2002 *SOUTHEASTERN NATURALIST* 1(2):149-158

AQUATIC INVERTEBRATES IN HARDWOOD DEPRESSIONS OF SOUTHWEST GEORGIA

JULIANN M. BATTLE [1] AND STEPHEN W. GOLLADAY [1]

ABSTRACT – Hardwood depressions in the southeastern United States have been extensively altered due to agriculture and other land management practices. They are small isolated wetlands dominated by oaks that typically become flooded every couple years for a few weeks to several months. We sampled the aquatic invertebrate assemblages of six depressions in 1998 and five depressions in 2001 and found they were composed primarily of clam shrimp, cladocerans, calanoid copepods, and chironomids. The primary functional feeding group was collector-filterers, which comprised >60% of the total numbers. Eubranchiopoda were well represented by two species of clam shrimp (*Lynceus gracilicornis* and *Limnadia lenticularis*) and one species of fairy shrimp (*Streptocephalus seali). L. lenticularis* is the first record of this species in Georgia. Consideration should be made for the conservation of hardwood depressions because of the rare invertebrates they accommodate.

INTRODUCTION

On the Coastal Plain of southeastern United States, the longleaf pine-grassland ecosystem was once the dominant vegetation; now only 3% of the forest remains (Lynch et al. 1986). Hardwood depressions occur as small islands within the expansive longleaf upland forest and are defined by a closed canopy of live oak (*Quercus virginiana* Mill.), as well as other species of oaks (*Q. hemisphaerica*, *Q. geminata*, *Q. laurifolia*) (Lynch et al. 1986). On the Dougherty Plain of southwestern Georgia, depressions occur on a mantled karst landscape and are sites of low plant diversity. Other features include an open and poorly developed understory and depauperate ground cover. Soils are sandy-loam and are primarily non-hydric with scattered hydric inclusions (Goebel et al. 1997). They are intermittently flooded by heavy rains every few years and remain wet for a few weeks to several months.

Historically, much of the longleaf pine-grassland ecosystem has been converted to agriculture and commercial pineland, resulting in the loss of hardwood depressions. Remnant longleaf pine forests are dependent on fire for regeneration and to prevent invasion by hardwoods, which can out-compete longleaf pine. In the past, frequent summer burns set by Native Americans and lightning strikes prevented

[1] J.W. Jones Ecological Research Center at Ichauway, Route 2, Box 2324, Newton, Georgia 31770; jbattle@jonesctr.org.

extensive hardwood intrusions within the longleaf pine forest (Lynch et al. 1986). Present day management practices prescribe low intensity fires during the dormant season (March-April) for the management of native game birds (e.g., quail) and for safety reasons. This has resulted in less intense fires.

It is believed that some hardwood depressions were once mesic areas dominated by pines and grasses (Coffey et al. 2001). Restoration of longleaf pine forests requires the removal of artificial hardwood stands, but it can be difficult if not impossible to discern natural depressions from those created through fire suppression. Once hardwood depressions are established they are difficult to eradicate with cool season burning because oak leaves are poor ignition fuel, most hardwoods have the ability to resprout vegetatively, and most saplings can tolerate low intensity burns if basal diameter is >5 cm (Jacqmain et al. 1999). Before mechanical removal of hardwood depressions, whether due to longleaf pine restoration or agriculture practices, their function and importance to local wildlife (i.e., invertebrates, amphibians, reptiles, songbirds, red-headed woodpecker, wild turkey, squirrels, deer, etc.) needs to be examined. Limited work has shown they provide an acorn crop that can be a considerable seasonal food source for wildlife, mainly squirrels and deer (Wharton 1978). In this paper, we describe for the first time the aquatic invertebrate assemblages associated with these temporary wetlands.

METHODS

The study site was located on the Dougherty Plain in southwestern Georgia on the Ichauway Reserve (31°22'N, 84°48'W; Fig. 1). Ichauway Reserve, the location of the J. W. Jones Ecological Research Center, contains approximately 11,600 ha of longleaf pine-wiregrass ecosystem. Hardwood depressions in the Reserve range in size from 0.1 to >2 ha and vary greatly in shape from narrow discontinuous bands to some that are circular. Study depressions tended to be circular, <1 ha, were not directly connected to other wetlands, and had an average water depth <0.5 m.

An El Nino event occurred in 1998, which resulted in a wet winter and southwest Georgia received approximately 20 cm of rain on 8 March. These circumstances resulted in depressions becoming flooded and created extensive surface flow over low areas of topography causing some hardwood depressions to become temporarily linked to neighboring limesink wetlands. We sampled six hardwood depressions on 2 April 1998 that had been flooded for roughly 3 wk (Fig. 1). From the summer of 1998 through 2000 southwest Georgia experienced a severe drought, but in March 2001, rainfall exceeded 33 cm (Georgia AEMN 2001). On 23 April 2001, after approximately 2 wk of inundation, we sampled only two of the six initial depressions, as the others remained dry, and sampled an additional three depressions that were inundated (Fig. 1).

Aquatic invertebrates were collected from three locations within each depression by taking five sweeps over the same 1-m distance using a 500-um-mesh D-frame sweep-net. Sweeps included sampling the water column, as well as the bottom, by collecting surface detritus. Invertebrate samples were preserved with 70% EtOH, hand-picked in the laboratory, and identified to lowest practical taxonomic level (Pennak 1989, Merritt and Cummins 1996, Epler 2001). For analyses, a sample was considered the sum of invertebrates from all three locations.

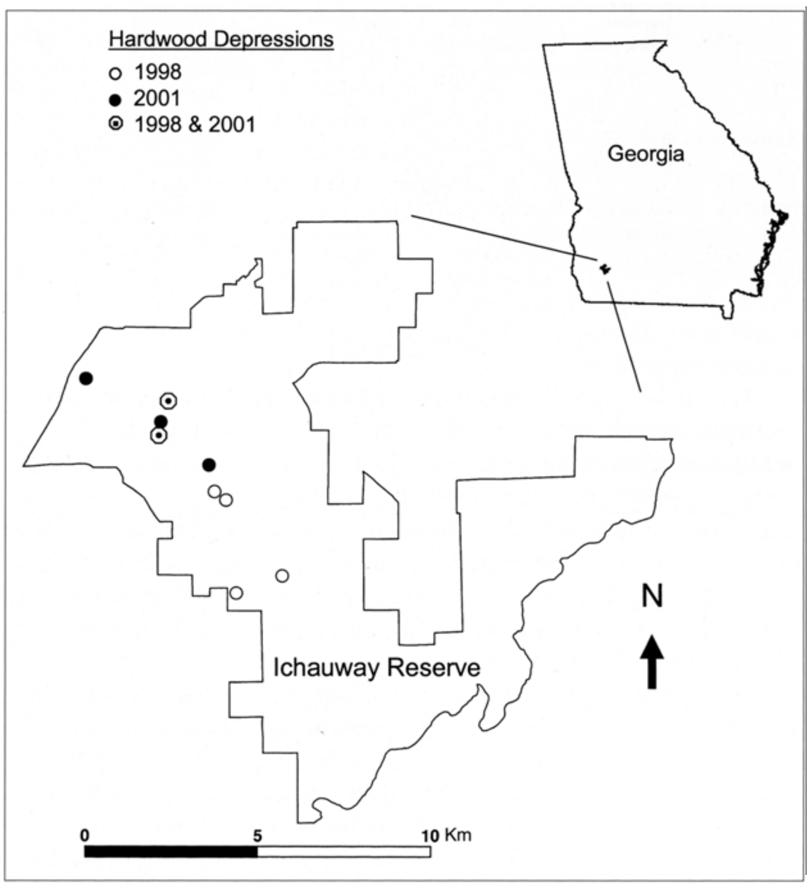

Figure 1. Hardwood depression study sites on the Ichauway Reserve, southwest Georgia.

Table 1. Mean abundance (# individuals/sample) of taxa in hardwood depressions during 1998 and 2001. Asterisk indicates taxon was present but mean abundance was <1. Functional feeding group (FFG) is listed for each taxon (coll. = collector). The '# of sites' indicates the number of depressions in which taxon occurred. Six depressions were sampled in 1998 and five were sampled in 2001.

Taxon				FFG	1998	2001	# of sites
ANNELIDA	Oligochaeta			detritivore	1	0	2
CRUSTACEA	Anostraca	Streptocephalidae	*Streptocephalus seali*	coll.-filterer	0	6	4
	Conchostraca	Lynceidae	*Limnadia lenticularis*	coll.-filterer	1	0	2
			Lynceus gracilicornis	coll.-filterer	143	406	11
	Cladocera (other than *Daphnia* and Sididae)			coll.-filterer	96	550	11
		Daphnidae	*Daphnia* spp.	coll.-filterer	10	653	10
		Sididae		coll.-filterer	6	16	5
	Ostracoda			coll.-filterer	0	12	2
	Calanoida			coll.-filterer	132	315	7
	Cyclopoida			coll.-filterer	21	26	10
	Isopoda	Asellidae	*Caecidotea*	detritivore	*	*	2
	Amphipoda	Crangonyctidae	*Crangonyx floridanus*	detritivore	19	*	5
	Decapoda	Cambaridae	*Cambarus*	detritivore	*	0	1
			Faxonella	detritivore	*	0	1
ARACHNIDA	Hydracarina			parasite	*	1	4
	Other Arachnida			predator	*	0	2
INSECTA	Odonata	Lestidae	*Lestes*	predator	*	0	1
	Hemiptera	Corixidae	*Hesperocorixa*	herbivore	8	0	5
		Gerridae	*Gerris*	predator	1	0	3
		Notonectidae	*Notonecta*	predator	4	0	6
	Coleoptera	Dytiscidae	*Acilius* larvae	predator	2	2	6
			Agabetes larvae	predator	*	0	1
			Agabus larvae	predator	0	*	1
			Copelatus larvae	predator	1	*	4
			Hydaticus larvae	predator	0	*	2
			Thermonectus larvae	predator	0	1	2
			Thermonectus adult	predator	*	0	1
		Gyrinidae	larvae	predator	*	0	1
	Diptera	Ceratopogonidae	*Bezzia* larvae	predator	*	0	1
		Chaoboridae	*Chaoborus* larvae	predator	0	89	5
			Chaoborus pupae		1	12	5
		Chironomidae	pupae		2	0	4
		Tanypodinae	*Procladius*	predator	2	0	4
			Zavrelimyia	predator	2	0	3
		Orthocladiinae	*Corynoneura*	coll.-gatherer	*	0	1
			Gymnometriocnemus	coll.-gatherer	*	0	1
			Psectrocladius	coll.-gatherer	*	0	1
		Chironominae	*Chironomus*	coll.-gatherer	40	9	9
			Chironomini genus III	coll.-gatherer	*	0	1
			Glyptotendipes	shredder	1	2	4
			Kiefferulus	coll.-gatherer	*	6	4
			Parachironomus	predator	*	0	1
			Polypedilum	shredder	25	6	9
			Tanytarsus	coll.-filterer	1	0	2
			Tribelos	coll.-gatherer	0	*	1
		Culicidae	*Culex*	coll.-filterer	0	4	1
	Lepidoptera	Noctuidae		shredder	0	*	1
		Pyralidae	*Crambus*	shredder	0	*	1

Dissolved oxygen and temperature were measured at sample locations with a dissolved oxygen meter (YSI Model 55, Yellow Springs, Ohio). Three 500-ml water samples were also collected for laboratory analyses. Using standard procedures (Eaton et al. 1995) we determined dissolved carbon levels (organic and inorganic) with a Shimadzu TOC-5050 analyzer. NH_4-N, NO_3-N and soluble reactive phosphorus (SRP) were measured with a Lachat Quikchem 8000 flow-injection colorimetric method (Lachat Instruments 1998). Alkalinity and pH were measured with a Mettler DL12 tritrator and apparent color was determined with a DR/2000 Spectrophotometer (HACH, platinum-cobalt standard scale, method #120).

RESULTS

Invertebrate assemblages in the hardwood depressions were chiefly composed of clam shrimp, cladocerans, calanoid copepods, and chironomid larvae (Table 1). There was greater invertebrate diversity in 1998 than 2001, but greater abundance in 2001. A total of 46 taxa were identified with 38 taxa occurring in 1998 and 26 taxa in 2001. Chironomids were notably less diverse in 2001 than 1998 (Table 1). In 1998, abundances averaged 518 individuals/sample, ranging from 134 to 1364. In 2001, mean abundance was 2118 individuals/sample and ranged from 131 to 3137. Eubranchiopoda were well represented. The clam shrimp, *Lynceus gracilicornis* (Packard), was present in all sites at fairly high numbers for both years. *Limnadia lenticularis* (L.) was found in two depressions in 1998. In 2001, the fairy shrimp, S*treptocephalus seali* (Ryder), occurred in all the wetlands (Table 1).

Collector-filterers, comprised primarily of clam shrimp, cladoceran, and calanoid copepods, were the predominant functional feeding

Table 2. Summary water chemistry values for hardwood depressions during 1998 (n = 6) and 2001 (n = 5).

	1998		2001	
	median	range	median	range
Dissolved oxygen (mg L^{-1})	1.3	(0.4 - 3.1)	1.0	(0.6 - 2.2)
Temperature (C)	20.2	(18.9 - 23.7)	20.5	(18.7 - 22.8)
Total carbon (mg L^{-1})		n/a	47.5	(36.7- 58.2)
Inorganic carbon (mg L^{-1})		n/a	4.0	(2.6 - 6.2)
Organic carbon (mg L^{-1})		n/a	43.1	(34.1 - 53.2)
NH_4-N (μg L^{-1})		n/a	120.5	(23.6 - 134.9)
NO_3-N (μg L^{-1})		n/a	8.4	(6.5 - 11.4)
SRP (μg L^{-1})		n/a	41.5	(3.9 - 178.7)
pH	6.2	(5.9 - 6.4)	5.4	(4.9 - 5.7)
Alkalinity (mg Ca CO_3 L^{-1})	11.1	(7.7 - 19.5)	7.9	(2.5 - 15.6)
Apparent color (Pt Co)	184	(148 - 228)	336	(231 - 493)

n/a = sample contamination precluded analyses.

group (FFG; Fig. 2). Collector-gatherers, herbivores, and shredders were more abundant in 1998 than 2001, while predators were more abundant in 2001 than 1998. Collector-gatherers were more abundant in 1998 due to greater numbers of chironomids. There were no scrapers present during either year, and scavengers, detritivores, and parasites were not abundant.

Water chemistry data for the hardwood depressions are shown in Table 2. Dissolved oxygen levels were extremely low (<2 mg L^{-1}) and water was heavily stained, as indicated by apparent color. Sample contamination in 1998 precluded analysis of several constituents. In 2001, dissolved organic carbon levels were greater than 34 mg L^{-1}, and SRP and NH_4-N levels were very high in certain wetlands (Table 2).

DISCUSSION

Compared to neighboring limesink wetlands (i.e., grass-sedge marshes, cypress savannas, and cypress-gum swamps) the invertebrate

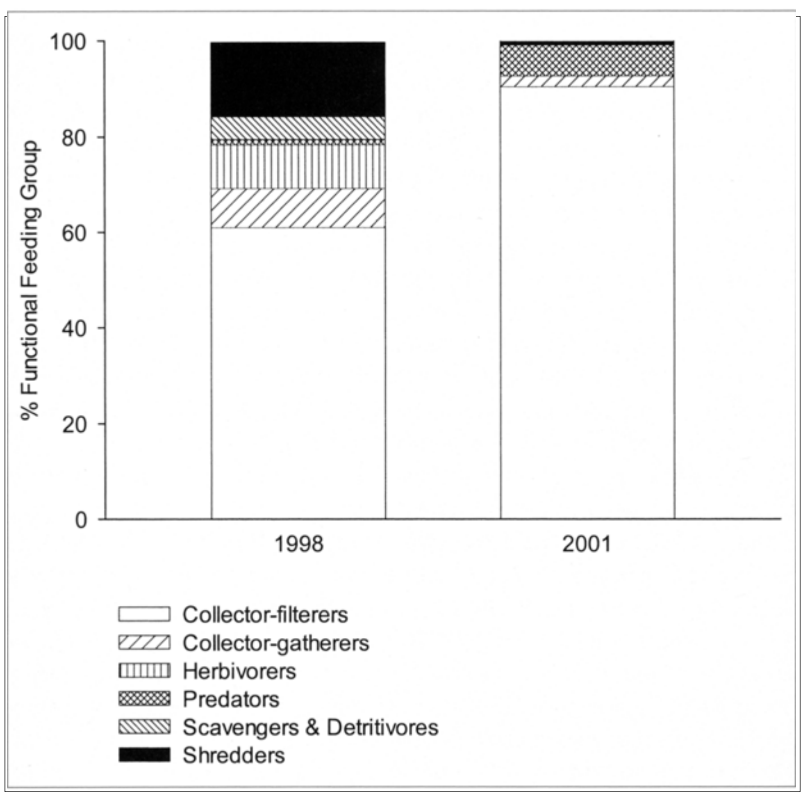

Figure 2. Percentages of aquatic invertebrate functional feeding groups for 1998 and 2001.

community was generally less taxonomically rich but had a greater diversity of Eubranchiopoda (Battle and Golladay 2001). Eubranchiopoda, composed of fairy, tadpole, and clam shrimp, are common inhabitants of temporary wetlands (Pennak 1989). In southwestern Georgia, grass-sedge marshes are the only other wetland type that *L. gracilicornis* and S. *seali* have been found. The clam shrimp *L. lenticularis*, although only found in two sites in 1998, has not been recorded in any other wetlands on the Ichauway Reserve (Table 1; Battle and Golladay 2001). The three species of Eubranchiopoda collected during our study have been found in Carolina bays on the Atlantic Coastal Plain, but only in a small percentage of the bays sampled (Mahoney et al. 1990, Taylor et al. 1999). As far as we know, *L. lenticularis* has not been reported in Georgia (Pennak 1989). It is not clear if *L. lenticularis*, as well as the other Eubranchiopoda, should be considered rare or endangered because of the lack of knowledge on their distribution, their ecology, and their sensitivity to human activities. Nevertheless, loss of further habitat will accelerate population declines (Tennessen 1997).

Collector-filterers were the most abundant of the FFGs in these wetlands, likely because of abundant microbial food. The hardwood depressions had dissolved organic carbon levels that were double the concentration recorded in Carolina bays and limesink wetlands (Newman and Schalles 1990, Battle and Golladay 2001). Microbial food-webs can convert dissolved organic carbon into harvestable food for filter-feeding invertebrates (Hall and Meyer 1998). Microbial populations may also be affected by the elevated levels of SRP and NH_4-N we observed. SRP and NH_4-N can occur in high concentrations when soils flood and anoxic conditions occur near the substrate (Mitsch and Gosselink 1993). These conditions likely result in a productive and rich microbial community that may be responsible for the rapid development of collectors by providing a plentiful food source.

As with all invertebrates in seasonal aquatic habitats, invertebrates in hardwood depressions have evolved evolutionary and ecological strategies to deal with recurring dry conditions (Wiggins et al. 1980). In hardwood depressions, many invertebrate taxa are capable of aerially dispersing. Invertebrates that have no active dispersal may be carried into the depression from neighboring wetlands through water movement or are year-round residents that have a resistant stage for tolerating droughts (Wiggins et al. 1980). Desiccation resistant eggs, or resting eggs, permit many species to persist from one flood-period to the next. There is also the potential that resting eggs are dispersed through wind (Brendonck and Riddoch 1999) or by salamanders (Bohonak and Whiteman 1999) as occurs for certain fairy shrimp. Upon hatching, most taxa show rapid development and reproduction to take advantage of the short hydroperiod (Pennak 1989).

The greater taxonomic richness in 1998 versus 2001 may have been related to inundation levels and hydroperiod length. In 1998, southwestern Georgia experienced a 100-year flood event and some depressions became briefly linked to limesink wetlands and a nearby 5th-order creek. Hardwood depressions tend to occur in low-lying areas and during flood events they act as corridors for water movement. The surface flow of water serves as a means for dispersal of non-aerial invertebrate taxa across the landscape and as a mechanism for nutrient pulses. Diversity may have also been higher in 1998 because of the extended hydroperiod (Schneider and Frost 1996, Morehead et al. 1998). The hydroperiod was approximately >1 mo in 1998 versus 2-3 wks in 2001, which would have allowed extended time for colonization by aerial dispersers and ovipositors. It is not well understood how flood frequency and timing of flooding affects invertebrate communities in hardwood depressions.

Some land managers may consider hardwood depressions to be of little value because of their low timber quality. However, they represent a unique and vital habitat within the longleaf pine ecosystem of the southeastern United States. It is important to maintain a number of hardwood depressions because they support a distinctive invertebrate fauna including rare Eubranchipoda. Undisturbed depressions serve as important refugia that may help enhance the recovery of disturbed sites in the future (Mahoney et al. 1990).

ACKNOWLEDGMENTS

We like to thank the following people for their assistance: F. Hudson, B. Clayton, C. Peeler, T. Humphries, N. Peneff, J. Warren, S. Kelley, and L. Cox. J. Epler verified identification of the chironomids and C. Rogers provided verification of the clam shrimp. R. King, K. Coffey, R. Jacobsen, and one anonymous reviewer provide helpful comments on an earlier version of this manuscript. Funding was provided by the J.W. Jones Ecological Research Center and the R.W. Woodruff Foundation.

LITERATURE CITED

BATTLE, J.M., and S.W. GOLLADAY. 2001. Water quality and Macroinvertebrate assemblages in three types of seasonally inundated limesink wetlands in southwest Georgia. Journal of Freshwater Ecology 16:189-207.

BOHONAK, A.J., and H.H. WHITEMAN. 1999. Dispersal of the fairy shrimp *Branchinecta coloradensis* (Anostraca): effects of hydroperiod and salamanders. Limnology and Oceanography 44:487-493.

BRENDONCK, L., and B.J. RIDDOCH. 1999. Wind-borne short-range egg dispersal in anostracans (Crustacea: Branchiopoda). Biological Journal of the Linnean Society 67:87-95.

COFFEY, K.L., L.K. KIRKMAN, S.B. JACK, and L.M. CONNER. 2001. Reintroducing fire to hardwood-dominated depressions in a longleaf pine-wiregrass savanna: an adaptive management approach. Pp. 106, *In* J.S. Cush (Ed.). Proceedings of the Third Longleaf Alliance. Longleaf Alliance Report 5. Alexandria, LA. 226 pp.

EATON, A.D., L.S. CLESCERI, and A.E. GREENBERG. 1995. Standard Methods for the Examination of Water and Wastewater, 19th Edition. United Book Press, Inc., Baltimore, MD. 800+ pp.

EPLER, J.H. 2001. Identification Manual for the Larval Chironomidae (Diptera) of North and South Carolina. <http://www.esb.enr.state.nc.us/BAUwww/Chironomid.htm> Accessed 5 February 2002.

GEORGIA AEMN (Automated Environmental Monitoring Network). 2001. <http://www.griffin.peachnet.edu/bae/.> Accessed 27 August 2001.

GOEBEL, P.C., B.J. PALIK, L.K. KIRKMAN, and L.R. WEST. 1997. Landscape ecosystem types of the Joseph W. Jones Ecological Research Center: Field Guide. Technical Report 97-1. Joseph W. Jones Ecological Research Center at Ichauway, Newton, GA, USA. 99 pp.

HALL, R.O., Jr., and J.L. MEYER. 1998. The trophic significance of bacteria in a detritus-based stream food web. Ecology 79:1995-2012.

JACQMAIN, E.I., R.H. JONES, and R.J. MITCHELL. 1999. Influences of frequent cool-season burning across a soil moisture gradient on oak community structure in longleaf pine ecosystems. American Midland Naturalist 141:85-100.

LACHAT INSTRUMENTS. 1998. Method list for QuikChem automated analyzer. QuikChem methods 10-107-06-1 G, 10-107-04-1-B, and 13-115-01-1-B. Zellweger Analytics, Inc., Lachat Instruments Division, Milwaukee, WI. 61 pp.

LYNCH, J.M., A.K. GHOLSON, and W.W. BAKER. 1986. Natural features inventory of Ichauway Plantation, Georgia. Volume I. The Nature Conservancy Southeast Regional Office, Chapel Hill, NC. 308 pp.

MAHONEY, D.L., M.A. MORT, and B.E. TAYLOR. 1990. Species richness of calanoid copepods, cladocerans and other brachiopods in Carolina bay temporary ponds. American Midland Naturalist 123:244-258.

MERRITT, R.W., and K.W. CUMMINS. 1996. An Introduction to the Aquatic Insects of North America. 3rd Edition. Kendall/Hunt Publishing Company, Dubuque, IA. 862 pp.

MITSCH, W.J., and J.G. GOSSELINK. 1993. Wetlands. 2nd Edition. Van Nostrand Reinhold, New York, NY. 722 pp.

MOORHEAD, D.L., D.L. HALL, and M.R. WILLIG. 1998. Succession of macroinvertebrates in playas of the Southern High Plains, USA. Journal of the North American Benthological Society 17:430-442.

NEWMAN, M.C., and J.F. SCHALLES. 1990. The water chemistry of Carolina bays: a regional survey. Archiv für Hydrobiologie 118:147-168.

PENNAK, R.W. 1989. Fresh-water Invertebrates of the United States. 3rd Edition. John Wiley & Sons, Inc., New York, NY. 628 pp.

SCHNEIDER, D.W. and T.M. FROST. 1996. Habitat duration and community structure in temporary ponds. Journal of the North American Benthological Society 15:64-86.

TAYLOR, B.E., D.A. LEEPER, M.A. McCLURE, and A. DeBIASE. 1999. Carolina bays, ecology of aquatic invertebrates and perspectives on conservation. Pp. 167-196, *In* D.P. Batzer, R.B. Rader, and S.A. Wissinger (Eds.). Invertebrates in Freshwater Wetlands of North America: Ecology and Management. John Wiley & Sons, Inc., New York, NY. 1100 pp.

TENNESSEN, K.J. 1997. Aquatic insect resource management. Pp. 259-268, *In* G.W. Benz, and D.E. Collins (Eds.). Aquatic Fauna in Peril: Southeastern Perspective. Special Publication 1, Southeast Aquatic Research Institute, Lenz Design & Communications, Decatur, GA. 554 pp.

WHARTON, C.H. 1978. The Natural Environments of Georgia. Geologic and Water Resources Division. Georgia Department of Natural Resources, Atlanta, GA. 227 pp.

WIGGINS, G.B., R.J. MacKAY, and I.M. SMITH. 1980. Evolutionary and ecological strategies of animals in annual temporary pools. Archiv für Hydrobiologie Supplement 58:97-206.