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Using data from an encounter sampler to model fish dispersal

A. OBAZA*†, D. L. DEANGELIS‡§ AND J. C. TREXLER*||

*Department of Biology, Florida International University, 3000 NE 151st Street, North Miami, FL 33181, U.S.A., ‡Florida Integrated Science Center, U.S. Geological Survey, Fort Lauderdale, FL 33315, U.S.A. and §Department of Biology, University of Miami, Coral Gables, FL 33124, U.S.A.

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A method to estimate speed of free-ranging fishes using a passive sampling device is described and illustrated with data from the Everglades, U.S.A. Catch per unit effort (CPUE) from minnow traps embedded in drift fences was treated as an encounter rate and used to estimate speed, when combined with an independent estimate of density obtained by use of throw traps that enclose 1 m² of marsh habitat. Underwater video was used to evaluate capture efficiency and species-specific bias of minnow traps and two sampling studies were used to estimate trap saturation and diel-movement patterns; these results were used to optimize sampling and derive correction factors to adjust species-specific encounter rates for bias and capture efficiency. Sailfin mollies *Poecilia latipinna* displayed a high frequency of escape from traps, whereas eastern mosquitofish *Gambusia holbrooki* were most likely to avoid a trap once they encountered it; dollar sunfish *Lepomis marginatus* were least likely to avoid the trap once they encountered it or to escape once they were captured. Length of sampling and time of day affected CPUE; fishes generally had a very low retention rate over a 24 h sample time and only the Everglades pygmy sunfish *Elassoma evergladei* were commonly captured at night. Dispersal speed of fishes in the Florida Everglades, U.S.A., was shown to vary seasonally and among species, ranging from 0.05 to 0.15 m s⁻¹ for small poeciliids and fundulids to 0.1 to 1.8 m s⁻¹ for *L. marginatus*. Speed was generally highest late in the wet season and lowest in the dry season, possibly tied to dispersal behaviours linked to finding and remaining in dry-season refuges. These speed estimates can be used to estimate the diffusive movement rate, which is commonly employed in spatial ecological models.

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Key words: Everglades; sampling bias; stratified movement model.

INTRODUCTION

Growing appreciation for the role of spatial dynamics in understanding and managing natural populations has heightened the need for improved methods to study animal movement (Turchin, 1998). Ideally, animals are directly tracked to obtain the information necessary to incorporate movement into models of population dynamics, but many animals cannot be marked or tracked because of practical limitations

||Author to whom correspondence should be addressed. Tel.: +1 305 348 1966; email: trexlerj@fiu.edu

†Present address: Ocean Associates, Inc., 501 W. Ocean Blvd, Long Beach, CA 90069, U.S.A.

such as small size. Indirect methods are required in such cases, permitting inference of movements from patterns of collections of unmarked animals (Hohausová *et al.*, 2003). Models of population spread by simple diffusion (D) that characterize individual movements as uncorrelated random walks are a valuable starting point for incorporating dispersal into population dynamical models (Turchin, 1998). Rejecting predictions of a diffusion-type model leads to more sophisticated models of directed dispersal in a mechanistic modelling framework (Andow *et al.*, 1990; Turchin, 1998). For this reason, estimating D is a useful target for field research on spatial population dynamics (Skalski & Gilliam, 2000). Random-walk models assume movements occur as a series of pulses that are characterized by the animal's speed, duration of movement and angle of turning before the start of the next pulse (Berg, 1983; Turchin, 1998). DeAngelis *et al.* (2010) illustrated the estimation of D from field estimates of fish speed obtained from an encounter sampler and independent estimates of density using an enclosure sampler. Their protocol is intended for study of small fishes in shallow marsh or floodplain habitats, but may have application in other contexts (Rudstam *et al.*, 1984; Olin & Malinen, 2003).

Understanding bias and efficiency in sampling is a critical step in use of all methods that study fish ecology, and fish capture data are notoriously sensitive to artefacts created by the sampling process (Hamley, 1975). Fish collection methods may be divided into active methods that move an apparatus through water to overtake and collect fishes and passive methods that require fishes to enter a collection device. Use of passive sampling techniques, such as stationary traps and nets (fyke, gill and hoop nets), is widespread in fisheries biology (LeCren *et al.*, 1977; Parkinson & Berkowitz, 1988; Amundsen *et al.*, 2003). Problems, however, exist with interpreting data from passive sampling because only those animals that encounter and enter the sampling device are recorded (Fago, 1998; Prchalova *et al.*, 2008), yielding data reported as catch per unit effort (CPUE) or activity density. If bias from trap avoidance and density is accounted for, passive sampling data can provide an estimate of the encounter rate of moving fishes. The goal of this study was to develop and test a model for using CPUE data to estimate speed.

Drift fences, a form of fyke net, a hoop-shaped trap usually attached to a weir, can be a reliable method for monitoring the movement of aquatic animals (Dodd & Cade, 1998; Hohausová *et al.*, 2003). Drift fences may also reveal qualitative direction of movement if they use traps facing at right angles [Fig. 1(a)]. Behavioural effects on catch data obtained by traps, such as internal predation, avoidance and escape,

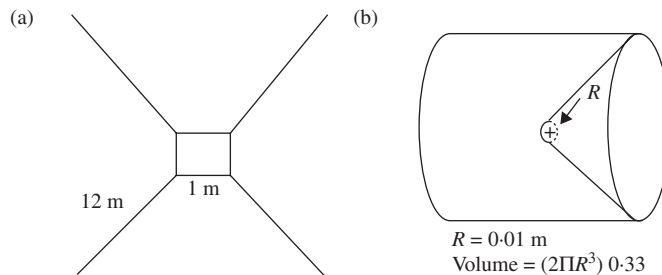


FIG. 1. Diagrams of (a) drift fence and (b) search volume used in the encounter equation. It is assumed that each fish encountering the search volume is caught.

diminish the value of drift-fence data (He & Lodge, 1990; Layman & Smith, 2001). Even if traps are not baited, they may in effect bait themselves by capturing animals that subsequently attract predators. Diurnal movement could bias capture rates downward or obfuscate interspecific comparisons of species with different patterns. Minimizing such bias and estimating the effects of what remains is an important step in applying trap data quantitatively.

In recent years, underwater video and high-resolution sonic devices have supplemented or replaced many traditional fish survey techniques (Ellis & DeMartini, 1995; Willis & Babcock, 2000; Cappo *et al.*, 2004). Underwater video is useful because it is less invasive than removal sampling, animals are not sacrificed, and some forms of biases are minimized. Unfortunately, gear and labour costs may limit the number of sites sampled simultaneously or samples processed, compared to traditional methods. Video can be used to provide a direct estimate of biases from escape and avoidance of traps and is increasingly used to improve, though not replace, passive sampling (Hatch *et al.*, 1994; Grant *et al.*, 2004; Ellis & Bell, 2008).

This article proposes a method to estimate fish speed (m s^{-1}) by application of an encounter rate model using estimates of CPUE and density. An empirical estimate of speed is an important step towards estimating D for use in spatial models of population dynamics; if no directional bias is assumed (the net turning angle is 0), D equals one-half the speed times the average distance moved between turns (*i.e.*, $D = 0.5 (\lambda\tau^{-1})\lambda$, where $\lambda\tau^{-1}$ is the speed and λ the distance between turns). This method is illustrated with a study of fishes in the Florida Everglades, U.S.A. The illustration includes studies that evaluate biases and provide correction factors that improve model parameterization.

MATERIALS AND METHODS

Research was conducted in the Shark River Slough, Everglades National Park, Florida, U.S.A., where the fish community is dominated by species too small to be studied by techniques that directly track fish movement (Loftus & Kushlan, 1987; Trexler *et al.*, 2001), including passive integrated transponder (PIT) tags (Cucherousset *et al.*, 2009). The movements of small fishes in response to seasonal drying of the marshes, however, are relevant to management of the ecosystem because these fishes are prey for wading birds that are a focal concern for the public (Trexler & Goss, 2009). Thus, there is a need for methods to document movement patterns quantitatively in a form that can be incorporated in models used to guide management (DeAngelis *et al.*, 2008).

Two types of study are reported in this article: analysis of bias in sampling by drift fences in the Everglades and use of resulting data to parameterize an encounter model for estimating speed.

SAMPLING BIAS

In the summer and autumn of 2007, the effect of sampling duration was studied to determine whether minnow traps would have higher catch rates during 2 h at crepuscular time-periods (dawn and dusk) or during 12 h overnight. Data were collected over five non-consecutive nights at short-hydroperiod sites, where minnow traps were set at either four or six drift fences 1 h before sunset. Six drift fences were sampled on each of the three nights and four others on two of the nights, for a total of 26 trap nights. At 1 h after sunset, animals were collected from minnow traps at half of the drift fences. The following morning, 1 h before sunrise, traps were set at the drift fences collected the previous night and animals from all the drift fences were collected 1 h after sunrise. The sampling design had three treatment

groups: sunrise (SR), sunset (SS) and a 12 h overnight sample (TH). Each night drift fences were randomly assigned to treatment groups, with the exception of one drift fence never being included in the 2 h treatment groups because of the difficulty in accessing at night. Moon phase was also noted on the night of sampling.

A mark–retention study was conducted at the same locations as the sampling-duration study to examine escape during a 24 h sampling regime. Samples were taken from two short-hydroperiod sites over three sampling days with 84 traps sampled. Two hours after minnow trap deployment, counts of species collected to that point were recorded, all fishes were marked with fin clips and returned to the traps and left for an additional 22 h, after which the contents of the trap were removed. The fishes from each trap were examined to determine whether they were marked to estimate retention and to document changes in catch and community composition during the 24 h sampling time.

A diel study of fish activity was used to determine the importance of time of deployment of minnow traps. Sampling was conducted over six non-consecutive days where data collection occurred with an equal frequency at sites containing one to three drift fences. Traps were set at four times of the day, midday (MD), sunset (SS), midnight (MN) and sunrise (SR), left for 2 h and collected for removal, euthanasia and preservation of all animals.

Catch-rate estimates from underwater videos were compared with catches from minnow traps set while the cameras were recording to evaluate sampling bias associated with fish avoidance and escape from traps. Underwater cameras (Sony HDD Handycams in a waterproof housing; www.sonystyle.com/Handycam) were placed in front of minnow traps, where they recorded activity at 2 h intervals. In the laboratory, the video footage was screened to count behaviours and identify species. Every entry, escape and avoidance of minnow traps by fishes were recorded for each video sample; animals in the video that failed to approach the trap were ignored. Avoidance refers to a fish that approached the trap and swam away without entering. All analyses assumed that if a fish escaped or avoided the trap, it did not return; it was impossible to determine whether the same individual returned multiple times.

Density and encounter data were collected concurrently from five sites over a 4 year period (2005–2008) from the Shark River Slough, Everglades National Park (sites 6, 7, 8, 23, 50; see map in Trexler *et al.*, 2001) to illustrate estimates of speed. Sampling took place in February, April, July, October and December each year to capture seasonal changes in water level. Drift fences yielded encounter data and throw traps yielded density data for each study site and time combination. Four of the study sites were located in long-hydroperiod marshes (inundated for >330 days) and one was in a short-hydroperiod marsh (inundated for *c.* 90–150 days). Drift fences collected fishes using 3 mm wire-mesh minnow traps (mouth diameter 1.25 cm) placed at the centre of drift fences constructed from greenhouse cloth supported by metal bars, similar to fences used to collect small mammals and herpetofauna (Ford *et al.*, 1999, 2002; Ryan *et al.*, 2002). The fences had four arms intersecting to form an 'X', creating four funnels with the midpoint facing at right angles [Fig. 1(a)]. Each arm was 12 m long and 0.7 to 1.5 m high, depending on water depth. The four arms intersected to form a box at the centre and each side of the box contained a hole where one or two (stacked vertically) minnow traps were placed depending on water depth; the trap openings facing the centre of the box were plugged. Drift fences could only be sampled when water depth was >15 cm and trap mouths were fully submerged. When water level exceeded 50 cm, two sets of four minnow traps were stacked vertically to capture fishes at two levels in the water column. Twenty-one 1 m² throw trap samples (Jordan *et al.*, 1997) were collected in the vicinity of each drift fence at each sampling period to provide density estimates. Throw traps were constructed with 2 mm mesh. Seven randomly located samples were collected from each of the three plots located in similar habitat and within 0.5 km of the drift fences. Fishes were euthanized upon collection by a high dose of MS-222 following standard procedures (UFR Committee, 2004) and afterwards they were preserved prior to processing.

ESTIMATING SPEED

A model of predator-encounter rate was modified to estimate prey speed from trap CPUE and density by treating the drift fence as a stationary predator (Gerritsen & Strickler, 1977; MacKenzie & Kiorboe, 1995). For a predator that can only search while paused, encounter

rate (E) is

$$E = VNF_P + AN\mu F_P D_P, \quad (1)$$

where V is the search volume (m^3), N the fish density (number m^{-3}), A the search area of the sampling device (m^2), μ the fish speed (m s^{-1}), F_P the predator pause frequency (numbers $^{-1}$) and D_P the predator pause duration (s). This is a simplified equation from MacKenzie & Kiorboe (1995) because several variables can be ignored when the predator is stationary and always searching; F_P and D_P equal 1.0 in this case, but are included here to make the units balance. Turbulent speed was treated as zero because of the very low current speed (typically $<0.02 \text{ m s}^{-1}$) in the Everglades. The radius of each trap's opening was treated as the search area ($A = 0.0003 \text{ m}^2$) and a half sphere from the opening of the minnow trap [Fig. 1(b)] was used as the search volume. These were selected because video data indicated that fishes entering this space typically entered the trap; considering a larger area, such as the triangle formed by the arms of the drift fence, yielded unrealistic results and was inconsistent with direct observation of fish captures from video data. Solving equation (1) for fish speed leaves

$$\mu = (E - NVF_P)(ANF_P D_P)^{-1}. \quad (2)$$

This equation was solved to estimate speed for several common fishes using 4 years of density data collected simultaneously at each study site by throw traps and encounter rates estimated from the drift fences. As in equation (1), F_P and D_P equal 1 and are included here only to make the units balance on the two sides of the equation. Only fishes $\geq 10 \text{ mm}$ standard length (L_S) were included to account for the slight difference in mesh in the throw trap and minnow traps. On the basis of the frontal measurements of fishes in the community and underwater video analyses, specimens $\geq 10 \text{ mm}$ are retained in both trap types.

DATA ANALYSIS

In the bias studies, changes in community structure were documented through a nested analysis of dissimilarity matrices estimated from species-by-sample matrices. Analysis of similarity (ANOSIM) was used to test hypotheses about sampling duration, mark retention, diel activity and moon phase with Bray–Curtis dissimilarity matrices calculated from fourth-root-transformed relative abundance data (Clarke & Green, 1988; McCune & Grace, 2002). Treatments were nested within site–date combinations to account for non-independence among drift fences and dates. Tests for community differences inside the minnow trap as a result of presence or absence of a piscivore during the mark–retention study were also conducted using ANOSIM. Piscivores included non-native cichlids, *e.g.* jewelfish *Hemichromis letourneuxi* Sauvage, Mayan cichlid *Cichlasoma urophthalmus* (Günther), jaguar guapote *Cichlasoma managuense* (Günther), sunfish *Lepomis* spp. and pike killifish *Belonesox belizanus* Kner. The tests for community differences were only conducted on samples from the 24 h collections, because there were no piscivores present in any of the traps after they were deployed for only 2 h. A similarity percentage-breakdown analysis (SIMPER) was used to determine how the relative abundance of a species affected the average similarity between groups (Clarke, 1993). This reports the relative contribution (%) of each species to similarity between groups as the ratio of their individual contribution to similarity and the average similarity (McCune & Grace, 2002). All community analyses were conducted using Primer 5.0 software (www.primers-e.com).

Univariate statistical tests were also conducted with treatments nested within site–date combinations to account for non-independence of sampling events. There was no replication within site–date combinations for the diel study, so bootstrap sampling (99 replicates) was used to estimate the error variance and perform hypothesis tests (Roff, 2006). All univariate statistical analyses used linear least-squares methods with transformations as necessary to meet the assumptions of the analyses. All minnow trap data were divided by the number of

hours of sampling to yield catch per hour (CPH). A general linear model with spatial autocorrelation was used to test for changes in the speed and migratory movements. Orientation, sampling period and the two-way interaction were treated as fixed effects over the five study periods and total catch was the response variable. Tests were conducted separately by site to avoid averaging across ecological regions. Univariate analyses were conducted using SAS 9.1 (www.sas.com) or SYSTAT 11.0 (www.systat.com); bootstrap analysis was conducted in R version 2.11.0 (<http://r-project.org>).

RESULTS

SAMPLING BIAS

Sample duration and time of day influenced both CPH and community composition. CPH was higher during the 2 h around sunset, followed by the 2 h around sunrise and the 12 overnight hours [nested ANOVA, d.f. = 26 and 129, $P < 0.05$; Fig. 2(a)]. Tukey's *post hoc* tests of paired contrasts averaged across days revealed

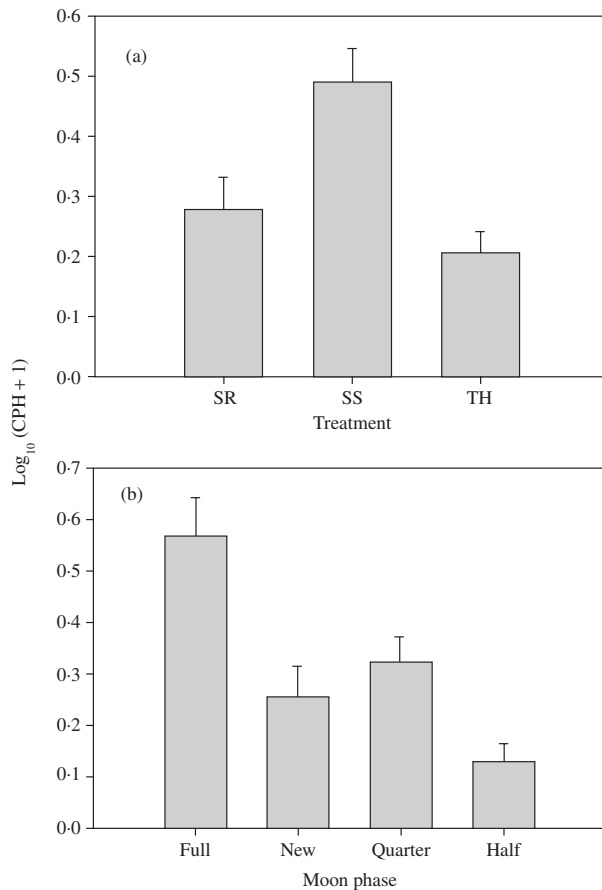


FIG. 2. Results from night-time fish movement study ($n = 144$ samples). Mean + s.e. [\ln catch per hour (CPH) + 1] (a) at each treatment (SR, sunrise; SS, sunset; TH, overnight) and (b) for each moon phase.

TABLE I. Similarity percentage analysis (SIMPER) results of sampling time study showing relative abundance at sunrise (SR) and sunset (SS) treatments and full and new moon treatments. Contribution (%) is the relative contribution of each species to overall differences between treatments

(a) Species	SR	SS	Contribution (%)
<i>Gambusia holbrooki</i>	0.48	0.61	22.65
<i>Lepomis marginatus</i>	0.22	0.09	18.25
<i>Fundulus confluentus</i>	0.07	0.1	12.85
<i>Lucania goodie</i>	0.1	0.06	12.83
Total	252	280	
(b) Species	Full	New	Contribution (%)
<i>Gambusia holbrooki</i>	0.72	0.32	20.69
<i>Fundulus confluentus</i>	0.09	0.17	15.75
<i>Lepomis marginatus</i>	0.06	0.21	15.59
<i>Lucania goodei</i>	0.04	0.17	14.13
Total	653	199	

no differences in CPH between sunrise and sunset and sunrise and overnight samples, but a difference between sunset and overnight (SS *v.* TH; $P < 0.01$). Two-way ANOSIM results on fourth-root-transformed community data indicated a difference between SR and SS treatments (global $R = 0.089$, $P < 0.05$). SIMPER showed that mosquitofish *Gambusia holbrooki* Girard and marsh killifish *Fundulus confluentus* Goode & Bean were more active at sunset than sunrise, whereas dollar sunfish *Lepomis marginatus* (Holbrook) and bluefin killifish *Lucania goodei* Jordan moved more at sunrise than in the evening [Table I(a)]. The full moon ($n = 36$) had the highest CPH (ANOVA, d.f. = 3 and 144, $P < 0.001$), but new ($n = 24$), quarter ($n = 60$) and half ($n = 36$) moons were not different from each other [Fig. 2(b)]. There was no interaction between treatment and moon phase. Analysis of similarity indicated that species relative abundance differed between new and full moons (global $R = 0.298$, $P < 0.01$). Similarly, SIMPER showed that *G. holbrooki* was more active during the full moon, whereas *F. confluentus*, *L. marginatus* and *L. goodei* were more active during the new moon [Table I(b)].

The mark–retention experiment demonstrated loss of fishes during a 24 h sample. Relatively few of the fishes marked after 2 h remained in the traps 22 h later; there was a high rate of escape from, or consumption within, the traps. The number of marked fishes in traps after 24 h was much lower than the number captured after the first 2 h (number of marked fishes in trap after 24 h mean = 1.63 and after 2 h mean = 8.12; t -test, d.f. = 82, $P < 0.001$). The total number of fishes inside the traps, however, increased over the same period (number of all fishes in trap after 24 h mean = 18.9 and after 2 h mean = 8.12; t -test, d.f. = 82, $P < 0.001$). Of the 683 fishes marked after 2 h, only 142 remained inside the traps at the time of collection, for a retention rate of only 20.8% (Table II). Total species richness also increased from 11 species after 2 h to 16 species after 24 h. Community structure inside the minnow trap changed between 2 and 24 h (ANOSIM, global $R = 0.055$, $P < 0.01$). *Gambusia holbrooki* and *L. goodei* were the most abundant species after 2 h, whereas *Lepomis* spp. and flagfish *Jordanella floridae* Goode & Bean were the most abundant

TABLE II. Total number of marked fishes at 2 and 24 h as well as per cent retained in the trap over the sampling period

Species	Number at 2 h	Number at 24 h	Retained (%)
<i>Gambusia holbrooki</i>	475	65	13.7
<i>Lepomis</i> spp.	72	40	55.6
<i>Poecilia latipinna</i>	34	9	26.5
<i>Lucania goodei</i>	27	10	37.0
<i>Jordanella floridae</i>	26	12	46.2
<i>Heterandria formosa</i>	25	2	8.0
<i>Fundulus chrysotus</i>	11	1	9.0
<i>Fundulus confluentus</i>	5	3	60.0
<i>Oreochromis aureus</i>	7	0	0

after 24 h [Table III(a)]. Presence or absence of a predator inside the minnow trap also influenced the community structure inside at the time of collection [Table III(b); ANOSIM, global $R = 0.14$, $P < 0.05$]. SIMPER demonstrated that *G. holbrooki* and *L. goodei* were more abundant in traps lacking predators, whereas *J. floridae* and *Lepomis* spp. had higher relative abundance when a piscivore was present.

The diel activity study indicated that Everglades fishes had distinct activity patterns during a 24 h period (Fig. 3). The bootstrap analysis indicated an effect of time-of-day treatment (bootstrap bias-corrected 95% C.I. for effect of treatment, -13.047 to 4.119). Averaging across days, the 95% C.I. for minnow traps set during the MD did not overlap with CPH of traps set at MN and overlapped marginally with those set at SS. CPH of SR and SS samples did not differ from each other or from samples collected at MN. An effect of moon phase was noted on these results, with moonless and cloudy nights yielding the lowest catches. Community structure differed

TABLE III. Similarity percentage analysis (SIMPER) results of mark-retention study. (a) The relative abundance by species in 2 and 24 h minnow-trap samples. (b) Relative abundance in communities with a piscivore present and absent. Contribution (%) is the relative contribution of each species to overall differences between treatments

(a) Species	2 h	24 h	Contribution (%)
<i>Lepomis</i> spp.	0.09	0.2	18.7
<i>Gambusia holbrooki</i>	0.66	0.44	18.39
<i>Poecilia latipinna</i>	0.05	0.04	10.24
<i>Jordanella floridae</i>	0.02	0.07	9.81
Total	683	1595	
(b) Species	Absent	Present	Contribution (%)
<i>Lepomis</i> spp.	0.13	0.23	18.04
<i>Gambusia holbrooki</i>	0.6	0.42	13.83
<i>Jordanella floridae</i>	0.04	0.1	10.91
<i>Belonesox belizanus</i>	0.0	0.08	10.3
<i>Lucania goodei</i>	0.08	0.02	8.81
Total	1551	727	

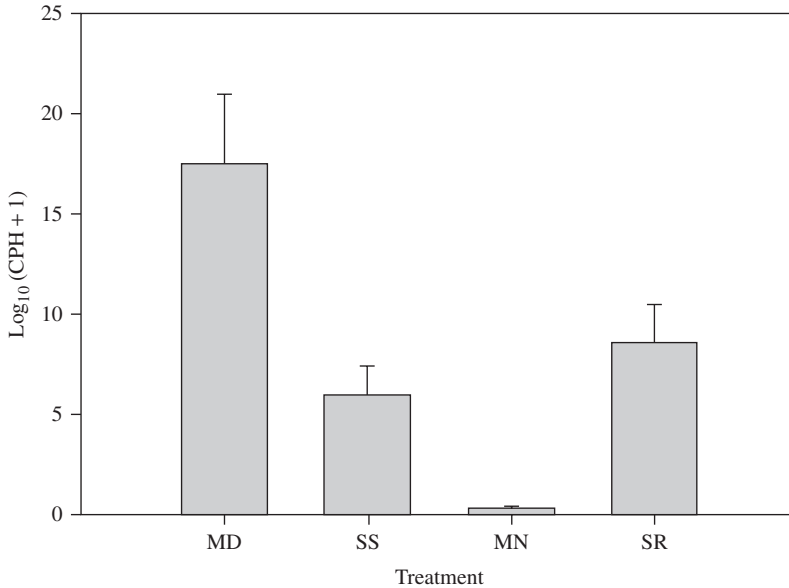


FIG. 3. Mean + s.e. [\log_{10} catch per hour (CPH) \pm 1] of fishes and invertebrates for each time of day ($n = 233$ samples) (MD, midday; SS, sunset; SR, sunrise; MN, midnight).

in two of the four treatments, with SR and SS being indistinguishable (Table IV). SIMPER showed that *G. holbrooki*, *L. goodei*, least killifish *Heterandria formosa* Girard and Everglades pygmy sunfish *Elassoma evergladei* Jordan were responsible for most differences among treatments (Table V). *Elassoma evergladei* was the only fish species that was consistently active at night, which affected community differences associated with time-of-day treatments.

Consistently, larger catches were expected based on video data than were obtained from the traps (t -test, d.f. = 19, $P < 0.05$). Specifically, the estimated CPH was lower in traps (mean \pm s.e. = 14.10 ± 7.09 fishes) than the number of fishes observed entering on video (mean \pm s.e. = 22.55 ± 10.58). The discrepancy between the two techniques was proportional to the level of fish activity [Fig. 4(a)]; when more fishes entered the trap the differences between video and trap increased.

TABLE IV. Results of analysis of similarities (ANOSIM) pair-wise tests during diel-movement study

Comparison	R statistic	P -value
MD–SS	0.074	<0.01
MD–MN	0.633	<0.01
MD–SR	0.039	<0.05
SS–MN	0.334	<0.01
SS–SR	0.016	>0.05
MN–SR	0.567	<0.01

MD, midday; MN, midnight; SS, sunset; SR, sunrise.

TABLE V. Similarity percentage analysis (SIMPER) results of diel-movement study. Relative abundance in midday (MD), sunset (SS), midnight (MN) and sunrise (SR) treatments. Contribution (%) is the relative contribution of each species to overall differences between treatments

Species	MD	SS	Contribution (%)
<i>Gambusia holbrooki</i>	0.47	0.44	18.42
<i>Lucania goodei</i>	0.12	0.1	13.04
<i>Heterandria formosa</i>	0.14	0.01	11.36
<i>Jordanella floridae</i>	0.1	0.04	10.43
Total	1032	346	
	MD	MN	
<i>Elassoma evergladei</i>	0.00	0.73	26.85
<i>Gambusia holbrooki</i>	0.47	0.08	21.64
<i>Heterandria formosa</i>	0.14	0.08	11.44
Total	1032	20	
	MD	SR	
<i>Gambusia holbrooki</i>	0.47	0.33	16.68
<i>Lucania goodei</i>	0.12	0.15	13.34
<i>Jordanella floridae</i>	0.1	0.11	11.92
<i>Heterandria formosa</i>	0.14	0.04	11.71
Total	1032	512	
	SS	MN	
<i>Elassoma evergladei</i>	0.08	0.73	30.19
<i>Gambusia holbrooki</i>	0.44	0.08	24.12
<i>Lepomis gulosus</i>	0.06	0.08	8.01
Total	346	20	
	MN	SR	
<i>Elassoma evergladei</i>	0.73	0.01	25.73
<i>Gambusia holbrooki</i>	0.08	0.33	18.29
<i>Lucania goodei</i>	0.00	0.15	9.67
Total	20	512	

Of the three behaviours recorded, avoidance was the most common, followed by entry, then escape (number of behaviours noted per 2 h: avoidance mean \pm s.e. = 111.9 ± 45.1 ; entry mean \pm s.e. = 28.7 ± 13.1 ; escape mean \pm s.e. = 6.1 ± 2.7). There was a linear relationship between fish escape and entry during 2 h samples for all species combined [Fig. 4(a); ANOVA, d.f. = 1 and 18, $P < 0.001$], but the slope was <1 (ANOVA, d.f. = 1 and 18, $P < 0.001$) indicating that these behaviours did not increase proportionately with the number of fishes in the trap. A similar relationship was noted between avoidance and number of fishes inside the trap for all species combined [Fig. 4(b); ANOVA, d.f. = 1 and 18, $P < 0.001$]; however, in this case the slope was not different than one (ANOVA, d.f. = 1 and 18, $P > 0.05$). Sailfin mollies *Poecilia latipinna* (LeSueur) had the highest escape rate (61.5%), whereas *L. goodei* had the lowest (0.0%). *Gambusia holbrooki* had the highest likelihood of avoiding the trap given an encounter and *Lepomis* spp. had the highest

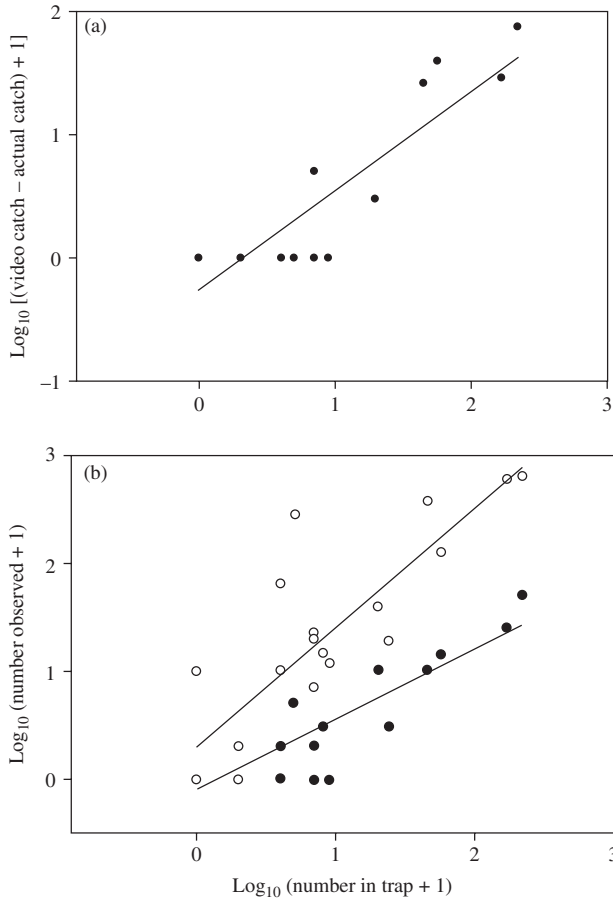


FIG. 4. Results from video analysis. (a) Relationship between the number of fish [$\ln(\text{number} + 1)$] observed by video entering traps and number of fish collected in the trap after 2 h [$\ln(\text{number in trap} + 1)$] ($y = 0.809x - 0.267$). (b) Relationship of number of fish [$\ln(\text{number} + 1)$] observed by video escaping (●, $y = 0.661x - 0.098$; $R^2 = 0.78$) and avoiding (○, $y = 1.101x + 0.300$; $R^2 = 0.72$) traps over 2 h sample time relative to the number of fish collected in the trap after 2 h [$\ln(\text{number in trap} + 1)$].

likelihood of entering the trap given an encounter (Table VI). On the basis of the video data, for most species the probability of escape during 2 h of trapping was lower than that observed during 22 h from the mark–retention study.

ESTIMATING SPEED

Estimates from throw traps of the density of fishes in Shark River Slough during the 4 year period from 2004 to 2007 showed that densities decreased through the dry season, reaching a minimum in April and remaining low through to July [Fig. 5(a)]. Densities then increased in October and December, though at levels similar to or less than that observed in February. Catch per day (CPD) of all fishes from drift fences at these sites showed a similar decline as density from February to April remained low in July and increased to the highest levels of the year in October and December

TABLE VI. Species-specific escape, avoidance and entry from video data where the total number of individuals is listed with per cent performing activity in parentheses

Species	Escape (%)	Avoid (%)	Enter (%)	Encounter
<i>Gambusia holbrooki</i>	97 (21.7)	1959 (81.4)	448 (18.6)	2407
<i>Jordanella floridae</i>	3 (7.1)	96 (69.5)	42 (30.4)	138
<i>Fundulus confluentus</i>	2 (11.8)	34 (66.7)	17 (33.3)	51
<i>Poecilia latipinna</i>	8 (61.5)	34 (72.3)	13 (30.4)	47
<i>Lepomis</i> spp.	5 (23.8)	23 (52.3)	21 (47.7)	44
<i>Heterandria formosa</i>	5 (38.5)	21 (61.8)	13 (38.2)	34
<i>Lucania goodei</i>	0 (0.0)	5 (55.6)	4 (44.4)	9

% Escape = 100 number escaped (N_{ES}) per number entered (N_{EN}); % avoid = 100 number avoided (N_A) per number encountered (N_{ENC}); % enter = 100 $N_{EN} N_{ENC}^{-1}$; encountered = $N_{EN} + N_A$.

[Fig. 5(a)]. Only one of the five sites provided evidence of differences in catch rate based on the direction of the trap, so data were pooled from the four directions for estimating speed. It was estimated for all fish species summed using equation (2) and these estimates of density and trap encounter rate. CPD was adjusted to account for underestimates of trap encounter because of escape and predation using species-specific correction factors from the mark-retention study (Table II). No correction factors were created for trap avoidance because 24 h data were lacking. Speed for all fish species summed was slowest in February and April ($c. 0.02 \text{ m s}^{-1}$) and then increased from April to October, with a slight increase from October to a maximum in December ($c. 0.04 \text{ m s}^{-1}$) [Fig. 5(a)].

Four species were abundant enough in the samples to analyse separately. *Lepomis marginatus* moved at a higher speed than the three small species examined: *G. holbrooki*, *L. goodei* and *J. floridae* [Fig. 5(b), (c)]. *Lepomis marginatus* moved more quickly in December and February than in other months, though s.e. were large in these 2 months because of large inter-sample variability in CPD [Fig. 5(b)]. *Gambusia holbrooki* also may have moved more quickly in December than *L. goodei* and *J. floridae*, but there were no differences in these species in the other months studied [Fig. 5(c); s.e. overlap]. There was large uncertainty, however, about the high December estimate for *G. holbrooki*.

DISCUSSION

This study demonstrates a methodology for obtaining indirect estimates of speed for fishes that cannot be tracked directly. The resulting estimates can be used in a simulation framework that assumes microscale fish movement as a random walk to estimate the diffusion coefficient D that is a common parameter in spatial ecological models (DeAngelis *et al.*, 2010). A random walk is a trajectory resulting from a sequence of steps in random directions, each beginning at the end point of the previous step. $D [= \lambda^2(2\tau)^{-1}]$ is estimated iteratively by solving for values that yield realistic encounter rates (τ) and average distance moved between turns (λ), constrained by field estimates of speed ($= \lambda\tau^{-1}$) obtained from methods described here. By assuming that these estimates describe short-distance movements (local or

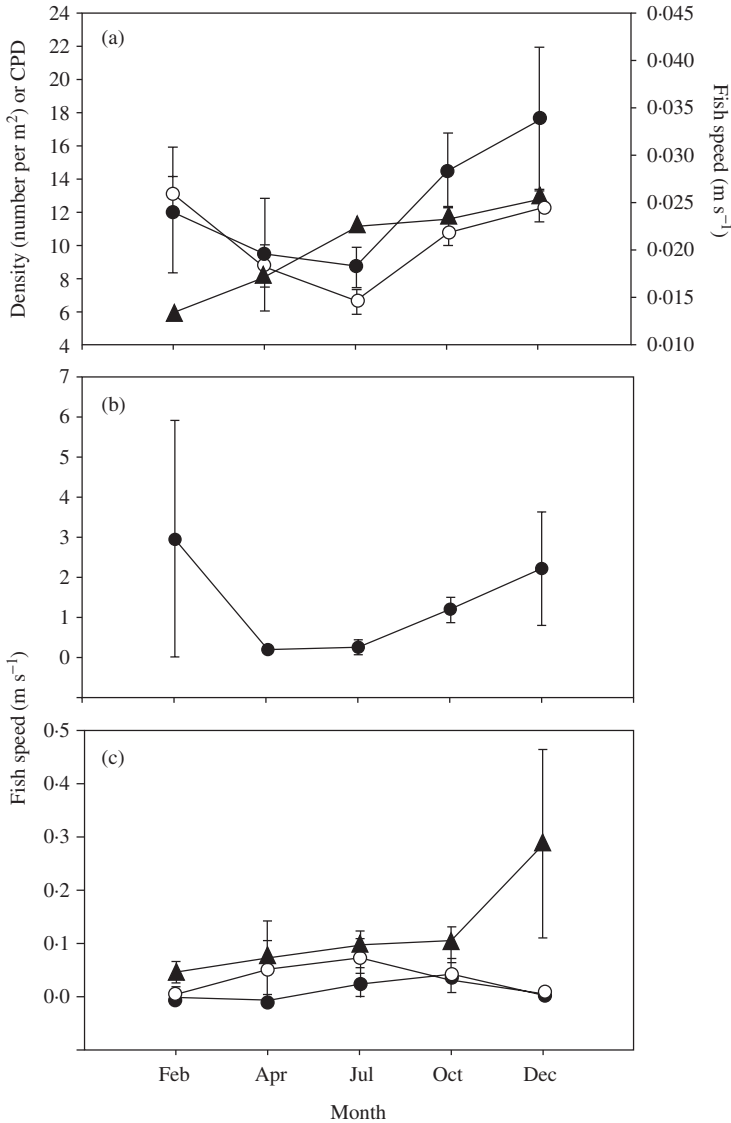


FIG. 5. Field estimates of mean \pm s.e. fish speed. (a) Density (\circ), catch per day (\bullet , CPD) and fish speed (\blacktriangle) of all fish species calculated from 4 years of throw trap and drift-fence data in Shark River Slough. CPD is given, rather than catch per hour as in previous figures, to facilitate scaling of the y-axis of this graph; these data can be adjusted to CPH by simply dividing by 24. Fish speed error bars were too narrow for the scale. (b) Fish speed and month for *Lepomis marginatus*. (c) Fish speed and month for three species of small fishes (\bullet , *Jordanella floridae*, \circ , *Lucania goodei*, \blacktriangle *Gambusia holbrooki*). Note scale changes on speed axes.

neighbourhood movements), these estimates of D can be applied in spatial population models for predicting the spread of species as they invade newly flooded habitats (Andow *et al.*, 1990) and for comparison to observations of invasion as a test for evidence of more complex dispersal modes (Turchin, 1998). A probable alternative

model to diffusion is a stratified diffusion model that assumes two or more classes of movements such as local and long distance (Shigesada *et al.*, 1995; Liebhold & Tobin, 2008). Although random-walk diffusion is a grossly simplistic description of fish movement, it can have useful application. For example, radio-tracking data indicate that Florida gar *Lepisosteus platyrhincus* DeKay make relatively small movements when water levels exceed 20 cm, but move longer distances in more shallow water (J. C. Trexler, unpubl. data), similar to a stratified model. Local movements may be well characterized by simple diffusion-based models, whereas the longer movements are better described by functions tied to directed movement to find dry-season refuges.

Although direct observation of movement would seem to be preferable to the present methods, direct observations have some limitations. For example, the study provides averages over long time-periods and many individuals. Tracking studies are often limited in the timeframe or number and diversity of demographic classes of fishes that can be studied. Also, values of speed from mark–recapture studies must assume linear movement between release and recapture, which could bias estimates downwards. Using the correction factor for loss, speeds were estimated to range from 0.001 to 0.300 m s⁻¹ for small poeciliids and fundulids living in the Everglades to 0.10 to >2.00 m s⁻¹ for a small species of centrarchid. These speeds are comparable to those estimated by direct observation in other studies (Fangue *et al.*, 2008; Jones *et al.*, 2008; Kavitha & Rao, 2008). For example, Bishop *et al.* (1995) directly observed speed of tropical fishes seeking dry-season refuge and found a range from 0.12 to 0.21 m s⁻¹. Although higher than the estimates for *L. goodei* and *J. floridae* reported here, their study species were larger (size >9 cm L_S) than those examined here (<4 cm L_S) and it is reasonable to expect larger fishes to move faster.

This study suggests that fish speed was not constant throughout the year. The two sampling periods with the lowest estimates for fish speed corresponded with the two driest months sampled. These data were collected from long-hydroperiod marshes and, presumably, by the time of the February and April samples, fishes had already moved there for refuge from drying marshes, seeking a hydrological refuge. Movement rates were greater in the wet-season samples, reaching a maximum in October and December. The margins of the Everglades begin to dry by December, possibly triggering fishes to move from those areas towards long-hydroperiod marshes where sampling was conducted.

Interpretation of minnow-trap data is difficult because of both bias in collections and confounding of density and speed. Several studies reported here demonstrated that minnow traps underestimate fish encounter rates and that the bias increases with the duration of sampling time. These effects, however, can be estimated and the speed estimated adjusted accordingly. Layman & Smith (2001) and Rotherham *et al.* (2006) demonstrated that minnow traps in some estuarine environments reach saturation relatively quickly, biasing capture rates. This study failed to find evidence of saturation, even after 24 h of sampling. Although a high rate of loss of marked fishes was noted, video data demonstrated that the net influx of fishes continued throughout the sampling interval. The Everglades is an oligotrophic ecosystem with a relatively low density of fishes compared to other shallow systems inhabited by fishes (Turner *et al.*, 1999). This could contribute to traps failing to become saturated in this study. It is also possible that as water levels drop and fishes become concentrated

in the dry-season pools in drought years, local densities could reach levels where traps would be saturated quickly.

The CPH changed as the length of samples increased, as did the species composition in the traps. The time of day also affected the estimates of CPH, undoubtedly tied to diurnal activity patterns of Everglades fishes (Loftus, 2000; Arrington *et al.*, 2002). The CPH was highest for 2 h at midday, followed by sunrise and sunset, and least at night (almost zero on moonless nights). Nocturnal catches were higher during a full moon, suggesting increased lighting of the marsh-permitted diurnal fishes to expand their activity period. Because the freshwater Everglades is not tidal, higher activity could not have resulted from changes in tidal water movement (Krumme & Saint-Paul, 2003) and there was no evidence that reproduction is associated with lunar phase (Taylor, 1984). A full moon that illuminates the marsh may make foraging easier for visual piscivores. Thus, diurnal activity in the fishes that were sampled may be triggered because large piscivorous species such as *L. platyrhincus* and bowfin *Amia calva* L. forage more at night (Helfman *et al.*, 1997; Snedden *et al.*, 1999). Large amphibians of the Everglades, such as greater siren *Siren lacertina* and amphiuma *Amphiuma means*, also eat small fishes and are primarily nocturnal foragers. The CPH at dusk and dawn was higher than at night, but lower than during the day, possibly because fishes were moving only for half of the sample time. Bishop *et al.* (1995) found a similar change from zero to high levels of fish movement during the dark and light segments, respectively, of crepuscular periods. Increased activity of *E. evergladei* at night compared with any other time was the primary reason for community differences between the midnight samples and all others. The relative abundance in traps of *G. holbrooki* was highest during the day, whereas *L. goodei* and *J. floridae* relative abundances were highest at sunrise. Such community differences among the treatments highlight the importance of selecting sampling times matched to questions being asked and accounting for this variation in data analyses (Ellis & Bell, 2008).

Almost 80% of the fishes marked and replaced in traps after 2 h of sampling were gone 22 h later, indicating high losses from either escape or predation. Piscivores were not present in every trap after 24 h, yet losses occurred in all but one, suggesting that escape accounted for much of the loss. Fishes were observed escaping traps on the videos, both swimming out of the opening and, for small individuals, through the wire mesh. Predation was also observed. For example, the gut contents of a *C. managuense* contained several marked *G. holbrooki* and a *B. belizanus* was preserved with a fish in its jaws. Breen & Ruetz (2006) found that predation typically did not exceed 10% inside a fyke net with known prey densities; similarly, low rates of predation were recorded for traps in this study.

On the basis of the video data, species differed in the probability of escape. *Gambusia holbrooki* and *H. formosa* had the lowest retention rates, probably because both species are small, increasing their chances of being eaten and of escaping through the 3 mm mesh. Additionally, individuals of *G. holbrooki* are active and inhabit the upper water column, allowing them more opportunities to encounter the exit of the trap. *Jordanella floridae* and *Lepomis* spp. had relatively high retention in traps. These taxa are demersal, with deeper body shapes less conducive to escape through the mesh. Species with higher retention times may have had lower motivation to escape, because they were less likely to be preyed upon. The higher retention of fishes associated with benthic habitats was similar to the results of Breen & Ruetz

(2006). An increase in species richness from 2 to 24 h was not surprising, as it was more likely that less abundant species, such as piscivores, encountered the trap during longer sampling times. The increase in species richness resulted in a community shift between the two sample times. As smaller fishes escaped or were consumed, individuals of larger species became relatively more abundant inside the traps. It appeared that the capture of small fishes may have baited the traps during the first 2 h or so and then attracted larger and more piscivorous species when left for longer periods.

Video recordings provided direct evidence for fishes escaping from the traps, as well as interactions in traps, including predators chasing small individuals. The video provided a conservative estimate of fish escape because the camera could focus only on the trap entrance and limited areas of the mesh. The number of fishes that avoided the trap was high when compared with number observed entering and even higher when compared to the number of fishes remaining in the trap after 2 h of sampling. Other studies found similar inefficiencies in passive sampling devices (Jury *et al.*, 2001; Cole *et al.*, 2004). Avoidance was independent of the number of fishes inside. Video recordings also revealed that the drift-fence wings produce a Venturi effect (Baylar, 2003) by concentrating moving water from the small currents that were present and flushing it through the opening where the trap was located. This current appeared to carry prey that attracted fishes to forage just outside the trap without actually entering it.

This study demonstrated a method to estimate fish speed that has application for analysis of dispersal with spatial population models. This work depends on information gleaned from an encounter-trap sampling device after adjusting for independent information on density. Success at removing density effects to reveal movement data underscores problems for studies that use such data as an index of density. If movement rate is constant across space and time, encounter-trap data can be used in a comparative study as an index for density differences. It seems unlikely, however, that the latter requirement holds in many cases. For example, Collins *et al.* (1983) concluded that predator density changed the activity patterns of crayfishes, leading to different capture rates in minnow traps. This study attempts to capitalize on artefacts of this type to glean useful information on movement that is usually ignored in trap data and difficult and at times impossible to obtain through direct measurements.

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