SEASONAL GROWTH RATES OF FISHES IN RELATION TO CONDITIONS OF LAKE STRATIFICATION

Glen E. Gebhart and Robert C. Summerfelt*

Oklahoma Cooperative Fishery Research Unit†, Oklahoma State University, Stillwater, Oklahoma

The effect of lake stratification and hypolimnetic anoxia on growth of gizzard shad (*Dorosoma cepidianum*), white crappie (*Pomoxis annularis*), and freshwater drum (*Aplodinotus grunniens*) was studied in Arbuckle Lake, Oklahoma. The percentage of total available fish habitat of Arbuckle Lake was decreased by anoxic conditions to 72.9% in 1973, 82.7% in 1974, and 72.7% in 1975. In 6 of 8 species-age group comparisons, the growth rate was highest in 1974 when more usable fish habitat was available than in other years. In 18 species-age group comparisons of fish growth rates in the summer stratified period with growth of the same age fish in the destratified overwinter period, the growth was faster in the destratified interval 12 times and faster in the stratified interval 6 times. It appears that lake stratification and the resultant loss of fish habitat retarded the growth of the fish.

INTRODUCTION

The objective of this paper is to examine the effect of lake stratification on fish growth. Most lakes and reservoirs in the United States are stratified in the summer, and dissolved oxygen (DO) in the hypolimnion is often depleted. Anoxia restricts fish from continuous occupancy of the hypolimnion of stratified lakes and reservoirs (1, 2). During middle and late summer, stratification commonly causes compression of even warm-water fishes into the stratum of water between the anoxic hypolimnion and the warm epilimnion where surface temperatures often exceed their thermal preferences. The compression effect of stratification may be lethal to cold-water fishes in lakes lacking cold, well-oxygenated water (3).

In Red Haw Lake, Iowa, Mayhew (4) noted that at the time of severe stratification and hypolimnetic stagnation most scales of bluegills (*Lepomis macrochirus*) developed false annuli, and their growth was greatly retarded in relation to the prestratification rate. Mayhew suggested that stratification is a primary controlling factor in growth of bluegills. Seasonal periodicity of growth has been reported which shows a reduced rate in midsummer. This coincides with the onset of summer stratification and severe hypolimnetic oxygen depletion. Beckman (5) found that 85% of the expected growth of bluegills in a Michigan lake was completed between the end of April and mid-July. Sprugel (6) found bluegill growth in Iowa was most rapid in June and little growth evident after July. Anderson (7) also found bluegill growth to be most rapid in June with most growth occuring in May, June and July and the total growing season extending from 1 May to 31 October. Winter temperatures are generally too low for optimum growth of most warm-water fishes, but even normal summer surface temperatures can exceed the optimum range for warm-water fishes as ascertained from laboratory and field studies of the preferred temperatures of fish (8).

In spite of an abundant literature on growth of fish, Mayhew's report remains the only direct examination of fish growth in relation to conditions of stratification. Since stratification is a well known limnological phenomenon having substantial ecological importance (9), it is surprising to find the lack of direct investigations relating stratification to fish growth.

The inimical water quality conditions occurring during stratification (high ammonia, hydrogen sulfide, and carbon dioxide and low DO) and their concomitant effects on production of benthic invertebrates are likely to retard the growth rates of fishes. Laboratory experiments in which conditions in stratified lakes are simulated show diminished fish growth rates at low DO levels and high tempera-

*Present address: Department of Animal Ecology, Iowa State University, Ames, Iowa 50011.

†Cooperators are the Oklahoma Department of Wildlife Conservation, the Oklahoma State University Environmental Institute, and the U.S. Fish and Wildlife Service.

tures. Stewart et al. (10) reported that growth rates of juvenile largemouth bass (*Micropterus salmoides*) were markedly reduced at DO levels below air saturation. The growth of bass subjected to fluctuating oxygen concentrations was also markedly impaired. Andrews et al. (11) found a similar decreased growth of channel catfish (*Ictaluris punctuatus*) held at reduced DO levels. Andrews and Stickney (12) observed a reduction in the growth rate of channel catfish when the temperature was increased from 30 C to 34 C.

Arbuckle Lake, Oklahoma, is typically stratified from mid-May through September with anoxic conditions occurring below 5 to 8 m (13). In each of the three years of our study, 1973-75, Arbuckle Lake was thermally stratified by mid-May and DO depletion followed the onset of thermal stratification (2). The lake remained stratified until September or October depending on the weather and on the artificial mixing which was attempted in these years. During the summer of 1973, the Bureau of Reclamation attempted destratification by using a compressed air gun similar to one described by Bryan (14). During the summers of 1974 and 1975 an attempt was made by J. E. Garton of Oklahoma State University to destratify the reservoir using an axial flow pump, larger than but similar to one described by Quintero and Garton (15).

The present study describes seasonal growth rates of gizzard shad (*Dorosoma cepedianum*), white crappie (*Pomoxis annularis*), and freshwater drum (*Aplodinotus grunniens*) in Arbuckle Lake from collections made in 1973-75.

METHODS

In 1973, fish collections were made for 15 continuous weeks from 14 May to 24 August and an additional collection was obtained 18-21 October. In 1974, collections began on 10-14 March 1974 with the weekly collection scheduled beginning 20 May and continuing through 23 August. A final 1974 collection was made 9-13 September to monitor growth and distribution of fish after the lake had destratified. In 1975, weekly collections began on 12 May and continued through 22 August; and a collection was made 22-26 September after the lake had destratified. The collection of fish at the beginning and end of the stratified period allowed for the measurement of growth during both the stratified and destratified periods.

Fish were sampled with experimental gill nets, 3.05 m deep by 45.73 m long, divided into six 7.62-m panels with mesh sizes (bar measure) of 1.27, 2.54, 3.81, 5.08, 6.35, and 7.62 cm. Nets were set in a horizontal position at depths of 0-5, 5-10, 10-15, and 15-20 m. The vertical distribution of fish, described from these net catches, showed the expected movement of fish out of the hypolimnion when it became anoxic (2). Weights from fish of the same age, collected at four sites, were pooled to obtain a mean weight for each period. Fish were weighed and measured, and scales were taken to determine the age of the fish by annular counts. Temperature and DO measurements were taken weekly at 1-m intervals at all sites with a DO probe and thermistor.

Instantaneous growth rates (G) were calculated for the stratified summer and the destratified overwintering periods for all age groups of the three species that were adequately represented in the sample. Values of G were calculated by the equation of Chapman (16). The growth rates and mean weight gains (*g*) were calculated from samples collected at the start and end of the stratified period.

RESULTS

In 7 of 8 destratified vs. stratified comparisons of G and *g* for gizzard shad, larger values were obtained in the destratified period (Table 1). Only in 1973, for age IV gizzard shad, were the G and *g* values larger in the stratified period. The results of t-tests showed significantly higher growth rates ($P < .05$) and mean weight gains ($P < .01$) of all age groups of gizzard shad combined in the destratified period than in the summer stratified period.

The mean weight gains for age group I white crappie were higher in the destratified period than in the stratified period in 2 of 3 yearly comparisons (Table 2). The G values for age I white crappie were higher in the stratified period in 2 of 3 years. Age II white crappie had larger absolute growth in the stratified interval in 2 of the 3 years, but higher growth rates in the destratified interval in 2 of 3 years.

TABLE 1. *Comparison of growth rates (G) and mean weight gain for gizzard shad for summer (stratified) and winter (destratified) intervals, 1973-76.*

Median collection date	Interval	Days	Age group III Growth rate	Age group III Weight gain (g)	Age group III Sample size	Age group IV Growth rate	Age group IV Weight gain (g)	Age group IV Sample size	Age group V Growth rate	Age group V Weight gain (g)	Age group V Sample size
5-23-73											
10-19-73	summer	149.0	−0.17	−2.0	237	1.33	29.2	88	−0.13	−3.8	21
5-29-74	winter	221.5	1.58	31.1	92	0.53	20.5	46	0.33	14.5	26
9-11-74	summer	105.5	0.98	8.7	87	1.40	16.8	10	−0.79	−14.7	25
5-21-75	winter	252.0	1.20	31.4	47	1.69	65.1	114	—	—	—
9-24-75	summer	128.0	0.71	7.2	48	1.13	18.8	39	−1.72	−37.0	120
5-19-76	winter	236.5	2.96	83.8	46	1.24	47.6	63	1.61	69.9	78

TABLE 2. *Comparison of growth rates (G) and mean weight gain for white crappie for summer (stratified) and winter (destratified) intervals, 1973-76.*

Median collection date	Interval	Days	Age group I Growth rate	Age group I Weight gain (g)	Age group I Sample size	Age group II Growth rate	Age group II Weight gain (g)	Age group II Sample size	Age group III Growth rate	Age group III Weight gain (g)	Age group III Sample size
5-23-73											
10-19-73	summer	149.0	6.30	21.7	6	1.42	30.2	50	0.08	2.9	26
5-29-74	winter	221.5	0.90[a]	19.7	19	2.06	102.0	5	—	—	—
9-11-74	summer	105.5	8.25	42.8	102	6.37	142.3	16	2.39[b]	74.2	6
5-21-75	winter	252.0	4.39	149.0	78	0.64	51.7	11	—	—	—
9-24-75	summer	128.0	0.12	0.8	167	−0.90	−24.4	56	1.54[c]	34.3	5
5-19-76	winter	236.5	1.35	19.4	255	−0.82	−35.0	45	—	—	—

[a]Interval was 241.5 days in length.
[b]Interval was 85.5 days in length.
[c]Interval was 62.0 days in length.

Since the mean weight gain and growth rate of age III white crappie was not represented in the destratified period, no seasonal comparison could be made. There was no significant difference (P > .05) in weight gain (*g*) or growth rate (G) between the stratified and destratified periods for all age groups of white crappie combined.

The mean weight gain of age II freshwater drum was higher in the destratified periods in 2 of 3 years but the growth rate was higher in the stratified interval in 2 of 3 years (Table 3). The one measure of weight gain and growth rate in the destratified period for age III fish was larger than any of the growth rates during the stratified period. The t-test indicated a lack of any significant difference (P > .05) in weight gain or growth rates for freshwater drum between the stratified and destratified periods.

DISCUSSION

The generally held view on seasonal variation in fish growth in North America is that growth is fastest in the spring and early summer, slows in the late summer and fall, and virtually stops in the winter (7). The stratified period in Arbuckle Lake includes the entire summer while the destratified period lasts the rest of the year. In 24 species-age group comparisons of fish growth in Arbuckle Lake, the growth rate was greater 12 times in the destratified period and 6 times in the stratified period (insufficient data for 6 other comparisons). The destratified period includes the long winter interval when growth is expected to be low because of low temperatures. Omission of the long winter interval would show an even larger differential between the balance of the destratified period versus the stratified period. The reason why the growth rate is higher in the destratified period, especially for gizzard shad, may be an increase in the available bottom feeding area during the destratified period.

Since the growth rates were mean population growth rates, they may be biased by selective mortalities. Tesch (17) generalized that the population growth is usually lower than the individual fish growth rate for fish older than age I or II because of selective mortality. In the present study, negative growth occurred in some age classes, mostly during the stratified interval. This negative growth should not reflect a bias from selective mortality of the fastest-growing fish, since selective mortality should have occurred throughout the year. Therefore, we do not believe that the frequency of faster growth in species-age group comparisons between the destratified and stratified intervals can be attributed to bias from selective mortality.

The comparison of the growth rates of fish of the same species and age over the three years of study for the stratified period indicates that 1974 was the best year for fish growth. In 6 out of 8 species-age group comparisons, the growth rate was highest in 1974. Vertical depth distribution of fish in Arbuckle Lake indicated that fish were generally absent from water with less than

TABLE 3. *Comparison of growth rates (G) and mean weight gain for freshwater drum for summer (stratified) and winter (destratified) intervals, 1973-76.*

Median collection date	Interval	Days	Age group II Growth rate	Age group II Weight gain (*g*)	Age group II Sample size	Age group III Growth rate	Age group III Weight gain (*g*)	Age group III Sample size
5-23-73								
	summer	149.0	−1.29	−34.7	33	−1.52	−59.9	37
10-19-73								
	winter	221.5	1.44	61.1	48	0.65	36.6	19
5-29-74								
	summer	105.5	0.75	14.7	37	0.63	15.4	51
9-11-74								
	winter	252.0	0.71	38.2	77	—	—	—
5-21-75								
	summer	128.0	5.26	99.0	32	0.16	4.8	71
9-24-75								
	winter	236.5	−0.01	−0.7	62	—	—	—
5-19-76								

2 mg/*l* DO (2). The percentage of the total volume of lake water with less than 2 mg/*l* DO was as high as 48% in 1973, 39% in 1974, and 59% in 1975. The average volume of stored water containing more than 2 mg/*l* DO during the 163-day interval from 11 May to 20 October (during a typical year this interval should encompass most of the summer stratification period) was 72.9% in 1973, 82.7% in 1974, and 72.7% in 1975. There was little difference between 1973 and 1975, but the percentage in both these years differed substantially from that in 1974 (2).

This variation in available habitat was reflected in yearly variations in the growth rate of fish during the stratified period. The fastest growth of age group III and IV gizzard shad and the second fastest growth for age V shad were observed in 1974 (Table 1). All three age groups of white crappies experienced greater growth in 1974 than in the other years (Table 2). The growth of age group II freshwater drum in 1974 was second to growth in 1975 but the maximum growth rate of age III drums was in 1974 (Table 3).

It appears that the seasonal cycle of stratification reduces fish growth by reducing the amount of fish habitat in a lake. The growth of fishes appears to slow down when lakes develop an anoxic hypolimnion due to stratification. Fish forced out of the cooler waters of the hypolimnion must remain in the transitional area of the thermocline if epilimnetic temperatures are thermally oppressive; or if they tolerate the higher temperatures of the epilimnion, food consumption must be increased to maintain a higher basal metabolism. It seems that the food supply is generally inadequate to provide for their basal metabolism needs, since many age groups lose weight during the summer.

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