MIDGE (DIPTERA: CHIRONOMIDAE AND CERATOPOGONIDAE) COMMUNITY RELATIONSHIPS WITH WATER QUALITY, VEGETATION, AND HYDROPERIOD IN EVERGLADES NATIONAL PARK

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Abstract

Effect of canal inflows on midge community composition: Quantitative samples of midge (Diptera: Chironomidae and Ceratopogonidae) pupal exuviae were collected along 5 suspected nutrient gradients in Everglades National Park (ENP) produced by canal inflows in order to determine midge community response to nutrient enrichment and identify possible indicators of water quality. Community abundance, species richness, and Shannon-Wiener diversity showed no consistent relationship with relative proximity to canal inflows. Eight species were significantly sensitive to canal inflows; 7 of these species were also sensitive to nutrient enrichment in Water Conservation Area 2A (WCA-2A) (King 2001). Seven species were significantly more abundant near canal inflows, none of these species were significantly tolerant to enrichment in WCA-2A. This discrepancy in tolerant species probably reflects differences in species responses to low gradients in ENP versus the much steeper gradient in WCA-2A.

Midge community response to experimental phosphorus enrichment: Midge community response to experimental phosphorus enrichment was examined at each of the 3 flume sites in Shark River Slough in 1999 and 2001. Community abundance, species richness, and Shannon-Wiener diversity showed no significant change with enrichment. Strong changes in individual species' abundance with increasing P-enrichment indicate that: (1) *Dasyhelea* c.f. *cincta*, *Tanytarsus "Nimbocera"* sp. A, and possibly *Cladotanytarsus* sp. A, may be sensitive to phosphorus enrichment; (2) *Chironomus stigmaterus*, *Chironomus* sp. B, *Dicrotendipes* sp. A, and *Pseudochironomus* c.f. *richardsoni* appear to benefit from enrichment. However, species' responses appear to be at least partially related to the relative position of treatments within the flumes, suggesting that preexisting, or flume-related, habitat gradients may exist at these sites that may confound detection of responses to enrichment.

The group of species identified as sensitive to enrichment in nutrient gradient studies in ENP were more responsive to P-enrichment than the taxa King (2001) listed as being sensitive to enrichment in WCA-2A. Tolerant species in the ENP gradient study were rare and inconsistently responsive to P-dosage, whereas WCA-2A tolerant species (King 2001) showed increases in abundance in high-dose channels relative to controls at all flumes, except Flume C in 2001. The greater responsiveness of ENP-sensitive species and WCA-tolerant species may reflect differences in the nutrient gradients sampled in the process of selecting these species as indicators.

Midge-plant community associations: Midge-plant community associations were examined by sampling pupal exuviae from (1) *Paspalidium/Eleocharis*, *Cladium*, *Pontederia*, *Typha*, and *Melaleuca* habitats in far eastern Northeast Shark River Slough (NSRS) in 2000, and (2) *Eleocharis* and *Cladium* habitats in NSRS and Taylor Slough in 2001. In 2000, *Paspalidium/Eleocharis* and *Cladium* habitats yielded the most individuals and species, whereas *Typha* and *Melaleuca* produced the fewest individuals and species. Midge communities from *Paspalidium/Eleocharis* habitats were quite similar, and were distinctly different from midge communities in the other habitats sampled. Midge communities in the other 4 habitats showed considerable variation and overlap with one another. The distinctiveness of

Paspalidium/Eleocharis midge communities was attributed to the greater amount of periphyton present at these sites. Most of the species found to be indicative of *Eleocharis* habitats in NSRS and Taylor Slough in 2001 were significantly associated with *Paspalidium/Eleocharis* habitats in eastern NSRS in 2000. Five species were indicative of *Cladium* habitats in 2001, but only *Beardius breviculus* was significantly associated with *Cladium* in 2000. The development of extensive periphyton growth in slough habitats with short emergent macrophytes, and the extensive detritus production and presumed low P/R ratios in tall emergent plant communities such as *Cladium*, *Typha*, and other plants whose physiognomy inhibits periphyton growth, appeared to be important determinants of midge community composition in these regions of ENP.

Midge associations with hydroperiod: Associations between midge species and hydroperiods were measured by comparing the mean relative abundances of each species in long-HP sites (HP > 9.5 months) versus that in short-HP sites (HP < 5 months). Seventy-nine midge taxa were categorized as long-HP species, 22 taxa were considered to be short-HP species. Most long-HP species are strongly associated with plants and substrates (peat) found in long-HP habitats. However, 19 species have spatially dynamic populations that are useful for assessing hydrological conditions in a variety of habitats. Twelve indices are proposed for measuring midge community response to hydropattern. Community indices based upon the richness and abundance of long-HP species present and mean hydroperiod scores for all species present, as well as multivariate ordination techniques that compare species composition at a site of interest against reference or 'target' communities, appear to be the most practical methods for assessing midge community response to hydrological conditions.

Emergence phenology of midges along hydroperiod gradients: The temporal and spatial responses of midge communities and species to hydrological conditions in the marl prairie and Rocky Glades were examined by sampling pupal exuviae at short time intervals along 2 hydroperiod transects throughout the wet season. All sites were characterized by communities comprised of a few abundant species and unusually large numbers of rare species. Total species richness increased with hydroperiod length along both transects. However, marl prairie and Rocky Glades sites exhibit similar: (1) Whittaker plots of species abundance versus rank, (2) slopes of cumulative species richness over time, (3) sample species richness, rarified species richness, and Shannon-wiener diversity during high water periods in late summer and fall, and (4) trajectories in ordination space through time. Collectively, these data suggest midge community structure is relatively unaffected by hydroperiod. However, at increasingly higher elevations, the emergence of rare species occurred progressively later in the wet season and, at the shortest-HP sites, coincided with high, and then receding, water levels in the fall. Rare species appearing at short-HP sites after September tended to be long-HP species, including seasonal species with fall and winter emergence. Compositional changes associated with increasing elevation included: (1) fewer long-HP species, (2) emergence of long-HP species increasingly limited to high water periods in the fall, (3) increases in proportions of Chironomini with decreases in Tanytarsini and Tanypodinae, and (4) Tanytarsini and Tanypodinae increasingly reduced or absent during the first 1-2 months after rewetting.

Several distinctive emergence patterns were observed among species including asynchronous emergence, highly synchronous emergence, summer seasonal emergence, fall-winter seasonal emergence, shallow-water emergence in both short-HP and long-HP species, and emergence confined only to deep water periods. Detrended correspondence analysis (DCA) of community succession along the Taylor Slough transect showed: (1) the high compositional dissimilarity, and strong differences in successional tracks, between the community in the main channel of Taylor Slough and those in the adjacent marl prairie and Rocky Glades, (2) convergence of communities at all sites during high water periods due to large emergences of ubiquitous species, the cessation of emergence of short-HP species (e.g., *Beardius reissi*), and the appearance of long-HP species at shorter-HP sites; and (3) divergence of communities in the fall was due to differences in distributions of seasonal species, and declines in deep-water emerging species with drops in water levels. Increasing hydroperiods and water depths in the marl prairie and Rocky Glades should increase species richness at any given site by: (1) allowing emergence of deep-water and late-seasonal, long HP species, (2) attracting more gravid females dispersing from sloughs, (3) and by providing a more suitable habitat for long-HP species to develop and emerge.

I. Changes in midge community composition along potential nutrient gradients caused by canal inflows into Everglades National Park

Introduction

The Everglades is an oligotrophic system that is phosphorus limited. Biotic commmunities in the Everglades are adapted to highly oligotrophic conditions and are quite sensitive to P-enrichhment (Steward and Ornes 1983, Walker et al. 1989, Hall and Rice 1990). Agricultural and urban inputs of P currently threaten the biotic integrity of the Everglades ecosystem. Enriched runoff from the Everglades Agricultural Area has already transformed natural sawgrass (*Cladium jamaicense*) stands and open-water slough habitats into dense stands of *Typha* near canal inflow structures.

Structural modifications and additions planned for the Central and South Florida Project as part of the Comprehensive Everglades Restoration Plan (CERP), will alter water deliveries into Everglades National Park. The increases of flow into Northeast Shark River Slough, and changes in sources of water will increase the potential for reductions in water quality and subsequent alteration of marsh community composition and function in Everglades National Park.

Effective biomonitoring methods need to be developed and implemented to ensure these modified water deliveries do not inadvertently degrade marsh systems in Everglades National Park.

Monitoring spatial and temporal changes in invertebrate community composition is a highly effective method of detecting changes in hydropattern, water quality, and overall function of aquatic ecosystems. Many invertebrate species are particularly sensitive, and quick to respond, to changes in their physical, chemical, and biotic environment. The reduction and disappearance of sensitive species, coupled with increases in species more tolerant of altered conditions, results in distinctive changes in community structure and composition among invertebrate communities that are differentially affected by environmental stressors.

Invertebrate bioassessment has become a widely accepted and applied method of evaluating aquatic ecosystem health, particularly for lotic systems. Much of its effectiveness rests in the high invertebrate species richness present in undisturbed freshwater habitats, and the sensitivity of many species and taxon groups to environmental degradation. Taxon groups such as the Ephemeroptera, Plecoptera, and Trichoptera (EPT) that generally require well-oxygenated waters for their survival, and that are relatively easy to identify, receive considerable attention in lotic bioassessment studies. The Chironomidae are often neglected in bioassessment studies because their identification is considered to be difficult and time-consuming (Rabeni and Wang 2001). However, chironomid midges are usually the most species-rich component of lotic invertebrate communities (Coffman and Ferrington 1996) and are known to be sensitive to a variety of stressors including nutrient enrichment (see reviews by Lindegaard 1995, Wright 1996),

The development of effective bioassessment protocols and indices for wetlands have received attention only recently (Danielson 1998) and consequently lag behind development of indices for running waters (e.g., Barbour et al. 1999). Many invertebrate-based indices of water quality for running waters are uninformative for wetlands bioassessment because of the relatively limited adaptive radiation, and consequent poor representation, of their constituent invertebrate groups in lentic habitats. For example, the relatively high dissolved oxygen requirements of most EPT families prevents their successful development in many pond and wetland habitats. In the

Florida Everglades, King (2001) found only 2 species of Ephemeroptera and 5 species of Trichoptera among the 252 invertebrate taxa he collected along the nutrient gradient present in WCA-2A. Accurate assessment of biological conditions in wetlands will require identifying indicators of water quality in organism groups that have not been traditionally used in stream bioassessment.

Chironomid and ceratopogonid midges have excellent potential as indicators of enrichment in freshwater wetlands, in part, because they have long been recognized as strong indicators of organic enrichment in lentic environments (reviewed by Rosenberg 1992; Lindegaard 1995). In recent wetlands studies, King and Brazner (1999) observed changes in chironomid communities that correlated with increasing levels of eutrophication in wetlands bordering Lake Michigan. Rader and Richardson (1994) observed density and composition changes in aquatic dipterans along the WCA-2A nutrient gradient in the northern Everglades. King & Richardson (2002) found that chironomid midges, when identified to species, were clearly the most informative group for detecting nutrient enrichment in the northern Everglades. Out of a total of 252 invertebrate species collected in their study, 41 species were determined to be significant indicators of water quality. Nineteen of these 41 species were chironomid midges, including 9 of the 15 species indicative of high water quality and sensitive to enrichment (King 2001).

Though midge community structure is responsive to nutrient enrichment, midges do not respond directly to increases in inorganic nutrient levels. Instead, invertebrates respond to nutrient-driven changes in food availability (changes in algal versus detrital food availability, changes within algal communities), plant community structure (both the physiognomy and composition of plant communities), and water chemistry (dissolved oxygen, ammonia, and hydrogen sulfide) in their environment. Since these variables may be influenced by factors other than nutrient enrichment (e.g., hydroperiod, geology), the responses of invertebrates to enrichment may vary considerably between different wetlands, and different plant communities within a wetland. Regional differences in other factors affecting food availability, plant community structure, and water chemistry likely account for conflicting classifications of midge species such

as *Polypedilum simulans* and *Nanocladius alternantherae* as both nutrient tolerant (Adamus and Brandt 1990) and nutrient sensitive (King 2001). Consequently, both the detection and application of indicator species for bioassessment should be regionally limited and specific to select habitats and plant communities. In the northern Everglades, King (2001) provided a list of 41 taxa that are potentially sensitive or tolerant of phosphorus-enrichment, including 19 chironomid taxa. However, his research was conducted in WCA-2A along a nutrient gradient that is far 'steeper' than those to be expected within Everglades National Park. Many of the indicators of water quality that he found may be either absent or unresponsive to biological changes along nutrient gradients in Everglades National Park. Furthermore, though King (2001) sought to quantify the responses of invertebrate communities to enrichment and identify the mechanisms that affect these changes, his study did not specifically examine the responses of a select group of invertebrates within a given plant community type.

In this study, we focus upon midge species and community responses to potential nutrient gradients created by canal inflows into Everglades National Park. Our objective was to identify species that may serve as indicators of either high water quality or impaired water quality, and search for community attributes that may be informative for detecting impairment.

SAMPLING WATER QUALITY AT INFLOWS INTO ENP

Sampling to evaluate midge community changes in response to potential reduced water quality in inflows into Everglades National Park was conducted along transects parallel to flow from: L-31W into Taylor Slough, S-332B into the Rocky Glades, and from 2 inflow structures along the Tamiami Canal near fish sampling sites 63 and 64 into Northeast Shark River Slough . Inflow near fish site 63 was sampled along 2 transects on successive days. A north-south transect consisting of fish sites 63, 56, and a site northeast of Mitchell Hammock was sampled on 18 December 2001. On 19 December, sampling was performed at 3 sites that were from 100-500 m west of the sites sampled on 18 December.

Two habitat types defined by their dominant plant species, *Eleocharis* marshes and *Cladium* stands, were sampled at each site along each transect. This design reduces the likelihood of identifying midge species as indicators of water quality that are really only

responding to changes in vegetation. Though these midge species may be indicative of changing water quality, their presence can be deduced from the plant community present at a site. Therefore, they provide very little useful information as indicators (useful indicators provide information that is otherwise difficult to obtain). *Eleocharis* and *Cladium* habitats were sampled in Taylor Slough and along all 3 transects in Shark Slough. In the S-332B area, *Cladium* and *Muhlenbergia* habitats were sampled at sites 50 m and approximately 1000 m west of the spillway outflow from the S-332B pond. Two additional pairs of samples were collected 100 m downstream of the inflow into the S-332B pond and 30 m east of the pond spillway into ENP. Table 1 summarizes the habitats and sites sampled along each inflow transect. Replicate quantitative samples of surface-floating midge pupal exuviae (1 meter-square of the water surface skimmed per sample) were collected at each site. Quantitative pupal exuviae samples were collected by skimming and removing all pupal exuviae contained within 0.25 m^2 plastic corrals (plastic storage containers with the bottoms removed) placed within a given habitat type. The total exuviae collected from 4 corrals situated next to each other (i.e., within an approximate 1.0 m^2 area) represented one sample. For each 0.25 m^2 corral area sampled, we recorded: the number of stems of each plant species present, a visual estimate of the percentage of stems covered by filamentous blue-green and other algae (epiphyton), a visual estimate of the amount of floating blue-green algal material (metaphyton), and water depth.

Plant tissue, whole water, and soil samples were collected from each sampling site for nutrient analyses. All nutrient analyses were performed by Dr. Yuncong Li's staff at the University of Florida Tropical Research and Educational Center in Homestead, FL. A total of 72 samples of midge pupal exuviae were collected during this survey.

Indicator species analysis (INSPAN, Dufrêne and Legendre 1997) was used to help identify taxa that may be useful as indicators of nutrient enrichment. INSPAN combines the relative abundance and relative frequency of occurrence of individual species in different treatment groups (in this study, sites closest to or farthest from canal inputs) into an indicator value (IV) for each group, and then assess the significance of IVs for each species using Monte Carlo simulations. Taxa that had significant IVs were considered to be sensitive to, or

Table 1. Vegetation habitats and sites sampled along each inflow transect sampled for assessing the relationships between midge communities and the quality of waters entering ENP along its eastern and northern boundaries.

Transect	Sites sampled	Habitats sampled (number of replicates collected)
Northeast Shark River Slough - 63A (outflow near site 63)	Fish sampling site 63	*Eleocharis* (2), *Cladium* (2)
	Fish sampling site 56	*Eleocharis* (2), *Cladium* (2)
	200 m east of north end of Mitchell Hammock	*Eleocharis* (2), *Cladium* (2)
Northeast Shark River Slough – 63B (outflow near site 63)	100 m west of site 63	*Eleocharis* (2), *Cladium* (2)
	500 m west of site 56	*Eleocharis* (2), *Cladium* (2)
	200 m west of north end of Mitchell Hammock	*Eleocharis* (2), *Cladium* (2)
Northeast Shark River Slough – 64 (outflow near site 64)	Fish sampling site 64	*Eleocharis* (2), *Cladium* (2)
	Fish sampling site 52	*Eleocharis* (2), *Cladium* (2)
	Fish sampling site 23	*Eleocharis* (2), *Cladium* (2)
S-332B pond outlet	100 m below S-332B pond inflow	mixed vegetation (2)
	30 m east of S-332B pond spillway	mixed vegetation (2)
	50 m west of spillway	*Cladium* (2), *Muhlenbergia* (2)
	~1000 m west of spillway	*Cladium* (2), *Muhlenbergia* (2)
Taylor Slough (outflow from L-31 canal)	L-31W 50 m south of S-332	*Eleocharis* (3), *Cladium* (3)
	50 m of Taylor Slough bridge	*Eleocharis* (3), *Cladium* (3)
	Fish sampling site 54	*Eleocharis* (3), *Cladium* (3)
	Fish sampling site 53	*Eleocharis* (3), *Cladium* (3)

tolerant of, enrichment if at least 75% of their relative abundance was concentrated in the group for which they are indicative of (Dufrêne and Legendre 1997). INSPAN was conducted using PC-ORD 4.08 (MjM Software, Gleneden Beach, Oregon, USA). Separate INSPAN analyses were performed on samples from *Eleocharis* habitats, *Cladium* habits, and all habitats combined in order to increase the overall power of significance tests. The balanced design of this study (equal numbers of samples were collected from each habitat type at equal numbers of sites close to, and far from, canal inputs along each transect) allows us to combine data from different habitat types.

It is important to note that INSPAN analyses represent simultaneous tests of multiple hypotheses, one for each species being tested. In these situations, a Bonferroni-adjustment of alpha is usually recommended in order to reduce the likelihood of designating species as significant indicators when, in fact, they are not (Type I error). However, Bonferroni-adjustments of alpha increase the likelihood that valid indicator species of water quality may be regarded as being uninformative (Type II error). Since the objective of this study was to determine which species may be useful for assessing water quality, all species hypotheses were pre-defined (i.e., for each species, H_0: species X is distributed randomly across treatments [relative positions to inflow]; H_1: species X is more abundant or less abundant nearer to inflows). For several species, information already has been written and compiled on their tolerance of eutrophication (Adamus and Brandt 1990: Table 9, and references therein), or anoxic conditions (Adamus and Brandt 1990: Table 10, and references therein), or their sensitivity/tolerance to phosphorus enrichment (King 2001:133). Certain species have previously been identified as being representative of communities that are not typical of the Rocky Glades and neighboring sloughs (2000a). Therefore, for many species, these analyses do not necessarily represent blind 'dredging' of data to find significant relationships. Furthermore, since our biomonitoring research will continue after this study, there is no real need for adjusting alpha to control Type I error. In this study, we set our alpha level at 0.05 for each species. Bonferroni-adjusted alpha levels were also calculated, but they are not considered critical cutoffs for determining biological significance. These species' reliability as indicators of water quality will be examined further, both in the P-dosing flume study, and in gradient sampling and other biomonitoring research in the future.

INSPAN analysis provides an unbiased, non-parametric method of identifying useful indicator species, but scoring of species is partially dependent upon their frequency of occurrence across all sites in a given treatment category. Strong indicator species whose abundance is concentrated in a given treatment category, but whose occurrence is relatively rare across all sites in this treatment category, will have lower IVs and reduced 'value' as indicators in the final Monte Carlo simulations to determine statistical significance. This may occur if inflow sources vary in their degree of effect upon midge communities receiving these inputs, or if species have

highly localized distributions. To further assess the effect of relative proximity to inflow points, we have listed changes in each species' absolute and relative abundances at sites near inputs versus sites removed from inputs, along each transect sampled. These data help to identify species with local distributions. Their recognition, along with perspectives on their ecology gained from prior midge work in Everglades National Park and published information on their responses to enrichment and anoxia by other researchers outside of ENP, provide insight into the relative effect of each input source on midge communities sampled in receiving marshes.

Results

COMMUNITY ATTRIBUTES

The mean abundance, mean areal species richness, total areal species richness, and Shannon-Wiener diversity for sites sampled in northeast Shark River Slough (NESRS), Taylor Slough (TS) and in the Rocky Glades adjacent to, and sites within, the 332B retention pond are plotted in Figures 1-3. Correlation coefficients for comparisons of mean numbers of exuviae, mean species richness, total species richness, and Shannon-Wiener diversity are listed in Table 13. Densities of midge pupal exuviae were highest within the 332B retention pond, Rocky Glades habitats close to the pond spillway, and in *Eleocharis* habitats along the 63A and 63B transects in NESRS. Midge pupal exuviae densities were lowest in *Cladium* habitats in NESRS, and *Eleocharis* habitats along NESRS transect 64. No consistent relationship was found between mean densities of pupal exuviae collected in samples and relative distance from inflow points. For example, densities declined with increasing distance from inflow points at the 332B pond spillway and Taylor Slough, but generally increased with distance along NESRS transects, though they were actually highest at mid-transect sites.

Densities in each of the 2 habitats sampled were weakly correlated along each transect sampled (e.g., for *Cladium* vs *Eleocharis* r=0.279, N=13, P=0.3567; densities of midge pupal exuviae in *Cladium* and *Muhlenbergia* habitats both decreased with distance). However, no habitat type consistently yielded greater densities of exuviae across transects (Table 2). This suggests that local conditions may affect both habitat-types at a site in a similar manner, but there

Table 2. Correlation coefficients for attributes of midge communities in samples of pupal exuviae collected from *Cladium* and *Eleocharis* habitats in northeast Shark River Slough, Taylor Slough, and Rocky Glades sites near the S-332B retention pond. * = P<0.05, ** = P<0.01, *** = P<0.001.

	Cladium				*Eleocharis*		
	mean # ind.	Total S^2	Mean S^1	Mean H	Mean # ind	Total S^2	Mean S^1
Cladium mean # ind.							
Cladium total S^2	0.868***						
Cladium mean S^1	0.834***	0.932***					
Cladium diversity	0.214	0.457	0.640*				
Eleocharis # ind.	0.279	-0.124	-0.148	-0.462			
Eleocharis total S^2	0.339	0.148	0.090	-0.089	0.546		
Eleocharis mean S^1	0.329	0.059	0.022	-0.236	0.735**	0.944***	
Eleocharis diversity	0.276	0.179	0.144	-0.098	0.004	0.730**	0.622*

[1] = same as species density (no. of species per unit area)
[2] = total number of species in a given habitat type at a site

is also considerable variation in midge density within a given habitat type among transects in a basin (NESRS), and among basins/regions sampled in ENP. For example, variation in midge densities within *Cladium* sites between transects may be due to differences in *Cladium* plant height. The greater height of *Cladium* in NESRS relative to other regions, may reduce periphyton growth, and thereby limit midge production. Variation in midge production in *Eleocharis* habitats may be linked with cycles of development, senescence, and mechanical disruption of calcareous algal mats that may vary temporally and spatially.

Mean species density (number of species / m^2) was significantly correlated with mean numbers of pupal exuviae collected from each habitat at each site (r=0.834, N=15, P=0.0001) and was highest at sites within, and adjacent to, the S-332B retention pond. Mean species density tended to decrease with increasing distance from inflow points in Taylor Slough and in the Rocky Glades near the S-332B retention pond. Only low emergence at Taylor Slough site 2 (just west of Taylor Slough along FL State Road 9336) breaks this trend. In NESRS, mean species density showed little change with distance from the Tamiami Canal.

Total species richness (the total numbers of taxa collected in pooled replicate samples from a given habitat at a given site) was significantly correlated with mean numbers of pupal exuviae collected from each habitat at each site (r=0.868, N=15, P<0.0001). Total species

richness was highest in the S-332B retention pond and in neighboring Rocky Glades habitats. Fifty species were collected from the 2 sites sampled in the S-332B retention pond (total of 4 $1m^2$-samples). *Cladium* and *Muhlenbergia* habitats located 50 meters west of the retention pond spillway yielded a combined total of 44 taxa (total of 4 $1m^2$-samples). Many of the species present at these sites (e.g., *Chironomus stigmaterus, Goeldichironomus holoprasinus*, *Goeldichironomus amazonicus*, *Procladius bellus, Dicrotendipes modestus*) are considered to be indicators of eutrophic conditions in wetlands (Adamus and Brandt 1990). Total species richness increased in the Rocky Glades with increased proximity to the S-332B retention pond, and in Taylor Slough near the L-31W canal, but essentially remained the same (*Eleocharis*) or dropped slightly (*Cladium*) in NESRS near the Tamiami Canal.

Shannon-Wiener diversity correlated significantly with mean areal species richness in both *Eleocharis* and *Cladium* habitats, and with total species richness in *Eleocharis* habitats, but was not correlated with mean numbers of exuviae collected, or with areal species richness in *Cladium* habitats. At Rocky Glades sites near the S-332B retention pond, diversity tended to increase, while total species richness declined, with increasing distance from the pond spillway. This reflected drops in the relative abundance of species such as *Tanytarsus "Nimbocera" limneticus*, and *Tanytarsus* sp. D, that dominate a rich fauna near the spillway comprised of many relatively rare species, some of which are indicators of enrichment.

SPECIES RESPONSES

A total of 70 midge species were collected in samples from sites within ENP, including 58 Chironomidae and 12 Ceratopogonidae (Table 3). The 4 samples collected from the S-332B retention pond yielded a total of 50 midge species, including an additional 8 chironomid species not found in ENP samples. These 8 chironomid species also were not found in wet prairie or *Cladium* habitats in previous studies. Most species (48 of 70) were present in more than one region of ENP, and many of those taxa that were found in only one region in this study have been collected in other regions in earlier studies. However, the midge community near the S-332 retention pond is notable in having the largest number of species unique to its region even though

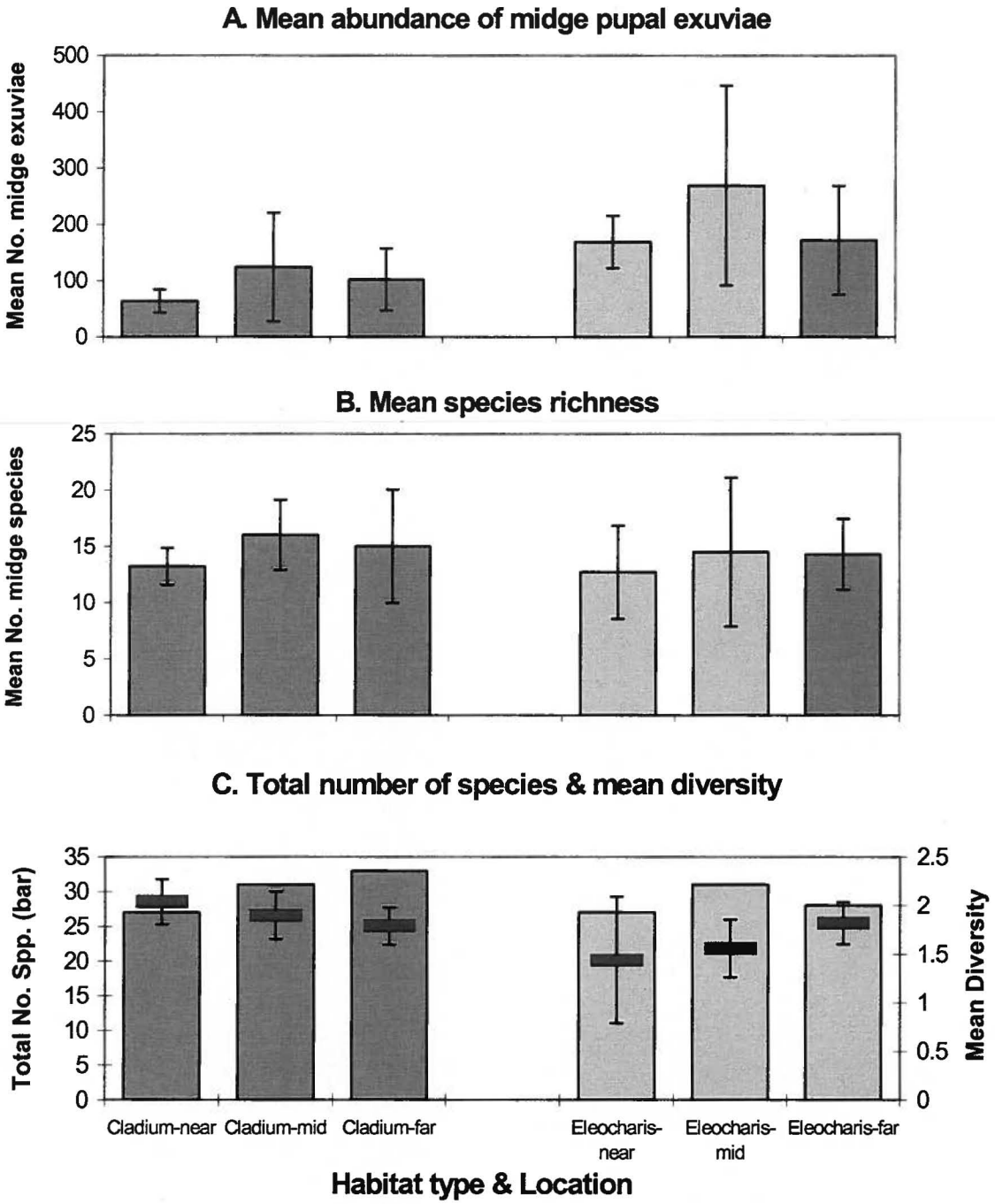


Figure 1. Abundance, species richness, and diversity of midge pupal exuviae collected in November-December 2001 samples from *Cladium* and *Eleocharis* habitats at 3 locations relative to inflow along 3 transects in northeast Shark River Slough. A. mean and 95% CI of midge pupal exuviae abundance. B. mean and 95% CI of species richness. C. Total numbers of species collected from each habitat at each site location, mean with 95% CI of Shannon-Wiener diversity for samples from each site and habitat.

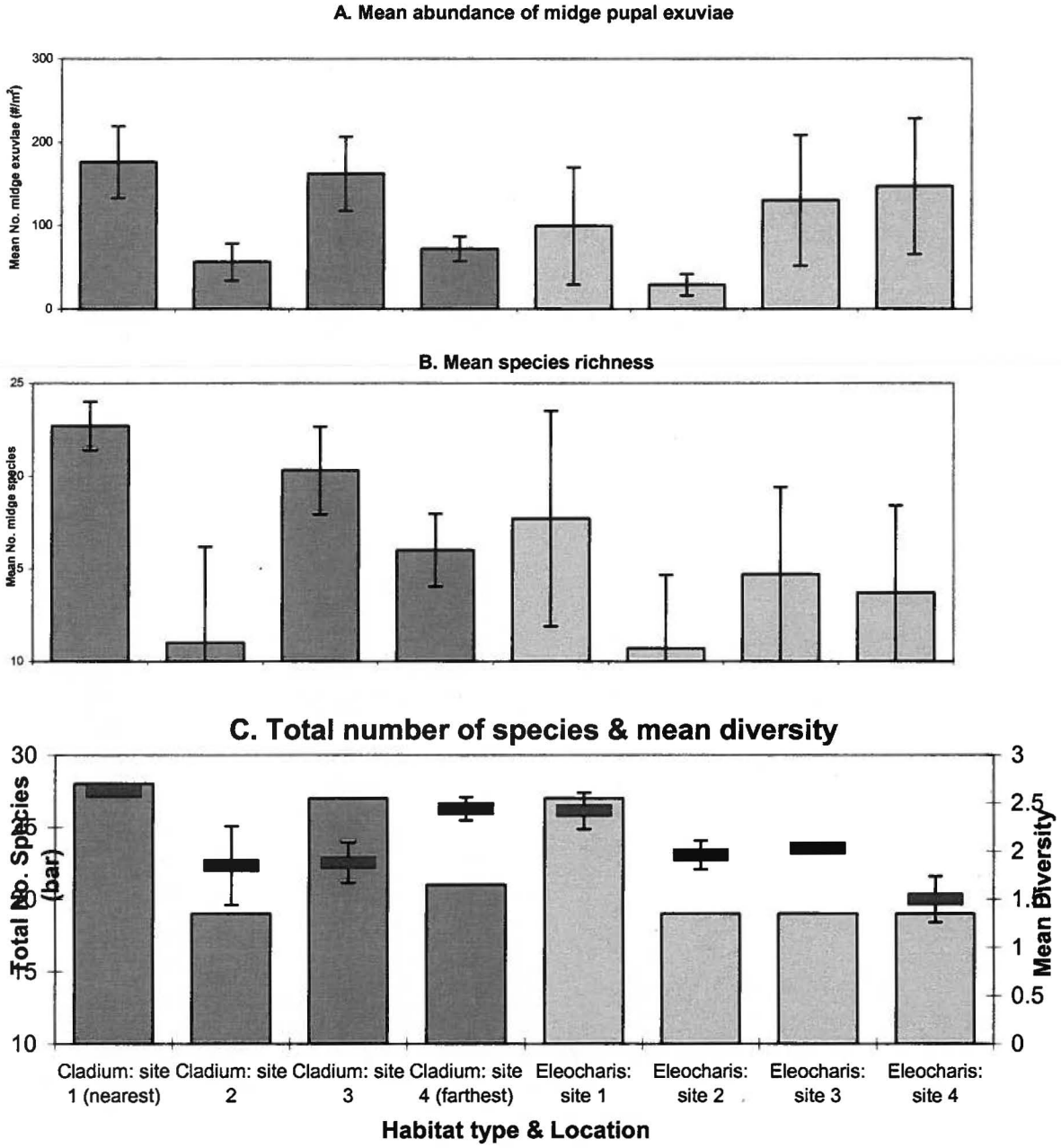


Figure 2. Abundance, species richness, and diversity of midge pupal exuviae collected in 31 October 2001 samples from *Cladium* and *Eleocharis* habitats at 4 sites in Taylor Slough at increasing distance from L-31W canal inflow. A. mean and 95% CI of midge pupal exuviae abundance. B. mean and 95% CI of species richness. C. Total numbers of species collected from each habitat at each site location, mean and 95% CI of Shannon-Wiener diversity for samples from each site and habitat.

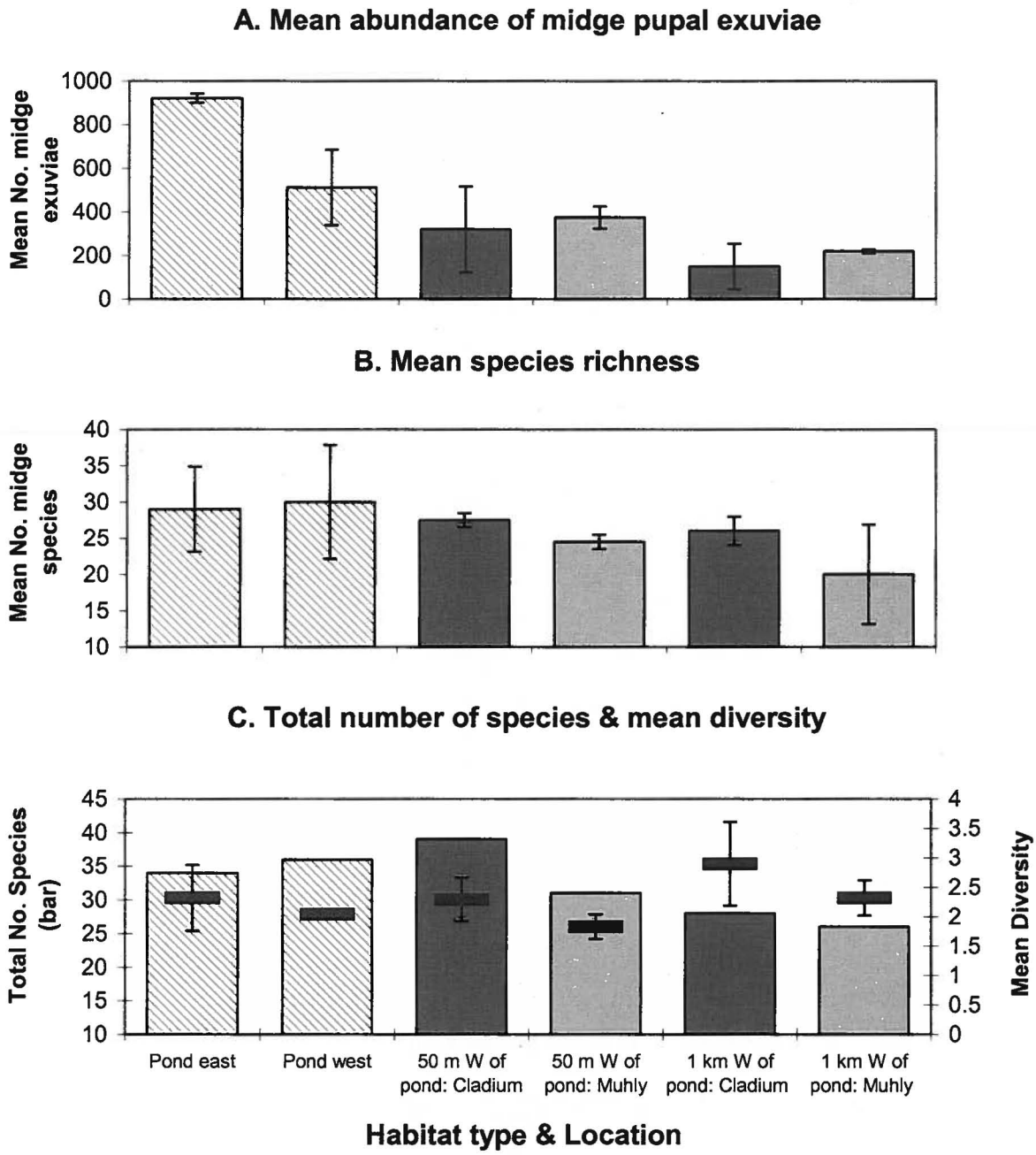


Figure 3. Abundance, species richness, and diversity of midge pupal exuviae collected in quantitative samples from sites within the 332B pond and from Rocky Glades sites and habitats just west of the 332B pond spillway on 14 November 2001. A. mean abundance with 95% confidence interval of midge pupal exuviae. B. mean species richness. C. Total numbers of species collected from each site/habitat, and mean with 95% CI of Shannon-Wiener diversity for samples from each site and habitat.

it was much less extensively sampled (12 species in 8 samples versus 3 species unique to Taylor Slough in 24 samples, and 7 species unique to NESRS in 36 samples), and in sharing an additional 7 species only with Taylor Slough (Tables 4 and 5). Several species unique to this region in this study, such as *Chironomus stigmaterus* and *Cladopelma forcipis* are known as indicators of enrichment. Other species such as *Tanytarsus* H, *Tanytarsus* sp. I, and Ceratopogonidae sp. AC are common to ditches around Homestead, but are rare in ENP (Fig. 4). Drops in species thought to be sensitive to nutrient enrichment occur near the pond spillway (Fig. 5).

The results of indicator species analyses for samples collected from *Cladium* habitats, *Eleocharis* habitats, and all habitats sampled in ENP are listed in Table 6. Taxa with P-values below 0.05 (not Bonferroni-adjusted) are given in Table 7. Fifteen species had significantly indicative responses to inflows (unadjusted $P<0.05$); 14 of these species were chironomids. In addition, *Chironomus* sp. B, *Polypedilum* sp. L, and *Tanytarsus* sp. F were sufficiently abundant, and 88-100% of their relative abundance at sites near canal inflows, but were not distributed across transects sufficiently enough (Tables 4 and 5) to produce significant indicator scores. *Chironomus stigmaterus*, *Cladopelma forcipis*, and *Dicrotendipes modestus* are considered to be strong indicators of enrichment (Adamus and Brandt 1990, Epler 2001, King 2001), and were found only at sites near canals, but were too local and rare to produce significant IV scores in this study.

Almost all of the species listed in Table 7 as being sensitive to canal inflows were also found to be sensitive to phosphorus enrichment by King (2001: 286). *Pseudochironomus* c.f. *articaudus*, a species that is abundant in the Rocky Glades and Taylor Slough, and that appears to be able to withstand drying, apparently is rare or absent in WCA-2A. *Corynoneura* sp. D, *Nanocladius alternantherae*, *Parachironomus alatus*, and *Paratanytarsus* sp. B were found to be significantly sensitive to enrichment by King (2001), but were too rare in this study for proper evaluation. *Dasyhelea* c.f. *cincta*, a species that is abundant in blue-green algal mats, was only slightly more abundant at sites distant from canals. Pupal exuviae densities of *D.* c.f. *cincta* were significantly correlated with a simple index of blue-green algae stem cover (= # plant stems X %

stem cover) in NESRS (R^2=0.3564, N=36, P=0.0001, but not in Taylor Slough (R^2=0.0682, N=24, P=0.2177).

At least 6, and possibly all 7 of the species listed in Table 7 as potential indicators of enrichment were not listed as tolerant of enrichment by King (2001). Many of the species that he lists as being tolerant were present, often exclusively, at sites near canals, but were collected in insufficient quantities, or from insufficient numbers of sites, to produce significant IV scores.

Discussion

Community metrics of species richness and diversity appeared to be somewhat inconsistent for reliably measuring water quality along these transects, but this needs to be reassessed when chemical analyses are received from the University of Florida. Species density and total species richness were highly dependent upon the intensity of emergence, which itself, varied considerably along each transect and showed no pattern among transects. Species density and total richness tended to increase with increased proximity to canal discharges in Taylor Slough and near the S-332B retention pond, but showed no response in NESRS. Changes in species composition along the transects at the S-332B pond and Taylor Slough suggest that nutrient gradients at these transects may be greater than those sampled in NESRS. Therefore, species density and total species richness may prove to be useful for detecting reduced water quality. Shannon-Wiener diversity shows no relationship with abundance, but also shows no consistent relationship with species richness and distance from canal inflows in ENP. For midge communities, Shannon-Wiener diversity essentially is uninformative for determining water quality.

Increases in species density with nutrient enrichment were observed in slough habitats by Rader and Richardson (1994). However, King (2001) found that species richness tended to show a unimodal, subsidy-stress response to enrichment in WCA-2A, and therefore, was unreliable as a measure of water quality there. In general, he found that metrics based upon taxonomic richness, taxonomic structure, and feeding ecology were essentially ineffective for assessment, because they fail to show monotonic relationships with enrichment. Therefore, aggregate indices of biological integrity that are based upon community attributes commonly used

in stream bioassessment (species richness, diversity, functional feeding groups, EPT), are likely to be less informative in wetland systems. Unless new community attributes can be found that respond in a monotonal or even an exponential fashion, analyses of compositional changes in invertebrate communities appear to be more effective and reliable for determining changes in water quality than multimetric approaches.

King (2001) observed strong changes in invertebrate community composition along the pronounced phosphorus (P) gradient in WCA-2A, and he identified 19 chironomid midge species as significant indicators of P-enrichment. Vegetation was the principle direct determinant of invertebrate community composition, with distance from the Hillsboro Canal, spatial relationships, P-levels (residuals), and hydropattern also influencing composition.

In this study, we attempted to control variation in community assemblages that were directly or indirectly attributable to changes in plant communities along gradients by sampling within only select plant communities at each site sampled. This was done in order to better resolve midge species that might be responsive to environmental change over relatively short time scales, as opposed to species whose presence is dependent upon changes in vegetation that occur over longer time scales. In NESRS, where *Eleocharis* and *Cladium* habitats were selected for sampling, our sites nearest canal inflows had to be located 200-300 m away from inflow points due to a lack of *Eleocharis* habitats closer to these points. Despite our experimental design, and the constraints they imposed on our selection of sampling sites, we found 15 species out of 70 total species (14 out of 58 chironomid midge species, or 24%) with distributions that were significantly related to distance from canal inflows. Undoubtedly, some of these species will be found to be unreliable indicators with additional collecting. However, a large number of species that are considered to be indicators of enrichment, but that were rare in this study, will likely be validated as indicators for the Everglades with further collecting. King (2001) and King and Richardson (2002) also found the Chironomidae to be particularly sensitive to P-enrichment in the northern Everglades. Though chironomid midges made up 21% of the taxa collected in WCA-2A (57 out of 272 taxa, including 23 microcrustacean taxa that are not typically regarded as

macroinvertebrates), they comprised 46.3% (19 out of 41 taxa) of those species that were determined to be significant indicators of water quality.

Midge communities appear to be extraordinarily responsive to the combined inherent sensitivity and severity of Everglades habitats, including their propensity to undergo anoxic stress with enrichment. The nature of Everglades marshes predispose them to strong diel changes in chemistry. *Cladium* marshes often attain sufficient height and density to restrict periphyton growth and limit photosynthetic activity. This reduced photosynthetic activity, combined with microbial processing of the large amounts of detritus produced yearly, may keep oxygen levels low in these stands. Slough habitats exhibit strong diel oxygen fluctuations created by intensive photosynthetic activity in extensive floating algal/*Utricularia* mats that offset high sediment, plant, and algal respiration rates throughout the day. In minimally-impacted sloughs, photosynthetic production approximately balances respiration rates. Photosynthetic production in sloughs may also relieve anaerobic conditions in adjacent Cladium stands (McCormick et al. 1997).

Additions of phosphorus can disrupt periphyton production and accelerate community respiration rates sufficiently enough to create prolonged periods of oxygen depletion, and effectively shift the competitive balance in the midge community toward taxa that are better able to cope with the resulting increased anoxic stress. The loss of periphyton also shifts the balance of trophic resources available to midges away from algal foods toward detritus and detritus-based foods. It is interesting to note that the 3 Orthocladiinae listed by King (2001) as being sensitive to enrichment (*Nanocladius alternantherae*, *Parakiefferiella coronata*, and *Corynoneura* sp. D), as well as other Everglades Orthocladiinae, are algal grazers that are likely to be associated with periphyton mats, and they lack hemoglobin, a physiological feature that is present in midge species found to be tolerant of enrichment. The fact that there are a large number of midge species that are adapted to high BOD, low oxygen environments, just as there are a large number of midge taxa that require well-oxygenated environments, may account for their extraordinary usefulness as indicators of enrichment in the Everglades. Midge community composition in the Everglades essentially teeters on changes in the ratio of production versus

respiration (P/R), a system parameter that is extremely sensitive to nutrient additions in this particular ecosystem.

Table 8 summarizes the indicator status of each species collected in this study based upon taxonomic and wetlands literature, and upon the results of this study. Almost all of the species found to be sensitive to enrichment in this study were also considered to be sensitive in WCA-2A (King 2001). The similarity of the findings of these two studies regarding sensitive species reflects the fact that the nutrient gradients examined in both studies incorporated relatively unimpacted habitats with similar chemistry and biology. This general agreement between 2 completely independent studies strengthens the validity of these species as indicators of excellent water quality. The addition of *Pseudochironomus* c.f. *articaudus* and *Nilothauma babiyi* are important additions to King's list that are relevant to future biomonitoring in ENP.

Dasyhelea c.f. *cincta*, an abundant species in blue-green algal (BGA) mats, is undoubtedly one of the most productive and important aquatic insect species in the Everglades. However, virtually nothing is known about its population ecology or its relationship with blue-green algal mat dynamics. If this species is strongly associated with BGA mats as is currently suspected, their populations should be greatly affected by canal waters with sufficient P-enrichment to disrupt BGA mat formation. *Dasyhelea* c.f. *cincta* appeared to be sensitive to phosphorus in P-dosing experiments, but it was only slightly more abundant at sites distant from canals. Apparently, phosphorus concentrations at many of the sites near canal outflow in ENP were not high enough to suppress BGA mat growth. Ryan King did not find "*Dasyhelea* sp." to be significantly sensitive to enrichment in WCA-2A; however, species of *Dasyhelea* are indistinguishable as larvae (at least 5 species are present in ENP, 4 were collected in this study). Much more work is needed on the ecology of this species and its sensitivity to enrichment.

In contrast to species that are sensitive to canal discharge, most, if not all, of the 7 species determined to be potentially tolerant of enrichment in this study were not found to be tolerant by King (2001). The species King found to be tolerant of enrichment were either not significantly responsive, were too rare, or were not sufficiently distributed among transects to produce significant IV's. There are several possible reasons for this discrepancy. The difference

in the degree of enrichment and gradient steepness between WCA-2A and those gradients sampled in ENP probably explain the disparity in the responses of most species. Phosphorus levels in the Hillsboro Canal are much higher than those found in the Tamiami Canal and the L-31W canal. Well known indicators of enrichment such as *Chironomus stigmaterus* and *Goeldichironomus holoprasinus* (Epler 2001) were abundant at enriched sites in WCA-2A, but were present only within and around the S-332B retention pond. Significant indicators of enrichment in ENP may show a unimodal subsidy-stress response over the nutrient gradient in WCA-2A and not be recognized as tolerant of enrichment there. Secondly, sampling in ENP was limited to *Cladium*, *Eleocharis*, and *Muhlenbergia* habitats. Eutrophic species associated with *Typha* would not have been collected in our study.

If inflows differ in water quality, legitimate indicators of poor water quality would be present near some inflows but not others. INSPAN analysis weights a species frequency of occurrence within sites in a given treatment group equally with its relative abundance in different groups. Low frequency of occurrence due to differences in water quality will cause possible legitimate indicators like *Chironomus* sp. B and *Polypedilum* sp. L to have non-significant IV scores.

Finally, differences in the sampling methods used and the relative ability to achieve species-level identification looking at pupae versus larvae may contribute to the differences observed between our study and King's. Sampling surface-floating pupal exuviae samples all microhabitats simultaneously without bias toward a certain substrate or microhabitat. Samples obtained using a D-frame net tend to be biased toward microhabitats that are easier to collect such as fine sediments, while often missing species that live on or in coarse substrates such as wood and large macrophytes. Also, larger species with longer larval life spans will be relatively more abundant in D-frame net samples than they will in surface-floating pupal exuviae samples. It is interesting to note that most of King's tolerant taxa are large species that tend to inhabit fine, peaty sediments.

Species-level identification is generally easier to achieve when one works with pupal exuviae rather than larvae. This is particularly true for the Ceratopogonidae. The difficulties in

identifying larval Ceratopogonidae to species may explain why King found only 8 taxa (out of 144,000 invertebrates identified; for comparison, 12 species of Ceratopogonidae were found in this study out of 13,004 midge exuviae identified), and none were considered significant indicators.

Though our sampling design attempts to control for midge community variation attributable to changes in habitat/plant community-types and their associated variables, there are other factors besides water quality that may influence midge community composition along these transects. Sites were selected on the basis of their relative proximity to canal effluents entering ENP. Water quality, expressed in terms of nutrient concentrations, was assumed to improve with increased distance from the canal input point. Presumably, the results of water, soil, and plant tissue sample analyses, when they are completed, will support this assumption. Yet one should also consider the fact that canals are an atypical habitat in the Everglades and would be expected to harbor species not typically found in natural Everglades habitats. A certain degree of penetrance of 'canal' species into neighboring Everglades slough and sawgrass habitats may occur by virtue of these sites' close proximity to gravid females dispersing from canals (i.e., a source – sink situation). These species would be considered to be tolerant of enrichment in this study, even if they actually require excellent water quality for their development. However, most of the species designated as indicators, or potential indicators, of enrichment in this study (Table 6) have been identified as indicators of either eutrophication, or as tolerant of anoxic conditions, in other studies (Adamus and Brandt 1990, Epler 2001, King 2001, Wirth 1979). Furthermore, though increased proximity to canal population sources might hypothetically account for increases in tolerant species near canals, it fails to explain the decreases and disappearance of species identified as being sensitive to enrichment near canal inflows.

King (2001) detected a significant residual variation in both plant and invertebrate composition in WCA-2A that was explained only by distance from the Hillsboro Canal. He suggested that one or a combination of factors may be occurring including: (1) other environmental variables besides nutrient levels that are directly influenced by canals, are affecting plant and invertebrate communities; (2) proximity to canals may influence plant and

invertebrate dispersal; (3) a "front" of successional changes in vegetation and invertebrate assemblages, perhaps initiated by canal water quality, has progressed into the marsh out of synchrony with environmental changes; and (4) other effects directly related to proximity to the canal (e.g., pathogens). Of these 4 possibilities, I feel that other environmental variables related to canal discharge such as toxic chemicals, and current, and precipitation of dissolved organic compounds and colloidal sediments (choice 1 above) might also be affecting midge communities.

The close proximity of the Everglades to urban and agricultural development suggests that toxic compounds are potentially a problem. The frequency and magnitude of deformity in midge larvae has been shown to correlate with levels of toxic and radioactive chemicals (Johnson et al. 1993, Williams et al. 2001). Abnormalities in chironomid pupal morphology are commonly observed (Langton 1995), but relationships between the frequency and magnitude of their occurrence and water quality have not been reported. I observed a curious instance of very strong variation in the shagreen fields on tergites of *Tanytarsus* sp. D at sites close to and within the S-332B retention pond. The cause of this variation is unknown and may involve factors other than water chemistry, but its prominent occurrence at these sites warrants further study.

Changes in midge communities along these transects may also be due to changes in current velocity. Though current velocities at all sites are probably low, they are likely to be slightly higher at sites near canal inflow points. Differentiating the relative influences of current and nutrient levels on midge communities in this study is difficult, because slight differences in current velocity can change the effective nutrient loading these sites receive, even if nutrient levels are equal. Slight differences in current velocity may affect midge community composition by altering their algal food base. Filamentous green algae appear to become more abundant with increasing current velocity near culverts under FL State Road 9336 (RJ, personal observation). Further research is needed to explore the effects that slight increases in current might have on midge community composition. Examining how midge communities differ with increasing distance from culverts along FL State Road 9336 and the road to Pa-hay-okee might help to identify midge species that are responsive to changes in current velocity.

Finally, phosphorus-dosing experiments performed in enclosures effectively control for current while allowing the investigator to examine the community response to nutrient enrichment. Sampling of midges in P-dosed mesocosms, or in P-dosed flumes, should be incorporated in future research on midge response to nutrient enrichment.

II. Midge community response to P-dosing

Introduction

Current Everglades restoration plans include reestablishing flow into northeast Shark Slough (NESS) and raising water levels in the Rocky Glades and Taylor Slough to provide hydropatterns that will enhance marsh food-web production. The increases of flow into Northeast Shark River Slough, and changes in sources of water will increase the potential for reductions in water quality and subsequent alteration of marsh community composition and function in Everglades National Park. Effective biomonitoring methods need to be developed and implemented to ensure these modified water deliveries do not inadvertently degrade marsh systems in Everglades National Park.

Our current understanding of invertebrate and fish community responses to nutrient enrichment in Everglades marshes is based on two studies with somewhat contradictory results and conclusions, and that also lack comparability due to differences in collecting methods and reporting of data. Whereas Rader and Richardson (1994) observed greater densities of both fish and invertebrates in enriched sites in the northern Everglades, but Turner et al. (1999) found that only fish biomass increased with enrichment and suggested productivity gains from enrichment cascade up and accumulate in fish, which effectively serve as the top trophic level in these systems. However, failure to account for midge biomass and productivity in food web studies often results in misinterpretation of food web structure and dynamics (Berg and Hellenthal 1993). Examining midge community response along nutrient gradients and in mesocosm studies will help clarify food web dynamics in Everglades marshes.

Considerable experimental effort is currently being expended to establish water quality standards that will preserve the character and function of Everglades marsh ecosystems (Jones et al. 2000). We

incorporated sampling of midge exuviae to more precisely determine the chemical thresholds and ecological consequences of nutrient enrichment and to develop better metrics for its detection. In the previous chapter, we examined how midge community structure and composition change at different distances from canal inflows into ENP. INSPAN analysis was performed to identify potential species that are responsive to enrichment based upon changes in their prevalence and abundance at sites close to, and distant from, canal inputs. The objective of this study was to examine (1) midge community response to experimental P-dosing, (2) evaluate the responsiveness of species identified as sensitive or tolerant to canal inflows, and (3) identify additional taxa that may be useful in nutrient bioassessment. This section is divided into two parts: the first part describes the response of the midge community and some select species to P-dosing; the second part examines the responses of species identified as being sensitive to inflows in ENP and WCA-2A in separate studies.

A. Midge response to P-dosing

Methods

Semi-quantitative samples of surface-floating pupal exuviae were collected from each of the 3 P-dosing flume sites in Shark River Slough in March 1999 and January 2001. The P-dosage levels for each flume treatment category and the positions of these treatment channels within each flume array are listed in Table 9. The position of each treatment channel in the flume array was determined by Florida International University researchers in a random fashion with one constraint – the control and high dose channels could not be next to each other. Note, however, that at all the Shark Slough sites, the zero-dose control channel is located in one of the first two channels (1st channel at sites A and C, 2nd channel at site B) and the high-dose channel is in one of the last two channels (the 4th channel at sites A and B, the 3rd channel at site C).

Three surface-floating pupal exuviae samples were collected in each flume channel and an additional sample was collected outside the first channel (a total of 13 samples per flume site). The within-channel samples were collected at approximately 10m, 45m, and 75m downstream from the header box in order to examine within-channel distance effects. Samples were collected at each site by skimming the water surface with a 2-quart sauce pot within an arms reach (approximately 1

Table 9. Phosphorus dosage levels and channel positions for each treatment category at each of the Shark Slough flume sites.

Flume site	Treatment category	P dosage level	Channel position at flume site1
Shark R. Slough - A	Outside control	0 ppb	outside 1st channel
	Control	0 ppb	2nd channel
	Low	+ 5 ppb P	3rd channel
	Medium	+ 15 ppb P	1st channel
	High	+ 30 ppb P	4th channel
Shark R. Slough - B	Outside control	0 ppb	outside 1st channel
	Control	0 ppb	1st channel
	Low	+ 5 ppb P	3rd channel
	Medium	+ 15 ppb P	2nd channel
	High	+ 30 ppb P	4th channel
Shark R. Slough - C	Outside control	0 ppb	outside 1st channel
	Control	0 ppb	1st channel
	Low	+ 5 ppb P	2nd channel
	Medium	+ 15 ppb P	4th channel
	High	+ 30 ppb P	3rd channel

1=channels numbered in sequence from left to right when looking upstream, e.g., the first channel is nearest to the dock.

meter) of the walkway along a two meter distance on each side of the channel. The exuviae were concentrated by pouring the captured exuviae into a 125-micrometer opening sieve. Thirty "pot-dips" were made over the 2 meters sampled along each side of the channel at a sampling site (60 dips total per site). The outside control sample was collected by skimming along a 4 meter stretch of the outer walkway adjacent to the first channel. Consequently, all samples represent the exuviae present in 60 pot-dips made within an approximate 4 meter-square area.

Results and Discussion

A combined total of 34,919 pupal exuviae representing 66 nematoceran dipteran species were identified in the samples collected from the Shark Slough P-dosing flumes in March 1999 and January 2001 (Tables 10 and 11).

Flume sites differed in the total numbers of species and numbers of exuviae collected during sampling (Tables 10 and 11, Figures 6 and 7) . Samples from flume site A yielded notably

more individuals and species than did samples taken from sites B and C. Samples from site A also tended to have slightly higher Shannon-Wiener diversity, though slightly lower evenness, than those from the other two sites (Figure 8).

Overall, the 3 Shark Slough flume sites were generally quite similar in species composition though the proportions of certain species may vary between sites and between sampling dates (Table 12). Thirteen species were unique to site A, whereas only 3 species were unique to site B and 2 taxa were found only at site C. However, all species unique to a given site were represented by only a few individuals. Perhaps the most obvious change between sampling periods at these sites has been the increase in abundance of *Dicrotendipes* sp. A Epler 1995 at flume sites A and B while numbers of *Parachironomus alatus*, *Corynoneura* sp. B, and *Cladotanytarsus* sp. A have declined.

No notable changes in community structure in response to P-dosing treatments were observed at the Shark Slough flume sites in March 1999 or in January 2001 (Tables 10 and 11, Figures 6-8). However, the changes in abundance for certain important taxa between (1) control channels versus high-dose channels and (2) sites at different distances from the doser in high P-dosage channels suggest these species may be responsive to phosphorus enrichment. *Dasyhelea c.f. cincta* (Figure 9), a species that is abundant in cyanobacterial mats, is generally much less abundant in the high dosage channels than in lower dosage and control sites. These drops presumably reflect the disintegration of these algal mats in response to phosphorus enrichment. Declines in numbers of *Dasyhelea* account for the noticeable shift in the relative proportions of the Ceratopogonidae and Chironomidae with increasing enrichment seen in Figure 10. Tanytarsus "Nimbocera" sp. A also appear to drop in numbers near the doser in the high dosage channel at each flume site.

While *Dasyhelea c.f. cincta* abundance declines in response to enrichment, certain species known to be tolerant of the reduced oxygen levels frequently found in enriched waters appear to increase in numbers. *Chironomus* sp. B and *C. stigmaterus*, perhaps the two largest chironomid species in the Everglades in terms of body size, appear to be significantly more numerous in the high dose channels than at the control and low-dosage sites in 1999 (Figures

11A and 12A). This pattern was less clear, though, in January 2001 samples. *Dicrotendipes* sp. A (Figure 13A) also appeared to show a strong increase in numbers in response to enrichment versus control sites during both sampling periods. Also, as mentioned above, this species became much more abundant with prolonged dosing. Nine out of 10 exuviae of *Pseudochironomus richardsoni*, a species that is common in enriched drainage ditches near Everglades National Park, but that is rare within the Park, were collected within the high P-dosage channels at Sites A and B.

The increases in the numbers of *Chironomus* spp. and *Dicrotendipes* sp. A may also be a function of channel treatment position within flume arrays rather than a response to enrichment. This channel position effect becomes evident when treatments are arranged graphically according to their orientation at each field site (Figures 11B and 13B). The generally more uniform patterns of response across the channels suggest that either preexisting, or flume-related, habitat gradients may exist across flume sites A and B, and perhaps site C that have a profound effect on the composition of the midge communities within these flume arrays. The degree of variation between sample sites due to this position effect will need to be accounted for in future analyses in order to accurately resolve the effects of nutrient enrichment on Everglades dipteran communities. The unfortunate arrangement of treatments within the three Shark Slough flume sites (control channels in the 1st two channels and the highest dosage channels among the last two channels) may make accounting for this position effect more difficult and/or reduce the sensitivity of these flume experiments in resolving midge responses to enrichment. In addition, the large scale of these flume experiments may render them more susceptible to confounding factors such as habitat heterogeneity and gradients that reduce the resolution of a response to nutrient additions.

B. Response of indicator species to P-dosing

Methods

We used the results of the nutrient gradient study conducted in ENP to identify 15 midge taxa as potential indicators of nutrient enrichment. The responses of this group of species to P-enrichment in the Shark River Slough Flume arrays was examined and compared against: (1) the

midge species King (2001) found to be significantly responsive to enrichment in WCA-2A, (2) a composite list of species from both of these studies, and (3) this composite list augmented by select species that were highly responsive to enrichment in the flumes, but that have not been shown to be indicators in other Everglades studies (Table 13). These species are *Tanytarsus "Nimbocera"* sp. A (sensitive), *Dasyhelea* c.f. *cincta* (sensitive), *Dicrotendipes* spp. (tolerant) and *Chironomus* sp. B (tolerant). The inclusion of these species with ENP and WCA-2A indicators to form the third group, and examining this group's response in the flume study, does not constitute an independent test of their validity as indicators. It is done here for comparative purposes. Further investigations are required to verify their usefulness as indicators.

Results

The total responses of species, identified as sensitive or tolerant to canal inflows in ENP, to P-dosing at the Shark River Slough flumes are shown in Figs 14-17. Sensitive species from the ENP gradient study (ENP-sensitive) collectively show strong drops in percent relative abundance at the beginning of the high dose channels at Flumes A and B in both years, but not Flume C. Flume C shows no change in percent relative abundance in 1999, and shows an increase in tolerant species relative to the control channel in 2001. The medium dosage channel actually had the highest percentage of sensitive taxa while the control channel had the lowest percentage (Outside control: 31.4%; Control: 24.5%; Low dose channel: 25.5%; Middle dose channel: 56.2%; High dose channel: 36.9%). All flumes showed increases in percent relative abundance of ENP-sensitive species with increased distance from the doser in the high dose channel in 1999. In 2001, sensitive species increased with distance from the high P-doser in Flumes A and B; Flume C showed decreases in these species. Percentages of sensitive species were lower in the control channel than in the sample collected outside of the flume array at all flumes except Flume C in 1999.

Species identified by King (2001) as sensitive to phosphorus enrichment in WCA-2A (WCA-sensitive), exhibited response patterns between channels and along the high dose channel similar to those of ENP-sensitive species, but the magnitude of response of this group of species

was not as strong (Figs. 14 and 16). At Flume B in 1999, WCA-sensitive species show an increase in the high dose channel relative to the control channel; ENP-sensitive species show the expected decrease. *Tanytarsus* sp. D (=sp. R Epler), *Parachironomus alatus* and *Paratanytarsus* sp. B

often showed increases in the high dose channels that weakened overall group response strength. WCA-2A-sensitive species included all ENP-sensitive species.

The combination of WCA-sensitive taxa, plus *Dasyhelea* c.f. *cincta* and *Tanytarsus* "*Nimbocera*" sp. A (All-sensitive), showed strong drops in percent relative abundance between control and high-dose channels at all sites except Flume B in 1999. These drops were not steady, monotonic declines with increasing dosage at Flumes A and B. The median dose channel had higher percentages of sensitive taxa than the low dose channel. Flume C showed monotonic declines. The All-sensitive indicator species group increase in percent relative abundance from the start to the end of the high dose channel at all flumes in both years except Flume C in 2001.

ENP-tolerant indicators were often absent from channels; when present, they were rare and inconsistently responsive to dosage (Fig. 15). WCA-tolerant indicators increased between controls and high dose channels in all flumes in both years except Flume C in 2001. Responses were not steady, monotonic increases with dosage, but typically showed a peak in the low dose channel. Within the high dose channel, the percentage of WCA-tolerant taxa drops with distance from the doser (Fig. 17). The control channel had higher percent WCA-tolerant taxa than the outside control at all flumes in both years except Flume C in 2001.

Adding *Chironomus* sp. B and *Dicrotendipes* sp A Epler to the WCA-tolerant group of indicator species greatly amplified the increases in tolerant species in the high dose channel relative to controls. However, Flume C had the highest percentage of tolerant species in the medium dose channel in both years. Tolerant taxa declined along the length of the high dose channel at all flume sites in both years except for Flume C in 2001 where they were highest at he end of the channel.

Table 13. Species considered to be sensitive or tolerant of nutrient enrichment in Everglades National Park (based upon INSPAN analysis of their abundance close to and distant from canal inputs), WCA-2A (King 2001: 286), and additional species that are responsive in the Shark River Slough flume project.

	ENP	WCA	SRS Flumes
Sensitive species			
Ablabesmyia sp. A	X	X[1]	
Ablabesmyia sp. B	X	X[1]	
Nanocladius alternantherae		X	
Parakiefferiella coronata	X	X[2]	
Pseudochironomus c.f. *articaudus*	X		
Nilothauma sp.	X		
Parachironomus alatus		X	
Polypedilum simulans	X	X[3]	
Cladotanytarsus sp. A	X	X[4]	
Cladotanytarsus sp. B	X	X[4]	
Paratanytarsus sp. B		X	
Tanytarsus "Nimbocera" sp. A			X
Dasyhelea c.f. *cincta*			X
Tanytarsus sp. D (=R Epler)		X	
Tolerant species			
Pseudochironomus richardsoni		X	
Asheum beckae	X		
Chironomus stigmaterus		X	
Chironomus sp. B			X
Chironomus (Lobochironomus) sp.	X		
Dicrotendipes modestus		X	
Dicrotendipes nervosus gr. sp.		X[6]	
Dicrotendipes sp. A Epler			X
Dicrotendipes tritomus			X
Goeldichironomus holoprasinus		X	
Goeldichironomus c.f. *natans*		X	
Kiefferulus pungens		X	
Polypedilum falciforme	X		
Polypedilum trigonus		X	
Polypedilum (Penta.) tritomus	X		
Tanytarsus sp. B (=sp. C Epler)	X		
Tanytarsus "Nimbocera" sp. D	X		
Tanytarsus sp. F Epler[7]			
Tanytarsus sp. J Epler[5]			
Ceratopogonidae sp. C	X		

1 = *Ablabesmyia rhampe* gr. in King (2001)

2 = *Parakiefferiella* sp. C Epler in King (2001)
3 = *Polypedilum halterale* gr. in King (2001)
4 = *Cladotanytarsus* sp. in King (2001)
5 = unassociated with pupa - Reared specimens of my sp. H may be this species
6 = *Dicrotendipes simpsoni* in King (2001)
7 = not collected in Everglades National Park

Discussion

ENP-sensitive taxa were more responsive and dependable indicators to nutrient enrichment than WCA-sensitive species. This was because *Tanytarsus* sp. D, *Paratanytarsus* sp. B and *Parachironomus alatus* often increased in abundance with enrichment in these flumes. These species may show negative responses to enrichment over the high nutrient gradients in WCA-2A, but they may benefit from the nutrient additions in these experiments.

ENP-tolerant species performed poorly in these flume experiments, whereas WCA-2A-tolerant species appear to respond well to P-dosing. The poor performance of ENP-sensitive species relative to WCA-2A taxa may have several explanations. The differences in performance may reflect differences in the nutrient gradients sampled in the process of selecting these species as indicators. The gradients sampled in the ENP nutrient gradient study may not have been high enough to elicit subsidy responses in species that are well known to be tolerant of enrichment. Indicator species such as *Chironomus stigmaterus*, *Dicrotendipes* spp, and *Pseudochironomus* c.f. *richardsoni*, were responsive to enrichment in both WCA-2A and these flume experiments.

ENP-tolerant species may simply not be reliable indicators. In the ENP nutrient gradient study, they may have been responding to other factors such as current and proximity to canals. These species distribution may also be patchy in the Everglades, and were not present in the area to respond. *Asheum beckae*, *Tanytarsus* "*Nimbocera*" sp. D, and *Tanytarsus* sp. B were not collected at the flumes at all. These species, as well as *Chironomus* (*Lobochironomus*) sp., were not collected in WCA-2A. *Kiefferulus pungens* was a significant indicator in WCA-2A, was present in northeast Shark River Slough, but was not collected at any flume sites.

Recommendations for future studies

(1) Expand nutrient gradient sampling to include more gradients over a wider area of Everglades National Park. Sampling should include areas to the west of the L-67 levee in Shark River Slough, and possibly in areas of far northeastern Shark River Slough near the *Melaleuca* stands. Expanding sampling will increase the power of INSPAN analyses and perhaps capture more individuals of species that are regarded as indicators of enrichment.

(2) Sampling should also include strong gradients outside of Everglades National Park. Sampling strong gradients will allow one to capture and assess the responses of all constituents of the Everglades community to nutrient enrichment. Sampling entirely within Everglades National Park allows one to get a good sense of which species may be sensitive to enrichment, but one cannot fully assess the responses of species that are tolerant of enrichment.

(3) Sampling should also be performed within canals and ditches in close proximity to Everglades National Park to gain some understanding as to what species live in these environments, and which species present in ENP are there because of the close proximity to these atypical environments. Investigations around some of the remaining burrow pits may be helpful in measuring the degree of penetrance into the surrounding natural environment these atypical species achieve.

(4) Studies that examine rates of larval deformities in midges may yield valuable information for assessing the quality of water entering ENP as part of the modified waters program, or emergency dumping of water to prevent flooding in urban areas.

(5) Research on the role of current in structuring midge communities would be helpful for identifying "tolerant" species that are actually responding to the currents near inflow points into ENP. Culverts along the Main Road in ENP provide excellent situations for studying invertebrate response to current.

III. MIDGE – PLANT COMMUNITY RELATIONSHIPS

Introduction

Plant communities typically have a profound effect on ecosystem structure and function in shallow water environments. The density and physiognomy of plant communities can greatly influence freshwater food webs by: (1) providing substrates for periphyton attachment, (2) reducing light levels for periphyton and plankton growth, thereby affecting rates of water column primary production and P/R ratios, (3) and affecting the degree to which food webs are detritus-based, and the oxygen demands detrital decomposition imposes on consumers, and (4) altering critical physical environmental factors such as water temperature and current, and aspects of community structure and function that are in equilibrium with these factors.

Undisturbed ridge and slough habitats in the Everglades are typically comprised of a mosaic of different plant communities that arise in response to differences in elevation, hydroperiod, fire frequency, and alligator activity. Plant community – invertebrate relationships in the Everglades are not well understood. Surveys of midge communities along hydroperiod transects indicate that there is considerable change in community composition with hydrological changes. Undoubtedly, changes in plant communities along these transects contribute to these compositional changes. A better understanding of plant – midge relationships, and how they change within this vegetation mosaic, is important for determining diversity patterns across Everglades landscapes. Knowledge of plant – midge relationships also provides insight into the biology of midge species and how they respond to environmental change.

This study consists of 2 separate investigations: (1) a survey of midge assemblages present in 5 plant communities in the northeastern corner of northeast Shark River Slough (NSRS), and (2) a more extensive survey of midge communities in NSRS and Taylor Slough, associated with Cladium stands and Eleocharis marshes, the 2 dominant plant communities in graminoid wetlands in the Everglades. The objectives of these studies were to: (1) expand surveys of midge communities in ENP to NSRS and Taylor Slough in order to understand distributions of species in ENP, and to search for new records for the Park and the Everglades system in general; (2) determine relationships between midge assemblages and plant communities.

Methods

In September 2000, samples of surface-floating pupal exuviae were collected from *Melaleuca* stands, as well as *Typha*, *Pontederia*, *Cladium*, and *Eleocharis* / *Paspalidium* macrohabitats. Each plant community was sampled at 3-4 separate locations within the study area. Surface-floating pupal exuviae were collected by skimming the water surface for 5 minutes with a 3-quart pot and concentrated using a 125 um sieve. Samples were preserved in 95% ethanol and identified to species or morphospecies in the laboratory. Water depth, temperature, conductivity, and dissolved oxygen measurements were also taken.

Midges associated with Cladium and Eleocharis habitats in western areas of NSRS and Taylor slough were sampled quantitatively in the fall of 2001 as part of an investigation into midge response to canal inflows into ENP. The locations of sampling sites in Taylor Slough and NSRS, as well as the number of replicate samples collected at each site, are given in Table 14 below.

Table 14. Vegetation habitats and sites sampled along each inflow transect sampled for assessing the relationships between midge communities and the quality of waters entering ENP along its eastern and northern boundaries.

Transect	Sites sampled	Habitats sampled (number of replicates collected)
Taylor Slough (outflow from L-31 canal)	L-31W 50 m south of S-332	*Eleocharis* (3), *Cladium* (3)
	50 m of Taylor Slough bridge	*Eleocharis* (3), *Cladium* (3)
	Fish sampling site 54	*Eleocharis* (3), *Cladium* (3)
	Fish sampling site 53	*Eleocharis* (3), *Cladium* (3)
Northeast Shark River Slough - 63A (outflow near site 63)	Fish sampling site 63	*Eleocharis* (2), *Cladium* (2)
	Fish sampling site 56	*Eleocharis* (2), *Cladium* (2)
	200 m east of north end of Mitchell Hammock	*Eleocharis* (2), *Cladium* (2)
Northeast Shark River Slough – 63B (outflow near site 63)	100 m west of site 63	*Eleocharis* (2), *Cladium* (2)
	500 m west of site 56	*Eleocharis* (2), *Cladium* (2)
	200 m west of north end of Mitchell Hammock	*Eleocharis* (2), *Cladium* (2)
Northeast Shark River Slough – 64 (outflow near site 64)	Fish sampling site 64	*Eleocharis* (2), *Cladium* (2)
	Fish sampling site 52	*Eleocharis* (2), *Cladium* (2)
	Fish sampling site 23	*Eleocharis* (2), *Cladium* (2)

Quantitative pupal exuviae samples were collected by skimming and removing all pupal exuviae contained within 0.25 m^2 plastic corrals (plastic storage containers with the bottoms removed) placed within a given habitat type. The total exuviae collected from 4 corrals situated next to each other (i.e., within an approximate 1.0 m^2 area) represented one sample. For each 0.25 m^2 corral area sampled, we recorded: the number of stems of each plant species present, a visual estimate of the percentage of stems covered by filamentous blue-green algae (epiphyton), a visual estimate of the amount of floating algal material (metaphyton), and water depth. All pupal exuviae collected were identified to species or morphospecies.

Results

2000 Survey

Fifty-six midge species, including 47 Chironomidae and 9 Ceratopogonidae were identified among the 2,946 pupal exuviae collected in samples from these 5 habitats (Table 15). Samples from *Paspalidium/Eleocharis* marshes yielded the largest numbers of exuviae; *Melaleuca* and *Typha* samples had the fewest exuviae.

Total species richness and mean sample richness were highest in *Paspalidium/Eleocharis* and *Cladium* habitats. All sites sampled in these habitats were quite uniform in species richness. On the other hand, samples from *Pontederia*, *Melaleuca*, and *Typha* communities were quite variable in species richness. *Pontederia* samples yielded from 5 to 25 species. *Melaleuca* and *Typha* stands had the lowest mean and total midge species richness of all habitats sampled.

Ordination of samples using nonmetric multidimensional scaling showed that *Paspalidium/Eleocharis* samples group together, and are somewhat distinct from all other samples except Cladium-2 (Fig. 18). Eight species were found to be significantly associated with *Paspalidium/Eleocharis* sites in indicator species analysis (INSPAN) (Table 16), including: *Labrundinia neopilosella*, *Larsia* sp. A, *Parakiefferiella coronata*, *Polypedilum trigonus*, *Cladotanytarsus* sp. A, *Paratanytarsus* sp. B, *Dasyhelea* c.f. *cincta*, and Ceratopogonidae sp. E (a *Dasyhelea* sp.). In addition, all 55 specimens of *Parachironomus alatus* were found at 2 of the 4 *Paspalidium/Eleocharis* sites. Many of these species (e.g., *Parakiefferiella*, *Dasyhelea* c.f. *cincta*) are strongly associated with blue-green algal periphyton. Field notes taken at the time of collection indicate that all *Paspalidium/Eleocharis* sites sampled had

Figure 18. Ordination plot of the first 2 dimensions of nMDS ordinations of midge communities in 5 habitats (*Paspalidium/Eleocharis*, *Cladium*, *Pontederia*, *Typha*, and *Melaleuca*) in eastern Northeast Shark River Slough, September 2000. PE = *Paspalidium/Eleocharis*, Cm = *Cladium*, Po = *Pontederia*, Ty = *Typha*, Me = *Melaleuca*.

extensive periphyton growth comprised primarily of filamentous blue-green algae. The close position of *Cladium*-2 is due to this sample having large numbers of *Parakiefferiella coronata* and *Paratanytarsus* sp. B, suggesting that periphyton growth may have been present there. Two-way indicator species analysis (TWINSPAN), splits all *Paspalidium/Eleocharis* samples and *Cladium*-2 from all other remaining samples at the second level on the basis of the former group having *Cladotanytarsus* sp. A (Fig. 19). *Cladotanytarsus* sp. A was associated with *Eleocharis* in the 2001 habitat study and is an indicator of good water quality.

Midge assemblages from the other plant communities were well spread out in ordination space and show considerable overlap with other plant community assemblages. *Pontederia* assemblages showed considerable spread, but appeared to be most similar to those of *Typha* stands. Significant indicators of *Pontederia* habitats include *Glyptotendipes* sp. B, *Kiefferulus pungens*, and *Polypedilum* sp. K. The first two species, and others such as *Dicrotendipes modestus* and *Chironomus* (*Lobochironomus*) sp., are tolerant of moderate enrichment and anoxia (Epler 2001, Adamus and Brandt 1990). They were present at sites in several of these plant communities, as well as at *Paspalidium/Eleocharis* sites. *Beardius breviculus* was significantly indicative of *Cladium* habitats. No taxa were found to be significantly indicative of *Typha* or *Melaleuca* stands.

Several species collected in this study have been rare or absent in samples from studies of Taylor Slough midges. *Glyptotendipes* sp. B and *Polypedilum* sp. L are new records for ENP. *Kiefferulus pungens*, *Polypedilum* sp. J, and *Polypedilum* K are species associated with gator holes and long-HP sites that were rarely collected in earlier surveys. Most of these species were particularly abundant in *Pontederia* habitats. Their perceived rarity likely reflects the emphasis on sampling drier habitats in previous studies.

2001 Survey

Quantitative samples from Taylor Slough and northeast Shark River Slough (NSRS) yielded 50 species of Chironomidae and 9 species of Ceratopogonidae. These species are listed in Table 17, along with results from INSPAN analysis. Seven species were significant indicators of *Eleocharis* marsh habitat: *Ablabesmyia* sp. A, *Ablabesmyia* sp. B, *Larsia* sp. A, *Parakiefferiella coronata*, *Cladotanytarsus* sp. A, *Tanytarsus* sp. G, and *Dasyhelea* c.f. *cincta* Out of these 7 species, 4 were significant indicators of

Paspalidium/Eleocharis habitat in the 2000 study, 2 species were not found in 2000 (*Ablabesmyia* spp.), and one species (*Tanytarsus* sp. G) tended to be indicative of *Pontederia*, with only 1 0f 92 specimens collected in *Paspalidium/Eleocharis* samples. *Tanytarsus* sp. G may be problematic as an indicator of habitat or nutrient enrichment, because it could very well consist of 2 or more species. This taxon belongs in the *mendax* group of species in *Tanytarsus*. Spies (1998) recently described two new species in this group that would both be considered *Tanytarsus* sp. G in my studies. The two species would be difficult to separate under a dissecting microscope. Further taxonomic work is needed to determine which species are present in ENP, and to determine how to reliably separate these taxa (if there are more than one species) under a dissecting microscope.

Five species were indicative of *Cladium* habitat: *Paramerina* sp., *Beardius breviculus*, *Cladopelma* sp. A, *Cladotanytarsus* sp. C, and *Dasyhelea* c.f. *atlantis*. Only one of these species (*Beardius breviculus*) was a significant indicator of *Cladium* habitats in 2000. However, *Cladopelma* sp. A tended to indicate *Cladium* (N=97, P=0.078), but was found in all other habitats as well. *Cladotanytarsus* sp. C tended to be indicative of *Paspalidium/Eleocharis* sites in 2000 (P=0.071, N=11).

Discussion

A number of midge species in ENP were previously known to have strong, direct associations with certain plants or animals:

> *Polypedilum* (*Pentapedilum*) undescr. sp. associated with *Nymphaea* and *Sagittaria* (Jacobsen, personal observation)
>
> *Endotribelos hesperium* associated with *Nymphaea*, *Sagittaria*, and *Typha* (Grodhaus 1987, Jacobsen, personal observation)
>
> *Stenochironomus* (*S.*) sp. associated with wood (*Salix* in ENP) (Borkent 1984)
>
> *Stenochironomus* (*Petalopholeus*) sp. associated with dangling leaves (host unknown) (Borkent 1984)
>
> *Polypedilum nymphaeorum* associated with *Nymphaea* leaves (Maschwitz and Cook 2000)
>
> *Xenochironomus* xenolabis associated with Porifera (Epler 2001)

Out of these species, only *Endotribelos hesperium* was collected in these studies (1 specimen in *Typha* stand). However, *Beardius breviculus* was determined likely to be directly asssociated with *Cladium*.

Besides the strong associations observed in these studies, *Beardius breviculus* (as "*B.* c.f. *truncatus*") was cited by King (2001: 168) as being strongly associated with *Cladium* in the northern Everglades.

The differences in results between the two studies suggest that strong, direct associations between midges and plants are not the prevailing pattern in the Everglades. In most instances where midge species distributions are associated with certain plant habitats, these associations are likely to be due to either: (1) other factors in these habitats that are favorable for both species' development, or (2) the plant community directly affects features of the habitat in a way that is beneficial for certain midge species. For example, the physiognomy of *Eleocharis* and *Paspalidium* allows ample light to reach the water column, enabling extensive periphyton development. Midge species that thrive in these mats, perhaps because of the food the mats harbor and the oxygen they generate and store, will then be associated with these species (and others with similar growth forms). Macrophyte communities with plant shapes and densities sufficient to inhibit periphyton growth will suppress midge species that are associated with periphyton. This poor periphyton growth, coupled with the high biological oxygen demand induced by the detritus that species like *Cladium* produce, create an oxygen-depleted environment that many 'tolerant' species can successfully exploit. Many of the species associated with *Cladium* in the *Cladium* versus *Eleocharis* study, were present in other plant communities sampled in eastern NSRS in 2000. Likewise, in the 2000 study, species that were significantly associated with *Pontederia* were also present in a variety of other habitats, including *Paspalidium/Eleocharis* marshes.

Perhaps the most interesting midge-plant community association is *Cladotanytarsus* sp. C associated with *Cladium*. This species is significantly associated with *Cladium* habitats, yet it is also very sensitive to enrichment (King 2001 as "*Cladotanytarsus* sp."; this report). *Nilothauma* sp. (all males are *N. babiyi*) also is sensitive to enrichment, but is about equally well represented in *Eleocharis* and *Cladium* habitats.

Finally, it is interesting to note the strong disparity in the numbers of individuals and species collected from *Paspalidium/Eleocharis* sites (means: 480.5 individuals, 17.75 species) and *Cladium* sites (means: 130 individuals, 18.33 species) compared with what was collected in *Typha* (means: 30 individuals, 8.7 species) and *Melaleuca* stands (means: 43.7 individuals, 8.7 species). Rader and Richardson (1994), sampling in open-water habitats because "they are the centers of biodiversity in the

Everglades" (P. 136), found greater numbers of individuals and species in enriched areas of WCA-2A and concluded that phosphorus enrichment increases species richness in the Everglades. Our results indicate *Typha* stands, which are the predominant plant community in enriched areas of WCA-2A (King 2001), are relatively species poor in terms of midges. Highest midge species richness was found in Cladium stands. Random sampling across all habitat types (i.e., not stratified) in enriched areas and unenriched areas may show that enriched areas (usually dominated by *Typha*), on average, will have less species richness than unenriched areas (see also King 2001).

IV. MIDGE ASSOCIATIONS WITH HYDROPERIOD

To examine midge species and community composition responses to different hydropatterns, we collected surface-floating midge pupal exuviae samples monthly for a year from 22 sites categorized as either short-hydroperiod, medium-hydroperiod, or long-hydroperiod sites based upon their plant community composition. The objective of this sampling was to describe: midge communities characteristic of certain hydroperiods and associated plant community types, how community composition changes between sites with different hydropatterns, and to identify species that might be useful as indicators of hydrological change in the Rocky Glades and neighboring slough habitats. The results of this investigation were presented in Jacobsen and Perry 2000b.

At each site, the relative abundance of each midge species was calculated by pooling all samples collected over a year. The mean relative abundance of each species for each site hydroperiod category was then calculated from relative abundance data for each site. Note that this approach weighs the relative abundances from each site equally, rather than assigning equal weight to each exuviae collected. This equal weighting of site data promotes detecting broad-scale patterns of species abundance and community change. The ratio of a species mean relative abundance at long hydroperiod sites versus its abundance at short-hydroperiod sites was used as a measure of that species hydroperiod 'preference'. As earlier reported in Kline et al. (2001: Tables 8 and 9), both families of midges (i.e., the Chironomidae and the Ceratopogonidae) were lumped together for relative abundance calculations. Both families were well represented at all sites in each hydroperiod category, so lumping them together seemed to be practical at that time. However, since the relative proportions of each midge family changed with hydroperiod (the proportion of midges that are Chironomidae increase with increasing hydroperiod length), it was more accurate to calculate hydroperiod preference scores for species in each family separately. Table 18 lists the scoring criteria for each species based upon their mean relative abundance data. Tables 19 and 20 list the mean relative abundances of all species of Chironomidae and Ceratopogonidae collected, various ratios of their relative abundances between different site hydroperiod categories, their assigned hydroperiod preference status, and their hydroperiod preference score.

Based upon the data presented in Tables 19 and 20 and the scoring criteria in Table 18, it is clear that there are numerous chironomid and ceratopogonid species that may serve as indicators of

hydrological conditions. Out of 100 chironomid species collected during this study, 66 species either had much higher relative abundances in, or were exclusively found in, long-HP habitats (Table 19). Eleven species were far more abundant in, or are exclusive to, short-hydroperiod habitats; 22 taxa either were more abundant in medium-hydroperiod sites or were common to habitats with a wide range of hydroperiods. Species that show markedly greater mean relative abundances in medium-hydroperiod environments include: *Ablabesmyia* sp. *A*, *Larsia* sp. *A*, *Pseudochironomus* c.f. *articaudus*, *Apedilum* sp., *Nilothauma babiyi*, *Tanytarsus* sp. *B*, *T.* sp. *D*, and *T.* sp. *G*.

Table 18. Scoring criteria and hydroperiod preference designations for midge species based upon comparisons of their mean relative abundance (MRA) between sites in different hydroperiod (HP) categories.

Score	Criteria	Assigned hydroperiod association
10	Found at "long"-hydroperiod sites only	Long
9	Found at "medium"- and "long"-hydroperiod sites only	Long
8	Ratio of MRA at long HP sites vs short HP sites > 10	Long
7	Ratio of MRA at long HP sites vs short HP sites = 5-10	Long
6	Ratio of MRA at long HP sites vs short HP sites = 2.5-5	Ubiquitous*
5	Ratio of MRA at long HP sites vs short HP sites = 0.4-2.5	Ubiquitous*
4	Ratio of MRA at long HP sites vs short HP sites = 0.2-0.4	Ubiquitous*
3	Ratio of MRA at long HP sites vs short HP sites = 0.1-0.2	Short
2	Ratio of MRA at long HP sites vs short HP sites < 0.1	Short
1	Found at "short"- & "medium"-hydroperiod sites only	Short
0	Found at "short"-hydroperiod sites only	Short

* = includes species with preferences toward "medium"-hydroperiod habitats

Thirty Ceratopogonid taxa were collected during this study (Table 20). Most species are either rare or were collected either shortly after rewetting or at low-water periods during dry-down (at long-HP sites), suggesting they prefer moist, semi-aquatic conditions and therefore, are of limited value as indicators of hydroperiod during the wet season. However, the 5 species highlighted in grey emerge throughout the wet season and are informative for assessing community responses to hydropatterns.

Midge species useful for measuring invertebrate community response to hydropattern change may be grouped conceptually into 2 general types based upon their spatial dynamics and degree of substrate affinity. The first group of species (called Type 1 species here) are those with relatively static

populations temporally and spatially that are strongly associated with certain substrates and plant taxa. The second group of species (Type 2 species) have dynamic populations that are responsive to short-term, seasonal changes in hydrological conditions and that apparently show no strong associations with bottom substrates and emergent plant species. This classification of midge species is simply one discernable pattern out of perhaps many trends that exist within, and help to describe, the midge community. This dichotomy may not be discrete, but instead, represent endpoints in a spectrum of species-substrate affinities within the midges. Nevertheless, these categories are instructive for understanding how midge communities respond to hydrological change and how their species composition may be used to assess hydrological restoration in the Everglades.

This dichotomous view of Everglades midge species based upon substrate affinity and spatial dynamics was initially conceptualized from, and is most manifest among, species that prefer longer hydroperiods. Type 1 species recognized so far from long-hydroperiod habitats are closely associated either with fine, peaty soils (e.g., *Coelotanypus* sp., *Tanypus* spp., *Procladius* spp., *Chironomus* spp.), specific plant taxa (e.g., *Polypedilum* (*Pentapedilum*) undescr. sp., *Polypedilum nymphaeorum*, and *Endotribelos hesperium* are associated with *Nymphaea* and/or *Sagittaria*), decaying wood (*Stenochironomus* sp., *Tribelos fuscicorne* found in rotting *Salix*), or sponge (*Xenochironomus xenolabis* obligately associated with sponge). These substrates and plant or animal "host" species are highly dependent upon long-term wet hydrological conditions for their existence. Consequently, their establishment or disappearance occurs over relatively long time-periods (i.e., at least a year and most likely over several years' time) rather than at seasonal time-scales. Likewise, most Type 1 species' populations show little spatial expansion over the course of the wet season. Type 1 species tend to be large, rare, and ecologically specialized, suggesting they have long developmental times and/or their microhabitat is relatively small and limits population size. However, there are quite a few of these species, and therefore, collectively, they are commonly encountered and represent a significant portion of the midge community species-wise at long-hydroperiod sites. Their ecology and life history features are somewhat analogous to k-selected species in life-history theory or late-successional to climax species in a successional sere. They are important in demonstrating the linkages between hydrological conditions, plant communities, and invertebrate communities. Due to their close affinity to biological features at long-

hydroperiod sites that are dependent upon long hydroperiods, they are strong indicators of long hydroperiods and comprise a large portion of those taxa in Table 19 with hydroperiod-preference scores of 9 or 10. However, the numerical and spatial size of their populations are likely to be unaffected by small or short-term changes in water levels or duration of hydroperiod. Therefore, they tend to be of limited value for monitoring invertebrate community response to hydroperiod change over short time periods. In addition, their presence or absence at a site can be generally inferred from the readily observable biological features they are dependent upon.

Type 2 long-hydroperiod species appear to be less substrate specific, or if they are specific to certain substrates and plant species, these substrates/plants respond quickly when hydrological conditions are appropriate for their development during the wet season (e.g., long hydroperiod species that feed upon filamentous green algae – they develop to maturity when water levels are high and current is sufficient for algal growth). Their populations are temporally and spatially dynamic, radiating outward from sloughs and other long-hydroperiod sites during the wet season and successfully emerging in shorter hydroperiod areas if hydrological, and hydrologically-driven biotic, conditions are sufficient for their successful development. Because they may be present at sites with a variety of hydroperiods, they tend to score lower (7-8) than Type 1 taxa using the scoring criteria in Table 18. However, they are very important as an assessment "tool" because of their sensitivity; they appear to respond to even slight changes in water depth and hydroperiod length over short time scales. Comparisons of their emergence phenology at different sites along hydroperiod gradients have revealed that their emergence periods become disproportionately shorter relative to the wetted period across sites with decreasing hydroperiod length. This attenuation of emergence time with hydroperiod is not seen in more widely distributed species. At short hydroperiod sites, the emergence of Type 2 long-hydroperiod species tends to be confined to late in the wet season and/or during high water periods. Therefore, their presence, abundance, species richness, and length of their emergence period at a site all may be used effectively as measures of biological response to changing hydropatterns at both long and short time-scales. These measures, as well as the relative richness and abundance of long- versus short-hydroperiod species, and hydroperiod-preference indices calculated from the preference scores listed in Tables 19 and 20,

represent a diversity of metrics that provide multiple perspectives of biological response to hydrological change.

For some species, emergence late in the wetted period may be due to life history strategies that result in seasonal development and emergence. Their classification as long-hydroperiod taxa reflects the prolonged wetting at longer-hydroperiod sites during the winter months (and therefore, greater relative abundance over a year). Though these seasonal species appear to respond more to hydroperiod timing than hydroperiod length, they can be effectively used to monitor hydroperiod length because of the highly seasonal nature of the annual hydrological cycles in the Everglades.

Species that do not prefer longer hydroperiods are somewhat difficult to categorize according to both their spatial dynamics and substrate affinity. The relationship between a species' substrate affinity and it's spatial stability becomes increasingly uncoupled in shorter hydroperiod habitats depending upon the nature and the spatial dynamics of the substrate preferred. Among short-hydroperiod species, *Beardius reissi* prefers certain grasses found in short-hydroperiod habitats (*Muhlenbergia, Schizachyrium*; Jacobsen and Perry 2000) and therefore, might be considered a Type 1 species. However, they may develop on other substrates and their populations can radiate to, and emerge briefly from, longer-hydroperiod sites – both of which are features of Type 2 species. Short-hydroperiod taxa such as *Pseudosmitta, Manoa, Paratendipes*, and *Dasyhelea* c.f. *atlantis* that prefer shallow water may be considered Type 2 species because they appear to be able to exploit shallow-water habitat at long-hydroperiod sites when they become seasonally available.

Among ubiquitous species, *Goeldichironomus natans/fluctuans* are closely associated with dead twigs and stems and can be considered to be a Type 1 species. Also, *Beardius breviculus* appears to be closely associated with *Cladium*, perhaps mining in senescent leaves. However, several species that are regarded as being either ubiquitous or preferring medium-hydroperiod habitats are strongly affiliated with blue-green algal mats (e.g., *Dasyhelea* c.f. *cincta*). Since algal mat development and disappearance can occur over short time-periods, they are perhaps best considered to be Type 2 species despite their substrate preferences.

Potentially useful indices for assessing biological response to changing hydrological conditions in the Rocky Glades and other Everglades marshes include:

(1) The proportion of all individual exuviae collected that represent long-hydroperiod species

(2) The number of long-hydroperiod species in samples

(3) The proportion of species in samples that prefer long-hydroperiod conditions

(4) The proportion of all individual exuviae collected that represent short-hydroperiod species

(5) The number of short-hydroperiod species in samples

(6) The proportion of species in samples that prefer short-hydroperiod conditions

(7) The ratios of the numbers of (a) individuals, and (b) species of long-hydroperiod species versus those of short hydroperiod species

(8) Community hydroperiod-preference indices based on a mean score for all exuviae collected

(9) Community hydroperiod-preference indices based on a mean score for all species collected

(10) Multivariate analyses of community composition that measure the relative conformity of the community composition at a site of interest to the mean or centroidal composition representative of a selected hydrological pattern.

(11) The numbers of exuviae collected, length of the emergence periods, and the proportion of the wetted period when emergence occurs, of select species that prefer long-hydroperiod environments such as *Tanytarsus* sp. C, *Polypedilum falciforme*, or *Paratanytarsus* sp. B.

(12) The numbers of exuviae collected, length of the emergence periods, and the proportion of the wetted period when emergence occurs, of select species that prefer short-hydroperiod environments such as *Beardius reissi, Paratendipes subequalis, Pseudosmittia sp, and Dasyhelea c.f. atlantis.*

The relative effectiveness of each of these indices in discerning different hydrological conditions needs to be examined in future investigations. Note that some indices require frequent sampling of midge communities over an entire wet season (e.g., 11 & 12) and, therefore, may be less practical than indices that require fewer samples. Indices that incorporate measures of the numbers of species and abundance of long-HP species (numbers 1, 2, and 3 above) may perform better than indices that incorporate short-HP species (4, 5, 6), because short-HP species may have different optimal habitats in

terms of hydroperiod length. *Beardius reissi*, an abundant short-HP species, increases in abundance with increasing hydroperiod length up to about 5 months; beyond 5-month hydroperiods, their abundance declines. Indices based simply upon the proportions of short-HP species, will tend to score sites with 5-month hydroperiods that have large emergences of *Beardius reissi* as being drier than sites with 3 month hydroperiods. On the other hand, this species' relationship with hydrology is well known, can be accounted for in these indices, and may even be used to estimate hydroperiod lengths below 6 months.

At this time, I feel the most reliable measures of hydrological conditions of those proposed above are: (1) The proportion of all individual exuviae collected that represent long-HP species; (3) The proportion of species in samples that prefer long-HP conditions; (9) Community hydroperiod-association indices based upon a mean score for all species collected, and (10) multivariate analyses that can measure the relative conformity of the midge community at a site of interest, to reference or 'target' communities. These indices do not require extensive sampling, only that samples be collected within a short time period (for comparative purposes) at strategic times during the wet season (e.g., end of rainy season).

V. EMERGENCE PHENOLOGY OF MIDGES ALONG HYDROPERIOD GRADIENTS

Introduction

Historically, the Florida Everglades was an extensive wetland system whose dynamic natural hydrological cycles and dependent food webs attracted and supported large numbers of wading birds and other vertebrate predators. Pronounced seasonal rainfall patterns generated annual cycles of wetland expansion and increased aquatic food web production during the summer rainy season, followed by concentration of prey and their exploitation by vertebrate predators when water-levels receded in autumn and winter.

Human activities over the past century, particularly canal construction, compartmentalization of the northern Everglades and redirection of flow into the park from levee construction, as well as poor management of water levels and flow within the existing system, have disrupted the natural dynamics of the Everglades and reduced its capacity to support wildlife (Gunderson and Loftus 1993). The higher portions of the eastern Everglades such as the Rocky Glades (RG) have experienced substantially shorter and more unnatural hydroperiods (in terms of their flooding duration and drydown frequency) since hydrological flow patterns throughout the Everglades were altered by drainage and canal construction. Construction of the L-67 levees and canals which divert water to western Shark Slough have particularly reduced water levels in northeast Shark Slough which borders the Rocky Glades (Loftus et al., 1986). Correlated reductions in water levels in the Rocky Glades have likely reduced invertebrate species abundance and species richness there (Loftus et al., 1992).

There are tentative plans to change water releases into Everglades National Park with the aim of restoring hydropatterns in the RG to regimes closer to those which existed prior to drainage and levee construction. Information on the responses of invertebrate communities to changes in hydroperiod is needed to assess the effects of present reduced and atypical water allotments into the RG and to model invertebrate response to changes in hydrological regimes in the future.

Midges (flies in the families Chironomidae and Ceratopogonidae) are the most species rich and abundant component of the Everglades macroinvertebrate community (King 2001, Rader 1994, Rader and Richardson 1994, Turner and Trexler 1997). With over 160 species collected from within Everglades National Park, midges comprise 30-40% of the total macroinvertebrate species richness in the

Everglades (Jacobsen and Perry 2000a). They are a major component in the Everglades food web, linking plant, algal, and microbial production to higher trophic levels.

Review of previous midge-hydroperiod research

In our previous research on midge communities in the Rocky Glades and adjacent sloughs, we found, through cluster and detrended correspondence analysis on total community composition data, that midge community composition differs considerably between sites with different hydropatterns. Compositional changes were most pronounced between long-hydroperiod (>10 month hydroperiod) slough and gator hole habitats and neighboring marl prairie habitats (< 10 month hydroperiods). Differences between slough and marl prairie habitats were largely due to hydroperiod-related differences in substrates and vegetation. Compositional differences were also found between MHP and SHP sites within marl prairie habitats. Short-hydroperiod sites harbored several abundant species with adaptations for surviving the harsh conditions at these sites (e.g., *Beardius reissi*, Jacobsen and Perry 2000b), suggesting that hydrological factors may directly limit community species composition in short hydroperiod areas.

Species rank/abundance curves for pooled long-hydroperiod (LHP) sites were also notably different from those of pooled medium-hydroperiod (MHP; hydroperiod of 8-10 months) sites and pooled short-hydroperiod (SHP; hydroperiod of 4-8 months) sites, suggesting that niche-space allotment at LHP sites was fundamentally different than in the marl prairie. Long-hydroperiod sites supported large numbers of relatively rare species, many of which are strongly associated with fine peat substrates and plant species found at these sites. Species rank/abundance curves for pooled MHP and pooled SHP sites were very similar, perhaps reflecting the prominent role that calcareous blue-green algal mats have in both habitats.

Mean community abundance (mean numbers of midges collected per monthly 10-minute CPUE sample) and cumulative species richness (total number of species collected in monthly samples over a year) increase with increasing hydroperiod length/water depth. Sample species richness generally increased with hydroperiod length and was highest at LHP sites. Sample species richness at marl prairie sites increases with water levels and approaches the richness levels found at LHP sites during high-water

periods. However, the similarity in species/rank curves between SHP and MHP marl prairie sites raises some questions about species richness – hydroperiod relationships in the marl prairie. Do shorter hydroperiods actually limit the composition and species richness of emerging midges? Or are declines in species richness simply an artifact of lower midge production, and consequently, fewer midges collected, in short hydroperiod areas?

To more closely examine the relationship between hydrological conditions and midge community richness, we examined the emergence phenology of midge communities at sites along hydroperiod transects in the Taylor Slough basin and Shark Slough basin near Pa-hay-okee over the course of the 1999-2000 wet season. Our intent was to investigate both community structural changes, as well as the responses of individual species, along hydroperiod gradients through the wet season. With respect to community-level responses, or specific objectives were:

1) *To more precisely estimate actual species richness at these sites.* By sampling surface-floating pupal exuviae, and sampling frequently, one can capture more rare species that would be missed by monthly sampling or conventional benthos sampling.

Total species richness = (Maximum sample richness + seasonal turnover) – rare species missed

2) *To determine if, and to what extent, there is a seasonal component to species richness in the Everglades.* Species richness (total number of species that a site produces over a year) at a site can be thought of as having (a) a maximum spatial component and (b) a temporal or seasonal component:

Total species richness = Maximum available niche space at a point in time + temporal niche space
(Maximum species richness at a point in time) (seasonal sp. turnover)

In temperate systems, seasonal changes in light, temperature, and food or substrate availability allow for a larger number of species to coexist than would be possible without this seasonality. In the Everglades, the degree to which seasonality contributes to species richness, and how this might be affected by hydroperiod, is not well known.

3) *To determine patterns of sample species richness, diversity, and species composition, and their relationship with hydropattern through time, in order to determine optimal times and schedules for midge sampling.*

Frequent sampling of sites along hydroperiod transects allows one to examine the response of individual species to hydropatterns. Our species-level objectives were:

1) To determine which species show seasonal emergence.

2) To determine how emergence phenologies across hydroperiod gradients differ between species categorized in our larger-scale hydroperiod study as preferring either "long-hydroperiod" or "short-hydroperiod" habitats, as well as those species that are ubiquitous .
3) To examine relationships between a species emergence periods and hydrological and hydrologically-related variables.
4) To detect species that may be able to resist desiccation. Species that emerge shortly after rewetting and that show strongly synchronous emergence afterward are likely to have adaptations, such as aestivation as larvae or pupae, that enable them to survive seasonal drydown.

Methods

Study sites

The hydroperiod transects sampled for this study are situated along the periphery of the eastern Rockland marshes, or Rocky Glades, region of Everglades National Park. The slightly higher elevations in the Rocky Glades cause marshes in this region to have naturally shorter hydroperiods than those found in neighboring Shark River Slough and Taylor Slough. As a result, the marl prairie marshes here have had little hydric soil development, and solution and weathering of the oolitic limestone bedrock has produced an uneven surface topography with shallow patchy soils found primarily in numerous solution holes and depressions. Marl prairie plant communities are consequently diverse and patchy, with *Cladium jamaicense* Crantz often a co-dominant with *Schoenus nigricans* L., *Panicum tenerum* Beyr., *Spartina bakerii* Merrill, *Schizachyrium rhizomatum* (Swallen), and *Muhlenbergia filipes* M. A. Curtis (Gunderson and Loftus 1993). During the wet season, bottom substrates and submerged plant stems develop thick periphyton growth comprised primarily of calcareous, filamentous blue-green algae.

Prior to development of the current water management system in south Florida, summer rainfall and sheet flow from Shark River Slough are believed to have maintained 8-10 month hydroperiods over most of the Rocky Glades (Fennema et al. 1994). Construction of canals through the Atlantic Coastal Ridge, compartmentalization of the northern Everglades, and redirection of water away from northeast Shark River Slough have lowered water tables in the Rocky Glades as much as 50 cm and have reduced hydroperiods to approximately 3-7 months in length (Loftus et al. 1992; Fennema et al. 1994). Consequently, transects extending 1-2 miles from neighboring sloughs into the Rocky Glades today, may cross through a variety of marl

Table 21. Location, and description of soils and plant communities at sampling sites along hydroperiod transects in Shark River Slough basin and Taylor Slough basin

Watershed	Site	Location	Descriptive location	Soil types	Soil depth Mean+SE	Dominant vegetation
Shark R. Slough	PAH	25 25' 55" N 80 46' 38" W	10 m E of Pa-hay-okee Road, 200 m N of FL 9336	marl, peat	27±4 cm	*Eleocharis. Cladium*
Shark R. Slough	WRR	25 26' 00" N 80 45' 27" W	20 m N of FL 9336, 400 m W of Rock Reef Pass	marl	16±3 cm	*Cladium*
Shark R. Slough	RRP	25 25' 59" N 80 44' 14" W	20 m N of FL 9336, 500 m E of Rock Reef Pass	rock, marl	13±5 cm	*Schizachyrium, Muhlenbergia, Cladium*
Taylor Slough	MTS-1	25 24' 05" N 80 36' 25" W	Taylor Slough N of bridge, near USGS hydrostation TSB	peat, marl	32±5 cm	*Cladium* (tall form), *Eleocharis; Salix, Nymphaea in vicinity*
Taylor Slough	MTS-3	25 24' 16" N 80 36' 39" W	20 m N of FL 9336, 150 m WNW of Taylor Slough bridge	marl	46±3 cm	*Cladium*
Taylor Slough	MTS-5	25 24' 32" N 80 37' 10" W	30 m N of FL 9336, 1.2 km WNW of Taylor Slough bridge	marl, rock	11±1 cm	*Cladium, Muhlenbergia*
Taylor Slough	MTS-7	25 25' 03" N 80 38' 21" W	10 m NE of USGS hydrostation NTS14	rock, marl	3±1 cm	*Muhlenbergia, Schizachyrium, Cladium*

prairie and rockland marsh plant communities with annual hydroperiods ranging from 3 – 12 months.

Sampling was conducted at 7 sites along 2 hydroperiod gradients in the Rocky Glades: 3 sites on the eastern edge of Shark River Slough basin, and 4 sites within the Taylor Slough basin. Sites were selected on the basis of the hydropattern-indicative plant communities that they supported, and collectively, were intended to cover a hydroperiod range of from <5 to >10 months in each transect. Table 21 lists the location of these sites and summarizes their plant communities and soils present. All sites except MTS-1 had primarily marl or rock soils, and were located within spatially large and uniform plant communities. MTS-1, located in the 20 m wide main channel of Taylor Slough north of FL 9336, has a variety of primarily peaty-soil habitats in

the vicinity, including tall *Cladium* stands, *Eleocharis*-dominated wet prairie, willow heads, and alligator holes. Sampling there was performed along a narrow, wood strewn pathway through tall *Cladium* bordered by wet prairie.

To determine the temporal pattern and abundance of midge emergence, samples of surface-floating pupal exuviae were collected at 7-10 day intervals from the onset of rewetting on the marl prairie in June until September, and then at 10-14 day intervals from September until drydown had occurred at all marl prairie and Rocky Glades sites. This design allowed us to examine midge community response to both temporal and spatial changes in hydrological conditions. Tropical storm and hurricane activity in Everglades National Park briefly delayed sampling during September and October. Sampling of surface-floating midge pupal exuviae was performed, according to USEPA protocols (Ferrington 1987b, Ferrington et al., 1991), with slight modification, by skimming the water surface for 10 minutes with a 3-quart pot, and concentrating the collected exuviae with a 125μm opening sieve. All pupal exuviae collected in samples were identified to the lowest taxonomic level possible - usually to species, but in a few instances where different species could not always be reliably separated, to species groups. Morphospecies designations were given to distinct taxa that could not be associated with current described species. Identification was typically performed at 40X with a dissecting microscope, with occasional spot-checking of specimens under a compound microscope. Slide-mounted specimens of all taxa have been deposited in the South Florida Collections Center.

Hydrological data was collected at each site by measuring water depth at "benchmark" stakes in order to develop linear regressions of water depth against stage height measurements recorded from nearby USGS hydrological monitoring stations. To estimate the onset of inundation and percent inundation during low water periods, the surface topography at each collection site was determined by taking water depth measurements at 100 points along a 10 m x 10 m grid overlaying the area where exuviae samples were collected. Rewetting and zero water depth was determined to occur when site water levels estimated from USGS stage heights reached a level whereby 1% of the surface at a site would be underwater. Water temperature, pH, dissolved oxygen, and conductivity adjusted to 25° C were measured during each site visit using a YSI field meter. Water temperature was recorded at long and short-hydroperiod sites using a temperature data-logger.

Species were assigned to hydroperiod preference categories based upon the ratio of their mean relative abundances at long-HP and short-HP in an extensive prior survey. Species that had more than 5 times greater mean relative abundance at long-HP sites than at short-HP sites, were considered to prefer long-HP habitats. Likewise, species whose mean relative abundance was more than 5 times greater at short-HP sites were considered to prefer short-HP habitats. Species with intermediate ratios of relative abundance were considered to be ubiquitously distributed with no hydropattern preference. Listings of chironomid and ceratopogonid taxa in each category are provided in Tables 19 and 20 in the previous section.

Results

Hydrology

The numbers of wetted days, and longest continuously wetted periods for each year from 1990-1999, for each site are listed in Table 22. Mean hydroperiod lengths among the Shark River Slough basin transect sites from 1995-1999 ranged from 4.8 months at RRP, to 9.6 months at PAH. Mean hydroperiods during this time period at Taylor Slough basin sites ranged from 3.5 months at MTS-7, to 11.5 months at MTS-1.

Midge community response

The total numbers of individuals and species of midges collected at each site are given in Table 23. The total numbers of species of all midges and chironomids increased with increasing hydroperiod length along each transect. More species of Ceratopogonidae were found at shorter HP sites than at longer HP sites in the Taylor Slough basin.

Whittaker plots of ranked abundance for all Rocky Glades and Marl sites appear to share features of both log normal and log series distributions, but show an atypically large number of rare taxa that increases with hydroperiod length. This was particularly true at MTS-1, where nearly 50% of the species (38 of 78 species) had relative abundances under 0.1%. Slopes of curves for midge communities at marl prairie (including PAH) and Rocky Glades sites were quite similar, and were steeper (showing less even distribution) than the curve for MTS-1 (Fig. 20).

Table 22

Table 23. Total numbers of individuals and species of Chironomidae, Ceratopogonidae, and both midge families combined, in surface-floating pupal exuviae samples collected from sites along hydroperiod transects in Shark River Slough basin and Taylor Slough basin during the 1999-2000 wet season.

Site	No. midge pupal exuviae collected	No. spp.	No. Chironomidae exuviae	No. spp.	No. Ceratopogonidae exuviae	No. spp.
Shark R. Slough Basin						
PAH	20,695	59	15,256	48	4,981	11
WRR	14,782	56	12,913	46	1,869	10
RRP	10,393	39	8,622	32	1,768	7
Taylor Slough Basin						
MTS-1	16,849	78	12,143	69	4,706	9
MTS-3	12,159	57	7,095	49	5,064	8
MTS-5	14,558	53	9,992	41	4,565	12
MTS-7	2,993	45	1,732	33	1,261	12
Total	92,429	89	67,753	71	24,214	18

Long-hydroperiod sites in both watersheds showed rapid increases in cumulative midge species richness (both Chironomidae and Ceratopogonidae combined) after rewetting up to August, and then very gradual species accumulation over the remainder of the wet season (Fig. 21). Cumulative species plots for intermediate-hydroperiod sites (WRR, MTS-3, MTS-5) were more linear, with new species appearing steadily well into December. Short-hydroperiod sites had similar linear rates of increase in cumulative richness, except they were interrupted by a dry period in August and underwent drydown in early winter.

The number of midge species in individual samples at SRSB sites, and TSB marl prairie and Rocky Glades sites were correlated with their water depths (for samples collected after 30 days of rewetting with water depth >15 cm: $r = 0.6278$, $N = 47$, $P<0.0001$). These correlations weakened but persisted even when all samples collected during shallow water periods (<20 cm) were excluded from analysis ($r = 0.4365$, $N = 41$, $P=0.0043$), suggesting that these correlations may not have been an artifact of lesser sampling effectiveness during low water periods. MTS-1 species richness was significantly correlated with depth even though all water depths on sampling days 30 days of rewetting were above 40 cm ($r = 0.64668$, $N = 22$, $P = 0.0011$)

Samples from MTS-1 yielded more species than all other sites in both SRSB and TSB transects on all but 3 sampling dates. MTS-1 species richness reached 31 species less than 3 weeks after rewetting, and ranged from 30-40 species per sample from August into January. Longer-hydroperiod marl prairie sites (PAH, MTS-3) exceeded shorter-hydroperiod Rocky Glades sites in sample species richness during the first 3 months after rewetting. After September, sample species richness at intermediate-HP and short-HP marl sites approached, and even surpassed (e.g., WWR), those at longer-HP marl sites. All sites peaked in species richness during the high water period after Hurricane Irene in October or November.

Numerical species richness (rarefaction to 100 exuviae) and Shannon-Wiener diversity patterns for each site were similar to sample species richness patterns, but show even less separation between sites after September. Large synchronous emergences of *Beardius reissi* produced brief drops in diversity during the summer at shorter hydroperiod sites (MTS-5, MTS-7, RRP). Zero diversity values at MTS-7 in late July and August are due to drydowns.

Cumulative species richness of Chironomidae rapidly exceeded sample species richness at long-HP sites shortly after rewetting (Fig 22). This relationship between cumulative and sample richness becomes increasingly less divergent at progressively higher elevations such that, at the shortest-HP sites, sample species richness remains almost equivalent to cumulative species totals until water levels peak in October. Divergence of curves during high emergence periods after water levels peaked (October – December at SRSB sites and MTS-7; October-February at MTS-1, 3, and 5) represented appearance of rare taxa, seasonal turnover, and cessation of emergence of certain long-HP species coincident with falling water levels (SRSB).

Plots of the percent occurrence of rare species (species with a total relative abundance <0.1% at a given site) at sampling sites over the wet season indicated that emergence of rare taxa at long-HP sites occurred throughout the wet season, but may be highest in the first month after rewetting (Fig. 23). At increasingly higher elevations, the emergence of rare species occurred progressively later in the wet season and, at the shortest-HP sites, coincided with high, and then receding, water levels in the fall. These patterns did not change when the criteria for

rarity was relaxed to <0.2%. Rare species appearing at short-HP sites after September tended to be long-HP species, including seasonal species with fall and winter emergence.

The numbers of individuals and species of Chironomidae collected in each hydroperiod-preference category at each site through the wet season are shown in Figures 24 and 25. Long-HP species were present, and usually well represented at long-HP sites throughout the wet season. Long-HP species with apparent seasonal emergence patterns, were particularly abundant at MTS-1 during winter. At increasingly higher elevations and shorter hydroperiods, long-HP species were fewer, less abundant, and appeared increasingly later in the wet season. Ubiquitous species such as *Labrundinia neopilosella*, *Cladotanytarsus* spp., and *Tanytarsus* sp. D, dominated the chironomid emergence at long-HP sites (PAH, MTS-1) and marl prairie sites (MTS-3, WRR). A few short-HP species were usually emerging at all sites throughout the wet season. The strong dominance of short-HP species at higher elevation sites in summer is due primarily to large synchronous emergences of *Beardius reissi.*

Chironomini were usually the dominant chironomid taxonomic group in species richness at all sites, followed closely by Tanytarsini and Tanypodinae, in samples grouped by month (Fig. 26). Chironomini were most abundant at short-HP sites, where *Beardius reissi* show large synchronous emergence during the summer (Fig. 27). Tanypodinae and Tanytarsini were most numerous at longer hydroperiod sites along each transect; Tanypodinae were notably reduced, and Tanytarsini were absent, at short-HP sites during the first 1-2 months after rewetting. Pseudochironomini were most abundant at marl prairie sites (WRR and MTS-3), and consisted almost exclusively of synchronously emerging populations of *Pseudochironomus* c.f. *articaudus.* Though only 6 species of Orthocladiinae were collected in this study, the subfamily is well represented at all sites, with *Parakiefferiella coronata* and *Pseudosmittia* sp. present throughout the year, and *Corynoneura* spp. showing large emergence during the late fall and winter.

Phenology of midge species

Table 24 lists the mean depths, mean emergence times, and hydroperiod preferences of all midges collected wthin the Taylor Slough basin. Hydroperiod preference categories were correlated with days since rewetting ($r = 0.3181$, $N = 84$, $P = 0.0032$), and weighted mean water depth at emergence ($r = 0.5329$, $N = 84$, $P < 0.00001$), but showed a weak relationship with mean date of emergence ($r = 0.19516$, $N = 84$, $P = 0.0752$). This weak relationship of hydroperiod category with emergence date is likely due to species that emerged shortly after rewetting, and then emerged again during the winter

Comparisons of the emergence phenologies of different species, and their response along hydroperiod gradients, revealed several distinctive emergence patterns among midge species. These emergence patterns provide a degree of insight into their biology and how their distributions may be indicative of hydrologic conditions. Below, I list and describe these distinctive emergence patterns and offer examples of species that show these patterns.

Type 1: Ubiquitous species – Ubiquitous species emerge continuously throughout the wet season in habitats with a wide range of hydroperiods. They may start emerging as early as 15 days after rewetting, but they show no obvious, large initial emergence or subsequent population synchrony that would suggest that they are resistant to desiccation and able to pass through the dry season. Many species are small, abundant, and are likely to be rapid dispersers with very short life-spans. Therefore, many have characteristics of "r-selected" species in life history theory. *Tanytarsus* sp. D (Fig. 28) and *Labrundinia neopilosella* (Fig. 29) are representative species.

Type 2: Synchronous, desiccation-resistant (?) species – For these species, emergence occurs shortly after rewetting, is highly synchronous, and subsequent emergences remain well synchronized throughout the wet season. This pronounced periodicity, with time intervals between emergence periods that are clearly longer than the interval of time from rewetting to their initial emergence, suggests that the immature stages are resistant to desiccation. The most dramatic examples of species with this type of emergence pattern are *Beardius reissi* (Fig. 30) and *Pseudochironomus* c.f. *articaudus* (Fig. 31). *Beardius reissi* starts to emerge approximately

10 days after rewetting. Subsequent emergence peaks occur every 5-6 weeks through the summer until emergence ends in October. Larvae are frequently collected from November until drydown, but no emergence occurs until the next wet season. *Paratendipes subequalis* may also show this emergence pattern (Fig. 32), but intervals between peaks may have also been caused by deep waters inhibiting emergence. *Polypedilum trigonus* may also be desiccation resistant, but their populations become asynchronous after the first or second emergence (Fig. 33).

Type 3: Shallow water, short-hydroperiod species – For shallow water, short-hydroperiod species, emergence occurs throughout the wet season at short-HP sites, but tends to be limited to shallow water periods at the beginning and at the end of the wet season at longer-HP sites. These species appear to require some habitat feature of, or derive some competitive benefit associated with, shallow waters, or they are inhibited by conditions in deep waters. *Paratendipes subequalis* (Fig. 32), *Pseudosmittia* sp. (Fig. 34) and *Dasyhelea* c.f. *atlantis* (Fig. 35) are examples. All are considered to be short-HP species in Everglades National Park.

Goldhammer and Ferrington (1992) found a strikingly similar community ("*Paratendipes subequalis*, *Dasyhelea mutabilis* gr. sp., and *Pseudosmittia* sp.") in epirheic capillary fringe habitats subject to high temperature (35° C) along the Cimarron River in Kansas. Ferrington (1987a) suggested that *Paratendipes subequalis* was adapted to withstand high temperatures much like its sister species, *P. thermophilus*, which is found along the margins of desert hot springs.

Type 4: Shallow water, long-hydroperiod species – These species were found to emerge from shallow waters in peaty habitats. Emergence occurs at the beginning of the wet season at long hydroperiod sites (e.g., *Chironomus* sp. B). These species may also emerge at the end of the wet season when water depth is low, and perhaps be able to survive a 2-3 month drydown within moist, peaty sediments

Type 5: Long-hydroperiod, deep water, aseasonal species – These species have long emergence periods at long-HP sites, but their emergence periods become strongly attenuated at shorter hydroperiod sites and coincide with maximum water depth at these sites. Emergence appears to occur only when water levels are above a certain minimum depth. Some feature of

the environment that is associated with water depth - possibly temperature, current, growth of certain algal species they feed upon, or protection from ultraviolet radiation – appears critical for their development and emergence. *Zavreliella marmorata* (Fig. 36) and Ceratopogonidae sp. G (Fig. 37) show this emergence pattern.

Type 6: Fall and winter seasonal species – These species show large emergences during the fall and winter. These species may not show a preference for water depth, but because longer-HP sites stay wet longer into the fall and winter, the relative abundance of these species will be greater at long-HP sites than at short-HP sites. *Corynoneura* sp. A (Fig. 38), *Corynoneura* sp. B (Fig. 39), and *Cryptochironomus* sp. B are examples.

Type 7: Summer seasonal species – Species that show emergence only during the summer. *Beardius reissi* (Fig. 30) fits into this category.

Community succession

Detrended correspondence analysis (DCA) of community succession (Figs. 40-44) along the Taylor Slough transect show, first of all, the general dissimilarity and differences in the successional tracks between the midge community at MTS-1 (which has primarily peaty substrates) with midge communities in the marl prairie and Rocky Glades. However, successional tracks of marl prairie and Rocky Glades sites are very similar, and these sites and MTS-1 converge in ordination space during high water periods. This convergence appears to be due to: (1) the influence of large emergences of ubiquitous species such as *Dasyhelea* c.f. *cincta* on their position in ordination space, (2) cessation of emergence of short-HP species such as *Beardius reissi*, and (3) the appearance of spatially dynamic long-HP species (Type II species) at marl prairie and Rocky Glades sites.

The initial community at MTS-1 was comprised of species with a variety of emergence patterns, but had a notably large number of rare taxa (e.g., *Labrundinia* sp. 6/10 Roback, *Labrundinia* sp. B Epler) and species that inhabit fine, organic sediments (*Chironomus* sp. B, *Chironomus* (*Lobochironomus*) sp., *Cladopelma* sp. A). Presumably, the combination of rich, organic soils and shallow water provide favorable environmental conditions for development and emergence.

The midge community during the initial months of the wet season at MTS-3 (marl prairie) was comprised of both shallow water species (*Pseudosmittia* sp.), desiccation-resistant synchronous emergers (*Pseudochironomus* c.f. *articaudus*), and ubiquitous species. Rocky Glades sites (MTS-5 & 7) were initially dominated by desiccation-resistant species (*Beardius reissi*), and later by shallow-water, short-HP species (*Paratendipes subequalis* and *Dasyhelea* c.f. *atlantis*), and ubiquitous species. The large, periodic, synchronous emergences of *Beardius reissi* during the summer cause these sites to oscillate in ordination space

Convergence of all sites during high-water periods (September-November) is due to: (1) increased prominence of ubiquitous species, many of which are associated with periphyton (*Dasyhelea* c.f. *cincta*, *Labrundinia neopilosella*, *Ablabesmyia* spp., *Parakiefferiella coronata, Cladotanytarsus* spp.); (2) decline and cessation of emergence in *Beardius reissi* and other short-

Figure 40. Midge community succession at MTS-1 (black triangle) relative to succession at other Taylor Slough basin sites (gray symbols) in DCA ordination space through the 1999-2000 wet season. Numbers next to triangles represent the sequence (sampling date) in which they were collected.

Figure 41. Midge community succession at MTS-3 (black triangle) relative to succession at other Taylor Slough basin sites (gray symbols) in DCA ordination space through the 1999-2000 wet season. Numbers next to triangles represent the sequence (sampling date) in which they were collected.

Figure 42. Midge community succession at MTS-5 (black diamond) relative to succession at other Taylor Slough basin sites (gray symbols) in DCA ordination space through the 1999-2000 wet season. Numbers next to triangles represent the sequence (sampling date) in which they were collected.

Figure 43. Midge community succession at MTS-7 (black dot) relative to succession at other Taylor Slough basin sites (gray symbols) in DCA ordination space through the 1999-2000 wet season. Numbers next to triangles represent the sequence (sampling date) in which they were collected.

Figure 44. Positions of midge species in DCA ordination space superimposed upon the positions of samples from all sites collected in the Taylor Slough basin during the 1999-2000 wet season

HP species; and (3) appearance of deep-water long-HP species (*Zavreliella marmorata*), and then fall-winter emerging long-HP species. Convergence in ordination space occurs increasingly later at progressively higher elevations – i.e., they converge in sequence according to their hydroperiod length.

Divergence later in the fall represented: (1) differences in distributions of seasonal species, presumably related to differences in soils and plant communities present at MTS-1 versus those at marl prairie and Rocky Glades sites; and (2) declines in deep-water long-HP species at marl prairie and Rocky Glades sites with drops in water levels (Ceratopogonidae sp. G, *Nimbocera* sp. A, *Zavreliella marmorata*).

Discussion

Hydroperiod clearly affects midge community composition. It is the primary determinant of plant communities in the Everglades, and plants represent a important dimension of the habitat template to which the midge community responds. Species such as *Endotribelos hesperius*, *Polypedilum nymphaeorum*, *Beardius breviculus*, and *Beardius reissi* show strong associations with different plant communities that are affected by hydrology. Other features of Everglades habitats that are hydrologically related, such as peat formation, presence of woody debris (*Salix*), *Utricularia* growth, and *Utricularia*/periphyton mat production, determine the distributions of midge species in the Everglades.

Hydrological and hydrologically-related features likely determine the initial emerging constituents of the community. Short-HP sites are initially dominated by species with physiological adaptations for withstanding desiccation and heat (e.g., *Beardius reissi*, *Paratendipes subequalis*), and these species remain significant components of the community over most of the wet season except when water levels are high. Long-HP sites produce species that utilize moist, peaty environments (*Chironomus* sp. B). Initial differences in community composition are even expressed among major taxonomic groups of midges, with Tanytarsini and Tanypodinae being conspicuously rare or absent at short-HP sites for 1-2 months after rewetting.

The initial differences in midge community composition relax through time, particularly during high water periods. This convergence appears to be due to dispersal and successful emergence of taxa characteristic of long-HP sites at short-HP sites during high water levels. At the same time, emergence of short-HP species appears to be depressed during these periods. Communities begin to diverge again when water levels begin to fall during the late fall and winter. Collectively, this suggests that midge communities are strongly affected by hydrological conditions.

Changes in slopes of Whittaker plots, differences in species richness, and relative positions and successional tracks of midge communities in ordination space largely corroborate observations from midge community surveys in 1998-1999, that there is a major shift in midge community structure when hydrological conditions become sufficient for slough plant communities to succeed, and peat formation to occur. MTS-1 communities were more evenly distributed and supported an inordinate number of rare taxa relative to species distributions typically seen in nature. The midge community there included a variety of species associated with peaty soils; taxa associated with periphyton on *Cladium* and, along the periphery of this site, Eleocharis; and species associated with relatively rare habitats present at long-HP sites such as wood, Nymphaea, Sagittaria, etc.

Whittaker plots for marl prairie sites show that their midge communities are not as rich and as evenly distributed as MTS-1. However, like MTS-1, they are dominated by a few abundant species, and have a large number of rare taxa. To determine whether hydroperiod affects community species richness in the marl prairie and Rocky Glades, sampling programs and methodologies need to address this feature (numerous rare species) of the community. Measures of species richness also have to be sensitive to this characteristic of these assemblages.

Sampling surface-floating pupal exuviae following EPA protocols (10 minute catch-per-unit effort sampling) developed for streams, is an excellent and efficient method for collecting large quantities of midges from all microhabitats simultaneously, increasing the likelihood the collector will encounter rare taxa. Ten-minute CPUE sampling yielded over 10,000 exuviae from

6 of the 7 sites sampled, and collected many taxa with relative abundances < 0.1%. Therefore, it provides an excellent picture of community composition at each site, and how it changes over the course of the wet season. Problems arise, however, when estimating community areal species richness from these collections, because the effective area sampled may vary with water depth. Sample abundance and species richness at all sites correlate with water depth. These increases in species abundance and richness seem reasonable, since increased water levels in these habitats, with their extensive emergent macrophyte growth, effectively increased the surface area of inhabitable substrate, and presumably increased available niche space as well. MTS-1 sample species richness correlated with depth, even though water depth on almost all days sampled was adequate for efficient sampling. However, at other sites, these correlations weakened, and in some instances, disappeared, when low water samples are excluded from analyses. This variation in the areal surface sampled may actually be small, but it is undeterminable, and therefore, becomes problematic in linking increased species richness with water depth. One can say, though, that more species are collected when water levels are high.

Slopes of cumulative species richness curves for marl prairie and Rocky Glades sites (all medium-HP and short-HP sites) were approximately equal. Breaks in slopes at MTS-7 may reflect hydrological conditions, but they may also be due to a sampling effect, i.e., an inefficiency of sampling emerging midges during low or, in this case, no water.

Richness comparisons using rarefaction (or numerical species richness) suggest that, after a couple of months have passed since rewetting, and water levels are high, there is little difference in richness between sites. Unfortunately, the degree to which rarefaction can express the contributions of rare species to overall community richness is limited by the size of the smallest sample (in this study, the cutoff was 100 individuals). If there is a large discrepancy in sample size, rarefaction essentially becomes a measure of diversity. Numerical species richness plots were very similar to those for Shannon-Wiener diversity.

So far, measures of community richness suggest that community structure is similar at marl prairie and Rocky Glades sites if one accounts for differences in the time of initial rewetting. Species richness may increase with water depth, but this may be confounded by a sampling

effect. However, comparisons of the relationship between cumulative species richness and sample species richness, and of the percent occurrence of rare taxa in samples, between sites along transects, revealed an important pattern in midge community organization that is related to hydropattern. The reduced divergence of cumulative species richness curves from sample richness curves, and the low occurrence of rare species at short-HP sites until water levels rise in October, indicated that with increasing elevation: (1) the community becomes comprised almost entirely of short-HP and ubiquitous species during the first four months, the occurrence of rare species is minimal; (2) community richness estimates from sample species richness were more accurate for these short-HP sites than for longer-HP sites - lower cumulative species richness values at short-HP sites are not attributable to inadequate sampling; and (3) increases in species richness with increasing depth at short-HP sites are real relationships and not an artifact of the sampling procedure used. Rare species do not appear at short-HP sites until water levels rise in September and October. At that time, species characteristic of long-HP sites begin to emerge, including species associated with deep water (e.g., *Zavreliella marmorata*, Ceratopogonidae sp. G), and seasonal species (*Corynoneura* spp.).

Everglades midge communities appear to be highly dynamic in response to hydrological changes over the wetted season. The initial distribution of midge species upon rewetting appears to be related to the relative severity of different habitats during the dry season. Rewetting initiates a dynamic process whereby midge populations disperse and expand with expanding suitable habitat. Gravid females disperse from sloughs, or in some instances (e.g., *Beardius reissi*), into sloughs, and lay eggs in these recently inundated areas. Successful development and emergence of long-HP species appears to be dependent upon hydrological conditions such as water depth, or on other factors affected by hydrology. These factors may include: protection from UV radiation, reduced thermal stress, increased current, and increased growth of preferred foods (e.g., filamentous green algae). Increasing hydroperiods and water depths in the marl prairie and Rocky Glades should increase species richness at any given site by: (1) allowing emergence of late seasonal species, (2) attracting more gravid females dispersing from sloughs, (3) and by providing a more suitable habitat for long-HP species to develop and emerge.

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