Freshwater mussels alter fish distributions through habitat modifications at fine spatial scales

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Abstract: Aggregations of freshwater mussels create patches that can benefit other organisms through direct habitat alterations or indirect stimulation of trophic resources via nutrient excretion and biodeposition. Spent shells and the shells of living mussels add complexity to benthic environments by providing shelter from predators and increasing habitat heterogeneity. Combined, these factors can increase primary productivity and macroinvertebrate abundance in patches where mussel biomass is high, providing valuable subsidies for some fishes and influencing their distributions. We performed a 12-wk field experiment to test whether fish distributions within mussel beds were most influenced by the presence of subsidies associated with live mussels or the biogenic habitat of shells. We used remote underwater video recordings to quantify fish occurrences at fifty 0.25-m^2 experimental enclosures stocked with either live mussels (2-species assemblages), sham mussels (shells filled with sand), or sediment only. The biomass of algae and benthic macroinvertebrates increased over time but were uninfluenced by treatment. We detected more fish in live mussel and sham treatments than in the sediment-only treatment but found no difference between live mussel and sham treatments. Thus, habitat provided by mussel shells may be the primary benefit to fishes that co-occur with mussels. Increased spatiotemporal overlap between fish and mussels might strengthen ecosystem effects, such as nutrient cycling, and the role of both fish and mussels in freshwater ecosystems.

Key words: Spatial subsidies, stream fish, unionid mussels, behavior, remote underwater video

Spatial subsidies are resources produced in one habitat that cross over into adjacent habitats (Polis et al. 1997, Nakano and Murakami 2001). Spatial subsidies can occur across discrete habitat boundaries at broad spatial scales such as the reciprocal flux of insects among terrestrial and aquatic habitats (Baxter et al. 2005). However, resources can also be spatial subsidies when they cross fine-scale boundaries within aquatic systems such as from pelagic to benthic habitats (Baustian et al. 2014, Jager and Diehl 2014). The effects of spatial subsidies are most pronounced when they substantially elevate resource abundance above that produced in the recipient habitat (Nakano and Murakami 2001, Marczak and Richardson 2007).

Some ecosystem engineers control the availability of spatial subsidies to other organisms by physically modifying, maintaining, or creating habitats (Jones et al. 1997). For instance, tree canopies create habitat suitable for other organisms by mediating understory and soil conditions (Holling 1992, Callaway and Walker 1997), and beavers use dams to create lentic habitat in otherwise flowing streams (Wright et al. 2002). The physical engineering activities of heterogeneously distributed organisms can amplify differences in resource production rates among habitat patches, thereby resulting in resource-rich and resource-poor patches (Wetzel et al. 2005, Chowdhury et al. 2016). Furthermore, mobile animals may track the activities of temporally stable but spatially heterogeneous aggregations of animals that benefit them. For example, prairie dogs (*Cynomys ludovicianus*) form spatially heterogeneous colonies that trigger numerous compositional, structural, and nutritional changes in the vegetation, and these changes attract bison (*Bison bison*) through both direct and indirect effects (Coppock et al. 1983). Understanding whether heterogeneous animal aggregations influence the distribution of co-occurring groups is fundamental to ecology because spatial and temporal overlap may enhance ecosystem functions, such as nutrient cycling (Hopper et al. 2018).

Freshwater mussels (family Unionidae) are common in eastern North American streams, where they are patchily distributed at multiple spatial scales. Mussels typically occur as dense, multi-species aggregations called mussel beds where mussels are 10 to 100 × denser than they are in areas outside of beds (Strayer 2008). Further, mussel densities within these beds can vary with stream size (Atkinson et al. 2012). Mussel beds often exist in river channels that experience significant sediment mobility, but beds can persist in the same stream locations and have similar abundance and species composition for decades, which may provide stable conditions for other organisms (Sansom et al. 2018b). Mussels are also heterogeneous within beds, with individual mussels aggregating in dense patches separated by areas with few or no mussels (Strayer and Ralley 1993, Vaughn and Spooner 2006). Mussels filter-feed and stimulate primary and secondary production through N excretion and biodeposition of feces and pseudofeces (Atkinson and Vaughn 2015, Vaughn 2018). Mussel beds, therefore, increase the amount of nutrients and resources, which provide spatial subsidies that link the water column and benthic foodweb compartments of streams. These spatial subsidies might facilitate other organisms at both broad and fine spatial scales.

The distribution and abundance of mussels are closely linked to the distribution and abundance of fishes. Mussels are dependent on fish hosts for dispersal of their ectoparasitic larvae (Barnhart et al. 2008, Strayer 2008, Schwalb et al. 2011) and are, therefore, only abundant and diverse where fish are abundant and diverse (Vaughn and Taylor 2000, Modesto et al. 2018). It has often been assumed that mussels have little effect on fish. However, in marine systems some organisms exploit the shells of mussels to reduce thermal stress (Stephens and Bertness 1991) and injury or to avoid removal by currents or predators (Skilleter 1994). In streams, mussel shells create biogenic habitat for other organisms (Gutiérrez et al. 2003, Spooner and

Vaughn 2006). In addition, nutrients excreted and biodeposited by mussels increase primary production and can shift the functional composition of algal assemblages (Atkinson et al. 2013). Densities of benthic macroinvertebrates are higher in sediment patches with mussels than patches without mussels (Vaughn and Spooner 2006, Spooner and Vaughn 2006). Further, the composition of benthic macroinvertebrate assemblages is different within mussel patches than in the surrounding habitat, probably because mussels provide shell habitat, stabilize sediments, and increase algal food resources (Howard and Cuffey 2006, Vaughn et al. 2008). In the Eel River, California, the growth of juvenile Pacific lamprey was significantly enhanced when the lamprey consumed mussel biodeposits (Limm and Power 2011). Thus, heterogeneously distributed mussels provide an opportunity to test whether fish abundance increases in response to spatial subsidies produced by freshwater mussels.

We hypothesized that patches of mussels would attract fishes through spatial subsidies that cause alga and invertebrate prey to be concentrated at fine spatial scales (Table 1). Further, we expected that piscivorous fishes would be attracted to increased abundance of prey fishes feeding on increased algal or invertebrate biomass within mussel bed hotspots (Table 1). We hypothesized that spatial subsidies (i.e., trophic resources) generated within patches of live mussels would attract more fishes than would empty shells or bare sediment (Table 1). To test this hypothesis, we manipulated mussel occurrence within enclosures in a field experiment and used remote underwater video to quantify the abundance of fishes across treatments with live mussels, mussel shells filled with sand, and controls (sediment only).

METHODS

Study system

We conducted our experiment in the Kiamichi River, a tributary (watershed area = 4560 km^2) of the Red River in the Ouachita Mountains of southeastern Oklahoma known for its high diversity of fishes and mussels (86 and 31 species, respectively) (Matthews et al. 2005). There is considerable variation in seasonal discharge in this system (Vaughn et al. 2015; Fig. S1), but mussels persist as temporally stable aggregations (Sansom et al. 2018b). To avoid confounding mussel effects within our treatments with effects of established mussels, we installed the experiment in a river reach without mussels upstream of known mussel beds (Atkinson and Vaughn 2015). We transplanted mussels to the site (see below) following a method similar to that of Atkinson et al. (2014). Our study site was a shallow ~50-m reach with relatively homogenous depth and flow (Table 2), and the stream bottom was comprised mainly of sand, gravel, and cobble. The lentic conditions of the experimental reach were representative of those in the Kiamichi River in late summer and fall, where mussel beds are contained in shallow, isolated reaches with long hydrologic residence times (Vaughn et al. 2004, Vaughn et al. 2015).

Experimental design

Mussel treatments___ We performed a 12-wk field experiment to test whether fish distributions within mussel beds were most influenced by the presence of subsidies associated with live mussels or biogenic habitat of shells. Variation in spatial subsidies among mussel patches may be influenced by the traits of mussels occupying those patches (Howard and Cuffey 2006, Vaughn et al. 2007). To account for this, we used 2 mussel species that are common in this river and have traits that can influence food web dynamics and ecosystem function (Spooner and Vaughn 2012, Atkinson et al. 2013). *Actinonaias ligamentina* and *Amblema plicata* are both characteristic of the Interior Highlands mussel fauna (Haag 2010) and together comprise >70%

130 of mussel biomass in the Kiamichi River (Vaughn and Pyron 1995, Hopper et al. 2018). The 2
131 species differ in morphological, physiological, and behavioral characteristics that influence their
132 functional role in ecosystems (Vaughn 2010, Atkinson et al. 2018). *Actinonaias ligamentina* has
133 a smooth shell and is more active than *A. plicata*, which has a ridged shell and tends to be
134 sedentary (Vaughn et al. 2004, Allen and Vaughn 2009). Differences in algal and invertebrate
135 abundances occur on the shells of the 2 species (Vaughn et al. 2008, Atkinson et al. 2013), and
136 abundances of invertebrates are higher in sediments that surround each species than bare
137 sediment (Spooner and Vaughn 2006). In addition, they have different temperature-dependent
138 excretion rates and different tissue and excretion stoichiometry, which can result in differences in
139 algal production and composition (Atkinson et al. 2018, Spooner and Vaughn 2012).
140 To represent natural variation in assemblage composition and density in the Kiamichi
141 River, we created mussel assemblages of 40 individuals (ind)/m^2 that were either dominated by
142 live *A. ligamentina* (7 *A. ligamentina* and 3 *A. plicata*) or by live *A. plicata* (3 *A. ligamentina* and
143 7 *A. plicata*). In addition, we had treatments that used sham mussels of both species in the same
144 combinations and density, as well as a sediment-only control. Sham mussels were clean, empty
145 shells filled with sand and glued together (Spooner and Vaughn 2006). We replicated each
146 treatment 10× (n = 50). This design allowed us to separate effects of trophic resources (live
147 mussels), structural features (sham mussels), and no mussels (sediment control) on fish
148 distributions. Mussels were collected from a downstream site, transplanted into enclosures, and
149 returned to their collection site following the experiment.
150
151 ***Enclosures***___We installed 50 enclosures (50 cm × 50 cm × 20 cm deep) on July 12, 2017.
152 Enclosure frames were made from 3.3 cm schedule 40 PVC pipe, and the sides and bottom were

153 enclosed with 2.5 cm diameter poultry wire (Spooner and Vaughn 2006). Enclosures were placed
154 in the stream reach >2 m from shore and ~2 m apart in a checkerboard pattern to minimize cage-
155 effects on downstream enclosures. Sediment was removed from the stream bottom and
156 homogenized. We then buried enclosures 20 cm into the streambed and filled them with
157 homogenized sediment so the tops of the enclosures were level with the streambed and mussels
158 could not escape. This method allowed us to maintain constant mussel densities throughout the
159 experiment while still allowing invertebrates and fishes to move freely through both the sediment
160 and water column.
161
162 **Remote underwater video**
163 We used camera-based methods that allowed detailed observations of many experimental
164 units simultaneously for extended periods. Remote underwater video (RUV) is commonly used
165 in descriptive studies of marine environments and has become increasingly common in
166 freshwater studies (Ebner et al. 2014, 2015, Wilson et al. 2015, Schmid et al. 2017). Few of these
167 studies have exploited the utility of RUV in an experimental setting, but they have demonstrated
168 the benefits of camera-based methods for quantifying ecological interactions among co-occurring
169 organisms.
170 We used Activeon CX high-definition cameras (San Diego, California) with fixed focal
171 length, continuous video, a wide-angle field of view, and a resolution of 1920 × 1080 pixels.
172 These action cameras are a cost-effective and reliable alternative to the handheld cameras
173 commonly used in marine-baited RUV studies (Struthers et al. 2015). The cameras were
174 powered by Li-ion batteries (1200 mAh) that allowed ~130 min of video recording, which we
175 used for each deployment. The entire camera system was secured in a watertight case and

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attached to a flexible clamp mount (Captain FlexMount; Captain, China). Fish abundances at enclosures were observed by clamping a single camera to a 10-cm PVC segment fitted into a "T" joint fixed to the top, upstream side of each enclosure. We used the 5.0 cm LCD screen on the back of each camera to position the camera to record in the downstream direction and ensure that the entire enclosure was within the field of view (Fig. 1).

We conducted underwater camera surveys at 9 and 12 wk exclusively during daylight between 0800 and 1730 h to avoid light limitation at other times of day. During surveys, each enclosure was filmed for ~5 h/d over 2 periods within a single day: 1 in the morning (~0800–1030 h) and 1 in the afternoon (~1500–1730 h). All video samples were standardized to ~36 min of footage for analysis, beginning after the first ~36 min of filming when water clarity returned to normal following camera deployment. The footage used for the analysis was divided into twelve 30-s segments that were viewed in real time, with 5 min separating each segment (Cousins et al. 2016). The number of fish we detected during morning (20.2 ± 6.7 [mean ± SD]) and afternoon 14.9 ± 5.7 surveys were similar, so we combined them to increase the number of 30-s samples to 24 for each enclosure. We scored the video quality for each survey by assigning a score from 1 to 10 (zero visibility to highest clarity) to each 30-s sample. Following data collection, we determined the lowest visibility score at which fish were detected and removed all samples below this threshold (3% of 30-s samples, $n = 2400$).

We determined the percentage of usable video for each enclosure at 9 and 12 wk separately and compared the 2 weeks across treatments (King et al. 2018; Fig. S2). We used 2 different metrics to determine fish response to the treatments. The 1st, total fish detections, is the maximum number of individual fish counted within a particular 30-s segment (MaxN). We summed the MaxN for all 30-s samples for each enclosure to calculate total fish detections. The

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199 2nd metric, detection probability, was calculated as the proportion of 30-s segments in which at
200 least 1 fish was detected. For instance, if at least 1 fish was detected in eight 30-s samples out of
201 24 samples at a single enclosure, the detection probability for that enclosure would be 0.33.
202 These metrics were quantified from the video samples that met the visibility criteria described
203 above. We identified all observed fish to the lowest taxonomic resolution possible and assigned
204 them to a size class (e.g., <50mm, 51–100 mm) by estimating their total length (mm) relative to
205 the known size of substrate baskets within the enclosures.
206
207 **Quantifying spatial subsidies**
208 To determine if live mussels and their shells increased spatial subsidies to fish, we
209 quantified the biomass of benthic algae, organic matter, and macroinvertebrates in each
210 enclosure 9 and 12 wk after we began the experiment. Benthic algal biomass was measured by
211 burying 2 ceramic tiles (width = 7.6 cm) in each enclosure. Each tile had a glass fritted disk
212 (diameter = 2.8 cm) mounted to it that remained flush with the sediment and, therefore, collected
213 algae. We removed and froze 1 disk from each enclosure during the 9- and 12-wk sampling
214 periods. We later cold-extracted chlorophyll *a* (Chl *a*) from these disks with acetone and
215 quantified Chl *a* with a spectrophotometer (APHA 2005).
216 We placed 6 square mesh plastic baskets (6 cm deep, 100 cm^2 surface area) filled with
217 homogenized substrate from the experimental reach in each enclosure to measure the biomass of
218 benthic organic matter and macroinvertebrates (Bertrand and Gido 2007). We removed 3 baskets
219 from each enclosure at 9 and 12 wk. We created a slurry by homogenizing the contents of the
220 collected baskets in a bucket with a known volume of stream water. A subsample of the slurry
221 was filtered (GF/F; 0.7µm pore size), frozen, and ashed to obtain ash-free dry mass (AFDM) of

benthic organic matter. Measurements of AFDM were then standardized to the volume of substrate sampled. The remaining slurry was processed for macroinvertebrates by elutriation followed by pouring it through a 0.175mm mesh sieve and preserving the sieved material in 70% ethanol (Bertrand and Gido 2007). In the laboratory, macroinvertebrates were enumerated, identified to order or family (Merritt and Cummins 2008), and measured for length. We then used standard length–mass relationships (Eckblad 1971, Benke et al. 1999, Johnston and Cunjak 1999, Miserendino 2001, Stoffels et al. 2003, Giustini et al. 2008, Miyasaka et al. 2008, Obaza and Ruehl 2013) to estimate biomass. Length–mass relationships were calculated as $\text{dry mass} = a \times \text{length}^b$. Odonates longer than 10 mm were analyzed separately from the total invertebrate biomass because they were rare (<1% of the data set) and, like fish, large odonates could be attracted by treatment effects. Macroinvertebrate biomass was then standardized to the area of substrate sampled.

Statistical analyses

We assessed variation in detection probability among treatments with analysis of variance (ANOVA) and compared total fish detections across treatments with a generalized-linear model with a Poisson distribution (Zuur et al. 2009). Fixed effects included treatment and sample date (wk 9 or 12). We tested assumptions of normality and heterogeneity of variances with Shapiro–Wilks tests and Levene's tests, respectively, for detection probability and total fish detections before we did the statistical tests. We arc-sin $\sqrt{x}$- transformed detection probabilities to meet assumptions of normality. We used the function Anova to conduct likelihood ratio tests and obtain *p*-values for the generalized linear model, as implemented in the R package *car* (Fox and Weisberg 2019).

We tested for differences in benthic invertebrate, large odonate, algal, and particulate organic matter biomass among treatments with ANOVA, with treatment and sampling date as fixed effects. Before analysis, we $\log_{10}$-transformed benthic invertebrate biomass and particulate organic matter data to conform to assumptions of normality and heterogeneity of variances. We used Tukey post-hoc tests to conduct multiple comparisons if the null hypothesis of no difference among treatment means was rejected for a dependent variable. Statistical analyses were done in R (version 3.5.1; R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

We detected 8 fish species from 580.5 h of video samples. Nearly 90% of the detections (total detections = 351) were of juvenile *Lepomis* spp. (total length ~20–50 mm) (Fig. 2A). Detections of darters (Percidae) and minnows (Cyprinidae) were much lower (Fig. 2B) than previous standardized fish surveys in a downstream reach (Hopper et al. 2018). Detection probability for fish did not vary significantly among treatments or sampling periods ($F_{4,90} = 1.36$, $p = 0.24$), although on average the probability of detection was lower at sediment-only treatments (0.08 ± 0.008 [mean ± SE]) compared with detection probabilities for live and sham treatments (mean for both assemblages combined 0.14 ± 0.01 and 0.14 ± 0.03, respectively; Fig. 3A). However, the total number of fish detections varied significantly among treatments ($\chi^2 = 21.20$, $p < 0.001$). Post-hoc tests indicated total fish detections for live and sham mussel treatments were significantly different than bare sediment treatments, regardless of mussel assemblage composition. Yet, the number of fish detected did not differ significantly among the live or sham mussel treatments and was not influenced by mussel assemblage composition (Fig. 3B). The total number of fish detected at either sham or live mussel treatments (mean for both

assemblages combined 3.6 ± 0.23 and 4.2 ±0.85, respectively) was nearly 2 × higher than sediment-only treatments (2 ± 0.69). The total number of fish detected was also influenced by sampling date, and detections increased from wk 9 (mean =, SE =) to 12 (3.0 ± 0.23 and 4.1 0.44, respectively; $\chi^2 = 8.65$, $p = 0.003$).

Spatial subsidies were not different among live, sham, or sediment only treatments, but some were influenced by incubation time. Benthic invertebrate biomass was highly variable across treatments (range = 0.0–2.93 g/m^2, mean = 0.87 ± 0.44 [SD] g/m^2) and did not differ significantly among them ($p = 0.32$). Benthic invertebrate biomass increased significantly in all treatments from wk 9 to 12 (mean = 0.07 ± 0.33 and 1.05 ± 0.48 g/m^2, respectively; $F_{1,88} = 61.37$, $p < 0.001$). Large odonate biomass did not differ among treatments or weeks (0.27 ± 0.24 g/m^2). Biomass of benthic algae was highly variable among treatments (0.96 ± 0.88 µg/cm^2) and did not differ significantly among treatments ($p = 0.10$). Particulate organic matter also did not vary significantly among treatments ($p = 0.80$), but decreased significantly from wk 9 to 12 ($p <0.001$) in all treatments.

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DISCUSSION

Mussel shells (live and sham) led to a heterogeneous distribution of fish within our experimental reach and appear to provide habitat for fish at fine spatial scales. The probability of fish detection did not vary significantly among treatments, but the number of fish detections was greatest in the live mussel and sham treatments compared with the sediment-only treatment. Our results are consistent with observations that both mussels and empty shells increase interstitial spaces in the substrate, which are important habitats for fish (Sechnick et al. 2011) and their prey (Cummins and Lauff 1969; Table 1). Specifically, mussels and their spent shells might offer

refuge from larger aquatic predators (Moy and Sparks 1991). For instance, small Green Sunfish (*Lepomis cyanellus*) wedge themselves horizontally beneath cobbles to avoid detection by observers who are confused as predators during snorkel surveys in Brier Creek, Oklahoma (W. J. Matthews, personal communication). Habitat complexity associated with mussel patches might also serve as a critical flow refuge for the small fishes detected in our experiment because mussel patches significantly reduce near-bed flow velocity relative to gravel beds (Sansom et al. 2018a). Furthermore, in previous field studies, we have regularly observed active sunfish nests within mussel beds (C. Vaughn, personal observation). Our previous observation may indicate that the stable stream sediments and the accumulation of dead shell material in and around mussel patches provide preferential spawning, nesting, or nursery habitat to certain fishes observed in other systems (Wisniewski et al 2013). Two species of cavity-spawning madtoms, *Noturus gyrinus* and *N. eleuthurus* (Miller and Robison 2004) have been captured inside abandoned mussel shells in this river and others in the region (G. Hopper, personal observation). Thus, habitat modifications by mussels at fine spatial scales may provide a long-term, stable flow refugia, facilitate aspects of fish life histories, and result in the heterogeneous distribution of fish within mussel beds.

Contrary to our hypothesis and the findings of previous studies in this river (Spooner and Vaughn 2006, Vaughn and Spooner 2006), live mussel patches did not increase algal or invertebrate resources to fishes relative to sediment patches. Increased nutrient cycling by mussels can modify benthic algal assemblage composition and increase primary production, which can lead to increased invertebrate densities (Spooner and Vaughn 2006, Atkinson et al. 2013). Those effects can differ depending on the mussel species, so we used 2 mussel species with different traits that both have documented effects on foodweb dynamics and ecosystem

function (Spooner and Vaughn 2012, Atkinson et al. 2013). However, trophic resources to fish were not influenced by the physiological, behavioral, or morphological traits of mussels occupying experimental patches.

Mussel effects can change with environmental context (Vaughn et al. 2004). To avoid legacy effects from mussels, we conducted our experiment upstream of known mussel beds, near the headwaters of the Kiamichi River. This area has a higher gradient than areas in which previous experiments have been conducted, which can influence macroinvertebrate assemblage composition and densities (Covich et al. 1996) because such areas experience frequent high shear stress events during high flows. Additionally, this area had relatively large substrate, which often has reduced macroinvertebrate densities compared with smaller substrates (Wise and Molles 1979). Spooner and Vaughn (2006) conducted an experiment similar to ours in the Kiamichi River with the same enclosure design and similar mussel species treatments (they had single species treatments rather than 2-species assemblages), but their experiment was further downstream in a lower gradient area of the river. In their 12-mo experiment Spooner and Vaughn (2006) found that patches of mussels increased benthic invertebrate abundances and that these effects were much greater during low-flow summer periods than higher flows in autumn.

We planned for our experiment to encompass the typical summer low-flow conditions in this river (Allen et al. 2013, Vaughn et al. 2015), but discharge was nearly 6× higher on average than the previous 30 y during the incubation time of the experiment (August). These flows may have homogenized or prevented establishment of invertebrates and algae within the treatments (Fig. S1). Furthermore, continuously high flows through the reach may have reduced light availability to the benthos, reducing the importance of the bottom-up effect of nutrient recycling by mussels. We hypothesize that longer periods of low-flow conditions would increase spatial

337 subsidies derived in patches of live mussels, as in previous work (Spooner and Vaughn 2006).
338 However, under the high-flow conditions of this experiment, fish were more attracted to the
339 structural features of mussel aggregations rather than their trophic resources.
340 Throughout the experiment, we did not detect high fish density or diversity. We
341 hypothesized that mussels would increase prey densities and influence the distribution of benthic
342 feeding fish such as darters (Percidae) and grazing minnows (e.g., *Campostoma spadiceum*) that
343 are prevalent in the system (Pyron et al. 1998; Table 1, Fig. 2B). The habitat in which we placed
344 our enclosures, a low-velocity pool with cobble substrate, was dominated by *Lepomis* spp. and a
345 few other species such as darters, which are more abundant in riffles, which could have lowered
346 our chances of detecting them. The daytime deployment of our RUV cameras also greatly
347 reduced the potential to detect nocturnal species, such as madtoms, that may have occurred
348 within enclosures. Indeed, we captured 2 madtoms in live and sham treatments during our basket
349 sampling, indicating that either madtom abundance was low in this reach or our ability to detect
350 their association with our treatments with RUVs was poor. Future studies addressing similar
351 topics might consider sampling diverse habitats with a variety of techniques to better understand
352 species interactions at fine spatial scales.
353 Like most other sampling techniques, RUV has specific biases and limitations. For
354 example, species identification may be difficult or impossible based solely on video footage
355 (Cappo et al. 2004, Pelletier et al. 2011), especially for smaller individuals, fish with similar
356 body shapes (i.e., *Lepomis* spp.), and fish that can inhabit interstitial spaces (i.e., darters and
357 madtoms). In addition, there is a nonlinear relationship between the abundance metric, MaxN,
358 that we used in our study and true fish abundance, such that fish abundance is increasingly
359 underestimated as fish abundance and mobility increase (Schobernd et al. 2014, Campbell et al.

2015). This system has high fish diversity (Pyron et al. 1998, Matthews et al. 2005; Table 1), so we assume that the abundance of some small, schooling and highly mobile species, such as cyprinids that inhabit the water column, was underestimated in this experiment (Table 1, Fig. 2B). Future studies might build on our results by conducting similar experiments along a gradient of stream conditions (e.g., depth or low flows), which might allow the responses of different suites of species to be quantified.

Activities of animals that modify both habitats and trophic resources can cause other species to aggregate (Coppock et al. 1983, Vaughn and Spooner 2006). We also found this effect in that mussel patches at fine spatial scales (<1 m^2) increased fish densities by modifying river habitat in which mussels and fish co-occur. Despite low total fish detections in our experiment, mussel shell presence affected fish distributions at fine spatial scales. This effect may become more apparent in downstream reaches because these reaches have higher mussel densities (Atkinson et al. 2012). Understanding whether fish and mussels aggregate at fine spatial scales is important because they may interact to spatially concentrate the ecosystem effects of each group. We predict the strongest ecosystem effects will occur where both mussel and fish densities are high (Hopper et al. 2018). Our experiment did not find a positive effect of mussel patches on the abundances of fish prey, but under different environmental contexts both habitat and nutrients supplied by mussels might be important. Investigators should seek out these types of interactions because overlapping aggregations of animals can form biogeochemical hotspots (McIntyre et al. 2008, Atkinson and Vaughn 2015) and can have important consequences for ecosystem structure and function (Atkinson et al. 2018).

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Author contributions: GWH, TPD, KBG, and CCV designed the study. GWH and TPD carried out the experiment. GWH analyzed the data and wrote the manuscript with input from all authors.

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FIGURE CAPTIONS

Fig. 1. A.—Example screen shots from remote underwater video (RUV) camera used to detect fish occurrence and diversity over experimental enclosures. View of live mussel enclosure and positioning of baskets used to quantify spatial subsidies. B.—Adult Longear Sunfish (*Lepomis megalotis*) detected at a control enclosure (sediment only). C.—Two juvenile Spotted Bass (*Micropterus punctatus*) detected at a sham enclosure. D.—Two juvenile sunfish (*Lepomis* spp.) detected feeding on live mussels. Black arrows show the location of individuals. E.—Longear Sunfish detected at a sham enclosure. Black arrow shows the location of the fish. F.—*Lepomis* spp. detected at a live mussel enclosure; small black arrow shows the location of the fish and a prominent mussel biodeposit is shown with a larger arrow.

Fig. 2. A.—Abundances for fishes and crayfish detected with remote underwater video at enclosures placed in the Kiamichi River, Oklahoma. Organisms were categorized to the lowest taxonomic level possible based on visibility and presented in order of their abundance. B.—Abundance of fish and crayfish at a site downstream of the — experimental reach (G. Hopper, personal observation). These data are organized for easy comparison to abundances measured by underwater video.

Fig. 3. A.—Detection probabilities for fish at treatments with live mussels, sham mussels, or sediment. B—Total number of fish detected in twenty-four 30-s samples across enclosure treatments. * indicates a significant difference among the treatments and control (sediment only). Black lines indicate the median, black circles indicate the mean, and box ends indicate the 1st through 3rd quartile of the data.

628 Table 1. Composition of fish communities in the Kiamichi River, Oklahoma, downstream of the experimental reach. These
629 measurements are based on fish collected with standardized seining and electrofishing (Hopper, unpublished). The predicted
630 numerical response (direction and cause) is based on the trophic guilds and vertical stream position for each species. The direction of
631 predicted response is described as either an increase (++) or no change (NA). Trophic guilds are coarsely split into: A = Algivore; D =
632 Detritivore; I = Invertivore; and P = Piscivore. Position in stream is either the surface, stream bottom (Benthic), or water column
633 (WC).

Species	Predicted numerical response to mussels/shams	Trophic guild	Position in stream	Predicted cause of numerical response
Etheostoma radiosum[a]	++	I	Benthic	Habitat and invertebrates
Lepomis megalotis[a]	NA or ++	I	WC	Habitat and invertebrates
Lepomis cyanellus[a]	NA or ++	I	WC	Habitat and invertebrates
Lepomis macrochirus[a]	NA or ++	I	WC	Habitat and invertebrates
Etheostoma nigrum[a]	++	I	Benthic	Habitat and invertebrates
Micropterus punctulatus[a]	NA or ++	P/I	WC	Invertebrate and fish
Orconectes palmeri[a]	++	D	Benthic	Habitat and detritus
Percina copelandi[a]	++	I	Benthic	Habitat and invertebrates
Campostoma spadiceum	++	A	Benthic	Habitat and algae
Lythrurus umbratilis	NA	I	WC	
Cyprinella whipplei	NA	I	WC	
Notropis boops	NA	I	WC	
Percina sciera	++	I	Benthic	Habitat and invertebrates
Labidesthes sicculus	NA	I	Surface	
Fundulus notatus	NA	I	Surface	
Gambusia affinis	NA	I	Surface	

Pimephales notatus	++	D/I	Benthic	Habitat and detritus
Etheostoma gracilis	++	I	Benthic	Habitat and invertebrates
Lepomis humilis	NA or ++	I	WC	Habitat and invertebrates
Lepomis gulosus	NA or ++	I	WC	Habitat and invertebrates
Pimephales vigilax	++	I	Benthic	Habitat and detritus
Ameiurus natalis	++	P/I	Benthic	Habitat and invertebrates
Micropterus salmoides[a]	NA or ++	P/I	WC	Invertebrate and fish
Lepomis microlophus	NA or ++	I	WC	Habitat and invertebrates
Moxostoma erythrurum	++	I	Benthic	Invertebrates
Noturus nocturnus	++	I	Benthic	Habitat and invertebrates
Pylodictis olivaris	NA or ++	P	Benthic	Fish

634 [a] Species detected at experimental enclosures at the Kiamichi River, Oklahoma with remote underwater video (RUV).

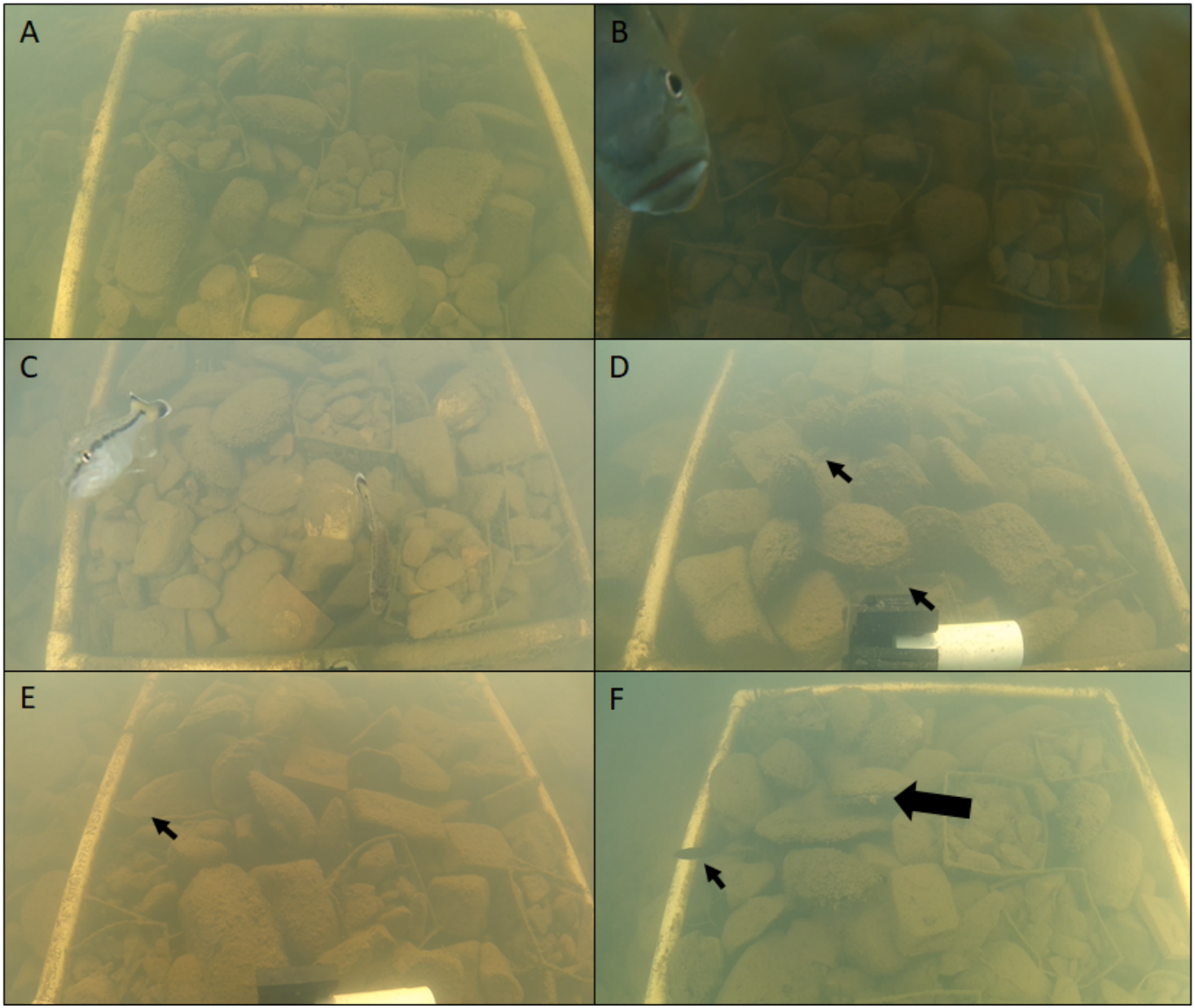
635

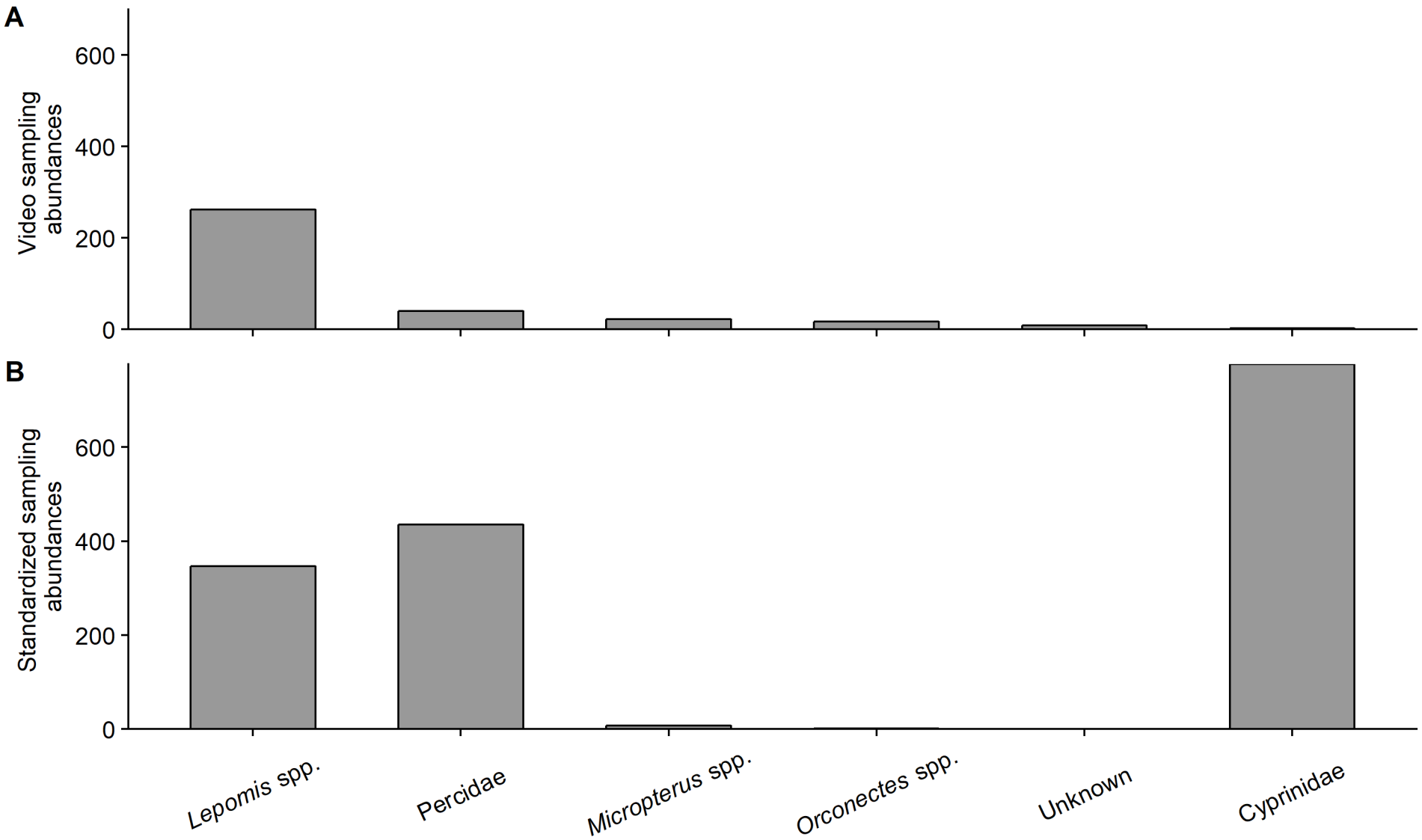
636 Table 2. Mean (SD) abiotic and biotic characteristics of each experimental treatment during wk 9 and 12. Od. Biomass = Odonate
637 biomass. Benthic organic matter (BOM) decreased significantly from wk 9 to 12, whereas invertebrate biomass increased significantly
638 from wk 9 to 12.

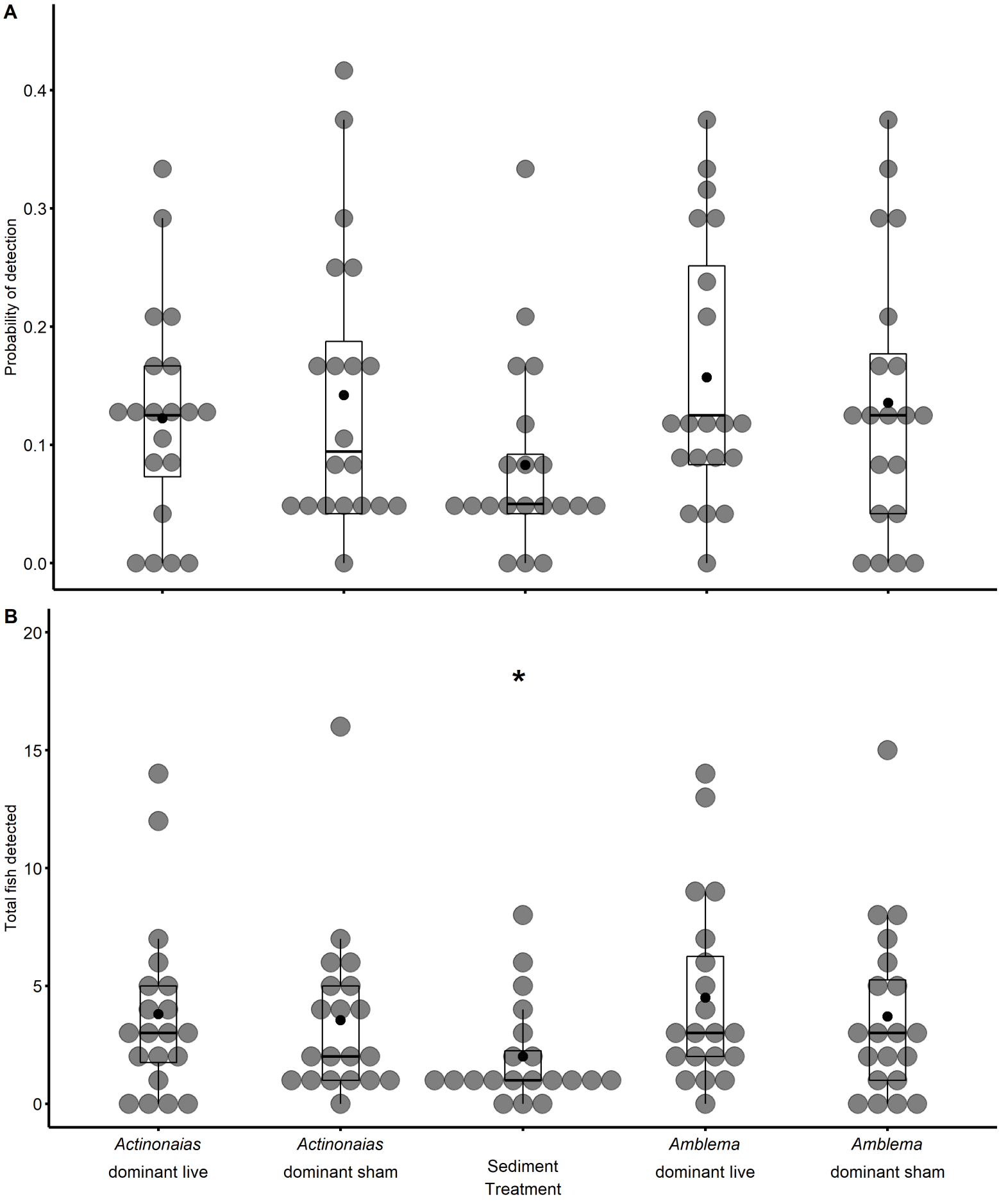
	Week 9						Week 12					
Treatment	Depth (m)	Current velocity (m^3/s)	Chl *a* (µg/ cm^2)	BOM (g/m^2)	Invert. biomass (g/m^2)	Od. biomass (g/m^2)	Depth (m)	Current velocity (m^3/s)	Chl *a* (µg/cm^2)	BOM (g/m^2)	Invert. biomass (g/m^2)	Od. biomass (g/m^2)
Actinonaias												
Dominant Live	0.56 (0.09)	0.02 (0.02)	0.79 (0.43)	1.50 (1.2)	0.54 (0.24)	0.01 (0.01)	0.55 (0.08)	0.02 (0.01)	0.87 (0.52)	0.3 (0.2)	1.00 (0.30)	0.02 (0.10)
Dominant Sham	0.56 (0.06)	0.01 (0.02)	1.58 (0.84)	1.70 (1.3)	0.66 (0.27)	0.02 (0.01)	0.59 (0.06)	0.02 (0.01)	1.33 (1.20)	0.2 (0.1)	1.06 (0.34)	0.03 (0.03)
Amblema												
Dominant Live	0.54 (0.07)	0.01 (0.01)	0.79 (0.35)	1.10 (0.4)	0.88 (0.43)	0.03 (0.03)	0.56 (0.06)	0.01 (0.01)	1.20 (1.05)	0.4 (0.1)	1.21 (0.71)	0.05 (0.04)
Dominant Sham	0.52 (0.09)	0.02 (0.02)	1.10 (0.72)	1.30 (0.6)	0.74 (0.29)	0.03 (0.03)	0.55 (0.07)	0.02 (0.02)	0.35 (1.63)	0.6 (0.16)	1.08 (0.63)	0.02 (0.01)
Sediment	0.58 (0.09)	0.02 (0.01)	1.08 (0.08)	1.30 (3.0)	0.69 (0.37)	0.02 (0.01)	0.59 (0.08)	0.01 (0.02)	0.80 (0.34)	0.4 (0.3)	0.88 (0.32)	0.02 (0.01)

639

640


A
B
C
D
E
F


A
Video sampling abundances
600
400
200
0
B
Standardized sampling abundances
600
400
200
0
Lepomis spp.
Percidae
Micropterus spp.
Orconectes spp.
Unknown
Cyprinidae


A
Probability of detection
0.0
0.1
0.2
0.3
0.4
B
Total fish detected
0
5
10
15
20
*
Actinonaias
dominant live
Actinonaias
dominant sham
Sediment
Treatment
Amblema
dominant live
Amblema
dominant sham