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INVERTEBRATES THAT AESTIVATE IN DRY BASINS OF CAROLINA BAY WETLANDS

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Abstract: Water levels fluctuate widely in Carolina bay wetlands and most dry periodically. Aquatic organisms inhabiting these wetlands have the capacity to either resist desiccation or to recolonize newly flooded habitats. The objective of this study was to determine which invertebrates aestivate in the soil of dry Carolina bays and to describe how differences in habitat affect the composition of aestivating invertebrates. Eight Carolina bays located on the Savannah River Site (SRS) near Aiken, South Carolina, USA were examined for this study. Although all of the wetlands dried seasonally, three of the wetlands were relatively wet (inundated 47–92% of the year on average), one was intermediate, and four were relatively dry (inundated 20% of year on average). Sections of soil were removed from each bay during August and November when all sites were dry, placed into tubs, flooded, and covered with fine mesh. Invertebrates were sampled from the water biweekly for four weeks. Invertebrate assemblages were contrasted between naturally inundated bays and rehydrated samples, wetter and drier bays, August and November collections, and remnant ditches and the main basins. Common aestivating fauna included midges, dytiscid beetles, copepods, and cladocerans. The Jaccard's coefficient of similarity for invertebrates emerging from dry substrate and from naturally flooded wetlands (with both aestivators and colonizers) averaged 0.22. More taxa emerged from rehydrated samples from wetter bays than drier bays. Season affected which taxa emerged. Remnant ditches supported fewer taxa than basins. Aestivating invertebrates make up a significant component of Carolina bay fauna.

Key Words: aestivation, rehydration, invertebrates, wetland ponds

INTRODUCTION

Alternating wet and dry phases of temporary ponds require special adaptations of their aquatic inhabitants (Kenk 1949, Wiggins et al. 1980, Williams 1987, 1996). Life histories with desiccation resistance, active (non-diapause) aquatic and terrestrial stages, or a combination of these two strategies allow invertebrates to exploit these habitats (Wiggins et al. 1980).

The degree to which invertebrates rely on desiccation resistance varies among different types of wetlands. For example, in desert rain pools (Anderson et al. 1999) and playas of Texas, USA (Hall et al. 1999), few invertebrate taxa possess desiccation-resistant stages because dry periods are prolonged and extreme, with high temperatures. In snowmelt ponds of Wisconsin, USA (Schneider and Frost 1996) and dry beaver wetlands of Pennsylvania, USA (Wissinger and Gallagher 1999), most of the invertebrates employ desiccation-resistant strategies. Among the aquatic invertebrates of Carolina bays and other isolated depressional wetlands, many microcrustaceans are known to produce resting stages (Taylor et al. 1990, Taylor et al. 1999). However, strategies of the diverse aquatic insects are essentially unknown. One goal of this study was to determine which of the aquatic insects and other invertebrates aestivate in these bays by experimentally rehydrating sediments from the dry basins. Comparing experimental results with extensive samples from the naturally flooded ponds enabled us to infer which species persist in dry basins and which species probably regularly recolonize.

Wissinger (1999) identified several features of wetland hydroperiod that might influence invertebrate community structure. Duration of flooding was considered particularly important. Habitats with long hydroperiods tend to support a more diverse fauna than habitats with short hydroperiods (Schneider and Frost

1996, Wellborn et al. 1996, Schneider 1997, 1999, Wissinger et al. 1999). However, much of the increase in diversity in long hydroperiod habitats comes from organisms unable to tolerate drying, and it is unknown how hydroperiod length influences the composition of desiccation-resistant invertebrates. A second goal of this study was to determine how variation in hydroperiod influenced aestivating invertebrates of Carolina bays.

Wissinger (1999) also indicated that the phenology of flooding might influence wetland invertebrate faunas. The different conditions that occur if ponds first flood in spring, summer, fall, or winter can affect the resultant invertebrate faunas. Higgins and Merritt (1999) found that in temporary ponds of Michigan, USA one fauna developed when the habitats flooded in spring, but a quite different fauna developed if the ponds reflooded in summer. Some species of copepods in Carolina bays break dormancy whenever the pond fills, others are specialized to narrower ranges of conditions (Wyngaard et al. 1991, Medland and Taylor 2001). Eggs of a common calanoid copepod, *Aglaodiaptomus stagnalis* Forbes, hatch immediately after inundation but only if the pond fills between November and April (Taylor et al. 1990). A third goal of this project was to examine how season of flooding affects the diversity and abundance of emerging aestivating invertebrates in Carolina bays.

Invertebrates that aestivate in low, moist areas of ponds may have increased odds of survival (Wiggins et al. 1980, Brown et. al 1996). Some invertebrates are behaviorally adapted to survive the dry phase by burying in mud, crawling under rocks or logs, or by living in crayfish burrows (Wiggins et al. 1980, Batzer and Wissinger 1996). Brown et al. (1996) suggested that remnant ditches in dry ponds serve as an important refuge for aestivating invertebrates. Broschart and Linder (1986) found that flooded habitats in ditches supported more invertebrates than the adjacent habitat. How ditches influence aestivating invertebrates in dry wetlands has not been established clearly, and contrasting aestivating invertebrate fauna in dry ditches and nearby dry basins of Carolina bays was the final goal of this study.

To address these goals, we took soil substrate samples from dry Carolina bays and flooded them in a greenhouse. We contrasted faunas in naturally flooded bays to the faunas that emerge from flooded substrate. We also contrasted emergent aestivating faunas from longer hydroperiod bays to shorter hydroperiod bays, August floodings to November floodings, and basins to ditches.

STUDY SITES

Carolina bays are elliptical, depressional wetlands of the Atlantic Coastal Plain of North America. Pond-ed water in bay basins is usually < 1 m deep (Taylor et al. 1999). On the Savannah River Site (SRS), where our study was conducted, nearly two-thirds of the bays were ditched or drained in the 1800s or early 1900s for agriculture or other uses. When the SRS was created in 1951, agriculture was discontinued. Many bays have become forested, although others remained open herbaceous meadows (Kirkman et al. 1996).

Eight partially drained Carolina bays (numbered 108, 118, 124, 126, 147, 5092, 5135, and 5239) on the SRS were examined for this study (Figure 1). Remnant ditches remain functional in each, but during wet periods, all eight bays support diverse wetland faunas (Dietz et al. 2001). Bay waters were generally acidic (pH ranged from 3.9–6.1). The four wetter bays flooded in spring of both 1998 and 1999, and the four drier bays flooded only in spring 1998. Subsequent hydrologic data revealed that one of the wetter bays (5135) actually had an intermediate hydroperiod (Table 1). Thus, we excluded bay 5135 from the wetter versus drier bay contrasts.

METHODS

Wet Season Sampling

To determine which aquatic invertebrates used the bays, we sampled all eight of the bays every two months from December 1998 through April 2000 when they held water. Macroinvertebrates were sampled with a 1-mm-mesh D-frame (30-cm width) sweep net. The sweep net was submerged so that the straight edge rested on top of the sediments, and the net was scraped along the bottom. One 1-m sweep was taken at the edge of each bay, a second 1-m sweep was taken in the center, and a third 1-m sweep was taken at either an intermediary point or in an additional sub-habitat. These samples were preserved, sorted, and identified in the laboratory using keys in Pennak (1989), Thorp and Covich (1991), and Merritt and Cummins (1996).

Microinvertebrate collections were taken with a 102-micron-mesh hand net swept through the water column. These samples were also preserved and organisms identified in the laboratory using keys in Edmondson (1959) and Thorp and Covich (1991).

Rehydration Experiment

To determine which aquatic invertebrates were aestivating in dry substrates of Carolina bays, we collected sediments from each of the eight Carolina bays while they were dry in August and November of 1999. Three sediment samples (50 cm $\times$ 50 cm $\times$ 10 cm) were collected from the main basin and three from the ditch of each bay. Care was taken to ensure that all

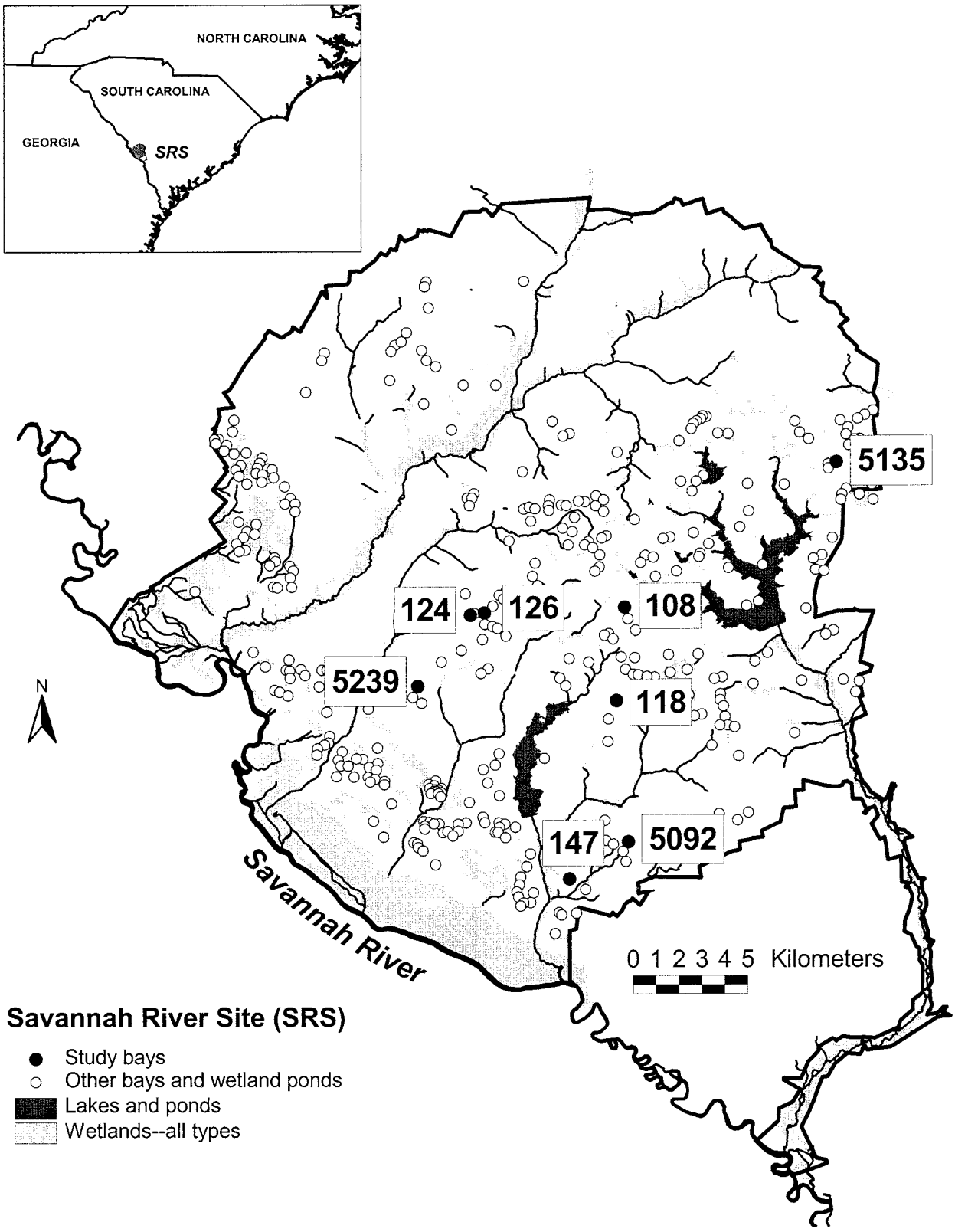

Figure 1. Carolina bays on the Savannah River Site near Aiken, South Carolina, USA.

Table 1. Environmental characteristics of the eight bays sampled in this study. Hydroperiod is an estimate of the average percentage of the year that the bay holds water. Hydroperiods for 51 bays, including Bay 118, were computed from monthly data for the 5-year period June 1996 to May 2000 (R. Lide and R. R. Sharitz, SREL, unpublished hydrologic survey). For each of the other seven bays in this study, we averaged hydroperiods of 2 to 5 bays from the hydrologic survey that had matching patterns of presence or absence of water (based on 12 months from February 1998 to April 2000). Area and vegetation were provided by C. Barton and J. Singer (Center for Forested Wetlands Research, Charleston, SC). Ranges of water temperature and pH were determined from measurements on each sampling date.

Bay #	Area (ha)	Hydroperiod (% of year)	Vegetation	Max. Depth (cm)	Temp. Range, °C	pH Range
108	1.05	20	Hardwoods, loblolly pines	32	12–23	5.6
118	1.04	70	Hardwoods, loblolly pines	84	9–23	5.7–4.9
124	0.86	47	Open-canopy pines	67	9–26	5.6–6.1
126	1.53	20	Bottomland hardwoods	56	10–26	5.5
147	3.32	92	Pond cypress	49	8–24	4.4–5.2
5092	1.36	20	Bottomland hardwoods	49	18–23	4.5–6.1
5135	0.28	27	Open-canopy pines	45	11–24	3.9–4.5
5239	1.70	20	Sweetgum, pines	66	10–23	5.6

soil layers remained intact during removal. The 10-cm depth was chosen because the soil below this level is very sandy. Each of the 48 substrate samples per sampling date was placed in a plastic container (50 cm × 50 cm × 22 cm), transferred to a greenhouse, covered with plastic lids with windows covered by 102-micron mesh, and filled with water. Water was kept at a constant level of 10 cm over the upper surface of sediment samples throughout the experiment. Tap water was used for the August rehydration, and de-ionized water was used for the November rehydration. Subsequent tests indicated that the water source had no effect on invertebrate emergence (Dietz 2001).

After substrate rehydration, invertebrates were sampled with a fine-mesh hand net (102 microns). The net was swept three times through the container to collect a quantitative measure of invertebrate abundance. Samples were collected from each of the 48 containers twice a week for four weeks and preserved in 95% ethanol. Organisms were identified to genus, except chironomids, which were identified to subfamily, and worms and copepods, which were identified to family. Processing procedures were identical in both August and November trials.

Statistical Analyses

t-tests were used to compare the number of taxa in rehydrated soil from the three wetter habitats (118, 124, 147) and the four drier habitats (108, 126, 5092, and 5239). Assemblages in wetter and drier bays were further compared using Jaccard's coefficient of community similarity (Brower and Zar 1977). Jaccard values can range from 0 to 1.0, with the former value indicating no similarity and the latter value indicating 100% similarity. When the same taxa were collected from both wetter and drier bays, individual *t*-tests were used to contrast their densities. Because not every organism could be classified to genus, density analyses were conducted at the family level.

Wilcoxon matched pair tests were used to contrast the number of taxa occurring in the August versus the November samples, basin versus ditch collections, and naturally inundated bays versus samples artificially rehydrated in the laboratory. Jaccard coefficient values were calculated for each paired collection, and we report the average and range of these measures. Wilcoxon tests were used to compare the densities of each family that occurred in paired collections.

RESULTS

Invertebrates that Aestivate in Dry Soils

At least 17 taxa (12 families) of invertebrates were collected and identified from rehydrated substrates. All of these taxa were also found in the Carolina bays when they flooded naturally (Table 2). However, at least 39 additional taxa (12 additional families) occurred in bays when they flooded naturally but were not collected from the rehydrated substrate. The number of taxa collected from the flooded bays and the rehydrated soil samples differed significantly ($p = 0.008$). The average Jaccard coefficient for invertebrates from rehydrated substrate and natural floodings was 0.22 and ranged from 0.15 to 0.35. The order Hemiptera, common in naturally flooded bays, was completely absent from the rehydrated sediments, and the order Odonata was poorly represented. The dipteran *Chaoborus* was also common in flooded bays and notably absent from rehydrated sediments.

Several crustaceans found during flooded periods

Table 2. Invertebrates found in eight Carolina bays after natural floodings (Dietz et al. 2001). Taxa that were also recovered from rehydrated sediment samples are indicated by an ''X.''

Group	Family	Taxon	Rehydrated sediments
INSECTS			
Odonata	Aeshnidae	*Aeshna*	
	Coenagrionidae	*Argia*	
	Libellulidae	*Erythrodiplax*	
		Libellula	
		Sympetrum	X
Hemiptera	Corixidae	*Sigara*	
	Gerridae	*Gerris*	
	Naucoridae	*Pelocoris*	
	Notonectidae	*Buenoa*	
		Notonecta	
Coleoptera	Dytiscidae	*Cybister*	
		Dytiscus	
		Hydaticus	X
		Hydroporus	X
		Hydrovatus	
		Laccophilus	
		Nebrioporus	
	Gyrinidae	*Dineutus*	
	Hydrophilidae	*Berosus*	X
	Noteridae	*Hydrocanthus*	
Diptera	Chaoboridae	*Chaoborus*	
	Chironomidae	Tanypodinae	X
		Non-Tanypodinae	X
	Culicidae	*Aedes*	X
		Culex	
	Tabanidae	*Tabanus*	X
CRUSTACEANS			
Anostraca	Chirocephalidae	*Eubranchipus*	
		Streptocephalus	X
Conchostraca	Lynceidae	*Lynceus*	
Cladocera	Bosminidae	*Neobosmina*	
	Chydoridae	*Acroperus*	
		Alona	
		Alonella	
		Camptocercus	
		Chydorus	X
		Disparalona	
		Ephemeroporus	
		Eurycercus	
		Kurzia	
		Pleuroxus	
		Pseudochydorus	
	Daphniidae	*Ceriodaphnia*	X
		Daphnia	X
		Scapholeberis	X
		Simocephalus	X
	Macrothricidae	*Acantholeberis*	
		Ilyocryptus	
		Iheringula	
		Lathonura	
		Macrothrix	
		Streblocercus	
	Sididae	*Diaphanosoma*	
		Pseudosida	
Isopoda	Asellidae	*Caecidotea*	X
Copepoda	Cyclopidae	—	X
ANNELIDS			
Oligochaeta	Tubificidae	—	X

Table 3. Taxa found in the rehydrated sediments from each bay. Letters indicate occurrence in August (A) or November (N) experiments.

Group	Family	Taxon	108	126	5092	5239	5135	118	124	147
INSECTS										
Odonata	Libellulidae	*Sympetrum*							A	
Coleoptera	Dytiscidae	*Hydaticus*				A, N		N	A	N
		Hydroporus						A	A, N	A, N
	Hydrophilidae	*Berosus*							A	
Diptera	Chironomidae	Tanypodinae	N	N	N	N	N	N	N	N
		Non-Tanypodinae								N
	Culicidae	*Aedes*				N	N	N		
	Tabanidae	*Tabanus*								N
CRUSTACEANS										
Anostraca	*Streptocephalidae*	*Streptocephalus*								A
Cladocera	*Chydoridae*	*Chydorus*								A
	Daphniidae	*Ceriodaphnia*								A, N
		Daphnia								A, N
		Scapholeberis		N	A				A, N	A
		Simocephalus	A, N	A, N	N		A, N	A, N	A, N	A, N
Copepoda	Cyclopidae	—					N	A, N	A, N	N
Isopoda	Asellidae	*Caecidotea*						A, N		A, N
ANNELIDS										
Oligochaeta	Tubificidae	—	A	A	A		A, N	A	A	A, N

were not recovered from rehydrated substrates (Table 2), despite the fact that they cannot actively colonize isolated wetlands. They either were missed in our sampling, did not emerge, or might aestivate in locations other than surface soils and leaf litter. Little is known about colonization in microinvertebrates, and we assume that most use desiccation-resistant techniques to survive in temporary habitats. However, we estimate that 48% of the aquatic insects that inhabit these Carolina bay wetlands depend on recolonization strategies.

Wetter Bays vs. Drier Bays

We collected 17 aestivating invertebrate taxa (12 families) in the rehydrated substrate from the three wetter sites (bays 118, 124, and 147) but only six taxa in the rehydrated substrate from the four drier sites (bays 108, 126, 5092, and 5239), (Table 3, Figure 2, *t*-test, $p = 0.003$). The six taxa found in the drier bay collections were also found in the wetter bay collections. In both habitats, the family Daphniidae (*Ceriodaphnia*, *Scapholeberis*, and *Simocephalus*) was the most abundant invertebrate (mean ± standard deviation among bays: 30.9 ± 10.3 animals/sample in wetter bays; 4.6 ± 4.3 animals/sample in drier bays), followed by the family Tubificidae (8.9 ± 6.7 animals/sample in wetter bays; 1.8 ± 1.8 animals/sample in drier bays). The genera *Caecidotea*, *Aedes*, *Sympetrum*, *Streptocephalus*, *Berosus*, *Chydorus*, and *Tabanus* were collected only from the wetter bay soils, although the latter four genera were uncommon even in those samples. The Jaccard coefficient between the invertebrate faunas aestivating in wetter and drier bays was 0.42. Of the families aestivating in both habitats, only the Daphniidae ($p = 0.005$) were significantly more abundant in wetter than drier sites.

August Emergence vs. November Emergence

We collected nine invertebrate families from sediment samples rehydrated in August and eight invertebrate families from samples rehydrated in November (Table 3). Although numbers of genera collected in the summer versus the fall were similar ($p = 0.279$), composition differed. The genera *Sympetrum*, *Streptocephalus*, *Berosus*, and *Chydorus* were found only after the August rehydration, although none was abundant. The family Chironomidae (primarily Tanypodinae) and the culicid genus *Aedes* were found only after the November rehydration, and each was abundant (5.3 ± 5.0 animals/sample for chironomids; 2.0 ± 3.2 animals/sample for the culicid). Jaccard coefficients of community similarity between August and November samples in the eight ponds ranged from 0.33 to 0.57, and the mean was only 0.43 (even though these comparisons were within rather than between bays). Of the four families emerging during both seasons, three of them (Daphniidae, Dytiscidae, and Cyclopidae) had similar densities in August and November. However, we collected significantly more Tubificidae in August than in November (8.4 ± 10.8 animals/sample in August, 0.2 ± 0.4 animals/sample in November; $p = 0.014$).

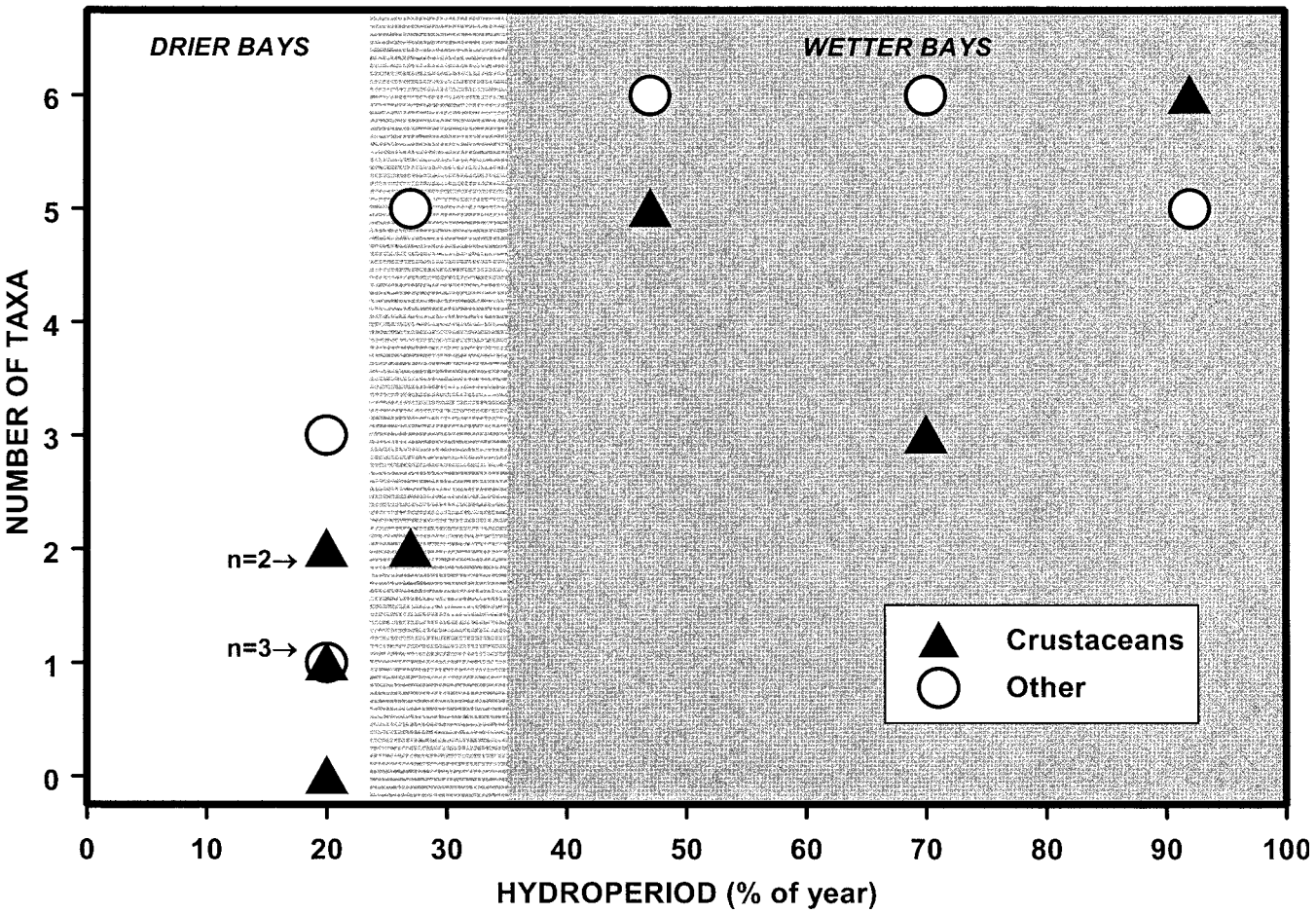

Figure 2. Number of taxa collected from rehydrated sediment samples as a function of hydroperiod.

Basins vs. Ditches

Twelve families (17 genera) were collected from samples removed from basins, and only eight families were collected from sediment samples removed from ditches (Wilcoxon matched pairs test, genus level, $p = 0.574$). All of the genera occurring in ditches were also found in basins. The Jaccard coefficients between the basins and the ditches for the eight bays ranged from 0 to 1.0, and the mean was 0.55. The family Daphniidae was the most abundant invertebrate in both the basin and ditch samples (21.3 ± 24.4 animals/sample in basins, 7.3 ± 9.7 animals/sample in ditches). Abundances did not differ significantly between basins and ditches for families occurring in both habitats. The families Streptocephalidae, Chydoridae, Tabanidae, and Hydrophilidae were collected only in rehydration samples from basins, but all of these organisms were relatively rare.

DISCUSSION

Our results demonstrate that desiccation resistance is an important strategy for invertebrates that inhabit Carolina bays. Some of the taxa collected when bays were flooded but not from rehydrated substrate probably have desiccation-resistant stages (e.g., Bosminidae and Diaptomidae), but they either did not emerge due to the absence of appropriate cues or were not detected in rehydration samples (Taylor et al. 1990, Medland and Taylor 2001). We also could have missed some of these organisms because they were aestivating deeper than 10 cm in the sediments or perhaps in refugia such as root holes or crayfish burrows (see Wiggins et al. 1980).

Comparing our results to others from different wetland types, it appears that snowmelt ponds of Wisconsin (Schneider and Frost 1996) and beaver wetlands of Pennsylvania (Wissinger and Gallagher 1999) have greater numbers of aestivating invertebrate taxa than Carolina bays. However, it also seems that Carolina bays have greater numbers of aestivating invertebrate taxa than do desert rain pools (Anderson et al. 1999) or playa lakes of Texas (Hall et al. 1999). Combined, these studies indicate that those wetland types with a longer hydroperiod and less intense dry phase will sup-

port more invertebrates that rely on desiccation resistance.

Even within Carolina bays, duration of hydroperiod strongly influenced aestivators. Many more invertebrates were able to use the longer (wetter) hydroperiod bays in this study. Our findings that shorter hydroperiod wetlands tend to support a lower diversity of aestivating invertebrates parallel the findings by Schneider and Frost (1996) and Wissinger (1999) for overall faunas (including non-desiccation resistant colonizers) and Taylor et al. (1999) for microcrustaceans.

We found few invertebrate predators in the rehydrated sediments from drier bays. This low intensity of predation, at least until the recolonizers arrive, may help explain some differences in the community composition between drier and wetter bays. For example, drier bays frequently support clam shrimp and fairy shrimp (DeBiase and Taylor, unpublished), large taxa that are very vulnerable to predators.

Faunas emerging from dry Carolina bay basins changed dramatically depending on the time of year that flooding occurred. While we collected almost the same number of families in the August versus the November samples (nine versus eight), the Jaccard coefficient indicated that there was only an average of 43% similarity between the August and November communities. Some of the dipterans (Chironomidae and Culicidae) may not emerge until fall because of critical short day lengths required to break aestivation (Chapman 1998). Tubificids are not typically considered aestivators (Wiggins et al. 1980), although they can be abundant in bays that dry regularly (Leeper and Taylor 1998), and the lower numbers of these worms in November than August may reflect mortality from prolonged drying.

Contrary to expectations (see Brown et al. 1996), the ditches supported fewer rather than more aestivating invertebrate families. Because temporary wetlands with longer hydroperiods generally support a greater diversity of invertebrates, we had expected to find more families in the bay ditches. Apparently, ditches are not serving as refuges. Alternatively, the ditches may serve as residual pools for non-aestivating predators, such as hemipterans, coleopterans, and odonates, and these predators might consume many of the potential aestivators in ditches.

The ecology of invertebrate aestivation and recolonization in wetlands merits further research. Aestivating invertebrates make up a large component of Carolina bay fauna, and the processes that regulate aestivation and affect survival of aestivating organisms are not well understood. These processes can strongly influence the composition of the assemblage that appears after the pond fills. Likewise, patterns of recolonization by non-aestivating organisms will also influence assemblages. The recolonizers of Carolina bays include many predatory taxa, such as odonates, notonectids, and *Chaoborus*, and these organisms are capable of strongly influencing the structure of the aquatic community (Woodward and Kiesecker 1994, Jeffries 1996, and Higgins and Merritt 1999). Thus, the structure of communities in temporary wetlands may depend not only on local conditions, but on the proximity to other aquatic habitats that can serve as sources of colonists.

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