

## ABSTRACT

OZEN, OZCAN. Population Dynamics of Largemouth Bass in Lucchetti Reservoir, Puerto Rico. (Under the direction of Dr. Richard L. Noble)

Juvenile largemouth bass Micropterus salmoides in Lucchetti Reservoir have a high mean daily growth rate (0.70 mm/d) and range (0.35 and 1.33 mm/d), and show an extended spawning period (January-June), making population monitoring demanding. A hand-held electrofisher effectively sampled age-0 largemouth bass within the size range 50-150 mm total length (TL). Mean catch-per-unit-effort (fish/h, CPUE) of age-0 fish between April and September was a reliable estimator of the year-class strength, and explained 83% ( $P < 0.05$ ) of the variation of age-1 CPUE data obtained with a conventional boom-mounted electrofisher the next year in February. Based on calculations using daily growth rates and spawning period, year-class strength can be reliably measured by with a hand-held electrofisher between April and September with a time interval of 76-d between the samplings. Hatch date distributions, estimated from sagittal otoliths, indicated that the major spawning of largemouth bass started in January, soon after photoperiod began to increase. The time lag between increasing day length and the start of spawning, however, was dictated by water level fluctuation. When water level began to decrease during the spawning season, spawning was interrupted but resumed when water level started to rise again resulting in bimodal hatch-date distributions. Because of its tropical geographic location, water temperature is relatively constant during the initiation of spawning and varies between 24-30°C annually. Water level increase could be used to stimulate largemouth bass spawning in systems where water temperature is suitable. CPUE of age-1 largemouth bass was positively correlated with water levels of the previous year and negatively correlated with water level

fluctuations. The effect of these hydrological variables on largemouth bass recruitment appeared to be exponential rather than linear. Age-1 largemouth bass comprise the majority of the fishable stock in Lucchetti Reservoir, and the stock is typically below carrying capacity. Thus, the potential exists to adopt a water level management plan during the spawning period of largemouth bass to ensure successful largemouth bass recruitment into the next year's fishable stock.

**POPULATION DYNAMICS OF LARGEMOUTH BASS IN  
LUCCHETTI RESERVOIR, PUERTO RICO**

by

**OZCAN OZEN**

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**APPROVED BY:**

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Kenneth H. Pollock

---

James A. Rice

---

Joseph E. Hightower

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Richard L. Noble  
Chair of  
Advisory Committee

## **BIOGRAPHY**

Ozcan Ozen was born in Solingen, Germany, on June 21, 1971. He graduated from the high school Muharrem Hasbi Koray Lisesi in Balikesir, Turkey, in 1989. He received his Bachelor of Science in Fisheries from Faculty of Fisheries, Ege University, Turkey, in September 1993. He received his Masters of Science in Fisheries from Auburn University in 1997. His thesis was entitled “Crappie Population Characteristics in Six Alabama Reservoirs”. He then entered the Department of Zoology at North Carolina State University in 1997 for his Ph.D. and upgraded his research interest from “Crappie” to “Bass” in 1998 when he joined the project under the direction of Richard L. Noble.

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## PREFACE

The life history of largemouth bass, Micropterus salmoides, native to the United States, has been investigated in many aspects including growth, mortality, spawning, and recruitment. However little was known about the population dynamics of this species when introduced to tropical regions. The project, undertaken in Puerto Rico by North Carolina State University in 1992 under the direction of Richard L. Noble, has been one of the most comprehensive to provide insight into largemouth bass life history in tropical reservoirs.

This long-term study over the years 1992-2001 provided information about length, weight, age, and relative abundance of juvenile largemouth bass in Lucchetti Reservoir. Moreover, adult largemouth bass population estimates were available for eight years. Data on habitat structure, limnological and hydrological variables were also available.

I joined this project in 1998 and was given the opportunity to utilize this large historical database. The data analyzed in the following chapters were primarily collected by several different personnel. Whereas only a minimal number of samples had been processed for juvenile ages of largemouth bass, I undertook the task of ageing all available otoliths to determine hatch periodicity and growth rates.

In the first chapter, I investigated the sampling method of juvenile largemouth bass that were collected with a hand-held electrofisher. This gear is relatively new for the use of largemouth bass sampling and not many studies (only one besides this, to my knowledge) investigated the efficiency of this gear. Previous reports indicated that catch-

per-unit-effort data were very erratic and that CPUE data may not be reliable. My primary goal was to determine if sampling with the hand-held electrofisher would allow prediction of year-class strength of largemouth bass.

In Chapter II, I examined the spawning periodicity of largemouth bass. This species spawns in early spring in temperate regions, and photoperiod and temperature are strong environmental cues. Previous reports suggested that largemouth bass spawning cycle was related to water level fluctuation. Using daily ring counts from otoliths, I determined the hatching periodicity of largemouth bass. I investigated the relation between water level fluctuation and spawning periodicity of largemouth bass in this tropical reservoir, where the water temperature varies very little throughout the year compared to temperate regions, but water level fluctuates markedly over the spawning season and the year.

In Chapter III, I assessed the effects of the hydrological regime on largemouth bass recruitment in Lucchetti Reservoir. Puerto Rico frequently encounters tropical storms and hurricanes, and reservoir water levels are dropped in preparation for the hurricane season. Previous studies provided conflicting results about the impact of water level fluctuations. Lucchetti Reservoir water level fluctuated as much as 17 m and therefore it should affect the littoral-zone dependent juvenile largemouth bass, and hence affect recruitment.

Finally, Chapter IV is a synthesis of the results of this study. Some management implications for largemouth bass populations and some future research needs are also discussed.

## **CHAPTER I**

# **Assessing Juvenile Year-Class Strength of Fast-Growing Largemouth Bass in a Tropical Reservoir**

## **Abstract**

Age-0 largemouth bass, Micropterus salmoides, were collected every 3 weeks from 1992-1994, every 6 weeks from 1995-1998, and about every 15 weeks from 1999-2000 using a hand-held electrofisher in Lucchetti Reservoir, Puerto Rico. The extended hatching period (January to June) and the high mean rate (0.70 mm/d) and wide range (0.35 and 1.33 mm/d) of juvenile daily growth, demands high sampling effort as age-0 largemouth bass keep recruiting into the sampling gear from February to September. To assess if the hand-held electrofisher catch-per-unit-effort (CPUE, fish/h) of age-0 largemouth bass was a reliable estimator of the year-class strength, I regressed age-1 largemouth bass CPUE, obtained with a conventional boom-mounted electrofisher between 1994 and 2001, on the CPUE of age-0 (< 150 mm) fish. Simple linear regression analyses suggested that 83% ( $P < 0.01$ ;  $N = 7$ ) of the age-1 CPUE variation could be explained with age-0 mean CPUE calculated from April to September. A 6-week sampling cycle between April-September also produced reliable estimates of year-class strength ( $P < 0.05$ ). Although a significant relationship ( $P < 0.05$ ) was obtained for the 15-week cycle with only two times sampling per year, it was sensitive to the sampling day. Based on calculations using daily growth rates and spawning period, sampling at least three times, starting in April with 76-d interval was necessary to obtain a representative sample of year-class strength with the hand-held electrofisher. Early year-class strength variation of largemouth bass can be detected efficiently with relatively minimal effort with the hand-held electrofisher, thereby allowing early evaluation of management options.

## **Introduction**

One of the most important parameters for fisheries managers is the abundance of the fish population. Management decisions for either game or commercial fish species based upon biased measurements or indices of population size may result in either the collapse of the fish population, due to overestimation, or underutilization of the fish resource by humans, due to underestimation. Catch-per-unit effort (CPUE) has been widely used as an index of the population size in fisheries (Ney 1993). Bias associated with this estimate is mainly due to gear bias, which includes failure to represent the population in proportion for different fish sizes. Fish at particular length may not be in the area sampled, or even if present, differences in capture probability for different sizes may occur.

Several studies have shown that electrofishing CPUE of adult largemouth bass was highly correlated with largemouth bass population density (Hall 1986; Coble 1992; McInerny and Degan 1993; Edwards et al. 1997), indicating that electrofishing could be used for largemouth bass relative abundance estimation. These and other studies have led to standardization of procedures for indexing of adult largemouth bass abundance with traditional boom-mounted electrofishing gear (Noble in press). Even if accurate, adult density indices have limitation for some management applications (e.g., supplemental stocking or temporary fishing limitations) because decisions have to be made well in advance for such management approaches. Therefore, population density indices are needed at early life stages.

A variety of methods, such as shoreline seining, littoral and cove rotenoning, and boom-mounted electrofishing have been used for sampling juvenile largemouth bass

populations (Kramer and Smith 1960; Miller and Kramer 1971; Hightower et al. 1982; Ludsin and DeVries 1997; Pine et al. 2000). However, each of these methods has some disadvantage in terms of bias, precision, applicability, or feasibility. Seining may be relatively less efficient for larger fish (>80 mm total length, TL) compared to boom-mounted electrofishing gear (Pine et al. 2000). Hightower et al. (1982) reported that shoreline rotenone was not an efficient tool to sample largemouth bass as they collected on average only 2.5 young-of-the-year per man-day. In addition, rotenone use may not be feasible in all water bodies due to environmental concerns. The boom-mounted electrofisher, on the other hand, does not sample small largemouth bass (< 130 mm) effectively enough to evaluate some early life processes of largemouth bass (Jackson and Noble 1995).

Jackson and Noble (1995) described a new method for collecting young-of-the-year largemouth bass by using a hand-held electrofisher. This gear has been used in some studies in recent years (Irwin et al. 1997; Phillips et al. 1997; Sammons et al. 1999; Jackson and Noble 2000) in temperate reservoirs where juvenile largemouth bass spawning occurs over two months (April-May; Phillips et al 1997; Sammons et al 1999). Mean daily growth rates of juvenile largemouth bass for these systems were less than 0.75 mm/d (Sammons et al 1999; Jackson and Noble 2000). The short spawning period accompanied by slow growth rates allow the entire cohort to be sampled and followed through the first growing season (Jackson and Noble 1995).

In Lucchetti Reservoir, Puerto Rico, largemouth bass spawning season extends from January to June (Ozen and Noble in press) and largemouth bass grow relatively fast (0.63-1.50 mm/d), according to micro-tagging studies (Churchill et al. 1995, Neal et al. in

press). Based on these statistics, the size distribution of juvenile largemouth bass in Lucchetti Reservoir could encompass over 150 mm, a size range for which no gear has been shown to sample effectively. Therefore, monitoring the young-of-the-year largemouth bass population dynamics in Lucchetti Reservoir requires frequent sampling events and a prolonged sampling period compared to temperate regions.

The main purpose of this study was to investigate if the hand-held electrofisher could be used as a sampling gear to measure year-class strength of young largemouth bass when there is a prolonged spawning period and fast growth rate. My approach was to relate age-0 CPUE to age-1 CPUE data from the following spring. Temporal frequency and periodicity of the sampling protocol were evaluated to provide a feasible sampling strategy while minimizing the sampling requirements. In addition, individual variations in juvenile largemouth bass daily growth rates were evaluated for refinement of the above stated objectives, related to the sampling frequency and periodicity.

## **Methods**

Lucchetti Reservoir is a 108-ha impoundment in southwestern Puerto Rico. When completed in 1952, the maximum water depth at spill level of 173.8 m above sea level was 54.3 m. Neal et al. (1999), however, reported the maximum depth that was encountered as 22.2 m in 1999. The watershed, largely agricultural land, is about 45.1 km<sup>2</sup> with a mean annual precipitation of 198 cm. The reservoir serves mainly as an irrigation and water supply and is therefore subject to high water level fluctuations (up to 17 m). The shoreline is defined as steep sloping with a mixture of rock and clay. In Lucchetti Reservoir the water temperature ranges between 24-30°C and conductivity

ranges between 200-350  $\mu\text{S}/\text{cm}$  (Churchill et al. 1995), which is in the optimum range for electrofishing efficiency (Reynold 1996). Secchi disk transparency varies between 0.8 and 2.0 m.

The species composition includes largemouth bass, redbreast tilapia Tilapia rendalli, Mozambique tilapia Tilapia mossambica, bluegill Lepomis macrochirus, threadfin shad Dorosoma petenense, channel catfish Ictalurus punctatus, and marbled bullhead Ameiurus nebulosus marmoratus. About 81% of the boat anglers target largemouth bass as their preferred catch (Corujo Flores 1991). Shoreline fishing access and a paved access ramp are provided.

Age-0 largemouth bass were sampled with a hand-held electrofisher (Jackson and Noble 1995) during nighttime using non-pulsed 260-V DC. Five representative electrofishing transect sites were chosen with regard to the most common shoreline habitat types in the reservoir; sites were dispersed around the shoreline so that all were at least partially accessible during periods of low water levels. The electrofishing sampling was not exclusively targeted for largemouth bass and continued until 75 fish, excluding threadfin shad, were collected. If in the random sampling fewer than 10 juvenile largemouth bass were collected, then electrofishing continued until the 10 age-0 largemouth bass were collected or 30 minutes of shocking time for the site had elapsed.

Age-0 largemouth bass were collected in 1992-1994 at 3-week, in 1995-1999 at 6-week, and in 1999-2000 at about 15-week intervals unless weather conditions or water levels interfered. In 1995, the age-0 largemouth bass sampling did not commence until July 20. Because largemouth bass start spawning between January and February, most largemouth bass would have outgrown the gear's effective sampling range by the end of

July (Jackson and Noble 1995). Therefore, I did not include the 1995 juvenile data in my analyses.

Sagittal otoliths removed from largemouth bass 100 mm TL and smaller (referred as juvenile hereafter) were processed for daily ring readings for the years between 1992-1994 and 1996-1999. Daily ring counts of sagittal sections of largemouth bass otoliths have been shown to be relatively unbiased and precise (i.e., deviation of < 5 d from true age) for the first 100 days after swim-up (Miller and Storck 1982). Daily growth rate for Lucchetti Reservoir largemouth bass was previously estimated using microtags as about 1 mm/d (Churchill et al. 1995). Therefore, I limited processing of otoliths to largemouth bass < 100 mm TL. Otolith processing procedures were described by Ozen and Noble (in press). Daily growth rates (mm/d) for juvenile largemouth bass were calculated from total length minus 6 mm (length at swim up) divided by daily ring counts (age since swim-up; Ludsin and DeVries 1997).

Adult largemouth bass CPUE data were obtained from mark-recapture population estimate studies conducted during 1994-2001 (Ashe et al 1998; Neal et al. 2001). For those studies, adult largemouth bass were collected lake-wide each year with a boom-mounted electrofishing boat using 240 V pulsed-DC, usually during January and February. CPUE data available for the recapture period, usually February, were utilized to index year-class strength at age-1.

Ageing of adult largemouth bass in Lucchetti Reservoir was not possible because of indiscernible otoliths rings (Neal et al. 1997). To obtain year-class strength estimations for age-1, length-frequency distributions were used to separate this cohort from the older cohorts using the Bhattacharya method (Sparre and Venema 1998). This

method was applied only to the recapture sampling periods when age-1 fish were larger than they were at mark sampling, and presumably equally susceptible to electrofishing over their length range. Catch-per-unit-effort was obtained by dividing the age-1 frequency by actual electrofishing time, which ranged from 5.4-7.8 h.

To evaluate the hand-held electrofisher catch rates for predicting year-class strength, CPUE of age-1 fish was linearly regressed against age-0 mean CPUE of largemouth bass (<150 mm TL). This analysis used seven data points; it was not possible to use the 1992 hand-held electrofisher CPUE data as a year-class strength indicator because there were no corresponding age-1 data.

Different sampling frequencies were also analyzed with linear regression by excluding sampling occasions of age-0 largemouth bass. For 1993 and 1994 sampling occasions were excluded in the analyses so that the time interval between sampling would be 6-week. A second analysis was performed by using the eliminated sampling dates and excluding the utilized data from the previous analysis. The same strategy was deployed for the years 1993-1994 and 1996-1998 for investigating the relationship between age-0 and age-1 CPUE for a 15-week interval.

Sampling scheduling (period and frequency) for age-0 largemouth bass was estimated by using the slowest and fastest daily growth rates. Parameters such as the spawning period and the size range that the hand-held electrofisher effectively sampled largemouth bass were incorporated for this estimate.

## Results

Using the hand-held electrofisher, 2,387 largemouth bass smaller than 150 mm TL (age-0) were collected in 57 surveys from 1992-1994 and 1996-2000. Distribution of CPUE varied annually in response to reproductive periodicity (Ozen and Noble in press) and sampling frequency (Figure 1). Mean annual CPUE of age-0 largemouth bass ranged from 17.0 to 64.0 fish/h. Monthly mean CPUE (averaged over years) were greater than 38 fish/h for the months between May-August (Figure 2). In January, February, and December, mean CPUEs were less than 1 fish/h. Annual peak catch rates of age-0 fish varied about 2.2-fold (1996 vs. 1999; Figure 1) and were observed between May and August.

Age-0 fish started to recruit into the hand-held electrofishing gear as small as 23 mm TL and some fish larger than 400 mm TL (age-1+) have also been captured in some sampling occasions. A pooled length frequency distribution for all sampling surveys suggests largemouth bass fully recruit to the gear at about 70 mm TL (Figure 3). Similar length-catch frequency distributions were observed from the 3-week (1992-1994) and 6-week (1996-1998) sampling period intervals. The 15-week (1999-2000) sampling period, however, exhibited a different frequency pattern than the other sampling period intervals.

Based on 792 otolith readings, juvenile largemouth bass mean daily growth rate was 0.70 mm/d (SD = 0.162) for the years 1992-1994 and 1996-1999 (Figure 4). The range for the growth rate was relatively large (0.35-1.33 mm/d). Most of the fish (94.4%), however, had estimated growth rates between 0.40-1.00 m/d. The growth distribution was significantly different ( $P < 0.01$ ) from normal distribution (Kolmogorov-

Smirnov test;  $D = 0.055$ ) and skewed to the right (Skewness = 0.485; Kurtosis = -0.0713).

Mean daily growth rate was probably underestimated because I only used fish smaller than 100 mm TL and thus the fast-growing individuals were represented less frequently in my sample. On May 2, 1999, because of the short 1999 spawning period (Ozen and Noble in press), a representative length range was captured where fish were between 40-126 mm TL with one sampling survey. The mean growth rate for the juvenile fish for that cohort was 0.62 mm/d. However, five individual fish (102-126 mm) were also aged from daily rings (not included in the daily growth distribution of fish <100 mm TL in Figure 4), and had a mean daily growth rate of 1.09 mm/d. Thus, the correct estimated mean daily growth rate should be 0.71 mm since swim up for the 1999 cohort.

Growth rate was also estimated for the 1999 cohort using mean lengths of age-0 and age-1 fish. A mean length increase of 222 mm was observed over a 286-day period resulting in a mean daily growth rate of 0.78 mm/d, based on the assumption that no differential mortality occurred.

Estimated age-1 CPUE was highest in 1997 with 76.4 fish/h and lowest in 2000 with 24.2 fish/h (Figure 5). In some years bimodal frequency distributions occurred for the age-1 largemouth bass (i.e., 1999 and 2001). The smaller fish modes from these bimodal cohorts had the smallest fish (~170 mm TL) compared to the other years. For those years the Bhattacharya method was applied to the second mode because it was evident from the previous years' age-1 length frequency distribution that these fish were not age-2 (Figure 5). In addition, Ozen and Noble (2000) estimated from microtagged

fish data using the von Bertalanffy growth equation that the mean TL of largemouth bass for this population should be about 275 mm for age-1 and 373 mm for age-2. In fact, those second modes of age-1 in 1999 and 2001 had estimated mean lengths of 280 and 275 mm TL, respectively, supporting earlier calculations of growth rates. The first modes on the other hand were 225 mm TL in 1999 and 212 mm TL in 2001. These fish probably were late-hatched fish (i.e., June) that did not grow a full year, but were still age-1 fish based on calendar year. Ozen and Noble (in press) found that the 1999 largemouth bass cohort had a very short hatching period compared to the other years. In fact, the age-1 length distribution in 2000 was the only unimodal distribution with an estimated mean TL of 294 mm. This is the greatest estimated mean TL compared to the other age-1 mean TLs, because late hatched fish (smaller at age-1 calendar year) did not affect the mean estimation of length, and probably as a result of the small cohort size that resulted in a high growth rate.

Simple linear regressions between age-1 CPUE and mean age-0 CPUE were highly significant, depending on the age-0 sampling period (Table 1). The highest correlation was for the period of June-December ( $R^2 = 0.90$ ;  $P = 0.001$ ). Using the catch rates between May-August (the period for which the monthly means were relatively high and the peak catch rates were observed) also resulted in a significant relationship ( $R^2 = 0.76$ ;  $P = 0.011$ ). A more conservative period that encompassed the period of available age-0 fish less than 150 mm, April-September, explained 83% ( $P = 0.004$ ) of the variation in age-1 CPUEs (Figure 6; Table 1). The data were generally aligned with a regression slope close to 1; with the exception of the 1998 cohort, age-1 CPUE was predicted very close with the mean CPUE of age-0 (Figure 6).

I chose to calculate the mean CPUE for age-0 largemouth bass smaller than 150 mm TL for the hand-held sampling unit based on the findings of Jackson and Noble (1995) that the hand-held electrofisher was not as effective as the boom-mounted electrofisher over 150 mm. However, by using fish smaller than 140 mm TL for the April-September period, the variation explained by age-0 mean CPUE of age-1 CPUE was 87% ( $\underline{P} = 0.002$ ) compared to the 83% ( $\underline{P} = 0.004$ ) obtained using fish smaller than 150 mm TL (Table 2). In addition, assuming the effective range of the hand-held electrofisher was between 50 and 150 mm TL (Figure 3) I performed the regression analyses for this length range of age-0 fish. The results were still statistically significant ( $R^2 = 0.85$ ;  $\underline{P} = 0.003$ ) when only age-0 CPUE of fish between 50-150 mm TL were included in the analyses for the period of April-September.

For the period of April-September, I evaluated if the relationship between age-0 and age-1 CPUEs would be still significant if sampling had been performed at 6-week intervals in 1993 and 1994. Examination of CPUE relationships by excluding the data of alternate sampling dates from the 3-week sampling cycle (1993-1994) still resulted in significant relations ( $\underline{P} < 0.05$ ). The relationship was significant whether calculated by excluding the first or the second and alternate sampling dates (Figure 7 a-b).

I also evaluated whether age-0 mean CPUE predicted age-1 CPUE if sampling had been conducted about every 15 weeks between April-September in 1993-1994 and 1996-1998. Data from sampling at a 15-week cycle resulted in a significant relationship when sampling cycle was begun with the first date ( $R^2 = 0.70$ ;  $\underline{P} = 0.014$ ; Figure 7 c). But this relationship was not significant ( $\underline{P} = 0.169$ ) if the 15-week sampling cycle started

with the second sampling occasion in April and performed at about 15-week intervals (Figure 7 d).

Sampling schedule and periodicity were estimated based on maximum hatching period (January-June) and maximum (1.33 mm/d; Figure 8, black lines) and minimum (0.35 mm/d; Figure 8, grey lines) daily growth rates of juvenile largemouth bass (<100 mm TL). Assuming that age-0 largemouth bass begin hatching as early as January 1 and have relatively high susceptibility to the hand-held electrofisher in the range of 50-150 mm TL (Figure 3), the latest date to start sampling would be April 19; the fast growing fish (1.33 mm/d) that hatched very early in the season (January 1) would outgrow the maximum susceptibility limit (150 mm TL) after that date (Figure 8). The subsequent sampling should be on July 4 (76 day interval), because fish that were 49 mm on the previous sampling date and were not as effectively sampled would again outgrow the 150 mm TL limit on July 4. A third sampling on September 18 would also be necessary to catch fish that were not sampled on the July 4 sample.

To fully encompass the year class, an additional (4<sup>th</sup>) sample would be required on October 18. Some of the slow growing fish (0.35 mm/d) that hatched as late as June 30 would not be represented in the September 18 sampling. However the majority of fish (94%) have a growth rate between 0.4 and 1.0 mm/d, and largemouth bass other than the 50-150 mm range are somewhat susceptible to the gear. Thus, use of this last (4<sup>th</sup>) sample would be somewhat conservative; whereas the late hatched slow growing fish were at least 38 mm TL on September 18, the latest sampling would probably not be necessary. Although age-0 largemouth bass were still recruiting into the gear until August, no major recruitment into the gear was evident after September (Figure 9).

## **Discussion**

My results were promising in the sense that very high correlation existed between mean CPUE of age-0 largemouth bass that were collected with a hand-held electroshocker and the corresponding cohort's CPUE at age-1 that were collected with a boom-mounted electrofisher. Comparisons of catch rates of different gear types commonly do not provide consistent results because each gear has different size selectivity (Hubert 1996; Hayes et al 1996). Some fishing gears are selective for the larger fish, while some gears are selective for a certain length range only, thus excluding the capture of very small and very large fish (Sparre and Venema 1998). The size ranges of largemouth bass in this study appeared to be representative for their age groups by the method they were sampled. For example, age-0 CPUE was calculated only for sizes less than 150 mm TL; the length that age-0 largemouth bass fully recruit to the hand-held electrofisher is probably somewhere below 70 mm TL (Figure 3) and relatively few fish have been captured less than 50 mm. For age-1 CPUE, on the other hand, the size range of age-1 largemouth bass was between 170-360 mm TL, with most of the age-1 fish (60%) being within a 250-300 mm TL. Thus, sampling for these two age groups of largemouth bass was in the effective length range for these two electrofisher types, respectively (Hill and Willis 1994; Jackson and Noble 1995).

Jackson and Noble (1995) found that the boom-mounted electrofisher sampled largemouth bass greater than 150 mm more effectively than the hand-held electrofisher in spring sampling, and that small size-classes (<125 mm) sampled with the hand-held electrofisher were not represented in the sample with the boom-mounted electrofishing unit. My high correlation of age-0 and age-1 CPUE is consistent with their findings that

largemouth bass larger than 150 mm are sampled effectively with the boom-mounted and that fish less than 150 mm are effectively sampled with the hand-held electrofisher. On the other hand, fish less than 150 mm TL were typically non-existent during February when samples were taken with the boom-mounted unit. In contrast, the pooled length-frequency graph (Figure 3) implies that efficiency of the hand held-held unit is relatively high between 50-150 mm TL. However, the declining right side of the distribution may also represent mortality as well as the selection curve, and no conclusion can be made that the hand-held electrofisher is not effective for fish larger than 150 mm. But the ascending left side of the distribution indicates that the hand-held electrofisher is not representing the largemouth bass population less than 50 mm TL, as smaller fish must be in higher numbers at some point. In fact, from 57 sampling occasions, only 143 of 2,387 largemouth bass smaller than 150 mm TL were smaller than 50 mm TL (Figure 3).

Seining is a commonly used gear for juvenile largemouth bass sampling (Noble in press). Seining was proven more efficient than the hand-held electrofisher for fish less than 60 mm (Jackson and Noble 1995). However, seining may not be feasible in shorelines with steep slopes and where logs and brush are present. In addition, Higginbotham (1995) found that the precision of seining was very low for young-of-the-year largemouth bass.

Gear selectivity also affects estimation of growth rates. Mean daily growth estimates of fish sampled with selective gear would always be erroneous regardless of whether the growth rates were obtained by ageing or from mean length of sequential sampling occasions. Mean calculations are related to the size distribution of the sample and therefore a biased sample would result. The range of growth estimated from otoliths,

however, might be a more accurate statistic because it is very likely that at least one fast growing and one slow growing fish will be captured, especially using multiple sampling occasions.

Assuming that daily growth rate is not related to mortality, a slow growing fish (0.35 mm/d) would have a probability of being captured about 13.6 times while it grows from 50 to 150 mm when sampled every 3 weeks (1992-1994). A fast growing individual (1.33 mm/d), on the other hand, would have the probability of being captured just 3.6 times. This ratio of capture probability based on differential growth would not change with the sampling periodicity since both fast and slow growing fish capture probability would change in the same magnitude. The ratio of the probability of a slow growing fish to fast growing fish would always be  $1.33/0.35$  for a given length range (e.g. 50-150 mm). Therefore, according to this example, a mean growth estimation based on selective gear would result in biased results. A true estimate of mean growth would only be obtained if there were no differences in capture probability between fish with different growth rates. The right-sided skewness of the growth distribution (Figure 4) suggests that slower growing individuals were sampled at higher rate.

The potential also exists for CPUE to be biased because of the under-representation of fast-growing fish. For a given hatch date, slow-growing fish would not be equally sampled as the fast growing fish, which would result in biased estimate of CPUE. If the true growth distribution were known, this bias could be adjusted if two or more sampling surveys through time were conducted. From a cumulative probability function of growth rate, the probability that an individual fish will be captured the next sampling period could be extracted from the previous sampling so that each individual

fish would have been captured just once. Then the adjusted catches for all sampling surveys could be summed to a total. By doing this, each fish would have the same capture probability regarding growth rate. If slow-growing fish, on the other hand, would have a higher mortality rate then the higher probability of being captured for these fish would be somewhat compensated.

I assumed that the age-1 CPUE of largemouth bass collected with the boom-mounted electrofisher was a valid index of year-class strength. Although some bias may exist in my age-1 CPUE, my assumption is convincingly supported by many studies that found adult largemouth bass CPUE significantly related to population density (Hall 1986; Coble 1992; McInerney and Degan 1993; Hill and Willis 1994; Edwards et al. 1997). In the absence of annual age data due to inability to detect annuli in Puerto Rico largemouth bass (Neal et al. 1997), I used the Bhattacharya technique to identify age-1 fish. However, the Bhattacharya method for splitting a composite distribution into separate normal distributions requires an uncontaminated (clean) slope of a normal distribution (Sparre and Venema 1998) where in fact the age-1 length distribution may have been influenced by the overlapping age-2+ cohort (i.e., 1998 population estimate; Figure 5). A large year-class in 1996 (CPUE = 76.4; Figure 5) apparently had a slow growth rate and the relatively smaller year-class 1997 (CPUE = 58.6; Figure 5) had a higher growth rate, resulting in overlap of age classes (see 1998 in Figure 5). In other years, however, the age-1 modes were reasonably distinguishable from age-2 and older fish. Distinctive bimodal distributions were evident in 1999 and 2001, probably as results of water level fluctuations during the hatching periods of these cohorts (Ozen and Noble in press), with medium year-class strengths (52.3 and 50.3, respectively). Nevertheless, the strong

correlation of age-1 CPUE with age-0 CPUE suggests that my technique produced reasonably good indices of age-1 abundance.

Based on the results from the regression analyses, a 3-week sampling interval may not be necessary, because a 6-week interval was equally precise in predicting age-1 CPUEs from the mean age-0 CPUEs (Figure 7). A 15-week cycle with only two sampling occasions, however, appeared to be sensitive to the date the sampling was conducted. In addition it produces a poor length distribution (Figure 3). The predicted 76-day (~11 week) sampling interval with at least three sampling occasions, given the daily growth range, would probably be more precise than a 15-week sampling cycle for year-class strength estimations.

My results also confirm that year-class strength of largemouth bass in Lucchetti Reservoir is fixed before August and by the time they reach a length of 150 mm TL. These findings are very consistent with the results of Chapter 3, that age-1 largemouth bass CPUE variation in February was related to hydrological variables between January-July from the previous year in Lucchetti Reservoir. This corroborates my conclusion that year-class strength is set before August for this population.

Juvenile black bass assessment is conducted mostly with electrofishing gear by the state agencies in the U.S. (Noble in press). Usually such sampling is done with boom shocker, shown by Jackson and Noble (1995) to be size-selective. The hand-held electrofisher provided promising results as an alternative for monitoring population dynamics of young-of-the-year largemouth bass. Besides this study, only one study (Jackson and Noble 1995) investigated the efficiency of the hand-held electrofisher.

Further investigation is necessary of its size selectivity to improve the precision of the estimates with this alternative sampling gear for age-0 largemouth bass.

Selectivity of electrofishing may vary from system to system because of environmental effects such as water temperature, transparency, and water conductivity, with the latter being the most important (Reynolds 1996). Hill and Willis (1994) demonstrated that water conductivity was a significant factor in predicting adult largemouth bass density from pulsed DC CPUE (but see Van Zee 1996). Therefore, studies of selectivity analyses of the hand-held electrofisher should incorporate water conductivity if standardization of this gear is to be accomplished.

Early year-class strength detection can provide valuable management options, especially for supplemental stocking. Churchill et al. (1995) showed that stocking 50 largemouth bass fingerlings per hectare produced detectable impacts on cohort size, especially when densities of wild-hatched fish were low. Neal et al. (in press) found that supplemental stocking of largemouth bass if performed off-season (September-November) in Lucchetti Reservoir, resulted in higher growth and survival rate than if it would be performed during the spawning season. This study revealed that year-class strength in this reservoir can be detected by August, and if stocking largemouth bass is considered when low recruitment is expected, preparation time would be adequate for the off-season supplemental stocking. Given that adult stock of largemouth bass in Lucchetti Reservoir seldom reaches carrying capacity (Ashe et al. 1998), supplemental stocking based on juvenile assessment could regularly enhance the population.

## References

- Ashe, D. E., T. N. Churchill, R. L. Noble, and C. G. Lilyestrom. 1998. Temporal variability in the littoral fish community of a Puerto Rico reservoir. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 52:39-48.
- Bennett, C. D., and B. E. Brown. 1968. A comparison of fish population sampling techniques on Lake Raymond Gary, Oklahoma. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 22:425-444.
- Betsill, R. K. 1996. Electrofishing catch of largemouth bass: Spatiotemporal variation and relation to angler catch. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 50:1-11.
- Buynak, G. L., B. Mitchell. 1993. Electrofishing catch per effort as a predictor of largemouth bass abundance and angler catch in Taylorsville Lake, Kentucky. *North American Journal of Fisheries Management* 13:630-633.
- Churchill, T. N., R. L. Noble, J. E. Gran, and A. R. Alicea. 1995. Largemouth bass recruitment in Lucchetti Reservoir. Final Report. Federal Aid in Sportfish Restoration Project F-16-2. Puerto Rico Department of Natural and Environmental Resources.
- Coble, D. W. 1992. Predicting population density of largemouth bass from electrofishing catch per effort. *North American Journal of Fisheries Management* 12:650-652.

- Corujo Flores, I. N. 1991. Reservoir sportfish survey. Final Report. Federal Aid in Sportfish Restoration Projects F-16, Study 1. Puerto Rico Department of Natural Resources.
- David L. Higginbotham. 1995. Comparison of 3 seines in Alabama small impoundments. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 49:195-204.
- Edwards, C. M, R. W. Drenner, K. L. Gallo, and K. E. Rieger. 1997. Estimation of population density of largemouth bass in ponds by using mark-recapture and electrofishing catch per effort. North American Journal of Fisheries Management 17:719-725.
- Hall, T. J. 1986. Electrofishing catch per hour as an indicator of largemouth bass density in Ohio impoundments. North American Journal of Fisheries Management 6:397-400.
- Hayes, D. B., C. P. Ferreri, and W. W. Taylor. 1996. Active fish capture methods. Pages 193-220 in B. R. Murphy and D. W. Willis, editors. Fisheries Techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Herring, J. 1979. Fish population estimate methods evaluated by a total drawdown. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 33:393-401.
- Hightower, J. E., R. J. Gilbert, and T. B. Hess. 1982. Shoreline and cove sampling to estimate survival of young largemouth bass in Lake Oconee, Georgia. North American Journal of Fisheries Management 2:257-261.

- Hill, T. D., and D. W. Willis. 1994. Influence of water conductivity on pulsed AC and pulsed DC electrofishing catch rates for largemouth bass. *North American Journal of Fisheries Management* 14:202-207.
- Hubert, W. A. 1996. Passive capture techniques. Pages 157-192 in B. R. Murphy and D. W. Willis, editors. *Fisheries Techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Irwin, E. R., R. L. Noble, and J. R. Jackson. 1997. Distribution of age-0 largemouth bass in relation to shoreline landscape features. *North American Journal of Fisheries Management* 17:882-893.
- Jackson, J. R., and R. L. Noble. 1995. Selectivity of sampling methods for juvenile largemouth bass in assessments of recruitment processes. *North American Journal of Fisheries Management* 15:408-418.
- Jackson, J. R., and R. L. Noble. 2000. Relationships between annual variations in reservoir conditions and age-0 largemouth bass year-class strength. *Transactions of the American Fisheries Society* 129:699-715.
- Kramer, R. H., and L. L. Smith, Jr. 1960. First-year growth of the largemouth bass, *Micropterus salmoides* (Lacépède), and some related factors. *Transactions of the American Fisheries Society* 89:222-233.
- Ludsin, S. A., and D. R. DeVries. 1997. First-year recruitment of largemouth bass: the interdependency of early life stages. *Ecological Applications* 7:1024-1038
- McInery, M. C., and D. J. Degan. 1993. Electrofishing catch rates as an index of largemouth bass population density in two large reservoirs. *North American Journal of Fisheries Management* 13:223-228.

- Miller, K. D., and R. H. Kramer. 1971. Spawning and early life history of largemouth bass (*Micropterus salmoides*) in Lake Powell. Pages 78-83 in G. E. Hall editor. Reservoir fisheries and limnology. American Fisheries Society, Special Publications 8, Bethesda, Maryland.
- Miller, S. J., and T. Storck. 1982. Daily growth rings in otoliths of young-of-the-year largemouth bass. Transactions of the American Fisheries Society 111:527-530.
- Neal, J. W., R. L. Noble, A. R. Alicea, and T. N. Churchill. 1997. Invalidation of otolith ageing techniques for tropical largemouth bass. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 51:159-165.
- Neal, J. W., R. L. Noble, and T. N. Churchill. In press. Timing of largemouth bass supplemental stocking in a tropical reservoir: impacts on growth and survival. Pages X-XX in D. P. Phillip and M. S. Ridgeway, editors. Black Bass 2000 Symposium. American Fisheries Society, Symposium in press.
- Neal, J. W., R. L. Noble, C. G. Lilyestrom, N. M. Bacheler, and J. C. Taylor. 2001. Freshwater Sportfish Community Investigations and Management. Final Report. Federal Aid in Sport Fish Restoration Project F-41-2. Puerto Rico Department of Natural and Environmental Resources, San Juan, Puerto Rico.
- Neal, J. W., R. L. Noble, C. G. Lilyestrom, T. N. Churchill, A. R. Alicea, D. E. Ashe, F. M. Holliman, and D. S. Waters. 1999. Freshwater Sportfish Community Investigations and Management. Final Report. Federal Aid in Sport Fish Restoration Project F-41-2. Puerto Rico Department of Natural and Environmental Resources. San Juan, Puerto Rico.

- Ney, J. J. 1993. Practical use of biological statistics. Pages 137-158 in C. C. Kohler and W. A. Hubert, editors. Inland fisheries management in North America. American Fisheries Society, Bethesda, Maryland.
- Noble, R. L. In Press. Reflections on 25 years of progress in black bass management. Pages X-XX in D. P. Phillip and M. S. Ridgeway, editors. Black Bass 2000 Symposium. American Fisheries Society, Symposium in press.
- Ozen, O., and R. L. Noble. 2000. Yield-per-recruit simulation analyses for a largemouth bass population in Lucchetti Reservoir, Puerto Rico. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 54:59-69.
- Ozen, O., and R. L. Noble. In press. Relationship between water level fluctuations and largemouth bass spawning in a Puerto Rico reservoir. Pages X-XX in D. P. Phillip and M. S. Ridgeway, editors. Black Bass 2000 Symposium. American Fisheries Society, Symposium in press.
- Phillips, J. M., J. R. Jackson, and R. L. Noble. 1997. Spatial Heterogeneity in abundance of age-0 largemouth bass among reservoir embayments. North American Journal of Fisheries Management 17:894-901.
- Pine III, W. E., S. A. Ludsin, and D. R. DeVries. 2000. First-summer survival of largemouth bass cohorts: is early spawning really best? Transactions of the American Fisheries Society 129:504-513.
- Reynolds, J. B. 1996. Electrofishing. Pages 221-251 in B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

- Sammons, S. M., L. G. Dorsey, P. W. Bettoli, and F. C. Fiss. 1999. Effects of reservoir hydrology on reproduction by largemouth bass and spotted bass in Normandy Reservoir, Tennessee. *North American Journal of Fisheries Management* 19:78-88.
- Sparre, P., and S. C. Venema. 1998. Introduction to tropical fish stock assessment. Part 1. Manual. FAO (Food and Agriculture Organization of the United Nations) Fisheries Technical Paper. No. 306.1, Revision 2. Rome, Italy.
- Van Zee, B. E., and six coauthors. 1996. Comment: clarification of the outputs from a Coffelt VVP-15 electrofisher. *North American Journal of Fisheries Management* 16:477-478.

Table 1. Coefficients of determination ( $R^2$ ) between age-1 CPUE and age-0 mean CPUE and the corresponding probability ( $P$ ; in parentheses). Regressions were analyzed for different time periods starting between January and June, and ending between July and December.

Month sampling started	Month sampling ended					
	Jul	Aug	Sep	Oct	Nov	Dec
Jan	0.394 (0.131)	0.700 (0.019)	0.734 (0.014)	0.743 (0.013)	0.812 (0.006)	0.815 (0.005)
Feb	0.384 (0.138)	0.687 (0.021)	0.726 (0.015)	0.742 (0.013)	0.806 (0.006)	0.809 (0.006)
Mar	0.361 (0.154)	0.658 (0.027)	0.709 (0.018)	0.738 (0.013)	0.796 (0.007)	0.799 (0.007)
Apr	0.512 (0.071)	0.804 (0.006)	0.832 (0.004)	0.834 (0.004)	0.842 (0.004)	0.842 (0.004)
May	0.543 (0.059)	0.756 (0.011)	0.779 (0.009)	0.778 (0.009)	0.757 (0.011)	0.757 (0.011)
Jun	0.840 (0.029)	0.800 (0.007)	0.853 (0.003)	0.860 (0.003)	0.895 (0.001)	0.900 (0.001)

Table 2. Regression coefficients ( $R^2$ ) and corresponding  $P$ -values between the age-0 mean CPUE (fish/h; April-September) collected with the hand-held electrofisher and age-1 CPUE (fish/h) collected next year with the boom-mounted unit, for different upper total length (TL; mm) limits of age-0.

TL (mm)	$R^2$	P
130	0.39	(0.135)
140	0.87	(0.002)
150	0.83	(0.004)
160	0.79	(0.007)
170	0.71	(0.017)
180	0.61	(0.037)
190	0.57	(0.049)
200	0.51	(0.071)

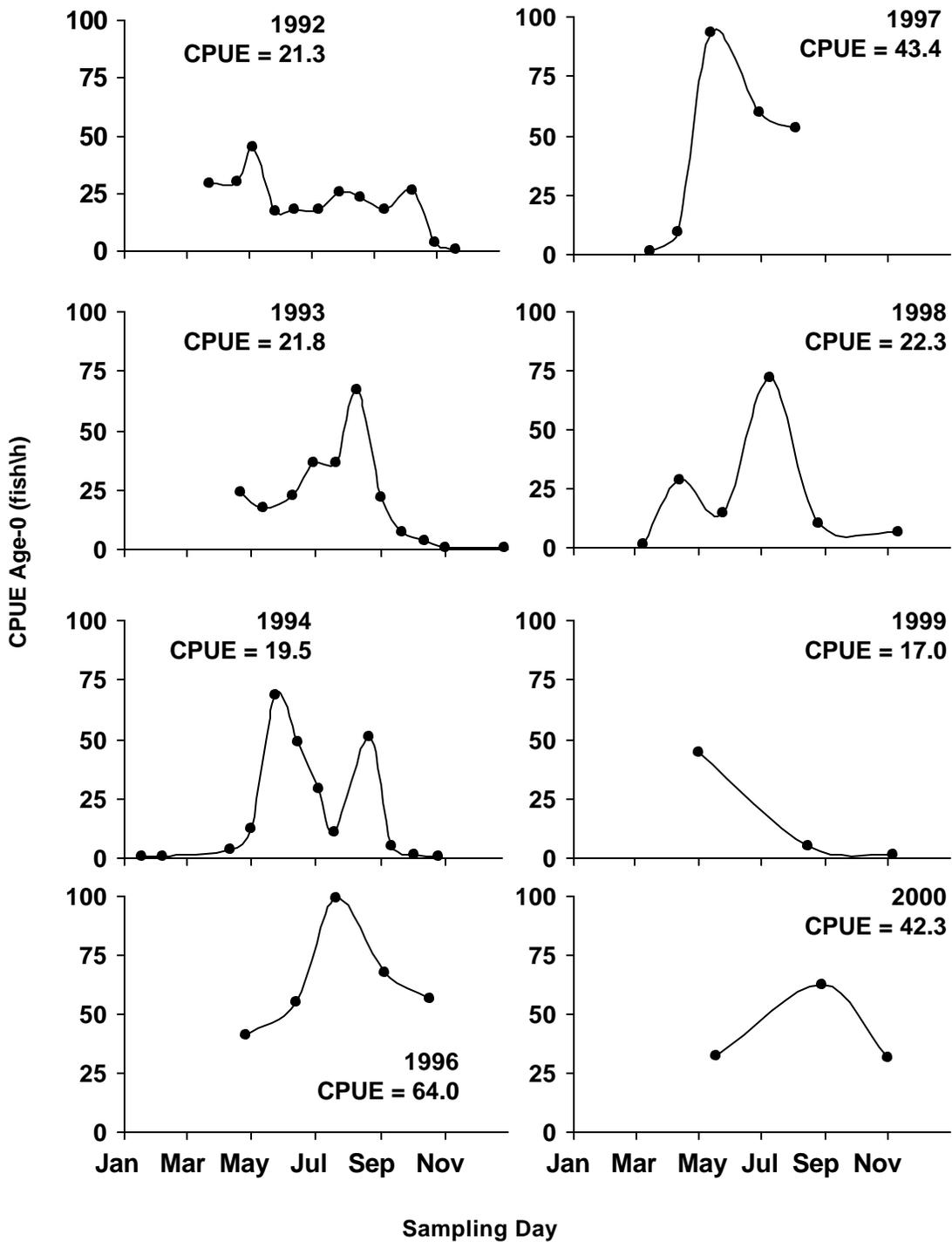


Figure 1. CPUE (fish/h) of each sampling date for age-0 (<150 mm TL) largemouth bass sampled with a hand-held electrofisher between 1992-1994 and 1996-2000. The CPUE value given represents the annual mean.

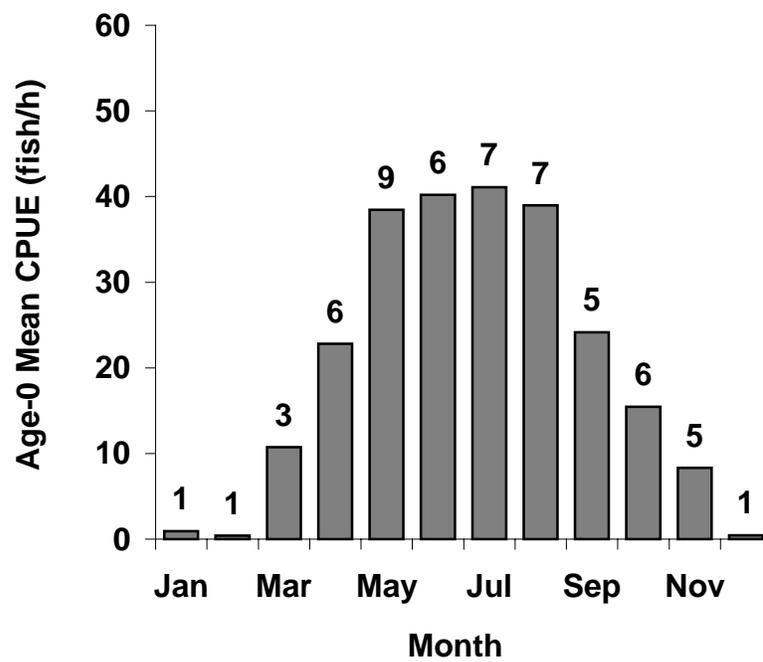


Figure 2. Monthly means of age-0 (<150 mm) CPUE from the hand-held electrofisher for the years 1992-1994 and 1996-1999 combined. The number above the bars represents the number of samplings for each month.

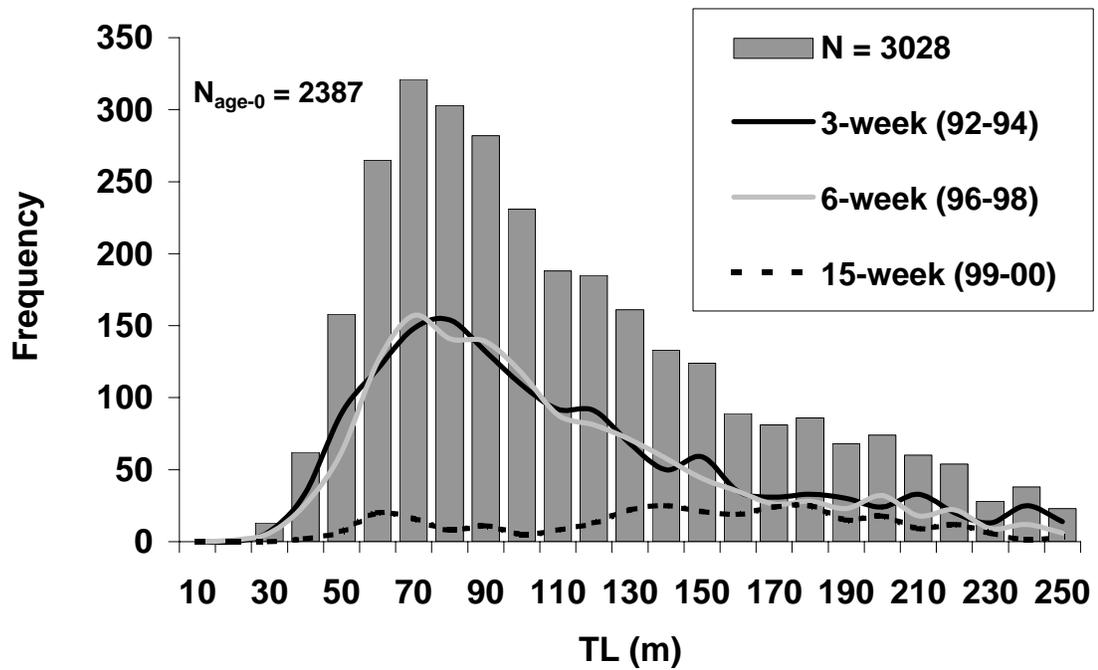


Figure 3. Pooled length-catch frequency (solid bars; 10 mm TL increment) of largemouth bass collected with the hand-held electrofisher in 57 sampling surveys with 3-week interval from 1992-1994 (black solid line), with 6-week interval from 1996-1998 (gray solid line), and with 15-week interval from 1999-2000 (black dashed line).

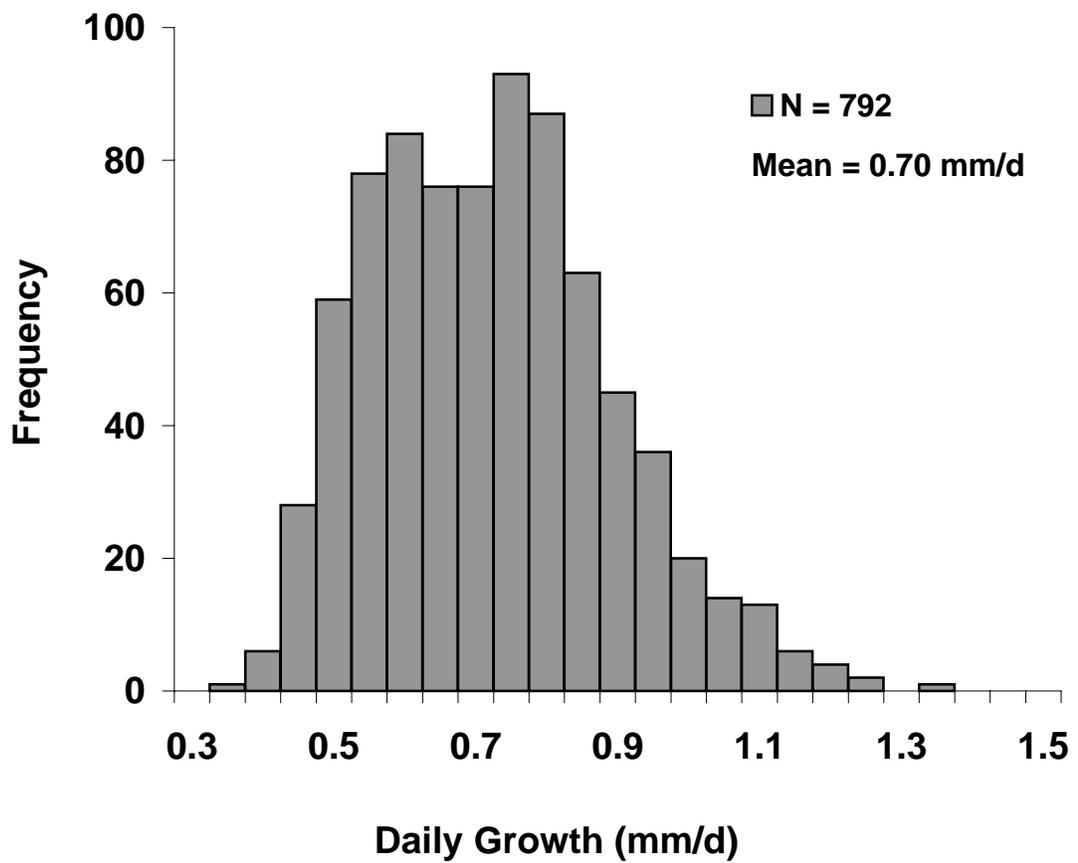


Figure 4. Daily growth distribution (mean = 0.70 mm/d; STD = 0.17; N = 792) of juvenile largemouth bass from swim-up until 100 mm collected with the hand-held electrofisher between 1992-1994 and 1996-1999.

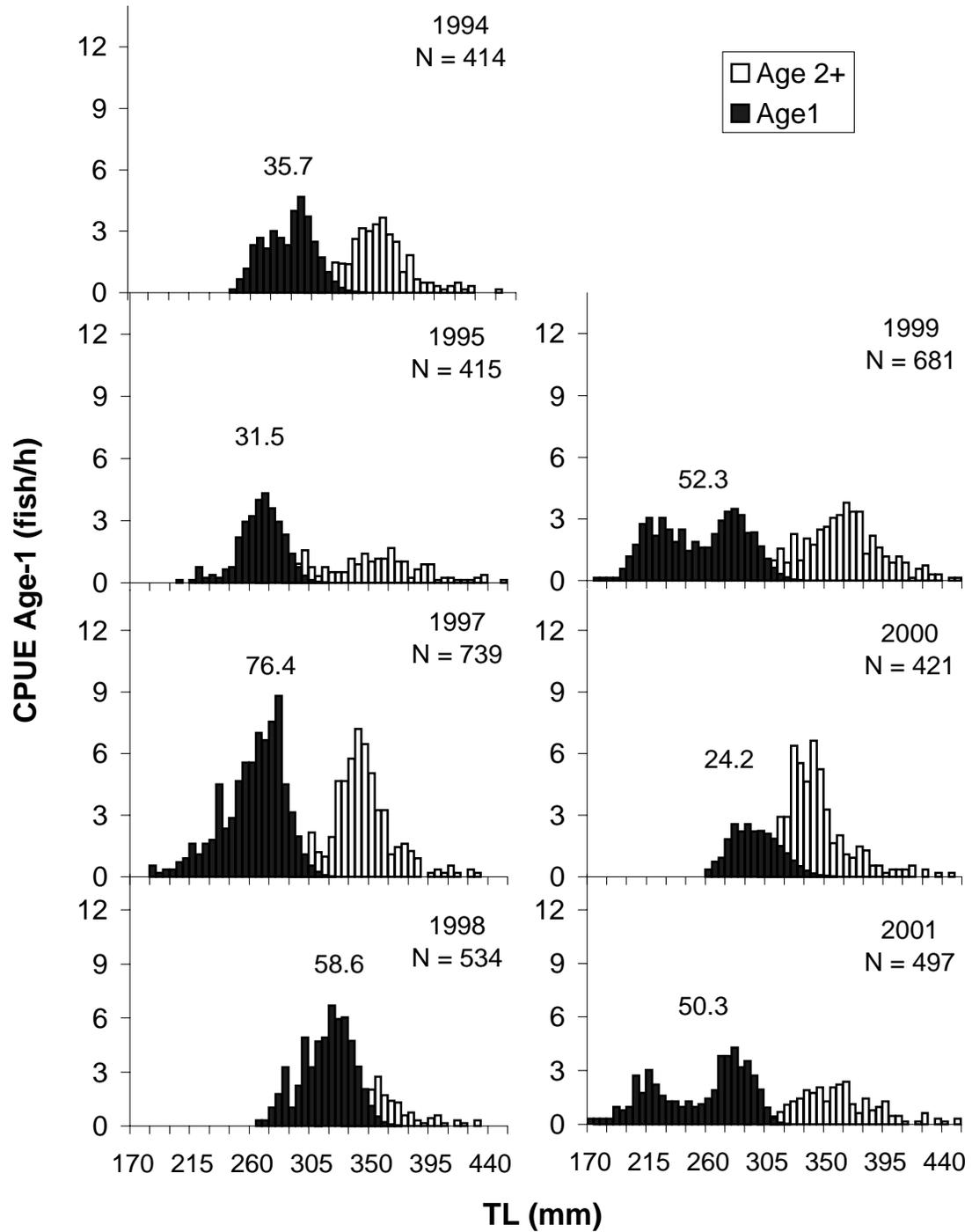


Figure 5. CPUE for age-1 largemouth bass (filled bars; 5 mm increments) collected with a boom-mounted electrofisher between 1994-1995 and 1997-2001. Number (N) includes age-2+ largemouth bass (open bars) but the CPUE above the filled bars represents only CPUE of age-1.

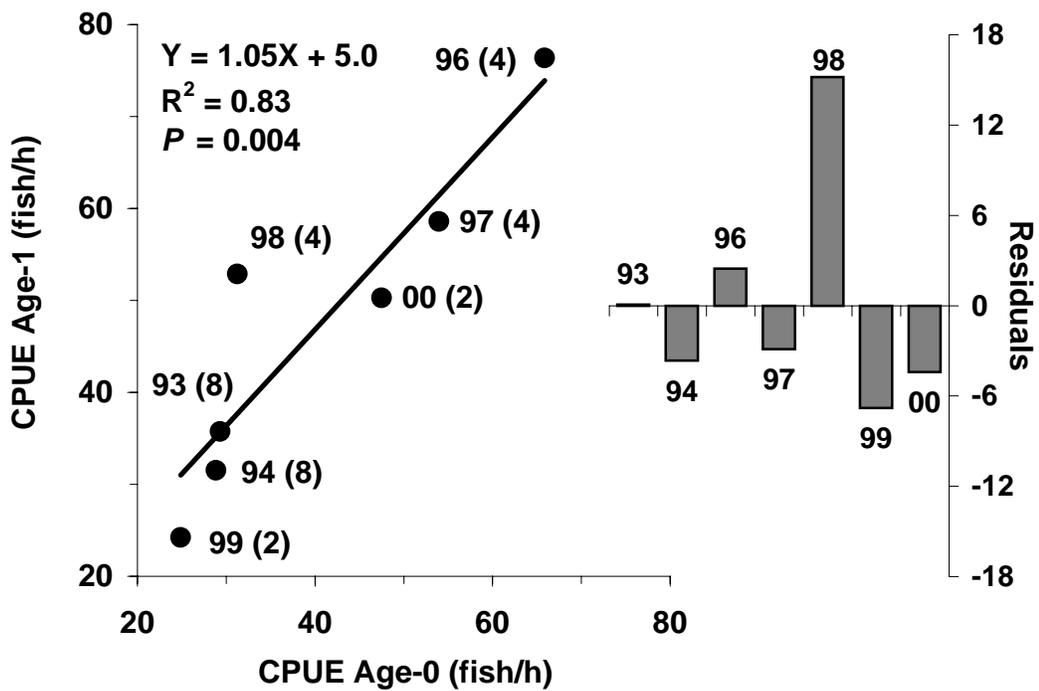


Figure 6. CPUE (fish/h) of age-1 vs. mean CPUE of age-0 (<150 mm TL) from April to September (left panel). The numbers are the last two digits of the cohort-year and in parentheses are the numbers of samplings. The right panel shows the residuals of the predicted values for each year.

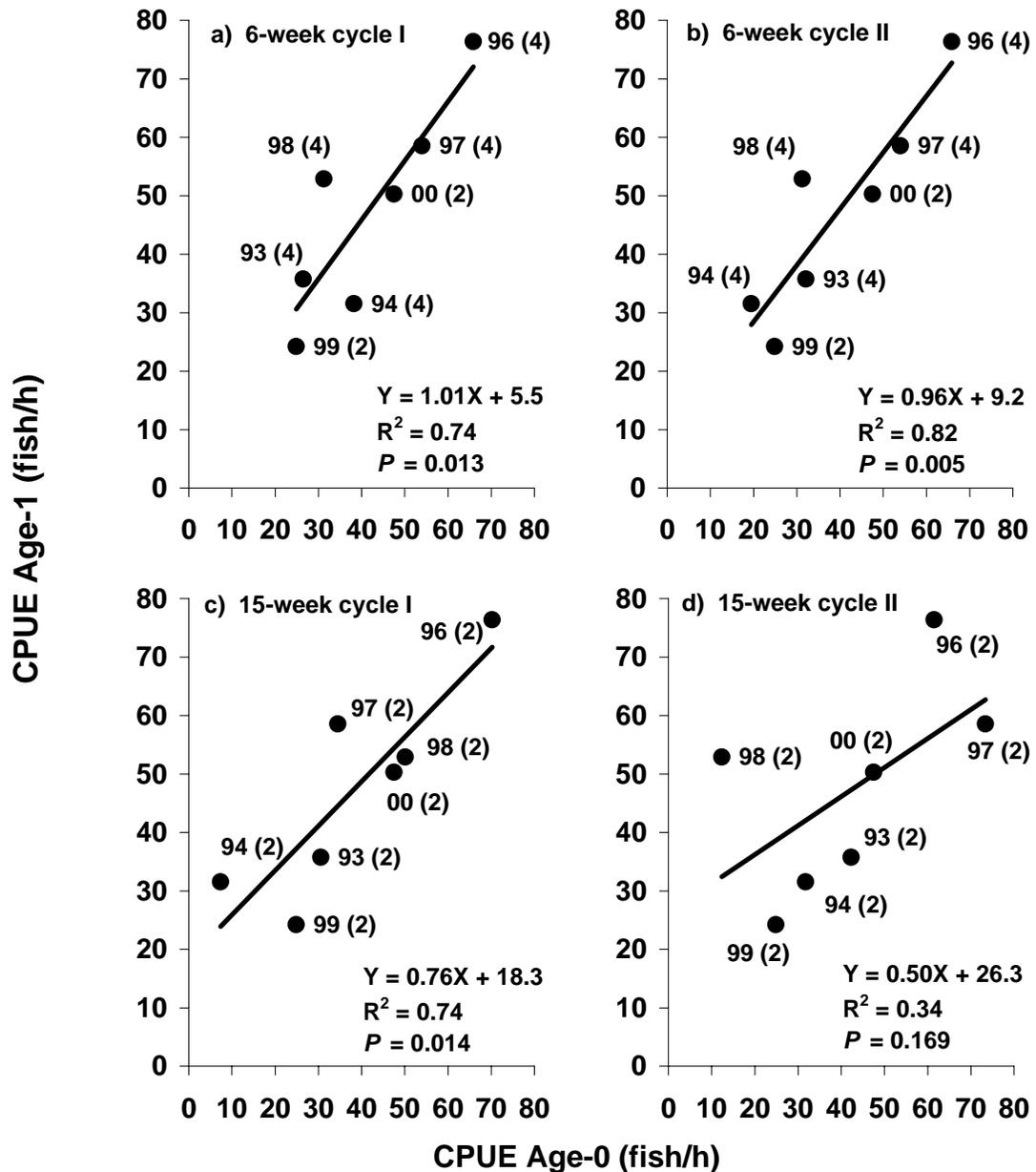


Figure 7. Reduced sampling occasion regressions between age-1 CPUE and age-0 mean CPUE (<150 mm TL; April-September). Excluding the samplings of every other sampling day from the 3-week samplings (1993-1994) by starting with the second (a) and with the first (b) and alternating sampling date so that the sampling cycle is about 6-weeks. Using the first sampling date (c) and the second sampling date (d) in April and excluding the samplings dates in 1993-1994 and 1996-1998 so that the sampling interval is about 15 weeks through September. The numbers represent the last two digits of the cohort-year and in parentheses are the numbers of samplings.

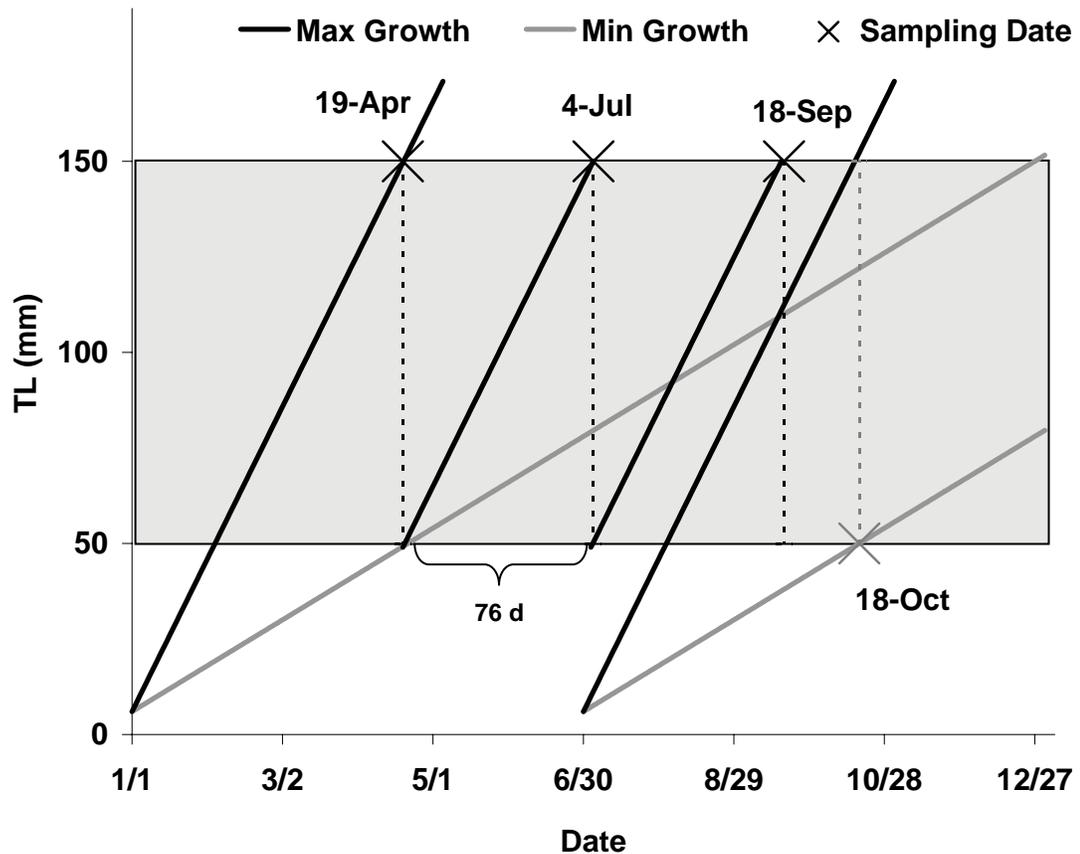


Figure 8. Estimated sampling schedule based on hatching period (January-June) and maximum (1.33 mm/d; black lines) and minimum (0.35 mm/d; grey lines) daily growth rates of juvenile largemouth bass (<100 mm TL). The grey background indicates the relatively effective range (50-150 mm) of age-0 largemouth bass to the hand-held electrofisher. Note that largemouth bass were 6 mm TL on hatching dates. See text for explanation on the estimation of the sampling schedule.

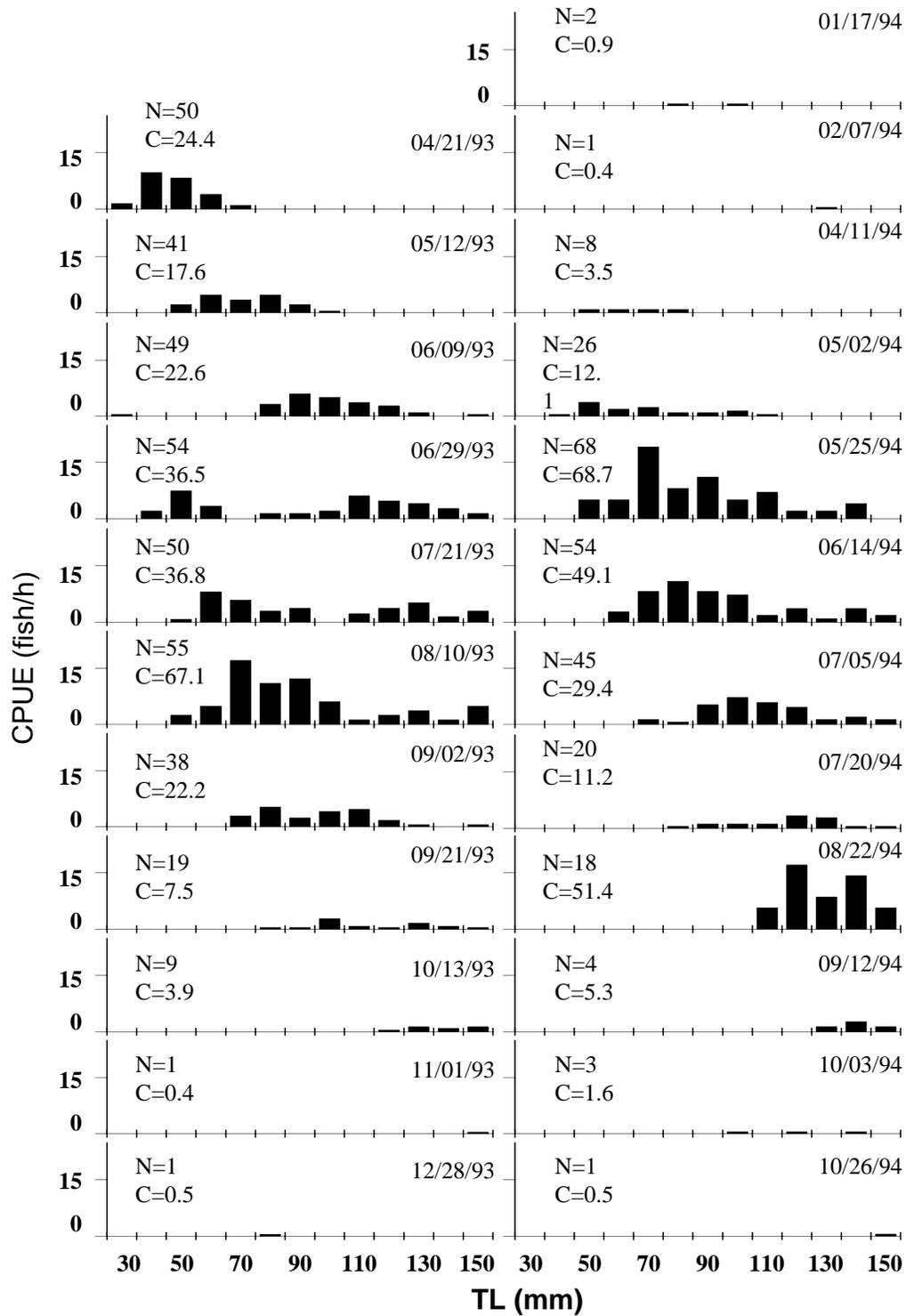


Figure 9 a). Length-CPUE distributions (10 mm increment) collected with the hand-held electrofisher for each sampling period from 1993-1994. The C value inside the graphs represents the CPUE for that sampling date.

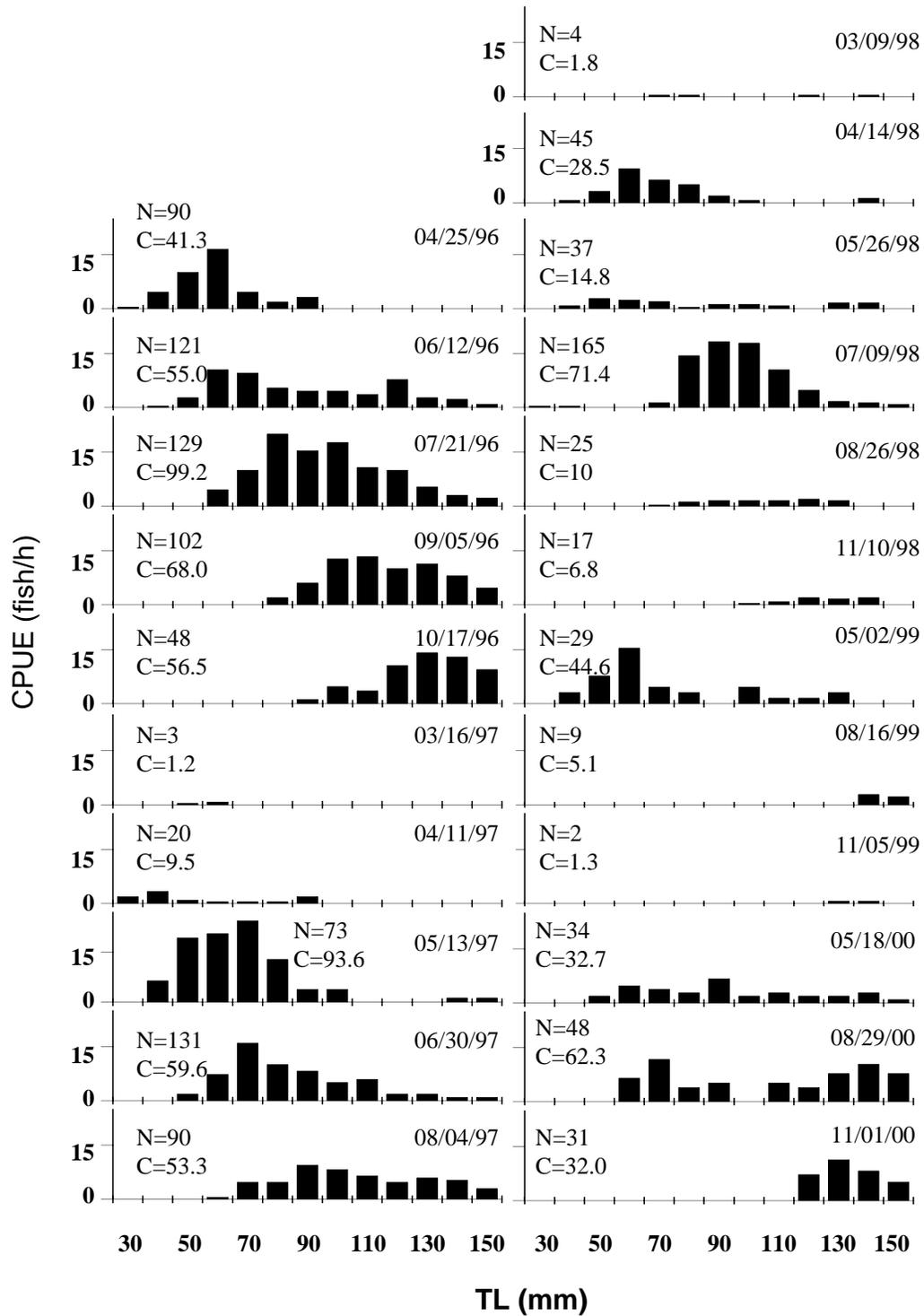


Figure 9 b). Length-CPUE distributions (10 mm increment) collected with the hand-held electrofisher for each sampling period from 1996-2000. The C value inside the graphs represents the CPUE for that sampling date.

## **CHAPTER II**

### **Relationship between Water Level Fluctuations and Largemouth Bass Spawning in a Puerto Rico Reservoir**

## **Abstract**

Age-0 largemouth bass, Micropterus salmoides, were collected over seven years throughout the spawning season in Lucchetti Reservoir, Puerto Rico. Sagittal otoliths were removed and daily ages determined to assess hatching periodicity. Hatch date distributions indicated that the major spawning of largemouth bass started in January, soon after photoperiod began to increase. The time lag between increasing day length and the start of spawning, however, was dictated by water level fluctuation. In some years, when the water level began to decrease during the spawning season, spawning was interrupted, but resumed when water level started to rise again, resulting in bimodal hatch-date distributions. Because of its tropical geographic location, Lucchetti Reservoir experiences temperature variations of 24-30°C annually, and relatively constant temperature during the initiation of spawning. My data indicate that, despite some role of photoperiod in defining the primary spawning season, the initiation of largemouth bass spawning was stimulated by water level increase in this tropical reservoir. The overriding role of water level was further evident by late-season pulses in spawning, related to rising water level, in some years. I hypothesize that water level increase could be used in systems where water temperature is suitable to stimulate largemouth bass spawning.

## **Introduction**

The effect of hydrological conditions on largemouth bass, Micropterus salmoides, population dynamics has been widely studied in lakes, rivers, ponds, and reservoirs. Raibley et al. (1997) found that strong year classes were produced in years when largemouth bass had access to flooded areas for a prolonged time in spring and summer in the Illinois River. Largemouth bass recruitment was higher in high-water years than it was in low-water years, but was unaffected by water level fluctuations during the spawning season in two Illinois reservoirs (Kohler et al. 1993). Maceina and Bettoli (1998) reported that largemouth bass recruitment in four Tennessee impoundments were not affected by fluctuating water levels during spawning, but was positively correlated with dry early summer conditions. Sammons and Bettoli (2000) found that strong largemouth bass year classes were produced in years when the water level was at or above pool level during spring and summer in Normandy Reservoir, Tennessee. Cove rotenone densities of young-of-the-year (YOY) largemouth bass showed a significant positive relationship to the duration and area flooded in the post-spawning period in Bull Shoals Lake, Missouri-Arkansas (Aggus and Elliot 1975), suggesting the importance of inundated terrestrial vegetation for early survival of largemouth bass (Fisher and Zale 1991).

However, year-class strength of largemouth bass may not necessarily be associated with water level fluctuations. Phillips et al. (1997) and Jackson and Noble (2000) found no relation between YOY abundance and water level in Jordan Lake, North Carolina. Likewise, Miranda et al. (1984) found that water level rise during spawning

period increased the spawning success of largemouth bass, but did not necessarily produce strong or weak year-classes because of varying mortality rates after hatching in West Point Reservoir, Alabama-Georgia.

The potential mechanisms of water level increase that would benefit fish are summarized by Keith (1975): inundated terrestrial vegetation initiates dying and decomposition of vegetation and causes the release of nutrients; increases in available nutrients and substrate increases phytoplankton and periphyton production which forms the bottom of the food chain for fish; desirable habitat and temporary cover for shoreline dwelling fishes are produced; and finally, inundation creates an area of water that is sparsely populated with fish life, which stimulates the natural reproductive and growth processes of fish. The general relationships between water level and fish have been reviewed in detail by Liston and Chubb (1985) and Ploskey (1986).

Largemouth bass typically spawn in water 0.3 to 1.3 m deep (Heidinger 1975), so successful reproduction may be influenced by water level declines. Miller and Kramer (1971) reported that spawning started on the shallower (mean depth of 1.64 m) and more gently sloping shore and, as the spawning season progressed, nest depth increased (mean depth of 4.54 m) as bass sought the protection of ledges and boulders, in Lake Powell, Utah-Arizona. Maraldo and MacCrimmon (1981) indicated that largemouth bass spawned in water depths between 0.2 and 1.4 m and observed largemouth bass nests exposed to air because of declining water level in Tadenac Lake, Canada. Declining water levels (0.88-3.94 cm/d) during largemouth bass spawning had little effect on hatching success in Lake Mead, Arizona, but declines as high as 6 cm/d would have caused more than 85% of nests to be susceptible to wind and wave action (Morgensen

1983). Miller and Kramer (1971) observed largemouth bass nests destroyed by strong wave action at 0.45-1.07 m water depths.

Water level increase has also been reported as a primary stimulus for spawning initiation for some fish species. Ali and Kadir (1996) reported that spawning of the cyprinid, Thynnichthys thynnoides, coincided with water level increase in the Chenderoh Reservoir, Malaysia. Bruton (1978) indicated that the final stimulus for Clarias gariepinus was the rise of water level in Lake Sibaya, South Africa. An experiment with weakly electric fish, Eigenmannia viresces, showed that final maturation and spawning occurred only with the combination of decreasing conductivity, rain, and water level increase whereas any other combination did not result in spawning (Kirschbaum 1979). Relation between water level increase and initiation of spawning for largemouth bass, however, has not been reported. Sammons et al. (1999), however, reported that the first day of realizing full pool was significantly correlated to the date of first hatch in Normandy Reservoir, Tennessee, which may imply a relation between initiation of largemouth bass spawning and water level rise.

Initiation of largemouth bass spawning in temperate regions has been attributed to increasing photoperiod and temperature (Heidinger 1975). Spawning activity of largemouth bass starts when temperature reaches 15° C to 24° C (Kramer and Smith 1960; Miller and Kramer 1971). In contrast to temperate regions, largemouth bass in Lucchetti Reservoir, Puerto Rico, have a prolonged spawning season (Gran 1995; Waters 1999) and multiple cohorts sometimes occur (Churchill et al. 1995). Largemouth bass have a high growth rate in Lucchetti Reservoir. Juvenile largemouth bass may grow about 0.63-1.50

mm/d in Lucchetti Reservoir, estimated from a micro-tagging study (Churchill et al. 1995, Neal et al. 2000), and typically reach maturity at age-1 (Neal et al. 1999).

The main objective of this present study was to investigate water level fluctuations and photoperiod as the cues for spawning initiation, the peak spawning, and the termination of spawning of largemouth bass in Lucchetti Reservoir. The effect of water level fluctuation on within-season periodicity of spawning was also investigated.

## **Methods**

Study site. Lucchetti Reservoir is a 108-ha impoundment in the mountain region of southwestern Puerto Rico. When completed in 1952, it provided about 20.35 ha-m<sup>3</sup> of usable storage for power generation and irrigation to the arid Lajas Valley. However, by 1978 the storage capacity dropped to 14.30 ha-m<sup>3</sup> with a mean sediment accumulation of 25 cm/year (Zack and Larsen 1993). The drainage area is about 45.1 km<sup>2</sup>.

Lucchetti Reservoir is divided into four embayments, corresponding to its four river confluences. The basin of the reservoir is located in a subtropical moist forest, where annual precipitation is about 198 cm. At the time of construction the retention time was about 0.66 years, which was above the average for reservoirs in Puerto Rico. Mean depth of the reservoir at pool level was about 11.6 m. A maximum depth of 54.3 m at the spill level of 174 m above the sea level was cited by Churchill et al. (1995), but Neal et al. (1999) found depths no greater than 22.2 m, supporting the earlier findings of heavy siltation.

Lucchetti Reservoir shoreline has a steep slope and the substratum consists of a mixture of rock and clay, resulting in a variety of habitat types. Water level may

fluctuate as much as 17 m annually with a constant decline over a period of about 4 months (Figure 1). These fluctuations result in dramatic changes of the shoreline distance and surface area. This extreme water level change limits aquatic macrophyte establishment. However, the tropical environment is conducive to continual rapid growth of terrestrial vegetation, which establishes on exposed clay banks during drawdown periods. The productivity level of Lucchetti Reservoir has been categorized from mesotrophic to eutrophic (Churchill et al. 1995).

Sampling and otolith procedures. Juvenile largemouth bass were sampled through timed nighttime electrofishing efforts using a 260-V DC hand held probe (Jackson and Noble 1995) at 3-week intervals from 1992 to 1994 and at 6-week intervals from 1995 to 1998. Young largemouth bass fully recruit to the electrofishing gear at 50 mm TL and susceptibility to the gear declines when they reach 130 mm TL (Churchill et al. 1995). Because hatching occurs over an extended period and growth rates are rapid, only a portion of a cohort is assessed during each sample, and therefore catch-per-unit-effort (CPUE) for each sampling occasion may not be an accurate indication of overall year-class strength.

In 1995, the juvenile largemouth bass sampling did not start until the end of July. Because largemouth bass start spawning between January and February, a precise spawning distribution could not be obtained from the delayed sampling survey and therefore I omitted the 1995 data in my analyses. In addition, a one-time sampling was conducted in May 1999. These data were included in the analyses because a very short spawning period in 1999 enabled us to capture a sample of the entire size distribution of this cohort in one collection event.

Sagittal otoliths removed from juvenile largemouth bass were aged according to the procedures of Miller and Storck (1982). These investigators found that age estimates were reliable for the first 80-100 days after hatching. I used only fish less than 100 mm TL for aging, corresponding approximately to the 100-day maximum described by Miller and Storck (1982). Two independent readers counted the daily rings twice. If any of the readings from the two readers agreed within 2 days, then the higher reading was assigned as the hatching age (Isely and Noble 1987). If the two readers did not agree within 2 days, a third reading was conducted and the same two-day agreement was checked. If there still was not an agreement within two days, no hatching age was assigned.

Hatch dates were estimated from the aged otoliths by adding 5 days, the time required for swim-up (Carr 1942; Kramer and Smith 1960), to the assigned number of day rings and then subtracting this total from sample date. Estimated hatching distributions were developed based on CPUE for the fraction of each sample that was assigned an age. At tropical temperatures, spawning dates would have occurred 2-3 days prior to the hatching dates (Carr 1942; Kramer and Smith 1960; Maraldo and MacCrimmon 1981).

Daily water levels of Lucchetti Reservoir from December 1991 to September 1999 were obtained from the United States Geological Survey. Missing data were estimated by using PROC EXPAND command with METHOD=JOIN in SAS® (1993) (Figure 1). This method simply fits a continuous curve to the data by connecting successive straight-line segments. Sunrise and sunset times for a full year, and moon phases from January 1991 to December 1999 were obtained from the Department of the U.S. Naval Observatory (<http://aa.usno.navy.mil/AA/data/>).

## Results

A total of 1505 juvenile largemouth bass measuring less than 100 mm in total length were captured with the hand-held electrofisher in the seven sampling years (1992-1994 and 1996-1999). About 58% ( $n = 870$ ) of these were processed for otolith readings of which 792 met the readers' agreement criterion and were assigned hatch dates.

Hatch-date frequencies indicated that largemouth bass spawning started soon after photoperiod began increasing (Figure 2). Hatching commenced as early as 25 December 1991, and as late as 5 February 1993. The one-month variation in the initiation of spawning suggested that factors in addition to photoperiod affected the start of spawning. Examination of relationships of initial spawning dates to lunar cycle and to absolute water level on 1 January (163-173 m ASL) revealed no detectable effects.

Despite wide annual variation in water levels on 1 January, early-year increases in water levels were typical of the water level regime. These increases varied from as little as 1 m (1994) to 4 m (1998). However, because of variation in absolute water level prior to the increase, there was also variation in absolute water level reached by the rising water levels.

In all years the initiation of spawning corresponded closely to the times when water level started to increase about 1m in less than a week (Figure 3). Spawning distribution consistently indicated a pulse of reproduction lasting a month or more. In years when water level started to decline during the spawning period, largemouth bass spawning diminished, but resumed when the water levels rose again. For example in 1992 and 1993 observed two distinctive spawning occasions corresponding to the water level oscillation can be observed. In 1994 and 1996, a small increase in water level

initiated spawning. A second greater water level increase resulted in a more intensive spawning in 1994 and in an extension of the spawning period in 1996. Spawning also started and ceased with the water level fluctuation in 1997.

During some years (1992, 1993, 1998) spawning continued into June. Termination of spawning at that time appeared unrelated to water level fluctuations. However, rapid declines in water level during the spawning season not only caused interrupted spawning, but also terminated reproduction for the year in some cases.

In January 1999, water level began declining just 2 weeks after the water level started to increase. The spawning distribution was almost identical to this water level pulse. Consequently, the spawning duration was only about 3 weeks. In 1998 a similar pattern of water level increase and decrease as in 1999 was evident, except that the water level rise and decline was over 12 weeks. The spawning distribution extended also over the 12-week period. A second but minor spawning was also observed in 1998, again corresponding to the increasing water level.

## **Discussion**

This long-term study suggests that largemouth bass spawning activity in this tropical reservoir is related to water level fluctuations, superimposed over the annual photoperiod cycle. Sammons et al. (1999) found that mean hatch dates of largemouth bass spawning were positively related to the first day water levels achieved full pool in Normandy Reservoir, Tennessee. This study indicates that, after the photoperiod starts to increase, water level rise coincides with the spawning of largemouth bass.

Depending on the magnitude of change, declining water level during the January-June spawning period reduces, pauses, or terminates spawning activity within the period. Spawning activity may increase or resume when water levels begin rising again. Summerfelt (1975) speculated that disjunctive spawning could result from water level fluctuation. Kohler et al. (1993) found disruptions of largemouth bass hatching success due to water level decline and rise. My results support their findings on the hatching success disruption during water level drops. In contrast to their findings, my results showed positive relation between hatching frequency and water level rise during the spawning period.

Largemouth bass apparently responded to miniscule increases in day length. Photoperiod increases only 6 min from December 22 to January 14 at the latitude of the study site. In some years, largemouth bass started to spawn even before mid-January. Subtle increases in water temperature ( $< 1^{\circ}\text{C}$ ) also occur over this period (Churchill et al. 1995) and could serve as a spawning cue for largemouth bass in Lucchetti Reservoir. However, unlike photoperiod, daily variation in temperature during the period overwhelms the subtle trend.

It is uncertain from my data if the late-spawned young-of-the-year were from the same parental group as the early spawn, or if different individuals spawned in the late period. Goodgame and Miranda (1993) reported that smaller largemouth bass tend to spawn later than the larger adults do. However, Gran (1995) found that female largemouth bass had mature eggs through the first half of the year, and were capable of spawning continually through that period in Lucchetti Reservoir.

For purpose of analyses, I assumed that the hatch-dates of collected fish were representative of the temporal distribution of spawning. I recognize that the sampled fish are only individuals that survived to the sampling date, and that the spawning distributions presented could be only “survivor distributions”. Consequently, speculation could be made that rising water levels increase survivorship by inundating habitat that provides refuge from predators or increased prey availability. Decreasing water levels, on the other hand, could cause abandonment of the nest by the parents, loss of broods when nests are exposed to air, or total mortality of offspring from predation or starvation. However, telemetry studies at the site by Waters (1999) indicated movement of males from spawning grounds when water level declined, suggesting that spawning could therefore be interrupted or terminated. Moreover, Gran (1995) found that gonadosomatic index (GSI) of female largemouth bass in Lucchetti Reservoir started to increase after the photoperiod started to increase in December, but substantial increase in GSI coincided with water level rise in January even though the water temperature was still dropping until February in 1994. A small increase of GSI was also observed in October 1993, again corresponding to water level increase during which period both water temperature and photoperiod were still declining.

Regardless of whether these are spawning distributions or survivor distributions, the recruitment process of largemouth bass is evidently shaped by water level fluctuation, and the relationships provide beneficial insight for management purposes. I believe that in addition to a water level stabilization management plan during the spawning period of largemouth bass, water level increase could be used to stimulate the initiation of

largemouth bass spawning in ponds and reservoirs where the water is at optimum spawning temperature.

## References

- Ali, A. B., and B. K. A. Kadir. 1996. The reproductive biology of the cyprinid, Thynnichthys thynnoides (Bleeker), in the Chenderoh Reservoir -- a small tropical reservoir in Malaysia. *Hydrobiologia* 318:139-151.
- Aggus, L. R., and G. V. Elliott. 1975. Effects of cover and food on year-class strength of largemouth bass. Pages 317-322 in. R. H. Stroud and H. Clepper, editors. *Black bass biology and management*. Sport Fishing Institute, Washington, D. C.
- Bruton, M. N. 1979. The breeding biology and early development of Clarias gariepinus (Pisces:Clariidae) in Lake Sibaya, South Africa, with a review of breeding in species of the subgenus Clarias (Clarias). *Transactions of the Zoological Society of London* 35:1-45.
- Carr, M. H. 1942. The breeding habits, embryology and larval development of the largemouthed black bass in Florida. *Proceedings of the New England Zoological Club* 20:43-77.
- Churchill, T. N., R. L. Noble, J. E. Gran, and A. R. Alicea. 1995. Largemouth bass recruitment in Lucchetti Reservoir. Final Report. Federal Aid in Sportfish Restoration Project F-16-2. Puerto Rico Department of Natural and Environmental Resources.
- Fisher, W. L., and A. V. Zale. 1991. Effects of water level fluctuation on abundance of young-of-year largemouth bass in a hydropower reservoir. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 45:422-431-401.

- Goodgame, L. S., L. E. and Miranda. 1993. Early growth and survival of age-0 largemouth bass in relation to parental size and swim-up time. Transactions of the American Fisheries Society 122:131-138.
- Gran, J.E. 1995. Gonad development and spawning of largemouth bass in a tropical reservoir. M.S. thesis, North Carolina State University, Raleigh, North Carolina.
- Heidinger, R. C. 1975. Life history and biology of the largemouth bass. Pages 11-20 in R. H. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fishing Institute, Washington, D.C.
- Isley, J. J., and R. L. Noble. 1987. Use of daily otolith rings to interpret development of length distributions of young largemouth bass. Pages 475-481 in R. C. Summerfelt and G. E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.
- Jackson, J. R., and R. L. Noble. 1995. Selectivity of sampling methods for juvenile largemouth bass in assessments of recruitment processes. North American Journal of Fisheries Management 15:408-418.
- Jackson, J. R., and R. L. Noble. 2000. Relationships between Annual Variations in Reservoir Conditions and Age-0 Largemouth Bass Year-Class Strength. Transactions of the American Fisheries Society 129:699-715.
- Keith, W. E. 1975. Management of water level manipulation. Pages 489-497 in. R. H. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fishing Institute, Washington, D. C.
- Kirschbaum, F. 1979. Reproduction of the weakly electric fish Eigenmannia virescens (Rhamphichthyidae, Teleostei) in captivity. 1. Control of gonadal recrudescence

- and regression by environmental factors. *Behavioral Ecology and Sociobiology* 4:331-355.
- Kohler, C. C., R. J. Sheehan, and J. J. Sweatman. 1993. Largemouth bass hatching success and first-winter survival in two Illinois reservoirs. *North American Journal of Fisheries Management* 13:125-133.
- Kramer, R. H., and L. L. Smith, Jr. 1960. First-year growth of the largemouth bass, *Micropterus salmoides* (Lacépède), and some related factors. *Transactions of the American Fisheries Society* 89(2):222-233.
- Liston, C. R., and S. Chubb. 1985. Relationships of water level fluctuations and fish. Pages 121-140 in H. H. Prince and F. M. D'Istri, editors. *Coastal Wetlands*. Lewis Publishers, Chelsea, Michigan.
- Maceina, M. J., and P. W. Bettoli. 1998. Variation in largemouth bass recruitment in four mainstream impoundments of the Tennessee River. *North American Journal of Fisheries Management* 18:998-1003.
- Maraldo, D. C., and H. R. MacCrimmon. 1981. Reproduction, distribution, and population size of largemouth bass, *Micropterus salmoides*, in an oligotrophic Precambrian Shield lake. *Canadian Field-Naturalist* 95(3):298-306.
- Miller, K. D., and R. H. Kramer. 1971. Spawning and early life history of largemouth bass (*Micropterus salmoides*) in Lake Powell. Pages 78-83 in G. E. Hall editor. *Reservoir fisheries and limnology*. American Fisheries Society, Special Publications 8, Bethesda, Maryland.
- Miller, S. J., and T. Storck. 1982. Daily growth rings in otoliths of young-of-the-year largemouth bass. *Transactions of the American Fisheries Society* 111:527-530.

- Miranda, L. E., W. L. Shelton, and T. D. Bryce. 1984. Effects of water level manipulations on abundance, mortality, and growth of young-of-the-year Largemouth Bass in West Point Reservoir, Alabama – Georgia. *North American Journal of Fisheries Management*. 4:314:320.
- Morgensen, S. A. 1983. The effects of water level fluctuations on the spawning success of largemouth bass (Micropterus salmoides) in Lake Mead. *Symposium on the Aquatic Resources Management of the Colorado River Ecosystem*. Chapter 33:563-578.
- Neal, J. W., R. L. Noble, C. G. Lilyestrom, T. N. Churchill, A. R. Alicea, D. E. Ashe, F. M. Holliman, and D. S. Waters. 1999. *Freshwater Sportfish Community Investigations and Management*. Final Report. Federal Aid in Sport Fish Restoration Project F-41-2. Puerto Rico Department of Natural and Environmental Resources.
- Neal, J. W., R. L. Noble, and T. N. Churchill. In press. Timing of largemouth bass supplemental stocking in a tropical reservoir: impacts on growth and survival. Pages X-XX in D. P. Phillip and M. S. Ridgeway, editors. *Black Bass 2000 Symposium*. American Fisheries Society, Symposium in press.
- Phillips, J. M., J. R. Jackson, and R. L. Noble. 1997. Spatial Heterogeneity in abundance of age-0 largemouth bass among reservoir embayments. *North American Journal of Fisheries Management* 17:894-901.
- Ploskey, G. R. 1986. Effects of water-level changes on reservoir ecosystems, with implications for fisheries management. Pages 86-97 in G. E. Hall and M. J. Van Den Avyle, editors. *Reservoir fisheries management: strategies for the 80's*.

Reservoir Committee, Southern Division American Fisheries Society, Bethesda, Maryland, USA.

Raibley, P. T., T. M. O'Hara, K. S. Irons, K. D. Blodgett, and R. E. Sparks. 1997.

Largemouth bass size distribution under varying annual hydrological regimes in the Illinois River. *Transactions of the American Fisheries Society* 126:850-856.

Sammons, S. M., and P. W. Bettoli. 2000. Population dynamics of a reservoir sport fish community in response to hydrology. *North American Journal of Fisheries Management* 20:791-800.

Sammons, S. M., L. G. Dorsey, P. W. Bettoli, and F. C. Fiss. 1999. Effects of reservoir hydrology on reproduction by largemouth bass and spotted bass in Normandy Reservoir, Tennessee. *North American Journal of Fisheries Management* 19:78-88.

SAS Institute, Inc. 1993. *SAS/ETS user's guide, version 6, second edition*. SAS Institute, Inc., Cary, North Carolina.

Summerfelt, R. C. 1975. Relationship between weather and year-class strength of largemouth bass. Pages 166-174 *in* R. H. Stroud and H. Clepper, editors. *Black bass biology and management*. Sport Fishing Institute, Washington, D. C.

Waters, D. S. 1999. Spawning season and mortality of adult largemouth bass (*Micropterus salmoides*) in a tropical reservoir. M. S. thesis. North Carolina State University, Raleigh, North Carolina.

Zack, A., and M. C. Larsen. 1993. Puerto Rico and the U.S. Virgin Islands. Pages 126-134 *in* A. R. De Souza, editor. *Water: reflections on an elusive resource*. Research & Exploration 9. National Geographic Society, Washington, DC.

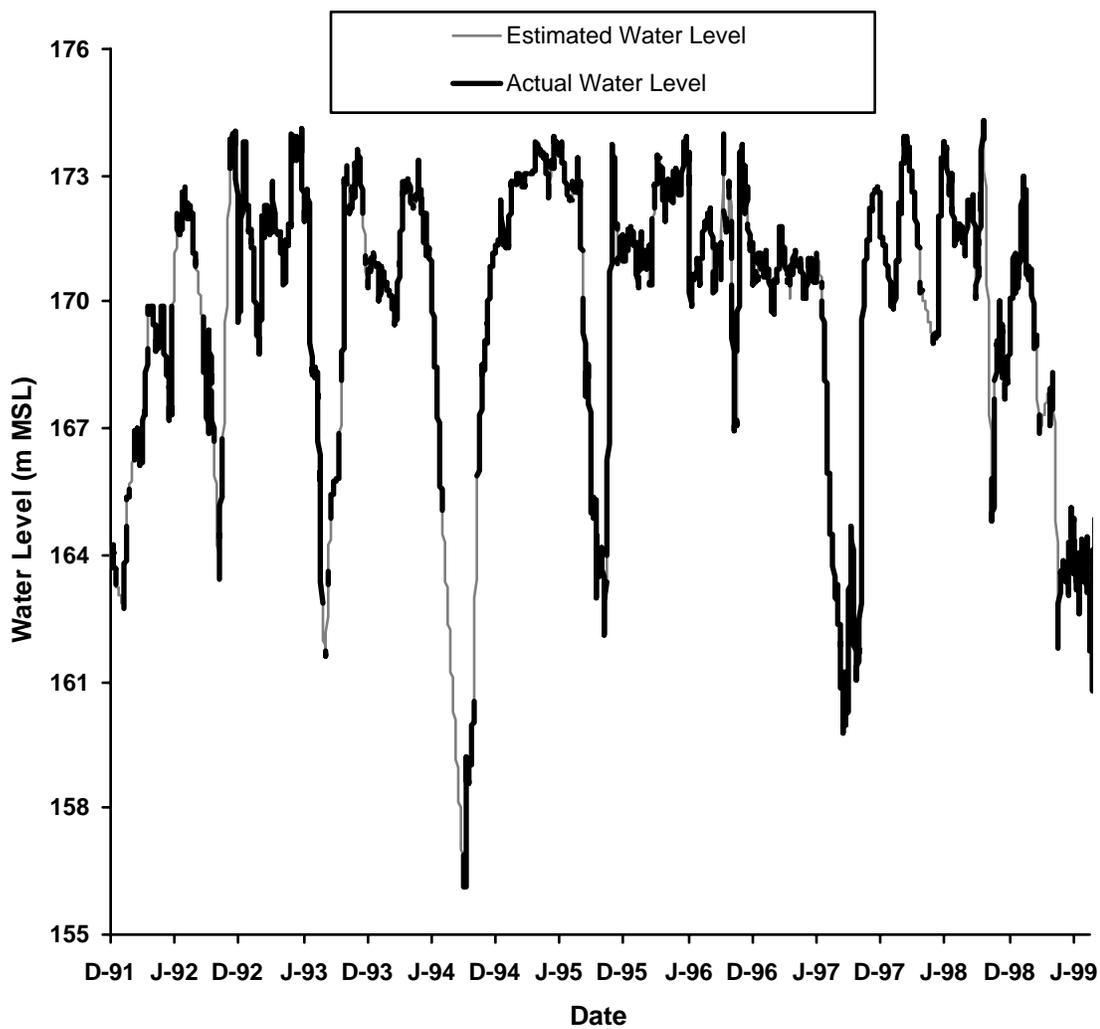


Figure 1. Water level fluctuations (m MSL) in Lucchetti Reservoir between December 1991 and June 1999. Solid lines represent actual water level; dashed lines are the estimated water level.

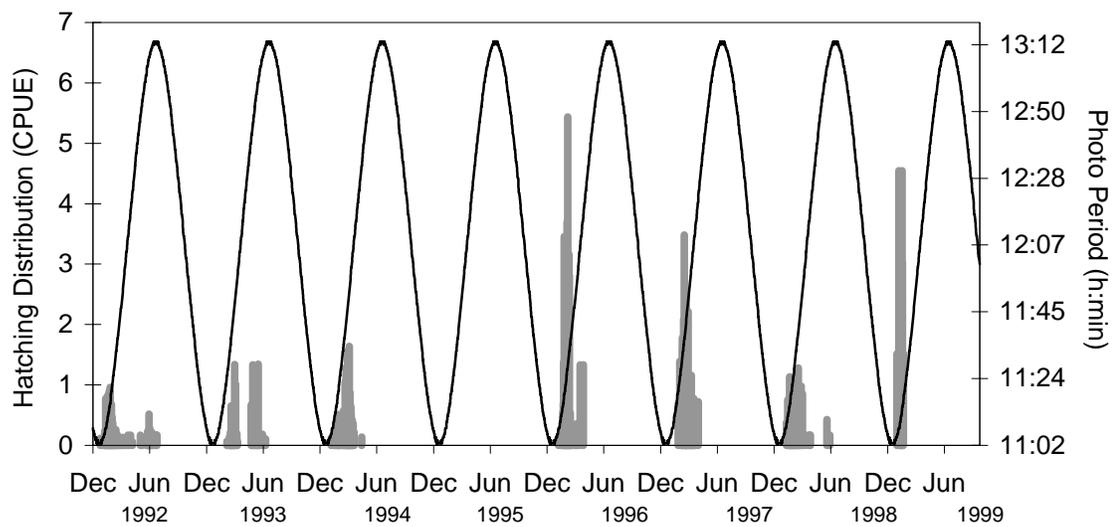


Figure 2. Hatching distribution histograms (CPUE of largemouth bass <100 mm TL) and photoperiod (h) in Lucchetti Reservoir, 1992 to 1994 and 1996 to 1999.

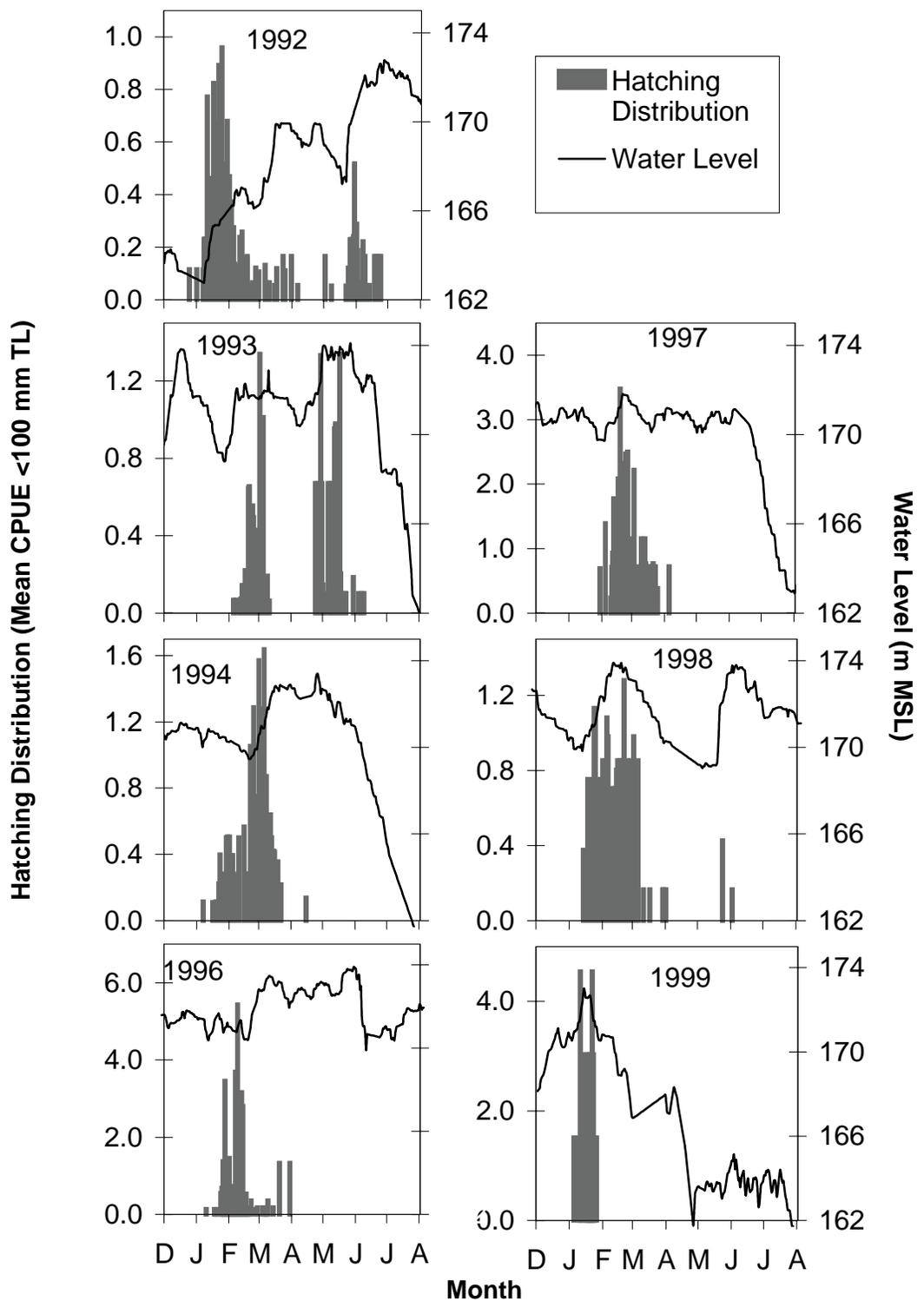


Figure 3. Largemouth bass hatching distributions (histograms) and water levels (solid lines) in Lucchetti Reservoir. Hatching distributions are derived from the annual mean CPUE for largemouth bass less than 100 mm TL.

## **CHAPTER III**

### **Relationship between Largemouth Bass Recruitment and Water Level Dynamics in a Puerto Rico Reservoir**

## **Abstract**

Age-1 largemouth bass electrofishing catch-per-unit-effort (CPUE) varied five fold between 1994 and 2001 in Lucchetti Reservoir, Puerto Rico. CPUE of age-1 largemouth bass was higher in years when the water level of the previous year (1993-2000) remained high during the spawning period (January-June). Year-class strength was also adversely affected by water level fluctuations. The greatest water level drop (11.2 m) during the spawning period was observed in 1999, resulting in a water volume decrease of 66.5 %, and corresponded to the lowest recruitment (CPUE 24.2 fish\*h<sup>-1</sup>) for the years studied. With only 2.6 m of water level drop and 18.3 % water volume decrease during the spawning period, the 1995 largemouth bass cohort appeared to be the strongest (CPUE 128.3 fish\*h<sup>-1</sup>). The effect of these hydrological variables on largemouth bass recruitment appeared to be exponential rather than linear. Age-1 largemouth bass comprise the majority of the fishable stock in Lucchetti Reservoir, and the stock is typically below carrying capacity. Thus, the potential exists to adopt a water level management plan during the spawning period (January-June) of largemouth bass to ensure successful largemouth bass recruitment into the next year's fishable stock.

## **Introduction**

Instability in fish recruitment challenges fisheries managers as these variations result in stock fluctuations, which in turn can cause annual disparities in catch rates for anglers. Consequently stock assessment programs frequently need to be conducted annually for managed fisheries.

Fluctuations in year-class strength of largemouth bass are common and therefore have been widely investigated in temperate North America (Ludsin and DeVries 1997) where the fishable stock typically is comprised of multiple age groups. In Lucchetti Reservoir, Puerto Rico, the adult largemouth bass population is comprised primarily of two age groups, age-1 and age-2 (Neal et al. 1999), i.e., recruitment occurs at age 1. Therefore, variation in year-class strength has a strong effect on the fishable largemouth bass stock, as two successive failures of largemouth bass recruitment would result in the collapse of the fishery. Ashe et al. (1998) reported that Lucchetti Reservoir experienced a 3-fold variation in adult largemouth bass population size over a 5-year period. Although age composition cannot be directly obtained for other Puerto Rico reservoirs because of indistinctive annuli (Neal et al. 1997), largemouth bass size composition in most Puerto Rico reservoirs is similar to that in Lucchetti Reservoir (Neal et al. 1999).

Year-class strength of largemouth bass has been attributed to several different biotic factors such as prey abundance (Aggus and Elliott 1975), growth of age-0 fish possibly affecting overwinter survival (Gutreuter and Anderson 1985; Ludsin and DeVries 1997; Garvey et al. 1998; Pine et al. 2000), spawning adult size (Miranda and Muncy 1987; Goodgame and Miranda 1993), and predators (Miranda and Hubbard

1994). Intracohort cannibalism, which can affect recruitment, has also been reported for largemouth bass (Johnson and Post 1996). In Lucchetti Reservoir, largemouth bass intracohort cannibalism may be more pronounced because fast growth and extended spawning broaden size distribution.

Abiotic factors may also be responsible for recruitment variation. Temperature (Summerfelt 1975; Jackson and Noble 2000), wind action (Kramer and Smith 1962; Summerfelt 1975), and hydrological conditions (Miranda et al. 1984; Willis 1986; Wright 1991; Yeager et al. 1992; Kohler et al. 1993; Reinert et al. 1995; Ploskey et al. 1996; Maceina and Bettoli 1998; Sammons and Bettoli 2000) have also been implicated in year-class strength variation of largemouth bass.

First year dynamics of largemouth bass are highly dependent upon the littoral zone (Noble et al. 1994). Habitat conditions in the littoral zone are essential for spawning, hatching, and feeding, as well as for cover. Water level regimes, through their extreme impact on the littoral zone, potentially affect recruitment directly or indirectly as they influence any of these essential dimensions for age-0 largemouth bass.

Although the relation of largemouth bass and water level regime has been investigated extensively for reservoirs, the types of hydrological conditions that influence largemouth bass recruitment differ in these studies. Reinert et al. (1995) found significant correlation between catch rates of age-0 largemouth bass and inflow to release ratio; but for one of their studied reservoirs the correlation was with mean surface area, which implies a water level effect. Ploskey et al. (1986) found correlation between largemouth bass recruitment and hydrological conditions including surface area. In some reservoirs, high water levels increased largemouth bass recruitment (Kohler et al. 1993;

Sammons and Bettoli 2000), but early dry summer (Maceina and Bettoli 1998) and drought conditions (Buynak et al. 1991), possibly associated with consistent water levels, have also been linked to stronger largemouth bass year-classes.

Water temperatures in Lucchetti Reservoir range only from 24 to 30° C and water level fluctuations as high as 17 m have occurred (Churchill et al. 1995). I hypothesized that largemouth bass year-class strength in this tropical reservoir, where over-winter mortality associated with low temperatures should not occur, was mainly dictated by hydrological conditions during the first year of life. My main objective was to evaluate the effects of water level fluctuation during spawning and early nursery period (age-0) on recruitment (age-1) with the goal of providing a feasible water level management plan for successful largemouth bass management in extremely fluctuating reservoirs.

## **Methods**

Lucchetti Reservoir is a 108-ha impoundment located on the river basin of Rio Yauco, in southwest Puerto Rico. The drainage area is about 45.1 km<sup>2</sup>. The basin of the reservoir is located in a subtropical moist forest, where annual precipitation is about 198 cm. Lucchetti Reservoir serves as the major and most important flow regulation structure within the basin (Quinones-Aponte 1986), and therefore is subject to high water level fluctuations. Retention time is about 0.66 years.

When completed in 1952, Lucchetti Reservoir provided about 20.35 ha-m<sup>3</sup> of usable storage for irrigation to the arid Lajas Valley. However, by 1978 the storage capacity decreased to 14.30 ha-m<sup>3</sup> with a mean sediment accumulation of 25 cm\*year<sup>-1</sup> (Zack and Larsen 1993). Mean depth of the reservoir at pool level was about 11.6 m in

1952. A maximum depth of 54.3 m at the spill level of 174 m above the sea level was cited by Churchill et al. (1995), but Neal et al. (1999) reported that the maximum depth encountered was 22.2 m, supporting the earlier findings of heavy sediment accumulation.

Lucchetti Reservoir was sampled by electrofishing twice each year from 1994-2001 for mark-recapture estimation of largemouth bass  $\geq 250$  mm total length (TL) (Ashe et al. 1998; Neal et al. 2001). For each sample, the entire shoreline was electrofished, typically over a 3-day period, using a boom-mounted electrofisher at 240-V pulsed DC. All age-1 and older largemouth bass were collected and measured. Effort was recorded as seconds of actual electrofishing. Catch-per-unit-effort (CPUE) of age-1 largemouth bass was calculated for the second sampling period each year, usually between January and early March.

Fish were classified as age-1 or 2+ based on the length-frequency distribution because annual ageing of largemouth bass with otoliths is not possible in Lucchetti Reservoir (Neal et al. 1997). Largemouth bass growth in Lucchetti Reservoir is relatively fast for the first year, and slows markedly by age 1; therefore some overlapping of length distributions with older fish groups occur in some years (Figure 1). To separate the age-1 from the older fish, I assumed normality of the length frequency distribution of age-1 fish and applied the Bhattacharya method (Sparre and Venema 1998) to each annual distribution (Figure 1). Frequencies of age-1 were divided by the electrofishing time (h) to obtain CPUE of age-1.

Daily water levels for Lucchetti Reservoir from January 1992 to December 2000 were obtained from the United States Geological Survey. Missing data (about 12%) were

estimated by using PROC EXPAND command with METHOD=JOIN in SAS® (1996) (Figure 2). This method simply fits a continuous curve to the data.

Water volume of the reservoir for some of the elevations was obtained from Díaz et al. (1998) (Figure 3). Different regression models were fit to these data and the model with the best fit was used to predict the capacity of the reservoir for the unavailable water level elevations (Figure 3).

To examine the effect of water level fluctuation on year-class strength, CPUE of age-1 largemouth bass was correlated to several hydrological variables from the previous year when these fish were age-0. The variables for the water levels were calculated from January to June, July, and August. Largemouth bass typically start to spawn in January, and in June most of the spawning is completed (Ozen and Noble in press). In July the reservoir water level is typically lowered sharply in preparation for the hurricane season. The January-August period was also analyzed because the stage at which the largemouth bass cohort is set was not known in Lucchetti Reservoir; water level dynamics during the summer could affect the largemouth bass year-class in early life stages.

Analyzing only the time intervals when the spawning occurred would not be appropriate for my analyses, because my main goal was to investigate if recruitment at age 1 was affected by hydrological variables. Spawning could have occurred at different time periods during the spawning season if the water level conditions were appropriate (Ozen and Noble in press). In addition, recruitment is not only the result of hatching but also of survival. Therefore, hydrological conditions during, between, and after spawning events may have an effect on recruitment processes.

The hydrological variables used in the analyses for each period and the theorized possible biological effects of these variables on the year-class formation were as follows:

- mean water levels (MWL), as an indicator of littoral habitat on average
- standard deviations of the daily water levels (STDWL), as stress put on the eggs and juveniles due to fluctuating water levels and thereby exposing life stages to different habitat and depths
- minimum water level attained (MinWL), as a index of the highest fish density realized
- maximum water level attained (MaxWL), as a index of how much littoral zone was available at maximum at a given day
- sum of the daily water declines (SumWLD), as an indicator of force to migrate to deeper water for both the parents that guard the nests and the juvenile largemouth bass
- sum of the water incline for consecutive days (SumWLI), as an index of how much allochthonous nutrients could have been added to the system
- maximum percentage change of the water volume between the maximum and minimum water level attained (PerWVC), as an index of how much space was lost and how much overall fish density increased

Although inter-correlations of some of these hydrological variables were anticipated (see Appendix), different implications were expected from the various analyses. My intention of using all these variables was to investigate what kind of water level management plan would improve recruitment the most, and also to provide different water level management plan options for the authorities.

Data were analyzed using single and multiple linear regressions. Nonlinear analyses were also conducted to investigate exponential relationships. All analyses were performed using SAS software (SAS 1998). Results were considered significant at  $P < 0.05$ .

## **Results**

Water volume-elevation relation was best described with a quadratic regression model (Figure 3). A significant ( $P < 0.01$ ) relation with very high predictability ( $R^2 = 1.0$ ) ensured that the predicted values between the measured data points were accurate. Also, the water levels used for predicting the unavailable water volume data were within the range of the provided data (156.1-176.2 m MSL).

Water level analyses for the whole calendar years between 1993 and 2000 revealed that highest water level attained in Lucchetti Reservoir was 174.3 m MSL on 21 September 1998, when Hurricane George passed over Puerto Rico (Figure 2). The lowest water level, 156.1 m MSL, was observed on 8 September 1994. For that year, the highest water level was 173.4 on 26 April, resulting in a water volume reduction of 86.4% in a time period of less than 5 months (Figures 2 and 3). Also, in 1994, the water levels had the highest fluctuation rate with a STD of 4.99 m MSL. The most stable water levels, on the other hand, were observed in 1996 and 2000 with STDs of 1.28 and 1.38 m MSL, respectively.

Age-1 fish comprised the majority of the largemouth bass stock in most years (Figure 1), and size distribution of age-1 fish was typically unimodal. Catch-per-unit-effort data indicated approximately 5-fold variation in year-class strength at age-1. Age-

1 CPUE of largemouth bass from electrofishing samples was highest for the 1995 cohort (128.3 fish\*h<sup>-1</sup>; Table 1), which coincided with the highest MWL during the spawning season (January-June) (173.1 m MSL; Figures 1-2). The lowest CPUE (24.2 fish\*h<sup>-1</sup>; Table 1) was observed for the 1999 cohort, corresponding to the lowest rate of MWL of 166.9 m MSL during the spawning period (Figures 1-2).

Significant positive relationships ( $P < 0.05$ ) were evident between age-1 CPUE and MWL and MinWL (Table 2). Significant negative relationships ( $P < 0.05$ ) existed between age-1 CPUE and STDWL, PerWVC, and SumWLD (Table 2). Maximum water level (MaxWL) and SumWLI were not significantly related ( $P < 0.05$ ) to the CPUE of age-1 largemouth bass. Maximum water levels attained were always observed earlier than June; therefore this value was the same for all three time periods analyzed (Table 1).

Multiple linear regression analyses produced no model including a second significant ( $P > 0.05$ ) variable. Multi-collinearity was typically high among the independent variables (see Appendix).

Using nonlinear analyses, 82% of the variation of age-1 CPUE was explained by STDWL between January and July ( $P < 0.05$ ; Figure 4). MWL explained 61% of the age-1 variation and PerWVC explained 78% of the variation ( $P < 0.05$ ; Figures 5-6).

## **Discussion**

Year-class strength of largemouth bass appeared to be highly affected by hydrological conditions during and after the spawning period (January-June) between 1993 and 2000 in Lucchetti Reservoir. For the periods analyzed, mean water level and the minimum water level observed were positively related to largemouth bass

recruitment, whereas the relation was negative for the standard deviation, sum of the successive daily water declines, and the percentage of water volume change. No significant relations were observed between largemouth bass year-class strength and the sum of water level inclines, and the maximum water level attained during or post spawning season.

In contrast to this study, Kohler et al. (1993) and Maceina and Bettoli (1998) found no relation between largemouth bass year-class strength and water level fluctuations. However, their observations were from reservoirs where water level fluctuations were most of the time less than 2 m during the spawning periods for the years they investigated. In Lucchetti Reservoir, the minimum water level fluctuation during the spawning period was 2.6 m (1995), corresponding to the strongest year-class (age-1 CPUE 128.3 fish\*h<sup>-1</sup>); the maximum water level fluctuation was 11.2 m (1999) corresponding to the weakest year-class (age-1 CPUE 24.2 fish\*h<sup>-1</sup>) in this study. My results support the findings of Garvey et al. (2000), who found that daily water level variations were negatively related to mean CPUE of age-0 largemouth bass in a study of four Ohio reservoirs.

I believe that the STD of water levels would provide more appropriate estimates of water level fluctuation effects on fish population dynamics than the overall difference of the maximum and minimum water levels. The water level may rise and drop several times as much as the maximum difference of the water levels. Such fluctuations may have more severe effects on the littoral fish population (e.g., juvenile largemouth bass) than a steady water level decline from the maximum to the minimum water level. In fact, the highest nonlinear relationship ( $R^2 = 0.82$ ) among the variables analyzed for

largemouth bass recruitment strength was obtained with the STDWL with an exponential effect for the period of January-July (Figure 5). Water level changes during and after the spawning would cause eggs or juvenile fish to be exposed to different habitat types and different depths. Neal et al. (In press) indicated that littoral cover is reduced and major substrate change occurs with a decline of only about 2 m in Lucchetti Reservoir.

Declining water levels (SumWLD) seem to affect recruitment of largemouth bass negatively, whereas increasing levels (SumWLI) showed no positive effect. Water level declines during the breeding cycle could cause male abandonment of guarded nests, or eggs could be exposed to air (Maraldo and MacCrimmon 1981; Morgensen 1983). Wind actions can also reduce hatching success during the breeding cycle when the water depths of the nests decline (Miller and Kramer 1971). Although not statistically significant ( $P > 0.05$ ), the SumWLI appeared to have negative impact on year-class formation. Ozen and Noble (in press) indicated that water level increases initiate spawning of largemouth bass in Lucchetti Reservoir, but my results suggest that increasing water levels do not contribute to year-class strength. However, any declining water level should increase eventually; therefore the water level increases were higher in years when the water level declines were also higher and therefore declining water levels may have obscured any positive impact of water level increases on largemouth bass recruitment.

Relatively high water levels (MWL) during the spawning periods resulted in stronger year-classes (Figure 4). Several studies have demonstrated that higher largemouth bass recruitment occurs when water levels remain relatively higher during the spawning period (Aggus and Elliot 1975; Morgensen 1981; Miranda et al. 1984; Reinert et al. 1995; Raibley et al. 1997; Sammons and Bettoli 2000). Waters (1999), in a

telemetry study of largemouth bass in Lucchetti Reservoir, found that adults quickly left spawning grounds when water levels declined. Spawners returned when water levels stabilized, even if water levels did not return to previous elevation. Mean water level can be considered as an index of average space available over time. Higher water levels cause extension of the littoral zone and thereby provide more habitat for the juvenile largemouth bass. Correlation coefficients between MWL and age-1 CPUE continued to increase as terminal period for the hydrological variable was extended from June to July to August (Table 1), suggesting possible effects of improved nursery habitat.

A water volume decline (PerWVC) of 66.5% was observed during the spawning period in 1999 that corresponded to the lowest recruitment of largemouth bass in this study (Figure 6). This decline began early in the season (Figure 2). A more drastic change of water volume (84.4 %) was observed in 1994 for the period of January-August and this year resulted in the second lowest largemouth bass production. This decline began about two months later than in 1999. It is possible that the PerWVC during the spawning period (January-June) has a greater effect than it has later in the season (August) and that largemouth bass year-class strength is primarily fixed somewhere in July. In fact, except for MWL for which the correlation was highest for the January-August period, all other variables had the highest correlation for the period of January-July.

Decrease in water volume would result in an increase of fish population density. Predators would benefit from this by having their prey closer and in higher density (Forbes 1887) and juvenile largemouth bass, especially the smaller ones, would be subject to higher mortality rates (Miranda and Hubbard 1994). In contrast, prey for

juvenile largemouth bass could also be concentrated, possibly improving growth and survival.

Maximum water level (MaxWL) achieved during the spawning period was not a significant factor for the years from 1993-2000 (Table 1). However, MaxWL ranged only from 171.8 to 174.1 m MSL. High water level attained for a period of time could provide allochthonous nutrients into the system (Liston and Chubb 1985). Therefore, a significantly lower MaxWL than was observed could have a possible effect on largemouth bass recruitment by reducing available food and thereby growth.

Based on the contradictory results in the literature, it is probably safe to conclude that hydrological factors affecting largemouth bass recruitment are both specific to the system and related to the magnitude of the variable. Morphology of the system should have effects on how hydrological impacts occur. Yeager et al. (1992) for example, reported largemouth bass densities were significantly related to different hydrological variables in four different systems of which two were mainstream and two were tributary Tennessee Valley Authority reservoirs.

Lucchetti Reservoir is characterized by a steeply sloping shoreline. In reservoirs with less steep slopes, water level fluctuations with similar magnitudes could affect year-class strength even more than they would in Lucchetti Reservoir, because the change in the amount of littoral zone for reservoirs with gentle shoreline slope would be much more pronounced. In contrast, Lucchetti Reservoir, with its high water level fluctuations, experiences dramatic changes in littoral zone composition despite steeper sloping shorelines.

## **Management Implications**

Jenkins (1970) stated that water level management may be deleterious if not carefully designed, but water level manipulation could be the most effective management tool in reservoirs if it is soundly planned. Water level management for black bass has been adopted by more than half of the state agencies in the U.S. (Noble in press).

Although Sammons and Bettoli (2000) claimed that water level management plans for black bass were usually impossible because of conflicts with other water level management plans, I believe that a compromise of water level management could be achieved despite the different user groups and the multiple purposes of the reservoirs. For example, a significant increase of largemouth bass electrofishing catch rates were reported after applying a stable or gradual declining water level plan in Eufaula Lake, Oklahoma (Wright 1991).

In this study I used age-1 largemouth bass electrofishing CPUE as an indication of year-class strength. Age-1 largemouth bass had a total length of 250 mm or greater in most of the years (Figure 1). The largemouth bass population in Lucchetti Reservoir is comprised of 2 or 3 year-classes, age-1 being the major fishable stock (Figure 1). Ashe et al. (1998) found that even at the highest largemouth bass population levels recorded, carrying capacity was not exceeded. Therefore, a water level management plan during the first six to eight months of the year would directly contribute to the largemouth bass fishery the following year.

Environmental factors cannot be controlled and the general social priority during hurricane season is not the recreational fishery. However, since the 16th century no hurricane or tropical storm affected Puerto Rico before July (Figure 7). If necessary for

hurricane season preparation, water levels should be declined gradually and as late as possible in the season. I believe that adopting a water level stabilization management plan, at least for the spawning period (January-June), in Lucchetti Reservoir would benefit the largemouth bass fishery through enhanced recruitment. Because of the contradicting results reported in the literature, I also believe that water level management plans should be based on long term studies and should be developed specifically for the systems where the plans are to be implemented.

## References

- Aggus, L. R., and G. V. Elliott. 1975. Effects of cover and food on year-class strength of largemouth bass. Pages 317-322 in. R. H. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fishing Institute, Washington, D. C.
- Ashe, D. E., T. N. Churchill, R. L. Noble, and C. G. Lilyestrom. 1998. Temporal variability in the littoral fish community of a Puerto Rico reservoir. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 52:39-48.
- Churchill, T. N., R. L. Noble, J. E. Gran, and A. R. Alicea. 1995. Largemouth bass recruitment in Lucchetti Reservoir. Final Report. Federal Aid in Sportfish Restoration Project F-16-2. Puerto Rico Department of Natural and Environmental Resources, San Juan, Puerto Rico. 74 pp.
- Díaz, P.L., Aquino, Zaida, Figueroa-Alamo, Carlos, Vachier, R.J., and Sánchez, A.V., 1998, Waterresources data Puerto Rico and the U.S. Virgin Islands Water Year 1997: U.S. Geological Survey Water-Data Report PR-97-1, 548 p.
- Forbes, S. A. 1887. The lake as a microcosm. Bulletin of Peoria Scientific Association pp. 77-87. Reprinted in Bulletin of the Illinois State Natural History Survey 15 (1925):537-550. Page 14-27 in L. A. Real and J. H. Brown, editors. Foundations of Ecology – Classical papers with commentaries. The University of Chicago Press, Chicago (1991).

- Garvey, J. E., R. A. Wright, and R. A. Stein. 1998. Overwinter growth and survival of age-0 largemouth bass (Micropterus salmoides): Revisiting the role of body size. *Canadian Journal of Fisheries and Aquatic Sciences* 55:2414-2424.
- Garvey, J. E., R. A. Wright, R. A. Stein, and K. H. Ferry. 2000. Evaluating how local- and regional-scale processes interact to regulate growth of age-0 largemouth bass. *Transactions of the American Fisheries Society* 129:1044–1059.
- Goodgame, L. S., L. E. and Miranda. 1993. Early growth and survival of age-0 largemouth bass in relation to parental size and swim-up time. *Transactions of the American Fisheries Society* 122:131-138.
- Gutreuter, S. J., and R. O. Anderson. 1985. Importance of body size to the recruitment process in largemouth bass populations. *Transactions of the American Fisheries Society* 114:317-327.
- Jackson, J.R. and R.L. Noble. 2000. Relationship between annual variations in reservoir conditions and age-0 largemouth bass year-class strength. *Transactions of the American Fisheries Society* 129:699-715.
- Jenkins, R. M. 1970. Reservoir fish management. Pages 173-181 in Benson N. G, editor. *A century of fisheries in North America*. American Fisheries Society, Special Publications 7.
- Kohler, C. C., R. J. Sheehan, and J. J. Sweatman. 1993. Largemouth bass hatching success and first-winter survival in two Illinois reservoirs. *North American Journal of Fisheries Management* 13:125-133.
- Kramer, R. H., and L. L. Smith, Jr. 1962. Formation of year classes in largemouth bass. *Transactions of the American Fisheries Society* 91:29-41.

- Liston, C. R., and S. Chubb. 1985. Relationships of water level fluctuations and fish. Pages 121-140 in H. H. Prince and F. M. D'Istri, editors. Coastal Wetlands. Lewis Publishers, Chelsea, Michigan.
- Ludsin, S. A., and D. R. DeVries. 1997. First-year recruitment of largemouth bass: the interdependency of early life stages. *Ecological Applications* 7(3):1024-1038.
- Maceina, M. J., and P. W. Bettoli. 1998. Variation in largemouth bass recruitment in four mainstream impoundments of the Tennessee River. *North American Journal of Fisheries Management* 18:998-1003.
- Maraldo, D. C., and H. R. MacCrimmon. 1981. Reproduction, distribution, and population size of largemouth bass, Micropterus salmoides, in an oligotrophic Precambrian Shield lake. *Canadian Field-Naturalist* 95(3):298-306.
- Miller, K. D., and R. H. Kramer. 1971. Spawning and early life history of largemouth bass (Micropterus salmoides) in Lake Powell. Pages 78-83 in G. E. Hall editor. Reservoir fisheries and limnology. American Fisheries Society, Special Publications 8, Bethesda, Maryland.
- Miranda, L. E., and R. J. Muncy. 1987. Recruitment of young-of-year largemouth bass in relation to size structure of parental stock. *North American Journal of Fisheries Management* 7:131-137.
- Miranda, L. E., and W. D. Hubbard. 1994. Winter survival of age-0 largemouth bass relative to size, predators, and shelter. *North American Journal of Fisheries Management* 14:790-796.

- Miranda, L. E., W. L. Shelton, and T. D. Bryce. 1984. Effects of water level manipulations on abundance, mortality, and growth of young-of-the-year Largemouth Bass in West Point Reservoir, Alabama – Georgia. *North American Journal of Fisheries Management*. 4:314:320.
- Morgensen, S. A. 1983. The effects of water level fluctuations on the spawning success of largemouth bass (Micropterus salmoides) in Lake Mead. *Symposium on the Aquatic Resources Management of the Colorado River Ecosystem*. Chapter 33:563-578.
- Neal, J. W., N. M. Bacheler, R. L. Noble, and C. G. Lilyestrom. In press. Effects of Reservoir Drawdown on Available Habitat: Implications for a Tropical Largemouth Bass Population. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 55: (in press).
- Neal, J. W., R. L. Noble, A. R. Alicea, and T. N. Churchill. 1997. Invalidation of otolith ageing techniques for tropical largemouth bass. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 51:159-165.
- Neal, J. W., R. L. Noble, C. G. Lilyestrom, N. M. Bacheler, and J. C. Taylor. 2001. *Freshwater Sportfish Community Investigations and Management*. Final Report. Federal Aid in Sport Fish Restoration Project F-41-2. Puerto Rico Department of Natural and Environmental Resources, San Juan, Puerto Rico. 96 pp.
- Neal, J. W., R. L. Noble, C. G. Lilyestrom, T. N. Churchill, A. R. Alicea, D. E. Ashe, F. M. Holliman, and D. S. Waters. 1999. *Freshwater Sportfish Community Investigations and Management*. Final Report. Federal Aid in Sport Fish

- Restoration Project F-41-2. Puerto Rico Department of Natural and Environmental Resources, San Juan, Puerto Rico. 113 pp.
- Noble, R. L. In press. Reflections on 25 years of progress in black bass management. Pages X-XX in D. P. Phillip and M. S. Ridgeway, editors. Black Bass 2000 Symposium. American Fisheries Society, Symposium in press.
- Noble, R. L., J. R. Jackson, E. R. Irwin, J. M. Phillips, and T. N. Churchill. 1994. Reservoirs as landscapes: Implications for fish stocking programs. Transactions of the North American Wildlife and Natural Resources Conference 59:281-288.
- Ozen, O., and R. L. Noble. In press. Relationship between water level fluctuations and largemouth bass spawning in a Puerto Rico reservoir. Pages X-XX in D. P. Phillip and M. S. Ridgeway, editors. Black Bass 2000 Symposium. American Fisheries Society, Symposium in press.
- Pine, W. E., S. A. Ludsin, and D. R. DeVries. 2000. First-summer survival of largemouth bass cohorts: is early spawning really best? Transactions of the American Fisheries Society 129:504-513.
- Ploskey, G. R. 1986. Effects of water-level changes on reservoir ecosystems, with implications for fisheries management. Pages 86-97 in G. E. Hall and M. J. Van Den Avyle, editors. Reservoir fisheries management: strategies for the 80's. Reservoir Committee, Southern Division American Fisheries Society, Bethesda, Maryland, USA.
- Quinones-Aponte, V. 1986. Simulation of ground-water flow in the Rio Yauco Alluvial Valley, Yauco, Puerto Rico. U.S. Geological Survey Water-Resources Investigations Report 85-4179. San Juan, Puerto Rico. Pages 32.

- Reinert, T. R., G. R. Ploskey, and M. J. Van Den Avyle. 1995. Effects of hydrology on black bass reproduction in four southeastern reservoirs. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 49:47-57.
- Sammons, S. M., and P. W. Bettoli. 2000. Population dynamics of a reservoir sport fish community in response to hydrology. North American Journal of Fisheries Management 20:791-800.
- SAS. 1996. SAS/STAT user's guide, release 6.12. SAS Institute, Cary, North Carolina.
- Sparre, P., and S. C. Venema. 1998. Introduction to tropical fish stock assessment. Part 1. Manual. FAO (Food and Agriculture Organization of the United Nations) Fisheries Technical Paper. No. 306.1, Revision 2. Rome, Italy. 407p.
- Summerfelt, R. C. 1975. Relationship between weather and year-class strength of largemouth bass. Pages 166-174 in R. H. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fishing Institute, Washington, D. C.
- Waters, D. S. 1999. Spawning season and mortality of adult largemouth bass (Micropterus salmoides) in a tropical reservoir. M. S. thesis. North Carolina State University, Raleigh, North Carolina
- Willis, D. W. 1986. Reviews of water level management on Kansas reservoirs. Pages 110-114 in G. E. Hall and M. J. Van Den Avyle, editors. Reservoir fisheries management: strategies for the 80's. Reservoir Committee, Southern Division American Fisheries Society, Bethesda, Maryland, USA.

- Wright, G. L. 1991. Results of a water level management plan on largemouth bass recruitment in Lake Eufaula, Oklahoma. Pages 126-130 in J. L. Cooper and R. H. Hamre, editors. Warmwater Fisheries Symposium I. USDA Forest Service, General Technical Report RM-207. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station Fort Collins, Colorado.
- Yeager, B. L., T. A. McDonough, and J. Taylor. 1992. Spring water level stabilization and relationships between hydrologic, biologic, and fishery characteristics of TVA reservoirs. Review of existing data summary report and recommendations – phase one of the fish spawning task team. Prepared for the reservoir resources re-evaluation task force water resources. Report TVA/WR—92/13.
- Zack, Allen, and Larsen, M.C., 1994, Island hydrology: Puerto Rico and the U.S. Virgin Islands: National Geographic Research & Exploration: Water Issue, p. 126-134.

Table 1. Age-1 CPUE (fish\*h<sup>-1</sup>) obtained from 1994-2001 as year-class strengths for the previous years. Hydrological variables between 1993-2000 for the mean water level (m MSL; MWL), standard deviations for the daily water levels (STDWL), minimum (m MSL; MinWL) and maximum water levels (m MSL; MaxWL), sum of the water level decreases (m; SumWLD) and increases (m; SumWLI) for consecutive days, and the percentage change of the water volume between the maximum and minimum water level attained (PerWVC) for the periods of January to June (Jun), July (Jul), and August (Aug).

Year	Age-1 CPUE	Period	Hydrological Variable						
			MWL	STDWL	MinWL	MaxWL	SumWLD	SumWLI	PerWVC
1993	35.7	Jun	171.6	1.4	168.3	174.1	16.0	12.7	37.6
		Jul	170.8	2.5	162.1	174.1	22.9	13.3	67.7
		Aug	169.9	3.3	161.6	174.1	23.4	17.5	69.8
1994	31.5	Jun	170.9	1.6	165.8	173.4	12.9	7.8	48.7
		Jul	169.8	3.2	161.1	173.4	17.6	7.8	70.2
		Aug	168.4	4.7	156.9	173.4	21.8	7.8	84.4
1995	128.3	Jun	173.1	0.6	171.3	173.9	4.5	5.6	18.3
		Jul	173.0	0.6	171.3	173.9	5.8	7.2	18.3
		Aug	172.5	1.5	166.5	173.9	12.9	8.1	47.0
1996	76.4	Jun	172.1	1.1	169.9	173.9	13.9	13.5	27.1
		Jul	172.0	1.1	169.9	173.9	14.8	15.2	27.1
		Aug	171.9	1.0	169.9	173.9	17.8	17.5	27.1
1997	58.6	Jun	170.7	0.5	168.5	171.8	9.7	7.3	24.8
		Jul	169.8	2.2	163.0	171.8	15.2	7.4	57.5
		Aug	168.8	3.5	159.8	171.8	20.8	10.3	71.8
1998	52.9	Jun	171.5	1.6	169.1	173.9	9.7	11.2	32.3
		Jul	171.5	1.5	169.1	173.9	11.0	12.1	32.3
		Aug	171.6	1.4	169.1	173.9	12.9	13.7	32.3
1999	24.2	Jun	166.9	3.1	161.8	173.0	21.4	14.6	66.5
		Jul	166.4	3.1	161.7	173.0	26.1	17.2	66.7
		Aug	166.1	3.0	160.8	173.0	32.2	25.9	70.5
2000	50.3	Jun	168.3	1.3	166.9	173.0	13.7	11.8	40.9
		Jul	168.3	1.2	166.9	173.0	14.1	13.7	40.9
		Aug	168.4	1.2	166.9	173.0	17.0	18.0	40.9

Table 2. Correlation coefficients between age-1 CPUE (fish\*h<sup>-1</sup>) and the hydrological variables from the previous year and the corresponding P-values (in parentheses). Mean water level (m MSL; MWL), standard deviations for the daily water levels (STDWL), minimum water level attained (m MSL; MinWL), maximum water level attained (m MSL; MaxWL), sum of the water level decreases for consecutive days (m; SumWLD), sum of the water increases for consecutive days (m; SumWLI), and the percentage change of the water volume between the maximum and minimum water level attained (PerWVC) for the periods of January to June (Jan-Jun), July (Jan-Jul), and August (Jan-Aug). Significant correlations (P<0.05) are in bold type.

Variable	Period		
	January – June	January – July	January – August
MWL	0.649 (0.082)	<b>0.737 (0.037)</b>	<b>0.767 (0.027)</b>
STDWL	-0.680 (0.062)	<b>-0.836 (0.010)</b>	-0.562 (0.147)
MinWL	<b>0.781 (0.022)</b>	<b>0.814 (0.014)</b>	0.525 (0.181)
MaxWL*	0.242 (0.565)	0.242 (0.565)	0.242 (0.565)
SumWLD	<b>-0.796 (0.018)</b>	<b>-0.833 (0.010)</b>	-0.693 (0.057)
SumWLI	-0.560 (0.149)	-0.438 (0.278)	-0.487 (0.221)
PerWVC	<b>-0.797 (0.018)</b>	<b>-0.840 (0.009)</b>	-0.501 (0.206)

\*Maximum water level was attained earlier than June and therefore the

correlations with age-1 CPUE were the same for all three periods.

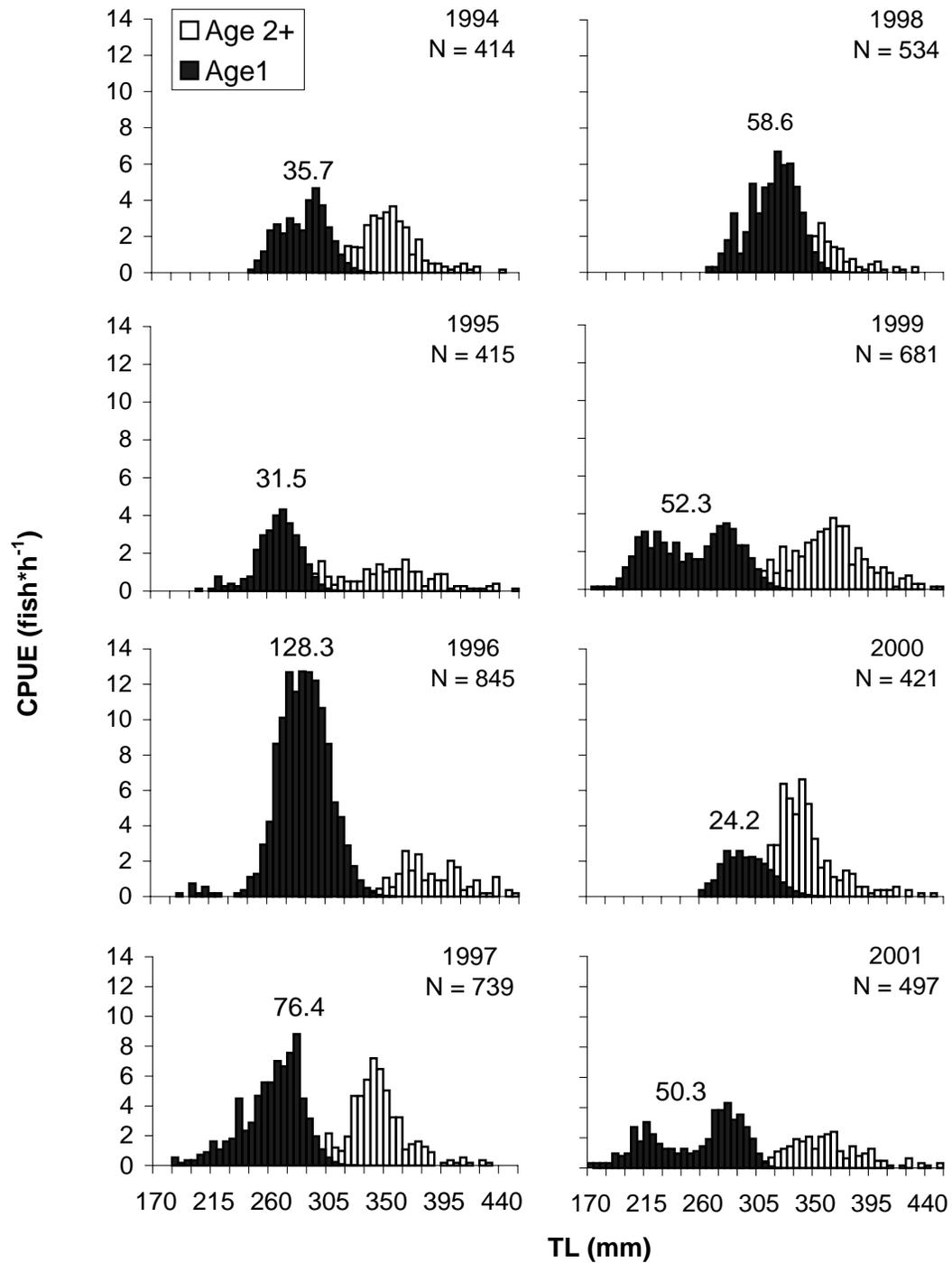


Figure 1. CPUE for age-1 (filled bars) largemouth bass separated from the older population (age 2 and older; open bars) with Bhattacharyya method. Number (N) represents the total frequency of the fish sampled for total length (TL) between 170-450 mm for the years 1994-2001. The number above the age-1 length distribution represents the CPUE for age-1 fish only.

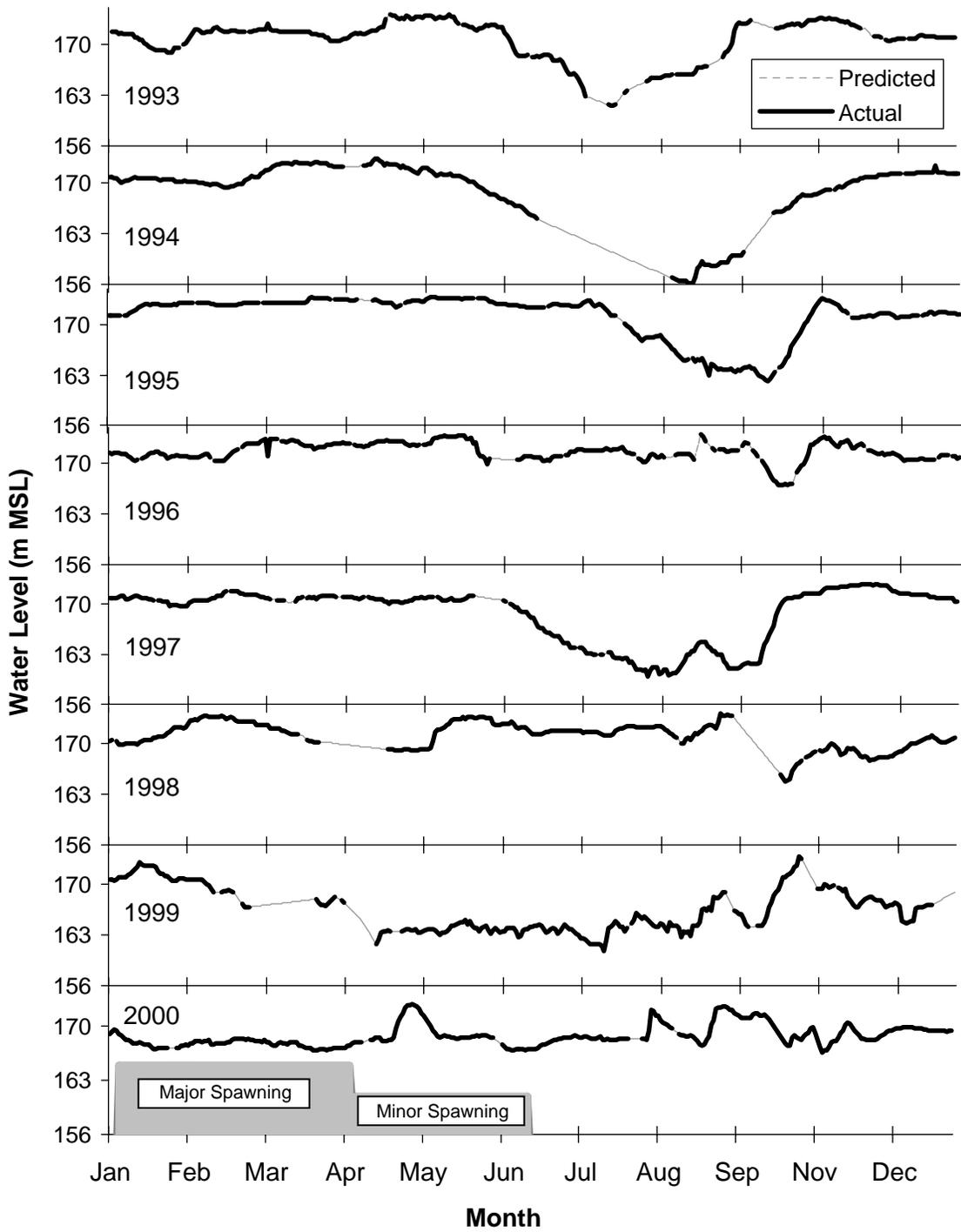


Figure 2. Water levels (m MSL) between January 1993 and December 2000 in Lucchetti Reservoir. Solid lines are the actual data and the dashed lines are the predicted (fitted) data. Spawning period is between January and June, but the majority of the spawning is between January and April.

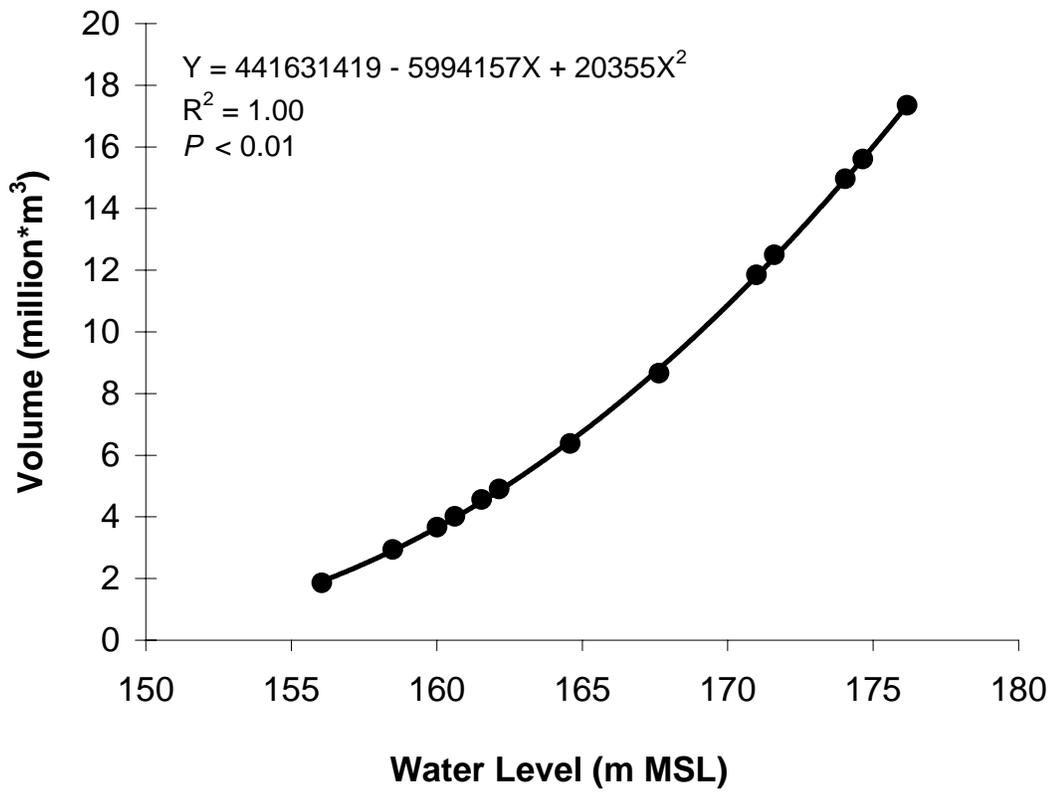


Figure 3. Water volume (m<sup>3</sup>×10<sup>6</sup>) of Lucchetti Reservoir for different water levels (m MSL) and the predicted quadratic regression line.

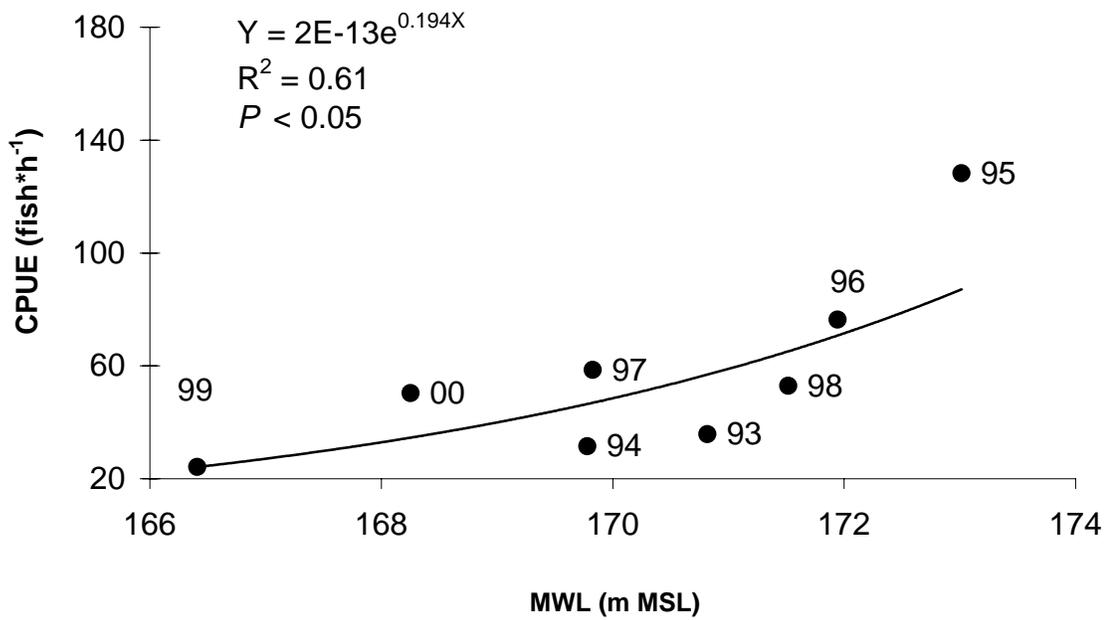


Figure 4. Relationship between CPUE of Age-1 largemouth bass and mean water level (MWL) from the previous year for the period of January-July. The numbers next to the dots represent the last two digits of the year for the cohorts.

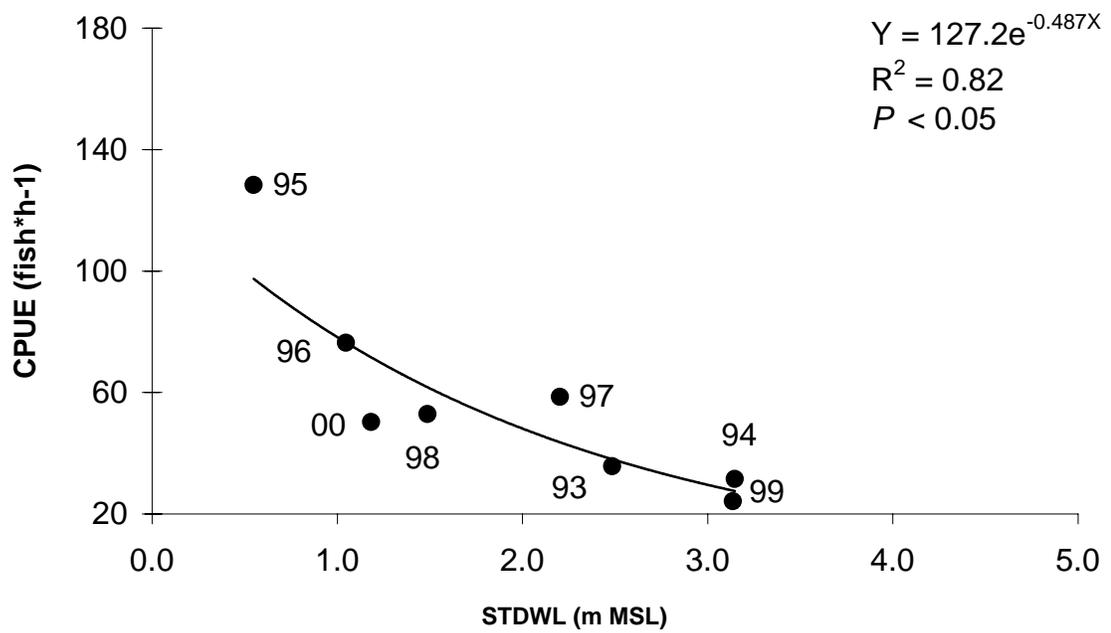


Figure 5. Relationship between CPUE of Age-1 largemouth bass and the standard deviations for the daily water levels (STDWL) from the previous year for the period of January-July. The numbers next to the dots represent the last two digits of the year for the cohorts.

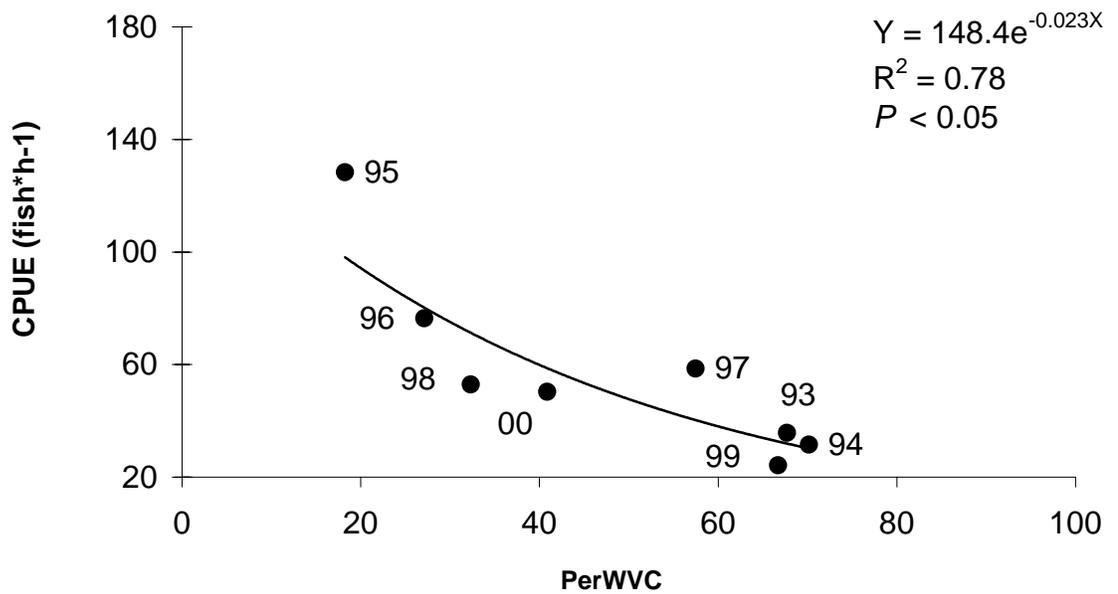


Figure 6. Relationship between CPUE of Age-1 largemouth bass and the percentage water volume change (PerWVC) from the previous year for the period of January-July. The numbers next to the dots represent the last two digits of the year for the cohorts.

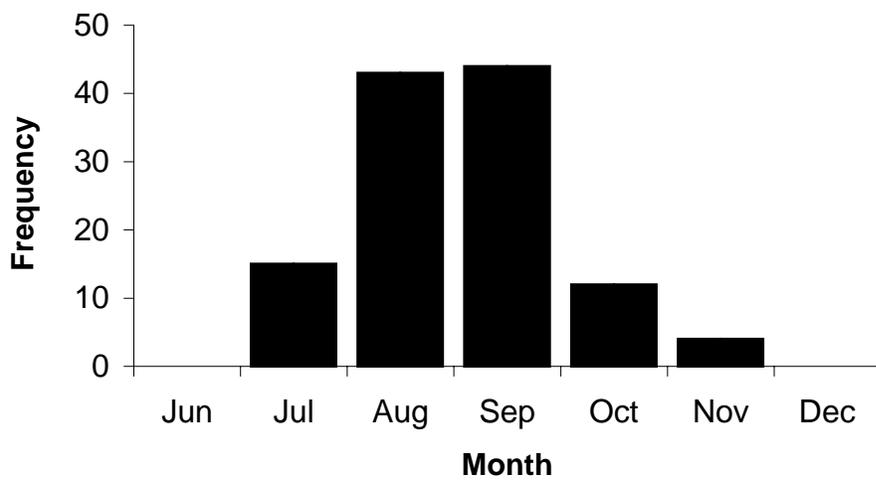


Figure 7. Frequency of tropical storms and hurricanes which passed within two degrees latitude of Puerto Rico and the Virgin Islands from 1515-1999 (Source: National Oceanic and Atmospheric Administration; <http://www.noaa.gov>).

## **CHAPTER IV**

### **Summary**

## **Introduction**

In this study, the dynamics of a tropical largemouth bass population were investigated from a fisheries management point of view in a region where largemouth bass is not native and where growing season is continuous. In temperate regions, several studies have indicated that winter mortality influenced recruitment processes of largemouth bass. In Puerto Rico where temperature exceeds 20°C all year, winter mortality associated with low temperature should not affect the recruitment of largemouth bass. Because largemouth bass in Puerto Rico experience a prolonged and extended spawning season, evaluation of factors other than temperature should provide clues of the causes of variation in the reproduction cycle and dictate year-class strength.

Sampling of juvenile largemouth bass in Lucchetti Reservoir demands high effort due to the high and wide range of growth rate and the prolonged spawning season. Nevertheless, rapid growth allows assessment of year class strength at age-1, thereby facilitating investigation of factors in recruitment.

## **Conclusion**

My results confirmed the findings of Jackson and Noble (1995), who indicated that a hand-held electrofishing unit could effectively assess variation in abundance of young-of-the-year largemouth bass. These results were based on age-0 CPUE data obtained from the hand-held unit and on age-1 CPUE data obtained with the conventional boom-mounted electrofisher. The hand-held electrofisher provides precise indices of age-0 largemouth bass year-class strength. My results also confirm the findings of many others that the traditional electroshocker is an efficient gear for adult largemouth bass

sampling. A high correlation between age-0 and age-1 CPUE indicates that largemouth bass year-class strength in Lucchetti Reservoir is set before young reach 150 mm total length, which is usually before September.

Similar to the findings regarding spawning periodicity in temperate regions, largemouth bass spawning period is determined primarily by the photoperiod. It is remarkable that largemouth bass apparently sense the daytime increase of 6 min from December 22 to January 14, and start to spawn early in January even though the water temperature drops during this period. The exact period of spawning, however, was determined by water level fluctuations in Lucchetti Reservoir. These results were consistent with the findings of Waters (1999) who found largemouth bass moving into deeper water as water levels dropped and returning to the spawning grounds as the water level again increased.

Water levels not only shaped the hatching distribution but also affected recruitment of largemouth bass. Conflicting results were obtained in the large number of studies of hydrological effects on largemouth bass recruitment processes in the Continental United States. Water level fluctuations during the period of January-August had a strong impact on the year-class strength of largemouth bass in Lucchetti Reservoir.

### **Management Implications**

Several options are available for the management of largemouth bass populations. Manipulating prey species (Noble 1981), restrictive regulations (Noble and Jones 1993), habitat manipulation (Noble et al. 1994), water level management (Irwin and Noble 1996), supplemental stocking of largemouth bass (Noble 1986), and using genetically

different subspecies (Isley et al. 1987) are some of the tools of largemouth bass management.

Alicea et al. (1995) found that largemouth bass growth was rapid and that prey was adequately abundant in Lucchetti Reservoir. Therefore prey species manipulation is probably not necessary and not a factor affecting year-class strength in Lucchetti Reservoir

Using restrictive regulations in Lucchetti Reservoir, such as minimum size limits as suggested by Ozen and Noble (2000), may not be feasible because the recruitment varies annually (Ashe et al. 1998). In addition, regulations in Lucchetti Reservoir are not effectively enforced (Waters 1999).

Habitat enhancement is not a feasible approach to largemouth bass management in Puerto Rico because of the highly fluctuating water levels. Irwin and Noble (1996) found that littoral habitat quality in Jordan Lake, North Carolina, changed markedly with a 2 m drop in water level, which most directly affects the littoral community. Similar morphometry of Lucchetti Reservoir suggests that adequate habitat likely exists at high water levels.

Water level management, on the other hand, such as stable water levels, at least from the beginning of the spawning season (January) until the hurricane season (August) could be an option for assuring constant and high recruitment of largemouth bass in Lucchetti Reservoir. Compromise of fishery management with the primary use of the reservoir, irrigation, should be sought.

Supplemental stocking was proven to have noticeable influence on cohort size, especially when wild-hatched largemouth bass densities were low. Since early detection

of year class strength has been proven possible with this study, stocking could be considered as a management option in years with relatively low recruitment. Supplemental stocking was more efficient when performed during the off-season (September-November) because of higher survival and growth rate (Neal et al. in press). Microtag studies suggested that supplemental stocked Florida largemouth bass, Micropterus salmoides floridanus, resulted in higher numbers than the usual Puerto Rico intergrades (Neal et al. 1999), and might provide a relatively longer life span.

### **Research Needs**

Young-of-the-year largemouth bass can be efficiently sampled using a hand-held electrofisher. However, further investigation of the hand-held electrofisher is needed for standardization purposes. A size selection curve would be very useful in the regard that the approximate size range of the efficiency can be adjusted and thereby more accurate interpretation of the sampling can be made. The improved predictability would result in more refined management decisions. For example estimated mean growth rates of juvenile largemouth bass may be biased due to the sampling selectivity. An approximate mean selection curve for this gear that incorporated several factors known to influence selectivity at most would be broadly applicable. Several selection curves in different types of habitats encompassing the range of water conductivity in Puerto Rico would be very useful.

My results showed that water level fluctuations can affect both the hatching distribution and year-class strength. However, the correlative results are by no means conclusive on the mechanisms that directly or even indirectly influence these processes.

A better understanding of these mechanisms would broaden the options for management and would help to influence policy decisions.

## References

- Alicea, R. A., R. L. Noble, and T. N. Churchill. 1997. Trophic dynamics of juvenile largemouth bass in Lucchetti Reservoir, Puerto Rico. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 51:149-158.
- Ashe, D. E., T. N. Churchill, R. L. Noble, and C. G. Lilyestrom. 1998. Temporal variability in the littoral fish community of a Puerto Rico reservoir. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 52:39-48.
- Irwin, E. R., and R. L. Noble. 1996. Effects of reservoir drawdown on littoral habitat: assessment with on-site measures and geographic information systems. Pages 324-331 in L. E. Miranda and D. R. DeVries, editors. Multidimensional approaches to reservoir fisheries management. American Fisheries Society, Symposium 16, Bethesda, Maryland.
- Isley, J. J., R. L. Noble, J. B. Koppleman, and D. P. Philipp. 1987. Spawning period and first-year growth of northern, Florida, and intergrade stocks of largemouth bass. Transactions of the American Fisheries Society 116:757-762.
- Neal, J. W., R. L. Noble, and T. N. Churchill. In press. Timing of largemouth bass supplemental stocking in a tropical reservoir: impacts on growth and survival. Pages X-XX in D. P. Phillip and M. S. Ridgway, editors. Black Bass 2000 Symposium. American Fisheries Society, Symposium in press.

- Noble, R. L. 1981. Management of forage fishes in impoundments of the southern United States. Transactions of the American Fisheries Society 110:738-750.
- Noble, R. L. 1986. Stocking criteria and goals for restoration and enhancement of warm-water and cool-water fisheries. Pages 139-146 in R. H. Stroud, editor. Fish culture in fisheries management. American Fisheries Society, Bethesda, Maryland.
- Noble, R. L., and T. W. Jones. 1993. Managing fisheries with regulations. Pages 383-402 in C. C. Kohler and W. A. Hubert, editors. Inland fisheries management in North America. American Fisheries Society, Bethesda, Maryland.
- Noble, R. L., J. R. Jackson, E. R. Irwin, J. M. Phillips, and T. N. Churchill. 1994. Reservoirs as landscapes: Implications for fish stocking programs. Transactions of the North American Wildlife and Natural Resources Conference 59:281-288.
- Ozen, O., and R. L. Noble. 2000. Yield-per-recruit simulation analyses for a largemouth bass population in Lucchetti Reservoir, Puerto Rico. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 54:59-69.
- Waters, D. S. 1999. Spawning season and mortality of adult largemouth bass (Micropterus salmoides) in a tropical reservoir. M. S. thesis. North Carolina State University, Raleigh, North Carolina.

## **APPENDIX**

Table 1. Correlation coefficients and their corresponding P-values (in parentheses) for the variables of daily water levels used in the analyses for the period of January-July. Hydrological variables between 1993-2000 for the mean water level (m MSL; MWL), standard deviations for the daily water levels (m; STDWL), minimum water level attained (m MSL; MinWL), maximum water level attained (m MSL; MaxWL), sum of the water level decreases for consecutive days (m; SumWLD), sum of the water increases for consecutive days (m; SumWLI), and the percentage change of the water volume between the maximum and minimum water level attained (PerWVC).

Hydrological Variable	Hydrological Variable						
	MWL	STDWL	MinWL	MaxWL	SumWLD	SumWLI	PerWVC
MWL		-0.713 (<0.05)	0.775 (<0.05)	0.581 (0.131)	0.735 (<0.05)	-0.524 (0.183)	-0.779 (<0.05)
STDWL	-0.713 (<0.05)		-0.956 (<0.05)	-0.478 (0.231)	-0.667 (0.071)	0.204 (0.628)	0.970 (<0.05)
MinWL	0.775 (<0.05)	-0.956 (<0.05)		0.678 (0.065)	0.623 (0.099)	-0.131 (0.757)	-0.997 (<0.05)
MaxWL	0.581 (0.131)	-0.478 (0.231)	0.678 (0.065)		0.281 (0.501)	0.028 (0.947)	-0.632 (0.093)
SumWLD	0.735 (<0.05)	-0.667 (0.071)	0.623 (0.099)	0.281 (0.501)		-0.321 (0.438)	-0.637 (0.090)
SumWLI	-0.524 (0.183)	0.204 (0.628)	-0.131 (0.757)	0.028 (0.947)	-0.321 (0.438)		0.166 (0.694)
PerWVC	-0.779 (<0.05)	0.970 (<0.05)	-0.997 (<0.05)	-0.632 (0.093)	-0.637 (0.090)	0.166 (0.694)	