THE INVASIVE SPREAD OF THE RUSTY CRAYFISH *FAXONIUS RUSTICUS* AND ITS IMPACTS ON THE ESTABLISHED VIRILE CRAYFISH *FAXONIUS VIRILIS* IN THE MONOCACY RIVER

By

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THESIS

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ABSTRACT

The rusty crayfish (*Faxonius rusticus*) has invaded lakes and rivers across North America, displacing resident crayfish species in the process. *Faxonius rusticus* has been moving down the Monocacy River since at least 2007 displacing the established population of the virile crayfish (*Faxonius virilis*). We quantified changes in the species composition of the crayfish community, size distribution and habitat preferences of crayfish over the length of the Monocacy River in Maryland. Invaded sites experienced an initial increase in *F. rusticus* (> 90% of crayfish) followed by a decrease approximately 5 years post-invasion (40-60 %). *F. virilis* numbers were greatly reduced during the initial invasion period but the population likely persisted due to a size refuge, with a small proportion of *F. virilis* exceeding the maximum size of *F. rusticus*. *Faxonius rusticus'* generalist habitat preferences may allow it to invade more easily to outcompete *F. virilis* by establishing itself in vacant habitats.

DEDICATION

I dedicate this paper to my Family: My parents Paul and Debra for raising me and trying their

hardest to answer the many weird questions I had about animals when I was little, and my

brothers Adam and Jason.

I also dedicate this paper to Lisa, who supported me and listened to me every step of the way and

shared my intense enthusiasm for nature and biology.

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INTRODUCTION

Invasive species are one of the most critical threats to any ecosystem or species today, as invasive organisms can utilize biological advantages they have in specific novel environments and can disturb or eliminate native species and disrupt ecological processes on a large scale (Pejchar & Mooney, 2009). This occurs through a variety of mechanisms such as direct competition, predation, or disruption of a common food source. The impacts on a single native species can potentially lead to subsequent negative effects on other species and the collapse of the original ecosystem. In fact, hundreds of native animal species have been driven to extinction by relatively few invasive species (Doherty et al., 2016). These reductions in ecosystem services greatly impact humans as well through declines in water quality, destruction of crops, and toxic bacterial blooms (Walsh et al., 2016).

Many invasive species impact native species through both predation and competition. Predation by invasive crustacean species may result in extirpation and extinction of a wide range of native animals due to most invasive crustacean species having a generalist diet consuming macroinvertebrates and fish eggs (Hänfling et al., 2011; Morse et al., 2013). The other primary mode of extirpation of native species by invasive species is interspecific competition. Interspecific competition from invasive decapods resulted in declines of native species numbers through direct predation and reduction of important food sources and has been documented multiple times in species such as invasive Asian shore crabs (*Hemigrapsus sanguineus*), green crabs (*Carcinus maenas*), and signal crayfish (*Pacifastacus leniusculus*) (Baillie & Grabowski, 2018; Dunn et al., 2009; Williams et al., 2009).

The rusty crayfish (*Faxonius rusticus*) is a species of freshwater Cambarid crayfish native to streams, lakes, and ponds in North America (U. S. Geological Survey, 2021). *Faxonius rusticus* has a highly generalist diet, consisting of plants, invertebrates, fish eggs, and small amphibians, although nearly 50% of their diet consists of detritus (Lorman & Magnuson, 1978; Lorman Jg, 1982; Momot, 1992; Tran & Manning, 2019). The spread and invasion of *F. rusticus* into surrounding waterways has been well documented by researchers over the past 40 years, with some observations ranging back over 130 years (Olden et al., 2006). *Faxonius rusticus* is believed to be native to freshwater habitats in the Ohio River basin primarily within the states of Ohio, Indiana, and Kentucky, although the exact native range is not well understood (Guiaşu & Labib, 2021). The range has expanded considerably over time, with populations becoming established throughout most of Wisconsin and Minnesota and in many other waterways west of the Mississippi River (Olden et al., 2006; U. S. Geological Survey, 2021). In addition to this, *F. rusticus* has become established in many states in the Mid-Atlantic region, including Maryland, Virginia, Pennsylvania, New York, and New Jersey, likely as a result of introduction via bait buckets by anglers (Hobbs et al., 1989; Kilian et al., 2010; U. S. Geological Survey, 2021).

Faxonius rusticus can alter abiotic factors of the environment through substrate modification, such as a reduction in sedimentation rates and changes in the substrate composition by overturning rocks during foraging and the construction of shelters (Albertson & Daniels, 2016). *Faxonius rusticus* invasions have also been linked to decreases in macrophyte biomass and abundance as this species consumes and destroys significantly more foliage than native crayfish and high *F. rusticus* densities can result in the complete eradication of macrophytes (Lodge & Lorman, 2011; Olsen et al., 1991; Peters et al., 2008). The destruction of macrophytes and increased substrate disturbance can lead to a reduction of refugia for both native crayfish

species and other macroinvertebrates, as well as a reduction in food sources for native species that feed on plants and periphyton (Lodge & Lorman, 2011; Peters et al., 2008).

The introduction of *F. rusticus* has been linked to consistent reductions in macroinvertebrate populations in multiple lake and river systems and it has been shown consuming and damaging gastropods at a far higher rate than its congeners, leading to increases in primary production due to grazer removal (Hanson et al., 1990; Mccarthy et al., 2006; Nilsson et al., 2012; Olsen et al., 1991). These changes in macroinvertebrate abundance have led to both top down effects due to grazer removal, and bottom-up trophic effects reducing the abundance of fish species that feed on macroinvertebrates (Charlebois & Lamberti, 1996; Kreps et al., 2016). In addition, invasive *F. rusticus* consume fish eggs at a much higher rate than native congeners and is correlated to decreased fish abundance (Morse et al., 2013; Wilson et al., 2004). These effects on macroinvertebrate and fish populations provide examples of how *F. rusticus* impacts biotic communities when it is introduced to lake and stream ecosystems.

Faxonius rusticus has been observed outcompeting and extirpating *Faxonius virilis* populations regardless of whether the *F. virilis* populations were native to the area or established before the rusty crayfish invasion. In Wisconsin lakes where *F. virilis* is native the elapsed time until extirpation of *F. virilis* has varied from lake to lake ranging from five years to over 17 years (Lodge et al., 1986; Olsen et al., 1991). One study found that the invasion of *F. rusticus* led to the near disappearance of both *F. virilis* and *F. propinquus*, another native crayfish species (Wilson et al., 2004). Most of these observations and studies were performed in lakes, and the displacement of native species by *F. rusticus* may be even more severe in stream environments, with models predicting *F. virilis* having a 10% greater probability of being displaced by *F. rusticus* in Wisconsin streams when compared to Wisconsin lakes (Olden et al., 2011).

Faxonius rusticus tends to be far more aggressive than its congener *F. virilis* despite *F. rusticus'* smaller body size (Capelli & Munjal, 1982). *Faxonius rusticus* won all direct aggression interactions against *F. virilis*, causing *F. virilis* to flee in all direct altercations, and was shown to outcompete *F. virilis* for shelter occupancy (Capelli & Munjal, 1982). *Faxonius rusticus* also dominated *F. virilis* in fights roughly 85% of the time regardless of whether or not each species was from native or invasive populations (Glon et al., 2018). Despite these results, observations indicate that *F. rusticus* is not directly dominant to *F. virilis* in the Monocacy river ecosystem when both species are matched by size and observed for directly aggressive behavior (Wright, 2011). Although direct fighting interactions may not be in favor of *F. rusticus* in the Monocacy river, *F. rusticus* may alternatively be dominant due to its ability to outcompete *F. virilis* for both shelter and food, as such events have been observed more directly by several studies (Capelli & Munjal, 1982; Garvey et al., 1994; Hill & Lodge, 1999; Pintor & Sih, 2009). In this way *F. rusticus* may be able to outcompete *F. virilis* in the Monocacy River ecosystem in a more indirect way as opposed to direct methods such as individuals directly combating each other.

When *F. rusticus* and *F. virilis* cohabitate in a mesocosm with a limited food source, *F. rusticus* always outcompetes *F. virilis* for food, and in more direct observations *F. rusticus* pirated food that was already captured by *F. virilis* (Hill & Lodge, 1999). The act of stealing food directly from other crayfish by invasive individuals of *F. rusticus* has been observed before in competitions with *F. propinquus* (Pintor & Sih, 2009). *Faxonius rusticus* also consistently outcompetes *F. virilis* for shelter when both species are given a single sheltering structure, and *F. rusticus* will even evict *F. virilis* from the shelter if *F. virilis* has been given a 30-minute

acclimation period to settle into the shelter before *F. rusticus* is introduced(Capelli & Munjal, 1982).

The eviction of *F. virilis* from shelters by *F. rusticus* may combine with predation to reduce *F. virilis* populations in invaded waters (Garvey et al., 1994). In an environment with limited shelters and the presence of predatory largemouth bass (*Micropterus salmoides*), *F. rusticus* displaced *F. virilis* individuals from their shelters exposing *F. virilis* to this predator. In addition to this, the act of swimming away from competitors made *F. virilis* far more susceptible to predation by fish, leading to *F. virilis* being consumed at a far higher rate than *F. rusticus* in mesocosm experiments (Garvey et al., 1994).

In situations involving fish predation where *F. virilis* was consumed at a far higher rate than *F. rusticus*, the predators selected prey based on chela size, favoring prey with proportionally smaller chelae (Roth & Kitchell, 2005) . *Faxonius rusticus* has proportionally larger chelae than *F. virilis*, and chela length has a positive effect on aggression in both *F. rusticus* and *F. virilis* (Glon et al., 2018). The typically larger chela size in *F. rusticus* may determine the winner in competitions for limited shelters between *F. rusticus* and *F. virilis*, and also result in differential predation on each species by fish, with both of these factors interacting to produce a strong negative effect on *F. virilis* in *F. rusticus*-invaded waters (Garvey & Stein, 1993; Roth & Kitchell, 2005).

Denial of specific macrohabitats by *Faxonius rusticus* is a potential mechanism for outcompeting *Faxonius virilis* (Garvey et al., 2003). *F. virilis* was seen actively seeking cobble-based substrate for shelter. It was also noticed that *F. rusticus* numbers increased in a region only if the substrate was > 16% cobble, indicating that *F. rusticus* desired it for shelter as well, and *F. virilis* and *F. propinquus* was displaced from the cobble by *F. rusticus* (Garvey et al., 2003). In a

separate study *F. virilis* was found in cobble in streams where the *F. rusticus* was absent, but in nearby streams where the *F. rusticus* was present, *F. virilis* was relegated to patches of macrophytes. *Faxonius rusticus* also destroys macrophytes, reducing the already small refuges that *F. virilis* could use in *F. rusticus*-infested waters (Smith et al., 2019).

Deep water is a potential macrohabitat that may provide *F. virilis* a spatial refuge from *F. rusticus* (Jansen et al., 2009). In Canadian lakes, although both species favor and compete for cobble-based substrate, *F. virilis* was found more often in areas greater than eight meters in depth (Jansen et al., 2009). *Faxonius rusticus* was not found below eight meters and would likely stay away from waters near or below the thermocline. This may be due to *F. rusticus* having a higher metabolic rate than *F. virilis*, indicating that it has a higher ideal temperature than *F. virilis* and would thus be averse to colder water (Mundahl & Benton, 1990). This higher metabolism has been theorized to assist in *F. rusticus*'s invasiveness allowing it to gather resources at a faster rate but may also provide *F. virilis* with a temperature refuge by preventing *F. rusticus* from tolerating colder water temperatures (Jansen et al., 2009).

Most of the reported observations in literature on *F. rusticus* invasion dynamics have been in lentic freshwater ecosystems such as Wisconsin lakes, and there is a paucity of research on *F. rusticus* invasions in river systems. One study examined Illinois waterways and found that *F. rusticus* tended to completely displace other crayfish species including *F. virilis* when invading streams, with *F. rusticus* eventually being the only crayfish species present at most of these river sites (Taylor & Redmer, 1996). The remainder of studies examining *F. rusticus* invasion dynamics in rivers and streams only monitored the rate of expansion, with average downstream speeds of 20 km yr^{-1}, 13.5 km yr^{-1}, and 3.7 km yr^{-1} (Messager & Olden, 2018; Momot, 1996; Sorenson et al., 2012). With *F. rusticus* spreading into rivers and streams and very

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few recorded observations of their impact on lotic ecosystems, further research, and observation of *F. rusticus* invasion dynamics in rivers would be valuable for managing and protecting these environments.

The Monocacy River is a sixth order tributary of the Potomac River, which empties into the Chesapeake Bay. The river begins in southern Pennsylvania and runs south through Maryland until meeting the Potomac at Maryland's border with Virginia. The Allegheny crayfish (*Faxonius obscurus*) and the spinycheek crayfish (*Faxonius limosus*) are native to the Monocacy River, being historically common throughout surrounding regions as well (Kilian et al., 2010). The virile crayfish (*Faxonius virilis*) is native to the Midwestern United States but has been present in Maryland rivers since the 1960's, and since its introduction to the Monocacy River, it has displaced *F. limosus* entirely and has almost completely displaced the native *F. obscurus* (Kilian et al., 2010). *Faxonius virilis* is now present in much of the Monocacy River and can be considered a resident species, being non-native but well established in the ecosystem.

Since the release of *F. rusticus* in the northern portion of the Monocacy River in southern Pennsylvania, the species has spread downstream into Maryland waters, and was first reported at the Sixes Bridge site in 2007 (Kilian et al., 2010, 2012) (Figure 1). Preliminary work by E. R. Annis (unpublished) suggested that *F. rusticus* may be displacing the resident *F. virilis* from its preferred macrohabitats in the Monocacy River as the invasion front spreads further downstream. In the Monocacy River *F. virilis* YOY had a higher mortality rate and lower growth rate in regions with *F. rusticus* than regions without *F. rusticus*, and *F. rusticus* YOY and juveniles had a higher growth rate in sites with *F. virilis* than in sites without *F. virilis*, indicating that *F. virilis* YOY are possibly consumed by *F. rusticus* (Selckmann, 2010).

Previous research in the Monocacy river has also shown that *F. virilis* is dominant to *F. rusticus* in size-matched trials, with *F. virilis* winning most aggression trials when matched with *F. rusticus* with a > 10% difference in size, indicating that size-matched direct competition is likely not occurring in the Monocacy River, but it is possible that interactions between the two species in the Monocacy River are not size-matched, allowing larger *F. rusticus* to win against smaller *F. virilis* individuals (Wright, 2011). A size refuge may exist for *F. virilis* in the Monocacy River that could allow a population of large-bodied (> 28 mm CL) *F. virilis* to persist in *F. rusticus*-present sites. Even if *F. rusticus* is dominating smaller *F. virilis* in non-size-matched trials, a small number of *F. virilis* individuals attaining a body size great enough to remove them from competition with smaller sized *F. rusticus* (Annis unpublished).

We examined the relative abundance of *F. rusticus* and *F. virilis* at sites along the length of the Monocacy river in Maryland to determine changes in the range and spread of both *F. rusticus* and *F. virilis* from 2009 to 2021. Based on previous data, we expected that *F. rusticus* would remain at a high density at invaded sites, relegating *F. virilis* to a small percentage of the crayfish community composition. We also quantified the invasion rate of *Faxonius rusticus* in the Monocacy River by comparing the present location of the invasion front to the previous location. We also searched for evidence of a size refuge of *F. virilis* in areas where *F. rusticus* is present. The presence of large-bodied *F. virilis* at *F. rusticus*-present sites many years post-invasion would indicate a stable population that is still persisting as a result of size refugia. We also determined if displacement of *F. virilis* from favorable habitats by *F. rusticus* was occurring by comparing the relative abundance of each species in macrohabitats at each site. Differential abundance of *F. virilis* between different macrohabitats as well as between *F. rusticus*-present sites versus non-*F. rusticus*-present sites would indicate that *F. rusticus* is likely denying use of

specific macrohabitats to *F. virilis* at these sites. We predicted that *F. virilis* would likely prefer

pools and vegetation patches based on previous observations (Annis unpublished).

METHODS

Study Sites

We sampled at multiple sites along the length of the Monocacy River in MD between 2009 and 2021 to document the location of the invasion front, changes in species composition, population structure, and sex ratios. The study was completed over a period of several years with many student participants, and collections in 2009, 2010, 2011, 2016, and 2021 (See Figure 1, Table 1). The Department of Natural Resources sampled crossings from 2008 to 2013 to identify locations of the invasion front, and data from those samplings were used in this study. Sites were chosen along a 79-kilometer stretch of the Monocacy River and identified by the road name of the nearest bridge crossing extending from Route 140 (upstream) to Park Mills (downstream). Sites in the 2009-2011 years were selected to span the advancing invasion front to include a single site with an established population of *F. rusticus*, a site with only *F. virilis*, and a site where the invasion was in process. In subsequent years the initial sites were revisited, and new sites were selected further downstream to track the invasion front. In 2021, 10 sampling sites were selected with the intent to provide 5 sites with established populations of *F. rusticus* and 5 sites with only *F. virilis*.
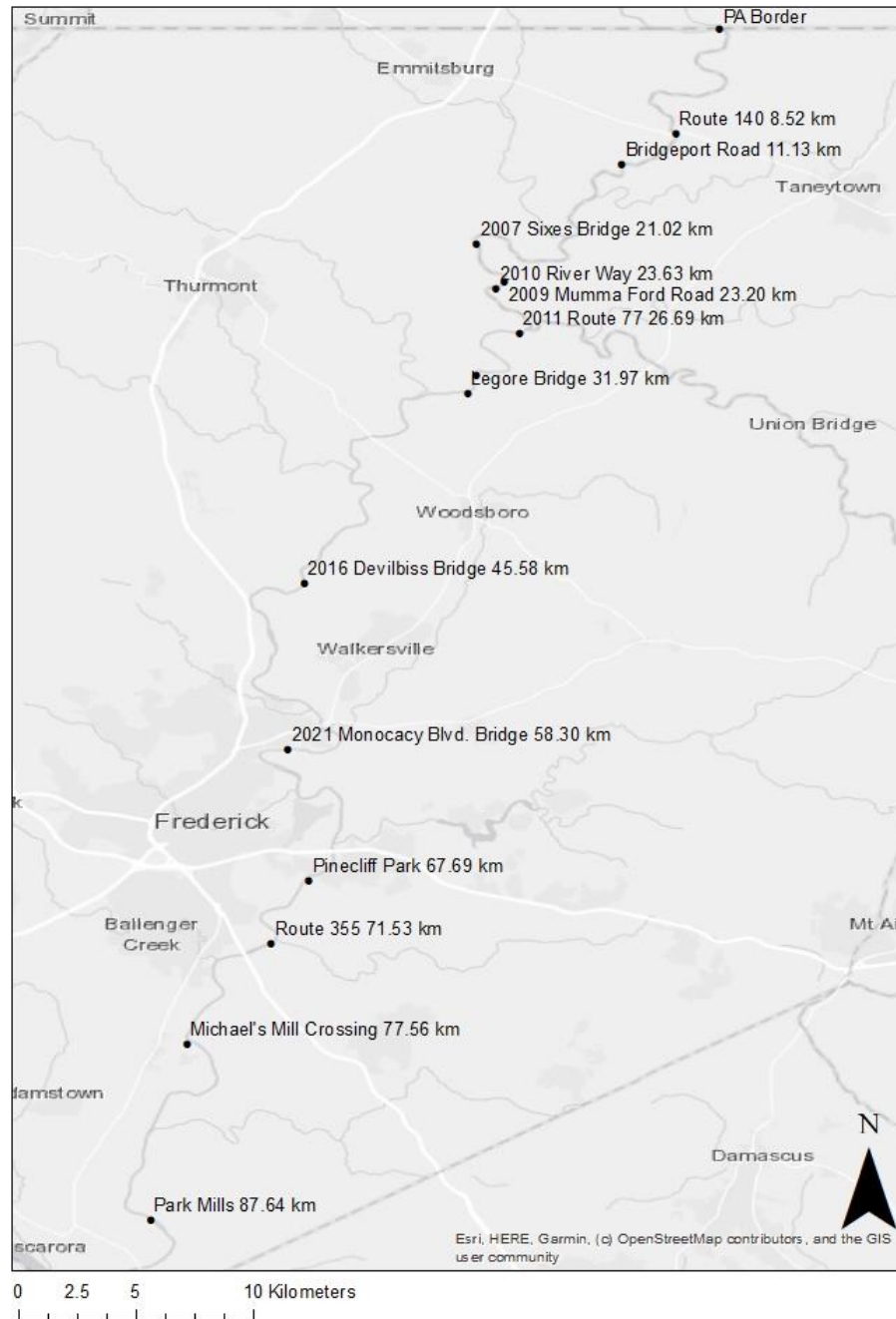
Figure 1: A map of the Monocacy River surrounding Frederick, MD with sampling sites denoted with circular markers with labels including the site name and cumulative river kilometers from the Maryland-Pennsylvania border. Sites where the invasion front was located are marked by the year.

Table 1: The coordinates, date of collection, and sample sizes (in quadrats) for each sampling period from 2009 to 2021 in the Monocacy River.

Site	Coordinates (lat/long)	2009		2010		2011		2016		2021	
		Dates	n	Dates	n	Dates	n	Dates	n	Dates	n
Route 140	39°40.652'N 77°14.076'W	6/3/2009	55	6/4/2010	25	8/2/2011	16	6/15/2016	12	8/16/2021	15
		6/8/2009		6/7/2010							
		6/23/2009									
		6/25/2009									
Sixes Bridge	39°38.219'N 77°17.905'W	6/16/2009	60	6/8/2010	25	6/15/2011	25				
		6/22/2009									
		6/24/2009									
Mumma Ford Road	39°37.391'N 77°17.964'W	6/9/2009	63	6/13/2010	25	8/1/2011	15	6/13/2016	12	8/12/2021	15
		6/16/2009									
		6/17/2009									
		7/11/2009									
Route 77	39°36.197'N 77°17.632'W					8/4/2011	15	6/15/2016	12	8/26/2021	15
LeGore Bridge	39°34.860'N 77°18.802'W							6/20/2016	12	8/15/2021	15
Links Brige	39°38.172'N 77°17.904'W							6/22/2016	12		
Devilbiss Bridge	39°30.247'N 77°22.382'W							6/21/2016	12	8/11/2021	15
Biggs Ford	39°28.824'N 77°23.288'W							6/22/2016	12		
Monocacy Blvd.	39°26.615'N 77°22.975'W							6/21/2016	12	7/20/2021	15
Pinecliff Park	39°23.721'N 77°22.301'W									8/2/2021	15
Route 355	39°22.126'N 77°23.468'W	6/29/2009	15							8/3/2021	15
Michael's Mill	39°19.823'N 77°25.129'W	7/1/2009	50	6/14/2010	25	6/9/2011	25			8/10/2021	15
		7/2/2009		6/15/2010							
		7/6/2009		6/16/2010							
		7/10/2009									
		7/13/2009									
Park Mills	39°15.783'N 77°26.135'W									8/25/2021	15

Sampling locations were selected to incorporate the five macrohabitat types (riffles, glides, runs, pools, and stands of vegetation) and an equal number of quadrat samples were taken in each of the macrohabitats. Macrohabitats were identified qualitatively based on characteristics described by Dodds (2002). At the site of each quadrat sample, we recorded the flow rate and depth (both using an average of 5 measurements), conductivity, and temperature using a flowmeter (Swoffer 3000 or OTT MF pro), a meterstick, and a YSI Pro2030 probe.

Sample Collection and processing

Each sample was collected using a quadrat sampling device consisting of a 1 m x 1m square wooden frame with 0.5m legs, with netting on all sides weighed down with chains and a downstream codend made of netting to collect the crayfish (Figure 2). We selected sample collection locations by identifying spots in each macrohabitat with the most suitable substrate for crayfish, generally consisting of rocks approximately between 10 and 50 cm (coarse cobble to fine boulders according to the Udden-Wentworth grain-size scale) to ensure substrate type consistency, outside of pools and vegetation patches which had varying substrates and were more defined by flow rate and vegetation respectively. Sample collection was performed by placing the quadrat sampler in a suitable region of substrate and lowering the weighed netting down to the riverbed, with the codend facing downstream. We agitated and raked the substrate for 30 seconds and manually removed larger rocks to expose crayfish before using paddles to sweep the water downstream to drive any remaining crayfish into the codend. After the codend was removed from the water we removed all crayfish including adults and YOY (young-of-year) and sealed them in plastic bags and kept on ice until processing. Crayfish were identified to species and sex, carapace length (CL) was measured, and they were examined for notable damage or injury such as regenerating chelae and damaged rostrums. Specimens were frozen for potential future study.

Data Analysis

The invasion front was defined as the furthest downstream site with a confirmed presence of *F. rusticus* and the average speed of the front's advancement in km yr^{-1} was determined by dividing the distance between two invasion fronts with the elapsed time and taking the average of these multiple front speeds. The density of each species at each site was calculated for both 2021 and all previous collection years (2009, 2010, 2011, and 2016), and compared to illustrate changes in species composition and density at each site over time. For density calculations, the
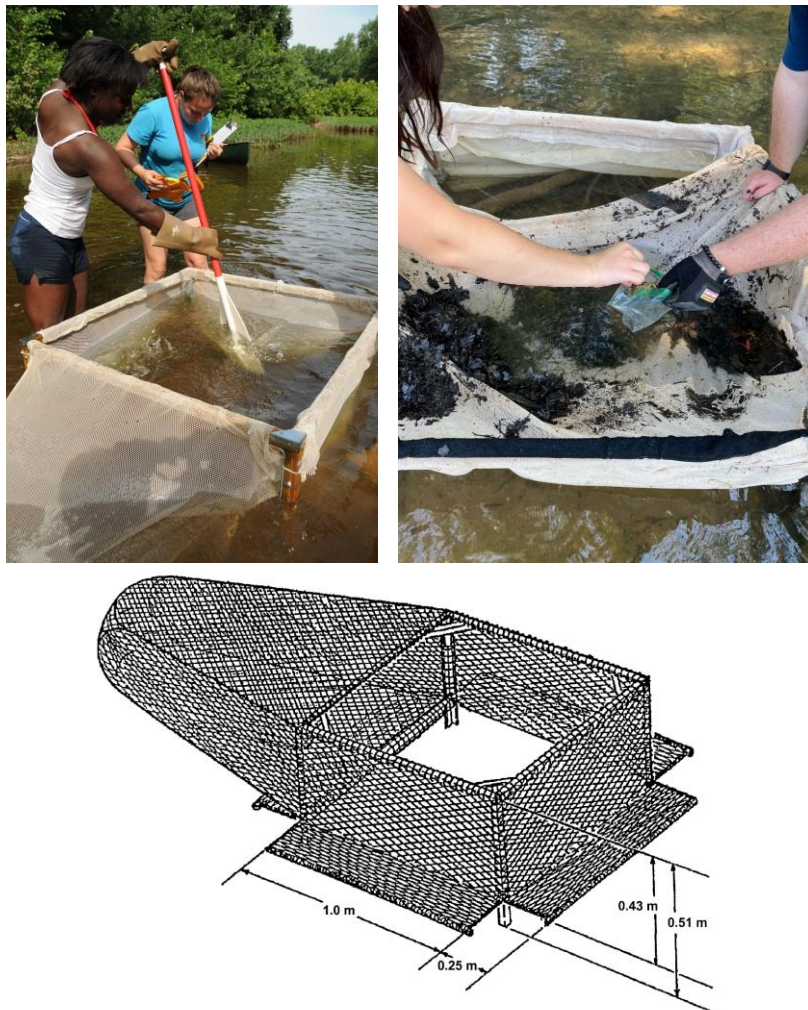

Figure 2: Students paddling water into the codend (left), manual removal of crayfish from the codend (right), and a diagram of the quadrat sampling device (bottom) (Students pictured: Meghan Coulbourne, Katie Geiger, Kierstyn Higgins, and Alex Marinelli, Sampler diagram from R. J. DiStefano et al., 2003).

YOY were removed from each sample to account for size differences due to sampling at different times throughout the season using carapace lengths described by Selckmann (2010).

To determine macrohabitat usage of both *F. rusticus* and *F. virilis*, we divided the 10 sites in 2021 into 6 sites with *F. rusticus* and 4 sites without *F. rusticus*. Kruskal Wallis tests were conducted using SPSS software to determine the effect of site and macrohabitat type on density of *F. virilis* in both *F. rusticus*-present sites and *F. rusticus*-absent sites, as well as *F. rusticus*, and *F. obscurus*. We performed a series of pairwise comparisons between macrohabitat types to identify statistically significant differences.

The carapace lengths of both *F. virilis* and *F. rusticus* individuals collected at *F. rusticus*-present sites were arranged in a histogram with 1 mm size bins to determine the size classes of persisting *F. virilis* in order to find evidence of a size refuge. We used length frequencies of persisting *F. virilis* to determine if they reached a size refuge above the maximum size of *F. rusticus*.

RESULTS

Downstream Advancement

In 2021, *Faxonius rusticus* was observed as far downstream as Monocacy Boulevard and made up nearly 40% of the total crayfish population at that site (Table 2, Figure 3). The invasion front had expanded downstream since their last observation in Devilbiss in 2016. *Faxonius rusticus* moved downstream from the first observed site near Sixes Bridge Road in 2007 to Monocacy Blvd in summer 2021; a distance of 37.29 km in 14 years and a rate of downstream expansion of 2.66 km yr^{-1} (SD = 1.12)(Figure 1).

Species Composition and Abundance

The species composition of the crayfish assemblage in *Faxonius rusticus*-invaded waters was characterized by an increase followed by a decrease in *F. rusticus* density. At Route 140, *F. rusticus* made up nearly 95% of the crayfish assemblage before decreasing to 60% 5 years later (Figure 4). Similar decreases in *F. rusticus* numbers after initial invasion were observed at Mumma Ford Road, Route 77, and LeGore Bridge, indicating an initial spike in *F. rusticus* individuals followed by a reduction. The percentage of *F. rusticus* in 2021 at Devilbiss Bridge and Monocacy Blvd. was higher than it was in 2016.

The Route 355 site showed a reduction in *F. obscurus* abundance and an increase in *F. virilis* abundance since 2009 (Figure 4). In 2021, species composition in sites without *F. rusticus* showed *F. virilis* being high in concentration at Pinecliff Park, but further downstream the composition shifted to a higher concentration of *F. obscurus* than *F. virilis*, indicating a possible invasion front of *F. virilis* (Table 2).
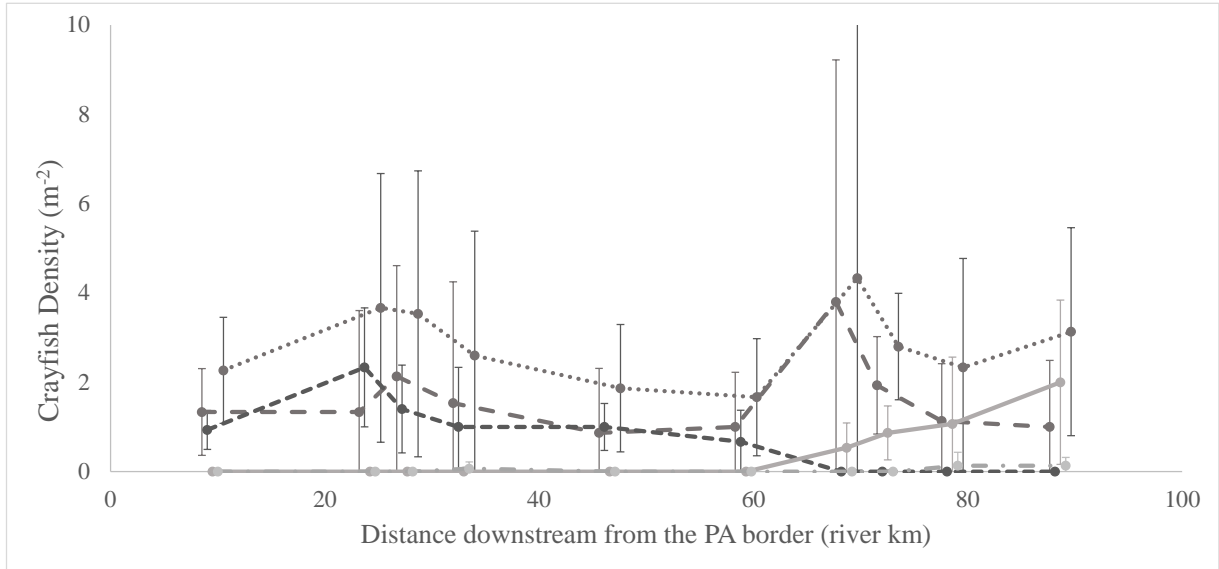
Figure 3: The average density of crayfish species *Faxonius rusticus* (square dotted line), *Faxonius virilis* (dashed line), *Faxonius obscurus* (solid line), and *Cambarus bartonii* (dot and dashed line) as well as the total crayfish density (round dotted line) at distances downstream from the Pennsylvania border in cumulative river kilometers in the Monocacy River in 2021. Error bars denote standard deviations, and the downstream distances have been offset for clarity.
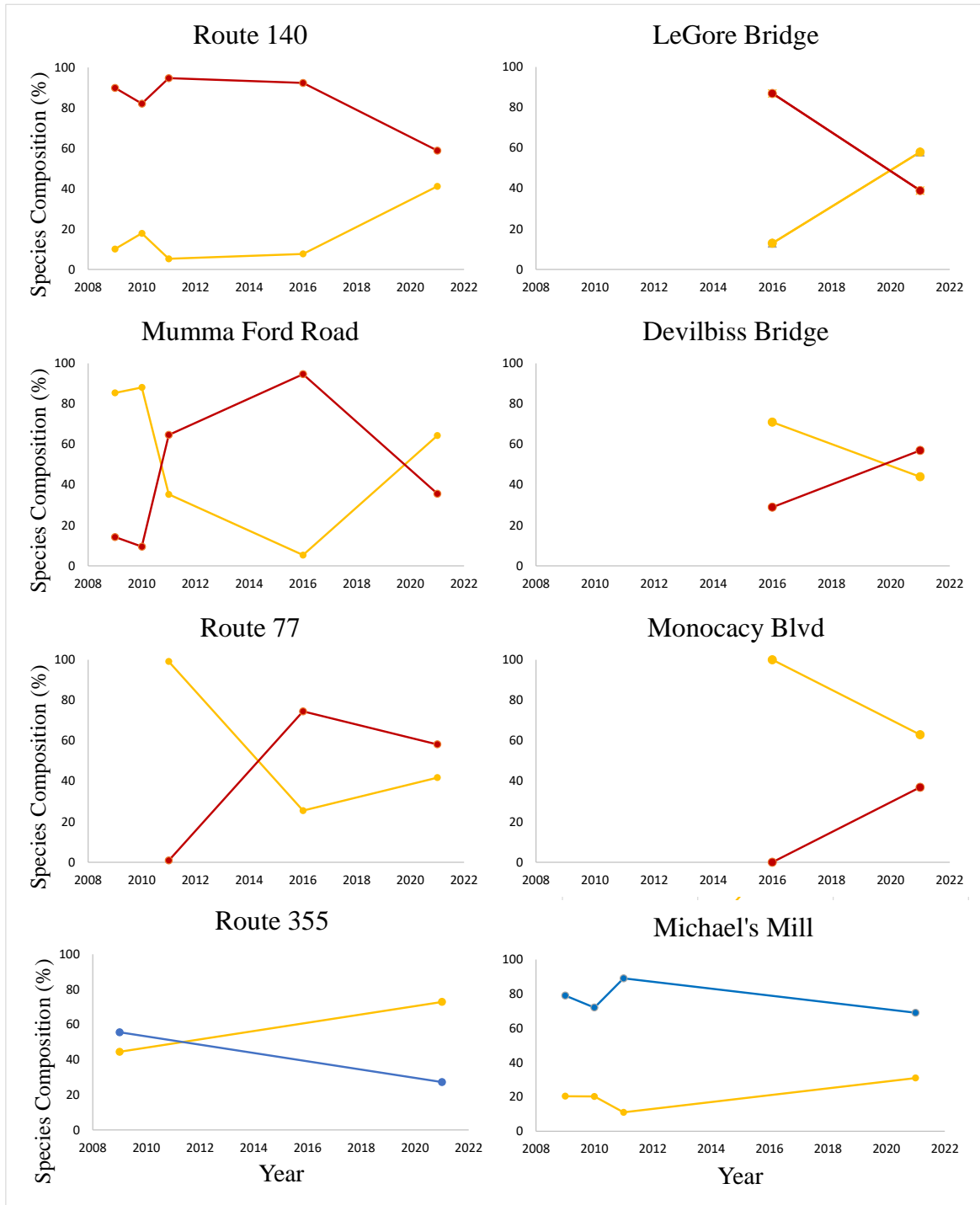
Figure 4: Species composition (%) of crayfish between *Faxonius rusticus* (red), *Faxonius virilis* (yellow), and *Faxonius obscurus* (blue) in the Monocacy River from 2009 to 2021.

Table 2: The average densities (in crayfish per square meter) of crayfish species *Faxonius virilis*, *Faxonius rusticus*, and *Faxonius obscurus* across all recorded sites in the Monocacy River from 2009 to 2021.

Site	Year	*F. virilis*	*F. rusticus*	*F. obscurus*	Other	Total density (Crayfish/m^2)
Route 140	2009	1.11	9.85	0	0	10.96
	2010	2.32	10.64	0	0	12.96
	2011	1.06	19	0	0	20.06
	2016	0.92	11	0	0	11.92
	2021	1.33	0.93	0	0	2.26
Sixes Bridge	2009	2.24	4.6	0.96	0	7.80
	2011	0.36	8.24	0	0	8.60
Mumma Ford	2009	5.88	0.98	0	0.02	6.88
	2010	10.4	1.12	0	0.28	11.80
	2011	2	3.67	0	0	5.67
	2016	0.75	13.33	0	0	14.08
	2021	1.33	2.4	0	0	3.73
Route 77	2011	7.93	0.07	0	0	8.00
	2016	2.17	6.33	0	0	8.50
	2021	2.13	1.53	0	0	3.66
Legore Bridge	2016	0.25	1.67	0	0	1.92
	2021	1.67	1.13	0	0.07	2.87
Links Bridge	2016	2.33	0	0	0	2.33
Devilbiss Rd	2016	0.42	0.17	0	0	0.58
	2021	0.87	1.13	0	0	2.00
Biggs Ford	2016	1.83	0	0	0	1.83
Monocacy Blvd	2016	2.83	0	0	0	2.83
	2021	1.47	0.87	0	0	2.34
Pinecliff Park	2021	3.8	0	0.8	0	4.60
Route 355	2009	1.07	0	1.33	0	2.40
	2021	2.33	0	0.87	0	3.20
Michael's Mill	2009	2.46	0	6.54	1.06	10.06
	2010	2.6	0.92	8	3.32	14.84
	2011	0.44	0	0	3.68	4.12
	2021	1.2	0	1.33	0.13	2.66
Park Mills	2021	1	0	2.07	0.13	3.20

Size Distribution

In 2009 both Route 140 and Sixes Bridge, two sites that had a high level of *Faxonius rusticus* presence, had a length-frequency distribution consisting of a large amount of young of the year (YOY) of *F. virilis*, a notable gap of individuals within the 16-30 mm carapace length range, and a small number of individuals with carapace lengths greater than 30 mm (large class individuals) (Figure 5). In these same sites, the most common *F. rusticus* size class was in the 16-30 mm range. In 2021, Mumma Ford, Route 77, LeGore Bridge, and Devilbiss Bridge had some large class *F. virilis* present (Figure 6). Of these sites only LeGore had any *F. rusticus* above 30 mm, and it was still smaller than all of the large class *F. virilis*. Both the earliest impacted site (Route 140) and the most recently impacted site (Monocacy Blvd.) had no large class *F. virilis*. Almost no large class *F. virilis* were present at sites downstream of the *F. rusticus* invasion front. Only three percent of collected crayfish had any noticeable damage, and no pattern was found in terms of differences in damage by species, site, or macrohabitat.

Figure 5: Size-frequency plots of the carapace length (in mm) of both *Faxonius rusticus* (red) and *Faxonius virilis* (yellow) at the route 140 crossing, Sixes Bridge, and Mumma Ford Road in the Monocacy River in 2009.
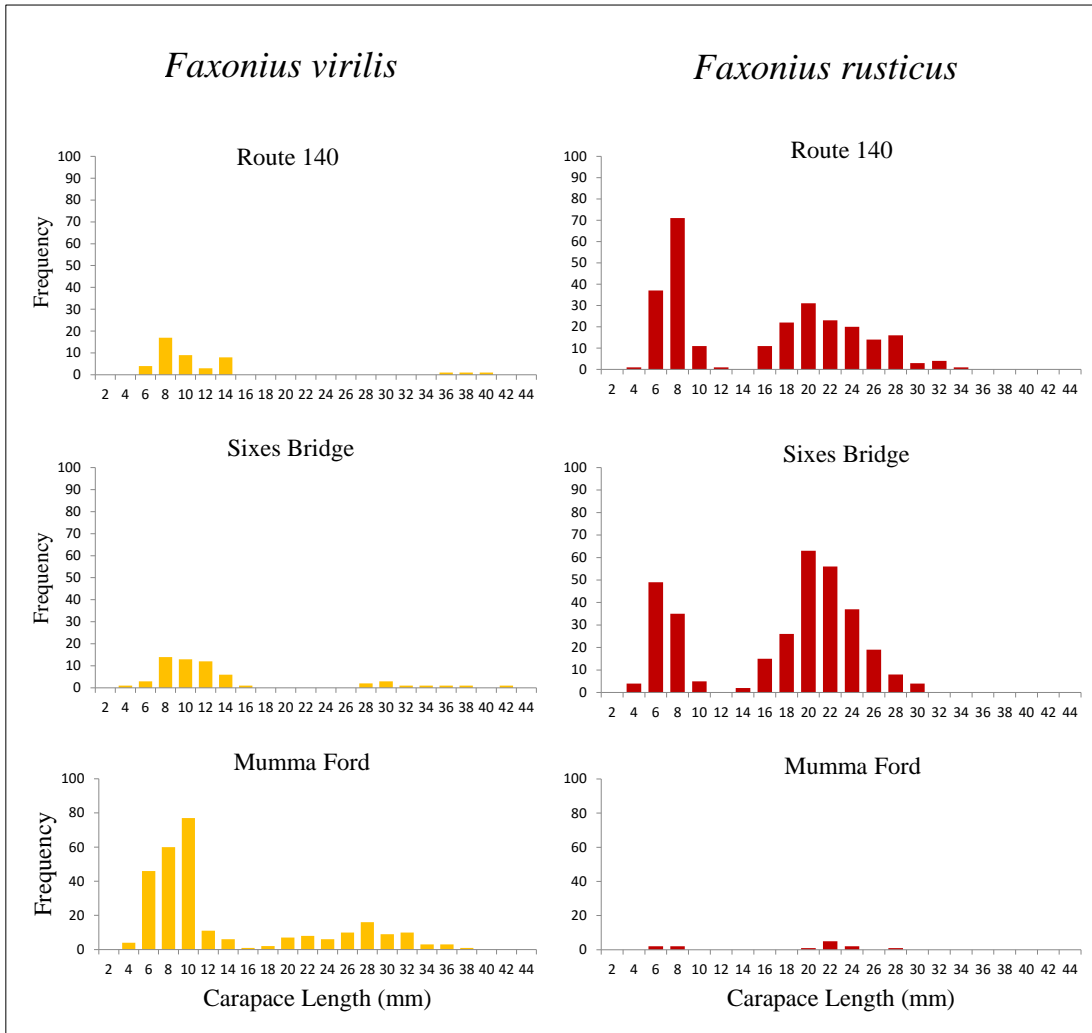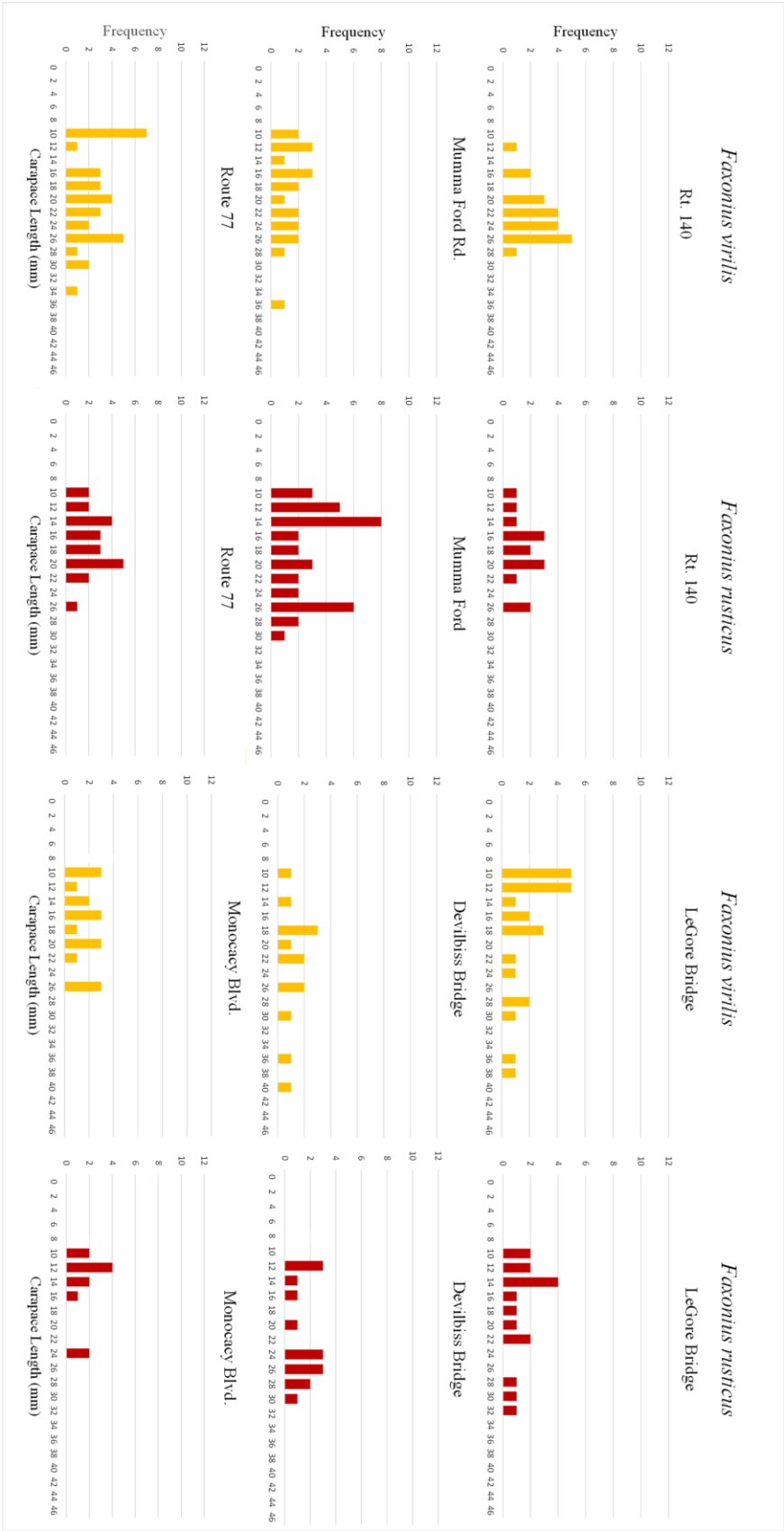
Figure 6: Size-frequency plots of the carapace length (in mm) of both *Faxonius rusticus* (red) and *Faxonius virilis* (yellow) at *F. rusticus*-present sites in the Monocacy River in 2021.

Habitat Distribution

There were no significant differences in *F. rusticus* density between sites or macrohabitats. For *F. obscurus*, there was no significant difference in density between sites, but the density in riffles and runs were significantly lower than in vegetation, pools, or glides ($p < 0.05$) (Table 3, Figure 7). *F. virilis* showed no significant differences in density among sites, but there were significant differences in macrohabitat use. In sites without *F. rusticus*, *F. virilis* had a significantly higher density in vegetation and pools than anywhere else ($p < 0.01$). In *F. rusticus*-present sites, *F. virilis* had a significantly higher density in vegetation than all others ($p < 0.01$), as well as a significantly higher density in pools than in runs ($p < 0.05$).
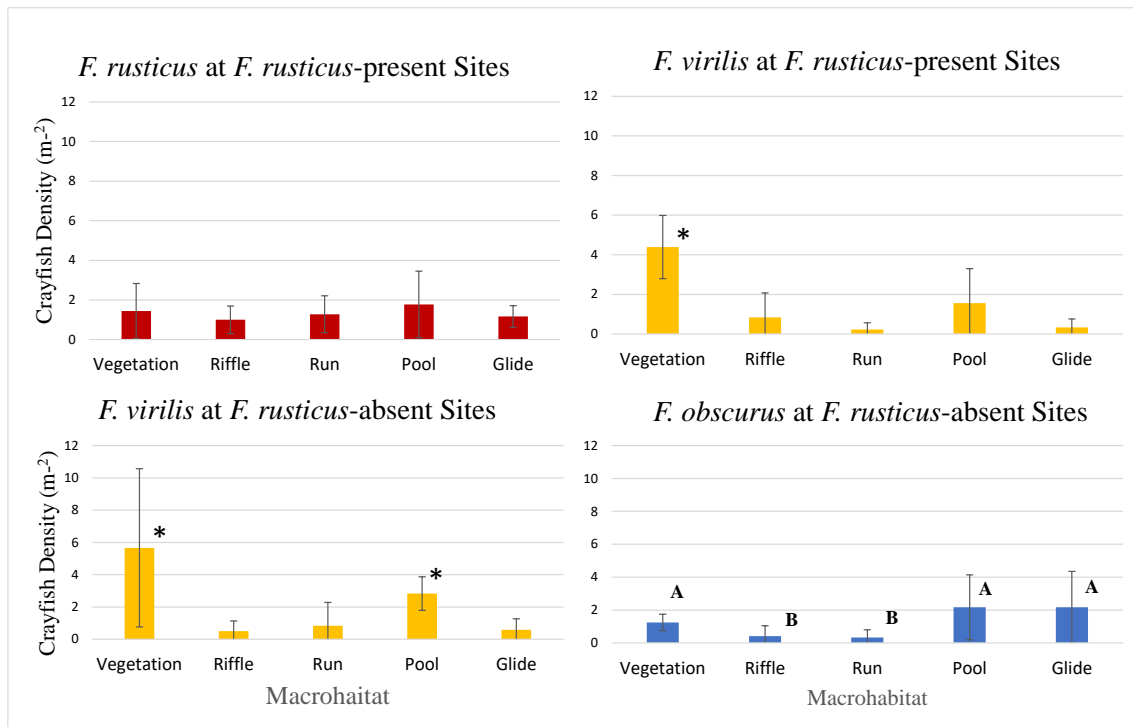

Figure 7: The average density of *Faxonius rusticus*, *Faxonius virilis*, and *Faxonius obscurus* in five different macrohabitats at sites where *F. rusticus* were present and not present in the Monocacy River in 2021. Error bars denote standard deviations, asterisks denote statistically significant differences, and letters denote statistically different groups.

Sex ratios

For *F. virilis* the sex ratios remained slightly female-dominant regardless of site (Table

4). For *F. obscurus* however, the sex ratio was highly skewed towards females, with the

population at Park Mills consisting of 98% females. For *F. rusticus* the ratios were similar to *F.*

virilis, except for Monocacy Blvd. where females made up over 90% of the total.

Table 3: Results from Kruskal-Wallis tests of the effects of site on density and macrohabitat density on
F. rusticus, *F. obscurus*, and *F. virilis* in the Monocacy River in 2021. Included are the results of
pairwise comparisons between macrohabitats on *F. virilis* in sites where *F. rusticus* is present and sites
where *F. rusticus* is not present. Bold values indicate statistically significant results.

Species	Independent Variable	Sig.
F. rusticus	Macrohabitat	0.977
	Site	0.141
F. obscurus	Macrohabitat	**0.01**
	Site	0.323
F .virilis	Macrohabitat	**<0.001**
	Site	0.349

F. virilis in sites with *F. rusticus*					
	Vegetation	Riffle	Run	Pool	Glide
Vegetation		**<.001**	**<.001**	**0.001**	**<.001**
Riffle	**<.001**		0.274	0.203	0.598
Run	**<.001**	0.274		**0.018**	0.572
Pool	**0.001**	0.203	**0.018**		0.072
Glide	**<.001**	0.598	0.572	0.072	
F. virilis in sites without *F. rusticus*					
	Vegetation	Riffle	Run	Pool	Glide
Vegetation		**<.001**	**0.001**	0.61	**<.001**
Riffle	**<.001**		0.855	**0.003**	0.91
Run	**0.001**	0.855		**0.006**	0.767
Pool	0.61	**0.003**	**0.006**		**0.002**
Glide	**<.001**	0.91	0.767	**0.002**	

Table 4: The male percentage of the population of each species of crayfish at each site in the Monocacy River in 2021.

Site	*F. virilis*	*F. rusticus*	*F. obscurus*
Route 140	18	27	-
Mumma Ford	48	44	-
Route 77	23	21	-
LeGore Bridge	47	31	-
Devilbiss Bridge	53	36	-
Monocacy Blvd.	42	6	-
Pinecliff Park	36	-	4
Route 355	16	-	13
Michael's Mill	33	-	3
Park Mills	30	-	2

DISCUSSION

Faxonius rusticus has advanced downstream in the fourteen years since its first detection in 2007 near the Maryland-Pennsylvania border. Their invasion of the Monocacy River was characterized by a sudden rapid increase in abundance followed by a decline. During this period of high abundance, they made up nearly 95% of the local crayfish assemblage, and they outcompeted other established species such as *Faxonius virilis*, which was reduced to the remaining 5% in invaded sites. The mechanism behind the reduction in *F. rusticus* density post-invasion is not yet understood. *Faxonius rusticus* has generalist macrohabitat preferences unlike *F. virilis* which prefers vegetation patches, and this generalist behavior may have allowed *F. rusticus* to establish itself in macrohabitats with low *F. virilis* density. During this initial spike of *F. rusticus* numbers, *F. virilis* likely persisted in low density due to a size refuge. *F. virilis* also appeared to be displacing the native *F. obscurus* further downstream although there was no evidence of the initial spike and reduction in numbers as seen in *F. rusticus*.

Downstream Advancement

The invasion front of *F. rusticus* advanced 37 km downstream since 2007 at a rate of 2.66 km yr^{-1}. This rate was low but within the range of most reported rates of *F. rusticus* expansions in lotic ecosystems. There is a paucity of research on invasion speed in streams and rivers and the published invasion speeds of *F. rusticus* are somewhat inconsistent. Observations in a Washington state river show *F. rusticus* having a downstream spread rate of 20 km yr^{-1} (Messager & Olden, 2018), and a rate of 13.5 km yr^{-1} was reported in the John Day river in Oregon, but a rate of only 3.7 km yr^{-1} was reported in Ontario streams (Momot, 1996; Sorenson et al., 2012).

Multiple limnological factors such as flow rate, morphometry, the presence of artificial barriers, and stream gradient may impact the speed of the downstream spread of *F. rusticus*, resulting in the wide range of observed invasion speeds. In Croatia, the invasive crayfish *P. leniusculus* had an 8-fold difference in downstream dispersal rate between 2 different streams due to differences in both streams shapes and discharge rates (Hudina et al., 2017). *Faxonius rusticus* dispersed on shores of a Wisconsin lake at a rate of 0.68 km year (Wilson et al., 2004), and at a rate of 2.1 km yr^{-1} in Lake of the Woods in Canada (Jansen et al., 2009), although these rates were in lentic systems with different abiotic factors than that of streams and rivers such as topography, substrate composition, and particularly flow rate which could facilitate easier downstream movement of invasive crayfish. The downstream invasion rate of *F. rusticus* seen in the Monocacy river was more comparable to that of populations in lentic systems, but despite being relatively low, a rate of 2.66 km yr^{-1} was within observed invasion rates of *F. rusticus,* although not in observed lotic invasion rates.

Changes in species composition

Invasive *F. rusticus* displaced resident crayfish species and maintained dominance post-invasion in freshwater environments according to previous observations and this was hypothesized to be the case in the Monocacy River (Kuhlmann, 2021; Olden et al., 2011; Wilson et al., 2004). Contrary to expectations there was an initial spike in *Faxonius rusticus*, followed five years post-invasion by a population decrease to 40-60 % of the total crayfish population. This fluctuation in population composition has not been previously reported in a lotic freshwater environment. Reductions of *F. rusticus* proportions have been observed post-invasion in freshwater lakes in Wisconsin (Tamisiea, 2021). Four of twenty-one lakes invaded by *F. rusticus* in Michigan showed sharp declines in *F. rusticus* density over a decade post-invasion, but the

remaining lakes maintained high *F. rusticus* density throughout the study, up to over 30 years post-invasion (Kreps, 2009). Oscillations of invasive populations of crayfish resembling a "boom and bust" cycle have also been observed in lakes in Sweden with the signal crayfish *Pacifastacus leniusculus*, with 41% of the invaded lakes having a reduction in *P. leniusculus* numbers 10-15 years post invasion (Sandström et al., 2014). These results are rare in the literature however, with most observations indicating *F. rusticus* populations maintaining a high abundance many years post-invasion (Kreps, 2009, p. 20; Olden et al., 2006; Wilson et al., 2004).

In a New York stream system, invasive *F. rusticus* increased in abundance over the course of 9 years with no signs of population reduction (Kuhlmann, 2021). Another study however found a decrease in the abundance of the invasive *P. leniusculus* in a California river system that coincided with a period of prolonged wet-seasons and a high discharge rate (Light, 2003). While much research has been done on invasion dynamics of *F. rusticus* in lakes, there are not many reported observations of *F. rusticus* in lotic environments, where abiotic factors may alter the abundance, competition dynamics, and invasion speed of *F. rusticus*. More observations are needed to determine long-term changes in the abundance of invasive *F. rusticus* populations in lotic ecosystems.

Possible mechanisms for this population decline of *F. rusticus* include habitat alteration, disease, and parasitism. One hypothesis is that an increase in the amount of *F. rusticus* results in increased destruction of macrophytes, leading to a loss of potential shelter (Larson et al., 2019). This in turn resulted in increased predation of *F. rusticus* driving their numbers back down in a form of self-sabotage. In the course of our study, we did not quantify macrophyte abundance, but we did not perceive any qualitative changes in the vegetation cover in invaded sites over time,

and there is little evidence to support this mechanism driving changes in crayfish species composition in the Monocacy River.

Parasitism has been found to decrease crayfish densities in temperate lakes. The trematode *Microphallus ssp.* has a multi-stage life cycle that uses crayfish as a vector before moving on to vertebrate hosts, and infected crayfish exhibit increased boldness around predators to facilitate transmission via consumption (Reisinger et al., 2015). *Faxonius rusticus* is susceptible to *Microphallus* infection, and exhibits less predator-avoidance and decreased growth rate as a result of hosting *Microphallus*, spending up to 20% more time outside of shelters (Reisinger & Lodge, 2016). The initial increase in *F. rusticus* population during the initial invasion may have facilitated the spread of this parasitic trematode due to the high crayfish density, resulting in a loss of fitness and subsequent reduction in the population of *F. rusticus*. There are no records in the literature of *Microphallus*-infected crayfish in the Monocacy river, but the genus of trematode is ubiquitous and has been found in crayfish in the Midwest and southeastern United States (Overstreet et al., 1992; Sargent et al., 2014).

The water mold pathogen *Aphanomyces astaci*, often called the crayfish plague, is found in *F. rusticus* populations all across the United States (Panteleit et al., 2019). Although it commonly only causes high mortality in European crayfish species, there are instances of strains of *A. astaci* reinfecting previously immune North American crayfish species such as *Pacifastacus leniusculus* (Aydin et al., 2014). In addition to this, the pathogen may increase stress and decrease fitness, resulting in increased vulnerability to predation or other pathogens in *F. rusticus* (Panteleit et al., 2019).

Size Refuge

In 2009 at the invaded sites, the size distribution of *F. virilis* and *F. rusticus* were consistent with those that would be present in a size refuge, with the *F. virilis* distribution containing few, very large individuals in addition to the YOY. During this period *F. virilis* individuals with carapace lengths between 16-28 mm were almost entirely absent. *F. virilis* mortality can be caused by predation by crayfish congeners or by fish, which can be influenced by a presence or lack of shelter for *F. virilis* (Garvey et al., 1994). Due to the lack of *F. virilis* individuals smaller than 30 mm CL, the YOY that were present at these sites may have been produced by the *F. virilis* that had < 30 mm CL. The presence of YOY and lack of immediately larger sizes of *F. virilis* may be a result of competition or predation by *F. rusticus* individuals of a larger size class, as *F. virilis* YOY in sites where *F. rusticus* is present have a far higher mortality rate than in sites where *F. rusticus* is absent, with a 23% difference in mortality between sites (Selckmann, 2010).

The invasion of *F. rusticus* may have resulted in selective pressure favoring larger carapace lengths in *F. virilis*. In 2021 Mumma Ford, LeGore, Route 77, and Devilbiss still had some large-sized individuals of *F. virilis*, after the initial maximum density of *F. rusticus* decreased (See Appendix Figure 12). The larger *F. virilis* individuals at these sites were all larger than the largest *F. rusticus* individuals, a phenomenon also observed in 2009. These may be the vestiges of the previous size refuges, which are no longer as apparent as in 2009, as the size distribution for *F. virilis* likely returned to a more normal distribution as the medium-sized *F. virilis* increased in density when the proportion of *F. rusticus* decreased. No large *F. virilis* were present at Route 140 or Monocacy Blvd., likely because the initial spike was a decade ago and most changes in size distribution have reverted back to normal at Route 140, and the *F. rusticus*

have not reached a high enough density to cause differential mortality in *F. virilis* forming the positively skewed size distribution at Monocacy Blvd.

Body size plays an important role in agonistic interactions by crayfish with individuals of larger body size winning in both intraspecific and interspecific aggressive interactions (Bovbjerg, 1956; Pavey & Fielder, 1996). A 10% difference in carapace length is enough to determine the dominant competitor in an interaction between crayfish, with competition outcomes being mostly random between individuals with less than a 10% size difference (Daws et al., 2002). Chelae size is also an important factor in aggressive competitions, and *F. rusticus* has larger proportional chelae than *F. virilis*, putting them at a competitive advantage even with a slightly smaller body size (Garvey & Stein, 1993). According to most literature *F. rusticus* tends to outcompete similar sized *F. virilis*, but in the Monocacy River *F. virilis* is dominant when competing against size-matched *F. rusticus* (Wright, 2011). *Faxonius rusticus* must be 10% larger than *F. virilis* in order to dominate in an agonistic interaction in the Monocacy River, so interactions that are not size-matched may occur with larger *F. rusticus* outcompeting or consuming smaller *F. virilis* individuals (Selckmann, 2010; Wright, 2011).

Differences in growth rate between *F. rusticus and F. virilis* may have facilitated the initial displacement of *F. virilis* in the Monocacy River by altering predation and competition dynamics between the two species. *Faxonius rusticus* is known to have a high degree of morphological and behavioral plasticity, particularly in differences between invasive and native populations. Individuals in invasive ranges exhibit a higher growth rate as a result of more time spent foraging, and this may provide *F. rusticus* an advantage in competitive interactions due to individuals achieving a larger body size in a shorter amount of time (Reisinger et al., 2017). The higher growth rate of *F. rusticus* compared to *F. virilis* was also observed in the Monocacy

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River, with *F. rusticus* YOY having a higher growth rate than *F. virilis* in sites where both species are present and *F. virilis* YOY having a decreased growth rate when in the presence of *F. rusticus* (Selckmann, 2010). The increased mortality of *F. virilis* YOY when in the presence of *F. rusticus* and the greater growth rate of *F. rusticus* compared to *F. virilis* may indicate that *F. virilis* YOY are consumed and outcompeted by larger size class *F. rusticus* (Selckmann, 2010). The predation and competition of *F. virilis* YOY by larger *F. rusticus* may result in the lack of medium sized *F. virilis* during the initial peak of *F. rusticus* density, even with an initially high density of *F. virilis* YOY in sites with *F. rusticus* during the initial invasion peak.

The importance of body size in competitive interactions means that *F. virilis* would likely gather fewer resources and be evicted from shelters as a result of losing competitions with *F. rusticus* individuals of larger size classes (Garvey et al., 1994; Wright, 2011). This in turn may increase their susceptibility to predation by fish, and drive the mortality seen in *F. virilis* individuals between 16 and 28 mm CL. The pressures of predation select for larger size in crayfish, as larger crayfish are more difficult to consume by fish (Stein, 1977). With predation and loss of competitions driving mortality in *F. virilis* individuals, the few individuals that were able to grow larger than 30 mm CL were able to gather food without competing with *F. rusticus* and could utilize shelters to prevent mortality from predation.

Habitat Distribution

Faxonius virilis utilized patches of vegetation significantly more than other types of macrohabitats ($p < 0.05$). On the contrary, *F. rusticus* did not have any specific macrohabitat preference, being found in similar abundance in all 5 macrohabitats. In lakes invaded by *F. rusticus*, *F. virilis* was often relegated to persisting in macrophyte beds, but was also found to coexist with invading *F. rusticus* longer than other species of crayfish such as *F. propinquus*

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(Kreps, 2009). In macrophyte beds *F. virilis* was consumed less often by predators than its congeners, making such habitats a refuge for *F. virilis* during invasions (Garvey et al., 2003).

Most research on habitat preferences between crayfish species has been performed in lakes, where flow rates do not impact crayfish as much as in lotic environments, and therefore habitats in these studies tend to be characterized by substrate type rather than flow rate or combinations of these attributes. In lentic ecosystems population and invasion dynamics are likely based more on biotic factors such as competition and predation (Perry et al., 2001). In contrast, streams provide far more abiotic factors that may influence invasion dynamics such as flow rate and habitat shape.

In lotic ecosystems crayfish prefer areas with low flow rates and high structural complexity and this is likely the case for *F. virilis* and *F. obscurus* in the Monocacy River as well. Out of 4 crayfish species examined in streams in Arkansas, 3 had a strong correlation between abundance and macrohabitat type, significantly preferring vegetation and pools, and avoiding riffles and runs (Flinders & Magoulick, 2007). Only one species, *Cambarus hubbsi*, preferred high flow and low flow habitats equally. These macrohabitat preferences are similar to those of the established species in the Monocacy River, with *F. virilis* and *F. obscurus* found at very low densities in runs and riffles, and *F. rusticus* having no significant preference between macrohabitat.

Faxonius rusticus is known to be a generalist with respect to substrate type and flow rate, showing no behavioral changes in flow velocities of up to 40 cm s^{-1}, and being able to persist in flow rates as high as 50 cm s^{-1}. By contrast *F. virilis* could only persist at flow rates < 30 cm s^{-1} (Maude & Williams, 1983; Messager & Olden, 2019; Perry et al., 2013). Crayfish can be dislodged from the riverbed or shelters if the current velocity is too high, and high flow rates can

result in reduced foraging in crayfish even if it is below a given species' slip-speed (Hart, 1992). The low slip-speed of *F. virilis* likely prevents individuals from foraging in high flow macrohabitats and staying in vegetation patches and pools, and this preference may leave the riffles, runs, and glides vacant for occupation by *F. rusticus*. In contrast, the ability of *F. rusticus* to tolerate high flow rates results in them having more generalist macrohabitat preferences, providing an avenue for colonization. *Faxonius rusticus* may become established in riffles runs and glides where it doesn't need to compete with *F. virilis* and can subsequently reproduce and compete with *F. virilis* in the slower water macrohabitats. This may provide an example of generalist habitat requirements allowing an invasive species to compete against a more specialist native species and may be responsible for *F. rusticus* being such a prevalent invasive species in streams in addition to lentic environments.

Sex Ratios

Sex ratios in *F. virilis* were typically non-skewed regardless of site, while *F. rusticus* and *F. obscurus* both had female-heavy sex ratios at Monocacy Blvd and every site downstream, with some populations being over 95% female (Table 4). *F. virilis* had a slightly higher proportion of males which may be due to differences in behavior because male *F. virilis* are more active than females leading to increased predation and mortality (Hazlett & Rubenstein, 1974).

It is possible that the extreme asymmetry of sexes downstream of Devilbiss Bridge may have been due to changes in water quality. Endocrine disrupting chemicals such as atrazine in freshwater ecosystems can impact crayfish (Yurdakok-Dikmen et al., 2020). Atrazine is used as an herbicide and alters the sex ratio of crayfish, resulting in a significantly higher proportion of females in *Cherax quadricarinatus* (Mac Loughlin et al., 2016). We did not collect data on

atrazine levels in the Monocacy River during this study and if endocrine disrupting chemicals are

causing the shift in sex ratio, *F. virilis* remains unaffected by it.

CONCLUSION

Understanding the invasion patterns of invasive species is critical to predicting their impacts on ecosystems as well as developing management plans for stopping their spread or mitigating damage to the environment. This is the first long-term study examining the invasion dynamics of the rusty crayfish in a river system and has revealed previously unreported dynamics in *F. rusticus* invasions. In lentic environments most observations indicate that *F. rusticus* tends to increase in abundance until it outcompetes its native congeners, but in the Monocacy River the abundance of *F. rusticus* decreased after an initial peak, with *F. virilis* avoiding extirpation following the initial invasion. The mechanism behind the decline of *F. rusticus* is unknown, although density-dependent factors such as pathogens or resource exhaustion could be partially responsible due to the high initial density. Further studies should address the possible causes of the reduction in *F. rusticus* numbers seen in the Monocacy River, such as examining the population for parasites or pathogens, or determining changes in habitat that could alter the species composition. More long-term observations could be done to determine further changes in the crayfish assemblage decades after the initial invasion, including the dynamics between *F. virilis* and the native *F. obscurus* further downstream. The observations of the invasion dynamics from this study may be useful for management of this invasive species in river ecosystems, as the rate of spread can be more accurately predicted in rivers and information on the long-term fate of congeners such as *F. virilis* may enable prioritization for more at-risk native crayfish species.
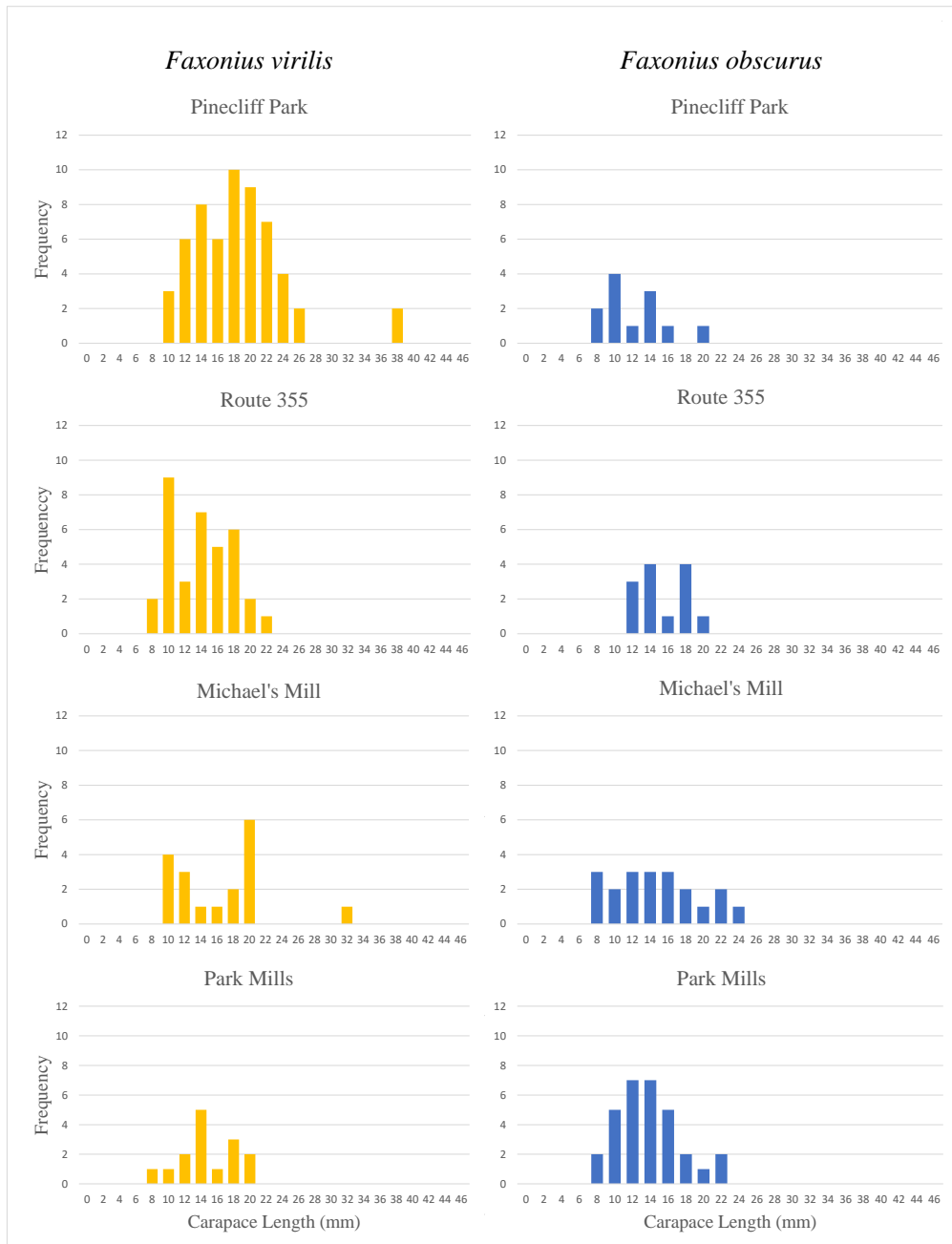
Figure A-1: Size-frequency plots of the carapace length (in mm) of both *Faxonius virilis* (yellow) and *Faxonius obscurus* (blue) at non-*F. rusticus*-present sites in the Monocacy River in 2021.

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