Experimental Population Reduction of Largemouth Bass from an Overpopulated Tropical Reservoir: Impacts on Predators and Prey

Cynthia F. Holt[1], *Texas Parks and Wildlife Department, Inland Fisheries Division, 6200 Hatchery Road, Fort Worth, TX 76114*

J. Wesley Neal, *Department of Wildlife, Fisheries & Aquaculture, Mississippi State University, Box 9690, Mississippi State, MS 39762*

Abstract: Behavioral shifts by bass (*Micropterus* spp.) anglers toward catch and release practices has severely decreased the ability of managers to control predator-prey dynamics and reduced effectiveness of harvest as a management tool. Lack of harvest reduces managers' ability to use harvest regulations to influence bass growth and can result in slower growth and poor condition due to excessive predator abundance and reduced prey availability. This scenario appears to have developed in a tropical reservoir where angler harvest has been limited. Largemouth bass (*M. nigricans*) were experimentally removed from Cerrillos Reservoir, Puerto Rico, to test if targeted population reduction could improve prey availability and condition of largemouth bass in tropical systems. Specific objectives were to 1) assess the response of prey species abundance and size distributions to reduced predator abundance, and 2) determine the response of largemouth bass size structure and relative weight to experimental population reductions. The experimental removals resulted in increased abundance and decreased mean size of sunfish (*Lepomis* spp.) and tilapia (*Coptodon* and *Oreochromis* spp.) as recruitment of prey species increased. Abundance of threadfin shad (*Dorosoma petenense*) also increased. Largemouth bass W_r increased, indicating improvement in prey availability and improved predatory success. However, recruitment of largemouth bass also increased, highlighting the need for harvest, either by anglers or managers, to maintain population abundance necessary to maintain improvements in size-structure and condition.

Key words: largemouth bass, mechanical removal, predator-prey dynamics

Journal of the Southeastern Association of Fish and Wildlife Agencies 12:10–18

The relationship between largemouth bass (*Micropterus nigricans*) or Florida bass (*Micropterus salmoides*) as predators and bluegill (*Lepomis macrochirus*) as prey is one of the most frequently described predator-prey interactions in fisheries management (Olson et al. 1995, Brenden and Murphy 2004, Oplinger et al. 2011). When bass and bluegill populations are balanced, bluegill populations yield abundant prey to multiple size classes of bass resulting in rapid growth and good condition in bass (e.g., Schramm and Willis 2012). Conversely, abundant bass populations can deplete prey resources resulting in slow growth and poor condition of bass, while the intense predation reduces bluegill abundance, lowers bluegill intraspecific competition, and can result in prey size structure dominated by fewer individuals and larger adults (McHugh 1990, Aday and Graeb 2012). Similar relationships have been reported between bass and other prey species (e.g., Olson 1996, Nakazawa et al. 2007, Einfalt 2015).

Bass and bluegill populations in small impoundments are usually manipulated through specific stocking and harvest regimes designed to control predator-prey dynamics to maximize desired fishery conditions (Willis 2010). Insufficient harvest can lead to overpopulation of bass, intense intraspecific competition, and slow growth. This scenario, known as bass crowding, is a common problem in small impoundments in the southern U.S. (Schramm and Willis 2012). The theoretical solution to crowded bass populations is to reduce numbers of predators to reduce intraspecific competition (Willis 2010; Aday and Graeb 2012). However, managing bass populations using harvest regulations has become more difficult in recent decades as bass anglers have shifted towards catch and release practices (Quinn 1996, Bonds et al. 2008, Myers et al. 2008).

Kim et al. (2022) recently split largemouth bass into two separate species with Florida bass retaining *M. salmoides* and renaming largemouth bass as *M. nigricans*. Populations of both species have been established in freshwater systems far beyond their native range, including subtropical and tropical regions, such as the island of Puerto Rico. Largemouth bass populations in Puerto Rico reservoirs are intergrade fish with variable genetic contributions from each species (Neal et al. 1999, Peterson et al. 2017). Whereas Neal and Noble (2002) reported significant differences in longevity between Puerto Rico's intergrade largemouth bass and pure Florida bass, we will hereafter refer to Puerto Rico fish as "largemouth bass."

Most management models for largemouth bass were designed for temperate systems, and although the knowledge base for bass

1. E-mail: Cynthia.fox@tpwd.texas.gov

management in tropical reservoirs is expanding (e.g., Dadzie and Aloo 1990, Aloo and Dadzie 1995, Neal et al. 2002, Neal and Noble 2002, Waters and Noble 2004, Neal and Noble 2006, Neal et al. 2008), many uncertainties still exist. Unlike in temperate regions, tropical largemouth bass grow more rapidly as juveniles and usually reach maturity in less than 1 year (Gran 1995). Spawning season is prolonged up to 6 months with multiple spawning events (Dadzie and Aloo 1990, Gran 1995), which is energetically expensive and may result in reduced somatic growth of adults (Neal and Noble 2006). Tropical waterbodies typically have bass populations composed of many mid-sized fish with few large fish because longevity is greatly truncated, with few fish surviving beyond age 3 (Neal et al. 2002).

The phenomenon of reduced maximum size and longevity occurs in several of the reservoirs in Puerto Rico, characterized by 3–4 distinct year classes observable in length distributions that typically consist of quality (300–379 mm TL) and preferred+ size (380+ mm TL) fish (Neal et al. 2009, Neumann et al. 2012). Cerrillos Reservoir in Puerto Rico does not follow this tropical pattern. Prey species were stocked in Cerrillos Reservoir by the Puerto Rico Department of Natural and Environmental Resources (DNER) in 1996, including threadfin shad (*Dorosoma petenense*), tilapia (*Coptodon* and *Oreochromis* spp.), bluegill, and redear sunfish (*Lepomis microlophus*). Largemouth bass were stocked the following year, with this species being the only trophic-level piscivore in the reservoir. The original stocking density is unclear, but Peterson (2015) reported that a total of 48,520 presumed Florida Bass were stocked in 1997 in Cerrillos, Guajataca, and Lucchetti Reservoir, combined, for an average stocking density of about 80 fish ha^{-1}. Whereas Cerrillos Reservoir was the only introductory stocking in that year, it is likely that a greater density of fish was allocated to Cerrillos Reservoir than the other two established reservoirs. This was the only reported stocking of *Micropterus* in Cerrillos Reservoir, yet Peterson (2015) reported introgression of the two species by 2011, and suggested that the stock was not pure when introduced. Redbreast sunfish (*Lepomis auritus*), channel catfish (*Ictalurus punctatus*), white catfish (*Ameiurus catus*), western mosquitofish (*Gambusia affinis*), and Amazon sailfin catfish (*Pterygoplichthys pardalis*) are also present, though the timing of their introductions is unknown.

From 1997 to 2000, the reservoir was not open to the public for fishing, allowing the bass population to quickly expand. In 2000, the reservoir was opened to fishing three to four days per week, although long periods of closure (weeks to months) were common. In 2003, a management station and boat ramp were constructed at the reservoir, and management biologists from DNER were stationed at the facility to provide reliable access Thursday to Sunday each week. No length or bag limits were imposed for any fish species; however, anglers were required to report harvest (species, lengths, and numbers) at the management station before leaving the reservoir. Despite the reliable access and lack of harvest restriction, prey populations became depleted, leading to slow bass growth, poor condition, and limited appeal to anglers. The most abundant size classes of bass displayed W_r values indicative of prey limitation and crowding (Anderson 1980, Neal et al. 2001).

Like classical bass crowding in the southern U.S. (Schramm and Willis 2012), condition of adult largemouth bass in Cerrillos Reservoir declined sharply as fish grew and entered a growth bottleneck (mean $W_r = 83$; Fox and Neal 2011). This resulted in a single slow-growing length mode comprised of multiple age classes, with only a few larger fish. In 2003, a protected slot (356–508 mm TL) limit was established to improve growth and condition in Cerrillos Reservoir by encouraging harvest of small largemouth bass and to protect larger fish. However, limited access, limited effort, and angler unwillingness to harvest small fish continued the inadequate harvest of smaller bass and prevented the success of the regulation (Fox and Neal 2011). The regulation was removed early in 2011, and the regulation was changed to a 10 bass per day bag with one bass ≥508 mm TL.

Experimental removals of largemouth bass from Cerrillos Reservoir were conducted to test if targeted population reductions could improve condition and size structure of largemouth bass in tropical systems. We hypothesized that reduction in predator abundance and biomass would reduce predatory pressure, allowing prey populations to expand, which would increase foraging success for the remaining bass population. Our objectives were to 1) assess the response of prey species abundance and size distributions to reduced predator abundance, and 2) determine the response of largemouth bass size structure and relative weight to experimental population reductions.

Methods

Study Site

Cerrillos Reservoir was impounded in 1992 and reached full pool in 1996. The reservoir is in the Cordillera Central (English: Central Mountain Range) of Puerto Rico, northeast of the city of Ponce. It is a 160-ha reservoir at full pool with mostly steep rocky shorelines and a maximum depth >80 m, and is a clear, oligotrophic system (Fox and Neal 2011). The primary purposes for the impoundment are flood control, hydropower, agricultural and drinking water supply, and recreation (USGS 2008), which can contribute to significant annual fluctuations in water level (≥10 m). The watershed is mostly composed of steep mountains with forest and coffee plantations (active and abandoned). Most angling occurs in boats and bank angling is negligible except at the management facility due to the steep rocky shoreline and surrounding terrain.

Largemouth Bass Population Collection, Estimates, and Removals

Boat-mounted electrofishing standardized to an output of 3000 W (range 3000–3500; Burkhardt and Gutreuter 1995) was used to collect largemouth bass. Mark-recapture population surveys were used to estimate largemouth bass population abundance, biomass, size structure, and condition (W_r) in spring from 2012 to 2014. The entire shoreline and available offshore habitats were systematically electrofished in March. Offshore habitats consisted of an island in the lower end of the reservoir and flooded timber and rocky ridges in the middle and upper reaches of the reservoir. All largemouth bass collected were measured (mm, TL) and weighed to the nearest 2 g, and stock-size fish (>200 mm) were marked by removing about 80% of one pelvic fin prior to release. Right and left fins were alternated between years. Marked fish were given 4–5 wk to reintegrate into the population prior to recapture efforts. During the recapture sampling, the entire shoreline and available offshore habitats were sampled using boat-mounted electrofishing and all largemouth bass were collected, measured (TL, mm), and examined for marks.

The number of stock-size largemouth bass was estimated using Chapman's modification to the Petersen index (Chapman 1951), with a target 95% confidence interval of no more than ±25% of population size (Robson and Regier 1964). Biomass and its confidence bounds were estimated by multiplying the mean weight (kg) of stock-sized largemouth bass by the estimated population size and its confidence bounds. Condition was determined on all largemouth bass (≥150 mm TL) using the largemouth bass W_r index developed by Wege and Anderson (1978) with Henson's (1991) modified parameters for intercept and slope.

Experimental removals of largemouth bass ranging from 200–380 mm TL were selected based on the density dependent growth impacts observed in Neal et al. (2010) and Neal et al. (2011). Bass population reductions were conducted in 2012 and 2013 during and immediately following recapture efforts for population estimation. Removal efforts continued until 20% of the estimated biomass for that year had been removed. The largemouth bass population was sampled again in 2014 to assess the response to consecutive population reductions.

Prey Fish Community Assessment

Abundance and size distribution of sunfish, tilapia, and threadfin shad were examined prior to (2012) and one year following (2014) the second removal of largemouth bass. Sunfish and tilapia were collected by electrofishing (3000–3500 W output power) at six sites throughout the reservoir in January and April (immediately prior to initiation of largemouth bass removals in 2012). Each site was divided into two transects (North and South). One transect from each site was randomly selected to be sampled during the day (0900–1500 h) and the second transect was sampled during the night (2100–0300 h). Each transect was sampled for 900 sec. All fish collected were identified, measured (mm; TL), and released. Catch per unit of effort (CPUE; fish h^{-1}) was calculated for the reservoir by combining all sampling events (day and night, January and April) per year as an estimate of sunfish and tilapia relative abundance.

Threadfin shad were collected using a frame trawl in January and April from six open water sites prior to (2012) and one year following (2014) the second removal of largemouth bass. A custom frame fry trawl with aperture dimensions of 3 × 3 m, with 6-mm mesh in the body of the trawl, 4-mm in the cod end, and total length of 10.5 m (Neal and Prchalova 2012) was used to sample open water habitat in Cerrillos Reservoir. The reservoir was divided into three sections: upper (river arm), middle, and lower (dam), with two sites sampled in each section. Three different water layers were sampled at each site: the upper open water with depth range 0–3 m, the middle open water 3–6 m, and the lower open water 6–9 m. The depth of towing was determined by the length of the rope between the buoy on the surface and the upper rim of the trawl frame (0, 3 and 6 m, respectively).

Trawling was conducted at night using a two-boat system. The first boat was used as a trawler, pulling the trawl on preset transects. The second boat was used to retrieve the cod end, empty the catch, and process the samples. Mean (SE) duration of each trawl tow was 119 (0.46) sec, which resulted in a mean trawled distance of 118 (0.82) m with average speed of 3.0 (0.01) km h^{-1} and a mean sampled volume of 1064 (7.35) m^3. Before beginning a tow, the trawl was flushed at sampling depth to remove any fish that may have entered the net during deployment by leaving the cod end open and towing the trawl for thirty seconds. At the end of each tow, the funnel section of the trawl was retrieved using the surface buoy, and the catch was moved down the funnel section through the open cod end to the bucket on board the retrieval boat. The catch was stored in a labeled zip-sealed plastic bag and placed on ice for processing in the laboratory.

Iced catches were processed the next day. Total length (TL) of each fish was measured to the nearest millimeter. When large numbers of threadfin shad were captured, sub-sampling was used. At least 50 subadult/adult (>30 mm TL) individuals per tow were measured, and the rest were counted collectively. Threadfin shad <30 mm TL were considered to be larvae and were counted and weighed separately. Abundance was calculated as number per unit effort (NPUE; fish 1000 m^{-3} water trawled) for January and April for each year by combining all trawl tows (sections and depths). Because lower abundance of threadfin shad was expected in January compared to April (Neal and Prchalová 2012), the two sampling periods were analyzed separately.

Statistical Analyses

Largemouth bass W_r was compared between 2012 (prior to removals) and 2013 and 2014 (following first and second removal). This allowed estimation of the response to population reduction. Condition was compared using general linear models (PROC GLM, SAS Institute 2013; Hansen et al. 2007) between pre-removal (2012) and post-removal (2013–2014) years, with year set as a class variable, length category (LCAT; Gabelhouse 1984) as a continuous variable, and the year × LCAT interaction included to determine if any of the parameters differed among years. Least squares means (LSMEANS, SAS Institute 2013) were calculated for each parameter to account for the unbalanced design and to provide appropriately adjusted means that take other model effects into account. For significant comparisons, differences among variables were determined using the pairwise differences (pdiff) option with the Sidak adjustment to control familywise error for multiple comparisons in the least squares means procedure. Length-frequency distributions were compared between 2012–2014 using Kolmogorov-Smirnov two-sample (Zar 1996) and chi-squared (Michaletz et al. 1995) tests.

Catch per unit effort of sunfish and tilapia was compared between pre (2012) and post-removal (2014) years using a paired two-sample *t*-test (McDonald 2014). Length-frequency distributions were compared between pre- and post-removal years using a Kolmogorov-Smirnov two-sample test (Zar 1996). Number per unit effort of juvenile and adult threadfin shad was compared by month using a paired two-sample *t*-test between pre- and post-removal years. For all statistical analyses, α = 0.05 was set as the level of significance.

Results

Largemouth Bass

Prior to the first experimental removal, the 2012 population estimate of stock-size bass was 9639 (SE = 908) largemouth bass, with an associated biomass of 3440.5 (165.4) kg and mean W_r = 83 (0.24) (Table 1). In April 2012, 2333 largemouth bass were experimentally removed, accounting for a biomass reduction of 715 (0.127) kg or 20.8% (0.9%) of the total population by weight (Table 1, Figure 1).

Table 1. Sampling effort and population estimate data for largemouth bass from Cerrillos Reservoir, Puerto Rico, spring 2012–2014. Error is the relative width of the confidence interval (target was less than 25%). CPUE is catch-per-unit-effort for all (overall) and for stock-size (200+ mm TL) largemouth bass. Marking and recapture effort is hours of electrofishing (pedal down time) recorded during sampling. Removal effort is an estimate of additional untimed electrofishing effort following completion of the population estimate that was required to reach the removal target.

	Year		
Variable	**2012**	**2013**	**2014**
Marking effort (h)	15.7	16.7	10.6
Recapture effort (h)	25.9	21.2	13.3
Removal effort (h)	~30	~30	0
Number marked	1493	956	1054
Number captured	1889	853	871
Number recaptured	292	101	81
Population estimate	9639	8011	11,218
95% confidence interval	908	1372	2206
Error (%)	9.4	17.1	19.6
CPUE overall (fish h^{-1})	98	74	116
CPUE stock (fish h^{-1})	95	57	99
Mean weight (g)	357	386	365
Total biomass (kg)	3440.5	3093.7	4100.0
Number removed	2333	1993	0
Biomass removed (kg)	715	620	0
% Biomass removed	20.8	20.0	0
Relative weight (W_r)	83	85	90

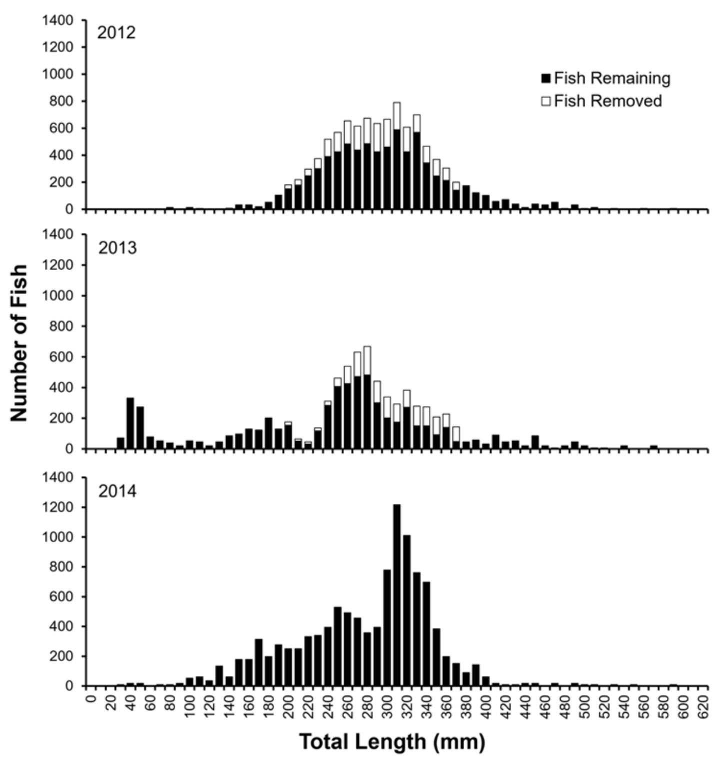

Figure 1. Estimated length distribution of largemouth bass in Cerrillos Reservoir, Puerto Rico, in 2012, 2013, and 2014. The population prior to experimental reduction is represented by the stacked white and black bars. White bars represent fish that were removed during that year's experimental reduction. Black bars represent the fish remaining in the population.

In 2013, the population was estimated to be 8011 (SE = 1372) largemouth bass, with an associated biomass of 3093.7 (270.4) kg. Mean condition increased, with mean (SE) W_r climbing two percentage points to 85 (0.31). A second biomass removal was conducted, with 1993 largemouth bass accounting for a biomass reduction of approximately 620 (0.130) kg or 20.0% (0.9%). Removal efforts in 2012 and 2013 began during the recapture phase of the bass population estimate sampling, and once the estimate was completed, continued with untimed electrofishing. It took approximately 5 days of electrofishing to reach the goal of removing 20% of the total biomass each year. We used two electrofishing boats, each with one operator and one or two netters to collect the fish. Additionally, we used a third boat with a single operator to transport fish to shore where they were loaded into hauling tanks on trucks for transport to a different reservoir.

One year after the second experimental removal, the population was estimated to be 11,218 (SE = 2206) largemouth bass with an associated biomass of 4100 (411.4) kg. Although population size and biomass in 2014 were greater than prior to removals, condition of largemouth bass increased across all length categories (Figure 2). Overall mean W_r increased 5 units to 90 (SE = 0.37; LSMEANS, $F_{5,11}$ = 117.09, P < 0.001). These increases were significant in all length categories (P < 0.001) except memorable-size fish (P = 0.71). Length frequency distributions differed among years (D = 0.09–0.14, P < 0.001). The lower end of the crowded size range shifted towards larger sizes, with a strong peak at 310–330 mm TL.

Prey Fish

Mean (SE) CPUE of sunfish increased from 38 (6) in 2012 to 72 (10) fish h^{-1} (t_{67} = 2.78, P = 0.007) in 2014 and for tilapia increased from 57 (9) to 162 (29) fish h^{-1} (t_{46} = 3.38, P = 0.001) following the removals (Figure 3). Concurrently, mean total length decreased among sunfish (D = 0.15, P = 0.002) and tilapia (D = 0.41, P < 0.001). Overall mean threadfin shad NPUE (fish 1000 m^{-3} water trawled) did not significantly increase (t_{51}= –0.89, P = 0.376) following the removals. However, mean NPUE of larval (<30 mm TL; t_{11} = 2.314, P = 0.041) and juvenile/adult shad (≥30 mm TL; t_{11} = 2.400, P = 0.035) from prior to the first removal in 2012 to 1 year after the second removal in 2014 within January samples were different (Figure 4). Similar results were found in April samples for juvenile/adult shad (t_{11} = 2.504, P = 0.029), but no difference was detected for larval shad density (t_{11} = 0.523, P = 0.611).

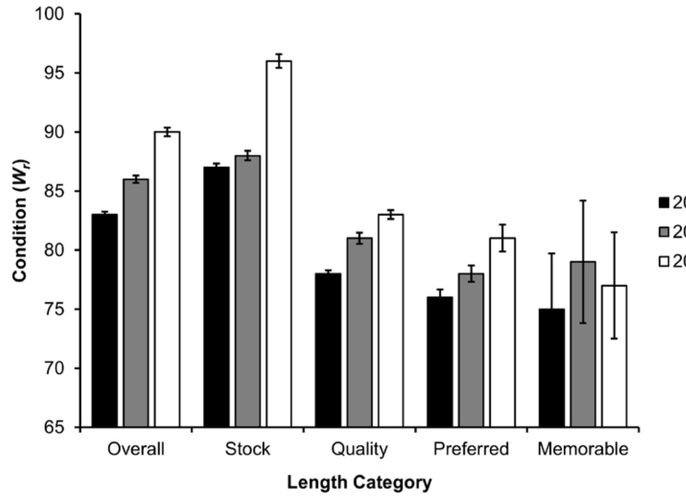

Figure 2. Mean (SE) condition (W_r) of largemouth bass for the total population (overall) and by length category in Cerrillos Reservoir from 2012, 2013, and 2014. Length classes are those for largemouth bass from Gabelhouse (1984).

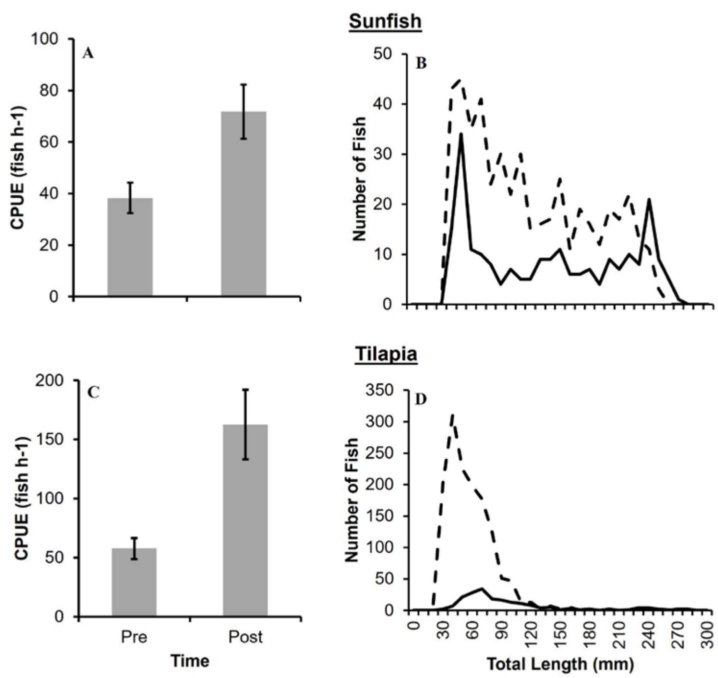

Figure 3. Mean (SE) catch-per-unit-effort (CPUE) and length distributions in 2012 prior to experimental largemouth bass population reduction (pre) and 2014 one year after second population reduction (post) for sunfish (Top A & B; *Lepomis* spp.) and tilapia (Bottom C & D; *Coptodon* and *Oreochromis* spp.). In B and D, the solid line is prior to largemouth bass population reduction and the dashed line following the second largemouth bass population reduction.

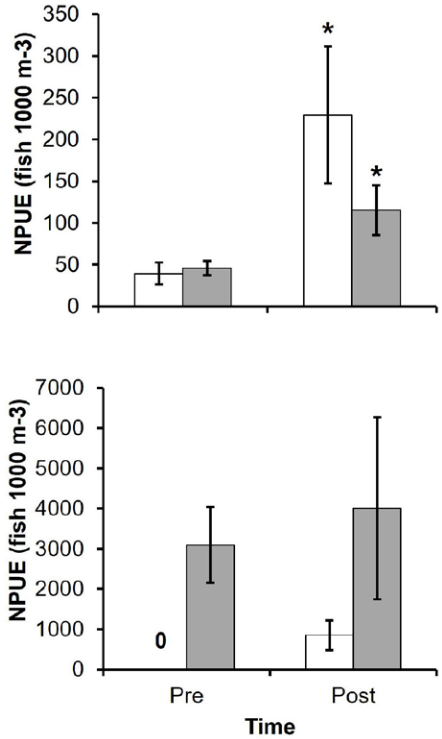

Figure 4. Mean (SE) larval (<30 mm TL; Top) and juvenile/adult (>30 mm TL; Bottom) threadfin shad number-per-unit-effort (NPUE) in 2012 prior to experimental largemouth bass population reduction (pre) and 2014 one year after second population reduction (post). Open bars = January, grey bars = April. Asterisk (*) denotes statistically significant difference.

Discussion

Neal et al. (2001) suggested that the rapid decline in condition of the largemouth bass population in Cerrillos Reservoir following initial introduction was due to predator overpopulation and subsequent prey limitation. That report recommended liberal harvest of small largemouth bass to reduce crowding and to increase growth rates and body condition for the remaining population. However, angler harvest was insufficient to test this recommendation (Fox and Neal 2011). The experimental removals in the current study demonstrated that largemouth bass mean condition can be increased when population size is reduced. Further, predator reduction led to increased prey availability and smaller size structure when recruitment increased. Positive correlations between relative weight and prey abundance have previously been documented for largemouth bass (Wege and Anderson 1978), pumpkinseed (*Lepomis gibbosus*; Liao et al. 1995), northern pike (*Esox lucius*; Paukert and Willis 2003), and walleye (*Sander vitreus*; Marwitz and Hubert 1997, Porath and Peters 1997).

This was the first significant increase in largemouth bass condition in this reservoir since it was initially stocked in 1997. The relationship between relative weight and growth has been demonstrated for several temperate species including largemouth bass (Wege and Anderson 1978, Neumann et al. 1994), hybrid striped bass (*Morone saxatilis* × *M. chrysops*; Brown and Murphy 1991), black crappie (*Pomoxis nigromaculatus*; Guy and Willis 1995), white crappie (*Pomoxis annularis*; Gabelhouse 1991), and northern pike (Willis 1989, Neumann and Willis 1996). Unlike condition, which can change over relatively short periods of time (weeks; Blackwell et al. 2000), changes in length tend to present more slowly, specifically in mature fish (von Bertalanffy 1938). Mosher (1984) suggested that there could be a threshold for relative weight that has to be met before growth in length can respond. Because largemouth bass were in reduced condition prior to the removal, it is likely that they would need to invest more energy into improving condition before significant investment in growth in length would occur.

Previous research in northern temperate climates found that population reductions are necessary for several consecutive years to be effective. Willis (2010) conducted annual harvests of subslot largemouth bass (<300 mm TL) from a high density, slow growing population in South Dakota, and reported that it took 3 years of removals before the size structure of the population began to shift towards target proportional size distribution (PSD) and condition. However, due to higher year-round temperatures, largemouth bass in Puerto Rico reservoirs experience a much longer growing season than those in South Dakota ponds, and population changes likely occur more rapidly. The Cerrillos Reservoir population responded with a 2 unit increase in W_r a year after the first removal and another 5 unit increase after the second removal.

Population abundance and biomass increased following the second removal, despite 20% of biomass being removed in two consecutive years. This may be due to the expanded size structure, which opens a wider breadth of potential prey to the population and allows greater recruitment success. When most of the population is crowded into a narrow size range, their potential population size and biomass is limited by the prey available to that size range (Shelton et al. 1979, Diana 1987, Heath and Roff 1996), and competition inhibits recruitment. Further, few prey survive the predator gauntlet to grow to adult sizes, thus limiting reproduction and recruitment of prey (Swingle 1950, Swingle 1956, Gabelhouse 1987). As the largemouth bass size structure expands, the population can exploit a greater available prey base leading to improved condition and increased growth. Conversely, the bass population responded to the biomass reductions with subsequent strong recruiting classes following each population reduction.

It is likely that removals of this magnitude will need to occur periodically in Cerrillos Reservoir to maintain the observed improvements or to reach ultimate target levels in condition and growth rate. In the South Dakota study, all harvest of largemouth bass ceased once the population reached target size structure and condition, and when the population was sampled again 7 years later, it had returned to its original state of high density, low condition, slow growing bass (Willis 2010). Likewise, Neal et al. (2016) reported that the Cerrillos Reservoir largemouth bass W_r declined to 86 by 2016, 3 years after the second removal. Thus, regular removals of small largemouth bass may be the best way to manage this and similar populations to maintain quality fishing opportunities (Novinger 1990, Neumann et al. 1994, Noble and Jones 1999, Wilson and DiCenzo 2002, Willis 2010). Concerted efforts to promote harvest of small largemouth bass with anglers could be successful, although it is unclear at this point whether angling pressure alone is sufficient to reach harvest goals even if anglers harvest all small fish caught. Regardless, this research demonstrated that prey abundance and size structure can be manipulated via targeted reduction in predator populations, and that predator condition will respond to increases in prey availability in closed tropical systems.

Literature Cited

Aday, D. D. and B. D. S. Graeb. 2012. Stunted fish in small impoundments: an overview and management perspective. Pages 215–234 *in* J. W. Neal and D. W. Willis, editors. Small impoundment management in North America. American Fisheries Society, Bethesda, Maryland.

Aloo, P. A. and S. Dadzie. 1995. Diet of the largemouth bass, *Micropterus salmoides* (Lacepède), in Lake Naivasha, Kenya. Fisheries Management and Ecology 2:43–51.

Anderson, R. O. 1980. Proportional stock density (PSD) and relative weight (W_r): interpretive indices for fish populations and communities. Pages 27–33 *in* S. Gloss and B. Schupp, editors. Practical fisheries management: more with less in the 1980's. American Fisheries Society, New York Chapter, Ithaca.

Blackwell, B. G., M. L. Brown, and D. W. Willis. 2000. Relative weight (W_r) status and current use in fisheries assessment and management. Reviews in Fisheries Science 8:1–44.

Bonds, C. C., J. B. Taylor, and J. Leitz. 2008. Practices and perceptions of Texas anglers regarding voluntary release of largemouth bass and slot length limits. Pages 219–230 *in* M. S. Allen, S. M. Sammons, and M. J. Maceina, editors. Balancing fisheries management and water uses for impounded river systems. American Fisheries Society, Symposium 62, Bethesda, Maryland.

Brenden, T. O. and B. R. Murphy. 2004. Experimental assessment of age-0 largemouth bass and juvenile bluegill competition in a small impoundment in Virginia. North American Journal of Fisheries Management 24:1058–1070.

Brown, M. L. and B. R. Murphy. 1991. Standard weight (W_s) development for striped bass, white bass, and hybrid striped bass. North American Journal of Fisheries Management 11:451–467.

Burkhardt, R. W. and S. Gutreuter. 1995. Improving electrofishing catch consistency by standardizing power. North American Journal of Fisheries Management 15:375–381.

Chapman, D. G. 1951. Some properties of the hypergeometric distribution with applications to zoological sample censuses. University of California Publications in Statistics 1:131–160.

Dadzie, S. and P. A. Aloo. 1990. Reproduction of the North American black bass, *Micropterus salmoides* (Lacepède), in an equatorial lake, Lake Naivasha, Kenya. Aquaculture and Fisheries Management 21:449–458.

Diana, J. S. 1987. Simulation of mechanisms causing stunting in pike populations. Transactions of the American Fisheries Society 116:612–617.

Einfalt, L. M., J. J. Parkos III, and D. H. Wahl. 2015. Effect of predator size and prey characteristics on piscivory of juvenile largemouth bass. Transactions of the American Fisheries Society 144:682–692.

Fox, C. N. and J. W. Neal. 2011. Development of a largemouth bass crowded population in a tropical reservoir. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 65:98–104.

Gabelhouse, D. W., Jr. 1984. A length-categorization system to assess fish stocks. North American Journal of Fisheries Management 4:273–285.

_____. 1987. Responses of largemouth bass and bluegills to removal of surplus largemouth bass from a Kansas pond. North American Journal of Fisheries Management 7:81–90.

_____. 1991. Seasonal changes in body condition of white crappies and relations to length and growth in Melvern Reservoir, Kansas. North American Journal of Fisheries Management 7:81–90.

Gran, J. E. 1995. Gonad development and spawning of largemouth bass in a tropical reservoir. Master's thesis, North Carolina State University, Raleigh.

Guy, C. S. and D. W. Willis. 1995. Population characteristics of black crappies in South Dakota waters: A case for ecosystem-specific management. North American Journal of Fisheries Management 15:754–765.

Hansen, M. J., T. D. Beard, Jr., and D. B. Hayes. 2007. Sampling and experimental design. Pages 51–120 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Heath, D. D. and D. A Roff. 1996. The role of trophic bottlenecks in stunting: a field test of an allocation model of growth and reproductions in yellow perch *Perca flavescens*. Environmental Biology of Fishes 45:53–63.

Henson, J. C. 1991. Quantitative description and development of a species-specific growth form for largemouth bass, with application to the relative weight index. Master's thesis, Texas A&M University, College Station.

Kim, D., A. T. Taylor, and T. J. Near. 2022. Phylogenomics and species delimitation of the economically important black basses (*Micropterus*). Scientific Reports 12:9113.

Liao, H., C. L. Pierce, D. H. Wahl, J. B, Rasmussen, and W. C. Legget. 1995. Relative weight (W_r) as a field assessment tool: relationships with growth, prey biomass, and environmental conditions. Transactions of the American Fisheries Society 124:387–400.

Marwitz, T. D. and W. A. Hubert. 1997. Trends in relative weight of walleye stocks in Wyoming reservoirs. North American Journal of Fisheries Management 17:44–53.

McDonald, J. H. 2014. Handbook of biological statistics, 3rd edition. Sparky House Publishing, Baltimore, Maryland.

McHugh, J. J. 1990. Responses of bluegills and crappies to reduced abundance of largemouth bass in two Alabama impoundments. North American Journal of Fisheries Management 10:344–351.

Michaletz, P., J. Boxrucker, S. Hale, and J. R. Jackson. 1995. Comparison of four trawls for sampling juvenile shad. North American Journal of Fisheries Management 15:918–923.

Mosher, T. D. 1984. Responses of white crappie and black crappie to threadfin shad introductions in a lake containing gizzard shad. North American Journal of Fisheries Management 4:365–370.

Myers, R., J. Taylor, M. Allen, and T. F. Bonvechio. 2008. Temporal trends in voluntary release of largemouth bass. North American Journal of Fisheries Management 28:428–433.

Nakazawa, T., N. Ishida, M. Kato, and N. Yamamura. 2007. Larger body size with higher predation rate. Ecology of Freshwater Fish 16:363–372.

Neal, J. W., R. Kroger, C. G. Lilyestrom, M. Muñoz, N. Peterson, M. C. Lloyd, K. Olivieri-Velázquez, and C. Fox. 2011. Freshwater sport fish management and enhancement. SFR Project F-53R. Annual Report of Mississippi State University, College of Forestry Resources, Department of Wildlife, Fisheries, and Aquaculture to Puerto Rico Department of Natural and Environmental Resources, Bureau of Wildlife and Fisheries, Division of Marine Resources, San Juan, Puerto Rico.

______, ______, ______, ______, M. Prchalova, N. Peterson, M. C. Lloyd, K. Olivieri-Velázquez, and C. Fox. 2010. Freshwater sport fish management and enhancement. SFR Project F-53R. Annual Report of Mississippi State University, College of Forestry Resources, Department of Wildlife, Fisheries, and Aquaculture to Puerto Rico Department of Natural and Environmental Resources, Bureau of Wildlife and Fisheries, Division of Marine Resources, San Juan, Puerto Rico.

______, C. G. Lilyestrom, C. N. Fox, and J. M. Bies. 2016. Fisheries research and management in Puerto Rico. SFR Project f-69 Final Report. Department of Natural and Environmental Resources, Bureau of Wildlife and Fisheries, Division of Marine Resources, San Juan, Puerto Rico.

______, ______, and T. J. Kwak. 2009. Factors influencing tropical island freshwater fishes: species, status, and management implications in Puerto Rico. Fisheries 35:546–554.

______, ______, and D. Lopez-Clayton. 2008. Tropical reservoir fisheries in Puerto Rico: Adaptive management through research. Pages 681–697 *in* M. S. Allen, S. Sammons, and M. J. Maceina, editors. Balancing fisheries management and water uses for impounded river systems. American Fisheries Society, Symposium 62, Bethesda, Maryland.

______ and R. L. Noble. 2002. Growth, survival, and movement of Florida and intergrade largemouth bass in a tropical reservoir. North American Journal of Fisheries Management 22:528–536.

______ and ______. 2006. A bioenergetics-based approach to explain largemouth bass size in tropical reservoirs. Transactions of the American Fisheries Society. 135:1535–1545.

______, ______, and T. N. Churchill. 2002. Timing of Largemouth Bass supplemental stocking in a tropical reservoir: impacts on growth and survival. Pages 691–701 i*n* D. P. Philipp and M. S. Ridgeway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.

______, ______, C. G. Lilyestrom, N. M. Bacheler, and J. C. Taylor. 2001. Freshwater sport fish community investigations and management. Puerto Rico Department of Natural and Environmental Resources, Federal Aid in Sport Fish Restoration Project F-41, Study 2. San Juan, Puerto Rico.

______, ______, ______, T. N. Churchill, A. R. Alicea, F. M. Holliman, and D. S. Waters. 1999. Freshwater sport fish community investigations and management. Puerto Rico Department of Natural and Environmental Resources, Federal Aid in Sport Fish Restoration Project F-41, Study 2. Final Report. San Juan, Puerto Rico.

______ and M. Prchalova. 2012. Spatiotemporal distributions of threadfin shad in tropical reservoirs. North American Journal of Fisheries Management 32:929–940.

Neumann, R. M., C. S. Guy, and D. W. Willis. 2012. Length, weight, and associated indices. Pages 637–676 *in* A. V. Zale, D. L. Parrish, and T. M. Sutton, editors. Fisheries techniques, 3rd edition. American Fisheries Society, Bethesda, Maryland.

______ and D. W. Willis. 1996. Application of relative weight (W_r) as a tool for assessment of esocid populations. Pages 21–28 *in* R. Soderberg, editor. Warmwater workshop proceedings: esocid management and culture. American Fisheries Society, Northeastern Division, Bethesda, Maryland.

______, ______, and D. D. Mann. 1994. Evaluation of largemouth bass slot length limits in two small South Dakota impoundments. Prairie Naturalist 26:15–32.

Noble, R. L. and T. W. Jones. 1999. Managing fisheries with regulations. Pages 455– 480 *in* C. C. Kohler and W. A. Hubert, editors. Inland fisheries management in North America, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Novinger, G. D. 1990. Slot length limits for largemouth bass in small private impoundments. North American Journal of Fisheries Management 10:330–337.

Olson, M. H. 1996. Predator-prey interactions in size-structured fish communities: implications for growth. Oecologia 108:757–763.

______, G. G. Mittelbach, and C. W. Osenberg. 1995. Competition between predator and prey: resource-based mechanisms and implications for stage-structured dynamics. Ecology 76:1758–1771.

Oplinger, R. W., D. H. Wahl, and M. A. Nannini. 2011. Effect of predators on growth and reproductive investment in bluegills: comparison of populations with differing size and age of maturation. Transactions of the American Fisheries Society 140:1532–1539.

Paukert, C. P. and D. W. Willis. 2003. Population characteristics and ecological role of northern pike in fish communities of shallow Nebraska natural lakes. North American Journal of Fisheries Management 23:313–322.

Peterson, N. R. 2015. Subspecies composition, genetic variation and structure of largemouth bass in Puerto Rico reservoirs. Master's thesis, Mississippi State University, Starkville.

______, D. Lutz-Carrillo, and J. W. Neal. 2017. Genetic composition of largemouth bass in Puerto Rico reservoirs. North American Journal of Fisheries Management 37:1199–1207.

Porath, M. T. and E. J. Peters. 1997. Use of walleye relative weights (W_r) to assess prey availability. North American Journal of Fisheries Management 17:628–637.

Quinn, S. 1996. Trends in regulatory and voluntary catch-and-release fishing. Pages 152–162 *in* L. E. Miranda and D. R. DeVries, editors. Multidimensional approaches to reservoir fisheries management. American Fisheries Society, Symposium 16, Bethesda, Maryland.

Robson, D. S. and H. A. Regier. 1964. Sample size in Petersen mark-recapture experiments. Transactions of the American Fisheries Society 93:215–226.

SAS Institute. 2013. SAS/STAT 13.1 user's guide. SAS Institute, Inc., Cary, North Carolina.

Schramm, H. L., Jr. and D. W. Willis. 2012. Assessment and harvest of largemouth bass-bluegill ponds. Pages 181–213 *in* J. W. Neal and D. W. Willis, editors. Small impoundment management in North America. American Fisheries Society, Bethesda, Maryland.

Shelton, W. L., W. D. Davies, T. A. King, and T. J. Timmons. 1979. Variation in the growth of the initial year class of largemouth bass in West Point Reservoir, Alabama and Georgia. Transactions of the American Fisheries Society 108:142–149.

Swingle, H. S. 1950. Relationships and dynamics in balanced and unbalanced fish populations. Alabama Polytechnic Institute Agricultural Experiment Station Bulletin Number 274, Auburn.

______. 1956. Determination of balance in farm fish ponds. Transactions of the North American Wildlife Conference 21:298–322.

U.S. Geological Survey (USGS). 2008. Water resources of the Caribbean. <http:// pr.water.usgs.gov/public/rt/prlakes/lake_50113950.html>. Accessed on 15 August 2011.

von Bertalanffy, L. 1938. A quantitative theory of organic growth. Human Biology 10:181–213.

Waters, D. S. and R. L. Noble. 2004. Spawning season and nest fidelity of largemouth bass in a tropical reservoir. North American Journal of Fisheries Management 24:1240–1251.

Wege, G. J. and R. O. Anderson. 1978. Relative weight (W_r): a new index of condition for largemouth bass. Pages 79–91 *in* G. D. Novinger and J. G. Dillard, editors. New approaches to the management of small impoundments. American Fisheries Society, North Central Division, Special Publication 3, Bethesda, Maryland.

Willis, D. W. 1989. Proposed standard length-weight equation for northern pike. North American Journal of Fisheries Management 9:203–208.

_____. 2010. A protected slot length limit for largemouth bass in a small impoundment: will the improved size structure persist? Pages 203–210 *in* B. R. Murphy, D. W. Willis, M. L. Davis, and B. D. S. Graeb, editors. Instructor's guide for case studies in fisheries conservation and management: applied critical thinking and problem solving. American Fisheries Society, Bethesda, Maryland.

Wilson, D. M. and V. J. DiCenzo. 2002. Profile of a trophy largemouth bass fishery in Briery Creek Lake, Virginia. Pages 583–592 *in* D. P. Phillip and M. S. Ridgway, editors. Black bass: ecology, conservation and management. American Fisheries Society Symposium 31, Bethesda, Maryland.

Zar, J. H. 1996. Biostatistical analysis, 3rd edition. Prentice-Hall, Inc., Upper Saddle River, New Jersey.