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Selection of Interstice Size by Juvenile Flathead Catfish

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Abstract.—Little is known about habitat requirements of juvenile flathead catfish *Pylodictis olivaris*. Previous studies indicate use of coarse substrates associated with riffle habitats in streams; however, limited information on microhabitat characteristics associated with habitat selection exists. To further our understanding of early life history habitat for flathead catfish, we used polyvinyl chloride half tubes (i.e., tubes cut in half longitudinally) of six different diameters (range, 13–76 mm) and depths (range, 25–152 mm) to simulate interstitial spaces provided by coarse substrates and determine (1) whether juvenile flathead catfish selected for interstice size, (2) relative importance of interstitial diameter and depth, and (3) if interstitial space size selection was related to fish body size. A total of 1,316 selection trials regarding interstitial diameter, depth, and the interaction of these characteristics was conducted using juvenile flathead catfish ranging in total length (TL) from 15 to 128 mm. Utilization of interstice diameters and depths was nonrandom (i.e., selection was occurring). Selection of interstice diameter was positively related to fish body size (i.e., total length), whereas all sizes of juvenile flathead catfish most often selected the greatest depth of interstitial space offered. We observed an ontogenetic shift in relative importance of interstice diameter and depth during interaction trials. Flathead catfish less than 40 mm TL selected for interstitial diameter, fish between 41 and 60 mm TL selected for both interstitial characteristics, whereas individuals larger than 60 mm TL selected for interstitial depth. Results of our study are among the first to identify microhabitat-scale characteristics that influence habitat selection by early life history stages of this species.

Introduction

The flathead catfish *Pylodictis olivaris* is a popular recreational sport species throughout its native range (Jackson 1999). However, introduced populations throughout many coastal rivers along the Gulf of Mexico and Atlantic slope of the United States have also negatively affected native fish communities (Guier et al. 1984; Thomas 1995; Sakaris et al. 2006). Many studies have characterized habitat use by adult flathead catfish (Robinson 1977; Grace 1985; Sandheinrich and Atchison 1986; Coon and Dames 1991; Grussing et al. 2001; Vokoun 2003; Daugherty and Sutton 2005), but few have investigated habitat requirements of juveniles (Irwin et al. 1999; Brewer and Rabeni 2008). An understanding of habitat needs at all life stages is important for management of desirable stocks of flathead catfish, as well as to aid in control of introduced populations.

Observations suggest that juvenile flathead catfish inhabit areas of shallow water depths, high velocities, and coarse substrates (Hubbs and Lagler 1947; Minckley and Deacon 1959; Pflieger 1975; Trautman 1981; Pierson et al. 1989); however, these studies did not quantitatively assess habitat use. Irwin et al. (1999) and Brewer and Rabeni (2008) provided the first quantitative information on juvenile flathead catfish habitat. Irwin et al. (1999) reported that 86% of juvenile (<150 mm total length [TL]) flathead catfish ($N = 95$) were collected in shallow (<35 cm) water depths associated with high (≥55 cm/s) flow rates and coarse substrates (i.e., gravel or larger substrata) in Alabama streams. Likewise, Brewer and Rabeni (2008) reported that the availability of coarse substrates was positively correlated with presence of juvenile (<277 mm standard length) flathead catfish in the Marais des Cygnes River, Missouri, though average water column velocity was negatively correlated with juvenile abundance. In-

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formation on physical habitat characteristics associated with selection by early life stages is needed to better understand habitat requirements for flathead catfish.

Association of fishes with coarse substrates has been attributed to the provision of cover (Minckley and Deacon 1959; Lobb and Orth 1991; Irwin et al. 1999; Brewer and Rabeni 2008). Coarse substrates create interstices (i.e., spaces between adjacent substrate particles) that provide protection from predation and vary in size based on grain size of the substrate. Interstice size has been documented to be an important factor in microhabitat selection for other structure-oriented fishes (Crowder and Cooper 1979; Walters et al. 1991). Walters et al. (1991) reported that bullheads *Ameiurus* spp. selected for small (40 mm) interstices offered by artificial pipe structures in ponds. Similarly, bluegills *Lepomis macrochirus* selected small interstices provided by brush habitat over larger ones created by tire or stake-bed structures (Brouha 1974; Wilbur 1978; Wege and Anderson 1979), and largemouth bass *Micropterus salmoides* have been reported to use interstitial spaces in relation to body size (Lynch and Johnson 1989). Results of these studies have provided useful information to further define and manage habitat for these species. Similar knowledge of interstitial space size selection of juvenile flathead catfish would advance our understanding of early-life history habitat needs and identify habitat characteristics associated with selection. Therefore, our objectives were to (1) determine whether juvenile flathead catfish select for specific interstitial space characteristics, and (2) examine relationships between fish body size and interstitial space selection using polyvinyl chloride (PVC) tubes as simulated interstitial spaces in a laboratory environment. Results of this study will further our ability to identify, protect, and enhance early life history habitat critical to production of strong year-classes of flathead catfish throughout their native range and aid in identification of systems that may support invasive stocks.

Methods

Fish Production

Reproductively mature flathead catfish were collected from Lake Buchanan, Texas during March through May 2008 and 2009 using pulsed-DC electrofishing. Fish were transported to the Texas Parks and Wildlife Department Heart of the Hills Fisheries Science Center (Mountain Home, Texas), gender was determined by visual examination of the urogenital area as described for channel catfish by Kelly (2004), and spawning pairs were randomly assigned to 1 of 20 outdoor spawning enclosures (one pair per enclosure). Enclosures were constructed of wire mesh fencing and measured 3 m long by 1 m wide with a maximum water depth of 1 m. A 56-L ceramic jar or a 114-L aluminum garbage can was placed in each enclosure to serve as a spawning receptacle, and receptacles were checked every 24 h for eggs. If spawning occurred, egg masses were removed, dematrified using a 2% sodium sulfite solution, and placed in McDonald jars at a maximum density of 10,000 eggs per jar. Eggs were incubated at water temperatures ranging from 21°C to 23°C and treated with 100 ppm formalin (15-min bath) every 48 h to inhibit fungal infection (Small 2006). After hatching, yolk sac fry were transferred to a 218-L raceway and, following yolk absorption, fed granulated feed (Silver Cup Granulated Salmon/Trout #1; Nelson and Sons, Murray, Utah [2008] or Starter Diet #0; Rangen, Inc.; Buhl, Idaho [2009]) ad libidum until about 20 mm TL. Larger age-0 flathead catfish were fed a combination of frozen bloodworms (Chironomidae) and fathead minnow *Pimephales promelas* fry.

Interstitial Space Selection Trials

We used PVC tubes (cut in half longitudinally) as simulated interstitial spaces (SIS). Fischer and Öhl (2005) used PVC tubes (in the round) as simulated shelter to study responses of juvenile burbot *Lota lota* and stone loach *Barbatula barbatula* to decreasing cover availability. The authors reported that the tubes were readily accepted as shelter and provided a measureable interstice space. In our study, preliminary trials ($N = 50$) indicated that juvenile flathead catfish accepted the PVC tubes as cover, with 100% of fish utilizing the tubes after 4 h and remaining under the tubes through 24 h. Based on these results, we concluded that PVC half tubes provided an acceptable form of SIS to meet the objectives of our study.

We examined interstitial space selection based on (1) interstice diameter, and (2) interstice depth (i.e., length of the half tube). In addition, we tested various combinations of interstice diameter and depth to determine relative importance of each characteristic. All selection trials were conducted in 114-L aquaria, housed indoors at water temperatures ranging from 18°C to 24°C.

Interstice diameter trials.— Six PVC tubes with diameters of 13, 25, 38, 51, 64, and 76 mm and a depth of 152 mm were placed over a layer of sand substrate (about 1 cm thick) on the bottom of each aquaria. Location (e.g., middle of tank, end of tank, etc.) and orientation (i.e., parallel or perpendicular to adjacent tubes) of each tube was randomized within each tank and trial to avoid potential biases associated with these factors. Juvenile flathead catfish were randomly selected from the pool of available fish, measured for total length (to the nearest millimeter), and placed in the aquaria (one fish per aquarium) for 24 h under a 12:12 h (light:dark) regime. At the conclusion of each trial, tubes in each aquarium were removed and diameter of the tube used as cover was recorded. Experimental trials were repeated weekly from July through December 2008 and 2009. An individual fish was used only once during the study. We used a chi-square analysis to test whether diameter of interstitial spaces used by juvenile flathead catfish differed significantly from random (i.e., selection was occurring). If selection did occur, we used a cumulative multinomial logit model (PROC GENMOD; SAS Institute 2010) to determine if selection changed as a function of fish body size (total length). Statistical analyses were considered significant at $P \leq 0.05$.

Interstice depth trials.—Six half tubes, all of the same diameter but with differing lengths (25, 52, 76, 102, 127, and 152 mm), were placed on the bottom of each aquarium as described previously. The diameter of half tubes used in these trials was based on results of diameter selection. For example, if juvenile flathead catfish 50–60 mm TL selected interstices with a diameter of 52 mm, then 52-mm-diameter tubes were used in interstice depth trials for fish of that size. Trials were conducted and statistical analyses performed as described for interstice diameter selection trials.

Diameter–depth interaction trials.—To examine relative importance of interstice diameter and depth characteristics, we conducted an additional series of selection trials using a randomized combination of the aforementioned tube diameters and depths in each aquarium. Juvenile flathead catfish were selected at random and trials were conducted as described for interstice diameter and depth trials. At the conclusion of each trial, diameter and depth of the selected tube were recorded. Limited sample sizes ($N = 154$ trials over 36 depth × diameter combinations) and unbalanced data precluded use of the cumulative multinomial logit model. To test whether fish of a given size selected for interstitial diameter, depth, or both, we calculated marginal probabilities (Agresti 1990) for each factor. We condensed data to five total length-classes (<40, 41–60, 61–80, 81–100, and >100 mm) and examined each size-class independently. We then compared marginal probabilities in the crossed trials (i.e., depth and diameter interaction) to selection probabilities of the independent interstice diameter and depth trials using Pearson's product-moment correlation. When a factor is important and strongly influences selection, the pattern of selection within the marginals of the crossed trials is similar to the pattern of selection observed within the individual trials. Alternatively, the pattern of selection within the marginals of the crossed trials differs from that in the individual trials, suggesting that influence of the factor on selection has been altered by the competing factor. Therefore, a high, positive correlation between marginal probabilities in the crossed trials (i.e., depth and diameter interaction) and selection probabilities of the independent interstice diameter and depth trials indicates the importance of that factor on selection. Conversely, a low correlation (positive or negative) indicates reduced importance of the factor in selection.

Results

We conducted a total of 1,316 selection trials during the study. Flathead catfish used in trials ranged from 15 to 128 mm TL (Figure 1). Use of the PVC half tube as cover during trials by flathead catfish was high (94%). Mortality of flathead catfish during trials was 0.9%.

Use of interstitial diameter by flathead catfish during trials was nonrandom ($\chi^2 = 523.1$, df = 5, $P = 0.0001$) and selection was related to fish total length ($\chi^2 = 335.8$, df = 1, $P < 0.0001$). Generally, interstice diameter selection was positively related to fish total length, and probability of selection for a given interstice diameter was greatest over a range of fish lengths (Figure 2). Probability of selection for the 25-mm-diameter SIS was greatest (range, 51–74%) among juvenile flathead catfish less than 45 mm TL, whereas fish 46 to 80 mm TL selected interstitial diameters of 25, 38, and 51 mm (Figure 2). Flathead catfish between 81 and 105 mm TL generally selected the 51-mm-diameter SIS, and fish greater than 105 mm TL selected the largest diameters offered (64 and 76 mm). Probabilities of selection for 64- and 76-mm-diameter SIS did not differ significantly (95% Wald confidence intervals for estimated beta

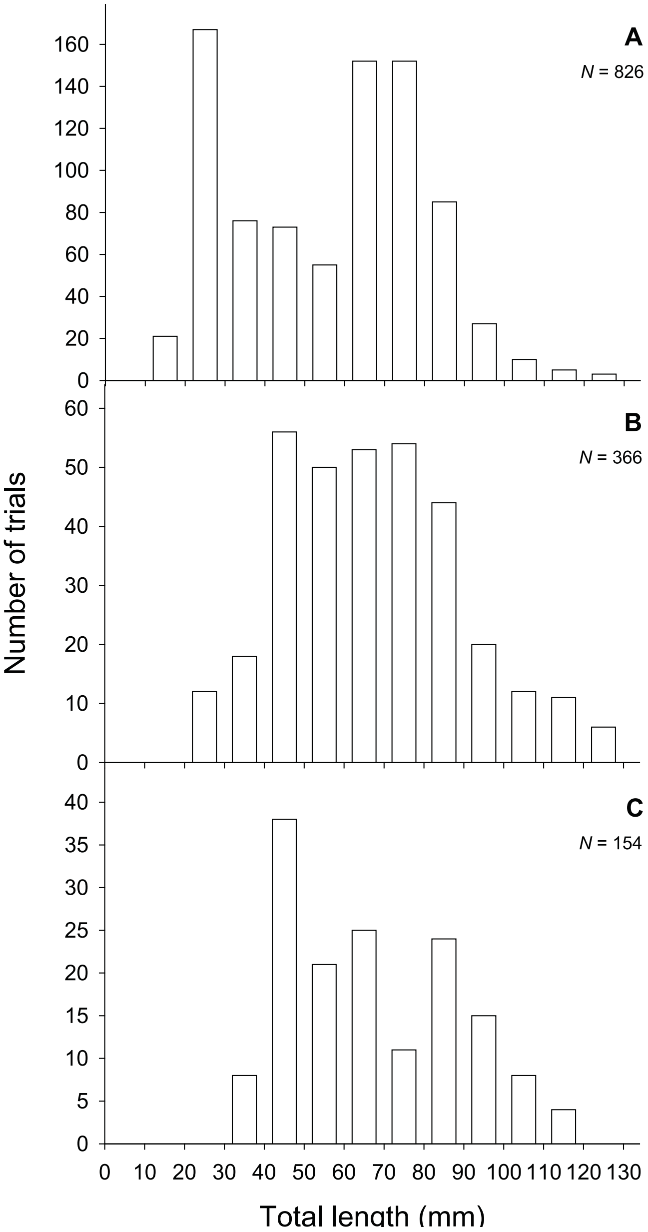

FIGURE 1. Number of trials (by fish length class) for (A) interstitial diameter, (B) interstitial depth, and (C) interstitial diameter-depth interaction effects. *N* refers to total number of trials.

coefficients: 7.33–8.72 for 64-mm-diameter SIS and 7.82–9.31 for 76-mm-diameter SIS). Therefore, we estimated a single selection probability for these interstitial diameters (Figure 2).

Juvenile flathead catfish use of interstitial depth was also nonrandom ($\chi^2 = 536.2$, df = 5, $P = 0.0001$). However, interstitial depth selection was not related to fish TL ($\chi^2 = 0.68$, df = 1, $P = 0.4081$). Flathead catfish consistently selected the greatest depth of interstitial space offered (152 mm) at all body sizes, and probability of selection declined with decreasing interstitial depth (Figure 3). Tubes 25 and 51 mm in depth were never used in the 336 interstice depth trials we conducted.

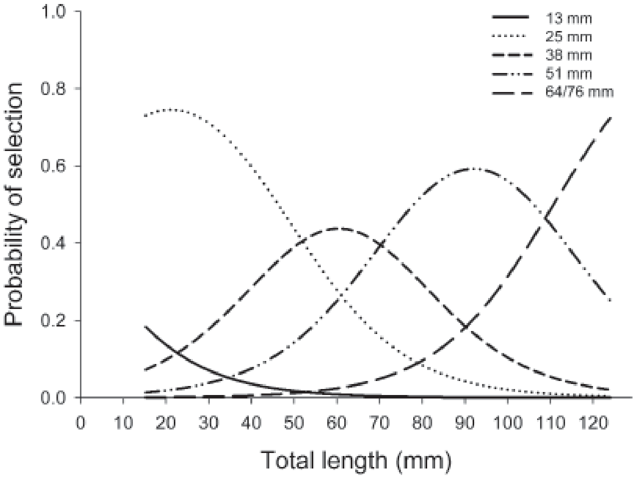

FIGURE 2. Relationships between probability of selection and juvenile flathead catfish total length for six diameters of simulated interstitial space. Relationships for 64- and 78-mm interstitial space diameters were combined because individual relationships did not significantly differ.

Analysis of diameter–depth interaction trials indicated that relative importance of interstice diameter and depth is related to fish size (Table 1). Correlation coefficients (*r*) for interstice diameter and depth indicated that selection of SIS by flathead catfish less than 40 mm TL favored diameter irrespective of interstice depth. However, interstice diameter and depth were of similar importance in selection of SIS by flathead catfish 41–60 mm TL (r = 0.82 and 0.96, respectively; Table 1). For juvenile flathead catfish 61 mm TL and larger, interstice depth was the important factor in selection of SIS (all $r \geq 0.95$), whereas importance of interstice diameter was reduced (all $r \leq 0.54$; Table 1).

Discussion

A comprehensive understanding of habitat needs for all life history stages is important for management of any fish population. However, quantifying habi-

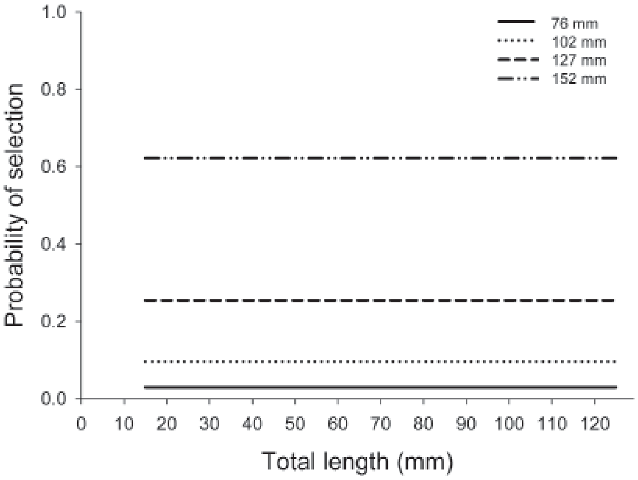

FIGURE 3. Relationships between probability of selection and juvenile flathead catfish total length for four depths of simulated interstitial space. Relationships for 25- and 51-mm interstitial space depths were omitted because they were not used during trials.

TABLE 1. Pearson's product-moment correlation coefficient between estimated probabilities of selection for interstitial diameter or depth (independent trails) and marginal probabilities of diameter × depth crossed trials for each total length class of flathead catfish. N_{Dia} and N_{Dep} refer to sample sizes of the independent diameter and depth trials, respectively, whereas N_{Cross} refers to sample size of the crossed trials.

	Correlation coefficient (r)				
Size-class (mm)	Diameter	Depth	N_{Dia}	N_{Dep}	N_{Cross}
<40	0.98	–0.05	225	20	7
41 to 60	0.82	0.96	112	85	50
61 to 80	0.24	0.95	287	107	36
81 to 100	0.51	0.97	129	66	38
>100	0.54	0.97	20	26	12

tat use and physical habitat characteristics associated with selection for life stages of a species that inhabit a relatively narrow range of environmental conditions is critical. Although flathead catfish have often been considered habitat generalists (Travnichek and Maceina 1994; Cloutman 1997; Jackson 1999), early life history stages have been consistently and exclusively associated with riffle habitat (Hubbs and Lagler 1947; Minckley and Deacon 1959; Pflieger 1975; Trautman 1981; Pierson et al. 1989; Jenkins and Burkhead 1993; Irwin et al. 1999; Jackson 1999; Brewer and Rabeni 2008). However, we understand little about the physical characteristics of this habitat type that define its use by juvenile flathead catfish. Our data are among the first to relate fish body size (total length) to cover size attributes for this species.

Previous studies have proposed many factors that may influence fish choice of cover, including food availability (Pardue 1973; Crowder and Cooper 1979; Prince et al. 1979) and refuge from predators (Glass 1971; Crowder and Cooper 1979; Savino and Stein 1982). Our study did not attempt to identify mechanisms associated with habitat selection of early life history stages of flathead catfish. However, we observed a high degree of selection for interstitial space habitat characteristics in the absence of both food and predators. Johnson et al. (1988) and Lynch and Johnson (1989) reported significant increases in use of small-interstice structures by juvenile bluegills in the presence of predators. The authors postulated this behavior reduced vulnerability to predation by physically excluding larger predators from their habitat. Lynch and Johnson (1989) also reported that adult bluegills with body sizes large enough to be relatively invulnerable to predation also occupied small interstitial spaces and suggested that bluegills are innately attracted to interstitial spaces that could provide a survival advantage. Our observation of a relationship between fish total length and interstitial size characteristics in the absence of predators may indicate a similar innate response by flathead catfish minimizing vulnerability to predation.

The size of a fish primarily determines its vulnerability to predation. Small body sizes are susceptible to a wider range of size- and gape-limited predators (Wootton 1998). Selection of an interstitial space diameter comparable to that of the occupant would serve to minimize the size range of potential predators that could exploit the habitat. This provides a plausible explanation of the relationship between interstice-diameter selection and body size that we observed in our study. Although our measure of body size was total length rather than body diameter, these measures were correlated (r = 0.98; D. J. Daugherty, unpublished data). Juvenile flathead catfish selected an interstitial space diameter comparable to that of their body, thereby minimizing the size range of potential predators. Lack of a relationship between juvenile flathead catfish body size and interstice depth may also be explained by selection of interstitial space characteristics that minimize vulnerability to predation. Regardless of body size, juvenile flathead catfish tended to select the greatest interstitial depths provided in experimental trials. Use of the deepest interstitial spaces available would minimize potential for prey to be extracted by predators too large to exploit the interstitial space, further reducing vulnerability to predation.

Based on relationships observed in the independent selection trials for interstice diameter and depth, we expected that juvenile flathead catfish in the interaction trials would select the interstitial diameter and depth combination that most closely matched their body diameter and maximized interstitial depth. However, we observed an ontogenetic shift in relative importance of interstice diameter and depth over the size range of fish we examined. It is unclear whether the observed relationship is an artifact of limited sample size (*N* = 154 trials over 36 depth × diameter combinations) or a true ontogenetic shift in relative importance of these microhabitat characteristics. However, larger juvenile flathead catfish are likely vulnerable to fewer, larger predators (Wootton 1998). Few large predators inhabit shallow, riffle habitats (Wootton 1998); predator communities in this habitat type are primarily smaller-bodied individuals that can only eat small prey. This may explain our observation that interstitial diameter was more important for small juveniles (<60 mm TL) and less important for larger fish. Future investigations of interstitial space selection by fishes should further examine relative importance of these characteristics.

Patterns of interstitial space selection that we observed provide plausible explanations for habitat use by juvenile flathead catfish observed in the field. Although Brewer and Rabeni (2008) did not examine microhabitat use in relation to flathead catfish total length, these authors reported evidence of ontogenetic shifts in habitat selection based on seasonal (i.e., summer and autumn) logistic models of habitat use. Variables explaining summer habitat use included water velocity (negatively correlated) and percent pebble, cobble, and boulder substrate (positively correlated). In contrast, their most parsimonious model of habitat use in autumn only included percent cobble and boulder substrate (positively correlated). Larger substrates are associated with higher water velocities (Kondolf and Wolman 1993); therefore, the negative correlation of velocity in the summer model, as well as the importance of percent pebble, indicated greater utilization of smaller substrates when fish are smaller. Retention of only percent cobble and boulder substrates in the autumn logistic model indicates increased use of larger substrates at greater body sizes. Interstitial space size is generally positively related to particle size (Platts et al. 1979), although the relationship can vary depending upon a number of factors, including substrate roundness, heterogeneity (Tickell and Hiatt 1938), and packing (Furnas 1931; Graton and Fraser 1935). In our study, smaller juvenile flathead catfish selected smaller diameter interstices, and selected interstitial diameter increased with fish total length. Therefore, our laboratory results corroborate those reported by Brewer and Rabeni (2008) and suggest that a range of coarse substrate sizes is required to provide appropriately sized interstitial cover for flathead catfish throughout early life history.

The results of our study suggest that the interstitial spaces provided by coarse substrates may play an important role in regulating survival and subsequent recruitment of early life history stages of flathead catfish. Association of coarse substrates with riffle habitats in lotic systems suggests that flathead catfish may be vulnerable to loss of this habitat type (Irwin et al. 1999; Brewer and Rabeni 2008). In regulated systems, reduced flows may increase sedimentation or dewater portions of riffles containing coarse substrates that provide appropriately sized interstitial spaces. Furthering our understanding of relationships between substrate particle-size measures and associated interstitial spaces will increase our ability to protect, create, and enhance juvenile habitat for native populations of flathead catfish and aid in identification and management of systems vulnerable to establishment of invasive stocks.

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