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STATE OF ILLINOIS • WILLIAM G. STRATTON, *Governor*
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This paper is a contribution from the Section of Aquatic Biology.

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WARMOUTH

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OVERPOPULATION among certain warm-water fishes is now commonly recognized as a cause of poor fishing in many lakes and ponds of the United States. More than a decade ago, Bennett (1944:186) suggested that perhaps some sunfish not prone to overpopulation would, with little control by man, produce good fishing over a prolonged period. This suggestion stimulated a search for a species that has a low reproductive potential, a species that does not tend to overcrowd its habitat, and yet has good sporting qualities. The warmouth, *Chaenobryttus gulosus* (Cuvier), appeared to be such a species. The study of its life history and ecology presented here may serve as a basis for an estimate of the potential value of the species as a companion for bass or other game fishes in lakes and ponds of Illinois and neighboring states.

The warmouth is a dark, thick-bodied sunfish (family Centrarchidae) which superficially resembles the somewhat better known rock bass, *Ambloplites rupestris* (Rafinesque). It is readily distinguished from the latter by the presence of three spines in the anal fin; the rock bass has six. A good color and morphometric description of the warmouth is given by Forbes & Richardson (1920:245).

The nomenclature of this robust sunfish was summarized by Jordan, Evermann, & Clark (1930:302–3), in whose check-list *Chaenobryttus gulosus* was the accepted name. Harper (1942:50) pointed out that Bartram in his *Travels,* 1791, had accurately described this species and called it *Cyprinus coronarius,* a name which antedates *Chaenobryttus gulosus* by 38 years. Recently, however, the Committee on Nomenclature of the American Society of Ichthyologists and Herpetologists agreed that, because Bartram was not consistently binomial in the work cited by Harper, the name *Chaenobryttus gulosus* should be reapplied (Bailey 1956:336). Of the 16 or more common names given to the species, warmouth, warmouth bass, and goggle-eye are the most widely known. The American Fisheries Society Committee on Common and Scientific Names of Fishes (1948:16) designates this fish the warmouth, the name used throughout this paper.

The warmouth occurs generally in suitable waters throughout the central and eastern United States and south to the Gulf Coast. Its distribution extends from Kansas and Iowa to the Mississippi River drainage in southern Wisconsin, includes the southern two-thirds of the Lower Peninsula of Michigan, Lake Erie, and the Allegheny River tributaries of Pennsylvania, and embraces the territory southward to Florida and west through the Gulf states to the Rio Grande (Hubbs & Lagler 1947:93). As a result of introductions, it is now found west of the Rocky Mountains. Introductions into California, Washington, and Idaho were made as early as the end of the last century (Smith 1896:441).

In Illinois, the warmouth has a wide, scattered distribution. Approximately a half century ago, Forbes & Richardson (1920:246) found it in glacial lakes of northeastern Illinois and showed that it increased in abundance from north to south; they gave it frequency ratios in their collections for northern, central, and southern sections of the state as 0.44, 0.78, and 1.78, respectively.

Leonard Durham, while employed by the Illinois Department of Conservation in 1950–1955, found a somewhat different pattern of warmouth distribution (unpublished data). In studying representative populations of fish in 426 Illinois ponds and lakes, some of them natural and some artificial impoundments, Durham found little difference in the frequency of occurrence of warmouths in the three zones of the state then recognized by the Department of Conservation. In the northern, central, and southern zones, warmouths were taken from 15.4, 17.1, and 15.4 per cent, respectively, of the waters sampled. These figures suggest that the distribution of warmouths in Illinois may have changed since Forbes and Richardson made their collections. The construction of many artificial impoundments requiring the widespread transportation of fishes for stocking purposes probably is responsible for some of the changes that have occurred in the distribution of this species.

Although principally a pond and lake fish, the warmouth occurs in the Rock, Mississippi, and Illinois rivers and is reported as common in small, sluggish streams of the southern part of the state. Its scattered distribution in Illinois coincides with the occurrence of suitable habitat.

ACKNOWLEDGMENTS

The research upon which this paper is based was a project of the Illinois Natural History Survey and was proposed and supervised by Dr. George W. Bennett, who gave guidance and help in all stages of the work.

Much of the material presented here was included in a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Horace H. Rackham School of Graduate Studies of the University of Michigan, 1950. As chairman of my doctoral committee there in the Department of Zoology, Dr. Karl F. Lagler directed my graduate studies, made many suggestions for my research, and helped me revise my thesis manuscript.

The paper published here was edited by Mr. James S. Ayars, the Natural History Survey's Technical Editor. His skill and patience have added considerably to the accuracy and clarity of reasoning, expression, and composition. Mrs. Darlene Ose, while secretary in the Section of Aquatic Biology, read and criticized the manuscript.

Dr. Leonard Durham, while employed by the Illinois Natural History Survey from April, 1947, to August, 1950, assisted in all of the field work and in many of the laboratory preparations; his continued interest added greatly to the completeness of this study and to the pleasure of conducting it. Mr. W. Leslie Burger, also while employed by the Natural History Survey, helped sort the contents of warmouth stomachs, after which members of the Section of Faunistic Surveys and Insect Identification of the Natural History Survey identified many of the invertebrate food items. Messrs. William J. Harth, James F. Opsahl, and William F. Childers, while with the Department of Conservation, assisted in some of the field work or in the tabulation of data. Other members of the Survey staff and my wife, Glenn E. Larimore, gave willing aid to the work.

I appreciate the permission to refer to unpublished observations by members of the Natural History Survey staff on warmouths in Illinois; observations of special value are those by Dr. Bennett at Ridge Lake, in Coles County, and at the Pollywog Association water area, in Vermilion County, and those by Dr. Donald F. Hansen at Lake Glendale, in Pope County. Credit for these and other unpublished observations is given in the text of this paper.

The Associated Tackle Manufacturers supplied certain equipment necessary for field work and gave financial support for my library studies at the University of Michigan.

The owners of several Illinois ponds in which warmouths were studied aided this investigation through their willing co-operation.

The picture of the warmouth reproduced as the frontispiece was painted by Mr. Maynard Reece and is used here through the courtesy of the Iowa State Conservation Commission.

AREAS OF INTENSIVE STUDY

As part of the investigation reported here, intensive studies of warmouths were conducted in two aquatic habitats, Park Pond and Venard Lake, figs. 1 and 2; these studies were then compared with more general observations on warmouths in other waters.

Both of the aquatic habitats in which the intensive studies were conducted were man-made: a flooded stripmine area and a small artificial lake. The many differ-

Fig. 1.—Southwest section of Park Pond, Vermilion County.

Fig. 2.—Part of Venard Lake (principally the east arm), McLean County.

ences between these two water areas permitted an evaluation of the effects of a considerable range of habitat conditions on warmouth populations.

Park Pond

Park Pond has a history that dates back many years. More than a quarter century ago, in Vermilion County, in east-central Illinois, an abandoned stripmine flooded with waters from the Salt Fork River was leased by a group of sportsmen and conservationists, who, in about 1929, had formed the Waste Land Reclamation Association. In 1932, this area was acquired by a group of sportsmen who had formed the Pollywog Association, an organization that has continued since that time to use the area for hunting and fishing. A few years after the formation of the Pollywog Association, the construction of two small dams raised the water level several feet. A major part of the investigation reported here was based on material from Park Pond, which in 1946 had an area of 18 acres, in the central part of the Pollywog Association area.

When field work for the warmouth study was begun in 1946, the old mining cuts from which coal had been taken in 1889 and 1890 had become filled with water and appeared as irregular lakes connected by many narrow channels, fig. 1. High banks, formed when soil was removed to expose underlying coal beds, had become covered with dense brush and small trees. Older trees, killed when the water level was raised by the two small dams, lined the water's edge.

The chemical composition of the water differed from that of many other Illinois lakes, primarily in its high mineral content, table 1. Sulfates were especially high in concentration, but the buffer effect of other substances eliminated the extreme acidity often associated with the sulfur of mine waters.

The fish fauna of Park Pond had been derived from two sources. Many species of fish had entered on flood waters from the nearby Salt Fork River. Fish of some of these species, as well as others not indigenous to the Salt Fork, had been placed in the pond by the Illinois Department of Conservation. Thirty-six species were recorded from this pond, table 2.

Table 1.—Chemical composition (parts per million) of water from Duck Pond, in the Pollywog Association area, Vermilion County, Illinois, and from five recently constructed United States Soil Conservation Service ponds in central Illinois.

Pond	Iron		Ca	Mg	Na and K	SO_4	NO_3	Cl	Methyl Orange Alkalinity	Total Hardness
	Filtered	Unfiltered								
Duck Pond July 15, 1938......	.....	0.2	74.8	38.2	43.2	236.0	9.0	23.0	152.0	343.5
Duck Pond October 7, 1942....	.....	0.1	58.8	44.6	......	......	3.5	33.0	146.0	329.0
Five Soil Conservation Service ponds (average) August-September, 1939...	1.1	2.78	26.9	15.1	11.6	17.2	2.0	2.8	130.8	127.1

The relative abundance of these species was disclosed by the poisoning of the fish populations in four ponds of the Pollywog Association; each of these ponds was isolated from other waters except during floods. The total area to which poison was applied equaled 9.07 acres and was supporting a fish population which averaged 455.5 pounds per acre. Gizzard shad, carp, and bluegills comprised high percentages of the total weight of all fish collected from these four ponds, table 3. Warmouths represented 1.1, 0.9, 1.5, and 10.4 per cent of the weight in the four areas, or 1.6 per cent of the combined weight of fish from these waters. They made up a greater proportion of the weight of the fish population in these waters of the Pollywog Association than in most other Illinois

Table 2.—List of fishes collected from Park Pond of the Pollywog Association, with information on the relative abundance of each kind.*

Species	Relative Abundance
Gizzard shad, *Dorosoma cepedianum* (Le Sueur)	Abundant
Quillback carpsucker, *Carpiodes cyprinus* (Le Sueur)	Common
White sucker, *Catostomus commersoni* (Lacépède)	Common
Lake chubsucker, *Erimyzon sucetta* (Lacépède)	Rare
Spotted sucker, *Minytrema melanops* (Rafinesque)	Common
Silver redhorse, *Moxostoma anisurum* (Rafinesque)	Rare
Northern redhorse, *Moxostoma aureolum* (Le Sueur)	Common
Carp, *Cyprinus carpio* Linnaeus	Abundant
Bluntnose minnow, *Pimephales notatus* (Rafinesque)	Rare
Fathead minnow, *Pimephales promelas* Rafinesque	Rare
Golden shiner, *Notemigonus crysoleucas* (Mitchill)	Common
Channel catfish, *Ictalurus punctatus* (Rafinesque)	Common
Yellow bullhead, *Ictalurus natalis* (Le Sueur)	Abundant
Black bullhead, *Ictalurus melas* (Rafinesque)	Common
Flathead catfish, *Pylodictis olivaris* (Rafinesque)	Rare
Madtom, *Noturus* sp.	Rare
Grass pickerel, *Esox vermiculatus* Le Sueur	Common
American eel, *Anguilla rostrata* (Le Sueur)	Rare
Banded killifish, *Fundulus diaphanus* (Le Sueur)	Common
Blackstripe topminnow, *Fundulus notatus* (Rafinesque)	Abundant
Yellow bass, *Roccus mississippiensis* (Jordan & Eigenmann)	Common
Yellow perch, *Perca flavescens* (Mitchill)	Rare
Logperch, *Percina caprodes* (Rafinesque)	Rare
Johnny darter, *Etheostoma nigrum* Rafinesque	Rare
Smallmouth bass, *Micropterus dolomieui* Lacépède	Rare
Spotted bass, *Micropterus punctulatus* (Rafinesque)	Rare
Largemouth bass, *Micropterus salmoides* (Lacépède)	Common
Warmouth, *Chaenobryttus gulosus* (Cuvier)	Common
Green sunfish, *Lepomis cyanellus* Rafinesque	Common
Pumpkinseed, *Lepomis gibbosus* (Linnaeus)	Common
Bluegill, *Lepomis macrochirus* Rafinesque	Abundant
Orangespotted sunfish, *Lepomis humilis* (Girard)	Common
Longear sunfish, *Lepomis megalotis* (Rafinesque)	Abundant
White crappie, *Pomoxis annularis* Rafinesque	Abundant
Black crappie, *Pomoxis nigromaculatus* (Le Sueur)	Common
Brook silverside, *Labidesthes sicculus* (Cope)	Common

*The common names used here and elsewhere in this paper follow those of the American Fisheries Society Special Publication Number 1, 1948, or the changes recommended by the Society (Bailey 1952, 1953); most of the scientific names are those given by Bailey 1956.

waters from which fish collections have been taken in recent years.

Venard Lake

Little is known of the early history of Venard Lake, fig. 2, an "old" artificial impoundment 1 mile south of Bloomington, near the junction of state highway 51 and United States highway 66, in McLean County, Illinois. In 1947, the lake had an area of 3.2 acres. Though there was a small spring at the upper end of the lake, most of the water came from surface runoff flowing into the lake from two shallow valleys. Settling basins, built in both of these valleys above the lake, removed much of the silt load carried by surface water; even so, during a period of several decades, the basin had accumulated much silt. In 1946, the lake was drained, a stunted fish population removed, and the basin allowed to refill with water. In April of 1947, Venard Lake was stocked with the following fishes: 225 yearling largemouth bass between 4 and 8 inches in total length, 15 largemouth bass between 9.6 and 13.7 (average 11.9) inches in total length, and 101 warmouths between 5.1 and 8.1 (average 6.8) inches in total length.

Extremely large broods of both bass and warmouths were spawned in 1947. The fish placed in the lake early in 1947 grew well and supported excellent fishing the following months. Many warmouths of the 1947 year class were caught in spring

Table 3.—Kinds of fish that were collected from four Pollywog Association water areas treated with rotenone and the percentage of the total weight of fish comprised by each kind. The total area of water treated was 9.07 acres and the average standing crop of fish was 455 pounds per acre.*

Kind of Fish	Per Cent of Total Weight
Largemouth bass	3.5
White crappie	3.8
Bluegill	14.4
Warmouth	1.6
Other fine fish	1.0
Catfish	0.8
Coarse fish	25.5
Gizzard shad	49.3
Other forage fish	0.1
Total	*100.0*

*Data from three of the water areas were collected by Dr. George W. Bennett. Data from the fourth, Park Pond, were collected by the author.

fishing of 1949, but very few were taken in the summer of that year. Most of the bass caught in 1949 were of the 1947 year class; many of them were still below the then legal size of 10 inches.

During several weeks in August of 1948, shallow parts of the lake were dredged. This operation killed many of the 1948 brood of warmouths, in particular those trapped in the large weed masses removed from the lake. The bass, on the other hand, were apparently unharmed.

HABITAT CHARACTERISTICS

Collections of the warmouth from many lakes, ponds, and streams of Illinois, and descriptions of the water areas in which this sunfish is found in other parts of its range, indicate that it is usually associated with certain habitat characteristics.

Vegetation and Bottom Materials

Dense weed beds and a soft bottom are two habitat characteristics with which the warmouth is usually associated. Brush and roots attract this sunfish, and in water areas lacking extensive weed beds, as in some of the bottomland lakes of the South, old tree stumps constitute the common hiding places of the warmouth (thus, the name "stump-knocker" is sometimes given to it). The quiet, almost sulky disposition of the warmouth and the customary association of this fish (particularly young and moderate-sized individuals) with protected hiding places cause members of this species to concentrate in weedy and stump-filled waters.

In the Everglades region of southern Florida, Bangham (1939:263–5) found warmouths second in abundance to gars. The waters were slow moving or still, dark-colored, usually choked with vegetation, and with bottoms composed of soft muck. Of five ponds in the Ocala National Forest in Florida censused by Meehean (1942), all contained warmouths, table 4. The population having the greatest concentration of warmouths was in an old pond (Little Steep Pond) with a thick layer of humus on the bottom and a mat of vegetation covering the entire surface. When Tarzwell (1942) applied poison to three backwater sloughs of Wheeler Reservoir in Alabama, he found warmouths in all populations, although in low percentages by weight; the highest proportion of these fish by weight (1.0 per cent) was associated with a soft silt or mud bottom, table 4.

The greatest proportion of warmouths that Bennett (1943:360) encountered in censusing 22 ponds and lakes of Illinois was in Delta Pond (10.7 per cent warmouths by weight), table 4. As only 2 years had passed since this pond had been stocked with game fish and pan fish, the fish population probably did not reflect the environment of the pond as much as it did the original stocking. Onized Lake, which contained the second greatest proportion of warmouths (6.5 per cent) that Bennett found in a population, was an old pond with heavy marginal vegetation that favored these fish. Warmouths in Onized Lake may have been favored also by extremely heavy and selective fishing that had resulted in the removal of large numbers of fish of other species.

The fish population in four shallow, mud-bottomed backwater areas of the Mississippi River contained low percentages of warmouths (Upper Mississippi River Conservation Committee 1947:25–7 and 1948:23–4). Two of the areas, near Savanna, Illinois, contained respectively 0.3 per cent and 1.0 per cent warmouths by weight. The two other areas, near Oquawka, Illinois, contained respectively 0.2 per cent and 1.4 per cent warmouths by weight, table 4.

Turbidity

Forbes & Richardson (1920: 246) concluded that the waters in which they found the warmouth in their Illinois collections indicated for this fish "a deliberate preference for muddy water over pure." Certainly the warmouth, now as in the time of Forbes and Richardson, is found more frequently and in greater abundance in muddy or turbid waters, usually characteristic of lowland lakes, backwater areas, and sluggish streams, than in less turbid waters.

However, the occurrence or abundance of the warmouth in turbid waters may not indicate a direct preference of this fish for these waters. Rather, it may show that the warmouth has a greater tolerance of turbid waters and conditions associated with turbidity than have most other sunfishes. This tolerance may give the warmouth certain advantages in a population in which it must compete with many species and may account for its frequently comprising greater proportions of the total fish population in turbid waters than in clear.

Turbidity may affect growth rate of and fishing success for the warmouth. The

Table 4.—Data from fish censuses of 29 water areas containing warmouths: for each area the approximate weight per acre of the standing crop of fish and the percentage of the total weight comprised by warmouths.

Body of Water	Surface Area, Acres	Estimated Weight of all Fish, Pounds per Acre	Warmouths: Per Cent of Total Weight	Source of Data
Little Steep Pond (Florida)	2.10	105	10.55	Meehean 1942
First Pond (Florida)	7.00	110	0.99	
Big Prairie Lake (Florida)	4.00	61	1.87	
Buck Pond (Florida)	18.00	33	6.61	
Clearwater Lake (Florida)	24.00	22	0.82	
Upper Railroad Pond (Alabama)	6.50	292	0.07	Tarzwell 1942
Powerline Slough (Alabama)	1.10	831	0.07	
Sweetwater Slough (Alabama)	4.40	188	1.00	
Southside Country Club Lake (Illinois)	8.40	719	tr.	Bennett 1943
Homewood Lake (Illinois)	2.83	699	tr.	
Fork Lake (Illinois)	1.38	539	tr.	
Farmer City Golf Course Lake (Illinois)	0.75	455	tr.	
Upper Twin Lake (Illinois)	1.08	392	tr.	
Black Jack Lake (Illinois)	4.00	280	tr.	
Delta Pond (Illinois)	0.80	234	10.7	
Onized Lake (Illinois)	2.14	206	6.5	
Duck Pond, Pollywog Assn. (Illinois)	3.10	673	1.1	
Triangle Pond, Pollywog Assn. (Illinois)	2.50	487	1.5	
Duck Island Farm Lake (Illinois)	4.90	316	tr.	
Sportsmen's Lake (Illinois)	3.70	341	tr.	
Lower Twin Lake (Illinois)	1.36	778	1.0	
Lake Glendale (Illinois)	82.00	86	5.0	Hansen unpublished
Park Pond Slough, Pollywog Assn. (Illinois)	0.47	371	10.4	Present study
Mississippi River				Upper Mississippi
Backwaters, Oquawka (Illinois)				River Conservation
Area 1	1.07	391	0.2	Committee 1947,
Area 2	1.76	695	1.4	1948
Backwaters, Savanna (Illinois)				
Slough 1	2.16	171	0.3	
Slough 2	0.96	423	1.0	
Lamer's Upper Pond (Illinois)	0.25	516	4.7	Elder & Lewis 1955
Lamer's Lower Pond (Illinois)	0.50+	285	3.3	

best fishing for warmouths in experimental areas of central Illinois is in moderately clear water, the poorest fishing in turbid waters. Jenkins, Elkins, & Finnell (1955:42) found the slowest growing Oklahoma warmouth populations in waters known to be continuously turbid.

In a comparison of fish populations in two southern Illinois ponds, one of which was more turbid than the other, Elder & Lewis (1955:394) reported that reproduction and the coefficient of condition of warmouths was better in the less turbid pond, although growth was somewhat better for the warmouths in the more turbid pond. As the two ponds differed in age, size, density of fish population, and fertility, turbidity was not the only factor that might have been responsible for differences in growth.

Depth

Several field observations indicate that small warmouths remain in shallow weed beds, or other dense cover, for their food and protection, whereas larger warmouths spend more time in deeper water.

In Venard Lake, small warmouths were collected in great numbers from the riprapping along the dam, fig. 3, where they were hiding beneath submerged rocks. Seldom were large warmouths taken from under these rocks; except during the spawning season, most of the fish of larger sizes were taken from deeper water.

Relatively few warmouths of desirable sizes were found in a weed-choked channel of Park Pond, although many large individuals were taken in Park Pond proper.

In Park Pond, winter collecting with an electric shocker turned up large numbers of small warmouths in shallow water close to the banks, although at that time the surface of the pond was covered with thin ice.

Apparently, small warmouths do not leave their protected hiding places in shallow water even during cold weather. This behavior contrasts sharply with that of bluegills. Bluegills, most numerous of the

Fig. 3.—Warmouths, stunned with an electric fish shocker, near the riprapping of the dam at Venard Lake.

kinds of fishes collected along the banks of Park Pond through summer months, were taken there in far fewer numbers after the beginning of cold weather. In the winter, bluegills of all sizes were ordinarily collected in compact schools in deeper water. Large warmouths were likewise in relatively deep water but showed little tendency to group together. The conclusions suggested here are that (1) warmouths of less than 5 inches total length remain in protective cover in shallow water the year around; (2) large individuals spend more time in deep than in shallow water; (3) warmouths exhibit no tendency to group together during the winter months.

Dissolved Oxygen

Observations in the field and laboratory indicate that warmouths may survive in habitats having low concentrations of dissolved oxygen. An example of the tolerance of warmouths for a low oxygen concentration was observed on April 27, 1947, when 23 of 50 fish in an overcrowded aquarium were found dead; of the 50 fish,

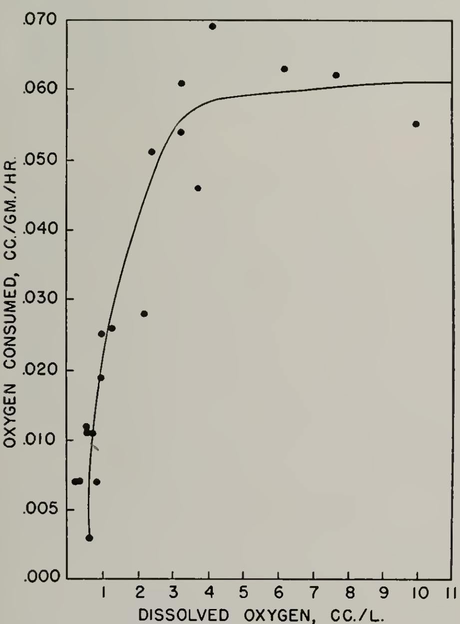

Fig. 4.—Amounts of oxygen consumed (cubic centimeters per gram per hour) by warmouths in water of different oxygen tensions (cubic centimeters per liter) at 20 degrees C.

about half were warmouths and half were bluegills. Of the 23 fish that were dead, all were bluegills. The few bluegills that were still living were light colored and obviously sick. All warmouths, however, were alive and showed very little or no distress.

Warmouths are among the last species of fish to die when collections of live fish are concentrated in tanks, tubs, or buckets containing water. For example, on November 12, 1949, between 9:30 A.M. and 2:15 P.M., many bluegills and warmouths were taken alive from Park Pond. The morning and afternoon collections were placed in separate fish tanks in a truck. No compressed air was supplied to the water in these tanks, and consequently many fish were dead when the tanks reached the laboratory late in the afternoon. In the tank containing the morning collection, all of the bluegills (about 30) were dead, whereas 40 warmouths in the same container showed only mild signs of distress. Of 50 bluegills collected in the afternoon, only a few remained alive, whereas 24 warmouths collected at the same time and kept in the same tank were in excellent condition.

In order to test the tolerance of warmouths for low concentrations of dissolved oxygen, Leonard Durham and I measured the oxygen consumption of warmouths confined in water containing different amounts of this gas. Dr. C. L. Prosser, Professor of Physiology, University of Illinois, suggested the laboratory procedures for these tests, the results of which supported our observations made in the field.

The Winkler method was used to determine oxygen concentrations of two samples of water, one sample taken at the beginning and one at the end of the test period. The difference between the two samples in cubic centimeters of oxygen per liter of water multiplied by the number of liters of water in the test jar (volume of jar minus volume of water displaced by fish) gave the total amount of oxygen consumed by the fish; the number of cubic centimeters of oxygen used per gram of fish per hour (cc./gm./hr.) was then calculated.

The amount of oxygen used by the test warmouths in water at 20 degrees C. ranged between 0.05 and 0.07 cc./gm./hr.

as long as the available dissolved oxygen in the water exceeded 3 cc. per liter, fig. 4. The consumption of oxygen by the warmouths dropped off abruptly from 0.03 cc./gm./hr. when the dissolved oxygen in the water was 2.5 cc. per liter to less than 0.01 cc./gm./hr. when it was 0.5 cc. per liter. The concentration of dissolved oxygen at which oxygen consumption by the fish declines abruptly is the critical oxygen tension or the oxygen concentration at which the metabolic rate of the fish begins to fall off rapidly. Even though this critical oxygen tension is not lethal immediately it will ultimately be so. For the warmouths in our tests, the critical tension figure was found to be 2.5 cc. per liter (3.6 p.p.m.) at 20 degrees C.

This critical tension figure is close to that determined by Moore (1942:327) after he had studied 13 species of freshwater fishes, including the largemouth bass, the bluegill, the pumpkinseed, and other species which are often associated with the warmouth. Moore stated, "In general, oxygen tensions of less than 3.5 p.p.m. at temperatures of 15-26° C. are fatal within 24 hrs. to most of the species tested."

Although the warmouths in our tests were removed before complete asphyxiation, several specimens had reduced the dissolved oxygen in the water to low concentrations. Only 0.21 cc. of oxygen per liter of water remained at the end of one test on warmouths, 0.24 cc. at the end of another.

Conclusions from the tests described above not only suggest reasons for survival of the warmouth during periods of water conditions that are generally considered unfavorable to fish but also indicate certain of the warmouth's physiological characteristics that are associated with its habitat selection. Turbid waters, organic silt deposits, and dense vegetation, usually regarded as typical features of warmouth habitats, are associated with high oxygen demands and, at times, low concentrations of dissolved oxygen.

Stream Gradient

The abundance of warmouths in flowing waters appears to be related to stream gradient; the occurrence of these fish increases from rare in fast-moving creeks to common in sluggish streams with a low gradient. I have collected warmouths in several central Illinois streams having gradients between 8 and 14 feet per mile, but I have never collected them in large numbers. Nelson (1876:37) mentioned that Professor S. A. Forbes found this species "very common" in the Illinois River and tributaries through central Illinois; and Forbes & Richardson (1920:246) reported it "common" in southern Illinois, "mainly in the smaller streams." The Illinois River has a generally low gradient, and the small streams of southern Illinois in which warmouths are now commonly reported have low gradients.

FOOD HABITS

The food habits of warmouths from Park Pond and Venard Lake were studied through a period of 12 months. The objectives of this study were to determine the kinds and amounts of food consumed and the ways in which food habits of the warmouths were influenced by habitat, season of year, daily feeding periods, size of individual fish, and competing species of fish. Consideration was given to the possible effects of two different computing methods on the interpretation of the data.

Methods of Study

For the food habits study, warmouths were collected from Park Pond and Venard Lake, for the most part at monthly intervals over a period beginning in October, 1948, and ending in September, 1949. Heavy ice prevented collecting from Park Pond in January and from Venard Lake in January and February. Extra collections were taken from Park Pond during the summer months as a means of determining diurnal feeding periods.

No attempt was made to measure the relative abundance of food organisms in the water areas.

A total of 515 warmouth stomachs were collected from Park Pond; of these, 124 were empty and 391 contained food in varying amounts. Of 413 warmouth stomachs taken at Venard Lake, 57 were empty and 356 contained food materials in measurable amounts.

All fish were taken with a rowboat fish shocker (Larimore, Durham, & Bennett 1950), fig. 5. Regurgitation of food by the fish was not caused by the shocker as it was used in this study. While the fish were fresh, their stomachs were removed and placed in cheesecloth bags; the bags were labeled and placed in formalin. Other parts of the digestive tracts were discarded.

In the laboratory, each stomach was first studied as a unit. The contents were removed and their total volume was measured. Then the contents were sorted under a dissecting microscope (magnification 9 to 48 times) into various taxonomic categories, table 5. The number of individual organisms and the volume of each kind of food were determined. Volumetric measurement was made by one of two methods: large, irregular masses of food were measured by water displacement in a calibrated centrifuge tube; small, compact items were measured by comparison with cork blocks of known volumes. This second method was devised by the late R. E. Richardson, for several years employed by the Illinois Natural History Survey. It was found to be convenient and reliable. When items were measured by both methods, the volume determined by one method agreed closely with the volume determined by the other. The sum of volumes of the different kinds of food in each stomach was checked against the total volume recorded for each stomach when the contents were removed.

Fig. 5.—An electric fish shocker being used from a rowboat to collect warmouths in Park Pond.

After data for the sorted food materials had been tabulated, calculations were made that involved (1) the percentage of stomachs in which each kind of food occurred (*frequency of occurrence*), (2) the average number of items of each kind of food in the stomachs containing the food (*average number of items*), (3) the average of the percentages of volume comprised by each of the kinds of food in each of the stomachs examined (*average of volume percentages*), and (4) the percentage of the total volume of all foods represented by each kind of food (*percentage of total volume*). These calculations and similar calculations for largemouth bass used with the warmouths of Venard Lake are summarized in tables 6–12.

Table 5.—Food organisms taken from the stomachs of 391 warmouths from Park Pond, 356 warmouths from Venard Lake, and 99 largemouth bass from Venard Lake; also, for each kind of organism taken from the stomachs, its occurrence rating, based on the number of stomachs in which it was found: abundant (A), common (C), rare (R), or present but with no record of abundance (X).

Food Organism	Park Pond	Venard Lake	
	Warmouth	Warmouth	Largemouth Bass
Cestoda			
Proteocephalidae	...	R	R
Bryozoa			
Plumatella sp.	R	R	...
Annelida			
Oligochaeta	...	R	...
Gastropoda			
Planorbidae			
Gyraulus probably *parvus* (Say)	C	...	...
Ancylidae	...	...	R
Lymnaeidae	C	...	...
Physidae			
Physa integra Haldeman	C	A	...
Physa probably *gyrina* Say	C	...	...
Cladocera			
Simocephalus sp.	A	A	A
Daphnia sp.	...	R	...
Chydorus (?) sp.	...	R	...
Alona (?) sp.	...	R	...
Copepoda			
Cyclops sp.	A	A	C
Ostracoda	A	C	...
Amphipoda			
Hyalella azteca (Saussure)	A	R	...
Isopoda			
Asellus sp.	C	A	...
Decapoda	A	A	A
Procambarus blandingii acutus (Girard)	X	X	X
Orconectes virilis (Hagen)	X	X	X
Orconectes propinquus propinquus (Girard)	X	...	...
Araneae			
Lycosidae	...	...	R
Pisauridae			
Dolomedes triton sexpunctatus Hentz	C	C	C
Hydrachnellae			
Limnesia fulgida Koch	...	R	R
Arrenurus sp.	R	...	...
Collembola			
Podura aquatica Linnaeus	...	R	...
Ephemeroptera			
Caenis sp.	A	A	A
Siphlonurus sp.	C	A	A
Hexagenia limbata (Serville)	R	...	...
Odonata			
Zygoptera	A	A	A
Argia apicalis (Say)	...	...	X
Enallagma basidens Calvert	...	...	X
E. carunculatum Morse	...	...	X
E. civile (Hagen)	...	...	X
E. signatum (Hagen)	...	...	X
Ischnura posita (Hagen)	...	X	...
I. verticalis (Say)	...	X	X
Perithemis tenera (Say)	...	...	X
Anisoptera	A	A	A
Celithemis sp.	...	X	X
Epicordulia princeps (Hagen)	...	X	...
Erythemis simplicicollis (Say)	...	X	...
Leucorrhinia sp.	...	...	X
Libellula pulchella Drury	...	X	X
Pachydiplax longipennis (Burmeister)	...	X	...

Table 5.—*Continued.*

Food Organism	Park Pond	Venard Lake	
	Warmouth	Warmouth	Largemouth Bass
Plathemis lydia (Drury)	...	...	X
Sympetrum obtrusum (Hagen)	...	X	...
Tetragoneuria sp.	...	X	...
Hemiptera			
Corixidae	C	C	C
Notonectidae	R	R	C
Nepidae			
Ranatra sp.	R	...	...
Belostomatidae			
Belostoma sp.	R	...	...
Veliidae			
Microvelia sp.	C	C	C
Rhagovelia sp.	C	...	R
Gerridae			
Gerris sp.	C	C	C
Homoptera			
Membracidae	...	...	R
Neuroptera			
Sisyridae	...	R	...
Megaloptera			
Sialidae			
Sialis sp.	R	...	...
Hymenoptera			
Formicidae	R	...	C
Apidae			
Apis mellifera Linnaeus	...	...	C
Coleoptera			
Haliplidae			
Haliplus sp.	R	C	...
Peltodytes sp.	C	A	A
Dytiscidae			
Ilybius sp.	R	...	R
Hydroporus sp.	...	C	...
Hydrophilidae			
Berosus sp.	C	C	...
Tropisternus sp.	R	C	...
Buprestidae	...	...	R
Chrysomelidae			
Phyllotreta sp.	...	...	R
Elateridae			
Melanotus sp.	R	...	...
Scarabaeidae			
Ataenius sp.	...	R	R
Phyllophaga probably *futilis*	R	...	...
Trichoptera			
Hydroptilidae	A	A	R
Oecetis cinerascens (Hagen)	X	...	...
Oecetis inconspicua (Walker)	X	...	...
Oxyethira sp.	...	X	X
Orthotrichia sp.	X	...	...
Phryganeidae	A	A	C
Diptera			
Chironomidae	A	A	A
Ceratopogonidae	...	A	C
Culicidae			
Chaoborus sp.	R	A	A
Syrphidae			
Eristalis sp.	R	R	...
Stratiomyidae	R	R	...
Tabanidae	R	...	...
Pisces			
Chaenobryttus gulosus (Cuvier)	C	C	A
Lepomis m. macrochirus Rafinesque	C	...	...
Micropterus salmoides (Lacépède)	...	C	C

The reason for calculating the volume of each kind of food by both average of volume percentages and percentage of total volume is that these two calculations give very different expressions of volume. The average of volume percentages is influenced by frequency of occurrence of a kind of food but not by the size of a stomach nor its fullness; thus, it gives the stomach contents of a small fish the same importance as those of a large fish and favors small food items that appear in a high percentage of stomachs. On the other hand, the percentage of total volume emphasizes the importance of large food items and therefore the diet of large fish. Since the percentage of total volume of a food is not affected by frequency of occurrence (the percentage of stomachs in which the food occurs), it does not reflect the food habits of individuals of a population but rather the foods consumed by the population as a whole. A few large items might be important as food to a few large fish but of no value to the smaller members of that population.

Although the above differences have been discussed in other food studies (Bennett, Thompson, & Parr 1940: 18; Martin, Gensch, & Brown 1946; Beck 1952: 398; Reintjes & King 1953: 96), a complete food analysis employing both methods has not been published to illustrate erroneous conceptions inherent in references to volume as a percentage without defining its derivation or meaning.

Principal Foods in Two Habitats

Food items of many kinds were found in the stomachs of warmouths collected from Park Pond and Venard Lake, table 5. Considerable differences exist in the taxonomic levels to which the food items were identified.* A similar situation is found in most food studies of fish and generally is due to difficulties in the exact identification of fragmentary animal remains. In groups such as Odonata, individuals of which were found in large numbers in the warmouth stomachs and which were represented by many species not distinguishable except by a specialist, only selected collections were identified to species. These identifications extended the number of species found in warmouth stomachs but provided no information as to the relative abundance of individual members of these species.

*Identifications of selected collections were made by the following persons: Dr. H. H. Ross (Trichoptera), Dr. M. W. Sanderson (Coleoptera and miscellaneous groups), Dr. L. J. Stannard, Jr. (Hydrachnellae), Mrs. Leonora K. Gloyd (Odonata), Mr. Robert Snetsinger (Araneae), Dr. T. E. Moore (Hemiptera), and Dr. W. R. Richards (Diptera), all at the time of this study with the Illinois Natural History Survey; Dr. B. D. Burks, with the Division of Insect Identification of the United States Department of Agriculture (Ephemeroptera); Mr. Glenn R. Webb, Ohio, Illinois (Gastropoda); and Dr. H. H. Hobbs, Jr., University of Virginia (Decapoda).

In both frequency of occurrence and volume, the foods of warmouths collected from Park Pond differed from the foods of warmouths collected from Venard Lake, tables 6–11. The six foods that, on the basis of their volume and the percentage of stomachs in which they were found, were judged to be most important for each of the two areas are considered below. Less important food groups that appeared to be significant in the warmouth diet are mentioned as miscellaneous foods.

Park Pond.—Four of the food groups listed among the six most important in Park Pond were included among the six most important in Venard Lake. These were the Decapoda, Ephemeroptera, Zygoptera, and Anisoptera. Trichoptera and Pisces, among the six most important in Park Pond, were comparatively unimportant in Venard Lake.

Decapoda.—Crayfish, which ranked first in bulk as a warmouth food at Park Pond, made up 50 per cent of the total volume consumed by warmouths collected from this pond. Decapods were found in 19 per cent of the stomachs; the average of their volume percentages amounted to 14. Crayfish were important for a few warmouths (generally the larger ones) but of relatively little value to the others.

Ephemeroptera.—Forty-one per cent of the warmouth stomachs from Park Pond contained mayfly nymphs (no adult mayflies were found). These nymphs comprised less than 1 per cent of the total volume, but the average of their volume percentages was 10. Nymphs of three genera were identified: *Caenis* sp. was the only mayfly abundant in the stomachs; *Siphlonurus* sp. was uncommon and *Hexagenia limbata* was rare.

Zygoptera.—Damselflies (mostly nymphs) occurred in 34 per cent of the stomachs of Park Pond warmouths. They made up 2 per cent of the total volume; the average of their volume percentages was 16. Eight species (four genera) were identified; no tabulation was made of the percentage comprised by each species.

Anisoptera.—Dragonflies were less important than damselflies in the stomachs of Park Pond warmouths. Dragonfly nymphs, found in 14 per cent of the stomachs, made up only 2 per cent of the total volume of food; 6 was the average of their volume percentages. Nine genera of dragonflies were identified.

Trichoptera.—Caddisfly larvae occurred in a high percentage (36 per cent) of the warmouth stomachs from Park Pond but amounted to only 3 per cent of the total volume; 13 was the average of their volume percentages. The specimens identified belonged to the families Hydroptilidae and Phyrganeidae.

Pisces.—Fishes ranked second to crayfish in total volume of food in the stomachs of Park Pond warmouths. They made up 36 per cent of the total volume and occurred in 18 per cent of the stomachs; 14 was the average of their volume percentages. Small sunfishes were most common, but single individuals of several species other than sunfishes were included.

Miscellaneous.—Among the food items somewhat less important in the diet of Park Pond warmouths than the six listed above were the amphipods. These occurred in 24 per cent of the stomachs from Park Pond but were absent from the Venard Lake collections. Diptera larvae or pupae (mostly chironomids) were identified in 38 per cent of the stomachs of Park Pond warmouths but comprised less than 1 per cent of the total volume of food. Sixteen per cent of the stomachs contained cladocerans.

Venard Lake.—The most striking difference in diet between the warmouths of the two water areas was in the number of fish consumed. Fish were found in less than 2 per cent of the warmouth stomachs from Venard Lake in contrast to 18 per cent of the stomachs from Park Pond.

Isopoda.—Eleven per cent of the total volume of food in the stomachs of warmouths collected from Venard Lake consisted of *Asellus* sp. (a form previously considered *A. communis*), which occurred in 27 per cent of the stomachs examined. Isopods were found in only about 1 per cent of the warmouth stomachs collected from Park Pond.

Decapoda.—Crayfish occurred in only 10 per cent of the warmouth stomachs collected from Venard Lake and comprised 15 per cent of the total volume of food in these stomachs. They ranked second in percentage of total volume in Venard Lake stomachs, but the percentage was low in comparison to that in Park Pond stomachs (50 per cent of total volume).

Ephemeroptera.—Mayfly nymphs, like crayfish, comprised 15 per cent of the total volume of food in warmouth stomachs from Venard Lake, but they could be considered more important as food because they were found in a larger percentage (43 per cent) of the stomachs. An average of 10 nymphs per stomach was found in the stomachs that contained mayflies. *Caenis* sp. was the mayfly most often found in warmouth stomachs from Venard Lake. *Siphlonurus* sp. was found in a larger percentage of stomachs from Venard Lake than from Park Pond.

Zygoptera.—Damselfly nymphs ranked fifth in frequency of occurrence (14 per cent of the stomachs) and fifth in total volume (7 per cent) of food in the warmouth stomachs from Venard Lake.

Anisoptera.—Dragonfly nymphs or emerging adults comprised the greatest volume of food (38 per cent of total volume) in the warmouth stomachs from Venard Lake. They were found in 17 per cent of the stomachs. Nine different species of dragonflies were recognized.

Diptera.—Forty-four per cent of the warmouth stomachs from Venard Lake contained Diptera larvae or pupae. Dipterans comprised only 2 per cent of the total volume; 12 was the average of their volume percentages. Five families of Diptera were represented.

Miscellaneous.—Caddisflies were found in 21 per cent of the stomachs from Venard Lake, a smaller percentage than in the stomachs from Park Pond. Cladocerans occurred in 51 per cent of the stomachs from Venard Lake, ostracods and copepods in smaller percentages of the stomachs. Cestodes, annelids, and collembolans were represented in the stomachs of warmouths from Venard Lake but not in the stomachs of warmouths from Park Pond.

Table 6.—Stomach contents of 64 warmouths collected

Food Item	Stomachs From 38 Fish of Less Than 5.0 Inches			
	Percentage of Stomachs Containing Organism	Average Number of Organisms in Stomachs Containing Them	Average of Volume Percentages	Percentage of Total Volume
Gastropoda	8	2	0.7	0.3
Cladocera	11	6	3.6	0.2
Copepoda	3	1	tr.	tr.
Amphipoda	13	2	3.2	0.3
Isopoda	3	1	2.1	0.1
Decapoda	0	0	0.0	0.0
Araneae	3	1	0.1	0.1
Ephemeroptera	32	3	16.9	1.5
Zygoptera	32	2	21.3	5.8
Anisoptera	21	1	18.6	20.9
Hemiptera	5	1	3.0	0.1
Neuroptera	3	1	0.1	1.4
Coleoptera larvae	3	12	2.6	5.0
Trichoptera	16	1	8.0	2.1
Diptera	24	1	3.2	0.4
Pisces	21	1	15.7	59.8
Filamentous algae	5	....	0.4	1.6
Higher plants	5	....	0.6	0.3
Organic debris	0	....	0.0	0.0

Table 7.—Stomach contents of 79 warmouths

Food Item	Stomachs From 52 Fish of Less Than 5.0 Inches			
	Percentage of Stomachs Containing Organism	Average Number of Organisms in Stomachs Containing Them	Average of Volume Percentages	Percentage of Total Volume
Bryozoa	0	0	0.0	0.0
Gastropoda	8	1	0.9	0.5
Cladocera	23	3	5.1	0.4
Copepoda	13	3	3.4	0.1
Ostracoda	4	2	0.5	tr.
Amphipoda	37	2	5.6	1.2
Isopoda	2	1	0.1	0.1
Decapoda	13	1	3.7	2.3
Ephemeroptera	56	2	10.7	3.5
Zygoptera	52	2	27.3	25.9
Anisoptera	8	1	2.4	3.2
Hemiptera	2	1	0.1	0.1
Hymenoptera	0	0	0.0	0.0
Coleoptera adults	0	0	0.0	0.0
Trichoptera	40	3	12.0	12.8
Diptera	23	5	15.3	6.4
Pisces	2	1	1.8	30.6
Filamentous algae	6	....	0.5	0 2
Higher plants	8	....	1.1	0.4
Organic debris	23	....	9.6	12 4

from Park Pond in December, 1948, and January, 1949.

Stomachs From 26 Fish of 5.0 Inches or More				Stomachs From All 64 Fish			
Percentage of Stomachs Containing Organism	Average Number of Organisms in Stomachs Containing Them	Average of Volume Percentages	Percentage of Total Volume	Percentage of Stomachs Containing Organism	Average Number of Organisms in Stomachs Containing Them	Average of Volume Percentages	Percentage of Total Volume
0	0	0.0	0.0	5	2	0.4	0.1
8	1	tr.	tr.	9	4	2.1	tr.
0	0	0.0	0.0	2	1	tr.	tr.
0	0	0.0	0.0	8	2	1.9	0.1
4	1	tr.	0.1	3	1	1.3	0.1
23	1	16.2	45.0	9	1	6.6	36.6
4	1	0.8	0.4	3	1	0.4	0.3
12	2	4.0	0.1	23	3	11.6	0.4
23	1	15.0	0.3	28	2	18.8	1.3
8	2	3.8	2.0	16	1	12.6	5.5
0	0	0.0	0.0	3	1	1.8	tr.
0	0	0 0	0.0	2	1	0.1	0.3
0	0	0.0	0.0	2	12	1.5	0.9
4	1	0.1	0.4	11	1	4.8	0.7
15	1	3.9	0.1	20	1	3.5	0.1
50	1	46.8	51.3	33	1	28.3	52.9
0	0	0.0	0.0	3	....	0.2	0.3
15	....	1.0	0.3	9	....	0.8	0.3
15	....	8.5	0.1	6	....	3.4	0.1

collected from Park Pond in March–May, 1949.

Stomachs From 27 Fish of 5.0 Inches or More				Stomachs From All 79 Fish			
Percentage of Stomachs Containing Organism	Average Number of Organisms in Stomachs Containing Them	Average of Volume Percentages	Percentage of Total Volume	Percentage of Stomachs Containing Organism	Average Number of Organisms in Stomachs Containing Them	Average of Volume Percentages	Percentage of Total Volume
4	1	3.7	tr.	1	1	1.3	tr.
4	1	3.5	tr.	6	1	1.8	0.1
0	0	0.0	0.0	15	3	3.4	tr.
0	0	0.0	0.0	9	3	2.2	tr.
0	0	0.0	0.0	3	2	0.3	tr.
4	1	0.2	tr.	25	2	3.8	0.1
0	0	0.0	0.0	1	1	tr.	tr.
59	1	43.1	60.9	29	1	17.1	56.2
11	2	0.8	1.1	40	2	7.4	1.3
40	1	8.4	0.8	47	2	20.9	2.9
15	1	4.5	0.8	10	1	3.1	1.0
4	1	tr.	tr.	3	1	0.1	tr.
4	1	3.0	0.2	1	1	1.0	0.1
7	1	0.5	tr.	3	1	0.2	tr.
19	2	3 2	0.3	33	3	9.0	1.3
30	2	1 4	0.2	39	4	10.6	0.7
15	1	11.6	29.7	6	1	5.1	29.7
4	....	0 6	0.1	5	....	0.6	0.1
52	....	6.0	5 1	23	....	2.8	4.7
26	....	9.4	0.9	24	....	9.5	1.8

Table 8.—Stomach contents of 131 warmouths

Food Item	Stomachs From 98 Fish of Less Than 5.0 Inches			
	Percentage of Stomachs Containing Organism	Average Number of Organisms in Stomachs Containing Them	Average of Volume Percentages	Percentage of Total Volume
Gastropoda	14	2	2.1	0.6
Cladocera	24	5	4.3	0.3
Copepoda	10	5	1.6	0.1
Ostracoda	5	4	0.1	tr.
Amphipoda	35	3	3.2	1.3
Decapoda	16	1	11.4	30.1
Araneae	1	1	tr.	0.1
Ephemeroptera	58	4	11.6	4.6
Zygoptera	47	2	19.5	12.4
Anisoptera	17	1	5.1	5.0
Hemiptera	6	1	0.5	0.3
Hymenoptera	0	0	0.0	0.0
Coleoptera larvae	1	1	tr.	tr.
Coleoptera adults	4	1	0.1	0.1
Trichoptera	52	5	17.3	15.9
Diptera	49	3	5.9	3.1
Pisces	16	2	9.8	22.4
Filamentous algae	4	....	0.2	0.3
Higher plants	11	....	1.2	1.0
Organic debris	17	....	5.1	2.4

Table 9.—Stomach contents of 117 warmouths collected from

Food Item	Stomachs From 93 Fish of Less Than 5.0 Inches			
	Percentage of Stomachs Containing Organism	Average Number of Organisms in Stomachs Containing Them	Average of Volume Percentages	Percentage of Total Volume
Gastropoda	11	2	2.2	0.4
Cladocera	20	17	3.7	0.6
Copepoda	15	9	1.7	0.3
Ostracoda	3	3	0.1	tr.
Amphipoda	35	2	6.8	0.7
Isopoda	1	11	1.1	0.6
Decapoda	4	1	3.5	20.7
Araneae	1	1	0.8	3.9
Hydrochnellae	1	1	0.1	tr.
Ephemeroptera	49	2	12.9	2.0
Zygoptera	24	2	10.9	3.5
Anisoptera	15	1	7.2	5.0
Hemiptera	7	2	2.7	2.0
Coleoptera larvae	1	1	0.1	tr.
Coleoptera adults	1	1	0.1	tr.
Trichoptera	46	3	18.8	7.5
Diptera	55	3	11.3	2.2
Pisces	11	1	8.0	48.9
Filamentous algae	3	....	0.5	0.1
Higher plants	8	....	0.9	0.8
Organic debris	14	....	6.3	0.7

collected from Park Pond in June–August, 1949.

Stomachs From 33 Fish of 5.0 Inches or More				Stomachs From All 131 Fish			
Percentage of Stomachs Containing Organism	Average Number of Organisms in Stomachs Containing Them	Average of Volume Percentages	Percentage of Total Volume	Percentage of Stomachs Containing Organism	Average Number of Organisms in Stomachs Containing Them	Average of Volume Percentages	Per-centage of Total Volume
3	1	tr.	tr.	11	2	1.6	0.1
0	0	0.0	0.0	18	5	3.2	0.1
0	0	0.0	0.0	8	5	1.2	tr.
0	0	0.0	0.0	4	4	0.1	tr.
3	1	tr.	tr.	27	3	2.4	0.3
55	1	49.4	73.3	26	1	21.0	64.3
3	1	tr.	tr.	2	1	tr.	tr.
30	1	0.5	0.1	51	3	8.8	1.0
15	1	5.8	0.3	39	2	16.0	2.8
9	1	6.3	2.7	15	1	5.4	3.2
3	1	0.2	tr.	5	1	0.4	0.1
6	1	0.1	tr.	2	1	tr.	tr.
6	1	0.8	tr.	2	1	0.2	tr.
6	1	3.1	0.2	5	1	0.8	0.2
27	1	2.4	1.0	46	4	13.5	4.1
6	4	1.0	tr.	38	3	4.7	0.7
30	1	23.8	21.8	20	2	13.4	21.9
27	....	1.2	tr.	10	....	0.5	0.1
24	....	1.4	0.4	14	....	1.2	0.5
12	....	2.2	0.1	16	....	4.3	0.6

Park Pond in September–November, 1948, and September, 1949.

Stomachs From 24 Fish of 5.0 Inches or More				Stomachs From All 117 Fish			
Percentage of Stomachs Containing Organism	Average Number of Organisms in Stomachs Containing Them	Average of Volume Percentages	Percentage of Total Volume	Percentage of Stomachs Containing Organism	Average Number of Organisms in Stomachs Containing Them	Average of Volume Percentages	Per-centage of Total Volume
4	1	1.2	tr.	9	2	2.0	0.1
0	0	0.0	0.0	16	17	3.0	0.2
0	0	0.0	0.0	12	9	1.3	0.1
0	0	0.0	0.0	3	3	0.1	tr.
8	2	0.4	tr.	30	2	5.5	0.2
0	0	0.0	0.0	1	11	0.8	0.2
29	1	27.4	36.1	9	1	8.4	31.9
12	1	8.3	3.4	3	1	2.4	3.6
0	0	0.0	0.0	1	1	0.1	tr.
4	1	2.8	tr.	40	2	10.8	0.5
12	1	6.4	tr.	21	2	10.0	1.0
8	2	0.4	0.5	14	1	5.8	1.7
8	1	0.1	tr.	9	2	2.2	0.6
0	0	0.0	0.0	1	1	0.1	tr.
8	1	0.6	tr.	3	1	0.2	tr.
25	2	16.5	3.2	42	2	18.3	4.4
12	2	1.1	0.1	46	3	9.2	0.6
33	1	26.4	55.6	15	1	11.8	53.8
0	0	0.0	0.0	3	....	0.4	tr.
21	....	5.4	0.5	10	....	1.8	0.6
12	....	3.2	0.5	14	....	5.6	0.5

Seasonal Trends

Each of the various seasons—winter, spring, summer, and fall—designated in the following discussion of seasonal trends in warmouth foods and feeding encompasses 3 months. The seasons are biological rather than astronomical; that is, they are based on similarities in the foods present and utilized by the fish. Winter includes December, January, and February; spring includes March, April, and May; summer includes June, July, and August; fall includes September, October, and November.

The degree to which the stomachs from individual warmouths of Park Pond and Venard Lake were judged to be full was found to be of little value as a measure for determining seasonal trends in feeding activities of the fish or relative amounts of food consumed by them in various seasons of the year. The stomachs from many fish contained one and one-half to two times as much food as apparently full stomachs from fish of similar sizes.

A better measure of seasonal feeding trends was found to be the average volume of stomach contents of warmouths of several size groups. This measure also proved to have its limitations, most important of which were concerned with differences in rates of digestion and daily feeding periods (discussed under "Daily Changes") that tended to mask the true seasonal trends.

Seasonal trends in average volume of stomach contents (empty stomachs excluded) were apparent in three length groups of warmouths taken from Park Pond. In the warmouths of each of two groups, 3.5–4.9 and 5.0–6.4 inches total length, the average volume increased progressively in the three seasons following winter; the average volume in the fall was two to three times that in the winter. In a group of smaller warmouths (2.0–3.4 inches total length), the average volume of stomach contents was greatest in summer;

Table 10.—Stomach contents of 71 warmouths collected in winter (December, 1948) and 81 warmouths collected in spring (March–May, 1949), all from Venard Lake.

Food Item	Stomachs From 71 Warmouths Collected in Winter				Stomachs From 81 Warmouths Collected in Spring			
	Percentage of Stomachs Containing Organism	Average Number of Organisms in Stomachs Containing Them	Average of Volume Percentages	Percentage of Total Volume	Percentage of Stomachs Containing Organism	Average Number of Organisms in Stomachs Containing Them	Average of Volume Percentages	Percentage of Total Volume
Bryozoa	0	0	0.0	0.0	1	2	tr.	tr.
Annelida	0	0	0.0	0.0	1	1	0.4	0.4
Gastropoda	3	1	0.7	0.2	0	0	0.0	0.0
Cladocera	96	18	28.9	13.4	56	11	9.6	0.8
Copepoda	45	7	3.0	1.6	20	3	1.0	tr.
Ostracoda	1	1	tr.	tr.	0	0	0.0	0.0
Isopoda	45	3	27.8	48.5	57	2	29.1	13.9
Decapoda	0	0	0.0	0.0	2	1	1.0	3.3
Hydrachnellae	0	0	0.0	0.0	1	1	tr.	tr.
Collembola	0	0	0.0	0.0	1	1	tr.	tr.
Ephemeroptera	56	3	21.2	12.1	60	24	20.8	20.4
Zygoptera	4	1	2.1	3.9	35	3	8.7	8.1
Anisoptera	6	1	3.1	15.8	36	3	23.4	47.8
Neuroptera	0	0	0.0	0.0	1	1	tr.	tr.
Coleoptera larvae	0	0	0.0	0.0	7	1	0.2	0.1
Trichoptera	3	1	0.2	0.1	26	5	2.3	2.1
Diptera	48	2	12.8	4.4	38	7	1.4	1.3
Filamentous algae	1	....	tr.	0.1	2	....	tr.	0.1
Higher plants	0	0	0.0	0.0	15	....	0.3	0.2
Organic debris	1	....	tr.	0.1	23	....	1.7	1.3

Table 11.—Stomach contents of 107 warmouths collected in summer (June–August, 949) and 97 warmouths collected in autumn (October–November, 1948, and September, 1949), ll from Venard Lake.

Food Item	Stomachs From 107 Warmouths Collected in Summer				Stomachs From 97 Warmouths Collected in Autumn			
	Percentage of Stomachs Containing Organism	Average Number of Organisms in Stomachs Containing Them	Average of Volume Percentages	Percentage of Total Volume	Percentage of Stomachs Containing Organism	Average Number of Organisms in Stomachs Containing Them	Average of Volume Percentages	Percentage of Total Volume
estoda	3	1	0.5	1.6	0	0	0.0	0.0
astropoda	5	2	2.1	1.5	10	3	3.0	5.6
ladocera	32	13	9.3	0.9	37	16	8.6	4.5
opepoda	11	3	0.8	tr.	37	7	7.4	0.3
stracoda	16	5	2.4	0.2	31	24	10.0	0.5
opoda	8	2	1.6	0.4	9	3	5.2	1.1
ecapoda	24	1	18.0	35.0	8	1	6.8	44.9
phemeroptera	33	4	9.7	6.1	31	6	5.9	3.3
ygoptera	9	1	5.0	3.6	10	3	4.5	4.7
nisoptera	10	2	7.2	25.0	16	2	10.1	22.8
emiptera	0	0	0.0	0.0	2	2	0.3	0.2
ymenoptera	0	0	0.0	0.0	1	1	tr.	tr.
oleoptera larvae	7	2	0.8	1.4	2	2	0.2	0.1
oleoptera adults	1	1	tr.	0.1	2	1	0.4	0.4
richoptera	34	4	18.7	8.4	16	3	7.4	3.0
iptera	40	2	12.5	1.2	49	7	18.5	4.2
isces	6	1	5.0	12.5	0	0	0.0	0.0
ilamentous algae	0	0	0.0	0.0	5	....	0.3	0.4
igher plants	9	....	1.1	0.9	8	....	0.8	1.0
rganic debris	10	....	5.1	1.6	20	....	10.7	2.9

he trend was downward through the seaons to the lowest figure of the year in pring.

Of some interest is the large number of mpty stomachs taken in the winter from he warmouths of Park Pond. Thirty-four er cent of the warmouth stomachs colected there in winter (44 per cent of the tomachs collected in January) contained o food. These high percentages may relect the influence of partial ice cover and old water on the feeding activities of warnouths. A large percentage of stomachs mpty at a time in which digestion was low indicated that the fish were going ong periods between feedings. A large roportion of stomachs empty in summer vas due to rapid digestion and reduced eeding activity after midday.

Tables 6–11 show seasonal changes in inds of food eaten by warmouths in Park Pond and Venard Lake, as indicated by nalysis of stomach contents.

The following discussion and figs. 6 and 7 emphasize the highs and lows of the seasonal trends in foods most commonly found in the warmouth stomachs from the two study areas.

Winter.—In the warmouth collections from Park Pond, fish (Pisces) were found in a larger percentage of stomachs in winter than in any other season, fig. 6. Crayfish (Decapoda), which ranked second to fish in percentage of total volume in winter, were present in only 9 per cent of the winter-collected stomachs examined (all of them from large fish) and did not comprise so large a percentage of the total volume in winter as during the spring and summer. Dipteran and caddisfly (Trichoptera) larvae, cladocerans, and amphipods were found in a smaller percentage of stomachs in winter than in any other season of the year.

In the warmouth collections from Venard Lake in winter, the animal groups

Table 12.—Stomach contents of 99 largemouth bass collected from Venard

Food Item	Stomachs From 23 Largemouth Bass Collected During March–May, 1949			
	Percentage of Stomachs Containing Organism	Average Number of Organisms in Stomachs Containing Them	Average of Volume Percentages	Percentage of Total Volume
Cestoda	0	0	0.0	0.0
Gastropoda	0	0	0.0	0.0
Cladocera	22	70	5.0	1.9
Copepoda	0	0	0.0	0.0
Isopoda	39	4	22.1	13.3
Decapoda	4	2	2.9	1.6
Araneae	0	0	0.0	0.0
Hydrachnellae	0	0	0.0	0.0
Ephemeroptera	83	17	10.3	7.4
Zygoptera	57	6	16.6	26.3
Anisoptera	61	3	36.9	37.8
Hemiptera	9	2	tr.	tr.
Homoptera	0	0	0.0	0.0
Hymenoptera	0	0	0.0	0.0
Coleoptera larvae	0	0	0.0	0.0
Coleoptera adults	0	0	0.0	0.0
Trichoptera	0	0	0.0	0.0
Diptera	39	5	1.0	0.5
Pisces	0	0	0.0	0.0
Filamentous algae	0	0	0.0	0.0
Higher plants	13	....	0.3	0.2
Organic debris	26	....	5.0	11.0

found in the largest percentages of stomachs were cladocerans, mayfly nymphs, dipteran larvae, copepods, and isopods; each of these groups was in winter at or near its peak for the year in the percentage of stomachs in which it was represented. Fish and crayfish, which in winter led all other food groups in percentage of Park Pond stomachs in which they were found, were not found in any of the Venard Lake stomachs during the winter.

Spring.—In the warmouth collections from both Park Pond and Venard Lake, the nymphs of damselflies were found in a larger percentage of stomachs, and comprised a somewhat larger percentage of total volume of food, in spring than at any other season. Mayfly nymphs were present in a larger percentage of the stomachs from Venard Lake in spring than at any other season; at this season, they were present in a large proportion of the stomachs from Park Pond, also.

In the Park Pond collections, the percentage of stomachs containing fish and the percentage containing dragonfly nymphs were lower in spring than at any other season. The fragments of so-called higher plants, mostly rootlets or parts of leaves, that were found in 23 per cent of the stomachs probably were taken accidentally with other organisms. About two-thirds of the stomachs that contained plant fragments also contained crayfish.

In the Venard Lake collections, isopods occurred in a larger percentage (57 per cent) of stomachs in spring than at any other season, fig. 7. They did not comprise so large a percentage of total volume in spring as in winter, but their average of volume percentages (29 per cent) was greater and it was greater than that of any other food item taken during the spring. Dragonfly nymphs were present in nearly half of the Venard Lake stomachs collected in spring; the percentage of stomachs containing these nymphs, the average of volume percentages, and percentage of the total volume were much greater during the spring than at any other season. Annelida, Collembola, Neuroptera, and Bryozoa were represented as Venard Lake

Lake during the period beginning October, 1948, and ending September, 1949.

Stomachs From 32 Largemouth Bass Collected During June–August, 1949				Stomachs From 44 Largemouth Bass Collected During October–November, 1948, and September, 1949			
Percentage of Stomachs Containing Organism	Average Number of Organisms in Stomachs Containing Them	Average of Volume Percentages	Percentage of Total Volume	Percentage of Stomachs Containing Organism	Average Number of Organisms in Stomachs Containing Them	Average of Volume Percentages	Per-centage of Total Volume
3	1	0.1	0.1	0	0	0.0	0.0
6	1	tr.	tr.	7	1	0.1	tr.
3	199	3.0	0.4	59	178	23.0	10.1
0	0	0.0	0.0	7	2	tr.	tr.
0	0	0.0	0.0	9	2	0.4	0.1
34	1	18.5	19.8	9	1	9.0	54.0
3	1	tr.	tr.	2	1	tr.	tr.
3	1	tr.	tr.	0	0	0.0	0.0
47	8	2.4	0.9	77	26	24.1	8.7
47	4	17.6	6.3	30	3	5.8	2.1
41	3	15.9	10.6	34	2	15.5	9.8
16	1	tr.	tr.	27	1	6.0	0.8
3	1	tr.	tr.	0	0	0.0	0.0
25	1	3.3	0.7	2	1	tr.	tr.
19	43	4.1	1.9	0	0	0.0	0.0
9	1	tr.	tr.	0	0	0.0	0.0
6	1	0.2	tr.	14	1	2.1	0.3
28	2	1.0	0.1	57	13	6.8	1.4
38	2	30.4	59.1	5	2	4.5	11.4
0	0	0.0	0.0	2	....	0.2	0.1
6	....	0.1	tr.	20	....	0.3	0.4
12	....	3.3	0.1	14	....	2.0	0.7

warmouth foods in spring but at no other time.

Summer.—As new broods of young fish became available in summer, a marked increase in the percentage of warmouth stomachs that contained fish was noted in the collections from both Park Pond and Venard Lake.

In the warmouth collections from Park Pond, crayfish occurred in a slightly smaller percentage of stomachs in summer than during the spring but attained a peak in the percentage of total volume of food —64.3 per cent, fig. 6. The percentage of stomachs containing mayfly nymphs and caddisfly larvae increased progressively from winter to summer; these groups were found in proportionately more warmouth stomachs taken during the summer than at any other time of year in Park Pond. The percentage of stomachs in which damselfly nymphs were found was smaller in summer than in spring.

In the warmouth collections from Venard Lake, caddisfly larvae were present in a larger percentage of stomachs in summer than at any other season. Caddisfly larvae comprised only a relatively small part of the total volume of food, but the average of volume percentages was greater for caddisflies than for any other food utilized in summer. Crayfish also were found in a large percentage of the stomachs collected in summer. Although crayfish made up a smaller percentage of the total volume of food in summer than during the fall months, the percentage of stomachs containing crayfish was three times as great in the summer as in the fall. Fish were found in the stomachs of only those warmouths collected in summer. Mayfly, damselfly, and dragonfly nymphs comprised smaller percentages of the total volume of food and were present in smaller percentages of stomachs in summer than in spring.

Fall.—In the warmouth collections from Park Pond, fish comprised a larger percentage of the total volume of food, and crayfish a smaller percentage of the total volume of food, in fall than in summer; the percentages in the fall were nearly equivalent to those observed during

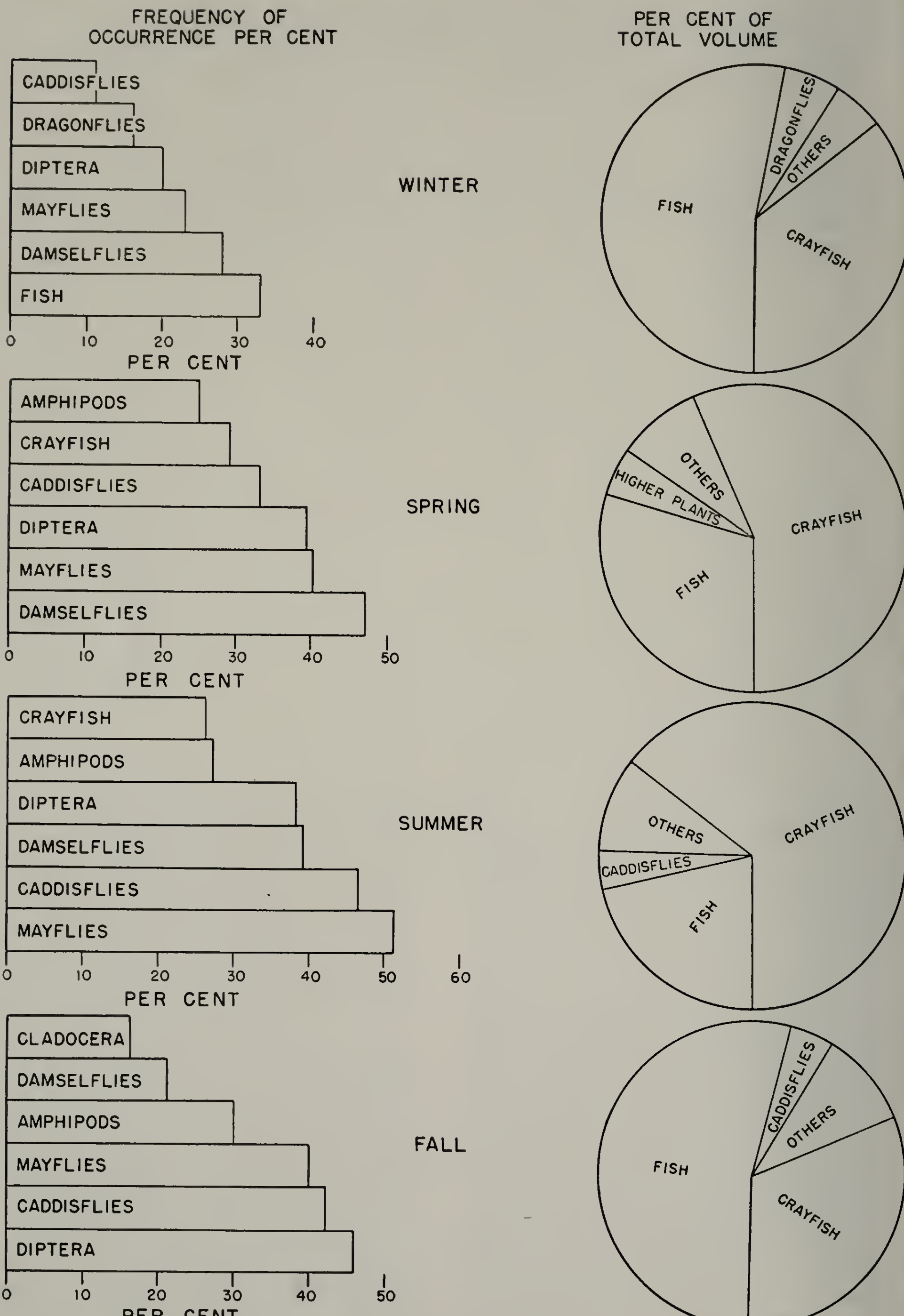

Fig. 6.—For each of the most important foods taken from the stomachs of warmouths collected from Park Pond in each of the four seasons of 1948 and 1949, the percentages of stomachs containing these foods (frequency of occurrence) and the percentage of the total volume of food represented by each of these important foods.

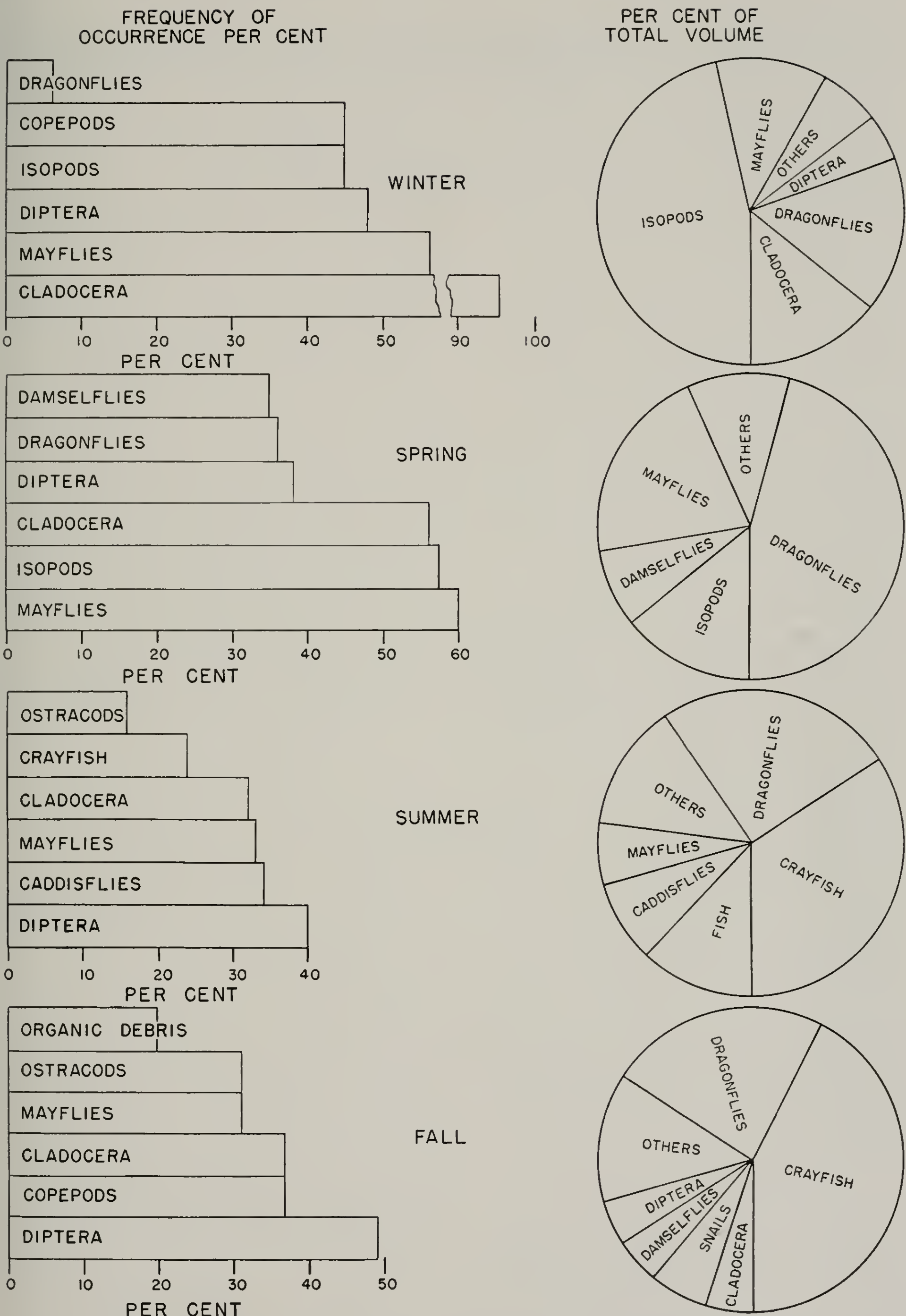

Fig. 7.—For each of the most important foods taken from the stomachs of warmouths collected from Venard Lake in each of the four seasons of 1948 and 1949, the percentage of stomachs containing these foods (frequency of occurrence) and the percentage of the total volume of food represented by each of these important foods.

the winter months, fig. 6. Although fish comprised more than one-half the bulk of food in winter, they were taken from only 15 per cent of the stomachs collected in the autumn. Dipteran larvae (largely chironomids) comprised less than 1 per cent of the total volume of food each season but occurred in a large percentage (33 per cent or more) of stomachs each season—the largest percentage in the fall. In the fall collections, dipteran larvae were present in 46 per cent of the stomachs; the average of volume percentages for these larvae was 9.2. Caddisfly larvae were present in a large proportion of stomachs and ranked first among all food groups in average of volume percentages. Mayfly and damselfly nymphs were found in a smaller proportion of stomachs collected during the fall than during the summer, whereas dragonfly nymphs were present in about the same percentages of stomachs in these two seasons.

In the warmouth collections from Venard Lake, mayfly and damselfly nymphs were present in about the same percentages of stomachs during the summer as during the fall. In November, nymphs of the mayfly, *Siphlonurus* sp., showed a sudden pulse of occurrence that extended into December. Caddisfly larvae were present in a smaller percentage of stomachs collected in fall than in the summer months. Throughout the four seasons, dipteran larvae were found in consistently high percentages of stomachs—38 to 49 per cent—the highest percentages in the fall and winter, fig. 7. *Chaoborus* sp., a dipteran larva, was found only occasionally during the spring and summer; but, during the fall months and in December, it was found in large numbers of stomachs. Gastropods (snails) and ostracods were found in higher percentages of Venard Lake warmouth stomachs in the fall than at other seasons.

Daily Changes

During the summer, when water temperatures were high, digestion in the stomachs of fish was rapid, and food remained in these stomachs for only a few hours. At this season, it was possible to determine daily feeding periods of warmouths at Park Pond by comparing the percentages of empty stomachs taken in morning collections with those taken in afternoon collections, table 13. The influence of individual fish size, and of size groups represented by few individuals, was reduced by eliminating from the calculations all warmouths less than 2.0 inches or more than 6.4 inches total length.

Only 4 per cent of the warmouth stomachs collected in the morning were empty, whereas 50 per cent of those collected in the afternoon contained no food.

On July 8 and August 1, 1949, collections were taken soon after sunrise and as late in the evening of the two days as fish could be taken with the shocking apparatus without the use of artificial lights. The daily feeding pattern was quite evident in these collections, table 13. Stomachs removed from fish collected between 6:00 and 7:15 A.M. on July 8 were "relatively full of very dark material"; in contrast, the stomachs collected between 6:15 and 7:45 P.M. "seemed rather empty, the upper intestine completely empty, with only the last three-fourths inch of the lower intestine containing heavy black material representing the early morning feeding."

In stomachs of fish of selected size groups (excluding fish with empty stomachs), total volumes of the food masses averaged consistently lower (by 24 per cent or more) for individuals taken in the afternoon than for those taken in the morning.

Monthly collections of stomachs from Venard Lake in the warm period of the year (1949) indicated for the warmouths of this body of water a daily feeding pattern somewhat similar to that of the warmouths of Park Pond. Of four collections from Venard Lake in the warm months, when the daily feeding pattern might be evident, two were taken in the morning and two in the evening; 13 per cent of the stomachs in the two morning collections and 26 per cent of the stomachs in the two afternoon collections were empty. The differences between morning and afternoon collections were less evident at Venard than at Park Pond, probably because the collections were taken from Venard late in the morning and early in the afternoon.

There was evidence of some feeding activity by warmouths in late afternoon. Although most of the food materials found

Table 13.—Number of warmouths in morning and afternoon collections from Park Pond, June 2–September 2, 1949, and number of those warmouths with empty stomachs. Figures include only those for fish between 2.0 and 6.4 inches total length.

Collection Date	Morning		Afternoon	
	Number of Fish	Number of Empty Stomachs	Number of Fish	Number of Empty Stomachs
June 2	...	...	5	1
June 10	25	3	...	...
July 5	...	...	23	8
July 8	25	0	18	11
August 1	19	1	16	11
August 15	16	1	...	...
September 2	28	0	...	...
Total number of fish	*113*	*5*	*62*	*31*
Per cent of stomachs empty	...	4	...	50

in stomachs collected in the afternoon during the summer were well digested, a few were fresh items; most of the materials were nearly digested or else quite fresh, a situation that suggested a resumption of feeding after a period of no feeding. Afternoon feeding during the summer was either very light or it occurred very late in the day, possibly just at dusk when it became too dark for fish to be collected without lights.

Influence of Fish Size

The yolk supply of warmouth larvae observed under laboratory conditions usually was exhausted within 4 days from hatching; without food, the larvae starved to death in 10 or 11 days at 24–25 degrees C. Ordinarily, the postlarvae began feeding at least by the seventh day of life. Stomachs of warmouth larvae collected from outdoor tanks contained a few flagellates and ciliates and many bacteria. One or two of the large protozoans made a rather big meal for an 8-mm. larva. When 14 days old, the warmouth larvae ate considerably larger organisms, feeding even on small mosquito larvae. Both in natural waters and in the laboratory, warmouths 19 mm. long were observed feeding voraciously on postlarval warmouths 5 mm. long.

In a study of differences in food taken by larger fish, the stomach contents of warmouths from Park Pond and Venard Lake were grouped according to sizes of fish from which the stomachs had been taken. Since it was necessary to present these analyses in compact tables, fish from Park Pond were grouped in two length ranges, tables 6–9, and fish of all lengths from Venard Lake were grouped together, tables 10 and 11. Some of the relationships between lengths of fish and foods taken, such relationships as are obscured in the tables by combining data for fish of various lengths, are given in the following general statements.

Cladocerans, copepods, and ostracods were taken mostly by warmouths less than 3.5 inches in length and were the principal foods of warmouths less than 1.7 inches in length, which only occasionally took small mayfly nymphs or dipteran larvae. Amphipods were an important food for small warmouths at Park Pond but were utilized by very few fish larger than 4.9 inches in length. Snails were eaten mostly by warmouths between 2.5 and 4.9 inches in length.

Crayfish were eaten by more large warmouths than small ones at Park Pond. In contrast, crayfish were eaten by more small warmouths than large ones at Venard Lake, presumably because large numbers of small crayfish were available to the fish there during the summer months.

In both study areas, mayfly nymphs were taken by a larger percentage of small warmouths than of large ones; however, at Park Pond in summer they were taken by 30 per cent of the warmouths over 5.0 inches long. At Venard Lake, where both *Caenis* and *Siphlonurus* occurred in large numbers, the nymphs of *Caenis* were taken mostly by warmouths between 2.0 and 3.4 inches, whereas the nymphs of *Siphlonurus,* which were larger, were eaten generally by larger fish, up to 5.2 inches in length.

Caddisfly larvae were eaten by a larger percentage of small warmouths than of large ones; the seasonal trend in consumption was somewhat similiar for fish of all sizes. Damselfly and dragonfly nymphs were utilized as food by warmouths of all sizes except those less than 2.0 inches long. Fish were eaten by a greater percentage of large warmouths (over 5.0 inches in length) than of small ones.

The average volume of food found in the stomachs of warmouths of various sizes was not directly proportional to the length or weight of the fish; the larger the warmouth the greater was the volume of food taken in proportion to its size. The stomachs of very small warmouths occasionally contained relatively great amounts of food, but small warmouths feeding on many small items seldom experienced the extreme distention of the stomachs that occurred in many large warmouths when feeding on comparatively large fish or crayfish.

The percentage of stomachs that were empty was smaller among small warmouths than among large ones. The percentages of Park Pond warmouths with empty stomachs were as follows: fish of 1.9 inches or less total length, 3 per cent; fish of 2.0–3.4 inches, 18 per cent; fish of 3.5–4.9 inches, 24 per cent; fish of 5.0–6.4 inches, 32 per cent; and fish of 6.5 inches or larger, 28 per cent. Small warmouths feeding on many small items apparently had a more certain food supply than had large warmouths, which had relatively fewer large organisms on which to feed.

Interspecific Competition

Largemouth bass stomachs were collected from Venard Lake at the same time the warmouth stomachs were obtained. Because only four largemouths were taken during the winter, their food habits for this season were omitted from consideration here. The majority of the bass taken (92 per cent) were between 5.5 and 9.0 inches total length. Of 107 bass stomachs collected, 99 contained food materials, table 12.

Cladocerans were found in surprisingly large numbers in the stomachs of largemouths up to 7.5 inches in length—791 of them in the stomach of one 6.4-inch bass. Of the largemouth stomachs collected in the fall months, cladocerans (almost exclusively *Simocephalus* sp.) were found in 59 per cent. Very few were found in the bass stomachs collected in summer. Cladocerans were found in relatively high percentages of the warmouth stomachs collected from Venard Lake throughout the year; they did not show an increase in utilization by warmouths during the fall months comparable to the increase in utilization by largemouth bass. Cladocerans were found in 32 and 37 per cent of the warmouth stomachs collected, respectively, in the summer and fall and in 96 per cent of the warmouth stomachs collected in December. Copepods were found in very few stomachs of the largemouth bass, and ostracods were found in none. Isopods were found in greater percentages of both largemouth and warmouth stomachs collected in spring than at any other season.

Fish and crayfish together comprised 64 per cent (36 and 28 per cent, respectively) of the total volume of largemouth bass food. The percentages of bass stomachs containing fish or crayfish were low in the spring, high during the summer, and low again in the fall. The seasonal trend was somewhat similar to that for warmouths at Venard Lake. Bass stomachs collected in August contained very few items except fish and crayfish.

That mayfly nymphs and midge (Diptera) larvae were important bass foods at Venard Lake was shown by the consistently large percentage of stomachs in which they occurred. Percentages were larger in spring and fall than in summer. Mayfly nymphs were found in at least as large a percentage of bass stomachs each season as was any other kind of food organism; they were found in a larger percentage of bass than of warmouth stomachs. The fall increase in utilization of mayfly nymphs by bass was not followed by a similar increase by warmouths. Nymphs of *Siphlonurus* sp. accounted for the fall increase in consumption of mayfly nymphs by bass; as many as 125 were found in each of several bass stomachs taken during November. Only in the spring collections did the nymphs of *Caenis* sp. occur in bass stomachs as frequently as those of *Siphlonurus*; *Caenis* was consistently the species of mayfly most abundantly taken by warmouths. The variation in utilization of these mayflies may have come from differences in their habitats: *Siphlonurus* is generally concentrated in deeper water than is *Caenis* and would be available to largemouths feeding in open areas of the lake. *Caenis* is a shallow-water mayfly and would be taken by warmouths feeding along the banks and in shallow weed beds.

The percentage of bass stomachs that contained damselflies (Zygoptera) and/or dragonflies (Anisoptera) decreased from spring to fall. A smaller percentage of warmouth than of largemouth stomachs contained nymphs of the Odonata. Largemouth bass stomachs contained more adults and subimagoes of damselflies than did warmouth stomachs; in the June collection of bass stomachs, these forms outnumbered the nymphs taken.

Larval and adult beetles (Coleoptera), bugs (Hemiptera), and bees and ants (Hymenoptera) occurred at peak abundance in bass stomachs during the summer, especially in June. The incidence of these insects was much greater in largemouth bass than in warmouths at Venard Lake. Larvae of the aquatic beetle *Peltodytes* sp. were eaten in large numbers by a few largemouths; in June, 131 of the larvae were found in the stomach of one individual and 115 in the stomach of another.

Certainly the foods and feeding areas of warmouths and largemouth bass overlapped in Venard Lake. However, even though largemouth bass and warmouths fed on the same kinds of organisms, and even though several of these organisms followed similar seasonal patterns of occurrence in the stomachs of the two fishes, the competition was somewhat reduced by differences in feeding habits. Warmouths tended to consume the organisms on the soft bottoms, in shallow waters, and along the banks; largemouths fed more on the surface organisms and free-swimming forms in deeper or more open parts of the lake.

General Conclusions on Food Habits

Considerable differences have been observed in the contents of the stomachs of warmouths taken in small numbers at different seasons or from widely separated localities, table 14.

Forbes (1903:48–9) analyzed the stomach contents of warmouths collected at scattered localities in Illinois and neighboring states and considered the foods uti-

Table 14.—Average of volume percentages for the food of warmouths studied by Forbes (1903), McCormick (1940), and Rice (1941) and for the food of warmouths of approximately the same sizes, and collected at about the same times of year, from Park Pond and Venard Lake.

Food Item	Forbes (1903) Illinois Autumn 6 Fish Length, Inches 3+	McCormick (1940) Reelfoot Lake Summer 69 Fish Length, Inches* 3.3–8.7 (5.4 Average)	Rice (1941) Reelfoot Lake Summer 45 Fish Length, Inches* 3.3–6.5 (4.8 Average)	Present Study Park Pond Summer 59 Fish Length, Inches 3.4–6.4 (4.7 Average)	Present Study Venard Lake Summer 27 Fish Length, Inches 3.4–6.4 (4.3 Average)
Crayfish	...	46.38	99.5	29.7	27.7
Entomostraca	...	2.90	tr.	0.7	0.7
Mayflies	25	2.90	tr.	2.9	5.7
Damselflies	...	1.59	...	15.7	3.8
Dragonflies	...	10.87	...	5.2	23.8
Hemiptera	18	7.68	...	0.3	...
Diptera larvae	...	10.03	tr.	4.6	3.9
Miscellaneous insects	10	5.07	...	12.2	17.3
Fish	47	7.94	...	20.5	5.9
Miscellaneous items	...	4.64	tr.	8.2	11.2

*Measurements here are equivalents of metric measurements given by author.

lized by fish of different sizes. The small warmouths in his study had eaten large numbers of Entomostraca, as had the small warmouths at Venard Lake and at Park Pond. In his six adult warmouths, table 14, crayfish were not represented, and fish made up a larger percentage of the food (47 per cent) than has been reported in other studies. Forbes related the especially piscivorous habit of this species to the large size of its mouth. Dragonflies were noticeably absent in all the warmouth stomachs he examined.

Data in studies made by McCormick (1940:73) and Rice (1941:26) at Reelfoot Lake, Tennessee, table 14, emphasized the differences in foods utilized by a species in successive years, even at the same location and during the same season of the year. McCormick examined 69 warmouth stomachs which contained food and found that the average of volume percentages of insects was 38.14 per cent. The comparable figure at Park Pond was 40.9 per cent. Crayfish were higher and fish were lower in the average of volume percentages of warmouth food at Reelfoot Lake than at Park Pond. A year after McCormick's study, Rice examined another series of warmouth stomachs from Reelfoot Lake. Of 45 stomachs which contained food, only 1 had food other than crayfish, table 14.

For the periods of time covered by the studies cited in table 14, warmouths at both Venard Lake and Park Pond utilized a greater variety of food items than did warmouths in the other places listed, as is indicated by the percentages of "miscellaneous insects" and "miscellaneous items."

Lewis & English (1949:321) examined the stomachs of 29 warmouths from Red Haw Hill Lake, Iowa. The fish were collected from April through July and ranged from 40 to 177 mm. in total length. In the 17 stomachs that contained food, "food items occurred as follows: 2- to 4-inch fish, 7; crayfish, 4; vegetable debris, 2; unidentified insect larvae, 4; leech, 1; dragon-fly naiad, 1; unidentified insects, 2; and snails, 1." These figures probably refer to the number of stomachs in which each kind of food was found and not to the numbers of individual food items. The conclusion from this study was that "On a volumetric basis, fish and crayfish were the most important food items."

In a rather general statement involving five fishes, Black (1945:463) mentioned that the warmouth in Shiner Lake, Indiana, hunts the northern mimic shiner, *Notropis volucellus volucellus* (Cope), to the exclusion of almost all other food. At Park Pond, where many species of minnows were present, small sunfish were more commonly taken by warmouths than were minnows.

Hunt (1953:29) examined 25 small warmouths from the Tamiami Canal west of Miami, Florida. Twelve of these fish, ranging from 1.4 to 3.5 inches in total length, contained food material composed exclusively of animals, including the following organisms: dragonfly, damselfly, and mayfly nymphs; dipteran larvae of various kinds; a few scuds and large ostracods; and a large number of small shrimps, *Palaemonetes paludosa.*

Huish (1947:15–6) examined 17 warmouths from Lake Glendale (southern Illinois) during the summer of 1946. These fish, caught on artificial flies, ranged from 5.0 to 7.5 inches in total length. Of the 14 fish whose stomachs contained food, there were 3 with small fish, 1 with a tadpole, 3 with dragonfly nymphs, and 7 with crayfish.

Fish, crayfish, and immature forms of aquatic insects comprised the important foods for most of the warmouths involved in the present study. Diets of the warmouths in Park Pond were found to differ from the diets of the warmouths in Venard Lake both as to the kinds and to the amounts of certain organisms eaten in various seasons and by fish of different sizes. This study and others, some of which have been cited above, make it seem very unlikely that there is any specific diet or highly restricted food preference for this species. Food items of many kinds are acceptable to the warmouth; this fish may feed upon any of those items that are readily available.

REPRODUCTION

Whether a fish population overcrowds its habitat is determined in part by its rate of reproduction—the development of sex products and the subsequent growth and survival of young fish.

Development of Sex Products

In interpreting the stages of development of sex products in a fish such as the warmouth, which spawns over a period of several months, one must keep in mind that all of the germ cells do not go through the cycle of maturation simultaneously; instead, small groups of these cells mature at intervals and are spawned. This process is accompanied by a continuous recruitment of additional cells from the primordial stock. Thus, in a gonad in spawning condition, in addition to the fully matured sex products, there are other groups of cells representing earlier stages in the maturation process.

Annual Sexual Cycle.—Terms descriptive of the appearance of the fish gonad are useful for designating stages of development associated with seasons, table 15. Some of the terms used here are the same as those used by Bennett, Thompson, & Parr (1940:17).

Partly because the gradual process of growth of germ cells varies among individuals and partly because the developmental process is influenced by climatological conditions, the periods during which the various designated stages may be found overlap and are not exactly the same from year to year for either individual fish or for populations. Overlapping of developmental stages was evident in warmouths

Table 15.—Appearance and significance of each stage in the development of warmouth gonads, related here to the seasonal occurrence of each stage in warmouths from Park Pond, 1948 and 1949.

Stage of Development of Gonads	Appearance of Gonads		Significance of Stage in Developmental Process	Season of Stage
	Male	Female		
Latent	Clear pinkish white to colorless; a narrow translucent strand	Light amber, often with small red dots; lobelike in form and somewhat translucent	A quiescent period; gonad containing only primordial germ cells	All year for fish under 3.5 inches; July 1–April 15 for fish over 3.5 inches
Poorly developed	Pinkish white, opaque, becoming ribbon-like	Pinkish orange to light yellow; slightly granular and somewhat enlarged	Initial maturation of sex products	March 1–May 1
Well developed	White, opaque; ribbon-like, with wavy margins	Bright yellow; very granular and fully distended, with opaque eggs	Advanced development of germ cells; heavy yolk accumulation in ova	April 15–June 1
Spawning condition	Appears as in preceding stage but flowing milt when gently pressed	Appears as in preceding stage but flowing eggs when gently pressed	Completed germ cells free in gonad, ready to be discharged	May 15–August 15
Partly spent	White to gray; more nearly flat than in spawning condition	Yellow to orange, with congested blood vessels; less distended than in spawning condition	No germ cells free in gonad, but a considerable stock of well-developed ova and sperm remaining	June 1–August 20
Spent	Muddy white, becoming smaller and less distended	Reddish-orange, flaccid, with congested blood vessels	Remaining matured germ cells resorbed; gonad reorganizing, but effect of spawning still evident	June 15–September 1

collected from Park Pond during the spawning season of 1949. These fish were divided into two size groups established on the basis of differences in maturation: in the first group were "large" warmouths, those of more than 5.4 inches total length; in the second group were "small" warmouths, those between 3.5 and 5.4 inches total length. Warmouths shorter than 3.5 inches were eliminated from this part of the study because they would not mature in the then current season. The following generalizations may be made regarding the season of greatest sexual activity of the warmouth, fig. 8:

1. The "large" warmouths (over 5.4 inches total length) attained spawning condition sooner and spawned over a longer period than did the "small" fish (3.5–5.4 inches total length).

2. All the "large" individuals took part in spawning activities, whereas a considerable proportion of the specimens between 3.5 and 5.4 inches remained immature during the entire nesting season.

3. The "small" warmouths recovered more quickly from the effects of spawning than did the "large" ones; all of the "small" warmouths were in a latent condition by August 1, whereas among the larger fish only 14 per cent of the males and 33 per cent of the females possessed gonads that had become reorganized by that date.

4. The males ripened slightly earlier in the season than did the females and remained sexually active somewhat longer.

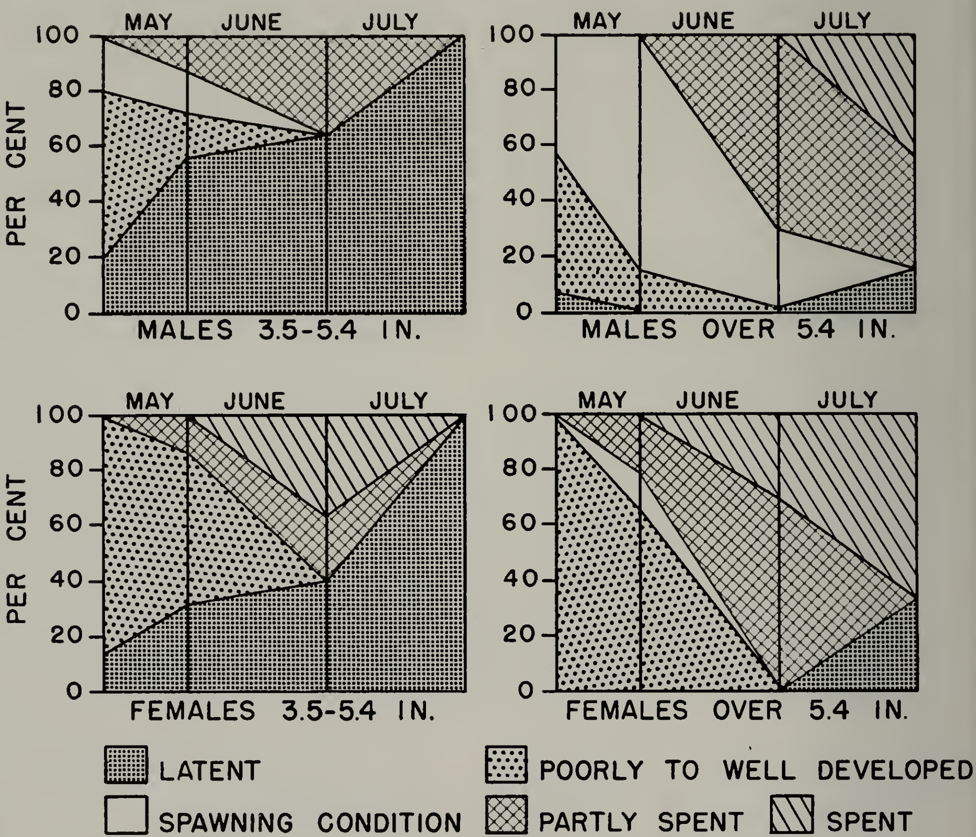

Fig. 8.—Percentage of warmouth males and females (two size groups) in each of five stages of sexual development during May, June, and July. These warmouths were collected from Park Pond, May 13 to August 1, 1949.

In the smaller size group (3.5–5.4 inches total length), a considerable proportion of both males and females had latent gonads after the first week in May, fig. 8. The continuous rise in percentage of latent gonads found in this size group during the nesting season may have resulted from (1) rapid reorganization of the gonads of early spawners, (2) failure of some small individuals to spawn and prompt return of these individuals to the latent condition, (3) growth of fish during May, June, and July, which resulted in the recruitment of some sexually undeveloped fish into the 3.5–5.4-inch group and the loss of some sexually mature fish from this group to the size group beyond 5.4 inches, and/or (4) inadequacy of collections and their failure to represent true proportions of individuals in the various developmental stages.

Field observations showed that sexually mature females do not have free ova (which can be forced out by gentle pressure on their sides) except immediately before and during the spawning act, whereas sexually mature males may be induced to extrude milt during much of the spawning season. These observations may explain the fact that many more males than females were classed as ripe. The scarcity of small males that were classed as completely spent was due probably to the difficulty of separating partly spent from completely spent individuals in the small sizes.

By expressing the weight of gonads at regular intervals through the year as per cent of body weight, one can follow the increase and diminution in size of the sex glands and fit the observed spawning condition of fish into the annual sexual cycle (James 1946 and others). Statistics on monthly gonad weight–body weight relationships for warmouths in Illinois were based on 222 females and 260 males collected in Park Pond from early October, 1948, to early September, 1949, fig. 9. The fish were divided into three size groups: (1) less than 3.5 inches total length, (2) 3.5–5.4 inches total length, (3) more than 5.4 inches total length. Most of the warmouths of 3.5 inches and longer total length were sexually mature; most below this length were sexually immature.

During the period beginning with September and ending with March, there was no appreciable change in gonad weights among warmouths. Soon after the initial rise of water temperatures in March, the gonads in warmouths longer than 3.5 inches began to enlarge, and they increased rapidly in weight during April and May. The ratio of gonad weight to body weight increased most rapidly in the large warmouths (over 5.4 inches); males in this group showed their greatest average gonad weight in May and females showed their greatest average gonad weight early in June. The ratio of gonad weight to body weight for both male and female warmouths between 3.5 and 5.4 inches in length averaged highest the first week in June. Soon afterwards, however, the ratio of gonad weight to body weight declined rapidly for females in the two larger size groups. Among males of both groups, there was a drop in weight of testes, but the males remained sexually developed later in the season than did females. The ratio of gonad weight to body weight may be at a minimum immediately following cessation of sexual activity, but it may increase slightly with reorganization of the gonads.

Evidence from the cycle of changes in the ratio of gonad weight to body weight lends support to the conclusion previously drawn that large warmouths mature earlier in the season than do small ones and also remain active reproductively over a longer period. In this series of specimens, initial ripening of the sex products occurred during the second week in May, 1949, fig. 9.

At the time other warmouths were spawning, warmouths under 3.5 inches total length showed no increase in the relative weight of the gonads; in fact, an apparent decrease took place. This decline was probably associated with an improvement in condition (an increase in the body weight) of the smaller fish during May, June, and July. The irregularities that appeared during winter months in gonad weight–body weight relationships of females in the two smallest length groups, fig. 9, were attributed to changes in body weight rather than to changes in gonad weight; these irregularities corresponded to changes in the coefficient of condition, fig. 17.

Increasing length of day and rising temperatures associated with spring are known to stimulate gonad development in fishes.

In 1949, the ratio of average gonad weight to average body weight of Park Pond warmouths began increasing early in March and roughly corresponded to an upswing in mean monthly air temperatures above 40 degrees F. (United States Weather Bureau 1948–1949, Danville Station). Spawning was actually initiated at water temperatures (12 inches deep) of about 70 degrees F. Low ratios of gonad weight to body weight for the summer months of July and August, 1949, indi-

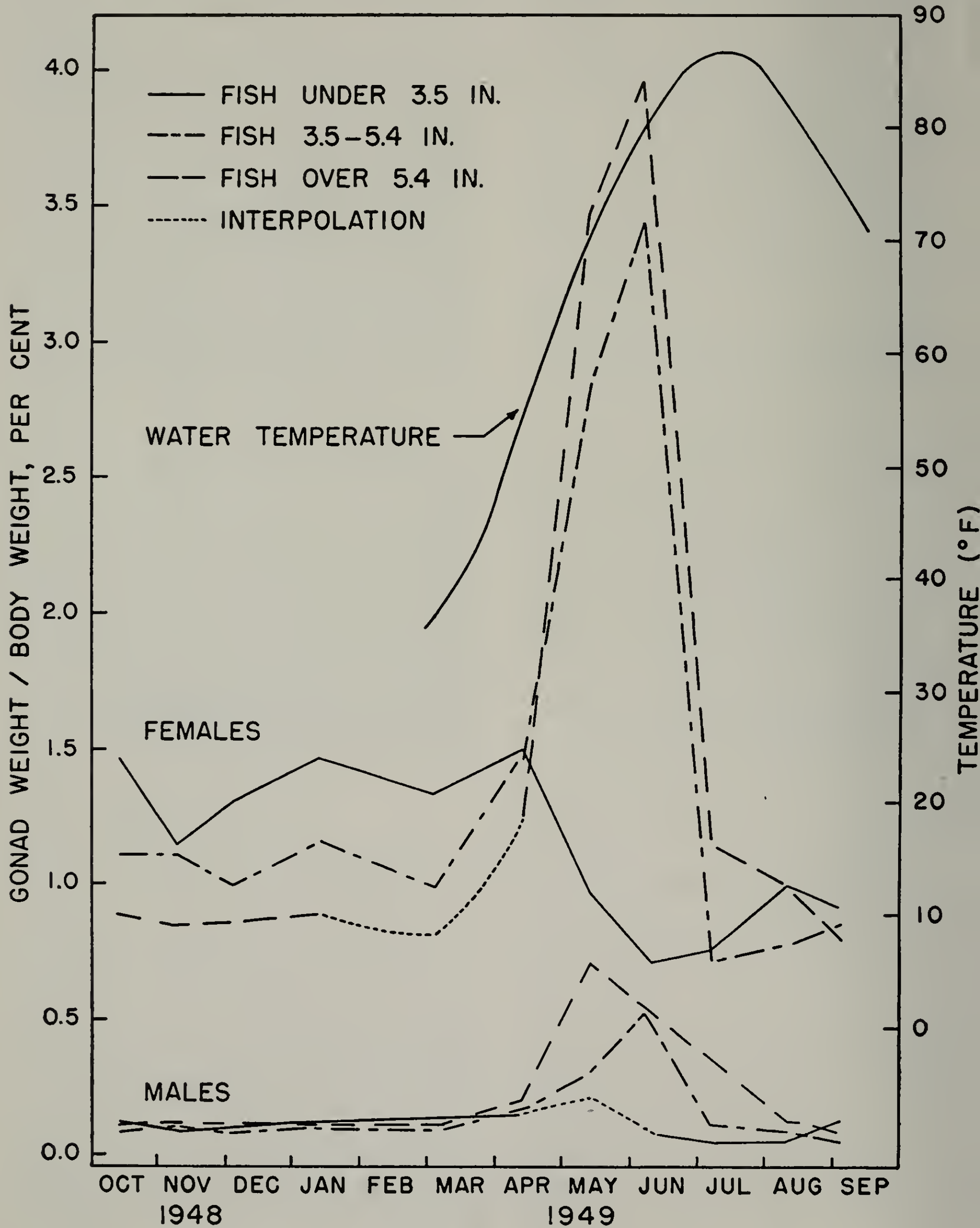

Fig. 9.—Curves illustrating the relationships of gonad weight to body weight (the per cent the gonad weight is of the body weight) for male and female warmouths of three size groups collected from Park Pond, early October, 1948, through early September, 1949, and water temperatures (degrees F.) taken with a mercury thermometer 12 inches below the water surface.

cated that most of the spawning was completed by early July. Information obtained from collections of warmouths made the previous summer suggested that the spawning season in 1949 may have been shorter than in most years.

Fecundity.—Probably one of the more difficult problems in studying the reproduction of a fish is how to estimate the total number of ova developed in a season by an individual female. The problem is especially complex in a fish that, like the warmouth, spawns an indefinite number of times over a rather long period and that contains large numbers of eggs too small to be counted without some magnification. Usually an extended period of sexual activity in fish is associated with a continuous maturation of eggs and sperm, so that sex products may ripen and be discharged at frequent intervals during the spawning season. Thus, at almost any time during the spawning season, in the ovary are several sizes of ova representing various stages of development from primordial germ cells to yolk-laden eggs ready for spawning.

The egg-counting problem presented by the warmouth was not solved by any of the methods previously reported for determining the number of eggs in fish ovaries. The method used—based on the dry weight of the egg mass in an ovary—was developed as an efficient way to estimate the numbers of ova of various sizes. The first step involved measuring several hundred ova and sorting them into seven size groups. A low power binocular microscope ($\times 18$) equipped with an ocular micrometer was used to measure each of the several hundred ova to the nearest 0.05 mm. The seven size groups were as follows: I, 0.15–0.30 mm.; II, 0.35–0.45 mm.; III, 0.50–0.60 mm.; IV, 0.65–0.75 mm.; V, 0.80–0.90 mm.; VI, 0.95–1.05 mm.; and VII, 1.10 mm. and over. Group I included most small ova except the undifferentiated germ cells in the ovigerous lamellae.

All ova diameters were measured as the ova appeared at random on the horizontal scale of the ocular micrometer. Clark (1925:5), in using a similar system of measurement, proved this was a reliable method of measuring eggs that were not spherical. The ova were separated into the various size groups as they were measured. Twenty ova belonging to each size group were then placed in a platinum crucible of known weight and put in a drying oven at 45 degrees C. After remaining in the drying oven for 48 hours, the eggs, in the crucible, were moved to a desiccator, where they were left until repeated weighings showed no changes in weight. (It is now believed that the use of a desiccator was not necessary.) Each sample was weighed to the nearest 0.01 mg.; through calculations, the tentative average dried weight for ova in each of the various samples was determined. For each size group, five additional samples of 20 eggs each were dried and weighed before a final average dried weight was determined. The average dried weight determined for eggs in each size group was assumed to be the same as the average dried weight for eggs in a similar size group in other ovaries.

Steps in processing each ovary for which a calculation of egg numbers was desired were as follows: (1) The connective tissue sheath surrounding the ovary was removed, and the eggs were teased apart; (2) a random sample of several hundred eggs was taken from the total mass of eggs in the ovary; the eggs in the sample were measured individually and separated into size groups, and the percentage of eggs in each size group was determined; (3) the mass of eggs remaining was washed, placed in a drying oven at 45 degrees C. for 48 hours, moved to a desiccator, and kept there until repeated weighings showed no changes of weight.

Steps in calculating the total number of eggs in an ovary were as follows:

1. The average weight (dry) determined for eggs of each size group was multiplied by the percentage of eggs of the random sample in that size group. The products from the calculations for all the size groups were added and the sum multiplied by 100 to give the calculated dry weight of 100 representative eggs of the sample.

2. The weight of the dried eggs (exclusive of eggs in the random sample) was divided by the calculated dry weight of 100 representative eggs, as determined from the random sample, and the resulting quotient was multiplied by 100; to this product was added the number of eggs

in the random sample. The sum of these numbers was the calculated total number of eggs in the ovary.

The calculated number of eggs in each size group in the ovary was determined by multiplying the calculated total number of eggs in the ovary by the percentage of the random sample represented by the size group.

A modification of the dry-weight method described above, and one that did not require the initial work of determining the average dried weight of eggs of each size group was as follows: After the eggs were teased apart and the connective tissue removed, (1) eggs in a random sample were counted (and measured if there was interest in size groupings), dried, and weighed, (2) the eggs remaining were dried and weighed, and (3) the total number of eggs was then calculated on the basis of the total dried weight of all eggs in the ovary including those in the random sample. This method was similar to that used by Katz & Erickson (1950:176) for estimating fecundity of herrings, in which only one size group of eggs was involved.

When the numbers of ova in only a few ovaries are to be calculated, this modified dry-weight procedure is faster than the method first described. However, once the average dried weight of ova of each size group has been determined, the first method requires less work and is faster because the sample ova that are measured, sorted, and counted do not have to be dried and weighed.

Ovaries for which estimates of numbers of eggs were made—38 ovaries from Park Pond and 10 from Venard Lake—had been divided into four groups: those taken from Park Pond warmouths in (1) January and March, (2) April, May, and June, (3) July and August, and (4) those taken from Venard Lake warmouths, May 25, 1949. In these ovaries, there was a positive correlation between estimated numbers of eggs in individual fish and total length of fish. Coefficient of correlation values ranged from 0.64 to 0.98.

Seasonal variations in the number of eggs in warmouth ovaries were considerable. There was a marked increase in number of eggs per ovary from late winter to the peak of the spawning period, fig. 10. Immediately after the peak of spawning activities, the number of eggs per ovary was considerably reduced. At that time, the correlation between number of eggs and size of fish was lowest; this low correlation was due to the depleted condition of the ovaries, some of them being partly spent, some entirely spent, and others partly recovered. Females showing recovery from spawning contained more eggs than did the spent fish. During the fall and winter months, the number of eggs per ovary increased gradually; the final and greatest increases took place in the spring when groups of small eggs were adding yolk and undergoing final maturation.

Fish of comparable sizes in different bodies of water did not produce comparable numbers of eggs. For example, a Venard Lake female, 5.3 inches in length, contained 40,400 eggs, whereas a female of this length from Park Pond contained only 12,500 eggs, table 16. This large difference may be explained in part by differences in environmental stresses upon these warmouth populations resulting from (1) a rapidly expanding population in Venard Lake in 1947 and 1948 in contrast to an older and more stable population in Park Pond, (2) a greater concentration of fish in Park Pond than in Venard Lake, and (3) a higher incidence of parasitic infestation in the more concentrated population of fish.

Venard Lake was stocked in the spring of 1947, and the fish population expanded rapidly during the 1947 and 1948 growing seasons. Although the population probably had attained its maximum size by the time ovaries were collected for egg counts in 1949, the rapid expansion of the population in the preceding two seasons may have been at least partly responsible for the fact that the number of ova per female warmouth was greater for fish collected from Venard Lake than for those from Park Pond.

Park Pond had a higher population density of fish other than warmouths than had Venard Lake, which had only warmouths and largemouth bass. Where many fish are concentrated within a limited volume of water, there may be severe competition for food and space among members of this population. The smaller number of eggs per warmouth in Park Pond may have been

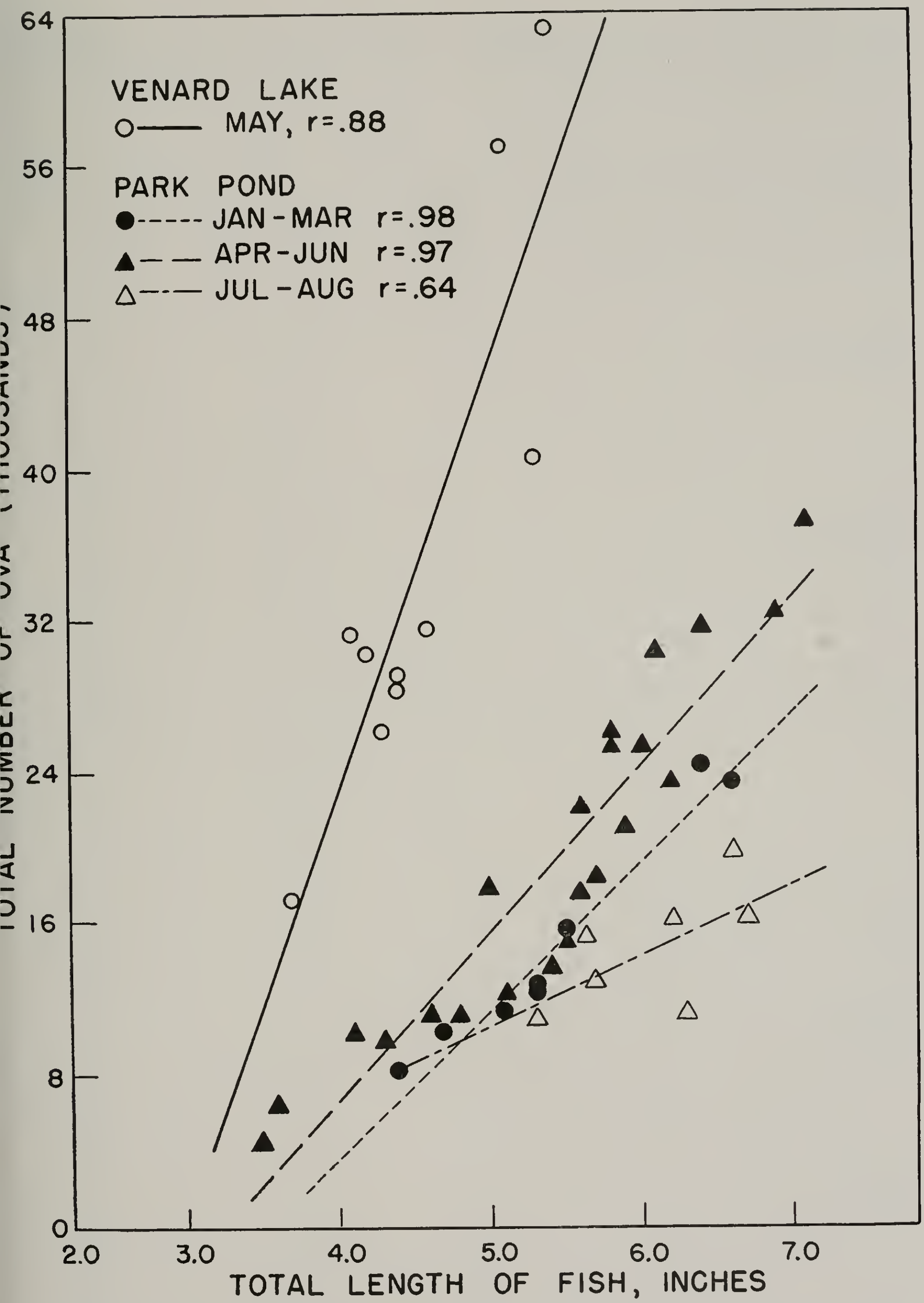

Fig. 10.—Estimated number of ova from warmouths of various total lengths in collections from Park Pond (January–March, April–June, and July–August) and Venard Lake (May), 1949. Scattergram, regression line, and coefficient of correlation (r) are given for each collection group. Elevations of the regression lines indicate seasonal changes in numbers of ova in three groups of Park Pond warmouths and also indicate that females from Venard Lake produced more ova than did females of similar sizes from Park Pond. Each graphic symbol represents one female from which the number of ova was estimated.

associated with interspecific competition among several species rather than intraspecific competition among warmouths.

Of the warmouths for which ova counts were made, the females from Venard Lake were in much better body condition (average of coefficient of condition 82.2) than were Park Pond females of similar sizes taken at about the same time (average of coefficient of condition 73.8). This differ-

Table 16.—Estimated numbers of ova in 38 warmouths from Park Pond and 10 from Venard Lake, 1949, arranged according to seasons and in order of increasing total length of fish.

Place and Time	Length of Fish, Inches	Weight of Fish, Pounds	Date of Collection	Estimated Numbers of Ova
Park Pond, January–March	4.4	0.06	March 2	8,100
	4.7	0.07	March 2	10,200
	5.1	0.09	March 2	11,200
	5.3	0.11	March 2	12,300
	5.3	0.11	March 2	12,500
	5.5	0.13	January 8	15,600
	6.4	0.21	January 8	24,300
	6.6	0.24	January 8	23,400
Park Pond, April–June	3.5	0.03	May 23	4,500
	3.6	0.03	April 9	6,200
	4.1	0.05	May 13	10,200
	4.3	0.05	April 9	9,800
	4.6	0.06	May 14	11,200
	4.8	0.09	May 13	11,200
	5.0	0.09	April 7	17,700
	5.1	0.10	May 13	11,600
	5.1	0.10	May 14	12,000
	5.4	0.12	May 13	13,900
	5.5	0.13	May 13	15,500
	5.6	0.12	June 10	17,900
	5.6	0.14	April 9	22,200
	5.7	0.15	June 10	18,300
	5.8	0.15	June 10	26,000
	5.8	0.15	May 13	25,600
	5.9	0.16	May 13	21,200
	6.0	0.18	May 14	25,500
	6.1	0.18	May 13	30,400
	6.2	0.17	May 14	23,700
	6.4	0.20	June 3	31,900
	6.9	0.28	May 14	32,700
	7.1	0.29	June 10	37,500
Park Pond, July–August	5.3	0.12	August 1	11,000
	5.6	0.14	August 15	15,100
	5.7	0.15	July 5	13,100*
	6.2	0.20	July 8	16,200
	6.3	0.16	July 5	11,300**
	6.6	0.24	August 15	19,800
	6.7	0.24	August 1	16,100
Venard Lake, May	3.7	0.04	May 25	17,200
	4.1	0.06	May 25	31,400
	4.2	0.06	May 25	30,200
	4.3	0.06	May 25	26,000
	4.4	0.07	May 25	28,200
	4.4	0.07	May 25	29,000
	4.6	0.08	May 25	31,600
	5.1	0.11	May 25	57,000
	5.3	0.12	May 25	40,400
	5.4	0.14	May 25	63,200

*Two plerocercoids of *Proteocephalus*.
**Four plerocercoids of *Proteocephalus*.

ence in body condition indicated that the Venard Lake females had a greater amount of reserve energy, which was available for the production of eggs.

Functions of the gonads of warmouths may be disturbed by internal parasites. Two ovaries in the series examined were parasitized by plerocercoid tapeworms and contained fewer ova than expected, table 16. However, in both Park Pond and Venard Lake there was such a high correlation between egg production and length of fish, regardless of differences in parasitic infestations, that it does not seem possible that parasites greatly influenced egg production in these populations.

Fecundity in warmouths may be reduced by lack of suitable nesting space, by overcrowding of the population, unfavorable weather conditions, or other circumstances which limit spawning opportunities and result in large numbers of mature eggs being retained and resorbed in the ovaries. Examination of ovaries from warmouths taken from Park Pond during the middle and last of June, 1949, revealed that only small percentages of mature eggs were present in these fish and that some of these eggs were being resorbed, indicating that not all the ova produced were actually discharged. It was found that the spawning period for warmouths was generally shorter in this water area than in other water areas under observation in Illinois.

Seasonal Development of Ova.—Development of warmouth ova through the seasons was observed in the fish collected from Park Pond, figs. 11 and 12. The development was followed by assigning the ova collected at various times to the size groups defined on page 35. The seasonal occurrence of eggs in these size groups was as follows:

1. From January to early April, ovaries contained only the smallest eggs (size group I, 0.15–0.30 mm. diameter).
2. During the second week in April, the ova began to increase in size; some ova were in group II.
3. By the middle of May, in some fish two-thirds of the eggs were of the smallest size, or size group I, and small numbers of eggs were in size groups II, III, IV, and V. In other fish only one-third of the eggs were in size group I, and group VI, as well as groups II, III, IV, and V, was represented. In still other fish, there were relatively more eggs in groups V and VI than in groups II, III, and IV.
4. Toward the end of May, all of the size groups of ova were well represented, and some of the eggs appeared to be ripe.
5. By the end of the first 2 weeks of June, the ovaries of all the mature fish had discharged most of the largest eggs. Some of the fish appeared to be preparing for a final spawn; about one-fourth of their eggs were in size group V and only low percentages in groups II, III, and IV. Other fish appeared to have completed spawning, and their ovaries appeared to have begun reorganizing, as small eggs again comprised three-fourths of the ova present.
6. On completion of spawning in July or early August, ovaries contained many pulpy eggs that were undergoing rapid resorption; the only other eggs present were those of group I. The ovigerous lamellae were poorly organized, showing no recovery from the production and crowding of large volumes of mature eggs.
7. By mid-August, ovaries were fully reorganized; the well-arranged ovigerous lamellae contained many small ova which comprised a part of the egg-stock for the next season.

Prespawning Activities

Nest building and spawning activities of the centrarchids probably have been studied more thoroughly than the spawning behavior of any other family of fishes (Breder 1936 and others). Although the reproductive behavior of the warmouth is much like that of other sunfishes, it may differ in the location and construction of nests, recognition of sex, courtship, care of eggs and larvae, and spawning schedule.

Location and Construction of Nests.—Warmouths appear to exercise selection in their choice of nesting sites. Both available bottom materials and cover influence this selection. In Venard Lake, where nesting was easily observed, the following types of bottom were available: loose silt, silt containing sticks and leaves, rubble, rubble covered with a thin layer of silt, sand with loose silt, and clean sand. No nests were found on clean sand (such as is often selected by bluegills and pumpkinseeds), and the only nests seen on loose silt were closely associated with tree roots or mats of submerged plants. Even though the Venard Lake warmouths used each of the bottom types (except sand) as nesting sites, they showed some preference for rubble lightly covered with silt and detritus.

The warmouths at Venard Lake were not so consistent in nesting on a particular kind of bottom as they were in selecting a spot near a stump, root, rock, clump of vegetation, or some similar object. This habitual preference for a location adjacent to a stationary object may account for the lack of nests on the clean sand bottom in Venard Lake. Nests were never found on an area of bottom completely exposed, such as the bluegill usually selects. In laboratory aquariums, the locations most often used by warmouths for nesting were near the vertical drain pipes.

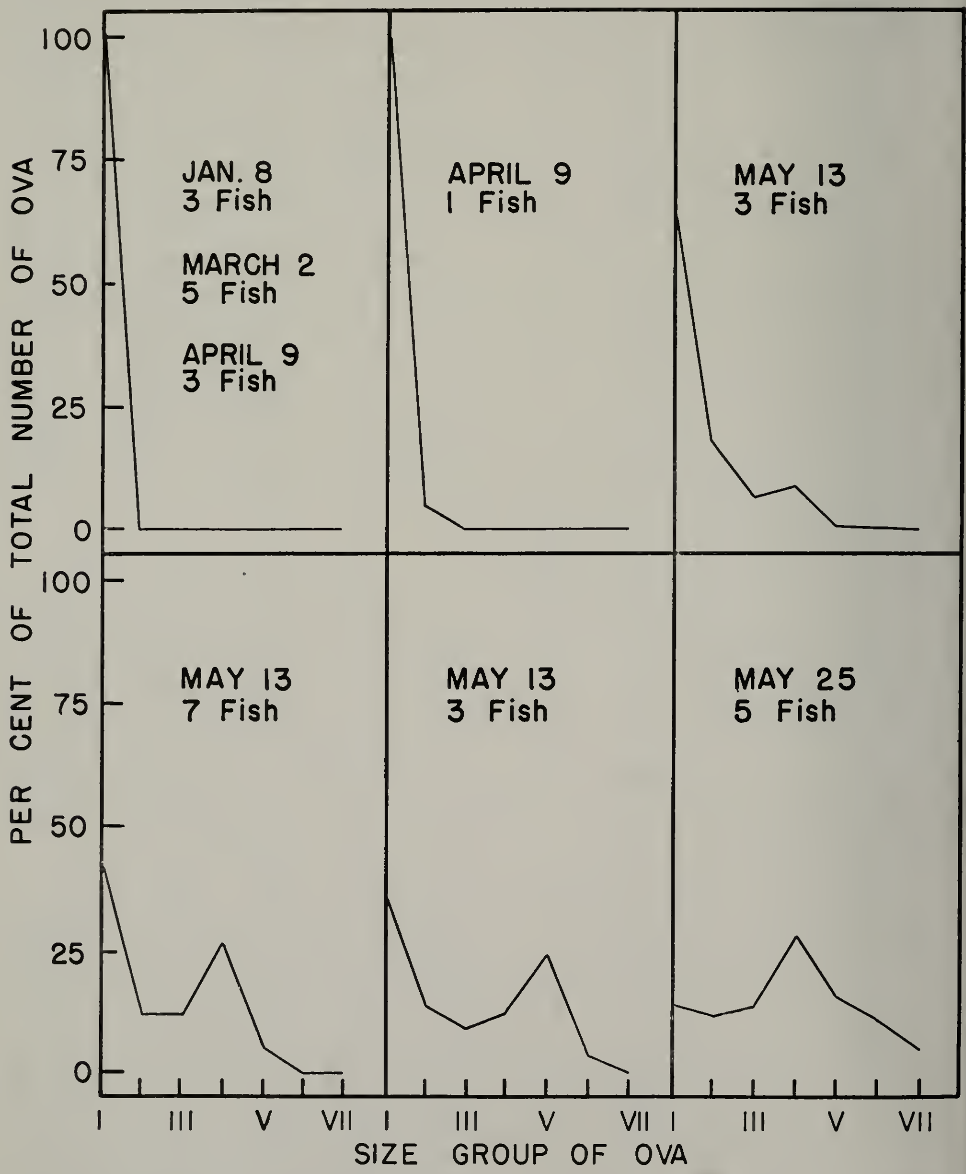

Fig. 11.—Percentage of total number of ova in each size group of ova found in warmouths collected from Park Pond and Venard Lake, January 8 to May 25, 1949.

In Park Pond, warmouths nested among weed masses, stumps, roots, and brush; they nested in areas where the water was less than 4 feet deep and were most frequently seen where the shale and rubble spread out at the ends of the old spoil banks or had filled in the back portions of the flooded strip channels. They were not seen nesting where the banks were steep and sloped off quickly into deep water.

Warmouths build nests within a wide range of water depths, and consequently nest locations vary in their distances from shore. Earlier observers of warmouths recorded a variety of water depths selected: 6 to 10 inches (Richardson 1913: 412); mostly 2 to 10 inches (Carr 1940:109); 3 feet (Hubbs 1919: 144); 2 or 3 feet (Toole 1946: 33). In Venard Lake, the depths of water over warmouth nests that

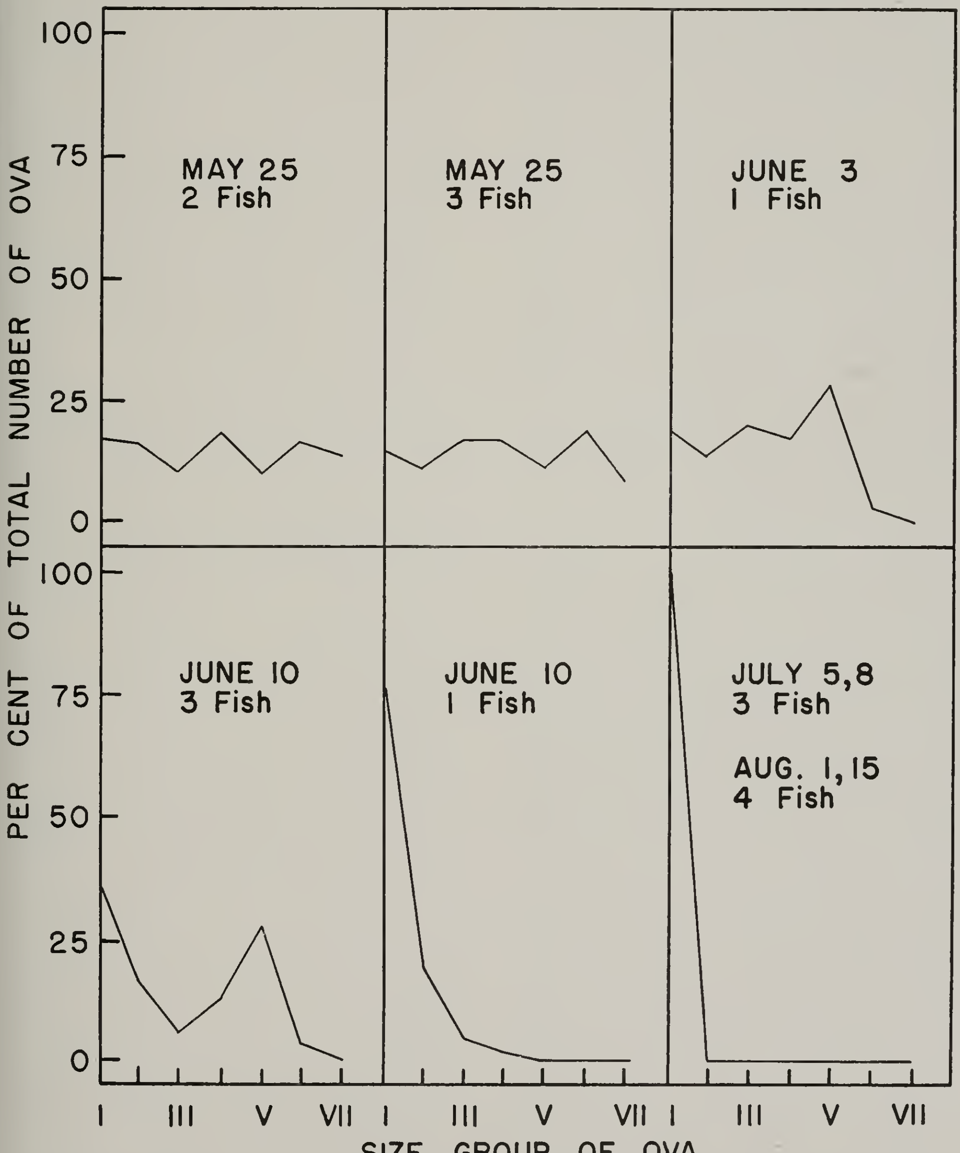

Fig. 12.—Percentage of total number of ova in each size group of ova found in warmouths collected from Park Pond and Venard Lake, May 25 to August 15, 1949.

were found ranged from 6 to 60 inches. Most of the nests were covered with 2 to 2.5 feet of water; nests in deeper water were more difficult to locate and may have been more common than counts showed. The limited areas of shallow water or the high transparency of the water in Venard Lake might account for the comparatively great depths at which nests were found in this body of water.

Reports of some observers indicate that the warmouth is gregarious in its nesting habits, forming colonies of nests (Richardson 1913:412; Carr 1940:110). It seems probable, however, that colony formation is a result of restricted nesting habitat. Observations of Carr (1940:109) in Florida and of the author in Illinois support the assumption that the reason warmouth nests are sometimes found close to each other is that the fish are tolerant of each other rather than gregarious in their habits. The warmouth colony studied by Carr was formed on what may have been the only bottom of suitable depth not covered with ooze. In Venard Lake, in May and June, 1947, nests were scattered in shallow water along the shore line with no indication of colonization. Three nests within a linear distance of 4 yards were the only ones that were found very close together.

Nest construction by warmouths in laboratory aquariums was observed many times in the course of the study reported here. As in other sunfishes, the male excavates the nest. Violent sweeping motions of the tail clear the loose debris away from the selected spot and produce a shallow, irregular concavity. The male begins each sweeping movement by approaching the nesting spot with his nose low and close to the bottom. As he enters the nest site, he turns abruptly upward, giving three or four violent sweeps with his tail while balancing in an almost vertical position and checking his forward motion with his pectoral fins. The loose material in the nest area is stirred up, and much of it settles outside the spot being cleared. The size and neatness of the nest depend to some extent on the amount of time the male spends in its construction. Many nests in natural waters are rather shapeless oval depressions of 4 by 8 inches from which loose silt has been cleared. The male may continue to improve the nest if a female is not immediately available for spawning. One warmouth male nesting in an aquarium worked on his nest until it was a beautifully symmetrical depression 18 inches in diameter and 5 inches deep. Though most warmouth males under natural conditions spend no more than a few hours in clearing small nesting spots, the male in the aquarium spent a week working on his nest while waiting for the female that was present to become ripe.

A mature female warmouth isolated in an aquarium during the breeding season constructed a shallow nest; her attachment to the nest was much weaker than that characteristic for a male.

Preliminary Courtship.—The preliminary courtship phase of warmouth nesting was observed by the author only in laboratory aquariums. Normally it appeared as an aggressive threat to other males, serving to drive them away, and as a persuasive gesture to females in spawning condition.

During the first week in May, 1947, three unripe warmouths were placed in each of four aquariums previously filled with water and supplied with a layer of sand and gravel. By the second day, some of these fish had selected favorite corners and were accepting food. Two of the three fish in each tank soon began constructing nests and making advances at the third fish. On the basis of behavior, only the nest-building warmouths appeared to be males; the third fish in each of the tanks showed no interest in nesting and apparently was being courted by the aggressive males. Courtship in each tank progressed to the act of driving the nonnest-building warmouth into the nest depression and going through motions of spawning. Vivid spawning colors (discussed in the following section) were displayed by only the aggressive males; no color changes were shown by the fish that were being courted. After these courtship activities had continued for several days, the fish were examined. Several had become ripe since being put in the aquariums and were flowing milt. Dissection of the nonaggressive, nonnest-building fish revealed that they, too, were males, although not in advanced stages of development, as were the aggressive males.

These initial observations of spawning suggest that (1) warmouth males begin construction of the nests in the absence of females and well before their testes are ripe; (2) sex recognition among warmouths is based on behavior and response to courting; and (3) in a small group of warmouths, during the breeding season some individuals assume dominance over less aggressive fish.

When a female that is not yet ready to spawn is placed in a tank with a nesting male, she is charged, nipped, and driven to the surface. She remains quiet and retiring, ignoring as much as possible the male's advances. Being unable to escape the male in an aquarium, she may finally be killed by his continued aggression. Under natural conditions, the female does not become exposed to the unavoidable advances of the nesting male before she is ready to spawn.

Spawning

In the warmouth, the mating act, which includes the deposition and fertilization of eggs, requires the simultaneous ripening of sex products and synchronization of behavioral attitudes in a male and female. Many environmental conditions, as well as the state of maturity of the fish, affect the spawning process.

Size and Age at Sexual Maturity.—The attainment of sexual maturity in fishes is influenced by both age and size. In the warmouth, size seems to be more important than age in determining when a fish attains maturity. However, there is considerable variation among warmouths in the size (and age) at which maturity is reached. As might be expected, this variation is greater between fish of different populations than among fish within a single population.

Sexual maturity is attained by warmouths when the fish are between 3 and 4 inches in length. In Venard Lake, both males and females matured at 1 year of age and at lengths between 3.1 and 3.4 inches. In Park Pond, warmouths did not mature until they were 2 years old and at least 3.5 inches in length. Thus, at the time the fish became sexually mature in Park Pond, they were somewhat larger than the sexually mature 1-year-old fish in Venard Lake. Hile (1941:319) found for the rock bass that rapid growth appears to be correlated with an early attainment of sexual maturity.

Nesting Season.—The observed nesting season for the warmouth in central Illinois begins during the second week in May, reaches its peak early in June, starts to decline after the first of July, but often extends well into August. The length of the nesting season differs among different populations of warmouths in different lakes and probably varies considerably from year to year. The length of the season varies also with the size of the fish; large warmouths spawn over a longer period than do small ones, fig. 8.

Although the exact length of the spawning season is difficult to determine for an individual fish, studies of gonads have shown that a fish may spawn several times during a summer. In Texas, Toole (1946:33) reported, "One pair of these fish was observed to spawn three different times during one year from April to October." At the Natural History Survey laboratory, two females that spawned early in June, 1948, were examined 2 weeks later and were found to have well-developed ova. These fish were not spent after the one spawning period and would undoubtedly have produced more ripe eggs during the same season. Warmouths that were collected in July, 1948, and that presumably had spawned at least once, were placed in a small pond on the following August 10; they produced a good brood of young in the pond that season.

Deposition and Fertilization of Eggs.—Only when a female is ready to lay her eggs will she allow a male to guide her to the nest for spawning. In getting the female to the nest, the male assumes a very aggressive attitude, approaching her with his opercles widely spread and his mouth open. The body of such a courting male becomes bright yellow in color and his eyes become blood red. The adjustment to these colors is very rapid, requiring only 5 to 10 seconds. If the female is ready to spawn, she is easily directed toward the nest, and spawning soon follows.

The number of females contributing to the complement of eggs in a nest may depend upon how many females are ripe and available to the male. It is probably not uncommon for more than one female to spawn in a single nest, as has been observed for other centrarchids. That such polygamy seldom occurs after the male assumes close guardianship of the eggs is indicated by the fact that freshly laid eggs are not commonly found in nests containing eggs in advanced stages of development. In a laboratory aquarium, however, a male guarding yolk-sac fry brought a female to the nest and proceeded with spawning activities.

One female observed in a large aquarium in which two males had nests only 10 inches apart alternated between the two nests during a continuous spawning sequence. During an hour of spawning activity, the female spawned with both males. When she was in one nest, the male in the other nest showed no concern for her; he would inspect the newly deposited eggs, stir the nest with his tail, and wait for the female to again approach his nest. The female spawned almost continuously for 40 minutes and for another 20 minutes at brief intervals and less vigorously. When spawning was finished, the female was temporarily removed from the aquarium; gentle pressure on the sides of this female did not cause the discharge of any eggs.

On entering the nest site, both male and female begin to circle, the female being nearer the center of the nest, slightly on her side and somewhat beneath the male, fig. 13. As they circle inside the nest, the female works her jaws three or four times and suddenly jerks her body violently, giving the male a sharp thump on the side. Each time the female jerks, she extrudes about 20 eggs. The thump she gives the male probably stimulates a discharge of sperm, although no milt was ever seen coming from the genital pore. After circling the nest several times, the female interrupts the activities and leaves the nest site. The male usually follows her a short distance but returns quickly to the nest to assume guardianship. At this point in the spawning activity, males often have been observed to fan the nest with sweeping motions of the tail in a manner similar to that exhibited when nest building.

Spawning activities like those observed in aquariums were carefully watched in Venard Lake. In nature, when a female

Fig. 13.—Warmouths spawning in an aquarium. The light-colored fish is the male; the darker fish below and slightly on her side is the female.

is ready to spawn, she makes her appearance near a nest and accepts the advances of the male. After a few spawning turns inside the nest, she retires, usually to a clump of weeds several yards away. The male remains over the nest for a few minutes before again making advances toward the female. This procedure is repeated until the female has discharged her ripe eggs. With spawning completed, the female swims away, and the male settles down quietly to protect and fan the eggs.

History of Embryos and Larvae

When the warmouth starts its life and development, it is confronted by greater stresses of physical and biological factors than it will face at any other time during its life. Temperature changes or temperature extremes, disease and predation, and dependence on the constant protection of a parent fish, which may at the same time be exposed to many dangers, result in high losses in the period of early development of the warmouth.

Development of Embryos.—Four groups of warmouth eggs, 10 in each group, were artificially inseminated in order to observe the gross development of the embryos and the exact length of the incubation period. The following account includes the time sequence of certain easily discerned stages of development at temperatures between 25.0 and 26.4 degrees C. Within this temperature range, the average developmental period of the 40 eggs was 34 hours and 30 minutes and the interval between hatching of the first egg and hatching of the last was 2 hours and 40 minutes.

When eggs and sperm were mixed in a petri dish and then immediately flooded with water, a high percentage of the eggs became fertilized. The inseminated eggs measured 0.95 to 1.03 mm. in their greatest diameters during their first and second minutes in water. These measurements are slightly below those of the largest ova taken from preserved ovaries. Differences in size measurements between preserved and live ova may have been due to differences in shapes: irregular shapes of the ova preserved intact in the ovaries and almost spherical forms of the live ova in water. Each of the live eggs, translucent and light amber in color, contained a single, dark amber oil droplet 0.35 mm. in diameter.

Within 3 minutes after an egg was impregnated by a sperm cell, a thin perivitelline space could be seen between the outer membrane (chorion) and the egg cell proper. Thirty minutes later, a blastodisc was evident as a slightly raised cap, giving the egg a somewhat oval appearance. The first division of the blastodisc occurred 43 minutes after impregnation. Each blastomere then measured 0.4 mm. across. The second, third, and fourth divisions took place at 60, 75, and 90 minutes, respectively. The resulting group of blastomeres appeared whitish, the yolk was very pale yellow, and the oil droplet remained dark amber in color.

After 2 hours and 15 minutes, the blastomeres formed an oval-shaped mass at one end of the yolk. The segmentation cavity was formed beneath this mass, and at 2 hours and 30 minutes the blastoderm began growing down over the yolk mass.

The blastoderm had grown over two-thirds of the yolk mass within about 11 hours after impregnation, and a thickened band of cells at the margin of the blastoderm had appeared as the germ ring. About an hour later (12 hours and 15 minutes after impregnation), the blastoderm covered all but a small plug of yolk, which contained the oil droplet. The first differentiation among the dividing cells was visible in the live egg after 14 hours and 15 minutes. A groove extended around the egg from a patch of opaque cells near where the yolk plug and oil droplet entered the blastoderm. This groove, formed by the neural plate and neural folds, became quite distinct during the following hour (15 hours and 10 minutes after impregnation).

After 16 hours and 30 minutes, the primordial form of the embryo was defined. The ensuing process of organ formation, however, could not be discerned. Movement of the embryo was first observed 25 hours after impregnation.

The first egg hatched 33 hours and 20 minutes after impregnation. All eggs had hatched by the end of the following 2 hours and 40 minutes (36 hours after impregnation). Fry emerging from the eggs early during the hatching period were smaller (2.30–2.60 mm. in total length)

Fig. 14.—Warmouths from hatching through postlarval stage: *A*, prolarva, 3.4 mm., soon after hatching; *B*, prolarva, 4.6 mm., 48 hours old; *C*, postlarva, 5.3 mm., 4 days old; *D*, postlarva, 7.6 mm.; *E*, postlarva, 8.8 mm.; *F*, postlarva, 12.0 mm.

than those emerging later (2.65–2.85 mm. in total length). The oil droplet in the newly hatched fish was the same size (0.35 mm. in diameter) and color as it was in the newly fertilized egg. The greatest depth of the fry was 0.80 mm. across the yolk sac.

It is interesting to note here that warmouth eggs fertilized with sperm from a green sunfish showed no difference in rate of development from the rate described above. There was a high percentage of survival of both embryos and fry of the warmouth and green sunfish cross.

Development and Growth of Larvae.—Specimens for a study of growth of larvae were collected from a nest in a laboratory aquarium. The eggs were laid during the morning of June 24, 1947. Daily collections were made until the postlarvae left the nest. Then the free-swimming larvae were transferred to an outdoor tank, where observation and sampling were continued. The specimens, preserved in alcohol, served as materials for the following descriptions of developmental stages. Observations indicated that total length of a larva is a better indicator of the stage of its development than is actual age, which was known for each specimen. Measurements made with an ocular micrometer to the nearest 0.01 mm. were used in the description of body form. In general, descriptions follow the procedure used by Fish (1932); terms for growth stages are those suggested by Hubbs (1943: 260).

Prolarva, 3.4 mm., soon after hatching, fig. 14*A*: Total length 3.4 mm.; length to anus 1.7 mm.; length of yolk sac 1.0 mm. Large oval yolk mass containing one oil droplet 0.3 mm. in diameter. Head deflected sharply downward in front of yolk sac, making the midbrain the most forward part of the body and the forebrain lying directly beneath it. Head from front of forebrain to end of hindbrain 0.65 mm. Optic capsule faint, 0.23 mm. in diameter. Notochord straight. Myomeres incomplete anteriorly, numbering about 8 in front of anus and 17 behind anus. Embryonic marginal fin fold complete except for faint break where intestine penetrates fin to outside. Fin extending forward on back to point 1.0 mm. from front of body. No visible ray development nor pigmentation.

Prolarva, 4.6 mm., 48 hours old, fig. 14*B*: Total length 4.6 mm.; length to vent 2.0 mm.; length of head 0.63 mm.; greatest depth of body in front of vent 0.70 mm.; greatest depth of body behind vent (excluding fin fold) 0.35 mm. Forebrain still somewhat deflected, with globular cerebellum extending high above anterior part of medulla. Eyes well pigmented, each 0.35 mm. in diameter; optic fissure still quite apparent. Mouth indistinct. Fin fold extending forward on back to point 1.2 mm. from front of body, entire except for break at anus. Very weak indications of fin rays below and above end of straight notochord, giving effect of diphycercal tail. Pectoral lobes present. Myomeres indistinct forward, about 10 to anus, 19 caudad from anus. Branchial elements forming.

Postlarva, 5.3 mm., 4 days old, fig. 14*C*: Total length 5.3 mm.; length to anus 2.2 mm.; greatest depth of body anterior to anus 0.6 mm.; greatest depth of body posterior to anus 0.35 mm.; diameter of eye 0.41 mm.; length of head 0.90 mm. Cranial flexures almost straightened, but cerebellum high and bulblike. Optic cavity distinct. Fin fold beginning on back 1.5 mm. from front of body, becoming slightly narrow on caudal peduncle but wide again at tail. Faint indication of rays forming in areas of the anal and soft dorsal fins. Distinct fin rays on either side at end of the straight notochord. Kidney apparent through body wall. Pectoral fin lobes well developed but with no rays. Myomeres 10 anterior to anus, 19 posterior to anus. Branchial arches well formed and with developing gills. Mouth gape extending obliquely forward from point below middle of eye. Dark row of spots on either side of ventral fin fold; two large chromatophores between bases of pectoral fins.

Postlarva, 7.6 mm., fig. 14*D*: Total length 7.6 mm.; length to anus 3.4 mm.; length of head 1.5 mm.; diameter of eye 0.55 mm.; greatest depth of body anterior to anus 1.15 mm.; greatest depth of body posterior to anus 0.65 mm. Myomeres 11 before anus, 19 behind anus. Fin fold still complete except for break at anus; high at soft dorsal fin region, quite low above and below caudal peduncle. End of notochord bent upward at 40-degree angle, giving appearance of heterocercal tail. Caudal fin rays well developed on lower side of notochord, with middle rays longest. Rays weak but distinct in unformed anal fin;

rays very weak in soft dorsal. Rays visible in pectoral fins. Mouth only moderately oblique. Pigmentation much more developed. Row of spots along ventral fin fold spreading as stellate chromatophores over ventral surface of body. Series of dark dashes indicating lateral line. Heavy chromatophore lying above anus. Some color apparent at base of caudal fin rays. Six stellate chromatophores between bases of pectoral fins and a row of five chromatophores on each side across branchiostegals. Distinct, dark chromatophores scattered over top of head.

Postlarva, 8.8 mm., fig. 14*E*: Total length 8.8 mm.; length to anus 3.9 mm.; length of head 2.0 mm.; length of snout 0.4 mm.; diameter of eye 0.75 mm.; depth of caudal peduncle 0.65 mm. Caudal peduncle long and narrow. Notochord with upturned end but tail appearing essentially homocercal. Fin fold present immediately anterior to anus. Anal and soft dorsal fins separate from caudal fin but each broad at base, due to some remaining parts of the embryonic marginal fin fold. Rays distinct in all fins present. Pelvic fins not developed. Otic region large and clear. Anus protruding from ventral line of body. Lateral line chromatophores quite distinct. Ventral spots larger, with more chromatophores scattered over head region.

Postlarva, 12.0 mm., fig. 14*F*: Total length 12.0 mm.; length to anus 5.4 mm.; length of head 2.8 mm.; diameter of eye 1.0 mm.; length of snout 0.7 mm.; greatest depth of body 2.45 mm.; length of caudal peduncle 2.4 mm.; depth of caudal peduncle 1.15 mm. Fin fold remaining only as short keel in front of anus. Pelvic fins present but weak and with indistinct rays. Spinous dorsal developed only as a row of short stubs. Distribution of pigment about the same as in 8.8 mm. stage, except spots appearing more distinct. More dark chromatophores around mouth; a vertical row present at base of caudal rays.

Juvenile, 15.7 mm. (not photographed). Body form essentially like that of adult fish. Total length 15.7 mm.; length to anus 7.0 mm.; length of head 4.35 mm.; diameter of eye 1.4 mm.; length of snout 0.85 mm.; greatest depth of body (at about anterior insertion of spinous dorsal) 3.7 mm.; length of caudal peduncle 2.9 mm., depth 1.5 mm. Anus protruding only slightly from abdomen. No trace of embryonic marginal fin fold. Pelvic and spinous dorsal fins well formed. Pigmentation much heavier than in earlier stages. More color apparent over head and caudal peduncle. Belly rather free of pigment. Many large chromatophores scattered over back. Heavy row of spots forming circle behind eye and distributed over top of head. Chromatophores noticeable on soft dorsal, anal, and caudal fins.

Behavior of Larvae.—Activities of the warmouth larvae during their early life in the nest were limited to a few feeble movements. There was definite sequence, however, in the behavioral development of these small fish. The following description of behavior was based on laboratory observations in aquariums with water of 24–25 degrees C. (75–77 degrees F.).

Immediately upon hatching, the delicate prolarvae dropped down onto the sand and silt between coarse gravel particles of the nest. As the heavy yolk sac restricted movement, the prolarvae were difficult to see in the nest. When the prolarvae were between 36 and 48 hours old, fig. 14*B*, they began making feeble jumps an inch or so above the bottom of the nest. Most of these prolarvae were between gravel particles in the nest, but a few could be seen resting on the flat surfaces of the largest particles.

Although the yolk supply was about exhausted by the fourth day, the young fish still limited their movements to poorly directed jumps above the nest. They did not begin active swimming until the end of the fifth day, when they appeared as in fig. 14*D*. At this time, they swam about the nest in rather compact groups. Their movements were well controlled, and they showed remarkable ability to avoid a dip net. In the aquariums, these small fish had no food supply and starved in 10 or 11 days after hatching, but in outdoor tanks they began feeding at least by the seventh day after hatching.

School formation among postlarval warmouths in natural habitats was not so obvious as in postlarvae of certain other sunfishes, for the warmouths remained either among dense submerged vegetation or else in small pockets of open water closely surrounded by plants. The individual shown in fig. 14*F* was taken from a school near the nest in which it had hatched. The schools gradually dissolved as individuals began independent searches for food. No juvenile warmouths were observed in large groups.

Factors Affecting Survival.—Rate of survival of warmouth eggs and young is influenced greatly by many physical and biological factors. Incubating eggs are readily affected by adverse weather conditions. Sudden drops in water temperatures promote the rapid growth of fungi infecting the eggs; often, entire nests of eggs are destroyed early in the spawning season as a result of low temperatures and fungi. For example, many warmouth nests in Venard Lake contained eggs during the last week in May, 1947, but, after several days of cold weather, the eggs in every nest observed were covered with fungi. Although heavy rains and high turbidity were not seen to affect nesting of adults or survival of fry, rapidly falling water levels might disturb nesting.

In several Illinois lakes, minnows and sunfishes were observed destroying eggs and larvae in unprotected warmouth nests. In laboratory aquariums, warmouths were seen to rob poorly guarded nests; they charged in to snap up eggs or larvae.

Postlarval and juvenile warmouths which have left the nest are eaten in great numbers by larger fish. Venard Lake supported a heavy spawn of both largemouth bass and warmouths in the summer of 1947. On June 30 of that year, bass 1.75 inches long were voraciously feeding upon warmouths 0.75 inch long, which had been eating large numbers of postlarval warmouths. In the laboratory, a 0.75-inch warmouth ate 11 postlarvae (4 days old) in 5 minutes; another ate 12 in the same length of time.

Survival of small warmouths is closely related to the density and composition of the fish population, the time of year, and the character of the habitat in which they are produced. Fry hatched late in the spawning season are in a population with a larger number of potential predators (fish only slightly larger than themselves) than are the fry produced earlier. However, because the density of aquatic vegetation increases during June and July, survival in the late summer broods is frequently higher than in early broods.

GROWTH

Whether one is studying a single species of fish or the entire fish population of a body of water, it may become necessary to consider the growth of individuals in the one or more species involved. An analysis of growth is not always the objective of such a study, nor is determination of the morphological relationships which must be known before an analysis of growth can be made. The ultimate value of a growth study may come from its use in determining the factors that govern or influence growth of fish under particular conditions.

Relative Growth

Various parts of a fish's body grow at differential rather than uniform rates. The differential rates are not necessarily the same even for closely related species in the same habitat, nor for fish of the same species in different habitats. Consequently, when making a growth analysis of a selected species in a given habitat, one must determine several morphological relationships, namely, those of body growth to scale growth, body growth to growth of tail fin, and growth in length to growth in weight. Lewis & English (1949) and Hennemuth (1955) have plotted some of these relationships for two populations of Iowa warmouths, and Jenkins, Elkin, & Finnell (1955) for several populations of Oklahoma warmouths.

Relation of Body Growth to Scale Growth.—A regression line to show the relationship between length of anterior radii of scales and length of body was constructed from measurements of 1,068 warmouths from Venard Lake and Park Pond, fig. 15. Data were obtained from collections made approximately monthly beginning in June, 1948, and ending in November, 1949. Regression lines constructed for warmouths from Venard Lake and for those from Park Pond proved to be so similar that data from the two lakes were combined.

Key or representative scales were taken from the side of each of the fish near a point where the tip of the pectoral fin laid backward touched the third row of scales below the lateral line. Fish were separated into total length classes at 0.5-inch

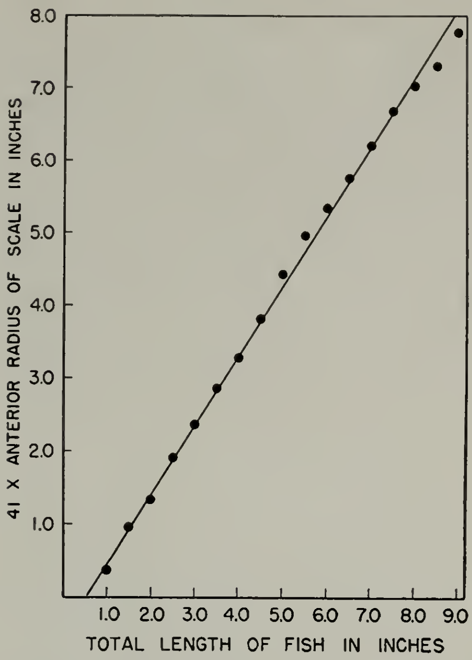

Fig. 15.—Regression line expressing the relationship between total length of fish and radius of scale for 1,068 warmouths collected from Park Pond and Venard Lake, early June, 1948, through middle November, 1949. The dots show the anterior radius of scale$\times$41 for fish of various total lengths (one-half-inch intervals).

intervals, and the average of the total lengths for the fish in each of these classes was determined. Scales of these fish were placed in a scale-reading machine that magnified 41 times, and images of the anterior radii of the scales were measured and averaged for the fish in each length class. Average total lengths of fish and corresponding average anterior radii of selected scales were used in developing the regression line shown in fig. 15 and the following equation:

$$L = 0.5278 + 1.048\ S$$

where L=total length of fish in inches and S=41$\times$anterior radius of scale in inches

Relation of Body Growth to Tail Growth.—Growth of the body of a fish in relation to growth of its tail, or caudal fin, may be ascertained by comparing the standard length of the fish with its total length. As defined by Hubbs & Lagler (1947:13), total length includes the caudal fin, whereas standard length does not.

The relationship between growth of body to growth of tail was calculated from measurements of 264 warmouths taken from Park Pond, summer, 1948, and November, 1949, and Venard Lake, October, 1949. As the average body length of the warmouths increased, the average tail length became relatively less, table 17. In fish less than 4.0 inches total length, the average total length was 1.259 times the average standard length; in fish of 4.0 to 6.9 inches, the average total length was 1.240 times the average standard length; and, in fish longer than 6.9 inches, the average total length was 1.211 times the average standard length.

Relation of Growth in Length to Growth in Weight.—The relationship between growth in length and growth in weight was calculated from data on 866 warmouths collected from Park Pond between early June, 1948, and early November, 1949. Size groups were established at 0.1-inch intervals. Average weights were determined for each group within the size range beginning with 3.3 and ending with 8.2 inches total length. The length-weight relationship for each of

Table 17.—Factors derived from measurements of warmouths from Venard Lake, October, 1949, and Park Pond, summer, 1948, and November, 1949, for converting standard length (S.L.) to total length (T.L.), and the reverse, with the same and with different units of measurement.

Total Length, Inches	Number of Fish	Conversion Factors			
		T.L. to S.L. (Same Units)	S.L. to T.L. (Same Units)	S.L. (Mm.) to T.L. (Inches)	T.L. (Inches) to S.L. (Mm.)
Under 4.0	130	0.795	1.259	0.0495	20.18
4.0–6.9	93	0.806	1.240	0.0488	20.48
Over 6.9	41	0.826	1.211	0.0477	20.98
Combined	264	0.809	1.240	0.0487	20.52

the specimens (866) was expressed by the equation:

$$\log W = -4.49867 + 3.04902 \log L$$

where W=weight in grams
and L=standard length in millimeters

Length-weight relationships were calculated for the especially heavy and especially light warmouths in the Park Pond population. For warmouths heavier than average, the equation was as follows:

$$\log W = -4.36191 + 3.01387 \log L$$

For those lighter than average, the equation was as follows:

$$\log W = -4.35603 + 2.95352 \log L$$

From these equations, it may be seen that fish either heavier in relation to length, or lighter in relation to length, than the average bore a systematic relationship of length to weight roughly paralleling that of the average. Such divergence from the average as was discernible was found particularly among the fish of greater lengths and weights, fig. 16.

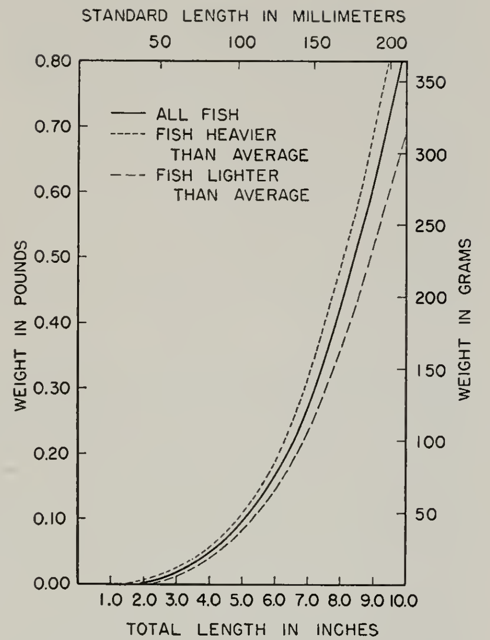

Fig. 16.—Curves illustrating the relationship between length and weight of warmouths collected from Park Pond, early June, 1948, through middle November, 1949.

Coefficient of Condition

The coefficient of condition (C), based on total length in inches and weight in pounds, was computed for the 866 Park Pond warmouths used in the analysis of length-weight relationships. Fish smaller than 3.3 inches total length were not considered because individuals were weighed only to the nearest 0.01 pound, and greater weighing preciseness would have been necessary if smaller fish had been used; warmouths of more than 8.2 inches total length were not used because few were available.

Condition (C) increased progressively with increased size of fish. The average C (weighted to compensate for differences in numbers of individuals in groups) for each of several size groups, 3.3–4.2, 4.3–5.2, 5.3–6.2, 6.3–7.2, and 7.3–8.2 inches total length, was 72.6, 74.8, 78.6, 80.9, and 82.6, respectively. Warmouths within the size range 3.3–4.2 inches total length showed a wide seasonal variation in condition (C). This variation among small warmouths may have been caused by their dependence upon food items that fluctuated widely in abundance from month to month, such as cladocerans and certain insects and their larvae. Larger warmouths, feeding more upon crayfish and fish, varied less in body condition from one season to the next than did small warmouths.

The condition (C) of warmouths for each of three size groups, 4.3–5.2, 5.3–6.2, 6.3–7.2 inches total length, was similar in seasonal fluctuations. A sudden, severe drop in condition occurred in September, 1948; a low level in condition lasted through October, and was followed by a rapid recovery by mid-November. Condition declined gradually during the winter and spring, but then began an increase that continued through May and June. Condition remained relatively high and constant throughout the summer of 1949 and then declined during the fall months. Fig. 17 suggests that for the warmouths of Park Pond a definite cycle of condition associated with seasons could not be established.

Since food habits were studied for these warmouths collected from early October, 1948, to early November, 1949, it was possible to associate the foods eaten with the seasonal variations in condition of the fish. The low level of condition in the winter (1948–49) was coincident with a comparatively low consumption of crayfish, dipteran larvae, amphipods, and mayfly nymphs and with a comparatively high consumption of fish and dragonfly nymphs, fig. 6. During the spring of 1949, when the warmouths were eating high percentages of crayfish (volume) and damselfly nymphs (frequency), the condition of these fish was steadily improving. The relatively good condition of warmouths during the summer of 1949 was associated with the extensive use of mayfly nymphs, caddisfly larvae, and crayfish.

There were no consistent differences in condition between male and female warmouths in Park Pond.

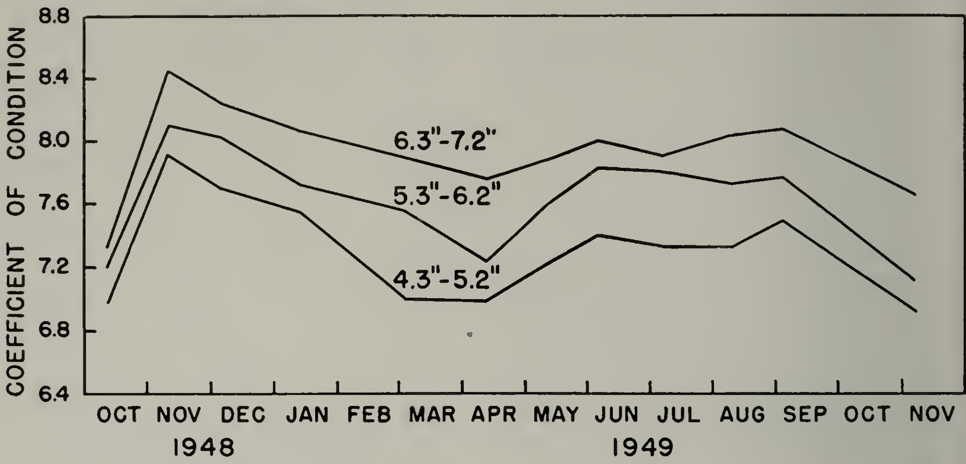

Fig. 17.—Coefficient of condition of 392 warmouths of three size groups (6.3–7.2 inches, 5.3–6.2 inches, 4.3–5.2 inches) collected from Park Pond, early October, 1948, through early November, 1949. Warmouths collected and weighed in the summer of 1948 were so few in number that data on them were not included in the graph.

Scale Method of Calculating Growth

The method of calculating warmouth growth from fish lengths and scale measurements is a composite of methods developed by several authors but generally follows the procedures suggested by Hile (1941).

Validity of the Annulus as a Year-Mark.—Age and growth studies made from the scales of warmouths in Venard Lake and Park Pond indicate that the annulus is a reliable year-mark in this species. Hile (1941:201–4) outlined the most important features of a valid annulus. Four points used to test the validity of the scale method of age determination for the warmouths used in the present study are as follows:

1. There was a regular increase in the number of annuli accompanying an increase in size of fish, and fish assigned to any single age group were within a certain length range, table 18.

2. Lengths calculated from scale measurements agreed reasonably well with actual lengths of fish of corresponding ages, tables 18 and 21.

3. Calculated lengths were similar for the same age groups of fish collected in different years and consistent for different age groups of fish collected in the same or different years. Because the calculated lengths were very similar for warmouths in the 1948 and 1949 Park Pond collections, data for these two collections were

Table 18.—Averages of total lengths of warmouths of various ages collected from Park Pond, June, 1949.

Year of Life	Number of Fish	Average Total Length, Inches	Range of Total Length
2	17	2.31	1.9–2.8
3	35	3.53	2.8–4.6
4	90	5.20	3.6–7.1
5	114	6.62	5.4–8.2
6	31	7.66	6.0–8.7

combined and are not shown separately; however, consistency in calculated lengths of fish of the same and of different age groups is shown in tables 21 and 26.

4. There was similarity among warmouths of different year classes with respect to growth rates in certain calendar years, tables 23 and 24.

Characteristics of the Annulus.—The true annulus on the warmouth scale appears as a result of resumption of growth of body and scales after the cessation of growth during winter months. True annuli or year-marks usually show several rather definite characteristics, fig. 18. Across the anterior field of the scale the annulus appears as a break in the arrangement of circuli; it is bordered on the inside by closely spaced, incomplete circuli and on the outside by complete, widely spaced circuli. The radii in the anterior field are slightly distorted in the region of the annulus. On the lateral fields of the scale, the annulus and newly formed circuli

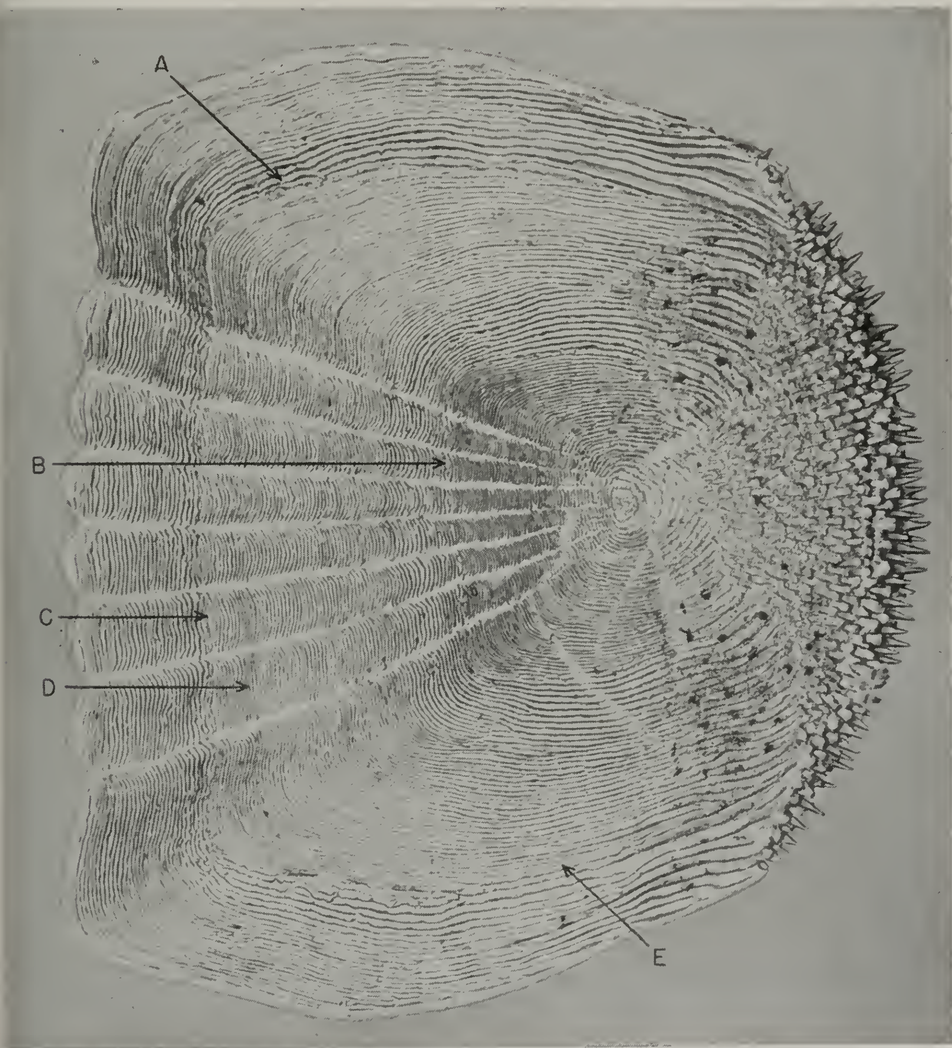

Fig. 18.—Warmouth scale: *A*, wide spacing of circuli especially evident following resumption of growth in spring; *B*, first annulus; *C*, second annulus; *D*, crowding of circuli during period of slow growth resulting from habitat disturbance; *E*, new circuli cutting across ends of circuli laid down in previous season.

"cut over" the circuli laid down near the end of the previous season. The annulus extends only part way across the posterior field of the scale. Slight differences in spacing of circuli and in the lengths of ctenii (small surface spines on scale) may aid in recognizing the location of the year-mark in the posterior field.

The first annulus formed on the warmouth scale does not show as much "cutting over" in the lateral fields as do later annuli, nor are the differences in spacing of circuli so apparent in the first as in later annuli. The differences which may exist in length and distribution of ctenii are most useful in recognizing the first annulus. Annuli formed later are generally more difficult to recognize with certainty, mainly because they are closer together than those earlier marks laid down when the fish was increasing rapidly in length.

Time of Annulus Completion.—In 1949, the time of annulus completion in warmouths at Park Pond was determined from 129 specimens collected between April 7 and May 20. Sixty-eight per cent of the warmouths collected May 13 and 14 had laid down the year's annuli on their scales, so that the average time of annulus completion appeared to be about the first week of May, table 19, at which time the water temperature 1 foot below the surface of the water was about 70 degrees F., fig. 9. Small fish usually lay down the year-mark earlier in the spring than do the larger ones, because the former begin to grow at an earlier date. Fifteen per cent of 39 fish collected from Park Pond on April 7 and 9 showed new annuli on their scales; all but one of these fish were less than 4 inches total length.

As annulus formation is associated with the resumption of growth of the fish in spring, the annuli on the scales of fish may not be completed at the same time each year, and the time may vary from one population to another. Warmouths in Venard Lake showed a period of annulus formation in 1949 that differed from the period shown by the warmouths in Park Pond. In the fish collected from Park Pond, some year-marks appeared before April 7, but only 68 per cent of the fish in the May 13–14 collections had completed annulus formation; the period in which annuli were being completed covered more than 6 weeks. In Venard Lake, on the other hand, none of the specimens collected on April 5 had formed an annulus; in the collection of May 12, about 5 weeks later, 30 of 31 fish (nearly 97 per cent) had completed annulus formation.

Ecological conditions in Venard Lake, where warmouths were confined to a small area having only minor fluctuations in depth, probably were more nearly uniform than in Park Pond, where warmouths were found in shallow sloughs, deep channels, and open waters. It seems reasonable to believe that a population inhabiting a pond with a wide variety of physical conditions might show annulus formation over a longer period than a population exposed to more nearly uniform physical conditions. Furthermore, in Park Pond, fish of many other species were competing with warmouths for the natural foods available in early spring.

Table 19.—Percentages of warmouths with and without new annuli, Park Pond collections, 1949.

Date of Collection	Number of Fish	Percentage Lacking New Annuli	Percentage With New Annuli
April 7–9....	39	85	15
May 13–14..	38	32	68
May 16......	40	20	80
May 20......	12	8	92

False Annuli.—Some scales of warmouths show false annuli, or marks which are not true year-marks but merely indications of physiological disturbances during growing seasons. False marks were found on the scales of many fish from Park Pond. Most of them could be recognized with confidence. They did not appear uniformly throughout a population or regularly at definite times of year.

False marks were formed on the scales of a large part of the warmouth population of Venard Lake during August of 1948. These marks could be distinguished, particularly in the 1947 year class, on the scales of fish collected in succeeding years. Since monthly collections allowed the false annuli to be originally dated and to be recognized by their location in relation to true annuli on the scales in later collections, these marks gave little trouble in age determinations. The formation of the marks coincided with a 4-week period of shoreline dredging with a dragline. Such a severe disturbance of the habitat must have reduced the food supply or its availability and caused a temporary stoppage of growth that produced the false marks.

Growth in Park Pond

Park Pond, an 18-acre lake in a flooded stripmine area, in 1948 and 1949 supported an old (60 years at least), rather large fish population of about 36 species native to the region. Most of these species had been introduced into the lake from the Salt Fork in times of flood, page 4.

Collection and Preparation of Materials.—In the period beginning June 7, 1948, and ending November 12, 1949, 1,420 warmouths were collected from Park Pond. Hoop nets, fig. 19, were used in collecting 367 warmouths; of these fish, 298 were collected between early June and mid-September, 1948, and 69 between June 27 and July 5, 1949. An electric shocker rigged for operation from a rowboat (Larimore, Durham, & Bennett 1950) was used to collect specimens for growth analyses and food studies. A total of 788 fish were taken by this method in collections made at monthly intervals from early October, 1948, to early November, 1949, except that no collections were made in February and October, 1949. Even though Park Pond supported the largest naturally established warmouth population that had then been examined in Illinois, warmouths were never taken there in great numbers; a good day's take might consist of 2 dozen warmouths from the usual set of six hoop nets or 50 warmouths from the operation of the electric shocker. Large specimens predominated in the hoop net catches; fish of all sizes were present in collections made by shocking. On August 22, 1949, rotenone was applied to a shallow, isolated, 0.47-acre slough in Park Pond, and a census was made of the fish population. Scales for growth studies were taken from 265 of the 504 warmouths collected from this area.

Fig. 19.—Collecting fish with a hoop net in Park Pond.

Ages were determined for 1,328 of the 1,420 warmouths collected (265 from the shallow, isolated slough and 1,063 from other parts of Park Pond). Scales from 84 fish were regenerated and unreadable; scales of 8 other specimens were so difficult to read that ages could not be determined with certainty. Fish from the slough that was treated with rotenone were considered separately because they showed growth rates significantly different from those taken in the other collections. Impressions of the warmouth scales were made on cellulose acetate slides, and the images of these impressions were projected for study at a magnification of 41 diameters. Measurements along the median, anterior radius of a magnified scale image were marked on a manila paper strip, and the strip was used for calculating past growth on a nomograph, as described by Carlander & Smith (1944). Calculated lengths, based on a straight-line relation between scale length and body length, were corrected for an intercept of 0.53 inch in body length (fig. 15 and equation on page 50).

The following sections, "Growth Differences Between Sexes," "History of Successive Year Classes," "Fluctuations in Annual Growth," and "Seasonal Growth," refer to Park Pond warmouths other than those from the slough.

Growth Differences Between Sexes.—Sex was determined by dissection or by visible discharge of sex products for 600 specimens in year classes 1944 through 1948. Calculated lengths of males and females of each of the year classes were averaged and compared, table 20. Fish in both the 1943 and 1949 year classes were represented by so few specimens for which sex was determined that they were omitted from the calculations.

Very consistent, although rather small, differences existed between the growth rates of males and females. Males were larger than females at the end of each year of life in the five year classes considered. The greatest differences occurred in the 1944 year class, but the small number of specimens (only seven females) made this growth comparison less reliable than that for other year classes. The next oldest brood, the 1945 year class, was represented by 187 specimens. Males in this group averaged only a little longer than females. Schoffman (1940:32) observed that the lengths and weights of male and female warmouths of the same ages in Reelfoot Lake, Tennessee, were either the same or only slightly different.

Since the actual differences in lengths of male and female warmouths were rather small in those year classes represented by substantial numbers of specimens, data for the two sexes were not separated in the growth analyses discussed in the following paragraphs.

History of Successive Year Classes.—All the specimens were assigned to year

Table 20.—Average calculated total lengths in inches for male and female warmouths, representing five year classes, collected from Park Pond, October, 1948, through November, 1949.

Year Class	Sex	Number of Fish	Average Calculated Total Length in Inches at End of Indicated Year of Life				
			1	2	3	4	5
1944.....	Male	15	1.64	3.51	5.39	6.68	7.32
	Female	7	1.46	3.01	4.72	5.73	6.35
1945.....	Male	102	1.73	3.49	4.89	5.88	
	Female	85	1.62	3.34	4.68	5.85	
1946.....	Male	84	1.56	2.85	4.21		
	Female	85	1.56	2.81	4.11		
1947.....	Male	79	1.58	2.99			
	Female	71	1.48	2.61			
1948.....	Male	33	1.62				
	Female	39	1.61				

Table 21.—Average calculated total lengths in inches for 1,063 warmouths, representing nine year classes, collected from Park Pond, June, 1948, through November, 1949.

Year Class	Number of Fish	Average Calculated Total Length in Inches at End of Indicated Year of Life*							
		1	2	3	4	5	6	7	8
1940........	1	1.61	3.08	4.20	5.50	6.33	6.93	7.94	8.61
1941........	6	1.58	2.86	4.39	5.75	6.89	7.91	8.58	8.54
1942........	10	1.47	2.89	4.54	5.98	7.37	8.04	8.43	
1943........	46	1.59	3.25	5.28	7.00	7.69	8.76		
1944........	122	1.62	3.77	5.73	6.75	7.10			
1945........	362	1.75	3.80	4.86	5.99				
1946........	239	1.59	2.90	4.26					
1947........	187	1.53	2.83						
1948........	90	1.63							
Weighted averages...	....	*1.64*	*3.38*	*4.91*	*6.40*	*7.44*	*8.02*	*8.47*	*8.56*

*Average for last year in each year class based on fish in which annulus for current year was present.

classes on the basis of number of true annuli on their scales. The length of each fish at the end of each year of life was calculated from its scale measurements. The calculated lengths for each year of life were then averaged for fish of each year class. In the length calculations for 1948 growth of fish collected in 1949, only those fish taken after annulus formation in May could be used. The calculated lengths for 1,063 warmouths, table 21, suggested the following conclusions:

1. Average calculated lengths for fish of the 1943, 1944, and 1945 year classes were greater in most years of life than the weighted averages for the fish of all year classes (averages were weighted to compensate for differences in numbers of fish in the various groups); fish of both the 1944 and 1945 year classes showed less than the average length for the last complete growing season (1948) prior to capture.

2. Average calculated lengths for fish of the 1946 and 1947 year classes were less in most years of life than the weighted averages for the fish of all year classes.

3. Average calculated lengths exhibited no large growth rate differences for the same years of life among warmouths caught at different ages—no phenomenon of apparent change in growth rates as described by Lee (1912:9). (However,

Table 22.—Average calculated total lengths in inches for each year of life of 1,063 warmouths collected from Park Pond, June, 1948–November, 1949, with equivalent standard lengths in millimeters and weights in pounds and grams. Calculated annual increments in lengths and weights are based on these averages.

Year of Life	Total Length, Inches	Standard Length, Inches	Weight, Pounds	Weight, Grams	Annual Calculated Increment of Total Length, Inches	Annual Calculated Increment of Weight, Pounds
1.............	1.64	33	0.004	1.8	1.64	0.004
2.............	3.38	68	0.026	11.8	1.74	0.022
3.............	4.91	101	0.088	39.9	1.53	0.062
4.............	6.40	131	0.200	90.7	1.49	0.112
5.............	7.44	153	0.337	152.9	1.04	0.137
6.............	8.02	168	0.432	196.0	0.58	0.095
7.............	8.47	178	0.510	231.3	0.45	0.078
8.............	8.56	180	0.527	239.0	0.09	0.017

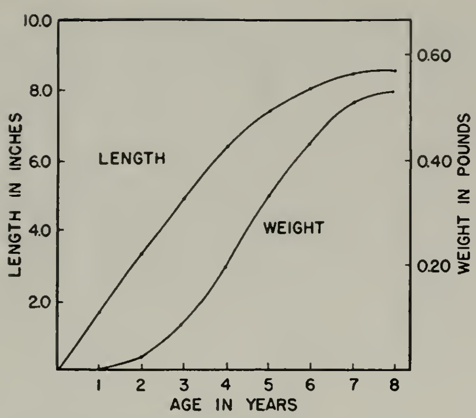

Fig. 20.—Averages of calculated total lengths and calculated weights at end of each year of life for 1,063 warmouths of various ages from Park Pond, early June, 1948, through middle November, 1949.

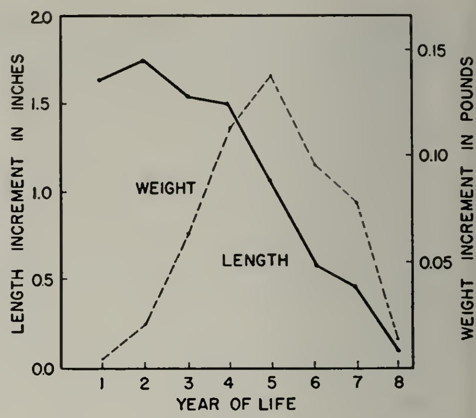

Fig. 21.—Averages of annual increments of calculated total lengths and calculated weights in each year of life for 1,063 warmouths from Park Pond, early June, 1948, through middle November, 1949.

Lee's phenomenon was evident in Venard Lake warmouths, figs. 23 and 24.)

Annual length increments based on calculated lengths were determined for each year of life of the 1,063 warmouths, table 22. These length increments were greatest for the second year of life and decreased thereafter; they declined rapidly after the fourth year and were very slight in the eighth year of life.

The pattern of weight increase was different from that of length increase. Average calculated weights in pounds, corresponding to average calculated lengths in inches (length-weight prediction equation, page 51), furnish evidence that in the warmouths studied the rate of weight increase was slow during the first 2 years, reached a peak the fifth year, and declined rapidly in the following years, table 22. Fig. 20 shows the average lengths and weights; fig. 21 shows the increments of length and weight for each year of life.

Fluctuations in Annual Growth.—There were calendar years of good and of poor growth for all year classes of warmouths at Park Pond. These years of good and of poor growth were evident even though warmouths in certain year classes were of consistently larger or smaller sizes than the average for all warmouths.

Using the average annual length increment for all warmouths in each year of life as a base, tables 21 and 22, one can calculate the percentage of the expected increment attained by each year class for

Table 23.—Average percentage of expected annual length increment attained in each year of life in eight separate year classes of 1,062 warmouths collected from Park Pond, June, 1948–November, 1949.

Year Class	Number of Fish	Average Percentage of Expected Annual Length Increment Attained in Indicated Year of Life						
		1	2	3	4	5	6	7
1941	6	96	74	100	91	110	176	149
1942	10	90	82	108	97	134	116	
1943	46	97	95	133	115	66		
1944	122	99	124	128	68	34		
1945	362	107	118	69	76			
1946	239	97	75	88				
1947	187	93	75					
1948	90	99						

each year of life and for each calendar year, table 23. Percentages of expected growth during selected calendar years may be read from table 23 in diagonal rows from lower left to upper right. The percentages of expected growth in each calendar year, when averaged, show clearly the fluctuations in annual growth, table 24.

Actual length increments exceeded the expected increments in only 1945 and 1946, table 24. Poor growth in 1942 and 1943 may have been due to heavy floods, which caused the water to remain muddy for 6 or 7 weeks during the early summer of each of these years.

The exceptionally good growth of warmouths during 1945 and 1946 may have resulted from an artificial thinning of the fish population. On June 26, 1945, May 15, 1946, and July 29, 1946, Dr. George W. Bennett and other members of the Illinois Natural History Survey staff sprayed most of the shallow waters of Park Pond with rotenone to reduce the numbers of small fish in the population. Although no estimate could be made of the percentage of the total fish population killed by these partial poisoning operations, the great number of small fish destroyed may well have allowed a substantial increase in growth rates of the surviving fish.

Seasonal Growth.—Growth patterns of the 1946, 1947, and 1948 year classes of warmouths in Park Pond during the summer of 1949 are shown in fig. 22. The length increment for each fish was calculated from scales. The growth increment on each scale used was measured on the median anterior radius from the outermost annulus to the margin of the scale. Average monthly length increments were calculated from scale collections made each month except October in a period that began in May and extended into November. When more than one collection was made in a single month, the collections were combined and an average date was used. In this particular analysis, year classes other than those of 1946–1948 could not be used because they were not represented by sufficient numbers of warmouths to give validity to the calculations.

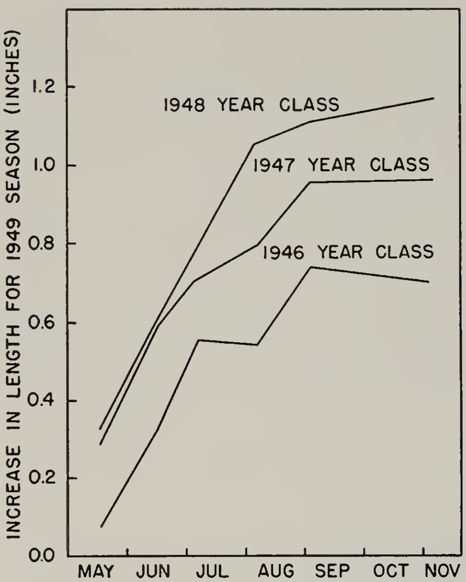

Fig. 22.—Averages of length increases of warmouths of the 1946, 1947, and 1948 year classes in Park Pond during the 1949 growing season. The growth increment for each warmouth was calculated from scale growth outside of the last annulus.

Table 24.—Average percentages of expected annual length increment attained in each calendar year by warmouths collected from Park Pond, June, 1948–November, 1949; year classes combined.

Calendar Year	Number of Fish	Average Percentage of Expected Annual Length Increment Attained in Each Year of Life
1941.....	6	96
1942.....	16	82
1943.....	62	93
1944.....	194	98
1945....	546	114
1946....	785	128
1947.....	972	91
1948...	526	74

Growth was rapid for the three year classes in May and June, and this good growth continued through July for the 1948 year class, fig. 22. Growth rates decreased in July for the 1946 and 1947 year classes and improved considerably in August. Little or no growth was evident in the three year classes after August. Certain general differences were discernible between the fish of these year classes. The oldest fish (1946 year class) showed a midsummer slump in growth and had completed their seasonal growth by September, whereas the youngest fish (1948 year class) grew rapidly through July and showed some growth in each of the months through October. The growth pattern for the 1947 year class was intermediate between the patterns for the 1946 and 1948 year classes.

Seasonal growth rates of three year classes of warmouths in Venard Lake are shown in figs. 23 and 24.

Measurements of warmouths from Park Pond, fig. 22, from Venard Lake, figs. 23 and 24, and from certain Oklahoma waters (Jenkins, Elkin, & Finnell 1955:42) indicated an apparent decrease in the average lengths of the fish of some age groups in July or August. This apparent decrease may have been due to changes in habits or distribution of the warmouths from the early part to the middle part of the summer, changes which might have affected the efficiency or selectivity of the collecting method, with a result that a proportionally smaller number of large members in each age group was taken.

Growth in Localized Population.—In the isolated, 0.47-acre Park Pond slough to which rotenone was applied in 1949, warmouths comprised 10.4 per cent of the weight of the fish population. Although this weight represented 504 individuals, only 18 were more than 6 inches long. Most of these warmouths were less than 3.5 inches in length.

Age determinations for 265 of the 504 warmouths revealed a growth rate considerably less than was found in other areas of Park Pond, table 25. Of the 265 specimens aged, very good growth was found in 23 large fish belonging to the 1944 and 1945 year classes. These fish did not seem to be representative of the population of the slough. Their history of rapid growth suggested they had only recently moved into this area.

Table 25.—Average of calculated lengths of 265 warmouths from which scale samples were taken, after being collected from Park Pond Slough, shown with similar calculated lengths of warmouths from other parts of Park Pond.

Group of Fish	Year Class	Number of Fish	Calculated Total Length at End of Indicated Year of Life					Average Total Length at Capture
			1	2	3	4	5	
Fast-growing warmouths from slough	1944	2	1.74	4.07	5.38	6.65	7.11	7.35
	1945	21	1.91	3.83	5.14	5.87		6.15
Slow-growing warmouths from slough	1945	10	1.56	2.90	4.00	4.86		5.27
	1946	74	1.54	2.85	3.97			4.59
	1947	93	1.46	2.54				3.34
	1948	52	1.48					2.50
	1949	13						1.65
Slow-growing warmouths from slough, average		242	1.50	2.64	3.64	4.62		
Warmouths from other Park Pond areas, average	Combined year classes	1,063	1.64	3.38	4.91	6.40		

All of the smaller specimens in this slough showed consistently poorer growth than warmouths from other areas of Park Pond. A study of the fish population of the slough indicated that (1) isolated populations of warmouths existed within the total warmouth population of Park Pond; (2) individuals of these isolated populations, most of them in dense weed beds, grew slowly; and (3) individuals of these populations appeared to remain in the same locations throughout their life spans.

Compensatory Growth.—Three hundred thirteen warmouths from Park Pond were separated into three size groups based on calculated lengths of fish at the end of the first year of life, table 26. The average length increment for each year of life was then calculated for each size group as a means of determining the growth rate—whether fast, intermediate, or slow.

Of the 313 warmouths considered, 94 had been collected with hoop nets during the summer of 1948; these 94 were fish of the 1944 year class and were faster-growing individuals than the specimens (219) that had been taken from the slough. Warmouths taken from the slough had been collected after being poisoned with rotenone; they belonged to the 1946, 1947, and 1948 year classes, table 26.

For the fish taken in hoop nets, the difference in average calculated lengths between the largest and smallest size groups was 0.55 inch for the first year of life, 0.74 inch for the second, 0.55 inch for the third, and 0.42 inch for the fourth. The decline in differences between these two size groups in the third and fourth years of life may indicate compensatory growth among individuals of the smallest group in these years. However, the compensatory growth that occurred was slight and it did not overcome the length advantage held by the fish that grew most rapidly during the first year of life.

In the slow-growing population from the slough, the maximum differences in length between the two extreme size groups of the various year classes declined little or not at all after the second year. In the 1946 year class, after an increase in length difference at the end of the second year, the differences were about the same at the end of the third and fourth growing seasons, table 26.

A study of compensatory growth in these four year classes of warmouths from Park Pond suggested the following conclusions:

1. Warmouths that were largest at the end of the first year of life increased this length advantage in the second year of life.

Table 26.—Compensatory growth, in inches, in four year classes of warmouths collected from Park Pond. Fish in the 1944 year class were collected in hoop nets from several parts of Park Pond in the summer of 1948; those in 1946–1948 year classes were taken from a slough to which poison was applied on August 22, 1949.

Year Class and Place of Collection	Group of Fish, Based on Calculated Total Length in Inches at End of First Year of Life	Number of Fish	Calculated Average Total Length at End of Indicated Year of Life				Calculated Average Length Increment in Indicated Year of Life			
			1	2	3	4	1	2	3	4
1944 (Entire pond)	Below 1.45	22	1.33	3.53	5.68	6.70	1.33	2.20	2.15	1.02
	1.45–1.70	42	1.58	3.80	5.74	6.76	1.58	2.22	1.94	1.02
	Over 1.70	30	1.88	4.27	6.23	7.12	1.88	2.39	1.96	0.89
	Maximum difference		0.55	0.74	0.55	0.42	.....	.....	.....	.....
1946 (Slough)	Below 1.3	13	1.20	2.49	3.61	4.25*	1.20	1.29	1.12	0.64*
	1.3–1.6	33	1.43	2.63	3.74	4.35*	1.43	1.20	1.11	0.61*
	Over 1.6	28	1.84	3.28	4.41	5.04*	1.84	1.44	1.13	0.63*
	Maximum difference		0.64	0.79	0.80	0.79	.....	.....	.....	.....
1947 (Slough)	Below 1.3	19	1.22	2.24	3.11*	.....	1.22	1.02	0.87*	.....
	1.3–1.6	55	1.41	2.47	3.27*	.....	1.41	1.06	0.80*	.....
	Over 1.6	19	1.81	3.03	3.79*	.....	1.81	1.22	0.76*	.....
	Maximum difference		0.59	0.79	0.68	.....	.....	.....	.....	.....
1948 (Slough)	Below 1.3	14	1.24	2.24*	.....	.....	1.24	1.00*	.....	.....
	1.3–1.6	24	1.41	2.42*	.....	.....	1.41	1.01*	.....	.....
	Over 1.6	14	1.82	2.89*	.....	.....	1.82	1.07*	.....	.....
	Maximum difference		0.58	0.65	.....	.....	.....	.....	.....	.....

*Empirical length representing growth to August 22, 1949.

2. Warmouths that were smallest at the end of the first year of life showed no compensatory growth in the second year but showed a slight compensatory growth in the third year.

3. Although warmouths that grew fast the first year of life underwent a decline in annual length increment after the second growing season, they retained their length advantage over warmouths that grew slowly the first year.

4. Warmouths that grew slowly the first year of life showed more compensatory growth in later years if they were members of fast-growing populations than if they were members of slow-growing populations.

These conclusions are in fair agreement with those from similar studies done on several other sunfishes. Hubbs & Cooper (1935:678) found no compensatory growth during the second year of life in the longear sunfish, pumpkinseed, or bluegill, or in bluegill×pumpkinseed hybrids. Their data did not include growth rates beyond the second year. For the rock bass, Hile (1941:332) stated: "First-year advantage in size may be retained over 1 or 2 additional years, but more probably it will be increased in the second and/or third year of life. Compensatory growth occurs in the later years."

Sizes and Longevity.—A 9.6-inch male was the largest warmouth collected from Park Pond. This fish weighed 1.0 pound and was 6 years of age. The majority of the large fish were males. Although the males grew slightly faster than the females, table 20, it did not necessarily follow that the males reached greater maximum sizes than did the females. The occurrence of more large males than large females in the collections may have indicated only that the former were more readily taken than were the latter—a logical hypothesis in view of the differences in behavior during the nesting season. The sedentary nest-guarding habits of the males would have made them very vulnerable to collection by shocking.

Schoffman (1940:36) mentioned spawning habits to explain the greater percentage of females than males in the groups of large warmouths he collected from Reelfoot Lake, Tennessee. As his collections were taken with traps operated during the breeding season, nest-guarding males were not caught so readily as females. The largest warmouth handled by Schoffman (1940:34) was a 9.29-inch female.

Growth in Venard Lake

In 1948 and 1949, warmouths in Venard Lake, an artificial lake of 3.2 acres, were associated with only one other species, the largemouth bass. Both species had been introduced in April, 1947, page 5.

The 1,102 Venard Lake fish used in this study were from collections made with an electric shocker each month (except January and February) in a period beginning September, 1948, and ending October, 1949. Methods used for scale preparation and age determination were similar to those described for the collections from Park Pond.

Since Venard was a recently stocked lake, it contained only a small number of year classes of warmouths: 1947, 1948, and 1949. A comparison of growth rates was made between warmouths of the first, fast-growing year class (1947) and those of the two following year classes (1948 and 1949). The following points seem apparent, figs. 23 and 24:

1. Both actual and calculated lengths of warmouths of the first year class to be spawned in the lake (1947) averaged more at the end of the first year and of each succeeding year of life than did those of later year classes.

2. The actual length range for members of the first year class was greater than that for members of each succeeding year class.

3. The average calculated lengths of warmouths of 1947 and 1948 year classes collected in successive months of 1949 showed a decline.

4. The average annual growth of warmouths in Venard Lake was very similar to that of warmouths in their first 3 years of life in Park Pond, table 27, in spite of large ecological differences in the two habitats.

Growth in Other Water Areas

The rate of growth of warmouths may be influenced by various environmental factors or combinations of them. This fact is illustrated by the differences observed in the growth rates of warmouths taken from 12 Illinois water areas, table 27.

The most rapid growth recorded in Illinois warmouths was in Enright Pond in McLean County in which some members of the first brood produced in the lake attained 6 inches in total length during their first 13 months. Thinning the total fish population by intensive angling resulted in an increase in the growth rate of warmouths in Onized Lake, a 2-acre body of water in central Illinois (Bennett 1945: 396–7).

Exceptionally rapid growth of warmouths usually accompanies the expansion of fish populations in new reservoirs. During the first 6 years after impoundment of

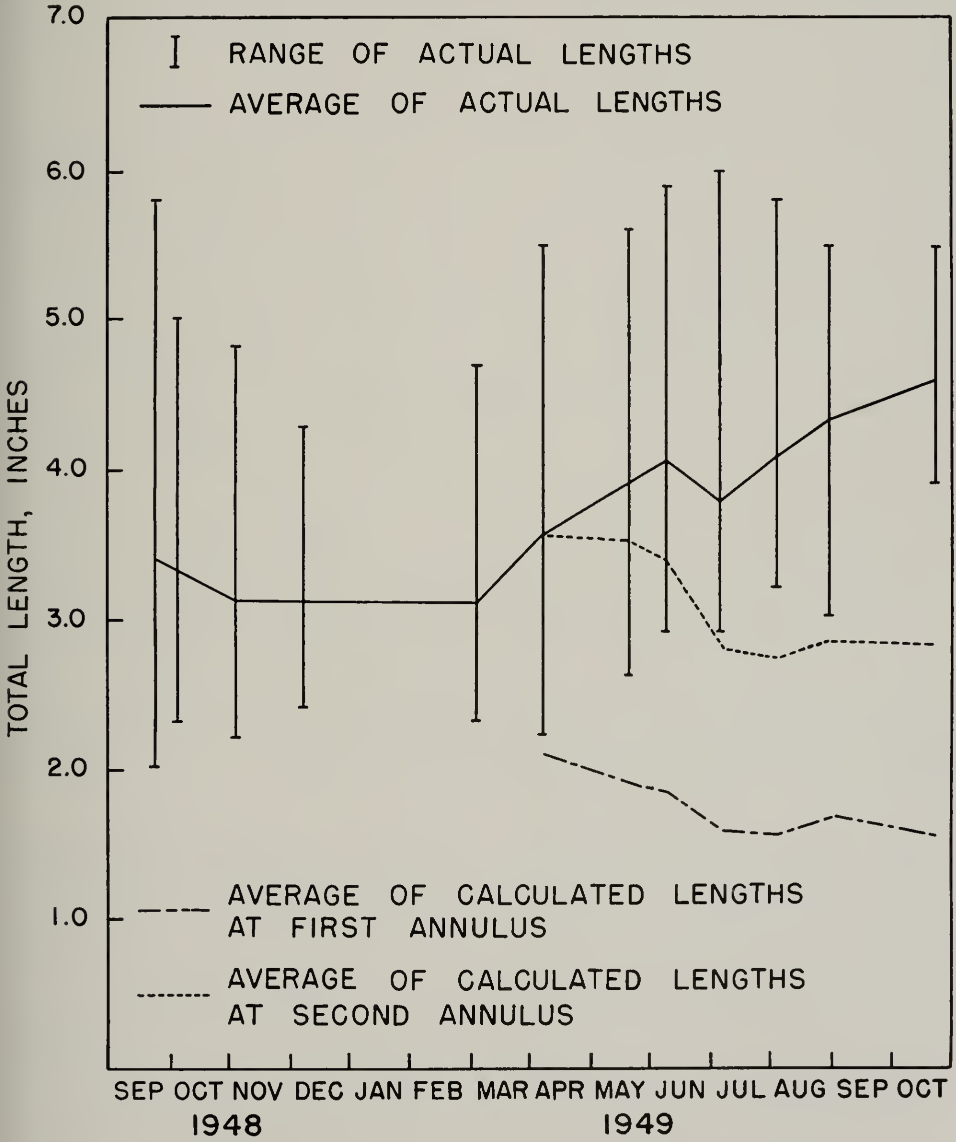

Fig. 23.—Averages of actual total lengths and averages of calculated total lengths at time of formation of first annulus and at time of formation of second annulus for warmouths of the 1947 year class taken in 12 collections from Venard Lake, late September, 1948, through middle October, 1949; also range of actual total lengths in each collection.

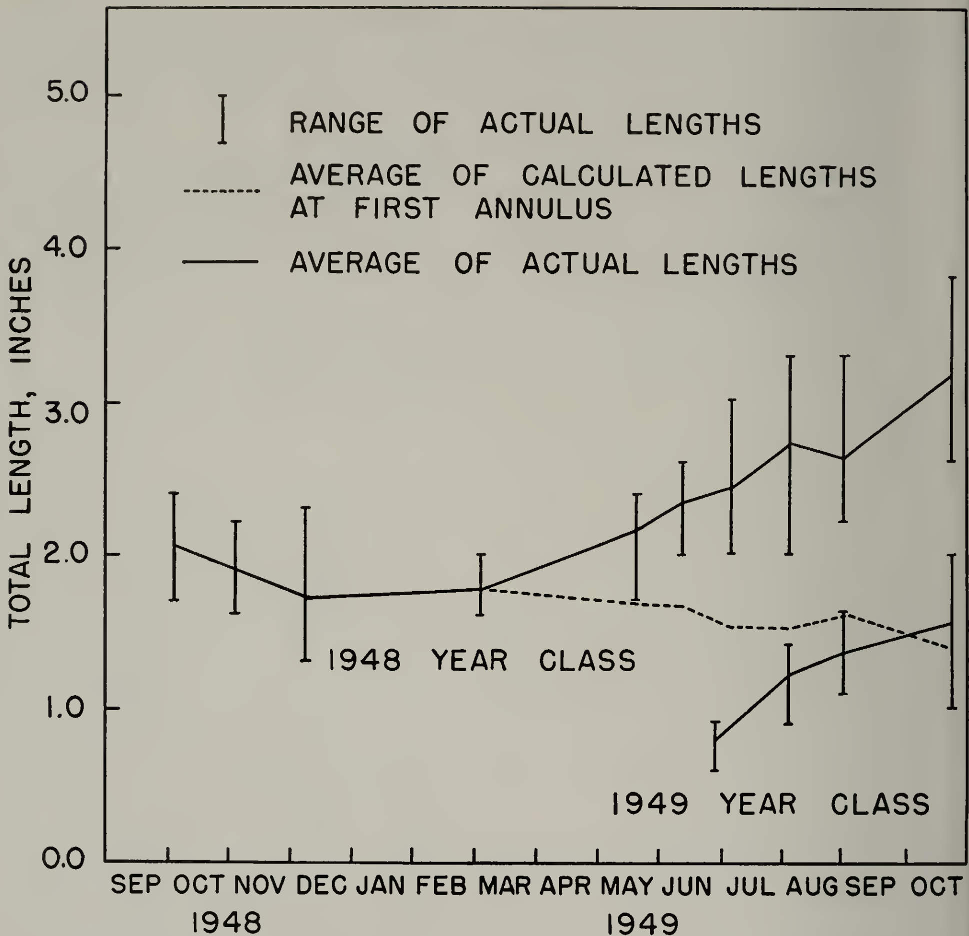

Fig. 24.—Averages of actual total lengths and averages of calculated total lengths at time of formation of first annulus for warmouths of the 1948 year class taken in 10 collections from Venard Lake, early October, 1948, through middle October, 1949; averages of actual total lengths of warmouths of the 1949 year class taken in 4 collections, late June through late October, 1949; also range of actual total lengths in each collection.

Lake Glendale, an 82-acre lake in Pope County, Illinois, warmouths showed a growth rate that was exceptionally fast for the species (Dr. Donald F. Hansen of the Illinois Natural History Survey, unpublished studies of Lake Glendale). Another example of improved growth rate in a new impoundment is given by Hall & Jenkins (1953:34); they found that, in Tenkiller Reservoir in Oklahoma, the growth rate of warmouths was rapid during the first year of impoundment. Jenkins (1953:79) found that in Grand Lake, Oklahoma, the growth rate of warmouths gradually declined during the years of impoundment.

Data from several studies of warmouth growth in other states are summarized by Carlander (1950:191–2; 1953:370–1). An inspection of these data and those given in table 27 reveals a wide range of differences in warmouth growth rates.

PARASITISM

No attempt will be made here to survey all published records concerning parasites of the warmouth. Reference should be be made, however, to several important studies involving autopsies of comparatively large numbers of warmouths. Holl (1932:99–100) examined 90 warmouths from North Carolina and discovered an interesting seasonal fluctuation in relative numbers of parasites and in percentages of fish infested. In a study of centrarchids from southern Florida, Bangham (1939: 265) examined 143 warmouths and found all of them infested with parasites of one or more species. The fish populations from which these specimens were taken contained relatively high concentrations of warmouths. Venard (1941:15) found that of 45 warmouths examined from Reelfoot Lake, Tennessee, all were parasitized. Bangham & Venard (1942:33) listed 22 species of parasites from 58 specimens examined from Reelfoot Lake; all of the specimens were infested with parasites.

A comprehensive investigation of warmouth parasites was not made in this study. The following brief discussions are of the general relationships between the hosts and four common parasites of warmouths from Venard Lake and Park Pond.*

The strigeid fluke, *Posthodiplostomum minimum* (MacCallum), was the most abundant parasite of the warmouths in Park Pond. Its hosts include a snail of the genus *Physa,* any one of several species of fish, and the great blue heron, *Ardes herodias* L. As little age immunity has been demonstrated in intermediate hosts of most flukes, the numbers of metacercariae of this strigeid probably continue to increase in the host warmouth until the fish dies. Extremely heavy infestations of metacercariae were found commonly in Park Pond warmouths over 5 inches in length, but seldom in smaller ones.

Table 27.—Growth rates of warmouths in 13 water areas in Illinois.

Water Area	County	Year of Collection	Number of Fish	Calculated Total Length at End of Indicated Year of Life						
				1	2	3	4	5	6	7
Park Pond	Vermilion	1948–49	1,063	1.6	3.4	4.9	6.4	7.4	8.0	8.5
Park Pond Slough	Vermilion	1949	242	1.5	2.6	3.6	4.6			
Venard Lake	McLean	1948–49	334	1.7	3.2	4.6				
Onized Lake*	Madison	1941	101	1.4	4.0	6.1				
Lake Glendale	Pope	1945–46	108	2.1	4.6	6.2				
Mississippi River†		1944	26	1.8	4.8	6.2	7.1			
Lake Chautauqua	Macon	1947	30	1.4	2.7	4.5	5.9	6.8		
40-and-8 Lake	Henry	1954	22	1.5	2.9	4.2	6.0	7.0		
Staunton Lake	Macoupin	1953	18	1.7	3.1	4.5	5.6			
Mount Clare Lake	Macoupin	1953	16	1.3	2.8	4.6	5.7			
McKenzie Lake	Montgomery	1952	12	1.3	2.4	3.5	4.4	5.0	5.4	
Weldon Springs	De Witt	1952	28	1.7	3.5	5.7				
Fairmount Quarries	Vermilion	1953	100	1.7	3.0	4.6	5.6			

*From Bennett 1945:397.
†From Upper Mississippi River Conservation Committee 1946:20.

The bass tapeworm, *Proteocephalus ambloplites* (Leidy), was present in all warmouths examined from Park Pond. As a plerocercoid larva, it occurred in most of the internal organs, especially in the liver, gonads, and mesenteries. Since the warmouths acquired these parasites by eating copepods containing the procercoids, the rate at which the fish acquired the parasites declined as the fish changed their food preferences from Entomostraca to larger items. Therefore, unlike *Posthodiplostomum,* plerocercoids did not occur in relatively greater numbers among the large warmouths than among the small ones at Park Pond.

An interesting nematode, *Camallanus oxycephalus* Ward & Magath, lives in the lower intestine of the warmouth. Blood-red worms of this species were so numerous in some warmouths from Park Pond that they often formed tangled masses in the lumens of the guts. Frequently *Camal-*

*Dr. L. J. Thomas, University of Illinois, checked the identification of the cestode and trematode parasites and suggested possible relationships between these parasitic worms and the fish population. The late Dr. H. J. Van Cleave, University of Illinois, identified the acanthocephalan; Professor R. V. Bangham, College of Wooster, identified the nematode; and Professor M. C. Meyer, University of Maine, identified the leech.

lanus worms were seen hanging as a red tuft from the anus of a fish taken from the water. *Camallanus* attaches to the inner intestinal wall. The warmouth serves as the final host, and infestation may take place at any time.

The only parasite which infested noticeable numbers of warmouths from Venard Lake was a leech, *Illinobdella moorei* Meyer. During the autumn and winter of 1948, leeches of this species were present in such large numbers that they appeared as compact fringes on the fins of the warmouths. The caudal fins of the fish were severely damaged, frequently suffering extensive destruction of the rays. Although the infestation was still heavy during the spring of 1949, only relatively few of the leeches were seen during the following summer months.

An examination of 25 ovaries from warmouths taken from Park Pond on November 12, 1949, revealed the following: (1) 14 ovaries contained one or more parasites; (2) ovaries of all sexually mature females were parasitized; (3) 24 plerocercoids of *Proteocephalus ambloplites* occurred in 12 ovaries, as many as 4 in 1 ovary; (4) 27 metacercariae of *Posthodiplostomum minimum* occurred in 10 ovaries, 12 in 1 ovary; and (5) 4 sexually undeveloped adult acanthocephalans, *Leptorhynchoides thecatus* (Linton), were found in 4 ovaries (1 in each ovary). In spite of these parasites, no sterile fish were found and no primary damage to the ovaries was evident.

Warmouths were collected in sufficient numbers from Venard Lake and Park Pond to permit tentative conclusions to be drawn relative to the influence of parasites on the general physical condition of these fish. Warmouths from Venard Lake had fewer internal parasites and a consistently higher coefficient of condition (C) than had warmouths of similar sizes taken from Park Pond. At the same time, among the heavily infested warmouths of Park Pond, no positive relationship could be shown between a fish's coefficient of condition and the number of parasites present. Therefore, it is believed that the difference in condition of warmouths from the two lakes was more directly a result of difference in densities of the total fish populations than of parasitism.

Even though no harmful effects of parasites on the condition (C) of warmouths in Venard Lake or Park Pond could be demonstrated, possibilities of some other harmful effects must be recognized. Female warmouths from Park Pond produced much smaller numbers of eggs than did Venard Lake females, table 16, which were less heavily infested.

BEHAVIOR

Observations on the behavior of the warmouth are scattered through many sections of this publication. For example, the aggressive behavior of the nesting male is described (page 43) under "Spawning" in the section on reproduction. It seems desirable to bring together here certain aspects of observed behavior of the warmouth, although to do so will mean some repetition.

General Activity and Disposition

The warmouth has a quiet disposition; it moves around relatively little and displays no showy activity except during the nesting season. It seeks the cover of weed masses, stumps, or rocky banks (pages 6 and 8), and avoids intense light.

Reproductive Behavior

Tinbergen (1953:23) describes synchronization, persuasion, orientation, and reproductive isolation as functions of mating behavior in animals. These functions, along with defense of the nest area, the spawning act, and parental care, are considered here as reproductive behavior in the warmouth.

Defense of the Nest Area.—The nesting warmouth male displays an aggressive threat toward other fish that approach his nest area (page 42). He assumes a belligerent attitude by swimming toward the intruder with his mouth open and his opercles spread; at the same time, his eyes become red and his body becomes light yellow in color. As the nesting male nears the intruder, he usually turns abruptly to one side or upward and, with vigorous movements of his tail fin, forces small pulses of water toward the intruder. He may also nip the intruder. The entire threat attitude associated with defense of the nest area is similar to the persuasive behavior employed by the nesting male in courting a female (page 43).

Synchronization.—The spawning period for warmouths extends over several months (page 43). Male warmouths become ready to spawn earlier and remain capable of spawning later in the season than do females. Thus, a ripening female generally encounters many males ready to spawn. More precise synchronization for the actual discharge of sex products is brought about by the preliminary courtship and persuasive gestures of the male and finally by the thump given the male as the female extrudes a group of eggs (page 44).

Orientation.—The special orientation for mating in warmouths consists simply of the male having an established nest, the female with ripening eggs wandering into the vicinity of the nest, and the male initiating the persuasive actions. A signal—such as sound, odor, or color display, used by many animals to attract a mate from considerable distances—is not known to be given by the male warmouth. However, the female probably receives some internal physiological stimulus to wander as her eggs ripen and they become free for discharge.

Persuasion.—The male warmouth's threat attitude, described above, serves to initiate the action for persuading the female to spawn. A female that is not ready to spawn responds to the threat as any other intruder would and is driven from the nesting area (page 43). On the other hand, a female that is ready to spawn quietly submits to the aggressive male. The threat, in which the male spreads his opercles and shows some display of color, is followed by attempts to guide the female to the nest depression. With only mild resistance and casual reluctance, the ripe female accepts more and more of the male's actions and soon enters the nest to remain with him for periods of time that become increasingly longer until spawning actually takes place.

The Spawning Act.—The series of signals and responses described above culminates when the male and female come together to deposit their sex products simultaneously. Although the aggressive attitude of the male makes it seem that he is controlling the spawning activities, the female enters the nest only when she is ready, she gives the final signal (thumping the male's side) for extrusion of eggs and milt, and she leaves the nest depression for short intervals between egg laying. The spawning signals and responses follow a definite sequence; it is interesting to recall that a female warmouth in a laboratory spawned alternately during one continuous spawning sequence with two male warmouths (page 44). After having been brought to a spawning attitude by one male, the female then responded to either of the two nesting males.

Reproductive Isolation. — Hybrids are produced between the warmouth and a great number of the species of *Lepomis,* and yet such hybrids seldom occur in large numbers in natural populations. What forms the reproductive isolation that prevents greater hybridization was not determined in this study. There is little spatial separation of the various sunfishes. The warmouth is usually found living and even nesting with several species with which it could genetically hybridize, and yet few hybrid individuals are formed. In the absence of any other observable isolating barrier, the isolation appears to result from a lack of the specific signals and responses necessary to bring a warmouth to successful spawning with an individual of another species. In the laboratory, male warmouths have courted green sunfish and bluegill females but have not succeeded in spawning with them and seldom are able to guide them to the nest depressions. Apparently, the series of specific signals and responses is not followed through to successful spawning.

Parental Care.—After the warmouth fry leave the nest area, they receive no parental care. In ponds and lakes, the fry scatter into dense weed masses (page 48), and thus it becomes impossible for the male parent to keep the young together for close care. Protection afforded by the dense weed masses eliminates most of the needs for parental care. The male warmouth seems to lack the drive to care for his free-swimming young; even in a laboratory aquarium without vegetation in which the young may hide, he shows little interest in his fry after they leave the nest.

Group Behavior

The warmouth is not a gregarious fish, even though large numbers of individuals may be concentrated in a comparatively small area. The following observations concern the social relations among warmouths.

Aggregations.—There is no school formation among warmouths except that immediately associated with the nest (page 48). Aggregations form around desirable cover, such as the riprapping along a dam (page 8), but little social structure can be detected in such groups. Even during the winter, when many fishes form groups, warmouths show no tendency to gather together except in response to choice habitats. The nesting colonies that have been reported (page 42) are probably due to restricted nesting habitat rather than to a gregarious nature of the species.

Hierarchy.—To what extent an order of dominance occurs in a natural warmouth population has not been observed. Attempts at observations on dominance are hampered by the difficulty of identifying individual fish in a natural setting; also, the order of dominance becomes complicated by nesting behavior, mating aggression, feeding activities, and local movements.

A hierarchy is quickly established among warmouths in a restricted group, such as that in an aquarium. The aggressiveness of a fish, as for food or space, and the dominance of the fish relative to other members of the group, determine its position in the hierarchy. The smaller the group the more stable and definite the order of dominance appears. In groups of more than three or four, the order may change frequently. Nesting studies in the laboratory revealed that a male in spawning condition tends to assume dominance over one not so sexually advanced (page 42). The attitude of aggression which initiates the breeding behavior temporarily affects any existing hierarchy.

Witt (1949:34) discovered a definite hierarchy among five warmouths in an aquarium. He found no correlation between the order of dominance and the errors the fish made in learning to distinguish a worm on a hook from a worm that is free.

Feeding Behavior

Warmouths have a simple pattern of taking food. When a food item is sighted, the fish turns toward it, judges its acceptability as food, and then may move in quickly to snap it up. An unacceptable food item may hold the warmouth's attention for several minutes. Seldom is a motionless object picked up by a warmouth.

Suction created as the warmouth quickly opens its wide mouth aids in the capture of food. This suction causes a loud noise when the fish gulps an item of food from the water's surface and may be responsible for taking a considerable amount of detritus with the food.

Learning

Witt (1949:27) found that warmouths could learn to distinguish a worm on a hook from a free worm. As isolated individuals, warmouths learned about as quickly as did bluegills and more quickly than did largemouth bass, but in groups the warmouths made more errors than did either largemouths or bluegills. Individuals of all three species exhibited a fair degree of learning, making the majority of their errors in the first two of the seven trial periods. After being penalized for making an error, the warmouth was not so cautious as the bluegill in its approach to a hooked worm.

Warmouths do not seem so cautious in taking fishing lures or so quick in recognizing artificial situations as most other sunfishes. In ponds and in laboratory aquariums, warmouths were seen to strike repeatedly at artificial lures without, apparently, becoming suspicious that the lures were unnatural. In an aquarium, a resting warmouth, molested by a succession of lures dangled before its face, apparently was so undisturbed by the experience that it turned to snap at a lure more attractive to it than the others. On several days at Ridge Lake, Coles County, Illinois, a fisherman repeatedly hooked and released what appeared to be the same large warmouth by dangling a worm in front of an old piece of tile. This warmouth may have learned, but, if so, its memory did not last from one fishing trip to the next.

The warmouth's gullibility toward baits

may be a desirable trait for a warm-water sport fish.

ECONOMIC RELATIONS

Warmouths attain their greatest importance as food and sport fish in the lower Mississippi River valley and states bordering the Gulf of Mexico. There they are commonly taken with live bait by canepole fishermen. In the midwestern and eastern states, warmouths usually are not taken in large numbers but are caught on a wide variety of baits and lures. Because of their gamyness and plumpness, they are attractive to most anglers.

The Warmouth as a Food Fish

The warmouth is now of little commercial value, partly because in most states its sale is illegal; where it can be legally sold, the warmouth is not an important food fish in comparison to the larger species now being marketed.

In North Carolina during the early part of this century the warmouth was taken in gill nets and other nets and sold throughout the year (Smith 1907:235). At Reelfoot Lake, Tennessee, in 1937, it was one of the seven sunfishes that as a group comprised approximately 10 per cent of the weight of the commercial catch (Kuhne 1939*b*:58).

Most people consider the warmouth an excellent table fish. At times, however, this fish may have a "muddy" flavor, which is generally blamed on its association with silt bottoms and muddy waters, but which is caused at least partly by the food organisms comprising its diet. Warmouths taken off silt-covered bottoms of Park Pond usually had an excellent flavor; they were intermediate between the bluegill and the largemouth bass in both flavor and texture of flesh.

The Warmouth as a Sport Fish

An early angling critic, Henshall (1903:59), was very enthusiastic about the warmouth; he wrote, "For its size, it is the gamest member of the family except the black-bass." In a discussion following a paper by Lovejoy (1903:120), Henshall pointed out that this sunfish takes a fly well, responds to almost any kind of bait, and is an excellent table fish. Evermann & Clark (1920:393), Baker (1937:44), Curtis (1949:266), and others have praised the fighting qualities of the warmouth or have termed it "an excellent small game fish."

The value of the warmouth as a sport fish is enhanced by the wide variety of natural and artificial lures that are effective in catching it. Through most of its range, the warmouth is taken more commonly on natural baits (earthworms, minnows, grasshoppers, crickets, or grubs) than on artificial baits.

The yield to the warmouth fisherman, using either natural or artificial lure, is often restricted by the difficulty of working the lure in close enough to weed masses, brush, and other dense cover to present it properly to the fish without getting the hook snagged. This difficulty increases during the summer as aquatic vegetation grows rank. Floating lures, such as poppers, are effective during the summer, because they can be dropped in pockets of open water among water weeds—where the warmouths may be hiding, feeding or nesting—and then be lifted out without becoming entangled. Worm fishing with a long pole offers similar advantages in fishing for warmouths around dense vegetation and heavy brush.

Most Illinois fishermen believe that warmouths may be taken in greater numbers during the spring and early summer than at other seasons. At the Pollywog Association property and at the flooded limestone quarries (Fairmount Quarries) near Fairmount, Vermilion County, good catches of warmouths are usually made in May and June but seldom later in the summer—at least not on the artificial lures that are relatively effective during the earlier months. Most of the warmouths caught at Ridge Lake (Dr. George W. Bennett, unpublished creel records from Ridge Lake, Coles County, Illinois) have been taken during the first month of the summer fishing season. Although the catch of warmouths at Lake Glendale (Dr. Donald F. Hansen, unpublished creel records from Lake Glendale, Pope County, Illinois) was distributed rather evenly in the period May through August in 1945, the catch of warmouths in 1946 was much higher in April and May than during the summer months. No warmouths were taken at Lake Glendale during September in either year. These records form an interesting contrast with the records of Ricker (1945:330) for Muskellunge Lake, Indiana, where a striking increase in the catch of warmouths occurred during September.

Censuses of sport fishing reported by Ricker (1945) for three Indiana lakes show that warmouths were taken regularly by anglers but not in abundance. Lewis & English (1949:317) recorded only four warmouths taken during 6,513 man-hours of fishing in Red Haw Hill Reservoir, Iowa, even though warmouths were fairly common in the lake. They suggested that the low catch was due to the difficulties of angling among the dense marginal vegetation of this lake. Kuhne (1939*a*:51) calculated a take of warmouths at Reelfoot Lake, Tennessee, that amounted to 1.02 per cent by weight of the anglers' catch for 1937. The combined catches of resident and non-resident fishermen amounted to only 0.02 warmouth per hour (Kuhne 1939*a*:48). In a creel census for the period March 1 through September 30, 1952 (Cobb 1953:21), warmouths comprised 2.05 per cent of the weight of all fish taken by sport fishermen at Reelfoot Lake.

Creel records for Illinois lakes show that the warmouth usually is not abundant in the anglers' catches.

In Onized Lake, Illinois, Bennett (1945:380–3) reported only 105 warmouths caught during 7,526.9 hours of fishing in a period beginning in 1938 and ending in 1941. This catch represented about 0.01 warmouth per hour. Even though this species comprised 18 per cent of the total number of fish (6 per cent by weight) in the final census of 1941, it made up only 2.6 per cent by numbers (2.9 per cent by weight) of all fish caught in the period of study. Since only a few warmouths were caught during a period when the other sport fish were being severely cropped in this 2-acre lake, one might have expected warmouths to replace the other fish of desirable sizes removed by angling. However, only 13 warmouths of 6 inches or more in length were recorded in the final census.

At Horseshoe Lake, Alexander County, in southern Illinois, 2 per cent of the fishermen's catch during the summer of 1956 was composed of warmouths (Bruce Muench, 1956, report to the Illinois Department of Conservation and Southern Illinois University).

At Venard Lake, 20 of the 101 warmouths planted in this lake early in 1947 were caught by anglers later in the same year. This take represented about 20 per cent of the number of warmouths planted but only 14 per cent of the total catch. About 52 per cent of the 240 largemouth bass that had been planted with the warmouths were taken by anglers in 1947.

In 1946 at Lake Glendale, in southern Illinois, the percentage of warmouths in the anglers' creel was not far below the percentage of warmouths in the total fish population. Warmouths were first caught in Lake Glendale the third summer after impoundment of the lake in 1940 and they increased in the anglers' catches during each of three summers following their first appearance (Dr. Donald F. Hansen, unpublished creel records from Lake Glendale, Pope County, Illinois). In the last year of the 3-year sequence, warmouths comprised 4.5 per cent of the total number of fish taken. When the lake was drained and the fish population censused, warmouths made up 6 per cent of the total number of fish and 5 per cent of the total weight; 57 per cent of the warmouths were over 6 inches in total length.

Several central Illinois ponds that, as part of the life history study reported here, had been stocked with warmouths produced hook-and-line yields that were low in proportion to the populations of these fish. The exploitation rate from angling was proportionally lower than for most other centrarchids inhabiting these waters. Fly and plug fishermen caught relatively few warmouths; most large catches of warmouths from these stocked ponds were taken on live baits.

Warmouth populations in the creeks and rivers in most parts of Illinois contribute very little to the creels of anglers. However, anglers who fish a few of the streams of southern Illinois report the common occurrence of warmouths in their creels. The warmouth is probably not abundant enough in the Mississippi River from Caruthersville, Missouri, to Dubuque, Iowa, to be considered of much importance in the sport fishery (Barnickol & Starrett 1951: 319).

The Warmouth as a Laboratory Fish

The warmouth is a desirable fish for laboratory experimentation. It is relatively easy to transport from the field and to keep alive in the laboratory. It is large enough to be easily handled and yet small enough to be accommodated in most aquariums. It has a quiet disposition, quickly becomes adapted to laboratory conditions, and readily feeds on a wide variety of foods.

In the laboratory, the warmouth will nest and spawn, apparently undisturbed by the presence of an observer. The wide variety of foods acceptable to it simplifies the task of keeping this fish for long periods in the laboratory. Such characteristics as its tolerance for low concentrations of dissolved oxygen, its rapid color responses to excitement, and its unusual individual and group behavior present interesting problems for study. The warmouth has been used in Natural History Survey laboratories in studies of food conversion, learning, group behavior, and marking techniques, as well as in studies reported in the present paper.

The Warmouth in Artificially Established Populations

Several combinations of species have been used by fisheries biologists in seeking to establish fish populations that will produce and maintain good sport fishing in lakes and ponds. In some waters, the largemouth bass and bluegill have seemed to be suitable companion species (Swingle & Smith 1941:271). In many Illinois lakes, however, this combination has not proved satisfactory, as bluegills have tended to overpopulate the water (Bennett 1944:186).

Lovejoy (1903:116–7) considered the warmouth one of the three best species to be used in stocking small ponds in the south. He wrote, "It grows to much larger size than the bream, thick and fleshy, with large mouth, and is to some extent cannibalistic, but not enough so to make it objectionable. It will eat a few of its own young, but not enough to miss them —just enough to make the balance grow well."

The stocking of inland waters with warmouths for sport fishing was begun before the turn of the century. Records indicate that the distribution of warmouths by state and federal agencies has been sporadic and probably never on a large scale. For example, an Oklahoma state agency distributed 36,300 fingerlings in the calendar year 1935, and the United States Bureau of Fisheries distributed 53,160 fingerlings in the fiscal year ending June 30, 1936 (Earle 1937:16, 23). In the 12-month period beginning September 1, 1946, a Texas state agency distributed 134,345 warmouth fingerlings, and in 1947 the United States Fish and Wildlife Service distributed 20,348 warmouth fingerlings and 20 warmouths at least 6 inches in length (Tunison, Mullin, & Meehean 1949:55, 58). The Fish and Wildlife Service distributed 64,040 warmouth fingerlings in 1949 and 710 in 1950 (Duncan & Meehean 1953:5–6); 4,600 warmouth fingerlings and 610 warmouths at least 6 inches long in 1951 and none in 1952 (Duncan & Meehean 1954:4–5).

In Alabama, Swingle (1950:49–73) stocked 10 of 34 experimental ponds with warmouths in combination with largemouth bass, bluegills, and other fishes. Seven of the 10 ponds containing warmouths produced populations that were considered balanced and 3 produced populations that were considered unbalanced. Warmouths comprised less than 6 per cent of the total weight of fish in all but 1 of the 10 ponds, a pond with a population judged to be unbalanced; in this pond warmouths made up 11.3 per cent of the weight. Bluegills far outnumbered the warmouths in each population.

The relatively low proportions of warmouths encountered (usually less than 10 per cent by weight, table 4) indicate that these fish have no tendency to become dominant at the expense of other kinds of fishes. However, even these low proportions may represent overcrowding for the warmouths themselves, as indicated by slow growth and the occurrence of a high percentage of small individuals reported in several censuses. Growth studies in Illinois indicate that as low a proportion of warmouths as 10.4 per cent by weight, found in Park Pond Slough (a weed-choked channel in Park Pond) may represent overcrowding for these fish. Growth of warmouths in this channel was considerably slower than was that of warmouths in Onized Lake, just preceding 1941, when warmouths made up 6.5 per cent of the total weight of the fish population (Bennett 1945:382, 397), and slower than that of warmouths in Lake Glendale just preceding 1946, when warmouths made up 5.0 per cent of the total weight (unpublished information from Dr. Donald F. Hansen of the Illinois Natural History Survey). In Onized Lake, the fish population had been thinned by excessive fishing, and in Lake Glendale the population had been expanding during the 6 years following impoundment of the water.

Experimental Species Combinations.—As part of a series of management experiments by the author, 17 ponds in central Illinois were stocked with warmouths in various combinations that included largemouth bass, smallmouth bass, several pan fishes, and minnows. Because these experiments have not yet been completed and because they are not an integral part of the life history study reported here, the stocking combinations are listed below with consideration given principally to the early development of the populations and such factors as directly relate to the life history of the warmouth.

Warmouths (Adults); Largemouth Bass (Fingerlings and Yearlings).—This combination of species and sizes was first tested in 3-acre Enright Pond over a period of 15 months. Sixteen adult warmouths, 4 yearling largemouths, and 60 fingerling largemouths per acre were released in May, 1947. Warmouths spawned the first summer, and both species produced broods of young the second summer. Growth of all fish was rapid; some of the first-brood warmouths attained lengths as great as 6 inches in a little more than a year. There was a desirable distribution of numbers in size groups of both species.

Warmouths (Fingerlings and Adults); Largemouth Bass (Fingerlings and Adults).—Both species were introduced in numbers and sizes simulating a "pyramid of numbers." This combination was tried in Enright Pond after termination of the experiment described above; the population was established during the early fall months of 1948 with 90 fish of each species per acre. Moderate-sized broods of both species were produced the next summer, and in each of the seven following summers the population was studied. The striking difference between what occurred in this warmouth-largemouth population and what usually occurs in a bluegill-largemouth population was that in the Enright Pond population the bass successfully produced a brood each year and fish of the companion species (warmouths in Enright) never produced such large numbers of young that they dominated the population. In 187 hours of recorded fishing during the sixth summer (there were fewer records for other years), 98 largemouths and 16 warmouths were caught at a rate that averaged 0.6 fish per hour. The number and sizes of fish of each species in this population were more nearly constant from year to year than in populations started with fish of one size.

Warmouths (Adults); Largemouth Bass (Yearlings and Adults).—Venard Lake was stocked in 1947 with 32 adult warmouths and 70 yearling and 5 adult largemouths per acre. The growth and competition for food in this population have been discussed previously in this paper. The bass gained an early dominance over the warmouths; by the end of the third growing season, the lake was becoming overcrowded with bass.

Warmouths (Adults); Largemouth Bass (Adults).— Fifteen adult warmouths and 22 adult largemouths per acre were released in Reece Pond in May, 1949. This 2.5-acre pond was characterized by a large proportion of shallow water and dense masses of aquatic vegetation (*Potamogeton foliosus*). Both species of fish spawned the first summer and they produced broods in each of the 7 succeeding years. The extensive vegetation permitted the survival of more young fish than could grow well in this pond.

Warmouths (Adults); Largemouth Bass (Adults) Added 1 Year Later.—In April and May, 1948, approximately 20 adult warmouths were released in a 1-acre pool above Venard Lake. They produced a large brood in the summer of 1948. The following spring about 20 adult largemouths were added to the pool. A small brood of bass was spawned, and the young grew well; by the end of the summer they were feeding on small warmouths. This combination and sequence of setting up the population allowed the warmouths to become well established, may have limited the size of the first bass spawn, and provided small forage fish for the bass.

Warmouths (Established Population); Largemouth Bass (Adults).—In June, 1951, Kearney Pond (2.5 acres), fig. 25, containing a small population of warmouths, principally yearlings, was stocked with 5 adult largemouths per acre. In the following October, 20 more adult bass per acre were added, along with 40 fingerling and adult warmouths per acre. The warmouths produced a moderate-sized brood in 1951. In 1952, the largemouths produced a large brood, the warmouths a relatively small one. This relative spawning success of the two species was maintained in each of the 3 following years, or until the study was terminated.

Warmouths (Adults); Largemouth Bass (Fingerlings); Minnows.—The influence of minnows—both as a forage item and as a predator on the eggs and fry of sport fishes—was investigated in three populations containing warmouths and largemouths.

Three adult warmouths and 30 fingerling largemouths per acre were released in June, 1952, in Parkhill Pond, a 3-acre pond which contained a large established population of the bullhead minnow, *Pimephales vigilax* (Baird & Girard). When the study was terminated at the end of about a year, which included parts of two breeding seasons, there was an abundance of minnows, the bass and warmouths had grown exceptionally fast, and the warmouths had produced broods the first and second summers. The largemouths, which were 10 to 12 inches in total length early in the second season, did not produce a brood. Since the warmouths spawned successfully even though an abundant minnow population was present, it seems likely that the largemouths would have produced a brood the next year.

In July, 1948, Lutz Pond contained a large population of several species of minnows, the most abundant of which was the bullhead minnow. This 1.5-acre pond was then stocked with 20 adult warmouths and 60 fingerling largemouths per acre. Warmouths spawned the first summer (1948) and produced a large brood; these young fish grew rapidly. The warmouths produced another brood (1949) before the

Fig. 25.—Central part of Kearney Pond, McLean County, stocked with warmouths and largemouth bass.

2-year-old largemouths spawned in 1950. The minnow population declined rapidly during the third summer.

Kearney Pond (2.5 acres) contained minnows (species unidentified) and darters, *Etheostoma nigrum* Rafinesque, when it was stocked in June, 1949, with 10 adult warmouths and 46 fingerling largemouths per acre. The warmouths, minnows, and darters reproduced well in the first summer. Growth of the sport fishes was good. The numbers of minnows and darters declined during the summer.

In Parkhill Pond and Lutz Pond, two broods of warmouths were produced before the first spawn of bass. In all three ponds, the abundance of small forage fish provided food for the warmouths and largemouths, which grew rapidly; largemouths provided some fishing the second summer; and a bass brood of moderate size was spawned the third summer in the presence of two broods of warmouths.

Warmouths (Fingerlings and Adults); Minnows.—In August, 1948, 34 fingerling and 14 adult warmouths per acre were introduced into Longworth Pond (2 acres), which contained a large population of fathead minnows, *Pimephales promelas* Rafinesque. The warmouths spawned successfully during the remainder of the 1948 season and again the following summer. The broods in both years were small; evidently the minnows had a depressive effect on the warmouth population.

Warmouths (Adults); an Established Sunfish Population.—Three experiments were conducted to see if a small number of warmouths could successfully reproduce and survive in an established population consisting of several species of sunfishes.

Seven large adult warmouths were planted in a one-half-acre pond, Green Gravel Pit, which at the time (June, 1947) contained a population of bluegills, redear sunfish, green sunfish, and largemouth bass. Only one warmouth (original stock) was recovered when poison was applied to the pond in August, 1948. The warmouths had failed to establish a brood during the two intervening spawning seasons.

In November, 1949, Taylor Pond (2 acres) was stocked with 69 adult warmouths per acre. A few weeks before, it had been stocked with 100 bluegill fingerlings, 100 largemouth fingerlings, and 15 largemouth adults per acre; a few adult green sunfish, longear sunfish, and bluegills also were added. The population was killed during the second spawning season (June, 1951); two adults, each a half pound in weight, were the only warmouths recovered from a rather large sunfish population (337 pounds per acre).

Twenty-three adult warmouths were released in June, 1952, in a 3-acre pond, McCarty, which contained a new but large population of bluegills and largemouth bass. No young warmouths (definitely identified) were taken from this pond during the following 4 years.

Warmouths (Adults); Redear Sunfish (Adults); Smallmouth Bass (Adults and Fingerlings).—This combination of species was tested in two ponds.

In July, 1951, 2-acre Taylor Pond (mentioned in connection with another experiment) was stocked with 21 adult warmouths per acre. These fish produced a small brood in the same summer. In the following fall and spring, 10 fingerling and 7 adult smallmouth bass and 17 adult redears per acre were added. A small brood of smallmouths, a moderate-sized brood of warmouths, and a relatively large brood of redears were produced in the summer of 1952.

Observations the next 2 years revealed the following: The smallmouths produced a very small brood in 1953 and no brood in 1954. Growth of the original stock of bass was good, but growth of both the 1952 and 1953 year classes was very poor. The warmouths and redears reproduced successfully each year and at first grew at satisfactory rates; however, by the spring of 1955 there were relatively few over 6.5 inches in length.

Sparks Pond (3 acres), fig. 26, was stocked with 22 adult smallmouth bass in November, 1949. The following spring the smallmouths spawned very successfully. In June, 25 adult warmouths and 34 adult redear sunfish were added to the population of this pond. Both of these species reproduced, although the brood of warmouths was quite small in numbers.

During the following 7 years, these observations were made: Smallmouth bass of the first brood (1950) did not grow well after the first summer. The bass spawned

Fig. 26.—South side of Sparks Pond, Woodford County, stocked with warmouths, redear sunfish, and smallmouth bass.

each year, but the fingerlings disappeared before attaining 1.5 inches in length. The only successful brood of bass after the first was that produced in 1954, which came after the redear sunfish population had been reduced in numbers by poison applied to part of the pond, a tremendous number of small sunfish had been lost over the spillway during a severe flood, and bass of the 1950 brood had become less numerous. Growth in this 1954 brood of bass was poor.

The redear sunfish spawned very successfully each year. The original stock and the first brood grew very well. Broods produced later showed much slower growth. After the fourth year, there were very few redears over 6 inches in length, although redears of smaller sizes were numerous.

The warmouth population was slow to develop. Warmouths spawned successfully each year, but the broods produced were small. However, by the fourth year warmouths were numerous and had become large enough to be attractive to anglers.

Warmouths; Largemouths; Bluegills (Adults of One Sex).—Four experiments were set up in attempts to produce warmouth×bluegill hybrids.

Kearney Pond (mentioned in connection with other experiments) contained a 4-year-old warmouth-largemouth population when 8 adult female bluegills per acre were added, July, 1955, in an effort to produce hybrids with the warmouths. No hybrids were found in the two spawning seasons after the bluegills were added.

Dunmire Pond (4.5 acres), fig. 27, was stocked in May, 1950, with 16 adult warmouths, 19 adult male bluegills, and 100 fingerling largemouth bass per acre. In July, 1955, 10 more adult male bluegills per acre were added. The warmouths and largemouths grew well, spawned successfully each year, and produced good fishing. The male bluegills grew exceptionally large (1.2 pounds), but no hybrids were observed in the first 6 years after the pond was stocked.

A shallow 3-acre pond on the University of Illinois Golf Course near Savoy was stocked with 45 adult warmouths, 185 adult female bluegills, and 907 largemouth bass fingerlings. These fish were placed in the pond in two groups, one group in each of the summers of 1949 and 1950. In the third summer following the original stocking, a large brood of bluegills was produced; one or more male bluegills must have been accidentally introduced in 1950. No warmouth×bluegill hybrids were collected from this pond.

During the summers of 1949 and 1950, 19 adult warmouths and 59 adult male bluegills were released in Green Gravel

Pit, mentioned in connection with another experiment. Broods of warmouths were produced in each of these two summers and the two following summers that the study was continued. The male bluegills built nests, but no warmouth×bluegill hybrids were collected. This half-acre pond, in which a substantial warmouth population had been developed, should have offered a desirable situation for hybrid production.

Fig. 27.—North arm of Dunmire Pond, Woodford County, stocked with warmouths, largemouth bass, and male bluegills.

General Conclusions About Species Combinations.—Several general conclusions may be drawn from the preliminary observations on these experimental populations. Usually when sexually mature warmouths are released in a pond before the middle of August, they will produce a brood the same summer. In established warmouth populations, a high proportion of each new brood is spawned so late in the season that the fish are too small in their second summer of life to reproduce then. Small numbers of warmouths when introduced into a pond overcrowded with other sunfish seem unable to establish a population. Warmouths reproduce successfully in the presence of a large minnow population and grow well when they become large enough to utilize the minnows as food.

Largemouth bass in a pond with warmouths apparently grow faster and produce better fishing than do smallmouth bass in a pond with warmouths. There is little difference in growth rates between warmouths that develop in a pond with largemouths and those that develop in a pond with smallmouths. Warmouths will not establish a large enough population to support angling and materially reduce the survival of young bass unless adult warmouths are introduced a year before adult bass are added, or unless fingerling bass, instead of adults, are introduced with the adult warmouths.

There is no assurance that hybrids will be produced when bluegills of only one sex are introduced into a warmouth population.

SUMMARY

1. The ecological life history of the warmouth, *Chaenobryttus gulosus* (Cuvier), was studied intensively in two habi-

tats of central Illinois: Venard Lake, a 3.2-acre artificial impoundment stocked only with warmouths and largemouth bass, and Park Pond, an 18-acre flooded strip-mine area containing a fish population of 36 species. The intensive investigations in these two areas were supplemented by observations in other habitats and by published records on warmouth habitats and populations.

2. Field observations and published records indicated that the warmouth is usually associated with habitats characterized by soft bottoms and dense stands of aquatic vegetation.

3. In the water areas under observation, small and medium-sized (less than 5 inches total length) warmouths remained in protected areas of shallow water throughout the year, whereas larger individuals spent more time in deep, open waters.

4. Laboratory experiments supported field observations demonstrating that warmouths are able to survive in water having very low concentrations of dissolved oxygen. The critical oxygen tension observed was 2.5 cc. per liter at 20 degrees C. Tolerance for low oxygen concentrations allows the warmouth to survive and grow in a wide range of habitats and to survive during periods of water conditions that are generally considered unfavorable to fish.

5. The food habits of warmouths from Park Pond and Venard Lake were studied through a 12-month period. In volume and frequency of occurrence, the various food items identified in warmouth stomachs showed little similarity in the two areas, although crayfish and nymphs of mayflies, dragonflies, and damselflies were abundantly utilized at both places. During the summer months, feeding activity was at a peak early in the morning; it practically ceased in the afternoon.

6. Postlarval warmouths observed in the laboratory fed first on protozoa and bacteria. There was a general increase in size of food items taken by warmouths of Park Pond and Venard Lake as the fish increased in size; the percentage of stomaches that were empty was higher among large fish than among smaller ones.

7. In Venard Lake, warmouths and largemouth bass consumed about the same kinds of foods, but differences in their feeding habits may have prevented extensive competition between these species.

8. Seasonal changes in appearance and weight of gonads indicated that the warmouths collected from Park Pond and Venard Lake attained sexual maturity when between 3.1 and 3.5 inches total length and that fast-growing fish matured earlier in life than did slow-growing ones. Warmouths over 5.4 inches total length attained spawning condition earlier in the nesting season, and spawned over a longer period, than did fish of smaller sizes. Males matured slightly earlier in the season than did females. In central Illinois, the spawning season for warmouths generally extends from mid-May through mid-August.

9. An estimation was made of the total number of eggs in ovaries of warmouths of different sizes, from different water areas, and taken at different times of year. Total egg counts ranged from 4,500 to 63,200 per ovary. Females from Park Pond consistently produced fewer eggs than did those from Venard Lake.

10. A month before the beginning of the spawning season, groups of developing eggs began moving away from the primordial egg-stock in sexually mature warmouth females. There was a gradual withdrawal of eggs from the egg-stock throughout the spawning season. Ova in advanced maturation were resorbed if not spawned before the cessation of nesting.

11. In all instances of warmouth nesting observed in the field, the male constructed the nest, usually near some projecting object and on a bottom of loose rubble containing some silt and detritus. No colony formation was observed.

12. Sex recognition among warmouths observed in the laboratory was based apparently on behavior and response to courting. Males displayed temporary color changes during courtship and spawning. There was evidence that many males and females spawned two or more times during a summer; in some instances, more than one female contributed to the complement of eggs in a nest.

13. In the laboratory, incubation of eggs lasted about 34.5 hours at temperatures between 25.0 and 26.4 degrees C. Immediately after hatching, the prolarvae dropped to the bottom of the nest. The

yolk supply was exhausted in 4 days, and the larvae attempted feeble, poorly directed jumps. By the fifth day, they swam actively. They began feeding by the seventh day; considerable pigmentation had developed and the caudal fin appeared homocercal. The 15.7-mm. young were essentially like an adult in body form.

14. The mathematical relationship (in inches) between the anterior radius of a warmouth scale magnified 41 times (S) and the total length of the fish (L) was expressed by the equation:

$$L=0.5278+1.048\ S$$

15. In the populations studied, as the body length of the warmouth increased, the tail became relatively shorter; different mathematical relationships between standard length and total length were found for fish of various sizes.

16. The relationship of standard length in millimeters (L) to weight in grams (W) was expressed for 866 Park Pond warmouths by the equation:

$$\log W=-4.49867+3.04902 \log L$$

17. The coefficient of condition (C) for 866 warmouths from Park Pond showed no consistent seasonal cycle. Seasonal variations in condition were greater in warmouths between 3.3 and 4.2 inches than in larger fish. Coefficient of condition increased progressively with increase in size of fish.

18. The annulus was found to be a reliable year-mark in the warmouth. Warmouths in Park Pond completed the 1949 annulus between April 7 and May 20. Warmouths in Venard Lake completed the 1949 annulus over a shorter period than did those in Park Pond, where ecological conditions in the habitat varied greatly. Dredging of the shore of Venard Lake during August, 1948, is believed to have caused the formation of a false annulus.

19. Females from Park Pond were consistently smaller than males of the same ages. The difference was small, however.

20. Age was determined for 1,063 warmouths from Park Pond; it was found that fish of certain year classes had consistently grown more rapidly than others. Growth for all year classes was better in certain years than in others.

21. The 1946, 1947, and 1948 year classes in Park Pond showed different growth patterns for the summer of 1949. The fish in each year class grew rapidly during May and June. Although growth continued through the summer for the younger fish, it declined rapidly after June for the 1946 year class. The 1947 year class showed a growth pattern intermediate between the earlier and later year classes. Growth rates were different for warmouths in different parts of Park Pond.

22. A comparison of length increments for the first and for later years of life showed that warmouths in Park Pond with the greatest length increment for the first year added to this length advantage the second growing season. Fish that grew slowly the first year showed a slight growth compensation during the third year, although they did not overcome the length advantage held by the larger fish.

23. Three year classes, represented by 1,102 warmouths, were studied in Venard Lake. Fish of the first year class spawned in the lake grew faster than did those of succeeding year classes. The length range in a single year class was greater during the first summer than in succeeding years. The average growth in length for warmouths in their first 3 years in Venard Lake was similar to that for warmouths of comparable ages in Park Pond.

24. Warmouths in Park Pond were heavily infested with *Posthodiplostomum minimum, Proteocephalus ambloplites,* and *Camallanus oxycephalus.* Except for an infestation of the leech, *Illinobdella moorei,* warmouths in Venard Lake were relatively free of parasites. No direct harmful effect of parasites was established.

25. Laboratory and field observations showed that the warmouth has a quiet disposition. In its reproductive and group behavior, it is similar to other centrarchids, but it displays certain behavioral characteristics peculiar to the species.

26. Reports and field observations demonstrated that the warmouth is caught on a wide variety of baits and lures, and that warmouth fishing is best during the spring and early summer months. The warmouth has been praised by sport fishermen for its fighting qualities. It is a useful fish for laboratory experimentation.

27. That warmouths have no tendency to become dominant at the expense of other kinds of fishes was indicated by the rela-

tively low proportions of warmouths reported in fish populations of Illinois and other states. In 17 ponds in central Illinois stocked with 11 different fish combinations that included warmouths with other species—largemouth bass, smallmouth bass, and several pan fishes—warmouths tended to establish small broods each year without seriously restricting the reproduction or growth of companion species.

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