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8 Carolina Bays

Ecology of Aquatic Invertebrates and Perspectives on Conservation

BARBARA E. TAYLOR, DOUGLAS A. LEEPER,
MORGAN A. McCLURE, and ADRIENNE E. DeBIASE

Carolina bays are geomorphically distinctive basins of the Atlantic Coastal Plain of North America. Most contain wetland ponds, and a few contain shallow lakes. They are abundant, and they constitute an important type of natural lentic habitat in the region. Fluctuating water level is a primary factor influencing composition and dynamics of the invertebrates. The occurrence of fish is also an important factor: occasional drying combined with absence of surface inlets or outlets eliminates fish from many bays. Many bays and much of their surrounding landscapes have been heavily altered by human activity. Because invertebrate assemblages are diverse among as well as within bays, maintenance of the diversity of invertebrates (and other animals) probably depends on protecting groups of these habitats, as well as the other aquatic habitats that can serve as seasonally alternate habitats for transient members of the bay assemblages.

INTRODUCTION

Carolina bays are shallow, isolated, oval basins that occur in the Atlantic Coastal Plain of North America, mainly in North and South Carolina. The basins generally contain palustrine wetland habitats, which we will refer to as *wetland ponds*. A few of the larger basins hold shallow permanent lakes.

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Aquatic invertebrates are abundant and diverse in Carolina bays. As habitat for aquatic invertebrates, Carolina bays have several notable attributes. The first is their hydrology. Water levels fluctuate widely in most Carolina bays, and many dry out seasonally, or at least occasionally. Their aquatic inhabitants must therefore have some capacity to resist desiccation or to disperse and recolonize as the wetlands dry and refill. The second is their isolation. Bays typically lack surface inlets and outlets, restricting the exchange of aquatic animals among bays or between bays and other aquatic habitats. Fish are absent from most bays that dry regularly. A third is the chemistry of their waters, which are typically acidic, soft, and moderately to heavily colored.

This chapter provides an overview of the composition, natural history, and ecology of invertebrates in Carolina bays and also discusses conservation issues and research needs.

DISTRIBUTION AND DESCRIPTION OF CAROLINA BAYS

Carolina bays occur in areas of sandy surficial sediments on Atlantic Coastal Plain from New Jersey to northern Florida (Fig. 8.1). Typically, the long axis of the oval basin has a northwest-southeast orientation (Johnson 1942, Prouty 1952), and an elevated sand rim may be present (Fig. 8.2). The largest bay, Lake Waccamaw in North Carolina, has a length of 8 km and an area of 3600 ha. Most bays are much smaller. On the Upper Coastal Plain on the Savannah River Site (SRS) in South Carolina, the median size of Carolina bays is 1 ha, with a range of 0.1–50 ha (Schalles et al. 1989). The basins are shallow. The seasonal maximum water depth in bays on the SRS is typically <1 m (Mahoney et al. 1990). For bay lakes in North Carolina, Frey (1949) reported maximum water depths of 2.2–3.6 m. Estimates of the number of bays are as high as 500,000, but the number is more probably 10,000–20,000 (Richardson and Gibbons 1993).

The distinctive shape and orientation of Carolina bays have been attributed to meteor impacts, solution depressions, and a variety of other causes (e.g., Johnson 1942, Savage 1982, Ross 1987). The most generally accepted explanation entails modification of shallow ponds through the action of waves generated by westerly winds (Thom 1970, Kaczorowski 1977, Grant et al. 1997); elongation of the basin occurs perpendicular to the direction of the prevailing wind. Basal dates from organic sediments in the basins range from 10,000 to more than 20,000 years B.P. The wetland habitats of the bays are thus probably at least as old as most North American lakes, although paleoenvironmental and archaeological records suggest that these habitats have been dynamic, with changes driven by climatic and geologic process as well as human activity (e.g., Frey 1951a, Watts 1980, Bliley and Burney 1988, Brooks et al. 1997, Gaiser 1997).

The substrate of the basin may be either peat or clay. Peat-based bays are common in the Lower Coastal Plain of North Carolina and the adjacent coun-

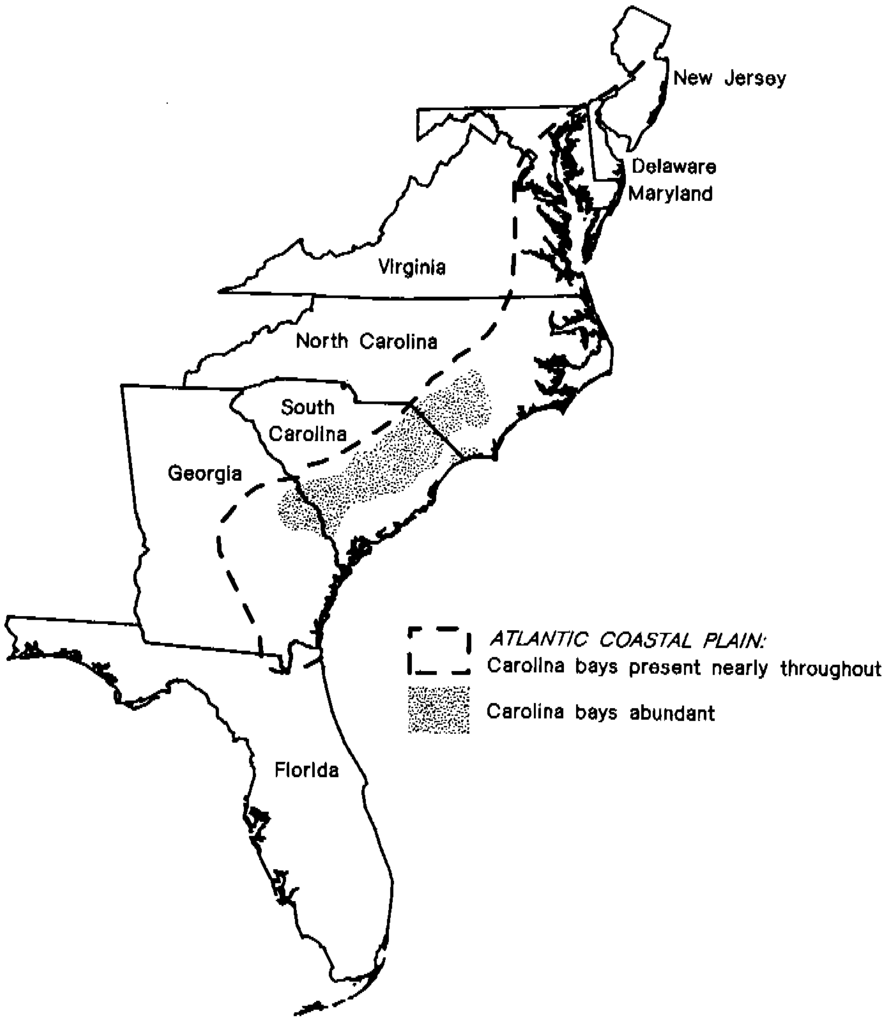

Fig. 8.1. Distribution of Carolina bays. Boundaries of the Atlantic Coastal Plain are based on Isphording and Fitzpatrick (1992). Regions of abundant bays are based on Johnson (1942) and Prouty (1952).

ties of South Carolina. These bays have thick deposits (1–2 m or more) of peat, and water is perched on an aquitard layer of humate-impregnated sand (Thom 1970). Clay-based or hard-bottomed bays are common in the Upper Coastal Plain of North Carolina (Nifong 1982) and throughout most of the Coastal Plain of South Carolina (Bennett and Nelson 1991). In these bays the upper layer of organically enriched sediment is shallow (often <20–30 cm), peat is usually absent, and a clay layer forms the aquitard. Clay-based bays may have hydrologic histories of more frequent or prolonged drying, which

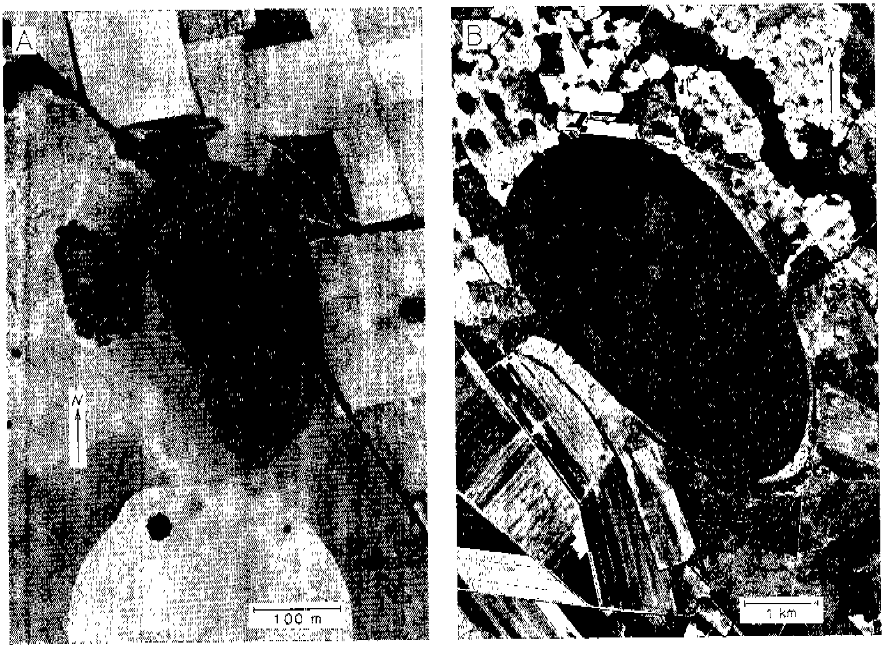

Fig. 8.2. Aerial photographs of two Carolina bays. The photographs illustrate characteristic oval shape, orientation, and sand rims, as well as recent human modifications. (*a*) Flamingo Bay, Aiken County, South Carolina, in 1943 (Cartographic and Architectural Branch of the National Archives, Washington, DC). The eastern side of the bay was plowed; the western side was probably pasture. The dark lines are trees along fence lines. Flamingo Bay is now protected as a DOE Research Set-aside Area on the Savannah River Site. (*b*) Woods Bay, Sumter and Clarendon Counties, South Carolina, in 1994 (U.S.G.S. Aerial Photography Field Office, Salt Lake City, Utah). The small impoundment on the eastern edge was constructed as a mill pond in the latter part of the nineteenth century, and cypress trees were harvested from the interior of the bay in the 1910s and 1920s (S. Wolfe, Woods Bay State Park, personal communication). Woods Bay is now protected as a state park.

would promote oxidation of organic material by biological processes or fire and thus retard accumulation of peat.

The Coastal Plain has a mild, moist temperate climate with rainfall distributed, on average, fairly evenly throughout the year. In the Coastal Plain of South Carolina the average monthly temperature ranges from 8°C in January to 27°C in July. The average annual rainfall is 123 cm, the wettest months occurring in summer and the driest months occurring in fall (30-year averages for divisions 4, 6, and 7, National Oceanic and Atmospheric Administration 1992). Snowfall is unusual, and ponds rarely ice over.

Water regimes of Carolina bays range generally from seasonally flooded to permanently flooded. Seasonally flooded bays typically fill in winter and dry in late spring. A few bays are known to be spring-fed, and groundwater may contribute substantially to the hydrologic budgets of others (Lide et al. 1995). Generally, however, fluctuations in water level are highly correlated with precipitation and evapotranspiration, and year-to-year variation can be large. At Rainbow Bay, a seasonally flooded wetland pond on the SRS in South Carolina, the median annual hydroperiod (main filling only) was 160 days, with a range of 3–391 days over 16 years (Semlitsch et al. 1996). Among nearly a hundred bays and other wetland ponds on the SRS for which some hydrologic record exists, most dry in most years, and only a few have never been observed to dry (Savannah River Ecology Laboratory, unpublished data).

The waters of Carolina bays are typically acidic, soft, and moderately to heavily colored. From a survey of 49 bays in North and South Carolina, Newman and Schalles (1990) reported a median pH of 4.6 (range 3.4–6.7); from a survey of 75 bays and other wetland ponds in South Carolina, Gaiser (1997) reported a mean pH of 4.8 (range 3.9–5.8). Dissolved organic carbon is moderate. Newman and Schalles (1990) reported a mean of 17.11 mg DOC L^{-1}. Levels of calcium are generally low. Newman and Schalles (1990) reported a median of 1.69 mg L^{-1} (range 0.16–11.75 mg L^{-1}); Gaiser (18 bays and other wetland ponds, 1997) reported a mean of 1.02 mg L^{-1} (range 0.15–3.09 mg L^{-1}). Other solutes are also generally low (see Newman and Schalles 1990, Pickens and Jagoe 1996). Most of these data come from clay-based, rather than peat-based, bays.

Less information is available about nutrient chemistry, but the concentrations of major nutrients appear to fall into ranges that would indicate meso-eutrophic or eutrophic conditions in lakes (see Wetzel 1983). In a winter and spring survey of 19 Carolina bays and other wetland ponds in South Carolina, DeBiase and Taylor (unpublished data) found median total Kjeldahl nitrogen concentrations of 0.83 mg L^{-1} (range 0.22–5.01 mg L^{-1}) and median total phosphorus concentrations of 0.037 mg L^{-1} (range 0.008–0.243 mg L^{-1}). Again, most of these data come from clay-based bays.

Wetland habitats of Carolina bays range from forests to wetland meadows to open water (Sharitz and Gresham 1997). Bennett and Nelson (1991) described plant communities of bays in South Carolina that are relatively undisturbed by human activity (according to their estimate, <20 percent of the bays are greater than 0.8 ha in area). The commonest types are: pond cypress pond, which has a closed canopy of pond cypress (*Taxodium ascendens*); nonalluvial swamp, which is dominated by hardwoods, such as swamp tupelo (*Nyssa sylvatica biflora*), red maple (*Acer rubrum*), and sweetgum (*Liquidambar styraciflua*), and may be codominated by pond cypress; and pocosin, which is dominated by a dense growth of shrubs such as fetter-bush (*Lyonia lucida*), titi (*Cyrilla racemiflora*), inkberry (*Ilex glabra*), blueberries (*Vaccinium* spp.), and loblolly bay (*Gordonia lasianthus*), vines such as greenbrier or "bamboo" (*Smilax laurifolia*), and stunted trees such as pond pine (*Pinus serotina*). Pond cypress savanna, which has an open canopy of pond cypress, is also common. Pond cypress pond, pond cypress savanna, and nonalluvial swamp vegetation are associated with clay-based bays; pocosin vegetation is associated with peat-based bays. Depression meadow, the only herbaceous palustrine community described by Bennett and Nelson, is uncommon among relatively undisturbed bays. It is dominated by grasses (*Panicum* spp. and *Leersia hexandra*) and sedges (*Carex* spp.). Open-water lakes are rare among bays in South Carolina. They support extensive floating and emergent aquatic vegetation, including water lily (*Nymphaea odorata*), water shield (*Brasenia schreberi*), and heartleaf (*Nymphoides* spp.), as well as many grasses and sedges.

The vegetation of most bays has been disturbed by human activity (Bennett and Nelson 1991, Kirkman et al. 1996). Row crops, pastures, and pine plantations represent the extremes. The short-term legacy of logging or clearing for agriculture is often the development of a herbaceous or shrub community (see Kirkman et al. 1996). Common species of these communities on the SRS include grasses, sedges, and the shrub buttonbush (*Cephalanthus occidentalis*) (De Steven, University of Wisconsin at Milwaukee, unpublished data).

Pond-breeding amphibians are the most abundant and productive of the vertebrates in Carolina bays (Richardson and Gibbons 1993). Common species in bays and other wetland ponds on the SRS (Gibbons and Semlitsch 1991) include the mole salamander (*Ambystoma talpoideum*), marbled salamander (*Ambystoma opacum*), dwarf salamander (*Eurycea quadridigitata*), red-spotted newt (*Notophthalmus viridescens*), southern cricket frog (*Acris gryllus*), southern toad (*Bufo terrestris*), eastern narrow-mouthed toad (*Gastrophryne carolinensis*), green treefrog (*Hyla cinerea*), spring peeper (*Pseudacris crucifer*), ornate chorus frog (*Pseudacris ornata*), southern leopard frog (*Rana sphenocephala*), and spadefoot toad (*Scaphiopus holbrooki*). In temporary ponds, including Carolina bays, of the sandhills region of North Carolina, the broken-striped newt (*Notophthalmus viridescens dorsalis*) and tiger salamander (*Ambystoma tigrinum*) are common (Morin 1983).

Hydrologic fluctuations limit the development of fish populations in many bays, but species such as lake chubsucker (*Erimyzon sucetta*), dollar sunfish (*Lepomis marginatus*), and mud sunfish (*Acantharchus pomotis*) occasionally colonize these habitats (Snodgrass et al. 1996). During times of high water, fish may gain access through ditches or overflows to bays that are otherwise isolated. Larger and more diverse populations of fish appear in continuously inundated habitats. The bay lakes of North Carolina support common southeastern pond species such as lake chubsucker, yellow bullhead (*Ameiurus natalis*), warmouth (*Lepomis gulosus*) and other centrarchids, and yellow perch (*Perca flavescens*); Lake Waccamaw also harbors several endemic fishes (Frey 1951b, Richardson and Gibbons 1993).

Reptiles, birds, and mammals also use Carolina bays (Clark et al. 1985, Schalles et al. 1989, Richardson and Gibbons 1993, Sharitz and Gresham 1997). Turtles such as the eastern mud turtle (*Kinosternon subrubrum*) and chicken turtle (*Deirochelys reticularia*) are common, as are various snakes and lizards (Gibbons and Semlitsch 1991). Alligators (*Alligator mississippiensis*) reside in some bays. More than a hundred species of nesting and summering birds were found at bays in North Carolina (Lee 1987); similar numbers of species were observed at two small bays on the SRS (SREL 1980). The larger nesting birds include wood duck (*Aix sponsa*), great blue heron (*Ardea herodias*), little blue heron (*Egretta cerulea*), great egret (*Casmerodius albus*), and anhinga (*Anhinga anhinga*) (Lee 1987; C. Eldridge, SREL, personal communication). Mammals such as oppossum (*Didelphis marsupialis*), raccoon (*Procyon lotor*), and white-tailed deer (*Odocoileus virginianus*) visit bays. Beaver (*Castor canadensis*) activity has been observed in a few bays on the SRS. Small mammals such as mice, shrews, moles, and bats are common.

INVERTEBRATE BIOTA

We provide an overview of composition and diversity, feeding, and life cycles, including adaptations to fluctuating water levels. Aquatic invertebrates in temporary habitats can be classified either as residents, adapted to persist during the dry season, or transients, adapted to recolonize during the wet season (see Wiggins et al. 1980, Batzer and Wissinger 1996). We classify life cycles, exclusive of the resting stage, as very short (a few days to a week), short (a week to a month), or long (months). Unless noted otherwise, information is derived from Barnes (1980), Brigham et al. (1982), Pennak (1989), Thorp and Covich (1991), Williams and Feltmate (1992), Merritt and Cummins (1996), and Batzer and Wissinger (1996).

Most of the research on invertebrates of Carolina bays has been conducted on the Savannah River Site (SRS), a large federal facility in Aiken and Barnwell Counties, South Carolina. The bays that have been studied are mainly clay-based, and there is little information on the invertebrates of peat-based bays.

The data discussed here are not all from wetlands whose basins have the characteristic shape and orientation of Carolina bays. In the field and in customary usage the distinction between Carolina bays and other types of isolated, depression wetlands is often unclear (Lide 1997). Of the best-studied sites on the SRS, Thunder Bay is unambiguously a bay, while Rainbow Bay is arguably not a bay. While we try to qualify the sources of data, our intuition is that the geomorphic distinction is not important ecologically.

The bay lakes of Bladen and Columbus Counties in North Carolina are shallow open-water lakes with extensive wetland margins. Because published information on their wetlands is sparse, we do not include them in the review below. Early accounts describe crustaceans of White Lake (Coker 1938) and benthic and planktonic invertebrates of Lake Waccamaw (Frey 1948, 1949). Lake Waccamaw, where the acidity of the water has been buffered by a natural outcrop of limestone, is the only bay or bay lake in which mollusks are abundant. The aquatic assemblage includes several endemic species, and an endemic land snail is found in the environs. Porter (1985) provides a detailed review of the older literature and collections. The evolution and ecology of these mollusks are topics of active research (e.g., Fuller 1977, Davis et al. 1981, Kat 1983, Johnson 1984, Cahoon et al. 1992, Stiven and Alderman 1992, Cahoon and Owen 1996).

Insects

A great variety of aquatic and semiaquatic insects live in Carolina bays (Table 8.1). A single bay may support more than 100 species (McClure 1994, Leeper and Taylor 1998, in press), and well over 300 species have been collected. Among the orders commonly found in aquatic habitats, only the Plecoptera (stoneflies), which live mainly in lotic habitats, are absent. Aquatic insects of Carolina bays range in length from about 0.3 mm for the earliest instars of odonates and 1 mm for the smallest dipteran larvae to >4 cm for the elongate hemipteran *Ranatra* (Leeper and Taylor 1998, in press).

For most aquatic insects, the complex life cycle with the winged adult stage facilitates dispersal into terrestrial and other aquatic habitats. In bays where the water is impermanent, many species persist as resting stages or as terrestrial adults when the bay dries; many others colonize seasonally or opportunistically. Batzer and Wissinger's (1996) review suggests that such patterns of "cyclic colonization" are generally important for the maintenance of insect populations in wetlands.

Dipterans. Larvae of dipterans, mainly chironomids, dominate the insect assemblages of Carolina bays. At Rainbow Bay on the SRS, where the most detailed studies have been conducted, 79 taxa, including 65 taxa of chironomids, were collected (SREL 1980, Leeper and Taylor 1998). Dipterans constituted 97 percent of the insects collected from benthic substrates and the water column (Leeper and Taylor, in press), and chironomids accounted for 93 percent of insect emergence (Leeper and Taylor 1998). Chironomids were the dominant insects at five other bays in the region, accounting for 63 percent of the insects collected (McClure 1994). Most dipterans, including the Chironominae, the most diverse and abundant subfamily of chironomids in these wetlands, are collector-gatherers as larvae. Larvae of *Chaoborus* and chironomids of the subfamily Tanypodinae consume small invertebrates, including other midge larvae. Life cycles of dipterans are typically short. Some species have desiccation-resistant eggs or larvae; others probably colonize from nearby aquatic habitats.

Coleopterans. Aquatic coleopterans, particularly the Dytiscidae and Hydrophilidae, are moderately diverse in Carolina bays. Fifty-three species of coleopterans were collected from Ashleigh Bay in Barnwell County, South Carolina (McClure 1994). At Rainbow Bay on the SRS, 23 genera were

TABLE 8.1. Aquatic and Semiaquatic Insects of Carolina Bays and Other Depression Wetlands in South Carolina

Order	Number of Species	Common Taxa
Ephemeroptera mayflies	5	Baetidae: *Callibaetis* Caenidae: *Caenis*
Odonata dragonflies and damselflies	37	Aeschnidae: *Anax* Libellulidae: *Erythemis, Erythrodiplax, Libellula, Pachydiplax, Sympetrum, Tramea* Coenagrionidae: *Anomalagrion, Argia, Enallagma, Ischnura* Lestidae: *Lestes*
Hemiptera true bugs	30	Corixidae: *Hesperocorixa, Sigara* Notonectidae: *Buenoa, Notonecta* Naucoridae: *Pelocoris*
Megaloptera dobsonflies	1	Corydalidae: *Chauliodes rastricornis*
Coleoptera beetles	86	Dytiscidae: *Coptotomus, Hydroporus, Thermonectus* Hydrophilidae: *Berosus, Enochrus, Tropisternus* Noteridae: *Hydrocanthus* Haliplidae: *Peltodytes*
Trichoptera caddisflies	35[a]	Leptoceridae: *Oecetis, Triaenodes*
Lepidoptera moths and butterflies	2	Pyralidae: *Synclita*
Diptera true flies	165	Chironomidae: *Ablabesmyia, Chironomus, Dicrotendipes, Kiefferulus, Polypedilum, Procladius, Psectrocladius* Culicidae: *Aedes, Culex* Chaoboridae: *Chaoborus* Ceratopogonidae: *Forcipomyia*

[a]May include lotic species

Source: Lists are based on surveys of Rainbow Bay and Sun Bay on the SRS (SREL 1980), longer-term studies at Thunder Bay on the SRS (Schalles 1979, Schalles and Shure 1989) and Rainbow Bay (Leeper and Taylor 1998, in press), and a survey of five bays in South Carolina, including two on the SRS (McClure 1994).

collected (Leeper and Taylor 1998). Generally, both larvae and adults are aquatic. Larval and adult dytiscids and larval hydrophilids are predacious; adult hydrophilids are largely herbivorous. Life cycles are generally long. Beetles produce desiccation-resistant eggs, some beetles pupate in terrestrial habitats, and the winged adults can disperse widely.

Odonates. Odonates are typically diverse and abundant in southeastern wetlands. However, their occurrence in Carolina bays may be limited by seasonal drying of aquatic habitats. In a study of five bays in South Carolina, McClure (1994) found 3–7 odonate species at three bays that dried during summer and 18–20 species at two bays that held water throughout the year. The aquatic odonate nymphs are predators, consuming micro- and macroinvertebrates, as well as larval amphibians and small fishes. Life cycles are long, and most species probably complete only one generation annually. Some nymphs can survive desiccation, but populations in ponds that have dried and refilled are probably more commonly reestablished by adults from other habitats. Adult odonates are strong fliers that range widely and oviposit freely. On the SRS the flight seasons for most anisopteran odonates are between April and September (Cross 1955; see also Kondratieff and Pyott 1987). Many species lay eggs in aquatic habitat; a few lay diapausing eggs on moist soil or in wetland plants (endophytic oviposition).

Hemipterans. The notonectids are the most abundant and conspicuous of the bugs in Carolina bays. Most of the aquatic bugs, including notonectids, are aggressive predators of invertebrates and small vertebrates. Corixids feed generally on a mix of microorganisms, detritus, and microinvertebrates. The habitat and habits of juveniles and adults are similar. Life cycles are typically long. Most aquatic bugs are winged as adults, and dispersal is probably good.

Trichopterans. Trichopterans are generally not abundant in Carolina bays. Some taxa may be limited by seasonal drying or lack of suitable materials for case construction (McClure 1994). The common trichopterans of bays are case-makers and are presumably collector-gatherers. Life cycles are typically long.

Other Orders. Other aquatic insect groups are less diverse or common in Carolina bays. The number of species of ephemeropterans in bays is low, although their abundances may be high (McClure 1994, Leeper, personal observation). The single species of *Chauliodes* is the only megalopteran recorded from Carolina bays. Aquatic and semiaquatic lepidopterans, including the pyralids *Synclita* and *Vogtia,* and several noctuids have been collected from bays in South Carolina (SREL 1980, McClure 1994, Ford, SREL, unpublished data). A few species of plecopterans (SREL 1980), which probably represent capture of transient adults from lotic habitats, have also been reported from bays. Aquatic collembolids are common, but only *Smithnurius* (McArthur, SREL, unpublished data) has been identified.

Crustaceans

Crustaceans in Carolina bays include members of the subclasses Branchiopoda, Copepoda, Ostracoda, and Malacostraca (Table 8.2). At least 90 species of cladocerans, other branchiopods, and calanoid copepods have been collected from Carolina bays in South Carolina. The assemblages rank among the richest in the world for temporary ponds (see Mahoney et al. 1990).

Most of the crustaceans of Carolina bays are small. The largest species of copepods, cladocerans, and ostracods attain only 3–4 mm in length; most range from <0.1 mm (for early naupliar stages of copepods) or 0.2 mm (for early stages of small cladocerans and ostracods) to 2 mm in length. Amphipods and isopods may reach 5–10 mm in length. Conchostracans and anostracans may reach 1.3 and 2.5 cm, respectively, in length. The crayfishes, which attain lengths of 5 cm or more, are the largest of the aquatic invertebrates found in bays.

Except for some decapods, most of the freshwater crustaceans have limited mobility in terrestrial habitats. Thus, most are permanent residents of bays. Many can produce resting eggs; others enter dormancy as juveniles or adults.

Branchiopods. Three of the major groups of branchiopods, the Cladocera, the Conchostraca, and the Anostraca, are found in Carolina bays; the Notostraca (tadpole shrimps) are absent. Cladocerans occur in nearly all lentic freshwater habitats, while anostracans and conchostracans, as well as notostracans, occur mainly in temporary ponds.

Cladocerans are present in virtually all Carolina bays. All of the families, except for Leptodoridae and Holopedidae (Mahoney et al. 1990, DeBiase and Taylor, unpublished data), are represented, although members of the Polyphemidae and Moinidae are rare. The greatest diversity occurs among the chydorids. In a typical bay on the SRS, one might find eight species of chydorids, five daphnids, two macrothricids, a sidid, and a bosminid (Mahoney et al. 1990). The only *Daphnia* species, *D. laevis,* collected in South Carolina surveys appears to be restricted to Carolina bays and other wetland ponds.

Most cladocerans are filter-feeders or scrapers, consuming algae and other fine particulate material or periphyton. An exception, *Polyphemus,* preys on small invertebrates. Some, including many daphnids and sidids, are planktonic or free-swimming in habit; others, including most chydorids and macrothricids, are associated more closely with benthic and littoral substrates. Life cycles of cladocerans are short, less than one week under warm temperatures, perhaps one to two weeks at cool temperatures, and they produce resting eggs to survive the dry season.

Anostracans and conchostracans are common and sometimes abundant, but not diverse, in Carolina bays. They are filter-feeders, consuming algae and

TABLE 8.2. Crustaceans of Carolina Bays and Other Depression Wetlands in South Carolina

Subclass and Order	Number of Species	Common Taxa
Subclass Branchiopoda		
Order Anostraca fairy shrimp	2	Streptocephalidae: *Streptocephalus seali* Chirocephalidae: *Eubranchipus holmani*
Order Conchostraca clam shrimps	2	Lynceidae: *Lynceus gracilicornis* Limnadiidae: *Limnadia lenticularis*
Order Cladocera water fleas	45[a]	Sididae: *Diaphanosoma, Pseudosida bidentata* Daphnidae: *Ceriodaphnia, Daphnia laevis, Scapholeberis armata armata, Simocephalus* Bosminidae: *Neobosmina tubicen* Macrothricidae: *Ilyocryptus, Macrothrix* Chydoridae: *Alona, Alonella, Chydorus, Ephemeroporus, Pseudochydorus* Polyphemidae: *Polyphemus pediculus*
Subclass Ostracoda seed shrimps	unknown	unknown
Subclass Copepoda copepods		
Order Calanoida	11	Diaptomidae: *Aglaodiaptomus, Leptodiaptomus moorei, Onychodiaptomus sanguineus* Centropagidae: *Osphranticum labronectum*
Order Cyclopoida	12	Cyclopidae: *Acanthocyclops robustus, Diacyclops, Macrocyclops fuscus, Tropocyclops*
Order Harpacticoida	unknown	unknown

TABLE 8.2. (Continued)

Subclass and Order	Number of Species	Common Taxa
Subclass Malacostraca	unknown	Asellidae: *Caecidotea*
Order Isopoda		
aquatic sow bugs		
Order Amphipoda	unknown	Crangonyctidae: *Crangonyx*
scuds		Gammaridae: *Gammarus*
		Talitridae: *Hyalella*
Order Decapoda	unknown	Palaemonidae: *Palaemonetes*
shrimps, crayfishes		Cambaridae: *Procambarus*

[a]Includes distinct but unidentified or undescribed species.

Source: Lists for Branchiopoda and Calanoida are based on surveys of 23 bays and depression wetlands on the SRS (Mahoney et al. 1990), 88 bays and depression wetlands on the SRS (DeBiase and Taylor 1993, and unpublished data), and three bays elsewhere in the Coastal Plain (DeBiase and Taylor, unpublished data). The list for the Cyclopoida is based on long-term studies at Rainbow Bay on the SRS (Wyngaard et al. 1991, Medland 1997), as are the lists for the Amphipoda and Isopoda (Leeper and Taylor, in press). Decapoda on the SRS were surveyed by Hobbs et al. (1978), but results were not reported specifically for Carolina bays.

other fine particulate material. Their life cycles are probably short, perhaps one to three weeks, depending on temperature. Both appear to be univoltine in bays, producing only resting eggs (Mahoney et al. 1990). Within a pond they may appear only sporadically, apparently persisting as resting eggs over multiple years (Taylor, unpublished data).

Copepods. All three orders of free-living freshwater copepods, the Calanoida, the Cyclopoida, and the Harpacticoida, are represented in Carolina bays. The calanoids are the best studied.

Calanoid copepods are present in many Carolina bays. As many as six species have been recorded from a single bay on the SRS, but the number is more commonly one or two (Mahoney et al. 1990, DeBiase and Taylor, unpublished data). About half of the Diaptomidae belong to the genus *Aglaodiaptomus,* including a locally common, newly described species, *Aglaodiaptomus atomicus* (DeBiase and Taylor 1997). Many of the bay calanoids, including all of the *Aglaodiaptomus,* are brightly pigmented with blue or red carotenoid pigments.

The diaptomid calanoids are free-swimming and planktonic in habitat; they feed on algae, other fine particulate material, and small invertebrates; the centropagid *Osphranticum labronectum* is epibenthic. The life cycle from hatching to egg production for *Aglaodiaptomus stagnalis,* the largest species, is completed in five to six weeks (Taylor and Mahoney 1990); smaller species probably require two to three weeks, depending on temperature. Calanoid copepods produce resting eggs to survive desiccation and other adversities.

Aglaodiaptomus stagnalis is strictly univoltine, producing only resting eggs, while *A. atomicus* and some other species are multivoltine.

Cyclopoid copepods are virtually ubiquitous in lentic habitats. Carolina bays are no exception (Mahoney et al. 1990), but their cyclopoids have received little attention. With the exception of work by Coker (1938) in North Carolina, detailed studies have been made only at Rainbow Bay on the SRS. Cyclopoid copepods are epibenthic or planktonic, feeding generally on algae, bacteria, detritus, and microinvertebrates. Most probably shift ontogenetically from herbivory in the early juvenile stages to omnivory in the late juvenile and adult stages. The life cycle of the active stages is short: one to several weeks, depending on temperature. Cyclopoid copepods survive adverse seasons in dormancy at a late juvenile stage (copepodid instar IV, the antepenultimate instar). Maturation and egg production may occur within a few days of emergence (Wyngaard et al. 1991, Medland 1997). Most species of cyclopoids at Rainbow Bay appeared to complete several generations before producing dormant stages (Medland 1997).

Harpacticoid copepods are also common and abundant in Carolina bays (Mahoney et al. 1990, Taylor and Mahoney 1990, Leeper and Taylor, in press), but have received even less attention than cyclopoids. They live in benthic microhabitats and feed generally on detrital material. Life cycles are probably short. Harpacticoid copepods also survive adverse seasons in dormancy at a late juvenile stage.

Ostracods. Ostracods are found in most Carolina bays (Mahoney et al. 1990). They may be rich in species (see Ebert and Balko 1987 and King et al. 1996 for accounts of their diversity in California vernal pools), but their composition has not been studied. They feed generally on fine particulate material, and life cycles are probably short. They can produce desiccation-resistant resting eggs.

Malacostracans. Amphipods and isopods are common but not ubiquitous in Carolina bays; decapods are less frequently encountered. Mahoney et al. (1990) found amphipods and isopods in about one third of 23 bays and other wetland ponds surveyed on the SRS. In their survey of decapods on the SRS, Hobbs et al. (1978) collected half a dozen species from lentic habitats, but did not specify which were found in bays. Members of all three orders are common in acidic depression wetlands on the Lower Coastal Plain of South Carolina (DeBiase and Taylor, unpublished data). Amphipods, isopods, and decapods are all benthic animals, variously feeding on periphyton or plants or scavenging. Their life cycles are typically long. They generally lack special adaptations, such as resting eggs, for surviving desiccation, but have some capacities to persist in moist substrates.

Annelids

Aquatic annelids, including oligochaetes and leeches, are common and abundant in Carolina bays (Mahoney et al. 1990). At least 14 species of oligochaetes, including an enchytraeid, the naidids *Dero, Nais, Pristina,* and *Stephensoniana,* the tubificids *Limnodrilus, Tasserkidrilus,* and *Tubifex,* and the lumbriculid *Eclipidrilus,* have been reported from bays on the SRS (McArthur, SREL, unpublished data, Leeper and Taylor, in press). Many of the aquatic oligochaetes in bays are small (<1–2 cm in length), and they are mainly benthic deposit feeders. Leeches are scavengers, ectoparasites, and predators. Life cycles are probably short. Aquatic oligochaetes and leeches can aestivate in mucus-lined cysts.

Nematodes

Nematodes are also common and abundant in Carolina bays (Mahoney et al. 1990, Leeper and Taylor, in press). Although the assemblages are probably quite diverse, only one genus, *Dorylaimus,* has been identified (McArthur, SREL, personal communication). These nematodes are small (1–2 cm in length). Nematode nutrition is diverse; they include predators, scavengers, and deposit feeders. Life cycles are probably very short. Eggs, larvae, and adults can survive desiccation.

Rotifers

Rotifers, like cyclopoid copepods, are virtually ubiquitous in lentic habitats. At Rainbow Bay on the SRS (Taylor and Mahoney 1990), more than a dozen taxa were present, of which *Polyarthra* sp. and *Conochilus unicornis,* a colonial form, were the most common. Rotifers are typically 0.1–0.2 mm in length. Most of the rotifers feed as collector-gatherers on algae and bacteria; others prey on very small invertebrates. Their life cycles are very short. Rotifers produce desiccation-resistant eggs.

Mollusks

Mollusks generally do not thrive in waters of low pH or low calcium concentration, which are typical conditions in Carolina bays. Only a few small gastropods, including the limpet *Ferrissia,* have been reported from bays other than Lake Waccamaw (Schalles 1979, Schalles and Shure 1989, Mahoney et al. 1990, McArthur, SREL, unpublished data). These mollusks feed as scrapers on epiphytic material. Life cycles are probably short, and the animals probably aestivate to survive dry seasons.

Other Aquatic Invertebrates

Other aquatic invertebrates, including poriferans, bryozoans, hydrozoans, tardigrades, turbellarians, and water mites, have also been reported from Carolina bays (Mahoney et al. 1990, Leeper and Taylor, in press, McArthur, SREL, unpublished data). Sponge spicules are frequently found in the surficial sediments (Stager and Cahoon 1987, Gaiser 1997), even in bays that dry completely. These occurrences contradict Williams's (1987) observation that sponges do not occur in temporary ponds.

Terrestrial Invertebrates

Assemblages of terrestrial invertebrates occurring at Carolina bays have received less attention than aquatic assemblages. At Sun Bay on the SRS a spring survey yielded specimens from 75 families of terrestrial insects, 10 families of spiders, 1 superfamily of harvestmen, 5 families of millipedes, and 1 family of centipedes (SREL 1980). Twenty-three species of ants were collected from the environs of three other bays on the SRS (Van Pelt and Gentry 1985). Semlitsch (1986) reported on the life history of the mole cricket, *Neocurtilla hexadactyla,* which is common in mesic and hydric habitats of bays of the SRS. Haddad (SREL, unpublished data) surveyed the SRS for butterflies and identified at least two hesperids, *Ancyloxypha numitor* and *Panoquina ocola,* which were associated with bays and swampy areas. Draney (SREL, personal communication) found that wolf spiders (Lycosidae) dominated the assemblage of ground spiders in the basin of Rainbow Bay on the SRS and that orb-weavers (Araneidae) were also common.

ECOLOGY

Assemblages

Most phyla of freshwater invertebrates are well represented in Carolina bays, and the invertebrate assemblages are rich in species. The only well-studied groups are insects and crustaceans. A single bay might support a more than 100 species of aquatic insects (see **Insects** above) and more than 30 species of crustaceans (see **Crustaceans** above; this tally omits speciose but unstudied groups such as ostracods), as well as unknown numbers of species of oligochaetes, rotifers, nematodes, and other invertebrates. We note that because hydroperiod and other environmental conditions are highly variable among years in bays, species lists based on a single year's study will almost certainly be incomplete, even if the hydroperiod during the study year seems "typical."

Microcrustacean assemblages are diverse among bays, as well as within bays (Fig. 8.3). Nearby ponds tend to be more similar than distant ones, but this effect is weak for ponds separated by more than 1 km. The pattern might reflect greater exchange of immigrants among nearby ponds, according to a stepping stone model, or greater similarity of habitat among nearby ponds. Corresponding data are unavailable for other invertebrates. Particularly for insects with cyclic colonization patterns, it seems plausible that assemblages would be influenced by proximity to other aquatic habitats, as well as to other bays.

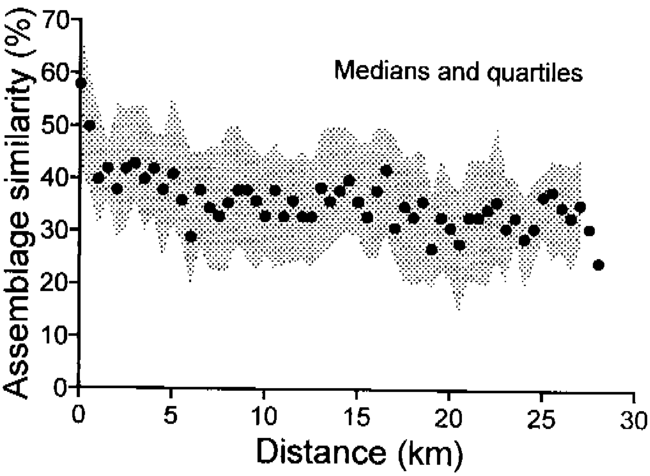

Fig. 8.3. Similarity versus distance for microcrustacean assemblages of Carolina bays and wetland ponds on the Savannah River Site in South Carolina. The Jaccard index of percentage similarity was computed for 88 ponds sampled in February, April, May, August, and November (DeBiase and Taylor, unpublished data). The comparisons are based on a list of 34 cladocerans (except chydorids and macrothricids), other branchiopods, and calanoid copepods that were consistently identified to species level. Medians (filled circles) are shown for 0.5-km distance classes; quartiles (shaded band) are shown if $N \geq 10$ observations. Among all pairs, the average similarity was 36 percent.

Genetic data indicate high levels of differentiation among populations of calanoid copepods and of the cladoceran *Daphnia laevis* (Boileau and Taylor 1991). The extent to which these patterns reflect persistent founder effects, ecological divergence, or low exchange of migrants is unresolved. Undoubtedly, wide-ranging vertebrates, including wood ducks, herons, egrets, deer, and humans, function as agents of passive dispersal for invertebrates among bays and other aquatic habitat. The frequency and magnitude of such transfers have not been measured.

Isolation among bays has not resulted in extensive speciation among the resident invertebrates. The only recognized endemics among the bay invertebrates are some of the mollusks of Lake Waccamaw, where the isolation is enhanced by the locally atypical water chemistry of the lake. Some of the calanoid copepods, such as *Aglaodiaptomus atomicus,* may also be endemic to the region, if not to Carolina bays, but too little is presently known about their distributions to make that judgement. The microcrustacean groups that yielded the greatest numbers of rare or undescribed species in California vernal pools (King et al. 1996) remain unstudied (ostracods and harpacticoid copepods) or poorly resolved (chydorid cladocerans and cyclopoid copepods) in Carolina bays.

Among temporary ponds, species richness often increases with duration of the hydroperiod (e.g., vernal and autumnal temporary pools in Ontario, Canada, Wiggins et al. 1980; vernal pools in California, Ebert and Balko 1987; temporary ponds in Wisconsin, Schneider and Frost 1996). A substantial amount of variation in invertebrate assemblages of Carolina bays seems to be associated with hydroperiod. Among 88 bays and other wetland ponds on the SRS, the median number of microcrustacean species (cladocerans except chydorids and macrothricids, other branchiopods, and calanoid copepods) ranged from 6 in ponds that hold water for only a few months annually to 12 in ponds that seldom dry (DeBiase and Taylor, unpublished data). Because all of these microcrustaceans have life cycles short enough to be completed in any of the ponds, the number of species is not determined simply by duration of the hydroperiod. Some of the microcrustaceans are distinctly seasonal in occurrence (see **Population Dynamics and Seasonal Succession** below). The longer hydroperiods, spanning more seasons, can support a greater variety of phenologies and thus more species.

Occurrences of invertebrates with longer life cycles may be affected directly by duration, as well as timing, of the hydroperiod. McClure (1994) observed that insect assemblages of three bays with intermittent hydrologies were dominated by multivoltine species with rapid larval development (mainly dipterans), while two bays with more persistent water were dominated by univoltine species with slow development (odonates, hemipterans, and coleopterans). A similar pattern occurs with pond-breeding amphibians in Carolina bays (Pechmann et al. 1989). The number of species of metamorphosing larvae increases with length of the hydroperiod, both among ponds within years and within ponds among years.

The size of the pond has a modest influence on the number of species. Species-area relations have been examined only for microcrustaceans. Among 23 Carolina bays and other wetland ponds on the SRS, Mahoney et al. (1990) found that the number of cladoceran taxa, but not of calanoid copepod taxa, was positively correlated with area of the wetland. The relationship is approximately log-linear. Because the effect is due mainly to chydorids, we speculate that it is associated with diversification of the littoral habitats favored by members of this family.

There are striking differences between the assemblages of Carolina bays and nearby manmade permanent ponds and reservoirs on the SRS, particularly among the free-swimming or "planktonic" microcrustaceans (DeBiase and Taylor, unpublished data). Relatively large or brightly pigmented microcrustaceans, such as *Daphnia laevis, Aglaodiaptomus* spp., anostracans, and conchostracans, are conspicuous in the bays but absent from the impoundments. Assemblages of these impoundments consist of species that are small or transparent, fitting a pattern that has been repeatedly associated with intense predation by fish or other vertebrates. Few or none of the bays on the SRS hold water permanently. Although there are other differences, such as water chemistry and morphometry, between bays and impoundments, we hypothesize that differences in assemblages are due mainly to the exclusionary effect of bay hydrology and isolation on fish populations (see Wellborn et al. 1996). Because the relatively large or brightly pigmented microcrustaceans do coexist with salamanders in many bays, we must also hypothesize that predation on microcrustaceans by salamanders in the bays is less intense than predation by fish in the impoundments.

Among the smaller epibenthic and littoral taxa, there are no obvious differences between assemblages of Carolina bays and impoundments. In a survey of 88 bays and other wetland ponds and 8 impoundments on the SRS, about half the cladoceran species found in Carolina bays were also found in permanent ponds and reservoirs (DeBiase and Taylor, unpublished data); chydorids and macrothricids were not identified in this study.

The bright carotenoid pigmentation of some calanoid copepods and other microcrustaceans in the Carolina bays may confer protection against ultraviolet radiation (Hairston 1976). However, because ultraviolet radiation should attenuate very rapidly in the dark-stained waters typical of Carolina bays (see Wetzel 1983), the photoprotective benefit is probably less important in bays than in other types of shallow ponds. Its other benefits are as yet unknown.

Population Dynamics and Seasonal Succession

In the annual hydrologic cycle of Carolina bays, winter is the time when water levels generally increase. Among bays that dry, refilling often occurs in winter, and even among bays that do not dry entirely, substantial areas may become reinundated. For most invertebrates in Carolina bays, the active aquatic phase of the life cycle is shorter than the hydroperiod, and many species are distinctly seasonal or even ephemeral in occurrence. The initial dominants are invertebrates that emerge from resting stages in the basin. For example, within hours after the sediments are inundated, calanoid, cyclopoid, and harpacticoid copepods appear; at Rainbow Bay they constituted the largest part of the zooplankton for about a month after the pond filled (Taylor et al. 1989). Most of the calanoid species are active only during the cooler months, but a few, such as *Aglaodiaptomus atomicus,* remain active through summer if the pond holds water (Mahoney et al. 1990, DeBiase and Taylor, unpublished data). Although cladocerans also hatch from resting eggs soon after the pond fills, their abundances are initially low (Taylor and Mahoney 1990). Abundances and diversity of cladocerans increase seasonally. Among bays and other wetland ponds on the SRS, Mahoney et al. (1990) found that the median number of species per pond increased from 7 in February to 13.5 in June; most of the increase was among chydorids and macrothricids, which are mainly epibenthic or littoral. Abundances in most other groups, including oligochaetes, dipterans, and other insects, at Rainbow Bay also increased seasonally, reaching maxima in mid- to late spring (Leeper and Taylor, in press).

For resident aquatic invertebrates that produce resting stages, breaking and reentering dormancy are critical features of population dynamics. These processes have been examined through detailed field and laboratory studies for some of the microcrustaceans at Rainbow Bay on the SRS; both ecological and environmental conditions seem, variously among species, to control them. The cyclopoid copepods are divided nearly equally between species that appear whenever the pond fills and those that seem to require more specific conditions, such as seasonal cues (Medland 1997). Resting eggs of the calanoid copepod *Aglaodiaptomus stagnalis* hatch only if the pond fills between late fall and early spring; if the pond fills earlier and retains water through the late fall and early spring, the eggs remain dormant (Taylor et al. 1990, and unpublished data). Some of the larger microcrustaceans, including *A. stagnalis* and the fairy and clam shrimps, produce only resting eggs. For many other species the return to dormancy seems to depend on ecological or environmental conditions. In the cladoceran *Daphnia laevis,* production of males and resting eggs coincided with declining fecundities and food resources, which occurred at different times in successive years (Taylor and Mahoney 1990, and unpublished data).

The resting stage itself is not exempt from demographic processes. The mortality, as well as the passive dispersal, that can occur during the resting stages may have important effects on dynamics of a population. After several years of drought at Rainbow Bay, numbers of emerging cyclopoid copepodids were reduced by about an order of magnitude, and numbers of hatching *Aglaodiaptomus stagnalis* nauplii were reduced by about two orders of magnitude (Taylor et al. 1990, Wyngaard et al. 1991). Populations of the cyclopoids, which include multivoltine species, recovered to predrought abundances within two months, but *A. stagnalis,* which is univoltine, did not recover until a subsequent year.

The populations of transient aquatic invertebrates in bays are subject to regulation in their alternate habitats, as well as in the Carolina bays. Phenology of dispersal, as well as success in alternate habitats, is obviously important to their success in bays. Bays that are dry during the flight seasons for odonates, for example, may be ignored by species that oviposit only in aquatic habitats.

Trophic Structure and Production

In Carolina bays many of the large aquatic invertebrates, including odonates, hemipterans, and some coleopterans, are predators, feeding generally on other invertebrates but occasionally on larval amphibians or small fishes. Insects and larval salamanders are probably the main aquatic predators of invertebrates in most bays, with fish assuming importance only in those that are permanently flooded.

Larval salamanders in Rainbow Bay on the SRS feed mainly on microcrustaceans and chironomid larvae (Taylor et al. 1988). Predation by salamander larvae has been shown experimentally to depress populations of microcrustaceans (Ginger's Bay on the SRS, Scott 1990; artificial ponds in

North Carolina, Morin et al. 1983b). Pond-breeding salamanders can be active as predators in bays during much of the year. Adults, depending on species, return to breed from autumn through late spring, and the larvae, depending again on species, are present from winter through late summer (Gibbons and Semlitsch 1991).

Most of the small aquatic invertebrates in Carolina bays are collector-gatherers, feeding on smaller particles of food, which may be algae, bacteria, detritus, protozoans, or smaller invertebrates. Shredders are underrepresented (McClure 1994, Leeper and Taylor, in press). With the exception of some beetles, the common aquatic invertebrates of Carolina bays do not consume the living macrophytes. Thus, the main support for their production is probably derived from periphyton, phytoplankton, and detritus, including the remains of both aquatic and terrestrial plants.

Invertebrate biomass has been estimated at only two Carolina bays, both on the SRS, and the data offer contrasting pictures of the relative importance of the two general classes of invertebrate consumers (Fig. 8.4). In Thunder Bay the invertebrate biomass is dominated by macroinvertebrate predators, mainly odonate nymphs. Schalles and Shure (1989) hypothesized that turnover among microinvertebrate prey must be extraordinarily high to support the biomass of predators. In Rainbow Bay the invertebrate biomass is dominated by collector-gatherers, mainly oligochaete worms (the bulk of which are tubificids and naidids), chironomid larvae, cladocerans, and isopods (Leeper and Taylor, in press). Odonates were notably sparse at Rainbow Bay, perhaps because the pond had dried during preceding summers (see ***Odonates*** above).

At Rainbow Bay demographic analyses indicated that populations of microcrustacean collector-gatherers, such as the cladoceran *Daphnia laevis,* were usually limited by food rather than by predation (Taylor and Mahoney 1990, and unpublished data), and observations of fecundities at other ponds suggest that the phenomenon is widespread. At both Rainbow and Flamingo Bays rapid declines in fecundity coincided with increases in cladoceran populations and great decreases in biovolume of phytoplankton (Taylor and Mahoney, unpublished data). Whether this apparent importance of algal resources to microcrustaceans applies to bays generally or extends to other invertebrate consumers is an open question. Batzer and Wissinger (1996) comment that "the importance of algae to wetland food webs has probably been underestimated."

There are only a few estimates of invertebrate production from bays. Annual production of the planktonic microinvertebrates at Rainbow Bay in 1984 was 6.2 g dry mass m^{-2}, a value that ranks as moderate in comparison with other shallow lakes and ponds (Taylor et al. 1989). In the same year, production of larval salamanders was 1.5 g dry mass m^{-2}, the bulk of which was probably sustained by dipteran larvae (Taylor et al. 1988). In a subsequent study at Rainbow Bay, annual production by oligochaetes, crustaceans, and rotifers was 37 and 15 g dry mass m^{-2} during two consecutive years (1992–

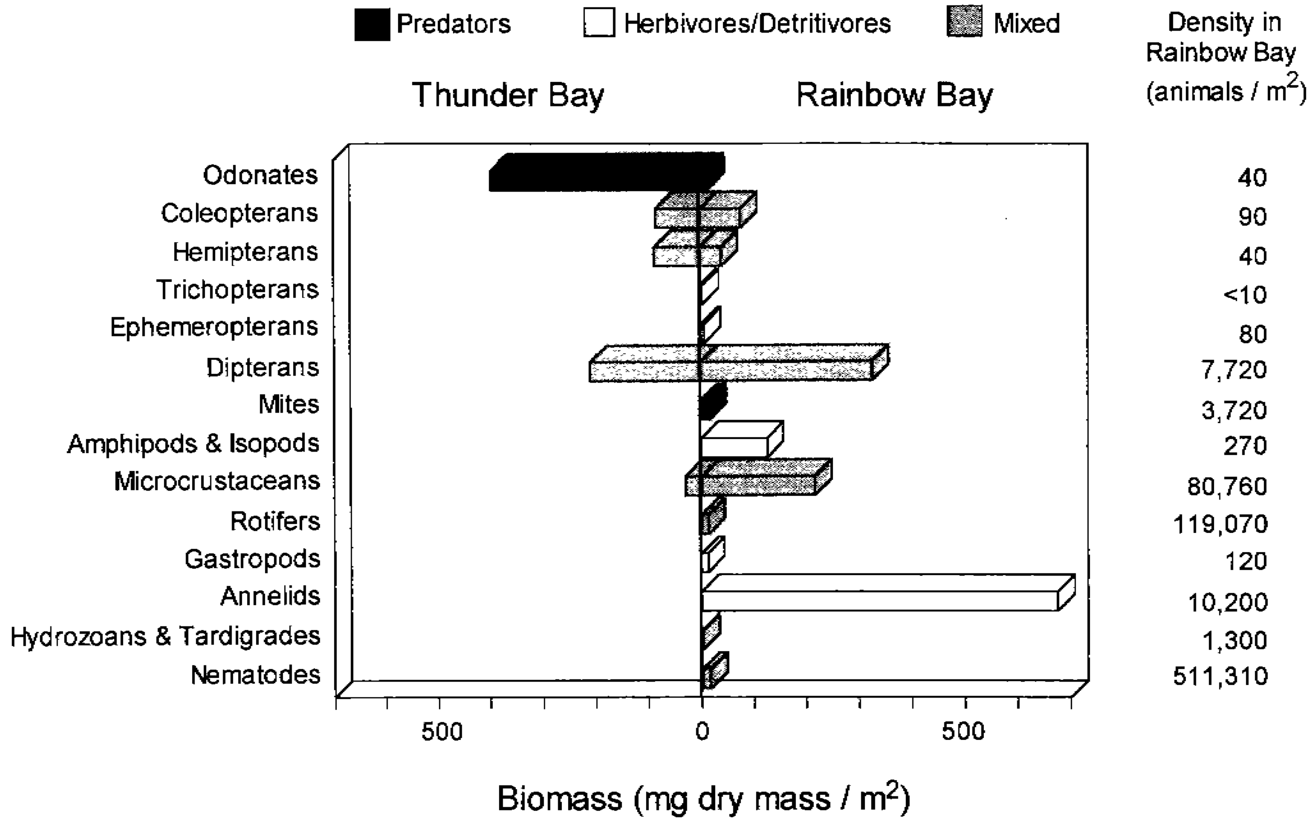

Fig. 8.4. Composition of the invertebrate assemblages at two Carolina bays on the Savannah River Site in South Carolina. Biomass density is shown for both bays. Population density is given only for Rainbow Bay; corresponding data for Thunder Bay were unavailable. Thunder Bay held water continuously during the one-year study by Schalles and Schure (1989); Rainbow Bay held water for 250 and 175 days annually during the two-year study by Leeper and Taylor (in press). In both studies quantitative sampling included sediments, the water column, and aquatic macrophytes. Micro- and macroinvertebrates were sampled at Rainbow Bay; only macroinvertebrates were sampled at Thunder Bay.

93, Leeper and Taylor, in press). The difference between these two years was due primarily to differences in production by benthic oligochaetes and chironomids. For Thunder Bay, Schalles and Shure (1989) argued that 15 g dry mass m^{-2} in annual production of invertebrates would be required to support the observed biomass of odonate and amphibian predators.

The magnitudes of trophic connections with terrestrial consumers remain unexplored. Birds such as wood ducks, herons, and egrets feed on aquatic invertebrates, as well as on the amphibian and piscine predators of aquatic invertebrates (e.g., Landers et al. 1977). Insectivorous birds and bats feed on adult insects emerging from the bays; these insects are also consumed by predatory invertebrates such as adult odonates and spiders.

CONSERVATION

Although Bennett and Nelson (1991) write that "bays have been historically regarded as very uninviting to humans," Carolina bays have a long record of human activity. Archaeological artifacts indicate that bays were used by the earliest people known to have lived in this region (Eberhard et al. 1994). Their activities included habitation on the rims during some prehistoric periods. With European settlement of the Coastal Plain during the eighteenth and nineteenth centuries, human usage and modification of the bays intensified. Many bays were ditched and drained for agriculture or silviculture (Ash et al. 1983, Gilliam and Skaggs 1981). Timber (pond cypress or pine) was harvested from some bays, and a few larger bays were used as mill ponds (see Fig. 8.2). Three additional threats to bays emerged in the 1980s: peat mining, tertiary wastewater treatment, and urbanization (see Richardson and Gibbons 1993, Kadlec and Knight 1995). Today only about 40 percent of the bays in South Carolina remain relatively intact (Bennett and Nelson 1991).

Four major federal programs regulate or protect Carolina bays. The Wetlands Advance Identification Program (ADID), jointly implemented by the United States Army Corps of Engineers and the Environmental Protection Agency, delineates and evaluates wetlands, designating those that are unsuitable for filling or other modification and recommending those that are suitable for restoration or mitigation. The Carolina bay ADID identifies approximately 250 bays (24,700 ha) in South Carolina. The National Environmental Policy Act applies to federal lands, including military reservations and national forests, which include more than 230 bays (5000 ha). The Wetland Reserve Program provides financial incentives to private landowners to protect and restore wetlands. Because so many bays were previously converted to agriculture, South Carolina gives high priority to bays in this program. Under the Emergency Wetlands Resources Act, the United States Fish and Wildlife Service evaluated wetlands to determine which were eligible for federal or federally assisted state acquisition. The Southeast Regional plan listed 28 eligible Carolina bays or bay complexes.

State and private programs also protect Carolina bays. Coordinated efforts between The Nature Conservancy and state natural resource agencies have purchased bays in Georgia (1 bay, 405 ha), South Carolina (32 bays, 3870 ha), and North Carolina (8 bays, 246 ha). These sites have been chosen mainly for their populations of rare or endangered plants. State parks protect all or part of five bay lakes in North Carolina and a large bay and a bay complex in South Carolina. Other bays are located in state forests and wildlife refuges. A few bays in North and South Carolina have been restored and protected under wetlands mitigation banking programs.

Conservation efforts often focus on a few representative examples of a type of habitat. The great diversity of invertebrate assemblages among Carolina bays suggests that this strategy would not protect all or even most of the species within an area, and preservation of insect diversity may depend on the maintenance of other types of aquatic habitats. Circumstances that afford protection of groups of bays are thus particularly fortunate. An outstanding example is the Lewis Ocean Bay preserve in Horry County, South Carolina, which is administered by the South Carolina Heritage Trust. Federal facilities, including Fort Gordon in Georgia and the Savannah River Site in South Carolina, also protect complexes of bays and other wetland and aquatic habitats.

Many Carolina bays on the Savannah River Site, now a National Environmental Research Park, had been severely altered by agricultural activity before 1951, when the land was acquired by the federal government. After more than four decades of passive, benign management, these bays support microcrustacean assemblages that rank among the richest in the world, as well as thriving populations of other invertebrates and amphibians. Whether the communities have returned to the predisturbance states of the late eighteenth or early nineteenth century is unknown, probably unknowable, and in most cases unlikely. In the long view, paleoenvironmental data suggest that the modern era of anthropogenic disturbance represents yet another change in a history that stretches back for 10 or more millennia. In the short view, ecological results reinforce the opinion that disturbed, as well as undisturbed, wetland habitats are worthy of protection.

Few invertebrates from Carolina bays appear on conservation lists. Some of the endemic mollusks of Lake Waccamaw in North Carolina are considered species of special concern, threatened, or endangered (Fuller 1977, Porter 1985). Lake Waccamaw also harbors three endemic fishes, one of which appears on the federal list of threatened species (Rohde et al. 1994). Lake Waccamaw seems to be unique among bays in its endemic invertebrate fauna. Two calanoid copepods found in South Carolina rated as "vulnerable" on 1996 IUCN Red List of Threatened Animals (IUCN 1996). *Hesperodiaptomus augustaensis* occurs in a few Carolina bays and other wetland ponds on the SRS, and *Aglaodiaptomus marshianus* occurs in wetland ponds on the Lower Coastal Plain of South Carolina (DeBiase and Taylor, unpublished data). Their recommender, Janet Reid of the Smithsonian Institution, comments that these and other narrowly distributed species in temporary ponds may become endangered because "ephemeral habitats are under particular pressure for human alteration worldwide" (Reid 1997).

RESEARCH NEEDS

Much of the present knowledge of the ecology of Carolina bays, particularly of the animals, is based on studies on the Savannah River Site. Additional basic research is needed to characterize the communities of bays, particularly elsewhere on the Atlantic Coastal Plain. Critical questions for further research have been summarized by Richardson and Gibbons (1993) and Sharitz and Gresham (1997). The potential effects of fire, hydrologic alteration, and other management techniques on the invertebrates are poorly known. The use of bay habitats by terrestrial invertebrates during both wet and dry seasons, as well as the ecology of aquatic invertebrates during dry seasons, deserves further attention. Paramount is the need to evaluate the roles, current and potential, of these wetlands in the functioning of the larger ecosystem of the Coastal Plain.

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