

## Research Article

## Evaluation of five trap designs for removal of invasive red swamp crayfish (*Procambarus clarkii* Girard, 1852) in Southern Michigan: catch per unit effort, body size, and sex biases

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### Abstract

Trapping and removing invasive crayfish is one of the most common forms of control, however gear-specific biases can limit effectiveness of such methods. We evaluated five trapping gears (Gee's minnow traps [GMT], pyramid traps [PYR], artificial refuge traps [ART], additional partition refuge traps [APART], and juvenile traps [JUV]) for their effectiveness in a *Procambarus clarkii* Girard, 1852 (red swamp crayfish) removal effort among four Southern Michigan ponds between May and October 2019. Our objectives were 1) determine which gear(s) produce the highest catch per unit effort (CPUE); 2) assess gears for body size and sex biases; 3) ascertain the degree of seasonality in gear-specific catches and biases. We found that baited GMT and PYR traps substantially outperformed the ART, APART, and JUV traps with respect to CPUE. However, catches of refuge-style traps trended positively over the season. Body size biases were prevalent, with GMT and PYR traps consistently recording individuals > 30 mm carapace length. The ART and APART traps caught relatively smaller individuals but trended towards capturing larger individuals later in the season. We observed no sex biases or biases between Form 1 and Form 2 males among the gears. Our findings support employing multiple gears for crayfish removals but demonstrated that baited traps can remove more crayfish than unbaited traps (on a CPUE basis) and both can capture body size trends by accounting for the timing of capture. Further, the lack of sex bias suggests any of these commonly used traps can be used to broadly sample females or male reproductive forms. Based on our results and recommendations, the Michigan adaptive response strategy has adopted a combination GMT-APART strategy to maximize CPUE while also targeting a wide range of crayfish sizes.

**Key words:** invasive species, gear comparison, seasonality, management, artificial impoundment, rapid response, adaptive protocol

### Introduction

Among the principal threats to biodiversity is human-facilitated introduction of non-native species. Efforts are ongoing to develop strategies aimed to control, alleviate, and prevent further invasions (Crystal-Ornelas and Lockwood 2020). Invasive species introductions are among the top forces of global change in the anthropocene and have heavily benefited from

human activity and environmental modification (Dukes and Mooney 1999). Their introductions typically alter interspecies and ecosystem dynamics, often causing losses of biodiversity and ecosystem functions crucial for environmental health and services (Tylianakis et al. 2008). Further, if control and removal of invasive species is left unprioritized, such species can integrate themselves into crucial functional relationships (Lurgi et al. 2018) that complicate biodiversity and ecosystem management and restoration goals (Kopf et al. 2017). Timely response to reports of detected invasive species is vital because removing established populations requires substantial investment of monetary and human effort (Vander Zanden et al. 2010; Jardine and Sanchirico 2018).

Particular attention is warranted towards invasive crayfishes. Several species are globally recognized as strongly consequential invaders of aquatic ecosystems (Lodge et al. 2000; James et al. 2015). Nearly all the recognized invasive crayfishes are North American species, and their documented impacts are wide-ranging (Lodge et al. 2012). Invasive crayfish are linked to declines of native crayfish primarily through resource competition (Hill and Lodge 1999; Usio et al. 2004; Sargent et al. 2011) and disease vectoring, particularly through the transmission of crayfish plague (Petrušek and Petrusková 2007; Skov et al. 2011; Strand et al. 2019). Other ecosystem-level impacts include the alteration of aquatic community food webs (Kershner and Lodge 1995; DiStefano 2005) and ecosystem engineering through terrestrial burrowing (Barbaresi et al. 2004; Faller et al. 2016; Haubrock et al. 2019). Invasive crayfish also negatively affect water quality, food provisioning, and infrastructure provided by invaded aquatic systems (Lodge et al. 2012). Managing for established invasive crayfish is challenging, and long-term control of crayfish invasions is rarely successful. The few successful eradications have generally been limited to small impoundments (e.g. Peay et al. 2019), and the success of other long-term control efforts are still being evaluated (Hein et al. 2006; Hansen et al. 2013; Nunes et al. 2017). Most eradication or control strategies also rarely generalize well across ecological, managerial, legal, and financial constraints to be broadly employed, which further contributes to poor success rates (Lodge et al. 2006; Kettenring and Adams 2011).

Among invasive crayfish species, the red swamp crayfish, *Procambarus clarkii* (Girard 1852; red swamp crayfish) has garnered global attention (Gherardi et al. 2011). Native to the Southern United States and an important economic resource throughout the region, *P. clarkii* have been widely transported world-wide for aquaculture, fisheries, and aquarium trade (Gherardi 2006; Aquiloni et al. 2011). Although they are considered to be the most widespread and best-documented invasive crayfish globally (McLaughlan et al. 2014), range expansions of *P. clarkii* in the US are only well-documented in states along the Pacific Coast (Larson and Olden 2011; Larson et al. 2017; Oficialdegui et al. 2019). Their invasiveness is attributed

to their relatively wide environmental tolerances, high fecundities, quick maturation and growth rates, aggressiveness, and ability to diversify resource preferences (Correia 2002; Loureiro et al. 2015; Vesely et al. 2015). Additionally, *P. clarkii* are known for their extensive terrestrial burrowing behaviors, which can destabilize lake and river banks and pose serious civil engineering risks in high densities (Arce and Diéguez-Uribeondo 2015; Haubrock et al. 2019). The diversity of suitable habitats has led to a wide variety of methods, protocols, and gear for sampling and removing *P. clarkii* (see Parkyn 2015). Up-to-date studies on effective trapping for removing *P. clarkii*, are needed to best inform management objectives.

Protocols for managing invasive crayfish frequently rely upon physical removal. There is substantial literature dedicated to evaluating gear performance on the basis of catch per unit effort (CPUE) (De Palma-Dow et al. 2020; Chadwick et al. 2021). Gear selection is a crucial step because poor removal rates could spur compensatory growth or simply fail to remove individuals (Zipkin et al. 2009). Baited traps are most commonly employed for capturing crayfish owing to their ease of deployment, standardization of effort, cheap cost, relative ease of use compared with active sampling techniques, and capacity to sample a variety of microhabitats within aquatic systems (Larson and Olden 2016). Intensive baited trapping effort over multiple seasons helped to control a *Faxonius rusticus* (Girard, 1852, rusty crayfish) invasion (i.e., temporally maintaining low CPUE) in a Wisconsin lake (Hansen et al. 2013). However, the effectiveness of baited traps in controlling *P. clarkii* populations is uncertain (Gherardi et al. 2011).

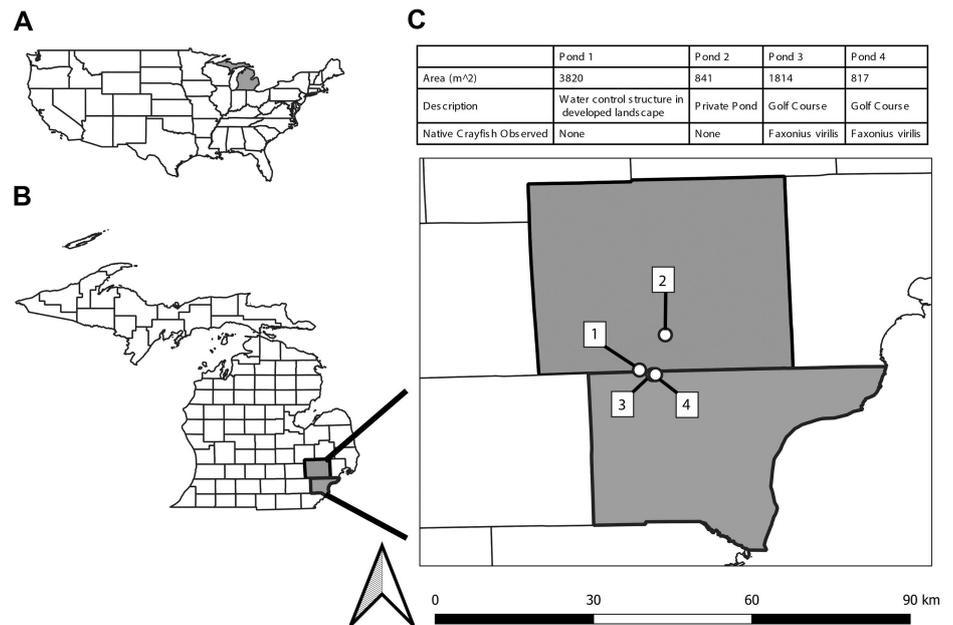
The uncertain efficacy of baited traps in removing crayfish can be partly attributed to gear biases. These biases vary depending on the type of aquatic system, target population life history, and study context (Rabeni et al. 1997; Dorn et al. 2005; Coignet et al. 2012). Large body size and male-dominant sex biases are commonly reported with these gears, possibly attributed to increased exclusion by sexually mature, aggressive males, or other dominant behaviors of larger-bodied individuals (Stuecheli 1991; Ogle and Kret 2008). Consequently, baited traps may result in selective removal, leaving considerable portions of the crayfish population undetected by these gears. The use of multiple gears is recommended to overcome this limitation and improve total population removal rates (e.g., Loureiro et al. 2018; García-De-Lomas et al. 2020). For example, supplementing baited traps with unbaited traps that mimic crayfish refugia could enhance overall CPUE and decrease the size and sex biases that are often reported with baited traps (Green et al. 2018; De Palma-Dow et al. 2020). The deployment of multiple gears might address some biases that lead to selective removal. However, the effectiveness of some gears may be constrained by seasonality (Larson and Olden 2016). Temporal patterns in catches and size/sex representation are associated with behavioral changes over the sampling season (Parkyn et al. 2011; Barnett and Adams 2018) or following changes

in environmental conditions (Somers and Stechey 1986). However, there is little information about seasonal effects for effective trap-based protocols for invasive crayfish from which to draw useful recommendations.

In 2017, *P. clarkii* were first reported in several ponds across Southern Michigan, USA (Smith et al. 2018). The source(s) of this invasion remains unclear, but the species has since received priority interest from the state to limit further spread and ultimately eradicate established populations. In this study, we evaluate and compare the efficacy, biases, and seasonality of several passive gears employed for an intensive removal effort of *P. clarkii* in these ponds. Up-to-date documentation of these efforts are important because the urgency of a species invasion may prevent managers from conducting *a priori* studies to assess optimal types or combinations of gear. Crayfish control studies may instead need to be conducted within an adaptive framework, wherein a design must be developed using the best available knowledge, executed, and then subsequently assessed for effectiveness (Reaser et al. 2020). Thus, this study is unique because we explore gear characteristics within the context of an ongoing removal effort, rather than at the onset of the effort.

The trapping gear studied herein include two baited trap types (Gee's Minnow Traps and Pyramid traps), two refuge-style trap types (PVC-based artificial refuge traps and additional partition refuge trap), and one juvenile refuge trap. Gee's Minnow Traps (GMTs) and Pyramid Traps (PYR), are commonly used for sampling crayfish in open water habitat (Parkyn 2015). Previous studies have demonstrated the effectiveness of baited traps from a CPUE perspective, however they also report biased sampling of larger, male crayfish (Stuecheli 1991; Paillisson et al. 2011; Barnett and Adams 2018). The other three trap styles we examined, artificial refuge trap (ART), additional partition artificial refuge trap (APART), and juvenile traps (JUVs) attempted to represent artificial habitats. Recent work suggests these traps may attract a wider range of crayfish sizes and less sex bias to offset baited trap biases (Green et al. 2018; O'Connor et al. 2018; De Palma-Dow et al. 2020). The juvenile trap used in this study was a particularly novel construction and we assess its effectiveness as there is broad interest in employing passive trap methods to assess juvenile *P. clarkii* year-class strength and recruitment (Fjälling 2011; Engdahl et al. 2013). While we expected to identify biases within this multiple gear assessment similar to what is already reported for these gears, we questioned if/how seasonal constraints in Michigan could influence the catch rates and biases among the trapping gears.

The principal goal with this study is to develop recommendations to refine trap-based removal protocols for *P. clarkii* in Southern Michigan pond system, that can be applicable to other active Midwestern USA infestations based on relative gear performances and biological characteristics of individuals removed. Within these contexts, we present findings that show



**Figure 1.** A) Map of the United States with the state of Michigan colored in gray. B) Michigan county map showing the counties where the 2019 sampling occurred colored in gray. C) Site summaries (table inset) for sample ponds (white circles). Numbers in boxes above circles indicate the pond corresponding to the pond number in the table inset.

their effectiveness in terms of CPUE and biases (size, sex, and seasonality). To achieve our study goal, we pursued the following objectives: 1) determine which trap(s) produce the highest CPUE; 2) assess trap types for size and sex biases; 3) ascertain the degree of seasonal dependency of trap-specific catches and biases.

## Materials and methods

### Site description

We implemented our gear comparison study at four ponds in Southeast Michigan with documented *P. clarkii* populations (Figure 1). These ponds were selected for this study because they were identified as the top priorities for eradication in Michigan based on *P. clarkii* relative abundance and potential for spread via adjacent stream networks. Extensive, unstandardized daily trapping efforts have occurred at the four ponds since the initial documentation in 2017 (Ponds 1 and 2) and 2018 (Ponds 3 and 4). We examined trapping data gathered in 2019, when other gear types were first used in addition to Gee's minnow traps. All four ponds were characterized as small “non-natural” systems (mean surface area = 1,823 m<sup>2</sup>) with one acting as a water control structure (Pond 1), a private pond (Pond 2), and two located on a public golf course (Ponds 3 and 4). Depths of these ponds all averaged < 1 m, all ponds were lacking complex habitat structure (e.g., rocks, boulders, tree limbs), and all pond substrates tended to be dominated by organic material. Although overall pond features were qualitatively similar, detailed quantitative measurements of habitat features at trap placement sites were not taken over the course of this study due to time, equipment, and personnel

constraints. Crayfish communities for all four ponds were dominated by *P. clarkii*, although native *Faxonius virilis* (Hagen, 1870, northern crayfish) were also captured at Pond 3 and 4.

### *Trap descriptions and strategy*

Gee's minnow traps (Tackle Factory®, Model G40M, 6.35 mm mesh) are barrel-shaped traps with funnel openings for crayfish entry at both ends of the trap (Supplementary material Figure S1). We modified these traps by spreading the opening slightly to approximately 4.5 cm to accommodate larger crayfish sizes, following protocols detailed by previous studies (Capelli and Magnuson 1983; Hein et al. 2006). Pyramid (PYR) traps are constructed of galvanized steel mesh (5 mm bar), and are approximately 35 mm on each of four sides at the base, narrowing to a 8 cm square opening at the top of the trap. The opening contains a spring-loaded hinged gate to prevent escape. We baited the GMTs and PYRs with approximately 100 g of dry dog food in a small mesh bag that was replaced as needed to maintain consistent bag fullness during daily trapping.

The other three trap styles, ART, APART, and JUV, were un-baited. These trap styles are intended to represent artificial habitats to attract a wider range of crayfish sizes and reduce sex bias (Green et al. 2018; O'Connor et al. 2018; De Palma-Dow et al. 2020). ART traps consisted of 7 PVC pipes tethered together in a single row and capped with nylon mesh at one end, whereas the APART traps were modified versions of ART traps where 3 pipes were stacked above the remaining 4 (i.e., horizontally partitioned). The pipes in both trap types were cut 20.32 cm in length and diameters of the pipes were arranged in decreasing order with one 5.08 cm diameter pipe and two pipes each of diameters 3.81 cm, 3.175 cm, and 2.54 cm. We created juvenile traps from nylon shower loofas, untied to create a strip of approximately 1 m of 2 mm mesh fabric that was then looped into fourths. The resulting trap was then weighted to the substrate with a large steel washer. This created a structure that we believed approximated broad-leaf macrophytes, containing numerous crevices and folds for juvenile crayfish to hide.

The removal protocol consisted of daily (Monday–Friday) physical removals of *P. clarkii* via overnight trapping at all four ponds from May 20, 2019 to October 15, 2019. At the onset of the study, the initial placement of each trap type was randomly determined around the pond perimeter. Traps were all equidistantly deployed at a density of one trap per five meters of shoreline, thus the total number of traps deployed was not equally balanced across ponds. The primary trap type used in the Michigan Red Swamp Crayfish Response program efforts were GMTs and therefore they made up the majority of the traps. Five of each “experimental” trap types were deployed in each pond, with the rest of the traps in each water body being GMTs (Table S1). This resulted in an unbalanced number of

traps for each type, which was determined to be appropriate based on the tradeoffs between conducting on-going removals using GMTs while simultaneously evaluating four experimental trap types. Additionally, external factors often encountered during the course of our daily removals such as flooding, lost/damaged/stolen traps, and time intervals until traps could be replaced resulted in inconsistent numbers of total traps pulled on a given day. We acknowledge these limitations, but this study design allowed us to address uncertainties related to gear biases while remaining respectful to management interests in maximizing the removal of invasive *P. clarkii*.

Each day, crayfish were removed from traps, visually identified to species, and counted. At the end of each week of daily trap pulls, the traps were all pulled and their positions randomly shuffled for the following week. All *P. clarkii* specimens were returned to the laboratory for euthanization (freezing) and disposal (incineration). We recorded the sex and carapace length of 30 crayfish that were randomly selected each week for each trap type on all ponds. We judged 30 crayfish to be reasonable to measure because of time and personnel constraints, which required us to balance to less intensive removal efforts at low-priority pond locations alongside the ponds requiring daily removals. The subsetting procedure at each pond consisted of placing all captured individuals from a specific trap type into a holding container (a 18.9 L bucket or larger container depending on number of individuals removed), mixing the crayfish in the container as best as possible, and blindly sampling individuals. If a trap type in a pond did not capture 30 individuals, we measured and sexed all individuals cumulatively captured by that trap type throughout the week until we reached 30 individuals. We measured carapace length of each crayfish using digital calipers (mm; dorsal length from base of cephalothorax to rostrum tip) and determined sex (female, male Form 1, and male Form 2) by examining gonopodia. Juveniles were generally specified as individuals below CL < 20 mm as we found no sexually mature males or gravid females below this threshold.

### *Statistical analysis*

We analyzed CPUE data (defined as the mean number of individuals counted per trap pulled), body size (as CL) and sex biases among trap types, and any seasonal dependencies with an analysis of covariance framework. Our analytical approach employed linear models (LM), linear mixed models (LMM), generalized linear models (GLM) or generalized linear mixed models (GLMM). When appropriate, we set the pond identity as the random effect and included in all models as fixed effects the gear type, Julian time (day or biweek depending on response variable, see below for details) as a covariate, and their interaction. If a fixed effects model was used, we used the general formulation:

$$Y_i = \beta_0 + \beta_1 * \text{Gear Type} + \beta_2 * \text{Julian Time} + \beta_3 * \text{Trap Type} * \text{Julian Time} + \varepsilon_i \quad (1)$$

where  $Y_i$  is an observed count of the  $i$ th trap ( $Y_i$  is size/sex of the  $i$ th individual for models of CL and Sex),  $\beta_0$  is the model intercept,  $\beta_1$  and  $\beta_2$  are slope coefficients for the categorical trap type and the Julian time covariate respectively, the  $\beta_3$  term represents the slope of the interaction term and  $\varepsilon_i$  represents residual error. If we used a mixed model, the formulation we used was:

$$Y_i = (\beta_0 + \tau_j) + \beta_1 * \text{Gear Type} + \beta_2 * \text{Julian Time} + \beta_3 * \text{Trap Type} * \text{Julian Time} + \varepsilon_i \quad (2)$$

where  $\tau_j$  represents the random effect (coded as random intercepts) of the  $j$ th pond.

For all analyses, the decision to use either a fixed effects or mixed effects model was made based on model AICs, with model ties (i.e., models with  $\Delta\text{AIC} < 2$ ) being broken in favor of the more parsimoniously parameterized model. Significance of fixed effects was assessed with type III Wald Chi-square tests at  $\alpha = 0.05$  to help account for the strongly imbalanced trap type category (R package “car”, version 3.0-10, Fox and Weisberg 2019). If the interaction term in the best fitting model was not significant, we refit the models without the interaction term and assessed mean pairwise differences among trap types with Tukey adjusted P-values. When the best supported model included a significant interaction term, we used estimated marginal means with functions from the R package “emmeans” (Lenth 2021) to examine pairwise differences among gears at fixed values of the Julian time covariate. We chose three covariate levels (mean  $\pm 1$  SD) that were treated as fixed constants in the model at which to make pairwise contrasts among the means of the trap types (Cohen et al. 2003). We further assessed the significance of the covariate slope for each trap type by determining whether its 95% confidence interval overlapped zero, which informed us as to the general seasonal trend for that trap type. Contrasts among covariate slopes between each trap type were tested with pairwise t-test and significance assessed using Tukey-adjusted p-values.

GLMMs and GLMs of the CPUE data were fit with both Poisson and negative binomial error distributions (log-link functions) and Julian day as the covariate. The lowest model AIC was used to discriminate which model distribution had the best quality of fit. However, because of the quantity of zeroes in the CPUE data, we also fit hurdle and zero-inflated versions of the GLMMs using R package “glmmTMB” (Brooks et al. 2017) and ascertained if these models showed better quality fits than the original GLMMs by AIC. Our motivation for examining a hurdle model along with a zero-inflated model is because the presence of bait may have a considerable influence on detecting an individual within a trap, which may be an important bias on the observed proportion of zeroes in the data. Thus, the hurdle models represented a mixture distribution that first used a logistic function to estimate a detection probability given that a trap was baited and then subsequently fit the negative binomial or Poisson error

distributions to model count probabilities. Contrastingly, the zero-inflated models assume the excess of zero counts is not from specific causes, and thus their probabilities are estimated with their own component nested within the original count models. In total, we assessed the fits of 12 GLMMs to the CPUE data consisting of two Poisson and negative binomial hurdle models, two zero-inflated models, two non-zero adjusted models, and respective versions of these models fit without a random effects term.

Carapace length data (CL) were initially analyzed with LMM and LM (i.e., linear modelling with Gaussian error), with Julian biweek set as the covariate and AIC used to discriminate the best quality fit. Julian biweek, a binned covariate consisting of Julian days comprising a two-week interval in the Julian calendar was selected over Julian day due to the weekly quantification of CL data. In preliminary assessments of model fits, we found that the normality of residuals assumption was violated (Shapiro-wilk tests,  $P < 0.001$ ) primarily because of left skew resulting from the inclusion of juveniles. However, a significant test is expected with the sample sizes we used, and the models' residuals nevertheless appeared approximately normal. We further explored potential CL biases in gears by determining whether the size distributions of the sampled CL varied across gears. For these analyses, we pooled all CL measurements across all biweeks and ponds and subsequently used pairwise Komolgorov-Smirnov tests ("DatascienceR" package, Lin 2021) between each pair of gears for each pond separately.

Sex data were recorded simultaneously during the measurement of CL and analyzed with logistic regression using GLM and GLMMs (binomial error distribution, logit link function). For sex data analyses we removed all juveniles as many were not developed enough to confidently sex (61 individuals). We then ran models to assess gear biases on 1) males versus females and 2) Form 1 males versus Form 2 males. All statistical analyses were performed in R (Version 4.0.2).

## Results

We captured 11,254 *P. clarkii* individuals across trap types over the course of this study. As expected, most individuals (9,945) were recorded in GMTs whereas the juvenile traps captured the fewest (144, Tables S2–S4). We also recorded 6,614 individuals of *F. virilis* from all gears combined and were the only other crayfish species sampled with these traps. This native species was only found in two of the four ponds we sampled, and individuals were immediately returned to the ponds after capture without any measurements taken (i.e., CL and sex).

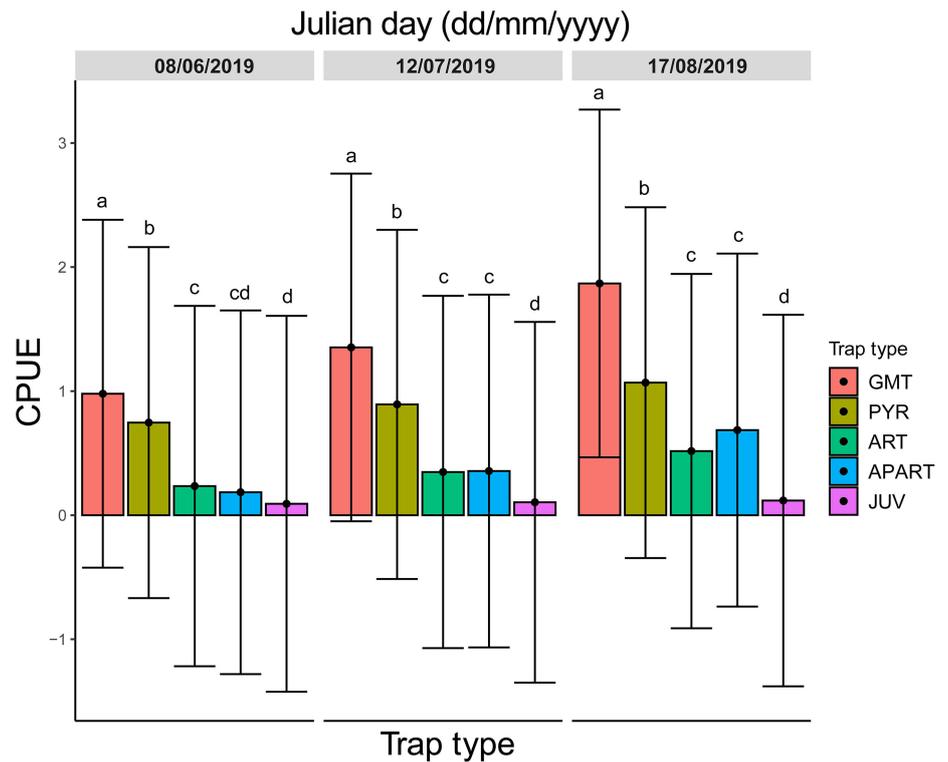
### *CPUE trends*

After subsetting the data to remove potential structural errors (e.g., observations noting lost/damaged/unbaited traps) and including only Julian

**Table 1.** Results of Wald Chi-square tests of significant parameters from LM, LMM, GLM, and GLMM fits examining CPUE differences and carapace length and sex biases among different trap types across Julian times (day or biweek). GMT = Gee’s minnow trap, PYR = pyramid trap, ART = artificial refuge trap, APART = additional partition refuge trap, JUV = juvenile mesh trap.

Response Variable	Parameter	DF	Wald $\chi^2$	P
CPUE	Trap Type	4	26.77	< 0.001
	Julian Day	1	28.24	< 0.001
	Trap Type X Julian Day	4	13.89	< 0.001
Carapace Length	Trap Type	4	54.78	< 0.001
	Julian Biweek	1	9.35	0.002
	Trap Type X Julian Biweek	4	37.38	< 0.001
Sex (Male versus Female)	Trap Type	3	1.63	0.654
	Julian Biweek	1	15.59	< 0.001
	Trap Type X Julian Biweek	3	6.75	0.080
Sex (Form 1 versus Form 2)	Trap Type	3	9.50	0.023
	Julian Biweek	1	35.57	< 0.001
	Trap Type X Julian Biweek	3	5.10	0.165

days with all 5 trap types recorded for that day across all 4 ponds (54 total Julian Days for each gear), the CPUE data consisted of 7,498 daily individual trap counts, ranging from 0 individuals to 31 individuals. Although a GLMM using a zero-inflated negative binomial error distribution showed the lowest AIC of 12 models fit to the CPUE data, the hurdle model version showed a similar AIC score ( $\Delta\text{AIC} < 2$ ). Therefore, we chose the parsimonious model and examined our CPUE data with a GLMM using a zero-inflated negative binomial error distribution. Examination of the model coefficients revealed a significant interaction of trap type with Julian day (Wald  $\chi^2 = 13.89$ ,  $P < 0.001$ ; Table 1; Figure 2), which justified examination of pairwise differences using estimated marginal means, assessed at Julian Days 159 (08 June), 193 (12 July), and 227 (17 August). In general, across all Julian days, CPUE of baited traps were between 2–5 times higher than that of ART and APART traps (all significant P-values:  $< 0.001$ , Table S5), and 9–10 times higher than JUV CPUE. Gee’s minnow traps and PYRs consistently demonstrated highest mean CPUEs of all trap types. Between the baited traps, CPUEs of GMTs were substantially (27% to 51%, all  $P < 0.02$ ) higher than the PYR traps. Mean CPUE between ART and APART traps were similar across all Julian days ( $P = 0.861$  at Julian day 159, and  $P = 0.354$  at Julian day 227), however both traps produced significantly lower mean CPUE than the baited traps across the whole study period (all  $P < 0.010$ ). Mean CPUEs of JUV traps were significantly lower (2–10 times on average; all pairwise  $P < 0.001$ ) than the other trap types across Julian days. Trends in the covariate slopes across all trap types were significantly positive (95% confidence intervals (CI): smallest 2.5 percentile = 0.002, largest 97.5 percentile = 0.025, Table S6), indicating that mean CPUE generally increased during the study period apart from JUV traps, which demonstrated no significant trend (95% CI =  $-0.0059$ , 0.0134). Pairwise t-test contrasts between covariate slope estimates indicated that the positive trends across all trap types were similar in magnitude (all  $P > 0.05$ ),

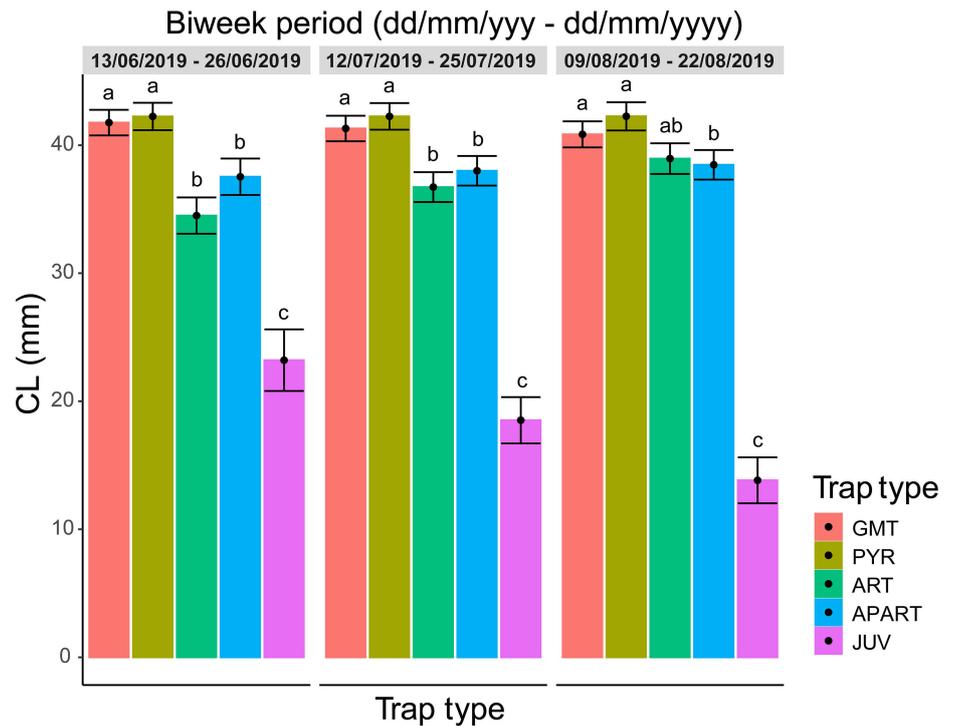


**Figure 2.** Pairwise comparisons of CPUE (mean count per trap) across different gear types given specific Julian days (presented as actual dates dd/mm/yyyy). Different letters denote statistical differences ( $P < 0.05$ ). Error bars represent standard error. Mean CPUE and standard error shown are back-transformed from model estimates on natural log scale while statistical differences in group means were assessed on  $\ln(\text{CPUE})$  scale and at fixed values of the Julian day covariable. GMT = Gee's minnow trap; PYR = pyramid trap; ART = artificial refuge trap; APART = additional partition refuge trap; JUV = juvenile mesh trap.

except for the PYR trap, which showed a significantly shallower slope than the APART trap ( $P < 0.001$ ).

### Carapace length biases

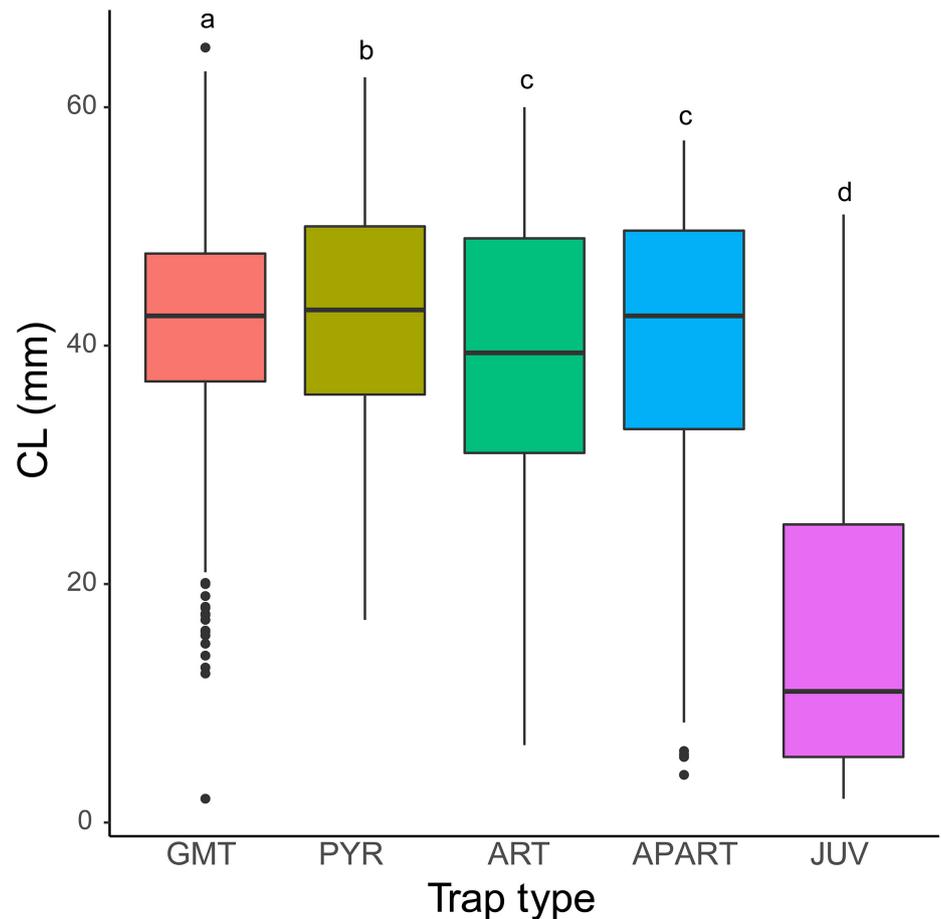
The data for assessing trap type biases towards specific CL were obtained with the aforementioned subsetting procedure, comprising a total of 3,800 individuals measured over the course of eight biweek periods (spanning approximately the same time frame as CPUE data). A LMM was found to best fit the CL data on the basis of AIC. Examination of LMM model coefficients indicated a significant interaction between trap type and Julian biweek (Wald  $\chi^2 = 37.38$ ; Figure 3), justifying our approach to make pairwise comparisons among trap types at biweeks 3 (encompassing 14 June–26 June), 5 (12 July–25 July), and 7 (09 August–22 August). Pairwise comparisons among trap types showed that on average GMT and PYR traps both generally captured the largest individuals (40.9 mm and 42.2 mm respectively) compared to non-baited traps (ranging 16 mm for JUV traps to 36 mm and 37 mm for ART and APART traps respectively, all  $P < 0.010$ , Table S7) until the end of the study season when ART and APART traps began to show similar mean CL as the PYR and GMT traps in some pairwise comparisons. Juvenile traps caught the smallest individuals throughout the



**Figure 3.** Pairwise comparisons of mean carapace length (CL, in mm) across different trap types at 3 fixed Biweek periods (dd/mm/yyyy–dd/mm/yyyy). Biweeks represent 2-week sampling periods encompassing 14 June–26 June 2021 [Biweek 3], 12 July–25 July 2021 [Biweek 5], and 09 August–22 August 2021 [Biweek 7]. Error bars represent standard error. Different letters denote significant pairwise differences ( $P < 0.050$ ). GMT = Gee’s minnow trap; PYR = pyramid trap; ART = artificial refuge trap; APART = additional partition refuge trap; JUV = juvenile mesh trap.

study period. ART and APART traps did not significantly differ from each other in size of crayfish captured across the study period ( $P = 0.225$  at Biweek 3, and  $P = 0.984$  at Biweek 7). CL trended significantly negative with Julian biweek for the GMT and JUV traps (95% CIs:  $-3.439$ ,  $-0.0822$ , Table S8) while the others trended positively, however positive slopes were only significant for the ART traps (95% CIs:  $0.528$ ,  $1.699$ ).

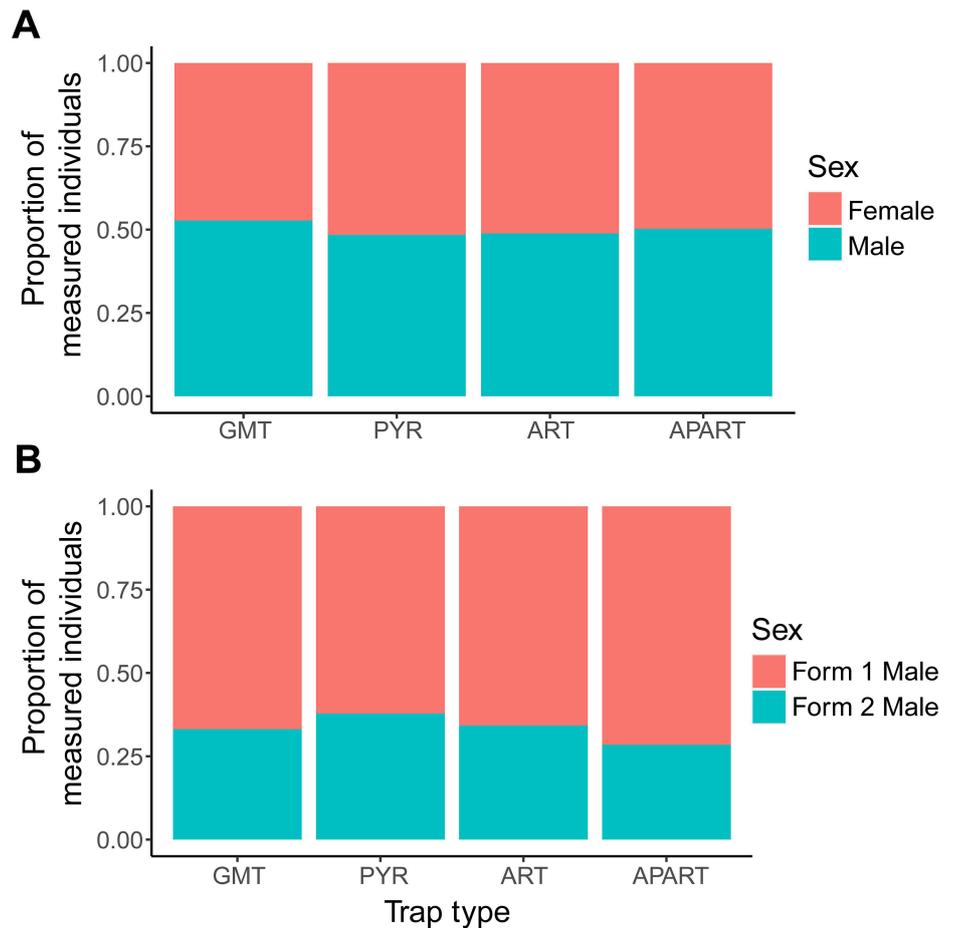
Visually, a strong overlap in the CL distributions among four trap types was observed, however, the bulk of the juvenile trap CL distribution fell mainly  $< 20$  mm (mean CL of JUV trap =  $17.3$  mm, 95% CI:  $12.7$  mm,  $21.91$  mm; Figure 4). Pairwise Komolgorov-Smirnov tests indicated that the traps differed in their overall distribution shapes and centers. Differences between the baited and unbaited traps (APART and ART) were mainly with respect to tail thickness (broader left tails in the ART and APART traps, or more representation of smaller CL) and kurtosis (GMT and PYR had narrower range of CL values). The CL distributions for GMT and PYR differed significantly from each other, and each differed from the unbaited traps (all  $P < 0.001$ ) whereas the ART and APART did not ( $P = 0.119$ ). The CL distribution for the JUV traps was visually and statistically distinct from all other traps (all  $P < 0.001$ ), being generally non-overlapping with the other trap types although with a strongly right skewed tail.



**Figure 4.** Boxplot representations of the carapace length (CL, in mm) frequency distributions for each trap type across ponds. Different letters above boxes indicate statistical differences in the frequency distribution as assessed by pairwise Komolgorov-Smirnov tests. GMT = Gee's minnow trap; PYR = pyramid trap; ART = artificial refuge trap; APART = additional partition refuge trap; JUV= juvenile mesh trap.

### *Sex biases*

We assessed trap types for sex bias using 1,772 female crayfish and 1,882 male crayfish (Form 2 = 635; Form 1 = 1,247). For the assessment of male (Form 1 + Form 2) versus female gear bias, we fit a GLM to these data as the GLMM produced a similar AIC score ( $\Delta\text{AIC} < 2$ ), which justified our choice of the more parsimonious model. Analysis of male versus female gear bias using GLM indicated that only the Julian biweek covariate was significant (Wald  $\chi^2 = 15.59$ ,  $P < 0.001$ ). Across all gears, ratios of male and female were equitable ( $\sim 50/50$ , Figure 5A), although the overall trend in the odds of sampling male crayfish was positive and increased on average by 4% (95% CI = 0.5% to 7.0%) per biweek over the sampling period. In contrast, GLMM fit to assess biases for sampling Form 1 versus Form 2 males found that both the trap type (Wald  $\chi^2 = 9.50$ ,  $P = 0.023$ ) and Julian biweek (Wald  $\chi^2 = 35.57$ ,  $P < 0.001$ ) were significant while the interaction was not (Wald  $\chi^2 = 5.10$ ,  $P = 0.165$ ). However, trap type was ultimately found to be insignificant as post-hoc comparison of pairwise means, after Tukey adjustment, demonstrated no significant pairwise differences among



**Figure 5.** Stacked bar plots showing proportions of (A) males and females and (B) Form 1 Males and Form 2 males among all crayfish individuals that were measured for carapace length for each trap type throughout the study period. Data are pooled from all ponds and from the entire season. GMT = Gee's minnow trap; PYR = pyramid trap; ART = artificial refuge trap; APART = additional partition refuge trap. Juvenile trap data not assessed.

trap types (all  $P > 0.05$ ). Measured males tended to be dominated by Form 1 individuals across all trap types (between 62% to 72% of all males, Figure 5B). The overall temporal trend in the probability of sampling Form 1 males over Form 2 males was positive with the likelihood of sampling a Form 1 male increasing on average by 20% (model slope 95% CI = 14%, 26.7%) per biweek.

## Discussion

Our study evaluated trap CPUE performances and biases of five different trap types in the midst of on-going removal efforts of *P. clarkii* in southeast Michigan. Our analysis achieved several objectives aimed at providing recommendations for future eradication planning. With respect to our first objective, baited traps generally outperformed unbaited refuge traps with respect to numbers caught with GMT and PYR traps capturing the greatest number of crayfish. Following our second objective, baited traps were consistently biased towards capturing larger individuals, unbaited refuge traps towards intermediate sized individuals, and juvenile traps towards

small individuals. No significant sex biases were recorded among the gears. However, all traps showed seasonal influences in their patterns of CPUE and body size bias, following objective 3.

When examined on count per trap bases (i.e., CPUE), the GMT and PYR traps both performed comparably better than the other three refuge traps, which suggests that baited trap designs are likely to maximize crayfish removal rates. Our results fall in line with oft-reported high CPUE in baited traps across crayfish species (Somers and Stechey 1986; Parkyn 2015; Larson and Olden 2016, but see Dorn et al. 2005), but contrasts recent findings that showed comparatively high CPUE of *Pacifastacus lenisculus* (Dana, 1852, signal crayfish) in artificial refuge traps (Green et al. 2018). One reason for this discrepancy may be because unbaited traps that simulate habitat could require deployment intervals longer than overnight to achieve comparable or higher CPUE than baited traps (Parkyn et al. 2011; Green et al. 2018). Therefore, we recommend exploring protocols that lengthen the sampling intervals of refuge traps while maintaining daily removal frequencies with baited traps. We do not recommend the use of JUV traps use for enhancing *P. clarkii* crayfish removal due to their extremely low CPUE and the ability of other traps to capture juvenile crayfish. We note that the presence and availability of alternative habitat structure across our ponds (e.g., submerged macrophytes and leaf packs) could affect captures at trap placement sites (Magoulick and Flinders 2007; Nolen et al. 2014). However, we did not take measurements of dynamic habitat variables at trap deployment sites that could be correlated with CPUE.

Our results for baited traps are consistent with Welch and Price (2009), who demonstrated baited traps tend to be biased towards larger individuals. The bias may result from aggression tendencies of larger bodied individuals excluding smaller ones (Stuecheli 1991; Ogle and Kret 2008). Our findings also point to an important source of sampling error in our existing trapping protocol because GMTs may be less effective at removing smaller (< 35 mm) reproductively capable *P. clarkii* individuals. The CL frequency distributions also demonstrated that unbaited refuge traps sampled distributions that are usually wider than either baited trap, although we note that statistical analyses of size distributions are not commonly performed for crayfish gear comparison studies. Size distribution specifics are not observable when assessing only group means and we emphasize that gear-comparison studies could benefit from a direct assessment of size frequency distribution data alongside trends in means. In all, we conclude that complementing baited traps with the ART and APART traps, which appear to be more inclusive of a wider CL range, benefits the overall removal effort.

Mesh JUV traps appeared to sample juvenile sizes as expected but captured too few to be a useful tool for managers. Sampling for juvenile-sized crayfish is of high research value because juvenile abundances yield

critical information about potential year-class strengths and overall recruitment rates for the following year (Momot 1984; Hansen et al. 2013). Although we do not recommend the particular mesh trap we used for eradication purposes due to low CPUE, other refuge-style designs demonstrate relatively higher juvenile CPUE across species (cedar bundles in hoop nets, Parkyn et al. 2011) or provide more relevant information about population-level densities (fixed-area net enclosures, Engdahl et al. 2013). Further examination of juvenile crayfish abundances could provide an important yardstick to assess eradication. Consequently, we strongly recommend that further work should examine how alternative designs could improve the representation of juvenile sizes in the total catch.

None of the five traps we examined demonstrate a particular sex bias, which runs counter to the typically reported male-sex catch biases across crayfish species, especially when using baited traps (Parkyn 2015; Larson and Olden 2016). An explanation for this documented bias is relatively higher male aggression that excludes or dissuades females and juveniles from entering the trap (Ogle and Kret 2008; Welch and Price 2009; Hilber et al. 2020). These interactions may be reduced in refuge-style traps (Barnett and Adams 2018; Green et al. 2018). Other studies have demonstrated equitable sex ratios of *P. clarkii* across 6 different styles of traps (five baited and one unbaited refuge trap similar in style to the ART, De Palma-Dow et al. 2020). In that case, the authors suggested the lack of sex bias stemmed from decreased male exclusionary biases, as the removal of large males may allow smaller individuals and females freer access to traps (see also Moorhouse and MacDonald 2011). Our data only weakly support the explanation of decreased male exclusionary bias as male captures increased through time across trap types, despite overall equitable sex ratios between gears. Sex biases of trapping gear have been previously correlated with microhabitat availability and diversity surrounding trap placement sites (Donato et al. 2018), but such data were not measured in our study to explore this possibility. In all, our ongoing removal effort will not likely be impacted by sex selectivity by the type of traps employed, but future work should attempt to measure the potential influence of habitat/microhabitat features around trap placement sites.

Although previous removals have occurred at these four study ponds in 2017 and 2018, removal rates, total captures, and trapping effort (data not shown) were not at the scale or intensity as that employed in this study. Therefore, we are confident that historical removals are not likely influential on this study's observed CPUE, size, or sex patterns. However, there are still two important caveats to our study design that likely played an important role in our CPUE and size/sex bias results. First, the protocol we followed for the daily removal effort was strongly imbalanced in favor of GMTs and limited our ability to increase the ratios of the other gear types. We concede that some CPUE variability was likely influenced by the

disproportionate representation of trap types, rather than purely reflecting catchability differences among them. This was unavoidable owing to logistic constraints imposed at the onset of the project. However, we attempted to manage these biases by restricting our analyses to those Julian days where all trap types were recorded to limit missing data and using statistical comparisons for imbalanced designs. Second, we cannot discount that one potential reason for the lack of bias in sex ratio in our study could be that the protocol of weekly random subsetting of 30 individuals per pond per trap type may not be frequent enough, or is not using large enough sample sizes, to detect sex biasing. In particular, the protocol of using the first 30 randomly picked individuals from the holding container may not have been *effectively* random at that sample size even though the container was well-mixed and individuals were randomly selected for measurements. While this explanation may partly apply to the GMTs, we note that the PYR, ART, and APART traps often failed to produce weekly catches of 30 individuals. Thus, we instead expect a confounding effect of small sample size for the other traps compared to GMTs. Nevertheless, our data suggest that any trapping strategy should focus on maximizing CPUE and capturing size diversity given the observed lack of sex bias. We also recommend that future trapping efforts consider increasing the subset size and more strictly balancing the use of alternative trap designs to increase statistical power if/when resources allow.

We determined that seasonal considerations are needed to improve trap CPUE and/or better record life history characteristics of the population (body size and sex ratios), although there are nuances. With respect to mean CPUE, all Julian day covariate slopes for each trap type were positive, likely reflecting warmer temperatures as the sampling progressed from May through to September and falling in line with historical trapping observations across crayfish species (Richards et al. 1996; Hein et al. 2007; Garcia et al. 2015). However, only the PYR and APART showed different rates of CPUE increase. This suggested that seasonal constraints on CPUE are weak and limited to relative efficiencies (i.e., CPUE/day) depending on the trap used. In contrast, seasonal CL slope magnitudes and patterns differed between baited traps versus unbaited refuge traps suggesting that seasonality is consequential to trap-specific size biases. Additionally, the overall increase in the proportion of males as the season progressed could indicate a slightly increasing likelihood of undersampling females. Results indicate our trapping design tended to be more size and sex inclusive early in the sampling season, and less so later on. The increase in male prevalence as the season progressed could reflect both generally fewer females in the population coupled with increasing fractions of females returning to underground burrows for oviposition (Loureiro et al. 2015). We caution that we cannot quantitatively disentangle trapping effort from general population dynamics/life histories, which are not assessed for *P. clarkii*

in Michigan. We conclude that the removal effort stands to benefit with increased effort (i.e., diversity and number of traps) during the early sampling period. However, this decision should be balanced by considering that relatively lower CPUE during this early period could likely and rapidly produce diminishing returns as effort increases.

Upon detecting a novel species invasion, management and legal priorities are likely to limit the temporal window for methodological research in favor of immediate response using existing knowledge, even if the data are out of date and context (Simberloff 2003; Lodge et al. 2006). Here, we demonstrate important potential sources of sampling variability in a multi-gear design, both from the trap and seasonal perspective. Our main recommendation is that the existing removal effort of *P. clarkii* in Southeastern Michigan, which relies mainly on GMT traps, should be modified and adapted by diversifying the types of traps used (e.g., APART) and considering the timing of efforts (early vs later season sampling). Because crayfish invasions are now becoming increasingly reported in the US and globally (e.g., Morningstar et al. 2020; Weiperth et al. 2020; Galinat et al. 2021), we believe studies such as ours are widely needed. We therefore strongly encourage other on-going crayfish management efforts to assess their protocols in a similar manner as this study, especially if the protocols integrate combinations of active and passive gears. With a larger body of literature devoted to gear bias, managers can hone their removal protocols for introductions of *P. clarkii*, and meet challenges associated with a diversity of environmental and management contexts.

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### Author's contributions

WRB designed statistical methodology, performed data analyses, interpreted data and wrote all drafts of the manuscript. BR, LRN, and SH conceptualized research, developed study design, obtained funding, and reviewed and edited drafts of the manuscript. SMT and KS developed study design and methodology, performed investigation and data collection, and reviewed and edited drafts of the manuscript. SNW reviewed and edited drafts of the manuscript.

## Ethics and permits

No institutional ethics review was required to conduct this study. All specimens collected and disposed during the course of this study were collected under a scientific collector's permit for crustaceans (Issued to BR for 2019; Michigan Department of Natural Resources).

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### Supplementary material

The following supplementary material is available for this article:

**Figure S1.** Photographs of trap types employed in the study.

**Table S1.** Modes (standard deviation) in number of traps sampled on a given Julian day.

**Table S2.** Summary of total individuals captured with each gear type across the study ponds.

**Table S3.** Summary of size data taken for *Procambarus clarkii* individuals subsampled from collections in traps.

**Table S4.** Summary of sex data taken for *Procambarus clarkii* individuals subsampled from collections from traps.

**Table S5.** Results of pairwise contrasts of mean catch per unit effort (CPUE) across gear types at specific Julian days (reported here as actual dates, dd/mm/yyyy).

**Table S6.** Model estimates of covariate slopes for each trap type and associated pairwise contrasts testing for differences in covariate slopes between each trap type.

**Table S7.** Results of pairwise contrasts of Carapace Length (CL, mm) across gear types at specific biweeks periods (reported here as actual week intervals dd/mm/yyyy–dd/mm/yyyy).

**Table S8.** Model estimates of covariate slopes for each trap type and associated pairwise contrasts testing for differences in covariate slopes between each trap type.

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