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RELATION OF DENSITY TO BROWN TROUT MOVEMENT IN A MICHIGAN STREAM

By

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ABSTRACT

RELATION OF DENSITY TO BROWN TROUT MOVEMENT
IN A MICHIGAN STREAM

By

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It has been suggested that among territorial stream fishes territorial competition may increase as density increases above some threshold level, and that this increase in competition results in a corresponding increase in the proportion of nomadic fish in the population. If this is true it seems reasonable to assume that the degree of movement shown by the population as a whole would increase also. To test this hypothesis a study of the relationship between trout density and the movement patterns of brown trout was undertaken.

During the summer of 1968 a mark and recapture experiment was performed on the brown trout in a 1400-foot section of the Pine River in Isabella County. This section was divided into seven, adjacent 200-foot stations and trout from each station and over 6-inches in total length were marked distinctively. Data on movement obtained from 106 recaptures in 1968 indicated that trout movement was oriented around the station of initial capture.

In 1969 a repetition of the above experiment was planned, with the inclusion of two new sections. Then, following reduction of the population, another mark and recapture experiment was planned. However, during the course of sampling in 1969 it became apparent that a decrease in abundance of trout over 6-inches in length had already occurred, probably as a result of reduced recruitment. Schnabel estimates indicated a 54.4% reduction in number, while subtraction of the recruitment estimate from the estimated mortality indicated a 55.7% reduction. Manipulation of density was therefore unwarranted.

Distribution of the 97 recaptures of fish marked in 1969 indicated that trout movement in each of the three sections was oriented around the station of initial capture, just as in 1968. Moreover, the movement patterns for trout in the three sections sampled in 1969 did not differ from the pattern recorded in 1968.

It is suggested that a positive relationship between density and the degree of movement shown by brown trout populations exists, but that it probably occurs primarily among the fry and becomes considerably diminished by the time the fish reach 6-inches in length. It is suggested that this relationship operates as a density regulating mechanism, with primary regulation occurring before the fish reach reproductive age. This mechanism would then act to conserve energy and insure adequate reproduction.

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INTRODUCTION

Movements of fishes have received much attention since the early 1950's. Effort has been directed toward both lotic and lentic environments, however, the lotic environment offers several advantages. One advantage is that streams can be sampled relatively efficiently compared to the deeper portions of the lacustrine environment. Also, the analysis of stream fish movement is simplified, since vertical movements are limited and horizontal movements are primarily directed in only two directions.

While many of these studies have indicated that movement by stream fishes is quite limited, little work has been done to determine the importance of this phenomenon or what factors are responsible.

Gerking has published two reviews concerning the restricted movements of stream fishes, and presents the possibility that territorial behavior or hierarchy may have an effect on the degree of movement shown by these populations (Gerking, 1953; 1959). He presented three postulates with regard to this possibility: (1) fish move rapidly into an area of underpopulation, (2) a foreign population when placed in an established population will be forced to move out, and (3) the established population will move about more than usual as a result of the competition. It would seem from these postulates that Gerking believes that territoriality operates to regulate density by altering the degree of movement shown by the population, or at least he feels that density and movement are in some way related.

If there is such a mechanism operating, and it functions in the manner suggested by Gerking, then it may be proposed that if the population in an area of stream was reduced, a decrease in movement would ensue. Jenkins (1969), in an excellent study of the social structure of populations of brown trout, *Salmo trutta*, has indicated a similar possibility. He suggests that the proportion of transient fish in a population may increase with population density, past some threshold level. According to this view, a decrease in density to a point below this threshold level would result in decreased movements of the population as a whole.

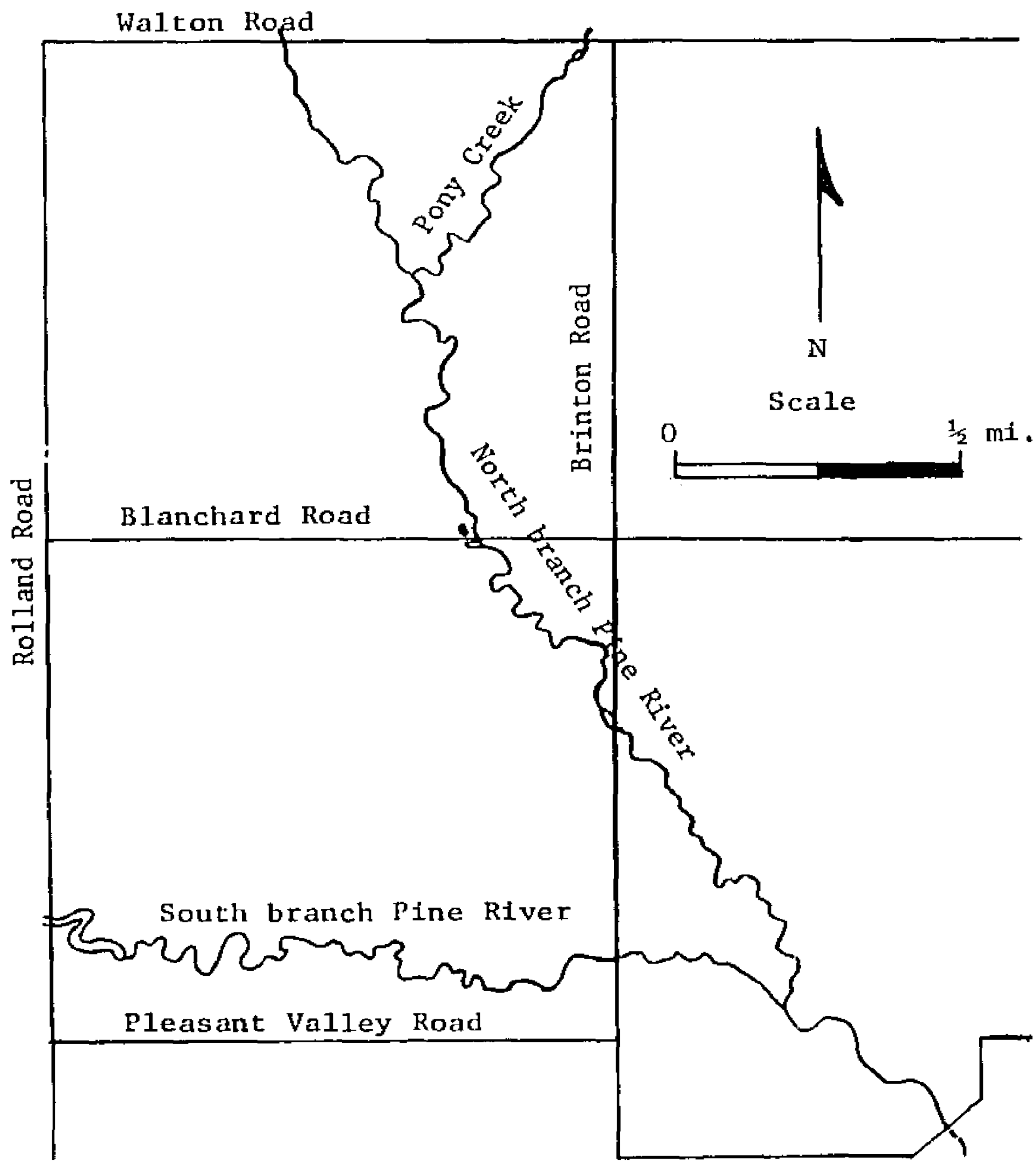
From these ideas, a working hypothesis may be formulated such that if the population density of a territorial stream fish was reduced, the degree of movement shown by that population would be reduced also. Since factual evidence to support this hypothesis is lacking, it was decided to attempt to determine the effect of a drastic decrease in density on the degree of movement shown by a brown trout population in a small, southern Michigan stream.

THE STUDY AREA

One of the problems inherent in studies of stream fish movement is the possibility of fish movement beyond the limits of the sampling area. However, choice of a localized population of stream fish with well-defined limits to its distribution would serve to minimize this bias. A short section of the Pine River in Montcalm County, Michigan, just south of the Isabella County line, seemed to meet this requirement. The area has been frequently stocked with small numbers of brown trout and adjacent sections of the stream are considered as marginal habitat for this species. Several samples taken in spring, 1968, revealed brown and brook trout, *Salvelinus fontinalis*, both in this area and a section of the river approximately six miles upstream. The abundance of brown trout in the upstream area was considerably greater, however, and the river was smaller and could be more thoroughly sampled. For these reasons the upstream area was selected for study.

The upstream area chosen for the study consisted of the North Branch upstream to West Walton Road (Fig. 1). The areas downstream from the junction of the South Branch for several miles and upstream from Walton Road were

Fig. 1.--A map of the Pine River study area.


Walton Road
Pony Creek
Brinton Road
N
Scale
0
½ mi.
Rolland Road
Blanchard Road
North branch Pine River
South branch Pine River
Pleasant Valley Road

considered uninhabitable by trout, at least during the summer months, and several rod and reel samples and three electrofishing samples taken in these areas contained only two brown trout. Both of these were taken a short distance below the confluence of the South Branch during August, 1969.

The stream between Walton Road and its confluence with the South Branch has an average gradient of about five feet per mile, and averages about 25 feet in width. Good cover is provided by shoreline trees and shrubs, predominantly willow, *Salix* sp., and alder, *Alnus* sp., the latter forming dense tangles in some places. In several places dense mats of watercress, *Nasturtium officinale*, provided excellent trout cover, although these mats were quite scarce. Fallen trees have produced some of the deeper pools in the study area and many bend holes are present along the river's meandering course. The deepest pool in the study area approached only four feet in depth during normal water levels, and could be quite readily sampled with the stream shocker. The stream bottom in the study area is composed of silt, sand, and gravel, with one or another predominating in any given stream section depending on the current velocity. The stream bottom as well as its banks remained quite stable throughout the study except for one pool just below the Brinton Road bridge. This pool began to fill with sand in the spring of 1969, resulting in the establishment of a sand bar in the middle of the pool by September. Another noticeable change in the stream in 1969 was the decrease in size of the few beds of watercress which had provided scarce but good trout cover in 1968. The reasons for this decline of watercress remain obscure.

Various parameters of selected chemical qualities of the water are included in Table 1. All samples were taken during daylight hours. These data indicate a relatively high basic productivity for the study area. Water temperatures were not considered limiting to brown trout, as the highest recorded temperature was 22.0°C on July 15, 1968. Strawn (1958) has listed 25.3°C as the upper critical limit for brown trout, while the upper instantaneous lethal temperature has been reported to be 27-29°C during the summer (Grudniewski, 1961). Dissolved oxygen values were also within an acceptable range, with the lowest reading of 5.4 mg/l recorded at 8:30 p.m. on September 5, 1969, during a rather prolonged warm-weather period. Grudniewski (1961) has reported minimum levels of dissolved oxygen for brown trout as between 2.5 and 3.0 mg/l during the summer. Doubtless, these recorded observations do not encompass the full range of values actually attained in the study area, but if more extreme conditions do exist, they are probably short-lived and of relatively rare occurrence. Overall, conditions appear to be favorable for

Table 1.--Water chemistry of the Pine River at the Blanchard Road bridge, Isabella County, Michigan, during 1968 and 1969. (all concentrations expressed in ppm)

	Alkalinity*	D.O.	pH	Total phosphate	Nitrate
Sample size	28	29	26	30	31
Mean	184.8	9.3	--	0.158	0.465
Standard dev.	17.1	2.2	--	0.083	0.211
Range	142-228	6.3-14.1	7.2-8.8	0.033-0.400	0.125-0.750

*Only methyl orange alkalinity was recorded, as phenolphthalein alkalinity was never observed.

survival of brown trout and it became apparent that the brown trout population in this section of the river has been able to reproduce and maintain itself over an extended period of time without the need for supplemental stocking.

Michigan Department of Natural Resources records indicate that the North Branch was stocked with a total of 13,000 brown trout in 1921 and 1924, while the South Branch received 41,500 browns from 1926 to 1932. The South Branch apparently no longer holds trout during the summer months, as an electrofishing sample taken there in August, 1969, did not contain a single trout. Pony Creek, a small tributary emptying into the North Branch between Blanchard and Walton Roads was also stocked with a total of 36,000 brown trout between 1922 and 1926, and one was caught in 1968 with rod and reel, so at least there is a possibility that a few still persist. Since 1932, however, no brown trout have been stocked in this area of the Pine River or its watershed. Direct evidence of reproduction was obtained in 1969, when a number of young-of-year brown trout were collected in the study area. A check with the Michigan Department of Natural Resources revealed that no brown trout plantings had been made in the stream system. The population in the study area can thus be considered as a naturalized, established population which has been able to maintain itself over an approximately 40 year period.

METHODS AND MATERIALS

Division of the Study Area

The study area, from a point 1,000 feet below the Brinton Road bridge upstream for 3,200 feet above this bridge, was divided into three, 1,400-foot sections, each comprised of seven, 200-foot stations. The end of each station was signified by a strip of white cloth tied to a nearby twig, while the end of a section was denoted by a red cloth strip. Occasionally the placement of these markers varied a few feet either up or downstream. For instance, if the endpoint of a station was located in the center of a pool, the flag was arbitrarily placed either at the head or tail of the pool, as these areas represented more distinct divisions to the human observer and presumably also to the fish. The three sections were denoted in order as A, B, and C, with C being the furthest downstream. Within each section, the stations were numbered 1 through 7 consecutively from downstream to upstream. The length of stream from the Pleasant Valley Road bridge to the downstream limit of section C will be denoted here as area D, while the length of stream from the upstream limit of section A to the Walton Road bridge will be termed area E.

Fish Sampling

Brown trout were captured with a 115 V, DC, electric stream shocker in 1968 and the early part of 1969, after which time a 115 V, pulsating AC unit was used. Both devices were similar with respect to wave shape and frequency and appeared to be equally efficient in practice. An auxiliary unit was also employed during the study so that voltage and amperage could be varied to suit the varying conductivity of the water. A reduction of amperage and voltage to the point where fish could still be captured, but where the visible effects on the fish were minimal was attempted. A satisfactory combination was found to be 60 to 70 V, and 0.7 to 1.0 amps, and this combination was used throughout the study. Some difficulty was encountered in capturing fish with this combination, but once captured, the fish usually recovered within a few minutes. Two notable exceptions occurred where brown trout failed to recover. Both of these fish were subjected to extremely long periods of shock when they became lodged in thick brush and could not be quickly netted.

No assumptions were made on the effect of electric shock on movement patterns of stream fishes, as information on this point is lacking. Although Gerking (1953) made some attempt to compare movements of shocker-caught rock bass, Ambloplites rupestris, with those of seine-caught fish, he was not able to catch enough fish with the seine to make a valid comparison. Fajen (1962) used the cresol method, suggested by Embody (1940), to sample smallmouth bass, Micropterus dolomieu, and his results approximated those of earlier studies of smallmouth movement where electric shockers were used. Also, cresol has a disadvantage of toxicity and for these reasons there appears to be little advantage in using the cresol method. The effects of electric shock on behavior, stamina, and mortality rates of trout have been studied to some extent (Bouck and Ball, 1966; Horak and Klein, 1967), with the results indicating some alteration of behavior and a decrease in stamina of shocked fish. However, no increase in mortality rates were detected even though the shock given the fish in each of these studies was apparently quite severe. Therefore, since no practical alternative method is available for capturing large numbers of fish in streams, it was hoped that a reduction of amperage and voltage would result in a corresponding reduction in effects on the fish.

After capture, fish were placed in a tub of stream water, which was refilled at the end of each station. After sampling a station, each captured fish was finclipped, or if it had previously received a clip, the type of clip was noted and recorded; the total length of the fish was quickly measured and recorded; and the fish was released. Separate data sheets were used for each station to avoid confusion. Maximum distance that a fish could have been displaced, using this procedure, was 200 feet and this distance can be considered negligible, since homing of brown trout has been shown to occur over much greater distances (Schuck, 1945).

The fish were marked with a maximum of two fin clips consisting of one median and one paired fin, or in some instances, two median fins (Table 2). Fin clipping was selected for marking fish in preference to other marking methods because it is long-lasting and apparently has a minimal effect on the fish as long as no more than two clips per fish are used (Nelson, 1960; Stauffer and Hansen, 1969; Brynildson and Brynildson, 1967; Shetter, 1967; Radcliffe, 1950). There is also some evidence that fin clipping may not alter the extent of fish movement (Gerking, 1953).

Mark and recapture runs were made approximately weekly from July through the first half of September in section B during 1968, and in all three delineated sections from June through August, 1969. The mark and recapture period encompassed an 81 day period in 1968 and an 80 day period in 1969. The entire study area, with the exception of that portion upstream from Blanchard Road, was sampled once during August, 1968. The area above Blanchard Road was sampled in part on July 1, 1968.

Table 2.--Types of fin-clips used to mark brown trout from 21 stations in the Pine River during 1968 and 1969.

Station	1968	1969
C1	--	anal-adipose
C2	--	upper caudal-adipose
C3	--	lower caudal-adipose
C4	--	left pectoral-adipose
C5	--	right pelvic-adipose
C6	--	right pectoral-adipose
C7	--	left pelvic-adipose
B1	anal	anal
B2	upper caudal	upper caudal
B3	lower caudal	lower caudal
B4	left pectoral	left pectoral
B5	right pelvic	right pelvic
B6	right pectoral	right pectoral
B7	left pelvic	left pelvic
A1	--	anal-dorsal
A2	--	upper caudal-dorsal
A3	--	lower caudal-dorsal
A4	--	left pectoral-dorsal
A5	--	right pelvic-dorsal
A6	--	right pectoral-dorsal
A7	--	left pelvic-dorsal

Total numbers and total lengths of all captured fish were recorded but no fin-clips were given. The captured fish were released periodically during sampling operations. These same areas, with the inclusion of the entire section of stream from Blanchard Road to Walton Road, and a portion of the South Branch for several hundred yards upstream from its mouth, were sampled in like manner during August, 1969. All brown trout captured downstream (area D) and upstream (area E) from the three study sections were given separate identifying clips. These fish could then be distinguished from fish marked in the study sections and an idea of the extent of movement into the study sections was possible. Although two samples were taken in the three study sections after marking these fish, only one marked fish from area D or E was recaptured.

In addition to the data collected and mentioned above, scale samples were taken from 97 brown trout captured in 1969 and 147 white suckers, *Catostomus commersonni*, taken during 1968 and 1969. Scales were taken from trout only during the last sampling period because of the possibility of infection or behavioral alterations which may have resulted from skin damage and the additional handling involved.

Trout scales were taken from an area located immediately below the lateral line and just behind the tip of the pectoral fin when that fin was pressed back against the body, while sucker scales were taken from the region anterior to the dorsal fin and just above the lateral line. Sucker scales were imprinted on clear plastic slides for examination, but trout scales, because of their small size, were mounted between two microslides. A magnification of 48X was sufficient for detection of annuli in both species, and measurement of scale radius as well as the distance from the focus to each annulus was taken at the antero-lateral margin under this same magnification.

RESULTS

The Fish Population

The abundance of fishes comprising electrofishing samples made in the study area during August and September, 1968, and August, 1969, are shown in Table 3. Brown and brook trout were the predominant sport fishes present, but a few small northern pike, *Esox lucius*, were taken on occasion. Other fishes collected in the study area included: stoneroller, *Campostoma anomalum*; northern brook lamprey, *Ichthyomyzon fossor*; central mudminnow, *Umbra limi*; mottled sculpin, *Cottus bairdii*; johnny darter, *Etheostoma nigrum*; black sided darter, *Percina maculata*; stonecat, *Noturus flavus*; bluegill, *Lepomis macrochirus*; black bullhead, *Ictalurus melas*; and rainbow trout, *Salmo gairdneri*. The latter five species were represented in the collections by only one specimen each and should be considered as uncommon inhabitants, or as strays from other areas of the drainage. From Table 3, it is apparent that the percentages for the more abundant species in the two 1968 samples are in close agreement. The differences in abundance of both brown and brook trout in the two samples is probably a reflection of the relatively poor

Table 3.--Abundance of fishes in electric shocker samples taken from the North Branch of the Pine River downstream from Brinton Road during August, 1968 and 1969 (A), and a sample taken upstream from Brinton Road during September, 1968 (B). (numbers in parentheses are percentages)

Species	1968 (B)	1968 (A)	1969 (A)
white sucker (*Catostomus commersoni*)	105 (50.2)	104 (48.4)	16 (10.7)
creek chub (*Semotilus atromaculatus*)	39 (18.7)	28 (13.0)	29 (19.5)
river chub (*Hybopsis micropogon*)	12 (5.7)	14 (6.5)	32 (21.5)
hog sucker (*Hypentelium nigricans*)	9 (4.3)	12 (5.6)	7 (4.7)
brown trout (*Salmo trutta*)	16 (7.7)	27 (12.6)	22 (14.8)
common shiner (*Notropis cornutus*)	21 (10.0)	12 (5.6)	12 (8.1)
brook trout (*Salvelinus fontinalis*)	3 (1.4)	13 (6.0)	27 (18.1)
rock bass (*Ambloplites rupestris*)	0 (0.0)	2 (0.9)	0 (0.0)
blacknose dace (*Rhinichthys atratulus*)	0 (0.0)	0 (0.0)	4 (2.7)
Others	4 (1.9)	3 (1.4)	0 (0.0)
Total	209 (99.9)*	215 (100.0)	149 (100.1)*

*Figures do not add to 100.0 because of rounding errors.

trout habitat found for some distance above the Brinton Road bridge. The agreement of the patterns of percentage values for the two 1968 samples indicates little change in relative species composition during the summer.

These data, although capable of indicating only gross changes in fish populations, do seem to show a decided increase in the abundance of river chubs and brook trout in 1969 and a decline in abundance of white suckers. Care should be exercised in interpreting data based on electrofishing samples, however, since the shocker is selective for larger fish. Thus the results may reflect not only abundance of the fish but also relative sizes of the fish.

Since the average size of white suckers comprising the 1969 sample was 19.6 cm in total length, only 2.4 cm less than the average of 22.0 cm obtained from the 1968 sample, it would seem that the bias resulting from the size selectivity of the electric shocker was negligible. However, if only the larger suckers had declined in abundance while the number of young-of-year had increased, an apparent decrease in abundance could result.

For example, suppose the population of larger suckers was 100 in 1968, and the population of young-of-year fish was also 100. In 1969 the number of fish in each of these size classes was 50 and 200 respectively. Now assume unequal capture rates for the two size groups:

50% for the larger fish and 10% for the young-of-year. Applying these capture rates to the proposed populations in the two years we have:

	1968	1969
Large fish	100 X 0.5 = 50	50 X 0.5 = 25
young-of-year	100 X 0.1 = 10	200 X 0.1 = 20
	N = 200 n = 60	N = 250 n = 45

It can be seen that although the total population in 1969 was greater than in 1968, the total number of fish in each of the samples indicates a decreased population in 1969.

A similar situation to the above apparently existed in the study area in 1968 and 1969. Since none of the 78 white suckers of various ages captured in the study area during 1969 were found to have attained lengths greater than 19 cm at the formation of the first annulus, it was assumed that fish under this length were young-of-year. When this assumption was applied to the samples of white suckers captured in the study area during 1968 and 1969, it was found that 26% of the August, 1968, sample were considered to be young-of-year, while 44% of the 1969 sample were considered young-of-year. Thus an increase in the number of young-of-year and a decrease in the number of older white suckers in the study area is indicated. An increased number of young-of-year were observed while sampling the study area in 1969 as compared to observations made during 1968.

The example given above apparently does not apply in the case of brook trout. Since the mean lengths of the 1968 and 1969 samples were 20.8 and 17.5 cm respectively, a bias resulting from size selectivity of the shocker would have tended to show a decrease in abundance of brook trout in the 1969 sample. To the contrary, however, the number of brook trout captured in 1969 showed a substantial increase over the number captured in 1968, indicating an increase in abundance in 1969.

In summary, only limited information is available concerning population changes in the study area over the period of study. Limitations were primarily due to selectivity of the shocker for larger fish and the impracticality of using other fish sampling devices in a relatively fast-flowing stream. We can, however, indicate possible fluctuations in the fish population over the two-year study period. The relative species composition of the study area is fairly stable during the summer, as indicated by the close agreement of the patterns of values obtained from the two 1968 samples. Both brook trout and river chubs showed an apparent increase in abundance in 1969. The population of larger white suckers was probably reduced in 1969, although the number of young-of-year most likely increased. No change in abundance of brown trout is indicated in 1969, although strong evidence for a decrease in abundance will be discussed in the following section of this paper.

The Brown Trout Population

Population Density.--The number of brown trout over 6-inches in total length declined markedly in the study area from 1968 to 1969. The fish population data already discussed gave no clear indication of this decline, but a more refined estimate is appropriate here. Totals of 64 and 29 brown trout respectively were marked in section B in 1968 and 1969, while the numbers of recaptures made were 105 and 36 respectively.[1] When the Schnabel multiple mark and recapture model was applied to these data, estimates of 68 and 31 were obtained. Thus a 54.4% numerical reduction in the number of brown trout over 6-inches in length is indicated. The agreement of the Schnabel estimates with the numbers of fish marked in each year indicates that over 90% of the fish in the study area were captured at least once during the course of sampling. The formula used to obtain these estimates took the form:

$$\hat{N} = \sum_{i=1}^{k} (n_i M_i)/[(\sum_{i=1}^{k} x_i) + 1]$$

where ni = the total number captured on the ith day,

M_i = the number of marked fish in the population on the ith day (prior to sampling on that day),

[1]Tables showing the numbers of fish marked and recaptures made in each station of each section and in each year can be found in the appendix.

x_i = the number of marked fish captured on the ith day,

and $\hat{N}$ = the estimate of the population size.

This model assumes the following: (1) there is no loss of marks, (2) there is equal mortality of marked and unmarked fish, (3) catchability of marked and unmarked fish does not differ and remains the same, and (4) there is no recruitment into the population or emigration of marked fish from the population. Many studies, notably Shetter (1952), have shown that clipped fins remain identifiable as marks for several years. Thus the first assumption can be accepted, since fin-clips were the type of mark used in the present study. Other studies (Bouck and Ball, 1966; Horak and Klein, 1967) have shown no additional mortality as a result of shocking fish with DC shockers, and Nelson (1960), Stauffer and Hansen (1969), and Brynildson and Brynildson (1967), among others, have shown that the loss of up to two fins does not decrease survival in trout. Therefore, the second assumption can be accepted for the present study. Assumption three is open to a good deal of criticism and the validity of assumption four is, of course, the concern of this study. The degree of spatial stability thus far shown for stream populations of brown trout (Schuck, 1945; Allen, 1951), and the stability found for the population in the present study, do not indicate a complete validation of this fourth assumption.

If this assumption is false, the population estimates would be biased upward to the same degree in both years, and the relative difference would remain approximately the same, assuming the same degree of emigration and immigration in both years. This last assumption then assumes that density has no effect on the degree of movement of the trout, which, of course, is the hypothesis being tested in this study. For purposes of comparing the population estimates, however, we will accept the assumption that emigration and immigration did not vary between years.

Cooper and Lagler (1956) have pointed out also that population estimates of this type are biased downward when all length groups are pooled before estimation. While this bias cannot be completely eliminated, they propose that individual estimates be made for various size groupings and the results pooled. However, the number of size groupings into which mark-and-recapture data can be broken is limited by the numbers of fish of each size group present and the number of recaptures made. In the present study, the number of fish present in the area was small, and the amount of data did not warrant a breakup into size groups. However, it was felt that exclusion of fish under 6-inches in length removed a substantial portion of the bias resulting from pooling. Schuck (1945) found that recapture rates for brown trout over 6-inches in length were very nearly the same but that recapture rates for smaller fish decreased drastically with size.

Additional evidence of a decrease in abundance was the recapture in 1969 of only 24 of the 64 brown trout marked in 1968. Assuming a complete recapture of all marked fish still present in the stream, this represents a mortality of 62.5% of the brown trout over 6-inches in length. This mortality estimate is well within the range of mortalities so far reported for stream populations of brown trout. McFadden and Cooper (1962), in a comparison of six stream brown trout populations, reported annual mortality rates from 44.6% for a stream closed to fishing to 81.1% for a stream where fishing was allowed. Their estimates of mortality, like that of the present study, were based only on age classes I through IV. Mortality of brown trout over 6-inches was 78% over one fishing season in one Wisconsin stream (Brynildson, Hacker, and Klick, 1963), while annual mortality (including emigration) of age II brown trout in the Hinds River, New Zealand, averaged 82% throughout their lives (Lane, 1964).

The 62.5% mortality estimate reported in this paper closely approximates the estimate of the reduction in numbers of trout over 6-inches in total length obtained from mark-and-recapture data (54.4%) and indicates little recruitment into the population over 6-inches in length from 1968 to 1969. Recruitment into the size class over

6-inches in length in 1969 would come mainly from the 1968 year class as indicated in Table 4. In fact, the probability of low recruitment into the 6-inch and greater size class in 1969 is supported by the presence of only one young-of-year brown trout in the 1968 samples as opposed to the 82 captured in 1969. Also, only 15.9% of the estimated 1969 population of brown trout over 6-inches in length were considered to be from the 1968 year class. This 15.9% estimate of the proportion of yearlings in the 1969 population represents 6.8% of the 1968 population, and by subtracting this recruitment estimate from the 62.5% estimated mortality, a 55.7% reduction is indicated; a very close agreement with the previous estimate of 54.4% obtained by comparison of population estimates from the two years. It is apparent, then, that the reduction in numbers of brown trout over 6-inches in total length exceeded 50% from 1968 to 1969.

Age and Size Structure.--Age and growth data obtained from 97 brown trout taken in the study area during August, 1969, are shown in Table 4. The body-scale relationship used to obtain the mean calculated lengths of the fish at each annulus took the form:

$$Y = 2.5078 + 0.5240\ X$$

where Y = total length of the fish in cm,
and X = scale radius in mm x 48.

Table 4.--Age and growth of 97 brown trout taken from the Pine River study area on August 11 and 25, 1969. (means, standard deviations, and ranges in total length are given in that order; all lengths are in centimeters)

Year class	Age class	N	Length at capture	Average calculated length at annulus 1	2	3	4
1968	I	10	19.3	11.0			
			1.96	1.42			
			16.3-22.9	8.8-13.4			
1967	II	30	27.8	10.7	20.6		
			3.32	1.48	2.68		
			20.0-32.6	7.9-13.6	15.2-26.6		
1966	III	55	36.6	11.0	22.1	30.8	
			3.11	1.77	2.99	3.03	
			29.8-43.8	7.5-14.9	16.8-30.6	24.0-38.0	
1965	IV	2	44.2	13.4	26.7	35.8	40.9
			2.97	0.14	2.83	3.11	2.00
			42.1-46.3	13.3-13.5	24.7-28.7	33.6-38.0	38.3-43.5
Grand average length				10.9	21.7	31.0	40.9
				1.66	3.04	3.15	2.00
				7.5-14.9	15.2-30.6	24.0-38.0	38.3-43.5
Number of fish				97	87	57	2
Average increment				10.9	10.7	8.7	5.1
Summed increments				10.9	21.6	30.3	35.4

An approximation of the proportionate age structure in both 1968 and 1969 can be constructed by utilizing the growth histories of the various year classes. Assuming a six-month growth period and linearity of growth from April through September, and no growth from October through March, the mean length and approximate range in length for a given age class can be estimated by back calculation to any previous month in the life of a fish. The assumed six-month growing period appears to be a reasonable approximation in light of the information available. Graham and Jones (1962) reported that brown trout in Llynn Tegid, Wales, grew most rapidly from June to August or September and showed little or no growth from November to March. In Welsh rivers, the period of rapid growth was from March or April to August or September (Thomas, 1964). In a paper perhaps more appropriate to the present study, Beyerle and Cooper (1960) reported that brown trout in Pennsylvania streams obtained half of their annual growth between mid-April and mid-June, with a cessation of growth from December through March. While a six-month growing season may be a reasonable assumption in the present study, a less reasonable assumption is that of linearity of growth during this time, since growth appears to be greater in the spring than during the rest of the growing season. In spite of this apparent error, the resulting approximations appear to be fairly accurate.

The results of these back calculations to the lengths of the various age classes at previous times in their lives, and the numbers and proportions of all marked fish estimated to be in each age class are indicated for both 1968 and 1969 in Table 5. The length ranges shown for each month are calculated for the midpoint of each month. As an indication of the accuracy of these predicted values, the lengths of the young-of-year collected in 1969 can be compared with the back-calculated lengths of the previous year classes during their first summer. Since an overlap in the length frequency distributions for age groups 0 and I did not occur, young-of-year brown trout could be clearly distinguished from age I fish on the basis of length. The range in total length for 81 young-of-year brown trout collected in the study area during the last week of July and the month of August, 1969, was 6.0 - 10.7 cm, which compares favorably with the predicted range of 6.6 - 10.0 cm for the month of August. Comparisons of mean values in this case would be of little value because of the strong selectivity of the shocker for larger specimens.

A problem developed in placing fish in appropriate age groups, since some overlap in predicted total length ranges occurred between age groups. However, few fish fell within these ranges of overlap, and in these cases, the value representing the total length of the fish was

Table 5.--Estimates of the number of marked brown trout in each age class, the percentage of the population contributed by each age class and the ranges in total length for each age class for three months during 1968 and 1969. (all lengths are in centimeters)

1968	Age class 0	I	II	III
Number	0	8	55	1
Percent of population*	0	12.5	85.9	1.6
Length range				
July	5.1-7.8	12.2-21.2	21.0-34.9	36.3-41.2
August	6.6-10.0	13.4-23.4	22.2-36.2	37.1-42.1
September	8.1-12.3	14.6-25.5	23.4-37.4	37.9-43.0
1969	**Age class I**	**II**	**III**	**IV**
Number	13	22	68	2
Percent of population*	15.9	20.7	61.0	2.4
Length range				
June	13.3-19.1	18.1-30.2	27.5-41.5	40.6-45.2
July	14.8-21.0	19.0-31.4	28.6-42.6	41.3-45.7
August	16.3-22.9	20.0-32.6	29.8-43.8	42.1-46.3

*The population as here defined includes only fish greater than 6" in T.L.

located more toward the center of the length frequency distribution of one age group than the other, and the fish was placed in the former age group. For example, the upper limit of the total length range of age II fish was 30.2 cm in June, 1969, while the lower limit of the length range of age III fish was 27.5 cm. A fish 27.6 cm in total length was then placed in age group II, as it was considered more likely that it was an age II fish than an age III fish.

As can be seen from Table 5, the 1966 year class was dominant in 1968, making up almost 86% of the population greater than 6-inches in total length. While this dominance was carried over into 1969, the relative strength of the year class had declined to 61% of the population. The 1967 and 1968 year classes appear to be very weak, but from the number of young-of-year brown trout collected in 1969, another strong year class appears to be in the making. This type of instability has been previously noted in two stream populations of brown trout in New Zealand (Burnet, 1959), and a suspected cause was cannibalism by a dominant year class on young-of-year. When this dominant year class had declined to a low enough level, it was proposed that survival rates of young fish would again increase to produce another dominant year class. Whatever the cause, this same phenomenon apparently also occurs in the Pine River population.

No five year old brown trout were captured in the study area during 1968 or 1969 sampling operations. In fact, trout over four years of age were quite uncommon (Table 5). The growth rates of brown trout in the study area were better than average for U.S. streams (Carlander, 1969), and this is in agreement with the productivity data presented for this area of the Pine River and the nutrient levels found there (Table 1).

Movement and Stability.--During 1968 an intensive study of the movements of brown trout within section B was undertaken. The numbers of fish marked and recaptured in each 200-foot station on each sampling date are shown in the Appendix. The mean time between initial capture and recapture for the 106 recaptures could not be accurately calculated because individual recognition became impossible as more and more fish were added to the marked population. As an indication of the degree of stability of the brown trout population, percentages of the total number of recaptures made within the home station and of recaptures made elsewhere in section B were calculated (Table 6). Home station is here defined as the station where the fish was originally captured and marked. Only about 33% of the recaptures made in section B occurred outside the home stations. To check the validity of this apparent stability, a Chi-square goodness of fit test based on the population density of each station was made on the data.

This procedure has been previously used by Gerking (1953) to determine stability in a stream population of rock bass. It was assumed that if the fish showed no attachment to their home stations, the distribution of recaptures of fish outside their home stations should be proportional to the relative proportion of fish marked in each of the various stations. This assumption then recognizes that some stations supply better habitat for trout than others, since the number of fish marked in each of the stations varied greatly.

Table 6.--Total number and percentage of brown trout recaptures made at given distances from the station of marking in 1968.

	Distance in 200-foot intervals						
	0	1	2	3	4	5	6
Number	71	20	11	2	2	0	0
Percent	67.0	18.9	10.4	1.9	1.9	0.0	0.0

Expected frequencies for this analysis were obtained by first calculating the expected recapture frequencies for each station as a function of the number of fish marked in each station (Table 7). Expected values for each cell in the table represent the product of the corresponding row total for observed and the percentage value found at the bottom of the corresponding column. Then, since the number of trout captured on any one date

Table 7.--Number of recaptures and expected frequencies of recaptures of brown trout from seven stations in the Pine River study area during 1968.

Marking station	Station of recapture 1	2	3	4	5	6	7	Total
1 observed	10	4	0	0	0	0	0	14
expected	1.75	5.47	0.66	1.09	1.97	0.22	2.84	14.00
2 observed	7	41	1	0	0	0	0	49
expected	6.12	19.14	2.30	3.83	6.89	0.76	9.95	48.99*
3 observed	6	1	4	0	0	0	0	11
expected	1.38	4.30	0.52	0.86	1.55	0.17	2.23	11.01*
4 observed	0	0	0	3	1	0	0	4
expected	0.50	1.56	0.19	0.31	0.56	0.06	0.81	3.99*
5 observed	0	0	0	5	7	0	4	16
expected	2.00	6.25	0.75	1.25	2.25	0.25	3.25	16.00
6 observed	0	0	0	0	0	0	0	0
expected	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
7 observed	0	0	2	2	1	1	6	12
expected	1.50	4.69	0.56	0.94	1.69	0.19	2.44	12.01*
Σ exp.	13.25	41.41	4.98	8.28	14.91	1.65	21.52	ΣΣ106.00
Percent of total fish marked	12.50	39.06	4.69	7.81	14.06	1.56	20.31	99.99*

*Deviations are due to rounding errors.

was small and the expected values for some of these stations on some dates were below 1.0, it was necessary to pool the data for each station (Cochran, 1952). The Chi-square test was then applied to these pooled data to compare the observed numbers of trout recaptured at various stations distant from the station of initial capture, or home station (Table 8). The pooling process consisted of

Table 8.--Chi-square goodness of fit of observed recaptures of brown trout to the number expected assuming recaptures to be distributed according to population size in seven stations comprising section B during 1968.

	Distance in 200-foot intervals						
	0	1	2	3	4	5	6
Recaptures observed	71	20	11	2	2	0	0
expected	26.41	21.49	14.73	16.65	7.52	14.86	4.34
deviation	+44.59	-1.49	-3.73	-14.65	-5.52	-14.86	-4.34

$X^2 = 112.47$*** df = (K-1) = 7-1 = 6

X^2 (.005,6) = 18.50

adding both the expected and observed values in Table 7 diagonally. For example to obtain the expected number of recaptures showing no movement in Table 8 (the value under the column headed 0), we would enter Table 7 at cell 1,1 and add all expected values lying on the diagonal ending at cell 7,7. This pooling procedure may be stated in terms of the formula:

$$F_{e_i} = \Sigma F_{e_{ij}}$$

where F_{e_i} = the expected frequency of recaptures made i stations distant from the station of marking (from Table 8),

and $F_{e_{ij}}$ = the expected frequency of recaptures made i stations distant from station j, where j is the station of marking (from Table 7).

The results of this Chi-square goodness of fit test are shown in Table 8. The resulting Chi-square value of 112.47 was highly significant ($X^2_{.005,6} = 18.50$), indicating that the fish did not distribute their movements over the various stations of section B in proportion to the population densities of the stations, but tended to spend most of their time in the vicinity of their home stations over the 81 days of the study.

It should be made clear that this phase of the study was not concerned with movement of brown trout out of the sampling area, but only with movement between stations of section B. That a portion of the population of stream fishes moves rather widely has been suggested by Funk (1955), and this may have been the case during the 1968 phase of the present study. However, one sample was taken from the Pleasant Valley Road bridge to the Blanchard Road bridge, about a half mile upstream from the area of intensive study, during 1968. While numerous trout were taken from the junction of the South Branch to the Blanchard Road bridge, only three recaptures were made outside section B. One of these was made about 500 feet downstream from station B1, while two were made within 25 feet upstream from station B7. No trout were taken below the confluence of the South Branch, making it extremely unlikely that any trout traveled further downstream.

Plans for the study originally included a threefold expansion of the sampling area and a division of the sampling period in 1969. During the first period, a repetition of the 1968 experiment was to be attempted; then, after a decimation of the brown trout population, the second sampling period would begin. This decimation was planned to test the hypothesis that a decrease in density would reduce the degree of movement shown by the remaining fish. During the first phase of the 1969 study, however, it became apparent that the population was already substantially reduced in number from the 1968 level, and thus a further reduction was not warranted. The first study period was then lengthened to encompass an 80 day period, approximately the same length of time as in 1968.

In 1969, the area of intense study was enlarged to include sections A and C, and in addition, one sample was taken from areas D and E. During the course of these sampling operations, 24 trout of the 64 marked in section B in 1968 were recaptured. The distribution of these recaptures was wider than the distribution of the 1968 recaptures, however all were taken within the three study sections. Apparently some redistribution had occurred between September, 1968, and June, 1969. Thirteen of these 24 trout were recaptured in section B and of these 13, seven (54%) were taken in stations other than their 1968 home station. This percentage is considerably greater than the 33% estimate of movement away from the home station in section B during the summer of 1968. Eleven of the 24 recaptured trout had moved into the adjacent sections A and C.

To determine if the population could still be considered to be oriented around the home stations after almost a year of residence, a Chi-square goodness of fit test was applied to these first 1969 recaptures of trout marked in 1968. The method of obtaining expected values was the same as for the previous test of the 1968 data, with the same assumption that the distribution of recaptures was proportional to the relative densities of trout in the 21 stations. The results of this test, shown in Table 9, indicate a significant X^2 value of 27.48 ($X^2_{.01,12} = 26.2$). Thus the trout appear to have restricted their movements over the winter or at least returned to areas occupied during the previous summer.

The mean distance moved by these 24 trout between 1968 and 1969 was 608 feet, with one trout moving 2,400 feet upstream. The net shift shown by the sample was 120 feet upstream, a not too significant shift when it is

Table 9.--Chi-square goodness of fit of observed numbers of recaptured brown trout to the number expected assuming recaptures to be distributed according to population size in 21, 200-foot stations approximately one year after marking.

	Distance in 200-foot intervals												
	0	1	2	3	4	5	6	7	8	9	10	11	12+
Recaptures													
observed	6	6	1	2	3	0	1	3	1	0	0	0	1
expected	1.43	2.37	2.10	1.90	2.59	2.17	2.03	2.52	1.32	1.77	1.03	0.90	1.38
deviation	+4.57	+3.63	-1.10	+0.10	+0.41	-2.17	-1.03	+0.48	-0.32	-1.77	-1.03	-0.90	-0.38

X^2 = 27.48**n.s. df = (K-1) = 13-1 = 12

X^2 (.05,12) = 21.0

remembered that movement was only estimated in 200-foot intervals. There seemed to be a possible tendency for older fish to move to a greater extent than the younger, as 17 fish estimated to be in age group III in 1969 had moved an average of 576 feet, while seven fish estimated to be in age group II had moved an average of only 486 feet. This same phenomenon has been previously observed in brown trout (Allen, 1951), and in various warm-water stream fishes (Gerking, 1953), but quite the opposite was found for stream fishes in Missouri (Funk, 1955). It is sufficient to state here that information is inconclusive on this point at present.

The subsequent movements of these 24 trout were recorded during sampling in 1969 (Table 10). Although recapture data on this small number of fish was limited, approximately 82% of the 33 recaptures made, occurred within 400 feet of the station of first 1969 capture, indicating that the population was still maintaining a relative spatial stability.

During 1969, movement of trout within section B was again studied. The same procedures were also used within sections A and C, allowing an estimate to be made of movement between these contiguous areas. Because both the low number of trout and the 21 different fin-clip combinations used made it extremely unlikely that two fish of the same size would receive the same mark, recognition of individual fish was possible. Therefore, mean time out, or the mean number of days between initial capture and recapture, could be calculated for the recaptures made in 1969.

Table 10.--Total number and percentage of brown trout recaptures in 1969 (exclusive of their first 1969 recapture) of fish marked in 1968, at various distances from the point of first capture in 1969.

	Distance in 200-foot intervals								
	0	1	2	3	4	5	6	7	8-20
Number	18	6	3	2	1	2	0	1	0
Percent	54.5	18.2	9.1	6.1	3.0	6.1	0.0	3.0	0.0

Mean time out, as well as the numbers and percentages of recaptures made in the home station and elsewhere in section B were again calculated, and the same calculations were performed for the recaptures made in sections A and C. Recaptures displaying movement between sections were not considered here so that the results could be compared to the 1968 results. The results of these calculations indicate little difference in the movement patterns of the fish either between different sections or between years (Table 11). It is possible that there was a change in the degree of long-range movement between the two years. In other words, more fish may have moved out

Table 11.--Total number, time out, and percentage of brown trout recaptures made at given distances from the station of marking during 1969. (stations were 200 feet in length)

Section A	Distance in 200-foot intervals						
	0	1	2	3	4	5	6
Number	24	5	4	0	1	0	0
Percent	70.6	14.7	11.8	0.0	2.9	0.0	0.0
Mean time out						23.3 days	

Section B	Distance in 200-foot intervals						
	0	1	2	3	4	5	6
Number	27	6	3	0	1	0	0
Percent	73.0	16.2	8.1	0.0	2.7	0.0	0.0
Mean time out						27.4 days	

Section C	Distance in 200-foot intervals						
	0	1	2	3	4	5	6
Number	18	3	2	2	1	0	0
Percent	69.2	11.5	7.7	7.7	3.8	0.0	0.0
Mean time out						24.9 days	

of the study sections in one year than in the other year. If this were true, it would be expected that fewer marked fish would remain in the sections and that the recapture rate would be less in those sections where emigration of marked fish was the greatest. The recapture rates within the section of original marking were 0.94, 1.24, and 1.37 for A, B, and C respectively in 1969; and 1.64 for section B in 1968. Given that the recapture rate is negatively related to movement of fish out of the recapture area, it is possible to examine the effect of density on the degree of emigration from each of these three sections in 1969. Since the number of fish marked in 1969 declined successively from section A to section C while the recapture rate increased in the same order, it might be assumed that the emigration rate increases with density. The highest rate of recapture, however, occurred in section B in 1968, when the population was at a peak and thus doubt is cast on this assumed relationship between density and emigration rate. Also, it is doubtful if the numbers of fish marked in each of the three study sections in 1969 reflect any 'real' density difference, but more likely reflect a difference in habitat quality of the three sections. These data suggest little change in long-distance movements of brown trout within the study area even with a drastic decrease in density.

Of the total of 120 recaptures of the 84 fish marked in 1969, only 24 displayed movement across sectional lines, and only one recapture was made farther than 1,600 feet from the home station. This one recapture was made 2,600 feet upstream. The percentages and numbers of these 120 recaptures made at various distances from the home station are shown in Table 12. Another Chi-square goodness of fit test was applied to these data, as was done for the 1968 recaptures in section B. The same method of obtaining expected values was used, and the assumption that the distribution of recaptures was proportional to the relative densities of trout in the 21 stations was again tested. Relative densities of fish in each station were again based on the number of trout marked in each station. Expected values can be obtained by utilizing the data in the appendix. The results of this test are included in Table 13. The calculated Chi-square value of 564.74 was highly significant ($X^2_{.005,12} = 28.3$), indicating that trout movements--just as in 1968--were not related to the density of trout in the various stations, but were oriented around the home station.

Table 14 shows the numbers of recaptures observed at various distances from the home station, as well as the expected numbers of recaptures at those distances. In calculating these expected values, it was assumed that the fish had an equal likelihood of moving

Table 12.--Total number and percentage of brown trout recaptured in 1969 at various distances from the point of first capture in 1969.

	Distance in 200-foot intervals														
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14-20
Number	69	18	10	6	6	6	0	2	2	0	0	0	0	1	0
Percent	57.5	15.0	8.3	5.0	5.0	5.0	0.0	1.7	1.7	0.0	0.0	0.0	0.0	0.8	0.0

Table 13.--Chi-square goodness of fit of observed recaptures of brown trout to the number expected assuming recaptures to be distributed according to population size in 21, 200-foot stations during 1969.

	Distance in 200-foot intervals												
	0	1	2	3	4	5	6	7	8	9	10	11	12+
Recaptures													
observed	69	18	10	6	6	0	2	2	0	0	0	0	1
expected	7.60	10.35	7.88	8.01	9.33	9.71	8.84	7.23	6.36	6.47	6.57	6.16	18.37
deviation	+61.40	+7.65	+2.12	-2.01	-3.33	-9.71	-6.84	-5.23	-6.36	-6.47	-6.57	-6.16	-17.37

$X^2 = 564.74$*** $\qquad$ df = (K-1) = 13-1 = 12

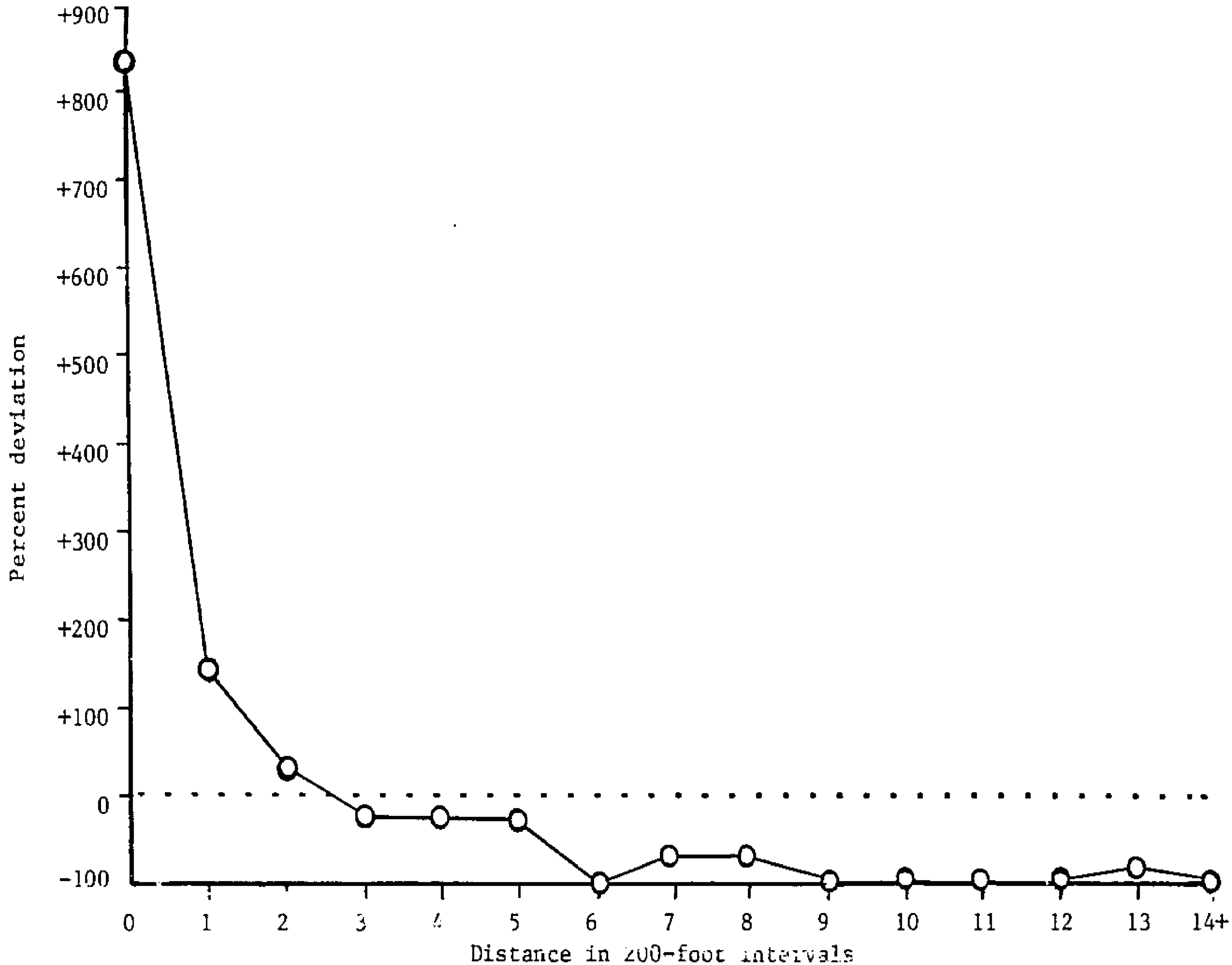
X^2 (.005,12) = 28.3

Table 14.--Expected and observed numbers of recaptures made at various distances from the point of initial capture during 1969.

Distance in 200-foot intervals	Number of marked fish which could be recaptured	Probability of recapture	Expected recaptures	Observed recaptures
0	43.5	0.0621	7.45	69
1	43.5	0.0621	7.45	18
2	43.5	0.0621	7.45	10
3	43.5	0.0621	7.45	6
4	43.5	0.0621	7.45	6
5	43.5	0.0621	7.45	6
6	43.5	0.0621	7.45	0
7	43.5	0.0621	7.45	2
8	43.5	0.0621	7.45	2
9	43.5	0.0621	7.45	0
10	43.5	0.0621	7.45	0
11	40.5	0.0588	7.06	0
12	35.5	0.0508	6.09	0
13	30.0	0.0428	5.14	1
14	27.5	0.0394	4.73	0
15	24.0	0.0343	4.11	0
16	21.0	0.0300	3.60	0
17	16.0	0.0229	2.75	0
18	12.0	0.0171	2.05	0
19	9.0	0.0129	1.55	0
20	5.5	0.0079	0.50	0

either up or downstream, and that the population densities of the stations did not affect their movements. A graph of the deviations between these expected and observed values is shown in Fig. 2. This graph shows that the recapture rate was much greater than expected up to 400 feet from the home station, at which point the observed rate declined to less than the expected rate. About 81% (97) of the 120 recaptures were made within 400 feet of the home station, and 96% (115) were made within 1000 feet. These data agree reasonably well with those of Allen (1951), who found that 92.5% of his recaptures of brown trout occurred within 450 feet of the marking site. His higher value can be at least partially attributed to the small size of his stations (900 feet as opposed to 4,200 feet in the present analysis), whereby fish moving distances greater than 900 feet did not remain in the recapture area, and could only be included in the analysis if they moved far enough to enter another sampling area. From this evidence, as well as from the data presented in the present study, it can be proposed that the usual movements of the brown trout encompass about 400 linear feet of stream, with longer movements being made only occasionally. Of course, these values may not be generally applicable, as the physical features of a particular stream may temper the range of fish movement to a great extent. Fish moving longer distances can be presumed to be in the

Fig. 2.--Percentage deviations of the observed from the expected numbers of recaptures made at various distances from the point of initial capture during 1969.


+900
+800
+700
+600
+500
+400
+300
+200
+100
0
-100
Percent deviation
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14+
Distance in 200-foot intervals

process of either changing their homesites or perhaps to represent the migratory portion of the population suggested by Funk (1955) and Jenkins (1969).

DISCUSSION

A great array of literature on the movement of stream fishes is available. All of these studies have indicated that stream fishes tend to maintain a relative spatial stability, or a tendency to remain in a limited area for periods of several weeks or months. As early as 1936 there was good information on the movement of brook trout that indicated a high degree of spatial stability (Shetter, 1936). Schuck (1945), working in New York, and Allen (1951), working in New Zealand, have recorded spatial stability in populations of brown trout, while populations of cutthroat trout, *Salmo clarki*, have also been shown to display limited movements (Miller, 1957). Shetter (1968), in a long-term study of brook and brown trout movement in three Michigan streams, has shown that movement of the population as a whole is limited even over periods of several years, although individual fish may move considerable distances.

Not all stream studies of fish movement have been limited to cold-water species. Several authors have shown that smallmouth bass display limited movement, even after periods of up to two years (Tate, 1950; Larimore, 1952; Funk, 1955; Brown, 1961; and Fajen, 1962). Linton (unpublished M.S. thesis, Michigan State University Library, 1964) and Gerking (1953) found spatial stability in stream populations of rock bass, and the same phenomenon has been recorded in stream populations of sharpfin chubsuckers, *Erimyzon tenuis* (Gunning and Shoop, 1964), and bluegills and longear sunfish, *Lepomis megalotis* (Gunning and Shoop, 1963).

It has been proposed that this spatial stability in stream fish populations may be a result of territoriality or hierarchy, and that an increase in density above some threshold level may generate a population of transient fish. This would then tend to increase the degree of movement shown by the population as a whole (Gerking, 1953; Jenkins, 1969). However, it appears that a decrease in density of brown trout over 6-inches in total length from an estimated 256 per mile of stream in 1968 to an estimated 106 per mile in 1969 in the Pine River resulted in no change in the degree of movement of this population.

It may be argued that the population in the study area was not, in fact, reduced in 1969, but that the number of young-of-year may have more than made up for the losses of the older fish. Thus a change in the degree of movement of the population would not be expected. Although no estimates of the population of smaller trout were made, the number caught with the electric shocker during 1969 was many times the number caught in 1968. However, even if the losses among the older fish were compensated by the addition of these young-of-year, a change in the movement patterns of the older fish--if it occurred--should still have been observed, since fry are not behaviorally equivalent to larger fish. Braddock (1945) and Greenburg (1947) have shown that size confers an advantage in hierarchies among fish kept in aquaria, while Jenkins (1969) has observed the same effect for territorial brown trout in streams. He also observed that prior residence conferred advantage among these fish. Chapman (1962) has shown the same size advantage among juvenile coho salmon, *Oncorhynchus kisutch*. This size advantage, coupled with the prior residence effect and the differences in habitat utilization between fry and adult salmonids (McCrimmon, 1954) makes it unlikely that fry could alter the movements of larger trout.

If social control is a strong regulatory mechanism in salmonids as has been suggested by Chapman (1966), then as density increased past some threshold level, presumably more fish would be forced to assume a transient role. LeCren (1965) notes that in territorial fishes dispersion may operate in a manner quite similar to mortality. This mechanism might then serve to maintain optimum stocking levels. These ideas seem consistent with the statements of Gerking and Jenkins.

In view of the present data it would appear that the necessary threshold level required for an increased degree of movement was not attained. If this was in fact the case, then we need not reject the hypothesis, and from work that has been completed, rejection seems impossible. Kalleberg (1958) has shown that in stream aquaria, as the density of juvenile Atlantic salmon, *Salmo salar*, increased, the population became divided into two groups: those which held territories and those which were repeatedly chased. The latter group would presumably become transients in a volitional population. The density necessary to cause the development of a transient population was considerably higher than would be expected in most natural populations if the entire area of stream is considered, being greater than 200-250 fry per 10 square feet of bottom area. However, not all areas of a stream can be considered as suitable habitat for young salmonids and it is possible that densities of this magnitude may be reached in natural populations when unsuitable habitats are excluded from consideration.

Indirect evidence that a transient fry population does develop under natural stream conditions is available. Elliott (1966) reported the occurrence of brown trout fry in drift samples, and cutthroat trout fry have been reported as moving downstream in artificial stream channels (Smith, 1944). Chapman (1962) also concluded that aggressive behavior appeared to be a major factor in causing downstream movements of juvenile coho salmon.

A density regulating mechanism of this type has not been demonstrated for adult salmonids to my knowledge, but if it occurs, the threshold level necessary to generate a transient population is likely never attained in an adult brown trout population in nature. If this is true, our hypothesis must be revised to include only the younger segment of the population. Social regulation of numbers would then be expected to occur only among the young fish. Competition for territories among the fry would result in movement of the excess fish to less favorable habitats where they would be subject to additional hazards. As growth occurred and new habitats were required, the fry would be thrown into competition with older fish. Since size and prior residence confer strong advantages on the older fish in contests for territory, the extent of recruitment of the younger fish into the adult population would appear to offer a further opportunity for social regulation to occur. The excess portion of young fish would then be forced to assume the role of transients. After these initial adjustments have taken place, the regulation of density in the population may depend upon the gradual dispersal of the older trout as was demonstrated in the present study. This would be necessary to compensate for the increased biomass resulting from growth. Jenkins (1969) has indicated this phenomenon in brown trout. In enclosed sections of artificial streams, he observed what he termed "roaming" in individual fish. In this behavior, which occurred spontaneously and for no apparent reason, a fish would be seen to leave his refuge and roam over the entire channel. It is probable that these fish would have left the enclosure if they had been given the opportunity. In observations in the Owens River, he observed that territorial fish maintained their territories for periods of from 5 to 70 days, but eventually left the observation area and did not return. No fish remained in the area throughout the entire period of observation. These periodic shifts of territory may be explained by the changing requirements of fish as they grow larger (Chapman, 1966). Further credence for this explanation of adult trout movement is lent by the remark by Miller (1957) that repopulation of poisoned sections of streams by adult cutthroat trout was quite slow. It has also been found that transient coho salmon fry were smaller than the residents (Chapman, 1962), and numerous authors, notably Chapman (1962) and Kalleberg (1958) have shown that despotic fish in hierarchies or successful territorial fish grow more rapidly than subordinates or refugees. The primary direction of movement of these transient fry is downstream and thus if a transient adult population were present it would be expected that a trend toward downstream movement would be detected. This was not the case in the present study, nor has it been the case in any other study of trout movement that I have encountered.

It is important here to recognize that this territorial shifting, which is proposed to account for the movements of the adult members of the population, may be an individual response to physical environment or food requirements, and not a result of contest for territory. In this context, density would play no role in effecting this movement.

If this line of reasoning is continued, it follows that the pioneering role of brown trout populations would fall primarily to the excess young which have been forced to assume a transient role, thereby minimizing the danger of losses to the mature, reproducing segment of the population.

In Jenkin's 1969 paper he mentions that he found a transient group of fish among the adult population in the Owens River. He was at a loss to explain where they might have come from or why they should exist. It is possible that these fish are the survivors of the group displaced at a younger age, but this is unlikely. Larkin (1956) has suggested that these transients would be most susceptible to predation because of their slower growth rates. Assuming a benign environment, some survival of transient fry may occur, however such a benign environment is difficult to conceive of for a fish species which has been reported to sustain annual losses of at least 40%. Jenkins indicated that a few of the transients were successful in displacing territorial fish, and thus there may have been some sort of equilibrium reached between the transients and territorial segments of the population whereby members of each group shifted their roles for a period of time. The smaller number of transient fish which were successful in displacing territorial fish would seem to obliterate this possibility. A further possibility exists, however, which appears to be the most likely explanation to account for these transient adults. This possibility is that the 'transients' observed by Jenkins may not have been free-roaming fish, but actually may have been territorial fish which were in the process of shifting territories. Jenkins stated that these 'transients' made up between 20 and 30% of the total population, which agrees quite well with the range of percentages (27-33) for recaptures showing movement in the present study. These recaptures were oriented around the sections of original capture, and thus cannot be considered as free-roaming fish. This may have also been the case with the 'transients' mentioned in Jenkin's paper.

It is concluded that if social regulation of density occurs among stream-dwelling brown trout populations, it must be operative only among the younger fish, reaching its peak soon after the fry emerge from the gravel, and gradually declining in importance as the fish become larger. This mechanism would then serve to pass the pioneering role down to the younger fish and reduce the hazards to the older, reproducing segment of the population. Strong social regulation during the fry stage would also function to reduce the degree of competition among the older fish, and thus increase the efficiency of energy utilization. The annual production of fry would then serve two useful purposes: recruitment into the population, consistent with optimum usage of the available habitat; and pioneering of areas of potentially new habitat. The necessary but dangerous task of pioneering would thus require only a minimum expenditure of energy. Social regulation may be proposed to insure that these dual functions are fulfilled with a minimum loss of energy to the population.

SUMMARY

1. Although information on changes in the fish population in the study area is limited, samples taken during 1968 and 1969 indicated an increase in the abundance of river chubs and brook trout in 1969 and a decline in abundance of larger white suckers.
2. Brown trout over 6-inches in total length declined in abundance from an estimated 256 per mile of stream in 1968 to an estimated 106 per mile in 1969. The reason for this decline was apparently due to a low recruitment from the 1968 year class.
3. The 106 recaptures recorded in 1968 from one 1400-foot stream section indicated a pronounced tendency for trout over 6-inches in total length to limit their movements during the summer.
4. Movement of trout over 6-inches in length during the summer of 1969 was again limited, as shown by the locations of the 97 recaptures of trout marked in 1969.
5. The locations of the first 1969 recaptures of 24 trout marked in 1968 indicated that the fish either moved very little over the winter or returned to areas occupied the previous summer. Further recaptures of

these 24 trout during the summer indicated that their movements had again become limited.

6. The patterns of movement of trout within the three sections sampled in 1969 did not differ from each other or from the movement pattern recorded for trout recaptured within one section sampled in 1968.
7. Apparently the decrease in the density of trout over 6-inches in length which occurred in the study area from 1968 to 1969 did not alter the movement pattern of the population of trout over 6-inches in length as was expected.
8. It is suggested that a positive relationship between density and the degree of movement shown by brown trout populations exists, and that this relationship acts as a density regulating mechanism by increasing emigration at higher densities. The mechanism probably acts primarily among the fry and becomes considerably diminished in effect by the time the fish reach 6-inches in length. This mechanism would then act to conserve energy and insure adequate reproduction within the population.

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APPENDIX

Numbers of brown trout marked and the numbers recaptured in the seven stations comprising section B on each sampling date during 1968. (numbers in parentheses represent recaptures)

Date	Station 1	2	3	4	5	6	7
July 6	5	14	2	1	6	1	9
July 16	1 (3)	6 (3)	0 (1)	1 (0)	0 (2)	0 (0)	1 (1)
July 19	1 (2)	2 (3)	1 (1)	1 (0)	0 (5)	0 (0)	1 (1)
July 23	0 (0)	0 (6)	0 (1)	1 (0)	0 (0)	0 (0)	2 (1)
Aug. 6	0 (0)	1 (2)	0 (1)	0 (0)	2 (1)	0 (0)	0 (0)
Aug. 19	0 (2)	1 (7)	0 (2)	0 (0)	0 (0)	0 (0)	0 (1)
Aug. 27	1 (2)	1 (7)	0 (1)	1 (0)	0 (2)	0 (0)	0 (2)
Sept. 11	0 (1)	0 (7)	0 (1)	0 (2)	1 (3)	0 (0)	0 (1)
Sept. 17	0 (2)	0 (6)	0 (2)	0 (1)	0 (2)	0 (0)	0 (3)
Sept. 25	0 (2)	0 (7)	0 (1)	0 (1)	0 (1)	0 (0)	0 (2)
Total	8 (14)	25 (48)	3 (11)	5 (4)	9 (16)	1 (0)	13 (12)
Grand total	64 (105)						

Numbers of brown trout marked in each station and the numbers of recaptures of fish marked in each station in the seven stations comprising section A on each sampling date during 1969. (numbers in parentheses represent recaptures of fish marked in section A in 1969, underlined numbers represent marked fish recaptured in other sections)

Date	Station 1	2	3	4	5	6	7
June 2	4	4	0	1	3	2	3
June 9	2	0	0	2	1	2	0
	1 (2)	(2)	(0)	(1)	(1)	(2)	(3)
June 16	1	1	1	0	0	0	2
	(2)	(0)	(0)	(3)	(1)	(0)	(1)
June 23	0	0	0	0	0	0	1
	(0)	(0)	(0)	(0)	(0)	(0)	(0)
July 9	0	0	0	1	0	1	0
	1 (0)	(0)	(0)	(0)	(1)	(0)	(1)
July 14	0	0	0	0	0	0	0
	(0)	(0)	(0)	(0)	(1)	(0)	(0)
July 22	0	0	0	0	1	0	0
	(1)	(1)	(0)	(0)	(1)	(1)	(1)
July 28	0	0	0	0	0	0	2
	(0)	(0)	(0)	(0)	(0)	(1)	(1)
Aug. 5	0	0	0	0	0	0	0
	(1)	(0)	(0)	(0)	(0)	(1)	(2)
Aug. 21	0	0	0	1	0	0	0
	(0)	(0)	(0)	(0)	(0)	(0)	(2)
Total	7	5	1	5	5	5	8
	2 (6)	(3)	(0)	(4)	(5)	(5)	(11)
Grand total	36 (34) 2						

Numbers of brown trout marked in each station and the numbers of recaptures of fish marked in each station in the seven stations comprising section B on each sampling date during 1969. (numbers in parentheses represent recaptures of fish marked in section B in 1969, underlined numbers represent marked fish recaptured in other sections)

Date	Station 1	2	3	4	5	6	7
June 2	1	3	3	3	1	1	3
June 9	0 (1)	1 (1)	3 (0)	0 1(1)	3 (1)	1 (0)	1 1(2)
June 16	0 1(0)	1 (0)	0 1(2)	0 (1)	0 (1)	1 1(1)	0 1(1)
June 23	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 1(0)
July 9	0 (0)	0 (3)	0 (1)	0 (0)	0 (2)	0 (0)	0 (1)
July 14	0 (0)	0 (1)	0 (0)	0 (1)	0 (1)	0 (0)	0 (0)
July 22	0 (0)	2 (2)	0 2(0)	0 (1)	0 (1)	0 1(1)	0 (0)
July 28	0 1(0)	1 (3)	0 3(0)	0 (0)	0 (0)	0 (1)	0 (0)
Aug. 5	0 (0)	0 1(2)	0 1(0)	0 (0)	0 (0)	0 1(1)	0 (0)
Aug. 21	0 1(0)	0 (0)	0 2(0)	0 (0)	0 (1)	0 (1)	0 (0)
Total	1 3(1)	8 1(12)	6 9(3)	3 1(4)	4 (7)	3 3(5)	4 3(4)

Grand total 29 (36) 20

Numbers of brown trout marked in each station and the numbers of recaptures of fish marked in each station in the seven stations comprising section C on each sampling date during 1969. (numbers in parentheses represent recaptures of fish marked in section C in 1969, underlined numbers represent marked fish recaptured in other sections)

Date	Station 1	2	3	4	5	6	7
June 2	1	2	1	2	3	0	0
June 9	1 (0)	0 (2)	0 (1)	1 (0)	3 (2)	0 (0)	0 (0)
June 16	0 $\underline{1}$(0)	0 (1)	0 (0)	0 (1)	1 (3)	0 (0)	0 (0)
June 23	0 (1)	0 (1)	0 (1)	1 (0)	0 $\underline{1}$(1)	0 (0)	0 (0)
July 9	0 (0)	0 (0)	0 (0)	0 (0)	0 (2)	0 (0)	0 (0)
July 14	1 (0)	0 (0)	0 (0)	0 (1)	0 (2)	0 (0)	0 (0)
July 22	0 (0)	0 (0)	0 (1)	0 (1)	1 (1)	0 (0)	0 (0)
July 28	0 (0)	0 (0)	0 (0)	0 (0)	0 (2)	0 (0)	0 (0)
Aug. 5	0 (0)	0 (0)	0 (0)	0 (0)	0 (1)	0 (0)	0 (0)
Aug. 21	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)	0 (0)
Total	3 $\underline{1}$(1)	2 (4)	1 (3)	4 (3)	9 $\underline{1}$(15)	0 (0)	0 (0)

Grand total 19 (26) $\underline{2}$