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Movement, production, and distribution in sympatric populations of brook and rainbow trout

Wilbur Eugene Whitworth

To the Graduate Council:

I am submitting herewith a thesis written by Wilbur Eugene Whitworth entitled "Movement, production, and distribution in sympatric populations of brook and rainbow trout." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.

Richard J. Strange, Major Professor

We have read this thesis and recommend its acceptance:

J.L. Wilson, B.L. Dearden

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

To the Graduate Council:

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and recommend its acceptance:

Accepted for the Council:

Vice Chancellor
Graduate Studies and Research

MOVEMENT, PRODUCTION, AND DISTRIBUTION IN SYMPATRIC POPULATIONS OF BROOK AND RAINBOW TROUT

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Wilbur Eugene Whitworth

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ABSTRACT

A typical Southern Appalachian second-order stream was partitioned into 30 meter sections which were then grouped into pure rainbow trout, mixed trout, and pure brook trout zones, and sampled by electrofishing every two months from September, 1978 to October, 1979. Each trout captured was uniquely cold-branded for identification, and scales were taken for aging. After length, weight, and section number were recorded, the trout were returned to the section from which they were taken. Overall average movement was upstream for both species, but averaged less than 2.0 sections (60 m). Zero-plus (1979 cohort) fish of both species were found in greatest densities in their respective pure zones. Two-plus and 3+ (1976-77 cohorts) rainbow trout were about equally distributed between the rainbow zone and the mixed zone, while there was 66% less density and biomass of 1+ (1978 cohort) rainbow trout in the mixed zone than in the rainbow zone.

Zero-plus brook trout grew faster in the pure brook zone than in the mixed zone, at least during the fall period. Brook trout and rainbow trout maintained equal size and equal relative growth rates until the spring (February through May) of their 1+ year at which time rainbow trout outgrew brook trout and thereafter maintained an absolute size advantage with relative growth about the same for older brook trout and

rainbow trout. Total mixed zone production (1.8 g/m^2/9 mo) was 62% lower than total rainbow zone production (4.8 g/m^2/ 9 mo) and 44% lower than total brook zone production. The most important single group of fish within the study area was 1+ rainbow trout accounting for 88% of the total rainbow zone production; 54% of the total, positive mixed zone production; and 37% of the total brook zone production; even though they accounted for only 12% of total brook zone density. Lower total production levels in the mixed zone and brook zone were caused by an absence of 1+ rainbow trout. This absence may be the result of displacement by brook trout. Competition, therefore, may be most intense between 1+ rainbow and brook trout, probably larger brook trout.

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CHAPTER I

INTRODUCTION

Throughout most of its range the brook trout (*Salvelinus fontinalis*) thrives and competes successfully with other species. In the southern-most part of its range, however--the Southern Appalachians and particularly East Tennessee--this popular native salmonid has lost habitat to introduced, invading rainbow trout (*Salmo gairdneri*) (Tatum 1969, Robinette 1978, and Whitworth 1979). Several Southern Appalachian states have maintained quality brook trout fisheries only through put and take stocking. In areas where this is neither desirable nor possible (i.e., National Park Service lands), it is essential to manage for naturally reproducing brook trout populations. To do this in the face of apparently expanding populations of rainbow trout requires as much information as possible about the ecology of these two species, especially where they live sympatrically.

In the Southern Appalachians, when brook trout are found living with an invading rainbow trout population, three areas, or "zones," of the stream typically prevail. Brook trout, usually in the headwaters of the stream, form a pure, or nearly pure, allopatric population called the "brook zone." Downstream from this, there is typically an area composed of both brook trout and rainbow trout, the

"mixed zone," which in turn phases into an area of pure rainbow trout known as the "rainbow zone." It has been generally believed that interspecific competition, either for space or for food, within the mixed zone is a key factor in allowing rainbow trout expansion within the stream. It would logically follow, therefore, that the area most important to understanding the dynamics of brook trout/ rainbow trout competition is the mixed zone. If distribution, growth, production, and other population parameters could be better understood in the mixed zone (as compared with the brook zone and rainbow zone), then the invasion characteristics of rainbow trout could also be better understood.

Many studies of rainbow trout and brook trout ecology have been performed. Apparently, however, none have addressed the problem of interspecific competition in areas of transition from one species to the other. McFadden (1961) performed one of the most comprehensive studies of brook trout ecology to date, dealing intensively with growth, population size, movement, mortality, and other population parameters. This study, however, was not a comparative study, and dealt only with brook trout ecology. Less comprehensive investigations of brook trout growth, production, and standing crop (biomass) include work by Wydoski (unpublished), Carline (1977), Cooper and Scherer (1967), Michaels (1978), Konopaky (1978), and Saunders and Power (1970). Again, however, these studies have dealt only with

brook trout growth, and give little insight into the ability of brook trout to effectively compete with other species. Similarly, studies examining rainbow trout population ecology were carried out by Alexander and MacCrimmon (1974) and Goodnight and Bjorn (1971). Although not strictly comparable, these works do provide valuable base-line information about brook and rainbow trout ecology.

Some studies comparing brook trout with other fish (usually rainbow trout) have, however, been performed. Aggressive interactions between brook trout and rainbow trout were examined by Newman (1956) and Wolfe, et al. (1978) and indicate that, behaviorally, brook trout can effectively compete with equal-size rainbow trout. Food habits were compared between brook trout and rainbow trout by Tebo and Hassler (1963) and Nyman (1970), and between brook trout and cutthroat trout (*Salmo clarki*) by Griffith (1974). All three studies showed the species involved to be indiscriminate carnivores, and thus potential competitors for food. These studies do not, however, examine growth comparisons between sympatric and allopatric areas. Flick and Webster (1975) examined movement, growth, and survival of stream brook trout as non-trout species were removed. Similarly, Moore (1979) examined changes in brook trout biomass as other salmonids (principally rainbow trout) were removed. While these studies provide much information about interspecific competition between brook trout and other

species, they fail to give any insight into competition within the critical transition areas.

This study, therefore, seeks to focus on growth, production, and other population parameters as indicators of interspecific competition between brook and rainbow trout. The use of growth as an indicator of competition has been established by several authors. Brown (1946) found that competition from larger juvenile brown trout (*Salmo trutta*) reduced the growth rate of smaller brown trout. Davis and Warren (1965) found that increased competition between sculpins (*Cottus carolina*) reduced growth, due to more food being utilized for maintenance and less for growth. Magnuson (1962) reported that, under limited food conditions, larger medaka (*Oryzias latipes*) outcompeted smaller ones for food, and thus grew faster.

More specifically than just looking at growth and production, this study seeks to compare these indicators of competition between the rainbow, mixed, and brook zones in the hope of gaining a better understanding of brook trout/rainbow trout interactions within these critical areas of the stream.

CHAPTER II

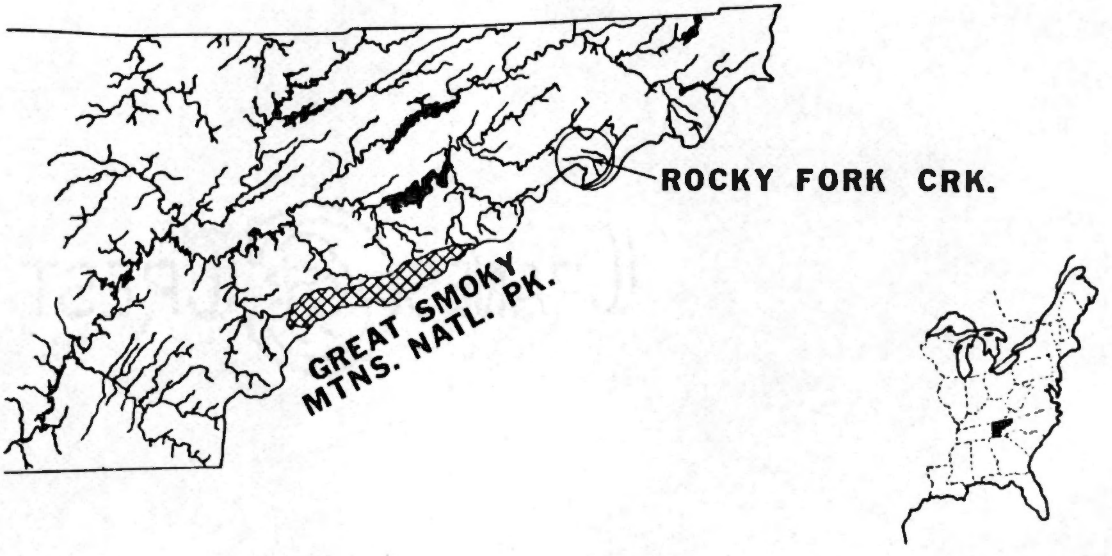
METHODS AND MATERIALS

Site

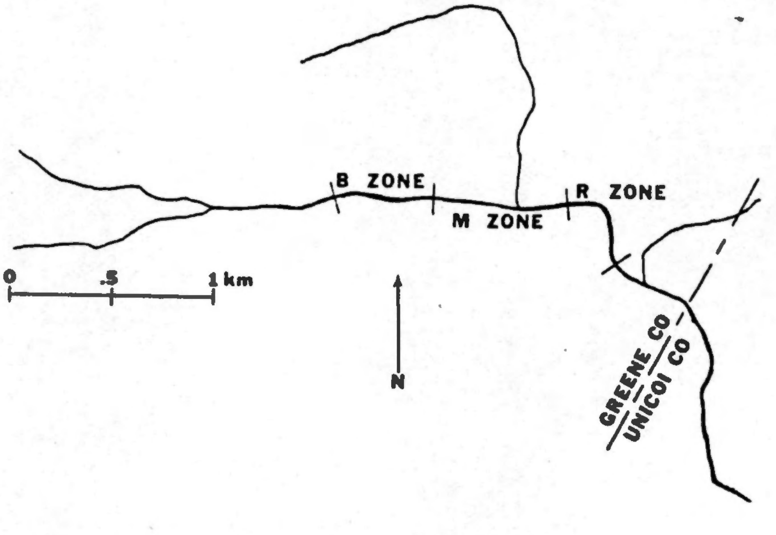
The study site, Rocky Fork Creek, is a typical second-order Southern Appalachian brook trout stream with an invading rainbow trout population. A South Indian Creek tributary in the Nolichucky River drainage, Rocky Fork flows from Green to Unicoi County, Tennessee (Figure 1), and has a total length of 8.2 km and an average slope of 6%. The actual study area was a 1.5 km section of stream starting at 975 m elevation and ending at 1,036 m.

It was felt that, although the stream was open to exploitation, fishing pressure within the actual study area was at a minimum. Because it is located on the 4,047 ha Unicoi County Bear Preserve, Rocky Fork is closed to public access except by foot travel. The approximately 5 km walk to the study area should have greatly reduced fishing pressure in the brook trout waters.

Habitat parameters such as bottom type and bank vegetation--measured using the methods of Seehorn (1970)--were used to classify differences between the three zones. Although the stream did change with altitude, no sudden or large differences between zones were noted. Pools in the lower end of the study area tended to be larger. More gravel



A. East Tennessee



B. Rocky Fork Creek Study Site

Figure 1. Rocky Fork Creek and Surrounding Area.

areas and bank vegetation, predominantly Rhododendron maximum, were noted near the head of this study area. All areas, however, appeared to have satisfactory pool-riffle-run ratios with plenty of cover in the pools. There were very few large, deep pools throughout this part of the stream.

The study area was divided into 50 contiguous sections which averaged 30 m each in length. Sections were usually delineated by such natural boundaries as heads of pools and small waterfalls; however, no artificial structures such as blocknets were erected between sections. Although one small waterfall of about 1 m height was located about midway of the study area, no barriers to movement existed.

The water characteristics of Rocky Fork--measured with a standard Hach kit in September 1978--were: pH=6.5, dissolved oxygen=10 ppm, hardness=17 ppm, and alkalinity=51 ppm. Water temperature ranged from a low of 1°C in February 1979 to a high of 16°C in September 1978.

Data Collection

From September 1978, through October 1979, the area was sampled every two months using backpack electrofishing equipment. After anesthetization with MS-222 (tricaine methanosulfate), each fish was weighed (nearest 0.50 g) with a triple beam balance, and measured (total length to the nearest mm). Scales were taken for age verification using the methods of Cooper (1951).

Using a coding system consisting of three letters, each fish was uniquely cold-branded with dry-ice for identification upon recapture. Except for the use of dry ice (without alcohol or acetone) instead of liquid nitrogen, the guidelines of Raleigh and McLaren (1973) were used. The fish were not double-marked; therefore, an estimate of mark-loss could not be made (Robson and Regier 1966). However, because there were very few misinterpreted recaptures (i.e., fish which either gained or lost excessive length and/or weight, thus indicating a mistaken number code), and very few fish with unreadable markings, mark-loss was not considered great enough to seriously affect the results.

Statistics

Parameters estimated include movement, population size, density, biomass, growth, and production. Movement of each recaptured fish was computed and divided by the number of sample intervals between the first and second capture to obtain mean bi-monthly movement. The t-test was used to test for significance from zero, and for significance between absolute up-stream and down-stream movement.

Population estimates were made using a computer program--POPAN-2 (Arnason and Baniuk 1978)--which utilized the "Jolly-Seber" estimation technique; published separately but simultaneously by Jolly (1965) and Seber (1965). After Pollock's test for recruitment (Pollock et al. 1974) determined that recruitment within cohorts (i.e., immigration)

was significant, the open population model (i.e., recruitment and mortality present) was used. In addition, Manly's test for type-1 loss (increased mortality due to marking and handling) (Manly 1971) was performed to insure agreement with this assumption. Because each estimate of the population at sample-time i depends on information about the population both before and after time i, estimates for the first and last sample times are unavailable. Because of this, biomass and production estimates were available only for the period from December 1978 through August 1979. This was only a nine-month period; however, because it covered the periods of greatest growth, the nine-month production estimates reported here should closely approximate the total yearly production.

To avoid unreliable POPAN-2 estimates of 0+ rainbow trout--caused by very low recapture rates--the size of this cohort was approximated in the following manner. The POPAN-2 estimate for all rainbow trout was multiplied by the ratio of 0+ rainbow trout to older rainbow trout in the sample. This is probably an underestimate for this cohort; however, it should, nevertheless, be more accurate than a direct POPAN-2 estimate for 0+ rainbow trout.

Population estimates--and thus density, biomass, and production estimates--were derived by first determining the population size for the entire study section. This was then apportioned-out to each zone based on the relative distribution of each cohort and species in the sample, to

obtain estimates for each zone. To have broken the sample down by zone and then estimated the population using POPAN-2 would have resulted in a very low sample size and thus an unreliable estimate. Assessments of mortality by zone, therefore, were unavailable.

After population estimates were computed, density (number fish/m^2) and mean biomass (g fish/m^2) estimates were made for each zone, species, cohort, and sample time. Mean density and biomass estimates for each zone, species, and cohort (averaged over sample time) were then computed for the year.

Absolute, relative, and instantaneous growth estimates were computed for all recaptured fish. Like movement, these were computed for successive captures (not necessarily contiguous sample times) of each recaptured fish. Unlike movement, however, these were divided by the number of months between capture times to get mean monthly growth. Since seasonal effects on growth were important, any growth interval which was averaged over more than two sample intervals--one sample interval is defined as the period from one sample time to the next, about two months--was rejected.

Relative growth, instantaneous growth, and production were computed using the formulas of Ricker (1975). In this case, production can be thought of as being synonymous with net production (Ricker 1975). Analysis of variance was used to test for the effects of species, cohort, zone, and sample interval on relative growth. Instantaneous growth was used

only in the computation of production which was estimated for each species, cohort, zone, and sample interval, and then summed for the nine-month period.

CHAPTER III

RESULTS

Movement

Because significant movement from one zone to the next would make it difficult to study the effects of zone on growth and production, overall and interzone movement were analyzed before growth was analyzed (Figure 2). Absolute brook trout movement (regardless of direction) averaged 1.4 sections (43 m) and absolute rainbow trout movement averaged 2.6 sections (78 m). Net movement (averaging up-stream with down-stream movement) was up-stream for both species, but averaged only 0.4 sections (13 m) for brook trout (Table 1) and 0.8 sections (24 m) for rainbow trout (Table 2). The t-test revealed that total net movement (combining all cohorts) was significant ($\alpha=0.05$) only for brook trout. Total absolute movement, however, was significant for both species. Although statistically significant, this movement was nevertheless very limited, and thus may not be biologically significant. The t-test also revealed that fish moved about as far up-stream as down-stream. This seems to indicate that, as a whole, movement in the population was random.

After analyzing absolute and net movement, the stream was divided into the three zones: rainbow zone, mixed zone, and brook zone; based on the distribution of first capture

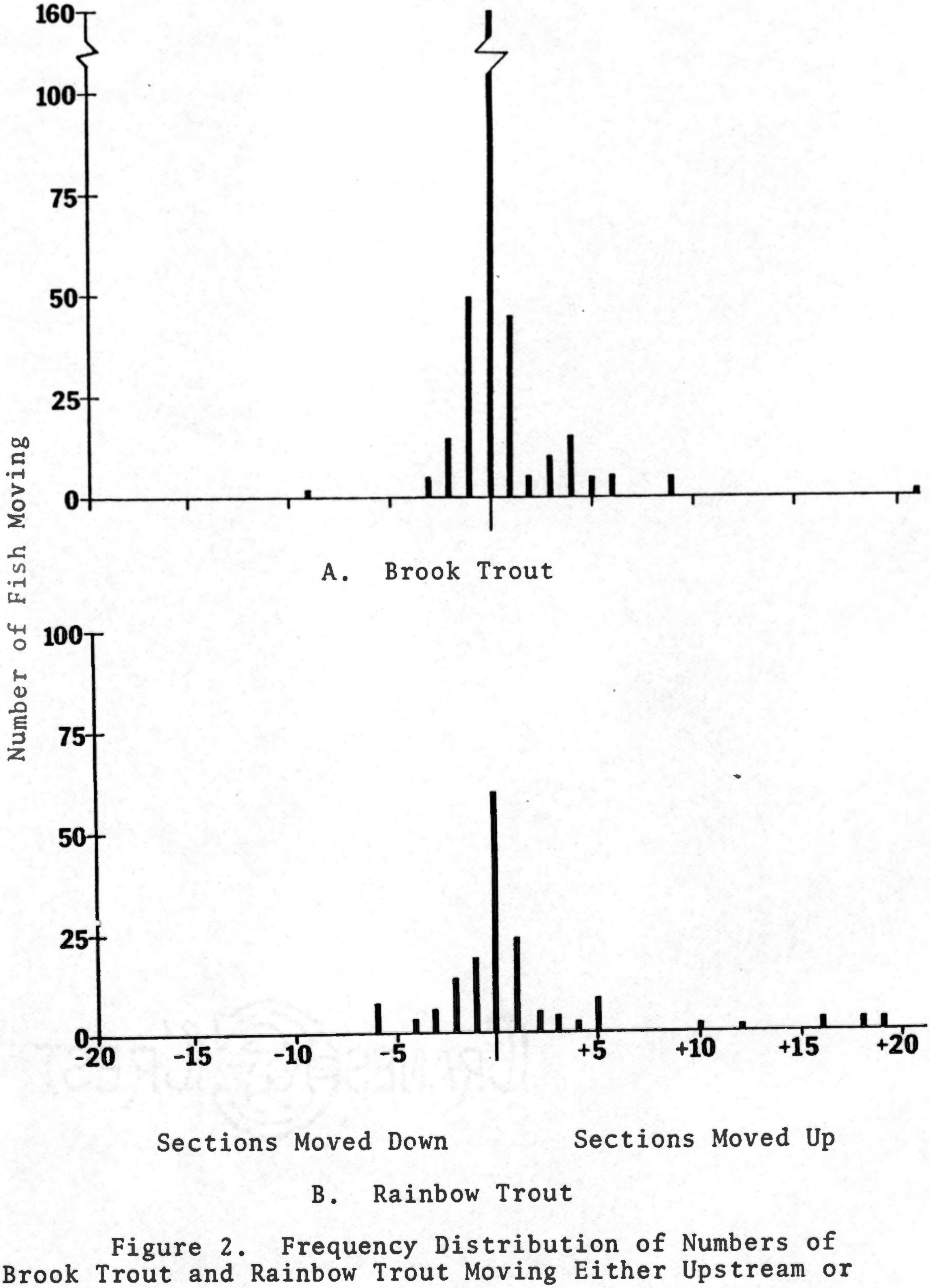


Figure 2. Frequency Distribution of Numbers of Brook Trout and Rainbow Trout Moving Either Upstream or Downstream.

Table 1. Brook trout movement in sections and meters with 95% confidence limits.[a]

		Absolute Movement				Net Movement			
Cohort	N	Number of Sections	95% C.L.	Meters	95% C.L.	Number of Sections	95% C.L.	Meters	95% C.L.
1979 (0+)	36	1.2	±0.5	35.7	±14.1	+0.1	±0.6	+2.7	±18.9
1978 (1+)	136	1.7	±0.5	49.8	±15.3	+0.8	±0.6	22.8	±17.0
1977 (2+)	107	1.4	±0.4	41.7	±10.8	+0.6	±0.4	18.9	±13.1
1976 (3+)	15	1.3	±0.5	39.9	±14.7	-1.3	±0.4	-39.9	±13.5
Total	321	1.4	±0.2	43.2	± 7.6	+0.4	±0.3	13.2	± 8.8

[a]Net movement was computed by averaging upstream with downstream movement, while absolute movement was computed as mean absolute distance moved, regardless of direction.

Table 2. Rainbow trout movement in sections and meters with 95% confidence limits.[a]

		Absolute Movement				Net Movement			
Cohort	N	Number of Sections	95% C.L.	Meters	95% C.L.	Number of Sections	95% C.L.	Meters	95% C.L.
1979 (0+)	3	5.0	±17.4	150.0	±521.2	+3.7	±20.2	+110.0	±606.3
1978 (1+)	75	1.6	± 0.7	48.9	± 20.3	+0.7	± 0.8	+ 22.2	± 22.7
1977 (2+)	50	3.6	± 1.6	106.8	± 49.4	+1.3	± 1.9	+ 39.6	± 57.3
1976 (3+)	21	2.3	± 1.4	69.9	± 42.0	-1.8	± 1.6	- 53.1	± 47.0
Total	161	2.6	± 0.7	77.7	± 21.2	+0.8	± 0.8	+ 23.7	± 24.1

[a]Net movement was computed by averaging upstream with downstream movement, while absolute movement was computed as mean absolute distance moved, regardless of direction.

brook trout throughout the study (i.e., each fish was counted only once regardless of how many times it was captured) (Figure 3). The zone boundaries were arbitrarily set with the rainbow zone containing about 96% rainbow trout and about 4% brook trout. The mixed zone was 52% brook trout and 48% rainbow trout, and the brook zone contained 22% rainbow trout and 78% brook trout.

Obviously some movement did take place; therefore, after zones were established, further movement analyses were performed to determine the extent and degree of movement from one zone to the next. As summarized in Table 3, very few fish actually moved outside their assigned zone (25 brook trout and 11 rainbow trout), and when they did move, the distance was very short. Consequently, interzone movement appeared to be by only those fish near the boundaries. This limited movement should not affect the permanent assignment of fish to one zone and subsequent analysis of growth. In addition to the limited but significant movement presented in Tables 1, 2, and 3, a few individual fish showed considerable movement. Considered as outliers, these "movers" were principally older fish and consisted of mainly rainbow trout. An indication of these movers can be obtained from Table 3. Although more brook trout than rainbow trout exhibited interzone movement, all but two moved only intermediate to short distances. More rainbow trout, on the other hand, appeared to move over greater distances. It can also be seen from these data that only three brook

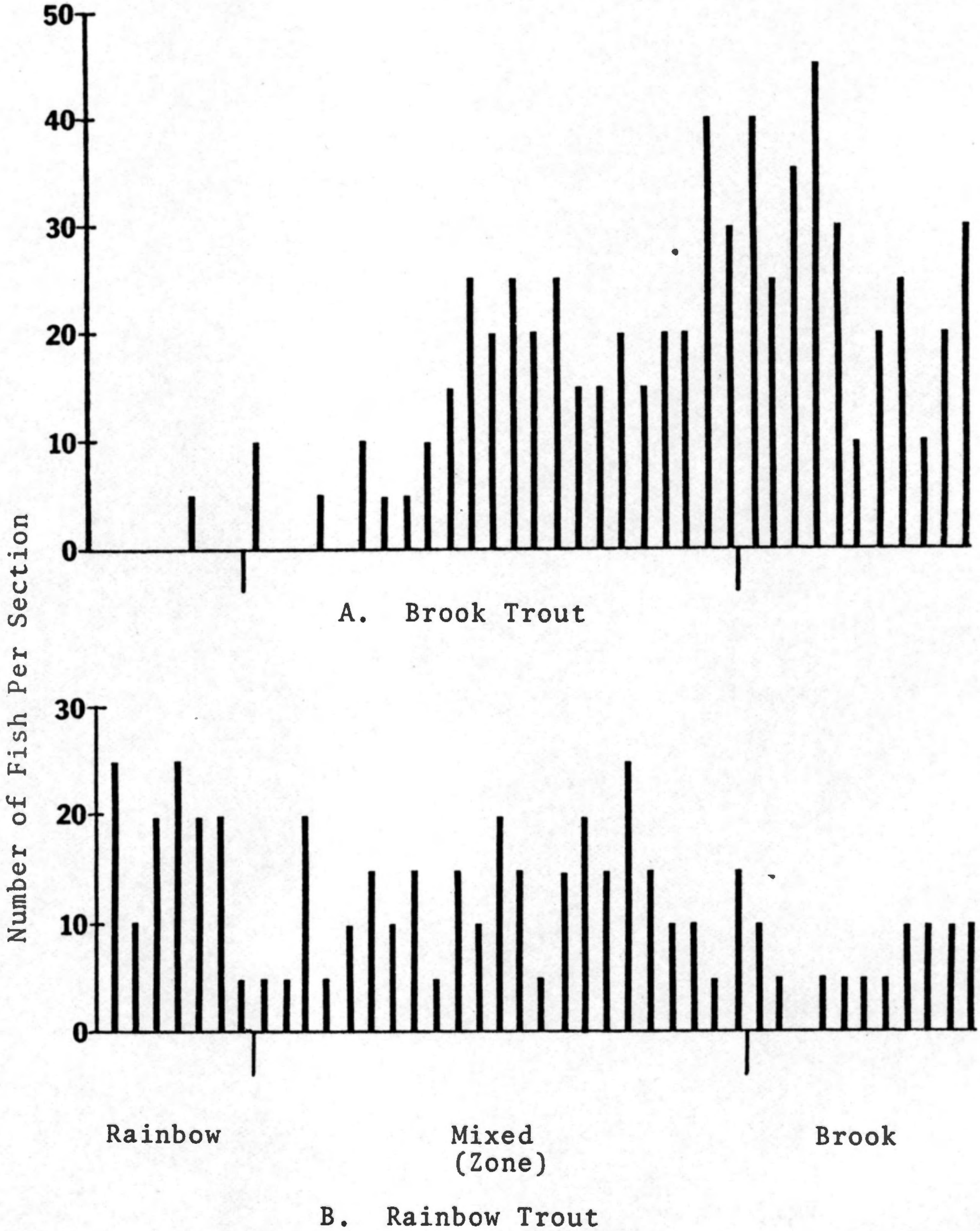


Figure 3. Frequency Distribution of Brook Trout and Rainbow Trout Throughout the Study Site. Distribution is based on the number of non-recaptured fish caught throughout the study.

Table 3. Brook trout and rainbow trout average interzone movement for each cohort.[a]

Interzone Movement	Cohort	Brook Trout N	Brook Trout Distance[a]	Rainbow Trout N	Rainbow Trout Distance[a]
Brook to Mixed	1979 (0+)	2	- 43.5 m	0	-
	1978 (1+)	0	-	0	-
	1977 (2+)	5	- 68.4 m	1	- 33.0 m
	1976 (3+)	2	- 45.0 m	0	-
Brook to Rainbow	1979 (0+)	0	-	0	-
	1978 (1+)	0	-	0	-
	1977 (2+)	0	-	0	-
	1976 (3+)	0	-	0	-
Mixed to Brook	1979 (0+)	1	+120.8 m	0	-
	1978 (1+)	7	+145.8 m	1	+300.0 m
	1977 (2+)	6	+155.1 m	1	+810.0 m
	1976 (3+)	0	-	0	-
Mixed to Rainbow	1979 (0+)	0	-	0	-
	1978 (1+)	0	-	0	-
	1977 (2+)	0	-	1	- 42.0 m
	1976 (3+)	0	-	2	- 57.0 m
Rainbow to Mixed	1979 (0+)	0	-	0	-
	1978 (1+)	0	-	0	-
	1977 (2+)	0	-	0	-
	1976 (3+)	0	-	0	-
Rainbow to Brook	1979 (0+)	0	-	1	+390.0 m
	1978 (1+)	1	+630.0 m	2	+555.0 m
	1977 (2+)	1	+450.0 m	2	+1080.0 m
	1976 (3+)	0	-	0	-

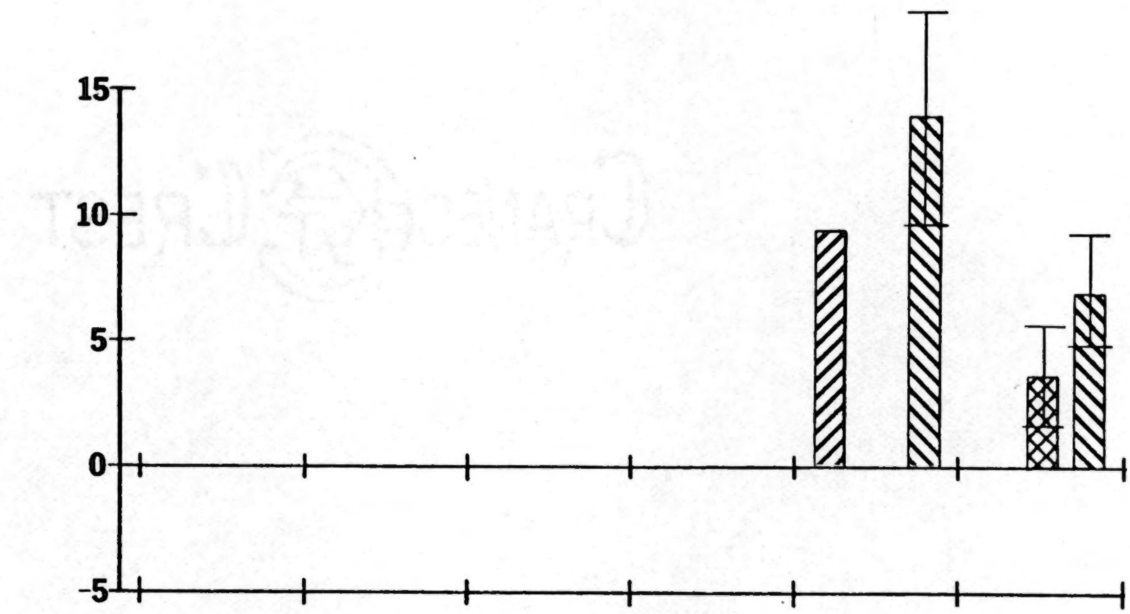
[a]Upstream movement is indicated by + and downstream movement is indicated by -.

trout and one rainbow trout of the 0+ cohort exhibited interzone movement. Furthermore, all but 11 brook trout and four rainbow trout were 2+ and older.

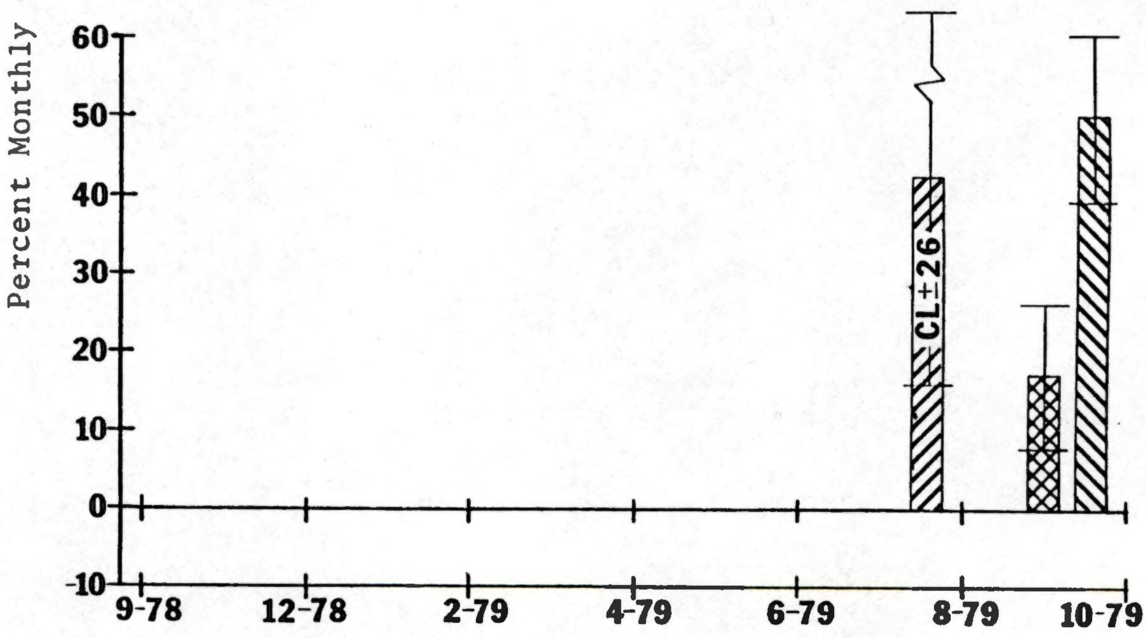
Growth

Relative growth was analyzed to study the effects of zones on growth. Zero-plus brook trout grew faster in the pure brook zone, at least during the fall, than in the mixed zone (Figure 4A,B). Although zone effect for 0+ brook trout relative length gain was not significant, there was a trend. Between August and October 1979 these fish averaged a 4% length gain per month in the mixed zone and about a 7% length gain in the brook zone (Figure 4A). Relative weight gain during this same period, however, did show a significant zone effect (Figure 4B). While mixed zone 0+ brook trout only gained about 17% of their body weight per month, brook zone brook trout gained 50% of their body weight per month during the same period.

Although there was no apparent zone effect for older fish of both species, there was a seasonal effect. The greatest period of growth for all older fish occurred between February and June 1979, and it was during this period that 1+ rainbow trout initially outgrew brook trout and thereafter maintained their size advantage. One-plus brook trout exhibited an average relative length gain of about 22% per month between April and June 1979, and 18% per month between February and April 1979. Conversely, the periods



A. Relative Length Gain



Growth Intervals Between Sample Times

B. Relative Weight Gain

Figure 4. Relative Growth of 1979 Cohort (0+) Brook Trout. ▨ - Rainbow Zone, ▩ - Mixed Zone, ▧ - Brook Zone.

from June through August, and August through October 1979 were among the lowest periods of growth, with averages of only 0.5% and 4% per month, respectively, for all zones (Figure 5A).

One-plus rainbow trout appeared to show the same trends as brook trout; however, spring growth data were somewhat unreliable due to very large confidence limits (Figure 5B). Nevertheless, it appeared evident that spring growth was great in relation to summer growth. This can be confirmed with Figure 6 and Table 4. The mean length for 1+ rainbow trout increased from 90.4 mm in February to 103.8 mm in April, to 147.1 mm in June; for increases of 13.4 mm and 43.3 mm, respectively. Summer increases, on the other hand, were only 11.1 mm from June through August and 0.7 mm from August through October.

Figures 6 and 7 clearly show that it was during the spring of their 1+ year that rainbow trout initially outgrew brook trout and thereafter maintained their absolute size and growth advantage, even though relative growth data indicated that adult (1+ and older) brook trout gained slightly more of their body length per month than adult rainbow trout (Figures 5 and 8). While 1+ brook trout and rainbow trout maintained about the same average length from September 1978 through February 1979, rainbow trout growth from February through April, and from April through June was 13.4 mm and 43.3 mm, respectively. Conversely, brook trout

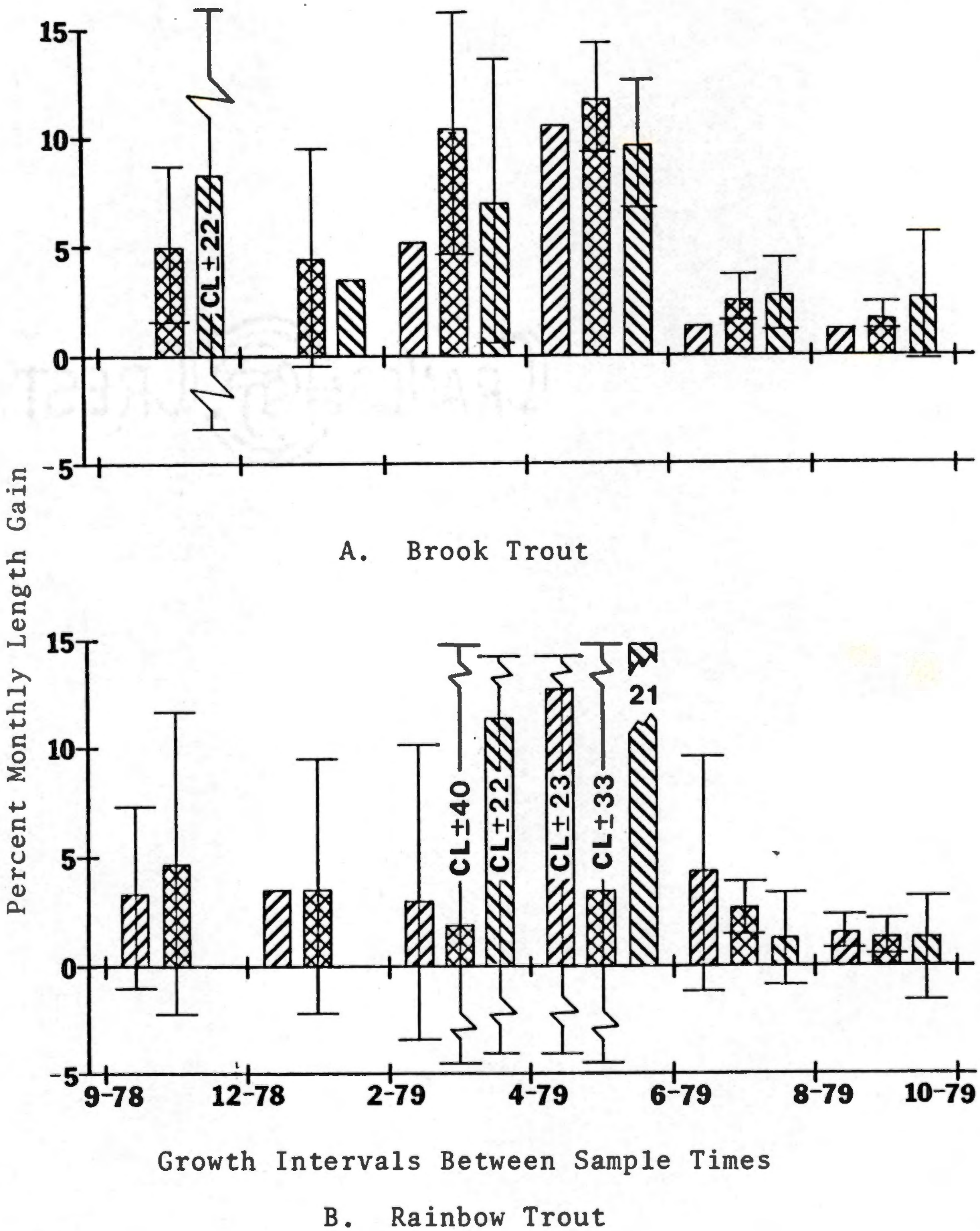


Figure 5. Relative Length Gain of 1978 Cohort (1+) Brook Trout and Rainbow Trout. ▨ - Rainbow Zone, ⊠ - Mixed Zone, ▧ - Brook Zone.

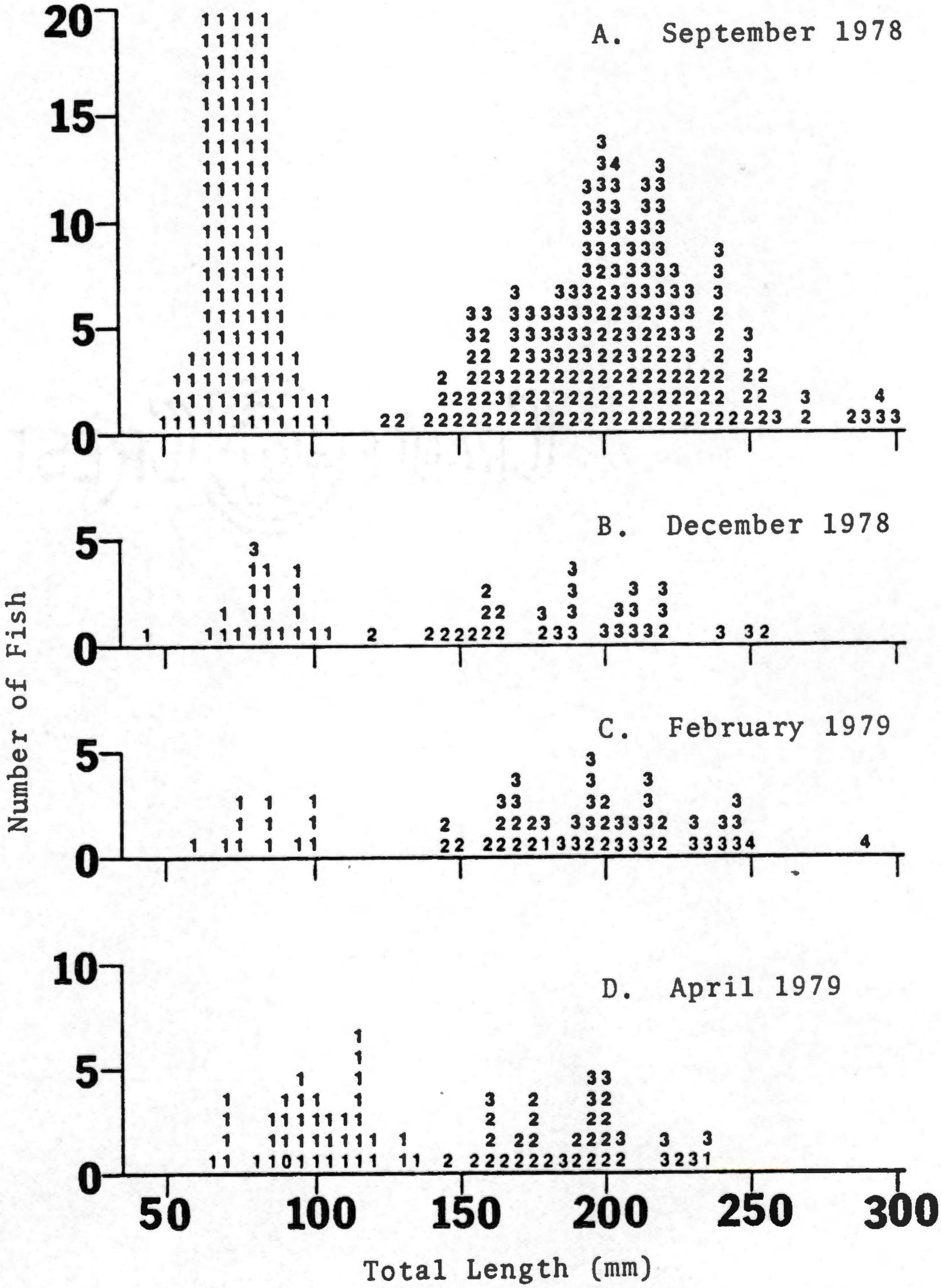


Figure 6. Rainbow Trout Length Frequency Distribution at Each Sample Time. Each number represents the age (determined by scales) of one fish.

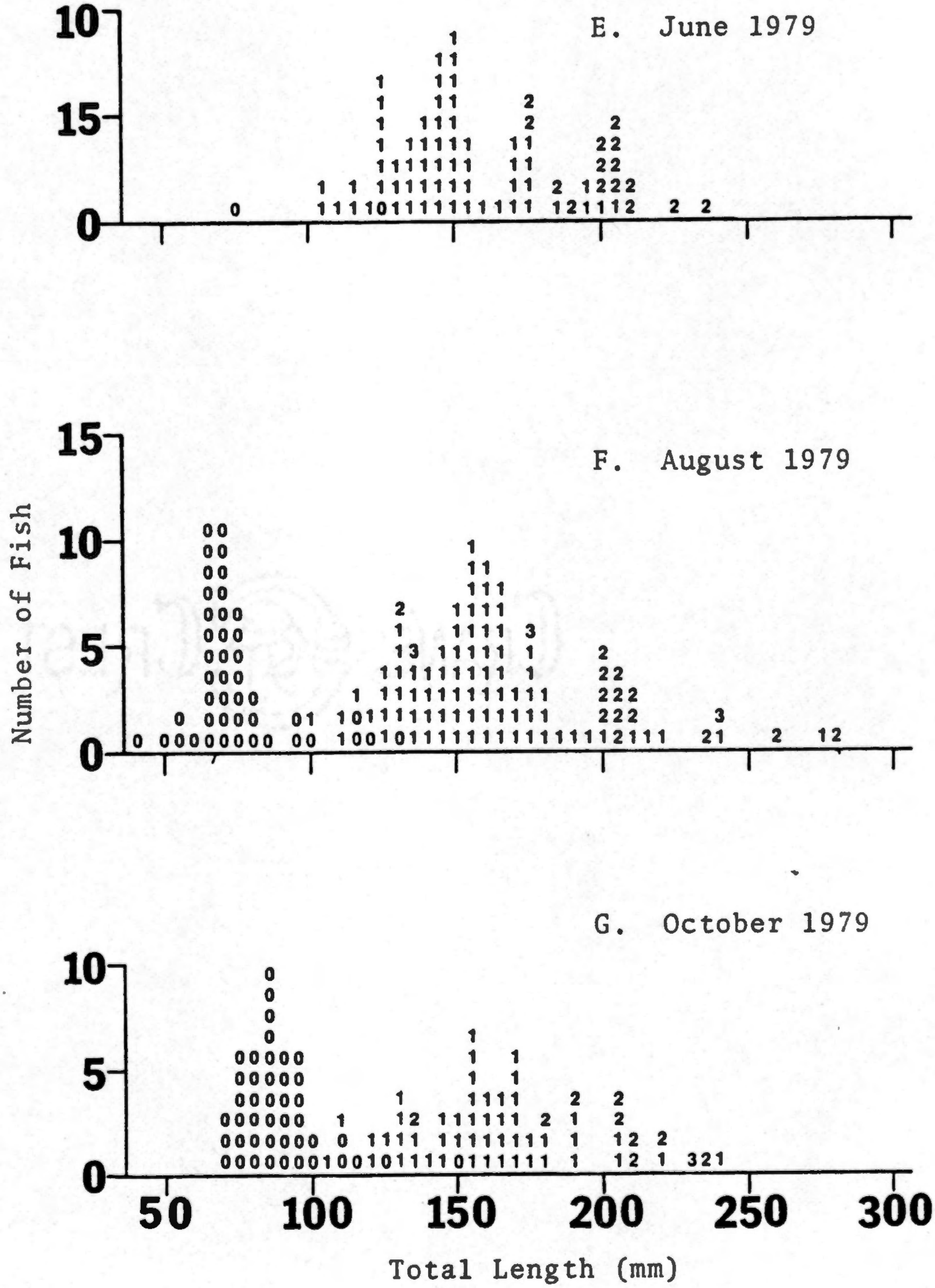


Figure 6. (Continued)

Table 4. Rainbow trout mean length (L), weight (W), and condition factor (K) [Fulton's K (Ricker 1975)] for each cohort at each sample time.[a]

	1979 Cohort (0+)		1978 Cohort (1+)		1976-77 Cohort (2-3+)	
	X̄	95% C.L.	X̄	95% C.L.	X̄	95% C.L.
9-78						
L			76.7	2.0	203.2	6.1
W			6.3	0.7	88.9	9.0
K			1.34	0.05	1.04	0.19
12-78						
L			81.0	79.6	185.6	26.7
W			*	---	*	---
K			*	---	*	---
2-79						
L			90.4	19.4	196.9	11.2
W			11.4	10.4	75.1	14.1
K			1.32	0.53	0.91	0.04
4-79						
L	92.0	**	103.8	9.3	185.7	9.6
W	8.0	**	15.5	7.1	59.6	7.5
K	1.03	**	1.10	0.04	0.91	0.04
6-79						
L	99.5	311.4	147.1	5.9	201.3	9.4
W	14.5	82.5	35.6	4.3	83.9	13.5
K	1.50	5.04	1.05	0.02	1.01	0.04
8-79						
L	74.9	5.5	158.2	6.5	189.6	23.6
W	5.4	1.4	43.6	6.7	76.2	18.3
K	1.30	0.46	1.00	0.03	1.00	0.04
10-79						
L	88.7	4.6	158.9	8.1	210.3	25.0
W	8.4	1.6	43.9	6.9	96.5	37.9
K	1.12	0.05	1.03	0.07	0.96	0.11

[a]*Weight and K unavailable for 12-78. **N=1.

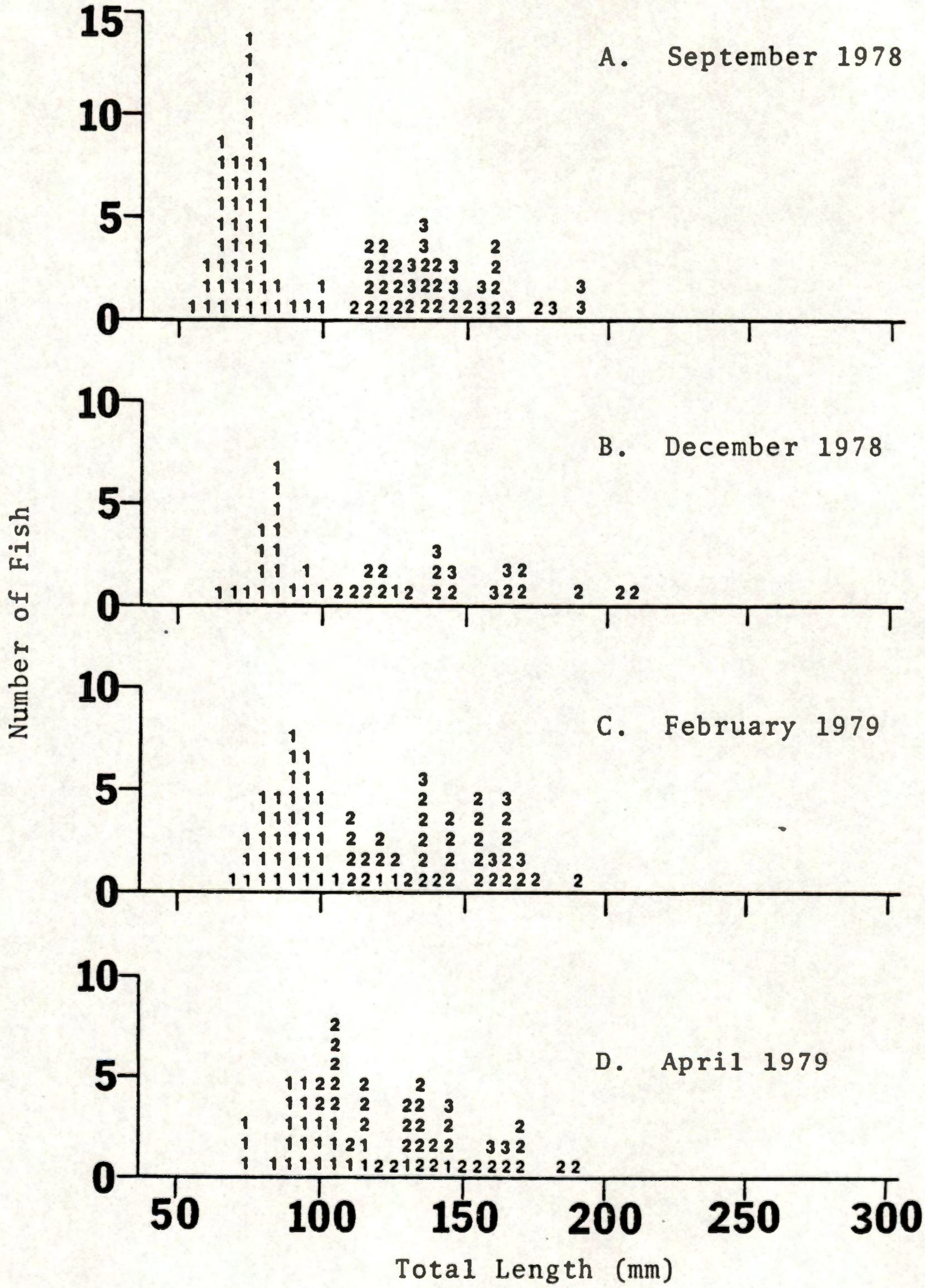


Figure 7. Brook Trout Length Frequency Distribution at Each Sample Time. Each number represents the age (determined by scales) of one fish.

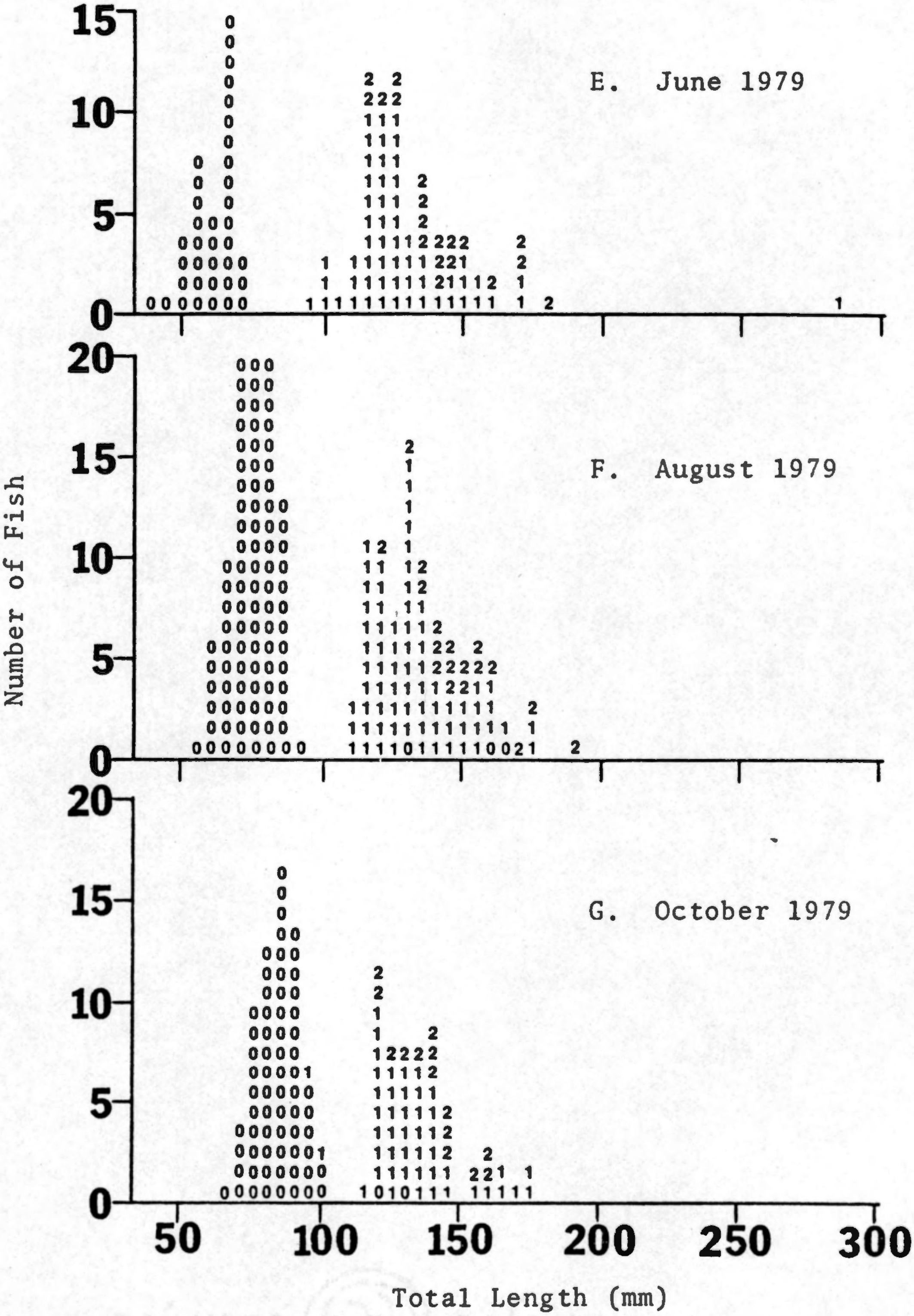


Figure 7. (Continued)

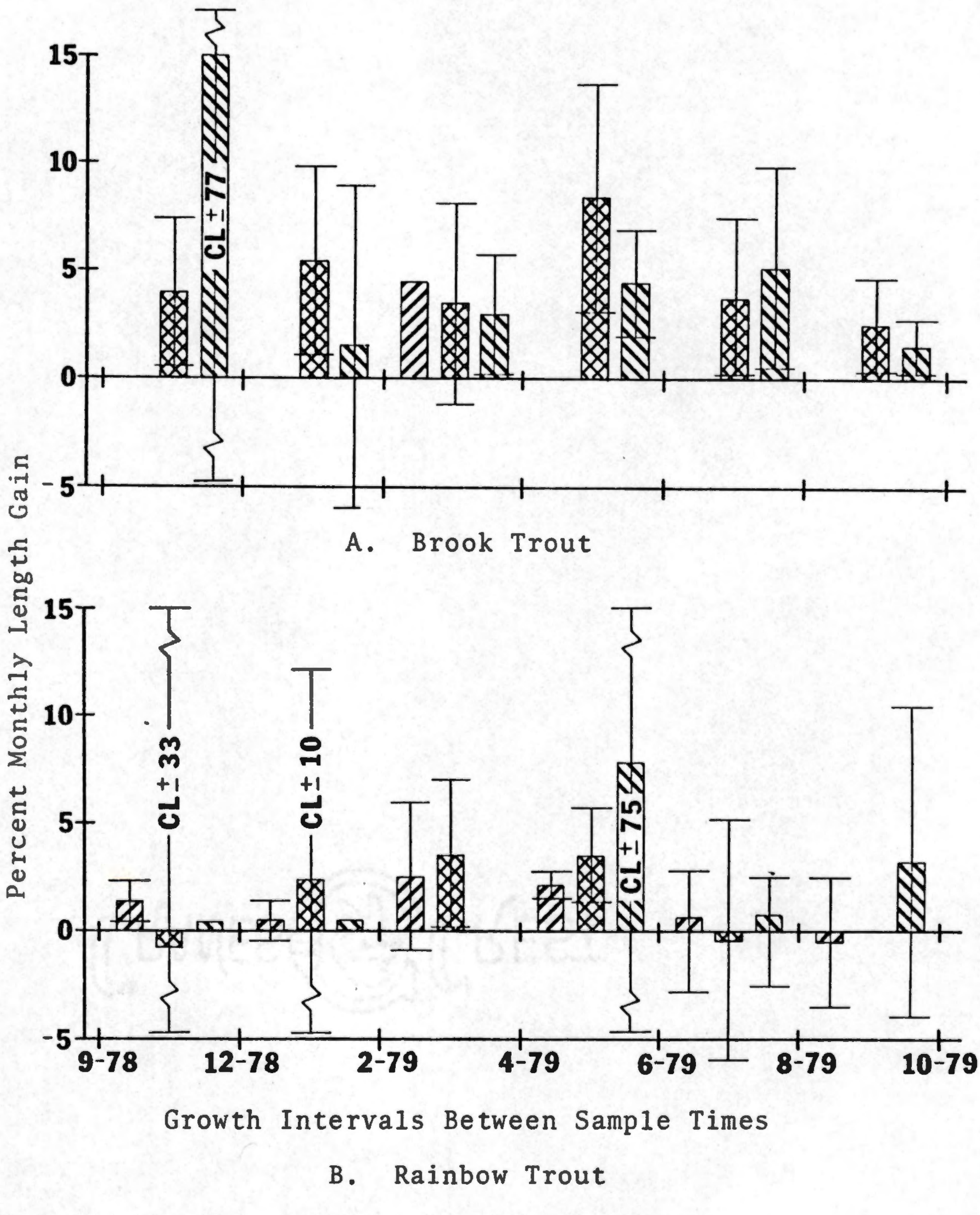


Figure 8. Relative Length Gain of 1976-77 Cohorts (2-3+) Brook Trout and Rainbow Trout. ▨ - Rainbow Zone, ▩ - Mixed Zone, ▧ - Brook Zone.

growth during these same periods was only 7.5 mm and 30.3 mm respectively (Figures 6 and 7 and Tables 4 and 5).

Mortality

The relationship between age and mortality is illustrated in Figures 6 and 7. It can be seen that 3+ brook trout and rainbow trout--as determined by scale verification--are in the population up until early spring (April). By June, however, these older fish have, for the most part, died.

Distribution

As summarized in Figure 9 and Appendix (Table 6), mean density distribution data reveal two important points. First, while older (2+ and 3+) rainbow trout maintained about equal densities from the rainbow zone to the mixed zone, 1+ rainbow trout showed a 66% decline. Meanwhile, total density dropped only about 20% from the rainbow zone to the mixed and brook zones. Thus, while older, larger rainbow trout maintained their presence in sympatric areas, 1+ rainbow trout did not. Secondly, 0+ fish of both species were found in greatest densities in their respective pure zones. Zero-plus rainbow trout were about 2.8 times as abundant in the rainbow zone as in the mixed zone, and 0+ brook trout were about 2.3 times as abundant in the brook zone as in the mixed zone.

Biomass distribution (Figure 10) was similar to the density distribution. While older rainbow trout maintained

Table 5. Brook trout mean length (L), weight (W), and condition factor (K) [Fulton's K (Ricker 1975)] for each cohort at each sample time.[a]

	1979 Cohort (0+)		1978 Cohort (1+)		1976-77 Cohort (2-3+)	
	$\overline{X}$	95% C.L.	$\overline{X}$	95% C.L.	$\overline{X}$	95% C.L.
9-78						
L			73.3	2.8	140.8	12.9
W			5.8	2.6	29.2	11.6
K			1.42	0.57	1.03	0.25
12-78						
L			86.0	6.3	139.2	14.5
W			*	---	*	---
K			*	---	*	---
2-79						
L			89.7	3.9	145.5	7.7
W			8.1	1.0	28.3	4.5
K			1.10	0.08	0.88	0.05
4-79						
L			97.2	7.4	133.5	7.7
W			10.5	2.4	24.4	3.9
K			1.08	0.06	0.96	0.03
6-79						
L	59.4	2.3	127.5	7.6	142.4	8.6
W	2.5	0.3	20.3	2.2	31.0	6.1
K	1.21	0.14	1.01	0.05	1.02	0.06
8-79						
L	76.1	2.1	131.1	3.9	148.7	8.5
W	5.2	0.8	23.3	2.5	34.8	7.6
K	1.15	0.08	0.98	0.02	1.00	0.04
10-79						
L	84.7	2.4	134.9	6.8	139.6	7.6
W	7.1	0.7	26.5	4.7	26.2	3.8
K	1.14	0.06	1.00	0.03	0.95	0.03

[a]*Weight and K unavailable for 12-78.

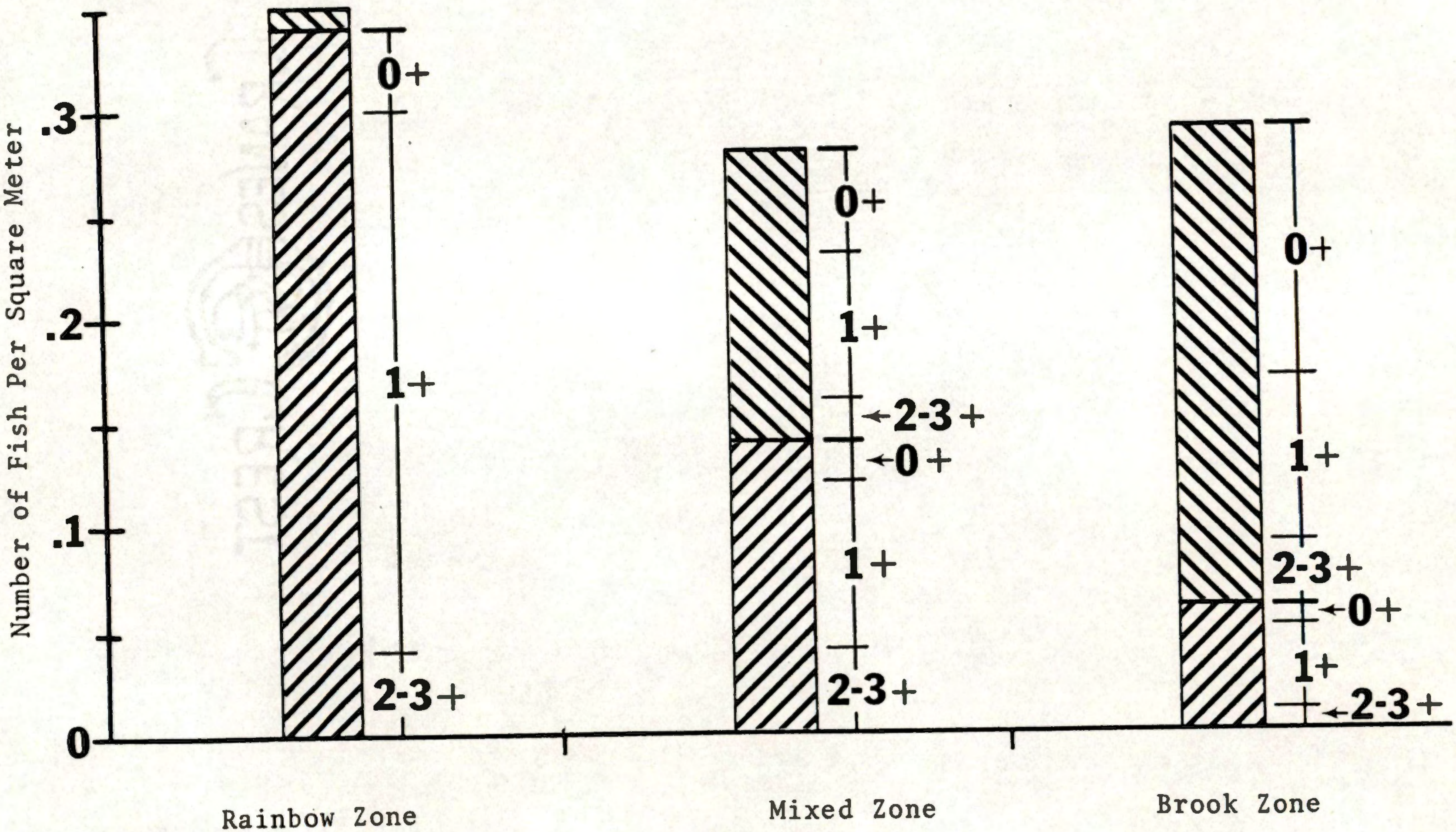


Figure 9. Mean Brook Trout and Rainbow Trout Density (Number Fish/m^2), by Zone and Cohort. Brook Trout, Rainbow Trout.

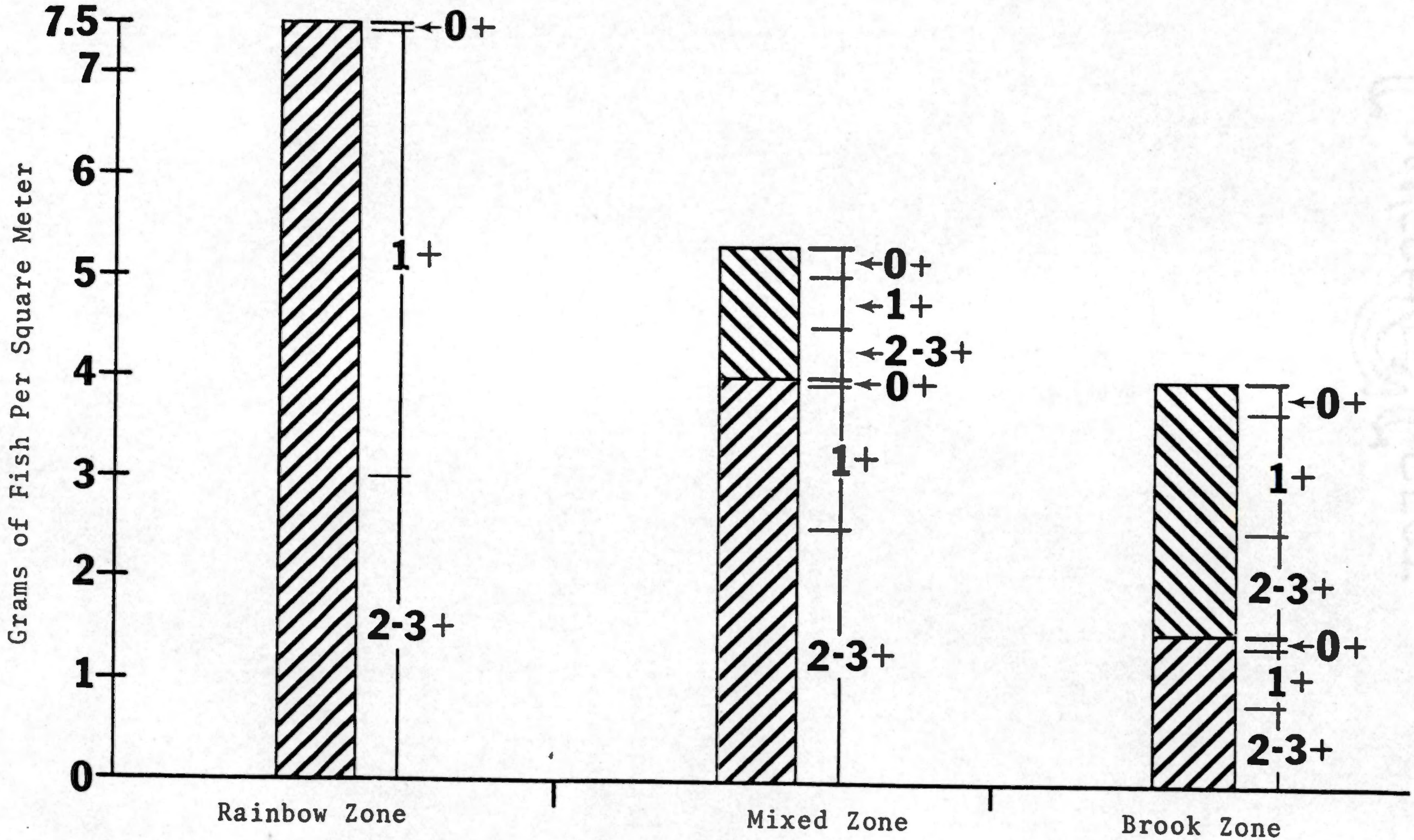


Figure 10. Mean Brook Trout and Rainbow Trout Biomass (g Fish/m^2), by Zone and Cohort. [legend swatch] Brook Trout, [legend swatch] Rainbow Trout.

equal biomass from the rainbow to the mixed zone, 1+ rainbows showed about a 66% decline. Total zone biomass showed a steady decline from the rainbow to the brook zone, a reflection of the increasing importance of brook trout to total density (Figure 9). Since the mean weight of brook trout was lower than that of rainbow trout--except for 0+ fish--(Tables 4 and 5, pages 25 and 30, respectively), total biomass was lower, even though total density remained approximately the same.

Production

Production was computed and is summarized in Figure 11 for the nine-month period. Four points emerge from these data.

Sympatric areas had lower levels of production than allopatric areas. Total (adding nine-month production for all cohorts of both species) rainbow zone production was highest at 4.8 $g/m^2/9$ mo, mixed zone production was lowest at 1.8 $g/m^2/9$ mo and brook zone production was intermediate at 3.2 $g/m^2/9$ mo. The mixed zone, which was roughly half-and-half brook and rainbow trout, had total production which was 62% lower than the rainbow zone. The brook zone, which was about 22% rainbow trout, showed total production which was 33% lower than the rainbow zone.

Rainbow trout were the major contributors to production within the stream. In addition to contributing virtually all of the rainbow zone production, these fish

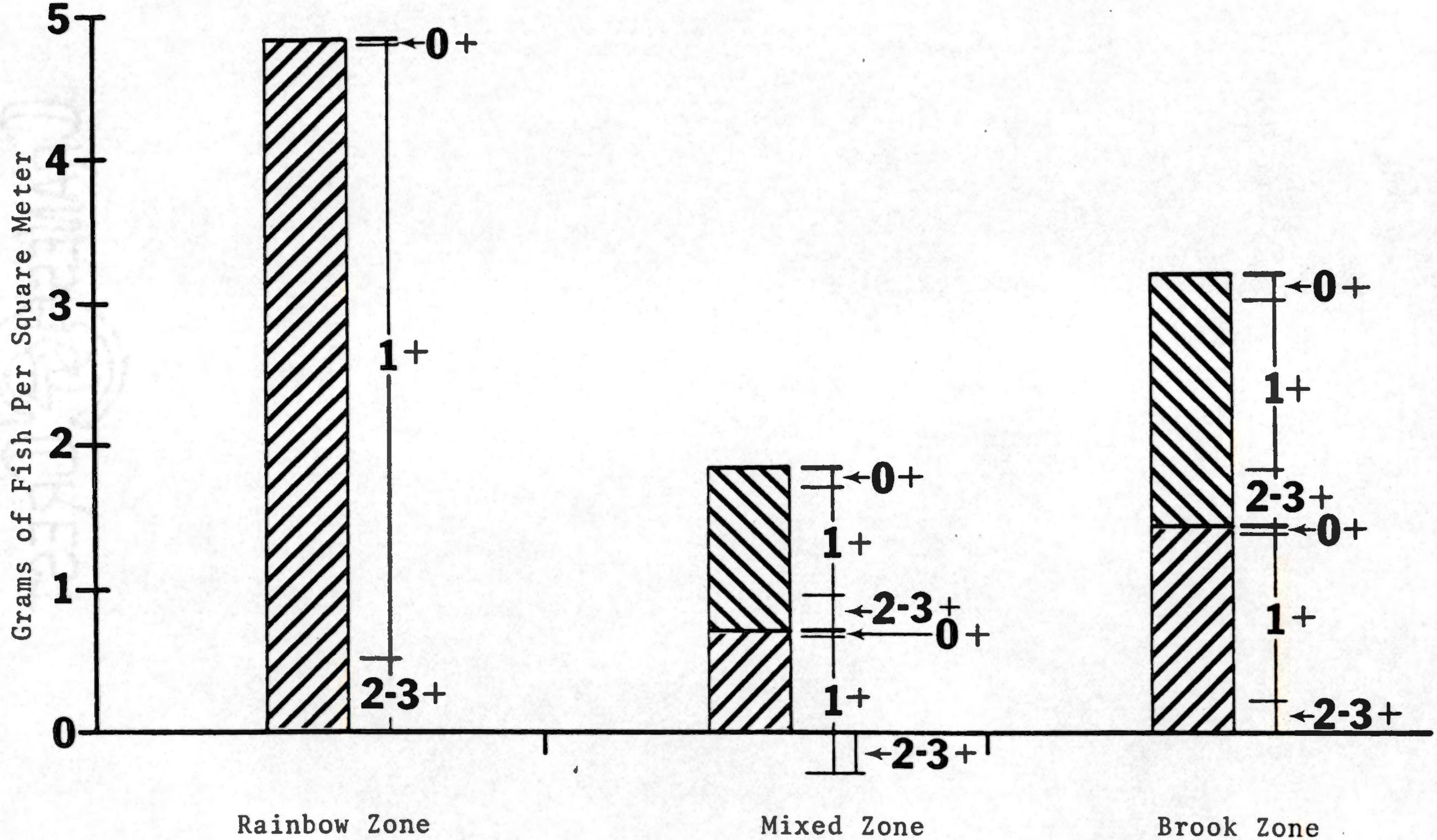


Figure 11. Total Brook Trout and Rainbow Trout Production ($g/m^2/9$ mo), by Zone and Cohort. [legend swatch] - Brook Trout, [legend swatch] Rainbow Trout.

contributed 54% of the total positive mixed zone production and 45% of the total brook zone production, even though they comprised only 21% of the number of fish in the brook zone.

In terms of production, the 1+ cohort was the most important cohort for both species, with 1+ rainbows having greater production than 1+ brook trout. One-plus brook trout contributed 65% and 69% of the total brook trout production in the brook and mixed zones, respectively. One-plus rainbow trout, on the other hand, accounted for 88% of the total rainbow zone production and 54% of the total positive mixed zone production (including brook trout production). They also accounted for 37% of the total brook zone production, even though they only accounted for 12% of the total brook zone density and 16% of the total brook zone biomass.

Older (2+ and 3+) mixed zone rainbow trout exhibited the only negative nine-month production throughout the study (Figure 11). This negative production was caused by a large negative instantaneous growth rate--and consequently a large negative production--from December 1978 through February 1979 (Appendix, Tables 7 and 8). This was not regained during the spring growth spurt, thus leaving a negative production for the nine-month period.

CHAPTER IV

DISCUSSION

Movement

Significant movement in fishes, and especially salmonids, has been well documented (Hall 1972, Moring and Buchanan 1978, Gerking 1959, and Erman and Leidy 1975). Funk (1955), in working with warm-water fishes, isolated two subgroups: movers and nonmovers. Furthermore, Flick and Webster (1975) isolated the same two subgroups in a population of brook trout in New York. They also found, however, that as non-trout species were removed, virtually all salmonid movement ceased. It seems, therefore, that not all populations of salmonids exhibit extensive, or even significant, movement. Newell (1957), in working with stocked brook trout and rainbow trout, found that brook trout moved more than rainbow trout, and most movement was downstream. Most fish of both species, however, stayed within about three-quarters of a mile of the point of stocking. Shetter (1936) found most brook trout stayed within about one mile of their original location. McFadden (1961), Bridges (1972), and Stefanich (1951) also found little movement by brook trout. In the Southeastern United States, Moore (1979) and Harned (1976) found limited movement by brook trout in the Great Smoky Mountains National Park.

For the most part, my data tend to agree with the literature; however, most previous workers have only been able to determine movement to within a kilometer or so, and at best, several hundred meters (Moore 1979). Data presented here, being much more precise, showed even more restricted movement than this previous work. These data, however, tend to disagree with those of Newell (1957), in that, in this study, not only did rainbow trout move more than brook trout, but net overall movement was up-stream. Although this movement was statistically significant on the part of certain groups, the distances were nevertheless very short; thus indicating a lack of biological significance. Certainly, very few fish mcved from one zone to the next. The possibility remains, however, that, if this small amount of movement is consistent from year to year, it may form very significant patterns that would not show up in this study. This, however, requires further investigation.

While the vast majority of fishes showed significant but very limited movement, it was also determined that a few older rainbow trout exhibited quite extensive movement. Hall (1972), in working with warm-water species, also found older fish to move up-stream. More importantly, however, these data appear to agree with Funk (1955) and Flick and Webster (1975), in that it suggests two subgroups to the population: movers and non-movers.

Growth

Rocky Fork age and growth and periodicity of growth data compare faborably with the literature. Rocky Fork brook trout average total length in April was 97.2 mm for one year old fish and 133.5 mm for two year old and older fish. Other authors report ranges of 99-170 mm at age 1 and 142-208 mm at age 2 (Cooper 1953, 1961 and Brasch et al. 1973). In several Southeastern streams, Konopaky (1978) reported total lengths--converted from standard lengths using his conversion of 1.28 (SL)=TL--of 87.0-102.4 mm at age one and 117.8-130.6 mm at age two. Rocky Fork rainbow trout averaged 103.8 mm at one year of age and 185.7 mm at two years of age. In comparison, Stauffer (1972) reported rainbow trout in a Great Lakes tributary to average 112 mm at one year, 180 mm at two years, and 226 mm at three years.

High spring growth and low summer and winter growth reported here are also seen in other fish populations. Both Shetter (1936) and Cooper (1953) reported brook trout growth to increase rapidly in the spring and decrease in the summer and winter. This phenomenon is thought to be food-related in the summer (Cooper and Benson 1951 and Ellis and Gowing 1957) and temperature-related in the winter (Leonard 1942).

Decreased relative growth of 0+ brook trout in the mixed zone indicated increased competition in this area. Whether competition was with other 0+ fish or with older fish, and whether competition was for food or for space, is

unclear. Griffith (1974) found that brook trout and cutthroat trout (Salmo clarki) both consumed invertebrate drift. Zero-plus fish of both species, however, concentrated on the smaller of these food organisms. Therefore, while there was probably a great deal of resource partitioning between younger and older fish in Rocky Fork, some degree of direct competition between these two cohorts for food may have occurred. It seems likely that older, more dominant fish may force 0+ fish into suboptimal microhabitats where food resources would not be as plentiful (Jenkins 1969). Distribution data supports the contention that competition for space among 0+ fish in the mixed zone was greater than in other areas, this apparently being due to the presence of both species. As stated previously, 0+ brook trout and rainbow trout were found in greatest densities in their respective pure zones. On the other hand, while the total combined density of 0+ brook trout and rainbow trout in the mixed zone was intermediate between that of the rainbow zone and brook zone, individual densities of 0+ fish were lowest in the mixed zone. This is consistent with the findings of Larson (personal communication) in the Great Smoky Mountains National Park.

Relative growth data of older fish indicated that competition directly affecting growth was not present after the first summer of life. Possibly as the fish grew larger they were better able to utilize larger, and thus more varied and plentiful, food items. This may reduce the

effect of suboptimal habitat, or direct competition with older fish. This point is only speculative, however, and requires further investigation.

Production and Distribution

Although low, Rocky Fork production estimates fell within the wide range reported by other workers. Brook trout production in Rocky Fork, a relatively infertile stream (pH=6.5, hardness=17 ppm, alkalinity=51 ppm), was 1.7 and 1.1 $g/m^2/9$ mo for the brook and mixed zones, respectively. Cooper and Scherer (1967), in examining the relationship of water chemistry to brook trout production in Pennsylvania, found production to range from 5.8 $g/m^2/yr$ in an infertile stream (pH=6.6, total alkalinity=5 ppm) to 30.0 $g/m^2/yr$ in a fertile stream (pH=7.3, total alkalinity= 130 ppm). Other authors have found similar ranges in brook trout production (Saunders and Power 1970, Goodnight and Bjorn 1971). Although lower than most other estimates, Rocky Fork production was higher than those estimates reported by Michaels (1978) for three infertile brook trout streams in Northern Georgia (production=0.31-0.73 $g/m^2/yr$, hardness= 3.75 ppm). It should be kept in mind, however, that, in Rocky Fork, rainbow trout were the most important producers. Even in the mixed and brook zones, where they were much less important to total density, they accounted for much of the production. Rainbow zone production, which was comprised of virtually 100% rainbow trout, was 4.77 $g/m^2/9$ mo. This

compares favorably with the estimates of Johnson and Hasler (1954) for rainbow trout production in five dystrophic lakes in Wisconsin and Michigan, which ranged from 1.9 to 8.4 $g/m^2/yr$. It is lower, however, than the estimates of Alexander and MacCrimmon (1974) for juvenile rainbow trout production in a Canadian stream of 13.2 $g/m^2/yr$.

There are two factors which have to be examined to explain lower levels of production in sympatric areas, and especially the mixed zone: (1) growth and (2) distribution (both biomass and density distribution).

The very low level of production in the mixed zone, as compared to the brook, and especially the rainbow zone, can be partially explained by a negative production rate for the nine-month period by 2+ and 3+ rainbow trout. This can in turn be explained by a large negative winter (December to February) production rate, caused by a high biomass combined with a negative instantaneous growth rate of 2+ and 3+ rainbow trout. An increased mortality rate in the spring combined with a lower growth rate for older fish in general did not allow this group to make up for the negative winter production. In-and-of-itself, negative winter production is not unusual. Hunt (1966) reported negative winter production for each year of a five year study in Lawrence Creek, Wisconsin. Negative production for the year, however, appeared to be somewhat unusual, and indeed, this observation of negative production for 2+ and 3+ rainbow trout in the mixed zone may be atypical. As mentioned earlier,

except for 0+ brook trout, there were no significant effects of zone on growth.

Another, and possibly more plausible, explanation for lower production in sympatric areas may be found by looking at density and biomass distribution. Overall density and biomass calculations fell well within the range established by previous workers. Total mean density (including brook trout and rainbow trout) in Rocky Fork ranged from 0.28 fish/m^2 in the mixed zone to 0.35 fish/m^2 in the rainbow zone. Total mean biomass ranged from 4.02 g/m^2 in the brook zone to 7.55 g/m^2 in the rainbow zone. Although there are no direct comparisons with zones in the literature, Alexander and MacCrimmon (1974) estimated the biomass for juvenile rainbow trout to be 7.05 g/m^2 in Bothwell's Creek Canada. Saunders and Power (1970) estimated brook trout biomass in a Canadian lake to be 0.31 g/m^2. Wydoski (unpublished) reported density and biomass of brook trout in a fished stream to be 0.13-0.26 fish/m^2 and 2.37-4.50 g/m^2, respectively. Computing mean biomass from the data of Michaels (1978) revealed that the three North Georgia brook trout streams had total mean biomass ranging from 1.58 to 7.22 g/m^2. Rocky Fork biomass estimates, comparing favorably with most of these authors, were higher than those of Saunders and Power (1970). The latter estimates were, however, for a lake habitat, and thus not directly comparable. Density estimates were only slightly higher than those of Wydoski (unpublished).

More important than overall mean density and standing crop estimates, however, were the differences in these estimates between the rainbow zone and mixed zone for 1+ and 2+ and 3+ rainbow trout. While these older rainbow trout maintained about the same density and biomass from the rainbow zone to the mixed zone, 1+ rainbow trout showed a 66% reduction. This, coupled with the overall importance of 1+ rainbow trout to total stream production, accounted for the lower production levels in sympatric areas. In other words, lower production in these areas was caused by a relative absence of 1+ rainbow trout, as they were apparently being "displaced" by brook trout.

One-plus, rather than older, rainbow trout showed a decline in density from the rainbow to the mixed zone. This suggests that competition was greatest between 1+ rainbow trout and brook trout, probably larger brook trout. Furthermore, this decline in density indicates that competition, to a great extent, may have been primarily for space rather than directly for food. Newman (1956) and Wolfe (1978) demonstrated that brook trout tend to be more aggressive than even slightly larger rainbow trout. This indicates that behaviorally, brook trout have the ability to effectively compete with rainbow trout of about the same size. It should be kept in mind that, in Rocky Fork, brook trout were essentially equal in size to rainbow trout throughout their first year. Even by the fall of their 1+

year, rainbow trout were only about 24 mm longer than equally-aged brook trout, and only about 10 to 20 mm longer than 2+ and 3+ brook trout (Tables 4 and 5, pages 25 and 30, respectively).

Even though relative growth data--the lack of zone effect on growth--did not clearly indicate any direct competition for food resources, there seems little doubt that some interspecific competition does exist. Both species have been described as indiscriminate carnivores (Griffith 1974, Miller 1974, and Power 1980), and in Western North Carolina, Tebo and Hasler (1963) reported these two species to have very similar food habits. Furthermore, Davis and Warren (1965) found that, in sculpins (*Cottus carolina*), increased competition caused more food to be utilized for maintenance and less for growth. Moore (1979) found no consistent increase in mean weight of brook trout after competing, sympatric rainbow trout were removed from streams in the Great Smoky Mountains National Park. This was apparently a general phenomenon throughout the Park which may be interpreted to indicate a lack of interspecific competition for food resources. Larson (personal communication), however, speculated that environmental factors may have masked any indicators of direct competition for food (i.e., growth). This may have been the situation in Rocky Fork. Competition for food directly affecting growth, therefore, may be evident only during times of low prey abundance. Magnuson (1962) found that when food was limited,

larger, dominate medaka (Oryzias latipes) chased smaller fish away from potential food, and thus, exhibited faster growth. Consequently, in larger fish with adequate food, spatial competition may be the most evident and important interaction between these two species. Without further evidence, however, this is only speculation, and thus requires further study.

CHAPTER V

SUMMARY AND RECOMMENDATIONS

(1) There was a significant but small amount of movement by several groups of fish; however, the above average movements of a few older fish indicated the possibility of two subgroups within the population: (a) movers and (b) non-movers.

(2) Zero-plus brook trout and rainbow trout were found in greatest concentrations in their respective pure zones, and 0+ brook trout grew better there.

(3) Except for 0+ brook trout, the zone in which fish were found had no effect on relative growth.

(4) While 2+ and 3+ rainbow trout maintained about the same density and biomass from the rainbow to the mixed zone, 1+ rainbow trout showed a 66% decline in density and biomass.

(5) The 1+ rainbow trout cohort was the single most important group of fish contributing to production. Consequently, it was the relative absence of these fish which contributed to lower production in sympatric areas of the stream.

(6) The lack of zone effect on relative growth of all fish except 0+ brook trout suggested that competition directly for food took place only among these younger brook trout. No doubt some competition for food was probably

present in older fish; however, the reduction in density of individual cohorts from their respective pure zone to the mixed zone indicated that, in these groups, competition may have been largely for space. The cohorts involved indicated that this competition was most intense between 1+ rainbow trout and brook trcut, probably larger brook trout.

Current brook trout management practices include, among other things, the rehabilitation of brook trout streams by the removal of rainbow trout; either by massive electrofishing efforts, or by extreme liberalization of rainbow trout fishing regulations. Although by no means conclusive, the data presented here suggest that the main threat to brook trout populations comes, not so much from 0+ and 1+ rainbow trout, but from older, larger rainbows. Not only are these the principal contributors to rainbow trout reproduction, but they also appear to outcompete brook trout more effectively than younger rainbows. Thus, while the importance of removing as many rainbow trout as possible, regardless of age and size, should be stressed, it appears to be even more important to remove the larger, more harmful rainbow trout first. The significance of this can be seen by looking at the cost versus benefits of the removal of rainbow trout from brook trout streams. Brook trout stream rehabilitation via massive electrofishing efforts is very labor intensive, and thus very costly. It seems possible, therefore, that the present effort used to

try and remove rainbow from a stream can be reduced and concentrated primarily on these older, larger rainbows.

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APPENDIX

Table 6. Mean densities (number fish/m^2) for each cohort, species, and zone.[a]

		Zone							
		Brook		Mixed		Rainbow		Average	
Cohort	Species	$\overline{X}$	95% C.L.	$\overline{X}$	95% C.L.	$\overline{X}$	95% C.L.	$\overline{X}$	95% C.L.
1979 (0+)	Brook	0.124	0.137	0.055	0.062	0.002	0.000	0.060	0.263
	Rainbow	0.015	0.016	0.014	0.015	0.039	0.042	0.023	0.061
1978 (1+)	Brook	0.073	0.137	0.074	0.140	0.010	0.014	0.052	0.158
	Rainbow	0.036	0.070	0.087	0.168	0.257	0.493	0.127	0.116
1976-77 (2-3+)	Brook	0.034	0.053	0.017	0.025	0.002	0.003	0.018	0.069
	Rainbow	0.012	0.031	0.036	0.092	0.044	0.109	0.031	0.072
All Cohorts	Brook	0.231		0.146		0.014		0.130	
	Rainbow	0.063		0.137		0.340		0.180	
Total		0.294		0.283		0.354		0.310	

[a]Confidence limits include only the variance due to time and do not include variance of the original population estimate.

Table 7. Distribution of rainbow trout mean biomass (B, g/m^2), instantaneous growth rate (G), and production (P, g/m^2) by cohort, zone, and time.

Growth Interval	1979 Cohort (0+)			1978 Cohort (1+)			1976-77 Cohort (2-3+)			Total	
	B/m^2	G	P	B/m^2	G	P	B/m^2	G	P	B/m^2	P
Brook Zone											
12-78 -- 2-79				0.44	0.08	0.04	1.75	0.03	0.05		
2-79 -- 4-79				0.66	0.60	0.40	0.83	0.06	0.05		
4-79 -- 6-79				0.85	0.89	0.76	0.38	0.29	0.11		
6-79 -- 8-79	0.05	0.12	0.07	0.56	0.03	0.01	0.27	0.04	0.01		
Total	0.05		0.07	2.51		1.20	3.23		0.22		1.43
Mean	0.05			0.63			0.81			1.49	
Mixed Zone											
12-78 -- 2-79				1.06	0.18	0.19	5.41	-0.13	-0.72		
2-79 -- 4-79				1.58	0.21	0.33	2.55	0.06	0.16		
4-79 -- 6-79				2.02	0.14	0.27	1.16	0.16	0.19		
6-79 -- 8-79	0.05	0.12	0.01	1.33	0.14	0.19	0.83	0.10	0.08		
Total	0.05		0.01	5.99		0.98	9.99		-0.29		0.70
Mean	0.05			1.50			2.49			4.03	
Rainbow Zone											
12-78 -- 2-79				3.12	-0.02	-0.05	6.49	0.01	0.09		
2-79 -- 4-79				4.65	0.06	0.27	3.06	0.09	0.27		
4-79 -- 6-79				5.67	0.58	3.47	1.39	0.11	0.16		
6-79 -- 8-79	0.14	0.12	0.02	3.94	0.13	0.58	9.99	0.02	0.02		
Total	0.14		0.02	17.69		4.21	11.94		0.54		4.77
Mean	0.14			4.42			2.99			7.55	

Table 8. Distribution of brook trout mean biomass (B, g/m^2), instantaneous growth rate (G), and production (P, g/m^2) by cohort, zone, and time.

Growth Interval	1979 Cohort (0+)			1978 Cohort (1+)			1976-77 Cohort (2-3+)			Total	
	B/m^2	G	P	B/m^2	G	P	B/m^2	G	P	B/m^2	P
Brook Zone											
12-78 -- 2-79				1.32	0.24	0.31	1.51	0.09	0.14		
2-79 -- 4-79				0.79	0.21	0.17	0.98	0.02	0.02		
4-79 -- 6-79				1.16	0.49	0.57	0.74	0.23	0.17		
6-79 -- 8-79	0.36	0.54	0.20	1.58	0.06	0.09	0.62	0.12	0.08		
Total	0.36		0.20	4.84		1.14	3.85		0.40		1.74
Mean	0.36			1.21			0.96			2.54	
Mixed Zone											
12-78 -- 2-79				0.64	0.24	0.15	0.72	0.06	0.05		
2-79 -- 4-79				0.38	0.49	0.18	0.46	0.10	0.05		
4-79 -- 6-79				0.56	0.57	0.32	0.35	0.28	0.10		
6-79 -- 8-79	0.22	0.54	0.12	0.76	0.15	0.11	0.29	0.13	0.04		
Total	0.22		0.12	2.34		0.77	1.83		0.23		1.12
Mean	0.22			0.58			0.46			1.26	

VITA

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