Selection of Habitat-Enhancing Plants Depends on Predator–Prey Interactions

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Abstract

Shallow areas of drawdown reservoirs are often devoid of adequate fish habitat due to degradation associated with unnatural and relatively invariable cycles of exposure and flooding. One method of enhancing fish habitat in these areas is to sow exposed shorelines with agricultural plants to provide structure once flooded. It remains unclear if some plants may be more suitable than others to provide effective fish habitat. To determine the fish habitat potential of various crops, we performed a replicated tank experiment evaluating the selection of agricultural plants by prey and predator fishes with and without the presence of the other. We submerged diverse treatments of potted plants in outdoor mesocosms stocked with prey and/or predator fish and monitored selection of plant species, stem density, and stem height over 0.5-h trials. Prey fish selected the densest vegetation, and selection was accentuated when a predator was present. Predators selected the second highest stem density and were more active when prey were present. Prey schooling was increased by predation risk, suggesting that cover was insufficient to outweigh the advantages of increased group size. Our data indicate that the perception of cover quality is reciprocally context dependent on predator–prey interactions for both predator and prey. Applications of the two most selected plant treatments in this study could enhance structural habitat for both predator and prey fishes in reservoirs, adding to their already reliable functionality as supplemental forage crops for terrestrial wildlife.

Keywords: drawdown; reservoir; habitat; enhancement; centrarchid

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Introduction

Man-made reservoirs provide invaluable services to societies globally, but require severe environmental alterations. In particular, flood control reservoirs experience large annual disturbances as water level fluctuations seasonally expose and inundate an interval of shoreline elevations known as the regulated zone (Miranda 2017). Because these reservoirs were created to catch flood waters, their water cycle has been altered to temporally mismatch natural flood cycles, which suppresses establishment of aquatic and wetland plants in the regulated zone during the plant growing season (Beard 1973; Bayley 1995; Baldwin et al. 2001; Greet et al. 2013). Cover is a key habitat component for most fish, but access to submerged structural cover is often inadequate in the regulated zone of drawdown reservoirs. Growth of upland vegetation during drawdowns temporarily provides submerged structure once flooded before it degrades, but drawdowns occur in late autumn and winter, mostly outside the growing season. The resulting barren mudflats are typically featureless, as they are smoothed out by wave action, erosion, and sedimentation (Miranda 2017). Littoral zones in lotic systems often possess heterogeneous habitat of varying architectural complexity that can serve as spawning habitat for adult fish and critical nursery habitat for juvenile fish (Winfield 2004). In drawdown reservoirs, the culmination of factors that homogenize the lake bottom can limit species diversity (Hatcher et al. 2019) and the productivity of fish assemblages by reducing reproductive success (Hassler 1970; Sutela et al. 2002; Zohary and Ostrovsky 2011) and juvenile recruitment (Heman et al. 1969; Ploskey 1983). The negative consequences of periodic drawdowns on aging reservoirs lead many natural resource managers to habitat enhancement to promote fish communities (Strange et al. 1982; Ratcliff et al. 2009; Norris et al. 2020).

One option for structural habitat enhancement during drawdowns is sowing shorelines with fast-growing cool season agricultural plants that can reach maturity after drawdown and before flooding (Norris et al. 2020). Upon inundation, plantings could provide complex habitat to local biota. Applications of cereal barley *Hordeum vulgare*, fescue *Festuca* sp., sudangrass *Sorghum bicolor* var. *sudanese*, sorghum *S. bicolor* sudangrass hybrid, and rye *Secale cereale* have been used for nutrient additions to the water column, turbidity reductions, and improved structural refuge for juvenile black bass *Micropterus* spp. (Hulsey 1959; Strange et al. 1982; Ratcliff et al. 2009). These studies reported increased juvenile densities in seeded areas compared with unseeded areas. However, the few plant species that were tested were not compared with one another in terms of benefit to fish. Additionally, the plantings of Strange et al. (1982) and Ratcliff et al. (2009) were intended to serve as juvenile fish refuge, but observations of adult piscine predator activity were limited. More information is needed on how fish use agricultural plants and if plants affect predator-prey interactions to understand what effects plantings may have on habitat enhancement.

Understanding how different agricultural plants affect predator-prey interactions could inform decisions about planting. Plants that conceal prey fish and exclude large predatory fishes could be used as refugia and potentially boost recruitment of structure-oriented juvenile fishes. Other plants that can be accessed by predators and prey and that facilitate moderate levels of predation could reduce predation enough to sustain prey fish populations while improving growth of predators by increased forage abundance (Sass et al. 2006). Plant-specific variations in growth and architecture could influence prey capture success and possibly explain differences in plant selection by fish. Perhaps one of the easiest quantified and widely used whole-plant architecture metrics is stem density, which alters the behavior and feeding activities of fishes (Savino and Stein 1982; Crowder and Cooper 1982; Gotceitas and Colgan 1987, 1990). Stem density describes plant structures on a horizontal axis, and when used in combination with a plant’s height, most of the plant architecture is described. Studying the influence of stem density and height on plant selection by common reservoir fishes could provide insight on why certain plant species are selected and how they may influence predator-prey dynamics and may inform environmental management programs.

We performed a controlled mesocosm experiment to investigate how various agricultural plants mediate interactions between a predator, adult Largemouth Bass *M. salmoides*, and prey, juvenile Bluegills *Lepomis macrochirus*. We selected these species because they are ubiquitous in reservoirs throughout North America, Largemouth Bass prey on Bluegills, and Bluegills use vegetation to reduce predation risk (Savino and Stein 1982; Mittelbach 1981; Gotceitas and Colgan 1987; Werner and Hall 1988). Specifically, our objectives were to 1) observe behavioral patterns of predator and prey in the presence and absence of one another in submerged agricultural plants, and 2) determine the selection of agricultural plants by Largemouth Bass and Bluegills in the presence and absence of one another. We hypothesized that selection of plant characteristics will differ between fish species, and that both behavior and selection will differ for both species in the presence and absence of one another. We predicted that Bluegills would select the highest stem densities and heights because of greater concealment from predators offered by the denser foliage, and that Largemouth Bass would select intermediate stem densities and heights for ease of prey capture. We also predicted that prey and predator would select a wider variety of plant species and plant characteristics when separated, but selected varieties would be narrower when the two species are in the presence of one another.

Methods

Experimental plants

We selected seven cultivars (i.e., varieties of domesticated agricultural plant species) that could be planted during autumn when reservoir bottoms are typically
exposed, that tolerate low-quality untreated soils of reservoir substrates, and that could be readily available for purchase in bulk from seed companies (Table 1). There were two clover species (family Fabaceae, legumes) and four grass species (family Poaceae). These species have diverse architectures, differing in compactness and height. Moreover, they require minimal seedbed preparation for planting, reach maturity prior to submergence from reservoir filling in the spring (Coppola et al. 2019), and have been used successfully in reservoir-regulated zones (Norris et al. 2020). Thus, the seven plant cultivars along with an unseeded treatment served as our eight plant treatments.

**Plant cultivation**

We filled plastic nursery pots (n = 42, diameter = 15 cm, height = 12 cm) with commercial topsoil and hand-sown seeds in the upper 1 cm of soil. We used cultivar germination and purity ratios to determine seeding rates to ensure that each pot received the correct percentage and quantity of pure live seed (Harper 2008). Plants grew outdoors beneath a hoop frame structure outfitted with herbivore-excluding netting. We applied fertilizer to pots every 2 weeks (6:2:1, N:P:K ratio). At the beginning of the mesocosm experiment, we recorded stem density (number of stems) and maximum height (cm) for all pots. We used six pots filled with soil from the same source as the plants as an unseeded treatment with no sown seeds in the upper 1 cm of soil. We used cultivar Arrowleaf clover

| Cultivar          | Scientific name  | Legume (family Fabaceae) or Grass (family Poaceae) | Planting date          |
|-------------------|------------------|----------------------------------------------------|------------------------|
| Arrowleaf clover  | *Trifolium vesiculosum* | Legume | August–October |
| Balansa clover    | *Trifolium micranthum* | Legume | September–October |
| Annual ryegrass   | *Lolium multiflorum* | Grass | August–October; February–April |
| Oat               | *Avena sativa* | Grass | August–October; February–March |
| Triticale         | *Trticoscale* | Grass | August–October |
| Wheat             | *Triticum aestivum* | Grass | August–October |

Bluegills because they depend on submerged vegetation as refuge in natural settings (Werner and Hall 1988). We selected the Largemouth Bass size range to mirror previous studies of predator-prey behavior mediated by habitat (Savino and Stein 1982; Goteitas and Colgan 1987, 1990; McCarrt et al. 1997). We housed prey and predator fish separately in two outdoor flow-through tanks (6,400 L) for 3 weeks before the first trial. Bluegills consumed commercially prepared pellet feed until satiation 3 d per week. We fed Largemouth Bass live, locally captured Bluegills at approximately 2% body weight 3 d per week (Barrows and Hardy 2001) and starved them between 24 and 72 h before trials. Water temperatures in the holding tanks averaged 22°C (±3°C SD) and dissolved oxygen (DO) averaged 7.4 ppm (±0.8 ppm SD); these values were not significantly different among tanks (two-sample t-tests, temperature [t = −0.4, df = 32, P = 0.66] and DO [t = 1.2, df = 28, P = 0.24]; Data S1, Supplemental Material).

**Experimental arenas**

We used three circular flow-through fiberglass tanks (2.44 m diameter, 1.37 m height) as the experimental arenas that were in the same location as the holding tanks. Circular wood platforms fit to the circumference of the tanks raised the bottom of tanks 21 cm to make the vegetation–soil interface even with the bottom of experimental arenas. Foam padding filled any gaps between the tank walls and platforms to prevent fish from entering space below the platforms. We cut two concentric rings of eight equally spaced holes into the platforms to hold the pots so that their tops were flush with the platform (Figure 1). The exterior and interior rings were 15 cm and 56 cm from the tank wall. We selected this arrangement to determine the effect of the tank wall on habitat selection of fish because other studies identified an affinity of Bluegills to tank walls (Savino and Stein 1982; Moody et al. 1983; Gotceitas and Colgan 1987, 1990; DeVries 1990). We fixed plastic rods suspending two cameras across the top of each arena, each recording one half of the arena during all experimental trials. Review of video footage following trials facilitated fish behavior observations. Cotton sheets
stretched over the camera arrangements covered the arenas to reduce glare and disturbances to fish while still allowing sunlight to penetrate and illuminate the tanks. Water drawn from a well filled tanks and maintained a depth of 76 cm (55 cm above platform). We held the flow of new water into tanks and aeration constant when trials were not taking place. We prepared plants for inundation by covering exposed soil with a layer of gravel to prevent suspension and by fixing bricks to the bottom of pots to reduce buoyancy. These conditions differ to those experienced in a reservoir mudflat. However, the purpose of this experiment was not to simulate reservoir conditions, but to create a controlled, easily observed environment with the experimental plants all equally available to fish for selection.

Experimental design

We first randomly assigned two replications of each plant treatment to each of the three tanks, and they remained in their respective tanks for the duration of the study \((N = 6\) per cultivar). Plant submergence began 2 d before the first trial, and plants remained underwater for 10 d total until the last trial. Before each trial, we rearranged plant configurations by first randomly assigning one pot of each plant treatment to the interior and exterior ring of platform holes, then we randomized the plant treatment order within rings. We replicated pot and plant treatment arrangements for all three tanks for each set of trials. During each rearrangement, we gently moved plants underwater to not damage plants or interrupt submergence. If rearrangement caused suspension of soil, then we removed coarse material using a fine mesh skimmer and added new water to tanks until there were no visible traces of soil. To assess if submergence altered plant architecture, we recorded stem density and maximum height at the end of the 10-d submergence period by measuring both variables in each pot while plants were still submerged.

Each arena housed one or two 0.5-h trials per day for 8 d. We initiated trials in the three arenas within 0.25 h of one another so that they were simultaneous. However, camera failure resulted in fewer tanks being observed at once during some sets of trials. We randomly assigned three ecological conditions, prey only (PY), predator only (PD), and prey and predator (PP), to the arenas for each set of trials. We began PY trials by releasing 10 Bluegills into the center of each tank for a 0.5-h acclimation period. Following acclimation, we counted fish in all regions of the tanks (see below) at 5-min intervals \((\text{Savino and Stein 1989})\) for 0.5 h, resulting in six observations. The PD trials followed the same protocol as the PY trials except using a single Largemouth Bass. We adapted the PP trials from Chick and McIvor (1997), and they consisted of releasing 10 Bluegills into the center of the tank and a Largemouth Bass in a permeable 62.5 L \((60 \text{ cm} \times 41 \text{ cm} \times 34 \text{ cm})\) container placed in the tank for a 0.5-h acclimation. The container separated predator and prey while allowing both to acclimate to tank conditions. We released the predator following acclimation and counted prey and predator locations at 5-min intervals for 0.5 h. We collected fish following trials by using a backpack electrofishing unit to immobilize fish and removed them using a dipnet to minimally disturb plants. We
Table 2. Categorical variables used to characterize zones of the experimental arenas that fish selected during trials. These experimental arenas housed all trials that consisted of observing predator (Largemouth Bass Micropterus salmoides) and prey (Bluegill Lepomis macrochirus) fish as they occupied different zones within arenas. We conducted the experiment at Mississippi State University’s South Farm Aquaculture Facility during May 2018. All classes of each variable are nonoverlapping zones of tanks. We quantified use of the different classes for each variable by counting fish within each class every 5 min for 30 min per trial. We chose the classes of the two variables that described zones based on characteristics of the nearest potted plant (i.e., stem density and maximum height) subjectively to distribute pots among classes as evenly as possible for each variable. We binned unseeded pots as well as all observations outside of pots into a no vegetation category.

| Predictor          | Description                                                                                                                                                                                                 |
|--------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Tank region        | Four regions were identified. The exterior region included all observations in plant treatments in the outer concentric ring of plants as well as observations outside of plants that were < 15 cm from the tank wall. The intermediate region included observations outside of plants between 15 and 56 cm from the tank wall. The interior region included observations within the plant treatments of the inner concentric ring of plants as well as all observations that were > 56 cm from the tank wall. The surface region was any point in the tank where fish were in the upper half of the water column. |
| Plant treatment    | Defined the plant each fish observation was near. Each plant treatment zone was defined as a region within 15 cm of each pot. Areas outside of plant treatment zones were delineated as per tank region.                                      |
| Stem density       | Presubmergence values were categorized in an ordinal scale as low (1–500 stems/m²), intermediate (501–1,000 stems/m²), high (1,001–2,000 stems/m²), and very high (2,001–10,000 stems/m²).      |
| Maximum height     | Presubmergence values were categorized in an ordinal scale as low (1–10 cm), intermediate (11–15 cm), tall (16–20 cm), and very tall (21–35 cm). Intervals that delineated categories were chosen to distribute pots as evenly as possible over all categories. |

measured TL of fish before each trial and did not use the same fish in more than one trial. In total, our sample size was 12 PY, 15 PD, and 9 PP trials.

Fish behavior
We counted the number of fish demonstrating different types of behaviors during each of the six sampling intervals previously described. For Largemouth Bass, behaviors were searching (moving), following (orienting toward prey), or inactive (motionless; Savino and Stein 1982). Behaviors of Bluegills were schooled (aggregating together while moving), shoaled (aggregating together but stationary), or dispersed (moving or stationary but not within the immediate vicinity of a conspecific; Pitcher 1986).

Selection predictors
For each of the six observations per trial, we used four predictors (i.e., tank region, plant treatment, plant stem density, and plant maximum height) to spatially divide arenas into different zones based on different features (Figure 1; Table 2). All predictors tested were categorical, and their classes each described independent zones of the tank. We summed observations that fell within zones. To describe the effect of tank wall on selection, the tank region variable delineated concentric zones that differed in their distance from the walls. The plant treatment variable described the cultivar each fish observation was near, and we described all other locations within the tank not adjacent to plants like the tank region variable. The stem density and maximum height variables each described the density of stems and the maximum height of plants that observations were near, and we grouped all other locations within the tank into a no vegetation category. We discretized these two numeric growth metrics into ordinal predictors by binning pots into four categories for each variable of their respective magnitude of maximum height and stem density with a fifth no vegetation category (Table 2).

Statistical analyses
Plant architecture before and after submergence. The test plants when submerged reportedly may continue to grow for a few days and eventually decay at different rates (Coppola et al. 2019). Because of this, it was important to determine the extent that submergence affected plants. To monitor the effect of submergence on plants, we compared their heights and stem densities among treatments before and after submergence using repeated measures analysis of variance models followed by Tukey’s least significant difference tests for pairwise comparisons. The categorical independent variables were cultivar, time (i.e., before or after submergence), and their interaction, and we included a within-subject error term that specified the individual pot that we repeatedly measured. We log₁₀ transformed stem densities to satisfy the homogeneity of variance assumption (we added one to stem densities because two arrowleaf clover pots had zero stems at the end of the experiment; see Discussion). To reduce type-1 error rates of the pairwise comparisons, we adjusted α to 0.007 using a Bonferroni correction.

Behavior of fish. For each trial, we summed frequencies of each behavior to have one observation for each behavior per trial. We compared the behavior of fish in different ecological conditions (i.e., PD, PY, and PP) using generalized linear models (GLMs). We used counts of fish as the interval response variable and behavior as a grouping categorical independent variable along with ecological condition and their interaction. We used
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Figure 2. Mean height (maximum heights of each potted plant, cm) and mean stem density (mean of \(\log_{10}\) transformed counts of stems per pot plus one) of the experimental cool season annual plant treatments that were available to Bluegills \(Lepomis macrochirus\) and Largemouth Bass \(Micropterus salmoides\) before submergence and after 10 d of submergence in experimental arenas. Experiments consisted of numerous trials where we added and removed fish from arenas. We conducted the experiment at Mississippi State University’s South Farm Aquaculture Facility during May 2018. We gently moved plants to other locations within arenas between trials, and submergence was not interrupted throughout the 10-d experiment. Stem densities were \(\log_{10} + 1\) transformed. Error bars represent standard errors.

Poisson distributions when dispersion parameters were <2; otherwise, we used quasi-Poisson models and defined the mean-variance relationships as the variance being equal to the product of the mean and dispersion parameters (Zuur et al. 2009). We did not include tank as a random or fixed effect because preliminary analysis indicated that tank did not have a significant effect. There was no predation or mortality in the trials.

Use, availability, and selection. We tested for selection or avoidance of the predator categories by comparing observed to expected proportions (Neu et al. 1974). We integrated counts of fish within trials by summing counts in each predator category, resulting in one observation for each predator category per trial. We then summed observations across trials for each predator category and ecological condition. We determined proportional use by dividing the integrated fish counts of the predator categories by the total fish counts of the predictor in each ecological condition. We defined expected use of each predator category as the two-dimensional area of each category available to fish divided by the total area of all categories available (Figure 1). We used chi-square goodness-of-fit tests to examine the null hypothesis that use and availability proportions did not differ. We tested species separately in the presence and absence of one another. Due to low Largemouth Bass use values that resulted from total counts of a single fish in tanks (as opposed to 10 fish in Bluegill trials), we simulated Largemouth Bass \(P\) values via permutational tests with fixed margins (Patefield 1981).

When chi-square tests were significant \((P < 0.05)\), we estimated simultaneous confidence intervals of the true proportion of use for each category. We obtained the 95% simultaneous confidence intervals for multinomial proportions using Goodman’s (1965) estimation, which produces shorter intervals with lower error rates than other methods (Cherry 1996). When expected values were not large enough \((<5)\), we estimated the confidence intervals based on truncated Poisson distributions, as described by Sison and Glaz (1995). We used the DescTools package (Signorell 2020) of R statistical software version 4.0.3 to estimate all confidence intervals (R Core Team 2020). We calculated selection or avoidance by dividing the estimates of use and their 95% confidence intervals by their respective proportions of availability. If the resulting confidence intervals overlapped one, then use was random, if they were >1, then selection occurred, and if they were <1, then avoidance occurred. We used the estimated confidence intervals of use to compare the magnitude of selection or avoidance among predictor categories.

Results

Vegetative structures of plant treatments available to fish differed in their height \((F = 21; \text{df} = 6,35; P < 0.01);\) Figure 2; Data S2, Supplemental Material). Before submergence, arrowleaf clover was significantly shorter than all treatments except balansa clover and wheat. The ryegrasses and oat were all similar heights and were taller than balansa clover and wheat before submergence, but not significantly. Triticale was significantly taller than all plant treatments. The effect of time (10-d submergence) on the maximum height of plant treatments was not significant \((F = 2; \text{df} = 1,35; P = 0.2)\); however, time significantly interacted with plant treatments \((F = 12; \text{df} = 6,35; P < 0.01)\), indicating opposing trends in height among treatments (Figure 2). The height of the ryegrasses increased following submergence (Figure 2), while the height of all other treatments decreased. Pairwise comparisons of each treatment’s height before and after submergence indicated that triticale was the only treatment that significantly differed from its presubmergence height (Figure 2).

The stem densities of plants differed among cultivars \((F = 55; \text{df} = 6,35; P < 0.01);\) Figure 2; Data S2, Supplemental Material). Before submergence, oat, tritica- le, and wheat had significantly lower stem densities than all plant treatments except arrowleaf clover. The ryegrasses had similar stem densities and were higher than arrowleaf clover before submergence; however, Marshall ryegrass stem density was not significantly higher than arrowleaf clover. Balansa clover stem density was significantly higher than all cultivars and was on average 5.4 times greater than the cultivar with the
GLM, dispersion parameter
distribution of Bluegill behaviors differed (quasi-Poisson
submergence period. Other treatments had vegetation at the end of the 10-d
four arrowleaf clover pots had, on average, 1.5 stems. All
vegetation by the end of the experiment, while the other
unchanged (Figures 2). Two arrowleaf clover pots in
densities while all other treatments remained relatively
explained by the clovers significantly decreasing in stem
(Figures 2) of one another in experimental arenas. We
performed a replicated mesocosm experiment by observing
Largemouth Bass and Bluegills in the presence and absence of
one another to determine their selection of habitat enhancing
plants. We conducted the experiment at Mississippi State
University’s South Farm Aquaculture Facility during May 2018.
Largemouth Bass behaviors were search (moving), stationary
(motionless), or follow (pursuing Bluegills), and Bluegill
behaviors were schooled (aggregating together while moving),
shoaled (aggregating together but stationary), and dispersed
(moving or stationary but not within the immediate vicinity of a
conspecific).

second highest stem density, Marshall ryegrass. Time
significantly affected stem densities of treatments ($F = 79$; $df = 1,35$; $P < 0.01$) and significantly interacted with
plant treatments ($F = 14$; $df = 6,35$; $P < 0.01$). This can be
explained by the clovers significantly decreasing in stem
densities while all other treatments remained relatively
unchanged (Figures 2). Two arrowleaf clover pots in
separate tanks completely degraded and did not have
vegetation by the end of the experiment, while the other
four arrowleaf clover pots had, on average, 1.5 stems. All
other treatments had vegetation at the end of the 10-d
submergence period.

Observed predator and prey behaviors depended on
the presence or absence of one another. Proportional
distribution of Bluegill behaviors differed (quasi-Poisson
GLM, dispersion parameter $= 3.5$; $F = 11$; $df = 2,60$; $P < 0.01$) and was influenced by Largemouth Bass presence
($F = 67$; $df = 2,57$; $P < 0.01$; Figure 3; Data S3,
Supplemental Material). Without a predator, Bluegills
primarily dispersed (58% total observations), and schooling
was the least common behavior (18%). When a predator was present, few Bluegills dispersed (9% total observations), and schooling was the dominant behavior (71%). Similarly, proportional distribution of Largemouth Bass behaviors differed (Poisson GLM, $X^2 = 20$; $df = 2,60$; $P < 0.01$) and was significantly influenced by Bluegill
presence ($X^2 = 6$; $df = 1,56$; $P < 0.01$; Figure 3). When
alone, Largemouth Bass were primarily inactive (69% total observations); when with Bluegills, Largemouth
Bass spent a similar amount of time searching (46%) as inactive (41%). There were few observations of Largemouth Bass following prey.

Fish selected for tank region, plant treatment, plant
stem density, and maximum height, as indicated by
statistically significant chi-square tests (Table 3; Data S3,
Supplemental Material). Inspection of 95% confidence intervals of selection revealed that Bluegills selected the
interior region of the tank when a predator was not
present but transitioned to selecting the exterior region
when a predator was present (Figure 4). Both species of
fish avoided the surface regardless of ecological condi-
tion; however, avoidance was significantly less evident
(nonoverlapping 95% confidence intervals) for Bluegills
when in the presence of Largemouth Bass. Selection of
tank regions by Largemouth Bass (Figure 4) remained
unchanged with and without prey, where Largemouth
Bass selected the exterior of the tank and avoided the
interior and surface.

Selection of most plant treatments by both species
changed little between ecological conditions. Plants
selected by Bluegills were triticale, balansa clover, and
both cultivars of ryegrass in the absence of a predator;
however, none differed from the unseeded treatment
(Figure 4; Data S3, Supplemental Material). Fish outside of
plant boundaries selected for the interior and avoided
the exterior and surface. When Bluegills and Largemouth
Bass occupied the same tank, Bluegills selected for
balansa clover and Marshall ryegrass and avoided the
interior and surface. Selection of balansa clover was
significantly greater than selection of the unseeded
treatment (nonoverlapping 95% confidence intervals).
When alone, Largemouth Bass selected balansa clover
and both cultivars of ryegrass, all of which were very
similar and not significantly different than the unseeded
treatment (Figure 4). When Bluegills were present,
Largemouth Bass selected areas outside of plant
treatments in the exterior region but also selected
Marshall ryegrass to a lesser extent. In all conditions,
Largemouth Bass avoided the surface, and all treatments
did not differ from the unseeded treatment. Although
use of most plant treatments did not differ from
unseeded pots, the 95% confidence intervals of propor-
tions of use of unseeded pots in all situations overlapped
with proportions of availability, meaning that all use of
unseeded pots could be due to randomness. Because of
this, comparisons of unseeded pots to other treatments
that were selected are less meaningful.

Changes in selection of stem categories between
ecological conditions were apparent for Bluegills but not
for Largemouth Bass (Figure 4; Data S2, Data S3,
Supplemental Material). Both species avoided sections
with no vegetation in all ecological conditions. Prey
selected for all stem densities greater than zero when
alone and selected the low and very high categories
most often. When combined with a predator, prey
selected the very high category more often than all other
stem density categories (nonoverlapping 95% confi-
dence intervals) and did not select the low category.
When prey were absent, Largemouth Bass selected the
two highest stem categories (Figure 4). However, when
prey were present, Largemouth Bass only selected the
high density.

Selection of plant height differed between species and
changed little between ecological conditions (Figure 4;
Data S2, Data S3, Supplemental Material). Prey selected all
Table 3. Chi-square tests used to determine if use of the classes of each variable that described different zones of experimental arenas by Bluegills Lepomis macrochirus and Largemouth Bass Micropterus salmoides differed from their availability. If use differed from availability, then the spatial distribution of fish in experimental arenas was not random and zones (i.e., classes of variables) were either selected or avoided. We quantified use by dividing counts of fish in zones by total counts of fish in all zones. We quantified availability by dividing the two-dimensional area of each zone by the area of all zones. We observed selection by Bluegills and Largemouth Bass in prey or predator ecological conditions in separate experimental arenas, and we observed selection in prey and predator conditions in a single arena. Largemouth Bass tests were permuted because some expected values were <5. We categorized zones of tanks using the four predictors: tank region (general location within tank), plant treatment (cultivar of plant), stem density (counts of stems per pot standardized to stems per m²), and plant height (cm). We conducted the experiment at Mississippi State University’s South Farm Aquaculture Facility during May 2018.

| Predictor        | Ecological condition | Bluegill (Χ², df, P value) | Largemouth Bass (Χ², P value) |
|------------------|----------------------|-----------------------------|--------------------------------|
| Tank region      | Prey                 | 703, 3, <0.001              | 165, <0.001                    |
|                  | Predator             |                             | 97, <0.001                     |
| Plant treatment  | Prey                 | 180, 3, <0.001              | 456, 11, <0.001                |
|                  | Predator             | 666, 11, <0.001             | 159, <0.001                    |
| Stem density     | Prey                 | 476, 4, <0.001              | 461, 4, <0.001                 |
|                  | Predator             | 107, <0.001                 | 36, <0.001                     |
| Plant height     | Prey                 | 485, 4, <0.001              | 98, <0.001                     |
|                  | Predator             | 266, 4, <0.001              | 34, <0.001                     |

plant height categories greater than zero with similar intensity. Predator selection generally increased with plant height when prey were absent, but they did not select the tallest category (21–35 cm). When the species were combined, Largemouth Bass selected the second tallest category (16–20 cm).

Discussion

Behavioral responses of predator and prey suggest that prey used vegetation for refuge when confronted with a predator but were not completely concealed by the vegetation. Previous studies showed that if enough structural refuge is present, then quantity of Bluegills demonstrating schooling behavior will either be unaffected or reduced by the presence of Largemouth Bass (Savino and Stein 1982, 1989). Similarly, another prey species known to congregate, the Eurasian minnow Phoxinus phoxinus, chose cover over grouping when few conspecifics and a predator were present (Magurran and Pitcher 1983, 1987). These studies suggest that if a threshold of suitable concealment by structural cover is not met, then prey fishes may use other antipredator behaviors. Savino and Stein (1982) reported that predatory activity of Largemouth Bass (i.e., searching, following, and attacking prey) was significantly reduced with increasing stem density of vegetation analogs. The low predator activity in our study may have resulted from the cover provided by vegetation to prey. Without a control ecological condition (i.e., predator and prey combined without vegetation) the true effect of plants on predation pressure is unknown; however, predator activity and visual orientation were not reduced enough to preclude prey antipredator behavior.

Affinity for regions within the tanks was likely driven by prey-pursuing and by predator-evading behaviors. Change in selection from interior to exterior of tanks by Bluegills when combined with a predator was most likely due to Bluegills maximizing distance away from the predator and using tank walls as refuge space. Edges of tanks can serve as refuge for cover-seeking Bluegills (Moody et al. 1983) that may choose the tank edge furthest from predators over other forms of available structure (Savino and Stein 1982; DeVries 1990; Gotceitas and Colgan 1990). Similarly, schooling at the surface may be selected over other forms of cover (Gotceitas and Colgan 1987). The increase in use of exterior walls and water surface by Largemouth Bass was likely driven by searching for prey in areas where they were previously detected.

The reciprocal changes in selection of balansa clover by both species could indicate its potential for nursery cover that excludes predators. A potential explanation for why Bluegills favored balansa clover and Largemouth Bass did not is that clovers grow short, broad leaves that form dense crown rosettes (Hall 2008; Harper 2008) compared with grasses, which generally form long leaves that grow vertically parallel to stems and allow for more light to penetrate through the canopy (Gibson et al. 2008; Mohammad et al. 2011). The leaf morphology of balansa clover along with its high stem density could have provided more concealment than other treatments. However, it is unclear whether Bluegills selected balansa clover based on leaf morphology, stem density, or both because no other cultivar with a different leaf morphology grew similar stem densities. Moreover, Bluegills also selected Marsh ryegrass to a similar extent as balansa clover, with the two differing in morphology and significantly differing in stem densities, although Marshall ryegrass was among the top three highest cultivar stem densities. For plant height, some categories possessed both selected and nonselected plant treat-
Figure 4. Bluegill *Lepomis macrochirus* and Largemouth Bass *Micropterus salmoides* selection and avoidance of zones within experimental arenas described by the four predictor variables: (A) tank region, (B) plant cultivar treatment, (C) plant stem density (counts of stems per pot standardized to stems per m²), and (D) plant height. Circles are proportions of use of each predictor level (counts of fish in each category divided by total counts of fish in all categories) divided by their respective proportions of availability (two-dimensional area of category divided by area of all categories). Circles are open when the two species are in separate experimental arenas and solid when they are combined in the same arena. Error bars are 95% simultaneous confidence intervals of the proportions of use of each class of the variable divided by their proportions of availability. The dotted line represents each category’s relative availability. If a category’s confidence interval does not overlap with availability and is to the right of the dotted line, then it was selected; if it is to the left, it was avoided. We conducted the experiment at Mississippi State University’s South Farm Aquaculture Facility during May 2018.
ment cultivars (e.g., arrowleaf and balansa clovers). This discrepancy suggests that plant height did not influence selection by prey; however, the range of plant heights may have been too small for a discernable relationship. It is likely that Bluegills selected crops based on stem densities rather than plant height or other unaccounted for morphological characteristics (e.g., leaf morphology), although this experiment was not designed to determine selection of fine-scale characteristics unique to each plant treatment. The general pattern of selection of high stem densities by prey in this experiment was similar to other experimental and observational studies where small-bodied prey species select for denser and more complex habitats as refuge (Goteitas and Colgan 1987, 1990; Hayse and Wissing 1996; Yeager and Hovel 2017).

Although plant height and stem density were affected by the 10-d submersion, plant selection by fish likely was not affected during this time. This is because plants did not change much in terms of how they generally compared with one another from least to greatest height and stem density. The clover species appeared to be the most affected by submergence, which agrees with other studies that identified that clovers degrade rapidly following submergence (Coppola et al. 2019). Regardless, balansa clover demonstrated the greatest change in stem density; however, it still possessed, on average, the most stems compared with all other treatments following submergence and was one of the highest selected cultivars by both species of fish. The stem density of arrowleaf clover also demonstrated significant deterioration following submergence; however, it had a low stem density initially, and so time probably did not affect selection. Although the height of triticale was significantly lower after submergence, it was still among the top three tallest cultivars following submergence, the other two being the ryegrasses that continued to grow throughout the experiment. The postsubmergence growth of the annual ryegrasses has been observed in other studies and demonstrates a tolerance of brief flooding events (Coppola et al. 2019); however, vegetative structures are more vulnerable to degradation following the rapid growth (Sauter and Kende 1992).

The patterns of plant use by fish in this mesocosm study partially agree with other studies documenting reservoir mudflats enhanced with agricultural plants. Like Bluegills’ high selection of annual ryegrass in this study, plantings of cool season annual grasses seeded by Strange et al. (1982) were marked by higher abundances of juvenile fishes than unseeded areas. Additionally, plantings of barley *H. vulgare*, a cereal grain like those in our study (i.e., oat, wheat, and triticale), had significantly higher densities of age-0 black bass *Micropterus* spp. than unplanted shorelines (Ratcliff et al. 2009). Use of cereal grains in our study was low, most likely due to the presence of other treatments demonstrating more favorable habitat quality, such as balansa clover and Marshall ryegrass (discussed further below). Of the three cereal grains tested, plantings of triticale could provide favorable habitat for juvenile fish. This is because Bluegills selected triticale (predator absent), and triticale demonstrated an ability to retain maximum height and complexity for longer than both balansa clover and Marshall ryegrass (Coppola et al. 2019).

The increased use of minimally vegetated areas of tanks (i.e., no vegetation and low stem densities; Figure 4) by predators when prey were present was most likely driven by attraction toward areas where prey were detected. Largemouth Bass are visually oriented predators that follow their prey (Savino and Stein 1982, 1989; Anderson 1984). Foraging efficiency of Largemouth Bass decreases in dense vegetation (Savino and Stein 1982) and can induce changes in diet to less mobile prey (Anderson 1984). Searching Largemouth Bass that are responding visually to prey will likely use areas where prey are visible more than where prey are not visible. Additionally, higher stem densities reduce the sizes of gaps between stems that can exclude large fishes (Johnson et al. 1988). However, this likely did not influence our observations because areas next to pots were included so fish of all sizes could access all stem densities.

Management implications

The results of this mesocosm study suggest that cool season agricultural plants may differ in their value as structural habitat to fish. Plants that grew high stem densities, such as balansa clover, may provide habitat for refuge-seeking prey fishes. Thus, plantings of balansa clover could be used in situations where enhanced nursery habitat is the primary management objective. Annual ryegrass cultivars, especially Marshall, could potentially be used for enhancements that target the entire fish community or larger-bodied adult fishes. However, selection of plants in reservoir environments may be different because submerged plantings could benefit other trophic levels, similar to how macrophytes do in other lotic systems. For example, benthic and epiphytic invertebrate communities increase in abundance and species richness with increasing periphyton, detritus, refuge, and living space afforded by submerged vegetation (Cyr and Downing 1988; Schramm and Jirka 1989; Jeffries 1993). Marshall ryegrass outperformed all crops and natural vegetation when planted on reservoir mudflats (Norris et al. 2020) and persisted once submerged for up to 3 months (Coppola et al. 2019). The results of our study further validate Marshall ryegrass suitability for reservoir mudflat applications. Annual ryegrass is native to Europe and is extensively used in the United States as a supplemental forage crop for livestock and wildlife (Harper 2008). Simultaneously, it is listed as an invasive species in some parts of the United States (USDA 2020a). Applications in reservoir regulated zones will most likely be short lived due to prolonged submergence during years of normal precipitation (Coppola et al. 2019), thus precluding long-term establishment. However, drought may leave plantings exposed during spring and summer, facilitating introductions to upland habitats. An ecologically conservative alternative to annual ryegrass could be triticale, a hybrid cereal grain that is a hybrid of wheat and rye and is highly beneficial for wildlife in the United States (USDA 2020).
with no documented occurrences of naturally reproducing populations in North America (USDA 2020b) that will likely not compete well with established upland plant communities due to slow growth during early life phases (Salmon et al. 2004).

Balansa clover has high potential as a mudflat enhancer in regulated zones, but caution should be used when considering this species. Balansa clover grew poorly on reservoir mudflats seeded by Norris et al. (2020), but this might have been due to low seeding rates, substandard soils, and drought rather than species performance. Maturing balansa clover specimens degraded rapidly when submerged in experimental tanks (Coppola et al. 2019); however, fully matured plants were not tested. A conservative approach to using balansa clover could be to mix it with a more tolerant and durable plant, such as Marshall ryegrass or triticale, that would enhance fish habitat regardless of balansa clover’s performance. This would also reduce the total costs of using grasses with high seeding rates (e.g., triticale) because balansa clover is relatively affordable (Harper 2008). Mixing legumes with grasses is a common technique that can improve the establishment of plantings. In grass-legume mixtures, grasses germinate and establish quickly, thereby partially acting as a weed suppressant and erosion control while legumes improve nutrient availability in the soil by fixing nitrogen (Harper 2008). Mixed plantings of the two top-performing species in this study, balansa clover and Marshall ryegrass, significantly increase total yield of biomass compared with ryegrass monocultures when planted in unfertilized conditions (Santos et al. 2015). Additionally, mixtures may maximize structural heterogeneity and minimize the risk of either species failing to grow in harsh environments or persist following inundation.

Supplemental Material

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Data S1. Bluegill Lepomis macrochiru and Largemouth Bass Micropterus salmoides Holding Tank Temperature (°C) and Dissolved Oxygen (ppm) Measurements. Holding tanks consisted of two 6,400-L outdoor flow-through tanks. The fish in these holding tanks served as our experimental animals that provided information on selection of habitat-enhancing plants. We housed the two species separately in two holding tanks and recorded measurements approximately once daily. Holding tanks were in the same location as experimental arenas beneath a pavilion and received constant aeration and flow of new well water. We transported fish to holding tanks from sources within Oktibbeha County, Mississippi, 3 weeks before the experiment. We conducted the experiment at Mississippi State University’s South Farm Aquaculture Facility during May 2018.

Data S2. Experimental Potted Plant Maximum Height (cm) and Stem Density (n/pot) Measurements Before and After Being Submerged for the Duration of the Experiment. Plants were those we presented to Bluegills Lepomis macrochiru and Largemouth Bass Micropterus salmoides in experimental arenas to determine selection by fish and to assess how they mediate predator–prey interactions. We conducted the experiment at Mississippi State University’s South Farm Aquaculture Facility during May 2018. Sample describes the time period (pre = before submergence, post = after experiment), tank ID (1–3) describes the experimental arena the plant was submerged in, pot ID is a unique identifier for each individual pot, and plant treatment describes the cultivar of the plant. Experiments consisted of multiple trials of adding and removing fish from tanks. Between each trial, we gently moved plants underwater to different locations within their respective tanks, and we did not interrupt submergence for the duration of the experiment.

Data S3. Raw Count Data of Bluegills Lepomis macrochiru and Largemouth Bass Micropterus salmoides and Their Behavior in Regions of Experimental Arenas. We used this information to assess selection of submerged habitat-enhancing plants by fish in the experimental arenas and whether predator–prey interactions influenced selection. We recorded observations every 5 min for 30 min, resulting in six observations total for each region of the experimental arena for each trial. For each set of trials (trials consisted of between one and three tanks being initiated at once), we recorded the date, trial set number (1–17), ecological condition (predator [PD] = 1 predator in an experimental arena, prey [PY] = 30 prey in an experimental arena, and prey and predator [PP] = 1 predator and 30 prey in an experimental arena), and tank ID (1–3, unique identifier for each experimental arena). Sample time (minutes 5–30) describes the six repeated measures of each tank region. Plant position describes the sequential clockwise position of each pot in the exterior ring (1–8) and the interior ring (9–16), and we randomly assigned plant position to pot IDs between trials. Pot ID is the unique identifier assigned to each individual potted plant. Plant treatment describes the plant cultivar and regions outside of plants. For each sample time, we recorded observations of Bluegills (n), Largemouth Bass (n), schooled Bluegills (n, quantity of Bluegill schooling), shoaled Bluegills (n, number of Bluegills shoaling), dispersed Bluegills (n, number of Bluegills dispersed), and Largemouth Bass behavior (stationary = motionless, search = moving, or follow = pursuing Bluegills) within each tank region. Schooled fish were those aggregating together while moving, shoaled were aggregating together but stationary, and dispersed were those moving or stationary but not within the immediate vicinity of a conspecific (Pitcher 1986). We

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conducted the experiment at Mississippi State University’s South Farm Aquaculture Facility during May 2018.
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