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Dynamics of One-Species Populations of Fishes in Ponds Subjected to Cropping and Additional Stocking

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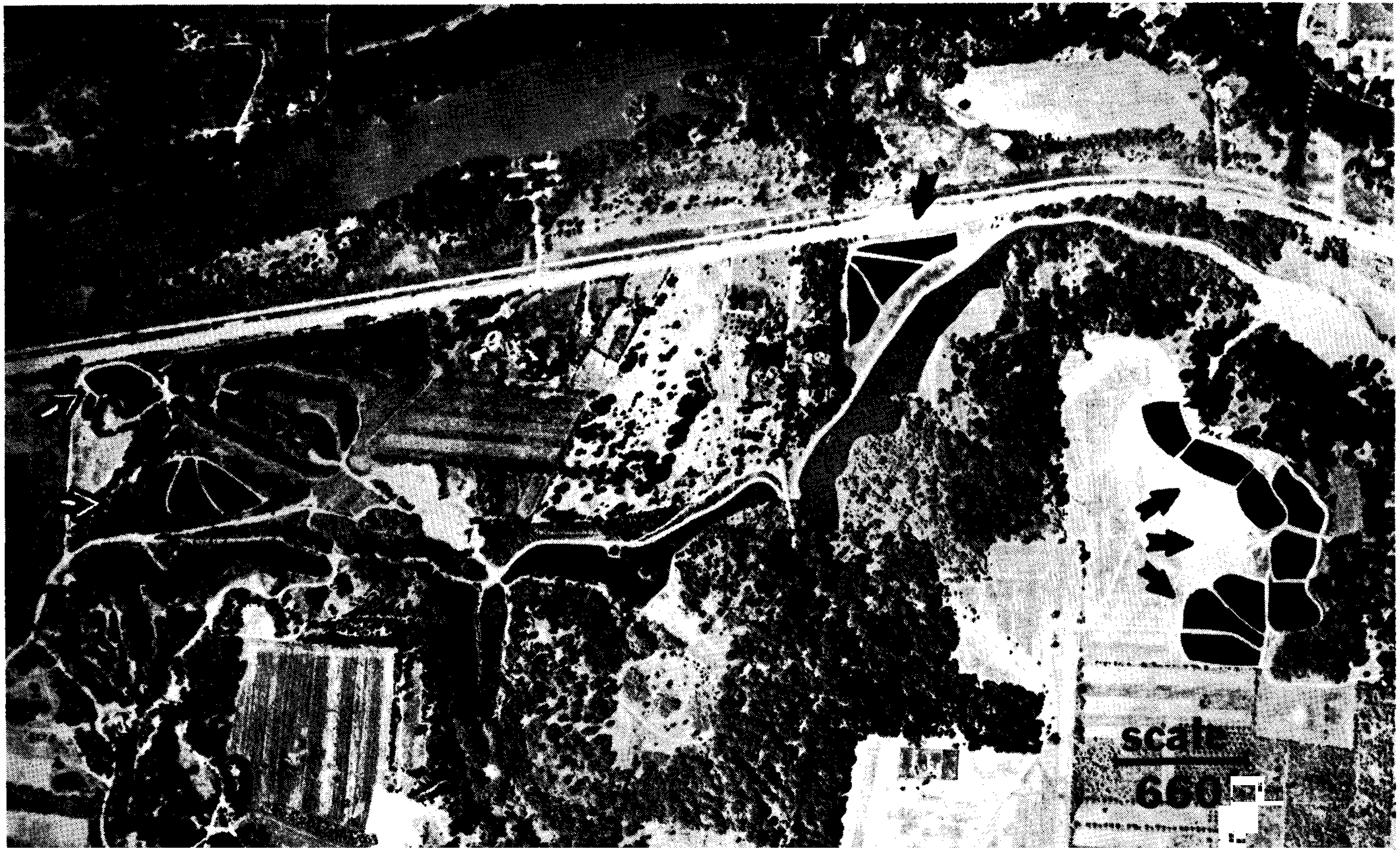

Fig. 1.—Aerial view of the McGraw Foundation area, showing shapes of the ponds used in studies reported on in this article and the arrangement of these ponds in units of three. Pond locations, indicated with arrows, are at right, right center, and left.

Dynamics of One-Species Populations of Fishes in Ponds Subjected to Cropping and Additional Stocking

D. Homer Buck
Charles F. Thoits Ill

THIS REPORT is based on several years of intensive studies of the production and related population dynamics of six kinds of warmwater fishes maintained as single species in 1-acre ponds. Species involved included the largemouth bass, *Micro pterus salmoides* (Lacépède); smallmouth bass, *M. dolomieui* Lacépède; bluegill, *Lepomis macrochirus* Rafinesque; yellow perch, *Perca flavescens* (Mitchill); brown bullhead, *Ictalurus nebulosus* (LeSueur); and the white crappie, *Pomoxis annularis* Rafinesque. Most production data published for these species have originated primarily from studies involving complex, multispecies populations. Only Bennett & Childers (1957), Cooper *et al.* (1963), and Eipper (1964) are known to have made comprehensive studies of the dynamics of populations having only a single species.

The principal aims of this investigation were to 1) increase our knowledge of the carrying capacities of ponds for warmwater fishes, 2) consider the relationship of carrying capacity to standing crop and to rate of production, and 3) measure the influence of controlled population increases and decreases on fish production.

It was assumed that physically similar, contiguous ponds would have reasonably similar characteristics and/or production potentials, and that differences in production could be related to treatments administered. Thus, emphasis was placed on the collection of fish population data, as opposed to intensive environmental analyses.

An attempt was made in these investigations to determine how nearly standing crops approximated carrying capacities. Although the data provided clear indications in some instances, we were dealing with a complex relationship that merits some preliminary examination.

The evolution of the carrying capacity concept has been quite thoroughly treated by Edwards & Fowle (1955). Somewhat later, Krumholz *et al.* (1957) reviewed the status of wildlife terminology and proposed the following definition of carrying capacity as one widely applicable to both fish and game biology: "the maximum number (or weight) of organisms of a given species and quality which can survive in a given ecosystem through the least favorable environmental conditions that occur within a stated interval of time." These writers further observed that in general the most appropriate "stated interval of time" is one year. By the terms of this definition, carrying capacity involves a minimum quantity which places limitations upon its practical application. If the interval of time is a year, the carrying capacity becomes the minimum population present during the annual cycle. Frequently, however, it is of more value to determine maximum rather than minimum rates of abundance. Only maximum rates, for example, permit the proper evaluation of the harvestable crop, or of the comparative production potentials of two species or combinations of species, or permit the proper evaluation of a remedial treatment in fisheries management. It would therefore seem desirable to measure carrying capacities at seasons other than when conditions for survival are poorest.

A more useful concept might therefore be that of Bennett (1962:59), who proposed the following definition of carrying capacity as one applicable for fishes: "the maximum poundage of a given species or complex of species of fishes that a limited and specific aquatic habitat may support during a stated interval of time." In eliminating the restrictive clause "through the least favorable environmental conditions," Bennett effectively removed the requirement for a minimum quantity, and in this respect his definition resembles the "current carrying capacity" of Edwards & Fowle (1955). One then becomes free to evaluate carrying capacity at any season for which suitable data may be obtained.

The question logically arises as to why standing crop may not in itself provide a satisfactory measure of carrying capacity, or of potential rates of abundance. It may, of course, at times. It is widely recognized, however, that the two are not necessarily the same, and that standing crop might be lower than, equal to, or in excess of the carrying capacity (Krumholz 1948, Bennett 1962, and others) due to changes in habitat, food supply, or population structure.

Carrying capacity is often conceived to be a relatively stable quantity, changing little from year to year. Theoretically, under comparatively stable conditions such as an extremely sterile lake or an extremely fertile, continuously fertilized pond, the carrying capacity could conceivably be quite stable. In the first instance one or more factors would be definitely and continuously deficient, or limiting, so that production would be at a continuously low level, as in a northern oligotrophic lake. In the second instance the essential nutrients would be supplied in a continuous abundance so that production might tend to remain near its potential maximum. Such a condition might be found in a southeastern pond so fertilized that available nutrients were channelled directly into the production of a continuous abundance of phytoplankton, zooplankton, and tertiary feeders with none diverted into the growing of higher plants. In both instances the flow of energy would tend to follow a reasonably regular and direct path. Between these two extremes exist those intermediately productive, unfertilized waters where the factors influencing production may exist in an almost infinite variety of combinations and the flow of energy may be channelled through a great variety of paths. The ponds of the present study typify such an intermediate category.

References made to carrying capacity in this paper are intended to represent the current or temporary carrying capacity which existed at the time of observation and may not necessarily represent the carrying capacity at the time when conditions for survival were poorest.

The investigations were conducted at the former McGraw Hydrobiological Laboratory near Dundee, Ill. Limited investigations were begun in 1956, but the majority of the data were collected in the years 1958-1963. The project was designed to continue for a minimum of 15 years as a cooperative program of the North American Wildlife Foundation, The Illinois Department of Conservation, the Illinois Natural History Survey, and the McGraw Foundation. As a result of organizational changes within the McGraw Foundation, the program was prematurely terminated in November 1963.

ACKNOWLEDGMENTS

The investigations were centered in 16 1-acre ponds constructed especially for this study. Pond construction was financed in part and an office and laboratory work space were provided by the North American Wildlife Foundation. Additional financial support for pond construction and other items of use in the program was provided by the Illinois Department of Conservation, and for the period 1956 through October 1961, that agency assigned to the project a full-time biologist. From

October, 1961, partial financial support was received through the Dingell-Johnson program, including salary and expenses for the assistant leader. Planning and administration of the program, financial support for the program leader, summer field assistance, and major equipment support was provided by the Illinois Natural History Survey throughout the course of the investigations.

We gratefully acknowledge the contributions of M. A. Whitacre of the Illinois Department of Conservation during the early years that he was assigned to the project as a fisheries biologist. We also owe a special debt of gratitude to the late Sam A. Parr for his many valued contributions to the program in his former capacity as Administrative Assistant to the Director of the Illinois Department of Conservation.

For assistance with summer field work, we are grateful to Robert M. Eichler and Warren U. Brigham.

The program was conceived and designed by Dr. George W. Bennett, and we gratefully acknowledge his suggestions and encouragement throughout the investigations as well as his critical review of the manuscript. We are additionally grateful to 0. F. Glissendorf for his editing of the final manuscript, and to Richard M. Sheets for drawing the figures.

DESCRIPTION OF THE AREA AND PONDS

The study area, in Kane County, Illinois, is approximately 35 miles south of the Wisconsin state line, and 30 miles west of Lake Michigan. It lies within the Wisconsin glaciation, with a rolling topography formed by the irregular deposition of glacial material. Major relief occurs only along waterways. The land is fertile and intensively devoted to the culture of corn and soybeans. Physiography and characteristics of the soils have been presented by Hopkins *et al.* (1917), and the climate of the area is described by the Atlas of Illinois Resources (1958).

The study ponds were located within a block of approximately 1,200 acres operated as a hunting and fishing club. This was an area of irregular topography, lying partly on high ground overlooking the Fox River to the west and dropping rather abruptly to the floodplain from points as high as 170 feet above the river. Steeper slopes were heavily wooded with native hardwoods and cut by frequent natural drainage ways to the river. Within this area were two series of club fishing lakes at two distinct levels. These contained mixed populations of warmwater sport fishes and were the source of water for most of our experiments. The only exceptions were three ponds used in our first series of smallmouth bass experiments which were filled by a partial diversion of an artificial spring-fed trout stream.

The major system of 15 ponds was constructed in five units, each containing three contiguous ponds. Because of differences in location, in types of bottom materials, and in age, or completion dates, the ponds presented a rather wide range of characteristics. Table 1 presents the names, dates of completion, and various chemical and physical characteristics of the ponds in each of the five units, plus the single pond Alpha.

All ponds were designed to have a surface area of 1 acre and a maximum depth of 8 feet, with average depths of between 3 and 5 feet. Pond banks were steep in slope (approximately 1:1) to minimize growth of shoreline plants. Grade of pond bottoms was established to provide 1 foot of rise in the first 50 feet from the drain, and 1 foot additional rise for each 100 feet thereafter. Pond shapes varied from approximately round to an irregular L-shape, depending upon topography, but the most common shape was triangular — wide at the shallow end, and forming a narrow apex at the drain (Fig. 1).

Table I.-Some physical and chemical data from ponds built on the property of the McGraw Foundation near Dundee, Illinois and used for carrying capacity experiments. When filled, each pond had a surface area of I acre.

Unit	*Pond*	*Year of Completion*	*Bottom Material*	*Relative Fertility*	*Average pH*	***pH* Range**	*Average Total Alkalinity*	*Average Transparency, Inches (Secchi disc)*	*Submersed Aquatic Vegetation*
	Alpha	1956	Black Dirt, Clay, & Gravel	Medium	8.6	**8.5–8.7**[b]	203	50.4	**None**[c]
1	Beta	1957		High	8.9	8.3-9.9	199	72.5	**Abundant**[d]
	Gamma				8.7	8.3-9.0	180	83.6	
	Delta	"		"	9.2	8.0-10.2	188	60.2	"
2	Zeta	1958	Sand & Clay	Low-Medium	8.8	8.6-9.0	161	41.6	Moderate
	Theta				9.4	9.0-9.8	117	44.0	
	Iota				9.2	8.7-9.9	149	35.8	
3	Kappa		Clay	Low	8.7	8.0-9.2	148	16.7	Scarce
	Lambda				9.2	8.7-10.2	113	22.0	
	Rho				8.9	8.6-9.4	145	22.5	
4	Sigma				8.9	8.6-9.4	134	26.0	
	Tau				9.1	8.6-10.1	105	36.0	
	Upsilon				9.1	8.4-9.8	106	32.0	
5	Phi	1960			8.8	8.4-9.7	91	22.4	None
	Chi				8.7	8.0-9.2	93	15.2	
	Psi				8.7	8.5-9.2	118	20.1	

Average alkalinities and pH and Secchi disc readings were based on weekly determinations, usually made between 9 A.M. and noon, throughout the 1962 growing season.
[b] In 1961, with abundant vegetation, pH in this pond exceeded 10.2 and caused total loss of a chain pickerel population. With no vegetation in 1962, pH remained low.
[c] Although weedless in 1962, this pond contained abundant stonewort *(Chara)* in other years.
[d] Beta, Gamma, and Delta were extremely variable, with weeds ranging from abundant to none in various years.

Descriptive data listed in Table 1 are generally self-explanatory, but two items deserve comment. Daytime pH values in most ponds ranged abnormally high. Since the testing apparatus used had an upper range of 10.2, the average pH, as well as the upper range, could have been higher in these ponds for which a high of 10.2 is listed. The high values were associated with intensive rates of photosynthesis, and consequent replacement of absorbed carbonate and bicarbonate ions by released hydroxyl ions. Such extremes are not uncommon in small ponds having poorly buffered waters (Ruttner 1953). High pH (10.2 or above) was credited with the deaths of an experimental population of chain pickerel, *Esox niger* LeSueur, at this station, and had some influence on the spawning of largemouth bass, as is discussed in a later section.

Density of submerged aquatic plants varied greatly from pond to pond, as well as from year to year, and was usually positively correlated with age, fertility, and clarity of the pond (Table 1). Weeds were not observed in Unit 5, were relatively scarce in Units 3 and 4, moderately abundant in Unit 2, and often extremely abundant in pond Alpha and in Unit 1. The most common forms were the curley-leaf pondweed, *Potamogeton crispus* L., and sago pondweed, *P. pectinatus* L.; almost as common was *P. foliosus* Raf. Less common were *Anacharis canadensis* (Michx.) and a bushy pondweed, probably *Najas flexilis* (Willd.). A water milfoil, *Myriophyllum exalbescens* Fernald was observed only in pond Theta, and horned pondweed, *Zannichellia palustris* L. only in pond Delta.

With the exception of pond Alpha, all ponds received at least one treatment of inorganic fertilizer. While each of the three ponds in a unit received equal treatments, those units thought to be the least fertile received additional amounts (Table 2).

Tablo 2. — Kinds and amounts of fertilizers used in the various pond units, and dates of application.

Fertilizer	*Pounds Per Acre*	*Pond Units Treated*	*Date*
0/20/0	100	1,2,3,4	6/02/59
0/20/0	100	4	6/29/59
10/10/10	100	3,4,5	5/14/62
0/46/0	26	3,4,5	5/25/62
0/46/0	28	3,4,5	6/25/62
0/46/0	28	5	7/20/62

EXPERIMENTAL DESIGN AND METHOD OF OPERATION

The original plan of study involved the simultaneous operation of the 15 ponds, divided into five units of three ponds each, with each unit devoted to a single species of fish. The 15 populations were to be studied through three growing seasons, following which all ponds would be drained and censused and the population of each unit rotated into a new unit for a similar study. This was to be continued through five 3-year periods, or until each of the five species had been rotated through each of the five units of ponds.

Due to the staggered completion date of the ponds it was not possible to initiate the original plan until the total of 15 ponds became available in 1961. However, prelim inary investigations were launched as the ponds became available and, when possible, these ponds were operated on a schedule similar to that originally planned. Where units of three ponds were available each pond was stocked with similar numbers and sizes of the same single species. One of these (the "cropped" pond) was then cropped at a predetermined rate from April through September, and the majority of those fish were marked and added to a second pond (the "add-stock" pond). The third pond in each unit (the "control" pond) w a s neither cropped nor "overstocked," and was left to develop naturally. All ponds were sampled at regular intervals to measure comparative fish growth and condition, and some fishable populations were subjected to limited hook-and-line fishing. The principal deviation of the pre-1961 experiments from the original design was in the interval of study. Final censuses were made after only one and one-half or two seasons, rather than after three growing seasons.

An additional part of the design was to drain and census the population in each "control" pond (one in each unit) at the end of the first growing season so that this early population development might be compared with that attained after longer periods. Additional spring and fall inventories were made by utilizing Petersen estimation procedures. Those few estimates which could be supported by supplementary draining censuses or other information have been utilized herein, but the majority of the estimates were believed to be too unreliable for presentation. In a study of these same populations, using seines for obtaining samples, we found that the Petersen procedures tended to provide a high proportion of gross underestimations (Buck & Thoits 1965).

In censusing the ponds, fishes and water were allowed to pass through the drains into a modified Wolf-type weir where the fish were trapped and transferred to holding tanks or live boxes. Data collected included individual lengths and weights of fish older than Age 0, individual lengths and weights of an adequate sample of Age 0 fishes, length frequency distributions, and total weight of all fishes. All fishes were then resorted into equal numbers of various size or age groups and randomly restocked in a different unit of ponds. Other observations recorded at this time included kinds and relative amounts of aquatic vegetation, abundance of tadpoles and crayfish, and kinds and abundance of the more common aquatic insects. As a part of one draining operation the waters from three ponds were strained through a special filter which retained all stages and sizes of aquatic insects, scuds, and larger zooplankters, and permitted an estimate of standing crops of these invertebrate forms.

Prior to 1963 all fish populations were sampled at intervals of 2 weeks throughout most of the growing season (usually April through September). In 1963, samples were collected every third week. Most sampling was by use of a large seine, 185 feet long, 12 feet deep, and with % -inch mesh. This was supplemented by sampling with smaller seines for small fish, wire traps for perch and bluegills, and hook-and-line fishing and a-c boat shocker for perch and smallmouth and largemouth bass. Only bullheads were collected exclusively by seining. Efforts were made to sample all age components of each population at each sampling period, with a sampling goal of at least 100 fish for each abundant age class. Whenever possible, sampling of an individual pond was accomplished in a single day. However, when samples were difficult to obtain, sampling of an individual pond often continued over several consecutive days. Fish were weighed and measured when caught, except that hook-and-line and boat shocker samples taken at night were usually not processed until the following morning. Cropping and the transfer of stock was integrated with sampling. Individual lengths and weights were taken of larger fish; smaller fish of uniform sizes were often weighed in groups of 10 or 20.

In this study index of condition (C) was arrived at by employing the method of Thompson & Bennett (1939) using the formula

$$C = \frac{10{,}000\ W}{L}$$

Various fin clips were used to indicate the age of fishes, to designate those being transferred, and to indicate the season of transfer. If a fish to be stocked at the beginning of a new experiment bore no previous age mark, census mark (including that of the first-year census of a control pond), or sampling mark, it was given a fin clip indicating its approximate age. Because of frequent spawning failures, year classes were in many cases easily distinguishable by size. This fortunately was true for the bluegill population where age distinctions would have been the most difficult. Even when consecutive year classes were produced there were periods when age separations were possible and unmarked fish could be marked, thereby defining the range of sizes for the several year classes in later draining censuses. All individuals in some year classes were marked, and in most cases a majority of individuals in each class had received an identifying mark by the time of the final census. The major exception was in the largemouth bass where cannibalism was responsible for considerable overlapping of age classes before the fish could be marked. In these instances the censused populations were divided into size classes, which to a large extent approximated age classes.

Mortalities from marking were generally quite negligible. Also, most clips were found to be permanent. When partially regenerated fins were encountered in sampling, the regenerated portions were removed. Fish with completely regenerated fins were identifiable by malformations of the fin.

PRESENTATION OF DATA

The data are presented by individual species. Primary subjects considered include growth, condition, reproduction and survival rates, mortality rates, and the influence of the experimental stocking and cropping on production. Included are standing crop totals, along with supplementary data, for 11 populations of smallmouth bass, 10 of largemouth bass, 6 each for yellow perch and white crappie, and 4 each for bluegills and brown bullheads. Supplementary data include number of growing seasons, pounds originally stocked, pounds added or pounds cropped, and pounds lost or gained over the course of the experiment.

The pounds lost or gained figure is intended to represent the weight of fish produced in the pond, less natural mortality. Thus, from the standing crop figure we subtracted pounds originally stocked, and pounds added, then added pounds cropped, to derive the sum of pounds lost or gained. This final summation is identical with Ricker's (1958) surplus production when computed for a single season, when no stock was added during the season, and when the poundage present at the start of the season approximated carrying capacity. It differed from Ricker's statistic when original stock was below carrying capacity, when stock was added to the population, or when computed for a period longer than one calendar year. Where applicable, our figure of pounds lost or gained is used interchangeably with Ricker's surplus production. This statistic provides a useful measure of production, and permits an evaluation of the influence of the population manipulations involved and how nearly the standing crops attained, or whether they exceeded, the carrying capacities of the ponds at the times of census.

SMALLMOUTH BASS

The stock of smallmouth bass used in these studies was obtained from small ponds located on the grounds of the former Fin 'n Feather Club, near Dundee, Illinois, where they had been maintained in club fishing ponds for a number of years. The source of the club's stock is not known. Smallmouth stocked in pond Alpha in July, 1956, spawned the following spring, and progeny from this stock were used in all subsequent experiments.

Pond Alpha was completed and first filled with water in July, 1956, and was stocked with 16.2 pounds of smallmouth consisting of 95 sub-adults (mostly Age I) in July of that year. Ponds in Unit 1 (Beta, Gamma and Delta) were cornpleted and first filled in May, 1957, but were first stocked with smallmouth in May, 1958. On May 13, each pond received a total of 5.6 pounds of smallmouth consisting of 10 adults averaging 9.8 inches total length, and 40 fingerlings (Age I) averaging 4 inches total length. Adults were observed to spawn in all three ponds in the first week following their release. These ponds were drained and censused in October, 1959, following two seasons of growth.

Following the 1959 censuses, age groups of smallmouth from all ponds were combined and randomly restocked in equal numbers of the several size (age) groups in each of the same three ponds. Total weights of these new populations were between 90 and 97 pounds. The ponds were drained and censused in October, 1960, following the single season of growth.

Ponds in Unit 4 (Sigma, Tau and Upsilon) had been completed in August, 1958, but were not available for the smallmouth experiment until 1960. Thus, the ponds were slightly over 2 years old when first stocked with smallmouth bass in October of 1960. Unit 1 was the source of fish for Unit 4. Stockings were heavy, being approximately 130 pounds per acre in each pond, composed principally (about 92 percent by weight) of Age II fish (1958 year-class). From a review of available information collected during the winter of 1960-1961, it was decided that the fall stocking of Age II fish had been excessive. Accordingly, in mid-April, 1961, 60 of the dominant age class (now Age III) were removed from ponds Sigma and Upsilon, and 59 were removed from Tau. Total weights of these fish were 20.93, 21.79 and 21.45 pounds from ponds Sigma, Tau and Upsilon, respectively. It was believed that these reductions might improve the food-feeder relationships between the food producing potential of the ponds and the bass populations. Additional population adjustments and transfers of stock are presented in subsequent text and tables.

Standing Crop Data

Table 3 presents standing crops in pounds per acre for 11 populations of smallmouth bass arranged according to experimental treatments given the populations, with an average standing crop presented for those ponds receiving

Table 3.—Standing crops in pounds per acre of smallmouth bass in ponds receiving different experimental treatments. All censuses were by pond drainage and count of fishes at the ends of the growing seasons.

Unit	*Pond*	*Number of Growing Seasons*	*Year of Census*	*Standing Crop in Pounds Per Acre by Treatment Received*		
				Control	Cropped	Add-stock
	Alpha [a]	1½	1957	64.7		
1	Delta	2	1959	26.4	. .	
1	Gamma	2	1959		73.0	
1	Beta	2	1959			
1	Beta	1	1960	169.0	. .	
1	Delta	1	1960		56.3	
1	Gamma	1	1960			173.4
4	Sigma	1	1961	84.9		
4	Sigma	2	1963	93.2		
4	Tau	3	1963		9.3	. .
4	Upsilon	3	1963			95.5
			Average	*87.6*	*46.2*	*149.6*

a Operation of this single pond was similar to that of the regular control ponds, and it is so classified here.

identical treatments. Table 4 shows the same standing crop data together with such pertinent supplementary data as pounds originally stocked, pounds added to or removed from the populations during the course of the experiments, and the net loss or gain in pounds of fish flesh by the termination of the experiment. All censuses presented in Tables 3 and 4 were by pond drainage with counts of all fishes at the ends of the growing seasons. Table 5 presents those standing crops obtained by estimation procedures in the spring, in addition to those obtained by draining censuses in the fall, for ponds Sigma, Tau, and Upsilon. Original stock, computations of pounds gained or lost, and other supplementary data in Table 5 were derived or computed from figures obtained from the previous census, whether it was by estimation or actual count.

Standing crops ranged from a high of 180 pounds per acre in the add-stock pond Beta in 1959 to a low of 9.3 pounds in grossly overcropped pond Tau in 1963 (Tables 3 and 4). Some of the known factors that contributed to these variations included 1) differences in experimental treatments received, 2)

Table 4. — Pounds of smallmouth bass per acre originally stocked, pounds added or removed, final standing crops in pounds per acre, and weights gained or lost in pounds per acre in ponds Alpha, Beta, Gamma, Delta, Sigma, Tau, and Upsilon for periods of 1, 1½ (Alpha), 2 and 3 years. All censuses were by pond drainage and count of fishes at the ends of the growing seasons.

Unit	Pond	Treatment	*Year* of Census	Number of Growing Seasons	Pounds of Original Stock	Standing Crop, Pounds Per Acre	Pounds Added	Pounds Removed	Pounds Lost or Gained
	Alpha	None	1957	1½	16.2	64.7	0.0	0.0	+48.5
1	Delta	Control	1959	2	5.6	26.4	0.0	2.5	+23.3
1	Gamma	Cropped	1959	2	5.6	73.0	0.0	69.8	+137.2
1	Beta	Add-stock	1959	2	5.6	180.0	41.7	1.1	+133.8
1	Beta	Control	1960	1	89.7	169.0	0.0	1.6	+80.9
1	Delta	Cropped	1960	1	97.4	56.3	0.0	86.2	+45.1
1	Gamma	Add-stock	1960	1	91.1	173.4	50.2	8.4	+40.5
4	Sigma	Control	1961	1	130.8	84.9	0.0	36.1	−9.8
4	Sigma	Control	1963	2	83.8	93.2	8.1	51.1	+52.4
4	Tau	Cropped	1963	3	133.1	9.3	5.5	126.9	−2.4
4	Upsilon	Add-stock	1963	3	129.6	95.5	84.9	50.8	—68.2

Table 5. — Standing crops of smallmouth bass in 1-acre ponds Sigma, Tau, and Upsilon, and pertinent supplementary data, from censuses in both spring and fall, by either drainage (exact count) or Petersen estimation procedures.

Pond	Season and Year of Census[a]	Type of Census	Number of Growing Seasons	Standing Crop, Pounds Per Acre	Pounds of Original Stock	Pounds Added	Pounds Removed	Pounds Lost or Gained
Sigma	F 1961	Drainage	1	84.9	130.8	0.0	36.1	−9.8
Sigma	S 1963	Estimate	2	56.4	83.8	8.1	50.5	+14.9
Sigma	F 1963	Drainage	1	93.2	56.4	0.0	0.6	+37.4
Tau	S 1963	Estimate	2	5.6	133.1	5.5	119.4	−13.6
Tau	F 1963	Drainage	1	9.3	5.6	0.5	7.5	+10.8
Upsilon	S 1962	Estimate	1	55.4	129.6	42.3	33.6	-82.8
Upsilon	S 1963	Estimate	1	64.5	55.4	36.5	15.8	—11.6
Upsilon	F 1963	Drainage	1	95.5	64.5	6.1	1.3	+26.2

[a] Symbols: F = fall, S = spring.

differences in pond fertilities and consequent differences in production of foods, and 3) differences in size and/or age composition of the populations. Except for the unusually low production in pond Delta in 1959, standing crops among contiguous ponds within the same experimental units were universally highest in the ponds which received additions of stock, lowest in those from which fish were cropped, and intermediate in those ponds which were maintained as controls.

Fertilities of the three ponds in Unit 4 were thought to be very similar, but ponds in Unit 1 exhibited rather marked differences in their productivities. These differences were believed to be related to the way these ponds were supplied with water while they were occupied by smallmouth. During this period the ponds were watered by partial diversion of the artificial, spring-fed trout stream mentioned earlier. The diverted water first entered pond Beta, from which it overflowed through a tube into the second pond, Gamma, and from which it again overflowed to fill the third pond, Delta. In addition, a small stream of water flowed into Beta for extended periods to make up losses through seepage and evaporation in all three ponds. Beta's productivity was probably enhanced by a greater water exchange, by an influx of drift organisms from the feeding stream, and from receiving nutrients not passed along in equal quantities to its companion ponds. The data indicated that productivity of smallmouth decreased in the order that the water filled and passed through the ponds, from Beta to Gamma to Delta. We thus may have experienced a progressive drain of both food and nutrients so that water reaching the last pond Delta was relatively sterile.

The rather wide range of differences in standing crops recorded in Table 3 merits additional discussion. The final standing crop of 64.7 pounds per acre in pond Alpha may have been short of the carrying capacity of this pond because 1) initial stocking was light (16.2 pounds) and little more than one effective growing season was involved, 2) the population contained only two year-classes, and 3) much larger standing crops were recovered from other ponds, including those believed to be less fertile, when more time was involved or initial stocking was larger.

The extremely low standing crop of 26.4 pounds of bass found in Delta in October, 1959, was due to a combination of low fertility, when compared with its two companion ponds, and to the virtual absence of the age classes 0 and I. No young could be found in Delta in 1958, and numbers of young bass were extremely limited in 1959. Weight gains of the population consisted almost entirely of flesh added to the original stock, which, at the time of census, included only 32 individuals. The absence of fish of Ages 0 and I was particularly critical in this instance since they comprised the greatest weight in both companion ponds. However, as the age and size distribution of fish in the three ponds was equalized at the time the ponds were restocked in November, 1959, the comparatively low standing crop in Delta in 1960 was believed to have been due to low productivity. Poor production in this pond in 1960 was evidenced by its low figure of "pounds gained" (45.1 pounds) (Table 4), in spite of a relatively heavy rate of cropping (86.2 pounds).

The similarity of standing crops in Beta in 1959, and in Beta and Gamma in 1960, and a consideration of "pounds gained" in the two periods (Table 4), suggested that from 170 to 180 pounds per acre was near the maximum carrying capacity of these ponds for smallmouth. This seems evident because final standing crops were similar in the three instances, and "pounds gained" was either high (133.8 pounds in Beta, 1959), or low (40.5 pounds in Gamma, 1960), depending upon the poundage required to attain this presumed maximum.

Large standing crops in Beta in 1959, and Beta and Gamma in 1960, suggested that these populations made highly efficient use of available foods, and it is of interest to examine their compositions. Table 6 presents numbers of each age class censused, with percentages of total weights and numbers of the entire population comprised by each.

A characteristic common to all three populations was the dominance of bass in the intermediate size ranges. In October, 1959, Age I fish in pond Beta ranged from 6.0 to 8.9 inches total length, and comprised 85.3 percent of the total populations by weight and 82.2 percent by numbers. In 1960, the principal component in both Beta and Gamma was Age II fish ranging from 7.5 to 10.9 inches in total length. By weight, these comprised 85.9 percent and 94.6 percent of the populations in Beta and Gamma, respectively. Predation of young may have made a major contribution to growth of the older fishes. In studies of the stomach contents of 59 Age I fish collected from these ponds, however, fish were a minor item, and various invertebrates strongly predominated. It seems obvious that the larger fish (6-11 inches) competed quite intensively with the smaller ones for invertebrate foods, and made efficient use of these foods when small fish were scarce or absent. This contrasts with the situation in pond Delta in 1959 where low production was attributed largely to an absence of small fish. In that instance, however, fish older than Age I were also limited, numbering only 32. An inference from the two populations may be that when a sufficient number of smallmouths are present to make efficient use of an abundant supply of invertebrate foods, size of the bass may be relatively unimportant, and the absence of young, small fish may cause little or no loss in total production of pounds of fish flesh.

Unfortunately, we had no population of large numbers of young fish only so that their efficiency could be compared with that of larger individuals of Ages I and II. However, we believe smallmouth of such intermediate sizes to be either superior foragers or more efficient converters of invertebrate foods than largemouth of a similar size, which, in our experience, exhibit more specific food requirements in the form of fish and other large food items.

Populations censused in 1959 had expanded through two seasons from an initial stock of 5.6 pounds, and ponds drained in 1960 had developed through one growing season from original stocks of 90, 91 and 97 pounds in Beta, Gamma and Delta respectively (Table 4). The data indicate that a sufficient amount of time had elapsed in both periods for carrying capacities to have been achieved. This conclusion is based on a comparison of "pounds gained" against standing crop totals. The data for pond Gamma provide one of several examples. When cropped in 1958 and 1959, the population in pond Gamma had a "pounds gained" figure of 137.2 over the 2-year period, as compared to only 40.5 pounds when "overstocked" in 1960. "Pounds gained" would probably have exceeded 40 pounds in 1960 had the pond not attained its carrying capacity at that point.

These results indicate substantial differences in productivities of ponds Beta, Gamma, and Delta during the smallmouth bass experiments. Beta and Gamma both clearly exceeded Delta in pounds of fish produced in both years of census. A greater productivity by Beta than Gamma in 1959 was indicated by the fact that although Beta received an addition of 41.7 pounds of stock, while Gamma was heavily cropped, surplus productions in the two ponds were

Table 6. —Numbers in each age group, and percents of total numbers and weights of each age group in censused populations of smallmouth bass in the single pond Alpha, in ponds Beta, Gamma, and Delta (Unit 1), and in ponds Sigma, Tau, and Upsilon (Unit 4), in years indicated.

Pond, Year of Census, Treatment[a]	*Total Number Censused in each Age Group*					*Percent of Total Number Censused in Each Age Group*					*Percent of Total Weight Censused in Each Age Group*					*Total, All Age Groups*	
	0	I	II	III	IV & Older	0	I	II	III	IV & Older	0	I	II	III	IV & Older	Number	Pounds
A 1957 0	1,157	0	76	0	1	93.8	0.0	6.2	0.0	Tr	50.5	0.0	46.1	0.0	3.4	1,234	64.7
D 1959 0	0	2	26	6	0	0.0	5.9	76.5	17.6	0.0	0.0	3.1	69.6	27.3	0.0	34	26.4
G 1959 —	1	357	0	0	0	0.1	99.9	0.0	0.0	0.0	1.0	99.9	0.0	0.0	0.0	358	73.1
B 1959 +	188	1,009	20	8	0	15.3	82.2	1.6	0.4	0.0	3.8	85.3	5.4	5.5	0.0	1,225	180.0
B 1960 0	889	0	406	4	3	68.3	0.0	31.2	0.3	0.2	9.7	0.0	85.9	1.6	2.8	1,302	169.0
D 1960 —	67	0	126	2	2	34.0	0.0	64.0	1.0	1.0	5.9	0.0	85.9	2.7	5.5	196	56.3
G 1960 +	23	0	506	14	0	4.2	0.0	93.2	2.6	0.0	0.3	0.0	94.6	5.1	0.0	543	173.4
S 1961 0	70	0	0	233	8	22.5	0.0	0.0	74.9	2.6	1.4	0.0	0.0	91.2	7.4	311	84.9
S 1963 0	729	24	47	8	59	84.1	2.8	5.4	0.9	6.8	11.9	4.3	23.6	4.8	55.4	867	93.2
T 1963 —	77	11	0	0	1	86.5	12.4	0.0	0.0	1.1	31.6	51.1	0.0	0.0	17.3	89	9.3
U 1963 +	1,534	59	44	6	86	88.7	3.4	2.5	0.4	5.0	14.4	10.0	16.5	3.2	55.9	1,729	95.5

Ponds are designated as: A = Alpha, B = Beta, G = Gamma, D = Delta, S = Sigma, T = Tau, and U = Upsilon. Pond treatments are designated as: O = none, = stock added, and — (minus) = cropped.

similar (133.8 and 137.2 pounds) . That the productivity of Beta was as great as, if not greater than, that of pond Gamma in 1960 was evidenced by the fact that final standing crops were similar even though Gamma received 50.2 pounds of additional stock while Beta, the control, received none.

Standing crops measured by fall draining censuses of ponds in Unit 4 (Sigma, Tau, and Upsilson) ranged from 9.3 pounds per acre in the grossly overcropped Tau, to fairly uniform levels of from 84.9 to 95.5 in the two companion ponds. The two fall standing crops in pond Sigma, and the final one in pond Upsilon were thought to either exceed or to approximate carrying capacities of those ponds in the fall season, and such levels were about one-half of those measured in the fall in the more fertile ponds (Beta and Gamma) of Unit 1. In Unit 4 ponds, however, censuses were also made in the spring by Petersen estimates, and these data indicated fall carrying capacities greatly exceeding those of the spring. This is illustrated by data in Table 5, and in the following review of the known history of each population in Unit 4.

As shown in Table 5, standing crops recorded for control pond Sigma were 84.9 pounds by a draining census in the fall of 1961, 56.4 pounds by a Petersen estimate in the spring of 1963, and 93.2 pounds by the final draining census in October, 1963. Related facts of importance were, briefly, as follows. As shown in Table 6, the 1961 standing crop of 84.9 pounds was comprised primarily (91.2 percent by weight) of 233 individuals of the dominant Age III class. From the original stock of 343 Age III fish, 105 had been removed in 1961, leaving an unaccounted for loss, or mortality, of five individuals by the end of that first year. From the time of stocking in October, 1960, to October, 1961, the 233 survivors of the original stock of 343 had made an average length increment of only 0.24 inches, had shown an average loss in weight of 0.012 pounds, and a loss in condition of from 4.5 to 4. None of the original 311 fingerlings stocked at Age 0 were recovered in 1961, apparently having been lost through predation, and the recovery of only 70 Age 0 fish in the 1961 census represented the total recruitment to the population. There was a deficit by October, 1961 of 9.8 pounds, as shown in the "pounds lost or gained" column of Table 5, in spite of the earlier cropping of 36.1 pounds. The combination of these facts indicated that the final standing crop of 84.9 pounds may have exceeded the carrying capacity of the pond at the time of the 1961 census. For this reason, all three populations in this unit were again thinned in May and June, 1962. The removal from pond Sigma was 143 8- to 10-inch bass (then Age IV), weighing a total of 50.5 pounds. Concurrent removals from the companion ponds were similar, and will be given in the discussions concerning each.

Pond Sigma was next inventoried by the Petersen method in the spring of 1963, and this inventory provided an estimated standing crop of 56.4 pounds. Recoveries made in the fall draining census indicated this estimate to be accurate. Using the figure of 56.4 pounds, we computed a pounds gained of only approximately 15 pounds since the previous inventory in October, 1961, in spite of the removal of 50.5 pounds of bass at the start of the 1962 growing season. It is therefore believed that the carrying capacity of pond Sigma in the spring of 1963 was quite low, and probably almost the same as the standing crop of 56.4 pounds estimated at that time.

The 1963 draining census of pond Sigma yielded a standing crop of 93.2 pounds. Based on an "original stock" of 56.4 pounds as provided by the 1963 spring estimate, we derived a pounds gained figure of 37.4 during the 1963 growing season. This rather substantial gain (as compared with those of 1961 and 1962) was coupled with an increase in condition by the dominant age group of from 4 in October, 1961, to 5 in October, 1963. We therefore believe that the carrying capacity of pond Sigma was substantially higher in the fall of 1963 than at either previous census, and that the increase was due primarily to an increasing fertility and a consequent greater food production, with the food increase being primarily in the production of scuds and crayfish.

Increased production in pond Sigma may also have been related to changes in population composition. The 1961 draining census contained only 70 fish of Age 0, none of either Ages I or II, and 241 that were Age III or older. The 1963 census contained 729 Age 0 fish, 24 of Age I, 47 of Age II, and 67 that were Age III or older. With its more normal distribution of sizes, the 1963 population would be expected to have made a more efficient use of available foods.

The cropped pond, Tau, was inventoried by a Petersen estimate in the spring of 1963, and by a draining census in October, 1963. We believe that the standing crop of about 5.6 pounds estimated in April, 1963, was quite accurate (Table 5). At the final draining census (October, 1963) the population contained only 89 fish weighing about 9.3 pounds, of which only 12 were older than Age 0 and only one older than Age I. Clearly, the cropping of a total of 119.4 pounds from this pond in 1961 and 1962 was excessive. Remaining fish grew fast, and were in excellent condition, but there were too few to efficiently exploit the increasing availability of food. Expansion of the population was further inhibited by a failure of reproduction in 1963, although reproduction was successful in both companion ponds. Though cropping had been heavy, our accounting indicated that a minimum of 30 adults should have been available for spawning in 1963. Mortalities apparently exceeded the expected, and may have left no breeding pairs. An additional cause for failure may have been the great abundance of crayfish in this pond at the time of spawning. In a later study, in a 4-acre pond containing smallmouth, lake chubsuckers, *Erimyzon succeta* (lacépède), and chain pickerel, we credited the foraging of an extreme abundance of crayfish with destroying the eggs and/or larvae of lake chubsuckers and chain pickerel.

By midsummer 1963, it was clear that no Age 0 fish were present in pond Tau, and on July 26, 97 Age 0 fingerlings were transferred to Tau from Upsilon. When censused in October, 77 of the 97 (79.4 percent survival) were recovered. Based on an original stock of 5.6 pounds, as estimated in April, 1963, and 7.5 pounds removed, this cropped pond made a gain of only about 10.8 pounds during 1963. The fish grew well in the presence of abundant food, but were simply too few in number to make additional gain.

Standing crops recorded for the add-stock pond Upsilon were 55.4 and 64.5 pounds from Petersen estimates in the springs of 1962 and 1963, respectively, and a total of 95.5 pounds from the draining census of October, 1963. The dynamics of this population are also quite thoroughly known, and will be reviewed in some detail.

Intensive sampling indicated that all 313 Age 0 fingerlings stocked in October, 1960, and all but few of a large 1961 brood were eliminated by fall of 1961, probably by predation.

From the original stock of 346 fish of the 1958 year-class, we had removed a total of 102 (early thinning, stomach samples, etc.), and during a scheduled transfer operation in the summer of 1961 we had added a total of 120, leaving a balance of 364 1958 year-class fish at the beginning of the winter of 1961—1962 (assuming no 1961 mortality) . The Petersen estimate of May, 1962, indicated that the total population consisted of 180 individuals. Based on average weights at that time the standing crop was computed to be 55.4 pounds, or about 43 percent of the total weight (129.6 pounds) originally stocked. This indicated a mortality of 184 bass of the 1958 year-class, weighing approximately 67 pounds. Since average condition of this year-class had declined during the previous season (1961) from 4.5 in April, to 3.6 in September, the mortalities were not unexpected. We decided, however, that the population should be further reduced. On May 10, 1962, 55 additional bass of this age were removed. Based on our previous estimate of 180 fish, this left a total of 125 of the 1958 brood to enter the 1962 growing season. A subsequent increase in condition from 3.7 in May, to 5 in July, indicated the thinning had significant results.

Over the course of the 1962 season 3 bass of the 1958 year-class were injured and removed, and 37 were added as a part of the regular transfer program. Assuming no additional mortalities, we should have ended the 1962 season with 159 individuals of the year-class in question.

The population in pond Upsilon was again inventoried by a Petersen estimate in May, 1963. The estimate indicated an overwinter mortality of about 78 fish, or about half the number that died during the previous winter. Such an estimate would have put us into the 1963 season with 81 fish of the still dominant 1958 brood. Finally, using the October, 1963 census figures, we can evaluate our previous estimates of standing crop and mortalities for this group. We entered the spring with an estimated 81 Age IV fish, and one fish of this age was transferred into Upsilon in July. The final census yielded 83 fish of this age, indicating that our earlier estimates of this dominant 1958 year-class had been surprisingly good.

The final standing crop (drain census) in pond Upsilon in October, 1963 was 95.5 pounds. Based on the 1963 spring estimate of 64.5 pounds, we derived a pounds gained figure for 1963 of 26.2 pounds. The carrying capacity of Upsilon apparently improved during this third season over what it had been at previous times of census, and to the level of that attained by pond Sigma at the end of its third year. Again, increased production was probably due to increased fertility, greater food production (principally crayfish and scuds), and a more efficient distribution of sizes within the 1963 population. Whereas the October, 1961 population was dominated by excessive numbers of adults of the 1958 year-class that were in extremely poor condition, the 1963 population contained a more normal and efficient distribution of sizes (Table 6).

As shown in Table 3, maximum standing crops attained in Sigma and Upsilon (Unit 4) were just about half of those attained in Beta in 1959 (180 pounds), and Beta and Gamma in 1960 (169 and 173.4 pounds). This difference in productivity was much larger than anticipated, and had caused us to grossly overstock the Unit 4 ponds at the time of transfer.

Effects of Cropping and Adding Stock

The effects of cropping and adding smallmouth stock on the production of fish flesh were largely obscured in these experiments by differences in the productivities of contiguous ponds in Unit 1, and by the effects of gross overstocking, and subsequent overcropping of the cropped pond, in Unit 4. The data to be considered are those listed under the column headed "pounds lost or gained" in Table 4. This figure of "pounds gained," closely analagous to the surplus production of Ricker (1958) and Cooper *et al.* (1963), should have been highest in cropped ponds, lowest in the ponds receiving added stock, and intermediate in the control ponds.

The highest individual gain was that of 137.2 pounds in cropped Gamma over the 1958-1959 period, but the average for cropped ponds was made abnormally low because of limited production in pond Delta in 1960, due to this pond's fertility being lower than in either companion pond, and by the low production in pond Tau caused by the severe overcropping of this population. The average for control ponds was also lower than should have occurred because of abnormally low production in pond Delta in 1959, due to the paucity of numbers available to add flesh, and in pond Sigma in 1961, because no gain was possible due to original, gross overstocking. On the other hand, the average gain in fish flesh probably was higher in the add-stock ponds than should have occurred because pond Beta was more fertile than either companion pond, and made the large gain of 133.8 pounds of fish flesh over the 1958-1959 period in spite of an addition of 41.7 pounds of stock. As mentioned previously, this higher production in Beta was probably related primarily to the manner in which this pond was supplied with water and the enrichment of its food supply by the entrance of drift organisms from the feeding stream.

Growth and Condition

Two types of growth data are presented. For comparison with smallmouth growths made in other waters, our data in Table 7 represent averages of all fish of the respective age classes recovered in the October censuses. Most ages were known by length ranges (particularly for the youngest age class present), or by the presence or absence of a particular fin clip. Fish of uncertain age were omitted from Table 7. Addi-

Table 7. — Growth of smallmouth bass in ponds used for carrying capacity experiments on the McGraw Foundation grounds, along with similar data on smallmouths in several other waters.[a]

Group	*Pond*	*Year*	*Treatment*	*Average Length in Inches (at Ends of Numbered Growing Seasons) with Number of Fish Used to Establish the Average in Parentheses*			
				1st	2nd	3rd	4th
......	Alpha	1957	None	4.0(1,157)			
Unit 1	Beta	1959	Add-stock	4.3(188)	7.1 (1,009)	10.4 (20)	
	Gamma	1959	Cropped	4.7(1)	7.6(357)		
	Delta	1959	Control	.	9.2(2)	11.3 (26)	
Unit 1	Beta	1960	Control	3.4(899)		9.3(406)	11.4(4)
	Gamma	1960	Add-stock	3.8(23)		9.0(506)	11.6(14)
	Delta	1960	Cropped	4.7(67)		9.4(126)	11.9(2)
Unit 4	Sigma	1961	Control	3.4(70)			9.4(233)
	Sigma	1963	Control	3.2(729)	70(24)	9.8(47)	
	Tau	1963	Cropped	4.1(77)	9.2(11)		
	Upsilon	1963	Add-stock	2.7(1,534)	6.8(59)	9.0(44)	10.0(6)
Other Waters		*Author*					
Jordan Creek, Ill.[b]		Durham (1955)		3.3	6.3	9.5	11.4
Malcomson's Pond, Ill.[c]		Bennett & Childers (1957)		5.3	9.3	11.1	12.2
Siloam Springs Lake, Ill.[b]		Rock (1966)		4.2	7.0	10.5	13.2
Michigan		Beckman (1949)		5.9	9.0	11.2	13.3
Norris Reservoir[b]		Stroud (1948)		3.1	8.9	13.3	15.8

All data from our ponds are for fish of known age.
[b] Lengths back calculated from scales.
[c] Average lengths of fish separated on the basis of ages assigned from scale analysis.

tional growth data are presented in Fig. 2 and 3 where growth curves are based on samples collected during the months indicated.

Linear growth in our single-species populations was somewhat intermediate to growth made in other waters through the first 2 years of life, but in some cases was quite poor thereafter (Table 7). Extremely poor growth by the third, fourth, and fifth year fish was due to overcrowding (most notably in Unit 4), or to the scarcity of large food items such as small fish or crayfish.

Fig. 2 presents growth and condition curves for the dominant 1958 brood through the 1960 season in ponds Beta, Gamma, and Delta. Near cessation of growth in ponds Gamma and Delta from mid-May to mid-June was paralleled by a deflection in condition curves. Condition of the cropped population made a sharp improvement in June and remained high for the remainder of the season, and this was paralleled by rapid and continuous growth through September. Data from the control pond illustrates an inconsistency that was rather common throughout this study. Here a high rate of growth was paralleled by a declining rate of condition. During this same period both growth and condition in the add-stock population remained low.

The growth and condition curves showed only moderate conformity to the differing densities of stock. When stocked in October, 1959, each pond had received approximately 455 bass of this dominant age group (Age II in 1960). Cropping and transfers of stock during 1960 included 321 bass of Age II weighing 75.5 pounds, cropped from pond Delta, of which 175 weighing 41.4 pounds were marked and released in pond Gamma. Comparative densities at the time of the October, 1960 censuses were 406 in the control pond, 126 in the cropped pond, and 506 in the add-stock population (Table 6). With a

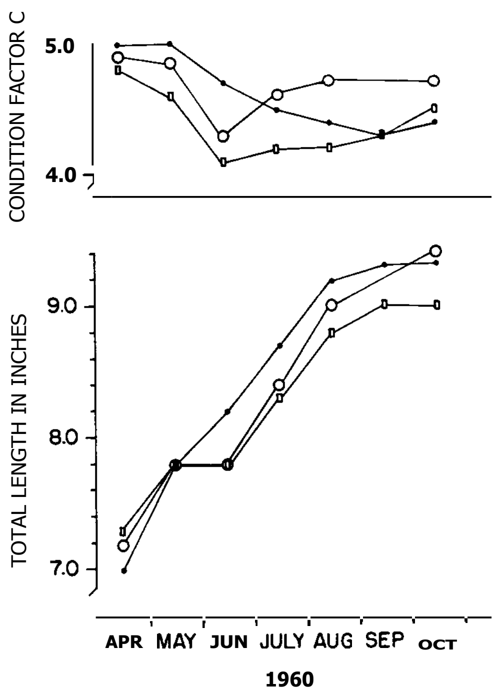

Fig. 2.—Growth and condition (C) of smallmouth bass of the dominant 1958 year-class in the control pond Beta (dots), add-stock pond Gamma (rectangles), and cropped pond Delta (circles) during the 1960 growing season.

final ratio of densities as great as 4:1 (506 to 126) between the add-stock and cropped populations, one would have expected a greater influence on growth and condition than seems to have occurred. Again, we suspect that the influence of the treatment was masked by differences in the ponds' productivities, with pond Delta again indicated to have a low productivity.

As mentioned earlier, growth by larger fish was extremely poor in the infertile, generally overcrowded ponds in Unit 4. This is emphasized in Table 8 which shows total length and weight increments of the dominant 1958 year-class over the period 1961-1963.

Growth and condition curves of the 1958 year-class through 1960 were plotted in Fig. 2, and following the transfer of the population to the new unit of ponds we may again trace this dominant age group through its 3-year

Table 8.— Length and weight increments over three seasons, 1961-1963, and final average coefficients of condition for the dominant 1958 year-class of smallmouth bass in ponds Sigma, Tau, and Upsilon.

Pond	*Treatment*	*Average Length Increment, Inches*	*Average Weight Increment, Pounds*	*Final Average Condition (C)*
Sigma	Control	2.68	0.80	4.9
Tau	Cropped	4.17	1.61	6.8
Upsilon	Add-stock	1.51	0.61	4.8

history in ponds Sigma, Tau, and Upsilon (Fig. 3). Again growth and condition were computed from the same samples. While mid-season samples were in some cases quite small, and a source of some error, those collected at the beginning and end of each season were large and believed to be highly representative. Because of initial overstocking of all three ponds with approximately 130 pounds per acre, growth was negligible, conditions remained poor, and the influence of the experimental treatment was only barely discernible in 1961. All three populations were heavily and equally thinned in early 1962, and the effects of subsequent cropping and transfer of stocks became increasingly apparent throughout 1962 and 1963.

The degree of conformity between the growth and condition curves indicates that for the 1958 year-class in Unit 4 ponds there was a rather close relationship between rate of growth and body condition, with fastest growth associated with best condition, and vice versa. The most dramatic response to population manipulation occurr ed among the dominant 1958 year-class in pond Upsilon. Average condition for these fish declined from 4.5 in April, 1961, to 3.6 in the following September, due to increased density of stock.

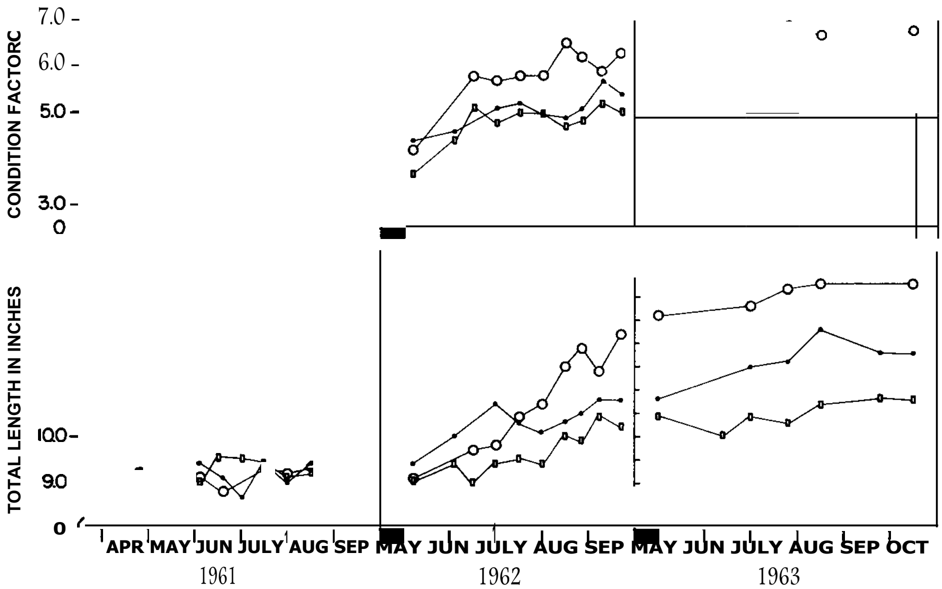

Fig. 3.—Growth and condition (C) of smallmouth bass of the dominant 1958 year-class through three growing seasons (1961-1963) in the control pond Sigma (dots), cropped pond Tau (circles), and add-stock pond Upsilon (rectangles).

A combination of overwinter mortality, and additional thinning by us in May, 1962, caused condition of this population to improve from 3.7 in May, 1962, to 5 by the following June.

Mortalities

Mortality data for the populations of smallmouth in ponds Beta, Gamma, and Delta were for three categories of fishes: 1) those of the original stock, 2) those transferred from the cropped to the add-stock pond, and 3) those fish captured, measured, weighed, marked, and released when and where caught. Mortalities over the 1958-1959 period for bass of the three year-classes transferred from Gamma to Beta in 1959 ranged from 50 percent for the 1956 year class, to 100 percent for the 1958 year class, averaging about 70 percent; whereas mortalities over a single season for those marked and transferred from Gamma to Beta in 1959 ranged from 38.1 to 75 percent, averaging about 51 percent. Among 294 fish of the 1958 brood transferred from Gamma to Beta during 1959, the mortality by the end of that season was 38.1 percent, while for 144 fish of the same age caught in Beta, marked, and returned to Beta, the comparable mortality was 34 percent. For older fish of the 1957 brood, comparable figures were 40 and 36.7 percent, in almost the same ratio. In this instance the transferred fish survived quite well in the new population, and the act of transfer was in itself no cause for a notable increase in mortality. In 1960, however, we found the mortality among 175 fish transferred to pond Gamma was 25.1 percent, as compared to 17 percent among the 168 fish which were caught in Gamma, marked, and returned to the same population in that pond. As in the 1959 data, mortalities of the younger and older fish in 1960 generally were higher than those of intermediate ages. Finally, average rates of mortality were greater in the add-stock pond, intermediate in the control pond, and lowest in the cropped pond.

Mortalities as related to densities of stock are best known for the 1958 year-class of bass during their third year of life in the 1960 season. When restocked in October, 1959, each pond received from 449 to 455 fish of this age class. Recoveries, numbers unaccounted for in the census, and percents of mortalities by October, 1960, for various categories of these bass are shown in Table 9. Following the removal of 321 individuals from the cropped population, only 8 fish were unaccounted for in the October census, indicating a mortality of 6 percent among that portion of the original population that was not cropped. Comparable figures were 7.9 percent in the control population, and 13.2 percent among the original stock in the add-stock population. Among those fish

Table 9.— Numbers of the dominant 1958 year-class of smallmouth bass originally stocked in ponds Beta, Gamma, and Delta in 1959, numbers cropped and added in 1960, and numbers of the different categories recovered in the draining censuses, with numbers of fish unaccounted for, and percents of mortality.

Pond	*Number Originally Stocked, Oct., 1959*	*Number Cropped from Pond in 1960*	*Number Transferred to Pond in 1960*	*Number of Original Stock Recovered in Census, Oct., 1960*	*Number of Transferred Fish Recovered in Census, Oct., 1960*	*Number Unaccounted for* Original Stock	*Number Unaccounted for* Transferred Fish	*Percent Mortality* Original Stock	*Percent Mortality* Transferred Fish
Beta	449	8	0	406		35		7.9	. .
Gamma	452	20	175	375	131	57	44	13.2	25.1
Delta	455	321	0	126		8		6.0	

transferred to the add-stock population, mortalities were 25.1 percent, approximately twice as great as among survivors of original stock in this same pond. It should be pointed out here that neither the marks used, nor the handling of fish involved in the transfer of stock, were in themselves causes for increased mortalities. The transfers were accomplished in conjunction with our regular sampling operations, and frequently more fish were caught, marked, and returned to the control pond than were marked and transferred from the cropped to the add-stock population. The transferred fish were simply carried a few feet farther, in water, before their release. Thus, where mortalities were greater among fish that were marked and transferred than among resident individuals that were marked and returned to the same pond, those mortalities must be attributed to something other than the purely physical effects of the marking and transfer. In this instance it was probably an inability to compete on even terms with those fish already resident in the overcrowded population.

The inability of transferred fish to compete effectively with those resident in an overcrowded population also was evident in a study made of rates of seasonal mortalities of smallmouth bass in 1960. Rates of mortalities were based on recoveries in the draining censuses of fish given distinctive fin clips for each month of the 1960 growing season (Table 10). Marked fish were principally of the 1958 brood. Errors due to incomplete recoveries are believed to have been small, and such errors would operate in favor of lower mortalities. Mortalities due to marking were erratic, and high for some marking periods, as is clear from a study of Table 10. For example, the returns of fish marked in April implied that percentages of from 26.7 (in Beta) to 30 (in Gamma) of all fish of the group in question that were living at the time of marking had died by October. Actually, total rates

Month	*Marked and Returned Directly to the Control Population, Beta*			*Marked and Returned Directly to the Add-stock Population, Gamma*			*Marked and Transferred to the Add-stock Population, Gamma*		
	Number Released	Number in Census	Percent Mortality	Number Released	Number in Census	Percent Mortality	Number Released	Number in Census	Percent Mortality
April	30	22	26.7	2[illegible]	2[illegible]	2[illegible].6	[illegible]	2[illegible]	30.[illegible]
May	30	28	6.7	[illegible]	2[illegible]	2[illegible].0	3[illegible]	22	[illegible]
June	30	29	3.3	30	2[illegible]	[illegible]3	[illegible]	30	[illegible]5
July	[illegible]	31	0	[illegible]	23	25	5[illegible]	48	[illegible]8
Aug.	30	30	0.0	29	2[illegible]	[illegible]	22	18	2[illegible]
Sept.	30	24	20.0	30	2[illegible]	20.0	. .	. .	
Total	*181*	*164*		*179*	*145*		*[illegible]38*		
Average			*9.4*			*18.9*			*7.9*

of mortality for the year-class in question (1958) over the entire 12-month period were only 9.6 percent in Beta, and 17 percent in Gamma. Marks used were clearly distinguishable at the time of the draining censuses, and there seemed to be small margin for error in their interpretation. These data indicated that such studies must be conducted with great care, and should involve large samples. In the present instance the "unnatural" death of as few as four or five fish projected serious errors.

Mortalities were not proportional to length of time marked, due possibly to greater deaths among marked fish in certain months than others. However, if such errors (deaths) may be assumed to have been reasonably proportional for each population, a significant and logical pattern appears when rates of mortality for fish marked each month are averaged for each category over the season (see averages in Table 10). Average rate of mortality was lowest in Beta, the control pond, intermediate for those marked and returned in the "add-stock" pond, and highest for those transferred from Delta to the add-stock pond.

Our principal data on mortalities in the ponds in Unit 4 are from fish of the dominant 1958 brood in the control and add-stock populations. As observed for our earlier smallmouth populations (Table 10), mortalities were lowest in the control pond and highest in the add-stock pond, and seemingly related to density of stock. For example, in the control pond Sigma, with an original stock of 343 Age III fish on October, 1960, the year-class had an unaccounted for loss of only 5 individuals by October, 1961, and an additional loss of only 29 individuals by October, 1963. In this instance, 105 fish had been removed in 1961 and five were unaccounted for, leaving 233 survivors in the 1961 fall census. Assuming removals and deaths had been nonselective as to size, over the 12-month period the 233 survivors had made an average length increment of only 0.24 inches, and had shown an average loss in weight of 0.012 pounds and a loss in condition of from 4.5 to 4. Living conditions were therefore quite poor, but not so poor as to have induced mortality.

Such low rates of mortality in pond Sigma in 1961 were verified by the following experiment. For each month from April through September, from 28 to 30 individuals of the 1958 brood were caught and released with a mark distinctive for that month. When censused following pond draining in October, 1961, recoveries were made of 28 of the 30 fish marked in April, 28 of the 30 marked in May, and of 100 percent of fish marked in each of the four remaining months. Of the two fish missing from each of the April and May samples, one for each month, or two of the total of four, were observed, accidental deaths. There were therefore only two unaccounted for individuals among the 176 fish marked, and mortalities for this group were less than 2 percent.

In the add-stock pond Upsilon, with its steadily increasing density of stock, mortalities became quite high. Assuming no mortalities, we would have entered the winter of 1961-1962 with 325 individuals of the 1958 year-class. Our 1962 spring estimate indicated a population of only 180, and a mortality to that date of 184 individuals. Average condition had declined through 1961 from 4.5 in April to 3.6 in September, so large overwinter mortality was not unexpected. Our next inventory by Petersen estimate in April, 1963, indicated that an additional 78 fish of this group were missing and unaccounted for. While both estimates could have been in error, the sum of estimated mortalities from both was verified by the 1963 final census. The two estimates had indicated 81 survivors by April-May, 1963, and a transfer from Tau raised the total to 82. Thus, a recovery of 83 individuals in the final census indicated that the estimates had been exceptionally good.

While mortalities were high in the add-stock pond, this population was subjected to considerable stress by virtue of the greater population density and a limited food supply. There may have been an additional stress owing purely to the transfer and adjustment to a new environment. Quite possibly the impact of the transferred fish may have created stress for the resident fish as well. On the other hand, mortalities in the control pond were extremely light. Results from the control pond indicated the adult smallmouth bass to be unusually hardy, even under the relatively poor conditions afforded by pond Sigma, and even when subjected to frequent sampling by seine, shocker, or hook-and-line, and to multiple marking by fin clip. In this respect, we experienced the smallmouth bass to be a much tougher and superior experimental fish than the largemouth.

Spawning Success

In 1960 an effort was made to study success of spawning and survival of young in relation to the differing densities of populations in the three ponds in Unit 1. Table 11 presents 1) estimates made of the number of potential spawners in each pond, 2) counts made of total numbers of nests and numbers of successful nests, 3) percentages of successful nests, 4) ratios of numbers of total nests and of successful nests to numbers of spawning adults, and 5) estimated numbers of fry produced and their rate of mortality by the time of the October draining censuses.

The potential number of spawning adults was taken as the number of fish of Age II (1958 brood) or older stocked in each pond the previous November, plus or minus those added to or removed from each pond prior to the advent of

nd	Estimated Number of Potential Spawners	Count of Nests	Count of Successful Nests	Percent of Successful Nests	Ratio of Nests to Potential Spawners	Ratio of Successful Nests to Potential Spawners	Estimated Number of Young Produced	[illegible]	[illegible]
E ma	63	[illegible]	40	32.8	[illegible]	1:11.6	21,930	899	95.9
[illegible]	526	[illegible]	6	3.8	[illegible]	1:87.7	3,290	cv	99 3
[illegible]	344	[illegible]	20	1	[illegible]	1:23.2	10,965	cc	99.4

spawning in late May, 1960. The assumption of no overwinter mortality is undoubtedly erroneous; however, deaths through the winter were known not to have been large. Counts of nests, and of successful hatches of fry were made by dividing each pond into small sections and making daily counts of all sections throughout the spawning period. Estimated production of fry was computed from an average number of fry per nest based on actual counts of fry taken from the nests. The black but still largely immobile sac-fry were siphoned out of the nests and spread over the bottom of a large white enameled tray having a grid marked in the bottom. Pictures were taken and later enlarged so that counts could be made in the laboratory. The fry were sucked off the nest by means of a ¾-inch tube attached to the bottom of a 5-gallon bucket. Slow submersion of the bucket from above created a gentle suction by which the fry could be moved from the nest into the bucket. When fry were returned to the nests the guarding males resumed their patrols, and all such spawns were observed to develop in a normal fashion. Successful counts were made of broods removed from eight nests, six from pond Beta, two from pond Delta. The overall range in numbers of fry per brood was from 190 to 787. The six broods from pond Beta averaged 542 fry per brood; the two from pond Delta averaged 568. The average of the eight nests was 548.25, and this figure was used as the basis for computing the total productions of fry listed in Table 11.

It may be significant that pond Gamma with both the largest number of potential spawners and the largest number of nests, had by far the lowest rate of spawning success (Table 11). This would appear to be a density-related factor whereby overcrowding brought about a reduced reproduction. Ricker (1954) presented reproduction curves exhibiting this phenomenon in a variety of animal populations, and Rose (1959) presented evidence of reduced reproduction as a result of overcrowding guppies. However, the relation of spawning success to density of the spawning population was not consistent in data from ponds Beta and Delta. Pond Beta had an intermediate number of spawners and the smallest number of nests, but had the greatest number of successful nests, whereas Delta with the smallest number of potential spawners had an intermediate number of nests and an intermediate number of successful nests. Though density related, rate of spawning success in the present data appeared related to additional factors as well. One such factor may have been the relative locations of the ponds, and the manner in which they received water. As mentioned earlier, the supply stream first entered Beta, from which it overflowed to fill Gamma, from which it again overflowed to fill Delta. It may be significant that pond Beta, the first pond in the series, is believed to have had the most successful rate of reproduction and/or survival in all 3 years, 1958-1960. Reproduction in Delta, the last in the series, was extremely limited in 1958, and believed to be nonexistent in 1959, and in both years was less than that achieved in pond Gamma, the middle pond in the series. Thus, in both 1958 and 1959 the rate of spawning success decreased in the exact order in which the ponds were located in the flow series, from Beta to Gamma to Delta. The order was partially reversed in 1960, with a greater production of fry in Delta than in Gamma. In this instance, however, the much greater density of breeding stock in Gamma than in Delta (Table 11) may have had an overriding influence.

The significance of the position of the ponds in the flow series could be related to an accumulation of an inhibitory product. Rose (op.cit.) demonstrated in aquaria that some fishes release waterborne products that limit growth and survival of their own or closely related species, though not limiting that of certain other distantly related forms. Rose's studies also suggested that self-inhibiting products produced by one species may be metabolized away by other species in the community. Thus, a species maintained alone might be more subject to such an inhibitory influence than when in a mixed population. Although the ponds contained no fish when filled, they received additions of "make-up" water throughout the course of the experiments. Thus, an accumulation of waterborne products would have been progressively greater in Gamma and Delta, and if such an inhibitory influence was operative it would have decreased production and survival of young in the order in which it occurred.

Total counts of nests and of successful nests were not possible in the Unit 4 ponds because of higher water turbidities. However, in the 1961 spawning season a reliable count was believed made of broods of fry just risen from the nests. Each such brood was marked with a float at the point first seen, which in most cases was very near to a nest. The totals of floats in each pond is believed to have closely approximated the totals of broods. Table 12 presents the number of broods seen, the time intervals over which they were seen, the number of potential breeders believed to have been present, and computed ratios of numbers of broods to number of potential spawners. As earlier observed in Unit 1 (Table 11), the fewest number of hatches was associated with the greatest density of breeding stock. Pond Upsilon with an estimated 348 breeders (1958 year-class and older), produced only 7 hatches, for a ratio of about 1:50. Comparable ratios were 1:14 in Sigma, with an estimated 292 breeders, and about 1:17 in pond Tau with approximately 237 potential spawners.

Brood counts were also made in 1962 and 1963, but poorer visibilities, due principally to frequent strong winds, probably made these counts less complete than those of 1961, and they were not included in the table. In 1962 our notes listed only five hatches observed in the add-stock pond, as compared to nine in the control, Sigma, and either "eight or nine" in the cropped pond Tau. No hatches were observed in pond Tau in 1963, due, possibly, to the absence of a breeding pair because of overcropping, or to predation of eggs or larvae by an abnormally large population of crayfish.

Foods of Smallmouth Bass

Information on foods eaten in ponds Beta, Gamma, and Delta is based on examination of 20 stomachs each from ponds Beta and Gamma and 18 from pond Delta, all of Age II, collected in June and August, 1960 (Table 13). Based on frequency of occurrence in stomachs, scuds and mayfly nymphs ranked first and second, respectively, in both June and August. Cladocerans and crawling water beetle larvae were also prominent in June, but much less so in August. Nymphs of damselflies were

Table 12.— Estimated numbers of potential smallmouth bass spawners, numbers of broods seen, time intervals over which they were seen, and ratios of numbers of broods to numbers of potential spawners in ponds Sigma, Tau, and Upsilon, 1961.

Pond	*Number of Potential Spawners*	*Number of Broods*	*When Broods Were Seen*	*Ratio of Broods to Potential Spawners*
Sigma	292	21	June 1-16	1:14
Tau	237	14	June 6-9	1:17
Upsilon	348	7	June 6-16	1:50

Table 13. — Food organisms found in stomachs of the dominant 1958 year-class of smallmouth bass collected from ponds Beta (control), Gamma (add-stock), and Delta (cropped) in June and August, 1960. Length ranges of the fish, in inches, were 7.8-9.8 in Beta, 7.4-9.3 in Gamma, and 7.2-9.7 in Delta.

Food Organisms		Total Number of Items, All Stomachs			Percent of Occurrence, All Stomachs		
		Beta [a]	Gamma [b]	Delta	Beta [a]	Gamma [b]	Delta [c]
AQUATIC INSECTS							
Plecoptera	adults	0	1	0	0.0	5.0	0.0
Ephemeroptera	nymphs	60	210	691	50.0	70.0	69.0
Odonata							
Zygoptera	nymphs	40	6	101	60.0	25.0	25.0
	adults	22	1	2	25.0	5.0	11.5
Anisoptera	nymphs	5	0	0	20.0	0.0	0.0
Hemiptera							
Corixidae	adults	1	2	1	5.0	10.0	5.0
Coleoptera							
Haliplidae	larvae	0	395	440	0.0	40.0	25.0
	adults	3	0	2	10.0	0.0	12.5
Dytiscidae	larvae	3	0	16	15.0	0.0	30.0
	adults	0	1	5	0.0	5.0	19.0
Hydrophilidae	adults	0	0	1	0.0	0.0	6.5
Trichoptera	larvae	8	1	1	25.0	5.0	5.0
Diptera							
Culicidae	larvae	0	2	1	0.0	10.0	6.5
Tendipedidae	larvae	1	104	36	5.0	35.0	34.0
	pupae	0	13	67	0.0	25.0	37.5
Ceratopogonidae	larvae	1	5	0	5.0	15.0	0.0
	pupae	0	1	0	0.0	5.0	0.0
OTHER AQUATIC ORGANISMS							
Annelida							
Hirudinea		0	1	0	0.0	5.0	0.0
Cladocera		452	242	1,099	15.0	50.0	20.0
Ostracoda		3	12	0	10.0	30.0	0.0
Amphipoda		716	598	962	55.0	85.0	75.0
Decapoda		2	0	1	10.0	0.0	6.5
Hydracarina		2	62	65	10.0	25.0	52.5
Pisces		1	0	1	5.0	0.0	5.0

[a] Twenty stomachs examined, 18 of which contained food.
[b] Twenty stomachs examined, 19 of which contained food.
[c] Eighteen stomachs examined, all of which contained food.

moderately prominent in both periods. The prevalence of cladocerans in the stomachs of these smallmouth bass in their third year of life emphasized their dependence upon invertebrate foods. Fish remains were found in one stomach in June, crayfish in three stomachs in August. Smaller fish of Ages O and I undoubtedly utilized the same invertebrate foods. Larger fish of Age III and older appeared to prey to a considerable degree on fishes in Age I, and made fair growth so long as they were present, and grew poorly when they were absent. For example, in 1959 Age I fish were available in all ponds and fish older than Age II increased in length from an average of 12.5 inches in May, to 14 inches in October. In 1960, when Age I fish were not available, seasonal growth of the older and larger fish was negligible. Absence of a prey fish of a suitable size caused the elimination of many of the larger predators in an indirect way. In the last weeks of the 1960 season several of the larger fish were found dead with an Age II fish lodged in the gullet. Their hunger was obviously such that they were forced to prey on fish larger than their gullets could accommodate.

In 1960 an attempt was made to measure the standing crops of invertebrates in ponds Beta, Gamma, and Delta by collecting them in a large filter box of saran screen as described by Buck & Whitacre (1960). As the ponds were drained the water was screened through the box and the organisms collected and weighed. The only separation possible was that between "plankton" and scuds. The "plankton" consisted in the main of cladocerans, a moderate number of phantom larvae, and occasional copepods, water mites, small beetles, various nonburrowing mayfly nymphs, and scuds. This group was collected at a fairly continuous rate throughout the draining, except that the scuds drained out at the end of the operation, or concentrated in and around the sump at the end of the drain tube inside the pond. The technique worked reasonably well except for the fact that an unknown percentage of such forms as scuds, and the immature stages of caddis flies and mayflies, remained in the abundant dewatered vegetation in Beta and Gamma, while a greater percentage flushed out of the much less densely vegetated Delta. Recoveries of scuds and other larger forms could not be considered complete or comparable for all ponds, but that of "plankton" may have been reasonably so.

Weights obtained were as follows:

Beta	"Plankton"	37 lbs.
	Scuds	20 lbs.
Gamma	"Plankton"	142 lbs.
	Scuds	20 lbs.
Delta	"Plankton"	670 lbs.
	Scuds	131 lbs.

Differences in standing crops suggest a greater productivity for pond Delta, a fact not substantiated by the fish data. The vegetation factor, as mentioned above, would have accounted for a part of the differential, and may have accounted for it all. It should also be pointed out that standing crops of smallmouth were at least three times as great in both ponds Beta and Gamma as in Delta. Heavier rates of cropping of the "plankton" and scuds by the larger populations of fish could have caused the difference in standing crops of the invertebrates. With heavier rates of cropping, rates of production of invertebrates actually may have been greatest in the ponds having the smallest standing crops of invertebrates.

Information on foods eaten by smallmouth in Unit 4 ponds is based on a collection of 119 stomachs, 40 each from ponds Tau and Upsilon and 39 from pond Sigma. About 10 specimens were collected from each pond in each of the four months June through September. All samples were collected by hook-and-line, and the monthly samples from each of the three ponds were collected on approximately the same dates — June 16-20, July 24-25, August 22, and September 19. All specimens were adults of the dominant 1958 brood and ranged in length from 7.7 to 10.2 inches total length in June and from 8 to 10.8 inches in September.

A total of 105, or approximately 88 percent, of the 119 stomachs contained food; 14 were empty. Determinations were made of the number of items of each identifiable taxonomic group, their total volume in each stomach, their frequency of occurrence, and the average volume of food in stomachs containing food. A total of 23 items were identified in the stomachs (Table 14), but many were occasional or rare, and only six items were encountered with sufficient frequency, or in sufficient volume, as to be considered prominent. On the basis of frequency of occurrence the six most common items were 1) midge larvae and pupae in 46 stomachs, 2) burrowing mayfly nymphs in 42, 3) nymphs of smaller, nonburrowing mayflies in 39, 4) caddis fly cases in 24, 5) damselfly nymphs in 18, and 6) crayfish in 14. By

Table 14. —Food organisms found in stomachs of the dominant 1958 year-class of smallmouth bass collected from ponds Sigma (control), Tau (cropped), and Upsilon (add-stock) in June, July, August, and September, 1961. Length ranges of the fish, in inches, were 8.5-10.9 in Sigma, 8.3-10.8 in Tau, and 7.7-10.4 in Upsilon.

Food Organisms		*Total Number of Items, All Stomachs*			*Percent of Occurrence All Stomachs*		
		Sigma	Tau[b]	Upsil	Sigma	Tau[b]	Upsil
AQUATIC INSECTS							
Ephemeroptera							
Nonburrowers	nymphs	14	426	33	35.5	47.5	35.0
Burrowers	nymphs[c]	61	59	55	54.0	30.0	27.5
	adults[d]	0	6	0	0.0	5.0	0.0
Odonata							
Zygoptera	nymphs	9	157	0	20.8	37.5	0.0
	adults	42	0	0	2.5	0.0	0.0
Hemiptera							
Notonectidae	adults	0	0	2	0.0	0.0	5.0
Corixidae	adults	5	11	4	12.8	20.0	7.5
Coleoptera							
Haliplidae	larvae	0	1	0	0.0	2.5	0.0
	adults	1	0	0	2.8	0.0	0.0
Dytiscidae	larvae	1	1	0	2.5	2.5	0.0
Trichoptera	larvae	146	40	116	27.5	15.0	25.0
Diptera							
Culicidae	larvae	0	0	1	0.0	0.0	2.5
Tendipedidae	larvae	432	5	71	47.5	7.5	30.0
	pupae	438	65	28	20.0	15.0	25.0
	adults	4	4	1	7.5	5.0	2.5
Ceratopogonidae	larvae	4	0	2	10.3	0.0	5.0
OTHER AQUATIC ORGANISMS							
Cladocera		903	2,246	3	7.5	25.0	2.5
Ostracoda		360	783	0	2.5	10.0	0.0
Decapoda		6	9	5	13.3	10.0	12.5
Hydracarina		14	1	0	17.5	2.5	0.0
Pisces		0	1	1	0.0	2.5	2.5
TERRESTRIAL INSECTS							
Coleoptera	adults	0	2	15	0.0	2.5	5.0
Diptera	adults	1	0	2	2.5	0.0	2.5

Thirty-nine stomachs examined, 37 of which contained food.
[b] Forty stomachs examined, 39 of which contained food.
[c] Forty stomachs examined, 29 of which contained food.
[d] Probably all *Hexagenia limbata* (Serville).

order of volume, the six ranked 1) crayfish, 2) burrowing mayfly nymphs, 3) nonburrowing mayfly nymphs, 4) caddis fly cases, 5) damselfly nymphs, and 6) midge larvae. On the basis of both categories, nymphs of large burrowing mayflies were the most frequent and important food item, followed by the nymphs of the smaller mayflies. Nymphs of both burrowing and nonburrowing mayflies were a prominent food item in all four months. Tendiped larvae were prominent in July only and of quite moderate occurrence in other months. Damselfly nymphs were a common item in August and quite scarce in other months. The cases of caddis flies were quite common in stomachs collected in both July and August, but were absent in those taken in June and September. Cladocerans occurred in nine of the ten stomachs taken in June, in only two in

July, and in one each in August and September. While young smallmouth bass were preyed upon when available, and their numbers frequently decimated, their remains were found in only two stomachs (one each in July and August), and on this basis they must be considered an item of minor importance. Scuds were not present in these ponds in 1961, but were undoubtedly a major food item following their establishment in 1963.

While a large proportion (88 percent) of the stomachs contained food, average volumes were small. In the control pond Sigma, 37 of 39 stomachs contained food, with an average volume for the 37 of only 0.49 milliliters. In the cropped pond Tau, 39 of 40 stomachs contained food, with an average volume of 0.39 milliliters. In the add-stock pond Upsilon, only 29 of 40 contained food, with an average volume of 0.92 milliliters. However, the picture of comparative volumes was distorted by two occurrences of comparatively large volumes of crayfish. If we remove crayfish volumes from the calculations, we then have averages of 0.25 in the control pond, 0.34 in the cropped pond, and only 0.12 in the overstocked pond. Though possibly fortuitous, these averages conform with the expected, where volume of food in stomachs was greatest in the cropped pond having the fewest fish, and smallest in the add-stock pond having a more dense population.

Review and Discussion of Smallmouth Bass Data

A survey of the literature revealed records of only five standing crops of smallmouth bass when maintained as a single species (Table 15). Maximum previous poundages were recorded by Regier (1962) from mark and recapture estimates made in a 0.09-acre pond in New York. These were at rates of 143, 146, and 139 pounds per acre over 3 consecutive years. The author observed that successful reproduction occurred in each of the 3 years, in spite of what he thought were high standing crops. Our three largest standing crops ranged from 169 to 180 pounds per acre (Unit 1 ponds), and our populations also reproduced successfully in all 3 years of census. While numbers of young-of-the-year surviving until fall in our three populations were in some cases small (188, 889, and 23), it should also be observed that none of our three populations was cropped to any substantial degree (maximum in any year: 8.4 pounds). Cropping of adult fish would be expected to enhance both reproductive success and survival of young, particularly when the populations were dominated by older and larger fish, as was true in both Regier's populations and ours.

Bennett and Childers (1957) recorded the next highest standing crop of 100.3 pounds (not including Age O) in a 1.4-acre gravel pit pond of "below medium" fertility in central Illinois. In the four years preceding the final census of this pond in June, 1955, it had produced successive hook-and-line yields ranging from 78 to 123 pounds per acre. The catches of 119 and 123 pounds per acre, made in 1952 and 1953 respectively, both exceeded the standing crop measured in 1955, and the authors believed this indicated that there was an annual replacement of fish flesh in this pond which exceeded the standing crop that the pond could support.

Our smallmouth populations produced no tangible evidence of a replacement potential of this species comparable to that provided by Bennett & Childers. We believe that this failure was due in part to the relative immaturity of our populations, to severe overcropping in at least one instance, and partly to chance. Our first cropped population (in Gamma, 1958-1959) had been initiated in May, 1958, with only 10 adults and 40 fingerlings, and in 1959 was so heavily cropped that too few fish remained to replace the flesh of those

Table 15.— Known published records of standing crops per acre of single species fish populations in small ponds.

Location	Method of Census[a]	Standing Crop, Pounds Per Acre: Bluegills	Largemouth Bass	Smallmouth Bass	Black Bullheads	Author
Kentucky	M & Ro	315.0				Turner, William R. (1959)
		328.0				
		664.0				”
Oregon	M & R	89.7				Isaac & Bond (1963)
		231.6				'
			62.0			
Texas	D		94.1			Brown, W. H. (1951)
	'		76.2[b]			
			50.3[b]			
Alabama			32.9			Swingle, H. S. (1952)
Illinois			48.2			Bennett, George W. (1954)
	Ro			100.3		Bennett & Childers (1957)
New York	M & R			143.0		Regier, Henry A. (1962)
				146.0		
				139.0		
				46.0		
Iowa	Ro				288.0	Carlander & Moorman (1956)
'	”				128.0	
	”				653.0	
	M & R				134.3	

[a] Symbols: M & Ro = marked and rotenone, M & R = marked and recaptured, D = drained, and Ro = rotenone
[b] Pond was fertilized.
[c] Same pond.

removed. We attempted to correct this situation in our next populations with initial stocks in Beta, Gamma, and Delta having weights ranging from 90 to 97 pounds. By unfortunate chance, however, the pond cropped during this experiment (Delta) simply did not have the productive potential to replace the weight of the fish that were cropped. Our third and last population to be cropped was that in pond Tau. A combination of overcropping of larger fish, and limited recruitment of younger fish (limited survival of young in 1961 and 1962, and no survival in 1963) left too few individuals to make an efficient conversion of available food. We therefore believe that the replacement potential of smallmouth bass in our ponds was not adequately tested.

Our oldest populations had completed three growing seasons when censused. Regier's data cited was from a population in its 6th, 7th, and 8th years, and the population studied by Bennett and Childers was in its 8th year when censused in 1955. All of these populations contained young-of-the-year when censused, and the heavily cropped population of Bennett and Childers had a normal composition, consisting of an estimated 5,000-6,000 young-of-the-year, 243 ranging in lengths of from 4 to 8.5 inches, and 49 fish longer than 10 inches. It should also be mentioned that none of these ponds received fertilization, which would have increased production. Str ong evidence therefore exists that the smallmouth bass is capable of high, sustained yields when maintained as a single species in warmwater ponds.

LARGEMOUTH BASS

Bass used in these studies were obtained mostly from private ponds, partly from a state hatchery, and partly from a public reservoir, all located within the northern half of the state.

Data presented here were obtained over two periods of approximately one and one-half growing seasons each (1958-1960) in Unit 2 ponds, and from a 3-year period (1961-1963) in Unit 1 ponds. Ponds Zeta, Theta, and Iota (Unit 2) were completed and first filled with water in the spring of 1958. Each pond was stocked with 10 adults 10-13 inches long in May, and with a total of 61 subadults over the period June through August, for a total in each pond of about 16 pounds. In this series, pond Zeta was the control, pond Theta was cropped, and pond Iota received additions of stock.

In July, 1959, largemouth bass in all Unit 2 ponds were found to be severely infested by a gill parasite, *Dactylogyrus* sp. Since it would be extremely difficult to measure or evaluate the extent of deaths due to the parasites, it was decided to census the ponds before mortalities became a serious factor. On July 27, all three ponds were treated with rotenone. Based on returns of marked fish, the recoveries were judged to be comparable and reasonably complete in all ponds.

Following drainage and spraying of residual pools with a solution of HTH (available chlorine 15 percent), the ponds were refilled and restocked by August 25. Each pond was stocked with 514 young-of-the-year largemouths, plus an assortment of yearlings and adults to a total of approximately 30 pounds. The ponds were next drained in October, 1960.

The 1960 drainage censuses revealed the only notable contamination by unwanted species that occurred throughout these investigations. Pond Zeta contained three adult bluegills and an estimated 15-20 pounds of young-of-the-year bluegills. Pond Theta contained a single white crappie. Pond Iota contained two adult bluegills and between one and two pounds of young bluegills. The impact of these contaminants is believed to have been small. Other things being equal, the most likely influence would probably have been an increase in condition of bass in proportion to the degree of contamination. There was, in fact, an inverse correlation. Pond Zeta, with the greatest contamination (15-20 pounds) contained bass with the poorest average condition (3.8) in the three ponds, and pond Theta, with only the single adult white crappie contaminant had the best-conditioned bass (4.5). There are, however, additional considerations. Cropping from Theta would be expected to cause the remaining bass to have a higher rate of condition than bass in the uncropped ponds, which it seems to have done. At the least, then, we may say that the influence of the contaminants was not such as to have masked the effects to be expected from cropping. In the remaining analyses we have assumed the influence of the contaminating fishes to have been negligible though this may not have been strictly true.

Following the draining censuses of the Unit 2 ponds in October, 1960, the bass were regrouped by size and age and stocked in Unit 1, with supplemental stock added from other local sources. The ponds in Unit 1 had just been refilled following the draining censuses of smallmouth populations previously described.

Standing Crop Data

Table 16 presents standing crops in pounds per acre as measured by draining censuses of 11 populations of largemouth bass. The data are arranged according to experimental treatments given the populations, with an average standing crop presented for those ponds receiving identical treatments. Table 17 presents the same standing crop data

Table 16.—Standing crops in pounds per acre of largemouth bass in ponds receiving different experimental treatments. All censuses were by pond drainage on the dates or seasons indicated.

Unit	*Pond*	*Number of Growing Seasons*	*Date or Season of Census*	*Standing Crop in Pounds Per Acre by Treatments Received*		
				Control	Cropped	Add-stock
2	Zeta	1½	7/27/59	21.7		
2	Theta	1½	7/27/59			
2	Iota	1½	7/27/59			37.6
2	Zeta	1½	F 1960	49.6		
2	Theta	1½	F 1960		47.4	
2	Iota	1½	F1960	. .		71.7
1	Beta	1	F 1961	126.8		
1	Beta	2	F 1963	87.4	. .	
1	Gamma	3	F1963		84.2	. .
1	Delta	1	S1962			120.6
1	Delta	2	F1963			160.2
			Average	*71.4*	*51.1*	*97.5*

Symbols: F = fall, S = spring.

together with such pertinent supplementary data as pounds originally stocked, pounds added to or removed from the population during the course of the experiment, and the net loss or gain in pounds of fish flesh by the termination of the experiment. Table 18 presents those standing crops obtained by estimation procedures in the spring in addition to those obtained by draining censuses in the fall, for ponds Beta, Gamma, a n d Delta. Original stock, computations of pounds lost or gained, and other supplementary data in Table 18 were derived or computed from figures obtained from the next previous census, whether it was by estimation or actual count.

Table 19 presents the numbers in each size or age group and percents of total numbers and weights of each group recovered in each draining census. Size and age separations in these censuses were less complete than those earlier made for smallmouth because of the multiple sources of stock and the degree of overlap between age groups.

Standing crops of largemouth in Unit 2 ponds ranged from a high of 71.7 pounds in the add-stock pond Iota in 1960 to lows of 21.7 pounds in both the control (Zeta) and cropped (Theta) ponds in 1959, all following approximately one and one-half seasons of growth. Standing crops in Unit 1 ponds ranged from a high of 160.2 pounds in the add-stock pond Delta in 1963 to a low of 84.2 pounds in the cropped pond Gamma in the same year. As in the smallmouth experiments, causes for variation included 1) the differences in experimental treatments received, 2) differences in pond fertilities, and 3) differences in size and/or age compositions of the populations. The effects of the experimental treatments are discussed quite fully in the text to follow. Without exception, however, standing crops among contiguous ponds within the same experimental units were highest in the ponds which received additions of stock, lowest in those from which fish were cropped, and intermediate in those ponds which were maintained as controls.

Unit 1 ponds, with basins of black dirt and clay, were much more productive than ponds in Unit 2 where bottoms were composed largely of sand overlayed with a blanket of clay. The visi-

Table 17. — Pounds of largemouth bass per acre originally stocked, pounds added or removed, final standing crops in pounds per acre, and weights gained or lost in pounds per acre in ponds Zeta, Theta, Iota, Beta, Gamma, and Delta for periods of 1, 1½, 2, and 3 years. Censuses of ponds Zeta, Theta, and Iota in July, 1959, were by use of rotenone; all other censuses were made by pond drainage.

Unit	*Pond*	*Treatment*	*Date or Season of Census*[a]	*Number of Growing Seasons*	*Pounds of Original Stock*	*Standing Crop, Pounds Per Acre*	*Pounds Added*	*Pounds Removed*	*Pounds Lost or Gained*
2	Zeta	Control	7/27/59	1½	16.0	21.7	0.0	2.2	+ 7.9
2	Theta	Cropped	7/27/59	1½	16.3	21.7	0.0	24.6	+ 30.0
2	Iota	Add-stock	7/27/59	1	15.1	37.6	23.0	3.1	+ 2.6
2	Zeta	Control	F 1960	1 3/b	29.6	49.6	0.0	3.5	+ 23.5
2	Theta	Cropped	F 1960	1 3/	32.4	47.4	0.0	34.6	+ 49.6
2	Iota	Add-stock	F 1960	1	30.2	71.7	33.6	0.0	+ 7.9
1	Beta	Control	F 1961	1	87.3	126.8	0.0	1.3	+ 40.8
1	Beta	Control	F 1963	2	105.7	87.4	18.2	3.6	- 32.9
1	Gamma	Cropped	F 1963	3	93.1	84.2	1.5	148.8	+138.4
1	Delta	Add-stock	S 1962	1	96.7	120.6	49.6	1.2	- 24.5
1	Delta	Add-stock	F 1963	2	120.6	160.2	100.5	4.6	- 56.3

Symbols: F = fall, S = spring.

Table 18.-Standing crops of largemouth bass in 1-acre ponds Beta, Gamma, and Delta and pertinent supplementary data, as determined by draining censuses (exact count), or Petersen estimates, in spring and fall.

Pond	Season and Year of Census[a]	Type of Census	Number of Growing Seasons	Standing Crop, Pounds Per Acre	Pounds of Original Stock	Pounds Added	Pounds Removed	Pounds Lost or Gained
Beta	F 1961	Drainage	1	126.8	87.3	0.0	1.3	+ 40.8
Beta	F 1962	Estimate	1	124.7	105.7	18.2	2.9	+ 3.7
Beta	F 1963	Drainage	1	87.4	124.7	0.0	0.6	- 36.7
Gamma	F 1963	Drainage	3	84.2	93.1	1.5	148.8	+138.4
Delta	S 1962	Drainage	1	120.6	96.7	49.6	1.2	- 24.5
Delta	F 1962	Estimate	1	164.5	120.6	66.5	3.9	- 18.7
Delta	S 1963	Estimate	0[b]	128.1	164.5	0.0	0.0	- 36.4
Delta	F 1963	Drainage	1	160.2	128.1	34.0	0.7	— 1.2

Symbols: F = fall, S = spring.

[b] There was no intervening period of growth between this spring estimate and that of the preceding fall. The deficit of 36.4 pounds in the pounds gained or lost column therefore indicates the estimated loss to overwinter mortality.

ble differences were the density of aquatic plants and the richness of the invertebrate fauna. The consequent differences in fish production are expressed by differences in standing crops in the control ponds of each unit. Maximum for a control pond in Unit 2 was 49.6 pounds per acre in Zeta in 1960, as compared to a maximum of 126.8 in pond Beta in 1961 (Table 17).

Fertilities of individual ponds within units were thought to be quite similar. This, for Unit 1, represented a marked change since the earlier period when rates of productivity and spawning success of smallmouth decreased in relation to their position in the flow series, i.e., from Beta to Gamma to Delta. During the summer of 1960 a water system was completed which permitted individual filling of each pond. With this new water system, productivities tended toward equalization. There was, in fact, some evidence that pond Delta, the least productive for smallmouth, may have had a narrow superiority in the production of largemouth.

The premature census of ponds in Unit 2 due to parasitism might be considered fortuitous, for it resulted in two sets of data rather than the intended one. Although the 1959 censuses occurred in July and the 1960 censuses in October, each period involved approximately one and one-half growing seasons, and the two are compared on that basis. A further difference was that the 1959 censuses were accomplished with rotenone, and those in 1960 by drainage. The clarity of the water and the high returns of marked individuals indicated a high recovery of the poisoned populations.

There is evidence that all populations in Unit 2 attained or exceeded the carrying capacities of their respective ponds under conditions which existed at times of census. Although the standing crops were quite small, particularly in 1959, it was verified that a potential for gain existed in these ponds by the surplus productions of 30 pounds in cropped Theta in 1959, and 49.6 pounds in the same pond in 1960. Larger gains would have been expected in the uncropped ponds if the carrying capacities had not been attained. Additional conclusions seem warranted by the almost perfect correspondence between the various quantities in the two different periods. In both study periods standing crop was highest in the add-stock pond and approximately equal in the control and cropped ponds; and surplus produc-

Table 19. — Numbers in each age or size group, and percents of total numbers and weights of each group in censused populations of largemouth bass in ponds Zeta, Theta, and Iota (Unit 2), and in ponds Beta, Gamma, and Delta (Unit 1), in years indicated.

Pond, Year of Census, *Treatment*[a]	Total Number Censused in Each Age or Size Group			Percent of Total Number Censused in Each Group			Percent of Total Weight *Censused* in Each Group			Total, All Age Groups	
										Number	Pounds
	Age 0	Age I & Older, Less Than 10" Long	Age I & Older, 10" or Longer	Age 0	Age I & Older, Less Than 10" Long	Age I & Older, 10" or Longer	Age 0	Age I & Older, Less Than 10" Long	Age I & Older, 10" or Longer		
Z 1959 0	103	59	7	61	35	4	4	78	18	169	21.7
T 1959 —	923	84	3	91	8	1	41	49	10	1,010	21.7
I 1959 +	319	122	8	71	27	2	8	78	14	449	37.6
Z 1960 0	32	191	24	13	77	10	3	57	40	247	49.6
T 1960 —	683	93	9	87	12	1	49	31	20	785	47.4
I 1960 +	20	262	48	6	79	15	1	44	55	330	71.7
	Age 0	Age I	Age II & Older	Age 0	Age I	Age II & Older	Age 0	Age I	Age II & Older		
B 1961 0	1,705	0	122	94	0	6	44	0	56	1,827	126.8
B 1963 0	203	54	189	46	12	42	3	8	89	446	87.4
G 1963 —	10,601	1	49	99	tr	1	61	tr	39	10,651	84.2
D 1963	363	0	388	48	0	52	2	0	98	751	160.2

Ponds are designated as: Z Zeta, T Theta, I Iota, B Beta, G Gamma, and D Delta. Pond treatments are designated as: 0 none, stock added, and — minus = cropped.

tion was significantly high in the cropped ponds, intermediate in the control, and lowest in the add-stock ponds. It also seems significant that in both instances surplus production in the cropped pond exceeded final standing crop in the control pond. The consistent similarities suggest that the effects of the experimental procedures were valid and reasonably free from additional unrecognized influences. If true, we then had a valid expression of the relationship of total production to rate of cropping or exploitation wherein cropping stimulated growth, reproduction, and/or survival in the residual population with the consequence of an increased total production. In 1958-1959, surplus production (pounds gained) in the cropped pond was approximately 3.8 times that of the control pond; and in 1959-1960, it was about 2.1 times that of the control pond.

It is interesting to speculate as to whether the standing crops might have been the same in pond Theta with or without cropping. It may be that we were achieving an optimum rate of turnover for this population, and that the additional production was a "bonus" stimulated by an optimum cropping rate.

If we assume final standing crops to have approximated carrying capacities, as interpreted here, carrying capacity appears to have approximately doubled in the period from July 1959 to October 1960. While parasitism probably depressed growth to some degree in 1959, the greater production of fish in 1960 was believed due primarily to an increase in available food, principally crayfish.

In our second series, ponds Beta, Gamma, and Delta (Unit 1) were inventoried by both drainage and Petersen estimation procedures. As shown in Table 18, the control pond Beta was inventoried by a draining census at the end of the first growing season, by Petersen estimate at the end of the second, and by draining census at the end of the third. Our intimate knowledge of this population, based on frequent sampling, indicated that the 1962 estimate was within acceptable limits If we accept this estimate we find that the standing crops were almost identical at near 125 pounds per acre in October of both 1961 and 1962, but dropped rather unaccountably to 87.4 pounds in October, 1963. The surplus productions in 1961 and 1962 were 40.8 and 3.7 pounds, respectively, being either moderately high or low as necessary to attain the presumed maximum. That these gains were not larger probably indicates that the standing crops in 1961 and 1962 approximated the carrying capacities of the pond at the times of census. These standing crops greatly exceeded those for largemouth bass measured in Unit 2 (Table 17), but were considerably below those of 170-180 pounds of smallmouth bass recovered from this pond (Beta) in earlier years.

Following the 1961 draining census, pond Beta was restocked with 105.7 pounds of bass, as shown in Table 18. The loss (pounds lost) of 36.7 pounds by October 1963 indicates that 1) the carrying capacity of pond Beta declined significantly during its third season, or 2) that the 1963 population was less efficient than those of 1961 or 1962. Decrease in standing crop implies a loss of efficiency by the population, or a decrease in available food. While no quantitative comparisons can be made, there was no evidence of a decline in available food. On the other hand, differences in population structure in the 3 years suggested possible differences in efficiencies of conversion of available food. From 1961 through 1963, progressively higher percentages of total weights were to be found in the larger sizes of bass. For example, in October 1961, 56 percent of the population (by weight) was made up of fish more than 8.5 inches long (Age II and older), while by October 1963, nearly 90 percent of the total weight of the population was represented by fish longer than 8.5 inches, most of which were now Age III or older. While an abundance of food may have been available for small bass in 1963, it possibly went largely unutilized because of the relative scarcity of small bass. With a more optimum size distribution of fish, the standing crop of pond Beta probably would have been higher. The obvious trend was a progressively greater depletion of small bass through predation by a progressively increasing proportion of larger bass. Had the larger bass been cropped by fishing the population would have assumed a more optimum composition and total production undoubtedly would have been higher. As previously observed, largemouth bass of larger sizes (in this case 8.5 inches and above) seem to lack the ability of smallmouth of similar sizes to forage for invertebrate foods, and are more dependent upon fish or other large food items.

For the cropped pond Gamma we have only the single final inventory of this population plus records of original stock and pounds cropped over the 3-year period. The total of about 148.8 pounds in the "pounds removed" column (Table 17) includes 31.04 pounds cropped in 1961, 81.34 pounds in 1962, and 36.40 pounds in 1963. In retrospect, it now appears that the removal of 81.34 pounds in 1962, followed by a cropping of 36.40 pounds in 1963, may have been excessive. While it caused accelerated growth and improved condition among the survivors, it left too few individuals of larger sizes to permit replacement of the pounds removed. This seems evident because the final standing crop was low as compared with those of companion ponds, and was comprised of 61 percent Age 0 fish by weight, and only 50 individuals older than Age 0. The final standing crop included only one fish in the Age I group, and only six fish in the 6.5-9.5-inch length range. We thus created quite the opposite condition of that found in the uncropped pond Beta. In that first instance we had an excessive number of slow-growing, poorly conditioned older fish (243 Age I or older) comprising about 97 percent of the population by weight, as compared with too few, faster-growing older fish (50 Age I or older) comprising about 39 percent of the population weight. In each instance, production was limited, and final standing crop was less than the carrying capacity of the pond due to an imbalance in population structure.

The add-stock pond Delta was inventoried by a draining census in the spring of 1962, by Petersen estimates in the fall of 1962 and the spring of 1963, and again by draining census in the fall of 1963 (Table 18). There is a reasonable probability that the estimates are usable because 1) both mark-and-recapture samples were large (probably equalling or exceeding 50 percent of the total population), 2) the estimates were credible when compared with known numbers stocked and numbers later recovered by draining census, and 3) estimates of standing crops made in the spring and fall agreed closely with those obtained by actual measurements (draining censuses) at the same seasons in other years. On the basis of experiments conducted to evaluate the estimates (Buck & Thoits 1965), such errors as existed probably would have been negative.

If we are to accept these estimates, certain inferences may be drawn:

(1) Standing crops in all inventories of pond Delta at least equalled and probably exceeded carrying capacities. This seems evident from the fact that all quantities in the pounds gained or lost columns are negative (Table 18), indicating that the additions of stock had overtaxed available resources.

(2) Overwinter mortalities were large and fall carrying capacities exceeded those for spring. This seems apparent because standing crops inventoried in the fall exceeded those obtained

in the spring by approximately 44 pounds in the first instance and approximately 32 pounds in the second. Since pounds were lost in all instances, we believe that the carrying capacities at times of censuses were probably close to, but possibly somewhat below, the figures for standing crops. As in Unit 2, surplus production was highest in the cropped pond, intermediate in the control pond, and lowest in the add-stock pond.

Effects of Cropping on Fish Production

The influence of cropping on fish production is best illustrated by referring again to Table 17 which features the figures on "pounds lost or gained." The data from ponds in Unit 2 (Zeta, Theta, and Iota) are most rewarding. The significant points in the data are that 1) in both periods of observation, standing crops of largemouths in the control and cropped ponds were similar, 2) in both periods surplus production in each cropped population equalled or exceeded the final standing crop in both cropped and control ponds, and 3) surplus production in the cropped pond was 3.8 times that of the control pond in 1958-1959 and 2.1 times that of the control pond in 1959-1960. The combination of these data indicate that we here approached the optimum rate of cropping for these populations and that the replacement of fish flesh during each period was approximately the same as the ponds could support at any one time (100 percent).

Data from the Unit 1 ponds were less precise. The fact that the final "pounds gained" figure of about 138 pounds made in the cropped pond was so much larger than the amounts of the companion ponds indicated that cropping did indeed stimulate production. This, however, was an accumulated gain over three seasons, which translates to an average gain of approximately 46 pounds for each of the 3 years. We may note that the final standing crop of 84.2 pounds in this cropped pond was lower than that for either companion pond, and was comprised of a larger number (10,601) of young-of-the-year with only one fish of Age I and 49 that were of Age II or older (Table 19). The total of about 148.8 pounds cropped from this pond (31.04 pounds in 1961, 81.34 pounds in 1962, and 36.40 pounds in 1963) may have represented overcropping, particularly among fish of larger sizes. A more optimum distribution of sizes in this population — specifically, fewer fish of Age 0 and more of Age I —would undoubtedly have increased its potential for replacement of the fish flesh that was removed.

Growth and Condition

Table 20 presents growth data for fish of known age in the final censuses of 10 of our populations of largemouth bass along with growths made in other waters. Precise growth data for largemouth in ponds Zeta, Theta, and Iota were limited because of the variety of origins, sizes, and ages in the original stock, and because small confidence was placed in the interpretation of scale samples collected. The data in Table 20 are, therefore, limited to first-year growths made in these ponds. For other purposes, however, we used length frequency distributions to make the less precise separations presented in Table 21, and these provide limited additional information on growth in these waters.

Growth rates listed for 1959 were those which were terminated at the time of the premature census on July 29. First-year growths over the full 1960 season ranged from 4.3 inches in Theta to 4.8 inches in Zeta, and these were quite intermediate to first-year growths made in other waters with which they are compared (Table 20).

The 1959 section of Table 21 shows numbers of fish within four different size ranges in the populations censused in July, 1959, the average condition for each size grouping, and a designation

Table 20.- Growth of largemouth bass in ponds used for carrying capacity experiments on the McGraw Foundation grounds, along with similar data on largemouths in several other waters.

Group	Pond	Year	Treatment	*Average Length in Inches (at Ends of Numbered Growing Seasons) with Number of Fish Used to Establish the Average in Parentheses*			
				1st	2nd	3rd	4th
Unit 2[a]	Zeta	1959	Control	2.6 (103)) [b]			
	Theta	1959	Cropped	2.8 (923) } [b]			
	Iota	1959	Add-stock	2.7 (319) [b]			
Unit 2[c]	Zeta	1960	Control	4.8 (32)			
	Theta	1960	Cropped	4.3 (683)			
	Iota	1960	Add-stock	4.4 (20)			
Unit 1	Beta	1961	Control	4.1 (1,705)			. .
	Beta	1963	Control	2.9 (203)	6.7 (54)	8:6 (152)	11.7 (37)
	Gamma	1963	Cropped	2.2 (10,601)	7.5 (1)	10.3 (40)	12.8 (8)
	Delta	1963	Add-stock	2.9 (363)	. . (0)	8.7 (221)	10.8 (167)

Other Waters	*Author*	1st	2nd	3rd	4th
Oklahoma Reservoirs[d]	Jenkins & Hall (1953)	5.48	9.66	12.5	14.91
Norris Reservoir"	Stroud (1948)	6.9	12.2	14.7	16.1
Pennsylvania Pond[e]	Cooper *et al.* (1963)	3.5	3.98		
Pennsylvania Pond[e]	Cooper *et al.* (1963)	5.25	8.42		
Johnson Sauk Trail Lake, Ill[f]	Rock (1966)	4.0	7.2	10.9	13.0
Ramsey Lake, Ill.[f]	Stinauer (1966)	4.3	8.8	11.3	13.7
Red Hills Lake, Ill.[f]	Price (1966)	4.7	7.7	10.5	11.9
Ridge Lake, Ill.[g]	Bennett (1954)	8.1	10.3	12.6	13.6

[a] From actual measurements of live fish on July 29, 1959.
[b] Growth to July 29 only.
From actual measurements of live fish at end of growing season.
[d] Lengths back calculated from scales.
[e] Based on measurement of live fish of known age.
Lengths were determined from analysis of scales, and represent averages of growths made in from 5 to 8 separate years.
[g] Age categories for fish of these lengths based on scale analysis and fin clips of bass marked for individual censuses.

of the age class to which a majority of fish within each size group probably belonged. Two trends are apparent in these data: 1) a decline in condition with increase in size of fish within the same population, more prominent in the control and add-stock populations, and 2) a strong relationship between condition and density of stock when comparing fish of the same age in different populations. Condition declined progressively from 5.7 for the Age 0 fish to 4.2 for the group comprising the largest individuals in pond Zeta, and from 5.1 to 3.6 for the same age groups in pond Iota. This relationship was absent in the cropped populations because of the greater densities of stock of the smaller sized fish and lesser densities in the groups of larger sized individuals, as a natural consequence of cropping. As one makes further comparisons between rates of condition and densities of stock of fish of the same age or size class in the three ponds, it is evident that, without exception, condition was poorest where numbers were greatest and vice versa. For example, numbers of Age 0 fish in the three ponds were 103, 319, and 923, and rates of condition for these groups were 5.7, 5.1, and 4.6, respectively.

The 1960 section of Table 21 presents similar data for fish censused in the same ponds during October, 1960. Conditions again ranged from poor to average by Bennett's (1948) standards, the low averaging 3.78 (rounded to

3.8) for 166 fish in the control pond, Zeta, and the high averaging about 5.2 for 9 fish of the oldest class in the cropped pond Theta. The tendency for increasing condition with increase in size of bass was present in these populations due in part to a change in shape as the bass become larger and in part to a greater abundance of food (notably crayfish) for larger fish in 1960 over that of 1959.

The correlation between strength of year-class and average condition in the respective ponds was also less apparent in the 1960 census. As an example, 166 fish of the "mostly Age I" category in pond Zeta had an average condition of 3.8, as compared to 4.2 for 233 fish of the same class in the add-stock pond. We may note, however, that average condition of all three of the oldest year-classes in 1960 ranked higher in the cropped than in either companion pond, due probably to their lesser abundance as a result of cropping. Transfer of better-conditioned fish from the cropped to the add-stock population could have contributed to the higher condition of certain age classes in pond Iota than in the control pond, but we believe the differences were due primarily to a slightly greater fertility of the add-stock pond.

Growth data of two types are also presented for largemouth from ponds in Unit 1 (Beta, Gamma, and Delta). Data presented for comparison with growths made in other waters (Table 20) are restricted to fish of known age, and represent an average of all fish in the final draining censuses for which ages were known. Additional growth data are presented in Fig. 4 where growth curves are based on samples collected during the months indicated.

As is evident in Table 20, growths in these single-species populations were slower than in most mixed populations with which they are compared, even in some instances when growth was stimulated by relatively heavy cropping.

								Mostly Age II			Age III or Older		
		m nsu	og. Ran e Inc	e d n	• su	og c es	erage di io	Number in Census	n• Range, che	• o d	N r Census	Length Range In	Average Condition
1959													
Zeta	Control	f08	3	5.7	18	6.1–7.7	5.4	4		5.	7	10.5–12 3	4.2
Theta	Cropped	92C8	2. 3	4.	76	4.6–8.3	4.7	8		5.2	3	10.7–11 7	4.9
Iota	Add-stock	3▯9	3	5.	44	5.0–7.8	4.9	8		4.	8	10.0–13.9	3.6
1960													
Zeta	Control	32	0– 2		1C8			Z5		4.	6	10. 13.9	4.5
Theta	Cropped	8C8	3		784				8.Eci	4.	9	10. 16.4	5.2
Iota	Add-stock	20			788					4.	8	10.0–16.9	4.7

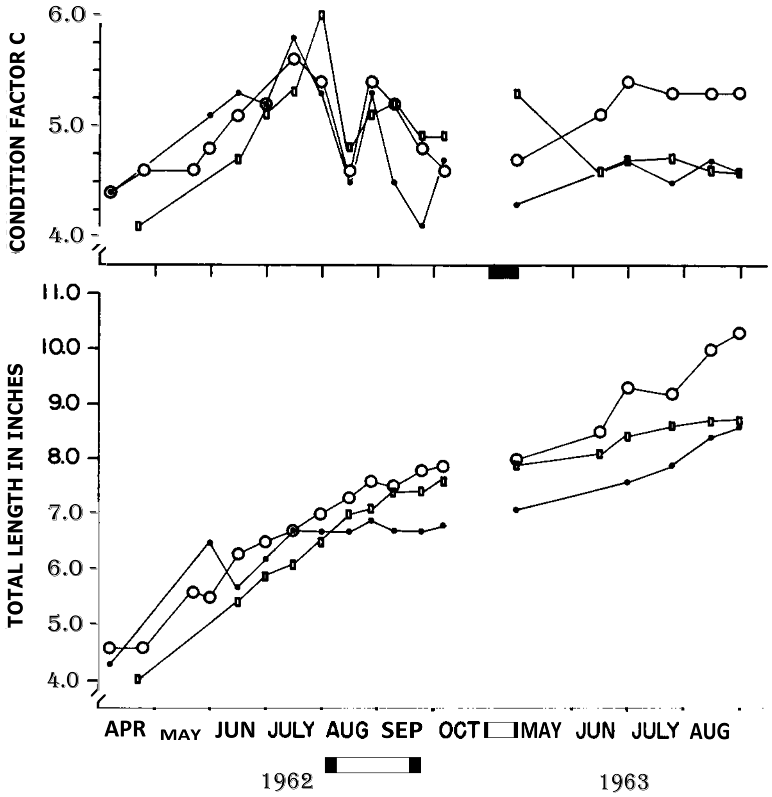

Fig. 4.—Growth and condition (C) of largemouth bass of the dominant 1961 year-class over the 1962 and 1963 growing seasons in the control pond Beta (dots), cropped pond Gamma (circles), and add-stock pond Delta (rectangles).

Cooper *et al.* (1963) demonstrated that heavy cropping of a population of yearling bass in a Pennsylvania pond caused substantial improvement in growth and condition, and in surplus production. It should be pointed out that the Pennsylvania study was a comparison of data from a single pond in different years while our comparisons were of data from different ponds in the same year. As emphasized earlier, differences in environments frequently masked the influences of our experimental treatments. While our rates of surplus production were consistently greatest in cropped ponds, and lowest in the add-stock ponds, rates of growth and condition showed less conformity.

Our most complete data comparing growth with condition are for the 1961 brood over the 1962 and 1963 growing seasons since this was the age group that was most abundant and the most heavily cropped over that period. Fig. 4 presents growth and condition curves for the 1961 year-class based on approximately bimonthly samples over most of the 1962 and 1963 growing seasons, with the terminal points in 1963 representing averages of all fish in the final censuses. Growth and condition curves are based on identical samples. After mid-June, 1962, the growth curve representing the cropped population ranked higher than that of either companion population and the margin of difference increased steadily throughout 1963.

Coefficients of condition computed from the same samples were extremely variable from one sampling period to the next throughout 1962, but all three populations exhibited similar patterns of seasonal variation. Condition in all ponds improved steadily from spring to a mid-summer peak, dropped sharply over the period from mid-July to mid-August, rose to a second but lower peak by early September, and then declined again. Differences in patterns between individual populations were not great in 1962, and showed little influence from the experimental treatment. In 1963, however, condition of the cropped population had achieved a distinct superiority by early June, and this was maintained throughout the 1963 season.

While the cropped population ranked high in both growth and condition in 1963 (Fig. 4), growth in the add-stock population was higher than, and condition was similar to, that in the control pond throughout much of both 1962 and 1963. Such an advantage in the add-stock population could have been influenced to the degree to which faster-growing, better-conditioned fish transferred from the cropped pond contributed to the samples obtained from the add-stock population. However, inspection of our samples showed that the transferred fish composed such a small part of the samples as to render their influence negligible. Faster growth and better condition of fish in the add-stock pond than in the control pond, in spite of the greater density of stock in the add-stock pond, were believed due to a higher productivity for the add-stock pond than for the control pond Beta. As mentioned before, this indicated a reversal in the comparative productivities of the two ponds since the earlier period with the stock of smallmouth bass.

The condition curves for our Age I fish in 1962 (Fig. 4) illustrate the degree to which the condition of such a population may fluctuate over short periods of time. The similarity of curves in all ponds suggests that the fluctuations were due to some natural phenomenon common to all ponds. Since our Age I bass were largely dependent upon zooplankton and other small invertebrate foods, the fluctuations were probably related to normal variations in the availabilities of these foods. The relative stability of the condition curves for these same fish when larger and one year older in 1963 suggests that they were then subsisting on larger food items of a more stable supply. This may well have been crayfish, or the 1963 spawn of bass, or both.

Fig. 5 shows rates of condition plotted against lengths of bass recovered from ponds Beta, Gamma, and Delta in the draining censuses of October 1963 and allows a comparison of the three curves

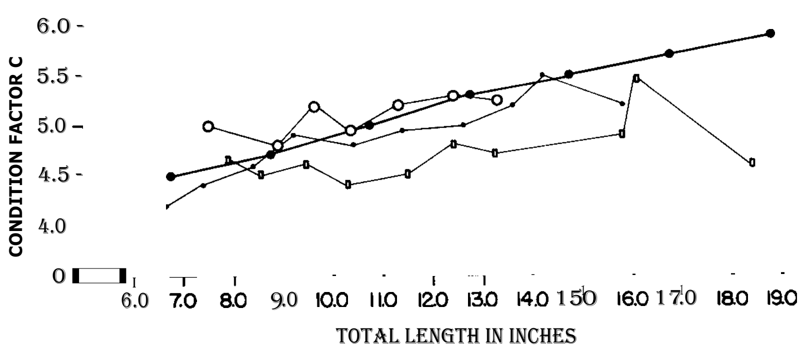

Fig. 5.—Coefficients of condition (C) in relation to lengths of largemouth bass for populations in the control pond Beta (small dots), cropped pond Gamma (circles), and add-stock pond Delta (rectangles) in 1963 compared with similar data (large dots) for bass from a mixed species population in an Illinois reservoir (Ramsey Lake: Stinauer 1966). Points plotted are the averages of condition for bass of convenient length groupings against the mid-length of each length grouping.

with a similar one for bass from a normal, mixed population from an Illinois reservoir (Stinauer 1966: Ramsey Lake). Conditions of our bass were commonly highest in the cropped pond, lowest in the add-stock pond, and intermediate in the control pond. While our bass showed a common though slight tendency for increased plumpness with increase in length, the tendency was less marked than in the normal population with which they are compared. This tendency may be typical of single-species populations of bass having no companion fish as a source of forage.

Mortalities

Rates of mortality for largemouths in ponds, Zeta, Theta, and Iota were poorly known because of incomplete knowledge of year-class strengths. Information is limited to those fish which were marked and transferred from Theta to Iota or were marked and released where caught. Since ages were poorly known, they usually were designated only as "Age I and Older" or "Age II and Older." The limited data permit three general observations: 1) mortalities of those fish marked and transferred were consistently a little higher than for those resident fish marked and released in the same (add-stock) population, 2) mortalities in the add-stock populations were slightly higher than for fish in the less densely populated companion ponds, and 3) known rates of mortality for largemouth were not notably different from those for similar categories of smallmouth in ponds Beta, Gamma, and Delta in 1959-1960, insofar as they could be compared.

In 1960 we attempted a study of rates of seasonal mortality based on recoveries in fall draining censuses of fish given distinctive fin clips at earlier periods in the growing season. Numbers marked in each period, numbers recovered in the final censuses, and percents of mortality are presented in Table 22. Because the fish marked were of a variety of sizes, and not of a single age class as in the earlier, similar experiment with smallmouth bass, the range in length and average length of each lot of marked fish are included in the table. Mortalities by the end of the 1960 growing season ranged from a low of 27.3 for 22 fish marked in pond Zeta in August to a high of 69.2 for 13 fish marked in pond Iota in April. Averages of mortalities (all ponds combined) for bass marked in each month showed a decrease from 48.9 percent for all fish marked in April to averages of 38.4, 37.9, and 30.5 for fish marked in the months of June, July, and August respectively. When rates of mortality for all fish marked in each pond were averaged (all marking periods combined), mortalities in the add-stock population (44 percent) exceeded those in either companion pond (33.2 percent and 39.6 percent in Zeta and Theta respectively). As in our smallmouth experiments, all mortality rates were abnormally high. The data indicated a rather high and fairly uniform mortality due to handling and marking, with a slight increase in mortality with increase in time the fish were marked.

Table 22 also reveals that mortalities were quite uniform over the size ranges marked, and not greater for either smaller or larger (younger or older) fish. This was evident from the rather normal and consistently small differences between those average lengths, as well as ranges in lengths, that were determined when the fish were marked and when they were recovered. A disproportionately high mortality among older fish would have been reflected by a lesser average length for those fish recovered than for those marked, and greater mortality of smaller fish would have had the opposite effect. A comparison of the lengths in Table 22 indicates a range of differences that in most cases would represent normal growth increments.

Rates of mortalities of the largemouth population from Unit 1 are more completely known because of greater knowl-

Table 22. —Numbers and sizes of largemouth bass marked and returned to ponds Zeta (control), Theta (cropped), and Iota (add-stock) in various months in 1960, and numbers and sizes recovered in the fall draining censuses, with percents of mortality.

Month	Number Marked and Returned, Number Recovered, and Percent *Mortality* [a]			Length Range and Average of Total Length in *Inches* [b]					
				When Marked			When Recovered		
	Zeta	Theta	Iota	Zeta	Theta	Iota	Zeta	Theta	Iota
April	26 17 34.6	14 8 42.9	13 4 69.2	3.4–14.9 7.3	3.9–11.3 7.7	3.6–16.3 *7.1*	6.4–15.0 *8.9*	6.2–11.5 *10.0*	5.8–10.8 *8.5*
June	27 16 40.7	25 15 40.0	26 17 34.6	4.7-16.0 *9.0*	4.2-15.5 *9.1*	6.7-15.7 *9.9*	6.9-16.2 *10.3*	6.2-15.4 ***10.2***	7.7-16.2 *10.9*
July	30 21 30.0	13 7 46.2	32 20 37.5	4.7-12.1 *6.6*	5.0-11.7 *7.3*	4.6-13.5 *6.7*	6.7-12.5 *8.1*	6.1-11.9 *8.4*	5.7-13.4 *7.8*
Aug.	22 16 27.3	41 29 29.3	23 15 34.8	5.6-11.3 *7.3*	5.3-16.0 *6.7*	5.3-15.2 *8.2*	6.2-11.4 *7.7*	5.5-15.9 *7.1*	5.9-15.2 *8.6*
Average Mortalities	*33.2*	*39.6*	*44.0*						

The sequence in each group of numbers corresponds to the order of categories as mentioned here; for example, in pond Zeta in April, 26 fish were marked and returned, 17 were recovered, and mortality was 34.6 percent.

[b] Total length averages are shown in italic.

edge of their age compositions. When possible, as during a draining census, entire year classes were given distinctive marks. These, plus marks given during normal sampling, and to fish transferred during each year, made it possible at times of census to compute rates of mortality for most components of the populations. Known rates of mortality for fishes stocked in or transferred to pond Delta are presented in Table 23.

Pond Delta contained 363 Age 0 bass when censused in October, 1963. This was particularly interesting since our observations had indicated no successful reproduction (and certainly no survival) in this pond in either previous year. We believe that the earlier failures were related to high pH levels, as discussed in the section devoted to spawning success.

Age I was completely missing in the 1963 fall census of pond Delta. The 1962 spawn had been unsuccessful, and the 451 Age 0 fish transferred from Gamma as 2-4-inchers in late August and September, 1962, had disappeared, probably through predation.

As indicated in Table 23, Age II fish (1961 year-class) in the final population of pond Delta contained four components for which mortalities ranged from 16.7 to 90.3 percent. Mortalities were higher among transferred than among resident bass and were highest among those fish transferred earliest and when smallest. We suspect, however, that higher mortalities were related more to the size of the fish when transferred than to length of time in the new population.

The Age III and older fish also had four separate origins. Mortalities (Table 23) ranged from 16.7 to 82 percent, and were again related to length of time in the population and/or to size of fish when transferred.

Known rates of mortality for bass in the control pond Beta are presented in Table 24, and are restricted to the original stock of October, 1960, or to those restocked following the draining census of October, 1961. A total of 1,705 young-of-the-year were recovered in the draining census of October, 1961, of which 892 were marked and restocked. The recovery of only 152 of this marked group in the census of October, 1963, indicated a mortality of 83 percent over the final 2-year period.

Table 23.— Mortalities of various categories of largemouth bass based on recoveries in the draining census of pond Delta (add-stock) in October, 1963.

Year Class or Classes	*Origin, or Number Originally Stocked*	*Recovery in Oct., 1963 of Bass Marked and Transferred to Delta in Year Indicated*	*Total Number Recovered*	*Percent Mortality*
1963	Spawned in Delta, 1963		363	Unknown
1962	Spawned in Delta, 1962		0	100.0
1962	Transferred from Gamma	0 of 451 (1962)	0	100.0
1961	581[a]		132	77.3
1961	Transferred from Gamma	7 of 72 (1961)	7	90.3
1961	Transferred from Gamma	52 of 191 (1962)	52	72.8
1961	Transferred from Gamma	30 of 36 (1963)	30	16.7
1960 or Older	478[b]	. .	86	82.0
1960 or Older	Transferred from Gamma	27 of 72 (1961)	27	62.5
1960 or Older	Transferred from Gamma	34 of 70 (1962)	34	51.4
1960 or Older	Transferred from Gamma	15 of 18 (1963)	15	16.7

[a] Since no spawning was observed in 1961, all 1961 year-class fish not transferred to pond Delta are believed to have originated from this stock of 581 1-inch fry in mid-June, 1961.

[b] The 478 included 231 Age 0 fingerlings, 212 that were mostly of Ages I and II, and 25 that were mostly Ages III and IV when stocked in October, 1960, and 10 of Ages II and Older stocked in May, 1961.

Table 24. — Mortalities of various categories of largemouth bass based on recoveries in the draining censuses of pond Beta (control) in October, 1961, and October, 1963.

Year Class or Classes	*Number Originally Stocked*	*Number Recovered in 1961*	*Percent Mortality*	*Origin, or Number Restocked in Oct., 1961*	*Number Recovered in 1963*	*Percent Mortality*
1963				Spawned in Beta, 1963	203	Unknown
1962				Spawned in Beta, 1962	54	Unknown
1961	585	1,705	Unknown	892	152	83.0
1960	132	0	100.0		. .	. .
1959 or Older	295	112	62.0	129	37	71.3

[a] Eight bass of the oldest group (1959 or older) were stocked in May, 1961, all 585 of the 1961 year-class were stocked as 1-inch fry in mid-June, 1961; all others (73.86 pounds) were stocked in October, 1960.

The remaining population was comprised of 37 older and larger individuals, none of which bore marks. Their origin traces back to the original stock of 295, nearly all released in October, 1960 as mixed Age I and older (mostly Age II and III). A total of 112 of these fish were recovered in October, 1961, representing a mortality of approximately 62 percent over the 12-month period. Seventeen fish of the same age were added to the group, bringing the total restocked in October, 1961 to 129. Our final total of 37 therefore represented a mortality of approximately 71 percent over the final 2-year period.

The original stock in the cropped pond Gamma numbered 1,014 individuals, including 585 fry of the 1961 brood, 132 fingerlings from the 1960 brood, and a total of 297 individuals that were Age II or older (mostly Age III and IV) in 1961. By time of final census in October, 1963, only 49 individuals remained of this original stock, including 40 of the 1961 year-class, none of the 1960, and only 9 individuals of the oldest group, by then Age IV or older. Of the 1961 brood, a total of 425 had been cropped over the 3 years. The total of the two figures (425 cropped plus 40 recovered 465) implies a much higher survival than one would expect from an original stock of 585 1-inch fish, and a small survival of the 1961 spawn is indicated.

Of the 132 fingerlings in the original stock, none was cropped in any year, and none was recovered in the 1963 census. It seems likely that this age group was decimated quite early by predation.

Of the original stock of 297 older fish, 72 were cropped in 1961, 71 in 1962, and 18 in 1963, for a total of 161. Only 9 of this group were recovered in the 1963 census, which meant that 127 must have died natural deaths over the 3-year period.

The final 1963 standing crop in the cropped pond Gamma also contained 10,601 young-of-the-year, as compared to only 203 and 363 of the same age in the two companion ponds. This large survival of young was coupled with the recovery of only 49 fish older than Age I, as compared with totals of 189 and 388 fish of similar ages in the control and add-stock ponds respectively. Differences in surviving young were probably related to differences in numbers of older fishes and corresponding differences in predation.

Spawning Success

Successful spawns of largemouth bass occurred in ponds Zeta, Theta, and Iota (Unit 2) in all years, 1958 through

1960, and young-of-the-year were recovered in all draining censuses. Attempts to obtain comparative counts of schools of fry in ponds of both Units 1 and 2 were unsuccessful, due primarily to concealment of the fry by either large mats of filamentous algae or submerged aquatic weeds. As may be seen in Table 19, the numerical abundance of young-of-the-year in all final standing crops was much higher in the cropped than in the companion ponds. This may have reflected higher rates of spawning success due to lesser densities of breeding stock in the cropped ponds than in the companion ponds, as observed in the smallmouth populations, or may have been due to lesser degrees of predation by lesser numbers of older and larger fish in the cropped ponds, or both.

In Unit 1, successful spawns were known to have occurred in all ponds in all years, 1961-1963, except in pond Delta in 1961. A series of observations made in 1963 suggested a possible reason for the apparent failure in pond Delta in 1961, as well as for limited production of young in that pond in 1962. On May 9 and 10, 1963, adults were observed to be building nests in ponds Gamma and Delta but not in pond Beta. By early June, young-of-the-year had been seen in both Gamma and Delta, but neither young nor spawning activities of any type were observed in pond Beta throughout May or early June. During May we also observed that weeds of various *Potamogeton* spp., particularly *P. crispus* L., were becoming extremely dense in pond Beta, and considerably more so than in either companion pond. As an apparent consequence to the dense vegetation and associated high rates of photosynthesis, the pH of the pond waters rose to levels above 10.2 in pond Beta, and to levels of between 9.5 and 10 in ponds Gamma and Delta. Fish of larger sizes in pond Beta were observed to be extremely listless, with some appearing to be dazed and gasping for air at the surface, while at the same time smaller fish of about 8-inch lengths appeared unaffected. On May 27 approximately 1.25 acre-feet of fresh water were introduced into pond Beta, and the pH receded to about 9.5 and the fish appeared to recover. The treatment proved quite temporary, however, and we decided to eliminate the weeds to reduce the high pH. On June 4, 1963, approximately one-third of the area of each of the three ponds was treated with enough endothal to provide a concentration of about 1 ppm in each treated area. On the basis of total pond volumes, the concentrations were probably between 0.3 and 0.5 ppm. The treatments proved to be effective in all ponds. As the weeds began to die and the pH levels declined, the bass in pond Beta were observed to build nests and commence spawning activities. Nests were first observed on June 19 and 20, approximately 6 weeks later than in either companion pond, and several successful hatches were later recorded. We have attributed this delayed spawning to the high pH during the normal spawning season. From observations made in the three ponds we believe that the critical level of pH was in the range of 9.6-10. These observations agree closely with those made by Jackson (unpublished) in some Wisconsin hatchery ponds where he reported no successful reproduction by bass in those ponds in which the pH remained at 9.6 or above during the spawning season. While adult bass have been known to tolerate pH levels exceeding 10 for short periods (Doudoroff & Katz 1950), reproduction may be restricted at somewhat lower levels. We believe, as did Jackson, that high pH may influence bass production in one or more ways:

1. High pH may inhibit spawning.
2. High pH may kill the eggs or larvae.
3. Emerging fry may starve to death due to elimination of zooplankton by high pH.

Since levels of 9.6-10.2 were common to our new, poorly buffered ponds in earlier years, we suspect that high pH may have eliminated or seriously reduced spawning of bass in those years.

Review and Discussion of Largemouth Bass Data, and Comparison with Smallmouth Data

Brynildson & Truog (1959) have recommended the stocking of Wisconsin warmwater ponds with largemouth bass alone because of unsatisfactory results from combinations of bass and bluegill. Brynildson (personal communication) has reported fairly good fishing from such single species populations providing the bass are not eliminated by winterkill or lack of natural reproduction. Bass alone have been stocked fairly extensively in both Illinois and Oregon. Bennett (1962) has achieved satisfactory results in Illinois ponds by stocking an assortment of bass larger than 10 inches, in addition to 100 fingerling bass per acre. The adults produced young at the first spawning season after stocking, and the fingerlings already present prevented the development of a dominant new brood subject to stunting. Bond (personal communication) has reported excellent fishing in some Oregon ponds and poor results in others (particularly in small, weedless ponds) due to stunting and limited reproduction, and he believes that best results may be obtained from use of ponds with areas of 2 acres or more. In a series of fishing trials, Bond and his associates found bass fishing to be much superior in single species populations than in populations containing both bass and bluegill. Largemouth are known to have been stocked as single species in ponds in other localities, but few such populations have been evaluated, due probably to early contamination by other unwanted species.

A search of the literature has provided only six listings of standing crops of bass as a single species (Table 15). The maximum poundage reported was 94.1 pounds per acre in a small, unfertilized pond in Texas (Brown 1951). However, Mraz (1964) has reported data from a stunted population of largemouths in a 1-acre pond in Wisconsin where the standing crop appeared to have exceeded 200 pounds per acre. The author reported removing 688 bass 5-9 inches long, and weighing about 100 pounds, in a single seine haul in the fall. The pond was heavily fished by hook and line both prior to this removal and during the following summer In the following fall an additional 707 bass were removed, having a total weight of 108 pounds and an average length of 7 inches, and which had made practically no linear growth during the year. A substantial population of small bass also remained following this second harvest. The data suggest that both harvests were from the same age and size class of bass, which means that the standing crop at the time of the first harvest must have exceeded 200 pounds per acre.

Our largest standing crop was 160.2 pounds per acre in pond Delta in October, 1963 (Table 17). However, this population had received heavy additions of stock (100.5 pounds) since the last previous inventory, and the deficit of 56.3 pounds in the "pounds lost or gained" column indicated that the pond's carrying capacity had been surpassed. The maximum poundage recovered from a control pond was 126.8 pounds per acre from pond Beta in October, 1961. This pond had received an original stock in the preceding October of 87.3 pounds, and upon drainage contained 1,705 Age O fish (55.6 pounds) ranging in length from 3 to 6.9 inches, no bass of Age I, and 122 bass (71.2 pounds) that were Age II or older, ranging from 8.5 to 18.6 inches in length. Additional inventories (Table 18) indicate that from 120 to 130 pounds per acre may have been the maximum carrying capacity of these ponds for largemouths. These compare with maximums of from 170 to 180 pounds of smallmouths earlier recovered from ponds in this same unit. Greater production of smallmouths than largemouths was believed due primarily to the superior ability of smallmouths of larger sizes to subsist on an invertebrate diet.

As observed in Oregon and Wisconsin, largemouth bass as a single species are sometimes self-limiting due to predation of young, or failures to reproduce. We observed a common tendency toward progressively greater proportions of older and larger fish in both smallmouth and largemouth populations, but elimination of young was less pronounced among largemouths than smallmouths in our studies. Table 25 compares the final compositions of 10 populations for each species (4 control, 3 cropped, and 3 add-stock populations). Higher average standing crops of smallmouth than largemouth bass were associated with greater numbers and greater percentages by weight of fish older than Age 0 in the final smallmouth than in final largemouth populations. For both species, numbers of fish older than Age 0 were highest in the add-stock ponds, lowest in the cropped ponds, and intermediate in the control ponds. One would suspect that numbers of Age 0 fish in the final censuses might be inversely correlated with numbers older than Age 0. This was true for largemouth, but not true for smallmouth populations. Average numbers of young smallmouths were 422 in four control ponds, 582 in three add-stock ponds, and only 23 in three cropped ponds. Comparable figures for largemouths were 511 in four control ponds, 234 in three add-stock ponds, and 4,069 in three cropped ponds. It is not clear whether smaller numbers of Age 0 smallmouths than largemouths in the final censuses were due to the lesser fecundity of the smallmouths, to greater predation on smallmouth young by their elders, or to more periods of high pH. The greater numbers of older smallmouths could have accounted for greater predation. However, the fact remains that all populations of largemouths contained young-of-the-year at the times of the fall censuses, ranging in individual ponds from 20 to over 10,000 survivors (Table 19), and average numbers of these survivors were higher in largemouth than in smallmouth populations (Table 25). Evidence therefore exists that largemouths alone also are capable of sustained, year-to-year production in 1-acre ponds, especially when subjected to cropping.

Numbers of surviving young-of-the-year in cropped largemouth ponds aver-

Table 25.- Comparison of final compositions of 10 populations of largemouth bass with 10 of smallmouth bass on basis of treatments received. Averages are presented for four control, three cropped, and three add-stock populations for each species.

Species of Bass	*Type and Number of Populations Averaged*	*Average Standing Crop, Pounds Per Acre*	*Average Percent of Weight of Fish in Specified Age Group*		*Average Number of Fish in Final Census in Specified Age Group*		*Average Percent of Numbers of Fish in Specified Age Group*	
			Age 0	Older	Age 0	Older	Age 0	Older
SMALLMOUTH	Control (4)	93.4	5.8	94.2	422	207	43.7	56.3
	Cropped (3)	46.2	12.5	87.5	23	166	40.3	59.7
	Add-stock (3)	149.6	6.2	93.8	582	584	36.1	63.9
LARGEMOUTH	Control (4)	71.4	13.5	86.5	511	159	53.2	46.8
	Cropped (3)	51.1	50.3	49.7	4,069	80	92.6	7.4
	Add-stock (3)	89.8	3.7	96.3	234	276	41.8	58.2

aged much higher than in companion largemouth ponds, as seems normal and expected, but numbers of surviving young in cropped smallmouth populations averaged much less than in companion smallmouth ponds (Table 25). As mentioned previously, the apparent spawning failure of smallmouths in cropped pond Tau in 1963 may have been due to the absence of a breeding pair, or to predation of eggs or larvae by an abundant population of crayfish. We suspect that other failures of smallmouths in cropped ponds were related more to physical or chemical limitations in the environment, as discussed in the sections devoted to spawning success, than to any significant difference in behavior of the two species.

Ponds in Unit 2 provided evidence that under an optimum program of cropping, largemouth populations are capable of a seasonal replacement of fish flesh equal to the poundage that the pond can support.

Our most efficient largemouth populations were believed to be those comprised of large weights of both small and large fishes, and this division of sizes was apparently more critical in largemouth than in smallmouth populations. As detailed earlier, standing crops of largemouths in pond Beta declined substantially as the population progressed from an approximate equal division of weights of fishes of Age 0 and those of Age II and older to one in which about 90 percent of the weight was comprised of fish longer than 8.5 inches (Age II and older). Populations of smallmouths in these same ponds attained maximum poundages (170-180 pounds) when over 90 percent of the weights were comprised of fishes that were Age I and older in one instance and Age II and older in two instances. The essential difference apparently lies in the greater ability of smallmouth of larger sizes to make efficient use of invertebrate foods. Probably none of our bass populations attained the maximum of which either species was capable. While we have little knowledge of what constitutes an optimum size distribution, and it would probably vary with the type and amount of available foods, we would presume it to be one in which all sizes and ages of fish had optimum representation. Since even our most productive populations had one or more age (and size) classes missing, possibly none achieved maximum efficiency.

As noted for the smallmouth populations, carrying capacities for largemouths were larger in the fall than in the spring. As shown in Table 18, standing crops measured in pond Delta in the spring were 120.6 pounds (drain census, 1962) and 128.1 pounds (estimate, 1963), as compared with fall standing crops of 164.5 pounds (estimate, 1962) and 160.2 pounds (drain census, 1963) in the same pond. Thus, carrying capacities in pond Delta in the spring were approximately 77 percent as large as those in the fall.

Carrying capacities of ponds in Unit 2 showed a marked increase over the period 1958-1960, due primarily to increased production of crayfish and other invertebrates, but there was no evidence that the carrying capacities of ponds in Unit 1 increased over the period 1961-1963. However, carrying capacities were evaluated by differences in standing crops, and these were influenced by differences in size and age compositions of the populations. Thus, differences in population structures in the different years could have masked any increase in carrying capacities.

As in the smallmouth populations, life histories of the largemouths were strongly influenced by differences in population densities. In general, rates of growth and condition were poorest, and rates of mortality highest, in those populations having the greatest densities of stock. Again, however, fastest growth rates were not always accompanied by highest rates of condition, and comparative rates of either were sometimes poor indicators of comparative rates of the other. Comparative rates of reproduction were poorly known, but numbers of young-of-the-year surviving through their first growing season were consistently by far the highest in the cropped populations.

YELLOW PERCH

We will present data obtained over 2-year (1958-1959) and 1-year (1960) periods from the single pond Alpha, earlier devoted to smallmouth bass, and a 3-year period (1961-1963) in ponds Zeta, Theta, and Iota (Unit 2), which earlier contained largemouth bass. The original stock of perch was transported from the Green Bay section of Lake Michigan where the fish had been trapped by personnel of the Wisconsin Department of Conservation.

Pond Alpha was first stocked with perch on April 30, 1958, receiving 79 males and 4 females, all adults of unknown age, having a total weight of 19.4 pounds. In spite of a loss of eggs, in transportation, by one or more of the 4 females a substantial spawn was obtained. Cropping in 1958 consisted of only 20 young weighing about 1 pound. Total cropping in 1959 was 78.7 pounds, including 57.2 pounds removed by summer hook-and-line fishing, and an additional 21.5 pounds taken by wire traps in October. Following the October draining census in 1959 the entire population was replaced in the pond. This included two of the original adults, 1,531 young-of-the-year, and 464 yearlings, representing a combined total weight of 123.4 pounds. In addition, 21 adults from a local lake were added to augment the breeding population, which brought the weight of the original stock for the 1960 experiment to 125 pounds. The pond was cropped of a total of 88.3 pounds in 1960, and when censused in October of that year had a standing crop of approximately 192 pounds. Perch obtained from the 1960 census of pond Alpha were immediately restocked in ponds Zeta, Theta, and Iota, with each pond receiving 3,771 young-of-the-year and 225 of mixed Ages I and II for total weights in each of about 52 pounds. These populations were sampled and observed through three growing seasons (1961-1963), and final censuses were accomplished in October, 1963. Pond Zeta was cropped, Theta received additional stock, and Iota was maintained as a control.

Standing Crop Data

Table 26 presents standing crop data for six populations of perch together with such pertinent supplementary data as pounds of original stock, pounds added to or removed from the populations during the course of the experiments, and the net gain or loss in pounds of fish flesh by the termination of the experiment. Table 27 presents numbers in each size or age group and percents of total numbers and weights of each group recovered in each draining census.

Standing crops of perch ranged from a low of 51.3 pounds per acre in the cropped pond Zeta in 1963 to a high of 191.9 pounds per acre in the cropped pond Alpha in 1960. Differences in standing crops of perch were due in part to differences in pond fertilities, differences in pond treatments, and differences in size and/or age compositions of the populations. Fertilities of the three ponds in Unit 2 were believed to be quite similar, but all were clearly less fertile than the single pond Alpha. The degree of differences is indicated by the fact that the cropped pond Alpha had a larger standing crop in 1960 than did pond Theta in 1963 when it received quite large additions of stock.

The differences in standing crops in pond Alpha in 1959 and 1960 were not as large as indicated (Table 26) because 21.5 pounds were cropped from Alpha just prior to the October draining census in 1959, and this poundage is included under the heading "pounds removed." Without this October removal the standing crop in 1959 would have been approximately 144 pounds rather than 123.4. However, the "pounds gained" would have remained the same at 183.7 in 1959, regardless of how the standing cr op was computed, which illustrates the usefulness of the pounds gained statistic.

Remaining differences in standing crops and in pounds gained or lost in pond Alpha in the two periods have been attributed to differences in schedules of cropping and in population composition. In 1959 cropping was poorly distributed over the growing season with a total of only 32.5 pounds removed by late July. Since average length increment of the dominant yearlings was only about 0.5 inch from May through September, 1959, and since coefficients of condition steadily declined from 4.25 to 3.78 during the same period, the removal apparently was too little to permit increased growth by survivors. In 1960 we wanted to determine if more intensive cropping of pond Alpha earlier in the season might have a more measurable effect on the survivors, and tend to increase total production. In 1960 24.5 pounds were removed in April, 22 in May, and a total of 77.2 pounds, or about 88 percent of the total season's cropping had b e en accomplished by July 20. Table 26 shows a marked increase in production during the second and shorter of the two periods. From an original stock of 19.4 pounds the first population showed a pounds gained figure of 183.7 pounds in two seasons, whereas the second population, with a much larger original stock (125 pounds), showed 155.2 pounds gained in only one growing season. The actual mechanisms were a greater production and/or survival of young, and increased growth by survivors of the original stock.

While the accelerated cropping surely increased production in 1960, there were also important differences in popu-

		a	s	Se'	o g	ou Orig to oj a	Standing Crop, Pounds Per Acre	Pounds Added	Pounds Removed	Pounds Lost or Gained
–	Alpha	OO p		59	2	19	123	0.0	79.7	' 8 7
—	Alpha	OO o d		9 0	1	12 0	19	0.0	88.3	55.2
2	Iota	OO ro		96	1	5 8	0	0.0	1 9[a]	┬ 5 8
2	Iota	ol		96	2	4 .7	0	0.0	2 [b]	1 7
2	Theta	10 d-s		96	3	5 3	00	149.9	39.5[c]	0
2	Zeta	O opp 1		96	3	53.3	5	0.0	22.8[d]	20.8

Table 27.- Numbers in each age group, and percents of total numbers and weights of each age group in censused populations of yellow perch in the single pond Alpha, and in ponds Zeta, Theta, and Iota (Unit 2), in years indicated. Age groups are shown in italic Roman numerals.

Pond, Year of Census, Treatment[a]	*Total Number Censused in Each Age Group*					*Percent of Total Number Censused in Each Age Group*					*Percent of Total Weight Censused in Each Age Group*					*Total, All Age Groups* Number	Pounds
	0	*I*	*II*			*0*	*I*	*II*			*0*	*I*	*II*				
A 1959 0	464	1,531	2			23.2	76.7	tr			12.7	86.6	0.7			1,997	123.4
	0	*I & II*				*0*	*I & II*				*0*	*I & II*					
A 1960 0	14,288	764				94.9	5.1				50.1	49.9				15,052	191.9
	0	*I*	*II & III*			*0*	*I*	*II & III*			*0*	*I*	*II & III*				
I 1961 0	0	2,210	66			0.0	97.1	2.9			0.0	89.8	10.2			2,276	94.7
	0	*I*	*II*	*III*	*IV*	*0*	*I*	*II*	*III*	*IV*	*0*	*I*	*II*	*III*	*IV*		
I 1963 0	0	3,079	0	372	19	0.0	88.7	0.0	10.7	0.6	0.0	59.2	0.0	30.7	10.1	3,470	100.3
T 1963 +	141	2,861	0	998	14	3.5	71.3	0.0	24.9	0.3	2.0	64.0	0.0	30.0	4.0	4,014	183.7
Z 1963 -	752	230	0	30	3	74.1	22.7	0.0	3.0	0.3	40.8	42.2	0.0	13.7	3.3	1,015	51.3

[a] Ponds are designated as: A = Alpha, Z = Zeta, T = Theta, and I = Iota. Pond treatments are designated as: 0 = none, + = stock added, and — (minus) = cropped.

lation compositions. The first relates to the increased abundance of breeding stock in 1960, which resulted in an increased production of young-of-the-year. The only mature females present in 1959 were survivors from the original stock of four, since females of the 1958 brood would not have matured by 1959. In 1960, however, the 1958 brood was in its third year, and is known to have spawned. Weight of Age 0 perch in the final censuses increased from 15.7 pounds in 1959 to 96.2 pounds in 1960.

A second important difference in composition of the two populations in pond Alpha was in their size distribution. In the 1959 census, in excess of 99 percent of the population, both by weight and by numbers, was contained within a length range of only 3.3 inches (from 4.1 to 7.4). Concentration into such a small size range undoubtedly intensified competition for food and greatly restricted predation of the smaller by the larger perch. In contrast, when censused in 1960 the population was quite normally distributed over a range of 7.2 inches (from 2.5 to 9.7), which could have permitted substantial cannibalism and a more efficient utilization of total food resources. Age 0 fish grew more slowly in 1960 than in 1959 because of their much greater abundance, but both growth and condition of fish older than Age 0 improved in 1960.

When this pond was devoted to smallmouth bass an initial stock of 16.16 pounds of small breeders produced a standing crop of 64.7 pounds after one and one-half growing seasons. The standing crop of perch in 1959 approximately doubled, and the 1960 crop approximately tripled this previous production of smallmouths.

Standing crops of perch in Unit 2 ponds ranged from 51.3 pounds in cropped Zeta in 1963 to 183.7 in the add-stock pond Theta in the same year (Table 26). The control pond Iota was drained and censused at the end of only one growing season (October, 1961), and was restocked and censused again after two additional growing seasons (October, 1963). Standing crops were similar at 94.7 and 100.3 pounds in 1961 and 1963 respectively. One might therefore conclude that the carrying capacity of this pond for perch was approximately 100 pounds per acre. It seems likely, however, that production may have been inhibited, and standing crops depressed by poor production of young in both census years. For reasons unknown no young were produced, or none survived, in 1961, a strong year-class was produced in 1962, and there was another complete failure in 1963. Thus neither the 1961 nor 1963 census contained young-of-the-year. The presence of young would have increased total poundages and would have provided food for older, cannibalistic individuals. The carrying capacity of this pond (Iota) may therefore have exceeded the poundages obtained from the two censuses. It should be noted that the maximum standing crop of largemouth bass in this pond had been 71.7 pounds when it was used as an add-stock pond in 1960.

As might be expected, pounds gained were lowest and standing crop highest in the add-stock pond, and pounds gained were highest and standing crop lowest in the cropped pond. The differentials reflect an increased productivity associated with cropping. For example, with the addition of stock the pounds gained figure in pond Theta amounted to only 19 pounds, compared with 220.8 pounds gained where cropping was heavy. Here pounds gained was almost equal to the total of pounds removed, indicating a complete turnover of the population.

Effects of Cropping on Fish Production

The influences of cropping on perch populations were perhaps less obscured by environmental differences than in experiments with either of the basses. We have already noted the increased production in pond Alpha in 1960, over that of the 1958-1959 period, due at least in part to accelerated cropping in the latter year. The same was equally evident in Unit 2 ponds where the figures for both pounds gained and growth (length of the fish) were greater in the cropped than in either companion population (Tables 26 and 28). Table 27 shows that the largest standing crop produced by perch was that containing the greatest abundance of young-of-the-year. Table 27 also shows that the strength of the Age 0 year-class was related to the abundance of older perch, particularly those of Age I. Thus where Age I perch were abundant in the final census, Age 0 perch were scarce or absent. We suspect that the absence of Age 0 perch was due in large part to predation by Age I perch when Age 0 perch were very young. We believe that the cropping of Age I perch increased the survival of young.

Table 28.- Growth of yellow perch in ponds used for carrying capacity experiments on the McGraw Foundation grounds, along with similar data on yellow perch in several other waters.

Group	*Pond*	*Year*	*Treatment*	*Average Length in Inches (at Ends of Numbered Growing Seasons) with Number of Fish Used to Establish the Average in Parentheses* 1st	2nd	3rd	4th
. .	Alpha	1959	Cropped	4.4 (100)	5.7 (100)		
. .	Alpha	1960	Cropped	2.7 (100)			
Unit 2	Iota	1961	Control		4.8 (300)		
Unit 2	Iota	1963	Control	. .	3.8 (200)		6.0 (155)
Unit 2	Theta	1963	Add-stock	3.9 (15)[a]	4.7 (230)		5.1 (202)[c]
Unit 2	Zeta	1963	Cropped	4.3 (200)	6.2 (230)		7.9 (29)
Other Waters		*Author*					
Lake Chautauqua, Ill.		Starrett and Fritz (1965)		. .	7.1	8.3	9.7
Lake Erie		Jobes (1952)		3.6	6.6	8.4	9.4
Red Haw Lake, Iowa		Lewis (1950)		3.7	7.2	10.3	
East Lake, Iowa		Lewis (1950)		3.4	5.7	7.1	7.6

[a] Determined from fish spawned in the pond.
[b] Determined from those fish spawned in the pond or transferred as fry from pond Iota in June, 1962.
[c] Determined from survivors of the original stock.

Growth and Condition

In the marking experiments in pond Alpha in 1960 we gained useful information on rates of seasonal growth. Table 29 includes figures indicating the percent by which each monthly lot increased its average length between time of marking and time of the October census. The greatest average length increment was 17.6 percent made by fish marked in May, and those marked in both May and June made larger increments than those marked in April. After May the rates declined quite regularly to a low of 4.9 percent for perch marked in mid-September.

The differences in growths made by perch marked in May and June and those marked in April are believed to be sex related. Samples for all three months were collected by wire traps, and length-frequency data indicated the samples to be almost equally divided between Age I and Age II individuals. More than 90 percent of the April sample was com-

Table 29.— Averages and ranges in total lengths of yellow perch marked in pond Alpha in spring and summer months indicated in 1960, and recovered in the fall draining census, with percents of mortality and length increments for each monthly lot.

Marked (During periods indicated, in 1960)				Recovered (Nov. 7-9, 1960)				
Date	Number	Range in Length, Inches	Average Length, Inches	Number	Range in Length, Inches	Average Length, Inches	*Percent Mortality*	*Percent Length Increment*
April 5-6	60	4.2-6.1	5.03	43	5.2-6.8	5.90	28.3	14.7
May 10-13	60	4.2-6.3	5.18	49	5.4-8.1	6.29	18.3	17.6
June 1-2	60	4.6-6.9	5.44	55	5.5-8.5	6.43	8.3	15.4
July 6-8	60	5.2-6.9	5.90	46	5.4-8.1	6.40	23.3	8.5
Aug. 29	52	5.5-8.2	6.83	38	6.0-9.7	7.19	26.9	5.0
Sept. 14-15	40	5.5-8.1	6.85	35	5.7-8.7	7.20	12.5	4.9

posed of ripe, freely milting males, and the few females caught at that time were retained for stocking a different pond. Fish marked and released in April are therefore known to have been all males. Spawning occurred in April, and fish marked in May and June were not sexed, but were believed to have had a more normal sex ratio. We therefore believe that the smaller increment made by the exclusively male sample marked in April reflects a poorer growth made by this sex. These data seem to be somewhat at variance with those of Herman *et al.* (1959) who showed that among Age I and Age II perch from Green Bay and Lake Mendota the males were of similar or slightly larger average size than females, but that the females were larger by Age III and thereafter.

Growth data presented for comparison with data from other waters (Table 28) are restricted to fish recovered in the draining censuses, and for which ages were known (not calculated). Data presented in the growth curves (Fig. 6 and 7) are based on samples collected on the dates indicated. Some such samples were collected on a single day and others represent a composite of small collections over periods which rarely exceeded 10 days. Perch samples were collected by wire traps, hook-and-line, and by boat shocker. Ages of fish were known by presence or absence of marks, or by distinct separations in size. First-year growths compared favorably with those from other waters (Table 28), except when the age class was unusually large, as in pond Alpha in 1960 in the presence of abundant, protective vegetation. Good first-year growth was probably related to heavy predation by older perch. Growth by perch older than Age O in our single-species populations was very poor, and poorer than for perch in most other waters with which they were compared. For example, growth increments of the 1960 year-class over a 2-year period (Ages II and III) in our control and add-stock ponds (Unit 2) were only 1.24 and 0.69 inches respectively. Concurrent growth in our cropped pond was higher, but still only 2.26 inches.

The influences of cropping and additions of stock are apparent in Fig. 6 and 7 which present growth and condition curves for the 1960 and 1962 year-classes throughout their existence in the populations. For the dominant 1960 year-class (Fig. 6) growth was fastest in the cropped pond, slowest in the add-stock pond, and intermediate in the con-

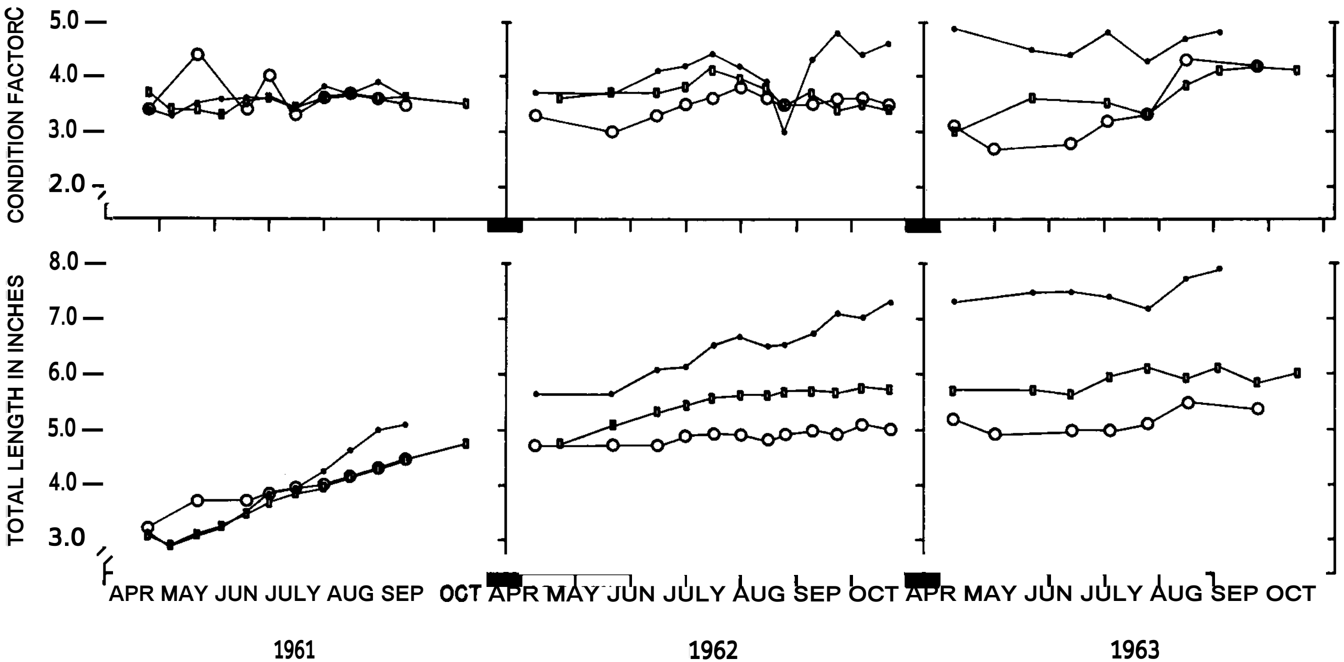

Fig. 6.—Growth and condition (C) of yellow perch of the 1960 year-class in the control pond Iota (rectangles), add-stock pond Theta (circles), and cropped pond Zeta (dots) during the 1961, 1962, and 1963 growing seasons.

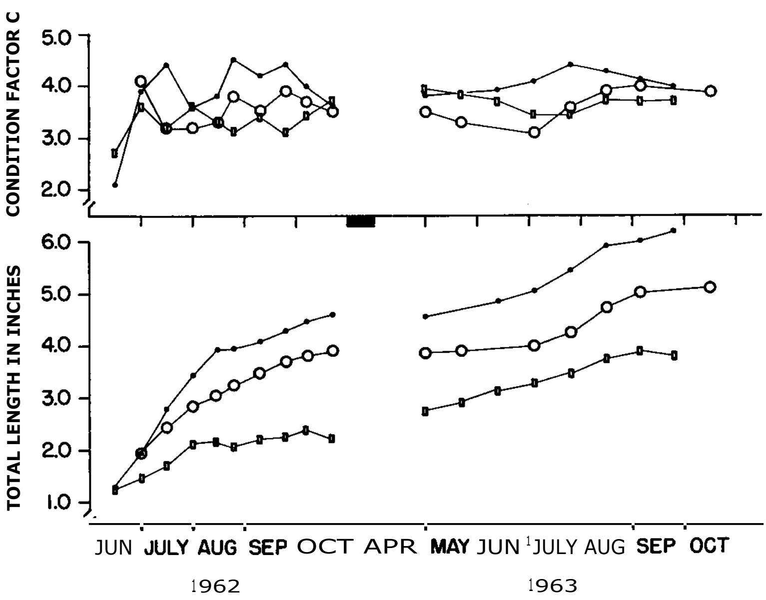

Fig. 7.—Growth and condition (C) of yellow perch of the 1962 year-class in the control pond Iota (rectangles), add-stock pond Theta (circles), and cropped pond Zeta (dots) during the 1962 and 1963 growing seasons.

trol pond, and the relationship of condition to growth was generally normal and consistent, with highest condition associated with fastest growth.

The next most dominant year-class through 1962 and 1963, both by weights and numbers, was that spawned in 1962. Fig. 7 shows that both condition and growth in the cropped population were again high, but that both growth and condition in the add-stock pond quite consistently exceeded that of the control pond. The explanation lies in the comparative abundance of the age class in the two populations. Spawning success was extremely poor in pond Theta in 1962, but exceptionally heavy in the control pond Iota. In June 1962, 2,380 Age 0 perch were transferred from Iota to Theta. The abundance in Iota was still such that an additional 14,664 fish of this age were thinned from Iota, mostly in 1962. By time of final census in October, 1963, this 1962 brood still numbered 3,079 in Iota, as compared to 2,861 in pond Theta, and only 230 in the cropped pond Zeta. In pond Theta the lesser number of this age class grew faster and maintained better condition, even though the number and total weight of older perch was much larger in this add-stock (Theta) than in the control (Iota) population. Thus, rate of growth was more dependent upon abundance of the year-class (intra-year-class, or size competition) than upon total standing crop, or total population pressure. This indicates a diversity of food habits by size, and that a group of one size can make fast growth in the presence of an abundance of larger, more slowly growing fish, the latter apparently offering little competition for food or other essentials of the environment.

Table 30 presents a comparison of the growth and condition of the various components of the Age I and Age III perch in the final census of pond Theta in relation to their origin or date of transfer. For both age groups final average lengths and weights were greater for perch of the original stock than for those perch moved to the add-stock pond in

Table 30.— Averages of total lengths, weights, and coefficients of condition of various components of Age I and Age III yellow perch in the final census of the add-stock pond Theta, 1963, in relation to their origin or date of transfer.

	Length, Inches	*Weight, Pounds*	*Coefficient of Condition*
Age I			
Original Stock	4.67	0.037	3.63
Transferred in 1962	4.54	0.034	3.63
Transferred in 1963	5.75	0.073	3.84
Age III			
Original Stock	5.07	0.046	3.53
Transferred in 1961	4.89	0.040	3.42
Transferred in 1962	6.94	0.130	3.89
Transferred in 1963	7.73	0.200	4.33

the first year in which each was transferred (1962 for Age I perch, 1961 for Age III perch). We know that in all cases fish transferred from the cropped to the add-stock population were of larger average size at time of transfer than perch of the same age among the original stock in the add-stock population. Since transferred fish received no harsher treatment than fish of the original stock which were sampled, weighed, marked, and returned to the add-stock population, the retardation of growth would have been due more to stresses encountered in the new environment than to handling. Progressively greater average sizes of perch transferred at later dates reflects the growth advantage obtained bef ore transfer from the cropped population. Comparative data on condition are generally consistent, with fish transferred latest having the highest coefficients of condition.

Mortalities

In 1960 we were able to compute total mortality of perch older than Age **O** in pond Alpha. From an original stock of 2,017 "older" fish, 1,089 were removed by cropping and 764 were recovered in the final census, leaving an unaccounted for loss of 164, or about 8.1 percent of the original stock.

In 1960 we also attempted to obtain rates of seasonal mortalities, along with rates of seasonal growth. From April through September a number of perch of Ages I and II were caught and released with a distinctive mark for each month. As in earlier, similar experiments with smallmouth and largemouth bass, the data provided little useful information on rates of seasonal mortality and emphasized the difficulties of such an experiment. For example, lowest mortalities were among fish marked in June, and mortalities for fish marked in July and August were much higher than for those marked in June and little different from mortalities of those marked in April (Table 29).

From marks given to various year-classes, and to fish transferred to pond Theta, we have information on mortalities of many components of the populations from ponds Zeta, Theta, and Iota. Our most complete information is from pond Theta, which received additions of stock. Among the 141 Age **O** fish recovered in the final census, 126 were survivors of the 408 transferred from pond Zeta in July and August, 1963 (69.1 percent mortality) and only 15 were survivors from the 1963 brood spawned in this pond. These returns indicate a rather heavy predation of young by older perch.

Recoveries in the draining censuses and computed mortalities for various categories of perch are presented in Table 31 for the control pond Iota, in Table 32 for the cropped pond Zeta, and in Table 33 for the add-stock pond Theta. Mortalities were generally quite irregular and not clearly density-related, *i.e.*, not notably or consistently higher **in** the add-stock population than in the cropped or control populations. This indicates that density probably was not a critical factor among our populations. However, mortalities were higher among fish transferred to a new population than among members of the original stock already resident in that population. For example, for three groups of perch, all of the 1960 brood, mortalities by October 1963 were 96.1 percent among 462 perch transferred in 1962 and 85.1 percent among 1,309 transferred in 1961, while mortality of original stock over the 3-year period was only 74.4 percent (Table 33). While fish densities did not appear to be critically high, transferred fish encountered stress in the new environment which increased their mortality. As mentioned before, the act of marking and transfer was not in itself cause for greater mortality because untransferred fish were also marked and handled.

Table 31. — Mortalities of various categories of yellow perch in the 1961 and 1963 October draining censuses of the control pond Iota, approximately 11 months and 24 months after stocking.

Year Class or Classes	*Recovery in Oct., 1961 of Fish Stocked in Nov., 1960*	*Recovery in Oct., 1963 of Fish Stocked in Oct., 1961*	*Number Removed by Other Than Natural Mortality*	*Percent Unaccounted for: Natural Mortality*
1960	2,210 of 3,771		140	39.1
1958-59	66 of 225		70	57.4
1960		372 of 1,000	30	61.6
1958-59		19 of 65	0	70.8

Table 32. — Mortalities of original stock of yellow perch in the October, 1963 draining census of the cropped pond Zeta.

Year Class or Classes	*Recovery of Fish Stocked in Nov., 1960*	*Number Removed by Other Than Natural Mortality*	*Percent Unaccounted for: Natural Mortality*
1960	30 of 3,771	2,877[a]	96.6
1958-59	3 of 225	216[b]	33.3

[a] Removed 1,704 in 1961, 1,088 in 1962, and 85 in 1963.
[b] Removed 213 in 1961, 0 in 1962, and 3 in 1963.

Table 33.— Mortalities of various categories of yellow perch in the October, 1963 draining census of the add-stock pond Theta.

Year Class or Classes	*Origin, or Number Orginally Stocked in Nov., 1960*	*Recovery in Oct., 1963 of Original Stock, or of Fish Marked and Transferred to Theta in Year Indicated*	*Number Removed by Other Than Natural Mortality*	*Percent Unaccounted for: Natural Mortality*
1963	Transf. from Zeta	126 of 408 (1963)		69.1
1962		299 of 385 (1962)		22.3
1960	"	58 of 83 (1963)		30.1
1960		18 of 462 (1962)	4	96.1
1960		194 of 1,309 (1961)	8	85.1
1960	3,771	728 of 3,771 (O.S.)[a]	926[b]	74.4
1958-59	Transf. from Zeta	3 of 3 (1963)		0.0
1958-59	225	10 of 225 (O.S.)[a]		95.6
1958-59	Transf. from Zeta	1 of 155 (1961)	50	99.0

[a] Indicates original stocking of November, 1960.
[b] Total of 926 includes 62 cropped in 1961, 855 in April, 1962, and 9 in May, 1963.

Spawning Success

Variations in spawning success and in year-class strengths were large and of particular interest in the perch populations. Adequate breeding stock was present in the form of Age III perch in all ponds in 1961, but all three populations failed to either spawn or produce a surviving year-class in this first spawning season in the Unit 2 ponds. In the control pond Iota a strong year-class was produced in 1962, having 3,079 survivors in the fall of 1963, and this was followed by an extremely light year-class in 1963, of which none survived to the end of that year.

Theta, the add-stock pond, produced no surviving young in 1961, and there was extremely light reproduction (or survival) in both 1962 and 1963.

Zeta, the cropped pond, after its 1961 failure, produced a large year-class in 1962. However, this class was drastically thinned by mortality of unknown origin. Over a 2-week period in early June, 1962, the 1-to 2-inch fingerlings could be seen at the surface periodically immobile and "belly-up" for a few seconds, from which they would suddenly recover as if under some sudden stimulation and swim rapidly away, only to repeat the process a few minutes later. While no mortalities were observed at the time, subsequent sampling revealed a greatly reduced population of the Age O fish. Only 230 survived until October, 1963. Fish older than Age 0 apparently were unaffected. The heavy 1962 spawn was followed by a weak brood in 1963, of which only 752 were recovered in October of that year.

A normal spawn was anticipated in 1961 because both ripe and spent females were observed, and developing eggs were found on wire traps. When the failures became apparent we speculated that the cause may have been due to the absence of submerged vegetation in ponds Zeta, Theta, and Iota, and that successful spawning in Alpha may have been facilitated by an abundance of Chara. Starrett & Fritz (1965) attributed poor spawning success of yellow perch in Lake Chatauqua to the lack of submerged vegetation. Though moderately thick growths of pondweeds (*Potamogeton* spp.) developed in the summer months in our ponds, none were present during the spawning period. As a spawning aid in 1962 and 1963 multibranched tree limbs were placed in the ponds. Eggs were deposited upon the limbs in both years, and eggs transferred from the limbs to the laboratory made normal development. Reproduction was heavy in Zeta and Iota in 1962, and light in Zeta and Theta in 1963, but no young were recovered from Iota in 1963. Obviously, some additional factor was limiting.

Our data indicated that high pH was not a limiting factor in the reproduction of perch, and that water quality was otherwise satisfactory. We suspect that under conditions of normal water quality, failures of reproduction are due less to failure of the adults to produce normal eggs and young than to a failure of the young to survive. Fluctuations in year-class strength are common to perch populations (Herman *et al.* 1959), as to most fish species. In the present instance we believe the most probable cause was predation on eggs or young. Failures occurred when either weight or numbers of companion perch (principally Age I) were large, and successes occurred when they were small (Table 27). Though the populations were not large by normal standards, they occurred in the absence of protective cover for young. Abundant spawns in pond Alpha could have been facilitated by the protective cover provided by the beds of Chara, but no such protection existed in the ponds in Unit 2. Predation of eggs or larvae by large populations of crayfish and tadpoles may have augmented that by perch. Both forms were of unusual abundance in 1962 and 1963 because of the absence of bass or other large predators.

Related Environmental Factors

Although quantitative data are limited, some observations can be made of such related ecological factors as abundance of associated plants and animals, and of the physical and chemical characteristics of the pond waters. Of particular note were the unusual abundances of tadpoles and crayfish, presumably because of the absence of bass or other more efficient predators. Table 34 presents weights of these forms, together with weights of perch collected during the final censuses. As indicated in the table footnote, poundages of crayfish were conservative, because many failed to be flushed from the pond with the water and were not available for weighing. Poundages presented, however, are believed quite representative of differences in weights which occurred.

Tadpoles were primarily those of the bullfrog, *Rana catx.sbeiana,* crayfish were identified as *Arconectes virilis.* There are several noteworthy associations in Table 34.

1. The largest poundages of perch were associated with the smallest poundages of crayfish, and vice versa, indicating some degree of control of crayfish by perch.
2. Tadpoles were abundant when crayfish were scarce, and vice versa, indicating some degree of control of tadpoles by crayfish.
3. At the time of the three 1963 drainages, weeds (principally *Anacharis* sp.) covered an estimated 90 percent of the bottom of pond Theta, which had the fewest crayfish, while the bottom was almost completely bare of weeds in pond Zeta with its comparatively great weight (231.2 pounds) of crayfish. Neither weeds nor crayfish were abundant at the two drainages of pond Iota. Actually, weeds in all three ponds had been quite drastically thinned by treatments with endothal in June, 1963, but the weeds had again become abundant where the crayfish were less abundant and had become increasingly scarce where the crayfish were most abundant.

Nymphs of the large burrowing mayfly, *Hexagenia limbata,* were abundant in ponds Iota and Zeta, but were absent from pond Theta at the time of drainage in October, 1963. At the time, the bottom of pond Theta contained thousands of small "craters" from 1 to 3 inches in diameter, and from 1 to 1½ inches deep, often with subsurface cavities larger than the openings. Since these craters were not present in the companion ponds having abundant burrowers, it suggests that the larger population of perch in Theta may have eliminated the mayflies by burrowing or sucking them out of the mud. Concurrently, however, scuds, phantom larvae, smaller mayflies, dragonflies, and assorted other

Table 34.—Standing crops of yellow perch, crayfish, and tadpoles, and relative abundances of rooted, submerged aquatic plants in ponds Zeta, Theta, and Iota at times of fall draining censuses.

Pond and Year	*Standing Crop, Pounds Per Acre*			*Relative Abundances of Aquatic Plants*
	Yellow Perch	Crayfish a	Tadpole	
Iota, 1961	94.7	27.7	297.4	Medium
Iota, 1963	100.3	84.3	312.1	Medium
Theta, 1963	183.7	34.1	247.5	High
Zeta, 1963	51.3	231.2	84.3	Low

Weights of crayfish are conservative because some did not flush out of pond.

invertebrates were of the same general abundance in Theta as in the companion ponds, suggesting no inordinate predation pressure on these forms.

Throughout most of each of the three growing seasons weekly observations were made of the surface pH, Secchi disc transparency, and the temperature profile of each pond. Because of differences in treatments of the populations, no interpretations can be made of the influence of these factors upon fish production. However, the data warrant the following observations.

Of the three years, thermal stratification was greatest, and transparency lowest in all ponds in 1963. The decrease in average transparency was negligible in the add-stock pond, but quite marked in the companion ponds, particularly the cropped pond Zeta (from 72 inches in 1961 to 20 inches in 1963). One therefore suspects that decrease in transparency was related to increase in the crayfish population, which was notably high in pond Zeta. Increase in thermal stratification was in turn probably related to decrease in transparency of the pond water.

Differences in pH were not believed to have had any important influence on fish production. Generally lower pH's in 1963 were probably related to the reduction of weeds by chemical treatment in all ponds in June, 1963. A lesser average pH in pond Zeta was probably related to the influence of crayfish in reducing vegetation in that pond.

Review of Perch Data, and Comparison with Largemouth and Smallmouth Data

Perch were maintained in ponds previously occupied by either smallmouth or largemouth bass. In Unit 2 ponds the maximum standing crop obtained from a control population of largemouths was about 50 pounds per acre, while that for a population of perch receiving the same treatment was about 100 pounds. The largest standing crop obtained from an add-stock population of largemouths in this unit was about 72 pounds, while that from the add-stock population of perch was about 184 pounds.

We have already noted that in pond Alpha the standing crop of perch in 1959 more than doubled, and that of 1960 approximately tripled, the standing crop of smallmouths earlier produced in this pond. We believe, however, that the differences in efficiencies in food utilization or conversion were less than indicated. Smallmouth bass probably did not attain their potential maximum in pond Alpha because of the relative immaturity of the pond when occupied by smallmouths, and because the population had developed over only one and one-half growing seasons and contained only two year-classes when censused.

Perch are believed to be more dependent upon an invertebrate diet than either of the basses, and their greater efficiency is probably related to their lower trophic level. However, in our data the yellow perch of intermediate size and age appeared to be less efficient in utilizing invertebrate foods than were smallmouth bass of the same category. The largest standing crops of perch were those having the largest numbers of young-of-the-year, and where young were scarce, older fish seemed incapable of taking up the slack or of making efficient use of the food that would have been eaten by the young-of-the-year. On the other hand, our largest standing crops of smallmouth bass were those dominated by fish older than Age 0, and production in these populations seemed very little inhibited by an absence or scarcity of young-of-the-year smallmouths. It may therefore be that in the absence of vertebrate food the smallmouth is a more efficient insectivore than the yellow perch.

Data from the add-stock population in Unit 2 indicate that the perch may be less versatile or adaptable in its food habits, and that there may be relatively less competition for food between different sizes and ages of perch than between different sizes and ages of smallmouths. We have seen, for example, that in the 1963 census of pond Theta, 2,861 perch of the 1962 brood had an average length only about 0.4 inches less than that of 728 perch of the 1960 brood. While the younger perch had grown almost 5 inches in 2 years, the older perch had grown less than 1 inch over the same period. Thus the younger, more abundant, faster-growing perch obviously utilized foods not taken by the older fish, which permitted them to literally grow into the size range of the older perch.

BLUEGILLS

Bluegills were studied in ponds Kappa, Lambda, and Rho (Unit 3) over a 3-year period, 1961-1963. This unit of ponds had been constructed in 1957, and for the period 1958-1960 was stocked with white crappies. Following the final census of crappies in October, 1960, each pond was stocked with 4,080 Age 0 bluegills from the state hatchery at Spring Grove, Illinois. Over the period May 11—June 23, 1961, each pond received an additional stock of 104 adult bluegills obtained by boat shocker from Fox Lake, Lake County, Illinois. The combined total weights of young and adults stocked in each pond were similar, ranging from 34 to 38.3 pounds (Table 35).

Standing Crop Data

Table 35 presents standing crop data for four bluegill populations together with such pertinent supplementary data as pounds of original stock, pounds added to or removed from the populations during the course of the experiments, and the net gain or loss in pounds of fish flesh by the termination of the experiments. Table 36 presents numbers in each size or age group and percentages of total numbers and weights of each group recovered in each

			Year of Census	*Number of Growing Seasons*	*Pounds of Original Stock*	*Standing Crop, Pounds Per Acre*	*Pounds Added*	*Pounds Removed*	*Pounds Lost or Gained*
3	Rho	Control	1961		3 .0		0.0	co	+ 96.8
3	Rho	Control	1963	2	38.5		0.0	7.5	+ 78.8
3	Kappa	Add-stock	963	co	3 .0	3	30.8	7.9	+ 93.4
3	Lambda	Cropped	1963	co	38.3		0.0	1 1.3	+204.0

Pond, Year of Census, Treatment[a]	*Total Number Censused in Each Age Group*					*Percent of Total Number Censused in Each Age Group*					*Percent of Total Weight Censused in Each Age Group*					*T ' ou s*	
	0					0	I									Number	Pounds
R 1961 0	•• 2	2.	45	0	0	97.1	2.9	*	0.0	0.0	41.8	49.1	9.0	0.0	0.0	77,698	127.1
R 1963 0	6 53	2	346	68	3	98.8	*	0.5	0.6	*	12.1	*	24.9	53.0	10.0	68,300	99.8
K 1963 +	98,7 8	0	9?3	62	3	97.4	0.0	1.9	0.6	*	17.3	0.0	48.8	26.7	7.3	101,431	173.3
L 1963 —	8,644	0	38	10	0	85.7	0.0	14.2	*	0.0	28.5	0.0	69.2	2.2	0.0	10,092	101.0

draining census. Small poundages were removed from both control and add-stock ponds in all years, primarily for study purposes. The total of 141.3 pounds shown removed (Table 35) from the cropped pond Lambda is a minimum figure. Of this total 16.9 pounds of mixed Age I and adults were cropped in 1961, of which 15.5 pounds were transferred to pond Kappa. Known cropping from Lambda in 1962 consisted of mixed Age I (37.4 pounds), Age II (17.3 pounds), and original adults (17.5 pounds) for a total of 72.2 pounds. However, a significant part of this cropping was achieved on May 31, 1962 by spraying rotenone over a 30- to 40-foot width of approximately one-half of the shoreline. We hoped to achieve an early-season kill of a large proportion of the abundant Age I fish. A 3-day pickup of all visible dead included 4,616 bluegills (12 adults, 115 Age II, 4,489 Age I) weighing 15.9 pounds, which are included in the total of pounds removed (Table 35). Many fish (particularly Age I) were observed to sink to the bottom and be attacked by an abundant crayfish population, and were thus lost from the records. This unknown weight is believed to have been something less than that recovered and recorded from the treatment. Thus, the true pounds cropped, and pounds gained, were in excess of those totals listed in Table 35.

In 1963 a total of 52.1 pounds was cropped from pond Lambda including 10,954 young-of-the-year weighing 16.9 pounds, removed in August, and 719 Age II fish weighing 35.2 pounds, removed in June, July, and August. Of this total, 626 Age II fish weighing 30.7 pounds were transferred to pond Kappa.

Standing crops of bluegills in pounds per acre ranged from 99.8 in the control pond Rho in 1963 to 173.3 in the add-stock pond Kappa in the same year. As in our previous experiments, variations in production by the separate populations were influenced by differences in 1) treatments received, 2) population compositions, and 3) pond fertilities; however, the relative importance of each factor was difficult to assess. We may first note that standing crops (pounds) were highest where numbers of both Age 0 and older bluegills were largest (Table 36). There is evidence, however, that the add-stock pond had the additional advantages of greater fertility and a larger carrying capacity. It seems significant that even with the much larger standing crop in the add-stock pond, its pounds gained figure was also greater than in the control population (Table 35). Thus, pond Kappa made a substantial production of fish flesh in addition to that transferred from the cropped pond. This suggests that the additions to pond Kappa had not exceeded the pond's carrying capacity. Since the numbers of both small and large fishes contained in pond Rho appeared sufficient to utilize available food resources, we must suspect that the carrying capacity of pond Rho was much smaller than that of pond Kappa in 1963.

We have evidence that the carrying capacity of the control pond Rho declined quite substantially between 1961 and 1963. Table 35 shows that in this pond both final standing crop and pounds gained figures were substantially higher in 1961 than in 1963. We may note (Tables 35 and 36) that final population structures were comparable, having similar abundances of both small and large bluegills, that original stocks were similar, and that differences in pounds removed were not significant. We thus have evidence that the carrying capacity of pond Rho had been attained in its first growing season (1961), that a greater weight of fish was produced in the first than in either of the two following seasons, and that the productivity of this pond declined quite substantially between 1961 and 1963 in spite of moderate fertilization in 1962. It also seems significant that final standing crops of both crayfish and tadpoles were also higher in Rho in 1961 than in 1963. Pounds of crayfish in 1961 (173.2) were more than triple the amount of 1963 (55.6), and pounds of tadpoles in 1961 (113.9) more than doubled the standing crop (55.9) of 1963.

The final population in pond Rho in 1961 contained 75,424 young-of-the-year which comprised about 42 percent of the total weight of the standing crop. The 1963 census of Rho also contained abundant Age 0 fish (67,453), but these comprised only 12 percent of the total weight due to their smaller average size. This smaller size suggests that spawning in 1963 may have been later than in 1961, or that food for young was in shorter supply. With regard to date of spawning, our field notes indicate that spawning occurred in late June or early July in both years, with young of similar sizes first found in early July in both years. Our sampling provided no evidence of a second and larger spawn in late 1963. We believe that the young-of-the-year simply grew more slowly in 1963, in spite of their lesser abundance.

We have no comparative data on abundance of benthos or zooplankton in the two years. However, data on mean seasonal transparencies (Secchi disc) show that pond Rho maintained a richer bloom in 1963 than in 1961. Means of weekly readings from April through October were 19 inches in 1963 and 45 inches in 1961. Higher turbidity in 1963 than in 1961 was not caused by crayfish since the standing crop of crayfish in 1963 was only about one-third as great as that in 1961 when turbidities were lowest. These ponds received very little erosion silt, and never appeared muddy. Turbidities were due primarily to phytoplankton. The greater plankton turbidity in 1963 indicated a condition favorable to fish production in that year, a fact not borne out by the standing crop data. It seems apparent that the principal food utilized by the bluegills was not dependent upon phytoplankton abundance.

Mortalities were frequently high and quite variable, but were not believed to have had an important influence upon size of final standing crops. Dead fish were rarely seen, and no large or sudden "kills" were observed just prior to the censuses, or at any other time. The most probable effect of mortalities on the table data was in some instances an artificial depression of the pounds gained figure. For example, of the 626 Age II fish transferred to pond Kappa in 1963, only 102 were recovered in October of that year. A major portion of this mortality was probably due to handling, with a large proportion of the fish dying so soon as to have had a minimum impact upon the existing population. In our computations of pounds gained, however, the total weight of transferred fish was treated as though all had survived. Since this was a minus (subtracted) quantity in the calculations, the figure of pounds gained was artificially depressed, and production of fish flesh in the population was higher than indicated. This factor was probably more critical among bluegills than among other species studied because in our experience the bluegill was the most susceptible to injury or death due to marking and handling.

Effects of Cropping on Fish Production

Increased production gained by cropping was probably more clearly evident in the bluegill study than in those for other species. The key figures were those of pounds gained (Table 35). The figure of 204 pounds gained in pond Lambda was a minimum one due to unknown losses from the use of rotenone, yet it was more than twice that of either companion pond. It is significant that even with the cropping of 52.1 pounds from Lambda in 1963, its standing crop in October slightly exceeded that of the control pond Rho. It is also noteworthy that numbers in the final censuses were less than one-sixth as great in cropped Lambda as in the control population in pond Rho. A total of 10,954 young-of-the-year were cropped from Lambda in 1963, and the smaller number of 8,644 remaining in the final census represented 29 percent of the total weight of the population, while the much greater number of 67,453 Age 0 bluegills censused in pond Rho represented only 12 percent of the total weight censused in that pond. The fewer fish had grown much faster, indicating that total numbers are in themselves not an overriding factor. With no evidence of a greater inherent productivity in pond Lambda than in pond Rho, greater production of bluegill flesh in pond Lambda must have been stimulated by cropping.

Growth and Condition

Growths of bluegills in our single-species populations through their first 3 years of life were in most cases slower than for bluegills from normal, mixed populations in Illinois reservoirs with which they are compared (Table 37). Again, our growth data were from large samples of known-age fish as collected in the final censuses at the ends of the growing seasons. Failure of certain age classes in our cropped pond to show faster growth than in the companion ponds was due in some instances to differences in abundance. For example, the average length after three growing seasons was greater in the control pond Rho (4.9 inches) than in the cropped pond Lambda (4.3 inches) (Table 37), because the group in question (Age Group II, Table 36) numbered only 346 individuals in the final census in pond Rho, as compared to 1,438 in pond Lambda. At the same time, total lengths of 3-year-old fish were little different in the cropped and add-stock populations even though the add-stock pond contained the greater number of 3-year-old fish (1,973, as compared to 1,438) and total population pressure of fish older than Age 0 was much greater

Table 37. — Growth of bluegills in ponds used for carrying capacity experiments on the McGraw Foundation grounds, along with similar data on bluegills in other Illinois waters.

Group	*Pond*	*Year*	*Treatment*	*Average Length in Inches (at Ends of Numbered Growing Seasons) with Number of Fish Used to Establish the Average in Parentheses* 1st	2nd	3rd	4th
Unit 4	Rho	1961	Control	1.13 (200)	3.57 (358)	..	
Unit 4	Rho	1963	Control	0.75	2.78 (2)	4.90 (205)	5.62 (365)
Unit 4	Kappa	1963	Add-stock	0.85 (100)	..	4.22 (253)	4.95 (141)
Unit 4	Lambda	1963	Cropped	1.82 (257)	..	4.30 (338)	6.76 (10)
Other Illinois Waters		*Author*					
Johnson Sauk Trail Lake		Rock (1966)		2.0	4.2	6.2	7.3
Ramsey Lake		Stinauer (1966)		2.7	3.7	5.0	5.5
Red Hills Lake		Price (1966)		2.6	4.0	5.4	6.0
Lake Chautauqua		Starrett & Fritz (1965)		1.8	4.8	6.2	7.1
Ridge Lake		Bennett (1954)		4.7	6.2	7.1	7.6

Data presented for this population were taken from fish of the original stock or those spawned in the pond.

(2,653, as compared to 1,448) (Table 36). It seems clear that pond Kappa must have had a higher carrying capacity than pond Lambda, at least in 1963.

Additional growth data are contained in Fig. 8 and 9 which present growth and condition curves for the dominant year-classes - the 1960 year-class through 1961 and 1962 and the 1961 year-class through 1962 and 1963. Mean lengths and conditions were computed from the same samples. All samples were collected by seine, and were in most cases large, never averaging less than 43 per sampling period in any year, and often approximating 100. Ages were known by presence or absence of marks previously given. Effects of cropping on growth of the 1960 year-class in 1961 was little apparent until late season when the average size for this group was largest in the cropped pond, smallest in the add-stock pond, and intermediate in the control population (Fig. 8). The rather narrow differences remained consistent throughout 1962. The corresponding curves for rates of condition computed from the same samples conformed poorly with growth curves. While the growth curves climbed quite consistently and regularly upward, indicating small sampling variation, those for condition were quite erratic from period to period, most notably for bluegills in pond Rho between mid-June and Mid-July, 1962 (Fig. 8). Here our samples showed condition to drop from 7.9 in mid-June to 4.4 on July 1, and to improve sharply to a high of 8.3 on July 15. We suspect that these major variations may have been related to the spawning act. No surviving young could be found in ponds Kappa and Lambda in 1962, and the only survivors from the 1962 brood were two recovered from pond Rho in the census of 1963. Since the major loss in condition occurred precisely at the time spawning would have been expected, and occurred only in pond Rho, spawning may have been restricted to this population, as our other observations indicated. It is of further interest that lengths increased while rate of condition continued to decline in the pond Rho samples over the period from July 1 to mid-September, 1962. Since lengths

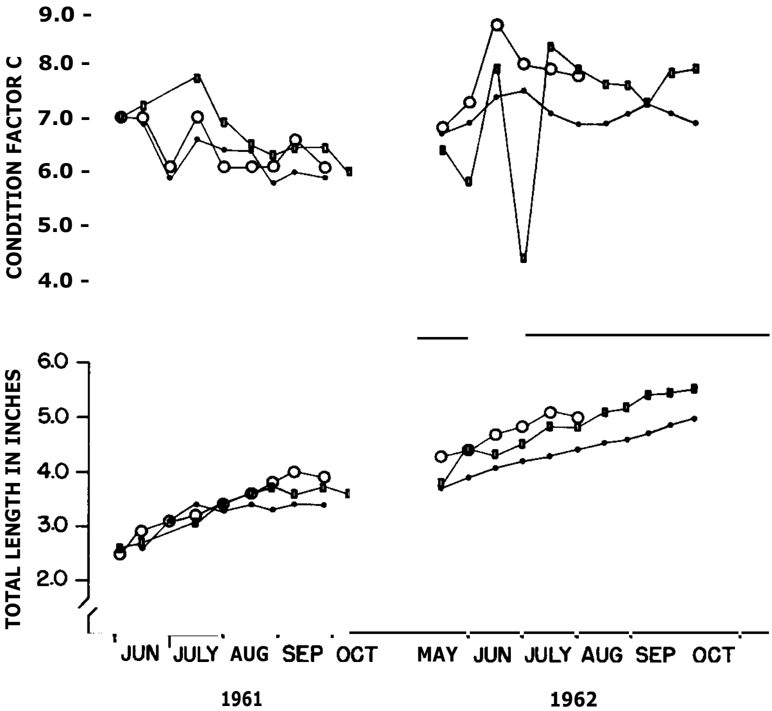

Fig. 8.—Growth and condition (C) of bluegills of the 1960 year-class in the control pond Rho (rectangles), add-stock pond Kappa (dots), and cropped pond Lambda (circles) during the 1961 and 1962 growing seasons.

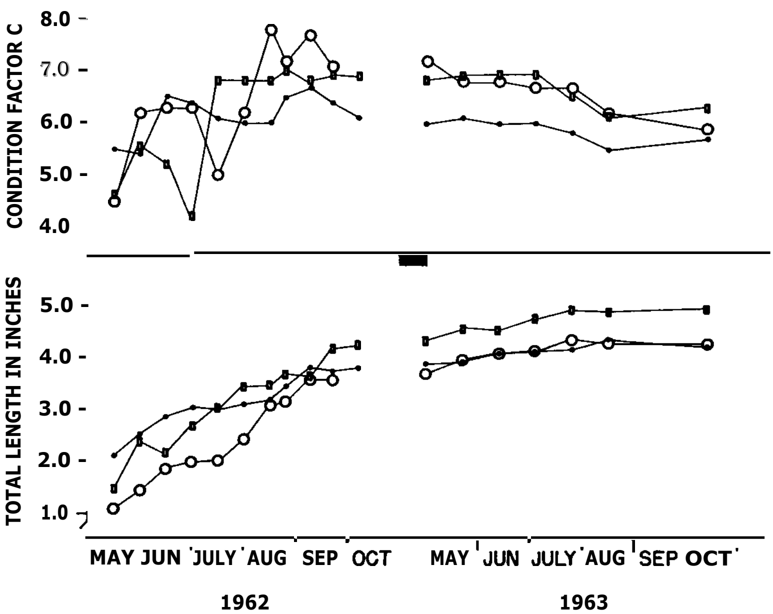

Fig. 9.—Growth and condition (C) of bluegills of the 1961 year-class in the control pond Rho (rectangles), add-stock pond Kappa (dots), and cropped pond Lambda (circles) during the 1962 and 1963 growing seasons.

showed a regular continuous trend, the source of variation was clearly in weights. A part of such variations could be attributed to differences in fullness of stomachs at times of measurement and a part to unusual sampling variation, but a principal source could have been a loss of weight by spawning females. It seems evident, however, that for a variety of possible reasons conditions can vary widely in fishes having similar patterns of linear growth, and that comparative rates of condition may be poor indicators of comparative rates of linear growth.

Fig. 9 presents similar data for the 1961 year-class in 1962 and 1963. Due to their greater numerical abundance, fish in the cropped pond grew the least in 1962, and their growth was little different from growth of those in the add-stock pond in 1963. However, growth curves climbed quite regularly and uniformly upward in all ponds before leveling off in August, 1963, indicating little sampling variability. Condition curves were again extremely irregular in 1962, but quite regular and comparatively stable throughout 1963. The difference in the two years may have been related to differences in feeding habits or in availabilities of food. When younger, in 1962, these fish may have been largely dependent upon zooplankton, with frequent, large fluctuations in condition corresponding to normal variations in the abundance of such food. When the fish were older and larger, in 1963, foods taken may have been more diversified, and of a more stable abundance, resulting in more stable rates of condition.

We have noted in Fig. 8 and 9 that comparative strengths of year-classes were reflected in rates of growth. We referred to comparative abundance of the same year-class in different ponds. It is of further interest to consider the influence of differing strengths of year-classes in the same pond. Dominant year-classes in our ponds derived from the original stock of 4,080 bluegills of the 1960 brood in each pond, and from the large broods spawned in all ponds in 1961. We should then remember that reproduction failed in all ponds in 1962. We may thus consider comparative growth of Age I fish in the presence or absence of the younger year-class. Based on our bimonthly sampling from April into October, Age I fish in all three ponds grew more in 1962 than 1961 (Fig. 8 and 9). The average length increment of the Age I fish in all three ponds in 1961 in the presence of abundant Age O fish was only 1.29 inches, compared to an average increment of 2.29 inches for Age I fish in 1962 in the absence of Age O fish. A large part of this difference was probably due to differences in degrees of competition between the two year-classes in the two years.

Mortalities

On the basis of returns of bluegills bearing distinctive fin clips given at the time of stocking or transfer we were able to compute mortalities for various age groups in the control pond Rho (Table 38) and the add-stock pond Kappa (Table 39). Mortalities for bluegills in the cropped pond Lambda could not be calculated because of the unknown loss occasioned by the use of rotenone in 1962.

Mortalities were frequently high, but quite erratic, and tended to be somewhat higher among those fish transferred to pond Kappa than for the original stock in either population. Highest mortality was among 626 Age II bluegills transferred to pond Kappa in June, July, and August, 1963. The recovery of only 102 in October represented a loss of 83.7 percent over a fraction of a growing season. These fish were handled in larger quantities than most groups sampled and/or transferred, and we believe that the longer period required for weighing, measuring, and marking these larger groups contributed to their higher

Table 38. — Mortalities of various categories of bluegills in the 1961 and 1963 October draining censuses of the control pond Rho, approximately 11 months and 24 months after stocking.

Year Class or Classes	*Recovery in Oct., 1961 of Fish Stocked in Oct., 1960, or May-June, 1961*	*Recovery in Oct., 1963 of Fish Restocked in Oct., 1961*	*Number Removed by Other Than Natural Mortality*	*Percent Unaccounted for: Natural Mortality*
1960	2,229 of 4,080		185	42.8
Unknown[a]	45 of 104			56.7
1961		346 of 10,756	6,343	92.2
1960		468 of 700	32	29.9
Unknown[a]		31 of 45	2	27.9

Designates the adults in the original stock for which ages were unknown.

Table 39. — Mortalities of various categories of bluegills in the October, 1963 draining census of the add-stock pond Kappa.

Year Class or Classes	*Origin or Number Originally Stocked*	*Recovery in Oct., 1963 of Original Stock, or of Fish Marked and Transferred to Kappa in Year Indicated*	*Numbers Removed by Other Than Natural Mortality*	*Percent Unaccounted for: Natural Mortality*
1961	Transf. from Lambda	102 of 626 (1963)	2	83.7
1960		36 of 87 (1962)	0	58.6
1960		74 of 374 (1961)	0	80.3
Unknown[a]		7 of 29 (1961)	0	75.9
Unknown[a]	. .	13 of 20 (1962)	0	35.0
Unknowns	104	33 of 104 (O.S.)[b]	1	68.0
1960	4,080	516 of 4,080 (O.S.)[b]	145	86.9

Designates original stock of adults for which ages are unknown.
[b] Designates original stock.

mortality. Bluegills transferred in smaller groups in earlier years had smaller mortalities over longer periods of time. For example, for 374 bluegills transferred at Age I in 1961, and for 29 original adults transferred at the same time, mortalities by October, 1963 were 80.3 percent and 75.9 percent respectively. Mortalities among the control population were generally lower, but tended to be highest among the smallest fishes. For 10,756 Age 0 bluegills restocked following the 1961 census the mortality by October, 1963 was 92.2 percent. For 700 Age I bluegills and 45 of the original breeding stock restocked at the same time, mortalities by October, 1963 were only 29.9 percent and 27.9 percent respectively.

In 1961 we attempted to measure rates of seasonal mortality from April through September in pond Rho. In samples in each of these months approximately 100 Age I fish were captured and released with distinctive fin clips for each month, and returns of each mark were counted in the final census. As shown in Table 40, only 52 of 100 marked in June were recovered in October, but recoveries for fish marked in other months were grouped within a range of only about 75-78 percent. Differences in mortalities of bluegills marked in April and September were less than 2 percent. The similarities in the returns may indicate that there was a rather uniform loss due to handling and marking and that mortalities due to

Table 40.— Numbers of bluegills marked by a distinctive fin clip and released in each month of the growing season in pond Rho in 1961, numbers recovered in the draining census of October, 1961, and percents of mortality.

Month of Marking	*Fin Clipped*[a]	*Number Released*	*Number Recovered*	*Percent Mortality*
April	R. P.	99	74	25.3
May	L. P.	99	77	22.2
June	S. D.	100	52	48.0
July	H. D.	102	80	21.6
Aug.	Anal	101	77	23.8
Sept.	Pelvic	100	77	23.0

[a] Abbreviations: R. P. = right pectoral, L. P. = left pectoral, S. D. = soft dorsal, H. D. = hard dorsal.

other causes were insignificant. We have seen, however, that mortalities among other groups of both marked and unmarked bluegills ranged both higher and lower than for fish marked for this experiment.

Spawning Success

All populations produced large broods in 1961 and 1963, but all suffered spawning failures in 1962. The failures may have been due to predation of their own eggs by an underfed, overcrowded population of bluegills, as observed by Swingle & Smith (1943), or possibly caused by lower water temperatures in 1962. Late morning surface water temperatures in our ponds ranged from the high 60's to the high 70's (Fahrenheit) throughout the summer, rarely attaining 80° F., and then for only brief periods. For example, our weekly records show that the highest temperatures recorded in pond Kappa were 81.9° F. in 1961, 78.8 in 1962 and 81.9 in 1963. Following each of these highs the next temperatures recorded had fallen to 75° F. or below. Swingle (1949) stated that in Alabama ponds no young bluegills are produced until the temperatures of the surface waters reach 80° F. or above. However, Snow *et al.* (1960) reported that bluegills have spawned as early as late May in Wisconsin in water temperatures of approximately 67° F.

Our breeding stock came from a series of large flowage lakes located about 20 miles north of our study ponds, and in which the bluegills commonly spawn in late May or early June. However, 1-acre ponds are subject to greater fluctuations of water temperatures with changes in air temperatures than such larger lakes. The peak spawning period for our bluegills was believed to occur in the last half of June, and we suspect that this lateness was due to frequent, rapid cooling of these small water volumes by the frequent periods of cool weather that are common to northern Illinois in the summer Lowest temperatures recorded in 1961 and 1963 from early June through July were 73.4 and 72.6° F. respectively. In 1962 a late morning temperature of 68.7° F. was recorded on July 16, with other June and July readings as low as 70° F. at mid-day. Since these temperatures were taken only once each week, we believe that interim, minimum temperatures probably fell into the middle 60's in all ponds at intervals in June and July, 1962. These frequent, sudden drops in temperature may have limited spawning in 1962.

Review and Discussion of Bluegill Data

We have four published listings of standing crops of bluegills when maintained as a single species (Table 15). These ranged in pounds per acre from 89.7 in a small Oregon pond to an estimate of 664 in an unfertilized 1.35-acre pond in Kentucky (Turner 1959). The highest standing crop reported in the Kentucky study for bluegills when in a mixed population was 547 pounds per acre. Both of these rather large poundages in Kentucky ponds were by estimates based on the return of marked fish when the pond was treated with rotenone. The highest bluegill poundage that we have seen recorded by Swingle (1950) was one containing 464.7 pounds per acre in a fertilized pond which also contained 49.4 pounds of largemouth bass. Bennett's (1954) highest recovery of bluegills per acre in his draining censuses of Ridge Lake was 193.3 pounds in 1947. Our highest standing crop of bluegills was 173.3 pounds per acre in the add-stock population in 1963, and the average of our four standing crops was 125.3. The comparative figures reveal the low fertility of our bluegill ponds.

Since the bluegill ponds were previously devoted to white crappies, we have some basis for comparing the relative efficiencies of the two species. In both instances Rho was the control pond, and fish were cropped from Lambda for transfer to Kappa. Tables 35 and 44 show that in all cases standing crops of bluegills exceeded those for white crappies. Maximums were 89.6 for crappies in the control pond Rho, and 173.3 for bluegills in the add-stock pond Kappa. A more legitimate comparison, however, might be that of the control ponds: 89.6 for crappies and 127.1 for bluegills. Greater productivity for the bluegill might be expected due to its greater fecundity and lower trophic level. It seems possible that the true differences may have been greater than indicated. There is strong evidence that the productivity of pond Rho declined over the period 1961-1963. If an equal decline occurred over the period 1958-1961, the differences in efficiencies of the two species would have been greater than indicated.

BROWN BULLHEADS

According to Forbes and Richardson (1920), the brown bullhead had an early but rather brief popularity as a commercial species in European ponds. Swingle (1957) developed procedures for its culture in Alabama ponds, but in later studies found the channel catfish to be more efficient and less subject to disease. Cross (1967) noted that the brown bullhead was propagated and distributed for use in ponds in Kansas in the 1950's but that the introduction was not a success. The species has apparently found small favor, and seems to have been very little studied. Brown bullheads were used in the present study because thriving populations of these fish of desirable size in post-glacial lakes near our study area indicated that they might have some value for sport fishing.

Ponds Phi, Chi, and Psi (Unit 5) were completed in the fall of 1960 and first filled with water in the early spring of 1961. Between May 11 and June 23, 1961, each pond was stocked with 28 adults obtained by boat shocker from Fox Lake, in Lake County, Illinois. Weights stocked in each pond were similar, ranging from about 19 to 21 pounds. The control pond Psi was drained and censused at the end of the first and third growing seasons, and the companion ponds only at the end of the third. Although several interim estimates were made by conventional estimating procedures, some were so strongly in error that none have been used as standing crop data.

No fish were cropped in 1961, and when drained in October the control pond showed a "pounds gained" of 21.2 pounds and a final standing crop of 40.6 pounds. The pond was restocked with 19 adults and 7,882 young-of-the-year having a combined total weight of 33.5 pounds. In 1962 the cropped pond Phi was harvested of 61.9 pounds, of which 33.5 were transferred to pond

Chi. In addition, both ponds Chi and Psi were cropped in 1962 to thin what were believed to be excessive numbers of small bullheads. From pond Psi, 1,670 Age I fish (12.7 pounds) were removed in May and June, and 562 Age O (3.5 pounds) were removed in July and August. From pond Chi, 3,031 Age I fish (16 pounds) were removed in May and June, and 2,458 Age 0 (9.6 pounds) were removed in July and August. The only additional cropping was 35.4 pounds removed from the cropped pond Phi in 1963, of which 33 pounds were transferred to the add-stock pond Chi. As in adjacent Units 3 and 4, this unit was lightly fertilized in 1962 (Table 2).

Standing Crop Data

Table 41 presents the standing crop totals for four populations of brown bullheads, together with pounds of original stock, pounds gained, and other pertinent supplementary data. Table 42 presents the numbers in each age group and the percents of total numbers and weights of each group recovered in each draining census.

The cropped pond Phi had the smallest standing crop (16 pounds), but the highest pounds gained figure (91.9); the add-stock pond had the largest standing crop (90.2) and the lowest figure for pounds gained (29.8); the control pond ranked intermediate in both respects. Data from the control pond Psi indicates that this pond had a carrying capacity of between 40 and 50 pounds per acre. We may note that its final standing crop was 40.6 pounds when consisting of only two age groups in 1961, but increased to only 49.3 pounds when having the full complement of four age groups 2 years later (1963). At the same time, however, the final standing crop of the add-stock pond was almost twice that of the control pond, and the fact that a substantial weight of fish flesh was produced in

			Year of Census	*Number of Growing Seasons*	*Pounds of Original Stock*	*Standing Crop, Pounds Per Acre*	*Pounds Added*	*Pounds Removed*	*Pounds Lost or Gained*
	P	Control	961		9 '	0.6		0.0	+21.2
	Ps	Control	963		3	9.3		18.0	+32.1
5	C ſ	Add-stock	oc8		9.'	0.2		25.6	+29.8
	P	Cropped	9c8		2 .4	6.		97.3	+91.9

Pond, Year of Census, Treatment	Total Number Censused in Each Age Group			Percent of Total Number Censused in Each Age Group				Percent of Total Weight Censused in Each Age Group				T e	
		I				A						Number	Pounds
P 961 0	·	0	0	99.8	•		0.2	3 9	0.0	0.0	6.	56˙	40.˙
P 1963 0	4,	23	325	+.4		32.	0.6	5	6	84.6		94	4 3
1963 +	9	6	47	7.8		2	0.6	5.	5	80		316	90.2
P 963 —	6		29	7	0.	2.6	0.6	3.	0.6	3	8.8	101	0

[a] Pond treatments are designated as: o• • • de •n • in •

1963, in spite of the addition of stock, indicates that the pond's carrying capacity had not been exceeded. The principal gains were made by bullheads of Ages 0 and I, most of which had been spawned in the pond, while practically no growth was made by fish of Age II and older which were the primary ages transferred into this population. Thus the limiting level of competition created among the larger and older fishes (Ages II and above) had little apparent influence upon the younger and smaller fishes. Average growth of Age 0 bullheads in 1963 was in fact substantially larger in the add-stock than in either companion pond, due, presumably to a lesser abundance than in the companion ponds (Table 42). The add-stock pond was probably somewhat more fertile than either companion pond, but we believe that the combination of greater total numbers and a more optimum distribution of sizes of bullheads contributed substantially to its larger standing crop.

Growth and Condition

Table 43 shows growth of brown bullheads of known age in our ponds as determined by actual measurements at the times of the fall draining censuses. Growth of bullheads in general, and brown bullheads in particular, seems to have been very little studied. Our growths were quite similar to those few records available for this species from New York and Illinois, as summarized by Carlander (1950). Our brown bullheads had growths similar to the black bullheads in Clear Lake, Iowa (Forney 1955), but grew more slowly than black bullheads in Oklahoma waters (Houser & Collins 1962).

Rate of growth was closely related to abundance. For example, first year growth in the cropped population in 1963 was less than in the add-stock pond because, in spite of cropping, the group numbered 1,065 in the final census in the cropped pond as compared to only 497 in the add-stock population.

Table 43. — Growth of brown bullheads in ponds used for carrying capacity experiments on the McGraw Foundation grounds.

Group	*Pond*	*Year*	*Treatment*	*Average Length in Inches (at Ends of Numbered Growing Seasons) with Number Censused in Parentheses*		
				1st	2nd	3rd
Unit 5	Psi	1961	Control	1.8 (10,547)	. .	
Unit 5	Psi	1963	Control	2.2 (640)	4.5 (23)	6.8 (325)
Unit 5	Chi	1963	Add-stock	2.6 (497)	4.6 (163)	6.2 (647)
Unit 5	Phi	1963	Cropped	2.2 (1,065)	5.5 (1)	7.7 (29)

The dominant class by weight (Table 42), and that which best reflected treatments in both 1962 and 1963 was the class spawned in 1961. Fig. 10 presents seasonal changes in average length, average weight, and condition for this dominant brood over the 1962 and 1963 growing seasons. Values for the cropped pond tended to rank high, and those for the add-stock pond low. Rates of condition declined in all ponds throughout 1963, and the decline was approximately as great in the cropped as in either companion population in spite of its much greater gains in both length and weight. Average seasonal length increments for the 1961 brood in inches were 1.64 in the cropped population, 0.95 in the add-stock, and 0.41 in the control population. Weight increments averaged 0.08 pounds in the cropped pond, as compared to 0.022 in the add-stock pond. Somewhat surprisingly, in the control pond Psi, average weight of individuals in this brood was less at the end than at the start of the growing season, in spite of an average length increment of 0.41 inches. In our sample of May 1, 1963, 100 Age II fish had an average length of 6.36 inches and an average weight of 0.131 pounds. In our fall census in late September, 1963, a sample of 182 bullheads of this brood had an average length of 6.77 inches and an average weight of 0.127 pounds. The loss in weight was reflected in the decline of average condition from 5.1 in April-May to 4.1 in October.

The rather sharp increase in condition in early 1962 (Fig. 10) is explained by the fact that for a short time in the spring we used a supplemental feed as bait in an attempt to concentrate the fish and expedite seining. While not notably successful for this purpose, it caused a temporary increase in condition.

The curves in Fig. 10 show that average lengths, weights, and condition of the 1961 brood were higher in all populations in the first spring sample of 1963 than they had been in the fall of 1962, and that condition was at a peak in the early spring and declined steadily throughout the following summer. These data show that surprisingly large percentages of total annual growth were made between the fall and spring samples. Mean lengths and weights for our fall samples of the 1961 brood were based on fish collected between September 30 and October 13 from ponds Chi and Psi and between October 14 and 27 from pond Phi. Mean weights for the first sample of 1963 were from samples collected between April 21 and May 11 from all ponds. The samples showed that for pond Phi 17 percent of the length and 31 percent of the weight increments made in 1963 (between October, 1962 and October, 1963) occurred prior to our first spring sampling period of 1963. Corresponding figures were 29 and 53 percent for pond Chi, 24 and 100 percent for pond Psi. While a part of the increase in weight could have been

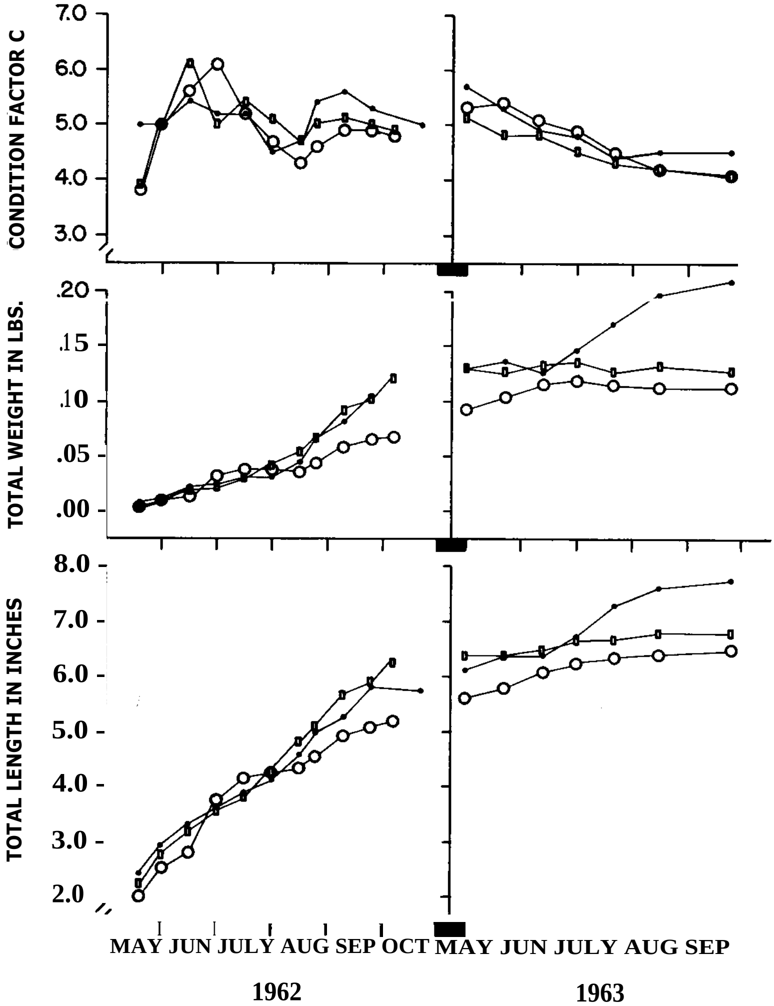

Fig. 10.—Length and weight increments and condition (C) of the 1961 year-class of brown bullheads in the control pond Psi (rectangles), add-stock pond Chi (circles), and cropped pond Phi (dots) during the 1962 and 1963 growing seasons.

due to gonadal development, lengths would not have been so affected.

Such overwinter growth was observed only among bullheads in our studies, and may be peculiar to this species. The fact that the bullheads had increased their lengths and weights, and were at their seasonal peak of condition in early spring suggests that they had found abundant food over much of the fall-to-spring period. Such a period of feeding and growth could conform with the seasonal fluctuation in abundance of some benthic fauna. As has been previously observed (Ball & Hayne 1952; Eggleton 1931; and others) invertebrate abundance (primarily midge larvae) typically increases in the fall to a mid-winter peak, and is followed by a continuous decline throughout the spring and summer and again increases in the fall. Exploitation of such a fall-to-spring abundance of invertebrate food could explain the pattern of growth by our bullheads. The spring-to-fall decline of the invertebrate population, coupled with increased competition from an abundant new year-class of bullheads, could explain the summer decline in growth and condition. It further implies small utilization or preference for the abundant crayfish, and little cannibalism by the larger and older bullheads.

Crayfish were abundant throughout 1962 and in the spring of 1963, and standing crops in pounds per acre in October, 1963 were 5.2, 6.2, and 38.8 in Phi, Chi, and Psi respectively. We had expected that the larger bullheads would make efficient gains on these abundant crayfish, a n d excretions by sampled fish indicated that the crayfish were commonly eaten. However, the fact that average size and condition of the original adult breeders actually declined over the 3-year course of the experiment indicates that crayfish were not heavily eaten, or were of little food value. It further suggests that competition for food among adults and Age II fish in 1963 may have been severe.

Mortalities

As in our previous presentations, mortality data are restricted to those groups for which both original and final numbers were exactly known. For bullheads we have data from only two year-classes — that of the original stock of 28 adults, and the 1961 brood, which was the only additional group present at drainage of the control pond in 1961 and the only group from which transfers were made. Because of their paucity, these data were not tabled but are presented here in the text.

Of the original 28 adults in the cropped pond Phi, 2 were removed in 1963 and 6 were recovered in the final census, representing a reduction of 20 individuals over the 3-year period, with a mortality rate of about 77 percent. Of the 28 adults stocked in the control pond Psi in May-June, 1961, 20 were recovered the following October, for a mortality rate of about 29 percent. For the 19 individuals restocked, mortality over the following two growing seasons was about 53 percent. Mortality was about 68 percent for 28 adults in the add-stock population over the full 3-year period, and 100 percent for the two adults transferred to this pond on August 13, 1963.

Mortalities among three groups of the 1961 brood by October, 1963 ranged from 6.5 percent for 200 bullheads transferred to pond Chi over the summer of 1963 to 94.8 percent for the 7,882 returned to the control pond Psi following the 1961 census. Mortality among 616 fish of this brood transferred in 1962 was 63.6 percent by October, 1963. The large mortalities recorded for the 1961 brood occurred during their second and third years when the fish ranged from 2 to 7 inches in total lengths. The absence of large cannibals among the 1961 brood, and the negligible growth and poor condition of the adult bullheads, indicate that cannibalism was not a major source of mortality. Since no large die-offs were observed, and sampled bullheads appeared to be healthy and vigorous at all times, the large mortalities among the 1961 brood appear to have been due to natural causes.

Spawning Success

New broods were produced in all ponds in all years, and reproduction was probably restricted to survivors of the original stock of adults. Table 42 shows that 10,547 Age 0 bullheads were recovered in the control pond in October, 1961, while recoveries of Age O bullheads in October 1963 ranged from a low of 497 in the add-stock population to 1,065 in the cropped pond. The numbers of Age 0 fish were highest where numbers of older fish were lowest, indicating a relationship to total density.

Review and Discussion of Brown Bullhead Data

No records of standing crops of brown bullheads could be found for comparison with ours, but we found four records from populations of single species of black bullheads which are listed in Table 15. All were from small Iowa ponds for which the standing crops were estimated by mark and recapture procedures or from the return of marked fish among those killed with rotenone. These estimated standing crops ranged from 128 to 653 pounds per acre, with an average for four populations of about 300 pounds per acre. It should be noted that this average was more than three times the maximum standing crop of brown bullheads produced in our ponds. It is also of interest that bullhead production ranked lowest for any species maintained in our ponds. We must therefore conclude that the Unit 5 ponds were not only extremely infertile, but probably afforded extremely poor habitat for this species.

Forbes & Richardson (1920) found that Illinois brown bullheads showed a preference for glacial lakes, lowland lakes, and larger rivers, in that order, and that they grew best in weedy ponds or quiet rivers. Trautman (1957) found Ohio specimens occurring most commonly in deep, clear ponds having some vegetation, preferring deeper water than either the yellow or black bullhead, and being less tolerant of turbid waters than the black bullhead. Limiting factors in our ponds probably included their small size and shallowness, the complete absence of weeds, and their moderate turbidity, which most commonly ranged 15-25 inches of Secchi disc visibility.

WHITE CRAPPIES

White crappies, although not one of the five principal species studied over the 3-year period 1961-1963, were used in two short-term experiments in ponds Kappa, Lambda, and Rho (Unit 4) in the period 1958-1960. The Unit 4 ponds had been completed in 1957, and in May of 1958 each pond was stocked with six male and five female white crappies in breeding condition. Lengths ranged from 7.2 to 9.3 inches, and total weight of the 11 fish released in each pond was about 3 pounds. All were collected by boat shocker from Fox Lake in Lake County, Illinois.

By early July of 1958 we became convinced that no fish remained alive in pond Lambda. Both ponds Lambda and Rho had been treated with rotenone on May 20, 1958 to remove green sunfish. Tests with live fish in cages indicated that both ponds were free of rotenone on May 27, and they were stocked with crappies on May 28. Despite evidence to the contrary, sufficient rotenone must have remained in pond Lambda to kill the breeding stock. Therefore, between July 7 and 22 1,750 young-of-the-year and 3 adults were transferred to Lambda from each companion pond so that Lambda received 3,500 young and 6 adults, having a total weight of about 4 pounds. There were no additional stock transfers, and all ponds were drained and censused in October.

All ponds were kept dry over the winter of 1958-1959 while a blanket of clay was spread over the base of the dams to help reduce seepage. Between May 7 and 14, 1959, each pond was stocked with 85 yearlings and from 10 to 12 adults, for a total weight in each pond of about 7.5 pounds. The yearlings were from our 1958 stock and the adults were new stock also obtained from Fox Lake. Over the 1959 and 1960 growing seasons pond Rho was maintained as a control and pond Kappa received crappies cropped and transferred from pond Lambda. Cropping was moderate in both years: 8.2 pounds in 1959, of which 7.9 pounds were released in Kappa and 22.8 pounds in 1960, of which 19.6 pounds were released in Kappa. All three ponds were drained and censused in October, 1960.

Standing Crop Data

Table 44 presents the standing crop totals for six populations of white crappies, together with pounds of original

		Year of Census	Number of Growing Seasons	Pounds of Original Stock	Standing Crop, Pounds Per Acre	Pounds Added	Pounds Removed	Pounds Lost or Gained
.ppa	8 ol	1958		2.9	3 .0[a]	.0	2	+38.
m'da	8 ol	1958		9.2	4 .4	.0	0.0	+3[illegible]
o [illegible]	[illegible]	958		3.0	3 .5	.0	2	+3[illegible]
ppa	[illegible]	960	2	5	69.7	.2	0.0	+35.
m'ca	[illegible]	960	2	5	6 .5	.0	30.5	+8[illegible]
O	O ol	960	2	5	89.6	.0	0.0	+8

ctea, [illegible]

stock, pounds gained, and other pertinent supplementary data. Table 45 presents the numbers in each age group and the percents of total numbers and weights of each group recovered in each draining census.

Actual standing crops in 1958 were 37, 43.4, and 35.5 pounds of crappies in ponds Kappa, Lambda, and Rho, respectively. However, since pond Rho had a greater loss of water through seepage, and an increasingly smaller pond area, its actual production in terms of pounds per acre was probably quite similar to that of pond Lambda.

Of special interest is the fact that pond Lambda, restocked in mid-July, produced the largest standing crop. From final census data it was clear that both weight and numbers of fish stocked in Lambda in July were only small percentages of those existing in the two companion ponds at that date. It is also clear that this smaller midsummer stock had only about one-half of the growing season in which to surpass total production in the companion ponds. Three possible explanations may be suggested:

1. Pond Lambda was much the most productive; or
2. The lesser abundance in pond Lambda permitted a more efficient conversion of available food; or
3. In the absence of fish there had been an accumulation of food which imparted a marked advantage when fish were stocked in mid-July.

Since no environmental differences were observed which would indicate a greater productivity for pond Lambda, we are inclined to favor the second and/or third of these possibilities. It may have been a combination of the two, either of which could have important connotations.

Also of interest is the fact that 3,140 of the mid-July stock of 3,500 in pond Lambda were recovered in October. This was a survival of about 90 percent which seems unusually high for fish of

Tr	*Total Number Censused in Each Age Group*				*Percent of Total Number Censused in Each Age Group*				*Percent of Total Weight Censused in Each Age Group*				*ou*	
													N[illegible]	P[illegible]
K 9 8 0	4	0	0	4	9.	0.	[illegible]		4.0	0.0	0.0	0	8.9 8	37
L 9 8 0	40	0	0	5	99.9	0.	0		5.0	0.0	0.0	0	3. 45	3
R 9 8 0	3 0[illegible]6	0	0	4	O9	0	0		2.0	0.0	.0	8 0	37,010	35
K 960 +	[illegible]0	84	60	6	0.0	[illegible]8		0	0.0	9 .0	6.0	3 0	4 190	6O
L O 0	[illegible]0	2, 89	37	6	0.0	98		0	0.0	80.0	6.0	4.0	2,8 2	64.
9 0 0	485	2,0 8	106	9	8 6	7	0	0	0.0	80	6.0	4.0	2,6 3	8

p a d = = oc d

this age. A high availability of accumulated food may have influenced survival.

Over the period 1959-1960 the actual production of fish flesh (pounds gained) was lowest (35 pounds) in the pond which received additions of stock, but only slightly higher in the cropped pond (87.5 pounds) than in the control pond (82.1 pounds). At the same time stand[illegible] crops were similar in the cropped and add-stock ponds at 64.5 and 69.7 pounds respectively, but considerably the highest (89.6 pounds) in the control pond. These data suggest that 1) ponds Kappa (add-stock) and Lambda (cropped) were similar in their poten[illegible], and that "pounds gained" were high (87.5 pounds in Lambda) or low (35 pounds in Kappa) in order to attain the presumed carrying capacity of 65-70 pounds, and 2) the control pond Rho, with its relatively large pounds gained figure and a final standing crop higher than that of the add-stock pond Kappa, had a considerably higher pro[illegible] than either companion pond.

While both of these observations may be true, there were differences in total densities and in the size and age [illegible]-[illegible] of the populations that probably had some influence upon production. All populations produced strong year-classes in 1959, but in 1960 young were recovered only from pond Rho. The low production (pounds gained) of crappies in pond Kappa was associated with the largest total number of fish (4,200) but the poorest distribution of sizes and ages, with over 98 percent by numbers and 91 percent by weight concentrated in Age I over a length range of only about 2.5 inches (2.5-5). The high pro[illegible] in pond Rho was associated with the smallest total number of fish in the final census (2,613), with the fish more evenly distributed in three age groups (O, I, and II) over a length range of about 6.3 inches (1.7-8). We may note also in Table 46 that growth of all ages of crappies was fastest in the control pond Rho.

Table 46. —Growth of white crappies in ponds used for carrying capacity experimenis on the McGraw Foundation grounds, along with similar data on white crappies in other Illinois waters.

Group	Pond	Year	Treatment	*Average Length in Inches (at Ends of Numbered Growing Seasons) with Approximate Number of Fish Censused in Parentheses* 1st	2nd	3rd
Unit 4	Kappa	1958	None	2.4 (8, 904)		
Unit 4	Lambda	1958	None	3.2 (3,140)		
Unit 4	Rho	1958	None	1.4 (37,006)	..	
Unit 4	Kappa	1960	Add-stock	.. (0)	3.4 (4,134)	5.9 (60)
Unit 4	Lambda	1960	Cropped	. (0)	3.8 (2,789)	6.3 (37)
Unit 4	Rho	1960	Control	2.8 (485)	4.5 (2,013)	7.0 (106)
Other Illinois Waters		*Author*				
Ramsey Lake		Stinauer (1966)		3.8	6.6	8.6
Red Hills Lake		Price (1966)		4.2	7.5	9.8
Lake Decatur		Hansen (1951)			7.3	9.1
Lake Chautauqua		Starrett & Fritz (1965)			7.5	9.3

We may again observe the association of the greatest weight of fish with the smallest numbers. This may simply have been an expression of a greater natural productivity of pond Rho in 1960; however, it may be recalled that the same phenomenon occurred in the 1958 populations, but in different ponds. On the earlier occasion pond Lambda, restocked in mid-July with a much smaller population, made a greater total production by October than either companion pond. As suggested in the earlier section devoted to bluegills, such data may indicate that there is an optimum density which contains sufficient digestive tracts to make efficient use of available foods, but which is not so abundant as to be self-inhibiting in growth.

In the crappie data we must also consider the possible influence of contaminating fishes, and the rather large differences in standing crops of tadpoles and crayfish. Table 47 shows abundances of fish and the associated forms. Green sunfish, *Lepomis cyanellus* Rafinesque, represent the only contamination of consequence encountered in these studies, other than that, previously described, in the largemouth bass ponds.

Table 47. —Standing crops of white crappies, crayfish, and tadpoles, and relative abundances of Chara in ponds Kappa, Lambda, and Rho at times of the draining censuses in 1958 and 1960.

Pond and Year	*Standing Crop, Pounds Per Acre* White Crappie	Crayfish	Tadpoles	*Relative Abundance of Chara*
Kappa, 1958[a]	37.0	0.0	Trace	None
Lambda, 1958	43.4	0.0	90.0	None
Rho, 1958	35.5	0.0	75.1	None
Kappa, 1960	69.7	127.7	92.1	None
Lambda, 1960	64.5	69.0	241.3	Medium
Rho, 1960	89.6	Trace	205.1	Heavy

[a] Also contained 7.0 pounds of green sunfish in this census.

This contamination was limited to 2 adult and approximately 800 young green sunfish (total weight, 7 pounds) recovered in the draining census of pond Kappa in 1960. There is some question, of course, as to whether the presence of the green sunfish may have increased or inhibited production of crappies. In this case the contaminants were small enough to have provided forage for the crappies, but too small to have preyed upon crappies. It is doubtful that competition was great, or that absence of the 7 pounds of green sunfish would have permitted production of 7 additional pounds of crappies. It seems likely that the rather small weight of green sunfish had little influence upon crappie production.

There is little known basis for evaluating the influence of differing weights of tadpoles and crayfish upon fish production. Both would probably contribute to the production of largemouth bass, but might inhibit production of such less predatious forms as bluegills or small crappies. While small tadpoles or crayfish might be eaten by bluegills or crappies, larger forms might offer competition. Although the competition might not be direct, one must suspect that production of a large weight of crayfish, and/or tadpoles must divert energy that might otherwise contribute to fish production. Crayfish might have a secondary influence when so abundant as to eliminate weeds or algae. Evaluation may be additionally complicated by the sudden death or disappearance of these forms. We have observed large die-offs of crayfish for reasons unknown. Tadpoles may transform sooner in one pond than in another so that ponds yielding greatly disparate weights at time of census may have had similar weights one week earlier. So the importance of these forms is difficult to evaluate in the light of present knowledge. However, there are several associations to be noted in Table 47. Densities of vegetation (chara) in these ponds at the time of final census in 1963 were inversely correlated with standing crops of crayfish — about 128 pounds of crayfish with no chara, 69 pounds with "medium" chara, and only a trace of crayfish where chara was heavy. The degree of control seemed related to density of crayfish, and such control could have considerable influence upon a pond's ecology. In this instance the highest production of crappies was associated with a scarcity of crayfish and the densest stand of chara.

In the 1958 census of these ponds neither crayfish nor vegetation of any type were present. In that year the highest production of fish was associated with the greatest standing crop of tadpoles.

Growth and Condition

White crappie broods were not given distinctive fin clips as were those of our other species, and ages were assigned on the basis of length frequency distributions. Thus, ages of crappies were less precisely known than those of our other species, but probably sufficiently so for the comparisons offered in Table 46. These data show that growth of white crappies as single species in our infertile ponds was slower than growth made by crappies from mixed populations in other Illinois waters with which they are compared (Table 46). Totals cropped and transferred were too small to alter the original differences in densities. The control pond, Rho, with the fewest fish older than Age 0 in the final census of 1960 (Table 45), had the largest 2- and 3-year old fish in that year, and pond Kappa, with the largest numbers, had the smallest fish of these ages (Table 46). This is further shown by comparative length increments made by Age I fish in 1960. Based on average lengths of samples collected in June and October, length increments wer e highest (1.59 inches) in the pond having the least density of fish (Rho) and lowest (1.09 inches) in the pond having the highest density of stock (Kappa).

Samples taken during the growing season were too few and too small to provide seasonal curves for growth and condition for these populations, but we may compare conditions of a few fish from each pond at the time of final censuses: 21 from Kappa ranging from 4 to 11 inches in length, 25 from Lambda from 6 to 10 inches long, and 80 from Rho from 6 to 12 inches long. Conditions in the add-stock pond Kappa averaged low (3.5), the cropped pond high (4.3), and the control pond intermediate (3.9). These rankings, however, did not conform with those of rates of growth, which were intermediate in the cropped pond with its denser population and high in the control pond with the lower population density (Table 46). As with some of our earlier species, rates of condition would here be poor indicators of comparative rates of linear growth.

Mortalities

We have already mentioned the remarkably low mortality among the Age O crappies that were transferred from ponds Kappa and Rho to pond Lambda in mid-July, 1958. When censused on October 1, 3,140 of the original 3,500 were recovered, a mortality of only about 10 percent over an approximately 2½-month period. Mortality of adults over the same period was 3 of 8, or about 37 percent.

The crappie broods were not identified by distinctive clips as were those of our other species, and data for crappies is therefore limited. Our only additional data were derived from an attempt in 1960 to measure seasonal rates of mortalities for Age I crappies given a distinctive fin clip for each of the three summer months. Approximately 100 were marked in each pond in June, July, and August, and returns were counted in the October census. The results were extremely erratic and indicated that mortalities from handling and marking were sometimes large and subject to large variations. For example, mortalities by October of Age I crappies were 77, 67, and 47 percent for those marked in June, 98, 100, and 43 percent for those marked in July, and 98, 100, and 93 percent for those marked in August, in ponds Kappa, Lambda, and Rho respectively.

Spawning Success

Reproduction was successful in ponds Kappa and Rho in 1958 and was absent in pond Lambda due to the elimination of brood stock by rotenone. Recoveries in October of young spawned in these ponds were 37,006 from pond Rho and 8,904 from pond Kappa. We have no knowledge of what caused such a wide difference in numbers of young produced in 1958.

Numbers of Age I crappies recovered in the 1960 census (Table 45) show that all three populations produced moderately large broods in 1959. In 1960, however, young-of-the-year were recovered only from pond Rho. Environmental factors which also showed marked variations in these ponds in 1960 were the abundances of older crappies, and the abundances of crayfish and chara. Age 0 crappies were present 1) where numbers of older crappies, particularly those of Age I, were least abundant (Table 45), 2) where crayfish were absent, and 3) where chara was the most abundant. Thus, the absence of Age 0 crappies in the two companion ponds may have been due to greater predation by greater numbers of older fish in waters having less chara and less protective cover. Predation of eggs or larvae of crappies by the abundant crayfish populations might also have been a factor.

Review and Discussion of White Crappie Data

The white crappie has been found to be undesirable in small ponds (Hall *et al.* 1954; Jenkins 1958; and others) because of overcrowding and slow growth. So far as is known it has not previously been used as a single species, but has produced large poundages in mixed populations. Jenkins (1958) reported an average standing crop of 72 pounds per acre of white crappies in mixed populations in 18 Oklahoma ponds, and a maximum standing crop of 205 pounds per acre when combined with black bullheads (107 pounds per acre) and mixed sunfishes (15 pounds per acre). The species finds its greatest value as a sport fish in larger lakes and reservoirs where catch rates are sometimes quite high. Buck & Cross (1951) reported a large catch from a 5,000-acre Oklahoma reservoir where the crappies were attracted by a temperature gradient. Over a 69-day period in late winter the hook-and-line catch totaled 626,897 crappies weighing 194,338 pounds which computed to approximately 39 pounds per acre for the entire 5,000 acres. A majority of this total was removed from a single cove in which the entrance of warmer water was creating a mild temperature gradient. Total catch from this 3-acre cove over the 69-day period was at a rate of over 22 tons per acre, practically all from a single year-class.

In an earlier section we noted that subsequent stocking of bluegills in these same ponds (Kappa, Lambda, and Rho) produced considerably larger standing crops than had been obtained from white crappies. Maximum standing crops in pounds per acre were 89.6 for crappies and 173.3 for bluegills. Comparing only control ponds, the poundages were 89.6 for crappies and 127.1 for bluegills. Such a difference indicates a lesser efficiency for white crappies, due probably to their subsistence at a higher trophic level.

As earlier observed for bluegills when stocked in the same unit of ponds, highest total production of crappies was not made in the pond containing the most fish. This encourages the speculation that there is an optimum density for maximum production. This optimum number would include enough individuals of proper sizes to obtain efficient utilization of the pond's resources, but they would not be so abundant as to stunt their own growth. We must also recognize that maximum production of fishes is dependent on high production of their invertebrate foods. Maximum production of invertebrates would occur under an optimum rate of exploitation. The optimum density of fishes might in some cases be that which provides optimum cropping and maximum production of the invertebrates used as food. Such optimum synchronization would result in maximum fish production. Variations in the degree of synchronization would produce variations in fish production.

GENERAL DISCUSSION

Table 48 summarizes standing crop data presented in earlier sections. For each species it includes an average standing crop for all ponds receiving each treatment, and in the last column an average for all populations in all seasons, regardless of treatment. In this last column of the table we can observe that standing crops of bluegills narrowly exceeded those for yellow perch, which were followed by smallmouth bass, largemouth bass, white crappies, and brown bullheads in that order. We must emphasize, however, that because of differences in environments this order of rank does not necessarily reflect the relative efficiencies of these species. Its principal value is to indicate the potential for variation in standing crops of the individual species. Direct comparisons between species have been limited to those instances where standing crops of two different species were measured in the same ponds in consecutive years. As detailed earlier, such comparisons indicated that smallmouth bass were more efficient than largemouth bass, that yellow perch produced larger poundages than either largemouths or smallmouths, and that weights of bluegills were larger than those earlier produced by white crappies in the same ponds.

Table 48.— Average standing crops (rounded) in pounds per acre for the six species of warmwater fishes studied as single species in 1-acre ponds, 1957-1963.

Species	*Standing Crop for All Ponds Receiving Each Treatment*			*Overall Average, All Populations*
	Control	Cropped	Add-stock	
Bluegills	114	101	173	125
Yellow Perch	98	122	184	124
Smallmouth Bass	88	46	150	93
Largemouth Bass	71	51	90	71
White Crappies	51	65	70	57
Brown Bullheads	45	16	90	49

Three sources of variation in our standing crops were: 1) differences in experimental treatments received, 2) differences in pond fertilities, and 3) differences in size and age composition of the populations. All species were generally responsive to cropping, or to the additions of stock, although the influences of the treatments were sometimes masked by differences in pond fertilities or in population compositions. As a general rule, however, standing crops were highest and rates of production (pounds gained) were lowest in those populations receiving additions of stock, standing crops were lowest and rate of production highest in cropped populations, and both values tended to be intermediate in the control populations. A primary effect of the experimental treatments was to create three differing levels of fish density for each species. In general, rates of growth and condition were poorest, rates of reproduction were lowest, and rates of mortality were highest in those populations having the greatest densities of stock.

The areas for greatest individuality among species were probably those of age and size structure of the populations and the influence of the differing structures upon production. Some species exhibited characteristics or relationships that were either unique to that species or less evident among the others and therefore it might be appropriate to briefly review these, making comparisons between species where useful.

In terms of efficient use of available food supplies, and the ability to sustain a high rate of production, it appears that the smallmouth bass was the most successful as a single species of any of the six species studied. We found it to be extremely hardy even when subjected to marking and frequent handling in seines and live boxes. It reproduced adequately under a variety of conditions, including ponds with bottoms of hard clay overlayed by claysilt, and in the absence of sand, rocks, or gravel. From original stocks as small as 5.6 pounds per acre (including some spawning adults), maximum standing crops were achieved in two growing seasons if successful reproduction occurred in both seasons. From original stocks approximating one-half of the carrying capacity of the ponds, maximum standing crops were achieved in a single season with only one successful reproduction period. Standing crops as high as 170-180 pounds per acre exceeded those of the largemouth bass (later used in the same ponds) by as much as 40-50 pounds per acre. The greater production of the smallmouth bass over that of the largemouth was attributed primarily to the more efficient utilization of lesser invertebrates as food by smallmouth of larger sizes. Our heaviest populations of smallmouth were those dominated by 6- to

11-inch individuals, and these larger fish seemed as efficient in utilizing the small invertebrates as were the young-of-the-year. In contrast, standing crops of largemouth bass declined progressively as the populations became increasingly dominated by largemouth of these same intermediate sizes. The smallmouth was unique in that high production was not dependent upon large numbers of both small and large fish. Data from Unit 1 indicated that when sufficient numbers were present to make efficient use of an abundance of invertebrates, size of the bass was relatively unimportant, and the absence of young, small fish might cause little or no loss in total production of fish flesh. When larger fish (about 11 inches and above) were present, however, their growth was inhibited when neither crayfish nor smaller bass were available as prey.

Standing crops of smallmouth bass measured in the fall exceeded those estimated in the spring. For the control and add-stock populations in Unit 4, three standing crops estimated in the spring ranged from 55.4 to 64.5 pounds per acre, averaging 58.8 pounds and three measured in the fall ranged from 84.9 to 95.5, averaging 91.2 pounds. Thus the spring standing crops averaged only about 64 percent as large as those measured in the fall. When numbers of bass were large, as in the add-stock populations, reductions to the spring levels were brought about by large over-winter mortalities, chiefly among the older and larger individuals. Where fish were less abundant, as in the control pond, the low spring level was due more to a failure of the older individuals to add flesh, in spite of large reductions made in their numbers, and their having eaten major portions of the smaller members of the population. Carrying capacities were higher in Unit 4 ponds in the fall of the third season than at any previous time due to improved fertility and greater food production in the ponds. Higher standing crops at this time were believed also due in part to a more optimum distribution of sizes and ages in the population than when formerly dominated by older and larger individuals of the 1958 brood.

Manipulations of stock produced differing levels of population densities, and these influenced the populations in a number of important ways. In general, rates of growth and condition were poorest, rates of reproduction were lowest, and rates of mortality were highest in those populations having the greatest densities of stock. Fastest rates of growth, however, were not always accompanied by highest rates of condition, and comparative rates of either frequently were poor indicators of comparative rates of the other.

Our largest standing crops, and presumably our most efficient populations of largemouth were those containing large numbers of both small and large fish. We believe that when largemouth populations contained few or inadequate numbers of young-of-the-year, the pond's carrying capacity was not attained and much of the pond's resources remained unutilized.

Our data from Unit 2 ponds provided evidence that when cropped at a proper rate largemouth populations are capable of a seasonal replacement of fish flesh equal to the poundage that the pond can support. Although we obtained no tangible evidence of such a replacement potential among our smallmouth populations, we believe that such failure was due primarily to our experimental procedures. The replacement potential of smallmouth in our ponds was not adequately tested by proper cropping, but the large standing crops and large gains made in uncropped ponds indicated that such a potential did exist. We suspect that the replacement ability of cropped populations of smallmouth would be at least equal to that of the largemouth.

The largemouth bass has been quite widely used as a single species in ponds, and probably considerably more so than the smallmouth. When so used, the largemouth has sometimes failed to sustain itself due to failures of reproduction, or of survival of young, and this is believed to be a common failing In the present experiments, however, young-of-the-year were present in all of 10 largemouth populations and 10 of 11 smallmouth populations at the time of the final censuses. We believe that our data show both species to be capable of a high sustained production as a single species in 1-acre ponds, and especially so when subjected to cropping. Since bluegills are also known to frequently overpopulate and to eliminate reproduction among coexisting bass, we believe that the chances for a sustained production of bass are as good when stocked alone as when mixed with bluegills.

Absence of a forage species for either of the basses has certain disadvantages. In our populations coefficients of condition were generally poor, fish were never fat, and growth of fish older than Age O was usually slower than for bass in mixed populations. On the other hand, our bass populations indicate that total weights of bass actually could be larger when a bass species is alone than when it is in a mixed population. In addition to their greater total weight and number, bass as single species would, in most cases, be more readily caught than when better fed through preying upon a companion species. As mentioned before, Bond and his associates in Oregon (personal communication) found bass fishing to be much superior in ponds where the bass were alone than when they were associated with bluegills. If a pond owner is primarily interested in bass, use of either bass species could prove rewarding. In our experience, however, we would have a slight preference for the smallmouth because it better withstood marking and frequent handling, suffered fewer mortalities, and was more able to subsist on an invertebrate diet.

So far as is known, the yellow perch has not previously been stocked as a single species, and no standing crop data are available for comparison with ours. The species can, however, attain large numbers and weights when in combination with other species in fertile waters. In 1920, the 10,000-acre Lake Mendota in Wisconsin was estimated to contain 15,000,000 adult perch (Hasler & Wisby 1958) which, using the average weight of adults caught at that time, projects to a standing crop of about 169 pounds per acre of adult perch only. Moyle *et al.* (1950) have recorded estimates as high as 184 pounds per acre in Minnesota game fish lakes, although the mean for 41 such lakes was only 32.1 pounds per acre. Our highest standing crop was 192 pounds per acre as a single species in pond Alpha, which only slightly exceeds the maximums estimated for perch in multispecies populations. These data suggest that the perch may be particularly well adapted to its own ecological niche, and relatively little affected by competition from companion species.

Perch growth was generally fastest in our cropped population and slowest in our add-stock population, and closely related to density of stock. There was strong evidence, however, that intrabrood density was more critical or controlling than total population density, with little apparent competition between perch of different ages or sizes. For example, perch of the 1962 brood in the add-stock population grew faster than their more numerous counterparts in the control population in spite of the much greater total weight (all age groups combined) of perch in the add-stock population. It was further notable that at the time of the final census in 1963, 2,861 perch of this 1962 brood had an average length (4.7 inches) only about 0.4 inch less than that (5.1) of 728 perch of the 1960 brood that had survived from the original stocking of October, 1960. The 1962 brood of perch had made an average length increment of about 3.5 inches in its first year and 1.2 inches in its second year, while the 1960 brood had made a length increment of less than 1 inch over the entire 2-year period.

It should be pointed out that numbers of perch older than the 1962 brood were being continuously augmented by perch transferred from the cropped pond Zeta. However, the total of all perch older than the 1962 brood in the 1963 census numbered only 1,012 as compared to the 2,861 in the faster-growing 1962 brood. While the older perch of the 1960 year-class had apparently attained a growth limit due to intraclass competition for some element within the environment (probably food), they obviously were offering little competition to the much more abundant and faster-growing perch of the 1962 brood. We had at the same time a small group of "cannibal" perch of the 1960 year-class that made excellent growth due to their cannibalistic tendencies. So we had within the add-stock population three distinct groups of perch, probably with different food habits, and which offered relatively little competition to each other: 1) the large, fast-growing cannibals of the 1960 brood, 2) the more abundant perch of the 1960 brood that had attained their growth plateau, obviously subsisting upon an invertebrate diet, but of a different composition than that utilized by the younger perch, and 3) the younger, most abundant and fastest-growing group in the population, which obviously utilized foods not taken by the older fish, and which permitted them to literally grow into the size range of perch that were 2 years older.

Some studies have shown the food habits of perch to change to some degree with increase in size. Tharratt (1959) found that immature insects were prominent as food for all size groups (2.5 inches and up) of perch in Saginaw Bay, but that mayfly nymphs, which were the largest insects available (presumably *Hexagenia* sp.), were found only in the stomachs of perch longer than 4.7 inches. Tharratt also found that copepods were the chief constituents in the food of young-of-the-year, but were absent from the stomachs of perch more than 5.4 inches long. On the other hand, Pearse & Achtenberg (1920) and Herman *et al.* (1959) have observed that adult perch commonly feed on cladocerans, utilizing gill rakers adapted to straining these small forms from the water. It therefore seems quite remarkable that in our studies one age group of perch could find sufficient food to grow well, while an older group of only slightly larger average size appeared to have done little more than subsist. We have previously noted that the nymphs of the larger burrowing mayfly, *Hexagenia limbata,* were apparently eliminated fr om the add-stock pond, while remaining abundant in the companion ponds. Possibly the 1960 brood in pond Theta had developed the habit of feeding almost exclusively on these mayflies and the perch were unable to change their feeding habits when this food was exhausted. The senior author observed a somewhat similar occurrence (unpublished) in which a large population of white bass in a large southern reservoir literally starved to death in a year when its principal food (gizzard shad) had a spawning failure, although other forage fishes of similar size were available.

The brown bullheads were used only in Unit 5 where they produced the lowest standing crops recorded in this study. We believe that this was because the Unit 5 ponds were the least fertile of our ponds, and because the brown bullheads were poorly adapted to our weedless, moderately turbid, moderately shallow ponds with their soft clay-silt bottoms. This poor adaptability was emphasized by the fact that survivors of the original stock of 28 adults failed to increase their average size over the 3-year period of study. There was no evidence of cannibalism in these populations. Although crayfish were usually abundant, and were known to be eaten by the larger bullheads, they obviously did not provide an adequate diet. With no cannibalism, food for all sizes of bullheads was limited primarily to invertebrates. It is therefore interesting that there was little apparent competition for food between the Age 0 fish and those older than Age 0. As in the yellow perch populations, competition among bullheads was greater within than between age classes. In this instance Age O bullheads in the add-stock pond (most of the bullheads added were older ones) grew faster than their counterparts in the companion ponds because of their lesser abundance, even though the population of fish older than Age 0 was much larger in the add-stock than in either companion pond.

We earlier noted that production of bluegills was greater than that of white crappies earlier maintained in the same ponds. Our standing crops of bluegills were low by common standards (Table 35) due to the low fertility of the ponds in which they were stocked. However, the bluegills produced the highest average standing crops, and were probably the most efficient of any of our six species.

Both bluegills a n d white crappies were stocked in Unit 4, and both exhibited the phenomenon whereby a smaller number produced a greater weight than a larger number of the same species. We had observed that our cropped pond Lambda had a larger standing crop (weight) of bluegills than the control pond Rho even though the total population numbered less than one-sixth that of Rho at the time of census. Also, the same association was apparent in the white crappie populations in both 1958 and 1960, with that of 1958 being the most distinct. We may recall that in 1958 the population in pond Lambda was inadvertently destroyed by rotenone, and the pond was restocked in mid-July with a smaller weight and number than were present in either companion pond. By the time of the census in October this smaller number had produced a larger poundage than either companion pond in only about one-half as much time. The differences in standing crops could have been caused by differences in pond fertilities. If so, however, in the case of the crappies pond Lambda would have been enormously more fertile than pond Rho in one period and slightly less fertile in the other. Differences in age structures of the populations could also have had some influence. We recognize that there may be other possible explanations, one involving the concept of an optimum density. The effects of an optimum density might be asserted in at least two ways:

1. The density of fishes would be in optimum relation to that of their prey if feeding activities maintained the prey species at population levels at which they most efficiently replaced their own numbers. Thus the maximum food supply would be provided for the predator fishes. Too few fish would make inefficient use of the prey species, whereas too many would cause overexploitation and a temporary collapse of both predator and prey populations.

2. There may be an optimum density which contains enough fishes to make efficient use of available foods, but not so dense as to be self-inhibiting. We know that some fishes attain densities at which they may inhibit their own growth and reproduction. Even when the food supply is not a limiting factor, it may be possible for a smaller number of fish to attain a greater total weight than a larger population so dense that it created an inhibitory barrier. Such a barrier might be either physiological or psychological, and could be more limiting upon a species maintained alone than when the fish are in a mixed culture. It it known that certain combinations of species may be extremely compatible and that one may actually en-

hance production of the other. Data reported by Rose (1959) suggest the engaging possibility that when two unrelated or distantly related species are combined, one may have the effect of metabolizing away self-inhibiting products produced by the other.

The influence of total fish densities, of differing densities by size or age group, and the influence of such associated organisms as tadpoles and crayfish upon fish production are difficult to measure and evaluate in ponds, but may be of great importance. This may be especially true in single species populations. We have seen that in our control pond Rho the standing crops of bluegills, crayfish and tadpoles were all much higher in October, 1961 than in October, 1963. We must therefore wonder if the carrying capacity of pond Rho declined so markedly over that period, or if the greater production of bluegills in 1961 was in some way enhanced by the greater numbers of crayfish and/or tadpoles.

Whether it may or may not be influenced by an inhibitory factor, an optimum density will exist for each population. In its simplest terms, the amount of new flesh produced in a population is dependent upon three things: 1) the carrying capacity of the pond for that species, 2) the number and weight of fish already present, and 3) the pounds being cropped (or otherwise removed) that are subject to replacement. If the carrying capacity has been attained, and no fish die or are otherwise removed, the fish cannot grow and no new flesh can be produced. On the other hand, the more pounds cropped the more that can be produced in replacement. The most efficient and productive arrangement will be one in which the optimum number is cropped, maintaining the population continuously below carrying capacity but not reducing the number of fish below the level that can by growth and recruitment efficiently replace those removed, as was done in two of our smallmouth populations. As indicated by studies of smallmouth bass (Bennett & Childers 1957) and by our largemouth experiments in Unit 2, under an optimum rate of cropping it may be possible to remove more pounds in a season than the pond can support at any time. For each pond there must exist an optimum population density, and an optimum rate of cropping, and these will differ and fluctuate as the productive potential of individual ponds must also differ and fluctuate. The rates of production to be obtained will be the result of the interaction of these complex and unstable forces, and the efficiency of production will be determined by how nearly the optimum rates of cropping and density can be maintained.

A primary purpose of this investigation was to consider the relationship of carrying capacity to standing crop. In doing so we should again clarify our usage of the two terms. Standing crop is universally recognized as the quantity of organisms present at the particular time of measurement, and is so used here. As defined by Krumholz *et al.* (1957), carrying capacity was considered to be that quantity surviving through the least favorable environmental conditions over a stated interval of time. By such terms it automatically becomes a minimum quantity. There are, however, many practical reasons for measuring maximum rather than minimum levels of abundance. Many researchers and commercial fish growers refer to their maximum standing crops as the carrying capacity of the unit involved. They interpret this to mean the maximum poundage that the pond can produce, or support, of the number and type of organisms involved, and under the environmental conditions that existed or were maintained. This usage is now very widely accepted. For our present purposes we have recognized what was termed a temporary carrying capacity by Edwards & Fowle (1955).

We have measured standing crops in both spring and fall and have evaluated these in terms of carrying capacities, recognizing that the poundage of fish supported by a pond in late winter or early spring may be quite different from the poundage that the same unit might support in late summer or fall.

In evaluating carrying capacity it is important to come to an understanding of its relative stability. Carrying capacity is sometimes conceived as being a relatively stable quantity, changing little from year to year. This is tantamount to saying that the environment itself is not subject to change. We recognize a number of factors other than changes in the environment as being capable of influencing the standing crop, but we believe that our data have shown that the pond environments were relatively unstable, and that variations in standing crops were frequently due to changes in the environments and in the ponds' carrying capacities.

Changes in carrying capacities of the ponds were believed to have had two principal causes: 1) changes in such physical elements of the environment as inorganic fertility, turbidity, or type and density of vegetation, and 2) changes in densities of associated invertebrates, including those utilized as food, such as scuds or mayfly nymphs, or those having a potential for either inhibiting or enhancing the production of fish, such as crayfish.

In working with our data, standing crops frequently were judged to have been either larger or smaller than the pond's carrying capacity. When larger, it was because of excessive additions of stock, and the excess was indicated by a loss in the pounds gained or lost column. We could not, of course, know when the point of equilibrium was reached and when additional losses would or would not occur. However, when a loss had occurred, and when additions of stock had been quite continuous up to near the time of census, we assumed that equalization was still in progress and that the standing crop probably still exceeded the pond's carrying capacity. It was more difficult to make a judgment as to when the standing crop was at or below the pond's carrying capacity. If the standing crop was medium to large, the pounds gained not overly large, and the population structure reasonably normal, we felt that the standing crop probably approximated carrying capacity. If the pounds gained figure was unusually large the question arose as to whether the carrying capacity was also unusually large and may not yet have been attained. We suspected our standing crops to be below carrying capacity when they were small and when total numbers of fish were small, or when one or more size or age groups of the population were inordinately small, or absent, due either to heavy cropping, excessive cannibalism, or reproductive failures. Among smallmouth bass, however, we found that absence of Age 0 fish was of little importance if a sufficient number of intermediate sized smallmouth were available to make efficient use of the invertebrate food supply.

While the standing crop is not necessarily a measure of carrying capacity the two are intimately related, and the former is limited by the latter. Both must be considered dynamic quantities dependent upon the interaction of all forces within the environment. As an expression of these forces, carrying capacity must also fluctuate, and can have no greater stability than that of the environment. As a finite quantity, carrying capacity may be extremely difficult to measure exactly, and might only by chance be the same at any two points in time. Standing crop might be conceived as the "tail on the kite," always tending to follow, either up or down, the movement of the controlling body.

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