WETLANDS, Vol. 17, No. 3, September 1997, pp. 383–393

INVERTEBRATE COMMUNITIES OF FORESTED LIMESINK WETLANDS IN SOUTHWEST GEORGIA, USA: HABITAT USE AND INFLUENCE OF EXTENDED INUNDATION

Stephen W. Golladay, Brad W. Taylor, and Brian J. Palik[1]
J.W. Jones Ecological Research Center
Rte 2, Box 2324
Newton, GA 31770 USA

[1]*Current address: Forestry Sciences Laboratory*
USDA Forest Service, 1831 Highway 169 E
Grand Rapids, MN 55744

Abstract: Limesink wetlands are a common aquatic habitat in southwest Georgia, USA. These wetlands are non-alluvial, occupying shallow depressions formed from dissolution of limestone bedrock and collapse of surface sands. They are seasonally inundated, with a typical hydroperiod extending from late February to early July. Little is known about factors influencing invertebrate community structure in limesink wetlands. Recently, it has been suggested that regular inundation and drying are important influences on community structure in some seasonal wetlands. We had an opportunity to examine this hypothesis in 3 forested limesink wetlands. Quantitative samples of invertebrates were taken monthly on benthic and wood surfaces from March 1994 through July 1995. This included a period of unusually heavy precipitation, summer and autumn of 1994, when the wetlands would normally be dry. Immediately following inundation, benthic samples were dominated by amphipods (*Crangonyx sp.*), isopods (*Caecidotea sp.*), cladocerans, and copepods. Maximum total densities (1000–4000 individuals per m^2) were observed within 3 months of inundation. During summer and autumn, densities decreased (< 500 individuals per m^2), and the benthos was dominated by larval chironomids. Wood surfaces were dominated by chironomids, with greatest densities (1000–3000 individuals per m^2) observed in summer and autumn. Although not quantified, freshwater sponge became very abundant on wood surfaces during autumn. During the following spring (1995), invertebrate densities on sediments remained low, and few amphipods, isopods, cladocerans, or copepods were collected. Chironomids remained very abundant on wood. Our results suggest that extended inundation is a disturbance to some elements of wetland invertebrate communities. Extended inundation may cause short-term reductions in populations by eliminating summer refugia (amphipoda, isopoda) or by altering environmental cues necessary for the completion of life cycles (cladocerans, copepods).

Key Words: wetlands, invertebrates, community structure, wood, extended hydroperiod, southwest Georgia

INTRODUCTION

In the southeastern USA, non-alluvial wetlands are a conspicuous feature of the landscape (Tansey and Cost 1990, Sutter and Kral 1994). These wetlands are often shallow basins, seasonally inundated, and isolated from streams or other permanent water bodies (Sutter and Kral 1994). While the ecological structure and function of perennially inundated wetlands (i.e., those associated with lakes or rivers) have been extensively studied, less is known about seasonal wetlands. The non-alluvial wetlands of the southeast have been recognized as sites of moderate productivity, high biological diversity, and important wildlife habitat (e.g., Sklar 1985, Taylor et al. 1988, 1989, Dodd 1992, 1995). They are also threatened by regional development and agriculture (Tansey and Cost 1990, Sutter and Kral 1994).

Traditionally, physical conditions of seasonal aquatic habitats have been thought of as adverse to aquatic organisms (e.g., Williams 1985). Common stresses include desiccation, high environmental temperatures, fluctuating or high salinity, low oxygen concentrations, and environmental unpredictability (Williams 1985). However, many taxa possess specific adaptations that make them well suited for life in seasonal wetlands. Adaptations include production of drought-resistant or diapausing life-cycle stages, migration to refugia within the habitat, or migration to perennial aquatic habitats within the region (Wiggins et al. 1980, Williams

1985). Although drying eliminates aquatic habitat, it may provide advantages to organisms with the appropriate adaptations. Seasonal drying prevents sediment anoxia, particularly in hot climates, thus ensuring a summer refuge in moist sediments (Sklar 1985). Drying reduces predator abundance by reducing colonization of seasonal wetlands by invertivorous fish (Wiggins et al. 1980, Batzer and Wissinger 1996). Although the invertebrate assemblages of seasonal wetlands have been recognized as unique and specialized to survive drying (e.g., Wiggins et al. 1980, Williams 1985), there have been few studies examining the affect of hydrologic variation on seasonal wetland invertebrates.

Little is known about factors influencing invertebrate community structure in limesink wetlands or many other southeastern seasonal wetlands. Although the length of the hydroperiod has been recognized as an important influence (e.g., Sutter and Kral 1994), there have been few studies of year-to-year hydrologic variation and its effect on invertebrates. In addition, the role of wood debris as a habitat has been virtually ignored, even though many southeastern wetlands are heavily forested (Mitsch and Gosselink 1993). Wood debris has been recognized as a site of high invertebrate activity, diversity, and productivity in southeastern Coastal Plain streams (Benke et al. 1985) and in forested wetlands on their floodplains (Thorp et al. 1985). To date, most studies of southeastern wetland invertebrates have focused on planktonic or benthic assemblages.

As part of a study of habitat use by invertebrates of forested limesink wetlands, we examined effects of extended inundation. During summer and autumn of 1994, a series of tropical depressions resulted in unusually heavy precipitation in southwest Georgia. Many limesink wetlands remained continuously inundated from March 1994 through July 1995, substantially extending the normal hydroperiod. Our objectives were to examine habitat use by invertebrates in three forested wetlands and to evaluate responses of these communities to unusual hydrologic conditions.

METHODS

Study Site

This study was conducted on the Gulf Coastal Plain of southwest Georgia in a physiographic region known as the Dougherty Plain. This area of about 11,400 km^2 is bounded by the Chattahoochee River and Fall-line Hills to the west and north and by Pelham Escarpment to the south and east (Beck and Arden 1983). It is an area of low topographic relief, with deep sandy soils overlying highly fractured limestone bedrock. Because of the porous soils, stream drainage densities are low and most water movement occurs through subsurface flow paths (Beck and Arden 1983).

A conspicuous feature of the Dougherty Plain is its numerous limesink wetlands. These shallow surface depressions form from dissolution of limestone bedrock followed by subsidence of overlying sands (Hendricks and Goodwin 1952). While most are isolated from permanent stream channels, some depressions become connected by ephemeral channels during periods of heavy rain. Limesink wetlands range from small sinks with steep sides to shallow flat expanses of several hectares (Wharton 1978) and have depths ranging from <1 to 8 m (Torak et al. 1991). Vegetation varies from open grassy meadows to forests composed of flood-tolerant cypress/hardwoods (Lynch et al. 1986). Many of the depressions have a confining layer of silt and clay that enables them to hold water following heavy rainfall (Hendricks and Goodwin 1952, Hayes et al. 1983).

Macroinvertebrate communities were sampled in three forested wetlands located on the Ichauway Ecological Reserve. The reserve is a 10,500-ha remnant tract of longleaf pine/wire-grass savanna. Study wetlands (Collins Pond, King Pond, and Predest Pond) ranged in size from 7.5 to 15 ha and showed little evidence of recent human disturbance, having mature forest stands (Lynch et al. 1986). Their vegetation is dominated by an open to dense canopy of pond cypress (*Taxodium ascendens* Brongn.) over a subcanopy of swamp blackgum (*Nyssa biflora* (Walter) Sargent) (Lynch et al. 1986). Based on canopy vegetation, they can be classified as swamp tupelo forests, one of 18 non-alluvial wetland communities recognized across the Coastal Plain (Sutter and Kral 1994). Swamp tupelo wetlands are generally nutrient-poor, with low alkalinity and a hydroperiod established by rainfall (Mitsch and Gosselink 1993, Sutter and Kral 1994). The wetlands we sampled are mostly shallow (< 1m), although a few small deeper depressions (~ 2m) are present (S. Golladay, personal observation). The primary habitats in the wetlands are benthos (i.e., leaf litter and fine organic detritus with little inorganic matter) and wood debris.

The timing of wetland inundation and drying are strongly influenced by regional patterns of precipitation. Annual precipitation in the region averages 130 cm (1895–1995, National Climate Data Center, National Oceanic and Atmospheric Adminstration, Ashville, North Carolina, Climate Division Drought Database). Rainfall varies greatly in intensity and duration. Winter storms (January through March) are typically of long duration and moderate intensity, while summer storms (June through August) are generally short in duration and relatively intense (Hayes et al. 1983). During winter, evapotranspiration is low and

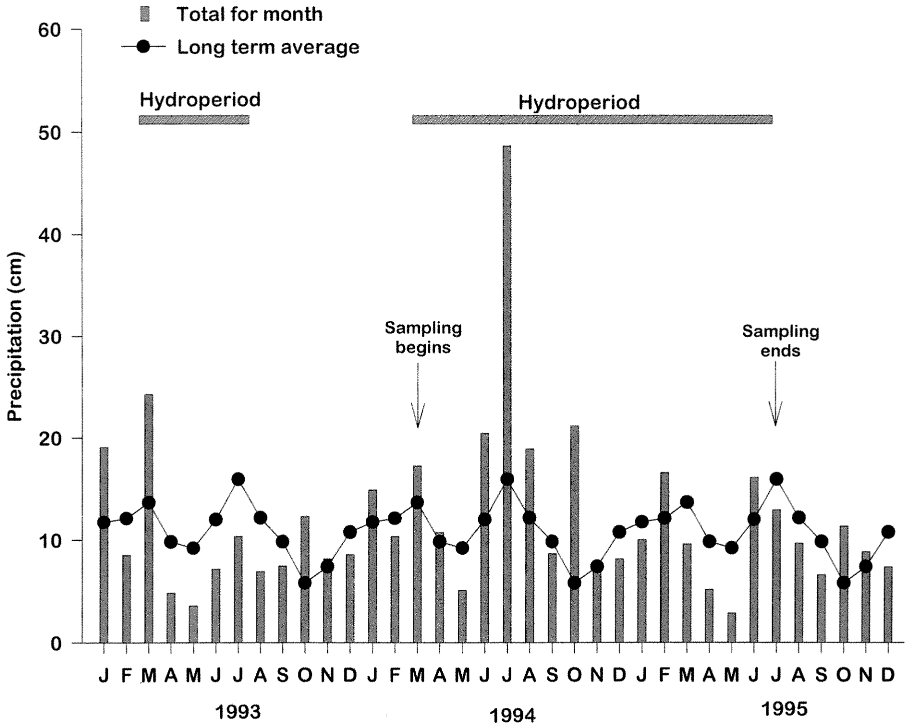

Figure 1. Annual and long-term monthly precipitation for southwest Georgia, USA. Data are from the National Climate Data Center, National Oceanic and Atmospheric Administration, Drought Division Database, Ashville, NC, USA. Long-term means are based on 100 years of data. Hydroperiod is the period of surface inundation and is based on observation of the wetlands.

wetlands fill in response to extended rainfall. Wetlands respond rapidly to precipitation, often filling within 24 to 48 hours of storms. During summer, most precipitation is lost through evapotranspiration, and wetlands dry over a period of a few weeks. Most wetlands in an area dry at about the same time.

A typical hydroperiod for limesink wetlands extends from late winter through early summer and was observed during 1993 (Lynch et al. 1986, Figure 1). Wetlands began filling during March 1994 in response to late winter storms and began to dry during early June 1994. A series of tropical storms and depressions beginning in late June 1994 and continuing through summer and autumn resulted in greater than average precipitation (Figure 1). Total amount of rainfall in 1994 was 192 cm, 48% greater than the long term average (130 cm), and was the greatest annual rainfall recorded in the region (1895–1995, National Climate Data Center, National Oceanic and Atmospheric Adminstration, Ashville, North Carolina, Climate Division Drought Database). As a result, wetlands remained inundated throughout 1994. During 1995, 119 cm of rainfall were recorded, and wetlands dried during July.

Sample Collection and Analysis

Invertebrate sampling began following wetland inundation in March 1994. At each wetland, three sampling transects were established at equal intervals around the perimeter. Transects extended from the outer edge of the wetland margin toward the center of wetland. At roughly monthly intervals, we collected one sample from the benthic surface and one from wood debris at each transect (i.e., 3 samples from each habitat per pond on each date). All collections were made within 5 to 10 m of the edge of the water at depths of 30 to 50 cm. Samples were collected randomly, and as ponds filled or dried, we moved along the transect so as to consistently sample at a 30 to 50 cm depth. Benthic samples were collected using a 25.4-cm-diameter core and hand operated bilge pump. Coarse organic matter (primarily whole leaves and leaf fragments) was removed from the core by hand and placed in a container. Water and fine material (primarily organic matter) were pumped from the core through a 500-μm-mesh net. The contents of the net were placed in a container, preserved in ethanol, and taken to the laboratory for processing and counting. The samples included organisms present in the water column, on the sediment surface, and within the sediment.

On each sampling date, a single piece of wood debris was sampled at each transect. Submerged wood was placed in a bucket and taken to shore. On shore, invertebrates were washed from wood surfaces into a bucket using a soft bristle brush and wash bottle.

Wood was carefully inspected following washing, and any remaining invertebrates were picked from the surface. Contents of the bucket were rinsed onto a 500-μm-mesh sieve, preserved in 70% ethanol, and taken to the laboratory for processing and counting. The length and diameter of wood was recorded and used to estimate area sampled. During preliminary studies, we transported representative pieces of rinsed wood to the laboratory and tested the efficiency of our collecting procedure. Wood was placed in a bucket containing a few cm of water and inspected daily for invertebrates leaving the wood as it slowly dried. This procedure verified that our field procedures were collecting a majority (>95%) of invertebrates present on wood surfaces.

In the laboratory, invertebrates were sorted by hand and identified using Merritt and Cummins (1984) and Pennak (1989). Based on information in taxonomic references, food habits of each taxon were determined and assigned to broad feeding categories (i.e., predator, detritivore, scavenger). Larval chironomids were excluded from the classification because this group contains both predators and detritivores. Predators were assumed to feed on other macroinvertebrates. While some taxa classified as detritivores derive substantial nutrition from bacteria, protozoans, or other microinvertebrates, we assumed most were feeding on the detrital aggregate. Scavengers were assumed to be opportunistic feeders on either plant or animal matter.

Invertebrate densities were expressed as number of individuals per m^2 of wood or benthic surface sampled. To improve homogeneity of variances, means for each pond/substrate/date combination were calculated using a $\ln(n + 1)$ transformation; back-transformed means were used in subsequent analyses (Sokal and Rohlf 1995). Detrended Correspondence Analysis (DCA) was used to examine patterns in community composition across habitats and over time. This ordination was exploratory, designed to formulate hypotheses about community composition rather than test them. The data were entered into a matrix consisting of taxon densities in each of 96 samples representing 2 habitat (benthos, wood), 3 pond (Collins, King, Predest), and 16 sampling date levels. Ordinations were performed using PC-Ord Version 2.0 (MJM Software Design, Gleneden Beach, OR, USA). A single ordination was used to compare community assemblages on wood and benthic surfaces, although for clarity, benthic and wood ordination scores were graphed on separate but identically scaled axes. Prior to ordination, taxa present in fewer than 5% of samples were eliminated from the data matrix, but no other transformations were performed on means.

Sample scores on axes 1 and 2 were derived from the ordination, averaged by season (spring 1994, summer 1994, autumn 1994, winter 1995, spring 1995), pond, and habitat, and then plotted to examine temporal trajectories in invertebrate community dynamics. Since the underlying distribution of axis scores was not known, inferential statistics could not be used to compare seasonal scores. A similar approach has been used by Palmer et al. (1995) to explore responses of benthic communities to disturbance.

Resistance indices for benthic and wood surface communities were calculated by comparing euclidean distances of average seasonal sample scores for spring 1994 and spring 1995. Resistance indices were assumed to reflect the ability of a community to resist displacement after a disturbance (*sensu* Webster et al. 1975). Resistance of the community to unusually long inundation was considered to be inversely proportion to a euclidean distance (e.g., Halpern 1988). Average total invertebrate density was calculated for spring 1994 and spring 1995 for each pond and habitat. Differences in density, before and after extended inundation, were compared using a paired t-test (Sigmaplot for Windows Version 2.0, Jandel Scientific Software, San Rafael CA, USA). However, because we sampled only one extended hydroperiod, differences in invertebrate density cannot be strictly attributed to extended inundation.

RESULTS

Invertebrate Densities and Habitat Use

The forested limesink wetlands we studied supported an abundant invertebrate fauna. Within a few weeks of inundation, densities of invertebrates in benthic samples were ~1000 individuals per m^2 in all ponds (Figure 2). Early benthic communities were dominated by amphipods (*Crangonyx* sp.) and isopods (*Caecidotea* sp.) (Figure 3). Most individuals collected were mature. After several months of inundation, cladocerans and copepods became abundant, and densities of amphipods and isopods declined. Maximum densities of invertebrates in benthic samples were observed within 3 months of inundation. Invertebrate densities were low during summer and autumn of 1994, and the benthic community was dominated by larval chironomids.Wood surface invertebrate densities peaked at 2000–3000 individuals per m^2 during late spring and summer. Larval chironomids were almost always the most abundant invertebrate collected from wood surfaces (Figure 4). Amphipods, isopods, copepods, and cladocerans, while present on wood surfaces, were never as abundant as in benthic samples. Invertebrate densities on wood decreased during the winter of 1995 and increased during the spring of 1995. Invertebrate

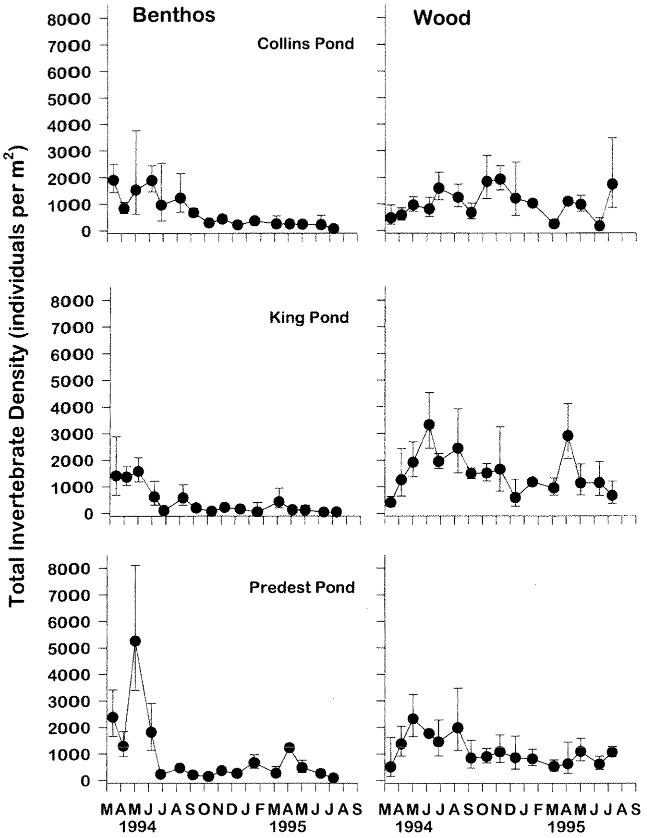

Figure 2. Total invertebrate densities in benthic samples taken from forested limesink wetlands in southwest Georgia, USA. Densities were calculated using a ln(n + 1) transformation and then back transformed. Values are means ± 1 standard error.

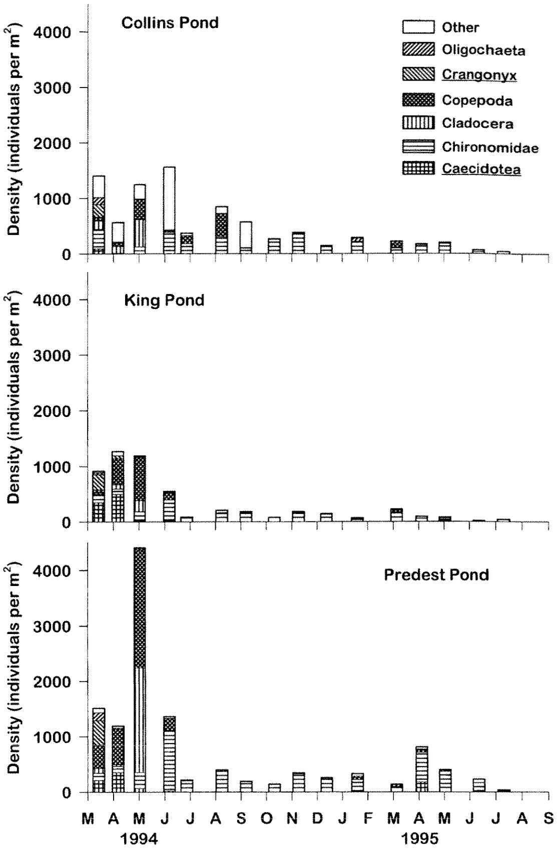

Figure 3. Densities of dominant invertebrate taxa in benthic samples taken from forested limesink wetlands in southwest Georgia, USA. Densities were calculated using a ln(n + 1) transformation and then back transformed. Values are means.

densities on wood during the spring of 1995 were comparable to those observed the previous year.

In all, 33 taxa from 12 invertebrate orders were collected on wood and benthic surfaces in our sites (Table 1). Most taxa were present in about the same frequency on benthic and wood surfaces. However, several exceptions were evident. Larval chaoborids and crayfish (Cambaridae) were found in greater frequency on benthic than wood surfaces. An aquatic neuropteran (*Sisyra* sp.) was found with greater frequency on wood than the benthos. *Sisyra* sp. is a predator of freshwater sponges. Although not quantified in our study, freshwater sponges were found almost exclusively on wood debris or on the submerged trunks of trees.

Of the 33 taxa collected, 6 dominated the community. Amphipods, oligochaetes, cladocerans, copepods, chironomids, and isopods were present on 60–100% of days sampled and accounted for >90% of invertebrate density on both substrates. Most of the non-chironomid invertebrate taxa were detritivorous, probably reflecting detritus-based food webs in these sites.

Temporal Trends in Community Structure and Responses to Extended Inundation

Ordination of invertebrate samples suggested a temporal change in benthic community structure strongly associated with axis 1 of the ordination (Figure 5, eigenvalue 0.501). The ordination is interpreted by noting relative associations among samples and taxa in ordination space. Samples closely associated in ordination space have similar taxa composition, while samples dissociated in the ordination have dissimilar composition. The sample scores for benthos and wood were derived from the same ordination but plotted separately for clarity.

Benthic sample positions from March, April, and May 1994 reflect the increasing importance of isopods, copepods, and cladocerans following inundation. The distribution of points for benthic samples was similar in all wetlands. An unidentified coleopteran (UNKC) was also very abundant in April 1994 benthic samples collected from Collins and Predest Ponds. With the exception of several outliers from Collins Pond, ben-

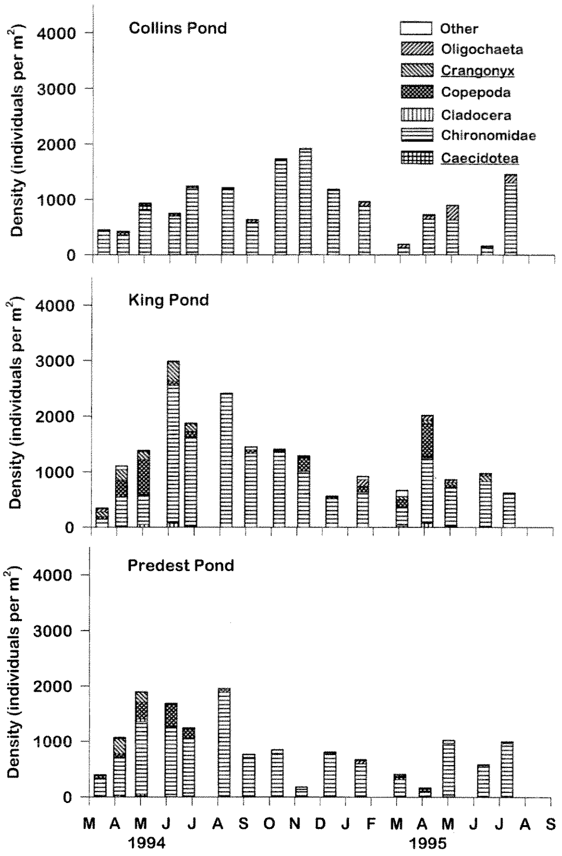

Figure 4. Densities of dominant invertebrate taxa in wood samples taken from forested limesink wetlands in southwest Georgia, USA. Densities were calculated using a ln(n + 1) transformation and then back transformed. Values are means.

thic samples from the rest of the study period were closely associated. The grouping of samples from summer 1994 through the end of the study (lower left of the joint plot) reflects the decreasing importance of early spring benthic taxa and their replacement by a community dominated by larval chironomids (CHIR), *Dineutus* sp. (DINE), Hydroptilidae (HYDR), and unidentified larvae (UNKL). The position of samples along axis 2 was strongly associated with an unidentified pupae (UNKP), *Hesperocorixa* sp. (HESP), Chaoboridae (CHAO), Libellulidae (LIBE), an unidentified dipteran (UNKD), *Faxonella* sp. (FAXO), and *Sisyra* sp. (SISY) (Figure 5, eigenvalue 0.304). The final group of samples from Collins Pond (Jun 94, Aug 94, and Jul 95) had UNKP and CHAO in very high densities and lacked UNKD, FAXO, SISY.

Wood samples did not show a strong temporal trend, nor was substantial dispersion observed along axis 2. The ordination scores of wood samples reflects their consistent domination by larval chironomids and their similarity to late study benthic samples.

Graphs of seasonal mean axis scores suggest an effect of extended inundation on benthic communities (Figure 6). In all wetlands, spring 1994 samples were substantially different from all other seasons. Euclidean distances between spring 1994 and spring 1995 benthic communities were relatively large (113–139 units, Table 2). These results suggest a very low resistance of the spring benthic invertebrate community to inundation extending into summer and autumn. Euclidean distances for wood-surface communities were smaller (Figure 6, Table 2), reflecting high resistance to extended inundation. These conclusions are also supported by the fact that total invertebrate density in benthic (paired t-test, $p = 0.05$, Table 2), but not wood samples (paired t-test, $p = 0.8$, Table 2), decreased following extended inundation.

DISCUSSION

Comparison with Other Studies of Seasonal Wetland Invertebrates

The ability to respond rapidly to the presence of surface water seems to be an important characteristic of invertebrate communities in seasonal wetlands. Often, extremely high invertebrate population densities are observed within a few weeks of inundation (Wiggins et al. 1980, Williams 1985, Watson et al. 1995). Our results are consistent with this observation, particularly for benthic samples. High invertebrate densities were observed within 1 to 3 months of inundation.

Several factors have been proposed as contributing to the rapid response of wetland invertebrates to seasonal inundation. In forested wetlands, the rapid response may be caused by the presence of high quality detrital food (e.g., Sklar 1985, Lake et al. 1989). Late winter standing crops of organic matter (leaves and wood) ranging from 2,000 to 5,400 g DW/m^2 have been reported in seasonally inundated wetlands of the Atlantic Coastal Plain (Day 1979). In addition, alternate drying and wetting has been suggested to enhance detrital quality (Wiggins et al. 1980), although as far as we know, this has not been tested. We did not quantify litter inputs, but leaf litter and other detritus were abundant throughout this study (S. Golladay, personal observation).

Sklar (1985) suggested that physical conditions, particularly water temperature and dissolved oxygen, regulate community abundance and composition in the forested wetlands of the Gulf Coastal Plain. In the southeast, as temperatures increase during spring, dissolved oxygen concentrations decrease in wetlands (Ziser 1978, Sklar 1985). Sklar (1985) suggested that high temperature and low oxygen stimulate behavioral or physiologic adaptations (discussed below) for

Table 1. Taxa list of invertebrates found in association with benthic and wood habitats in forested wetlands of southwest Georgia. Code is the abbreviation used in ordination diagrams. Classification is the dominant food habits of the group. Numbers are frequencies with which invertebrates were collected during monthly sampling from March 1994 through July 1995. To be counted, a taxon had to be present on 1 of 9 samples taken from the ponds on a particular date. Frequency was calculated as (months present/months sampled) * 100.

Group	Family	Genus	Code	Classification	Benthos	Wood
Amphipoda	Crangonyctidae	*Crangonyx*	CRAN	detritivore	87.5	93.8
Oligochaeta			OLIG	detritivore	75.0	93.8
Cladocera			CLAD	detritivore	62.5	81.3
Coleoptera	Dytiscidae	*Agabus*	AGAB	predator	6.3	12.5
		Dytiscus	DYTI	predator	6.3	6.3
	Gyrinidae	*Gyrinis*	GYRI	predator	6.3	18.8
		Dineutus	DINE	predator	6.3	31.3
	Haliplidae	*Peltodytes*	PELT	predator	6.3	0.0
	Heliodidae	*Scirtes*	SCIR	detritivore	0.0	25.0
	Hydroptilidae		HYDR	unknown	12.5	12.5
	unknown		UNKC	unknown	31.3	37.5
Copepoda			COPE	detritivore	93.8	100.0
Decapoda	Cambaridae	*Faxonella*	FAXO	scavenger	62.5	18.8
Diptera	Ceratopogonidae	*Bezzia*	BEZZ	predator	75.0	75.0
	Chaoboridae		CHAO	predator	81.3	18.8
	Chironomidae		CHIR	unknown	100.0	100.0
	Culicidae	*Culex*	CULI	detritivore	0.0	6.3
	Stratiomyidae		STRA	detritivore	0.0	6.3
	unknown		UNKD	unknown	25.0	31.3
Ephemeroptera	Baetidae	*Callibaetis*	CALL	detritivore	6.3	12.5
Hemiptera	Corixidae	*Corisella*	CORI	predator	6.3	0.0
		Hesperocorixa	HESP	predator	37.5	25.0
	Gerridae	*Gerris*	GERR	predator	0.0	6.3
	Notonectidae	*Buenoa*	BUEN	predator	18.8	0.0
		Notonecta	NOTO	predator	6.3	6.3
Isopoda	Ascellidae	*Caecidotea*	CAEC	detritivore	75.0	87.5
Megaloptera	Corydalidae	*Chauloides*	CHAU	predator	0.0	18.8
Neuroptera	Sisyridae	*Sisyra*	SISY	predator	18.8	75.0
Odonata	Coenagrionidae	*Enallagma*	ENAL	predator	6.3	18.8
	Lestidae	*Lestes*	LEST	predator	6.3	0.0
	Libellulidae		LIBE	predator	31.3	56.3
unknown larvae			UNKL	unknown	18.8	18.8
unknown pupae			UNKP	unknown	68.8	56.3

avoiding stresses associated with summer. For invertebrates intolerant of low oxygen, rapid response to inundation would maximize opportunities for population growth prior to stressful summer conditions. In this study, water temperature and dissolved oxygen were not measured on each sampling date. However, we have made occasional surveys of physical conditions at our sample sites. During summer surveys, we observed water temperatures of 28–32 °C and dissolved oxygen concentrations ranging from < 1mg/L at the sediment/water interface to 2 mg/L at the water surface (S. Golladay, personal observation). To date, the role of environmental stress in regulating wetland invertebrate community structure has not been systematically investigated in wetlands. Clearly, more experimental research is needed on biological and physical factors influencing community organization in these systems.

Densities of benthic invertebrates observed in this study (1000–4000 per m^2) are low compared to other studies of southeastern wetlands. Sklar (1985) reported average invertebrate densities >12,000 per m^2 in cypress-hardwood wetlands on the floodplain of the Mississippi River in southern Mississippi. Duffy and LaBar (1994) reported invertebrate densities ranging from 10,000 to 25,000 per m^2 in winter and spring samples taken from seasonal floodplain wetlands in east-central Mississippi. However, Duffy and LaBar

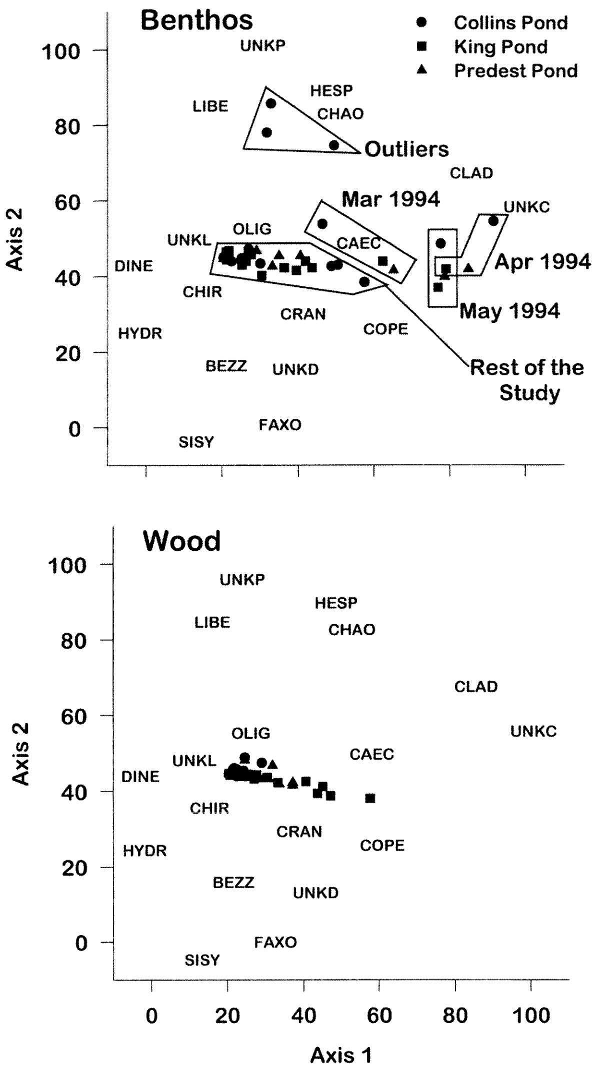

Figure 5. Detrended Correspondence Analysis of invertebrate communities of forested limesink wetlands of southwest Georgia, USA. A single ordination was used to compare communities on wood and benthic surfaces. However, for clarity, wood and benthic communities are graphed on separate axes. Taxa associated with abbreviations are listed in Table 1. Symbols are sample scores and abbreviations are taxa scores derived from the ordination.

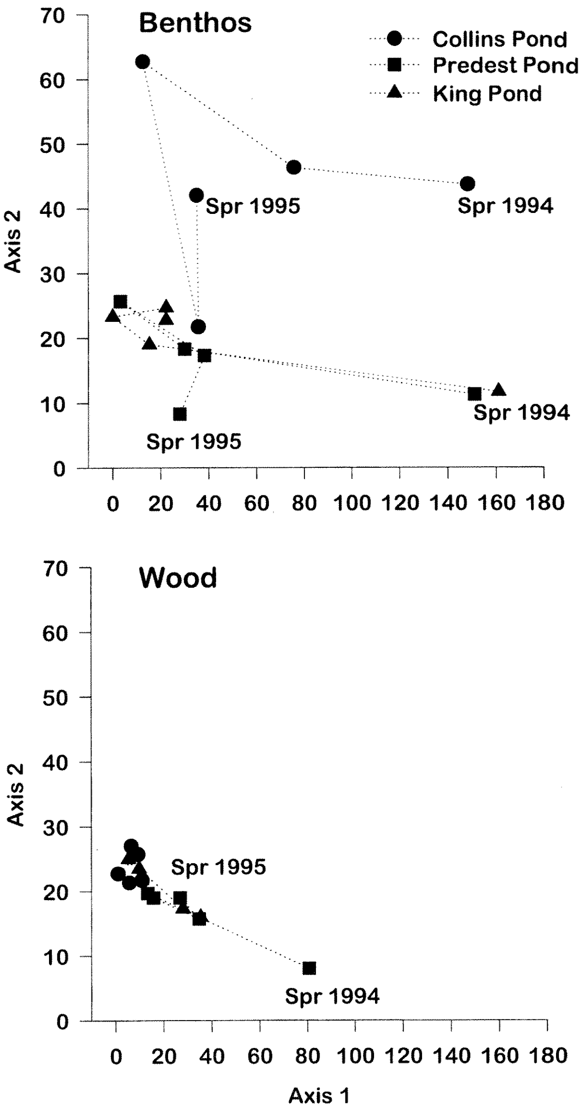

Figure 6. Seasonal mean axis scores from Detrended Correspondence Analysis of invertebrate communities of forested limesink wetlands of southwest Georgia, USA. A single ordination was used to compare communities on wood and benthic surfaces. However, for clarity, wood and benthic communities are graphed on separate axes.

(1974) used a smaller mesh (250 μm) sampler than Sklar (1985) or our study. The smaller mesh may have resulted in more efficient collection of copepods and cladocerans, which contributed significantly to total invertebrate population density but little to total biomass (Duffey and LaBar 1974).

The low invertebrate population densities we observed also may be due to the isolated nature of limesink wetlands. Wetlands associated with river floodplains, like those described above, probably receive seasonal subsidies of nutrients during floods. Downstream drift might also be an important source of colonists to floodplain wetlands. Sklar (1985) also noted high invertebrate densities in mats of floating aquatic vegetation, a habitat not present in forested limesink wetlands. As observed in our study, crustaceans, oligochaetes, and larval chironomids were very abundant in other southeastern wetlands (Ziser 1978, Sklar 1985, Duffy and LaBar 1994).

While wood debris is abundant in some forested wetlands (e.g., Thorp et al. 1985), its importance as invertebrate habitat has been largely ignored. Thorp et al. (1985) reported invertebrate densities averaging 3000 to 6000 per m^2 on wood debris in a southeastern

Table 2. Comparison of community composition on benthic and wood substrates before (Spring 1994) and after (Spring 1995) extended inundation of limesink wetlands. Euclidean distances in 2-dimensional ordination space were calculated from average seasonal axis scores based on Detrended Correspondence Analysis. Low values suggest a high degree of similarity between sample times and, thus, high resistance to extended inundation. Large values suggest a low degree of similarity and low resistance to extended inundation. Changes in average density were calculated as the difference in average total invertebrate density between Spring 1994 and Spring 1995. Negative values indicate a decrease, positive values an increase in density. Differences were compared using a paired t-test.

Substrate	Site	Euclidean Distance	Change in Average Density (# per m^2)	Paired t-test
Benthic	Collins Pond	113	−1231	$t = 4.327$ $p = 0.05$, $n = 3$
	King Pond	123	−1362	
	Predest Pond	139	−2458	
Wood	Collins Pond	7	319	$t = -0.153$ $p = 0.8$, $n = 3$
	King Pond	55	272	
	Predest Pond	27	474	

cypress-gum swamp. Gladden and Smock (1990) reported average invertebrate densities of ~1900 per m^2 on wood debris on the floodplain of a stream in Virginia. Densities we observed were similar (1000–3000 per m^2) to those reported by Gladden and Smock (1990). The cypress-gum wetlands studied by Thorp et al. (1985) received perennial flow from an adjacent stream, and higher densities they reported may have been associated with nutrient subsidies from the stream and downstream drift of colonists. Gladden and Smock (1990) reported that seasonal drying eliminated invertebrates from floodplain wood, reducing densities compared to wood debris in perennial stream channels.

Effects of Extended Inundation on Limesink Invertebrate Assemblages

There has been considerable interest in adaptations that permit invertebrates to survive in seasonal wetlands (e.g., Wiggins et al. 1980, Williams 1985, Batzer and Wissinger 1996). Organisms lacking a desiccation-resistant life cycle stage or ability to migrate tend to be eliminated by seasonal drying (Williams 1985). Conversely, in some cases, prolonged inundation during normally dry seasons may represent a disturbance to the wetland community. Neckles et al. (1990) reported that extended inundation decreased densities of cladocerans, ostracods, and larval mosquitos (Culicidae) in seasonally flooded prairie marshes in south-central Manitoba, Canada. Neckles et al. (1990) did not see any changes in food resources or predation pressure and attributed negative impacts of extended inundation to elimination of environmental cues required for life cycle progression.

In our study, altered benthic community structure and decreases in total invertebrate density following extended inundation suggest an adverse effect on some of the invertebrate fauna of forested limesink wetlands. Detrital organic matter was abundant throughout our study (S.W. Golladay, personal observation), and non-chironomid predators were never common (Figures 3–5). Thus, altered food availability or predation pressure did not seem responsible for changes in the invertebrate community. Altered physical and chemical conditions, particularly during summer flooding, have been reported to affect wetland invertebrate populations (e.g., Wiggins et al. 1980, Sklar 1985). Amphipods and isopods lack terrestrial life stages and are not known to produce desiccation-resistant eggs (Wiggins et al. 1980). However, they are common in southeastern wetlands (e.g., Sklar 1985) and probably survive summer conditions by aestivating in moist but not saturated sediments (Wiggins et al. 1980, Sklar 1985). Cladocerans and copepods survive seasonal drying by producing drought-resistant eggs (both groups) or have drought-resistant developmental stages (copepods) (Wiggins et al. 1980). In these groups, egg hatching or emergence is not only dependent on the presence of water but also on receiving the right sequence of seasonal cues (Wiggins et al. 1980). In limesink wetlands, extended inundation altered the typical seasonal progression of temperature and moisture conditions in sediments. We hypothesize that low population densities resulted from delayed development of desiccation-resistant life cycle stages.

In our study, extended inundation did not limit all taxa. Larval chironomid densities were highest in benthic and wood samples during late spring and summer. Larval chironomids are tolerant of low oxygen conditions (Ziser 1978, Wiggins et al. 1980, Butler and

Anderson 1990), and this undoubtedly contributed to their persistence during extended inundation. Much of the wood we sampled was in the water column above the sediment surface, and its proximity to water surface may provide higher dissolved oxygen concentrations than in the sediments. Thus, wood debris may be an important refuge for some invertebrates during extended inundation.

Limesink wetlands of southwest Georgia support an abundant and dynamic invertebrate fauna. Little is known about factors regulating invertebrate populations in these and other seasonal wetlands. Our results suggest that the presence of surface water extending into summer and autumn may be a disturbance to some elements of the invertebrate community. Extended inundation may reduce invertebrate populations by eliminating summer refugia (amphipods, isopods) or by altering environmental cues necessary for life-cycle development (cladocerans, copepods). Invertebrates capable of tolerating low oxygen conditions or successfully colonizing wood debris (i.e., larval chironomidae) seem resistant to altered hydrologic regimes. The invertebrate communities of limesink wetlands are strongly linked to hydrology, with the seasonal timing of inundation and drying being critical for community persistence.

ACKNOWLEDGMENTS

We thank Frankie Hudson for her assistance with coordinating the processing and sorting of invertebrate samples. Dorothy Garrett and Cookie Hudson also assisted with sample processing. Matt Lauck and Kevin Watt assisted with the field work. Funding for this research was provided by the J.W. Jones Ecological Research Center and the R.W. Woodruff Foundation. We thank Drs. D. A. Wilcox, M. A. Hanson, and two referees for their help in revising this paper. We thank Kevin Watt for many helpful comments on the final draft of this paper.

LITERATURE CITED

Allard, D. J. 1990. Southeastern United States Ecological Community Classification, Interim Report, Version 1.2. The Nature Conservancy, Southeast Regional Office, Chapel Hill, NC, USA.

Batzer, D. P. and S. A. Wissinger. 1996. Ecology of insect communities in nontidal wetlands. Annual Review of Entomology 41:75–100.

Beck, B. F. and D. D. Arden. 1983. Hydrology and Geomorphology of the Dougherty Plain, Southwest Georgia. Southeastern Geological Society, Tallahassee, FL, USA.

Benke, A. C., R. L. Henry III, D. M. Gillespie, and R. J. Hunter. 1985. Importance of snag habitat for animal production in southeastern stream. Fisheries 10:8–13.

Butler, M. G. and D. H. Anderson. 1990. Cohort structure, biomass, and production of a merovoltine *Chironomus* population in a Wisconsin bog lake. Journal of the North American Benthological Society 9:180–192.

Day, F. P. Jr. 1979. Litter accumulation in four plant communities in the Dismal Swamp, Virginia. The American Midland Naturalist 102:281–289.

Dodd, C. K. 1992. Biological diversity of a temporary pond herpetofauna in north Florida sandhills. Biodiversity and Conservation 1:125–142.

Dodd, C. K. 1995. Reptiles and amphibians in the endangered longleaf pine ecosystem. p. 129–131. *In* E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac (eds.). Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems., U.S. Department of Interior—National Biological Service, Washington, DC, USA.

Duffy, W. G. and D. J. LaBar. 1994. Aquatic invertebrate production in southeastern USA wetlands during winter and spring. Wetlands 14:88–97.

Gladden, J. E. and L. A. Smock. 1990. Macroinvertebrate distribution and production on the floodplains of two lowland headwater streams. Freshwater Biology 24:533–545.

Halpern, C. B. 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology 69:1703–1715.

Hax, C. L. and S. W. Golladay. 1993. Macroinvertebrate colonization and biofilm development on leaves and wood in a boreal river. Freshwater Biology 29:79–87.

Hayes, L. R., M. L. Maslia, and W. C. Meeks. 1983. Hydrology and Model Evaluation of the Principal Artesian Aquifer, Dougherty Plain, Southwest Georgia. Georgia Geological Survey Bulletin 97.

Hendricks, E. L. and M. H. Goodwin. 1952. Water-Level Fluctuations in Limestone Sinks in Southwestern Georgia. Geological Survey Water Supply Paper 1110-E.

Lake, P. S., A. E. Bayly, and D. W. Morton. 1989. The phenology of a temporary pond in western Victoria, Australia, with special reference to invertebrate succession. Archiv fur Hydrobiologie 115:171–202.

Lynch, J. M., A. K. Gholson Jr., and W. W. Baker. 1986. Natural Features Inventory of Ichauway Plantation, Georgia: Volume I. The Nature Conservancy Southeast Regional Office, Chapel Hill, NC, USA.

Merritt, R. W. and K. W. Cummins. 1984. An Introduction to the Aquatic Insects of North America. Kendall/Hunt Publishing Company, Dubuque, IA, USA.

Mitsch, W. J. and J. G. Gosselink. 1993. Wetlands. Van Nostrand Reinhold, New York, NY, USA.

Neckles, H. A., H. R. Murkin, and J. A. Cooper. 1990. Influences of seasonal flooding on macroinvertebrate abundance in wetland habitats. Freshwater Biology 23:311–322.

Palmer, M. A., P. Arensburger, P. S. Botts, C. C. Hakenkamp, and J. W. Reid. 1995. Disturbance and the community structure of stream invertebrates: patch-specific effects and the role of refugia. Freshwater Biology 34:343–356.

Pennak, R. W. 1989. Fresh-water Invertebrates of the United States: Protozoa to Mollusca. John Wiley and Sons, Inc., New York, NY, USA.

Sklar, F. H. 1985. Seasonality and community structure of the backswamp invertebrates in a Louisiana cypress-tupelo wetland. Wetlands 5:69–86.

Sokal, R. R. and F. J. Rohlf. 1995. Biometry, 3rd Edition. W.H. Freeman, New York, NY, USA.

Sutter, R. D. and R. Kral. 1994. The ecology, status, and conservation of two non-alluvial wetland communities in the South Atlantic and Eastern Gulf Coastal Plain, USA. Biological Conservation 68:235–243.

Tansey, J. B. and N. D. Cost. 1990. Estimating the forested-wetland resource in the southeastern United States with forest survey data. Forest Ecology and Management, 33/34:193–213.

Taylor, B. E., R. A. Estes, J. H. K. Pechmann, and R. D. Semlitsch. 1988. Trophic relations in a temporary pond: larval salamanders and their microinvertebrate prey. Canadian Journal of Zoology 66: 2191–2198.

Taylor, B. E., D. L. Mahoney, and R. A. Estes. 1989. Zooplankton production in a carolina bay. p. 425–435. *In* R. R. Sharitz and J. W. Gibbons (eds.) Freshwater Wetlands and Wildlife. USDOE Office of Scientific and Technical Information, Oak Ridge, TN, USA.

Thorp, J. H., E. M. McEwan, M. F. Flynn, and F. R. Hauer. 1985. Invertebrate colonization of submerged wood in a Cypress-Tupelo swamp and blackwater stream. The American Midland Naturalist 113:56–68.

Torak, L. J., G.S . Davis, G. A. Strain, and J. G. Herndon. 1991. Geohydrology and evaluation of water-resource potential of the upper Floridan Aquifer in the Albany area, Southwest Georgia. U.S. Geological Survey Open-File Report 91–52.

Watson, G. F., M. Davies, and M. J. Tyler. 1995. Observations on temporary waters in northwestern Australia. Hydrobiologia 299: 53–73.

Webster, J. R., J. B. Waide, and B. C. Patten. 1975. Nutrient recycling and the stability of ecosystems. p. 1–27. *In* F. G. Howell, J. B. Gentry, and M. H. Smith (eds.) Mineral Cycling in Southeastern Ecosystems. ERDA Symposium Series Conf-740513. Washington, DC, USA.

Wharton, C. H. 1978. The Natural Environments of Georgia. Georgia Department of Natural Resources, Altanta, GA, USA.

Wiggins, G. B., R. J. Mackay, and I. M. Smith. 1980. Evolutionary and ecological strategies of animals in annual temporary pools. Archiv fur Hydrobiologie Supplement 58:97–206.

Williams, W. D. 1985. Biotic adaptations in temporary lentic waters, with special reference to those in semi-arid and arid regions. Hydrobiologia 125:85–110.

Ziser, S. W. 1978. Seasonal variations in water chemistry and diversity of the phytophilic macroinvertebrates of three swamp communities in southeastern Louisiana. The Southwestern Naturalist 23:545–562.

Manuscript received 6 August 1996; revision received 3 February 1997; accepted 12 June 1997.