

## Sources of Sampling Bias in Enclosure Fish Trapping: Effects on Estimates of Density and Diversity

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### ABSTRACT

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Enclosure traps have been increasingly used to sample fish populations in shallow aquatic habitats because they have proven to be practical, effective and sufficiently precise. However, they are somewhat biased, usually underestimating fish densities. Large fish are under-sampled, due either to escape or scarcity, consequently affecting biomass estimates. Using computer simulations and an extensive enclosure-trap data base, we found that the most consistent explanation for the reduced densities observed was a reduced effective sampling area, rather than an inappropriate sampling model. Corrections for density bias could be made by considering that a 1-m<sup>2</sup> trap effectively samples a 0.81-m<sup>2</sup> area of marsh. Using an index of species diversity, we confirmed that, despite the bias in density estimates, the composition of the fish community could be accurately described using data obtained from enclosure trapping. Enclosure trapping could effectively be argued to be either with- or without-replacement sampling. Thus, under field conditions, fish may be either removed or replaced without violating the sampling model.

### INTRODUCTION

The existence and structure of biotic communities are matters of intense debate (Strong et al., 1984; Diamond and Case, 1986) and fish communities are playing important roles in this discussion (Tonn et al., 1983). In the analysis of fish communities, not only should the accuracy and precision of the sampling technique be known, but the estimators used should have underlying probability distributions appropriate to the sampling methods. The appropriate sampling of communities of small fishes in shallow-water environments, such as marshes, swamps and lake shores, has proven to be an especially complex sampling situation (Kushlan, 1981). Unresolved questions of potential

bias, particularly with regard to the use of appropriate estimators, remain unexamined.

Enclosure traps, open-bottomed traps that quickly enclose a known area of water, have been increasingly used for quantitative sampling of fish (Hellier, 1959; Kahl, 1963; Higer and Kolipinski, 1967; Moseley and Copeland, 1969; Wegener et al., 1973; Kjelson and Johnson, 1973; Kjelson et al., 1975; Aneer and Nellbring, 1977; Gilmore et al., 1978). In a review of sampling devices, Kushlan (1974) concluded that enclosure traps provided an appropriately consistent and practical methodology, and later (Kushlan, 1981) showed that a 1 m<sup>2</sup> throw-trap provided statistically precise density information and could be employed in a logistically feasible sampling program. Kushlan (1981) also found, however, that sample densities from his 1 m<sup>2</sup> throw-trap underestimated true population density with a consistent bias in accuracy of 73%. The source of bias was not identified and its effect on estimates of community structure was not known.

In this study, we further examine the apparent sampling error inherent in the design and use of enclosure traps. Although enclosure traps sample fish populations precisely, a bias may result because estimators based on assumptions of simple random sampling, which are commonly used for estimates of density and diversity, may not be appropriate (White et al., 1982). Fishes may not, in fact, be randomly dispersed throughout the marsh. Spatial heterogeneity of the marsh or patterns of fish dispersion, such as schooling, may affect the accuracy of density estimates derived from enclosure trapping and may subsequently affect estimates of community diversity derived from this same data base. We use simulated sampling of communities containing fishes having one of several spatial distributions to determine if model bias affects the accuracy of estimates of density and biomass derived from enclosure trapping of shallow-water fish populations. We evaluated one index of species diversity by comparing expected values of diversity with empirical results. We also hypothesized that the reported bias in density estimates might be caused by the trap having a reduced effective sampling area and we examined this hypothesis using computer simulations. Through these analyses, we evaluate the ability of enclosure trapping to provide reliable estimates of fish community parameters.

## MATERIALS AND METHODS

### *Field studies*

Tests of the enclosure trap were conducted in the marshes of the Florida Everglades in areas of medium to sparse herbaceous vegetation dominated by *Eleocharis cellulosa*, *Panicum hemitomom* and *Utricularia* spp. (Kushlan, 1981, 1987). Seventeen fish species occurring in these marshes included golden shiner

(*Notemigonus crysoleucas*), yellow bullhead (*Ictalurus natalus*), diamond killifish (*Adinia xenica*), sheepshead minnow (*Cyprinodon variegatus*), golden topminnow (*Fundulus chrysotus*), marsh killifish (*F. confluentus*), Seminole killifish (*F. seminolis*), flagfish (*Jordanella floridae*), bluefin killifish (*Lucania goodei*), mosquitofish (*Gambusia affinis*), least killifish (*Heterandria formosa*), sailfin molly (*Poecilia latipinna*), Everglades pygmy sunfish (*Elassoma evergladei*), warmouth (*Lepomis gulosus*), bluegill (*L. macrochirus*), dollar sunfish (*L. marginatus*) and redear sunfish (*L. microlophus*).

Standard application of the enclosure trap involves throwing the trap into the marsh to enclose a 1 m<sup>2</sup> area, then dip-netting to remove all fish. Collected fish are poisoned in the field (i.e., without replacement sampling) for subsequent measurement in the laboratory. The trap is randomly thrown again and the sampling process repeated until it is possible to detect a pre-determined density difference among sampling events by parametric statistical analysis (Kushlan, 1974). The purpose of deriving the density estimate is to compare fish densities among different marsh sites and to correlate fish density with water levels.

The accuracy and precision of the 1 m<sup>2</sup> throw-trap was determined by field sampling under conditions of low and high fish densities (9 fish m<sup>-2</sup> and 33 fish m<sup>-2</sup>, respectively), within two large block-netted areas, 190 and 232 m<sup>2</sup> in size, respectively. Inside the block-netted areas, 20 enclosure-trap samples were taken and data were recorded on the size (standard length in millimeters) and species of each fish captured. Fish were returned to the block-netted area (sampling with replacement) after each enclosure trap was thrown. When sampling by the enclosure trap was completed, the entire block-netted area was treated with rotenone and dead fish were collected over a 3-day period. Data from each enclosure trapping session were combined to form pooled 20-trap samples, from which empirical estimates of density and diversity were calculated. Fish poisoned in the block-netted areas represented the true populations.

#### *Density estimates*

We used computer simulations to evaluate the effects on density and biomass estimates of proposed spatial patterns of fish distribution and of the potential bias in the physical properties of the trap. Two grid sizes (140×140 and 150×150 units) represented the two areas from which fish populations were removed in the field at low- and high-density sites, respectively. The total number of fish known to exist in the enclosed areas (1791 and 7584, respectively) were distributed on the simulation grids according to pre-determined probability functions by assigning each fish (identified by species and size) to a grid location using a random number generator. Two random numbers (for X- and Y-axes) were multiplied by the size of the grid along each axis (i.e.,

140 or 150 units) to provide coordinates, such that after all fish were assigned locations, the number of fish per grid unit was a Poisson variate. The double Poisson distribution was used to simulate a clumped distribution, in which fish were aggregated in clumps of random size, which were then located randomly on the grid. We varied the size of the clumps, the second parameter of the double Poisson, to simulate low and high levels of clumping by bounding clump sizes at a maximum of 5 and 25 fish per clump, respectively. Simulated clumping tended to group together similar species and secondarily, similar sizes, because this was how the data file was structured. These are realistic characteristics of the fishes under study.

To simulate enclosure trapping, the center of each trapping area was assigned a grid location without replacement using a random number generator. The total area of the trap (representing 1 m<sup>2</sup>) around the assigned center location was sub-divided and a decreased trapping area (representing 0.81 m<sup>2</sup>) was simulated by removing fish located along the outer edge of the 1 m<sup>2</sup> trapping area from density calculations. Statistics were compiled on the number, size and species of each fish included in the trapping area. Twenty replications of 20-trap samples for each of 12 density/spatial distributions yielded 12 distributions of mean fish densities. The grand mean density is the mean of 20 replications of 20 enclosure-trap samples. The percent relative bias (White et al., 1982) of the simulated grand mean density of each of the 12 distributions was evaluated with respect to the empirical (enclosure-trap) and true (block-netted) mean fish densities determined through field sampling.

#### *Diversity estimates*

In this analysis, diversity is defined as the expected number of species encountered when '*m*' individuals are drawn at random from a population (Smith and Grassle, 1977). This index, first proposed by Hurlbert (1971), uses the maximum likelihood solution based on random selection from all possible combinations to reveal the most likely number of species for a given sample size (Hessler and Jumars, 1974) and suggests the probability of inter-specific encounters in a community of mobile organisms (Hurlbert, 1971). The formula given by Hurlbert (1971) is the without-replacement estimator for a multi-nomial if the population is completely known and is sub-sampled, and provides the maximum likelihood estimate for a new sample of size, *n*, taken at random from the original, incompletely known population.

The with-replacement equivalent of the above estimator, as given in Hurlbert (1971), can be used if it can be assumed that no inter-specific encounters within a community are lethal, i.e. if individuals are "replaced" after each inter-specific encounter. An advantage of the with-replacement index is that a minimum variance unbiased estimator exists (Smith and Grassle, 1977). The multinomial sampling model, however, assumes an infinite population (i.e., with-

replacement sampling) and the absence of patchiness within species (Smith and Grassle, 1977). Because fish are not replaced during enclosure trapping (Kushlan, 1974) and because mobile species are not usually homogeneously distributed (Fager, 1972), we suspected that the expected species diversity estimator may give biased estimates of community diversity. The effect of replacement is addressed later in this study, while the effect of patchiness is examined by using the heterogeneity  $\chi^2$  index proposed by Jumars (1975a). Based on the variance-to-mean ratio (Pielou, 1979), the heterogeneity  $\chi^2$  index tests the assumption that species are randomly dispersed among traps.

By graphical analysis, we tested the sensitivity of the diversity index of the estimated degree of aggregation (Jumars, 1975b). Using a range of values for  $n$  (the number of individuals in a hypothetical sample), we generated an asymptotic curve based on the expected species diversity estimator. The curve relates the expected number of species ( $Y$ -axis) in a sample with a given number of fish ( $X$ -axis). Empirical data (observed number of species in samples having measured numbers of fish) are plotted on the same set of axes. If species were randomly distributed among samples, the curve derived from the expected species diversity index should bisect empirical data points, given that the distribution of samples is normal such that the mean and median are approximately equivalent. If a significant number of samples were to fall below the curve, the species would be considered aggregated in their distribution among the traps (Hessler and Jumars, 1974) and we would conclude that the index was biased by the spatial patterns of the species in the community.

## RESULTS

### *Dispersion*

There was an increase in the variance of the density estimates within 20-trap samples from random dispersion, to low clumping, to high clumping (Table I). Low- and high-clumped distributions exhibited much greater variance than what was observed under field sampling and the low variance of the random spatial distribution was most consistent with empirical results. Thus, comparisons of simulated with empirical data suggest that the shallow water fish populations from which enclosure trapping samples were drawn were randomly distributed in space. Spatial heterogeneity, therefore, is not a factor of concern with regard to the appropriateness of assumptions of simple random sampling.

### *Effective trapping area*

The grand mean densities resulting from simulated sampling (Table I) decreased from the full ( $1 \text{ m}^2$ ) to reduced ( $0.81 \text{ m}^2$ ) trap areas, as might be expected. The  $1 \text{ m}^2$  trap simulations closely approached the true population

TABLE I

Simulation results showing the grand mean, standard error, maximum and minimum means of density (fish m<sup>-2</sup>), variance in density and fish size (mm) for 20 replicates of 20-trap samples

	Density				Variance in density				Fish size			
	Grand mean	Std. error	Max. mean	Min. mean	Grand mean	Std. error	Max.	Min.	Grand mean	Std. error	Max. mean	Min. mean
Low density												
Full trap	8.98	0.604	10.15	7.50	7.30	1.968	10.84	3.79	19.39	0.505	20.60	18.47
Low clump	9.01	1.515	12.00	6.65	36.33	7.868	50.30	20.45	19.75	1.277	21.95	17.45
High clump	8.46	3.268	15.65	3.05	205.66	106.362	507.71	48.36	18.95	2.237	22.88	14.20
Reduced trap	7.07	0.422	7.85	6.35	7.88	2.854	16.54	3.59	19.24	0.568	20.41	18.53
Low clump	7.40	1.362	10.25	5.25	30.12	9.495	47.25	13.94	20.12	1.371	22.10	18.05
High clump	7.10	2.891	12.10	2.80	167.92	123.036	539.04	33.25	18.91	2.379	23.00	14.20
High density												
Full trap	33.54	1.270	35.85	31.75	38.39	18.445	95.61	17.83	19.72	0.576	20.80	18.75
Low clump	32.48	2.901	38.15	27.65	131.27	35.478	205.10	55.50	19.84	0.670	21.95	18.85
High clump	29.12	3.263	35.50	21.65	562.58	178.415	1019.48	292.89	20.00	1.983	23.75	16.70
Reduced trap	27.04	0.601	29.00	24.75	35.52	16.331	86.93	10.74	19.82	0.736	21.10	18.50
Low clump	26.17	1.794	31.05	23.40	120.79	38.840	224.89	47.82	19.95	1.415	22.50	16.30
High clump	24.80	4.490	32.90	16.00	502.81	155.750	852.17	278.17	19.90	2.264	23.72	14.94

Under low- and high-density fish population levels, three spatial distributions simulated included random, low clumping and high clumping. Full and reduced trapping areas were also simulated. Empirical values were: density — 7.4 (low), 25.0 (high); variance in density — 15.52 (low), 44.09 (high); fish size — 17.0 ± 6.70 (low), 15.0 ± 8.00 (high). True population values were: density — 9.4 (low), 32.6 (high); fish size — 19.86 ± 6.67 (low), 20.8 ± 10.80 (high).

TABLE II

Percent relative bias (*PRB*) of simulated grand mean density (fish  $m^{-2}$ ) and simulated grand mean fish size (mm) from the respective true population means and from empirical means obtained during sampling trials

		Percent relative bias			
		Mean density		Mean size	
		True	Empirical	True	Empirical
Low density					
Full trap	Random	-4.47	21.35	-2.07	14.06
	Low clump	-4.15	21.76	-0.25	16.17
	High clump	-10.00	14.32	-4.29	11.47
Reduced trap	Random	-24.79	-4.46	-2.83	13.18
	Low clump	-21.28	0.00	1.62	18.35
	High clump	-24.47	-4.05	-4.49	11.24
High density					
Full trap	Random	2.88	34.16	-5.19	31.47
	Low clump	0.37	29.92	-4.62	32.27
	High clump	-10.67	16.48	-3.85	33.33
Reduced trap	Random	-17.05	8.16	-4.71	32.13
	Low clump	-19.72	4.68	-4.09	33.00
	High clump	-23.93	-0.80	-4.33	32.67

$PRB = ((\text{simulated} - \text{observed}) / \text{observed}) \times 100$ . Simulated values are from low- and high-density fish population sites, using random, low-clumped and high-clumped spatial distributions and using full and reduced trap areas.

means of 9.4 and 32.7 fish  $m^{-2}$  for low- and high-density populations, respectively, whereas the reduced trap simulations consistently underestimated the true means (Table I). The empirical means, 6.6 and 24.1 fish  $m^{-2}$  for low- and high-density populations, respectively, were more closely represented by the reduced trap samples under both densities (Table I). This is confirmed by the low percent relative bias exhibited by the reduced trap means (Table II). This result supports the hypothesis that the effective sampling area of the enclosure trap is  $< 1 m^2$ .

#### Fish size

Sizes of fish sampled during simulations provided standards against which empirical sizes could be compared to evaluate the potential bias in sampling large fishes. The true population mean fish size was closely estimated in all computer simulations, as indicated by a consistently low percent relative bias (Table II). The mean size resulting from field sampling, however, was consis-

tently lower than both the true population mean and the simulated means (Table II). Clumping of fishes of similar size, which resulted under computer simulations, had no apparent effect on overall size of trapped fish, giving similar results to the random distribution at both low and high densities. The size of the effective trapping area had no apparent effect on mean fish size. Thus, field sampling does not give accurate estimates of fish size and our simulated changes in dispersion patterns cannot explain this inaccuracy. We conclude that some component of fish biology, other than patterns of dispersion, interacts with the sampling procedure to result in an underestimate of the true mean fish size. Such components may include variation in avoidance behavior with fish size, or the vertical segregation of large and small fishes in the water column.

### Diversity

The test for heterogeneity  $\chi^2$  was significant at both low ( $\chi^2=172.14^{***}$ ,  $df=76$ ) and high ( $\chi^2=203.72^*$ ,  $df=152$ ) densities. These tests suggest that species do not enter the enclosure trap sample in proportion to their true abundances. Data from enclosure trapping may, therefore, reflect the aggregation of similar species under natural conditions. Of concern, is whether this aggregation effect is great enough to affect our estimates of fish community diversity.

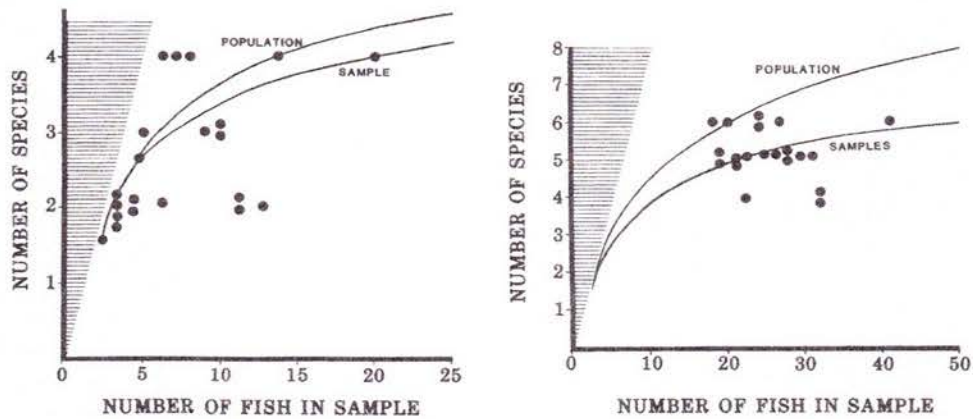


Fig. 1. Observed numbers of fish and species in each of 20 traps (points) in relation to the Hurlbert curve for expected number of species in the pooled samples and in the known population. (a) Left, low-density fish populations. (b) Right, high-density fish populations. Curve indicates the number of species expected in a hypothetical smaller sample taken from the distribution of individuals among species in a larger sample. Shaded edge delimits hypothetical condition of maximum diversity, where every fish belongs to a different species. Shaded area to the left excludes the possibility of trapping more species than individuals.  $\chi^2$  statistics test for deviation of individual trap results from expected values, based on pooled samples (a:  $\chi^2=1.44$ , ns; b:  $\chi^2=0.00$ , ns). Because rare species are missed during trapping, the pooled field sample curves lie below the true population curves.



To further test for the extent of aggregation effects, the sensitivity of the diversity estimator was evaluated graphically (Fig. 1). In this figure, the pooled sample and true population curves represent the expected number of species, based on proportions given by the pooled trap samples and population totals, respectively. Points indicate the number of species (ordinate) that were present in samples of a given number of fish (abscissa) taken during field sampling. The expected species diversity curve for the pooled samples lies below (i.e., underestimates) the diversity curve generated from the true composition of the population, suggesting that rare species are not represented in the samples in proportion to their abundances. It can be seen that the expected species diversity curve for the pooled samples bisects the empirical data points under both low ( $\chi^2 = 1.42$ , ns,  $df = 14$ ) and high ( $\chi^2 = 0.00$ , ns,  $df = 14$ ) densities. This suggests that the diversity estimator is unaffected by the degree of aggregation detected by the heterogeneity  $\chi^2$  statistic (Jumars, 1975b).

#### DISCUSSION

Spatial distributions simulated in this study provided biologically realistic hypotheses of fish aggregation, which may result from schooling or habitat heterogeneity in shallow wetland environments (Taylor, 1977). By simulating an aggregated fish community using the double Poisson probability distribution, we have confirmed an expected result that clumping results in a greater amount of open area and a greater probability of obtaining an empty trap on any throw. Thus, aggregated fish show a higher variance in density among traps when compared with estimates from randomly dispersed fish. However, the variance under simulated conditions of aggregated fish distribution was higher than the variance observed during actual field sampling, suggesting that in Everglades marshes, large aggregations of fish are not occurring and that under natural conditions fish are effectively distributed randomly with respect to the size of the trapping area. Thus, enclosure trapping for density estimates meets the assumptions of probability sampling that underlie estimators based on simple random sampling. Small aggregates of two to three fish were commonly formed using the simulated random distribution and consequently, small groups of fish that were commonly observed under field conditions are not inconsistent with an overall random distribution.

Regarding the consistent underestimates of fish density provided by enclosure trapping, it has been suggested (Freeman et al., 1984) that lower fish densities may result when detrital material is discarded during sampling. Our field methodology, however, minimizes this possibility because detrital material is carefully examined in the field. Using a similar enclosure device in a study of benthic deep-water communities, Jumars (1975a) found that a rush of water out of the bottom edges of his enclosure swept individuals out of the sampled area as the device was lowered, resulting in an underestimate of true

benthic diversity when the full area of the enclosure was considered to be the effective sampling area. In shallow-water habitats, a similar rushing of water out of the bottom of the enclosure trap as it is lowered may sweep fish out as well, or the fishes on the edge of the trap may swim out of the way of the trap side. These ideas provide a reasonable explanation for the consistent underestimates of density observed during field studies. We can consider that a 1 m<sup>2</sup> enclosure trap effectively samples only a 0.81 m<sup>2</sup> area of wetland habitat because of physical properties of the trapping methodology and we can correct estimates of fish density accordingly.

The enclosure trap apparently underestimates mean fish size, with important implications for using density measurements in estimates of biomass. Such a size bias [as noted by Kushlan (1981)] is probably caused by larger fish escaping a falling trap more easily than smaller fish, as well as by large fish being relatively scarce.

The question of whether to replace fish following each sample during enclosure trapping is of practical interest. Enclosure trapping is effectively without-replacement sampling, in that the disruption of habitat that results when fish are removed from inside a trap requires that the trap be thrown in a different, randomly chosen location each time. Although fish are mobile, it is unlikely that a replaced fish would be trapped a second time since this is avoided through the sampling protocol. Thus, in practical terms, enclosure trapping can be effectively argued to be either with- or without-replacement sampling depending on how much care is taken to throw traps at great distances from each other. Regardless, estimators used for the sample mean density are identical under with-replacement (WR) and without-replacement (WOR) simple random sampling. The unbiased variance estimators, however, differ

$$\text{WR: } S_y^2 = S^2/n$$

$$\text{WOR: } S_y^2 = (S^2/n) (1-f)$$

where  $f$ , the sampling fraction ( $n/N$ ), reduces to 0 when  $N$ , the total population size, is large relative to  $n$ , the size of the sampled population, such that  $(1-f)$  approaches 1. In enclosure trapping, where  $n$  is usually very small relative to  $N$ , the simpler WR estimator can be used. With small sampling fractions, both variance estimators are essentially equal, although at large sampling fractions, sampling WOR has large superiority over sampling WR because the variance of the WOR estimator approaches 0 as  $n$  approaches  $N$ . This latter situation, however, is extremely unlikely under field conditions, where large marshes are sampled and the sampling fraction is generally very small. It is thus of little consequence to the probability sampling procedure whether fish are collected at the time of sampling, held until sampling is completed, or returned immediately to the marsh.

An important conclusion to our evaluation is that estimates of species diver-

sity can be calculated with confidence from the same data used in calculating density. Thus, the sampling protocol using 1 m<sup>2</sup> enclosure-traps (Kushlan, 1981) not only provides acceptably precise estimates of density, but also provides acceptably accurate estimates of both density and diversity. Rare species (and as a consequence larger fish) are under-sampled [as noted by Kushlan (1981)] and corrections for density must be made to account for the reduction in effective sampling area that occurs with enclosure trapping in shallow wetland environments.

#### CONCLUSIONS

Enclosure trapping of small fishes in shallow wetland environments provides reliable estimates of fish community diversity, despite providing underestimates of fish density. The source of the sampling bias in density estimation is most likely the reduced effective sampling area of the enclosure trap, which must be corrected in calculating accurate density estimates. Spatial aggregation of fish under natural conditions does not appear to bias the use of a random sampling model. Biomass estimates may underestimate true population values due to the under-representation of large fish in enclosure samples.

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