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MICHIGAN DEPARTMENT OF CONSERVATION
COOPERATING WITH THE
UNIVERSITY OF MICHIGAN

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March 10, 1948

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Report No. 1166

THE SPAWNING HABITS, PRODUCTION AND SURVIVAL OF CENTRARCHID

FISHES IN DEEP LAKE, OAKLAND COUNTY, MICHIGAN

by

W. F. Carbine

Abstract

Observations were made at Deep Lake, Oakland County, Michigan on the spawning habits, the number of fry that are produced per nest, the total fry production and the percentage survival of these fry during the four-year period from 1938 to 1941, for the bluegill (Lepomis macrochirus), the pumpkinseed sunfish (Lepomis gibbosus), the rock bass (Ambloplites rupestris) and the largemouth bass (Huro salmoides).

All of the types of bottom material, or combinations of the various types, found in Deep Lake were used for nest construction and resulted in successful reproduction, by all of the species studied, although rock bass and largemouth bass seldom nested on peat bottom. One aspect of the study that was most striking was the variation in nest building. The characteristics of the nest are not specifically associated with the species occupying it. Some of the nests of all of the species were almost identical as to size, shape and type of bottom.

The average depth of water in which the nests were located during the 4-year period was 27.6 inches for the largemouth bass; 17.2 inches for the rock bass; 25.8 inches for the pumpkinseed; and 24.7 inches for the bluegill. The average diameter of all largemouth bass nests used for spawning in the 4-year period was 13.9 inches; rock bass, 9.7 inches; pumpkinseed, 18.0 inches; and the bluegill, 20.6 inches.

Every nest actually used for spawning during the period of observation was counted for each species. The number varied during the 4-year period from 23 to 56 for the largemouth bass, 28 to 67 for the rock bass, 97 to 188 for the pumpkinseed sunfish and 369 to 679 for the bluegill.

The spawning season during the 4-year period of observation averaged 26 days (range 17 to 51) for the largemouth bass; 43 days (range 25 to 53) for the rock bass; 54 days (range 49 to 63) for the pumpkinseed; and 65 days (range 44 to 78) for the bluegill. Correlation between the water temperature and the dates of spawning suggest that temperature regulates spawning to some extent, but for the bluegill it is believed that the time required for the development of the ova regulates spawning. Given proper temperatures, bluegills will spawn whenever a new batch of eggs matures.

When the first attempt was made to count eggs it was immediately evident that eggs of all sizes, from tiny immature eggs to large ones, were present in the ovaries of all mature largemouth bass, rock bass, pumpkinseed sunfish and bluegills collected during the spawning season. Therefore a detailed study was made of the growth history of the ova of the bluegill which led to the following conclusions: 1. The immature ova (0.0 to 0.4 mm. in diameter) are present in the ovaries of every adult bluegill during all seasons of the year. 2. All bluegills collected from the beginning to the

end of the spawning season, contained eggs of intermediate size (0.4 to 0.8 mm. in diameter). 3. Mature ova (0.8 to 1.5 mm. in diameter) were present in the ovaries of all adult bluegills collected from the beginning until the end of the spawning season, except for several fish that had just completed spawning. 4. When one group of ova matures and is spawned out, it is replaced by a new class moving outward from the intermediate group. This movement occurs at a faster rate in some individuals than in others and the rate is probably increased during periods of warmer weather and decreased toward the end of the spawning season. 5. The presence of at least 3 modes in the ova diameter frequency curves, the fact that intermediate-sized eggs started development towards maturity immediately after spawning and the fact that occasional large, ripe, unspawned eggs are found in some ovaries containing a batch of newly ripening eggs are probably evidence enough to justify the conclusion that some female bluegills spawn more than once in a season. Literature is cited to further substantiate this theory.

The estimated number of eggs contained in 42 bluegills ranged from 1,124 to 59,552 and averaged 17,261. The number of eggs contained in 7 rock bass ranged from 965 to 2,182 and averaged 1,685 eggs per female. Egg counts were not made for the pumpkinseed sunfish and largemouth bass.

The actual number of fry contained in the 53 bluegill nests that were sampled ranged from 2,657 to 61,815 and averaged 16,240 fry per nest. The number of rock bass fry per nest varied from 213 to 5,389 and the average total number in the 33 nests counted was 1,466. The number of pumpkinseed sunfish fry per nest varied from 1,509 to 14,639, for an average of 6,012 for each of the 14 nests counted. Counts of the fry collected from 11 largemouth bass nests averaged 5,654 (range 751 to 12,502). A number

of factors are discussed which may account for some of the mortality of the eggs and fry.

The fish population in Deep Lake was destroyed by means of powdered derris root. Although an effort was made to recover as many of the fish as possible, it is admitted that the recovered population may have been considerably short of the actual population, particularly of the smaller fish. Production figures are presented in this paper that are based upon the number of nests actually used for spawning, the average number of fry per nest and the number of fish of each year class from 1938 to, and including, 1941 that were actually recovered. The number of largemouth bass fry produced varied from 130,000 to 317,000 for the 4-year period, and the percentage survival for each year class ranged from 0.0123 to 0.2518. Between 41 and 98 thousand rock bass fry were produced each of the 4 years and the percentage survival ranged from 0.0341 to 0.9658. The production of pumpkinseed sunfish varied from 583,000 to 1,130,000 each year, and the percentage survival ranged from 0.0126 to 0.4875. The estimated number of bluegill fry produced each year varied from 5,993,000 to 11,027,000, and the percentage survival ranged from 0.0007 to 0.0970.

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This investigation on the spawning habits, production and survival of centrarchid fishes in Deep Lake was undertaken in 1938 with a view toward providing the Michigan Department of Conservation with a larger body of data needed for improved fishery management.

Many methods have been devised by fishery workers in an effort to solve the problem of the depletion of our fishery resources and of maintaining the production necessary to meet the demands of an ever increasing army of anglers. Artificial propagation, the introduction of exotic species, protection, law enforcement, measurements of angling intensity and environmental improvements have all been resorted to. Recently, it has been recognized that efficient fishery management depends upon a thorough knowledge of the complete life history of every species of fish present in a given body of water. By determining the various factors involved in the life cycle of any species, measures can then be applied to improve production.

Fish culture was one of the first developments to be used in an effort to improve sport as well as commercial fishing. Ever since, the planting of artificially propagated fish has been the panacea for all fishing ailments. In an effort to improve fishing, hatchery output has been tremendously increased. These well-meaning attempts to increase the fish supply have been carried out despite the apparent failure to maintain good fishing. As early as 1924, Kendall (1924) stated that early fish culture was in the nature of a venture rather than a rational procedure or experiment and deplored the fact that scarcely any attempt had been made to determine the practical value of artificial propagation.

Hatcheries have always been popular and have impressed the sportsmen because of the large numbers of fish that could be produced. Little did people realize that millions of young were produced naturally in many lakes and streams. Most of the fish raised in hatcheries until recently were planted as eyed eggs, fry or fingerlings, and the number planted in any lake or stream often amounts to fewer fish than are produced naturally in that same lake by one pair of spawners.

The introduction of certain species, such as perch and bluegills, frequently leads to natural overstocking and is often responsible for the poor fishing in many lakes. This has resulted in stunted populations many times (Eschmeyer, 1938a; Hubbs and Eschmeyer, 1938). Overcrowding has also resulted from certain conditions where natural reproduction has been exceptionally good, coupled with an abundance of cover and a lack of, or a diminished population of, predators.

The introduction of exotic species has provided excellent fishing in some waters that formerly produced little or no fishing. But this addition to the fauna of one or several bodies of water has not released the fishing pressure on all waters as a whole.

Relatively pure water of a certain optimum temperature, sufficient food, adequate spawning facilities and shelter are the essential requirements of fish. The lack of any one of these requirements will hold down the production of any species, whereas the excessive development of any requirement may throw any one species out of balance with the remainder of the population. The regulation of the number of fish in a given body of water depends upon the rate of reproduction, growth rate and the mortality during the normal life cycle. Great numbers of young are produced by most species of fish. It is necessary then that a drastic reduction in the number of young should occur in order to maintain the balance with the rest of the population. As Dr. Needham so aptly remarked (Needham, Juday, et al., 1922, p.52): "The number of young produced is proportioned to the vicissitudes of life; there are only enough to insure the continuance of the species under natural conditions. This is what is known as the natural balance.--This means that any two parents, despite the large number of their eggs, succeed in leaving on the earth but one pair of descendents that in turn reproduce."

The success of reproduction and the rate of survival of the young fish vary with the season, and with each particular body of water. The water temperature, amount of cover, the number of predators, the number of spawners and the amount of angling are all contributing factors. Ordinary survey technique often fails to determine the success of reproduction and survival and its relation to the catchable fish present.

Production studies in the past have been directed primarily toward determining the amount of fish that could be harvested. This has been accomplished by investigations of populations and by creel census. It is important to determine the spawning habits, egg production, fry production, and the relation between the chemical, physical and environmental factors, because these all affect the number of fish available to the angler. It is apparent that natural spawning would have to be studied in any problem involving lake productivity.

The present study was undertaken to obtain accurate knowledge of the number of eggs, fry and adults that result from natural reproduction and to ascertain the losses that occur during the various stages of development so that the final returns to the angler may be determined.

Observations were made at Deep Lake on the spawning habits, the number of fry that are produced per nest, the total fry production, and the percentage survival of these fry during a four-year period (1938-1941) for the bluegill (Lepomis macrochirus), the pumpkinseed sunfish (Lepomis gibbosus), the rock bass (Ambloplites rupestris) and the largemouth bass (Huro salmoides).

In order to control the production of any species it is important to determine the population, by age groups, for each species present in a lake. To increase any species that is to be favored in a lake, it

might be necessary to control the populations of several species. The number of nests actually used for spawning by each species and the average number of fry per nest will provide information on the total production of fry. If certain species produce large numbers of fry, it may be advisable to abolish all protection given the adults during the spawning season or destroy the nests containing eggs, to avoid overcrowding. Swingle and Smith (1939) found that heavy stocking of ponds did not always result in an increase in the number of pounds of fish produced per acre of water, but did result in the decrease in the average size of the fish. Overcrowding therefore could result in the fish being more numerous, yet smaller, and not as desirable to the angler. A quantitative measure of the initial productivity in a particular lake, computed from the number of fry produced and the expected survival, might yield results that could be used in determining the necessity for stocking; the relation between the number of fry and the abundance of future year classes; and the relation between the number of fry produced by each species and the possibility of the development of a dominant predator age-group.

It is conceded that the number of eggs deposited and the number of fry that hatch vary from year to year, from lake to lake, and in the same or similar spawning areas in the same and in different seasons.

Data on the amount of available spawning territory in a lake can be determined by obtaining the depth of water in which nests are found and the type of bottom used for nest building. This information should indicate whether or not an adequate hatch could be expected, provided that ample spawners were present. If necessary bottom types are absent, improvements could be made.

Regulations governing the fishing seasons can be determined for a species if the duration of the spawning season is known. The time of year that spawning occurs varies from year to year according to the weather conditions during a particular season. With this information at hand it is reasonable to believe that a more precise open season can be formulated. If any one lake is overpopulated with fish of a certain species the open seasons could be regulated to enable fishermen to catch this species during the spawning season.

The present investigation was conducted on Deep Lake, owned by Messrs. James Inglis and Ben E. Young. The lake is located in Oakland County, Rose Township, Michigan, between the villages of Clyde and Rose Center, and about 40 miles north of Ann Arbor.

Deep Lake fits more or less perfectly into the category of pit lakes (Scott, 1921). The lake is surrounded by high, steep banks. The soil of the surrounding country is moranic in character. Most of the land in the immediate vicinity is either under cultivation, used for pasture or is wooded. The high banks from the water level to the plain above the lake are sparsely wooded.

The lake has a surface area of 14.84 acres, a maximum length of 1,230 feet in a W.N.W.-E.S.E. direction, and a maximum width of 660 feet. The lake is approximately oval in shape and consists of two basins, an eastern, with a maximum depth of 61 feet and a western, with a maximum depth of 51 feet. The intervening area averages approximately 45 feet in depth. The lake has a shoreline development of 1.12, which means that the lake has a shoreline over 1.12 times as long as a perfectly circular lake of the same area. The drop-off from shore toward the center is so sharp that the amount of shoal area (the term shoal as used in this paper is that

zone between 0 and 5 feet in depth) is limited to 11.77 percent of the lake's surface area (Figure 1). The northern, southern and eastern shoal areas, varying from 12 to 62 feet in width, are composed chiefly of sand, with patches of gravel, rocks, roots and vegetation interspersed. The bottom of the western shoal area, varying from 20 to 70 feet in width, is composed principally of fibrous peat, decaying vegetation, roots and aquatic plants with some underlying sand and gravel. Patches of clay are present in some parts of the shoal area, and apparently is deposited by the run-off from adjoining property. Marl in the form of decomposed Chara is also present in some parts of the shoal area.

Deep Lake has neither an outlet nor a permanent inlet. One 6-inch tile, located at the southwest end of the lake, drains a nearby pasture, and was thought by the owners to be a spring. The lake is supplied and drained principally by the seepage of ground water. The entire lake receives the run-off from less than 10 acres of land. The fluctuation of the lake level seldom varies more than one foot per year. Between 1938 and 1942 there was a fluctuation, representative of high and low lake level, of about 1-1/2 feet.

The water of Deep Lake is relatively clear. A Secchi disk when lowered into the water, disappears from view at depths of 20 to 24 feet. The degree of transparency of Deep Lake is much greater than average for southern Michigan lakes. The extent of light penetration is closely correlated with the depth at which the higher aquatic plants are found in the lake.

A routine fisheries survey was conducted at Deep Lake on July 24, 1939, by the writer and members of the Huron River survey party.¹ At the time

¹ This party consisted of Dr. James Moffett, leader, of K. E. Goellner, La Rue Wesley, and Frank Lydell, assistants.

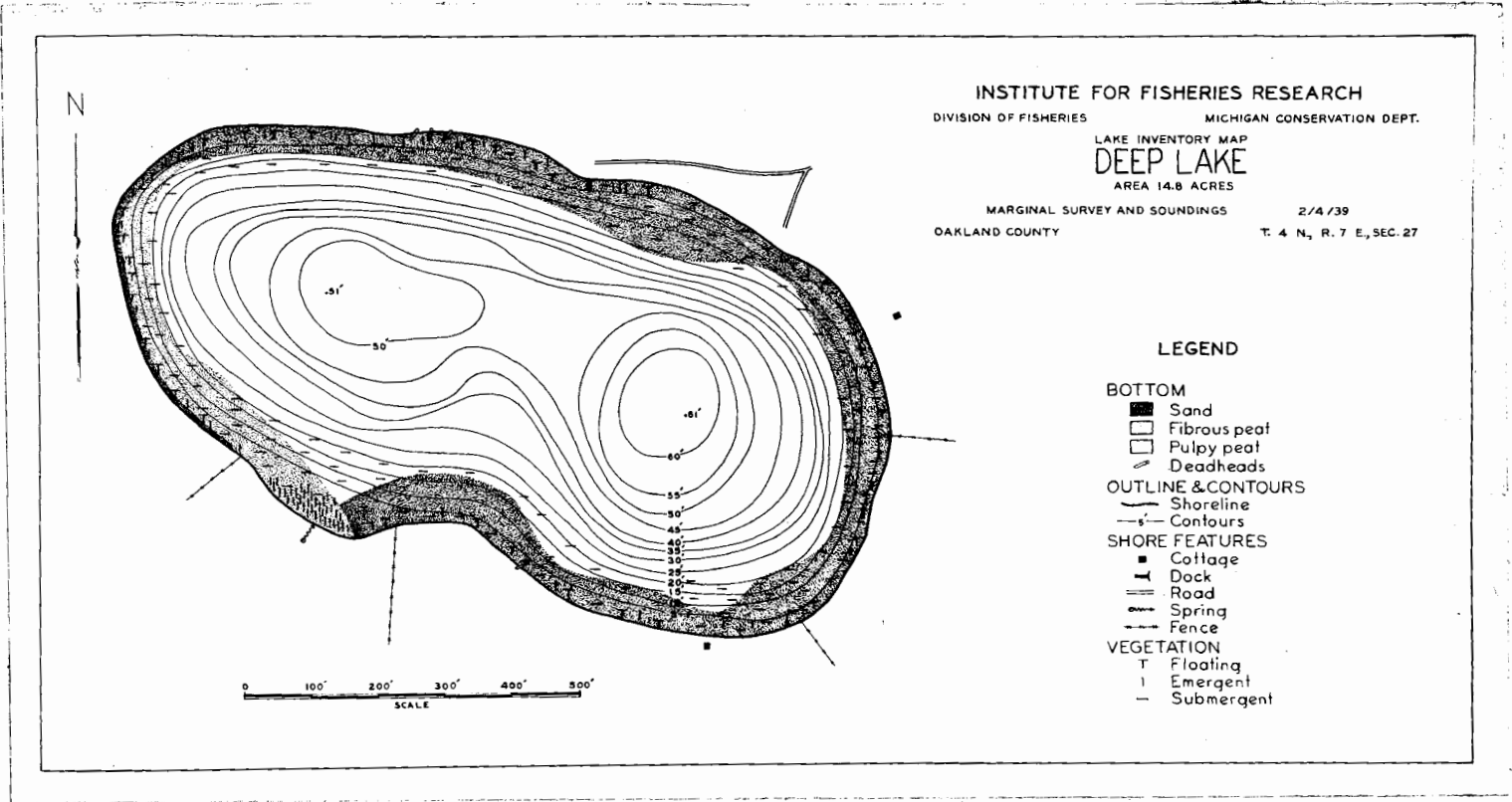


Figure 1.--Map of Deep Lake showing bottom types.

of the survey the lake was both thermally and chemically stratified. A thermocline was present between 16 and 39 feet. The temperature of the water varied from 79° F. at the surface to 42.8° F. at the bottom (61 feet). At the time of the survey, oxygen was found in a quantity sufficient to maintain fish life to depths of about 50 feet. Chemical analyses made at Deep Lake in late August and late September indicate that oxygen was plentiful in most of the deeper and colder waters.

The methyl orange alkalinity varied from 84 to 93 parts per million at the time of the survey, indicating that the lake can be classed as a moderately "hard" water lake.

The hydrogen ion concentration, or pH, of Deep Lake varied from 8.6 at the surface to 6.9 at 61 feet.

The aquatic vegetation can be judged as fairly abundant in Deep Lake, considering the limited amount of narrow, sandy shoal that is present (Figure 1). The aquatic plants that are found in Deep Lake are listed in Table 1.

Occasional rather dense patches of bulrushes with a scattering of others are found all along the sandy shoal in Deep Lake, in water from 0 to 3 feet in depth. Water lilies are pretty well scattered around the entire lake. On the widest shoal area (with a bottom of fibrous peat), floating-leaved and other pondweeds, water lilies and chara form a rather dense mat. Cattails (a dense stand) are found in only one place in Deep Lake; at the outlet of the tile drain. Some portions of the sandy shoal are relatively free of aquatic plants. A dense band varying in width from several to 20 feet, of floating-leaved pondweeds (P. natans and P. vaseyi), interspersed with other pondweeds, is found around the south, west, and north-west portions of the lake in water varying from 2 to 8 feet in depth. The

Table 1.--The aquatic plants found in Deep Lake.

Species	Scientific name [↓]	Abundance
Water marigold	Megalodonta Beckii	Sparse
Coontail	Ceratophyllum demersum	Sparse
Swamp loosestrife	Decodon verticillatus	Common
Bushy pondweed	Najas flexilis	Common
Needle rush	Eleocharis acicularis	Common
White water lily	Nymphaea odorata	Common
Yellow water lily	Nuphar advena	Common
Pickerelweed	Pontederia cordata	Common
Pondweeds:	Potamogeton americanus	Common
	Potamogeton amplifolius	Common
	Potamogeton angustifolius	Common
	Potamogeton gramineus	Common
	Potamogeton gramineus var. graminifolius f. myriophyllus	Common
	Potamogeton natans	Abundant
	Potamogeton vaseyi	Common
	Potamogeton zosteriformis	Common
Bulrush	Scirpus validus	Common
Cattail	Typha angustifolia	One patch--abundant
Chara	Chara sp.	Common

[↓] Identifications by B. M. Robertson, Department of Botany, University of Michigan.

water in Deep Lake is sufficiently transparent to permit the growth of submerged aquatic plants to depths as great as 25 feet.

The following species of fish were found to inhabit Deep Lake:

Bluegill - Lepomis macrochirus

Pumpkinseed sunfish - Lepomis gibbosus

Largemouth bass - Hure salmoides

Rock bass - Ambloplites rupestris

Yellow perch - Perca flavescens

Yellow bullhead - Ameiurus natalis

Green sunfish - Lepomis cyanellus

Mud pickerel - Esox vermiculatus

Hybrids: Bluegill X Pumpkinseed sunfish

Bluegill X Green sunfish

Green sunfish X Pumpkinseed sunfish

One horned dace (Semotilus atromaculatus) and one common shiner (Notropis cornutus chrysocephalus) were collected by seining during the course of the investigations. When Deep Lake was poisoned (to be discussed later), five common suckers (Catostomus c. commersonii), three mud minnows (Umbra limi), and one golden shiner (Notemigonus c. chrysoleucas) were found. These fish were undoubtedly introduced either as bait or in the several unsuccessful attempts that were made in 1936 and 1937 to establish minnows in the lake.

Bluegills were the dominant fish in the lake, with pumpkinseeds and largemouth bass following in that order. Perch were seldom taken. Before 1939, rock bass were frequently taken, but seldom entered the catch during the last few years. All of the game species in the lake,

with the possible exception of the largemouth bass, were growing slower than the state average¹ for the species.

Deep Lake has never been heavily fished. The owners and a few friends and neighbors have been the only ones to fish the lake from 1938 to 1941. Previous to 1937, Deep Lake, under different ownership, was reported to have been heavily fished. In 1938, there was someone fishing the lake almost every day. From 1939 on, the amount of fishing dropped off considerably because the owners were able to control the use of the lake much better. The best fishing was usually had during late spring and early summer. A few good catches of bass and bluegills were made occasionally.

We have been unable to locate any records of fish ever having been planted in Deep Lake prior to 1941, except for an experimental planting of minnows.

The present investigation was initiated by Dr. R. W. Eschmeyer, formerly a member of the Institute staff. Dr. Eschmeyer was well acquainted with most of the lakes in the state and selected Deep Lake for this investigation because it possessed so many natural advantages. The following were probably the most important reasons for his choice of Deep Lake:

1. Proximity to Ann Arbor, which would allow the observer to use all of the laboratory facilities.

2. Deep Lake is a small, private lake, not fished a great deal. This would allow the investigator to proceed with nest marking, collection of fry, construction of experimental pens, etc., without interruption and with the lake under complete control at all times. Being a

¹ Beckman, William C. Growth rate of some Michigan game fishes. I.F.R. Report No. 741, February, 1942.

private lake, sportsmen could not object to the removal of large numbers of fry from the lake for fry counts.

3. Relatively clear water and the narrow shoal were decided advantages for making life history observations. This enabled the investigator to work from shore, or from a rowboat with the same degree of ease. Because of the narrow shoal the nests were not as difficult to find and to count as would be the case with a lake having a broad shoal area which would require the observer to row back and forth in order to cover all of the area with the possibility of missing some nests. Another advantage of a narrow shoal was that observations were greatly speeded up; therefore fish that were guarding nests were not driven away from the nest for more than a few minutes at a time.

4. The presence of a great variety of bottom types near shore, provided practically all kinds that one would expect to find in any ordinary lake. (Sand, gravel, clay, marl, muck, fibrous peat, sticks, brush, logs, stones, leaves, aquatic plants and many combinations of these bottom conditions are present).

Previous Investigations

The details of nest construction and the spawning act of certain centrarchids have been studied by many previous investigators, notably by Jordan and Evermann (1937), Reighard (1906), Forbes and Richardson (1920), Evermann and Clark (1920), Adams and Hankinson (1928), and Breder (1936), and will not be discussed in detail in this paper.

Of all of the methods used to determine production in inland waters, creel census is perhaps the most common (Eschmeyer, 1936; Needham, 1937). Other methods used in the study of fish populations

of inland waters are poisoning (Smith, 1938 and 1940; Eschmeyer, 1937; Thompson and Bennett, 1939), netting (Thompson, 1941; Krumholz, 1944), and by the use of weirs (Foerster, 1931, 1936 and Pritchard, 1940). Such procedures permit the removal of the entire fish population or the mathematical computation of the standing population of catchable fish. A few studies (Eschmeyer, 1938b and 1939) have been designed to yield information on the production and survival from the fry stage to adult, or the species composition of an entire fish population by age groups. A great deal of information is available on fish hatchery production, but these data cannot be applied to normal lake or stream production.

One of the first attempts to obtain definite information on the total production of young resulting from natural reproduction was that of Coggeshall (1924) on Winona Lake. Coggeshall counted the entire number of bluegill nests in the lake, and the number of fry per nest in a few typical nests. These data were used to estimate the total production of fry in Winona Lake, by multiplying the average number of fry per nest by the total number of nests in the lake. Coggeshall estimated that approximately 207,751,000 young bluegills were hatched in 1923.

The following information on Lime Lake, Van Buren County, Michigan, was supplied us by Mr. Jay Marks, formerly Supervisor of Fisheries Operations, Wolf Lake Fish Hatchery. (Lime Lake has an area of 30.7 acres, and was used as a source of supply for bluegill fry^{by} the Wolf Lake Hatchery). During a nine-year period (1934-1942) a total of 31,600,000 (from 1 to 7 million yearly) bluegill fry have been removed from this lake for stocking the bluegill rearing ponds at the hatchery. During this same period, a total of 305,000 (from 10 to 115 thousand yearly) fingerling bluegills

have been restocked in the lake. The hatchery men collect fry in the early part of the spawning season only, and do not take all of the fry from the nests. This indicates that large numbers of bluegill fry are produced in some of our lakes.

The first real answer as to the returns that could be expected from naturally produced fish was shown by the brilliant work of Foerster (1931, 1936). Foerster obtained data on the actual number of sockeye salmon produced naturally as compared with the results of artificial propagation at Cultus Lake. Weirs were constructed to ensure a complete count of all adult males and females running upstream to spawn. By determining the number of eggs per female, an estimate of the total number of eggs capable of deposition was obtained. Counts were also obtained of all fry, yearlings and two-year-old migrants leaving Cultus Lake for the sea. From various marking experiments, Foerster obtained an estimate of the total number of seaward migrants that returned to spawn. Foerster's work demonstrated that at Cultus Lake, artificial propagation had no significant advantage over natural spawning.

A study of the life history of the smallmouth bass in Ontario waters was made by Tester (1930). Counts were made of the number of successful smallmouth bass nests at Goose Islands in Lake Nipissing. Estimates of the number of fry per nest yielded data on the number of bass fry added to Lake Nipissing by natural propagation each year. Briefly, his conclusions were that where conditions favor smallmouth bass and where a sufficient stock of breeders is present, natural reproduction should be adequate to maintain the stock providing protection is given and that no periods of unfavorable weather occur.

Hart and Tester (1934) made a study of the typical spawning grounds of the herring (Clupea pallasii) at Departure and Nanoose Bays on the east coast of Vancouver Island. Quantitative estimates were made on the number of spawning fish, the number of eggs deposited, the mortality of the eggs on the spawning grounds, and an estimate of the number of eggs that survive to the adult fish stage.

Surber and Gutsell (1937) and Surber (1943) counted the number of smallmouth bass nests in the South Branch of the Potomac River and the average number of fry per nest and estimated the number of fry produced per mile of stream.

A study of the natural propagation of the pink salmon (O. gorbuscha) was made by Pritchard (1940). Weirs were used to obtain counts on the number of adults migrating upstream to spawn and the fry returning to the sea. The production of fry from five spawnings varied from 6.9 to 23.8 percent of the number of eggs calculated to be contained in all of the females released above the weir to spawn.

The production of rainbow trout in Paul Lake, British Columbia, was determined by Mottley (1940). An egg collecting station was maintained on the only tributary into which trout from Paul Lake could migrate to spawn. A depletion in the fishery began to appear after several years of drouth combined with heavy fishing pressure and the great demand for eggs. A definite stocking policy was formulated and provided for an annual planting of a certain number (200,000) of fish each year. Mottley determined that about 5 percent of these planted fish reached the anglers' creel. Thus, the number of fish needed to support a heavy fishing pressure had been determined.

Carbine (1942) made a study of the number of fry and fingerling northern pike that resulted from natural reproduction at Houghton Lake, Michigan. Weirs were installed to capture the adult pike entering the spawning area and the young that resulted from this spawning.

Acknowledgements

The investigation of Deep Lake was made possible through the courtesy of the owners, Messrs. James Inglis and Ben E. Young. I am indebted to Dr. R. W. Eschmeyer for the initial data and for suggestions offered for the continuance of the investigation. I wish to thank Drs. A. S. Hazzard and Carl L. Hubbs for guidance during the progress of the investigation. Most of the Institute staff have aided in various phases of the study and without their aid this study would not have been so complete. I am indebted to A. S. Hazzard for a critical reading of the manuscript and for suggestions in the presentation of data.

Methods

The data presented in this paper are based on field and laboratory observations. Field studies were initiated each year (1938-1941) soon after the ice had left the lake and were continued until late fall. During the actual spawning season, daily observations were made. Some days it was impossible to make complete observations because of rain, wind, or cloudy weather. Other duties at times also caused the writer to miss a day or two, but this seldom happened. Data were secured at frequent intervals immediately before and after the regular spawning season. Just a few observations and collections were made during the winter.

Field observations were made from a rowboat or from the lake shore. The nests and the majority of the fish were easily distinguished in the

shallower waters during periods of calm weather, but windy weather frequently hampered the work. The majority of the observations were made during early morning, late afternoon, or at night when the water was more uniformly calm than during the middle of the day. A five-cell flashlight and an automobile battery equipped with a spotlight were used at night. There was usually less wind action at night and the majority of the fish were not frightened as readily as during the day. Polaroid glasses were effective in eliminating the surface reflection on the water during the daytime. It frequently took as much as four hours just to make one complete trip around the lake making observations, although at times this could be done in one hour.

Photographs (movies and still pictures in color and black and white) were made of representative types of spawning beds, nest construction, the spawning act, and of the nest guarding activities both during the day and at night (Plate 1). Special technique and apparatus for the photography were developed for the Institute by Mr. F. W. Ouradnik (a professional photographer) and by Dr. W. C. Beckman of the Institute. These men were largely responsible for the excellent photographs obtained.

Ordinary air and surface water temperatures were taken with a Taylor pocket thermometer in 1938 and 1939. In 1939, two Taylor maximum and minimum registering thermometers were placed in Deep Lake at depths of three inches and five feet. In 1940 and 1941, nine Taylor and Trerice maximum and minimum registering thermometers were in the lake throughout the spawning season. Five of these thermometers were placed on the lake bottom at the west end of Deep Lake at depths of 1, 2, 3, 4 and 5 feet. The lake bottom at these depths was composed mainly of fibrous peat.



Plate 1.--Method used in taking photographs of spawning beds. (Courtesy of Jack Van Coevering).

The other four thermometers were placed on sand bottom at depths of 1, 3, 4 and 5 feet at the east end of the lake. A Friez, weekly recording, combined air and distance thermograph with a bourbon tube for air temperature, and an extra sensitive grid bulb with 20 feet of capillary tubing for water temperature was used in 1940 and 1941, at the east end of the lake, inshore from the maximum and minimum thermometers (Plate 2). The thermograph recorded the water temperature at a depth of 18 inches, which was considered to be about the average depth of most fish nests in Deep Lake. Because of the high banks surrounding the lake, the sun's rays seldom reached the thermometers placed on the east side of the lake until 9:00 or 10:00 a.m. Similarly, the sun usually disappeared behind the trees on the west bank between 5:30 and 6:30 p.m.

A water level gauge was installed each year except in 1938. The gauge consisted of a heavy yardstick and was fastened to a steel fence post in 1939 and to the thermograph house in 1940 and 1941. Water level readings were made each day during the spawning season.

Nests were usually located by noting the presence of the guarding male, a recently cleaned area or nest depression. The species to which the nest belonged could usually be identified positively only when the guarding male was present in the case of bluegills and pumpkinseeds. Largemouth bass and rock bass nests could usually be told apart when eggs or fry were present. The characteristics of the nest are not specifically associated with the species occupying it. Some nests of the rock bass, largemouth bass and pumpkinseed were identical as to size, shape, depth of water and nature of the bottom deposits. Certain individuals of those species studied constructed well defined nests, while others occupied poorly defined nests. Fish of one species sometimes appropriated nests

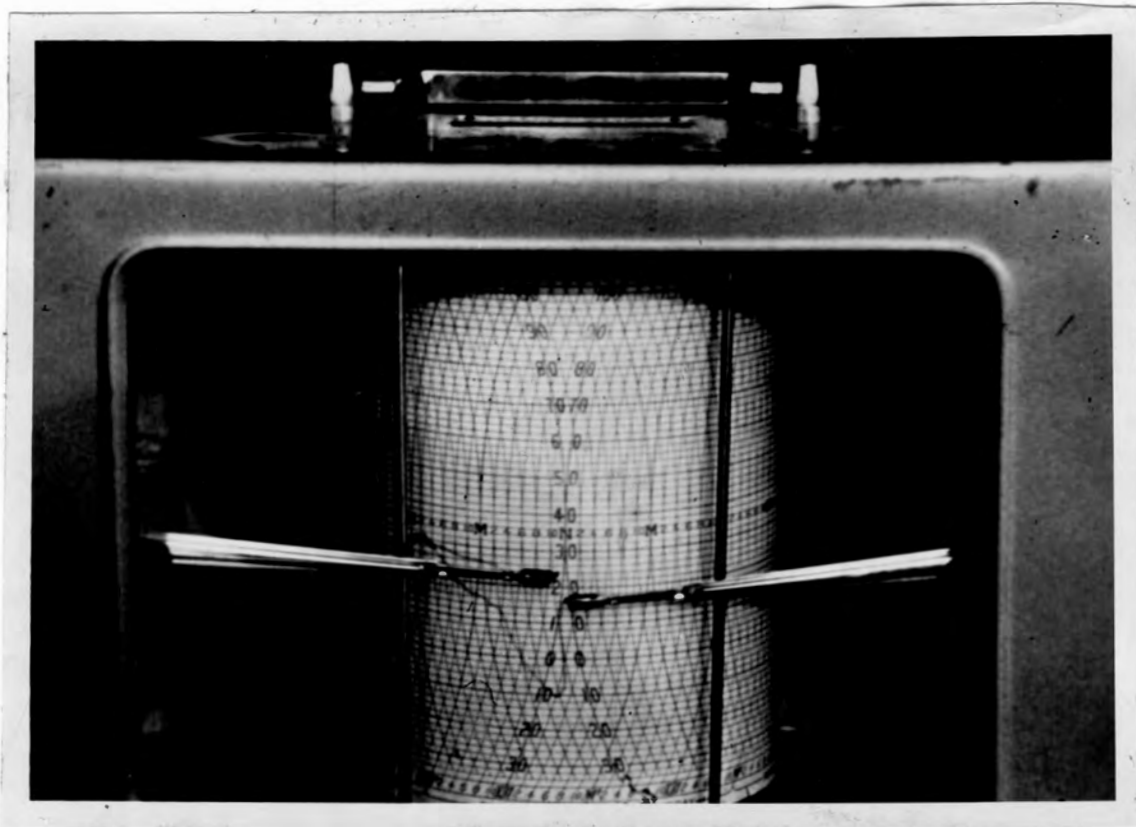


Plate 2.--Friez weekly recording, air and water thermograph used in Deep Lake.

built by individuals of another species. This intrusion, except in several cases which will be explained later, took place only after the original owner had finished spawning and the fry and adults had left. For example, largemouth bass used rock bass nests. Rock bass used pumpkinseed and largemouth bass nests. Pumpkinseeds appropriated the nests of bluegills and vice versa. Some individual nests of the bluegill and pumpkinseed were also used several times during one season.

All spawning beds actually containing eggs or fry were marked and counted. The nests were marked to prevent any possible duplication of counts. It was found that many nests were constructed that were never used for spawning. Some nests were built and abandoned before being put to use, and others were occupied by several successive tenants; therefore it was necessary to make daily observations and to mark and count only those nests actually containing eggs for fry. In 1938, the spawning beds were marked with colored glass marbles as follows: blue - largemouth bass; green - rock bass; yellow and red - pumpkinseed sunfish; blue - bluegill.^{1/} Some fish objected to the introduction of "foreign objects" into their nests. Rock bass, at times, carried the marbles from one to several feet from the nest. About half of the guarding males of this species (estimated) immediately moved the marbles from their nests. On one occasion the writer unsuccessfully tried to introduce a marble into one rock bass nest 3 times. In such cases the marble was placed beside the nest. Some bluegills and sunfish buried the marbles while fanning their nests.

In 1939, 1940 and 1941, three and four-foot lengths of one-half inch dowel were used in place of marbles for marking all nests. This eliminated

^{1/} In 1938 the largemouth bass had completed their spawning activities before the bluegills started to spawn.

the difficulty encountered with the use of marbles. One end of the dowel sticks was sharpened. The unsharpened end of some of the dowel sticks were painted to different colors to distinguish nests of the various species. The following colors were used: unpainted - largemouth bass and bluegills; blue - rock bass; red - pumpkinseed. When marking a nest with a dowel, the stick was always placed at the shoreward edge of the nest. At times some nest-guarding fish objected to these sticks and would bunt them a few times shortly after they were introduced. Some bluegill colonies composed of a large number of nests appeared from the distance as a young forest (Plate 3) because of the close proximity of the nests and the large numbers of sticks used. There were several advantages in using dowel sticks. Dates of spawning could be written on a stick which would enable the observer to obtain definite information on the time required for hatching, and the number of days that the fry remained on the nest after hatching. Another advantage obtained from the use of dowel pins was that individual nests and colonies of nests could be spotted from a distance. A numbered, metal tag, nailed in the unsharpened end of a dowel stick was used to mark each bluegill colony. Whenever there was any doubt as to the presence of eggs or fry on any nest a sample of the nest contents was obtained through the use of a glass tube (Plate 4).

Measurements of nest dimensions and depth of water were made for each nest with a special measuring rod (Plate 5). This measuring device consisted of two pieces of 1- by 2-inch oak. The longer of the two pieces was six feet in length and was hinged to the shorter three-foot stick. A piece of lead was fastened to the end opposite the hinge on the shorter stick to prevent this part of the measuring rod from floating when measuring the nest diameters. The measuring rod was painted white with black marks at intervals of six inches.

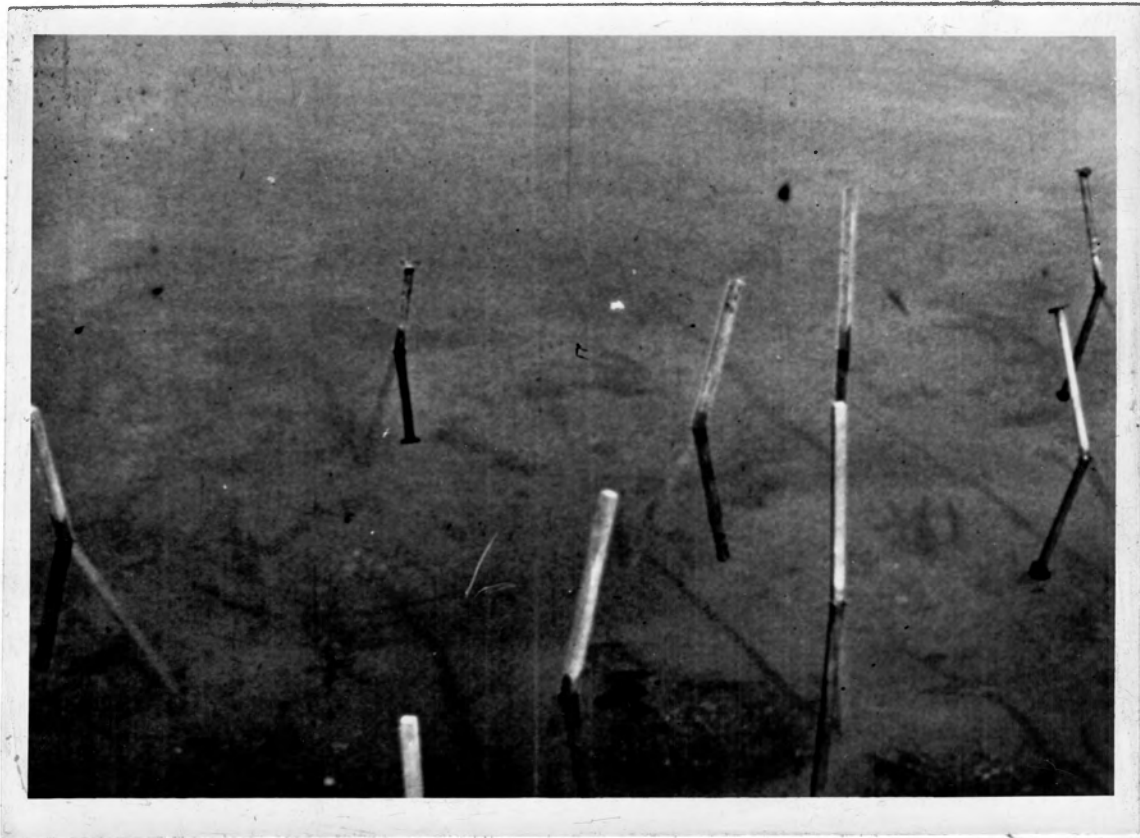


Plate 3.--Colony of bluegill nests showing the dowel sticks that were used for marking those nests that contained eggs or fry.



Plate 4.--Demonstrating the use of the glass tube used in sampling the contents of centrarchid nests in Deep Lake.



Plate 5.--Demonstrating the rod used for measuring the depth and diameter of centrarchid nests in Deep Lake.

The composition of the bottom was noted for each nest. Any shelter or cover such as logs, rocks or aquatic plants near any nest was also recorded at the time observations were made.

Fish were collected by angling, seines and fyke nets at intervals during each season. Some of the fish collected were fin-clipped or tagged, others were preserved as specimens for egg counts, or for parasite examination. Scale samples and measurements were obtained from a random sample of the fish collected. Methods of jaw-tagging and fin-clipping were the same as described by Shetter (1936).

All of the fish that were taken from Deep Lake for study were brought to the laboratory. Ovaries removed from the females were placed in 10 percent formalin. Because so much detail and analysis are required for a thorough understanding of the methods used in counting the eggs, the description of the methods used will be discussed under the section on egg counts.

The various phases of this study are presented in the following order:

- I. Observations on the spawning habits.
 - A. The spawning act
 - B. Type of bottom material used in nest construction.
 - C. Depth of water in which nests are found. Diameter of nests.
 - D. Number of nests used for spawning by each species.
 - E. Multiple use of nests.
 - F. Duration of the spawning season.
- II. Growth history of the ova and the number of eggs per female.
- III. Number of fry per nest.
- IV. Production and survival of fry.

In a study of this kind, there is bound to be some overlap between the various subdivisions; however, an effort has been made to hold this to the minimum necessary to clarify each section. Reference is frequently made in this report to other species of centrarchids not found in Deep Lake. Since all centrarchids are so closely related and because they have similar spawning habits, we feel justified in making comparisons between the various species.

The Spawning Act

The details of the spawning act of certain centrarchids have been studied in detail by many previous investigators, notably by Reighard (1906), Evermann and Clark (1920), Adams and Hankinson (1928), Breder (1936), and will not be discussed in detail in this paper because our findings correspond with those made by other workers. In brief, the male constructs the nest. During the period of actual spawning the male and female lie side by side with their ventral surfaces touching, and slowly circle the nest. The male remains in a vertical position while the female reclines to one side and is sometimes in a horizontal position. While circling about the nest the female is usually in the center with the male in the outside position. After spawning the female leaves the nest and does not return. The male takes up a position over the nest, setting up a fanning motion and carefully looks after the eggs. The male chases away all intruders and at times, both night and day, is kept extremely busy chasing away the hordes of smaller fish attempting to sneak in and eat the eggs or fry.

The following miscellaneous notes and anomalies, which should be of interest, were noted during the four-year period of investigation on Deep Lake.

Nest construction: On several occasions small (6 - 8-inch) largemouth bass were observed making nests, but eggs were never found on these nests. Mr. Claude Lydell, Supervisor of Fisheries Operations, Comstock Park Hatchery, Michigan, has told the writer that small-sized smallmouth bass often build nests that are never used for spawning.

At certain periods in June and July of 1939 and 1940, some fish of all of the species present in Deep Lake were found dead along the shores of the lake. Fish of all sizes and of both sexes were represented. On at least one occasion this mortality followed a period of intensive nest building and spawning. It is well known that many male fish injure themselves during the process of nest construction when the anal and caudal fins are often eroded, especially by those fish making nests on gravel bottom. The writer has observed many fish whose anal fins have been worn down to a "bloody stump." Fighting among nest building males has never been observed to reach serious proportions at Deep Lake and any mortality from this cause can be discounted entirely. A great many of the dead fish found at Deep Lake have been examined by the writer and others. In no one case has the exact cause of death been determined. Injuries received in spawning, disease, malnutrition, and fluctuations in temperature (water temperatures seldom fluctuated more than several degrees in one 24-hour period) could not have been wholly responsible at any time. Very few of the male fish that were found dead had badly eroded fins. In fact, the writer has found male fish apparently in good health and extremely active with fins in worse shape than some of the dead fish. The presence of both males and females among the dead fish would tend to eliminate to some extent the "egg-bound" factor as the cause of death of females. Examination of the ovaries of many females showed that the fish were in various

stages of maturity--some females were "green" and others were about ready to spawn. It is admitted that all fish, and especially the male centrarchids, undergo a period of stress and strain during the period of nest construction, spawning, and guarding of the nest. The violent efforts of the males in keeping hordes of small fish from robbing the nest of its eggs or fry may sometimes keep up for hours. Probably this overexertion plus a combination of other factors may be responsible for at least a part of the mortality. That this was not always the case is proven by the fact that the mortality was sporadic during one or two seasons and was not present in the lake every year. In this regard it would be well to mention that members of the staff of the Institute for Fisheries Research have been called upon to check similar mortalities during June and July on Michigan lakes almost every year. The exact cause of death has never been ascertained in any instance.

Bluegills have been observed, on many occasions, building and cleaning nests at night. However, most of the nest building and cleaning was done during the day by the bluegill. Largemouth bass, pumpkinseed, and rock bass did all of their work during the day.

Spawning act: All of the species studied spawned only during the day.

No actual spawning was ever observed at night. On the night of May 21, 1941, Dr. K. E. Goellner and the writer made observations on the habits of Deep Lake fish at night. Two largemouth bass were observed occupying the same nest. As both fish would leave the nest when we approached to within 20 feet of the nest with our light, we were unable to determine the sex of either fish, or whether or not they were actually spawning. When the observers would leave the immediate vicinity, these two bass would again occupy the nest. No eggs were found on the nest during the hour or

more that we were there that night. This nest contained eggs on the following morning at 8:00 a.m. when the writer again returned to the lake. Although this does not definitely prove that these largemouth bass spawned during the night, it is possible to entertain such a thought.

During actual spawning the males and females would remain on the nest except for the occasional forays made by the male to chase intruders away. When the observer would approach a nest where spawning was underway, the spawners would usually leave the nest. This was especially true of bluegills and largemouth bass. The majority of the spawning pairs of rock bass and pumpkinseeds, though, were quite unconcerned about nearby movements of a boat and would usually continue spawning. Many times the writer has anchored his boat beside a nest and has looked directly down on spawning rock bass and pumpkinseed sunfish. All four species have been observed in the act of spawning. (Deep Lake was especially well suited for this because of the narrow shoal and the high banks nearby where the observations could be made in relative comfort, sitting on the ground in the shade of a tree). The male bluegill was always the first to leave the nest upon the approach of the observer. The female bluegill that has been deserted suddenly by the male will sometimes continue to circle the nest several times in the characteristic horizontal position assumed in spawning, or will remain motionless over the nest until the male returns. The female is also frightened away from the nest at times.

Actual spawning has been observed in Deep Lake in the daytime when the waves were very high and the water so rough that the nest could hardly be seen. These observations disprove the theory that wind action plays a part in the selection of a nesting site.

On June 10, 1939, bluegills were observed spawning on a dark, cloudy day. A huge black thunderhead was over the lake and it was as dark outside as it usually is at dusk.

On June 28, 1940, bluegills were observed cleaning nests and spawning while it was raining and a strong wind was blowing. The water in Deep Lake was murky from the rain and wind. Pumpkinseed sunfish and rock bass were also observed spawning. On June 29, 1940, male bluegills, pumpkinseeds, and rock bass were still guarding their nests despite the fact that it was still cloudy, windy, and the water was roiled. It also sprinkled several times during the day. Some fish were observed spawning at different times of the day. On June 30, bluegills were observed spawning during a rain storm.

During the actual spawning act, the spawners have been observed circling the nest in both a clockwise and counter clockwise direction. The male fish always occupied the outside position.

On two different occasions the writer has observed three male bluegills spawning with one female at the same time. Another time, five male bluegills (4-7 inches in length) were observed spawning with one female (about 9 or 10 inches in length) at the same time. In the above examples all of the males remained in an upright (vertical) position, with their sides pressed closely together.

The writer has spent many hours watching fish of the various species spawning, but never more than one female was ever observed spawning in one nest at one time. On several occasions small females were observed spawning in certain nests. Later observations have indicated that there were more eggs in these nests than could normally have been deposited by such small females. This may indicate that perhaps the eggs of more than one

female are actually deposited in one nest. In late afternoon on May 18, 1941, the writer found one large male largemouth bass cleaning a nest in a bed of chara. Two large female bass were also nearby. The females would barely move and every now and then one female would swim over to the nest or out in deeper water about ten feet from the nest where she would swim back and forth, parallel to shore. The male would move out of the nest occasionally to one of the females. Sometimes he would return again to the nest, but at other times he would bite the tail of one female or swim under the female and touch her abdomen. These fish were not observed spawning. The following morning, eggs were found on the nest and notes taken at the time indicate that the writer had never before observed so many eggs on one bass nest. Probably both females deposited their eggs in this one nest.

Lamkin (1900) states that largemouth bass spawn several times during the season. He found one large male that fathered eight different nests of eggs from April 9 to July 4, at one time taking care of a large brood of fry and a nest of eggs at the same time.

The writer has never actually observed more than one female spawning in one nest at one time, or evidence that more than one female will spawn with one male. Lamkin (1900) observed 2 female largemouth bass on a nest with one male on several occasions. Reighard (1906) cites evidence that female smallmouth bass may spawn in more than one nest. Also that a male smallmouth bass may receive into his nest two females in succession. He also states that male largemouth bass habitually receives more than one female into his nest or receives the same female a second time after a considerable interval, as shown by presence in nests of eggs recently laid and some 48 hours old.

Breder (1936) declares that in the pumpkinseed one female may visit many nests. He cites one example where every nest in a small colony (pumpkinseeds) was visited by one female. Breder also states that one male and three female pumpkinseeds were placed in an aquarium. The male constructed a nest and spawned repeatedly with one or another of the females. At one time the male was spawning with two females at the same time. The male was in the middle of the group with one female on either side, reclined at nearly a 90 degree angle and all three were headed in the same direction and all were apparently taking an active part in the spawning.

Ingram and Odum (1941) mention one case in which two female pumpkinseeds spawned with one male in immediate succession.

Observations indicated that numerous bluegills, not actually participating in the spawning, were to be found in the immediate vicinity of the nests in almost every instance when other bluegills were spawning. These fish would be over and above the nests or they might be swimming leisurely and lazily about a few inches below the surface of the water just out from the nests. On one day a school of at least 25 bluegills of all sizes was observed hovering over and just out from the nests in Colony No. 17, where five pair of bluegills were spawning on five different nests. At times perhaps as many as one hundred fish were to be found in these schools near the spawning beds. Mature males and females of all sizes were represented in these schools of fish because many were captured with hook and line. At various times the writer would capture as many as twenty fish from one school. Examination revealed that all of the males and some of the females were nearly "ripe." (Abdomens of "ripe" or nearly "ripe" bluegills are distended with spawn. Milt can be expressed from male fish by exerting

gentle pressure with thumb and forefinger near region of the vent. "Ripe" male bluegills are always darker in color than the female and are usually a deep bronze color on the sides and ventral surface just behind the head. The male fish also (usually) have a larger jet-black opercular flap). On July 17, 1940, a pair of bluegills was spawning in a single nest (not a colony). About 30 other bluegills that ranged in length from 3 to 9 inches were hovering about the nest. In 1941, the writer noted similar concentrations of bluegills over or near all colonies or nests in which bluegills were spawning. In all cases these fish would stay away from the spawning fish except for an occasional male fish which would dash over to a nest and attempt to chase the spawning male away. Just why these surplus male and female bluegills should be hanging around spawning fish and yet not take any immediate part in the spawning activities is not known. Perhaps this may explain, at least in part, the fact that more than one female will spawn in one nest. As soon as one female finishes spawning, the male may venture out and select another. No explanation can be offered to explain the presence of ripe males in this group. It is extremely odd that they did not construct nests of their own. This is certainly an interesting feature of bluegill spawning and merits further study.

Males of all sizes and females of all sizes were observed spawning on the same day during most of the spawning season. Therefore, ^{the} theory that has been propounded by some fishery workers that the young fish spawn late in the season and the older ones spawn early in the season is probably not valid for the species studied at Deep Lake.

The actual deposition of eggs by female pumpkinseeds was observed on several different occasions when the writer was able to look directly down

(distance of about 2 feet) on spawning fish. The actual deposition of eggs would occur at intervals, and in all cases observed, while the female was in a horizontal position.

During the spawning act the male was frequently forced to leave the nest in order to chase other fish away. The female would usually remain in the nest until the male returned. At times male bluegills would be interrupted in this manner every few seconds. On one occasion the male pumpkinseed seemed to have trouble keeping a female in the nest. The male and female, in typical spawning position, would make several circuits of the nest and then the female would attempt to run away. The male would head her off by placing his body in front of her, his ear flaps extended and mouth open, or else he would bite her caudal fin and chase her back in the nest.

Pumpkinseed sunfish have been observed on many occasions spawning in a bluegill colony at the same time that bluegills were spawning. It would be fairly easy for a female bluegill to spawn with the male pumpkinseed at this time. On two occasions the writer has definitely observed bluegills spawning with pumpkinseeds. While approaching a bluegill colony on May 22, 1941, a pair of bluegills was observed spawning. As the writer approached the colony, the male bluegill left the nest. A large male pumpkinseed immediately darted into the nest and continued spawning with the female for several minutes until something frightened the spawning fish and they left the nest. On May 23, 1941, a male bluegill was observed spawning with a female pumpkinseed.

Actions of the guarding male: The male fish of the species studied guard the nests, eggs, and fry (Plate 6). The largemouth bass is the only species that guards the young fish after they leave the nest. With but few



Plate 6.--Male pumpkinseed sunfish chasing intruders away from nest.

exceptions, the male bluegills would leave the nest during the day when the observer would approach. This procedure was reversed at night when the majority of the fish would stay on their nests. Most male rock bass and pumpkinseed sunfish would remain on their nests both day or night when the observer approached. Some males of these two species would bunt the glass tubes used to collect fry when it would be inserted by the observer. Male largemouth bass were never observed to remain on their nests when the observer would approach in the daytime, and they would seldom remain there more than a few seconds after the approach of the observer at night. Most largemouth bass males would swim back and forth about 15 to 20 feet from their nests until the observer left. On July 8, 1938, a male bluegill remained on his nest while the writer collected the fry. This fish very obligingly kept other fish away from the nest and would bunt the glass tube occasionally. This same bluegill was guarding the same nest on July 16, when the writer again collected all of the fry from this nest. During the four-year period of this study, three other male bluegills also remained on their nests while fry were collected.

Only once during the four-year period of this investigation did a largemouth bass male remain fairly close to the nest while the fry were being collected (observed by Dr. R. W. Eschmeyer). This male was about ten inches in length and would chase small bluegills and sunfish away when they approached the nest.

At various times bluegill-pumpkinseed hybrids were observed guarding nests at Deep Lake. The first record was on July 13, 1939, when a huge hybrid was positively identified guarding a nest in a bluegill colony. On July 25, 1939, a hybrid was found guarding a nest in a bluegill colony. Some of the fry were collected from this nest and were taken

to the Drayton Plains Hatchery where they were placed in an experimental pond that contained no other fish. In October, this experimental pond was drained and the several hundred fish that remained were identified by Dr. Carl L. Hubbs as bluegills. Apparently the hybrid had chased the guarding male bluegill away and had taken over the protection of the nest. Several other hybrids were found guarding bluegill nests at other times. In one nest guarded by a hybrid, all of the eggs were dead and the bottom of the nest was a cottony-mass of fungus. A hybrid on another nest was not too faithful a guardian and would stray from the nest occasionally, allowing small fish to come in and eat the eggs. One nest in which bluegills were observed spawning on August 5, was guarded by a hybrid on August 6. In 1941, another nest in which bluegills were observed spawning was occupied by a pumpkinseed sunfish the next day. Observations revealed that the pumpkinseed male would conscientiously chase all intruders away and when all was peaceful would leisurely eat the eggs. This particular nest was watched closely for over an hour. At the end of this period the male pumpkinseed left the nest and did not return. Almost all of the eggs were eaten by this time. The male bluegill did not return.

On June 20, 1941, a medium-sized largemouth bass was found guarding two nests. The one nest was located in 39 inches of water and was spawned in on June 15. Eggs were deposited in the other nest located in 15 inches of water on June 20. These two nests were only 5 feet apart. On June 20, the deeper nest contained bass fry. The male bass would go from one nest to the other. On June 21, small bluegills and pumpkinseeds were observed eating the eggs in the nest in shallow water while the male was fanning the fry on the other nest. Before this day ended, all of the eggs in the

nest were eaten and the male fish began to spend more time on the nest in deeper water. On June 22, the male was not observed visiting the nest in shallow water.

Some bluegill nests containing eggs or fry were found in Deep Lake from June 1 until about the first of August in 1941. Males were guarding these nests despite the fact that there were periods of high wind, cloudiness, rain, etc. Apparently weather conditions and changes in water temperature do not cause the guarding male to leave the nest, once spawning has occurred, until the fry have left the nest. One male bluegill was observed guarding a nest of eggs when silt and clay were washed in the lake during sudden downpour of rain. For an entire day the water over this nest was so muddy that the fish could just barely be seen. After the water had cleared the following day, the male was still on his nest. Approximately one-quarter of an inch of fine silt and clay had been deposited over the entire colony of nests, but about 6 inches of the very center of this nest was still quite clean and fry were present. This shows that the male is capable of keeping the nest clean. It was not determined whether any mortality occurred, but many live fry were still present in this nest four days after the storm.

Rock bass and pumpkinseed sunfish could be caught on hook and line while guarding their nests. Bluegills could also be taken in this manner, but not as readily as rock bass and pumpkinseeds. Largemouth bass could seldom be caught on hook and line while guarding the nest. The writer and various co-workers tried to catch bass on at least forty different nests, but failed. Only one nest-guarding male largemouth bass was caught at Deep Lake as far as the writer knows. The writer and two other people spent at least an hour before finally hooking this fish. All sorts of artificial

lures and natural bait were cast over the nest or were pulled through the nest. The fish finally took a huge gob of worms. This bass was returned to his nest after measurements were taken. A number of fish of the different species were removed from their nests by hook and line, placed in a pail of water and taken to shore where they were photographed. These fish were always returned to their own nests. In only one instance did the male refuse to stay on his nest after being returned to it. This particular fish, a pumpkinseed sunfish, wandered away from the nest and never did return.

On May 31, 1938, Dr. R. W. Eschmeyer and the writer tried out a method of killing guarding fish by using rotenone (derris root). The powdered derris was mixed into a thick dough-paste. This paste was molded into a ball about one-half inch in diameter which was dropped in a rock bass nest. In the first nest in which it was tried, the male grabbed the derris in his mouth in an attempt to remove it from the nest. When he tried to eject it from his mouth, the pellet broke up. A good deal of the derris passed through the gills and a dense brown cloud of this material settled over the bottom of the nest. During this time the rock bass remained in this "cloud" of derris. The fish showed distress in two and a half minutes (checked, not estimated) and broke the surface of the water in three minutes and then left the nest. In five minutes the fish turned on one side and then swam away, very unsteady and wobbling. The fish was last seen about fifty feet from the nest and did not return. Derris was also placed in three other rock bass nests and in two pumpkinseed nests. None of these other fish grabbed the derris. All left their nests, however, but all but one fish (a pumpkinseed) returned in about an hour. While the

fish were gone, small fish were active in the nests and undoubtedly ate the eggs. On June 1, the two sunfish nests were still occupied, but we were not certain whether the same fish was on the one nest. All four rock bass nests were vacant and all eggs had been eaten. Whether the male rock bass deserted their nests because the eggs had been eaten or whether the fish had been killed is not known. This little experiment was not continued or repeated and is mentioned only because of the interest that it may evoke. It was thought that some such method could be employed to eliminate spawning fish in lakes that were over-crowded.

Some nests containing eggs and fry are deserted by the guarding male. No reason for this can be advanced. The eggs of many of these nests were covered with fungus, but whether this occurred before the nest was deserted is not known. Some nests of all of the species studied were found deserted and the desertion took place at all times during the spawning period, every year. The writer has observed nests in which all of the eggs or fry were eaten by other fish and yet the male has continued to guard the nest just as jealously as if eggs or fry were still present.

In 1940 it was decided that a pen should be constructed to conduct the following bluegill experiments: (1) To determine if bluegills would spawn if confined in a small pen; (2) if male fish spawn more than once during one spawning season; (3) if a female will deposit all of her mature eggs during one spawning and if a female will spawn more than once during a season. This pen was installed on the east side of Deep Lake. Inch mesh, poultry wire was used. The shore end of the pen was left open. The sides were about 17 feet long and the width varied from 11 feet on the lake end to 15 feet at the shore end. The depth of water varied from

0 to 3 feet. The bottom materials were sand, gravel, leaves, and sticks. This area was similar to that used for spawning by bluegills in other parts of the lake. In 1941, five such pens were constructed in Deep Lake.

In 1940, the pen was completed on June 6, and two males and one female were placed in the pen on June 12. No spawning activity was noted until July 5, when the males started to clean separate nests, in opposite corners of the pen. Spawning took place sometime on July 7, and eggs were present in the nest located in the north corner of the pen. Neither eggs nor fry were present on this nest on July 9. They were probably eaten by small fish. The female bluegill was removed from the pen on July 9, and was saved for laboratory examination. Another female was placed in the pen on July 10. On July 16, the two males started to prepare nests again. The nest in the south corner of the pen that was first prepared on July 5 was cleaned again. The nest in the north corner which was used for spawning before was left alone and a new nest was prepared which was located about half way between the other two. Both male fish were of about the same size and appearance; therefore it was impossible for the writer to distinguish between the two. It is assumed that the male fish that spawned on July 7 is the one that constructed the new nest on July 16, and the male that did not spawn just cleaned his old nest. Eggs were found in the south nest on July 21. All of the fry were collected from this nest.

In 1941, only two nests were used for spawning by the bluegills in all five pens. A great deal of trouble was experienced in 1941 in keeping the fish in the pens alive. At least one male died in each pen during the spawning season, and several of the females also died.

The following results were obtained from the experiments conducted in the pens:

1. Bluegills will spawn, even though confined in a small screen enclosure.
2. Male bluegills will build more than one nest in one spawning season. Presumably, males will also spawn more than once; otherwise they would not build more than one nest.
3. The information obtained on eggs and fry will be discussed later.

Types of Bottom Material used
in Nest Construction

The character of the bottom of the shoal area of Deep Lake varies in different parts of the lake, but most of the bottom types commonly found in lakes are present. The various types are as follows:

1. Inorganic soils.--Almost three-fourths of the shoal area of Deep Lake is composed of sand (Figure 2). Gravel is associated with the sand in certain areas, and varies from a few scattered pebbles to spots containing almost pure gravel. Some rubble and rock are to be found, but their presence is extremely spotty. Clay and silt from surface run-off of surrounding country is also present as a top coating over the sand in several places.

2. Organic soils.--The remaining quarter of the shoal area is composed of organic soils. All stages in the decomposition of plant life are present from accumulations of undecayed plant materials through fibrous peat, pulpy peat, marl (from chara), and muck. All of these organic soils are listed on the map (Figure 1) as fibrous peat because it is the most abundant type and because it was not feasible to attempt to break down the various components into separate units.

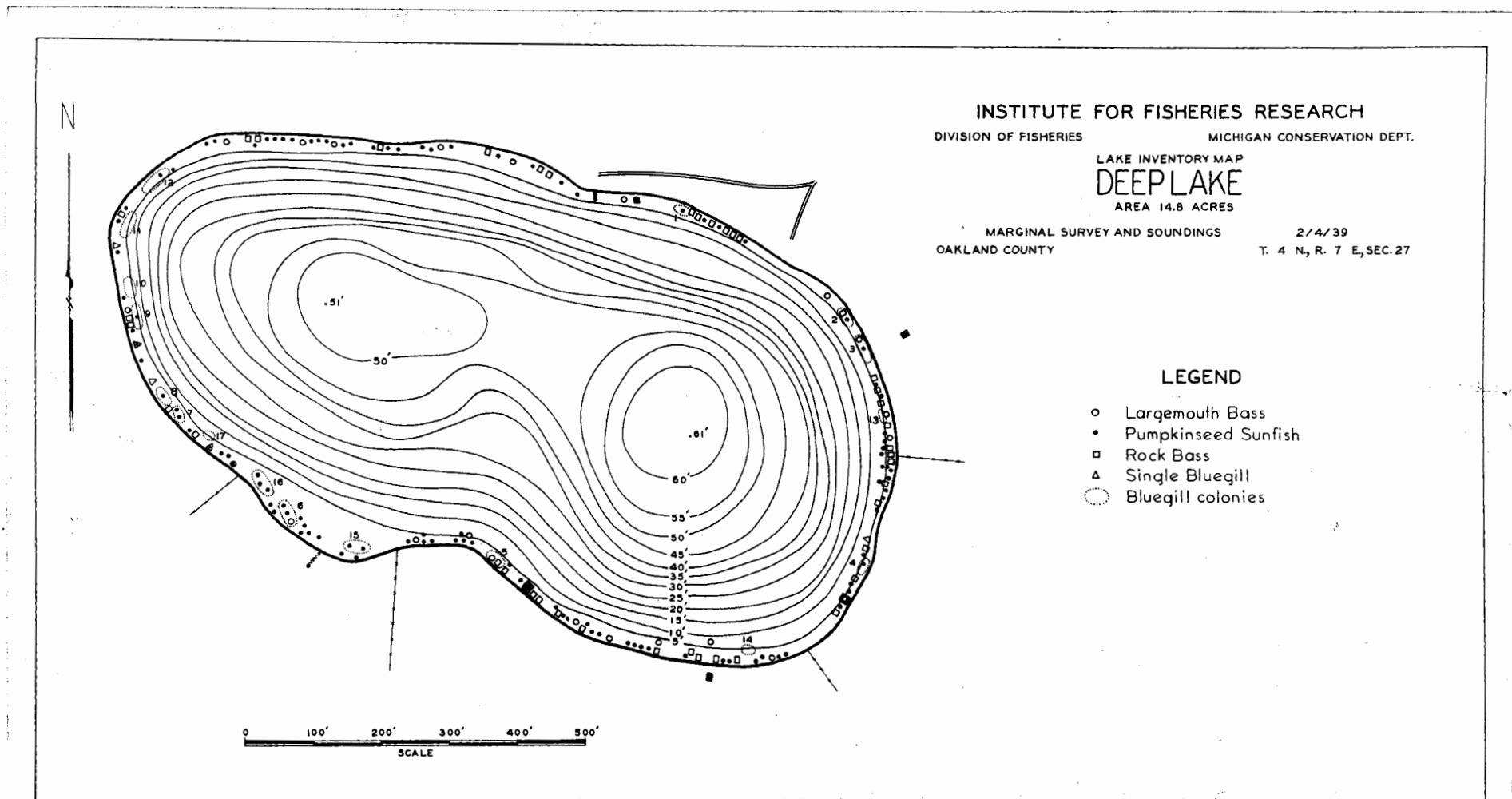


Figure 2.--Map of Deep Lake showing the approximate location of spawning beds of Deep Lake centrarchids during the entire 1939 spawning season.

Sticks, logs, and fallen trees are found about the entire lake. These are sometimes used as shelter for spawning fish or as shelter for the nests. They also form part of the nest or are associated with the nests of some of the species.

Occasionally Chara and Potamogeton were found in the nests of various species. The needle rush (Eleocharis acicularis) and the bushy pondweed (Najas flexilis) were frequently found in the nests of the largemouth bass, rock bass, and pumpkinseed sunfish. These species of fish actually deposited their eggs on these plants. Roots of the various aquatic plants were also used for egg deposition. The black roots of the bulrush and willow tree roots were most frequently used.

The bottom materials listed above were found singly or in combination in all of the nests observed at Deep Lake during the period of this investigation. Usually during the period of nest construction the majority of the finer, more flocculant bottom material was fanned away by the male fish. For example, if a fish was building a nest in muck, all of the loose, finely divided material would be swept away until firm bottom of roots, sticks, leaves, or fiber remained in the bottom of the redd. If roots were used, usually just enough cleaning was done to expose them. Some fish made no more than a pretense at cleaning an area for a nest. In such cases the male would just fan away the ooze that covered the sand. Other examples of this may also be cited. One largemouth bass made no attempt to remove the organic ooze from the chara on which eggs were deposited. A pumpkinseed sunfish about eight inches in length was found guarding a clutch of eggs located on newly-deposited clay (from run-off). Every time this fish sallied forth to chase some intruder away he would raise a cloud of clay and silt.

At Deep Lake, the composition of the bottom of the nest was noted at the time that each largemouth bass, rock bass, pumpkinseed, and single bluegill nest was marked and measured. The bottom material for all of the bluegill nests located in colonies was recorded at intervals throughout the spawning season. Data are available on the composition of the bottom of all bluegill nests used for spawning during the four-year period of this investigation, but only for the last three years for the remaining species. A total of nine major bottom types or combination of bottom types is used in this discussion of the bottom materials used in nest construction, as follows:

1. Sand
2. Sand and gravel
3. Sand, gravel, and green plants
4. Sand, gravel, and roots
5. Peat
6. Peat, sand, and gravel
7. Peat and roots
8. Peat and green plants
9. Peat, sand, and roots.

One aspect of the study that was most striking was the variation in nest building. The characteristics of the nest are not specifically associated with the species occupying it. Largemouth bass, rock bass, and pumpkinseed nests varied from almost no nest at all to very elaborate structures. Some of the nests, both elaborate and poorly defined, of these three species were almost identical as to size, shape, type of bottom, and varied decidedly in depth of water, kind of bottom, size, etc.

All of the species studied preferred some combination of sand or gravel for nesting, but all would use a great variety of bottom types. This indicates that the presence of sand or gravel is not necessary for successful nesting of any of the four species studied. Apparently all that is needed is a firm material in the nest for the deposition of the eggs. The eggs of these four species are slightly adhesive, and stick to anything that they come in contact with.

The pumpkinseed sunfish was not very selective as to the type of bottom used for nest construction at Deep Lake (Table 2, Figure 3). The pumpkinseed used all of the major types and combinations of bottom types found in the lake. The nests occurred singly, in groups of 2 to 6, and occasionally nests were found within a bluegill colony. The majority of the nests were clearly defined, but occasional nests were used for spawning that were located only by the presence of the guarding male. Usually nests constructed on sand bottom were approximately circular in outline and saucer-shaped. Saucer-shaped nests were sometimes constructed that had a clump of roots present in some part of the nest. In such nests the eggs were deposited on the roots and the bulk of the nest was therefore not used. Other fish made nests on sand where the only cleaning of the nest consisted of fanning off the ooze. Nests located in peat bottom were usually, but not always, larger than those located in sand bottom. The largest pumpkinseed nest found in Deep Lake was a huge crater-like nest located in sand bottom. At times pumpkinseed sunfish, and other species appropriated the nests of other species. These nests would usually be revamped somewhat by the new occupant, regardless of the type of bottom in which the nest was located.

Table 2.--The number and percentage of the nests of each species found in each bottom type or combination of bottom type in Deep Lake, 1938-1941.

	Sand and gravel	Sand, gravel, and roots	Sand, gravel, and green plants	Sand	Peat, sand, and gravel	Peat, sand, and roots	Peat and roots	Peat and green plants	Peat	Total number of nests
Largemouth bass										
1938	↓
1939	2	17	2	1	1	23
1940	6	22	12	8	2	5	1	56
1941	2	16	10	6	1	5	...	40
Total	10	55	24	15	3	...	1	10	1	119
Percentage	8.4	46.2	20.2	12.6	2.5	...	0.8	8.4	0.8	...
Rock bass										
1938	↓
1939	7	38	2	1	1	49
1940	3	15	9	1	28
1941	2	32	31	1	1	67
Total	12	85	42	3	2	144
Percentage	8.3	59.0	29.2	2.1	1.4
Pumpkinseed										
1938	↓
1939	28	48	...	15	6	9	8	...	7	121
1940	25	70	16	16	5	2	2	2	3	141
1941	9	42	12	6	5	4	10	8	1	97
Total	62	160	28	37	16	15	20	10	11	359
Percentage	17.2	44.5	7.8	10.3	4.5	4.2	5.6	2.8	3.1	...
Bluegill										
1938	166 ²	107	96	369
1939	270	61	290	621
1940	421	79	179	679
1941	289	77	261	627
Total	1,146	324	826	2,296
Percentage	49.9	14.1	36.0	...

↓ Bottom types not recorded on all nests in 1938

↕ Bottom type consists of sand and/or gravel for each year.

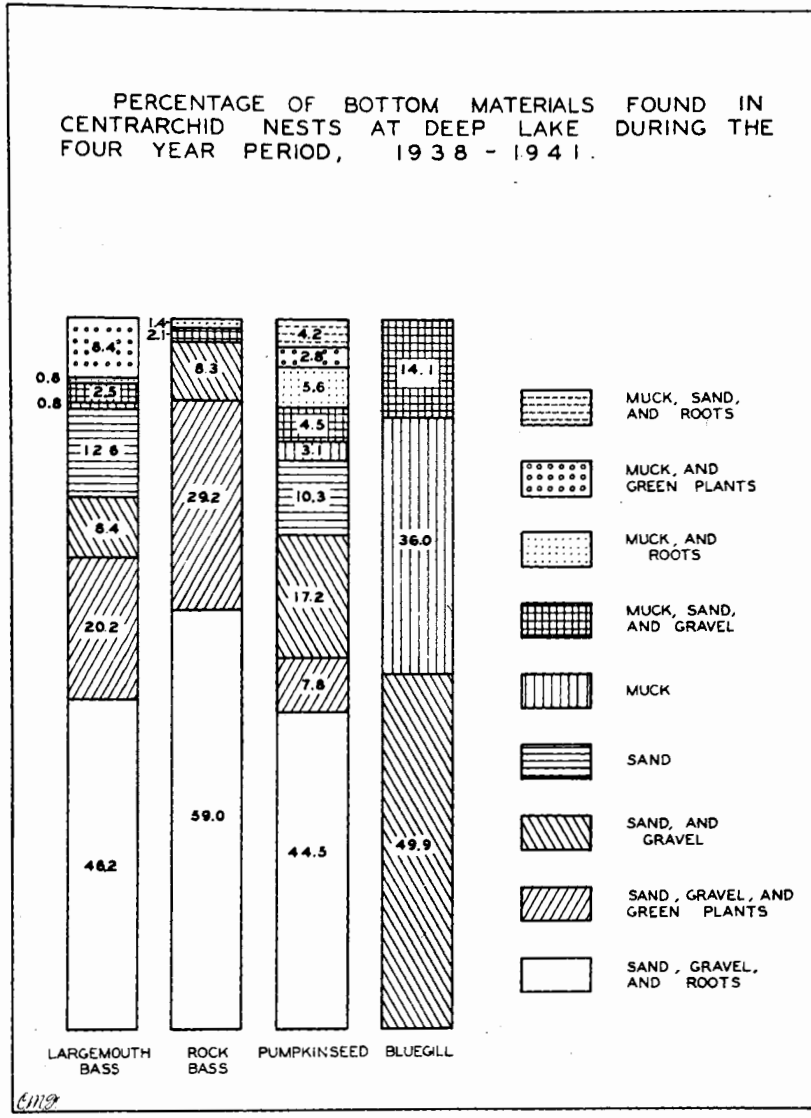


Figure 3.--Percentage of bottom materials found in centrarchid nests at Deep Lake.

The largemouth bass and rock bass were just a little more discriminating as to the type of bottom used for nesting. These species used all of the major types and combination of bottom types found in Deep Lake, although only a few nests were found in peat bottom. In general, most of the nests of these two species were poorly defined, but an occasional nest was constructed that was well defined and saucer-shaped. These species preferred to deposit their eggs on roots or aquatic plants and therefore did not require an elaborate, well defined nest.

The bluegill was perhaps the most selective as to the type of bottom used in nest construction. Almost all bluegill nests were well-hollowed out and clearly defined. Those nests located on sand and/or gravel bottom were approximately circular in outline and all were of about the same diameter. In fact, in no other species were the nests so nearly alike as to size, shape, and type of bottom material. The nests located in peat bottom were usually considerably larger than those on sand-gravel, and these nests were not always circular in outline. Bluegill nests were found in most of the common types of bottom.

All combinations of bottom material associated with sand and gravel were used more frequently by all of the species studied (Table 3) than were other bottom materials. The rock bass seldom nested on peat bottom, apparently preferring to deposit eggs on roots or green plants found on sand or gravel bottom. The rock bass and largemouth bass were similar in this respect. Bluegills nested in peat more often than any of the other species. Also, the bluegill was the only species that never picked a site where roots and green plants were present. On occasion a few roots might be found in a bluegill nest, but the eggs were not distributed on the

Table 3.--Percentage frequency of nests of Deep Lake fishes found in the major types of bottom and combinations of bottom types from 1938 through the 1941 spawning season.

Bottom types	Largemouth bass	Rock bass	Pumpkinseed	Bluegill
Sand and/or gravel	21.0	10.4	27.5	49.9
Peat	0.8	...	3.1	36.0
All combinations with sand and/or gravel	89.9	98.6	88.5	64.0
All combinations with peat	12.5	1.4	20.2	50.1
All combinations with roots or green plants	75.6	89.6	64.9	...

roots alone but were scattered over the entire bottom of the nest. In the other species that used roots or green plants for nesting, the majority, if not all, of the eggs were attached to the roots or green plants.

It is apparent from the data presented above and from an examination of Tables 2 and 3 that all of the species studied used similar types of bottom material for their nests. This overlap in the nesting grounds between the species was not serious enough to limit the spawning of any one species as will be shown later when the distribution of the nests is discussed.

The findings described above agree with observations that the writer has made on many other lakes in Michigan. They are also in harmony with the facts recorded in the literature which are summarized below:

1. Largemouth bass.--Nests containing roots or eggs deposited on roots - Lamkin (1900), Lydell (1903), Hankinson (1908), Richardson (1913), and Reighard (1915). Nests in gravel (fine and coarse) - Hubbs (1919), and Evermann and Clark (1920). Nests in sand - Carr (1942). Nests in silt - Carr (1942). Reighard (1906) states that largemouth bass prefer fibrous roots, but will deposit their eggs on dead leaves, roots, low-growing shoots of water plants, sand, and gravel. Smith (1907) declared that this species will use fine gravel, gravel, clay, or mud bottom for their nests. Hubbs and Eschmeyer (1938) report that the largemouth will spawn on gravel if available, but often breed successfully on roots or hard fragments exposed in digging nests. Thorpe (1942) stated that the largemouth bass nests may be found under varying local conditions in almost any type of bottom. Leuth (1942) pointed out that the largemouth

bass will spawn on leaves, rootlets, sand, gravel, or other hard bottom. Swingle and Smith (1943) list the following bottom types used by spawning largemouth bass: gravel, sand, firm clay, leaves, roots, brush, and other similar material.

2. Rock bass.--Hankinson (1908) found rock bass nests in marl bottom covered with small stoneworts. Reighard (1915) states that rock bass made their nests by exposing the fibrous roots of plants. The bottom material removed may be sand, marl, muck, or mud, but the essentials of the nest are the rootlets which form the bottom of the nest. Evermann and Clark (1920) describe rock bass nests that were found on clean, coarse sand or fine gravel. Hubbs and Eschmeyer (1938) say that rock bass prefer to use gravel if it is available.

3. Pumpkinseed sunfish.--Sunfish construct nests on the following types of bottom: bulrush roots, sand and marl (Hankinson, 1908); fine gravel, sand, roots, (Leathers, 1911); gravel but more often roots (Reighard, 1915); sand, pebbles, clam shells, pieces of wood (Krecker, 1916); fibrous turfy bottom, some on sand (Evermann and Clark, 1920); sand (Adams and Hankinson, 1928); mud is brushed away until firm, earth bottom is exposed and eggs adhere to roots and fragments of vegetation in the bottom of the nest (Reid, 1930); clay, sand, gravel with considerable variation (Breder, 1936); mud, gravel, mud and sticks, mud and small flat shale rocks, rounded stream-carried pebbles and sticks, and gravel and small, flat, shale rocks (Ingram and Odum, 1941); fine gravel, sand, or mud (Thorpe, 1942).

4. Bluegill.--Hankinson (1908) and Reighard (1915) found bluegill eggs attached to bulrush roots. Richardson (1913) found bluegill nests on hard bottom of sand and mud with a little vegetation, fine dead

drift, grass, and twigs. Coggeshall (1924) reported that bluegills nested in gravel or marl containing shells or roots. Adams and Hankinson (1928) cite instances of bluegills nesting on sand bottom containing roots or other objects on the bottom. Brass (1938) has pointed out that bluegills prefer sand or gravel for nesting but if these are not available they will use mud or marl. Leuth (1942) declared that a muddy or sandy bottom was preferred by nesting bluegills. To quote from Swingle and Smith (1943 - Page 3) - bluegills "apparently preferred to lay their eggs on fine gravel, but where this was not available, any firm surface, such as clay, sand, roots or pine needles was utilized."

Location and Distribution of Spawning Beds
in Deep Lake by Species

The centrarchids in Deep Lake utilized practically the entire shoal area for spawning, regardless of the type of bottom. In 1939, the approximate location of all of the nests of each of the four species was plotted on a map (Figure 2) at the time that each nest was actually used for spawning. The location of the spawning beds of all species was approximately the same each year, i.e., the same locations are selected year after year with only slight variations, and frequently the same nest will be used year after year. It is for this reason that only one map is being used for this discussion and this map exhibits the essential location of the nests for all species during the four-year period. In 1939, the actual spawning season began on May 12 (largemouth bass) and lasted until August 3 (the last bluegill spawned on this day). Therefore, the location of new nests was being recorded on the map over

a period of 84 days. If the same nest was used for spawning more than once during the season by the same species, it was not recorded. For example, only 44 rock bass nests are recorded on the map, although 49 nests were used for spawning. This means that 5 rock bass spawned in nests used previously by rock bass. Our records show that one nest was used three different times in one season by rock bass. If the same nest was used by two or more different species during the same season, it was recorded as such. Because of the large number of nests used by bluegills, only the colonies were listed on the map. The five single bluegill nests used for spawning in 1939 are located on the map.

From a casual glance at Figure 2, it would appear that the spawning grounds at Deep Lake were rather crowded. If all of the fish spawned at the same time this would be so. But it must be remembered that these nests were used over a period of 84 days. Another interesting thing is that the nests are distributed around the entire lake, regardless of the type of bottom or the width of the shoal area. Blank areas (areas without nests) on the northeast, east, and southeast shoals correspond fairly close to rather dense growths of rushes. These areas were used to some extent in 1938, 1940, and 1941, but not in 1939 by nesting largemouth bass, rock bass, and pumpkinseed sunfish. The location and distribution of the nests will be discussed separately for each species.

Largemouth bass - Largemouth bass nest singly and never in colonies. As was pointed out in a previous section, largemouth bass seldom constructed nests on peat bottom; therefore few nests are to be found in the west and southwest portion of the lake. One striking feature is the wide spacing (about 50 feet) between largemouth bass nests (Figure 2).

This was so evident while the writer was making daily observations during the four-year period that it must be stressed as being a very important factor in the spawning habits of this species. All observations made by various workers on the spawning habits of the smallmouth bass indicate that this species prefers to nest more or less away from other smallmouth bass. In fact, in brood ponds all smallmouth nests are provided with side-board shelters on two sides of the nests to act as "blindings" so that larger numbers of nests will be used because the guarding male cannot be seen by fish on adjoining nests. Apparently largemouth bass likewise do not care to nest very close to one another. The presence of pumpkinseed sunfish and rock bass nests near a largemouth bass nest does not seem to make any difference to the male largemouth guarding a nest. On several occasions rock bass or pumpkinseed nests were located as close as five feet from largemouth bass nests and males of both species were busy guarding their own nests and paid little attention to one another. Only on one occasion (on June 10, 1940) did the writer find two largemouth bass nesting close together, and in this case the two nests were only four feet apart.

The majority of the largemouth bass nests were located rather close to shore. In 1941, actual measurements were made and aside from a few nests, all were within 3 to 6 feet from shore. More largemouth bass nests per unit of area were found along the sandy, south shore of Deep Lake. No definite reason can be given for this except that nests located in this area were probably better shaded than nests located in any other place in the lake.

Rock bass - Rock bass never nest in colonies. The rock bass seldom constructs a nest in bottom composed of peat, preferring to nest in sand or gravel. Rock bass nests were found all around the lake except where pure peat bottom was located. To a certain extent, but to a lesser degree than the largemouth bass, the rock bass nested quite a distance apart (at least 8 or 10 feet). Rock bass nests were located close to shore, some as close as two feet. Rock bass, more than any of the other species, prefer to build their nests next to or under some sort of shelter such as large boulders, fallen trees, sticks, or in thick vegetation. Although not all rock bass nests are found in such situations, many of them are. Almost every year about 8 or 10 rock bass nests were located under fallen trees. Rock bass more than any of the other species would build their nests in dense patches of bulrushes.

Pumpkinseed sunfish - The pumpkinseed sunfish frequently nests in colonies, although at Deep Lake the majority of them nested singly. When they do nest in colonies, there were usually no more than six nests together. Pumpkinseed spawning beds were found around the entire lake. Although the pumpkinseed and the bluegill selected similar bottom types for nesting, they seldom used the same areas for spawning (Figure 2). The majority of the pumpkinseed nests were found outside and some distance away from bluegill colonies. Frequently, however, one or more pumpkinseeds would occupy nests within a bluegill colony (Figure 2). Pumpkinseed sunfish would sometimes occupy nests not more than two feet from rock bass nests and in nests adjoining those of bluegills. The guarding males of these different species apparently paid little attention to one another.

Bluegill - Bluegills almost always nest in colonies. At Deep Lake the number of nests in a colony varied from 3 to 54. Coggeshall (1924) found that the number of nests in a colony varied between 10 and 180. Very seldom do bluegills nest singly. In 1939, only 5 of the 621 bluegill nests were isolated. Despite the fact that bluegills preferred to nest in groups, the colonies of nests were scattered about the lake (Figure 2). If this species preferred to spawn on gravel, sand, or peat, all of the fish could have spawned in one large colony on either of these types of bottom. A total of 17 different spawning colonies occurred in 1939. Most of these same colonies were present year after year, and in most of them the same nests were used year after year. Bluegills spawned over a long period each summer and many of the nests in each colony were used several times during the same spawning season. During some years certain colony locations were not used. In 1941, several areas were frequented that were not used in previous years. There were usually fewer nests in the new colonies than in the permanent ones.

The location of spawning areas in a lake may be determined by such factors as the type of bottom, depth of water, degree of slope of the bottom, wind action, shade, or cover. Because our observations were made at Deep Lake, the discussion of these factors will necessarily be confined to this lake except for several pertinent observations made by other workers that can be compared with similar findings of the writer.

Apparently all spawning fish desire some sort of cover in the vicinity of the spawning area. The rock bass frequently constructs its nest beside or under some object. Most of the other species though, did not require this sort of cover at Deep Lake. Because of the sharp

drop-off at Deep Lake, most fish when frightened would retire to deep water which served as "cover" for the fish. Because Deep Lake is probably not a typical lake in this respect, no further discussion of this subject will be made.

The rock bass, and to some extent the largemouth bass and pumpkinseed, would select sites for spawning where some shade would be furnished by aquatic vegetation, trees, etc. The bluegill is the only species that consistently spawned in exposed areas.

No correlation can be made between the selection of nesting sites and wind action at Deep Lake. The prevailing winds were from a southwesterly direction at Deep Lake, yet nests were scattered around the entire lake. Consideration must be given to the fact that Deep Lake being a small lake surrounded by high banks never did get very rough. As was pointed out above, the fact that more largemouth bass nests were located on the south and southeast shore may be correlated with protection from wave action.

Very few nests were found in Deep Lake at a depth greater than five feet. The slope of the bottom in water deeper than five feet is steep. Rock bass nests were never found on sloping bottom. The deepest nests in a bluegill colony were frequently located on a sloping bottom, but the floor of the nest itself was hollowed out until it was horizontal. The same was true of pumpkinseed sunfish nests that were located on a sloping bottom. Several largemouth bass nests were located on sloping bottom and no attempt had been made by the male fish to hollow out a nest. Every one of these largemouth bass nests was first located only by observing the presence of the guarding fish, because he had just barely fanned the ooze and algae off the sand and the nest was not well

defined. Eggs were merely scattered over the cleaned area of the nest. In some nests the lower edge of the egg mass might be at a depth of at least a foot greater than the upper edge of the egg mass. Several times it was noted that many of the eggs had slid down the slope and there was definitely a "pile-up" of eggs at the lower edge of the nest. Fry were later observed on most of these nests.

The narrow shoal may account for the variety of bottom materials used for nest construction by the fishes in Deep Lake. But if the fish had preferred any particular type of bottom for their nests, there would have been a sufficient area of sand, sand and gravel, or peat to accommodate all of the nests found in Deep Lake in any one year. Because the largemouth bass nests are single and are usually located some distance apart, the number of nests might exceed the area available of a particular type of bottom. But this would have required the presence of several hundred bass breeders. Rock bass seldom build nests on peat bottom, but unlike the largemouth bass, they are not averse to nesting close together. Therefore suitable bottom for rock bass spawning was not limited in Deep Lake. Since pumpkinseed and bluegill nests are usually more or less closely grouped, all nests could have been located on a single type of bottom. It is believed that the gregarious instinct which causes males to build nests in groups may be due to the fact that the choice of a favorable area for spawning by one fish is the natural choice of others. Or perhaps these fish group together for the added protection of eggs and fry. To the writer it appears that the spawners of the species studied may not thoroughly investigate all areas before spawning, but tend to use whatever type is most available or any type that they happen to reach upon entering the shoal area from deeper water.

If sufficient room were not available for spawning, it is probable that spawning beds would be worked over and over, thus destroying previously deposited eggs. Any decrease in available spawning area would also increase the amount of fighting by males of the same and of different species. Observations made at Deep Lake over a four-year period did not reveal evidence to substantiate either of the above statements.

It is apparent that the four species studied at Deep Lake can reproduce successfully on any type of bottom present in a lake. It is only necessary for the nest to be clean of any flocculent or loose material which is fanned away until fibres, roots, green plants, shells, sticks, or any other fairly solid material is left for the eggs to adhere to. Possibly the only bottom type that may prevent successful spawning is the soft mud described by Breder (1936 - Pages 11-13) and this writer believes that some solid material would be present in this type of bottom if it was worked enough. From all of the observations that have been made on Deep Lake and other Michigan lakes by this writer, and from reading all of the available literature on the subject, it is apparent that it is not necessary to make any improvements in lakes for the spawning of the largemouth bass, rock bass, pumpkinseed sunfish, and bluegill. To further substantiate the above statement we quote from Swingle and Smith (1943 - Page 3) - "bluegills have been found to reproduce successfully under widely varied conditions and the construction of special spawning areas by the pond owner was unnecessary." (1943 - Page 4) - The largemouth bass "was able to find suitable spawning areas in all ponds, and the construction of special spawning areas was unnecessary."

Depth of Water in Which Nests are Found

Space available for spawning beds might have been somewhat limited in Deep Lake because of the very narrow shoal area. The abrupt drop-off starts at a depth of about 5 or 6 feet and few nests were found beyond this. The steep angle of the slope might be the factor limiting available spawning area. Any drop in the general water level at Deep Lake would further limit the amount of available spawning area.

The depth that individual nests (from the rim to the center of the bottom of the nest) are excavated varies according to the bottom type. Nests constructed in sand seldom vary more than 3 to 6 inches in depth from the rim to the center. In soft bottom such as mud, peat, muck, or marl, there may be a difference of a foot or more between the rim and the center of the nest. The eggs are usually deposited over the bottom (center) of the nest and measurements of the depth of water in which nests were found were always made at the bottom of the nest. Occasionally a nest would be found on the steep slope of the drop-off. In some of these the difference in depth from the upper edge to the lower edge may have been as much as one, or in one instance, two feet. The average between these measurements was usually taken for the depth of the nest.

The water depth in which the nests of each of the species were found over the four-year period is summarized in Table 4 and Figure 4.

Largemouth bass - The average depth of water in which largemouth bass nests were found during the four-year period was 27.6 inches, with the yearly average varying from 25.5 to 31.9 inches (depth of individual nests ranged from 10 to 74 inches). There was only a difference of 6.4 inches in the average depth of the nests during the four-year period.

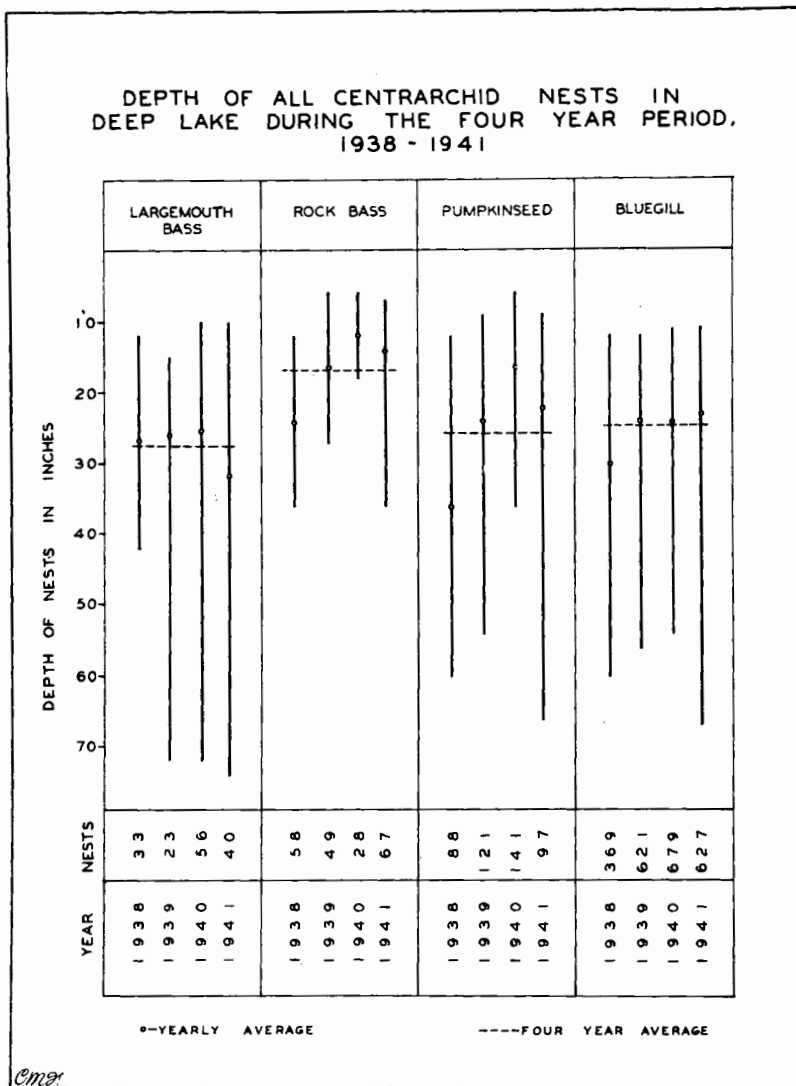


Figure 4.--Depth of all centrarchid nests in Deep Lake during the four-year period, 1938-1941.

Table 4.--Average water depth in inches of the spawning beds found in
Deep Lake, 1938-1941. Minimum and maximum depths in parentheses.

Species	1938 [↓]	1939	1940	1941	Four-year average
Largemouth bass	27.0 (12-42)	26.3 (15-72)	25.5 (10-72)	31.9 (10-74)	27.6 (10-74)
Rock bass	24.0 (12-36)	16.4 (6-27)	12.0 (6-24)	14.1 (7-36)	17.2 (6-36)
Pumpkinseed	36.0 (12-60)	24.2 (10-54)	16.3 (6-36)	22.0 (9-66)	25.8 (6-66)
Bluegill	30.0 (12-60)	24.1 (12-56)	24.3 (11-54)	23.2 (11-67)	24.9 (11-67)

↓ Measurements were not made of all nests in 1938

Hankinson (1908) found largemouth bass nests in Walnut Lake in from 1 to 2-1/2 feet of water. Richardson (1913) gives 6 to 36 inches as the depth at which bass nests are found. All largemouth bass nests in a Park Lagoon in Chicago were found at depths greater than 2 feet according to Hubbs (1919). Evermann and Clark (1920) found largemouth bass nesting in 6 feet of water. According to Breder (1936), this species spawns in shallow water which probably averages close to 2 feet in depth. Carr (1941) states that bass were nesting in water varying in depth from 4 inches to 8 feet.

Rock bass - The average depth of water in which rock bass nests were located ranged from 12 to 24 inches and averaged 17.2 inches for the four-year period (Table 4, Figure 4) and the extreme depths varied from 6 to 36 inches. Other workers found rock bass nesting in water ranging from a few inches in depth, Bensley (1915) to less than two feet (Hankinson, 1908).

Pumpkinseed sunfish - During the four-year period the average water depth of all pumpkinseed nests was 25.8 inches (range - 16.3 to 36.0 inches, Table 4 and Figure 4). The extreme range in depth varied from 6 to 66 inches. The following depths have been recorded for pumpkinseed nests: between one and two feet Hankinson (1908); from water barely deep enough to cover the fish to 18 inches, (Krecker, 1916); a foot or two of water, (Adams and Hankinson, 1928); usually in less than two feet of water (Breder, 1936); between 7 and 23 inches (Ingram and Odum, 1942). Employees of the Drayton Plains Hatchery of the Michigan Department of Conservation state that pumpkinseeds usually nest closer to shore and in shallower water than bluegills (personal com.).

Bluegill - Bluegill nests were found in water ranging in depth from 11 to 67 inches during the four-year period, with an average depth of 24.7 inches (Table 4 and Figure 4). The writer has found bluegill nests in water as deep as 8 feet in several other Michigan lakes. Hankinson (1908) found bluegill nests in from 5 to 6 inches to 2 feet of water. Other investigators noted the following depths: 1 to 1-1/2 feet of water (Richardson, 1913); 4 to 8 feet (Evermann and Clark, 1920); 0.5 to 2 meters, some to 10 feet (Coggeshall, 1924).

The difference in the water level from year to year partially explains some of the variation in the average depth of water in which nests of the various species were found during the four-year period. Definite figures on the fluctuation of the water level cannot be given because a permanent water gauge was not installed in Deep Lake. The water level of Deep Lake was higher in 1938 than in any of the other years, and was probably lowest in 1941. During mid summer in 1941, many spawning beds that were used in other years were high and dry.

Variation between species - The largemouth bass nested in deeper water than any of the other species studied, while the rock bass constructed their nests in much shallower water than any species. Bluegills and pumpkinseeds nested in about the same depth of water.

According to Breder (1936), the smaller the fish and the smaller the nest, the shallower the water will be over the nest. He found that the relationship of nest size to species and the nest size to depth was referable to the size of the fish, that is, fish more or less "fit" their nests, the length of the fish being approximately half the diameter of the nest they occupied. The depth and diameter of all of the

largemouth bass, rock bass and pumpkinseed nests actually used for spawning in 1940 is presented in Table 5. It is believed that these figures are typical and are comparable with those of the other three years, and also hold for those of the bluegill. Although some of these nests may have been constructed by other species (as suggested by Breder) before being occupied by another species, the writer found that these were not any larger on the average than those built by this latter species. In fact the largest and smallest nests constructed by the pumpkinseed were not used by other species, and most of the few nests of other species that were taken over by the pumpkinseed sunfish were equal in size or smaller than the average pumpkinseed nest. In general then, according to our information, the diameter of the nests increased slightly with an increase in the depth of the water, but no definite correlation between the depth of the water and the diameter of the nest can be made (Table 5).

Likewise the observations that were made at Deep Lake for four years lead the writer to conclude that there was very little correlation between the size of the fish, diameter of the nest and the depth of the water in which the nest is located. The writer has observed large and small fish, of the various species studied, spawning in both shallow and deep water, although there is a slight tendency for the larger fish to seek out deeper water for spawning. The writer has observed several pumpkinseeds that did not bother to build an elaborate nest, in fact all they did was to sweep the small accumulation of silt off the sand and deposit their eggs. These nests seldom averaged larger than 6 inches (covered by eggs) in diameter and were found at water depths up to about 3 feet.

Table 5.--Depth and diameter in inches of individual largemouth bass, rock bass and pumpkinseed nests in Deep Lake during 1940

Largemouth bass				Pumpkinseeds					
Depth	Diameter	Depth	Diameter	Depth	Diameter	Depth	Diameter	Depth	Diameter
10	9	39	12	6	9	12	30	18	18
10	12	48	15	6	12	13	18	18	18
12	12	49	15	7	9	13	24	19	7
12	12	51	18	8	6	13	24	19	12
12	15	52	15	8	15	14	6	19	18
12	18	72	18	8	18	14	10	19	24
12	24			9	6	14	12	20	8
13	21			9	6	14	18	20	12
15	12			9	9	14	24	20	12
16	18			9	12	15	6	20	24
18	12	6	8	9	12	15	6	20	24
18	15	8	6	9	12	15	8	21	4
18	21	8	12	9	12	15	8	21	9
18	24	9	4	9	12	15	9	21	9
18	24	9	4	9	15	15	9	21	12
19	15	9	6	9	15	15	9	21	12
19	18	9	6	9	15	15	9	21	15
20	18	9	9	9	15	15	10	22	12
20	18	9	9	9	18	15	12	23	21
21	9	9	12	10	6	15	18	23	24
21	12	10	6	10	8	15	18	24	6
21	12	10	6	10	9	15	18	24	6
21	21	10	9	10	12	15	24	24	6
22	12	11	5	11	12	15	24	24	8
22	18	12	6	11	24	15	30	24	15
22	24	12	6	12	6	15	30	24	18
23	12	12	6	12	6	16	12	24	18
23	18	12	8	12	6	16	12	24	18
23	21	13	4	12	7	16	12	24	24
24	12	13	6	12	9	17	18	24	27
24	12	14	8	12	9	17	18	27	9
24	12	14	12	12	9	17	24	27	9
24	18	15	6	12	9	18	6	27	18
25	15	16	6	12	12	18	6	27	18
26	18	18	4	12	12	18	9	30	15
26	21	18	6	12	12	18	12	30	15
27	9	18	15	12	12	18	12	32	11
27	12	24	6	12	12	18	12	33	12
27	20			12	12	18	12	33	15
27	24			12	15	18	12	34-35	15
30	18			12	15	18	12	36	15
30	30			12	18	18	15		
30	33			12	18	18	15		
31	12			12	18	18	15		
31	30			12	18	18	15		
33	9			12	21	18	18		
34	24			12	21	18	18		
36	8			12	21	18	18		
36	12			12	24	18	18		
36	21			12	30	18	18		

Fluctuations in water level could probably result in preventing a species from spawning successfully. At Deep Lake, a lowering of the water level by 5 or 6 feet would probably result in preventing most, if not all of the fish from spawning because of the steep slope of the remaining lake bottom. Fluctuations in level have definitely been the cause of poor production for some species in some lakes as observed by Carbine (personal observation) and Thorpe (1942, page 41). It is suggested that this method could be used in certain lakes and reservoirs where the water level is controlled by dams, to reduce the population of any certain undesirable species by preventing spawning or by exposing the eggs or fry during the spawning period.

Diameter of Nests

The details of nest construction of the centrarchids have been observed by many investigators, and Breder (1936) has recently summarized the available information on this subject. It might suffice here to mention that the nest is constructed by the male, by standing almost vertically over the nest and making sweeping motions with the tail. Bluegills sometimes shape the nest by making rapid circuits around the circumference of the nest. The currents thus created carries the finer material out of the nest and tends to make the nest as nearly circular in outline as the bottom features permit. The diameter of the nest depends to some extent on the type of bottom. Nests located in soft material are usually larger, more elaborate and better defined than those built over harder bottom. Nests constructed on solid, gravel bottom and in roots are usually smaller, less conspicuous and usually poorly defined than those built in sand, marl, muck or peat. Regardless of the type of

bottom, individuals of some species may spawn in nests where little or no arrangement of the bottom material to form a nest could be seen and the eggs or fry were discovered only by the presence of the guarding male. Illustrations of the diverse types of nests built and used by the various species are presented in Plates 7 - 22.

Although data were not obtained on the estimated length of the guarding males, observations indicated that little correlation existed between the size of the fish and the diameter of the nest. Large or small individuals of the several species built both large and small nests.

Measurements were made of all individual nests at the time that they were discovered and marked except in the case of the bluegills. Nests in bluegill colonies were measured at intervals when none of the nests, or very few were occupied. This prevented much of the predation of the eggs and fry by other fish which usually took place when the nests were left unguarded when the observer approached. (Male bluegills invariably left their nests when the observer approached. Usually little or no predation occurred during the time it took to locate, mark and measure one new nest, while a great deal of time was usually required to measure and record all of the nests in any one bluegill colony). The inside edge or rim of the cleaned area of the nest was always considered as the boundary of the nest when the diameter was measured. The average of the widest and narrowest diameters of irregular shaped nests was always used as the diameter of that nest.

Largemouth bass - The nests of this species always occur singly. The majority of the nests were simple and rather inconspicuous. In most



Plate 7.--Largemouth bass nest located in sand bottom. Notice eggs
(many fungused) on roots. Depth of water, 2 feet.

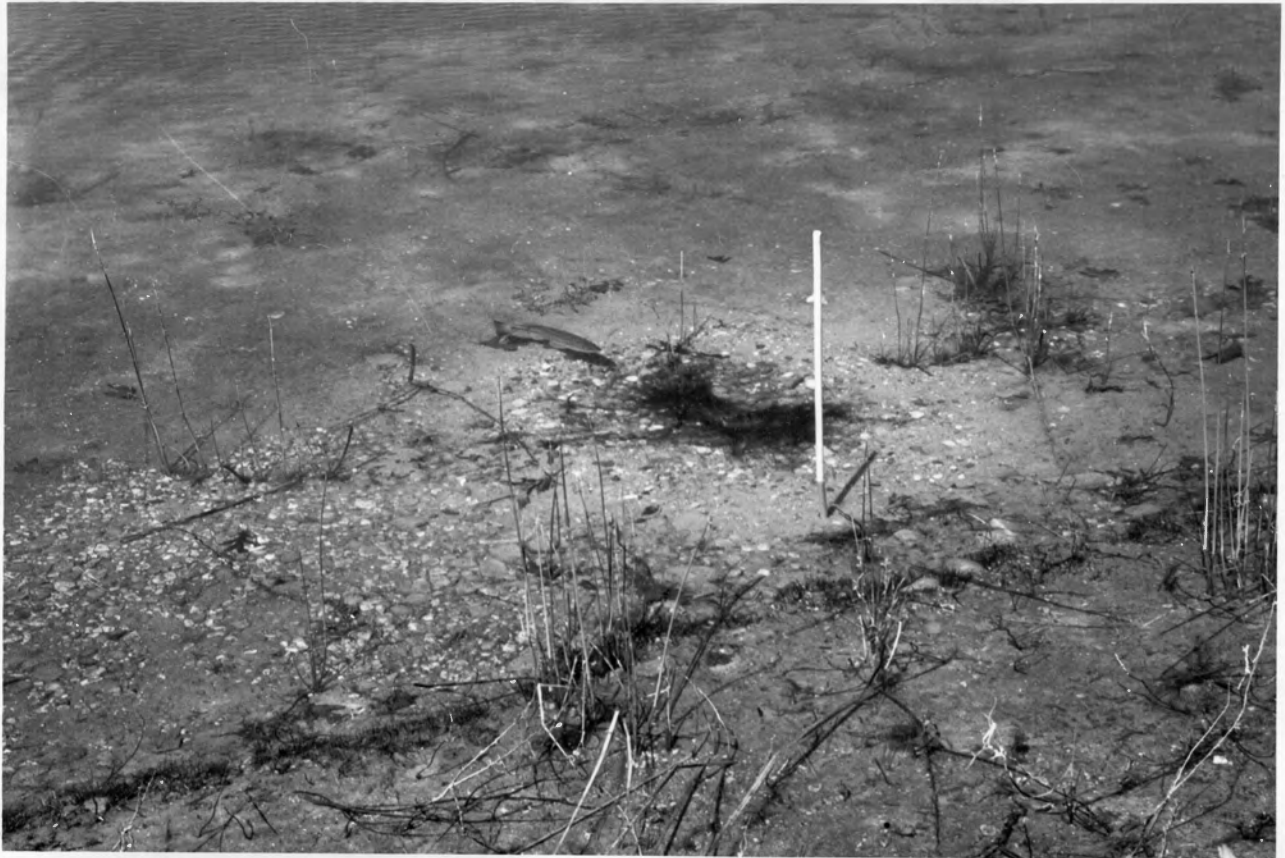


Plate 8.--Largemouth bass nest of roots, gravel and sand, located in
1 foot of water.



Plate 9.--Largemouth bass nest located on gravel bottom with very small amount of sand. Diameter 1-1/2 feet and depth of water 1-1/2 feet.

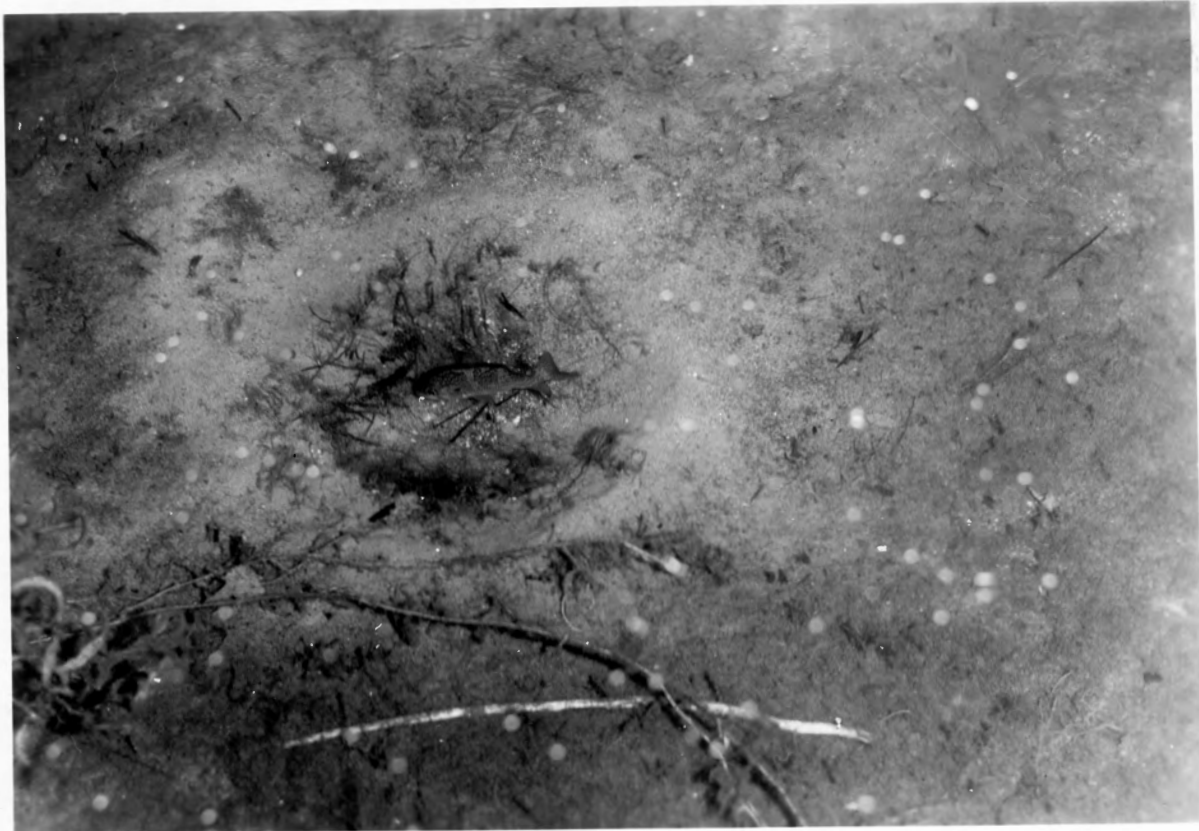


Plate 10.--Rock bass guarding nest of roots and sand.



Plate 11.--Rock bass guarding clutch of fungused eggs. Depth of water, 1-3/4 feet. This nest was used previously by a pumpkinseed sunfish and the rock bass just cleaned a portion of the old nest.



Plate 12.--Rock bass nest located in bulrushes. Bottom of nest is sand, but one rock is present in center. Eggs were deposited on the roots. Depth of water 26 inches and diameter of nest is 9 inches.



Plate 13.--Rock bass guarding nest of gravel with small amount of sand.

Note the large boulder near the edge of the nest. This same nest was also used by a largemouth bass earlier in the same season. Depth of water-23 inches.

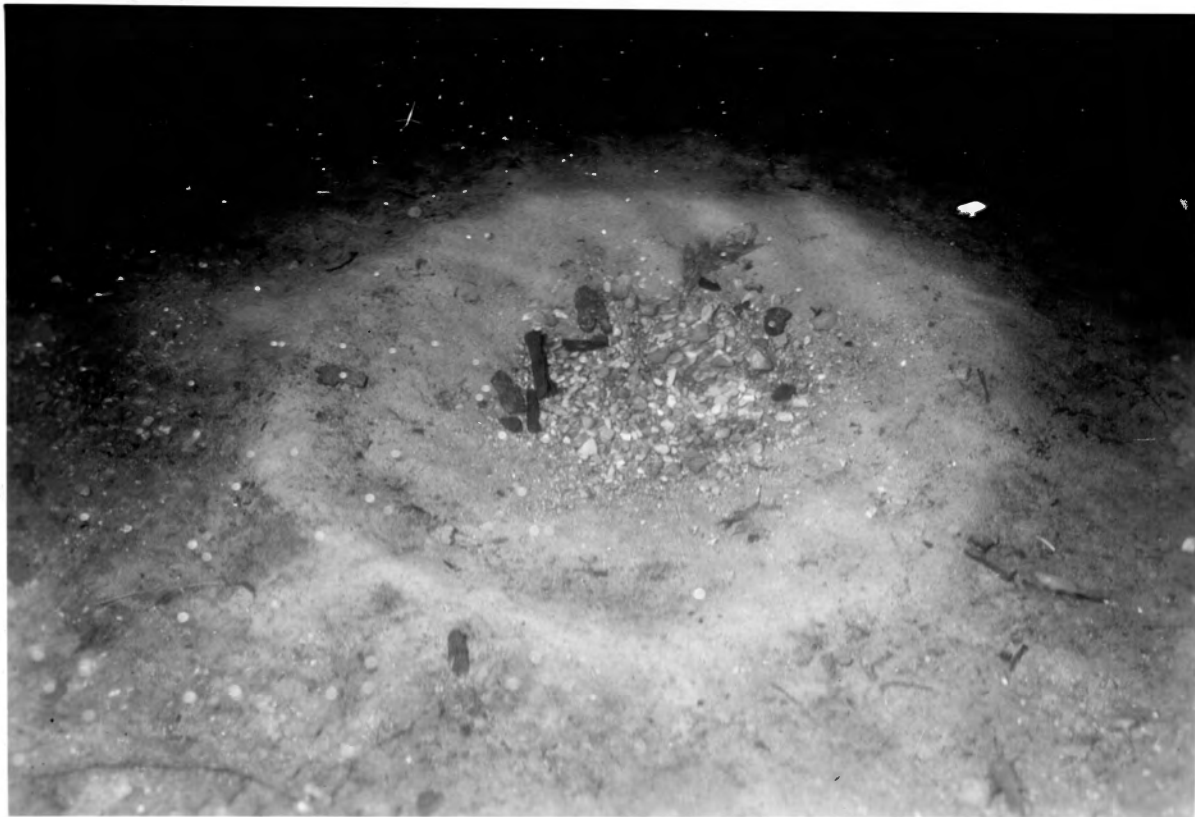


Plate 14.--Pumpkinseed sunfish nest located in three feet of water.

Diameter of the nest is 3 feet and the bottom is composed of sand with some gravel in the center.

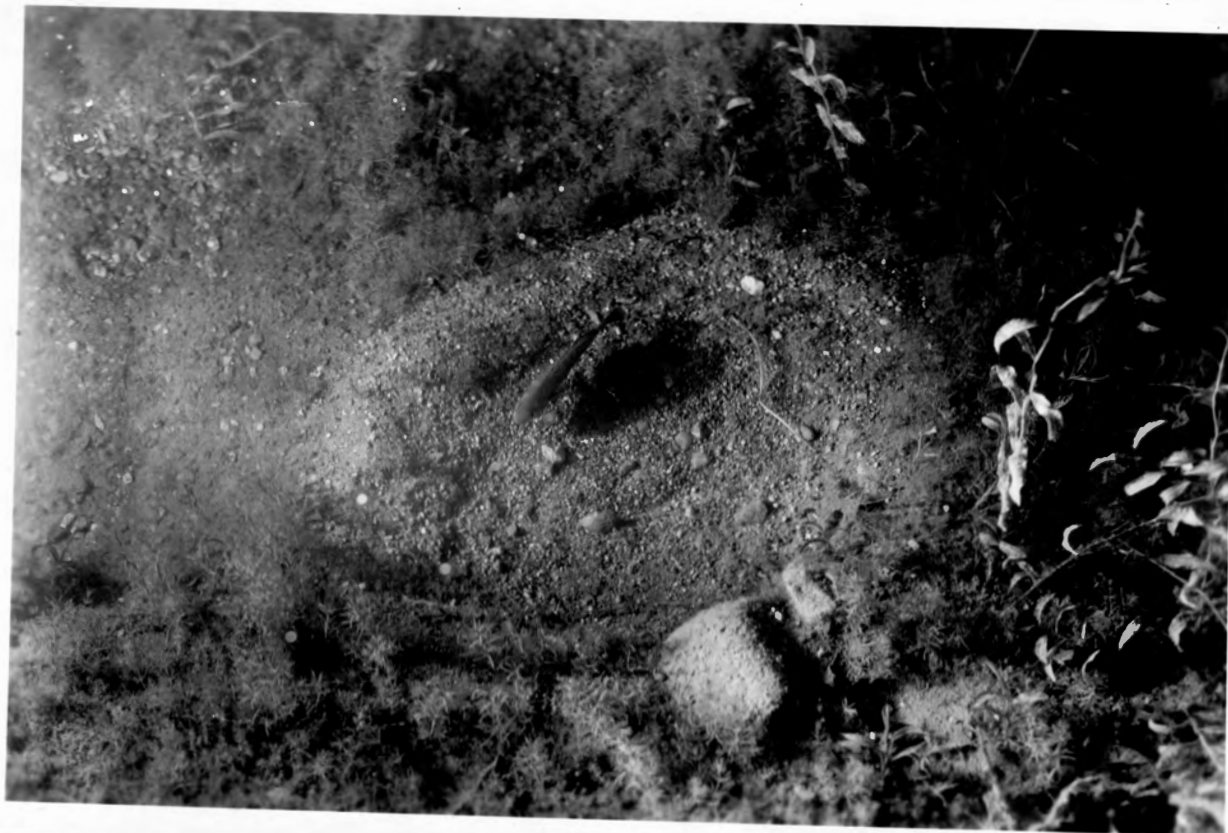


Plate 15.--Pumpkinseed sunfish nest 2-1/2 feet deep and 20 inches in diameter. Bottom of sand and gravel.



Plate 16.--Pumpkinseed guarding nest of gravel, rock and sand.



Plate 17.--Pumpkinseed sunfish guarding nest on level sand bottom in
27 inches of water. The eggs are adhering to the roots.
Note marble used in marking nest.



Plate 18.--Pumpkinseed sunfish nest in roots, leaves and sand in water
one foot deep.

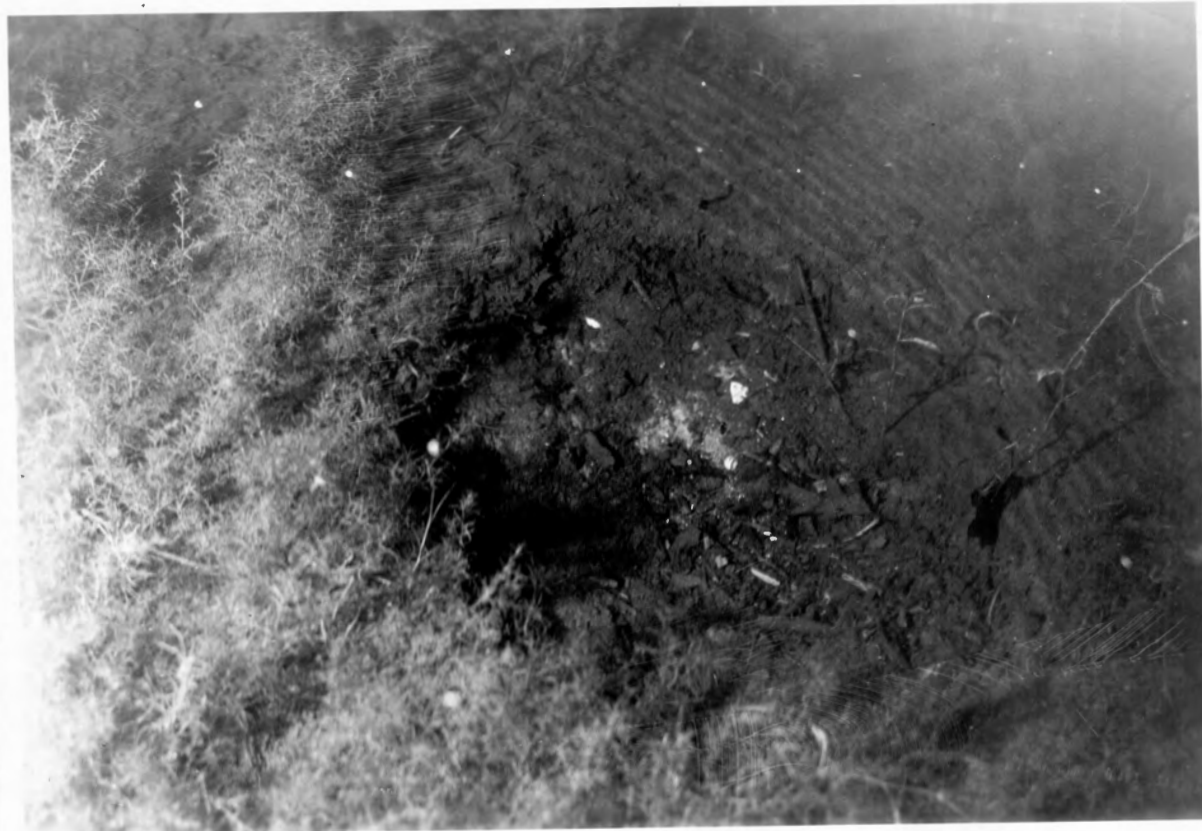


Plate 19.--Bluegill nest located in area of fibrous peat. Loose, flocculent material has been cleaned away and sticks, small gravel and some sand remains in the bottom of nest. Depth of water is 2 feet and the bottom of the nest is 2-3/4 feet below the surface of the water. Greatest diameter of nest is 26 inches.

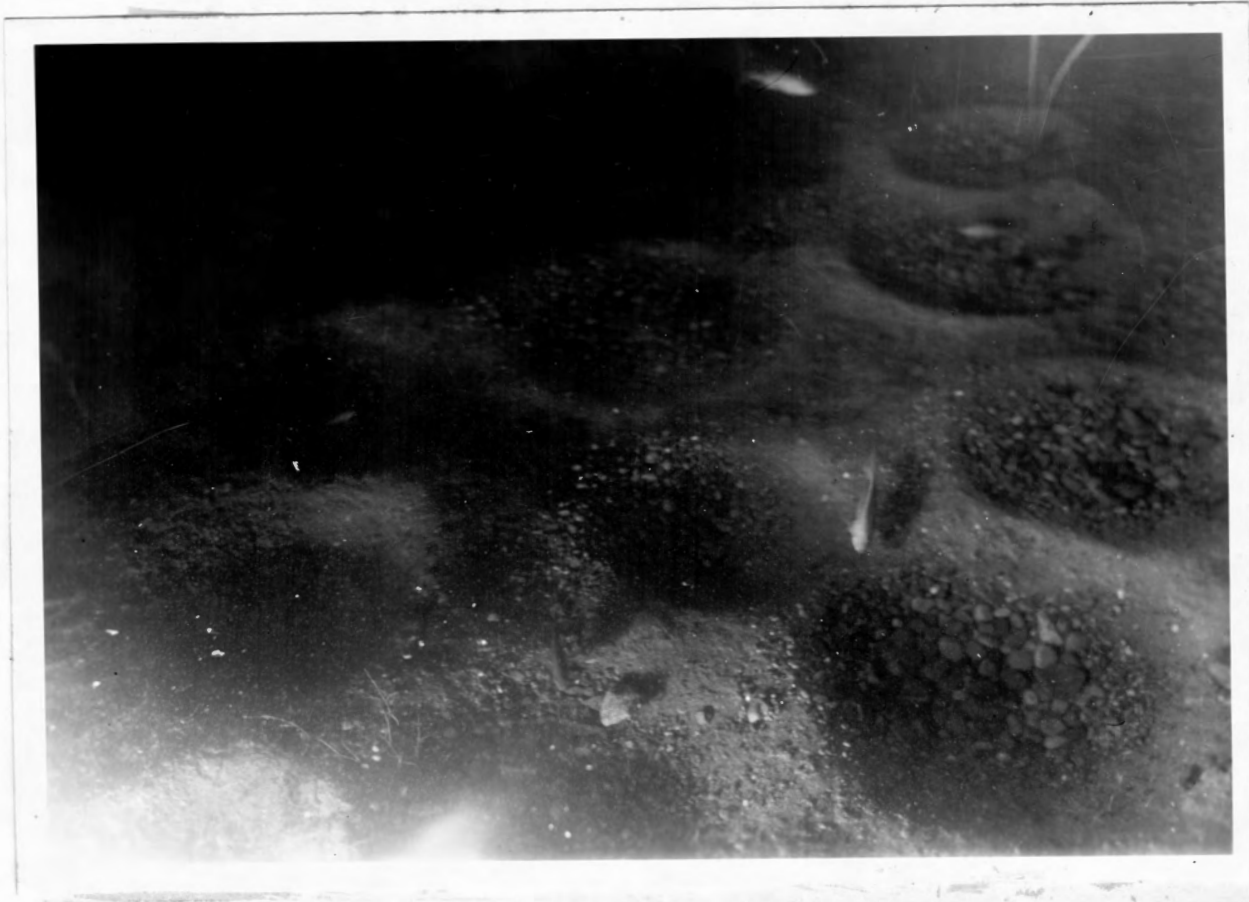


Plate 20.--Colony of bluegill nests. Average depth of water, 3 feet.
Bottom of sand and gravel.

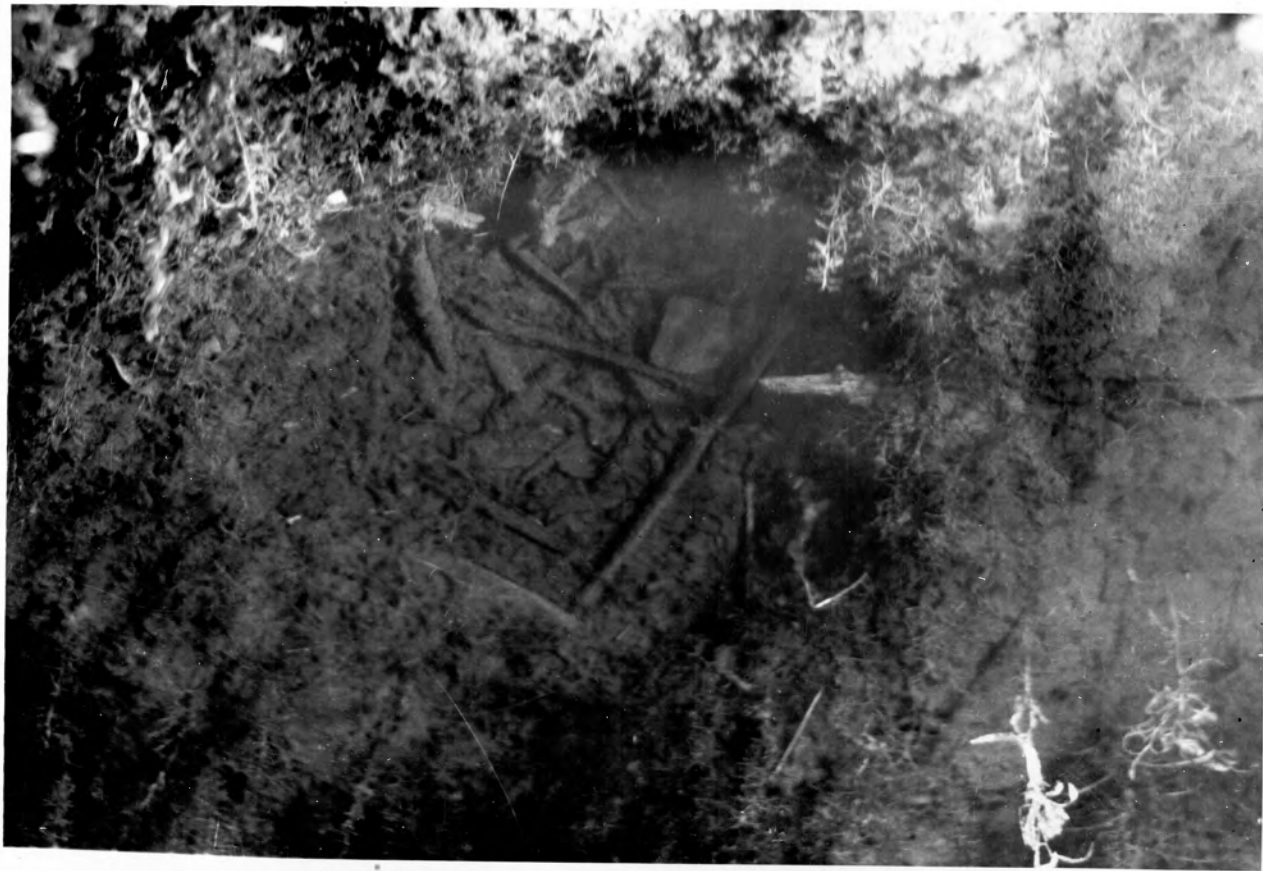


Plate 21.--Bluegill nest located in fibrous peat. The loose flocculent material has been swept out of the nest leaving a few sticks for the eggs to adhere to. Depth is 2 feet to the edge of the nest and 2 feet 10 inches to the center of the nest. Greatest diameter is 2 feet.



Plate 22.--Colony of bluegill nests located in sand and gravel. There are 21 nests in this colony and the depth of water ranges from 1-1/2 to 4 feet.

instances the male merely swept away the thin layer of ooze and detritus that covered a patch of roots, sand or gravel. Very few largemouth bass nests were found in Deep Lake that were saucer-shaped depressions. All inconspicuous nests were usually found by observing the presence of eggs or of the guarding male (Plates 7-9). The diameter of the bass nests in Deep Lake ranged from 6 to 33 inches and averaged 13.9 inches during the four-year period (Table 6 and Figure 5). The bottom of the small nests was almost always composed of roots, whereas the larger nests were in sand and/or gravel bottom.

Reighard (1906) states that largemouth bass nests were usually less conspicuous than were the nests of the smallmouth bass, but did not give any figures on the actual diameter. Smith (1907) lists the diameter of largemouth bass nests as 1-1/2 to 2 feet. Richardson (1913) found largemouth bass nests that were nearly round, well excavated and with diameters that ranged from 12 to 18 inches. Bensley (1915) states that the nests may be 3 feet in diameter. Largemouth bass nests, more or less circular in outline, with the center of the nest varying from 1 to 2 feet in diameter and with extreme diameters of from 1-1/2 to 3 feet were described by Hubbs (1919). Evermann and Clark (1920) state that the diameter of largemouth bass nests vary from 1 to 2-1/2 feet. Carr (1942) found that largemouth bass nests varied from 12 to 60 inches in diameter and the average for 30 nests was 30.2 inches.

Rock bass - Rock bass nest singly and the majority of the redds were poorly defined. In most of the nests, the thin layer of detritus and ooze was merely swept away from the roots, sand or gravel to expose the bottom. The nest of the rock bass was seldom hollowed out to any extent. Several nests found on sand bottom could barely be distinguished from the

Table 6.--Average diameter in inches of the spawning beds found in Deep Lake, 1938-1941. Minimum and maximum depths in parentheses.

Species	1938 [↓]	1939	1940	1941	Four-year average
Largemouth bass	10.5 (6-15)	16.1 (6-24)	16.8 (8-33)	11.7 (6-21)	13.9 (6-33)
Rock bass	11.0 (6-15)	11.0 (6-18)	7.2 (4-15)	8.8 (6-15)	9.7 (4-18)
Pumpkinseed	21.0 (6-36)	18.7 (6-36)	14.2 (4-30)	16.8 (6-30)	18.0 (4-36)
Bluegill	19.0 (12-30)	19.4 (12-30)	21.5 (12-36)	21.7 (10-40)	20.6 (10-40)

↓
Measurements were not made on all nests in 1938.

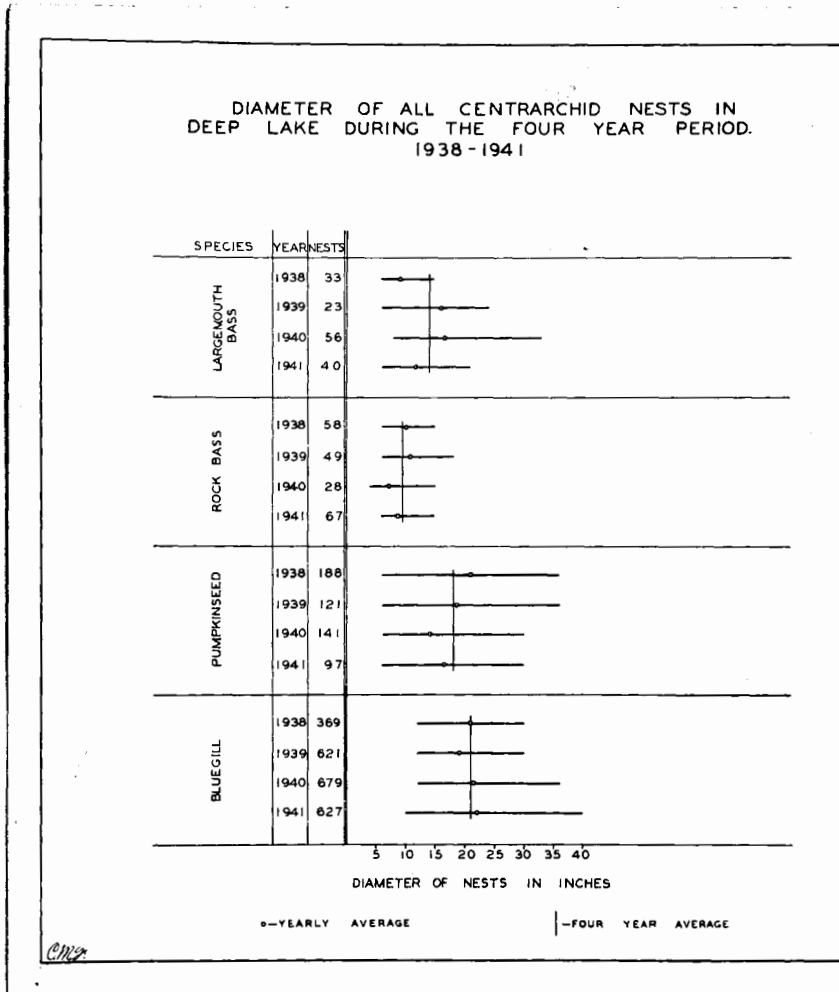


Figure 5.--Diameter of all centrarchid nests in Deep Lake during the four-year period, 1938-1941.

surrounding bottom. These were discovered by noting the presence of the guarding male, and verified by noting the presence of eggs or fry (Plates 10-13). The average diameter of rock bass nests in Deep Lake during the four-year period of this investigation was 9.7 inches and varied from 4 to 18 inches (Table 6 and Figure 5).

Hankinson (1908) found that rock bass nests varied considerably; from small shallow depressions of two or more inches in depth, to nests where no arrangement of the bottom material could be seen, and the presence of the nest was discovered by observing the guarding male. Rock bass nests usually varied from 8 to 9 inches in diameter in Lake Maxinkuckee, according to Evermann and Clark (1920).

Pumpkinseed - At Deep Lake, pumpkinseed sunfish either nested singly or in colonies, although the colonies usually consisted of only two or three nests. The redds of this species varied greatly as to shape and size, depending upon the type of bottom. Some were so poorly defined that they could hardly be distinguished from the surrounding bottom, while others were elaborate structures (Plates 14-18). Some large, bowl-shaped nests of the pumpkinseed that were located in sand bottom were as much as three feet in diameter and varied as much as 6 to 12 inches in depth (from the rim to the center of the nest). The bottom of the smallest nests were usually composed of roots or gravel, whereas the larger nests were constructed in bottom material of sand or peat.

The average diameter of all pumpkinseed nests that were used for spawning during the four-year period was 18.0 inches (Table 6 and Figure 5) and individual nests ranged from 4 to 36 inches. Leathers (1911) observed that pumpkinseed nests were about 18 inches in diameter.

A total of 419 nests were counted in Beimiller's Cove (Sandusky Bay) by Krecker (1916). The large nests found on sandy bottom were crater-like depressions, sometimes circular, but more often oval and were 36 by 27 inches in diameter. The smaller nests which averaged 7 inches in diameter were approximately circular in outline and were found on pebbles among the reeds. Adams and Hankinson (1928) state that the diameter of the nest is twice the length of the fish, but that one nest was found that was 36 inches in diameter. Reid (1930) claimed that pumpkinseed nests were about 1-1/2 feet in diameter. Breder (1936) noted that pumpkinseed nests are as nearly circular as the bottom features will permit and the diameter is commonly equal to twice the length of the fish. Breder found that the diameter of the nest rim varied from 8 to 40 inches, although the larger nests were probably built by Lepomis or Aplites. Ingram and Odum (1941) lists the variation in the diameter (to the nest rim) as 12 by 16 to 32 by 36 inches.

Bluegill - Bluegills usually nest in colonies containing two or more nests, although occasionally a single bluegill nest was found (Plates 19-22). Bluegills constructed larger and more elaborate nests than any of the other species studied. The nests were usually well excavated, bowl-shaped, and were always well defined. Even nests that were found in rather coarse gravel were easily identified. In contrast with the other species, bluegill nests seldom contained any roots. Bluegills were found to use the same nests, located in the same colonies year after year (this will be explained in more detail later).

The average diameter of all bluegill nests that were found in Deep Lake during the four-year period averaged 20.6 inches (range - 10 to 40 inches, Table 6 and Figure 5). The smaller nests were usually found

in gravel and the largest nests in fibrous peat. Nests located on sand bottom were surprisingly uniform as to size and shape.

In 1940, the writer had occasion to visit Lime Lake, Van Buren County, Michigan. This small, marl lake supports a good population of bluegills, and the average diameter of the several hundred bluegill nests that were found in this lake ranged from 9 to 24 inches. Hankinson (1908) states that the bluegill nests found in Walnut Lake were circular depressions about 2 feet in diameter. Richardson (1913) claimed that bluegill nests varied from 8 to 12 inches in diameter. Evermann and Clark (1920) lists the diameter of bluegill nests in Lake Maxinkuckee as about one foot. Coggeshall (1924) declared that the diameter of bluegill nests in Winona Lake averaged 28 inches and some were as large as 36 inches.

Some of the variation in the diameter of the nests of the species studied at Deep Lake is probably due to the difference in water level from year to year. When the water level is low, certain bottom types usually used by spawning fish may not be available, and other bottom types are of necessity used. Nests in soft bottom are generally larger than those in hard, firm bottom.

Of the four species studied, the nests of the rock bass exhibited the least variation in diameter, and were smaller. The nests of the pumpkinseed were larger than those of the rock bass, but smaller than those of the largemouth bass and the bluegill. The bluegill built the largest nests, some of which were 40 inches in diameter. In contrast with the other species, bluegills seldom constructed nests that were smaller than 12 inches in diameter. The characteristics of the nests are not specifically associated with the species occupying it. Bluegills and

pumpkinseeds often constructed nests that were very similar as to size, shape, and depth, and these nests did not resemble those built by the other two species. Also, some nests of the largemouth bass, rock bass, and pumpkinseed were almost identical in size and shape. Consequently, the species to which a nest belonged could only be identified positively either by noting the presence of the guarding male, or in some instances by the size, and characteristics of the eggs or fry.

Number of Nests

Every nest actually used for spawning during the period of observation by the largemouth bass, rock bass, pumpkinseed sunfish, and bluegill was counted during each of the four years covered by this investigation. As the largemouth bass and rock bass were already spawning when the first observations were made at Deep Lake in 1938, the total number of nests enumerated for these species probably does not represent the total number actually used. It is also possible that a few nests of all species might have been overlooked in other years.

The number of nests actually used for spawning varied considerably from year to year for each of the species studied (Table 7). The bluegill constructed more nests than any of the other species each year; the pumpkinseed sunfish, rock bass, and largemouth bass follow in that order. The number of nests used for spawning during each of the four years varied from 23 to 56 for the largemouth bass, 28 to 67 for the rock bass, 97 to 188 for the pumpkinseed sunfish, and 369 to 679 for the bluegill.

The data presented in Table 7 have also been plotted in graphic form (Figure 6). There is no correlation between the yearly variation in the number of nests between the various species. A decrease in the number

Table 7.--The number of nests actually used for spawning in Deep Lake by the largemouth bass, rock bass, pumpkinseed sunfish and bluegill from 1938 to 1941.

Year	Largemouth bass	Rock bass	Pumpkinseed sunfish	Bluegill
1938	33	58	188	369
1939	23	49	121	621
1940	56	28	141	679
1941	40	67	97	627
Total	152	202	547	2,296

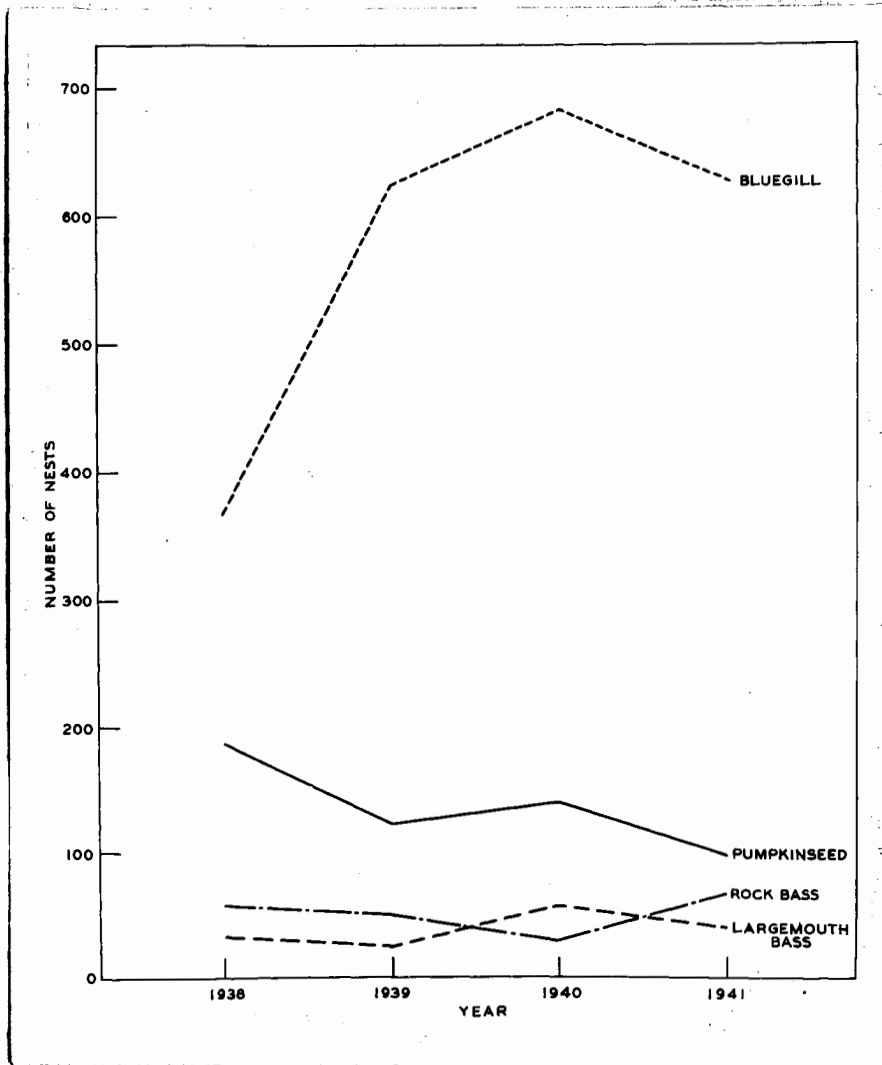


Figure 6.--Correlation between the number of nests used for spawning in Deep Lake by the various species of centrarchids from 1938 to 1941.

of nests from one year to the next for one species does not mean that all species would likewise show a decrease. When a decrease in the number of nests occurred for one species, another species would show an increase in the number of nests. This variation in the number of nests from year to year is probably due to the number of adults of each species that were present in the lake each year. It is interesting to note that in each year three species would show either an increase or a decrease in the number of nests over the preceding year, while the fourth species would react in the opposite direction (Table 7, Figure 6). For example, between 1938 and 1939 there was an increase in the number of bluegill nests while the number of nests for the other three species decreased. From 1939 to 1940 the rock bass was the only species showing a decrease in the number of nests while the other three species showed an increase. Between 1940 and 1941 all species except the rock bass showed a decrease in the number of nests. The rock bass then was the only species deviating from the general pattern two years in succession. Why this increase or decrease in the number of nests should affect three of the four species each year is not known. But since different species are involved each year, it would appear that it is caused by the number of the adults of each species present in the lake from year to year. The presence of a dominant age group of one species may cause a decrease in the population of the other three species. Also, poor survival of the eggs or fry of one or more species due to unfavorable conditions may account for this. The presence of a dominant bluegill population is evident after 1939 (Figure 6), and this large population may have eaten a large number of the eggs and fry of the other species or offered such severe competition

for food that the populations of the other three species was reduced. Angling is another factor that may enter the picture, but its significance cannot be ascertained.

Data on the daily number of new nests actually used for spawning by each of the species are available for all years except 1938. The Deep Lake study was started in 1938, and it was not possible for us to make daily observations that year. At times a period of several days elapsed between trips to Deep Lake. It is because of this that we are unable to summarize the data obtained on the number of nests in 1938 either by daily or weekly periods. Because the tables listing the daily number of nests used for spawning in 1939, 1940 and 1941 were so long, these data have been summarized by weekly periods (Tables 8, 9, 10 and Figures 7, 8, 9, 10).

The spawning season for each of the species was prolonged and the time that spawning occurred varied to some extent with the temperature of the water and other factors that will be discussed ^{later} in another section of this paper.

In 1939 and 1940 (Tables 8, 9, 10 and Figure 7), more than half of the largemouth bass spawned during the first week of the season whereas in 1941, the majority of the fish spawned during the third week of the season. The spawning gradually decreased after the first week in 1939. The 1940 and 1941 seasons are characterized by two peak spawning periods, in the first and third weeks. One interesting thing that occurred only in 1941 was that spawning took place in two nests after a lapse of over two weeks when there was no largemouth spawning (Figure 7). No explanation can be given for this. Surber (1943) found that a second spawning

Table 8.--The number of new nests found in Deep Lake each week for all species during the spawning season of 1939.

Weekly period	Largemouth bass	Rock bass	Pumpkinseed	Bluegill
May 12 - 18	15	1
19 - 25	7	16	13	...
26 - June 1	1	10	65	163
June 2 - 8	...	13	19	152
9 - 15	...	3	11	28
16 - 22	...	4	3	108
23 - 29	...	1	5	49
30 - July 6	...	1	3	41
July 7 - 13	1	13
14 - 20	9
21 - 27	1	48
28 - August 3	10
Totals	23	49	121	621

Table 9.--The number of new nests found in Deep Lake each week for all species during the spawning season of 1940.

Weekly period	Largemouth bass	Rock bass	Pumpkinseed	Bluegill
May 28 [↓] - June 3	35	4	1	...
June 4 - 10	6	11	62	63
11 - 17	15	8	28	122
18 - 24	...	4	8	88
25 - July 1	...	1	7	101
July 2 - 8	13	88
9 - 15	12	33
16 - 22	10	112
23 - 29	38
30 - August 5	19
August 6 - 12	13
13 - 19	2
Totals	56	28	141	679

[↓]The first observations were made at Deep Lake on June 1, by the writer; Dr. D. S. Shetter visited the lake on the afternoon of May 27, at which time only one largemouth bass nest had been completely cleaned and other largemouth bass were just beginning to clean nests. Therefore, actual spawning first occurred sometime between May 28 and June 1.

Table 10.--The number of new nests found in Deep Lake each week for all species during the spawning season of 1941.

Weekly period	Largemouth bass	Rock bass	Pumpkinseed	Bluegill
May 1 - 7	9
8 - 14	5
15 - 21	21	6	26	1
22 - 28	3	10	17	97
29 - June 4	0	9	18	87
June 5 - 11	0	18	15	86
12 - 18	1	9	2	3
19 - 25	1	12	14	140
26 - July 2	...	2	2	86
July 3 - 9	...	1	3	70
10 - 16	19
17 - 23	6
24 - 30	23
31 - August 6	9
Totals	40	67	97	627

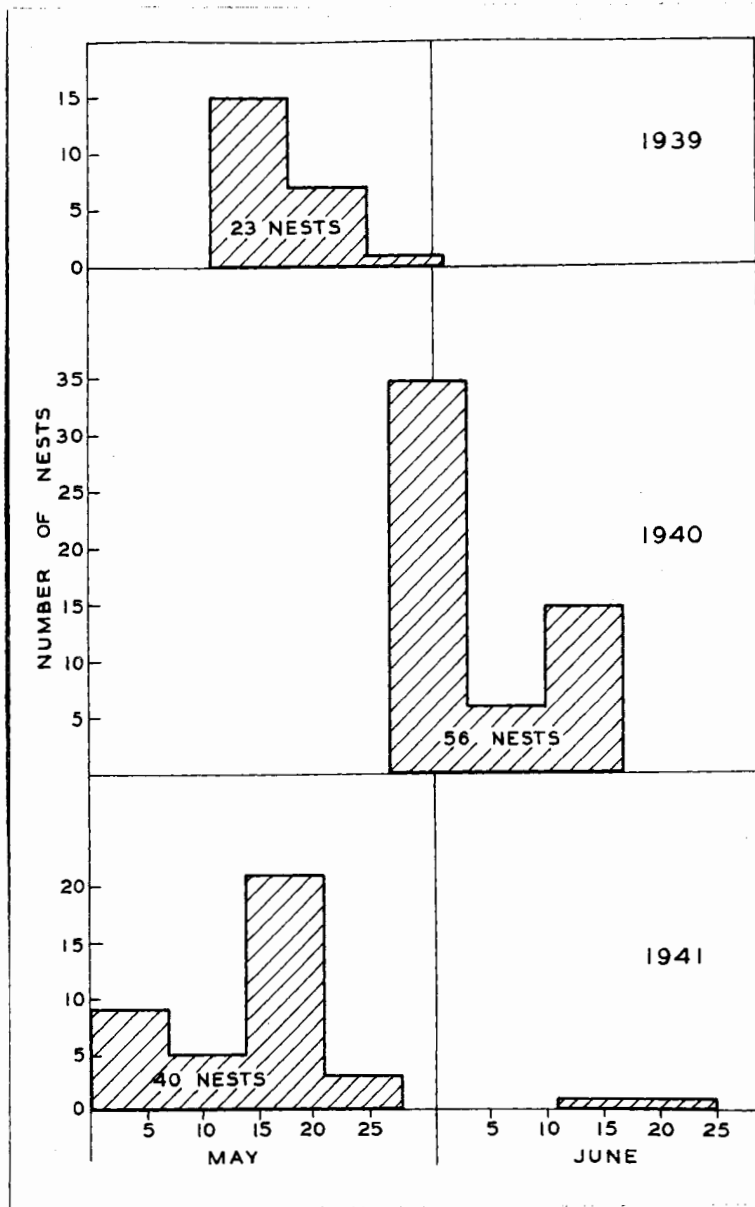


Figure 7.--The number of new largemouth bass nests in Deep Lake each week of the spawning seasons of 1939, 1940 and 1941.

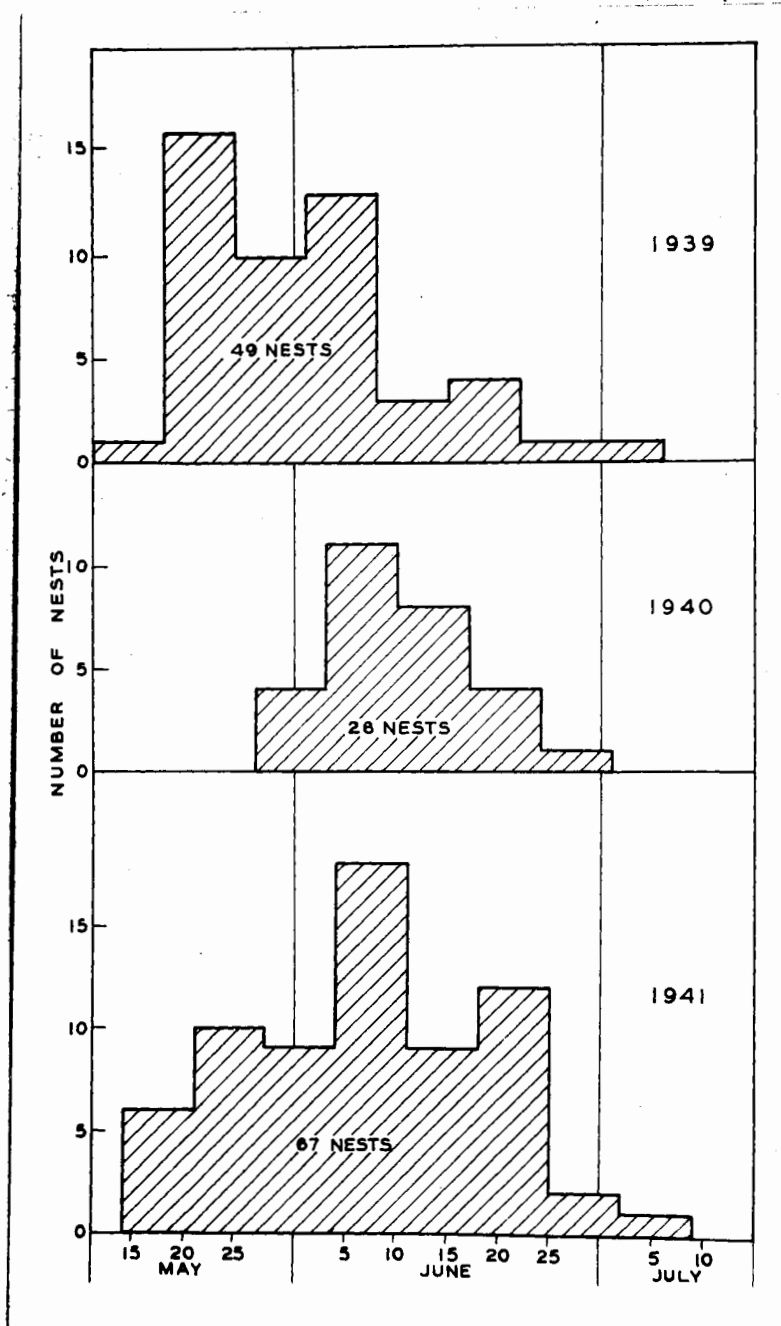


Figure 8.--The number of new rock bass nests in Deep Lake each week of the spawning seasons of 1939, 1940 and 1941.

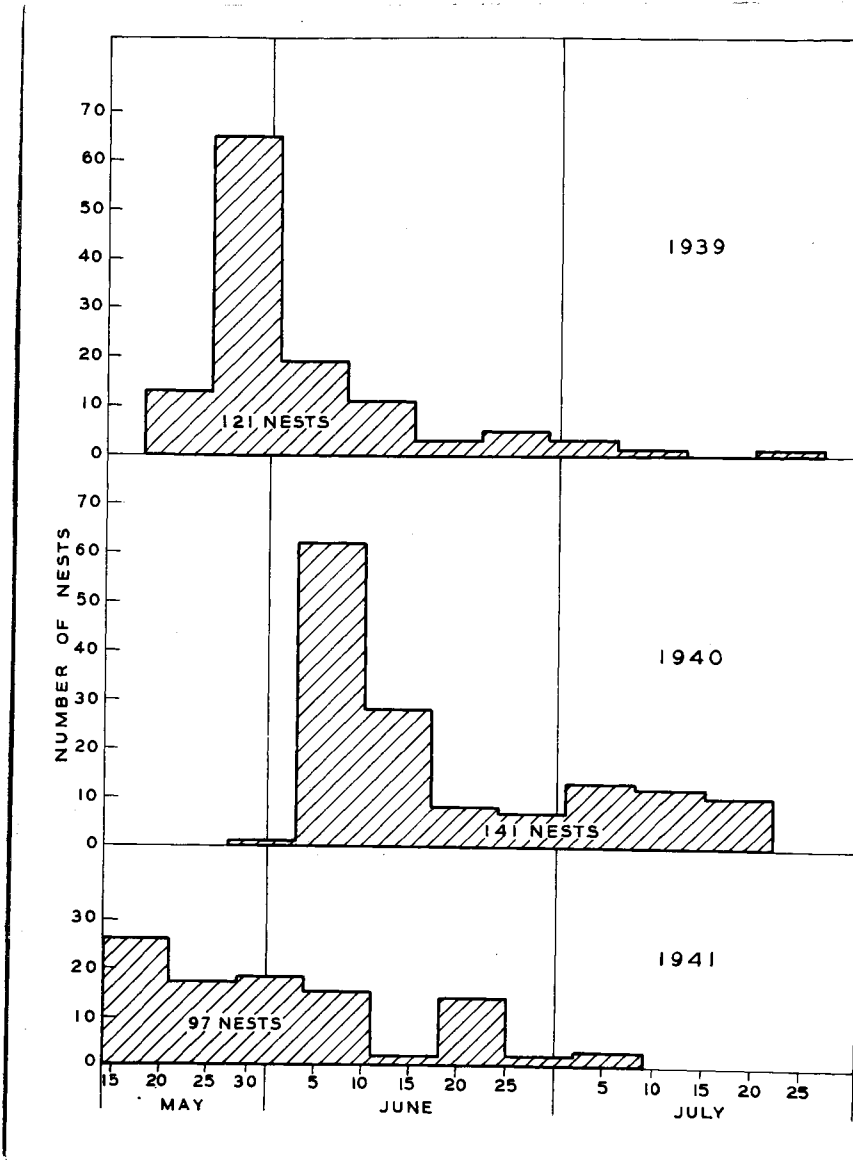


Figure 9.--The number of new pumpkinseed sunfish nests in Deep Lake each week of the spawning seasons of 1939, 1940, and 1941.

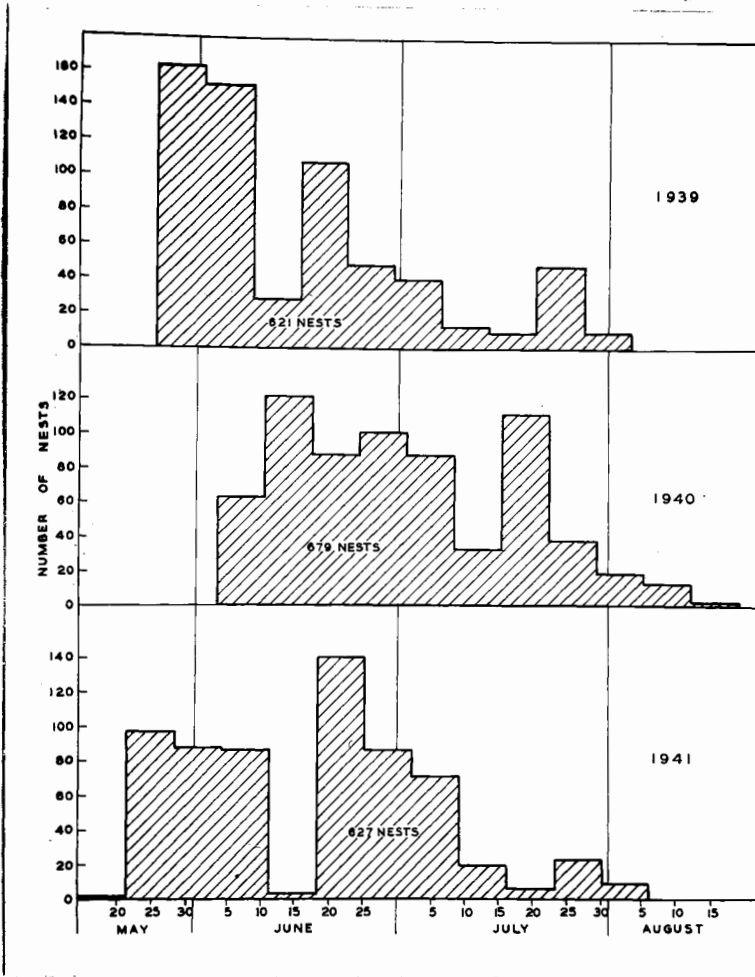


Figure 10.--The number of new bluegill nests in Deep Lake each week of the spawning seasons of 1939, 1940 and 1941.

period of considerable consequence occurred in the smallmouth bass in the South Branch of the Potomac River. The fry that resulted from the first spawning were all destroyed by a sudden rise in the water level. The second spawning of smallmouth occurred after a month of cold weather and amounted to about one-quarter of the principal spawning. In Deep Lake it was found that almost all largemouth bass nests contained some dead eggs or fry and occasionally all eggs on some nests were dead. Whether or not these two largemouth bass had all of the eggs or fry on their first nests destroyed (if they had spawned previously) is not known. But if this did happen, how would the particular females concerned know that this happened? Or why didn't some largemouth bass spawn late each year? It may be that weather conditions (the water temperatures were actually on the downgrade from late in May until June 15 when the first bass spawned) in 1941 were such that several females matured another batch of eggs. Or it may be that the eggs of several small females did not mature until later in the season and at that time they found males that were also ripe and spawning occurred.

In general it appears that given ideal conditions (favorable temperatures, etc.) the majority of the largemouth bass will spawn during the first week of the season.

The 1939 and 1941 rock bass spawning seasons are characterized by three distinct periods of intensive spawning (Figure 8). These peaks occur in the second, fourth, and sixth weeks of the spawning period. Only about half as many fish spawned in 1940 as in either of the other two years, and the peak of the spawning occurred in the second week that year and then gradually decreased.

Although the pumpkinseed sunfish spawning season is prolonged, the majority of the fish spawned during the first three weeks of the season in each of the three years (Figure 9). In the sixth week each year a slight increase in spawning was noted. After these periods of intensive activity, spawning gradually decreased toward the end of the season.

The spawning season for the bluegill was longer than for any of the other species. The majority of the bluegills spawned during the first part of the season (Figure 10). In each year there were three major periods of intensive spawning. Toward the end of the season, the number of nests decreased more or less gradually.

Some nests constructed by individuals of each of the species were never used for spawning. This was particularly noticeable in the bluegill, to a lesser extent in the pumpkinseed sunfish and rock bass and least of all in the largemouth bass. It is for this reason that the only nests that were counted were those actually containing eggs or fry. The data in Table 11 are presented as an example of the number of nests that were actually constructed by bluegills and the number of these used for spawning during one period of intense activity between May 21 and 26, 1941. The next spawning period did not start until May 30, 1941. Male bluegills cleaned a total of 154 nests in Deep Lake during this 6-day period and only spawned in 95 (61.7 percent) nests. The number of nests used for spawning in the various colonies ranged from 16.7 to 100.0 percent of the total number of nests constructed. The writer estimated that at least as many more bluegill nests are cleaned during each season as are actually used for spawning. Perhaps this is caused by a preponderance

Table 11.--Number of bluegill nests cleaned and the number of nests actually used for spawning in Deep Lake between May 21 and 26, 1941.

Bluegill colony number	Number of nests counted each day in each bluegill colony												Total nests clean	Total nests - eggs	Percentage
	May 21		May 22		May 23		May 24		May 25		May 26				
	Clean	Eggs	Clean	Eggs	Clean	Eggs	Clean	Eggs	Clean	Eggs	Clean	Eggs			
1	↓	...	13	4	25	10	25	8	25	0	25	0	25	22	88.0
4		...	3	1	3	1	3	1	3	0	3	0	3	3	100.0
14		...	6	0	7	0	7	1	7	0	7	1	7	2	28.6
5		...	10	1	10	0	10	3	10	0	10	0	10	4	40.0
15		...	24	3	24	0	24	4	24	0	24	0	24	7	29.2
6		...	9	2	9	2	9	0	9	1	9	0	9	5	55.6
16		...	12	7	17	6	17	0	17	0	17	0	17	13	76.5
17		...	3	1	3	2	3	0	3	0	3	0	3	3	100.0
8		...	5	1	5	2	5	0	5	0	5	0	5	3	60.0
9		1	30	13	30	5	30	0	30	1	30	0	30	20	66.7
11		...	4	0	6	1	6	0	6	0	6	0	6	1	16.7
12		...	12	2	12	8	15	2	15	0	15	0	15	12	80.0
Total or average		1	131	35	151	37	154	19	154	2	154	1	154	95	61.7

↓ Bluegills were cleaning spawning beds on this day and none were counted.

of males in the population and there were not enough females to occupy every nest. But the writer does not believe that this was actually the case. It appears that a better explanation would be that not all female fish are ready to spawn at the same time. Observations have shown that most male bluegills are ripe (running milt) before actual spawning occurs and many males remain in this condition for a short time after the spawning season has ended. All females on the other hand do not mature at the same time. Examination of the ovaries of female bluegills collected during one period of intensive spawning revealed that the various individuals were in all stages of maturity from fish that were already spent, to fish with intermediate-sized eggs, and others about ready to spawn. Also some bluegills spawned almost every day during the spawning season which extends over a period of several months. This would not occur if the eggs in all females matured at about the same time.

Observations that have been made on other lakes in Michigan indicate that many nests are constructed by the bluegill and pumpkinseed sunfish that are not used for spawning. There are usually some nests in some colonies that do not contain either eggs or fry.

An attempt has been made to correlate the number of nests that were actually used for spawning with the number of mature males and females (Table 12). Deep Lake was poisoned on September 12, 1941, at which time the entire fish population was killed. All of the fish recovered were sorted out by species and individual fish were sexed, weighed, and measured. Scale samples were taken from a random sample of the smaller fish and from all fish over 100 millimeters in length. In each of the species mature fish were considered to be: (1) bluegill and pumpkinseed

Table 12.--Correlation between number of nests in Deep Lake and number of mature males and females present when the lake was poisoned.

Species	Number nests in 1941	Total number mature fish ¹ at poisoning	Range in total length (millimeters)	Number males	Number females	Percentage males	Percentage females
Bluegill	627	728	100-272	303	425	41.64	58.36
Pumpkinseed	97	306	96-205	125	181	40.69	59.31
Rock bass	67	116	107-210	54	62	46.38	53.62
Largemouth bass	40	112	205-527	48	64	42.48	57.52

↓

The following were considered to be mature fish: bluegill, all fish in their fourth year of life, or older; pumpkinseed, all fish over 100 millimeters that were in their third summer, and all fish in their fourth year or older; rock bass and largemouth bass, all fish in their third year of life, or older.

sunfish - all fish over 100 mm. in length that were in their third year of life and all fish in their fourth year of life and older; (2) rock bass and largemouth bass - all fish in their third year of life and older. It is believed that all of the fish listed above would have been mature. Observations made at Deep Lake, and the examination of hundreds of fish at spawning time have shown that the division of mature and immature fish, as indicated, is quite accurate.

It is not known whether the number of males and females of each of the species that were taken when Deep Lake was poisoned on September 12 was the same as during the spawning season. Very little fishing was done after the close of the spawning season in 1941, and it is believed that the few fish taken by anglers and the fish that died of disease and from natural causes was probably compensated for by other fish that matured after the spawning season or by other fish that reached the size range and age of fish considered to be mature. Nevertheless, there are some discrepancies in these data, but they are all that we have and we must use them with certain reservations.

From the data presented in Table 12, it is evident that there was a decided difference between the number of male and female bluegills and the number of nests that were used for spawning during 1941 (303 males, 425 females, and 627 nests). The bluegill spawning period extended from May 21 to August 6, 1941. During this prolonged spawning period the largest number of nests counted in any period of intensive spawning was 95, between May 21-26. In other periods of intensive spawning, the following number of nests were counted: May 28-31, 90 nests, June 8-9, 86 nests; and June 16-19, 89 nests. Some bluegills were spawning almost

every day from June 20 to August 6. The largest number of nests counted during this period was 37 and the next highest number was 33. There were only two days when there were over 20 and less than 30 nests found, four days when between 10 and 20 nests were found, and on all other days there were less than 10 new nests enumerated. These data for the bluegill give added proof to the theory that the ova of all females do not mature at the same time and that both males and females spawn more than once during one spawning season.

A total of 67 rock bass nests were counted in 1941, and there were only 54 males and 62 females present in the lake. The rock bass spawning season extended from May 15 to July 6. Although the difference between the number of males and females and the number of nests is not as great for the rock bass as it was for the bluegill, the conclusion that both males and females spawn more than once during the spawning season also applies for this species.

In the pumpkinseed sunfish there were many more mature males (125) and females (181) than there were nests (97). The same was also true, but to a lesser degree, for the largemouth bass (48 males, 64 females, and 40 nests). These data for the pumpkinseed sunfish and largemouth bass do not necessarily mean that the males and females of these species spawn only once during the spawning season. Perhaps more than one female will spawn in one nest. It is also possible that our figures on the size or length at which males and females reach maturity may be too low. Evidence will be presented later in this paper to lend added proof that males and females of these species may spawn more than once during a season. Beeman (1924) records one instance where one male

smallmouth bass spawned with two different females in two different nests and another time when a male spawned alternately with two females in one nest. As the smallmouth bass and largemouth bass have similar spawning habits it is possible that male largemouth bass may spawn with more than one female.

Although some males and females of all of the species covered in this study may spawn more than once during a spawning season, the writer does not want to imply that all males and females will spawn more than once. As was mentioned in a previous section of this paper, some males of all of the species build nests that are never used for spawning. This might be due to an actual shortage of females or a shortage of mature females. As will be mentioned in the next section, the spawning season for all of the species was prolonged and there were periods during the season when spawning was more intensive than at other times. In between these periods of intensive spawning, all nests not containing eggs and fry were generally vacated by the guarding male. When new nests were made or old nests reclaimed for each cycle of spawning, the nests were occupied by new males or in some instances the same male was known to occupy the same nest. Therefore, the evidence indicates that only a portion of the available mature males and females spawn at one time.

Multiple Use of Nests

One of the most striking things brought out by this investigation was the multiple use of nests either by the same individual fish or by other fish of the same species or by fish of different species (Figure 2). There have been a few instances of this in the literature. Evermann and Clark (1920) found pumpkinseed sunfish nesting in bluegill colonies.

They did not state whether these nests were made by the pumpkinseed sunfish or by the bluegill. Because of the prolonged spawning season for both species, it is possible that either could have used the nests of the other sometime during the spawning season. Coggeshall (1924) found that bluegills use some of the same areas for spawning year after year. Ingram and Odum (1941) record one pumpkinseed sunfish nest that was used by three different occupants during one spawning season. Carr (1942) records two instances of two different largemouth bass nests that were used twice during one season; one of these nests was used twice by the same parent fish.

Many observations were made on the multiple use of nests at Deep Lake. It is possible that more observations could have been recorded had we left the nest markers (dowel sticks) in the lake for longer periods. Many of the observations that are enumerated below were made possible because of: (1) the presence of the different colored marbles that were

used to mark the nests at the beginning of this investigation; (2) because of the presence of the dowel stick nest markers; (3) because of the accurate description of the location of a nest recorded in the daily notes; and (4) because certain fish were found to be readily recognizable through individual peculiarities such as an injury, size of fish, etc.

The following observations are discussed separately according to the year and species.

1938

Bluegills cleaned and used nests (in colonies) that were apparently used the year before by bluegills.

Three different bluegills used nests that were previously prepared and spawned in by pumpkinseeds.

The same male bluegill fathered two different batches of fry on the same nest. This nest was used three times during this spawning season by bluegills.

The nests in one bluegill colony were used at least three times during the season.

A pumpkinseed used a nest for spawning that had been used previously by a largemouth bass.

One nest was spawned in by a pumpkinseed, rock bass, and another pumpkinseed.

Two different rock bass spawned in two nests previously used by pumpkinseeds (Plate 11).

Observations indicated that the fish that used a nest prepared by another fish usually revamped the nest a bit. For example, several pumpkinseed sunfish were observed using nests prepared previously either

by a largemouth bass or a rock bass. In these instances the pumpkinseed used only a portion of the nest; where the largemouth bass used roots, the pumpkinseed used gravel and sand.

1939

Bluegills spawned in colonies 1, 2, 3, 4, 5, 7, 8, 9, 10, 11, 12, 13, 15, and 16 in 1938 (See Figure 2). Colonies 6 and 17 were used in 1939 but not in 1938. Colony 14 was used previous to 1938 and in 1939.

Five different bluegills used nests prepared and used in 1939 by pumpkinseed sunfish and these were located in bluegill colonies. Two different single bluegill nests were previously used by pumpkinseeds.

Two bluegills spawned in nests constructed by largemouth bass.

Two different pumpkinseeds spawned in nests built by bluegills in 1938.

Three different pumpkinseed males used nests that were constructed by pumpkinseeds in 1938.

Six pumpkinseeds used nests previously spawned in by pumpkinseeds in 1939.

Four pumpkinseeds spawned in nests built by largemouth bass.

Four pumpkinseeds used nests built by bluegills.

Four different nests were used twice during the season by pumpkinseeds. One of these nest had also been used by a largemouth bass previously the same year.

Three rock bass used three nests constructed by largemouth bass.

Three rock bass spawned in nests previously used by pumpkinseeds.

Six different nests were used twice during the season by rock bass. One of these nests was originally built by a largemouth bass.

One rock bass used a bluegill nest.

One nest was used three times during the season by rock bass - twice by the same male.

On June 14, one rock bass nest was found containing eggs. On June 15, a pair of fish were found spawning in the same nest; the newly deposited eggs were scattered over the previously laid eggs. Presumably the same male was responsible.

Two largemouth bass were found on nests used by the same species in 1938.

One largemouth bass nest found containing eggs on May 20 was used for spawning again on May 22 before the other eggs had hatched.

1940

Bluegills used the following colonies for spawning in 1940: 1, 2, 3, 13, 4, 14, 14A, 5, ^{15,} 15A, 6, 16, 17, 7, 8, 9, 10, 11, 12, and 12A. Colonies 12A, 14A, and 15A were not used for spawning in 1938 and 1939.

Bluegill colony 5 was first used for spawning on June 5, 6 and 7 in 1940 when 11 nests were constructed. On June 12 these same nests were used for spawning for the second time. During the 1940 season some of the same nests were used by bluegills seven different times.

One nest was used by bluegills twice, once by a pumpkinseed and twice by largemouth bass in 1940.

Bluegill fry were collected from the same nest on three different occasions in 1940.

One single bluegill nest was used four different times, and another three different times in 1940.

Two pumpkinseed sunfish used nests that were constructed by largemouth bass.

As many as three pumpkinseeds have been found occupying nests within a bluegill colony of only eight nests.

A large hybrid bluegill-pumpkinseed was observed guarding a bluegill nest containing eggs. It is known that a male bluegill was in attendance on that nest on the previous day so the hybrid undoubtedly chased the male bluegill away.

Two different nests were used twice by pumpkinseeds during 1940.

A rock bass used a nest built by largemouth bass in 1940.

Three nests used by largemouth bass in 1939 were used again in 1940 by this species.

One nest was used twice by largemouth bass in 1940.

1941

The bluegill used the same colonies for spawning in 1941 that were used in 1940.

Observations on the other species were similar to those of previous years and will not be recorded here because no special effort was made to keep track of the multiple use of nests in 1941.

Duration of the Spawning Season

Pre-spawning period.--All of the Michigan centrarchids spawn during the spring and summer. The nests of all species are usually completed before actual spawning takes place. Spawning may occur from a few minutes to several days after the nests have been prepared (Figure 11). The pre-spawning period as used in this study, refers to that time when the nests were under construction or were already built, but no eggs had yet been deposited. (The post-spawning period is that interval immediately after the fry have left and the male fish was guarding an

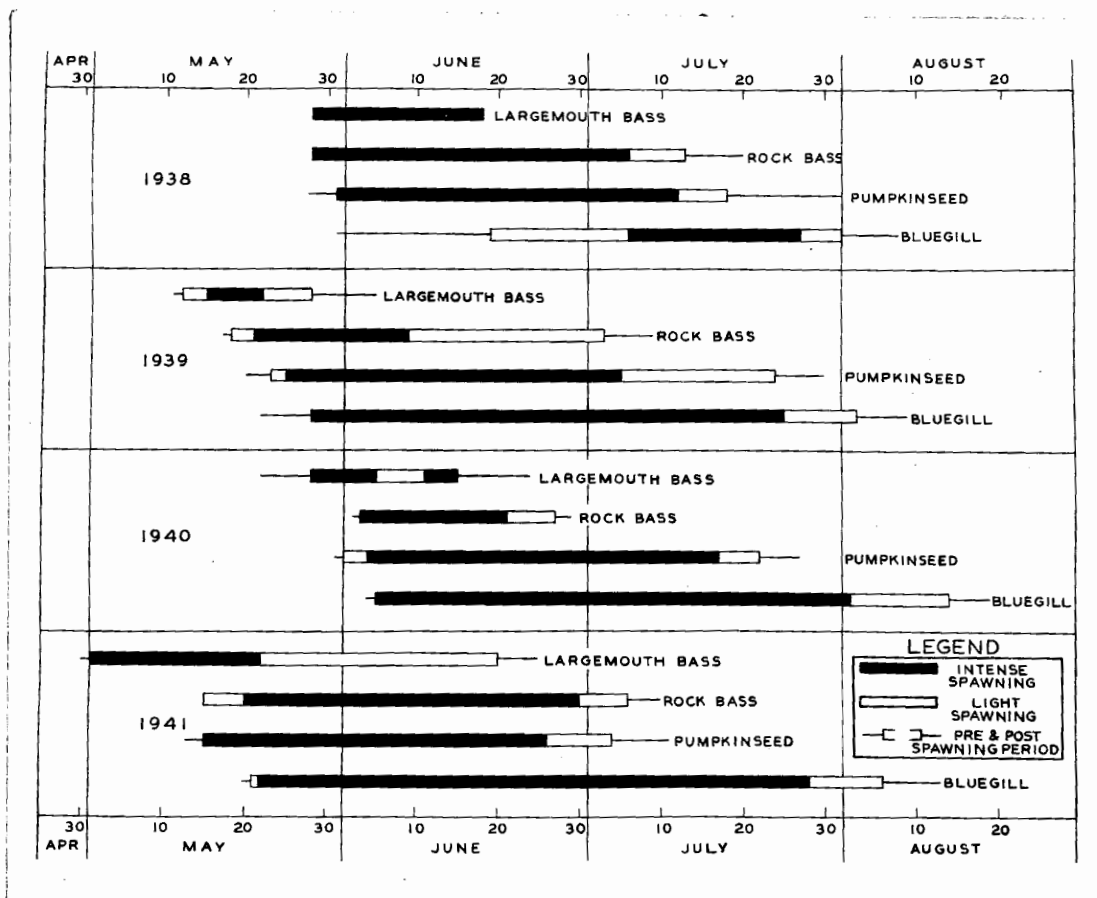


Figure 11.--Duration and intensity of the spawning season at Deep Lake, 1938-1941.

empty nest). Largemouth bass and rock bass usually spawn soon after the nest is prepared. Reighard (1906) found that smallmouth bass may spawn as soon as the nest is clean or some days later, depending upon the water temperature. Lamkin (1900) records an instance in which a largemouth bass guarded an empty nest for nine days. Carr (1942) states that largemouth bass guard empty nests for a longer period during the first of the season than later on. She cites records of four and five day intervals between nest construction and spawning. The pumpkinseed sunfish may also spawn soon after the spawning bed has been completed or several days thereafter. In the case of bluegills, spawning usually takes place a number of days after the nest has been finished, although in several instances nest construction and spawning occurred on the same day. From observations that the writer has made on fish caught throughout the season, it appears that the male fish usually ripens before the female, which may account in part for the male cleaning the nests some time before actual spawning takes place. Some nests are prepared that are never used. From observations made at Deep Lake, large numbers of nests will be cleaned on some warm days, but cool nights followed by cold days may inhibit spawning and none of these nests will be used.

Most of the species studied clean their spawning beds during the daytime. Bluegills, however, have been observed cleaning their nests at night.

Spawning season.--The spawning season as referred to in this paper includes the interval from the time the first spawning was observed until the fry have left the nest. There was considerable variation in the date of the first spawning of each of the species studied during the period covered by this investigation (Figure 11, Table 13). The

Table 13.--Dates on which spawning occurred in Deep Lake from 1938 to 1941.

Year	Largemouth bass	Rock bass	Pumpkinseed sunfish	Bluegill
1938	Before May 28-June 18	Before May 28-July 13	May 31-July 18	June 19-August 1
1939	May 12-May 28	May 18-July 3	May 23-July 24	May 28-August 3
1940	May 28 [↓] -June 15	June 3-June 27	June 1-July 22	June 5-August 14
1941	May 1-June 20	May 15-July 6	May 15-July 4	May 21-August 6

↓
The first observations in 1940 by the writer were made on June 1. Dr. D. S. Shetter visited the lake on the afternoon of May 27, at which time he found only one nest completely finished and numerous males cleaning nests. Spawning occurred sometime between May 28 and June 1.

largemouth bass was always the first species to spawn in Deep Lake. In 1938, the first spawning of this species took place just before May 28; in 1939, May 12; in 1940, between May 28 and June 1; and in 1941, May 1. The rock bass and pumpkinseeds started to spawn soon after the largemouth. The bluegill was always the last of the four species to start spawning each year. Centrarchids continued to spawn in Deep Lake until sometime during the month of August each year (Figure 11, Table 13).

The duration, in days, of the spawning season for each of the species in Deep Lake is summarized in Table 14.

The largemouth bass spawning period usually covered a shorter period of time than that of the rock bass, pumpkinseed, and bluegill, in that order. The considerable variation that is noted in the duration of the spawning season for each of the species in different years is undoubtedly tied in to some extent with the water temperature. But, the changes in the water temperature alone cannot be responsible for the extended spawning season. Some workers have observed that the largest fish of certain species are the first to spawn in any one spawning season (Clark, 1925; Hubbs, 1921, 1925). This may cause a prolonged spawning season. The depth of any particular body of water might also have some effect upon the maturation of the ova of fishes. Some fish may remain in the deeper, colder waters, while others of the same species may spawn earlier because they remain in the upper, warmer waters. That is not true at all times and with all species was determined by observations that the writer has made at various Michigan fish hatcheries. At the Drayton Plains Hatchery (Oakland County) where all of the bluegill rearing ponds are stocked with breeders, young of the year bluegills removed from rearing ponds in late fall are not always (but were for the

majority of the ponds drained), of the same general size, which indicates that the eggs must have hatched at about the same time. At the Fenton rearing ponds (Genesee County) which is also stocked with breeder fish, the young bluegills removed in the fall are of distinct size groups indicating that several spawnings occurred in these ponds. The presence in the ovary of eggs of varying sizes (to be discussed in more detail in a later section) has been definitely correlated with an extended spawning season. Bennett, Thompson and Parr (1940) observed that male bluegills matured at an earlier date than females, and that the apparent lag in the sexual development of the females continues throughout most of the summer.

In 1939, the writer had an opportunity to make a few observations on other Oakland County lakes in the general vicinity of Deep Lake. The last spawning in Deep Lake occurred on August 3, in 1939. The following observations were made:

August 3. Cruised most of the shallow water area of Pine Lake. Did not see any bluegill beds that appeared as though they had been used recently. Longear sunfish were still spawning.

August 4. Rowed around Deer Lake. Found several bluegill colonies on the sunken island in the middle of the lake that were still occupied. A few nests contained eggs and fry.

Rowed around Huntoon Lake. Saw better than 100 bluegills on nests many of which contained eggs and fry.

August 5. Rowed around Loon Lake. Many bluegill colonies were found, only two nests contained fry. Rowed around Lake Oakland. Found that bluegills were still occupying nests, although no eggs or fry were found.

August 7. Rowed around Orchard Lake. Found many bluegill nests. Some were still occupied, although neither fry nor eggs were observed.

From the observations listed above, it appears that bluegills in other lakes in the same general region were spawning at least a late in the summer as those found in Deep Lake. From fish hatchery records we know that bluegills start spawning in other lakes at about the same time in the spring and summer as they do in Deep Lake.

Most male fish of the species studied remain on their nests until the eggs have hatched and the fry have left. Largemouth bass usually guard their fry for periods varying up to two weeks or more after they leave the nest. Some fish will leave their nests as soon as the fry have risen, while others hover over their nests for days after all fry have left. We have one record of a fish remaining on its nest for two weeks after the fry departed. Precocious males, especially of largemouth bass, often construct nests that are never used for spawning and these males stay on their nests for varying periods of time. A partial explanation of why most males (outside of the largemouth bass) remain on their nests so long after all spawning is stopped, is that males (bluegills and pumpkinseeds) may remain ripe (actually "running" milt) long after all spawning has ceased.

Perhaps the best summary of the literature that can be found on the duration of the spawning season is that given in Adams and Hankinson (1928), and Breder (1936). Hankinson (1908) found that the breeding season for the pumpkinseed extended from May 21 until at least July 7 in Walnut Lake, Michigan. Leathers (1911) states that pumpkinseeds containing ripe eggs were taken as early as June 23, and males containing milt as late as August 20 in the region around the south shore of

Saginaw Bay, Michigan. Brass (1938) states that bluegills spawn from early June to the middle of July in south-central Michigan. According to the hatchery employees at the Wolf Lake Hatchery (Michigan) bluegills spawn over a period of about two months in many of the lakes used to supply their hatchery ponds with fry.

Stranahan (1912) states that the bluegill in the southern states spawn from early May till the latter part of September. He also found a school of bass on August 4, that had not been off the spawning bed for more than 2 or 3 days. Richardson (1913) observed bluegills building nests from May 1 to the second week in August near Havana, Illinois in 1911. The rock bass in Lake Maxinkuckee (Evermann and Clark, 1920) were spawning from the middle of May until June 15, whereas the pumpkinseed began nesting early in June and continued throughout the summer. According to James (1929) suitable temperatures for black bass spawning prevail in the more southerly states as early as February; in Tennessee it is March; and in southern Illinois, April; in Iowa, May; and in northern Minnesota, in June. He also says that sunfish and rock bass will spawn from one to two months longer than bass in the same waters, and that sunfishes and rock bass will continue nesting until the approach of cold weather in the fall. In 1938, Thompson and Bennett (1939) planted bluegills in Fork Lake between June 11 and 18. On June 22, the first spawning was noted and it continued throughout the summer. On September 15, some of the young bluegills varied in length from 3-3/4 inches to less than 3/4 of an inch. Bennett, Thompson and Parr (1940) found bluegills occupying nests from May 28 until September 18, 1939, in Fork Lake. Ingram and Odum (1941) observed pumpkinseeds constructing nests

on May 20, 1940, and actually observed spawning from June 15 to July 17, although spawning might have begun earlier. All nests were abandoned by August 3. Lueth (1942) gives the spawning season for Illinois largemouth bass as May or early June, and for bluegills as May to September. Carr (1942) found largemouth bass spawning from March 12 to 29, 1939. Swingle and Smith (1943) state that bluegills in Alabama spawn at irregular intervals each month from April to October. They also found that small largemouth bass spawned later than large bass and that bass began to spawn in 1942 within a five-mile radius of Auburn, Alabama, in different ponds in April, May, June and early July.

Perhaps one of the most interesting things brought out in this study has been that the spawning period was prolonged for all species studied except the largemouth bass (Tables 13, 14, and Figure 11). This important fact has quite an effect on several basic problems dealing with the availability and amount of suitable bottom for spawning, the opening of the fishing seasons, the maturation of ova, and the necessity for planting bluegills in our inland lakes. These subjects will be discussed later in this paper under separate headings.

Spawning vs. fishing season. The fishing season for bass and sunfish opens on June 25 in Michigan. By this time each year the largemouth bass have completed their spawning in most lakes (Figure 11). The majority of the rock bass in Deep Lake had also completed spawning on this date, but the pumpkinseeds were usually just at the height of their spawning and the bluegills were not quite half through. The duration of the spawning season for Deep Lake fishes is thought to be more or less the same for similar species in the same general region in Michigan.

Considering the prolonged spawning season for these species this writer believes that it would be unnecessary to change the opening of the fishing season to a later date, because enough fish, both adults and young, would survive to maintain the population. In fact any decrease in the numbers of adults and young would probably result in better growth and survival of those fish that were left. The following is quoted from Swingle and Smith (1943, p.3): "With such a long period during which spawning (bluegills) is possible, protection during the spawning period would certainly appear unnecessary. It is significant that nowhere in the United States have carefully controlled experiments shown that such protection is necessary for bluegill bream."

Correlation between spawning and water temperature. Just what effect the temperature of the water has on the time of spawning of centrarchids has never been clearly explained. Various workers have noted that the spawning season for many centrarchids is prolonged and that cycles, i.e., several periods of intensive spawning activity each followed by periods of less intense spawning, frequently occur. Seldom have sufficient temperatures been compiled from any one body of water during one or more spawning seasons to give the true correlation between temperature and spawning. Most investigators have given the dates of spawning but have omitted temperatures, or if the temperature is given, it is for the first day of the spawning season.

Lamkin (1900) reported that largemouth bass started to prepare their redds on April 1 when the water temperature was 56° F. and spawning took place on April 9 when the water temperature was 66° F.

Reighard (1906) states that largemouth bass spawning may start as soon as the nest is clean or some days later depending on the water temperature.

James (1929) observed that the suitable temperature for ^{the} spawning of black bass is between 58° and 68° F.

Tester (1930) pointed out that the time of spawning for smallmouth bass, depending on the temperature of the water, varies with the geographical latitude, with the size of the body of water, and the earliness or lateness of the season.

Wiebe (1935) states that it is assumed that largemouth bass do not spawn at temperatures much below 64° F.

Breder (1936, page 2) writes "apparent differences in the reproductive dates are probably to be associated in most cases with the speed of the rise to the temperature at which they spawn....It may also be mentioned that the reaching of a certain absolute thermal value has relatively little to do with the actual spawning. It is rather the antecedent temperatures, their duration and fluctuations, that determine to a considerable measure the metabolic rate of the gonadal development in such poikilothermal animals." He also states that the size and depth of the lake, pond or stream, the temperature, and the amount of water entering a lake or stream and general weather conditions influence the seasonal change. This is further borne out by the examination of Figure 2. Breder found largemouth bass nesting at a water temperature of 70° F.; bluegills, 76° F.; and pumpkinseeds, 68 to 84° F.

Brass (1938) claimed that bluegills spawn when the water temperature is between 62° and 70° F., and is intermittant because of temperature changes.

Bluegills were first observed nesting on May 28, in Fork Lake, Illinois (Bennett, Thompson and Parr, 1940) when the water temperature was 77° F. Average water temperatures in Fork Lake remained well above

70° F. from early May until the middle of September and bluegills were observed on their nests until late in September.

Breder (1940) found that the temperature of the water had an effect in controlling the abandonments and reoccupation of pumpkinseed nests. This, however, was not completely responsible because on one day two nests were abandoned and one was begun.

Ingram and Odum (1941) found no noticeable difference in the activity of nesting pumpkinseed sunfish on cold days (water temperature 50-60° F.), and on warm days (water temperature 61-70° F.).

Pumpkinseeds were found to be guarding nests in Connecticut (Thorpe, 1942) when the temperature ranged from 71° to 80° F.

Swingle and Smith (1943) declared that it was evident that there was no particular temperature of water at which egg-laying began because in 1942, largemouth bass spawning began in the middle of April in one pond, during May and June in others, and in the first week in July in another pond. All of these ponds were within a five-mile radius of Auburn, Alabama.

The comparison between the number of nests and the water temperature for the years of 1940 and 1941, for the species studied at Deep Lake is presented in Figures 12 and 13. During these two years sufficient water temperatures were taken for a comparison of this kind. In both years a total of 9 minimum-maximum thermometers were in the lake for the duration of the spawning season. An air and water thermograph was also present these two years, and was installed long before spawning started in the spring and was not removed until long after all spawning had ceased in the fall. The data presented in Figures 12 and 13 are the minimum-maximum water temperatures taken from the thermograph which was set at

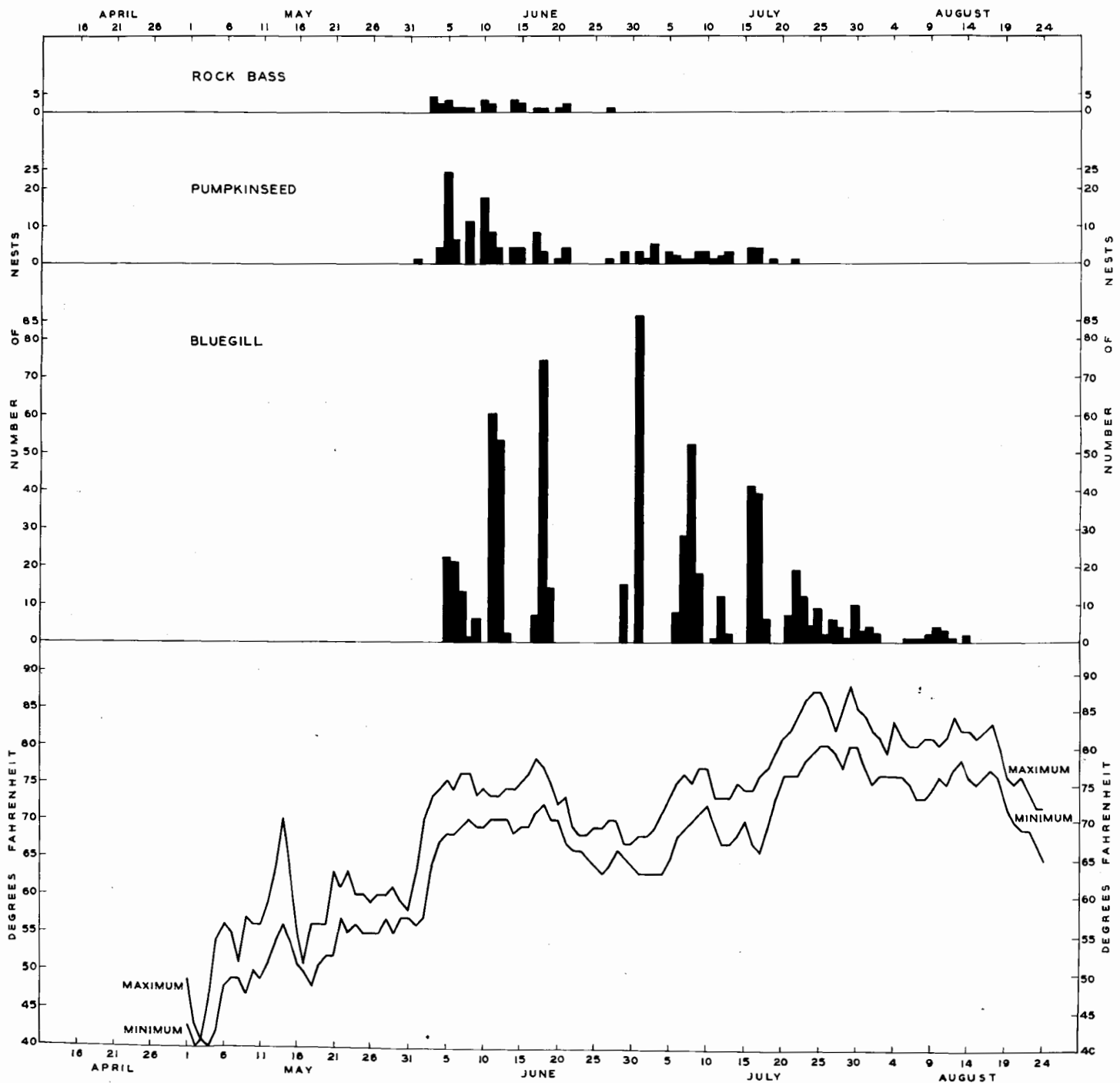


Figure 12.--Correlation between the minimum and maximum daily water temperature (recording thermograph, depth 18 inches) and the number of nests in Deep Lake in 1940.

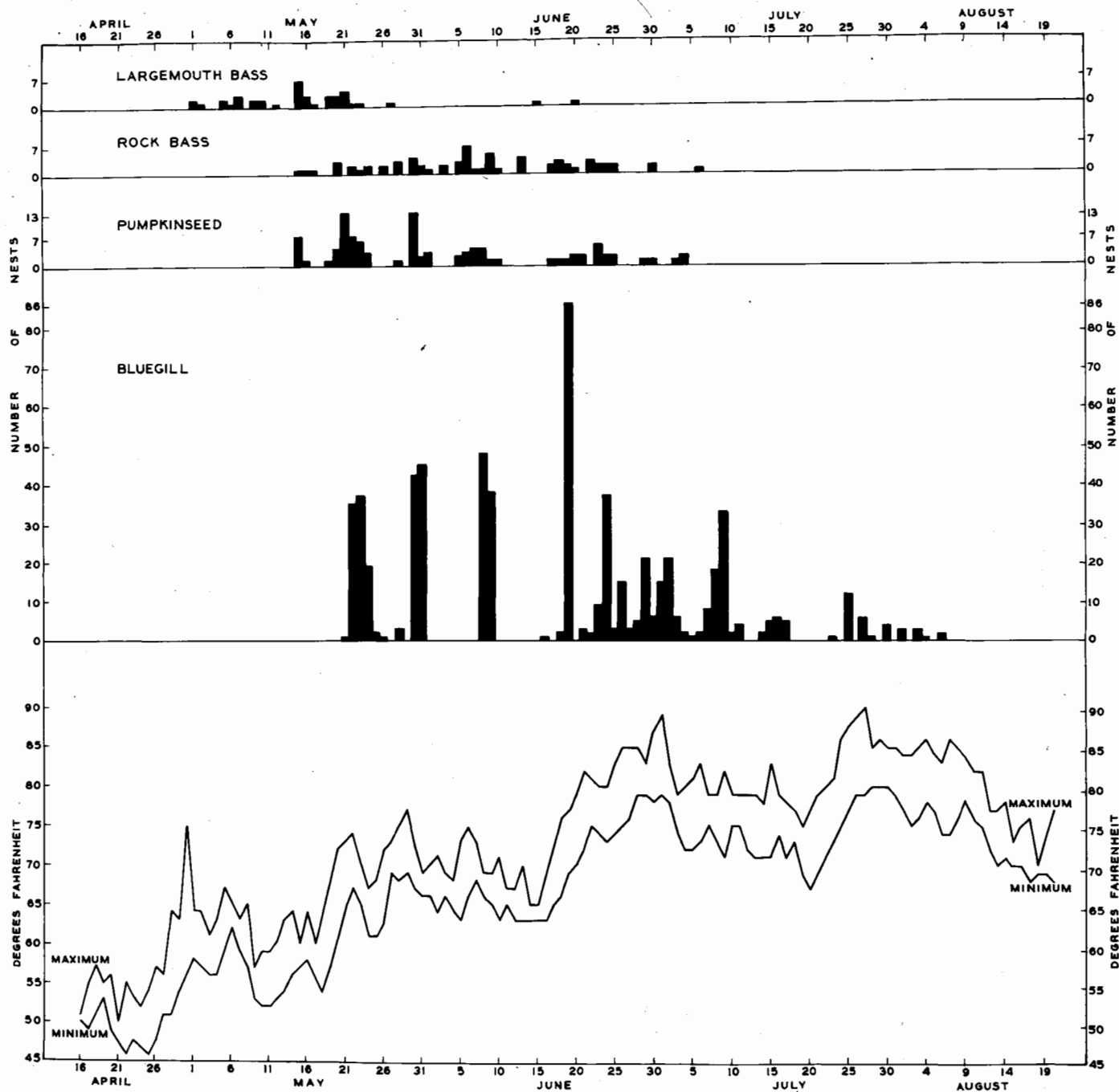


Figure 13.--Correlation between the minimum and maximum daily water temperature (recording thermograph, depth 18 inches) and the number of nests in Deep Lake in 1941.

a depth of 18 inches. These temperatures are similar to the temperatures provided by the minimum-maximum thermometers and were used because they are probably more accurate and show the trends in temperature much better. The minimum-maximum thermometers were not read at the same time each day, consequently if one reading was made late on the afternoon of one day and early on the morning of the following day, the minimum or the maximum temperatures for either day may not have been reached. It must also be noted here that the minimum-maximum thermometers were not always placed in the lake until a few days after spawning had started. All of the temperatures recorded for the minimum and maximum thermometers are listed in the Appendix. Although some temperatures were taken in 1938 and 1939^{1/}, (with a pocket thermometer) the temperature records were more inclusive in 1940 and 1941.

Correlation between number of nests and water temperature - 1940. The data on the number of largemouth bass nests for 1940 was not included in Figure 12, because spawning was already underway when the first observations were made, and had probably been going on for several days (no observations were made between May 28 and June 1). Therefore the large number of nests listed for the first day (June 1) would present a false picture and could therefore not be correlated with the temperature of the water.

Besides largemouth bass, one pumpkinseed spawned on June 1, when the water temperature was 56° F. (minimum for the day), and this was preceded for a 10-day period when the water temperatures did not drop below 55° F. After the other species started to spawn on June 3, 1940, the temperature of the water did not drop below 63° F. at any time. Periods when no spawning took place can be correlated with a drop in

^{1/} A comparison of the temperature data from 1939 with those of 1940 and 1941, showed that a similar correlation existed between the temperature and the number of nests, as exhibited for 1940 and 1941.

temperature whereas periods when spawning occurs can be correlated with a rise in temperature or immediately following a rise in temperature.

Rock bass. The first rock bass spawned on June 3, 1940, when the minimum temperature reading for the day was 63° and the maximum, 73° F. (Figure 12). Some spawning occurred each day until June 9, when no new nests were found. On June 9, the water temperature had dropped from 70° F. (on June 8) to 69° F. On June 10 another "wave" of spawning occurred which was followed by a two-day lull. On June 14 and 15 another peak of spawning was followed by a day on which spawning did not take place despite the fact that the temperature was rising. On June 17 and 18 spawning was again resumed. The water temperature on June 17 was the highest found during the rock bass spawning season. The temperature started to fall on June 18. Rock bass did not spawn on June 19. On June 20, spawning was resumed again. The slight increase in the number of rock bass nests on June 21 is correlated with a slight rise in temperature. No spawning was noted between June 22 and June 27, on which date the last rock bass nest was found. Water temperatures took a decided drop between June 28 and 30, but then started to increase.

From a close examination of the number of rock bass nests as presented in Figure 12, it will be seen that there are seven distinct periods of intense spawning activity. Two of these occurred when the temperature of the water was definitely on the upgrade, four are correlated with a peak temperature, while one started when the temperature was high and continued, despite a drop in temperature.

Pumpkinseed sunfish. The first pumpkinseed spawned on June 1, 1940, when the water temperatures ranged from 56° to 63° F. No spawning took

place during the next two days, when the temperatures were increasing. From June 4 until July 22 when the last pumpkinseed spawned, a total of 16 separate periods of spawning are found (Figure 12). Five of these occurred while the temperature was increasing, eight when the temperature was at its peak and two while the temperature was going down. One period started when the temperature was at a low point and continued the next day when the temperature was going up.

Bluegills. In 1940 the first bluegills spawned on June 5, when the temperature ranged from 68° to 75° F. A total of 22 fish spawned on this day. All spawning peaks are closely correlated with an increase of temperature. Of the 13 major spawning periods, three occurred while the temperature was increasing (going up) one at the peak temperature and nine immediately after a peak temperature when it had started going down. This correlation between the lag in spawning and water temperature for the bluegills suggests that gonadal development is speeded up (a cumulative process) by an increase in water temperature. This apparent lag was very noticeable in 1939 and in 1941 (the latter to be explained later). Although this lag or retardation in spawning, following a rise in temperature, is more pronounced in bluegills, it nevertheless occurs in the other species studied.

The major peaks of spawning activity of one species are comparable with those of most of the other species studied. However, there is a closer correlation between the rock bass and pumpkinseeds than between these two species and the bluegill where the peaks of spawning usually occur a day or more after the temperature starts to rise.

It is interesting to note that there is a more or less even spacing of the major periods of bluegill spawning activity (Figure 12). The

number of days that elapsed between the major spawning periods were 6, 6, 12, 2, 5, 5, 5, ⁵16 and 8 days. This might mean that a period of either 6, 12, or 18 or 5, 10, ^{or}15 days might be required after one spawning before a new batch of eggs matures for a second spawning. Whereas the periods are 6, 12, or 18 days apart during the first of the season when the temperature of the water is colder, the periods are 5, 10, or 15 days apart as the water warms.

Correlation between number of nests and temperature - 1941. Again in 1941 (Figure 13) periods when no spawning took place are correlated with a drop in the water temperature, and periods when spawning occurred are definitely correlated with a rise in the water temperature, or follow immediate rises in temperature.

Largemouth bass. The first largemouth bass spawned on May 1, in 1941, (Figure 13) when the temperature of the water ranged from 58 to 64° F. The maximum temperature on April 30 was 75°. The lowest temperature recorded during the bass spawning period was 52° and more than half of the fish had spawned before the minimum temperature reached and stayed above 60° F. No spawning occurred on May 3 and 4, when the water temperature was as low as 56° F. On May 10 and 11, the minimum water temperature dropped to 52° F. Fish spawned on May 10 when the maximum temperature was 59° F. as compared to 57° F. on May 9, but no spawning was noted on May 11, although the maximum temperature was also 59° F. The peak of the spawning occurred on May 15 when the water temperature ranged from 57° to 60° F. following two days when the temperatures were higher (54° to 63° F. on May 13 and 56° to 64° F. on May 14). The next sharp rise in spawning occurred on May 21 when the temperature ranged from 65° to 73° F. which followed several days of steadily increasing

temperatures. Only three nests were found after May 23; one on May 27, during an increase in temperature and the other two on June 15 and 20 when the temperature ranged from 63° to 65° F. and 70° to 79° F., respectively. Of the six main spawning peaks, four are correlated with a drop in temperature immediately following a rise, and two occurred when the temperature was going up.

Rock bass. The first rock bass spawned on May 15, 1941, (Figure 13) which was also the day on which the largest number of largemouth bass spawned. The lowest temperature recorded during the rock bass spawning period was 54° F. (May 18), but the temperature never fell below 61° F. after May 20. No spawning was recorded for May 18 when the temperature was again low. The largest amount of spawning occurred on June 6, when the temperature ranged from 66° to 75° F., which was a peak temperature. The second high in spawning was on June 9, when the temperature ranged between 65° and 69° F. The last rock bass spawned on July 6, when the temperature was rising again. Of the 13 major peaks of rock bass spawning, 5 occurred when the temperature was rising, 3 when the crest of the temperature for that period had been reached, and 5 when the temperature was going down or had reached a low point.

Pumpkinseed sunfish. The pumpkinseed sunfish also spawned first on May 15. The temperatures during the spawning period are the same for as those listed above the rock bass. The first big spurt in spawning came on May 21 when the temperature was going up and before it had reached the peak. The next high in spawning occurred on May 30, immediately following the highest temperature (77° F.) recorded for the period of May 1 - June 18. The last pumpkinseed spawned on July 4. Of the 7 main

spawning peaks recorded for this species, 3 occurred while the temperature was increasing and 4 while the temperature was decreasing.

Bluegill. The first bluegills spawned on May 21 in 1941. On this day the water temperatures ranged from 63° to 73° F. The lowest temperature recorded during the bluegill spawning period (May 21 to August 6) was 61° F. (on both May 24 and 25) and spawning took place on both of these days. The minimum water temperature reached 63° on three occasions, June 5, 10 and from June 12 to 16. No spawning took place on any of these days except on June 16, the fifth successive day on which the water had remained at 63°, when one bluegill spawned. After June 20, the minimum temperature of the water fell below 70° F. only between July 19-21, and no spawning was noted on these days. Some bluegills spawned each day from June 21, the first day that the minimum water temperature failed to dip below 70°, until July 11 (a period of 21 days). On July 12 and 13 no spawning occurred although the water temperatures were 72 and 71° F., respectively. Spawning was again resumed on July 14 and continued through July 17. The minimum water temperatures were 71, 71, 74, and 71 for this four-day period. The highest water temperature recorded during the 1941 bluegill spawning season was 90° F. (with a minimum temperature that same day of 79° F.) and six fish spawned that day. The next highest water temperature listed for the season was 89° F. (with a minimum temperature on the same day of 79° F.) on July 1. On this day 15 new nests were found and on July 2, a total of 21 fish spawned. Of the total of 15 peak spawning days, five were on days when the temperature was rising, ^{two} when the temperature was at a high point, five when the temperatures were decreasing and three when the temperature was at the low point between two rises (peaks).

The first apex, on the curve illustrating the bluegill spawning period in 1941, occurred just 2 days later than a similar one for the pumpkinseed and the second one was just one day later than that for pumpkinseed. The fourth big spawning period for the pumpkinseed covered two days (Figure 13), and the second day corresponded with the third bluegill crest. The fourth and largest period of spawning activity for the bluegill occurred just two days later than a similar one for the rock bass. The fifth major peak for the bluegill came a day later than similar ones for the pumpkinseed and two days later than one for the rock bass.

The number of days that elapsed from one major spawning pinnacle (Figure 13) to the next in 1941 were 8, 8, 11, 5, 2, 3, 3, 7, 7, and 9, respectively. The temperature was going down throughout the entire third period. With a rise in temperature at the end of this period the following number of days elapsed between the cycles: 5, 2, 3, 3, 7, 7, and 9. Again, as in 1940, there is a suggestion of some more or less definite spacing between these periods of intensive spawning. Although correlated to a certain extent with water temperatures, it is entirely possible that the time necessary to complete ova development may enter into the picture. The periods of 8, and 8, may mean that either 8 or 16 days are necessary for ova development, and similarly the 11, 5, 2, 3, 3, 7, 7, and 9 suggests that this period may be some multiple of 5 days.

All major spawning peaks come during, at, or just after a rise in temperature, and most periods where spawning did not occur come when the temperatures were on the downgrade. This certainly suggests that temperature regulates spawning. But, how can water temperatures alone account

for the fact that spawning is still spotty during that period when water temperatures remain above 70° F.? Although spawning does take place each day, why such distinct peaks? It appears to the writer that the development of the ova is tied in with water temperatures and is the factor that regulates spawning. Given proper temperatures, spawning will occur whenever a new batch of eggs matures.

From an examination of the literature it was obvious that many investigators have mentioned the temperatures of the water when spawning began, but they do not list the temperatures during the period preceding the first day of spawning. The water temperatures for a period just prior to the first day of spawning at Deep Lake in 1940 and 1941 is presented in Table 15. A detailed examination of these data shows that none of the species studied started to spawn until the maximum water temperature reached 60° F. A closer correlation is found between the antecedent temperatures than for the temperatures on the first day. Apparently the cumulative effect of several days of warmer water are necessary to bring about the final spurt of development of the ova. Also, bluegills require a much higher average temperature before spawning than do any of the other species studied. No apparent difference either in the average antecedent, or first day temperatures is noted in the table for the largemouth bass, rock bass and pumpkinseed despite the fact that the largemouth usually is the first to spawn. It may be that rock bass and pumpkinseeds either require a slightly longer period for egg development than the largemouth bass, or else a rise in temperature of only one, or at the most, several degrees may be necessary for the former. Apparently then, the water temperature on the first day is not as important as the water temperatures immediately preceding the spawning.

Table 15.--Water temperatures on the first day and prior to the first day of spawning of centrarchids in Deep Lake in 1940 and 1941. All temperatures in degrees Fahrenheit.

Species and year	Temperature first day of spawning		Date of first spawning	Average antecedent temperatures		
	Minimum	Maximum		Number of days	Minimum	Maximum
Bluegill						
1940	68	75	June 5	5	60	68
1941	65	73 ^{1/2}	May 21	5	57	66
Rock bass						
1940	64	73	June 3	7	56	61
1941	57	60	May 15	7	54	61
Pumpkinseed						
1940	56	63	June 1	8	56	60
1941	57	60	May 15	8	54	61
Largemouth bass						
1941	58	64	May 1	7	50	60

^{1/2} Only one bluegill spawned on this day. On the following day a total of 35 bluegills spawned and temperatures ranged from 67° F. to 74° F.

From the data obtained on the correlation of the water temperature and the number of nests of Deep Lake centrarchids (Figures 12 and 13) it is evident that the theory that water temperatures alone regulate spawning activities does not satisfactorily explain the extended spawning season. For example, there are many cycles of spawning, that is, periods when spawning was intensive, and intervening periods of reduced activity, or when spawning ceased altogether. One theory that is proposed to account for the prolonged spawning season is that all eggs do not ripen simultaneously, but are deposited in "batches" at intervals. The development of the ova of females takes place at a slower rate at low temperatures and may require several days of high or increasing water temperatures for the sudden spurt necessary for maturity. This may explain in part the frequent occurrence of spawning when the temperature is on the downgrade after reaching a peak. During, or at a period of low temperature following spawning, the intermediate sized eggs (eggs which will develop that same season into mature eggs) develop slowly, but when the temperature starts to rise, these eggs develop at a faster rate until mature; consequently, spawning takes place when the temperature is actually on the downgrade. Spawning may cease, even if the water temperatures are up, if all females containing mature eggs have spawned and an indefinite period of time is required before the eggs of these or other females have matured. Further proof of the latter may lie in the more or less definite spacing of the major peaks of spawning (Figures 12 and 13).

Growth History of the Ova and the Number of Eggs per Female

When the writer first attempted to make egg counts on the bluegill, rock bass, pumpkinseed sunfish, and largemouth bass, it was immediately evident that eggs of all sizes, from tiny immature eggs to large ones, were present in the ovaries of all mature fish collected during the spawning season. It was also discovered that it would be extremely difficult, especially in the bluegill and pumpkinseed sunfish, to separate the mature eggs from the maturing (or intermediate-sized) eggs when making counts.

A survey of the available literature revealed that several sizes of eggs were reported present in the ovaries of mature largemouth bass at spawning time. But no hint of this was to be found in the literature for the other three species. Workers have also found that fish having more than two size groups of eggs in their ovaries (1) have a prolonged spawning season; (2) may spawn more than once in a season; and (3) may shed only a part of their ripe ova at one time (Calderwood, 1892; Fulton, 1899; Reighard, 1906; Thompson, 1915; Clark, 1925, 1929, 1934; Walford, 1932; Hickling and Rutenberg, 1936; Farran, 1938; Atkinson, 1939; Carbine, 1944).

Therefore at the suggestion of Dr. C. L. Hubbs, it was decided to make a detailed study of the growth history of the ova of the bluegill in an attempt to shed some light on the following questions: (1) does each female spawn but once in a season, or more than once? and (2) what is the size range of the mature eggs that are deposited by a spawning female?

METHODS

Collection of Materials

All fish used for this study were collected either by angling, netting, or by spearing. Most of the specimens were taken by hook and

line fishing and only a few with fyke nets. A spear was usually carried in the boat and several female fish that were actually spawning were speared. Three fish were collected after spawning in experimental pens. Each of the three fish was left in the pens for varying lengths of time so that a complete picture could be obtained of the growth of the ova after spawning. Samples were obtained throughout the spawning season and during the fall, winter, and early spring each year from 1938 through 1941. As complete a size range as possible was obtained each year.

Shortly after its capture each fish was weighed to the nearest gram and standard and total lengths were measured in millimeters. The ovaries when removed were preserved in 10 percent formalin. A sample of scales was also obtained from each fish.

Measurement of the Ova. To trace the growth of the eggs and the relationship between the various sizes present in an ovary, diameter measurements of ova were made by means of an ocular micrometer in a compound binocular microscope. The magnifications used gave a value of 0.04 mm., and 0.2 mm. for each micrometer unit. The diameter of the ova was determined by placing the micrometer in a horizontal position with respect to the field of the microscope and reading the vertical diameter of each egg without regard to its shape or position in the field of the microscope. Owing to distortion in the process of preservation, some ova are not perfectly spherical, and this method obviated any selection of the longest or shortest diameter. It gave measurements of the longest diameter of some eggs, the shortest of others, and intermediate ones for still others.

In an effort to test the dependability of this method, a random sample of eggs was obtained after all eggs in an ovary had been teased

apart. Measurements were made of the longest and shortest diameter and the vertical diameter of 500 eggs. The average between the longest and shortest diameter was then compared with the vertical diameter by plotting each as a frequency curve. When compared, the two curves showed very little variation and it was considered accurate enough to continue to take just the vertical diameter of all eggs. Clark (1925), who made similar tests of this method, found it to be reliable and the most satisfactory for constant use.

Because of the small size of even the mature eggs and the difficulty encountered in teasing apart all of the eggs contained in the ovaries of one fish, it was decided that the best method of making diameter measurements of ova would be to take random samples from various parts of the ovaries. A total of thirteen samples of eggs was taken from the ovaries of each fish. The location from which these samples were taken are as follows:

- 1 and 2 Right and left ovaries - anterior ventral.
- 3 and 4 Right and left ovaries - anterior dorsal.
- 5 and 6 Right and left ovaries - posterior ventral
- 7 and 8 Right and left ovaries - posterior dorsal
- 9 and 10 Right and left ovaries - anterior mesial third.
- 11 and 12 Right and left ovaries - posterior mesial third.
- 13 Region just above oviduct.

Careful measurements were made on the ova of twelve bluegills using this sampling method. The number of eggs in each size frequency in all of the samples was totaled for each fish. By this method of sampling, the various sizes of eggs appear in proportions approximating those in which they occur in the ovary. In the ovaries of all fish

collected before and after the spawning season, and for a few collected during the spawning season, all sizes of all of the eggs present in the samples were measured. Only those eggs over 0.2 mm. in diameter were measured for four fish that were collected during the spawning season (Figure 14). Because each polygon in Figure 14 is based on the percentage of the eggs in each size class, the areas of the polygons for those fish where only the larger eggs were measured are not proportional to the polygons for which all eggs were measured. The exaggeration thus produced though presents an excellent picture of the development of the maturing and mature eggs present in these ovaries. The number of ova actually measured for each of the twelve bluegills varied from 1,758 to 19,282. Fewer ova were enumerated from those fish where only the large eggs were measured.

Between two and four hours was required to measure each sample of eggs. The time required to complete the measurements for one fish placed a limit on the number of individuals used in this study. It is believed that enough data were taken to justify the general conclusions drawn here.

Because of the tremendous amount of time required to complete a study of this nature and the vast amount of material required, we were unable to trace the development of the ova for the rock bass, largemouth bass, and pumpkinseed sunfish.

GROWTH HISTORY OF THE OVA

Description of the Ovary and Eggs. The ovary of a female bluegill during the fall, winter, and early spring is flaccid and does not fill the body cavity. This contrasts sharply with the turgid condition just

before and during the spawning season. The greatest volume of the ovary is reached just before the extrusion of the first ova. The abdominal wall of the female during the spawning season is much distended and the female is easily distinguished from the male. This turgid condition causes the female at spawning time to swim awkwardly and rather sluggishly.

The ova of all mature fish are recognizable from external observation of the ovary at all times of the year. During the prespawning and spawning seasons, there is no sharp line of demarcation between the immature, intermediate, and maturing ova. The gradation from the smallest to the largest ova is gradual. In such fish as the northern pike and trout (Carbine, 1944) the demarcation between the immature and mature ova is so great that many workers have never suspected the presence of the smaller ova in the ovary.

During prespawning growth the immature, intermediate, and maturing ova show no segregation in the ovary. Only five ripe bluegills were collected during this investigation. Cross sections of the ovaries of these fish revealed that when entirely mature, the ova are freed from their follicles and collect in the lumen of the ovary (Plate 23). Other mature ova were still to be found intermingled among the immature and intermediate-sized ova. The length of time that the ripe eggs remain in the lumen of the ovary before deposition is probably brief. Two females that were speared in the act of spawning were stripped of a part of their ripe eggs. The eggs from one female ran freely whereas slight pressure was exerted to strip the eggs from the other. It was apparent from examining the ovaries of these ripe females that not all ripe ova are freed from the follicles at the same time. It is probable that the ripe ova are extruded at intervals.

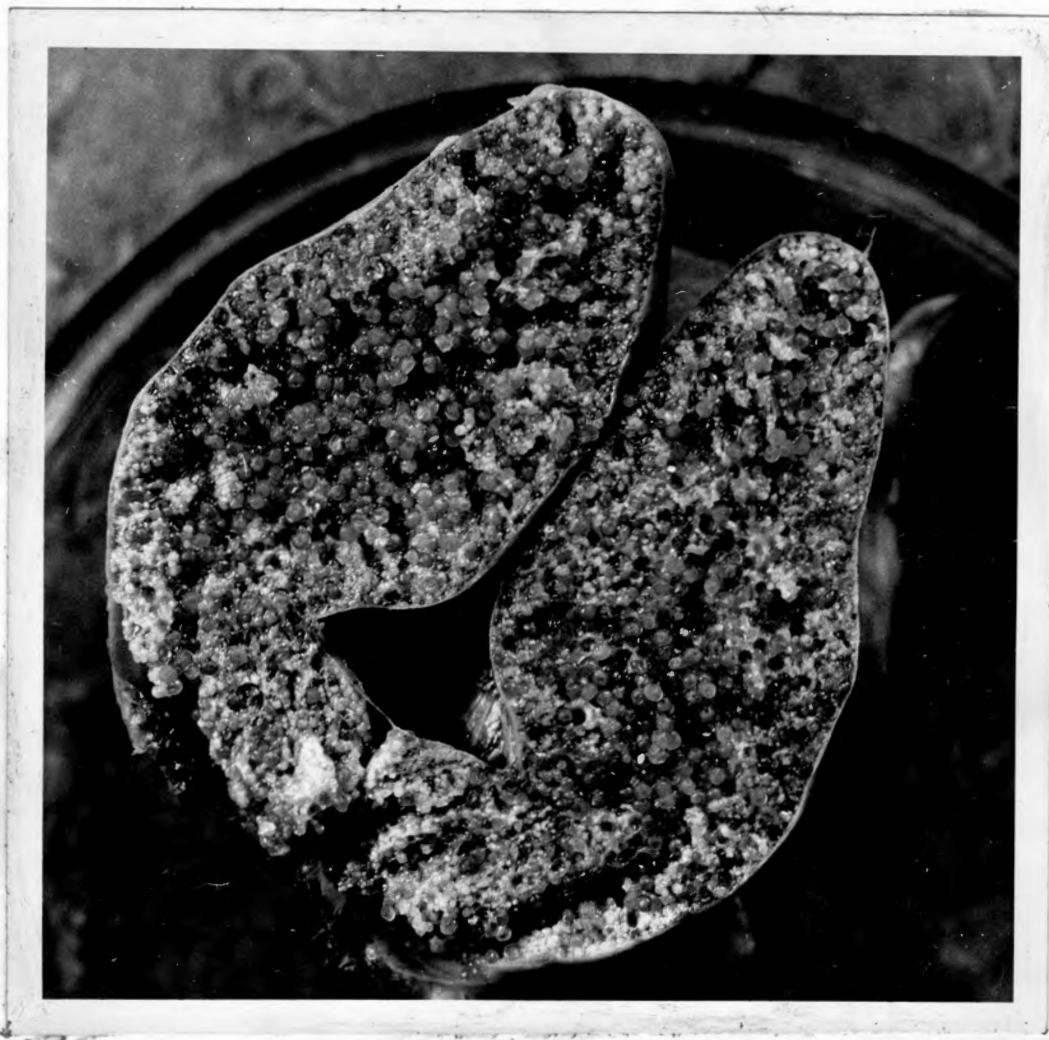


Plate 23.-Cross section of the ovary of a bluegill removed from the spawning bed while spawning. Mature ova, freed from their follicles, have moved to the lumen of the ovary. Many eggs have already been spawned from this ovary.

Three distinct groups of ova are present in all mature bluegills during the spawning season. The first, between 0.0 and 0.4 mm. in diameter, represent the immature eggs and are present in the ovary throughout the entire year. The second group, between 0.4 and 0.8 mm. in diameter are yellowish-opaque eggs present in the ovaries only during the prespawning and spawning seasons. (A very few may be present during the entire year). The third group, between 0.8 and 1.4 mm. in diameter, includes eggs ready or almost ready for spawning. If examined some time before spawning, all of this group will appear opaque, but will display a deeper yellow color than the intermediate-sized eggs. Ripe ova range in size from 0.9 to 1.4 mm., and are translucent. A batch of ripe eggs when placed in a small bottle or in a white pan are a golden-yellow color. The ripe egg of the bluegill is exceedingly delicate and ruptures at the slightest touch.

In several fish about ready to spawn, that were collected during the spawning season, several large (1.5 mm. in diameter), irregularly shaped, reddish-yellow eggs were found. It is believed that these large ripe eggs were left over from a previous spawning. Whether they were being resorbed or whether they would be extruded at the next spawning is not known. It was observed that these large eggs were extremely well embedded in the ovary and were exceedingly difficult to dislodge from their follicles.

Growth History of the Ova. In collections that were made after the spawning season and during the winter and early spring, all adult female bluegills contained eggs that were small (immature ova). Most of these eggs were under 0.4 mm. in diameter. Measurements of the ova resulted in a frequency polygon with only the one characteristic mode

at 0.05 mm. In the winter very few eggs were found that exceeded 0.4 mm., and the upper limit did not exceed 0.8 mm. This condition is illustrated in the uppermost polygon of Figure 14. In this fish, only 0.58 of one percent of the eggs were 0.4 mm. in diameter and over, and only 0.16 of one percent (17 ova out of 10,658) were over 0.4 mm. The condition of the ova of a fish taken more than a month after the spawning season is illustrated in the bottom polygon in Figure 14. In this fish, 85 ova (1.11 percent) out of the 7,653 ova measured ranged from 0.4 mm. to 1.0 mm. in diameter and only 60 ova (0.78 of one percent) were over 0.4 mm. Apparently a few of the larger eggs were retained from the previous spawning season in the ovaries of the two fish illustrated above.

This immature class of eggs (0.0 to 0.4 mm.) is present in the ovaries of every adult female bluegill during all seasons of the year. Any increase in size of the ova beyond this point has been considered as an indication of the beginning of the growth of the ova toward maturity for the approaching spawning season. Unfortunately we have not recorded the measurements showing the growth of the maturing ova just before the spawning season so that we cannot demonstrate the gradual development in size of the ova from the immature, to intermediate, to maturing stages. All bluegills that were collected from the beginning of the spawning season until the end of the spawning season, except those that had just completed spawning, contained eggs of intermediate size (0.4 to 0.8 mm.) and maturing ova (0.8 to 1.5 mm.). If all bluegills matured at the same time the growth of the ova to maturity could be readily traced. Because this is not the case in the bluegill, no chronological arrangement of the data obtained from ova diameter measurements could be made to show the

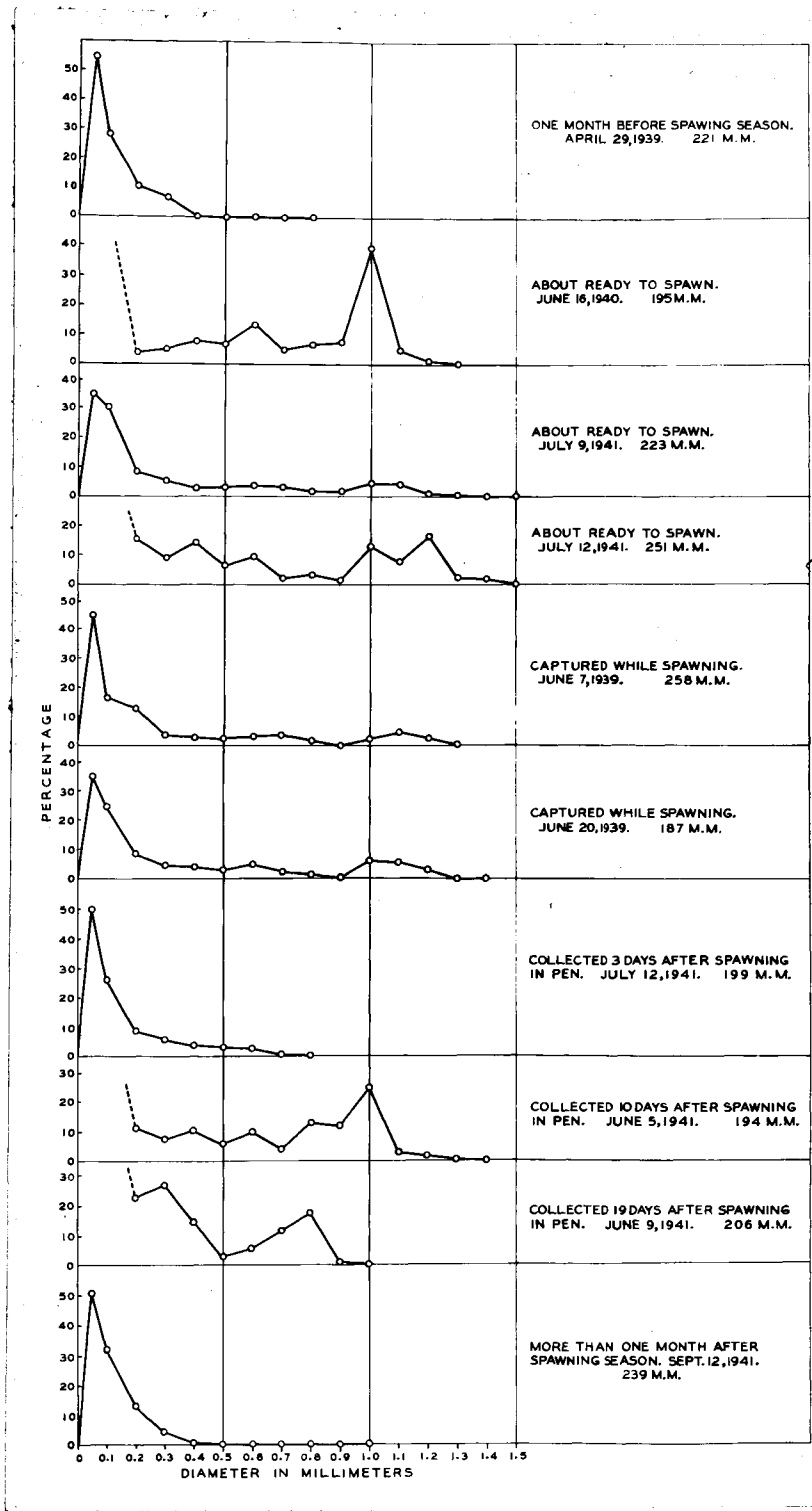


Figure 14.--Frequency polygons showing the growth history of bluegill eggs collected before, during and after the spawning season at Deep Lake in 1939, 1940 and 1941. See text for data concerning the collection of specimens and technique used in measuring eggs.

various stages through which the eggs pass before spawning. The closest approach to data of this type were obtained from fish that were kept in pens, allowed to spawn, and then killed at definite periods after spawning (Figure 14).

The polygons (second, third, and fourth from the top in Figure 14) for the fish that were collected before they had spawned during the spawning season, take on a multimodal character. It is possible to consider that each of these modes might represent eggs that have started to develop from the immature and intermediate classes of eggs at the same time. This growth from the immature to the intermediate class, and from the intermediate to the maturing class, probably occurs periodically as one group attains a constantly greater diameter. The second polygon from the top of Figure 14 probably represents a fish that is about ready to spawn, as do the two polygons below it. These last two fish though are nearer to actual spawning than the other. It is also possible that the two fish represented in these third and fourth polygons had spawned previously that same season, because one egg in each fish of the thousands measured was 1.5 mm. in diameter. These large eggs were irregularly shaped, firmly attached in their follicles and were of a deep yellowish-red color, and were very probably ova that were being resorbed. In none of the other fish were such large ova present.

Two fish were captured while in the act of spawning. Measurements that were made on the eggs from these fish are illustrated in the fifth and sixth polygons (from the top) of Figure 14. Three modes are visible in each polygon. In each of these polygons a group of immature eggs has started to develop to a larger size. It is this latter group of ova

that will probably develop into intermediate sized eggs soon after spawning has been completed and after the intermediate eggs start to mature.

Mature eggs of the bluegill range in diameter from 0.9 to 1.4 mm. The average diameter of the eggs stripped from these two females that were captured while spawning was 1.08 and 1.1 mm., respectively.

Figure 15 has been prepared to show the difference in size of the ripe eggs stripped from one of the female bluegills collected while spawning and the large eggs present in the ovary of the same fish. Only those eggs remaining in the ovary that ranged between 0.9 and 1.4 mm. were used for this figure because they were comparable in size with the eggs stripped from the fish. The eggs contained in the ovary were slightly smaller in diameter than the eggs that were stripped from the fish. This difference in size may be accounted for by the absorption of water after the eggs were stripped. But it is probable that this difference was due to the fact that the majority of the ripe eggs had either been deposited during spawning or stripped from the fish, leaving only a few mature and many maturing eggs in the ovary.

We were fortunate to obtain three females which were held for periods ranging from 3 to 19 days after spawning in experimental pens. The first one (seventh polygon from the top of Figure 14) was killed just three days after spawning. No eggs were present that were over 0.8 mm. in diameter. The absence of maturing and mature eggs can be accounted for by the fact that all eggs of these sizes were deposited while spawning. No decided growth of intermediate and immature eggs had yet occurred.

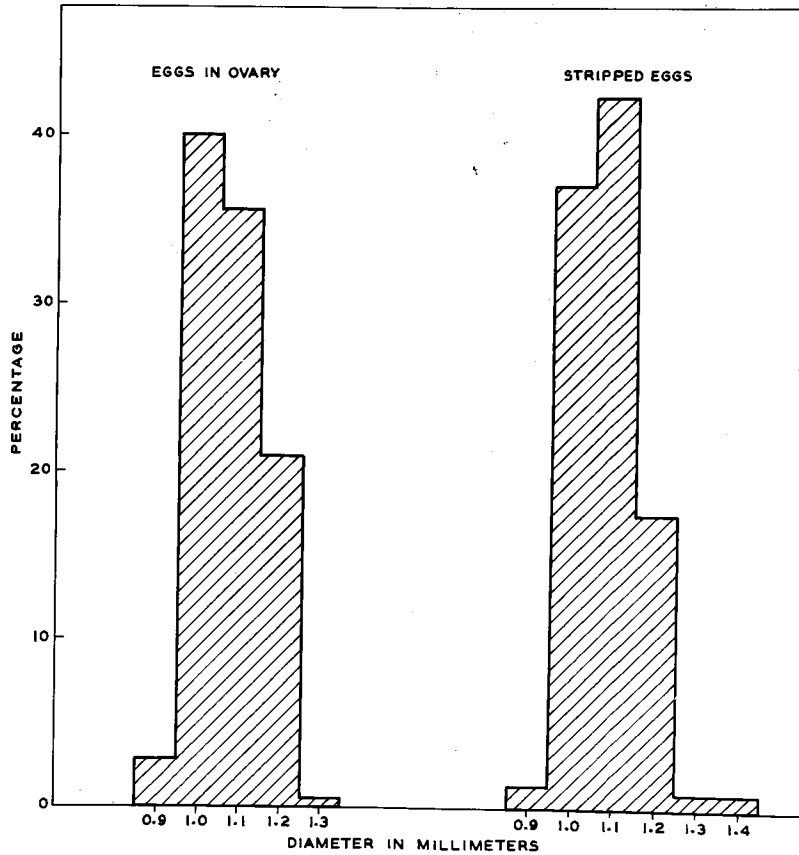


Figure 15.--Comparison between the size of eggs remaining in the ovary and eggs stripped from a bluegill collected at Deep Lake while in the act of spawning.

One fish was killed just ten days after spawning in a pen (ova measurements are illustrated in the eighth polygon from the top of Figure 14). The multimodal character of this polygon is an excellent illustration of the simultaneous growth and increase in size of various classes of ova. The large number of maturing eggs in this fish might indicate that spawning would occur again very soon.

Another fish was killed just 19 days after spawning in a pen. Measurements of the ova from this fish are illustrated in the polygon that is next to the bottom of Figure 14. Although the growth of the ova in this fish have not proceeded as rapidly as in the fish killed 10 days after spawning, it does illustrate the increase in size of one group of immature ova (mode at 0.3 mm.) and just one mode (0.8 mm.) for the intermediate sized ova. Perhaps this particular polygon could be used to illustrate the growth of the ova during the prespawning period. The lag in the development of ova in this fish as compared to the previous one (collected 10 days after spawning) might be accounted for by lower water temperatures or because the spawning season was farther advanced (by more than a month) than when the previous one was collected. When one group of ova matures and is spawned out, it is replaced by a new class moving outward from the intermediate group. But this movement probably occurs at a faster rate in some individuals than in others and the rate is probably increased during periods of warmer weather.

Calderwood (1892), from his observations on marine fishes in general, found three different sizes of eggs in all ripening ovaries. He considered that the large ova would be spawned during the present season, the medium sized ova the next year, and the minute ova in succeeding years.

Fulton (1899) states that species containing intermediate-sized eggs have a prolonged spawning period and that only a few eggs are deposited at one time or else they shed their eggs in more than one batch during the season.

Reighard (1906) describes three groups of eggs present in the ovaries of largemouth and smallmouth bass. He considered that the large eggs would be spawned during the present season, the intermediate eggs the following year, and the small eggs in subsequent years.

Thompson (1915) found three groups of eggs in the halibut: ripe ova, ova for the next season, and ova for future seasons. He traced the growth of the intermediate eggs and established the fact that they would mature the following season. He further divided the ripe ova into two groups: translucent ova which were ready to be spawned and large opaque eggs which would be spawned later that same season.

Clark (1925) made a careful investigation of the development of the ova for the grunion (Leuresthes tenuis), and found that when one batch of ova is spawned out, a batch of intermediate eggs develops to maturity and will be spawned out about two weeks later. Thus, after an individual starts to spawn, it continues spawning periodically throughout the breeding season. Clark (1929) determined, by ova diameter measurements, that the California jack smelt contains more than two sizes of eggs and spawns more than once in a season. Clark (1934) also studied the growth history of the ova of the California sardine, another species having more than two size classes of eggs, and concluded that individuals spawn more than once during a spawning season.

Walford (1932) determined from ova diameter measurements that the California barracuda spawns more than once during a spawning season. The

ovaries of the barracuda contain more than two sizes of eggs during the spawning season.

Hickling and Rutenberg (1936) have made a study of the ovary as an indicator of the spawning period in fishes. They conclude that there is an egg-stock of small eggs in the ovaries of all adult fishes. From this egg-stock, a quota is withdrawn each year to be matured and spawned and that each year a fresh supply of small eggs is added to this egg-stock. They measured the diameters of the ova contained in four species of fish with known spawning habits. They conclude that the diameter frequencies of the ova of a fish will serve as an index to the frequency of spawning.

The presence of several modes in the frequency polygons of ova diameters of maturing bluegills collected during the spawning season, before, during, and after actual spawning occurs, strongly suggests that individual bluegills spawn more than once in each spawning season. This cannot be accepted until it is proven that the intermediate sized ova are not spawned in succeeding years or that they never ripen and are resorbed at the end of the spawning season.

That the intermediate eggs of the bluegill are not spawned in succeeding seasons has been shown by measurements that were made of ova from fish collected after the spawning season had ended and before the next season. Only a small percentage (less than one percent) of intermediate-sized ova (0.4 to 0.8 mm.) were present in the ovaries of such fish. As this size class of ova were present during the entire spawning season, their disappearance was not due to spawning and was probably due to resorption.

Evidence has also been presented to show that after one batch of eggs has been spawned, groups of intermediate eggs start to grow towards maturity and also, that some immature eggs start to develop to intermediate size. Although distinct batches of intermediate ova do grow to the mature size in the ovaries of individual bluegills, this does not mean that more than one batch of eggs is actually spawned during the season by all female bluegills. Succeeding batches may never mature. The female bluegill that was killed 10 days after spawning in the experimental pen had actually developed ova to mature size after spawning once. The two modes (0.3 and 0.8 mm.) in the bluegill that was killed 19 days after spawning indicate that this fish was developing a new batch of mature eggs and a new batch of intermediate eggs. But it is not known whether either of these bluegills would have spawned again if they had not been killed.

From the microscopic study that was made on the eggs, it appears that the evidence justifies the belief that some female bluegills may spawn more than once each season. If there was only one spawning a season, it should seem reasonable to expect: (1) the presence of spent fish in the catch throughout the spawning season; and (2) the presence in the ovary of only 2 groups of eggs - mature and immature.

Since throughout each spawning season the ovaries of mature female bluegills contain intermediate-sized and maturing eggs and that no fully spent females were taken during the course of this investigation (except those in the pens), it seems fair to conclude that female bluegills may spawn more than once during a spawning season.

The presence of at least three modes in the ova diameter frequency curves, the fact that intermediate-sized eggs started development towards

maturity immediately after spawning, and the fact that occasional large, ripe, unspawned eggs are found in some ovaries containing a batch of newly ripening eggs are probably evidence enough to justify the conclusion that some female bluegills spawn more than once in a season.

Because of the body shape and the small abdominal cavity present in the bluegill it may be impossible for the female to retain all of the ripe ova it sheds during one season in its ovary at the same time. It can, therefore, be theorized that a gradual shedding of the ripe ova must occur. The gradual shedding of ripe ova at intervals would also help explain the prolonged spawning season for the bluegill.

The writer could find only one record in the literature in which it was definitely known that a female centrarchid actually spawned more than once during a season. Hubbs and Hubbs (1932) had one female green sunfish that spawned three times in an aquarium in one year. The dates of spawning were April 29, June 4, and July 12. (A total of 36 days elapsed between the first to second spawning and 38 days between the second and third spawning).

The immature eggs greatly outnumber the maturing eggs in the ovary of a bluegill about ready to spawn, but the volume of the maturing eggs vastly exceeds that of the immature eggs (Figure 16). To illustrate this relationship, measurements were made of the diameter of 6,657 ova comprising a random sample from the ovaries of a bluegill killed while in the act of spawning on June 20, 1939. This fish measured 187 millimeters, total length, and weighed 142 grams. The volume of the eggs in each size class was computed mathematically from the average diameter of each class. The number and volume of the eggs in each size class were computed and expressed as the percentage of the total number and of the

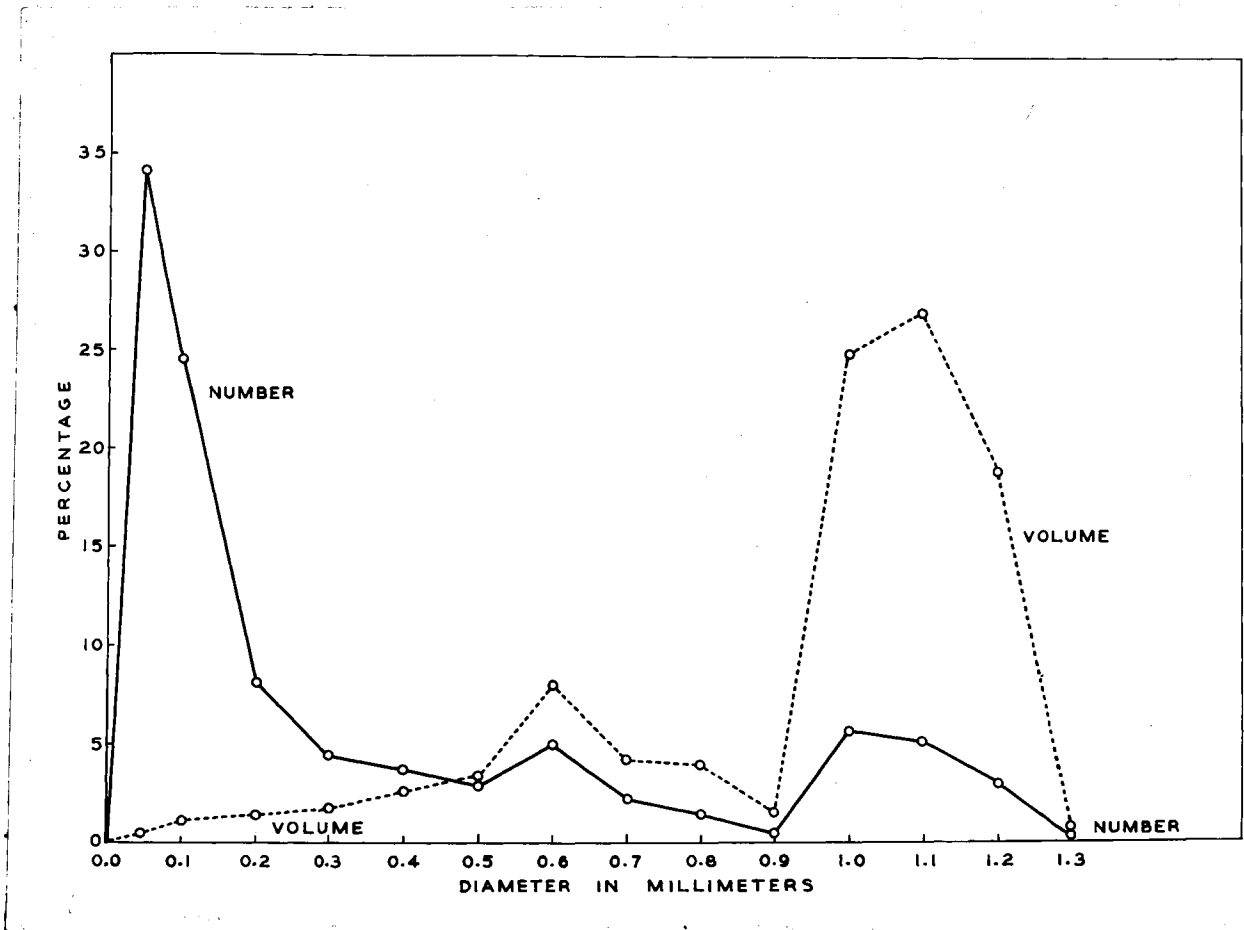


Figure 16.--Frequency polygons showing the proportionate number and proportionate volume of the eggs of each size class in the ovary of a mature bluegill. Based on measurements of 6,657 eggs, comprising a random sample of the ovary of a fish collected June 20, 1939, while spawning in Deep Lake.

total volume, respectively. Of the 6,657 eggs measured, the immature eggs (0.0 to 0.4 mm.) constituted 74.8 percent by number and 7.3 percent by volume; the intermediate ova made up 11.4 percent of the number and 19.9 percent of the volume; and the mature eggs composed 14.0 percent of the number and 72.8 percent of the volume (Figure 16).

The size group of eggs between 0.0 and 0.2 mm. far exceeded the numbers in all of the other size groups. This was true despite the fact that some of these small eggs might have been overlooked when measurements were being made. It would be extremely easy to overlook some of these no matter how careful the investigator was in teasing them apart.

An estimate was made of the number of eggs of the various size groups present in the ovaries of a bluegill. A nearly ripe fish, 223 mm. in length, collected on July 9, 1941, was selected for this study. The ovaries of this fish were weighed on a set of analytical balances and a sample comprising 4.785 percent of the entire ovary was removed and all ova in the sample were measured and counted. A total of 19,282 eggs was present in this sample. It is estimated that this bluegill contained a total of 402,968 eggs, of which 308,270 were immature, 47,550 of intermediate size, and 47,147 mature. Enough small eggs for several spawning were therefore present in the ovaries of this fish.

Number of Eggs per Female. Because so few bluegills were taken that were ripe and ready to spawn, and because individual fish may spawn more than once in a season, determinations of the number of eggs spawned by each female was difficult. This was due primarily to the uncertainty introduced as to whether any enumeration has included all of the eggs destined to be spawned during the current season and none that are to be

spawned during the following season. It was impossible to determine the number of eggs that would be deposited by one female during the entire spawning season. The data presented here include only the number of eggs capable of being deposited at one spawning. These counts, although not complete, are considered minimal, and will make it possible to compute the number of eggs that can be produced by a population in any one spawning.

Because there is no gap between the various size classes of ova and because of the individual variation in the size of the ova contained in different females, it was found that it was necessary to measure a sample of the maturing and mature eggs from each female before a count could be made. The following procedure was used: The whole ovaries were removed from the preservative, drained of excess moisture for several minutes, and weighed to the nearest milligram. Following this, several samples of eggs were taken from each ovary, placed in a weighing bottle, and weighed. About 1,000 eggs over 0.7 mm. in diameter in each sample were measured. If the majority of the eggs were in the 1.0 or 1.1 mm. size classes and very few in the 0.8 and 0.9 mm. size classes, this ovary was acceptable for egg counts. If the majority of the eggs were smaller than 1.0 mm., the ovary was discarded. During the spawning seasons from 1938 through 1941, a total of 215 specimens of female bluegills was secured for egg counts. Only 42 of these were actually used and the rest were discarded.

Because none of these fish used for egg counts were quite ready to spawn and because it was assumed that further growth of the ova would occur before reaching maturity, it was decided to count all eggs 0.8 mm. and over as mature eggs ready to be spawned. There were very few ova much greater than 0.8 mm. in diameter in any of the samples used for egg counts. It was necessary to use a microscope equipped with an ocular micrometer in making all of the egg counts.

After making measurements of a random sample of eggs from each weighed sample, the remainder of the eggs in the sample were counted. The number of eggs per gram was determined and calculations made to give the number of eggs per female (Table 16). Actual total counts of all of the mature eggs were made on 15 specimens. These were mostly small fish containing few eggs. Between 25.72 and 52.65 percent of the eggs present in the ovaries of another 15 specimens was counted and for the remaining 12 individuals (all large fish) between 10.32 and 22.98 percent of the eggs were counted (Table 16).

In as much as some bluegills may spawn more than once in a season, the number of eggs per female, as presented in this paper, probably does not represent the total egg production for a breeding season.

The estimated number of eggs contained in the 42 females (Table 16) ranged from 1,124 (for a fish having a total length of 4.9 inches and weighing 35 grams) to 59,552 (for a 9.1-inch bluegill weighing 258 grams). The following are average figures: number of eggs produced, 17,261; total length, 168 mm. (6.6 inches); weight, 108.9 grams (3.75 ounces).

The number of eggs increases rapidly with increase in length of the fish and is roughly proportionate to the weight (Figures 17, 18). (The weight of some of the larger bluegills (Table 16) was estimated from the weights of other female bluegills of similar sizes taken at Deep Lake. But it is believed that these estimated weights might be a trifle low. It is for this reason that the upper part of the curve in Figure 18 is a broken line instead of a solid line. An additional 25 or 30 grams added to each of the larger bluegills would straighten out this curve in Figure 18). The number of eggs in fish of any particular length or weight varies greatly.

Table 16.--Data on collection, size, age, weight of ovary, percentage of ovary and the estimated number of eggs for forty-two bluegills collected at Deep Lake.

Date collected	Total length (mm.)(inches)	Weight (grams)	Number of annuli	Weight of ovary (grams)	Percentage ovary counted	Number of eggs
6-6-38	116 - 4.6	28	IV	1.183	100.00	2,355
6-18-38	123 - 4.8	31	IV	2.041	100.00	3,060
6-28-39	125 - 4.9	35	III	0.753	100.00	1,124
7-2-39	127 - 5.0	32	IV	1.355	100.00	2,287
6-28-39	128 - 5.0	37	III	0.963	100.00	2,042
5-27-39	133 - 5.2	41	III	2.205	100.00	4,578
6-20-39	135 - 5.3	40	IV	1.685	100.00	3,462
6-6-38	136 - 5.4	43	IV	3.463	38.58	6,646
6-4-38	137 - 5.4	50	IV	1.963	100.00	3,411
6-6-38	143 - 5.6	51	IV	2.050	100.00	1,355
6-4-38	144 - 5.7	59	IV	4.627	52.58	8,761
6-20-39	144 - 5.7	53	IV	4.487	100.00	6,703
6-28-39	145 - 5.7	56	IV	1.803	100.00	4,154
7-3-41	148 - 5.8	53 [↓]	III	2.764	47.03	5,075
6-8-39	148 - 5.8	57	IV	2.928	100.00	6,144
6-20-39	149 - 5.9	61	IV	2.881	100.00	5,982
6-13-38	152 - 6.0	56	IV	2.050	100.00	3,569
6-4-38	156 - 6.1	79	IV	3.205	48.99	5,432
6-20-39	157 - 6.2	71	IV	5.455	37.27	12,040
6-20-39	158 - 6.2	71	IV	6.834	34.53	10,393
6-13-39	161 - 6.3	80	IV	3.588	47.32	9,435
6-16-40	162 - 6.4	75 [↓]	V	6.907	22.98	11,623
6-4-38	165 - 6.5	93	IV	6.558	43.12	11,810
6-20-39	166 - 6.5	88	IV	6.476	32.18	11,958
6-8-39	168 - 6.6	110	V	7.514	52.65	14,893
6-5-39	173 - 6.8	125	III	8.296	33.08	18,869
7-7-39	176 - 6.9	100	IV	2.621	100.00	7,316
7-13-39	177 - 7.0	106	V	6.180	30.66	14,874
6-20-39	178 - 7.0	97	IV	9.517	25.72	15,648
6-6-38	179 - 7.0	128	IV	7.338	25.78	14,761
6-20-39	191 - 7.5	153	V	19.722	19.39	28,406
5-27-39	196 - 7.7	205 [↓]	V	28.153	13.24	47,907
6-5-41	197 - 7.8	161 [↓]	VI	11.882	30.66	23,666
6-10-39	201 - 7.9	179	V	16.394	19.37	33,010
5-21-41	205 - 8.1	163 [↓]	VI	17.513	11.75	37,072
6-5-41	205 - 8.1	163 [↓]	V	13.503	12.11	26,426
6-3-40	213 - 8.4	212 [↓]	VI	16.185	12.53	45,858
6-5-41	214 - 8.4	190 [↓]	V	30.412	14.27	51,002
7-9-41	223 - 8.8	249 [↓]	VI	39.935	16.72	47,147
6-5-41	231 - 9.1	258 [↓]	VI	33.440	10.32	59,552
6-19-41	233 - 9.2	286 [↓]	VII	49.081	13.36	40,808
7-8-41	240 - 9.4	349 [↓]	VI	36.177	13.27	54,349
Averages	168 - 6.6	108.9	17,261

[↓] Fish not weighed. These are estimated average weights of other female bluegills of similar size taken from Deep Lake.

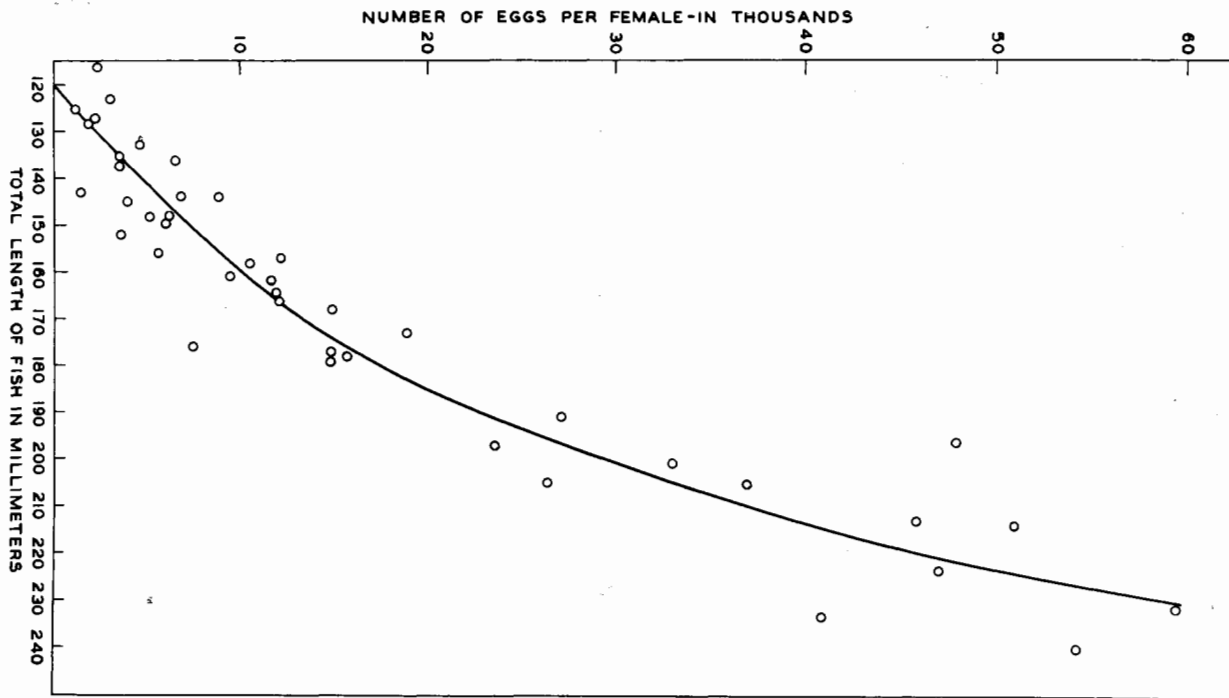


Figure 17.--Relation between the number of eggs and the total length of fish for 42 bluegills collected at Deep Lake.

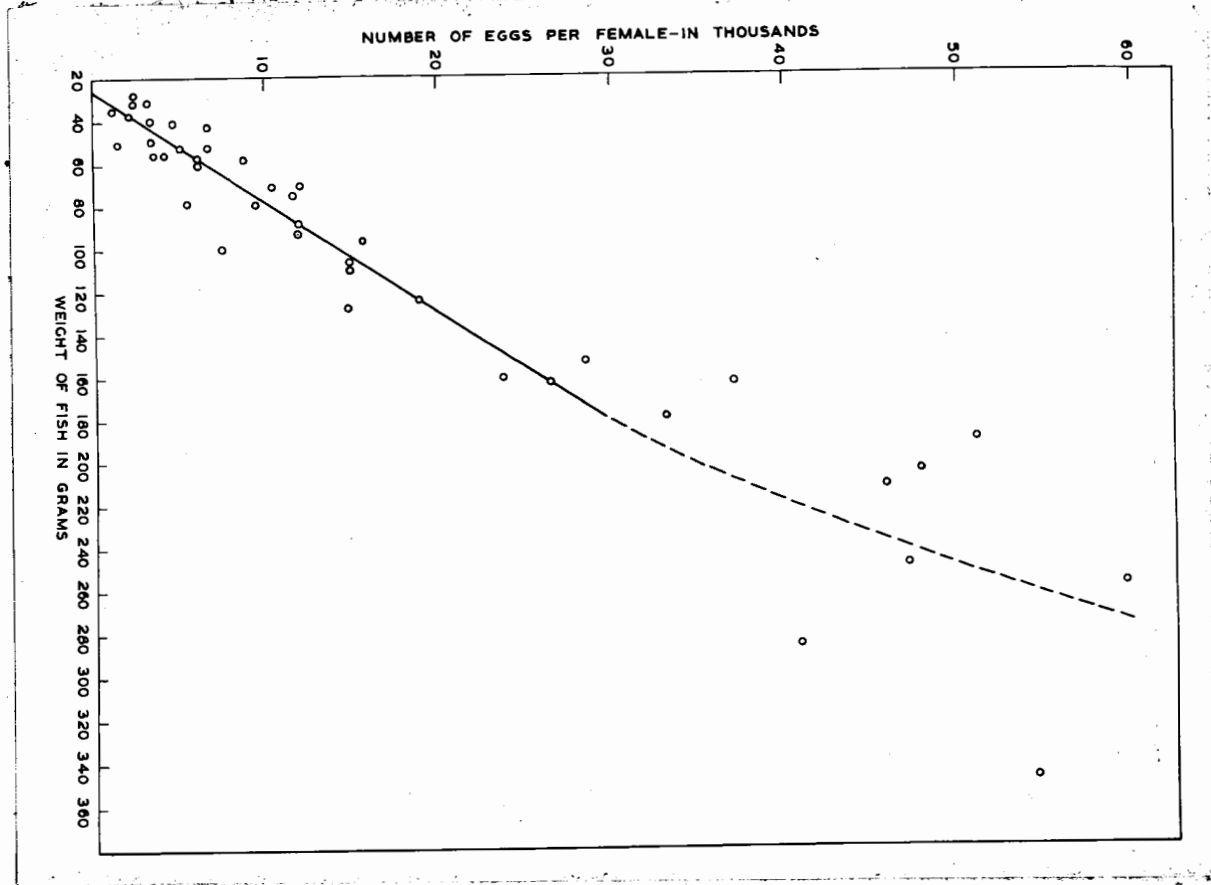


Figure 18.--Relation between the number of eggs and the weight of fish for 42 bluegills collected at Deep Lake.

In general, the older fish produce more eggs than the younger fish, but in any particular age it varies greatly. The average number of eggs produced by each age group is as follows: III, 6,338; IV, 7,122; V, 28,518; VI, 44,021; VII, 40,808.

In all of the literature pertaining to the number of eggs in the bluegill, no mention has been made of the various sizes of eggs contained in the ovary or which sizes of eggs were counted. A summary of the literature follows:

Coggeshall (1924) counted 11,257 eggs in a 14 cm. bluegill.

The number of eggs contained in two-year-old fish varies from 6,000 to 12,000 (Outdoor Indiana, 1936).

Brass (1938) states that the number of eggs per bluegill varies from 3,500 to 32,000.

A two-year-old, six and a half ounce bluegill was reported to contain 32,950 eggs by Culler (1938).

The Ohio Conservation Bulletin (October, 1938) places the number of eggs for the bluegill as between 5,000 and 10,000, the number depending upon the size of the female.

Ulrey, Risk, and Scott (1938) give the following figures for the bluegill: 7 two-year-old fish averaged 3,820 eggs (range, 2,360 - 5,066); 9 three-year-old fish averaged 9,264 eggs (range 6,518 - 13,137); and 2 four-year-old fish averaged 19,169 eggs (range 16,220 - 22,119).

Leuth (1942) states that the number of eggs per female in the bluegill ranges from 2,000 to 20,000.

None of the estimates and actual counts listed above are comparable with the counts obtained by this writer.

During the spawning season of 1938, a number of female rock bass were collected for egg counts. In the fall of 1938, the writer examined this material.

Seven of the females collected at various times during the summer contained large, translucent eggs averaging about 2.0 mm. in diameter. These fish were obviously about ready to spawn. Eggs of all sizes were present in the ovaries of these fish. Besides the large, translucent ova, there were also some large, yellow opaque eggs about the same size as the translucent eggs, and some slightly smaller (between 1.5 and 2.0 mm.). There were many eggs in the 1.0 mm. size class and many in the smaller size classes (0.0 to 0.3 mm.). Because of other duties it was impossible to work out the growth history of the ova for the rock bass.

All of the large translucent and opaque eggs contained in the ovaries of these seven rock bass were counted (Table 17). The number of eggs ranged from 965 to 2,182 and averaged 1,685 eggs per female.

Some largemouth bass and pumpkinseed sunfish ovaries were also collected from Deep Lake, but not enough material was obtained for a complete study of the growth history of the ova. Egg counts were not made for these two species.

The number of eggs per female^{for} the largemouth bass as given by various workers is as follows: 17,000 eggs for a two and a half pound fish is listed in the Rept., U. S. Fish Comm. for 1898; 2,000 to 3,000 eggs per nest, Richardson (1913); 1,000 to 10,000, Foley (1933); 10,000 eggs, Wiebe (1935); 10,000 to 15,000 eggs, Outdoor Indiana (1936); 30,481 eggs are produced by a 1 pound, 3 ounce bass, 22,300 eggs by a 1 pound, 10.5 ounce bass, 31,008 eggs by a 1 pound, 12 ounce bass,

Table 17.--Size and number of eggs for seven rock bass collected at
Deep Lake.

Total length (mm.) (inches)		Weight (grams)	Number of eggs
160	6.3	95	2,015
165	6.5	103	1,717
168	6.6	71	965
168	6.6	90	1,613
170	6.7	95	1,612
172	6.8	112	1,688
179	7.0	123	2,182
Averages	168.8 6.6	98.4	1,685

109,314 eggs by a 2.5 pound bass, and 79,000 eggs by a 2.75 pound bass, Culler (1938); the Ohio Conservation Bulletin (October, 1938) states that between 1,500 and 10,000 (average 3,500 to 5,000) eggs are produced by largemouth bass; and 2,000 to 20,000 eggs, Leuth (1942).

For the pumpkinseed sunfish, Culler (1938) states that an 8 ounce, two-year-old fish will produce 27,320 eggs and a four ounce, two-year-old will produce 12,000 eggs. Ulrey, Risk and Scott (1938) list the following number of eggs for the pumpkinseed sunfish: 8 two-year-old fish contained an average of 1,034 eggs (range 600 to 1,684); 11 three-year-old fish averaged 1,491 eggs (range 1,108 - 2,366); 3 four-year-old fish averaged 2,422 eggs (range 2,580 - 2,740 -- evidently there was an error made some place by the authors); 2 five-year-old fish averaged 2,436 eggs (range 1,950 - 2,923).

Number of Fry per Nest

Newly hatched fry are reddish-gold or yellow-gold in color and exhibit little or no movement in the nest. The majority of the fry was collected while in the golden stage and the rest of the fry was collected while in the black stage. A length of heavy glass tubing (boiler-gauge glass) with an inside diameter of one-half inch, or Pyralin (Du Pont) plastic tubing was used for the collection of all fry from the nests. The collection of fry from the nests was a tedious task that required from 1 to 5 hours per nest. At times it was possible to make 23 pulls per minute with the tube, but it would probably average 10. To be certain that all fry were obtained, samples were taken from the bottom of the nest until no fry were taken. Each nest was visited at least twice after the initial collection of fry had been made; either several hours later or on

the following day. It was easier to collect fry from the nests containing a sand bottom. Nests containing gravel caused more difficulty because pieces of gravel were continually getting stuck in the tube. Fry in nests with peat bottom were seldom collected because of the endless time required to sort out the fry.

Several difficulties were encountered in 1938 during the process of collection of fry. Individuals of other species (young bluegills and pumpkinseed sunfish were the worst offenders) continuously attempted to rush in and eat the fry. On several occasions partially collected nests had to be discarded when the collector was unable to keep these fish away. This difficulty was minimized when the guarding male remained on or near the nest. But sometimes the guarding male left the nest and occasionally in so doing would scatter the newly-hatched fry. Nests so disturbed could seldom be used for counts. To eliminate the difficulty produced by the predation of other fishes, a circular, fine-meshed screen wire fry trap (of the type employed in smallmouth bass culture) was dropped over each nest before the fry were collected. This permitted the collector to proceed at his leisure, and if necessary, to take time out at intervals without danger of losing the fry.

The fry, together with any sand, gravel, debris, and water taken with them, were placed in a 5-gallon pail. At times, more than 25 gallons of this material were taken from a single nest. The water in the sample was strained through a plankton net to prevent the loss of any fry. The majority of the fry remained on or above the sand and debris when the sample settled and were collected in the plankton net by repeated washings with water. The balance of the fry and the sand and debris containing them were preserved separately in 10 percent formalin

solution. Sometimes as many as 9 quarts of sand and debris containing fry were preserved from some nests.

The number of fry per nest was determined by actual count. A Baugh and Lomb magnifier mounted on an adjustable standard was used to facilitate fry counting. Volumetric and weighing methods of estimating the number of fry were attempted, but were not used because of the error introduced by the varying amounts of sand and debris invariably included with the fry. The calcium chloride floatation method (a modification of the method of Beak, 1937, and similar to the method used by Moffett, 1943) was found effective in removing the fry from the sand and gravel. About 250 cc. of the sample were placed in a large (10 inch) evaporating dish and the dish was filled with the super-saturated calcium chloride solution. This solution caused all fry, insects, and organic material to float to the surface when the sample was stirred. The fry and organic material were poured through a funnel covered with a piece of grit cloth after vigorous stirring and before settling could occur. This procedure was repeated until fry failed to appear on the surface of the calcium chloride solution. The sand and gravel were then washed repeatedly with water in an attempt to discover additional fry. Usually about five washings with calcium chloride and five with water sufficed to remove all of the fry. The calcium chloride method cannot be used if samples are composed entirely of inert organic material because the entire sample will float. The sand and gravel remaining after the removal of the fry was not examined in the majority of samples after washing with calcium chloride and water.

The sand and gravel from a number of samples was carefully examined to determine the number of fry that remained after the addition of calcium

chloride and the removal of the floating fry. From a critical study of a sample containing more than 500 cc. of sand (the amount taken from one nest), the following information was obtained: (1) the number of fry removed by repeated washings with water (immediately after collection and before preservation), 9,781; (2) number of fry removed by calcium chloride floatation, 2,282; and (3) number picked out of the sand, 28. Therefore, of the total of 12,091 fry contained in the nest, the washing with water and the floatation treatment resulted in the recovery of all but 28 of the fry or 99.8 percent of the fry from that nest. The percentages similarly recovered from two other samples were 99.8 and 99.7 percent.

A number of dead and/or fungused eggs and fry were present in almost every sample of fry collected. Some counts were made of the total number of these dead and fungused eggs and fry so that a comparison could be made between these and the fry that were alive when the collection was made.

Several times when the bass fry screen was dropped over a nest immediately before the fry were collected, one or more small fish were trapped over the nest. These fish were dipped out and preserved. The fry contained in the stomachs of these fish were counted and were included in with the total number of fry contained in the nest. Data will be presented later on the number of fry which were consumed by small fish of various sizes and species.

No selection of nests used for fry collections was practiced except that the fry in nests containing peat bottom, roots, and green plants were seldom collected. Some fry were collected early and some late in the spawning season each year. It is believed that an adequate sample of the nests of the bluegill (53 nests) and rock bass (33 nests) were

made to present fairly accurate counts on the average number of fry per nest. The fry from only a few pumpkinseed sunfish (14 nests) and largemouth bass (11 nests) nests were collected, and these probably do not constitute adequate samples. Because similar data are lacking for these last two species, the average number of fry per nest presented below will be used in all computations of production and survival figures for Deep Lake.

The actual number of fry contained in the 53 bluegill nests that were sampled (Table 18) ranged from 2,657 to 61,815 and averaged 16,240 fry per nest. The total number of rock bass fry per nest varied from 213 to 5,389, and the average total number in the 33 nests counted was 1,466. The number of pumpkinseed sunfish fry per nest varied from 1,509 to 14,639, for an average of 6,012 for each of the 14 nests counted. Counts of the fry collected from 11 largemouth bass nests averaged 5,654 (range - 751 to 12,502).

Coggeshall (1924) counted the fry obtained from four bluegill nests in Winona Lake, Indiana. The figures obtained were 11,257, 30,374, 80,000, 224,900, for an average of 86,631 (average given by Coggeshall is in error--correct average is 86,633) fry for the four nests. Coggeshall made actual counts of the number of fry obtained from the smaller collections and the number was estimated for the larger collections by counting out a sample of approximately 1,500 which were weighed and the total number of young calculated from the total weight of all of the fry taken from the nest. The weight method used by Coggeshall for determining the number of fry per nest is open to some criticism as mentioned earlier in this section of this paper. But it is still possible for such tremendous numbers of fry to be found on some nests. The writer has observed

Table 18.--Actual counts of the number of fry per nest collected from bluegill, rock bass, largemouth bass and pumpkinseed sunfish nests in Deep Lake.

Bluegill		Rock bass		Pumpkinseed sunfish		Largemouth bass	
Date	Number of fry	Date	Number of fry	Date	Number of fry	Date	Number of fry
7-5-38	4,670	6-2-38	575	6-29-38	1,509	5-29-38	11,457
7-8-38	22,333	6-3-38	352	7-13-38	14,639	5-30-38	1,967
7-8-38	8,124	6-3-38	1,056	6-5-39	11,383	6-1-38	751
7-8-38	38,703	6-13-38	1,407	6-8-39	6,106	6-3-38	4,189
7-8-38	23,169	6-17-38	1,756	6-13-39	5,515	6-3-38	3,511
7-9-38	9,162	6-29-38	774	6-21-39	8,535	5-24-39	12,502
7-9-38	16,974	7-2-38	344	6-22-39	8,718	5-29-39	3,576
7-9-38	21,974	7-10-38	401	6-23-39	2,681	5-29-39	4,421
7-10-38	8,345	7-11-38	499	6-24-39	4,059	6-4-40	7,141
7-10-38	10,351	5-29-39	3,137	6-27-39	1,640	6-4-40	4,019
7-12-38	8,559	5-29-39	4,193	6-27-39	2,447	5-18-41	8,661
7-13-38	7,161	5-29-39	1,497	6-27-39	8,815	Average	5,654
7-14-38	39,903	5-30-39	809	6-27-40	6,187		
7-16-38	12,091	5-31-39	1,208	7-19-40	1,938		
7-17-38	61,815	6-1-39	1,561	Average	6,012		
7-21-38	4,819	6-1-39	5,389				
7-21-38	6,389	6-1-39	1,329				
6-6-39	12,136	6-7-39	2,263				
6-6-39	3,749	6-8-39	4,891				
6-6-39	7,911	6-8-39	213				
6-12-39	32,010	6-13-39	1,195				
6-17-39	32,721	6-13-39	2,108				
6-13-39	11,904	6-20-39	2,027				
6-13-39	12,412	6-22-39	2,411				
6-14-39	5,524	6-22-39	1,173				
6-21-39	4,415	6-16-41	485				
6-23-39	22,929	6-19-41	1,528				
6-23-39	4,505	6-21-41	647				
6-24-39	9,347	6-21-41	230				
6-24-39	14,908	6-25-41	791				
6-24-39	18,551	6-26-41	923				
6-24-39	19,685	6-27-41	728				
6-25-39	17,987	6-30-41	468				
6-26-39	16,653	Average	1,466				
6-26-39	28,939						
6-26-39	30,664						
7-20-40	23,790						
7-21-40	11,729						
7-22-40	9,670						
7-23-40	31,694						
7-23-40	7,755						
7-24-40	11,747						
7-24-40	36,834						
7-26-40	16,696						
7-27-40	19,609						
7-30-40	11,484						
7-31-40	17,587						
8-2-40	5,458						
8-2-40	2,657						
8-12-40	5,393						
6-28-41	19,178						
7-12-41	7,037						
7-27-41	10,940						
Average	16,240						

nesses in Deep Lake that must have contained well over one hundred thousand bluegill fry.

Other records of the number of fry produced per female bluegill, rock bass, and pumpkinseed sunfish in hatchery ponds are recorded in the literature, but seldom was the actual number of males and females known exactly. Consequently, these figures are not given in this paper. There are a number of figures in the literature on the number of fry produced for female largemouth bass, as given below. But it must be pointed out that these figures are not too accurate because these workers were never certain that all of the fry had been seined up. All of the figures listed below are for free swimming fry.

Reighard (1906) states that the number of fry produced per female largemouth bass varies from 1,200 to 10,000 in different ponds.

Richardson (1913) records between 2,000 and 3,000 eggs per nest, and in some instances considerably more.

Davis and Wiebe (1930) found that one group of female largemouth held at the Fairport Station produced an average of over 6,500 fry to each female. Also, that 10 two-year-old largemouth bass females produced 12,219 fry or an average of over 1,200 fry per female.

Wiebe (1935) gives the following production figures for largemouth bass fry an average of 14,000 fry produced by several females averaging 5 pounds in weight; 7,600 fry per female for several fish averaging 4 pounds; 7,740 fry per female for 2.5 pound fish; and 4,884 fry for each of several 2-pound female largemouth bass. In another experiment, 17 females averaging just over 2 pounds produced an average of 8,000 fry per female, and 4 females just one year old and each weighing 0.75 pounds produced an average of 7,500 fry per female.

It is rather difficult to correlate the number of eggs produced by one female centrarchid at one spawning with the number of fry produced per nest because it is known that more than one female may spawn in one nest. Coggeshall (1924) states that more than one female bluegill will sometimes spawn in one nest. Lamkin (1900), Reighard (1906) and Adams and Hankinson (1928) record instances where more than one female largemouth bass spawned in one nest. Ingram and Odum (1941) describe one instance where two female pumpkinseed sunfish spawned with one male in immediate succession.

Despite the fact that more than one female may spawn in one nest, there is a close correlation between the number of eggs (range 1,124 to 59,552 with an average of 17,261) produced by the bluegill and the number of fry produced per nest (range 2,657 to 61,815, with an average of 16,240). Coggeshall (1924) counted 11,257 eggs in one female bluegill and the number of fry in the four nests that he counted ranged from 11,257 to 224,900 with an average of 86,631.

Fry were collected from two bluegill nests located in experimental pens at Deep Lake. A total of 7,755 fry were obtained from a nest which had been spawned in by a 6.2-inch female. In the other nest, 7,037 fry were produced by a 7.8-inch female. According to the egg counts that were made on Deep Lake bluegills, the 6.2-inch female should have produced between ten and twelve thousand eggs and the 7.8-inch female at least 23,000 eggs. It is possible that some cannibalism occurred on each of these nests before the fry were collected. Three other nests that were also used for spawning in experimental pens were entirely cleaned of their eggs by egg predators.

Although egg counts were made on only seven rock bass, the following figures are presented for comparison: the number of eggs per female ranged from 965 to 2,182 and averaged 1,685; the number of fry ranged from 213 to 5,389 and averaged 1,466.

According to the literature the number of eggs contained by the pumpkinseed sunfish range from 600 to 27,300 per female. The number of fry per nest at Deep Lake ranged from 1,509 to 14,639 and averaged 6,012.

The following figures are recorded in the literature for the largemouth bass: number of eggs per female ranged from 1,000 to 109,314; the average number of fry produced by each female varied from 1,200 to 14,000. Our figures obtained from Deep Lake place the range in the number of fry per nest at between 751 and 12,502 with an average of 5,654.

According to the information obtained at Deep Lake between 2 and 3 (seldom 4) days are required for the hatching of bluegill, pumpkinseed sunfish, and rock bass eggs, depending upon the water temperature. Largemouth eggs will hatch in from 5 to 6 days.

Lamkin (1900) states that largemouth bass eggs hatch from 48 to 72 hours after deposition. Reighard (1906) found that largemouth bass eggs will hatch in between 3 and 4 days. Observations made by Carr (1942) indicate that largemouth bass eggs will hatch in from 47 to 64 hours after deposition.

Some dead and/or fungused eggs or fry were found in almost every nest examined at Deep Lake. The nests of all species were affected and at all times during the spawning season, although this condition was more pronounced at certain times than at others. Some nests containing dead and/or fungused eggs or fry were still being guarded by the male fish. At no time were all of the nests in one colony (in the case of

the bluegills), or in the entire lake, ever fungused. Some nests in the same colony or elsewhere in the lake always contained live eggs or fry. At times only those nests located in sand bottom were thus affected, while at other times only those in peat bottom and still other times when some nests located on a variety of bottom materials. No matter how badly fungused, some live eggs or fry could still be found in almost every nest. Largemouth bass nests seemed to contain a greater percentage of dead and fungused eggs or fry than any other species, and the pumpkinseed sunfish was probably next. This is one reason that fry were collected from fewer largemouth bass and pumpkinseed sunfish nests than for the other species.

The cause of the death of eggs and fry in nests is not known, but it may have been due to any one or a combination of any of the following factors:

1. Unfertilized eggs. It is doubtful whether all of the eggs deposited by one female are fertilized. It is certainly possible for one or more eggs to be missed. Also, the writer has many times observed the female continue the spawning act (circling the nest in a horizontal position) after the male has left to chase away some intruder. Although it is not known whether the female actually deposits eggs during the absence of the male, it is entirely possible.

2. It is possible for a female to deposit a few small eggs, intermediate-sized eggs, or even large eggs held over from a previous spawning. It is doubtful whether these eggs could be fertilized.

3. Some eggs or fry are undoubtedly injured during spawning, hatching or even by the guarding male.

4. The presence in a nest of fungused eggs or fry from a previous spawning. Fungus adheres closely to sand and gravel in all nests. Many nests containing newly-deposited eggs were sampled in which the unmistakable odor of fungused eggs or fry from a previous spawning was noted as soon as the sampling tube was removed from the water. In still other nests containing newly-laid eggs, the "mat" of fungus from a previous spawning could be seen under the new eggs. When fungus is present in such concentrations, it will attack newly-laid eggs and spread over them rapidly.

5. Silting of a nest during periods of rain and wind undoubtedly kill many eggs and fry. Many deserted nests have been completely filled by debris in one afternoon during a heavy wind. Surber (1943) found that considerable mortality occurred in the smallmouth bass due to silting and high water.

6. Spawning of hybrids with either of the parent species. Hubbs and Hubbs (1933) attempted numerous back crosses between male hybrids and females of one of the parent species. Although eggs were deposited in many cases, the eggs showed no segmentation and later died and became fungused. At Deep Lake, male hybrids were occasionally observed spawning and guarding nests. It is possible that a few of the nests containing fungused eggs were the result of the spawning of hybrids with one of the parent species.

7. Desertion of the nest by the guarding male. Nesting fish at Deep Lake were frequently disturbed by the observer. Great blue herons and other birds might also have frightened and eaten some of the guarding males. This desertion of the nests may have been frequent enough to have caused some loss of eggs and fry, other than eggs and fry that were eaten

by predators. Production of smallmouth bass fry at hatcheries has been found to be higher if the nesting fish are seldom disturbed.

Reighard (1906) found that some times the eggs of the smallmouth bass died after developing normally for about two days. He therefore conducted a series of experiments to determine if the death of the eggs and fry could be attributed to the disturbance of the guardian fish. Reighard found: (1) that some of the best nests were situated where the guardian fish was disturbed frequently and that some of the poorest nests were far from where they could be disturbed; (2) three nests were examined at intervals and a few eggs were collected from each of these nests and later examined under a microscope. After a few days a large percentage of the eggs were dead and this mortality increased until all of the eggs were dead. In the meantime, the first eggs that died were attacked by fungus which soon spread over the entire nest. In each case the male continued to guard the eggs until all were dead and they did not desert the nests until a considerable portion of the nest was covered with fungus. Reighard concluded that the cause of death was due to a lack of vigor on the part of one or both parents. He maintained that certain fish produce eggs lacking in vitality because they suffer from lack of food, disease, or other factors which tend to lower their vitality. He found that in years when there was good production of fry, few deaths of the parent fish resulted. Also, when the fry production was low, a heavy mortality of adults occurred. This could be attributed only to a lack of vigor on the part of the adults, because Reighard was unable to detect any disease or infestation of parasites or to assign any other specific cause for the deaths.

In 1934 in Ohio, Langlois (1935) stated that the lack of vitality of eggs caused a poor hatch of smallmouth bass in hatchery ponds.

Carr (1942) found that a heavy mortality of largemouth bass fry occurred when the guarding fish were driven away from their nests or were caught by anglers who anchored their boats over or near spawning beds.

Bluegills, pumpkinseed sunfish, and rock bass in Deep Lake were found to be growing slower than average for the same species in Michigan. This can be attributed to the competition for food brought on by overpopulation. It is possible that some of the loss of eggs and fry in Deep Lake was due to the lack of vitality in the adults. Also, it was found that at times during the spawning season at Deep Lake, in some years, large numbers of adult fish died. No specific cause for their deaths could be determined although many fish were examined. Likewise, no correlation could be found between the number of dead adults and the number of nests containing dead or fungused eggs or fry. There were usually only a few nests containing eggs and fry when the heavy mortality of adults was observed. Apparently this mortality was heaviest at the beginning of a new cycle of spawning. A larger percentage of the nests of the largemouth bass at Deep Lake contained dead or fungused eggs or fry. Yet, dead largemouth bass were seldom found at Deep Lake.

Twice during the four-year period covered by this investigation at Deep Lake, clusters of tapeworms were found beside largemouth bass nests. (All of the eggs died and became fungused on one of these nests in 1940). Apparently these tapeworms were voided during the spawning act. Identification of these parasites by Dr. Leonard N. Allison, pathologist at the

Institute for Fisheries Research, revealed that they were Proteocephalus ambloplites. It is possible that the presence of the tapeworm in the bass may have reduced their vitality somewhat. Eggs would be robbed of a part of their yolk which would result in insufficient food for the developing embryo. The plerocercoid stage of Proteocephalus ambloplites was present in the ovaries of some of the Deep Lake bluegills, pumpkinseed sunfish, and rock bass. Its presence in these fish is expected in Deep Lake since the adult is present in the largemouth bass and the copepods are available as intermediate hosts. As all of the centrarchids in Deep Lake were infested with the bass tapeworm, it is possible that eggs could have been or were of poor quality.

Stranahan (1898) found that the greatest loss in whitefish eggs in Lake Erie hatcheries occurred from the time the embryo forms until hatching. This loss, he found, was caused by an insufficient food supply because the yolk was undersized. When the store of food was exhausted, the embryo dies of starvation. This accounted for 31 percent of the total loss of eyed eggs.

Some of the nests in Deep Lake that contained dead or fungused eggs and/or fry were still guarded by the male fish, while others were deserted. It is not known whether the guarding fish deserted the nests before or after the death of the eggs.

Stranahan (1898) states that the greatest loss of whitefish eggs in Lake Erie hatcheries was caused by an insufficient food supply (as discussed above) and that the next greatest loss was from abnormal development of the embryo.

Lamkin (1900) described several instances where two female largemouth bass spawned with one male. He claimed this usually proved to be disastrous

because the eggs were scattered over several square feet of bottom and many of these died and later became fungused. The writer made one similar observation at Deep Lake.

Doan (1940) while making observations on the nesting habits of the smallmouth bass in Georgian Bay found that the nests guarded by large male bass were more successful than those guarded by small males. Sixty-four percent of the nests were guarded by small bass (10-11 inches) and only 43 percent of their nests were successful. The remaining 36 percent of the guarding fish were 12 inches or over in length and their nests were 100 percent successful.

Another source of loss and destruction of eggs and fry was caused by the various predators. Most of the predation occurred while the nests were temporarily deserted by the guarding males. By far, the worst offenders were the young of all of the species found in Deep Lake. A number of these small fish were trapped on bluegill nests when the fry trap was dropped over a nest preparatory to collecting the fry. None of these fish were allowed to remain on a nest for more than one or two minutes before they were caught and preserved. The stomachs of these fish were later examined (Table 19). The results indicate that small fish (range in length from 73 to 113 mm.) of the several species were capable of devouring between 226 to 2,270 fry each in the several minutes they were on the nests. Several fish could thereby consume all of the eggs and fry from one nest in just a few minutes.

Turtles (snapping turtle, Chelydra serpentina, western painted turtle, Chrysemys bellii marginata, and musk turtle, Sternotherus odoratus) were frequently found in nests at Deep Lake that contained eggs and fry. Unfortunately, none of these turtles could be captured so that stomach

Table 19.--Number of fry removed from stomachs of Deep Lake fish trapped
in bluegill nests.

Species	Total length (millimeters)	Number of fry
Largemouth bass	83	810
Bluegill	93	471
Bluegill	78	226
Bluegill	87	1,446 ¹
Bluegill x pumpkinseed	98	
Bluegill x pumpkinseed	81	
Bluegill x pumpkinseed	113	540 ²
Bluegill x pumpkinseed	87	324
Bluegill x pumpkinseed	105	413
Bluegill x pumpkinseed	111	1,906
Bluegill x pumpkinseed	75	456
Bluegill x pumpkinseed	73	634
Bluegill x green sunfish	106	2,270

¹ A number of fry were regurgitated by these three fish after they were preserved in the same bottle. It was therefore impossible to determine the number of fry each fish had eaten.

² Includes 76 eggs.

examinations could be made to prove whether or not they had been eating eggs or fry. Fish hatchery employees in Michigan have found that turtles will consume large quantities of bluegill fry that are placed on trays in rearing ponds. It is for this reason that screen covers are now placed on all bluegill trays. Lagler (1943) counted 20,520 eggs (believed to be bluegill) in the stomachs of three snapping turtles.

Crawfish, various species of insect nymphs (chiefly damsel and dragon flies), and larvae were frequently observed in nests containing eggs and fry. No direct evidence can be presented by the writer to prove that these animals were actually eating either eggs or fry.

Dr. Ralph Hile (personal communication) has told the writer that he spent three days making observations on the nesting habits of the longear sunfish. Between nightfall and dawn of the third night all of the eggs disappeared. At dawn when observations were resumed, large snails (Goniobasis) were found in the nest and a total of 44 snails were found on or around the nest. Dr. Hile claims that it was possible that these snails could have eaten all of the eggs in this nest. Stomach examinations made on 10 of these snails revealed the presence of an albuminous substance that could have been the remains of fish eggs.

Other workers have recorded other instances of the predation of eggs and fry on nests.

Stranahan (1912) found that yearling bluegills would eat young-of-the-year bluegills and that the largest young (fish hatched) ate young that were just hatching.

Barney and Anson (1923) state that the young of the orangespot sunfish (Lepomis humilus) were eaten by darters and spot-tailed minnows (Notropis hudsonius).

Hubbs and Bailey (1938) report that crayfish, minnows, sunfishes, and young bass are known to prey heavily upon the eggs and young of the small-mouth and largemouth bass.

Bennett, Thompson and Parr (1940) declare that yearling largemouth bass feed upon the eggs and fry of the bluegill.

The barred killifish, bridled minnow, and other small fishes were found to feed upon the eggs contained in a pumpkinseed sunfish nest as soon as the guarding male was removed by seining (Thorpe, 1942).

Carr (1942) found that large numbers of largemouth bass eggs and fry were eaten by bluegills and Gambusia whenever the nest guardian would leave his nest for only a few seconds.

Bennett (1943) attributes the poor yield of bluegills in 1941 at Fork Lake (Illinois) to the fact that during the spawning season of 1939, young bass (5 - 7") fed upon the bluegills before they left the nest. This was verified by stomach examinations.

According to Swingle and Smith (1943, p. 3), "When sufficient food was not available (in ponds), bluegills commonly ate their own eggs. Each year the earliest eggs laid were usually eaten by the male bluegills with the result that although eggs were often laid in April at Auburn, few or no bluegills were produced from the earliest spawning." They state that this egg-eating habit was not detrimental to this species but was actually beneficial. Swingle and Smith found that in ponds that were overcrowded with bluegills, largemouth bass were not able to guard their nests successfully. When the bass would chase one bluegill away, four or five other hungry bluegills would dash in and eat the bass eggs. As a result of this, most of the eggs were eaten before they hatched, and in one pond the bass failed to reproduce successfully for four years.

8. The effect of temperature changes on the mortality of eggs and fry. Although sufficient water temperatures are available from Deep Lake for 1940 and 1941, the lack of certain other data prevent correlating the death of eggs and fry to abrupt changes in temperature. For example, we do not know how much time is required at different water temperatures before dead eggs and fry become covered with fungus. Not realizing the importance of such correlations, no attempt was made to obtain some of this vital information. Notations were made, however, on the number of partly or wholly fungused nests each day in 1941. From these data it is apparent that there is a lag of several days after a period of minimum water temperature before nests become fungused. However, some nests were found that were badly fungused on the same day that minimum water temperatures were recorded.

Other factors make it difficult to make any correlations between water temperatures and subsequent fungusing of nests in that there were always some nests adjacent to fungused nests or in the same depth of water or on the same type of bottom that still contained live eggs or fry. Also, some nests were found containing dead and fungused eggs or fry during the entire spawning season. It was also observed that one or more nests of one species would be partly or wholly fungused and nests of the same and other species would be entirely free of fungus. At other times, only a portion of the eggs in some nests would be dead and fungused, and the writer seldom found nests that did not contain at least a few live eggs or fry.

It does not seem that temperature could have been entirely responsible for the death of eggs or fry. If temperature were wholly responsible, it

would be more likely that all nests at one particular depth or on one type of bottom would be killed, and all eggs and fry in one nest would also be killed.

Because our data were not adequate to make definite correlations between changes in water temperature and the death and fungusing of eggs or fry, only the following general conclusions will be drawn.

Abrupt changes in temperature probably causes the death of some eggs and fry. Many nests containing dead and fungused eggs were observed immediately following a period of cold weather. Some nests containing dead and fungused eggs and fry were also observed immediately after a period in which water temperatures reached 90° F. Nests in deeper water and nests located on dark (peat) bottom were apparently affected to a lesser extent than nests located in shallow water and light colored (sand) bottom. It is also believed that certain other factors (as discussed previously) may also be responsible for some of the mortality of eggs and fry and it is probably coincidental that some nests containing dead and/or fungused eggs and fry were noted on or immediately after days when minimum or maximum water temperatures prevailed.

Other workers have found that the death of eggs and fry are correlated with abrupt changes in temperature.

James (1929) states that a drop below 55° F. is invariably fatal to the basses, rock bass, pumpkinseed sunfish, and other pond fishes, while the percentage hatch below 58° F. is greatly reduced.

Tester (1930) found that smallmouth bass embryos at the stage just prior to hatching were killed when the temperature of the water rose as high as 73.5° F.

Langlois (1936) states that all or almost all of the smallmouth bass eggs in a pond were killed when cold weather succeeds the warm weather which brings on the spawning.

It is difficult from the data at hand to determine the percentage mortality of eggs to the fry stage because this mortality varies from at least one dead egg to almost 100 percent dead eggs in various nests. The percentage of dead eggs contained in some nests at Deep Lake were obtained by counting dead and live eggs obtained from ^{four} nests (2.02 percent, 4.59 percent, 10.21 percent, and 20.12 percent), but these mean very little because of the extreme variation. The nests containing the lowest percentage of dead and fungused eggs were more or less average nests while the other two were selected. No attempt was made to obtain the percentage of live and dead eggs or fry in a nest that was really covered by a blanket of fungus.

Production and Survival of Fry

In the management of any species of fish it is important to know the probable yield from any spawning. In the experiments conducted at Deep Lake, a complete count was obtained of all of the nests used for spawning by the largemouth bass, rock bass, pumpkinseed sunfish and bluegill for the four-year period covered by the investigation. Counts were also made of the average number of fry per nest. From these data the estimated number of fry produced in Deep Lake each year by each species has been made. On September 12, 1941, the fish population of Deep Lake was killed by poisoning and the fish recovered and counted. It is possible, therefore, to present figures indicating the survival of the young of each year class from 1938 to 1941, from the fry stage until the lake was poisoned.

The destruction of the fish population of Deep Lake was accomplished by means of powdered derris root (5 percent rotenone content). The method of applying the poison was similar to that used by Eschmeyer (1937, 1938a) and Greenbank (1940). In order to distribute the poison in the colder waters of the thermocline and hypolimnion, burlap bags were filled with a stiff paste of derris, weighted and towed systematically at various depths behind a motorboat for 18 hours. The remainder of the poison was mixed with water to form a very thin suspension and was poured onto the surface of all parts of the lake from a motorboat.

The later examination of cages containing live fish placed in the lake before poisoning revealed that the poison penetrated to depths greater than 40 feet. The failure to take any fish in later netting operations indicates that all fish in Deep Lake succumbed to the poison.

A concerted effort was made to collect as many fish as possible after the poisoning. Visits were made daily for 17 days following the poisoning to assure as complete a recovery as possible. It is believed that almost all of the fish one year old and over that came to the surface were picked up. No estimate can be offered as to the percentage of the young of the year that were found. A special effort was made to recover as many of these small fish as possible. However, it is believed that the recovery of the young-of-the-year bluegills, pumpkin-seeds and rock bass was far from complete. The problems incident to the locating of the small fish after poisoning are manifold. The roiling of the water by collectors conceals many specimens on the bottom with a layer of silt and detritus. Many more are hidden in beds of vegetation. Furthermore, in the poisoning of a lake, the smaller fish

die first, and Eschmeyer (1939) has shown that numbers of them are eaten by larger fish before the latter are affected by the poison. Snakes, turtles, birds and insects also take advantage of this unusual source of food.

All of the fish collected at Deep Lake were sorted and identified in the field and in the laboratory by Dr. Carl L. Hubbs and Mr. Walter R. Crowe. Scale samples and length measurements were obtained from all fish over 100 millimeters in length, except for the bluegills of which only a sample of approximately half of the specimens over 100 millimeters was taken. Similar data were obtained also for a large random sample of all fish less than 100 millimeters long. Aggregate weights were secured of all of the fish recovered while individual weights were taken on only a random sample of the fish of each species. Measurements of standard and total length were made in millimeters and the fish were weighed to the nearest gram on a platform balance.

The production figures listed in Table 20 are based upon the number of nests of each species that were actually used for spawning and the average number of fry per nest. Any mortality that occurred before or during the fry stage has not been considered because no definite percentage mortality could be assigned. Therefore, the production figures presented in this report are probably higher (but not excessively so) than the actual production of fry. (The estimated production figures then are technically the maximum average production of fry possible if all eggs had hatched and if none of the fry had died until reaching the free-swimming stage).

In all of the discussions based on the survival, the number of legal (or undersized) fish removed by anglers has not been taken into

Table 20.--The number of nests, estimated number of fry produced and the survival rate of each year class of the four species of centrarchids in Deep Lake.

Species	Year class	Total number of nests used	Estimated number of fry produced [↓]		Estimated total number of fish in year class	Total length (inches)		Percentage survival	Survival per million fry produced
			In lake	Per acre		Range	Average		
Largemouth bass	1938	33	187,000	12,600	25	9.3-11.6	10.6	0.0134	134
	1939	23	130,000	8,800	16	8.1-10.5	9.5	0.0123	123
	1940	56	317,000	21,300	104	4.7-7.5	5.9	0.0328	328
	1941	40	226,000	15,200	569	1.6-4.0	2.7	0.2518	2,518
Total or average		152	860,000	57,900	714	0.0830	830
Rock bass	1938	58	85,000	5,700	29	5.2-6.9	6.0	0.0341	341
	1939	49	72,000	4,900	56	4.2-5.9	4.8	0.0778	778
	1940	28	41,000	2,800	396	2.4-3.7	3.0	0.9658	9,658
	1941	67	98,000	6,600	73	1.3-2.0	1.6	0.0745	745
Total or average		202	296,000	20,000	554	0.1872	1,872
Pumpkinseed sunfish	1938	188	1,130,000	76,100	142	3.8-5.6	4.6	0.0126	126
	1939	121	727,000	49,000	119	3.1-4.4	3.7	0.0164	164
	1940	141	848,000	57,100	4,134	1.5-3.0	2.2	0.4875	4,875
	1941	97	583,000	39,300	1,402	0.8-1.8	1.6	0.2405	2,405
Total or average		547	3,288,000	221,500	5,797	0.1763	1,763
Bluegill	1938	369	5,993,000	404,000	183	4.5-6.7	5.4	0.0031	31
	1939	621	10,085,000	680,000	69	3.6-4.8	4.2	0.0007	7
	1940	679	11,027,000	743,000	5,390	1.8-3.8	2.5	0.0489	489
	1941	627	10,182,000	686,000	9,872	0.6-2.6	1.8	0.0970	970
Total or average		2,296	37,287,000	2,513,000	15,514	0.0416	416
Grand total or average		3,197	41,731,000	2,812,400	22,579	0.0541	541

↓ All figures rounded off to nearest hundred or thousand. All figures are based on average of 5,654 fry per nest for the largemouth bass, 1,466 for the rock bass, 6,012 for the pumpkinseed and 16,240 for the bluegill (see Table 18). Deep Lake has an area of 14.84 acres.

consideration. The exact number of fish that were removed from Deep Lake by anglers during the period covered by this investigation, and especially during 1941, is not known. Observations indicate that fishing was practically nil during the 1941 fishing season. Also, it is believed that recruitment of small fish (and immature fish) to legal size or to maturity, at least equalled the angler's catch.

Of all of the fish picked up at the time of poisoning, a random sample of the more numerous species and all of the scale samples obtained from other species were used for age determinations. The balance of the fish were assigned to age groups according to the observed percentage age composition within the individual length intervals (Carbine and Applegate, 1947). The representations of the different age groups in all species were decidedly unequal (Table 20). The low number of young of the year recovered for each species can be attributed to the difficulties of recovery (many, doubtless were not found), to a low production of young in the 1941 season and to natural death and cannibalism. In presenting these data it is recognized that the recovered population is probably less than the actual population. Therefore, the survival figures quoted are minimal. Even if the recovered population was only half that of the actual population in Deep Lake, the percentage survival is still very low.

The presence of strong and weak year classes in fish populations has been commonly observed. It is not known whether the 1941 year class was good or bad. Considerable mortality probably occurred between the time of hatching and poisoning (a period of slightly less than two months had elapsed since the end of spawning in Deep Lake). It is natural to expect that the number of young of the year fish of all

species would be greatly reduced at the time of poisoning by death from various causes including cannibalism.

These data (Table 20) suggest a weakness in the 1939 year class in all species aged with the exception of the rock bass. In general, the differences in the strength of year classes do not follow the same pattern for all species. The representations of the different age groups were decidedly unequal and is probably due to the varying degrees of success of natural reproduction in different calendar years and the result of natural mortality over a period of years.

Largemouth bass. The estimated production of largemouth bass fry each year (Table 20) and the number and percentage survival of each year class up to the time Deep Lake was poisoned on September 12, 1941, was as follows:

Year class	Estimated number of fry produced	Estimated total number of fish in each year class	Percentage survival	Percentage mortality
1938	187,000	25	0.0134	99.9866
1939	130,000	16	0.0123	99.9877
1940	317,000	104	0.0328	99.9672
1941	226,000	569	0.2518	99.7482

The fry of the largemouth bass suffered an enormous mortality in Deep Lake each year from 1938 to September of 1941. The 187,000 fry estimated to have been produced in 1938 yielded only 25 fish when Deep Lake was poisoned--a mortality of 99.9866 percent. In 1939, only 16 fish resulted from the estimated production of 130,000 young (mortality--99.9877 percent). The approximately 317,000 fry estimated to have been produced in 1940, resulted in only 104 fish (mortality--99.9672 percent).

The 1941 production of fry (estimated at 226,000) showed a survival of 569 fish to September 12 (mortality--99.7482 percent). As was to be expected, a larger number of fish survived to the end of their first summer than remained at the end of the second summer of life. The 1939 year class was much weaker than the 1938 year class and may be classed as an exceptionally weak year class. This irregular representation between the year classes may not have been due entirely to a smaller production of fry in 1939, but to a poorer survival of young which may have been caused by predation.

Rock bass. The estimated production of rock bass fry (Table 20) and the number and percentage survival of each year class up to the time Deep Lake was poisoned is presented in the following table:

Year class	Estimated number of fry produced	Estimated total number of fish in each year class	Percentage survival	Percentage mortality
1938	85,000	29	0.0341	99.9659
1939	72,000	56	0.0778	99.9222
1940	41,000	396	0.0658	99.0342
1941	98,000	73	0.0745	99.9255

The production and survival of rock bass varied considerably each year. The young rock bass suffered an enormous mortality in Deep Lake. The percentage survival of the 1940 year class was much greater than that of the 1941 year class. This cannot be attributed solely to incomplete recovery of the young of the year fish because large numbers of young bluegills and pumpkinseeds were recovered and these fish were smaller on the average than the rock bass. The percentage survival of the 1939 year class was also greater than that of the 1941 year class.

Pumpkinseed sunfish. The estimated production of pumpkinseed fry each year (Table 20) and the number and percentage survival of each year class up to the time of poisoning on September 12, 1941, was as follows:

Year class	Estimated number of fry produced	Estimated total number of fish in each year class	Percentage survival	Percentage mortality
1938	1,130,000	112	0.0126	99.9874
1939	727,000	119	0.0164	99.9836
1940	848,000	4,134	0.4875	99.5125
1941	583,000	1,402	0.2405	99.7595

The production and survival of the pumpkinseed sunfish varied considerably from year to year. As in the rock bass, the percentage survival was greater for the 1940 class of the pumpkinseed than for the 1941 year class. The mortality of the pumpkinseed was extremely high, but this species also had a higher production of fry than did the largemouth bass and the rock bass. The 1938 year class was exceedingly strong, probably because of the original higher production of fry.

Bluegill. The estimated production of the bluegill fry each year (Table 20) and the number and percentage survival of each year class up to the time Deep Lake was poisoned, is summarized below.

Year class	Estimated number of fry produced	Estimated total number of fish in each year class	Percentage survival	Percentage mortality
1938	5,993,000	183	0.0031	99.9969
1939	10,085,000	69	0.0007	99.9993
1940	11,027,000	5,390	0.0489	99.9511
1941	10,182,000	9,872	0.0970	99.9030

The production and survival of bluegills in Deep Lake varied considerably in all years. As in the largemouth bass and the pumpkinseed sunfish, the 1939 year class showed a poorer survival than the 1938 year class. Also similar to the pumpkinseed was the high survival of both the 1940 and 1941 year classes. The mortality suffered by the young bluegills during the four-year period covered by this investigation was much greater than for any species. But, more bluegills were produced each year during the four-year period than were produced by the other three species in all four years.

The total production of fry per acre and the total survival of each year class per acre of all species combined up to the time Deep Lake was poisoned is summarized in the following table:

Year class-	1938	1939	1940	1941
Total fry production	498,300	742,700	823,200	747,100
Total survival	25.5	17.5	675.5	803.0

The total production of fry per acre for all species was much lower in 1938 than in any other year, while the 1940 production was the highest. More young of the year fish survived until the time of poisoning than fish that were produced in other years. The 1939 year class showed the poorest survival. The total production of fry for all species was tremendous when we consider that between 498,300 and 823,200 fry were produced per acre in Deep Lake. It is obvious from these data why such a high mortality of the fry is necessary.

The rate of survival per million fry produced by each species each year also varied considerably (Table 20). The rock bass which produced the smallest number of fry each year had the greatest survival and the bluegill which produced the greatest number of fry showed the poorest

survival. The heaviest survival for any species in any year occurred for the 1940 year class in the rock bass where the survival was at the rate of 9,658 fish per million fry produced.

The assumption that in order for a species to maintain a constant population, greater numbers of fish must survive until the end of the first year than to the end of the second year, and more fish must survive from the end of the second year, than to the end of the third year, etc., apparently does not hold for all of the species studied at Deep Lake. The fluctuation in the abundance of various year classes explains the cyclic phenomena so frequently observed between the populations of various species of fish.

The production and survival varied greatly for each of the four species during each of the four years covered by this investigation conducted at Deep Lake. The poorest production of rock bass fry was obtained in 1940 and this year class showed the best survival to September 12, 1941. The smallest number of bluegill fry was produced in 1938 and resulted in a better survival than for the 1939 year class when nearly twice as many fry were produced. Fewer largemouth bass fry were produced during the 1939 season and resulted in the lowest survival rate for the four-year period. For the pumpkinseed, the lowest production was obtained in 1941 and the resultant survival of this year class was lower than that for the 1940 year class.

The best production of fry and the survival for this dominant year class during the four-year period for each of the four species was as follows: largemouth bass - 1940, and the survival was between that of the 1939 and 1941 year classes; pumpkinseed - 1938, this dominant year class resulted in the lowest survival during the four-year period;

bluegill - 1940, the survival was between that of the 1939 and 1941 year classes; rock bass - 1941, and the survival for this year class was lower than that for either 1939 or 1940.

From the data presented above it is apparent that in certain years survival for most species was either exceptionally good or exceptionally poor. For neither 1939 nor 1940 did we find that some species had strong year classes and other species weak year classes. Also, that when a good hatch of several species was evidenced by a strong year class (such as 1940) a weak year class developed the following year (1941). This phenomenon in all probability is due only to predation. The fluctuation in abundance of various year classes offers suggestions of cycles which are more prominent in earlier year classes than in older year classes. A strong representation of an old age group indicates a much richer year class than does an equally large number of fish several years younger (Hile 1941).

It becomes apparent that variable survival conditions rather than the number of young produced in any one season determines the number of fish that later reach a catchable size. The greatest mortality is known to occur during the first summer and is also high during subsequent years. The stage, during the first year, at which the greatest loss occurred was not determined. Observations at Deep Lake indicated that large numbers survived through hatching and the period of yolk absorption and that the number of young dwindled after this. Cannibalism and predation was observed and might prove to be the most important source of loss. The reproductive capacity of fishes is high, apparently as an adaptation for living with predators.

Other species of fish also have a high rate of mortality as is evidenced by a review of the literature which is summarized as follows:

Carbine (1944) estimated that the survival of northern pike (Esox lucius) from the egg stage until the young left the spawning marshes amounted to 0.18 percent in 1939, 0.07 percent in 1940 and 0.44 percent in 1942. These estimates were made possible by actual counts of migrating adults and young.

Foerster (1936) found that of all of the eggs of the sockeye salmon (O. nerka) that are deposited naturally in the Cultus Lake region, a mortality of 97.5 percent to the seaward migrant stage occurs. The mortality in the ocean varied from 88.3 to 96.5 percent. Therefore, the total loss during the life cycle amounted to approximately 99.75 percent.

From marking experiments conducted on the Karluk River (Alaska), Barnaby (1944) ascertained that the average mortality of the red salmon (O. nerka) to the seaward migrant stage amounted to over 99 percent, and that the ocean mortality was 78.55 percent. Therefore, only between 0.1 and 0.2 percent of the progeny return as mature fish.

Pritchard (1940) who worked on the pink salmon (O. gorbuscha) states that the production of downstream migrant fry from five different spawnings varied from 6.9 to 23.8 percent of the possible egg deposition in McClinton Creek, British Columbia.

The mortality of the herring (Clupea pallasii) from the egg to adult was estimated to be at least 99.99 percent by Hart and Tester (1934).

The total mortality of the Atlantic mackerel (Scomber scombrus) from the deposition of eggs to the end of the planktonic existence (approximate length of fish - 2 inches) amounted to 99.9996 percent (Sette, 1943). Therefore, between 1 and 10 fish resulted from each million eggs spawned.

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