Habitat evaluation of native fishes in the Gila River basin

by

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Abstract

Habitat loss and alteration is a major cause of declining native fish diversity in streams across the southwestern United States. Much of this habitat alteration is a consequence of human's actively extracting or diverting water from lotic systems. The Gila River and its tributaries are home to multiple dams, diversions and also supply water to agricultural and industrial municipalities throughout the region, leading to continued decline of native fishes. We conducted a range-wide habitat assessment in an effort to identify critical habitat needs of two endangered minnow species, spikedace (*Meda fulgida*) and loach minnow (*Tiaroga cobitis*). This habitat assessment was conducted across multiple spatial scales in an effort to identify at what scale habitat variables most strongly influence the presence of these species. Further, we conducted an enclosure experiment using these two endangered fishes, as well as two other native cyprinids, speckled dace (*Rhinichthys osculus*) and longfin dace (*Agosia chrysogaster*), to test mechanisms influencing resource availability and growth rates. Our results point towards water velocity as the driving variable associated with presence and performance of endangered species in this system. We provide guidance on priority habitats and potential repatriation efforts, to ensure that these native species are not lost from this basin.

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Acknowledgements

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Chapter 1 - Multi-scale Habitat Assessment of Loach Minnow and Spikedace Across the Gila River Basin

Abstract

Habitat loss and alteration is a major cause of declining native fish diversity and abundance in streams across the southwestern United States. Much of this habitat alteration is a consequence of humans extracting or diverting water from lotic systems. The Gila River and its tributaries have multiple dams and diversions that supply water to agriculture, industry, and municipalities throughout much of Arizona, contributing to the decline of native fishes. To counter these declines, repatriation efforts have been implemented throughout the basin. While repatriation efforts have successfully re-established some populations, others have been unsuccessful. To aid in future management of imperiled Gila basin fishes, we conducted a range-wide habitat assessment in an effort to identify critical habitat needs of two federally-protected species, spikedace (*Meda fulgida*) and loach minnow (*Tiaroga cobitis*). This habitat assessment was conducted across multiple spatial scales, 1-km, 0.1-km, and the mesohabitat scale, to identify at what scale measured habitat variables most strongly predicted the presence of each species. We included minimum, maximum, and average depth, velocity, and substrate sizes within our model to predict the presence of both of these species. At our two broadest scales, average velocity was the variable that best predicted the presence or absence of both species. At the finest scale, loach minnow associated with very specific habitats while spikedace occurred across a range of habitats. Data were used to rank streams based on habitat suitability and suggested that future habitat assessments should be conducted at larger spatial scales to evaluate if a location should be repatriated.

Introduction

Repatriation, the placement of native animals in areas they have since been extirpated, is an increasingly common conservation strategy for restoring extirpated or enhancing diminished populations of terrestrial and aquatic species globally (Ripple & Beschta, 2003; King, Berg & Hay, 2004; Lamothe & Drake, 2019). Although there is a long history of fish stocking aimed at enhancing recreational or commercial fisheries, there is only recent interest for species that do not possess economic value (Lamothe & Drake, 2019; Desert Fishes Team, 2003; Marsh, Kesner & Pacey, 2005). Typically, repatriation of imperiled species and populations takes place in historically occupied habitat, presumably following the amelioration of factors that influenced the initial extirpation (Marsh, Kesner, & Pacey, 2005). Management actions to restore natural environmental characteristics include mimicking the natural flow regime, removal of nonnatives, and habitat improvements (Knopf et al. 1988; Tyus, 1992; Dodrill et al. 2015). Presumably, some combination of habitat restoration and eradication of nonnatives should set the stage for successful reintroduction of native fishes.

Our focus in this paper is to characterize habitat requirements of native Gila basin fishes, which can be challenging because habitat needs observed at one spatial scale may not be representative of what is needed at other scales (Winemiller, Flecker, & Hoeinghaus, 2010; Logue et al. 2011). With this in mind, studies evaluating habitat requirements for a species, as well as evaluating habitat for repatriation requirements, should be conducted at multiple spatial scales. Our goal with this approach was to provide additional information to inform future management in regard to the repatriation of imperiled species, to consider what spatial scale measurements should be taken, and what processes affected our observations. Until recently, community ecology focused on fine scale interactions, such as the mesohabitat scale, with the assumption that broad scale approaches, such as those occurring over multiple kilometers, were less important (Fausch et al. 2002). In the past, research was conducted only within short reaches of rivers due to the assumption that individuals complete their life cycle within this confined area (Gatz & Adams, 1994; Fausch et al. 2002). By assessing habitats at multiple scales, we hope to gain a better understanding of what scale is most appropriate to characterize habitats amenable to repatriation of native fishes.

Native fish declines in the American Southwest have been ongoing for decades and management efforts have been aimed at combating these declines (Propst, Williams, Bestgen, & Hoagstrom, 2020). The Gila River basin is home to multiple imperiled native fishes, all of which have been negatively affected by a combination of habitat loss and introduction of nonnative species (Propst, Gido, & Stefferud, 2008; Ruhi, Olden, & Sabo, 2016). In response to these declines, multiple management approaches have been implemented within the basin. Specifically, there have been extensive efforts to isolate reaches above natural or artificial barriers after eradication of nonnatives and establishment of native populations. However, due to continued declines, extensive evaluation of factors affecting successes or failures in establishing naturally reproducing populations in these renovated waters or elsewhere are needed.

We conducted a multi-scale habitat assessment in streams across the Gila River basin in an effort to identify variables associated with the presence-absence of loach minnow (*Tiaroga cobitis*) and spikedace (*Meda fulgida*), two federally-protected cyprinids that have been extirpated from > 80% of their native ranges (U.S. Fish and Wildlife Service, 2012). Whereas large-scale repatriation efforts have attempted to protect these populations from extinction (Desert Fishes Team, 2003), knowledge of the appropriate scale to conduct habitat measurements for the successful establishment of populations is critical (Lamothe & Drake, 2019). Repatriation of spikedace and loach minnow has been taking place for many years, but results have been mixed in regard to establishing reproductive populations (Desert Fishes Team, 2003; Clarkson & Marsh, 2010).

To gain an understanding of the habitat requirements of loach minnow and spikedace that might enhance success of repatriation efforts, we selected reaches throughout the Gila River basin where spikedace and loach minnow either have natural populations, extirpated populations, successfully repatriated populations, or unsuccessfully repatriated populations to test if habitat variables are driving population persistence. The main objectives of this study were to 1) identify abiotic variables associated with successfully establishing naturally sustaining populations of loach minnow and spikedace and 2) identify the spatial scales at which to measure habitat variables to best predict the presence-absence of these species. We used a nested design where habitat data from our mesohabitat spatial scale were grouped together to represent our 0.1-km spatial scale, but habitat at our 1-km scale was defined by transects taken throughout the reach (Figure 1.1). Fish were collected at the mesohabitat spatial scale and grouped together to represent both the 0.1-km and 1-km spatial scales.

Previous research on these species has provided insight into their habitat associations. Loach minnow are a riffle obligate species completing most essential life-history processes in high velocity habitats (Rinne, 1989; Propst & Bestgen, 1991). For spikedace, increased water velocity is necessary for reproduction and feeding; although they do not solely occupy high velocity habitats for extended periods of time (Barber & Minckley, 1983; Propst & Bestgen, 1986). Assuming loach minnow are riffle obligates, we predicted flow velocity and depth will predict occurrences at fine scales due to their direct influence on species well-being and habitat occupation. At broader scales, increasing mean velocity should also provide an index of the total amount of suitable habitat, and over some threshold value, should predict the occurrence of this species. For spikedace, we predicted that at fine scales they will require moderate flow velocity that sustains drifting invertebrates while not imposing excess energy expenditure. At the broader scales, we also predicted that intermediate mean flow velocity would associate with sites with a mosaic of intermediate and fast velocity habitats that might optimize feeding efficiency and energy use of this species. While we predicted velocity would predict occurrences of both species across all scales, we predict loach minnow would occur in higher velocities than spikedace.

Methods

Study area

The Gila River and its tributaries are part of the lower Colorado River basin and flows southwesterly through southwestern New Mexico, then in a westerly direction once it reaches Arizona, where it eventually drains into the Colorado River in southwest Arizona, near the town of Yuma, AZ. The upper Gila River basin remains free flowing with relatively low human impact due to its remoteness and presence of federally-administered lands. However, the other sub-basins of the catchment have moderate to heavy human impacts, running through populated areas as well as having multiple dams and diversions. We sampled 31 1-km stream reaches between October 2018 and October 2019 (Figure 1.2). Eighteen reaches were sampled in October 2018 and June 2019. During October 2019, 11 reaches previously sampled were replaced with new reaches. Six reaches were sampled throughout the study, because they either were highly dynamic or had variable occurrences of loach minnow or spikedace. Dropping and adding sites was done to increase overall sample size to provide a more comprehensive view of the range of habitats currently and potentially occupied by each species. The elevation of reaches sampled over the course of the study ranged from 953 to 2185 m above sea level. Individual reaches were selected based on accessibility to each location and in consultation with various state agencies.

Fish Sampling

Fish communities were sampled using a combination of backpack electro-fishing (Smith-Root LR 20B, 200-250 V, Freq: 30 Hz, Duty Cycle: 30%) and seining (4.6 x 1.8 m, 3.2-mm mesh). Every stream was evaluated at three different spatial scales: 1-km reach, 0.1-km reach, and mesohabitat (0.5-72 m^2). Mesohabitats were identified and selected on site by individuals conducting the sampling based upon their habitat characteristics (Table 1). All available habitat types present within each 1-km reach were sampled. Sampling was conducted by capturing fish in each mesohabitat independently of other samples. Fish captured within each mesohabitat were identified and measured to total length prior to release. Fish were released downstream of the sampling area in an effort to not capture the same individual more than once. All fish data were pooled across mesohabitats to represent our 0.1-km reach. Finally, fish data from all 0.1-km reaches were pooled to represent the fish community at the 1-km reach.

Habitat Measurements

Within each mesohabitat, three point measurements were taken across three transects. Each point measurement included depth, velocity, substrate (clay, silt, sand, gravel, pebble, coble, boulder, bedrock), based on the scale set by Wentworth, 1922, and presence-absence of cover (i.e., overhanging vegetation or macrophyte presence-absence). All habitat data collected from the 8-10 mesohabitats within the downstream, midstream, or upstream 0.1-km reach were pooled to represent the habitat variables at the intermediate spatial scale. To capture the habitat variables at our 1-km scale, habitat transects were taken along the entire 1-km reach, providing an independent habitat assessment of habitat availability at this broad spatial scale. These transects were taken perpendicular to the thalweg every 25 or 50 m throughout the 1-km reach and habitat was measured at points 0.5, 1.0, or 2.0 m increments across the entirety of the stream. Transect intervals were chosen to yield approximately 200 individual habitat measurements within each 1-km reach.

Data Analysis

Classification trees were used to identify variables associated with the presence of spikedace and loach minnow across three spatial scales. Variables included in the models were the mean, maximum, and minimum of velocity, depth and substrate size. Classification trees use a recursive partitioning method to identify which variables most strongly affect the differentiation in the presence-absence of these species across the basin and across spatial scales (Strobl, Malley, & Tutz, 2009). Trees are initially overfitted using as many variables as possible to predict presence-absence and are then pruned to remove nodes in an effort to minimize error within the model (Khoshgoftaar & Allen, 2001). Random forest was conducted, with 500 iterations (Archer & Kimes, 2008), to identify variable importance within each classification tree by identifying the degree to which each variable affects the Mean Decrease Gini (MDG). MDG is a metric that shows the purity of a particular node split within classification trees, where larger values indicate increased variable importance within the model (Han, Guo, & Yu, 2016). By conducting this analysis, we were able to identify habitat variables that were important drivers of presence or absence of loach minnow and at which scale habitat measurements should be conducted to assess a location’s suitability for either species. If a significant model was derived at the mesohabitat scale, we calculated the percent of suitable habitat for a species by using each individual points within the habitat transects throughout the 1-km reach. The percent suitable habitat was used to predict fish density using linear regression. Classification trees were generated in program R version 3.5.2 using the packages *rpart* and *randomForest,* while linear models were made using package *glm* (R Core Team, 2018). Sites were ranked based on their suitability for repatriation based on our ability to classify occurrences at the different spatial scales and the percent of adequate habitat throughout the reach.

Results

Classification trees indicated that mean velocity was the strongest predictor of presence-absence of both loach minnow and spikedace across all spatial scales, with the exception that no variable was able to predict presence-absence of spikedace at the mesohabitat scale (Figures 1.3 & 1.4). Further, random forest analysis suggested that for both species and at all scales, mean velocity was always the most important variable for predicting the presence-absence of these species (Table 1.2). At the 1-km reach scale, loach minnow presence was more likely in reaches with mean velocity > 0.19 m/s, and spikedace presence was more likely when average velocity was > 0.21 m/s. At the 0.1-km reach scale, mean velocity greater than 0.38 and 0.39 m/s were associated with the presence of loach minnow and spikedace, respectively. At the mesohabitat scale, mean velocity, depth, and substrate size predicted loach minnow presence, identifying two different habitat types that can describe this species presence. The first included deeper water (≥ 0.21 m) with very high velocities (≥ 0.91 m/s). The second was characterized by shallow, high velocity mesohabitats with coarser substrate sizes (< 0.21 m depth, ≥ 0.57 m/s velocity, < 4.6 substrate size [indicating gravel/pebble substrate]).

Of the 51 1-km reaches sampled, 25 had average velocities that were predicted to be occupied by loach minnow. However, loach minnow only occupied 16 (64%) of the 25 1-km reaches, as indicated by the numbers within the classification trees (16/25 reaches with velocity that met threshold had loach minnow occupying them). Of the 153 0.1-km reaches sampled, loach minnow occupied 20 of the 22 (91%) reaches where they were predicted to occur. Locations with adequate habitat without loach minnow were Eagle Creek and the lower San Francisco River. Of the 1246 mesohabitats sampled, loach minnow occupied 34 of the 47 (72%) classified as suitable habitat. Nine 1-km reaches sampled possessed at least one adequate mesohabitat without loach minnow present (Table 1.5). To further illustrate the importance of adequate fine-scale habitat, we found the percent of suitable mesohabitats was positively correlated with loach minnow density across the basin (p-value = 0.005).

Spikedace occupied 14 of 19 1-km reaches (74%) classified as suitable habitat. Five of the locations with suitable broad scale habitat locations were not currently occupied: Tularosa River at Hell's Hole, Eagle Creek, Lower Tularosa River, San Francisco River (not present at the time, have since inhabited this location), and the lower San Francisco River. Fifteen of the 20 (75%) 0.1-km reaches classified as possessing suitable habitat were occupied by spikedace. Of these 0.1 km reaches, Campbell Blue River, Gila River at Grapevine campsite (x2; was present in one of the three 0.1-km reaches), and the lower San Francisco River (x2) did not have spikedace. We were not able to classify occurrences of spikedace at the scale of mesohabitats, thus we were not able to compare densities to suitable habitat for this species.

Discussion

Classification trees described loach minnow and spikedace presence-absence using the same habitat variables across the two broadest spatial scales. As predicted, mean velocity was the environmental factor driving the model for both species. Water velocity influences multiple processes within streams and mediates many essential activities in the life history and well-being of fishes, such as increased food availability and required habitat (Barber & Minckley, 1983;

Facey & Grossman, 1992), and both species exhibit increased growth in high velocity habitats (CH, unpublished data). At the mesohabitat scale, loach minnows appear to require either shallow or very deep habitats with elevated velocity and coarse substrate sizes, aligning with our initial hypothesis. While loach minnow occurrences are very well described at the mesohabitat scale, no variables were able to predict spikedace presence-absence at this scale, contradicting our hypothesis. This is likely because spikedace is a vagile species, moving between a variety of high and low velocity mesohabitats and thus leading to our observation of no variable predicting their presence at this fine scale. Further, we believe higher flow velocities at the broader scales are indicative of higher habitat heterogeneity, potentially suggesting the importance of a variety of mesohabitats at the 0.1 km scale. Loach minnow seemingly require very specific fine scale requirements to be able to persist in a stream, while spikedace might require several mesohabitats at fine scales.

While some studies have highlighted the need to control for spatial scale in fisheries research (Fausch et al. 2002; Hale et al. 2019), others highlight the importance of incorporating multiple scales (Rowe, Pierce, & Wilton, 2009; Cheek et al. 2016; Bruckerhoff, Pennock, & Gido, 2020). The differentiation of velocity required across scales highlights the discrepancy of what these values indicate. Habitat measured at the fine spatial scale predicts specific requirements for an individual at a point in time, while at broader scales, habitat might represent requirements of the population or individuals over larger time scales. Taking a layered approach to characterizing habitat needs for both species, enabled the incorporation of spatial considerations in regard to habitat and expands our current knowledge on species habitat requirements.

Spikedace and loach minnow have been repatriated to locations throughout the Gila River basin with varying degrees of success (Desert Fishes Team, 2003; Robinson, et al. 2009). Our data suggests that some areas where they have been repatriated, but failed, should not be considered in the future. In addition, our examination identified several potentially suitable locations for stocking these species (Tables 1.3-1.5). These determinations were made by considering suitable habitat at all scales, as well as using transect data to identify the percent of habitat that meets the mesohabitat criteria for loach minnow. We found a positive correlation with percentage of suitable habitat in relation to the density of loach minnow across the basin. With this analysis, we determined that Eagle Creek in Arizona (average velocity: 1-km = 0.21 m/s, one 0.1-km reach meeting criteria, 2.39% of stream possessed suitable fine scale habitat) is a potential location to repatriate loach minnow, as this species is not currently found in this stream, although historically it occupied it (Marsh et al. 2003), and it meets the requirements at all spatial scales. We also identified locations that should be avoided in regard to repatriating these species in the future as they do not appear to have suitable habitat. Specifically, Bonita Creek (average velocity: 1-km = 0.02 m/s, no 0.1-km reaches meet criteria), Oak Creek (average velocity: 1-km = 0.14 m/s, no 0.1-km reaches meet criteria), the San Pedro River (average velocity: 1-km = 0.15 m/s, no 0.1-km reaches meet criteria), Clear Creek (average velocity: 1-km = 0.12 m/s, no 0.1-km reaches meet criteria), Saliz Canyon (average velocity: 1-km = 0.12 m/s, no 0.1-km reaches meet criteria), and Redfield Canyon (average velocity: 1-km = 0.02 m/s, no 0.1-km reaches meet criteria) do not have an adequate amount of elevated velocity habitats at broad scales for either species, as well as having no suitable habitat for loach minnow at the fine scale.

With continued alteration of stream habitats coupled with ongoing stream dewatering in the American Southwest, elevated velocity habitats are declining and, in turn, diminishing suitable habitats for native species throughout the basin (Davey, Kelly, & Biggs, 2006; Stradmeyer et al. 2008). With continued loss and alteration of aquatic habitats, identifying the needs of imperiled species, especially at differing scales, is essential for sustaining these populations. For both species evaluated in this study, we found that transects spaced out at equal intervals are the most objective approach to depicting habitats available within a reach. For loach minnow, transect data can be used to calculate the percentage of habitat available for it using the mesohabitat scale model. For spikedace, transects provides a more general measure of habitat suitability that might reflect habitat heterogeneity. Because habitat requirements for both species are very similar at intermediate and broad spatial scales, suitable areas could have the potential for the management of both of these species.

This study presents key variables that need to be considered prior to repatriation of loach minnow and spikedace and how spatial scale affected the variables driving these patterns. The three tier approach, in regard to spatial scale, used during this study provided a robust assessment of a streams ability to support the two species in question. Of the variables included within our models, water velocity had the greatest predictive power. While other factors must be considered in regard to repatriating these species, such as the presence of nonnative fishes, we provide a baseline for the abiotic requirements for these species. We recommend a widespread habitat assessment, using habitat transects, to identify locations throughout the basin where we can expand our current repatriation program and establish more self-sustaining populations of loach minnow and spikedace.

Acknowledgements

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Figures

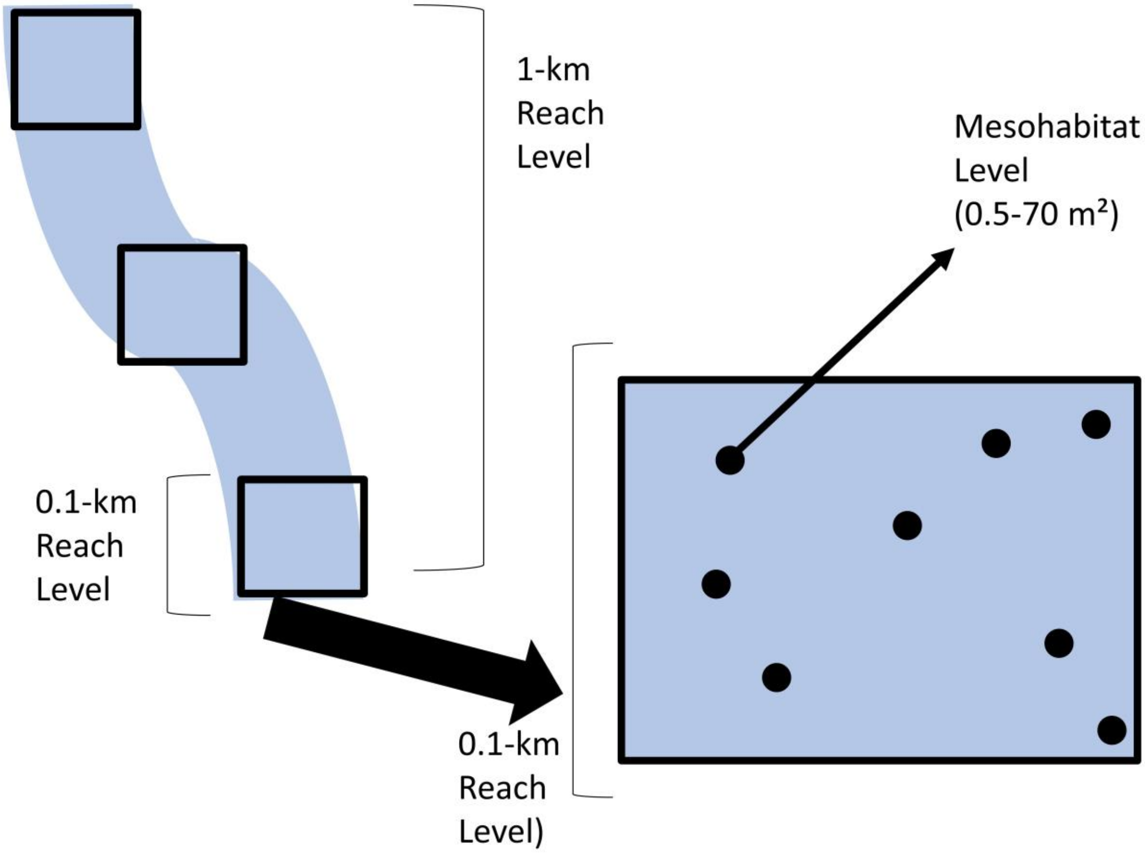

Figure 1.1. Visual representation of the three differing spatial scales sampled at each reach throughout the Gila River basin.

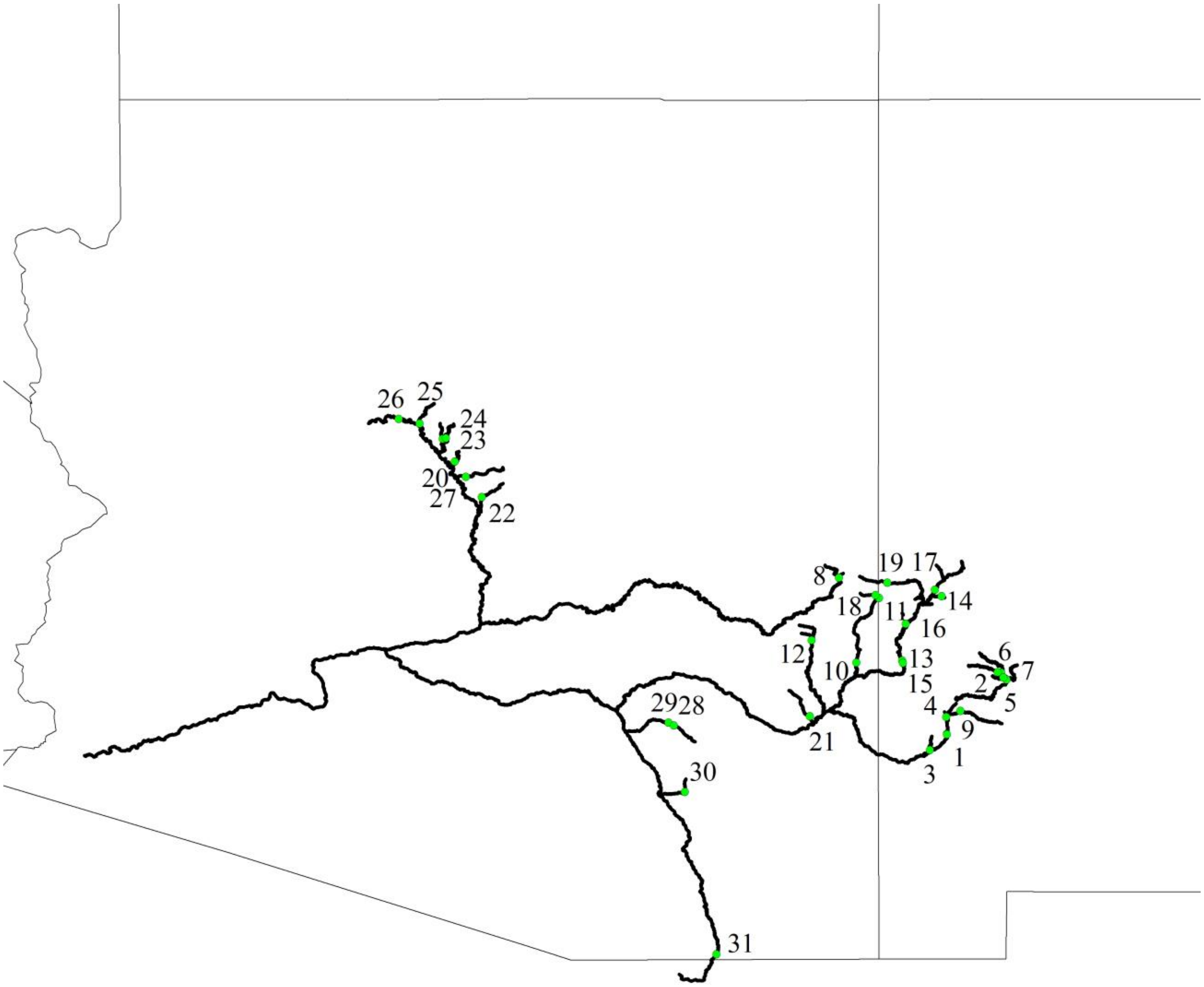

Figure 1.2 Map of reaches sampled throughout the course of this study in 2019 and 2020 in Arizona and New Mexico. Numbers correspond to locations reported on Table 1.3.

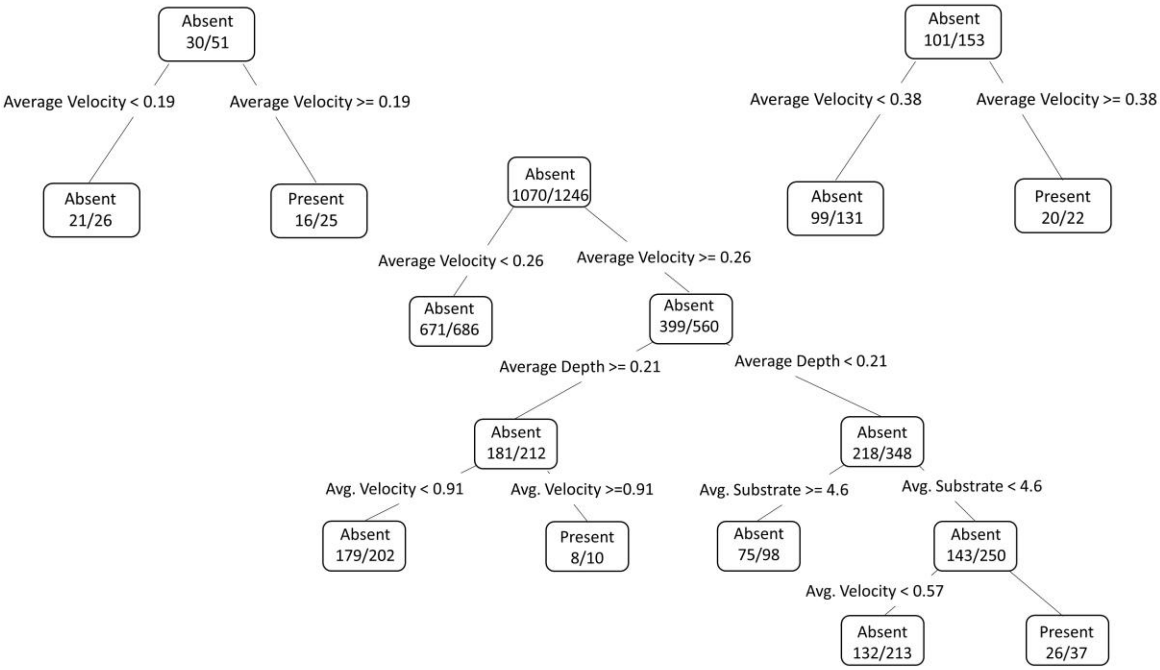

Figure 1.3 Classification tree for the loach minnow describing variables that predict species presence-absence at three differing spatial scales: 1-km reach (top left), 0.1-km reach (top right), and mesohabitat (bottom). Numbers within each box denote the number of observations where this species is truly present or absent (numerator), and the number of habitats that meet the requirements being described with no reference to fish presence absence (denominator).

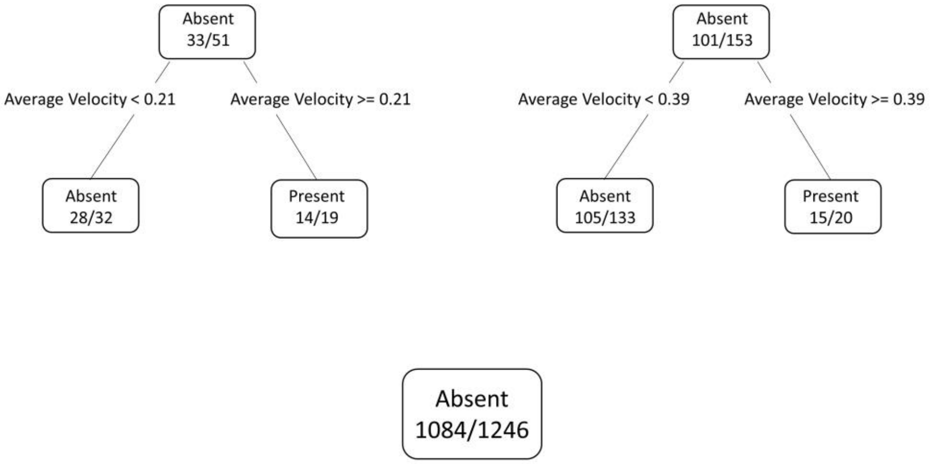

Figure 1.4 Classification tree for the spikedace describing variables that predict species presence-absence at three differing spatial scales: 1-km reach (top left), 0.1-km reach (top right), and mesohabitat (bottom). Numbers within each box denote the number of observations where this species is truly present or absent (numerator), and the number of habitats that meet the requirements being described with no reference to fish presence absence (denominator).

Tables

Table 1.1 List of habitats sampled over the course of this study throughout the Gila River basin. Means and standard deviations are reported for depth, velocity, and substrate sizes.

Habitat	Average Depth (m)	Average Velocity (m/s)	Average Substrate Size	Standard Deviation of Depth	Standard Deviation of Velocity	Standard Deviation of Substrate Size
Backwater	0.12	0.02	2.67	0.17	0.03	1.57
Chute	0.27	0.50	4.04	0.20	0.32	1.66
Eddie	0.19	0.04	3.39	0.14	0.07	1.68
Embayment	0.15	0.02	2.56	0.07	0.04	1.86
Plunge Pool	0.23	0.09	3.33	0.14	0.06	2.89
Pool	0.47	0.05	2.96	0.33	0.08	1.65
Pool-Run	0.28	0.20	3.39	0.18	0.14	1.40
Pool-Shore	0.22	0.04	2.83	0.18	0.09	1.57
Riffle	0.12	0.32	4.14	0.10	0.23	1.06
Riffle-Run	0.15	0.30	4.15	0.11	0.21	1.06
Run	0.19	0.25	3.65	0.15	0.17	1.31
Run-Shore	0.13	0.11	3.32	0.10	0.13	1.46
Shoal	0.12	0.07	3.08	0.12	0.09	1.33

Table 1.2 Values for Mean Gini Decrease for loach minnow and spikedace at all spatial scales in which Classification Trees generated from Random Forest with 500 iterations that were able to describe the presence of these species. Values indicate node purity identifying which variables were able to most accurately predict the presence of these species.

Loach Minnow

Variable	Mean Decrease Gini
Mean Depth	6447
Mean Velocity	21577
Mean Substrate Size	3784

0.1-km Reach

Spikedace

Variable	Mean Decrease Gini
Mean Depth	8719
Mean Velocity	35366
Mean Substrate Size	11876

Variable	Mean Decrease Gini
Mean Depth	24907
Mean Velocity	31721
Mean Substrate Size	6343

1-km Reach

Variable	Mean Decrease Gini
Mean Depth	42263
Mean Velocity	45898
Mean Substrate Size	21163

Variable	Mean Decrease Gini
Mean Depth	4018
Mean Velocity	4534
Mean Substrate Size	1672

Mesohabitat

Table 1.3 Number of 1-km reaches that meet habitat requirements for loach minnow and spikedace. Areas where spikedace currently occur are denoted with the superscript SD, while areas where loach minnow currently occur are denoted with the superscript LM.

Location	Meets Loach Minnow Requirements	Meets Spikedace Requirements	Key in Reference to Site Map
Gila River - Bird Area ^{LM,SD}	Yes	Yes	1
Gila River – Grapevine ^{LM,SD}	Yes	Yes	2
Gila River - Middle Box ^{LM}	Yes	No	3
Gila River - Riverside	Yes	Yes	4
Gila River West Fork ^{LM,SD}	No	No	5
Gila River Middle Fork	Yes	No	6
Little Creek	No	No	7
Black River	No	No	8
Bear Creek ^{LM}	No	No	9
Blue River	No	No	10
Campbell Blue River ^{LM}	No	No	11
Eagle Creek^{SD,}	Yes	Yes	12
Lower San Francisco River	Yes	Yes	13
Lower Tularosa River	Yes	No	14
San Francisco River - Glenwood ^{LM,SD}	Yes	Yes	15
Saliz Canyon	No	No	16
Tularosa River - Hell's Hole ^{LM}	Yes	No	17
Upper Blue River ^{LM}	Yes	No	18
Upper San Francisco River	No	No	19
Wet Beaver Creek	No	No	20
Bonita Creek	No	No	21
Fossil Creek ^{SD}	Yes	Yes	22
Oak Creek	No	No	23
Spring Creek ^{SD}	No	No	24
Sycamore Creek	No	No	25
Upper Verde River	No	No	26
West Fork Clear Creek	No	No	27
Aravaipa Creek ^{LM,SD}	Yes	Yes	28
Lower Aravaipa Creek ^{LM,SD}	Yes	Yes	29
Redfield Canyon	No	No	30
San Pedro River	No	No	31

Table 1.4 Number of 0.1-km reaches that meet habitat requirements for loach minnow and spikedace. Areas where spikedace currently occur are denoted with the superscript SD, while areas where loach minnow currently occur are denoted with the superscript LM.

Location	0.1 km Reaches that Meet Loach Minnow Requirements	0.1 km Reaches that Meet Spikedace Requirements	Total 0.1 km Reaches Sampled
Gila River - Bird Area ^{LM,SD}	0	0	3
Gila River – Grapevine ^{LM,SD}	2	2	3
Gila River - Middle Box ^{LM}	0	0	3
Gila River - Riverside	4	4	6
Gila River West Fork ^{LM,SD}	2	2	6
Gila River Middle Fork	0	0	3
Little Creek	0	0	6
Black River	0	0	6
Bear Creek ^{LM}	0	0	3
Blue River	0	0	6
Campbell Blue River ^{LM}	1	1	6
Eagle Creek^{SD,}	1	0	6
Lower San Francisco River	2	2	3
Lower Tularosa River	0	0	6
San Francisco River - Glenwood ^{LM,SD}	2	2	6
Saliz Canyon	0	0	6
Tularosa River - Hell's Hole ^{LM}	1	0	3
Upper Blue River ^{LM}	0	0	3
Upper San Francisco River	0	0	3
Wet Beaver Creek	0	0	6
Bonita Creek	0	0	6
Fossil Creek ^{SD}	0	0	9
Oak Creek	0	0	3
Spring Creek ^{SD}	0	0	9
Sycamore Creek	0	0	3
Upper Verde River	0	0	6
West Fork Clear Creek	0	0	3
Aravaipa Creek ^{LM,SD}	5	5	6
Lower Aravaipa Creek ^{LM,SD}	3	3	3
Redfield Canyon	0	0	3
San Pedro River	0	0	6

Table 1.5 Number of habitat points and percentage of suitable habitat from transect data that meets the fine scale habitat requirements for loach minnow. Streams that currently have loach minnow present are denoted with the superscript LM.

Location	Points That Meet Loach Minnow Requirements	Total Points Taken	Percent of Suitable Habitat
Aravaipa Creek ^{LM}	82	666	12.31
Lower Aravaipa Creek ^{LM}	32	288	11.11
Fossil Creek	20	276	7.25
Gila River - Riverside ^{LM}	20	342	5.85
Lower San Francisco River*	7	217	3.23
Eagle Creek	10	418	2.39
Spring Creek	6	395	1.52
San Francisco River - Glenwood ^{LM}	5	344	1.45
Gila River - Bird Area ^{LM}	3	209	1.44
Lower Tularosa River	7	499	1.40
Gila River - Grapevine ^{LM}	2	247	1.21
Gila River West Fork ^{LM}	6	544	1.10
Little Creek	3	273	1.10
Upper Verde River	4	565	0.71
Campbell Blue River	3	587	0.51
Gila River - Middle Box ^{LM}	1	196	0.51
Upper San Francisco River	1	282	0.35
Beaver Creek	1	301	0.33
Blue River ^{LM}	1	305	0.33
Upper Blue River ^{LM}	1	333	0.30
Bonita Creek	1	353	0.28
Bear Creek ^{LM}	0	225	0
Black River	0	542	0
Tularos River - Hell's Hole ^{LM}	0	99	0
Middle Fork Gila River	0	266	0
Oak Creek	0	163	0
Redfield Canyon	0	216	0
Saliz Canyon	0	411	0
San Pedro River	0	415	0
Sycamore River	0	264	0
West Fork Clear Creek	0	172	0

Chapter 2 - How Fast it too fast? Water velocity differentially effects growth of four Gila River, native cyprinids

Abstract

Lotic systems are highly heterogeneous, providing a range of habitats for stream fishes. Understanding trade-offs associated with occupying various habitats provides a mechanistic understanding of habitat needs that can be used to evaluate the consequences of habitat loss or alteration. The objective of this study was to identify how velocity affects the growth rates of four native species in the upper Gila River basin, USA: spikedace (*Meda fulgida*), loach minnow (*Tiaroga cobitis*), longfin dace (*Agosia chrysogaster*), and speckled dace (*Rhinichthys osculus*). Elevated velocity was predicted to increase food delivery through drift or through stimulating benthic primary production. Energetic costs of high velocity habitat were predicted to vary with morphology and behavior and would be lowest for speckled dace and loach minnow, because they are adapted to living in interstitial spaces of the substrate in riffles. Spikedace and longfin dace should perform best in moderate velocities, where there is a trade-off between exposure to drifting macroinvetebrates and the energetic costs of maintaining position in the water column. As predicted, growth rates of loach minnow and speckled dace increased in higher velocities but, contrary to our initial predictions, spikedace growth rates also increased in high velocity habitats while longfin dace grew fastest in low velocity habitats. These results indicate that for spikedace, the increased abundance of drifting macroinvetebrates in high velocity habitats out-weighs the energy expenditure, but for longfin dace the energetic costs of occupying high velocity habitats out-weighs the benefit to increased food availability. Our experimental manipulations provide a mechanistic understanding of habitat requirements across species and might inform predictions on how modifications or restoration of riverine ecosystems influence native fish diversity.

Introduction

Habitat use by stream fishes can be influenced by resource availability, energetic costs, predator avoidance, and competition (Werner et al. 1983; Hill & Grossman, 1993; Thompson, Petty & Grossman, 2001). Partitioning of resources along habitat gradients (i.e. depth, velocity, substrate, cover) can facilitate species coexistence (Fausch et al. 2002) and influences the composition of fish assemblages (Ross, 2013). As specific habitats are reduced or eliminated from aquatic systems, species either cannot survive because those habitats are critical for their survival or they are forced into habitats with other species where coexistence may be compromised. The loss or reduction of essential habitats facilitates the biotic homogenization of fish assemblages by reducing native species and potentially favoring the invasion of new species (Walters, Leigh, & Bearden, 2003). Therefore, gaining a mechanistic understanding of species habitat use can aid conservation efforts by providing information to focus habit preservation and restoration activities on biologically relevant attributes.

Water velocity is tied to both abiotic and biotic characteristics of habitats in lotic systems (Frissell et al. 1986). Elevated velocity habitats typically have a higher biomass of benthic macroinvertebrates, due to increased exchange of nutrients that increase algal and insect production (Buffagni & Comin, 2000). While food availability is elevated in these high velocity habitats, energetic costs associated with increased swimming exertion can also be higher, but is not always the case due to body morphology and behavior (Hill & Grossman, 1993). The trade-off between increased food availability and increased energetic costs of high velocity habitats contributes to shaping a species niche in a way that promotes the maximum amount of energy intake (feeding) while minimizing the amount of energy expenditure, although other factors are in play. Thus, the velocity gradients that occur naturally within lotic systems should include habitats to which their life history traits optimize energy intake to expenditure trade-offs. Conversely, a species that are forced to occupy habitat that does not align with its autecology should suffer from negative fitness consequences.

In this study, we used a stream enclosure experiment to investigate how velocity influenced adult growth of four small-bodied cyprinids native to the Gila River basin: longfin dace (*Agosia chrysogaster*), speckled dace (*Rhinichthys osculus*), spikedace (*Meda fulgida*), and loach minnow (*Tiaroga cobitis*) (Figure 2.1). In 2019, this experiment was conducted with speckled dace and longfin dace, while in 2020 it was conducted with the federally-endangered loach minnow and spikedace (U.S. Fish and Wildlife Service, 2012). To visualize our predictions for this study, we modified a conceptual figure that builds upon the work of Hill & Grossman (1993), depicting the differences in energy expenditure, food availability and feeding efficiency in response to a velocity gradient for both drift and benthic feeding fishes (Figure 2.2). Of the focal species, speckled dace and loach minnow are benthic, feeding primarily on benthic macroinvertebrates and are typically found in elevated velocity habitats (Figure 2.2B; Schreiber & Minckley, 1981; Moyle & Baltz, 1985; Bonar, Mercado-Silva & Rogowski, 2010; Pilger, Gido & Propst, 2010). While both of these species are typically found in elevated velocity water, loach minnow is a riffle obligate, very rarely making forays out of these habitats, while speckled dace are not obligate and can be found in a variety of habitats. Longfin dace and spikedace feed higher in the water column and occupy an array of habitats including pools, runs, glides, and riffles (Figure 2.2A; Stefferud, Gido & Propst, 2011). Longfin dace are omnivores feeding on drifting invertebrates, benthic macroinvetebrates, algae, and terrestrial inputs (Bonar, Mercado-Silva & Rogowski, 2010; Pilger, Gido & Propst, 2010). Spikedace are less omnivorous than longfin dace and rely more strongly on drifting invertebrates and terrestrial inputs. We predicted that adult speckled dace and loach minnow would have increased growth in high velocity habitats and the lowest growth in moderate to low velocity habitats (Figure 2.2B). This is due to their morphology and behavior allowing them to remain on the substrate while minimizing energy expenditure. Furthermore, elevated velocity habitats typically have increased production and increased aquatic macroinvertebrate biomass, enhancing fish growth (Hintz & Wellnitz, 2013). We further predicted that longfin dace and spikedace would have the highest growth in moderate velocities and the lowest growth in low and high velocity habitats (Figure 2.2A). This is due to increased energetic cost associated with elevated velocities for a water column species (Hill & Grossman, 1993), as well as the lower amount of resource availability in low velocity habitats (Buffagni & Comin, 2000). While we predicted these species would have similar responses in growth to velocity; spikedace should perform better at marginally higher velocities than longfin dace due to their fusiform body and embedded scales, presumably adaptations to elevated velocity.

Methods

Study Site

This experiment took place in the West Fork Gila River in southwestern New Mexico, USA. The experiment was conducted approximately 0.65 km downstream of the confluence of the West and Middle forks Gila River. The Gila River upstream of our study site has a natural flow regime and the watershed is almost entirely within US Forest Service managed lands. The stream in this area has an average width of 6.9 m and an average discharge of 0.23 m^3/s in the months this experiment was conducted. The upper Gila River possesses a cottonwood-boxelder-willow riparian area in a narrow valley at an elevation of approximately 1700 m.

Enclosure Experiment

In June 2019, three speckled dace (mean total length [TL] = 57.5 mm, SD = 3.4; mean weight = 2.04 g, SD = 0.40) and three longfin dace (mean TL = 55.3 mm, SD = 4.1; mean weight = 1.98 g, SD = 0.43) were placed together (6 individuals per cage) in each of 18 enclosures (0.914 x 0.914 m, 6.35 mm mesh) across a velocity gradient (range: 0.00 – 0.57 m/sec) to test how velocity and aquatic invertebrate abundances affected the growth of these species. Enclosures were maintained for 30 days. Fishes for the experiment were collected using a combination of backpack electrofishing (Smith-Root LR 20B, 200-250 V, Freq: 30, Duty Cycle: 30) and seining (4.6 x 1.8 m, 3.2 mm mesh) from the experimental reach. In July 2020 this experiment was repeated with spikedace (mean TL = 58.8 mm, SD = 3.4; mean weight = 1.8 g, SD = 0.37) and loach minnow (mean TL = 57.5 mm, SD = 3.5; mean weight = 2.00 g, SD = 0.37) across a velocity range of 0.00 – 0.97 m/sec. Enclosures were maintained for 46 days. For all four species, only age-1 individuals over 50 mm were used during this experiment so that fish would not be able to escape through the mesh of the enclosures. Because this study took place during the breeding season for each species, each fish was carefully evaluated to ensure that no gravid individuals were placed in enclosures. Prior to the beginning of the experiment, each individual was anesthetized with MS-222 while being measured, weighed, and uniquely marked (to enable individual identification) with a distinguishable Visible Implant Elastomer (VIE) Tag, and assigned cage placement. To minimize handling, fish were only measured prior to placement in enclosures and following extraction at the conclusion of the experiment. Following measurement, fish recovered in a cooler for a minimum of 10 minutes before being released into enclosures. When mortality occurred in an enclosure, the individual was replaced as long as there was at least 2 weeks remaining in the experiment. All analyses were converted to growth per-day because individuals were held for different lengths of time. Depth, velocity, and substrate composition within each cage were measured every 10 days during the experiment. We filled enclosures with substrate that was representative of the habitat they were placed in (e.g., silt/sand in low velocity habitats and pebble/cobble in high velocity habitats). All cages were given a few large cobbles to provide cover for fish. Cage mesh was cleaned of algae two to five times daily to minimize the effect of algae and debris accumulation on velocity within each enclosure. To estimate drifting invertebrate biomass, drift net samples (0.22 x 0.23 m opening, 1 mm mesh) were taken over thirty minutes in the evening (between 1700 and 1900 hrs) for three to seven nights a week in randomly selected enclosures. Two to three samples were taken in each enclosure over the course of the experiment. In 2019, nets were placed inside enclosures and directly adjacent to enclosures to determine if enclosure mesh reduced the biomass of drifting aquatic invertebrates available to fish. To test if biomass of benthic macroinvertebrates were affected by velocity, core samples were taken every two weeks. Only invertebrates ≤ 6 mm in length were analyzed, because we assumed larger invertebrates would not pass through the mesh. All macroinvertebrates were identified to order, with the exception of common dipterans and hemipterans that were identified to family.

Data analysis

We used mixed-effects models to test for differences in daily growth rates (change in length and change in weight per day) as a function of water velocity. Models were fit using the *lmer* function in the *lme4* package implemented in R, version 3.5.2 (Bates et al., 2014; R Core Team, 2018). We included cage number as a random effect to account for differences in potentially confounding factors such as depth and substrate composition across cages and focused on the fixed effect of velocity. We evaluated significance by comparing an intercept only model to a model with additive fixed effects of velocity using a Wald chi-square test. Further, we used the *lm* function in the *lme4* package to test if drifting and benthic macroinvertebrate biomass increased with velocity. To evaluate potential cage effects on invertebrate biomass, paired t-tests were used to test for differences between the average biomass of samples taken in the enclosures versus those collected in the river for both benthic and drifting invertebrates.

Results

Each species in this experiment experienced significant changes in total length or mass, or both, in response to the velocity gradient, with three species responding positively to increased velocity and one responding negatively. Further, in both years of this study the average velocity within each cage decreased throughout the study (Figure 2.3). In 2019, longfin dace in low velocity enclosures gained more weight compared to individuals in high velocity enclosures, increasing by as much as 0.015 g/d at low velocities relative to high velocities ($p = 0.02$; Figures 2.4 & 2.5). However, no significant differences were observed in length ($p = 0.30$; Figure 2.4). In contrast, speckled dace grew faster as measured in total length ($p < 0.001$; Figure 2.4), increasing by as much as 0.30 mm/d, and in weight ($p = 0.03$; Figure 2.4) increasing by as much as 0.05 g/d in high velocity habitats.

Both spikedace and loach minnow performed better in high velocity habitats in 2020. Spikedace gained more weight in elevated velocities ($p = 0.03$) growing by as much as 0.26 g/d more than in lower velocity enclosures (Figure 2.5). While spikedace weight increased in response to elevated velocity, change in length did not respond to velocity ($p = 0.48$; Figure 2.4). In one enclosure, with an average velocity of 0.57 m/s, spikedace were not able to maintain themselves for more than 24 hours at the beginning of the experiment, potentially indicating a physiological threshold for what this species can tolerate for prolonged periods of time. Lastly, total length ($p = 0.01$) and mass ($p < 0.001$) for loach minnow were positively correlated with velocity (Figures 2.4 & 2.5).

In 2019, biomass of both drifting and benthic invertebrates did not differ between inside and adjacent to the cages. Drifting invertebrates had increased biomass in higher velocity in both the enclosures and the river ($p = 0.008$ & 0.04 respectively), while benthic invertebrates did not respond to velocity in either the enclosures or river ($p > 0.21$; Figure 2.6). In 2020, drifting aquatic invertebrate biomass was 3.6 times greater in high velocity rather than in lower velocity habitats, although a significant relationship was not observed ($p = 0.056$). Benthic invertebrate biomass increased with velocity in 2020 ($p = 0.04$; Figure 2.7). There was a shift in invertebrate community composition with velocity; chironomidae and trichopteran larvae were collected in highest abundance in elevated velocity, while corixid adults were the most abundant species collected in slower velocity habitats. Lastly, t-tests showed that there was no difference in invertebrate biomass of either benthic ($p = 0.29$) or drifting invertebrates ($p = 0.38$) between samples within enclosures and those adjacent to enclosures in 2019.

Discussion

Three of the four species tested in the enclosures experienced increased growth with increasing velocity, confirming our initial hypotheses for loach minnow and speckled dace, but not spikedace. In field studies conducted to evaluate the habitat use of native fish in the Gila River basin, loach minnow occupied habitats had an average velocity of 0.59 m/s (±0.93 SD) and speckled dace occupied habitats with an average velocity of 0.30 m/s (± 0.21 SD; CH, unpublished data), which is similar to the maximum velocities in our field enclosures for loach minnow in 2020 (maximum velocity 0.57 m/s) but not for speckled dace in 2019 (maximum velocity 0.44 m/s). Further, the slope of the relationship between velocity and growth for loach minnow was greater than that for speckled dace or spikedace, indicating loach minnow might gain a larger benefit from high velocity habitats. Whereas both loach minnow and speckled dace are benthic species with a hydrodynamic morphology (e.g. down turned snout, large pectoral fins, and flat ventral), speckled dace can be found in habitats with relatively low velocity while loach minnow are a riffle obligate. Moreover, loach minnow has a reduced swim bladder, a trait not shared with speckled dace (Propst & Bestgen, 1991), providing it an enhanced ability to maintain position and navigate in elevated velocities with minimal energy expenditure.

Linear increase in growth of spikedace with velocity contradicted our expectation of a unimodal distribution in response to a velocity gradient. Spikedace have an extremely streamlined body with deeply embedded scales, adaptations for occupying habitat with elevated velocity. Our results suggest this morphology allows spikedace to occupy elevated velocity habitats, with increased food supply, without exacerbating energetic costs. However, we did have one enclosure, with an average velocity of 0.57 m/s, where spikedace could not sustain themselves for more than 24 hours, and were unable to include this in our analyses. Although we were not able to identify a threshold where energy expenditure outweighed the costs of increased food supply, this observation, albeit only a single enclosure, suggests a threshold response at where this species can no longer maintain itself for extended periods of time. Douglas et al. (1994) observed that in the presence of nonnative red shiner (*Cyprinella lutrensis*), spikedace occurred mainly in higher velocity habitats (mean velocity 0.40 m/s) than when red shiner is not present (mean velocity 0.36 m/s), a marginal difference. Interestingly, the shift to higher velocity was close to the optimal velocities for growth found in our experiment questioning if the shift in habitat was detrimental to the species. While this displacement affects multiple factors in a species life, combined field observations and our results generally suggest a performance benefit associated with elevated velocity habitats for spikedace.

Longfin dace fared best in low velocity habitats, contradicting our hypothesis that they would perform best in moderate velocities and indicating that its well-being is not linked to availability of drifting invertebrates. Field observations suggest longfin dace occupy a range of habitat types with an average overall velocity of 0.30 m/s (SD 0.18; CH, unpublished data)), which is only slightly less than for spikedace and contradicts results from our experiment. While field data shows this species can be found in moderate velocity habitats, the energetic costs of occupying these habitats for prolonged periods of time might offset the benefits for longfin dace. Further, longfin dace is an omnivore (Minckley 1973; Grimm, 1988; Pilger, Gido & Propst, 2010), thus growth rates might not be dependent on biomass of invertebrate prey. We also noted a slight increase in temperatures in lower velocity habitats; lowest velocity enclosure was 2° C warmer than highest velocity enclosure, which serve as a potential benefit for this species if this pushes them closer to their optimal thermal requirements (Bonar, Mercado-Silva & Rogowski, 2010). In contrast to the other species evaluated, the trade-off between energetic costs and resource availability along a velocity gradient are different for longfin dace.

In both 2019 and 2020, the biomass of drifting invertebrates was higher in enclosures with higher velocity, which was not surprising with an overall increase in water volume moving through these cages. In 2019, the biomass of benthic invertebrates did not change with velocity but in 2020 significantly increased with velocity, as reported in other studies (Gibbins, Vericat & Batalla, 2010). It is possible that any increases in benthic invertebrates associated with velocity in 2019 were offset by consumption by fish, which may not have occurred in 2020 because of higher overall production. Thus, higher abundance of invertebrates in high velocity treatments is likely responsible for increase growth rates. Indeed, shifts in assemblage composition towards more chironomidae larvae in high velocity habitats, is also consistent with findings in Pilger et al. (2010), where chironomid larvae are a frequent item in the diet of loach minnow, speckled dace, and spikedace while contributing less to the diet of longfin dace.

This study suggests mechanisms that drive habitat use of different species, highlighting that the two endangered species in the Gila River basin prefer elevated water velocity. Repatriation of spikedace and loach minnow is ongoing and has had varying degrees of success across the basin. We found a comparatively narrow range of velocities influenced growth of native cyprinids; nonetheless there are other factors limiting repatriation success. Increased growth rates of endangered species in higher velocity habitats also might suggest consequences of habitat alteration. Dewatering is known to degrade and cause the loss of certain habitats, particularly those of elevated velocity (Davey, Kelly, & Biggs, 2006; Stradmeyer et al. 2008; Perkin et al. 2015), which might disproportionately affect speckled dace, loach minnow, and spikedace. It has been observed that during dewatering events, fishes that typically occupy riffles are forced to relocate to pool habitats due to the loss of these high velocity areas (Stradmeyer et al. 2008). As velocity changes from what a species prefers the muscle composition, growth, and body condition of an individual can also change over time, and, thus, loss of habitat will negatively affect the individual being displaced (Hill & Grossman, 1993; Young, Cech Jr., & Thompson, 2011). Moreover, as drought is projected to become more common across the American Southwest in the coming decades, which likely will cause diminished water levels in rivers, knowledge of how this affects the habitat and well-being of a variety of species within the region (Morehouse, 2000; Cook, Ault, & Smerdon, 2015) will be critical to their conservation.

Acknowledgements

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Figures

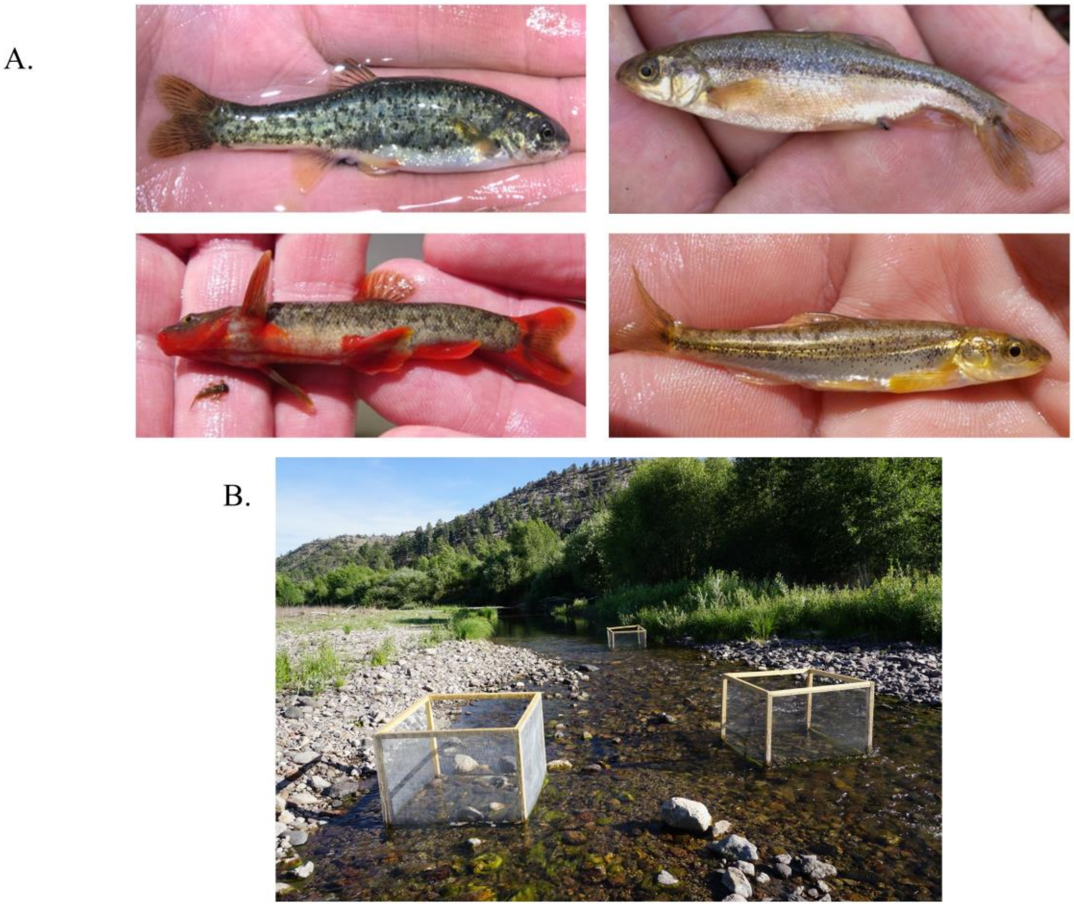

Figure 2.1 The four native species used in the enclosures experiment (A) and the enclosures within the West Fork of the Gila River (B). The four species used in the experiment are: Speckled Dace (top left), longfin dace (top right), loach minnow (bottom left), and spikedace (bottom right).

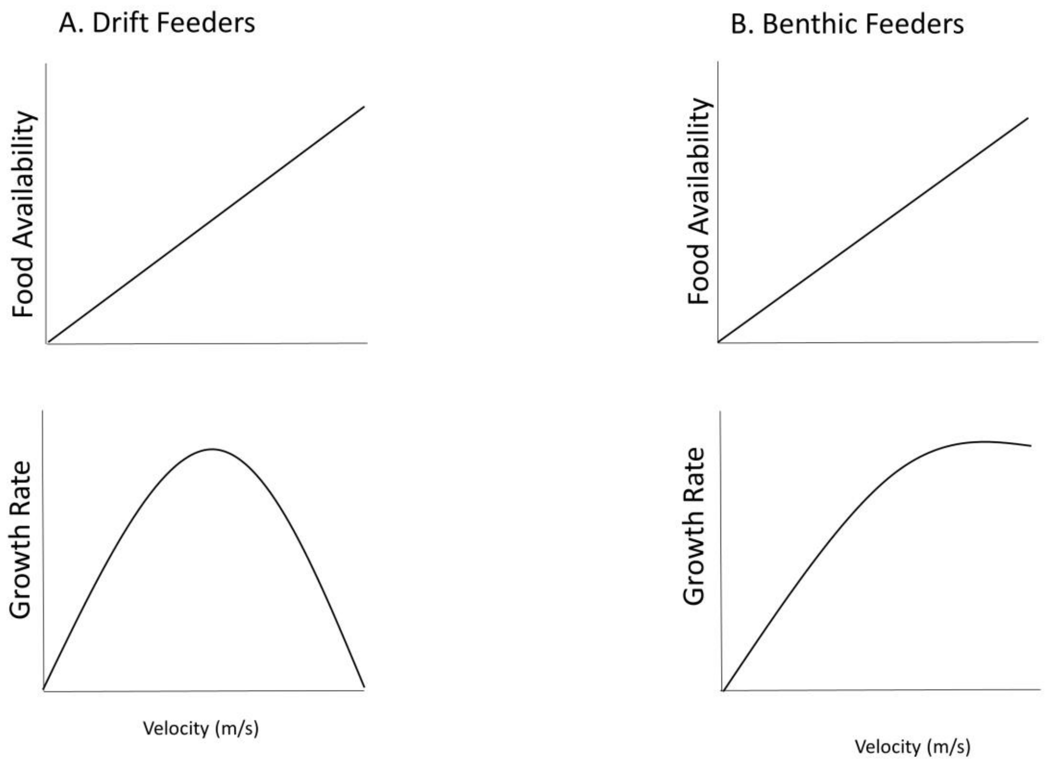

Figure 2.2 A graphical depiction of our predictions in regard to the response of food availability and growth rate of drift and benthic feeders.

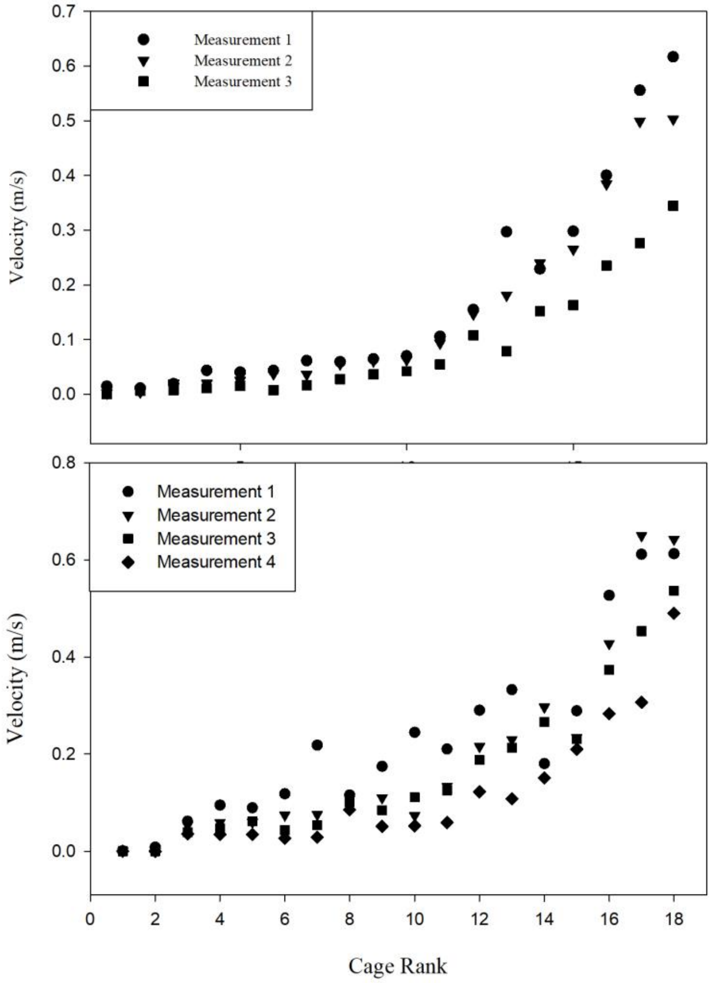

Figure 2.3 Variation in velocity within each enclosure over the course of the study in 2019 (top) and 2020 (bottom). Cage rank (1 = lowest mean velocity enclosure, 18 = highest mean velocity enclosure) is on the x-axis and velocity (m/s) is on the y-axis.

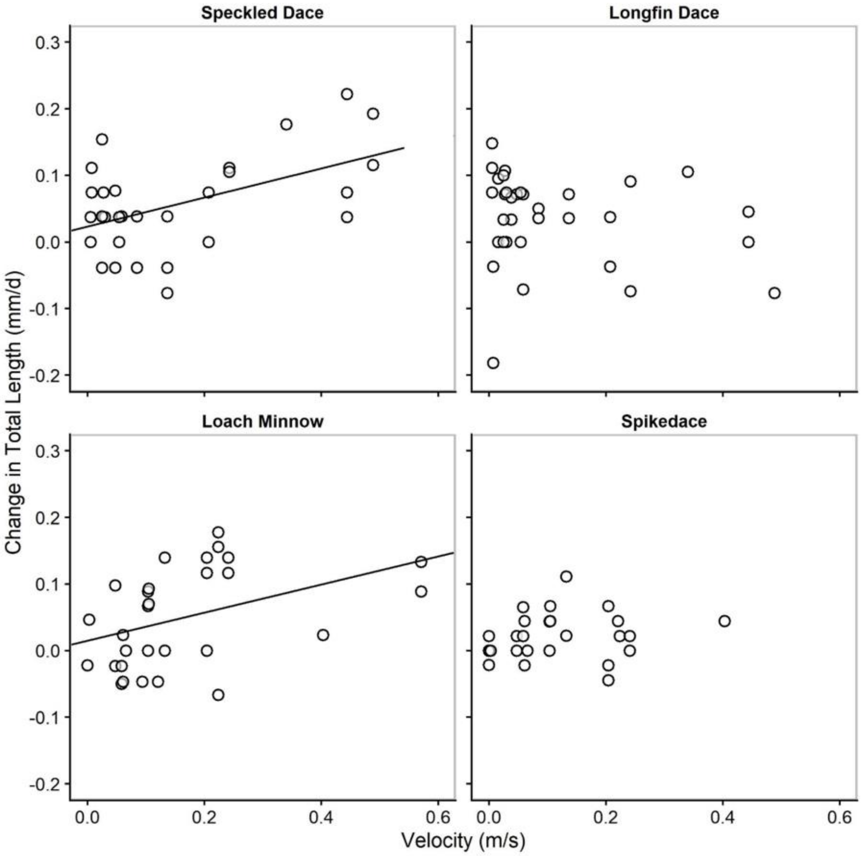

Figure 2.4 Relationship between enclosure velocity and individual growth rate, measured as change in total length (mm/d) between the beginning and end of the experiment for speckled dace, longfin dace, loach minnow, and spikedace. Each dot represents an individual fish and trend-lines are only included for significant relationships.

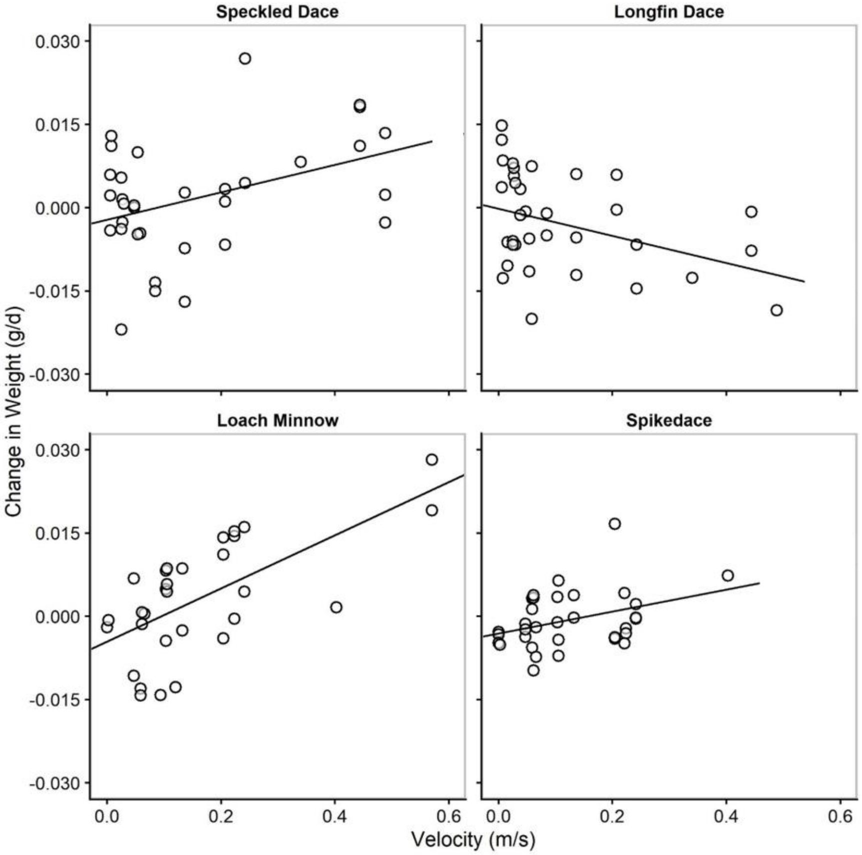

Figure 2.5 Relationship between enclosure velocity and individual growth rate, measured as change in mass (g/d) between the beginning and end of the experiment for speckled dace, longfin dace, loach minnow, and spikedace. Each dot represents an individual fish and trend-lines are only included for significant relationships.

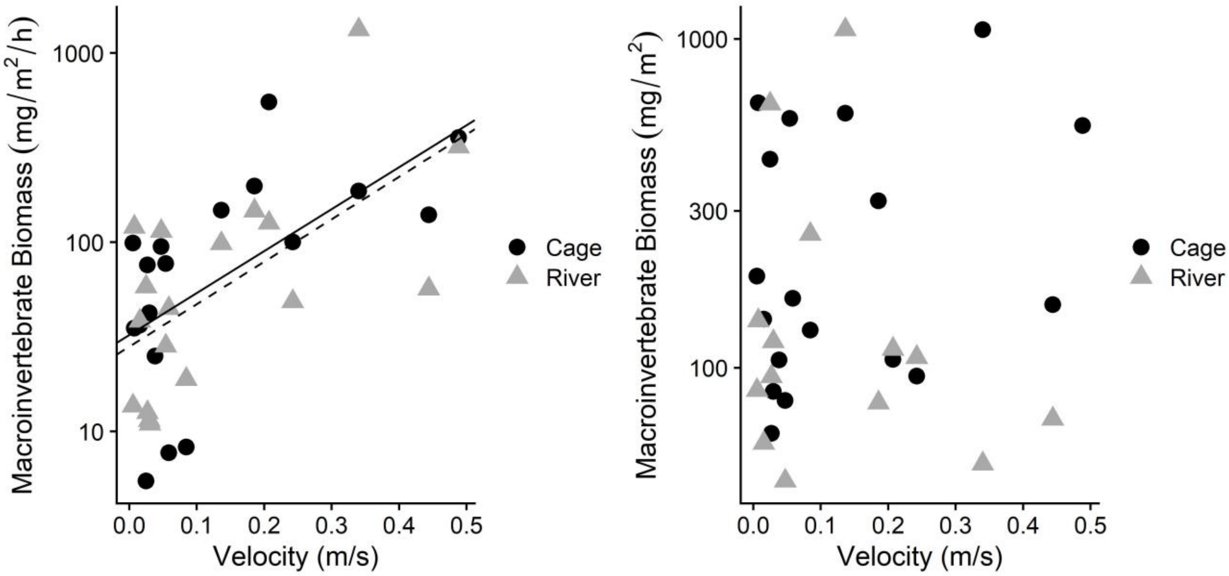

Figure 2.6 Biomass of drifting (left) and benthic (right) macroinvertebrates < 6 mm in enclosures (circles, black) and outside of enclosures (triangles, grey) across a velocity gradient in 2019. Both Y-axes are log transformed.

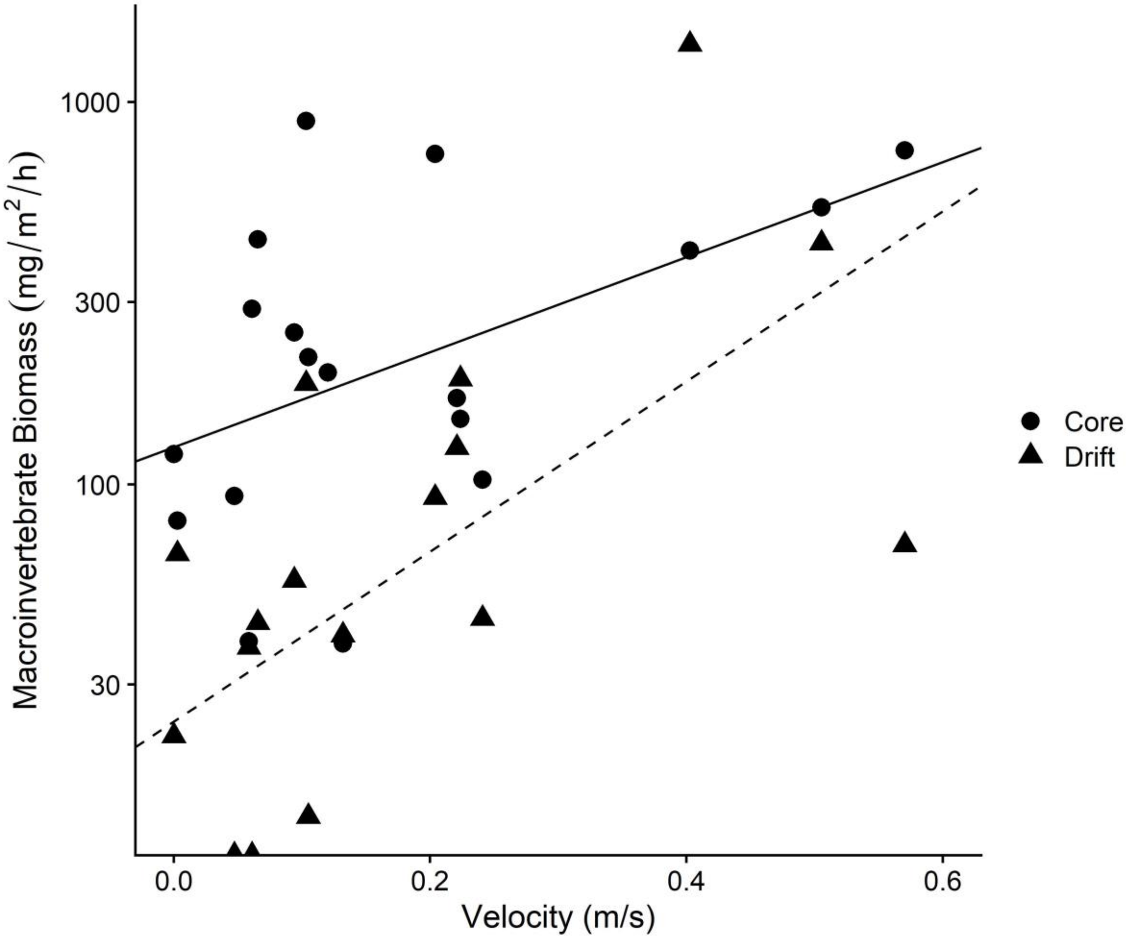

Figure 2.7 Biomass (< 6 mm) of drifting (triangles) and benthic (circles) macroinvertebrates in enclosures across a velocity gradient in 2020. Y-axis is log transformed. Each dot represents the average biomass of invertebrates in each enclosure.

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