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SOME OBSERVATIONS, AGE, GROWTH, FOOD HABITS AND VULNERABILITY OF LARGE BROOK TROUT *(SALVELINUS FONTINALIS)* FROM FOUR CANADIAN LAKES

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Résumé

La plupart des ombles de fontaine *(Salvelinus fontinalis)* capturés de quatre lacs étaient d'une taille supérieure à 40 cm. Les individus de classes d'âge V et VI étaient abondants, et un spécimen atteignait la classe d'âge IX. Des analyses de contenus stomacaux révèlent qu'aucune nourriture spéciale ne fut capturée par ces individus de grande taille, dans les eaux du nord. Les grands brochets *(Esox lucius)* sont présents dans tous les lacs, tandis que le doré *(Stizostedion vitreum)* se rencontre dans les bassins d'eau du Québec. L'omble de fontaine est exposé à une capture facile dans les lacs où ont été faits les étiquetages ; ce fait, en plus de la taille des populations, doit être sérieusement considéré dans l'établissement d'un programme d'aménagement.

Abstract

Most specimens of brook trout *(Salvelinus fontinalis)* collected from the four lakes were over 40 cm in length. Brook trout of age V and VI were common with one fish reaching age IX. Stomach analysis did not disclose any particular food item that might account for the large size reached by brook trout in some northern waters. Northern pike *(Esox lucius)* were present in all lakes and walleye pike *(Stizostedion vitreum)* were present in the Québec waters. Large brook trout were vulnerable to angling in the lake where trout were tagged and this, plus population size, should be given careful consideration when setting management regulations.

Introduction

Few lakes consistently produce brook trout over five pounds. Sportsmen (Wulff, 1969) and biologists (LeJeune, 1964; Power, 1966) have pointed out the vulnerability to angling of populations of large brook trout but data are scanty on this point, as are explanations on why certain waters produce unusually large fish.

In 1959 Cornell University and the Department of Tourism, Province of Québec became interested in obtaining brook trout eggs from populations where specimens reached unusually large size. In connection with these operations data on species composition, growth and stomach contents were collected from three lakes in Québec and similar data, plus information on recapture of tagged trout from one lake in Labrador. Time and funds were insufficient to conduct detailed studies but the results obtained contribute to our meager knowledge of these unique populations about which almost nothing has been published.

Materials and methods

ASSINICA LAKE

Assinica Lake is located approximately 241 km east of the southern tip of James Bay (longitude 75°15′W, latitude 50°30′N) in the Province of Québec. The lake is approximately 10 000 ha in area but is very shallow, running mostly under 7 m in depth (LeJeune, 1962). Rocky islands and shoals are common. Brook trout commonly reach weights of 3 kg with some specimens running to nearly 5 kg. In the 1960 Field and Stream contest 14 of the 20 awards for brook trout came from Assinica Lake and its outlet, the Broadback River.

Trout from the lake are believed to move into the river in late summer. The river is precipitious with a rocky bottom. Impassable falls prevent fish from James Bay entering the upper portion of the Broadback River or Assinica Lake.

LAKE ALBANEL

Lake Albanel is approximately 96 km northeast of Assinica Lake (longitude 73°10′W, latitude 51°10′N) and drains into Lake Mistassini and then via the Rupert River into James Bay. A falls below Lake Albanel prevents fish from Lake Mistassini from reaching this water. The lake is approximately 26 000 ha in area and differs from Assinica Lake in that it has a much greater average depth. Depths of 12 m were common a short distance from shore.

The main inlet to Lake Albanel is the Temiscamie River. A brook trout spawning area is located approximately 128 km above the lake and it is presumed a portion of the trout from the lake spawn here. The brook trout from Lake Albanel and the Temiscamie River commonly reach 2 kg with some fish reaching 3,5 kg. The maximum size is believed less than Assinica Lake.

Large mayfly hatches (presumably Hexagenia) reportedly occur during mid-July but were not observed during the survey of July 17-22, 1965.

LAKE MISTASSINI

This is one of the largest lakes in Québec and part of the Lake Albanel system. It is located approximately four km west of Lake Albanel (longitude 73°40′W, latitude 51°10′N). Brook trout for stomach analysis were obtained from the Indians at Mistassini Post. The lake contains brook trout of 3-4 kg, although those collected ran only 0,6-2 kg.

LAKE ANNE MARIE

Lake Anne Marie (longitude 60°40′W, latitude 52°25′W) is part of the Minipi Lake system and is located approximately 95 km southwest of Goose Bay, Labrador. The lake is approximately 2 300 ha in area and is mostly shallow with rocky islands and shoals, similar to Assinica Lake. Brook trout of 2 kg are common with some occasionally reaching 3-4 kg; during late summer trout reportedly move into the outlet and inlet from the lake.

Fishing camp rules are designed to preserve fishing quality and each angler is allowed to kill one trophy brook trout. Angling is by flies only.

During July large hatches of mayflies *(Hexagenia)* occur and at this time large brook trout feed readily on the surface throughout the lake. Later in the season few trout are taken in the lake and fishing is carried on in the outlet or inlet.

DATA COLLECTION

Scales were used for age determination from all waters except Assinica Lake where otoliths were used. Annuli on scales were normally distinct through age 4 but beyond this point the possibility of error increases with age. It is doubtful, however, if misinterpretation was greater than plus or minus 1 year.

Assinica Lake and Lake Albanel were gill netted to obtain information on species composition, and gather data on brook trout populations. Lake Anne Marie was gill netted with small mesh nets to sample fish species that might be of a size suitable for brook trout forage. Seining was unsuccessful for collecting fish samples due to the rocky bottoms of all the lakes. Angling was a major method of collecting brook trout samples in Lake Anne Marie and Assinica Lake.

Trout were tagged in Lake Anne Marie. A minimum tagging size of approximately 1 kg was established to reduce possible predation by northern pike, because of the shiny hog ring jaw tag used. The tagging period extended through the angling season of June 21 to the middle of August.

Stomach samples were collected from trout taken by angling in Lake Anne Marie and from specimens collected by gill netting in Lake Mistassini and Lake Albanel.

Results

SPECIES ASSOCIATION

Northern pike are present in all four lakes and walleye pike in the three Québec waters. In Assinica Lake and Lake Albanel walleyes made up nearly 50 percent of the total catch (Table I). Brook trout made up less than 4 percent of the fish handled. Netting and angling indicated brook trout under 35 cm were scarce in all lakes and most specimens were over 40 cm. Nearly all of the small trout taken were captured in the outlets or inlets of the lakes.

Walleyes were not present in Lake Anne Marie and white suckers made up the major part of the catch in this water. Larger mesh size would undoubtedly

TABLE I

Species composition in gillnet samples from three Canadian lakes.

Species	*Québec*						*Labrador*		
	Lake Albanel[1]			*Assinica Lake*[2]			*Lake Anne Marie*[3]		
	Total no. caught	Percent total	Size range (cm)	Total no. caught	Percent total	Size range (cm)	Total no. caught	Percent total	Size range (cm)
Stizostedion vitreum	376	44	20-64	247	50	Not available	0	—	—
Catostomus commersoni	191	22	48-55	56	11		23	74	16-27
Catostomus catostomus	113	13	20-58	6	1		2	7	16-17
Coregonus clupeaformis	91	11	20-60	103	21		0	—	—
Salvelinus fontinalis	31	3	19-23	11	2		1	3	29
Prosopium cylindraceum	21	2	19-41	0	—		0	—	—
Salvelinus namaycush	14	2	45-69	0	—		0	—	—
Coregonus artedi	8	1	19-29	1	—		0	—	—
Esox lucius	8	1	55-77	73	15		2	7	16-42
Lota lota	7	1	20-80	0	—		1	3	10
Salvelinus alpinus	0	—	—	0	—		2	7	22-29

[1] 86 gillnet units,* 16-178 (mm) stretched mesh — July 1967.
[2] 153 gillnet units,* 51-102 (mm) stretched mesh — September-October 1962 (Le Jeune, 1962).
[3] 8 gillnet units,* 25-36 (mm) stretched mesh — August 1973.
* 1 gillnet unit represents 100 feet net set 24 hours.

TABLE II

Brook trout growth in four Canadian waters. Length in cm, weight in kg.

Water	*Item*	*Age in years*								
		I	*II*	*III*	*IV*	*V*	*VI*	*VII*	*VIII*	*IX*
Assinica Lake, PQ	Number fish	7[1]	4[1]	2	3	2	4	4		
(Aug-Sept 1962)	Length	19,8	31,0	30,7	42,7	62,7	61,2	66,0		
	Weight	,08	,26	—	—	—	—	3,80		
Lake Albanel, PQ	Number fish	2	2	6	4	12	8	2		
(Jul 1967)	Length	20,1	20,1	39,1	46,5	55,1	58,7	61,2		
	Weight	,08	,06	,65	1,02	1,55	1,80	2,08		
Lake Mistassini, PQ	Number fish	0	2	14	17	16	4			
(Jul 1967)	Length	—	36,6	44,5	49,5	53,3	57,9			
	Weight	—	,48	,91	1,24	1,45	1,74			
Lake Anne Marie, Lab.	Number fish	4	17	38	43	30	33	18	2	1
(Jul-Aug 1973-74)	Length	17,0	23,1	33,0	44,2	51,8	54,9	55,6	57,9	64,8
	Weight	—	—	,63[2]	1,27	1,78	2,10	2,46	2,50	2,61

[1] Stream habitat.
[2] Only 30 fish weighed.

have taken a larger number of fish in Lake Anne Marie and the catch is not considered representative of abundance of various species, except possibly for suckers.

Forage Species

The fine mesh gill net used in Lake Anne Marie and Lake Albanel failed to reveal any fish species in sufficient abundance to be considered important as brook trout forage. Suckers were common in both lakes but most specimens in the samples were of a size too large to be utilized by brook trout.

BROOK TROUT GROWTH

Growth rates were similar in all waters. The large size obtained by some individuals was the result of good growth at ages III to VI, rather than unusually fast growth during the early years (Table II). Trout of age VI were taken in all lakes and except for Lake Mistassini age VII was well represented. Assinica Lake produced the largest specimen with one fish at age VII reaching 71 cm in length. During two summers of observation in Lake Anne Marie no trout under age III were taken in the lake proper and it may be assumed that trout from the tributaries and outlet move into the lake as they reach a large size. Scale examination showed a wide range in size at age III and IV which would support this hypothesis.

TAG RECOVERIES

Fifty-seven trout were tagged in 1973 and the same number in 1974, in Lake Anne Marie. Fishing pressure in 1974 was light, less than 0,1 rod day per ha, yet 16 percent of the trout tagged the previous season were recaptured. In 1974 nearly all (93 percent) tagging took place during the last three weeks of the season. Although these tagged fish were available for only a short period, 14 percent were recaptured within the season.

Approximately one half of the twenty five recoveries made during the 1973-

74 season were taken in the same general area as tagged. There were 4 recoveries of fish that had traveled either to or from the inlet to outlet, a distance of approximately 10 km.

FOOD HABITS

Sixty percent of the brook trout stomachs containing food from Lake Albanel held fish remains, as did forty five percent of those from Lake Mistassini (Table III). Small ciscoes were the dominant species in the stomachs of specimens from both lakes. Insects were present in over one half of the stomachs containing food from the two Québec Lakes. Ephemeroptera was the major insect order utilized from Lake Albanel, with terrestrial Coleoptera dominant from Lake Mistassini (Table III).

None of the stomachs examined from Lake Anne Marie specimens contained fish. A variety of insects were eaten and Odonata, Diptera and Coleoptera (mainly terrestrial) dominated (Table III).

No benthic organism was abundant in the Ekman dredge (15 × 15 cm) samples taken from 18 locations in Lake Anne Marie in mid-August. Chironomid larvae were most common and were found in eleven of the samples with an average number of 6 per sample. Oligochaeta were found in 7 samples (average 4 per sample and second in occurrence). Mayflies, which hatched in large numbers in July, were taken in only 4 samples (average 1 per sample).

TABLE III

Frequency of occurrence of fish and invertebrate food in brook trout from three Canadian Lakes.

Water	*Lake Albanel*		*Lake Mistassini*		*Lake Anne Marie*	
Number fish examined	*20*		*35*		*35*	
Size range trout (cm)	*25-63*		*33-60*		*33-61*	
Food items	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
FISH						
Coregonus artedi	6	30	9	26	0	—
Percina caprodes	3	15	0	—	0	—
Stizostedion vitreum	1	5	0	—	0	—
Unidentified	4	20	7	20	0	—
Total containing fish	12	60	13	37	0	—
INVERTEBRATES						
Annelida	1	5	0	—	0	—
Coleoptera	2	10	23	66	20	57
Copepoda	0	—	0	—	1	3
Diptera	1	5	6	17	22	63
Ephemeroptera	10	50	2	6	16	46
Hemiptera	0	—	5	14	1	3
Hymenoptera	0	—	15	43	1	3
Neuroptera	0	—	0	—	14	40
Odonata	0	—	1	3	23	66
Trichoptera	3	15	2	6	2	6
Unidentified	2	10	27	77	8	23
Total containing invertebrates	12	60	26	74	35	100

Discussion

The coexistence of northern pike and brook trout is often encountered in northern waters and a departure from the species association encountered in the southern part of the brook trout range. Walleyes and brook trout are an even rarer species association in more southerly waters. The factors permitting this association of predator species and brook trout may require recruitment of trout of 12 to 14 inches from a relatively mitigated stream environment.

The trout in all waters investigated had greater longevity than is usual in the southern part of their range (Cooper, 1953; Hoover, 1939; Green, 1951). Although age determination was uncertain in some older individuals in natural populations it can be substantiated up to 9 years from known age Assinica strain brook trout naturalized in the Adirondack Mountains of northern New York State (Flick and Webster, 1971).

The food supply that produces rapid growth and large size in these northerly trout populations remains obscure. Movement from a stream to a lake environment is often reflected in improved growth but it would seem that a large forage organism (e.g. fish) would be necessary to produce the size fish involved. Obviously, data from more than 2 months of the year are required to satisfactorily investigate this aspect of life history. This information is of great importance if we are to successfully manage waters for large sized brook trout.

The tagging data from Lake Anne Marie indicates the vulnerability, of brook trout to angling and the possibility of over exploitation even with light fishing. Data on Assinica Lake strain brook trout in a New York lake also indicate high vulnerability with approximately 50 percent of the population recovered by flyfishing in 4 hours of angling on a ten ha pond (unpublished data of author). The vulnerability of brook trout to angling was also noted by Power (1966) in the Ungava area and LeJeune (1964) in Assinica Lake. The large trout in these areas apparently move out of the lake and concentrate in the fast water during the summer where they are readily taken by angling. The combination of high vulnerability and apparent low population densities of large brook trout in some northern waters are critical factors to be considered in setting angling regulations.

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References

COOPER, Edward L., 1953. Growth of brook trout *(Salvelinus fontinalis)* and brown trout *(Salmo trutta)* in the Pigeon River, Otsego County, Michigan. — Pap. Mich. Acad. Sci., 38 : 151-162.

FLICK, W. A. and D. A. WEBSTER, 1971. Brandon Park Fish Management Report. — Dep. Nat. Resour., Cornell Univ., 40 p.

GREEN, W. Willard, 1952. Results from stocking brook trout of wild and hatchery strains at Stillwater Pond. — Trans. Am. Fish. Soc., 81(1951):43-52.

HOOVER, Earl E., 1939. Age and growth of brook trout in northern breeder streams. — J. Wildl. Mgmt, 3(3): 81-91.

LEJEUNE, Roger, 1964. Inventaire de la faune ichtyologique du lac Assinica. — Service de la faune, Ministère du Tourisme, de la Chasse et de la Pêche, Province de Québec, Rapp. N° 3, (1963): 257-267.

POWER, Geoffrey, 1966. Observations on the speckled trout *(Salvelinus fontinalis)* in Ungava. — Naturaliste can., 93: 187-198.

WULFF, Lee, 1969. The wonderful brookies of Minipi. — Sports Afield (July), 4 p.

ably because there were more large fish in deeper waters.

Although 58 kokanee and 50 trout examined in July 1963 did not utilize the same foods, we cannot postulate presence or absence of competition. As Larkin and Smith (1953) indicated for two fishes competing for food in Paul Lake, B. C., food analysis showing discrete food habits after several years of interspecific competition may be misleading. Even common utilization of the same food items might not constitute competition unless the foods concerned were in short supply.

Fish populations in Elk Lake have been supported entirely by stocking roughly equal numbers of kokanee and brook trout in recent years. Since the two species shared the same waters in late summer, for the most part, the greater catch of brook trout per net reflects either differing vulnerability of kokanee and trout to the gear or a somewhat lower survival of kokanee. Creel census in 1961[2] showed that 201 anglers in Elk Lake had caught 455 kokanee, 60 brook trout, and 41 rainbow trout. In 1962[2] there were 33 anglers checked with 193 kokanee, 26 brook trout, and 10 rainbows. It seems quite possible that fishing mortality was much higher for kokanee than for brook trout. Anglers in Elk Lake were usually fishing for kokanee in 1962–63.

[2] Annual Reports of the Fishery Division, Oregon State Game Commission for 1961 and 1962.

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LITERATURE CITED

Echo, John B. 1954. Some ecological relationships between yellow perch and cutthroat trout in Thompson Lake, Montana. Trans. Amer. Fish. Soc. 84: 239–248.

Flick, William A., and Dwight A. Webster. 1962. Problems in sampling wild and domestic stocks of brook trout (*Salvelinus fontinalis*). Trans. Amer. Fish. Soc. 91: 140–144.

Horak, Donald L., and Howard A. Tanner. 1964. The use of vertical gill nets in studying fish depth distribution, Horsetooth Reservoir, Colorado. Trans. Amer. Fish. Soc. 93: 137–145.

Larkin, P. A., and S. B. Smith. 1953. Some effects of introduction of the redside shiner on the Kamloops trout in Paul Lake, British Columbia. Trans. Amer. Fish. Soc. 83: 161–175.

Northcote, T. G., H. W. Lorz, and J. C. MacLeod. 1964. Studies on diel vertical movement of fishes in a British Columbia Lake. Verh. Internat. Verein. Limnol. XV: 940–946.

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Comparative Survival of Wild and Domestic Strains of Brook Trout in Streams

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ABSTRACT

Survival and growth of progeny of domestic, domestic × wild, and wild strains of brook trout (*Salvelinus fontinalis*) were compared after these trout were released during the fall as fingerlings 9 to 10 months old in selected sections of streams. One group of the wild strain was hatched and reared in the wild. Other groups were hatched and reared in the hatchery. The domestic strain had the highest over-winter survival in three of five streams. In only one stream did the wild strain have the highest over-winter survival. In the four streams investigated during the fall, the wild strain had the highest summer-survival. Survival of the domestic and domestic × wild strains through the summer fishing season was generally too low to evaluate survival of these strains through the second winter. The domestic strain grew most rapidly in the hatchery followed by the domestic × wild strain. This growth advantage was not maintained after release into streams.

Brook trout of the domestic strain were harvested early in the fishing season and did not contribute to the late-season catch, whereas the domestic × wild and wild strains were harvested throughout the fishing season.

INTRODUCTION

Domesticated brook trout (*Salvelinus fontinalis*), propagated for 30 or more years in Wisconsin hatcheries, do not survive in streams as well as resident wild brook trout. This is especially evident when the brook trout are released as fingerlings in early summer and in the autumn. Moreover, after introduction into streams with suitable habitat for brook trout, the domesticated brook trout do not survive exposure to a fishing season in adequate numbers to constitute a breeding stock (Brynildson and Christenson, 1961).

To determine whether "wilderness" is a factor influencing survival of hatchery-reared brook trout in Wisconsin streams, progeny of domestic, domestic × wild, and wild brook trout were reared in the Hatchery and subsequently released in streams. Wild fingerling brook trout from an upper section of one stream were transferred to a lower section where hatchery-reared brook trout were released in order to compare survival of stream-reared and hatchery-reared brook trout.

METHODS

Strains of trout

"Strains" are various groups of brook trout of different parentage. Although genetic differences among groups are unknown, behavior in the hatchery supports separation of the groups into strains.

Domestic strain.—This strain is over 30 years old and originated at the Osceola State Trout Hatchery at Osceola, Wisconsin. Brood stock was selected for uniformity in appearance and rapid growth. Most of the males mature as fingerlings (age group 0) during their first autumn of life; females mature 1 year later.

Wild strains.—Source of the wild strains reared in the hatchery and in the wild were from Lawrence Creek and Big Roche-a-Cri Creek, respectively, two streams in which the wild stock is maintained by native brook trout.

Hatchery procedure

Progeny from domestic and wild strains were hatched from eggs fertilized as follows: domestic strain (domestic ♂ × domestic ♀); wild strain (wild ♂ × wild ♀); WD Hybrid (wild ♂ × domestic ♀); and DW Hybrid (domestic ♂ × wild ♀).

Trout fry and fingerlings were fed 50% meat and 50% dry diet until 4 months old, then placed on a complete dry diet until released in streams.

Streams stocked

Various strains of brook trout, 9 to 10 months old, were released over a 1-mile section in each of five streams. Streams selected were Big Roche-a-Cri and Campbell Creeks which flow in the infertile central Wisconsin

TABLE 1.—Characteristics of the different brook trout strains before release into five Wisconsin streams

Streams stocked	Date stocked	Strain and symbol	Fins[1] removed	Number stocked	Length range (inches)	Average length (inches)	Average weight (grams)	Average K
Big Roche-a-Cri	20 Sep. 1962	Domestic (D)	RVLP	1,000	4.9–6.1	5.4	30	1.93
		WD Hybrid (WD)	ARP	1,000	4.0–6.0	4.8	22	1.95
		Wild (W-L)[2]	LVRP	1,000	3.0–4.6	3.5	8	1.70
		Wild (W-R)[2]	ALP	844	2.3–4.4	3.3	6	1.07
Black Earth	19 Sep. 1962	Domestic (D)	A	1,000	5.2–6.5	5.8	41	2.02
		WD Hybrid (WD)	ARV	1,000	4.7–6.4	5.5	32	1.95
		Wild (W-L)	ALV	1,000	3.5–5.1	4.2	13	1.73
Campbell	29 Oct. 1962	Domestic (D)	RV	1,000	5.9–7.5	6.6	62	2.09
		WD Hybrid (WD)	ARV	1,000	4.0–5.9	4.8	24	2.00
		Wild (W-L)	ALV	1,000	2.9–4.6	3.5	9	2.03
Big Spring	16 Sep. 1963	Domestic (D)	LV	1,000	5.0–6.7	5.8	35	1.78
		WD Hybrid (WD)	RV	1,000	5.0–6.3	5.5	29	1.75
		DW Hybrid (DW)	ALV	1,000	4.1–5.5	4.6	17	1.71
		Wild (W-L)	ARV	1,000	2.9–4.0	3.2	5	1.51
Story	20 Sep. 1963	Domestic (D)	ALV	1,000	4.6–6.8	5.4	28	1.78
		WD Hybrid (WD)	ARV	1,000	4.7–6.6	5.3	27	1.72
		DW Hybrid (DW)	LV	1,000	4.0–5.6	4.6	17	1.69
		Wild (W-L)	RV	1,000	2.7–4.0	3.2	6	1.62

[1] Abbreviations for fins removed: A—adipose; L—left; P—pectoral; R—right; V—ventral.
[2] W-L = wild strain native to Lawrence Creek which was hatched and reared in the hatchery.
W-R = wild strain native to Big Roche-a-Cri Creek which was hatched and reared in this stream.

sand plains area, and Big Spring, Black Earth, and Story Creeks which flow in the fertile predominately limestone area of southern Wisconsin.

The section stocked in Big Roche-a-Cri Creek had relatively deep, low velocity (less than 1 fps) water flow that was ice-covered during winter. This section contained approximately 18 pounds of resident wild brook and brown trout per acre plus approximately 30 pounds of white suckers (*Catostomus commersoni*) and minnows per acre.

The stocked section of Campbell Creek had low velocity water flow which was ice-free during the winter. In April, 1963, this section contained 11 and 270 pounds per acre, respectively, of wild brook and brown trout and 234 pounds of stocked brook trout of various strains, but only a sparse population of white suckers and minnows. The total poundage of stocked brook trout and wild resident trout combined was 516 pounds per acre.

The stocked section of Big Spring Creek had relatively shallow, high velocity (more than 1 fps) flow, typical of southwest Wisconsin coulee streams. Ample ground water discharge kept the entire stream free of ice during the winter. In April, 1963, this section contained approximately 15 pounds of carry-over stocked brown trout per acre and approximately 60 pounds per acre of white suckers and minnows, mainly creek chubs (*Semotilus atromaculatus*).

The section stocked in Black Earth Creek was ice-free during the winter and had relatively deep, low velocity water flow. Black Earth Creek is a fertile stream and has a high fish carrying capacity. In April, 1963, this section contained 319 and 200 pounds per acre of trout and white suckers, respectively. Of this biomass, 129 pounds per acre were wild brown trout, 20 pounds per acre were carry-over stocked domestic brown trout, and 30 pounds per acre were carry-over domestic rainbow trout (stocked as fingerlings in June, 1962), and 140 pounds per acre of the various strains of stocked hatchery-reared brook trout.

The stocked section of Story Creek was mainly ice-free during the winter and had relatively deep, low velocity water flow. In April, 1963, this section contained only 32 pounds of wild and carry-over stocked brown trout per acre; however, a high density of the redside dace (*Clinostomus elongatus*) was observed in April, 1963. Population levels of other minnows and white suckers were relatively low.

Groups of 1,000 brook trout of each strain (Table 1), reared at the Westfield Research Station in 1962 and 1963, were graded into narrow length frequency ranges, and marked, by removal of various fins, for future identification. After a random sample of 100 trout was measured and weighed from each group, the 1,000 trout of each strain were placed in a tank-truck and scatter-planted in the same section of a given stream. Following this procedure, the streams stocked first received the largest trout from the various groups. The 844 wild brook trout (W-R) collected on upper Big Roche-a-Cri Creek were marked, 100 measured and weighed, and then placed in a tank truck with the hatchery-reared strains, and all were released together in a section of Big Roche-a-Cri 4 miles below the upper section. Further data on the stocked trout are presented in Table 1.

Population estimates

Before trout population estimates were made, each stream study area was sub-divided into approximately 1-mile sections and 300-yard stations. Population estimates were made just prior to the opening of the trout fishing season in May, and in September or October after the trout fishing season closed in September. Electrofishing operations, using a 230-volt, 2,500-watt, direct-current electric shocker, covered approximately 2 miles in Campbell Creek, 5 miles in Big Spring, 6 miles in Black Earth and Story Creeks and 11 miles in Big Roche-a-Cri Creek. In September 1964, the upper 1-mile section of the 6-mile study area of Story Creek could not be electrofished because the stream channel was choked with reed canary grass. The Peterson-type mark and recapture method was employed. For details on procedure and efficiency of the electrofishing gear, see McFadden (1961) and Hunt, Brynildson, and McFadden (1962). Recapture values during the second run with the electric-shocker on trout 6 to 10 inches in total length was 60 to 90% of the original number captured, marked, and released during the first run. Population estimates of the trout were made by 1-inch length intervals in each of the approximately 1-mile stream sections within each stream.

All trout captured with the electric-shocker within and at each 300-yard station within the approximately 1-mile stream sections were measured to the nearest 0.1-inch in total length and a representative sample was weighed to the nearest gram on 500 or 1,000 gram capacity Hanson dietetic scales.

Creel census

A creel census was conducted on Big Roche-a-Cri and Black Earth Creeks during the 1963 trout fishing season. Only one man patrolled the stream and obtained an estimated 80% record of the total brook trout harvest during the season.

RESULTS

Survival and growth in the hatchery

The wild strain of brook trout had higher early mortality in the hatchery than the domestic and domestic × wild strains. Higher mortality of the wild strain occurred because some of these trout never acquired feeding patterns necessary for survival and growth in the hatchery. Mortality after several weeks declined rapidly and was low during the remainder of the rearing period.

Timid or excitable behavior of wild brook trout reared in the hatchery was reported by Greene (1952) and Vincent (1960). Such timid behavior was exhibited by the wild strains of brook trout at the Westfield Hatchery and was probably reflected in rates of growth in the hatchery. The domestic strain grew more rapidly than the hybrids which in turn grew more rapidly than the wild strain. During feeding, the domestic strain moved toward the man dispensing feed; the wild strain moved away; while the hybrids exhibited behavior patterns of both the domestic and wild strains. The domestic strain would feed readily off the surface where food, when dispensed, was immediately abundant, whereas the wild strain would stay near the bottom and take excess feed settling to the bottom. The hybrids fed off the surface but were more wary than the domestic strain.

The somewhat smaller size (av. 0.6 in. TL) of the DW Hybrid (domestic ♂ × wild ♀) in comparison to the size (av. 1.0 in. TL) of the WD Hybrid (wild ♂ × domestic ♀) when stocked may have been partly a result of hatching from the smaller eggs of the smaller wild female trout. Alm (1939) compared fry from small eggs, of the small brown trout in rivers, and large eggs from the larger

Table 2.—*Percentage survival of original stocks of different brook trout strains after release into five Wisconsin streams during autumn*

Streams	Time in stream (years)	Strains of trout: D	WD	DW	W-L	W-R	Average
Big Roche-a-Cri	½	32.4	43.6	–	50.7	54.8	45.4
	1	0.6	4.3	–	17.8	19.7	10.6
	1½	0.0	1.7	–	11.8	10.8	6.1
	2	0.0	0.1	–	0.3	1.1	0.4
Black Earth	½	40.0	35.4	–	30.0	–	35.1
	1	0.7	4.6	–	7.2	–	4.2
	2	0.0	0.5	–	0.5	–	0.5
Campbell	½	49.8	42.2	–	27.0	–	40.0
	1	0.0	2.9	–	9.7	–	4.2
Big Spring	½	33.6	31.7	20.1	9.1	–	23.6
Story	½	34.1	44.9	39.7	9.9	–	32.2
	1	1.5	2.7	3.9	6.1	–	3.6
	1½	0.7	3.4	4.5	7.9	–	4.1
Average	½	38.0	40.0	29.9	25.3	54.8	
	1	0.7	3.6	3.9	10.2	19.7	
	1½	0.4	2.6	4.5	9.8	10.8	
	2	0.0	–	–	0.4	1.1	

brown trout from lakes, under hatchery conditions. The fry were 0.9 inches and 1.1 inches, respectively, and after a year the length ranges were 1.9–2.9 inches and 2.2–3.2 inches, respectively.

Survival in streams

The domestic strain of brook trout had a significantly higher survival (Table 2) than the WD hybrid, during the closed season for fishing and first winter in Black Earth, Campbell Creeks ($P < 0.01$, by Chi square), and in Big Spring Creek ($P < 0.05$). The WD Hybrid, in turn, had a significantly higher survival ($P < 0.01$) than the wild strain (W-L) during the first winter in all streams except Big Roche-a-Cri Creek. In Big Roche-a-Cri Creek, the wild strains had a significantly higher survival ($P < 0.01$) than the WD Hybrid during the first winter while the latter had a significantly higher survival ($P < 0.01$) than the domestic strain. The WD Hybrid survival was also significantly higher ($P < 0.01$) than the domestic strain, during the first winter in Story Creek. In the two streams where released, the WD Hybrid survived the first winter better than the DW Hybrid (Big Spring Creek, $P < 0.01$ and Story Creek, $P < 0.05$). In pond environments during the first winter, wild strains of brook trout generally exhibited a higher survival than domestic strains (Flick and Webster, 1964).

Trout population estimates were made on all the streams except Big Spring Creek during September or October after the trout fishing season closed in September. The wild strain of brook trout survived the period open to fishing significantly better ($P < 0.01$) than the domestic and hybrid trout (Table 2). It is possible to demonstrate that the WD Hybrid survived the period open to fishing significantly better ($P < 0.01$) than the domestic strain in Black Earth and Campbell Creeks, but not in Big Roche-a-Cri and Story Creeks.

Except for the domestic strain, the estimated population of stocked brook trout was slightly higher in Story Creek, at the end of one and a half years than at the end of one year (Table 2). Because of a dense September 1964 aquatic plant growth, the upper-most mile of trout water in Story Creek could not be electrofished as it had been in April, 1964. However, after most of the aquatic plants disappeared, during the winter of 1964–65, this section of stream was successfully electrofished and a larger total number of trout were captured in the spring of 1965 than during the fall of 1964. No reliable comparison can therefore be made of relative survival of the various strains of trout during their second winter in Story Creek. However, from the spring of 1964 to the spring of 1965, the survival of the wild strain was significantly higher ($P < 0.01$) than the survival of the hybrid trout, which in turn exhibited a significantly higher survival ($P < 0.01$) than the domestic strain.

Survival during their second winter of life and exposure to a closed fishing season in Big Roche-a-Cri Creek was highest for the Lawrence Creek wild strain (W-L), followed by the Big Roche-a-Cri Creek resident wild trout (W-R) which had been transferred from an upper to the lower study area of Big Roche-a-Cri Creek (Table 1). The better survival of the Lawrence Creek wild strain compared to the WD hybrid was highly significant ($P < 0.01$) and the survival of the Big Roche-a-Cri Creek wild strain was significantly better ($P < 0.05$) in comparison to the survival of the WD hybrid. No trout of the domestic strain was found during electrofishing in April 1964, when these survival estimates were made (Table 2).

Table 3.—*Average total length in inches of different brook trout strains before and after release into five Wisconsin streams during autumn*

Streams	Stocking and collecting dates[1]	Strains of trout: D	WD	DW	W-L	W-R
Big Roche-a-Cri	(Sep., 1962)	5.4	4.8	–	3.5	3.3
	Apr., 1963	6.4	5.6	–	4.3	4.3
	Sep., 1963	9.7	7.5	–	6.3	6.7
	Apr., 1964	–	8.6	–	7.3	7.9
	Sep., 1964	–	9.3	–	9.5	10.3
Black Earth	(Sep., 1962)	5.8	5.5	–	4.2	–
	Apr., 1963	7.9	7.0	–	5.4	–
	Sep., 1963	9.2	10.7	–	9.1	–
	Sep., 1964	–	14.6	–	12.7	–
Campbell	(Oct., 1962)	6.6	4.8	–	3.5	–
	Apr., 1963	8.2	5.7	–	4.6	–
	Oct., 1963	–	6.9	–	6.4	–
Big Spring	(Sep., 1963)	5.8	5.5	4.6	3.2	–
	Apr., 1964	7.7	7.3	6.3	4.8	–
Story	(Sep., 1963)	5.4	5.3	4.6	3.2	–
	Apr., 1964	7.7	7.4	6.6	5.2	–
	Sep., 1964	9.7	9.4	8.5	7.3	–
	Apr., 1965	10.8	11.4	10.5	9.1	–

[1] Dates of stocking in parentheses.

Growth in streams

Although the domestic strain grew faster in the hatchery than the hybrids and the wild strain, they did not consistently maintain this growth advantage in the fall and winter environment of the streams where the trout were released (Table 3). Similar growth patterns of wild and domestic strains of brook trout in the wild environment were reported by Vincent (1960) and Flick and Webster (1964).

Comparative summer growths of the different strains of brook trout in a particular stream are obscured because the larger individuals of a given strain were probably creeled at a higher rate than smaller individuals. This may have been particularly true when comparing growth with the smaller-sized wild strains, some of which were still below the 6-inch minimum size limit after the fishing season closed. Moreover, most of the captured trout of the domestic strain were creeled because of their desirable size. Angling and natural mortality was so high that no trout of the domestic strain were collected by electrofishing in September in Campbell Creek. In the other streams investigated, only a small number of the domestic strain was still present after the close of the trout fishing season in September, and these probably represented smaller or slower-growing fish.

The only significant data available on comparative growth of the stocked strains, during their second season in waters closed to fishing and second winter of life, are from Big Roche-a-Cri and Story Creeks (Table 3). In these two streams, the growth of the wild strains and the hybrids was similar.

Table 4.—*Average coefficient of condition (R) of different brook trout strains before and after release into five Wisconsin streams during autumn*

Streams	Stocking and collecting dates[1]	Strains of trout: D	WD	DW	W-L	W-R
Big Roche-a-Cri	(Sep., 1962)	1.93	1.95	–	1.70	1.67
	Apr., 1963	1.66	1.65	–	1.49	1.52
	Sep., 1963	1.90	1.80	–	1.63	1.67
	Apr., 1964	–	1.75	–	1.63	1.68
	Sep., 1964	–	1.82	–	1.65	1.74
Black Earth	(Sep., 1962)	2.02	1.95	–	1.73	–
	Apr., 1963	1.87	1.78	–	1.62	–
	Sep., 1963	1.66	1.90	–	1.74	–
	Sep., 1964	–	2.14	–	1.94	–
Campbell	(Oct., 1962)	2.09	2.00	–	2.00	–
	Apr., 1963	1.71	1.70	–	1.70	–
	Oct., 1963	–	1.84	–	1.57	–
Big Spring	(Sep., 1963)	1.78	1.75	1.71	1.51	–
	Apr., 1964	1.68	1.66	1.56	1.46	–
Story	(Sep., 1963)	1.78	1.72	1.69	1.62	–
	Apr., 1964	1.85	1.81	1.72	1.65	–
	Sep., 1964	1.78	1.66	1.62	1.56	–
	Apr.–May, 1965	1.82	1.97	1.82	1.72	–

[1] Dates of stocking in parentheses.

Of the five streams containing the stocked brook trout, only Story Creek trout had an average coefficient of condition (R) which was higher in April than in September (Table 4). The domestic strain in all the streams had somewhat higher average coefficients of condition (R) than the average R of the hybrids or wild trout strains. Domestic strains of brook trout had higher average coefficients of condition than wild strains after various periods in ponds (Greene, 1952; Vincent, 1960; Flick and Webster, 1964) and in a stream (Vincent, 1960).

Harvest

The domestic strain was harvested early in the fishing season whereas the hybrids and wild strains contributed to the fishery throughout the season (Table 5).

DISCUSSION

The Wisconsin domestic strain of brook trout grows rapidly in the hatchery because through selection it has become adaptable to hatchery rearing. One of the characteristics of domesticated trout is the lack of wildness

TABLE 5.—*Recorded harvest in percentage of pre-fishing season (April) stock of different brook trout strains in 1963*

	Black Earth Creek			Big Roche-a-Cri Creek			
Month	D	WD	W-L	D	WD	W-L	W-R
May	26.2	8.2	1.2	13.9	7.3	0.2	0.7
June	0.5	2.5	0.9	0.3	0.4	0.0	0.0
July	0.0	0.8	0.7	0.6	5.3	0.4	1.8
August	0.3	0.6	1.7	0.0	4.4	2.4	3.1
September	0.0	0.0	0.9	0.3	0.7	1.4	1.3
Total	27.0	12.1	5.4	15.1	18.1	4.4	6.9

and hence willingness to feed in the presence of man, which in turn results in rapid growth. The WD Hybrid grew nearly as well in the hatchery as the domestic strain and was sufficiently tame to rear satisfactorily. The DW Hybrid, hatched from small eggs, had a size disadvantage and never did attain the size of the WD Hybrid. The wild strain, however, was too wary to feed satisfactorily when feed was dispensed by man and therefore grew slowly. By utilizing automatic feeders, and thus minimizing the human element in trout feeding, perhaps brook trout of wild origin can be more successfully reared in hatcheries. Mason, Degurse and Brynildson (1965) subsequently employed automatic feeders to successfully rear lake trout obtained from wild stock.

The better survival of the domestic and hybrid strains during the closed season for fishing and the first winter in four of the streams investigated appears to be related to their larger size. Densities of competing trout and other fishes were high in these four streams. Where low densities of resident fish were present, as in Big Roche-a-Cri Creek, the fifth stream, the larger and more domesticated strains of trout did not survive as well over-winter as did the smaller wild strains. When competition from trout and other fishes is low, those results suggest that wildness in yearling brook trout, within the length ranges of the various strains stocked (Table 1), is more important to over-winter survival in streams than relative size. Moreover, wildness may provide trout greater protection from terrestrial predators than does larger size. Vincent (1960) reported 20 and 33% summer survival estimates of domestic and wild strains of fingerling brook trout, respectively, in a relatively small unfished stream which contained only 27 pounds of resident brook trout per acre.

Shetter (1947) concluded after an extensive review of studies of fall-stocking that trout exhibited the highest over-winter survival in streams with abundant spring-water (no ice-cover) or low populations of native trout. Nielson, Reimers, and Kennedy (1957) and Reimers (1963) associated ice formation and ice-cover with low over-winter survival of stocked hatchery-reared rainbow trout. Brynildson and Christenson (1961) concluded that highest over-winter survival of fall-stocked domesticated brook, brown, and rainbow trout in streams occurred where the following conditions were met: 1) ice cover rare during winter, 2) adequate instream cover, and 3) low populations of resident trout.

Of the five streams stocked with the different strains of brook trout, only Big Roche-a-Cri Creek was permanently ice-covered during the cold months, and instream cover appeared to be adequate in all five streams. That the wild strains survived better than did the other strains, during the period including ice-cover on Big Roche-a-Cri, it suggested that the wild strains were hardier during the period of lowest water temperatures than the strains with domestic traits. In the other four streams, perhaps benefits to survival, if any, of ice-free water in winter were offset by competition from trout and other fishes because survival of the wild strain in these streams during the season closed to fishing was significantly lower than in ice-bound Big Roche-a-Cri Creek.

Significantly higher summer survival of the wild strain, in all streams investigated, is probably a result of wildness and smaller size, which make them more difficult to catch and less desirable for the creel. Many trout of the wild strain may have been caught by anglers, but because of their small size could have been returned to the streams.

Although the hybrids can be reared more successfully in the hatchery than the wild strain, the degree of wildness of the hybrids is apparently not adequate to prevent high angling and natural mortality during exposure to a fishing season, in the streams investigated. Hybrids could contribute only a small portion to a spawning stock needed to establish and maintain a wild brook trout population. Because the wild strains of brook trout survived longer in the streams investigated than did the domestic and the hybrid trout, we suggest that wild strains be introduced into potential brook trout streams. Because the wild strains are as yet difficult to rear in hatcheries, wild brook trout stock could be obtained during early autumn from streams with large standing crops of adult wild brook trout and transferred to streams lacking brood stock. Because the WD Hybrid and wild strains of brook trout supported a more sustained fishery throughout the fishing season in Big Roche-a-Cri and Black Earth Creeks, these strains would be a desirable addition to the hatchery-reared domestic strain of brook trout released in many Wisconsin streams lacking resident wild trout.

LITERATURE CITED

ALM G. 1939. Kgl. Lantbruksstyrelsen Medd. 15. (Investigations on growth, etc., by different forms of trout—English summary). *In* Margaret Brown E. (ed.) 1957. The physiology of fishes, Vol. 1. Academic Press, Inc. New York. 447 p.

BRYNILDSON, OSCAR M., AND LYLE M. CHRISTENSON. 1961. Survival, yield, growth and coefficient of condition of hatchery-reared trout stocked in Wisconsin waters. Wis. Conserv. Dept. Misc. Res. Rep. 3 (Fisheries), 23 p.

FLICK, A. WILLIAM, AND DWIGHT A. WEBSTER. 1964. Comparative first year survival and production in wild and domestic strains of brook trout, *Salvelinus fontinalis*. Trans. Amer. Fish. Soc. 93: 58–69.

GREENE, C. WILLARD. 1952. Results from stocking brook trout of wild and hatchery strains at Stillwater Pond. Trans. Amer. Fish. Soc. 81: 43–52.

HUNT, R. L., O. M. BRYNILDSON, AND J. T. MCFADDEN. 1962. Effects of angling regulations on a wild brook trout fishery. Wis. Conserv. Dep., Tech. Bull. 26, 58 p.

MASON, JOHN W., PAUL E. DEGURSE, AND OSCAR M. BRYNILDSON. 1965. Dry diets for trout. Successful diets to rear trout in the hatchery. Wis. Conserv. Dep., Res. Rep. 13 (Fisheries), 6 p.

MCFADDEN, J. T. 1961. A population study of the brook trout, *Salvelinus fontinalis*. Wildlife Monogr. No. 7, 73 p.

NIELSON, REED S., NORMAN REIMERS, AND HARRY D. KENNEDY. 1957. A six-year study of the survival and vitality of hatchery-reared trout of catchable size in Convict Creek, California. Calif. Fish and Game, 43: 5–42.

REIMERS, NORMAN. 1963. Body condition, water temperature, and over-winter survival of hatchery-reared trout in Convict Creek, California. Trans. Amer. Fish. Soc., 92: 39–46.

SHETTER, DAVID S. 1947. Further results from spring and fall plantings of legalsized, hatchery-reared trout in streams and lakes of Michigan. Trans. Amer. Fish. Soc. 74: 35–58.

VINCENT, R. E. 1960. Some influence of domestication upon three stocks of brook trout (*Salvelinus fontinalis* Mitchill). Trans. Amer. Fish. Soc. 89: 35–52.

PRECISION WITH WHICH SPECKLED TROUT (SALVELINUS FONTINALIS) RETURN TO THE SAME SPAWNING GROUNDS

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DURING the last four years, several thousand Speckled Trout were marked with jaw tags[1] in the Laurentides Park, Quebec. Often fish were tagged in the fall, on the spawning beds, which are usually located at the inlet or outlet of a lake. During the summer no adult trout were noticed over these grounds. However, the next fall several marked fish were recaptured on the same places where they were tagged a year before. These observations led to the following experiments.

Lake Grand Epaule, which is situated at an altitude of 2,127 feet above sea level and about 40 miles north of Quebec city, was chosen. It is nearly two miles long by a quarter of a mile wide, with an area of 300 acres and a maximum depth of 28 feet. There are two inlets, one at the northern end about three miles long, which will be called "A", and the other at the southeastern extremity only one mile long, "B".

Inlet "A" has its source in Lake Petit Epaule (53 acres), which is located 400 feet higher than Grand Epaule. Inlet "B" flows from Lake Noël (188 acres), situated approximately 175 feet above Lake Grand Epaule. In all these three lakes only one species of fish is found, namely speckled trout (*Salvelinus fontinalis*).

Grand Epaule trout do not spawn in the lake proper, but only in the inlets. The principal spawning ground of inlet "A" is located at a distance of about one mile from the wharf at Camp Devlin, along the eastern shore of this lake, while the main spawning bed of inlet "B" is approximately half a mile from the wharf (Fig. 1).

During September, 1938, over 400 trout taken with seines on the spawning grounds, were tagged and released in Grand Epaule, almost equal numbers being marked in each of the two inlets.

In the summer of 1939 no adult trout were seen in either inlet. Only seven tagged fish were recovered during the warm season of that year, all of them taken on the fly in the lake proper, not far from Devlin's wharf. The ratio between the tagged and untagged fish caught was 1 to 1,000.

Trout on the approach of the spawning season left the lake and moved towards either one or other of the inlets. In seining in September 1939 on the spawning beds, three tagged fish were recaptured in inlet "A" and

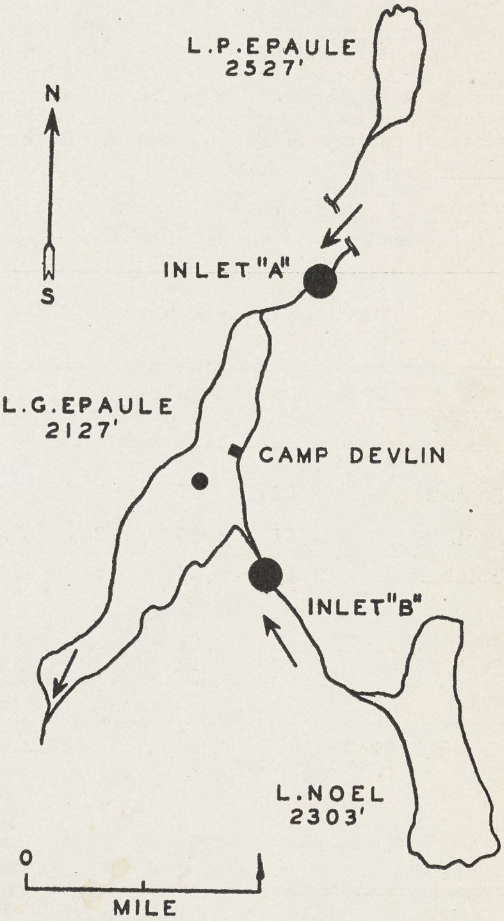

Figure 1. *Lake Grand Epaule in the Laurentides Park.* Large black dots show the location of spawning beds in both inlets, from which trout for tagging experiments were used. Small black dot within Grand Epaule Lake indicates the position of the station, where observations on hydrographic conditions of this lake were made and referred to in Table III, Inlet "A", which is about three times as long as Inlet "B", is shown in part.

[1] Description of this method is given by Shetter (1936).

one in inlet "B", all of which had been caught and released a year previously exactly on the same spots. These places had been marked by logs and rocks to facilitate finding their locations.

Of these recaptures, the recovery of a female (tag no. 722) is particularly interesting. This trout measuring 160 millimeters[2] was tagged, on September 19, 1938, in inlet "A" and was recaptured in 1939 on the exact spot, where it had been tagged a year before. This fish was then brought alive to Devlin's wharf and liberated there on September 12; two days later it was caught a second time at the original tagging place in inlet "A", at a distance of about one mile from the wharf.

During the fall of 1940, it was decided to repeat the experiment with Grand Epaule trout. On September 24 and 25, 110 trout were seined in inlet "A" and 116 in inlet "B". The fish ranged in length from 122 to 258 millimeters. Each group was brought separately from the place of capture to Devlin's wharf. During the trip in a motor boat, water in the tub was renewed several times. Then fish were tagged and liberated at the wharf.

Twenty-four and forty-eight hours later, seining was repeated exactly over the same beds in each of the inlets. During this short interval twenty trout were recovered: twelve in inlet "A" and eight in "B". Details of the recaptures are summarized in Table I. Without exception every one of the tagged fish recaptured had returned to the same ground as that to which it had previously resorted. Unfortunately it was impossible to continue these observations that fall.

Physico-chemical conditions in each of the inlets and the lake proper are given on Tables II and III.[3] Although only small differences in various factors were observed, they were

2 Throughout the present note, the size of fish is the length measured from the tip of the snout to the extremity of the middle caudal rays.

3 The determination of dissolved oxygen was made by the Nicloux method (1930) and that of free carbon dioxide by the American Public Health Association technique (1925, pp. 36-37, procedure 7a). For the determination of pH values, the Lovibond Comparator was used. Water analyses referred to in the present note were made by Mr. V. Legendre, assistant to the Biological Station.

TABLE I. TAGGING EXPERIMENT MADE WITH TROUT FROM LAKE GRAND EPAULE, DURING SEPTEMBER 24 - 26, 1940

	Fish released at wharf				Fish recaptured on respective spawning beds			
Date	♂ ♂	♀ ♀	?	Total	After	♂ ♂	♀ ♀	Total
				Trout from inlet "A"				
Sept. 24	32	17	3	52	24 hours	2	...	2
					48 "	4	1	5
Sept. 25	31	25	2	58	24 "	4	1	5
Total	63	42	5	110	24-48 hours	10	2	12
				Trout from inlet "B"				
Sept. 24	56	28	...	84	48 hours	2	3	5
Sept. 25	18	12	2	32	24 "	2	1	3
Total	74	40	2	116	24-48 hours	4	4	8

Remark: The lengths in millimeters of released trout varied from 122 to 258, and those of recaptured from 145 to 238.

TABLE II. PHYSICO-CHEMICAL CONDITIONS OF TWO INLETS: "A" AND "B" IN LAKE GRAND EPAULE, DURING SEPTEMBER, 1938-1940

Date	Temperature, °C.		O_2, p.p.m.		CO_2, p.p.m.		pH	
	A	B	A	B	A	B	A	B
Sept. 18 and 19, 1938[1]	9.8	12.6	10.0	9.2	1.0	2.0	6.3	6.0
Sept. 14, 1939	9.0	11.2	9.3	9.4	2.5	2.5	5.8	5.9
Sept. 20, 1939	10.0	13.0	8.5	8.0	2.0	3.0	6.1	6.0
Sept. 22 and 24, 1940[2]	11.9	10.5	9.0	8.9	2.0	2.0	6.5	5.9
Average	10.2	11.8	9.2	8.9	1.9	2.4	6.2	6.0

1 On Sept. 18, 1938, observations were made in inlet "B" and the following day in inlet "A".
2 On Sept. 22, 1940, observations were made in inlet "A". Two days later, a cool heavy rain lowered the temperature in both inlets; unfortunately only in inlet "B" was it possible to make observations.

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

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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.

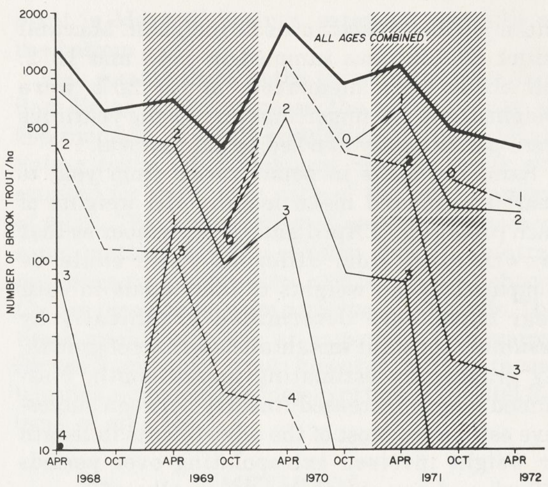

FIGURE 1.—Estimated numbers of brook trout in Clubhouse Springs, 1968-72. Numbers designate age-groups and hatched areas separate calendar years.

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.

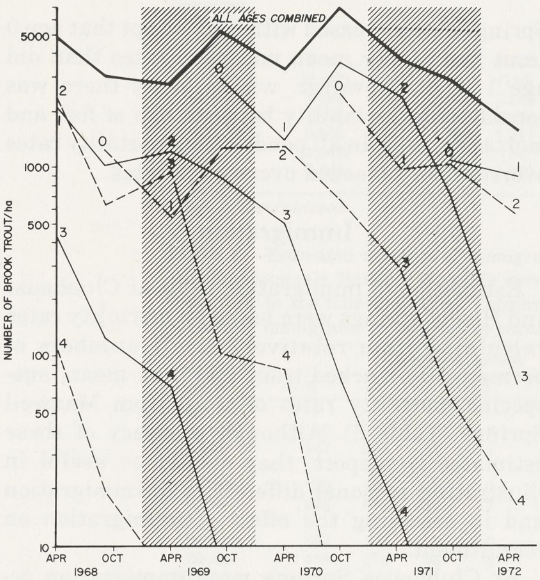

FIGURE 2.—Estimated numbers of brook trout in Hoglot Springs, 1968-72. Numbers designate age-groups and hatched areas separate calendar years.

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

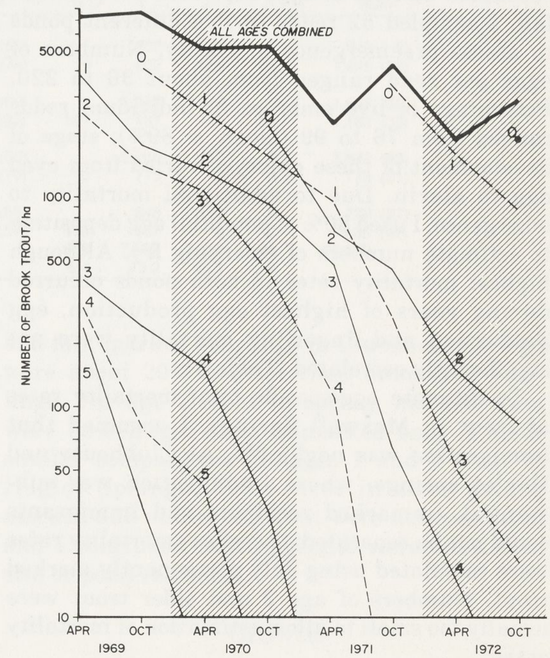

FIGURE 3.—Estimated numbers of brook trout in Maxwell Springs, 1969-72. Numbers designate age-groups and hatched areas separate calendar years.

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).

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

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

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 [1]0	Maxwell Springs 1	Maxwell Springs 2	Maxwell Springs 3	Maxwell Springs 4	Hoglot Springs 1	Hoglot Springs 2	Clubhouse Springs 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 0	Clubhouse Springs 1	Clubhouse Springs 2	Clubhouse Springs 3	Clubhouse Springs Sum	Hoglot Springs 0	Hoglot Springs 1	Hoglot Springs 2	Hoglot Springs 3	Hoglot Springs 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 $\bar{L}$	Age 0 $\bar{W}$	Age 1 $\bar{L}$	Age 1 $\bar{W}$	Age 2 $\bar{L}$	Age 2 $\bar{W}$	Age 3 $\bar{L}$	Age 3 $\bar{W}$	Age 4 $\bar{L}$	Age 4 $\bar{W}$
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*

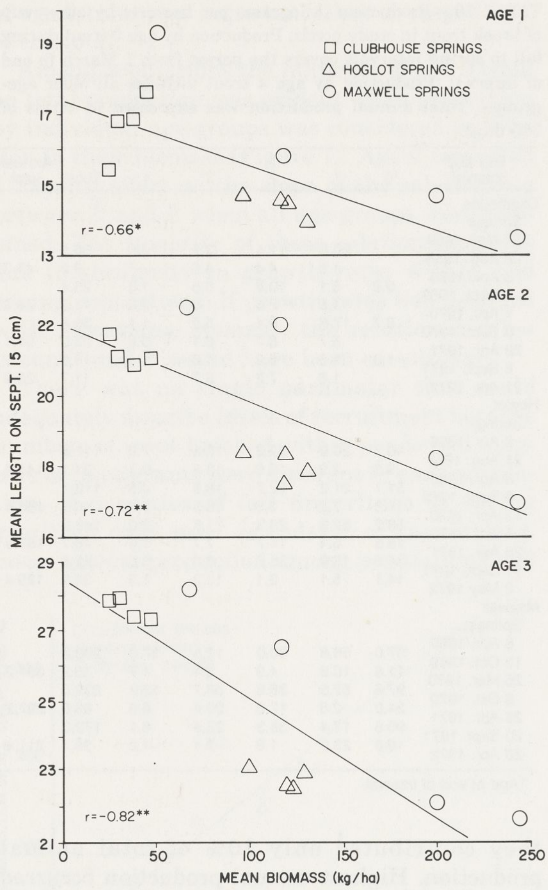

FIGURE 4.—Relationships between mean biomass of all ages of trout and mean lengths of ages 1, 2, and 3 trout on 15 September. (*$P<0.05$; **$P<0.01$.)

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;

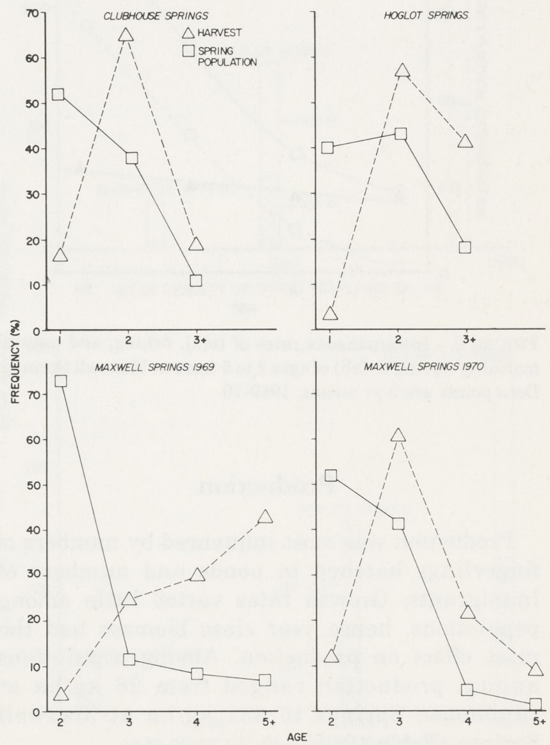

FIGURE 5.—Age-frequency distributions of harvests and populations of legal-sized trout in spring. Data points for Clubhouse and Hoglot springs are means of data from 1968 to 1970, and 1972.

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.

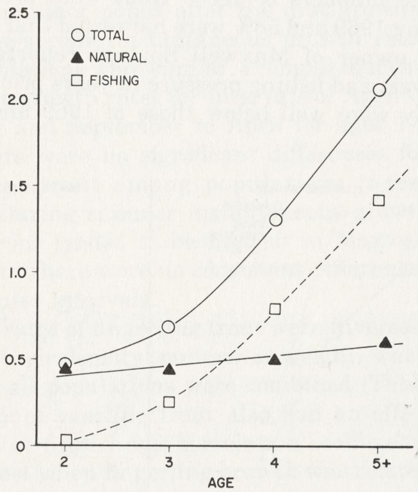

FIGURE 6.—Instantaneous rates of total, fishing, and natural mortality (spring to fall) of ages 2 to 5 trout at Maxwell Springs. Data points are 2-yr means, 1969-70.

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

[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

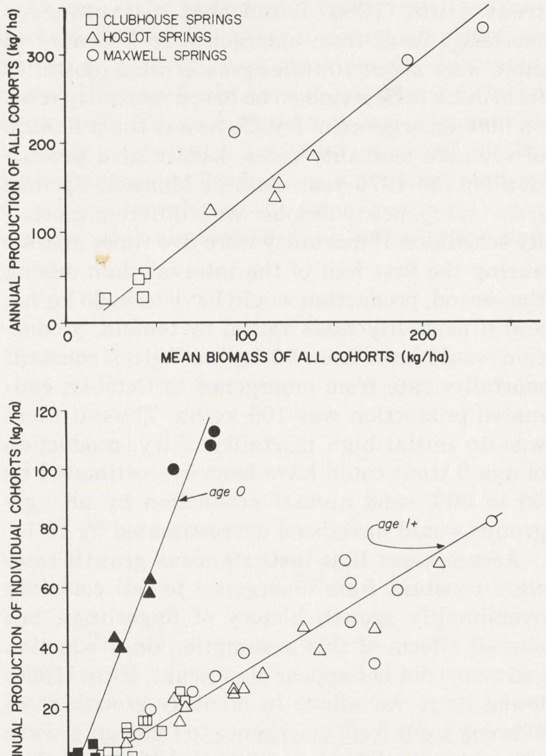

FIGURE 7.—Relationships between mean annual biomass and annual production. Production and biomass of all cohorts are combined in upper panel. In lower panel each point represents a single cohort. Lines fitted by inspection.

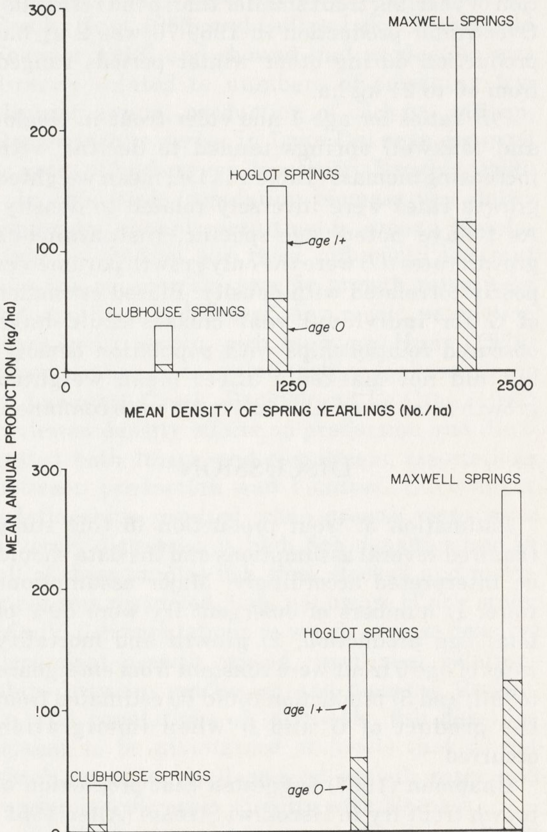

FIGURE 8.—Mean annual densities of spring yearlings and fall fingerlings in relation to mean annual production of age 0 and age 1 and older trout.

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

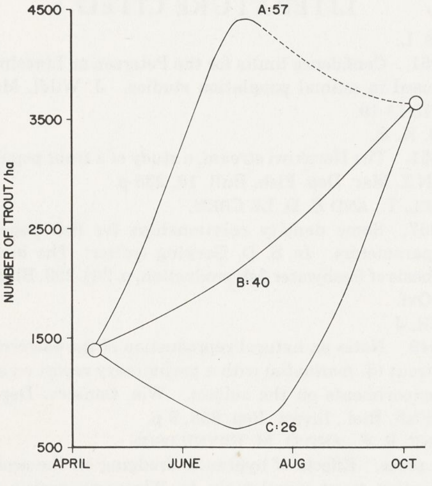

FIGURE 9.—Three hypothetical immigration patterns for a single age-group. Production for each curve was calculated monthly using the same instantaneous growth rate (G = 0.99, t = 0.5 yr). Total production for each curve is given next to letter designation.

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/m² to 64 g/m², but in most studies they were <20 g/m² (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/m²) 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/m²). 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.

ACKNOWLEDGMENTS

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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.

Information from the Freshwater Laboratory, Drottningholm
No. 4, 1969
Translated by Goran Blomberg

Cited in:
Nyman, O.L. 1970
Ecological interactions of brown trout and brook trout in a stream.
Can. Field-Natur.
84: 343-350.

Some Data on the Brook Char

by
Gösta Kjellberg

Introduction

During different times during the last few years I have had the opportunity to make short notes on the ecology of the brook char (Salvelinus fontinalis). The studies have mainly been conducted in connection with fishing (primarily brook fishing) when I have helped fish management organizations with smaller investigations in different parts of Hälsingland, Medelpad and Härjedalen. (TN*- these are different provinces in Sweden)

Stomachs, scales and gill covers have been collected and analyzed by the Limnological Institution in Uppsala, where I have received the competent help of doctoral candidate Evert Andersson, among others.

I want to point out that the results I have gathered together below from my notes should not be regarded as a major scientific undertaking, but only consist of shorter notations and observations made during normal free-time fishing.

Spawning

In 1950 brook char fry were implanted in a 2 hectare pond in southern Hälsingland (pH = 5.8-6.1, hardness = 30, water color 90 mg Platinum/l). The brook char has formed a self-sustaining population in the pond and its system of brooks (see map). The growth in the brooks is poor, 14-16 centimeters in four years. In the pond the growth is somewhat better, 20-22 cm

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*TN means translator's note.

Trout "strains" 8762

Mason, J.W., O.M. Brynildson, and P.E. Degurse
Comparative survival of wild and domestic strains of brook trout in streams. (ms. submitted to Am. Fish. Soc.)

Wisconsin strains used

Osceola St. Hatchery	Lawrence Crk.	Big Roche-a-Cri Crk.
strain over 30 yrs. old. selected for rapid growth; most ♂ mature first year 0 age; " ♀ " second " I.	not stocked for over 20 years. - hatched and reared at Westfield trout Res. Sta.	naturally reproduced in upper section - fingerlings transfered to lower section. - stocked w/ hatchery brook trout but survival thought too low to matter.

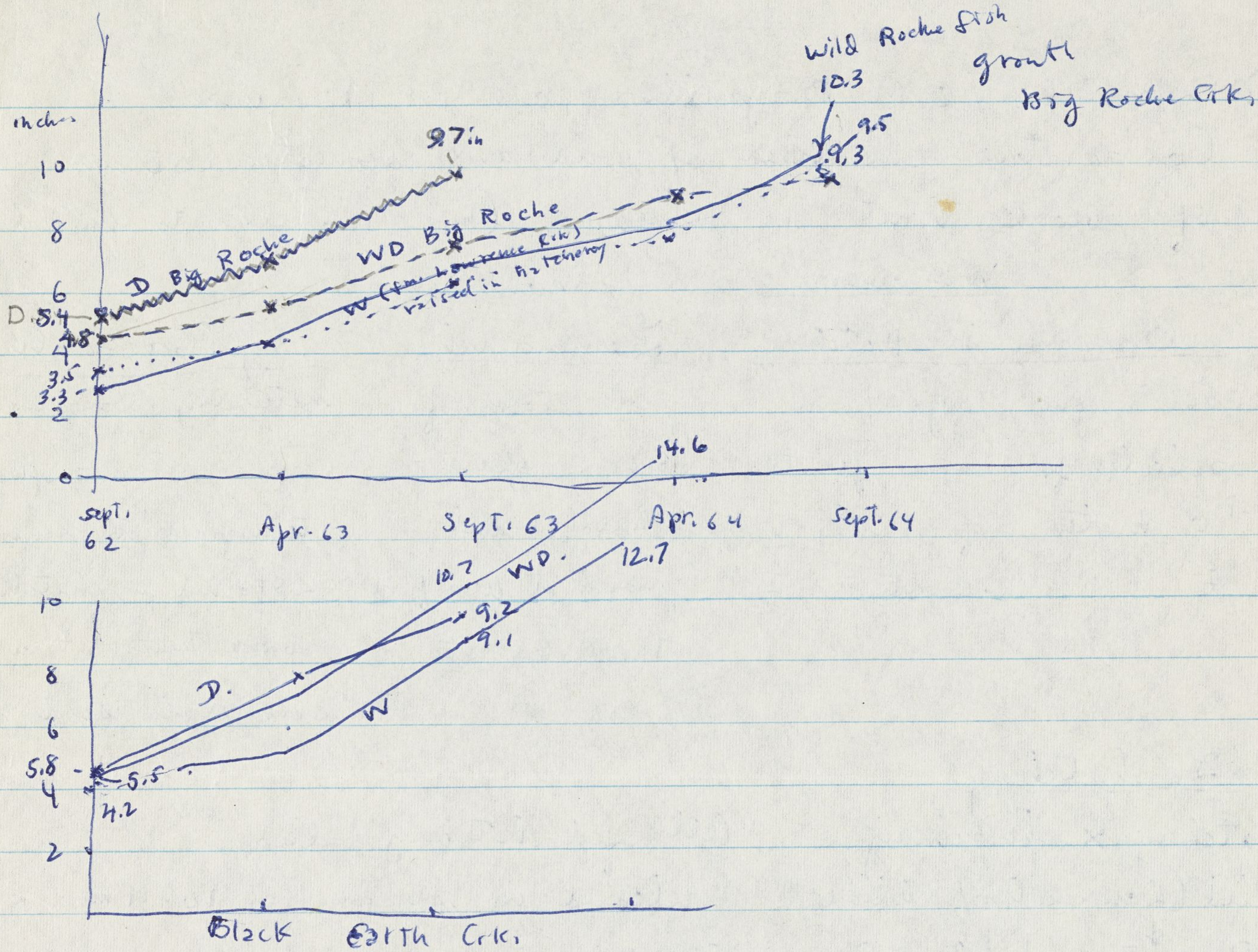
In hatchery:

Hatchery × hatchery
Wild (Lawrence Crk.) × Wild (")
WD ♂ × hatchery ♀
DW ♀ × ♂

All fed hatchery diet
released in streams at 10-11 mo. age.
- Planted in 1 mi. sections of 5 streams

Big Roche-a-Cri	Campbell	Big Spring	Black Earth	Story
infertile soil	infertile soil	fertile	fertile	fertile
deep, slow, ice covering	slow, no ice	shallow, fast no ice.	deep, slow	deep, slow
18 lb. brook & brown + 30 lb. white sucker & minnow /acre (s.e. ca. sampled in Apr.)	11 lb. brook * 270 lb. brown /acre few suckers & minnows	15 lb. brown 60 lb. suckers minnows	179 lb. trout. spp.?? 200 lb. suckers. 129 wild browns 20 hatchery holdovers 30 hatchery rainbows	32 lb. wild & stocked browns - high density of redside dace

1000 of each strain fin clipped
(844 wild Big Roche - used & stocked only in Big Roche -)
4 mi. downstream



-harvest-

Black Earth Crk.

27% caught
26.2% caught in May } Domestic - others more spread out (smaller size)

Big Roche Crk.

15.1% caught
13.9% in May } Domestic

(?)
Eggs
stock
① Wild strains — ~~Stock~~ from Lawrence Creek ^ ~~descr~~ —
— — — — were hatched and reared — — —.
— — — — —. Naturally reproduced fingerlings
from Big Roche-a-Cri Creek — — — —
— — were collected and transferred — — —.

(- What was the origin of these trout ?? - Were
brook trout native to these streams? - Where did
hatchery stock come from that were introduced?)

- Tense had or has (stream characteristics)

- How Stand. Crop. estimates made ??

Donaldson's cutt. interracial hybrids.
- Not Brook trt. habitat

- Genetic Dif. . - Non genet. dif.
- behavior - growth (in part)
- longevity?
- age at spawning? ? ?catchability??
- no. eggs, egg size?
? survival?

D×W
W×D crosses - size & survival

Hatchery stock - harvested early
Wild fish - caught throughout season

- better survival thru winter prob. mainly due to larger size
(In the 4 streams where hatchery & hybrids had better survival they had high population densities & competition).

* - Perhaps not! - Wild fish survived best in area w/ least fish - but fewer fish not due to ~~under~~ over exploited pop. - but rather to ~~[illegible]~~ limits of environment - food & cover - whereas rich sections - more heavily fished higher pop. density actually more food to go around & competition less.

	Big Roche-a-Cri	Campbell	Big Spring	Black Earth	Story
Stocked	Sept. 20 1962	Oct. 29, 62	Sept. 16, 63	Sept. 19, 62	Sept. 20, 63
	1000 D 4.9-6.1 (5.4) in. (30 gm.) K = 1.93	1000 D 5.9-7.5 (6.6) ~~5.2-6.5 (5.8)~~ 62 gm. ~~41 gm.~~ K = 2.09	1000 D 5.0-6.7 (5.8) 35 gm. K = 1.78	1000 D. 5.2-6.5 (5.8) 41 gm. K = 2.02	1000 D 4.6-6.8 (5.4) 28 gm. K = 1.78
	1,000 WD (♂ ♀) 4.0-6.0 (4.8) in 22 gm. K = 1.95	WD 1000: 4.0-5.9 (4.8) 24 gm. K = 2.00	1000 WD 5.0-6.3 (5.5) 29 gm. K = 1.75	WD 1000 4.7-6.4 (5.5) 32 gm. K = 1.95	1000 WD 4.7-6.6 (5.3) 27 gm. K = 1.72
	1000 W 3.0-4.6 (3.5) 8 gm. K = 1.70	W 1000: 2.9-4.6 (3.5) 9 gm. K = 2.03	DW 1000: 4.1-5.5 (4.6) 17 gm. K = 1.71	W 1000: 3.5-5.1 (4.2) 13 gm. K = 1.73.	1000 DW 4.0-5.6 (4.6) 17 gm. K = 1.69
	844 W^N from headwaters 2.3-4.4 (3.3) 6 gm. K = 1.67		W 1000: 2.9-4.0 (3.2) 5 gm. K = 1.51		W 1000: 2.7-4.0 (3.2) 6 gm, K = 1.62

Survival %

	Big Roche-a-Cri	Campbell	Big Spring	Black Earth	Story
	½ yr. / 1 yr	½ yr	½ yr.	½ yr. / 1 yr.	½ yr. / 1 yr. / 1½ yr
	D. 32.4% - 0.6%	D. 49.8%	D. 33.6	D 40.0% - 0.7	D 34.1% - 1.5 - 0.7
	WD 43.6% - 4.3%	WD 42.2	WD. 31.7	WD 35.4% - 4.6	WD 44.9% - 2.7 - 3.4
	W 30.7% - 17.8%	W 27.0	DW. 20.1	W 30.0% - 7.2	DW 39.7% - 3.9 - 4.5
	W^N 54.8% - 19.7%		W 9.1		W 9.9% - 6.1 - 7.9 (in error)
	1½ yr. / 2 yr.	1 yr.		2 yr.	
	D. - 00 - 0.0	D - 0.0		D - 0.0	
	WD 1.7 - 0.1	WD 2.9		WD - 0.5	
	W. - 11.8 - .3	W 9.7		W - 0.5	
	W^N - 10.8 - 1.1				

· Trout "strains"

Mason et. al. II

pop. estimates made in Apr.-May before season opened
and in Sept.-Oct. after close.

- electro fishing . covered 2 mi. Campbell Crk.
5 mi. Big Spring "
- fish marked 6 mi. Black Earth Crk. - migration of various strains ??
- second sample 11 mi. Big Roche -
60-90% captured again 6 mi. Story
weighed & measured.

- Creel census - est. 80% {catch reported - ??

- wild strain had higher early mortality in hatchery - wouldn't feed correctly - avoided people & surface feeding - timid & excitable
hybrids intermediate in behavior.

hatchery ♂ x wild ♀ . offspring smaller than wild ♂ x hatchery ♀
believed due to smaller eggs of wild ♀.

- overwinter survival better for hatchery > hybrids > wild in all except Big Roche Crk. (opposite) - In 2 streams where compared -
wild ♂ x hatchery ♀ had better survival than hatchery ♂ x wild ♀ } * only genetic dif. here - only inf. of egg size & early growth differential.

- wild strain survived fishing season better
due to behavior & smaller size.

i Storey Crk. - 1½ yr. estimates higher than 1 yr. estimate
Spring 65 estimates higher than Fall 64 due to plants interfering w/ stocking - but from Spring 64 → Spring 65 wild trout higher survival than hybrids > hatchery.

- Big Roche - Lawrence Crk ~~wild~~ (raised in hatchery) > Big Roche transferred natives >
hybrids > (no domestic fish found in Apr. 64)

- Growth: biased prob. due to fishermen catch of larger specimens
- but seemed comparable after stocking.