

EVIDENCE FOR THE CONCEPTS OF HOME RANGE AND TERRITORY IN STREAM FISHES¹

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INTRODUCTION

The size and structure of fish populations have received much attention in recent years. Contributions in this field have provided ideas concerning the theory of animal populations as well as a sound basis for the management of sport and commercial fishing. Among the factors influencing fish populations, most study has been accorded food, feeding habits, reproductive behavior, reproductive potential, growth, and mortality. The fish population has been considered an aggregate of animals in most studies of this sort. Very little attention has been given to the interaction between individuals of a fish population and to the effect such interaction might have on the size and structure of the group. The present work attempts to interpret a population of stream fishes as the result of competition among the individuals of which it is composed. The movements of the fish have been followed in detail and the possible importance of these activities is discussed.

Evidence will be presented to show that many stream fishes live in very restricted areas during most, if not all, of their lifetime. The movements of fish will be considered from two viewpoints: (1) home range, and (2) territory. Home range is a term borrowed from the mammalogists who have found that many mammals live within rather narrowly circumscribed limits. Such small mammals as the meadow vole, woodland deer mouse, woodmouse, and chipmunk

have received most attention in this respect, but even larger species like the coyote and rabbit have shown a similar pattern though on a larger scale. Although the home range is a well-recognized phenomenon among mammals, it has been defined in many ways. Burt (1943) defines home range as "the area, usually around a home site, over which the animal normally travels in search for food." This is an acceptable definition of the term in many respects, but the element of the "search for food" is over-emphasized. The main purpose of many activities may not involve the search for food. The home site implies a nest, a burrow, or some other attraction for the animal. Many animals have no such attraction during times when they are not breeding and yet confine their movements to restricted areas. For these reasons, home range will be redefined as "the area over which the animal normally travels." This is the same definition that Hayne (1949) used in his discussion of the calculation of the size of the home range.

The concept of territory had its beginnings in ornithology (Altum 1868), and the bulk of the work has been confined to these animals. The writer will use the term territory as Noble (1939) did: "Territory is any defended area." Nice (1941) accepted this definition. According to Allee *et al.* (1949), "territoriality includes homing or the defense of a given area or both." The writer believes that homing and the defense of an area are distinct phenomena, motivated by different stimuli. Noble's definition is preferred because it does not confine the idea of territory to the reproductive season, to one sex, or to animals of a specified age.

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To distinguish between home range and territory it must be emphasized that defense of a territory is the aggressive response of an animal for the protection of an area from invasion. Home range implies no aggressive action. When territory and home range boundaries coincide, the term "territory" should be used.

Aggressive behavior is very common and widespread among vertebrates (Collias 1944), and may be expected to be observed whenever the behavior of a number of individuals is studied. Burt (1943) rightly points out, however, that territoriality cannot be assumed, but that the aggressive behavior must be observed. It has not been possible to observe such behavior among the fishes in the murky southern Indiana streams, although it may be expected to occur on the basis of Greenberg's (1947) studies with the green sunfish. An experiment was designed to test this assumption in lieu of direct observational evidence.

Home range is a new concept as applied to fish behavior, but it has been realized that fishes have reproductive territories ever since the habits of nest-building fishes, particularly the sunfishes, began to be studied seriously. Breder (1936), Reighard (1920), Langlois (1936, 1937), Raney (1940) and many others have described this behavior. Ter-

ritory is considered here in a more general sense inasmuch as the experiments were conducted after the main spawning period. The term "home range" will be used when the behavior of the fish can be interpreted as a response not necessarily attributable to aggressive action. Territory will be associated with responses which can be interpreted as an indication of aggressive action. Home range and territory were not sharply distinguished by the field procedure that was used.

DESCRIPTIONS OF THE CREEKS

Richland Creek, a bedrock stream in Greene County, Indiana, was described in a previous paper by the writer (1950), who found its population to be stable during one summer in spite of the stress of a flash flood. Floods and high water have been typical during four years of observation. The portion of the stream selected for these studies is characterized by two main pool areas separated by a shallow riffle, 242 feet long. The extremities of the experimental area were bounded by other riffles. The site was selected because it was felt that the long riffle, designated as section D, would be a mechanical barrier to fish moving between the two pools. The downstream pool was subdivided into two sections, designated A and B, 242 and 184 feet long respectively. The upstream pool was also divided into two sections called E and F (Fig. 1), 246 and 117 feet long. The designation of section C has been changed since the previous report. This section, a 40-foot portion of the long riffle immediately above section B, has been included in section B because it has developed pool characteristics.

Stott's Creek, in Morgan County, Indiana, was investigated in order to compare the results of similar experiments of one-summer duration performed on creeks with different biological and physical characteristics. Biologically, Richland Creek and Stott's Creek were dissimilar in the species composition of the

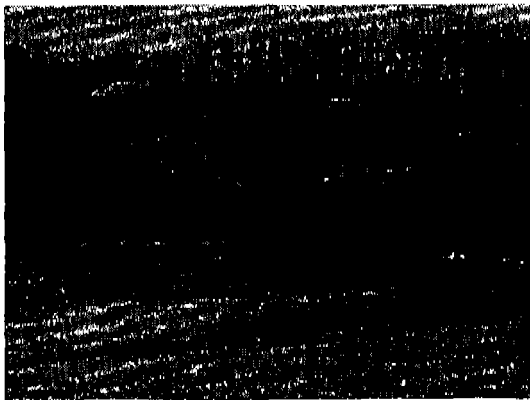


FIG. 1. A view of section F, Richland Creek, Greene County, Indiana. Rock outcrop can be seen on the hillside. A rock face about 15 feet high, shown on the extreme right, has been exposed by stream action.

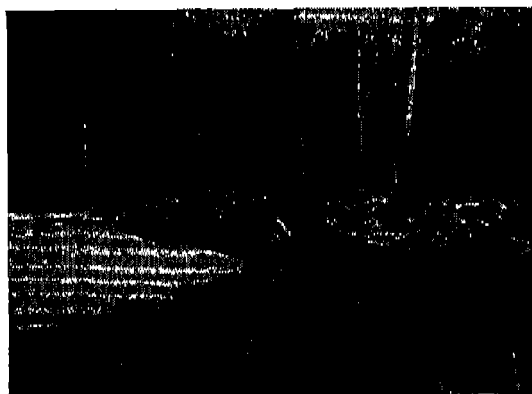


FIG. 2. A view of section A, Stott's Creek, Morgan County, Indiana. The sand and gravel nature of the stream is illustrated by the bar at the left. The stream meanders a great deal, being deflected by abundant stream debris.

fish fauna and in the relative abundance of species common to both creeks. Physically, the two streams diverged widely. Stott's Creek flows through the broad White River Valley in glaciated country. Its gravel and sand bottom is advantageous for a distinct riffle-pool development (Fig. 2). Fallen trees, stumps and logs make the pools small and deep. The stream bed shifts greatly from year to year, but the characteristics of the pools and riffles remain relatively constant for a summer season. The pools are almost isolated during low water, but there are several opportunities each summer for fish to move because the creek rises rapidly after a moderate rain. The bedrock bottom of Richland Creek makes it much more resistant to change from year to year. Its pools are longer and in general are less well defined than the pools in Stott's Creek.

EXPERIMENT I—YEAR-TO-YEAR MOVEMENT

Design of Experiment I

All experiments to be described here have a common rationale. If fish are marked distinctively in a given section of stream and are caught in the same section at some later time, it is assumed that the fish have confined their activities

to that particular section. Conversely, if a fish is found in a section some distance away from its point of original capture, it is considered to have moved from the particular section where it was marked. In the first case, the fish will be called "home" fish and in the latter case they will be called "stray" fish.

Richland Creek. The fish were marked by removing a pectoral or ventral fin. Fish in section A were marked LP (left pectoral fin removed); section B fish were marked RP; section E fish were marked LV (left ventral fin removed); RV was the mark used in section F. No difficulty was encountered recognizing missing fins as long as four years after the fish had been marked. All fish were captured with the electric fish shocker by working subsections about 60 feet long that had been blocked off by nets with $\frac{1}{2}$ inch mesh. A similar method was described by Shetter (1948), and our modification is described by Gerking (1950).

Fish were marked in late June of 1948 and an attempt was made to recapture them in early August of the same year. The area was traversed again in early July of 1949 when recaptures were sought and more fish were marked in the manner previously described. Mid-July of 1950 dated a similar operation, but individuals were not marked in that year. Late July of 1951 was the last time the stream was examined in this connection. Thus, in August of 1948, recaptures were being sought from fish marked in June of the same year. In 1949, individuals which had been marked in 1948 were sought. In 1950, the 1948 and 1949 marks were subject to recapture and the same was true in 1951. Although a different time element prevailed between the time of marking and the time recaptures were made in different years, the data are homogeneous enough for direct comparison.

A part of the data from the 1950 paper is incorporated into the analysis and in-

terpretation of results to be presented here.

Stott's Creek. The Stott's Creek experiment was planned similar to that above. The area was subdivided into four contiguous sections (A, B, C, and D). Each section contained 2 small pools separated by shallow riffles. Section A was 460 feet long; section B was 300 feet long; section C was 500 feet long; and section D was 640 feet long. Each section was at least twice as long as the Richland Creek sections.

Fish were caught by the electric fish shocker and were marked in the same way as described for Richland Creek. Marking took place July 15–22, 1949 and the search for recaptures was made August 18–24 of the same year. The Stott's Creek data will be referred to briefly for comparative purposes.

Experimental errors

Systematic errors

1. The 1950 paper pointed out that fin-clipping might influence the fish so that their movements might not be normal. The assumption that fin-clipped fish behave normally is fundamental to the interpretation of the data. To test this assumption, the movement of fin-clipped fish was compared with that of a group of fish made recognizable by an india ink tattoo mark which avoided amputation. Aquarium fish showed no harmful effects from this kind of mark, but the tattoo mark faded in three weeks. Thus, the time between marking and recapture in the field experiment was limited to two weeks.

An experimental area in Stott's Creek, several hundred yards upstream from the one already described, was divided into three sections. Fish of several species studied in both Richland Creek and Stott's Creek were captured with the electric shocker and marked distinctively in the three sections: 109 fish were fin-clipped and 69 were tattooed. Two fins were removed instead of the custo-

mary one, in order to elicit a maximum response to the effect of fin removal. A greater proportion of the tattooed fish moved, but a test of independence (Snedecor 1946) between the two classifications indicated that the difference between them could be accounted for by random sampling from a homogeneous population (Table I). As a result of this test more confidence can be placed in the assumption that the movement of fin-clipped fish is representative of normal fish.

2. There is a possibility that fish which have been subjected to an electric field behave differently than those which have not received such treatment. This source of error is subject to experiment, but an attempt to measure it was unsuccessful because of our inability to capture enough fish by netting to make the test conclusive. During the four years that the electric shocker has been operated in Indiana, no difference in behavior between shocked and normal individuals has been observed in the field, and in laboratory aquaria no behavioral differences have been noticed between fish caught by shocking and netting. Consequently, the effect of shocking on the movement of marked fish is considered to be negligible.

3. The most important error in the analysis involves the fish which have strayed completely away from the study area. These fish should be included among the strays, but circumstances prevented a thorough search for them in Richland Creek. A pool 15 feet deep was present a short distance downstream

TABLE I. *A comparison of the movements of fish marked by fin-clipping with those marked by tattooing in 3 sections of Stott's Creek*

Type of mark	Home	Stray	Total
Fin-clip	32	3	35
Tattoo	14	4	18
Total	46	7	53

$$\chi^2 = 0.884 \text{ with 1 d.f., } p = .40.$$

from the study area, and a long stretch of water 6-8 feet deep was adjacent to the upstream end of the area. A search was made below the deep downstream pool the first three years, and only one rock bass originally marked in the study area was discovered during this time.

A rough estimate of the number of fish that left the experimental area can be made from the composition of the known strays. In the extreme sections, A and F, fish could have escaped sampling by moving only a short distance. The 32 strays of all species which remained in the experimental area might have been matched by an equal number which escaped from the area by moving in the opposite direction. Those in sections B and E had to move at least twice as far to escape the sampling area. Six fish from sections B and E were known to have strayed at least two sections away from the place where they were marked, and an equal number might have escaped. But the riffles at the extremities of the experimental area could have acted as barriers to fish movement as the long riffle between sections B and E did. Seventeen of a total of 80 strays crossed the long riffle during four years of observation. This can be considered as a rough measure of the resistance of the riffle to fish movement. An estimated $32 + 6 = 38$ fish might have escaped if there had been no riffle at each end of the area, so $17/80 \times 38 = 8$ fish which might have been recaptured had they not escaped from the experimental area. This amounts to 2.5 per cent of the total number of recaptures caught during this time, which may well be an underestimate. Probably the loss of marked fish amounts to no more than 5 per cent of the number of recaptures. This unavoidable error does not affect the main conclusions of the experiment.

4. The use of arbitrary boundaries between stream sections places the investigator at a slight disadvantage because some fish might have home ranges which

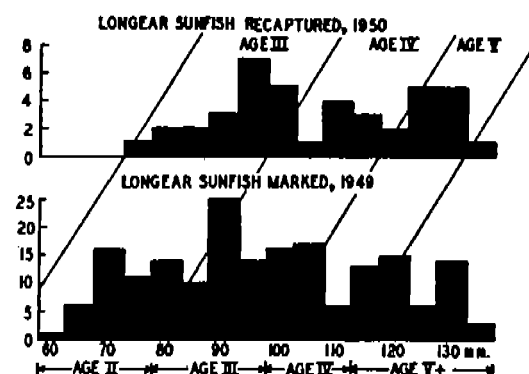


FIG. 3. Length frequency distribution of longear sunfish marked in 1949 and recaptured in 1950 in Richland Creek. Age determinations were made by the scale method on a sample of fish from the experimental area of the creek.

coincide with a boundary. These might be classed as strays even though they were exhibiting the same movements as home fish. This difficulty was unavoidable.

Sampling Errors

1. Not all species are represented by equal numbers among the fish marked and recaptured due to a difference in their relative abundance in the stream. The data to be presented are, therefore, not equally reliable for all species. In order to overcome this difficulty, the movement of each species has been analyzed statistically.

2. Since the electric shocker is not equally effective on all sizes of fish, the data are not applicable over the complete size range of a particular species. Large fish are the more easily collected. The fish marked and those recovered (Fig. 3) include an undue proportion of the older year classes.

3. It becomes more and more apparent that the electric fish shocker is not a random sampling device. Such factors as water conductivity, murkiness, depth, amount of stream debris, and persistence of the workers affect the size and quality of any sample. These factors can change from year to year or, in respect to the

workers' persistence, may change during one day's or week's operation. This error becomes important in population estimates but will not affect our observations on fish movement.

Species with restricted home range

Longear sunfish (*Lepomis megalotis*)

The longear sunfish is a very abundant, if not the most abundant, centrarchid fish in the smaller mid-western streams. It generally lives in quiet pools rather than in swift currents. Like the other centrarchids, it is a nest-building species. The main spawning is in May and June, although some breeding can be observed throughout the summer.

Richland Creek. The marked fish were distributed quite evenly in 3 of the 4 stream sections; there were fewer marks in section F because it was the shortest (Table II). Ages II, III, IV, V, and possibly a few age VI were included among the marked fish (Fig. 3). Because the size range of the different ages overlaps considerably, the age boundaries shown in the figure are arbitrary. Very few longears live more than five years, so that the five-year-old fish marked in any year have practically all disappeared from the population by the next year. By the same token, it was necessary to mark many small fish (age II), in order to insure a sufficient number of recaptures the following year.

The chi-square method can be used to test the hypothesis that the marked fish, as represented by the recaptures from all four years, distributed themselves at random throughout the area after being re-

TABLE III. Number of longear sunfish recaptured in Richland Creek during four years

	Population percentage	Area of recapture			
		Section A	Section B	Section E	Section F
Section A Fish marked LP	32.8	27	10	1	0
Section B Fish marked RP	28.7	11	41	1	1
Section E Fish marked LV	27.0	1	1	73	6
Section F Fish marked RV	11.5	0	0	3	15

$$\chi^2 = 350.41 \text{ with 12 d.f., } p = <.01.$$

leased (Table III). If the marked fish moved at random in the area, they could be expected to be distributed in relation to the population in each section. For each section Petersen-type population estimates (Ricker 1948) have been expressed as percentages of the total population for the whole area (the actual population size is not necessary for the analysis). The number of recaptures, associated with each kind of mark, which could be expected to occur in each section on the basis of random distribution of the marked fish, can be calculated and the χ^2 test performed. The χ^2 value of 350.41 with 12 d. f. (degrees of freedom) is far above the 1 per cent level of significance ($\chi^2_{.01} = 26.22$ with 12 d. f.). It is concluded that the marked fish did not move at random after they were released. Consistent results were obtained in the analysis of each year's recaptures.

Since the marked fish did not move at random after their release, the question arises as to the nature of their distribution. There was very little interchange between the two large pool areas. Only 5 of the 191 recoveries moved across the long intervening riffle during the four years' observations. A somewhat greater interchange between sections within each of the long pool areas occurred, but by far the majority of longears were found within 100-200 feet from where they were originally marked. The concentra-

TABLE II. The distribution of marked longear sunfish in a 0.2 mile region of Richland Creek

Year	Section A LP/	Section B RP	Section E LV	Section F RV	Total
1948	94	123	86	31	334
1949	45	42	57	44	188
Total	139	165	143	75	522

tion of recaptures diagonally across the table demonstrates that most of the fish were caught in the section where they were first found. Home fish made up 81.7 per cent of the total number of recaptures. A calculation of χ^2 for the fish in sections A and B showed that they did not move at random in the downstream pool ($\chi^2 = 27.17$ with 2 d. f., $\chi^2_{.01} = 9.21$ with 2 d. f.). A similar value of 43.01 for the fish of sections E and F shows that there would be less than one chance in 100 that this distribution could have resulted from a random movement of the fish in the upstream pool. It is concluded that the majority of longear sunfish, living in a small bedrock stream, confine their activities to about 100–200 feet.

Stott's Creek. Longear sunfish were not as abundant in Stott's Creek as in Richland Creek. Sixty-seven of various sizes were marked and 12 were recaptured one month later. Of those recaptured, 11 or 80.1 per cent remained in the same section where they had been marked. This sample compares favorably with Richland Creek. Since Stott's Creek has different physical characteristics from Richland Creek, it becomes very probable that this behavior of longear sunfish is not confined to one particular stream. The tendency for most longear sunfish to limit their activities to rather small areas may hold throughout the range of the species.

Rock bass (*Ambloplites rupestris*)

Rock bass were not as numerous as the longear sunfish in either stream. They generally live in quiet pools or

TABLE IV. The distribution of marked rock bass in a 0.2 mile region of Richland Creek

Year	Section A LP	Section B RP	Section E LV	Section F RV	Total
1948	22	21	25	8	76
1949	8	16	14	10	48
Total	30	37	39	18	124

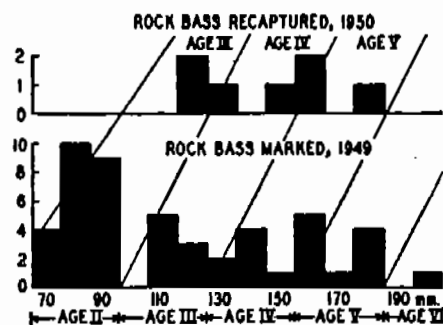


FIG. 4. Length frequency distribution of rock bass marked in 1949 and recaptured in 1950 in Richland Creek. Age determinations were made by the scale method on a sample of fish from the experimental area of the creek.

around rocks and other sheltering obstructions. Rock bass construct nests and spawn principally in early spring.

Richland Creek. Fewer rock bass were marked in section F than the other sections where the number of marks were about equal, averaging 35 per section (Table IV). Fish of ages V and VI which were marked in 1949 had disappeared from the population by 1950, presumably by natural mortality (Fig. 4).

Rock bass had the same pattern of distribution as described for the longear sunfish (Table V). The χ^2 value of 155.00 (12 d. f.) indicates that the fish did not move at random in the experimental area. Only one rock bass which had moved across the long riffle was taken in four years. The experiment demonstrated a real tendency for rock bass to remain within 100–200 feet of

TABLE V. Number of rock bass recaptured in Richland Creek during four years

	Population percentage	Area of recapture			
		Section A	Section B	Section E	Section F
Section A Fish marked LP	15.3	6	1	0	0
Section B Fish marked RP	56.0	1	7	0	0
Section E Fish marked LV	17.0	0	0	15	1
Section F Fish marked RV	11.7	0	1	2	0

$$\chi^2 = 155.00 \text{ with 12 d.f., } p = <.01.$$

their original location from year to year. The marks LP, RP, and LV were concentrated in the section where they were first caught. Only 3 rock bass marked RV were taken and these were all strays; 2 were caught in section E and one in section B.

Stott's Creek. Nine rock bass were caught and marked in Stott's Creek. Three of these were recaptured and all 3 were found in the section where they were marked. This limited information agrees with the main conclusion above, *i.e.*, that rock bass have a restricted home range. This phenomenon seems to occur in more than one stream.

Green sunfish (*Lepomis cyanellus*)

The green sunfish reaches its greatest abundance in small bodies of standing water, and is less frequent in small streams. It spawns principally in the spring.

Richland Creek. The green sunfish was too scarce in Richland Creek to obtain adequate numbers for positive judgment concerning their movement behavior, but the available information suggests that they moved very little. In 1948, 6 of 8 recaptures were in the same area where they had been marked 42 days previously. In another Richland Creek experiment to be described later, 10 of 11 recaptures remained at home during the summer. This behavior parallels that of the rock bass and longear sunfish very closely, and the tendency for the green sunfish to remain in a restricted area appears to be real. The principal restriction that should be placed on the conclusion is that the observations were conducted over a one-summer period and cannot be regarded as a year-to-year phenomenon as can that of the longear sunfish and rock bass.

Stott's Creek. No conclusion can be reached regarding the behavior of the green sunfish in Stott's Creek since only 2 of 20 marked there were recaptured. One of these was found at the place of

original discovery and the other had moved one section away from its original point of capture.

Species with a larger home range

Smallmouth bass (*Micropterus dolomieu*)

Individuals of this sport fish weighing two pounds were caught in Richland Creek, but they reach greater size elsewhere. The smallmouth bass is more abundant in larger streams with a fast flow of water. It builds nests and spawns principally in the spring. In contrast to the insect larvae, small snails and the like that longear and green sunfishes feed upon, the mature smallmouth bass feed upon larger animals, such as other fishes and crayfish.

Richland Creek. The marked fish used to judge the movement of smallmouth bass ranged in size from 106 to 305 mm fork length and averaged 179 mm. A tabulation of the recaptures similar to that for the longear sunfish and rock bass indicated that they were not moving at random in the experimental area ($\chi^2 = 27.11$ with 12 d. f.), but the pattern of distribution was distinctly different. Of 11 recaptures which had been originally marked in sections A and B, 5 were found in their home section and 6 had strayed. In sections E and F, 5 of 8 recaptures had remained in section E where they were originally marked and 3 had strayed to another section. The smallmouth bass obviously did not confine their activities to areas as small as the other sunfishes. However, all species need not have home ranges of the same size. Even the smaller sunfishes may not all have home ranges of the same size, but under the conditions of the experiment it was only possible to demonstrate its presence or absence in a distance of 100–200 feet.

Since the stream was divided into two pool areas separated by a long riffle, it is possible to reclassify the data; the two sections A and B can be combined to form the downstream pool (now called

TABLE VI. *Number of smallmouth bass recaptured in Richland Creek during four years*

	Popula- tion per- centage	Area of recapture	
		Area I	Area II
Area I Fish marked LP and RP	65.1	11	0
Area II Fish marked LV and RV	34.9	2	6

$$\chi^2 = 11.5 \text{ with 2 d.f., } p = <.01.$$

area I), and the two sections E and F can be combined to form the upstream pool (now called area II). The marks LP and RP represent area I and the marks LV and RV represent area II. Analysis of the data based on this reclassification demonstrates that only 2 of 19 recaptures crossed the long riffle (Table VI). There is little chance that this pattern of distribution could be accounted for by fish moving at random after their release. This suggests that the smallmouth bass has a home range about twice as great as the other sunfishes under the conditions of this experiment. This is not a completely unexpected result because larger and more predatory animals generally have greater home ranges than smaller and less precaceous ones.

Stott's Creek. Twenty-one smallmouth bass were marked in Stott's Creek and 7 were recaptured. All 7 of the recaptures were made at the place where they were marked. Data from adjacent sections were not combined as they were in Richland Creek. Smallmouth bass, therefore, exhibit home ranges in at least two creeks and the phenomenon may be more widespread.

Spotted bass (*Micropterus punctulatus*)

The habits of the spotted bass are similar to the smallmouth bass. Generally speaking, the spotted bass does not become as large as the smallmouth bass,

but in this study the average size was about the same.

Richland Creek. The size range of the marked spotted bass was 102–270 mm fork length and the average length was 161 mm. The remarks regarding the movement of smallmouth bass apply to this species as well. Only 1 of 16 recaptures moved across the long riffle (Table VII). This pattern of movement would not be expected on the basis of random distribution of the marked fish after their release. It is concluded that the spotted bass, like the smallmouth, has a home range about twice as great as that of the smaller sunfishes.

Stott's Creek. No spotted bass were found in Stott's Creek.

Golden redhorse (*Moxostoma erythrum*)

The golden redhorse was the most abundant sucker in Richland Creek, and it is a common species in the smaller streams of the mid-west. It can easily be confused with other redhorse species, so each specimen was identified carefully. The golden redhorse feeds on bottom organisms. In the spring it spawns on riffles by depositing eggs in small depressions which are untended.

Richland Creek. The movement of golden redhorse resembled the behavior of the previous two species. Eighty-nine marked fish averaged 181 mm fork length with a range of 92 mm to 322 mm. Only 4 of 28 recaptures moved across the long

TABLE VII. *Number of spotted bass recaptured in Richland Creek during four years*

	Popula- tion per- centage	Area of recapture	
		Area I	Area II
Area I Fish marked LP and RP	70.2	10	0
Area II Fish marked LV and RV	29.8	1	5

$$\chi^2 = 12.41 \text{ with 2 d.f., } p = <.01.$$

TABLE VIII. Number of golden redhorse recaptured in Richland Creek during four years

	Population percentage	Area of recapture	
		Area I	Area II
Area I Fish marked LP and RP	53.7	15	2
Area II Fish marked LV and RV	46.3	2	9

$$\chi^2 = 13.72 \text{ with 2 d.f., } p = <.01.$$

riffle in four years, (Table VIII), which is significantly different from the distribution to be expected on the assumption of random movement ($\chi^2 = 13.72$ with 2 d. f.). It is concluded that golden redhorse confine their movements to an area of about 300–400 feet in this stream.

It was a surprise to find that golden redhorse moved about so little. These fish ascend tributary streams to spawn in the spring and may move far. Richland Creek has no permanent tributaries within a few miles of the sampling site, and the spawning activities of this species are probably limited to the main stream itself.

Stott's Creek. Twelve golden redhorse were marked in Stott's Creek, and one was recaptured in the region where it was originally released.

Hog sucker (*Hypentelium nigricans*)

The hog sucker is common in small streams where it usually lives in the riffles or at the heads of pools. The writer is aware of no migratory movement of these fish coincident with spawning activities. In the flowing water of gravel streams the hog sucker deposits eggs in shallow cup-like depressions where they are left untended.

Richland Creek. Forty-one marked fish averaged 160 mm fork length and ranged from 140 to 204 mm. Most of the hog suckers were caught just below the riffle areas at the upper end of sections B and F. Of the 14 recaptures, 11 had remained in one or the other of

the main pool areas where they had been marked and the other 3 had crossed the long riffle. A χ^2 value of 15.34 with 2 d. f. indicates a significant departure from random movement. The size of the home range is similar to that of the golden redhorse.

Stott's Creek. In Stott's Creek, where the species is more abundant, 196 hog suckers were marked and 73 were recaptured a month later. Most of these fish were small; they ranged from 80–235 mm fork length and averaged 104 mm. Sixty-six of the 73 recaptures (90.4 per cent) were found at the point of original capture. This indicates a strong tendency to remain at home and reinforces the impression obtained from the Richland Creek fish. Comparison between the creeks is done with some hesitancy because the fish did not represent the same size groups, but the conclusion that hog suckers have a home range seems to be substantiated.

EXPERIMENT II—MOVEMENT OF A SELECT GROUP FOR FOUR YEARS

Design of Experiment II

It became increasingly important to learn how long the fish occupied the same home range. The 1948 data for Richland Creek and the 1949 data for Stott's Creek showed that the majority of these fishes occupy a home range for a one-summer period. The 1949 and 1950 samples from Richland Creek showed the same tendency from one year to the next. The 1951 sample was taken two years after the last marking had been done, and this sample had the same characteristics as the others. According to this information, a majority of the fish occupied the same home range for two and possibly three years (some of the 1951 recaptures could have been derived from 1948 marking).

A method of re-marking the fish was devised whereby the movement of groups could be interpreted for more than two years. In 1949 the recaptures (derived

from 1948 marked fish) were fin-clipped in a fashion so that the section where they had originally been marked in 1948 could be recognized as well as whether they were home fish or stray fish. This required the removal of two more fins; only the pectoral and ventral fins were used. Recaptures of these "double-marks" were available in 1950 and 1951. It was possible to follow the movement of some individuals during most of their lifetime in this way. Only rarely do longear sunfish, rock bass or green sunfish reach age VI, and the smallmouth and spotted bass in Richland Creek were no older. The chance of catching these double-marks was small, and it was realized that the numbers of recaptures would hardly give a conclusive demonstration whether or not fish live in one place over a long period of time. However, the tendencies are for the most part clear-cut and the data may offer suggestions to others who are interested in the problem.

None of these double-marked fish were included in the data of Experiment I.

Results of Experiment II

1950 recaptures of double-marked fish. Four longear sunfish, 4 smallmouth bass, 1 golden redhorse and 1 hog sucker were recaptured which had been originally marked in 1948 and re-marked in 1949. One of the longear sunfish was found in section B in 1948, again in 1949 and again in the same place in 1950. Two longear sunfish were caught in section E in all three years. One longear was caught in section B in 1948, had moved to the adjacent section A in 1949 but was back in section B in 1950. It had confined its activity to the downstream pool area. Three of the four longear sunfish recaptured had remained in the same section for three years, and the other moved very little. No longears were caught which had moved across the long riffle.

Experiment I indicated that the majority of smallmouth bass confined their

activity to one or the other of the two main pool areas and the same was true here. Three of the 4 smallmouth bass recaptures had remained in the same pool area for three years; the other had moved from the downstream pool across the riffle to the upstream pool.

The golden redhorse was found in the downstream pool in all three years and had confined its activity to section A.

The hog sucker was found in the upstream pool area for three years. It had remained in section F for two years and was located in section E in 1950.

Although the data are limited, there is nothing to disturb the conclusion that these species have a rather restricted home range. It can now be postulated that this behavior is characteristic over a three-year period.

1951 recapture of double-marked fish. Fifteen fish were caught in 1951 which had a double-mark: 8 longear sunfish, 2 rock bass, 4 smallmouth bass, and 1 hog sucker. Some of these recaptures could have been the same as were caught the previous year, but the extent to which this was true is unknown because individuals could not be recognized. Nothing is known about the activity of these fish in 1950; it is only known that they were marked in 1948, re-marked in 1949 and found again in 1951. The 1950 behavior might have been determined if they had again been re-marked in that year. However, further mutilation was not justified because the chance of recovery was very small.

Five of the 8 longear sunfish recaptures were discovered in the same section in 1951 where they were originally marked in 1948. Two sunfish which had occupied the same section in 1948 and 1949 had moved to an adjacent section in 1951. Only one longear had moved across the long riffle; it had moved from section E to B sometime between 1949 and 1951. All of these recaptures could be assigned to either age IV or V. Their average length was greater than the dou-

ble-marked recaptures of 1950; 1951 fish averaged 115 mm fork length and the 1950 fish averaged 102 mm.

One rock bass was found in section E in 1948, 1949 and 1951. This fish had probably remained within about 200 feet of the place where it was marked for four years. Another individual had moved from section E to F between 1948 and 1949, and it was found in section F in 1951. The movement of this rock bass suggests, as have the movements of other individuals, that an "old" home range may be abandoned and a "new" one adopted.

Smallmouth bass show a different pattern. Three of 4 fish had moved from the downstream pool across the long riffle to the upstream pool, while the other had remained in the same pool for four years. Possibly this species ranges over a wider area as it grows older.

The hog sucker was found in the same pool in 1948, 1949 and 1951.

The tendency to remain in restricted areas is not so pronounced among the 1951 recaptures. As fish grow older there seems to be a greater freedom of movement. Examination of the lengths of longear sunfish strays as compared to home fish of Experiment I suggests this same view (Table IX). In all four years the stray longear sunfish had a greater average length than the home fish. Other species showed this characteristic as well. There was considerable overlap in size among those that remained at home and those that strayed, but on the average it appears that the larger fish have the greater tendency to stray. Allen (1951) found that older brown trout travelled

more freely than younger fish. Either the older fish have a larger home range or they may have a greater tendency to shift from one home range to another.

EXPERIMENT III—A TEST OF THE TERRITORY HYPOTHESIS

Design of Experiment III

The home range phenomenon is not inalterably bound to territoriality, since aggressive behavior is not necessarily involved, but territoriality is suspected when evidence for home range is convincing. An experiment was designed to determine whether the fishes of Richland Creek maintain territories.

Provisionally accepting the hypothesis that territoriality is a real phenomenon among at least some of the species, the fish population was imagined as being under a constant state of tension. Competition for territories would create aggressive situations among the members of the population. Some fish would be eliminated or be buffeted about from place to place under such conditions. It might also be imagined that the weaker members of the population become the strays. However, as Greenberg (1947) found for immature green sunfish, the fish may have varying degrees of dominance, so that if one member was ousted from its territory it might compete successfully with a member close by. Large fish probably do not compete directly

TABLE IX. *A comparison of the average fork length of longear sunfish classified as "home" and "stray" in Richland Creek*

	1948 mm	1949 mm	1950 mm	1951 mm
Home fish	86	99	106	110
Stray fish	104	103	111	113

TABLE X. *Fish marked in Richland Creek, 1951. Section B fish were transplanted to section E*

Species	Section A LP	Section B RP*	Section E LV	Section F RV	Total
Longear sunfish	53	55	63	36	207
Green sunfish	5	1	15	3	24
Rock bass	19	32	13	12	76
Smallmouth bass	4	3	4	1	12
Spotted bass	6	1	0	2	9
Golden redbreast	32	9	7	19	67
Hog sucker	0	19	7	21	47
Total	119	120	109	94	442

*6 longear sunfish, 2 rock bass, and 1 hog sucker bearing the RP mark from a previous year were also transplanted. Stray fish found in section B were destroyed.

TABLE XI. *The distribution of marked longear sunfish in Richland Creek two weeks and six weeks after transplanting section B fish to section E*

Mark	Two weeks after transplanting				Six weeks after transplanting			
	Section A	Section B	Section E	Section F	Section A	Section B	Section E	Section F
LP	15	4	0	0	9	8	0	0
RP*	0	26	6	3	0	18	4	7
LV	0	0	37	2	0	1	23	9
RV	0	0	5	11	0	0	2	14

* Had been transplanted to section E.

with small ones at any given time because they usually occupy different niches. In Richland Creek, as is usual, the small fish live in shallow water and the large ones in pools. Some time during their lifetime the younger, faster-growing fish must enter deeper water and compete with larger fish, of the same or other species. These illustrations by no means exhaust the possible variety of phenomena associated with territoriality.

Assuming that territoriality may be a true behavior pattern among some or all the species considered here, at least 3 postulates may be made. (1) Fish move rapidly into an underpopulated area. (2) A "foreign" population, on suddenly entering a well-established population, competes with the others, but the residents have some advantage in the competition, as Braddock (1949) has shown for *Platy-poecilus maculatus*. As a result the "foreign" fish move to a greater extent than the others. (3) The well-established individuals move more than they usually do as a result of the competition. If these hypotheses could be satisfied by experiment, then evidence regarding territoriality would be more convincing.

The physical features of Richland Creek were ideal for an experiment to test the territorial hypotheses. Section B was underpopulated by removing all fish of all species that could be caught. The section B fish were placed in section E immediately after they were weighed, measured, and marked in the usual way. Section E thus became overpopulated. Before section B fish were transplanted,

all other sections had been traversed and the fish marked in the typical manner (Table X).

The small residual population of marked fish in the stream presented little difficulty in the interpretation of the data because most of them were home fish. The whole experimental area was traversed twice after the fish were transplanted in order to follow their movement, once two weeks after transplanting and again six weeks after transplanting. No high water or other unusual circumstance occurred between the time the fish were marked and their subsequent recapture.

The success of the experiment hinged on the assumption that the size of the population in all sections prior to the transplantation was near or at its maximum. This assumption seems to be reasonable since no drastic changes in the abundance of individual species or in the species composition were evident during the four years.

Results of Experiment III

Longear sunfish. The most striking feature of the transplantation experiment is that a majority of the longears, which had been transferred to section E, moved downstream over the long riffle to their original home (Table XI). This movement indicated that the riffle was a behavioral rather than a mechanical barrier. Twenty-six of 35 RP recaptures were taken in section B two weeks after transplanting, 18 of 29 recoveries in the six-week sample. A χ^2 test of independence

indicated that there was no significant difference between these samples ($\chi^2 = 0.575$ with 1 d. f.). Thus, the entire movement could be accounted for within two weeks after the fish were transplanted. This movement agrees with hypothesis 2, above.

The migration back to the original point of capture could also be interpreted as "homing," a well-known phenomenon among some anadromous fishes like the salmon. Until recently such behavior had never been described for non-migratory fishes. Larimore (1952) has performed some homing experiments with smallmouth bass and longear sunfish by following the movement of individuals after transferring them from their home pool to other parts of a stream. He cites strong evidence that smallmouth bass show homing behavior. In the light of this evidence, the homing interpretation cannot be eliminated. However, Larimore's experiments did not conclusively demonstrate a tendency for longear sunfish, the species under discussion here, to return to their home pool after being transferred to a new location. Therefore, the movement in our experiment will be interpreted as a result of competition between "foreign" and well-established individuals.

The redistribution of the transplanted longears that remained above the riffle was interesting, since 6 of 9 recaptures (67 per cent) were found in section E two weeks after they were transplanted, but only 4 of 11 (36 per cent) were in section E six weeks after transplanting. Though the sample was smaller than desirable, the results suggest that increased competition led to increased movement of the transplanted longears out of the area.

In the two-week sample of section E fish, 37 of 39 were found at home. Of 33 fish in the six-week sample, 23 were at home. A chi-square comparison of these data indicates that the difference between the samples is significant ($\chi^2 = 6.44$, with 1 d. f., $p = .012$). Some of

the longears which were well-established in the area moved away after it became overpopulated (see hypothesis 3 above).

Five of 16 longears originally marked in section F were strays into section E in the two-week sample, but only 2 of 16 were present in section E in the six-week sample. This could have been the result of chance ($\chi^2 = 0.732$ with 1 d. f.), but the migration away from the overpopulated area agrees with the trends already reported.

A progressive movement into the underpopulated area (section B) from section A seems to have taken place, as would be expected if the first hypothesis were true. Four of 19 longears (LP) had strayed into the underpopulated area two weeks after the fish had been removed and 8 of 17 were strays into section B in the six-week sample. This movement is also in accord with expectation.

The tentative conclusion is offered that territory competition was the cause of the movement, but it is tempered with the knowledge that it is based on fewer recaptures than desirable and also that it is not based on direct observation of such competition. The expected movements were all confirmed, however, and there would be little chance that they were the result of random movement.

Rock bass. The movement of 32 transplanted rock bass, and the movement of the well-established fish were similar to that of the longear in most respects (Table XII). Two differences were noticed: (1) the majority of the rock bass stayed above the long riffle after transplanting and (2) the fish from section A (LP) did not show a progressive movement into the underpopulated section. So few LP recaptures were made that sampling error could account for the difference between the two samples, although the data may reflect the actual movement that occurred. The fact that some rock bass moved back across the long riffle in such a short time again proved that the riffle was not a mechan-

TABLE XII. *The distribution of marked rock bass in Richland Creek two weeks and six weeks after transplanting section B fish to section E*

Mark	Two weeks after transplanting				Six weeks after transplanting			
	Section A	Section B	Section E	Section F	Section A	Section B	Section E	Section F
LP	7	2	1	1	4	0	0	0
RP*	0	3	4	2	1	2	6	6
LV	0	0	5	1	0	0	2	4
RV	0	0	1	3	0	0	0	5

* Had been transplanted to section E.

ical barrier to fish movement. The pattern of movement resembled that of the longear and it is tempting to interpret the limited data by the same hypothesis, i.e. the movement was caused by a competition for territories.

Other species. The information about the green sunfish, smallmouth bass, spotted bass, golden redhorse, and hog sucker was not sufficient to interpret their movement in the light of the territory hypothesis.

DISCUSSION

If the data have been interpreted correctly from the point of view of home range and territory, some new light is thrown on the general characteristics of fish populations in small streams. In streams with riffle-pool development, such as Richland Creek and Stott's Creek, each pool can be considered as a more or less isolated unit containing a natural population of its own. The chances are great that once a fish becomes established in an area it will remain there for most, if not all, of its lifetime. This sounds much like the statement by Burt (1940) concerning the wood mouse (*Peromyscus leucopus*): "Once a mouse settles down and establishes a territory, it usually, but not always, remains there for life." The tendency for fish to remain in familiar surroundings may be a more common characteristic than is generally realized. It is interesting in this connection to read Fraser-Brunner's (1950) statement that for six months he observed a butterfly fish (*Chaetodon melapterus*), identifiable

by a scarred fin, in the same position near a rock. Scott (1949) found that rock bass in the Tippecanoe River in Indiana moved very little from year to year. Shuck (1943) found this true for brook trout (*Salvelinus fontinalis*), Shetter (1937) described a similar situation for brown trout (*Salmo trutta*), and Larimore (1952) has shown that smallmouth bass are associated with "home pools." It appears that the fish population of a small stream may be thought of as a series of discrete, natural units rather than as a single, homogeneous, freely-mixing group. The natural intraspecific and interspecific changes in a fish population in one part of a stream may bear no relation to events occurring in another part of the stream.

Since this paper was written, Allen's (1951) work on the Horokiwi Stream of New Zealand has come to hand and some of his results are strikingly similar to ours. In a situation quite comparable with ours, 42 recaptures of brown trout were made and all but 2 were found where they were tagged. Allen regards the trout population of the Horokiwi as being not only isolated and self-contained, but also composed of a succession of distinct local populations. This is borne out further by his discovery that the trout had different growth rates in different parts of the stream.

Home range and territory have not been satisfactorily distinguished by the experimental procedure. They may or may not be independent of one another. The purely arbitrary selection of a boun-

dary between sections A and B and between sections E and F make it impossible to calculate the actual size of the home range. It is conceivable that a determination of this sort might be made by studying sections of progressively smaller size. If the home range concept is valid, a section size would finally be reached where the tendency to stay in one place would no longer be evident. In effect this is what was described in Richland Creek where the majority of longear sunfish and rock bass were found to remain within the 100–200 foot sections, while the larger species showed no tendency to remain in such small areas. When the boundaries were increased, the home range of the larger species was revealed.

The territory seems to be a much more satisfactory way of thinking about the interaction between members of a population than the home range. Territory stresses the type of competition which seems to have been developed in the overpopulated area of Experiment III. It is gratifying to get direct evidence for the territory concept among fishes from Greenberg's (1947) laboratory experiments with immature green sunfish. In his excellent paper he states: "Even under our laboratory conditions, with oversimplification of habitat and limitations of space, territoriality is an outstanding phenomenon in the social life of immature sunfish." Greenberg also proves that green sunfish have social rank built up much like the peck-order of chickens. Braddock (1945) shows that *Platyepocilus maculatus* has a social order although it does not have territories. Noble and Curtis (1939) described the social behavior in the jewel fish (*Hemichromis bimaculatus*) which has reproductive territories. Concepts of territory and social rank lead to the consideration that the amount of food and the number of young produced by fish are not the only limitations placed on natural populations. The natural aggressive action

of fish toward one another also limits the population size.

Greenberg and others have observed that as a general rule larger fish dominate smaller fish. If this is the case, the smaller fish would become the strays of our experiments. However, it was shown that in Richland Creek the larger fish of a given species wandered more than smaller ones. This discrepancy might be explained by the limitations of the aquarium experiments. Greenberg used only small fish of about the same size within the confines of small aquaria. Fish of all sizes are living together in the same general area in nature. In a rapidly growing population, the young fish which are being recruited into the older group will sooner or later be thrown into direct competition with the older fish. The younger fish might then have the advantage of youth and be able to dominate an older one and force him to seek territory elsewhere.

The importance of the stray fish should not be overlooked. Here is a reserve supply which is available to occupy territories left vacant for one reason or another. They become the elements which can move and repopulate decimated areas. They may also be important in the distribution of the species over the geographic limits of tolerance.

Intense competition such as pictured here does not lead to chaos in a population but rather forms the structure for stability among members of a group. Greenberg's aquarium fish usually retained a stable relationship with one another after the hierarchy and territories had become established. Once a fish learned his place in the group he was usually content, or forced, to remain there. Greenberg says, "Territories are stable but may undergo changes such as elimination of one, transfer of ownership, shifts in position and boundaries, and variations in relative aggressiveness of the possessors."

The tendency for fish to stay within circumscribed limits may not be limited

to streams. There is some evidence that certain species show the same behavior in lakes. A few examples can be cited where the information is clear. Lagler and Ricker (1942) studied the fish populations of Fouts Pond in Indiana (47.5 acres). They found that the fish in the south end of the pond did not mix freely with those in the north end. They stated: "Of 67 marked white crappies (*Pomoxis annularis*) recaptured in the southern part of the pond . . . , only 4 had moved in from the north; and only 3 of 22 retaken in the northern part had come from the south." These fish were not moving randomly in the pond. Omand (1951), who netted three Canadian lakes intensively, found that the nets fished well for a few days and then the catches dropped off. Good catches could be made if the nets were moved only a short distance (200 yards). Omand says, "The entire impression was one of exploitation of a series of local populations, usually in sheltered bays." Worthington (1950) noticed a similar phenomenon while fishing intensively for perch in Lake Windemere. It is a custom in studies of fish populations in Indiana lakes to move traps each day or two in order to avoid such occurrences, because circumstances similar to Omand's have been noticed often.

Ball (1947) tagged several species in Third Sister Lake, Michigan (10 acres). Eighteen of 27 bluegill (*Lepomis macrochirus*) recaptures had moved no more than 65 yards from their point of original capture and 12 were reported not to have moved at all. Yellow bullheads (*Ameiurus natalis*) showed the same tendency; 19 of 27 had moved no more than 100 yards from where they were marked and 11 had not moved at all. He reported that largemouth bass (*Micropterus salmoides*) showed no tendency to remain in one location. Shoemaker (1952) described an experiment in a 90-acre lake in which pumpkinseeds (*Lepomis gibbosus*) and yellow bullheads had affinity for definite areas in the lake. This experiment

also provided some evidence that these species have homing behavior. Rodeheffer (1941) fin-clipped and tagged many fish of various species in Douglas Lake, Michigan, during several years of investigation. The movement of his fish was restricted. One of his most interesting statements in this connection is: "It is most striking that not a single fish of the 4,557 marked at Grapevine Point from 1937 to 1939 were recovered at any other point in the lake." Sportsmen and collectors from the University of Michigan Biological Station were active in all these years and had been informed about the marked fish.

Other examples could be brought forward to support the fact that some lake species move very little. The fact itself is important, but when interpreted with regard to the social habits of fishes, it acquires even greater meaning, for now some insight is obtained as to why such behavior might be expected to occur.

The practical application of the social habits of fishes has received very little attention. Langlois (1936) used such information in his program of rearing smallmouth bass in ponds, but this is the only case of which the writer is aware. The lack of success in stocking fish in streams and lakes with either fingerlings or larger fish may in part be due to the intense competition in an already "saturated" environment. The social habits of fish deserve more attention in the future as the reward seems promising.

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SUMMARY

Investigation of the factors influencing fish populations has centered on food, feeding habits, reproductive behavior, reproductive potential, growth, and mortality. These factors have been studied from the viewpoint of the population as an aggregate of animals. The present work on the fish populations of two streams attempts to investigate the competitive interaction between individuals as another factor affecting the size and structure of the group.

The information concerning the movement of fishes in a bedrock stream and a gravel stream was interpreted with respect to home range and territory, phenomena best known among mammals and birds. Experimental areas in each stream were subdivided into four sections and the fish of each section were marked distinctively by fin-clipping. The movements of the fish in the bedrock stream were traced for four years. The gravel stream was studied for one summer.

Longear sunfish, rock bass and green sunfish moved about very little in the stream from one year to the next and some of them remained in one stream section for as long as four years, which is near their life-span. The size of the home range of these small sunfish in the stream could be estimated at 100–200 feet under the conditions of our experiment. The movement of the smallmouth bass, spotted bass, golden redhorse and hog

suckers was greater than the sunfishes. These species had home ranges of about 200–400 feet in the stream.

All of the species respected the stream riffles as boundaries. It is concluded that the fish population of a small stream with riffle-pool development may be considered as a series of discrete, natural units rather than a single homogeneous, freely-mixing group.

The concept of competitive territories develops logically from a convincing demonstration of home range. Aggressive behavior of the fish in the streams could not be observed, so an experiment was designed to test the hypothesis that fish have territories. Separate sections in an experimental area were underpopulated and overpopulated. The movements of longear sunfish and rock bass under these circumstances suggested that the territory hypothesis may be true. Aggressive behavior among individuals of a fish population may be one of the factors determining the characteristics of fish populations.

LITERATURE CITED

- Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. Principles of animal ecology. Phila. and London: Saunders, xii + 837 pp.
- Allen, K. Radway. 1951. The Horokiwi Stream. A study of a trout population. New Zealand Marine Department, Fisheries Bull. No. 10: 1–231.
- Altum, Bernard. 1868–1903. Der Vogel und sein Leben. Münster. 240 pp.
- Ball, R. C. 1947. A tagging experiment on the fish population of Third Sister Lake, Michigan. Trans. Am. Fish. Soc., 74: 360–369.
- Braddock, J. C. 1945. Some aspects of the dominance-subordination relationship in the fish *Platyphacelus maculatus*. Physiol. Zool., 18: 176–195.
- . 1949. The effect of prior residence upon dominance in the fish *Platyphacelus maculatus*. Physiol. Zool., 22: 161–169.
- Breder, C. M., Jr. 1936. The reproductive habits of the North American sunfishes (family Centrarchidae). Zoologica, 21: 1–48.
- Burt, W. H. 1940. Territorial behavior and populations of some small mammals in south-

- ern Michigan. Misc. Publ. Mus. Zool., Univ. Mich., No. 45, 1-58.
- . 1943. Territoriality and home range concepts as applied to mammals. Jour. Mamm., 24: 346-352.
- Collias, N. E. 1944. Aggressive behavior among vertebrate animals. Physiol. Zool., 17: 83-123.
- Fraser-Brunner, A. 1950. *Holocanthus xanthotis* sp. n. and other chaetodont fishes from the Gulf of Aden. Proc. Zool. Soc. London, 120: 43-48.
- Gerking, S. D. 1950. Stability of a stream fish population. Jour. Wildl. Manag., 14: 193-202.
- Greenberg, B. 1947. Some relations between territory, social hierarchy and leadership in the green sunfish (*Lepomis cyanellus*). Physiol. Zool., 20: 269-299.
- Hayne, Don W. 1949. Calculation of size of home range. Jour. Mamm., 30: 1-18.
- Lagler, K. F., and W. E. Ricker. 1942. Biological fisheries investigations of Fouts Pond, Gibson County, Indiana. Investigations of Indiana Lakes and Streams, 2: 47-72.
- Langlois, T. H. 1936. A study of smallmouth bass (*Micropterus dolomieu* Lacépède) in rearing ponds in Ohio. Ohio Biol. Surv. Bull., No. 33, 191-225.
- . 1937. Sociological succession. Ecology, 18: 456-461.
- Larimore, R. W. 1952. Home pools and homing behavior of smallmouth black bass in Jordan Creek. Ill. Nat. Hist. Surv. Div., Biol. Notes No. 28: 3-12.
- Nice, M. M. 1941. The role of territory in bird life. Am. Midl. Nat., 26: 441-487.
- Noble, G. K. 1939. The role of dominance in the life of birds. Auk, 56: 253-273.
- , and B. Curtis. 1939. The social behavior of the jewel fish, *Hemichromis bimaculatus*. Bull. Am. Mus. Nat. Hist., 76: 1-76.
- Omand, D. H. 1951. A study of populations of fish based on catch-effort statistics. Jour. Wildl. Manag., 15: 88-98.
- Raney, E. C. 1940. Comparison of the breeding habits of two subspecies of black-nosed dace (*Rhinichthys atratulus* Hermann). Am. Midl. Nat., 23: 399-403.
- Reighard, J. 1920. The breeding behavior of the suckers and minnows. Biol. Bull., 38: 1-32.
- Ricker, W. E. 1948. Methods of estimating vital statistics of fish populations. Indiana Univ. Publ., Science Series, No. 15, pp. 1-101.
- Rodeheffer, I. 1941. The movements of marked fish in Douglas Lake, Michigan. Pap. Mich. Acad. Sci., Arts and Lett., 26: 265-280.
- Scott, D. C. 1949. A study of a stream population of rock bass (*Ambloplites rupestris*). Investigations of Indiana Lakes and Streams, 3: 169-234.
- Shetter, D. H. 1937. Migration, growth rate, and population density of brook trout in the north branch of the Au Sable, Michigan. Trans. Am. Fish. Soc., 66: 203-210.
- . 1948. The electric "shocker" and its use in Michigan streams. Prog. Fish. Cult., 10: 43-47.
- Shoemaker, H. H. 1952. Fish home areas of Lake Myosotis, New York. Copeia, 1952: 83-87.
- Shuck, H. A. 1943. Survival, population density, growth and movement of the wild brown trout in Crystal Creek. Trans. Am. Fish. Soc., 73: 209-230.
- Snedecor, G. W. 1946. Statistical methods applied to experiments in agriculture and biology. Ames, Iowa: Iowa State College Press, xvi + 485 pp.
- Worthington, E. B. 1950. An experiment with populations of fish in Windemere, 1939-48. Proc. Zool. Soc. London, 120: 113-149.