910	.787
1971–1970	1.116	142.984	.491
1970–1969	.745	196.951	.523
1969–	.964	212.115	.905

by a computer program that used an iterative, least squares approach to fitting curvilinear equations (Bevington, 1969). The results of this effort are listed in Table 4. This model of migration was then extrapolated to estimate the missing data.

Estimation of density

Because preliminary work showed that densities were low and the probabilities of capture were high, a two-catch, removal method was employed to calculate the periodic density of a year class. Since data from the trap revealed that fish were leaving the sections between units of effort, an adjustment was added to the case of two trappings of Zippin (1958) as a compensation. The above compensation can be derived from the assumptions in the removal method. Robson and Regier (1971) state that the probability of capture must remain constant over all units of effort. If only two units of effort are employed, the probability of capture in the first unit must be equal to that in the second, and is expressed as:

$$c_1/N = c_2/\ (N - c_1 - m) \qquad (1)$$

where

N = the number of fish,

c_1 = the number of fish caught during the first unit of effort,

c_2 = the number of fish caught during the second unit of effort, and

m = the number of fish that left the area between the first and second units of effort.

If the variables are algebraically rearranged, equation (1) becomes:

$$\hat{N} = (c_1{}^2 + c_1 m)/(c_1 - c_2) \qquad (2)$$

Table 4. The normalized density function that describes emigration of the 1974 cutthroat trout year class in the first summer of their life. The equation was taken from Parton and Innis (1972) and was fit to the observed data of emigrating density via an iterative technique as described by Bevington (1969). The fitted equation was used to predict via extrapolation the emigration of this year class from June 25 to August 27, 1974

$$M_{E_t} = M_{E_{max}} [(b-t)/(b-a]^c \, e^{\{(c/d)(1 - [(b-t)/(b-a)]^d)\}}$$

M_{E_t} = the number of individuals that emigrated in week t

$M_{E_{max}}$ = the seasonal maximum of weekly emigrants

χ^2 = the chi-square test for goodness-of-fit (Bevington, 1969)

df = the degrees of freedom

Statistics	Standard deviations
a = 91.94	1.7666
b = 72.27	15.0516
c = 10.29	14.9455
d = 5.28	5.3348
χ^2 = .1	
df = 8	

where

$\hat{N}$ = the estimate of the number of fish.

Because the probability of capture in the above estimator approximates a Poisson distribution, the δ-method of Darrock (1958) was used to derive its variance. Robson and Regier (1971) state that if the fishing intensity and the rate of mortality in a removal estimator remain constant during the sampling period, the probability of capture follows the forementioned distribution. In this study of the fish population in Spawn Creek, the fishing intensity (number of fishing efforts per estimate) was held constant by design, and because the necessary time to complete the sampling procedure was short, a dramatic change of the mortality rate for the involved year classes was highly unlikely. Therefore, according to the previously mentioned technique, each parameter was multiplied by the square of its partial derivative from equation (2), and the three products were summed to become:

$$V\ (\hat{N}) = [c_1{}^5 - 2c_1{}^3 c_2 (2c_1 + m) + c_1 c_2{}^2\ (2c_1 + m)^2]/ \\ (c_1 - c_2)^4 + [N^2 c_2 + c_1{}^2 m]/(c_1 - c_2)^2 \qquad (3)$$

Since the stream was electrofished by section always in an upstream direction, the statistics $\underline{c_1}$, $\underline{c_2}$, and $\underline{m}$ for the entire stream were calculated as follows:

$$c_1 = \sum_{i=1}^{k} a_i \qquad (4)$$

$$c_2 = \sum_{i=1}^{k} b_i \qquad (5)$$

$$m = nL \qquad (6)$$

where

k = the number of sections that were sampled,

a_i = the number of individuals that were caught in the first unit of effort in the ith section,

b_i = the number of individuals that were caught in the second unit of effort in the ith section,

n = the number of sections where a representative of the particular year class was found, and

L = the number of fish that leave a section between units of efforts.

The data obtained from the special collections at the trap were used to calculate L. Since L was directly obtainable from only the section of stream immediately upstream from the trap, estimates of this parameter had to be calculated for the other sections to obtain the expected number of dislodged individuals in the entire stream. The observed data from the first section and trap were used in attempts to regress L with density, probability of capture, and the size of catches for each size group of fish. All such attempts at linear and curvilinear correlation provided such poor results that an average over time of the observed data was used to estimate L. These averages were stratified vis-a-vis the size of the migrant and were used in calculations with the appropriate year class.

A comparison of estimated densities that were calculated via several, multi-catch methods was made with the data from special collections (Table 5).

Table 5. Comparison of calculated densities from various removal estimators on hypothetical cutthroat trout populations from the combined samples of July 25 thru 26, 1973, January 18 thru 21, 1974. Standard errors are in parenthesis

Year Class	Modified Two-catch	Removal methods[a]				Delury[b]
		Two-catch	Three-catch	Four-catch	Five-catch	
1972	25.9 (3.35)	25.0 (1.53)	25.5 (1.33)	25.1 (.34)	25.0 (.14)	24.7 (.80)
1971	24.2 (18.96)	20.3 (9.80)	14.5 (.97)	15.3 (.61)	15.1 (.35)	15.1 (.78)
1970	17.8 (1.87)	15.1 (.38)	16.1 (.80)	16.0 (.10)	16.0 (.00)	15.8 (.80)
1969	4 (0)	4 (0)	4 (0)	4 (0)	4 (0)	

[a] Values were calculated as outlined by Zippin (1958).

[b] For Delury estimators the value within parentheses are the coefficients of determination (r^2).

Because the numbers of fish that were caught were small, the catch data from the special collections conducted in July, 1973, and January, 1974, were combined to improve precision. Although the calculated estimates from the combined data did not correspond to an actual population, the combination violated none of the underlying assumptions in the two-catch method and was, therefore, realistic when used in the following manner.

A comparison of the number of units of effort that were employed per estimate showed that as the number of units increased, the calculated density was reduced. Although this reduction is slight vis-a-vis the standard errors that are involved, the trend in the change in estimation from left to right in Table 5 is downward. This is as expected if between each unit of effort a number of fish emigrated from the study section.

Since the intensity of the bias and the steepness in the decline of estimated densities are directly related, Table 5 shows that groups of large and small fish were resistant to this type of bias while groups of moderately sized fish were not. This situation was probably due to the selectivity of the gear and the limitation of visually locating and recognizing stunned fish. As the length of an individual increases, the probabilities of recruitment and location after electric narcosis increase. The 1972 year class was poorly recruited, therefore, few stunned individuals floated out of a section and bias was negligible. The 1971 year class had better recruitment but visual recognition was poor, and the bias was great. The last two year classes were both well recruited and recognition was good, therefore bias was reduced.

Density

Mortality was assumed to be density independent. Although this is usually the case for adult salmonids, often it is not for juveniles (Kramer, 1969). Because electrofishing is least effective on smaller fish (Sullivan, 1956), these animals were rarely recruited into the samples. This absence precluded any attempt to determine compensatory mortality. Since some year classes contained migratory constituents, migration had to be incorporated into models of density; however, data from the trap was not directly employable, since the facility was in operation for only part of the study. Therefore, trigonometric components were added to some models as a compensation for migration. This addition consisted of a sine wave that exhibited various amplitudes, phases, and frequencies among the different year classes. These trigonometric components were placed in the exponent of the equations of time-dependent density as supplements to the relative rate of mortality. The purpose of the wave in each new function of density was to exacerbate the decline in the density during periods of emigration and create an increase in numbers during periods of immigration.

These modified models of depensatory mortality have constraints beyond those specified by Ricker (1958) for the original form. The statistic for the amplitude C is relative to the progression of time. As the weeks pass the product of time and the relative rate of mortality r dwarfs the value of the trigonometric component in the exponent, and the effects of migration on the density subside. This characteristic forces migration to be the most intense in the earlier years. When the total history of a trout is viewed, the largest potential for migration occurs just after maturation (Carlander, 1969). Therefore, if the modified models are applied to year classes beyond the age of maturation, the probability of a bias in this area is lessened.

The trigonometric part of the exponent forces the migratory frequency (b) to remain constant throughout the life span of the individual. If the patterns of migration do not remain so constant, the trigonometric component can be dropped or added from the model to lessen the amount of bias. Such a situation occurred in the model of the 1971 cutthroat trout year class. The trigonometric form was used in the calculation of time-dependent density from late October, 1973, to late August, 1974, and was fit to the data from this period. Since migrational information was unavailable for the spring of 1973 and the individuals in this year class did not immigrate in the fall of 1974 (Figure 2), these periods were modeled without the trigonometric component on the appropriate data.

Another such instance is the absence of immigration in the 1+ age group in the spring of the year. Since individuals in the 1972 cutthroat trout year class were this age in the spring of 1973, they could not have been expected to immigrate into Spawn Creek. However, these individuals immigrated in the fall of 1973, the spring, and the fall of 1974 as evidenced via data from the trap and the stream. There, the trigonometric component was dropped from the model of time-dependent density for this year class until the late summer of 1973.

The models of density were fitted to the data with the aid of a computer program that used an iterative, least squares approach for curvilinear fits (Bevington, 1969). All estimates of density ($\hat{N}$) were weighted by the reciprocal of their variances in the calculations.

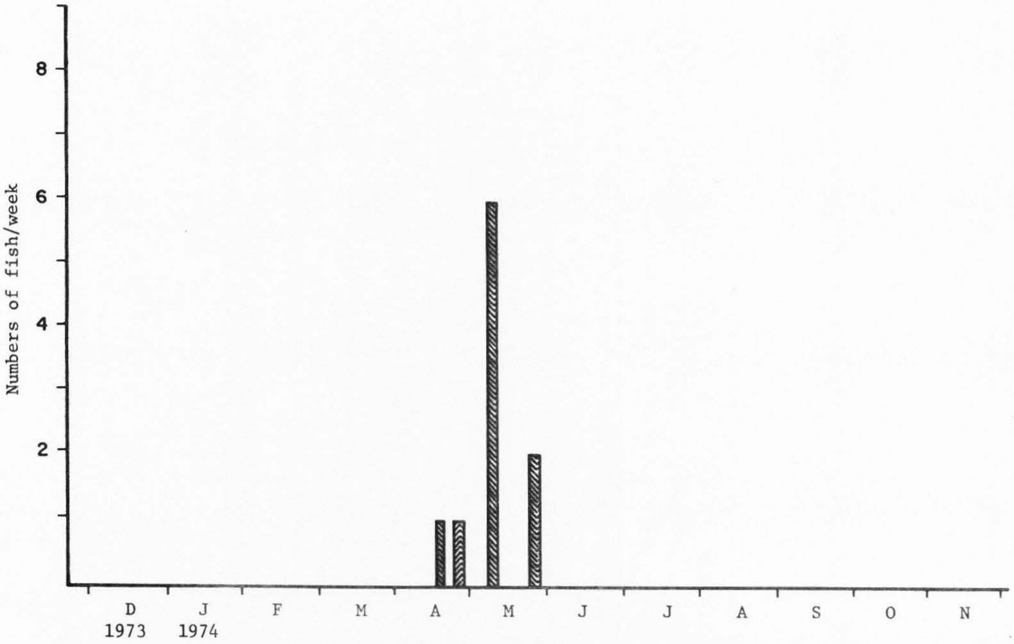

Figure 2. Graph of the immigration of individuals in the 1971 cutthroat trout year class into Spawn Creek from November 21, 1973, to November 20, 1974

The exact, mathematical constructions of these models are displayed in Tables 6 and 7. A plotted example of how these models fit the observed data is provided for the 1972 year class of cutthroat trout (Figure 3).

Because not enough points were available to fit a trigonometric function, the 1973 cutthroat trout year class was modeled with a parabolic curve of a logarithmic transformation of the data set. The specific, instantaneous rate of change $\underline{z}$ incorporated both the effects of mortality and emigration. The quadratic term $\underline{it^2}$ is an empiricism to provide for immigration in the fall of 1974.

Because only one estimate of density was available for the 1974 cutthroat trout year class, the value of $\underline{z}$ from 1973 was borrowed and incorporated into a model of exponential decay.

The method with which the change in density was modeled for the 0+ cutthroat age group was probably incorrect and biased subsequent estimates of production downward. A better model of the instantaneous rate of change for this age group would be:

$$\frac{dN}{dt} = -rN_t - \frac{dM}{dt}E \qquad (7)$$

where

$\frac{dN}{dt}$ = the instantaneous rate of decrease,

r = the specific, instantaneous rate of mortality,

N_t = the density at time t, and

$\frac{dM}{dt}E$ = the instantaneous rate of emigration (Table 4)

The solution of this differential equation would be the model of time-dependent density for this cohort. This model was not used because the

Table 6. Descriptive, mathematical models of time-dependent density for brown and brook trout year classes in Spawn Creek from April, 1973, to November, 1974

Year Class	Description	
	Brown Trout	Brook Trout
1974		$N_t = N_o e^{-rt}$
1973		"
1972	$N_t = N_o e^{-(Csine\{2\pi[t-s]/b\}+rt)}$	"
1971	$N_t = N_o e^{-rt}$	"
1970	"	"

N_t is the year class number at time t
N_o is the year class number at time zero
r is the specific, instantaneous rate of mortality
t is the time in weeks
C is the amplitude for the trigonometric component
s is the phasing of the trigonometric component
b is the frequency of the trigonometric component

Table 7. Descriptive, mathematical models of time-dependent density for cutthroat trout year classes in Spawn Creek from April, 1973, to November, 1974

Year Class	Description
1974	$N_t = N_o e^{-zt}$
1973	$N_t = N_o e^{-(z-it)t}$ $\{\ln N_t = \ln N_o - zt + it^2\}$
1972	$N_t = N_o e^{-(C\mathrm{sine}\{2\pi[t-s]/b\}+rt)}$ and $N_t = N_o e^{-rt}$
1971	" and $N_t = N_o e^{-rt}$
1970	"
1969	"
1968	$N_t = N_o e^{-rt}$

N_t is the year class number at time t

N_o is the year class number at time zero

z is the specific, instantaneous rate of decrease

t is the time in weeks

i is the empirical constant for numbers increase

C is the amplitude of the trigonometric component

s is the phasing of the trigonometric component

b is the frequency of the trigonometric component

r is the specific, instantaneous rate of mortality

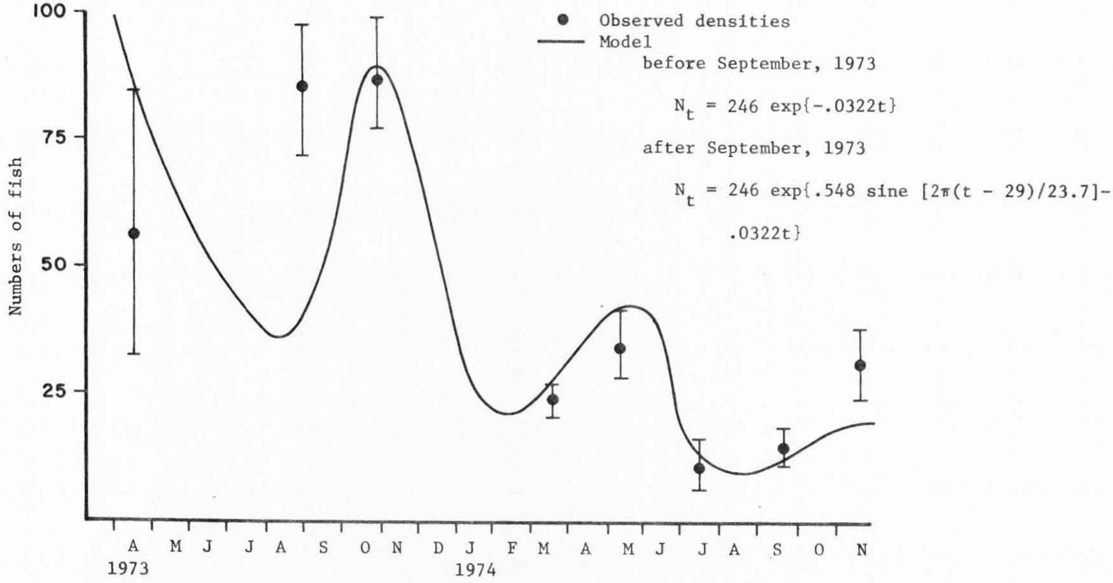

Figure 3. Plot of the observed densities of the 1972 cutthroat trout year class and the predictions by the fitted model of time-dependent density for that group. The observed densities are bracketed by an interval whose length is twice the calculated standard error for the appropriate estimate

integral of equation 7 was incompatable with the data. The trap samples would provide the necessary information to fit $\frac{dM_E}{dt}$, but at least two viable estimates of density during periods of no or low emigration would be necessary to find the specific, instantaneous rate of mortality. Only one viable estimate was accomplished.

Because only two and one viable estimates of density were calculated for the 1973 and the 1974 brown trout year classes, respectively, no models of time-dependent density were fitted for these groups.

Growth

Even though the general growth of an individual fish tends to be asymptotic in its life (Beverton and Holt, 1957; Parker and Larkin, 1959) seasonal variations of accelerated gain or loss of weight do occur (Chapman, 1971). As a compromise in these two trends, von Bertalanffy growth equations (Beverton and Holt, 1957) and trigonometric multipliers were combined and used to model growth in all but the 1974 year classes (Table 8). Unlike the trigonometric components in the models of density, these sine waves were not used in the exponents, but as multipliers of the asymptotic segment of the growth equations. These multipliers caused the new equation to undulate around the old as time progressed, thereby describing seasonal fluctuations in mean weight around a general trend.

The model of asymptotic growth as described by von Bertalanffy is based on various assumptions of the metabolism, ingestion, and the volumetric characteristics of the modeled animal (Beverton and Holt, 1957). The asymptotic weight ($\underline{W}_\infty$) is a function of the food availability;

Table 8. Descriptive, mathematical models of time-dependent growth for brown, cutthroat, and brook trout year classes in Spawn Creek from April, 1973, to November, 1974

Year Class	Description
1974	$\bar{w}_t = W_o e^{gt}$
1973	$\bar{w}_t = W_\infty(1 + C\text{sine}[2\pi\{t-s\}/b])(1-e^{-k[t-to]})^3$
1972	" and $\bar{w}_t = W_o e^{gt}$ [a]
1971	"
1970	"
1969	"
1968	"

$\bar{w}_t$ is the mean year class weight at time t in grams
W_o is the mean year class weight at time zero in grams
g is the specific, instantaneous rate of growth
t is the time in weeks
W_∞ is the asymptotic weight in grams
C is the amplitude of the trigonometric component
s is the phasing of the trigonometric component
b is the frequency of the trigonometric component
k is the coefficient of catabolism
t_o is the time at which the mean year class weight is zero

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[a] Cutthroat trout only

the coefficient of catabolism (k) is partly an expression of temperature; and the cubic exponent is an expression of the isometric relationship of weight with respect to the length of the fish.

The trigonometric multipliers place constraints on the models in Table 8 as well as those previously mentioned. These multipliers force the fluctuations in the growth of the modeled fish to be symetrical with a given amplitude (C) and a given frequency (b). The amplitude is set at a specific percentage throughout the life of the fish. For instance, the seasonal weight of a yearling and a seven year old fish will vary the same percentage around the general, sigmoid trend in growth, even though their respective changes in weight would be considerably different. This uniformity in the relative amount of fluctuation in weight does not segregate the particular causes of the deviations from the general trend. These models state that the relative change in weight is the same whether this change is due to increased reproductive activity or winter quiescence. Also, the frequency of the fluctuations in weight is set for the life span of the fish. Accordingly, such things as maturation should not cause the models to deviate.

These added assumptions in the models of time-dependent growth were fulfilled to various degrees for the populations of trouts in Spawn Creek. In populations of fish that spawn in the autumn, the main causes for the seasonal fluctuations in mean weight, reproduction and winter quiescence (Chapman, 1971), are contiguously confounded. The loss of weight due to reproductive activity immediately precedes the cessation of growth in the winter. The chronological intimacy of spawning vis-a-vis the winter season in autumnal spawners mitigates the effect of maturation on the frequency of the cycle of change in weight. Also, since the loss of weight in the winter due to the cessation of growth is the common denominator between juveniles and adults in the cycles of these populations, the relative change in weight probably doesn't vary that much throughout the life span of the fish.

Since brown and brook trouts spawn in the late fall, their populations in Spawn Creek probably fulfilled the models of modified asymptotic growth well. However, since the cutthroat trout adult does not spawn in the fall, the cycles in seasonal change in weight differ before and after maturation in the individual of this species. Those year classes of cutthroat trout whose individuals had either maturated before the start of the study or after the end, had constant frequencies throughout the study. Only the 1972 year class maturated during this time. As a compensation the modified model of asymptotic growth was used from November 21, 1973, to November 20, 1974, for this year class, while a model of exponential growth was used to describe their dynamics prior to that time. Unfortunately the major causes of seasonal fluctuations in growth were not chronologically dependent for the cutthroat adults and may have introduced some error into the following calculations.

The statistics for these models were calculated via the same computer program as those from the models of density (Bevington, 1969) with two exceptions. Because the short duration of the study did not expose enough of the asymptotic trend in the growth of every year class, the asymptotic weight $\underline{W}_\infty$ was estimated by a series of Walford plots (Walford, 1946) for each species. For each sampling period, the cubic roots of the mean weights of an individual for several, chronologically contiguous year classes were graphically regressed against the roots of the mean weight from the next youngest age group. The cube of the intercept of the regression line with the 45° diagonal through the origin provided an estimate of $\underline{W}_\infty$. These estimates were summed over time for all these species to provide the yearly, specific constant.

The second independently estimated statistic was the metric relationship of the length vis-a-vis the weight of the individual. This relationship is expressed by the exponent in the length-weight formula (Beverton and Holt, 1957). The models in Table 8 assume that this relationship is cubic (isometric). The length-weight regressions that were calculated via least-squares techniques (Snedecor and Cochran, 1967) for most samples, and their respective deviations from isometry are listed in Table 9. Although many deviations did exist, most were due to either seasonal fluctuations in growth due to reproduction or high degrees of freedom in the model (>200).

A plotted example of how these models fit the observed data is provided for the 1972 year class of brown trout (Figure 4).

The growth of the 1974 year classes was exponentially modeled. For those 0+ age groups that had some emigrants, models were constructed with data from both the stream and the trap (Appendix).

Production

Production is the elaboration of fish flesh by a population irregardless of the ultimate fate of the individuals that elaborated it (Ivlev, 1945). Only the gain or loss of weight by the individual and not migration or mortality affect the amount that has been produced (Chapman, 1971). Weight is gained by the individual when its metabolic

Table 9. Tests for significance of deviations from isometric growth in the periodic samples of fish taken in Spawn Creek from April, 1973, to November, 1974. The values for the slopes (b) of the log-log transformation of the length-weight regression were calculated via least-squares techniques (Snedecor and Cochran, 1967)

	b		
Date	Brown Trout	Cutthroat Trout	Brook Trout
1973			
April	2.558*	2.203**	2.616**
April		3.042	2.952
May		2.935	2.772
June			2.156**
June		3.820**	3.434**
July	2.978	2.421**	3.116
August	2.682**	2.933**	3.371
October	2.945	2.983**	3.010
December	2.685	2.490**	2.970
1974			
January		2.652**	4.150**
February		2.675*	
March		3.130	2.756
April		2.959**	2.996
May		2.784**	
June		3.026	
July		2.915	
August	3.165	3.004	2.985
September		3.031	
November	3.111	3.057	3.361

*Significance at the 95 percent level ($H_o: b = 3$)
**Significance at the 99 percent level ($H_o: b = 3$)

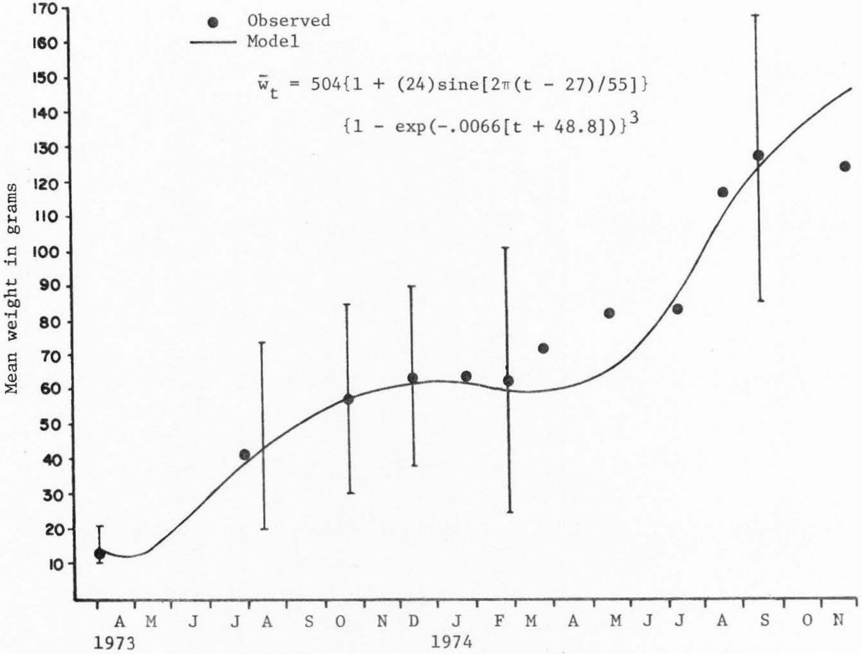

Figure 4. Plot of the observed mean weights of the 1972 brown trout year class and the predictions by the fitted model of time-dependent growth for that group. The observed weights are bracketed by 95 percent confidence intervals when more than 3 degrees of freedome were present

and excretory losses of energy are less than its gain through ingestion. Weight is lost when the above situation is reversed, or reproductive products are expelled from the body. Since this latter loss is not due to metabolic or excretory demands, compensation must be made in calculations of production.

Because low densities made significant sampling for size-fecundity relationships detrimental to the integrity of the populations, these relationships were gleaned from the literature (Table 10). The year class density and sex ratio were used to obtain estimates for loss of weight from the expulsion of eggs.

Because the relationships between the size of the male and the loss of the reproductive products are either poorly documented or unknown for the salmonids in Spawn Creek, and this loss is usually negligible in comparison to that of the female (Lagler, Bardach, and Miller, 1967; Royce, 1973), the masculine loss of weight from the expulsion of milt was ignored.

Production was calculated by the attachment of the weight of lost, female reproductive products to equation 9.19 from Beverton and Holt (1957):

$$P = \int_{t_a}^{t_b} \left(\frac{d\bar{w}}{dt}\right)_t N_t dt + R \tag{8}$$

where

P = the production in grams of wet weight from times t_a to t_b,

$\left(\frac{d\bar{w}}{dt}\right)_t$ = the derivative of the chosen growth equation at time t,

N_t = the population number at time t, and

R = the calculated weight of lost, female reproductive products from times t_a to t_b.

Table 10. List of mathematical functions for the yearly calculation of the lost reproductive products for each adult female in the populations of fishes in Spawn Creek

R = (the spawning population of females) x (the weight of reproductive products of the individual)

Brown trout		
$\log W = -4.29 + 3.85 \log (TL_{cm}) + .0038d$	$r^2 = .92$	McFadden, Cooper, and Anderson (1965)
Cutthroat trout		
$E = (46.9/1.05)^a \; TL_{cm}$ $W = EV^b$	No error structure available	Rounsefell (1957)
Brook trout		
$\log E = - .5361 + 3.23 \log TL_{inches}$ $W = EV^c$	$r^2 = .76$	Wydoski and Cooper (1966)

W = the mean weight of the egg mass of the individuals within a given cohort
TL = the mean total length of the individuals within a given cohort
d = the number of days past 4 September when spawning occurs
E = the mean number of eggs from the individuals within a given cohort
V = the volume in cc of a single egg $(4/3\pi r^3)$

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[a] Transformation of fork to total length (Carlander, 1969)
[b] Radius in millimeters is 2.35 (Rounsefell, 1957)
[c] Diameter in millimeters is $2.71 + .23 (TL_{inches})$; $r^2 = .42$ (Wydoski and Cooper, 1966)

The fitted equations of time-dependent growth from Table 8 were differentiated with respect to time for each year class. The resultant derivatives were then multiplied by the appropriate, fitted equations of time-dependent density from either Table 6 or 7. These subsequent products were then integrated, and the calculated weights of lost reproductive products were added to the solutions of the respective integrals.

The calculations of production were divided into several parts per year class according to various periods of time throughout the study. These periods roughly corresponded to the growing season in 1973 (April 13 to November 20), the growing season in 1974 (April 13 to November 20), and the period of operation for the trap (November 21, 1973, to November 20, 1974). These periods were somewhat different for the 1974 and the 1973 year classes than previously mentioned, since the times of emergence for these groups varied from the above dates. Although the periods of calculation for these groups were based on shorter intervals, the calculated estimates still corresponded to the production during the delimited growing season because no production occurred prior to emergence.

When solutions from particular integrals were not explicitly obtainable, these values were calculated by numerical integration with the aid of a digital computer and the subroutine HPCG of the IBM Scientific Subroutine Package. This alogirathm uses Hamming's Modified Predictor-Corrector Method (Ralston and Wilf, 1960) to solve ordinary differential equations. The required inputs for HPCG consisted of the limits for the definite integral, the value of the integral at time t_a, an initial time increment, and an upper limit of error. When HPCG was used to calculate P for the various year classes, the values of t_a and t_b for each integration varied according to the respective seasons of interest; the value of P at t_a was always zero; the initial increment in time was 0.01 weeks; and an error bound of 0.001 gm was chosen. As output the program provided cumulative estimates of P at given points between t_a and t_b. Since the estimate of P at t_a was set at zero, the solution of the integrand in equation 8 was the calculated estimate of P at t_b.

RESULTS

Density

The numbers of the 0+ age groups of both brown and cutthroat trout varied greatly between corresponding months in 1973 and 1974 (Tables 11 and 12). In the former year the estimated densities of both species were considerably greater. Brown trout fry in October in 1973 were almost four times as numerous as in that month in 1974; cutthroat trout fry in late summer of 1973 were approximately 10 times as numerous in late summer of 1974.

The general trend in the estimated densities of brown and cutthroat trout show that as the individuals in a particular year class age, fewer of them survive. This is as expected, since the older individuals have been exposed to the forces of mortality longer. A notable exception was the 1971 cutthroat trout year class. This cohort was almost as numerous as the 1972 year class before it on most sampling dates. This prominance in the older group denotes a dominant year class as dominance was defined by Lagler, Bardach, and Miller (1967).

The relative densities among the age groups of the brook trout population did not follow the previously mentioned trend in 1973, but did in 1974 (Table 13). The estimated densities of these cohorts show that the 1970 and the 1971 year classes dominated the population vis-a-vis numbers in 1973. These two year classes were estimated to compose 63 percent of the population of brook trout in April of 1973, and 58 percent in August of the same year. The 1970 and the 1971

Table 11. List of viable estimates of density for brown trout year classes in Spawn Creek. Concomitant standard errors are in parentheses

Year Class	April 1973	August	October	March 1974	May	July	September	November
1974								13 (1.866)
1973		54 (16.159)	51 (23.292)					
1972			5 (7.18)	1 (0)	1 (0)		4 (.707)	2 (0)
1971			9 (1.684)	1 (0)	1 (0)	1 (0)		
1970	9 (2.135)	7 (1.969)	1 (---)					

Table 12. List of viable estimates of density for cutthroat trout year classes in Spawn Creek. Concomitant standard errors are in parentheses

Year Class	April 1973	August	October	March 1974	May	July	September	November
1974							42 (6.379)	
1973			483 (143.361)		35 (12.908)	28 (6.506)	118 (61.828)	121 (34.719)
1972	60 (25.191)	81 (16.542)	89 (11.231)	25 (3.016)	33 (6.464)	12 (1.898)	18 (2.584)	42 (5.868)
1971	50 (20.319)	46 (4.320)	77 (8.447)	18 (4.762)	32 (6.619)	25 (30.311)		19 (1.826)
1970	37 (11.990)		27 (6.756)	16 (1.721)	13 (1.892)	9 (0)	2 (0)	
1969	20 (2.348)	14 (1.747)	9 (13.416)			7 (1.292)		
1968	5 (0)	5 (0)	5 (1.5)					

year classes were respectively 4 and 3 years of age in the winter of 1974 and were at the end of their life span (McAfee, 1966). When these dominant groups passed from the scene in 1974, the population of brook trout contained age groups whose relative densities more closely showed a descending abundance with age as is typical for most streams (Hunt, 1966; McFadden, 1961).

Although a more normal relationship among densities within the population of brook trout was established in 1974, the density of the population as a whole declined. The population dropped from an estimated level of 101 in October of 1973 to 35 in November of 1974 (Table 13). This reduction can be attributed to the poor recruitment and/or survival of the 1973 and 1974 year classes vis-a-vis the other cohorts during the same stage in life.

The estimates of relative, instantaneous rates of mortality for all year classes in the stream ranged from 0.004 to 0.07 mortalities per week per individual (Tables 14, 15, and 16). Because concomittant variances for these estimated values varied widely among themselves, no attempt was made to correlate these relative rates to age or density.

Growth

The growth of brown trout in 1974 was similar to that in 1973, as mean weights of year classes were similar in both years (Table 17). Only the 0+ age group exhibited a disparity in growth between years. The 1973 year class averaged 9.8 gm as fry in the third week in October while the 1974 year class averaged only 5.8 gm in the same month a year later.

Table 13. List of viable estimates of density for brook trout year classes in Spawn Creek. Concomitant standard errors are in parentheses

Year Class	April 1974	August	October	March 1974	May	July	September	November
1974							23 (14.349)	17 (12.483)
1973		13 (4.085)	28 (4.014)	12 (4.937)	16 (8.490)	5 (7.180)		17 (12.323)
1972	33 (2.589)	26 (12.290)	41 (2.285)			6 (5.750)		1 (0)
1971	28 (6.400)	44 (10.532)	20 (3.706)	4 (1.118)		3 (.913)	1 (0)	
1970	29 (4.530)	9 (2.581)	12 (1.581)					

Table 14. List of estimated coefficients for the models of time-dependent density of brown trout year classes in Spawn Creek from April, 1973, to November, 1974. Concomitant standard deviations are in parentheses

Year Class	Coefficients[a]						
	N_o	C	s	b	r	χ^2	df
1974							
1973							
1972	15.9 (33.509)	-.853 (.3979)	26.3 (3.873)	52.0	.0265 (.021917)	.0	1
1971	175.7 (178.700)				.0701 (.022599)	.2	2
1970	19.8 (11.414)				.0479 (.020299)	3.0	1

χ^2 = criterion for goodness-of-fit (Bevington, 1969)

df = degrees of freedom

---

[a] Definitions for the identifiers are in Table 6

[b] Graphically set constants

Table 15. List of estimated coefficients for the models of time-dependent density of cutthroat trout year classes in Spawn Creek from April, 1973, to November, 1973. Concomitant standard deviations are in parentheses

Year Class	Coefficients[a]								
	N_o	C	s	b	r	z	i	χ^2	df
1974	2×10^{16}[b]					.384470			
1973	4.729×10^7 (6.291)[c]					.384470 (.194370)	.002623 (.001412)	.3	2
1972	245.8 (87.655)	-.548 (.1372)	29.0 (1.735)	23.7 (.969)	.0322 (.004971)			5.4	3
1971	272.6 (88.110)	-.941 (.2952)	29.1 (.752)	24.1 (.763)	.0361 (.006095)			1.6	2
1970	48.6 (52.820)	-.095 (.2982)	35.0[d]	52.0[d]	.0169 (.017866)			.0	3
1969	23.4 (1.971)	.031 (.0976)	31.0[d]	52.0[d]	.0151 (.001670)			.1	1
1968	10.4 (77.718)				.020 (.177370)			.0	1

χ^2 = criterion for goodness-of-fit (Bevington, 1969)   df = degrees of freedom

---

[a] Definitions of the identifiers are in Table 7

[b] Coefficients lifted from 1973 data and applied to the 1974 year class data point

[c] Standard deviations from a logarithmic fit

[d] Graphically set constants

Table 16. List of estimated coefficients for models of time-dependent density for brook trout year classes in Spawn Creek from April, 1973, to November, 1974. Concomitant standard deviations are in parentheses

Year Classes	Coefficients[a]			
	N_o	r	χ^2	df
1974	441.9 (---)[a]	.033587 (----)		
1973	28.4 (24.154)	.00440 (.019543)	.7	4
1972	87.9 (5.140)	.03986 (.001250)	70.3	3
1971	60.8 (16.626)	.03674 (.005975)	2.1	4
1970	42.3 (18.053)	.031386 (.011393)	.5	1

χ^2 = criterion for goodness-of-fit (Bevington, 1969)

df = degrees of freedom

---

[a] Definitions of identifiers are in Table 6

[b] Standard deviations undefined

Table 17. List of the estimates of individual mean weight for brown trout year classes in Spawn Creek. Concomitant standard deviations are in parentheses and measurements are in grams

	Year classes							
Months	1974	1973	1972	1971	1970	1969	1968	1967
April 1973			12.7 (2.215)	40.0 (5.656)	66.6 (4.704)	201.0 (---)		
April				59.0 (6.429)	142.0 (---)			
May				62.0 (---)	153.0 (---)			
July		3.3 (.882)	39.0 (---)[a]	90.0 (11.000)	163.0 (---)			
August		6.2 (.282)	44.9 (11.205)	125.3 (.477)	191.5 (4.766)			
October		9.8 (.376)	55.7 (6.333)	119.5 (9.428)	208.0 (---)			600.0 (---)
December		9.7 (1.017)	61.7 (5.783)	104.0 (---)				
January 1974			62.0 (--)					
February			60.7 (8.686)	127.0 (---)				

Table 17. Continued

	Year classes							
Months	1974	1973	1972	1971	1970	1969	1969	1967
March 1974		9.5 (.707)	70.0 (---)	118.0 (---)				
May			80.0 (---)	127.0 (---)				
June				167.0 (---)				
July			79.5 (19.092)	154.0 (---)				
August	2.0 (.333)		114.0 (---)		230.0 (---)			
September	4.8 (.944)	66.3 (9.452)	124.0 (9.452)		205.0 (---)			
October	4.0 (.167)	71.5 (30.500)			239.0 (---)			
November	5.8 (.269)	57.0 (22.730)	121.5 (26.500)	174.0 (---)				

[a] Standard deviation is undefined.

The cutthroat trout as a species grew much the same as did the brown trout. Again all age groups exhibited similar growth for 1973 and 1974, save the young-of-the year (Table 18). The 1973 year class averaged 2.5 gm as fry in the third week in October while the 1974 year class averaged only 1.1 gm in the same month a year later.

The growth of the brook trout took the same pattern with one exception. The 1974 year class as fry outgrew the 1973 year class (Table 19). The latter cohort was 6.9 gm in the third week in October while the former was 9.8 gm a year later.

The estimates of the asymptotic weight for the individual brown, cutthroat, and brook trouts and the concomittant standard deviations were 504 gm (SD = 157), 622 gm (SD = 730), and 353 gm (SD = 334), respectively.

The amplitude of the seasonal fluctuations in the mean weight of the individual (C) of the brown trout varied from 59 to 24 percent of the sigmoid growth (Table 20). The standard deviations in these estimates increased with the age of the year class. The amplitudes for the cutthroat trout varied from 46 to 14 percent, and their standard deviations were lowest in the 1971 year class and rose in younger and older cohorts (Table 21). The amplitudes for the brook trout varied from 51 to 23 percent of the general trend in growth (Table 22). The standard deviations of these estimates ranged similarly to those for the estimates from year classes of cutthroat trout.

The estimates of the phasing of the seasonal fluctuations in growth (s), the frequency of these fluctuations (b), and the time of null weight for the individual (t_o) varied among species and year classes

Table 18. List of estimates of individual mean weight for cutthroat trout year classes in Spawn Creek. Concomitant standard deviations are in parentheses and measurements are in grams

Months	Year Classes 1974	1973	1972	1971	1970	1969	1968	1967	1966
April 1973			6.5 (.566)	24.8 (1.345)	56.6 (3.203)	115.2 (6.313)	191.4 (15.518)		
April			2.1 (.398)	14.8 (1.551)	49.7 (4.321)	140.8 (41.500)		331.0 (5.657)	
May			4.8 (2.588)	27.1 (11.086)	83.0 (6.706)	173.0 (21.024)			
June				36.0 (---)[a]	100.0 (---)	118.0 (---)			
June			2.0 (1.000)	28.0 (11.314)	60.0 (7.071)	107.3 (33.292)	151.5 (44.548)		
July		1.0 (---)	16.5 (2.414)	53.3 (8.876)	95.7 (5.781)	127.5 (19.092)			
August		.6 (.122)	17.2 (.992)	71.4 (3.549)		142.6 (6.737)	222.4 (39.488)		425.0 (---)
October		2.5 (.063)	17.2 (.847)	61.3 (2.535)	127.8 (5.528)	185.0 (8.626)	205.8 (22.261)		
December		4.0 (.707)	21.8 (8.408)	48.1 (4.453)	109.0 (23.000)				
January 1974		3.1 (1.168)	18.5 (1.230)	49.6 (3.386)	97.1 (4.487)	167.0 (29.547)			

Table 18. Continued

Months	Year Classes								
	1974	1973	1972	1971	1970	1969	1968	1967	1966
February 1974		5.0 (2.828)	19.9 (1.877)	51.0 (3.606)	100.7 (13.781)				
March		2.2 (1.134)	18.6 (1.348)	55.4 (3.718)	94.4 (10.048)		200.0 (---)		
May		4.2 (.370)	40.4 (3.202)	94.9 (2.941)	150.1 (13.317)				435.0 (---)
June		6.1 (.766)	33.5 (5.500)	54.5 (12.500)	100.4 (14.436)	163.2 (26.694)			362.0 (---)
July		8.2 (.569)	32.5 (1.614)	64.2 (16.135)	105.3 (13.416)	173.1 (14.121)			
August		13.9 (1.235)	54.7 (4.003)	92.0 (4.359)	165.0 (17.059)				382.0 (---)
September	.8 (.002)	18.4 (2.814)	76.3 (4.082)	127.2 (23.964)	189.0 (---)				
October	1.3 (.006)	19.3 (2.256)	87.8 (8.880)	163.7 (8.433)			339.0 (---)		
November	1.1 (.224)	15.8 (.801)	71.7 (3.271)	143.8 (4.185)	182.0 (---)				

[a] Standard deviation is undefined

Table 19. List of estimates of individual mean weight for brook trout year classes in Spawn Creek. Concomitant standard deviations are in parentheses and measurements are in grams

	Year Classes					
Months	1974	1973	1972	1971	1970	1969
April 1973			11.3 (8.318)	30.6 (2.044)	64.3 (4.287)	
April			9.7 (3.467)	41.5 (12.748)	68.3 (11.805)	106.0 (---)[a]
May			9.9 (1.099)	41.3 (4.187)	77.3 (4.500)	116.0 (---)
June			27.3 (2.171)	50.8 (5.762)	77.2 (17.712)	150.0 (5.657)
June			20.2 (1.483)	51.3 (4.031)	93.0 (18.056)	
July		3.3 (.882)	35.0 (2.739)	84.1 (5.501)	137.7 (13.051)	
August		5.5 (.871)	36.1 (2.611)	83.1 (4.123)	149.0 (7.303)	
October		6.9 (.878)	52.1 (2.361)	91.7 (5.270)	131.2 (3.760)	
December		5.0 (-)	35.0 (--)	68.3 (6.303)	119.5 (11.500)	

Table 19. Continued

Months	Year classes 1974	1973	1972	1971	1970	1969
January 1974		4.0 (--)	36.3 (5.239)			
March		13.8 (2.104)	43.0 (7.000)	62.7 (16.623)		
May		18.6 (1.661)	66.0 (9.900)	74.5 (6.637)		
July		19.0 (4.509)	52.6 (12.772)	88.0 (8.000)		
August		28.0 (4.000)	43.0 (4.041)	98.0 (---)		
September	8.2 (.618)	41.2 (8.048)	77.0 (18.908)	131.0 (---)	218.0 (---)	
October	8.0 (1.000)	74.0 (7.241)		139.0 (---)		
November	9.8 (1.161)	51.6 (5.393)	121.0 (---)			

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[a] Standard deviation is undefined

Table 20. List of estimated coefficients of models of time-dependent growth for brown trout year classes in Spawn Creek from April, 1973, to November, 1974. Concomitant standard deviations are in parentheses

Year Class	Coefficients[a]								
	W_o	C	s	b	k	t_o	g	χ^2	df
1974	.0064 (.005322)						.0702 (.008214)	2.7	7
1973		.588 (.081509)	20.6 (2.677)	53.0 (4.978)	.0063 (.000507)	-2.7 (3.451)		1.4	3
1972		.238 (.094954)	27.0 (8.419)	55.1 (10.723)	.0068 (.000844)	-45.6 (10.349)		.2	8
1971		.425 (.108910)	19.8 (2.798)	52.0 (6.533)	.0066 (.000902)	-91.4 (16.670)		1.1	8
1970		.584 (.393100)	19.1 (12.430)	66.2 (10.000)	.0059 (.001888)	-134.1 (52.457)		.3	4

χ^2 = criterion for goodness-of-fit (Bevington, 1969)

df = degrees of freedom

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[a] Definitions of identifiers are in Table 8

Table 21. List of estimated coefficients of models of time-dependent growth for cutthroat trout year classes in Spawn Creek from April, 1973, to November, 1974. Concomitant standard deviations are in parenthesis

Year Class	Coefficients[a]								
	W_o	C	s	b	k	t_o	g	χ^2	df
1974	.0051 (.007297)						.0593 (.016034)	.0	11
1973		-.456 (.048256)	15.7 (3.779)	41.7 (2.158)	.0032 (.000112)	-6.5 (3.152)		.9	9
1972	1.5634 (.194130)	.215 (.035323)	63.9 (.481)	22.5[b]	.0075 (.000379)	-8.3 (3.351)	.0587 (.003459)	19.9 23.7[c]	5 8[c]
1971		.194 (.021677)	65.9 (.410)	22.1 (.388)	.0052 (.000213)	-66.9 (4.845)		16.8	14
1970		-.156 (.030337)	7.7 (1.366)	21.6 (.716)	.0045 (.000428)	-130.0 (15.691)		6.1	12
1969		.136 (.033556)	16.6 (2.094)	21.9 (1.417)	.0037 (.000915)	-237.9 (63.098)		1.1	6
1968		-.177 (.195260)	16.2 (2.554)	26.0[b]	.0036 (.003220)	-278.8 (274.690)		.5	1

χ^2 = criterion for goodness-of-fit (Bevington, 1969)   df = degrees of freedom

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[a] Definitions of identifiers are in Table 8

[b] Graphically set constants

Table 22. List of estimated coefficients of models of time-dependent growth for brook trout year classes in Spawn Creek from April, 1973, to November, 1974. Concomitant standard deviations are in parentheses

Year Class	Coefficients[a]								
	W_o	C	s	b	k	t_o	g	χ^2	df
1974	1.6554 (2.0032500)						.0179 (.014916)	.2	3
1973		-.230 (.051559	4.4 (3.102)	52.0[b]	.0068 (.000372)	-3.5 (3.331)		3.2	8
1972		.509 (.040821)	29.0[b]	60.0 (1.811)	.0048 (.000676)	-88.3 (17.214)		4.7	12
1971		.402 (.030551)	25.3 (.968)	49.6 (1.714)	.0027 (.000207)	-225.0 (19.748)		1.7	10
1970		.360 (.042194)	22.5 (.963)	52.0[b]	.0035 (.000945)	-279.5 (82.507)		1.7	6

χ^2 = criterion for goodness-of-fit (Bevington, 1969)

df = degrees of freedom

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[a] Definitions of identifiers are in Table 8

[b] Graphically set constants

as would be expected for groups with dissimilar periods of reproduction, stages of maturation, and ages. The adults in the populations of brown and brook trouts spawn in the late autumn of the year, and hence their reproductive loss in weight is contiguous with the cessation of growth in the winter. The adults in the cutthroat trout population spawn in late spring and early summer with periods of growth before and after this season. Juveniles in the cutthroat trout population do not have a loss of weight during the reproductive season, and as such, exhibited approximately half the frequency in their pattern of seasonal fluctuation of growth as did the adults of that species.

The estimates of the coefficients of catabolism ($\underline{k}$) varied from 0.0075 to 0.0027. The brown trout year classes showed the least amount of age-dependent variation as compared to the other species.

Migration

Little immigration occurred until the middle of April when adult cutthroat trout (2+ and older) began to move (Figure 5). This movement continued until the second week in June and peaked the first week in May. Peak spawning activity was observed on the second week in that month. When the trap was placed back into operation after the bed-load sedimentation problem was alleviated, an immigration of juvenile cutthroat trout was monitored. This movement ended on the second week in November and peaked on the first week in October. The constituents of this run were members of the 1+ and 2+ age groups.

Brown trout immigration occurred in the fall of the year only and consisted of all age groups (Figure 6). The numbers of immigrants were

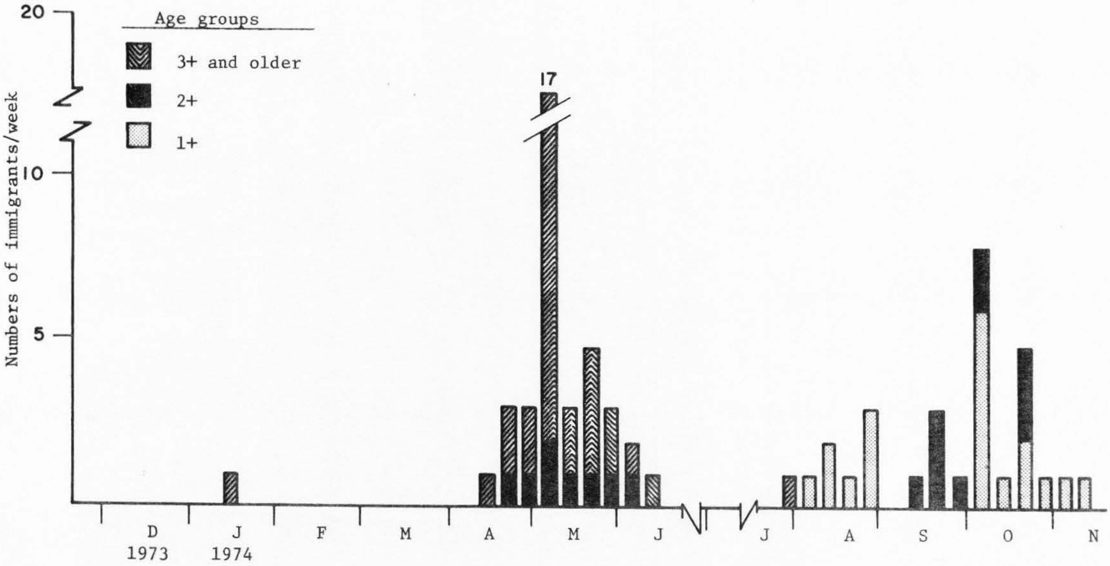

Figure 5. Graph of the immigration of individuals of all age groups of cutthroat trout (save the 0+ age group) into Spawn Creek from November 21, 1973, to November 20, 1974. The break in abscissa corresponds to the period when bed-load sedimentation halted sampling at the trap

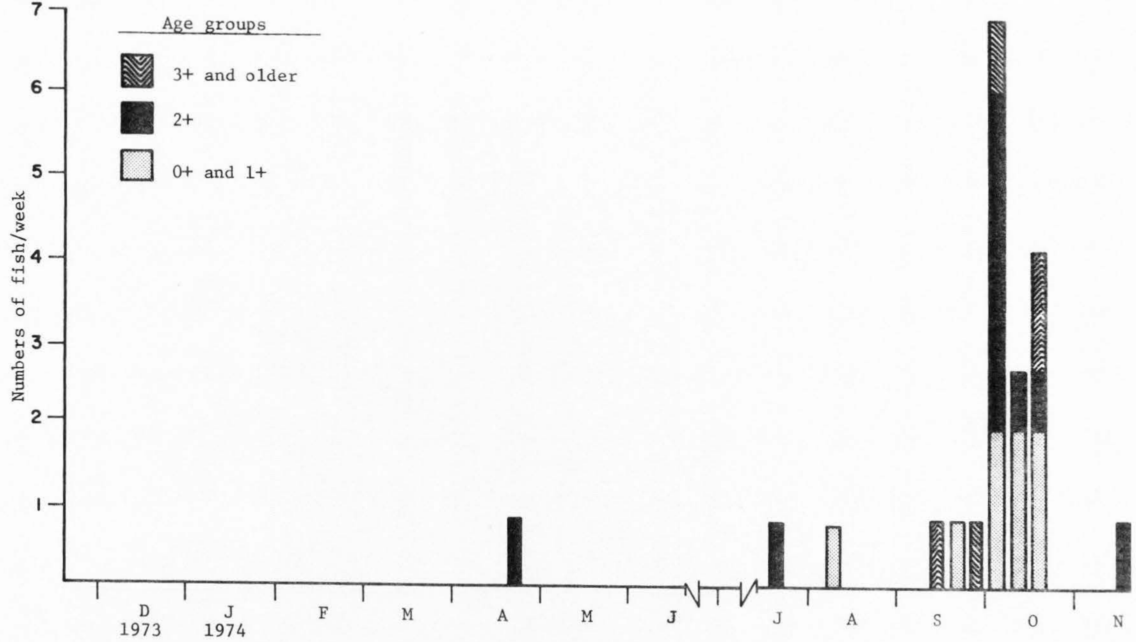

Figure 6. Graph of the immigration of individuals of all age groups of brown trout into Spawn Creek from November 21, 1973, to November 20, 1974. The break in the abscissa corresponds to the period when bed-load sedimentation halted sampling at the trap

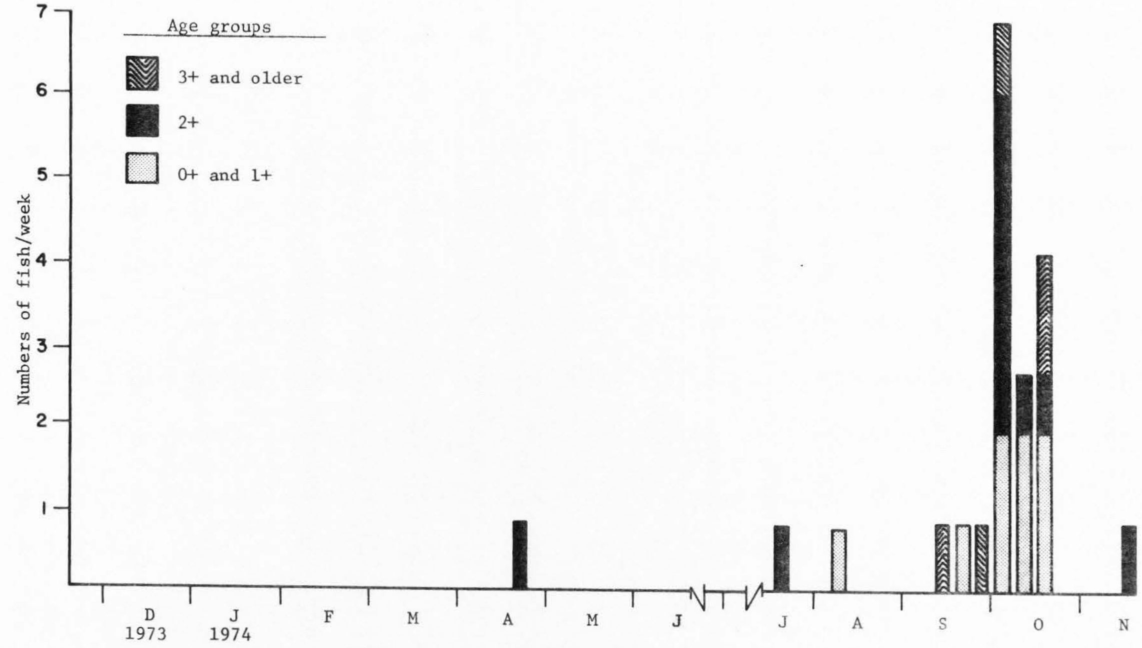

Figure 6. Graph of the immigration of individuals of all age groups of brown trout into Spawn Creek from November 21, 1973, to November 20, 1974. The break in the abscissa corresponds to the period when bed-load sedimentation halted sampling at the trap

quite low in comparison to the earlier cutthroat migration in the spring (Table 23). The adults immigrated primarly in October and the numbers of these migrants peaked in the first week of this month.

Emigration of the 0+ cutthroat trout age group occurred primarily in October (Figure 7). These animals remained in Spawn Creek from approximately 10 to 22 weeks before wintering in lower waters. Emigration of the 0+ brown trout age group occurred in conjunction with the cutthroat trout of the same age; however the number of emigrants was in no way as large as that of the other species (Table 23).

Emigration in the 1+ and older age groups of brown and cutthroat trouts occurred in a more uniformly random fashion (Figure 8).

The year classes of brook trout did not as a rule have migratory constituents. Only five brook trout were caught in the trap in 1974. Four of these individuals were emigrating juveniles while the other was an adult that was caught twice.

Production

A salient feature in the pattern of production by the trouts in Spawn Creek between the growing seasons in 1973 and 1974 was the larger amounts of produced biomass in the former year (Figure 9 and Table 24). Every age group save one exhibited greater production in 1973 than in 1974; the lone exception was the 0+ brook trout age group. The amount of produced biomass was so reduced in 1974 that actual losses occurred in several age groups. Three times as many age groups showed a loss in produced biomass in 1974 as opposed to 1973. All losses of production during the growing seasons occurred in cutthroat trout age groups.

Table 23. List of the numbers and biomasses of brown and cutthroat trout migrants into and out of Spawn Creek from November 21, 1973, to November 20, 1974. Biomass is in grams

Year Class	Brown trout				Cutthroat trout			
	Emigrants		Immigrants		Emigrants		Immigrants	
	Numbers	Biomass	Numbers	Biomass	Numbers	Biomass	Numbers	Biomass
1974	12	65	2	13	229	269		
1973	18	180	6	203	43	317	18	250
1972	5	319	9	489	31	1085	20	950
1971	2	366	3	588	37	3597	10	807
1970	1	170	2	462	8	1087	6	1237
1969					4	713	6	1147
1968					2	557	6	1585

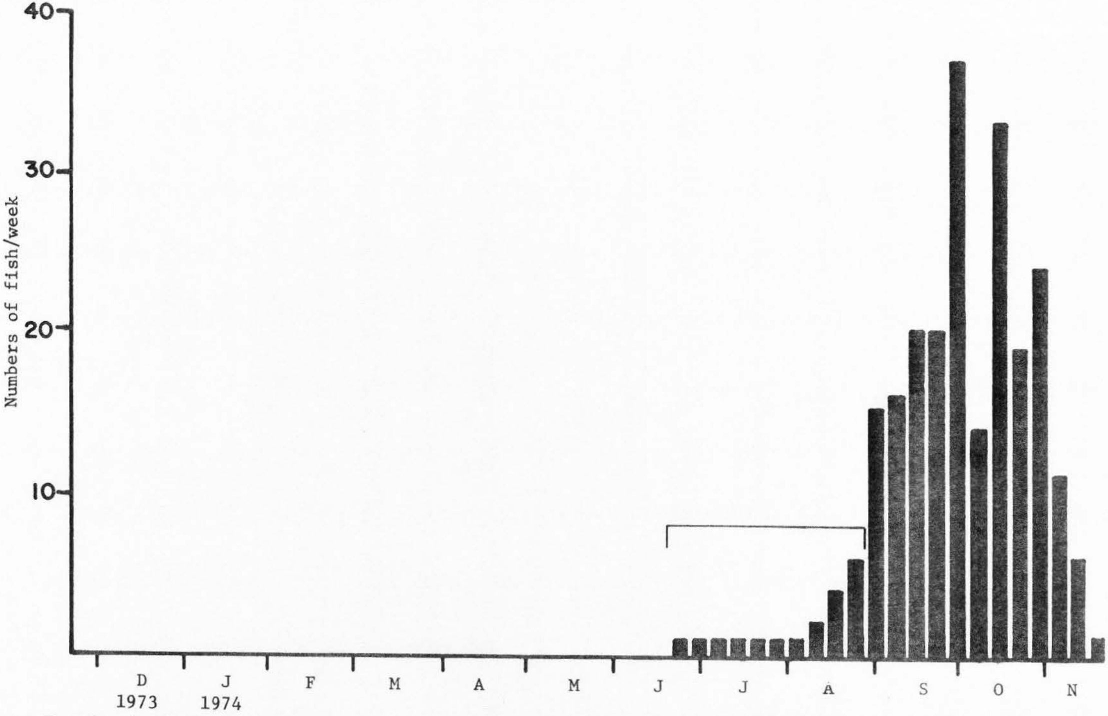

Figure 7. Graph of the emigration of individuals of the 0+ age group of cutthroat trout out of Spawn Creek from November 21, 1973, to November 20, 1974. The bars under the bracket correspond to estimated desnsities as calculated by the fitted equation in Table 4

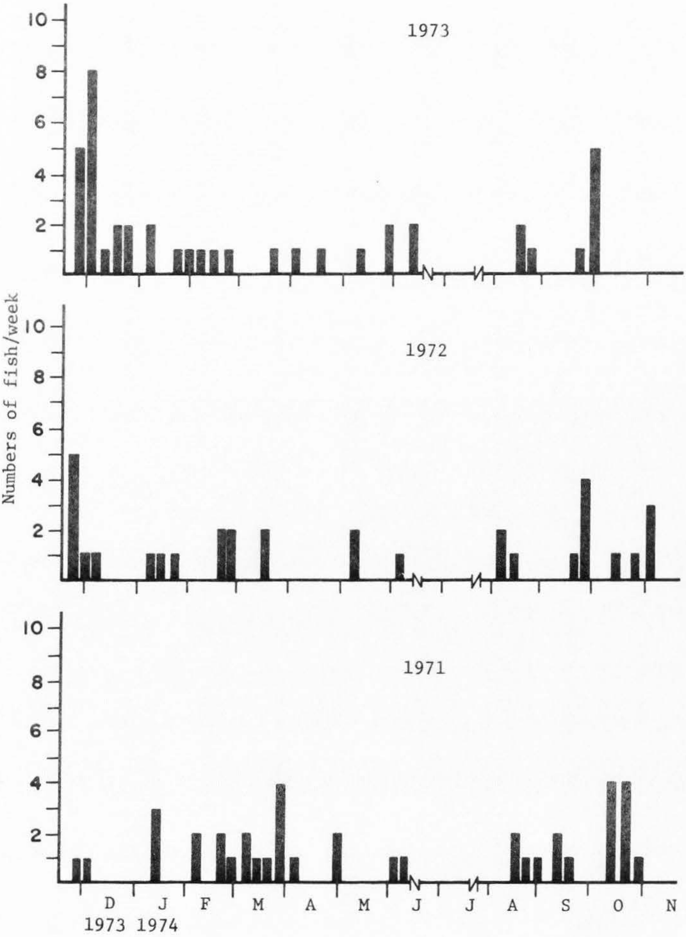

Figure 8. Graph of the emigration of individuals of the 1973, 1972, and 1971 year classes of cutthroat trout out of Spawn Creek from November 21, 1973, to November 20, 1974. The breaks in the abscissas correspond to the period when bed-load sedimentation halted sampling at the trap

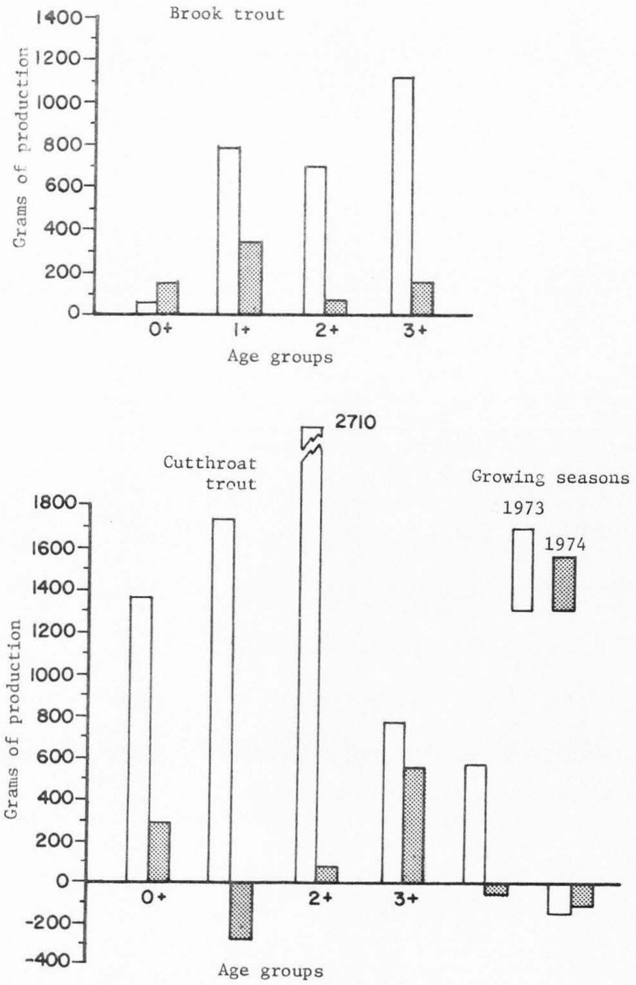

Figure 9. Graph of the calculated estimates of production for the different age groups of cutthroat and brook trouts for both the 1973 and the 1974 growing seasons. Each estimate encompasses the entire area of study

Table 24. Estimates of production in Spawn Creek by brown, cutthroat, and brook trout year classes for the three periods April 1 to November 20, 1973 (G73), April 1 to November 20, (G74), and November 21, 1973, to November 20, 1974 (TO). All the values for the production by the adult cohorts of trout were adjusted by the loss of female reproductive products (Appendix). All values are in grams

Year classes	Periods	Brown trout	Cutthroat trout	Brook trout
1974[a]	G74 & TO		257	141
1973[b]	G73		1351	46
	G74		-336	307
	TO		-545	138
1972	G73	147	1711	741
	G74	124	88	74
	TO	45	-170	-129
1971	G73	78	2710	696
	G74	24	235	145
	TO	81	-470	-7
1970	G73	653	775	1118
	G74	66	-39	283
	TO	-109	-208	-85
1969	G73		552	
	G74		-145	
	TO		-146	
1968	G73		-167	
	G74		134	
	TO		-130	

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[a] Production was calculated from the estimated time of emergence (cutthroat trout: June 24-30; brook trout: March 4-10)

[b] Production was calculated from the estimated time of emergence (cutthroat trout: June 11-17; brook trout: March 11-17)

Another trend was the loss of production in the year that is represented by the operation of the trap (Table 24). The year classes that lost production in this period were the 1970 brown trout, all the cutthroat save for the 1974 year class, and all the brook trout save the 1973 year class.

Because no models of time-dependent density were constructed for the 1974 and the 1973 brown trout year classes, no estimates of production were made for these groups.

The estimates of production for the period of trap operation were compared to the net emigration in various year classes of brown and cutthroat trouts (Table 25). These comparisons show that for the cutthroat trout only the 0+ age group was able to produce and export biomass. The next three older groups all lost biomass through production but still exported biomass. The three oldest age groups imported biomass but still showed a net loss through production. All three year classes of brown trout showed an importation of biomass while only the 1970 year class showed a loss of biomass due to production.

Table 25. Comparison of net migration, production, and their ratio for the brown and cutthroat trout year classes from November 21, 1973, to November 20, 1974. Net migration and production are in grams

Year Class	Brown trout			Cutthroat trout		
	M_N[a]	P	$\lvert M_N/P \rvert$	M_N	P	$\lvert M_N/P \rvert$
1974				269	257	1.047
1973				67	-545	.123
1972	-170	45	3.778	135	-170	.794
1971	-222	81	2.741	2790	-470	5.936
1970	-292	-109	2.678	-150	-208	.721
1969				-434	-146	2.973
1968				-1028	-130	7.908

[a] M_N = emigration minus immigration

DISCUSSION

Density

The density of a particular year class of fish greatly influences not only its own productive capacity, but also that of its population. When a population is composed of a small number of numerically dominant year classes, often these groups dominate the productive capacity of the population as well. A good example of the effects of numerical dominance on productive capacity can be made with the population of brook trout in Spawn Creek. The 1970 and 1971 year classes were numerically and productively dominant in 1973 (Table 24 and Figure 9). The total, estimated, production for that species during that growing season for the entire stream was approximately 2.6 kg, while during the corresponding season in the next year, the estimated amount of produced biomass was only 0.95 kg. Since growth was virtually the same for the individuals in corresponding age groups in both years, only the heavy mortality in the dominant year classes in the intervening, winter months could explain this dramatic loss of productive capacity in the population.

If numerical dominance in a year class greatly affects the dynamics of production in their population, those factors that regulate this dominance are of great importance. Often, when intraspecific competition occurs, a population of fish is structured with a single, almost exclusively dominant year class. However, in populations of salmonids with such structure, the numerical dominance of a particular year class is usually determined by the severity of abiotic factors in the environment in the first year of life relative to those factors for other year classes in previous years (Kramer, 1969). The productive capacity of such a population in a given year is then partially dependent on the history of the abiotic environment as manifested through the survivorship of the first year of presence for each year class.

The causes behind the formation of dominant year classes of brook trout in Spawn Creek are probably not intraspecific, but are abiotic. When intraspecific competition is the reason behind dominance, usually the presence of a dominant year class is cyclical over a period of years (Royce, 1973). As the dominant year class passes from the scene, the intensity of competition is momentarily relaxed, and their progeny form the new dominant group. The 1974 year class of brook trout was numerically very weak in comparison to what the density of the 1970 and 1971 year classes must have been at a similar age (Table 13). A more probable reason for the lack of establishment of dominant year classes over the past few years would be a diminishing amount of available or suitable habitat. Often the robustness of populations of brook trout in many streams is directly related to the presence of beaver (McAfee, 1966; McFadden, 1961). If this relationship holds in Spawn Creek, the abandonment of the beaver ponds on this stream probably was the reason for the poor survivorship in the 0+ age group and the subsequently poorer productive capacity of the population in 1974.

Because the population of brook trout in Spawn Creek is a closed population, the decline of the beaver is of great importance to the fisheries manager. If the loss of suitable habitat is not reversed the presence of dominant year classes, the productive capacity, and subsequently the angling yield from this fishery will continue to decline.

Growth

The relative growth of the various age groups of fish varied little between the growing seasons of 1973 and 1974, save for the 0+ age groups. These groups showed the greatest relative discrepancy between these two periods. One factor in this difference could be the variance in the time of growth past emergence of each of the appropriate year classes. The estimated time of emergence for cutthroat trout fry in 1973 was around June 14, while the estimate for the 1974 year class was June 27 (Table 24). This difference was due largely to the later spawning of cutthroat trout in 1974 as opposed to 1973. This allowed the 0+ age group in 1973 to attain approximately a two-week longer growing season than their counterparts in 1974. Since no observations on the spawning of brook or brown trouts were made in the late fall of 1972, no estimates of the times of emergence for the 1973 year classes of these species were made, and subsequently no comparison of these times could be made as was done for the cutthroat trout.

Another factor in the discrepancy between the attained weight of the 0+ age groups in the growing seasons of 1973 and 1974 could be the water temperatures in those respective years. The temperature of ambient waters has long been known to have a pronounced affect on the growth of fish (Brown, 1957; Davis and Warren, 1971; Kinne, 1960; and Lagler, 1967). Unless the population of fish is living near its upper limit of thermal tolerance, the rate of growth is directly proportional to the ambient water temperature.

The mean, daily water temperatures of Spawn Creek were colder at the trap site in the summer of 1974 as opposed to the summer of 1973.[1] An average of these daily values over June, July, and August was calculated for each year; the difference, 1.4 C, was significant at the 99 percent level of confidence. The differential in water temperatures probably shrank as the source of the stream was approached, and the water temperature was more influenced by inflows of groundwater.

The relationship of the weight of an individual fish and its metabolic rate has been described both as linear and as allometric (Phillips, 1969). Although no specific work on this relationship has been done for cutthroat trout to date, Beamish (1964) tried to elucidate this mechanism for the brown and brook trouts. Although he did find allometric deviations from linearity between weight and metabolic rate, most of these deviations were not statistically significant.

If the matabolic rates of the fish in Spawn Creek were allometrically related to temperature such that the relative metabolic rate increased with a decrease in weight, the smaller fish in the stream would be more responsive to changes in temperature than would be the larger. If a gram of biomass metabolizes faster in a small fish as opposed to a larger one at a given water temperature, the effects of a change in temperature on growth should be amplified in the smaller animal. This

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[1] Personal communication. Tom Twedt, Graduate Research Assistant, Department of Civil and Environmental Engineering, Utah State University, Logan, Utah 84322. March 15, 1975.

amplification could partially explain why the 0+ age groups and not the older trouts exhibited a relative differential in growth between the two growing seasons. Since the cutthroat and brown trouts occupy the lower elevations of stream vis-a-vis the brook trout, their 0+ age groups would be expected to show a greater response in growth to the colder growing season in lower waters.

Migration and Production

The patterns of immigration for both the brown and cutthroat trouts were closely aligned with the reproduction of each species with one exception. Since no precedent could be found in the literature, the immigration of some juvenile cutthroat into Spawn Creek in the fall of 1974 remained a mystery. Also, a rise in the estimated density of the 1+ and 2+ age groups occured in the stream in the fall of the previous year before the trap was placed into operation. Since most of these animals at this age were not reproductively mature, and since this migration occurred beyond the spawning season for cutthroat in this stream (Fleener, 1952), reproduction probably was not the cause. A behavioral response to some condition within the stream, such as large densities of emergent insects or the activities of fall spawning trout, might have triggered this phenomenon, but the energy demands of migration would have somewhat offset any dietary advantage. Whatever the reason, this immigration appeared in more than a single year and was an important factor in the dynamics of time-dependent density and production.

The gap in the data from the trap probably had little bearing on the overall picture of migration. The immigration of individuals in both the brown and cutthroat trouts appeared peaked with the gap well away chronologically from any intense immigration (Figures 5 and 6). Probably some individuals did emigrate during this period. However, the random fashion in which this emigration took place (Figure 8), probably kept the missed number of emigrants to a minimum relative to the total sum. The number of emigrating individuals from the 0+ age group of cutthroat trout was estimated.

One of the estimates of production in Table 25 was blatantly incorrect. Since no immigration of individuals in the 1974 cutthroat trout year class occurred during the year of trap operation, this group could not have exported more biomass than was produced in its first year of life. This discrepancy arose from two errors. The first such error was in the descriptive mathematics of the time-dependent density for that age group. This bias caused an underestimation of the production by emigrating individuals out of the stream before they could grow. The second error concerned the poor recruitment by the sampling techniques. The lone estimate for the density of this age group was obviously incorrect. On the week of September 9, the density of the 1974 year class of cutthroat trout was estimated at 42 individuals for the entire stream (Table 12). From that date to November 20, 179 individuals of the 0+ age group of cutthroat trout emigrated (Figure 7). This gross error in the estimate was probably due to insufficient recruitment of these fish by the electro-fishing gear. The smaller growth of the fish in the 1974 year class as compared to those of previous years at this time of the growing season probably was part of the cause of this poor recruitment.

The estimate of the amount of biomass produced by the 1973 year class of cutthroat trout in the growing season of 1973 was probably biased as well. Again the members of this age group were probably modeled as evacuating the stream too soon and thereby reducing the amount of produced biomass. Like the 1974 year class a year later, only one viable estimate of density was made, but this estimate probably was more realistic. The larger sizes of individuals in the 0+ age group in 1973 relative to those in 1974 would have enhanced recruitment by electro-sampling.

In the 1971, 1972, and 1973 year classes of cutthroat trout, the exportation of biomass was probably the reason for the loss of production during the year of operation of the trap. These three year classes exported 18, 16, and 26 individuals respectively between November 21, 1973, and April 1, 1974 (Figure 8). Along with those individuals who died during this period, these losses of individuals represented losses in the means of production. As these lost animals either emigrated or died during the debilitating winter months, not only did their seasonal loss of weight up to their time of departure subtract from the amount of production that year, but their passage from the scene deprived the stream of the means of regaining that lost biomass. Whether the immigrants that moved into Spawn Creek in the spring and/or fall migrations in 1974 were originally from this stream or not, had no bearing on this loss in production. These immigrants had grown outside the stream and as such the resultant production did not come from Spawn Creek. Therefore, the large amounts of exported biomass were the reason for the loss of productive capacity in the 1971, 1972, and 1973 year classes.

The 1970 and older year classes of cutthroat trout also lost production in the year of operation of the trap, but they, unlike the younger groups, imported biomass from lower waters. This situation denotes extremely poor growth in these groups. If these additions of immigrants to the population represented supplements for the productive capacity of their respective year classes, these additions were not used in such a manner. These immigrating individuals moved into the stream after the cold winter months during the spring when the conditions for growth were optimal.

The imported biomass of the 1970 and older year classes of cutthroat trout did not represent added productive capacity, but reproductive potential. These individuals immigrated into Spawn Creek, reproduced, and then either emigrated or died in a state of reduced weight. Since the values for production had been corrected for the loss of reproductive products, the loss of production represents a metabolic loss of weight in the individual that was not regained. Cope (1957b) observed a large degree of agression and defense of territory by cutthroat males during the spawning season in most streams. Ball and Cope (1961) reported an average loss in weight of 94 gm per female and 74 gm per male during the spawning season in Arnica Creek. Also these authors noted a 48 percent mortality among spawners, mostly males, during said season. Obviously, since males lose only about 1 percent of their body weight in the expulsion of reproductive products while spawning (Lagler, Bardach, and Miller, 1967; Royce, 1973), the loss of weight in the males in this situation was due largely to their associated, reproductive behavior. Their emigration or death after reproducing would have denied the stream the means to regain this lost weight.

The salient feature of the cutthroat trout as a population, excluding the 1974 year class, was that they lost approximately 1.7 kg of biomass. These losses for such a small population would be catastrophic if said population were closed. However, the simple existance of this population under such conditions, the large number of migrants, and the stratified manner in which they migrate with the juveniles emigrating and the adults immigrating biomass, showed that the population of cutthroat trout in Spawn Creek was really an extension of the population of this species from lower waters. The main function of this stream vis-a-vis the population of cutthroat trout in the lower waters was as a repository of reproduction. The stream first acts as a vehicle for spawning and then as a brood area for the young.

Although the brown trout year classes acted similarly to those cutthroat groups previously described, the conclusions similar to those drawn for the cutthroat trout population could not have been as firm. Again all the older year classes imported biomass during the year of trap operation but failed to respond with increased production (Table 25). Since brown trout also show much aggressive behavior and exacerbated rates of mortality during spawning (Greeley, 1932; O'Donnell and Churchill, 1954), this loss of production probably represented the use of the imported biomass as reproductive potential. However, no estimates of production were made for the juveniles of this species and few were seen emigrating. The numbers of individuals of brown trout of all ages in the population made the use of descriptive mathematics extremely difficult, and subsequent estimates must be viewed with some trepidation. Also, since the termination of the study was concurrent with the peak of the brown trout spawning season in 1974, the loss of production was probably a manifestation of the previous season in 1973. These qualifying factors reduce the firmness of any inferred conclusion similar to the illation for the population of cutthroat trout.

CONCLUSIONS

The brook trout were members of a closed population whose productive capacity fluctuated dramatically with the presence or absence of dominant year classes. Because brook trout spent their total existance in Spawn Creek and could not rely on the importation of reproductive potential, these fish were more proficient in the compensation of seasonal losses of production than were the other indigenous trouts. The failure to produce new, dominant year classes was perhaps a function of the declining suitability of habitat for fry.

The cutthroat trout were members of an open population whose dynamics were dominated by migration and reproduction. The stream provided a vehicle whereby the reproduction of this species within the Logan River system could at least be supplemented. Immigrating adults in the spring moved into and reproduced in Spawn Creek; their progeny remained in the stream for a length of time and then emigrated. Although an immigration of some juvenile cutthroat did occur in the fall of 1974, the phenomenon was not associated with the reproductive process, and the advantage of migration at this time was unknown.

The brown trout were also members of an open population and probably used Spawn Creek much as did the cutthroat trout although no off season run occurred.

The primary role of Spawn Creek vis-a-vis cutthroat trout within the Logan River drainage was to supply spawning and brood habitat to at least supplement the reproduction of this species in lower waters. Although brown trout utilized the stream in much the same manner, low densities and the lack of estimates of production for the younger year classes weakened any conclusion along the lines of the aforementioned.

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APPENDIX

Table 26. Chronological description of the sampling regime for fish populations in Spawn Creek

Months	Dates	Weeks	Sections	Comments
April 1973	4-8	13	All	
	20-21	16	7-12, 23-24	
May	5, 6, 8	19	7-12, 23-24	
June	13	24	23-24	Personal injuries limited sampling in May, June, and July.
	29-30	26	17, 23-24	
July[a]	25-26	30	3, 7, 11-12, 17, 24	
August	7, 9, 11, 13	32	All	
September	------------			
October	16-18, 23-24	42	All	
November	------------			
December	4	49	1, 3, 8, 20, 24	
January[a] 1974	18, 20-21	55	1, 3, 8, 14, 17	
February	18, 20	60	1-9	
March	20-22	64	All	
April	18	67	1	Aborted due to run-off
May	7, 9, 11, 14	71	All	
June	5/30, 6/3	74	1, 3, 5, 7-8, 10-13	
July	2-3, 5, 7, 9-10	79	All	
August	7-8	84	1, 3, 5, 10-13, 17-20, 31	
September	3-6, 9-10	88	All	
October	1-2	92	1-2, 4-5, 8, 10, 12-13, 18, 21, 23-24, 31	
November	10/28, 11/4-7	97	All	Early attempt to begin sampling failed due to weather.

[a] Dates of regular and special collections (multi-catch population estimators).

Table 27. List of the calculated weights of lost, female reproductive products by the trout populations in Spawn Creek in 1973 and 1974

Year Class	Brown trout	Cutthroat trout		Brook trout
	1973	1973	1974	1973
1974				
1973				
1972				100
1971	104		1149	128
1970	25	1325	424	72
1969	___[a]	472	231	
1968	___	280	122	
1967	89	___	___	

[a] Estimate not available

Table 28. List of the weekly mean weights of emigrating 0+ aged brown and cutthroat trouts that were used in the fitting of models of growth. Concomitant standard deviations are in parentheses and measurements are in grams

Species	August, 1974				September			October			November	
Brown		5.0					6.0		7.0	6.0	4.8	
Cutthroat	1.0	.9 (.22)	.9 (.46)	1.1 (.27)	1.2 (.46)	1.2 (.46)	1.1 (.60)	1.3 (.40)	1.5 (.77)	1.3 (.60)	1.5 (.63)	1.2 (.54)

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