The Wetlands of Lakes Pontchartrain and Maurepas: Past, Present and Future

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Abstract: One of the largest wetlands along the Gulf Coast of North America (ca. 150 000 ha) occurs around the shorelines of Lake Pontchartrain and Lake Maurepas in southeastern Louisiana, just north and west of New Orleans. We provide an introduction to the environmental history of the marshes and swamps in the upper Lake Pontchartrain basin, a review of the existing vegetation patterns and their possible causes, and a discussion of restoration targets and priorities. The Mississippi River produced the St. Bernard Delta 3000–4000 years ago, trapping fresh water to produce both Lake Maurepas and Lake Pontchartrain (Frazier 1967). The natural vegetation of much of the region remains fresh or brackish marshes, mixed with swamps dominated by bald cypress (*Taxodium distichum*) and tupelo (*Nyssa aquatica*). Yearly flooding by the Mississippi River was once a major factor controlling vegetation patterns, but these processes have been greatly impaired by the construction of artificial levees for flood control. Humans also removed most of the cypress swamps in a pulse of logging between 1876 and 1956. Continued subsidence of the land, slowly rising sea levels, salinity pulses from hurricanes, and canals from the Gulf of Mexico, add further stress to these wetlands. Over the past century there has been a steady loss of wetland area, and a gradual conversion of fresh water to salt water vegetation types. Biotic processes are also important. An exotic species of mammal, nutria (*Myocastor coypus*), consumes both aboveground and belowground parts of wetland plants. Reforestation is strictly limited by the combination of salt pulses, competition, and nutria. Alligators are the top predator in this system, but their potential for reducing the impacts of nutria has received minimal attention from biologists. There are many potential future states for this ecosystem. In the extreme case of rising sea level and warmer climate, the area may become a salt and brackish embayment fringed with mangroves. The state closest to historical conditions would be large areas of bald cypress swamp. Two important priorities are to increase flow of freshwater into the system from multiple pulsed fresh water diversions, and to decrease saltwater intrusions by closing canals such as the Mississippi River Gulf Outlet.

Key words: Louisiana, Maurepas, Mississippi River, Pontchartrain, wetlands, restoration.

Résumé : Une des plus grandes surfaces de terres humides le long du golfe du Mexique en Amérique (ca. 150 000 ha) se retrouve sur les rives des lacs Pontchartrain et Maurepas, dans le sud-ouest de la Louisiane, au nord et à l'ouest de la Nouvelle-Orléans. Les auteurs présentent une introduction à l'histoire environnementale des marais et des marécages à la tête du bassin du lac Pontchartrain, une revue des patrons de végétation actuelle et de leurs causes, et une discussion sur les cibles et les priorités de restauration. Le fleuve Mississippi à engendré le delta St-Bernard, il y a 3000–4000 ans, en retenant de l'eau douce, pour produire les deux lacs, Maurepas et Pontchartrain (Frazier 1967). La végétation naturelle d'une bonne partie de la région demeure constituée d'eau douce ou saumâtre, avec des savanes dominées par le cyprès chauve (*Taxodium distichum*) et le tupelo (*Nyssa aquatica*). Chaque année, la crue des eaux du Mississippi était autrefois un facteur majeur qui déterminait les patrons de végétation, mais ces processus ont été largement affectés par la construction de digues artificielles pour maîtriser les inondations. On a également supprimé la majeure partie des cyprès chauves, au cours d'un épisode de coupe, entre 1876 et 1956. Affaissement continu des terres, augmentation lente des niveaux de la mer, intrusions salines lors des ouragans, ainsi que les canaux provenant du golfe du Mexique, ajoutent aux stress reçus par ces terres humides. Au cours du dernier siècle, on a observé une perte continue de la surface de terres humides, et une conversion graduelle à des types de végétation d'eau douce vers des types d'eau salée. Les processus biotiques sont également importants. Une espèce exotique de mammifère, le ragondin (*Mycocastor coypus*), consomme les parties souterraines et aériennes des plantes des terres humides. La reforestation est strictement limitée par une combinaison d'intrusions salines et de compétition, incluant les ragondins. Les alligators sont les prédateurs à la tête de ce écosystème, mais leur potentiel pour réduire les impacts des ragondins n'a reçu que peu d'attention de la part des biologistes. Plusieurs possibilités existent pour le future de cet écosystème. Dans une situation extrême d'augmentation du niveau de la mer et du réchauffement climatique, cette surface pourrait se transformer en baie entourée de mangroves. La situation la plus proche des

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conditions historiques serait une grande surface marécageuse couverte de cyprès chauves. On doit accorder deux grandes priorités, soit l'augmentation de l'apport en eau douce dans le système à partir de multiples diversions périodiques d'eau douce, et la diminution des intrusions d'eau salée, en fermant les canaux comme le Mississipi River Gulf Outlet.

Mots-clés : Louisiane, Maurepas, fleuve Mississippi, Pontchartrain, terres humides, restauration.

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Introduction

One of the largest freshwater wetlands along the Gulf Coast of North America occupies the shorelines of Lake Pontchartrain and Lake Maurepas in Southeastern Louisiana (Moore 1992), just northwest of New Orleans. This area includes some 147 000 ha of wetland, largely bald cypress and water tupelo swamp, with increasing areas of marsh and open water (Penland et al. 2001). This area is the southeastern extension of one of the world's ten largest wetlands (Fraser and Keddy 2005), the Mississippi River alluvial plain (Shaffer et al. 2005). The socio-economic well-being of southern coastal states is tied to the ecological health of their wetlands, and consequently, there is considerable interest in conserving and maintaining such areas. Despite this interest and concern, coastal wetland loss in Louisiana averaged 34.9 mi.^{2}/year (1 mi^2 $\approx$ 2.59 km^2) from 1978 through 1990 (Barras et al. 1994).

Although there have been many studies of selected aspects of the Lake Pontchartrain and Lake Maurepas wetlands, no one has synthesized the available literature, particularly that which is available largely (or only) as unpublished reports and student theses. The primary focus of this review is plant communities and their ecological drivers, since these provide both the physical structure of the system and supply the energetic basis for wildlife production.

To put the Lake Pontchartrain and Maurepas marshes in context, the largest wetland along the Gulf Coast is the Atchafalalya Swamp. Depending upon how one draws the boundary around this ecological region, there are at least 400 000 ha still somewhat wet and wild, and possibly nearer to 800 000 ha if we include "the entire Atchafalaya backwater complex lying west of the Mississippi River between Baton Rouge and the Gulf of Mexico" (Reuss 1998; U.S. Army Corps of Engineers 1982). The largest interior marsh along the Gulf Coast is the Everglades (4.45 million ha), although expanses of freshwater marsh, wet prairie, or wet meadows occur elsewhere (Penfound and Hathaway 1938; Moore 1992; DeSelm and Murdock 1993). In Louisiana, Chabreck (1972) estimated there are over 1 million hectares of natural marsh in the coastal region alone, an area 1/4 the size of the Everglades. A number of nationally and regionally significant protected areas occur in the Lake Pontchartrain and Maurepas wetlands, including, from east to west, Bayou Sauvage National Wildlife Refuge (9315 ha), Big Branch National Wildlife Refuge (6917 ha), Fontainebleau State Park (1133 ha), the Joyce Wildlife Management Area (6511 ha), the Manchac Wildlife Management Area (3369 ha), and the new Maurepas Swamp Wildlife Management Area (25 293 ha), for a total in excess of 52 000 hectares or just over 1/3 of the total wetland area.

Acquiring and protecting land is a crucial first step in conservation, but equally important is the design and implementation of management practices based on a thorough understanding of ecosystem processes. The freshwater wetlands draining into the northern Gulf of Mexico have been the subject of active research, and entire books (Messina and Conner 1998; Turner and Streever 2002) have summarized their ecological processes and conservation status. Similarly, the Mississippi River drainage basin has been subjected to multiple studies (Shaffer et al. 2005). However, a comprehensive review specifically dealing with Lake Maurepas and Lake Pontchartrain is lacking. Many of these wetlands around Lake Pontchartrain are threatened by salt water intrusion and subsidence (Barras et al. 1994; Gosselink et al. 1998; Shaffer et al. 2005), a problem attributed in part to the many levees that prevent the Mississippi River from delivering fresh water, nutrients, and sediment to the region (Turner 1997; Davis 2000; Lopez 2003; Shaffer et al. 2003, 2005). Although southern wetlands have a pool in excess of a thousand wetland plant species (e.g. Godfrey and Wooten 1981), most coastal marshes in Louisiana, and in the Pontchartrain–Maurepas area have a small subset of the wetland flora. For example the entire Manchac Wildlife Management Area (3369 ha) has only 87 species of vascular plants (Platt 1988). This low diversity suggests that environmental factors such as salinity and flooding are strongly constraining the biological diversity of the marsh (Flynn et al. 1995; Grace and Pugesek 1997; Howard and Mendelssohn 1999).

It is imperative that an understanding of the ecological processes that maintain these wetlands be gained to ensure their conservation and restoration. Our goal is to provide a reference for researchers in this area, and a guide for administrators and policy makers involved in making conservation and restoration decisions. We, therefore, provide an introduction to the environmental history of the marshes and swamps at the west end of Lake Pontchartrain, a review of the existing vegetation patterns and their possible causes, and a discussion of potential restoration targets. There are a number of related topics that we do not cover, but which readers may wish to explore later — these include the unique habitats associated with longleaf pine savannas in uplands adjacent to these wetlands (Smith 1991; White et al. 1998; Keddy et al. 2006), the naval stores industry in the longleaf pine forests (Gamble 1920; Williams 1989), aquatic organisms of Lakes Pontchartrain and Maurepas such as rangia clams, paddlefish, and sturgeon (e.g. Smith 1985; Rutherford 2002; Lopez 2003), the effects of the historic plume industry on birds of Louisiana wetlands in the late 1800s (Rolfe 1900; Hornaday 1913), the effects of clam shell mining on adjacent aquatic ecosystems in Lake Pontchartrain (Lopez 2003), changes in water quality of Lakes Pontchartrain and Maurepas (Penland et al. 2001; LPBF 2005), the travels of Audubon in the region (Chancellor 1978; Dormon

1990), and the great Mississippi River flood of 1927 (Barry 1997). The combined effects of Hurricanes Katrina and Rita in 2005 had catastrophic effects upon humans in southern Louisiana, but the ecological effects are only slowly emerging. We include some short-term observations on the effects of these hurricanes on the wetlands of Lakes Pontchartrain and Maurepas where data are available.

Regional context: The Mississippi Delta

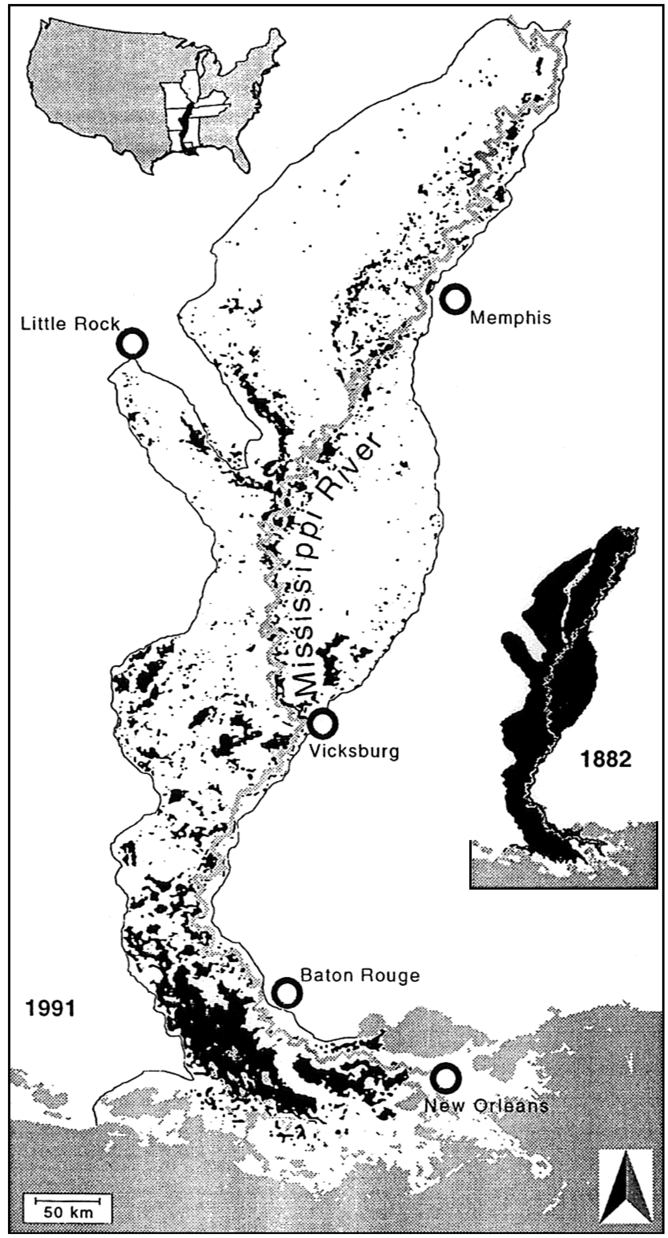
Louisiana is located on the Gulf of Mexico on the Gulf coastal plain. The sediments that form contemporary Louisiana eroded from uplands far to the northwest (Rocky Mountains) and northeast (Appalachian Mountains), being carried here primarily by the Mississippi River (Fig. 1). The central feature of southern Louisiana is the 3 million hectare deltaic plain of the Mississippi River; overviews of this region include Bernard and Leblanc (1965), Boyd and Penland (1988), Coleman et al. (1998), Boesch et al. (1994), and Gosselink et al. (1998). The origins of this plain can be traced to events at the end of the last ice age, as these controlled sea level and rates of discharge down the Mississippi River, and consequently the location and volume of sediments deposited in coastal Louisiana (Table 1). Each of the high water periods of the four interglacial periods left flat terraces with distinctive types of sediment deposited all along the coast of modern Louisiana (Holland 1944). During the last ice age, the Mississippi drained much of the melt waters from continental glaciers. A complex series of events involving ice margins and glacial Lake Agassiz, a huge glacial lake in midwestern United States and central Canada also produced five surges of melt water (from 30 to 200 years in duration) down the Mississippi River between 11 700 and 9270 years before present (Teller and Thorleifson 1983; Teller 1988, 2003). There is also marine evidence of megafloods approximately every thousand years since 5300 years before present (Brown and Kennett 1999). With deglaciation, changes in climate simultaneously produced changes in plant composition in southern Louisiana (Table 1).

Today the Mississippi River may be considered a scenic landscape, but the region left a forbidding impression on some early visitors. In 1837 one traveler from Europe wrote:

> *It is not like most rivers, beautiful to the sight … not one that the eye loves to dwell upon as it sweeps along …. It is a furious, rapid, desolating torrent, loaded with alluvial soil …. [I]t sweeps down whole forests in its course, which disappear in tumultuous confusion, whirled away by the stream now loaded with the masses of soil which nourished their roots, often blocking up and changing the channel of the river, which, as if in anger at its being opposed, inundates and devastates the whole country round…* (Barry 1997 p. 96)

The youngest parts of Louisiana have been newly built out into the Gulf of Mexico over the past 5000 years. As the Mississippi River enters the delta, the sediments (an annual load of some 6.2 x 10^{11} kg, Coleman et al. 1998) begin to settle and accumulate below the surface of the water. When not in flood, river sediments reach the sea. Coarse sediments accumulate closest to where the river enters the sea, whereas fine particles are carried further. An engineer named Eads once lowered himself to the bottom of this river in a self-made diving bell and later described his experience:

Figure 1. The lower Mississippi River basin, showing those regions that remain forested (from Llewellyn et al. 1996). The box indicates the general area covered by this review.



> *The sand was drifting like a dense snowstorm at the bottom …. At sixty-five feet below the surface I found the bed of the river, for at least three feet* [0.91 m] *in depth, a moving mass and so unstable that, in endeavoring to find a footing on it beneath my bell, my feet penetrated through it until I could feel, although standing erect, the sand rushing past my hands, driven by a current apparently as rapid as that on the surface*. (Barry 1997 p. 26)

During flood periods, the river flows up and over older deposits, depositing new layers of sediment. Coarse sediments deposit first and form natural levees while finer sediments deposit in back marsh and swamp wetlands. Thus, the deltaic sediments build up above the level of the ocean

Table 1. A summary of important events in the lower Mississippi River valley during the last major ice age. Much of the evidence comes from fossil pollen and plant debris, some of which was found along Nonconnah Creek (along the Tennessee–Mississippi border) associated with the skeletal remains of American mastodon (after Delcourt et al. 1980). Times preceding 22 000 BP were taken from the USGS LITE (Last Interglacial: Timing and Environment) site, esp.cr.usgs.gov/info/lite, accessed 12 July 2006.

Time before present	Climate	Other events	Floodplains	Bluffs
125 000 – 115 000	warm and dry	few glaciers	warm temperate forests	oak–pine forest and prairie
115 000 – 22 000	Cooling	increased depth of ponds		prairies invaded by forest
22 000 – 17 000	coldest era glacial maximum	American mastodon dies and is covered by sediment wind erodes silt and deposits it to the east (loess)	northern conifer forests with white spruce, fir and larch river forms braided streams	mesic forest with beech, oak, tulip tree, hickory, black walnut wind-carried silt (loess) accumulates on blufflands
17 000 – 11 000	warmer climate	glaciers generate pulses of meltwater into the Mississippi River	intense periods of flooding	gum, chestnut and bayberry migrate north to Memphis
12 500		continued warming	spruce disappears from lower Mississippi Valley	
9200		last pulse of meltwater from Lake Agassiz	severe flooding	
8700 – 5000	warmer and drier	falling water tables	river begins meandering and cuts terraces swamps become open marsh	increased frequency of fire and possible expansion of prairie
5000 – present	cooler and wetter	rising water tables	marsh reverts to swamp with willows, river birch, gums and bald cypress	mixed mesic forest with southern trees

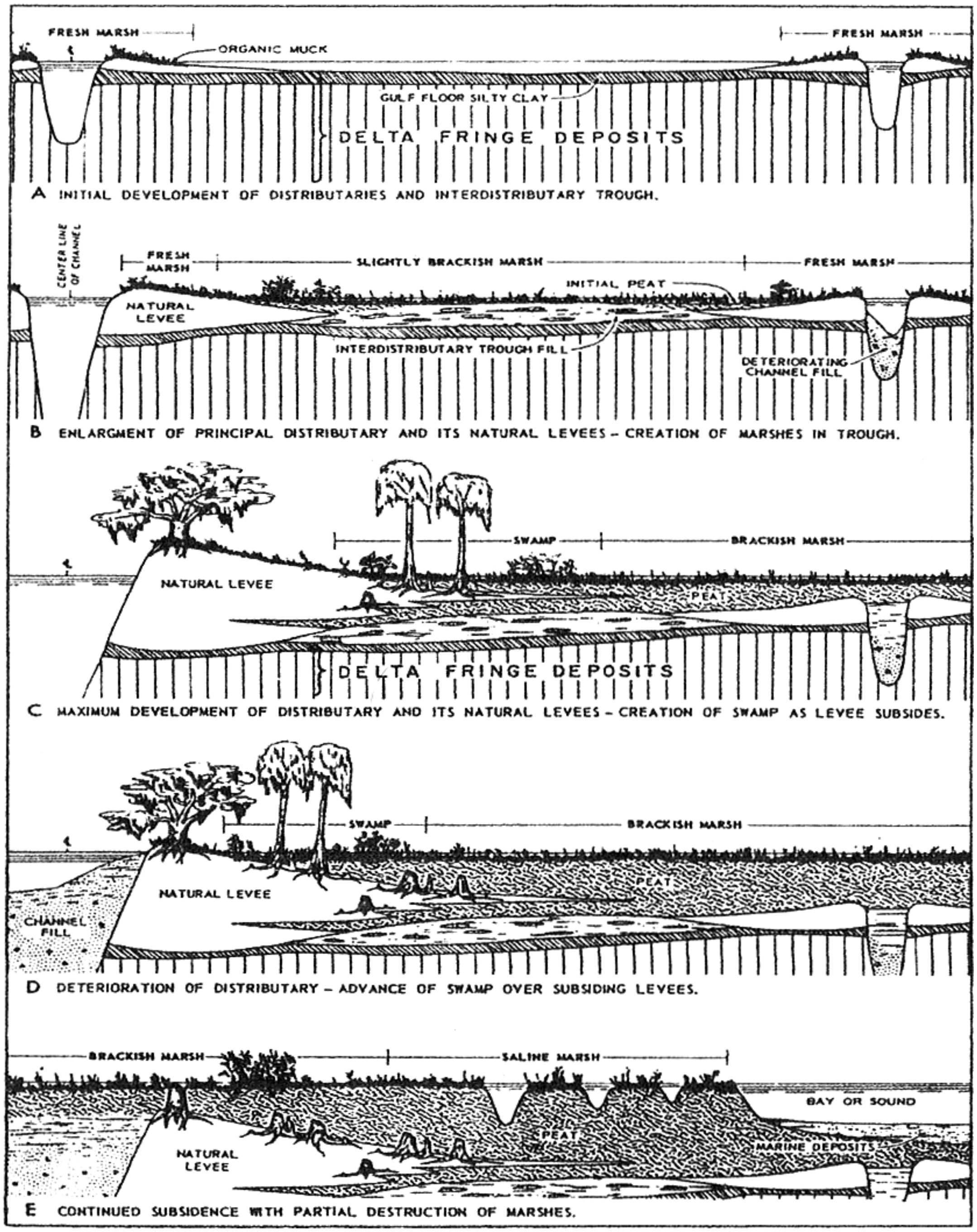
(Fig. 2*a*–2*c*). The natural vegetation of much of southern Louisiana would therefore be fresh or saltwater marshes, with higher elevations dominated by bald cypress (*Taxodium distichum*) and tupelo (*Nyssa aquatica*) swamps (taxonomy follows ITIS 2005). During periods of falling sea level, such as occurred during the ice ages, land formation would accelerate. During periods of rising sea levels, deposition by the river may fail to keep pace, and saline water may move inland, converting the fresh water swamps and marshes back into brackish marsh, salt marsh, or open water (Fig. 2*d*–2*e*). Since the 1930s, the Louisiana coastal plain has lost some 395 000 ha of wetlands, and there is an ongoing debate as to how much this rate of loss is natural and how much it has been accelerated by human intervention in the natural deltaic cycles (Turner 1997; Day et al. 2000, 2001; Houck 2006). Even without human intervention, it would be part of the natural deltaic cycle for a delta to subside until only a small chain of islands or even just a shoal remains (Boyd and Penland 1988). Hurricanes would occasionally accelerate this tug-of-war by eroding barrier islands and destroying outlying marshes (Boyd and Penland 1988; Cahoon et al 1995) as well as redistributing sediment (Turner et al. 2006).

If it were possible to view the last 10 000 years from a satellite with a time-lapse camera, the Mississippi River would be seen to snake back and forth from east to west across the northern Gulf of Mexico, switching deltas every 1000 to 2000 years. At least five major deltas can be distinguished (Fig. 3), each with an average thickness of 35 m (Coleman et al. 1998) corresponding to a period of active sedimentation by the Mississippi River. The oldest sediments are now those furthest to the west. About 3000–4000 years ago, the Mississippi swung back to the east, laying down the St. Bernard Delta and trapping fresh water to produce both Lake Maurepas and Lake Pontchartrain.

Since it was produced by flowing water, southern Louisiana is very flat. As the Mississippi River approaches the ocean, it flows down a negligible slope. For the last 724 km the bed of the river is actually below sea level- 4.6 m below sea level at Vicksburg and over 52 m below sea level at New Orleans! In the words of Barry (1997) “for 450 miles [724 km] or more, the water on the bottom of the river has no reason to flow at all” (p. 39).

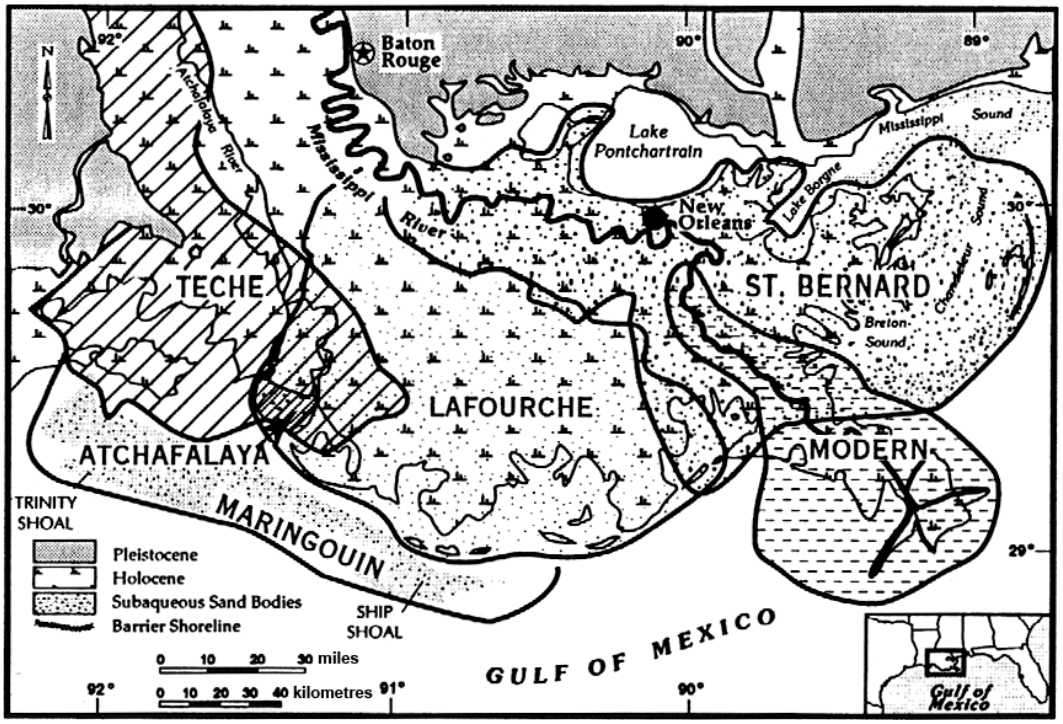
Even a difference of a few centimetres in elevation can make a huge difference in the duration of flooding, and hence the plant communities (Penfound and Hathaway 1938; Reuss 1998; Reyes et al. 2000). Sediment deposited by deltaic processes, and the associated increase in elevation and nutrients, has been shown to enhance productivity in deteriorating marshes (e.g. Pezeshki et al. 1992; Mendelssohn and Kuhn 2003). Where trees cannot tolerate flooding, marshes form, dominated by herbaceous species such as *Cladium mariscoides*, *Spartina* spp., *Phragmites australis, Schoenoplectus* spp., *Peltandra virginica, and Sagittaria* spp. The areas that are less inundated can become forested, with the tree species determined by flood duration.

Figure 2. Progressive stages in the development of the Mississippi River levees and marshes (from Bernard and Leblanc 1965).



Occasional floods can breach natural levees and deposit large fans of sediment. The land-building power of a single breach in a levee was demonstrated in 1890 on the Nita Plantation, some 80 km upstream from New Orleans (Saucier 1963). This breach began on 13 March 1890, and soon eroded to more than 0.8 km in width with a discharge of nearly 1/3 of the normal flow rate of the entire Mississippi River. The land to the north was quickly inundated: 9 days later the floodwaters reached Lake Maurepas and Pass Manchac, and by the end of the month, the flooding halted the Illinois Central railway that runs north from New Orleans to Chicago along the Manchac land bridge. The water rose to within 2.4 km of Ponchatoula Station, and continued to block trains for more than 2 months. Seen from the short term, this flood was probably a catastrophe yet the flood built land: it left a fan-shaped deposit of sand and silt covering some 2849 ha (Saucier 1963). Further east, the marshes south of Ponchatoula were covered with a fine "yellowish or bluish-brown clay". Another example occurred even closer to New Orleans, just 40 km upstream, where levees near Bonnet Carré were repeatedly breached by floods: 1849, 1857, 1867, 1871, 1874, and 1882. In 1849, the breach was nearly 1.61 km wide. The result of these events was vertical accretion over 9065 ha; the southwest shores of Lake

Figure 3. The active delta of the Mississippi River has shifted positions repeatedly over the last 7,000 years. The St. Bernard Delta (estimated age 3000–4000 years BP) formed the embayment that contains Lakes Maurepas and Pontchartrain (from Boesch et al. 1994).



Pontchartrain alone received more than 1.83 m of sediment. The total volume was calculated at 141 584 234 m^3 (Saucier 1963).

Left alone, the Mississippi would now swing back westwards and drain directly down the Atchafalaya basin (Fig. 3). The new delta at the mouth of the Atchafalaya is being built at a rate of some 121 to 202 ha/year (Coleman et al. 1998). If not for the massive Old River Control Structure built by the Army Corps of Engineers, it is likely that the Mississippi River would cease flowing through New Orleans. Started in 1955 and completed in 1963, the Old River Control Structure has 11 gates, each 13 m across that divert some 2/3 of the Mississippi away from the Atchafalya and toward New Orleans (Reuss 1998).

A brief environmental history for human impacts

Native Americans and early European exploration:

Superimposed upon the above geological processes are those driven by human beings. In southeastern North America, Native American populations achieved their greatest density. The Caddo, Atakapa, Tunica, Natchez, and Chitimacha were the five dominant cultures in Louisiana (Kniffen and Hilliard 1988). Most relied heavily on farming, with the women planting and harvesting corn, beans, squash, and sweet potatoes. Not only did these produce a high yield of quality food, but all could easily be dried and stored for later use. Sunflowers and tobacco were also cultivated. Fertile soils along rivers were favored for settlement. One of the most important American Indian settlements in North America occurs upstream from New Orleans at Poverty Point; here natives constructed an enormous bird-shaped mound of earth about 23 m high, along with six concentric ridges marking out a circle more than 0.8 km in diameter (Gibson 1996).

The American Indian way of life ended with the arrival of the Europeans. By far the most devastating effect was the spread of European diseases, such as smallpox, against which the American Indians had no immunity. Even one of the earliest European explorers, De Soto, in 1540, reported finding Indian villages virtually devoid of people. In one deserted village De Soto encountered houses "filled with the bodies of people who had died of the pestilence" — perhaps the consequence of an epidemic started by an earlier Spanish expedition in 1526 (Silver 1990).

The area known as Manchac Swamp was visited by the French explorer Pierre LeMoyne, Sieur d'Iberville, on 26 March 1699. According to Iberville's diaries (McWilliams 1981), while exploring the Mississippi River for a high-ground site to establish a fort to secure the basin near the mouth of the river, Iberville encountered two American Indian tribes (Bayogoula and Mogoulacha), who described an alternate route to the Gulf of Mexico. This alternate route began with a turn off of the Mississippi onto a small distributary named by Iberville's crew as *Riviere d'Iberville*, which was later re-named Bayou Manchac (Manchac is a Choctaw word meaning "rear entrance". From there the bayou joins with the larger Amite River that flows into Lake Maurepas (after Jerome de Phelypeaux, Comte de Maurepas) and then on to Lake Pontchartrain (after Maurepas' father, Louis Phelypeaux, Comte de Pontchartrain, Minister of Marine for France at the time) through the connecting Pass Manchac. From Lake Pontchartrain Iberville was able to make his way out to the Gulf of Mexico through Lake Borgne, where he finally reached his fleet of ships moored off the Mississippi coast at Ship Island.

Sieur de Bienville established New Orleans between the Mississippi River and Lake Pontchartrain in 1718, and the impacts of Europeans have continued to increase with population growth and industrialization. Edward King, looking back from 1875, painted this colorful picture of New Orleans in the early 1700s:

> *Imagine a low-lying swamp, overgrown with a dense ragged forest, cut up into a thousand miniature islands by ruts and pools filled with stagnant water. Fancy a small cleared space along the superb river channel, a space often inundated, but partially reclaimed from the circumambient swamp, and divided into a host of small correct squares, each exactly like its neighbor, and so ditched within and without as to render wandering after nightfall perilous. The ditch which ran along the four sides of every square in the city was filled with a composite of black mud and refuse, which, under a burning sun, sent forth a deadly odor. Around the city was a palisade and a gigantic moat; tall grasses grew up to the doors of the houses, and the hoarse chant of myriads of frogs mingled with the vesper songs of the colonists.* (*p. 22)*

The great American naturalist, William Bartram visited Louisiana in autumn 1777, towards the end of his journey, which included 9656 km on horseback, across the southeast (Earnest 1940). He describes traveling from east to west through Lakes Pontchartrain and Maurepas. Near the Pearl River, just east of Lake Pontchartrain he made the following observations:

> *I made frequent, indeed I may say daily excursions in and about this island, strolling through its awful shades, venerable groves and sublime forests, consisting of the Live Oaks and Magnolia grandiflora, Laurus Borbonia, Olea Americana, Fagus sylvatica, Laur. Sassafras, Quercus hemispherica, Telea, Liquid-amber styraciflua, Morus, Gleditsia, Callicarpa, Halesia, &c*. (p. 421)

Although the names of the plants have changed somewhat in two centuries, the live oaks, magnolias, red bay, ash, beech, and sassafras still occur. Many of these forests have, however, vanished under subdivisions spreading in the same direction Bartram traveled, eastwards along the north shore of Lake Pontchartrain. He next set off for:

> *Manchac on the Mississipi* (sic)*, in a handsome large boat with three Negroes to navigate her; leaving the friendly Mr. Rumsey's seat on Pearl Island, we descend a creek from the landing near his house; this creek led us about a mile, winding through salt sedgy marshes, into Lake Pontchartrain, along whose North shores, we coasted about twenty miles, having low, reedy marshes, on our starboard: these marshes were very extensive between us and the far distant high forests…. We came to in a little bay, kindled a fire, and after supper betook ourselves to repose … on clean sand banks; we rested quietly, though sometimes roused by alarms from the crocodile, which are here in great numbers, and of an enormous bulk and strength.*

He, of course, was referring to the dense population of alligators in the Manchac area. He next arrives at the Tangipahoa River (Taensapaoa in his notes):

> *we still coasted Westward, three or four miles* [4.83–6.44 km]*, to the straits that communicate to the lake Mauripas(sic); entering which and continuing six or eight miles* [9.66–12.87 km]*, having low swampy land on each side, the channel divides, forming an island in the middle of the pass, we took the right hand channel, which continuing three or four miles* [4.83–6.44 km]*, when the channels reunite in full view of the charming lake* [Lake Maurepas]. (p. 425)

He next sails up the Amite River, seeing

> *the land on each side a level swamp, about two feet* [0.61 m] *above the surface of the water, supporting a thick forest of trees, consisting chiefly of Fraxinus, Nyssa aquatica, Nyssa multiflora, Cupressus disticha, Quercus phillos, Acer rubrum, Ac. negundo, Acer glaucum, Sambuces(sic), Laurus Borbonia, Carpinus, Ulmus and others*. (p. 425)

Many of the species of trees grow along the Amite today, including, following the order in Bartram's notes, ash, tupelo, bald cypress, willow oak, and red maple, respectively. Eventually Bartram reaches the Mississippi River by traveling overland:

> THE *depth of the river here, even in this season, at its lowest ebb is astonishing, not less than forty fathoms* [73 m]*, and the width about a mile* [1.61 km] *or some what less….The banks of the river … though frequently overflowed by the vernal inundations, are fifty feet* [15.2m] *perpendicular height above the surface of the water (by which the channel at those times must be about two hundred and ninety feet deep* [88 m]*) and these precipices being an accumulation of the sediment of muddy waters, annually brought down with the floods, of a light loamy consistence(sic), are continually cracking and parting, present to view deep yawning chasms, in time split off, as the active perpetual current undermines, and the mighty masses of earth tumbe (sic) headlong into the river, whose impetuous current sweeps away and lodges them elsewhere.* (p. 427–428).

Early colonization, levees, the railway and logging:

Bartram arrived before humans had their greatest impacts on the landscape. Lopez (2003) divides human impacts in the basin into five periods of activity (supported by his appendix A with a 30 page chronological list of environmental events from 1711–2002).

(1) 1718–1844 Natural levee and ridge utilization.
(2) 1812–1895 Mississippi River severed from Pontchartrain basin
(3) 1890–1938 Commercial deforestation
(4) 1932–1990 Dredging and armoring of estuary
(5) 1950–1989 Water pollution

The two of these with the greatest continuing impact on wetlands are likely those that occurred largely between 1812 and 1938 — the construction of artificial levees and the destruction of upland and swamp forests (Davis 2000; Lopez 2003). The former has minimized the flow of fresh water, nutrients, and sediment into Lakes Maurepas and Pontchartrain. The latter removed natural forest cover and left the land permanently scarred. Both of these events will be a recurring theme in the remainder of this review. One specific, more recent, event — the construction of the Mississippi River Gulf Outlet in 1963–1965 — has amplified the effects of levee construction by providing direct access of salt water to the Lake Pontchartrain Basin (Lopez 2003). The original dredge width of the canal removed 527 ha of wetland, but the canal has expanded from bank erosion.

Moreover, the direct impacts are minor compared to the extensive damage from salt-water intrusion. Locally known as Mr. Go, the shipping channel continues to be one of the most important causes of salinization in both Lakes Pontchartrain and Maurepas (Lopez 2003; The Nature Conservancy 2004).

Levees were built steadily during the late 1800s and early 1900s, although even then there were vigorous debates among engineers about how to best control floods along the river (Barry 1997). But levee construction continued.

> *By 1851 most of the levees between New Orleans and the Red River had risen to at least four and a half feet – the largest was eight feet, with a base of thirty-five feet. With time these embankments extended from New Orleans to the mouth of the Arkansas River, a distance of about 600 miles* (Barry, J.M. 1997)

Almost as soon as the levees were built, they were breached. Davis (2000) describes how over time the frequency of crevasses grew from under ten crevasses a year before 1850, to 16–45 between 1858 and 1874, to more than 200 per year over the three years from 1882 to 1884. Crevasses increased in frequency as the levees grew in stature. Even so, as the levees grew in length and height, vital water, nutrients, and sediment were diverted away from wetlands along the river.

The Manchac land bridge is a prominent feature that separates Lakes Pontchartrain and Maurepas (Fig. 4), and its history mirrors that of the region as a whole. This peninsula was produced by the Mississippi River during the St. Bernard stage of delta construction (ca. 5000 years BP), when deltaic deposits created present day Lake Pontchartrain. Simultaneously, a branch of the Mississippi flowed, carrying sediment and building a narrow land bridge that severed modern Lake Maurepas from Lake Pontchartrain (Saucier 1963). In 1852, railroad construction began to link New Orleans to Jackson, Mississippi (Woolfolk 1979). Two bridges were built across Pass Manchac, a 213 m span at North Pass and a 549 m trestle span at South Pass, each with a steam drawbridge. Cypress crib work and pilings supported the rails. The *New Orleans, Jackson, and Great Northern Railway* opened the 142 km of track from New Orleans to the Mississippi border just 2 years later in 1854. A turntable at Pass Manchac allowed engines to be turned around on the single-track line, and a wooden loading platform constructed on pilings on the north side of Pass Manchac allowed boats to transfer freight to the train. This railway played a notable role in the Civil War, until it was burned with "nothing remaining at Pass Manchac more combustible than railroad iron and water-soaked piles" (Perrin 2000).

When the Civil War ended in 1865, the railway was rebuilt. The towns of Frenier and Ruddock grew up along the tracks, based upon truck farming and services for the logging industry. The black soil was apparently well-suited to growing cabbage and lettuce. The residents built a system of levees to control flooding of each farm, while the houses and sidewalks were built on pilings at least eight feet above the ground. The towns became well-known for shipping produce north to Chicago. By 1910, Ruddock had over 700 residents and Frenier had close to 200 (Heleniak and Dranguet 1987). Both towns were obliterated by the unnamed hurricane, which struck on 29 September 1915. The history of this era is recounted at four scales: for the south as a whole by Conner and Buford (1998), for Louisiana by Norgress (1947), for pull boat technology by Mancil (1980), and for the Manchac area local accounts such as Woolfolk (1979), Dranguet and Heleniak (1992), Heleniak and Dranguet (1987), and Perrin (2000).

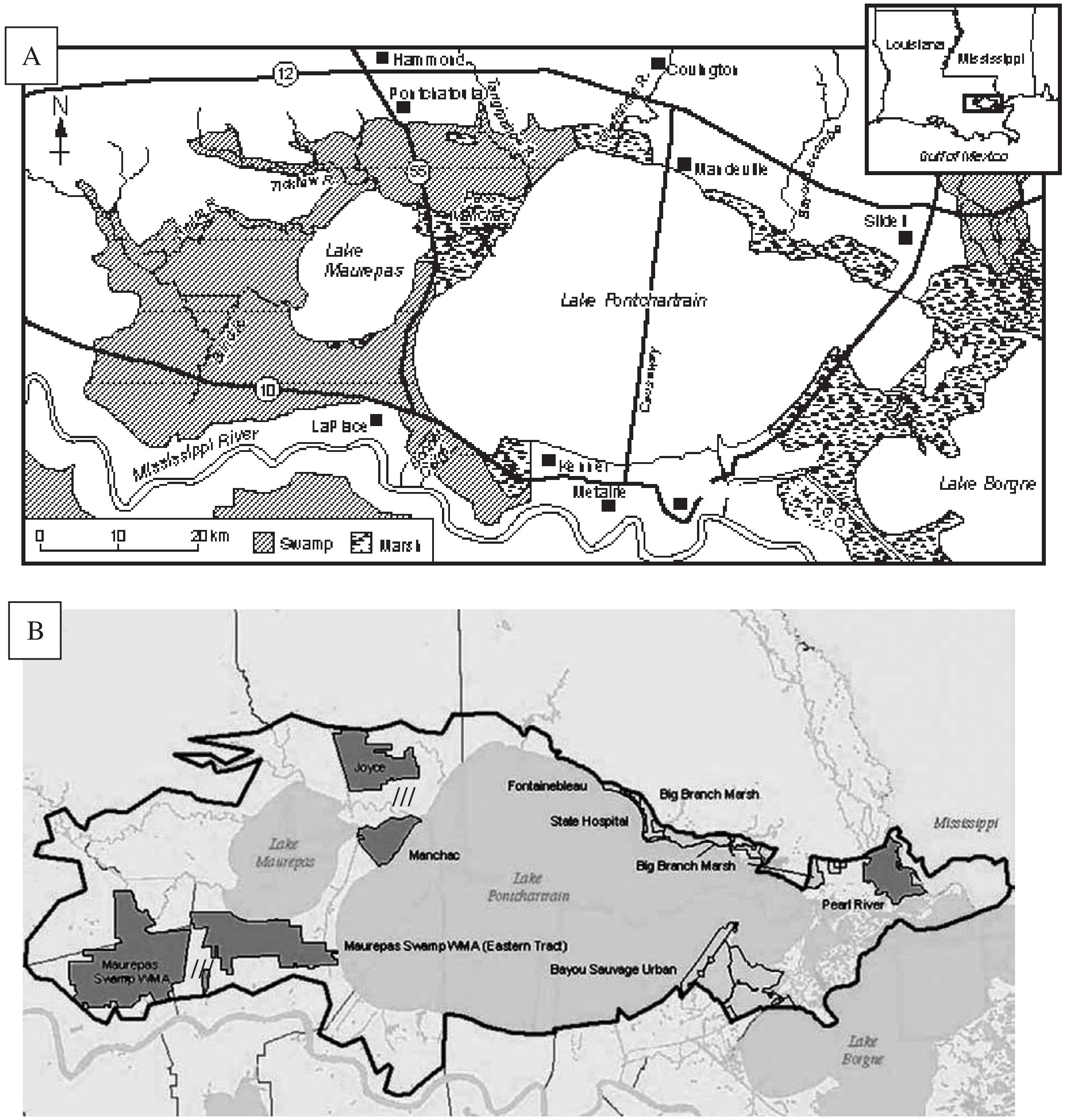
The railroad also provided a route for logging. The first advance towards large-scale commercial logging of cypress was driven by changes in legislation (Norgress 1947). When the Homestead Act of 1866 was repealed and replaced by the Timber Act of 1876, swampland was simultaneously declared unsuitable for cultivation and unavailable to private individuals. Large tracts sold for 25 to 50 cents per acre (0.4 ha). Several large transactions are known from this era (Dranguet and Heleniak 1992). Between 1885 and 1892, Leonard Strader, for example, acquired over 2833 ha of cypress swamp northeast of Pass Manchac as the Strader Cypress Lumber Company, later sold to the Owl Bayou Cypress Company, a West Virginia corporation. He constructed a sawmill at a site that became known as Strader. In 1902, the Joyce Lumber Company was established to the south and west, and two other companies acquired land near Pass Manchac and Lake Maurepas (Fig. 5). Other timber barons of that era included Charles Hackley, Thomas Hume, and Joseph Rathborne. The latter opened a mill in Ponchatoula in 1921 (C.A. Dranguet and R. J. Heleniak, personal communication, 2005). Lumber extraction reached a maximum in the early 1900s, and by 1934, the state had more than 647 497 ha of cutover swamp, with only 8903 ha remaining in cypress forest (Norgress 1947 p. 1047)

Shortly after the Timber Act passed, in 1891, pull boats further mechanized logging (Mancil 1980). Teams of loggers felled the enormous cypress trees (Fig. 6). Pull boats then used cables and winches to drag the fallen trees to the open water (Fig. 7), from as far away as 1524 m. Canals were excavated at 3048 m intervals, allowing entire forests to be stripped systematically. The logs were winched towards the larger canals along "runs" spaced 45 m apart. Each run was cleared of trees and stumps, and served as a pathway for repeated skidding of logs, which gradually scoured a mud and water filled ditch 1.8–2.4 m deep. In some places, logs were winched into canals from one point, in which case the pull boat runs radiate outwards like spokes of a wheel. Both parallel and wheel-shaped markings are still evident to visitors flying over the Manchac Swamp into New Orleans (Fig. 8). Dredges dug larger canals for pull boats causing further damage. These canals were 3 to 12 m wide and 2.4 to 3 m deep, resulting in the partial drainage and increased tidal exchange within many swamps.

In 1929, both the Williams and Rathbourne cypress lumber mills near Pass Manchac announced that they had exhausted the trees on their land and would, therefore close; there would be only a short reprieve while the wood already cut was processed through the mills. When reorganized as the Louisiana Cypress Lumber Company, the mill produced a mean of 14.3 million board feet of lumber per year between 1936 and 1956 (Dranguet and Heleniak 1992). In summarizing the impact of the industry on the local economy, J.H. Foster of the United States Forest Service said the lumber industry:

> *. . . obtained their lands at low prices and have made fortunes from the increase in the value of the timber. The*

Figure 4 (*a*) The study area (after Conner et al. 1980) (*b*), public lands and protected areas. Dark gray: state lands; medium gray: federal lands (from The Nature Conservancy 2004). Ongoing land acquisition indicated by ///.



> *industry does not develop the country permanently and the earnings are seldom invested where they are of any benefit to the community.* (Norgress, R.E. 1947).

With the loss of the swamp forests, the biota too certainly declined, but no wildlife census data from this era in the Manchac are available. One can either rely on the testimony of persons who lived in the area to describe losses of waterfowl, furbearers, and deer, or extrapolate from general trends in wildlife documented in that era. We can certainly infer the loss of three birds, one now on the edge of extinction (ivory-billed woodpecker), and two extinct (Carolina parakeet, passenger pigeon), as likely former inhabitants of these swamps.

The ivory-billed woodpecker was described admiringly by Alexander Wilson, a naturalist who pre-dated Audubon by about one generation, and who prepared an early volume guide to the birds of North America, called *American Ornithology* (Brewer 1840). Wilson says:

> *This majestic and formidable species, in strength and magnitude, stands at the head of the whole class of Woodpeckers hitherto discovered. He may be called the king or chief of his tribe; and Nature seems to have designed him a distinguished characteristic in the superb carmine crest and bill of polished ivory with which she has ornamented him…. the royal hunter now before us … seeks the most towering trees of the forests; seeming particularly attached to those prodigious cypress swamps…. his trumpet-like note and loud strokes resound through the solitary, savage wilds, of which he seems the sole lord and inhabitant.* (Brewer 1840)

Figure 5. Three tracts of cypress swamp acquired ca 1900.

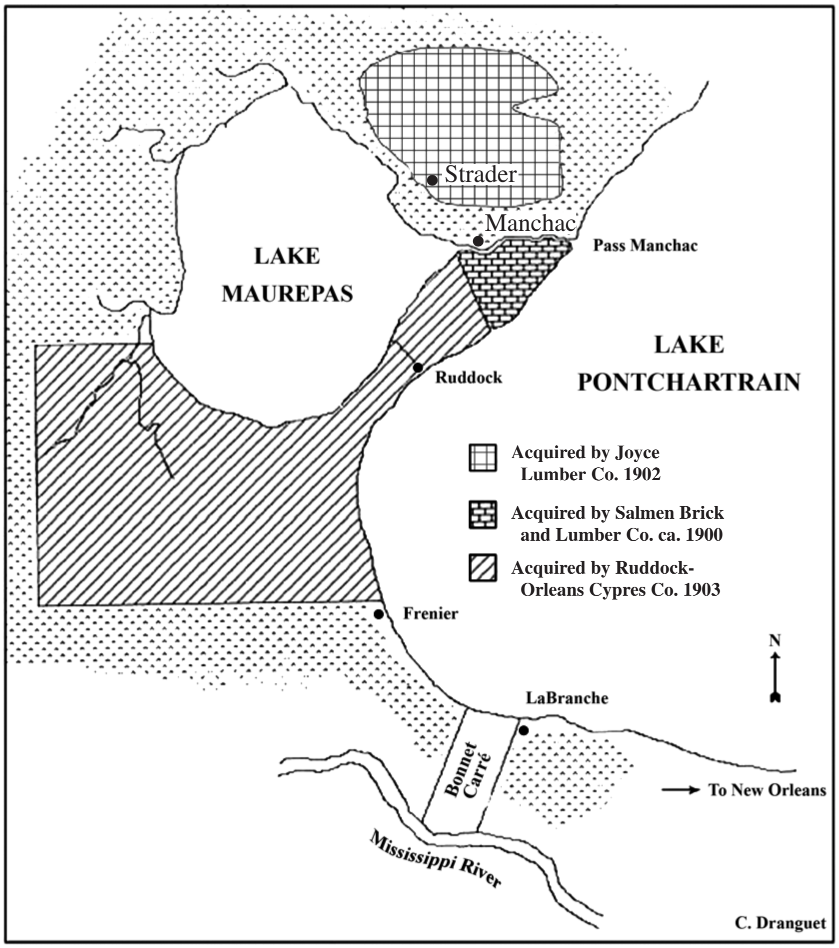


Figure 6. Giant tree cut by the Lyon Lumber Company in the Maurepas Swamp. (source: Al Dranguet.)

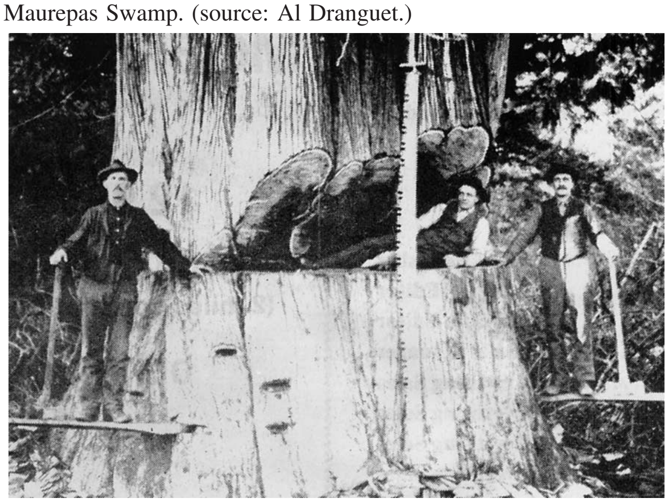
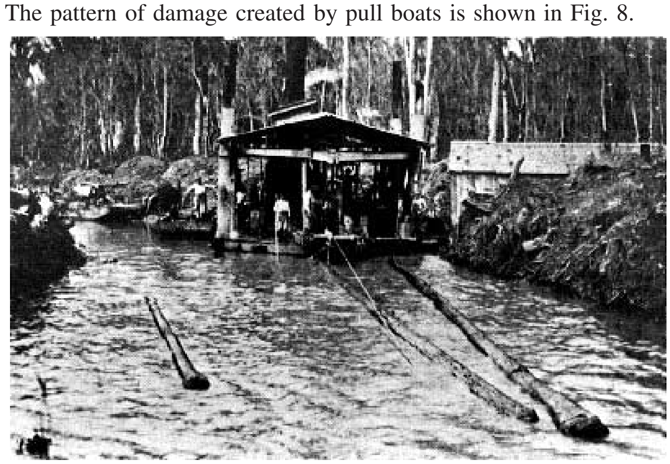


Figure 7. A two drum pull boat working in a canal cut into a cypress swamp in Louisiana. (Date unknown, from Williams 1989). The pattern of damage created by pull boats is shown in Fig. 8.



The gradual decline of these woodpeckers is described in Stolzenburg (2002).

Carolina parakeets, like passenger pigeons, are now extinct. In describing Carolina parakeets, Wilson wrote:

> *When they alighted on the ground, it appeared at a distance as if covered with a carpet of the richest green, orange, and yellow: they afterwards settled, in one body, on a neighboring tree, which stood detached from any other, covering almost every twig of it, and the sun, shining strongly on their gay and glossy plumage, produced a very beautiful and splendid appearance.* (Brewer 1840)

Carolina parakeets preferred alluvial forests and swamp, where Wilson says they were particularly attracted to:

> *large sycamores, in the hollow of the trunks and branches of which they generally roost, thirty or forty,*

Figure 8: Aerial view of the Manchac wetlands between Lake Maurepas and Lake Pontchartrain. Parallel and wheel-shaped markings are mud and water-filled ditches made by pull boats dragging trees through the swamp during logging operations in the early twentieth century (Thomson 2000).

and sometimes more, entering at the same hole. Here they cling close to the sides of the tree, holding fast by the claws and also by the bills. They … often retire to their holes during the day, probably to take their regular siesta*. They are extremely sociable, and fond of each other, often scratching each other's heads and necks, and always, at night, nestling as close as possible to each other, preferring, at that time, a perpendicular position, supported by their bill and claws.* (Brewer 1840)

Audubon's specimen of the Carolina parakeet is said to have been collected about 1821 at Bayou Sara near St. Francisville (Oberholser 1938), not far from the present day Cat Island National Wildlife Refuge. The last known Carolina parakeet died in the Cincinnati Zoo in 1918.

With the end of the cypress industry, two other industries ended (Heleniak and Dranguet 1987). One was the gathering of Spanish moss, which brought moss gatherers up to six cents per pound (0.45 kg). The moss was then pressed into bales and shipped for use in the furniture industry and for the expanding business of automobile upholstery. Boat building also was affected, particularly the larger boats that might require cypress planks over 7 inches thick. Although Manchac skiffs are still built locally, fiberglass has taken the place of cypress. A few other residents still harvest sunken logs, known as sinker cypress, for lumber.

One other noteworthy event occurred with the end of logging. The millionaire brewer and businessman from New Orleans, Edward Schlieder, acquired a 2226 ha tract of cut-over cypress land on the south side of Pass Manchac from the Salmen Brick and Lumber Company. Here Schlieder built a 2 1/2-story building, a boathouse, and a caretaker's residence. The camp was an island of luxury with electric lights and a walk-in refrigerator powered by a gas generator (Heleniak and Dranguet 1987). This building later became the Turtle Cove Environmental Research Station, the land became the Manchac Wildlife Management Area, and the Schlieder Foundation eventually funded the creation of the Schlieder Endowed Chair for Environmental Studies at Southeastern Louisiana University (Hastings 2004).

The story of the Manchac Swamp, therefore, illustrates the pattern of events that occurred across much of Louisiana — land built by the Mississippi River, early exploration by the Spanish and French, settlement, the Civil War, levee construction, cypress logging, decline in animal species from woodpeckers to sturgeon, and then mills closing as the cypress was exhausted. The state of the Pontchartrain and Maurepas wetlands today is largely a result of these events.

The Manchac area retains a distinctive culture — "the automobile is of little use to the people who live and work in the marsh between (the towns of) LaPlace (to the south) and Ponchatoula (to the north)" (Dranguet and Heleniak 1985), and after 3000 years of human habitation of the Manchac land bridge, the only surviving and permanent community is that of the Village of Manchac.

Flooding and salinity

In coastal wetlands, flood duration and salinity are the two main gradients that control species composition, although other factors including nutrients, herbivory, and rates of sediment deposition also are important (e.g., Moore 1992; Gough and Grace 1998; Keddy 2000; Mitsch and Gosselink 2000). These factors have been well-studied in wetlands along the Louisiana coast (e.g., Penfound and Hathaway 1938; Baldwin et al. 1996; Boesch et al. 1994; Gosselink et al. 1998) and manipulated in greenhouse experiments (e.g. Pezeshki et al. 1987*c*; Flynn et al. 1995; Baldwin and Mendelssohn 1998*b*; Hester et al. 1998, 2001; La Peyre et al. 2001). They are considered key factors for coastal wetlands in general (Keddy 2000; Mitsch and Gosselink 2000). Flood duration and salinity combine to produce the gradient of vegetation from herbaceous vegetation in the most flooded areas to forests in the least flooded areas. Table 2 summarizes the changes in production associated with this gradient. Within the herbaceous vegetation, salinity also produces changes in species composition and diversity (Table 3).

To explore patterns of flooding and salinity within the Manchac area, Thomson (2000) analyzed historical data from a stage and salinity gage (#85420) maintained by the United States Army Corps of Engineers (USACE), New Orleans District, attached to a piling on the southern end of the Interstate 55 bridge across Pass Manchac. The datum for the monitor currently is set to NGVD sea level (1983 adjustment), and the Louisiana Department of Transportation has stated that Interstate 55 does not subside with the surrounding wetlands, so this datum is assumed stable. These data were used to calculate the rate of eustatic sea level rise for the waters surrounding the study area, flood duration, and inter-annual variability.

For any single year, the stage is bimodal (Fig. 9) — it generally rises in the spring, then falls to its lowest level during summer, rises to its highest level in the fall, and again falls to low levels in the winter. The high stages recorded in the fall are attributed to tropical storms such as Hurricane Katrina in late August of 2005. During the period from 1956 to 1999, flood duration increased significantly, producing flood durations of 30% near Schlieder's Ditch and 60% near First Canal (Fig. 10). Salinity increased dramatically during the drought in 1999–2000, exceeding 8 ppt early in the growing season, and staying in the vicinity of 5 ppt until the heavy rains in July that ended that drought (Fig. 11). By early 2003, levels had returned to below 2 ppt.

Increased flood duration can be attributed to two causes. First, data from the gage (#85420) shows that from 1957 to 2000, there has been a rise in mean sea level of 1.6 mm per annum for a total rise in mean sea level of 0.07 m in this period (Thomson 2000). Second, local subsidence has been estimated to be 2.0 mm per annum at the southern Manchac land bridge (Penland and Ramsey 1990). As a consequence, the marshes in the Manchac area are flooded twice as much as they were 50 years ago. Increased submergence results in sulfide accumulation, a phytotoxin, which also reduces plant uptake of nitrogen (Koch et al. 1990), an important limiting primary nutrient in wetland plant productivity (Valiela and Teal 1974; Keddy 2000). This combination of increased flood duration and increased salinity are likely to convert fresh water swamps and marshes to salt marshes and open water, a process already well documented in historical photographs (Barras et al. 1994).

Zedler and Beare (1986) have argued that southern marshes in general are subjected to cycles of fresh and saline conditions driven by drought cycles, with regeneration from buried seed controlled by pulses of fresh water that allow germination and establishment. In the same way, pulses of saline water driven inland by tropical storms, and exacerbated by altered hydrology (Lopez 2003), are thought to significantly reduce plant diversity in fresh marshes (O'Neil 1949; Brewer and Grace 1990) and prevent the regeneration of swamps (Penfound 1952; Shaffer et al. 2003). One such pulse appeared when Hurricane Katrina passed over Louisiana in August 2005 (Fig. 12). The long-term effects of this pulse upon these wetlands remains unknown.

Major vegetation types

Because the large-scale picture of these gradients in coastal wetlands is well-documented, our focus here will be upon those studies that illustrate how these forces apply to the Pontchartrain–Maurepas area. Overall, the vegetation of the area can be approximately divided into two types, marsh and swamp. In many cases the distinction is arbitrary as many areas represent transitions between the two.

Several ecological factors acting in combination can create marsh. Further north, fluctuating water levels seem to be the single major cause of marsh formation, with high water periods killing colonizing woody plants, and intervening low water periods allowing regeneration of herbaceous species (Toner and Keddy 1997; Keddy 2000). In contrast, southern marshes have more complex and diverse origins. Fluctuating water levels are likely important in some cases, particularly in the Everglades (White 1994), at the mouths of large rivers (Brewer and Grace 1990), and certainly in adjoining pine savannas (Christensen 1988; Peet and Allard 1993). Fire also is known to be significant in maintaining and regenerating marshes in both coastal Louisiana (O'Neil 1949) and the Everglades (Loveless 1959; Brewer and Grace 1990; Herndon et al. 1991; White 1994), as well as marshes near Mandeville, Louisiana. Newly deposited deltaic sediments create conditions for the formation of new areas of marsh (Shaffer et al. 1992; White 1993; Boesch et al. 1994). Pulses of salt water associated with hurricanes and other tropical storms can cause significant changes in the species composition of marshes, and may kill trees or inhibit regeneration (Brewer

Table 2. Biomass and primary productivity for the major wetland types, and the effects of salinity upon the productivity in each (adapted from the literature review and analysis in Visser et al. 2004). Area from Coast 2050 (The Louisiana Coastal Wetlands Conservation and Restoration Task Force and the Wetlands Conservation and Restoration Authority. 1998).

Wetland type	Salinity (ppt)	Above ground biomass (g^{-2})	Total production (g^{-2} $year^{-1}$)	Percent decrease in productivity per 1 ppt	Area in Lake Pontchartrain/Maurepas wetlands (ha)
Bottomland hardwood	< 2	16 100	1374		44 515
Swamp forest	< 4	37 500	400–1780	8.4	86 392
Fresh marsh	< 2	635	7430	11.1	13 233
Intermediate marsh	2-6	291–1499	1414–7285	6.8	11 210
Brackish Marsh	6-15	441–1781	2143–8656	2.6	16 997
Saline wetlands	> 15	447–1750	1614–6318	2.1	

and Grace 1990; Gosselink et al. 1998). Herbivores may maintain, or possibly expand, marshes by feeding upon tree seedlings (Wilsey et al. 1991; Brantley and Platt 1992; Myers et al. 1995).

A major cause of open marsh is humans. Given the intensive and extensive history of logging (e.g. Norgress 1947; Conner and Buford 1998; Lopez 2003), it is often reasonable to suspect anthropogenic rather than natural origins. Large stumps emerging from mud, or troughs cut into the marsh by draglines, confirm that such areas were once forest. Further, these anthropogenic marshes are now at risk from another anthropogenic factor: salt water intrusion caused by a combination of rising sea levels, levees along rivers, altered hydrology that provides direct links to more saline waters, and subsidence of sediment (Boesch et al. 1994; Gosselink et al. 1998) along with increased exposure to salt water from storm surges (Michener et al. 1997; Thomson 2000). At the same time, proposals to divert fresh water from the Mississippi River (Shaffer et al. 2003) or to pump partially treated sewage into the Joyce Wildlife Management area could result in expanded areas of swamp and more eutrophic conditions.

In 2003, species composition was measured in 40 10 m × 10 m quadrats stratified among four a priori vegetation types in the Manchac wetlands to better describe the different vegetation types (Kandalepas 2004). The sample sites extended from the Tchefuncte River in the east to the Blind and Amite Rivers in the west. After removing infrequent species and floating aquatics, the resultant database consisted of 79 species out of the 107 species originally detected.

Marshes tended to have fewer plant species and less variation in species composition than swamps. TWINSPAN showed ten natural groupings (Fig. 13). There was no clear separation between anthropogenic and natural marshes, but rather the differences appear to be attributable to the salinity gradient, with the added occurrence of shrub-scrub community type that may reflect past logging activities. *Morella cerifera* is a common component of this community type. The swamps divided into two major groups: one, with the occurrence of *Sphagnum* moss, the other with saplings of *Taxodium distichum*. This suggests a fertility difference, with *Sphagnum* documenting sites of low fertility. The most speciose plots were those dominated by *Acer rubrum* and *Taxodium distichum*; the mechanism seems to be that many marsh plants can grow in small gaps in the forest, in which case forests contain not only woody plants, but a moderate number of marsh species in addition.

The status of the swamps

The original swamps were heavily logged, as described above. Apart from faded photographs, our other information on old growth cypress come from remnant stands, many outside the study area (e.g., Conner and Buford 1998; Devall 1998), although Hall and Penfound (1939*a*, 1939*b*) provided reliable descriptions of swamps nearby along the Pearl River. According to Devall, *Taxodium distichum* trees can reach 3.6 m in diameter (measured above the swollen base of the tree) and live up to 1000 years old. Dead snags and downed logs occurred at densities of "several" per 1.2 ha. *Nyssa aquatica* and *Nyssa biflora* were common associates.

The second growth swamps south of Lake Maurepas have received intensive study documenting variation among years and hydrologic regimes (Shaffer et al. 2003). Twenty study sites with two 625 m^2 replicates each were selected to capture four different hydrological regimes within the swamp: lake, intermediate, interior, and throughput. Interior sites were located away from any direct water exchange with Lake Maurepas and were only accessible by airboat. Intermediate sites were located closer to the lake in the vicinity of larger bayous or canals that made direct water exchange with the lake probable. Lake sites were close enough to Lake Maurepas to render tidal exchange common. Throughput sites were located near canals or natural waterways that were likely to provide regular inundation and sheet flow.

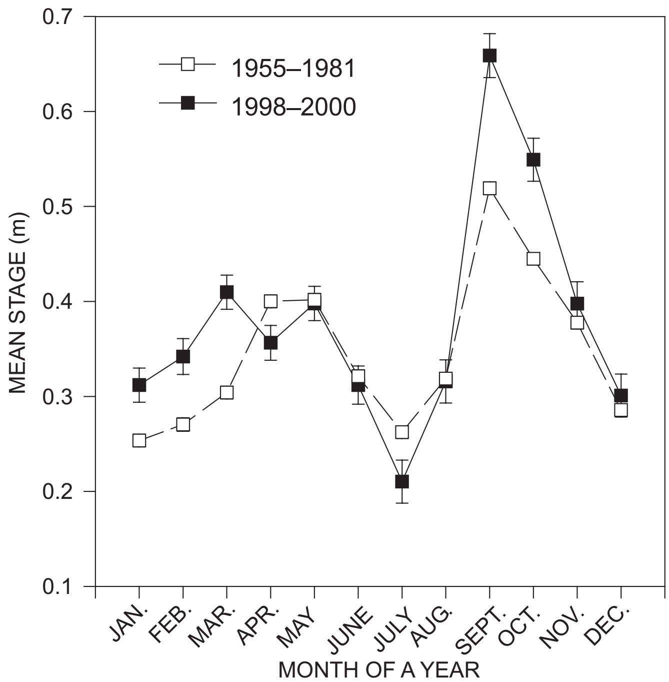
An intensive monitoring program measured factors including rates of subsidence, accretion, flooding, surface-water salinity, and soil variables such as soil water salinity, pH, bulk density, redox potential (Eh), sulfide concentrations, and concentrations of nitrate, ammonia, and phosphorus. Forest structure, production, and tree mortality were measured within each of forty 625 m^2 plots where all *Taxodium distichum* and *Nyssa aquatica* were tagged, as well as trees and large shrubs of other species, such as *Fraxinus pennsylvanica*, *Acer rubrum* var. *drummondii*, *Nyssa biflora*, *Quercus laurifolia*, *Salix nigra*, *Morella cerifera*, *Cephalanthus occidentalis*, and *Triadica sebifera*.

The results varied in both time (across years) and space (across the four habitat types). The drought during 1999–2000 had pronounced effects on the vegetation throughout the area, with effects including the invasion of herbaceous wetlands by shrubs and the increase in abundance of annuals such as *Amaranthus australis*. During the drought, the salinity of wells was highest in the lake plots (> 4 ppt), and lowest (< 2 ppt) in the interior and throughput plots. Although

Table 3. Common plant species, total number of plant species observed, and area for coastal marsh types in Louisiana (after Chabreck 1972). Salinity levels are from Visser et al. 2004.

	Saline	Marsh type: Brackish	Intermediate	Fresh
	Salinity (ppt)			
	>15	6-15	2-6	<2
Species				
Spartina alterniflora	1	4		
Distichlis spicata	2	2		
Juncus roemerianus	3	5		
Spartina patens	4	1	1	5
Batis maritima	5			
Scirpus olneyi (*Schoenoplectus americanus*)		3		
Phragmites communis (*Phragmites australis*)			2	
Sagittaria falcata (*Sagittaria lancifolia ssp.* media)			3	2
Bacopa monnieri			4	
Eleocharis sp.			5	3
Panicum hemitomon				1
Alternanthera philoxeroides				4
Total no. species	17	40	54	93
Area (ha)	323 344	479 957	263 855	494 526

Figure 9. Intra-annual variability of monthly mean stage comparing the periods 1955–1981 (historical) and 1998–2000 (drought period) (± standard error of the mean). The duration of flooding (percentage of the year that the marshes by Schleider's Ditch flood) more than doubled over the period of record for the USACE tide gage ($Yi = 11.527 + 0.450Xi$, $R^2 = 0.253$) from 11.5% in the mid-1950s to 30.5% in 2000 (from Thomson 2000, Thomson et al. 2002).



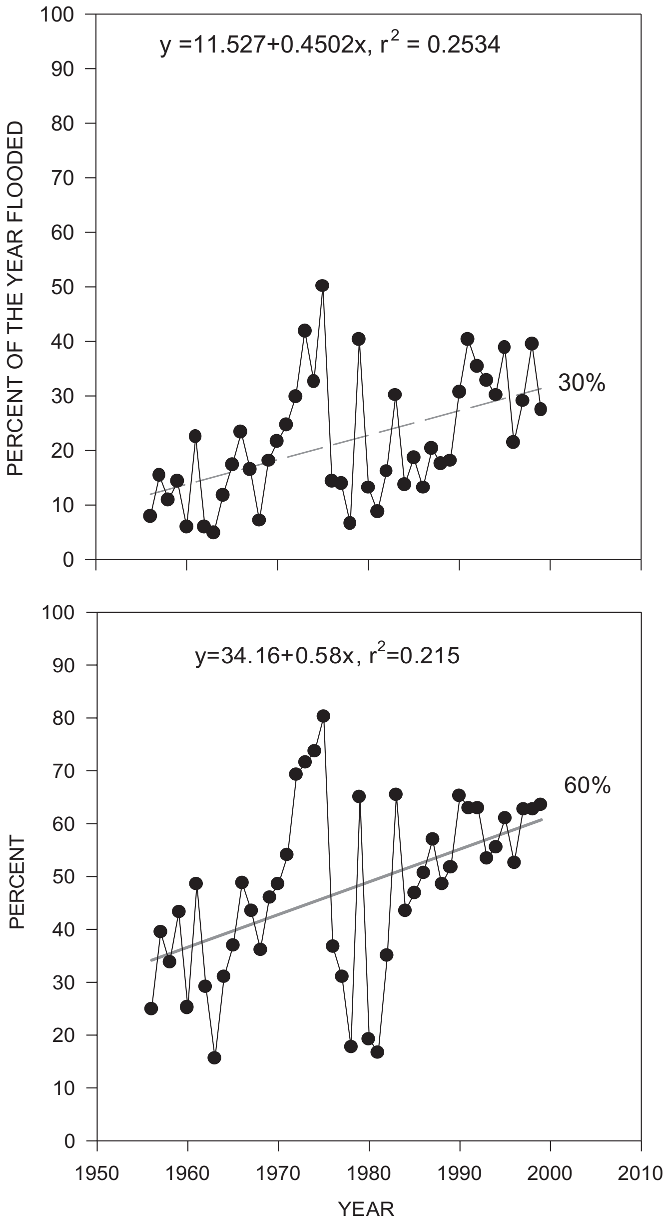
the trend remained the same 2 years later, values had fallen to below 2 and 1 ppt, respectively.

Overall, *Taxodium distichum* was the most productive species followed by *Nyssa aquatica*. These two species are the canopy dominants, make up the majority of the basal area found at each site, and are the most flood-tolerant tree species in this system. There was an increase in production the first year after the drought, and then production declined (Shaffer et al. 2003). Production was lowest at the lake sites and highest in the throughput sites. Tagged trees revealed mortality rates of about 2% in throughput, interior, and intermediate sites, but 10% in lake sites, with one, at Jones Island near Pass Manchac, showing rates as high as 25%.

Throughput sites had the highest productivity (Fig. 14), but comprised less that 15% of the area. Even the most productive throughput sites in the Maurepas, however, do not compare well with natural, periodically flooded cypress-tupelo swamps elsewhere in the southeastern United States (Carter et al. 1973; Conner and Day 1976; Conner et al. 1981; Megonigal et al. 1997). The vast majority of the Maurepas swamp, including interior, intermediate, and lake sites, was typical of swamps identified as either nutrient-poor and stagnant (Schlesinger 1978), stagnant (Taylor 1985; Mitsch et al. 1991), or near-continuously flooded (Megonigal et al. 1997).

All of these observations suggest that the majority of the Maurepas swamp consists of relic forests. The high rates of mortality are consistent with losses of swamp forest documented in Barras et al. (1994). Existing swamps are continuously flooded and largely impounded, which prevents seed germination and recruitment of *Taxodium distichum* and *Nyssa aquatica* (e.g., Conner and Day 1976; Harms et al. 1980; Conner and Day 1988; Myers et al. 1995; Souther and Shaffer 2000). Moreover, on average, flood durations in the Maurepas Swamps have doubled over the past half-century (Thomson et al. 2002). Continuous flooding, although not immediately detrimental to cypress-tupelo swamps, will lead to their gradual death over time (e.g., Harms et al. 1980; Pezeshki et al. 1987*a*; Conner and Day 1988; Conner and Day 1992). The four different habitat types identified within the Maurepas swamp appear to be in various stages along this trajectory of swamp decline. Moreover, if the high mortality rates continue, some areas along the southern

Figure 10. Percentage of the year that the marshes adjacent to Schleider's Ditch (top) and First Canal (bottom) flooded for the period 1956–1999 (Thomson 2000).

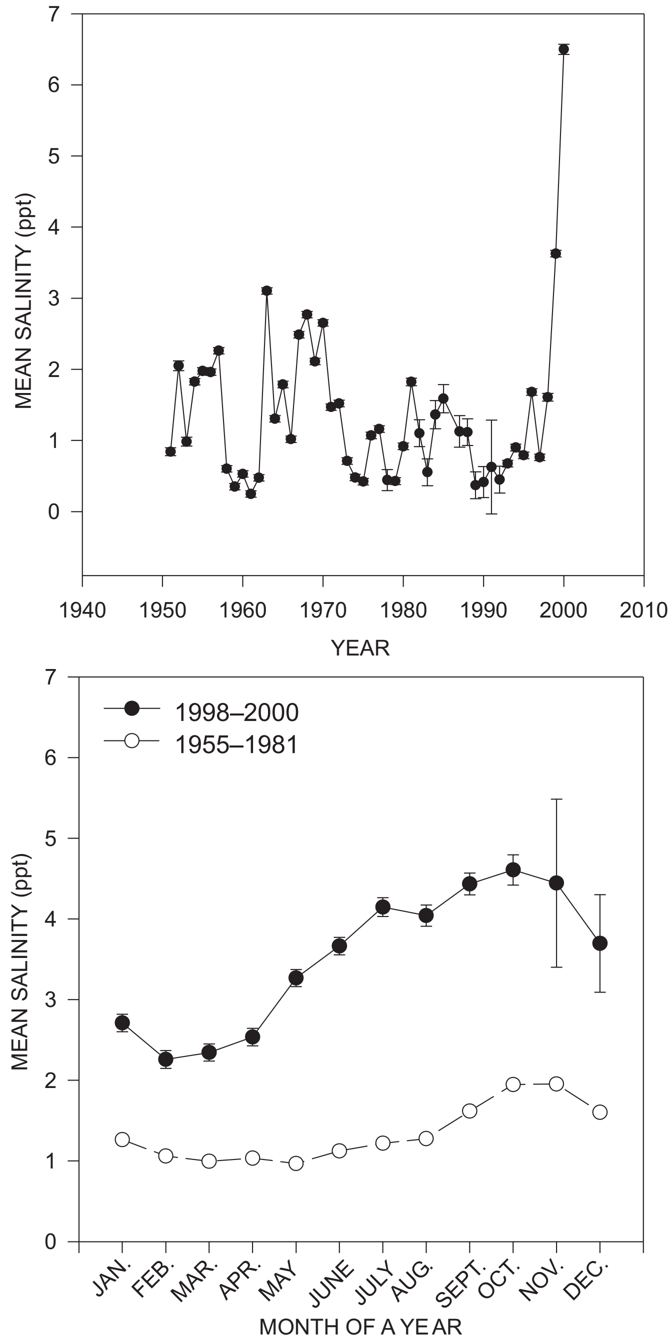


shore of Lake Maurepas may be completely deforested within the next 2–5 years.

Forests at slightly higher elevation are at risk from human development, as well as altered hydrology. White and Skojac (2002) have documented a few remnant forests in the region, several of which have already been destroyed by development. As a consequence, cypress swamps, along with bottomland hardwood forests, and relict ridge woodlands, are targets for conservation planning according to the criteria of The Nature Conservancy (2004).

In summary, Shaffer et al. (2003) have shown that most of the swamps in the Maurepas region appear to be converting to marsh and open water primarily due to the lack of riverine input. At lake sites, salt stress is the primary cause of mortality, whereas in interior sites, stagnant standing water and nutrient deprivation appear to be the largest stres-

Figure 11. Yearly mean salinity for Pass Manchac 1951–2000 showing the impact of the 2000 drought on patterns among years (top) and within years (bottom) (Thomson 2000).

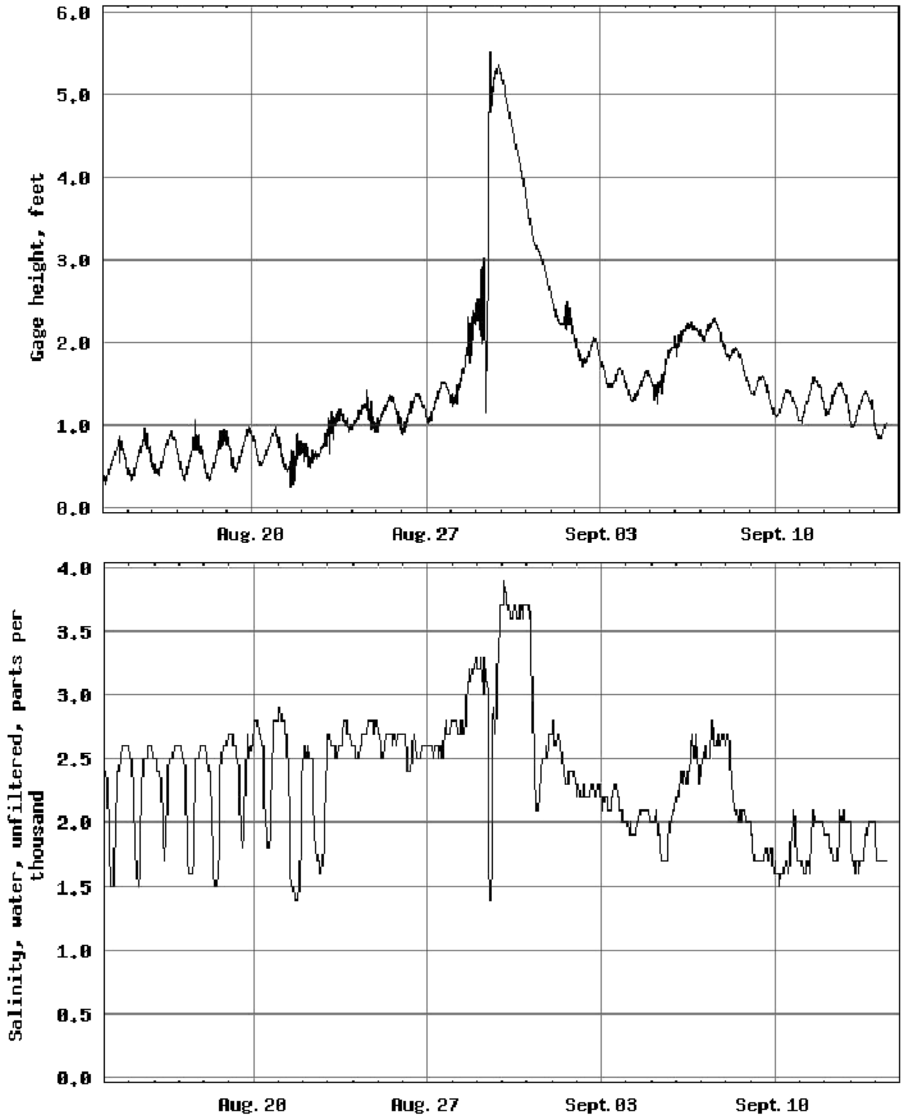


sors. Irrespective of their relative importance among site and years, both stressors would be simultaneously reduced by increased flows of water from the Mississippi River. These sites are, however, all potentially at risk from unsustainable logging (Shaffer et al. in review), while those at slightly higher elevations are at risk from urban sprawl.

Composition of marshes

To put the marshes in context, Table 3 summarizes the composition of wetlands along the coast of Louisiana along a salinity gradient of saline, brackish, intermediate, and

Figure 12. Changes in water level and salinity with the arrival of Hurricane Katrina (measured by USGS 301748090200900 Pass Manchac at Turtle Cove near Ponchatoula, LA; provisional data from USGS).



fresh. In general, this large-scale variation is repeated at a smaller scale in Lakes Pontchartrain and Maurepas, with the most saline marshes occurring further to the southeast. Table 4 shows the species commonly found in the marshes and swamps of Lakes Pontchartrain and Maurepas.

One of the best-described natural marshes occurs at the mouth of the Tchefuncte River (Conner et al 1980; Brewer and Grace 1990; Baldwin and Mendelssohn 1998*a*). Along a gradient extending between a bald cypress swamp and the lake, there are three major marsh types, *Cladium mariscus ssp. jamaicense*, *Sagittaria lancifolia*, and *Spartina patens*. The plant distributions are attributed largely to flood regime and soil organic matter, along with the occasional impacts of salinity pulses associated with storms (Brewer and Grace 1990). Although *Cladium mariscus* ssp. *jamaicense* (sawgrass) is common elsewhere along the Louisiana coast, this appears to be the largest stand in the Lake Pontchartrain–Maurepas area. *Cladium mariscus* ssp. *jamaicense* is considered to be particularly tolerant of low soil nutrient levels (Newman et al.1996; Lorenzen et al. 2001). In the Tchefuncte River marshes, more than 37 species of vascular plants were found in a total sample area of only 78 m^2 (Brewer and Grace 1990). Further to the east, at Little Lagoon, Conner et al. (1980) sampled a total of 2.5 m^2 (25–0.1 m^2 plots), and reported only seven species including *Spartina patens*, *Fimbristylis castanea*, *Symphyotrichum subulatum*, and *Sabatia dodecandra*.

To better quantify characteristics of anthropogenic marshes for comparison with natural marshes, we established seven nested plots in sites representing the anthropogenic marshes in the wetlands south of pass Manchac near the Turtle Cove Environmental Research Station (Hastings 2004). Each plot consisted of 11 nested circular quadrats (from 0.25 to 200.0 m^2). Dr. G. Montz confirmed all identifications, and voucher specimens were deposited in the Southeastern Louisiana University herbarium. In 2000, we identified only 19 species of vascular plants representing 17 genera in this area of 1400 m^2. The dominant species were *Amaranthus australis*, *Cuscuta indecora*, *Symphyotrichum subulatum*, *Echinochloa walteri*, and *Sagittaria lancifolia.*

Figure 13. A TWINSPAN classification of vegetation types in the northwestern portion of the Lake Pontchartrain Basin (Kandalepas 2004). Numbers directly above vegetation types indicate the number of locations out of 40 assigned to each group. The numbers in parentheses are mean number of plant species found within each group.

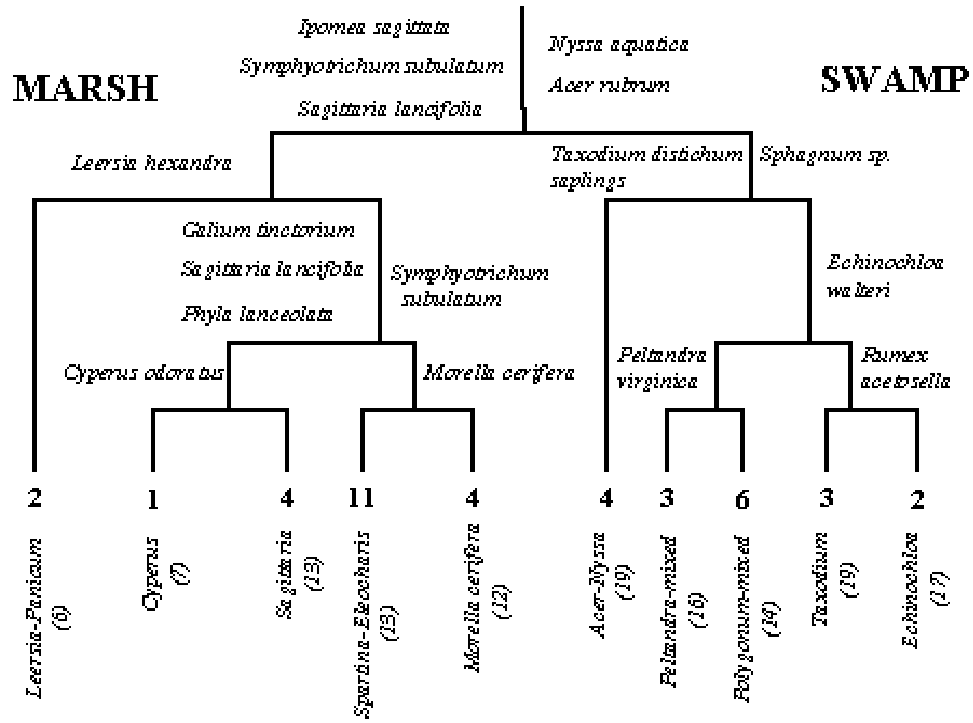
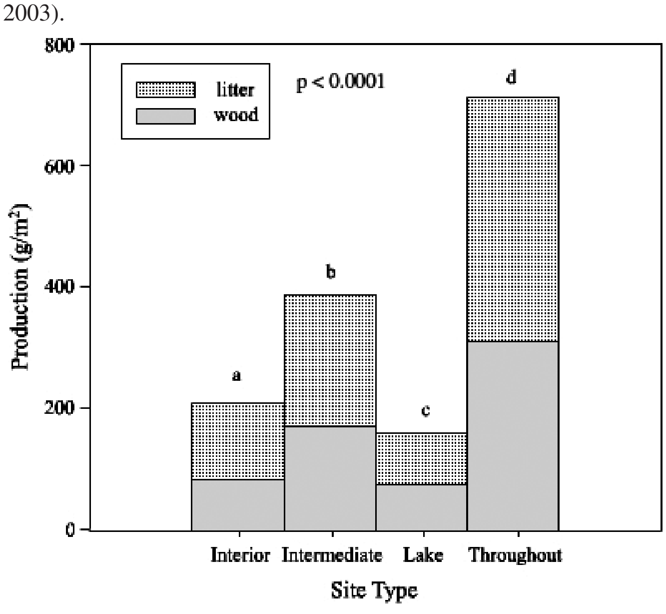


Figure 14. Annual production of swamps was lowest at the lake sites exposed to salt water intrusion and highest in the sites with throughput. The wood: litter ratio is about 1:1 (after Shaffer et al. 2003).



In later years, with less drought effects, dominance shifted to *Polygonum punctatum*, *Schoenoplectus americanus*, and *Eleocharis cellulosa*. Table 5 shows species composition overall, and as subdivided into four types by correspondence analysis.

Frequently, Louisiana wetlands are treated in isolation from the rest of the Gulf Coast. We wish to emphasize, as did Penfound (1952), that similar vegetation types are widespread along the Gulf Coast. Thus, scientists can share basic understanding and apply restoration techniques across a much wider geographic range than is normally done. For example, central Florida, on the margins of Blue Cypress Lake, Lowe (1986) describes wet prairie (37% of the marsh area) with the dominant being *Panicum hemitomon* along with *Sagittaria lancifolia* and *Cephalanthus occidentalis*. Other species included *Peltandra virginica*, *Crinum americanum*, and *Pontederia cordata*. He notes (p. 225) that this community is “quite similar to the wet prairies dominated by maidencane (*Panicum hemitomon*) which occupy large areas of the northern Everglades”. A further 23% of the marsh is dominated by *Cladium mariscus* ssp. *jamaicense*. Although this species does not occur in the anthropogenic marshes at Turtle Cove, it is common in other coastal marshes of Louisiana. Much like *Cephalanthus occidentalis*, it only occurs in fresh marshes, and likely only in those with adequate sheet flow (Chabreck 1972; Brewer and Grace 1990). The most extensive community type in the Everglades, which “covers vast areas throughout the entire marsh”, is *Cladium mariscus* ssp. *jamaicense,* stands “in association with” *Sagittaria lancifolia*, *Panicum hemitomon*, *Pontederia cordata*, *Typha domingensis*, and *Typha angustifolia* (Loveless 1959). Other species include *Peltandra virginica* and *Crinum americanum* (Loveless 1959). Loveless even describes the effects of drought in allowing species such as *Acnida cuspidata* (*Amaranthus australis*) and *Rhynchospora corniculata* to become abundant. Louisiana marshes, then, need not be studied in geographic isolation from those along the entire Gulf Coast; equally, results for studies carried out in Louisiana can be extrapolated to areas well beyond the mouth of the Mississippi River.

Table 4. Species commonly found in the marshes and swamps of the western Lake Pontchartrain and Maurepas area (adapted from Kandalepas 2004).

Marsh species	% Total cover	Swamp species	% Total cover
Sagittaria lancifolia	15.8	*Nyssa aquatica*	31.7
Eleocharis sp.	8.4	*Taxodium distichum*	12.7
Ipomoea sagittata	6.4	*Acer rubrum*	8.6
Polygonum punctatum	6.3	*Peltandra virginica*	7.8
Spartina patens	5.9	*Alternanthera philoxeroides*	5.2
Lythrum lineare	5.8	*Zizaniopsis miliaceae*	4.4
Eleocharis cellulosa	5.8	*Eleocharis vivipara*	3.6
Symphyotrichum subulatum	4.5	*Acer rubrum* seedling	3.5
Cuscuta indecora	4.0	*Cephalanthus occidentalis*	2.2
Leersia hexandra	3.3	*Morella cerifera*	2.2
Paspalum vaginatum	3.0	*Sacciolepis striata*	2.2
Panicum spp.	2.5	*Sparganium eurycarpum*	1.5
Cladium mariscus ssp. Jamaicense	2.5	*Echinochloa walteri*	1.3
Vigna luteola	2.3	*Hibiscus moscheutos ssp. lasiocarpos* seedling	1.1
Myrica cerifera (*Morella cerifera*)	1.9	*Pontederia cordata*	0.9
Eleocharis quadrangulata	1.7	*Leersia hexandra*	0.8
Echinochloa walteri	1.4	*Eleocharis* spp.	0.7
Baccharis halimifolia	1.4		
Peltandra virginica	1.2		
Alternanthera philoxeroides	1.2		

Possible mechanisms for patterns in marshes

To understand the current patterns in this wetland complex, and to predict changes in response to salt water intrusion or fresh water diversions, it is necessary to understand some of the mechanisms producing the above patterns. The first class of explanations assumes that environmental factors provide strong filters that exclude most of the native species pool (van der Valk 1981; Keddy 1992). There is broad consensus that deltaic wetlands in general, and the Lake Pontchartrain wetlands in particular, are likely controlled by a few over-riding ecological factors: salinity (Penfound and Hathaway 1938; Chabreck 1972; Taylor and Grace 1995), hydrology (Boesch et al. 1994; Myers et al. 1995), sedimentation rates (Milliman and Meade 1983; Keddy 2000), herbivory (O'Neil 1949; Brantley and Platt 1992; Myers et al.1995; Taylor et al. 1997; Evers et al. 1998), and fire (O'Neil 1949; Smith and Kadlec 1985*a*, 1985*b*; Nyman and Chabreck 1995).

Further, the biomass of these communities also could be setting a limit on the number of species. It may be that the physical factors control the amount of biomass forming a canopy, thereby excluding species intolerant of shading (Grace 1999; Keddy 2000; Keddy and Fraser 2002). The first two factors in the preceding paragraph (salinity and sedimentation) tend to control the rates at which biomass is produced, while the latter factors (herbivores and fire) tend to control the rates at which biomass is removed.

All of the above explanations, however, tend to assume that immediate physiological processes (or surrogates such as shading or competition) are sufficient to explain low plant diversity. Disturbance treatments that ameliorate effects of shading and competition should increase species richness, although experiments by Thomson (2000) and McFalls (2004) did not find corresponding increases in richness with disturbance.

The second class of explanations invokes dispersal. Because these marshes are anthropogenic in origin, they likely originated rapidly (over a few decades, probably from nearby seeds or as seeds dispersed by logging activities). Thus, the few founders of these plant communities may have given rise to the existing marshes. From this perspective, the low diversity of these marshes may be simply a founder effect, maintained by limited dispersal. Further, the few founder species may have rapidly filled the clearings and provided a closed canopy within a few years. A closed canopy would further reduce opportunities for successful establishment by newly arrived propagules. In most natural marshes, large deltaic networks provide vast areas of open mud flats where colonists may establish (Shaffer et al. 1992; White 1993). There is evidence from other vegetation types, that the size of the pool of colonists has an important effect on plant species diversity at local scales (Eriksson 1993; Grace and Pugesek 1997). Dispersal limitations in the Manchac area have been hypothesized (Gough et al. 1994).

The experimental introduction of plant species can test dispersal as a limiting factor, and allow the exploration of the relative importance of specified factors as controls on plant distribution. A large transplant experiment (Geho et al. 2007) was conducted to measure the relative importance of competition, herbivory (mammalian herbivores, primarily nutria), and sedimentation in controlling the number of species in the marsh. Sixteen species were introduced to these marshes (12 herbaceous species: *Acorus calamus*, *Cladium mariscoides*, *Eleocharis* sp., *Juncus effusus*, *Panicum hemitomon*, *Peltandra virginica*, *Pontederia cordata*, *Rhynchospora corniculata*, *Rhynshospora inundata*, *Saururus cernuus*, *Schoenoplectus americanus, Typha domingensis*;

Table 5. List of dominant plant species in the Manchac marshes near the Turtle Cove Environmental Research Station and the mean percent cover in four vegetation types identified by correspondence analysis. Only species that have greater than 10% mean cover in a vegetation type are included here. The areas being invaded by shrubs and having abundant *Amaranthus australis* became more noticeable during the drought, but later declined.

	Vegetation type			
	Polygonum	Shrubs (*Baccharis*, *Iva*, etc.)	*Eleocharis*	*Schoeno-plectus*
Annuals				
Amaranthus australis	1	34	1	1
Symphyotrichum subulatum	33	32	12	3
Echinochloa crus-galli	3	21	9	1
Polygonum punctatum	31	0	15	23
Perennials				
Alternanthera philoxeroides	1	16	0	0
Eleocharis cellulosa	1	1	28	1
Lythrum lineare	3	2	9	3
Sagittaria lancifolia	13	19	0	1
Schoenoplectus americanus	0	0	0	58
Schoenoplectus robustus	5	5	7	0
Vines				
Ipomoea sagittata	8	7	6	6
Vigna luteola	13	5	4	6
Parasites				
Cuscuta indecora	1	38	1	1
Shrubs				
Baccharis halimifolia	1	11	0	0
Iva frutescens	4	16	0	1

and 4 woody species: *Acer rubrum*, *Cephalanthus occidentalis*, *Nyssa aquatica*, and *Taxodium distichum*). Adult plants were transplanted into 3 m × 3 m plots either inside or outside of herbivore exclosures, with or without competition (removed by Rodeo™) from established vegetation, and with or without added sediment (1 cm thick). Each of these four treatments contained one representative of each species, and the four treatments were replicated three times. At the end of one growing season (7 months), above- and below-ground dry biomass was measured.

The treatments had significant effects on seven species (Table 6). The exclusion of herbivores resulted in significant biomass increases (2 to 26 times) for *Typha domingensis* and *Taxodium distichum* (Table 6). Removal of competition from neighbors resulted in significant biomass increases (2 to 10 times) for five species: *Acorus calamus*, *Cephalanthus occidentalis*, *Panicum hemitomon*, *Pontederia cordata*, and *Rhynchospora corniculata* (Table 6). In summary, the effects of competition from established plants may be preventing establishment after dispersal. Further, competition is apparently more important than herbivory, and, at least in the short term, added sediment, like that from a freshwater diversion, is unlikely to influence the number of species found. Despite studies supporting the prevalence of flooding and (or) salinity at reducing germination, recruitment and survival (McKee and Mendelssohn 1989; Baldwin et al. 1996), the increase in elevation created by the sediment addition, which would ameliorate flooding pressures, did not increase plant diversity over the short term (McFalls 2004). Longer-term experiments are needed to properly assess this hypothesis.

Effects of disturbance and fertility on marshes

The interactions of grazing, flooding, and salinity — three of the key ecological factors in this ecosystem — were experimentally explored in the Manchac marshes by Grace and Ford (1996). Sods of *Sagittaria lancifolia* were exposed to factorial combinations of salinity, flooding, and simulated herbivory. None of these factors alone significantly affected the test plants (Fig. 15), but all three factors combined caused negative effects on the plants. However, other studies have shown that increased flooding and salinity can negatively affect plants such as *Sagittaria lancifolia* (Pezeshki et al. 1987*b*). Low levels of salinity (≤ 6 ppt) combined with permanent flooding allow the expansion of *Sagittaria lancifolia* (Martin and Shaffer 2005) and *Peltandra virginica* (Watkins 2005) at the expense of less stress-tolerant species.

To better document the effects of natural disturbances in marshes, Baldwin and Mendelssohn (1998*a*) created three levels of disturbance in plots in the Tchefuncte River marshes: (1) no disturbance, (2) non-lethal clipping above ground vegetation, and (3) killing above and below ground vegetation with herbicide. They repeated the experiment in two vegetation types, a community dominated by *Sagittaria lancifolia* and another dominated by *Spartina patens*. Although treatment effects were significant in both communities ($P < 0.001$), the Spartina community was less resilient to disturbance. In the *Sagittaria* community (Fig. 16*a*), non-lethal disturbance had minimal effects, while lethal disturbance slightly decreased the number of species observed. In contrast, in the *Spartina patens* community (Fig. 16*b*),

Table 6. Effects of herbivory, competition, and sediment addition upon eight species transplanted into the anthropogenic marsh. Significant *P*-values (ANOVA, $p < 0.005$, Bonferroni adjustment of $\alpha = 0.05$ to adjust for multiple comparisons) are bold and marked with an asterisk (*). Empty cells indicate the interaction term was pooled into the error term ($F < 1.70$) (Bancroft and Han 1983). Species that were unaffected by any treatment are not shown. (Adapted from Geho et al. 2007)

Species	Herbivores (Exclosure)	Competition (Herbicide)	Sediment	Herbivores + Competition	Herbivores + Sediment	Competition + Sediment	Herbivores + Competition + Sediment
Acorus calamus	0.1589	**0.0003***	0.0377		0.1494	0.0593	0.1811
Cephalanthus occidentalis	0.0283	**0.0000***	0.1179	**0.0044***	0.1824	0.1978	
Panicum hemitomon	0.8656	**0.0000***	0.0053	0.1041	0.0283		
Pontederia cordata	0.2044	**0.0000***	0.075		0.0472		
Rhynchospora corniculata	0.2848	**0.0002***	0.8181	0.0086			
Taxodium distichum	**0.0024***	0.0931	0.2819	**0.0022***			0.0694
Typha domingensis	**0.0000***	0.0111	0.1722	0.0126	0.1383	0.0375	0.1158

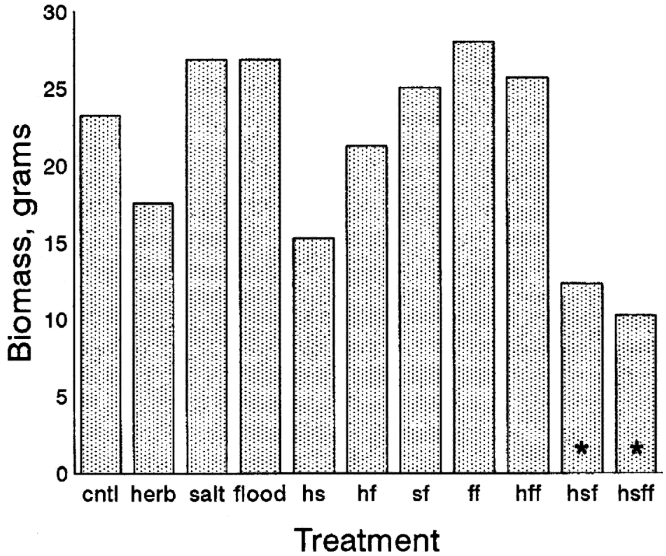
non-lethal disturbance increased plant richness, and lethal distance tripled the number of species observed. Overall, Baldwin and Mendelssohn (1998*a*) concluded that vegetation quickly recovered from non-lethal disturbance, since the plants quickly resprouted. In contrast, lethal disturbance created longer-term effects, in part because of delays in recovery, and in part because of increased establishment of species from buried seeds (Table 7). The *Spartina* community had nearly ten times the seed density (>32 000 as opposed to > 2500 seeds/m^2).

Inspired by this study, a much larger and more realistic experiment was conducted to measure how biomass and richness of entire plant communities respond to these and related factors. This larger experiment was conducted at Turtle Cove Experimental Marsh located on the Manchac land bridge (Fig. 17). The vegetation here was dominated by three species: *Schoenoplectus americanus* (39.0%), *Polygonum punctatum* (18.9%), and *Sagittaria lancifolia* (7.4%). The research treatments were designed to provide both multiple disturbance and fertility treatments ranked by intensity and combined in a factorial design (McFalls 2004). Disturbance, defined as any event that destroys plant biomass (Grime 1977, 1979), strongly influences species diversity and biomass patterns by creating heterogeneity in ecological communities (e.g., Connell 1979; Grime 1979). Disturbance intensity, measured as the proportion of biomass killed (Grime 1979; Sousa 1984), dictates how much the system is perturbed, while resource availability determines the rate of recovery. In 2002, five disturbance treatments, ranked by order of probable intensity, were applied: no disturbance (control), prescribed fire, herbivory (manipulated with exclosure cages), a single vegetation removal treatment, and a double vegetation removal treatment. The fertility treatments were designed to include factors that might affect production in Louisiana's rapidly submerging coastal areas, and also were ranked by probable intensity: no fertility enhancement (control), sediment addition, fertilizer addition, and a sediment + fertilizer addition (McFalls 2004).

In early 2002, three 40 m × 60 m herbivore exclosures were constructed and paired with 3 areas of equal size that were open to herbivory. Exclosures were designed to prevent nutria (*Myocastor coypus*), the principal vertebrate herbivores of the marsh, from entering the plots, but the exclosures also excluded other less common herbivores such as feral hogs (*Sus scrofa*), marsh rabbits (*Sylvilagus aquaticus*), and muskrats (*Ondatra zibethicus*). The main plots were constructed parallel to one another with a large boardwalk separating them. Access inside of the main plots was provided by 670 m of catwalk (Fig. 17). Subplots (3 m × 3 m) for the factorial combinations of the disturbance and fertility treatments were randomly allocated within the main plots. Above ground biomass was measured in July 2003 using destructive sampling techniques near the perimeter of each plot (McFalls 2004). The data were analyzed as 2×4×4 randomized block design split plot factorial analyses of covariance.

The main effects of disturbance and fertility treatments roughly followed our intensity rankings (Fig. 18). Linear contrasts showed that the sediment + fertilizer treatment, which simulated Mississippi River flooding events, resulted in increased biomass compared to plots with no fertility enhancement and plots with the sediment only treatment. The

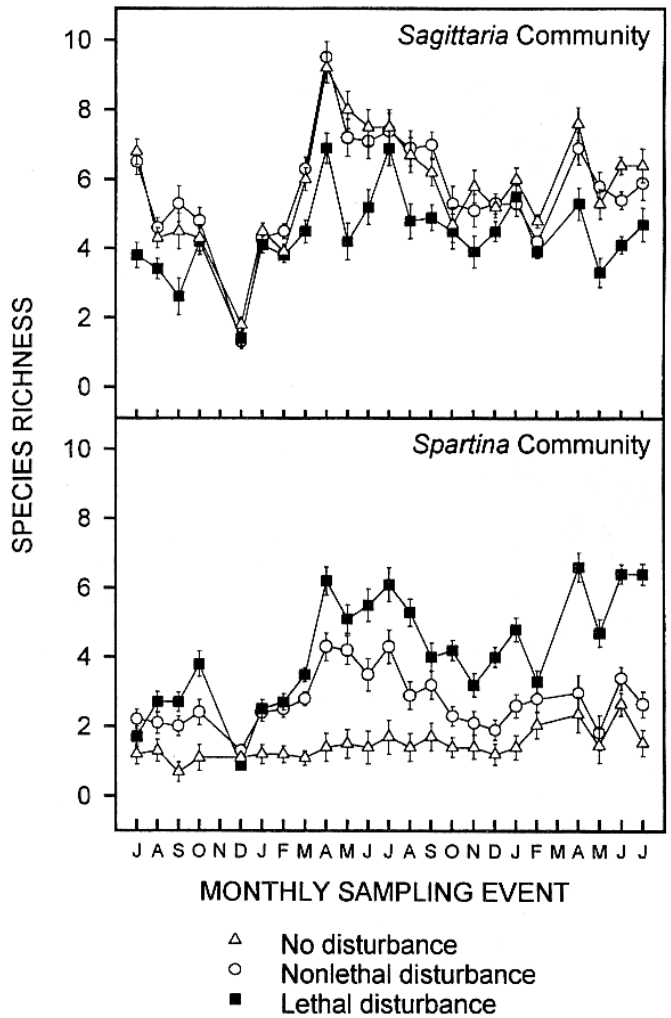
Figure 15. The response of one common marsh plant, *Sagittaria lancifolia,* to simulated herbivory (herb), increased salinity (salt), prolonged flooding (flood) and all possible combinations of these (e.g., hs is simulated herbivory + increased salinity). Although each effect is insignificant, when these effects are combined (hsf is herbivory + salinity + flood; hsff is herbivory + salinity + flood + fertilizer), plants were strongly negatively affected (from Grace and Ford 1996).



sediment treatment was statistically similar to the fertilizer treatment. Linear contrasts demonstrated that fire and the single vegetation removal reduced the amount of biomass relative to the control. Herbivory significantly reduced biomass ($p < 0.0001$). On average, areas protected from nutria herbivory had 1.4 times the biomass of areas open to herbivory.

There were complicated two- and three-way interactions (McFalls 2004) that are not shown here, but will be briefly summarized. Without grazing, biomass increased as fertility increased, whereas outside the exclosures, biomass did not change with fertility. This suggests that nutria consumed a great deal of the increased vegetation that results from enhanced fertility. Further, biomass decreased monotonically with disturbance outside the exclosures while this was much less noticeable inside the exclosures. Apparently, nutria only had an impact upon biomass if another disturbance was present, and they tended to amplify effects of disturbance. The likely mechanism is a preference for newly-growing vegetation, a common phenomenon in herbivores (White 1993). Overall, the results show that freshwater diversions that carry sediment and nutrients into the marsh are likely to increase production. These responses are likely to be reduced in the presence of nutria. Although fire occurs in Louisiana marshes, and is a management tool applied to selected marshes (O'Neil 1949; Nyman and Chabreck 1995), the short-term results of this experiment indicate that plants regenerating after fire are particularly attractive to nutria and increase impacts of herbivores upon the vegetation. Further, in dry periods fires can consume organic matter in the soil, leading to reduced elevation and increased flooding. This could initiate a positive feedback cycle for further reduction in plant cover and marsh elevation.

Figure 16. Effect of three levels of disturbance on the number of plant species (species richness) in two oligohaline marsh communities near the mouth of the Tchefuncte River over a 2 year period. Richness was measured in 0.5 m x 0.5 m quadrats and error bars are ± SE (from Baldwin and Mendelssohn 1998*a*).



Nutria, alligators, trophic networks, and top down control

Thus far, we have described these wetlands using the traditional paradigm in coastal management — a view that is entirely bottom up — that is, rivers deposit sediments, sediments raise elevation and allow plants to grow, and then the plants are converted into useful products that are harvested. There is undoubtedly a geological component to the creation of wetlands (e.g., Boyd and Penland 1988; Reyes et al 2000), and a certain bottom up logic is unavoidable: without sediments, there can be no plants. However, once sediment has been deposited, and a food web established, a new alternative emerges: top down control or trophic cascades in which a top predator like the American alligator could reduce herbivore populations, and thereby increase growth and biomass accumulation of plants (Keddy et al. In press).

The term trophic cascade refers to top down control, where a predator controls the abundance of herbivores, thereby controlling the biomass and species composition of

Table 7. Species occurring in the seed banks of two oligohaline marshes near the mouth of the Tchefuncte River. Values are mean ± SE of density (number m^{-2}). Each sample consisted of five shallow cores 5 cm deep by 4.8 cm in diameter in June 1994. Species names in brackets indicate current nomenclature. (Baldwin and Mendelssohn 1998*a*)

Species	*Sagittaria* community	*Spartina* community
Amaranthus australis	22 ± 22	177 ± 79
Ammannia latifolia	0	6587 ± 2973
Aster subulatus (*Symphyotrichum subulatum)*	111 ± 49	44 ± 29
Cyperus haspan	376 ±155	22 ± 22
Cyperus odoratus	0	5305 ± 1263
C. polystachyos var. *filicinus (Cyperus filicinus)*	22 ± 22	0
Diodia virginiana	44 ± 29	0
Echinochloa crus-galli	22 ± 22	1304 ± 455
Eleocharis fallax	774 ± 256	0
E. parvula	0	17 352 ± 5869
Lythrum lineare	597 ± 437	420 ± 217
Phyla nodiflora	22 ± 22	0
Polygonum punctatum	243 ± 61	221 ± 93
Sagittaria lancifolia	309 ± 124	140 ± 244
Scirpus tabernaemontani (*Schoenoplectus tabernaemontani*)	0	486 ± 279
Sesbania exaltata (*Sesbania herbacea*)	0	66 ± 47
Vigna luteola	22 ± 22	0
Total	2564 ± 570	32 826 ± 8638

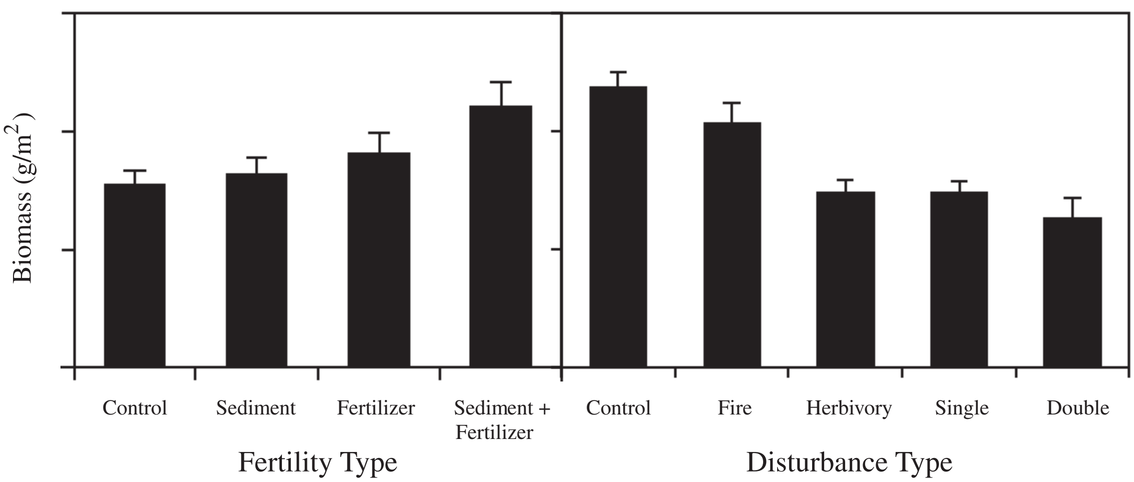
plant communities. When predators decline, the herbivores may increase in population size, become limited by food availability rather than predation, and cause significant damage to vegetation. One well-known (but still imperfectly understood) example in terrestrial habitats has been the major increase in populations of deer (*Odocoileus virginianus*) in North America, which in turn, affect forest composition and tree regeneration (Alverson et al. 1988; Tilghman 1989; Botkin 1990; Russell et al. 2001). There are multiple possible causes including human-induced changes in forest composition, increased edge habitat, and changing agricultural practices, but the loss of natural predators such as wolves and cougar also is implicated as a causal agent. There are more examples from aquatic habitats. Lobsters, for example, may control sea urchins on the east coast of North America, thereby influencing both the area and biomass of kelp beds (Mann and Breen 1972, but see Elner and Vadas 1990). Freshwater fish can reduce the abundance of herbivorous zooplankton in lakes, and may thereby increase phytoplankton (Carpenter and Kitchell 1988). In southern salt marshes, blue crabs (*Callinectes sapidus*) may help protect salt marshes from overgrazing by consuming periwinkles (Silliman and Bertness 2002). In northern marshes, exploding goose populations have damaged nearly two thirds of the approximately 55 000 ha of salt marsh along the coast of Hudson and James Bays (Jefferies and Rockwell 2002;Abraham and Keddy 2005). Overall, Sinclair et al. (2000) postulate that the effects of removing predators attenuate less in aquatic than in terrestrial systems. Hence, we need to consider the possibility that some of the patterns and processes seen in the study area reflect these sorts of trophic relationships.

Some evidence strongly suggests that trophic relationships are important in controlling the composition of the Pontchartrain–Maurepas wetlands. The first body of evidence is the impact of nutria on these wetlands. (Muskrats also are a part of the story, but seem to have usually been less common than nutria (Keddy et al. In press)). To put this problem in the Louisiana context, nutria were introduced to Louisiana in the late 1930s (Lowery 1974; Bernard 2002) and quickly became a common herbivore. Nutria and other herbivores have significant effects on wetland vegetation loss and composition (Bazely and Jefferies 1986; Myers et al. 1995; Lodge et al. 1998; Carter et al. 1999). Annual aerial surveys beginning in 1998 indicated that 321 km^2 to 415 km^2 of Louisiana's 14 164 km^2 coastal wetlands were severely damaged by nutria (LDWF 2006). These estimates are conservative because only the most obvious damage can be detected during aerial surveys (LDWF 2006). This damage occurred almost exclusively in the Mississippi River Deltaic Plain (unpublished map, Louisiana Department of Wildlife and Fisheries). Marshes in the Mississippi River Deltaic Plain probably are more sensitive to nutria damage because submergence (i.e., the combination of local subsidence and global sea-level rise) exceeds 1 cm/year in the Mississippi River Deltaic Plain, but averages only 0.57 cm/year in the Chenier Plain (Penland and Ramsey 1990), and because as noted, nutria increase the sensitivity of vegetation to flooding and (or) salinity stress (Gough and Grace 1998; Grace and Ford 1996). In 2002, the Coastal Wetlands Planning, Protection and Restoration Act (CWPPRA) Task Force initiated a US$68 million statewide nutria-control program designed to reduce damage to coastal wetlands resulting from nutria activity (CWPPRA 2003).

We already have provided evidence that simulated herbivory can increase the sensitivity of plants to flooding (Grace and Ford 1996) and that nutria reduce biomass in wetlands (McFalls 2004). Nutria even have a significant effect upon tree regeneration, which is particularly important for restoration, given the declining area of swamp and the possibility of reforesting areas of anthropogenic wetlands (Myers et al. 1995). In the transplant experiment conducted by Geho et al.

Figure 17. Turtle Cove Experimental Marsh. Left, aerial view with boardwalks and catwalks highlighted. The three 40 m × 60 m herbivore exclosures were randomly assigned to left or right of the main boardwalk. Schlieder's ditch runs to the east of the experiment, and the field station (not shown) is just beyond the bottom of the photograph. Note the parallel ditches left by logging nearly a century earlier. Right, entrance showing anthropogenic marshes in foreground and a cypress swamp along First Canal in the distance.

Figure 18. The short-term effects upon biomass of increasing fertility (left, including all herbivory and disturbance treatments, mean ± 1 SE, n = 96, $F_{3,70}$ = 10.004, p = 0.000) and increasing disturbance (right, including all herbivory and fertility treatments, mean ± 1 SE, n = 96, $F_{3,70}$ = 30.297, p = 0.000). Herbivory is included in the latter figure for visual comparison, but was not tested against the other types of disturbance (from McFalls 2004).



(2007), all cypress seedlings outside of exclosures were killed, often being cut off near the ground level by nutria. Larger trees may have their bark stripped.

Myers et al. (1995) explored possible restoration techniques for bald cypress, planting 400 trees in the Manchac Wildlife Management Area in a three-way factorial arrangement that included nutrient augmentation, control of entangling vegetation, and three types of protection from herbivores. All three of these factors strongly affected diameter growth of the seedlings. Unprotected trees suffered 100% mortality. Given the impacts of nutria on herbaceous and woody plants, it is reasonable to ask if a natural factor might control their abundance. Alligators are well known generalist predators in wetlands. Determining their diet from stomach content is always difficult, since the input of prey will vary with habitat, season and predator size, while volume and digestibility differs among prey species (compare fish and turtles). Turning first to a classic source, Dundee and Rossman (1989) say that alligators more than 1 m long "will eat anything they can catch and swallow . . . especially muskrats… and nutria.” In a recent review, Gabrey (2005) summarized the literature reporting alligator stomach contents. Nutria were not detected in alligator stomachs until 1961 (Valentine et al. 1972). In subsequent studies nutria comprised a significant portion of adult alligator diet throughout coastal Louisiana, while muskrat declined in importance (Wolfe et al. 1987).

Juvenile alligators (less than 1.2 m long) feed primarily on fish, insects, and crustaceans (reviewed in Gabrey 2005). Blue crabs can account for 70% of prey biomass in brackish marsh (Elsey et al. 1992), but crawfish can dominate prey in fresher areas (Platt et al. 1990). In coastal Louisiana, mammalian prey of adult alligators (>1.2 m) are dominated by nutria and muskrat (Wolfe et al. 1987). Quantitative simulations of such food webs show that alligators can have major impacts through indirect linkages to lower trophic levels (Bondavalli and Ulanowicz 1999). But the stomach content data from Louisiana show that the food webs may in fact be dominated by a few strong interactions — invertebrates being favored by smaller alligators, and nutria by larger alligators (Gabrey 2005). The diet also is controlled by salinity, with increasing salinity shifting the diet from nutria to blue crabs (Fig. 19).

There are no systematically collected data, but descriptions indicate that alligator populations in Louisiana declined precipitously between 1850 and 1960. The naturalist Bartram (1791), a frequently accurate but sometimes overzealous observer wrote:

> *Should I say, that the river (in this place) from shore to shore, and perhaps near half a mile* [0.8 km] *above and below me, appeared to be one solid bank of fish, of various kinds, pushing through this narrow pass of St. Juans into the little lake, on their return down the river, and that the alligators were in such incredible numbers, and so close together from shore to shore, that it would have been easy to have walked across on their heads, had the animals been harmless.* (p. 123)

Audubon (1827) was also impressed by their abundance:

> *On the Red River … they were so extremely abundant, that, to see hundreds at a sight along the shores, or on the immense rafts of floating or stranded timber, was quite a common occurrence, the smaller on the backs of the larger…. The shores are yet trampled by them in such a matter that their large tracks are seen as plentiful as those of sheep in a fold. It was on that river particularly that thousands of the largest size were killed, when the mania of having either shoes, boots or saddle-seats, made of their hides, lasted.* (p. 271)

McIlhenny (1935), who was a keen naturalist and can be considered a particularly reliable witness, reported that alligators “fairly swarmed” prior to harvest that began in the 1880s; they remained common until 1900, but were exterminated from many areas of Louisiana by 1935. All trapping was suspended in 1962 (Joanen and McNease 1987), and alligators were declared a federally endangered species in 1967. Poaching was virtually eliminated in parts of southwest Louisiana by the early 1960s (Tarver et al. 1987). Alligator populations then recovered enough that by 1972 there was an experimental harvest of 1337 animals in southwest Louisiana (Tarver et al. 1987). Alligator numbers continued to increase and by 1981 the harvest was state-wide and 15 534 hides were taken (Joanen et al. 1984). Larger alligators still are preferentially harvested (Taylor and Neal 1984), making it highly probable that mean size is well below that of the 1850s.

In summary, it is plausible, but by no means proven, that alligators could have several largely-overlooked direct and indirect impacts upon marsh vegetation through their impacts upon nutria (and to a lesser degree, muskrats):

(1) Increased biomass of plants in marshes
(2) Shifts in species composition towards species more favored by grazers
(3) Increased land accretion from increased organic matter accumulation
(4) Increased rates of regeneration of trees, particularly bald cypress

In view of the significant skepticism about such possibilities, and the continued practice of single species management, we draw again upon a terrestrial example. In northern forests, grazing by white tailed deer is changing the composition of both the forest canopy and the understory flora, with some species of herbaceous plants at risk of extirpation from high deer densities (Tilghman 1989; Russell et al. 2001; Latham et al. 2005). Regeneration of some tree species, particularly the conifer *Tsuga canadensis*, is all but eliminated by high deer populations. The absence of large predators like timber wolves and cougars is one of several explanations for these high deer population densities (Russell et al. 2001; Latham et al. 2005). Just as wolves may exert top down control upon the regeneration of northern forests, alligators may exert top down control on the regeneration of trees in southern swamps. So long as this possibility is ignored, we will lack the evidence to fairly evaluate it. Possible avenues for future work to test this proposition are discussed in Keddy et al. (In press). All require comparison of multiple treatment and control areas. The Manchac Wildlife Management Area may provide an example of an area where alligators are hunted; while nearby Jean Lafitte National Park may provide an example of an area where alligator populations are approaching historical density and size class distribution.

Conservation and restoration possibilities

Three conservation plans

To summarize processes in these wetlands, Fig. 20 shows the relationships between wetland area and key natural constraints. It is immediately apparent that these wetlands face multiple natural constraints (salinity, flooding, nutrient limitation, grazing) acting simultaneously. Further, when human impacts are super-imposed, it is apparent that humans have increased the severity of these natural constraints. The loss of wetland area, and conversion of swamp to marsh or open water, is a logical consequence of these natural and human impacts. Were we to add the projected effects of global climate change to Fig. 20, we could anticipate increased salinity, flooding, and storm pulses from rising sea levels. Other effects such as increased salinity from droughts or increased storm frequency and intensity would have additional negative effects. Consequently, at least three attempts have been made to develop comprehensive plans for the future of these wetlands.

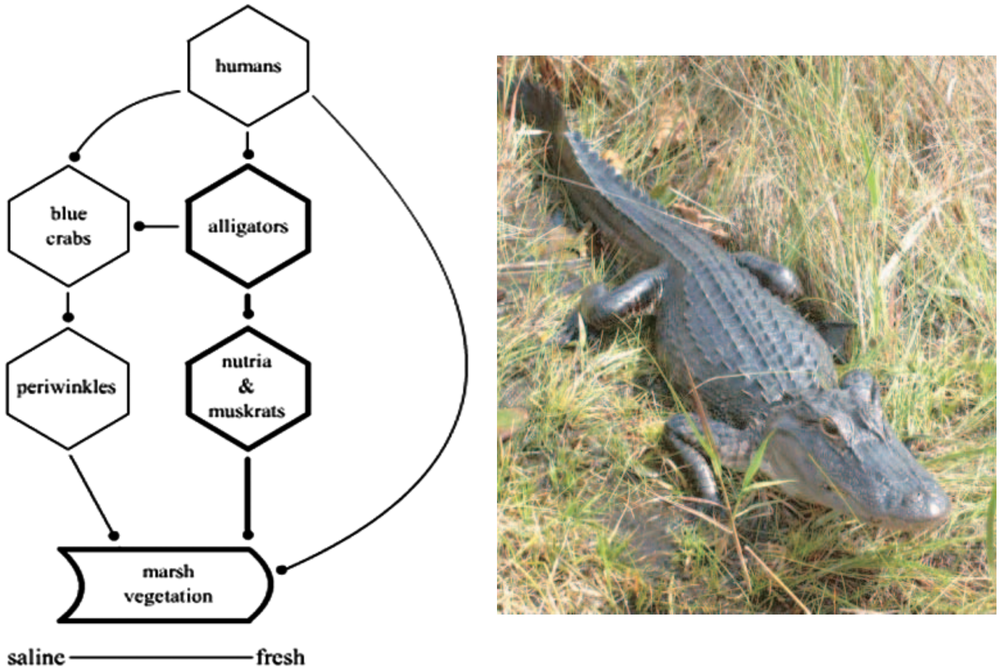
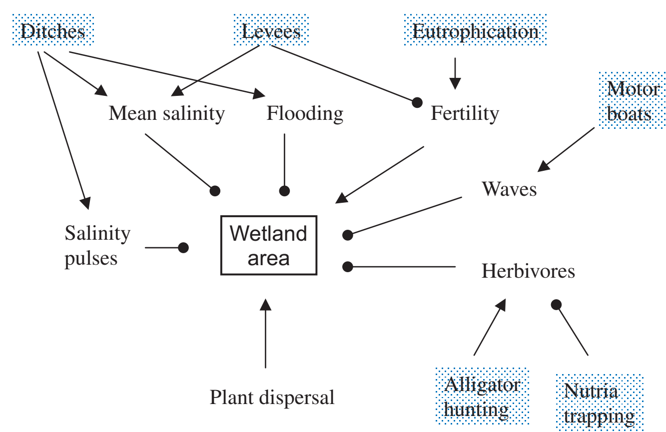


Figure 19. Alligators may have a positive indirect effect upon marsh vegetation by their negative direct effect upon nutria and muskrats. The symbol —● indicates a negative effect. There is also a possible link to the blue crab – periwinkle vegetation food web at higher levels of salinity.

The Louisiana Coastal Wetlands Conservation and Restoration Task Force and the Wetlands Conservation and Restoration Authority (1998) published a report entitled *Coast 2050: Toward a Sustainable Coastal Louisiana*. In it, they review coastal processes, and review causes for the loss of coastal wetlands including rising sea levels, subsidence, altered hydrology, storms, and herbivory. Their Region 1 encompasses the Pontchartrain–Maurepas wetlands and extends to the Gulf. In the Lake Maurepas area, they recognized 44 500 ha of bottomland hardwoods, 77 500 ha of swamps, 5200 ha of fresh and intermediate marshes. Surrounding Lake Pontchartrain they recognized 8800 ha of swamps, 8000 ha of fresh marshes, 11 000 ha of intermediate marshes, and 17 000 ha acres of brackish marshes. Their restoration strategies included freshwater diversions into the Maurepas swamps, maintaining "shoreline integrity" of the north shore of the lake, and phasing out of the Mississippi River Gulf Outlet. In view of the recent impacts of Hurricane Katrina, let us also record their concerns about New Orleans, "virtually an island already", in which "45% of the metropolitan core is at or below sea level" (p. 63). They add that "None of the current or planned protection measures would be effective" (p. 64) if an intense hurricane were to strike the city.

The Nature Conservancy completed a conservation area plan for the Lake Pontchartrain estuary in 2004 (The Nature Conservancy 2004). Their wetland target groups were fresh and intermediate marshes, brackish and salt marshes, cypress swamp, bottomland hardwood forest, and alligator snapping turtles. For the adjoining aquatic systems, these targets were gulf sturgeon, paddlefish, the open water ecosystem, submersed aquatic vegetation, and rangia clams. The primary stressors are largely a consequence of altered hydrology, with its consequent reduction in sediment and nutrients. More locally, urban sprawl has affected turbidity and nutrient loading. The highest priorities for action, according to their report are (1) fresh water diversions from the Mississippi River, (2) land use planning and growth management, (3) conservation land acquisition, and (4) a stricter wetland permitting process. High ranking priorities include (1) an invasive species action plan, (2) sustainable management of cypress forests, (3) watershed planning, (4) reduction of non-point source pollution, (5) protecting critical habitat for Gulf sturgeon, and (6) hunter and fisher education for target species.

Figure 20. A summary of the natural forces acting upon the area of wetlands in the Pontchartrain–Maurepas basin. The symbol → indicates a positive effect while the symbol —● indicates a negative effect. Superimposed, and marked with stippling, are the effects of humans; these largely amplify the natural forces that reduce wetland area.



The Lake Pontchartrain Basin Foundation (LPBF 2005) completed a new conservation management plan in 2005 to set future priorities for the organization. This plan covers a larger area than the Nature Conservancy plan, but two of the four sub-basins in this plan approximately correspond to the area under review (our Lake Maurepas region is termed "the Upper Sub-basin", while our Lake Pontchartrain region is termed "the Middle Sub-basin"). For the Lake Maurepas region, they recommend fresh water diversions from the Mississippi River, the use of treated sewage to enhance marsh production, and the prohibition of cypress logging where it is unsustainable. Recommendations for the Lake Pontchartrain region also include fresh water diversions, as well as restoration of littoral habitat and marshes, and strict control on urban development in wetland habitats. Reduction of the Mississippi River Gulf Outlet (or, in the senior author's opinion, immediate filling of the canal) is discussed in another sub-basin, but would simultaneously have many positive effects for both Lakes Maurepas and Pontchartrain.

Minor adjustments to these plans may be needed in the aftermath of Hurricanes Katrina and Rita; some of these are described in Boesch et al. (2006). Overall, while these plans are laudable, there is a significant gap between their aspirations and the actual actions of local and state governments. Houck (2006) offers the opinion that Lobbyists for the forest industry continue to assert their rights to log all coastal forests, whether sustainable or not, irrespective of the value and irrespective of whether they were restored at the public's expense. Senator Vitter has promoted changes that, in our opinion, would end or at least minimize protection for many swamp forests (Schleifstein 2005). New development and reconstruction along the lakeshore continues, and indeed has accelerated in the wake of hurricanes Katrina and Rita. The "senseless" (Houck 2006) Mississippi River Gulf Outlet continues to direct salt water toward Lake Pontchartrain and Lake Maurepas, and was a principal cause of flooding from Hurricane Katrina. Although multimillion dollar fresh water diversions already have been constructed, their value may be exaggerated, because existing diversions have been run at a fraction of capacity owing to lobbying by oyster fishers, hunters, camp owners, and local politicians who each object to either fresher conditions (e.g., oyster fishers) or higher water levels (e.g., hunters) when they want to use the marsh. At the same time, large-scale diversions appear to be the only tool that will substantially improve the area of coastal wetlands. To date, Houck (2006) concludes that the primary function of funding for flood control is the transfer of federal subsidies to Louisiana, nearly 2 billion dollars in the past 5 years.

> *What we have here, then, is a game that is not focused on flood control, and never has been. It has been focused on making money first for people with boats and then for as many people as possible, even when that has meant increasing hurricane risks and putting other people right into harm's way. It has been in denial about its impacts, and remains largely in denial.* (p. 17 Houck 2006)

Vegetation state changes with different restoration scenarios

Overall, as the length of this review shows, the area is comparatively well studied, and the major factors that are driving the systems are understood in at least a qualitative way. Let us therefore consider the options for large and small-scale restoration of the area. Setting targets for restoration of ecosystems is not an easy task and the goals set by restoration have to consider both the original state of the system as well as the desired state (Cairns 1989). If, for example, we use the map of historical vegetation types in Saucier (1963), one might set a target of 5% of the area as fresh marsh, 5% as intermediate marsh, and 90% as cypress and tupelo swamp. The plausibility of recreating these conditions depends upon the relative importance of the ecological forces acting upon these wetlands. Given the relative strength of these forces, one could imagine multiple ecological states for the anthropogenic marshes, in particular, as well as the wetlands as a whole (Fig. 21). Consider the range of options clockwise from the top.

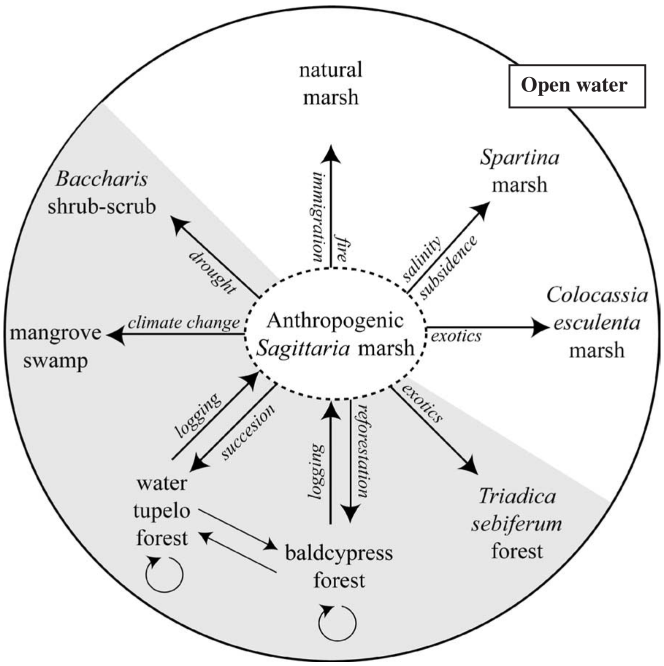
(1) Natural marsh — With appropriate management, the marshes could be fully restored to resemble the sawgrass marshes of the Tchefuncte River and the Everglades. This is likely to require fresh water diversion of Mississippi River water combined with enhanced dispersal of wet prairie and marsh species, and possibly combined with regular burning. Under appropriate conditions of fresh water flow intermingled with low water periods, it may even be possible that these sites would become wet prairies (Lowe 1986) or wet meadows (Keddy 2000), which are usually distinguished by higher plant species richness.

(2) *Spartina* marsh — With rising sea levels and little change in climate, combined perhaps with storms expanding the entrance to the lake, the area may become brackish marsh, with the vegetation dominated by species such as *Spartina patens* and *Juncus roemerianus*. Examples are described in Penfound and Hathaway (1938). Further subsidence of land or rising sea level would lead to open water.

(3) Exotic wetlands — Invasive plants could create entirely new communities. In 1949 O'Neil observed "...two new exotics, water hyacinth (*Eichhornia crassipes*) and alligator grass, (sic) (*Alternanthera philoxeroides*) ... have almost completely dominated the indigenous plants of the active delta and are now possibly in a position to change completely the plant communities of the area." (p. 11). More recently, *Colocasia esculenta* (Elephant's Ear, a common garden escape) has been spreading in wetter areas and now even forms distinctive vegetation patches in the Mississippi River delta (White 1993). *Triadica sebifera* (Chinese Tallow) is simultaneously invading these wetlands along natural and artificial levees (Broussard 1997). Global climate change is likely to accelerate the invasion of wetlands by invasive species since most invaders are native to warmer climates (Twilley et al. 2001). Nearer the Louisiana–Texas border one can see stands of forest where Chinese Tallow appears to be the dominant overstory tree.

(4) Bald cypress forest — It may be possible to restore existing swamps and convert anthropogenic marsh back into cypress swamp. The current limitation seems to be a combination of multiple stressors including salinity, nutrient limitation and herbivory (Myers et al. 1995) combined semi-permanent flooding (Shaffer et al. 2003). Freshwater diversions could ameliorate three of these

Figure 21. The constraints acting upon the wetlands of the Lakes Pontchartrain and Maurepas, along with possible future states for the ecosystem depending upon different combinations of climate change, rising sea levels, fresh water diversions, fire, and invasion by exotic plants. Areas in grey represent forest.



four stressors (Shaffer et al. 2003; Visser et al. 2004). Both inorganic sediments from the river, and the resulting increase in production would lead to increased elevation, while the fresh water would reduce impacts of salt water intrusion and sulfide accumulation. Currently, the Hope Canal near the southern edge of the Maurepas Swamp is a candidate for such a fresh water diversion (Lane et al. 2003; Shaffer et al. 2003). Hall and Penfound (1939*a*) describe a virgin example of such as swamp that could serve as a reference point for restoration

(5) Water tupelo swamp — With sufficient fresh water sheet flow and increased rates of sedimentation, it also is possible that *Nyssa aquatica* and *N. biflora* forest, and perhaps associated bottomland hardwood species, would reestablish. Fresh water diversions (Lane et al. 2003; Shaffer et al 2003; Visser et al. 2004) are again a significant tool in establishing such forests. Hall and Penfound (1939*b*) describe a virgin example of such as swamp that could serve as a reference point for restoration.

(6) Shrub scrub — With frequent drought, it may become *Baccharis halimifolia*, *Iva frutescens*, and *Morella cerifera* dominated shrub scrub. Shrub cover rapidly increased during the 1999–2000 drought, but decreased thereafter. Another drought is in progress, suggesting that the area of this wetland type may be tied to projections for climate change along the Gulf Coast (e.g., Twilley et al. 2001).

(7) Mangrove swamp — Rising sea levels and a warmer climate in coastal Louisiana might lead to a gradual conversion to mangrove swamp. *Avicennia germinans* occurs only a short distance to the south on the margin of the deltaic plain (Penfound and Hathaway 1938; Chabreck and Condrey 1979). Presently, occasional winter frosts appear to set the northern limit of this species and the associated mangrove ecosystem (Chabreck and Condrey 1979; Twilley et al. 2001).

Setting precise targets for ecosystem restoration requires information including (1) the constraints that are currently operating, (2) the degree to which humans can ameliorate these constraints (which includes both cost and ecological feasibility), (3) the probable trajectories of future stresses such as rising sea levels and changing climate, and (4) the ecological value and services likely to be produced by each of these future states. We suggest that it is not unreasonable to use the historical vegetation types in Saucier (1963) as a target — that is, a compositional goal of 5% of the wetlands as fresh marsh, 5% as intermediate marsh, and 90% as bald cypress – tupelo swamp. A total area somewhat greater than present — ca. 162 000 ha — appears practical given science knowledge and managerial capability. While we have not documented the economic value of all the goods and services produced by these wetlands, the historical data show that these areas of wetland were capable of supporting a wide array of activities and that most of these could probably continue, if practiced in a sustainable manner within a restored wetland landscape. Newer activities such as ecotourism could also be accommodated and expanded.

Priority actions for restoration

The wetlands we have described are driven by two primary processes. Both processes occur as pulses — short term, high impact events. The land building activities that maintain and restore freshwater wetlands are caused by flooding, primarily, but not exclusively, from the Mississippi River. The overall importance of such pulse events in rivers is well understood (Keddy 2000; Middleton 2002; Shaffer et al. 2005), although the impacts of pulses from hurricanes is less well understood (Michener et al. 1997, Boesch et al. 2006; Turner et al. 2006). As Fig. 2 illustrated, these flood pulses from rivers build freshwater wetlands in deltas, but these freshwater wetlands deteriorate over time as sea water returns (Boyd and Penland 1988; Coleman et al. 1998). This salt water often arrives in pulses associated with storms (Fig. 12), although the slower processes of subsidence and erosion also are responsible for loss of wetland area. Under natural conditions, the balance between these two sets of forces determines the relative amount of open salt water as opposed to fresh water wetlands. The future state of this system will therefore depend upon the dynamic equilibrium attained between these two opposing sets of pulses. There will not be a single stable state in future, but rather a dynamic equilibrium around a mean, with the deviations from that mean depending upon the magnitude and direction of the most recent pulses.

Humans have shifted this dynamic equilibrium by amplifying the pulses that enable salt-water intrusion events (e.g., construction of the Mississippi River Gulf Outlet), and all but terminating the pulses carrying sediment and fresh water into this system (e.g., construction of levees along the Mississippi River). The science of this situation is well understood, even down to the precise salinity levels that interfere with tree photosynthesis (Pezeshki 1990). Although the salinity levels that cause transitions from one vegetation type to another are less exactly determined (Visser et al. 2004), the direction of the change is equally clear. Priority actions must focus upon redressing this imbalance. That is, we need to increase the frequency and magnitude of fresh water pulses, and reduce the frequency and magnitude of salt-water pulses. We simultaneously need to avoid activities that will interfere with our ability to carry out these tasks — allowing new construction in wetlands, for example, will create more opposition to flood pulses. We propose seven actions. The first is the overriding factor, while the remaining six are refinements.

(1) More and larger fresh water pulses. The levees along the Mississippi River are incompatible with the long-term survival of deltaic wetlands. These levees interfere with water flow from as far upstream as the Bayou Manchac area (due south of Baton Rouge and not to be confused with the Pass Manchac within our mapped area). These pulses must be restored. In the short run, there are plans for a small diversion at the Hope Canal area which would add water and nutrients to the southern Maurepas area (Shaffer et al. 2003, 2005). The Bonne Carré spillway just west of New Orleans also provides a possible route for fresh water pulses. It leaks some 8000 cfs (1 $ft^3/s \approx 0.0283\ m^3/s$) during flood stage of the Mississippi, and could be routed up the I-55 Canal to spread across the Maurepas Swamp (Day et al. 2006). Its location near New Orleans makes it less than desirable, since it also is possible that the fresh water and sediment would directly enter Lake Pontchartrain rather than the wetlands to the west. In the immediate term, only the Bonne Carré is a viable option for adding fresh water. In the short term, the Hope Canal may provide some amelioration for southern regions of the swamp. In the long run, we must divert more fresh water into the swamps in sufficient volume to carry sediment and nutrients at least as far as the Manchac land bridge. Further diversions upstream as far as Bayou Manchac will be required. These events occurred historically (Thomson 2000), and they are urgently needed now. We strongly recommend at least two more large freshwater diversions into this area, with volumes capable of replicating the original flood levels that built these wetlands (candidate sites, and possible flows, are discussed in LPBF 2005).

(2) Re-establishment of sheet flow. Once water enters the system carrying sediment and nutrients, it must be able to flow through the entire system. Shallow flow over the surface of the soil, called sheet flow, was almost certainly a principle way in which water and nutrients moved through this system. Now, however, even if floods occur, canals and road and rail beds interfere with water movement. Canals decrease overbank flooding accelerate the flow of water and nutrients out of the area, while spoil banks and road and rail beds block sheet flow. Existing canals therefore need to be plugged and their levees need to be gapped every 500 m, while existing road and rail beds need to be removed, or at least breached with many large openings. It is important to re-establish such sheet flow across the entire Manchac land bridge — floods that simply flow out Pass Manchac into Lake Pontchartrain will continue to starve most of the Manchac land bridge of sediment and nutrients, and continue the ongoing conversion of swamp to marsh and open water. In contrast, the elevated Interstate 55 (contiguous to the land bridge from LaPlace to Ponchatoula) illustrates a more compatible transportation corridor. The old construction canal and spoil banks from I-55 likely also interfere with sheet flow; although there are large culverts. Newer methods of end-on construction are less damaging. In contrast, the road bed of old Highway 51 and the parallel rail line illustrate the scale of the obstacles that have been created; although these have culverts, many are now plugged and need maintenance.

(3) Limit salt-water intrusion. Salt-water intrusion from storms (e.g., Figs. 10, 12) remains a significant negative factor. The damaging effects of the Mississippi River Gulf Outlet continue to be documented, most recently with the flooding of New Orleans (Houck 2006). The Mississippi River Gulf Outlet needs to be closed, or at least reduced greatly in size with engineering additions to reduce salt water flow inland.

(4) Terminate land development within wetlands. The construction of camps, homes, and commercial enterprises in these wetlands is largely incompatible with the forgoing processes. First, flood pulses for restoration may place these structures at risk. Second, even if the structures are built on pilings capable of withstanding the flood pulses, previous experience has shown that land owners are frequently unwilling to tolerate flooding. As described above, through much of its history, the massive Caernarvon project has been run at a fraction of its flow capacity, and without large spring pulses, because of objections from landowners. Given strong landowner rights, there seems to be little prospect of convincing landowners to allow their land to be flooded in the public good. Therefore, if the Pontchartrain and Maurepas wetlands are to be managed appropriately, no further creation of obstacles to management can be tolerated. Every new subdivision, and every new camp, is an impediment to management and conservation.

(5) Acquire land for the public trust. In view of the foregoing problems, land acquisition is essential. Easements may provide a partial solution, but even when they are signed, management is constrained by elements not anticipated in the easements. Landowners may assert other rights, and each new right must be purchased. Even in the best case, easements can create long lag times in response to management problems, since each landowner must be contacted, negotiations must proceed, and single landowners can refuse the needed management. Hence, it is imperative that most of these lands be eventually placed in the public trust. Figure 4*b* and Table 8 summarize the public areas that now exist. At the same time, each of these is surrounded by privately owned land, which constrains the management of the public land. Large tracts remain from former logging leases may provide an opportunity for rapidly expanding land additions.

(6) Terminate logging in coastal swamps. In spite of the enormous pressure upon these swamp forests, including cumulative impacts of past logging, salt-water intrusion,

and nutrient starvation, private land in this area is still being logged, particularly for cypress. Given the history of degradation caused by logging, the sensitivity of many of these areas to disturbance by logging, and the evidence that significant areas of these forests are already converting to shrub scrub, marsh and open water we believe that no further logging should be permissible within the wetlands of this area. This restriction could be revisited once restoration measures are established to ensure sustainability. In theory, the U.S. Army Corps of Engineers can restrict logging near waterways, but in 2005, when a U.S. Senate committee drafted the Water Resources Development Act of 2005 to give Louisiana funding for coastal restoration, a provision, without public notice or discussion, was added by Senator David Vitter to remove these powers from the Corps. This action was strongly supported by the Louisiana Forestry Association because it would allow more logging in swamps (Schleifstein 2005). The Louisiana House voted 92-6 in support of this provision; on 25 May 2005 the Louisiana Senate approved the provision unanimously (Capitol News Bureau 2005). A recent 121 page report to the governor with 12 authors and 4 special contributors (Chambers et al. 2005) has concluded that there are three regeneration classes for cypress: class I (sites with potential for natural regeneration), class II (sites with potential for artificial regeneration only), and class III (no potential for either natural or artificial regeneration). After several years of activity, the report recommends (p. ix) "Place an interim moratorium on harvesting on state-owned Condition Class III lands. Develop mechanisms to delay timber harvesting on privately owned Condition Class III lands". We urge the Louisiana legislature to implement these recommendations. Still, given a hundred years of experience with the negative effects of logging, and decades of scientific study of wetland loss, these recommendations are surely insufficient.

(7) Create a special planning zone. The lack of regional planning exacerbates pressures upon these wetlands. Subdivisions continue to be developed in flood prone areas, logging upstream alters fresh water flow down rivers draining into the swamp, and overall, there is little consideration of the degree to which activities on adjoining uplands might impact the wetlands. We therefore recommend that a special planning zone be designated, extending, perhaps ten miles from the wetland boundary. Within this zone, added restrictions would be placed upon land use to prevent incompatible development from further interfering with conservation of the Lake Pontchartrain and Maurepas wetlands.

In conclusion, we have shown that the science of this area is comparatively well-understood. There is now a need for action; we have recommended management strategies. Lacking such action, the conversion of swamp to open water can be expected to continue or even accelerate, and the Lake Pontchartrain – Maurepas area will likely become an embayment open to the Gulf of Mexico. The potential loss of fresh water fisheries and recreation opportunities, and the consequent flood threats to New Orleans, would argue strongly against allowing this scenario to unfold. To restore this wetland to its original composition and productivity, and to support the local economy and offer new opportunities for ecotourism, the preceding seven steps need to be implemented without delay.

Table 8. Protected wetlands within the Pontchartrain–Maurepas area.

Protected wetland	Area (ha)
Maurepas Swamp Wildlife Management Area	25 293
Bayou Sauvage National Wildlife Refuge	9308
Big Branch National Wildlife Refuge	6917
Joyce Wildlife Management Area	6511
Manchac Wildlife Management Area	3369
Fontainebleau State Park	1133
Total	52 531

Acknowledgments

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