PRODUCTION BY THREE POPULATIONS OF WILD BROOK TROUT WITH EMPHASIS ON INFLUENCE OF RECRUITMENT RATES

ROBERT F. CARLINE[1]

ABSTRACT

Populations of wild brook trout, *Salvelinus fontinalis,* in three small ponds in northern Wisconsin were studied for 4 yr to determine annual production with particular emphasis on influence of recruitment rates. Recruitment included trout hatched in ponds and immigrants from adjacent waters. Age-specific growth rates and densities of trout were estimated in spring and fall. Harvest of trout was estimated through partial creel surveys.

Among populations annual production ranged from 26 to 331 kg/ha and was directly related to recruitment rates. Production was most influenced by population biomass. Instantaneous growth rates did not vary significantly within or among populations despite large differences in population densities; hence, variations in production appeared unrelated to growth rates. Among populations, yield of trout ranged from 25 to 72 kg/ha and fishing pressure ranged from 154 to 1,405 h/ha. Proportion of annual production that was harvested was directly related to fishing pressure.

Production of fry during the first 9 mo of life may have been overestimated because mortality rates from emergence to fall were assumed constant. Estimates of production of adult trout could have been positively or negatively biased depending upon immigration patterns. Despite these possible errors, it was clear that recruitment was the most important factor affecting production.

Estimation of fish production has gained widespread acceptance because it provides some measure of a system's capacity to support species of interest (Gerking 1967). Production is defined as the total elaboration of tissue by a population during a specified time interval, regardless of the fate of that tissue (Ivlev 1945). Unlike standing crop estimates, production is a dynamic population parameter that is useful in evaluating the environmental performance of a fish population (Le Cren 1972). Studies by Ricker and Foerster (1948), Allen (1951), and Hunt (1971) are good examples of how fish production has been related to predation, the food supply, and habitat suitability. While many studies have considered the effects of standing crops, growth rates, and mortality on production, the importance of recruitment has not been well defined.

In northern Wisconsin, standing crops of wild brook trout, *Salvelinus fontinalis,* in spring-fed ponds vary greatly. Some ponds have filled-in naturally and living space is limiting. In others, living space appears to be adequate, but spawning areas are small or nonexistent and recruitment seems to be limiting standing crops of trout. The objective of this study was to determine annual production by three populations of wild brook trout with particular emphasis on the influence of recruitment rates. Recruitment includes all trout hatched in the ponds plus all immigrant trout.

The ponds were chosen because they differed greatly in areas available for spawning and numbers of immigrating trout. Ponds were similar in size and watershed characteristics, and springs were the primary sources of water. Outlet streams, which flowed into larger streams and/or lakes, provided convenient sampling boundaries, but did not impede movement of trout into or out of the ponds. I estimated densities and growth rates of trout every spring and fall from 1968-72 and conducted partial creel surveys during 3 yr of the study to estimate trout yields.

DESCRIPTION OF STUDY AREA

The study ponds, situated in a terminal moraine, are located within 7 km of each other in Langlade County, north central Wisconsin. The moraine is composed of glacial till ranging in size from sand to large boulders. These permeable

[1]Wisconsin Department of Natural Resources, Route 1, Box 203, Waupaca, WI 54981; present address: Ohio Cooperative Fishery Research Unit, Ohio State University, 1735 Neil Avenue, Columbus, OH 43210.

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materials permit a relatively uninhibited flow of ground water that is the main source of water for all ponds. Hoglot and Clubhouse springs are on state-owned land and Maxwell Springs is privately owned. The ponds are located in wooded lowlands and all three drain into trout streams that are part of the Wolf River drainage, a major Lake Michigan watershed.

The ponds are similar in size and have relatively short exchange times due to large inflows of ground water (Table 1). Because all ponds are supplied by the same aquifer, concentrations of common ions are similar. Bottom materials consist mostly of marl and organic matter. About 10% of the shorelines in Maxwell and Hoglot springs are composed of gravel with emerging ground water and brook trout spawn in these areas. Numbers of trout redds in Hoglot Springs ranged from 85 to 105/ha of pond area, and in Maxwell Springs redd densities ranged from 165 to 230/ha. Clubhouse Springs lacks gravel areas with upwelling ground water and brook trout do not spawn there.

Continual inflow of ground water and rapid exchange times tend to moderate pond temperatures and maintain relatively high concentrations of dissolved oxygen. Ground water temperatures typically range from 6° to 7°C and concentrations of dissolved oxygen, from 8 to 9 ppm. Pond temperatures in summer at depths of 15 cm rarely exceed 16°C. Concentrations of dissolved oxygen rarely fall below 5 ppm at any depth throughout the year and they usually exceed 7 ppm. Ponds are ice-covered from early November to late March.

All ponds supported dense beds of aquatic vegetation. *Chara vulgaris* covered about 40% of the bottom in Clubhouse Springs and 15% in Hoglot Springs. *Anacharis canadensis*, the only common plant in Maxwell Springs, extended over 50% of the bottom.

TABLE 1.—Some physicochemical features of study ponds in north central Wisconsin. Chemical measurements were taken in April 1970.

Item	Clubhouse Springs	Hoglot Springs	Maxwell Springs
Surface area (ha)	0.81	0.38	0.97
Mean depth (m)	1.11	0.64	0.86
Outlet discharge[1] (m^3/s)	0.03	0.005	0.05
Exchange time[2] (days)	3.3	5.6	2.0
Specific conductance (μmho/cm)	341	335	310
Total alkalinity (mg/l as $CaCO_3$)	180	153	168
Calcium (mg/l)	42	40	39
Nitrate (mg/l-N)	0.5	0.7	1.1
Dissolved phosphorus (mg/l-P)	0.02	0.01	0.03

[1]Summer base flow.
[2]Pond volume/discharge.

Fish communities in the three ponds were similar. Brook trout composed the major portion of fish biomass. A small population of brown trout, *Salmo trutta*, in Clubhouse Springs never accounted for more than 10% of the total number of trout. The white sucker, *Catostomus commersoni*; mottled sculpin, *Cottus bairdi*; Central mudminnow, *Umbra limi*; and brook stickleback, *Culaea inconstans*, were common in all ponds. The brook stickleback was an important food source for age 3 and older trout; however, benthic invertebrates composed the major portion of the diet for trout of all sizes.

METHODS

Trout populations were estimated in spring and fall using Bailey's modification of the Petersen mark and recapture method (Ricker 1975). Trout were captured at night with electrofishing gear and held overnight in screen cages. The following day, fish were anesthetized, measured to the nearest 2 mm (total length), weighed to the nearest gram, given a temporary mark by clipping the tip of the caudal fin, and released. A second electrofishing run was made two or more days later. Proportions of marked trout captured during the second electrofishing sample were used to calculate confidence limits for population estimates (Adams 1951).

Age structures of trout populations were determined from length distributions of known age fish and scale analyses. Fall fingerlings and spring yearlings, determined from length-frequency distributions, were permanently marked by fin removal. Estimated numbers of trout in each 25-mm length group were placed in appropriate age-groups based on relative proportions of known age fish. The electrofishing gear was size selective. Efficiency was lowest for smallest fish and increased until fish size reached about 12 cm. Separate estimates for 25-mm length intervals avoided bias due to size selectivity of electrofishing gear.

Maxwell outlet and Elton Creek, the stream into which Clubhouse Springs flowed, were sampled with electrofishing gear to obtain data on growth rates of trout in outlet waters and on movement of trout between ponds and adjoining streams. A 1-km section of Elton Creek was sampled five times from 1968 to 1971; Clubhouse outlet joined this section at its midpoint. Maxwell outlet (200 m) was sampled in 1969 and 1972. All trout were measured, about 25% were weighed, and fall fingerlings and spring yearlings were permanently marked by fin removal.

Sampling dates in ponds varied from year to year. I estimated mean lengths and weights of each cohort on 15 April and 15 September so that growth rates from different years could be compared. Mean weights of individuals in each year class were determined graphically by assuming constant instantaneous rates of growth. By graphically estimating mean length, I assumed length increased linearly between successive estimates. Most of the adjustments in length or weight involved extrapolating over periods <2 wk and size changes were usually <5%.

Year class biomass was estimated by multiplying mean weights of individual trout by year class density. Biomasses in spring and fall were averaged to calculate mean biomass ($\bar{B}$). I followed procedures suggested by Ricker (1975) to calculate instantaneous rates of growth by weight (G), total mortality (Z), natural mortality (M), and fishing mortality (F). Production, the product of G and $\bar{B}$, was computed semiannually for each cohort. Production by fingerling trout was calculated from emergence (1 March) to time of spring population estimate and from spring to fall. A mean weight of 0.04 g was assigned to emergent fry (Hunt 1966). I assumed that instantaneous growth and mortality rates from emergence to fall were constant. Mean annual biomass of each cohort was calculated by weighting mean biomasses in the two intervals according to interval lengths. Annual production was calculated by summing production during the two intervals and expressing the sum for 365-day periods.

Potential egg production for each population was estimated from numbers of mature females in fall and from a relationship between total length of females and number of eggs. Fecundity of trout was determined from 83 females that were collected from two ponds in the same watershed as the study ponds. Trout were collected in early October, about 2 wk prior to spawning. Mature ova could be easily distinguished from recruitment eggs on the basis of size and color (Vladykov 1956). Data on trout length, weight, and total number of eggs were fitted to linear, curvilinear, and logarithmic regression models. A linear regression of total trout length and number of eggs yielded the highest correlation coefficient.

At Clubhouse and Hoglot springs, densities of some year classes increased during sampling intervals because of immigration from outlets or adjoining streams. Numbers of immigrants were estimated by first calculating expected densities at the end of sampling intervals by using mean, age-specific mortality rates; expected densities were then subtracted from actual densities. If the expected number of trout at the end of an interval was within 10% of the actual number or the difference was negative (suggesting emigration), it was assumed no immigration had occurred. Age-specific mortality rates for trout in Clubhouse and Hoglot springs were estimated from permanently marked fish. For some age groups, mortality rates could not be estimated because of insufficient numbers of marked fish. In these instances I used age-specific mortality rates of the population in Maxwell Springs, where immigration did not influence year class densities (discussed later).

Harvest of trout from Clubhouse and Hoglot springs was estimated from partial creel surveys in 1969, 1970, and 1972. State-wide angling regulations included a bag limit of 10 trout/day and minimum length of 154 mm (6 in). Census clerks worked five randomly chosen days per week during the entire fishing season, mid-May to mid-September. Catch rates were estimated from data collected during interviews of anglers, and fishing pressure was calculated from instantaneous counts of anglers (Lambou 1961). Harvest was estimated monthly from the product of the hours of fishing and numbers of trout caught per hour. Harvested trout were measured, examined for permanent marks, and scales were collected from a sample of the catch. Harvest data from Maxwell Springs were compiled by the owner and others who fished the pond. Ages of harvested trout from Clubhouse and Hoglot springs were determined from scales and size distributions of permanently marked fish. Ages of trout harvested from Maxwell Springs were estimated from comparisons of lengths of harvested trout with lengths of known age fish in spring and fall.

RESULTS

Population Densities and Biomass

Electrofishing was the most efficient method of collecting trout in these shallow ponds. Population estimates derived from collections with trap nets and seines showed that collecting trout with just electrofishing gear did not yield biased estimates (Carline unpubl. data). Efficiency of the electrofishing gear usually increased with trout size (Table 2). Mean proportions of marked trout captured during the second electrofishing sample for age 0 to 3 fish were 0.18, 0.31, 0.35, and 0.39, respectively. Recapture efficiencies were always lowest for age 0 trout and values ranged from 0.05 to 0.30. For age 1 and older fish, precision of estimates depended mostly upon sample size and confidence limits for the oldest age groups were generally broad because of their low densities (Table 2).

TABLE 2.—Examples of trout population estimates and 95% confidence limits by age-groups. Data were collected in fall 1970.

Item	0	1	2	3	4
Clubhouse Springs:					
Mean length (mm)	99	175	211	274	
Proportion of marked fish recaptured	0.30	0.40	0.41	0.50	
Population estimate (no./ha)	386	363	84	6	
95% confidence limits	234	279	47	0	
	782	466	124	40	
Maxwell Springs:					
Mean length (mm)	92	147	182	220	287
Proportion of marked fish recaptured	0.05	0.43	0.53	0.34	0.22
Population estimate (no./ha)	2,195	1,572	909	433	28
95% confidence limits	1,183	1,408	845	367	17
	3,944	1,778	1,003	507	56

Clubhouse Springs

The brook trout population in Clubhouse Springs was the smallest of the three populations. Because no spawning areas were present, this population was entirely dependent upon immigration from downstream areas. Trout densities usually declined from spring to fall and only age 0 trout appeared to immigrate in substantial numbers oversummer (Figure 1). Total trout numbers in 3 of 4 yr increased overwinter due to immigration. Numbers of trout in spring ranged from 390 to 1,750/ha and densities in fall ranged from 390 to 840/ha. Age structure of the population was at times atypical because young age groups were less numerous than older ones, owing to differential rates of immigration.

Changes in population biomass closely paralleled numerical changes. Biomass in spring averaged 45 kg/ha and in fall 26 kg/ha (Table 3). In all years, population biomass increased from fall to spring, the period when immigration appeared greatest.

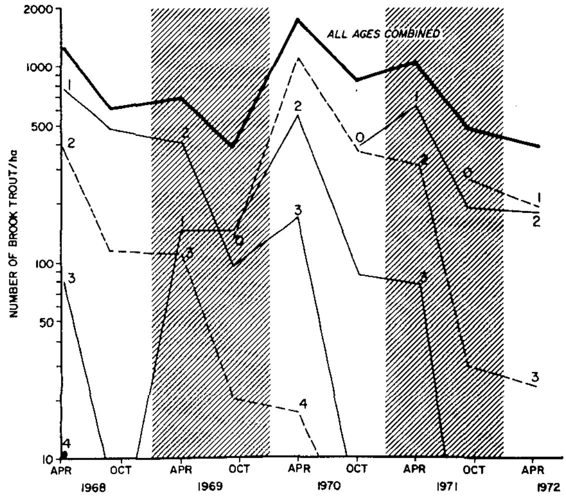

FIGURE 1.—Estimated numbers of brook trout in Clubhouse Springs, 1968-72. Numbers designate age-groups and hatched areas separate calendar years.

TABLE 3.—Estimated biomass (kilograms per hectare) by age-group of brook trout in study ponds, 1968-72. Mean weights of individuals in each age-group were multiplied by estimated density of the age-group to calculate biomass.

Site and date	0	1	2	3	4	5	Total
Clubhouse Springs:							
27 Mar. 1968		10.9	15.6	8.7	3.5		38.7
28 Aug. 1968		22.9	10.8	1.2	1.7		36.6
8 Apr. 1969		3.0	23.7	14.4	5.2		46.3
8 Sept. 1969	1.8	7.6	10.4	4.3	0.4		24.5
1 Apr. 1970		17.2	26.2	20.4	4.6		68.4
8 Sept. 1970	3.5	17.4	7.0	1.2			29.1
29 Apr. 1971		12.0	22.9	12.2	2.3		49.4
8 Sept. 1971	2.1	6.6	3.1	0.2			12.0
21 Apr. 1972		3.0	13.1	4.4	0.7		21.2
Hoglot Springs:							
2 Apr. 1968		22.6	69.1	26.5	11.2		129.4
26 Aug. 1968	6.8	26.1	35.8	13.6	3.6		85.9
8 Apr. 1969		5.0	37.2	66.8	8.1		117.1
8 Sept. 1969	15.9	33.7	47.6	12.5	2.3		112.0
13 Apr. 1970		13.0	38.3	38.5	13.3		103.1
8 Oct. 1970	16.9	91.0	36.4	9.1	0.7		154.1
28 Apr. 1971		10.8	70.7	21.5	2.1		105.1
21 Sept. 1971	7.0	26.6	40.7	5.6	0.2		80.1
2 May 1972		10.8	17.0	6.5	2.5		36.8
Maxwell Springs:							
9 Apr. 1969		34.4	50.8	26.3	41.6	80.3	233.4
13 Oct. 1969	27.0	55.8	88.8	29.3	20.8	16.1	237.8
26 Mar. 1970		25.3	47.3	69.6	16.2	12.4	170.8
6 Oct. 1970	22.0	56.6	63.6	53.7	6.9	2.6	205.4
26 Apr. 1971		8.2	48.0	46.9	17.6	0.5	121.2
20 Sept. 1971	24.6	19.2	32.6	13.8	0.9		91.1
26 Apr. 1972		27.1	7.3	7.1	3.7		45.2
29 Sept. 1972	14.8	46.6	11.0	4.5	1.4		78.3

Hoglot Springs

Although some fingerlings were hatched in Hoglot Springs, numbers of immigrating trout, particularly age 1 fish, had the most impact on population size. In 3 of 4 yr, densities of yearling trout increased oversummer, and during the winter of 1968-69 fall 2-yr-olds increased by 50% (Figure 2). Mean population densities were higher in fall than in spring (4,480 vs. 3,200/ha) because of recruitment by age 0 trout and age 1 trout.

Trout migrating into Hoglot Springs had a marked effect on population biomass. Biomass was highest in fall 1970 because of the large stock of yearlings (91 kg/ha), most of which were recent immigrants (Table 3). Little immigration occurred oversummer in 1971 and overwinter in 1971-72. As a result, population biomass in spring 1972 reached its lowest level of the 4-yr period.

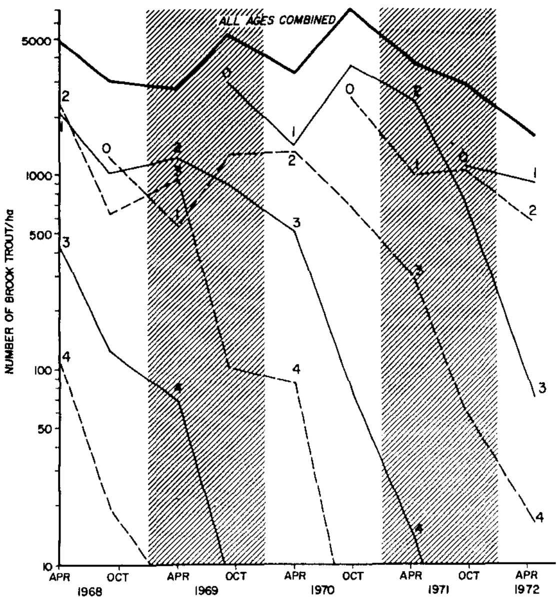

FIGURE 2.—Estimated numbers of brook trout in Hoglot Springs, 1968-72. Numbers designate age-groups and hatched areas separate calendar years.

Maxwell Springs

Except for 1972, Maxwell Springs supported the largest of the three populations, and natural reproduction accounted for nearly all recruitment. Two experiments were conducted to evaluate the extent of immigration from Maxwell outlet into the pond. In June 1969 and April 1972, a total of 602 ages 0 and 1 trout were captured in the outlet and marked. In subsequent surveys of the pond, I examined over 4,000 trout, only 3 of which had been marked in the outlet. Hence, I concluded that trout reared in the outlet did not materially affect recruitment in the pond.

From April 1969 to September 1972 trout densities in Maxwell Springs declined markedly (Figure 3). Spring densities steadily decreased from 7,300/ha in 1969 to 1,810/ha in 1972. Fall populations followed a similar trend. This decline was due in part to decreasing numbers of fall fingerlings. Densities of age 0 trout ranged from 4,085/ha in October 1969 to 1,940/ha in September 1972. However, even the 1969 year class, which was larger than the succeeding three year classes, had to be smaller than the 1968 and 1967 year classes, based on their densities as ages 1 and 2 fish in April 1969 (Figure 3). I estimated numbers of fall fingerling for the 1967 and 1968 year classes by using average mortality rates of succeeding year classes. The 1967 year class was estimated at 16,000/ha and the 1968 year class at 8,300/ha. Thus, numbers of fall fingerlings had steadily declined from 1967 to 1972 with one exception, the 1971 year class.

The reduction in year class strength in Maxwell Springs may have been related to the installation of a weir in the pond outlet in 1968. The weir, which was used to monitor discharge, was located 132 m downstream from the pond and it created

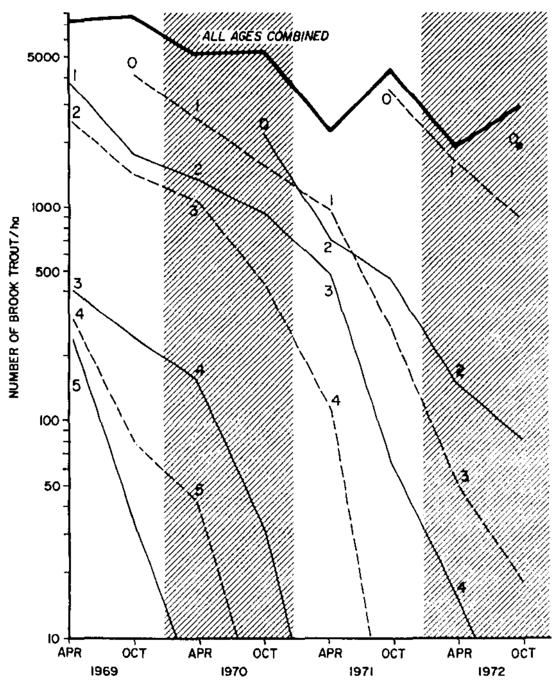

FIGURE 3.—Estimated numbers of brook trout in Maxwell Springs, 1969-72. Numbers designate age-groups and hatched areas separate calendar years.

an impoundment that extended to within 5 m of the pond. The impounded area was heavily silted by fall 1968 and I counted only four redds there. The owner had reported that large numbers of brook trout spawned in this area prior to weir installation. In fall 1974, 1 yr after the weir had been removed, I counted 34 redds and about half the streambed was covered with silt. Since effects of impoundment were still evident, this portion of the outlet may have provided much more spawning area than was evident in 1974. Possibly, immigration was an important source of recruitment prior to this study.

Population declines at Maxwell Springs were accompanied by changes in age structure. In April 1969, density of age 3 and older trout was nearly 1,000/ha and they totaled 233 kg/ha, or 63% of population biomass (Table 3). By September 1972, density of age 3 and older trout was 22/ha and biomass was about 6 kg/ha, the lowest in the 4-yr period.

Mortality

Numbers of fall fingerlings in Hoglot and Maxwell springs represented from 0.2 to 1% of the estimated number of eggs deposited the previous fall. I sampled 52 redds in five different ponds to assess preemergence mortality. Numbers of eggs per redd ranged from about 30 to 220. Percentage of live embryos in individual redds ranged from 76 to 99 (mean = 89%); stage of development of these embryos varied from eyed egg to alevin. Due to additional mortality to emergence, I used 80% of potential egg deposition to estimate numbers of emerging fry. Although highest mortality rates in both ponds occurred during years of highest egg production, egg production and fingerling mortality were not significantly correlated (Table 4).

TABLE 4.—Estimated egg production of brook trout populations and densities of fall fingerlings. Egg deposition was estimated from number of mature female trout in fall and the relationship of fecundity (Y) and trout length in millimeters (X); $Y = -588 + 6.14X$. Instantaneous mortality rates (Z) were based on 80% of egg production and were corrected for 182-day intervals.

Pond	Year class	No. eggs/ha	No. fall fingerlings/ha	Z/182 days
Hoglot Springs	1969	281,000	2,938	4.111
	1970	276,000	2,481	3.681
	1971	433,000	1,049	5.148
	Mean	330,000	2,156	4.313
Maxwell Springs	1969	543,000	4,085	3.742
	1970	550,000	2,195	4.384
	1971	739,000	3,519	4.549
	1972	212,000	1,945	3.800
	Mean	511,000	2,936	4.119

To estimate age-specific total mortality rates of trout in Maxwell Springs, I assumed that immigration was negligible. At Clubhouse and Hoglot springs, where immigration was substantial, unmarked residents and immigrants could not be separated; therefore, mortality rates were calculated using only permanently marked trout. Numbers of age 2 and older trout were usually too small to allow estimation of mortality rates.

Mean rates of oversummer mortality in Maxwell and Hoglot springs increased with age (Table 5). Overwinter mortality rates at Maxwell Springs also increased with age, except that age 0 trout had higher mean mortality rates than did age 1 trout. However, within years there was considerable variability between age of fish and mortality rates. In all ponds mean mortality rates oversummer exceeded overwinter rates.

Immigration

Estimation of immigration rates at Clubhouse and Hoglot springs were based on mortality rates calculated from relatively small numbers of permanently marked trout and from mean, age-specific mortality rates of trout from Maxwell Springs (Table 5). Although accuracy of these estimates is suspect, they should be useful in illustrating seasonal differences in immigration and in assessing the effect of immigration on recruitment.

At Clubhouse Springs most immigration occurred overwinter and age 0 trout made up 55% of all migrants (Table 6). Largest migrations into Hoglot Springs occurred between April and September when age 1 trout accounted for 73% of all migrants. In both populations periods of peak immigration coincided with highest population densities. Immigration was the only source of recruitment at Clubhouse Springs; at any one time more than half the population consisted of fish that had immigrated within the previous 6 mo. At Hoglot Springs percentages of recent immigrants ranged from 8.2 to 54.9 (mean = 34%).

If estimates of trout migrating into Hoglot Springs are reasonable, immigration accounted for a major portion of total recruitment. The four year classes produced in the pond from 1968 to 1971 amounted to 7,700 fall fingerlings/ha. About 3,800 of these fish survived to the following spring.

TABLE 5.—Instantaneous total mortality rates for 182-day intervals. Mortality rates of trout in Maxwell Springs were calculated from year class densities. Mortality rates of trout in Hoglot and Clubhouse springs were calculated from permanently marked fish. Estimated numbers of trout at the end of sampling intervals given in parentheses.

Interval and year	Maxwell Springs					Hoglot Springs		Clubhouse Springs
	0[1]	1	2	3	4	1	2	1
Oversummer:								
1968						2.254		1.238
						(72)		(75)
1969		0.766	0.573	0.510	1.521	0.408	2.151	1.914
		(1,691)	(1,368)	(233)	(109)	(110)	(7)	(13)
1970		0.448	0.373	0.850	1.492	0.725	1.080	1.489
		(1,525)	(882)	(420)	(31)	(158)	(8)	(81)
1971		0.500	1.552	2.439	4.404	1.382	1.631	1.522
		(442)	(264)	(62)	(3)	(33)	(20)	(65)
1972		0.681	0.670	1.185	1.532			
		(863)	(82)	(17)	(4)			
Mean		0.599	0.792	1.246	2.237	1.192	1.742	1.541
Overwinter:								
1968-69						0.175		0.804
						(58)		(28)
1969-70	0.530	0.282	0.306	0.826	1.085	1.312		1.662
	(2,457)	(1,310)	(1,039)	(110)	(41)	(23)		(2)
1970-71	1.048	0.444	0.606	1.243	2.498	0.687		0.573
	(664)	(931)	(450)	(106)	(2)	(74)		(39)
1971-72	0.659	0.917	1.398	1.211	0.926	0.826		1.186
	(1,549)	(147)	(49)	(14)	(1)	(12)		(15)
Mean	0.746	0.548	0.770	1.093	1.503	0.750		1.056

[1]Age at start of interval.

TABLE 6.—Estimated numbers of immigrant brook trout present by age-groups at the end of sampling intervals. Summer intervals were from April to September and winter intervals from September to the following April. Percent of population at the end of the interval composed of recently immigrated trout given in parentheses.

Year and interval	Clubhouse Springs					Hoglot Springs				
	0	1	2	3	Sum	0	1	2	3	Sum
1968										
Summer	0	346	0	0	346 (57)		207	42	0	249 (8)
Winter	147	277	65	14	503 (74)	0	802	659	34	1,495 (55)
1969										
Summer	130	104	0	0	234 (60)		1,046	619	0	1,665 (32)
Winter	955	514	130	12	1,611 (92)	191	767	149	56	1,163 (36)
1970										
Summer	387	102	0	0	489 (58)		3,205	417	0	3,622 (53)
Winter	451	215	46	6	718 (70)	0	773	0	0	773 (21)
1971										
Summer	262	0	0	0	262 (55)		645	133	0	778 (27)
Winter	86	128	12	0	226 (57)	478	157	0	0	635 (41)
Sum	2,418	1,686	253	32	4,389	669	7,602	2,019	90	10,380
Percent	55.1	38.4	5.8	0.7		6.4	73.2	19.5	0.9	

During this 4-yr period over 9,700 age 1 and older trout immigrated into the pond, hence, migrants accounted for about 70% of total recruitment of yearling and older trout.

It is likely that trout migrating from Elton Creek into Clubhouse Springs were smaller than pond residents because: 1) trout in Elton Creek grew more slowly than those in Clubhouse Springs and 2) permanently marked trout in the pond, i.e. residents, were larger than unmarked trout, which were mostly recent immigrants. From 1968 to 1970 fall fingerlings in Elton Creek averaged 4.2 g and those in Clubhouse Springs were 9.6 g. Fall yearlings in Elton Creek averaged 30 g and yearlings in the pond were 46 g. In spring and fall, marked yearlings in Clubhouse Springs were about 20% heavier than unmarked yearlings. For age 2 trout in spring, marked trout were 58% larger than unmarked ones. I made similar comparisons for ages 1 and 2 trout in Hoglot Springs; differences in sizes among marked and unmarked trout were not consistent and I concluded that migrants were similar in size to pond residents.

Growth

Among populations, mean size attained by trout of a given age was greatest in Clubhouse Springs (Table 7). After the first full year of life trout in

TABLE 7.—Estimated mean annual lengths (millimeters) and weights (grams) of brook trout on 15 April and 15 September. Data from Clubhouse and Hoglot springs were from 1968-71 and those from Maxwell Springs were from 1969-72.

Pond and month	Age 0		1		2		3		4	
	$\bar{L}$	$\bar{W}$	$\bar{L}$	$\bar{W}$	$\bar{L}$	$\bar{W}$	$\bar{L}$	$\bar{W}$	$\bar{L}$	$\bar{W}$
Clubhouse Springs:										
April			126	19	176	55	229	127		
September	105	13	166	49	212	105	276	238		
Hoglot Springs:										
April			107	10	150	31	199	72	241	136
September	88	6	130	26	178	56	226	118		
Maxwell Springs:										
April			106	12	154	38	203	89	264	172
September	89	7	147	34	200	88	246	168	300	284

Clubhouse Springs were from 58 to 90% larger than spring yearlings in Hoglot or Maxwell springs. Although trout in Clubhouse Springs maintained a size advantage over their counterparts in the other ponds after the first growing season, age-specific instantaneous growth rates for all populations were similar. I compared mean age-specific growth rates for intervals of April to September and September to April for ages 1-3 trout. There were no significant differences for similar age trout among populations (t-test $P>0.05$). During summer instantaneous growth rates of trout tended to be highest in Maxwell Springs, but there were no consistent differences during winter intervals.

Growth rates of fingerling trout were inversely related to their density (number or weight) when data from all populations were combined (Table 8). Density of yearling trout also had an effect on growth of fingerlings; correlation coefficients were highest when fingerling growth was related to combined density of fingerlings and yearlings. Effects of density on growth rates of age 1 and older trout were inconsistent. When instantaneous growth rates were used as the dependent variable and density in numbers or weight was the independent variable, correlation coefficients were consistently low (Table 8). When age-specific growth was expressed as mean weight or length in September or weight gain from April to September, correlation coefficients were consistently high (Figure 4). The lack of correlation between instantaneous growth rates and density may have been due to underestimation of mean weights of trout in fall, particularly in Clubhouse Springs. Biases could have resulted from: 1) immigration of trout smaller than pond residents, 2) differential exploitation of faster growing individuals in a year class, and 3) errors in estimating year class densities. The lack of correspondence between instantaneous growth rates and other growth parameters has been noted in other studies (Eipper 1964).

Harvest

Fishing success and harvest of trout were influenced by trout densities and fishing pressure. Maxwell Springs supported the largest trout population in 1969 and 1970 and catch rates were highest (Table 9). Among populations annual catch rates were positively related to spring densities of age 1 and older trout ($r = 0.88$; $P<0.01$). There was a significant correlation between biomass of trout harvested (yield) and the

TABLE 8.—Linear correlation coefficients for growth and density of trout ages 0 to 3 in study ponds. (df = 10; $^*P<0.05$, $^{**}P<0.01$.)

Independent variable	Age-group of dependent variable	Instantaneous growth rates	Mean length on 15 Sept.	Mean weight on 15 Sept.	Weight gain Apr.-Sept.
Mean trout biomass (kg/ha) of:					
Age 0	0	−0.62*	−0.59		
Age 1		−0.86**	−0.72*		
Ages 0 and 1		−0.85**	−0.76**		
Age 1	1	−0.08	−0.38	−0.61*	−0.53
All ages		0.13	−0.66*	−0.72**	−0.59*
Age 2	2	0.04	−0.81**	−0.79**	−0.62*
All ages		0.14	−0.72**	−0.68*	−0.48
Age 3	3	−0.05	−0.68*	−0.64*	−0.58*
All ages		−0.07	−0.82**	−0.79**	−0.68*
Mean trout density (no./ha) of:					
Age 0	0	−0.78*	−0.84**		
Age 1		−0.67*	−0.64*		
Ages 0 and 1		−0.82**	−0.85**		
Age 1	1	0.01	−0.57	−0.70*	−0.62
All ages		0.01	−0.66*	−0.77**	−0.63*
Age 2	2	0.06	−0.87**	−0.86**	−0.68*
All ages		0.17	−0.71**	−0.69*	−0.46
Age 3	3	−0.09	−0.82**	−0.76**	−0.67*
All ages		−0.12	−0.81**	−0.80**	−0.69*

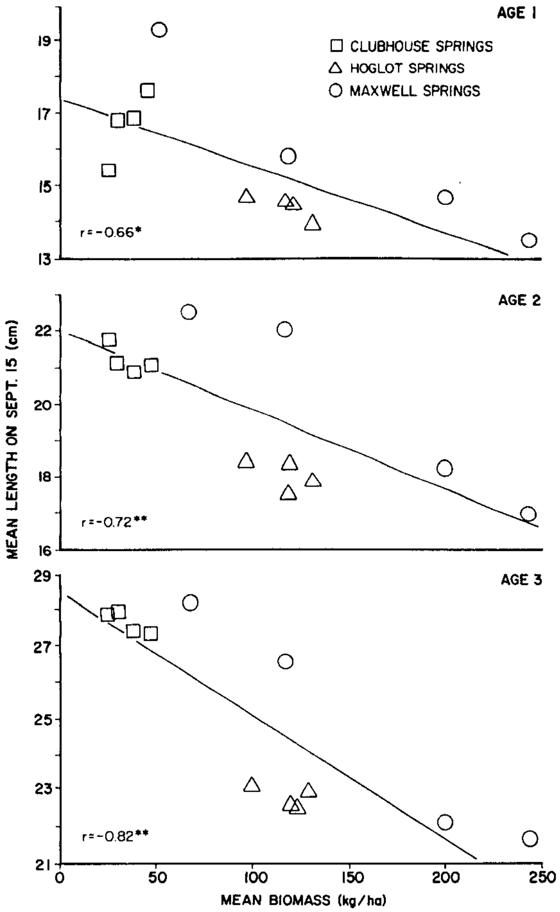

FIGURE 4.—Relationships between mean biomass of all ages of trout and mean lengths of ages 1, 2, and 3 trout on 15 September. (*$P<0.05$; **$P<0.01$.)

TABLE 9.—Annual fishery statistics for brook trout populations in study ponds.

Pond and year	Fishing pressure (angler h/ha)	Total harvest (no./ha)	Catch rate (no./h)	Mean size (cm)	Yield (kg/ha)
Clubhouse Springs:					
1969	1,069	580	0.55	21.8	68.4
1970	1,405	392	0.28	21.4	37.2
1972	809	298	0.37	20.3	27.4
Hoglot Springs:					
1969	835	926	1.11	18.3	54.6
1970	526	391	0.74	19.3	25.4
1972	401	218	0.54	18.8	13.5
Maxwell Springs:					
1969	189	334	1.77	27.2	71.8
1970	154	320	2.08	23.1	39.7

independent variables of fishing pressure and trout biomass in spring ($r = 0.88$; $P<0.05$). Fishing pressure was lowest at Maxwell Springs because the pond was privately owned and public access was restricted. The largest trout (up to 430 mm) were harvested from Maxwell Springs which supported the greatest number of age 4 and older trout. In spring 1969 there were about 530 age 4 and older trout/ha in Maxwell Springs and only 16/ha and 69/ha in Clubhouse and Hoglot springs, respectively.

Age 2 trout made up the major portion of the harvest in Clubhouse and Hoglot springs (Figure 5). In both populations, proportions of age 2 and older trout in the harvest were higher than their proportions in the spring populations, suggesting some size selection by anglers.

The fishery at Maxwell Springs differed significantly from the public ponds in 1969 when age 5 and older trout dominated the catch (Figure 5). Large numbers of age 5 trout were present in spring 1969 and 58% were harvested that season. The owner of Maxwell Springs reported that harvest and fishing pressure in years prior to the study were well below those of 1969 and 1970;

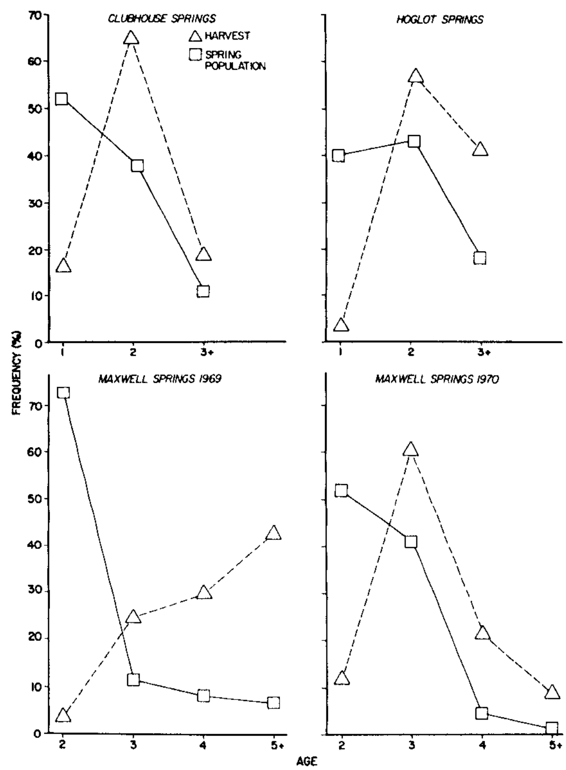

FIGURE 5.—Age-frequency distributions of harvests and populations of legal-sized trout in spring. Data points for Clubhouse and Hoglot springs are means of data from 1968 to 1970, and 1972.

it is likely that the population had been lightly exploited prior to 1969. Results of electrofishing surveys apparently stimulated greater fishing effort. Shape of the 1970 catch-frequency curve resembled those of public ponds, except that substantial numbers of age 4 and older trout were harvested.

Size selection by anglers at Maxwell Springs was reflected in the relative rates of natural and fishing mortality. For ages 2-5 trout, mean total mortality rates from spring to fall increased with age and were paralleled by fishing mortality (Figure 6). Natural mortality changed little with age of fish. Differences between natural and fishing mortality were greatest for age 5 trout and fishing mortality accounted for 69% of their total mortality.

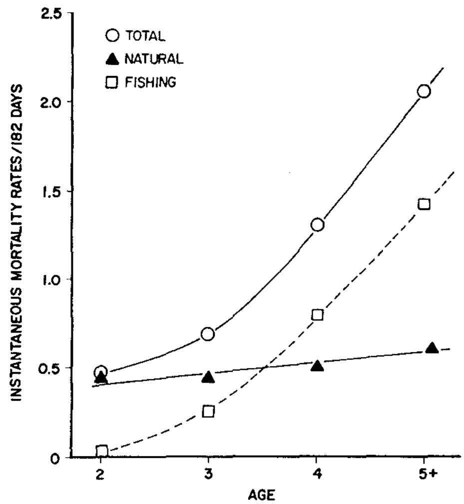

FIGURE 6.—Instantaneous rates of total, fishing, and natural mortality (spring to fall) of ages 2 to 5 trout at Maxwell Springs. Data points are 2-yr means, 1969-70.

Production

Production was most influenced by numbers of fingerlings hatched in ponds and numbers of immigrants. Growth rates varied little among populations, hence year class biomass had the most effect on production. Among populations annual production ranged from 26 kg/ha at Clubhouse Springs to 331 kg/ha at Maxwell Springs (Table 10).

Annual production in Clubhouse Springs was dependent upon biomass of ages 1 and 2 trout. Few fingerlings immigrated into the pond and

TABLE 10.—Production (kilograms per hectare) by age-group of brook trout in study ponds. Production by age 0 trout during fall to spring intervals covers the period from 1 March to end of interval. Production by age 4 trout includes all older age-groups. Total annual production was expressed in terms of 365 days.

Site and interval	[1]0	1	2	3	4	Total	Annual total
Clubhouse Springs:							
27 Mar. 1968 – 28 Aug. 1968		20.8	11.4	3.9	0.5	36.6	
28 Aug. 1968 – 8 Apr. 1969		1.5	4.4	4.0	—	9.9	45.3
8 Apr. 1969 – 8 Sept. 1969	0.9	5.1	10.8	5.6	1.0	23.4	
8 Sept. 1969 – 1 Apr. 1970		1.8	− 2.0	1.5	0.6	1.9	25.8
1 Apr. 1970 – 8 Sept. 1970	2.7	17.8	9.4	5.5	1.4	36.8	
8 Sept. 1970 – 29 Apr. 1971		5.7	8.7	6.1	0.8	21.3	54.1
29 Apr. 1971 – 8 Sept. 1971	1.0	5.6	5.2	1.8		13.6	
8 Sept. 1971 – 21 Apr. 1972		1.8	7.2	2.7		11.7	25.9
Hoglot Springs:							
2 Apr. 1968 – 21 Aug. 1968	40.1	20.9	32.2	10.6	7.9	111.8	
21 Aug. 1968 – 8 Apr. 1969	9.5	2.9	5.6	13.4	−0.3	31.1	141.4
8 Apr. 1969 – 8 Sept. 1969	51.1	21.2	22.7	18.5	4.6	118.1	
8 Sept. 1969 – 13 Apr. 1970	11.3	7.2	3.8	15.5	2.7	40.5	156.4
13 Apr. 1970 – 8 Oct. 1970	56.2	52.9	23.3	11.5	3.0	146.9	
8 Oct. 1970 – 28 Apr. 1971	18.5	6.4	14.7	7.7	1.4	48.7	187.9
28 Apr. 1971 – 21 Sept. 1971	34.8	15.9	35.7	5.9	0.6	92.9	
21 Sept. 1971 – 2 May 1972	14.1	5.1	3.1	10.2	1.3	33.9	125.4
Maxwell Springs:							
6 Apr. 1969 – 13 Oct. 1969	97.0	56.8	80.0	17.5	37.0	288.3	
13 Oct. 1969 – 26 Mar. 1970	11.6	10.9	4.9	2.4	1.7	30.2	331.2
26 Mar. 1970 – 6 Oct. 1970	97.5	52.5	38.6	38.7	12.2	239.5	
6 Oct. 1970 – 26 Apr. 1971	34.0	2.8	17.2	20.4	8.6	83.0	297.2
26 Apr. 1971 – 20 Sept. 1971	90.6	17.4	35.3	22.9	6.1	172.3	
20 Sept. 1971 – 26 Apr. 1972	10.6	23.0	1.8	3.1	1.2	39.7	211.4

[1]Age at end of interval.

they contributed only 10% of total annual production. Highest annual production occurred in 1970 when the population was bolstered by high levels of immigration during winter 1969-70 and in summer 1970. Low biomass in spring and below average rates of immigration in 1969 and 1971 resulted in low annual production.

At Hoglot Springs, annual production was most affected by numbers of fingerlings hatched in the pond and numbers of immigrants. Age 0 trout accounted for nearly 32% of average annual production. Annual production peaked in 1970 (Table 10) when large numbers of age 1 trout immigrated oversummer and cohort biomass increased from 13 kg/ha in spring to 91 kg/ha in fall.

Annual production in Maxwell Springs was related to the number of strong year classes present and their subsequent biomasses. The highest annual production was in 1969 when two large age-groups were present (1968 and 1969 year classes), and there was a high biomass of age 2 and older trout (Table 10). In 1971, the year of lowest production, the only large age-group was the fingerlings. In all years, production of age 0 trout was important; they averaged 44% of the total.

Among populations the influence of age 0 trout on total production was evident when production by individual age-groups was considered in relation to their biomass (Figure 7). Age 0 trout had a marked effect on the slope of the relationship between $\bar{B}$ and P when all age-groups were combined. The linearity of these relationships was due to similarity in growth rates within and among populations. If growth rates had declined with increasing biomass, the relationship between $\bar{B}$ and P would have been curvilinear.

There was no single parameter that could adequately describe levels of recruitment because numbers of trout hatched within ponds and numbers of immigrants were different in each population. If densities of fall fingerlings or spring yearlings were used as indexes of recruitment, mean annual production among populations and recruitment were directly related (Figure 8). Although age 0 trout made up a substantial portion of total production in Hoglot and Maxwell springs, production of just age 1 and older trout was also related to recruitment.

The ratio of annual production to mean annual biomass ($P/\bar{B}$) has been called "turnover rate" and "efficiency of production." The $P/\bar{B}$ ratio is, in fact, the weighted mean growth rate of the population. Population production is the sum of $G \times \bar{B}$ for each year class, hence, dividing total production by the sum of year class biomasses yields population growth rate, weighted according to the biomass of each age-group.

Among populations annual $P/\bar{B}$ ratios for age 1 and older trout varied by more than 100% (Table 11). The $P/\bar{B}$ ratio in 1969 at Clubhouse Springs (0.63) was probably underestimated. Growth rates

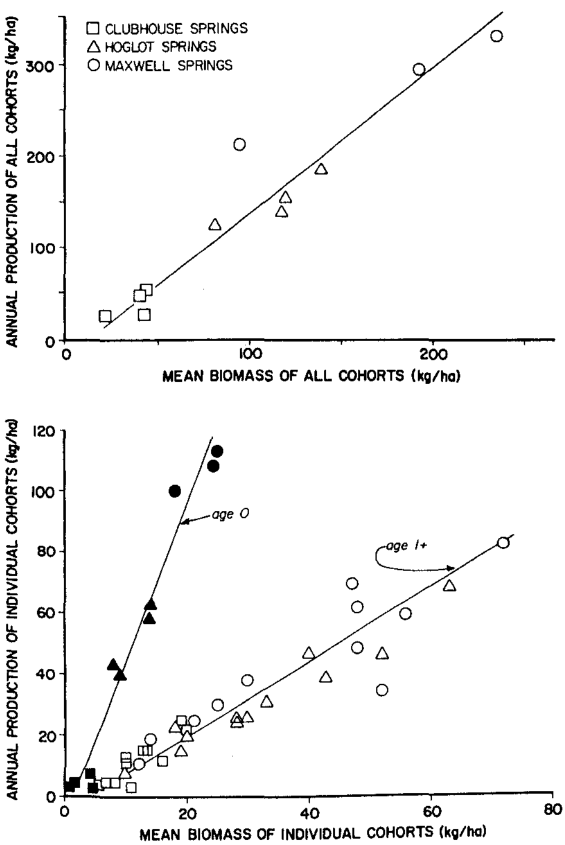

FIGURE 7.—Relationships between mean annual biomass and annual production. Production and biomass of all cohorts are combined in upper panel. In lower panel each point represents a single cohort. Lines fitted by inspection.

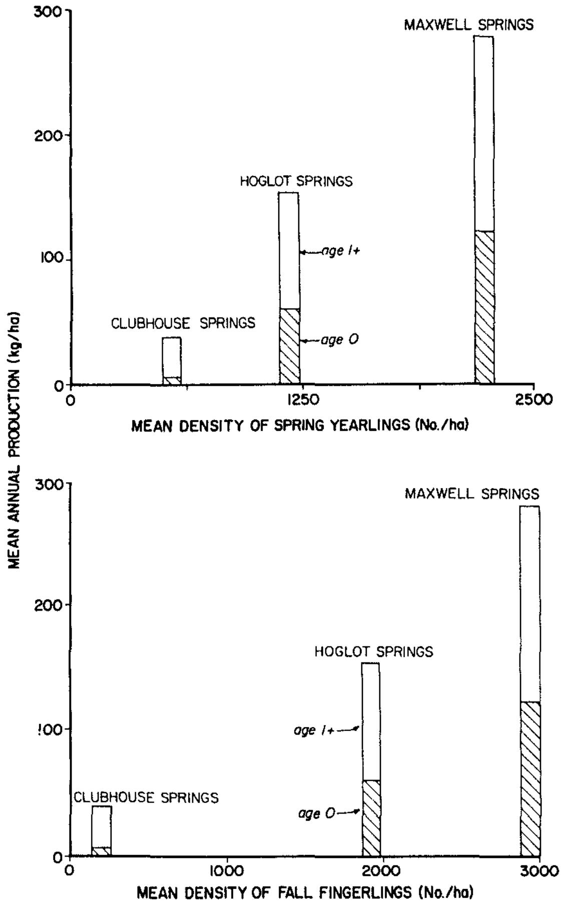

FIGURE 8.—Mean annual densities of spring yearlings and fall fingerlings in relation to mean annual production of age 0 and age 1 and older trout.

TABLE 11.—Total annual production (P), mean biomass ($\bar{B}$), and $P/\bar{B}$ ratios for all age 1 and older brook trout.

Pond and year	P (kg/ha)	$\bar{B}$ (kg/ha)	$P/\bar{B}$
Clubhouse Springs:			
1968	43.4	39.0	1.11
1969	23.0	36.5	0.63
1970	45.7	36.3	1.26
1971	23.0	20.1	1.14
Hoglot Springs:			
1968	89.3	103.1	0.87
1969	95.2	100.0	0.95
1970	110.0	118.2	0.93
1971	71.9	65.9	1.09
Maxwell Springs:			
1969	206.9	199.8	1.04
1970	173.6	162.2	1.07
1971	87.7	64.2	1.37

of individual age-groups during winter 1969-70 were well below average and age 1 trout lost weight. This was the only period in which an age-group in Clubhouse Springs had a negative growth rate, and it was probably due to immigration of yearling trout smaller than pond residents. Overwinter production in 1969-70 was 2 kg/ha; production during other winter periods ranged from 10 to 21 kg/ha.

$P/\bar{B}$ ratios for age 1 and older trout in Hoglot and Maxwell springs tended to decline with increasing biomass (Table 11), i.e., mean weighted growth rates were inversely related to density. As I have noted, age-specific, instantaneous growth rates (G) were the only growth parameters poorly correlated with density. Biased estimates of G for individual year classes could have obscured relationships with population density, but did not markedly affect mean weighted growth rates when all adult trout were combined.

DISCUSSION

Estimation of trout production in this study required several assumptions and the data should be interpreted accordingly. Major assumptions were: 1) numbers of emergent fry were 80% of total egg production, 2) growth and mortality rates of age 0 trout were constant from emergence to fall, and 3) production could be estimated from the product of G and $\bar{B}$ when immigration occurred.

Chapman (1967) suggested that production of brown trout fry in Horokiwi Stream (Allen 1951) could have been overestimated by fourfold due to errors in estimating egg deposition and emergence. I used fecundity data from two populations of wild brook trout that were collected from ponds in the same watershed as the study ponds. Fecundity differences among populations were probably not large since growth rates of the trout were similar. I assumed that all eggs were spawned because egg retention was insignificant in other stream populations of wild brook trout (Wydoski and Cooper 1966). In addition, I assumed emergent fry represented 80% of total egg production. Percentage of live embryos in individual redds exceeded 80% in my study. Brasch (1949) studied brook trout reproduction in several ponds; he found survival from egg to emergence was 79%. In laboratory experiments, emergence of brook trout fry exceeded 80% when the substrate was composed of 5% or less sand and concentrations of dissolved oxygen exceeded 7 ppm (Hausle 1973). Therefore, I do not believe estimates of egg production or emergent fry seriously biased production estimates.

The assumption of constant mortality rates from emergence to fall represents potentially large errors in production estimates for age 0 trout. Hunt (1966) found that instantaneous mortality rates from emergence in February to June were about 10 times greater than mortality from June to September; he based mortality rates on 90% emergence of fry. To assess the influence of variable mortality rates, I calculated production for the 1970 year class at Maxwell Springs from emergence to October with different mortality schedules. If mortality were five times greater during the first half of the interval than during the second, production would have been 63 kg/ha, and if mortality rates varied by tenfold, production would have been 60 kg/ha. With a constant mortality rate from emergence to October, estimated production was 109 kg/ha. Thus, if there was an initial high mortality of fry, production of age 0 trout could have been overestimated by 50 to 60%, and annual production by all age-groups would have been overestimated by 19%.

Assumptions that instantaneous growth rates were constant from emergence to fall certainly oversimplify growth history of fingerlings, but overall effects of this assumption on production estimates did not appear significant. Hunt (1966) found large variations in monthly growth rates of brook trout from emergence to October; growth rates increased to a maximum in May and then declined the rest of the year. Average monthly growth rates from February through April were not different than those from May to October (t-test $P>0.05$). These periods correspond to periods for which I calculated production by age 0 trout. If changes in growth rates of trout fry in my study were similar to those in Lawrence Creek, then assumptions of constant growth rates are much less serious than those regarding mortality rates.

To estimate production with the Ricker formula ($G \times \bar{B}$) one assumes that no emigration or immigration occurred (Chapman 1967). Effects of emigration on production are similar to those of mortality. Recognition of emigration allows one to demonstrate the fate of production, but does not directly affect calculated values. Immigration, however, can have serious effects upon production estimates. The Ricker formula integrates two simultaneous processes, growth and mortality. Numbers of fish are assumed to decrease exponentially and their mean weights are assumed to change in a similar fashion. When immigration occurs and an age-group increases in number, the Ricker formula treats this increase as an exponential one.

To assess the influence of immigration on production, I simulated three different immigration patterns in which year class density increased from 1,400 trout/ha in April to 3,600/ha in October (Figure 9). Curve B represents an exponential increase in density, i.e., that assumed in the Ricker formula. Production was calculated at monthly intervals and the same growth rate was used for each simulation. If all immigration had

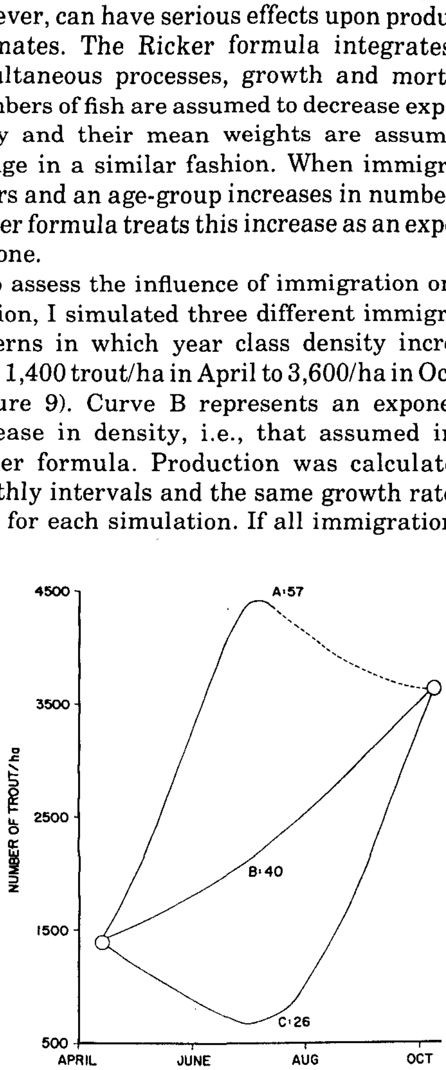

FIGURE 9.—Three hypothetical immigration patterns for a single age-group. Production for each curve was calculated monthly using the same instantaneous growth rate (G = 0.99, t = 0.5 yr). Total production for each curve is given next to letter designation.

occurred in the first half of the interval (A), estimation by the Ricker formula would have underestimated production by 30%, and if trout had immigrated in the latter half of the interval (C), production would have been overestimated by 54%. This increase in cohort size was similar to that of age 1 trout in Hoglot Springs in 1970, the largest increase that occurred in either Hoglot or Clubhouse springs. Therefore, potential errors in production estimates for other intervals would have been less serious.

Recruitment, via immigration and spawning within ponds, appeared to be the most important factor influencing production. Even though production by age 0 trout could have been overestimated, production by age 1 and older trout was closely tied to recruitment rates. In other studies, only a few attempts have been made to link production to recruitment. Backiel and Le Cren (1967) analyzed data from Lawrence Creek (Hunt 1966) and Cultus Lake (Ricker and Foerster 1948) and showed that production was directly related to numbers of emerging fry. Highest annual production of sockeye salmon, *Oncorhynchus nerka,* in Lake Dal'neye occurred in years of highest egg deposition (Krogius 1969).

In this study population biomass was determined by annual recruitment. Among populations, production was most influenced by trout biomass because age-specific growth rates were not significantly different. As a result, production increased linearly with biomass. Hunt (1974) found similar linear relationships for brook trout in Lawrence Creek. Backiel and Le Cren (1967) reviewed density effects on production and illustrated both linear and curvilinear associations between production and biomass. Curvilinear relationships resulted when growth rates were severely depressed at high fish densities and in all of these studies fish were stocked and movement was restricted. I am not aware of any study of wild fish populations in which inverse density-dependent growth caused curvilinear relationships between production and biomass. Rather, in wild populations of salmonids, fish densities appear to be maintained at levels that do not result in seriously depressed growth rates and production increases directly with biomass.

Standing crops of harvestable trout (age 1 and older) in the three populations declined over a year's time because total mortality exceeded growth rates, even though immigration bolstered density of some age-groups (Table 12). The actual

TABLE 12.—Comparison of annual yield of brook trout with potential yield and biomass loss to natural mortality. Data are for trout age 1 and older. All values are in kilograms per hectare.

Pond and interval	(1) Annual biomass loss	(2) Annual production	(1 + 2) Potential yield	(3) Actual yield	[(1 + 2) − 3] Biomass loss to natural mortality	Actual/ potential yield (%)
Clubhouse Springs:						
1970-71	31.0	49.7	80.7	68.4	12.3	85
Hoglot Springs:						
1969-70	27.0	89.0	116.0	54.6	61.4	47
1970-71	8.8	114.5	123.3	25.4	97.9	21
Maxwell Springs:						
1969-70	87.9	200.3	288.2	71.8	216.4	25
1970-71	57.8	188.2	246.0	39.7	206.3	16

biomass loss includes both the change in standing crops from one year to the next and the production during that interval. In all three populations, the actual annual loss in biomass exceeded average standing crops. This loss in biomass may be viewed as the potential yield (Table 12). Biomass lost to natural mortality was calculated as the difference between potential and actual yields. Fate of potential yields appeared dependent upon fishing pressure. In Clubhouse Springs fishing pressure was highest (Table 9), and yield in 1970 was 85% of the potential. Only 16 and 25% of potential yields were taken in Maxwell Springs, where fishing pressure was lowest. The relatively low level of exploitation in Maxwell Springs resulted in substantial biomass losses to natural mortality.

Estimates of fish production in lentic waters have varied from less than 1 g/m^2 to 64 g/m^2, but in most studies they were <20 g/m^2 (Le Cren 1972). Highest reported values were for juvenile sockeye salmon in Lake Dal'neye (Krogius 1969). Production estimates for Maxwell Springs (21-33 g/m^2) are among the highest values currently available. Even if contributions of age 0 trout in Maxwell Springs are ignored, production estimates still rank high (11-22 g/m^2). Carline and Brynildson (1977) suggested that high levels of trout production in ponds similar to Maxwell Springs were due to extensive littoral areas and high standing crops of benthic organisms. While prevailing food densities determine the level of potential fish production, attainment of this potential level is dependent upon annual recruitment of some minimum number of fish.

In this study differences in spawning areas among ponds were obvious and trout production varied accordingly. In many instances quantity and quality of spawning sites are unknown or cannot be readily determined. Where recruitment is limiting, fish production will be relatively low, regardless of the water's general productivity. If production is to be used as a measure of a system's capacity to support species of interest, recruitment of that species should be at or near maximum levels.

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LITERATURE CITED

ADAMS, L.
1951. Confidence limits for the Petersen or Lincoln Index used in animal population studies. J. Wildl. Manage. 15:13-19.

ALLEN, K. R.
1951. The Horokiwi stream, a study of a trout population. N.Z. Mar. Dep. Fish. Bull. 10, 238 p.

BACKIEL, T., AND E. D. LE CREN.
1967. Some density relationships for fish population parameters. *In* S. D. Gerking (editor), The biological basis of freshwater fish production, p. 261-293. Blackwell, Oxf.

BRASCH, J.
1949. Notes on natural reproduction of the eastern brook trout (*S. fontinalis*) with a preliminary report on several experiments on the subject. Wis. Conserv. Dep., Div. Fish. Biol., Invest. Rep. 653, 9 p.

CARLINE, R. F., AND O. M. BRYNILDSON.
In press. Effects of hydraulic dredging on the ecology of native trout populations in Wisconsin spring ponds. Wis. Dep. Nat. Resour. Tech. Bull.

CHAPMAN, D. W.
1967. Production in fish populations. *In* S. D. Gerking (editor), The biological basis of freshwater fish production, p. 3-29. Blackwell, Oxf.

EIPPER, A. W.
1964. Growth, mortality rates, and standing crops of trout in New York farm ponds. N.Y. Agric. Exp. Stn., Ithaca, Mem. 388, 68 p.
GERKING, S. D.
1967. Introduction. *In* S. D. Gerking (editor), The biological basis of freshwater fish production, p. xi-xiv. Blackwell, Oxf.
HAUSLE, D. A.
1973. Factors influencing embryonic survival and emergence of brook trout (*Salvelinus fontinalis*). M.S. Thesis. Univ. Wisconsin, Stevens Point, 67 p.
HUNT, R. L.
1966. Production and angler harvest of wild brook trout in Lawrence Creek, Wisconsin. Wis. Conserv. Dep. Tech. Bull. 35, 52 p.
1971. Responses of a brook trout population to habitat development in Lawrence Creek. Wis. Dep. Nat. Resour. Tech. Bull. 48, 35 p.
1974. Annual production by brook trout in Lawrence Creek during eleven successive years. Wis. Dep. Nat. Resour. Tech. Bull. 82, 29 p.
IVLEV, V. S.
1945. The biological productivity of waters. [In Russ.] Ups. Sourem. Biol. 19:98-120. (Translated by W. E. Ricker. 1966. J. Fish. Res. Board Can. 23:1727-1759.)
KROGIUS, F. V.
1969. Production of young sockeye salmon (*Oncorhyncus nerka*)(Walb.) in Lake Dal'neye. [In Russ.] Vopr. Ikhtiol. 9:1059-1076. (Transl. in Prob. Ichthyol. 9:852-865.)
LAMBOU, V. W.
1961. Determination of fishing pressure from fishermen or party counts with a discussion of sampling problems. Southeast. Game Fish Comm. Proc. 15th Annu. Conf., p. 380-401.
LE CREN, E. D.
1972. Fish production in freshwaters. Symp. Zool. Soc. Lond. 29:115-133.
RICKER, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can., Bull. 191, 382 p.
RICKER, W. E., AND R. E. FOERSTER.
1948. Computation of fish production. Bull. Bingham Oceanogr. Collect., Yale Univ. 11:173-211.
VLADYKOV, V. D.
1956. Fecundity of wild speckled trout (*Salvelinus fontinalis*) in Quebec lakes. J. Fish. Res. Board Can. 13: 799-841.
WYDOSKI, R. S., AND E. L. COOPER.
1966. Maturation and fecundity of brook trout from infertile streams. J. Fish. Res. Board Can. 23:623-649.