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Interference in White Bass Reproduction by Two Introduced Predators in Barren River Lake, Kentucky

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INTERFERENCE IN WHITE BASS REPRODUCTION BY TWO INTRODUCED PREDATORS IN BARREN RIVER LAKE, KENTUCKY

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Master of Science

By
Jacob Franklin Fose

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INTERFERENCE IN WHITE BASS REPRODUCTION BY TWO INTRODUCED PREDATORS IN BARREN RIVER LAKE, KENTUCKY

Date Recommended 4 November 2013

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To my parents
Ronald and Mary Fose

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White bass *Morone chrysops* are native to the Mississippi River and its tributaries. This range includes the Barren River in south central Kentucky. Over the last thirty years, the population of white bass in Barren River Lake, a reservoir of the Barren River, has been in decline. During that same time, two congeners of white bass have been introduced to the lake. Hybrid striped bass *Morone chrysops* × *Morone saxatilis* were introduced in 1979 and yellow bass *Morone mississippiensis* were first discovered in 2000. Due to the similar life histories and spawning strategies of all three *Morone* species, I hypothesized that the two introduced species are interfering with reproduction of the native white bass. In the springs of 2012 and 2013 I sampled fish from within a five kilometer stretch of Barren River upstream of the lake. I collected 144 white bass, 111 yellow bass and 29 hybrid striped bass. Detection of species at spawning sites was staggered with yellow bass and hybrid striped bass arriving after white bass but leading to a period of co-occurrence. White bass on the spawning sites appeared healthy: fecundity (75,200 to 741,150 eggs per female), mean gonadosomatic indices (peaked at 10.7% and 23.7% in sequential years), mean relative weight (93.8), and length at age (above the 50th percentile). Of the yellow bass stomachs examined, 21.6% contained fish eggs or larval fish. Based on arrival times and evidence of egg and larval fish predation, it is likely that yellow bass are directly impacting white bass spawning success through reproductive interference and the consumption of white bass offspring. Schoener’s index values revealed a significant degree of dietary overlap between white bass and yellow bass in larval fish, post larval fish, and arthropods (C_{xy} = 0.992,0.994, and 0.804, respectively), and between white bass and hybrid striped bass in arthropods (C_{xy} = 0.851). Information from this study may elucidate causes of the declining white bass population and aid in its management in Barren River Lake.

Introduction

Throughout North America, fish have been introduced into aquatic systems to which they are not native (Whittier and Kincaid 1999; Rahel 2000). Initially, during the late 1800's and early 1900's, fish were introduced as a way to improve the food supply and fishing opportunities for anglers (Moyle 1986). Through the first half of the twentieth century, as dams were constructed and many new impoundments formed, fish habitat changed drastically (Baxter 1977; Benke 1990). Many fish hatcheries were developed to produce fish that could be stocked into these new reservoirs for both food and recreation (Moyle 1986; Stickney 1994). Eventually, a few select species of fish were dispersed to nearly every body of water in which they could survive, often to the detriment of native fish communities (Rahel 2000). Currently, in North America, intentional introductions are occurring at a slower rate and scientists are learning to manage the effects of the past century's fish dispersal (Clark and Rose 1997).

Aside from stocking by fisheries managers, fish may be introduced to systems through other means. Fish can be introduced unintentionally by way of accidental releases and other human activities (Whittier and Kincaid 1999). Most introductions are harmless, however some unintended fish releases result in newly established populations that disrupt existing fish communities and the fisheries they support (Moyle and Light 1996; Rahel 2000). Effects of introductions are often indirect and can be overlooked because of their gradual onset (Ross 1991). Negative effects of fish introductions can vary from moderate changes in the behaviors of preexisting members of the community to severe ecological shifts and extirpations (Cucherousset and Olden 2011). Efforts are being made to understand the effects of introductions and minimize their negative impacts on fisheries (Li and Moyle 1999; Whittier and Kincaid 1999). More often, limited foresight of humans provides undesirable fish species the means to continue to spread and leaves fisheries managers mitigating the negative effects (Li and Moyle 1981; Whittier and Kincaid 1999; Rahel 2000; Steinhart et al. 2004; Cucherousset and Olden 2011).

Researchers continue to attempt to model unwanted introductions and predict their effects on aquatic ecosystems (Gido et al. 2004). Introduced fish often have the most pronounced negative effect on their closest relatives in the new system, due to their similarities in life histories and niches (Li and Moyle 1999). Competition resulting from overlap in diet and spawning habitat can occur between introduced and established fish species (Clark and Rose 1997; Cucherousett and Olden 2011). When different species interact and compete during spawning events, reproductive interference can result (Li and Moyle 1999). Reproductive interference is any kind of interspecific interaction during the process of mate acquisition that adversely affects the fitness of at least one of the species involved, and is caused by incomplete species recognition (Gröning and Hochkirch 2008). Interspecific interactions during native fish reproduction can lead to decreased population size, hybridization, and a subsequent loss of genetic variation through introgression (Forshage et al. 1988; Taylor et al. 2013).

Over the past century, fisheries management techniques have shifted in response to changing aquatic systems (Nielson 1999). Scientists are increasingly considering the entire ecosystem and ecological theory when making management decisions (Johnson and Martinez 1995; Li and Moyle 1999). This ecosystem approach requires gathering information in a scientific way and using it to apply informed management practices (Johnson and Martinez 1995; Moyle and Light 1996).

It is important that fish occurring within a system be managed to sustain a healthy fishery that reflects the needs of the shareholders and the ecosystem on which they rely (Churchill et al. 2002). Often, shifts in fish populations and angler success rates trigger fisheries managers to modify their strategies. Central to making these management decisions is knowledge of the niches of all species within a system and the ecological interactions among those species (Moyle and Light 1996; Cucherousset and Olden 2011). As an example, because some sport fish require flowing water to reproduce, there has been increased emphasis placed on management within the inflowing streams of reservoirs (Betsill and Pitman 2002).

Management strategies can vary according to angler preferences and the needs of the ecosystem as a whole. When populations of beneficial or popular sport fish appear to be in decline, managers will typically employ one of two strategies to boost the population. They may impose restrictions on the harvest of certain species, and/or implement supplemental stocking of an existing species (Stickney 1994). Historically, fish were stocked without a full awareness of underlying causes for the reduced population, resulting in failed population recovery attempts. Due to a lack of success from some stocking programs, emphasis has been placed on the need to use fish of appropriate brood stocks and to understand the effects that stocking may have on the fish community already in place (Neal et al. 1999; Lewin et al. 2006).

Along with stocking, the construction of dams has led to the restructuring of fish communities throughout watersheds (Sheehan and Rasmussen 1999). A reservoir is formed when a dam causes a stream to inundate a portion of the surrounding land area, leaving large open-water areas where a shallow stream previously existed (Stanford et al. 1996). As this environmental shift occurs, fish assemblages change drastically; some species increase in numbers and move higher into the watershed while others decline in population or are extirpated from the system (Benke 1990; Agostinho et al. 2008). Most native fish will not use the new pelagic habitat of a reservoir, and without stocking most of the open-water regions remain depauperate (Agostinho et al. 2008). The lentic habitat created by a dam provides the appropriate conditions for pelagic predators that otherwise would not occur in that system (Benke 1990). It becomes the responsibility of the surrounding municipalities to manage this artificial environment and conserve the associated resources in a sustainable way (Sammons and Betoli 2000).

One way managers attempt to improve reservoir fisheries is by stocking pelagic predators (Li and Moyle 1981; Eby et al. 2006). Stocking predators into reservoirs is used as a way to enhance fishing opportunities and to reduce populations of planktivorous fish within the lake (Neal et al. 1999). Without the presence of a predator, planktivores such as shad and herring can reach very large population sizes that exceed the carrying capacity of their aquatic system (Eby et al. 2006).

One predatory species that is frequently stocked into reservoirs throughout North America is the hybrid striped bass *Morone chrysops* X *Morone saxatilis* (Axon and Whitehurst 1985; Neal et al. 1999; Olson et al. 2007). Hybrid striped bass were first cultured in a laboratory setting in 1965 by fertilizing eggs of a striped bass *Morone saxatilis,* with milt from a white bass *Morone chrysops* (Bishop 1967; McCraren 1984). They have been favored for their rapid growth, large size, and hardiness (Germann 1982;

Patrick and Moser 2001). Hybrids are often stocked as a way to enhance the fishery and to control the population of shad *Dorosoma* spp. within a system (Neal et al. 1999; Olson et al. 2007). Hybrid striped bass are pelagic predators and are known to travel upstream to spawning locations during the same time frame as their parent species (Patrick and Moser 2001; Avise and Van Den Avyle 1984). Additionally, scientists documented a few cases of hybrids producing viable offspring with other hybrids or with one of their parent species (Avise and Van Den Avyle 1984; Forshage et al 1988; Taylor et al. 2013). Due to their impacts on native fish assemblages, some managers have attributed loss of fishery quality to the introduction of this predator (Patrick and Moser 2001). However, because of their popularity as a sport fish and relative ease of management, hybrid striped bass stocking has been viewed as an overall benefit (Olson et al. 2007).

The yellow bass *Morone mississippiensis* is another predatory species that has been introduced to reservoir systems throughout the North America. Historically yellow bass were stocked intentionally into a few systems and viewed as a way to improve fisheries (Wright 1968). Yellow bass have declined in popularity as a sport fish compared to other predatory fish, likely because of their slow growth and small size at maturity (Pfleiger 1997). Yellow bass have also been introduced to systems unintentionally; they presumably followed canals along the Tennessee Tombigbee waterway to enter the Tombigbee River (Boschung 1992). They have also spread through entire river systems in Wisconsin upon introduction into two reservoirs (Wright 1968). Their current range extends throughout the Mississippi River drainage and its tributaries (Driscoll and Miranda 1999).

Yellow bass introductions are often viewed as detrimental to existing sport fish communities. Following establishment, yellow bass have displaced popular sport fish and regularly hybridize with their congeners in sympatry (Wright 1968; Fries and Harvey 1989). Yellow bass thrive in pelagic habitat and migrate into streams to spawn in the spring (Pfleiger 1997). They are generalist feeders and consume large quantities of fish eggs during certain times of the year (Driscoll and Miranda 1999). Due to their lack of popularity as a sport fish, little research focuses on yellow bass. Understanding the effects of predators such as yellow bass on existing fish communities upon introduction is crucial for determining management strategies where they occur (Moyle et al. 1986).

Stocking of predators into a poorly studied system can have negative outcomes (Li and Moyle 1981; Clarkson et al. 2005). Top down ecosystem effects caused by predator introductions have been thoroughly documented (Halpern et al. 2005; Tronstad et al. 2010). Two predatory sport fish, rainbow trout *Oncorhynchus mykiss* and largemouth bass *Micropterus salmoides,* have been stocked across North America and have had harmful effects on existing fisheries and ecosystems (Clark and Rose 1997; Pilger et al. 2008). Understanding the biology of a new species being introduced to a fishery and its probable effects on the ecosystem is valuable to the conservation of that fishery (Cucherousset and Olden 2011). Fewer predators are being introduced as a management tool while fisheries biologists expand their knowledge of the potential negative impacts (Li and Moyle 1999).

One system with a history of repeated stockings is Barren River Lake (KDFWR 2006). Located in south central Kentucky, Barren River Lake is a flood control reservoir completed in 1964 through the damming of the Barren River by the U.S. Army Corps of

Engineers (Carter 1969). At full summer pool, the impoundment covers 4,047 hectares (Jacobs and Swink 1983). Before inundation, the Barren River was an unbroken flowing system stretching 263 kilometers from the headwaters in Monroe County, Kentucky to the Green River, a tributary of the Ohio River. Presently, 132 kilometers of stream exist between the dam and the furthest reaches of the headwaters upstream (Carter 1969). The lake is mesotrophic with a Trophic State Index (TSI) of 50 (Lander 1998).

White bass are native to the Barren River. A pre- and post-impoundment survey confirmed their presence in the upper portions of the Barren River (Carter 1969). White bass spend much of the year in open water habitat and spawn in reservoir tributaries in the spring when water temperatures range from 13°C to 18°C (Sigler 1949; Ruelle 1977; Becker 1983; Guy et al. 2002; Teletchea et al. 2009). Along with temperature, spawning in white bass is stimulated by photoperiod and stream inflow volumes (Hasler et al. 1958; Colvin 2002; DiCenzo and Duval 2002). White bass spawn in groups where one female's eggs are fertilized by multiple males (Becker 1983). Eggs are demersal, adhere to substrate upon fertilization, and hatch after about five days in 16°C water (Teletchea et al. 2009). Typical spawning lasts between two weeks and a month for white bass (Pflieger 1997; Quist et al. 2002). Larval white bass resist stream flow and drift at a slightly slower rate than the current until reaching the lentic portions of the upper reservoir (Starnes et al. 1983; Quist et al. 2002). Within reservoirs, white bass population sizes are cyclical in nature and tend to fluctuate drastically, with cycles taking up to a decade to complete (Becker 1983; DiCenzo and Duval 2002; Sammons and Betoli 2000; Willis et al. 2002).

Following the completion of the dam, the Kentucky Division of Fisheries released 322 adult white bass into the reservoir (KDFWR 2006). For the next couple of decades, white bass in the reservoir supported a well populated fishery and during their spring spawning migration into tributaries, were targeted by anglers (Lander 1998). White bass reproduced naturally in the Barren River reservoir tributaries and until recently, no supplementary stocking of white bass was deemed necessary (Lander 1998). However, for the past few decades, the white bass population slowly diminished. Sampling records indicated that the population steadily declined from about 1985 to 2002 (KDFWR 2010). The "last decent spawn" of white bass reportedly occurred in 1994 (Lander 1998).

Although the cause for their decline was not identified, it was speculated by District Fisheries Biologist, B. D. Laflin that white bass were experiencing poor reproduction caused by low rain levels during the springs of multiple years (Lander 1998). In an attempt to revive the failing fishery, supplemental stocking of white bass was initiated by the state in 2003 and continued at a rate of about 300,000 fingerlings per year until 2008 (KDFWR 2006; Dreves and Russell 2007).

Since its creation, at least two additional species of predatory fish were introduced to Barren River Lake. Hybrid striped bass were first stocked into the lake in 1979 (KDFWR 2006). Additional hybrid striped bass continue to be stocked into the reservoir and support a strong fishery (KDFWR 2010). Yellow bass are also present in the lake in large numbers (KDFWR 2010). The means by which yellow bass have entered the reservoir are unknown, yet reports of their presence exist as early as 2000 (Personal communication, Eric Cummins, Southwest District Fisheries Biologist, KYDFWR, 970 Bennett Lane, Bowling Green, KY 42101). Yellow bass are now commonly caught by anglers in Barren River Lake, and mostly released (KDFWR 2010).

Likely the introduction of two predatory *Morone* species to Barren River Lake is negatively affecting the white bass population. I hypothesize that yellow bass and hybrid striped bass are contributing to the decline of white bass recruitment, specifically during reproductive events.

To test my hypothesis, I assessed evidence of co-occurrence and possible competition among the three congeners with a focus on their reproductive strategies. I determined time of occurrence of all three species in a spawning stream of white bass. Overlap of fish present in the Barren River upstream of the lake would indicate the potential for direct interactions among these three populations. I also examined stomach contents of yellow bass and hybrid striped bass for predation on white bass eggs and larvae. To a lesser degree, overlap in diet of all three species signifies interference through interspecific competition for food during spawning times.

Additionally, it is possible that reduced recruitment is occurring as a result of biological and reproductive deficiencies within the white bass population. I assessed population characteristics of the reproductive white bass of Barren River Lake and compared them to those reported in other studies of white bass. I measured fecundity, average egg size, gonadosomatic indices (GSI), relative weights ($W_{r)}$, and length at age indices.

Methods

Sampling for this study took place within a five kilometer stretch of the Barren River upstream of the reservoir from April to June, 2012, and April to May, 2013 (Figure 1). Primarily, I used monofilament gill nets, but also collected supplemental fish on sampling days via hook and line angling. The Kentucky Department of Fish and Wildlife Resources (KDFWR) contributed one sample of 54 white bass that were collected during routine boat mounted electrofishing.

The gill nets used in this study were 23 meters long consisting of three 7.62 by 1.8 meter panels with mesh sizes of 25, 40 and 51 millimeters bar length. I placed gill nets in the stream perpendicular to the stream bank. Nets were weighted on each end with a five kilogram cement anchor secured to the lead-line of the net. Large plastic jugs were tied to the float line near each end to assume vertical orientation of the gill net and to warn boaters of the presence of a submerged net. Nets were deployed in the evening before dark and retrieved the following morning.

Fish were taken from the nets and placed on ice for immediate transport to the laboratory for further analysis. In the laboratory, fish were measured for total length (TL) in millimeters and weight in grams. Gonads and stomachs were removed from each fish, weighed, and stored in 70% ethanol. Sagittal otoliths were extracted from the skull, cleaned of debris, and stored dry until they could be examined under a dissecting microscope.

Gonadosomatic Index

Because the gonads in fish develop just prior to the spawning season, they can be used to assess reproductive readiness. I calculated gonadosomatic indices (GSI) (the proportion of the gonads to the total mass for each individual fish). Mean GSI values on each sample date were monitored to determine when fish were spawning. All fish collected after a distinct decrease in mean GSI were considered post-spawning fish and were not included in calculations of potential fecundity.

Fecundity

Fecundity in fish is described as the total number of mature ova produced by females in a single reproductive season. Often in fisheries studies, potential fecundity, defined as the total number of ova present in both ovaries before spawning, is given as fecundity (Ruelle 1977). I calculated potential fecundity here to compare the sample population in this study to those of other populations of white bass.

To assess fecundity, gonads were removed from ethanol and blotted on a dry paper towel. Excess tissue was removed from gonads and a new mass was recorded. A small sample of eggs (≈0.05g) was then extracted from each gonad and weighed to the nearest 0.01g. All of the eggs from the subsample were counted under a dissecting microscope. Potential fecundity was then calculated using the following equation:

$$Total\ eggs = \frac{Mass\ of\ gonad}{Mass\ of\ subsample} \times no.of\ eggs\ in\ subsample$$

A regression on non-transformed data was generated for total eggs at length of female white bass consistent with methods from Newton and Kilambi (1973) and Madenjian et al. (2000).

Egg size is one factor considered when assessing the health of spawning females (Newton and Kilambi 1969; Ruelle 1977; Brooks et al. 1997). Maturity of eggs was determined by assessing size (Newton and Kilambi 1969). To measure egg sizes, I obtained an additional subsample from each gonad and measured diameters of individual eggs. Each subsample was placed in a 10-ml vial of 70% ethanol and agitated until eggs moved freely in the fluid. Eggs were then placed in a small Petri dish with 70% ethanol, and photographed on a scanner. All egg images were then converted to black and white in Adobe® Photoshop® photo editing software. Next the images were processed on iXRF Iridium Ultra™ digital imaging software and feret diameter means of all eggs in the image were derived. Feret diameter is the distance between two parallel planes restricting an object perpendicular to that direction. Mean egg diameters were assessed according to sizes determined by Newton and Kilambi (1969).

Robustness

Relative weight (W_r) is a common measurement used to evaluate the health of individual fish (Brown and Murphy 1991). Relative weight compares the actual weight of a fish to what is expected for an average individual of that species at its specific length, (standard weight, W_s) (Wege and Anderson 1978). The equation for W_s was derived by Brown and Murphy (1991) by analyzing all available white bass data comprising 95 populations from 16 states (N=21,980). Comparing the weight of a white bass from this study to the W_s of all other white bass provides accurate means to assess robustness. The W_r was calculated through the equation:

$$W_r = W/W_s$$

Where W is the actual weight of the fish in grams and W_s is the standard weight for white bass at that specific length. The equation for standard weight of white bass,

$$\log_{10} W_s = -5.066 + 3.081 \log_{10} TL,$$

was used to calculate the expected weight of each fish based on its total length (TL).

I examined sagittal otoliths from each fish to assess the age structure of the spawning population. Otoliths were submerged in DI water and examined with a Leica L2 dissecting microscope with a variable light source. Similar to methods described by Soupir et al. (1997), otoliths of fish age three and older were cracked along the lateral axis, perpendicular to the dorsal edge, and examined as a cross-section. The von Bertalanffy growth equation (von Bertalaffy 1938; Van den Avyle and Hayward 1999) was used to calculate the mean lengths at age of white bass. Since fish were only collected in the spring (i.e. little error was introduced by capture date), all fish were used in modeling growth using the equation,

$$l_t = L_\infty[1 - e^{-K(t-t0)}],$$

where L_∞ is the theoretical maximum length for a white bass in this system, the constant, K, is the growth coefficient, l_t is the length at time (or age) t, and t_0 is the theoretical time at which the length of a fish is zero.

Growth parameters were obtained using the Chapman method where K was derived from the natural log of the slope of the regression of l_{t+1} on l_t. L_∞ was calculated from the negative slope of that regression and its intercept, and t_0 was derived from a regression of $ln(L_\infty - l_t)$ (Chapman 1951). Total length and age in years estimated from otoliths were used as the input data.

Stomach Content Analysis

Stomachs were removed from ethanol and contents examined under a dissecting microscope. Contents were then identified to the most specific practical taxon and separated into four categories: fish eggs, fish larvae, post-larval fish, and arthropods. Frequency of occurrence of stomach contents were then calculated for all four food types in each of the three fish species according to methods outlined by Hyslop (1980). Stomachs containing no food items or only detritus were counted as empty.

Schoener's Index, described by Hurlbert (1978), was used to test for overlap between white bass and yellow bass diets, and between white bass and hybrid striped bass diets. Schoener's index is calculated using the equation,

$$C_{xy} = 1 - \tfrac{1}{2} (\sum | p_{xi} - p_{yi} |),$$

where p_{xi} is the proportion of fish x that contained food item i and p_{yi} is the proportion of fish y that contained food item i. A Schoener's Index value of 0.0 indicates no diet overlap and a value of 1.0 indicates complete overlap in diets.

Results

A total of 144 white bass, 111 yellow bass, and 29 hybrid striped bass were collected in 2012 and 2013 (Figure 2 and Figure 3). In both years, white bass were the first *Morone* species detected at the spawning grounds. In 2012, white bass were initially captured in early April when water temperatures reached 18.5°C and remained in the river until mid June. Yellow bass were first captured in late May at temperatures of 23°C. Only two hybrid striped bass were collected in 2012. In 2013, white bass arrived again in early April when water temperatures were 12°C. Yellow bass and hybrid striped bass were detected simultaneously in mid April of 2013 during a high flow event at water temperatures of 13.5°C. Frequent and heavy rainfall limited sampling in 2013 (Figure 3). White bass were the only species detected in the river through mid May of 2013.

Gonadosomatic Index

In 2012, mean GSI values were greatest for female white bass in mid April at 10.7% (N = 25) while water temperatures were 18.5°C. In 2013 mean GSI reached its greatest values again in mid April at 23.7% (N = 4) at water temperatures of 13.5°C (Figure 4). Mean GSI values for male white bass peaked in early April of 2012 and 2013 at 4.3%; N = 102 and 5.2%; N = 12 respectively. The greatest frequency of spawning, as indicated by GSI, was mid April of both years.

Fecundity

I estimated potential fecundity for 23 female white bass collected in the springs of 2012 and 2013. Potential fecundities ranged from 75,269 to 741,152 eggs per adult female with an average of 250,896 eggs. A regression was generated for total eggs at length (Figure 5). The number of eggs per female increased linearly with total length as represented by the equation,

$$y = 2{,}115.2x + -429{,}251,$$

where y is the number of eggs per female and x is the total length in millimeters of female white bass. This regression explained only 20 % ($R^2 = 0.20$) of variation in potential fecundity of white bass.

A mean of 59 eggs from each female white bass (N = 25) were measured for diameters. Mean egg diameter per individual ranged from 0.45 mm – 0.77 mm. Egg diameters were largest in mid April of both years. The greatest mean egg diameter per female recorded for 2012 was 0.61 mm on April 15th, and the greatest for 2013 was 0.73 mm on April 14th. On average, gonads lost 7.76% of their total mass after preservation in ethanol. Consequently, I estimate that some shrinkage occurred among eggs during preservation. Eggs of white bass vary uniformly in size throughout the gonads, thus location in each gonad from which samples were extracted was not considered as a source of error in this portion of the study (Newton and Kilambi 1969).

Robustness

The mean relative weight (W_r) of all adult white bass was 93.8. According to Brown and Murphy (1991), this reflects a population that is 93.8% as heavy as average white bass for specific lengths. To assess the effect of gonad development on W_r, a regression was formed to compare W_r to GSI of male and female white bass (Figure 6). In females GSI was positively correlated to and explained 75% of variation in W_r. Changes in GSI explained 4% of variation in W_r in males.

The mean age of all white bass collected from this study was 2.08 years, females: 2.25 years (N = 28) and males: 2.03 years (N = 116). The mean age of yellow bass, (N = 88) was 3.71 years; all yellow bass sampled were males. The mean age of hybrid striped bass was 3.72 years; females: 3.17 years (N = 6) and males 3.87 (N = 23) (Figure 7). The maximum age was 4, 7, and 6, for white bass, yellow bass, and hybrid striped bass, respectively.

According to the von Bertalanffy growth equation, the calculated growth parameter values for K and L_∞ were 0.8686 and 362.97 mm respectively. Thus, the lengths at age were calculated for each age group using the equation:

$$l_{\mathrm{t}} = 362.97\ [1 - e^{-0.8686(\mathrm{t}-0.003814)}]$$

The predicted mean lengths at age were 210.2 mm, 298.9 mm, 336.1 mm, and 351.7 mm for white bass ages 1-4, respectively (Figure 8).

Stomach Content Analysis

Fish larvae were detected in 2.7% (4/144) of white bass stomachs and 1.1 % (1/88) of yellow bass stomachs. Fish eggs were detected in 20.5% of yellow bass stomachs, but were not detected in white bass or hybrid striped bass stomachs. Post-larval fish were found in 2.1% of white bass, 3.4% of yellow bass, and 27.6% (8/29) of hybrid striped bass stomachs. Arthropods were present in the stomachs of all three species and comprised the most frequent dietary item of white bass (36.8%) and yellow bass (76.1%).

A majority of white bass (59.7%) and hybrid striped bass (65.5%) stomachs were empty; only 18.2% of yellow bass stomachs were empty (Table 1).

Schoener's index values indicated high dietary overlap between white bass and yellow bass in larval fish, post larval fish, and arthropods: C_{xy} = 0.992, 0.994, and 0.804, respectively. Dietary overlap was also high between white bass and hybrid striped bass (C_{xy} = 0.851) in arthropods (Table 1).

Discussion

Adult white bass traveled upstream of Barren River Lake and into the Barren River during the springs of 2012 and 2013. As indicated by GSI and egg diameters, peak spawning among white bass likely occurred during mid April of both years. Due to low rain levels, spawning in 2012 was likely gradual, while large flood pulses in 2013 probably triggered a more punctuated spawning duration. I detected overlap in occurrence of white bass, yellow bass, and hybrid striped bass in both field seasons. White bass were detected in the river prior to the two introduced congeners. All three species were found in the river at the end of the white bass spawning period. The timing of the arrival of yellow bass and hybrid striped bass at the spawning site suggests a short period of overlap with white bass spawning. While in the river, yellow bass and hybrid striped bass may be interfering with white bass reproduction through site selection, and various forms of interspecific competition and/or predation. Evidence exists of both yellow bass and hybrid striped bass breeding with other *Morone* where they occur in sympatry (Avise and Van Den Avyle 1984; Forshage et al 1988; Fries and Harvey 1989; Taylor et al. 2013). Given the typical duration of white bass spawning (from two weeks to one month) and the overlap in arrival of yellow bass from this study, reproductive interference through interspecific mating may be occurring and limiting the success of white bass spawning.

In addition to reproductive interference, yellow bass may be directly feeding on white bass eggs and larvae. While in the river, yellow bass are aggressively feeding. Most yellow bass examined in this study (81.8%) had stomachs containing food. Additionally, 21.6% of yellow bass stomachs contained fish eggs or larvae. The occurrence of fish eggs in yellow bass diet from this study is consistent with reports by Driscoll and Miranda (1999). I detected no evidence of hybrid striped bass predation on white bass. When white bass spawn in the Barren River, they do so at a time that appears to directly precede the migration of yellow bass into the same stream. If yellow bass prepare for spawning similar to their congeners, then they will congregate in large numbers near the mouth of the river. This leaves white bass eggs susceptible to predation by yellow bass during spawning, and larvae remain vulnerable throughout their journey to the reservoir. The effects of predation by yellow bass on white bass are more pronounced in the river than they might be later in the summer when both species are in the reservoir.

Significant overlap in dietary components among all three species indicates competition for food during reproductive events. Although competition for food in the river likely has little impact on reproductive fitness, it may be indicative of competition occurring when the three species co-occur in the reservoir. The condition of fish in this study supports the idea that there is competition occurring within the lake through the rest of the year.

When assessing the invasion of yellow bass into Barren River Lake, it is important to consider the pre-existing environmental conditions. According to Moyle and Light (1996) there are twelve empirical rules governing the success and effects of species introductions. Five of these rules apply to this study (Table 2): 1) ecosystems that are low in species richness are more susceptible to the successful establishment of an invasive species. Although Barren River Lake and the inflowing river are not considered to be nutrient limited, and overall species richness is high, within the system very few fish use the pelagic habitat (Carter 1969; Jacobs and Swink 1983). Before the introduction of hybrid striped bass in 1979, and yellow bass twenty years later, white bass were the primary open-water predator of Barren River Lake. As a result, most of the lake was very low in species richness. 2) Piscivores are typically more likely to alter fish assemblages in new habitats. 3) Fish with a close physiological match to the system, are more likely to establish long-term success. 4) Invasions are most likely to occur in systems where populations of native species are already below normal. White bass were already in decline potentially leaving available resources that could be exploited by the newly introduced yellow bass. Finally, 5) systems permanently altered by human activity are more susceptible to invasions. This is especially true for reservoirs which drastically change the available habitat in systems that were once lotic. Consistent with these rules and historical population surveys, the conditions in Barren River Lake were optimal for the successful invasion of yellow bass. It is likely that during a relative trough in the recruitment cycle, the introduction of two closely related species provided the catalyst this vulnerable population needed to collapse.

Evidence suggests that spawning white bass from this study are in overall good health. Robustness estimates place this population in average length and weight categories. Mean relative weights of 93.8 ± 12 (1 SD) were within the 50th percentile determined by Brown and Murphy (1991), indicating that white bass from Barren River Lake are heavier than half of the known individuals at specific lengths. For three of the four year classes identified, mean lengths at age were above the 50th percentile determined by Jackson et al. (2008) from 69 white bass populations, indicating growth is above average for this population. Gonadosomatic indices for females exceeded those described by Ruelle (1977), and eggs, as indicated by their diameters appeared to be reaching healthy sizes before deposition (Newton and Kilambi 1969). The apparent health of individuals captured at the spawning grounds raises questions as to why the population of white bass remains at low levels. These results are consistent with a population that has suitable conditions for juveniles and adults yet suffers from low levels of recruitment. Potentially, recruitment is being hindered by yellow bass consuming eggs and larvae of white bass on the spawning grounds, and by yellow bass and hybrid striped bass interfering with white bass reproduction.

White bass from this study were below average in one category of health. Estimated potential fecundity from this study was lower on both ends than those reported by Newton and Kilambi (1973): 140,000 – 994,000, Ruelle (1977): 250,000 – 1,113,000, and Madenjian et al. (2000): 128,897 – 1,049,207 eggs. Fecundity estimates herein are not considered to be at unhealthy levels, as white bass often retain about 50% of their eggs after spawning (Ruelle 1977). However, reasons for lower fecundity from this population are unknown. One explanation may be the age of females from this study as compared to other reports. Most white bass from this project were age two and three whereas other studies reported most fish being ages three to four (Newton and Kilambi 1973; Ruelle 1977; Madenjian et al. 2000). Subsequently, the female fish from this study were smaller, as indicated by total lengths. Among white bass, there is a significant correlation in TL to potential fecundity, R = 0.65 (Newton and Kilambi 1969), and R = 0.85 (Madenjian et al. 2000). Fish from this study however had a high degree of variation between TL and potential fecundity (Figure 5). It is likely that a population of older fish would reflect greater potential fecundities with less variation. These fecundity estimates may be indicative of a young spawning population. The age structure of the spawning fish from this study is typical of a population that is receiving high fishing pressure on older fish (Van Den Avyle and Hayward 1999).

The 2013 fishing regulations for Barren River Lake limit the daily harvest of white bass and hybrid striped bass to 15 fish with no more than five fish exceeding 15 inches (381mm). The 2013 daily limit of yellow bass is 30 fish with no size restrictions (KDFWR 2013). More conservative creel limits on white bass within the Barren River upstream of Barren River Lake (e.g., five white bass per day) may help to preserve the white bass fishery. Removing regulations that limit the harvest of yellow bass may also limit the effect of yellow bass on white bass reproduction.

As previously noted, the white bass population was already in decline before yellow bass were detected in the lake. Research into other factors that may have contributed to this initial decline is warranted. Poor water quality is often closely linked to low spawning success rates (Berkman and Rabeni 1987). Water quality within the Barren River should be investigated for its possible role in declining reproductive success. Direct assessment of successful hatching and larval white bass transport to the reservoir should also be examined. During April of 2012 I performed exploratory larval fish sampling with drift nets and found no white bass larvae. A well designed sampling plan for drifting larval white bass would greatly elucidate spawning success. White bass year class strength in reservoirs is often closely associated with spring rain and water levels of inflowing streams (DiCenzo and Duval 2002; Willis et al. 2002). Monitoring rainfall and rates of inflow from the Barren River and other tributaries to the lake for potential correlations to white bass recruitment may reveal trends in the white bass population. Management strategies could be modified to limit harvest during periods of poor recruitment.

I documented overlap in habitat use of all three species in the river while white bass are spawning. In both years white bass were the first *Morone* species on the spawning grounds. Given that white bass are spawning, the arrival of yellow bass at the same spawning site provides ample opportunity for yellow bass to consume white bass eggs and larvae. I showed that yellow bass are eating eggs while on the white bass spawning ground. Eggs were not identified to species, as would be beyond the scope of this study. However, if yellow bass are consuming eggs during white bass spawning, then any eggs in the system are susceptible to predation. Through predation on eggs and larvae, yellow bass pose a threat to white bass recovery. To a lesser extent, hybrid striped bass are affecting white bass through diet and habitat overlap. I have shown the potential for these congeners to impact white bass in early stages of their life histories. In order to manage the fishery in a sustainable way, more efforts should be made to ameliorate the effects of yellow bass on white bass reproduction.

TABLES AND FIGURES

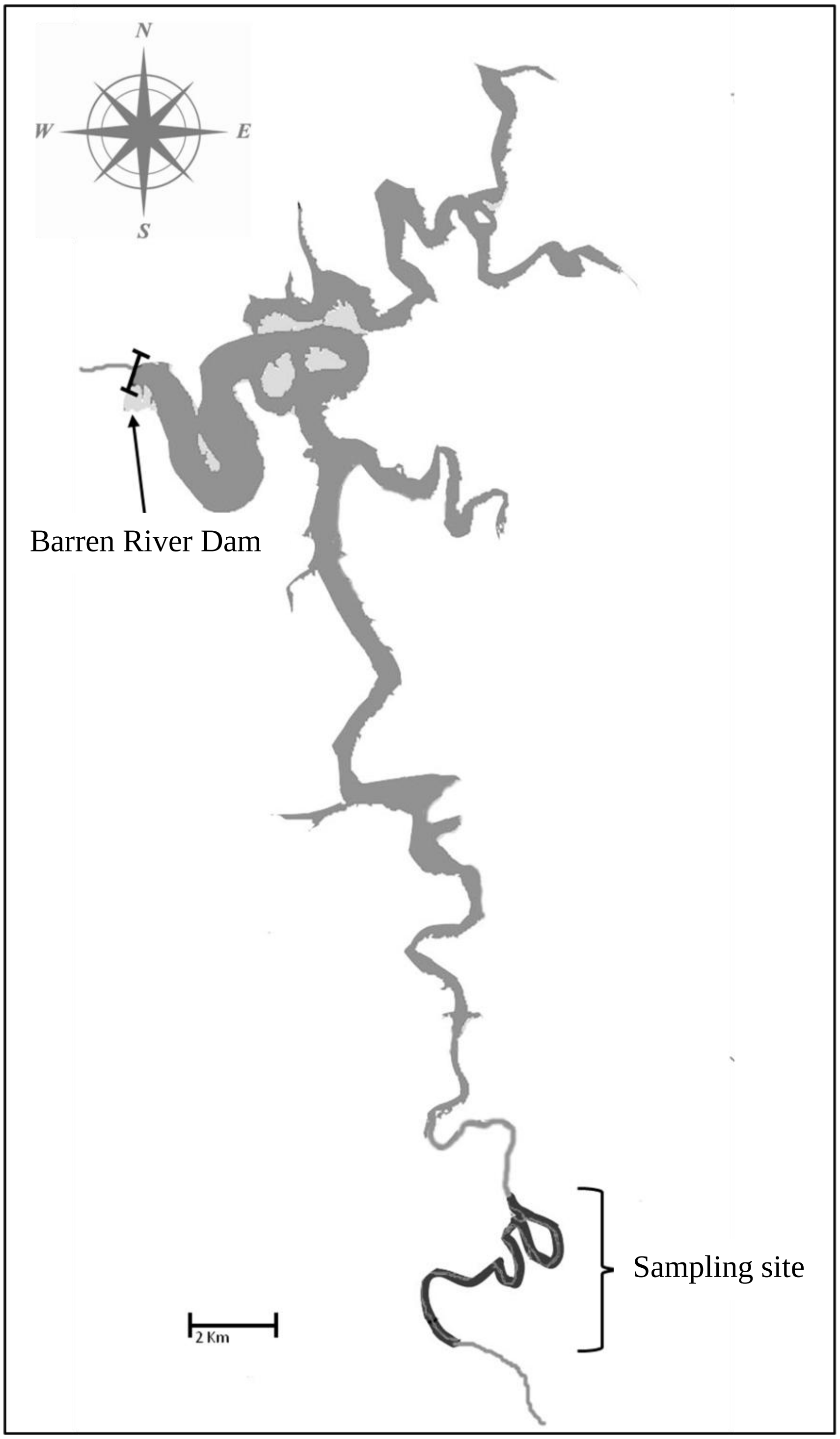


Figure 1. Map of Barren River Lake, Kentucky, showing sampling location on the Barren River, upstream of the lake.

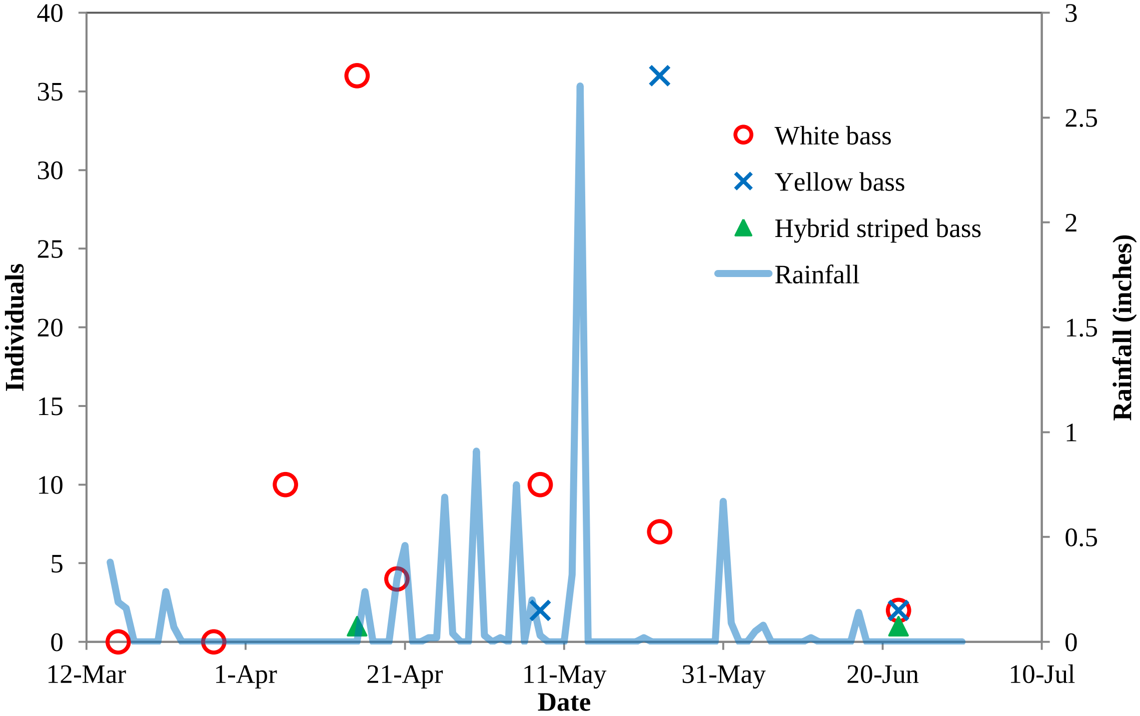


Figure 2. Diagram of the number of individual fish of each species collected in 2012 with rainfall during that period. Sampling periods before 3-April with no fish captured are show to illustrate the first date in which white bass were collected. Zeros are not shown for other species.

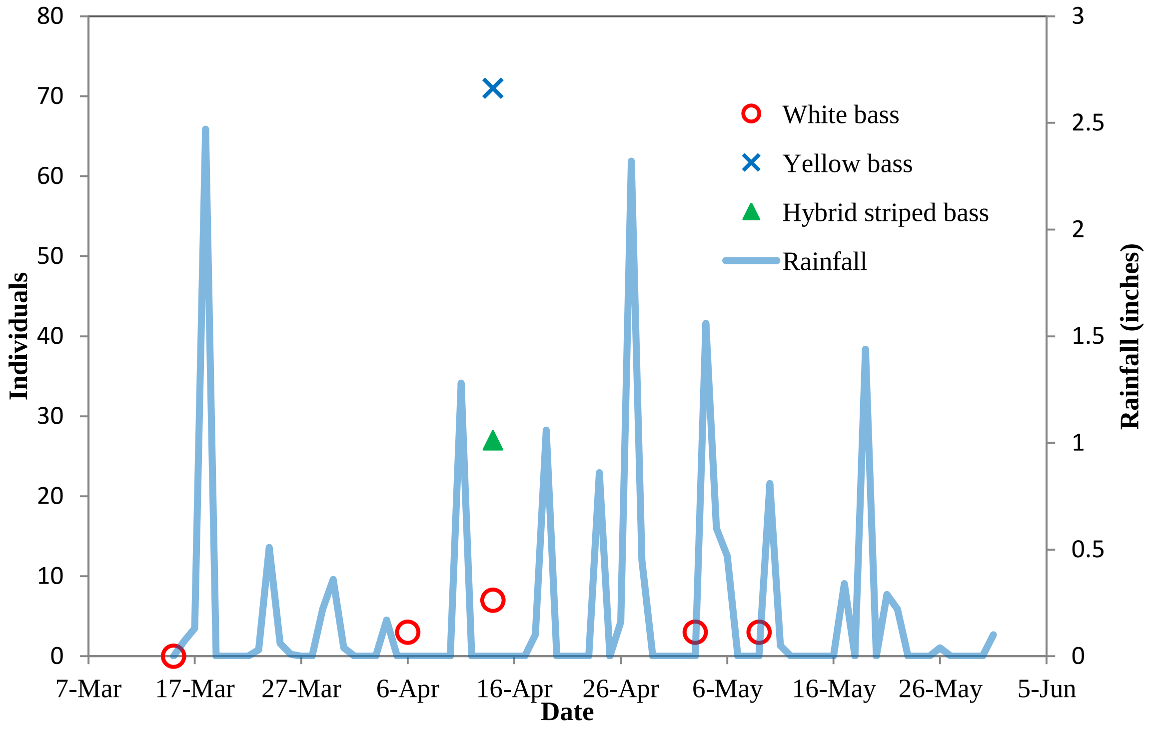


Figure 3. Diagram of the number of individual fish of each species collected in 2013 with rainfall during that period. Sampling periods before April-6 with no fish captured are shown to illustrate the first date in which white bass were collected. Zeros are not shown for other species.

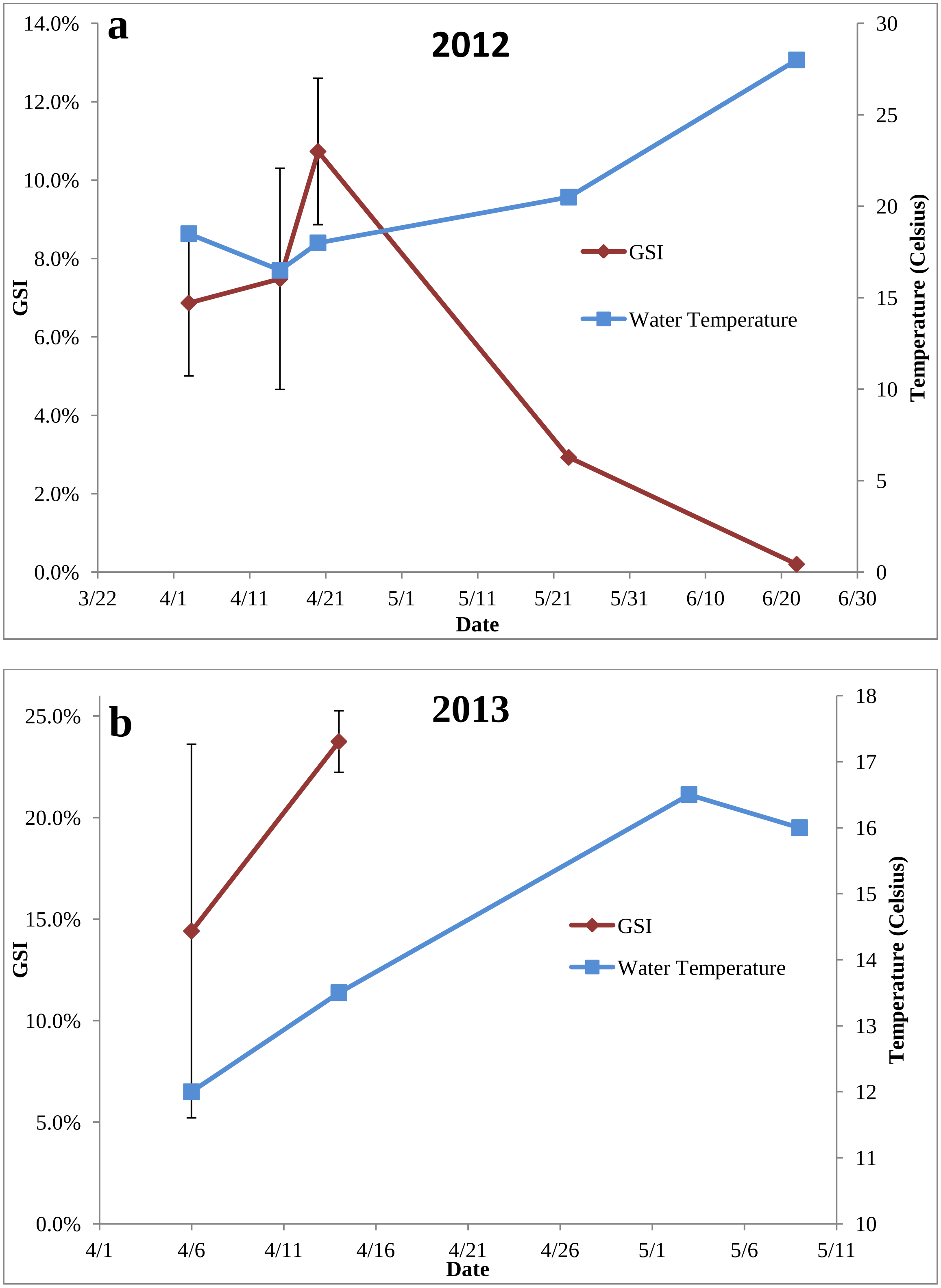


Figure 4. Mean gonadosomatic indices (GSI) (with error bars representing ± 1 SD) of female white bass with water temperatures during 2012 (**a**) and 2013 (**b**). Females were only collected on two sampling days in 2013.

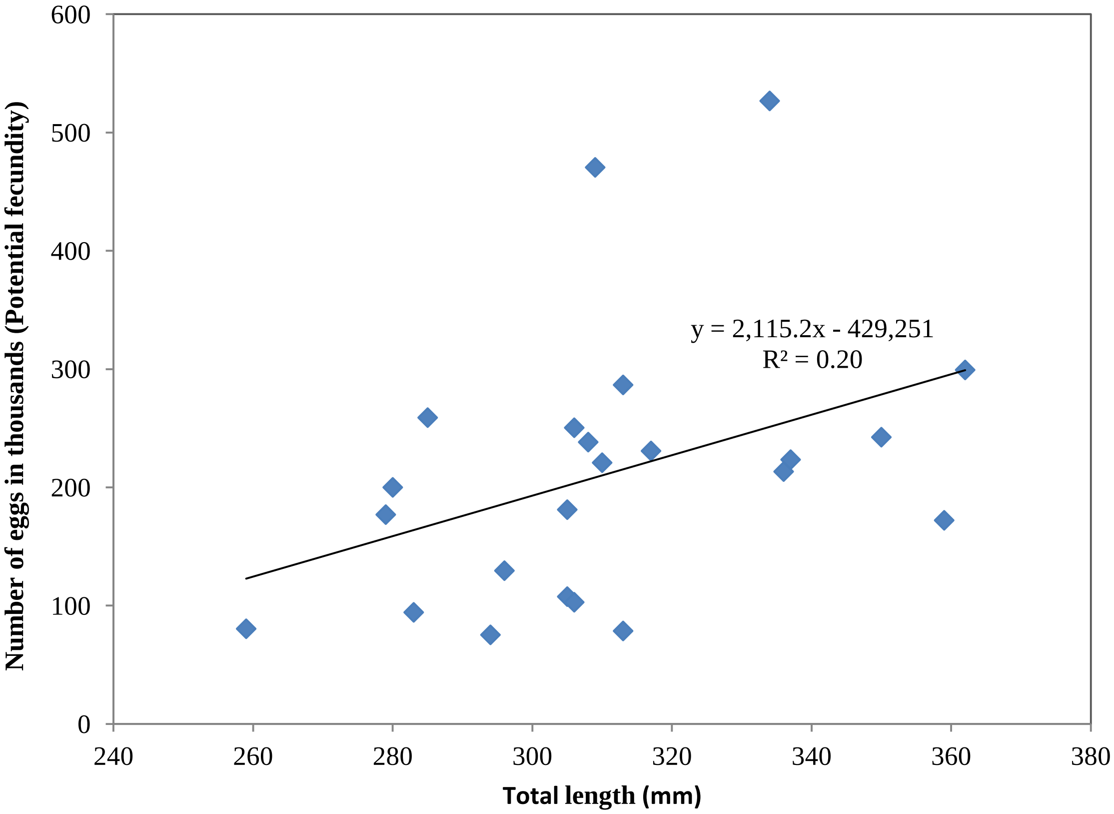
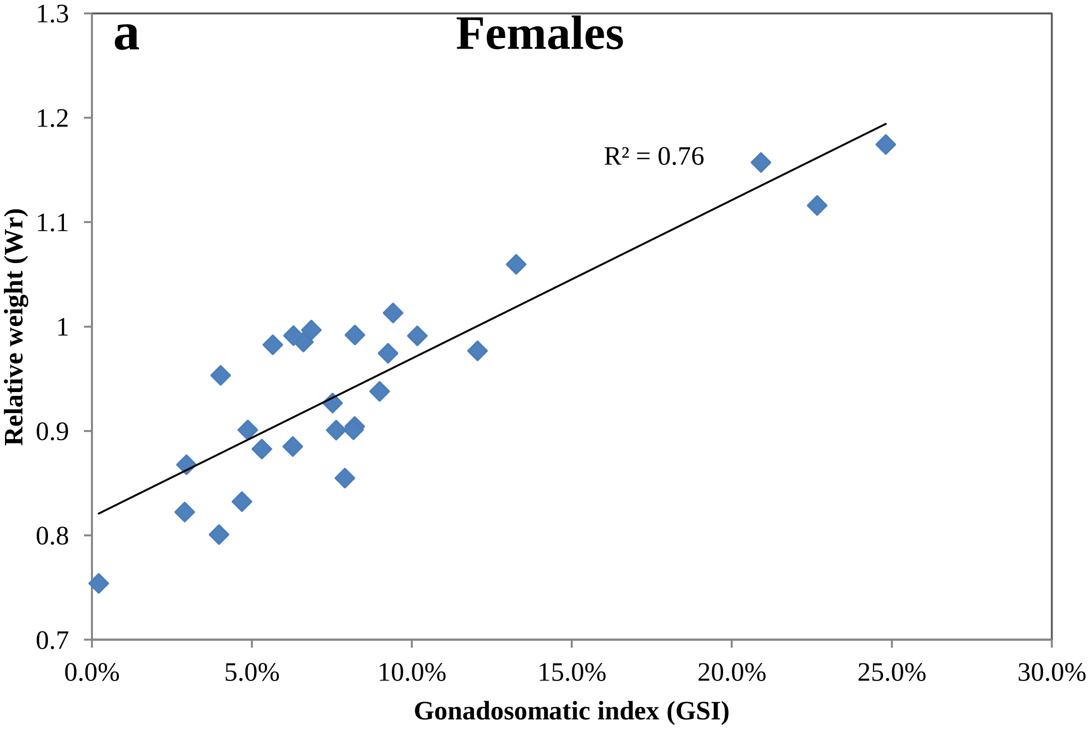


Figure 5. Comparison of the number of eggs to total lengths of 23 female white bass. Line of best fit explained 20.1 % of variation in egg counts at length.



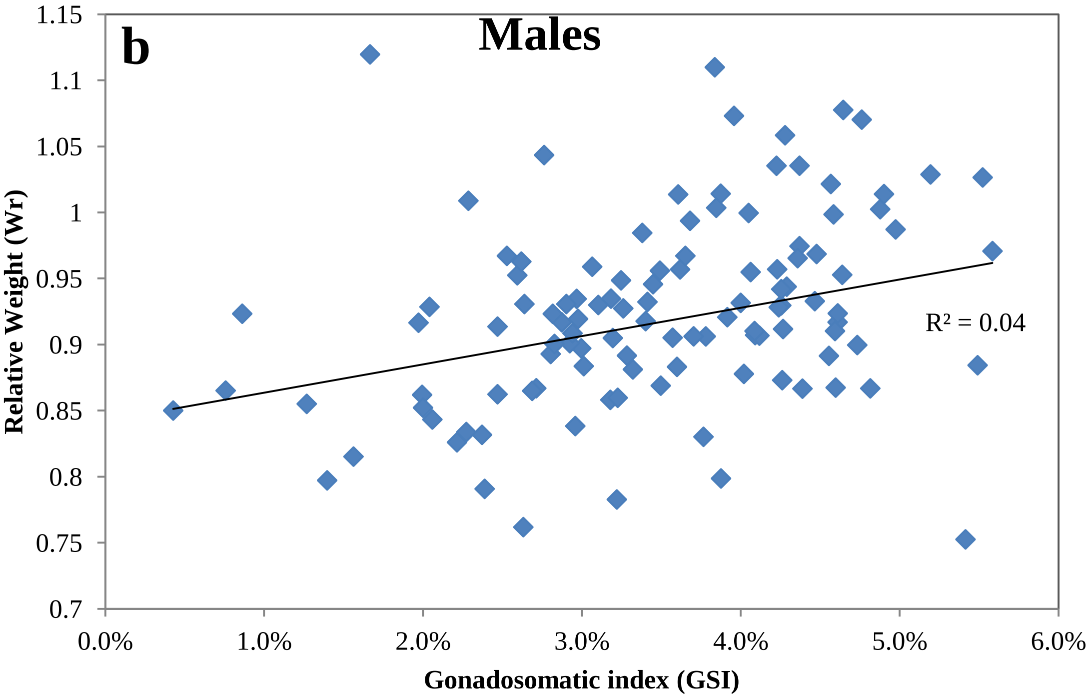


Figure 6. Comparison of gonadosomatic indices (GSI) to relative weights (W_r) of female (a) and male (b) white bass. GSI accounts for 75% of variation in female W_r and only 4% of variation in male W_r.

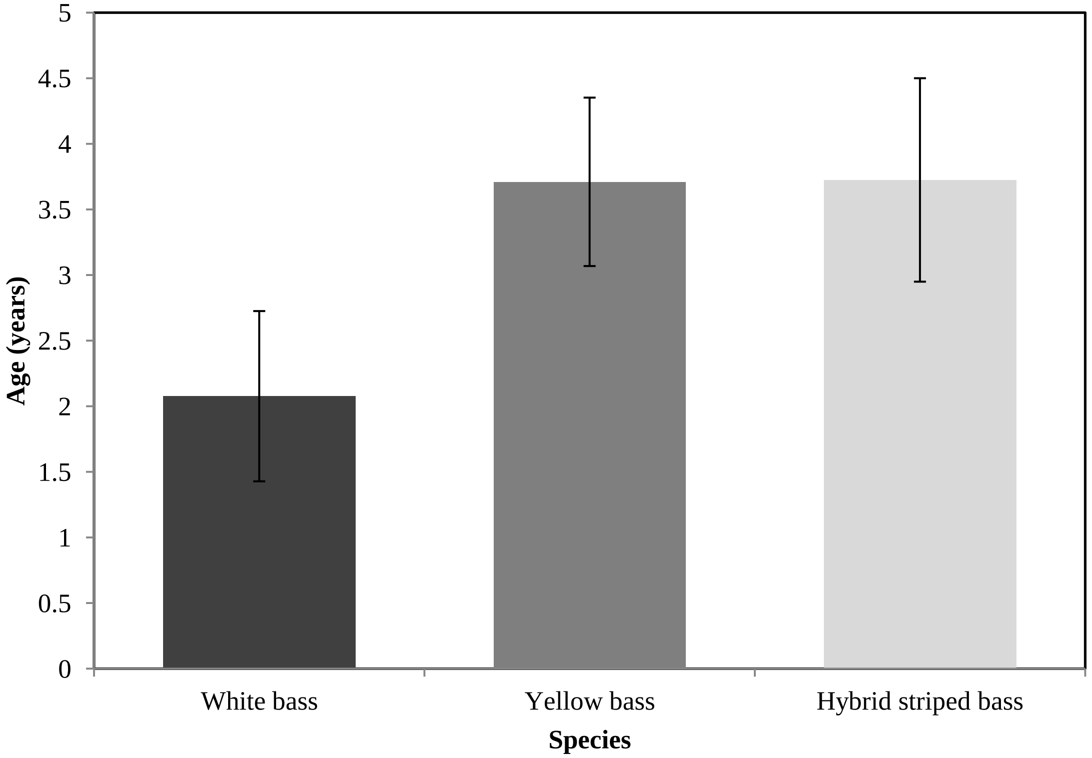


Figure 7. Mean ages with error bars representing ± (1 SD) of 144 white bass (2.07 years), 88 yellow bass (3.71 years), and 29 hybrid striped bass (3.72 years)

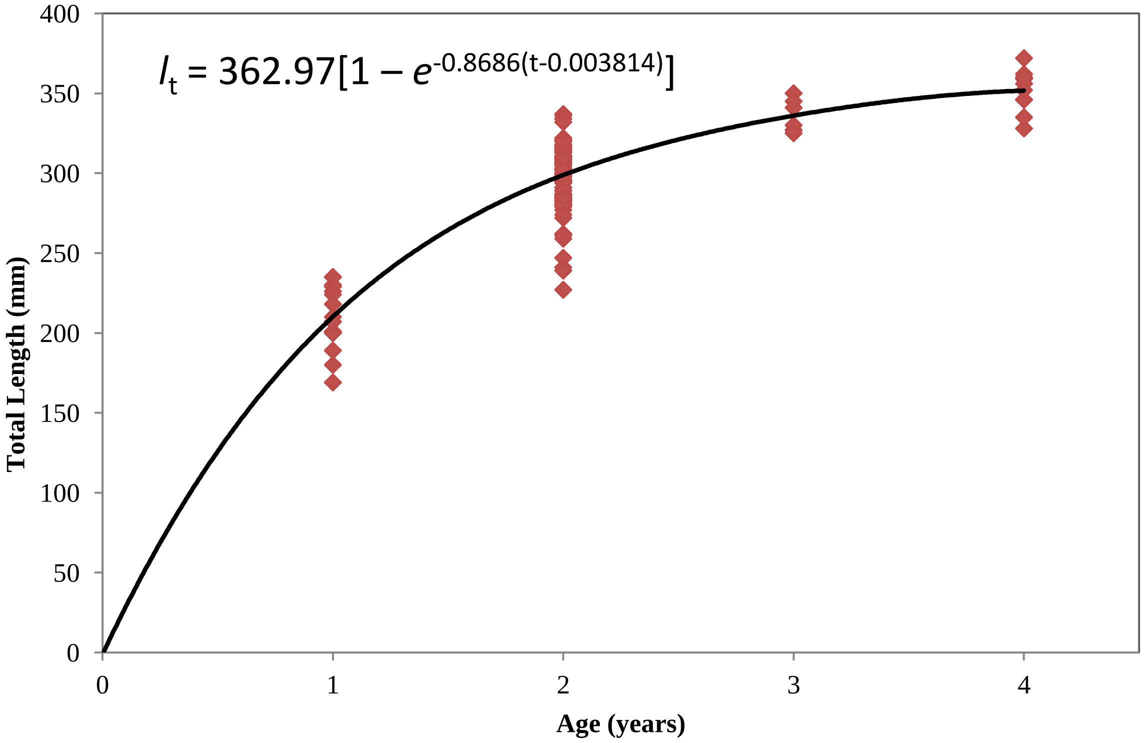


Figure 8. The von Bertalanffy growth equation and individual total lengths at age of 144 white bass.

Table 1. Dietary items by frequency of occurrence for white bass, yellow bass, and hybrid striped bass. Overlap is indicated by Schoener's values where 0.0 indicates no overlap and 1.0 indicated full overlap in diets.

	White bass	Yellow bass	Hybrid striped bass	White bass and yellow bass overlap	White bass and hybrid striped bass overlap
Fish eggs	0.0%	20.5%	0.0%	0	0
Fish larvae	2.7%	1.1%	0.0%	0.992	0
Post larval fish	2.1%	3.4%	27.6%	0.994	0.873
Arthropods	36.8%	76.1%	6.9%	0.804	0.851
Empty	59.7%	18.2%	65.5%	-	-
N	144	88	29	-	-

Table 2. Five of twelve empirical rules adopted from Moyle and Light (1996) that explain the invasion of yellow bass in Barren River Lake.

	Rule	Barren River Lake
1	Ecosystems with low species richness are more susceptible to invasion.	The open water area was mostly used by only a few species and was subsequently depauperate.
2	Piscivores are more likely to alter fish assemblages in new habitats.	Yellow bass and hybrid striped bass from this study exhibited piscivory.
3	Fish with a close physiological match to the system, are more likely to establish a population in that system.	Habitat and food items are similar those of which yellow bass are native.
4	Invasions are most likely to occur in systems where populations of native species are already below normal.	The white bass population was in decline since the 1980s.
5	Systems permanently altered by human activity are more susceptible to invasions.	The lake was formed by a dam constructed on the Barren River in 1964.

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