

THE AGE, GROWTH, AND GENETIC STRUCTURE OF
BLACK AND WHITE CRAPPIE POPULATIONS
IN A NEW OKLAHOMA RESERVOIR

By

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PREFACE

The purpose of this research was to study the genetic structure of founding populations of black and white crappie in a new Oklahoma reservoir. Additional objectives were incorporated into the study in order to examine the relationships between age, growth, and foraging strategies in founding crappie populations. The creation of Copan lake was a serendipitous event, and it was hoped that this study would provide baseline data for future research as well as new insight on reservoir crappie problems. Funding was made available through the Oklahoma Department of Wildlife Conservation. In addition, computer funds were provided by the Oklahoma State University Zoology Department.

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TABLE OF CONTENTS

Chapter	Page
I. AGE AND GROWTH OF BLACK AND WHITE CRAPPIE IN COPAN LAKE	1
Introduction	1
Study Area	3
Methods	4
Results	6
Discussion	13
Conclusions	21
Literature	22
Tables	27
Figures	55
II. THE GENETIC STRUCTURE OF BLACK AND WHITE CRAPPIE IN COPAN LAKE	76
Introduction	76
Study Area	79
Methods	80
Results	83
Allozymic Variation	83
Genetic Variation	87
Discussion	93
Literature	99
Tables	104
III. THE INCIDENCE OF F1 BLACK CRAPPIE X WHITE CRAPPIE HYBRIDS IN COPAN LAKE	127
Introduction	127
Study Area	129
Methods	130
Results	132
Discussion	133
Conclusions	136
Literature	137
Tables	141

Chapter	Page
IV. FORAGING STRATEGIES OF BLACK AND WHITE CRAPPIE IN COPAN LAKE	146
Introduction	146
Study Area	149
Methods	150
Results	151
Discussion	153
Literature	159
Tables	162

LIST OF TABLES

Table	Page
CHAPTER I	
1. Length frequency distribution by age group for black and white crappie captured in Copan lake during 1983	27
2. Year class distribution of black and white crappie captured at different sites in Copan lake during 1983	28
3. Sex ratio and age distribution of black crappie from sample locations in Copan lake during 1983	29
4. Sex ratio and age distribution of white crappie from sample locations in Copan lake during 1983	30
5. Monthly mean Gonadosomatic Index (GSI) for black and white crappie sexes captured in Copan lake during 1983	32
6. Monthly mean Gonadosomatic Index (GSI) for white crappie age groups captured in Copan lake during 1983	33
7. Monthly mean Gonadosomatic Index (GSI) for black crappie age groups captured in Copan lake during 1983	34
8. Mean relative weight (standard error) for black and white crappie sexes captured from sample locations in Copan lake during 1983	35
9. Monthly mean relative weight (standard error) for black crappie age groups collected from sample locations in Copan lake during 1983	36

10.	Monthly mean relative weight (standard error) for male and female black crappie captured in Copan lake during 1983	37
11.	Monthly mean relative weight (standard error) of pooled white crappie age groups captured from sample locations in Copan lake during 1983	38
12.	Mean relative weight (standard error) for white crappie age groups captured from sample locations in Copan lake during 1983	39
13.	Mean relative weight (standard error) for male and female white crappie captured from Copan lake during 1983	40
14.	Common log length-weight equations for black and white crappie captured from Copan lake during 1983 and other Oklahoma waters	41
15.	Natural log length-weight equations for black and white crappie captured from several locations in Copan lake during 1983	42
16.	Contrast analysis on regression slopes of natural log length weight equations of white crappie captured from sample locations in Copan lake during 1983	43
17.	Mean total length (mm) of black crappie captured from Endacott's pond during 1983	44
18.	Mean total length (mm) at annuli for white crappie from combined sample locations in Copan lake during 1983	45
19.	Total length (mm) increments between annuli for black crappie captured in Endacott's pond during 1983	46
20.	Total length (mm) increments between annuli for white crappie captured in Copan lake during 1983	47
21.	Mean total length (mm) at annuli for black and white crappie from sample locations in Copan lake during 1983	48

Table	Page
22. Mean length (mm) increments between annuli for black and white crappie captured from several locations in Copan lake during 1983	49
23. Mean total length (mm) at annuli for black and white crappie sexes captured from sample locations in Copan lake during 1983	50
24. Mean total length at annuli for black crappie captured in Copan lake during 1983 and other Oklahoma waters	51
25. Mean total length (mm) at annuli for black crappie captured in Copan lake during 1983 and other waters in the southern United States	52
26. Mean total length at annuli for white crappie captured in Copan lake during 1983 and other waters in Oklahoma	53
27. Mean total length at annuli for white crappie captured from Copan lake during 1983 and other waters from the southern United States	54

CHAPTER II

1. Genotype distributions and allele frequencies for IDH-2 and CK-3 in combined samples of black and white crappie captured in Copan lake during 1983	104
2. Mean observed and expected heterozygosities for IDH-2 and CK-3 in black and white crappie captured in Copan lake during 1983	105
3. Genotype distributions and allele frequencies for IDH-2 in black and white crappie sexes captured in Copan lake during 1983	106
4. Genotype distributions and allele frequencies for CK-3 in black and white crappie sexes captured in Copan lake during 1983	107

5.	Chi-square tests for conformance to Hardy-Weinberg equilibrium and indices for allele fixation and heterozygote deficiency for IDH-2 and CK-3 in black and white crappie captured in Copan lake during 1983	108
6.	Mean observed and expected heterozygosities for IDH-2 and CK-3 in black and white crappie age groups captured in Copan lake during 1983	109
7.	Genotype distributions and allele frequencies for CK-3 in black and white crappie age groups captured in Copan lake during 1983	110
8.	Genotype distributions and allele frequencies for IDH-2 in black and white crappie age groups captured in Copan lake during 1983	111
9.	Chi-square tests for conformance to Hardy-Weinberg equilibrium and indices for allele fixation and heterozygote deficiency for IDH-2 and CK-3 in black and white crappie age groups captured in Copan lake during 1983	112
10.	Mean observed and expected heterozygosities for IDH-2 and CK-3 in black and white crappie Relative Weight (Wr) groups captured in Copan lake during spring, summer, and fall 1983	113
11.	Mean observed and expected heterozygosities for IDH-2 and CK-3 in black and white crappie total length classes and age groups captured in Copan lake during 1983	114
12.	Genotype distributions and allele frequencies for IDH-2 in black and white crappie Relative Weight (Wr) groups captured in Copan lake during spring, summer, and fall 1983	115
13.	Genotype distributions and allele frequencies for CK-3 in black and white crappie Relative Weight (Wr) groups captured in Copan lake during spring, summer, and fall 1983	116

14.	Chi-square tests for conformance to Hardy-Weinberg equilibrium and indices for allele fixation and heterozygote deficiency for IDH-2 and CK-3 in black crappie Relative Weight (W_r) groups captured in Copan lake during summer and fall 1983	117
15.	Genotype distributions and allele frequencies for IDH-2 in black and white crappie total length (mm) classes and age groups captured in Copan lake during 1983	118
16.	Genotype distributions and allele frequencies for CK-3 in black and white crappie total length (mm) classes and age groups captured in Copan lake during 1983	119
17.	Chi-square tests for conformance to Hardy-Weinberg equilibrium and indices for allele fixation and heterozygote deficiency for IDH-2 and CK-3 in total length classes of black crappie age groups captured in Copan lake during 1983	120
18.	Matrix of similarity and distance coefficients for black and white crappie captured in Copan lake during 1983	121
19.	Genotype distribution and allele frequencies for IDH-2 in black and white crappie captured from sample locations in Copan lake during 1983	122
20.	Genotype distributions and allele frequencies for CK-3 in black and white crappie captured from sample locations in Copan lake during 1983	123
21.	Chi-square tests for conformance to Hardy-Weinberg equilibrium and indices for allele fixation and heterozygote deficiency for IDH-2 and CK-3 in black and white crappie captured from three sample locations in Copan lake during 1983	124

22. Chi-square tests for conformance to Hardy-Weinberg equilibrium and indices for allele fixation and heterozygote deficiency for IDH-2 and CK-3 in white crappie Relative Weight (Wr) groups captured in Copan lake during spring and summer 1983	125
23. Chi-square tests for conformance to Hardy-Weinberg equilibrium and indices for allele fixation and heterozygote deficiency for IDH-2 and CK-3 in total length classes of white crappie age groups captured in Copan lake during 1983	126

CHAPTER III

1. Enzyme, tissue, and buffer used in electrophoretic analysis of black crappie, white crappie, and their F1 generation interspecific hybrid crosses captured in Copan lake during 1983	141
2. Summary of six electrophoretically detected F1 black crappie x white crappie hybrids captured in Copan lake during 1983	142
3. Mean capture length, weight, and condition (Wr) for black crappie, white crappie, and F1 black crappie x white crappie hybrids captured in Copan lake during 1983	143
4. Mean back-calculated length at otolith annuli for black crappie, white crappie, and F1 black crappie x white crappie hybrids captured at two locations in Copan lake during 1983	144
5. Natural log length weight regressions for black crappie, white crappie, and F1 black crappie x white crappie hybrids captured from two locations in Copan lake during 1983	145

CHAPTER IV

1. Age distribution by diet classes of black and white crappie captured in Copan lake during 1983	162
2. Back calculated length at annuli for diet classes of black and white crappie captured in Copan lake during 1983	163
3. Mean capture length and weight and back calculated length at annuli for black and white crappie diet classes captured in Copan lake during 1983	164
4. Mean relative weight (standard error) at age for black and white crappie diet classes captured in Copan lake during 1983	165
5. Monthly mean relative weight (standard error) for black and white crappie diet classes captured in Copan lake during 1983	166
6. Percent increase in monthly mean relative weight in black and white crappie diet classes captured in Copan lake during 1983	167

LIST OF FIGURES

Figure	Page
CHAPTER I	
1. Collection locations in Copan lake during 1983	55
2. Length frequency distribution and proportional stock density (PSD) for black crappie captured in Endacott's pond during 1983	56
3. Length frequency distribution and proportional stock density (PSD) for black crappie captured in Copan lake north section during 1983	57
4. Length frequency distribution and proportional stock density (PSD) for white crappie captured at Highway 10 bridge east side in Copan lake during 1983	58
5. Length frequency distribution and proportional stock density (PSD) for white crappie captured in Little Caney river during 1983	59
6. Length frequency distribution and proportional stock density (PSD) for white crappie captured in Washington's cove of Copan lake during 1983	60
7. Length frequency distribution and proportional stock density (PSD) for all white crappie captured in Copan lake during 1983	61
8. Length frequency distribution and proportional stock density (PSD) for white crappie captured in Endacott's pond during 1983	62
9. Length frequency distribution and proportional stock density (PSD) for white crappie captured in Copan lake north section during 1983	63
10. Length frequency distribution and proportional stock density (PSD) for white crappie captured at Copan dam during 1983	64

Figure	Page
11. Gonadosomatic Index (GSI) for male and female white crappie captured in Copan lake during 1983	65
12. Mean capture weight and relative weight for black crappie size classes captured in Copan lake during 1983	66
13. Mean capture weight and relative weight for white crappie size classes captured in Copan lake during 1983	67
14. Mean relative weight and total length at capture for black crappie in Copan lake north section during 1983	68
15. Mean relative weight and total length at capture for black crappie in Endacott's pond during 1983	69
16. Mean relative weight and total length at capture for white crappie in Endacott's pond during 1983	70
17. Mean relative weight and total length at capture for white crappie in Copan lake north section during 1983	71
18. Mean relative weight and total length at capture for white crappie at Copan dam during 1983	72
19. Mean relative weight and total length at capture for white crappie in Washington's cove in Copan lake during 1983	73
20. Mean relative weight and total length at capture for white crappie at Highway 10 bridge on east side Copan lake during 1983	74
21. Mean relative weight and total length at capture for white crappie in Little Caney river during 1983	75

CHAPTER I

AGE AND GROWTH OF FOUNDING BLACK AND WHITE CRAPPIE POPULATIONS IN COPAN LAKE

INTRODUCTION

The black and white crappie (Pomoxis nigromaculatus and P. annularis, respectively) are important gamefish in midwestern reservoirs due to their abundance and large size. Field observations indicate that when both species occur together, black crappie usually predominate in clear, cooler, slightly acidic water, whereas, white crappie predominate in water that is warmer, more turbid, and slightly basic (Goodson 1966). Hall et al. (1954) reported that white crappie were more abundant and had higher growth rates than black crappie in turbid Oklahoma lakes.

Crappie populations often increase dramatically in new midwestern reservoirs. Growth rates are generally high the first few years after impoundment, but subsequently decline (Rutledge and Barron 1972). Abundance of black crappie also declines, and while white crappie remain relatively abundant, the population is often composed of many "stunted" or small fish (Jenkins 1953; Glass 1982). Decreased growth rates have been associated with declining nutrient levels in aging reservoirs (Ball and Kilambi 1972), interspecific competition (Keast 1968; Li et al. 1976), and severe intraspecific competition due to overcrowding

(Huish 1953; Burris 1956; Rutledge and Barron 1972). In addition, "stunted" populations may result from the absence of large fish due to overfishing or differential natural mortality (Colvin 1982).

Ellison (1984) reported age related mortality in older black crappie that failed to switch to piscivory at the appropriate size (> 200 mm TL). Apparently, the forage of older, nonpiscivorous crappie was not sufficient to supply the annual energy requirements, which resulted in an "energy trap" during summer. This explanation cannot be universal, however, because many black crappie are opportunistic feeders that forage primarily on the more abundant prey (May and Thompson 1974; Barwick and Lorenzen 1984), and switch to piscivory at older ages (Ager 1975). In addition, balanced black crappie populations can be maintained on a diet of only zooplankton and aquatic insects (Gablehouse 1984).

Severe intraspecific competition is generally reflected by dominant, weak, or missing year classes. The theory is that a large year class survives and severely crops young-of-year from subsequent hatches. This trend continues until the original year class can no longer control the reproduction of other year classes, and the cycle may be repeated (Rutledge and Barron 1972; Triplett 1976). However, year class strength is also correlated with reservoir water level management (Cichra et al. 1981; Mitzner 1981; Beam 1983), water temperature during spawning and incubation (Siefert 1968), the influence of cover on larval survival and recruitment (Ball and Kilambi 1972) and lower nutrient levels. The effect of lower nutrient levels in midwestern reservoirs is reflected by the fact that condition of black and white crappie in newly impounded midwestern reservoirs may be high the first few years, but

decline as the reservoir ages.

There is a need to document changes in founding crappie populations of new reservoirs over time. Knowing the beginning conditions in reservoirs and crappie populations may enable us to better understand the changes that occur later as the reservoir ages. Copan lake offers a unique opportunity to study the growth and condition of sympatric founding crappie populations in a new reservoir.

The objectives of this paper are to :

- (1) Describe the age and sex distribution of founding black and white crappie populations in the Copan lake basin.
- (2) Describe the growth histories and condition of founding black and white crappie populations in the Copan lake basin.

STUDY AREA

Copan Lake is located on the Little Caney River, approximately 3.7 km west of Copan, Washington County, in northeastern Oklahoma. The drainage area above the dam site is approximately 1,308 square kilometers, and is characterized by rolling hills, oak-hickory forests with numerous rock outcroppings interspersed with lowlands of tall grass prairie. At conservation pool elevation (209.5 m - 216.4 m), the lake covers approximately 1,962 hectares and inundates 23.3 kilometers of the Little Caney River. The Copan Lake Project was constructed by the Tulsa District U.S. Army Corps of Engineers, under the authorization of the 1962 Flood Control Act, for the purpose of flood control, water supply, water quality control, recreation, and fish and wildlife (U. S. Army Corps of Engineers 1972).

The Little Caney River is a tributary to the Caney River, which is part of the Verdigris River System in southeastern Kansas and northeastern Oklahoma. The Little Caney River is generally described as a sluggish, moderately turbid, clay-silt bottom stream. Fish fauna collected by the Corps of Engineers and the University of Oklahoma include: Notropis lutrensis, Pimephales notatus, P. promelas, Notemigonus crysoleucas, Ictalurus melas, Labidesthes sicculus, Gambusia affinis, Lepomis cyanellus, L. macrochirus, and Pomoxis annularis. (U.S. Army Corps of Engineers 1972).

The area above the dam consists of the lake proper and a periodically isolated pond, Endacott's pond, located on the west shore. The mean depth in the pond before inundation was 1.8 m and secchi readings averaged 1.2 m. The pond has historically stratified every year, and presently is the only site in Copan Lake that stratifies.

METHODS

White crappie and black crappie were collected with barrel net traps, gill nets, and modified trap nets. Sampling began in Endacott's pond (EP) and the Little Caney river (10W) during March 1983, one month prior to the impoundment of Copan lake (Figure 1). Thereafter, 4 additional sites were chosen in the new lake, and sampling continued through November 1983. All specimens were preserved with dry ice or 10% formalin and returned to the laboratory. At the laboratory, all crappie were weighed to the nearest gram and total length was determined to the nearest millimeter. Gonads were removed from a portion of adults from both crappie populations. Sex of all crappie was determined by visual

inspection and otoliths (sagittae) were removed for age determination. Otolith radius was measured from the center of the kernel to the anterior tip of the otolith. Distance to each annulus was measured along the radius from the center of the kernel to the proximal margin of the opaque band (Pannella 1974).

Estimated total lengths at time of formation of otolith annuli were back-calculated using the direct proportion method with an intercept of zero (Lagler 1956). A general linear model determined the natural and common log length weight relationships by using the least squares method: $\text{Log}(\text{WT}) = a + b[\text{Log}(\text{TL})]$. Analysis of covariance was used to compare regression slopes of the length weight data for each site (Snedecor and Cochran 1978). Significant differences in regression slopes were examined by contrast analysis (Zar 1974).

Population structure was examined with Proportional Stock Density (PSD). "Stock" and "quality" total length (mm) for black and white crappie were 130 and 200, respectively. Fish condition was calculated as Relative Weight (W_r), where $W_r = W_s / W_t$. Standard Weights (W_s) were derived by $\text{Log}_{10} (W_s) = -4.914 + 3.052[\text{Log}_{10} (\text{TL})]$ and $\text{Log}_{10} (W_s) = -5.102 + 3.112[\text{Log}_{10} (\text{TL})]$ for black and white crappie, respectively (Anderson 1980). Variances of sample mean relative weights were tested for equality in crappie samples of unequal size (Sokal and Rohlf 1969, p. 186). Significant differences in mean relative weights between crappie samples were determined by t-test for means of equal variances (Sokal and Rohlf 1969, p. 222) and for means of unequal variances (Ott 1977, p. 116). Gonadosomatic Index (GSI) was calculated as gonad weight/body weight X 100.

RESULTS

Population Structure

White crappie were the predominant crappie species in Copan lake. A total of 647 white crappie and 114 black crappie were collected during this study. Black crappie collections were represented by 6 year classes; however, 4 were very small (Tables 1 and 2). The majority of individuals were Age 0 (54%) and Age 4 (30%) from the 1983 and 1979 year classes, respectively. White crappie collections were represented by 7 year classes, with abundant Age 2 (31%) and an unexpected high number of Age 4 (13%) fish from the 1981 and 1979 year classes, respectively. Few individuals older than Age 4 were collected from either population.

Population mean PSD's were 0.63 and 0.52 for black and white crappie, respectively, and ranged from 0.18 to 0.76 for fish collections among sites (Figures 2-10). A bimodal length frequency distribution of black crappie in EP resulted from the greater abundance of 1983 and 1979 year classes (Figure 2). The small sample of black crappie in Copan north end (CNE) resulted in a distribution that was skewed toward smaller fish (Figure 3). Non-normal distributions were also evident in smaller samples of white crappie from sites 10 East (10E) and 10W, however, a normal distribution was found in the white crappie sample from Washington's cove (WC) (Figures 4, 5, and 6, respectively). Overall the length frequency distribution for white crappie was normal (Figure 7), as generally were length frequency distributions for fish from sites EP, CNE, and Riprap (RR), where larger collections were made (Figures 8, 9, and 10, respectively).

The black crappie population in EP was characterized by dominant, weak, and missing year classes (Table 2). Few black crappie were collected at CNE; however, 4 year classes were present in the sample. White crappie collections reflected more even year class distribution than black crappie collections, although, Age 0 fish of both species were captured primarily from EP and CNE (Table 2). White crappie samples in the Little Caney river (10W) and sites from Copan lake south (RR, WC, 10E) were characterized by an abundance of younger (Ages 1 and 2) fish, whereas, samples from EP and CNE were characterized by an abundance of slightly older (Ages 2 and 3) fish. However, the majority of Age 4+ crappie in the collections (1979, 1978, and 1977 year classes) were captured in Endacott's pond.

Sex ratios in the collections were skewed toward males at all sites except for white crappie in the Little Caney river. Black crappie males were twice as common as females in total collections, and ranged 1.6 : 1 to 15 : 1 between sites (Table 3). White crappie males were 1.2 : 1 more common than females in total collections, and ranged from 0.4 : 1 to 1.6 : 1 between sites (Table 4). Unequal sex ratios were generally more pronounced in smaller samples. In addition, female crappie were the predominant sex in older age groups of both species (Tables 3 and 4).

Gonad weights were measured in 22 (25%) black crappie and 81 (44%) white crappie. Although monthly gonad data were incomplete for black crappie during May, mean GSI in male black crappie was comparable to mean GSI in male white crappie (Table 5). Monthly mean GSI of pooled male age groups ranged from 0.33 to 0.82% in black crappie and from 0.01 to 0.77% in white crappie. Maximum GSI levels occurred in May for males

of both species. However, a second increase in male GSI was evident in Fall samples (Tables 6 and 7).

Mean female GSI's were generally greater in white crappie than black crappie at all ages (Tables 6 and 7). The data indicated sexual maturity occurred by Age 2 and 3 in female white and black crappie, respectively. Mean GSI's for pooled female age groups ranged from 0.17 to 4.18% in black crappie and from 0.07 to 6.40% in white crappie. Maximum female gonadal development appeared to occur one month earlier (April) in white crappie than black crappie; however, black crappie were not collected in April. The female Age 2 GSI for April (6.82%) was derived from one individual (276 mm, 450 g) captured at CNE. Monthly mean GSI's increased and peaked more rapidly in female white crappie than in male white crappie; however, mean GSI's in male white crappie declined more gradually through summer and fall months (Figure 11).

Condition Of Crappie

White crappie grew to greater size than black crappie in Copan lake (Figures 12 and 13). The largest black crappie sampled (297 mm, 550 g) was an Age 3 male, whereas, the largest white crappie sampled (354 mm, 864 g) was an Age 6 female with ripe ovaries (71 g). Sample means indicated that black crappie had lower relative weights than white crappie at all sample locations in Copan lake (Table 8). Black crappie had higher mean relative weights than white crappie until 150 mm total length, and greater mean actual weights until they reached 210 mm total length. However, white crappie had broader relative and actual weight ranges, and smaller standard errors than black crappie. Both species approached 100% relative weight at 150 mm total length; however, mean

relative weight in black crappie fluctuated thereafter. Mean relative weights in white crappie remained near 100% until they reached 250 mm total length, and above 100% thereafter (Figures 12 and 13).

Black crappie in Endacott's pond had higher mean relative weights (0.83%) and less variation between individuals as indicated by small standard error than black crappie collected at other locations (Table 8). Relative weights were greater in adult black crappie from the north section (CNE) and in Age 0 crappie from the south section (RR and 10E) (Table 9). Monthly mean relative weight data was incomplete for black crappie sexes and age groups due to the small sample and seasonal variation in catch distribution.

Condition was significantly greater in female black crappie than in males ($t = 2.55$, $df = 15$, $P < 0.05$) at CNE and in males than females ($t = 3.30$, $df = (32,52)$, $P < 0.005$) in Endacott's pond (Table 8). Seasonal relative weight changes in older black crappie were not evident due to the small sample; however, relative weights increased in Age 0 black crappie between October and November samples at 3 locations (EP, CNE, and 10E) in Copan lake (Table 9). Further analysis revealed significant differences between sexes in monthly samples of black crappie (Table 10). Age 0 males had higher relative weights than females in October samples ($t = 4.61$, $df = 8$, $P < 0.005$). However, Age 0 females had higher relative weights than males in November samples ($t = 9.51$, $df = 45$, $P < 0.001$), and Age 4 females had higher relative weights than males in June samples ($t = 15.3$, $df = 14$, $P < 0.001$) (Table 10).

Mean condition in all white crappie age groups decreased during summer (Table 11). However, analysis of variance of pooled ages revealed no significant differences in mean relative weight among

capture months ($F = 1.09$, $df = (7,23)$, $P > 0.25$) or seasons ($F = 1.24$, $df = (2,9)$, $P > 0.25$). Mean relative weights of crappie samples also varied in relation to capture site; they were lower in fish from Endacott's pond and Little Caney river, and higher in fish from the north (CNE) and south (RR, WC, and 10E) sections of Copan lake (Table 8). Analysis of variance tests of pooled white crappie age groups, however, revealed no significant differences ($F = 0.39$, $df = (5,20)$, $P > 0.75$) in mean relative weights of fish among capture sites (Table 12).

Relative weights were significantly different ($F = 18.30$, $df = (4,21)$, $P < 0.001$) among pooled white crappie age groups from different sample locations (Table 12). Relative weight increased with ascending age until the 4th year. Age 2 white crappie (1981 year class) had consistently high relative weights during the sample period. Condition in Age 3 crappie (1980 year class) was also high, but was inconsistent across months, with greater variation among individuals as indicated by higher standard errors.

Mean relative weights were similar between white crappie sexes in Endacott's pond and 10E (Table 8). However, males had significantly higher relative weights than females ($t = 5.53$, $df = 24$, $P < 0.001$) in Little Caney river. Condition of females was higher than that of males ($t = 1.36$, $df = (86,51)$, $P < 0.1$) at CNE, and was significantly higher than that of males from south lake sites RR ($t = 3.82$, $df = (76,66)$, $P < 0.005$) and WC ($t = 8.12$, $df = 21$, $P < 0.005$). Monthly differences between white crappie sexes at different ages were inconsistent (Table 13). Where sample sizes permitted analysis, significantly higher monthly mean relative weights were revealed more often in samples of male white crappie than of female white crappie.

Mean total lengths and relative weights at capture were plotted for black crappie age groups at 2 sample locations in Copan lake (Figures 14 and 15). Mean relative weights were higher in Age 0 black crappie from EP than from CNE; mean relative weight varied less among fish of different ages in samples from EP than from CNE. However, mean total lengths indicated that "quality" size fish (TL > 200mm) were more likely captured from samples of Age 2+ crappie in CNE and Age 4+ crappie in Endacott's pond.

Mean relative weights increased steadily with age and reached 100% in Age 2 crappie at all 6 sample locations in Copan lake except Little Caney river (Figures 16-21). Relative weights remained near 100% in Age 3 fish from the river (10W) and from 2 major sample locations (EP and RR), and above 100% in CNE and from 2 minor sample locations (WC and 10E). There was a decline in relative weight from Age 3 to Age 4 in all crappie. Mean total length at capture of Age 4 crappie was also below Age 3 mean length. Total lengths steadily increased in Ages 0-3 at all sites, and appeared to asymptote near 300 mm in older white crappie.

Length Weight Relations

Length weight relations for total samples of black and white crappie are $\text{Log}_{10}(\text{WT}) = -5.745 + 3.390[\text{Log}_{10}(\text{TL})]$ and $\text{Log}_{10}(\text{WT}) = -6.452 + 3.691[\text{Log}_{10}(\text{TL})]$, respectively (Table 14). Regression slopes for Copan crappie were greater than Oklahoma averages listed in Mense (1976). Common and natural log regression slopes ranged from 2.7 to 3.9 among sample locations (Tables 14 and 15, respectively). Analysis of covariance on natural log regression slopes revealed significant differences between species ($P < 0.001$). Within species analyses

revealed significant differences between main lake and pond samples of black crappie ($P < 0.001$), and between all sample locations of white crappie ($P < 0.001$). Contrast analysis identified significant differences in regression slopes of natural log length weight relationships in white crappie samples captured from 3 general areas of Copan lake (Table 16). Regression slopes were significantly different between fish samples from EP and CNE ($P < 0.0001$), both of which were significantly different from fish pooled from samples from south lake sites (RR, 10E, WC, and 10W) ($P < 0.0001$).

Crappie Growth Histories

Black crappie exhibited slower growth rates than white crappie, reaching "quality" length in the 3rd year instead of the 2nd year (Tables 17 and 18, respectively). White crappie had greater mean length increments and mean length at all but the 4th annuli, at which mean lengths for both species were below averages (Tables 19 and 20). Ages 2 and 3 white crappie (1981 and 1980 year classes, respectively) exhibited above average growth rates. Lee's phenomenon was not evident in back-calculated length at annuli of older (Ages 5 and 6) fish.

Black and white crappie growth rates varied between sample locations (Tables 21 and 22). The fastest growth in the study was found in black crappie from CNE. Above average growth rates and length increments between annuli were found in white crappie from the north (CNE) and south lake sites (RR, 10E, and WC). The poorest growth was found in white crappie from 10W. However, mean lengths in fish from Endacott's pond were below averages for both species. In addition, no significant differences were revealed between sexes (Table 23).

Mean back-calculated total lengths in Copan lake black crappie were comparable to Oklahoma and regional averages until Age 4 (Tables 24 and 25, respectively). Growth rates in EP were greater than averages for small Oklahoma lakes (5-110 acres), but less than averages of "new" waters (< 4 years). Black crappie at CNE had growth superior to all Oklahoma waters, and all regional waters but Norris Reservoir, listed in Table 25.

Growth rates of Copan lake white crappie were superior to those from all other Oklahoma waters except "new" waters (Table 26), and were comparable to those in regional waters (Table 27). Only 3 studies (Hansen 1951; Carter 1953; and Stevens 1959) listed greater mean lengths for Ages 1-4. Mean lengths in Copan lake were generally greater than means reported for other midwestern waters (Table 27). Growth rates of white crappie at EP were above Oklahoma and regional averages for Ages 1-2, after which they were only comparable to growth in small midwestern impoundments reported by Gablehouse (1984). In general, mean lengths of Age 3+ white crappie were below all means reported in Tables 26 and 27.

DISCUSSION

Although white crappie were more abundant than black crappie in Copan lake, both species had access to the reservoir. Both species were reported to be present in the Verdigris river system by Jenkins and Finnell (1957), however, only white crappie were listed for Little Caney river (U.S. Army Corps Engr. 1972). Hall et al. (1954) reported that black crappie were as widely distributed in Oklahoma as white crappie, although generally not as abundant. Black crappie were generally

restricted to Endacott's pond, where hatchery stocking occurred in 1945 (Paul Endacott, pers. comm.). It is assumed that present stocks of black crappie in Copan lake originated from hatchery stocks in EP, and, that white crappie stocks are derived from the indigenous population in the Little Caney river.

The weak 1980-82 black crappie year classes are characteristic of crappie populations in small impoundments and seem to fit the scenario of intraspecific competition presented by Rutledge and Barron (1972) and Gablehouse (1984). Overharvest might also partially explain missing age groups. A large number of "crappie" were reportedly removed from the pond by illegal methods when public access was established (1981). This removal may have drastically reduced effective population number in the pond. The few remaining breeding adults may have produced small cohorts, which were cannibalized at a disproportionately higher rate. Ball and Kilambi (1972) reported that adult crappie were cannibalistic in Tablerock reservoir, preferring Age 0 crappies over all other forage. Reduction of population size may also have resulted in greater survival of Age 4 crappie in the pond by reducing intraspecific resource competition and increasing growth rates.

The absence of Age 3+ fish in the main lake is typical of crappie populations in midwestern reservoirs (Hansen 1951; Gablehouse 1984). Faster growing individuals may have lower survivorship beyond Age 3 because of physiological "burnout". Ellison (1984) reported age related mortality when black crappie did not switch to piscivory at the appropriate size (> 200 mm) and thereby failed to increase daily ration above maintenance levels. Apparently, increasing water temperatures increased maintenance requirements and created an "energy trap" for

larger crappie during summer.

Physical factors could also be responsible for age specific mortality. Copan lake has undergone dramatic fluctuations in water levels and temperatures for 7 years prior to complete filling (1983). Heavy spring rains are usually followed by long, hot summers of little or no rainfall. The summer of 1980 recorded more than 30 consecutive days of ambient temperatures above 100°. The absence of older crappie in collections from the main lake could be associated with a combination of physiological stresses related to spawning, summer water temperature, and failure to maintain adequate condition.

The slower growth and older age structure of fish from the pond vs. those from the reservoir could be explained if the pond were a more benign environment than the reservoir. Endacott's pond was less turbid and more wind sheltered than Copan lake. In addition, a complex Centrarchid community was present in the pond, possibly suggesting that a more stable environment existed in the pond. Vanderpuye and Carlander (1971) reported that greater longevity in black crappie was correlated with slower growth rates after reservoir stabilization.

Seasonal changes in sex ratios such as I saw in Copan lake have been reported by other authors. A "shifting sex ratio" in Lake George black crappie collections was attributed to a changing sex ratio and shifting age composition in the population (Huish 1953). Hansen (1951) reported high annual mortality of Age 3 male white crappie in Illinois. He found that male white crappie dominated Fall and early Spring collections, and females dominated late spring and summer collections and suggested that males were missing from spring and summer because of their involvement with nest construction and guarding. Copan

collections did not indicate any lack of males in Spring and Summer collections. However, the increased presence of younger male white crappie in Fall samples was probably due to greater precocious vagility at earlier age.

Normally, crappie mature between the 2nd and 3rd year but there is evidence in my data of early maturation and prolonged spawning of males. Mean GSI's (0.82% and 0.77%) during May for male black and white crappie were greater than the mean of Age 4+ black crappie (0.52%) in the Ottawa river (Hanson and Quadri 1980), but were comparable to a small sample of Illinois white crappie (< 1.0%) (Hansen 1951). Greater Age 0 growth rates may allow black crappie to mature at an earlier age (Siefert 1969). Prolonged spawning periods for males may be indicated in my data because male GSI's decreased more slowly than female GSI's. This trend has also been reported in blacknose dace (Tarter 1969) and in silverjaw minnow (Hoyt 1971). However, this apparent delayed gonad attenuation could have been an artifact from the relatively lesser amount of gonad weight per body weight in male crappie compared to female crappie.

There is also evidence for high fecundity and early age of spawning of both black and white crappie in my data. Fecundity has been correlated with total length and weight (rather than age) for white crappie (Mathur et al. 1979) and black crappie (Barwick 1981). White crappie females appeared reproductively mature at Age 2 (Table 6). Despite low catch frequencies of Ages 2-3 black crappie, it is assumed that spawning also begins at Age 2 (Table 7). Hansen (1951) noted that age and sex composition in the catch distribution were positively correlated with crappie spawning activity. Fecundity may be unique for a year class, and may vary between years, populations, and habitat

types. Mathur et al. (1979) found evidence for a fecundity compensating mechanism in white crappie that tended to increase egg production at lower population density or at higher growth rates. Mean female GSI's during May for black and white crappie (4.18% and 5.95%, respectively) in Copan lake were greater than mean GSI of Age 5+ black crappie (3.3%) from a relatively slow growing population in the Ottawa river (Hanson and Quadri 1980). These higher GSI values suggest greater fecundity in Copan lake crappie stocks due to faster than average growth rates in the new reservoir.

There is no evidence for stunting in Copan lake crappie populations. Proportional stock densities (PSD) for all crappie samples indicated an abundance of "quality" size crappie in the lake. Gablehouse (1984) reported PSD's of 30-50% in "balanced" white crappie populations in small midwestern impoundments. The low site PSD's for white crappie (WC and 10W) and black crappie (CNE) in Copan lake are probably due to small samples.

Population structure, as indicated by length frequency indices (i.e. PSD), reflect growth rates over time intervals of a year or more. At the same time, condition indices (i.e. Wr) reflect growth rates over shorter time intervals. Environmental conditions in a reservoir vary by season, influencing changes in length and condition, which affects population fecundity, growth, and survivorship.

Growth rates were positively correlated with condition (Wr) in fish from different sample locations in Copan lake. Faster growth was associated with higher relative weight in the main body of Copan lake (RR, CNE, WC, and 10E). However, slower growth and lower relative weight was evident in Endacott's pond and Little Caney river (EP and

10W). Burris (1954) reported that condition was poor in slow growing crappie, but increased with total length in fast growing crappie. Mosher (1984) suggested a relative weight "threshold" was responsible for growth in white crappie, in which high relative weight was necessary for a response to new forage to result in rapid growth. Thus, stability of condition could be site specific, relating to habitat quality and population density.

The summer decrease in relative weight that was seen in Copan lake crappie species is similar to that reported in other crappie populations (Hansen 1951; Mosher 1984). Relative weights declined in Age 4 crappie, however, the majority of Age 4+ fish were collected in Endacott's pond, where mean condition of fish was generally lower than in fish from the main lake (Table 8). Nevertheless, the absence of older fish in late summer and fall samples suggests an increase in age related mortality that may result from lower condition. Ellison (1984) and Gablehouse (1984) suggest this phenomenon is responsible for reduced PSD in midwestern reservoir populations of black crappie and white crappie, respectively.

Back calculated total lengths indicated black crappie grew faster than white crappie the first year, whereas white crappie grew faster thereafter (Table 22). This tendency has also been noted in other sympatric crappie populations (Li et al. 1976), however, this difference in first year growth is not universal (Hansen 1951; Stevens 1958). In addition, first year growth of crappie must be interpreted with caution due to the extended spawning period (Siefert 1969).

Site related growth differences in Copan lake may indicate pre-impoundment subpopulations in the basin. Pre-impoundment crappie

stocks in the lake may not have been resource limited during the 7 years prior to filling. Fast growth in new reservoirs is generally associated with low population density and increased nutrients. White crappie in Lake Barkley had significantly greater growth rates and conditions than stocks in the small adjacent impoundments (Gasser and Johnson 1977). This difference was attributed mainly to high relative abundances in the adjacent waters. Slow crappie growth and low relative weights in Endacott's pond may be due to interspecific competition with the abundant centrarchids in the pond. However, crappie growth varies with habitat productivity as well as population size.

Growth of white crappie in pre-impounded Little Caney river was the lowest in the study, and was below the Oklahoma average for turbid waters (Table 26). Growth rates and condition of planktophagic crappie are reduced by the limitations increased turbidity places on visibility and foraging efficiency (Ellison 1984). Hall et al. (1954) attribute "extremely poor growth" of crappie in turbid lakes to the presence of post oak (Quercus stellata) and blackjack oak (Q. marilandica) forests in the drainage. Copan lake drainage is "characterized" by sandy soils and primarily post oak and blackjack oak forests (U.S. Army Corps Engr. 1972).

Growth and condition of crappie in the river probably result from constraints determined by turbidity and its influence on temperature and oxygen regimes. In addition to normally high levels of suspended solids, the river has historically undergone fluctuations in flow and temperature (U.S. Army Corps of Engineers 1972). Low summer flow may limit survival by reducing total habitat and increasing water temperatures. If the Little Caney river continues to deliver high

sediment loads into the lake, growth of future crappie populations may continue to be impacted by factors in the drainage.

The future of black and white crappie in Copan lake depends on recruitment, growth, and mortality. The decline of crappie growth in aging reservoirs is well documented (Rutledge and Barron 1972). The most abundant year class typically occurs the first year of impoundment. The 1983 year classes of black and white crappie were 59% and 22% of total samples, respectively (Table 1). The white crappie population has good year class balance and exhibits above average growth and condition.

Although excellent growth was seen in black crappie samples from CNE, black crappie were not widespread in Copan lake. The future of black crappie in Copan lake may depend entirely on the 1983 year class. Survival of the 1979-80 year classes will likely be too low to significantly affect 1984 reproduction in the lake. However, habitat degradation as the lake senesces may more directly affect black crappie life history. Age 0 white crappie move into the pelagic zone soon after leaving the nest, while Age 0 black crappie tend to stay longer near shoreline cover. The loss of submerged vegetation will reduce available cover and possibly result in a decline of black crappie recruitment (Ball and Kilambi 1972).

Ellison (1984) reported black crappie were poorly adapted to capturing fish in turbid water, which resulted in an energy trap during summer. It is conceivable that turbid midwestern reservoirs represent marginal habitat for black crappie. White crappie are usually the more abundant crappie in turbid reservoirs (Goodson 1966). Branson and Moore (1962) suggest that white crappie may be the more recently evolved crappie species. Perhaps the white crappie is a form with greater

adaptive plasticity which can exploit the relatively recent proliferation of reservoirs in midwestern states.

CONCLUSIONS

White crappie were generally in better condition, more fecund, and more widespread than black crappie in Copan lake. Growth rates of black crappie, however, were generally higher than those of white crappie during the first year of impoundment. As the reservoir ages and stabilizes, white crappie will probably remain the dominant crappie species. White crappie year class stability may be controlled by age related mortality and recruitment. It remains to be seen whether black crappie become established in the lake. The first few years of recruitment will be critical to establishing an effective population (especially of black crappie) with desirable growth and age structure.

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Table 1. Length frequency distribution by age group for black and white crappie captured in Copan lake during 1983.

Total Length	Age												
	Black Crappie						White Crappie						
	0	1	2	3	4	5	0	1	2	3	4	5	6
60-79							1						
80-99	15						52	3	1				
100-119	29	2					54	1					
120-139	16	3					13	11	9				
140-159	2	3					43	13					
160-179			1	1			46	28	2	5			
180-199				3	4		16	37	10	29			
200-219		1		1	13		3	38	8	25			
220-239					16	1	2	28	5	6	1		
240-259				1				22	11	3			
260-279								15	34	2			
280-299				1	1			3	27	6	1		
300-319									1	4	2		
320-339										1			
340-359													1
N	62	9	1	7	34	1	120	125	195	102	78	2	1
TL*	110	144	179	211	219	233	103	160	206	258	213	257	354

* Mean total length at capture.

Table 2. Year class distribution of black and white crappie captured at different sites in Copan lake during 1983.

Year Class Age	<u>White Crappie</u>						<u>Black Crappie</u>		
	<u>Capture Sites</u>						<u>Capture Sites</u>		
	CNE	EP	RR	WC	10E	10W	CNE	EP	
1983	0	52 (37.1)	58 (21.9)	2 (1.4)	0 (0)	7 (24.1)	1 (3.6)	6 (37.5)	44 (50.6)
1982	1	6 (4.3)	28 (10.6)	50 (35.5)	17 (73.9)	6 (20.7)	18 (69.2)	8 (50.0)	2 (2.3)
1981	2	34 (24.3)	73 (27.7)	73 (51.7)	4 (17.4)	8 (27.6)	3 (11.5)	1 (6.3)	0 (0)
1980	3	46 (32.9)	29 (11.0)	13 (9.2)	2 (8.7)	8 (27.6)	4 (15.4)	1 (6.3)	5 (5.7)
1979	4	2 (1.4)	74 (28.0)	2 (1.4)					35 (40.2)
1978	5		1 (0.4)	1 (0.7)					1 (1.2)
1977	6		1 (0.4)						
Total		140	264	141	23	29	26	16	87

* Percent frequency.

Table 3. Sex ratio and age distribution of black crappie from sample locations in Copan lake during 1983.

Year Class	Age	<u>CNE</u>		<u>EP</u>		<u>Total Sample</u>	
		Male	Female	Male	Female	Male	Female
1983	0	5 (33.3)	1 (100.0)	35 (66.0)	9 (27.3)	40 (58.8)	10 (29.4)
1982	1	8 (53.3)	0 (0)	2 (3.8)	0 (0)	10 (14.7)	0 (0)
1981	2	1 (6.7)	0 (0)	0 (0)	0 (0)	1 (1.5)	0 (0)
1980	3	1 (6.7)	0 (0)	2 (3.8)	2 (6.1)	3 (4.4)	2 (5.9)
1979	4			14 (26.4)	21 (63.6)	14 (20.6)	21 (61.8)
1978	5			0 (0)	1 (3.0)	0 (0)	1 (2.9)
Sex Ratio		15 : 1		53 : 33		68 : 34	

Table 4. Sex ratio and age distribution of white crappie from sample locations in Copan lake during 1983.

Year	Class Age	<u>CNE</u>		<u>RR</u>		<u>EP</u>		<u>WC</u>	
		Male	Female	Male	Female	Male	Female	Male	Female
1983	0	26 (29.5)	26 (50.0)	1 (1.3)	1 (1.5)	41 (30.1)	17 (13.3)	0 (0)	0 (0)
1982	1	6 (6.8)	0 (0)	29 (38.6)	21 (32.3)	13 (9.6)	15 (11.7)	11 (73.3)	6 (75.0)
1981	2	30 (34.1)	4 (7.7)	38 (50.0)	35 (53.8)	42 (30.9)	31 (24.2)	4 (26.7)	0 (0)
1980	3	26 (29.5)	20 (38.5)	7 (9.2)	13 (9.2)	13 (9.6)	16 (12.5)	0 (0)	2 (25.0)
1979	4	0 (0)	2 (3.8)	0 (0)	2 (3.1)	27 (19.9)	47 (36.7)		
1978	5			1 (1.3)	0 (0)	0 (0)	1 (0.8)		
1977	6					0 (0)	1 (0.8)		
Sex Ratio		88 : 52		76 : 65		136 : 128		15 : 8	

Table 4. Continued.

Year Class	Age	<u>10W</u>		<u>10E</u>		<u>Total Sample</u>	
		Male	Female	Male	Female	Male	Female
1983	0	0 (0)	1 (5.6)	6 (33.3)	1 (9.1)	74 (21.7)	46 (16.4)
1982	1	5 (62.5)	13 (72.2)	3 (16.7)	3 (27.3)	67 (19.6)	58 (20.6)
1981	2	2 (25.0)	1 (5.6)	4 (22.2)	4 (36.4)	120 (35.2)	75 (26.7)
1980	3	1 (12.5)	3 (16.7)	5 (27.8)	3 (27.3)	52 (15.2)	50 (17.8)
1979	4					27 (7.9)	51 (18.2)
1978	5					1 (0.3)	1 (0.4)
1977	6					0 (0)	1 (0.4)
Sex Ratio		8 : 18		18 : 11		341 : 281	

Table 5. Monthly mean Gonadosomatic Index (GSI) for black and white crappie sexes captured in Copan lake during 1983.

	Months								
	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV
Black Crappie									
Male	0.33	-	0.82	-	-	-	-	0.70	0.38
Female	-	-	4.18	0.94	-	-	-	1.39	0.17
White Crappie									
Male	0.20	0.22	0.77	0.04	0.19	0.01	0.03	0.16	0.04
Female	1.53	6.40	5.95	0.33	0.31	0.22	0.35	0.25	0.07

Table 6. Monthly mean Gonadosomatic Index (GSI) for white crappie age groups captured in Copan lake during 1983.

AGE	Months								
	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV
0 Male							0.0	0.04	0.01
Female							-	0.15	0.02
1 Male	0.0	0.0		0.0	0.17	0.0	0.0	0.41	0.17
Female	-	-		-	0.25	0.18	0.34	0.43	0.33
2 Male	0.11	0.14	0.44	0.03	0.27	0.01	0.14	0.48	0.54
Female	1.30	6.82	3.06	0.27	0.40	0.28	0.39	0.99	-
3 Male	0.37	0.33	0.74	-		0.0		0.77	0.23
Female	1.59	6.12	7.04	0.33		-		-	-
4 Male		-	1.10	0.11	-	-			-
Female		7.90	7.74	0.43	0.44	0.29			1.26
5 Male									
Female									
6 Male			-						
Female			8.22						

Table 7. Monthly mean Gonadosomatic Index (GSI) for black crappie age groups captured in Copan lake during 1983.

AGE	Months									
	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	
0 Male								1.00	0.38	
Female								1.39	0.17	
1 Male	0.41							0.39		
Female	-							-		
2 Male	0.0									
Female	-									
3 Male	0.28		0.85							
Female	-		2.57							
4 Male			0.81	-						
Female			4.98	0.94						

Table 8. Mean relative weight (standard error) for black and white crappie sexes captured from sample locations in Copan lake during 1983.

	Sample Locations					
	CNE	EP	RR	WC	10E	10W
Black Crappie						
Total Sample	0.76(.06)	0.83(.01)	0.62(.05)	-	0.72(.06)	0.90(-)
Male	0.78(.07) ²	0.80(.01) ³	0.62(.05)	-	0.79(.04)	0.90(-)
Female	0.68(.04)	0.88(.02)	-	-	0.60(.11)	-
White Crappie						
Total Sample	0.94(.04)	0.91(.01)	0.97(.02)	0.94(.04)	0.96(.06)	0.86(.03)
Male	0.91(.04) ¹	0.91(.02)	0.95(.02) ³	0.90(.04) ⁴	0.99(.08)	0.91(.06) ⁴
Female	1.00(.09)	0.92(.01)	1.00(.04)	1.00(.07)	0.96(.07)	0.86(.03)

1 = P < 0.1 ; 2 = P < 0.05 ; 3 = P < 0.005 ; 4 = P < 0.001

Table 9. Monthly mean relative weight (standard error) for black crappie age groups collected from sample locations in Copan lake during 1983.

AGE	MONTH									
	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	
0	-	-	-	-	-	0.71 (-)	0.70 (-)	0.59 (0.05)	0.79 (0.01)	
						0.57 (-)		0.52 (0.13)	0.64 (0.14)	
								0.65 (0.21)	0.72 (-)	
1	1.01 (0.21)	-	-	-	-	-	-	0.69 (-)	-	
	0.86 (-)									
2	0.63 (-)	-	-	-	-	-	-	-	-	
3	1.28 (-)	-	0.87 (0.02)	0.91 (-)	-	-	-	-	-	
	0.90 (-)									
4	0.94 (0.03)	-	0.82 (0.02)	0.96 (0.02)	0.90 (-)	-	-	-	-	
5	-	-	-	0.94 (-)	-	-	-	-	-	

1 = EP; 2 = CNE; 3 = 10E; 4 = RR; 5 = 10W.

Table 10. Monthly mean relative weight (standard error) for male and female black crappie captured in Copan lake during 1983.

AGE	Months									
	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	
0 Male	-	-	-	-	-	0.57(-)	-	0.62(.06)	0.76(.02)	
0 Female	-	-	-	-	-	-	-	0.56(.05)	0.79(.03)	
1 Male	1.00(-)	-	-	-	-	-	-	0.69(-)	-	
1 Female	-	-	-	-	-	-	-	-	-	
2 Male	0.63(-)	-	-	-	-	-	-	-	-	
2 Female	-	-	-	-	-	-	-	-	-	
3 Male	1.08(.19)	-	0.83(-)	0.91(-)	-	-	-	-	-	
3 Female	-	-	0.90(.00)	-	-	-	-	-	-	
4 Male	0.94(-)	-	0.82(.02)	0.90(.03)	0.90(-)	-	-	-	-	
4 Female	0.94(-)	-	0.80(.04)	0.98(.03)	-	-	-	-	-	
5 Male	-	-	-	-	-	-	-	-	-	
5 Female	-	-	-	0.94(-)	-	-	-	-	-	

1 = P < 0.005 ; 2 = P < 0.001

Table 11. Monthly mean relative weight (standard error) of pooled white crappie age groups from all sample locations in Copan lake during 1983.

AGE	MONTH									SEASON		
	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	SPRING	SUMMER	FALL
0	-	-	-	-	-	-	0.65 (-)	0.60 (0.02)	0.66 (0.02)	-	-	0.64 (0.01)
1	1.00 (0.15)	0.94 (0.07)	1.47 (-)	0.87 (0.03)	0.86 (0.04)	0.79 (0.01)	0.75 (0.02)	0.77 (0.01)	0.78 (0.02)	1.00 (0.08)	0.84 (0.02)	0.76 (0.01)
2	1.07 (0.03)	1.34 (0.02)	1.04 (0.03)	1.06 (0.02)	1.00 (0.02)	1.03 (0.03)	1.04 (0.06)	1.13 (0.03)	1.15 (-)	1.15 (0.06)	1.03 (0.01)	1.07 (0.03)
3	1.25 (0.06)	1.20 (0.14)	1.00 (0.03)	1.00 (0.04)	0.96 (0.05)	0.95 (-)	-	1.06 (0.15)	1.23 (0.13)	1.19 (0.03)	0.97 (0.03)	1.16 (0.10)
4	0.91 (0.04)	1.06 (0.11)	0.98 (0.02)	1.00 (0.02)	0.93 (-)	0.87 (0.03)	-	-	1.01 (-)	0.98 (0.02)	0.93 (0.02)	1.01 (-)
5	0.84 (-)	-	1.00 (-)	-	-	-	-	-	-	0.92 (-)	-	-
6	-	-	1.28 (-)	-	-	-	-	-	-	1.28 (-)	-	-

Table 12. Mean relative weight (standard error) for white crappie age groups captured from sample locations in Copan lake during 1983.

AGE	Sample Locations						POOLED AGE GROUPS
	CNE	EP	RR	WC	10E	10W	
0	0.55 (0.02)	0.69 (0.02)	0.60 (0.06)	-	0.68 (0.03)	-	0.64 (0.01)
1	0.91 (0.02)	0.80 (0.01)	0.86 (0.05)	0.85 (0.02)	0.69 (0.07)	0.57 (0.16)	0.90 (0.04)
2	1.02 (0.13)	1.03 (0.02)	1.02 (0.02)	1.12 (0.02)	1.08 (0.03)	0.84 (0.05)	1.02 (0.05)
3	1.07 (0.02)	1.01 (0.03)	1.11 (0.04)	1.29 (0.03)	1.32 (0.09)	1.04 (0.10)	1.16 (0.07)
4	1.10 (0.07)	0.97 (0.01)	1.04 (0.11)	-	-	0.97 (0.07)	0.97 (0.01)
5	-	0.84 (-)	1.01 (-)	-	-	-	0.93 (0.14)
6	-	1.28 (-)	-	-	-	-	1.28 (-)

Table 13. Mean relative weight (standard error) for male and female white crappie captured from Copan lake during 1983.

AGE	Sex	Month									
		MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	
0	Male	-	-	-	-	-	-	-	0.65(-)	0.59(.02)	0.66(.02) ²
	Female	-	-	-	-	-	-	-	-	0.61(.02)	0.62(.03)
1	Male	0.84(.45)	0.90(.02)	-	0.87(.03)	0.80(.01) ¹	0.78(.01)	0.77(.04)	0.78(.02)	0.76(.03)	
	Female	0.73(-)	-	1.47(-)	-	0.94(.10)	0.80(.01)	0.74(.02)	0.75(.00)	0.81(.02)	
2	Male	0.85(.02)	0.87(.02)	1.06(.05)	1.08(.02) ²	1.03(.02) ²	1.08(.03)	1.10(-)	1.13(.04)	1.15(-)	
	Female	0.84(.04)	1.44(-)	1.02(.03)	1.02(.03)	0.98(.03)	0.99(.04)	0.98(-)	1.11(-)	-	
3	Male	1.31(.04) ²	1.32(.03)	0.99(.04)	1.00(-)	0.95(.07)	0.95(-)	-	1.20(-)	1.11(-)	
	Female	1.16(.05)	1.35(.03)	1.02(.04)	1.00(.05)	0.98(-)	-	-	0.91(-)	1.36(-)	
4	Male	0.92(.04)	-	0.98(.03)	0.99(.04)	-	-	-	-	-	
	Female	0.90(.05)	1.06(.11)	0.97(.02)	1.00(.02)	0.93(-)	0.87(.03)	-	-	1.01(-)	
5	Male	-	-	1.00(-)	-	-	-	-	-	-	
	Female	0.84(-)	-	-	-	-	-	-	-	-	
6	Male	-	-	-	-	-	-	-	-	-	
	Female	-	-	1.28(-)	-	-	-	-	-	-	

1 = P < 0.005; 2 = P < 0.001

Table 14. Common log length-weight equations for black and white crappie captured from Copan lake during 1983 and other Oklahoma waters.

Sample	N	Length-weight equation	PR>F	R-Square
<u>Black Crappie</u>				
CNE	16	$\text{LOG}_{10}(\text{WT}) = -6.271 + 3.629[\text{LOG}_{10}(\text{TL})]$.0001	.9720
EP	89	$\text{LOG}_{10}(\text{WT}) = -5.598 + 3.326[\text{LOG}_{10}(\text{TL})]$.0001	.9875
TOTAL	114	$\text{LOG}_{10}(\text{WT}) = -5.745 + 3.390[\text{LOG}_{10}(\text{TL})]$.0001	.9831
* OK AVG	226	$\text{LOG}_{10}(\text{WT}) = -4.938 + 3.029[\text{LOG}_{10}(\text{TL})]$.987
<u>White Crappie</u>				
CNE	134	$\text{LOG}_{10}(\text{WT}) = -6.952 + 3.913[\text{LOG}_{10}(\text{TL})]$.0001	.9835
EP	275	$\text{LOG}_{10}(\text{WT}) = -6.308 + 3.628[\text{LOG}_{10}(\text{TL})]$.0001	.9798
RR	146	$\text{LOG}_{10}(\text{WT}) = -5.895 + 3.446[\text{LOG}_{10}(\text{TL})]$.0001	.9460
WC	22	$\text{LOG}_{10}(\text{WT}) = -6.302 + 3.631[\text{LOG}_{10}(\text{TL})]$.0001	.9696
1OE	29	$\text{LOG}_{10}(\text{WT}) = -6.756 + 3.821[\text{LOG}_{10}(\text{TL})]$.0001	.9887
1OW	30	$\text{LOG}_{10}(\text{WT}) = -4.284 + 2.729[\text{LOG}_{10}(\text{TL})]$.0001	.7470
TOTAL	647	$\text{LOG}_{10}(\text{WT}) = -6.452 + 3.691[\text{LOG}_{10}(\text{TL})]$.0001	.9679
* OK AVG	913	$\text{LOG}_{10}(\text{WT}) = -5.367 + 3.194[\text{LOG}_{10}(\text{TL})]$.978

* Referenced in Mense (1976)

Table 15. Natural log length weight equations for black and white crappie captured from several locations in Copan lake during 1983.

Sample	N	Length-weight equations	PR>F	R-Square
<u>Black Crappie</u>				
CNE	16	$\text{LN}(\text{WT}) = -14.439 + 3.629[\text{Ln}(\text{TL})]$	0.0001	0.9720
EP	89	$\text{Ln}(\text{WT}) = -12.892 + 3.326[\text{Ln}(\text{TL})]$	0.0001	0.9875
<u>White Crappie</u>				
CNE	134	$\text{Ln}(\text{WT}) = -16.007 + 3.913[\text{Ln}(\text{TL})]$	0.0001	0.9836
EP	275	$\text{Ln}(\text{WT}) = -14.524 + 3.628[\text{Ln}(\text{TL})]$	0.0001	0.9798
RR	146	$\text{Ln}(\text{WT}) = -13.574 + 3.446[\text{Ln}(\text{TL})]$	0.0001	0.9460
WC	22	$\text{Ln}(\text{WT}) = -14.510 + 3.631[\text{Ln}(\text{TL})]$	0.0001	0.9696
10E	29	$\text{Ln}(\text{WT}) = -15.555 + 3.821[\text{Ln}(\text{TL})]$	0.0001	0.9888
10W	30	$\text{Ln}(\text{WT}) = -9.865 + 2.729[\text{Ln}(\text{TL})]$	0.0001	0.7470

Table 16. Contrast analysis on regression slopes of natural log length weight equations of white crappie captured from sample locations Copan lake during 1983.

Contrast			Df	SS	F Value	PR>F
EP	V	CNE	1	1.15063829	44.76	0.0001
EP	V	WC	1	290.49192167	11299.11	0.0001
EP	V	RR	1	301.61413823	11731.72	0.0001
EP	V	10E	1	118.86270750	4623.34	0.0001
EP	V	10W	1	207.10994461	8055.84	0.0001
CNE	V	WC	1	227.34709079	8843.00	0.0001
CNE	V	RR	1	235.00097751	9140.71	0.0001
CNE	V	10E	1	97.52337042	3793.31	0.0001
CNE	V	10W	1	165.65332634	6443.33	0.0001
WC	V	RR	1	0.01086989	0.42	0.5158
WC	V	10E	1	0.00075491	0.03	0.8640
WC	V	10W	1	0.00523014	0.20	0.6521
RR	V	10E	1	0.00062941	0.02	0.8757
RR	V	10W	1	0.00001470	0.00	0.9809
10E	V	10W	1	0.00041244	0.02	0.8993

Table 17. Mean total length (mm) of black crappie captured in Endacott's pond during 1983.

Age	N (%)	I	II	III	IV	V
		*				
0	46 (52.3)	111.7				
1	1 (1.1)	92.6				
2	0 (0)	.	.			
3	5 (5.7)	88.7	156.8	194.5		
4	35 (39.8)	98.8	164.3	194.6	215.5	
5	1 (1.2)	116.5	186.9	200.5	211.3	222.1
Total		37	36	32	15	1
Mean TL		97.7	163.9	194.7	215.2	222.1
Mean Increment		97.7	66.2	30.8	20.5	6.9

*

Mean total length at capture.

Table 18. Mean total length (mm) at annuli for white crappie from combined sample locations in Copan lake during 1983.

Age	N (%)	I	II	III	IV	V
0	123 (19.0)	103.4				
1	111 (17.2)	95.8				
2	222 (34.3)	106.7	190.9			
3	102 (15.8)	98.5	179.4	240.1		
4	86 (13.3)	97.3	157.4	183.5	213.0	
5	2 (0.3)	106.7	182.8	200.6	215.8	
6	1 (0.2)	127.9	175.5	232.0	291.5	321.3
Total		438	269	135	26	1
Mean Length		101.5	178.1	210.0	216.2	321.3
Mean Increment		101.5	76.2	43.5	21.1	29.7

*

Mean total length at capture.

Table 19. Total length (mm) increments between annuli for black crappie captured in Endacott's pond during 1983.

Age	0-I	I-II	II-III	III-IV	IV-V
0	111.7	*			
1	92.6				
2	-	-			
3	88.7	68.1	37.7		
4	98.8	65.5	30.3	20.9	
5	116.5	70.4	13.6	11.2	10.8
MEAN	97.7	66.2	30.8	20.5	6.9

Table 20. Total length (mm) increments between annuli for white crappie captured in Copan lake during 1983.

AGE	0-I	I-II	II-III	III-IV	IV-V
	*				
0	103.4				
1	95.8				
2	106.7	84.2			
3	98.5	80.9	60.7		
4	97.3	60.1	26.1	29.5	
5	106.7	76.1	17.8	15.2	
6	127.9	47.6	56.5	59.5	29.5
MEAN	101.5	76.2	43.5	21.1	29.7

Table 21. Mean total length (mm) at annuli for black and white crappie from sample locations in Copan lake during 1983.

<u>Sample</u>	<u>N</u>	<u>I</u>	<u>II</u>	<u>III</u>	<u>IV</u>	<u>V</u>
<u>Black Crappie</u>						
CNE	11	119.9	216.9	280.3		
EP	42	97.7	163.9	194.7	215.2	222.1
<u>White Crappie</u>						
CNE	88	97.5	183.6	252.9	279.0	
EP	206	98.6	169.5	185.4	218.8	321.2
RR	140	110.6	196.4	248.7	280.9	
WC	23	95.9	179.9	260.0		
1OE	22	105.7	191.6	265.1		
1OW	25	94.4	166.5	183.8		

Table 22. Total length (mm) increments between annuli for black and white crappie captured from several locations in Copan lake during 1983.

Site	N	Annuli				
		0-I	I-II	II-III	III-IV	IV-V
<u>Black Crappie</u>						
CNE	11	119.9	90.1	63.4		
EP	42	97.7	66.0	29.7	17.5	10.8
<u>White Crappie</u>						
CNE	88	97.5	84.6	74.8	51.0	
EP	206	98.6	70.7	26.4	19.1	29.7
RR	140	110.6	82.8	73.1	36.2	
WC	23	95.9	83.9	59.9		
10E	22	105.7	81.4	60.4		
10W	25	94.4	53.0	17.2		

Table 23. Mean total length (mm) at annuli for black and white crappie sexes captured from sample locations in Copan lake during 1983.

Site	Sex	N	Annulus				
			I	II	III	IV	V
<u>Black Crappie</u>							
			*				
CNE	Female	1	112.0				
	Male	10	119.9	216.9	280.3		
EP	Female	24	100.7	165.5	194.1	214.3	222.1 (1)
	Male	18	93.7	161.7	195.7	218.7	
<u>White Crappie</u>							
CNE	Female	26	99.0	184.4	250.6	279.0	
	Male	62	96.8	182.8	255.5		
EP	Female	111	100.0	169.0	184.3	211.7	321.2 (1)
	Male	95	97.3	169.9	188.0	211.1	
RR	Female	65	107.0	183.1	248.8	280.8	
	Male	75	113.4	204.3	248.5		
WC	Female	8	105.8	202.3	262.0		
	Male	15	90.6	168.7			
10E	Female	10	99.8	185.6			
	Male	12	110.9	195.5	265.1		
10W	Female	17	95.3	166.5	183.8		
	Male	8	88.1				

* Total length at capture.

Table 24. Mean total length at annuli for black crappie captured in Copan lake during 1983 and other Oklahoma waters.

Site	N	Annulus							
		I	II	III	IV	V	VI	VII	
Endacott's Pond	42	97	163	194	215	222			Present Study
Copan North End	11	119	216	280					Present Study
Oklahoma Average	-	80	123	181	210	289			Mense (1976)
Oklahoma Average	2406	77	157	205	247	290	337	380 [†]	Hall et al. (1954)
OK Reservoirs (> 500 acres)	448	86	182	224	283	315	405 [†]		Hall et al. (1954)
OK Lakes (110-500 acres)	340	63	131	176	229	281	333	380 [†]	Hall et al. (1954)
OK Lakes (5-110 acres)	1220	75	154	202	236	287	308 [†]		Hall et al. (1954)
New Water (< 4 years)	-	125	207	245	292 [†]				Hall et al. (1954)
Turbid Waters	-	65	127	180	242	290	332 [†]		Hall et al. (1954)

[†] Mean total length was re-calculated into metric from inch X25. Decimals were truncated (77.6 = 77).

Table 25. Mean total length (mm) at annuli for black crappie captured in Copan lake and other waters in the southern United States.

Site	N	I	II	III	IV	V	VI	VII	VIII	IX	Source
Endacott's Pond	42	97	163	194	215	222					Present Study
Copan Lake North	11	119	216	280							Present Study
Oklahoma Average	2406	77	157	205	247	290	337	380			Hall et al. (1954)
Norris Res., TN	925	80	237	295	317	342					Stroud (1948)
L. Moultrie, SC	198	57	157	265	310	330	350	375	375		Stevens (1959)
L. Marion, SC	239	45	120	197	252	285	315	312	335		Stevens (1959)
L. Eustis, FL	292	50	110	170	207	235	260	280	292		Huish (1957)
L. Harris, FL	403	47	105	165	212	245	280	305	325	345	Huish (1957)
L. George, FL	943	110	202	247	287	312	302				Huish (1954)
L. Powell, UT	-	121	210	263	300	322					Hepwork and Pettingill (1980)
Lewis and Clark L., SD	-	68	118	148	185	200	239	267	286	314	Vanderpuye and Carlander (1971)
College L., CO	144	81	149	188	222	246	286				Willis et al. (1984)
Osage L., KS	-	62	133	188	239	272	290				Mosher (1984)
Clear L., CA	229	57	127	180	217	262	290	297			Erickson (1952)
Clear L., CA	78	77	136	158	168	175	193				Li et al. (1976)

* Mean total length re-calculated into metric from inch by X25. Decimals were truncated (77.6 = 77).
 † Referenced in Goodson (1966). ** Referenced in Huish (1954).

Table 26. Mean total length at annuli for white crappie captured in Copan lake during 1983 and other waters in Oklahoma.

Site	N	I	II	III	IV	V	VI	VII	VIII	Source
Copan Lake	298*	101	186	256	279					Present Study
Endacott's Pond	206	98	169	185	218	321				Present Study
Oklahoma Average	-	77	139	195	230	290				Mense (1976)
Oklahoma Average	10560	72	147	195	245	297	330	355	375 [†]	Hall et al. (1954)
OK Reservoirs (> 500 acres)	7300	82	172	205	247	297	322	330	352 [†]	Hall et al. (1954)
OK Lakes (110-500 acres)	1998	62	122	172	235	285	310	355	375 [†]	Hall et al. (1954)
OK Lakes (5-110 acres)	727	72	142	200	250	307	335	352 [†]		Hall et al. (1954)
New Waters (< 4 years)	-	127	232	255	307	367 [†]				Hall et al. (1954)
Turbid Water	-	62	125	175	227	292	320	347 [†]		Hall et al. (1954)

* Combined samples from Copan lake (CNE, RR, WC, 10E, and 10W).

† Mean total lengths re-calculated into metric from inch X25. Decimals were truncated (77.6 = 77).

Table 27. Mean total length at annuli for white crappie captured from Copan lake during 1983 and other waters from the southern United States.

Water	N	I	II	III	IV	V	VI	VII	VIII	Source
	**									
Copan Lake	298	101	186	256	279					Present Study
Endacott's Pond	206	98	169	185	218	321				Present Study
Oklahoma Average	10,560	72	147	195	245	297	330	355	375	Hall et al.(1954)
L. Marion, SC	129	47	172	247	280	307	315	327	*	Stevens (1959)
L. Moultrie, SC	37	55	205	282	335	365	375	372	*	Stevens (1959)
Kentucky L., KY	925	115	197	260	297	320				Carter (1953) †
L.Decatur, IL	3,507	182	227	262	265	305	307	*		Hansen (1951)
Small impoundments (IA,KS,MO,NB)	-	77	152	195	222	227	267		*	Gablehouse (1984)
Lewis and Clark L., SD	-	79	171	231	256	289	306	315		Siefert (1969)
Osage St. L., KS	-	64	146	216	269	321	341			Mosher (1984)
Campus L., CO	75	78	146	200	245	264	284			Willis et al. (1984)
Clear L., CA	149	70	145	178	189	213	193			Li et al. (1976)

** Combined samples from CNE, RR, WC, 10E, and 10W.

* Mean total length re-calculated into metric from inch by X25. Decimals were truncated (77.6 = 77).

† Referenced in Goodson (1966).

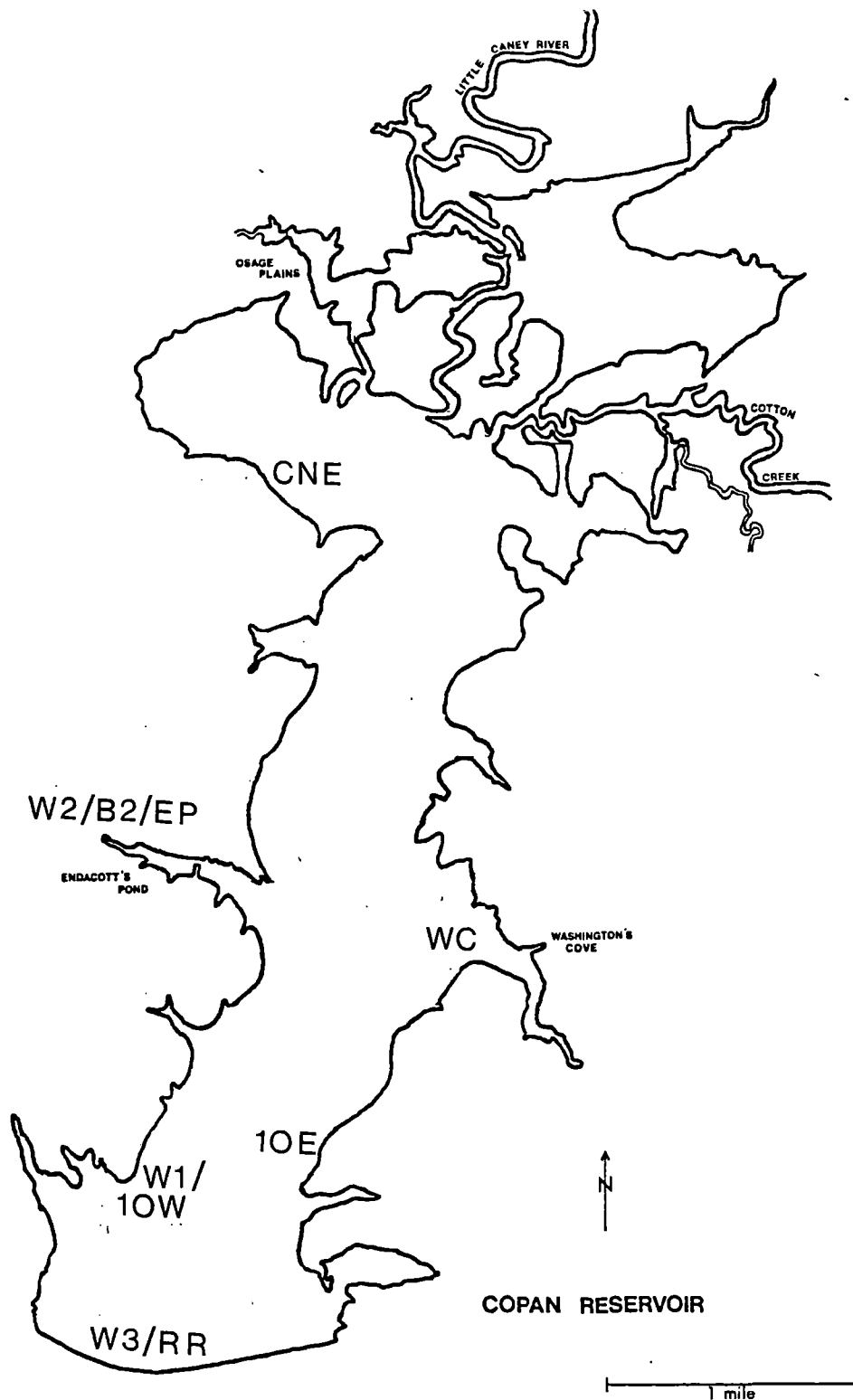


Figure 1. Collection locations in Copan lake during 1983.

LENGTH FREQUENCY DISTRIBUTION

SITE=EP

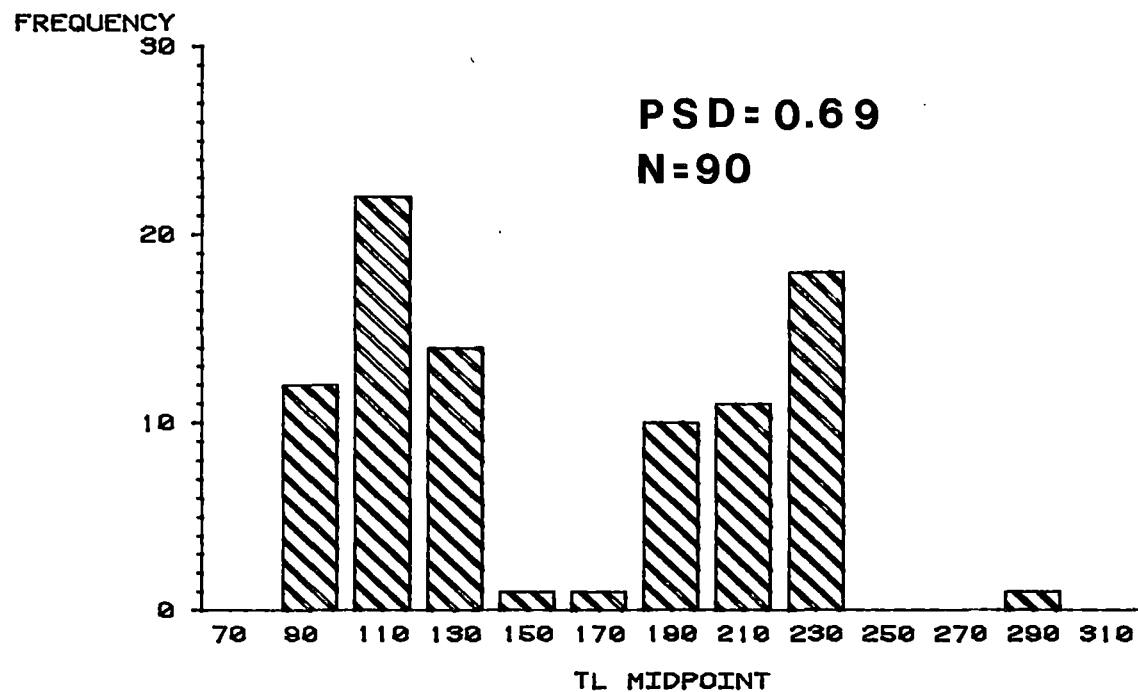


Figure 2. Length frequency distribution and proportional stock density (PSD) for black crappie captured in Endacott's pond during 1983.

LENGTH FREQUENCY DISTRIBUTION

SITE=CNE

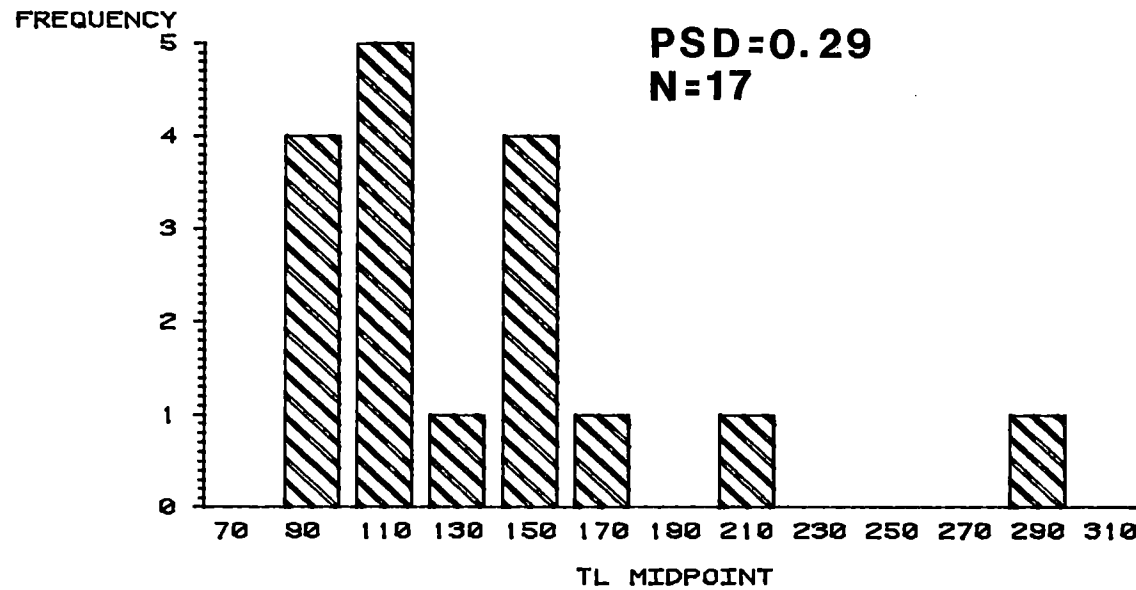


Figure 3. Length frequency distribution and proportional stock density (PSD) for black crappie captured in Copan lake north section during 1983.

LENGTH FREQUENCY DISTRIBUTION

SITE=10E

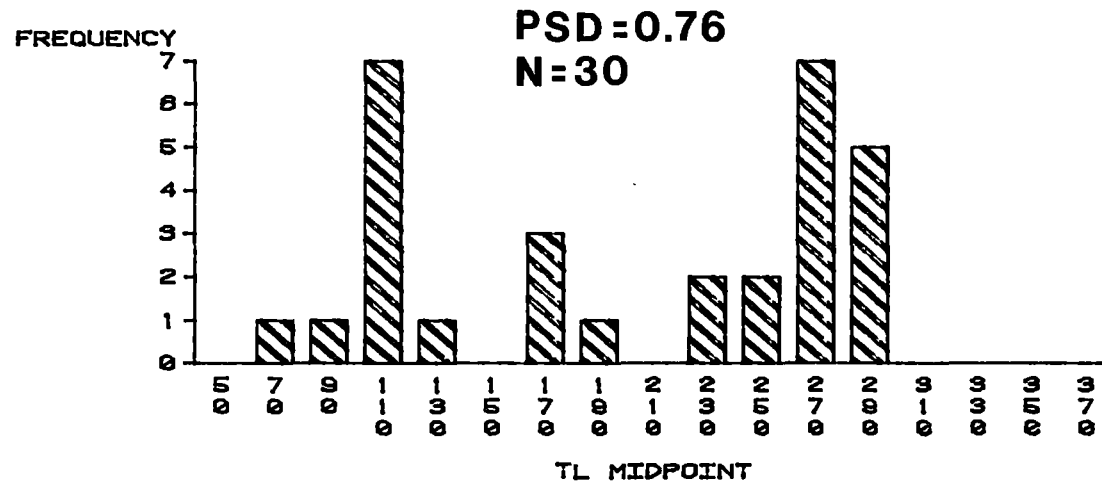


Figure 4. Length frequency distribution and proportional stock density (PSD) for white crappie captured at Highway 10 bridge east side in Copan lake during 1983.

LENGTH FREQUENCY DISTRIBUTION

SITE=10W

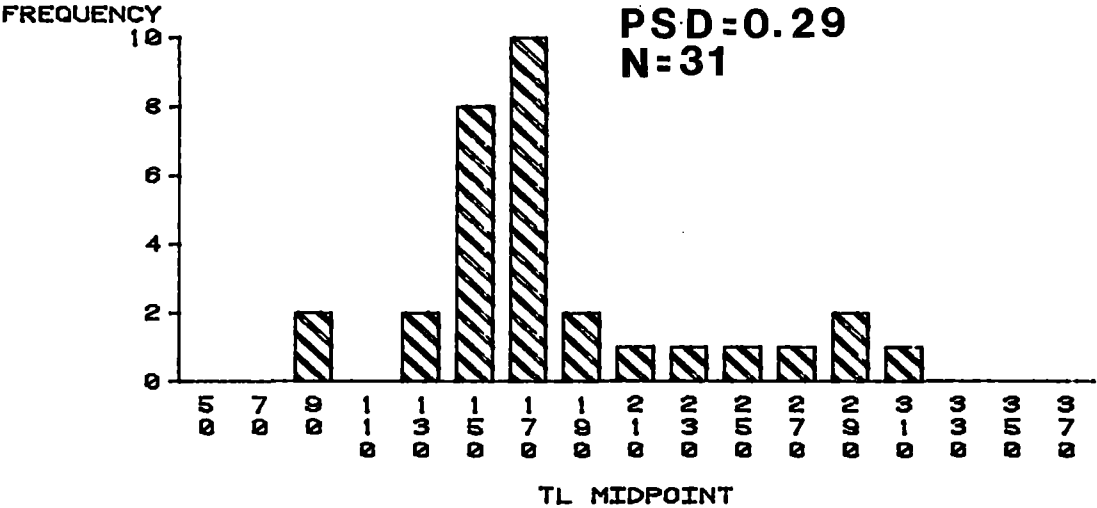


Figure 5. Length frequency distribution and proportional stock density (PSD) for white crappie captured in Little Caney river during 1983.

LENGTH FREQUENCY DISTRIBUTION

SITE=WC

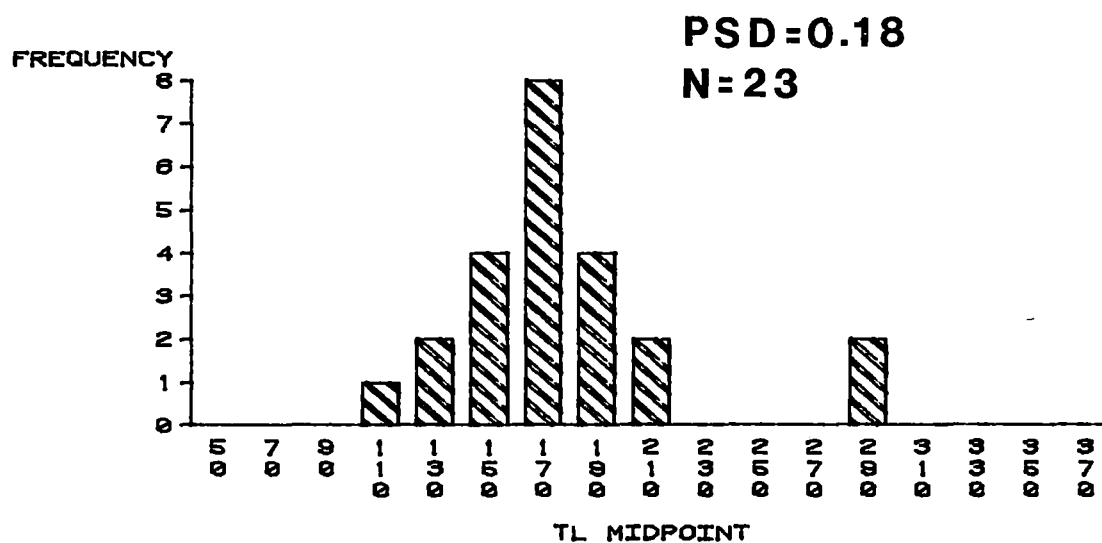


Figure 6. Length frequency distribution and proportional stock density (PSD) for white crappie captured in Washington's cove of Copan lake during 1983.

WHITE CRAPPIE LENGTH FREQUENCY DISTRIBUTION

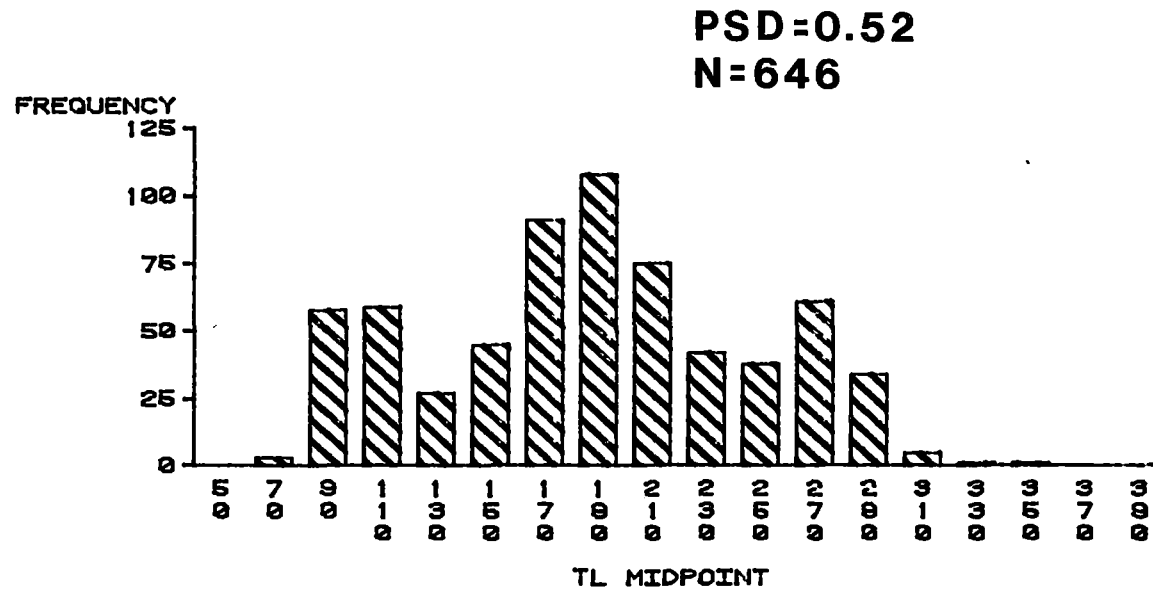


Figure 7. Length frequency distribution and proportional stock density (PSD) for all white crappie captured in Copan lake during 1983.

LENGTH FREQUENCY DISTRIBUTION

SITE=EP

PSD=0.47

N=286

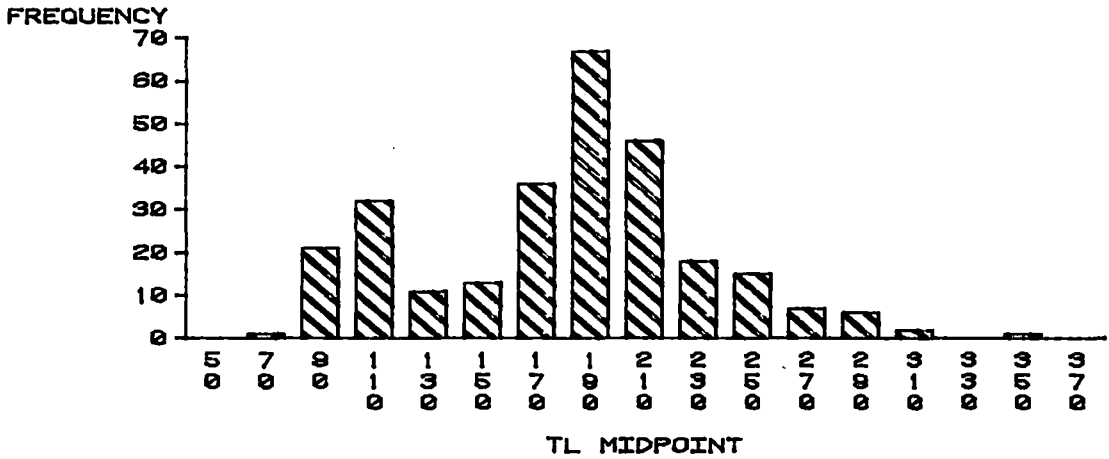


Figure 8. Length frequency distribution and proportional stock density (PSD) for white crappie captured in Endacott's pond during 1983.

LENGTH FREQUENCY DISTRIBUTION

SITE=CNE

PSD=0.75
N=135

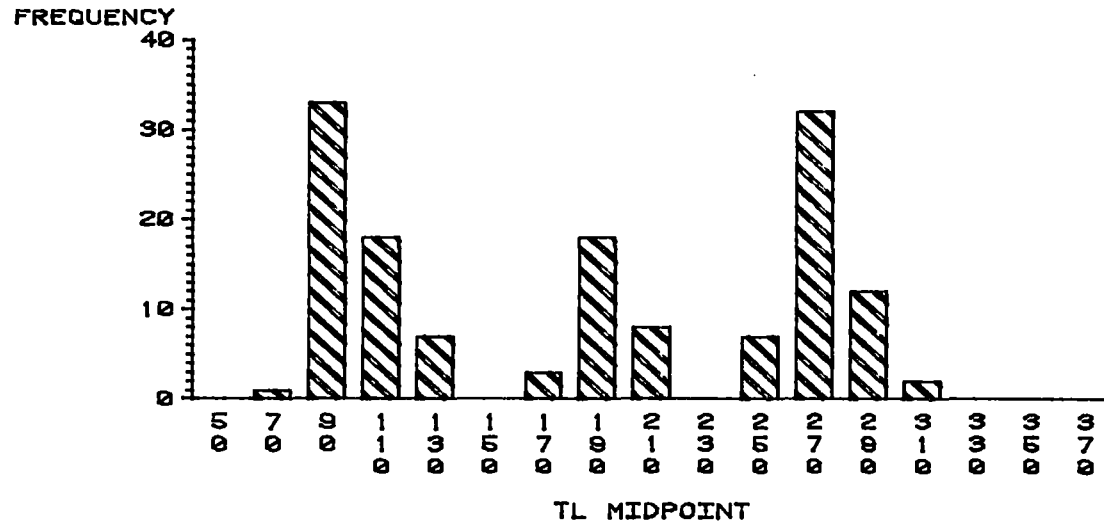


Figure 9. Length frequency distribution and proportional stock density (PSD) for white crappie captured in Copan lake north section during 1983.

LENGTH FREQUENCY DISTRIBUTION

SITE=RR

PSD=0.52

N=147

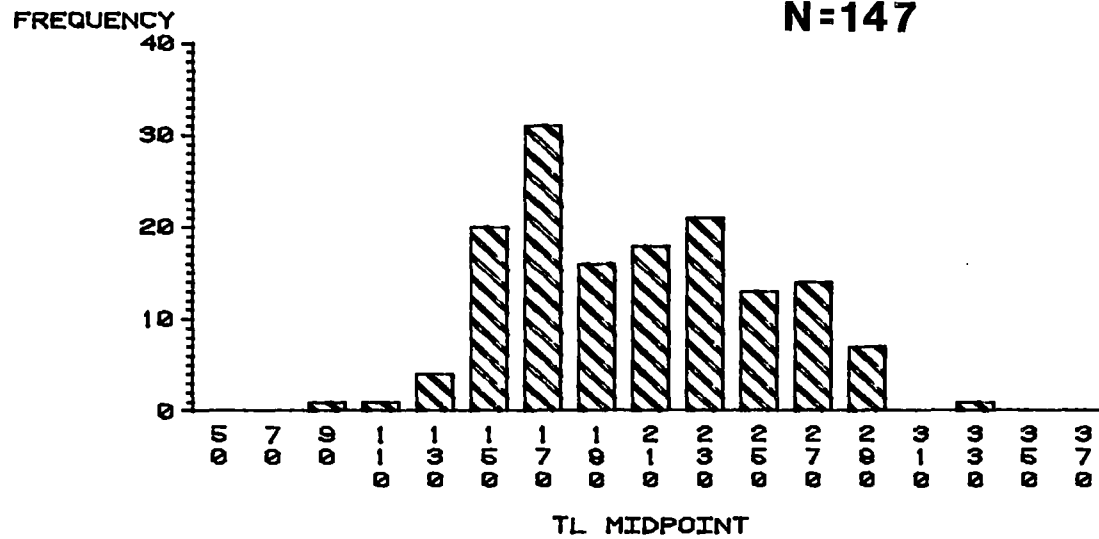
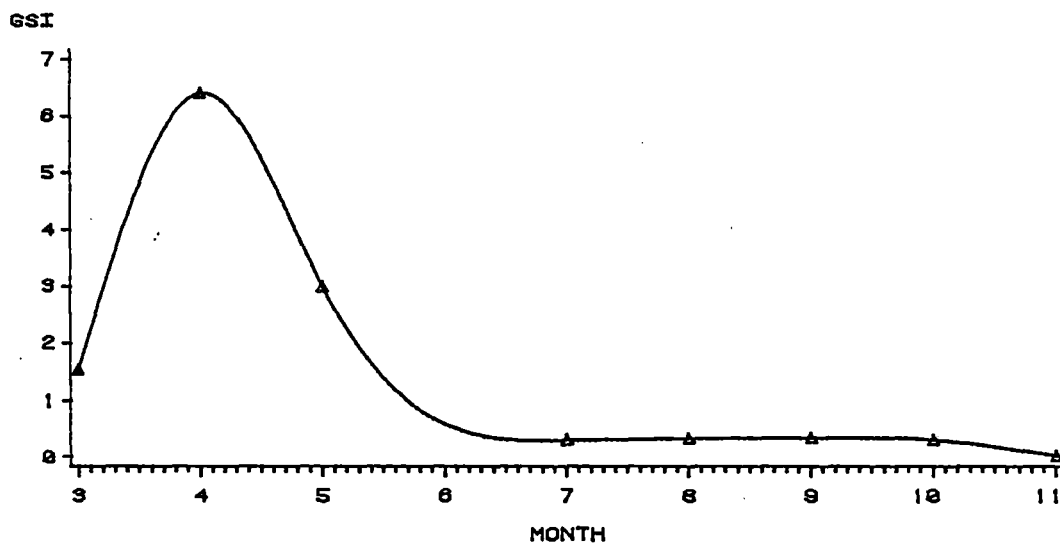


Figure 10. Length frequency distribution and proportional stock density (PSD) for white crappie captured at Copan dam during 1983.

FEMALE WHITE CRAPPIE GSI



MALE WHITE CRAPPIE GSI

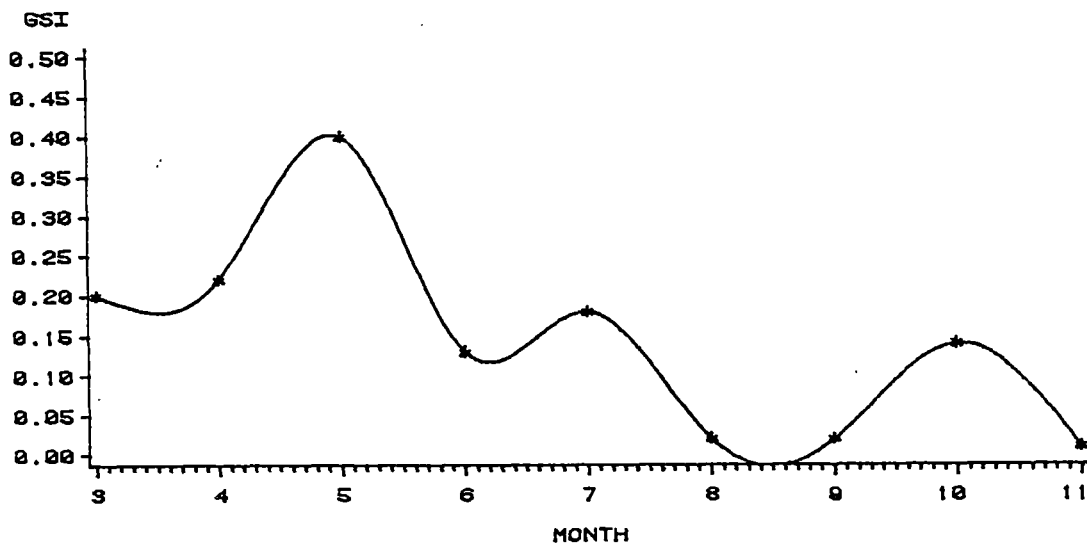
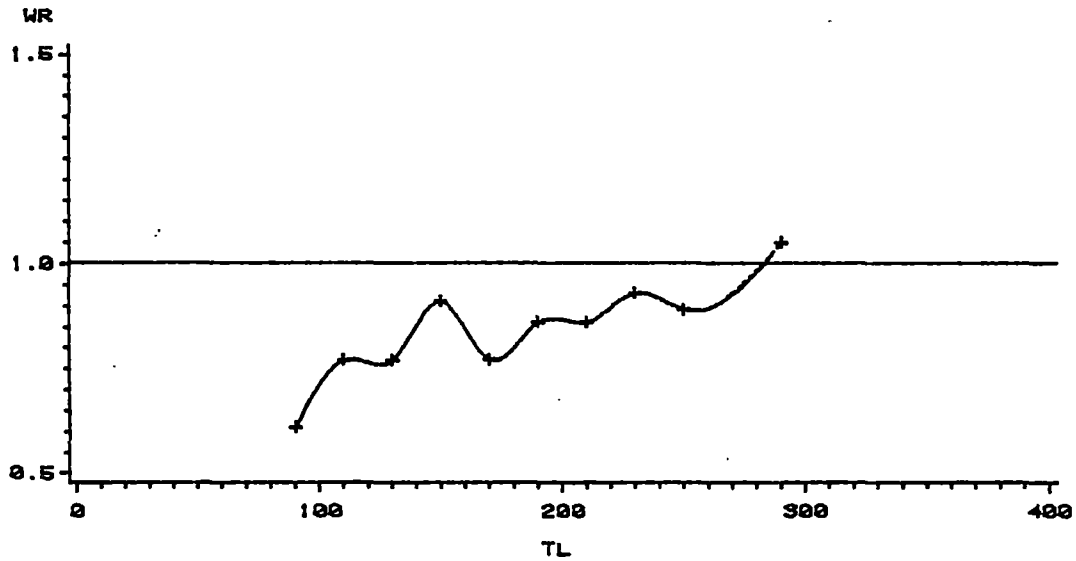


Figure 11. Gonadosomatic Index (GSI) for male and female white crappie captured in Copan lake during 1983.

MEAN RELATIVE WEIGHT AT TOTAL LENGTH



MEAN WEIGHT AT TOTAL LENGTH

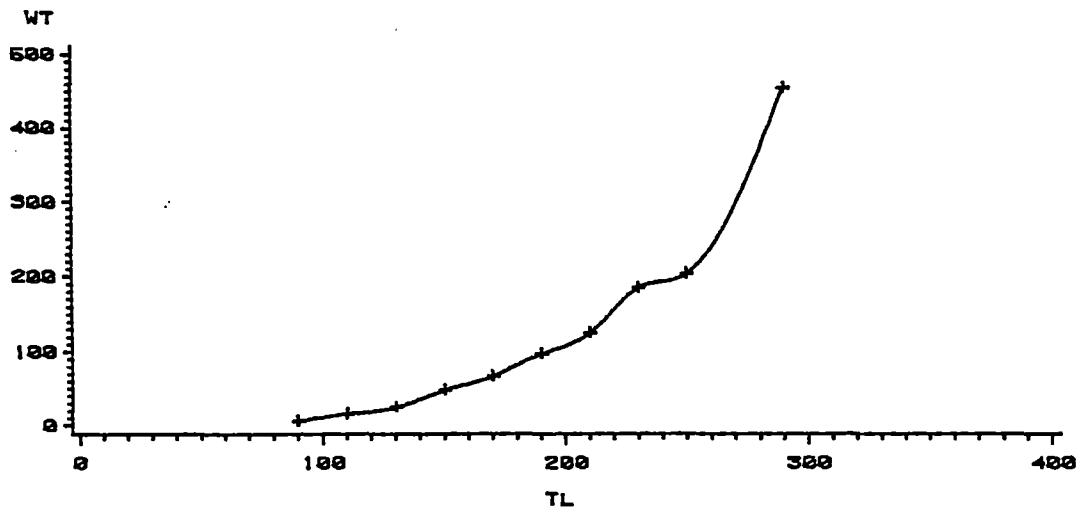
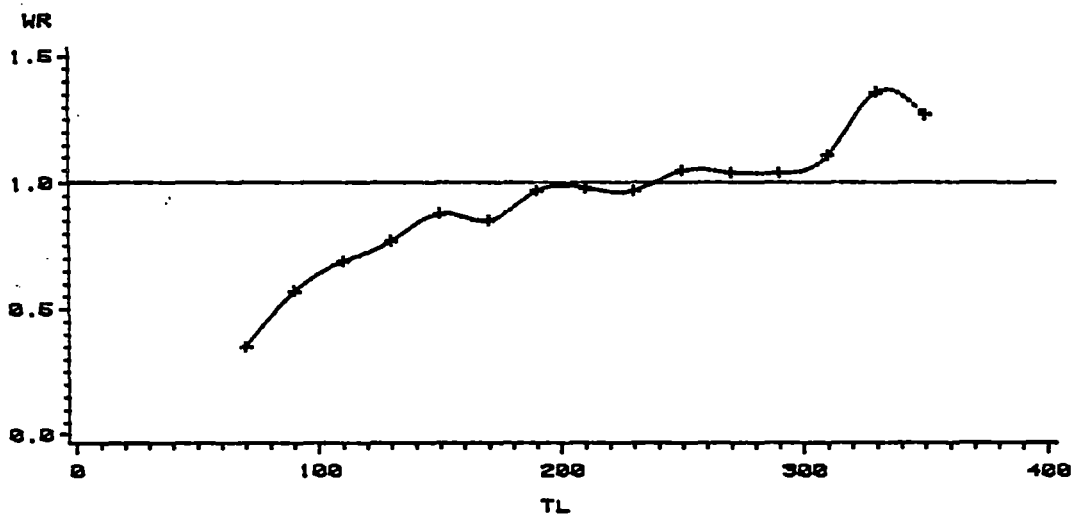


Figure 12. Mean capture weight and relative weight for black crappie size classes captured in Copan lake during 1983.

MEAN RELATIVE WEIGHT AT TOTAL LENGTH



MEAN WEIGHT AT TOTAL LENGTH

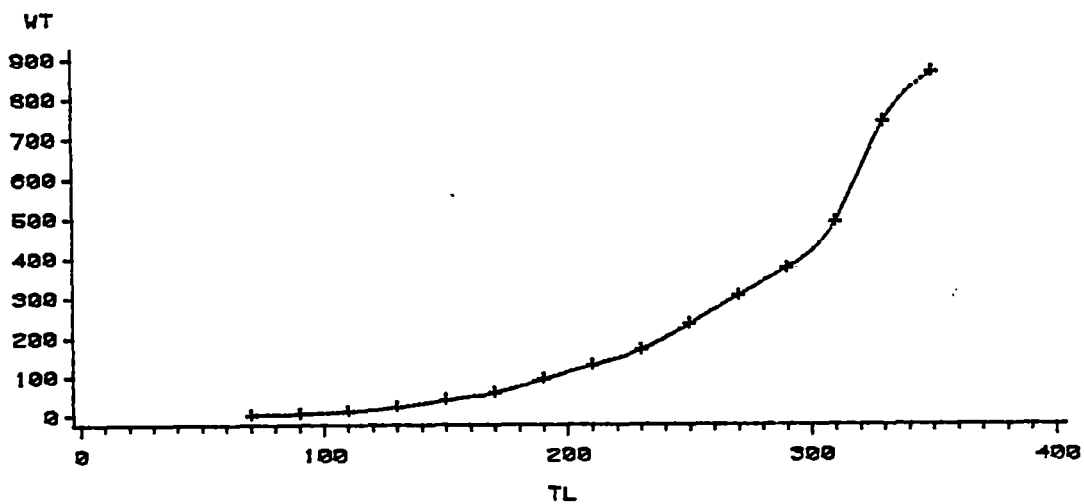


Figure 13. Mean capture weight and relative weight for white crappie size classes captured in Copan lake during 1983.

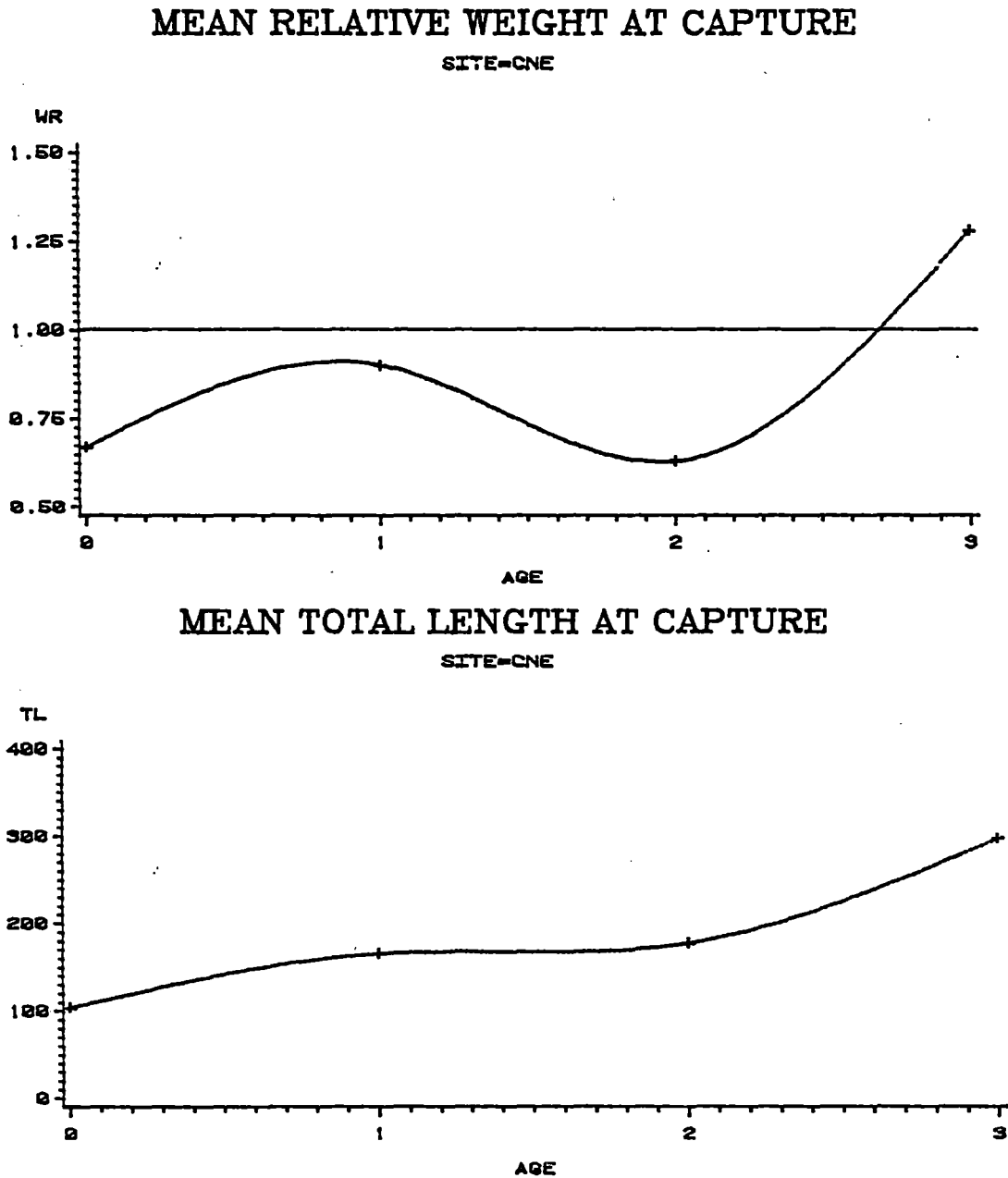


Figure 14. Mean relative weight and total length at capture for black crappie in Copan lake north section during 1983.

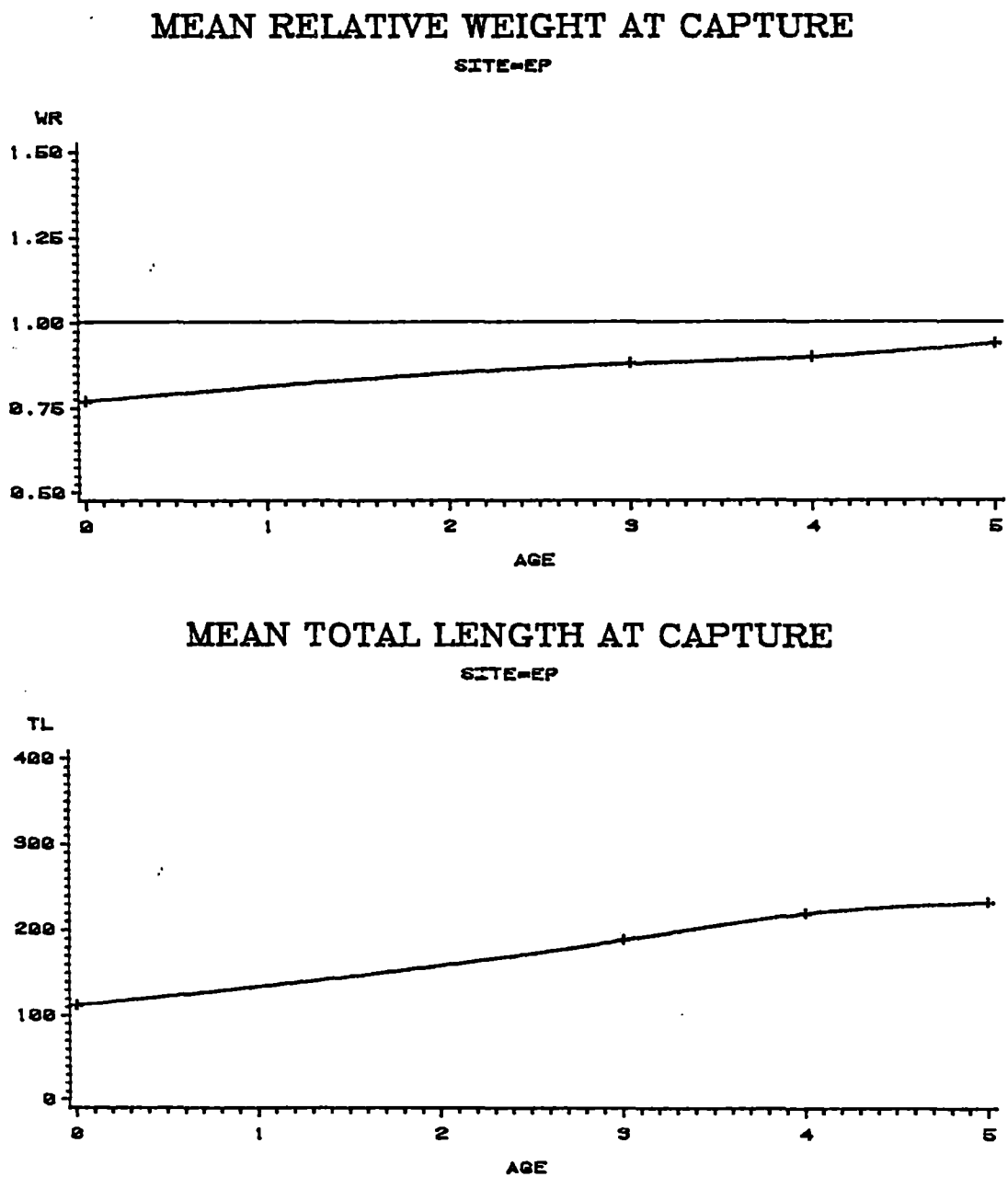
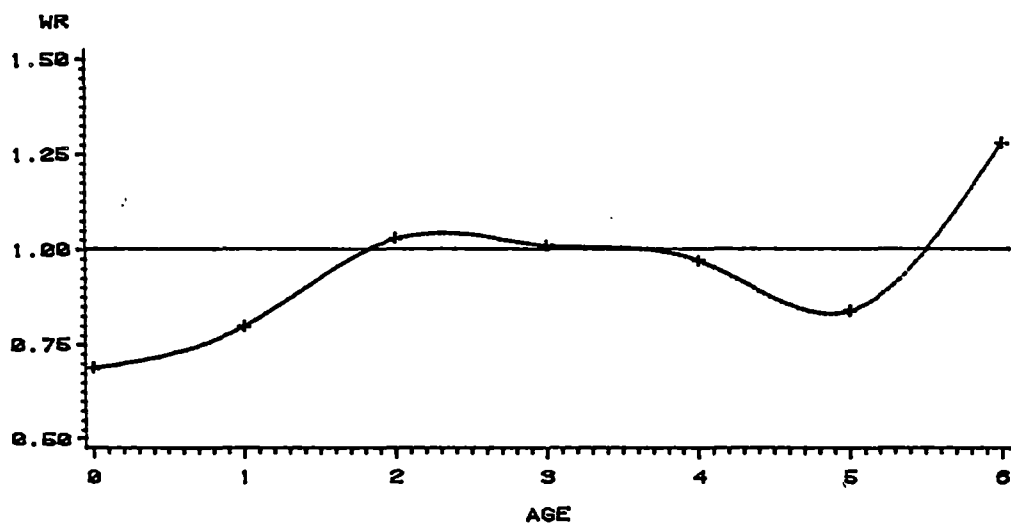


Figure 15. Mean relative weight and total length at capture for black crappie in Endacott's pond during 1983.

MEAN RELATIVE WEIGHT AT CAPTURE

SITE=EP



MEAN TOTAL LENGTH AT CAPTURE

SITE=EP

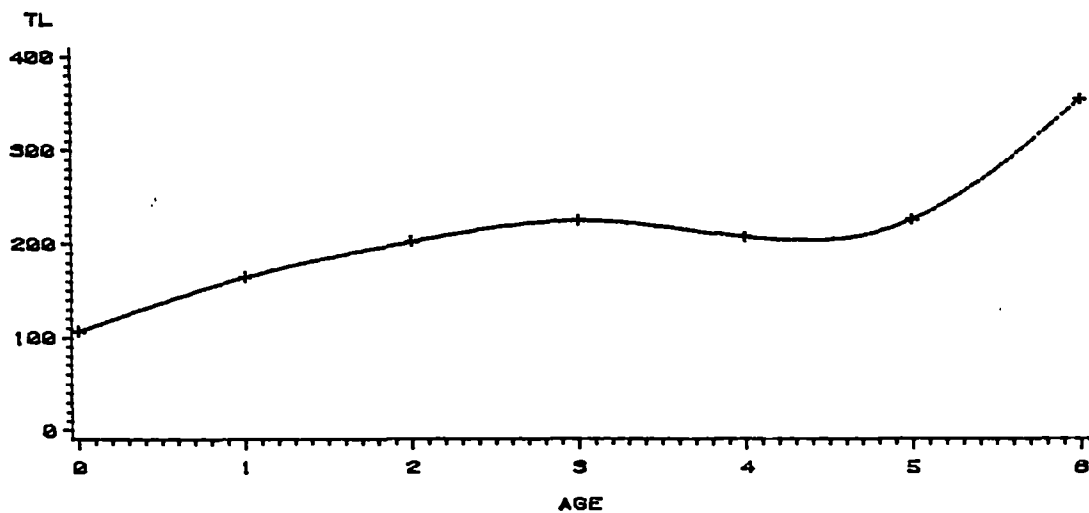


Figure 16. Mean relative weight and total length at capture for white crappie in Endacott's pond during 1983.

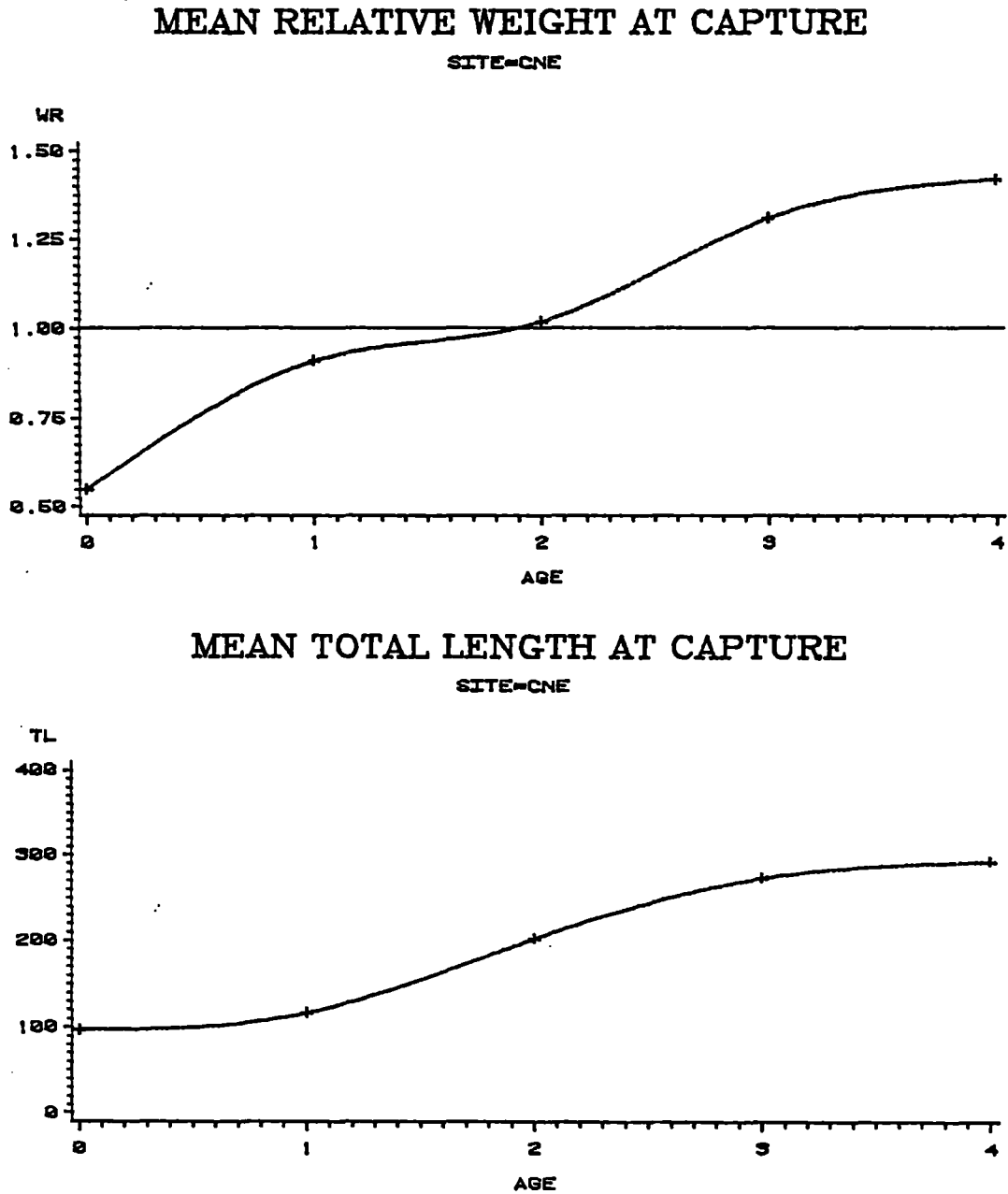
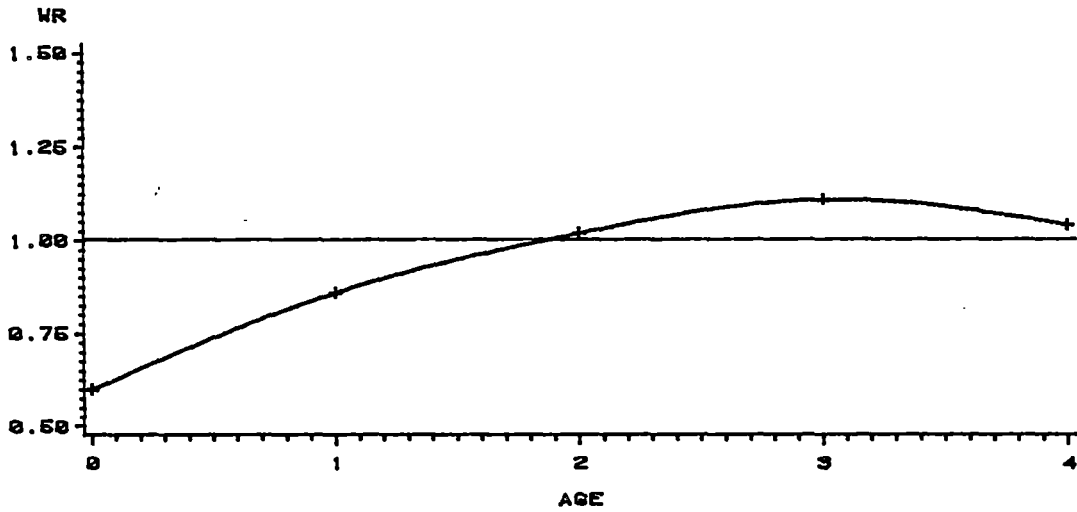


Figure 17. Mean relative weight and total length at capture for white crappie in Copan lake north section during 1983.

MEAN RELATIVE WEIGHT AT CAPTURE

SITE=RR



MEAN TOTAL LENGTH AT CAPTURE

SITE=RR

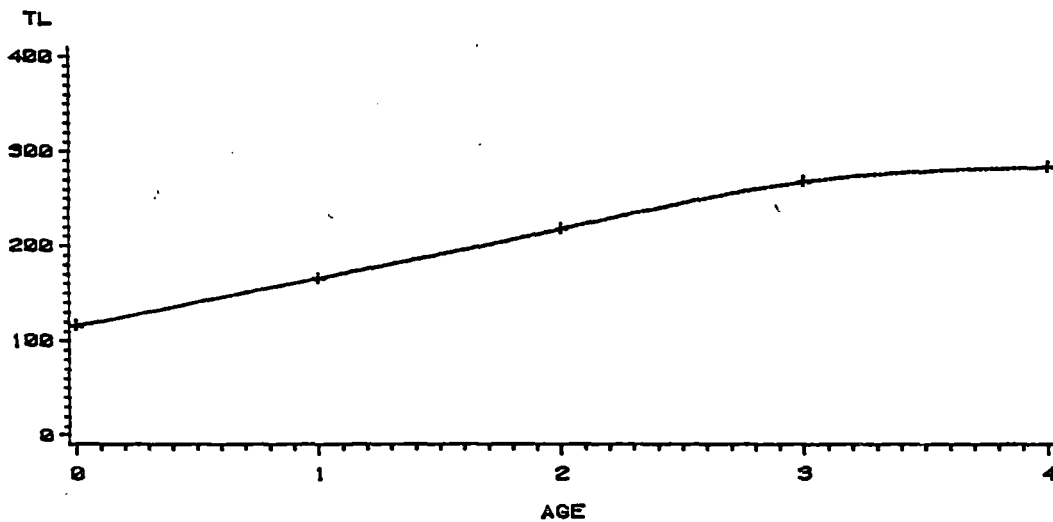


Figure 18. Mean relative weight and total length at capture for white crappie at Copan dam during 1983.

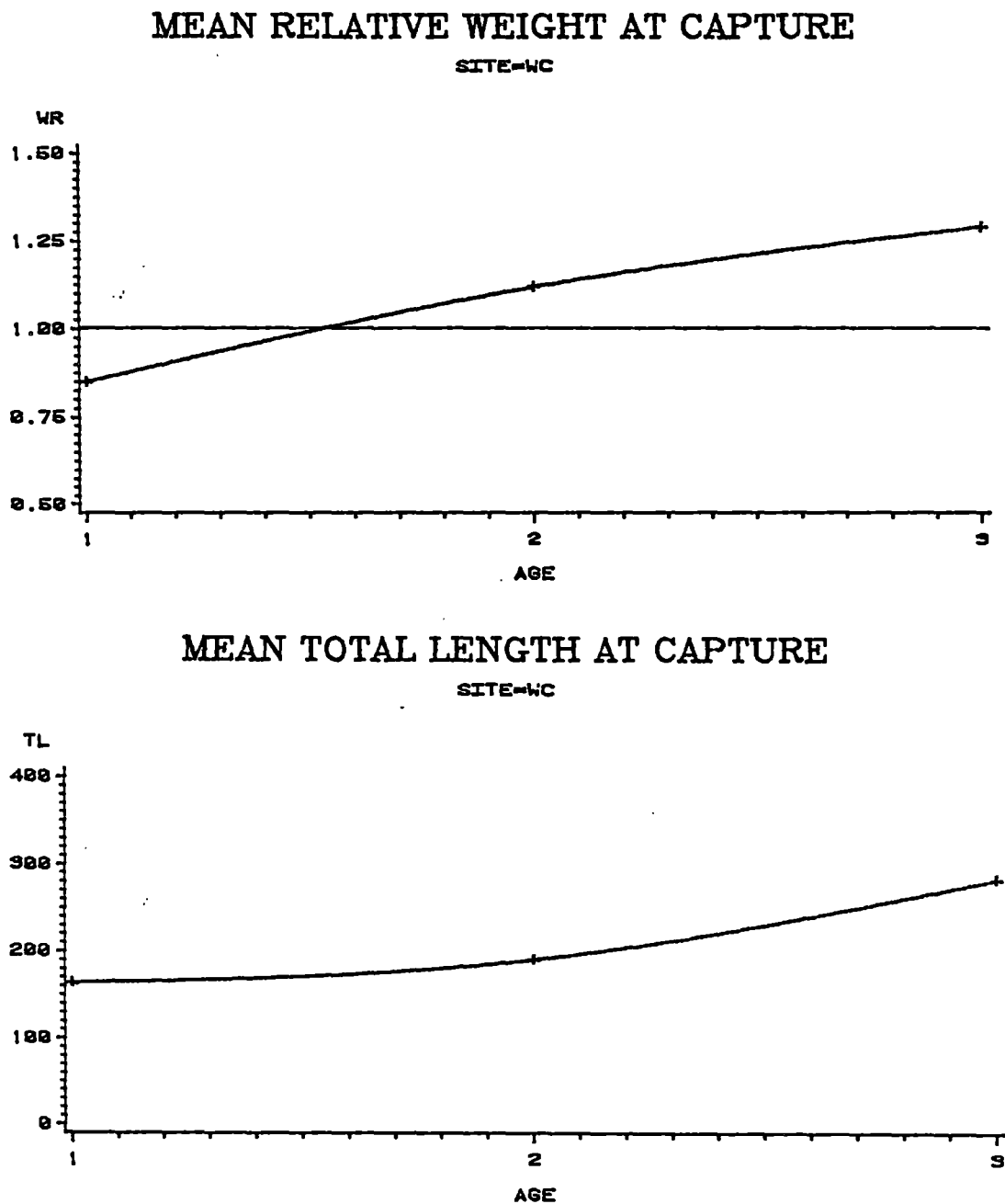
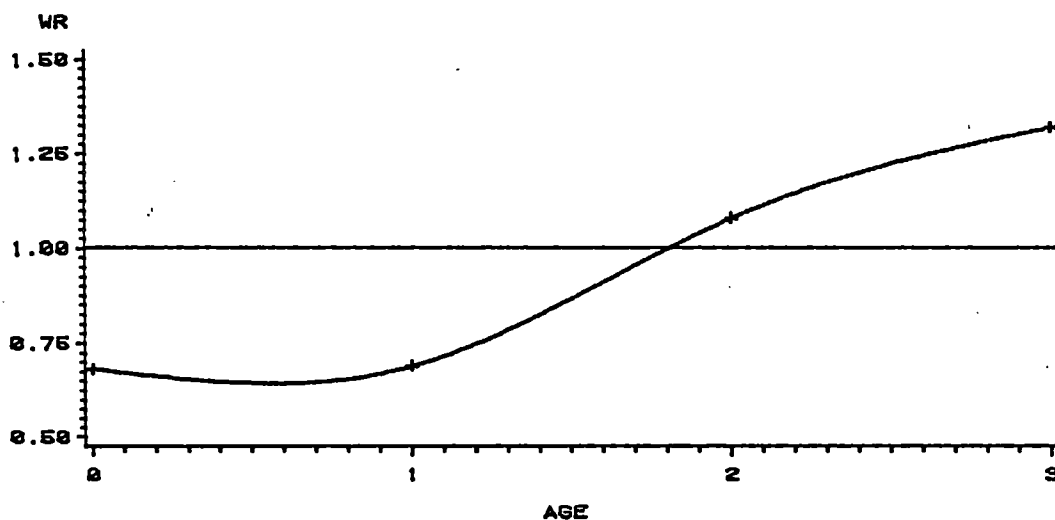


Figure 19. Mean relative weight and total length at capture for white crappie in Washington's cove in Copan lake during 1983.

MEAN RELATIVE WEIGHT AT CAPTURE

SITE-10E



MEAN TOTAL LENGTH AT CAPTURE

SITE-10E

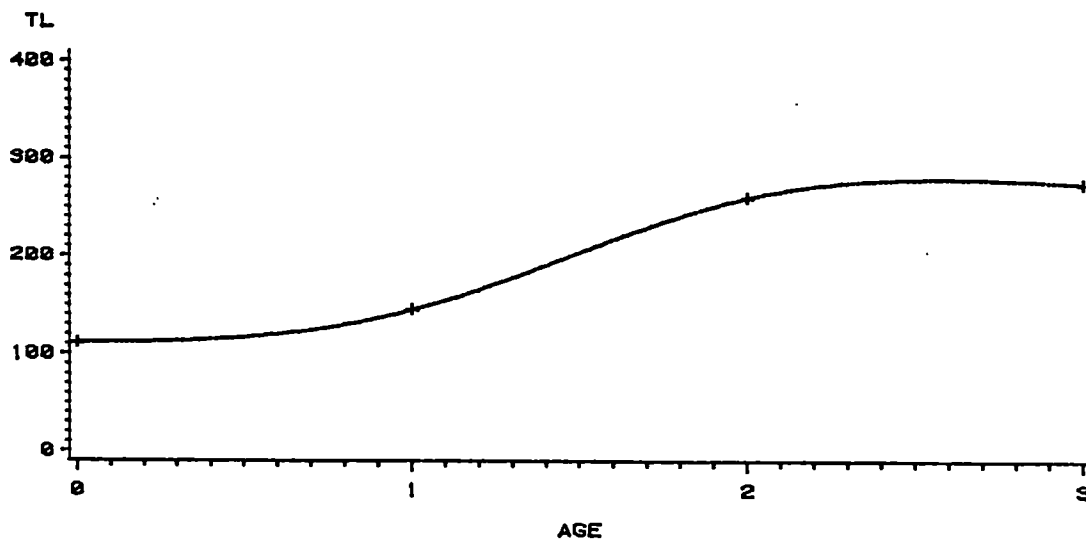
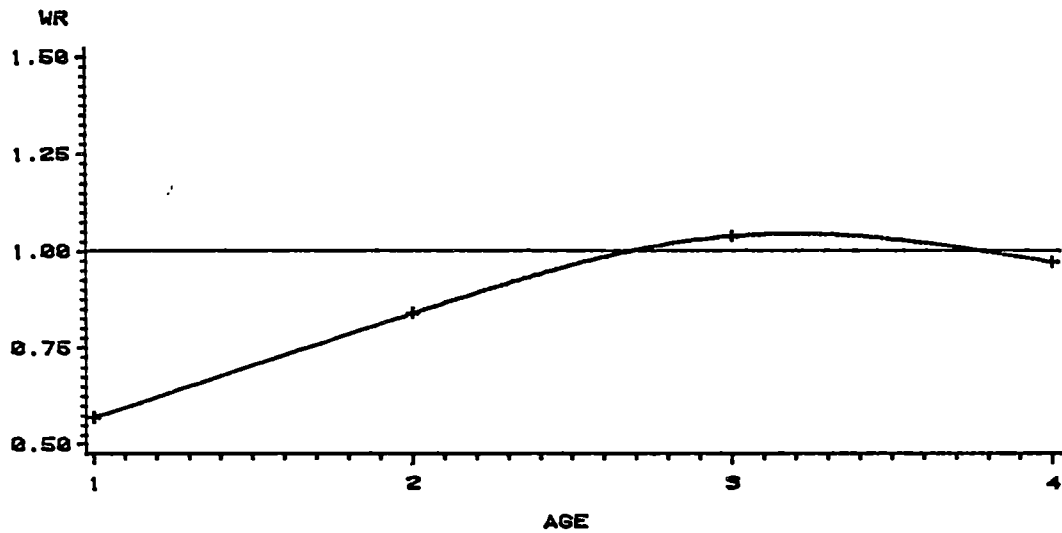


Figure 20. Mean relative weight and total length at capture for white crappie at Highway 10 bridge on east side Copan lake during 1983.

MEAN RELATIVE WEIGHT AT CAPTURE

SITE=10W



MEAN TOTAL LENGTH AT CAPTURE

SITE=10W

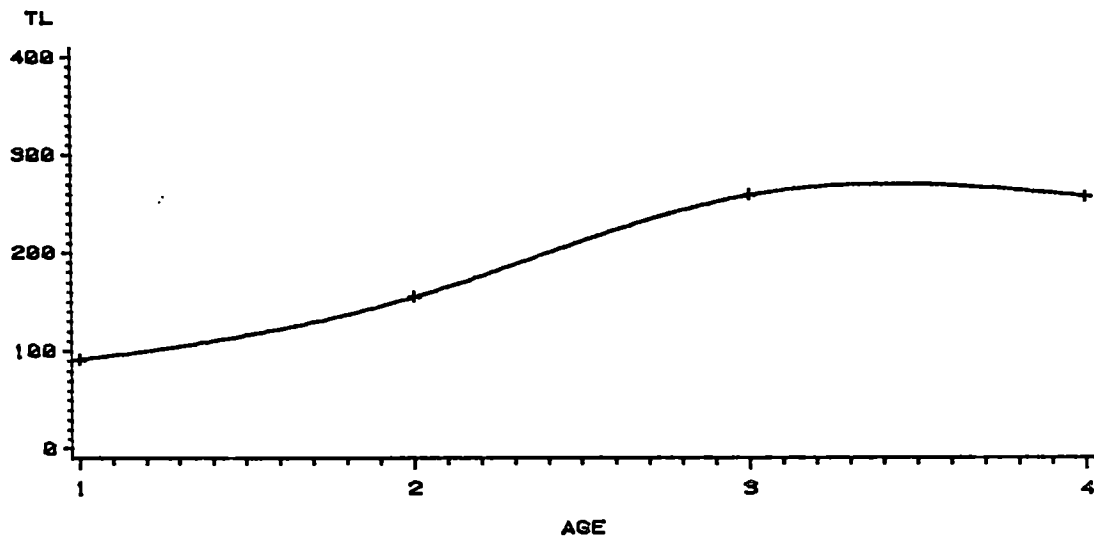


Figure 21. Mean relative weight and total length at capture for white crappie in Little Caney river during 1983.

CHAPTER II

THE GENETIC STRUCTURE OF FOUNDING BLACK AND
WHITE CRAPPIE POPULATIONS IN COPAN LAKE

INTRODUCTION

Black and white crappie (Pomoxis nigromaculatus and P. annularis, respectively) are widely distributed throughout North America. Field observations indicate that when both species occur sympatrically, black crappie usually predominate in clear, cooler, slightly acidic water, whereas white crappie predominate in water that is warmer, more turbid, and slightly basic (Hall et al. 1954; Goodson 1966).

Crappie populations often increase dramatically in newly created midwestern reservoirs. Growth rates of sympatric black and white crappie are generally high the first few years after impoundment, but subsequently decline (Rutledge and Barron 1972). Abundance of black crappie also tends to decline, and although white crappie remain relatively abundant, the population is often composed of many "stunted" or small fish (Jenkins 1953; Glass 1982). In general, midwestern reservoir crappie populations tend to be characterized by dominant, small, or missing year classes (Cichra et al. 1981; Mitzner 1981; Beam 1983).

Several hypotheses have been presented to explain the decline of black crappie populations in aging midwestern reservoirs. Generally,

researchers speculate that the decreased growth rates of black crappie in aging reservoirs and the selective advantage white crappie have in older midwestern reservoirs is related to interspecific competition for limited forage (Stevens 1958; Keast 1968; Li et. al. 1976) and severe intraspecific competition due to overcrowding (Huish 1953; Rutledge and Barron 1972; Hanson et al. 1983; Gablehouse 1984). In addition, more recent studies have identified specific foraging behaviors of black crappie that might limit population levels in southern reservoirs (May and Thompson 1974; Barwick and Lorenzen 1984). For example, in some warmwater reservoirs, large black crappie often have higher mortality rates than similar size white crappie because they feed primarily on invertebrates and fail to meet their energy requirements. Large white crappie, conversely, successfully meet their energy requirements by feeding on fish (Ellison 1984). However, many larger black crappie are piscivorous (Ager 1975). Therefore, none of the previously proposed hypotheses fully explain why black crappie often decrease in abundance over time.

One contributing factor to the decline of quality crappie populations in midwestern reservoirs may be the erosion of genetic variability in populations as they persist in aging reservoirs. Genetic variation is critically important in allowing adaptation to temporal and spatial changes in environmental conditions (Antonovics 1971; Avise and Selander 1972; Utter et al. 1973; Powers and Place 1978). Management programs usually operate on the assumption that the genetic makeup of crappie populations is fairly homogeneous and constant through time. It is also assumed that populations are composed of fish that are genetically capable of fast growth and can reach a large size if forage

is available. These assumptions may not be valid when reservoir stocks of crappie are derived from indigenous populations in an inundated river (Hall et al. 1954), where previous riverine selective pressures have determined the genetic structure of the founding population. New reservoirs present a myriad of new selective pressures that possibly alter gene frequencies in crappie populations after impoundment.

Population size is the single most important factor in sustaining high levels of genetic variation within a population (Meffe 1986). All populations become increasingly inbred with time, but inbreeding occurs much sooner in smaller populations and could be important in black crappie populations in aging midwestern reservoirs. Inbreeding depression, resulting in increased homozygosity, tends to lower individual fitness as measured by growth rates, developmental stability, survivorship, and fecundity (Meffe 1986). The ideal population is infinitely large. However, the effective breeding population is usually a subset of the total population, and is a function of the total number of breeding individuals, sex ratio, mating system, and variation in fecundity. Maintaining effective population size is important in resource management because it influences the genetic stability of populations, in that inbreeding and changes in gene frequency through sampling error (genetic drift) are inversely related to effective population size (Tave 1984).

Recent developments in techniques (primarily electrophoresis) have allowed natural resource managers to determine levels of genetic variation in natural populations (Smith et al. 1976). No previous study has examined the genetic structure of founding populations of black and white crappie in a new midwestern reservoir. Information on the genetic

structure of founding populations is essential before the genetic structure of crappie populations in aging reservoirs can be evaluated. Therefore, the purposes of this paper are to:

- (1) Describe the genetic structure of founding populations of black and white crappie in a new reservoir.
- (2) Discuss differences in allele frequencies between geographic localities, sexes, age groups, and growth and condition categories.

STUDY AREA

Our study took place in Copan Lake, located on the Little Caney River, approximately 3.7 km west of Copan, Washington County, in northeastern Oklahoma. The drainage area above the dam site is approximately 1,308 square kilometers, and is characterized by rolling hills and oak hickory forests, interspersed with lowlands of tall grass prairie and numerous rock outcroppings. At conservation elevation (209.5 m -216.4 m), the lake covers approximately 1,962 hectares and inundates 23.3 km of the Little Caney River. The lake has 55.6 km of shoreline and a shoreline development index of 3.1 (Oklahoma Water Resource Board 1984). Mean and maximum depths are 2.7 m and 10.6 m, respectively. Turbidity levels in the lake are high due to the relatively high concentrations of suspended solids in the river.

The area above the dam consists of the lake proper and a periodically isolated pond, Endacott's pond, located on the west shore. The mean depth in the pond before inundation was 1.8 m and secchi readings averaged 1.2 m. The pond has historically stratified every

year, and presently is the only site in Copan Lake that stratifies.

METHODS

Explanation of Collection Sites

Preliminary fish sampling began in Copan Lake basin in March 1983, one month before filling the reservoir. The purpose was to sample founding crappie stocks in different areas to determine if electrophoresis could identify genetic markers indicating reproductive isolation. Indigenous white crappie were first collected from the Little Caney River (10W) at the crossing of Oklahoma Highway 10 on the western shore of Copan lake (Figure 1; Oakey 1986, p. 55). Concurrently, white crappie and black crappie were collected from Endacott's pond (EP). On April 5, 1983, during a week of heavy rainfall, Copan dam was officially closed by the U.S. Army Corps of Engineers. Copan lake reached pool elevation three days later. This action connected Endacott's pond, now a cove, to Copan lake and allowed crappie free access to all areas of the lake basin. The third collection site for white crappie was located at the south shore riprap on Copan dam (RR). This area attracted large numbers of crappie during spawning season, and was adjacent to large "borrow" pits which were used during dam construction. During the seven years of reservoir construction, fish stocks were concentrated in these pits in the summer periods due to low water levels in the remainder of the basin.

Fish Collections

Black crappie and white crappie were collected with barrel net traps, gill nets, and modified trap nets. White crappie were collected primarily during spring and summer of 1983. Black crappie were collected over a longer period and, for purposes of analysis, were grouped into summer and fall samples. All specimens were frozen on dry ice before being returned to the laboratory. At the laboratory all crappie were weighed to the nearest gram and total length was determined to the nearest millimeter. During dissection, sex of all crappie was determined by visual inspection and otoliths (sagittae) were removed for age determination. Otolith radius was measured from the center of the kernel to the anterior tip of the otolith. Distance to each annulus was measured along the radius from the center of the kernel to the proximal margin of the opaque band (Pannella 1974). Fish condition was calculated as Relative Weight (Wr), where $Wr = W_s / W_t$. Standard Weights were derived by $\text{Log}_{10} (W_s) = -4.914 + 3.052 [\text{Log}_{10} (TL)]$ and $\text{Log}_{10} (W_s) = -5.102 + 3.112 [\text{Log}_{10} (TL)]$ for black and white crappie, respectively (Anderson 1980).

Electrophoresis

Separate extracts of liver, white muscle, and eye/brain from each individual were homogenized with an equal volume of buffer (0.1 M Tris, 0.001 M EDTA, and 5×10^{-5} M NADP, pH adjusted to 7.0 with HCl). The homogenate was centrifuged at 4° C for 15 minutes and supernatants were stored at -70° C for 3-10 weeks. This procedure resulted in no obvious decrease in enzyme activity, except in the case of Isocitrate

dehydrogenase (IDH). Personnel from the Illinois Natural History Survey kindly assisted in gel interpretation of the IDH-2 locus. Supernatants were subjected to standard methods of horizontal starch-gel electrophoresis as modified from Siciliano and Shaw (1976) and Philipp et al. (1979).

A total of 30 (12%) white crappie and 10 (12%) black crappie were surveyed for variation at 38 enzymes. Polymorphic loci were defined as those in which the frequency of the common allele was less than 0.95. Analysis of genetic structure was performed with BIOSYS-1 FORTRAN program (Swofford and Selander 1981).

Allele frequencies were compared within hierarchical subdivisions by geographic location, sex, and age. In addition, variation was examined between individual fish of greater or lesser "plumpness" (relative weight) at capture, and between fish of greater or lesser total length for age at capture. Relative weight categories were created by pooling all age groups into upper and lower 50 percentiles for each month. Consideration for seasonal variation in relative weight was made by further separating black crappie samples into summer and fall seasons, and white crappie samples into spring and summer seasons. Total length classes were created for each age group by separating individuals into upper and lower 50 percentiles for each month. In order to equalize the sample sizes, smaller samples were pooled in younger white crappie (Ages 0 and 1), older white crappie (Ages 4, 5, and 6), and older black crappie (Ages 3, 4, and 5).

RESULTS

Allozymic Variation

A total of 77 black crappie and 235 white crappie were analyzed by electrophoresis. Of 38 enzymes assayed in black and white crappie, 4 did not produce banding on the gels, and 10 were not useful because of difficulty in interpretation. The following is a list of the 24 enzymes (with results and comments) used to characterize the allozymic variation of the founding populations of black and white crappie in Copan lake.

Alcohol dehydrogenase . The ADH locus was monomorphic and migrated cathodally in all liver samples of black and white crappie. Two alternate alleles were reported fixed in black and white crappie populations surveyed in Illinois (Koppleman, per. comm.).

Lactate dehydrogenase . Homozygotes at the LDH loci appeared as three bands in muscle, liver, and eye/brain, indicating the presence of two loci coding a homotetramer each. All individuals were monomorphic at these loci. The same was reported in a small sample of black crappie from South Carolina (Avisé et al. 1977). In addition, a "nothing-dehydrogenase" was noted in liver and muscle during our preliminary survey.

Aldolase . ALD-1, ALD-2, and ALD-3 were stained under Histine-Citrate (HC) electrophoretic conditions from muscle, liver, and eye/brain, respectively. All electromorphs were monomorphic in addition to being badly smeared on all gels.

Adenylate kinase . Two AK loci, AK-1 in muscle, and AK-2 in liver and eye/brain were monomorphic and badly smeared under HC electrophoretic

conditions.

General Protein . Two alternate alleles were fixed in muscle samples: the faster migrating allele was present in white crappie. GP was not scorable in liver and eye/brain under HC electrophoretic conditions.

Mannose-6-Phosphate Isomerase . MPI was not scorable under HC electrophoretic conditions.

Sorbital dehydrogenase . The SDH locus was fixed for alternate alleles in liver. The allele present in white crappie migrated anodally, and the allele present in black crappie migrated cathodally.

a - Glycerophosphate dehydrogenase . a -GPDH-1 and a-GPDH-2 were monomorphic for all individuals in muscle and liver tissues, respectively.

Peptidases . PEP did not produce banding in any tissue under Tris-Citrate (TC) and EDTA-Borate-Tris (EBT) electrophoretic conditions, however, Avise et al. (1977) reported PEP fixed in black crappie.

Phosphoglucosomerase . Avise et al. (1977) reported that PGI-1 was polymorphic in black crappie for the common and slower allele (0.94 and 0.06, respectively). PGI-2 was fixed in the same population. PGI-1 and PGI-2 were fixed for alternate alleles in Copan lake black and white crappie. The faster migrating alleles for PGI-1 in eye/brain, and PGI-1 and PGI-2 in muscle, were present in white crappie. Illinois crappie populations were also reported with fixed alternate PGI alleles (Koppleman, per. comm.).

Fumerase . Copan lake crappie populations were fixed for a single FUM allele in liver. However, Illinois crappie populations were reported to be fixed for alternate alleles (Koppleman, per. comm.).

Isocitrate dehydrogenase . IDH-2 was polymorphic with 4 alleles in liver: alleles A, B, and C were present in white crappie, and alleles A and D were present in black crappie. IDH-1 was monomorphic in muscle for all individuals.

Creatine kinase . Three CK loci were present in Copan lake crappie populations. CK-1 was monomorphic in eye/brain, however, CK-2 was fixed for alternate alleles in muscle. The faster allele was present in white crappie. CK-3 was polymorphic for 3 alleles in liver and eye/brain of white crappie, and for 2 alleles in eye/brain of black crappie.

6 - Phosphogluconate dehydrogenase . 6 -PGD was monomorphic in liver samples of both crappie species under EBT electrophoretic conditions. This locus was also reported fixed in black crappie (Avisé et al. 1977).

Glyceraldehyde-3-Phosphate dehydrogenase . Three GA₃-PDH loci were monomorphic in Copan lake black and white crappie. Under HC electrophoretic conditions, GA₃-PDH-1 and GA₃-PDH-2 were badly smeared in muscle and liver tissues, respectively. However, GA₃-PDH-3 produced bands of exceptional clarity in eye/brain.

Esterases . EST-1 and EST-2 were fixed for alternate alleles in eye/brain of Copan lake crappie species. The faster migrating allele was present in the black crappie. Metcalf et al. (1972) reported tissue specific activity of esterases in white crappie, black crappie, and artificially reared F1 and F2 hybrids.

Phosphoglucomutase . PGM was fixed for alternate alleles in muscle of Copan black and white crappie. The same was reported for Illinois crappie populations (Koppleman, pers. comm.). PGM was fixed in black crappie in South Carolina (Avisé et al. 1977).

Catalase . CAT was monomorphic in liver for all individuals examined.

Malate dehydrogenase (NAD dependent). MDH-1 and MDH-2 were fixed for alternate alleles in Copan crappie species. The faster migrating allele of MDH-1 in liver, MDH-2 in muscle, and both loci in eye/brain were present in white crappie.

Adenosine deaminase . ADA was fixed in muscle for two alternate alleles in Copan lake black and white crappie. This fixation was also reported for crappie populations in Illinois (Koppleman, per. comm.). The faster migrating allele was present in Copan lake white crappie.

Xanthine dehydrogenase . Copan lake black and white crappie were monomorphic for two alternate alleles of XDH in liver. The allele present in black crappie was the faster migrating allele. Illinois crappie populations were also reported fixed at alternate XDH alleles (Koppleman, per. comm.).

Superoxide dimutase . The SOD locus appeared to be fixed in liver samples of both crappie species. However, one white crappie was heterozygous for the common allele and a slower migrating allele, producing a double banded phenotype under EBT electrophoretic conditions.

Glutamate oxaloacetate aminotransferase . GOT was monomorphic at three loci in Copan lake crappie species. GOT-1 and GOT-2 were scored in liver, GOT-2 and GOT-3 were scored in muscle, and three loci were scored in eye/brain.

Aconitase . ACO was monomorphic in liver for all individuals, however, Koppleman (per. comm.) reported two fixed alternate alleles in Illinois black and white crappie populations.

Genetic Variation

Total variation at 24 enzymes indicated white crappie were more variable than black crappie, although both species were below average levels recorded in fish populations (Powell 1975). Percent polymorphic loci per individual (P) and mean heterozygosities per locus (H) for all white crappie loci were 0.059 and 0.019, respectively. Two loci (CK-3 and IDH-2) were polymorphic in white crappie. A third locus (SOD) was variable below 0.05 frequency. Black crappie had small amounts of variation at CK-3 and IDH-2; however, both were below 0.05 frequency. Mean heterozygosity (H) for all loci that were examined in black crappie from Copan lake was 0.003. Black and white crappie were fixed for alternative alleles in 12 of the scorable enzymes. The majority of alleles that were present at loci of both species migrated anodally. However, SDH migrated cathodally in black crappie, and ADH migrated cathodally in both crappie. Genetic identity (the probability that two alleles, one from each population, are identical) between black and white crappie for all loci was $I = 0.65$ (Nei 1972). Genetic similarity (S) between black and white crappie for CK-3 and IDH-2 was 0.60 (Rogers 1972).

Genetic Variation in Black Crappie

Genetic variation in black crappie was very low and occurred only at two loci, IDH-2 and CK-3 (Table 1). Allele frequencies for both CK-3 and IDH-2 were monomorphic at 0.05 criterium. In addition, rare alleles were present only in heterozygous genotypes. Observed mean

heterozygosities at the two variable loci were near expected levels (Table 2).

Variation In Black Crappie Sexes

Mean heterozygosity was higher in female black crappie than in male black crappie. Females had slightly more heterozygotes at CK-3 and were polymorphic at IDH-2, whereas, males were monomorphic at both loci (Tables 3 and 4). Allele frequencies for both sexes conformed to Hardy-Weinberg frequencies (Table 5).

Variation In Black Crappie Age Groups

Our collections were missing 2 black crappie year classes, therefore, 2 data sets were partitioned, composed of Age 0 and Age 3+ fish, respectively. Young-of-year fish had slightly more variation than older crappie (Table 6). However, this difference was due to older crappie being monomorphic at CK-3. Allele frequencies at IDH-2 were identical in the 2 age groups (Tables 7 and 8). Observed heterozygotes were close to expected levels in both age groups, except for CK-3 in older crappie (Table 9).

Variation In Black Crappie Condition (Wr) Groups

Observed heterozygosity at both CK-3 and IDH-2 was close to expected levels (Table 10). CK-3 was monomorphic in both summer condition groups. In summer samples, IDH-2 was polymorphic in fish in better condition, and monomorphic in fish in lower condition (Tables 12 and 13). However, in fall samples nearly identical allele frequencies were found in both condition groups (Table 14).

Variation In Black Crappie Total Length Classes

Total length classes were sorted and analyzed by age, i.e. Age 0 and Age 3+ fish. Greater genetic variation appeared associated with the faster growing Age 0 fish, and with the slower growing adult fish (Tables 11, 15, and 16). Allele frequencies in all total length classes were in Hardy-Weinberg equilibrium (Table 17).

Genetic Variation in Total White Crappie Samples

Of 38 enzymes surveyed in Copan lake white crappie, only 2 (IDH-2 and CK-3) were polymorphic at the 0.05 criterion. Mean heterozygosities for all loci ($H = 0.019$) was much lower than the mean value obtained in 31 fish studies reported by Powell (1975). Percent polymorphic loci per individual for white crappie was $P = 0.058$. Heterozygosity by direct count for IDH-2 and CK-3 were $h = 0.476$ and 0.178 , respectively (Table 1).

However, the mean heterozygosities for IDH-2 and CK-3 were lower than expected under completely random mating (Table 2). Allele frequencies for IDH-2 deviated significantly ($\chi^2 = 17.36$, $df = 3$, $P = 0.001$) from Hardy-Weinberg frequencies (Table 5), apparently because of a deficiency of heterozygotes ($D = -0.197$) at IDH-2. The Fixation Index ($F = 0.195$) indicated that approximately 20% of all individuals were homozygous at IDH-2 .

In the case when more than 2 alleles were present in a sample, the Chi-square goodness of fit analysis was performed on pooled genotypes. Frequencies of homozygotes for the common allele were compared against frequencies of common/rare heterozygotes, and rare homozygotes and other

heterozygotes. The χ^2 test for pooled genotypes ($\chi^2 = 10.16$, $df = 1$, $P = 0.001$) indicated significant deviation from Hardy-Weinberg expectations at IDH-2 due to an excess of homozygotes for common and rare alleles (Table 1).

Variation Among 3 Geographic Localities

Mean genetic identity among white crappie stocks from 3 sites in Copan lake was $I = 0.988$ (Table 18). Mean genetic similarity between sites was $S = 0.91 + 0.04$. Allele frequencies were variable at IDH-2 and CK-3 loci for all sites (Tables 19 and 20). However, CK-3 was monomorphic in fish from the Little Caney river (10W). Mean heterozygosities for both loci were lowest in river stocks, and were below levels expected under random mating for all 3 sites (Table 2). The CK-3 locus in river stocks was heterozygous deficient ($D = -0.31$), and deviated significantly ($\chi^2 = 31.00$, $df = 3$, $P < 0.001$) from Hardy-Weinberg frequencies (Table 21). The CK-3 locus in Endacott's pond (EP) was in equilibrium; however, there were fewer than expected homozygotes for the rare alleles, but greater than expected rare/common allele heterozygotes. The 3 CK-3 alleles were in heterozygous genotypes in stocks from Copan lake (RR), however, homozygotes for the 2 rare alleles were not found (Table 20).

Fewer than expected heterozygotes for IDH-2 were found in all 3 sites (Table 21), however, homozygotes for the 3 IDH-2 alleles were present in all sites (Table 19). IDH-2 in EP deviated significantly ($\chi^2 = 18.33$, $df = 3$, $P < 0.001$) from Hardy-Weinberg frequencies. Pooled genotypes did not conform to Hardy-Weinberg expectations ($\chi^2 = 7.69$, $df = 1$, $P = 0.006$). High fixation ($F = 0.29$) and heterozygote

deficiency ($D = -0.29$) indices indicated an excess of homozygotes for the 2 rare alleles at IDH-2. Allele frequencies in fish from RR were in equilibrium, and were represented by homozygotes and heterozygotes of all 3 IDH-2 alleles present.

Variation In White Crappie Sexes

There was less genetic variation in female white crappie than in males (Table 2). IDH-2, the more variable locus, was much more heterozygous in male white crappie (Table 3). This effect on mean heterozygosities was somewhat reduced by CK-3, which, although less variable than IDH-2, was nearly twice as heterozygous in the females (Table 4). The differences between male and female crappie were mainly attributed to genotype distribution at IDH-2 and CK-3. Female crappie deviated significantly ($\chi^2 = 20.21$, $df = 3$, $P < 0.001$) from Hardy-Weinberg frequencies at the IDH-2 locus (Table 5). This deviation was due to excess homozygotes of the 3 alleles present. The effect of pooling the rare alleles continued to result in disequilibrium ($\chi^2 = 11.84$, $df = 1$, $P = 0.001$). Females were heterozygote deficient ($D = -0.28$), appearing to be fixed ($F = 0.29$) for IDH-2 in 30% of individuals.

Variation In White Crappie Age Groups

Allele frequencies appeared to fluctuate at CK-3 and IDH-2 in an age dependent manner, suggesting that directional selection may be occurring at these loci in Copan lake (Tables 7 and 8). The common allele frequencies increased and decreased in progressively older age groups at IDH-2 and CK-3, respectively. The 2 rare alleles of CK-3

behaved oppositely: in progressively older age groups allele A decreased and allele C increased. While the common IDH-2 allele increased in older fish, the 2 rare alleles behaved erratically. The C allele appeared to stabilize in Age 2 white crappie, while the A allele apparently declined after peaking in the Age 2 fish.

Mean heterozygosities at CK-3 increased with older age groups. However, mean heterozygosities in IDH-2 appeared to peak in the Ages 2 and 3 white crappie (Table 6). All age groups except the older fish were in Hardy-Weinberg equilibrium (Table 9). Heterozygosities of IDH-2 in Ages 4, 5, and 6 fish deviated significantly ($\chi^2 = 18.89$, $df = 3$, $P < 0.001$) from Hardy-Weinberg frequencies. Homozygotes for the rare alleles in IDH-2 were greater than expected, resulting in a deficiency of heterozygotes, and fixation at approximately 32% of older individuals sampled.

Variation In White Crappie Condition (Wr) Groups

There were no major trends in genetic variation between relative weight groups for spring and summer samples (Tables 12 and 13). Mean heterozygosities for IDH-2 in all age groups were below levels expected under Hardy-Weinberg equilibrium (Table 10). This excess of homozygotes was reflected in positive allele fixation indices but showed no apparent trends between groups (Table 22).

Genetic Variation Between White Crappie Total Length Classes

Allele frequencies did not show strong trends between size classes of white crappie age groups (Tables 15 and 16). IDH-2 lacked conformity to Hardy-Weinberg frequencies due to excess homozygotes in Age 0-1 and

Age 4+ fish. This lack of conformity was especially significant ($\chi^2 = 8.01$, $df = 3$, $P = 0.046$) in smaller Age 0-1 fish (Table 23). The average frequency of heterozygous individuals at IDH-2 was greater for larger fish of all ages, while the opposite was true for CK-3. Nevertheless, mean heterozygosities for most age groups were below expected level and tended to fluctuate between size classes without apparent cause (Table 11).

DISCUSSION

Crappie populations in Copan lake had very little variation in the enzymes examined in this study. Mean heterozygosities (H) for black and white crappie (0.019 and 0.003, respectively) were considerably lower than the average (0.058) cited for fish studies where 10 or more loci were examined (Powell 1975). Avise et al. (1977) reported mean heterozygosities (0.01) in black crappie, however, the number of individuals and loci examined were small. Our study reports on a moderately high number (38) of enzymes, and may represent a true description of variation in the population. However, Turner (1974) cautions "genes normally sampled electrophoretically may only represent a subset of the genotype that is relatively unresponsive to selection". However, this discussion will be restricted to the extent and possible mechanisms of genetic variation in Copan lake crappie populations. In the presence of few polymorphic loci, it is unusual that both crappie species were variable at the same two loci. Nevertheless, black and white crappie are expected to share large portions of their genomes due to close genetic identity (0.65) and the success of interspecific

hybrids (Philipp et al. 1979).

Population fitness characteristics (growth, survivorship, and fecundity) are positively correlated with genetic variation (Meffe 1986). Analyses were performed on Copan crappie populations to see if differences in heterozygosities were apparent in fish groups of higher or lower relative weight and greater or lesser total length per age group. The time interval necessary to see measurable changes are different for the two categories. Relative weight is more related to weight gains over short time intervals than gains in total length. No major trends in allele frequencies were found in this analysis. Low variation in black crappie prevented any useful interpretation of the data. Faster growing white crappie were slightly more heterozygous. However, this difference was not significant, as the frequency of all genotypes were evenly spread throughout age groups, and the majority were below expected heterozygote levels.

The low genetic variation in Copan lake black crappie may have several explanations. The absence of variation might imply that environmental heterogeneity in Endacott's pond was low, resulting in low selective pressures on black crappie (Awise and Selander 1972). However, our 1982 survey found a diverse species assemblage, indicating diverse habitat in the pond. The environmental heterogeneity in the pond is further increased through interactions with other fish species (Antonovics 1971).

Population size of black crappie in Endacott's pond is very low. The author was informed that illegal fishing with telephone hand-generators removed large numbers of "crappie" from the pond shortly after public access was established. This "bottleneck", and any

subsequent genetic drift, may be responsible for the low variation in black crappie. Even over short amounts of time, genetic drift can reduce percent polymorphism, the average number of alleles per locus, and the average heterozygosity per individual (Meffe 1986). For example, Bonnell and Selander (1974) reported no variation in elephant seals from a population that had been previously reduced to a population size of 20 individuals. In addition to small numbers and low selective pressures in the marine environment, the authors attributed increased inbreeding to decreased effective population number because of polygamous mating.

However, initial levels of genetic variation in the black crappie population may have been due to the effects of inbreeding in the hatchery stocks used to originally stock Endacott's pond in 1945. Ryman and Stahl (1980) reported low variation in hatchery stocks of brown trout (Salmo trutta) that resulted from reduced numbers of brood stock. They recommended that founding fish stocks should have at least 30 individuals from each sex. The effective population size (the number of reproducing individuals in a population) for black crappie in Endacott's pond was $N_e = [4 (\text{Males})(\text{Females}) / (\text{Males}) + (\text{Females})] = 41$ (Meffe 1986). This number was below the minimum of 50 individuals recommended by Soule (1980) that is needed to keep the loss of heterozygotes ($1/2 N_e$ per generation) below the 1% threshold. The effective population size is further reduced by a skewed sex ratio or disproportionate distribution of progeny (Meffe 1986). Greater longevity of female black crappie was evident in the pond, resulting in a sex ratio (18 Males : 24 Females) that departed from parity. Thus, the low variation found in black crappie from Endacott's pond was most likely due to the

combined effects of genetic drift and inbreeding.

White crappie generally had higher levels of genetic variation than black crappie. The presence of 3 alleles at each of the polymorphic loci indicates the possibility of more than one source of white crappie in Copan lake, although the mean genetic identity ($I = 0.98$) among the 3 sample locations suggests one population. However, Roger's (1972) mean similarity ($S = 0.91$) among locations was below mean similarity in a "quasi-panmictic assemblage of local populations" of reservoir bluegill (Avisé and Smith 1974). The greater similarity of (recently immigrated) white crappie in Endacott's pond with those in the lake ($S = 0.97$), and lesser similarity with those in the river ($S = 0.87$), suggests that pond and lake fish are a recent assemblage of closely associating stocks (Table 18).

White crappie were sampled in the river before impoundment and, assuming that fish show some degree of site fidelity, these fish were representative of original stocks in the river. Low variation at CK-3 in river fish may be due to small sample size. However, our data suggests that selection against the rarer A and C alleles may have occurred in the river, possibly during summers, when low water levels reduced the habitat to a series of semi-isolated, shallow pools. One of two AC heterozygotes of CK-3 was found in river fish, indicating that these rare alleles have existed historically in river stocks. The frequency has probably been low, however, because homozygotes for the A and C alleles were not found at any site.

Higher heterozygosities at CK-3 were found in Endacott's pond fish than in lake fish, while the opposite was true for IDH-2. White crappie were recent (and probably intermittent) immigrants in the pond.

Therefore, it is difficult to say whether selection for or against heterozygotes was correlated with specific mechanisms in the pond site. Further analysis, however, revealed that white crappie females were more heterozygous at CK-3 and more homozygous at IDH-2 than white crappie males. Allele frequencies were also found to change in an age dependant manner, indicating the possible accumulative effects of selection in favor of the CK-3 C and IDH-2 B alleles. In progressively older white crappie age groups, the CK-3 C allele increased in frequency as a heterozygote with the common allele. In addition, observed CK-3 heterozygotes were greater than expected in the Ages 4, 5, and 6 white crappie. This increased frequency may indicate the presence of heterosis occurring at CK-3 in white crappie. However, all allele frequencies were in Hardy-Weinberg proportions.

Homozygotes for the 3 IDH-2 alleles were in excess proportions in all white crappie age groups, sexes, and in 2 of the 3 sampling sites. This excess indicates inbreeding which may result from a history of non-random mating in reproductively discrete subpopulations in Copan lake basin (Futuyma 1979). The recent filling of the reservoir and the subsequent mixing of crappie stocks could obscure the evidence of subpopulations in the lake, especially if isolation is incomplete or intermittent.

The Little Caney river is known to overflow its banks and recede again, leaving behind isolated pockets of water. For seven years, the complete filling of Copan lake was delayed while court litigation resolved railroad access rights in the upper basin. It is conceivable that subpopulations of white crappie were isolated in various size pools, prevailing in spite of varying selection regimes. Since changes

in allele frequencies can occur over short periods of time, it is possible that allele fixation could have happened more than once and at more than one location. The cumulative excess of homozygotes in progressively older age groups may offer evidence to support this argument.

The high allele fixation found in female white crappie influenced fixation in older crappie as well as in the pond. The majority of older white crappie in the study were females, and almost all were collected in Endacott's pond. Females generally lived longer than males, and may have demonstrated more site fidelity as well. Females that continue to remain at a site are more likely to mate with homologous genotypes. This mating results in increased inbreeding and disproportionate distribution of progeny. Since more females than males were collected, the white crappie population may have had an unequal sex ratio which could have outweighed normal outbreeding effects of dispersing males, in addition to further reducing effective population size. The effect of impoundment will tend to decrease isolation and increase the occurrence of outbreeding among crappie stocks in Copan lake basin and slow normal levels of inbreeding. However, our data indicated that the founding populations of black and white crappie in Copan lake had low levels of genetic variation. Low genetic variation may jeopardize the potential adaptability of future crappie stocks to temporal and spatial changes in Copan lake as it ages.

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Table 1. Genotype distributions and allele frequencies for IDH-2 and CK-3 in combined samples of black and white crappie captured in Copan Lake during 1983.

Sample	N	h*	Genotype Distribution								Allele Frequency			
IDH-2			<u>AA</u>	<u>BB</u>	<u>CC</u>	<u>DD</u>	<u>AB</u>	<u>AC</u>	<u>AD</u>	<u>BC</u>	<u>A</u>	<u>B</u>	<u>C</u>	<u>D</u>
White Crappie	229	0.476	8	79	33	0	37	19	0	53	0.157	0.541	0.301	0.000
Black Crappie	77	0.091	70	0	0	0	0	0	7	0	0.955	0.000	0.000	0.045
CK-3			<u>AA</u>	<u>BB</u>	<u>CC</u>	<u>AB</u>	<u>AC</u>	<u>BC</u>						
White Crappie	230	0.178	0	189	0	4	2	35						
Black Crappie	78	0.026	0	76	0	0	0	2						

* h = Frequency of heterozygous individuals in sample.

Table 2. Mean observed and expected heterozygosities for IDH-2 and CK-3 in black and white crappie captured in Copan lake during 1983.

Sample	N	No. Alleles	Mean H*	Exp. H**
<u>Total Samples</u>				
White Crappie	229.5	3	0.327 (0.149)	0.382 (0.210)
Black Crappie	77.5	2	0.058 (0.033)	0.056 (0.031)
<u>Division by Sex</u>				
White Crappie Females	123.5	3	0.317 (0.085)	0.394 (0.171)
White Crappie Males	96.5	3	0.347 (0.220)	0.366 (0.247)
Black Crappie Females	29.0	2	0.103 (0.069)	0.097 (0.063)
Black Crappie Males	44.5	2	0.034 (0.012)	0.034 (0.011)
<u>White Crappie at three sites</u>				
Little Caney River	32.0	3	0.281 (0.219)	0.368 (0.276)
Endacott's Pond	100.0	3	0.334 (0.072)	0.403 (0.172)
Copan Lake	97.5	3	0.336 (0.205)	0.359 (0.225)

* Mean frequency of heterozygous individuals by direct count.

** Expected frequencies under Hardy - Weinberg equilibrium.

Table 3. Genotype distributions and allele frequencies for IDH-2 in black and white crappie sexes captured in Copan Lake during 1983.

Sample	N	h*	Genotype Distribution								Allele Frequency			
			AA	BB	CC	DD	AB	AC	AD	BC	A	B	C	D
White Crappie Females	122	0.402	4	51	18	0	19	8	0	22	0.143	0.586	0.270	0.000
White Crappie Males	97	0.567	4	26	12	0	18	8	0	29	0.175	0.510	0.314	0.000
Black Crappie Females	29	0.172	24	0	0	0	0	0	5	0	0.914	0.000	0.000	0.086
Black Crappie Males	44	0.045	42	0	0	0	0	0	2	0	0.977	0.000	0.000	0.023

* h = Frequency of individuals heterozygous at IDH-2 by direct count.

Table 4. Genotype distributions and allele frequencies for CK-3 in black and white crappie sexes captured in Copan Lake during 1983.

Sample	N	h*	Genotype Distribution						Allele Frequency		
			AA	BB	CC	AB	AC	BC	A	B	C
White Crappie Females	125	0.232	0	96	0	3	2	24	0.020	0.876	0.104
White Crappie Males	95	0.126	0	83	0	1	0	11	0.005	0.937	0.058
Black Crappie Females	29	0.034	0	28	0	0	0	1	0.000	0.983	0.017
Black Crappie Males	45	0.022	0	44	0	0	0	1	0.000	0.989	0.011

* h = Frequency of individuals heterozygous at CK-3 by direct count.

Table 5. Chi-square tests for conformance to Hardy - Weinberg equilibrium and indices for allele fixation and heterozygote deficiency for IDH-2 and CK-3 in black and white crappie captured in Copan lake during 1983.

Sample	Locus	N	χ^2	df	P*	Obs. Het.	Exp. Het.	F**	D†
<u>Total Samples</u>									
White Crappie	IDH	229	17.363	3	0.001	109	135.7	0.195	-0.197
	CK	230	6.681	3	0.083	41	39.5	-0.039	0.037
Black Crappie	IDH	77	0.149	1	0.700	7	6.7	-0.048	0.041
	CK	78	0.007	1	0.936	2	1.9	-0.039	0.037
<u>Division by Sexes</u>									
White Crappie Female	IDH	122	20.212	3	0.000	49	68.9	0.286	-0.289
	CK	125	0.012	3	0.912	29	27.7	-0.048	0.044
White Crappie Male	IDH	97	0.124	3	0.725	55	59.4	0.070	-0.075
	CK	95	0.394	3	0.530	12	11.3	-0.062	0.056
Black Crappie Female	IDH	29	0.203	1	0.652	5	4.6	-0.094	0.075
	CK	29	0.000	1	1.000	1	1.0	-0.018	0.000
Black Crappie Male	IDH	44	0.012	1	0.914	2	1.9	-0.023	0.012
	CK	45	0.000	1	1.000	1	1.0	-0.011	0.000

* Exact P; ** Fixation Index; † Heterozygote Deficiency Index.

Table 6. Mean observed and expected heterozygosities for IDH-2 and CK-3 in black and white crappie age groups captured in Copan lake during 1983.

Age	N	No. Alleles	Mean H*	Exp. H**
<u>White Crappie</u>				
Age 0-1	23.5	2.5	0.225 (0.185)	0.316 (0.276)
Age 2	97.5	3.0	0.329 (0.217)	0.365 (0.248)
Age 3	39.5	3.0	0.365 (0.160)	0.385 (0.196)
Age 4-5-6	68.0	3.0	0.338 (0.039)	0.416 (0.147)
<u>Black Crappie</u>				
Age 0	44.0	2.0	0.068 (0.023)	0.066 (0.021)
Age 3-4-5	33.5	1.5	0.045 (0.045)	0.044 (0.044)

* Mean frequency of heterozygous individuals by direct count.

** Expected frequencies un Hardy - Weinberg Equilibrium.

Table 7. Genotype distributions and allele frequencies for CK-3 in black and white crappie age groups captured in Copan Lake during 1983.

Sample	N	h*	Genotype Distribution						Allele Frequency		
			AA	BB	CC	AB	AC	BC	A	B	C
<u>White Crappie</u>											
Age 0-1	25	0.040	0	24	0	0	0	1	0.000	0.980	0.020
Age 2	98	0.112	0	87	0	3	1	7	0.020	0.939	0.041
Age 3	39	0.205	0	31	0	1	0	7	0.013	0.897	0.090
Age 4-5-6	67	0.299	0	47	0	0	1	19	0.007	0.843	0.149
<u>Black Crappie</u>											
Age 0	44	0.045	0	42	0	0	0	2	0.000	0.977	0.023
Age 3-4-5	34	0.000	0	34	0	0	0	0	0.000	1.000	0.000

* h = Frequency of individuals heterozygous at CK-3 by direct count.

Table 8. Genotype distributions and allele frequencies for IDH-2 in black and white crappie age groups captured in Copan Lake during 1983.

Sample	N	h*	Genotype Distribution								Allele Frequency			
			AA	BB	CC	DD	AB	AC	AD	BC	A	B	C	D
<u>White Crappie</u>														
Age 0-1	22	0.409	1	6	6	0	1	1	0	7	0.091	0.455	0.455	0.000
Age 2	97	0.546	3	31	10	0	17	14	0	22	0.191	0.521	0.289	0.000
Age 3	40	0.525	1	14	4	0	8	3	0	10	0.162	0.575	0.262	0.000
Age 4-5-6	69	0.377	3	28	12	0	11	1	0	14	0.130	0.587	0.283	0.000
<u>Black Crappie</u>														
Age 0	44	0.091	40	0	0	0	0	0	4	0	0.955	0.000	0.000	0.045
Age 3-4-5	33	0.091	30	0	0	0	0	0	3	0	0.955	0.000	0.000	0.045

* h = Frequency of individuals heterozygous at IDH-2 by direct count.

Table 9. Chi-square tests for conformance to Hardy - Weinberg equilibrium and indices for allele fixation and heterozygote deficiency for IDH-2 and CK-3 in black and white crappie age groups captured in Copan Lake during 1983.

Age	Locus	N	χ^2	df	P*	Obs. Het.	Exp. Het.	F**	D†
<u>White Crappie</u>									
Age 0-1	IDH	22	7.804	3	0.050	9	13.0	0.293	-0.309
	CK	25	0.000	1	1.000	1	1.0	-0.020	0.000
Age 2	IDH	97	4.566	3	0.206	53	59.4	0.103	-0.108
	CK	98	4.636	3	0.200	11	11.4	0.037	-0.042
Age 3	IDH	40	1.230	3	0.746	21	23.2	0.058	-0.097
	CK	39	0.441	3	0.932	8	7.3	-0.101	0.086
Age 4-5-6	IDH	69	18.898	3	0.000	26	38.8	0.325	-0.330
	CK	67	7.323	3	0.062	20	17.9	-0.120	0.112
<u>Black Crappie</u>									
Age 0	IDH	44	0.074	1	0.786	4	3.8	-0.048	0.036
	CK	44	0.012	1	0.914	2	1.9	0.023	0.012
Age 3-4-5	IDH	33	0.049	1	0.825	3	2.9	-0.048	0.032
	CK		--monomorphic at this locus--						

* Exact P; ** Fixation Index; † Heterozygote Deficiency Index.

Table 10. Mean observed and expected heterozygosities for IDH-2 and CK-3 in black and white crappie relative weight (Wr) groups captured in Copan Lake during spring, summer, and fall 1983.

Sample	N	Mean Wr	No. Alleles	Mean H*	Exp. H**
<u>White Crappie</u>					
Spring Wr Low	86.0	0.88	3.0	0.349 (0.105)	0.406 (0.167)
Spring Wr High	84.5	1.08	3.0	0.323 (0.154)	0.354 (0.198)
Summer Wr Low	28.5	0.86	2.5	0.311 (0.244)	0.335 (0.269)
Summer Wr High	30.5	0.99	3.0	0.298 (0.169)	0.391 (0.267)
<u>Black Crappie</u>					
Summer Wr Low	16.5	0.84	1.0	0.000 (0.000)	0.000 (0.000)
Summer Wr High	18.0	0.93	1.5	0.083 (0.083)	0.079 (0.079)
Fall Wr Low	20.0	0.66	2.0	0.075 (0.025)	0.074 (0.024)
Fall Wr High	23.0	0.92	2.0	0.065 (0.022)	0.064 (0.021)

* Mean frequency of heterozygous individuals by direct count.

** Expected frequency under Hardy - Weinberg equilibrium.

Table 11. Mean observed and expected heterozygosities for IDH-2 and CK-3 in black and white crappie total length classes and age groups captured in Copan lake during 1983.

Age	Mean TL	N	No. Alleles	Mean H*	Exp. H**
<u>White Crappie</u>					
Age 0-1 TL Low	124	24.0	2.5	0.216 (0.176)	0.341 (0.301)
Age 0-1 TL High	160	23.5	2.0	0.261 (0.261)	0.315 (0.315)
Age 2 TL Low	173	34.5	3.0	0.379 (0.179)	0.401 (0.191)
Age 2 TL High	214	35.0	3.0	0.343 (0.229)	0.355 (0.244)
Age 3 TL Low	203	19.0	3.0	0.342 (0.079)	0.422 (0.182)
Age 3 TL High	260	20.5	2.5	0.385 (0.235)	0.350 (0.208)
Age 4-5-6 TL Low	190	35.0	2.5	0.343 (0.029)	0.437 (0.169)
Age 4-5-6 TL High	244	33.0	3.0	0.332 (0.051)	0.394 (0.122)
<u>Black Crappie</u>					
Age 0 TL Low	97	22.0	1.5	0.023 (0.023)	0.023 (0.023)
Age 0 TL High	126	22.0	2.0	0.114 (0.023)	0.109 (0.021)
Age 3-4-5 TL Low	207	18.0	1.5	0.056 (0.056)	0.054 (0.054)
Age 3-4-5 TL High	222	15.5	1.5	0.033 (0.033)	0.033 (0.033)

* Mean frequency of heterozygous individuals by direct count.

** Expected frequency under Hardy - Weinberg equilibrium.

Table 12. Genotype distributions and allele frequencies for IDH-2 in black and white crappie relative weight (Wr) groups captured in Copan Lake during spring, summer, and fall 1983.

Sample	Mean Wr	N	h*	Genotype Distribution								Allele Frequency			
				AA	BB	CC	DD	AB	AC	AD	BC	A	B	C	D
<u>White Crappie</u>															
Spring Wr Low	0.88	86	0.453	3	33	11	0	13	6	0	20	0.145	0.576	0.279	0.000
Spring Wr High	1.08	86	0.477	3	34	8	0	17	4	0	20	0.157	0.610	0.233	0.000
Summer Wr Low	0.86	27	0.556	0	6	6	0	3	3	0	9	0.111	0.444	0.444	0.000
Summer Wr High	0.99	30	0.467	2	6	8	0	4	6	0	4	0.233	0.333	0.433	0.000
<u>Black Crappie</u>															
Summer Wr Low	0.84	16	0.000	16	0	0	0	0	0	0	0	1.000	0.000	0.000	0.000
Summer Wr High	0.93	18	0.167	15	0	0	0	0	0	3	0	0.917	0.000	0.000	0.083
Fall Wr Low	0.66	20	0.100	18	0	0	0	0	0	2	0	0.950	0.000	0.000	0.050
Fall Wr High	0.92	23	0.087	21	0	0	0	0	0	2	0	0.957	0.000	0.000	0.043

* h = Frequency of individuals heterozygous at IDH-2 by direct count.

Table 13. Genotype distributions and allele frequencies for CK-3 in black and white crappie relative weight (Wr) groups captured in Copan Lake during spring, summer, and fall 1983.

Sample	Mean Wr	N	h*	Genotype Distribution						Allele Frequency		
				AA	BB	CC	AB	AC	BC	A	B	C
<u>White Crappie</u>												
Spring Wr Low	0.88	86	0.244	0	65	0	2	2	17	0.023	0.866	0.110
Spring Wr High	1.08	83	0.169	0	69	0	1	0	13	0.006	0.916	0.078
Summer Wr Low	0.86	30	0.067	0	28	0	0	0	2	0.000	0.967	0.033
Summer Wr High	0.99	31	0.129	0	27	0	1	0	3	0.016	0.935	0.048
<u>Black Crappie</u>												
Summer Wr Low	0.84	17	0.000	0	17	0	0	0	0	0.000	1.000	0.000
Summer Wr High	0.93	18	0.000	0	18	0	0	0	0	0.000	1.000	0.000
Fall Wr Low	0.66	20	0.050	0	19	0	0	0	1	0.000	0.975	0.025
Fall Wr High	0.92	23	0.043	0	22	0	0	0	1	0.000	0.978	0.022

* h = Frequency of individuals heterozygous at CK-3 by direct count.

Table 14. Chi-square tests for conformance to Hardy - Weinberg equilibrium and indices for allele fixation and heterozygote deficiency for IDH-2 and CK-3 in black crappie relative weight (Wr) groups captured in Copan Lake during summer and fall 1983.

Sample	Mean Wr	Locus	N	χ^2	df	P*	Obs. Het.	Exp. Het.	F**	D†
Summer Wr Low	0.84	IDH	16							
		CK	17							
Summer Wr High	0.93	IDH	18	0.097	1	0.756	3	2.9	-0.091	0.061
		CK	18							
Fall Wr Low	0.66	IDH	20	0.027	1	0.869	2	1.9	-0.053	0.026
		CK	20	0.000	1	1.000	1	1.0	-0.026	0.000
Fall Wr High	0.92	IDH	23	0.023	1	0.879	2	1.9	-0.045	0.023
		CK	23	0.000	1	1.000	1	1.0	-0.022	0.000

* Exact P; ** Fixation Index; † Heterozygote Deficiency Index.

Table 15. Genotype distributions and allele frequencies for IDH-2 in black and white crappie total length (mm) classes and age groups captured in Copan Lake during 1983.

Sample	Mean TL	N	h*	Genotype Distribution								Allele Frequency			
				AA	BB	CC	DD	AB	AC	AD	BC	A	B	C	D
<u>White Crappie</u>															
Age 0-1 TL Low	124	23	0.391	1	7	6	0	2	4	0	3	0.174	0.413	0.413	0.000
Age 0-1 TL High	160	23	0.522	2	5	4	0	0	3	0	9	0.152	0.413	0.435	0.000
Age 2 TL Low	173	34	0.559	0	12	3	0	6	5	0	8	0.162	0.559	0.279	0.000
Age 2 TL High	214	35	0.571	1	11	3	0	9	3	0	8	0.200	0.557	0.243	0.000
Age 3 TL Low	203	19	0.421	1	7	3	0	1	2	0	5	0.132	0.526	0.342	0.000
Age 3 TL High	260	21	0.619	0	7	1	0	7	1	0	5	0.190	0.619	0.190	0.000
Age 4-5-6 TL Low	190	35	0.371	3	13	6	0	6	1	0	6	0.186	0.543	0.271	0.000
Age 4-5-6 TL High	244	34	0.382	0	15	6	0	5	0	0	8	0.074	0.632	0.294	0.000
<u>Black Crappie</u>															
Age 0 TL Low	97	22	0.045	21	0	0	0	0	0	1	0	0.977	0.000	0.000	0.023
Age 0 TL High	126	22	0.136	19	0	0	0	0	0	3	0	0.932	0.000	0.000	0.068
Age 3-4-5 TL Low	207	18	0.111	16	0	0	0	0	0	2	0	0.944	0.000	0.000	0.056
Age 3-4-5 TL High	222	15	0.067	14	0	0	0	0	0	1	0	0.967	0.000	0.000	0.033

* h = Frequency of individuals heterozygous at IDH-2 by direct count.

Table 16. Genotype distributions and allele frequencies for CK-3 in black and white crappie total length (mm) classes and age groups captured in Copan Lake during 1983.

Sample	Mean TL	N	h*	Genotype Distribution						Allele Frequency		
				AA	BB	CC	AB	AC	BC	A	B	C
<u>White Crappie</u>												
Age 0-1 TL Low	124	25	0.040	0	24	0	0	0	1	0.000	0.980	0.020
Age 0-1 TL High	160	24	0.000	0	24	0	0	0	0	0.000	1.000	0.000
Age 2 TL Low	173	35	0.200	0	28	0	1	1	5	0.029	0.886	0.086
Age 2 TL High	214	35	0.114	0	31	0	2	0	2	0.029	0.943	0.029
Age 3 TL Low	203	19	0.263	0	14	0	1	0	4	0.026	0.868	0.086
Age 3 TL High	260	20	0.150	0	17	0	0	0	3	0.000	0.925	0.075
Age 4-5-6 TL Low	190	35	0.314	0	24	0	0	0	11	0.000	0.843	0.157
Age 4-5-6 TL High	244	32	0.281	0	23	0	0	1	8	0.016	0.844	0.141
<u>Black Crappie</u>												
Age 0 TL Low	97	22	0.000	0	22	0	0	0	0	0.000	1.000	0.000
Age 0 TL High	126	22	0.091	0	20	0	0	0	2	0.000	0.955	0.045
Age 3-4-5 TL Low	207	18	0.000	0	18	0	0	0	0	0.000	1.000	0.000
Age 3-4-5 TL High	222	16	0.000	0	16	0	0	0	0	0.000	1.000	0.000

* h = Frequency of individuals heterozygous at CK-3 by direct count.

Table 17. Chi-square tests for conformance to Hardy - Weinberg equilibrium and indices of allele fixation and heterozygote deficiency at IDH-2 and CK-3 in total length classes of black crappie age groups captured in Copan Lake during 1983.

Sample	Mean TL	Locus	N	χ^2	df	P*	Obs. Het.	Exp. Het.	F**	D†
Age 0 TL Low	97	IDH	22	0.000	1	1.000	1	1.0	-0.023	0.000
		CK	22							
Age 0 TL High	126	IDH	22	0.077	1	0.782	3	2.8	-0.073	0.049
		CK	22	0.024	1	0.876	2	1.9	-0.048	0.024
Age 3-4-5 TL Low	207	IDH	18	0.030	1	0.862	2	1.9	-0.059	0.029
		CK	18							
Age 3-4-5 TL High	222	IDH	15	0.000	1	1.000	1	1.0	-0.034	0.000
		CK	16							

* Exact P; ** Fixation Index; † Heterozygote deficiency index.

Table 18. Matrix of similarity and distance coefficients for black and white crappie captured in Copan Lake during 1983.

Species	Collection Site	1	2	3	4
White Crappie	Little Caney R.	xxxxx	0.977	0.988	0.725
White Crappie	Endacott's Pond	0.130	xxxxx	1.000	0.670
White Crappie	Copan Lake	0.087	0.044	xxxxx	0.683
Black Crappie	Endacott's Pond	0.354	0.420	0.387	xxxxx

Above Diagonal : Nei (1978) Unbiased Genetic Identity

Below Diagonal : Rogers (1972) Genetic Distance

Table 19. Genotype distributions and allele frequencies for IDH-2 in black and white crappie captured from sample locations in Copan Lake during 1983.

Species	Site	N	h*	Genotype Distribution								Allele Frequency			
				AA	BB	CC	DD	AB	AC	AD	BC	A	B	C	D
White Crappie	W1**	32	0.500	2	7	7	0	3	5	0	8	0.188	0.391	0.422	0.000
White Crappie	W2	101	0.406	5	42	15	0	16	5	0	20	0.153	0.574	0.272	0.000
White Crappie	W3	96	0.542	1	32	11	0	18	9	0	25	0.151	0.557	0.292	0.000
Black Crappie	B2	77	0.091	70	0	0	0	0	0	7	0	0.955	0.000	0.000	0.045

*

h = Frequency of individuals heterozygous at IDH-2 by direct count.

**

W1 = Little Caney River; W2 = Endacott's Pond; W3 = Copan Lake; B2 = Endacott's Pond.

Table 20. Genotype distributions and allele frequencies for CK-3 in black and white crappie captured from sample locations in the Copan Lake basin.

Species	Site	N	h*	Genotype Distribution						Allele Frequency		
				AA	BB	CC	AB	AC	BC	A	B	C
White Crappie	W1**	32	0.063	0	30	0	0	1	1	0.016	0.953	0.031
White Crappie	W2	105	0.263	0	99	0	1	0	25	0.005	0.869	0.126
White Crappie	W3	99	0.131	0	86	0	3	1	9	0.020	0.929	0.051
Black Crappie	B2	78	0.026	0	76	0	0	0	2	0.000	0.987	0.013

*

Frequency of individuals heterozygous at CK-3 by direct count.

**

W1 = Little Caney River; W2 = Endacott's Pond; W3 = Copan Lake; B2 = Endacott's Pond.

Table 21. Chi-square tests for conformance to Hardy - Weinberg equilibrium and indices for allele fixation and heterozygote deficiency for IDH-2 and CK-3 in white crappie captured from 3 sample locations in Copan Lake during 1983.

Sample	Locus	N	χ^2	df	P*	Obs. Het.	Exp. Het.	F**	D†
Little Caney River	IDH	32	3.627	3	0.305	16	20.6	0.212	-0.224
	CK	32	31.000	3	0.000	2	2.9	0.308	-0.319
Endacott's Pond	IDH	101	18.335	3	0.000	41	58.1	0.291	-0.294
	CK	99	2.166	3	0.539	26	22.8	-0.145	0.139
Copan Lake	IDH	96	3.358	3	0.340	52	56.1	0.069	-0.021
	CK	99	3.548	3	0.315	13	13.2	0.016	-0.021

* Exact P; ** Fixation Index; † Heterozygote Deficiency Index.

Table 22. Chi-square tests for conformance to Hardy - Weinberg equilibrium and indices for allele fixation and heterozygote deficiency for IDH-2 and CK-3 in white crappie relative weight (Wr) groups captured in Copan Lake during spring and summer 1983.

Sample	Locus	N	χ^2	df	P*	Obs. Het.	Exp. Het.	F**	D†
Spring Wr Low	IDH	86	7.061	3	0.070	39	49.3	0.204	-0.209
	CK	86	7.129	3	0.068	21	20.5	-0.031	0.025
Spring Wr High	IDH	86	4.811	3	0.182	41	47.5	0.131	-0.136
	CK	83	0.650	3	0.885	14	12.9	-0.085	0.079
Summer Wr Low	IDH	27	0.904	3	0.824	15	16.3	0.062	-0.080
	CK	30	0.018	1	0.895	2	1.9	-0.034	0.017
Summer Wr High	IDH	30	6.413	3	0.093	14	19.7	0.278	-0.290
	CK	31	0.109	3	0.991	4	3.6	-0.055	0.038

* Exact P; ** Fixation Index; † Heterozygote Deficiency Index.

Table 23. Chi-square tests for conformance to Hardy - Weinberg equilibrium and indices of allele fixation and heterozygote deficiency for IDH-2 and CK-3 in total length classes of white crappie age groups captured in Copan Lake during 1983.

Sample	Locus	N	χ^2	df	P*	Obs. Het.	Exp. Het.	F**	D†
0-1 year TL Low	IDH	23	8.018	3	0.046	9	14.7	0.377	-0.391
	CK	25	0.000	1	1.000	1	1.0	-0.020	0.000
0-1 year TL High	IDH	23	8.425	3	0.038	12	14.5	0.155	-0.173
	CK	24		-locus was monomorphic-					
2 year TL Low	IDH	34	2.974	3	0.396	19	20.1	0.042	-0.056
	CK	35	4.551	3	0.208	7	7.3	0.035	-0.049
2 year TL High	IDH	35	1.098	3	0.778	20	20.9	0.032	-0.046
	CK	35	0.095	3	0.992	4	3.8	-0.045	0.030
3 year TL Low	IDH	19	4.716	3	0.194	8	11.4	0.285	-0.304
	CK	19	0.341	3	0.952	5	4.5	-0.124	0.095
3 year TL High	IDH	21	1.873	3	0.5999	13	11.7	-0.138	0.110
	CK	20	0.086	1	0.770	3	2.8	-0.081	0.054
4-5-6 year TL Low	IDH	35	12.823	3	0.005	13	21.2	0.378	-0.387
	CK	35	1.093	1	0.296	11	9.4	-0.186	0.169
4-5-6 year TL High	IDH	34	8.166	3	0.043	13	17.5	0.248	-0.259
	CK	32	6.586	3	0.086	9	8.7	-0.049	0.033

* Exact P; ** Fixation Index; † Heterozygote deficiency index .

CHAPTER III

THE INCIDENCE OF F1 BLACK CRAPPIE X WHITE CRAPPIE
HYBRIDS IN COPAN LAKE

INTRODUCTION

Black and white crappie (Pomoxis nigromaculatus and P. annularis, respectively) are widely distributed throughout North America. Field observations indicate that when both species occur sympatrically, black crappie usually predominate in clear, cooler, slightly acidic water, whereas white crappie predominate in water that is warmer, more turbid, and slightly basic (Hall et al. 1954; Goodson 1966).

Crappie populations often increase dramatically in newly created midwestern reservoirs. Growth rates of black and white crappie are generally high the first few years after impoundment, but subsequently decline (Rutledge and Barron 1972). Abundance of black crappie also declines, and while white crappie remain relatively abundant, the population is often composed of many "stunted" or small fish (Jenkins 1953; Glass 1982). In general, midwestern reservoir crappie populations tend to be characterized by dominant, small, or missing year classes (Cichra et al. 1981; Mitzner 1981; Beam 1983).

Several hypotheses have been presented to explain the decline of black crappie populations in aging midwestern reservoirs. Generally,

interspecific competition for limited forage (Stevens 1958; Keast 1968; Li et. al. 1976) and severe intraspecific competition due to overcrowding (Huish 1953; Rutledge and Barron 1972; Hanson et al. 1983; Gablehouse 1984) are thought to lead to decreased growth rates of black crappie and to a selective advantage for white crappie. In addition, more recent studies have identified specific foraging behaviors of black crappie that might limit population levels in southern reservoirs (May and Thompson 1974; Barwick and Lorenzen 1984). For example, in some warmwater reservoirs, large black crappie often have higher mortality rates than similar size white crappie because they feed primarily on invertebrates with which they fail to meet their energy requirements. Large white crappie conversely successfully meet their energy requirements by feeding on fish (Ellison 1984). However, many large black crappie are also piscivorous (Ager 1975). Therefore, none of the previously proposed hypotheses fully explain why black crappie often decrease in abundance over time.

One contributing factor in the decrease in abundance of black crappie when they are in sympatry with a much larger white crappie population is reduction of effective population size through gamete competition. Species integrity may be governed more by pre-reproductive isolating mechanisms than by post-reproductive mechanisms. The creation and stocking of reservoirs has often mixed otherwise isolated populations of black and white crappie and forced them to share spawning sites (Jenkins 1953). Thus, it is possible that they hybridize wherever they occur together.

Although there is little information on the frequency of natural hybridization, Burr (1974) reported a white crappie X flier (Centrarchus

macropterus) hybrid, and other studies have attempted artificial hybridization of Pomoxis spp. with other species of Centrarchidae (West and Hester 1966; Tyus 1973; Merriner'1971). Metcalf et al. (1972) demonstrated that artificially reared F₁, F₂, and back-crossed black crappie X white crappie interspecific hybrids were hardy and fertile. In addition, they found that F₁ hybrids were not morphologically intermediate between black or white crappie but instead were fairly typical of black crappie, making field identification difficult. The vigor and fertility of experimental hybrid crappie populations led Metcalf et al. (1972) to suggest that natural hybridization may occur more frequently than expected and may have management implications.

Little is known about the frequency of hybridization, growth, survival, or reproductive potential of crappie hybrids in natural populations. Therefore, the purpose of this paper is to report electrophoretically detected natural hybridization between sympatric populations of black and white crappie and to discuss the possible effects that this interbreeding may have on reservoir populations of black crappie.

STUDY AREA

Our study took place in Copan Lake, located on the Little Caney River, approximately 3.7 km west of Copan, Washington County, Oklahoma. The drainage area above the dam site is approximately 1,308 square kilometers, and is characterized by rolling hills and oak hickory forests, with numerous rock outcroppings interspersed with lowlands of tall grass prairie. At conservation elevation (209.5 m -216.4 m), the

lake covers approximately 1,962 hectares and inundates 23.3 km of the Little Caney River. The lake has 55.6 km of shoreline and a shoreline development index of 3.1 (Oklahoma Water Resource Board 1984). Mean and maximum depths are 2.7 m and 10.6 m, respectively. Turbidity levels in the lake are high due to the relatively high concentrations of suspended solids in the river.

The area above the dam consists of the lake proper and a periodically isolated pond, Endacott's pond. The mean depth of this pond before inundation was 1.8 m and secchi readings averaged 1.2 m. The pond has historically stratified every year, and presently is the only site in Copan Lake that stratifies. A pre-impoundment survey (1982) of crappie in the pond found a low density of mostly older black crappie. Few white crappie were captured.

METHODS

Black and white crappie used for the electrophoresis study were collected by barrel net traps, gill nets, and modified trap nets in Copan lake during 1983 (Figure 1; Oakey 1986, p. 55). Specimens were field-identified by dorsal spine number and body coloration (Miller and Robison 1973). A total of 77 phenotypic black crappie and 235 phenotypic white crappie were captured and frozen on dry ice before being returned to the laboratory. At the laboratory, all crappie were weighed to the nearest gram and total length was determined to the nearest millimeter. During dissection, sex of all crappie was determined by visual inspection and otoliths (sagittae) were removed for age determination. Otolith radius was measured from the center of the

kernal to the anterior tip of the otolith. Distance to each annulus was measured along the radius from the center of the kernal to the proximal margin of the opaque band (Pannella 1974).

Separate extracts of liver and eye/brain from each individual were subjected to standard methods of horizontal starch-gel electrophoresis (Siciliano and Shaw 1976). Three enzymes were used to identify pure stocks of black and white crappie and their interspecific hybrids: malate dehydrogenase (MDH, E.C. 1.1.1.37), esterases (EST, E.C. 3.1.1.2), and phosphoglucoisomerase (PGI, E.C. 5.3.1.9).

Electrophoretically, these enzymes were monomorphic within both species, and exhibited fixed differences between pure crappie stocks in Copan reservoir (Oakey 1986). Combinations of enzymes, buffer system, and tissues used in this study are listed in Table 1.

Total lengths and weights of hybrid crappie were averaged and compared with those of equivalent-age black and white crappie. Estimated total lengths at time of formation of otolith annuli were back-calculated using the direct proportion method (Lagler 1956) with an intercept of zero. Linear relationships of length-weight were determined for black, white, and hybrid crappie stocks with the least squares method: $\ln(WT) = a + b[\ln(TL)]$. An analysis of covariance was used to compare the regression slopes of the length-weight data for each stock (Snedecor and Cochran 1978). Relative weight (W_r) was calculated as $W_r = W_s / W_t$, where W_s and W_t represent standard weight and captured weight, respectively. Standard weights were derived by $\text{Log}_{10}(W_s) = -4.914 + 3.052 [\text{Log}_{10}(TL)]$ and $\text{Log}_{10}(W_t) = -5.102 + 3.112 [\text{Log}_{10}(TL)]$ for black and white crappie, respectively (Anderson 1980). Gonosomatic index (GSI) was calculated as gonad weight/body weight X 100.

RESULTS

Six of the 312 crappie examined from Copan Lake were identified as black crappie X white crappie F₁ hybrids. All diagnostic loci of F₁ hybrids had heteromorphic phenotypes indicating contributions of co-dominant alleles from the parent species (Table 2). No F₂ or F₃ individuals were identified. Of the 77 morphologically identified black crappie, 5 (6.4 %) were subsequently re-identified as F₁ hybrids. In addition, one male, originally field-identified as a white crappie, was re-identified as an F₁ hybrid.

The age of hybrid crappie ranged from young-of-year (YOY) to 4 years old (Table 2). The 3 four-year-old hybrids represented 15.4 % and 8.3 % of the 1979 year class of black crappie that were field identified and electrophoretically surveyed from Endacott's pond during May and June 1983, respectively. The 2-year-old hybrid, originally identified as a white crappie, represented 20 % of the 1981 year class of field identified white crappie surveyed in Endacott's pond during June 1983. Only 1 black crappie of the 1981 year class was collected from Copan Lake during this study. The remaining 2 hybrids were YOY and represented 66 % of the 1983 year class of black crappie collected and surveyed from the north end of Copan Lake during October 1983.

Adult hybrid crappie in Endacott's pond were generally larger and in better condition than either parent species of equivalent year class (Table 3). The 2 YOY hybrids from the north end of Copan Lake were the largest YOY crappie collected during the study. Mean back-calculated total lengths at otolith annuli indicated that although adult hybrids

grew faster than either black or white crappie in Endacott's pond, adult black and white crappie growth was greater at the north end of Copan Lake than was hybrid growth in Endacott's pond (Table 4). However, growth rates of crappie, in general, were slower in Endacott's pond than in the main body of the lake (Oakey 1986).

Slopes of length-weight regressions between hybrid and parent stocks in Endacott's pond were significantly different ($P < 0.0001$), with that of hybrids superior to those of parents (Table 5). However, slopes were not significantly different ($P < 0.2682$) between hybrid and parent stocks from the north end of Copan lake. In addition, the Gonosomatic index (GSI) for 1 gravid female hybrid (4.5 %) was lower than the average of 4 equivalent age white crappie (8.0 %) and 2 equivalent age black crappie (4.9 %) that were captured at Endacott's pond at the same time.

DISCUSSION

These data are the first verification of F_1 hybrid crappie from natural sympatric populations of black and white crappie. The occurrence of interspecific hybrid crappie in Copan Lake is not a recent, single event, because hybrids represented several age classes (Table 2). The sex ratio for the adult hybrids was 50:50, however 2 of the 3 four-year-old hybrids were female. Dominance by females in age classes is fairly typical in older crappie (Hansen 1951).

These data indicate the possibility of two distinct hybrid phenotypes in Copan Lake. One F_1 hybrid crappie was originally field-identified as a white crappie, but the majority of F_1 hybrid

crappie had key characteristics of black crappie. Hybrids represented 6.4 % of the morphologically identified black crappie examined in this study. Many crappie in the field that are morphologically intermediate between black and white crappie may actually be F₂ or F₃ hybrids (Metcalf et al. 1972).

Our study suggests that hybrid crappie benefited from heterosis. Four adult hybrid crappie had greater than average back-calculated length at annuli (Table 4) and, in general, greater total lengths and weights at capture than equivalent age black and white crappie captured in the same area (Table 3). Young-of-year hybrid crappie were collected only at the north end of Copan Lake, but these fish were the largest YOY crappie collected at that site during October (Table 2). Fast growth during the first year is important because it decreases the probability of juvenile mortality and increases the probability of reaching sexual maturity. Experimental hybrid crappie grew faster the first year in Illinois than black or white crappie (McClellan 1985). The late W. F. Childers suspected that hybrid crappie occurred throughout Illinois, and believed that several 4 to 5 pound crappies that he examined were hybrid crappie (McClellan 1985).

Hybridization between black and white crappie could affect the parent populations in several ways. Superior hybrid growth may indicate that hybrids are better adapted to reservoirs than black crappie. Being morphologically very similar to black crappie, hybrids might outcompete blacks over a long time period. Low competitive status would increase the vulnerability of black crappie to stress-related mortality. Faster growing hybrids may reach the size necessary for piscivory earlier in the growing season. Thus, by extending the range of accessible forage,

hybrid crappie more easily maintain good relative weight. Copan lake hybrids generally grew faster and had higher relative weight than equivalent age black and white crappie. In addition, sexual maturity and fecundity are related with size rather than age in crappie (Mathur et al. 1979).

Hybrid crappie are fertile and can back-cross with parent populations (Metcalf et al. 1972). It is possible that hybridization may result in genetic swamping of the smaller (black) crappie population through gene introgression. However, hybridization between crappie species in Copan lake may not be occurring on a large enough scale for genetic swamping to be a factor in the decline of black crappie. Hybridization between black and white crappie in Copan lake could result in the addition of new alleles into the gene pools of the parent populations. Although, before gene flow can occur, the incoming alleles must prevail despite selective pressure to remove them from the population (Ehrlich and Raven 1969). The addition of genetic material through gene introgression may be beneficial by increasing genetic variation in the parent populations. Conversely, a hybrid zone could be deleterious to the parent crappie populations if it disrupts co-adapted gene complexes and results in non-viable hybrid genotypes.

The absence of F_2 or back-crossed crappie hybrids in our study may be due to the small sample; however, it is possible that post-zygotic selection may be operating against hybrid reproduction in Copan lake. The breakdown of reproductive isolating mechanisms between black and white crappie in Copan lake may result in wasted reproductive effort (Ayala 1982). When black crappie occur in low density relative to white crappie, black crappie gametes may be limiting, and gamete competition

with white crappie and F_1 hybrids may further reduce total black crappie reproductive effort. Faster growth rates for the hybrid crappie probably increases their reproductive potential by allowing more individuals to be recruited into the breeding population and increasing the number of gametes per individual. Competition for gametes with white crappie and hybrid crappie would reduce the effective population size of black crappie.

CONCLUSIONS

The black crappie population in Copan lake is already small, and vulnerable to loss of genetic variation due to genetic drift. Further reduction of effective population size through gamete competition may lead to inbreeding depression, which could reduce fecundity, growth, and survivorship in the population (Meffe 1986). The continuation of hybridization between black and white crappie, when black crappie are relatively uncommon compared to white crappie, may reduce the black crappie to a small, inbred population that lacks adaptive plasticity and is vulnerable to stochastic environmental conditions.

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Table 1. Enzyme, tissue, and buffer used in electrophoretic analysis of black crappie, white crappie, and their F1 generation interspecific hybrid crosses captured in Copan Lake during 1983.

Enzyme	Tissue	<u>Allele Designation</u>		Buffer Systems For
		BC*	WC*	Gels and Chambers
Malate dehydrogenase	Eye / Brain	Slow	Fast	Tris-Citrate, pH 6.9
Esterases	Liver	Fast	Slow	Tris-Citrate, pH 6.9
Phosphoglucosomerase	Eye / Brain	Slow	Fast	Tris-Citrate, ph 6.9

* BC = Black Crappie; WC = White Crappie

Table 2. Summary of six electrophoretically detected F1 black crappie X white crappie hybrid captured in Copan Lake during 1983.

Field ID	Sex	Age	Year Class	TL	SL	WT	Site*	Capture Date
BC	Female	4	1979	221	173	150	EP	1 May 1983
BC	Female	4	1979	307	250	496	EP	10 May 1983
BC	Male	4	1979	236	184	180	EP	14 June 1983
WC	Male	2	1981	249	197	240	EP	17 June 1983
BC	Male	0	1983	145	110	35	CNE	24 October 1983
BC	Male	0	1983	150	118	39	CNE	24 October 1983

* EC = Endacott's Pond; CNE = Copan Lake North End

Table 3. Mean capture length, weight, and condition (Wr) for black crappie, white crappie, and F₁ black crappie X white crappie hybrids in Copan lake.

Species	N	Sex	Age	TL	WF	Wr
<u>Endacott's Cove 4 May 1983</u>						
White Crappie	2	Male	4	208	113	.87
White Crappie	1	Female	4	312	592	1.29
Black Crappie	1	Male	4	219	135	.80
Black Crappie	1	Female	4	194	112	.96
Hybrid Crappie	1	Female	4	221	150	.96 / .86*
<u>Endacott's Cove 10 May 1983</u>						
White Crappie	3	Male	4	198	100	.89
White Crappie	4	Female	4	186	92	1.00
Black Crappie	3	Male	4	201	116	.89
Hybrid Crappie	1	Female	4	307	496	1.19 / 1.04
<u>Endacott's Cove 14 June 1983</u>						
White Crappie	3	Male	4	205	128	1.03
White Crappie	2	Female	4	206	129	1.03
Black Crappie	2	Male	4	230	175	.90
Black Crappie	6	Female	4	223	181	1.02
Hybrid Crappie	1	Male	4	236	180	.94 / .85
<u>Endacott's Cove 17 June 1983</u>						
White Crappie	3	Male	2	215	155	1.07
White Crappie	1	Female	2	232	190	1.04
Hybrid Crappie	1	Male	2	249	240	1.06 / .96
<u>Copan Lake North End 24 October 1983</u>						
White Crappie	9	Male	0	109	11	.58
White Crappie	4	Female	0	109	11	.55
Hybrid Crappie	2	Male	0	148	37	.83 / .72

* Wr for white and black crappie, respectively.

Table 4. Mean back-calculated length at otolith annuli for black crappie, white crappie, and F1 black crappie X white crappie hybrids captured at 2 locations in Copan Lake during 1983.

Species	N	Annulus				
		1	2	3	4	5
<u>Endacott's Pond</u>						
White Crappie	206	98	169	185	210	321(1)
Black Crappie	42	97	163	194	215	222(1)
Hybrid Crappie	4	101	183	229	227(1)	
<u>Copan Lake North End</u>						
White Crappie	88	97	183	252	279	
Black Crappie	11	119	216	280		
Hybrid Crappie	2	147*				

* Total Length Of YOY Captured On 24 October 1983.

Table 5. Natural log length weight regressions for black crappie, white crappie, and F1 black crappie X white crappie hybrids captured from 2 locations in Copan Lake during 1983.

Species	N		PR < F	R ²
<u>Endacott's Pond</u>				
White Crappie	275	$\text{Ln}(\text{WT}) = -14.254 + 3.627[\text{Ln}(\text{TL})]$	0.0001	0.9798
Black Crappie	89	$\text{Ln}(\text{WT}) = -12.891 + 3.326[\text{Ln}(\text{TL})]$	0.0001	0.9875
Hybrid Crappie	4	$\text{Ln}(\text{WT}) = -14.929 + 3.692[\text{Ln}(\text{TL})]$	0.0025	0.9949
<u>Copan Lake North End</u>				
White Crappie	134	$\text{Ln}(\text{WT}) = -16.007 + 3.913[\text{Ln}(\text{TL})]$	0.0001	0.9835
Black Crappie	16	$\text{Ln}(\text{WT}) = -14.439 + 3.629[\text{Ln}(\text{TL})]$	0.0001	0.9720
Hybrid Crappie	2	$\text{Ln}(\text{WT}) = -6.079 + 3.523[\text{Ln}(\text{TL})]$	0.0000	1.0000

CHAPTER IV

FORAGING STRATEGIES OF FOUNDING BLACK AND WHITE
CRAPPIE POPULATIONS IN COPAN LAKE

INTRODUCTION

Black and white crappie (Pomoxis nigromaculatus and P. annularis, respectively) are among the most popular sportfish in the United States. Crappie populations often increase dramatically in new midwestern reservoirs. Growth rates are generally high the first few years after impoundment, but subsequently decline (Rutledge and Barron 1972). Decreased growth rates have been associated with decreased nutrient levels in aging reservoirs (Ball and Kilambi 1972), interspecific competition (Li et al. 1976), and severe intraspecific competition due to overcrowding (Burris 1956; Rutledge and Barron 1972). White crappie are often more abundant than black crappie in turbid, warmwater reservoirs and white crappie usually have higher growth rates than sympatric black crappie (Hall et al. 1954).

The differences of growth and survival of black and white crappie populations may be related to their feeding biology. Crappie feed primarily on zooplankton as fry, and begin feeding on aquatic insects at 120 mm, and switch to fish at 150 mm (Heidinger et al. 1985). White crappie are considered more piscivorous than black crappie and often

switch to piscivory at a smaller size. Ball and Kilambi (1972) found that foraging differences may have accounted for a decline of black crappie and an increase of white crappie in subsequent years following impoundment of Beaver reservoir. During the early period of impoundment, both species of crappie ate earthworms in winter and spring, and fed on gizzard shad (Dorosoma cepedianum) during the remainder of the seasons. White crappie apparently concentrated on shad even when earthworms were available. However, in the later impoundment period, black crappie ate benthic insects during spring, and fish in other seasons, whereas, white crappie ate shad year round.

Foraging behavior of black and white crappie may be specific for each population. Black crappie have been reported to be opportunistic; small crappie feed on zooplankton and invertebrates but many larger crappie switch to piscivory (Keast 1968; May and Thompson 1974; Ager 1975). Although large black crappie may be piscivorous, they do not necessarily stop feeding on invertebrates. Ager (1975) found that larger black crappie (> 239 mm TL) consumed more fish than did smaller black crappie, but there was no drop in the frequency of crustaceans and insects in their diet. The introduction of forage fish, however, significantly changed the forage behavior of black crappie in Lake Powell (May and Thompson 1974). Before the introduction of forage fish, Lake Powell black crappie fed on zooplankton and insects when they were small and added fish to their diets when they grew larger. After the introduction of threadfin shad (Dorosoma petenense), all size classes of black crappie fed on shad.

Increased growth rates and condition have been reported for black and white crappie that switched to piscivory in comparison to crappie

that remained nonpiscivorous (Ellison 1984; Heidinger et al. 1985). In addition, Ellison (1984) reported age related mortality in older black crappie that failed to increase daily ration by switching to piscivory at the appropriate size (> 200 mm TL). Apparently, the forage of older, nonpiscivorous crappie was not sufficient to supply the annual energy requirements, which resulted in an "energy trap" during summer. Nevertheless, some balanced midwestern crappie populations can be maintained on a diet of zooplankton and insects (Gablehouse 1984).

Not all crappie switch to piscivory at the same size (if at all). Keast (1968) and Heidinger et al. (1985) found feeding habits highly variable between and within crappie populations. Keast (1968) reasoned that even large black crappie could consume planktonic crustacea, possibly throughout life, because of a "specialized screen" of gill rakers (25-29) on the first arch. Tucker (1972) attributed the ability of young black crappie to maintain good condition throughout the growing season to gill raker count. However, crappie larger than 150 mm TL were less adapted to feeding on small zooplankton because large spaces developed between gill rakers that prevented the retention of small food organisms (Wright et al. 1983).

Clearly, the feeding biology of crappie is variable and may vary between individuals in a population. Such variation probably affects the growth rates of individuals and populations. Paloheimo and Dickie (1966) found relatively large variation in growth efficiencies among individuals and within individuals at different times. The effects of diet changes on growth, condition, and survival of crappie are poorly understood. Copan lake offers a unique opportunity to study the diets of sympatric founding crappie populations in a new reservoir.

The objective of this paper is to examine the affects of different foraging strategies on the growth, condition, and survival of founding populations of black and white crappie in Copan lake.

STUDY AREA

Our study took place in Copan Lake, located on the Little Caney River, approximately 3.7 km west of Copan, Washington County, Oklahoma. The drainage area above the dam site is approximately 1,308 square kilometers, and is characterized by rolling hills and oak hickory forests, interspersed with lowlands of tall grass prairie and numerous rock outcroppings. At conservation elevation (209.5 m - 216.4 m), the lake covers approximately 1,962 hectares and inundates 23.3 km of the Little Caney River. The lake has 55.6 km of shoreline and a shoreline development index of 3.1 (Oklahoma Water Resource Board 1984). Mean and maximum depths are 2.7 m and 10.6 m, respectively. Turbidity levels in the lake are high due to the relatively high concentrations of suspended solids in the river.

The area above the dam consists of the lake proper and a periodically isolated pond, Endacott's pond. The mean depth of this pond before inundation (1983) was 1.8 m and secchi readings averaged 1.2 m. The pond has historically stratified every year, and presently is the only site in Copan Lake that stratifies.

METHODS

Black and white crappie were collected with barrell net traps from the riprap on the south shore of Copan lake and Endacott's pond from March through November 1983 (Figure 1; Oakey 1986, p. 55). All crappie were weighed to the nearest gram and total length was determined to the nearest millimeter. Sex of all crappie was determined by visual inspection and otoliths (sagittae) were removed for age determination. Otolith radius was measured from the center of the kernel to the anterior tip of the otolith. Distance to each annulus was measured along the radius from the center of the kernel to the proximal margin of the opaque band (Pannella 1974). Fish condition was calculated as Relative Weight (W_r), where $W_r = W_s / W_t$. Standard Weights were derived by $\text{Log}_{10} (W_s) = -4.914 + 3.052 [\text{Log}_{10} (TL)]$ and $\text{Log}_{10} (W_s) = -5.102 + 3.112 [\text{Log}_{10} (TL)]$ for black and white crappie, respectively (Anderson 1980).

Stomach samples were removed in the field by making an anterior cut at the esophagus and a posterior cut at the intestine. Stomachs were placed in 10% formalin and returned to the laboratory, where each stomach was rinsed in water and stored in 70% isopropyl alcohol prior to analysis. Food items were enumerated and identified to the lowest taxonomic unit possible (Mearns 1985). Diet classifications were based on the presence of prey type in the stomach at the time of capture. For the purposes of this paper, it was assumed that gut contents at the time of capture were representative of the principal food items of an individual. Piscivores were classified as having only fish in their stomachs; insectivores were classified as having primarily aquatic

insects and zooplankton in their stomachs; omnivores were classified as having both prey types present in their stomachs.

Total length (mm) classifications were based at 2 size thresholds that are reported critical to crappie life history patterns. Growth and condition were examined in crappie above and below 150 mm total length, which is the length crappie reportedly switch from eating zooplankton and invertebrates to eating fish (Ball and Kilambi 1972). Length and condition were also compared in fish above and below 200 mm total length. Ellison (1984) reported increased mortality during summer of larger black crappie (> 200 mm) in small midwestern reservoirs. Daily ration in these fish declined during summer as a result of their failing to switch to piscivory, which resulted in increased mortality due to an "energy trap."

RESULTS

Stomach contents were analyzed for 40 black crappie and 45 white crappie from Copan lake basin (Table 1). Due to the small number of crappie captured from the founding populations, diets were not analyzed by season. Age 0, Age 3, and Age 4 black crappie were represented in our sample. The majority (81.1%) of insectivorous black crappie were Age 0, while an equal number (5) of Age 4 black crappie were either piscivorous or omnivorous. Six white crappie age groups were analyzed. An age related diet shift was more apparent in white crappie than in black crappie, due to the more even age distribution in the sample. White crappie insectivores were composed of younger age groups, while piscivorous and omnivorous samples were composed of increasingly older

age groups, respectively (Table 1).

Evidence of superior growth rates was present in all crappie samples that had piscivorous components in their diets (Table 2). Piscivorous white crappie had greater mean capture lengths and weights than omnivores or insectivores at all ages represented in the data (Table 3). White crappie Ages 2 and 3 had the fastest growth of all diet classifications in the study. Although back calculated lengths at annuli were greater in piscivorous white crappie, longevity was apparently greater in piscivorous black crappie and pooled omnivorous crappies, all of which were slower growing fish. The oldest fish in the study was an Age 5 omnivorous white crappie.

Slower growth was evident at all annuli of black and white crappie insectivores. Insectivorous white crappie appeared to grow faster than black crappie during the first 2 years (Table 2). However, the higher mean lengths in pooled ages were probably inflated by the superior growth that was evident in all Age 1 and 2 white crappie (Table 3). Mean lengths back calculated in Age 4 insectivores indicated that black crappie insectivores were larger at all annuli than white crappie insectivores.

Relative weights in pooled diet classifications were generally lower in Age 0 and Age 4 crappie, and highest in Age 2 crappie (Table 4). The incomplete sample prevents comparisons between species at all ages; however, Age 0 black crappie insectivores had higher relative weights than Age 0 white crappie insectivores. All ages of piscivores and omnivores had higher relative weights than equivalent age insectivores, with the exception of Age 2 white crappie insectivores (Table 4).

Insectivorous crappie were collected over a longer duration (May–November) than fish with other diet classes, yet adults had the lowest relative weights for each sample month (Table 5). Fall samples were composed almost entirely of insectivorous Age 0 crappies. Mean condition and percent increase between October and November (+ 41.1%) was higher in Age 0 black crappie. Omnivores were collected over a longer duration than piscivores, and had higher relative weights during summer months (Table 5). Percent increase in relative weights of omnivores was greater than for other diet classifications from spring to summer (+ 23.5%) and during summer months (+ 11.7%) (Table 6). In addition, relative weight increases were also evident for piscivorous white crappie during summer (+ 8.5%), and for adult black crappie insectivores during late spring and early summer (+ 9.1%).

DISCUSSION

Age related diet shifts were more apparent in white crappie than black crappie because of the larger white crappie sample. Although the majority of black crappie (74%) were Age 0 insectivores, the older age groups were highly variable in foraging strategies. The variation in stomach contents observed suggests that a choice for particular prey is operating between species and age groups in Copan lake.

White crappie are considered to be more piscivorous than black crappie, often switching to piscivory at a smaller size when sympatric with black crappie. The length classes at which this occurs range from 110–230 mm in a variety of systems, including natural systems where forage fish have not been stocked (Keast 1968; Ball and Kilambi 1972;

Ager 1975; Hanson and Quadri 1980; Heidinger et al. 1985) and systems where forage fish populations have been introduced (May and Thompson 1974; Li et al. 1976; Heidinger 1977). In addition, in many balanced crappie populations fish remain non-piscivorous throughout all age classes (Gablehouse 1984). Apparently, crappie that undergo a diet shift are responding to different arrays of factors in each body of water. The underlying assumption is, however, that crappie are similar throughout their range, and the differences in diet schedules and growth patterns are the result of diet decisions in the context of the characteristic features in each system.

Crappie are prolific and can quickly overpopulate small and medium size lakes. At higher densities, intraspecific competition may reduce available resources, resulting in overall poor growth and condition in a size class. Growth can be improved by reducing population number by means of harvest, mechanical methods, or introducing crappie predators (Rutledge and Barron 1972). Crappie may be reducing competition by partitioning resources through diet shifts. Burris (1956) attributed the differences between populations of fast and slow growing crappie to the growth and condition in crappie < 150 mm TL. Crappie that switch to piscivory at 100-150 mm TL may find relatively less competition and greater caloric return per feeding bout. In selecting one prey over another, individual crappie must meet dual requirements of growth incrementation and maintenance of good condition (relative weight). The results of prey selection will, over a period of time, determine if the individual survives annual stress periods and reaches the size necessary for sexual maturity.

Length and relative weight are closely interrelated, although, as responses to growth they are differentiated by time scale. Length increments occur over longer duration than fluctuations in relative weight. Changes in relative weight depend partially on body length, i.e., disproportionately greater increases in weight are necessary to increase relative weight as total length increases. Mosher (1984) found that a critical level of relative weight in white crappie must be reached in order for growth to result. However, as length increases, growth efficiency decreases, and more energy is converted to maintaining condition than to growth (Paloheimo and Dickie 1966). Similarly, Brown (1946) reported regular fluctuations in growth and appetite of individual trout that were related to deviations from an average condition factor. These fluctuations tended to restore condition to its' average value, although a time lag was present in the regulatory response.

Seasonal relative weight fluctuations in Copan lake crappie suggests varying successes with different foraging strategies. Each size class may have different growth efficiency with alternate prey, and different successes in meeting condition requirements. These differences in growth efficiencies were evident in the low relative weights of larger (Age 3-4) insectivores (Table 4). Keast (1968) reported that black crappie could be capable insectivores/ planktivores for much of their lives due to the high number (25-29) of gill rakers on the first gill arch. However, due to higher temperature extremes, crappie in the southern portion of their range may have metabolic costs that are too high to permit them to continue as insectivores beyond a critical size. Ellison (1984) suggested that midwestern reservoir

crappie (>200 mm) could not grow on a non-piscivorous diet, and that the low relative weights that resulted were responsible for temperature/age related mortality in summer.

Copan lake crappie that switched to piscivory presumably improved their growth efficiency (as indicated by growth rates and condition). Mearns (1985) reported that resources were not limiting to crappie during the first year (1983) of impoundment in Copan lake. The abundance of forage fish populations (primarily gizzard shad) in Copan lake are a critical factor in the continued success of piscivorous crappie. In Rend Lake, Illinois, Heidinger et al. (1985) reported significantly greater growth rates in piscivorous white crappie than sympatric non-piscivorous white crappie, yet piscivores were few in number and growth rates of fish in both diet classes were below regional averages due to limiting resources in the lake.

As Copan lake ages, there will probably be fluctuations in zooplankton, aquatic insect, and fish populations. Thus, individual crappie could potentially optimize their growth efficiency by being able to switch to a substitute prey. However, large piscivorous crappie may not be able to successfully switch to non-piscivorous prey (Ellison 1984). Rather than switching completely to piscivory, crappie that retain an insectivorous component in their diet may feed more continuously throughout the year than obligate piscivores. Copan lake omnivores had intermediate growth rates compared to piscivores and insectivores, yet they had the highest relative weights during summer. This increased summer weight may be attributed to a low energy budget associated with the intermediate length range when compared to larger piscivores of equivalent age (Paloheimo and Dickie 1966). Thus, the

relatively smaller omnivores (>200 mm) may more easily maintain good condition, which may insure greater survival during summer than obligate piscivores and insectivores. Such a trend is suggested by the age distribution of omnivores in Copan lake (Table 1).

Omnivorous crappie may have greater fitness than faster growing piscivorous crappie. Faster growing crappie reach reproductive size sooner and have greater gametic contribution per spawn than slower growing crappie; however, slower growing crappie may have greater cumulative fitness if they live longer and participate in more spawns than faster growing crappie. The best evolutionary stable strategy (ESS) for crappie populations would be for all individuals to be omnivorous. However, this strategy may be unlikely due to the variation of foraging behaviors within a population (Keast 1968).

A possible mechanism for a crappie population ESS is for individual crappie to be opportunistic and feed primarily on locally abundant prey. Diet shifts and associated changes in growth efficiencies would then be determined by environmental conditions, prey abundances, and individual energy budgets. Keast (1968) reported that black crappie fed on midwater Dipteran larvae until it became uneconomical, then switched to young-of-year yellow perch (Perca flavescens) that shared the same midwater habitat. Opportunistic foraging behavior was evident in Copan lake crappies, and was responsible for prey differences between piscivorous black and white crappie. Piscivorous black crappie were collected exclusively in Endacott's pond where they fed on Lepomis spp. and Pomoxis spp., whereas, piscivorous white crappie were collected exclusively from the open water adjacent to Copan dam and fed on gizzard shad (Dorosoma cepedianum) (Mearns 1985). Crappie populations had

slower growth rates and greater longevity in Endacott's pond than in Copan lake (Oahey 1986). In addition, the majority of omnivores (83%) in this study were collected from the pond. Apparently, conditions in the pond promoted omnivory, slower growth, and better energy budget management, whereas conditions in Copan lake promoted piscivory at the risk of growing large quickly and becoming vulnerable to energy deficits during summer.

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Table 1. Age distribution by diet classes of black and white crappie captured in Copan lake during 1983.

AGE	WHITE CRAPPIE			BLACK CRAPPIE		
	PISC	OMNI	INSECT	PISC	OMNI	INSECT
0	-	-	5 (33.3)	1 (14.3)	-	26 (81.3)
1	1 (5.6)	-	6 (40.0)	-	-	-
2	11 (61.1)	4 (33.3)	3 (20.0)	-	-	-
3	6 (33.3)	-	1 (6.7)	1 (14.3)	-	1 (3.1)
4	-	7 (58.3)	-	5 (71.4)	1 (100.0)	5 (15.6)
5	-	1 (8.3)	-	-	-	-
N	18	12	15	7	1	32

Table 2. Back calculated length at annuli for diet classes of black and white crappie captured in Copan lake during 1983.

CLASSES	N	ANNULI				
		1	2	3	4	5
<u>WHITE CRAPPIE</u>						
Piscivores	18	137	222	243		
Omnivores	12	98	174	189	206*	290**
Insectivores	15	110	174	178		
<u>BLACK CRAPPIE</u>						
Piscivores	7	100	169	200	217	
Insectivores	32	100	164	192		
<u>COMBINED SPECIES</u>						
Piscivores	25	128	208	212	217	
Omni/Pisc	38	117	196	201	212	290**
Insectivores	47	106	169	189		

* 7 White Crappie : 1 Black Crappie; ** Total length at capture.

Table 3. Mean capture length and weight and back calculated length at annuli for black (BC) and white crappie (WC) diet classes in Copan lake during 1983.

AGE	CLASS	Annuli				Mean TL	Mean WT
		1	2	3	4		
1	WC PISC	-				181	86
	OMNI	-				-	-
	INSECT	120				168	54
	BC PISC	-				-	-
	INSECT	-				-	-
2	WC PISC	145	226			254	252
	OMNI	94	184			201	117
	INSECT	103	182			235	203
	BC PISC	-	-			-	-
	INSECT	-	-			-	-
3	WC PISC	89	192	243		266	285
	OMNI	-	-	-		-	-
	INSECT	-	-	-		-	-
	BC PISC	-	-	-		-	-
	INSECT	-	-	-		-	-
4	WC PISC	-	-	-	-	-	-
	OMNI	100	168	189	206*	213	132
	INSECT	92	151	177	-	200	96
	BC PISC	100	169	200	217	230	185
	INSECT	100	164	192	-	214	126

* 7 White Crappie : 1 Black Crappie.

Table 4. Mean relative weight (standard error) at age for black and white crappie diet classes captured in Copan lake during 1983.

Diet Class	AGE					
	0	1	2	3	4	5
<u>SPECIES</u>						
WC PISC	-	1.03 (-)	1.04 (0.02)	1.00 (0.03)	-	-
WC OMNI	-	-	0.91 (0.06)	-	0.93 (0.03)	1.02 (-)
WC INSECT	0.57 (0.12)	0.80 (0.02)	0.97 (0.03)	-	0.84 (-)	-
BC PISC	0.72 (-)	-	-	0.88 (-)	0.95 (0.01)	-
BC INSECT	0.73 (0.02)	-	-	0.93 (-)	0.76 (0.03)	-
<u>POOLED SPECIES</u>						
ALL OMNI/PISC	0.72 (0.00)	1.02 (-)	1.00 (0.02)	0.98 (0.03)	0.93 (0.02)	1.02 (-)
ALL PISC	0.72 (-)	1.03 (-)	1.04 (0.02)	0.98 (0.02)	0.95 (0.01)	-
ALL OMNI	0.73 (-)	-	0.91 (0.06)	-	0.91* (0.03)	1.02 (-)
ALL INSECT	0.70 (0.03)	0.80 (0.02)	0.97 (0.03)	0.93 (-)	0.77 (0.03)	-

* 7 White Crappie : 1 Black Crappie.

Table 5. Monthly mean relative weight (Standard Error) for black and white crappie diet classes in Copan lake during 1983.

CLASS	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV
WC PISC	-	-	-	0.94 (-)	1.03 (0.02)	-	-	-	-
WC OMNI	0.93 (-)	-	0.85 (0.03)	0.99 (0.03)	1.05 (0.03)	-	-	-	-
WC INSECT	-	-	0.84 (-)	-	0.84 (0.03)	1.01 (-)	-	0.51 (-)	0.59 (0.15)
BC PISC	-	-	-	0.94 (0.02)	0.90 (-)	-	-	-	0.72 (-)
BC INSECT	-	-	0.76 (0.03)	0.93 (-)	-	0.71 (-)	-	0.56 (0.05)	0.79 (0.02)
OMNI/PISC	0.93 (-)	-	0.85 (0.03)	0.94 (0.02)	1.03 (0.01)	-	-	0.73 (-)	0.72 (-)
ALL PISC	-	-	-	0.94 (0.01)	1.02 (0.02)	-	-	-	0.72 (-)
ALL OMNI	0.93 (-)	-	0.85 (0.03)	0.94 (0.04)	1.05 (0.03)	-	-	0.73 (-)	-
ALL INSECT	-	-	0.77 (0.03)	0.93 (-)	0.84 (0.03)	0.86 (-)	-	0.55 (0.05)	0.75 (0.03)

Table 6. Percent increase in monthly mean relative weight in black and white crappie diet classes captured in Copan lake during 1983.

CLASSES	MAY - JUL	JUN - JUL	OCT - NOV
<u>SPECIES</u>			
WC PISC	-	+ 9.6 %	-
WC OMNI	+ 23.5 %	+ 6.1 %	-
WC INSECT	-	-	+ 15.7 %
BC PISC	-	-	-
BC INSECT	+ 22.4 %*	-	+ 41.1 %
<u>POOLED SPECIES</u>			
OMNI/PISC	+ 21.2 %	+ 9.6 %	-
ALL PISC	-	+ 8.5 %	-
ALL OMNI	+ 23.5 %	+ 11.7 %	-
ALL INSECT	+ 9.1 %	-	+ 36.4 %

* Increase from May to June.

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