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## Signal from the noise: model-based interpretation of variable correspondence between active and passive samplers

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**Abstract.** Combining information from active and passive sampling of mobile animals is challenging because active-sampling data are affected by limited detection of rare or sparse taxa, while passive-sampling data reflect both density and movement. We propose that a model-based analysis allows information to be combined between these methods to interpret variation in the relationship between active estimates of density and passive measurements of catch per unit effort to yield novel information on activity rates (distance/time). We illustrate where discrepancies arise between active and passive methods and demonstrate the model-based approach with seasonal surveys of fish assemblages in the Florida Everglades, where data are derived from concurrent sampling with throw traps, an enclosure-type sampler producing point estimates of density, and drift fences with unbaited minnow traps that measure catch per unit effort (CPUE). We compared incidence patterns generated by active and passive sampling, used hierarchical Bayesian modeling to quantify the detection ability of each method, characterized interspecific and seasonal variation in the relationship between density and passively measured CPUE, and used a predator encounter-rate model to convert variable CPUE–density relationships into ecological information on activity rates. Activity rate information was used to compare interspecific responses to seasonal hydrology and to quantify spatial variation in non-native fish activity. Drift fences had higher detection probabilities for rare and sparse species than throw traps, causing discrepancies in the estimated spatial distribution of non-native species from passively measured CPUE and actively measured density. Detection probability of the passive sampler, but not the active sampler, varied seasonally with changes in water depth. The relationship between CPUE and density was sensitive to fluctuating depth, with most species not having a proportional relationship between CPUE and density until seasonal declines in depth. Activity rate estimates revealed interspecific differences in response to declining depths and identified locations and species with high rates of activity. We propose that variation in catchability from methods that passively measure CPUE can be sources of ecological information on activity. We also suggest that model-based combining of data types could be a productive approach for analyzing correspondence of incidence and abundance patterns in other applications.

**Key words:** active and passive sampling; activity rate; catchability; detection probability; encounter-rate model; incidence; occupancy models.

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## INTRODUCTION

Multi-method data sets have the potential to increase inference about biodiversity dynamics, but also present challenges for the data analyst. Different sampling methods are often sensitive to different ecological processes and vary in their ability to detect rare species or specific life stages (Elphick 2008, Magurran et al. 2010, Jiménez et al. 2016). Nonetheless, if differences in method performance are understood and they are used in a complementary fashion, combining observations from different sampling methods can increase statistical power to characterize biodiversity, temporal trends, and population status (King and Porter 2005, Manley et al. 2005, Nichols et al. 2008). Data from different sampling methods can be combined within models that account for method-specific detection probabilities (Nichols et al. 2008), such as hierarchical Bayesian occupancy models (Coggins et al. 2014, Jiménez et al. 2016). Furthermore, aggregating data from multiple detection methods through an ecological model that reconciles their relationships can yield emergent biological information (Miller et al. 2015). Combining information from complementary sampling methods can produce novel information that cannot be gleaned from each method considered separately or the aggregation of data by linear approaches that lack an underlying conceptual basis.

Combining information from active and passive sampling of mobile animals presents both pitfalls and opportunities. Active sampling for density (individuals per unit area) involves overcoming or enclosing mobile animals and yields counts of organisms standardized by sampling area or volume. Examples of active-sampling gear include enclosure samplers, quadrats, and sweep nets. Passive measurement of catch per unit effort (CPUE) consists of counts of organisms that move into (encounter) and are retained by sampling devices such as gill nets, Malaise traps, sticky traps, and pitfall traps, deployed for a standard sampling time (Southwood and Henderson 2000). Because active measures of density are discrete point estimates in time, the probability of not detecting animals that are present can bias results. This detection issue produces the veil-line effect (Preston 1948), where rare species are not observed in a random

sampling of community members because of inadequate effort relative to their density. By continuously sampling over longer periods of time, passive samplers may increase the likelihood to detect cryptic and sparse species (Ribeiro et al. 2008). CPUE derived from passive sampling is not an estimate of abundance but provides an index proportional to it that can inform temporal or spatial comparisons if movement rates are constant (Quinn and Deriso 1999). However, detection rates from passive encounter-sampling devices, such as camera traps and gill nets, are related to both local density and activity patterns (Rudstam et al. 1984, Hancock and Legg 2012, Burton et al. 2015). In some cases, patterns obtained from passive samplers are related more to variation in movement behavior of the targeted animals than to variation of their density (He and Lodge 1990, Dorn et al. 2005, Burton et al. 2015, Miller et al. 2015). Agreement between active and passive measures of abundance can vary among locations and time periods (Rotherham et al. 2012), with the potential for misinterpretation of changes in CPUE as changes in abundance, when only catchability was changing (Quinn and Deriso 1999).

The importance of catchability, the relationship between capture rate and density, has long been appreciated by fishery biologists conducting stock assessments that rely on CPUE to assess abundance trends (Hilborn and Walters 1992, Quinn and Deriso 1999). Entomologists that collect insects with passively sampled traps (Miller et al. 2015) and wildlife biologists using trail-camera methods (Burton et al. 2015) are also confronting this challenge. More recently, concerns over detection probability, the odds of detecting a species that is present, in applications such as occupancy modeling have expanded the appreciation of this issue to questions of occupancy, distribution, and community dynamics (MacKenzie et al. 2002, Rota et al. 2011, MacManamy et al. 2014). Catchability as the proportion of a population captured per unit of sampling effort emerges from the probabilities of a given gear-type encountering and then capturing a particular target (Engstrom-Heg 1986). Given that detections could be considered successful captures, this conceptual model of catchability as an emergent pattern of encounter and capture probabilities is similar to detection probability, the probability

per unit effort of detecting at least one individual of a targeted taxon given that it is present in the sampled area (Seber 1982, MacKenzie et al. 2002). Both parameters share a sensitivity to probabilities of encounter and capture, with a key difference being their response to increasing abundance. As abundance increases, encounter probability should also rise, but capture probability, and not detection probability, may decrease because of gear saturation (Harley et al. 2001). This saturation point is where catchability and detection probability diverge and is associated with the condition of hyperstability, where CPUE exhibits little change over moderate to high densities (Harley et al. 2001). A growing body of work has called into question the practice of ignoring variation in catchability and detection probability (Archaux et al. 2012, Villegas-Rios et al. 2014, Gwinn et al. 2016), but what is less appreciated is the possibility that variation in catchability can itself provide ecological information.

Obaza et al. (2011) proposed treating catches from a passive encounter sampler as an encounter rate that could be modeled as though the trap is a stationary sit-and-wait predator. They used the MacKenzie and Kiorboe (1995) version of the Gerritsen and Strickler (1977) predator encounter-rate model:

$$E = VN + \mu AN \quad (1)$$

In this Eq. 1,  $\mu$  is the speed of the prey,  $A$  is the search area of the predator, and  $V$  is volume searched per unit time ( $A$  and  $V$  can be treated as constants for a passive sampler), and  $N$  is the density of fish. Therefore, fish speed is proportional to the relative difference between the encounter rate and population density:

$$(\mu \propto [E - N]/N) \quad (2)$$

Obaza et al. (2011) and Hoch et al. (2015) found that this approach yielded reasonable estimates of movement speed (m/s) when compared to independent estimates from the literature, but recommended use of these values as an index of relative speed or activity. Activity rates have numerous implications for ecological dynamics, such as spatiotemporal patterns of colonization and the interaction strength between predators and prey (Leibold et al. 2004, Navgar et al. 2008).

The objectives of this study were to compare incidence patterns generated by active and passive sampling, quantify the detection ability of each method, characterize how interspecific and seasonal variation in activity changes the relationship between density and passively measured CPUE, and use a predator encounter-rate model to convert variable CPUE–density relationships into ecological information on activity rates. This investigation was conducted within the context of monitoring freshwater fish in the Florida Everglades, where fish biomass is dominated by small-bodied species with an annual life history whose spatiotemporal distribution is shaped by the interaction between seasonal fluctuations in rainfall and landscape structure (Lofthus and Kushlan 1987, Trexler et al. 2002, Ruetz et al. 2005). We predicted that passive sampling would have higher detection probabilities at low densities than active sampling because passively sampled gear continuously samples over longer intervals of time than point collections by active samplers. We also predicted that CPUE would increase with density at a faster rate during seasonal declines of water depth because seasonal dispersal and reduced water volume would increase encounter rates with passively sampled gear. Using the approach of Obaza et al. (2011), we translated variable catchability into novel information on activity rates and used this information to assess interspecific responses to changing water levels and identify locations with high non-native fish activity.

## METHODS

### Data collection

Sampling was conducted in three surveys at 31–35 fixed sampling plots (Table 1) encompassing three different regions of the Florida Everglades (Everglades National Park [ENP], Water Conservation Area 3 [WCA], and the Departmentalization Physical Model area [DPM]; Fig. 1). Surveys were conducted at the end of the wet season (survey 1: October and November 2014), the transition between seasons (survey 2: December 2014 and January 2015), and in the early dry season (survey 3: February 2015). Depending on region, the active-sampling method consisted of 3–7 replicate collections per plot with a 1-m<sup>2</sup> throw trap shown to provide an

Table 1. Number of plots sampled (Plots) and samples collected per plot (Samples) with throw traps and drift fences.

Survey	Region	Plots	Throws	Fences	3-mm traps	6.4-mm traps
1	ENP	10 (4)	7	3	3	3
	WCA	6	5	3	0	3
	DPM	15	3	3	0	3
2	ENP	14 (6)	7	3	3	3
	WCA	6	5	3	0	3
	DPM	15	3	3	0	3
3	ENP	9 (9)	7	3	3	3
	WCA	10 (10)	5	3	3	3
	DPM	15 (15)	3	3	3	3

Notes: Everglades National Park (ENP), Water Conservation Area 3 (WCA), and the Decentralization Physical Model area (DPM) were regions that differed in the number of throw trap samples (Throws) collected per plot. All samples (i.e., all four gear types) were combined to determine which plots were occupied by target species, with occupied plots then used to estimate detection probabilities. This included 6.4-mm wire-mesh minnow traps (6.4 mm) that were deployed in every plot and 3-mm wire-mesh minnow traps (3 mm) that were deployed in a subset of ENP plots (reported parenthetically in the Plots column) during the first two surveys and all plots during the third survey.

accurate estimate of plot-level fish density (Jordan et al. 1997). Fishes were passively collected for 24 h per sample event by using three X-shaped drift fences consisting of four plastic ground-cloth wings extending 12 m from a central square at 45-degree angles. Four unbaited, 3-mm wire-mesh minnow traps, only open on one end, were embedded on each side of the square such that wings directed fish into trap openings facing each of the cardinal directions (Obaza et al. 2011, Hoch et al. 2015). Concurrent sampling with 3-mm and 6.4-mm wire-mesh minnow traps not embedded in drift fences was not the focus of this study, but when present, detections by these gear types were used to refine estimates of detection probability by identifying plots where target species were present but not detected by either throw traps or drift fences (Table 1). In all analyses, fish catches were censored to only include individuals >10 mm standard length to eliminate size-related retention issues with 3-mm minnow traps (Obaza et al. 2011, Gatto and Trexler 2019) and focus on differences arising from encounter rate and rarity. Water depth change at each plot was estimated over a 30-d period ending on sampling date with

Everglades Depth Estimation Network models that integrate real-time data collection from water gauges with models of surface elevation (<http://sofia.usgs.gov/eden/>).

#### Detection probability and density–CPUE relationship

Incidence (proportion of plots with at least one specimen of a target species), detection probabilities (probability that a target species was present in at least one sample if known to be present), and relationships between capture rate and density were derived from simultaneous use of active measurements of density and passive measurement of CPUE. Data for detection probabilities and incidence patterns were aggregated by regions with the same throw trap sampling effort (Table 1), corresponding to marsh plots downstream (ENP) and upstream (WCA) of the L29 levee and the DPM region (Fig. 1). Incidence data were aggregated as the sum of plots within each region where at least one individual of a particular species was detected, while detection probabilities were aggregated from the detection history (i.e., number of detections and non-detections) of each plot within a focal region. Incidence patterns derived from drift fences and throw traps were compared within each region, while regional detection probabilities were estimated for six species: Bluefin Killifish *Lucania goodei*, Eastern Mosquitofish *Gambusia holbrooki*, Flagfish *Jordanella floridae*, Sailfin Molly *Poecilia latipinna*, Dollar Sunfish *Lepomis marginatus*, and African Jewelfish *Hemichromis letourneuxi*. Bluefin Killifish, Eastern Mosquitofish, Flagfish, and Sailfin Molly are among the most abundant native species in this system and have been documented to vary in their recovery time from hydrological disturbance (Ruetz et al. 2005), and, along with the Dollar Sunfish, differ in their behavioral response to hydrological cues (Hoch et al. 2015). African Jewelfish was included as it is a non-native species currently undergoing rapid range expansion within Everglades National Park (Kline et al. 2014).

Region-specific detection probabilities for each sampling method were estimated for each of the six focal species with a Bayesian modeling approach with hierarchical priors that incorporated detection histories from all three surveys.

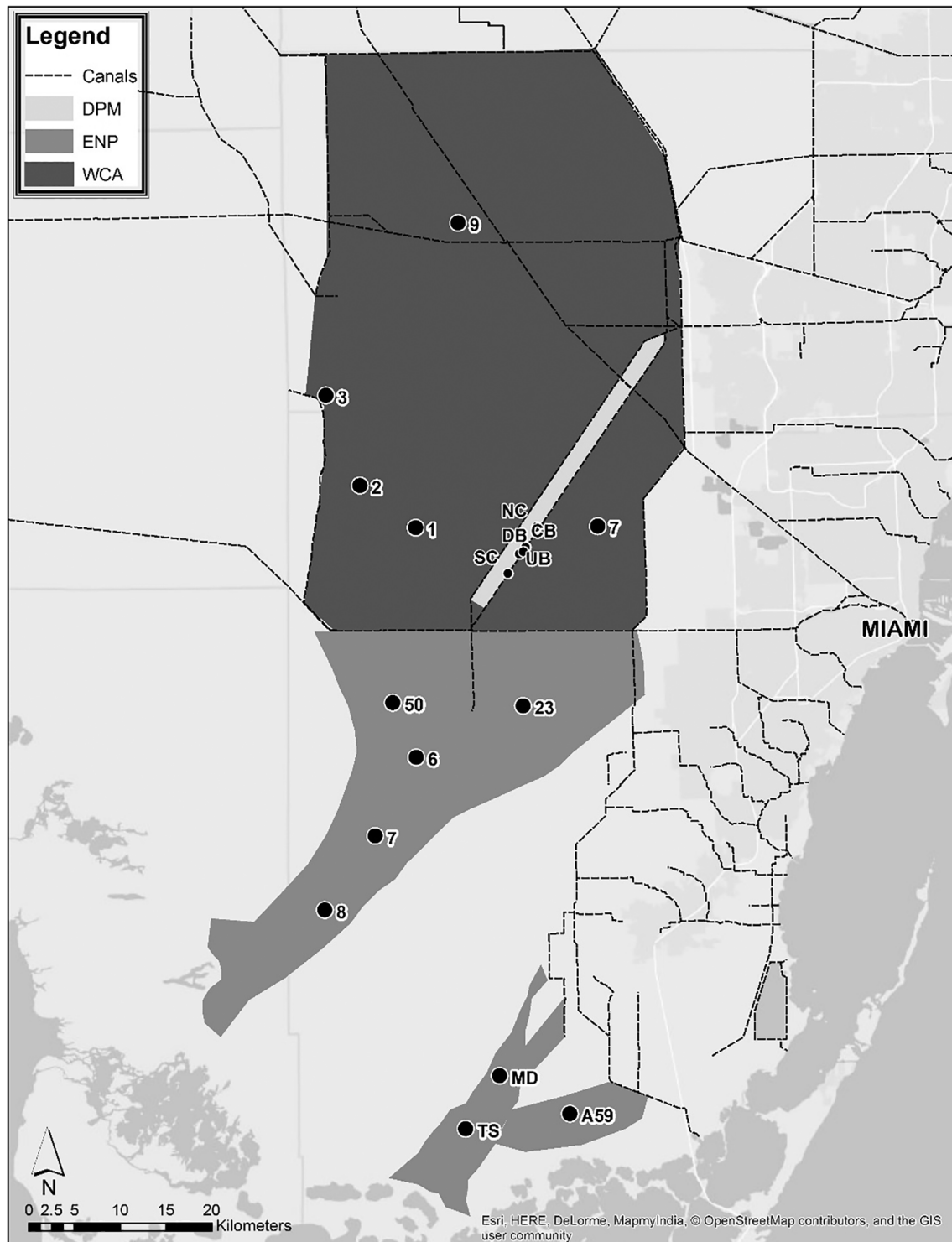


Fig. 1. Map of plots simultaneously sampled with drift fences and throw traps for fish abundance and occupancy in the Florida Everglades. Plots were located inside Everglades National Park (ENP), Water Conservation Area 3 (WCA), and the Decompartentalization Physical Model Area (DPM).

We used method-specific detection histories from plots where species presence was confirmed by any of the four sampling gears. In the program OpenBUGS, each plot-specific detection probability ( $\theta$ ) was modeled as a beta distribution shaped by two region-wide hyperparameters, region-scale detection probability ( $p$ ), and dependence of  $\theta$  on this region-scale probability ( $\kappa$ ):  $\theta = \text{beta distribution } (a, b)$ , where  $a = (p \times \kappa)$  and  $b = [(1 - p) \times \kappa]$ . Prior belief for  $p$  was also modeled as a beta distribution, and the  $\kappa$  prior was modeled with a gamma distribution. Parameters were first modeled with data from a single survey, and then, parameter distributions and priors were updated with data from subsequent surveys. Detection probability was initially modeled with flat beta and gamma priors, with the priors of each subsequent run informed by the previous posterior distribution. To build the most informed priors possible, initial flat-prior analyses were run with data from surveys with the largest sample size (i.e., greatest number of occupied plots). Based on subsequent sample sizes, parameters of the informed priors were adjusted to have mixing weight of the prior set at 0.40, allowing new survey data to have more influence than the prior when calculating new posterior means. Markov Chain Monte Carlo sampling of the posterior distribution was conducted with two chains that were considered to have converged when the ratio of between- to within-chain variance was close to 1.0 and neither chain systematically increased or decreased (Kruschke 2011). Chains were started at an initial value of 0.5, and based on assessments of convergence, burn-in period was 10,000 iterations followed by 40,000 further updates to generate the reported sample of the posterior distribution. Monte Carlo errors of the parameters were less than 5% of sample deviation in every case; therefore, 40,000 updates were considered sufficient to produce an accurate sample of the posterior distribution (Spiegelhalter et al. 2014). To assess how species-specific seasonal changes in density and activity rate might be associated with seasonally varying detection probabilities for active and passive gears, we estimated seasonal detection probabilities in the DPM region, where all plots were sampled during each survey, with the same Bayesian modeling approach used to estimate regional probabilities but using flat priors.

Interspecific and seasonal variation in the relationship between density and CPUE was investigated by testing the hypothesis of a proportional relationship between density and CPUE across multiple species and hydrologic conditions. In the 15 plots of the DPM region, CPUE from drift fences ( $N/24 \text{ h}$ ) was related to density from throw traps ( $N \text{ m}^2$ ) for four species whose average detection probability in this region was at least 40%. CPUE was regressed on density with the log-linear form of a power-curve function:  $\text{Ln}(\text{CPUE} + 1) = \text{Ln}(\text{intercept}) + \beta \text{Ln}(\text{density} + 1)$ . The slope of the resulting regression model,  $\beta$ , is a shape parameter that measures if CPUE either increases proportionally with density ( $\beta = 1$ ) or has a non-linear relationship with density ( $\beta \neq 1$ ), such as might result when sampling gear saturates at moderate to high densities ( $\beta < 1$ ; Harley et al. 2001, Erisman et al. 2011). Species-specific slope estimates were predicted to change across seasonal depth conditions from seasonal and species-specific differences in vulnerability and activity rates. Capture rates of demersal species were predicted to increase with declining water depth because of increased activity rates associated with movement away from shrinking habitat, while capture rates of species that are primarily active in the upper water column were predicted to increase both from increased activity rates and from decreased distance between traps and the water surface. Increased vulnerability and movement should increase encounter rates with passive-sampling gear, thereby resulting in a more proportional relationship between CPUE and density.

#### *Estimating activity rates*

We used a model-based interpretation of variation in catchability to examine interspecific patterns of activity rate and response to seasonal changes in depth. We used these data to quantify the relative contribution of non-native fishes to overall fish activity and encounter rate for prey and competitors across locations in the Everglades aquatic landscape. We estimated activity rates at each plot using Eq. 2, with predator (i.e., trap) search area ( $A$ ) and search volume ( $V$ ) based on a previous underwater video study of drift fence sampling (Obaza et al. 2011). Sometimes, a species was detected by drift fences but not throw traps, and so the minimum possible

density estimate,  $0.14/\text{m}^2$ , was added to every density value to avoid zeros in the denominator of the activity rate model. For species vulnerable to capture by drift fences, this type of discrepancy in detection between throw traps and drift fences was assumed to result from relatively high activity at low density. Seasonal activity rates in the DPM region for two demersal species, Flagfish and Bluefin Killifish, were plotted against change in depth over a 30-d period prior to sampling. Based on differences between these two species in seasonal dispersal behavior (Hoch et al. 2015), we expected them to also differ in the sensitivity of their activity rates to declining depth. The products of activity rates and densities were summed for native and non-native fishes at each sample plot in ENP and WCA and used as an index of potential interaction rates with these species. The constant  $0.14/\text{m}^2$  was added to all density values in this calculation and 0.008 was added to all activity rates to convert all rates to positive values. This index was calculated for data collected during the dry season (i.e., third survey), a time when encounters with potential competitors and predators may increase because of reduced habitat volume (Magoulick and Kobza 2003). DPM data were excluded from this analysis because there were few observations of non-native fishes in this region (Fig. 2).

## RESULTS

Over the course of this study, 32,530 fish were captured, representing 27 native and seven non-native species (Appendix S1). Using catches in survey 3 to illustrate a pattern found in all surveys, incidence of Dollar Sunfish, Marsh Killifish, Sailfin Molly, Pike Killifish, and African Jewelfish was higher as measured by drift fences than by throw traps (Fig. 2). Throw traps consistently measured higher incidences than drift fences for Everglades Pygmy Sunfish and Least Killifish (Fig. 2). During survey 3, five non-native species were detected in the ENP region, with one unique detection for throw traps (Walking Catfish) and two for drift fences (Black Acara, Mayan Cichlid; Fig. 2). Pike Killifish and African Jewelfish were detected by both methods in all three surveys of the ENP region. In WCA, none of the four non-native fishes detected by

drift fence sampling were captured by throw traps (Fig. 2). Of the four non-native species captured by drift fences in the WCA region, Black Acara and African Jewelfish were the only species detected in all three surveys. The DPM region had the fewest non-native detections, with no non-native fishes detected during survey 2 and only single-plot detections during the other surveys. Unlike the other regions, most of these non-native detections were by throw traps (Fig. 2).

### *Detection probability and CPUE–density relationship*

Throw trap and drift fence detection probabilities overlapped over a wide range of regional densities (Fig. 3A), except at sparse densities ( $\leq 0.84 \text{ fish}/\text{m}^2$ ) where drift fence detection probabilities were generally higher than throw trap probabilities (Fig. 3B). Detection probabilities for Dollar Sunfish and African Jewelfish, two species found at low local densities, were consistently lower for throw traps than for drift fences (Table 2). The probability of detecting Sailfin Mollies generally overlapped between the two sample methods, except in the ENP region where this species had low densities and was more readily detected with drift fences (Table 2). Regardless of sampling method, detection probabilities were high for Bluefin Killifish and Eastern Mosquitofish, two species with high regional densities (Table 2). Throw trap detection probabilities for Flagfish were not as sensitive to low density as they were for other species (Fig. 3) and overlapped for both sampling methods (Table 2).

Seasonal detection probabilities in the DPM region generally overlapped for both sampling methods (Table 3). Drift fence detection probabilities for Eastern Mosquitofish and Sailfin Molly during the third survey increased and had reduced overlap with drift fence detection probabilities from the first survey when depths were increasing (Table 3). The only non-overlapping seasonal detection probabilities between methods were for Eastern Mosquitofish sampled during the first survey, when throw traps had higher detection probabilities than drift fences (Table 3).

Species-specific relationships between drift fence CPUE and throw trap density varied over seasonal changes in water depth. Seasonal



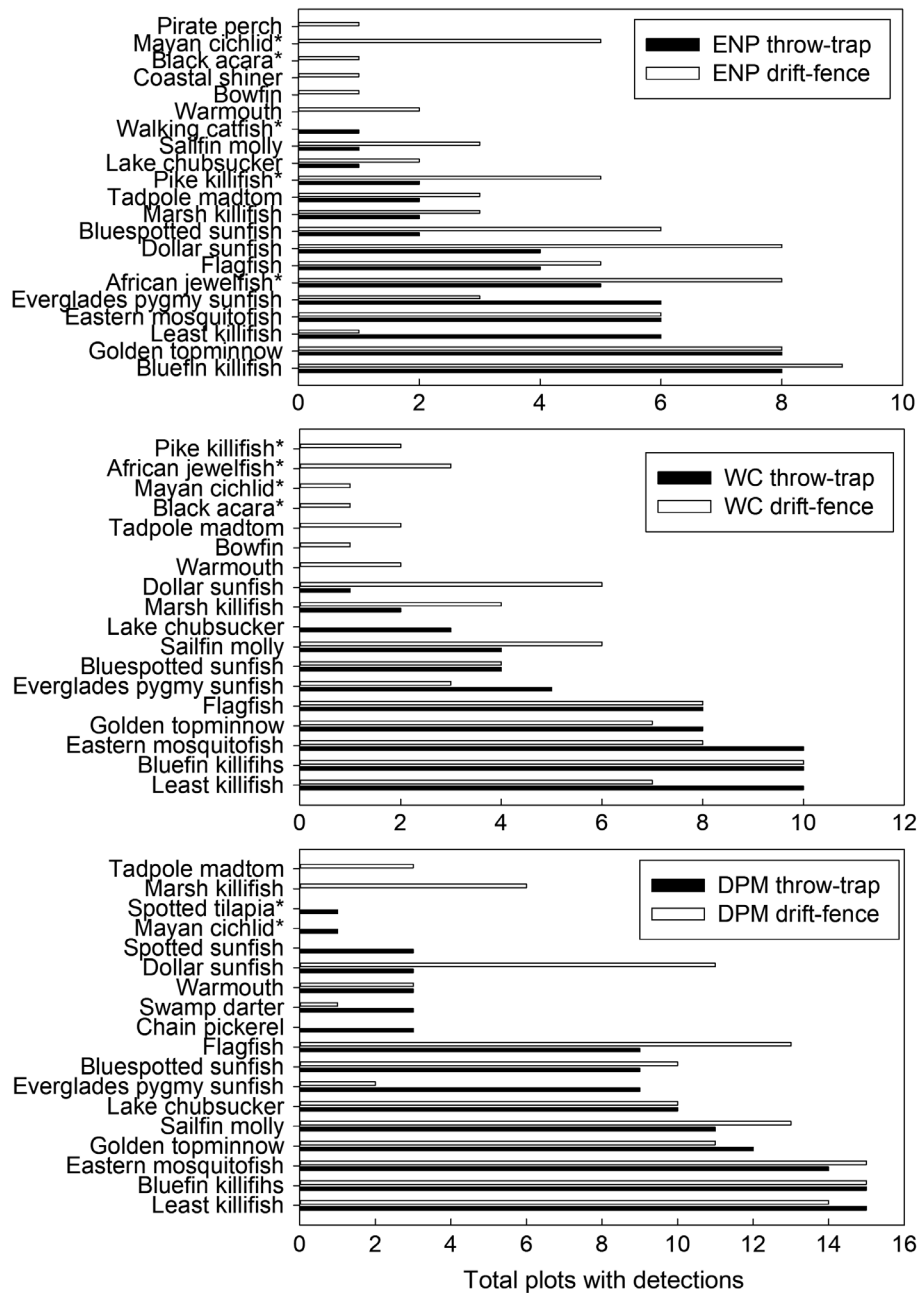


Fig. 2. Incidence (total plots where at least one individual was detected) of fishes in the ENP, WCA, and DPM regions as measured by throw traps (black bars) and drift fences (white bars) during survey 3. Non-native species are identified by \*.

hydrological dynamics in the DPM during the surveys went from slowly increasing, to a slow decline, to a relatively fast decline (Table 4). For most of the four investigated species, CPUE was

not correlated with density until water depths began to seasonally decline (Table 4). Bluefin Killifish were distinct in that they were the only species in this group whose CPUE was related to

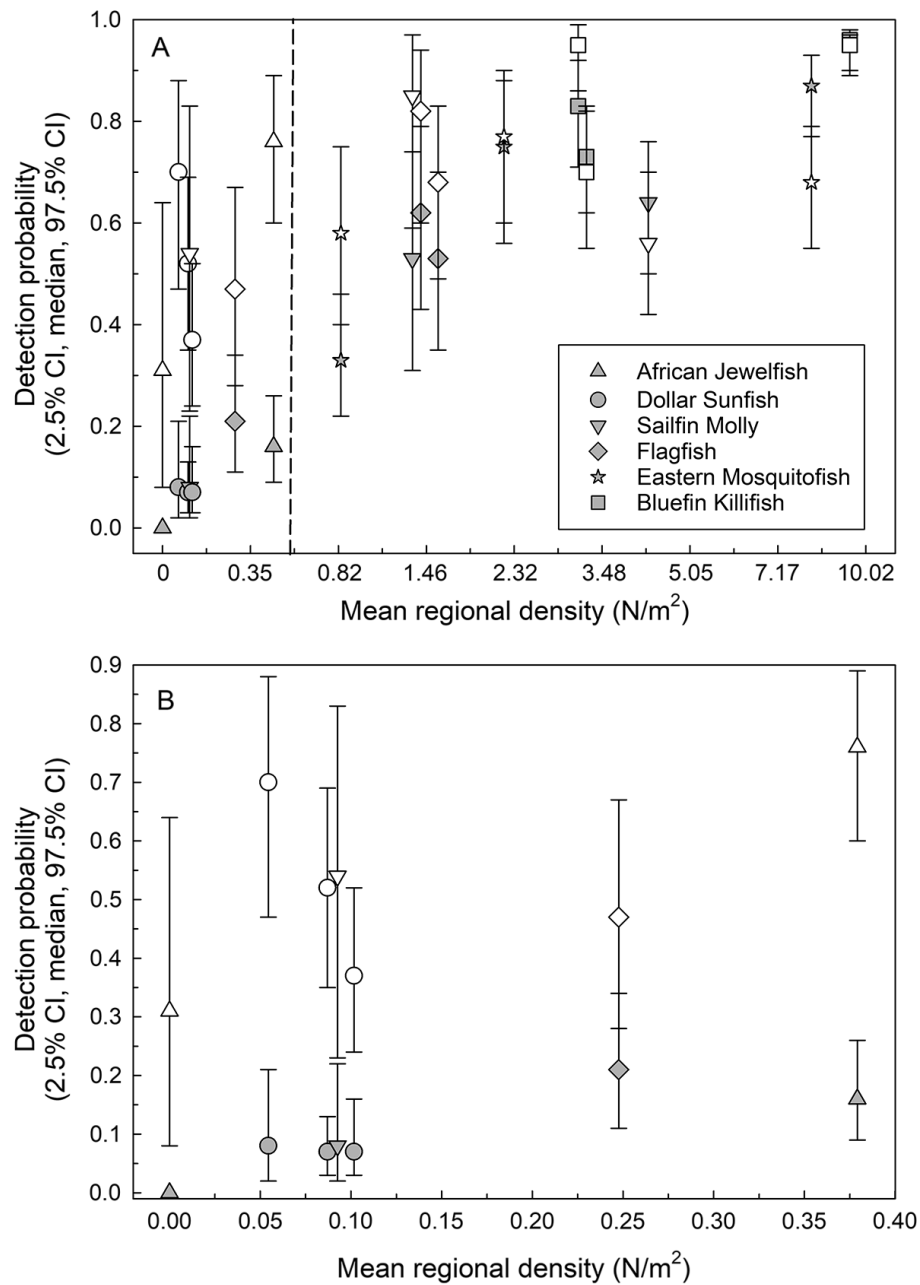


Fig. 3. (A) Regional detection probabilities (median probabilities with 2.5% and 97.5% credible intervals) for throw trap (gray symbols) and drift fence (open symbols) versus mean regional density of six fishes. (B) Low regional densities from panel A expanded to show median detection probabilities and their credibility intervals at low end of the distribution of regional densities (left of vertical dashed line in panel A).

density only when water levels were rising. Under these hydrologic conditions, Bluefin Killifish CPUE was proportional to density (Table 4). During the gradual depth declines of the second

survey, Sailfin Molly were the only species with a relationship between CPUE and density. Furthermore, this was the only circumstance where there was evidence of hyperstability (i.e.,  $\beta < 1$ ;

Table 2. Species-specific posterior probabilities of detection (median, 2.5% and 95% credible interval [CI]) for each region and sampling method (throw traps and drift fences).

Species	Region	Throw trap		Drift fence	
		Median	2.5–97.5% CI	Median	2.5–97.5% CI
Flagfish	ENP	0.21	0.11–0.34	0.47	0.28–0.67
Flagfish	WCA	0.62	0.43–0.79	0.82	0.60–0.94
Flagfish	DPM	0.53	0.35–0.70	0.68	0.49–0.83
Bluefin Killifish	ENP	0.73	0.62–0.82	0.7	0.55–0.83
Bluefin Killifish	WCA	0.83	0.71–0.92	0.95	0.86–0.99
Bluefin Killifish	DPM	0.96	0.90–0.98	0.95	0.89–0.97
Eastern Mosquitofish	ENP	0.33	0.22–0.46	0.58	0.40–0.75
Eastern Mosquitofish	WCA	0.75	0.60–0.88	0.77	0.56–0.90
Eastern Mosquitofish	DPM	0.87	0.77–0.93	0.68	0.55–0.79
Sailfin Molly	ENP	0.08	0.02–0.22	0.54	0.23–0.83
Sailfin Molly	WCA	0.53	0.31–0.74	0.85	0.59–0.97
Sailfin Molly	DPM	0.64	0.50–0.76	0.56	0.42–0.70
Dollar Sunfish	ENP	0.07	0.03–0.13	0.52	0.35–0.69
Dollar Sunfish	WCA	0.08	0.02–0.21	0.7	0.47–0.88
Dollar Sunfish	DPM	0.07	0.03–0.16	0.37	0.24–0.52
African Jewelfish	ENP	0.16	0.09–0.26	0.76	0.60–0.89
African Jewelfish	WCA	0	0	0.31	0.08–0.64

Table 3. Survey- and method-specific posterior probabilities of detection (median, 2.5% and 95% credible interval [CI]) in the DPM region for four species sampled with throw traps and drift fences.

Species	Survey	Throw trap		Drift fence	
		Median	2.5–97.5% CI	Median	2.5–97.5% CI
Flagfish	1	0.57	0.35–0.77	0.65	0.41–0.85
Flagfish	2	0.57	0.34–0.78	0.64	0.37–0.85
Flagfish	3	0.36	0.22–0.53	0.62	0.45–0.77
Bluefin Killifish	1	0.95	0.88–0.99	0.89	0.76–0.96
Bluefin Killifish	2	0.92	0.82–0.97	0.91	0.79–0.97
Bluefin Killifish	3	0.91	0.79–0.96	0.95	0.88–0.99
Eastern Mosquitofish	1	0.9	0.79–0.96	0.51	0.35–0.68
Eastern Mosquitofish	2	0.81	0.67–0.91	0.6	0.41–0.77
Eastern Mosquitofish	3	0.87	0.72–0.95	0.89	0.77–0.96
Sailfin Molly	1	0.69	0.51–0.84	0.49	0.30–0.68
Sailfin Molly	2	0.52	0.34–0.70	0.46	0.29–0.64
Sailfin Molly	3	0.57	0.39–0.74	0.82	0.64–0.92

Note: Survey 1 was conducted at the end of the wet season (October and November 2014), survey 2 during the transition between seasons (December 2014 and January 2015), and survey 3 during the early dry season (February 2015).

Table 4), which is indicated by similar levels of CPUE across a fairly wide range of moderate to high densities of Sailfin Molly (Fig. 4). The most proportional relationships between CPUE and density of Eastern Mosquitofish, Flagfish, and Sailfin Molly occurred during conditions with the fastest declines in depth (Table 4, Fig. 4).

There was little evidence for saturation of passive gear at high densities, with no evident plateau in CPUE with increasing density. Instead, CPUE was similar between high and moderate densities until water levels began dropping more rapidly, resulting in a more proportional relationship between CPUE and density (Fig. 4).

Table 4. Mean rates of depth change during three surveys and associated regression analyses of CPUE–density relationships for four species sampled in 15 plots of the DPM region.

Survey	Depth change (cm/30 d)	Species	N	R <sup>2</sup>	p	β (SE)	H <sub>0</sub> : β = 1	
							F	p
1	0.046 ± 0.027	Bluefin Killifish	15	0.38	0.01	1.065 (0.376)	0.03	0.86
		Eastern Mosquitofish	15	0.03	0.53	...	...	...
		Flagfish	7	0.12	0.46	...	...	...
		Sailfin Molly	12	0.26	0.09	...	...	...
2	−0.067 ± 0.003	Bluefin Killifish	15	0.01	0.77	...	...	...
		Eastern Mosquitofish	14	0.03	0.58	...	...	...
		Flagfish	7	0.51	0.07	...	...	...
		Sailfin Molly	14	0.37	0.02	0.552 (0.209)	4.61	0.05
3	−0.251 ± 0.007	Bluefin Killifish	15	0.04	0.46	...	...	...
		Eastern Mosquitofish	15	0.27	0.05	0.552 (0.252)	3.16	0.10
		Flagfish	15	0.58	0.001	0.909 (0.216)	0.18	0.68
		Sailfin Molly	15	0.34	0.02	0.606 (0.236)	2.79	0.12

Notes: Depth change (mean ± 1 SE cm) was change in depth over a 30-d period ending on the day fish were sampled. Regression models tested a log-linear relationship between catch per unit effort (CPUE) measured by drift fences and throw trap measures of density. Sample sizes (N), coefficients of determination (R<sup>2</sup>), and p-values for each regression model are presented along with hypothesis tests for a proportional relationship between CPUE and density, as quantified by the slope of the model (β ± 1 SE). Ellipses indicate no data are available because regression model was not significant.

### Estimating activity rates

Model-derived estimates of activity rates in the DPM region revealed interspecific differences in behavioral response to changing water depth and identified locations where non-native fishes were a large fraction of plot-level fish activity. Bluefin Killifish activity rates were similar during the relatively stable depth conditions of the first two surveys. During faster rates of depth decline, activity rates greatly increased for Flagfish while changing very little for Bluefin Killifish (Fig. 5).

Potential contact rates of stationary prey by mobile fishes, as measured by the products of fish activity rates and densities, exhibited spatial variation within and among regions, with a higher mean index in WCA (1.17 ± 0.20 SE) than ENP (0.53 ± 0.10 SE; Fig. 6). The higher index in WCA was not from higher densities because mean native fish density (±1 SE) overlapped between ENP (7.82 ± 1.36 N/m<sup>2</sup>) and WCA (9.68 ± 1.42 N/m<sup>2</sup>), and non-native species densities were relatively low in both regions during this study. In ENP, 2–67% of fish activity inside sample plots was from non-native species (Fig. 6). The majority of non-native activity was from African Jewelfish, whose mean activity rate was among the highest measured across the regions (Table 5).

### DISCUSSION

This study demonstrates how an ecological model can transform nuisance variation in CPUE–density relationships into novel ecological information. Information content of actively collected counts that are integrated over space is affected by sampling effort needed to detect rare or low density species, while encounter-rate data from passive samplers that integrate catches over time are influenced by both density and movement patterns (Burton et al. 2015, Miller et al. 2015). As movement can vary across taxa and environmental contexts, movement-driven variation in catchability by passive samplers complicates combining data from these two general types of methods. This was evident in the current study, where the relationship between CPUE and density varied among seasons and species, and was proportional only under particular conditions. For species too small to directly measure movement patterns in the wild through telemetry and other tagging methods, novel methods are needed to assess patterns of activity related to detection and catchability. A predator encounter-rate model provided a framework for estimating activity rates from the combined information of active and passive samplers.

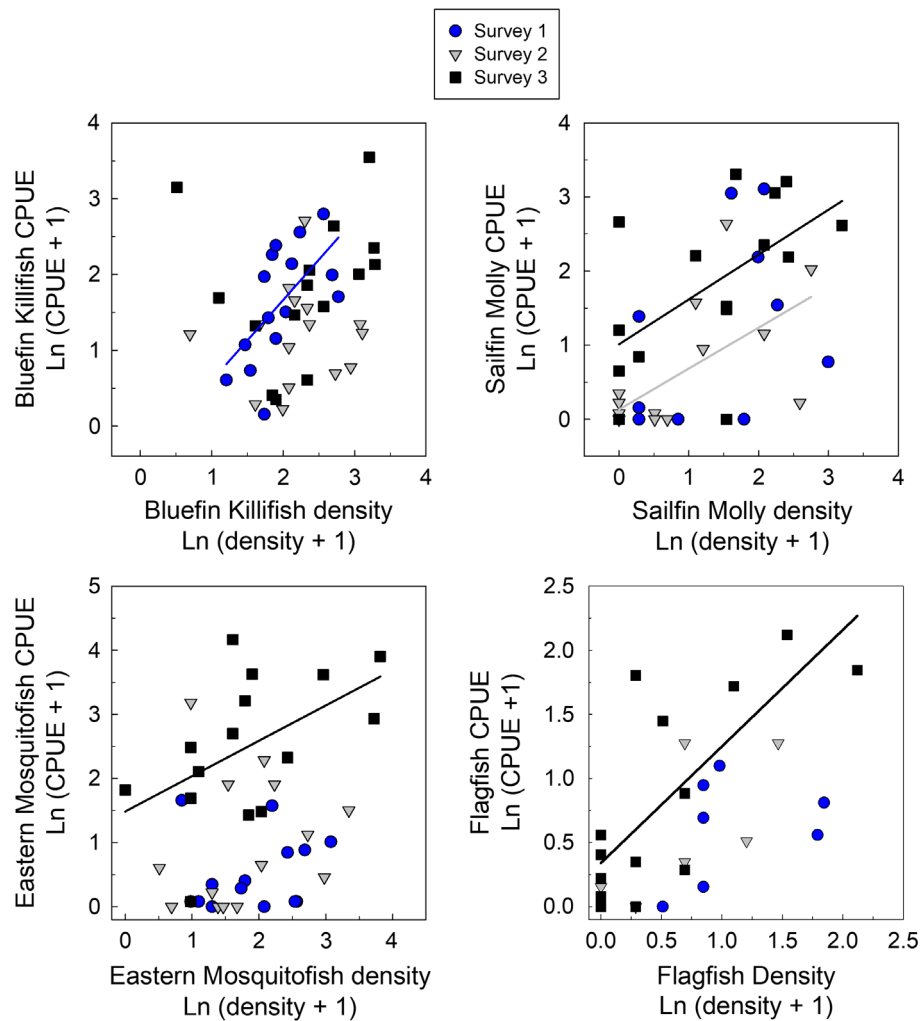


Fig. 4. Relationship between active measurements of density (throw traps;  $N/m$ ) and passive catch per unit effort (drift fences;  $N/24$  h). Solid lines are predicted CPUE from significant regressions. Symbols and regression lines are color-coded by survey (blue = survey 1, gray = survey 2, black = survey 3).

Active- and passive-sampling methods produced inconsistent views of fish distribution in the Florida Everglades because of differences in their ability to detect fishes present at low densities. Furthermore, the only sampling method to have spatial variation in detection probability was the active sampler because of inter-regional variation in density of target species. Given sufficient sampling effort, if rare species are active, passive samplers, by sampling continuously over a longer time window than point collections, should have a higher per-unit-effort detection probability for sparse individuals. Passive

samplers, such as camera traps and pitfall traps, are often used to assess occupancy of rare, mobile animals (e.g., Ribeiro et al. 2008, Blanc et al. 2014, Burton et al. 2015). In the current study, most fishes present at low densities had a much higher probability of being detected by drift fences set over a 24-h period than repeated point collections with  $1\text{-m}^2$  throw traps. This difference in detection probability even extended to the Dollar Sunfish, a species that was not rare in terms of its distribution across the sample regions (67–85% occupancy across study area), but where present, was not abundant, as

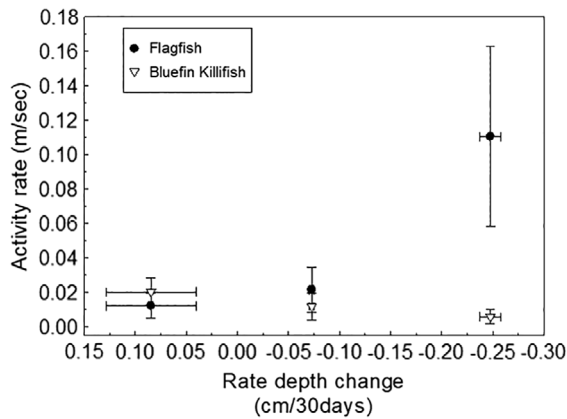


Fig. 5. Survey estimates of activity rate (m/s ±1 SE) and rate of depth change (cm/30-d ±1 SE) in the DPM region for Flagfish and Bluefin Killifish.

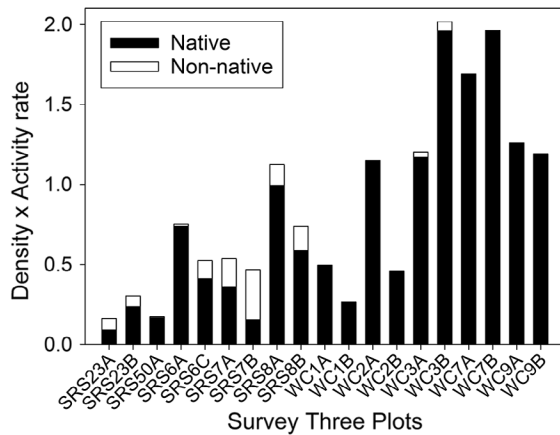


Fig. 6. Distribution of native and non-native fish activity index across plots sampled during the early dry season (survey 3). Sample plots were in Shark River Slough (SRS) of Everglades National Park (ENP region) and Water Conservation Area 3 (WC region). Products of species-specific density estimates and model-derived estimates of activity rate are summed by native (black) and non-native (white) status for each sampled location.

measured by either CPUE (mean regional CPUE (±1 SE) = 0.038 ± 0.01/h; mean regional relative CPUE = 0.11, maximum = 0.26) or density (mean regional density (±1 SE) = 0.39 ± 0.09/m<sup>2</sup>; mean regional relative density = 0.07, maximum = 0.13). The Everglades Pygmy Sunfish provides an informative exception to higher capture by passive than active sampling. This

Table 5. Mean (m/s ± 1 SE) activity rates and sample size (N) for all fishes captured by throw traps and drift fences in ENP and WCA during survey 3.

Species	Activity rate (m/s)	N
<i>Amia calva</i>	0.017	2
<i>Notropis petersoni</i>	0.017	1
<i>Erimyzon sucetta</i>	0.006 ± 0.01	5
<i>Noturus gyrinus</i>	0.018 ± 0.01	5
<i>Clarias batrachus*</i>	0.001	1
<i>Aphredoderus sayanus</i>	0.02	1
<i>Fundulus chrysotus</i>	0.021 ± 0.01	18
<i>Fundulus confluentus</i>	0.148 ± 0.09	8
<i>Jordanella floridae</i>	0.096 ± 0.03	15
<i>Lucania goodei</i>	0.06 ± 0.01	19
<i>Belonesox belizanus*</i>	0.021 ± 0.01	8
<i>Gambusia holbrooki</i>	0.181 ± 0.06	17
<i>Poecilia latipinna</i>	0.181 ± 0.07	10
<i>Elassoma evergladei</i>	0.006 ± 0.01	14
<i>Enneacanthus gloriosus</i>	0.052 ± 0.02	11
<i>Lepomis gulosus</i>	0.016 ± 0.001	4
<i>Lepomis marginatus</i>	0.348 ± 0.08	14
<i>Cichlasoma bimaculatum*</i>	0.019 ± 0.001	2
<i>Mayaheros urophthalmus*</i>	0.025 ± 0.01	6
<i>Hemichromis letourneuxi*</i>	0.343 ± 0.10	11

Note: Non-native species are indicated by an asterisk.

species was present at low densities but detected at more locations by throw trap than drift fence. It also had one of the lowest activity rate estimates of the study; therefore, drift fences may be less efficient than throw traps for capturing species with low activity rates.

Our results demonstrate that caution is needed when interpreting passively measured CPUE as an index of fish abundance. As with past work on crayfish (Dorn et al. 2005), we found that fish CPUE can be insensitive to changes in density and, for fish, varied among seasons (see also Obaza et al. 2011). Lack of proportionality between CPUE and density was not driven by gear saturation of the passive sampler because CPUE did not plateau over the range of densities observed in this study. Instead, we interpret the lack of linear relationships between passive CPUE and active measures of density as resulting from the influence of encounter rates with passively fished traps on CPUE. Factors that decrease encounter rates with passive samplers, such as low activity rates, will also decrease the correspondence between density and CPUE, resulting in a form of hyperstability whereby CPUE is not sensitive to variation in density. For

species such as Eastern Mosquitofish and Sailfin Molly, which are primarily active in the upper portion of the water column (Loftus and Kushlan 1987), stronger CPUE–density relationships in the dry season may have resulted from increased encounter rates with minnow-traps set on the substrate. As water depth dropped, traps would be closer to the upper portion of the water column where these species are concentrated. For demersal species like Flagfish and Bluefin Killifish (Loftus and Kushlan 1987), seasonal changes in capture rates relative to density may be related to their dispersal responses to fluctuating hydrology (Hoch et al. 2015). Seasonal changes in CPUE–density relationships were not associated with corresponding changes in detection probabilities, possibly because of greater uncertainty and reduced power associated with vague, uninformed priors (Linden and Roloff 2015). There was a general pattern of increase in drift fence detection probability between dry-season and wet-season surveys, but use of flat priors in our seasonal models yielded credibility intervals that were wide and overlapping. The Everglades undergoes large seasonal fluctuations in habitat availability for fishes, resulting in seasonal changes in extent of space use and regular cycles of dispersal and re-colonization (Ruetz et al. 2005, Parkos et al. 2015). Synchronizing passive-sampling effort with seasonal changes in activity levels could be a strategy for increasing catchability and providing CPUE measures more closely related to density (Chambert et al. 2012, Villegas-Rios et al. 2014).

Passive methods may be best for detecting sparse, active, non-native species (e.g., Britton et al. 2011) because of the link between activity rate and detection. Species introductions often begin from small numbers of individuals, especially relative to other species in the recipient community (Hudina et al. 2012, O'Connor 2014), making them difficult to detect until the population size has become too large to easily eradicate (Lockwood et al. 2007). Characterizing the rate and direction of invasive spread is also a challenge because of the paucity of data on dispersal and occupancy at invasion fronts, where density is likely to be low (Bahn et al. 2006) making detection difficult (Carey 1996). In the Everglades, drift fence data produced a different picture of non-native relative abundance and

occupancy than throw traps, including detecting four non-native species inside WCA that were undetected by throw traps. However, we noted unique detections of non-native fishes by both gear types, indicating that use of multiple methods provides the most effective form of monitoring for biological invasions (Hoffman et al. 2016).

Treating drift fence CPUE as the encounter rate in a foraging model permits estimation of activity levels in units usable in models of animal movement (DeAngelis et al. 2010). Applications of information on activity levels include investigating patterns of spread, dispersal, and ecological impact. Data on interspecific, seasonal, and spatial patterns of dispersal have the potential to improve models of community assembly and dynamics (Griffen and Byers 2006). For example, active predators and non-native species may have larger ecological impacts than predicted from density alone because of increased contact with native species and high rates of spread (Schmidt and Schaubert 2007, Mosnier et al. 2008). In some areas of the Everglades, non-native fishes were a substantial fraction of overall predator activity experienced by small fishes and macroinvertebrates. Of the non-native fishes collected during this study, African Jewelfish contributed the most non-native predator activity and, therefore, may have the largest effect on native fauna. Activity patterns can also be used to investigate threshold conditions that trigger dispersal behavior. For example, Flagfish and Bluefin Killifish exhibited different patterns of activity increase across the same range of depth changes. The higher level of Flagfish activity relative to Bluefin Killifish in this study conforms to previous observations that of the two, Flagfish have a more rapid response to declining water levels and more rapidly re-colonize re-inundated habitats (Trexler et al. 2002, Ruetz et al. 2005, Hoch et al. 2015).

## SUMMARY AND CONCLUSIONS

We used active- and passive-sampling data to illustrate how two types of data with particular sources of error and varying in their correspondence with one another can be treated as complementary in an ecological model, producing emergent information not available from either

data set on its own. In the case of active- and passive-sampling methods, the detection probabilities and rates of these approaches differ in their sensitivity to the activity patterns of targeted species. This situation is prevalent across the wide variety of mobile taxa surveyed with passive measures of incidence and relative abundance (Ribeiro et al. 2008, Villegas-Rios et al. 2014, Burton et al. 2015, Miller et al. 2015). The dynamic relationship between these different data sources can be interpreted through the lens of a predator-prey encounter-rate model to provide insight into the activity patterns affecting data correspondence. We propose that variable catchability from methods passively measuring CPUE is not only useful for adjusting abundance estimates, but also sources of information on behavioral variation (Stoner 2004, Miller et al. 2015).

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