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FINAL REPORT

RESEARCH AND SURVEYS

FEDERAL AID PROJECT NO. F-41-R

FACTORS INFLUENCING FISH POPULATIONS
IN OKLAHOMA LAKES AND PONDS

JOB NO. 2

STUNTED CRAPPIE INVESTIGATION
OCTOBER 1, 1978 THROUGH JUNE 30, 1981

FINAL REPORT

State: OKLAHOMA Project Number: F-41-R

Project Title: Factors influencing fish populations in Oklahoma lakes and ponds

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ABSTRACT

The small average size of black and white crappies (*Pomoxis nigromaculatus* and *P. annularis*) in many of Oklahoma's reservoirs is an important management problem. A literature review indicated that both slow growth and high mortality of crappies that are age IV and older contribute to the problem. Relatively little work has been done on the causes of mortality; although preliminary studies indicate that fishing mortality may be significant. Growth appears to be density dependent; therefore, slow growth would seem to be correlated with competition for scarce resources (possibly food). However, several attempts to relate growth rates to the quantity or types of forage consumed have produced conflicting results.

We investigated the relationship between diet and growth by comparing populations of fast and slow growing white and black crappies intraspecifically. No consistent relationships were found between type or quantity of forage consumed and growth rates. Based on these results and the conflicting findings of similar studies, it appears that growth rate is not dependent on diet. Behavioral or physiological differences between populations may sometimes be responsible for differences in growth and deserve additional study. Also, causes of mortality of age IV and older

crappies merit further investigation.

I. Objective:

To identify factors leading to stunted crappie populations.

II. Background:

Populations of black and white crappies (Pomoxis nigromaculatus and P. annularis) in many of Oklahoma's lakes (small reservoirs) and larger reservoirs are comprised mostly of individuals that are too small to be kept by fishermen. Considering that a recent survey of Oklahoma anglers found that crappies were the third most preferred, and the second most frequently sought after fish (Mense 1978), the small average size of crappies in many bodies of water is an important management problem in the state.

The relatively low proportion of large fish in many populations is the result of both high mortality of older fish and of slow growth. For example, age IV white crappies in Boomer Lake averaged 208 mm (total length), and only 9.7% of the population was age IV and older (Crawley 1954; Burris 1956). In Lake Texoma more rapid growth (to an average of 257 mm for age IV fish) and higher survival of older fish (24.0% of the population was age IV or older) combined to produce a much higher percentage of crappies large enough to be creeled (Whiteside 1974).

Numerous biological and physical factors may result in small average size (Fig. 1). The traditional explanation is that the crappies are overabundant, and that competition for food is intense, resulting in slow growth. The assumption that absence of older fish is due to natural mortality from stresses associated with overcrowded conditions is supported by several studies. High natural mortality of age III crappies was

observed by Starrett and Fritz (1965). A relatively abundant year class of crappies experienced 60 to 75% mortality during the fourth year of life. Of that mortality, 5% was due to fishing and 95% was natural. The authors did not indicate what may have caused the natural mortality. Certain lakes in Kansas were found to contain few crappies age IV and older, even though fishing pressure was low (Stafford 1979).

Based on the traditional explanation that intense competition causes slow growth and high mortality of older fish, it follows that increased fishing pressure will alleviate the situation by reducing the level of competition (Rutledge and Barron 1972). Recent work in Missouri, however, indicated that harvest may be a major source of mortality (Vasey 1979). Fishing pressure on crappies in the James River Arm of Tablerock Reservoir was much greater than in the Long Creek Arm. Growth rates were similar and rapid for both arms, but very few older crappies were present where fishing pressure was relatively high. The abundance of crappies that were age IV and older in the Long Creek Arm indicated that fish in the James River Arm had the potential to live longer than they actually did. A creel survey showed that, in the James River Arm, fishermen were harvesting the largest crappies available. The mortality due to fishing was not measured, but it probably accounted for the scarcity of older, larger crappies where harvest was high (Vasey 1979). Preliminary results indicate that reduction of harvest through a size and possession limit has increased survival of crappies that are age IV and older.

Although Vasey observed fast growth and high mortality of older crappies, slow growth in Oklahoma is often associated with high mortalities of older crappies. Where this combination exists, the possibility that increased exploitation of crappies would reduce densities and improve

growth appears unlikely. Crappies are extremely prolific (Jenkins 1957), and even a major reduction in the spawning stock of older, larger individuals seems unlikely to reduce recruitment to younger age classes. Therefore, relative to harvest of species where recruitment is more directly related to the spawning stock, intense harvest of crappies seems less likely to affect abundance of sub-harvestable individuals.

The ability of increased harvest to increase growth rate and reduce competition also appears unlikely when feeding habits are considered. Fish tend to become important in the diet of crappies at about 150 mm in length (Reid 1949; Burris 1956; Green and Murphy 1974); whereas crappies less than 150 mm eat mostly invertebrates and zooplankton. Thus the diet generally changes from invertebrates to fish when the crappies are less than, or first approaching the size which fishermen begin to keep. If anglers remove only the larger crappies, the increased exploitation may not reduce the degree of competition among the smaller crappies that feed on different foods than the larger fish.

As support for these hypotheses we would conclude that if harvest is reducing competition among larger crappies but not among smaller crappies, then growth should change only in older groups. Studies by Crawley (1954) and Burris (1956) of slow growing populations of crappies indicated that growth was slow up to about 150 mm in length, and more rapid after that. Similar patterns were suggested by data collected by the Oklahoma Department of Wildlife Conservation from other lakes (unpublished data). Harvestable crappies were relatively rare in lakes Carl Blackwell, Boomer, and Wewoka but relatively common in lakes Texoma, Arbuckle and Markham Ferry. Growth increments were similar for yearlings and older, larger crappies from both types of populations (Figure 2), but differed

considerably for young, subharvestable crappies.

Increased harvest of older crappies may also increase competition among younger age classes by reduction in predation. Adult crappies in Beaver Reservoir in Arkansas were cannibalistic. For two years the relative abundance of forage fish--threadfin shad (Dorosoma petenense), gizzard shad (D. cepedianum), brook silversides (Labidesthes sicculus), sunfish (Lepomis) and small crappies--were compared to abundance in stomachs of adult black and white crappies. The electivity index indicated that both species preferred young-of-the-year crappies over any of the other forage fish available (Ball and Kilambi 1972). Because cannibalism by adults could be a density dependent control on the abundance of young, overharvest could increase competition among smaller crappies. Large numbers of adults could limit survival of, and competition among, young, and therefore growth of young would be enhanced. Heavy angler harvest could reduce cannibalism, and increase competition among future year classes.

In summary, the literature does not always support the common belief that slow-growing populations of crappies should be intensely harvested. Careful considerations of individual situations are required prior to final management decisions.

In some populations of crappies natural mortality of older age classes may result in small average size. Parasites and diseases are possible causes of natural mortality; however, the literature does not indicate that they are widespread or severe enough to cause the 60 to 75% natural mortality that has been observed (Rutledge and Barron 1972). In Lake Texoma, up to 8% of the crappies had lymphocystis (Whiteside 1964), and approximately 9% of the crappies in Benbrook Lake, Texas were infected

(Green and Murphy 1974). In Benbrook Lake average condition factors of infected fish were slightly lower than for uninfected crappies, but neither study indicated that disease was a likely source of mortality. The causes of high mortality of age IV and older crappies are obscure. It has often been presumed to be associated with overcrowding, but this relationship has not been demonstrated.

Slow growth of crappies has been related to a variety of conditions, including physical factors. Hall et al. (1954) found that in Oklahoma growth was generally better in clear water than in turbid water. In a Missouri reservoir, growth increased from an average of about 0.3 to 1.0 m (Vasey 1979). Crappies are primarily sight feeders, so high turbidities could reduce feeding efficiency. However, crappies also grew slowly in some relatively clear waters (Leonard 1951; Martin 1952; Crawley 1954). High turbidities may be one cause of slow growth, but is not the only cause.

Crappies frequently grow relatively fast in new reservoirs and reservoirs on fertile watersheds (Hall et al. 1954). Such bodies of water generally have high productivity and would be expected to support either a greater biomass of fish, or faster growing fish.

Growth rates also appear to be related to the size of a reservoir (Hall et al. 1954). On the average, crappies in large reservoirs grew more slowly than those in smaller bodies of water; however, these data are weakened by the fact that many of the small reservoirs (lakes) were also new. Crappies generally do not grow rapidly in older small lakes.

Competition for space where crappies are very abundant could possibly limit growth (Bennett 1970). However, crappies are schooling fishes so competition for some factor other than space appears most likely.

Insufficient cover is also a possible cause of slow growth, since crappies concentrate in and around cover such as sunken brush and timber (Miller and Robison 1973). However, the literature gives no indication whether an absence of such cover could affect the well-being of crappies.

Slow growth of crappies is generally believed to be related to food, and a variety of conditions could produce an overabundance of fish relative to the food supply. One condition is insufficient predation on small crappies. Pierce et al. (1963), Swingle and Swingle (1967), and Tucker (1972), working with largemouth bass (Micropterus salmoides), and Powell (1973), working with northern pike (Esox lucius), found that abundance of predators was directly related to growth of crappies. Predation continuously thinned the population, reducing competition and increasing growth.

Year class strength varies greatly in many populations of crappies. A strong year class could lead to intense competition and slow growth, or at the other extreme, a weak year class could limit overall abundance and allow good growth (Thompson 1941). Such variations of year class could be cyclic or random. Apparent cycles of three to five years have been reported by Starret and McNeil (1952), Swingle and Swingle (1967), Siefert (1969), and others. Cycles could result from increased competition and slow growth following one or two strong year classes. Cannibalism would limit the abundance of subsequent year classes until mortality reduced the abundance of the dominant year classes. A period would follow in which crappies were scarce but grew relatively fast. Then reduced cannibalism would allow production of another strong year class.

The diets of individual crappie pass through three generalized stages. Very small crappies, particularly young of the year, feed primarily on

zooplankton. Crappies up to about 150 mm total length eat mostly benthic invertebrates whereas larger crappies eat mostly fish (Burris 1956). Thus, the size and quantity of forage apparently can determine whether or not crappies grow well. Recently, populations of threadfin shad and Mississippi silversides (Menidia audens) have been established in various lakes and reservoirs. Crappies will feed heavily on these species, and their introductions have in some instances been associated with increased growth of crappies (Beers and McConnell 1966; Li et al. 1976). In these instances the availability of forage fish may have been limiting growth; however, both studies noted that the introduced species may compete with young crappies. Li et al. (1976) found that even though over-all growth of crappies increased, growth during the first two years of life actually decreased. Competition with forage species could have increased mortality of young and improved growth of older fish may have been the result of reduced densities. Insufficient data were taken before the introduction of these forage species to evaluate this hypothesis. Crappies grew well where small threadfin shad were available throughout most of the year. However, in lakes where threadfin shad had a short spawning season, small shad were available for a limited time and crappies grew poorly (McConnell and Geddes 1964; Menn 1965; Beers and McConnell 1966).

Burris (1956) compared food habits of slow and fast growing populations of crappies and found fish were common in the diet of crappies under 150 mm where growth was good, and absent where growth was slow. This observation suggested that the quantity of forage fish available to small crappies determined rates of growth. Crawley (1954) and Siefert (1969), however, suggested that forage fish were not required for fast growth of crappies under 150 mm. Crawley found larger insects, including

Ephemeroptera, Diptera and Coleoptra, were important in the diet of faster growing fish. The diet of slow growing populations consisted primarily of smaller invertebrates. Siefert (1969) found a positive correlation between growth of crappies and numbers of Hexagenia nymphs in the diet. Both studies indicated that the kinds and abundance of invertebrates available influenced growth.

In summary, food habits appear to be related to growth rates of crappies; however, it is difficult to make generalizations. Crawley (1954) and Burris (1956) both indicated that the diet of fish under 150 mm long was important, but Burris concluded that fish were necessary for good growth, while Crawley suggested the size of invertebrates consumed was more significant. Li et al. (1976) found the introduction of threadfin shad was associated with an overall increase in growth of crappies even though growth during the first two years actually decreased. It is possible that competition between young crappies and forage fish such as threadfin shad and subsequent reduced survival of young crappies explains these results.

Various attempts have been made to increase growth rates of crappies. The relative success of these attempts offer insight as to the causes of slow growth, and of high mortality of fish older than age III. One common method has been to remove part of the population. Rutledge and Barron (1972) give a very extensive review of these projects, so only general conclusions will be presented here. Netting and poisioning have been used to remove a portion of the population of crappies from lakes where growth was slow, under the assumption that high densities produce intense competition and slow growth. Generally, when 30% or more of the population was removed growth of the remaining fish increased. However, without continued thinning, the populations rapidly expanded and reverted to the

high-density, slow-growing state. The results of thinning and predator-stocking experiments, as discussed above, indicate that growth rates in some lakes are density dependent, which suggests that either the forage base, space, or cover were limiting growth of crappies.

The relation between water level fluctuations and growth of crappies has been studied in Kansas (Beam 1979). Water levels were lowered throughout the summer, allowing terrestrial vegetation to grow on exposed portions of the reservoir bottom. In spring the reservoirs were allowed to refill, flooding the vegetation. Although it was expected that annual flooding of this nature would produce conditions similar to those in a newly filled reservoir, and therefore promote good growth, growth was unaffected (Beam 1979).

The small average size of crappies in many of Oklahoma's ponds and reservoirs is a complex problem. Physical factors such as turbidity appear to limit growth in some bodies of water. Also, studies of food habits, forage introductions, and reductions in density suggest that competition for food may limit growth in some populations. In other systems it appears that natural and fishing mortality may contribute to low abundance of fish age IV and older and thus explain smaller size crappies. Any one of these factors may be important in a given reservoir, and the interaction of two or more may be significant in many bodies of water. It is necessary to know which of these factors are limiting, and how they may interact, before populations of crappies can be managed effectively.

The objective of this study was to evaluate the relation between various aspects of the forage supply and growth. We compared growth rates and condition factors for populations of fast growing crappies to those of slow growing crappies. We also determined the important food items in

stomachs of crappies and estimated relative abundance of these primary forage organisms.

III. Procedures:

Experimental Design

Four fish populations, including fast and slow growing white and black crappie, were studied. We tested the following null hypotheses:

H_o: Forage was equally abundant in lakes (small reservoirs) where growth of crappies was fast and slow.

H_o: The average amount of food in stomachs of crappies was the same in lakes where growth was fast and slow.

Rejection of either of these hypotheses would suggest that forage abundance was related to growth of crappies.

Discrepancies between abundance, as measured by the sampling equipment, and the actual availability of food items to crappies could have confounded the results, however. This is a very basic problem with no feasible solution, although the consequences of such discrepancies were minimized by the following:

1. The same procedures were used in each lake to estimate abundance of forage. If the availability of a given organism was misrepresented by those procedures, then the bias should be the same for all lakes, and the results comparable on a relative basis.
2. Abundance was estimated only for organisms important in the diet. This assured that bias of the sampling gear for organisms not eaten did not influence the relative importance of items actually in their diet.

Bias due to gear selectivity was probably minimal if the types of organisms consumed were similar in all lakes and abundance changed in direct proportion to changes in diets. The sampling gear was likely to underestimate or overestimate the abundance of some organisms. If those organisms made up similar proportions of the diets for fish from different lakes then the effect of the bias was similar between lakes. If those organisms made up different proportions of the diet between lakes then the effect of the bias was different between lakes.

The quantity of stomach contents may not have been a relative measure of caloric content of food eaten, since caloric content can vary from one type of forage to another. Therefore, the types of forage consumed by each population were also compared.

Description of the Study Area

Four lakes were selected for study based on the following criteria:

1. Populations of crappies with different growth rates. The four lakes included relatively fast and slow growing fish of both species.
2. Relatively old lakes. Fast growing crappies have previously been studied in new lakes (Crawley 1954; Burris 1956). Since crappies usually grow well for the first three to five years in a new reservoir, after which growth rates may decrease (Thompson et al. 1951), Burris and Crawley may have observed temporary conditions, and possibly conditions eventually leading to poor growth. The lakes with fast growing crappies selected for this study were over ten years old and probably provided stable conditions supporting good growth.

3. Small size of the lakes. Lakes under 40 ha were selected so that sampling problems were minimized and results were applicable to state owned reservoirs (under 65 ha) where the management potential is greatest.

4. Low turbidity. Since growth of crappies may be reduced by high turbidity (Hall et al. 1954), we selected lakes with relatively low turbidity (for Oklahoma waters).

5. Convenient location. It was necessary that lakes be located where labor, equipment, and inexpensive lodging were available.

Two of the study lakes contained white crappies and two contained black crappies. The lakes with black crappies were:

1. Ham's Lake, west of Stillwater, Oklahoma (Section 22, Township 19N, Range 1E). Ham's Lake has a surface area of 40 ha, a capacity of 115 hectare meters, and a spillway elevation of 287 msl (Steichen 1974). Ham's Lake is relatively deep, with a maximum depth of 9.4 m. The lake tends to stratify in the summer and dissolved oxygen is reduced in the deeper waters (Figure 3). A mechanical mixing device is operated on Ham's Lake (Steichen 1974). The mixer shortens the period of stratification, as indicated by the August dissolved oxygen profile.

Ham's Lake was relatively clear during the first year of the study, but became very turbid during the second year. Secchi disk transparency averaged 1.05 m from July 1979 to April 1980. Then, apparently due to intense and prolonged rains, transparency decreased to an average of 0.30 m in May 1980 and averaged 0.32 m from then to September 1980. Extensive beds of macrophytes grew

to a depth of roughly 1.5 m during the first year; however, after the dramatic decrease in transparency, macrophytes were rare during the summer of 1980.

Vernon very fine sandy loam and Vernon loam soils make up almost all of the watershed. These are shallow to very shallow soils (13-38 cm deep) underlaid by clay. Infiltration of water is slow, and erosion is a problem when the land is cultivated. Therefore, most of the area is range land and native vegetation (Cobb and Hawker 1918).

2. Comanche Lake on the Wichita Mountains Wildlife Refuge (Section 1, Township 3N, Range 15W). Comanche Lake has a surface area of 21 ha, a conservation storage capacity of 111 hectare meters, and a spillway elevation of 554.7 msl (Oklahoma Water Resources Board 1976).

Comanche Lake has a maximum depth of 9.9 m, about the same as Ham's Lake. However, because of its steeper profile, Comanche has an average depth of about 5 m compared to 3 m for Ham's Lake. Comanche Lake stratifies during the summer and dissolved oxygen is low in the deeper waters (Figure 3).

Comanche Lake was clear throughout the study. The average Secchi disk reading was 2.2 m and it ranged from 1.25 to 3.0 m. Dense beds of macrophytes extended from the shoreline to areas as deep as 5.5 m. Myriophyllum sp. was the dominant macrophyte; Ceratophyllum sp. was common and some Potamogeton sp. were present.

The entire watershed of Comanche Lake consists of rock land and stoney rock land. These are very shallow soils over granite

bedrock, with gentle to moderately steep slopes. Range land is the only appropriate use for these areas, and they are managed as such for wildlife as part of the Refuge (U.S. Department of Agriculture 1967).

The lakes with white crappies were:

1. Lake George on Fort Sill Military Reservation (Section 15, Township 2N, Range 11W). Lake George is listed as having a surface area of 119 ha, a conservation storage capacity of 555 hectare meters, and a spillway elevation of 347 msl (Oklahoma Water Resources Board 1976). However, on the basis of planimeter readings from air photographs, we estimated the surface area to be about 37 ha. That figure seems more realistic based on casual observations of the lake's size during the study. The maximum depth in Lake George is about 6 m. The lake stratified to some degree; however, the zone of oxygen depletion was not as pronounced as in Comanche or Ham's lakes (figure 4).

   Lake George remained relatively clear throughout the study. Secchi disk transparencies averaged 1.03 m and ranged from 0.75 to 1.5 m. Substantial beds of macrophytes grew to a depth of about 2 m. During 1979, when water levels were near the drainpipe level, the macrophytes produced a broad, dense border around the lake, but the majority of the lake remained open. In 1980 the water level ranged from about 1 to 2 m below the drain pipe. The reduced depth allowed macrophytes to grow over a much larger area, and approximately half of the lake area consisted of dense growths of macrophytes. Myriophyllum sp. was the only macrophyte observed.

Soils have not been surveyed near Lake George or on Fort Sill in general. This watershed, like the watersheds of the other lakes involved in the study, consists largely of native vegetation. None of the land is cultivated.

2. Logan Lake on th Fort Sill Military Reservation (Section 16, Township 2N, Range 13W). The surface area and storage capacity of Logan Lake are unknown; however, we estimated the size to be 11 ha based on planimeter readings from air photographs. The surface elevation is 390 msl.

The maximum depth of Logan Lake is about 5 m. The lake stratified during summer; however, like Lake George, the zone of oxygen depletion was not as pronounced as in Ham's and Comanche lakes (Figure 4). Logan Lake remained relatively turbid throughout the study. Secchi disk readings averaged 0.31 m and ranged from 0.20 to 0.50 m. Only a few sparse patches of Myriophyllum were present.

Soil types are unknown, and natural vegetation covers the watershed. There are frequent fires near both lakes George and Logan, which maintain grassland on these watersheds.

Data Collection an Analysis

Crappies:

Adult crappies were collected primarily with hoop nets similar to those described by Houser (1960). Seines, a 3700 watt AC electrofishing boat (4.9 m), 45.7 m experimental gill nets (19 to 63.5 mm bar mesh), trap nets, and hook and line were also used. Lengths to the nearest mm and weights to the nearest g were measured on all fish in smaller catches.

When catches were larger, all of the fish in some nets were weighed and measured by length, whereas the catch in other nets was only counted by species.

Scales (collected from the side near the tip of the pectoral fin) and stomachs were removed from individuals representing the full size distribution of fish collected. When fish were being collected for stomach analysis the nets were generally emptied every morning and evening, and frequently more often.

Growth rates were determined from cellulose acetate impressions of the scales (Tesch 1971). Scales were aged independently by two people. When they disagreed either the two readers came to subsequent agreement, or a third person decided. Growth rates were back-calculated by computer. First the relation between total scale radius and total length was determined. (In all instances a linear relation was found.) Next, correction factors and slopes were computed and used in a second program that back-calculated lengths. Growth increments during each year of the study were then determined and tested for significant differences, with analysis of variance.

Fish used for stomach analysis were usually collected in the morning because food in their stomachs was less-digested than food in stomachs of fish caught in the evenings (unpublished data). Immediately after the fish were taken from the nets, stomachs were surgically removed from the larger crappies and wrapped in cheese cloth. Smaller fish were preserved whole and stomachs later removed in the lab. Fish and stomachs were preserved in 10% formalin.

Food was analyzed in the following manner:

1. The contents were removed from the stomachs and blotted dry.

2. The total volume of the contents was measured by water displacement in a graduated centrifuge tube.
3. Organisms were generally identified to family or order (Pennak 1953; Usinger 1956) under a dissecting microscope and the number of items in each taxon was determined.
4. The volume of each taxon was measured by displacement. When the volume of a taxon from a stomach was too small to be measured, it was based on the number of individuals and an average volume per individual estimated from stomachs where quantities for that taxon were larger, and from forage collected by dredge and plankton net.
5. Percent occurrence of each taxon was based on the number of stomachs that contained food.

Average volume of stomach contents per crappie and per gram of crappie were calculated for each month and year. The sign test (Conover 1971) was used to test for a consistent relation between monthly averages of growth and volume of food.

Catch-per-unit-effort was not used as an estimate of relative abundance because the various methods of capture gave conflicting results. For example, of the four study lakes Comanche had the highest catch-per-unit-effort by electrofishing and the lowest catch-per-unit-effort in hoop nets. Differences in turbidity and macrophyte abundance could explain the relative success of each method. However, a valid measure of relative abundance could not be determined.

Sampling of larval crappies was attempted by taking horizontal tows with a 0.5 m diamter Wisconsin-type net. Some larval crappies were collected, however, samples were collected too infrequently (two to four weeks between samples) to determine the reliability of this method.

Forage Abundance:

Zooplankton was collected from May to October 1979 and from May to September 1980. Four horizontal tows each month were made with a 0.115 m diameter Wisconsin-type plankton net having 80 μ mesh. When possible two surface and two deep (∿1.5 m) tows were made; however, in some instances macrophytes and shallow water limited collection to surface tows. If the combination of surface and deep tows had to be modified on one lake, then it was also modified on the other lake containing the same species of crappies so that the sampliing bias would be similar. Generally two tows were made adjacent to the dam and two in the upper end of each lake.

The average distance of a two was 170 m, taken at a speed of about 57 m/min. A flow meter mounted on the side of the boat determined the volume strained by each tow. Samples were preserved in 10% formalin. Zooplankton was identified (Pennak 1953) and enumerated using 1 ml subsamples in a Sedgewick-Rafter counting chamber. Three subsamples per tow were counted and densities were estimated as follows:

$$\text{No./m}^3 = \frac{[(\text{Average No./ml of sample}) \times (\text{Volume of sample (ml)})]}{[(\text{Area of net opening (m}^2) \times (\text{Length of two (m)})]}$$

Benthic invertebrates were collected with an Ekman dredge (225 cm^2) monthly from May to October 1979 and from May to September 1980. On each date, eight sites were chosen at random in areas of each lake where it was possible to sample. Samples were washed through a #30 mesh sieve at the lake, and preserved in 10% formalin. Invertebrates were separated, identified (Pennak 1953; Usinger 1956), and counted in the lab. The volume of each taxon was measured and the volume of invertebrates important in the diet of crappies was calculated per unit area.

IV. Findings:

Lakes George and Logan contained relatively fast and slow growing white crappies, respectively, and Comanche and Ham's lakes contained relatively fast and slow growing black crappies, respectively (Figures 5 and 6).

Conditions in a lake can change greatly from year to year, as can growth rates of fish. Therefore, it was important to confine the measure of growth to the period when environmental factors were also measured. Fish collected in 1980 were used to determine growth increments during all 1979. However, fish could not be collected in 1981 to determine growth during all of 1980. Instead fish collected during August and September 1980 were used. Thus the 1979 and 1980 growth increments were calculated for different lengths of time, and should not be compared to each other.

Growth increments were greater (by 18-52%) for white crappies age I and older from Lake George than Logan Lake for both years (Table 1). The differences were non-significant in 1979 ($p = 0.098$), but significant in 1980 ($p = 0.0001$). In 1979 yearling crappies in Logan Lake grew slightly faster than those in Lake George; however, the opposite was true for all of the older year classes. Overall growth was therefore greater in Lake George than Logan Lake. Gear selectivity limited the number of yearlings collected for stomach analysis. Stomachs were collected primarily from the older crappies which grew significantly faster in Lake George than in Logan Lake and consequently it is appropriate to refer to the stomach data from Lake George as representing faster growing fish than that from Logan Lake. Growth increments were greater (by 6-36%) for black crappies of given ages from Comanche Lake than Ham's Lake in 1979 ($p = 0.046$), but were statistically similar (greatest difference = 18%) in both lakes in 1980

($p = 0.424$ level; Table 2). Thus, contrasting growth could be related to other factors for both years with white crappies, but for only 1979 with black crappies. (Detailed data on age and length frequencies are presented in Appendix A. Condition factors are presented in Appendix B.)

Relative volumes of stomach contents were not closely correlated with growth. The sign test showed no relations between the monthly average volume of stomach contents per individual and growth (significant at the 0.48 level; Table 3). Monthly average volume per gram of fish was negatively related to growth. The relation was significant at the 0.10, but not at the 0.05 level (Table 4).

Annual average volumes of stomach contents indicate the same patterns. In two instances (white crappies in 1980 and black crappies in 1979), the annual average volume of stomach contents per gram of fish (Table 5) was greater (by 48-69%) where growth was slow than where growth was fast. When growth rates of white crappies also differed in 1979, however, populations contained nearly identical mean volumes of food per biomass. Also, in 1980 black crappies grew at similar rates in both lakes, yet the mean volume of food eaten per biomass was 39% greater in Comanche Lake. Although the pattern was not consistent, the average volume of stomach contents per gram of fish tended to be greater when growth was slow than where growth was fast.

Annual average volumes of stomach contents per fish also were not closely related to growth (Table 6). Volumes per black crappie were 42% greater in Comanche Lake in 1980, yet growth rates in Ham's Lake were similar to those in Comanche Lake. The second greatest difference was between the white crappie populations in 1980, when slow growing individuals in Logan Lake had eaten 29% more than the fast growing

individuals in Lake George. In 1979, the pattern was reversed for both black and white crappies; i.e., 23-42% more food per fish was eaten where growth was fast (lakes George and Comanche) than where growth was slow. Food habits do not support the hypothesis that fast growing fish ate more than slow growing fish. Overall the results were inconsistent, and the results of approximately one-half of the comparisons were the opposite of what would be expected.

We assumed that average volume of stomach contents was an approximation of caloric intake. However, caloric content per gram of wet weight varies greatly between different types of forage (Table 7). If slow and fast growing fish consumed different types of forage, then the caloric content per unit volume of stomach contents may have been different. According to previous workers (Crawley 1954; Burris 1956) differences in types of forage consumed may be more significant than total quantity in determining growth.

The results of this study, however, did not indicate that the type of forage consumed was closely related to growth. The relative importance of fish, benthic invertebrates, and zooplankton in the diet (Table 8) was highly variable for both fast and slow growing fish. For crappies from 100 to 149 mm total length, fish and benthic invertebrates were more important in 1979 in the diet of fast growing crappies than in slow growing crappies. Zooplankton constituted most of the food of slow growing crappies and a relatively small percentage of the diet where growth was fast. In 1980, however, the patterns were very different. Fish were more important, and zooplankton was scarce in the diet of slow growing white crappies relative to fast growing white crappies. Benthic invertebrates remained abundant where growth was fast relative to where growth was slow. On the other

hand, the importance of benthic invertebrates differed greatly in the diets of the two black crappie populations where growth rates were similar.

The relative importance of each type of forage was also highly variable for crappies greater than 150 mm total length (Table 8). Where growth was fast the percentage of fish, benthic invertebrates, and zooplankton in the diet varied from 11 to 79, 13 to 57, and 0.4 to 22, respectively. Where growth was slow fish made up from 35 to 87% of the diet, benthic invertebrates from 11 to 50% and zooplankton from less than 0.1 to 5%. Fish tended to be rare, and benthic invertebrates and zooplankton were more common in stomachs where growth was fast relative to where growth was slow. However, the differences were probably not significant. Also, in the instance where growth rates were similar (black crappies in 1980), the diets of the two populations were very different.

The next question was whether actual abundance of forage in the environment, rather than growth (a possible function of forage abundance), was related to diet. This factor was difficult to investigate, however, because different units were used to measure the abundance of different organisms, so a single estimate of total forage abundance could not be made. For example, the abundance of zooplankton was estimated per unit volume of water so that it was pertinent to a discussion of fish feeding. However, benthic invertebrates were encountered on a unit area basis and their densities needed to be measured over only two dimensions. The approach used here was to ordinally compare abundance of a given organism in two lakes or years with the importance of that forage in the diets of the corresponding sample of crappies. For example, if benthic invertebrates were more abundant during 1980 than during 1979 in Lake George, then it would be expected that they made up more of the diet during 1980 than 1979.

However, the abundance of benthic invertebrates and zooplankton in the diet of fish within a lake did not appear to be correlated to the organism's relative abundance in the environment in different years. Although benthic invertebrates are generally considered to be the main component in the diet of crappies 100 to 149 mm in length, abundance in the environment changed in the same direction as the change in importance in the diet only in Lake George (Table 9). In two lakes (Logan and Ham's) the changes were in opposite directions, and in Comanche Lake abundance in the environment remained constant but importance in the diet declined. For 16 similar comparisons made between years within lakes for both benthic invertebrates and zooplankton and for both size groups of crappies (Table 10), higher environmental abundance was associated with greater importance in the diet only eight times. Thus, although benthic invertebrates and zooplankton tended to be more abundant where growth was fast than where growth was slow, these differences in abundance did not appear to be directly related to differences in diets.

V. Analysis:

The data indicated growth appeared to be independent of food intake (based on average volume of stomach contents per fish) or negatively correlated with food intake (based on average volume of stomach contents per gram of fish). The analysis based on the average volume of stomach contents per fish may be the more appropriate measure, because the ultimate concern of this study was production of crappies of harvestable size (absolute growth of individuals), rather than maximization of total crappie production. These results are at odds with much of the published literature. For example, Paloheimo and Dickie (1965, p. 527) stated

"...the same absolute ration appears to lead to the same absolute growth rate no matter what the size of fish." This conflict with accepted conclusions led us to carefully review the assumptions of our methods and design.

Because of interaction of numerous factors, the relation between food consumption and the resulting growth is very complicated. The equation $pR = T + \Delta w/\Delta t$, where R is the ration consumed, p is a factor to adjust for incomplete digestion of the food consumed, T is the total energy metabolized, and $\Delta w/\Delta t$ is growth, has been presented by Paloheimo and Dickie (1965, 1966a, 1966b) as a useful guide for organizing discussion of this relation. The equation basically states that energy that is consumed and not excreted is either metabolized or used for growth. Given the following assumptions:

1. Average volume of stomach contents provided a relative measure of the energy consumed (average volume was directly proportional to R).
2. Of the energy consumed the proportions excreted were the same for the crappie populations being compared (p for white crappies in Lake George = p for white crappies in Logan Lake, and p for black crappies in Comanche Lake = p for black crappies in Ham's Lake).
3. Total metabolism was similar for the populations being compared (T for white crappies in Lake George = T for white crappies in Logan Lake, and T for black crappies in Comanche Lake = T for black crappies in Ham's Lake).

If these three assumptions are true, then it follows that a greater average volume of stomach contents would result in greater growth. Since our data did not show this relationship, one or more of the above assumptions may have been invalid.

Several factors, including caloric content and seasonal and daily variations in feeding patterns, affect the validity of assuming that average volume of stomach contents was a relative measure of energy intake. For example, variations in daily feeding patterns could have biased the observed volume of stomach contents. As a result of a short period of intense feeding each day, volume of stomach contents is large shortly after feeding and small just before the next period of feeding. In contrast, extended periods of feeding each day result in more consistent volumes of food in the stomach (Eggers 1977). If the crappies tended to feed intensively for short periods, and if this feeding period occurred at different times in the various lakes, then the volume of stomach contents (which we collected in the morning) would be highly variable, and the bias produced in each lake would have differed depending on the times of feeding.

The literature does not seem to support the idea of short intense feeding periods for crappies. Numerous studies have indicated that crappies tended to feed continuously rather than for a short period each day (Burris 1956; Seaburg and Moyle 1964; Keast 1968; Tucker 1972). In addition, other authors have also found a negative correlation between food volume and growth. Crawley (1954), who varied his sampling throughout the day in order to eliminate any bias due to a short period of feeding, found a greater average volume of stomach contents where growth was slow than where growth was fast. Altogether, the literature suggests that daily feeding patterns should not have had a great influence on our relative measure of energy intake.

Different digestive rates among populations also limit the usefulness of volume of stomach contents as a relative measure of energy intake.

Given the same food intake, fish that are rapidly digesting food will at any given time have a smaller volume of stomach contents than fish that digest food more slowly. The digestive rate of fish is temperature dependent (Tolg 1962; Kitchell and Windell 1968). In this study relative high temperatures (up to 27.2°C) could have caused the measure of food (energy) consumed to be underestimated; however, metabolism would also have been higher and proportionally less energy would have been available for growth. To some degree the two effects would cancel each other, producing an unknown, but smaller net effect. Regardless, differences in temperature did not appear to be the cause of the unexpected results. In 1980, when slow growing white crappies in Logan Lake apparently consumed more than fast growing white crappies in Lake George, temperatures were similar in areas of the two lakes where levels of oxygen were suitable for fish survival (Table 11). Temperatures were often the same, and never differed by more than 1.6°C.

Seasonal variations in feeding could also influence the usefulness of volume of stomach contents as a relative measure of total energy intake. In 1979 stomachs were collected for a six-month period in all of the lakes except Ham's, where samples were collected for only four months. However, growth was estimated for the entire year. In 1980 stomach samples were collected for five months whereas growth was measured for a nine-month period. It is possible that fish in one population did most of their feeding and growing when samples were not being collected, while fish in other lakes happened to feed and grow primarily during the months of sampling. If this hypothesis were true, food habits as measured during one part of the year would not have been representative of what occurred during the remainder of the year. This prospect seems unlikely, however. Samples

were collected throughout the warmer seasons (May to October in 1979 and May to September in 1980), when feeding, growth and digestive rates should have been greater than during the colder seasons. Presumably, much of the energy consumed during spring was expended for spawning. Thus, even if feeding patterns during the warmer months were very different from those during the remainder of the year, it seems that the period most significant, in terms of feeding and growth, was studied.

Another posibility is that fast and slow growing populations consumed foods with different caloric values. The caloric content of various forage organisms is highly variable; however, there was no indication that fast growing fish consistently ate items with different per unit volume caloric content than those eaten by slow growing fish. In summary, the assumption that average volume of stomach contents is a relative measure of energy intake can not be categorically accepted; however, a variety of evidence tends to support the assumption and none was found that discredited it.

The assumption that digestive efficiency was similar for all the crappie populations also defies absolute verification. Digestive efficiency is presumably dependent on the type of organisms being digested, but there is little specific information on the digestibility of the various taxa. To properly evaluate this assumptions, detailed information on caloric content and digestibility of the various food items, year round sampling of diel feeding habits, and knowledge of temperature selection of crappies in each lake are needed. Such information is not currently available but it appears that this assumption is not unreasonable. If this assumption is valid then we are left with only the third assumption of differences in total metabolism between fish from the different lakes to explain our results.

Total metabolism as discussed by Paloheimo and Dickie (1965; 1966a, 1966b) includes energy used for maintenance and activity. Ration size and temperature are two of the factors that affect total metabolism of fish. As temperature increases total metabolism increases and, given a constant energy supply, less energy is available for growth (Paloheimo and Dickie 1966b). However, as discussed previously, the effect of a temperature difference on total metabolism was countered by differences in digestion rates, a bias in how food consumption was measured, and by the fact that there were no differences in temperature among the lakes.

Total metabolism also is expected to increase as ration size increases. This relationship is not direct because as the ration size of fish increases the proportion of the ration used for maintenance and activity increases, and the proportion available for growth decreases. As the proportion available for growth decreases, however, the absolute amount available for growth increases (Paloheimo and Dickie 1965). The result of this interaction is that a given change in the ration size is associated with a proportionally greater change in ration size available for growth Therefore, in this study where growth rates were statistically different, a clear difference in ration size would be expected. Based on these observations we must conclude that neither temperature or ration size explain the lack of relationship between food intake and growth and must look to physiological factors to explain the data.

Physiological factors, that induce stress (high salinity, concentration of metabolic wastes, lack of cover, predation) and changes in behavioral activity also affect total metabolism. High salinity or concentrations of metabolic wastes have been shown to increase the energy required to maintain osmotic balance in fish, thereby increasing total

metabolism (Paloheimo and Dickie 1966b). Laboratory studies have shown that for certain species, a fish held as an individual has a higher metabolism than if it is allowed to form a group with other fish (Schuett 1933; Delco and Beyers 1963). In addition, the formation of hierarchies within groups of fish has been shown to affect growth efficiency (Paloheimo and Dickie 1966b).

Feeding behavior can also influence total metabolism. For example, active chasing of prey would require more metabolic expenditures than filtering or stalking. In addition, type of forage, cover, forage abundance, variance in food distribution (Ivlev 1961) and a wide variety of other factors could also influence feeding bahavior and total metabolism.

The data did not show any relationship between the abundance of forage in the environment and importance in the diet of crappies. One possible explanation is that changes in abundance of forage fish, which were not measured, may have had a greater influence on the food habits of crappies than changes in abundance of benthic invertebrates and zooplankton which were measured. In addition, the estimates of benthic invertebrates and zooplankton abundance were probably not strictly comparable between lakes, and may not have been entirely comparable for different years within a given lake. Extent of macrophyte growths determined where forage organisms could be sampled and this growth differed among lakes and between years.

In spite of these limitations, in summary we find the quantity and types of forage consumed did not appear to be related to the growth rates of fish in the four lakes studied. We conclude that in these lakes physiological and/or behavioral factors affected the metabolism and, therefore, the efficiency with which food was utilized. These conclusions appear to be consistent with the results of other studies on the

relationship between diet and growth of crappies (Crawley 1954; Burris 1956; Seaburg and Moyle 1964); although they are inconsistent with the current accepted explanation of stunting. Crawley found that the quantity of food consumed was unrelated to growth and concluded that differences in the nutrient content of the items consumed were responsible for the differences in growth. He mentioned the relatively small quantity of food and high occurrence of insect larvae in the stomachs where growth was fast and suggested that insect larvae were responsible for the rapid growth. Burris found that some fast growing fish contained more food than slow growing fish; however, the opposite was true for the size groups of crappies he concluded were "most severely stunted." He emphasized that fish were more important in the diet where growth was faster and probably were responsible for the differences in growth. Seaburg and Moyle (1964) found that a population of young fast growing crappies contained more than twice as much food as a population of older, slower growing individuals. The instances where fast growing crappies contained more food than slow growing crapppies can easily be attributed to chance but a consistent pattern seems to exist. Most authors have seemed reluctant to attribute the negative or no relationship between quantity and types of forage to physiological differences. Almost as an afterthought, previous workers seem to have concluded that since the quantity of food consumed did not determine growth rate, the types of forage did. The contrasting conclusions of Crawley (1954) and Burris (1956) and the lack of a consistent pattern in the present study, taken together, however, suggest that the types of forage consumed were also not closely related to growth.

Conclusions

Growth rates did not appear to be determined by the quantity or types of forage present or consumed in the four lakes studied. However, several assumptions made in this study need to be tested for validity. Seasonal and daily variations in feeding patterns could have biased the results. However, other studies suggest that possibility is unlikely. Evaluation of the types of forage consumed did not indicate that differences in caloric content per unit volume of food were related to differences in growth; however, this aspect may warrant further investigation. Temperatures did not appear to differ enough to be responsible for a difference in digestive rates or total metabolism and it appears unlikely that digestive efficiency would have been significantly different between populations. By a process of elimination, we suggest that physiological factors (stress), such as high salinities or concentrations of metabolic wastes, or differences in feeding and schooling behavior could have resulted in differences in the total metabolism of individuals in the four populations.

Recommendations:

Future studies should concentrate on evaluating potential biases encountered in this study and investigating the physiological difference hypothesis presented. Since many studies indicate that growth is density dependent, monitoring of physiological and behavioral aspects potentially related to growth while altering densities might be a feasible approach.

Factors affecting mortality of crappies should also be investigated, since many populations of crappies contain both slow growing individuals and a large proportion of fish that are age III and younger. Black crappies in Comanche Lake (which was unfished grew at moderate rates, yet a

very large proportion (83%) of these invididuals were of a harvestable size (Appendix A). The same appears to be true in nearby Grama Lake, which is also unfished (unpublished data). Fishing mortality and predator-prey interactions of largemouth bass and crappies, as described by the theory of proportional stock density (Anderson 1976), may be important.

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Table 1. Growth increments of white crappies of various ages from lakes George and Logan during 1979 and 1980.

Year of life	Lake and growth (mm)			
	January-December 1979		January-September 1980	
	George[1]	Logan[1]	George[2]	Logan[2]
0-1	76	83	-	74
1-2	49	39	67	29
2-3	35	23	18	12
3-4	-	24	13	11
4-5	33	25	-	9
5-6	-	38	-	-

[1]Statistically different at the 0.098 level.

[2]Statistically different at the 0.0001 level.

Table 2. Growth increments of black crappies of various ages from Comanche and Hams lakes during 1979 and 1980.

Year of life	January-December 1979 Comanche[1]	Hams[1]	January-September 1980 Comanche[2]	Hams[2]
0-1	117	99	-	74
1-2	61	50	-	45
2-3	37	35	45	38
3-4	32	23	24	24
4-5	-	-	15	14
5-6	9	-	-	-

[1]Statistically different at the 0.046 level.

[2]Statistically different at the 0.424 level.

Table 3. Relative growth rate and monthly average volume of stomach contents (X 10^3) per individual black and white crappies from various lakes, 1979 and 1980. [The symbol in parentheses indicates if the amount of food was greater in the lake with faster (+) or slower (-) growth.[1]]

Year	Species	Lake	Growth rate	Month and mean volume (ml)/individual X 10^3					
				May	June	July	Aug.	Sept.	Oct.
1979	White crappies	George	Fast	18.2	267.0	74.2	-	95.2	421.1
		Logan	Slow	89.0	426.8	135.3	-	100.0	11.5
				(-)	(-)	(-)	-	(-)	(+)
	Black crappies	Comanche	Fast	63.0	145.0	121.9	-	261.5	0.0
		Hams	Slow	-	-	58.8	58.3	55.6	160.0
				-	-	(+)	-	(+)	(-)
1980	White crappies	George	Fast	76.2	28.8	350.0	146.8	94.1	-
		Logan	Slow	171.4	163.6	254.5	0.0	312.5	-
				(-)	(-)	(+)	(+)	(-)	
	Black crappies	Comanche	Similar	966.7	140.0	198.1	261.5	306.3	-
		Hams	Similar	88.9	97.9	200.0	347.4	375.0	-

[1]Sign test: 13 trials, 5 were (+); statistically different at the 0.48 level (two-tailed test).

Table 4. Relative growth rate and monthly average volume of stomach contents per gram ($X\ 10^3$) of black and white crappies from various lakes, 1979 and 1980. [The symbol in parentheses indicates if the amount of food was greater in the lake with faster (+) or slower (-) growth.[1]]

Year	Species	Lake	Growth rate	Month and mean volume (ml)/g $X\ 10^3$					
				May	June	July	Aug.	Sept.	Oct.
1979	White crappie	George	Fast	0.47	4.96	2.22	-	2.83	5.64
		Logan	Slow	2.27	6.23	3.88	-	3.31	0.51
				(-)	(-)	(-)	-	(-)	(+)
	Black crappie	Comanche	Fast	0.42	1.25	0.77	-	2.04	0.00
		Hams	Slow	-	-	1.43	1.11	1.04	1.74
				-	-	(-)	-	(+)	(-)
1980	White crappie	George	Fast	1.08	0.70	5.31	3.90	2.24	-
		Logan	Slow	2.57	4.05	6.98	0.00	8.73	-
				(-)	(-)	(-)	(+)	(-)	
	Black crappie	Comanche	Similar	9.55	0.84	1.26	1.87	2.73	-
		Hams	Similar	1.43	1.51	2.96	5.34	0.43	-

[1]Sign test: 13 trials, 3 were (+); statistically different at the 0.092 level (two-tailed test).

Table 5. Yearly average volume of stomach contents per gram (X 10^3) of black and white crappies from various lakes, 1979 and 1980.

Species and lake	Mean volume (ml)/g X 10^3 1979	1980
White crappie		
George	3.22	2.65
Logan	3.24	4.47
Black crappie		
Comanche	0.90	3.25
Hams	1.33	2.33

Table 6. Yearly average volume of stomach contents (X 10^3) per individual black and white crappies from various lakes, 1979 and 1980.

Species and lake	Mean volume (ml)/individual 1979	1980
White crappie		
George	175.1	139.2
Logan	152.5	180.4
Black crappie		
Comanche	118.3	374.5
Hams	83.2	263.1

Table 7. Caloric content of various organisms found in stomachs of black and white crappies.

Taxon	Calories[1] Gram wet weight	Gram dry weight
Cladocera	-	5241
Daphnia	814	5028
Copepoda		
Diaptomidae	550	5741
Cyclopidae	-	5788
Amphipoda	934	4022
Insecta	759	4823
Ephemeroptera	-	5469
Odonata	-	5117
Diptera	613	4276
Chironomidae	656	5424
Centrarchidae	-	4677
Clupeidae	1927	6360

[1]From Cummins and Wuycheck (1971).

Table 8. Relative importance of fish, benthic invertebrates, and zooplankton in the diets of black and white crappies from four lakes, 1979 and 1980. (Unidentified remains bring totals up to 100 percent.)

Size class of crappie (mm)	Year	Taxon	Species, lake and percent (by volume) of stomach contents			
			White crappie		Black crappie	
			George	Logan	Comanche	Hams
100-149	1979	Fish	5	<0.1	49	0
		Benthic invertebrates	73	41	43	7
		Zooplankton	18	59	0	63
	1980	Fish	<0.1	73	87	8
		Benthic invertebrates	95	25	12	75
		Zooplankton	5	1	1	4
150-over	1979	Fish	77	87	11	35
		Benthic invertebrates	13	11	57	50
		Zooplankton	10	2	22	5
	1980	Fish	79	83	9	76
		Benthic invertebrates	18	15	82	12
		Zooplankton	0.4	<0.1	4	0.4

Table 9. Abundance of benthic invertebrates in the environment relative to importance in the diet of black and white crappies 100-149 mm total length, 1979 and 1980.

	Species and lake							
	White crappie				Black crappie			
	George		Logan		Comanche		Hams	
Year	Environment (no./m^2)	Diet (% total volume)	Environment (no./m^2)	Diet (% total volume)	Environment (no./m^2)	Diet (% total volume)	Environment (no./m^2)	Diet (% total volume)
1979	0.028	73	0.024	41	0.101	43	0.056	7
1980	0.054	95	0.031	25	0.101	12	0.032	75
Change	+0.026	+22	+0.007	-16	0.0	-31	-0.024	+68

Table 10. Abundance of forage types in the environment relative to importance in the diet of crappies of two sizes.

Crappie size group (mm)	Forage type	Comparison of changes between years within lakes		Comparison of changes between lakes within years	
		Expected[1]	Not expected	Expected[1]	Not expected
100-149	Benthic invertebrates	1	3	3	1
	Zooplankton	2	2	2	2
>149	Benthic invertebrates	3	1	4	0
	Zooplankton	2	2	3	1
	Totals	8	8	12	4

[1]Expected means greater abundance in the environment was associated with greater importance in the diet.

Table 11. Minimum and maximum water temperatures (^{o}C) in areas of lakes George and Logan that had dissolved oxygen concentrations of 3.0 ppm or more.

	Date and lake							
	May 1980		June 1980		August 1980		September 1980	
	George	Logan	George	Logan	George	Logan	George	Logan
Maximum	20.0	20.0	26.1	26.7	26.6	27.2	25.0	25.6
Minimum	20.0	19.4	24.4	25.0	25.6	26.7	23.9	24.4

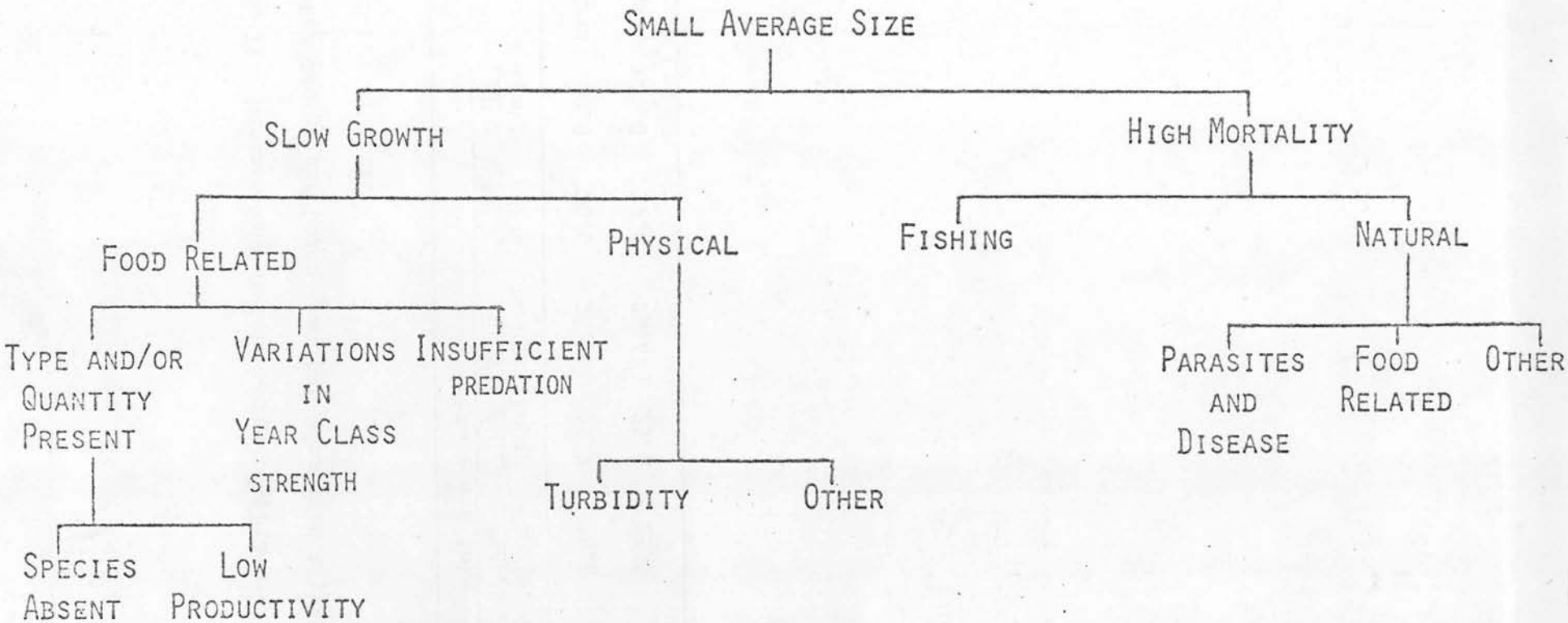


Figure 1. Flow chart of factors affecting the average size of crappies.

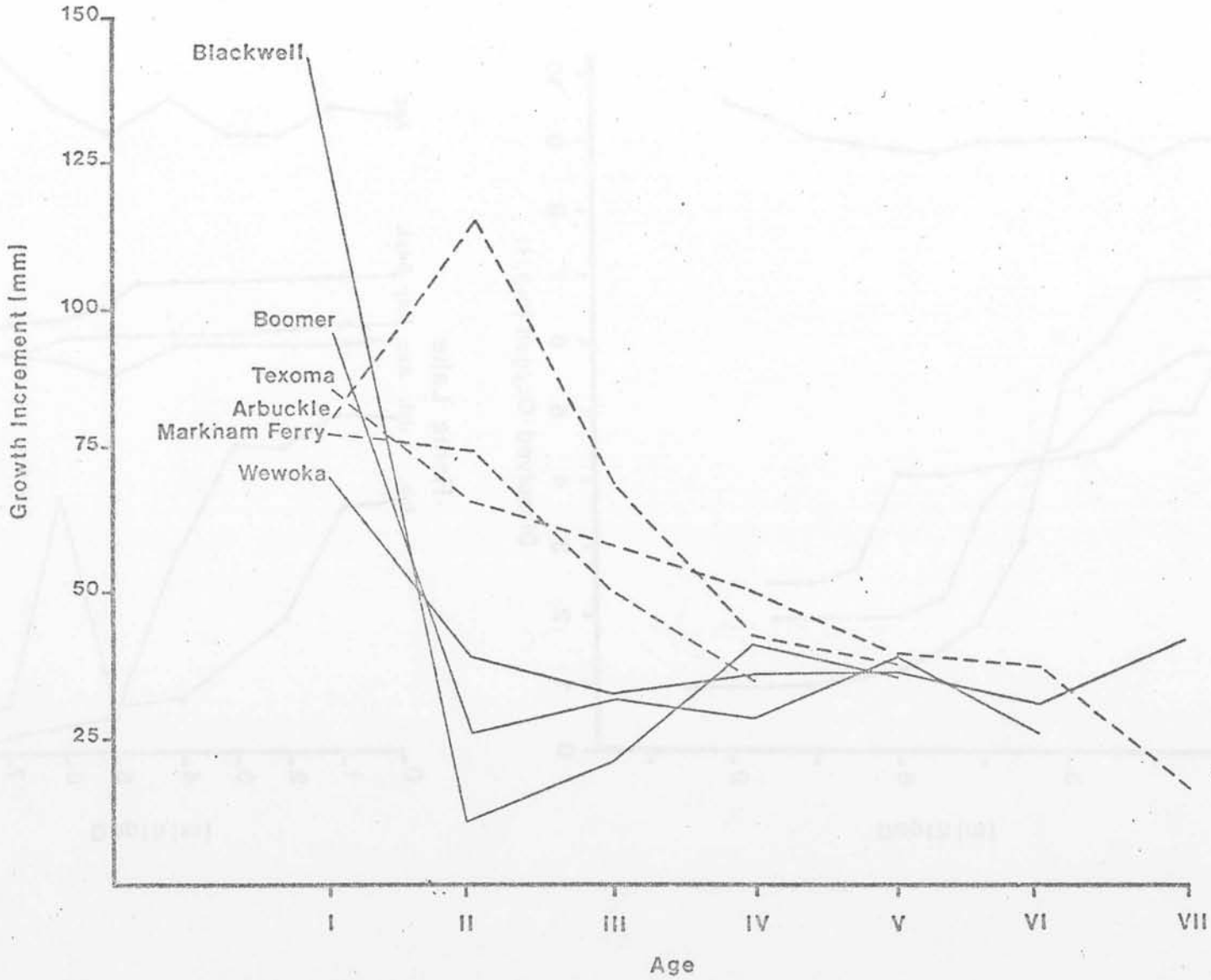


Figure 2. Annual growth increments of white crappies from lakes where growth is relatively good (--) and relatively poor (—).

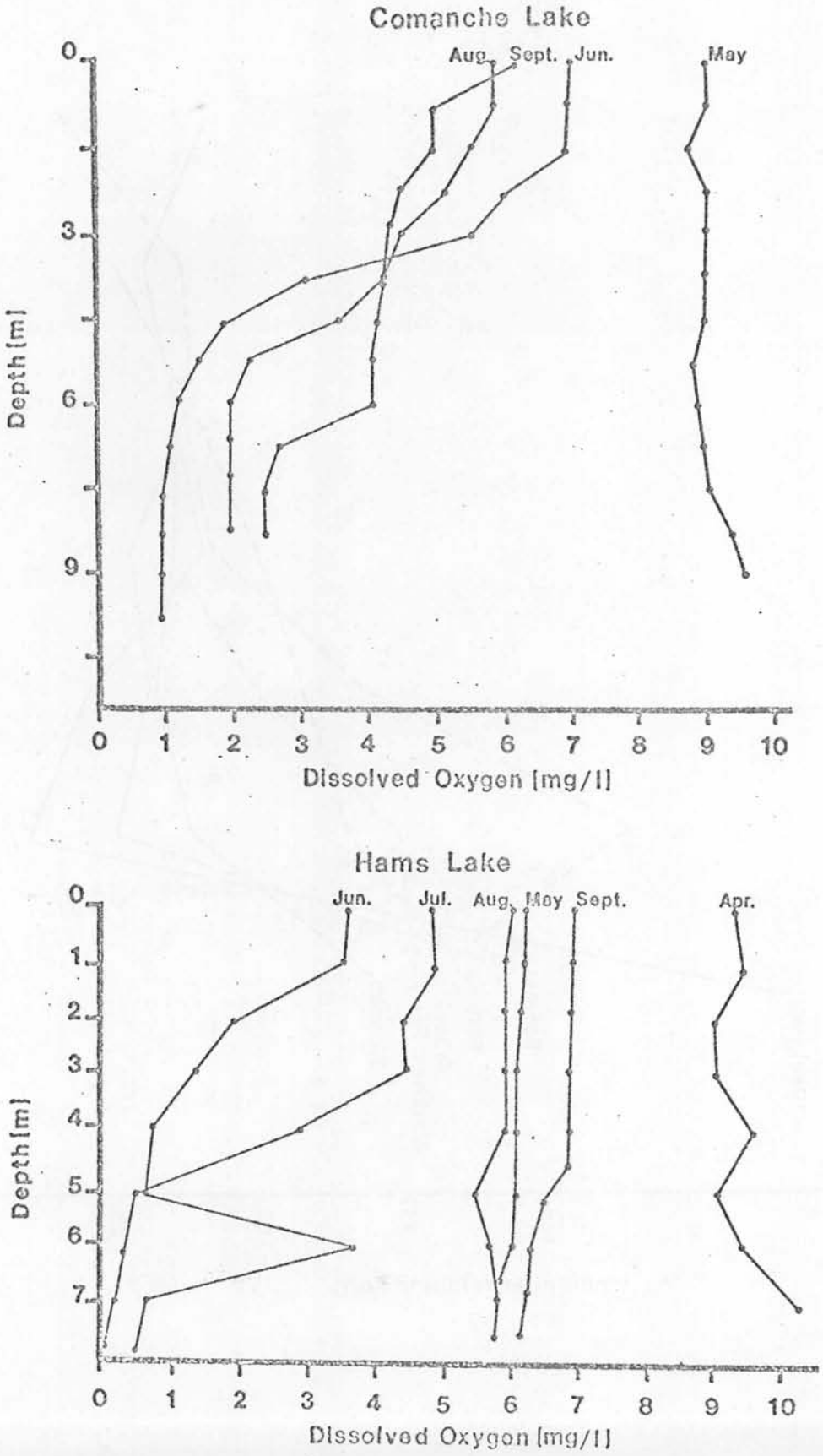


Figure 3. Dissolved oxygen profiles of Comanche and Hams lakes during various months.

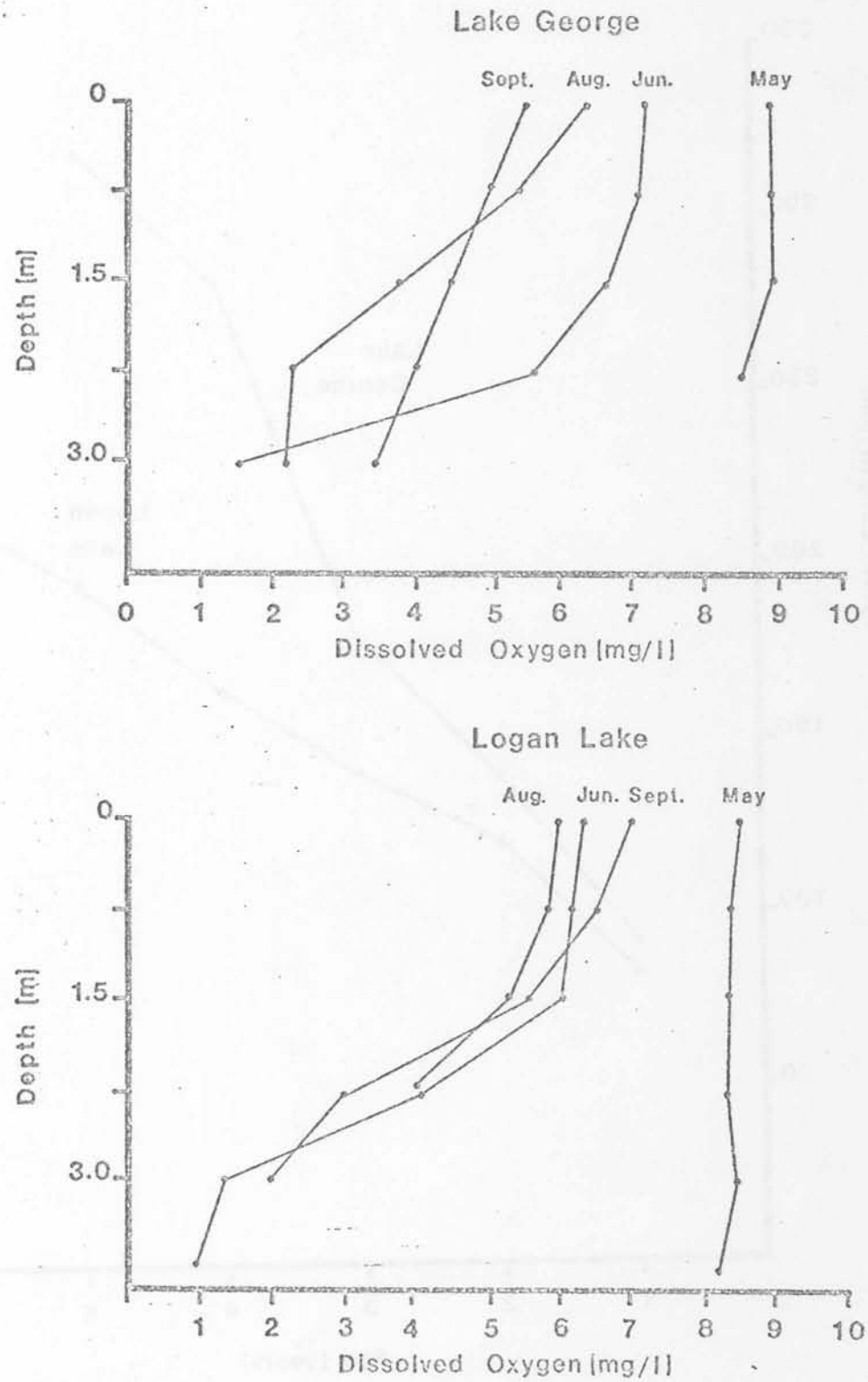


Figure 4. Dissolved oxygen profiles of lakes George and Logan during various months.

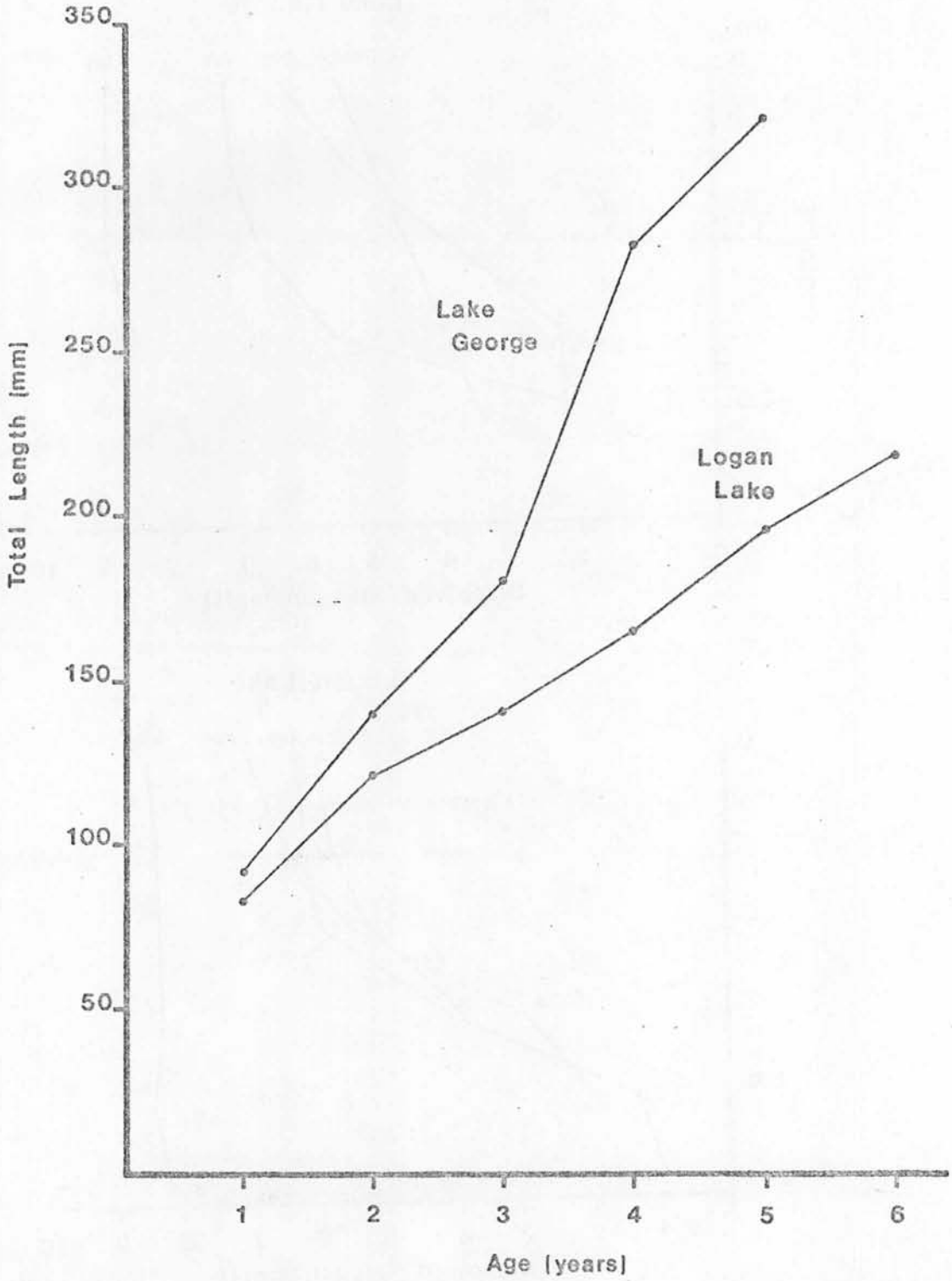


Figure 5. Average total length of white crappiesof various ages from lakes George and Logan during 1979 and 1980.

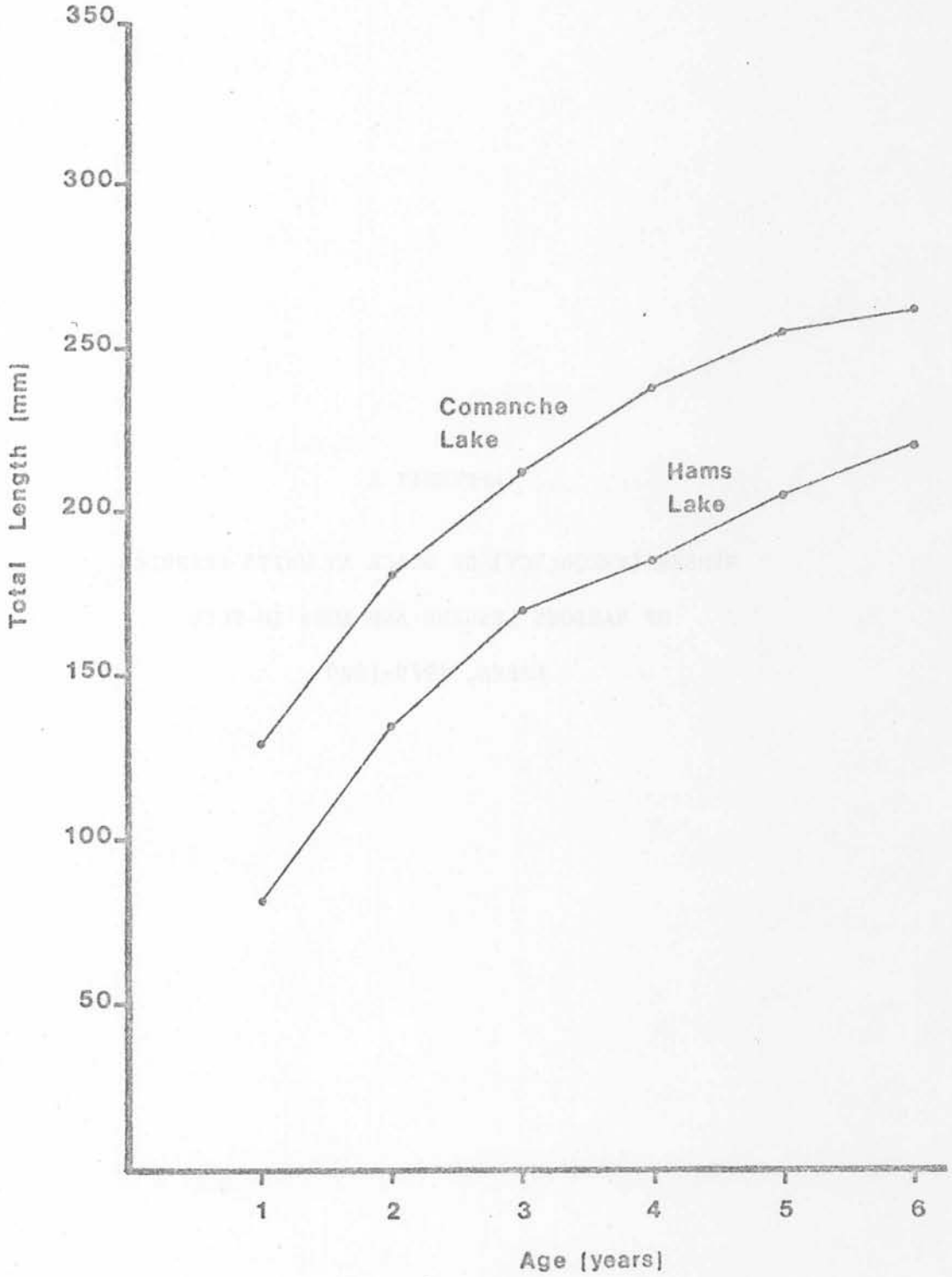


Figure 6. Average total length of black crappies of various ages from Comanche and Hams lakes during 1979 and 1980.

APPENDIX A

NUMBER (FREQUENCY) OF BLACK AN WHITE CRAPPIES OF VARIOUS LENGTHS AND AGES IN FOUR LAKES, 1979-1980

Some observations can be made from length and age frequencies; however, additional information would be required before any final conclusions can be made. The graphs indicates that angler harvest and proportional stock density (Anderson 1976) could be more important than growth rates in determining the proportion of crappies of harvestable size in a population.

Fishing pressure varied greatly between the lakes. No fishing has been allowed in Comanche Lake; a very limited number of people have access to Ham's Lake for fishing; and fishing pressure was relatively heavy on lakes George and Logan. Fishing from the bank was the primary method used on lakes George and Logan. Because Lake George was much larger and had dense beds of macrophytes along the shoreline for much of the year, harvest undoubtedly had much less impact on the fish populations in that lake than in Logan Lake.

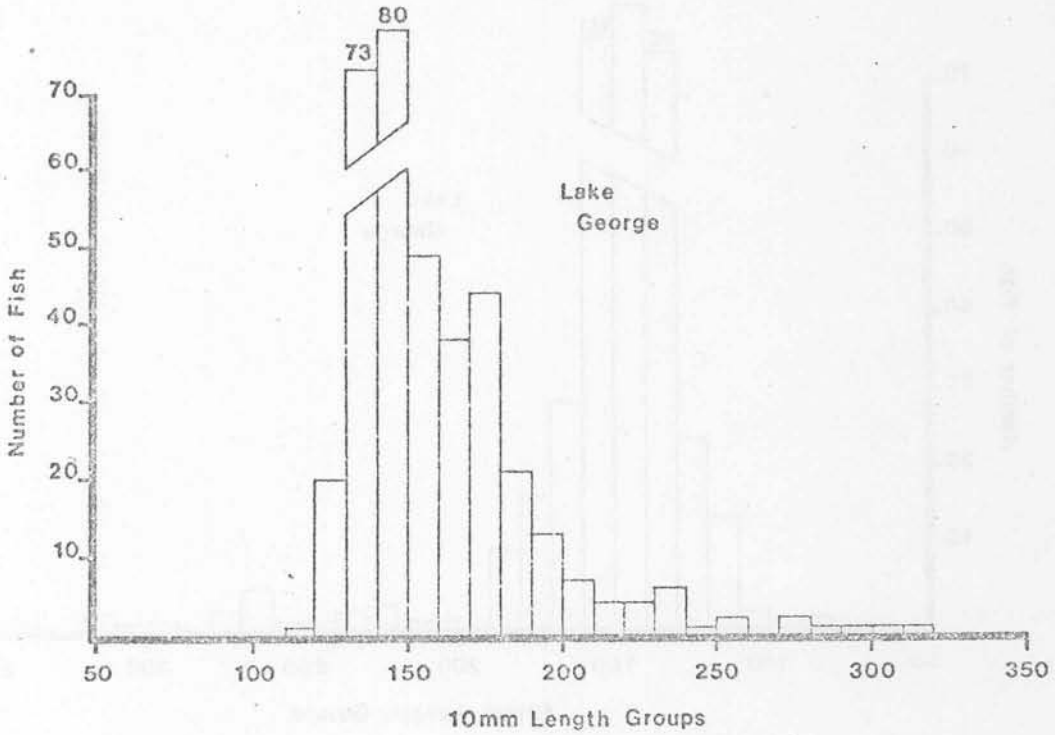
The proportion of harvestable size crappies was inversely correlated with fishing pressure. The majority of black crappies in Comanche Lake (where no fishing has been allowed) were 200 mm or longer (Figures 9 and 10). Ham's Lake, with limited fisherman access, had moderate numbers of black crappies over 200 mm; however, crappies in Lake George were slightly larger, on the average, than white crappies in Logan Lake (Figures 7 and 8).

Growth rates did not appear to be correlated with the proportion of crappies of harvestable size. Overall growth in Lake George was similar to growth in Comanche Lake and better than growth in Ham's Lake (Figures 5 and 6), yet relatively few crappie of harvestable size were present in Lake George. In lakes George and Logan size distributions of white crappies were similar, although growth rates were different. Crappies from Ham's and Logan lakes grew at similar rates (Figures 5 and 6), and their size

distributions were very different.

The absence of a relation between growth rates and size distributions in 1979 changed relatively little in 1980. Thus the age distribution seem to be basically stable (Figures 11, 12, 13, and 14). The same age groups of crappie remained dominant instead of particular year classes.

The negative correlation between fishing pressure and proportion of large fish does not mean that angling was directly responsible for the lack of large crappies. Since interviews with fishermen indicated they had little interest in, and caught few crappies in the lakes, harvest of crappies did not appear to be great enough to be solely responsible for the observed differences in size distributions. Since most anglers fished for largemouth bass, predator-prey interactions between bass and crappie were probably the link between fishing pressure and size distribution of crappies. Unfortunately, we did not catch enough largemouth bass to determine their abundnce and relative size in the four lakes.



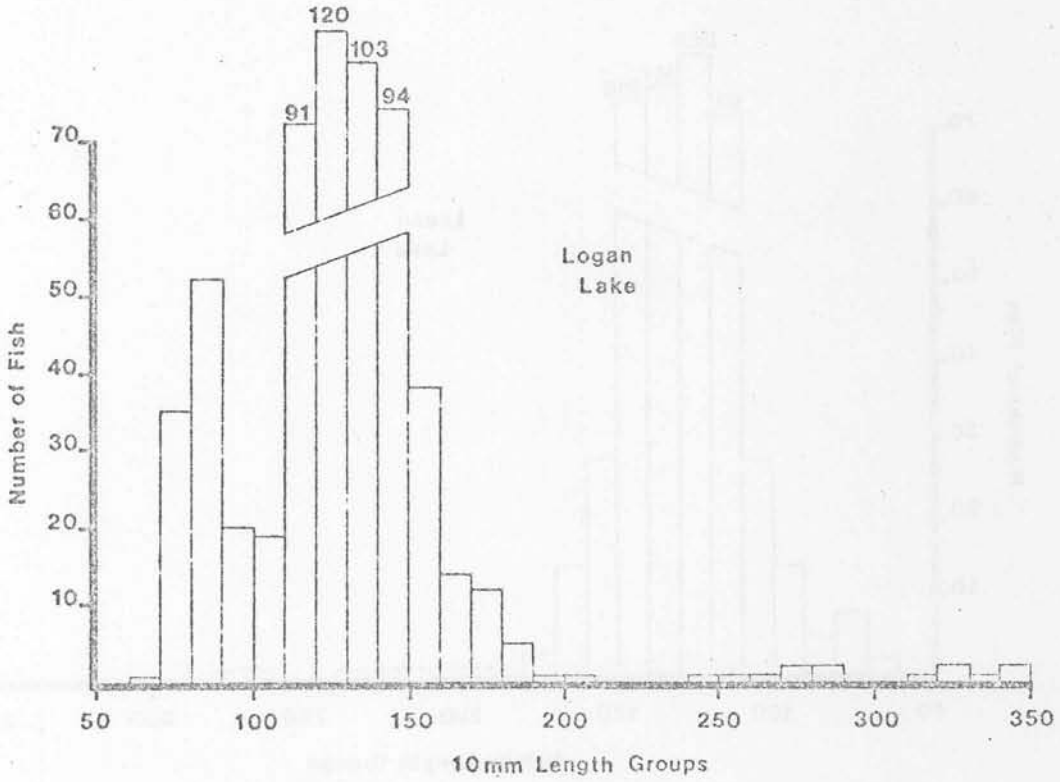
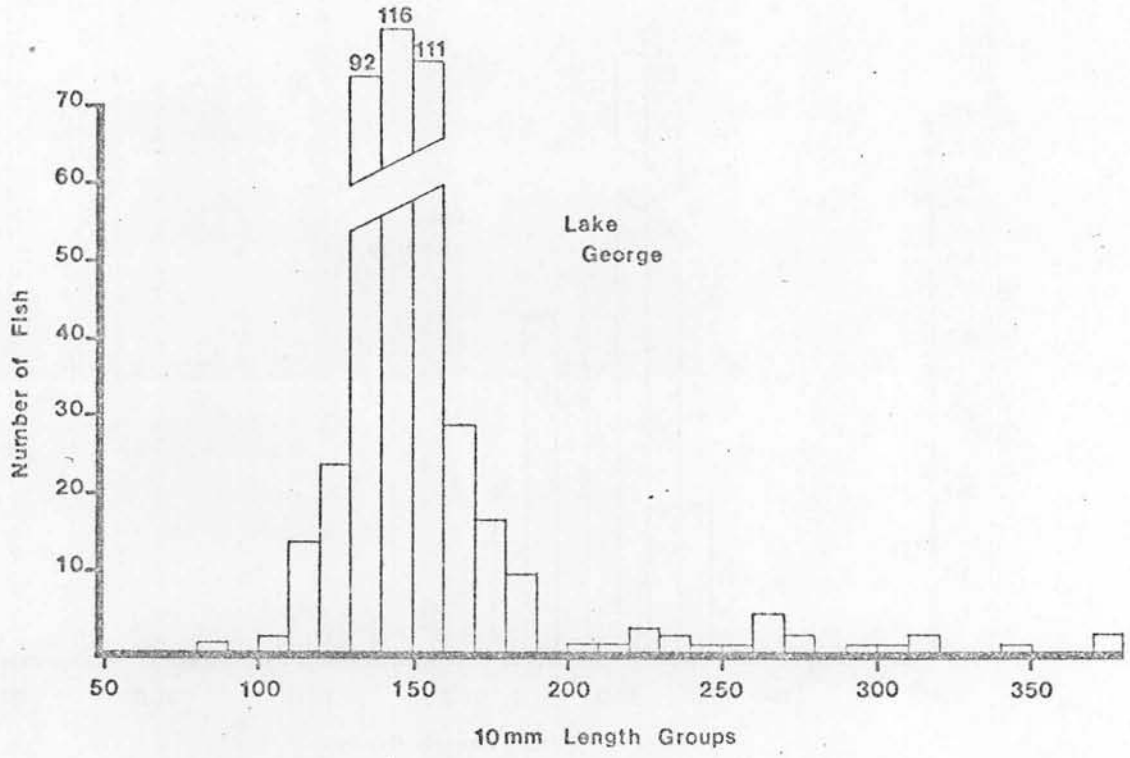


Figure 7. Length frequencies for white crappiesfrom lakes George and Logan, 1979.



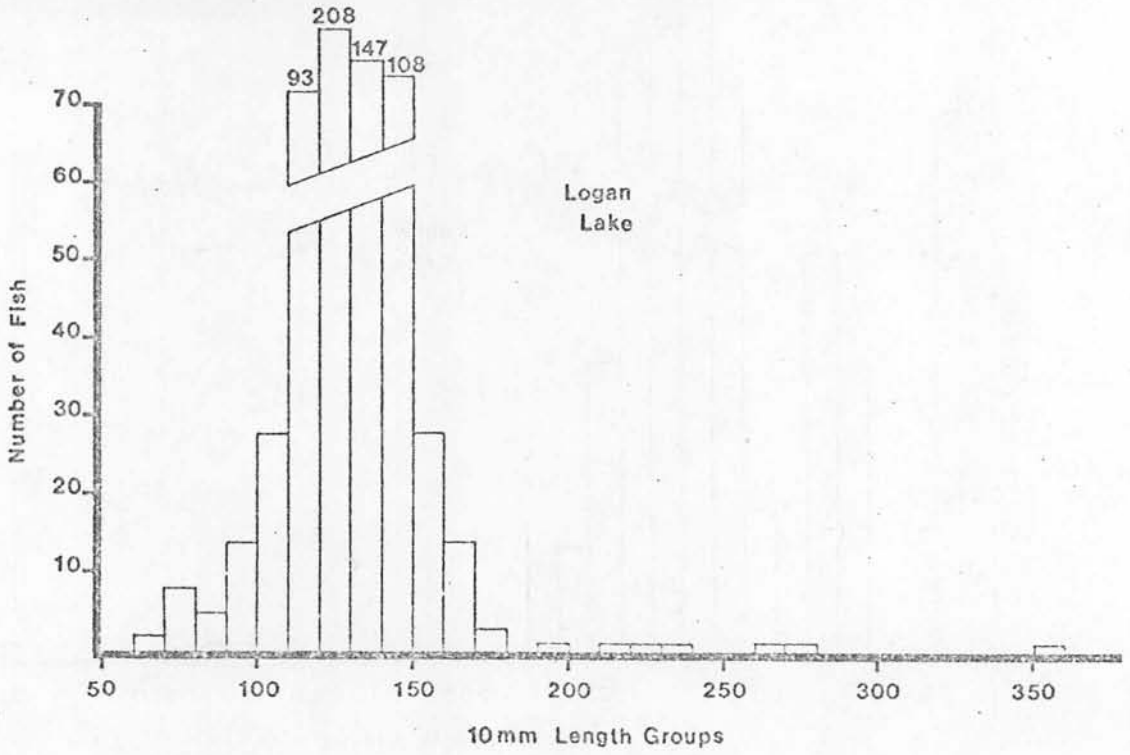
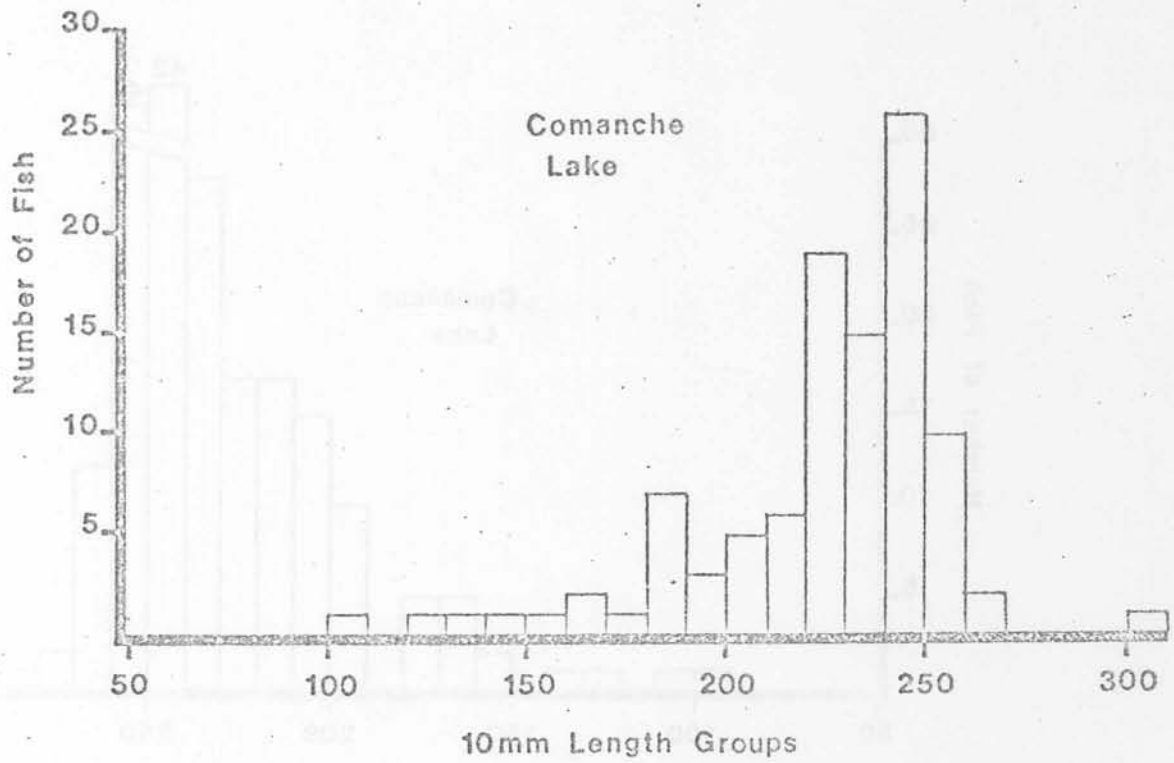


Figure 8. Length frequencies for white crappiesfrom lakes George and Logan, 1980.



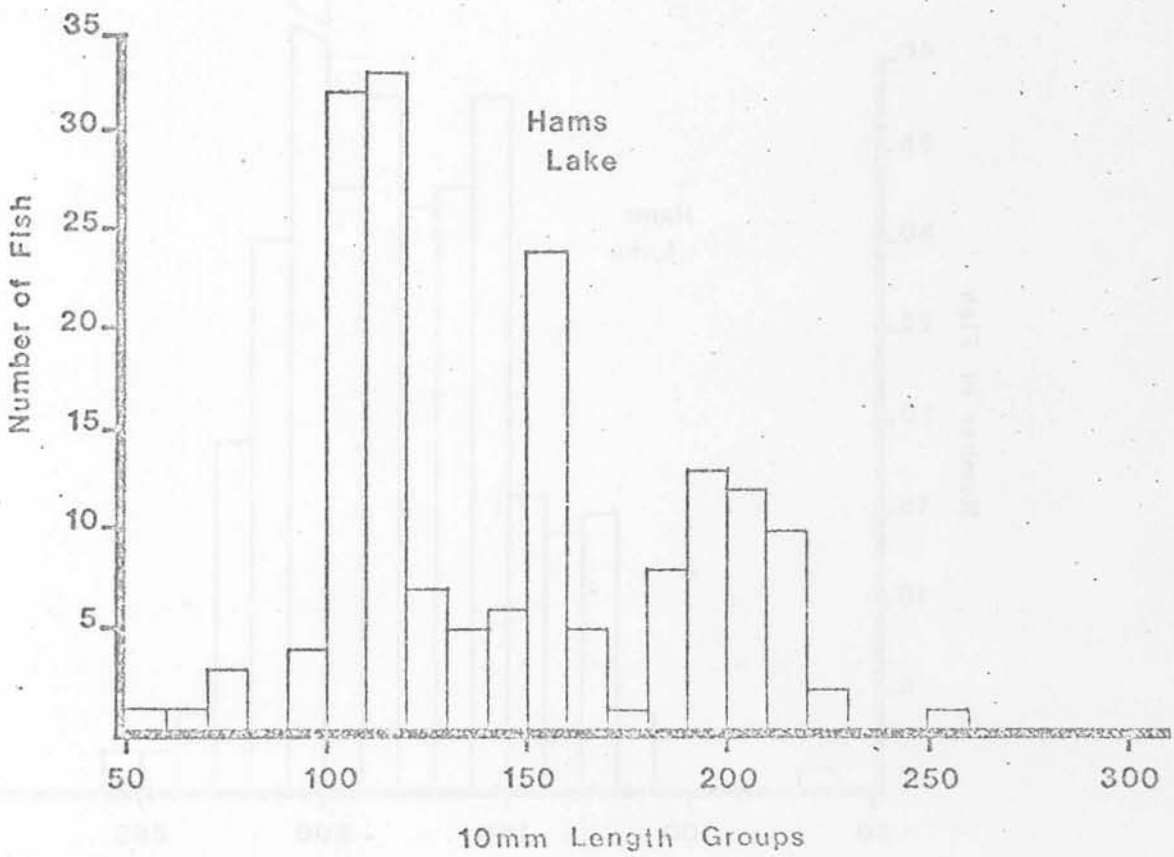
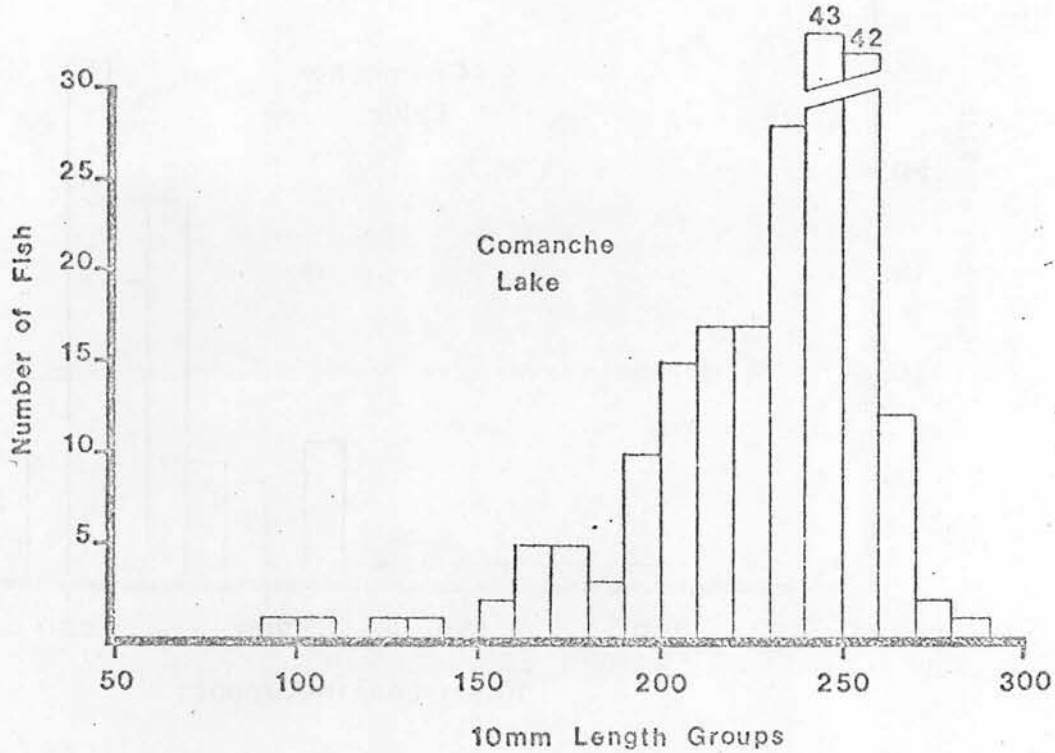


Figure 9. Length frequencies for black crappies from Comanche and Hams lakes, 1979.



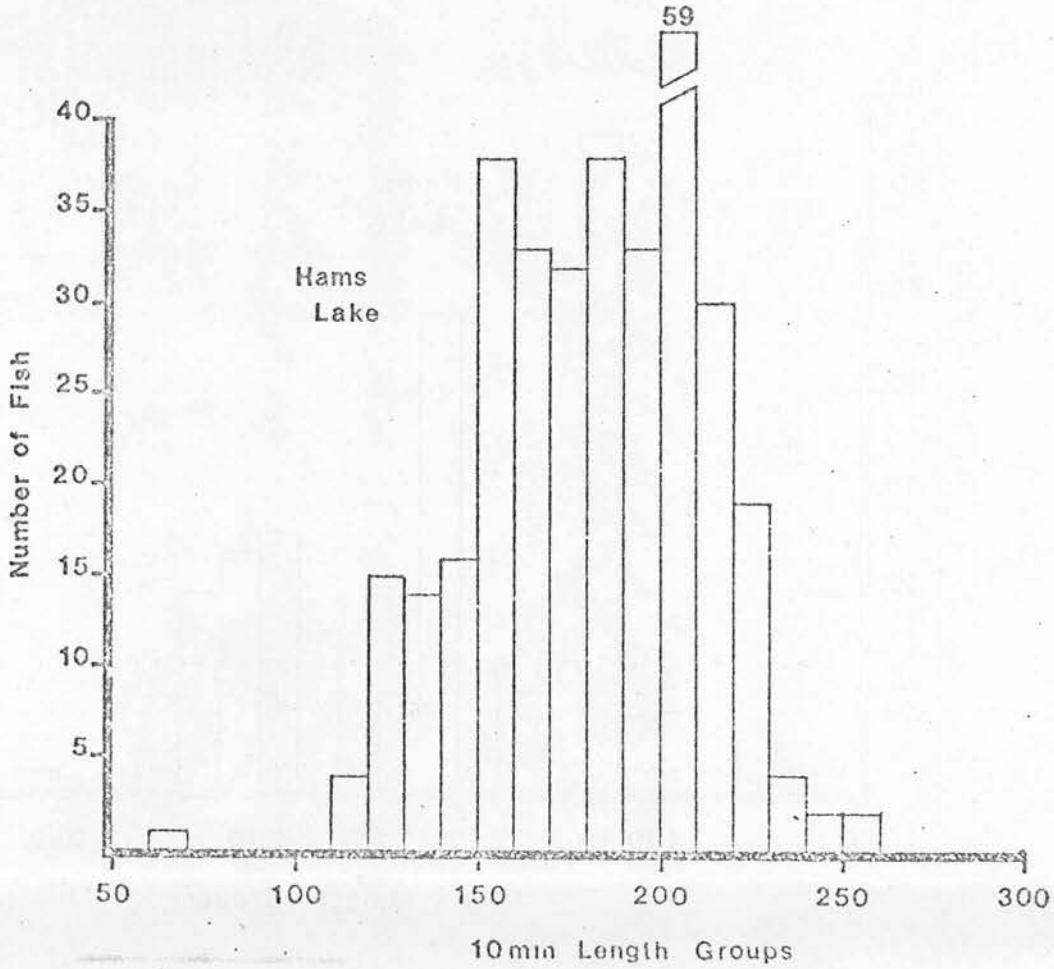


Figure 10. Length frequencies for black crappies from Comanche and Hams lakes, 1980.

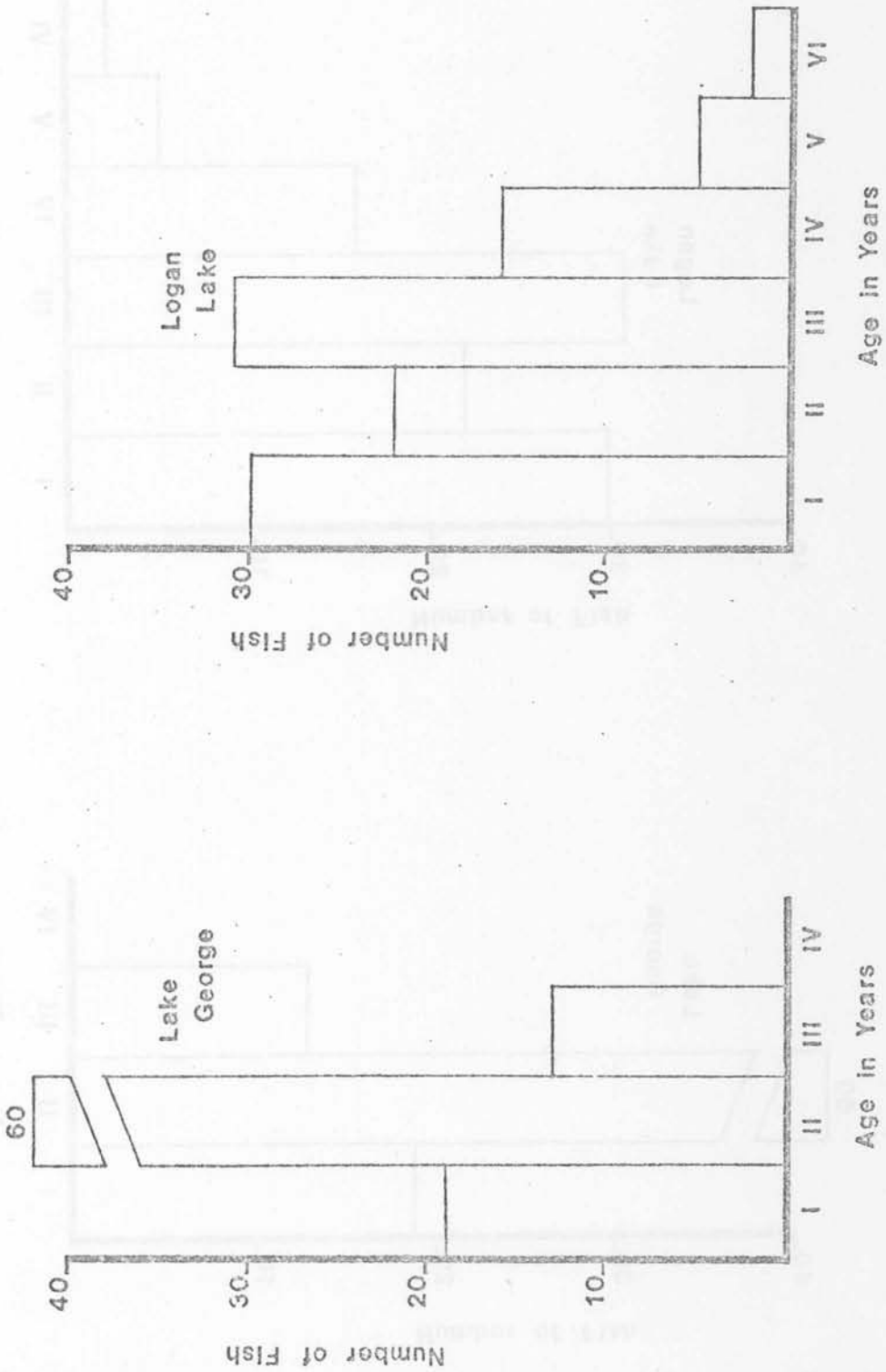


Figure 11. Age frequencies for white crappies from lakes George and Logan, 1979.

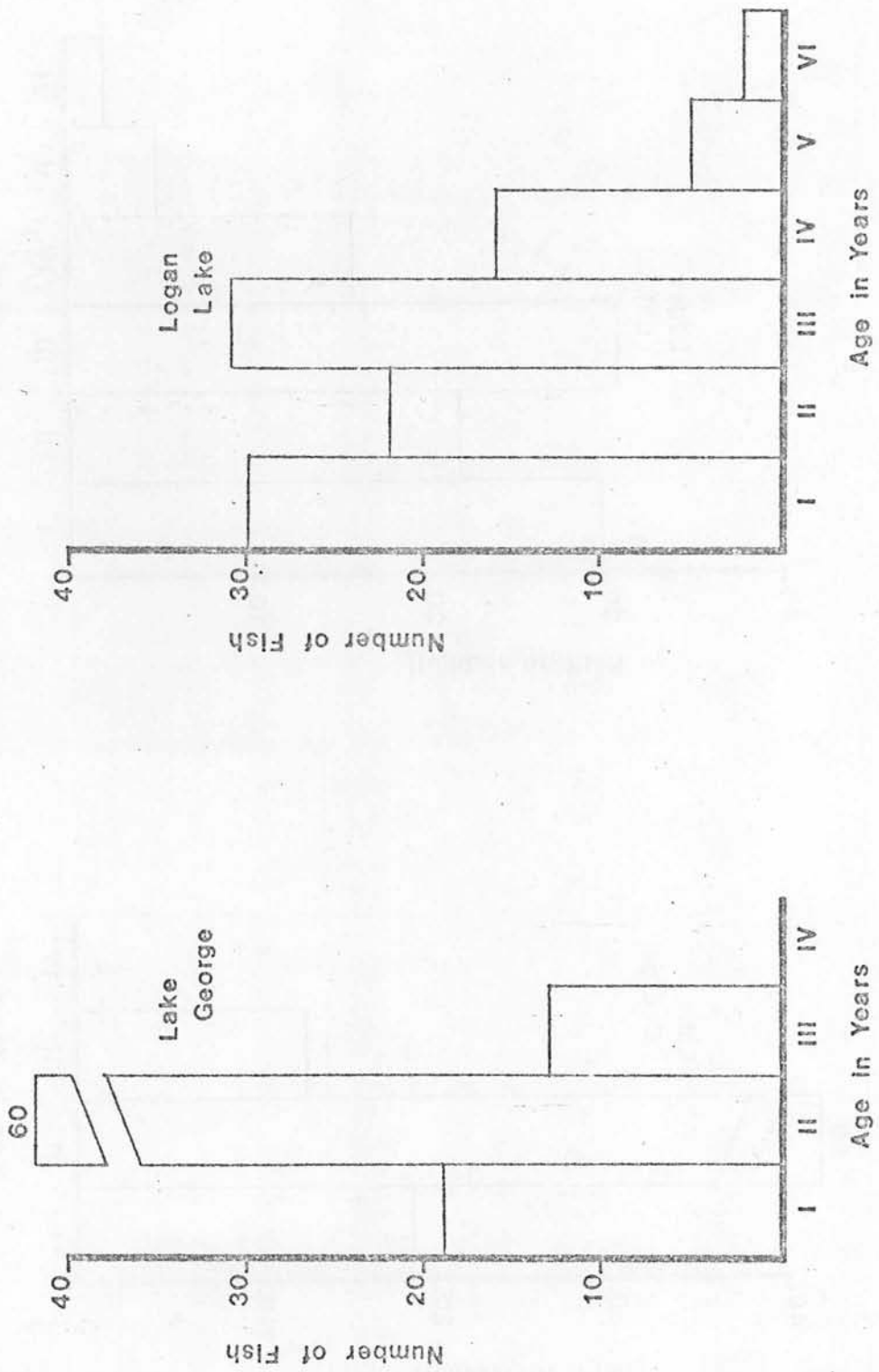


Figure 12. Age frequencies for white crappies from lakes George and Logan, 1980.

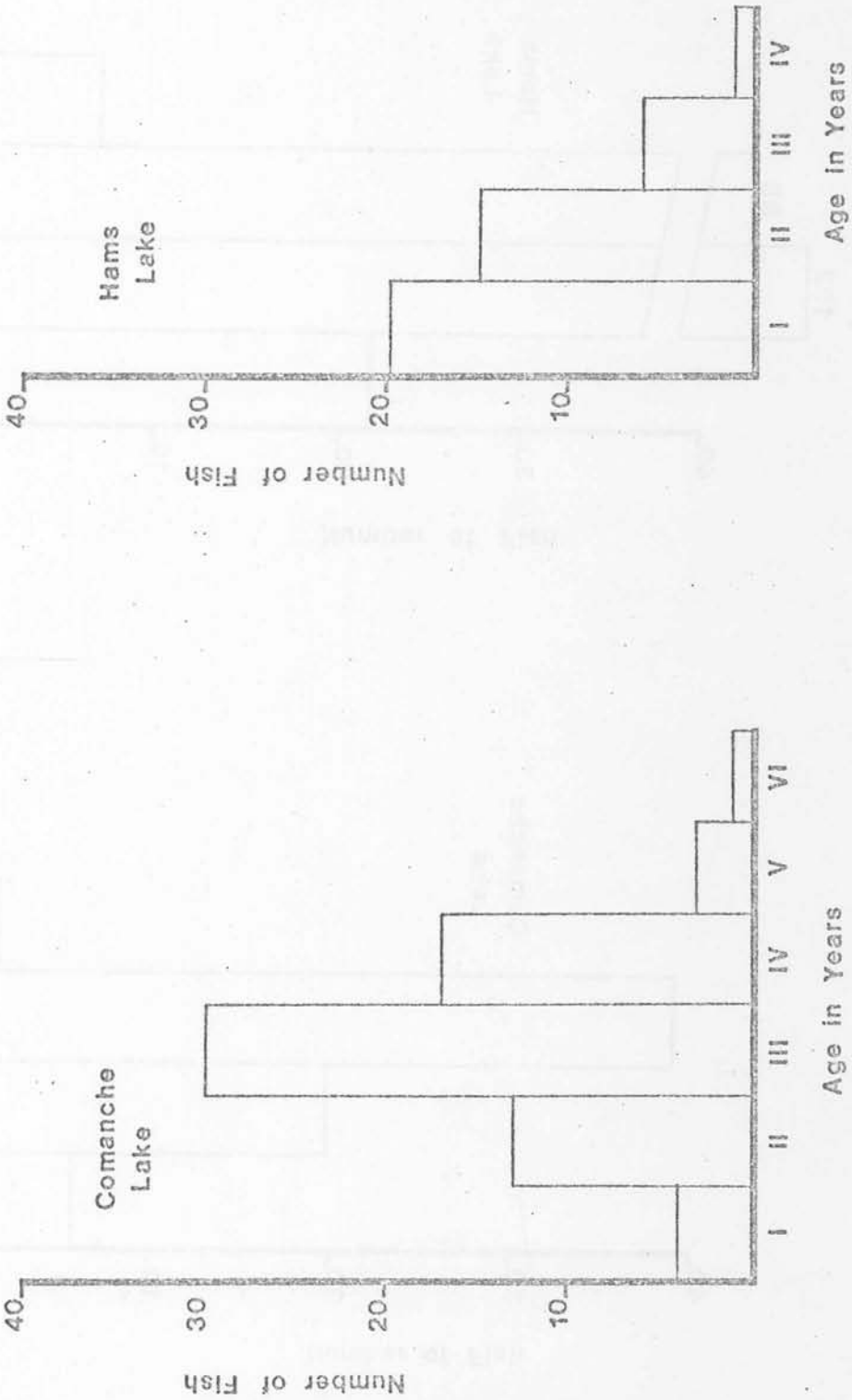


Figure 13. Age frequencies for black crappies from Comanche and Hams lakes, 1979.

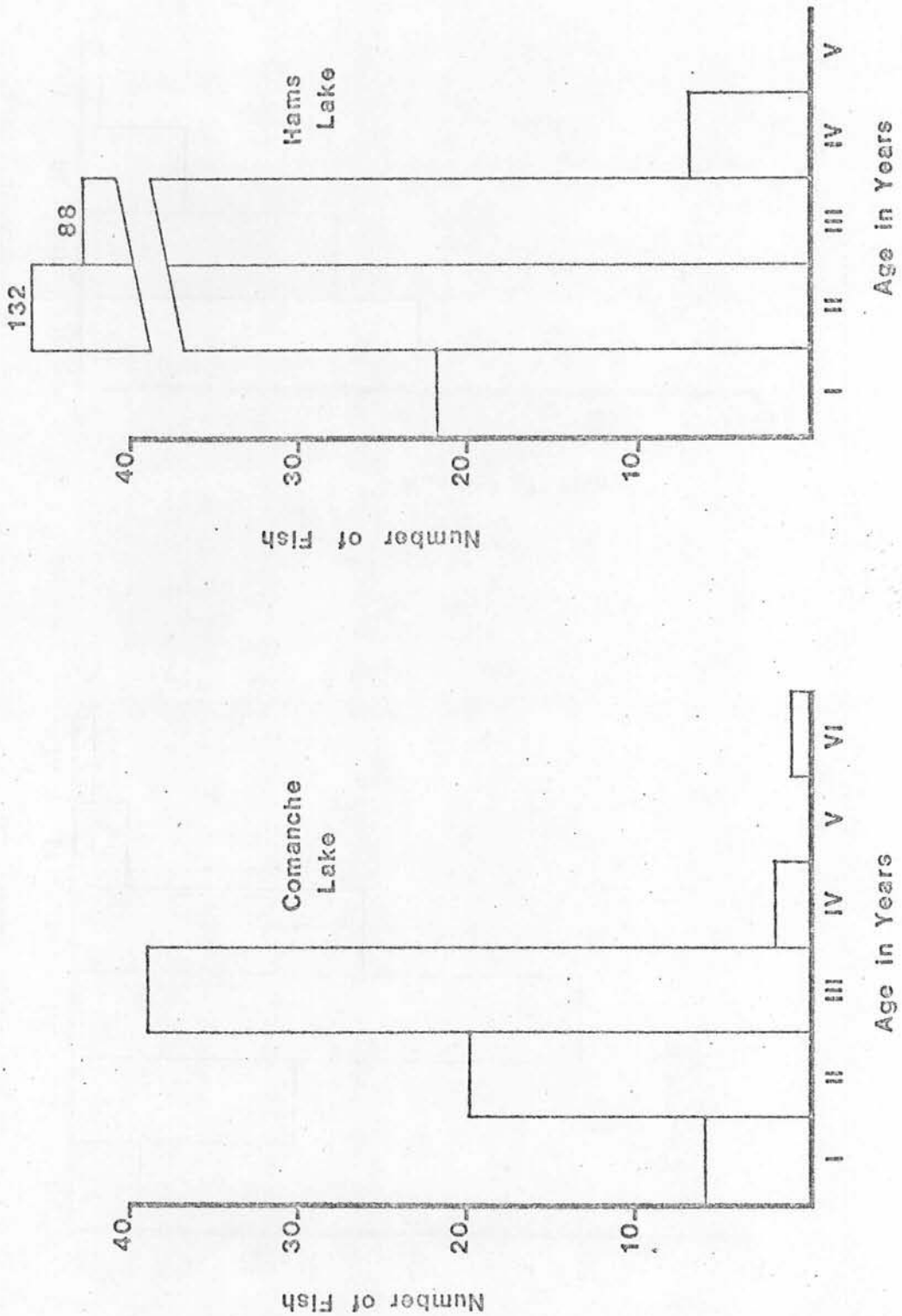


Figure 14. Age frequencies for black crappiesfrom Comanche and Hams lakes, 1980.

APPENDIX B

NUMBERS AND MEAN COEFFICIENTS OF CONDITION (K)

OF WHITE AND BLACK CRAPPIES OF VARIOUS

LENGTHS, DURING 1979 AND 1980

Table 12. Numbers and mean coefficients of condition (K) of white crappiesof various lengths from lakes George and Logan, April to August 1979.

Length (mm)	Lake George		Lake Logan	
	Number	K	Number	K
81 - 100	-	-	21	0.940
101 - 120	-	-	29	1.029
121 - 140	34	1.035	52	0.965
141 - 160	49	0.998	22	0.860
161 - 180	28	0.937	9	1.016
181 - 200	12	0.989	2	0.987
201 - 220	7	1.021	2	1.045
221 - 240	7	1.113	-	-
241 - 260	2	1.096	2	1.378
261 - 280	-	-	4	1.229
281 - 300	-	-	1	1.528
301 - 320	2	1.325	-	-
321 - 340	-	-	1	1.311
341 - 360	-	-	1	1.363

Table 13. Numbers and mean coefficients of condition (K) for black crappiesof various lengths from lakes Comanche (March to June) and Hams (July), 1979.

Length (mm)	Hams Lake		Comanche Lake	
	Number	K	Number	K
81 - 100	6	1.215	-	-
101 - 120	49	1.097	1	1.224
121 - 140	7	1.131	-	-
141 - 160	17	1.137	1	1.145
161 - 180	2	1.368	2	1.362
181 - 200	6	1.236	4	1.364
201 - 220	12	1.100	1	1.456
221 - 240	4	1.157	9	1.312
241 - 260	1	1.168	3	1.001

Table 14. Numbers and mean coefficients of condition (K) for white crappiesof various lengths from Comanche and Hams lakes, 1980.

Length (mm)	Comanche Lake		Hams Lake	
	Number	K	Number	K
81 - 100	1	1.13	-	-
101 - 120	1	1.28	5	1.09
121 - 140	2	1.23	27	1.15
141 - 160	2	1.30	62	1.23
161 - 180	11	1.20	69	1.25
181 - 200	13	1.22	66	1.28
201 - 220	30	1.22	81	1.25
221 - 240	49	1.22	19	1.22
241 - 260	86	1.10	3	1.41
261 - 280	15	1.02	-	-
281 - 300	1	0.77	-	-

Table 15. Numbers and mean coefficients of condition (K) for white crappies of various lengths from lakes George and Logan, 1980.

Length (mm)	Lake George		Lake Logan	
	Number	K	Number	K
61 - 80	-	-	8	0.73
81 - 100	1	1.01	17	1.01
101 - 120	15	0.98	105	0.98
121 - 140	131	1.03	224	0.96
141 - 160	220	0.99	81	0.91
161 - 180	49	0.96	8	0.93
181 - 200	4	1.06	2	0.98
201 - 220	3	1.14	1	1.30
221 - 240	5	0.97	1	0.98
241 - 260	1	1.21	-	-
261 - 280	5	1.09	1	1.35
281 - 300	1	0.91	1	1.51
301 - 320	2	1.22	-	-
321 - 340	-	-	-	-
341 - 360	1	1.19	2	1.42
361 - 380	1	1.12	-	-

APPENDIX C

STOMACH CONTENTS OF BLACK AND WHITE CRAPPIES

IN VARIOUS SIZE CLASSES, 1979 AND 1980

Table 16. Stomach contents of white crappies in various size classes from lakes George and Logan, 1979.

Size class (mm)	Food item	Measurement and lake: Percent occurrence		Percent of total volume	
		George	Logan	George	Logan
0-99	Diptera larvae				
	Chironomidae	-	50.0	-	7.7
	Chaoboridae	-	7.1	-	0.3
	Ceratopogonidae	-	7.1	-	0.3
	Diptera pupae	-	14.3	-	1.2
	Coleoptera larvae	-	7.1	-	<0.1
	Amphipoda	-	7.1	-	0.2
	Cladocera	-	64.3	-	73.7
	Copepoda	-	57.1	-	13.9
	Ostracoda	-	64.3	-	2.7
100-149	Fish	13.3	2.9	5.4	<0.1
	Fish eggs	2.7	0.0	<0.1	0.0
	Diptera larvae				
	Chironomidae	36.0	41.4	9.6	21.8
	Chaoboridae	40.0	34.3	51.9	12.3
	Ceratopogonidae	10.7	1.4	2.1	<0.1
	Diptera Pupae	30.7	20.0	4.4	2.2
	Ephemeroptera nymphs				
	Hexagenia	0.0	2.9	0.0	1.3
	Caenidae	8.0	1.4	1.3	0.1
	Odonata nymphs				
	Dragonfly	1.4	0.0	1.3	0.0
	Damselfly	0.0	5.3	0.0	1.3
	Hemiptera	0.0	1.4	0.0	<0.1
	Trichoptera larvae	0.0	2.9	0.0	<0.1
	Insect parts	20.0	10.1	2.4	1.9
	Amphipoda	0.0	2.9	0.0	<0.1
	Cladocera	33.3	50.0	13.5	39.5
	Copepoda	68.0	74.3	3.3	19.5
	Ostracoda	64.0	15.7	1.6	<0.1
	Unidentified remains	12.0	2.0	3.2	<0.1

Table 16. Continued.

Size class (mm)	Food item	Measurement and lake: Percent occurrence		Percent of total volume	
		George	Logan	George	Logan
150-	Fish	23.3	43.8	77.4	86.7
	Diptera larvae				
	Chironomidae	44.6	31.3	2.6	4.9
	Chaoboridae	26.8	18.8	3.7	0.3
	Ceratopogonidae	23.2	0.0	0.4	0.0
	Diptera pupae	37.5	18.8	2.3	<0.1
	Ephemeroptera nymph				
	Hexagenia	3.6	18.8	0.7	1.9
	Caenidae	14.3	0.0	0.4	0.0
	Odonata nymphs				
	Dragonfly	1.8	12.5	0.4	4.1
	Damselfly	14.3	0.0	1.8	0.0
	Hemiptera				
	Coriidae	1.8	12.5	<0.1	<0.1
	Coleoptera adult	3.6	0.0	<0.1	0.0
	Insect parts	10.7	18.8	<0.1	<0.1
	Amphipoda	14.3	0.0	0.2	0.0
	Cladocera	33.9	18.8	9.6	1.4
	Copepoda	35.7	25.0	0.1	0.8
	Ostracoda	48.2	6.3	0.1	<0.1
	Unidentified remains	12.5	0.0	0.3	0.0

Table 17. Stomach contents of white crappies in various size classes from lakes George and Logan, 1980.

Size class (mm)	Food item	Measurement and lake: Percent occurrence, George	Percent occurrence, Logan	Percent of total volume, George	Percent of total volume, Logan
0-99	Diptera larvae				
	Chironomidae	100.0	0.0	89.5	0.0
	Chaoboridae	0.0	45.5	0.0	15.8
	Ephemeroptera nymphs				
	Hexagenia	0.0	9.1	0.0	76.5
	Coleoptera adult	0.0	9.1	0.0	<0.1
	Cladocera	0.0	45.5	0.0	6.9
	Copepoda	100.0	63.6	9.5	0.7
	Ostracoda	100.0	0.0	1.0	0.0
100-150	Fish	5.8	9.2	<0.1	73.6
	Diptera larvae				
	Chironomidae	20.9	18.5	9.5	4.3
	Chaoboridae	57.0	53.8	34.6	8.0
	Ceratopogonidae	7.0	6.2	0.2	1.1
	Diptera pupae	2.3	0.0	0.4	0.0
	Ephemeroptera nymph				
	Hexagenia	2.3	4.6	0.1	9.9
	Caenidae	2.3	0.0	0.1	0.0
	Odonata nymph				
	Dragonfly	5.8	1.5	32.3	1.8
	Damselfly	17.4	0.0	17.9	0.0
	Amphipoda	4.7	0.0	<0.1	0.0
	Cladocera	58.1	50.8	3.3	1.0
	Copepoda	67.4	41.5	1.4	0.3
	Ostracoda	44.8	4.6	0.1	<0.1
150-	Fish	26.9	35.3	79.2	83.2
	Diptera larvae				
	Chironomidae	34.6	17.6	1.9	0.3
	Chaoboridae	51.9	29.4	7.9	0.5
	Ceratopogonidae	11.5	17.6	0.1	<0.1
	Ephemeroptera nymphs				
	Hexagenia	0.0	5.9	0.0	1.3
	Odonata nymphs				
	Dragonfly	7.7	0.0	2.4	0.0
	Damselfly	21.2	0.0	5.3	0.0

Table 17. Continued.

Size class (mm)	Food item	Measurement and lake: Percent occurrence		Percent of total volume	
		George	Logan	George	Logan
150-	Coleoptera adult	1.9	0.0	<0.1	0.0
	Crayfish	0.0	5.9	0.0	13.1
	Cladocera	32.7	23.5	0.4	<0.1
	Copepoda	36.5	17.6	<0.1	<0.1
	Ostracoad	17.3	5.9	<0.1	<0.1
	Unidentified remains	80.8	64.7	2.8	1.6

Table 18. Stomach contents of black crappies in various size classes from Comanche and Hams lakes, 1979.

Size class (mm)	Food item	Measurement and lake: Percent occurrence		Percent of total volume	
		Comanche	Hams	Comanche	Hams
0-99	Fish	-	14.3	-	47.0
	Diptera larvae				
	Chironomidae	-	14.3	-	1.2
	Insect parts	-	28.6	-	<0.1
	Copepoda	-	85.7	-	51.9
100-149	Fish	66.7	0.0	49.1	0.0
	Diptera larvae				
	Chironomidae	33.3	21.1	0.8	4.9
	Chaoboridae	33.3	15.8	29.8	0.7
	Ceratopogonidae	0.0	10.5	0.0	0.4
	Diptera pupae	66.7	5.3	6.0	0.8
	Odonata nymphs				
	Damselfly	33.3	0.0	3.3	0.0
	Insect parts	0.0	21.1	0.0	<0.1
	Amphipoda	66.7	5.3	2.7	0.2
	Cladocera	0.0	15.8	0.0	0.7
	Copepoda	0.0	89.5	0.0	62.1
	Unidentified remains	33.3	15.8	8.2	30.3
150-	Fish	22.0	19.2	11.0	34.6
	Diptera larvae				
	Chironomidae	54.0	19.2	7.2	2.9
	Chaoboridae	28.0	15.4	18.1	1.0
	Ceratopogonidae	38.0	0.0	2.3	0.0
	Diptera pupae	44.0	14.4	15.0	3.7
	Ephemeroptera nymph				
	Hexagenia	0.0	15.4	0.0	13.9
	Caenidae	32.0	7.7	7.3	0.6
	Baetidae	0.0	3.8	0.0	2.8
	Odonata nymph				
	Dragonfly	0.0	15.4	0.0	10.4
	Damselfly	4.0	7.7	0.3	4.2
	Coleoptera larvae	-	3.8	-	<0.1
	Hemiptera corixidae	2.0	0.0	<0.1	0.0
	Insect parts	14.0	11.5	5.7	10.4
	Amphipoda	34.0	7.7	1.4	<0.1
	Cladocera	62.0	15.4	20.4	0.2
	Copepoda	44.0	15.4	1.4	4.6
	Ostracoda	4.0	0.0	<0.1	0.0
	Unidentified remains	16.0	30.8	10.0	10.4

Table 19. Stomach contents of black crappies in various size classes from Comanche and Hams lakes, 1980.

Size class (mm)	Food item	Measurement and lake: Percent occurrence		Percent of total volume	
		Comanche	Hams	Comanche	Hams
0-99	Diptera larvae				
	Chaoboridae	100.0	50.0	57.0	8.6
	Odonata nymph				
	Damselfly	50.0	0.0	16.5	0.0
	Cladocera	0.0	50.0	0.0	1.1
	Copepoda	100.0	100.0	26.4	90.1
	Ostracoda	0.0	50.0	0.0	0.2
100-149	Fish	100.0	11.5	87.2	8.4
	Diptera larvae				
	Chironomidae	100.0	11.5	2.4	0.9
	Chaoboridae	100.0	50.0	1.8	36.5
	Ceratopogonidae	0.0	15.4	0.0	1.2
	Ephemeroptera nymphs				
	Hexagenia	0.0	23.1	0.0	27.7
	Caenidae	0.0	3.8	0.0	0.3
	Odonata nymphs				
	Dragonfly	0.0	3.8	0.0	5.0
	Damselfly	100.0	3.8	5.8	2.5
	Amphipoda	100.0	11.5	1.9	0.7
	Cladocera	0.0	38.5	0.0	1.6
	Copepoda	100.0	34.6	0.9	2.6
	Ostracoda	0.0	3.8	0.0	<0.1
	Unidentified remains	100.0	23.1	<0.1	12.5