

Sampling Aquatic Invertebrates from Marshes: Evaluating the Options Author(s): Andrew M. Turner and Joel C. Trexler Reviewed work(s): Source: Journal of the North American Benthological Society, Vol. 16, No. 3 (Sep., 1997), pp. 694-709 Published by: Society for Freshwater Science Stable URL: <u>http://www.jstor.org/stable/1468154</u> Accessed: 02/09/2012 11:49

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Society for Freshwater Science is collaborating with JSTOR to digitize, preserve and extend access to Journal of the North American Benthological Society.

# Sampling aquatic invertebrates from marshes: evaluating the options

ANDREW M. TURNER<sup>1</sup> AND JOEL C. TREXLER

# Southeast Environmental Research Program and Department of Biological Sciences, Florida International University, Miami, Florida 33199 USA

*Abstract.* Designing an effective sampling program and accurately interpreting the results requires a knowledge of the sampling characteristics of the various devices which might be used, but such knowledge is lacking for invertebrate samplers that can be used in heavily vegetated wetlands. We evaluated the sampling characteristics of 8 invertebrate samplers in vegetated habitats by employing them side-by-side in the Florida Everglades. The samplers differed in the number of individuals captured, number of species captured, and the equitability of species abundances. A funnel trap, a D-frame sweep net, and a stovepipe collected more individuals, more taxa, and a more even distribution of individuals among taxa, than did a 1-m<sup>2</sup> throw trap and Hester-Dendy artificial substrates. Three other samplers, a minnow trap, a benthic corer, and a plankton net, captured very few individuals. Most importantly, samplers differed consistently in the taxonomic composition of the invertebrates each captured. These differences argue for the use of several complementary methods in order to gain a complete representation of the invertebrate assemblage. We discuss issues involved in choosing samplers and recommend the use of 3: the funnel trap, the D-frame sweep net, and the 1-m<sup>2</sup> throw trap, for studies of aquatic invertebrates in heavily vegetated wetlands such as the Everglades.

*Key words:* sampler bias, aquatic invertebrates, aquatic macrophytes, species richness, rarefaction, relative abundance, species composition, marsh, wetlands, Everglades.

Aquatic ecologists have devised a wide variety of methods with which to sample invertebrates from aquatic habitats (Cummins 1962, Hellawell 1978, Downing and Rigler 1984, Merritt et al. 1984). Deciding which methods to include in a sampling program requires consideration of the sampling characteristics of each, the relevance to the question at hand of the taxa captured by each sampler, and the labor requirements. Comparisons have been made of devices used to sample invertebrates in lakes (review in Downing 1984), and fish in shallow, marsh habitats (Kushlan 1974, 1981, Freeman et al. 1984, Chick et al. 1992, Loftus and Ekland 1994) but only a few comparative studies have been made of methods used to sample invertebrates in freshwater marshes and other vegetated wetlands (e.g., Murkin et al. 1983, Chael et al. 1993, Brinkman and Duffy 1996).

Heavily vegetated wetlands present several challenges to those wishing to study aquatic invertebrates. First, choosing appropriate sample sites is not straightforward. Marshes are usually patterned into a mosaic of discrete vegetation associations (Gunderson 1994), and sampling

<sup>1</sup> Present address: Pymatuning Laboratory of Ecology, University of Pittsburgh, 13142 Hartstown Road, Linesville, Pennsylvania 16424 USA may need to be stratified with respect to these large-scale patterns (Elliott 1977, Green 1979). The vegetation may also be very dense. For example, sawgrass (*Cladium jamaicense*) covers great expanses of the Florida Everglades with >50 stems/m<sup>2</sup> (Urban et al. 1993), so any sampler used in these habitats must be able perform effectively in thick vegetation. Finally, marsh water levels may vary seasonally and spatially, and invertebrate samplers must be able to function at various depths.

Here we describe how we evaluated 8 methods of sampling aquatic invertebrates from heavily vegetated wetlands by employing them side-by-side. Our goal was to describe how commonly used samplers differ from one another in the numbers and kinds of invertebrates they capture, thereby aiding aquatic ecologists in making informed choices of sampling methods and in the interpretation of studies using different methods. Therefore, we chose for comparison a diverse group of sampling devices reflecting the range that might actually be used to sample marshes. Because our objective was to see how the methods differed, we did not attempt to standardize sampler mesh sizes or any other aspect of sampler use. Instead, we used each in the manner that they are most often em-

	Saw	grass	Spik	erush	Ca	ttail
Fish species richness <sup>a</sup>	6		6		5	
Fish density (no./m²)ª	32.5		13.1		91.9	
Fish standing crop (g/m²) <sup>a,b</sup>	0.2		0.3		1.1	
Sawgrass stems (no./m <sup>2</sup> )	128.9	(23.1)	2.1	(9.8)	43.8	(63.9)
Spikerush stems (no./m²)	0		184.5	(97.3)	0	. ,
Cattail stems (no./m <sup>2</sup> )	0		0		19.4	(15.0)
Submerged plant cover (%)	8.5	(17.8)	81.2	(22.3)	2.8	(11.2)
Floating mat biovolume (cm <sup>3</sup> /m <sup>2</sup> )	225.0	(438.4)	5384.8	(2057.3)	47.5	(87.7)
Total phosphorus—soil (µg/g) <sup>c</sup>	254.1	(50.2)	135.9	(112.6)	269.2	(73.0)
Total phosphorus—water (µg/L) <sup>c</sup>	20.0	(2.9)	23.5	(7.3)	31.5	(3.6)
Water depth (cm) <sup>d</sup>	31.5	(1.5)	44.1	(2.4)	25.8	(4.0)

TABLE 1. Environmental characteristics of the study site. Fish species richness and densities are from the 1-m<sup>2</sup> throw trap, and stem densities are from 20 randomly selected 1-m<sup>2</sup> quadrants. Floating mat consists of periphyton and vascular plants; biovolume estimated with 1000-mL graduated cylinder. All values are means for the plot ( $\pm$ 1 SD), n = 10, except for vegetation and periphyton (n = 20).

<sup>a</sup> Fish summary statistics do not include the occasional large fish (i.e., largemouth bass *Micropterus salmoides* and warmouth *Lepomis gulosus*)

<sup>b</sup> Dry mass

<sup>c</sup> Phosphorus concentrations in soils and water supplied by R. Jones, Florida International University

<sup>d</sup> Water depths at beginning of study in early April

ployed. We included devices which sampled invertebrates from each of the marsh's sub-habitats: the benthic infauna, the epibenthic and epiphytic fauna, and the planktonic fauna. In addition, we employed both passive samplers (funnel traps and an artificial substrate) and active samplers (nets, enclosure traps, and a corer). We compared their measurements of variables most commonly measured by aquatic ecologists: invertebrate abundance, species richness, relative abundance, and taxonomic composition. In addition, we compared the precision with which each sampler estimated invertebrate abundance, and we estimated the labor costs associated with using each sampler.

#### Methods

# Study area

We conducted our study in the marshes of the Florida Everglades, a widely known but littlestudied example of a vegetated wetland. The Everglades occupies a shallow limestone depression near sea level and historically received most of its water and nutrients from seasonal rainfall (Davis 1994). Oligotrophic waters, seasonal sheet flow, and a subtropical climate are thought to be responsible for the characteristic fauna and flora of the Everglades (Steward and Ornes 1975, Davis 1991). Despite recent interest in the effects of altered hydroperiod and nutrient enrichment on the aquatic communities of the Everglades, only a few studies of aquatic invertebrates there have been published (e.g., Loftus et al. 1990, Rader and Richardson 1992, 1994, Rader 1994). Therefore, an ancillary goal of our study was to present a preliminary description of the patterns of abundance and diversity of aquatic invertebrates in the marsh.

We chose for study an area in the southwest corner of Water Conservation Area 3B. The Everglades has several distinct vegetation associations, the most widespread being densely vegetated sawgrass marshes (Cladium jamaicense) and sparsely vegetated slough communities dominated by the emergent rush *Eleocharis* spp. (spikerush), submerged Utricularia spp., and periphyton (Loveless 1959, Craighead 1971, Gunderson 1994). Recent changes in nutrient loading, hydroperiod, and fire regime are causing a conversion to cattail marsh (mostly Typha domingensis) in some areas (Davis 1994, Davis et al. 1994, Gunderson and Snyder 1994). We established a study plot in each of these 3 vegetation associations, hereafter referred to as the sawgrass plot, spikerush plot, and cattail plot (environmental characteristics of each plot are summarized in Table 1). For each of the 3 vegetation plots, we established a square sampling grid containing 100 stations uniformly arranged in a

45-m by 45-m quadrat and randomly selected 10 stations. We then used the 8 methods described below to sample each of the 30 stations, taking care not to overlap the actual areas sampled. Thus, each sampler generated 30 samples (10 from each plot), and each set of 30 samples was taken from the same set of sampling stations. Sampling was conducted in the spring of 1995, except for the plankton, which was sampled in March of 1996. Mean water depth was 34 cm at the beginning of sampling, fell to 17 cm by mid May, and then rose to 39 cm by the end of the sampling period in mid June 1995.

# Sampling methods

Sweep net.-We used a conventional D-frame sweep net (mesh size = 1.2 mm, mouth area 690 cm<sup>2</sup>). We took one sweep of 0.5 m length at each sample station (a floating meter stick was used for reference), yielding an estimated volume filtered of 34,500 cm<sup>3</sup> (assuming 100% sampling efficiency). In shallow-water conditions such as those experienced during this study, the net mouth spans most or all of the water column, and the net is used by bumping it horizontally along the bottom (Usinger 1956, Macan 1977, Chael et al. 1993), thereby sampling epibenthic as well as epiphytic invertebrates. Samples were taken to the laboratory, washed through a 0.5-mm sieve, and placed into a white enamel pan where live animals were manually separated from plant material. Animals were then preserved in 10% formalin for identification and enumerated under a dissecting scope in the laboratory.

Stovepipe.—The stovepipe sampler was a cylindrical enclosure trap 34 cm in diameter and 60 cm tall. Similar samplers are often used to sample benthic and littoral habitats (Merritt et al. 1984) and are sometimes called Wilding samplers (Wilding 1940). Like the sweep net, this method samples epibenthic as well as epiphytic habitats. We used the stovepipe by quickly forcing it down through the vegetation to the marsh bottom and firmly seating it in the peat. We then removed material through the open top of the sampler by hand and by dipping with small nets (12 cm  $\times$  14 cm, 1.0-mm mesh). We standardized netting effort by having two people dip continuously for a total of 5 min. Animals were sorted and processed as described for the sweep net.

Throw trap.—The throw trap was a square cage (1 m on a side) open at the top and bottom, with 2 mm mesh enclosing the sides. The trap was thrown into the marsh, and the interior of the trap was then cleared with a 2-mm-mesh bar seine (Kushlan 1981, Chick et al. 1992). The bar seine was a 1 m  $\times$  0.5 m rectangular frame with netting stretched across it. We seined until 2 consecutive hauls yielded no invertebrates, and then used 2 dip nets, with 5-mm and 1.2-mm mesh respectively, until 10 consecutive nettings yielded no invertebrates. Invertebrates (as well as fish) were hand picked from each bar seine haul or dip net sweep as it was taken, and were preserved in formalin for identification and enumeration.

Benthic corer.—We collected 1 sediment core from each sample station using a plexiglass corer 6.5 cm in diameter which was inserted 8 cm deep into the sediments (Flannagan 1970, Kajak 1971). The cores were washed through 2 stacked sieves, 0.5-mm and 0.125-mm mesh, and the contents of the 0.5-mm sieve were placed in a tray and searched for 1 h. The contents of the 0.125-mm sieve were placed in a 20% solution of MgSO<sub>4</sub> for flotation of animals, which were then picked from the surface of the solution by hand. All animals recovered were then preserved in 10% formalin for laboratory identification and enumeration.

Funnel trap.—The funnel trap consisted of 9 funnels 65 mm in diameter and with necks 55 mm long set into an acrylic frame and emptying into 30-mL bottles (Szlauer 1963, Whiteside and Williams 1975, Brakke 1976, Whiteside and Lindegaard 1980). Neck diameter of the funnels was 4.5 mm, limiting passage to animals with a body width smaller than this dimension. The sampler was placed on the substrate of the marsh in mid-morning with the funnels facing downwards, allowed to remain in place for 24 h, and removed the following day. The contents of the 9 bottles were pooled into a single sample and preserved in 10% formalin. Samples were rinsed through a 0.153-mm-mesh screen, and invertebrates were enumerated under a dissecting scope.

Minnow trap.—Minnow traps were constructed of galvanized wire (6-mm mesh), were 44.5 cm long, 22.9 cm diameter, and had a funnel opening of 3.1 cm (Memphis Net and Twine Co., Memphis, Tennessee). The trap was deployed, unbaited, on the marsh bottom in midafternoon and left in place for 24 h. Captured invertebrates were identified, enumerated, and released in the field.

Hester-Dendy artificial substrate.-The Hester-Dendy sampler (Hester and Dendy 1962) consists of a series of 75-mm-diameter hardboard disks alternating with 25-mm disks (Forestry Suppliers, Jackson, Mississippi). Spacing between the 75-mm disks ranged from 3.5 mm to 14 mm. Each substrate was suspended 15 cm below the surface of the water for 6 wk. At the end of this time, the substrate was removed, disassembled, and carefully washed and scraped clean. Material removed from the substrate was washed on a 0.153-mm screen, preserved in the field with 10% formalin, and later stained with Rose Bengal. Animals were sorted from detritus and enumerated under a dissecting scope in the laboratory.

Plankton net.—We sampled planktonic fauna by dipping surface water from the marsh with 1-L beakers and pouring 20 L through a 0.153mm-mesh net at each sample station. Samples were then filtered through a 0.153-mm screen and preserved in 10% formalin for laboratory identification and enumeration. The thick vegetation, shallow water, and extensive periphyton mats made it difficult to obtain samples free of benthic or epiphytic material, and we accidentally entrained large insects, oligochaetes, and gastropods that were obviously not planktonic; these taxa were excluded from our counts.

# Analyses

We evaluated sampler efficacy from the number of animals captured, number of taxa represented, and the precision of abundance estimates. We also characterized the taxonomic composition of the animals sampled and their patterns of relative abundance. We considered the number of invertebrates per sample, rather than the number per standardized sample area or volume, because the effort associated with obtaining samples, as well as the power to make statistical inferences, is proportional to the number of samples taken, and not necessarily the size of the samples. We evaluated sampler precision by calculating the coefficient of variation  $(CV = (standard deviation / mean) \times 100)$  for each sampler in each vegetation plot. Research on aquatic invertebrates has shown that sampling variance typically increases with the mean (Downing 1979, Downing and Downing 1992), so we used the CV instead of the standard deviation to compensate for unequal means among samplers. We chose the variable of total invertebrate abundance for evaluation of sampler precision; preliminary analyses showed that the CVs of the abundance estimates for individual taxa were correlated with those for total invertebrate abundance. We considered the number of invertebrates per sample and the precision of the abundance estimates in an initial screening of the 8 samplers, and 5 samplers were retained for further analyses.

We used 2-way ANOVA to test the hypotheses that the mean number of animals captured and the total number of species captured differed among samplers and vegetation types. Because the total number of species captured is a plot-level variable, no within-plot replication is present. We used Tukey's (HSD) test to make post-hoc comparisons of species richness.

Each sampler was used with equal effort in terms of the number of samples gathered, but the area sampled and number of individuals captured was not equal. Observed differences in total species richness may result from 1) differences in the number of animals collected, or 2) real differences in the species richness of the assemblage sampled (Sanders 1968, Simberloff 1972, 1978, 1979). To distinguish between these 2 possibilities, we standardized the species richness estimates to account for differential numbers of individuals (rarefaction). We pooled data from the 3 plots and estimated the number of species each sampler would recover if capture rates ranged from 0 to 500 organisms per sampler (calculations performed by modified version of the FORTRAN program RAREFACT found in Krebs 1989).

We tested the hypothesis that these samplers differed in the equatability of species abundance estimates by calculating Simpson's index of diversity (SI) for each sampler in each vegetation type. Simpson's index is a non-parametric measure of equitability and provides an estimate of the probability that 2 randomly picked individuals will be different species. The index can range from 0 (low equitability) to near 1 (high equitability). We calculated Simpson's index for each sampler with the following formula developed for finite populations (Simpson 1949, Pielou 1969):

$$SI = 1 - \sum_{i=1}^{s} \left[ \frac{n_i(n_i - 1)}{N(N - 1)} \right]$$

where s = total number of species,  $n_i =$  number of individuals of species *i* in the sample, and N = total number of individuals in the sample.

We characterized the taxonomic composition of the catch for each sampler by reducing the data set to a small number of uncorrelated variables with principal components analysis (PCA). To reduce the influence of rare taxa as potential outliers (Gauch 1982), we included in this analysis only the 20 taxa most frequently encountered by each sampler, for a total of 55 taxa. Because we were interested in patterns of taxonomic composition and not patterns of abundance, we standardized the abundance of each taxon in a sample by the total number of animals in that sample. We then angularly transformed these relative abundances (Sokal and Rohlf 1981) and performed PCA on the transformed relative abundance matrix. We extracted 4 principal components and rotated them using the varimax technique (Stevens 1986). Each principal component can be conceptualized as describing a unique axis of variation in the patterns of relative abundance. We then tested the hypotheses that the catch of samplers differed in taxonomic composition, and that the invertebrate assemblages of the vegetation plots differed in taxonomic composition, by performing a 2-way multivariate analysis of variance (MANOVA) on the 4 principal components (5 samplers and 3 plots; n = 10 replicate collections for each sampler-plot combination). This overall test was followed by Tukey's (HSD) test to detect which samplers and vegetation plots differed. All analyses were done using the Statistical Analysis System (Release 6.09, SAS Institute Inc., Cary, North Carolina).

Developing an optimal sampling program demands consideration of the costs associated with collecting and processing each type of sample (Sheldon 1984, Downing and Cyr 1985, Brinkman and Duffy 1996). The primary costs are the labor requirements, and we considered those associated with each sample method in terms of person-hours invested. For invertebrate sampling major requirements are time spent 1) collecting samples from the field, 2) sorting invertebrates from associated periphyton, vegetation, or sediments, and 3) identifying and counting the sorted samples. Because the time spent identifying and counting a sample is largely independent of the technique used to gather it (depending primarily on the number of animals in the sample), we shall not consider it further. Collecting and sorting times were recorded for each sample as the work was performed.

#### Results

# Invertebrate abundance

The first and most fundamental question associated with any sampler is "will it catch anything?" The number of animals captured depended both on the sampler used and on the vegetation type (Table 2; 2-way ANOVA: sampler effect, p < 0.01; vegetation effect, p < 0.01). Of the 8 candidate samplers, 3 captured very few animals. Averaged across plots, the benthic corer captured 1.1 invertebrates per core, the minnow trap captured less than 0.1 invertebrates per trap, and the plankton net captured 9.3 invertebrates per sample. The remaining 5 samplers had overall capture rates of 20 or more invertebrates per sample (Table 2).

The CV associated with estimates of invertebrate abundance in each plot ranged from 36% to 211% (Table 2). The funnel trap, sweep net, throw trap, stovepipe, and Hester-Dendy artificial substrate had the lowest CVs, with overall values ranging from 43% to 108%. In addition to capturing the fewest number of invertebrates, the benthic corer, minnow trap, and plankton net also yielded the most variable estimates of invertebrate abundance, with overall CVs ranging from 112% to 211%. Because the benthic corer, minnow trap, and plankton net caught so few animals, and because their abundance estimates were relatively variable, the remaining analyses will focus on the funnel trap, sweep net, throw trap, stovepipe, and Hester-Dendy artificial substrate.

#### Species richness

Our study site yielded 114 taxa of invertebrates. The total number of taxa collected, however, depended on both the sampler used and the vegetation type sampled (Fig. 1; 2-way ANOVA: sampler effect, p < 0.01; vegetation effect, p < 0.01). Of the 5 samplers, the funnel trap and sweep net collected the most taxa, with the funnel trap collecting a total of 67 taxa and the

TABLE 2. Mean number of invertebrates captured by 8 different sample in each of the 3 vegetation plots, ranked by the coefficient of variation (CV, %) associated with the means (n = 10). Invertebrate numbers are for all taxa pooled together. Samplers are ranked by their overall CV; the overall CV is calculated by averaging the CV across the 3 vegetation plots.

	Area or	Numbers of invertebrates per sample and CV							
Sampler	volume cleared	Sawgrass		Spikerush		Cattail		Overall mean and CV	
Funnel trap <sup>a</sup>		415.5	(51)	55.6	(43)	550.8	(36)	340.6	(43)
Sweep net	34.5 L	140.7	(75)	47.2	(55)	77.7	(37)	88.5	(56)
Throw trap	1 m <sup>2</sup>	36.4	(46)	6.8	(67)	28.6	(64)	23.9	(59)
Stovepipe	908 cm <sup>2</sup>	28.4	(74)	62.3	(80)	45.5	(73)	45.4	(76)
Hester-Dendy <sup>a</sup>		518.0	(98)	2.9	(110)	100.0	(116)	207.0	(108)
Plankton net	20 L	15.6	(174)	4.6	(55)	7.6	(107)	9.3	(112)
Benthic corer	33.2 cm <sup>2</sup>	0.6	(161)	1.1	(157)	1.5	(130)	1.1	(149)
Minnow trap <sup>a</sup>		0	(-)	0	(-)	0.2	(211)	<0.1	(211)

\* Passive sampler

sweep net 70 taxa when the 3 habitats were combined. The throw trap collected fewer invertebrate taxa than any other sampler, and the Hester-Dendy substrate accumulated fewer taxa than the funnel trap and the sweep net but was not distinguishable from the stovepipe sampler (Fig. 1; Tukey's test, p < 0.05).

When the estimates of species richness were standardized to a common sample size of 500



FIG. 1. Total species richness of invertebrates captured by each sampling method in each vegetation plot. Each bar represents the number of taxa captured in 10 replicate samples in each vegetation type. Horizontal lines show groups of samplers that do not significantly differ (Tukey's test, p = 0.05).

individuals, the rarefield estimates fall into 2 groups: the funnel trap, sweep net, and stovepipe sampler estimates were between 36 and 47 species, while the Hester-Dendy substrate and throw trap estimates were only 21 and 17 species, respectively (Fig. 2).

#### Equitability of species abundances

The assemblage of invertebrates we sampled from Everglades marshes comprised a large number of species that were not equally abundant. We evaluated the contribution of rare taxa to overall catch in 2 ways. First, we plotted the relative abundance of the 25 most abundant invertebrate taxa in rank order for each sampler to illustrate the equitability of relative abundances (Fig. 3). The pattern of relative abundances illustrated in Fig. 3 is one of the most repeatable patterns in community ecology (Krebs 1989), but Fig. 3 shows that the slope of the relationship depends on the method used to sample a community. The funnel trap, stovepipe, and sweep net yielded relative abundance patterns that appear to be more evenly distributed than the Hester-Dendy substrate and the throw trap (Fig. 3).

The rank order of Simpson's index of equitability showed the same pattern as species richness (species richness shown in Fig. 1): the funnel trap sampler had the highest equitability (SI = 0.87), followed by the sweep net (SI = 0.85), the stovepipe sampler (SI = 0.74), Hester-Dendy artificial substrates (SI = 0.66) and the throw trap (SI = 0.64). Thus, samplers that captured a



FIG. 2. Rarefaction curves for each sampling method with data from the 3 vegetation plots pooled together. Curves are estimates of the expected number of species that would be sampled at the corresponding level of effort. Vertical bars represent 1 SD.

wide variety of taxa also succeeded in capturing relatively more individuals from rare taxa.

#### Species composition

An examination of the 10 taxa most frequently captured by each sampler shows that each sampler yielded an unique taxonomic list (Table 3). For several comparisons, pairs of samplers shared none of the most frequently encountered species (e.g., funnel trap versus throw trap; Hester-Dendy versus throw trap), and the other sampler comparisons showed that at most only 5 of the 10 most frequently captured species were shared by a pair of samplers (stovepipe and sweep net). Because each method was employed at the same locations, and in the same season, differences in invertebrate species composition among samplers suggests a pattern of consistent bias. While it is hardly surprising that a particular sampler selects for some taxa and against others, it is necessary to characterize the

nature of this bias in order to allow sound interpretations of the data.

The taxonomic composition of the invertebrates captured by each sampler, as summarized by PCA, depended on both the sampler employed (MANOVA: Wilks' Lambda = 0.0009; p < 0.0001), and on the vegetation plot from which samples were gathered (MANOVA: Wilks' Lambda = 0.314; p < 0.0001). Most importantly, post-hoc comparisons (Tukey's HSD) show that each of the 5 samplers differed significantly (p < 0.0001) from the other samplers along at least 1 axis of variation, demonstrating that no 2 samplers gathered the same assemblage of invertebrates.

We illustrate the taxonomic array of invertebrates that is characteristic of each sampler by plotting principal components 1 through 4 in bivariate space and identifying the taxa most strongly associated with each principal component. PC 1 discriminated most strongly between the funnel trap and all other samplers (Fig. 4,



FIG. 3. Relative abundance of invertebrate taxa relative to their rank abundance for 5 samplers. Data are pooled across the 3 vegetation plots; n = 30 samples for each method. The 25 most abundant taxa are shown for each sampler except for the throw trap, which sampled 19 taxa.

funnel trap different from all other samplers at p < 0.0001, Tukey's test). Seven species of Cladocera, Copepoda, and Ostracoda were strongly associated with PC 1 (strong association defined as correlation coefficient  $r > \pm 0.45$ ). Thus, small crustaceans accounted for a much larger portion of the funnel trap samples than of the other 4 sample types (the 7 taxa associated with PC 1 have mean body lengths < 0.5 mm). The 2nd axis of variation is almost as strong: PC 2 discriminated strongly between the throw trap and the other 4 samplers (the throw trap was different from all other samplers at p < 0.0001, Tukey's test). Four taxa showed a strong positive association with PC 2: the grass shrimp Palaemonetes paludosus, the dragonfly Pachydiplax longipennis, the pulmonate snail Pseudosuccinea columella, and the damselfly Ischnura ramburii. These species are among the largest invertebrates of the Everglades, and may prove to be important grazers (shrimp and snails) and key predators (dragonflies and damselflies).

Principal components 3 and 4 also strongly discriminated among samplers (Fig. 5). On PC 3, the stovepipe and sweep net are indistinguishable (Tukey's test, p > 0.25) but differ from the funnel trap, the Hester-Dendy artificial substrate, and the throw trap (Tukey's test, p <0.0001). PC 3 is strongly and positively associated with 4 medium size invertebrates: the aquatic mite Limnesia sp., the larval dipteran Chironomus sp., the beetle Celina sp., and another mite, Oxus sp. These and other similar taxa composed most of the catch by the sweep net and stovepipe samplers (Table 3). Finally, PC 4 discriminated the Hester-Dendy artificial substrate from the other 4 samplers (Tukey's, p < 0.0001). PC 4 showed a very strong positive association with 2 groups, nematodes (r = 0.76) and oligochaetes (r = 0.77), and a strong negative association with amphipods (r = -0.61). Thus, nematodes and oligochaetes composed a larger portion, and amphipods a smaller portion, of the invertebrates sampled by this artificial sub-

Funnel trap		Sweep net		
Copepoda	Cyclopoida <sup>a</sup> (30)	Amphipoda	Hyalella azteca (28)	
Ostracoda	Cypridae (30)	Hydracarina	Limnesia sp. (23)	
Oligochaeta	Naididae (28)	Diptera	Chironomus sp. (21)	
Diptera	Chironomus sp. (27)	Ostracoda	Cypridae (21)	
Diptera	Tanytarsus sp. (27)	Ephemeroptera	Caenis diminuta (19)	
Copepoda	Osphranticum labronectum (26)	Odonata	Coenagrionidae <sup>b</sup> (19)	
Cladocera	Chydorus sp. (26)	Gastropoda	Physella hendersoni (18)	
Diptera	Larsia decolorata (26)	Hydracarina	Oxus sp. (14)	
Copepoda	nauplii (23)	Hemiptera	Pelecoris femoratus (14)	
Ephemeroptera	Caenis diminuta (22)	Odonata	Pachydiplax longipennis (13)	
Stovepipe		Hester-Dendy		
Amphipoda	Hyalella azteca (27)	Oligochaeta	Naididae (21)	
Coleoptera	Celina imitatrix (20)	Ostracoda	Cypridae (18)	
Hydracarina	Limnesia sp. (19)	Nematoda (16)		
Diptera	Chironomus sp. (14)	Copepoda	Cyclopoidaª (15)	
Coleoptera	Celina sp. larvae (12)	Amphipoda	Hyalella azteca (13)	
Coleoptera	Hydrovatus pustulatus (10)	Diptera	Chironomus sp. (13)	
Decapoda	Palaemonetes paludosus (9)	Cladocera	Grimaldina brazzai (13)	
Gastropoda	Physella hendersoni (9)	Cladocera	Camptocercus rectirostris (11)	
Odonata	Pachydiplax longipennis (8)	Cladocera	Macrothrix rosea (11)	
Diptera	Larsia decolorata (8)	Cladocera	Chydorus sp. (7)	
	Throw trap			
Decapoda	Palaemonetes paludosus (28)			
Odonata	Pachydiplax longipennis (20)			
Hemiptera	Pelecoris femoratus (19)			
Odonata	Coenagrionidae <sup>b</sup> (14)			
Gastropoda	Pseudosuccinea columella (11)			
Diptera	Odontomyia sp. (7)			
Hemiptera	Belostoma sp. (5)			
Gastropoda	Physella hendersoni (4)			
Hemiptera	Palmacorixa gillettei (3)			
Odonata	Erythemis simplicicollis (3)			

TABLE 3. Taxa most frequently collected by each of the 5 samplers. Numbers in parentheses indicate the frequency with which the associated taxon was sampled (30 occurrences possible).

<sup>a</sup> The predominant cyclopoid species were *Macrocyclops albidus*, *Microcyclops rubellus*, and *Microcyclops varicans* (Reid 1992)

<sup>b</sup> The coenagrionids were approximately evenly split between *Ischnura ramburii* and *Enallagma pollutum* (A. M. Turner, personal observation), but these 2 taxa were not distinguished during sample processing

strate relative to the catch yielded by the other samplers.

# Labor requirements

Samplers varied greatly in their labor requirements (Table 4), reaffirming the importance of considering these costs. The throw trap required more field time per sample gathered than the other methods, but because animals were separated from associated plant material in the field, we spent no laboratory time on sorting (Table 4). Included in the estimate of labor involved with throw trap sampling is time devoted to gathering data on plant abundance and composition within the enclosure. The stovepipe sampler and sweep net, in contrast, both required a considerable investment of laboratory time to sort small invertebrates from periphyton, plant material, and peat sediments (Table 4). Hester-Dendy samplers required a moderate amount of time for deployment, retrieval, and scraping material from the substrates. The funnel traps were the most cost-effective because



PC 1

FIG. 4. Principal component 1 (x-axis) plotted against principal component 2 (y-axis) for each sampler (n = 30 scores). Error bars represent 1 SD and include variation among vegetation plots as well as variation among replicate samples within a plot. Taxa shown are those most strongly associated with the corresponding principal component ( $r > \pm 0.45$ ), and the arrows show whether the taxon is positively or negatively correlated with the principal component.

they required little field time for deployment and retrieval and did not require any further sorting, but collected large numbers of invertebrates (Table 4).

# Discussion

We found that the methods we employed for sampling invertebrates from the Everglades varied greatly in numbers of individuals collected, precision of the abundance estimates, number of species collected, equitability of species abundances, and species composition of the catch. Methods also varied with respect to the labor costs. If four performance criteria are: maximum number of individuals per sample, maximum number of taxa sampled, and highly precise abundance estimates, then the samplers considered here fall into 3 distinct classes. The funnel trap, sweep net, and stovepipe sampler performed best; the throw trap and the Hester-Dendy artificial substrate were intermediate; and the minnow trap, benthic corer, and plankton net performed worst.

A fundamental distinction among samplers is that of passive techniques (e.g., artificial substrates and funnel traps) versus active techniques (e.g., nets and enclosures). Artificial substrates and funnel traps are a popular means of sampling aquatic invertebrates, but data collected with these samplers are difficult to interpret for several reasons. First, because the capture rate of any passive sampler is a product of the abundance of animals in the environment and their movement rates into/onto a sampler (which are rarely known), it is usually impossible to convert the capture rates of passive samplers into abundances of animals in the envi-



FIG. 5. Principal component 3 (x-axis) plotted against principal component 4 (y-axis) for each sampler (n = 30 scores). Error bars represent 1 SD and include variation among vegetation plots as well as variation among replicate samples within a plot. Taxa shown are those most strongly associated with the corresponding principal component ( $r > \pm 0.45$ ), and arrows indicate whether the taxon is positively or negatively correlated with the principal component.

ronment. In addition, environmental differences may confound comparisons of invertebrate abundance among habitats (Whiteside and Lindegaard 1980, Murkin et al. 1983), because the movement rates of aquatic invertebrates depend

TABLE 4. Mean time (h) required to collect each sample from the field and to sort invertebrates from associated plants, periphyton, and sediments. Values are averaged across vegetation types. Times < 1 h are rounded to the nearest 0.1 h, times > 1 h are rounded to the nearest h.

Sample	Collecting	Sorting
Funnel trap	0.2ª	b
Sweep net	0.1	4
Stovepipe	0.2	6
Hester-Dendy	$0.4^{a}$	b
Throw trap	0.5	0°

<sup>a</sup> Includes both deployment and recovery time

<sup>b</sup> Because animals were sorted under the dissecting scope as they were identified and enumerated no separate estimate of sorting time is available

<sup>c</sup> Samples are sorted during collection

on environmental characteristics that can vary from place to place (e.g., predator abundance and food availability: Peckarsky 1980, McPeek 1990, Turner 1996). Because active samplers enclose, or filter, an estimable area or volume of water, their capture rates can be converted into estimates of abundance in the environment. Active samplers are also less prone to biases associated with reduced movement rates. They are often destructive to the environment, however, and may not be appropriate for use in long term experiments. Passive samplers minimize disturbance to the substrate and are useful in situations in which nondestructive sampling is necessary (Macan and Kitching 1972, Mason 1976, Macan 1977), allowing collection of data from locations that cannot be sampled effectively by other means (Rosenberg and Resh 1982).

Of the passive samplers evaluated, the funnel trap captured the most individuals, as well as the most diverse array of species, including many small crustaceans (cladocerans, copepods, and ostracods) that were not captured by other methods. Because the labor requirements for funnel traps are relatively low, they yield a large amount of data for a given level of labor investment. The performance of the Hester-Dendy artificial substrate contrasted sharply with the funnel trap. Although the Hester-Dendy yielded, on average, large numbers of invertebrates, these numbers varied a great deal among samples. The overall CV associated with the mean number of invertebrates on each substrate was 108%, the highest value of the 5 samplers considered here (Table 2). Our data also show that the substrate attracted a very restricted array of species (70% of the catch consisted of oligochaetes and nematodes), but these taxa were not captured in large numbers by any other sampler. Artificial substrates should ideally mimic a feature of the environment into which it is placed (e.g., Peterson and Cummins 1974, Sedell et al. 1975, Rosenberg and Resh 1982, Reeder and Davis 1983), but the Hester-Dendy mimics the wooden crevices of tree snags, which are not found in the Everglades. This alien substrate may be colonized by taxa that are rare in the environment, and responses of these taxa to environmental change may be different from those of more abundant taxa. Thus, Hester-Dendy substrates could potentially provide misleading results.

Of the active samplers, we found that the sweep net and stovepipe collected the most diverse array of invertebrates, and they showed relatively little variability among samples. Their favorable sampling characteristics argue for their inclusion in a sampling program, but they collected similar assemblages of invertebrates, making the use of both samplers redundant and raising the question of which one to use. One might think that the stovepipe sampler, being a walled enclosure, would yield less variable abundance estimates than the unenclosed sweep net, but we found no support for this idea (Table 2). To evaluate more carefully the sampling variability of the stovepipe and sweep net, we divided the invertebrates most commonly captured into 20 taxonomic groups and calculated the CV for each taxon in each set of replicate samples (20 taxa  $\times$  3 vegetation plots = 60 comparisons). The CV for the stovepipe sampler was higher than for the sweep net in 39 of 48 comparisons (12 of the 60 comparisons involved taxa with an abundance of zero). Clearly, the often cited concern that the sweep net is less

"quantitative" than the stove pipe (e.g., Merritt et al. 1984) is not borne out by these data (given that "quantitative" can be equated with sampler precision). Our stovepipe sampler was inoperable in deep water (though a larger version could have been used) and required more time for sorting (Table 4). In sum, the sweep net captured comparable numbers of invertebrates, yielded less variable estimates of invertebrate abundances, and was more cost effective than the stovepipe sampler. Other studies have also validated the utility of the sweep net for quantitative sampling. Kaminski and Murkin (1981) found that the sweep net and an enclosure sampler captured comparable numbers of invertebrates, and Cheal et al. (1993) concluded that the sweep net was the most suitable sampler for classifying wetland invertebrate communities.

Compared to the sweep net and stovepipe sampler, the throw trap sampled a more restricted array of invertebrate species. Because the invertebrates were sorted from the detritus in the field, only the larger or more conspicuous taxa were effectively sampled by this method. However, a number of studies suggest that the large invertebrates sampled by the throw trap are likely to be ecologically important players in marsh ecosystems. Dragonflies are often keystone predators in aquatic communities (e.g., Van Buskirk 1988, McPeek 1990, Werner and McPeek 1994), and grass shrimp and pulmonate snails are important grazers of periphyton (Beck and Cowell 1976, Doremus and Harman 1977, Lowe and Hunter 1988). Therefore, any study purporting to assay invertebrate community structure must do an adequate job of sampling large, but relatively rare, invertebrate taxa. Because these macroinvertebrate taxa are relatively uncommon, precise estimates of their abundance requires sampling a relatively large area. Using large samplers, with large mesh sizes, is a cost effective means of achieving this goal.

A general result of our study is the observation that each method consistently collected different invertebrate taxa. The funnel trap tended to capture a wide array of small crustaceans, the stovepipe sampler and sweep net tended to capture an equally wide array of medium sized invertebrates, the throw trap catch consisted of a few taxa of large invertebrates, and the Hester-Dendy artificial substrate collected oligochaetes and nematodes. These differences reflect differences in sampler sizes, mesh sizes, sorting pro-

cedures, sub-habitats sampled, and modes of operation. Sampling studies in other systems have shown that multiple sampling methods may be required to obtain representative samples of the fauna (Whiteside and Lindegaard 1980); our data reaffirm the need to use several complementary procedures when conducting a survey of invertebrate communities, or to choose a sampler effective at capturing the target taxon if the goal is to conduct a populationlevel survey. For example, 2 previous studies of Everglades invertebrates were based largely on data gathered with a single type of sampler (Loftus et al. 1990: funnel traps; Rader and Richardson 1992, 1994: sweep nets). Our results confirm that funnel traps and D-frame sweep nets gather more individuals and a wider array of taxa than do other methods, but we have also shown that any one method will only capture a subset of the overall invertebrate assemblage.

Finally, we note that although our study was unreplicated with respect to vegetation effects on invertebrate assemblages, the results show that invertebrate abundances and species composition can differ among vegetation associations. It is possible that restricting sampling to a single habitat type (e.g., Kushlan 1981, Loftus et al. 1990, Rader and Richardson 1992, Loftus and Eklund 1994, Rader and Richardson 1994) may result in an incomplete description of a marsh's aquatic communities. For example, Rader and Richardson (1994) sampled invertebrates from slough habitats along a nutrient gradient in the northern Everglades because these habitats "are the centers of biological diversity in the Everglades". The data presented here, however, show that emergent vegetation (cattails and sawgrass) can contain higher densities of fish and invertebrates than spikerush sloughs. In a more extensive study, Jordan (1996) compared invertebrate abundances in the sloughs and sawgrass stands of the northern Everglades and found that macroinvertebrates (individuals of all taxa summed) were more abundant in sawgrass stands than in sloughs. Clearly, a comprehensive strategy of sampling each major vegetation association will yield the most reliable conclusions about the overall composition and abundance of a marsh's aquatic fauna.

# Acknowledgements

Lourdes Rojas, Paul Rehage, Rachel Loubeau, and Walter Deloach helped collect and sort samples from the marsh. John Epler provided expert invertebrate identifications, and Bill Loftus shared his experience in sampling the Everglades. Tom Turner provided advice and encouragement throughout the project. We appreciate the thoughtful comments of Jack Meeder, Dan Johnson, Walter Duffy, Rosemary Mackay, and 2 anonymous reviewers on earlier versions of the paper. Financial support for this research was provided by Cooperative Agreement 5000-3-903012 issued to R. Jones et al. and 5280-3-9014 issued to J. Trexler et al. by the United States Department of the Interior, Everglades National Park. This is contribution #38 of the Southeast Environmental Research Program.

# Literature Cited

- BECK, J. T., AND B. C. COWELL. 1976. Life history and ecology of the freshwater caridean shrimp, *Palae*monetes paludosus. American Midland Naturalist 96:52–65.
- BRAKKE, D. 1976. Modification of the Whiteside-Williams pattern sampler. Journal of the Fisheries Research Board of Canada 33:2861–2863.
- BRINKMAN, M. A., AND W. G. DUFFY. 1996. Evaluation of four wetland aquatic invertebrate samplers and four sample sorting methods. Journal of Freshwater Ecology 11:193–200.
- CHAEL, F., J. A. DAVIS, J. E. GROWNS, J. S. BRADLEY, AND F. H. WHITTLES. 1993. The influence of sampling method on the classification of wetland macroinvertebrate communities. Hydrobiologia 257:47–56.
- CHICK, J. H., F. JORDAN, J. P. SMITH, AND C. C. MCIVOR. 1992. A comparison of four enclosure traps and methods used to sample fishes in aquatic macrophytes. Journal of Freshwater Ecology 7:353– 361.
- CRAIGHEAD, F. C. 1971. The trees of South Florida, volume 1: natural environments and their succession. University of Miami Press, Coral Gables, Florida.
- CUMMINS, K. W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. American Midland Naturalist 67:477–504.
- DAVIS, S. M. 1991. Growth, decomposition, and nutrient retention of *Cladium jamaicense* Crantz and *Typha domingensis* Pers. in the Florida Everglades. Aquatic Botany 40:203–224.
- DAVIS, S. M. 1994. Phosphorus inputs and vegetation sensitivity in the Everglades. Pages 357–378 in S. M. Davis and J. C. Ogden (editors). Everglades: the ecosystem and its restoration. Lucie Press, Delray Beach, Florida.

- DAVIS, S. M., L. H. GUNDERSON, W. A. PARK, J. R. RICHARDSON, AND J. E. MATTSON. 1994. Landscape dimension, composition, and function in a changing Everglades ecosystem. Pages 419–444 in S. M. Davis and J. C. Ogden (editors). Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida.
- DOREMUS, C. M., AND W. N. HARMAN. 1977. The effects of grazing by physid and planorbid freshwater snails on periphyton. Nautilus 91:92–96.
- DOWNING, J. A. 1979. Aggregation, transformation and the design of benthos sampling programs. Journal of the Fisheries Research Board of Canada 36:1454–1463.
- DOWNING, J. A. 1984. Sampling the benthos of standing waters. Pages 87–130. *in* J. A. Downing and F. H. Rigler (editors). A manual on methods for the assessment of secondary productivity in fresh waters. IBP Handbook No. 17, 2nd edition Blackwell Scientific Publications, Oxford, UK.
- DOWNING, J. A., AND H. CYR. 1985. Quantitative estimation of epiphytic invertebrate populations. Canadian Journal of Fisheries and Aquatic Sciences 42:1570–1579.
- DOWNING, J. A., AND W. L. DOWNING. 1992. Spatial aggregation, precision, and power in surveys of freshwater mussel populations. Canadian Journal of Fisheries and Aquatic Sciences 49:985–991.
- DOWNING, J. A., AND F. H. RIGLER (EDITORS). 1984. A manual on methods for the assessment of secondary productivity in fresh waters. IBP Handbook No. 17, 2nd edition. Blackwell Scientific Publications, Oxford, UK.
- ELLIOTT, J. M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biology Association Scientific Publication No. 25:1–142.
- FLANNAGAN, J. F. 1970. Relative efficiencies of various grabs and corers in sampling freshwater benthos. Journal of the Fisheries Research Board of Canada 27:1691–1700.
- FREEMAN, B. J., H. S. GREENING, AND J. D. OLIVER. 1984. Comparison of three methods for sampling fishes and macroinvertebrates in a vegetated freshwater wetland. Journal of Freshwater Ecology 2:603–610.
- GAUCH, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, UK.
- GREEN, R. H. 1979. Sampling design and statistical methods for environmental biologists. Wiley, New York.
- GUNDERSON, L. H. 1994. Vegetation of the Everglades: determinants of community composition. Pages 323–340 in S. M. Davis and J. C. Ogden (editors). Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida.

GUNDERSON, L. H., AND J. R. SNYDER. 1994. Fire pat-

terns in the southern Everglades. Pages 291–306 *in* S. M. Davis and J. C. Ogden (editors). Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida.

- HELLAWELL, J. M. 1978. Macroinvertebrate methods. Pages 35–90 *in* Biological surveillance of rivers. A biological monitoring handbook. Dorset Press, Dorchester, UK.
- HESTER, F. E., AND J. S. DENDY. 1962. A multiple sampler for aquatic macroinvertebrates. Transactions of the American Fisheries Society 91:420–421.
- JORDAN, C. J. 1996. Spatial ecology of decapods and fishes in a northern Everglades wetland mosaic. PhD dissertation. University of Florida, Gainesville, Florida.
- KAMINSKI, R. M., AND H. R. MURKIN. 1981. Evaluation of two devices for sampling nektonic invertebrates. Journal of Wildlife Management 45:493– 496.
- KAJAK, Z. 1971. Benthos of standing water. Pages 25– 65 in W. T. Edmondson and G. G. Winberg (editors). A manual of methods for the assessment of secondary productivity in fresh waters. IBP Handbook No. 17. Blackwell, Oxford, UK.
- KREBS, C. J. 1989. Ecological methodology. Harper and Row, New York.
- KUSHLAN, J. A. 1974. Quantitative sampling of fish populations in shallow, freshwater environments. Transactions of the American Fisheries Society 103:348–352.
- KUSHLAN, J. A. 1981. Sampling characteristics of enclosure fish traps. Transactions of the American Fisheries Society 110:557–562.
- LOFTUS, W. F., J. D. CHAPMAN, AND R. CONROW. 1990. Hydroperiod effects on Everglades marsh food webs, with relation to marsh restoration efforts. Pages 1–22 in G. Larson and M. Soukup (editors). Fisheries and coastal wetlands research: proceedings of the 1986 conference on science in national parks. US National Park Service and the George Wright Society, Fort Collins, Colorado.
- LOFTUS, W. F., AND A. EKLUND. 1994. Long-term dynamics of an Everglades small-fish assemblage. Pages 461–484 *in* S. M. Davis and J. C. Ogden (editors). Everglades: the ecosystem and its restoration. St. Lucie Press, Delray Beach, Florida.
- LOVELESS, C. M. 1959. A study of the vegetation in the Florida Everglades. Ecology 40:1–9.
- LOWE, R. L., AND R. D. HUNTER. 1988. Effects of grazing by *Physella integra* on periphyton community structure. Journal of the North American Benthological Society 7:29–36.
- MACAN, T. T. 1977. The fauna in the vegetation of a moorland fish pond as revealed by different methods of collecting. Hydrobiologia 55:3–15.
- MACAN, T. T., AND A. KITCHING. 1972. Some experiments with artificial substrata. Verhandlungen

der Internationalen Vereinigung für theoretische und angewandte Limnologie 18:213-220.

- MASON, J. C. 1976. Evaluating a substrate tray for sampling the invertebrate fauna of small streams, with comment on general sampling problems. Archiv für Hydrobiologie 78:51–70.
- MCPEEK, M. A. 1990. Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. Ecology 71:83–98.
- MERRITT, R. W., K. W. CUMMINS, AND V. H. RESH. 1984. Collecting, sampling, and rearing methods for aquatic insects. Pages 11–26 in R. W. Merritt and K. W. Cummins (editors). An introduction to the aquatic insects of North America. Kendall/Hunt, Dubuque, Iowa.
- MURKIN, H. R., P. G. ABBOTT, J. A. KADLEC. 1983. A comparison of activity traps and sweep nets for sampling nektonic invertebrates in wetlands. Freshwater Invertebrate Biology 2:99–106.
- PECKARSKY, B. L. 1980. Predator-prey interactions between stoneflies and mayflies: behavioral observations. Ecology 61:932–943.
- PETERSEN, R. C., AND K. W. CUMMINS. 1974. Leaf processing in a woodland stream ecosystem. Freshwater Biology 4:343–368.
- PIELOU, E. C. 1969. An introduction to mathematical ecology. Wiley, New York.
- RADER, R. B. 1994. Macroinvertebrates of the northern Everglades: species composition and trophic structure. Florida Scientist 57:22–33.
- RADER, R. B., AND C. J. RICHARDSON. 1992. The effects of nutrient enrichment on algae and macroinvertebrates in the Everglades: a review. Wetlands 12: 121–135.
- RADER, R. B., AND C. J. RICHARDSON. 1994. Response of macroinvertebrates and small fish to nutrient enrichment in the northern Everglades. Wetlands 14:134–146.
- REEDER, P. B., AND S. M. DAVIS. 1983. Decomposition, nutrient uptake, and microbial colonization of sawgrass and cattail leaves in Water Conservation Area 2A, Technical Publication 83-4, South Florida Water Management District, West Palm Beach, Florida.
- REID, J. W. 1992. Copepoda (Crustacea) from fresh waters of the Florida Everglades, U.S.A., with a description of *Eucyclops conrowe* n. sp. Transactions of the American Microscopical Society 111: 229–254.
- ROSENBERG, D. M., AND V. H. RESH. 1982. The use of artificial substrates in the study of freshwater macroinvertebrates. Pages 175–235 in J. Cairns (editor). Artificial substrates. Ann Arbor Science Publications, Ann Arbor, Michigan.
- SANDERS, H. L. 1968. Marine benthic diversity: a comparative study. American Naturalist 102: 243–282.
- SEDELL, J. R., F. J. TRISKA, AND N. M. TRISKA. 1975. The

processing of conifer and hardwood leaves in two coniferous forest streams. I. Weight loss and associated invertebrates. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 19:1617–1627.

- SHELDON, A. L. 1984. Cost and precision in a stream sampling program. Hydrobiologia 111:147–152.
- SIMBERLOFF, D. 1972. Properties of the rarefraction diversity measurement. American Naturalist 106: 414–418.
- SIMBERLOFF, D. 1978. Use of rarefraction and related methods in ecology. Pages 150–165 in K. L. Dickson, J. Cairns, and R. J. Livingston (editors). Biological data in water pollution assessment: quantitative and statistical analyses. American Society for Testing and Materials STP 652.
- SIMBERLOFF, D. 1979. Rarefaction as a distribution-free methods of expressing and estimating diversity. Pages 159–176 in J. F. Grassle, G. P. Patil, W. K. Smith, and C. Taille (editors). Ecological diversity in theory and practice. International Cooperative Publishing House, Fairland, Maryland.
- SIMPSON, E. H. 1949. Measurement of diversity. Nature 163:688.
- SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. W. H. Freeman and Company, New York.
- STEVENS, J. 1986. Applied multivariate statistics for the social sciences. Lawrence Erlbaum and Associates, Hillsdale, New Jersey.
- STEWARD, K. K., AND H. ORNES. 1975. The autecology of sawgrass in the Florida Everglades. Ecology 56: 162–171.
- SZLAUER, L. 1963. Diurnal migrations of minute invertebrates inhabiting the zone of submerged hydrophytes in a lake. Schweizerische Zeitschrift für Hydrologie 25:56–64.
- TURNER, A. M. 1996. Freshwater snails alter habitat use in response to predation. Animal Behavior 51: 747–756.
- URBAN, N. H., S. M. DAVIS, AND N. G. AUMEN. 1993. Fluctuations in sawgrass and cattail densities in Everglades Water Conservation Area 2A under varying nutrient, hydrologic and fire regimes. Aquatic Botany 46:203–213.
- USINGER, R. L. (EDITOR). 1956. Aquatic insects of California. University of California Press, Berkeley, California.
- VAN BUSKIRK, J. 1988. Interactive effects of dragonfly predation in experimental pond communities. Ecology 69:857–867.
- WERNER, E. E., AND M. A. MCPEEK. 1994. Direct and indirect effects of predators on two anuran species along an environmental gradient. Ecology 75: 1368–1382.
- WHITESIDE, M. C., AND C. LINDEGAARD. 1980. Complementary procedures for sampling small benthic invertebrates. Oikos 35:317–320.
- WHITESIDE, M. C., AND J. B. WILLIAMS. 1975. A new

sampling technique for aquatic ecologists. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie. 19: 1534–1539.

WILDING, J. L. 1940. A new square-foot aquatic sam-

pler. Limnological Society of America Special Publication 4:1-4.

Received: 1 November 1996 Accepted: 18 March 1997