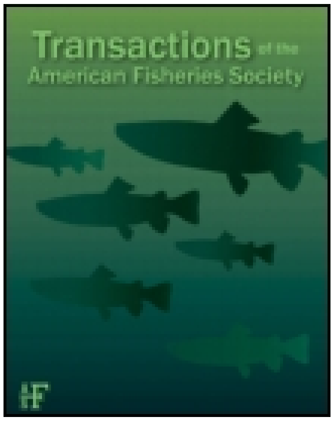

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ARTICLE

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Abstract
State and federal agencies typically introduce aquatic vegetation to increase the recruitment of sport fishes, particularly Largemouth Bass *Micropterus salmoides*. However, due to frequent turbidity and water-level fluctuations, managers in the southern United States are often left to introduce emergent macrophytes instead of submersed macrophytes. Emergent macrophytes have less underwater structural complexity than most submersed macrophytes and therefore may not be as effective in reducing the predation risk of Largemouth Bass. Therefore, the objective of this study was to determine if American water willow *Justicia americana*, a common emergent macrophyte species introduced in reservoirs, increases the survival of juvenile Largemouth Bass when exposed to predation. Predator–prey interactions between 10 juvenile and 1 adult Largemouth Bass were observed in tanks with natural densities of American water willow and compared with similar trials in vegetation-free control tanks. Each adult Largemouth Bass was tested once in each treatment (vegetation present or absent). Water willow significantly reduced the capture-to-attack ratio of adult Largemouth Bass and decreased the amount of time spent searching and the number of captures, resulting in significantly higher juvenile survival in the vegetated trials. Although water willow provided a similar increase in survival compared with previous studies using submersed macrophytes, the mechanism underlying this change differed, likely resulting from the more rigid stem design of water willow. We conclude water willow is an excellent candidate for establishment in reservoirs because it is easier to establish than many other macrophyte species yet still reduces predation risk on juvenile Largemouth Bass.

At moderate densities, aquatic macrophytes provide many benefits to reservoir ecosystems. Macrophytes improve habitat quality by preventing shoreline erosion (Summerfelt 1999) and reducing turbidity (Scheffer 1990). Macrophytes may also enhance the recruitment of juvenile fishes in reservoirs through multiple pathways. Macrophytes provide habitat for invertebrates, which increases the prey abundance for invertivorous juvenile fishes (Gotceitas and Colgan 1990; Savino et al. 1992). Macrophytes also provide shelter for some juvenile fishes, which in turn reduces predation risk (Miranda and Hubbard 1994; Dibble and Harrel 1997). However, the role of macrophytes in the recruitment process of most fishes is poorly understood, with the notable exception of Bluegill *Lepomis macrochirus* (Mittelbach 1981; Werner and Hall 1988; Turner and Mittelbach 1990). Because Bluegill are the only species well studied in this regard, knowledge regarding the role of vegetation in mediating predator–prey dynamics of this species is often applied to other fish species where research is lacking (e.g., Miranda and Pugh 1997; Olson et al. 1998; Lundvall et al. 1999; Havens et al. 2005).

Largemouth Bass *Micropterus salmoides* are one of the most pursued fish species within the United States (USFWS 2012), and recruitment variability is a common issue limiting these populations (Miranda and Pugh 1997). Several factors have been correlated with Largemouth Bass recruitment, including hatching date (Pine et al. 2000), forage availability (Parkos and Wahl 2010), water-level fluctuations (Kohler et al. 1993), predation (Miranda and Hubbard 1994), and

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availability of cover (Miranda and Hubbard 1994). Anecdotal field observations suggest that the presence of littoral vegetation may minimize the effects of many of these recruitment-limiting factors for Largemouth Bass (Miranda and Pugh 1997); however, this has not been tested directly.

Because of the potential benefits of macrophytes to juvenile fish recruitment, vegetation plantings have been attempted in many reservoir systems (Doyle et al. 1997; Smart et al. 1998; Smiley and Dibble 2006). However, turbidity levels (DeVries 1990) and fluctuating water levels (Strakosh et al. 2005) in southern U.S. reservoirs are often greater than in northern U.S. lakes, making submersed macrophytes difficult to establish in southern reservoirs. Therefore, lake managers often must overcome several challenges when attempting vegetation plantings in reservoirs (Collingsworth et al. 2007). Given the effort required to establish aquatic macrophytes in reservoirs, it is important to understand if these habitat enhancement projects truly improve recruitment for the target species.

One macrophyte species that can be successfully planted in turbid reservoir systems is American water willow *Justicia Americana* (hereafter, "water willow"). Water willow plantings have been used as a management tool to increase macrophyte coverage in the reservoirs of several states (Collingsworth et al. 2009; Strakosh et al. 2009). Often, a major objective of the plantings is the increased recruitment of juvenile Largemouth Bass by providing a refuge from predation. However, few studies have directly quantified the effects of aquatic macrophytes on Largemouth Bass recruitment, so it is not clear if these plantings are effective. Increased levels of aquatic vegetation have been correlated with increased age-0 Largemouth Bass abundance in field studies (Moxley and Langford 1985; Radomski et al. 1995; Hoyer and Canfield 1996; Tate et al. 2003), possibly due to increased refugia from predation (Miranda and Hubbard 1994). However, numerous environmental factors associated with the increased vegetation in these experiments could alternatively explain these patterns (e.g., changes in invertebrate abundance or competitor densities, altered sampling efficiency in different habitats producing inaccurate abundance estimates, concentration of the same number of age-0 fish near vegetation giving the appearance of increased production, etc.). Because predation is a major source of mortality for juvenile Largemouth Bass (Aggus and Elliott 1975; Durocher et al. 1984), understanding how macrophytes may mitigate the mortality of juvenile Largemouth Bass is essential for proper management and warrants further study. Additionally, water willow is an emergent macrophyte species that provides less underwater structural complexity than many submersed macrophyte species and, therefore, may not improve predator avoidance to the same degree as other species known to improve juvenile Bluegill survival (Savino and Stein 1982; Gotceitas and Colgan 1989). Therefore, additional research is needed to evaluate the effectiveness of water willow in reducing the predation mortality of juvenile Largemouth Bass. The objective of this study was to determine if water willow reduces the predation risk of juvenile Largemouth Bass and, if so, to elucidate the behavioral mechanisms involved. This information will be useful in explaining patterns observed in the field and will help to guide future management efforts aimed at reducing the predation mortality of juvenile Largemouth Bass.

METHODS

Five hundred forty juvenile Largemouth Bass (58–81 mm TL) were collected via seining and 17 adult Largemouth Bass (253–343 mm TL) were collected via boat-mounted electrofishing from ponds and reservoirs near Stillwater, Oklahoma. Collected fish were transported to the Oklahoma State University Fisheries and Aquatic Ecology Wet Laboratory (OSU FAEWL) and housed in tanks separate from the study tanks until they were used in the trials. Mean water temperature was 23 ± 2°C for the study tanks during the course of the experiment. Water willow was collected from Sanborn Lake, Payne County, Oklahoma, and immediately transported to the OSU FAEWL. Prior to collection, water willow stem densities were measured from 1-m quadrats at 10 distinct, haphazardly chosen water willow stands within Sanborn Lake. The average stem density (170 ± 11.7 stems/m^2 [mean ± SE]) from these 10 measured stands was used in the experiment. Water willow stems had a mean diameter of 10.4 ± 0.3 mm (mean ± SE; N = 50 measured). During collection, water willow stems were removed from the soil, leaving the root masses intact. Above-water leaves that obstructed the overhead camera view were removed from the stem. Each stem was cut at the first node above the root mass and planted haphazardly in gravel on one-half of the vegetation treatment tank.

To determine the effects of water willow on the predation risk posed by adult Largemouth Bass to juvenile Largemouth Bass, we conducted trials similar to those of Savino and Stein (1982) in round polyethylene tanks (1.98 m diameter, 0.86 m deep) at the OSU FAEWL. Trials were conducted in a vegetation treatment tank (with water willow in one-half of the tank) and a control tank (void of vegetation). Gravel was placed in the bottom of both the control and vegetated tanks. Water willow was only planted in one-half of the vegetation tank to give both predator (adult Largemouth Bass) and prey (juvenile Largemouth Bass) a choice between vegetated and open-water habitats.

Each adult Largemouth Bass was tested once in both the control and the vegetation treatments with a repeated-measures design to account for individual variation in predator behavior. Ten juvenile Largemouth Bass were used in each treatment trial, producing a density of juvenile Largemouth Bass within the range of densities found within natural water willow habitats (i.e., 3.25 fish/m^2; Strakosh 2006). Juvenile Largemouth Bass were matched to 20–25% of the adult Largemouth Bass TL, as this is considered the optimal prey size given the body shape of juvenile Largemouth Bass (Hoyle and

Keast 1987). Juvenile Largemouth Bass were not used in multiple replicates to ensure that predator avoidance did not increase during later trials.

To begin a trial, one adult Largemouth Bass was placed within a cylindrical hardware cloth cage (0.64-mm square mesh) in the study tanks and acclimated 24 h prior to the trial. All adult Largemouth Bass were trained to this confinement until they readily pursued prey when released. Juvenile Largemouth Bass were also acclimated 24 h prior to the experiment within the study tanks but were not restricted within the tank. Trials were initiated by lifting the hardware cloth cage so that the predator could gain access to the entire tank. Video cameras installed above the study tanks recorded adult and juvenile Largemouth Bass interactions during 1-h trials. Video recordings were subsequently reviewed to quantify the amount of time the predator and prey spent in each of several behavioral categories. The same observer was used for all video analyses to reduce potential bias.

Predator behavior was categorized following the approach of Savino and Stein (1982): searching, defined as movement by the predator when not oriented to prey; following, defined as movement by the predator while oriented to an individual prey; pursuing, defined as following while at burst speed; attacking, defined as the predator striking at a prey organism; capturing, defined as the predator successfully ingesting prey; and inactivity, defined as the predator resting motionless and not oriented towards prey. The number of captures per number of attacks (capture : attack ratio) and the number of attacks per number of follows (attack : follow ratio) were used to quantify predator foraging success. Following, pursuing, attacking, and capturing behaviors were all analyzed as counts, and inactivity and searching behaviors were analyzed as the proportion of time spent exhibiting the behavior during the trial.

Every 5 min, both predator and prey location (vegetated [left] or open-water [right] side in the treatment tank or corresponding locations [left versus right side] in the control tank) were recorded, predator activity (inactive versus one of the predatory behaviors [searching, following, etc.]) was recorded, and prey behavior was quantified as schooled or dispersed (Savino and Stein 1982). The camera above each tank was orientated such that water willow was as always on the "left" side of the tank and open water was on the "right" for the vegetated treatment. The camera was oriented the same way for the control treatments. Therefore, the left and right sides of both tanks were the same in terms of tank geography and orientation. This study design allowed not only for direct comparison of the use of vegetation versus open water (i.e., comparing the use of the left and right sides of the tank in the vegetation treatment) but also served as a control for potential environmental conditions in the laboratory (e.g., light, noise, etc.) that might have influenced which side of the tank was most used by the fish (i.e., comparing the use of the left and right sides of the tank in control treatments where both tank sides were the same to see if they actually spent 50% of their time on each side). Schooling was defined as individuals aggregated and moving about as a unit, and dispersed was defined as individuals not being closely associated with each other (Savino and Stein 1982).

To compare the effects of predation risk on juvenile Largemouth Bass behavior, 10 additional trials in both the vegetation and control treatments were conducted without a predator present. Juvenile Largemouth Bass used in the predator-absent trials were also not reused between trials. Juvenile Largemouth Bass behavioral metrics (i.e., the side of the tank used, schooling or dispersed) employed in the predator-present trials were also used to quantify behavior in the predator-absent trials.

The frequency of measured predator behaviors was compared between the vegetation and control treatments using one-way ANOVAs with repeated measures (predators treated as subjects to account for any individual variation in behavior). Juvenile Largemouth Bass behaviors were compared using a two-way ANOVA with repeated measures using two separate analyses to investigate both predator activity and treatment effects in predator-present trials. The percentage of juveniles on the left side of the tank was compared using both treatment (vegetation versus control) and the location of the predator in the tank at the time of observation as main effects, with observations taken within trial treated as repeated measurements. The percentage of juvenile Largemouth Bass schooled was compared using both treatment and predator behavior as the main effects, with observations taken within trial treated as repeated measurements. Lastly, juvenile Largemouth Bass behaviors were compared between the predator-present and predator-absent trials using a two-way ANOVA, with predator presence and treatment as main effects and observations taken within trials treated as repeated measurements. Variables whose residuals were not normally distributed (the percentage of juveniles on the left side of the tank and the percent of juveniles schooled) were arcsine-square root transformed. When significant differences were identified, a Tukey's honestly significantly different (HSD) posthoc test was performed to determine where those differences occurred. All statistical comparisons were performed using SAS PROC MIXED (SAS Institute 2011), with a significance level of $\alpha = 0.05$.

RESULTS

Adult Largemouth Bass (Predator) Behavior

Vegetation increased the survival of juvenile Largemouth Bass as the number of captures by adult Largemouth Bass was lower within the vegetation treatment than within the control treatment ($F_{1,\ 16} = 10.56$, $P = 0.005$; Figure 1). Predators were less active in the vegetation treatment (percent of time inactive, $F_{1,\ 16} = 14.90$, $P = 0.001$; Figure 2) and spent more

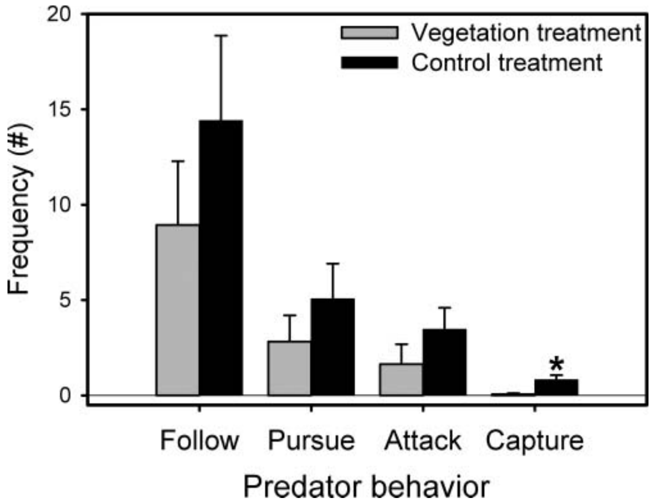

FIGURE 1. Mean frequency of predatory behaviors exhibited by adult Largemouth Bass in vegetated and unvegetated control treatments (error bars = SE). Asterisks denote significance ($P < 0.05$) between vegetation and control treatments.

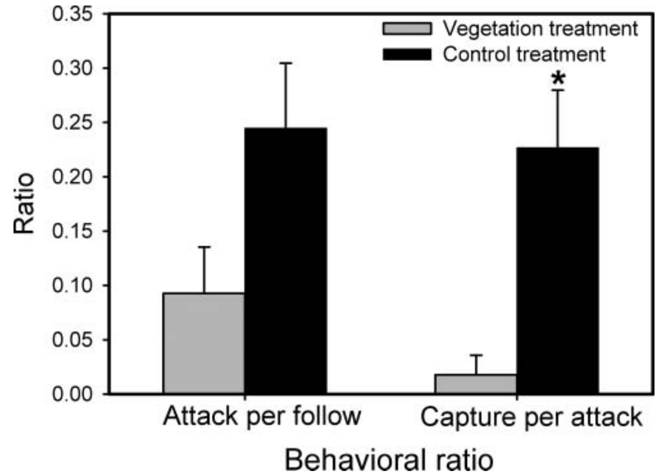

FIGURE 3. The number of attacks per follow and the number of captures per attack by adult Largemouth Bass in vegetation and control treatments (error bars = SE). Asterisks denote significance ($P < 0.05$) between vegetation and control treatments.

time searching in the control treatment ($F_{1,\ 16} = 11.72$, $P = 0.003$; Figure 2). However, the number of follows ($F_{1,\ 16} = 1.95$, $P = 0.181$), pursuits ($F_{1,\ 16} = 1.92$, $P = 0.185$), and attacks ($F_{1,\ 16} = 2.377$, $P = 0.143$) were not different between treatments (Figure 1), suggesting that the increased vulnerability of juvenile Largemouth Bass in the control tank was not simply a function of an increased encounter rate. A total of 28 attacks were made within the vegetation tank and 59 attacks within the control tank. All 28 attacks made within the vegetation tank were on the left (vegetated) side of the tank, while the attacks in the control treatment were more evenly distributed (30 on the left side, 29 on the right side). There was no difference in the attack : follow ratio between the two treatments ($F_{1,\ 13} = 2.84$, $P = 0.116$; Figure 3), indicating that predators were just as likely to strike in both treatments once they started following a prey item. However, predators were more successful in capturing the prey they attacked in the control treatment than in the vegetation treatment (capture : attack ratio: $F_{1,\ 2} = 21.20$, $P = 0.044$; Figure 3). The observed difference in the capture : attack ratio was only based on $N = 4$ adult Largemouth Bass because only predators that had quantifiable ratios in both their vegetation and control trials could be used in the analysis. However, all four predators for which the ratio could be calculated showed the same pattern, with at least a three times greater capture success in open water than in their control trial (i.e., the pattern was not driven by an outlier that overwhelmed the small sample size).

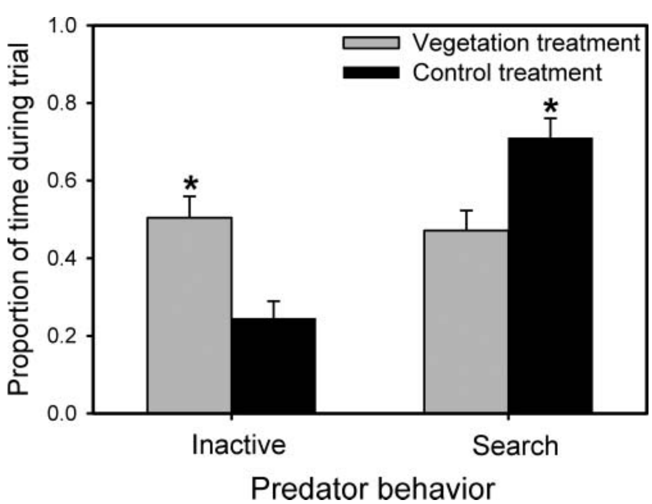

FIGURE 2. Proportion of time spent by adult Largemouth Bass in inactive and searching behaviors between vegetation and control treatments (error bars = SE). Asterisks denote significance ($P < 0.05$) between vegetation and control treatments.

Juvenile Largemouth Bass (Prey) Behavior

Juvenile Largemouth Bass typically used the opposite side (left versus right) of the tank from the predator in the control tank, but predator location was not related to prey location in the vegetation treatment (treatment × predator location interaction: $F_{1,\ 12} = 12.08$, $P = 0.005$; Tukey's HSD: $P < 0.001$ for all pairwise comparisons with the predator on the left side, $P > 0.330$ for all other comparisons; Figure 4). Juveniles were found on the vegetated side of the tank (left side) 66–73% of the time in the vegetation treatment, even when the predator was also on the same side (Figure 4).

Predator activity alone (inactivity compared with all other predatory behaviors) had no effect on the amount of juveniles schooling in either the vegetation (Tukey's HSD: $P = 0.80$; Figure 5) or control treatments (Tukey's HSD: $P = 0.13$; Figure 5). However, juveniles schooled more when vegetation

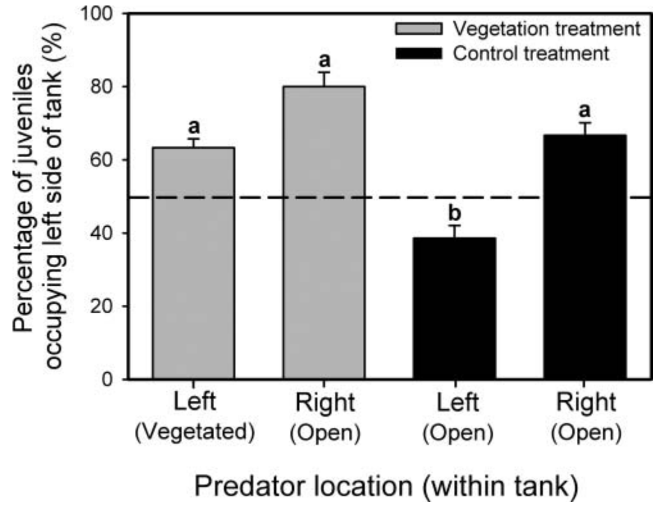

FIGURE 4. Percentage of juvenile Largemouth Bass on the left side of the study tank in vegetation or control treatments based on predator location (error bars = SE). Horizontal dashed line indicates prey using both sides of the tank equally; bars extending above this line indicate disproportionate use of the left side of the tank (vegetated side in the vegetation treatment, open water in the control treatment), bars below this line indicate disproportionate use of the right side of the tank (open water in both the vegetation treatment and control trials). Means with different letters denote significance at the 0.05 level.

was not available regardless of whether the predator was active or inactive (vegetation treatment × predator activity interaction: $F_{1,\ 12} = 10.30$, $P = 0.008$; all Tukey's HSD comparisons: $P < 0.001$; Figure 5).

Juvenile Largemouth Bass location did not differ between trials with and without a predator ($F_{1,\ 7} = 1.70$, $P = 0.233$). A greater proportion of juvenile Largemouth Bass used the left side of the tank (vegetated side) in the vegetation treatment trials than in the control trials ($F_{1,\ 16} = 33.0$, $P < 0.001$; Figure 6), whether the predator was present or not. Juvenile Largemouth Bass schooled more when a predator was present ($F_{1,\ 7} = 9.96$, $P = 0.016$), and juveniles schooled less in the vegetation treatment regardless of the presence of a predator ($F_{1,\ 16} = 166.55$, $P < 0.001$; Figure 6).

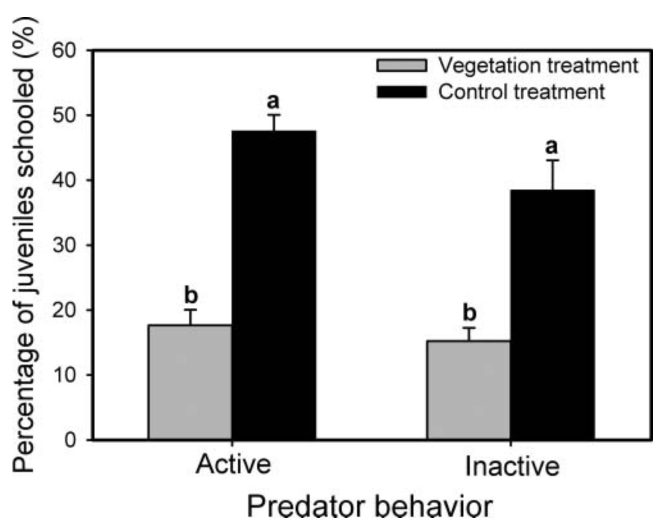

FIGURE 5. Percentage of Juvenile Largemouth bass schooled in vegetated or control treatments based on predator activity (error bars = SE). Means with different letters denote significance at the 0.05 level.

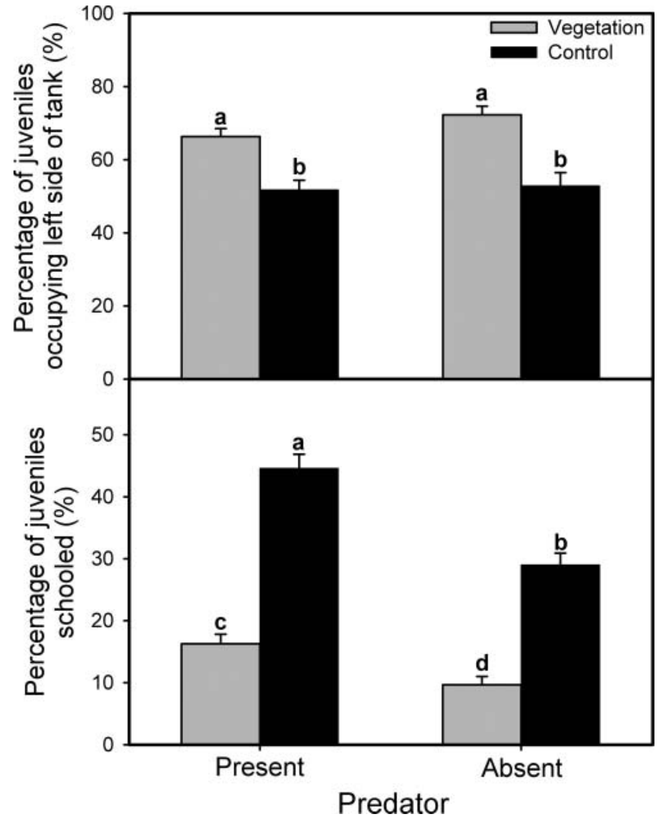

FIGURE 6. Effect of predator presence on juvenile Largemouth Bass habitat selection and schooling behavior. Top panel: percentage of juvenile Largemouth Bass on the left side of the study tank (vegetated side in the vegetation treatment), in vegetated or control treatments (error bars = SE). Bottom panel: percentage of juvenile Largemouth Bass schooled in vegetated or control treatments based on predator presence (error bars = SE). Means with different letters denote significance at the 0.05 level.

DISCUSSION

No studies have quantified the direct effects of aquatic macrophytes on juvenile Largemouth Bass predator avoidance behavior and survival. Several studies have inferred the effects of macrophytes on juvenile Largemouth Bass survival using field observations (e.g., Moxley and Langford 1985; Bettoli et al. 1992; Miranda and Pugh 1997); however, multiple factors differed between the vegetated and unvegetated conditions in these studies, so predation mortality cannot be separated from other factors influencing recruitment and therefore the role of macrophytes in reducing predation mortality is left unclear. We found water willow reduced the predation vulnerability (the total number of captures per hour) for juvenile Largemouth Bass. Our behavioral analysis provides insight into several of the mechanisms underlying this reduction in predation risk as we observed differences in both adult and juvenile Largemouth Bass behavior between the vegetated and unvegetated treatments.

The presence of water willow reduced adult Largemouth Bass activity (i.e., less time spent searching and more time spent inactive), which is consistent with previous observations that Largemouth Bass switch from active predatory behavior to an ambush style of behavior as structural complexity increases (Savino and Stein 1982, 1989a). All attacks made during the vegetation trial occurred within water willow, likely indicating that the adult Largemouth Bass preferred to wait for an opportune time to strike within the vegetation (consistent with the observations of Savino and Stein 1989a that adult Largemouth Bass become ambush predators at high vegetation densities). In contrast, attacks were equally frequent on the left and right sides of the tank for the control treatment as Largemouth Bass continually searched for available prey. However, the stem density used within our experiment was lower than the densities where this change in Largemouth Bass behavior has been observed previously (i.e., our stem density was 170 stems/m^2 compared with 350 stems/m^2 in Gotceitas and Colgan 1989 and 250 stems/m^2 in Savino and Stein 1982). The change in adult Largemouth Bass behavior likely occurred at a lower density with water willow because this plant has a more rigid growth form (i.e., inflexible stems) than most submersed macrophytes, thereby restricting adult Largemouth Bass movement even at a lower stem density. We observed that Largemouth Bass typically had to physical maneuver around individual water willow stems to pursue and attack prey within or near the edge of the vegetation.

Macrophytes create a predation refuge for Bluegill by reducing the visual contact between predator and prey (Savino and Stein 1982; Gotceitas and Colgan 1989), but we found that predator success was limited by capture efficiency rather than by visual contact in water willow. Water willow did not impede adult Largemouth Bass from detecting and positioning themselves to capture prey (i.e., there was no difference in the number of follows, pursues, or attacks between the vegetation and control treatments). Adult Largemouth Bass were also frequently observed orienting and following prey from deep within water willow, indicating that water willow did not severely obstruct the predator's visual contact with prey. Rather, vegetation allowed the juvenile Largemouth Bass to evade capture (i.e., cover reduced the capture : attack ratio). In dense submersed macrophytes, Largemouth Bass likely cannot locate prey as easily but instinctively attack prey when it is detected in close proximity, leading to reduced encounter rates but increased capture efficiency once prey are encountered (Savino and Stein 1982). In our study with macrophytes that were only moderately dense but had inflexible stems, adult Largemouth Bass were able to visually locate prey within water willow but could not effectively capture them when they were in vegetation. Therefore, our results show that aquatic vegetation can impact the predation process even when it is not dense enough to obstruct visual contact.

We found juvenile Largemouth Bass differ from other more well-studied prey (e.g., Bluegill and Fathead Minnows *Pimephales promelas*) with respect to their predator avoidance behavior in vegetated and open-water habitats. Juvenile Largemouth Bass, like Fathead Minnows, schooled more when a predator was present, regardless of the predator's behavior (Savino and Stein 1989b). In contrast, Bluegill do not school in response to the mere presence of a predator but school only in response to specific predator activities (DeVries 1990). Further, we found that juvenile Largemouth Bass selected vegetated habitat over open water, regardless of predator presence or location. For both Bluegill and Fathead Minnows, cover utilization was directly related to predator presence; Bluegill used cover more when predators were present (Savino and Stein 1989b; DeVries 1990), whereas Fathead Minnows used cover more when predators were absent (Savino and Stein 1989b). Because juvenile Largemouth Bass responded differently than other well-studied prey to predation risk in vegetated and unvegetated habitats, changes in vegetation could result in shifts in prey selection by predators (i.e., different prey types may be better adapted to evade predation at different vegetation densities).

Bluegill face a trade-off between utilizing dense vegetation to reduce predation risk and having greater foraging efficiency in open water (Werner and Hall 1988; Gotceitas 1990; Dionne and Folt 1991; Harrel and Dibble 2001). However, prepiscivorous juvenile Largemouth Bass do not suffer lowered foraging rates in complex submersed macrophytes with stem densities up to 1,000 stems/m^2 (Stahr 2014). Therefore, macrophytes should provide better overall recruitment for juvenile Largemouth Bass, as the current study demonstrates a predator avoidance advantage at macrophyte densities that do not impede juvenile Largemouth Bass foraging rates.

Although numerous studies have investigated the effectiveness of submersed macrophytes as a predation refuge for juvenile fish, few have considered emergent macrophytes in this role. Young of year Largemouth Bass are more abundant when reservoir water levels are high, presumably due to increased areas of flooded terrestrial and emergent vegetation (Aggus and Elliott 1975; Willis 1975; Shirley and Andrews 1977; Fisher and Zale 1993; Kohler et al. 1993). Our study is the first to consider how emergent macrophytes affect predator–prey interactions involving juvenile Largemouth Bass, and we found that the more rigid cover provided by water willow (a characteristic common to most emergent vegetation species) decreased the foraging success of adult Largemouth Bass at lower stem densities than previously reported. Therefore, water willow and other emergent macrophytes may provide an ideal level of complexity for juvenile Largemouth Bass even though they do not have as much structural complexity as many submersed vegetation species.

In large reservoirs common throughout the southern United States, water fluctuations and turbidity can impede submersed macrophyte colonization (Smart et al. 1998). Therefore, managers attempting to establish macrophytes must often work with emergent macrophyte species (such as water willow) that can withstand the extremes in these environments (Collingsworth et al. 2009). Water willow grows above the water's surface, reducing the influence of high water turbidity on vegetation establishment. Also, water willow is resistant to drought conditions (Strakosh et al. 2005). These attributes can make water willow easier to establish than many other macrophyte species. As with any species introduction, careful consideration should be given to any potential negative effects (e.g., competition with native species, potential to spread beyond intended area, etc.) before an introduction is carried out. If water willow is considered a suitable species for introduction in a given system, our results demonstrate that it can effectively increase survival of juvenile Largemouth Bass by reducing predation mortality. Future studies should test whether water willow plantings truly increase the recruitment of Largemouth Bass (i.e., not just increasing densities near plantings, as has previously been established [Strakosh et al. 2009], but increasing recruitment to age 1) and determine what level of plantings are needed to achieve a population-wide objective in reservoir ecosystems.

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