An evaluation of three trap designs for invasive rusty crayfish (*Faxonius rusticus*) suppression on critical fish spawning habitat in northern Lake Michigan

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Abstract

High densities of invasive rusty crayfish on critical spawning reefs present a potential impediment to the recovery of native fish in the Laurentian Great Lakes. Suppression of rusty crayfish on spawning reefs to protect fall spawning native fishes in the Great Lakes is hampered by regular storm events and ambient weather conditions, limiting the number of practical days traps can be checked, cleared, and re-baited. The Gee minnow trap design is the most common gear for sampling and managing crayfish, yet design constraints of the standard Gee minnow trap manifest as tradeoffs between capture efficiency and retention for users. In this study, we compared catch rates from a semi-controlled field experiment and escapement probabilities from laboratory controlled trials for a Gee minnow trap, a modified Gee minnow trap with intention to reduce escapement, and an experimental flat-bottomed pyramid design which showed potential promise during prototype-stage development. Bayesian parameter estimation of generalized linear models applied to catch data suggested that standard Gee minnow traps performed at least as well and often better than both novel trap designs in catch rate and escapement probability. Escapement during laboratory controlled trials was high for all trap designs, demonstrating that retention of trapped individuals is a persistent problem for crayfish monitoring and management. We conclude from our data that standard Gee minnow traps are a sensible gear choice for monitoring and/or potential suppression efforts for invasive rusty crayfish on nearshore spawning reefs in the Great Lakes. However, modifications to its design to improve retention should yet be pursued.

Key words: aquatic invasive species, trap comparisons, invasive crayfish management, Gee minnow trap, Laurentian Great Lakes

Introduction

Invasive crayfish pose severe ecological and economic threats to freshwater ecosystems globally, resulting in international calls to develop strategies for managing their spread, establishment, and impact (Gherardi 2010; Gherardi et al. 2011). Many methods have been developed for invasive crayfish sampling and control, but the most common technique is baited trapping due to its versatility, accessibility, and inexpensiveness to...
implement (Mangan et al. 2009; Parkyn 2015; Larson and Olden 2016). Despite its advantages, numerous problems persist with the use of traps for invasive crayfish surveillance and management. For example, trapping can be labor-intensive, inefficient, and lead to size or sex bias in population estimates (Brown and Brewis 1978; Abrahamsson 1981; Stuecheli 1991; Dorn et al. 2005; Almeida et al. 2013; Chadwick et al. 2021). Trapping is also dependent on crayfish behavior (e.g., territoriality), bait strength and attractiveness, habitat, and seasonality (Rach and Bills 1987; Richards et al. 1996; Ogle and Kret 2008; Pallisson et al. 2011; Kvistad et al. 2021). In addition, trap escapement as a function of soak-time is a long-recognized problem (Westman et al. 1979). Nonetheless, trapping can reduce population abundance, especially when a high effort is sustained (Stebbing 2016), or when paired with other control measures such as fisheries management (Hein et al. 2006), or other biological, chemical, or physical control methods (Hyatt 2004; Freeman et al. 2010; Gherardi et al. 2011; Stebbing et al. 2014).

One of the most common trap designs is a cylindrical galvanized steel trap, commercially manufactured and sold as the Gee’s® G-40 Minnow Trap (Tackle Factory; Fillmore, NY; hereafter referred to as Gee minnow traps), which is often modified with wider openings to accommodate entry for larger individuals. Previous criticisms of Gee minnow traps cite low retention rates and inconsistent capture probabilities, which can lead to gross underestimates of true population abundances (Riley and Fausch 1992; Dorn et al. 2005; Peterson et al. 2015; Smith 2020). Specifically, the widened opening, while increasing capture of large individuals, also increases the probability of escape for smaller individuals (Nulk 1978; Miller 1990). Attempts to ameliorate this problem have resulted in alternative trap designs or modifications at the trap entrances intended to reduce escapement (Slater 1995; Mangan et al. 2009; Ulikowski et al. 2017; Smith 2020). Many aspects of trap design, from shape to the position and size of the entrances, influence crayfish capture and retention inside traps (Westman et al. 1979; Fjälling 1995; Mangan et al. 2009). Hence, there is ongoing interest in trap design innovation to improve trapping efficiency, increase retention, reduce selectivity biases, and lower costs to managers (Slater 1995; Mangan et al. 2009; Larson and Olden 2016; De Palma-Dow et al. 2020).

In recent decades, non-native rusty crayfish *Faxonius rusticus* (Girard, 1852) have become pervasive in Lake Michigan along the shoreline, in stream tributaries, and on nearshore cobble reefs used by several fall-spawning fish (Jonas et al. 2005; Peters et al. 2014; Kvistad et al. 2021; O’Shaughnesssey et al. 2021). Fall-spawning fish such as lake trout *Salvelinus namaycush* (Walbaum, 1792), lake whitefish *Coregonus clupeaformis* (Mitchill, 1818), and cisco *Coregonus artedi* (Leseur, 1818) release their eggs over nearshore rock and cobble reef habitats in the Great Lakes where they mature over winter (Marsden et al. 1995; Scott and Crossman 1998). Egg and fry consumption of native fish eggs by rusty crayfish is a potential
impediment to natural recruitment of native fish stocks (Jones et al. 1995; Savino et al. 1999; Bronte et al. 2003; Claramunt et al. 2005; Forsythe et al. 2018). Several species of native crayfish, most prominently virile crayfish *Faxonius virilis* (Hagen, 1870) and northern clearwater crayfish *Faxonius propinquus* (Girard, 1852), also inhabit reefs in the nearshore waters of the Great Lakes and have been gradually replaced by rusty crayfish in the past decades (Peters et al. 2014). However, ambient weather conditions and regular yet unpredictable storm events impose challenges to successfully implementing an effective rusty crayfish suppression strategy in the Great Lakes by limiting the number of days that traps can be set, checked, and rebaited. In addition, previous rusty crayfish monitoring and suppression effort on northern Lake Michigan reefs suggests a narrow time window in which rusty crayfish appear susceptible to capture by baited traps, as evidenced by a rapid but fleeting increase in catch-per-unit-effort from mid- to late-October (Buckley 2017; Kvistad et al. 2021). Therefore, investigation of trap design modifications to accommodate challenging conditions, chiefly through improving catch and retention rates, is warranted if there is interest in locally suppressing invasive crayfish through trapping on Great Lakes reefs.

In this study, we compare the three trap types during a targeted rusty crayfish suppression effort on spawning reefs in northern Lake Michigan. We compared common Gee minnow traps, an altered Gee minnow trap with a throat modification intended to reduce escapement, and a novel pyramid shaped trap designed to increase catch and retention. We used a Bayesian multilevel modeling approach to evaluate relative catch rates between trap types across two major substrate categories, escapement probabilities using data from controlled laboratory trials, and the implied optimal soak time for maximizing rusty crayfish catch. We discuss the implications of our findings pertaining to rusty crayfish management on Great Lakes spawning reefs.

### Materials and methods

**Trap designs**

We evaluated three trap designs for capture and retention of rusty crayfish on Great Lakes spawning reefs, standard and modified Gee’s® G-40 minnow traps and a novel pyramid trap during removal efforts (Figure 1). Preliminary laboratory trials indicated increased capture and reduced size bias and escapement in pyramid traps compared to standard Gee minnow traps. The standard Gee minnow trap, commonly used for crayfish sampling, is made from 0.64 cm steel wire mesh (height: 23 cm, length: 45 cm) with 6 cm entrances at both ends, hereafter referred to as a non-flashing (NF) trap. The modified Gee minnow trap is identical to the unmodified Gee minnow trap, but with a thin reinforcement of aluminum sheet metal...
“flashing” around the throat, and hereafter referred to as a flashing (F) trap. The purpose of the sheet metal reinforcement was to lower the escapement probability by decreasing traction near the exits. The pyramid trap (depth: 18 cm, base: 50 cm × 49 cm) is made from 0.64 cm steel wire mesh and a single 18.5 cm × 19.5 cm entrance at the top, hereafter referred to as a pyramid (PYR) trap. The novel pyramid trap was based on a prototype designed in collaboration with, and subsequently commercially produced, by Tackle Factory™. Minor changes were made to the entrance of the commercially produced pyramid trap for manufacturing convenience. In the prototype, four equal pieces of metal flashing at a 90° slope with respect to the top of the trap came together to form a square funnel. In contrast, the commercially produced trap entrance consisted of two long pieces of metal flashing at roughly 45° angles on opposite sides and two shorter (~ 5 cm) flashing sections affixed to the adjacent sides. The pyramid trap was designed to allow crayfish to enter the trap regardless of the direction from which it was approached and metal flashing was intended to facilitate capture and prevent escapement. Preliminary laboratory trials using the prototype pyramid trap suggested a high rate of capture compared to standard Gee minnows.

All traps were baited with a mixture of generic dry dog food and coarsely chopped fish (e.g., alewife [Alosa pseudoharengus]; smelt [Osmerus mordax]; bloater chubs [C. hoyi]) held in a perforated plastic container. Traps were
replenished with fresh bait each time they were checked. All traps were fished for variable lengths of time throughout the suppression period (median soak time: 4 days; minimum soak time: 1 day; maximum soak time: 13 days), dependent on weather and sampling logistics.

**Trapping field trials**

We compared traps from late September to early November 2019 at known spawning sites for native salmonids in Little Traverse Bay (LTB), Lake Michigan, where rusty crayfish are abundant (Jonas et al. 2005; Kvistad et al. 2021). The reef in LTB is an artificial crib structure, approximately 1500 m² and in shallow water (≤ 5 m), located in the northern end of the bay near the city of Harbor Springs, MI (45°25′N; 84°56′W, hereafter; LTB Crib). For the first 50 m from the shore, the major substrate at LTB Crib is sand, then there is a continuous band of cobble on either side of the crib structure that extends offshore for approximately 35 m, followed again by sand (Figure 2).

Eight 90 m traplines consisting of seventeen traps spaced 5 m apart were set perpendicular to shore and starting roughly 10 m from the main cobble habitat. Traplines ran parallel to the artificial crib structure, which extends from shore to approximately 100 m out into the bay. Traps were placed on lines in random order to ensure an unbiased distribution of trap types.
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across major substrate categories. Because we had a limited number of pyramid traps available, only two pyramid traps were placed on each line while approximately equal numbers of flashing and non-flashing Gee minnow traps were placed in the remaining 15 spots.

We recorded the locations of the inshore and offshore anchors for each trapline with a marine GPS to map later in GIS software. Major substrate at each trap location was classified ex post facto in QGIS 3.12.1. We used the GPS coordinates at the end positions of each trap line to recreate the approximate locations of each trap. We overlaid the positions of each trap on Google Earth (Google, Menlo Park, CA) satellite background imagery and assigned a major substrate category for each trap based on underlying substrate, either “sand” or “cobble”. We only classified down to broad substrate categories because the precision of our classification estimates was probably low, and trap lines did shift occasionally (~ 1–2 m) between sampling events due to wind and waves. However, these sites were in water shallow enough (2–5 m) to be able to clearly distinguish cobble from sand in the satellite images.

In total there were 170 traps set in LTB, of which 17 were pyramid traps, 76 were flashing traps, and 77 were non-flashing traps. We replaced damaged or lost traps with new traps of the same type when possible. When no spare pyramid or flashing traps remained, we replaced damaged traps with standard non-flashing traps instead. By the fourth week of trapping, inclement weather reduced the amount of time each day that we could safely check all of the traps. Therefore, we reduced the number of traps on each line for the remainder of the trapping period from 17 to 14. The traps that were removed from each line were the first trap closest inshore and the last two furthest offshore. These traps were chosen primarily because early data indicated low catch rates compared to traps further inshore. We did not remove pyramid traps from any line due to the lower initial sample size.

As each trap was emptied, we recorded the total numbers of rusty crayfish, native crayfish, invasive round goby *Negobius melanostomus* (Pallas, 1814), and any other species caught. Any fish were measured for total length (mm). We calculated catch rate as the average number of rusty crayfish caught per trap and catch per unit effort as the number caught per trap per day. Any crayfish were measured for carapace length (mm) and sexed. We retained all rusty crayfish and round goby to be euthanized and discarded. All native species were returned unharmed to the reefs.

A concurrent study evaluating the effectiveness of experimental vinyl crayfish barriers, based on a modified fyke wing design, also took place at LTB Crib. Experimental fyke wing barriers were deployed with the intention of slowing rusty crayfish recolonization on to key habitat features on the reef. However, these experimental barriers are not the primary focus of the present study and consequently will not be discussed in detail. We acknowledge
the presence of experimental barriers at our study site as a potential source of additional variance and take steps to account for them in our statistical models (see details below).

**Escapement experiment**

We tested escapement of rusty crayfish (carapace length range: 26.0–46.3 mm) out of traps for each trap design under laboratory conditions. We placed a representative example of each trap design around the perimeter of a round plastic tub (120 cm diameter × 75 cm depth) and placed a porous plastic cup filled with a mixture of dry dog food and fish in the middle of the tub. We filled water in the tub until the top of the pyramid trap was covered in at least 6 inches of water. A randomly selected rusty crayfish was placed in each trap and allowed 24 hours to escape. Rusty crayfish were obtained during trapping field trials and held in recirculating aquaria to acclimate for at least 48 hours prior to testing. Each rusty crayfish was individually marked on its carapace with BIC Wite-Out® so it could be identified by the trap in which it was originally placed. After 24 hours, the traps were checked, and we noted whether any individuals had escaped. We repeated the escapement trials ten times for each trap type. Our escapement experiments assumed that no recaptures into the same trap occurred.

**Treatment of missing data**

Occasional missing data entries during the trapping field trials occurred due to human error and several storm events, which caused some traps to become lost or damaged to a point where they did not fish effectively. Roughly 3.7% of the total dataset contained missing values. We assumed any such missing values were missing completely at random; that is, no systematic process could explain which traps in the dataset became damaged or lost (Bhaskaran and Smeeth 2014). We then imputed the missing values using multivariate imputation by chained equations, with a predictive mean matching algorithm, using the “mice” R package (van Buuren and Groothuis-Oudshoorn 2011).

**Statistical analyses**

We used a Bayesian multilevel modeling approach to determine the relative catch and retention performance of the three trap types. Bayesian models were fit using Stan, a probabilistic programming language which employs a Hamiltonian Monte Carlo sampling algorithm (Carpenter et al. 2017), and implemented with the “rethinking” package in R as an interface to Stan (McElreath 2020). We used weakly informative regularizing priors that were consistent with our assumptions about the data generating processes, but which allowed the Hamilton Monte Carlo algorithm to
sample over a large parameter space. Values for the weakly informative priors were chosen by prior predictive simulation. Weakly informative regularizing priors are recommended in cases in which the amount of prior knowledge available is limited or when the expectations of model outcomes are highly uncertain, because they encourage the parameter estimates to be determined mostly by the data and likelihood functions, while still having a regularizing effect on influential data points (Gelman et al. 2008; McElreath 2020).

Catch rate model
We modeled rusty crayfish catch rate ($\lambda_i$; n trap$^{-1}$) with a hierarchical model, where a unique parameter was estimated for each level of all variables included in the model. All variables included in the model were categorical and therefore treated as factors in the analysis. We assumed the observed rusty crayfish counts ($y_i$) were generated from a Poisson likelihood function. The full Bayesian model expression is as follows:

$$y_i \sim \text{Poisson} (\lambda_i)$$

$$\log(\lambda_i) = \beta_{\text{Trap}[i]} + \beta_{\text{Substrate}[i]} + \beta_{\text{Zone}[i]} + \beta_{\text{Date}[i]} + \log \tau_i$$

$$\beta_{ij} \sim \text{N}(\bar{\mu}_i, \sigma_i)$$

$$\bar{\mu}_i \sim \text{N}(0, 1)$$

$$\sigma_i \sim \text{Exp}(1)$$

The estimated rate of capture ($\lambda_i$) was expressed as an additive function of trap type ($\beta_{\text{Trap}}$), major substrate ($\beta_{\text{Substrate}}$), sampling zone ($\beta_{\text{Zone}}$), and sampling date ($\beta_{\text{Date}}$). An offset term ($\log \tau_i$) was added to correct for differences in trap soak time across sampling events. Each parameter was assigned its own adaptive prior ($\beta_{ij}$), in which their respective means ($\bar{\mu}_i$) and standard deviations ($\sigma_i$) were estimated directly from the data.

Trap escapement model
We evaluated the escapement probability for each trap type using a simple hierarchical model in which a single parameter ($\alpha_{TID}$), indexed by trap type, was estimated:

$$E_i \sim \text{Bin}(1, p_i)$$

$$\logit(p_i) = \alpha_{TID[i]}$$

$$\alpha_{TID} \sim \text{N}(\bar{\alpha}, \sigma_{\alpha})$$

$$\bar{\alpha} \sim \text{N}(0, 1)$$

$$\sigma_{\alpha} \sim \text{Exp}(1)$$

The number of successful escapes ($E_i$) were predicted using a binomial trial with a probability of escape ($p_i$). The estimated parameter $\alpha_{TID}$ represented the probability of escape from each trap type. Partial pooling of information across trap types was achieved by specifying an adaptive prior distribution for $\alpha_{TID}$ in which $\bar{\alpha}$ and $\sigma_{\alpha}$ were estimated from the data directly. Numerical arguments for the hyperpriors on $\bar{\alpha}$ and $\sigma_{\alpha}$ were chosen to be weakly informative.
Soak time model

We ran a robust regression, using a Student’s *t*-distribution to represent the likelihood, to determine the optimal soak time to maximize the number of rusty crayfish caught per trap (n trap⁻¹). We used a Student’s *t*-distribution because it is considered a reasonable choice for the observation model when outliers in the data may have outsized influence on the model predictions (Vanhatalo et al. 2009; Gelman et al. 2013). The full model is expressed as follows:

\[ y_i \sim \text{t}(\mu, \sigma, \nu) \]
\[ \log(\mu) = \alpha_{TID[i]} + \beta_1 x + \beta_2 x^2 \]
\[ \beta_i \sim N(0, 1) \]
\[ \alpha_{TID} \sim N(\bar{a}, \sigma_\alpha) \]
\[ \bar{a} \sim N(0, 1) \]
\[ \sigma_\alpha \sim \text{Exp}(1) \]
\[ \sigma \sim \text{Exp}(1) \]
\[ \nu \sim \text{Gamma}(4, 1) \]

The number of rusty crayfish caught per trap (y_i) was modeled on a *t* distribution described by some mean (μ) and variance (σ), with unknown degrees of freedom (ν) and fit to a second order polynomial with a log-link function. The intercepts were allowed to vary by trap type (α_{TID}), but assumed a common adaptive prior distribution.

Model checking and derived quantities

After fitting each model, we checked the potential scale reduction factor (R*) on each parameter to assess convergence of the Markov chains (Gelman and Rubin 1992; Supplementary material Table S1). We determined Markov chain convergence when \( R* \approx 1.00 \) (± 0.01). We evaluated the fit of each model to the data by calculating a Bayesian p-value with the general formula \( P_B = Pr(T(y^{rep}, \theta) > T(y, \theta) | y) \) (Gelman 2005; Hobbs and Hooten 2015). Bayesian p-values are interpreted as the probability that some test statistic, in our case the mean, calculated from the reference distribution \( T(y^{rep}, \theta) \) exceeds the same value calculated from the data \( T(y, \theta) \). We considered models to have adequate support in the data if \( P_B = 0.1 \leq P_B \leq 0.9 \) (Gelman et al. 2013). Then, we performed graphical posterior predictive checks, in which simulated values were replicated and compared to the observed data to look for systematic discrepancies between our models and the data (Gelman and Shalizi 2013). We described differences in the estimated effects on trapping rate (\( \lambda_i \)) and escapement probability (\( E_i \)) between trap types by using the marginal posterior distributions of the parameters in each model to calculate effect sizes and other derived quantities of interest (Hobbs and Hooten 2015).
Results

Trapping field trials

Over the course of the field trials, non-flashing traps caught a total of 847 rusty crayfish with a male:female ratio of 1.09. Flashing traps caught a total of 245 rusty crayfish with a male:female ratio of 0.85. Pyramid traps caught a total of 105 rusty crayfish with a male:female ratio of 0.60. The length-frequency histograms for each trap type were approximately normally distributed across both substrate and sex categories with an overall average carapace length (mm; μ ± SD) of 31.70 ± 4.67 for females and 33.50 ± 4.30 for males (Figure 3). During the entire trapping period, we replaced 44 non-flashing traps, 76 flashing traps, and 8 pyramid traps, corresponding to failure rates of 4.2%, 11.6%, and 5.2%, respectively.

Figure 3. Sex-length frequencies of rusty crayfish caught in each trap type across both major substrate categories.
Non-flashing traps had the highest cumulative catch rate (corrected for number of traps) at 10.50 (n trap$^{-1}$), followed by the pyramid traps 9.18 (n trap$^{-1}$), then flashing traps at 5.39 (n trap$^{-1}$). Average (± SD) catch per unit effort (CPUE; n trap$^{-1}$ day$^{-1}$) over the trapping field trials was 0.17 ± 0.32 for non-flashing traps, 0.11 ± 0.27 for flashing traps, and 0.17 ± 0.48 for pyramid traps. Pairwise comparisons of CPUE between trap types suggested that flashing traps caught fewer rusty crayfish relative to non-flashing and pyramid traps, while CPUE between non-flashing and pyramid traps was roughly equal (Figure 4).

Pairwise comparisons of the parameter estimates using samples from the posterior suggested a 76% probability that the catch rate for non-flashing traps was higher than for flashing traps, a 54% probability that the catch rate for non-flashing traps was higher than for than pyramid traps, and only a 27% probability that the catch rate for flashing traps was higher than for pyramid traps. The median pairwise differences in the marginal posterior distributions of the parameter estimates for trap type (i.e., effect size) were 0.30 for the NF-F comparison, 0.002 for the NF-PYR comparison, and −0.29 for the F-PYR comparison (Figure 5).

Mean observed and predicted catch per trap within trap types differed across substrate categories (Table 1; Figure S1). During our study, average catch per trap for non-flashing traps was 14% greater on cobble versus sand, while flashing traps performed roughly equally on both substrate types, with only a 4% difference between cobble and sand substrates, slightly in favor of sand. By contrast, average catch per trap for pyramid traps was 48% greater on sand than on cobble. However, regularized predictions from the fitted model suggested that non-flashing traps are only expected to catch 6% more rusty crayfish on cobble compared to sand, flashing traps are expected to catch 4% fewer rusty crayfish on cobble compared to sand, and pyramid traps are expected to only catch 7% more rusty crayfish on cobble compared to sand.
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Figure 5. Pairwise differences in the posterior parameter estimates for each trap type from the model of trap performance. Dashed vertical lines indicate the median estimate for each comparison.

Table 1. Summary statistics for empirical observations and model predictions of rusty crayfish catch rates (n trap\(^{-1}\)) across each combination of trap type and substrate category.

| Trap type | Major substrate | Sample size (n) | Mean observed (SD) | Mean predicted (89% HDI) |
|-----------|----------------|----------------|-------------------|-------------------------|
| NF        | Cobble         | 280            | 0.75 (1.25)       | 0.72 (0.21 – 1.73)     |
|           | Sand           | 340            | 0.66 (1.08)       | 0.68 (0.20 – 1.75)     |
| F         | Cobble         | 178            | 0.42 (0.75)       | 0.44 (0.13 – 1.12)     |
|           | Sand           | 276            | 0.46 (0.90)       | 0.46 (0.05 – 1.07)     |
| PYR       | Cobble         | 43             | 0.51 (0.94)       | 0.72 (0.21 – 1.65)     |
|           | Sand           | 113            | 0.76 (1.51)       | 0.67 (0.22 – 1.71)     |

Posterior predictions of the model of trap performance generally resembled the empirical data, but the variability in catch across trap and major substrate types was high (Figure 6). Pairwise comparisons of the parameter estimates using samples from the marginal posterior distributions suggested > 99% probability that non-flashing traps performed better than flashing traps, a 67% probability that non-flashing traps performed better than pyramid traps, and a < 0.001% probability that flashing traps performed better than pyramid traps. The median estimates of the percent difference in expected catch was +34% (89% HDI: +24%–+42%) for the NF-F comparison, +5% for the NF-PYR comparison (89% HDI: −11%–+22%, and +31% (89% HDI: +16%–+44%) for the F-PYR comparison. The Bayesian p-value describing the overall fit of the trapping model was p = 0.68.

Escapement experiment

The median posterior probability of escape, based on predictions from the trap escapement model, was 49.6% (89% HDI: 27.8–71.0%) for non-flashing traps, 75.9% (89% HDI: 57.9–96.2%) for flashing traps, and 59.7% (89% HDI: 39.1–77.7%) for pyramid traps (Figure 7). Using samples from the posterior distributions of the parameter estimates, we calculated that
Figure 6. Mean posterior predictions (closed points) with 89% HDIs (vertical bars) compared to the observed means (open points) and one standard deviation (error bars) on each sampling event.

there was a 91% probability that the true probability of escape from flashing traps was higher than for non-flashing traps. Likewise, there was an 83% probability that the true probability of escape from flashing traps was higher than for pyramid traps. Finally, we estimated that there was a 72% probability that the true probability of escape from pyramid traps was higher than for non-flashing traps. The Bayesian p-value for the escapement model was \( p = 0.37 \).

**Soak time**

The soak time that maximized catch (n trap\(^{-1}\)) implied by the model of catch versus nights fished was 5.6 nights (Figure 8). The expected number of rusty crayfish per trap after fishing for 5.6 nights was 1.10 (89% HDI: 0.71–1.48) for non-flashing traps, 0.77 (89% HDI: 0.48–1.07) for flashing traps, and 0.99 (89% HDI: 0.71–1.23) for pyramid traps. The Bayesian p-value for the soak time model was \( p = 0.42 \).
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Discussion

Our objective in this study was to compare trapping efficacy for a common and widely used trap design (Gee minnow) against two experimental trap designs (a modified Gee minnow and a novel pyramid shaped design). We

Figure 7. The mean posterior probability of escape from each trap type across all trials (n = 10). Filled points are the model predicted probabilities and the line ranges are the 89% highest posterior density intervals. Open points are the observed proportions of successful escapes. The solid line marks the 50% probability line, while the dashed line represents the grand mean escapement probability (59%) across all three trap types.

Figure 8. Mean predictions (solid line) and 89% HDI (shaded regions) for the robust regression of catch (n trap⁻¹) against the number of nights fished. Observed data (open points) and standard errors (vertical lines) are displayed for reference. The optimal number of nights fished for all trap types implied by the model was 5.6 nights.
evaluated each design on measures of catch rate, escapement probability, and soak time. Average catch rates were similar between non-flashing and pyramid traps, but our modeling suggests that the modified Gee minnow with metal flashing had both the lowest expected catch rate and the highest expected escapement. Contrary to our expectations, the addition of metal flashing to the throat of the standard Gee minnow traps resulted in overall worse performance compared to unmodified Gee minnows and pyramid traps.

Our experiments revealed that rusty crayfish catch rates were not enhanced by the novel pyramid design when compared to the standard non-flashing Gee minnow traps. In spite of a lower sample size, catch rates and retention in pyramid traps were at least comparable to non-flashing traps. However, the pyramid traps were more difficult to work with in the field. The approach used to secure the base of the trap door used for clearing the trap was slower and harder to open. In addition, the bulkier design created issues with storage on the boat when clearing lines of multiple traps and, while the pyramid shape was designed to be stacked, in practice our teams avoided stacking to reduce risk of damage to the flashing devices at the entrances. The flat bottom of the pyramid traps occasionally caused them to sit incorrectly when used on uneven substrates (e.g., large cobble and boulders), potentially impacting their ability to fish. Our perception was that we experienced more practical difficulties using the pyramid traps than either of the Gee minnow trap designs. Partly because we set rows of multiple traps tethered to a single line, we also noticed a tendency for pyramid traps to tip over when wind and wave activity was high, which caused the lines to shift and dragged the traps across the substrate. More importantly, minor changes made to the final design of the pyramid traps for production convenience, specifically to the trap entrance, may have contributed to higher escapement than we anticipated based on preliminary results from its prototype design. Lastly, pyramid traps were roughly three times the cost of a standard Gee minnow trap, although costs would come down if they were produced at scale. Until issues of escapement, clearance, ease of use, and versatility can be resolved, our judgement is that standard non-flashing Gee minnow traps remains a sensible option for rusty crayfish control on Lake Michigan reefs.

**Escapement**

Escapement resulting from design weaknesses, trap saturation, bait depletion, and other reasons present major limitations for developing long-term fishing strategies in many decapod crustacean fisheries (Miller 1979; Robertson 1989). While the pyramid design we tested did not reduce the probability of escape compared to a standard Gee minnow design, others have seen success with flat-bottomed top-entry traps. For example, Ulikowski et al. (2017) tested a flat-bottomed design with a top entrance
compared to cylindrical Evo traps and found that it reduced escapement. Kozak and Policar (2003) investigated escapement rates from Evo traps and found escapement rates similar to what we observed in our study ($\mu \pm SD = 40\% \pm 29\%$). Similar escapement trials run by Smith (2020) also showed high escapement rates nearing 50% in unmodified minnow traps, and also found that the rate of escape increased as traps became more densely crowded. Smith (2020) developed a simple plastic trap mouth modification for standard Gee minnow traps to restrict the size of the entrances from the inside, which successfully doubled the maximum saturation level compared to unmodified Gee minnow traps in a semi-controlled field study. The application of a simple throat restriction like the one developed by Smith (2020) could potentially allow for a cost-effective rusty crayfish suppression strategy in the Great Lakes.

Crayfish are generally crepuscular and commonly found in murky environments, leading to a reliance on tactile and chemical stimuli to aid navigation through their surroundings (McMahon et al. 2005). Tactile cues are important for helping crayfish find preferred cover (Alberstadt et al. 1995). A frequently observed behavior in laboratory experiments is “wall-following” in which animals walking parallel to a wall will trail the end of one of its antennae along the wall, using the surface texture to navigate (Basil and Sandeman 2000; Koch et al. 2006; Patullo and Macmillan 2006). Basil and Sandeman (2000) also suggested that changes in topography motivates exploratory behavior in crayfish. Furthermore, it is well understood that crayfish are capable of learning and adapting to environments with novel topography quickly (Basil and Sandeman 2000; Shuranova et al. 2005). We hypothesize that the abrupt change in surface texture from wire mesh to solid sheet metal on the inside of the flashing traps may have provided a tactile cue for captured rusty crayfish to orientate themselves inside of the traps, thereby facilitating high escapement rates.

**Soak time**

Our study found that average rusty crayfish catch (n trap$^{-1}$) maximized at roughly 5.6 nights, a longer soak time than is typically recommended for crayfish sampling using baited traps. Baited traps are conventionally set for 24 hours to achieve maximal catch efficiency (Capelli and Magnuson 1983; Lewis 1997; Montgomery 2005; Larson and Olden 2016). Hardee (2009) noted that catches of red swamp crayfish *Procambarus clarkii* (Girard, 1852) in 24 hour sets were 36% higher than 48 hour sets, possibly explained by bait depletion. Pfister and Romaine (1983) recommended even shorter soak times reporting maximal catch rates between 6 and 12 hour sets. Given the generally crepuscular behavior of crayfish, Edsman and Söderbäck (1999) recommended setting traps at dusk and removing them at first light. However, the observed peak in catch occurring after
more than five days indicates that catch maximization may occur slower on Lake Michigan reefs than in other contexts, at least during the fall when our study took place.

Storm events at our study sites are common during the time of year in which our study took place. Therefore, unaccounted for sources of variance imposed by extreme weather may have influenced our inferences regarding soak time. While it is unknown how rusty crayfish respond to such weather events, their susceptibility to capture is almost certainly influenced. However, rusty crayfish are most susceptible to trapping during the fall months on Lake Michigan reefs (Buckley 2017; Kvistad et al. 2021). As such, unique challenges persist in developing invasive crayfish suppression strategies on Lake Michigan reefs. Future developments in technologies or methodological approaches in these environments must place inordinate focus on the influence of weather and seasonality compared to similar endeavors in inland lakes and streams. For example, it may be more effective to employ alternative removal methods (e.g. diver hand removals) starting earlier in the summer before switching to trapping in the fall to achieve greater cumulative removals before extreme weather events begin to preclude suppression operations. Such a strategy that leverages multiple removal methods would be consistent with the bulk of the current literature which emphasizes the use of numerous strategies to provide broad coverage of all life-history stages (Larson and Olden 2016; Green et al. 2018; Chadwick et al. 2021).

**Size and sex biases**

All three trap designs were ineffective at capturing juvenile and sub-adult rusty crayfish (< 20 mm carapace length). While such a size bias is common among many trap designs, it should be acknowledged that if conventional traps are to be used as a primary approach for a suppression strategy that the juvenile population will likely be unaffected. This could have important implications for the overall effectiveness of a suppression strategy. For example, harvest strategies that disproportionately target adults can result in an overcompensatory recruitment response in the juvenile population for some species (Zipkin et al. 2008, 2009). Therefore, caution should be advised to avoid unintentionally producing undesirable population-level outcomes.

We observed female dominant sex biases for both flashing and pyramid traps, and a slight male bias for non-flashing traps. Biased sex ratios in trapping methods are common, but a male bias is typically reported (Brown and Brewis 1978; Stuecheli 1991; Matthews and Reynolds 1995; Price and Welch 2009). Some have reported seasonal differences in sex biases, noting that sex ratios which typically skew male become female dominated in late summer and fall (Mason 1975; Byrne et al. 1999).

Artificial refuge traps may be a pragmatic alternative to conventional baited traps in certain situations to help reduce sex and size biases in sampling and removal programs. For example, Green et al. (2018) observed
approximately equal sex ratios of signal crayfish (*Pacifastacus leniusculus*) caught in novel artificial refuge traps compared to a significant male bias in conventional baited funnel traps. Although there is disagreement as to whether artificial refuge traps can remove as many crayfish as conventional baited traps using the same level of effort (Green et al. 2018; De Palma-Dow et al. 2020), their ability to reduce size and sex biases is clear (Green et al. 2018; Curti et al. 2021). As such, Curti et al. (2021) recommended the combined use of artificial refuge traps and baited minnow traps for red swamp crayfish removal from California streams. Further experimentation with alternative trap designs, such as artificial refuge traps, on Great Lakes reefs may provide insights into best practices for localized rusty crayfish suppression.

**Trap loss and damage**

The rate of damage and/or loss for the flashing traps was nearly triple that of non-flashing and pyramid traps, raising concerns for the potential of ghost fishing. Ghost fishing occurs when lost or un-retrieved fishing gear continues to ensnare organisms long after it is beyond the control of the fisher, leading to increased mortality (Matsuko et al. 2005). Ghost fishing occurring from derelict crab and lobster traps has been a non-trivial conservation concern for fishery managers along the coastal waters of the United States for several decades (Pecci et al. 1978; Smolowitz 1978). Recent evidence suggests that derelict crab pots are capable of effectively fishing for up to seven years, indicating potential for long-term cumulative effects on a fishery (Maselko et al. 2012). While we had few instances of bycatch of non-target organisms at our study sites, the potential long-term threat to native fish and crayfish from derelict gear cannot be entirely discounted. Therefore, reinforcements to current trap designs to prevent excess damage and/or losses may be prudent when considering trap removal programs in nearshore waters of the Great Lakes.

**Conclusions**

Invasive crayfish management is a global problem in need of technological and strategic solutions (Stebbing 2016). Intensive trapping is a common control strategy for invasive crayfish populations due to its simple concept. However, trapping alone using conventional baited traps is likely insufficient to successfully manage invasive crayfish populations outside of a few special circumstances, such as in small isolated water bodies (Gherardi et al. 2011; Hudina et al. 2017). Myriad other control methods have been suggested and/or attempted with some success such as drainage (Chadwick et al. 2021), biocides (Peay et al. 2006; Sandodden and Johnson 2010), and predator enhancement (Hein et al. 2006). Regardless, most alternative crayfish management strategies have been tested in inland lakes and streams and are unlikely to scale successfully to large continuous water bodies, like the nearshore zones of the Great Lakes. Nonetheless, practical limitations leave
baited traps as one of few effective options for invasive crayfish sampling and management in large lentic systems (Mangan et al. 2009; Larson and Olden 2016). Although the trap design modifications tested in this study ultimately did not improve trapping efficiency, our study highlights the difficulties inherent in trapping crayfish on Great Lakes reefs. Finally, our study underscores the importance of solving escapement issues with a common trap design used for crayfish sampling and suppression.

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Authors’ contribution

JTK: research conceptualization; sample design and methodology; investigation and data collection; data analysis and interpretation; ethics approval; original draft. TLG: research conceptualization; sample design and methodology; investigation and data collection; ethics approval; funding provision; review/editing. DFC: research conceptualization; sample design and methodology; investigation and data collection; ethics approval; funding provision; review/editing. WLC: research conceptualization; sample design and methodology; investigation and data collection; ethics approval; funding provision; review/editing. AJT: research conceptualization; sample design and methodology; investigation and data collection; ethics approval; funding provision; review/editing. MEH: research conceptualization; sample design and methodology; investigation and data collection; ethics approval; funding provision; review/editing.

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Supplementary material

The following supplementary material is available for this article:

**Table S1.** Marginal posterior parameter estimates on the linear predictor scale of each of the three models fit to describe catch rates, escapement, and soak time.

**Figure S1.** Mean predicted and observed rusty crayfish catch in all three trap types tested.

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