# Evaluating active and passive sampling methods to quantify crayfish density in a freshwater wetland 

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#### Abstract

We evaluated the sampling efficacy of $1-\mathrm{m}^{2}$ throw traps (active sampler) and baited minnow traps (passive sampler) across an experimental density gradient ( $1,2,4,6,8,10$, and $15 / \mathrm{m}^{2}$ ) of the slough crayfish (Procambarus fallax) in 2 trials with different crayfish populations. In both trials, throw-trap density estimates were highly correlated with actual crayfish density ( $r^{2}=$ 0.96 ). The form of the relationships between density estimates and stocked densities was consistent between trials, and indicated that throw traps captured a similar proportion of the stocked crayfish regardless of the stocked density. When we adjusted the relationships to account for clearing efficiency (proportion of captured animals actually recovered from the trap), the slopes of the regressions were not significantly different from 1 in either trial. Size distributions and sex ratios of crayfish collected by the throw traps accurately reflected those of the stocked populations. Baited minnow traps performed inconsistently between the 2 trials. Catch-per-unit-effort (CPUE) and density were significantly correlated only in Trial $2\left(r^{2}=0.82\right)$. The slope of the regression in Trial 2 ( 0.621 ) was significantly $<1$, and the intercept was positive and nearly significant ( $p=0.074$ ), indicating that minnow traps captured increasingly smaller proportions of the stocked crayfish as the stocked density increased (i.e., differences between CPUE values underestimated actual differences between stocked densities along the gradient). Minnow traps were biased toward capturing large male crayfish, but the form of the relationships between CPUE and density did not improve when large-male CPUE was used in the regressions. Our results suggest that 1-m² throw traps provide better estimates than baited minnow traps of crayfish densities in shallow vegetated habitats.


Key words: population size, crayfish, density, throw trap, minnow trap, Procambarus fallax, wetland.

Sampling aquatic animals to estimate population size (or density) and community composition is an important issue that has received considerable attention in a variety of settings including lakes (Chick et al. 1992, Lamontagne and Rasmussen 1993), streams (Rabeni et al. 1997, DiStefano et al. 2003), freshwater wetlands (Jordan et al. 1997), and estuaries (Rozas and Minello 1997, Kneib and Craig 2001). A major hurdle in obtaining good population estimates is verifying the effectiveness of the sampling method. Passive sampling methods usually involve a trap of some sort that can be left in the environment to catch animals that come in contact with it. Passive sampling methods integrate density over an unspecified area, and they depend on animal abundance and animal activity levels. Therefore, they actually measure activi-ty-density (e.g., Collins et al. 1983). In contrast, active sampling methods usually involve many collections or counts of animals within small units of volume or area scattered around an en-

[^0]vironment. The overall effectiveness of a sampling method depends critically on the ability of the method to quantify differences in population density and assemblage structure in space and time.
Monitoring crayfish populations is of particular interest to researchers and resource managers for several reasons. First, crayfish can have high standing-stock biomass and secondary production rates in a variety of systems (Momot et al. 1978, Rabeni et al. 1995), and they are often important prey items for larger, vertebrate predators (Rabeni 1992, Robertson and Frederick 1994, Dorn and Mittelbach 1999). Second, crayfish strongly influence community structure and ecosystem function through a variety of trophic and nontrophic activities (e.g., predation, herbivory, bioturbation, macrophyte removal; Lodge et al. 1994, Nyström et al. 1996, Dorn and Wojdak 2004). Third, crayfish are actively harvested for human food or fish bait (Roell and Orth 1992, Gherardi and Holdich 1999). Last, crayfish diversity in North America is threatened by continued introduction of nonindigenous species from other watersheds or continents (Lodge et al. 2000). Thus, monitoring
crayfish populations has many benefits for management and conservation priorities.

Crayfish are an integral part of the Everglades food web, and they provide food for wading birds, frogs, alligators, and fish (Robertson and Frederick 1994). Therefore, crayfish populations and assemblages have been targeted as performance measures to assess the success of the Comprehensive Everglades Restoration Plan (CERP) (Ogden et al. 2003). At present, no basis exists for choosing among crayfish sampling methods, particularly in wetland environments like the Everglades.

Many active and passive methods have been used to sample crayfish from aquatic habitats (e.g., baited traps, electrofishing, diver collections, quadrat sampling devices; Roell and Orth 1992, Lamontagne and Rasmussen 1993, Richards et al. 1996, Rabeni et al. 1997, DiStefano et al. 2003) and some researchers have used a combination of active and passive methods (Harper et al. 2002). Different methods have been compared to one another in a relative sense (e.g., Capelli 1975, Collins et al. 1983, Rabeni et al. 1997), but no studies have compared the efficacy of sampling methods across a known density gradient.

We evaluated the ability of active ( $1-\mathrm{m}^{2}$ throw traps) and passive (baited minnow traps) sampling methods to estimate crayfish density and demographic population measures (i.e., size structure and sex ratio) of the slough crayfish (Procambarus fallax) in field enclosures with a known experimental density gradient. We defined throw-trap accuracy as the congruence between the density estimates and the actual density in the environment. We also estimated clearing efficiency of the throw traps (average proportion of animals enclosed by the throw trap that is collected) to determine the extent to which clearing inefficiency can cause inaccurate density estimates (see Jordan et al. 1997, Rozas and Minello 1997).

## Study System

Our research was conducted in emergent wet prairies of Water Conservation Area 3B (WCA 3B) in Dade and Broward Counties, Florida (density-gradient experiment location: lat $25^{\circ} 49.8^{\prime} \mathrm{N}$, long $80^{\circ} 31.8^{\prime} \mathrm{W}$ ), from September through November 2003. WCA 3B is a $320-\mathrm{km}^{2}$, state-managed portion of the greater Everglades
ecosystem that lies north of Everglades National Park and immediately west of Miami, Florida. These marshes are normally dry ( $<5 \mathrm{~cm}$ depth) in late May to early June, but during most of the year, water depths range between 30 and 80 cm (JCT, unpublished data). WCA 3B vegetation consists primarily of discrete patches of spikerush (Eleocharis spp.) or sawgrass (Cladium jamaicensis) with emergent stem densities ranging from 20 to $>2000 / \mathrm{m}^{2}$. The communities and vegetation dynamics typical of these marshes have been detailed elsewhere (Busch et al. 1998, Turner et al. 1999). The slough crayfish can be found in both patch types (Hendrix and Loftus 2000) throughout Everglades National Park and the WCAs, but our work focused on spikerush habitat because current programs for monitoring of fish and other species target this habitat. Natural crayfish densities can range between 0 and $>40 / \mathrm{m}^{2}$ in spikerush habitat, but are commonly between 1 and $4 / \mathrm{m}^{2}$ (JCT, unpublished data). Similar densities occur in sawgrass habitat (Hendrix 2000).

## Methods

## Experimental design

Between October 30 and November 20, we constructed experimental crayfish-density gradients in an Eleocharis cellulosa-dominated marsh found in WCA 3B. Mean crayfish density in the experimental site was 1.82 individuals $/ \mathrm{m}^{2}(1 \mathrm{SE}$ $=0.21, n=39$ samples). We stocked 7 experimental enclosures ( $3.2 \times 3.2 \mathrm{~m}$, open on top and bottom, aluminum and plastic walls) with different numbers of crayfish. We made the bottoms of the enclosure walls of heavy aluminum sheeting and sank them 25 cm into the sediment to prevent crayfish escape. We attached heavygauge, flexible black plastic to the top edge of the aluminum sheeting with rivets ( 3 mm ) and washers (\#6) placed every 7 cm to seal the plastic tightly to the metal. The plastic part of the wall extended 95 cm up from the sediment and extended 25 cm above the water line. We suspended the top edges of the plastic walls by ropes that were strung through and attached to polyvinyl chloride (PVC) stakes along the sides and at the corners of the enclosure. To access the enclosures for throw trapping, we climbed over the walls using 2 stools.

We conducted 2 separate trials using the same

TABLE 1. Crayfish population parameters and habitat characteristics in the density-gradient trials. Population parameters are based on the crayfish added to the enclosures. Habitat characteristics are means for the marsh habitat within the enclosures, as measured in throw traps. NA $=$ not applicable.

|  | Trial 1 |  | Trial 2 |  |
| :---: | :---: | :---: | :---: | :---: |
|  | Mean (1 SE) | Limits | Mean (1 SE) | Limits |
| Crayfish |  |  |  |  |
| Size (mm carapace length) | 17.7 (0.05) | 9-31.5 | 18.6 (0.4) | 9-29.9 |
| Sex ratio (male:female) | 1.02 | NA | 1.55 | NA |
| Habitat |  |  |  |  |
| Water depth (cm) | 72.6 (3) | 68.5-77 | 70.4 (1) | 69-72 |
| Stem density ( $\mathrm{no} . / \mathrm{m}^{2}$ ) | 49.3 (7.5) | 28-85 | 64 (5.9) | 45-91 |
| Total periphyton volume (mL) | 4683 (550) | 2400-6700 | 4250 (512) | 1800-6000 |
| Fish density (no./m²) | 34.6 (5.9) | 24.5-66.5 | 23.3 (2.5) | 13.5-31.5 |
| Macroinvertebrate density ${ }^{\text {a }}$ (no. $/ \mathrm{m}^{2}$ ) | 11.5 (2.5) | 2.5-22 | 12.5 (1.9) | 7-22 |

${ }^{\text {a }}$ Mostly grass shrimp, dragonfly larvae, and large snails
experimental densities $(1,2,4,6,8,10$, and 15 individuals $/ \mathrm{m}^{2}$ ) of marked crayfish. We randomly assigned the densities to the enclosures, and we took care to ensure similar size distributions and sex ratios in each enclosure within a trial. We set up the enclosures for the trials in areas that were 50 to 100 m apart, and we used different collections of crayfish in each trial. Habitat features were similar between the trials (Table 1), but the crayfish used in Trial 2 were significantly larger than those used in Trial 1 (paired $t$-test on enclosure means, $\mathrm{df}=6, t=$ $-10.8, p<0.001$; Table 1). We began Trial 1 on 3 November and Trial 2 on 17 November, a week after Trial 1 trial ended.

We collected crayfish for the trials with minnow traps and throw traps from a variety of areas around WCA 3B during the 2 to 5 wk preceding the trials. The size distributions were skewed toward relatively large animals because most crayfish came from minnow-trap collections, and we did not use the smallest (most fragile) crayfish ( $<9 \mathrm{~mm}$ carapace length [CL]). We housed crayfish in laboratory tanks and fed them macrophytes and shrimp pellets prior to marking. We marked crayfish that were $>15$ mm CL by punching a hole in the left uropod with a sewing needle (Guan 1997). We marked smaller crayfish by clipping the left uropod ( $\sim 50-60 \%$ removed) with a fingernail clipper. On 3 November, we placed 460 measured and marked crayfish in the experimental enclosures. After stocking, we allowed the marked crayfish
to settle for 40 h (over 2 nights) before sampling began on 5 November.

## Throw-trap sampling

The $1-\mathrm{m}^{2}$ throw trap consisted of a $90-\mathrm{cm}-$ deep copper frame covered by $1.5-\mathrm{mm}$ nylon mesh on the sides (open on top and bottom). The throw trap captured only those crayfish within the $1-\mathrm{m}^{2}$ area of the trap. To account for patchy crayfish distributions within the enclosures, we took 2 throw-trap samples from each enclosure $(20 \%$ of the total area of the enclosure). We estimated sample densities obtained from throw traps by calculating the mean of the 2 throw-trap samples in each enclosure. To make 2 throws in each enclosure without trampling vegetation, we set both throw traps within a 20 -s interval. Each trap fell from the surface to the sediment in $\sim 1 \mathrm{~s}$. We set the $1^{\text {st }}$ throw trap in the center and the $2^{\text {nd }}$ trap in a randomly chosen position around the perimeter of the enclosure. We used this partially randomized scheme, rather than a completely randomized one, to minimize potential biases resulting from edge (wall) effects on crayfish distributions or behaviors.

After setting both throw traps, we entered the enclosures and cleared the traps. We measured water depth and vegetation parameters (stem counts and periphyton-mat volume; Jordan et al. 1997) in the traps before removing animals. We measured water depth with a meter stick. The
thick floating or attached algal mats characteristic of Everglades marshes are a mixture of live and dead algae, Utricularia spp., and detritus (Turner et al. 1999). We quantified the mat volumetrically by removing it from each trap and placing it in a large graduated cylinder (with holes in the sides that allowed water to drain). We collected crayfish and other animals by passing a $1 \times 0.3-\mathrm{m}$ bar seine through the trap (sometimes bumping along or scraping the bottom) until $\geq 3$ consecutive sweeps returned no fish or macroinvertebrates. We followed this procedure by sweeping the trap 10 times with a dip net. We alternated between using a fine ( $0.5-\mathrm{mm}$ mesh) and a coarse ( $1.5-\mathrm{mm}$ mesh) net during sweeps.

We preserved all fish and invertebrates except crayfish in $10 \%$ formalin; we euthanized fish with MS222 before preserving them. We sexed and measured recovered crayfish, examined them for marks, and released them after each trial.

## Throw-trap clearing efficiency

The accuracy of throw-trap density estimates can be affected if animals escape while the trap is falling (capture efficiency) and by the efficiency of the clearing technique used to collect enclosed animals from the trap (Jordan et al. 1997). We estimated clearing efficiency by attempting to recapture a known number of crayfish that we had placed in a trap. We estimated throw-trap clearing efficiency 10 times in a variety of water depths ( $63-72 \mathrm{~cm}$ ), stem densities ( $416.5 \pm 219$ stems $/ \mathrm{m}^{2}$, range $=34-2239$ ), periphyton biovolumes ( $4360 \pm 743 \mathrm{~mL} / \mathrm{m}^{2}$, range $=1600-10,000$ ), and fish densities ( $23.4 \pm 5.7$ fish/trap, range $=7-65$ ). We used crayfish that ranged from 7.4 to 26.5 mm CL (mean $=16.7$ $\pm 0.48 \mathrm{~mm}$ [SE]). For each of 10 clearing-efficiency tests, we measured 10 crayfish (nearest $0.1-\mathrm{mm} C L)$, marked them, and placed them in a throw trap that we already had set in the marsh. We did these tests outside the enclosures, but in similar habitats. We allowed the crayfish to settle for 15 to 50 min before we started clearing with the bar seine. We examined captured crayfish for marks and measured them to look for size biases in clearing efficiency.

## Minnow-trap sampling

At 0800 h on 5 November (the day before we conducted the throw-trap sampling), we set one cylindrical Gee Exotic Fish trap (minnow trap) ( $3-\mathrm{mm}$ mesh, $2-\mathrm{cm}$-diameter openings, Memphis Net and Twine catalog number G40CF) in the center of each enclosure. We removed the minnow trap after 24 h . We baited each minnow trap with a cob of corn ( 210 g damp mass). Previous sampling with a variety of traps (baited and unbaited) in nearby marshes showed that corn-baited minnow traps captured more crayfish than similar unbaited traps and, unlike liv-er-baited traps, did not attract vertebrate predators (NJD, unpublished data). We used 1 trap/ enclosure because minnow traps are not area (density) samplers, and $\geq 2$ minnow traps in close proximity would have competed for the same animals. Furthermore, the unit of effort in most field studies is a single trap. We sexed and measured recovered crayfish, examined them for marks, and placed them back in their respective enclosures. Thirty minutes later, we sampled the enclosures with throw traps. We always used minnow traps before throw-trapping because throw-trapping is a destructive sampling technique that could have altered crayfish behaviors by disturbing the vegetation and sediment.

## Statistical analysis

We fit density estimates and CPUEs from the respective capture methods (sample density) to the stocked-density gradient using linear regressions with stocked density as the predictor variable, and we determined whether the slopes of the regressions differed from 0 (SAS, version 9.0, SAS Institute, Cary, North Carolina). Our primary objective was to determine whether the capture methods sampled consistent proportions of the stocked crayfish regardless of the stocked density. We determined how well sample densities obtained from each capture method reflected the gradient of stocked densities by comparing the slopes of each regression to 1 with 2 -tailed $t$-tests.

We did additional regression analyses for each capture method using information about efficiency and capture biases to determine whether the additional information improved the form or fit of the regressions. Throw-trap

Table 2. Regression statistics describing the relationship between stocked crayfish density and throw-trap density estimates or minnow-trap catch-per-unit-effort (CPUE) in the density-gradient trials. Adjusted stocked density was calculated based on throw-trap clearing efficiency (see text for details).

|  | Variable | df | Coeficient | SE | $t$ | $p$ | 95\% confidence limits |  | $r^{2}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  |  |  | Upper | Lower |  |
| Throw-trap density vs stocked density |  |  |  |  |  |  |  |  |  |
| Trail 1 | Intercept | 1 | 0.163 | 0.634 | 0.26 | 0.807 | -1.467 | 1.793 |  |
|  | Density | 1 | 0.899 | 0.079 | 11.32 | $<0.001$ | 0.695 | 1.103 | 0.96 |
| Trial 2 | Intercept | 1 | -1.103 | 0.616 | -1.79 | 0.133 | -2.686 | 0.479 |  |
|  | Density | 1 | 0.820 | 0.077 | 10.63 | <0.001 | 0.622 | 1.018 | 0.96 |
| Throw-trap density vs adjusted stocked density |  |  |  |  |  |  |  |  |  |
| Trial 1 | Intercept | 1 | 0.163 | 0.634 | 0.26 | 0.807 | -1.467 | 1.793 |  |
|  | Density | 1 | 1.017 | 0.090 | 11.32 | $<0.001$ | 0.786 | 1.248 | 0.96 |
| Trial 2 | Intercept | 1 | -1.103 | 0.616 | -1.79 | 0.133 | -2.686 | 0.479 |  |
|  | Density | 1 | 0.928 | 0.087 | 10.63 | <0.001 | 0.703 | 1.152 | 0.96 |
| Minnow-trap total-crayfish CPUE vs stocked density |  |  |  |  |  |  |  |  |  |
| Trial 1 | Intercept | 1 | 2.270 | 1.396 | 1.94 | 0.110 | -0.883 | 6.295 |  |
|  | Density | 1 | 0.219 | 0.175 | 1.25 | 0.267 | -0.231 | 0.668 | 0.24 |
| Trial 2 | Intercept | 1 | 2.346 | 1.041 | 2.25 | 0.074 | -0.332 | 5.024 |  |
|  | Density | 1 | 0.621 | 0.131 | 4.76 | 0.0005 | 0.622 | 1.018 | 0.82 |
| Minnow-trap large-male CPUE vs stocked density |  |  |  |  |  |  |  |  |  |
| Trial 1 | Intercept | 1 | 1.606 | 0.723 | 2.22 | 0.077 | -0.252 | 3.464 |  |
|  | Density | 1 | 0.103 | 0.091 | 1.14 | 0.305 | -0.129 | 0.336 | 0.21 |
| Trial 2 | Intercept | 1 | 2.402 | 1.232 | 1.95 | 0.109 | -0.765 | 5.569 |  |
|  | Density | 1 | 0.526 | 0.154 | 3.41 | 0.019 | 0.129 | 0.922 | 0.70 |

density estimates are influenced by clearing efficiency, so we used the estimate of clearing efficiency to adjust the stocked crayfish density (i.e., we calculated the estimable number of crayfish, given clearing efficiency). We recalculated the regressions for each trial using the adjusted stocked densities and tested again to see whether the slopes differed from 1 (i.e., to see whether clearing efficiency accounted for the difference between density estimates and stocked density). Minnow-trap samples often are biased toward large males, and large-male CPUE often is used as an index of population density (Capelli and Magnuson 1983, France 1985, Lodge et al. 1986), so we recalculated the minnow-trap regression substituting large-male (CL > 19 mm ) CPUE for total-crayfish CPUE. Substituting one CPUE value for another theoretically could change the slope or fit of the relationship.
We compared the size distributions of crayfish captured by throw traps and minnow traps to the size distributions of the stocked crayfish to evaluate size biases of the capture methods.

For each trial, we pooled all crayfish captured by throw traps into a single sample, and we pooled all crayfish captured by minnow traps into a single sample. We calculated the size distributions of each pooled sample and of the crayfish stocked in the enclosures, and we used graphical inspection and separate KolmogorovSmirnov tests (one for each trial and capture method) to assess differences between the size distributions of the stocked crayfish and the captured crayfish (Systat, version 10.0, SPSS, Chicago, Illinois).

## Results

## Throw-trap performance

In both trials, the regressions describing the relationships between stocked density and throw-trap density estimates were positive, significant, and had high coefficients of determination (Table 2, Fig. 1A). The slopes of the relationships were similar between trials ( 0.899 vs 0.820 ), but more crayfish were caught in the $1^{\text {st }}$


Fig. 1. Relationships between throw-trap density estimates and the stocked density of marked crayfish (A), and the adjusted density of marked crayfish (B). Adjusted density was calculated based on throw-trap clearing efficiency (see text for details). See Table 2 for regression statistics. The dashed line indicates the idealized relationship (1:1) between density estimates and stocked density.
trial than in the $2^{\text {nd }}$ (Fig. 1A). The slope from Trial 1 did not differ significantly from $1(t=$ 1.27, $p>0.1$ ), but the slope from Trial 2 was significantly $<1(t=2.34,0.025<p<0.05)$.

The size distribution of crayfish caught in the throw traps did not differ significantly from the stocked distribution (Fig. 2A, B) in either trial (Trial 1: $D=0.144, p=0.104$; Trial 2: $D=0.15$, $p=0.184$; Fig. 2C, D). The sex ratios (male:female) of crayfish caught by throw traps (1.07 and 1.4) did not differ from the sex ratio of the stocked crayfish (1.02 and 1.55) in either trial (G $<0.17, p>0.5)$.

## Throw-trap clearing efficiency

The mean \% of marked animals recaptured in clearing-efficiency tests was $88 \%$ ( $1 \mathrm{SE}=2$, limits $=80-100 \%$ ). The time allowed for settling had no obvious influence on clearing efficiency
( $r^{2}=0.03, p=0.63$ ). The \% of crayfish recovered was not related to vegetation characteristics (periphyton: $r^{2}=0.01, p=0.79$; stem density: $r^{2}=$ $0.17, p=0.24)$, but we found an overall bias against recapturing the smallest crayfish (Fig. $3)$.

When the stocked density of crayfish (predictor variable) from the enclosure experiment was adjusted to account for clearing efficiency (i.e., the adjustment reduced the stocked densities by $12 \%$ ), the slopes of the regression lines in Trials 1 and 2 increased to 1.017 and 0.928 , respectively (Table 2, Fig. 1B). The adjusted slopes for both trials were not significantly different from $1(t=0.19$ and $0.91, p>0.25$ and 0.1 , respectively), indicating that clearing efficiency accounted for nearly all of the difference between estimated and stocked densities.

## Minnow-trap performance

In Trial 1, the slope of the relationship between stocked density and minnow-trap CPUE was not significantly different from 0 (Table 2, Fig. 4A), indicating that minnow-trap CPUE did not change as a function of stocked density. The regression from Trial 2 was significant and positive $\left(r^{2}=0.82\right.$; Table 2, Fig. 4A). The slope (0.621) was significantly $<1 \quad(t=2.92, p<$ $0.025)$, and the $y$-intercept was positive (2.346) and close to significant ( $p=0.074$, Table 2). The form of the Trial-2 regression indicated that comparing CPUE values (when used as an index of density or population size) will yield underestimates of actual differences in density (i.e., differences between density estimates and differences between corresponding stocked densities are disproportionate) and the underestimates become increasingly large as more disparate densities are compared. Substituting large-male CPUE for total-crayfish CPUE did not improve the fit or form of these regressions (Table 2, Fig. 4B). Relative to the regressions for total-crayfish CPUE vs stocked density, the regressions for large-male CPUE vs stocked density in both trials had lower $r^{2}$ values, shallower slopes, and similar large, positive y-intercepts.
The size distributions of crayfish caught by the minnow traps were significantly different from those of the stocked populations ( $D=$ 0.542 and $0.583, p<0.001$ ), and they clearly were skewed toward large ( $\mathrm{CL}>19 \mathrm{~mm}$ ) individuals in both trials (Fig. 2E, F). Captures

Trial 1
Trial 2


FIG. 2. Summed size-frequency distributions of carapace lengths (CL) of crayfish added to the enclosures at the beginning of Trials $1(\mathrm{~A})$ and $2(\mathrm{~B})$, captured with throw traps in Trials $1(\mathrm{C})$ and $2(\mathrm{D})$, and captured with minnow traps in Trials 1 (E) and 2 (F).
were slightly male-biased in the $1^{\text {st }}$ trial but were significantly male-biased in the $2^{\text {nd }}$ trial; the sex ratios of the stocked populations were 1.02 and 1.55 in the 2 trials (Table 1), whereas the sex ratios of crayfish captured in the min-now-trap ratios were $1.42(G=0.78, p>0.25)$ and 4.17 ( $G=8.13, p<0.005$ ), respectively.

## Discussion

## Active sampling with throw traps

Throw-trap sampling provided accurate estimates of density, size distributions, and sex ratios of the slough crayfish in Everglades spikerush habitats. After adjusting for clearing efficiency, the slopes from both trials did not differ
significantly from 1 (Fig. 1B), indicating that the throw traps sampled the same proportion of the population regardless of stocked density, and differences between density estimates and the actual density in the enclosure could be explained by less-than-perfect clearing efficiency. The size distributions of crayfish captured in throw traps were similar to the size distributions of crayfish stocked in the enclosures. However, we stocked few small crayfish ( $<11 \mathrm{~mm}$ CL ) in the enclosures, and small crayfish were recovered infrequently in clearing efficiency tests. Thus, the close correspondence of the stocked and sample size distributions may have been affected by the relative scarcity of small individuals in the stocked populations.

Throw traps yielded good estimates of


Fig. 3. Proportions of marked crayfish recaptured in throw-trap clearing-efficiency tests. Numbers within the bars indicate the total number of crayfish of each carapace-length (CL) size class used in the efficiency tests.
stocked densities, but we consistently caught fewer crayfish per trap in Trial 2. The difference in capture rates between trials probably was a result of differences in the populations used in the 2 trials. Large crayfish, which were more abundant in Trial 2, may have been better able than small crayfish to escape the throw traps as the traps fell to the bottom of the enclosure. Also, the individual condition and survival of animals may have differed between the trials, as several small crayfish molted and a few died ( $<10$ total) during the marking and transportation process of Trial 2.

We estimated $88 \%$ clearing efficiency for crayfish. Jordan et al. (1997) found a similar (83\%) clearing efficiency for small ( $<8 \mathrm{~cm}$ standard length) fish in similar wetland habitats. Throw traps and other similar enclosure samplers give good population density estimates of fish in freshwater marshes (Jordan et al. 1997) and shallow vegetated zones of lakes (Chick et al. 1992), and both fish and decapods in shallow marine and estuarine habitats (Pihl and Rosenberg 1982, Rozas and Minello 1997). Conceptually similar area-based (quadrat) sampling methods are used commonly to measure crayfish densities in streams (Creed 1994, DiStefano et al. 2003, Flinders and Magoulick 2003) and lakes (Lamontagne and Rasmussen 1993, Kershner and Lodge 1995), but Rabeni et al. (1997) noted that quadrat sampling devices could be used effectively in only a subset of stream hab-


Fig. 4. Relationships between catch-per-unit-effort (CPUE) and stocked density for total crayfish (A) and large (carapace length [CL] $>19 \mathrm{~mm}$ ) male crayfish (B) captured in corn-baited minnow traps. See Table 2 for regression statistics. The dashed line indicates the idealized relationship (1:1) between CPUE estimates and stocked density.
itats. Similarly, the throw trap is probably less effective in wetland habitats with hard or uneven substrate surfaces (Kobza et al. 2004). Similar experimental studies of sampling method effectiveness across known density gradients have not been conducted in lakes or streams.

## Passive sampling with minnow traps

Minnow-trap CPUE did not adequately reflect differences in crayfish densities along the stocked gradient. The slope of the regression was not significantly different from 0 in Trial 1 and was significantly $<1$ in Trial 2. In general, minnow traps do not provide a clear estimate of density because they are not area-specific, so predicting how minnow-trap CPUE values should vary with changes in crayfish density is difficult. A relationship that adequately reflects changes in density could have any significant
positive slope if the $y$-intercept were close to 0 (e.g., CPUE could always be $1 / 2$ or $2 \times$ the density). However, $y$-intercepts for our minnowtrap regressions were $>0$ (but not significant), whereas the slopes were $<1$. The combination of a positive $y$-intercept and a slope $<1$ meant the regression line actually intersected the ideal regression line, and that intersection indicated relative overestimation of low stocked densities and underestimation of high stocked density. For example, we had an enclosure with 1 crayfish $/ \mathrm{m}^{2}$ and another with $8 / \mathrm{m}^{2}$, an $8 \times$ true difference in density between enclosures. When we sampled those enclosures with minnow traps in Trial 2, we perceived from the CPUE estimate that the population in the higher-density enclosure was only $3 \times$ greater than that in the lowerdensity enclosure (i.e., a $3 \times$ perceived difference vs an $8 \times$ true difference). Comparing the predicted CPUE values from the Trial- 2 regression (instead of the actual CPUE values) yielded even greater underestimates. Thus, CPUE either failed to discriminate any differences in density (Trial 1) or changed disproportionately with regard to true density and underestimated real differences between levels of the stocked density gradient (Trial 2). Differences in the slopes (and fits) of the regressions between the trials could have been influenced by demographic differences between the 2 populations used in the trials; specifically, the greater proportion of large males stocked in Trial 2 may have lowered the trap-shyness or inhibition of the entire population.

The minnow traps did not capture many small or medium crayfish ( $<18 \mathrm{~mm} \mathrm{CL}$ ), indicating that minnow traps were biased toward capturing animals in the largest size classes. The prevalence of large crayfish (especially large males) in traps has been reported before (e.g., Brown and Brewis 1978, Capelli and Magnuson 1983, Lodge et al. 1986) and has caused others to use adult-male CPUE as an index of population density (France 1985, Lodge et al. 1986). In our study, using large-male CPUE in the place of total CPUE did not improve the regressions (Table 2).
Minnow traps have proven ineffective for sampling stream crayfish (Rabeni et al. 1997), but studies in north temperate lakes indicate that minnow-trap CPUE can be positively correlated with other measures of crayfish density (e.g., diver counts) (Capelli 1975, Capelli and

Magnuson 1983, Collins et al. 1983). In Trial 2 of our study, large-male CPUE and total-crayfish CPUE were both positively related to stocked crayfish density. Nevertheless, simply indicating a positive correlation between minnow trap CPUE and other estimates of density (diver counts, quadrat counts, stocked density, etc.), does not mean that minnow-trap CPUE (used as an index of density) accurately quantifies differences in population density. In our study, the form of the relationship indicated that using CPUE as an index of density underestimated actual differences in population density.
Lake-wide average minnow-trap CPUE for large male crayfish in 4 Wisconsin (USA) lakes was positively correlated with mean population density estimates from SCUBA quadrat counts (Capelli 1975), but CPUE apparently overestimated differences in density between the lakes (negative $y$-intercept and a slope of $\sim 2.8$; estimated from re-plotting Capelli 1975). Minnowtrap CPUE was sometimes, but not always, positively correlated with diver counts of crayfish density in a larger study of 17 Ontario lakes (Collins et al. 1983). CPUEs of Orconectes spp. and Cambarus robustus were lower than expected based on diver counts in 4 of the lakes where densities of fish predators (Micropterus spp. and Ambloplites rupestris) were high (Collins et al. 1983). Crayfish in those lakes were less active and entered traps less often than in lakes with fewer predators, presumably because of the greater encounter rate with predators. In the remaining 13 lakes, most of which had lower predator densities, CPUE was strongly correlated with crayfish counts, but the form of the relationship suggested that CPUE, used as an index of density, underestimated differences in density. Predators were apparently absent (no observations or captures) from our enclosures, so we think it unlikely that predators could have been responsible for the lack of a significant relationship in Trial 1 or the shallow slope of the relationship between CPUE and density in Trial 2. We suggest that small differences in the habitat (e.g., stem density, periphyton quality, or periphyton quantity) among enclosures or social interactions among crayfish in and around traps could have caused the inconsistent or weak relationships in our study.
Regardless of the mechanism, the generally shallow slopes produced by minnow traps in our study suggest that CPUE with minnow
traps will, at best, provide underestimates of total crayfish density, and at worst, not reflect changes across density gradients at all. Others have detailed similar problems with using minnow traps to estimate fish densities quantitatively (He and Lodge 1990, Rozas and Minello 1997, Robichaud et al. 2000, Kneib and Craig 2001). Minnow-trap CPUE integrates activity and density, and we suggest that minnow traps might be better used to estimate movement or activity rates (when combined with independent density estimates) rather than simple densities. We recommend throw traps for reliable estimates of crayfish densities and size distributions in vegetated wetland habitats such as those found in the Everglades.

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