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Hydroecological monitoring of benthic invertebrate communities of marsh habitat in the upper and middle St. Johns River

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Biological Sciences

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Abstract Monitoring of benthic invertebrate communities in aquatic ecosystems has been used to evaluate a variety of environmental effects, including changes in hydrology. As part of a hydroecological assessment of the St. Johns River, FL, we studied invertebrate communities of shoreline and floodplain marsh habitats at locations in the middle and upper St. Johns River. A total of 112 invertebrate taxa were identified. Most were aquatic insects in the orders Odonata, Hemiptera, Coleoptera and Diptera. We examined a variety of metrics of invertebrate community structure and a surrogate measure of ecosystem function. Some of these metrics displayed patterns that could be related to hydrology. Preliminary sampling in floodplain marsh habitats with varying duration of inundation suggested some hydroecological patterns; relative abundance of taxa indicative of more permanent aquatic habitats (Ephemeroptera and Amphipoda) had a positive relationship with duration of inundation. Taxa able to undergo diapause during dry periods (Oligochaeta), those able to disperse to new habitats (Diptera, Coleoptera), and those with short life cycles adapted to temporary habitats (Diptera) had negative relationships between relative abundance and duration of inundation. We propose three new metrics that may be useful for future monitoring.

Keywords Bioassessment, Florida, hydroecology, macroinvertebrate, St. Johns River, wetland invertebrate communities

Introduction

The St. Johns River is a low gradient, hardwater, colored river in northeast FL, USA. Approximately two thirds of the 499 km length of the river lies at or near mean sea level, giving it a more lentic character than most other southeastern US river systems. The river is a former coastal lagoon, and has many "in-line" lakes, which are widened portions of the river channel. The river supports a moderately diverse benthic invertebrate community; to date a total of 1,063 taxa of freshwater, estuarine and marine invertebrates have been collected and identified from the system (Mattson et al. 2012).

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The river has been identified as a potential source of potable water to supplement groundwater withdrawals, which have traditionally been the main water source for communities in the region. Increased groundwater pumping over the past 60 years is now reaching the limits of sustainability for the Floridan Aquifer, the principal groundwater source, and thus alternative sources, such as surface water withdrawals from the river, are being considered (SJRWMD 2006). To develop tools to evaluate the potential impacts of surface water withdrawals, the St. Johns River Water Management District (SJRWMD) undertook a comprehensive hydroecological investigation of the river, beginning in 2007, to evaluate relationships between river hydrology and ecological responses. This investigation included evaluation of hydrology and hydrodynamics (both river and estuarine, using empirical data and modeling), water quality, phyto- and zooplankton communities, fish populations, floodplain wetland plant and wildlife communities, soil biogeochemistry, submerged aquatic vegetation, and benthic invertebrate communities.

Monitoring of benthic invertebrate communities (benthic communities) of lakes, rivers and wetlands has been used to assess the effects of environmental drivers such as water quality, hydrology, and habitat (Rosenberg and Resh 1993, Davis and Simon 1995). There are no long-term monitoring data on benthic communities of the St. Johns River, but a few short-term ($\leq$ 1 year) studies conducted on benthic communities in freshwater regions of the river were completed (the middle and upper reaches of the river, reviewed in Mattson et al. 2012). Therefore, the data available to evaluate relationships between hydrology and benthic communities were very limited. Previous studies were mostly conducted on the benthic communities of the main river channel bottom, sampling with various dredge-type samplers (mostly petite ponar grab). Based on our (R. Mattson, K. Cummins, and R. Merritt) collective experience in large Florida rivers (Kissimmee, St. Johns, Suwannee, Caloosahatchee), and our judgment, channel bottom invertebrate communities exhibit little or no response to changes in water level due to the bottom depths. Water level changes would likely be most influential on benthic invertebrate communities of the shallow river shoreline and floodplain wetland habitats, where no benthic invertebrate data from the St. Johns River were available. Therefore, we undertook a short-term survey of benthic invertebrates of shoreline and floodplain marshes in order to: 1) develop a baseline data set to compare with future benthic community sampling that might be conducted after any commencement of surface water withdrawals from the river; 2) employ a methodology to sample benthic invertebrate communities of shoreline and floodplain marshes of the St. Johns River previously developed in south Florida rivers; and 3) evaluate measures of benthic invertebrate community characteristics that potentially could be sensitive to water level change and hence useful metrics in evaluating impacts of hydrologic change due to water withdrawal or other causes.

Materials and Methods

Sampling was conducted at two locations in the St. Johns River: Lake Poinsett, in the upper basin (Orange and Brevard Counties, FL), and Lake Monroe, in the middle basin (Volusia and Seminole

Table 1. Summary of habitats sampled, number of locations, and number of dip net samples taken in each.

Lake	Month	Habitat	# Locations	# Samples/ Location	Total # Samples
Poinsett	July	Bulrush	3	3	9
		Spatterdock	3	3	9
		Deep marsh	1	1	1
		Deep marsh	1	1	1
		Deep marsh	1	1	1
		Shallow marsh	1	1	1
		Shallow marsh	1	1	1
		Shallow marsh	1	1	1
		Para grass/Cypress	1	1	1
		Wet prairie	1	1	1
		Giant reed	1	1	1
Poinsett	November	Bulrush	3	3	9
		Spatterdock	3	3	9
Monroe	July	Bulrush	3	3	9
		Spatterdock	4	3	12
Monroe	November	Bulrush	3	3	9
		Spatterdock	4	3	12

Counties, FL). Comparison of these two lakes was made because Lake Poinsett is more hydrologically dynamic, exhibiting greater changes in water level over the course of a year and among years than downstream Lake Monroe [based on lake level data from U.S. Geological Survey gaging sites: St. Johns River near Cocoa, FL (State Road 520 at the Lake Poinsett outlet) and St. Johns River near Sanford, FL (State Road 17/92 at the Lake Monroe outlet)].

The principal habitats sampled at both lakes were two types of shoreline marsh communities that are continuously inundated: spatterdock (*Nuphar advena*) and bulrush (*Scirpus* sp.). Sampling was conducted in July (beginning of wet season) and November (beginning of dry season) 2009. Additionally, in July 2009, we sampled a variety of marsh habitats in the floodplain of Lake Poinsett subject to varying amounts of inundation, generally less than the shoreline marsh habitats (i.e., wetter vs. drier marshes). Geographic coordinates of the actual sampling stations in each lake are available from the corresponding author and in Appendix B in Mattson et al. (2012).

Sampling methods employed to collect invertebrates followed those used by Merritt et al. (1996, 1999, 2002) in marsh habitats in south Florida rivers. This consisted of timed (30 seconds) sampling with a dip net (500 micron mesh) within a 1 m^2 quadrat. Three dip net samples were collected at each of three or four separate locations in spatterdock and bulrush habitats, in July and November in both lakes (Table 1). As a supplement to the shoreline marsh sampling, one dip net sample was collected at each of nine Lake Poinsett floodplain marsh locations in the July sampling period (Table 1) to evaluate invertebrate community structure along a gradient from wetter to dryer marsh floodplain habitats. All material collected was retained and preserved in 90% isopropanol. In the laboratory, samples were sorted in their entirety, or if a sample was particularly voluminous, it was split with a Folsom plankton splitter™ and half of the sample sorted. All invertebrates sorted were identified to the lowest practical taxonomic level using Merritt et al. (2008), Thorp and Covich (2001), and Pennak (1989). Invertebrates were assigned to various functional feeding group (FFG) categories as described in Cummins et al. (2008) and Merritt and Cummins (2006). Invertebrate biomass was calculated from length measurements on all taxa of invertebrates using a computer program (INVERTCAL) developed by Merritt et al. (2002) based on length/mass regressions published in Benke et al. (1999) and direct measurements (K. W. Cummins, Michigan State Univ. unpublished data).

Our sampling methodology was semi-quantitative, so for purposes of comparing the invertebrate communities in Lakes Poinsett and Monroe, we examined a variety of invertebrate community measures based on relative abundance (% of total abundance), rather than absolute abundance (as #/unit area). We examined relative abundance by major group (e.g., % Odonata, % Gastropoda, % Diptera), relative abundance by combined groups (% Ephemeroptera/ Odonata/ Trichoptera [EOT], % Molluscs+all Crustacea), and diversity (Shannon-Weaver diversity index). These reflected a variety of community characteristics, such as the relative abundance of long-lived taxa (e.g., Odonata), short life-cycle, highly motile taxa (e.g., Diptera), taxa regarded as "sensitive" to various stressors (e.g., EOT taxa), and basic community descriptors such as richness, taxon relative abundance, and diversity. We also examined a variety of metrics developed by Merritt et al. (1996, 2002) that serve as "surrogate measures of ecosystem function." This included the P:R (production:respiration) surrogate ratio, calculated (using either abundance or biomass data) as the proportion of live plant feeders (sum of shredder-herbivores, herbivore-piercers, and scrapers) to detrital plant feeders (sum of all collectors and shredder-detritivores). Cummins et al. (2008) showed that an invertebrate surrogate ratio value of 0.75 corresponds to the traditional P:R ratio of 1 as the threshold between heterotrophy (<0.75 or 1) and autotrophy (>0.75 or 1; after Odum 1956, King and Cummins 1989).

Statistical comparisons of mean metric values between lakes Poinsett and Monroe within a given month (July and November, tested separately) were made using the non-parametric Mann-Whitney U test (conducted using Mini-Tab™ Version 16). High levels of heteroscedasticity, uncorrectable for many metrics even by transformation of the data, negated the use of parametric methods such as ANOVA. Statistical analysis of the single dip net samples collected in the Lake Poinsett floodplain marshes were conducted by comparing selected invertebrate community measures (selected based on the basic biology of the taxon) with the duration of inundation at a particular sampling site using the nonparametric Spearman rank correlation coefficient (calculated using an EXCEL™ spreadsheet program written by R. Mattson). We calculated the covariance statistic between duration of inundation and invertebrate community measures (using Mini-Tab™ version 16) to assess support for the existence of a relationship between inundation and invertebrate community measures. Duration of inundation of each floodplain site was determined using land elevation survey data in combination with the stage-duration relationship for the lake.

Results

Plots of mean daily gage height in Lakes Poinsett and Monroe are shown in Figure 1. We selected the period 1/1/2000 to 12/31/2005 because it encompasses a severe dry period (2000–2001) and an extremely wet period (2004–2005). Lake Poinsett exhibits a greater range of stage fluctuation both within and among years (4–8 feet) than Lake Monroe (2–3 feet).

A total of 112 taxa of aquatic invertebrates were identified (Table 2). The total number of invertebrate taxa collected (Table 2) was greater in Lake Monroe in both July and November (65 and 74 taxa, respectively) than in Lake Poinsett (60 and 60 taxa, respectively). Major taxonomic groups with the most number of taxa (Table 2; "taxa" in this case counting families and genera) were all aquatic insects: Odonata (13 taxa), Hemiptera (13), Coleoptera (21) and Diptera (18). Mean taxa richness across the individual sampling sites in spatterdock and bulrush habitat in both lakes was highly variable, with no clear trends apparent (Figure 2) among habitats or lakes; a pattern seen for the other measures we looked at as well. In spatterdock habitat, mean taxa richness was significantly higher in Lake Monroe than in Lake Poinsett in both July and November (Table 3), but the pattern was reversed in bulrush habitat, with Poinsett having slightly higher mean taxa richness both months (Table 3). Relative abundance of Odonata (as %), Trichoptera, Ephemeroptera,

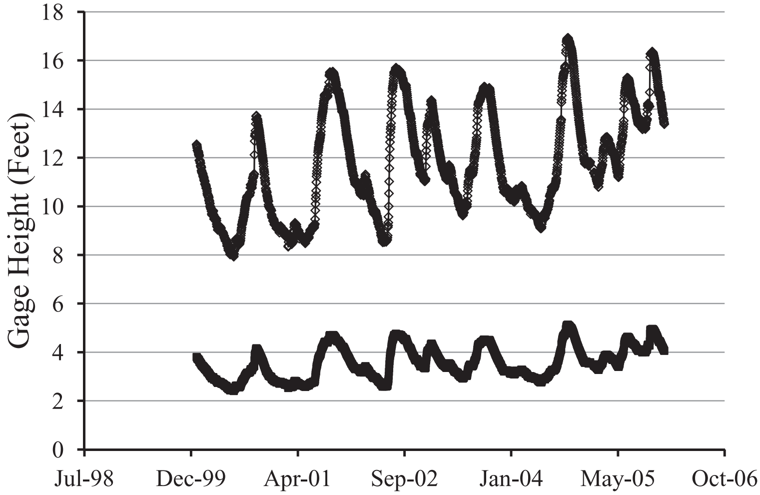


Figure 1. Gage height (feet; daily mean plotted) in Lake Poinsett (top series) and Lake Monroe (bottom series) for the period 1/1/2000 to 12/31/2005.

Gastropoda, Molluscs + all Crustaceans, and Oligochaeta tended to be significantly higher in Lake Monroe in one or both shoreline marsh habitats (Table 3). Relative abundance of Coleoptera, Diptera, and Amphipoda tended to be significantly higher in Lake Poinsett in one or both habitats (Table 3). Overall, in July more invertebrate community measures were significantly higher in Lake Monroe (15) than in Lake Poinsett (7), while in November the number of measures significantly higher were about equal (9 measures higher in Monroe and 8 in Poinsett).

Shoreline habitats in both lakes (bulrush and spatterdock) were primarily heterotrophic ecosystems as indicated by the P:R (production:respiration) surrogate ratio (Table 3). Both biomass and abundance data generally gave the same result (Figure 3); in this case showing bulrush marsh communities of both lakes were heterotrophic ecosystems most of the time (Figure 3), although biomass data indicated an autotrophic state in July in both lakes. Based on abundance, Lake Poinsett appeared to "switch" to an autotrophic state in July, in spatterdock habitat as well (Table 3).

The dipnet samples taken from Lake Poinsett floodplain marsh in July displayed a pattern that could be related to duration of inundation. Taxa characteristic of more permanent aquatic habitats (Ephemeroptera and Amphipoda) had significantly higher relative abundance in habitats inundated for longer periods (Figure 4). Odonata, indicative of taxa characteristic of aquatic habitat, and also including a number of long-lived larval stages, displayed a non-significant positive relationship with duration of inundation. Both the Spearman correlation coefficient and the covariance statistic were positive for all three comparisons (duration of inundation vs. % Odonata, % Ephemeroptera, and % Amphipoda), suggesting that as inundation duration increased, so did the relative abundance of these taxa in the invertebrate community. Short life cycle and multivoltine taxa (Diptera), motile taxa capable of dispersing to other habitats by flight (Coleoptera, Diptera), and taxa capable of diapause during dry conditions (Oligochaeta) all had a significant negative correlation with duration of inundation, suggesting higher relative abundance in shorter-duration marsh habitats (Figure 4). In these three comparisons, the Spearman correlation coefficient and the covariance statistic were all negative, suggesting higher relative abundance of these taxa in shorter-duration wetland habitats. Note also that, based on graphical inspection (Figure 4), a key "breakpoint" appears to be 9 months of inundation, with Amphipoda, Ephemeroptera and Odonata all exhibiting higher relative abundance above this and Coleoptera, Diptera, and Oligochaeta generally exhibiting highest relative abundance below this level.

Discussion

Hydrology, and in particular changes in water level, has been shown to influence many benthic invertebrate community characteristics in wetland habitats (Ward 1992, Wellborn et al. 1996). Frequency, duration, and depth of inundation all influence the habitat available to aquatic invertebrates and thus characteristics such as taxonomic composition, relative abundance, biomass and productivity (Wissinger 1999). For the St. Johns River, changes in water level were anticipated to be the most important hydrologic driver affecting benthic communities, primarily due to its influence in shoreline and floodplain habitats that support more diverse invertebrate communities than those found in unvegetated sediments of the main river channel bottom (Mattson et al. 2012).

This study was one of the few conducted to date in wetland habitats of the St. Johns River. A few studies of benthic invertebrates were previously conducted in headwater marshes of the river, upstream of our study sites (St. Johns River Water Management District unpublished data), and a limited amount of dip net sampling in shoreline marshes has been conducted in the middle river downstream of our Lake Monroe sampling area (pers. comm. D. Denson, Florida Dept. of Environmental Protection, March 2010). Blue Cypress Marsh, in the river headwaters, supports many of the same taxa found in the marsh habitats of Lakes Monroe and Poinsett (St. Johns River Water Management District unpublished data). These included hemipterans (*Belostoma* sp. and *Lethocerus* sp), odonates (aeshnid nymphs, *Pachydiplax* sp., *Erythemis* sp., *Enallagma* sp.), the mayfly *Callibaetis* sp., the amphipod *Hyalella azteca*, gastropod mollusks and chironomid midge larvae. Shoreline and floodplain marshes of the Kissimmee River in south Florida (Merritt et al. 1996, 1999) and marsh and slough habitats in the northern Florida Everglades (Rader 1994) also supported a similar benthic invertebrate assemblage. Odonata, Hemiptera and Coleoptera were the major invertebrate predator groups in the St. Johns, Kissimmee and Everglades marshes. The taxonomic composition of the major insect groups also were similar in all these systems;

Table 2. List of aquatic and semi-aquatic macroinvertebrate taxa collected in Lake Monroe and Lake Poinsett in this study. Functional feeding group designation (FFG; as described by Cummins et al. 2008) is shown: PR=predator, SC=scraper, PA=parasitic, CF=collector-filterer, CG=collector-gatherer, SH-DT= shredder-detritivore, SH-HB=shredder-herbivore, PCR=herbivore-piercer. Abundance category as used by Rader (1994): A=abundant (>100 individuals collected); C=common (20–100 individuals collected); R=rare (< 20 individuals collected).

Taxon	FFG	Monroe Jul	Monroe Nov	Poinsett Jul	Poinsett Nov
Cnidaria					
Hydra sp.	PR	R	R	R	
Platyhelminthes					
Turbellaria	SC	R	R		
Nematoda					
Unidentified spp.	CG/PA		R		R
Mollusca-Gastropoda					
Hydrobiidae	SC	C			
Planorbidae	SC	A	A	A	C
Helisoma sp.	SC	C	A		R
Gyraulus sp.	SC				R
Ancylidae	SC	A	A	A	C
Physidae	SC	C	C	A	C
Physa sp.	SC	R			
Lymnaeidae	SC		A		R
Prosobranchia	SC	A	C	C	R
Mollusca-Bivalvia					
Unionidae	CF				R
Sphaeriidae					
Pisidium sp.	CF		R		R
Annelida					
Oligochaeta	CG	A	A	A	A
Hirudinea	PR/PA	C	C		R
Crustacea					
Ostracoda	CF	A	A	A	A
Cladocera	CF	A	A	A	A
Copepoda	CG	A	A	A	A
Harpacticoida	CG		C	R	C
Argulus sp.	CG	R			
Amphipoda					
Hyalella azteca group	SC	A	A	A	A
Isopoda					
Asellidae	SH-DT	C	R	R	R
Decapoda					
Cambaridae	SH-DT/PR	R	R	R	C
Palaemonidae					
Palaemonetes sp.	SH-DT	A	A	C	A

Table 2 Continued

Taxon	FFG	Monroe Jul	Monroe Nov	Poinsett Jul	Poinsett Nov
Chelicerata					
Aranae	PR	R	R	R	R
Acari	CG/PR	A	A	A	C
Hydracarina	CG/PR	R		R	
Insecta					
Collembola	CG	R	C	C	C
Ephemeroptera					
Baetidae	CG	R			
Callibaetis sp.	CG	A	A	C	R
Caenidae					
Caenis sp.	CG	A	A	A	A
Odonata					
Anisoptera	PR	C	C	R	R
Aeshnidae	PR	R	R		
Coryphaeschna sp.	PR		R		
Macromiidae	PR				R
Corduliidae	PR		R		
Somatochlora sp.	PR				R
Libellulidae	PR	R	R	R	
Erythemis sp.	PR		R		R
Libellua sp.	PR	R			
Pachydiplax sp.	PR	R			R
Sympetrum sp.	PR		R		R
Zygoptera					
Coenagrionidae	PR	A	A	R	C
Enallagma sp.	PR	C			
Ischnura sp.	PR	A	C	C	
Coleoptera					
Haliplidae					
Peltodytes sp.	SH-HB		R	R	
Dytiscidae	PR	R	R	C	
Acilius sp.	PR			R	
Agabus sp.	PR			R	
Celina sp.	PR			R	
Desmopachria sp.	PR			R	
Liodessus sp.	PR		C		
Thermonectus sp.	PR				R
Noteridae	PR	R			
Hydrocanthus sp.	PR	R	R	R	R
Suphis sp.	PR		R	R	
Suphisellus sp.	PR		R	C	R
Ptilidae	SC			R	
Hydrophilidae (larvae)	PR	R		R	R

Table 2 Continued

Taxon	FFG	Monroe Jul	Monroe Nov	Poinsett Jul	Poinsett Nov
Hydrophilidae					
Berosus sp.	PCR/CG	R		C	R
Derallus sp.	CG			C	R
Enochrus sp.	CG				R
Paracymus sp.	PCR/CG	R			
Tropisternus sp.	PR			R	
Hydraenidae	PR		R	R	C
Chrysomelidae	SH-HB				R
Diptera					
Ceratopogonidae	PR				R
Forcipomyia sp.	CG	R	R		R
Mallochohelea sp.	PR	R	R		
Probezzia sp.	PR		R		R
Chaoboridae	PR				R
Chaoborus sp.	PR		R		R
Chironomidae	CG/CF/PR	A	A	A	A
Culicidae					
Aedes sp.	CF			R	
Anopheles sp.	CF		R	R	
Culex sp.	CF	R	R		
Mansonia sp.	CG		R		
Uranotaenia sp.	CF			R	
Psychodidae	CG		R		
Simuliidae	CF		R		
Stratiomyidae	CG	C	R	C	R
Odontomyia sp.	CG	A	R	R	
Ephydridae	CG		R	R	R
Cirrula sp.	SH-HB	R			
Sciomyzidae	PR		R		
Hemiptera					
Hydrometridae					
Hydrometra sp.	PR	R	R	R	
Belostomatidae	PR	R			R
Belostoma sp.	PR	R	R	C	R
Lethocerus sp.	PR		R		
Nepidae					
Ranatra sp.	PR	R	R	R	R
Pleidae	PR		R		
Paraplea sp.	PR			R	R
Naucoridae					
Ambrysus sp.	PR		R		
Pelocoris sp.	PR	R	R		

Table 2 Continued

Taxon	FFG	Monroe Jul	Monroe Nov	Poinsett Jul	Poinsett Nov
Corixidae	SC/CG	R	R	R	
Trichocorixa sp.	SC/CG	R	R		
Mesoveliidae					
Mesovelia sp.	PR	C	C	C	R
Hebridae	PR	R	C	R	R
Trichoptera					
Polycentropodidae	CF			R	R
Cyrnellus sp.	CF	R		R	C
Hydroptilidae	PCR	R	R	R	
Orthotrichia sp.	PCR	R	A		R
Oxyethira sp.	PCR	R			
Leptoceridae	CG			R	
Nectopsyche sp.	SH-HB	R	R		
Oecetis sp.	PR	C	R	R	R
Lepidoptera					
Crambidae	SH-HB		R		
Argyractis sp.	SH-HB		R		
Noctuiidae	SH-HB	R	R	R	R
Bellura sp.	SH-HB	R		R	
Pyralidae					
Paraponyx sp.	SH-HB	R	C		
Total Taxa		65	74	60	60

e.g., baetid and caenid Ephemeroptera; leptocerid, hydroptilid, and polycentropodid Trichoptera; hydrophilid, noterid, dytiscid and haliplid Coleoptera. Several dipteran groups collected in our study (chironomid and certatopogonid midges; ephydrids, culicids, and chaoborids) also were found in the Kissimmee River floodplain marshes and the Everglades. The amphipod *Hyalella azteca* (now referred to as the *Hyalella azteca* group) and the grass shrimp *Palaemonetes* sp. (most likely *P. paludosus*) were important species by both numbers and biomass in the Kissimmee River floodplain marshes (Merritt et al. 1999, Wessell et al. 2001). *Hyalella* also was a major component of the invertebrate community in the St. Johns marshes, while *Palaemonetes paludosus* was present, but not as abundant.

Comparison of the benthic invertebrate communities in similar shoreline habitats in Lake Poinsett (more hydrologically dynamic) and Lake Monroe (less dynamic) indicated a few trends related to hydrology that might be used to derive predictions of changes due to water withdrawal. Higher taxa richness and diversity in spatterdock habitat and higher relative abundance of Odonata (as %) and % 'Molluscs + all Crustaceans' in both shoreline marsh habitats in Lake Monroe could be due to the more stable hydrology in this lake. However,

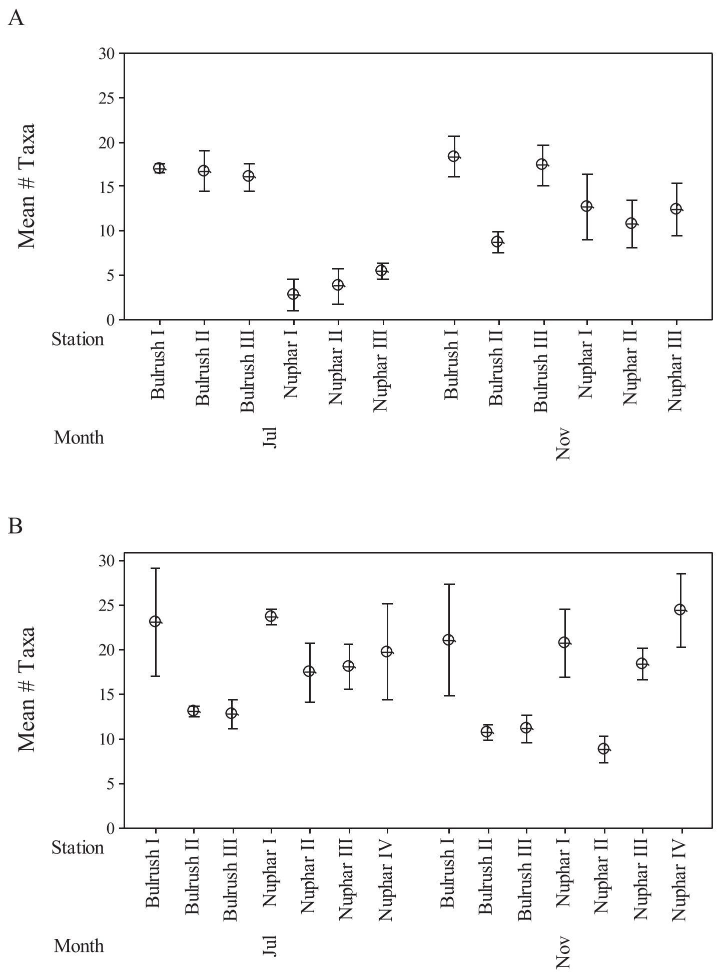


Figure 2. Mean macroinvertebrate taxa richness (± standard error) in spatterdock (= "Nuphar") and bulrush habitat at sampling sites in (A) Lake Poinsett and (B) Lake Monroe. N=3 at each sampling site.

they also could be a result of factors such as greater food resource availability, differences in water quality, and/or predation (although these also may be related to hydrology). High variability typical of benthic communities precluded identification of consistent patterns among all of the metrics examined. Even so, the benthic invertebrate communities of the shoreline and floodplain wetland habitats are most likely to be sensitive to changes in water levels. Additional data collected over time will enable better resolution of variation among and within the shoreline wetlands of these two lakes and a better understanding of the influences of hydrology. The baseline data reported here will be useful for future comparisons and the methodology developed for this study can be used in any new sampling program.

Table 3. Mean (standard error) of benthic community metrics in spatterdock and bulrush habitats in Lakes Monroe and Poinsett, St. Johns River. Values expressed as % are % of total abundance. Significant differences between the two lakes for a given month (Mann-Whitney U test) indicated by different letters. No letters indicates not significantly different. N shown in Table 1.

		Monroe Jul	Poinsett Jul	Monroe Nov	Poinsett Nov
Total taxa richness	Spatterdock	19.67 (1.64)a	3.89 (0.90)b	18.00 (2.18)a	11.89 (1.60)b
	Bulrush	16.22 (2.49)a	16.56 (0.84)b	14.22 (2.53)a	14.78 (1.84)b
% Odonata	Spatterdock	4.91 (1.23)a	0b	2.47 (0.65)a	0.84 (0.47)b
	Bulrush	3.02 (0.61)a	0.50 (0.27)b	2.02 (0.87)a	0.25 (0.17)b
% Trichoptera	Spatterdock	0.76 (0.25)a	0.59 (0.59)b	0.57 (0.20)a	0.44 (0.23)b
	Bulrush	0.95 (0.34)a	0.22 (0.14)b	1.04 (0.72)a	3.90 (1.21)b
% Diptera	Spatterdock	3.13 (0.69)a	9.63 (3.37)b	10.35 (2.64)	9.08 (3.13)
	Bulrush	4.89 (1.28)	6.54 (0.78)	10.51 (2.15)a	26.81 (4.80)b
% Coleoptera	Spatterdock	0.02 (0.02)a	3.70 (2.45)b	0.01 (0.01)a	0.16 (0.16)b
	Bulrush	0.01 (0.01)a	0.31 (0.12)b	0.03 (0.03)a	0.31 (0.18)b
% Ephemeroptera	Spatterdock	6.75 (1.65)a	3.70 (2.45)b	6.21 (0.90)a	4.72 (1.00)b
	Bulrush	4.02 (1.32)	3.37 (0.75)	3.27 (1.34)a	3.37 (1.46)b
% Ephemeroptera/ Odonata/Trichoptera	Spatterdock	12.41 (1.83)a	4.29 (2.41)b	9.25 (1.44)	6.00 (1.21)
	Bulrush	8.00 (1.69)a	4.09 (0.98)b	6.33 (1.59)a	7.53 (1.96)b
% Gastropoda	Spatterdock	6.98 (1.75)a	0.93 (0.93)b	3.74 (1.31)a	2.97 (1.29)b
	Bulrush	11.0 (1.69)a	4.07 (1.37)b	4.25 (1.27)a	0.47 (0.27)b
% Amphipoda	Spatterdock	12.37 (5.23)a	24.80 (9.73)b	14.02 (3.21)	8.34 (3.19)
	Bulrush	8.21 (1.90)	10.30 (3.23)	11.68 (3.13)	18.69 (3.35)
% Molluscs+all Crustacea	Spatterdock	49.73 (5.52)a	6.20 (2.64)b	39.79 (4.55)	16.52 (6.82)
	Bulrush	67.30 (5.34)	31.23 (6.70)	52.85 (6.45)	17.94 (2.35)
% Oligochaeta	Spatterdock	12.72 (4.04)a	0b	18.54 (4.01)a	14.08 (5.67)b
	Bulrush	4.14 (2.37)a	3.01 (0.55)b	5.07 (1.68)a	6.22 (1.76)b
% Cladocera/Copepoda/ Amphipoda	Spatterdock	49.18 (4.14)a	25.34 (9.99)b	38.69 (3.61)	18.22 (6.73)
	Bulrush	53.81 (6.47)	28.09 (5.89)	49.14 (6.66)	23.46 (3.48)
Shannon-Weaver Diversity (H′)	Spatterdock	1.92 (0.09)a	1.02 (0.24)b	2.11 (0.08)	1.49 (0.10)
	Bulrush	1.70 (0.15)	1.82 (0.10)	1.95 (0.11)	1.82 (0.11)
Pielou's Evenness	Spatterdock	0.65 (0.03)a	0.66 (0.13)b	0.76 (0.03)	0.62 (0.05)
	Bulrush	0.61 (0.04)	0.65 (0.03)	0.76 (0.03)	0.72 (0.04)
P:R Surrogate Ratio	Spatterdock	0.44 (0.15)a	2.35 (1.10)b	0.53 (0.14)a	0.18 (0.06)b
	Bulrush	0.38 (0.08)	0.45 (0.15)	0.35 (0.10)	0.61 (0.13)
# TIMES SIGNIFICANTLY HIGHER	15	7	9	8	

The patterns of relative abundance in the floodplain marsh sampling (Figure 4) are regarded as preliminary because without replication parametric statistical analyses are not possible. We also recognize that the existence of an association between duration of inundation and invertebrate community metrics (as indicated using correlation and covariance analysis) does not indicate causation. However, a basic understanding of the biology of the groups we looked at would argue that the relationships we saw in our data are at least in part related to hydrology of the habitat. Supporting evidence is that the patterns we saw in these preliminary data were very similar to those of

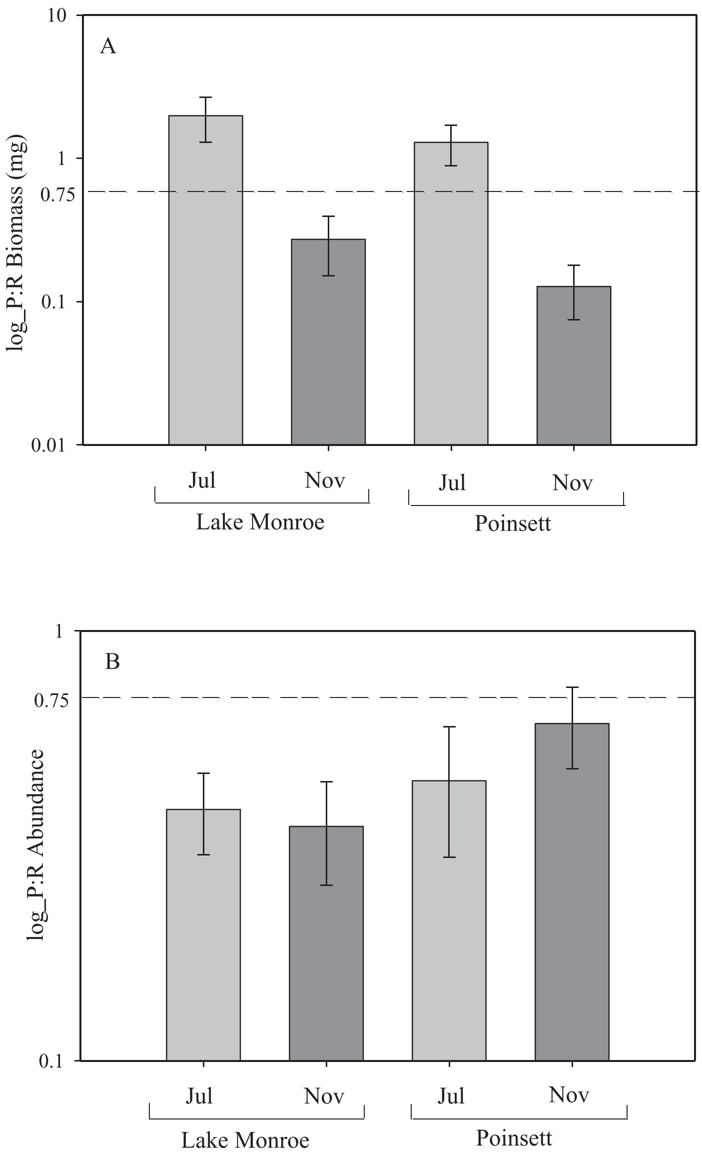
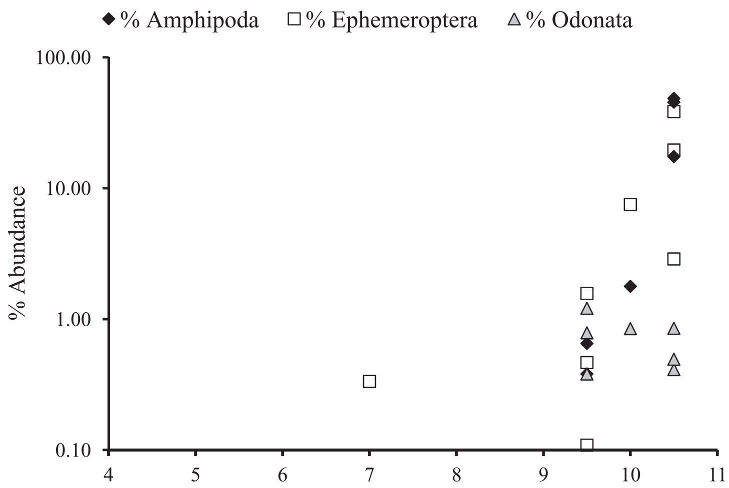


Figure 3. Mean production:respiration surrogate ratio, derived as ratio of live plant feeders to detrital plant feeders (± standard error), in bulrush habitat in Lakes Monroe and Poinsett. Threshold of 0.75, indicating break between heterotrophy (<0.75) and autotrophy (>0.75) is shown: (A) biomass data, (B) abundance data.

Lillie (2003), who found higher abundance of some of the same taxa (Ephemeroptera and Amphipoda) in Wisconsin wetlands with >8 months of inundation and higher abundance of some Diptera species in wetlands with <8 months of inundation, similar to our suggested threshold of 9 months.



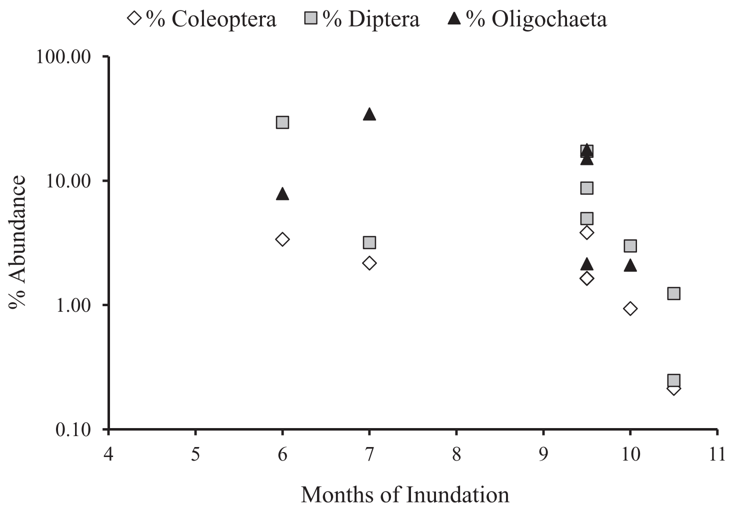


Figure 4. Relative abundance (%) of selected aquatic invertebrate taxa vs. duration of inundation in Lake Poinsett floodplain marsh habitats. Spearman rank correlation coefficients (** = significant at $p < 0.05$): Amphipoda rho= 0.93**, Ephemeroptera rho= 0.90**, Odonata rho= 0.52, Coleoptera rho= −0.81**, Diptera rho= −0.80**, Oligochaeta rho= −0.77** Covariance statistics: Amphipoda= 18.01, Ephemeroptera= 10.45, Odonata= 0.45, Coleoptera= −1.59, Diptera= −11.12, Oligochaeta= −11.31 Top: Amphipoda r = 0.93, …. Bottom: Coleoptera r = 0….. N=1 for each data point.

Future sampling of benthic invertebrates in the St. Johns River should include a variety of floodplain wetlands with varying hydroperiod to better discern the influences of hydrology (*sensu* Wellborn et al. 1996).

Some of the taxa that we collected in the shoreline and floodplain habitats could be highly useful for future monitoring of hydrologic conditions. Dragonflies and damselflies (Odonata) are long-lived taxa that would be sensitive to changes in water levels that limit the aquatic habitat required for completion of their life cycle. These taxa are easy to identify and enumerate in the field and could be a focus of future monitoring efforts using in-the-field, "rapid bioassessment" techniques. Crayfish (found in all habitats at both lakes; Table 1) could be another group sensitive to water level changes (e.g., Acosta and Perry 2001, Dorn and Trexler 2007), and they are also easy to collect and identify in the field. Brooks et al. (2011) listed Dytiscidae, Hydrophilidae, Haliplidae, Baetidae, Ceratopogonidae, and Corixidae (all of which we collected in St. Johns River shoreline and floodplain marshes) as having a "high likelihood of adverse effect" due to hydrologic changes caused by water withdrawals in river shoreline edge habitat in Australia. However, life history differences between the Australian and Florida fauna may render the latter less sensitive to hydrologic change (e.g., in Florida, corixids are probably the most mobile of the taxa cited above).

We propose three new functional surrogate metrics that could be useful for future hydroecological monitoring in shoreline and floodplain marshes: dissolved oxygen requirement index; mobility index and voltinism index. The dissolved oxygen requirement index (DORI) is calculated as the ratio of taxa that respire dissolved oxygen to those that are air breathers. Taxa that obtain oxygen from the water (via gills, plastron or cutaneous respiration) would be vulnerable to reduced DO levels resulting from decreased flow or increased decomposition of dead plant material related to falling water levels. Taxa that respire air or those with mechanisms to withstand periods of hypoxia (e.g., those with hemoglobin in their tissues) would be resistant to reduced DO levels. Values of this metric >1.0 would indicate a benthic community potentially susceptible to withdrawal because a majority of the taxa in the community require dissolved oxygen in the water to survive. A preliminary threshold of 1 (essentially a "50/50" split) is conservatively proposed pending additional work to develop a more defensible threshold. This metric could be calculated using biomass or abundance data. Examination of the 61 genera identified in this study (Table 2) revealed that 34 of these taxa utilize aquatic respiration and 27 were air breathers. The DO Index of 1.26 (34 water : 27 air) suggests that the benthic community would be more likely to be vulnerable to water level reductions if lower dissolved oxygen conditions result.

The mobility index (MI) is calculated (by biomass or abundance) as the ratio of invertebrate taxa with low or very low dispersal ability to those with high dispersal ability. Those taxa with low capability for dispersal cannot readily move to adjacent inundated aquatic habitat as areas where they reside dry up. Some of these non-motile taxa (e.g., amphipods, grass shrimp) are important food items for fish and wildlife, and reductions in their populations could impact wetland food webs. The motile taxa would be largely unaffected by drying due to water withdrawal, as they could follow receding water levels or disperse to adjacent inundated areas (e.g., adult Coleoptera and Hemiptera). All of the aquatic insects (except Collembola) have winged adult life stages and thus have a higher, although variable, potential for dispersal. An MI threshold value > 1.0

would indicate a community susceptible to withdrawal because a majority ($> 50\%$) of the community would consist of individuals with limited motility and dispersal capability. A value < 1.0 would suggest that the benthic community would be resistant to withdrawal effects because a majority of the taxa would be able to disperse to new habitat. This metric could be affected depending upon whether abundance or biomass data were used, as variation in the proportion of large-bodied taxa could influence the outcome. Of the 61 genera collected in this study (Table 2), 15 were classified as having low to very low mobility and 46 as having a potential for high mobility. The Mobility Index of 0.33 (15 low mobility:46 high mobility) predicts that the macroinvertebrate fauna would not be highly vulnerable to reductions in water level because a majority of the taxa would be able to disperse to adjacent wetted habitats.

Finally, a voltinism index (VI) is the ratio of invertebrate taxa with longer life cycles (semivoltine >1 yr) to those with shorter life cycles (univoltine or multivoltine ≤ 1 yr; i.e., one or more generations per year). Voltinism (as well as life cycle length) would be an indicator of the rapidity with which a taxon can respond to loss of habitat due to drying. If relative abundance of longer life cycle taxa is reduced, this could also have food web effects both because of loss of food base for fish and wildlife, and because many of these taxa (e.g., odonates) are important intermediate predators in wetland and aquatic food webs. Timing of life history could also be important but is not addressed here. Again, a preliminary threshold of 1.0 is proposed, with values > 1.0 suggesting the community could be vulnerable to water withdrawal effects due to a majority of the taxa being longer life cycle organisms. Of the 61 genera collected in this study, 13 were tentatively classified as semivoltine and 48 as uni- or multivoltine, although very little data exist on invertebrate life histories in Florida. This yields a VI of 0.21 (life cycle >1yr 13 : life cycle ≤ 1 yr 48) suggesting that a majority of the fauna collected were short life cycle taxa that would, in general, be less vulnerable to water level reductions because the majority of the taxa could rapidly recolonize habitats when they became inundated again. The differing results indicated by each of these three metrics (i.e., the DO metric indicating sensitivity to withdrawal, while the MI and VI indicating not) shows that multiple traits/measures must be examined to get a complete picture of the invertebrate community.

The data in hand suggest that the hydrologic changes caused by proposed surface water withdrawals directly from the river will have little effect on the invertebrate benthic community of the upper and middle St Johns River. However, the extreme variability always associated with studies of riverine benthic invertebrate community distribution and abundance leaves this conclusion subject to significant uncertainty. A precautionary approach dictates that further monitoring would be the best hedge against unpredicted effects of water manipulation of the river. We argue that the functional analyses and related measures evaluated here could provide an efficient and sensitive approach to meet this objective.

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