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BENTHIC MACROINVERTEBRATES OF SMALL FLORIDA PONDCYPRESS SWAMPS AND THE INFLUENCE OF DRY PERIODS

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Abstract: Benthic macroinvertebrate communities were sampled bimonthly from December 1993 to April 1995 in three small pondcypress swamps. Eighty-five taxa were collected, with Chironomidae, Dytiscidae, and Hydrophilidae contributing large numbers of genera. Annual mean density was 4,229 individuals/m^2, and monthly densities for individual ponds ranged from 950 to 11,623 individuals/m^2. Three genera, *Crangonyx* (Amphipoda), *Polypedilum,* and *Chironomus* (Chironomidae), accounted for 70% of the total density. High levels of temporal and inter-pond variability were documented. Taxon richness and total density of communities sampled during drawdown were similar to those of wet months. The large number of taxa unique to the dry period contributed substantially to overall taxon richness. The benthic macroinvertebrate communities of these systems seem to be adapted to unpredictable drawdown.

Key Words: pondcypress swamps, drawdown, forested wetland, macroinvertebrates

INTRODUCTION

Pondcypress swamps (also known as cypress domes, cypress ponds, and cypress heads) are small basin wetlands found throughout the pine flatwoods of the southeastern coastal plain (USA). These wetlands are characterized by a canopy of pondcypress (*Taxodium distichum* var. *nutans* (Ait.) Sweet) and water levels that normally fluctuate dramatically each year. Even though these systems are very common, there has been little research on the aquatic invertebrates of pondcypress swamps, with the exception of Brightman's (1984) study of invertebrate response to wastewater application.

Aquatic invertebrates process organic matter (Cummins 1973) and serve as food for higher trophic levels (e.g., Dannell and Sjoberg 1977, Jarvis and Noyes 1986). Most research on invertebrates of southern forested wetlands has documented communities of river swamps, such as backswamps, floodplain pools, and green-tree reservoirs (Parsons and Wharton 1978, Ziser 1978, Sklar 1985, White 1985, Gladden and Smock 1990, Duffy and LaBar 1994), in which periodic inputs of allochthonous nutrients may support the development of high density and biomass. Pondcypress swamps, however, are more isolated water bodies, rainfall being the primary source of water (Heimburg 1984). These swamps are characterized by low pH, high color, and slow litter decomposition and are generally considered nutrient-limited (Ewel 1990). Pondcypress swamps vary in hydroperiod, size (<1–10 ha), and understory vegetation (Marois and Ewel 1983).

Small pondcypress swamps are characterized by an unpredictable regime of drying and wetting, in some years remaining flooded all year and in others drying completely four times or more. Aquatic invertebrates of other temporary water bodies have evolved various tactics to withstand desiccation, including the ability to fly or burrow and drought resistance in the larval or egg stage (Wiggins et al. 1980, Williams 1987, Batzer and Wissinger 1996). Although there has been interest in the response of aquatic invertebrate communities to rewetting (McLachlan 1974, Butler et al.

1992, Bataille and Baldassarre 1993), most studies have ignored the dry period itself (e.g., White 1985, Duffy and LaBar 1994).

The objectives of this study were (1) to examine benthic macroinvertebrate communities of small pondcypress swamps in order to document sources of variability and (2) to describe the community present during drawdown.

METHODS

Study Sites

The pondcypress swamps used in this study were located within a managed pine plantation approximately 25 km north of Gainesville, Florida. The dominant canopy tree in all ponds was *Taxodium distichum* var. *nutans,* accompanied by subdominants *Pinus elliottii* Engelm. and *Nyssa sylvatica* var. *biflora* (Walt.) Sarg. Three ponds within a 30 ha block were selected for study. Pond 1 (1.4 ha) was covered with a thick bed of emergent macrophytes, including *Carex* sp. and *Woodwardia virginica* (L.) Smith. Pond 2 (2.5 ha) had a dense understory of shrubs, including *Lyonia lucida* (Lam.) Koch and *Myrica cerifera* L., and sparse clumps of *Carex* sp. and *W. virginica.* Pond 3 (0.6 ha) had virtually no emergent macrophytes. A dense cover of mosses, primarily *Sphagnum* sp., was present in all ponds.

Sampling Methods

Benthic macroinvertebrates were sampled bimonthly from December 1993 to April 1995 using a stainless steel corer (7.1-cm-diameter, 26.5-cm-long cylinder with 64-cm attached handle). All ponds were sampled each period, regardless of water depth, except in December 1993 and February 1994 when only Ponds 2 and 3 were sampled. During each sampling period, 20 sediment cores (approximately 15 cm depth, including the entire coarse organic material layer) were taken at randomly determined stations within a 20-m radius of the deepest point in the pond. Except in June 1994, when ponds were dry, only wet areas within the ponds were sampled. Cores were sieved on-site using a U.S. Standard No. 30 sieve (0.6 mm openings), preserved with 80% ethanol, and stained with rose bengal. Water depth was measured at each coring site.

During each sampling month, dissolved oxygen, water temperature, and pH were measured once in the center of each pond 10 cm above the sediment surface. Water levels at the deepest point in Pond 11 were measured daily by a float-pulley water-level recorder.

In the laboratory, macroinvertebrates were picked from the sediment and identified to genus or to the lowest taxonomic level practical. Zooplankton were not counted. Taxonomic keys used included Young (1954), Usinger (1956), Peterson (1960), Wiggins (1977), Pennak (1978), McCafferty (1981), Brigham et al. (1982), Merritt and Cummins (1984), Daigle (1991, 1992), and Epler (1995). Specimens difficult to identify were compared with collections maintained by the State of Florida or were brought to taxonomists for identification.

Statistical Analysis

Taxon richness and total density were calculated using only aquatic and semi-aquatic taxa; data were pooled for the 20 cores sampled in each pond. In order to compare macroinvertebrates of non-dry ponds with dry ponds, differences in total density and richness between the April 1994 and June 1994 sampling periods were tested with a paired t-test. A $x^{1/2}$ transformation was applied to densities in order to stabilize variances. Annual mean density was calculated with data from April 1994 to April 1995 using the average of the two April densities as one month. Functional feeding groups were assigned using classifications by Pennak (1978) and Merritt and Cummins (1984).

Sources of variance (time, pond, core) were estimated for all taxa combined and taxa accounting for ≥ 2% of the mean density over time for unpooled core counts using PROC VARCOMP (SAS Institute, Inc., 1989). A $x^{1/2} + (x + 1)^{1/2}$ transformation, used for datasets with zero counts (Freeman and Tukey 1959), was applied to the data.

RESULTS

Water Depth and Quality

Water depth in the pondcypress swamps fluctuated during the year and a half of observation and was lowest during the summer (Figure 1). All ponds were dry during and at least one month prior to the June 1994 sampling period and for at least one week in September 1994. Pond 3 was deeper than Ponds 1 and 2 during most sampling periods.

Dissolved oxygen concentrations and water temperature were similar in all ponds, bimonthly means ranging from 1.4±0.7 to 4.8±0.9 mg/L and from 8.2±0.9 to 24.3±0.6 °C, respectively. pH was low and ranged from 3.4 to 4.4 (W. Casey, unpublished data).

Benthic Macroinvertebrates

Eighty-five aquatic and semi-aquatic macroinvertebrate taxa were collected from the three pondcypress swamps (see Appendix). Diptera and Coleoptera were

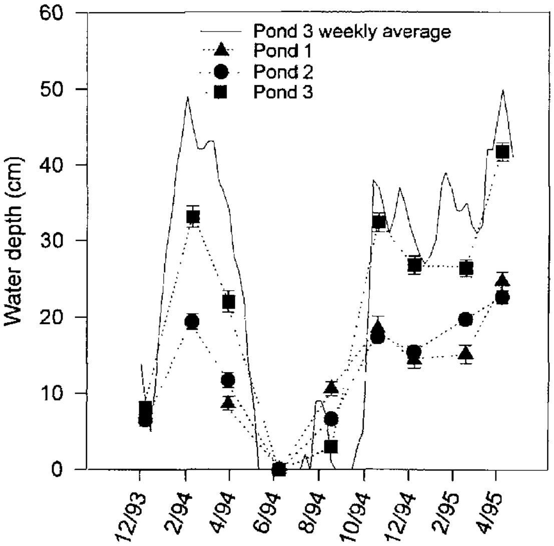

Figure 1. Water depth in cypress ponds. Weekly average water depth for Pond 3 was determined for the deepest point (H. Riekirk and L. Korhnak, unpublished data). Bimonthly means (±SE) were calculated from 20 measurements taken in each Pond (1, 2, and 3). Bimonthly sampling did not include the September 1994 dry period.

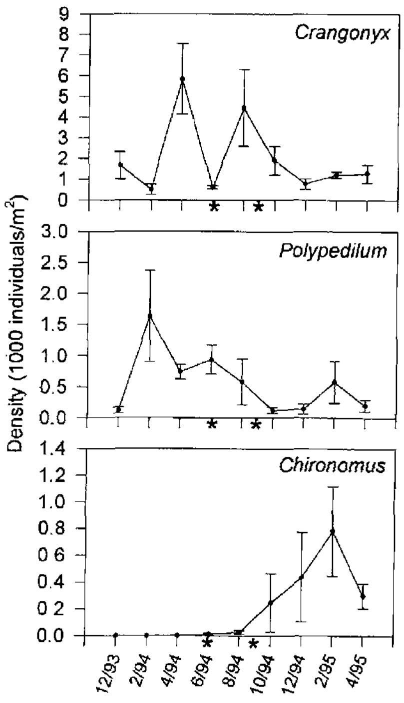

Figure 2. Mean density (±SE) of *Crangonyx, Polypedilum,* and *Chironomus* in cypress ponds. All means were calculated for three ponds except in December 1993 and February 1994, when only two ponds were sampled. * denotes time when all ponds were dry.

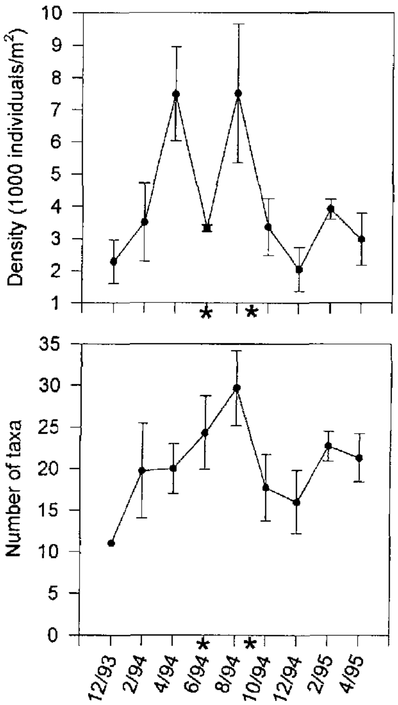

Figure 3. Mean total density (±SE) and number of taxa in cypress ponds. All means were calculated for three ponds except in December 1993 and February 1994, when only two ponds were sampled. * denotes time when all ponds were dry.

the most taxonomically rich groups, each accounting for 35% of total richness. Within these orders, Chironomidae (Diptera), Dytiscidae, and Hydrophilidae (Coleoptera) contributed large numbers of genera.

Annual mean density of benthic macroinvertebrates was 4,229 individuals/m^2. *Crangonyx* (Amphipoda), a dietary generalist, was the most dominant invertebrate, accounting for 52% of total density. Two generalist chironomids, *Polypedilum* and *Chironomus,* were also common, contributing 13% and 5% of overall density, respectively (Figure 2).

Total density peaked in April and August 1994, when *Crangonyx* was very abundant, and it remained relatively low the rest of the year (Figures 2 and 3). Bimonthly densities in individual ponds ranged from 950 individuals/m^2 in December 1994 to 11,623 in August 1994, both in Pond 2. *Polypedilum* was found throughout the study, was particularly abundant in the spring and early summer of 1994, but less so in the following months (Figure 2). *Chironomus,* on the other hand, became abundant only after October 1994.

Variability among ponds in most months was great for total density, density of dominant taxa, and taxon richness (Figures 2 and 3). Pond 3 was lowest in taxon richness for every sampling period except December 1993 and contained only 43 taxa overall, as opposed

Table 1. Variance among transformed macroinvertebrate counts and densities. Variance estimates were determined from macroinvertebrate counts of 420 core samples (twenty cores taken in three cypress ponds in each of seven months).

	Variance Source (core counts)				
Taxon	Pond	Time	Time × Pond	Core	Total
Total taxa	0.00	2.61	2.43	5.62	10.66
Cecidomyidae	0.00	0.01	0.13	0.50	0.64
Ceratopogonid larva 1	0.29	0.27	0.39	0.74	1.69
Chironomus	0.02	0.35	0.53	1.60	2.50
Crangonyx	0.72	3.90	2.18	5.91	12.71
Culicoides	0.01	0.02	0.04	0.38	0.45
Monopelopia	0.16	0.14	0.10	0.61	1.01
Polypedilum	0.49	0.46	0.21	2.69	3.85

to 72 and 59 taxa for Ponds 1 and 2, respectively. Taxa usually found in other ponds, especially Ceratopogonid larvae 1, 2, and 3 and tanypod chironomids (*Larsia, Monopelopia*), were often absent in Pond 3. *Polypedilum* was often present at greater densities in Pond 3 than in Ponds 1 and 2.

Sources of variance (pond, time, core) were estimated for core counts (Table 1). Core to core variability was the largest source of variance for all taxa analyzed.

Drawdown

Ninety percent of the individuals identified from the dry ponds of June belonged to taxa sampled in previous wet months. Total density during June was not significantly lower than during April (t = 3.05; df = 2; P; eq 0.09) and was similar to that of other months (Figure 3). As in wet months, *Polypedilum* and *Crangonyx* were dominant in June, accounting for 28% and 18% of total density, respectively. Chrysomelid larva 1 was abundant only in June.

There was no loss of taxon richness from April to June (t = 2.33; df = 2; P = 0.14) (Figure 3). Of the 40 taxa sampled in June, 12 were exclusive to that sampling period; an average of 3 taxa were exclusive to each wet sampling period. Among those taxa unique to June were many semi-aquatic taxa, including the beetles *Hydraena, Stenus,* and Carabidae and larvae of Dolichopodidae (Diptera). Mean density of larvae of the terrestrial Sciaridae (Diptera; 135 individuals/m^2) was greatest in June.

DISCUSSION

The pondcypress swamps in this study supported a large number of benthic macroinvertebrate taxa (85). Although not as taxonomically rich as some floodplain swamps (e.g., Gladden and Smock 1990), these systems are richer than other southern swamps. For instance, 66 invertebrate species were identified over two years in a cypress-tupelo swamp (Sklar 1985), and only 27 genera were found in a deep pondcypress swamp in Florida (Brightman 1984). Both of the previous studies employed methods that sampled both the sediment and water column. Because we only sampled the sediment, total aquatic macroinvertebrate richness likely was underestimated.

Many of the taxa sampled were characteristic of temporary ponds. The pondcypress swamps supported a taxonomically rich assemblage of Coleoptera, especially the families Dytiscidae and Hydrophilidae, which have been observed in other temporary water bodies (e.g., Nilsson 1986, Balla and Davis 1995). Many Coleoptera found in temporary waters are characterized by great mobility (Fernando and Galbraith 1972, Gray and Fisher 1981), which allows them to colonize suitable habitats. Some of the taxa exclusive to the dry ponds, including those in the semi-aquatic families of the Carabidae, Hydraenidae, and Staphylinidae, were adults and may have flown into the ponds during the dry period. The large number of taxa found only in the dry ponds contributed greatly to total taxon richness. Sampling invertebrates in temporary water bodies only during wet periods may substantially underestimate taxon richness.

The annual mean density (4,229 individuals/m^2) of these pondcypress swamps falls within a range found in other southern swamps: from 442 individuals/m^2 in a Florida cypress slough (Haack 1984) to 10,934 individuals/m^2 (discounting zooplankton) in a highly productive blackwater floodplain in Virginia (Gladden and Smock 1990). Compared to other non-alluvial basin swamps, including Florida deep pondcypress (Brightman 1984) and hardwood (Camp et al. 1992) swamps, densities found in this study were high. Detrital food quality in the swamps we studied may have been increased by drawdown and subsequent rewetting. Detrital protein levels increase with fungal and bacterial colonization during drawdown (Barlocher et al. 1978) and may account for large invertebrate densities.

Chironomids, amphipods or isopods, and oligochaetes are dominant in many southern swamps (e.g., Brightman 1984, Haack 1984, Sklar 1985, Camp et al. 1992, Duffy and LaBar 1994). In the pondcypress swamps, three generalist feeders, *Crangonyx* (Amphipoda) and chironomids *Polypedilum* and *Chironomus,* accounted for 70% of overall density. In April and August 1994, *Crangonyx* density increases accounted for peaks in total density. Whereas *Polypedilum* was present in the ponds throughout the study, *Chi-*

ronomus only reached appreciable densities after October. Intra- and interannual variability is characteristic of aquatic invertebrate populations (e.g., Parsons and Wharton 1978, Sklar 1985, Neckles et al. 1990).

Generalists are a large component of the invertebrate community in many forested wetlands, but collectors such as oligochaetes and some chironomids are often the most abundant group in alluvial swamps (e.g., Haack 1984, Sklar 1985) where fine particulate organic matter is prevalent (Anderson and Sedell 1979). In basin wetlands like pondcypress swamps, there are mostly autochthonous inputs of organic matter in the form of coarse particulate matter, which is fed upon by generalists or shredders, not collectors (Anderson and Cummins 1979). The large proportion of generalists found may also enable the invertebrate community to withstand disturbance (e.g., drawdown) when food resources change (Cummins and Merritt 1984).

Densities of benthic macroinvertebrates in ponds that had been dry for over one month were surprisingly similar to those of wet months. Many of the taxa sampled in the dry ponds were present in previous wet months. These taxa were therefore able to survive drawdown *in situ,* as opposed to leaving the system as adults before drawdown. *Crangonyx* can burrow into moist sediments to avoid desiccation, and some chironomids, including *Polypedilum,* can withstand drawdown as larvae (McLachlan and Cantrell 1980, Wiggins 1980, Williams 1987). Taxa unable to weather desiccation in the sediment must complete their aquatic stage and leave the system before drawdown. In systems with unpredictable drawdowns such as these pondcypress swamps, the ability to withstand desiccation *in situ* is advantageous.

Variability of taxon richness was high among the pondcypress swamps sampled. Although dominant taxa were similar, subdominant assemblages often differed. Except in December 1993, Pond 3 was lowest in taxon richness. Several taxa relatively abundant in Ponds 1 and 2 were rarely, if ever, sampled in Pond 3, including ceratopogonid and tanypod chironomid (*Larsia, Monopelopia*) taxa. Although variables such as dissolved oxygen, pH, and water temperature were similar among ponds, there was much variability in water depth and vegetation that may have resulted in differences in invertebrate communities. Deeper water in Pond 3 may have hindered capture of more mobile invertebrates with our short coring device.

Vegetation can influence both density and taxonomic composition of invertebrates, providing a food source and substrate (e.g., Voigts 1976, Beckett and Aartila 1992, Ward 1992). Pond 1 (72 taxa) was characterized by a thick cover of emergents, but Pond 3 (43 taxa) had virtually no emergent vegetation. *Crangonyx* dominance was linked to high *Sphagnum* cover in a study of these and other pondcypress swamps (Leslie 1996).

A broad approach to sampling should be adopted for studies of wetland invertebrate communities, particularly given the important role they play as a link between detrital and primary production and higher trophic levels. Future studies should document the importance of sampling all parts of the aquatic invertebrate community, including those associated with the sediment, vegetation, and water column. In addition, high core to core variability observed in these pondcypress swamps and in marshes (Streever and Portier 1994) emphasizes the importance of sample replicates within a wetland. The macroinvertebrate community of pondcypress swamps in this study was characterized by high taxon richness, due in part to the large number of taxa unique to dry ponds. Excluding dry periods from sampling in temporary ponds may affect estimates of overall taxon richness and density.

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Appendix. Mean density (individuals/m^2) over time for all cypress ponds. Presence in wet ponds (w) and dry ponds (d) is noted.

Taxon		Mean Density	Wet/Dry
ARACHNIDA	Hydracarina	19.2	w, d
	Other Arachnida	38.4	w, d
OLIGOCHAETA		32.7	w, d
CRUSTACEA			
Decapoda	Cambaridae	5.6	w
Amphipoda	*Crangonyx*	2052.4	w, d
Isopoda	*Asellus*	54.3	w, d
ENTOGNATHA			
Collembola	Entomobryomorpha	22.9	w, d
	Sminthuridae	1.4	w
INSECTA			
Coleoptera	Carabidae	1.4	d
	Chrysomelidae		
	Chrysomelid larva 1	59.4	w, d
	Chrysomelid larva 2	50.5	w, d
	Chrysomelid larva 3	15.9	d
	Dytiscidae		
	Agabus	0.5	w
	Bidessonotus	5.6	w
	Celina	8.4	w
	Copelatus	0.5	w
	Coptotomus	0.5	w
	Desmopachria	17.8	w, d
	Hydaticus	0.9	w
	Hydroporinae larva	48.2	w, d
	Hydroporus	0.9	w
	Matus	5.6	w
	Thermonectes	0.5	w
	Uvarus	3.7	w, d
	Gyrinidae		
	Gyrinus	4.2	w
	Haliplidae		
	Haliplid larva 1	0.5	d
	Hydraenidae		
	Hydraena	10.8	d
	Hydrophilidae		
	Berosus	1.9	w
	Enochrus	19.2	w, d
	Helocombus	0.5	d
	Helophorus	0.9	d
	Hydrobius	2.3	w, d
	Hydrochus	1.9	w, d
	Tropisternus	12.6	w
	Other Hydrophilidae	3.7	w, d
	Histeridae		
	Histerid adult 1	0.5	w
	Noteridae		
	Hydrocanthus	0.9	w
	Notomicrus	2.8	w, d
	Scirtidae		
	Cyphon	10.8	w
	Staphylinidae		
	Stenus adult	0.5	d
	Other Staphylinidae	1.4	d
	Other Coleoptera	26.7	w, d

Appendix. Continued.

Taxon		Mean Density	Wet/Dry
Diptera	Cecidomyidae	73.9	w, d
	Ceratopogonidae		
	Culicoides	91.7	w, d
	Ceratopogonid 1	151.1	w, d
	Ceratopogonid 2	9.8	w, d
	Ceratopogonid 3	3.7	w, d
	Chaoboridae		
	Chaoborus	22.9	w
	Chironomidae		
	Ablabesmyia	11.2	w
	Chironomus	201.1	w, d
	Corynoneura	3.3	w
	Keifferulus	5.1	w
	Labrundinia	0.5	w
	Larsia	43.5	w, d
	Limnophyes	0.9	w
	Monopelopia	99.6	w, d
	Polypedilum	491.1	w, d
	Procladius	1.9	w
	Psectrocladius	5.1	w
	Tanytarsus	0.9	w
	Other Chironomidae	11.2	w, d
	Corethrellidae		
	Corethrella	3.3	w
	Culicidae		
	Culex	0.5	w
	Culiseta	3.3	w
	Mansonia	0.5	w
	Dolichopodidae	5.6	d
	Ephydridae	8.4	w, d
	Psychodidae	0.5	d
	Sciaridae	16.4	w, d
	Tabanidae	8.9	w, d
	Tipulidae	2.8	w, d
	Other Diptera	45.8	w, d
	Diptera 1	4.7	w
	Diptera 2	2.3	d
	Diptera 3	5.1	w, d
Ephemeroptera	Caenidae		
	Caenis	2.8	w
Hemiptera	Gerridae	0.5	w
	Belostomatidae		
	Belostoma	0.9	w
	Mesoveliidae		
	Mesovelia	4.2	w, d
	Veliidae		
	Microvelia	0.5	w
	Notonectidae		
	Buenoa	1.4	w
Lepidoptera	Pyralidae	0.5	d
Megaloptera	Sialidae		
	Neohermes	0.9	w
Odonata	Aeshinidae		
	Anax	0.5	w
	Epiaeschna	0.5	w

Appendix. Continued.

Taxon		Mean Density	Wet/Dry
	Gomphaeschna	0.9	w
	Coenagrionidae		
	Ischnura	3.7	w
	Lestidae		
	Lestes	0.9	w
	Libellulidae		
	Libellula	9.8	w
	Pachydiplax	1.9	w
	Tramea	0.5	w
	Other Libellulidae	1.4	w
Trichoptera	Hydroptilidae		
	Oxyethira	3.3	w