(Hand and Jackman 1982, 1984). Below this point, macroinvertebrates have been reduced to fewer than ten pollution-tolerant species. The Milton plant is being extensively upgraded, which is expected to improve the area water quality. Fish and macroinvertebrate populations in the remainder of the river are considered exceptionally healthy (Bass 1983) despite agricultural runoff and several point-source effluent dischargers.

Biological water-quality stations in the basin were sampled during 1973–78 (Ross and Jones 1979). A station in Big Coldwater Creek had a high Biotic Index from qualitative sampling, indicating no significant organic pollution. A station in the upper Blackwater River near SR 4 exhibited high macroinvertebrate diversities for two types of quantitative sampling and a high Biotic Index for qualitative samples. Occasionally high total and fecal coliform counts were attributed to pasture and other agricultural runoff. These numbers sometimes exceeded Class III (i.e.,recreation, propagation and maintenance of a healthy , well-balanced population of fish and wildlife) water quality standards. A station at the mouth of the river in East Bay had a moderate species diversity and a low number of species per sample, which was attributed to the estuarine conditions. The occurrence of frequently high total coliform bacteria counts were attributed to the Milton sewage treatment plant upriver and to area runoff.

The USGS is monitoring a waste injection well near Milton for potential ground-water contamination (Pascale and Martin 1977).

4.7.10 Escambia River Basin (Figure 56)

The Escambia River drains 10,960 km² of which approximately 10% (1,080 km²) is in Florida and 90% (9,880 km²) is in Alabama. The river is formed by the confluence of Escambia Creek and Conecuh River at the Florida border. The basin has a limestone base with poorly drained organic surface soils near the coast, such that the river flows through a generally low, swampy area with many sloughs and backwaters from Molino, Florida, to Escambia Bay (Hand and Jackman 1984). These conditions change to well-drained sandy soils in the northern portions of the drainage. Despite these well-drained soils, topographic relief is sufficient to render this area susceptible to erosion (FDER 1986c).

The basin is lightly populated with only two cities, Cantonment and Century, having populations greater than 5,000. Most of the basin is forested and, together with some agriculture, this constitutes the major land use. There are approximately 260 km² of floodplain crop and pasture land. Flood peaks occur primarily in April and May, with high river stages also common in December. It is recommended that crops be planted and construction take place at least 7 m above the mean river stage to minimize flood damage (USACE 1980b).

Historic baseline water quality data for the Escambia River includes a study by Patrick (1953). Thirteen point-source dischargers have State or Federal permits to discharge into this basin. Five sewage treatment plants and five industrial sources (primarily paper and chemical companies) discharge into the basin in Alabama including the Container Corporation of America—Brewton Mill (U.S. EPA 1971a). In Florida, Monsanto Chemical discharges inorganic effluents into the Escambia River, and two small towns near the Alabama-Florida border, Jay and Century, discharge effluent from sewage treatment plants. The Escambia River has a history of water quality problems (U.S. Dept. of the Interior 1970b). U.S. EPA water-quality index values for DO, color, and bacteria downstream of Alabama point sources in the past have been fair to poor (Hand and Jackman 1984).

Recent samplings show that bacterial standards for Florida Class III waters (i.e., recreation, propagation and maintenance of a healthy, well-balanced population of fish and wildlife) are not being met in the Escambia River near the Alabama border (Hand and Jackman 1984). Fish communities are recovering from past degradation; however, they remain less healthy than expected (Bass 1983). Fishery investigations by the Florida Game and Fresh Water Fish Commission suggested that the river was in an intermediate stage of recovery from the past pollution (Bass and Hitt 1978, Bass 1983). Effluent from the sewage treatment plant for the Florida town of Century causes bacterial violations downstream in the Escambia River. The recent reduction in monitoring activity has made it impossible to distinguish between river impacts originating in Alabama and in Florida. At the lower end of the Escambia River at the mouth of Governors Bayou three of five DO measurements taken during 1981–83 were below 3 mg/l (Hand and Jackman 1984).

Canoe Creek, a tributary of the Escambia River, has experienced some water quality problems from nonpoint source runoff (FDER 1978). The 1978 study noted increasing bacterial levels, decreasing pH, and relatively high nitrate concentrations from 1975 to 1978. Only one point source discharges to the stream, Bluff Springs Campground sewage treatment plant. FDER concluded that this source was not responsible for the problems and tentatively attributed the low pH to substantial input of the unbuffered water of the Sand and Gravel Aquifer and the bacteria and nitrate levels to pasture and woodland runoff. The creek demonstrated bacterial violations in 1983, attributed by the FDER district office to dairy and other agricultural stormwater runoff. In addition, siltation and turbidity remain problems in Canoe Creek, especially after rainfall.

In the central part of this basin, near the town of Jay, the University of Florida operates an IFAS (Institute of Food and Agricultural Sciences) agricultural research center. The FDER investigated the site in 1984 following complaints that the pesticides and herbicides tested at the center were being improperly disposed of (Busen et al. 1985). Three separate sampling trips confirmed pesticides at high levels as deep as 4.5–6 m in the soil at the pesticide mix-wash area, in the drainage ditch, and in the field to which the runoff was diverted. Leftover pesticides and wash water were dumped into the drainage ditch, which flowed to gravel-filled pits built to increase percolation. An on-site dump in which pesticide containers containing chemicals were found also showed soil contamination from pesticides. No ground-water contamination, however, was detected. The deep water table and numerous clay layers in the soil limit the potential for pesticide migration into the ground water. This incident raised concerns about the other 22 IFAS centers where similar disposal methods and the normal sandy soils of the State might pose a hazard to area ground water.

Macroinvertebrate diversity was monitored at three stations in the Escambia River from 1973 to 1978 (Ross and Jones 1979). These data suggested that the river was recovering from the massive pollution present during the 1950's and 1960's (FDER 1986c). The station in the river near the Alabama border showed significant improvement during the study period. Diversity indices and the Biotic Index indicated a fairly healthy, stable macroinvertebrate community. However, the combination of very high total coliform bacteria populations and low fecal coliform populations suggested a marked impact from a large paper mill upstream. A second station at Upper Bluffs, approximately 18 km upriver from the river's mouth had high macroinvertebrate diversities, high Biotic Index values, and also showed a significant trend of improvement. Occasionally high bacteria counts were attributed to runoff. The salt wedge from Escambia Bay reaches this station during low flow conditions and estuarine forms are found here. The third river station was at the mouth at US 90. It was tentatively concluded that the estuarine conditions found there, combined with thermal effluents, oil and grease spills, and PCB-containing sediments, may have lowered macroinvertebrate diversities. Occasional high coliform counts were apparently caused by runoff.

4.7.11 Escambia Bay and Coastal Area (Figure 56)

The Escambia Bay coastal area (including Pensacola, Escambia, East, and Blackwater Bays and Santa Rosa Sound) drains approximately 1,410 km². The bay system receives flow from a watershed including the Yellow, Blackwater, and Escambia Rivers and totalling some 18,130 km², of which 6,525 km² (36%) is located in Florida and 11,605 km² (64%) in Alabama. Major inflows to the bay system are from the Escambia River (185 m³/s) and the Blackwater River (11 m³/s). The bay is relatively shallow, ranging from less than 1 m to 6 m deep and averaging 2.5 m at mean low water (U.S. EPA 1971a). Water depth increases from the northern end southward. Ellis (1969) described some of the basic dynamics of the estuary and labeled it a low energy estuary.

Escambia Bay was studied during a period of low river flow in 1969 (U.S. Dept. of the Interior 1970a) with a follow up during high river flow in 1970 (U.S. EPA 1971b). These studies found that Escambia Bay sediments are highly organic and that tidal circulation in upper Escambia Bay is poor. Therefore, disturbing the sediments (e.g., dredging) can cause severe oxygen depletion and massive fish kills. These studies reported unconsolidated bottom sediments ranging from approximately 0.5 m to greater than 2 m, with about one-third of the bay covered to a depth greater than 2 m. Circulation in the bay is generally clockwise during high and low river stages. Water flows out the west side of the bay and saline water flows into the east side. During low flow periods the small creeks in the extreme northern end of the bay do not discharge sufficient water to flush the area, and pollutants are effectively trapped. The studies further determined that the pilings (most of which were unused and unnecessary) of the railroad bridge across the middle of the bay restricted circulation between the upper and lower bay. An investigation of bottom benthos (U.S. EPA 1971b) suggested that wastes discharged along the eastern shore from American Cyanamid and Escambia Chemical companies were generally swept northwestward and deposited along with wastes from Monsanto and Container Corporation in the central and western portions of the upper and lower bay.

An enforcement conference in the late 1960's (U.S. Dept. of the Interior 1970b) led to bay recovery studies by U.S. EPA during 1972–73. These studies resulted in more stringent controls on municipal and industrial discharges. In 1975, following a study of the area's capability to deal with the pollutant loads it was generating (Henningson, Durham & Richardson, Inc. 1975, Olinger et al. 1975), it was concluded by the West Florida Regional Planning Council that (1) there should be no additional nutrient loads discharged to Pensacola Bay, and (2) all domestic sewage discharges should be removed from: Perdido Bay, Big Lagoon, Escambia Bay, East Bay, Blackwater Bay, and Santa Rosa Sound. Hand and Jackman (1984) report that most of the bay system has good water quality; however, several of the bayou areas which receive treated sewage, industrial wastes, and urban runoff exhibit significant water quality problems.

Bayou Chico drains part of the Pensacola urban area, receives treated industrial waste and treated sewage from Warrington Sewage Treatment Plant via Jones Creek and until recently from Pen Haven Sewage Treatment Plant via Jackson Creek, and has bacteria and nutrient problems (Hand and Jackman 1984). The Pen Haven plant has been closed and its waste load diverted to the Main Street Plant. As a result Jackson Creek is improving.

Bayou Texar drains the center of Pensacola and, though there are no permitted point sources in its drainage, has shown bacteria and low DO problems. This bayou is on the western side of Escambia Bay and the only stream flowing into it is Carpenter Creek. The creek and bayou are over 13 km long but the bayou varies in width from about 30 m to a maximum of about 425 m (NWFWMD 1978b). The creek is intermittent in some sections and apparently receives little base flow, depending on runoff to maintain flow. Bayou Texar undergoes wide fluctuations in depth depending on local weather conditions, experiencing "flooding" caused by water pile-up as well as exposure of large expanses of bottom when water is blown away. In 1974 a restoration study was prepared for the State (Henningson, Durham & Richardson 1974). This study concluded that the major cause of water quality degradation was sediment deposits on the bottom resulting from uncontrolled development in the basin. Further studies ensued to determine the nature and extent of siltation in the bayou and the effect of the siltation on local hydrology (NWFWMD 1978b). This study detailed changes in the bayou since 1893 and described erosion problems of surrounding lands and subsequent transport of the eroded sediments through the bayou. Hand and Jackman (1984) report no recent (since 1981) data on this area. Water quality problems exist in the northern part of Escambia Bay with reduced DO concentrations and bacteria problems around the mouth of the Escambia River. The University of West Florida Sewage Treatment Plant effluent and Monsanto industrial effluents are discharged to the river just upstream of the mouth.

Mulatto Bay, on the east side of Escambia Bay, has had DO, nutrient and bacteria problems but Hand and Jackman (1984) report no data since 1981. Blackwater Bay exhibits water quality problems primarily attributable to nutrients at the Blackwater River mouth. These are attributed to the nutrient loads carried by the river.

Pensacola Bay, particularly the area near Pensacola, was monitored as part of an investigation of the effects of discharges from the Main Street

Wastewater Treatment Plant (McAfee 1984). This study showed the bay to be highly stratified and poorly flushed. They reported improved conditions from studies taking place in the mid-1970's.

The western half of Santa Rosa Sound was studied for its potential for reclassification as a shellfish harvesting water (Florida Department of Health and Rehabilitative Services 1970). The study concluded that, at that time, the western part of the Sound should be reclassified for shellfish harvest since it had excellent water quality, no sources of industrial pollutants, and a watershed little larger than the area of the Sound. Five sewage treatment plants did, however, discharge into the Sound. It was recommended that these be forced to find alternative discharge points outside this area.

Santa Rosa Sound was studied again in 1977–79 (Moshiri et al. 1980). The researchers concluded that the Sound exhibited serious degradation of water quality relative to other local estuarine systems; during warm months red tide outbreaks were possible. Additionally, Little Sabine Bay, on the western end of the gulf side of Santa Rosa Sound, exhibited signs of eutrophication evidenced by high nutrient concentrations, low water transparency, increased algal populations, and low DO. They recommended no further discharges be allowed to Little Sabine Bay.

A biological station sampled in Escambia Bay during 1973–78 showed macroinvertebrate diversities ranging from near zero (very poor) to 3.3 (good) with no trend of improvement evident (Ross and Jones 1979). The apparent instability was attributed to the estuarine environment and stresses from variable industrial discharges into the bay. A similar station in Pensacola Bay was well flushed with marine waters and population and species diversity values suggested a fairly stable macroinvertebrate community. A final station in Santa Rosa Sound at Upper Pritchard Point generally exhibited moderate macroinvertebrate diversities with no significant trend and no notable bacteria problems. This last station is probably more closely associated with Choctawhatchee Bay than with the Escambia Bay system.

The American Creosote Works, Inc. has treated wood at a site in Pensacola for 70 years and discharged effluents into two unlined surface impoundments which are in direct contact with the Sand and Gravel Aquifer, the principal source of water in the area. The USGS chose this site in particular for further study because it is typical of other industrial storage impoundments, the phenols involved are very toxic, and it gave ease of access for sampling (Troutman et al. 1984). They have placed monitoring wells surrounding the site and are sampling the nearby area in Pensacola Bay (Troutman et al. 1984, USGS 1984). Total phenol concentrations in water samples from a test well 30 m south of the impoundment were 36,000 µg/l at a depth of 12 m but less than 10 µg/l at a depth of 27 m (Troutman et al. 1984). Other test wells indicated that contaminated ground water may not be discharging directly into Pensacola Bay. However, phenol concentrations in samples from a drainage ditch discharging directly in Bayou Chico exceeded 20 µg/l.

Deep-well waste injection is used by several of the industries in the Pensacola area. The USGS has been doing substantial investigations of this method, studying movements of the injected wastes (Pascale 1976, Pascale and Martin 1978, Hull and Martin 1982, Merritt in press) and chemical changes in the wastes following injection (Ehrlich et al. 1979, Hull and Martin 1982, Vecchioli et al. in press) to ensure that it will not contaminate area ground water. These programs are ongoing.

The USGS performed an early ground-water investigation near Gulf Breeze in Santa Rosa County, identifying two shallow aquifers separated by a clay confining layer (Heath and Clark 1951). They have also constructed maps showing flooding along the coast during Hurricane Frederick in 1979 (Franklin and Bohman 1980, Franklin and Scott 1980, Scott and Franklin 1980) and published a summary of ground water and surface water data for Pensacola and Escambia County (Coffin 1982).

4.8 Potential Hydrology and Water Quality Problems

4.8.1 Hydrologic Concerns

The frequency and magnitude of floods usually increase as drainage basins are developed. Flooding is a necessary and desirable part of the river basin ecosystem's energy flow; however, their frequency and magnitude can easily exceed levels needed to maintain the ecosystem if improper development takes place. Enforcement of prudent construction practices designed to retain or slow runoff can minimize this increase and its effects on human development. Minimizing vegetation removal (especially trees), prohibiting ditch-and-drain operations as well as dredge-and-fill construction (particularly in wetland areas), and preventing, or tightly controlling, construction and development in river flood plains are all necessary to minimize excessive flooding.

Summer rainfall may be reduced if future development increases the area's albedo (surface reflectivity). It has been proposed that convective rainfall has been reduced by albedo changes from extensive wetland draining in south and east Florida (Gannon 1982). The Panhandle has a lower percentage of wetlands than did these regions originally, yet summer rainfall patterns are similar, with afternoon seabreezes reacting with updrafts from the heated land mass to form thunderheads. The potential for human alterations of Panhandle albedo causing altered rain patterns seems likely; however, programs underway by State and Federal agencies appear to be minimizing those alterations.

A hydrologic change certain to have substantial impact in at least the coastal areas of the Panhandle is the rising sea level. Projections in reports published by the U.S. EPA (Hoffman et al. 1983, 1986) and the National Academy of Sciences (Revell 1983) predict a global sea level rise ranging from as little as 38 cm to as much as 211 cm over the next 100 years. The most recent estimates (Hoffman et al. 1986) predict a global rise of between 57 and 368 cm by 2100. This rise, coupled with coastal subsidence in the Panhandle from tectonic activity totalling approximately 13 cm would result in a net sea level increase along the Panhandle coast of from 70 to 381 cm (roughly 2.3 to 12.5 ft). This compares to a net increase over the last century of approximately 10–15 cm (Gornitz et al. 1982, Barnett 1983). The rate of rise increases with time; the 25-year estimates and cumulative totals through the year 2100 are given in Table 5 and Figure 57.

Impacts from sea level rise will be manifold but can be placed in three broad categories: shoreline retreat, temporary flooding, and salt intrusion. Besides inundating lowlying coastal areas, coastal erosion will progress inland a great distance. Statewide, average horizontal encroachment by the oceans in the next 100 years is expected to be approximately 100 times the vertical rise (i.e., 51–224 m) (Bruun 1962). The actual encroachment experienced will be strongly dependent on the local terrain. This high ratio is an effect explained by the Bruun Rule. Briefly, this rule states that beach erosion occurs to provide sediments to the shore bottom so that the shore bottom can be elevated in proportion to the rise in sea level. Thus sufficient beach will erode to provide the same shore bottom-beach slope from some distance offshore that was stable prior to the sea level rise (Figure 58).

The current trend of sea level rise may be responsible for serious erosion taking place in many coastal resorts (New Jersey Department of Environmental Protection 1981, Pilkey et al. 1981). Most of the Panhandle can probably expect a ratio lower than the Florida average since maintaining the relatively steep nearshore slope of the mostly high energy coastline will result in somewhat less lateral encroachment. However, the barrier islands along much of the Panhandle will be strongly affected, migrating landward where possible and experiencing heavy erosion on the seaward faces.

Table 5. Scenarios of future sea-level rise (in cm) (Hoffman et al. 1986).

Scenario	2000	2025	2050	2075	2100
High	5.5	21	55	191	368
Low	3.5	10	20	36	57

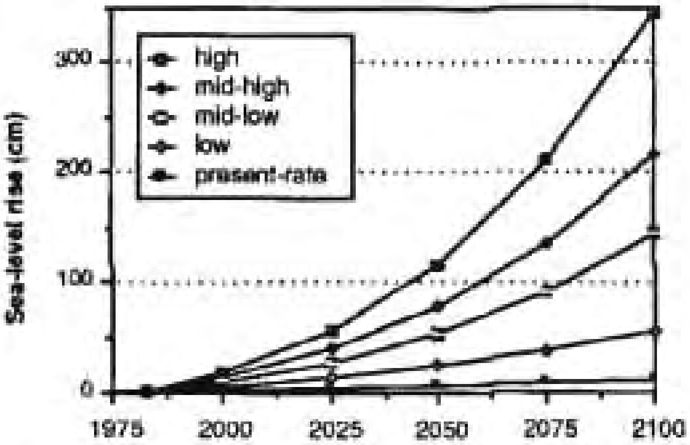

Figure 57. Projected sea-level rise using different scenarios (data from Hoffman et al. 1983).

The increased depth of the water near shore in those areas where artificial or natural structures prevent sediment erosion from the beach, according to the Bruun Rule, will allow more energetic waves to strike the coastline. Areas suffering temporary flooding will increase behind these structures since storms, including hurricanes, will result in higher "storm surge" levels. Many present coastal developments and cities will be much more vulnerable to storm damage. Impact scenarios have been developed for Galveston, Texas, and Charleston, South Carolina (Barth and Titus 1984). These models indicate that substantial damage will occur in these two cities, but that the extent can be ameliorated and substantial losses prevented by taking anticipatory actions.

Although buildings are frequently designed assuming a 30 year life, the patterns of development resulting from construction of roads and certain key commercial property (e.g., factories, utilities, airports) may determine patterns of development for centuries. Consideration of the changing sea level should be made a part of planning and permitting, particularly for these key structures. Barrier island development is probably foolish in nearly all instances.

The rising sea level will, by increasing the hydraulic pressure of the saltwater, increase saltwater intrusion into the aquifers in coastal areas. The potentiometric pressures in the aquifers along the coast suggest that the saltwater intrusion will be felt along the entire Panhandle near-coastal area and will have the greatest effect in those areas where the aquifer potentiometric pressures have already been reduced to levels near or below sea level (Figure 52). Southern Okaloosa county is presently the most extreme case of ground water over-pumping in the Panhandle.

Areas in the Panhandle most affected by sea-level rise may be the barrier islands, coastal wetlands, and those coastal areas with present elevations less than a few meters above sea level. The wetlands will tend to migrate inland except where development prevents it.

4.8.2 Water Quality Concerns

a. Surface water. The further reduction of point-source, surface-water pollutants from Panhandle

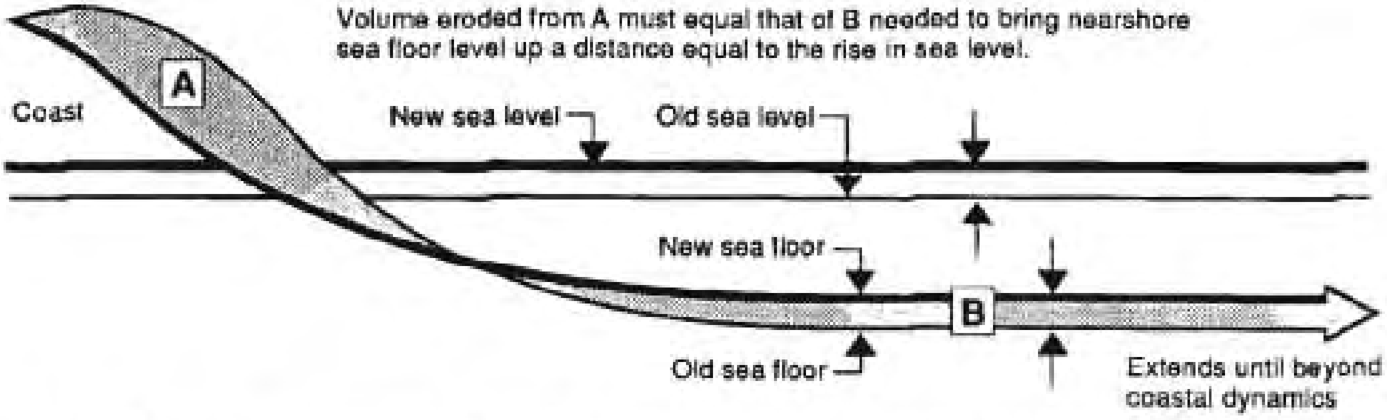

Figure 58. Diagram showing Bruun Rule for beach erosion following increase in sea level.

sources through State and Federal efforts looks promising; however, the water quality of Panhandle rivers is presently most affected by out-of-state pollution. Any improvements in this problem will result from either improvement in the regulatory programs of Alabama and Georgia or efforts by Federal authorities. The State of Florida has been carrying on negotiations with these States for several years in an efforts to encourage their help.

The outlook for control of nonpoint-source pollutants is not as promising. Nonpoint-source pollution is generally the result of rainfall runoff carrying dilute amounts of polluting agents such as petroleum products and nutrients. Since runoff almost invariably increases with development, nonpoint-source pollution also increases with development. The problems with nonpoint-source pollution have less to do with the concentration of the pollutants in the runoff than with the total pollutant load that is carried to our waters each year by the enormous volume of rainfall that runs off the Panhandle. The impacts of this type of pollution tend to be less noticeable than those of point sources because they lack the localized nature of the sometimes massive effects which bring a point-source site to the attention of the public. The nonpoint-source pollutants are nevertheless important and their area of effect often widespread. Detecting and preventing their proliferation will require that regulating agencies establish baseline and monitoring biological and chemical studies in area waters and that future development be planned and controlled to minimize creation of nonpoint-source pollution.

Acid rain is potentially damaging to the surface waters of parts of the Panhandle. Studies are presently underway to determine the sources, amounts, and effects of acid rain (Environmental Science and Engineering, Inc. 1982a, 1982b, 1984; FDER and Florida Public Service Commission 1984; FDER 1985b). Preliminary findings suggest that acid rain results from sulfate emissions by powerplants and other industry, that it tends to be concentrated over land by the sea-breeze/land-breeze phenomenon, and that it develops most strongly during the summer when it is transported northward by the prevailing winds. The already acidic and unbuffered streams and lakes formed by swamp drainage are probably the most likely surface water bodies to be affected. The Panhandle seems to be receiving rainfall that is more acidic than the rest of the State receives except for the area immediately to the east.

Metal-containing sediments are a possible source of water quality problems. Some anaerobic sediments have been identified as potential sources of heavy metal pollution. When iron and sulfur are present in anaerobic sediments (they are especially common in marine sediments) pyrite is formed. When disturbed and exposed to aerobic conditions (e.g., dredging and disposal of resulting spoil), the pyrites rapidly oxidize, forming sulfuric acid. Interstitial porewater pH's as low as 2–3 occur and these conditions can release substantial quantities of any metals bound in the sediments into surrounding waters. This problem has been identified in European harbors (harbor sediments commonly have substantial metal loads [FDER 1986b]) and its potential is being investigated in the Mississippi delta. Possible Panhandle sites where this could be a problem include Pensacola Bay, Apalachicola Bay, and the Dead Lakes along the Apalachicola River.

b. Ground water. The single greatest concern for ground water is contamination from landfills. Panhandle ground-water supplies are very easily contaminated by toxic substances percolating from the surface through the porous ground. With growth comes the necessity of disposing of increasing amounts of waste. Many old landfills were established without regard to their potential for ground-water contamination. These must be located and, where necessary, closed and their contents disposed of safely. New landfills and other forms of surface disposal must be established and managed to prevent contamination of ground water.

The intrusion of saline ground water into the potable aquifers is the second greatest future problem. The increasing consumption of ground-water supplies by a growing population will cause this to be increasingly common. Historically in south Florida, this type of water problem was addressed by local governments with temporary improvements which were not cures and which often simply increased the size of the area of saline contamination. Comprehensive plans have not been instituted until the situation bordered on collapse. In the western Panhandle a water distribution system to prevent this nearly irreversible contamination needs to be instituted before the intrusion increases.

Degraded water quality may occur in Panhandle areas where ground water is pumped for irrigation. The water in excess of plant needs percolates back through the ground to the shallow aquifer from which it was pumped, carrying residual concentrations of the fertilizers used on the crops. It is pumped and used repeatedly and the fertilizer residuals tend to increase in the aquifer. The constant percolation increases the porosity of the ground, minimizing the time before more irrigation is necessary and therefore speeding the cycle. As a result of this process, places in west-central Florida south of Weeki Wachee are unfit for farming. Care must be taken in areas where this recycling might occur to limit irrigation to levels necessary for good crop growth, thereby minimizing the amount percolating back to the underlying ground water.

The direct forms of waste water disposal to the aquifers (e.g., drainage wells and injection wells) which are being used must be investigated carefully and instituted with great caution. The opportunity for large scale pollution of ground water with these methods is very real.

The problems of the future stem largely from the need to balance the pressure for "progress" against the maintenance of those factors necessary to support that progress. Given the near inevitability of the growth, it is sensible to pay extra attention to maintaining the ecosystem.

Chapter 5. TERRESTRIAL HABITATS

5.1 Introduction

Animals and plants are directly affected by the physical nature of the environment. All of Florida's habitats can be ordinated along one or more physical gradients. Among the most important are (1) slope, (2) soil moisture, (3) soil particle size, (4) soil pH, (5) fire frequency, (6) stream order (e.g., Strahler 1964), (7) temperature, (8) light intensity, (9) duration of inundation, and (10) humidity. Each physical factor varies in intensity or quality, often determining the presence, absence, or numbers of individuals in a species population. Groups of species can be found together in a community or habitat more or less predictably over a geographic region, wherever the same physical aspects of the environment occur.

The plant communities that develop in response to background physical and chemical conditions are integrating links between the watershed as a physical unit and the watershed as a habitat for fish and wildlife. Plants and animals possess a wide variety of adaptive mechanisms to reduce competition with one another and for responding to changes in their local environment. They may in turn induce changes in their surroundings that shift the competitive balance in their favor and lead to the succession of one community into another. In plants, such changes include the production of flammable plant parts to promote the probability of fire (Mutch 1970), the production of secondary plant compounds that inhibit the growth of other plant species (allelopathy), local control of microclimate, local erosion control, the alteration of topographic patterns, and the accumulation and recycling of organic matter, as well as many others. In animals, such changes include altering the environment by their behavior such as territoriality, grazing, burrowing, or excavating holes in trees. The outcome of all these interactions is that biotic communities are dynamic rather than static systems.

The watersheds of Panhandle Florida, because of their unique geographical position and geological and hydrological history, have a diverse array of habitats supporting a variety of vegetative communities. Bottomland hardwoods predominate in the river floodplains, and pines mixed with a variety of other tree species and shrubs prevail in the uplands. Wetlands dominate the coastal fringe of the bay systems and large parts of the river floodplains. Dune vegetation and salt marshes are common and important habitats of the barrier islands, beaches, and spits that border the coastline. Seagrass meadows and oyster reefs provide habitat diversity to the intertidal and subtidal areas within the bays.

For more than 400 years northern Florida has been explored by naturalists. Some of the reports and writings of the early naturalists (LeMoyne in DeBry 1591, Catesby 1743, Bartram 1791, Williams 1827, Muir 1917) provide numerous descriptions of plant species, but surprisingly few details of habitats and community types. Although considerable surveys and observations have been made on the flora of the region, until recently a general lack of understanding of the delineation of plant communities and of the factors that control their structure, distribution, and successional relationships has prevailed. According to Clewell (1971), the reasons for this lack of understanding include (1) the general complexity and diversity of Panhandle flora; (2) the subtle patterns of vegetation associations and the dramatic shifts that occur with little obvious change in physiochemical conditions; (3) the lack of information on the effects of fire and flood on vegetation; and (4) the lack of information on the environmental tolerances and reproductive strategies of many important species.

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For more than 400 years northern Florida has been explored by naturalists. Some of the reports and writings of the early naturalists (LeMoyne in DeBry 1591, Catesby 1743, Bartram 1791, Williams 1827, Muir 1917) provide numerous descriptions of plant species, but surprisingly few details of habitats and community types. Although considerable surveys and observations have been made on the flora of the region, until recently a general lack of understanding of the delineation of plant communities and of the factors that control their structure, distribution, and successional relationships has prevailed. According to Clewell (1971), the reasons for this lack of understanding include (1) the general complexity and diversity of Panhandle flora; (2) the subtle patterns of vegetation associations and the dramatic shifts that occur with little obvious change in physiochemical conditions; (3) the lack of information on the effects of fire and flood on vegetation; and (4) the lack of information on the environmental tolerances and reproductive strategies of many important species.

Past and present land use also affect distributions. Although sparsely populated and industrialized compared to the rest of Florida, the watersheds of the Panhandle already have experienced severe environmental modifications affecting plant communities and will continue to do so. Among the impacts are forestry, logging, agriculture, and land and waterway development for commerce and urbanization. Nonetheless, knowledge of the factors which affect the processes important for these communities is necessary to predict the future changes that will be induced by human alterations and provide information to employ proper management practices.

The Panhandle is richly endowed with animals and plants. A general map of the distribution of vegetative communities (habitats) discussed is shown in Figure 59. Aquatic organisms, understandably, are limited in their geographic ranges by the continuity, or lack thereof, of the water in which they live. Therefore, all of the larger stream basins of Panhandle Florida have their aquatic endemics. Terrestrial animals and plants are not so limited by drainage divisions as they are by water in the stream courses of the drainage basin. Even so, numerous terrestrial species are restricted by, or at least have ranges terminating in, a specific Panhandle drainage.

Florida's richest region of endemicity is located in the Apalachicola Bluffs and Ravines, but other parts of the Panhandle have their own distinctive identities also. Between the Apalachicola and Ochlockonee Rivers, and between Telogia Creek on the north and the Gulf of Mexico on the south, lies another region of endemicity (Means 1977), and the vicinity of western Eglin Air Force Base seems also to be emerging as an area having narrowly restricted species, including a frog new to science (*Rana okaloosae*), a darter (*Etheostoma okaloosae*), a cyprinid minnow (*Notropis* new species), possibly a desmognathine salamander, the Panhandle lily (*Lilium iridollae*), and others.

Table 6 lists all the known Panhandle endangered, threatened or commercially exploited plants listed by the State of Florida and USFWS (Wood 1986) and the Panhandle counties in which they are found (Ward 1978). Table 7 lists the endangered or threatened animals (Wood 1986).

5.2 Native Habitats

5.2.1 Longleaf Clayhill Uplands

Harper (1906) recognized the biological distinctiveness of the red hill country in the Coastal Plain of Georgia, calling it the Altamaha Grit Region. In Panhandle Florida, this same physiographic region reaches coastward from the Georgia border to its termination at Cody Scarp and is called the Tallahassee Red Hills (Harper 1914), a subdivision of the Northern Highlands (Puri and Vernon 1964). At least half of the terrestrial environments of Panhandle Florida are developed on red clay soils of the Northern Highlands (Figure 59 and Figure 5).

a. Flora. Longleaf pine (*Pinus palustris*) was the principal tree species on upland soils (valley slopes and ridges) of the Coastal Plain in pre-Columbian times. At least 70 million acres (Wahlenberg 1946) were reported to have supported longleaf, or yellow pine. Typically the canopy is sparse or open, allowing direct or weakly filtered sunlight to the forest floor. This condition fosters a species-rich groundcover flora, containing more than 200 species of forbs and grasses per hectare (Clewell 1971, 1978). One grass particularly, pineland three awn, or wiregrass, (*Aristida stricta*) is a groundcover dominant that is always present. Other wiregrasses (*Aristida* spp., *Sporobolus* spp. and bluestems *Andropogon* spp.) are common herbs, and bracken fern (*Pteridium aquilinum*) is always present and often abundant. Forbs include numerous species of composites (*Aster* spp., *Eupatorium* spp., *Solidago* spp., etc.), legumes (*Desmodium* spp., *Lespedeza* spp., *Tephrosia* spp., etc.), and heaths (*Vaccinium* spp., *Gaylussacia* spp.). Woody low shrubs such as the runner oaks (*Quercus pumila* and *Q. minima*), chinquapin, (*Castanea pumila*), and others are common. See Clewell (1978) for a full list of the plants found on three longleaf clayhill habitats near Thomasville, Georgia. On ridges and high slopes in clayhill country where rains have leached clays from the topsoil, the scrub oaks *Quercus laevis, Q. marilandica*, and *Q. incana* are found. These were suppressed by the frequent natural fires of these communities in pre-Columbian times, and occurred

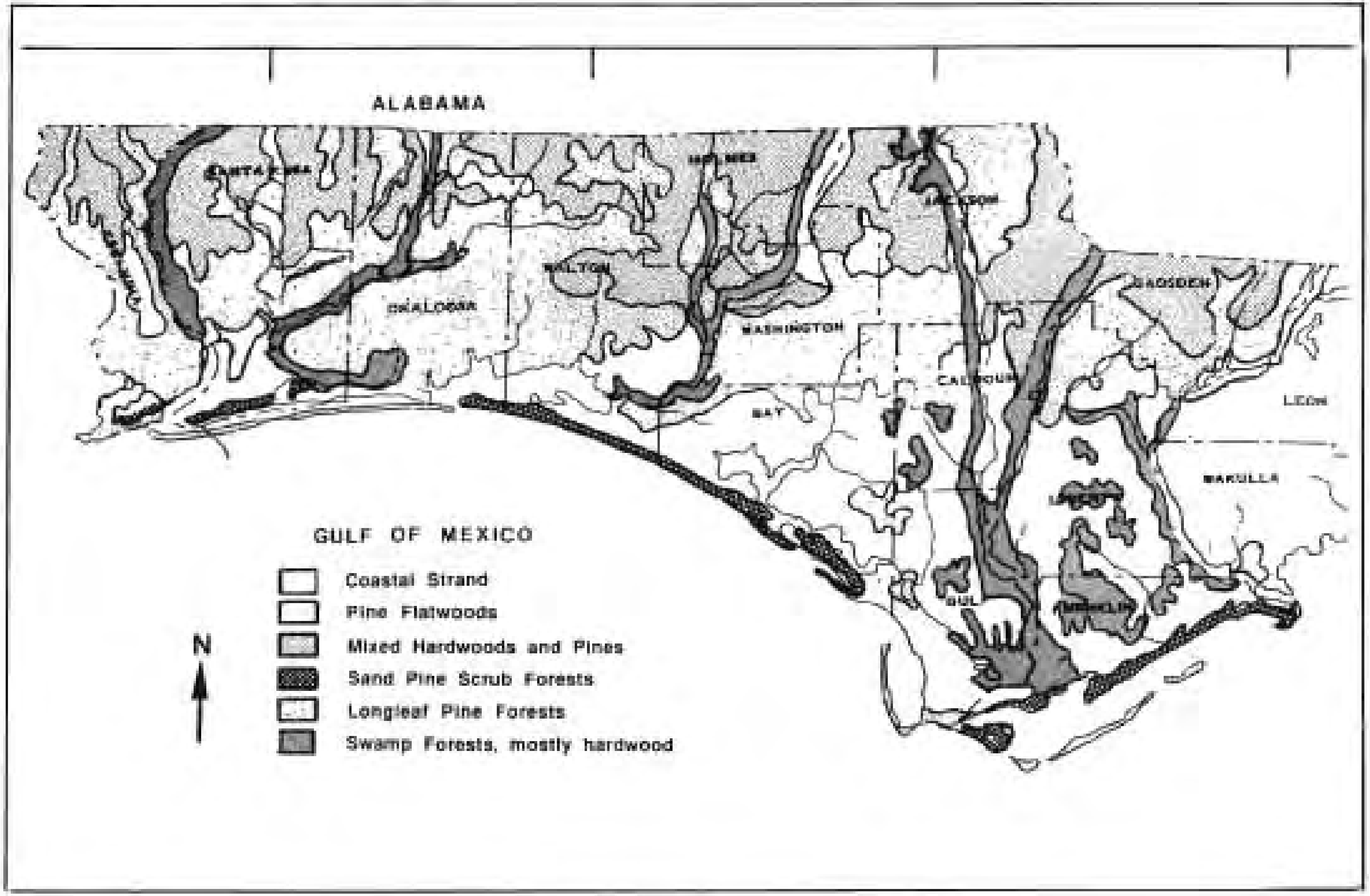

Figure 59. Vegetative communities of the Florida Panhandle (after Davis 1967).

Table 6. Panhandle plants listed as Endangered (E), Threatened (T), Commercially Exploited (C), and Under Review (UR) by the State of Florida (FDA) and USFWS (from Wood 1986) and counties where they are found (from Ward 1978).

			Bay	Calhoun	Escambia	Franklin	Gadsden	Gulf	Holmes	Jackson	Leon	Liberty	Okaloosa	Santa Rosa	Walton	Washington
Actaea pachypoda	T															
Adiantum capillus-veneris	E		•	•		•	•	•		•						•
Aquilegia canadensis	E	UR								•						•
Baptisia hirsuta	T	UR							•				•	•	•	
Baptisia megacarpa	T	UR		•			•		•	•						
Brickellia cordifolia	T	UR								•						
Bumelia lycioides	T			•												
Callirhoe papaver	T															
Cheilanthes microphylla	T															•
Chrysopsis cruiseana	E	UR											•	•		
Conradina glabra	T	UR														
Cornus alternifolia	T			•			•									
Croomia pauciflora	E	UR					•									
Cryptotaenia canadensis	T						•									
Drosera intermodia	T		•	•	•	•		•					•	•	•	•
Epigaea repens	E				•								•	•		
Erythronium umbilicatum	T						•									
Gentiana pennelliana	F	UR	•	•		•	•	•							•	
Harperocallis flava	E	E				•										
Hedeoma graveolens	E	UR	•													
Hepatica nobilis obtusa (=americana)	E						•									
Heterotheca (=Chrysopsis) cruiseana	E	UR			•								•	•	•	
Hexastylis arifolia	T				•		•						•	•	•	•
Hydrangea arborescens	T															
Hypericum lissophloeus	E	UR	•													•
Juncus gymnocarpus		UR													•	
Kalmia latifolia	T			•	•		•		•	•			•	•	•	•
Liatris provincialis	E	UR				•		•								
Leitneria floridana	T	UR				•										
Lilium iridollae	E	UR			•								•	•	•	
Linum westii	T	UR		•		•		•		•						
Litsea aestivalis	T	UR											•			

(continued)

Table 6. Concluded

	FDA	USFWS	Bay	Calhoun	Escambia	Franklin	Gadsden	Gulf	Holmes	Jackson	Leon	Liberty	Okaloosa	Santa Rosa	Walton	Washington
Lupinus westianus	E	UR	•			•		•					•	•	•	
Macbridea alba	E	UR	•			•		•								
Magnolia acuminata	T								•						•	
Magnolia ashei	E	UR					•				•	•	•	•	•	•
Malaxis unifolia	T						•					•				
Matelea alabamensis	E	UR										•				
Medeola virginiana	T						•				•			•		
Melanthium (=Veratrum) woodii	E						•			•						
Nolina atopocarpa	E	UR				•						•				
Oxypolis greenmanii	E	UR	•	•				•								
Pachysandra procumbens	E									•						
Parnassia grandifolia	E					•										
Polygonella macrophylla	T	UR	•		•	•		•					•	•	•	
Polygonum meisnerianum	T										•					
Rhapidophyllum hystrix	C	UR					•			•	•	•			•	
Rhexia salicifolia		UR	•								•				•	•
Rhododendron austrinum	E	UR	•	•	•		•	•	•	•	•	•	•	•	•	•
Rhododendron chapmanii	E	E					•	•				•				
Salix floridana	T	UR								•						
Sarracenia leucophylla	E		•	•	•	•		•	•	•		•	•	•	•	•
Sarracenia rubra	E	UR	•		•								•	•	•	
Schisandra glabra	T	UR					•			•		•				
Staphylea trifolia	T											•				
Stewartia malacodendron	E		•	•	•		•		•	•		•	•	•	•	•
Taxus floridana	E	UR					•					•				
Thalictrum(=Anemonella) thalictroides	T						•									
Torreya taxifolia	E	E					•			•						
Trillium lancifolium	E						•									
Verbesina chapmanii	T	UR	•					•				•				
Viola hastata	E						•									
Xyris longisepala	E	UR	•								•				•	

Table 7. Vertebrate animals of Panhandle Florida whose status is threatened (T), endangered (E), under review (UR), or of special concern (SSC) (after Wood 1986).

		Status	
Scientific name	**Common name**	**State**	**Federal**
Fish			
Acipenser oxyrhynchus desotoi	Atlantic sturgeon	SSC	UR
Ammocrypta asprella	Crystal darter	T	UR
Etheostoma histrio	Harlequin darter	SSC	
Etheostoma okaloosae	Okaloosa darter	E	E
Fundulus jenkinsi	Saltmarsh topminnow	SSC	
Micropterus notius	Suwannee bass	SSC	
Micropterus sp. (undescribed)	Shoal bass	SSC	
Notropis callitaenia	Bluestripe shiner	SSC	UR
Notropis sp. (undescribed)	Blackmouth shiner	E	UR
Amphibians			
Ambystoma cingulatum	Flatwoods salamander		UR
Haideotriton wallacei	Georgia blind salamander		UR
Hyla andersonii	Pine barrens treefrog	SSC	
Rana areolata	Gopher frog	SSC	UR
Rana okaloosae	Bog frog	SSC	UR
Reptiles			
Alligator mississippiensis	American alligator	SSC	T (S/A)[a]
Caretta caretta caretta	Atlantic loggerhead turtle	T	T
Chrysemys (=Pseudemys) concinna suwanniensis	Suwannee cooter	SSC	UR
Dermochelys coriacea	Leatherback turtle	E	E
Drymarchon corais couperi	Eastern indigo snake	T	T
Gopherus polyphemus	Gopher tortoise	SSC	UR
Graptemys barbouri	Barbour's map turtle	SSC	UR
Lepidochelys kempii	Atlantic ridley turtle	E	E
Macroclemys temmincki	Alligator snapping turtle	SSC	UR
Pituophis melanoleucus mugitus	Florida pine snake	SSC	UR
Birds			
Aimophila aestivalis	Bachman's sparrow		UR
Ammodramus maritimus juncicolus	Wakulla seaside sparrow	SSC	UR
Aramus guarauna	Limpkin	SSC	

(continued)

Table 7. Continued

Scientific Name	Common Name	Status	
		State	Federal
Birds (continued)			
Buteo swainsoni	Swainson's hawk		UR
Campephilus principalis	Ivory-billed woodpecker	E	E
Charadrius alexandrinus tenuirostris	Southeastern snowy plover	T	UR
Charadrius melodus	Piping plover	T	T
Cistothorus palustris marianae	Marian's marsh wren	SSC	
Dendroica dominica stoddardi	Stoddard's yellow-throated warbler		UR
Dendroica kirtlandii	Kirtland's warbler	E	E
Egretta caerulea	Little blue heron	SSC	
Egretta thula	Snowy egret	SSC	
Egretta tricolor	Tricolored heron	SSC	
Elanoides forficatus	Swallow-tailed kite		UR
Falco peregrinus tundrius	Arctic peregrine falcon	E	T
Falco sparverius paulus	Southeastern kestrel	T	UR
Grus canadensis pratensis	Florida sandhill crane	T	
Haematopus palliatus	American oystercatcher	SSC	
Haliaeetus leucocephalus	Bald eagle	T	E
Lanius ludovicianus migrans	Migrant loggerhead shrike		UR
Mycteria americana	Wood stork	E	E
Pelecanus occidentalis	Brown pelican	SSC	
Picoides borealis	Red-cockaded woodpecker	T	E
Rostrhamus sociabilis	Snail kite	E	E
Sterna antillarum	Least tern	T	
Vermivora bachmanii	Bachman's warbler	E	E
Mammals			
Felis concolor coryi	Florida panther	E	E
Mustela vison lutensis	Florida mink		UR
Myotis austroriparius	Southeastern bat		UR
Myotis grisescens	Gray bat	E	E
Myotis sodalis	Indiana bat	E	E
Neofiber alleni	Round-tailed muskrat		UR
Peromyscus floridanus	Florida mouse	SSC	UR
Peromyscus polionotus allophrys	Choctawhatchee beach mouse	T	E
Peromyscus polionotus leucocephalus	Santa Rosa beach mouse		UR
Peromyscus polionotus peninsularis	St. Andrews beach mouse		UR
Peromyscus polionotus trissyllepsis	Perdido Bay beach mouse	E	E
Plecotus rafinesquii	Southeastern big-eared bat		UR

(continued)

Table 7. Concluded

Scientific Name	Common Name	Status State	Status Federal
Mammals (continued)			
Tamias striatus	Eastern chipmunk	SSC	
Trichechus manatus latirostris	West Indian manatee	E	E
Ursus americanus floridanus	Florida black bear	T	UR

[a]S/A = similarity of appearance

mostly as woody herbs in the groundcover. At best they were small trees of the understory, probably rarely attaining 30 years of age.

The second-growth forests of this community type today are somewhat different from their presettlement prototypes in several important ways. First, the age-class composition of clayhill longleaf forests is truncated; most stands are less than 60 years old, containing no trees 350–400 years old as is possible for longleaf pine (Wahlenberg 1946). Second, the cycle of summer fires has been halted or, in the case of controlled burning, shifted to winter burns. Alteration of the fire cycle has had a dramatic effect upon the reproduction of many of the species of plants in longleaf communities. Because many plants require fires in summer to stimulate flowering (Parrott 1967, Davis 1985, Means and Grow 1985), the absence of fire or the shifting of fire to the season of plant dormancy has prevented these species from reproducing. Moreover, many of these same species, and others that do not require summer fires for flowering, have vastly diminished recruitment because their seeds require a bare mineral soil on which to germinate. Longleaf pine itself has this requirement; summer burns open the rank groundcover and create bare mineral soil which lies exposed when longleaf seeds normally fall to the ground during fall and winter.

b. Ecology. The life cycle of the longleaf pine is important to the ecology of the clayhills, sandhills, and flatwoods ecosystems it inhabits and will be discussed to provide an understanding of the functioning of these ecosystems. Even though fully grown specimens of most of the species of southern pines can withstand fire, they are killed in the seedling and sapling stage. Longleaf pine alone, is physically adapted to tolerate fire when young. Instead of growing upward right away as most saplings do, longleaf seedlings stay flat on the ground for periods of 3 to 15 years (Croker and Boyer 1975).

During the "grass stage," the young tree grows a long, heavy taproot that probably helps it reach far down into the sandy soil toward moisture; this tap root also serves as a nutrient storage organ. When the young plant finally starts to grow tall, the stored food in the taproot helps it shoot rapidly upward. At the same time that it is racing skyward, the tree delays putting out branches, giving young saplings of this species a distinctive bottlebrush appearance. By growing rapidly upward in a single spurt, the young tree minimizes the amount of time its growing tip is vulnerable to destruction by ground fires. A young tree growing steadily year by year and putting out multiple branches would be vulnerable to ground fires over a far longer period of time. Moreover, longleaf pines have thick, corky bark and dense tufts of needles surrounding its apical buds. These two characteristics insulate the young longleaf pine and are obvious adaptations for resisting heat.

Like many conifers, the seeds of the longleaf require open sunlight and bare mineral soil on which to germinate. Beneath longleaf pines, however, the ground is densely carpeted with wiregrass and many other native grasses and forbs. The only open places readily available to longleaf seeds are very small bare patches of soil created by burrowing animals (e.g., gopher tortoise, *Gopherus polyphemus*; pocket gopher, *Geomys pinetus*) and the tip-up mounds of wind-thrown longleaf trees. More than any other single agent, it is fire that creates the bare mineral soil conditions necessary for the germination of longleaf seeds. In the longleaf pine belt, summertime is the season of natural fires. The pines drop their seeds in the autumn and those seeds germinate when other plants are dormant from October to March, a timing that is adapted to the yearly cycle of the fires.

The periodicity of natural fires depends mainly upon two major factors: (l) number of local lightning ignitions, and (2) the occurrence of broad, sweeping fires. It is obvious that summers with more lightning storms also had more fires. The amount of lightning, however, varies considerably from summer to summer, as meteorological data for the past half century show. About once every decade, summer lightning reaches a peak. During those peak summers, there are enough lightning storms to set enough local fires to burn off most of the longleaf pine sites in the Coastal Plain.

There is good reason to believe that the original longleaf forests typically burned every 2 to 3 years, but sometimes they burned annually and, during periods of low lightning incidence and wet summers, sometimes as seldom as once in 5 years (Clewell 1971, Means and Grow 1985, Christensen, in press).

Lightning is usually attracted to older, larger pines. Older pines are more likely to have heart-rot, a fungal infection that makes the heartwood porous and more flammable, and to have more resins in their heartwood than younger trees. Even when alive, the older trees are more likely than younger trees to be set afire, or to be set smouldering, even during heavy rains. A smouldering tree can ignite a ground fire days later, when the storm is past and the ground is dry again. Dead trees may start groundfires more readily than live ones do. The original longleaf forest not only was able to survive fire, it even depended upon fire, and it may actually have helped start and sustain the fires that regularly burned it (Mutch 1970).

Old-growth trees—living or dead—are exceedingly rare in the Coastal Plain today because almost all of the original timber has been cut. Furthermore, the present generations of longleaf pines are destined to be harvested when their commercial value peaks out at 40–50 years, and there will be very few forests, indeed, that contain old longleaf pines, living or dead.

In the original forests of the Coastal Plain, longleaf communities dominated the uplands and spread downslope from ridgetops all the way to the saturated soils. Longleaf pine forests have been labeled as fire "disclimax" or "subclimax" forest, because, to survive, they need fires to suppress the scrub oaks and other hardwoods that would otherwise take over. Most hardwoods are thin barked and fire tender, and in the original forests, they could only survive in the Coastal Plain in areas that were naturally fire protected, such as valley bottoms and lower down on the moist soils of valley sidewalls.

There still are many places where the pine woods grade naturally into the hardwoods. As one travels downslope from the dry uplands, the first hardwoods one sees are typically shrubby, small-leaved evergreen species. Further downslope, these grade into more substantial hardwood trees at the toe of the valley sidewall and thereafter, the species composition changes according to the hydrology of the stream course.

c. Soils. The soils of the clayhills are developed from the Miocene Miccosukee Formation in the Tallahassee Red Hills subdivision of the Northern Highlands, and from the Citronelle Formation in the Western Highlands. Clayhills soils tend to hold moisture over a long period of time. On ridgetops, rain leaches the clay particles from the top 6 inches of soil, creating slightly more xeric soil conditions for plants and animals. Hilltops are the sites in the clayhills communities of the Tallahassee Red Hills, Grand Ridge, New Hope Ridge, and the Western Red Hills where the best agricultural lands lie, and the lands that have been most impacted by agriculture and development.

d. Trophic dynamics. Although no measures have been found in the literature, the primary productivity in longleaf clayhill associations is probably about equally divided between the overstory and the groundcover. Primary consumers of the longleaf pines are mostly insects, but there is some consumption of young longleaf seedlings and saplings by grazing and browsing vertebrates. Feral hogs are known to be particularly damaging to young longleaf pines by digging and eating the long tap roots. (Wahlenberg 1946).

The high primary productivity and species richness of the plants support a rich consumer community. In addition to leaf-, stem-, and root-consuming insects (i.e., lepidoptera, orthoptera, coleoptera, diptera, hemiptera) and other invertebrates, the many species of flowering forbs attract numerous species of pollinating insects. Because the groundcover plants bring their insect consumers close to the ground surface, insectivores abound there and include predaceous beetles (coleoptera), dragonflies (odonata), bugs (hemiptera), mantises (mantida), and spiders (arachnida). The invertebrates are also the food base for dozens of vertebrate insectivores including lizards, frogs, mammals and birds.

e. Fauna. The following animals are principal species found in open, longleaf pine forests: red-tailed hawk *(Buteo jamaicensis)*, great horned owl (*Bubo virginianus*), fox squirrel (*Sciurus niger*), eastern diamondback rattlesnake (*Crotalus adamanteus*), pine snake (*Pituophis melanoleucus*), gopher tortoise (*Gopherus polyphemus*), Bachman's sparrow (*Aimophila aestivalis*), and bobwhite (*Colinus virginianus*).

In a drift-fence study of the amphibians and reptiles inhabiting a 200-acre tract of old growth longleaf pine in the Tallahassee Red Hills (Means and Campbell 1981), 20 different species were recorded in over 6,000 trap weeks during one 2-year period (Table 8). Engstrom (1982) reported the largest number of breeding birds from any known Florida habitat from the same site (Table 9).

f. Rare and endangered species. Panhandle Florida longleaf clayhill communities support a large number of species that are rare, endangered, threatened, or of special concern. The gopher tortoise, a species of special concern, is found in clayhills from the Perdido to the Ochlockonee drainages, but does not do as well in clayey soils as it does in sandy soils. The gopher tortoise is a keystone species (Eisenberg 1983) whose presence is vital to the existence of other species. The burrows of the gopher tortoise are a haven for dozens of vertebrates and invertebrates, including a few strict obligate commensals that are totally dependent upon the gopher tortoise. More about the interdependencies of the tortoise and its commensals is discussed under sandhills habitat. The federally endangered red-cockaded woodpecker (*Picoides borealis*) once was common in clayhills longleaf forests, but most of the native longleaf forest has been replaced in clayhills habitats by the mixed shortleaf-loblolly pine hardwood community in which the red-cockaded woodpecker does very poorly. Mature longleaf pine forests such as those that originally clothed the clayhills habitats of the Northern Highlands are nearly nonexistent today. Their absence is the principal reason why the red-cockaded woodpecker is endangered. Because so much of the original longleaf pine clayhills communities have been converted into ruderal communities, the native biota of longleaf clayhills has been severely reduced or fragmented.

5.2.2 Longleaf Sandhill Uplands

The term "sandhills" has been applied to this community by a long list of its students (Laessle 1958, Bozeman I971, Campbell and Christman 1982, Means and Campbell 1981, Christensen in press). Other common names that have been applied to this community are high pinelands (Clewell 1971), longleaf pine, and xerophytic oaks (Davis 1967), and dwarf oak forests (Wharton 1977). In Panhandle Florida, sandhills habitats can be roughly classed into two types: (1) the longleaf sandhill uplands in the interior, especially those occurring as a broad band of deep sand deposits below Cody Scarp, including Eglin Air Force Base, Greenhead Slope, Fountain Slope, and Beacon Slope; and (2) sandhills along the coast that are vegetated with coastal scrub vegetation (overstory of either slash pines or sand pine, and understory of coastal scrub oaks). The former are discussed here, the latter in 5.2.7.

a. Soils. The well-drained white-to-yellowish sands usually are 100 cm (40 inches) or more deep above finer textured subsoils. They are relatively sterile, nearly flat to strongly sloping, acidic, moderately to excessively well drained, and coarsely textured. Water moves so rapidly through the soil that shortly after rains and in the interim between

Table 8. Numbers of amphibians and reptiles captured on two annually burned pine stands and an unburned hardwood stand in north Florida (Means and Campbell 1981).

Species	Longleaf pine clayhills[a]	Shortleaf loblolly clayhills[b]	Beech magnolia[c]
Ambystoma opacum	0	3	264
Ambystoma talpoideum	0	0	22
Ambystoma tigrinum	99	13	0
Notophthalmus viridescens	4	0	1
Eurycea bislineata	0	0	1
Eurycea quadridigitata	1	0	0
Plethodon glutinosus	0	3	18
Scaphiopus holbrooki	41	21	24
Bufo quercicus	294	0	0
Bufo terrestris	38	66	28
Acris gryllus	0	0	8
Hyla cinerea	0	0	2
Hyla crucifer	0	0	2
Hyla gratiosa	2	0	0
Hyla chrysocelis	0	0	1
Pseudacris nigrita	3	0	0
Pseudacris ornata	152	0	0
Rana catesbeiana	0	3	2
Rana clamitans	0	1	6
Rana sphenocephala	4	4	9
Gastrophryne carolinensis	39	22	20
Kinosternon subrubrum	3	0	0
Terrapene carolina	3	1	0
Deirochelys reticularia	2	0	0
Anolis carolinensis	0	2	12
Sceloporus undulatus	0	3	0
Cnemidophorus sexlineatus	16	2	4
Eumeces inexpectatus	2	0	0
Eumeces laticeps	7	14	2
Leilopisma laterale	0	0	1
Ophisaurus ventralis	7	0	0
Cemophora coccinea	2	0	0
Coluber constrictor	0	0	2
Elaphe guttata	0	1	0
Elaphe obsoleta	0	0	1
Heterodon platyrhinos	0	1	0
Thamnophis sauritus	2	0	0
Thamnophis sirtalis	0	4	0
Total	**721**	**164**	**430**
Total number species	**20**	**17**	**21**

[a] 64 traps running continously 16 March 1979–6 Feb 1981 = 6,272 trap weeks.

[b] 16 traps running continously (except 11 Apr–24 Sep 1978) 1 Feb 1976–6 Feb 1981 = 2,760 trap weeks.

[c] 3 traps running continously 14 Apr 1976–18 Apr 1978, then 16 traps 12 Oct 1978–6 Feb 1981 = 1,840 trap weeks.

Table 9. Breeding birds of clayhill longleaf old-growth forest (from Engstrom 1982). The number of individuals per trip in Winter Bird Population Study (WBPS-79, 58.3 ha), the number of breeding pairs per tract in Breeding Bird Censuses (BBC-79, 58.3 ha; BBC-80, 20 ha), and residency status.

Species	WBPS-79[a]	BBC-79	BBC-80	Status[b]
Wood duck (*Aix sponsa*)	+	2	2	WB
Bobwhite (*Colinus virginianus*)	-	2.5	2.5	BO
Mourning dove (*Zenaida macroura*)	2	10.5	3	WB
Great horned owl (*Bubo virginianus*)	1	1	-	WB
Common flicker (*Colaptes auratus*)	4	5	1.5	WB
Pileated woodpecker (*Dryocopus pileatus*)	+	1	+	WB
Red-bellied woodpecker (*Melanerpes carolinus*)	8	8.5	3.5	WB
Red-headed woodpecker (*M. erythrocephalus*)	-	13.5	3.5	BO
Yellow-bellied sapsucker (*Sphyrapicus varius*)	3	-	-	W
Red-cockaded woodpecker (*Picoides borealis*)	17	5	1.5	WB
Hairy woodpecker (*Picoides villosus*)	+	1	1	WB
Downy woodpecker (*Picoides pubescens*)	+	1	+	WB
Eastern kingbird (*Tyrannus tyrannus*)	-	3	+	B
Great crested flycatcher (*Myiarchus crinitus*)	-	13	4	B
Eastern wood pewee (*Contopus virens*)	-	8.5	4.5	B
Blue jay (*Cyanocitta cristata*)	2	8	2	WB
Common crow (*Corvus brachyrhynchos*)	-	2	-	WB
Tufted titmouse (*Parus bicolor*)	-	1	-	WB
White-breasted nuthatch (*Sitta carolinensis*)	7	5	2.5	WB
Brown-headed nuthatch (*Sitta pusilla*)	7	7	4.5	WB
House wren (*Troglodytes aedon*)	9	-	-	W
Carolina wren (*Thryothorus ludovicianus*)	4	4	2.5	WB
Northern mockingbird (*Mimus polyglottos*)	-	1	-	BO
Brown thrasher (*Toxostoma rufum*)	-	3	1	BO
American robin (*Turdus americanus*)	8	-	-	W
Eastern bluebird (*Sialia sialis*)	3	3	2	WB
Loggerhead shrike (*Lanius ludovidianus*)	1	1	+	WB
Solitary vireo (*Vireo solitarius*)	2	-	-	W
Yellow-throated vireo (*Vireo flavifrons*)	-	1.5	+	B
Yellow-rumped warbler (*Dendroica coronata*)	2	-	-	W
Pine warbler (*Dendroica pinus*)	11	10	6.5	WB
Palm warbler (*Dendroica palmarum*)	2	-	-	W
Common yellowthroat (*Geothlypis trichas*)	12	14	4.5	WB
Yellow-breasted chat (*Icteria virens*)	-	11.5	2.5	B
Eastern meadowlark (*Sturnella magna*)	5	7.5	3	WB
Red-winged blackbird (*Agelaius phoenicus*)	60	2	-	WB
Common grackle (*Quiscalus quicala*)	-	1	-	BO
Brown-headed cowbird (*Molothrus ater*)	-	5	4	BO
Orchard oriole (*Icterus spurius*)	-	2	1	B

(continued)

Table 9. Concluded

Species	WBPS-79	BBC-79	BBC-80	Status[b]
Summer tanager (*Pirangra rubra*)	-	4	1.5	B
Cardinal (*Cardinalis cardinalis*)	1	4	-	WB
Blue grosbeak (*Guiraca caerulea*)	-	11	3.5	B
American goldfinch (*Carduelis tristis*)	1	-	-	W
Indigo bunting (*Passerina cyanea*)	-	14.5	6.5	B
Rufous-sided towhee (*Pipilo erythrophthalmus*)	16	30	11	WB
Bachman's sparrow (*Aimophila aestivalis*)	-	16.5	8	B
Swamp sparrow (*Melospiza georgiana*)	1	-	-	W
Total species	**25**	**39**	**27**	
Total estimated density	**189**	**245**	**94.5**	

[a] averaged <1

[b] WB = permanent resident, winter and breeding season; BO = permanent resident, breeding season only; W = winter resident only; B = breeding resident only.

rains, the soil is dry and often hot. Only plants adapted for such xeric conditions can survive in sandhills. One botanist has described the sandhills community as a desert in the rain (Wells 1967).

b. Flora. The community has a distinctively open canopy with widely spaced longleaf pines comprising the overstory and smaller (dwarf or scrub) oaks in the understory. The scrub oaks are turkey oak (*Quercus laevis*), blackjack oak (*Q. marilandica*), and bluejack oak (*Q. incana*). Turkey oak and bluejack oak are almost universally found together. Blackjack oak and often sand post oak (*Quercus stellata margarettae*) are more often found with turkey oak and bluejack oak on the moister and loamier soils of the clayhills. In addition, particularly near the coast, the understory may also contain live oak (*Q. virginiana*). Ground cover is usually dominated by wiregrass and bracken fern plus a variety of low woody shrubs, such as ground huckleberries (*Gaylussacia* spp.), dwarf blueberries (*Vaccinium* spp.), runner oaks (*Quercus pumila, Q. minima*), gopher apple (*Licania michauxii*), and blackberry (*Rubus cuneifolius*). Important herbs are *Dichanthelium* spp., *Tragia* spp., *Andropogon* spp., *Heterotheca graminifolia*, and numerous legumes and composites.

c. Ecology. The combination of longleaf pine and wiregrass indicates that fire plays a dominant role in maintaining this community (Greene 1931, Garren 1943, Clewell 1971, Vogl 1973, Christensen in press). Dry during much of the year, the water table remains 4 ft or more below the surface except after heavy rains. Longleaf communities depend upon fire (Clewell 1971, Komarek 1974, Christensen 1986). This is nowhere more evident than in the sandhills, which are the driest, most fire prone of all Panhandle habitat types. Fire mediates the dominance relationship between pines and hardwood species that live in this, Florida's most xeric ecosystem. The above ground parts of turkey oak, blackjack oak, and bluejack oak are highly vulnerable to fire, which readily kills the stems and branches. But their roots, like the roots of many hardwoods, survive to throw up other stems. Moreover, most of these scrub oaks produce underground runners that put up stems in every direction, so that what appears to be 50 or more separate trees growing over areas as large as an acre may actually be separate stems of a single, cloning plant. This may be one way that these oaks cope with fire.

Because of their large root systems and elaborate runners, scrub oaks are constantly ready to clayey sand, or sandy clay, well drained, and moderately-to-steeply sloping. Occasionally Tertiary limestones are exposed and the stream channel may even be etched into hard limestone bedrock (as above Aspalaga Landing on the Apalachicola River).

The soils of the stream valley bottom in its first and second order (Figure 60) reaches are eroding and are composed of the same materials of the valley sidewalls immediately upslope. Soils of the floodplain of the third and higher orders are alluvial, contain more silts and clays, and are distinguished by the presence of partially decomposed vegetation in the form of fluid muck or fibrous peat.

b. Ecology. Rainwater works its way to the sea by (1) evaporation off the land surface and direct transport to the sea via precipitation; (2) by percolation downward and seaward through underground passageways ranging in size from the interstitial spaces between sand or clay particles to 30-m diameter tunnels dissolved in limestone; and (3) over the top of the ground as surface runoff. This latter means by which water moves to the sea is extremely important to plants and animals because the erosive power of surface runoff sculpts the physical topography of the land. Where soil particle size (clays and silts) is so small as not to allow much percolation, surface runoff is proportionally higher than where soils are coarser grained and more friable. Gullying of the land surface, therefore, is more extensive in tighter soils. The tightly packed soils of the Western Highlands, Grand Ridge, New Hope Ridge, and the Tallahassee Red Hills physiographic regions are the most susceptible to gullying of all the Panhandle soils. Combined with the greatest elevations in the Panhandle, the highlands contain some of the most deeply entrenched ravine valleys in Florida. Gully-eroded ravines are most abundant and deepest along the valley wall escarpments of the larger river systems. Those along the eastern valley wall of the Apalachicola River are among the very best examples of deeply incised small-tributary ravine valleys in the entire Coastal Plain, and have been famous the world over for their biological uniqueness for 140 years (Gray 1846, James 1961, Graham 1964). The Apalachicola Bluffs and Ravines area is recognized as biologically distinct (Means 1977, 1985c).

Other ravines in the Northern Highlands are clustered along the Holmes Valley Scarp (see Figure

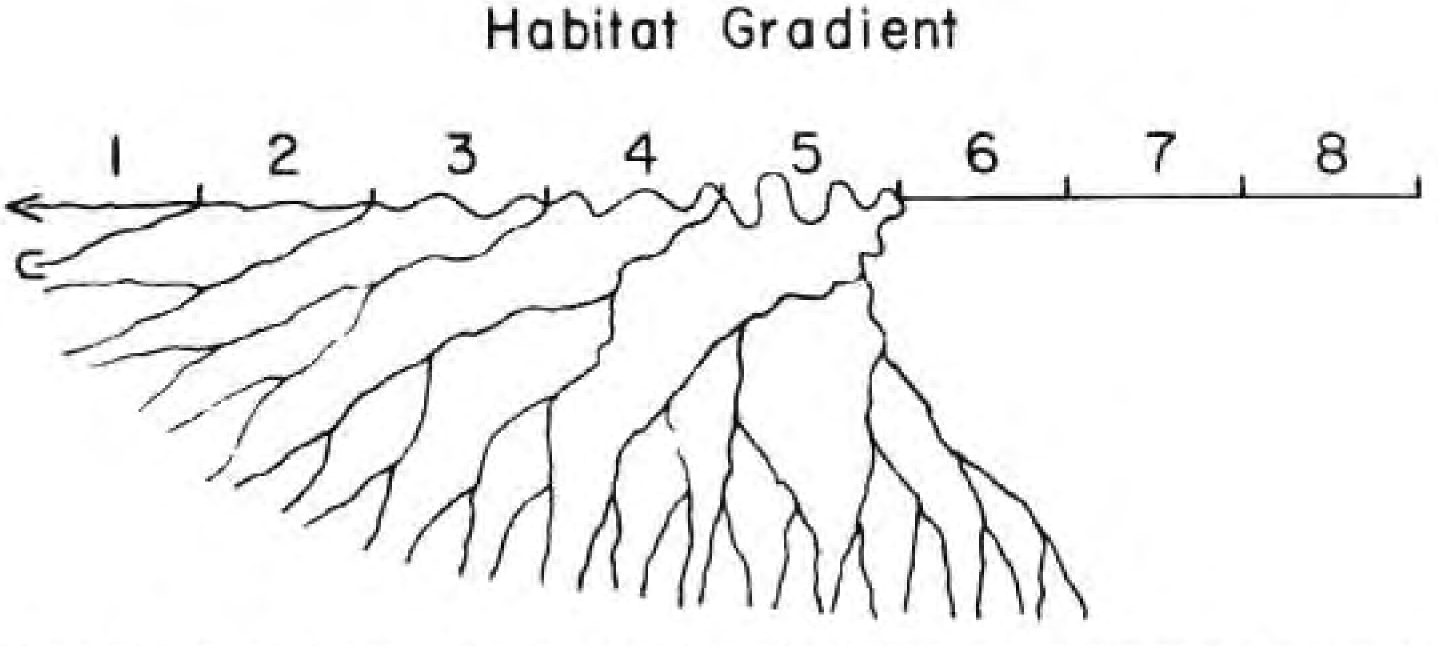

Figure 60. Stream habitat classification (Strahler 1964): (1) order 1 streams including gully erosion (V-shaped) and steephead (U-shaped) ravines; (2) order 2 streams; (3) order 3 streams; (4) order 4 streams; (5) order 5 streams; (6) streams greater than order 5, but less than about order 8; (7) large river floodplain sloughs and alluvial swamp habitats; (8) lake and pond margins.

5), along parts of the southern and western valley wall of the Choctawhatchee River, along the southwestern valley escarpment of the Escambia River, the western tributaries of the Escambia River, and along the Yellow River system and its major tributaries. All these ravine systems are poorly explored, but offer considerable promise of being biologically interesting (Means and Longden 1970; Means 1974a,b, 1975, 1985c).

The heads of gully-eroded stream systems are hydrologically similar throughout the Panhandle. From catchment divides downslope for some distance, the water channels in catchment bottoms are subject to extreme fluctuations in streamflow. Typically, water flows only during and shortly after a rainfall. The persistence of flowing water is strictly dependent upon the regularity and amount of rainfall. During normal dry periods and particularly during extended drought, these stream channels are quite dry, and are inhospitable to aquatic or wetland plants and wildlife.

At some point down the stream gradient, the moisture in the catchment soils upslope becomes great enough, notwithstanding the relatively impermeable clay soils, to slowly leak into the stream bottom, creating a more mesic to hydric condition. This usually is along portions of the creek gradient of Strahler order 2 or 3 (Figure 60). During a drought, even in these reaches streamflow dries up, but the soil moisture remains high enough to support a wetland vegetation of evergreen shrubs and hardwoods. These parts of headwater catchments are clearly erosional, showing little alluviation in the valley bottom, and having relatively steep valley sidewalls. Further downstream, when the slope of the stream bottom becomes shallower, stream flow slows down and loses its scouring ability. The stream drags its sediments along and spreads them all over the valley bottom (alluviation), creating a more or less flat surface with minor depressions. A low-water channel develops that carries stream water during low water stages, but during heavy rains, the water rises out of the meandering channel and flows over the entire flat surface of the floodplain. When the water recedes, it is trapped in the shallow basins where partially decomposed organic debris builds up as muck or peat. This portion of the Strahler gradient is characterized by a stream channel incised into the floodplain floor with clayey-sandy-organic banks that rise sometimes 2 to 3 ft above the channel bed. During dry weather the alluvial portions of ravine streams are mesic, and support many of the members of the beech-magnolia community. During wet weather, however, water flows or stands in the floodplain long enough that a number of hydric trees often are found here too. One value of gully-eroded ravines is to preserve the terrestrial habitat gradient from longleaf pine clayhills to beech-magnolia mesic forest. Where slopes are gentle, ravines are not present because people have replaced the natural forest types with agriculture, silviculture, and urban and suburban developments. The steep slopes of ravine valleys preserve some of the natural terrestrial communities from gross alteration by human activities. Ravines also have a higher and more continuous humidity during summer because of the greenhouse effect under the closed canopies and confining valley sidewalls of ravines. The variety in slope shading, results in north-facing effects (protection from direct sunfall), south facing effects (dryer microclimates because of more direct year-round sunfall), and combinations of these.

c. Flora. Generally, the lower valley sidewalls support a beech-magnolia community (see Section 5.2.5). In the saturated soils of the alluvial floodplain on both sides of the stream channel, one finds hydric species such as the star anise (*Illicium floridanum*), sweet bay magnolia (*Magnolia virginiana*), tulip tree (*Liriodendron tulipifera*), and sweetgum (*Liquidambar styraciflua*). A classic example of a gully eroded ravine in reasonably undisturbed condition is located just north of the city limits of Tallahassee.

The gully-eroded Apalachicola ravines between Sweetwater Creek in Liberty County and the Florida-Georgia border are replete with northern relicts and species endemic to the ravines. Leonard and Baker (1982) reported 52 species of trees, shrubs, and herbs that were endemics, relicts, or rare.

d. Fauna. Wildlife that utilize gully eroded ravines include species tolerant of a wide range of moisture fluctuations. At the heads of gullies near the catchment divides, the vegetation and animal life are characteristic of the longleaf pine clayhills, but shortly downstream woody evergreen shrub species appear, then grade into the beech-magnolia forest with its characteristic wildlife (see sections on longleaf pine clayhills and beech-magnolia forest). The stream itself is the beginning of a developing aquatic gradient, and the water column has its own peculiar wildlife associated with it (see Chapter 6.3.1).

The fauna of the uppermost reaches of gully-eroded ravines is typical of that found in the upland vegetation clothing the watershed (see longleaf clayhills and beech-magnolia sections). When soil moisture increases, and gully-eroded stream valleys begin to have some permanence of flow, a stream side litter fauna is found. The highly distinctive fauna of these streamsides features dozens of species of invertebrates found only in ravines, including earthworms (*Diplocardia* spp., *Sparganophilus* spp.), crayfish (*Procambarus* spp.), trap-door spiders (*Cyclocosmia torreya*), and plethodontid salamanders (*Eurycea bislineata, Pseudotriton ruber, Plethodon glutinosus*, and *Desmognathus* spp.). When studied systematically, the ravines across Panhandle Florida should reveal a great deal of biological diversity presently unrecognized.

5.2.4 Steepheads

Steepheads are highly distinctive stream valley habitats (Means 1975, 1981, 1985c) known presently only from Florida, where they first were discovered and named in the Panhandle (Sellards and Gunter 1918). They are found in the deep sands of the Citronelle Formation and in younger deposits below Cody Scarp (Puri and Vernon 1964, Brooks 1981b) and are aligned east-west (Figure 61) in a manner suggesting an old shoreline (Means 1981, 1985c).

Steepheads and their stream valleys are formed when ground water leaks out on a sloping surface through porous sand at the head of a stream catchment. If the volume of escaping ground water is substantial, sand will be carried away downstream, creating a semicircular horizontal nick in the sloping sand body. Over time, as more sand is carried away, a U-shaped (in vertical cross-section) valley forms as the steep, amphitheatre-shaped valley head migrates headward into the sand. It is this process of lateral sapping of the water table and the resulting headward undercutting that makes steepheads and the valleys they form fundamentally different from typical gully eroded stream valleys. Stream valleys normally are formed as the surface of the land is carried away by the scouring action of rainwater surface runoff, a process called gully erosion. Steephead-origin streams are the same as the seepage streams listed by the Florida Natural Areas Inventory.

Proceeding east across the Panhandle, steepheads first occur in the Panhandle in the deep sands of western Eglin Air Force Base. Large stream valleys cut deeply into the Citronelle sands there and

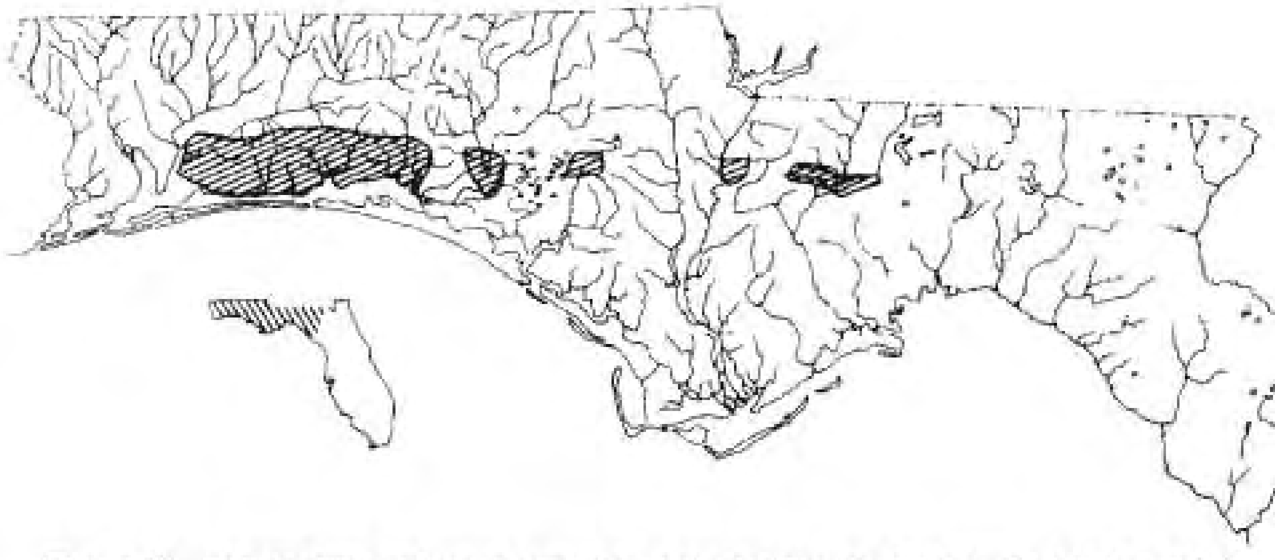

Figure 61. Distribution of known steepheads in the Florida Panhandle (Means 1981).

drain north into the lower reaches of the Yellow River, and south into East Bay River and Choctawhatchee Bay. A few have been etched into the landform along the eastern side of Econfina Creek in Washington County, and into sinkholes in northern Bay County. Below the main axis of Big Sweetwater Creek in Liberty County, every stream valley feeding into Big Sweetwater Creek was formed by steephead migration, and each stream supports a magnificent steephead that is still actively eroding its way headward. A few steepheads are found in the Telogia Creek drainage and along Ocklawaha and Bear creeks draining into the west side of Lake Talquin on the Ochlockonee River. Going east across north Florida, the last steepheads are found along the east side of Lake Talquin in the short tributaries etched into the western end of Beacon Slope.

a. Soils. Soils of steephead valley slopes are exceedingly porous, coarse sands whose angle of repose is about 45°. They are between 25 and 100 ft deep, depending upon geographical location. The soils of steephead valley bottoms are the same Citronelle and Recent sands of the valley walls, but have an occasional veneer of organic deposits along the stream margin and the lower, seepage slope of the valley wall. Downstream in third order portions of steephead valleys, alluvial matter and organic sediments become more prevalent as substrates for plants and animals to live on, or burrow in.

b. Ecology. The physical and chemical characteristics of steepheads are the result of their special hydrological conditions. Steephead waters are filtered through tons of sand, and emerge relatively neutral in pH. Waters of gully-eroded streamheads take on chemical characteristics of the substrate over which the waters flow. Runoff waters characteristically are turbid with suspended clays and silts picked up from the parent material of the soil, and they contain leachates and organic particulates that sweep into the stream course. Since the porous sands soak up rainwater, there is little opportunity for surface runoff to deliver organic or inorganic materials downslope into the stream. Steephead springs usually are continuously flowing, giving a perennial nature to the watercourse at and downstream from spring sources. The bottom of a steephead valley at its head can be up to 30 m deeper than the top of the uplands it drains.

Water chemistry is not the only quality of steephead streams that is different from runoff streams. The temperature of steephead waters is thermally buffered because it emerges from subterranean perched aquifers. Steephead waters have ground-water temperatures at all times of the year, but warm up by ambient processes progressively downstream. Even so, the temperature of steephead-origin streams such as Sweetwater Creek in Liberty County and Liveoak and Turtle Creeks in Okaloosa County are much cooler than the waters of surface runoff streams. Runoff waters are subject to considerable temperature fluctuation seasonally because of the air temperature on the catchment, but ground water tends to track the annual average temperature of the surface of the ground; in the Panhandle, steephead spring-water temperatures are 68–72 °F, year around.

Because steepheads are highly localized phenomena and have formed de novo in each of the larger Panhandle drainages in which they are found, they are rather isolated environments, separated by drainage divides upstream and by changing lotic environments downstream. Biologically, steepheads are natural laboratories providing a potential for ecological and evolutionary processes. Some populations of animals and plants in steepheads may differ from regional populations genetically because of the founder effect or strong local selection; populations of other species demonstrate ecological release in steepheads where more competitive congeners are precluded from immigration for some reason (Means 1975).

c. Flora. Steepheads throughout the Panhandle generally possess a similar cross-sectional gradient of vegetation along a vertical transect running from the top of the basin or watershed they drain to the stream bed. Xeric longleaf pine-scrub oak (*Pinus palustrus, Quercus laevis, Q. incana, Q. marilandica*, and often *Q. virginiana*) communities are found on drainage divides surrounding steepheads. From about where the crest of the slope breaks to about halfway down the transect, the forests are a closed-canopy assemblage of xeric, deciduous trees commonly containing *Carya tomentosa, Quercus hemisphaerica, Q. nigra*. In this xeric zone, are sometimes found stumps and cut logs—signs of a once more extensive occurrence of northern red cedar, *Juniperus virginiana*.

About halfway down steephead slopes one enters a mesic forest containing many elements of the beech-magnolia climax type including *Magnolia grandiflora, Fagus grandifolia, Quercus nigra, Pinus glabra, Carya glabra, Ostrya virginiana, Quercus michauxii*, and *Q. alba*. In this zone in steepheads of the Apalachicola River basin, *Magnolia pyramidata, M. ashei*, and *Stewartia malacodendron* also occur.

On the lower one-third of steephead slopes that are protected from the sun (north-faces or particularly deep cuts), an evergreen shrub zone is developed. This zone contains shrubby species such as *Vaccinium arboreum, Kalmia latifolia, Lyonia lucida, Rhododendron austrinum*, and others.

In steepheads of the Apalachicola River basin, the evergreen shrub zone is especially well-developed and contains many of Florida's endemic and rare northern plants. Among these are *Kalmia latifolia, Rhododendron austrinum, Torreya taxifolia, Taxus floridana, Asarum arifolium, Croomia pauciflora*, and others.

The valley floor of steepheads is a wetland community as demonstrated by an abrupt change to wetland plants and animals. *Illicium floridanum* and *Magnolia virginiana* are indicator species that are almost invariably found rooted in the inundated to saturated soils of steephead bottoms across the entire Panhandle.

d. Fauna. The fauna of steepheads is mostly confined to the litter of the valley bottom, where a detritus-cycling community of litter arthropods feeds a number of small vertebrates on the moist valley floor. Almost every steephead across the Panhandle supports breeding populations of three species of lungless salamanders of the family Plethodontidae. Two of these species are always found: the two-lined salamander, *Eurycea bislineata*, and the red salamander, *Pseudotriton ruber*. One of three species of dusky salamanders completes the trio: *Desmognathus auriculatus* is found in a few steepheads on Eglin Air Force Base and in the steepheads of Econfina Creek in Bay County; *D. fuscus conanti* is found in all others west of the Chipola River basin (Means 1974a,b). An undescribed species is endemic to the Apalachicola-Chipola and Ochlockonee river basins (Karlin and Guttman 1986). The creek chub, *Semotilus atromaculatus*, often is found within a few meters of the sapping waters of steepheads when the volume is large as it is on Eglin Air Force Base. Downstream from the steephead proper, in streams at the western end of Eglin Air Force Base, a frog new to science, *Rana okaloosae*, was just described as occurring in bogs along the margins of streams (Moler 1985). When Panhandle steepheads are thoroughly investigated, numerous relict or endemic invertebrates and possibly some nonvascular plants will be found.

5.2.5 Beech-Magnolia Climax Forests

In the long-term absence of fire, hardwood forests eventually replace the fire-perpetuated longleaf pine ecosystems on all the upland soils of Panhandle Florida. One particular association, in which American beech (*Fagus grandifolia*) and southern magnolia (*Magnolia grandiflora*) are among the dominant trees, is composed of about 40 hardwoods and a few conifers just downslope from the fires in the pinewoods and just upslope from places where the soil is permanently wet (Figure 62). This forest type has been widely touted as the climax forest of the Gulf Coastal Plain (Delcourt and Delcourt 1977), even though old-growth stands are patchily distributed, rather rare, and confined to small areas protected by slopes.

a. Soils. The beech-magnolia forests of the Panhandle are capable of growing in a wide range of soils, ranging from the loamy soil at the bases of slopes, on the higher reaches of floodplains, and on the overflow zones of small creeks to xeric, sandy soils. Because fires keep the species of the beech-magnolia forest off of ridge crests and the upper slopes of stream valleys, the actual soils on which the beech-magnolia forests are rooted are not so variable as they might otherwise be. Usually, soils of beech-magnolia forests are moderately to well-drained sandy loams, which become clayey within a few feet of the surface. On flat, small stream terraces, organic and clay content is higher than on steep slopes of steephead ravine valleys. In the Marianna Lowlands, the Apalachicola Bluffs and Ravines region, and the Coastal Lowlands where limestone is close to the surface of the ground, beech-magnolia forests seem to be especially well developed.

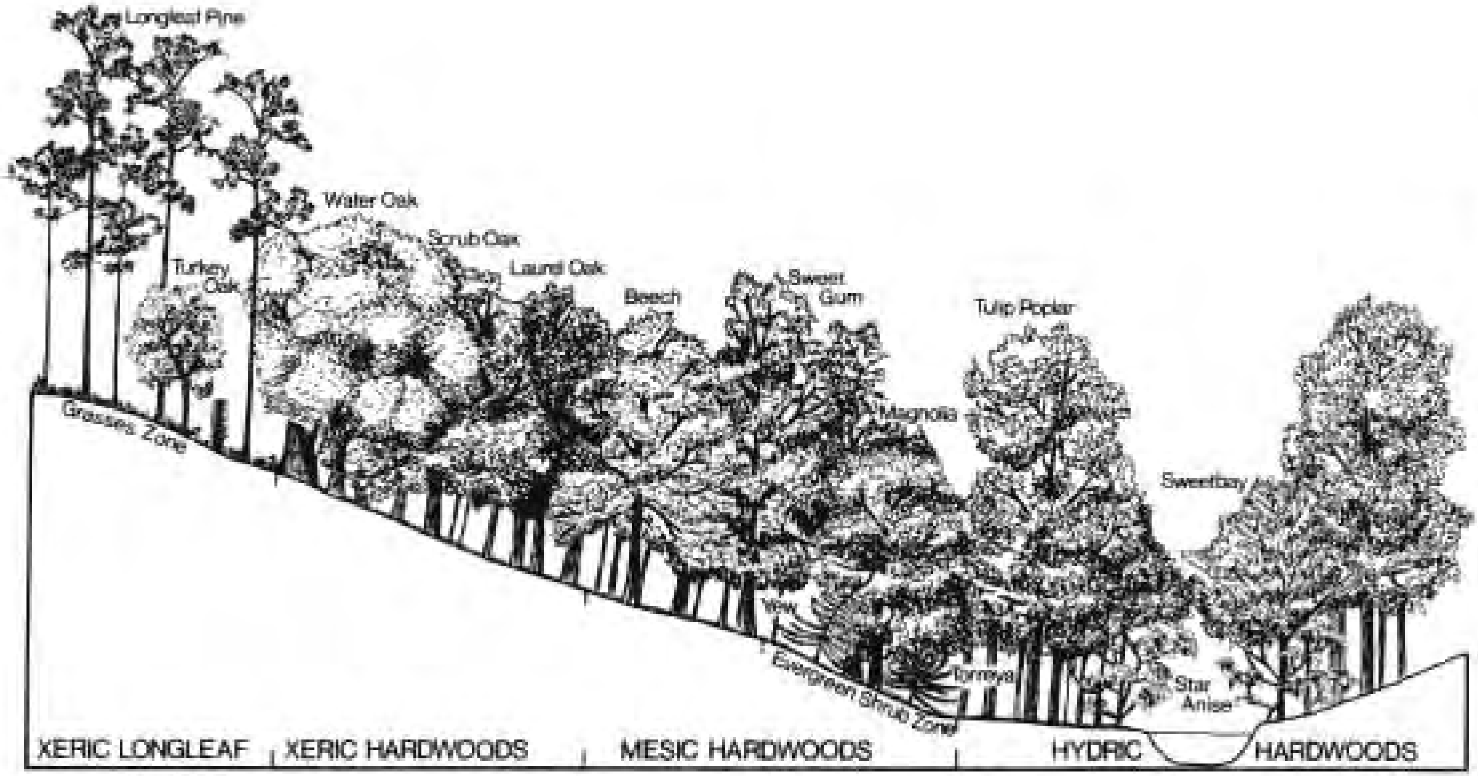

Figure 62. Pine–hardwood continuum developed over a steep slope/moisture gradient.

b. Ecology. Experimental studies of beech-magnolia forests at Tall Timbers Research Station near Tallahassee, Florida have demonstrated that the regular fires that sweep downslope from longleaf forests in clayhill regions of the Coastal Plain keep elements of the beech-magnolia forest downslope in mesic soil zones where fires are naturally retarded by soil and litter moisture. They also indicate that the mixed pine-oak-hickory forests of Quarterman and Keever (1962) are ruderal successional forests involving elements of the beech-magnolia forest mixed with shortleaf and loblolly pines and other colonizing vegetation. The latter forest type, one of the most common habitat types in the Panhandle today, is human-created, and is discussed in Chapter 5.3.1.

When fires are eliminated from the native longleaf pine forests, the hardwoods begin to encroach in an upslope direction (Mutch 1970). Among the hardwoods that are first able to get a roothold in the wiregrass community are sweetgum, laurel oak (*Quercus laurifolia*), and water oak (*Q. nigra*). In the absence of natural fire, the hardwood forest moves slowly up toward the ridgetops. The drier, sandier soils on ridgetops are less suitable for these species; nevertheless, most species of the beech-magnolia forest can, in time, grow in even the highest, driest sites.

This displacement has happened both naturally and experimentally. There are places in north Florida where an unusual configuration of steep slopes has naturally kept broad, sweeping fires away from isolated ridgetops. Under natural circumstances, longleaf pines would occur on those dry ridgetops but instead, beech-magnolia forests occur there—in a continuous transect from the moist valleys to the high, dry hilltops. Apparently there are not enough lightning fires on such ridges to kill back the new hardwood growth. Once established, this forest is self-perpetuating. The beech-magnolia forest, therefore, is the climax forest type on the Coastal Plain uplands, even though those high places are usually the domain of the pines.

The term "hammock" broadly refers to any grouping of hardwood trees. Where it occurs on clayey-loamy soils, it is termed a mesic hammock, and the beech-magnolia climax is often found in these environments. Mesic hammocks are particularly rich in numbers of species of trees. Most mesic hammocks in the Panhandle occur on the lower slopes of stream valleys throughout the Western Red Hills and Tallahassee Red Hills regions. Hammocks can also be found on sandy, or xeric, soils.

Xeric hammocks are often found within sandhill or pine flatwoods communities or on the fringes of lakes and ponds. Clewell (1971) notes that hardwood hammock vegetation often surrounds high pineland depressions especially along the steep slopes of lime sink holes. Overstory trees consist of a mixture of mockernut (*Carya tomentosa*) and pignut hickory (*C. glabra*), persimmon (*Diospyros virginiana*), and southern red oak (*Quercus falcata*) on drier sites.

Hydric hammocks are on the wet end of the soil moisture scale and consequently intergrade imperceptibly with swamp forests. For this reason they are treated in 6.2.2.

Two of the more prominent characteristics of beech-magnolia associations are their overall diversity as a floristic unit and their compositional variation from site to site. In seeking to determine why different tree species were more prominent in one stand than another, Monk (1965) examined species composition in terms of soil moisture, calcium, phosphorus, potassium, and magnesium. His conclusions, summarized in Wharton (1977, p. 167) are as follows:

"(1) Calcium is extremely important; soils high in calcium produce the maximum diversity;

(2) Soils low in calcium, potassium, phosphorus, and moisture support a community dominated by evergreen trees;

(3) Some trees, such as water oak [*Quercus nigra*], swamp chestnut oak [*Q. prinus*], sugarberry [*Celtis* sp.], spruce pine [*Pinus glabra*], and blackgum [*Nyssa sylvatica*], favor wetter environments;

(4) Some trees such as sweetgum [*Liquidambar styraciflua*] and live oak [*Q. virginiana*] do well at both extremes of wet and dry [meaning that factors like fire and longevity may be more important when these trees do or do not appear in the forest];

(5) American holly [*Ilex opaca*] and wild olive [*Osmanthus americanus*] prefer dry areas, dogwood [*Cornus* spp.] and hop hornbeam [*Ostrya virginica*]

prefer dry to mesic conditions, and ironwood [*Carpinus caroliniana*] prefers more hydric soils;

(6) Some shrubs and herbs also prefer xeric conditions (sparkleberry [*Batodendron arboreum*], *Elephantopus* [elephant's foot], horse-sugar [*Symplocos tinctoria*], sarsaparilla vine [*Smilax pumila*]);

(7) Of the 49 tree species, Monk found only four; cabbage palm [*Sabal palmetto*], red bay [*Persea borbonia*], wild olive, and buckthorn [*Bumelia temax*], to be of subtropical affinities."

c. Flora. Dominant trees include southern magnolia (*Magnolia grandiflora*), American beech, sweet gum, spruce pine (*P. glabra*), pignut hickory (*Carya glabra*), American holly (*Ilex opaca*), laurel oak (*Quercus laurifolia*), white oak, swamp chestnut oak (*Q. michauxii*), hop-hornbeam (*Ostrya virginiana*), ironwood (*Carpinus caroliniana*), dogwood (*Cornus florida*), and a host of others. Table 10 lists the tree species found in several unpublished studies of mesic hardwood forests in the eastern Panhandle (Means, unpubl. data).

Common shrubs include wild olive (*Osmanthus americanus*), sparkleberry (*Vaccinium arboreum*), witch hazel (*Hamamelis virginiana*), fringe tree (*Chionanthus virginicus*), horse sugar (*Symplocos tinctoria*), strawberry bush (*Euonymus americanus*), red bay (*Persea borbonia*), and others. Woody vines are abundant in the beech-magnolia forest. The giant vines of the muscadine (*Vitis rotundifolia*), smeared with the orange slime mold (*Dictyostelium* sp.) in the spring, the spiked catbrier (*Smilax bona-nox*), and the distinctive leaves of poison ivy (*Toxicodendron radicans*) are always present. Partridge berry (*Mitchella repens*), trillium (*Trillium underwoodii*), violet (*Viola floridana*), Indian pipe (*Monotropa uniflora*), and ferns (*Polystichum acrostichoides*, *Thelypteris* spp., *Asplenium* spp. and others) are common herbs in these forests.

d. Fauna. Hardwood forests are quite different from the open pine forests of the Panhandle in ways very important to animals. Most of the photosynthesis in hardwood forests goes on high in the lofty canopy where new buds, leaves, flowers, fruits, and nuts abound. The animals that are primary consumers, therefore, are generally arboreal. Lepidopteran larvae in the canopy and a host of sucking and chewing insects are the base of the food web comprised of arboreal insectivores. These mostly are birds, including vireos, warblers, woodpeckers, and other foliage and bark gleaners. The gray squirrel (*Sciurus carolinensis*) is the most prominent mammal in the canopy.

The forest floor food web in hardwood forests is litter driven. The leaves, sticks, twigs, flower parts, and seeds of the trees accumulate on the forest floor and are immediately eaten by a host of terrestrial invertebrates. Among the more important groups

Table 10. Species of trees in the beech-magnolia forest association over 100-m transects compared among selected old-growth forests in Panhandle Florida (from reports on beech-magnolia forests on file with the Florida Natural Areas Inventory, Tallahassee). o = overstory; u = understory.

	Marianna Caverns State Park	Timberlane Hammock	Woodyard Hammock	McBride's Slough Hammock	Indian Lake Hilltop Hammock	Sweetwater Hill Hammock
Acer barbatum	o			o		
Acer rubrum		u	u	u		
Aesculus pavia	u					
Amelanchier arborea						u
Broussonetia papyrifera		u				
Carpinus caroliniana	u	u	u	u		

(continued)

Table 10. Concluded

	Marianna Caverns State Park	Timberlane Hammock	Woodyard Hammock	McBride's Slough Hammock	Indian Lake Hilltop Hammock	Sweetwater Hill Hammock
Carya glabra	o	o	o	o	o	
Carya pallida						o
Carya sp.	o					
Celtis laevigata	u					
Cercis canadensis			u			
Cornus florida	u	u	u	u		u
Crataegus sp.				u		
Fagus grandifolia	o	o	o	o	o	o
Fraxinus caroliniana	o					
Fraxinus pennsylvanica			u			
Halesia diptera	u					
Hamamelis virginiana	u					
Ilex opaca	u		u	u	u	
Juglans nigra	o					o
Juniperus nigra	u					
Liquidambar styraciflua	o	o	o	o	o	
Liriodendron tulipifera		o	o			
Magnolia grandiflora	o	o	o	o	o	u
Magnolia virginiana			u	o		
Morus rubra	u		u			
Myrica cerifera				u		
Nyssa sylvatica		o	o	o		
Osmanthus americana						u
Ostrya virginiana	u	u	u	u	u	u
Oxydendrum arboreum			u			o
Persea borbonia	u	u		o	o	o
Pinus echinata	o					
Pinus glabra	o	o	o	o	o	o
Pinus taeda		o	o			
Prunus caroliniana			u			
Prunus serotina	o	o	u	o		o
Quercus alba		o	o	o	o	
Quercus hemisphaerica	o	o	o	o	o	o
Quercus michauxii	u	u	o	o	o	
Quercus nigra		o	o	o	o	
Quercus phellos	u		o			
Quercus shumardii	o		o			
Quercus stellata	o					
Quercus virginiana			o			o
Sabal palmetto				u		
Symplocos tinctoria		u	u			o
Tilia americana	o				o	
Ulmus alata	u					
Ulmus americana	o		o			
Vaccinium arboreum						u
Viburnum dentatum						u

are springtails, mites, harvestmen, beetles, hemipterans, millipedes, dipterans, isopods, orthopterans, and earthworms. Spiders, feeding on the detritivores, create another source for the higher consumer levels. The rich litter infauna drives a surprisingly complex predator community. Table 8 lists the terrestrial vertebrates captured in a drift-fence sampling of an old growth beech-magnolia forest (Woodyard Hammock) on Tall Timbers Research Station in northern Leon County. Many other primary and secondary consumers visit the beech-magnolia forest ecosystem, but are not restricted to it. In fact, there seems not to be a single vertebrate that is strictly found in the hardwood habitats. However, a suite of highly visible, large vertebrates are more characteristic of hardwood forests than the pine forests further upslope. These are the gray squirrel, the red-shouldered hawk (*Buteo lineatus*), and barred owl (*Strix varia*)—ecological analogs of the fox squirrel species, red-tailed hawk (*Buteo jamaicensis*), and great horned owl (*Bubo virginianus*) in the open pine forests.

5.2.6 Longleaf Flatwoods

Longleaf pine flatwoods are open woodlands that lie between the drier sandhill community upslope and the evergreen shrub dominated wetlands downslope. A drop of only 5 ft in elevation over a distance of 200 m in the Coastal Lowlands will have a longleaf-turkey oak-gopher tortoise sandhills xeric community at the high end, a broad, flat, longleaf flatwoods with no understory over 90% of the transect, and an evergreen shrub bog appearing abruptly at the lower end. Standing anywhere along the slope-moisture gradient, however, the casual observer would be unable to visually detect the elevational drop. Flatwoods often are much broader than 200 m.

The longleaf pine-wiregrass association was undoubtedly the presettlement dominant forest type of the southeast Coastal Plain. It is estimated to have originally covered about 24 million acres from Mobile Bay, Alabama, eastward throughout Florida and then northward through the Coastal Plain in Georgia, South Carolina, and southern North Carolina. Vast flatwood acreages still stretch across the Gulf Coastal Lowlands between the Choctawhatchee River and the Ochlockonee River, and between Cody Scarp and the coast. Scrub oaks, common in the sandhills, are absent from this community and the grassy aspect of the ground cover is sometimes obscured by saw palmetto.

a. Soils. The soils in pine flatwoods are sandy, ground-water podzols with much organic matter in the upper few inches associated with the roots of the dominant ground cover, wiregrass. An organic pan is usually present a foot or two into the soil profile. Soils are generally moist at shallow depths with the water table at or near the surface to about 4 ft deep under drier conditions.

b. Ecology. Working in the Apalachicola National Forest, Clewell (1971) identified four variants of the pine flatwoods based on dominant species. These include: (1) a longleaf pine phase, (2) a slash pine (*P. elliottii*) phase, (3) a longleaf-slash pine phase, and (4) a pond pine (*P. serotina*) phase. The pond pine phase usually contains a compliment of cypress and blackgum and is a true wetland ecosystem. It will be discussed in Chapter 6.2.2.

Before the influence of people, longleaf pine was far more common in the overstory of Coastal Plain flatwoods than it is today. Before about 1920, pond and slash pine were generally restricted to wetter areas, as were some of the brush species characteristic of present-day bay swamps. Reasons for the increase in these species in the flatwoods are still largely unresolved, but are probably related to the disruption of the longleaf pine and wiregrass association by logging practices, silviculture, and most of all, by the interruption of the natural fire cycles. The key to deciding whether a Gulf Coastal Lowlands site is a low sandhill or a flatwood site is the water table. When it is between 0 and 4–5 ft beneath the surface, a flatwoods prevails.

As noted in Clewell (1971, p. 35), "Notes of early naturalists indicated that these pinelands contained nearly pure stands of longleaf pine, as many still do today. Only during recent decades of fire suppression have loblolly, pond, and particularly slash pine invaded some of these pinelands. Longleaf pine, which is the only southeastern tree able to survive fire as a seedling and sapling, owes its existence to the highly flammable wiregrass. Wiregrass and the needle-drop from the longleaf pine comprise a highly combustible fuel that is ignited by lightning and more recently by people. The density of wiregrass and the overlap of the blades of adjacent bunches assures that a fire, once ignited, will spread for miles over that flat or gently rolling pinelands with nothing to stop its course. In pre-colonial days these fires must have burned at intervals of every 3–4 years in order to have destroyed the seedlings and saplings of all other tree species that had seeded in the pineland since the previous fire."

Both species, longleaf pine and wiregrass, have adaptive competitive abilities to maintain their mutual existence. Beside their tolerance to fire, these include an ability to acquire and maintain moisture and nutrients in poor, well-drained soils, the ability to eliminate competitive plants via growth patterns, and the ability to perpetuate themselves under adverse conditions.

Longleaf pine depends upon the dense carpet of wiregrass for the elimination of competitive tree species that would otherwise replace the pine and prevent its future reproduction, while the pine provides an open canopy (light) and soil conditions (pH and nutrients) conducive to wiregrass cover and associated plants (e.g., yellow fox glove [*Aureolaria pedicularia*], dwarf huckleberry [*Gaylussacia dumosa*], and blazing star [*Liatris* spp.]).

Wiregrass does not readily become reestablished once uprooted because it does not reproduce sexually or asexually except under the most exacting environmental conditions (Clewell 1974). These include temperature, photoperiod, moisture, and fire. According to the picture drawn by Clewell (1974, p. 45), the required conditions may no longer exist, leaving the theory that the wiregrass left today "may have germinated from seeds centuries ago when earlier, post-Pleistocene climates provided the environmental conditions needed for reproduction." Once disrupted by logging or agricultural practices, this shallow-rooted grass is eliminated from the ground cover, resulting in a permanent successional change to other forest conditions.

c. Flora. In addition to the wiregrass and saw palmetto (*Serenoa repens*), gallberry (*Ilex glabra*), runner oaks (*Quercus minima, Q. pumila*), a low blueberry (*Vaccinium myrsinites*), a ground huckleberry (*Gaylussacia dumosa*), and bracken fern are dominant ground cover plants in the pine flatwoods. According to Clewell (1971), there may be 200 or more species of ground cover, with 75 or more found in any given stand of a few acres. A list of groundcover species found in four Panhandle flatwood sites is given in Table 11.

d. Fauna. The flatwoods of the Gulf Coastal Lowlands, especially in the Apalachicola National Forest, support a robust population of native earthworms of the genus *Diplocardia*. One species, particularly, *D. mississippiensis*, is the focus of a large fishing bait industry. Many local residents of Calhoun, Liberty, and Wakulla counties make a good living by gathering this species by means of the technique called "grunting." A wooden stake is driven into the ground and vibrated by drawing an ax handle, shovel handle, or similar device across it. The vibrations in the ground agitate the earthworms, driving them to the surface where they are collected. Bait collectors like to "grunt" recently burned flatwoods, where densities of *D. mississippiensis* are on the order of thousands per acre. This species, alone, must do a considerable job in recycling organic nutrients back into the soil.

The groundcover of flatwoods is usually quite luxuriant because water is readily available during rains which do not percolate far into the soil to local water tables. Furthermore, under the natural conditions of regular fires, nutrients tied up in dead and slowly decomposing organic litter are quickly made available to the plants of flatwoods by the rapid oxidation and nutrient-cycling effect of fire.

Because the primary productivity of the groundcover vegetation is so high, flatwoods support a rich invertebrate fauna of herbivores. These, in turn, drive a surprisingly rich vertebrate insectivore fauna, comprising salamanders (*Ambystoma talpoideum, A. tigrinum, A. cingulatum, Notophthalmus viridescens, N. perstriatus, Eurycea quadridigitata*), frogs (*Gastrophryne carolinensis, Bufo terrestris, B. quercicus, Hyla squirella, H. femoralis, H. gratiosa, Pseudacris ornata, P. nigrita, Limnaoedus ocularis, Rana sphenocephala, Scaphiopus holbrookii*), and lizards (*Eumeces inexpectatus, Scincella lateralis, Cnemidophorus sexlineatus, Ophisaurus ventralis*). Snakes that feed upon the herbivores are abundant also (*Coluber constrictor, Lampropeltis getulus, L.*

Table 11. Comparison of floral diversity among four flatwoods sites in Panhandle Florida. Site 1=Liberty County flatwoods; site 2=Tate's Hell Swamp; site 3=grass-sedge savannah, Liberty County; site 4=Buckhorn Hunt Camp (from research summaries 6, 7, 9, & 5, respectively, in Clewell 1981).

Species	Site 1	Site 2	Site 3	Site 4
Agalinis aphylla	•		•	
Agalinis filicaulis			•	
Agalinis linifolia		•		
Agalinus purpurea		•	•	
Ageratina aromatica	•			
Aletris aurea	•		•	
Aletris lutea	•	•	•	
Aletris obovata	•			
Angelica dentata	•			•
Andropogon virginicus	•			•
Andropogon sp.			•	
Anthaenantia rufa			•	
Aristida affinis			•	
Aristida stricta	•		•	•
Arnoglossum ovatum			•	
Aronia arbutifolia		•		
Asclepias cinerea	•			•
Asclepias convivens			•	
Asclepias lanceolata			•	
Asclepias longifolia	•		•	
Asclepias michauxii	•			
Ascyrum (=Hypericum) hypericoides				•
Asimina longifolia	•			•
Aster adnatus	•		•	•
Aster chapmanii		•	•	
Aster concolor	•			
Aster dumosus	•			
Aster eryngiifolius	•		•	•
Aster linariifolius	•			
Aster reticulatus	•		•	•
Aster tortifolius	•			•
Aureolaria pedicularia	•			
Balduina uniflora		•	•	•
Baptisia lanceolata	•			
Baptisia simplicifolia	•			•
Bartonia paniculata		•		
Berlandiera pumila	•			
Bigelowia nudata			•	
Callicarpa americana	•			
Calopogon pallidus		•	•	
Calopogon tuberosus (=C. pulchellus)			•	
Carphephorus pseudoliatris	•	•		•
Cassia fasciculata	•			•
Cassia nictitans	•			
Chamaecyparis henryae		•		
Chaptalia tomentosa			•	
Chondrophora nudata		•		
Chrysopsis mariana	•			•
Cirsium horridulum	•			
Cirsium lecontei	•		•	
Cleistes divaricata				•
Clethra alnifolia		•	•	
Cliftonia monophylla		•		
Cnidoscolus stimulosus	•			
Coreopsis gladiata			•	
Coreopsis leavenworthii		•		
Coreopsis nudata			•	
Crotalaria purshii	•			•
Ctenium aromaticum	•		•	
Cuscuta compacta		•		•
Cyrilla racemiflora parvifolia		•	•	
Cyrilla racemiflora		•		•
Desmodium ciliare	•			
Desmodium lineatum	•			•
Desmodium paniculatum	•			•
Dichanthelium acuminatum	•		•	•
Dichromena colorata			•	
Dichromena latifolia		•	•	
Diospyros virginiana			•	
Drosera capillaris		•	•	•
Drosera filiformis		•		
Dyschoriste oblongifolia	•			
Elephantopus elatus	•			
Erianthus giganteus			•	
Erigeron vernus	•		•	
Erigeron tomentosum	•			
Eriocaulon compressum			•	
Eriocaulon decangulare		•	•	
Eryngium yuccifolium	•		•	•
Eupatorium album	•			
Eupatorium compositifolium	•			•
Eupatorium leucolepis			•	
Eupatorium recurvans	•	•	•	
Eupatorium rotundifolium	•		•	

(continued)

Table 11. Continued

Species	Site 1	Site 2	Site 3	Site 4
Eupatorium semiserratum	•	•		
Euphorbia inundata	•		•	
Euthamia minor		•	•	
Fraxinus caroliniana			•	
Fuirena squarrosa			•	
Galactia erecta	•			
Gaylussacia dumosa	•		•	
Gaylussacia frondosa	•			•
Gaylussacia mosieri		•		
Gelsemium rankinii		•		
Gelsemium sempervirens	•			
Gnaphalium purpureum falcatum	•			
Heleanthemum carolinum	•			
Helenium pinnatifidum	•		•	
Helianthus floridanus		•		
Helianthus heterophyllus	•		•	
Helianthus radula	•			•
Heterotheca (=Pityopsis) aspera	•			
Heterotheca (=Chrysopsis) gossypina	•			
Heterotheca (=Pityopsis) graminifolia	•			•
Heterotheca (=Pityopsis) oligantha	•		•	•
Hibiscus aculeatus	•			
Hieracium gronovii	•			
Houstonia (=Hedyotis) procumbens	•			
Hypericum brachyphyllum		•	•	
Hypericum fasciculatum	•	•	•	
Hypericum microsepalum	•		•	
Hypericum myrtifolium	•		•	
Hypericum tetrapetalum	•			
Hypericum stans	•			
Hypoxis hirsuta		•	•	•
Hyptis alata			•	
Ilex coriacea		•	•	•
Ilex glabra	•	•	•	•
Ilex myrtifolia		•	•	•
Iris tridentata			•	
Justicia crassifolia	•			
Kalmia hirsuta				•
Lachnanthes caroliana		•		
Lachnocaulon anceps	•	•		
Lespedeza capitata	•			
Lespedeza repens	•			•
Liatris chapmanii				•
Liatris gracilis	•			
Liatris spicata		•	•	
Liatris tenuifolia	•			
Licania michauxii	•			•
Lilium catesbaei		•	•	
Lobelia brevifolia			•	
Lobelia floridana	•	•	•	
Lobelia paludosa	•		•	•
Lophiola americana		•	•	
Ludwigia linearis		•		
Ludwigia pilosa		•		
Lycopodium alopecuroides		•	•	
Lycopodium carolinianum		•		
Lycopodium prostratum			•	
Lygodesmia aphylla	•			
Lyonia ferruginea				•
Lyonia fruticosa		•		
Lyonia lucida		•	•	•
Magnolia virginiana		•	•	
Muhlenbergia capillaris			•	
Myrica cerifera	•	•	•	•
Myrica heterophylla	•		•	
Myrica inodora	•	•		
Nolina atopocarpa	•			
Nyssa sylvatica biflora		•	•	
Onosmodium virginianum	•			
Osmanthus americanus	•	•		
Osmunda cinnamomea			•	•
Oxypolis filiformis		•	•	
Panicum anceps				•
Panicum rigidulum			•	
Parnassia caroliniana			•	
Paspalum plicatulum			•	
Paspalum sp.	•			
Persea palustris		•	•	
Petalostemon albidum	•			
Phoebanthus tenuifolia	•			
Physostegia leptophylla			•	
Pieris phillyreifolia		•		
Pinguicula sp.			•	
Pinus elliottii	•	•	•	•

(continued)

Table 11. Continued

Species	Site 1	Site 2	Site 3	Site 4
Pinus palustris	•			•
Plantanthera ciliaris		•		
Plantanthera nivea		•	•	
Pleea tenuifolia		•	•	
Pluchea camphorata		•		
Pluchea foetida		•		
Pluchea odorata		•		
Pluchea rosea		•		
Pogonia ophioglossoides			•	
Polygala baldwinii			•	
Polygala crenata	•		•	
Polygala cruciata		•	•	
Polygala cymosa		•	•	
Polygala grandiflora	•			
Polygala harperi			•	
Polygala incarnata	•			
Polygala lutea	•	•		
Polygala nana	•			•
Polygala ramosa			•	
Polygala setacea				•
Proserpinaca pectinata		•		
Pteridium aquilinum	•			•
Pterocaulon pycnostachyum (=P. virfatum)	•			•
Quercus falcata	•			
Quercus incana	•			
Quercus laevis	•			
Quercus minima	•			•
Quercus nigra	•		•	
Quercus pumila	•			•
Rhexia alifanus	•	•	•	•
Rhexia lutea			•	
Rhexia petiolata			•	
Rhexia virginica		•		
Rhododendron serrulatum		•		
Rhynchospora chapmanii			•	
Rhynchospora corniculata			•	
Rhynchospora globularis			•	
Rhynchospora microcephala			•	
Rhynchospora mollissima	•			
Rhynchospora plumosa			•	
Rhynchospora sp.	•			
Rubus argutus			•	
Rubus cuneifolius	•			
Rudbeckia graminifolia			•	
Rudbeckia mohrii			•	
Ruellia pedunculata			•	
Sabatia bartramii			•	
Sabatia brevifolia	•			
Sabatia difformis				•
Sabatia quadrangula		•		
Sabatia stellaris			•	
Sagittaria graminea		•		
Salvia azurea	•			
Sarracenia flava		•	•	
Sarracenia psittacina		•	•	
Schrankia microphylla	•			
Scleria baldwinii			•	
Scleria hirtella	•		•	
Scleria nitida				•
Scleria reticularis			•	
Scleria triglomerata				•
Scutellaria integrifolia	•			
Serenoa repens	•			•
Seymeria cassioides	•		•	•
Sisyrinchium arenicola	•		•	
Smilax auriculata	•			•
Smilax glauca			•	•
Smilax laurifolia		•	•	
Smilax pumila	•			•
Solidago odora	•			
Solidago stricta	•			
Spiranthes praecox			•	
Stylisma patens	•			
Stillingia sylvatica	•			•
Stylosanthes biflora	•			
Styrax americana		•		
Syngonanthus flavidulus		•		•
Taxodium distichum nutans (=T. ascendens)		•	•	
Tephrosia hispidula				•
Tephrosia virginiana	•			
Tofieldia racemosa			•	•
Tragia urens	•			•
Trichostema dichotomum	•			
Trilisa (=Carphephorus) odoratissimus	•		•	•
Trilisa (=Carphephorus) paniculatus	•			
Utricularia cornuta		•		

(continued)

Table 11. Concluded

Species	Site 1	Site 2	Site 3	Site 4
Utricularia juncea		•	•	
Vaccinium darrowi	•			•
Vaccinium fuscatum		•		
Vaccinium myrsinites	•			•
Verbesina chapmanii			•	
Viola septemloba	•			
Viola sp.	•			
Vitis rotundifolia	•		•	•
Vitis sp.		•		
Woodwardia virginica		•		
Xyris ambigua		•		
Xyris baldwiniana		•	•	
Xyris caroliniana	•		•	•
Xyris elliottii		•		
Xyris stricta		•	•	
Zigadenus densus	•		•	•
Zigadenus glaberrimus		•	•	
Total species	**134**	**87**	**127**	**71**

triangulum, L. calligaster, Masticophis flagellum, Drymarchon corais, Sistrurus miliarius, Elaphe guttata, E. obsoleta).

Mammals of the flatwoods are most of the same species found in sandhills. They include the mammalian insectivores: shrews (*Blarina brevicauda, Cryptodus parva, Sorex longirostris*) and the mole (*Scalopus aquaticus*). Mammalian herbivores are abundant: cottontail and marsh rabbit (*Sylvilagus floridanus, S. palustris*), cotton rat and cotton mouse (*Sigmodon hispidus, Peromyscus gossypinus*), harvest mouse (*Reithrodontomys humulis*), pine vole (*Microtus pinetorum*), white-tailed deer (*Odocoileus virginianus*), and others. Most of the mammalian carnivores (skunk, opossum, raccoon, bobcat, gray fox) not strictly associated with water are found in flatwoods. Since watercourses meander through the flatwoods, the aquatic mammals (otter, mink, beaver) occasionally enter the piney woods. The threatened black bear is found in small numbers in deep swamps like Bradwell Bay Wilderness Area located in the flatwoods of the Apalachicola National Forest.

The avifauna of flatwoods is of four feeding guilds: an arboreal, needle and bark gleaning suite of species; a flycatching group that sallies out from their perches to catch insects in the air; a seed-eating terrestrial assemblage; and a group of aerial predators. Preeminent among the birds of the first guild is the federally endangered red-cockaded woodpecker (*Picoides borealis*).

The last strong bastion of this species is the Coastal Lowlands of Panhandle Florida. Eglin Air Force Base and the Apalachicola National Forest probably harbor more than 50% of the remaining individuals of this species. The aerial predators are nocturnal and diurnal, including the great horned owl (*Bubo virginianus*), red-tailed hawk (*Buteo jamaicensis*), and chuck-will's-widow (*Caprimulgus carolinensis*). The Bachman's Sparrow (*Aimophila aestivalis*) is a fully terrestrial bird that requires the open, shrubless prairie groundcover typical of flatwoods.

5.2.7 Beach, Dune, and Scrub

The beach and dune coastal strand vegetative associations are restricted to the high energy shorelines along the seaward boundary of the spits and barrier islands of Panhandle Florida. The barrier islands are Santa Rosa, Shell, St. George, St. Vincent, and Dog Island; the larger spits are Moreno Point, Crooked Island, St. Joseph Spit, and Alligator Peninsula. One small stretch of mainland exposed to the open gulf, from Alligator Point to Dog Island, has a small amount of strand vegetation. Coastal marshes and salt flats found along low-energy coastlines are not considered components of the strand community, nor are the upland communities, such as the pine flatwoods found inland of the dune system and along shorelines being eroded by the sea.

a. Soils. Soils of the coastal strand, as the beach, dune, and coastal scrub are often called, are sandy, grading from unsorted, mixed grain sizes and shells thrown up as berms by storms to finely graded and sorted grain sizes on aeolian dunes. These latter dunes occur perched on the interdune flats or are developed on top of the berms thrown up by storms.

b. Ecology. The scrub community, which is unique to the southeastern Coastal Plain and especially to Florida, has two variants, one dominated by sand pine (*P. clausa*), and one dominated by slash pine (*Pinus elliottii*). On Panhandle barrier islands, treeless scrub occurs just behind the foredunes in the lee of winds heavily laden with salt spray off the Gulf of Mexico. Going inland, the treeless scrub changes to scrub with a slash pine canopy. Further back from the first or second beach-dune ridge, one encounters sand pine scrub. This transect is obvious on St. Joseph Spit, St. George Island, and St. Vincent Island.

As in peninsular Florida, pine scrub of the Panhandle is also found on relict sand dunes and beach ridges created when sea level was higher than at present. Soils on such relict dunes are well-washed, well-drained sterile white-to-yellowish sands. Unlike peninsular Florida scrub communities, however, the Panhandle scrub community tends to be closer to the coast, positioned between the coast and the pine flatwoods. The pine scrub habitats of Panhandle Florida are isolated from those in the north central peninsula by the low-energy coastline of the Florida Big Bend region, where few dunes have been formed.

c. Flora. Though variable from site to site, dune and beach vegetation can have three distinguishable zones: (1) the shifting beach sands; (2) the produne vegetation; and (3) the scrub zone.

The shifting beach sand zone is, by definition, devoid of living, rooted vegetation. The primary energy sources for the often numerous consumers that frequent this zone are imported by wind and wave action or brought down from more inland areas. Seagrasses washed onto the shoreline by storm tides and waves, drifting plant debris, shells, and carcasses of fish and other marine life, collectively called seawrack, serve as food for the primary consumers that include many insects and their larvae, amphipods, ghost crabs (*Ocypode* sp.), and other burrowing invertebrate species. These, in turn, provide food for gulls, terns, and probing shorebirds.

Inland from the shifting beach sand zone, the produne zone is the first large dune. Produne vegetation is characterized by pioneer plants that are able to establish themselves in the shifting, arid sands and to tolerate salt spray and intense heat. Examples include sea oats (*Uniola paniculata*), railroad vine (*Ipomoea pes-caprae*), beach morning glory (*I. stolonifera*), evening primrose (*Oenothera humifusa*), sand spur (*Cenchrus tribuloides*), grasses (*Paspalum vaginatum, Schizachyrium maritimum, Panicum amarum*), sand cocograss (*Cyperus lecontei*), and sea purslane (*Sesuvium portulacastrum*) (Kurz 1942; Clewell 1971). Limited quantitative data on the density of these dune plants on St. George Island are provided by Carlton (1977).

The produne affords limited protection to the interior dune system from wind and salt spray and is crucial for the establishment of subsequent plant communities. On the backsides of these dunes Spanish bayonet (*Yucca aloifolia*), myrtle oak (*Quercus myrtifolia*), green brier (*Smilax auriculata*), saw palmetto (*Serenoa repens*), and other plants characteristic of the interior dunes may grow.

Farther inland from the foredunes is the "scrub" zone, characterized by stunted, wind and salt spray-pruned scrubby oaks and other evergreen, small-leaved shrubs. This area is referred to as the "scrub" zone by Kurz (1942), because of its similarity to scrub oak growing on relict sand dunes of interior Florida. The scrubby, gnarled, thick-leaved evergreen oaks that are characteristic of the scrub community almost always include sand-live oak (*Q. virginiana geminata*), Chapmans oak (*Q. chapmanii*), fetterbush (*Lyonia lucida*), and very rarely in the Panhandle, myrtle oak (*Quercus myrtifolia*). Other common shrubs include different types of rosemary (*Ceratiola ericoides, Conradina canescens*) and gopher apple (*Licania michauxii*). Ground cover is usually sparse, leaving large patches of bare white sand interspersed with reindeer moss (*Cladonia rangifera*) and other lichens. The scrub community is typically two layered, with slash or sand pine in the canopy and the scrub oaks and shrubs in the understory.

Scrub communities are quite variable. The coastal scrub forest is dominated by a mixture of sand and slash pine in most locations (Carlton 1977). However, according to Clewell (1971), sand pine was represented by a single tree in his survey of St. George Island. Comparable dunes near Carrabelle and on St. Joseph Spit have dense forests of sand pine (*Pinus clausa*). Sand pine seems to be less tolerant of salt spray than slash pine. Therefore, it is common to find sand pine on the interior dunes or bayside beach ridges and dunes on the Panhandle's barrier islands. Across the lagoon, where sand pine is somewhat better sheltered from heavy winds and salt spray, it occurs in dense stands on relict dunes and beach ridges along the continental margin. Eglin Air Force Base is noted for a variety of sand pine having open, rather than serotinous cones, such as the sand pine has in central Florida. Sand pine forests include monospecific stands of uniform age, indicating regeneration about the same time. This coincides with theories about natural replacement of sand pine by fires in central Florida (Laessle 1958). It is common to find sand pine growing with other pines, such as longleaf pine on Eglin Air Force Base. Apparently sand pine will encroach under the canopy of longleaf pine in the absence of fire. In stands of old sand pine, wind seems to be able to blow over large individuals, opening the sand pine forest up for invasion by hardwoods, other pines, and shrubs. The successional relationships of Panhandle sand pine have yet to be fully studied.

Open areas of the scrub zone are sometimes occupied by lichens, St. Johns wort (*Hypericum reductum*), nettles (*Cnidoscolus stimulosus*), stunted sea oats, and jointweed (*Polygonella polygama*). Swales between dunes may occasionally retain water after heavy rains. These shallow interdunal depressions may be distinguished from sloughs in that they drain surface runoff vertically into the soil, whereas sloughs hold surface runoff or carry it into the bay (Clewell 1971).

On St. George Island, sloughs are generally flanked by pine flatwoods and are delineated by a dense zone of medium-sized oaks. These mesic to xeric-like hammock communities are composed primarily of laurel oak (*Quercus laurifolia*) and live oak with some sand-live oak (*Q. virginiana geminata*), as well (Clewell 1971). A variety of woody plants form an understory in this more protected habitat, including gallberry (*Ilex glabra*), wax myrtle (*Myrica cerifera*), greenbrier, bamboo vine (*Smilax laurifolia*), poison oak (*Toxicodendron quercifolia*), muscadine (*Vitis rotundifolia*), wild olive (*Osmanthus americanus*) yaupon (*Ilex vomitoria*), buttonwood (*Cephalanthus occidentalis*), royal fern (*Osmunda regalis*), and sawgrass (*Cladium jamaicense*). Where standing water remains nearly all year pond habitat may form, supporting freshwater marsh plants such as sawgrass, water lilies (*Nymphaea odorata*), and umbrella grass (*Fuirena scirpoidea*).

The vegetation of the coastal community is subjected to harsh conditions. High winds, shifting sands, intense heat, and salt spray are chronic stress factors which define not only species composition, but growth form as well. Many plants found in the coastal region appear to be gnarled and stunted, perhaps as adaptations to or consequences of environmental stress.

Despite the fact that many plants may appear stunted or small, they are frequently quite old. Clewell (1971) reports a myrtle oak 2 m in height to be at least 11 years old; a 2.3 m sand live-oak to be 25 years old; a 1.3 m rosemary bush to be 15 years old; and a 25.4 cm diameter slash pine to be 75 years old. Though they appear stressed, many of the scrub species survive quite well under such conditions. Their success is essential to the stabilization of the dune system, which is constantly subjected to the eroding force of onshore winds and storms.

Although fire tends to be infrequent in the coastal community, it does occur (Clewell 1971) and is important in maintaining other more typically inland community types on barrier island systems (i.e., pine flatwoods, pine scrub). Because of the openness of the scrub zone and the lack of fuel in the ground cover, fewer fires occur and they rarely spread very far in the dune system.

The slash pine scrub community described by Clewell (1971) in the Apalachicola National Forest possesses more than just scrub oak understory. Sand-live oak (*Quercus virginiana geminata*), sweet bay magnolia (*Magnolia virginiana*), southern magnolia (*Magnolia grandiflora*), and stagger bush (*Lyonia ferruginea*) were common stunted trees, 10–30 ft tall. Others included black titi (*Cliftonia monophylla*), wild olive (*Osmanthus americanus*), water oak (*Quercus nigra*), and others. The overstory, which has been cut, was solely slash pine (*Pinus elliottii*), up to 120 years in age before logging. The scrub layer in this community contains fetterbush (*Lyonia lucida*), stagger bush, gallberry (*Ilex glabra*), dwarf huckleberry (*Gaylussacia* spp.), dangleberry (*Vaccinium erythrocarpum*), and sand-live oak (*Quercus virginiana geminata*). Saw palmetto (*Serenoa repens*) grows sparsely. Only 51 species are recorded from this upland site.

On St. George Island, a slash pine dominated scrub community lies behind the dune system, often intergrading into sand pine scrub and pine flatwoods (Clewell 1971). In this particular location, myrtle and sand-live oak form large patches and saw palmetto covers up to 15% of the ground. Chapmans oak and rosemary were also reported.

Two trends in this community's distribution have been noted: (1) the invasion of sand pine into sandhill sites as fire is eliminated (Gatewood and Hartman 1977); and (2) the establishment of a slash pine overstory at sites formerly dominated by sand pine as the sand pines reach old age and begin to fall down and thin out (Clewell 1971). Fire suppression in sandhill communities may slow the recycling rate of organic nutrients in the forest litter and eliminate wiregrass, lowering overall soil fertility and thus favoring the invasion by sand pine. The deliberate planting of slash pine may promote its invasion into adjacent scrub communities by increasing the relative numbers of seeds reaching available sites. Fire suppression may also play a role in promoting slash pine. In south Florida sand pine scrub is recycled by catastrophic fire (Laessle 1958, Bozeman 1971). Much less is known about the role of fire in north Florida scrub communities, and extrapolation from the ecology of central Florida scrub may be invalid.

d. Fauna. The dunes are so arid and hot that few amphibians can tolerate the severely stressful conditions. Southern toads (*Bufo terrestris*) occasionally take refuge in burrows and forage at night at the base of dunes, especially in the interdune flats. Toads can be abundant in coastal strand environments as can the southern leopard frog (*Rana sphenocephala*) because both breed in temporary ponds of the interdune flats.

Coastal strand environments are well endowed with reptiles. Reptiles are the vertebrates best adapted for dry terrestrial environments, and the kinds of foods eaten by most reptiles (insects, small vertebrates) are themselves abundant in the highly productive coastal habitats. The garter snake (*Thamnophis sirtalis*), black racer (*Coluber constrictor*), coachwhip (*Masticophis flagellum*), cottonmouth (*Agkistrodon piscivorus*), and pygmy rattlesnake (*Sistrurus miliarius*) are also exceedingly abundant along strands. Mammals of the coastal strand include the eastern mole (*Scalopus aquaticus*), shrews, beach mice (*Peromyscus polionotus* sbspp.), rice rat (*Oryzomys palustris*), cotton rat (*Sigmodon hispidus*), cottontail (*Sylvilagus floridanus*), and marsh rabbit (*S. palustris*).

Panhandle scrub communities are depauperate in animals when compared to the central Florida interior scrubs. Apparently the Panhandle scrubs are only as old as the barrier islands and the coastline where it is confined geographically. Present coastal features are only about 6,000 years old, but interior scrubs in central Florida are relicts stranded from higher stands of the sea, possibly as long ago as late Pliocene, and may be up to 2 million years old.

Coastal scrub communities from Santa Rosa Island to St. Joe Spit have populations of light-colored beach mice that burrow in the sand. These, cotton rats, and rice rats probably are eaten by the coachwhip and black racer, common snakes in the scrub that actively hunt their prey. They also eat the six-lined racerunner (*Cnemidophorus sexlineatus*), one of the commonest scrub vertebrates. Southern toads are the most common frog, but the southern leopard frog is also abundant. Many of the animals encountered in scrubs are visitors from adjacent wetlands, forests, or grassland vegetation. Two federally listed endangered subspecies, the Choctawhatchee beach mouse (*Peromyscus polionotus allophrys*) and Perdido Key beach mouse (*P. polionotus trissyllepsis*) are found on some of these barrier islands.

5.2.8 Caves

Caves filled with air rather than water are generally rare in Florida but are more prevalent in the Panhandle than in the peninsula. This type of habitat is found in regions with limestone formations. Two distinct limestone (karst) regions exist in north Florida west of the Suwannee River, each biologically and geologically distinct from the other: the Woodville Karst Plain in the Florida Big Bend region and the Marianna Lowlands in the Panhandle. Air-filled caves are virtually nonexistent in the subterranean limestone passageways of the Woodville Karst Plain, but they are abundant in the Marianna Lowlands. The reason seems to be that the water table in the Marianna Lowlands is lower than the general elevation of the upper limestone passageways, allowing air, rather than water, to fill the caves. The air-filled passageways are connected by vertical shafts to water-filled passageways in horizontal cave systems at lower levels. The biological resources of water-filled caves are described in the chapter on freshwater wetlands (Chapter 6.5.1).

The Marianna Lowlands physiographic region of Panhandle Florida is the southwestern end of a large karst plain known in Georgia as the Dougherty Plain. This limestone region extends northeast from Marianna, Florida, to about 25 mi beyond Albany, Georgia. The Tertiary limestones which lie close to the ground surface, mantled with a thin veneer of sand, have been subject to erosion by dissolution for millions of years, and both vertical and horizontal solution channels are extensive in them. Vertical shafts dissolve as surface waters percolate downward through joints, cracks, fissures, and faults; horizontal caves are formed as ground water flows downhill underground along bedding planes between limestone terranes (sediment layers). Over millions of years, horizontal tunnels can widen to become 30–50 ft in diameter, or even larger in places.

When in time sea levels drop, as they periodically do in Florida in response to the waxing and waning of continental glaciation, ground water levels also fall. When ground water drops, it abandons upper horizontal cave systems through vertical interconnecting shafts and occupies horizontal systems at lower levels in the limestones. Once the water in the passageways is replaced with air, they are available for colonization and use by terrestrial animals and plants.

Because light is always a limiting factor in food webs (except some deep sea ones), it is no surprise that light, or the lack of it, plays a role in cave ecosystems. Light intensity declines as the square of distance, so that the intensity of light available for photosynthesis falls off very rapidly back from the cave mouth. Very few caves exist into which sunlight falls directly. The area near the mouth of a cave where any amount of light falls is called the "twilight" zone. This is not an abstract category; animals and plants that use and/or need light are specifically found in this zone in caves, and their distributions in the twilight zone are quite demonstrable on inspection. The dark portions of caves are, of course, just as well-defined by the absence of any light at all, and the simplified food webs in the dark (troglobitic) zones of caves are driven entirely by detritus.

Most of the caves of biological importance in the Marianna Lowlands are privately owned, but two systems now belong to the State of Florida. The caves in the Marianna Caverns State Park include a few thousands of feet of passageways. None of these caves is particularly important biologically, and the main commercial cavern is disturbed daily by the tourist traffic. Some of the park's smaller caves, such as Indian Cave, are being managed in hope of the return of the endangered grey bat (*Myotis grisescens*), which is known to have once used them. One of the most important caves in the region, biologically, is known as Judge's Cave. This cave now is owned by the Florida Game and Fresh Water Fish Commission. It is the major maternity cave for the grey bat, whose pregnant females seem to require a roost over water in caves (Tuttle 1974, Humphrey and Tuttle 1978).

Other privately owned caves that are important biological resources are known by the following names: Bump Nose Cave, Honey Comb Hill Cave, Stoney Cave, Fears Cave, Sam Smith's Cave #1 (also known as Gerard's Cave), Sam Smith's Cave #2, and Baxter Cave, all in Jackson County. Many more occur in Jackson County. Some are clustered along the Chipola River valley between Marianna Caverns State Park and U. S. Highway 90, and others are found to the west in the direction of the town of Cottondale. Another cluster of caves lies along Waddell's Mill Creek and its tributaries west of the Chipola River. The Florida State Cave Club, a grotto (branch) of the National Speleological Society and operating out of Florida State University in Tallahassee, maintains records on the caves of the Panhandle and has maps of many.

a. Flora. It may come as some surprise that the twilight zones of caves in the Panhandle have a distinctive flora. Cave plants are mostly microscopic species, and in the Panhandle are limited to algae, fungi, and bacteria. While cave flora have not yet been thoroughly investigated in Florida caves, at least two species of algae have already been described as endemic to Panhandle caves (Friedmann and Ocampa 1974). Liverworts and fungi are common about the mouths of caves, and fungi occur far back in the dark zones, especially on bat guano.

b. Fauna. There are many animals that use caves casually because they provide shelter and buffered air temperatures. For many animals caves may seem to be no more than just larger cracks and burrows that they normally inhabit. The Florida wood rat (*Neotoma floridana*) commonly builds its stick nests just inside caves in the twilight zone, usually under large rocks or in fissures in the walls. The slimy salamander (*Plethodon glutinosus*), two-lined salamander (*Eurycea bislineata*), and long-tailed salamander (*Eurycea longicauda*) are three common casual visitors to the Marianna caves. The camel cricket (*Ceuthophilus* spp.) is found abundantly in Panhandle caves, in the twilight zone and throughout the dark zone. *Cambala annulata* is a cave millipede found in Marianna caves, along with the cave spider, *Islandia* sp.

5.3 Human-created Habitats

5.3.1 Fallow Lands, Succession, and Mixed Hardwood Forests

Today, most of the pine forests in the Coastal Plain are very different from the native longleaf communities they have replaced. First, the pines themselves are different. Shortleaf (*Pinus echinata*), loblolly (*P. taeda*), and slash pine (*P. elliottii*) have replaced longleaf pine. Second, these areas are as much hardwood communities as they are pine forests. These replacement forests are old field successional communities, and they result from the most serious of human impacts to longleaf forests: soil disturbance.

a. Soils. The soils of fallow lands are usually the richest and the highest in elevation—those that are naturally best suited for agriculture. In the Panhandle, the best agricultural soils are the loamy soils of the Northern Highlands. The sediments of the Miccosukee and Citronelle Formation in the Northern Highlands, and the nutrient rich calcareous soils of the Marianna Lowlands attracted the first settlers and consequently, have been disturbed by the plow the longest. In the Coastal Lowlands cultivated and, later, fallow land have always been less abundant because the sandy soils are poor for agricultural use. Site preparation for silviculture has had similar impacts in the Coastal Lowlands (see Section 5.3.3).

b. Ecology. At one time or another, most of the naturally richer soils of the Coastal Plain have been farmed. In the pre-Civil War South agriculture was the primary industry of the Coastal Plain, and it still is important today. Until the 1940's and 1950's, when commercial fertilizers began to be used on a grand scale, farmers had to rotate their crops from site to site and let fields lie fallow for a few years to restore their fertility naturally.

But in the Coastal Plain no land lies unclaimed for long. Many plants spread seeds using the wind, water, animals, or birds for distribution. Soon a rich flora develops on the old field sites. Several species of hardwoods from beech-magnolia forest may take root. The first of these are usually sweet gum, laurel oak, and water oak. A pine from that same forest, the loblolly pine, may recruit and establish itself provided that it can escape death by fire in the first decade of its life. The shortleaf pine also invades the old fields. It followed settlers coastward from its natural habitat in the Piedmont.

Today, many of the pine forests of the southeast grow on former longleaf sites that were cleared, farmed, and abandoned. Where these forests are burned each year, the hardwoods are suppressed, and an open, parklike panorama of large old field pines can be produced. When these stands are 40 to 80 years old, they begin to resemble the native longleaf vistas, but a closer look reveals that the replacement forests contain a very different mix of plants than the original longleaf forests. For one thing, hardwoods that grow up with the replacement pines are rarely eliminated, because their persistent roots keep putting up new shoots. If fire is kept out long enough, the large hardwood roots can thrust up stems very rapidly and grow big enough to survive the next fire.

With infrequent fires, old fields inevitably become hardwood stands. The hardwoods make it species, and in the Panhandle are limited to algae, fungi, and bacteria. While cave flora have not yet been thoroughly investigated in Florida caves, at least two species of algae have already been described as endemic to Panhandle caves (Friedmann and Ocampa 1974). Liverworts and fungi are common about the mouths of caves, and fungi occur far back in the dark zones, especially on bat guano.

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With infrequent fires, old fields inevitably become hardwood stands. The hardwoods make it even more difficult for fire to sweep through, and young shortleaf and loblolly pines cannot survive under the dense shade of the hardwoods. The old field site eventually changes into a hardwood community as the original shortleaf and loblolly individuals age and die.

The strong dependency of many native groundcover plants (and longleaf pines as well) on summer fires for sexual reproduction is probably a major reason that fallow land does not recruit the same mix of species that make up a virgin forest, even if adjacent to one. Another reason, however, is that among the species of any community, some are better adapted for colonizing bare soil than others. Bare soil of the sizes left by humans following agriculture or other artificial soil disturbance are unusual site conditions that probably never existed in presettlement times. Large patches of bare soil are quickly colonized, not by a random sample of the native flora, but by a highly biased subset of the native flora involving mostly the good colonizers (sometimes called "weeds"). These species naturally occur at very low densities under normal conditions. Broomsedge (*Andropogon virginicus*) and dog fennels (*Eupatorium* spp.), whose density on old fields can be almost impenetrable, are good examples of native species that in longleaf ecosystems are relatively rare because they are found on a few bare patches of soil that exist only for short periods. Such bare patches are created by tree tip-up mounds when trees fall over, or consist of soil pushed up by burrowing animals such as the gopher tortoise or pocket gopher. Because these patches are small and rare, the plants that are adapted for finding and utilizing them usually have high fecundity and high dispersability. Lots of seeds, produced every year and carried by the wind, ensure that these species will find the rare and fleeting bare soil sites in native longleaf communities. Fallow soil, however, is selectively colonized by these species, creating vast instead of normally tiny populations.

Weeds introduced from Asia, Europe, Africa, South and Central America, and elsewhere in North America by people have also invaded the Coastal Plain. These join with native weeds and are called ruderal "communities."

c. Flora. The mixed pine-oak-hickory forests of Quarterman and Keever (1962) are not, as they believed, the natural climax community. These communities are late successional stages of fallow lands. Numerous grasses and forbs dominate the early stages of field abandonment. Woody perennials succeed the succulent annuals, and include *Eupatorium* spp., *Rubus* spp., sassafras (*Sassafras albidum*), winged sumac (*Rhus copallina*), beautyberry (*Callicarpa americana*), and young stems of several hardwood species, including sweet gum (*Liquidambar styraciflua*), water oak (*Q. nigra*), laurel oak (*Q. laurifolia*), black cherry (*Prunus serotina*), pignut hickory (*Carya glabra*), mockernut hickory (*Carya tomentosa*), southern red oak (*Quercus falcata*), occasional live oak (*Quercus virginiana*), persimmon (*Diospyros virginiana*), and others. When these tree species begin to rise above the perennials, they are in a race skyward with the old field pines (shortleaf and loblolly). At first the pines win the race, establishing a canopy above the slower growing hardwoods. If regular fires sweep these forests after about 7 or 8 years, the hardwoods will be pruned back to rootstocks after every burn, allowing the pines to dominate the site. If no fires sweep the site, or they come at great intervals, the hardwoods will reach the canopy and share it a while with the pines. The hardwoods, however, can replace themselves with new recruits when an opening occurs in the closed canopy; the pines, being intolerant of shade, can not. Eventually, as the old-field pines die, the mixed pine-oak-hickory forest becomes an exclusively hardwood community. Most of the arable land of the Panhandle, if not presently under cultivation, is in some stage of successional recovery from it or has been totally converted into living space for people.

d. Fauna. Many of the animals that inhabit the longleaf pine clayhills uplands are found in the short leaf loblolly pine woodlands, if these are burned regularly (annually). But dense stands of young hardwoods and pines were not present in the Panhandle in pre-Columbian times, and few animals are preadapted to do well in this now common community type. A recent study of the breeding birds of an 80-year old, annually burned old-field community showed two things: (1) The fauna of the forest, which was similar physiognomically, to a longleaf pine forest, was not too different from that habitat; and (2) when the annual burning ceased, there was a measurable decline in the presence and abundance of birds that favor open, prairie-like pinelands. (Engstrom et al. 1984). In a drift-fence study comparison of an original growth longleaf pine forest with an 80-year old, annually burned shortleaf loblolly pine forest, Means and Campbell (1982) showed little difference between the terrestrial herpetofauna (Table 8). It is not known, however, what happens to the suite of species if annual fires are stopped.

5.3.2 Silvicultural Communities

Probably as much of the terrestrial environment of the Panhandle is devoted to silviculture as comprises all other terrestrial habitat types combined. The largest timber growers are private pulp and lumber corporations who have holdings in every county. Next in total area are the State and Federal lands devoted to tree farming, including the Blackwater River State Forest, Apalachicola National Forest, Eglin Air Force Base, and St. Marks National Wildlife Refuge. Tree farming by small private land owners is also extensive and may approach, in sheer acreage, the sum of the large corporate holdings.

a. Soils. Soils range from ultisols to spodisols to entisols. Pine tree silviculture is carried out on the sandiest soils throughout the Panhandle, the loamy soils of the Western Red Hills and Tallahassee Red Hills, and the acid wetland soils of flatwoods.

b. Ecology. Most of the silviculture in the Panhandle involves monospecific stands of one of three kinds of native pines: slash pine (*Pinus elliottii*), loblolly pine (*P. taeda*), and sand pine (*P. clausa*). About as much acreage in the clayhill regions of the Northern Highlands is devoted to pine tree farming as in the flatwoods country of the Coastal Lowlands. Therefore, many community types, ranging from the driest longleaf and scrub oak forests downslope to the evergreen shrub wetlands bordering flatwood streams, have been replaced by uniform silviculture. This has erased natural beta diversity and simplified site-specific community structure.

c. Flora. Usually slash pine (*Pinus elliottii*) is found on flatwoods soils or sandhill soils of the Gulf Coastal Lowlands; slash or loblolly pine (*P. echinata*) on clayey loamy soils of the Northern Highlands; and, sometimes, sand pine (*P. clausa*) on sandy soils in the Gulf Coastal Lowlands. Other trees that may occur in silvicultural stands are native hardwood species that either resprout from rootstocks or seedstocks left after site preparation, or seed into the site in the early years after planting with trees. In the clayhill regions of the Panhandle these are colonizing members of the beech-magnolia forest, including especially sweet gum (*Liquidambar styraciflua*), laurel oak (*Quercus laurifolia*), black cherry (*Prunus serotina*) and water oak (*Q. nigra*). Later, if fires are kept out of silviculture stands, even the slower colonizers such as pignut hickory (*Carya glabra*), dogwood (*Cornus florida*), and southern magnolia (*Magnolia grandiflora*) will encroach if stands are left alone for 40 to 50 years.

In flatwoods regions, silvicultural stands become rapidly invaded by many of the evergreen shrub species that attain small tree stature, such as black titi (*Cliftonia monophylla*), swamp cyrilla (*Cyrilla racemiflora*), and sweetbay magnolia (*Magnolia virginiana*). Often a plethora of shrubby evergreen species encroaches as well, including fetterbush (*Lyonia lucida* and *Leucothoe racemosa*), stagger bush (*L. ferruginea*), large gallberry (*Ilex coriacea*), pepperbush (*Clethra alnifolia*), and St. Johnswort (*Hypericum* spp.). As one approaches the coast in the Panhandle, the water table rises nearer to the surface of the ground. The increased moisture greatly stimulates the groundcover, producing rank growth. Scarified wet flatwoods soils in the Panhandle are dominated by a luxuriant growth of St. Johnswort.

On sandhills, site preparation does not eliminate species of scrub oaks that occur in the original xeric longleaf pine communities. Usually the cloning species resprout from root fragments, these are turkey oak (*Quercus laevis*), blackjack oak (*Q. marilandica*), and bluejack oak (*Q. incana*).

Some shrubs found in silvicultural areas are sparkleberry (*Vaccinium arboreum*) and plums and cherries (*Prunus* spp.), but the closed canopy in pine tree forests after about 5–8 years of growth usually shades out most of the shrub species.

Several herb species are common to all silviculture sites. Some of these are species of bluestem grasses (*Andropogon* spp.) and blackberry (*Rubus* spp.). It is notable that vines of the genus Smilax are also invariably present in pine tree farms.

Succession of a limited sort is obvious in pine silviculture. At first, the planted pines grow in an open prairielike environment with grasses and forbs abundant. After 8–15 years, however, depending on soils, the pine canopy closes and shades the ground so severely that often only a brown carpet of pine needles is visible on the forest floor.

d. Fauna. The pine trees of pine tree farms produce resinous, acid litter that neither decomposes readily nor is readily eaten by many primary consumers. Among those that do eat the dead needles are harvestmen, which are reasonably numerous in silvicultural sites. Other insects are generally restricted to lepidopteran larvae adapted to eating pine needles or beetle larvae and adults that eat the cambium of trees.

Amphibians are restricted to those species that enter silviculture sites from adjacent communities. Most notable is the southern toad (*Bufo terrestris*); others are the oak toad (*B. quercicus*), and, usually, the pinewoods tree frog (*Hyla femoralis*). These eat the insects and other arthropods found in the litter or on boles of trees.

Lizards are scarce because of the paucity of insects, but usually the ubiquitous anole (*Anolis carolinensis*) can be found at least near the edges of silvicultural sites. Sometimes the eastern glass lizard (*Ophisaurus ventralis*) is present, and in pine tree farms in sandhills, the fence swift (*Sceloporus undulatus*) can be found. Snakes are almost nonexistent in pine tree farms because they feed at higher trophic levels than insects, but if a snake is to be found it most likely is the black racer (*Coluber constrictor*), which feeds on lizards. It is common to see the gopher tortoise (*Gopherus polyphemus*) dig out of its burrow after site preparation, and gopher tortoise populations flourish after replanting on silvicultural sites; invariably after about 10 years, when the canopy closes and shades out the valuable herbaceous groundcover food of the tortoise, the species becomes locally extinct. This holds true for the entire community of herbs, shrubs, vines, insects, and vertebrates. For the first 5 to 10 years, a productive groundcover flourishes and forms the basis for a rich animal food web. After canopy closure, and until clearcutting 20–40 years later, the entire understory community nearly vanishes.

Before canopy closure, grassland birds are common and do well as both winter visitors and summer residents. After canopy closure, very little bird life visits pine tree farms except those that glean foliage, and feed in the canopy. Few species breed in silvicultural sites.

Mammals are restricted to low density populations of those species that normally inhabit the natural pine forest lands on which a given site is developed. Species usually include the cotton rat (*Sigmodon hispidus*), cotton mouse (*Peromyscus gossypinus*), short-tailed shrew (*Blarina brevicauda*), and the least shrew (*Cryptodus parva*). White-tailed deer (*Odocoileus virginiana*) use pine tree farms in early successional stages when forage is close to the ground and abundant. After canopy closure, whitetail use falls off dramatically. Other mammals usually are transients.

In drift fence studies on silvicultural plots on the Apalachicola National Forest, Means (unpubl. data) trapped the rare southeastern shrew (*Sorex longirostris*) in a flatwood slash pine forest that was bedded. Generally, no rare, endangered, or threatened species are restricted to pine tree farms, or even commonly found there.

Chapter 6. FRESHWATER HABITATS

6.1 Introduction

We define the freshwater habitats of Panhandle Florida as beginning where the water table first rises to the elevation of the soil surface. This usually happens at the lower sides of catchment slopes, somewhere near the stream valley bottom. Habitats that are neither strictly aquatic nor strictly terrestrial are called wetlands. Downslope, water from wetlands flows in an ever increasing volume as it works its way to the sea. As it joins other water to form larger and larger channels, the increasing volume of water and its changing physical attributes create a continuum of changing aquatic habitats. These habitats as well as ponds, swamps, and lakes are all considered in this chapter.

The U. S. Fish and Wildlife Service (USFWS) (Cowardin, et al. 1979, p. 3) defines wetlands to be "...lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface or the land is covered by shallow water...wetlands must have one or more of the following three attributes: (1) at least periodically, the land supports predominantly hydrophytes; (2) the substrate is predominantly undrained hydric soils; and (3) the substrate is nonsoil and is saturated with water or covered by shallow water at some time during the growing season of each year."

Under the unpublished classification scheme of the Florida Natural Areas Inventory (FNAI), communities in Florida having these characteristics are classified as "palustrine." These are "...lands regularly inundated or saturated by freshwater and characterized by wetland vegetation." The FNAI list contains 19 palustrine community types of which all are found in Panhandle Florida. Below we use the FNAI designations, expand upon them where we believe it warranted, or at least mention them under our own heading.

The terms "lotic" and "lentic" are usually used in aquatic systems to refer to bodies of open water either running (lotic), such as rivers, creeks and streams; or standing (lentic), such as ponds and lakes. Wetlands that are periodically or ephemerally covered with water may be incorporated into this scheme depending on their source and period of inundation. In this particular case the term lotic is expanded to include not only the aquatic portions of streams but their associated floodplain wetlands as well. Likewise, standing water wetlands such as swamps, marshes, and savannas which may fringe the margin of lakes and ponds are called lentic systems.

The treatment of freshwater habitats will follow the same pattern as that in the section on terrestrial habitats: freshwater habitats are considered to be aligned along a soil moisture and stream gradient. The first freshwater habitats discussed are those immediately downslope from dry ground, called wetlands, or palustrine habitats. Next, we will discuss streams and rivers that form as water flows downhill from palustrine habitats into channels sculpted by water in the landform.

It is important to note that the slope of the catchment valley sidewalls has a very strong influence upon the type of wetland or stream encountered. In catchments with steep slopes cut by gully erosion, streams and the adjacent wetlands are confined to a narrow band where the two slopes intersect. The hydrology and biology of such streams is very different from streams with gently sloping valley walls. When stream catchments are not deeply etched into the landform, such as those in the flatwoods of the Coastal Lowlands, the wetlands adjacent to the stream form very broad fringing zones.

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6.2 Native Palustrine Habitats

6.2.1 Herb Bogs and Savannahs

Much of the geological structure underlying the Florida Panhandle is deep, porous sand often containing relatively impermeable clay lenses. In combination with the high annual rainfall, this condition causes the buildup of small reservoirs of perched groundwater. Where slopes are very steep, such as those in steepheads that characteristically are 45° or more, seepage escapes into a well-defined stream channel, and little boggy wetland exists. But where the sloping ground surface is very gentle, such as in the Gulf Coastal Lowlands (Figure 5), it intersects the horizontal water table over a fairly broad zone. Here the water seeps laterally, forming wetlands called bogs (Figure 63).

The first of the wetland zones normally encountered downslope from longleaf pine forests in stream valleys with gentle slopes, is called a "seepage bog," or a "herb bog." Panhandle Florida and the adjacent lower Gulf Coastal Plain of Alabama and Mississippi were once nearly continuous bogs (Bartram 1791, Harper 1914), containing one of North America's most unusual assemblages of animals and plants, including many that are rare, endangered, or endemic. Calculations by Folkerts (1982) indicate that nearly 97% of the original herb bog habitat has been destroyed throughout the Gulf Coastal Plain. The largest acreage and some of the best remaining examples of this unique wetland type are found in the Coastal Lowlands areas in Panhandle drainage basins from the Perdido to the Ochlockonee Rivers. Seepage bogs decline rapidly in both acreage and number to the east of the Ochlockonee, and are not a particularly important habitat type in the Florida Big Bend.

Although defined as wetlands, seepage bogs of various types are sometimes quite dry. During periods of wet weather when the perched aquifers are fully charged, seepage is continuous and the soil of herb bogs is moist and difficult to walk in because of sinking into the wet organic deposits. At the other extreme, during seasonal or extended droughts, the soil of herb bogs tends to dry out and sometimes crack. In order to tolerate the drastic soil moisture changes animals and plants must have specific adaptations to resist death or physiological stress.

Because of the activity of the mineral components of the soils, bog soils typically are low in pH. Values range from 3.4 to 5.0 (Wharton 1977, Clewell 1981, Folkerts 1982). This, coupled with low-nutrient soils, makes bogs home to only those plants that can tolerate such extreme conditions.

a. Flora. Typically, Panhandle seepage bogs contain insectivorous plants, including two or more species of *Drosera*, the sundews; two or more species of *Sarracenia*, the pitcher-plants; two or more of *Pinguicula*, the butterworts; and occasionally *Utricularia*, the bladderworts. Because the distinctive leaves of some species of pitcher plants are so conspicuous, these bogs are often called "pitcher plant bogs." Many other genera of forbs characteristic of highly acid sites are associated with the carnivorous plants, including *Sphagnum*, *Eriocaulon*, *Calopogon*, *Habenaria*, and *Burmannia*. Wiregrass (*Aristida stricta*), beaked rushes (*Rhynchospora*), panic-grasses (*Panicum*), and sedges are among other dominant herbs.

When the seepage slopes of flatwoods stream valleys are extremely gently inclined, the herb bog zone can be hundreds of meters wide (Figure 64). In this case, the open, treeless plain often is called a savannah. The region located in the western half of the Apalachicola National Forest between the settlements of Wilma and Sumatra is particularly noted for extensive seepage bog savannahs developed on fine clays and silts (Clewell 1971).

Clewell (1971) has studied these savannahs and believes there are four variations:

(1) *Verbesina* phase. This is an open savannah with loamy surface soils. The indicator species is Chapman's crownbeard, *Verbesina chapmanii*, a summer flowering composite.

(2) *Pleea* phase. This too is an open savannah, but with sandy soil. The indicator species in the ground cover is an autumn flowering lily, rush featherling (*Pleea tenuifolia*).

(3) Hatrack phase. This is a less open savannah with one to many stunted slash pines (*Pinus elliottii*) with spindly trunks and abbreviated limbs.

(4) Pine-titi phase. This is an even less open savannah with some *Pleea* and larger slash pine, pond pine (*Pinus serotina*), titi (*Cyrilla* spp., *Cliftonia monophylla*), cypress (*Taxodium distichum* var. *nu-*

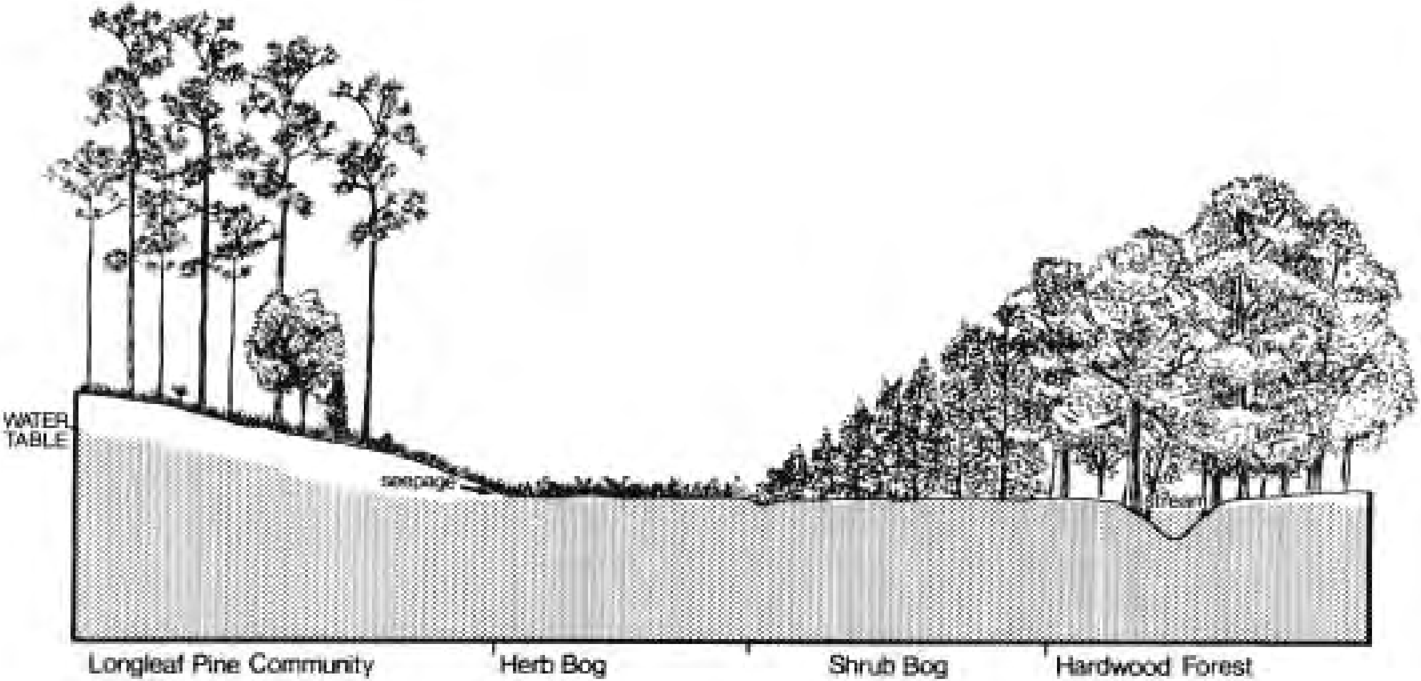

Figure 63. Flatwoods seepage bog developed along a gentle slope/moisture gradient.

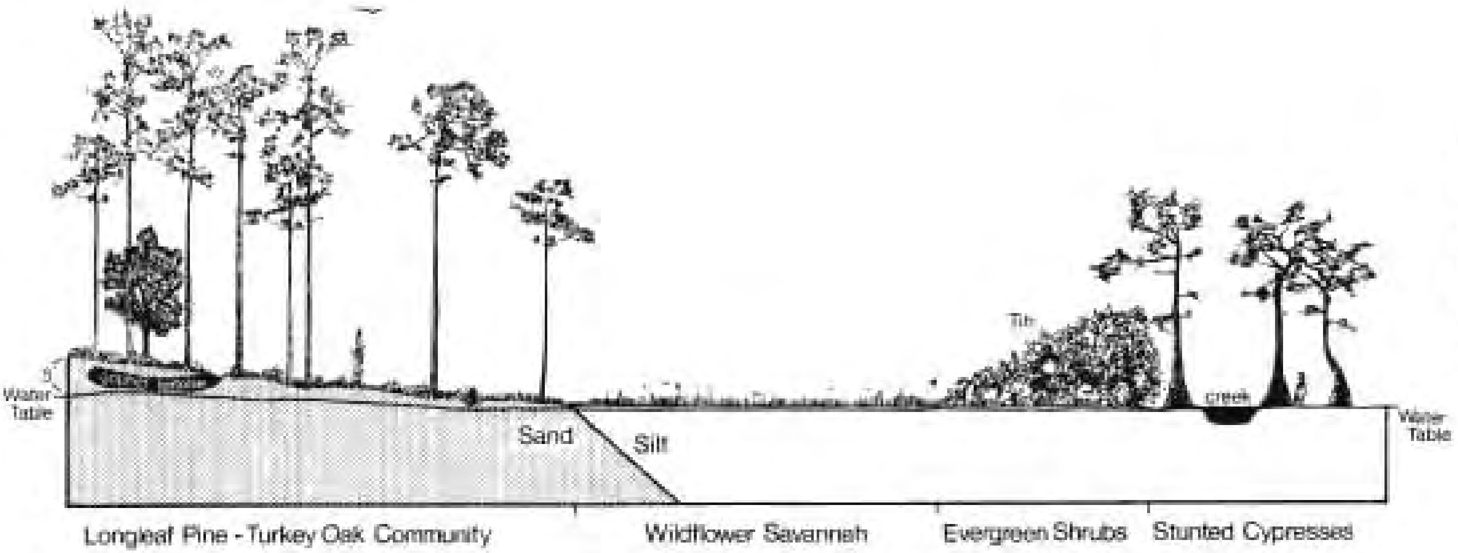

Figure 64. Flatwoods savannah, a special case of a seepage bog that is underlain by silt and has a nearly level slope.

tans), sweet bay (*Magnolia virginiana*), wax myrtle (*Myrica cerifera*), fetter-bush (*Lyonia lucida*), myrtle-leaf holly (*Ilex myrtifolia*), and large gallberry (*Ilex coriacea*).

This fourth phase is regarded as continuous with titi swamps. Were it not for the lack of saw palmetto (*Serenoa repens)* and the presence of pitcher-plants and other characteristic savannah species, the pine-titi phase could be considered transitional to titi swamps.

These communities are noted for their dense growth of grasses and sedges interspersed with an abundance of wild flowers numbering well over a hundred species. Among these are many orchids and insectivorous plants. Wiregrass usually dominates although it may be absent from the *Pleea* phase. Species of *Panicum* are also important. Beak rush (*Rhynchospora chapmanii, R. plumosa*) and several nut rushes (*Scleria baldwinii, S. reticularis*) are among the more important sedges. A pseudocanopy of St. Johnswort (*Hypericum* sp.) often covers the entire community. The needlelike leaves apparently allow considerable light to reach the ground cover below.

The level of soil moisture in savannahs is consistently higher than in pine flatwoods and even in some bay communities. The heavy loams and highly organic sands are indicative of a perched water table. After heavy rains the soils may be totally saturated for extended periods, giving rise to the name herb bog.

In addition to the ecotone between the pine-titi phase and the titi swamps, savannahs also intergrade with savannah swamps and longleaf pine flats. Clewell (1971) summarizes the ecological relationships of savannahs to other vegetation and theories on their origin and maintenance. According to Clewell, *Verbesina chapmanii* grows only in heavy soils and *Pleea tenuifolia* only in sands or sandy loams; they do not grow together. Barbara's-buttons (*Marshallia graminifolia*) may also be a good indicator of the *Pleea* phase. Several other species seem to be associated only with *Verbesina* savannahs. The *Verbesina* phase is generally freer of shrubs and does not contain black titi, fetterbush, or large gallberry. The clays underlying the *Verbesina* phase extend downward at least 8 ft. The proximity of these clays to the Apalachicola River suggests that they represent alluvial deposits, which accumulated as the river shifted course during the Pleistocene. Ripples of sand on top of these clays provide the elevated knolls upon which longleaf pines grow.

The curious hat rack slash pines may have become established during periods of fire suppression. The poorly adapted pines were able to grow sufficiently to withstand the next fire. Pritchett (1969) studied slash pine growth in a savannah having a weston fine sandy loam, which is a humic gley soil. He found that the poor drainage caused by a sandy clay substrate within 25 cm of the surface, reduced the aeration needed for growth in pine roots. He also found that low levels of phosphorus restricted growth. Applications of phosphate on an unditched site with minimal site preparation raised the site index (a numerical evaluation of the quality of a habitat for plant productivity used by the U.S. Forest Service) from 28 to 68 .

The question has been raised whether southeastern savannahs are successional, permanent, or artifactual communities. Penfound (1952) suggested that savannahs could be created by excessive fire or logging. Wells and Shunk (1928, 1931) in a classic study on a savannah in North Carolina noted that nearly all savannah vegetation grew on hammocks which they believed to be the soil around former root systems in a shrub-bog of blackgum (*Nyssa sylvatica*) and swamp titi (*Cyrilla racemiflora*). With a drop in the water table in post-Pleistocene times, the savannah replaced the shrub-bog, at least in part because of increase in the incidence of fire associated with a drier habitat.

Pessin and Smith (1938) noted that the logging of longleaf pines resulted in a higher water table in successive years and in a subsequent invasion of pitcher-plants and other savannah species which had been absent previously. They suggested that removing the trees reduced the evapotranspiration sufficiently to raise the water table, or rather to prevent its being lowered. Wahlenberg (1946) expressed the same opinion on savannah formation.

Quintus A. Kyle (pers. comm. to Clewell 1971) added substance to that theory. He said that some of the present savannahs west of Bradwell Bay in the Apalachicola National Forest (ANF) were formerly low, wet longleaf pine flatwoods that were not as densely stocked as pine-palmetto flatwoods usually are. These pines were cut in about 1915, and thereafter the water table rose and savannah vegetation became evident. It seems likely that the acreage of savannahs has increased since the initial logging in the ANF. If so, much of the *Pleea* phase may have once been low flatwoods, which are now being converted to savannah because of a rise in the water table. The pine-titi phase would then represent additional areas being converted to savannahs, but lack of fire has allowed the invasion of brush.

Of course the reduction in evapotranspiration is not necessarily the only mechanism for raising water tables and thereby creating savannahs. Clewell (1971) suggested that slumping of the surface could be creating wet depressions as organic acids dissolve calcareous deposits in underlying Miocene clastics.

The *Verbesina* savannahs lack pine stumps, but adjacent longleaf pine flats still retain stumps remaining from the original timber harvest. This observation suggests that the *Verbesina* phase is a permanent, edaphic vegetation type, and was not created via recent reductions in evapotranspiration. The heavy soils probably retain water much more effectively than sands. Evidence for this comes from a somewhat loamy savannah of the *Pleea* phase near Fort Gadsden (SW 1/4 Sec. 29, T6S R7W), where the savannah is actually a foot or so higher in elevation than the adjoining, sandier, drier pine-palmetto flatwoods (Clewell 1971).

Changes in savannahs in northwest Florida resulting from disturbance were indicated by Pullen and Plummer (1961). They resurveyed a savannah studied in 1906 by R. M. Harper, which had since been drained and intensively grazed. They counted 98 species not listed by Harper, many of them weedy, that were introduced because of disturbance. They also said that about 50 species had been eliminated, including spectacular species of pitcher-plants (*Sarracenia* spp.), sundew (*Drosera* spp.), *Agalinis*, *Aster*, *Coreopsis*, colic-root (*Aletris* spp.), meadow-beauty (*Rhexia* spp.), cone-flower (*Rudbeckia* spp.), *Sabatia* spp., and *Balduina* spp.

Wells and Shunk (1928) noted the complete lack of legumes in a savannah in North Carolina. Legumes are rare or absent in savannahs of the ANF, although many species are represented, some abundantly, in adjacent pinelands. Perhaps the nitrogen-fixing bacteria in leguminous roots cannot survive the long hydroperiods of savannah soils.

Wells (1967) remarked on the large number of species with leaves appressed against their stems, which he interpreted as a mechanism to prevent transpiration. Plants of savannahs may be physiological xerophytes, even though they grow in wet soils, because high acidity prevents the rapid absorption of water.

b. Fauna. As expected in a plant community lacking trees and shrubs, no arboreal fauna is present. The herb-dominated bogs and savannahs of the Panhandle support a rich diversity of insects that feed upon the numerous species of groundcover plants. These in turn feed a small group of vertebrate insectivores, including most notably the pine woods tree frog (*Hyla femoralis*), the ornate chorus frog (*Pseudacris ornata*), and the Florida chorus frog (*P. nigrita*). Burrowing crayfishes of the genera *Cambarus* and *Procambarus* (Hobbs 1942) can be unusually abundant in herb bogs. Although never studied, it appears quite probable that burrowing crayfishes have a strong beneficial influence upon other animals that use the burrows for protection from enemies and the elements. Among these species are the two-toed amphiuma (*Amphiuma means*), southern dusky salamander (*Desmognathus auriculatus*), and the mud salamander (*Pseudotriton montanus*).

In the western Panhandle from Washington to Santa Rosa Counties, the pine barrens tree frog (*Hyla andersonii*) seems to be exclusively dependent upon herb bog seepage sites for breeding (Means and Longden 1976, Means and Moler 1979).

Reptiles that use herb bogs include the garter, ribbon, and mud snakes (*Thamnophis sirtalis*, *T. sauritus*, *Farancia abacura*). The mud turtle (*Kinosternon subrubrum*) and box turtle (*Terrapene carolina*) are also common herb bog inhabitants.

Grassland birds like the meadow lark (*Sturnella magna*) and the red-winged blackbird (*Agelaius* *phoeniceus*) are visitors in herb bogs occasionally and the common yellowthroat (*Geothlypis trichas*) is found along shrubby edges. The rice rat (*Oryzomys palustris*) and cotton rat (*Sigmodon hispidus*) are important and common small mammals that live in herb bogs, the rice rat being more at home during wet weather when the bogs are wet, and the cotton rats more so during drought.

6.2.2 Shrub Bogs, Titi Swamps, and Bay Swamps

Downslope from herb bogs, a dense growth of evergreen shrubs is encountered in Panhandle flatwoods. When fire cycles are operating normally, the transition from open herbaceous prairie to dense, small- and leathery-leaved shrubs is often abrupt (Figure 63). Predominant among these shrubs are the titis of the family Cyrillaceae, with either black titi (*Cliftonia monophylla*) or swamp titi (*Cyrilla racemiflora*), or both, present. Other evergreen shrubby species usually present with the titis are the fetterbushes (*Lyonia lucida* and *Leucothoe racemosa*), myrtles (*Myrica cerifera* and *M. inodora*), dahoon holly (*Ilex cassine*) and large gallberry (*I. coriacea*), sweet pepperbush (*Clethra alnifolia*), and others. In Panhandle Florida evergreen shrub communities of this type usually fringe swamp forests of several types. The shrub zones are rarely extensive, but form a very distinctive transition from the dry soil uplands or moist soil herb bogs to the stream or pond gallery forests described below.

Pine flatwoods are frequently dotted with swampy depressions and minor drainageways occupied by shrub-bog species and small trees, mostly evergreens. Such systems are loosely referred to as "bays" or "bay swamps." These swamps may support primarily titi (*Cyrilla racemiflora, Cliftonia monophylla*), in which case they are called titi swamps. Titi swamps may contain scattered pond pines (*Pinus serotina*) or slash pine (*P. elliottii*) extending above a dense growth of titi. Small, round bay or titi swamps of a few acres or less are locally called ponds, even if they contain no standing water.

Larger bay swamps usually contain taller trees toward the center and are fringed with titi. Sweetbay magnolia (*Magnolia virginiana*) and slash pine are common species. Where such swamps form the headwaters of a small creek, they are known as "bayheads." Intermittent streams lined with elongated bay swamps are known as bay branches. Where Atlantic white-cedar (*Chamaecyparis thyoides*) grows conspicuously within bay or titi swamps the area is locally called a juniper swamp.

Large bay swamps may also encircle moister sites occupied by cypress or blackgum swamps. Cypress swamps that are circular in shape are known as cypress domes or heads because the trees in the center tend to be taller than those along the margins, giving a circular dome shape to the canopy. The center trees may be taller because conditions there are more optimum for cypress growth than the margins. Elsewhere in Florida, researchers have noted that the taller trees in the center may or may not be older than the fringing trees (Duever et al. 1976). Kurz (1933b) hypothesized that the shape of cypress domes was created by the pruning effect of fires. Shorter, younger trees would be produced at the margins by more frequent fires there, and larger, taller trees would result from fewer fires as one moved toward the deeper water in the center of domes. Cypress swamps that are elongated along a slough or other small drainageway are called cypress strands.

Within large areas of bay, cypress, or blackgum swamps, small patches of pine flatwoods may occur. These pine islands usually occupy the more elevated sites.

The ecotonal changes from pineland to titi, bay, cypress, and blackgum swamps usually involve an elevation drop of less than 4 m (12 ft). The horizontal distance may be as small as 16–66 m (50–200 ft). Below this point or as the size of the swamps increase, the community type changes to bottomland hardwood forest or cypress-gum swamp forest.

a. Bay swamps. Clewell (1971) identified four phases of bay swamps; (1) Sweetbay phase where sweetbay (*M. virginiana*) is dominant with a few slash pines, swamp bay (*Persea borbonia*) and loblolly bay (*Gordonia lasianthus*); (2) Slash pine phase, with sweetbay present but slash pine dominant; (3) Mixed swamp phase, with dominance shared by sweet bay, blackgum, cypress, sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), water oak (*Quercus nigra*), and diamond-leaf oak (*Q.*

laurifolia); and (4) Atlantic white cedar phase, as mentioned above; Atlantic white cedar (*Chamaecyparis thyoides)* is a conspicuous member of the community.

The patchy, often dense understory of bay swamps contains a mixture of switch cane (*Arundinaria gigantea*), wax myrtle (*Myrica cerifera*), swamp titi (*Cyrilla racemiflora*), sweet pepperbush (*Clethra alnifolia*), and black titi (*Cliftonia monophylla*). Other common species include wild azalea (*Rhododendron canescens*), fetter-bush (*Lyonia lucida*), large gallberry (*Ilex coriacea*), muscadine (*Vitis rotundifolia*), myrtle leaf holly (*I. myrtifolia*), odorless wax myrtle (*Myrica inodora*), climbing fetterbush (*Pieris phyllyreifolia*), an epiphytic shrub on pine or cypress, red chokeberry (*Aronia arbutifolia*), highbush blueberry (*Vaccinium corymbosum*), odorless yellow jessamine (*Gelsemium rankinii*), and poison ivy (*Toxicodendron radicans*).

Ground cover consists of patchy beds of peat moss (*Sphagnum* spp.), Virginia and netted chain ferns (*Woodwardia virginica, W. areolata*), sedges (e.g., *Carex glaucescens*), and grasses (e.g., *Panicum tenerum*). Cane (*Arundinaria gigantea*) may occur in openings.

The soil in bay swamps is highly organic sand often overlain by peat. The peat may erode into hammocks and hollows giving some microrelief to the terrain. The soil is usually moist and at times may be inundated with several inches of water. The water table seldom lies more than 1 m below the ground level. Pines are not common in bay swamps primarily because of the wetness and the buffer provided by fringing titi swamps.

b. Titi swamps. Titi swamps come in five varieties, three of which have a pine overstory: (1) A titi phase with no overstory of pines, (2) A pond pine phase, (3) A slash pine phase, (4) A pond pine-slash pine phase, and (5) A holly phase with neither a pine overstory nor titi, having myrtle-leaf holly as the dominant shrub. Atlantic white cedar may be locally common.

This community is distinguished by its understory of dense shrubbery. The dominant species include one or more of two titi species, black titi (*Cliftonia monophylla*) and swamp titi (*Cyrilla racemiflora*). Black titi is the most common and tends to occur on higher sites than swamp titi. Other common species of shrubs include fetter-bush, large gallberry, and switch cane. Less common but still frequent species include staggerbush (*Lyonia ferruginea*), sweet pepperbush (*Clethra alnifolia*), and odorless wax myrtle. Ground cover is generally absent. Saplings of swamp bay or sweet bay may be present.

Soils in titi swamps are similar to those in bay swamps: highly organic sand overlain by peat. Generally the roots of the shrubs bind the peat soils, but under the influence of fire and intense rainfall erosional channels may develop, leaving little islands of thicker peat between swales burned down to mineral soils. As in bay swamps the water table is always close to the surface. During wet periods standing water pockets are common.

Titi swamps often border on pine flatwoods and may form along the borders between bay swamps and pine communities as well. Titi swamps tend to be poor fuel for the frequent fires that maintain pine dominance in neighboring flatwoods. Usually no more than the outer fringes of titi swamps burn. Thus they act as a protective buffer between pine communities and more fire sensitive bay swamps. In places the titi swamp may also border cypress or blackgum swamps, affording them the same buffer.

During prolonged summer droughts when humidity is low and the water table depressed, fire may spread into the titi swamps or be started there by lightning. Clewell (1971) estimated these conditions could occur once every 5 to 10 years. Wharton et al. (1976) estimated that the fire period in titi swamps was 20–50 years in monospecific stands of black titi. When such fires do ignite, they tend to be very hot and hard to contain. Usually all aerial stems are destroyed and some or all of the peat may also burn. Larger pines if present may survive, but most of the trees and shrubs will be killed if fires burn deeply into the peat and kill their roots.

Subsequent to fires that do not burn into the peat, the titi and other shrubs resprout from root crowns, directly regenerating the swamp without going through successional stages. Often several sprouts may arise from each crown, creating trees and bushes with multiple trunks. It has been suggested that the root crowns of these multitrunk resprouted trees and shrubs may be centuries old (Clewell 1971).

Titis (Cyrillaceae) are but one group of evergreen shrubs or small trees that in the pre-Columbian Coastal Plain naturally occurred downslope from the fire-frequent longleaf pine forest in places where soil moisture was high enough to preclude fires in most normal years. The titis and the other evergreen woody species associated with them are fire-tender hardwoods that die when their stems are heated. The evergreen shrub zone naturally occurs just upslope along the margin of stream hardwood forests occupying creek bottoms where stream valley soils usually are saturated. This was the narrow, original zone of slash pine, also.

When fires are kept out of the flatwoods in the Coastal Lowlands for long periods of time, as they have been in Florida National Forests by anthropogenic factors, the evergreen shrub species of stream hardwoods migrate upslope by seeding and root propagation. This has a twofold effect upon the ecology of the herbaceous wetlands. First, the vegetative species composition obviously changes, and so too does the vegetative structure. Instead of a grass-forb meadow habitat, the herb bog sites become closed-canopied forests of small-diameter, densely stocked evergreen trees. Because woody plants have higher evapotranspiration rates than grasses and forbs, the sheet flow that occurs in herb bogs due to seepage from the intercepted water table is depressed, changing the hydrology of the site. In flatwoods where drainage valley slopes are so gentle that they often cannot be perceived by the naked eye, the woody evergreens and other stream hardwoods expand their distribution well upslope into the longleaf-wiregrass zone. Site preparation probably is more damaging ecologically in titi areas that are to be reclaimed than in any other soil type because the delicate, gentle slope and moisture gradients are severely interrupted by chopping, disking, and bedding, and by running a fire plow through them, channelizing the water flow.

c. Fauna. The animal life of shrub bogs has not been the target of specific studies, but many Panhandle animals are known to use shrub bogs. Two frogs seem to be restricted almost exclusively to shrub bogs and the adjacent herb bogs. One is the pine barrens tree frog, *Hyla andersonii*, which uses the stems of evergreen shrub plants as foraging habitat (Means and Longden 1976, Means and Moler 1979). The other is the bog frog (*Rana okaloosae*), known from wetlands along the margins of the steephead streams of Eglin Air Force Base and a few localities in Santa Rosa, Okaloosa, and Walton counties (Moler 1985 and P. Moler, Florida Game and Fresh Water Fish Commission, Gainesville; pers. comm.).

When enough water is present for breeding, shrub bogs also support populations of the bronze frog (*Rana clamitans*), southern leopard frog (*R. sphenocephala*), green tree frog (*Hyla cinerea*), pine woods tree frog (*H. femoralis*), and spring peeper (*H. crucifer*). The five-lined skink (*Eumeces fasciatus*) and sometimes the coal skink (*E. anthracinus*) are common lizards while the green anole (*Anolis carolinensis*) and ground skink (*Scincella lateralis*) are sometimes abundant at the margins of shrub bogs. Garter snakes (*Thamnophis sirtalis*) and ribbon snakes (*T. sauritus*) forage in shrub bogs for frogs, as does the black racer (*Coluber constrictor*) and the endangered indigo snake (*Drymarchon corais*).

6.2.3 Bottomland Hardwood Forests

The forested floodplain of the Apalachicola watershed is the largest in Florida, covering approximately 450 km² (173 mi²) (Wharton et al. 1976). The predominant species in terms of cover include water tupelo (*Nyssa aquatica*), ogeechee tupelo (*N. ogeche*), baldcypress (*Taxodium distichum*), carolina ash (*Fraxinus caroliniana*), swamp tupelo or blackgum (*Nyssa sylvatica biflora*), sweetgum (*Liquidambar styraciflua*), and overcup oak (*Quercus lyrata*). These species are typical of alluvial floodplains in the southeastern United States and occur in such areas partially because of their ability to withstand saturated and inundated soils (Wharton et al. 1976).

The distribution of floodplain trees in the Apalachicola basin has been described in detail by Leitman (1978, 1984) and Leitman et al. (1983). In these studies vegetative composition was shown to be

Table 12. Types, species composition, and distinguishing characteristics of bottomland hardwood forests of the Apalachicola River (from Leitman et al. 1983).

Name	Definition	Chief associates	Common associates
Type A: Sweetgum–sugar-berry–water oak.	Sweetgum, sugarberry, water oak, American hornbeam, possumhaw, are predominant.[a]	Diamond-leaf oak, green ash.	American elm, American sycamore, water hickory.
Type B: Water hickory–green ash–overcup oak–diamond-leaf oak.	Water hickory, green ash, overcup oak, diamond-leaf oak, sweetgum, American elm are predominant.[a]	Sugarberry, red maple.	Water oak, possumhaw, American hornbeam, water tupelo, Ogeechee tupelo, baldcypress.
Type C: Water tupelo–Ogeechee tupelo–baldcypress.	Water tupelo, Ogeechee tupelo, baldcypress, swamp tupelo, Carolina ash, planertree are predominant but not pure.[a]	Overcup oak, pumpkin ash, red maple.	Water hickory, American elm, green ash, diamond-leaf oak, sweetbay.
Type D: Water tupelo–swamp tupelo.	Water tupelo, swamp tupelo, Ogeechee tupelo, baldcypress, Carolina ash, pumpkin ash, planertree, sweetbay are pure[a, b]	—	—
Type E: Water tupelo–baldcypress.	Water tupelo, baldcypress, Ogeechee tupelo, Carolina ash, planertree are pure.[a]	—	—

[a] Predominant: comprising 50% or more of basal area; pure: comprising 95% or more of basal area.
[b] Swamp tupelo, pumpkin ash, or sweetbay serve as indicator species to distinguish this type from type E.

highly correlated with depth of water, duration of inundation and saturation, sediment grain size, and water level. These hydrologic conditions are, in turn, controlled by the height of natural riverbank levees and the size and distribution of levee breaks along the river. A description of forest types, their species composition, and distinguishing characteristics is presented in Table 12 from transect plots surveyed by Leitman et al. (1983).

Alluvial rivers have broad floodplains that are dominated by two very important hydrological processes: high water and low water. During low water stages, the water flows in a meandering channel that, with time, wanders back and forth across the floodplain and continually resculpts it. The scouring action of water at the outside bends of meander loops continually undercuts the channel bank, causing the stream channel to migrate in the direction of the meander loop. Sediment eroded from the outside bends of meander loops is deposited downstream on the inside of the next bend in the river, on the advancing end of the point bar. Point bars have successional stages of plant communities developing on them from the youngest pioneer stages on new sand berms at water's edge to stable hardwood forests farther back from the water.

When rising water leaves the low-water channel, it loses its velocity—and thus its sediment carrying power—creating piles of coarser sediments called levees, or berms, along the channel banks. The coarser sediments are dropped first, and finer sediments such as silts and clays are carried farther out into the floodplain. It is not uncommon for silt and clay several inches to a few feet deep to be deposited on the floodplain floor away from the low water channel after every high water rise.

Each Panhandle river has its great annual rise sometime between midwinter and midspring (January to April), when water volume may exceed 100 times or more the normal volume in the low water channel (Foose 1983). During this 3-month period, water extends across the entire floodplain from one valley sidewall to the other. Only flood-tolerant species of plants and animals can survive in floodplains. Floodplain communities, therefore, are true wetlands, characterized by specialized wetlands species. True terrestrial vegetation is found above the level of the annual high water at the extreme lateral margins of the floodplain. The inundated floodplain of the Apalachicola River during the annual high water levels ranges from 2300 m (1.4 mi) to 6500 m (4.0 mi) wide (Leitman et al. 1983). The Apalachicola River floodplain remains inundated annually for periods ranging from 1 to 5 months (Foose 1983).

a. Ecology. A sweetgum-water oak-loblolly pine (*Liquidambar styraciflua-Quercus nigra-Pinus taeda*) association is found in dry to damp soils on elevated slopes. This forest association is most prevalent in the middle reach of the river, decreasing in area as the water hickory-overcup oak-sugarberry (*Carya aquatica-Quercus lyrata-Celtis laevigata*) association increases. This association covers approximately 43% of the floodplain, mainly in the upper and middle reaches of the river basin, and becomes increasingly uncommon in the lower reaches of the river valley where it occupies a narrow band along the river. Dominant in the lower reaches of the river basin is a tupelo-cypress-mixed hardwood association covering over 38% of the lower floodplain. Found in dry to saturated soils, this association is concentrated along existing and relict waterways just upland from the water hickory-overcup oak-sugarberry association. A somewhat similar tupelo-baldcypress (*Nyssa aquatica-Taxodium distichum*) association is located in damp to saturated soils along the entire length of the river. In addition to these major forest associations a pioneer community, dominated by black willow (*Salix nigra*), occupies a narrow zone in areas inundated more than 25% of the time.

When all forest types are considered, tupelo, baldcypress, and ash (*Fraxinus* spp.) are the three most abundant species in descending order (Table 13). Total leaf production follows the same general ranking with only a few exceptions (Elder and Cairns 1982). It is surprising, however, that relative leaf production per stem biomass of individual tree species displays a different trend. Low abundance trees such as sugarberry, overcup oak, American hornbeam (*Carpinus caroliniana*), and elm (*Ulmus* spp.) are high in relative leaf productivity while tupelo, cypress, and ash are low (Figure 65). Although no explanation for this has been advanced, it seems possible that trees occurring in saturated (and anaerobic) soils such as tupelo, cypress, and ash may be nutrient limited or may be investing energy in stem and trunk biomass. The expanded basal areas of these trees relative to other tree species strongly suggest that they invest more than an average amount of energy into stem and trunk biomass production, perhaps to aid in stabilization. This may be done at the cost of leaf production. In contrast, the more upland species can afford greater leaf production which may improve their competitive ability for light and canopy space. The higher rates of leaf production may result from investing less energy in stem and trunk biomass and perhaps from higher nutrient concentrations.

A plot of total leaf production versus hydroperiod would yield a bell-shaped curve according to productivity data of Elder and Cairns (1982). At the peak of this curve is a forest characterized by high tree species diversity and low to moderate inundation. Although speculative, this peak in leaf production

Table 13. Species abundance for all forest types combined (from Leitman et al. 1983). Species are ranked in order from most important to least important in terms of basal area. Absolute basal area and density upon which these percentages are based are 201 ft^2/acre (46.2 m^2/ha) and 623 trees /acre (1.540 trees/ha), respectively. Because of rounding, percentages given will not necessarily total 100.

Species	Relative basal area (%)	Relative density (%)
Water tupelo (*Nyssa aquatica*)	29.9	12.8
Ogeechee tupelo (*Nyssa ogeche*)	11.0	6.6
Baldcypress (*Taxodium distichum*)	10.6	5.5
Carolina ash (*Fraxinus caroliniana*)	5.4	11.5
Swamp tupelo or blackgum (*Nyssa sylvatica biflora*)	5.0	2.0
Sweetgum (*Liquidambar styraciflua*)	4.8	3.2
Overcup oak (*Quercus lyrata*)	3.2	2.0
Planertree[a] (*Planera aquatica*)	2.9	9.4
Green ash (*Fraxinus pennsylvanica*)	2.9	2.7
Water hickory (*Carya aquatica*)	2.9	0.8
Sugarberry or hackberry (*Celtis laevigata*)	2.8	2.1
Diamond-leaf or laurel oak (*Quercus laurifolia*)	2.5	1.4
American elm (*Ulmus americana*)	2.4	1.2
American hornbeam (*Carpinus caroliniana*)	2.0	4.7
Pumpkin ash (*Fraxinus profunda*)[b]	1.9	4.4
Water oak (*Quercus nigra*)	1.8	0.5
Red Maple (*Acer rubrum*)	1.5	4.8
Sweetbay (*Magnolia virginiana*)	1.0	0.5
River birch (*Betula nigra*)	0.8	0.7
Possumhaw (*Ilex decidua*)	0.8	10.5
American sycamore (*Platanus occidentalis*)	0.6	0.3
Swamp cottonwood (*Populus heterophylla*)	0.4	0.4
Black willow (*Salix nigra*)	0.4	0.4
Swamp chestnut oak (*Quercus prinus*)[c]	0.3	0.1
Box elder (*Acer negundo*)	0.3	0.8

Other species found:

Green haw (*Crataegus viridus*)
Cabbage palmetto (*Sabal palmetto*)
Water locust (*Gleditsia aquatica*)
Red mulberry (*Morus rubra*)
Swamp-privet (*Forestiera acuminata*)
Winged elm (*Ulmus alata*)
Slippery elm (*Ulmus rubra*)
Cherrybark oak (*Quercus falcata* var. *pagodaefolia*)
Stiffcornel dogwood (*Cornus foemina*)[d]
Chinaberry (*Melia azedarach*)[e]
Black tupelo or sourgum (*Nyssa sylvatica*')

Buttonbush (*Cephalanthus occidentalis*)
Spruce pine (*Pinus glabra*)
Loblolly pine (*Pinus taeda*)
Buckthorn bumelia (*Bumelia lycioides*)
Parsley haw (*Crataegus marshallii*)
Common persimmon (*Diospyros virginiana*)
Black walnut (*Juglans nigra*)
Titi (*Cyrilla racemiflora*)
Witherod viburnum (*Viburnum cassinoides*)
Little silverbell (*Halesia parviflora*)
Plus a total of 22 additional species.

[a] Water elm according to Little (1979).

[b] Some trees identified as pumpkin ash may have been Carolina ash or green ash. Samaras (winged seeds) had dropped from the trees and seeds of all three species were mixed on the ground beneath the trees.

[c] *Quercus michauxii* according to Little (1979).

[d] Swamp dogwood (*Cornus stricta*) according to Little (1979).

[e] Introduced exotic species.

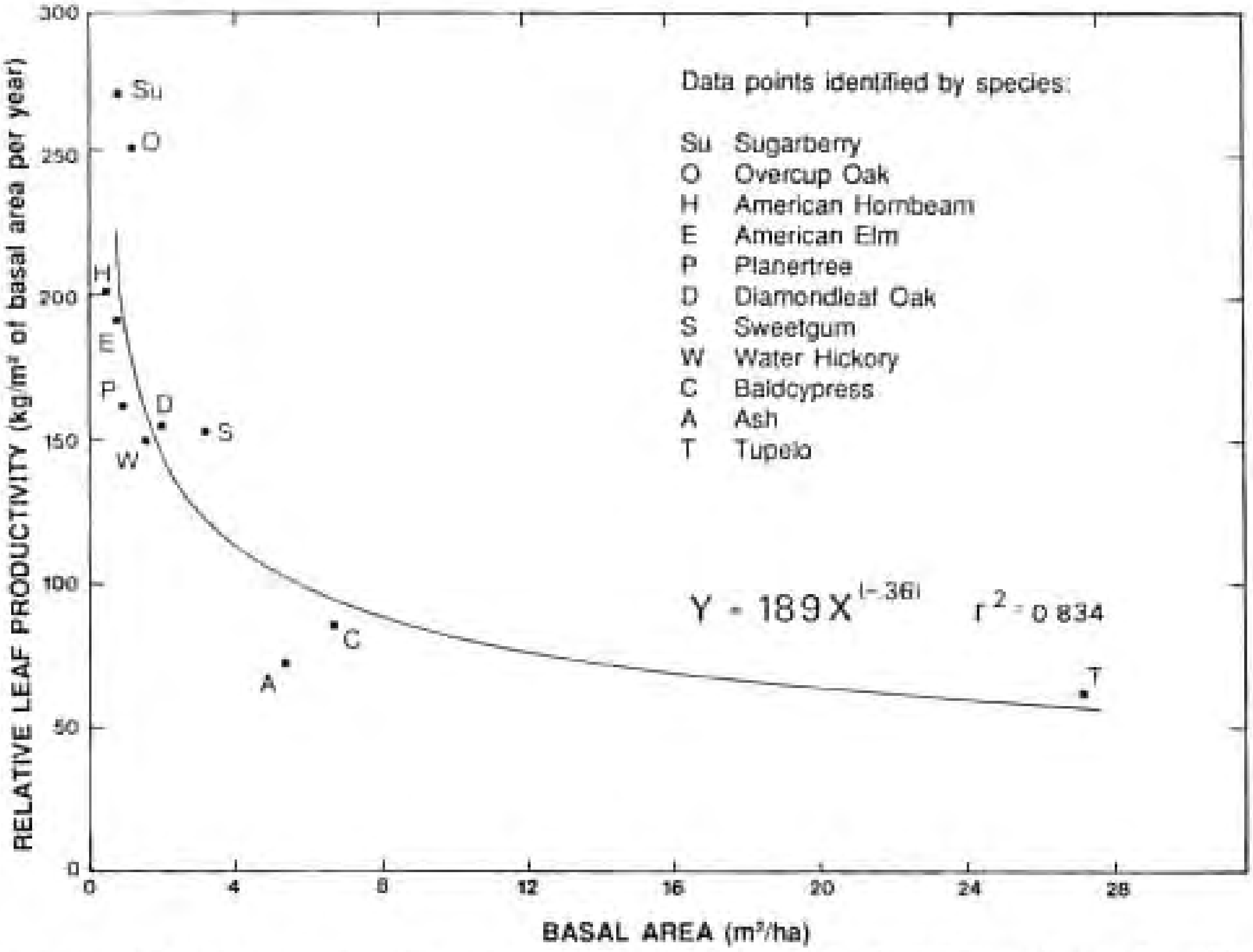

Figure 65. Relative leaf productivity per stem biomass of 11 major leaf–fall producers (trees) in the Apalachicola River flood plain (Elder and Cairns 1982).

may reflect the location of optimum conditions for floodplain forest growth. Further upland, forest productivity may be limited by competition for canopy space, nutrients, and less than optimum hydroperiod; closest to the river, productivity may be limited by the physical and chemical stresses of the increasing hydroperiod. This possibility is reminiscent of the theoretical maximum proposed for mangrove forest productivity within the freshwater to saline gradient (Carter et al. 1973).

The rate of leaf and litter production varies not only seasonally, but also as a function of forest type, individual species, and background conditions. Three patterns of seasonality are identified by Elder and Cairns (1982). The first pattern is one of high rates of leaf fall in September through December, followed by no leaf fall through late spring and only minimal rates in summer. Representative species exhibiting this pattern include water hickory, baldcypress, ash, American elm, grape (*Vitis rotundifolia*), and American hornbeam. A second pattern of leaf fall is represented by tupelo and sweetgum. These trees begin to shed leaves in the early spring and steadily increase the rate through late fall. By midwinter no leaves are falling. The third pattern is exemplified by diamond-leaf oak (*Quercus laurifolia*), overcup oak, sugarberry, and planer tree (*Planera aquatica*). These species start shedding leaves in early fall followed by a sustained release that peaks in December and January. During spring the rate decreases and by May or June leaf fall has ceased. Examples of these seasonal leaf fall patterns for three representative species are shown in Figure 66.

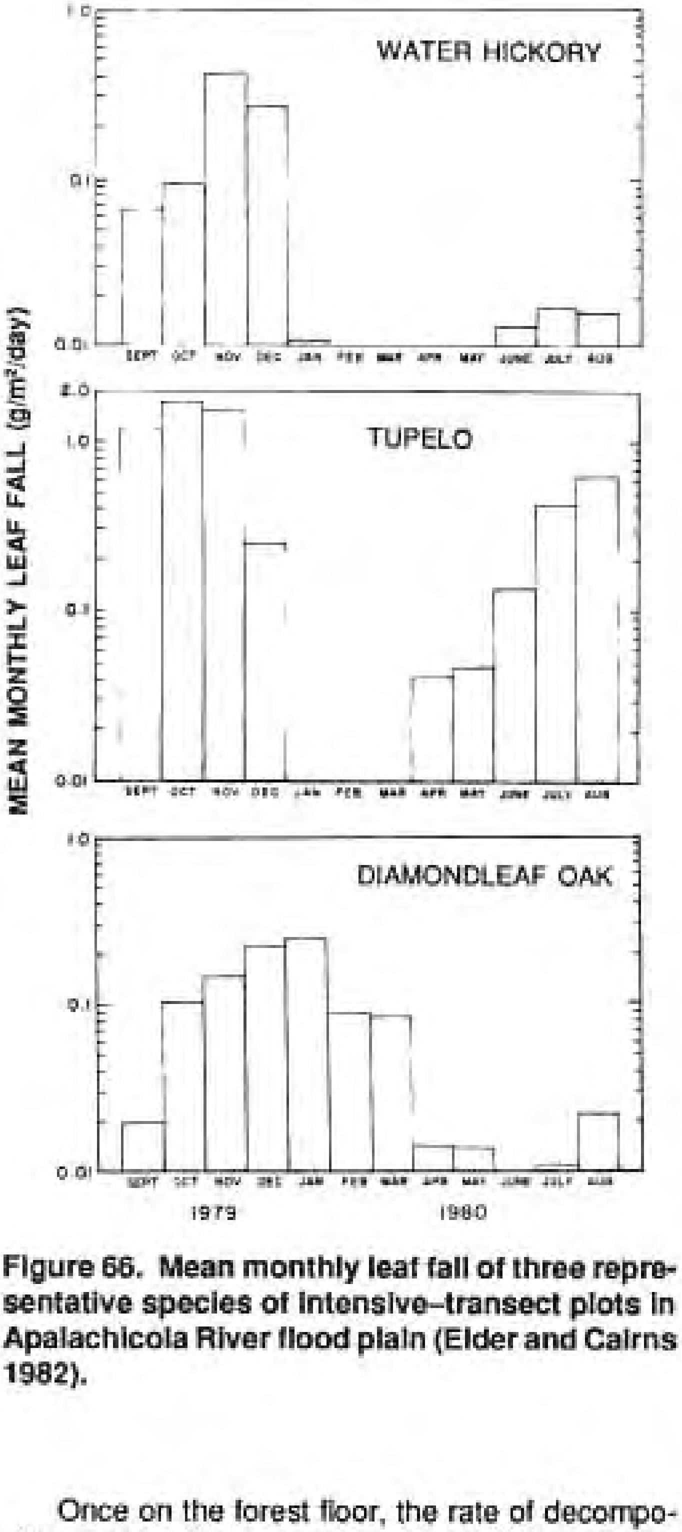

Figure 66. Mean monthly leaf fall of three representative species of intensive–transect plots in Apalachicola River flood plain (Elder and Cairns 1982).

Once on the forest floor, the rate of decomposition varies with species, environmental conditions, and the supply of chemical substance (i.e., nitrogen, phosphorus, carbon). Of five tree species monitored on continuously flooded sites, tupelo and sweetgum leaves degrade the fastest, losing essentially all of their biomass in 6 months. Baldcypress and diamondleaf oak degrade the slowest losing only 40% of their biomass in the same time period. Water hickory is intermediate in decomposition rate, and it is the most variable, with 25%–30% remaining after 6 months. On dry sites, decomposition rates are considerably lower, though the relative species rankings remain the same. The fast decomposers have approximately 60% remaining after six months, the slow ones 90%. It appears that inundation by flood waters increases the decomposition rate, a finding similar to that reported by Heald (1969) for red mangrove leaves.

Another factor controlling decomposition rate is the physical-chemical nature of the water and soil. The rate of loss of carbon, nitrogen, and phosphorus from litter are slowest in the floodplain, higher in river water, and highest at submerged locations influenced by estuarine waters. Phosphorus and nitrogen decline exponentially, with phosphorus being lost more rapidly. Carbon and total leaf material show a linear rate of decrease (Figure 67).

Apalachicola floodplain forests are an important source of energy to the river and estuary. The quantity of nutrients generated from litterfall is more than that from any other source except the upstream drainage basin (i.e., Flint and Chattahoochee Rivers). What makes the floodplain source even more important is the form in which it supplies nutrients, as particulate matter. Although the upstream basin may supply a greater load of nutrients, the bulk of this energy is in the dissolved form. Lake Seminole acts as a large settling basin for particulate matter, lowering the load delivered downstream. This causes partially decomposed leaves and other forest litter from floodplain forests to take on a relatively more important role in the metabolism of the estuary (Elder and Cairns 1982). Considerable evidence indicates that detritus in particulate form is essential to maintaining high levels of estuarine productivity (Livingston 1984).

b. Fauna. The floodplains across the Panhandle are richly endowed with animal life to match their plant species-richness. Productivity available to herbivores in floodplain forests is mostly in the canopy overstory. There, a wealth of consumer insects abounds that feed on the many kinds of leaves, mostly of palatable hardwood species. Feeding on the insects is a rich avifauna dominated by wood

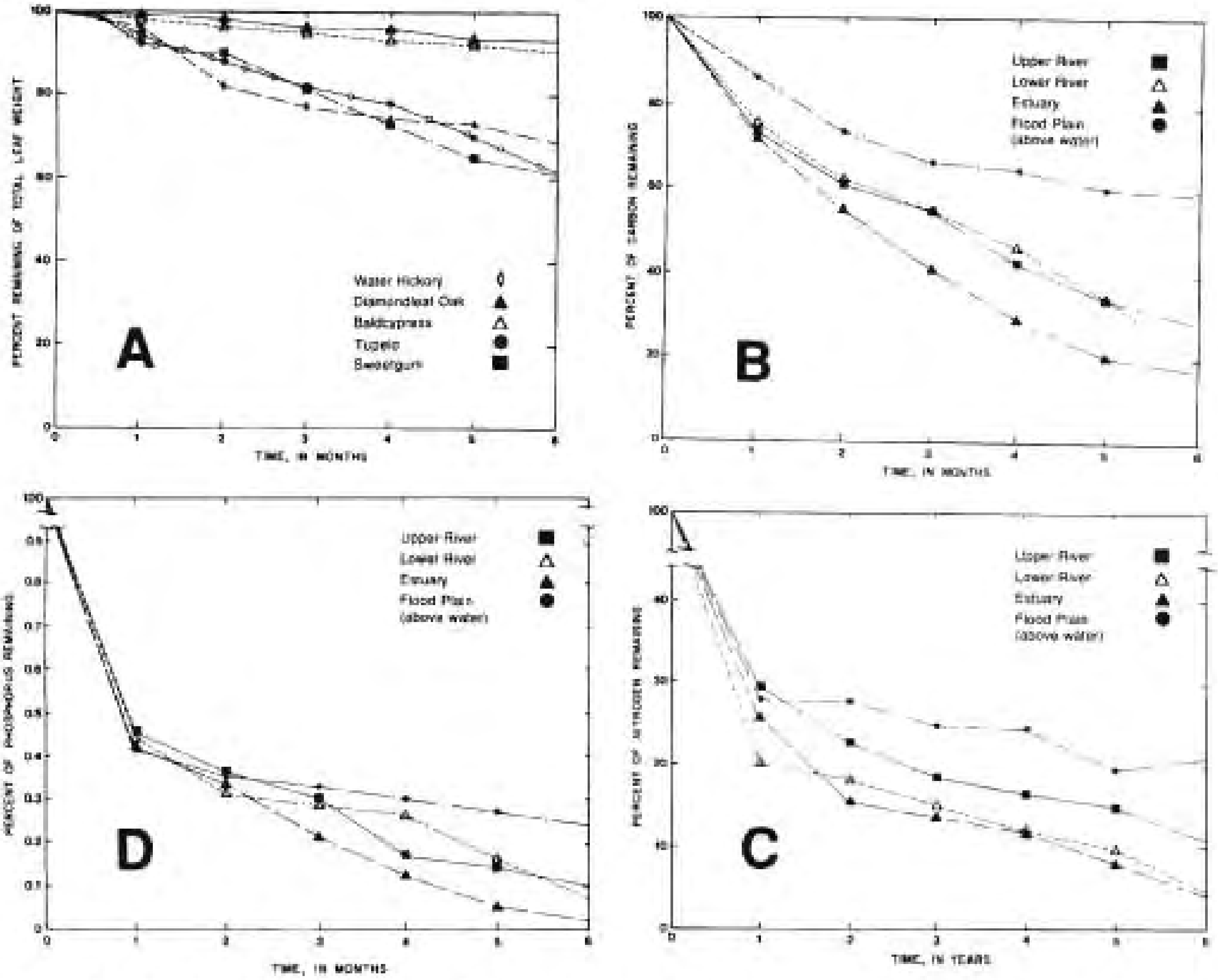

Figure 67. Decline in carbon, phosphorus, nitrogen, and total leaf mass during decomposition in Apalachicola River system (Elder and Cairns 1982).

warblers, many of which breed in these bottomland forests and in no other terrestrial habitats. The parula warbler (*Parula americana*) is one example. The only reptile that capitalizes on the canopy insects is the ubiquitous broad-headed skink (*Eumeces laticeps*).

On the floodplain floor, notwithstanding the lack of primary productivity, a rich fauna exists which is based on (1) decomposing litter from the canopy above, (2) imported litter from tributary streams, (3) nut and seedfall from overstory trees such as sweetgum, water hickory, tupelo gum, blackgum, diamondleaf oak, overcup oak, and others, and (4) the sparse herbaceous groundcover that exists on heavily filtered sunlight. Harvestmen, millipedes, springtails, isopods, and other macroinvertebrates feed directly on the detritus and are themselves food for litter-inhabiting insectivores.

Panhandle floodplains are the home of some vertebrate insectivores that are found only in floodplains. These species eat both litter consuming invertebrates and the surprising number of canopy-inhabiting invertebrates that fall to the forest floor. Among these are Fowler's toad (*Bufo woodhousii fowleri*), upland chorus frog (*Pseudacris triseriata*), northern cricket frog (*Acris crepitans*), southern dusky salamander (*Desmognathus auriculatus*), mud salamander (*Pseudotriton montanus*), one-toed salamander (*Amphiuma pholeter*), and coal skink (*Eumeces anthrocinus*).

The American beaver (*Castor canadensis*), once nearly extirpated from Florida, now is found throughout Panhandle floodplains. Its diet consists of loblolly pine, sweetgum, silverbell (*Halesia diptera*), sweetbay, and ironwood (*Carpinus caroliniana*, predominantly, but other plants employed to one degree or another are tupelo (*Nyssa* spp.), box elder (*Acer negundo*), wax myrtle (*Myrica cerifera*), witch-hazel (*Hamamelis virginiana*), spruce pine (*Pinus glabra*), and others. Beavers are responsible for damming up small streams by creating stick and mud dams across them. In the Panhandle, beaver ponds are commonly found in the abundant water in backswamps, floodplain creeks, and sloughs of the larger river bottomlands.

The eastern wood rat (*Neotoma floridana*) is common in hardwood bottomlands (Lowery 1974), building large stick and debris nests often on bare ground at the base of a tree, in a hollow log, or especially under tangles of muscadine vines (*Vitis spp.*). This rodent is one of the commonest herbivores in bottomland hardwood forests, eating buds, seeds, tubers, roots, nuts, succulent herbs, grasses, berries, and especially oak mast.

6.3 Native Riverine Habitats

There has been very little effort to make comparative studies of the streams and rivers of Florida. Furthermore, there are very few intensive studies of the ecology and limnology of any Panhandle Florida river. We have been unable to find any ecological characterization of the physical, chemical, and biological properties of Panhandle rivers. What knowledge is available resides in many separate studies of single species or specific water quality and hydrology studies.

Beck (1965) made an admirable early attempt to analyze Florida streams and delineate the natural categories he felt they represented. For our purposes, the streams and rivers of Panhandle Florida are loosely organized into three categories, following Beck (1965): (1) alluvial streams, (2) blackwater streams, and (3) spring-run streams. Streams and rivers of the Panhandle, however, while mostly exhibiting the characteristics of one of the above categories, in fact also possess characteristics of the other two stream types. The large, alluvial Apalachicola River for instance, blends its waters with the Chipola River, its largest Florida tributary and a spring-run stream. Another example is the alluvial upper Ochlockonee River which joins the blackwater stream, Telogia Creek.

Unfortunately no student of Florida's streams has made a study of the changes that occur with increasing water volume, showing, for instance, how the ecology of streams may change and be classified along a water volume gradient. Clearly the limnology at the source of a steephead seepage stream differs in the extreme from that of the middle of the Apalachicola River.

When speaking of the size of a stream, we refer to the same stream classification scheme (Figure 60) we referred to when describing the upland vegetation along a stream valley gradient (Strahler 1964).

6.3.1 First-order Ravine Streams

Just as the vegetation and animal life in the terrestrial portion of ravine valleys is distinctive from all other types of upland habitats, the biota of the water column in ravines is very different from other types of aquatic systems. No specific comparative studies of the limnology of Panhandle Florida ravine waters has been carried out, but numerous studies of aquatic invertebrates, and a few studies of aquatic vertebrates, indicate that ravine streams form a special class of aquatic habitats. Moreover, there may be different types of ravine streams as well.

Studies of crayfish (Hobbs 1942), freshwater snails (Thompson 1984), mayflies (Berner 1950), dragonflies (Byers 1930), water beetles (Young 1954), caddisflies (Franz 1982), stoneflies (Stark and Gaufin 1979), and salamanders (Means 1974a,b, 1975; Means and Karlin, in press) indicate that ravine-type headwater streams in the Panhandle are unique aquatic habitats having a specialized fauna of their own. There are good reasons also why ravines of a special type called steepheads (see Chapter 5.2.4) may have entirely different aquatic life than ravines formed by gully erosion (Chapter 5.2.3) (Means 1981, 1985c).

a. Flora. Little is known of the aquatic submerged vegetation of Panhandle ravine streams, but algae and diatoms are commonly visible to the naked eye or using a hand lens, growing on the pea-sized gravels and coarse sands in steephead stream beds. Primary productivity in these streams is most likely somewhat limited because the streams are almost always heavily shaded by a closed hardwood canopy. Productivity derives mostly from litter that falls or washes into ravine streams from the productive hydric hardwood forests of the stream valley bottom (*Magnolia virginiana, Illicium floridanum, Smilax bona-nox)*, and the mesic hardwood forests clothing the lower valley sidewalls. These latter forests usually are the beech-magnolia type (see Chapter 5.2.5 for a description).

b. Fauna. The aerated, cool (65–70°F) clear spring water of steepheads flows over sandy-gravelly substrates from the point on the valley sidewall where ground water seeps laterally. Many of these streams originate from an amphitheatre-shaped valley head where spring sapping takes place along a 270° arc. Water in some Panhandle steepheads has so much volume that fishes such as the creek chub (*Semotilus atromaculatus*), mosquitofish (*Gambusia affinis*), and darters (*Etheostoma* spp.) can be seen within 3–5 m of the spring source. Steephead streams flowing into western Choctawhatchee Bay from Eglin Air Force Base contain the entire distribution of the federally endangered Okaloosa darter (*Etheostoma okaloosae*). All across the Panhandle in first-order streams, Means (1974a,b) discovered a specific suite of plethodontid salamanders that are not found in any other habitats. The larva of these three species live in benthic habitats in ravine streams from 6 months in the case of the central and Apalachicola dusky salamanders (*Desmognathus fuscus conanti, D.* n. sp.) to 3 years in the case of the two-lined salamander and the red salamander (*Eurycea bislineata, Pseudotriton ruber*).

Among the many crayfishes that inhabit Panhandle ravine streams, species of *Procambarus* and *Cambarus* are the diet of the queen snake (*Regina septemvittata*), a crayfish-eating specialist that is relatively rare in Florida, and which lives mostly in Panhandle ravine streams. Occasionally, banded water snakes (*Nerodia fasciata*) find their way into ravine streams, probably to eat fish. The mud turtle (*Kinosternon subrubrum*), loggerhead musk turtle (*Sternotherus minor*), and juvenile snapping turtles (*Chelydra serpentina*) all forage in ravine stream waters (Means, personal observation). Panhandle Florida ravine streams apparently have no aquatic mammals or birds that use aquatic habitats as their homes, but the opossum (*Didelphis virginiana*) and raccoon (*Procyon lotor*) are common visitors. The raccoon, adroit fisher that it is, possibly has the most impact on the system. Raccoon tracks in the wet sands and organic soils adjacent to ravine streams attest to their presence.

6.3.2 Alluvial Streams and Rivers

Four Panhandle streams are noteworthy for their alluvial character. They are the Escambia, Choctawhatchee, Apalachicola, and Ochlockonee Rivers. All four have blackwater tributary streams, and the Choctawhatchee and Apalachicola have substantial inputs from spring-run tributaries. The alluvial character of these rivers derives from the fact that the greatest portions of their stream catchments are north of the Florida boundary in clastic-dominated sediments of the Coastal Plain or, in the case of the Apalachicola River, in the southern Appalachian Mountains.

The development of rooted aquatic vegetation in the rivers of the Panhandle is limited by the influence of one or more of four factors: (1) current velocity, (2) water depth, (3) turbidity and color, and (4) fluctuating water levels. Factors 1 and 2 tend to be limiting in channels where water flow and depth are greatest. Rainfall runoff, into the larger Panhandle rivers particularly, is usually quite turbid, limiting light penetration. The only suitable areas for the development of rooted aquatic species are narrow shelves between the floodplain vegetation and the main channel.

Where the Panhandle rivers drain sandy swampy lowlands, the water flowing in the turbulent areas has a brown color. The water in these streams is frequently high in organic acids, tannins, and lignins leached from the decomposing plant litter, giving the water the look of tea. Many Panhandle rivers and streams cut steepsided ravines beneath the closed canopies of their mature floodplain forests. Light penetration is limited first by the forest canopy, second by the dark color. Also, the steep sides of stream channels generally insure that water depth fluctuates widely in response to rainfall and runoff, creating an unstable background environment, especially for submergent plants. These conditions act together to limit the growth of submergent, emergent, and floating aquatic vegetation.

In contrast, the Panhandle rivers and their tributaries support a rich and varied assemblage of aquatic animals (Means 1977, Yerger 1977, Swift et al. 1977). This situation underscores the close interdependence between the streams and their floodplains. Detritus from upland runoff and leaf fall appears to be the major energy source for the Panhandle rivers as well as for their estuaries. The highly diverse animal community appears to result from the diversity provided by bank vegetation and regularly flooded swamp forests rather than by instream plant communities.

a. Flora. The aquatic habitats of the alluvial streams of Panhandle Florida can be classified by the water column and by different types of substrates. In the water column, the free-swimming aquatic organisms are plankton (microscopic plants and animals) and nekton (macroscopic motile organisms such as crayfish and true fish). Benthic substrates are masses of attached algae, compact clay, sand, mud, fixed organic debris (submerged brush, logs, roots, leaf packs), and rock and gravel (Gold et al. 1954). Because alluvial rivers are turbid with fine suspended sediments, and because river waters continually move and fluctuate in volume, phytoplankton levels often are quite low in this type of coastal plain aquatic habitat compared to those in standing water (Patrick et al. 1967).

Wharton (1977) lamented that "general descriptions of Coastal Plain streams are rare...I could find few studies of submerged, floating, or emergent higher plants in Georgia rivers." While scientists are beginning to generate considerable knowledge about the ecology of Panhandle estuaries (see Chapter 7), few detailed studies are available on Panhandle rivers. Information on the ecology of the Savannah River in Georgia may not be strictly applicable to Panhandle rivers, but a few generalities may be extrapolated.

Most algae are common in summer and fall, others in the spring, and a few in winter. A few green algae (*Oedogonium* spp.), red algae (*Compsopogon* spp., *Batrachospermum* spp.), and filamentous diatoms form long streamers in faster water. Some blue-green algae (*Lyngbya* spp.) form long filaments in still water. The green algae *Vaucheria* and *Oedogonium* form algal mats on sand or mud in shallow water, while *Spirogyra* exists a little deeper.

b. Fauna. The animal life of large Panhandle alluvial rivers is extensive and more well known than the plants. Each river system across the Panhandle has a core of wide-ranging species shared by all the rivers, but each system also possesses many species of invertebrates and fish not found in the other rivers. The Escambia River, farthest west of the alluvial streams, is most abundantly endowed with the animal life typical of the western Gulf of Mexico streams such as the Mississippi River. The Escambia has its headwaters in the upper Coastal Plain of southern Alabama, adjacent to the much larger Alabama-Tombigbee drainage on its west. The Ochlockonee River, by contrast, receives a large share of its species from the Atlantic Coastal Plain. This may be a result of a shared drainage divide with the Withlacoochee River (a tributary of the Suwannee River) as well as a possible connection with the Suwannee on the exposed Continental Shelf during the Pleistocene. The Apalachicola River is distinctive because it is the only Florida drainage whose headwaters originate outside the Coastal Plain in the southern Appalachian Mountains.

The wide variety of animal life in alluvial rivers is related to the diversity of the physical environments of these streams. For instance, the 68 species of freshwater fishes in the Ochlockonee River (Swift et al. 1977) are distributed among diverse habitats: shallow swift water and slow deep pools, sandy riffles and organic muck, under cut banks and in midstream, ravine tributaries and main channels. A severe change takes place in these streams annually that affects much of the wildlife. Runoff of rainwater falling on the catchments during winter and spring tends to be greater than at any other time of the year (Foose 1983, Means 1986), causing water to spill out of the low water channel into extensive floodplains. Many riverine species such as catfishes

(*Ictalurus* spp.), centrarchids, bowfin (*Amia calva*), gars (*Lepisosteus* spp.), and minnows (*Notropis* spp.) benefit by moving into the expanded aquatic environment during the 1–5 months that annual high waters stand in the floodplain. In addition, species that live in the backwaters of floodplains benefit by the high annual rises which rejuvenate the backwater aquatic systems by providing them with nutrients and water. During winter and spring high water periods, for instance, some species of riverine amphibians breed in the floodplain and spend their larval life in the receding waters outside the main low water channel. These are the upland chorus frog (*Pseudacris triseriata*), Fowler's toad (*Bufo woodhousii fowleri*), and southern leopard frog (*Rana sphenocephala*). Others breed in the same floodplain backwaters during the summer. Among these are the river swamp frog (*Rana heckscheri*), bronze frog (*Rana clamitans*), bird-voiced tree frog (*Hyla avivoca*), gray tree frog (*Hyla chrysoscelis*), green tree frog (*Hyla cinerea*), southern dusky salamander (*Desmognathus auriculatus*), mud salamander (*Pseudotriton montanus*), long-tailed salamander (*Eurycea longicauda*), and dwarf four-toed salamander (*Eurycea quadridigitata*).

Alluvial rivers of the Panhandle, while not possessing a great deal of primary productivity in the water column for filter feeding animals, compensate by being rich in nutrients supplied by litter that washes into the system from floodplain forests and from tributary streams. Thus alluvial rivers are replete with benthic organisms that attack the litter and, in turn, feed a robust food web of higher feeding levels. Among the many important invertebrate groups are caddisflies (Wiggins 1977), mayflies (Berner 1950), crayfish (Hobbs 1942), freshwater snails (Thompson 1984), bivalves (Clench and Turner 1956), stoneflies (Stark and Gaufin 1979), and carnivorous groups such as dragonflies (Byers 1930) and water beetles (Young 1954).

The invertebrates are the food base, in turn, for a wealth of fish species. Some fish groups feed on the bottom, such as the sturgeons (*Acipenser* spp.), suckers (*Catostomus, Minytrema, Erimyzon*), darters (*Etheostoma* and *Percina*), and catfishes (*Ictalurus, Noturus*). Some feed at or near the water's surface, such as many species of the Cyprinodontidae, Poeciliidae, and Centrarchidae, and others feed in the water column, such as species of those families just mentioned plus the gars, bowfin, pickerels (*Esox* spp.), minnows, shad (*Dorosoma* and *Alosa*), and others.

Alluvial rivers support a great wealth of reptile life beginning with large numbers of many species of turtles. The world's largest freshwater turtle, the alligator snapping turtle (*Macroclemys temminckii*), is largely confined to the deep waters of alluvial streams, and Panhandle Florida rivers are one of the important holdouts of their populations. The Mississippi River and other western Gulf of Mexico drainages have had severe fishing pressure brought to bear on the alligator snapper for use in commercial production of turtle soup. Common omnivores in alluvial rivers are the large river cooters and sliders, most notably the Suwannee and Mobile cooters (*Pseudemys concinna* sspp.), the peninsula cooter (*P. floridana*), and the yellowbelly slider (*P. scripta*). Other important turtles are species of map turtles (*Graptemys* spp.) found exclusively in large rivers, including a species endemic to the Apalachicola River system, Barbour's map turtle (*G. barbouri*), species of musk turtles (*Sternotherus odoratus* and *S. minor*), and mud turtles (*Kinosternon subrubrum*).

Alligators (*Alligator mississippiensis*) are very common in the large alluvial rivers where they have not been harassed or killed out. They eat mostly fish, but turtles are next in importance. While no lizard is specialized for aquatic life in Florida Panhandle rivers, several snakes are. The most abundant snake seen along overhanging branches and along the banks of alluvial rivers is the brown water snake (*Nerodia taxispilota*) usually mistaken for the cottonmouth (*Agkistrodon piscivorus*). The latter rarely is found in the main channel of alluvial streams, but it flourishes in the backwater slough and swamps in the floodplain. The red-bellied water snake (*Nerodia erythrogaster*) is also a common riverine species, often seen at the water's edge where it feeds on fish.

Otter (*Lutra canadensis*) and beaver (*Castor canadensis*) are the only truly aquatic mammals sometimes seen in the main channel of alluvial rivers, but both are more common in the tributary streams and backwaters. Historically, the manatee (*Trichechus manatus*) apparently made forays up into the alluvial rivers of the Panhandle, but this is probably rare or nonexistent today.

Alluvial rivers are the feeding grounds for many species of wading and aquatic birds. Wading birds such as the great blue heron (*Ardea herodias*), great egret (*Casmerodius alba*), and little blue heron (*Egretta caerulea*) are commonly seen feeding along the banks of alluvial rivers. Diving birds such as the anhinga (*Anhinga anhinga*), double-crested cormorant (*Phalacrocorax auritus*), and species of ducks use alluvial rivers extensively. The osprey (*Pandion haliaetus*) and bald eagle (*Haliaeetus leucocephalus*) are common raptors that grab fish from the surface of river waters.

Although no definitive study of the fauna of alluvial rivers has been done, Means (1977) has surveyed the significance of the Apalachicola River basin to vertebrates, and more information, including a vertebrate species list, is available in the publication.

6.3.3 Blackwater Streams

The most widely distributed type of stream in Panhandle Florida we call here the blackwater stream. We combine Beck's (1965) sand-bottomed stream with his swamp-and-bog stream because the latter is merely a slower moving, lower volume version of the former; the swamp-and-bog stream dominated by organic sediments in its bed, grades downstream into a sand-bottomed stream if the drainage system is large enough. The Perdido River, Blackwater River, Shoal River, Titi Creek, Pine Log Creek, Bear Creek, Telogia Creek, New River, and others are examples of blackwater streams that have organic-bottom tributary streams that come together to form the sand-bottomed, blackwater master stream.

The highly acid, sluggish swamp-and-bog streams are found throughout Panhandle Florida, and are particularly common in the Gulf Coastal Lowlands (Figure 5). They originate in herb bogs and shrub bogs and show a definite relationship to the sand-bottomed streams in that all chemical differences are functions of velocity (Beck 1965). An increase of gradient would convert them to the sand-bottomed type by increasing turbulence, which in turn increases reaeration, reduces carbon dioxide, increases pH and alkalinity, and removes the finer bottom sediments of organics and silt, replacing them with sand.

The swamp-and-bog version of blackwater streams has the following characteristics: pH 3.8 to 6.5, alkalinity and hardness both normally well below 40 mg/l, color sometimes as high as 750 units, turbidity low, and carbon dioxide at times above 100 mg/l. The velocity of these streams is slow to moderate. The larger volume, sand-bottomed version of the blackwater stream is mildly acid to circumneutral (pH 5.7–7.4), has alkalinity ranging from 5 to 100 mg/l, hardness from 2 to 120 mg/l, color moderate to high, and moderate to swift velocity (Beck 1965).

a. Flora. Plant life in blackwater streams has not been studied across the Panhandle. While diatoms and algae no doubt make up a considerable portion of the phytoplankton of blackwater streams, the primary productivity of blackwater streams is lower than a typical spring-run stream because of the differences in light levels. One emergent that catches the eye in shallow blackwater streams is golden club (*Orontium aquaticum*), whose green emergent leaves accentuate the golden-tipped spathe rising from dark, sometimes inky, waters.

b. Fauna. Blackwater streams support a surprising fish and amphibian fauna, with many species present that are normally considered sensitive to high carbon dioxide values, e.g., sunfishes (*Lepomis* spp.) and darters (*Etheostoma* spp.), waterdogs (*Necturus* spp.), and plethodontid salamanders.

According to Beck (1965), the invertebrate fauna of the organic-bottomed blackwater streams differs little from acid ponds. Running water forms and species that thrive in running water are universally lacking. Mollusks are represented only by *Physa pumilia*, and the general fauna give the impression of being composed almost totally of species highly resistant to organic pollution, even though the streams are not polluted by anthropogenic sources. Typical elements are hydropsychid and philopotamid caddisflies, mayflies of the genera *Stenonema* and *Isonychia*, simuliid larvae, Plecoptera, orthocladiine chironomids, elmid beetles, and *Corydalis cornutus* (Beck 1965). The fishes are an exception.

Farther downstream in sand-bottom reaches of the catchment, flowing water species dominate.

The floodplains of blackwater streams, particularly where there is seepage, are the breeding sites of several salamanders found more commonly in blackwater streams than anywhere else. These are the long-tailed salamander (*Eurycea longicauda guttolineata*), southern dusky salamander (*Desmognathus auriculatus*), and mud salamander (*Pseudotriton montanus*). Other salamanders living in the water column as adults are the two-toed amphiuma (*Amphiuma means*), lesser siren (*Siren intermedia*), and the gulf coast waterdog (*Necturus beyeri*).

Common reptiles of blackwater streams are the alligator (*Alligator mississippiensis*), common snapping turtle (*Chelydra serpentina*), peninsula cooter (*Pseudemys floridana*), stinkpot (*Sternotherus odoratus*), mud turtle (*Kinosternon subrubrum*), glossy water snake (*Regina rigida*), banded water snake (*Nerodia fasciata*), and cottonmouth (*Agkistrodon piscivorus*).

Wading and diving birds tend to use blackwater streams infrequently for two possible reasons: less food may be available because of the reduced productivity or visibility in black water, and the danger from subsurface attack from alligators and other aquatic predators is greater than in alluvial rivers and spring-run streams. No aquatic or semiaquatic mammals are known exclusively from blackwater streams, but the raccoon, beaver, and otter use blackwater streams extensively.

6.3.4 Spring-fed Streams

Panhandle Florida is not so well endowed with large springs as is central Florida and the Florida Big Bend region, but Rosenau et al. (1977) mapped 37 different springs in Panhandle Florida ranging in discharge from under 5 ft^3/s to more than 250 ft^3/s. Panhandle Florida has only two first order magnitude springs (having a discharge of more than 64.6 million gallons per day), Gainer Springs in Bay County and Blue Springs in Jackson County (Fernald and Patton 1984). Most of the Panhandle springs average in the range of 15–35 ft^3/s.

Spring-fed streams are very different from other Panhandle stream types in several important ways. First, spring waters are usually clear because they have been filtered through limestones. Second, spring-fed streams have relatively constant temperatures at their spring-heads, that persist to a diminishing extent downstream, making them somewhat thermally buffered. Third, they are chemically different from other rivers because they issue from carbonate terranes (limestone sediments) where the waters have picked up ions of calcium, magnesium, iron and other minerals. Spring-fed rivers and streams are notably less acidic than other rivers because of their high mineral ion content and seem to be heavily populated with mollusks, possibly because of the high levels of available calcium in the water.

Only two major streams of the Panhandle can be classed as spring-run streams, but both are also heavily influenced by inputs from blackwater stream tributaries. The Chipola River of Jackson, Calhoun, and Gulf Counties receives a large percentage of its flow from springs discharging the Floridan Aquifer from limestones in the southern Marianna Lowlands physiographic region. Many springs discharge directly into the floodplain of the Chipola River north of Marianna, but other springs have outlets into smaller spring-run stream courses that join the Chipola, such as Blue Springs Run. The Floridan Aquifer also discharges into Econfina Creek in Bay County through limestone conduits. A substantial portion of each stream catchment above the zone of the springs receives water as runoff from the surrounding landform, so that immediately below the springs, the waters of both rivers are a blend of calcareous spring waters and acid blackwater stream waters. Holmes and Wright Creeks in Washington and Holmes Counties are also fed by spring waters. During droughts, the waters of Chipola River, Holmes, Wright, and Econfina creeks become clear and dominated by spring-flow. At these times, these streams are more like the classic spring-flow streams of the Big Bend (Wakulla and Wacissa Rivers). During normal rainfall periods, however, all four streams can be so dominated by runoff that their waters are quite dark, and the streams appear superficially as blackwater streams.

According to Beck (1965), spring-run streams (called calcareous streams by Beck) typically are alkaline (pH 7.0–8.2), the alkalinity ranging from 20 to 200 mg/l, hardness from 25 to 300 mg/l, water normally clear, and velocity ranging from slow to swift. The beds of Panhandle spring-run streams consist of sand and limestone in the vicinity of springs, changing to sand, clay, pebbles, mollusk shells (of the introduced clam *Corbicula manilensis*), and organic detritus downstream.

a. Stream flora. The clear waters allow much more light to penetrate at depth, and therefore spring-fed streams have the highest primary production of all Panhandle streams. This is manifest more in macrophytic plants rooted in the subaquatic stream bed than in the water column. Diatoms and filamentous algae also abound but are attached to the physical substrate and the macrophytes. Thermal buffering prevents both low temperatures that slow down plant and animal metabolism and high temperatures that lead to anoxic conditions during summer.

Unfortunately, there are no ecological studies of the flora of Panhandle spring-fed streams, so that quantitative information about the roles of different species in primary productivity, and therefore their role as food and cover for aquatic wildlife, is lacking.

b. Stream fauna. According to Beck (1965), the invertebrate fauna of spring-run streams is less current-loving than sand-bottomed blackwater streams. The most obvious benthic faunal feature is their high mollusk populations, originally consisting of native genera *Goniobasis, Campeloma, Viviparus*, and *Pomacea*. Today, because of the overwhelming dominance of the introduced clam *Corbicula manilensis*, the bottom sediments are full of the living and dead shells of this bivalve, to the literal extirpation of many of the native species. Other current-loving invertebrates listed by Beck (1965) are hydropsychid caddisflies, mayflies of the genus *Stenonema*, a great variety of chironomid midges, *Corydalis cornutus*, and occasionally Simuliidae and Plecoptera.

Spring-run streams of the Panhandle are noteworthy for their mollusk-eating turtles. Females of Barbour's map turtle (*Graptemys barbouri*) are several times larger than males, but differ even more in possessing powerful crushing jaws and jaw musculature, enabling them to feed upon the abundant mollusks. A similar adaptation has taken place in the loggerhead musk turtle (*Sternotherus minor*). Both sexes, however, feed upon mollusks and show enlarged feeding apparatus. Omnivorous turtles are also very common, possibly because light penetrates deeply in spring-run streams and there is much more aquatic plant productivity than in the other two types of Panhandle streams. Commonly found are the Suwannee Cooter (*Pseudemys concinna*), peninsula cooter (*P. floridana*), and sometimes the yellowbelly slider (*Pseudemys scripta*).

The brown water snake (*Nerodia taxispilota*) is by far the most common aquatic snake encountered in Panhandle spring-run streams, but the red-bellied water snake (*N. erythrogaster*), and the cottonmouth (*Agkistrodon piscivorus*) are also found regularly, the latter more often off the main open-water channel in the fringing river swamps. The spectacularly colored rainbow snake (*Farancia erytrogramma*), specialized to eat freshwater eels (*Anguilla rostrata*), seems mostly to be found in spring-run streams.

Two freshwater fishes are known almost exclusively from spring-fed stream waters in the Panhandle. These are the redeye chub (*Notropis harperi*) and the bluefin killifish (*Lucania goodei*). Other fishes common to Panhandle spring-run streams include: bowfin (*Amia calva*), spotted sucker (*Minytrema melanops*), blacktail redhorse (*Moxostoma poecilurum*), pugnose minnow (*Notropis emiliae*), sailfin shiner (*N. hypselopterus*), coastal shiner (*N. petersoni*), blacktail shiner (*N. venustus*), longnose shiner (*N. longirostris*), weed shiner (*N. texanus*), silverjaw minnow (*Ericymba buccata*), bigeye chub (*Hybopsis amblops*), speckled madtom (*Noturus leptacanthus*), tadpole madtom (*N. gyrinus*), golden shiner (*Notemigonus chrysoleucas*), mosquitofish (*Gambusia affinis*), least killifish (*Heterandria formosa*), blackbanded darter (*Percina nigrofasciata*), spotted sunfish (*Lepomis punctatus*), bluegill (*L. macrochirus*), spotted bass (*Micropterus punctulatus*), largemouth bass (*M. salmoides*), brook silversides (*Labidesthes sicculus*), and others.

6.4 Native Lacustrine Habitats

The Panhandle has less water-bearing limestone near the surface of the ground than the rest of to 200 mg/l, hardness from 25 to 300 mg/l, water normally clear, and velocity ranging from slow to swift. The beds of Panhandle spring-run streams consist of sand and limestone in the vicinity of springs, changing to sand, clay, pebbles, mollusk shells (of the introduced clam *Corbicula manilensis*), and organic detritus downstream.

a. Stream flora. The clear waters allow much more light to penetrate at depth, and therefore spring-fed streams have the highest primary production of all Panhandle streams. This is manifest more in macrophytic plants rooted in the subaquatic stream bed than in the water column. Diatoms and filamentous algae also abound but are attached to the physical substrate and the macrophytes. Thermal buffering prevents both low temperatures that slow down plant and animal metabolism and high temperatures that lead to anoxic conditions during summer.

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6.4 Native Lacustrine Habitats

The Panhandle has less water-bearing limestone near the surface of the ground than the rest of the State, so lakes formed by solution subsidence of the ground surface to levels below the piezometric surface of ground water are less common. Most of these lakes are in northern Bay and southern Washington Counties. Lake Wimico may represent a depression in a relict sea bottom. The second most common type of lake is formed by the natural meandering processes of Panhandle streams and rivers, and we will call them floodplain lakes.

The two largest lakes of the Panhandle (Lakes Seminole and Talquin) are impoundments of the Apalachicola and Ochlockonee rivers, respectively. The three largest natural lakes, Dead Lake, Ocheesee Pond and Lake Wimico, are associated in one way or another with the Apalachicola River.

Lakes are not very long lived geological phenomena because they receive sediment-laden water from the surrounding uplands, and eventually are filled in. The filling process involves both inorganic sediments that are washed in by streams and other surface runoff and organic sediments that accumulate from the incomplete decomposition of plant matter. Organic lake sediments are derived mostly from primary productivity in the lake itself and to a lesser degree from imported litter. Young, recently formed Florida lakes usually are relatively deep, sand-bottomed, and possess open surface waters. Later in the filling cycle these lakes become shallow, with deep organic sediments in their beds, and begin to support a highly productive macrophyte community of emergent aquatic grasses, forbs, shrubs, and trees. We classify young, deep, sand-bottomed lakes as karst lakes and the shallow, peat-dominated lakes as swamp lakes. The latter usually are simply late successional stages of the former.

6.4.1 Karst Lakes

Panhandle Florida has fewer natural lakes than the adjacent Florida Big Bend region or peninsular Florida, but where lakes are found in the Panhandle, they usually have a limestone solution origin similar to those in the peninsula. Most of the natural lakes in the Panhandle are located in Bay and Washington Counties on the sandy uplands called Greenhead Slope between the Choctawhatchee River and Econfina Creek (Puri and Vernon 1964). These lakes and a few others such as De Funiak Springs Lake, Lake Mystic, Camel Pond, Wright Lake, Moore Lake, and Silver Lake are all of karst origin.

The karst lakes of the Panhandle seem to fit the FNAI Sandhill Upland Lake category better than their Sinkhole Lake type. These generally are rounded solution depressions in deep sandy uplands, usually without surface inflows or outflows. A few lakes on both sides of Econfina Creek in Bay County, however, have or had a steephead stream develop from their margins at the time the sink lake depression formed. In one case, a steephead stream flows over more than a mile into a sinkhole lake . The sand resulting from erosion of the steephead valley partially fills these lakes. They typically have a sandy substrate with organic accumulations near their deeper portions. They are characteristically clear, circumneutral to slightly acidic, and moderately free of minerals.

a. Flora. Little research on Panhandle lakes has been published. The karst lakes in Bay and Washington Counties are known to have several interesting plants, and a systematic investigation may discover more. Smooth-barked St. Johnswort (*Hypericum lissophloeus*) is an endangered species endemic to Lake Merial and one other sinkhole lake nearby (Ward 1978). One of the Bay County lakes is a known locality of the threatened karst pond xyris (*Xyris longisepala*), which is also found in karst lakes in southern Leon County and Walton County (Ward 1978). Other rare plants are known from these lakes, and a pine barrens sundew, *Drosera*, may be disjunct in the bed of Lake Merial and other Bay County lakes; other populations of this species are known only from North Carolina to New Jersey (R. K. Godfrey, Florida State Univ., Tallahassee; pers. comm.).

The phytoplankton of Panhandle karst lakes has not been described. Many karst lakes have sandy, treeless shores with zones of successional herbaceous vegetation fringing the waterline. Other lakes have a scattering of cypress around their margins.

b. Fauna. Almost nothing is known about the fauna of Panhandle karst lakes. Plankton, benthic algae, and submerged aquatic plants are the basis of the food web, which consists of turtles (*Pseudemys scripta*, *P. floridana*) and invertebrates. Macroscopic predators are fish (centrarchids, topminnows (*Fundulus* spp.), poeciliids, catfishes (*Ictalurus* spp.), bowfin (*Amia calva*), two-toed amphiuma

(*Amphiuma means*), bullfrog (*Rana catesbeiana*), bronze frog (*R. clamitans*), southern leopard frog (*R. sphenocephala*), pig frog (*R. grylio*), snapping turtle (*Chelydra serpentina*), mud turtle (*Kinosternon subrubrum*), green water snake (*Nerodia cyclopion*), mud snake (*Farancia abacura*), black swamp snake (*Seminatrix pygaea*), and alligator (*Alligator mississippiensis*).

6.4.2 River Floodplain Lakes

The low water channels of rivers migrate over their floodplains through the centuries in wandering loops. These loops eventually are cut off during high water by newly eroded channels, forming the familiar oxbow lakes that are dammed up at both ends by levees thrown up by subsequent high water stands. Thereafter, following each high rise of the river, the fine particles settle out of the turbid waters that refill the oxbow lake. Over time, oxbow lakes fill in with silt and clay.

a. Flora. At first, a newly cut off oxbow lake is only a portion of the river with standing, rather than flowing water in its channel. As the oxbow lake fills in, floodplain vegetation grows in from its sides, eventually closing the open water channel with a canopy of baldcypress (*Taxodium distichum*), and gum trees (*Nyssa aquatica, N. ogeche*).

b. Fauna. While the lotic river channel and lentic oxbow lake faunas may differ somewhat because of differences in current, Panhandle Florida oxbow lakes have not been intensively studied and compared. The species of aquatic vertebrates in oxbow lakes is a subset of those of deeper, slower waters in the main river channel, including the bowfin (*Amia calva*), alligator, spotted, and longnose gars (*Lepisosteus spatula, L. oculatus, L. osseus*), chain pickerel (*Esox niger*), suckers (*Moxostoma* spp.), catfishes (*Ictalurus* spp.), pirate perch (*Aphredoderus sayanus*), flier (*Centrarchus macropterus*), largemouth bass (*Micropterus salmoides*), warmouth (*Lepomis gulosus*), bluegill (*L. macrochirus*), dollar sunfish (*L. marginatus*), black crappie (*Pomoxis nigromaculatus*), siren (*Siren lacertina*), two-toed amphiuma (*Amphiuma means*), larvae of the river swamp frog (*Rana heckscheri*), alligator (*Alligator mississippiensis*), alligator snapping turtle (*Macroclemys temminckii*), Florida softshell turtle (*Trionyx ferox*), river cooter (*Pseudemys concinna*), peninsula cooter (*P. floridana*), and yellowbelly slider (*Pseudemys scripta*).

6.4.3 Swamp Lakes

Large swamp lakes such as Lakes Miccosukee, Iamonia, and Tsala Apopka of the Florida Big Bend are rare in the Florida Panhandle. Most of the Panhandle lakes are relatively deep limestone solution lakes that have not yet reached an advanced stage of filling in with sediments. There are, however, a number of small swamp lakes in Holmes and northern Walton Counties that appear to be nearly filled in solution basins. In addition, two large lakes in the middle stages of filling in and becoming swamps are of river origin and are not solution basins. Dead Lake on the lower Chipola River is an interesting example of a small river (Chipola) that is naturally impounded by the alluvial sediments of a larger river (Apalachicola) at the confluence of the two rivers. The waters of the Chipola have been backed up long enough for the lake margin to have accumulated massive organic deposits that ultimately will fill in at least the backswamps in time. Ocheesee pond is an even better example of a swamp created by the filling in of a lake. This wetland lies in an abandoned bed of the Apalachicola River, and the lake basin may later have been enlarged partially by downward and lateral solution of limestone.

There is virtually no scientific literature on the biota of the swamp lakes of Panhandle Florida, and we have no insights as to how Ocheesee Pond and Dead Lake differ from river floodplain lakes.

6.4.4 Ponds

Panhandle Florida possesses hundreds of small (less than 1 acre) ponds scattered throughout all the physiographic provinces. These water bodies collectively deserve mention as a major lotic type because they are the breeding sites of so many animals. No comparative studies of these ponds have ever been made for the eastern United States so far as we are able to determine, even though these ponds are known to field biologists as the only places to find certain invertebrates and vertebrates in larval and even adult stages.

We are also unable to subclassify ponds into natural groups, but we do recognize that there are major physical differences in their properties. Some are deep woods ponds formed in the hardwood forests of bottomlands that are not inundated by annual high rises of a large stream. Some are flatwoods ponds, and these may be marshy with no trees, or only a thin scattering of cypress or gum, or both. Some are just depressions in sandy flatwoods, with sandy bottoms that grass over during dry spells, and some have organic sediments perched on sand. The water cycle of most of these ponds is ephemeral, but some are permanent or nearly so.

a. Flora. The truly ephemeral ponds sometimes have very little distinctive flora except diatoms and other one-celled algae in the water column when water is present. Sometimes these temporary ponds form in depressions in wiregrass flatwoods or in low places in sandhills where little difference is notable in the groundcover between the rare times when the site is wet and when it is dry. As the hydroperiod increases, plant response increases, and often a low swale is evident by its herbaceous distinctiveness, indicating the beginnings of a true wetland. Certain grasses and many sedges seem to be the first indication that the hydroperiod is longer on some sites than on others. All degrees of plant response, depending upon hydroperiod, are evident among the many Panhandle ponds, including those with cypress (*Taxodium*) and gum (*Nyssa*) fringing them. In those ponds with a longer hydroperiod, organic sediments build up, and are obvious underfoot during drought periods. A study of small ponds and their physical and biological characteristics would begin to provide an understanding of an important, and often overlooked, habitat type.

b. Fauna. A great many unusual species of invertebrates and vertebrates use ephemeral ponds to complete their life cycles. A major reason may be the absence of fish predators. Several rarely seen crustacean groups become dense in these ponds after rains, including the fairy shrimps (Anostraca) and clam shrimps (Conchostraca). Other crustaceans that bloom in ephemeral ponds are species of isopods, amphipods, and decapods, including grass shrimps (Penaeidae) and crayfishes (*Procambarus*).

The invertebrate life and algae form a rich food resource and a number of amphibian vertebrate carnivores have evolved to take advantage of it. Ephemeral ponds are often the only places larvae of ambystomatid salamanders can be found. Panhandle Florida has four: the marbled salamander (*Ambystoma opacum*) is found in ephemeral ponds in hardwood bottomlands, breeding in river floodplain temporary standing water bodies or temporary ponds in low lying woodlands along smaller stream courses; the flatwoods salamander (*A. cingulatum*) uses temporary ponds in flatwoods, usually temporary cypress or cypress-gum ponds; the tiger salamander (*A. tigrinum*) also breeds in flatwoods ponds, especially deeper ones with slightly longer water cycles, including ponds with fish; and the mole salamander (*A. talpoideum*) which has a catholic preference, using almost any temporary pond, in any major terrestrial habitat.

Another group of salamanders that depend upon ephemeral ponds for their larval life is the Salamandridae, or newts. *Notophthalmus viridescens* commonly breeds in ponds and the larvae spend one or more years of their life in the ponds. Newts metamorphose into terrestrial salamanders called efts, and migrate away from ponds to take up a fossorial life in adjacent woodlands of various types. Later, when the breeding urge comes upon them, they migrate back to ponds and undergo another series of morphological changes that assist them with aquatic life. Both newts and the mole salamander mentioned above have the unique life history strategy of retaining their larval morphology (process of neoteny) until sexually mature and breeding if water levels remain substantial for one or more years. If water levels recede or the pond dries up, however, they quickly metamorphose and wander off to live on land until water returns and they are able to migrate back to the pond and breed.

Temporary ponds of the Panhandle are quite important to frogs and a couple of turtles. The chicken turtle (*Deirochelys reticularia*) is known almost exclusively from small ponds. It and the mud turtle (*Kinosternon subrubrum*) are among the most common turtles seen crossing roads. The ability to disperse from one drying pond to another is certainly an important adaptation found in animals that live in drying ponds. But frogs, among the vertebrates, seem to use temporary ponds the most, possibly because of the absence of predaceous fishes. Frogs rely on temporary ponds so much that several species in Panhandle ponds even breed only during cold weather in the middle of the winter.

The spring peeper (*Hyla crucifer*), ornate chorus frog (*Pseudacris ornata*), and Florida chorus frog (*P. nigrita*) use these ponds from November to February when there is ample winter rain. A definite spring breeding burst occurs in these ponds from February–April during very heavy rains, when the southern toad (*Bufo terrestris*), gopher frog (*Rana areolata*), and southern leopard frog (*R. sphenocephala*) breed, sometimes with huge numbers of the spadefoot (*Scaphiopus holbrookii*). But it is the summer rains that bring out the largest number of breeding species. Beginning in May and continuing until September, ponds in the Panhandle are teeming with breeding activity and tadpoles. The following are species of frogs that mostly depend upon small ephemeral summer ponds for the larval portion of their life cycle: oak toad (*Bufo quercicus*), narrowmouth toad (*Gastrophryne carolinensis*), pinewoods tree frog (*Hyla femoralis*), barking tree frog (*H. gratiosa*), squirrel tree frog (*H. squirella*), little grass frog (*Limnaoedus ocularis*), cricket frog (*Acris gryllus*).

Other frog species which are more catholic in the selection of their breeding habitats such as the green tree frog and gray tree frog (*H. cinerea, H. chrysoscelis*), also breed in these ponds.

When fish are found in ephemeral ponds, they almost always include the following: pygmy sunfishes (*Elassoma* spp.), pirate perch (*Aphredoderus sayanus*), mosquitofish (*Gambusia affinis*), and often the banded topminnow (*Fundulus cingulatus*).

No aquatic mammals are known to use ponds exclusively, but opportunistic predators such as raccoon and opossum are common, especially when water levels begin to go down and the large numbers of larvae are concentrated. These ponds support one of Florida's endangered birds, the wood stork (*Mycteria americana*), which feeds on small fish and amphibian larvae when ponds are drying up.

The fact that so many animals are found only in ponds, or have special adaptations for pond life, indicates that the pond is a very important true habitat type, and not an artifact of human attempts to define nature. Studies on Panhandle ponds are urgently needed.

6.4.5 Coastal Ponds

Between sets of aeolian dunes or wave-created sandy berms along the coastal barrier islands and the mainland lie interdune depressions, or flats. Often these depressions have water standing in them for periods ranging from a few days to nearly always. The FNAI designation for these water bodies is Coastal Dune Lake. These ponds are very important to the wildlife of coastal strands, and we single them out here for recognition.

The bottoms of coastal ponds are predominantly composed of sand, with some organic matter. The amount of organic matter depends upon hydroperiod—short hydroperiods allow faster decomposition of organic sediments, so that some interdune flats that have water standing for only a few days to weeks after rains have almost no organic sediments at all. The salinity of coastal ponds is variable and subject to saltwater intrusion from beneath during drought, from storm surges, and from salt spray transported by the wind. Coastal ponds are slightly acidic, but often have hard waters with high mineral content (especially sodium chloride).

Coastal ponds, occurring at the continental margin and on barrier islands, are very young geologically. Those on Panhandle barrier islands such as St. George, St. Vincent, and Dog islands are no more than 6,000 years old. Because the barrier island ponds have formed in isolation from the mainland, each pond is likely to have its own distinctive subset of waif plants and animals in it. On St. Vincent Island, for instance, almost no titis (Cyrillaceae) fringe the coastal ponds in the manner that they do on the mainland. Instead, the evergreen shrubs in many St. George Island ponds are replaced with persimmon, *Diospyros virginiana*. No studies are available comparing coastal pond biota. Many species typical of ephemeral water bodies can be expected in coastal ponds, partly because of the dearth of fish in them. Ostracods, amphipods, anostracans, conchostracans, and isopods should be looked for after rains. A few frogs and toads use coastal ponds, including the southern toad (*Bufo terrestris*), southern leopard frog (*Rana sphenocephala*), and pig frog (*Rana grylio*). The first fish to appear in these ponds usually are the mosquitofish (*Gambusia affinis*), but some larger, permanent ponds on St. Vincent Island contain the spotted gar (*Lepisosteus osseus*), bowfin (*Amia calva*), lake chubsucker (*Erimyzon sucetta*), brown bullhead (*Ictalurus nebulosus*), golden topminnow (*Fundulus chrysotus*), pygmy killifish (*Leptolucania ommata*), least killifish (*Heterandria formosa*), sailfin molly (*Poecilia latipinna*), tidewater silverside (*Menidia beryllina*), everglades pygmy sunfish (*Elassoma evergladei*), warmouth (*Lepomis gulosus*), bluegill (*L. macrochirus*), redear sunfish (*L. microlophus*), largemouth bass (*Micropterus salmoides*), striped mullet (*Mugil cephalus*), and the fat sleeper (*Dormitator maculatus*) (Christman 1984).

Coastal ponds are very important to wildlife, especially on barrier islands, because usually they provide the only water available. For this reason they are extremely important to incoming migrant birds that are returning from cross-Gulf migration.

6.5 Subterranean Habitats

6.5.1 Water-filled Caves

Beginning with Lonnberg (1894a, 1894b), studies of the animal life of caves and sinkholes in Florida and adjacent parts of the Coastal Plain of Georgia and Alabama have revealed a number of cave-adapted organisms that are endemic in the Apalachicola River drainage basin. Because Panhandle Florida solution cavities are presently filled with water, the number of aquatic troglobites (phreatobites) is large in contrast with the number of troglobites (cave-adapted animals) in air-filled cave ecosystems of the Appalachian region of the eastern United States.

Means (1977) recognized three groups of troglobites in Florida and Georgia by the following names: the Chattahoochee fauna, named for the anticline which brought limestone terranes to the surface in the Marianna Lowlands-Dougherty Plain physiographic region (same as Pylka and Warren's (1958) northern region); the Woodville fauna, named for the Woodville Karst Plain of the Gulf Coastal Lowlands physiographic region (Hendry and Sproul, 1966); and the Ocala fauna, named for the Ocala Uplift in peninsular Florida. These last two areas plus sinkholes breaching the Hawthorne Formation along the Peninsular Arch.

In Panhandle Florida only one fauna, the Chattahoochee fauna, is present. At least eight caves in the Marianna Lowlands-Dougherty Plains region share the Chattahoochee fauna (Figure 68). A number of springs and subterranean water-filled passages which probably contain the Chattahoochee fauna are located along the west bank of the Apalachicola River for several miles south of Sneads. The nature of the barrier isolating the Chattahoochee fauna from other troglobites is now better known because of geological and hydrological studies carried out in the past decade (Figure 69). A faulted syncline complementary to the Chattahoochee anticline is present between the Apalachicola and Ochlockonee Rivers, and contains clastic sediments of low permeability (Veatch and Stephenson 1911, Applin and Applin 1944, Herrick and Vorhis 1963, Sever 1964, Kaufman et al. 1969). Also, limestone underlying the clastic sediments in the trough does not show evidence of significant solution or secondary permeability (Hendry and Sproul 1966). This geomorphic feature has been called the Gulf Trough (Hendry and Sproul 1966). The eastern edge of the Gulf Trough contains another structure, the Ochlockonee fault (Kaufman et al. 1969), which may also serve as an impediment to hydrologic flow to the southeast (Figure 69). Recent studies of disequilibrium patterns of naturally occurring uranium isotopes demonstrate that "...the Gulf Trough and Ochlockonee Fault act as a hydrologic barrier that prevents any significant southeastward flow of groundwater" (Kaufman et al. 1969, p. 384).

Much of what is known about phreatobites of the eastern gulf region came from studying specimens brought up from wells which penetrate cavities in the Floridan aquifer (Carr 1939; Hobbs 1942, 1971; Hobbs and Means 1972). In many cases, the nearest entrance to the aquifer is through sinkholes or springs several miles from the well. After Carr (1939) described the Georgia blind salamander (*Haideotriton wallacei* Carr) from a deep well in Albany, Georgia, specimens were discovered in caves in Jackson County, Florida (Pylka and Warren 1958). All troglobitic salamanders presently known from this karst region are *Haideotriton wallacei*.

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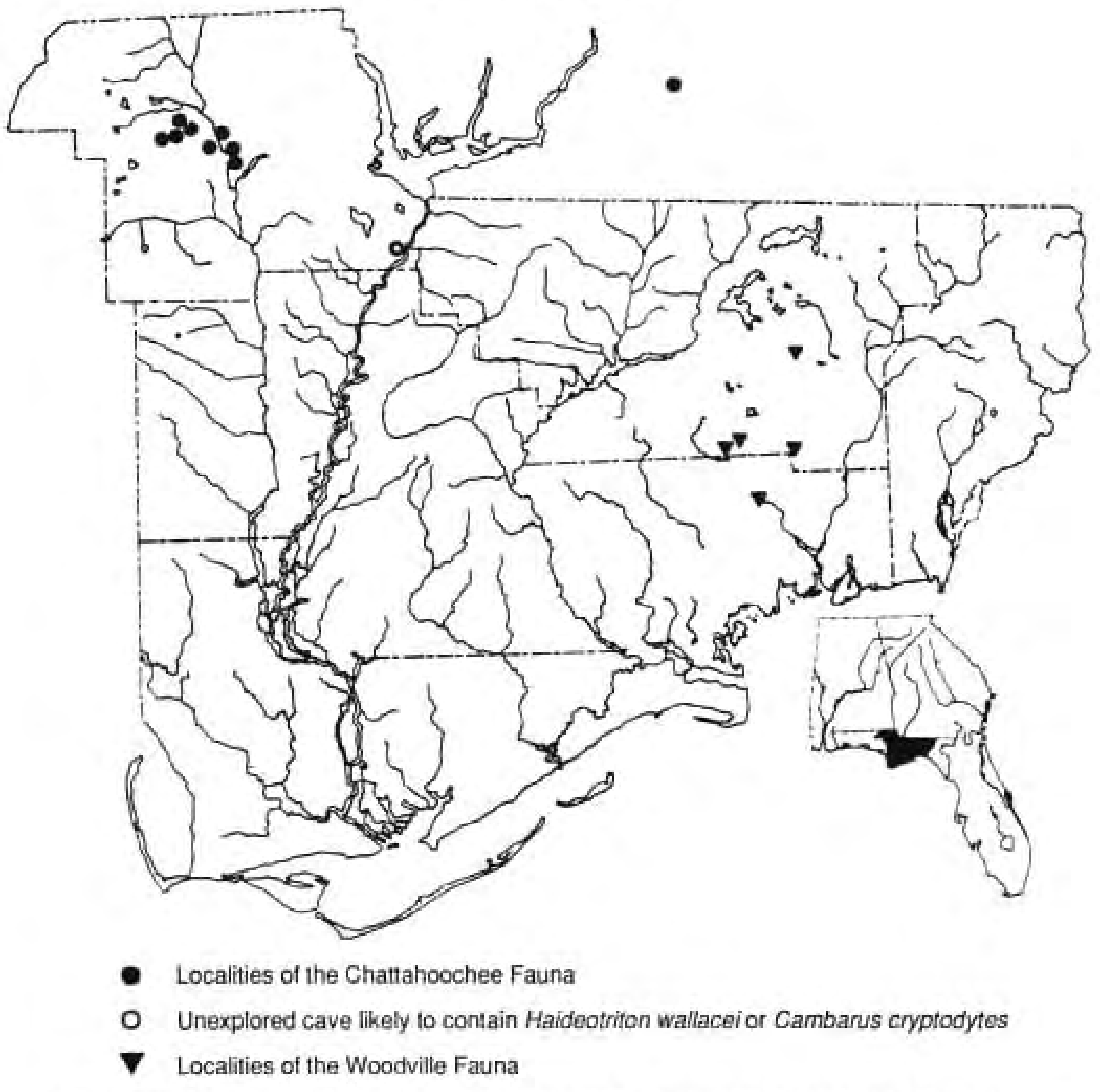

Figure 68. Distribution of caves and phreatobites in Panhandle Florida (after Means 1977).

Haideotriton wallacei is not closely related to any known troglobitic salamanders, but several species of troglobitic salamanders whose epigean (living on ground surface) ancestry probably belongs to the same genus occur in the Balcones Escarpment (Edwards Plateau) region of Texas. The epigean ancestors of all these species probably belonged to the genus *Eurycea*. *Haideotriton* probably evolved from this genus independently and is similar morphologically to the most cave-adapted species, *Typhlomolge rathbuni* from the Balcones Escarpment, by evolutionary convergence.

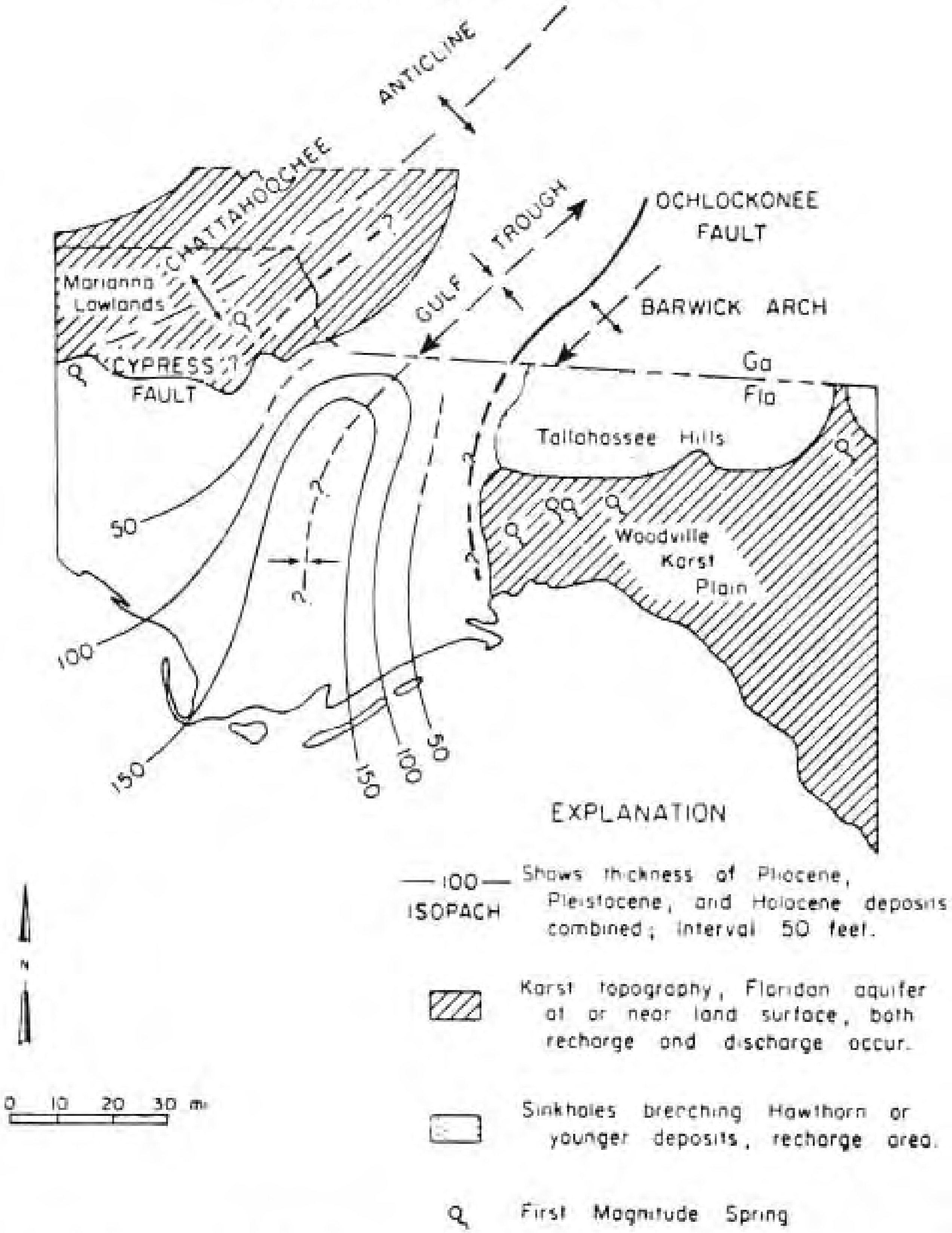

Figure 69. Regional structure of eastern Panhandle Florida showing the Gulf Trough putative barrier to dispersal between the Chattahoochee and Woodville phreatobite faunas. (Kaufman et al. 1969).

Two epigean species (*Eurycea bislineata*, *E. longicauda*) are known troglobites in caves of the Marianna Lowlands and in Climax Cave, Georgia. Larvae of both species have been found in and near the mouths of caves in pools and streams issuing from the underground water system (Means, personal observation). Both of these species of *Eurycea* are typically northern animals. It is not known whether either gave rise to *Haideotriton wallacei*, but they or their ancestors are the most likely candidates. The species *H. wallacei* and *T. rathbuni* of Texas share the distinction of being the most highly cave-adapted salamanders in North America.

The endemic crayfish, *Cambarus cryptodytes* , was also described from the specimens obtained from a well; they, too are now known to be abundant in caves in Jackson County. Both *Cambarus cryptodytes* and *Haideotriton wallacei* live together in the water column, especially near nutrient inputs such as subterranean streams beneath bat roosts in caves. Gerard's Cave (Pylka and Warren 1958) in Jackson County has several vertical cracks in the cave floor under bat roosts where these species are common year around. Apparently the crayfish forage on detritus from bat excreta and carcasses, and on other aquatic life that feeds on the same fare. Middle-sized and large crayfishes are capable of capturing and feeding upon *Haideotriton wallacei*. The crayfish probably also feed upon some of the food items that have been identified in the diet of the cave salamander, including ostracods, amphipods, isopods, copepods, insects and a species of mite (Lee 1969).

The troglobitic isopod, *Asellus hobbsi* is found in the Marianna Lowlands in the Panhandle and in cave waters of peninsular Florida. However, its occurrence in crayfish burrows in Calhoun County south of Blountstown (Maloney 1939) and the tendency for other subterranean isopods to occur in epigean waters (Minckley 1961) indicates surface dispersal and would not require continuous limestone connection between the two regions in the study area. Peck (1973) identified an amphipod (*Crangonyx floridanus*) and a copepod (*Macrocyclops albidus*) from guts of *Haideotriton wallacei*.

The extensive system of subterranean waters and solution cavities drained by the upper Apalachicola basin contains an isolated and unique ecosystem of cave-adapted aquatic organisms. Major threats to this ecosystem are impacts from pollution (municipal waste effluents, siltation, and turbidity due to surface erosion in open recharge areas) and alteration of the water table (by impounding local streams, including the Apalachicola and Chipola Rivers, or from heavy drawdown by wells). Serious consideration should be given to influences on the local water table.

6.6 Human-Created Lacustrine Habitats

People have created numerous lotic environments over Panhandle Florida, mostly of the small, ephemeral type along roadsides and railroad rights-of-way. Roadside ditches are so common that biologists commonly use them for collecting and teaching, yet almost no studies of the biota of roadside ditches, per se, are available. The closest natural lotic environments to roadside ditch ponds are the ephemeral ponds described in Chapter 6.4.4. Somewhat larger than roadside ditches are the borrow pits created by roadbuilders for road construction. These water bodies are quite sterile, even more so than roadside ditches, because they usually are deeper. In the Panhandle, particularly the Coastal Lowlands region, borrow pits are characterized by the dense growths of St. Johnswort (*Hypericum* spp.) that flourish after mechanical disturbance to a wetland.

6.6.1 Impoundments

The largest of all human-created lotic environments, however, are the impoundments of streams and rivers. These are numerous over the entire Panhandle. Many are fish management areas maintained by the Florida Game and Fresh Water Fish Commission Some of the small- to medium-sized impoundments are Bear Lake (107 acres) in Santa Rosa County, Hurricane Lake (400 acres) in Okaloosa County, Juniper Lake (665 acres) in Walton County, Lake Stone (130 acres) in Escambia County, Lake Victor (134 acres) in Holmes County, Merritt's Mill Pond (202 acres) in Jackson County, and Smith Lake (160 acres) in Washington County. There are surprisingly few impoundments of the larger rivers, however, even when compared to the upstream reaches of these rivers north of the Florida State line. The three largest are Lake Talquin on the Ochlockonee River (4,004 acres), Deer Point Lake (5,000 acres) on Econfina Creek north of Panama City, and Lake Seminole (37,000 acres).

The Florida Department of Environmental Regulation recently completed a 1-year study of water quality in Panhandle impoundments (FDER 1986d). This investigation included the monitoring of benthic macroinvertebrate and periphyton populations upstream of, in, and downstream of 17 Panhandle impoundments. This study found that the nutrient enrichment in the impoundments resulted in oxygen depletion, depauperate populations of benthic macroinvertebrates, and enhanced growth of algae. Not only were there effects within the impoundments, but there were profound adverse effects downstream of the impoundment that resulted in reduced macroinvertebrate populations.

The largest lake in Panhandle Florida is Lake Seminole, an artificial impoundment of the Chattahoochee and Flint rivers, backed up behind Jim Woodruff Dam exactly at their point of confluence at the beginning of the Apalachicola River. This large lake, with a surface area of 152 km^2 and a total volume of 9,439 km^3, is the last of 16 impoundments in the drainage basin, and the only one on the Florida reaches of the river.

a. Flora. Phytoplankton in Lake Seminole are dominated by diatoms (*Melosira distans, Asterionella formosa*), which during the cooler months make up as much as 77% of the population. During the warmer months, blue-green algae become dominant, making-up 76% of the total numbers. Coincident with this seasonal pattern is a switch in limiting nutrients from phosphorus in the cool months to inorganic nitrogen in the summer and fall. Cell numbers also vary seasonally, averaging lowest in winter months (1,951 cells/ml) and highest in September (14,729 cells/ml). An average of 37.5 taxa (13 to 51) of phytoplankton were reported from 17 stations in the lake over a 6-month period (USACE 1981).

Aquatic macrophytes cover approximately 40% of the surface area of Lake Seminole and virtually 100% of the area less than 2 m in depth (USACE 1981). Over 700 taxa of macrophytes have been identified, with 73 being reported as common to abundant (Table 14).

b. Fauna. We were unable to find comparative studies of the trophic relationships within Panhandle impoundments, although various lakes have been monitored for various periods by the Florida Game and Fresh Water Fish Commission. The fauna of impounded lakes derive mostly from the native faunas of the rivers in question, and partly from lentic water species that find their way into the lake by means of chance dispersal and by human transport. All of the impoundments in the Panhandle have been stocked with game fishes, mostly bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), and channel catfish (*Ictalurus punctatus*), and with other species on a more limited basis (Gatewood and Hartman 1977). The fish, mammal, and waterfowl recreational values of these impoundments were summarized by Gatewood and Hartmann (1977).

Table 14. Aquatic macrophytes noted to be common to abundant in Lake Seminole during 1978–79 field surveys by the Army Corps of Engineers (USACE 1982). S = Submersed; E = Emergent; F = Floating.

Algae	S	E	F	Vascular	S	E	F
Chara spp.; chara	•			*Justicia americana*; water willow		•	
Lyngbya/Spirogyra; algal mat			•	*Sagittaria latifolia*; common arrowhead		•	
Nitella spp.; nitella	•			*Alternanthera philoxeroides*; alligator-weed		•	
				Colocasia esculenta; wild taro		•	

(continued)

Chapter 7

ESTUARINE, SALTWATER WETLAND, AND MARINE HABITATS

7.1 Introduction

Classification of the saltwater habitats follows the scheme of Cowardin et al. (1979) as closely as possible (Table 15). Two systems, estuarine and marine, make up the saltwater environment. Included within each system are two subsystems— subtidal and intertidal. It is not possible to classify many of the Panhandle habitats as strictly subtidal or intertidal. For example, oyster reefs are primarily intertidal, but some are entirely intertidal and some may have both intertidal and subtidal regions. Given these problems, most habitats within the two systems are not subdivided further into strict subsystems. Class (henceforth "habitat") definitions are maintained and are based upon substrate composition (e.g., oyster reef) or primary vegetation (e.g., seagrass bed). In this document, the water column is treated as a separate habitat—open water—and includes fish and truly planktonic forms that cannot be assigned to specific habitats.

The short and very arbitrary naming and delineation of habitats are made with the following caveats: (1) the environment is a continuum of habitats, each one unique (e.g., not all oyster reefs are exactly the same) and each one dependent to varying degrees upon the others, and (2) many organisms use multiple habitats during different times of the day or different life stages and, therefore, cannot be assigned precisely to a single habitat. Wherever possible, major discrepancies in the classification are underscored.

A gross-level classification of the fauna is made according to the size of the organism, especially the benthos (bottom-dwelling organisms), for which size categories have traditionally been based upon retention on various sieve sizes: macrofauna (>0.500 mm), meiofauna (0.500–0.062 mm), and microfauna (<0.062 mm). This scheme has limitations. Some macrofaunal organisms are included as meiofauna early in their development, hence both temporary and permanent meiofauna distinctions are made. Nevertheless, the categories roughly follow taxonomic lines such that the macrofauna generally includes echinoderms, polychaetes, bivalves, oligochaetes, and crustaceans, such as decapods, amphipods, and isopods. The meiofauna includes harpacticoid copepods, nematodes, ostracods, kinorynchs, polychaetes, and gastrotrichs. The microfauna includes ciliates, fungi, and bacteria. Within this overall organization, there are trophic (i.e., deposit feeders and suspension feeders) and life-position (i.e., epifaunal and infaunal) distinctions.

The classification of flora is also based roughly on size: macrophytes (e.g., seagrasses and salt marsh grasses) and microphytes (e.g., phytoplankton and benthic diatoms). The boundaries, however, are less rigidly defined.

Given the large area of coast covered in the Panhandle region, it is unrealistic to report every species present or the small, albeit interesting, differences among watersheds. Primarily, dominant and ecologically important organisms are reported. An attempt has been made to highlight general patterns and interactions observable throughout the different locales. In addition, the role and natural history of some commercially important organisms are reported.

Within each habitat description, assessments and projections were made on potential and realized human impacts. Because they are semienclosed and have limited circulation, coastal estuaries and lagoons are very sensitive to pollution impacts, even though they ordinarily possess much higher nutrient concentrations than the marine or freshwater areas.

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Table 15. Definition of estuarine and marine systems (after Cowardin et al. 1979).

Estuarine System	Marine System
Consists of deepwater tidal habitats and adjacent tidal wetlands that are semienclosed by land but have open, partly obstructed, or sporadic access to the open ocean. It contains ocean water that is at least occasionally diluted by freshwater runoff from the land. The salinity may periodically increase above that of open ocean due to evaporation.	Consists of the open ocean overlying the Continental Shelf and its associated high-energy coastline. Salinities exceed 30 ppt with little or no dilution except outside the mouths of estuaries. It includes habitats exposed to the waves and currents of the open ocean.
Limits—extends: (1) upstream and landward to where salinities do not fall below 0.5 ppt during the period of average annual low flow; (2) to an imaginary line closing the mouth of a river, bay, or sound; (3) to the seaward limit of wetland emergents, shrubs, or trees where they are not included in (2).	**Limits**—extends from the outer edge of the Continental Shelf shoreward to one of three lines: (1) the landward limit of tidal inundation (extreme high water of spring tides), including the splash zone from breaking waves; (2) the seaward limit of wetland emergents, trees, or shrubs; (3) the seaward limit of the Estuarine System.
Subsystems— (1) Intertidal—substrate exposed and flooded by tides; includes the splash zone; (2) Subtidal—substrate continuously submerged.	**Subsystems**— (1) Intertidal—substrate exposed and flooded by tides; includes the splash zone;

Estuaries act as nutrient and pollutant sinks through three major mechanisms: (1) sediment adsorption—the abundant clay-sized sediment particles tend to adsorb nutrients and other chemicals; when concentrations in the water column decline, sediments release their nutrients; (2) the basic circulation pattern of the estuaries—there are usually only limited tidal- and wind-generated currents in estuaries, and retention times are generally long; (3) biodeposition—large numbers of suspension-feeding mollusks (e.g., oysters) and crustaceans remove suspended materials and package them into feces and pseudofeces. These act as large particles that sink to the bottom and are buried; the nutrients and pollutants contained in them may later be released by erosion, sediment reworking by the benthos, and dredging.

In this document, human perturbations are generally grouped into two broad classes. The first includes those destructive impacts (usually the most easily detected), such as dredging and construction, that result in changes in habitat quantity. The second includes those impacts, such as excessive organic loading, that alter and degrade habitat quality. In some instances, the classes overlap. In many cases, specific impact studies on Panhandle sites are lacking and projected effects were derived from examples outside the immediate area.

7.1.1 Tides and Salinity Ranges

There are two types of tides along the Panhandle coast: semidiurnal from Ochlockonee Bay to Apalachicola Bay and diurnal (daily) from Apalachicola Bay westward to Perdido Bay. The semidiurnal tides are mixed (i.e., have unequal highs and lows) and range from 0.67 m to 1.16 m (Stout 1984). Diurnal tides have smaller amplitudes, ranging from 0.37 m to 0.52 m. Local daily tidal conditions are highly dependent upon meteorological conditions such as wind speed and direction.

Nearby gulf coastal water salinities are characteristically marine and stable through the year, averaging between 34 and 35 ppt. On the other hand, the bays and estuaries demonstrate fluctuating salinities that depend on a variety of physical factors such as river flow, rainfall, and tidal and wind conditions. The bays, except for St. Joseph and Alligator Harbor, which do not have rivers and streams supplying freshwater inputs, usually have definable haloclines that intensify during heavy rainfalls and dissipate during droughts. The interface between brackish bay water and saline gulf water approaches the surface on incoming tides and falls during outgoing tides. Northerly winds (especially strong in the winter) can cause the surface water of bays to move gulfward and can lower salinities up to 7 ppt (Salsman and Ciesluk 1978). Bay water salinity is low near river mouths and ranges between 20 and 38 ppt through most of their area.

7.2 Estuarine Habitats

7.2.1 Introduction

The discussion of the estuarine habitats follows a general format: first, the habitat is introduced with general background information; second, the flora, fauna, or both typically found in the habitat is discussed; third, the distribution of the habitat is provided; fourth, the trophic interactions within the habitat are given; and last, the natural and human impacts are presented. Sections will not be included where information was not available.

7.2.2 Brackish Marshes

a. Introduction. The brackish vegetation habitat includes both emergent and submergent forms. The habitat is primarily limited to salinities in the range of approximately 0 to 15 ppt and is generally located along river mouths subject to tidal influence.

b. Vascular species. Clewell (1978) investigated the extensive brackish marshes (i.e., emergent vegetation) at the mouth of the Apalachicola River. The marshes were primarily dominated by sawgrass (*Cladium jamaicense*). However, large patches of black needlerush (*Juncus roemerianus*) interrupted the sawgrass in places, particularly near the river channels and its distributaries. Other herbs were also common within a few meters of the banks of the channels, especially *Cicuta maculata*, *Ipomoea sagittata* (morning glory), *Rumex verticillatus*, *Sagittaria lancifolia* (arrowhead), *Spartina patens* (saltmeadow cordgrass), and *Teucrium canadense*. These and others are generally incidental or absent in the interior expanse of the sawgrass meadow.

The dominant brackish-water submergent vegetation includes three species: *Vallisneria americana*, *Potamogeton* sp., and *Ruppia maritima*.

East Bay in the Apalachicola Bay system has been the most extensively studied (Livingston 1980, 1984). Harper (1910) published the only other account of emergent brackish marshes in the Panhandle (specifically the Apalachicola).

Brackish vegetation is perennial, with annual diebacks starting in the fall and continuing at low biomass through the winter. This vegetation probably serves as an important source of detrital material providing energy for the species in the area.

c. Associated fauna. McLane (1980) described 33 species of benthic infauna from an area of East Bay (north Apalachicola Bay) brackish vegetation (Table 16). The dominant macrophytes were *Vallisneria americana* and *Ruppia maritima*. The six most abundant macrofaunal organisms (in descending rank) were *Grandideriella bonneroides* (amphipod), *Dicrotendipes* sp. (insect larva), *Laeonereis culveri* (polychaete), a nematode, *Mediomastus californiensis* (polychaete), and *Amphicteis gunneri* (polychaete). The number of macrofauna ranged from approximately 1,000 to 10,000 individuals/m². Peak numbers were recorded from September through March. Lowest densities were recorded from May through August. Biomass peaked in February to March and August to September.

Purcell (1977) described the epibenthic fauna associated with tape weed (*Vallisneria americana*) beds in East Bay and discussed that this habitat is an important nursery area especially for blue crabs (*Callinectes sapidus*).

d. Human impacts. Timber clear cutting increases runoff and sediment load in streams leading

Table 16. Common benthic macroinvertebrates found in brackish vegetation in the Panhandle (McLane 1980).

Type	Species	Type	Species
Crustaceans	*Cerapus* spp. (amphipod)	Polychaetes	*Amphicteis gunneri*
	Corophium lousianum (amphipod)		*Laeonereis culveri*
	Gammarus macromucronatus		*Mediomastus californiensis*
	Grandideriella bonneroides (amphipod)		*Streblospio benedicti*
	Callinectes sapidus	Mollusks	*Littorina sphictostoma*
			Mactra fragilis
Insects	*Dicrotendipes* sp.		*Spisula solidissima*

into the estuaries. The increased turbidity and sediments and lower pH (i.e., higher acidity) cut down on light for photosynthesis. The increased sedimentation also smothers plants and animals.

7.2.3 Salt (or Tidal) Marshes

a. Introduction. Salt marshes are plant communities of the intertidal zone that represent a transition between terrestrial and marine ecosystems. Generally, marshes develop along low-energy coasts under stable or emergent conditions (Chapman 1960). Salt marshes develop in estuaries, behind the shelter of spits, offshore bars, and islands, in protected bays, and along very shallow seas. All these environments provide the marsh with protection from high-energy waves and allow for sediment accumulation and plant community expansion.

Numerous factors influence the areal extent of salt marshes. The most important of these are:

(1) the relation of land to sea level (i.e., whether the coastline is stable, emerging or submerging);

(2) the composition of the substrate;

(3) the amplitude of local tide;

(4) winds, currents, and waves—through their effects on sedimentation and aggradation (i.e., detrital loading)—and;

(5) the nature of the body of water facing the marsh.

The coastal marsh system is highly productive, exceeding natural upland vegetation and in some cases even agricultural crops (Odum et al. 1974). The high productivity is generally attributed to a large input of nutrients and particulate organic matter (of freshwater and marine origin), river flow and rainfall fluxes, tidal energy input, and basic physiographic and biological features. Three groups of organisms are responsible for the high productivity: phytoplankton, algae (on sediments and plants), and vascular plants. Both the above- and below-ground productivity make very important contributions.

The detrital food web appears the most important in salt marshes (Odum and de la Cruz 1967). Very few animals feed directly upon *Spartina* or *Juncus*.

Salt marshes perform four major ecological functions:

(1) They produce relatively large quantities of organic matter per unit area per time. Some of this organic matter is stored in the marsh in the form of peat, some is recycled in the marsh through a variety of food chains, and some is transported out of the marsh and dissipated into the estuaries.

(2) They are the exclusive habitat of a few species of algae and seed plants, of a large variety of invertebrates, of a large number of birds, and of a few reptiles and mammals.

(3) They provide substantial protection to adjacent low-lying uplands from saltwater intrusion, coastal erosion, and quantities of drifting debris, and, in expansive marshes, from salt spray.

(4) They are important nursery grounds and refuges for commercial and sport species.

Three different plant communities can be delineated within salt marshes (Stout 1984):

(1) saline marshes that experience tidal waters of marine salinity;

(2) brackish marshes where tidal waters are routinely diluted before flooding of the marsh; and

(3) transitional communities between brackish and freshwater marshes (also called "intermediate marshes"). Note: the brackish marshes were discussed in the previous section.

Salt marshes are usually characterized by large, homogeneous expanses of dense grasslike plants. Typically, the marshes are dominated by one plant species and named accordingly (e.g., *Juncus* marsh). The marsh community is usually low in macrophyte species diversity (see Table 17) with incidental species having a patchy occurrence and represented by only a few species.

b. Major physiographic features. Three types of surface irregularities occur in Panhandle salt marshes: tidal creeks, natural levees, and barrens.

Tidal creeks form when minor irregularities in marsh substrate cause the tidal water to be guided into definite channels (Chapman 1960). Once channels are formed, tides cause further scouring and prevent recolonization by vascular plants. Channels also deepen by accretion on their banks of sediments trapped around the roots of plants bordering the creek. As sedimentation increases and the marsh floor builds, creeks may lengthen and branch. Where the surface slope is gradual, creeks are less branched and the main channels are sinuous. The sinuosity of tidal-creek channels facilitates flooding and drainage, and promotes extension of the marsh by reducing the time required for the inward movement of seawater with each rising tide. Creek banks often support different vegetation from that immediately beyond the bank.

Natural levees develop from sand deposited on upper beaches by very high tides. Most natural levees slowly move landward through the action of tides. Very high tides continually remove sand from the seaward side and redeposit it on the landward side of levees.

Barrens (or salt barrens and salt pans) develop during the initial stages of marsh formation because of the irregular colonization patterns of salt marsh "pioneer" plants, which surround low bare areas and cause them to lose their outlets for tidal waters. These areas fill during spring tides and hold water for long periods of time. In summer, evaporation causes the salinity to rise and plants cannot invade the area. The characteristic round shape of salt pans may result from eddies that form on their borders during flooding. Barrens can also form by deposition of sand and silt in irregularly flooded areas (Kurz 1953, Kurz and Wagner 1957) and from debris tossed up on the marshes by tides and storms that sometime smother the marsh vegetation. In addition, they may

Table 17. Common vascular plants (in order of abundance) present in Panhandle salt marshes (Stout 1984).

Species	Common name	Species	Common name
Juncus roemerianus	Black needlerush	*Scirpus robustus*	Leafy sedge
Spartina alterniflora	Smooth cordgrass, oystergrass	*Salicornia bigelovii*	Annual glasswort
Spartina patens	Saltmeadow hay, saltmeadow cordgrass	*Salicornia virginica*	Perennial glasswort
Spartina cynosuroides	Giant cordgrass, rough cordgrass	*Batis maritima*	Saltwort
Distichlis spicata	Salt grass	*Phragmites australis*	Common cane, Roseau cane
Scirpus olneyi	Three-square sedge	*Baccharis halimifolia*	Sea myrtle
		Iva frutescens	Marsh elder

form behind a levee as a narrow strip devoid of vegetation. Most are temporary and usually recolonize within a few years, depending on salinity levels and depth of the barren (Kurz 1953).

c. Distribution. The marshes in the Panhandle are developing on the seaward edge of the Pamlico terrace of the late Pleistocene (Kurz 1953, Coultas 1980). The Pamlico terrace is a low upland with an elevation up to 8 m.

The Ochlockonee and Apalachicola Rivers supply alluvium downdrift to the west that results in the development of a system of beaches, spits, and barrier islands, as well as bars at the river mouths. Within these low-energy zones, marshes are located in the lee of barriers and within bays protected from wave action (Tanner 1960b, Kwan 1969). No barriers are found in the region west of St. Joseph Bay. Moderate-energy waves from the Gulf of Mexico strike the beaches; marshes protect shores only in major bays such as St. Andrew Bay and Choctawhatchee Bay. Steep mainland bluffs along the western shore of Escambia Bay in the Pensacola system do not support broad salt marshes.

Marshes occur sporadically along the lagoonal interface of Alligator Point peninsula, especially at the extreme east end of Alligator Harbor (Livingston 1984). Marshes are limited along the mainland east and west of the Apalachicola River mouth. In areal coverage, East Bay marshes dominate the system with lesser marsh development along St. Vincent Sound and the landward portions of Dog Island and St. George Island. The marshes of the Apalachicola Bay system cover approximately 14% of the surface (Livingston 1984).

d. Vascular plants present. The saline marshes of the Panhandle are dominated by halophytic monocotyledonous grass or rushlike plants, primarily *Juncus roemerianus* (black needlerush), *Spartina alterniflora* (saltmarsh cordgrass), *Spartina patens* (saltmeadow hay or cordgrass), and *Distichlis spicata* (salt grass). Fleshy, dicotyledonous plants—*Salicornia*, *Batis*, and *Borrichia*—are commonly present but less abundant. Table 17 gives a list of dominant plant species in Panhandle salt marshes. Tidal marshes of the northwest Florida coast are dominated by *Juncus roemerianus*. Thirty-one percent of the marsh area in the Panhandle is dominated by this species (Eleuterius 1976).

The vascular plants form distinctive patterns of species zonation within the salt and brackish marshes of the Panhandle. Four zones are discernible: *Spartina alterniflora*, *Juncus roemerianus*, salt flat or barren, and high meadow (Stout 1984) (Figure 70A).

The *Spartina alterniflora* zone is closest to sea level in the intertidal zone and experiences regular or daily inundation. Since this zone is regularly flooded, substrate salinity is approximately that of tidal concentration. The zone lies typically within an elevation from -0.24 m to 0.54 m MLW. If the shore topography is broad and gently sloping, *S. alterniflora* can exhibit differences in morphology and flowering. Taller plants with flower heads occur in the lower elevations of the zone, while shorter sterile plants occupy the upper area (Stout 1984). The zone is usually monospecific. On shores with greater slope, *S. alterniflora* may be found mixed with *Juncus roemerianus*. Shores with greater wave energy may form a levee upslope from the *Spartina* (Figure 70B). The vegetation of the levee is usually typical of higher elevations.

The *Juncus roemerianus* zone is at a slightly higher elevation and subjected to less flooding than the *Spartina alterniflora* zone (Figure 70A). *Juncus* comprises the bulk of the biomass in most Panhandle marshes. There is usually a sharp demarcation between the *Spartina* and *Juncus* zones. The *Juncus*-demarcation zone generally corresponds to the MHW mark, but edaphic conditions and biotic factors may also be important. The *Juncus* zone occupies a more restricted elevation range (0.54 m–0.75 m MLW) but spans greater horizontal distances than *Spartina*. The *Juncus* zone can reach several kilometers in width.

Tidal flooding of this zone is irregular and higher elevations may be flooded only during spring or storm tides. Because of longer more frequent periods of exposure and evaporation, interstitial water salinities may be higher in *Juncus* than *Spartina alterniflora* zones. The high organic content (and associated acid conditions) of *Juncus* soils may impede percolation of tidal water and rainwater into the substrate.

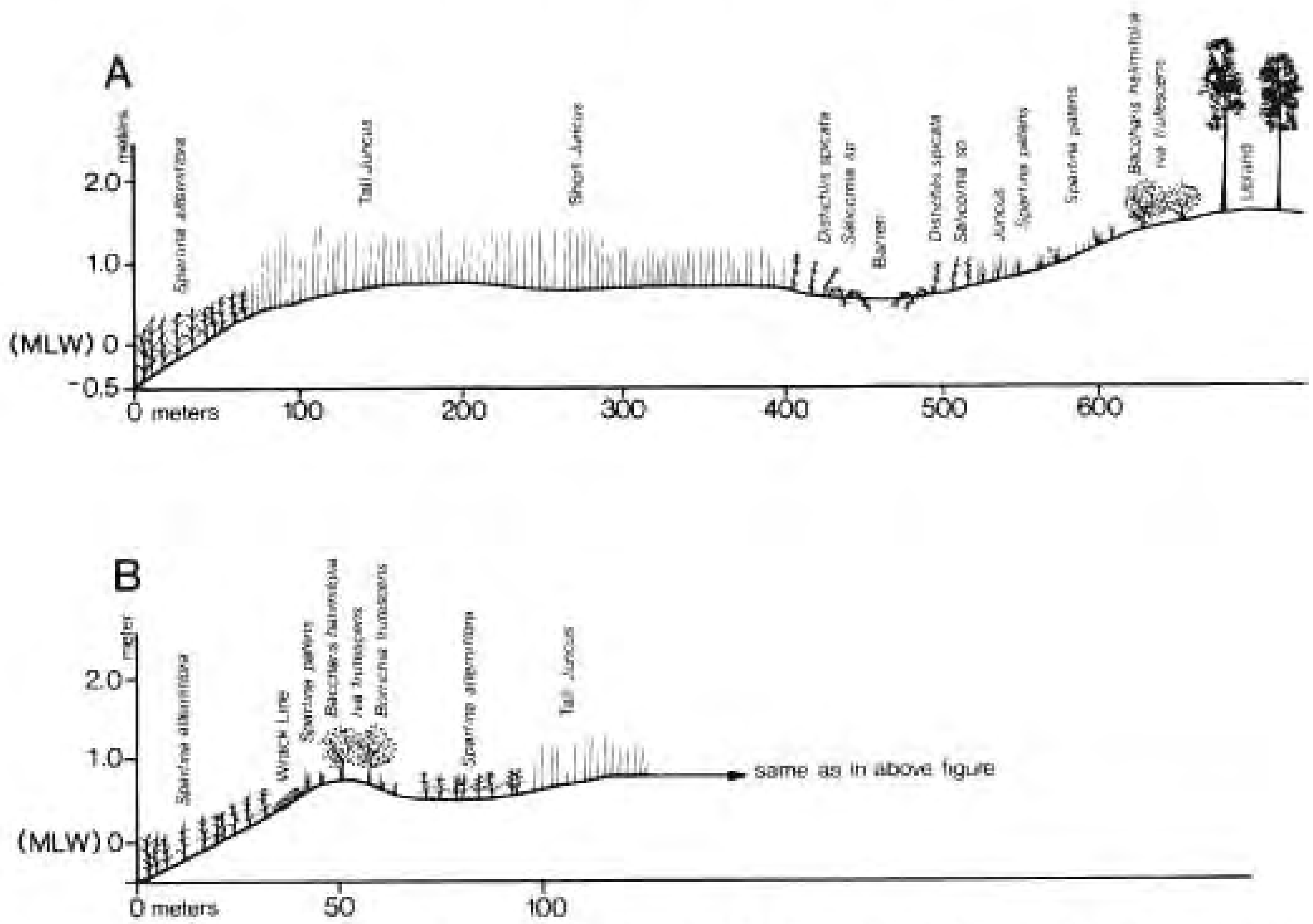


Figure 70. Schematic views of gulf coast salt marshes on protected low-energy shorelines (A) and open moderate energy shorelines (B) (after Stout 1984).

A *Juncus* marsh community may be represented by two or more height forms that possibly reflect microhabitat differences in the zone. The tallest plants are nearest the tidal source and so are more frequently flooded. Stem height and diameter decrease with distance from shore, while stem densities and new leaf production increase. Soil texture and salinity gradients may a play role in morphology (Coultas 1980).

There is a decline in sexual reproduction in *Juncus* and *Spartina alterniflora* plants at higher elevations in a marsh. The shortest *Juncus* plants (height ≤0.5 m) are usually sterile and are found adjacent to salt flats. Unlike most of the other marsh grasses, *J. roemerianus* grows throughout the year and represents a climax vegetational type (Eleuterius 1976).

The salt flat zone, just upland from the *Juncus* zone, has a sandy, hypersaline soil and includes portions of the zone vegetated by halophytic species. These ecotonal areas are called "barrens" because they are devoid of plants. This zone is rarely inundated by tidal water and when it is flooded, water quickly percolates through the coarse substrate. Interstitial water salinities are extremely high.

The seaward and upland margins of the salt flat are usually mirror images of plant communities on either side of the barrens (Stout 1984). Salt grass

(*Distichlis spicata*) extends in parallel stands from the upper edge of the *Juncus* and the lower edge of the high meadow into the salt flat. As salinities increase toward the barrens, *Distichlis* no longer grows. Interior to the *Distichlis* margins of the salt flats only three species occur: *Salicornia virginica* (perennial); *S. bigelovii* (annual) and *Batis maritima*. All three species are obligate halophytes.

The size of the barrens varies with local conditions and may change over short periods of time (i.e., days) with rainfall fluctuations and tidal flooding, and over long periods of time with changes in elevation. If salinity decreases within the barrens, seedlings of the annual *Salicornia bigelovii* and rhizomes of other salt flat species rapidly colonize the area.

The extent of the high meadow zone (or high marsh) varies greatly from a narrowly vegetated fringe between the salt flat and upland vegetation to a broad meadow of grasslike vegetation. *Juncus* is usually very abundant and shares dominance with *Spartina patens*, the latter being most common upland. This zone contributes most to the diversity of the marsh with numerous incidental species present in the shrub-forest ecotone. Species common in this zone include: *Fimbristylis caroliniana*, *Scirpus robustus*, *Aster tenuifolius*, *Phragmites australis*, *Cynanchum angustifolium*, *Pluchea* sp., and various shrubs (e.g., *Baccharis halimifolia*, *Iva frutescens*, and *Myrica cerifera*).

e. Nonvascular (and microbial) plant community. The highest density of nonvascular plants is always found on other plants above the soil surface. Twenty-five species of filamentous fungi occur on *Spartina*, all of which are on the aboveground parts of the plant. Two infectious fungi occur on *Spartina*: the ergot fungus *Claviceps purpurea* and the rust fungus *Puccinia sparganiodes*.

Of the algal communities found in Panhandle marshes, only diatoms and blue greens of *Juncus*-dominated marshes have been examined (Stout 1984). The epiphytic algae *Bostrychia* spp. and *Enteromorpha* spp. are the most frequently encountered (Table 18). Diatoms constitute a continuous benthic marsh cover in areas with and without a spermatophyte canopy. The most abundant diatom species is *Navicula tripuncata*. The greatest number of diatom species is found on *Distichlis spicata*, the lowest on *Juncus*. Diatom distributions are primarily

Table 18. Zonal relationship of algae with spermatophyte community in Panhandle marshes (from Kurz and Wagner 1957, Stout 1984).

Dominant algae	Location
***Spartina alterniflora* community**	
Bostrychia spp.	attached to culms
Enteromorpha flexuosa	attached to culms
Melosira spp.	attached to culms
Microcoleus chthonoplastes	channel bottom
Phormidium fragile	attached to oyster shells
Lyngbya confervoides	attached to oyster shells
soil diatoms	sediment
Chondria spp.	drift fragments
Digenia spp.	drift fragments
Enteromorpha spp.	drift fragments
Sargassum spp.	drift fragments
Polysiphonia spp.	drift fragments
Champia spp.	drift fragments
Fosliella spp.	drift fragments
***Juncus roemerianus* community**	
Bostrychia spp.	attached to culms
Cladophora spp.	attached to culms
Chaetomorpha spp.	attached to culms
Enteromorpha spp.	attached to culms
Lyngbya aestuarii	attached to culms
***Distichlis spicata* community**	
Bostrychia spp.	attached to culms
Cladophora spp.	attached to culms
Chaetomorpha spp.	attached to culms
Enteromorpha spp.	attached to culms
Lyngbya aestuarii	attached to culms

regulated by marsh surface elevation and canopy height.

f. Marsh-associated fauna. Animal members of the marsh ecosystem fall into three broad categories: (1) permanent residents that spend their entire lives in the marsh; (2) transitory residents that spend only part of their lives (e.g., foraging) in the marsh; and (3) animals that spend only the juvenile portion of their lives in the marsh (Shipp 1977). The third category emphasizes the importance of the role of salt marshes as "nursery ground" for many species.

Salt marsh organisms are frequently exposed to harsh and variable conditions. Waters within the marsh change daily with the tide, resulting in salinity, temperature, oxygen, and pH fluctuations. Salinity can also vary from one area to another with temperature, wind, freshwater inflow, rainfall, and evaporation. The marsh fauna change along the gradient from the low marsh to the upper marsh (Figure 71).

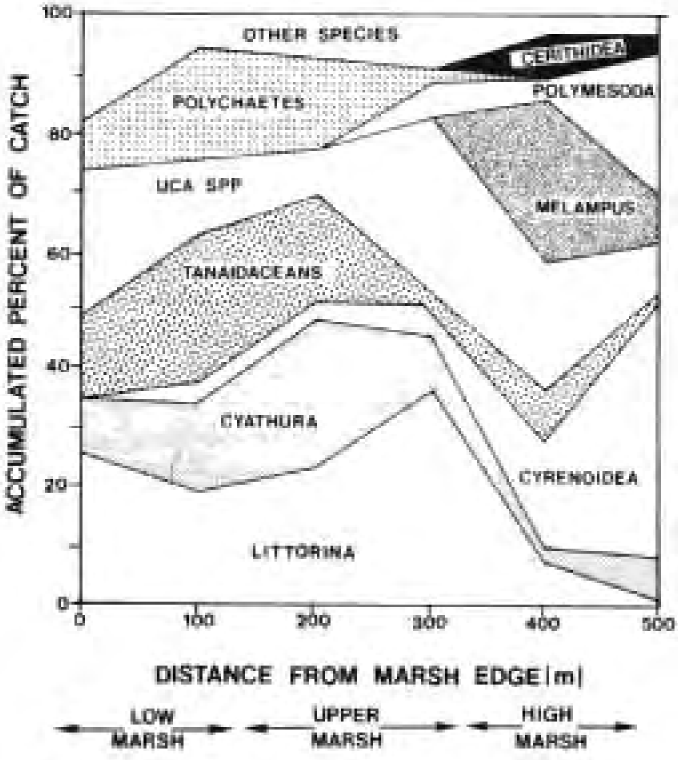


Figure 71. Horizontal distribution of macrofauna in a typical Panhandle tidal marsh (after Stout 1984).

Of the marsh invertebrates (Table 19), insects are very abundant, with all major orders being recorded (McCoy 1977). The insects can be divided into aquatic, subterranean, and surface-living groups. Diptera, Coleoptera, and Hemiptera dominate. Gastropods and fiddler crabs (*Uca* spp.) are the most common visible mollusks and crustaceans, respectively.

Fish are seasonally very abundant and diverse. Over 80 fish species have been reported from the creeks, ponds, and open water of salt marshes in the Panhandle. Table 20 shows those that are most common. Fish community structure is influenced by (1) season and tides, (2) species breeding activity, (3) species feeding behavior, (4) habitat diversity

Table 19. Common invertebrates of Panhandle salt marshes (Stout 1984).

Group	Species or order
Zooplankton	*Uca* spp.
Meiofauna	Nematoda
	Harpacticoid copepods
Insects	Diptera
	Coleoptera
	Hemiptera
Polychaetes	*Scoloplos fragilis*
	Neanthes succinea
	Amphicteis gunneri
	Laeonereis culveri
Mollusks	*Littorina irrorata* (marsh periwinkle)
	Polymesoda caroliniana (bivalve)
	Neritina usnea (gastropod)
	Melampus bidentata (gastropod)
	Cerithidea scalariformis (gastropod)
	Detracia floridana (gastropod)
	Succinea ovalis (gastropod)
Crustaceans	*Halmyrapseudes bahamensis* (tanaid)
	Cyathura polita (isopod)
	Palaemonetes pugio (grass shrimp)
	Palaemonetes intermedius
	Callinectes sapidus (blue crab)
	Uca spp.

Table 20. Common fishes of Panhandle salt marshes (Stout 1984).

Species	Common name	Residence status
Menidia beryllina	Tidewater silverside	permanent
Fundulus similis	Longnose killifish	permanent
Fundulus grandis	Gulf killifish	permanent
Fundulus confluentus	Marsh killifish	permanent
Cyprinodon variegatus	Sheepshead minnow	permanent
Adinia xenica	Diamond killifish	permanent
Poecilia latipinna	Sailfin molly	permanent
Leiostomus xanthurus	Spot	nursery user
Lucania parva	Bluefin killifish	permanent
Anchoa mitchilli	Bay anchovy	nursery user
Mugil cephalus	Striped mullet	nursery user
Lagodon rhomboides	Pinfish	nursery user

and available space, and (5) proximity to estuarine and nearshore waters. Panhandle marshes, like other Gulf of Mexico marshes, are dominated by cyprinodont species (Stout 1984).

A number of reptile species are commonly encountered in the marsh, but amphibians are not as well represented. Common reptiles are shown in Table 21.

Birds are an important component of the marsh system. Over 60 species are reported to use habitats within Panhandle salt marshes. Table 22 lists those species that are common, however, only a few are permanent residents. The marsh offers food sources, nesting areas, and refuges. Wading birds and shore birds often feed near the marsh intertidal zone and creeks. Only clapper rails and seaside sparrows nest in the *Juncus* marshes. The majority of others nest in small trees and shrubs growing on shell and sand berms or spoil deposits within the marsh. Snowy and great egrets are the most abundant nesting species within the brackish marshes. Tricolored herons are the most abundant species in the salt marshes (Stout 1984).

Table 21. Common reptiles of Panhandle salt marshes (Stout 1984).

Species	Common name
Malaclemys terrapin pileata	Mississippi diamond back terrapin
Pseudemys alabamensis	Alabama red-bellied turtle
Pseudemys floridana floridana	Florida cooter
Alligator mississippiensis	America alligator
Nerodia fasciata clarkii	Gulf salt marsh water snake

Mammals can be categorized into three major groups: (1) marsh residents, (2) inhabitants of the marsh-upland interface, and (3) upland mammals entering the marsh to feed (Table 23).

g. Species of special concern. The American bald eagle (*Haliaeetus leucocephalus*) is listed as federally endangered and occurs in Panhandle salt marshes.

h. Trophic dynamics/interactions. Marshes are characterized by an extremely high level of primary productivity and, subsequently, serve as the base of the detrital food web for the entire estuarine ecosystem. Few animals feed directly upon live *Juncus* or *Spartina*, but marsh detritus that results from the decomposition (both biological and mechanical) of plant material is a rich food source for many marsh and estuarine organisms.

Table 22. Common birds of Panhandle salt marshes (Stout 1984). Note for Occurrence: P = permanent resident; B = breeding population; M = migrant; W = winter visitor; S = summer resident; C = casual; T = threatened species (State of Florida).

Order	Species name	Common name	Occurrence
Gruiformes	*Rallus elegans*	King rail	PB
	Rallus longirostris	Clapper rail	PB
	Rallus limicola	Virginia rail	MW
	Porzana carolina	Sora	MW
	Coturnicops noveboracensis	Yellow rail	W
	Laterallus jamaicensis	Black rail	PB
	Fulica americana	American coot	PB
Charadriiformes	*Sterna nilotica*	Gull-billed tern	M
	Sterna forsteri	Forster's tern	PB
	Sterna caspia	Caspian tern	W
	Charadrius semipalmatus	Semipalmated plover	W
	Pluvialis squatarola	Black-bellied plover	WM
	Catoptrophorus semipalmatus	Willet	MB
	Calidris minutilla	Least sandpiper	WM
	Calidris alpina	Dunlin	WM
	Limnodromus griseus	Short-billed dowitcher	SM
	Calidris himantopus	Stilt sandpiper	M
	Calidris pusilla	Semipalmated sandpiper	M
	Calidris mauri	Western sandpiper	WM
Ciconiiformes	*Ardea herodias occidentalis*	Great white heron	CS(T)
	Ardea herodias	Great blue heron	PB
	Butorides striatus	Green-backed heron	SB
	Egretta caerulea	Little blue heron	PB
	Casmerodius albus	Great egret	PB
	Egretta thula	Snowy egret	PB
	Egretta tricolor	Tricolored heron	SB
	Nycticorax nycticorax	Black-crowned night heron	PB
	Eudocimus albus	White ibis	S
Anseriformes	*Anas rubripes*	American black duck	PB
	Anas strepera	Gadwall	W
	Anas americana	American wigeon	W
	Aythya americana	Redhead	MW
	Aythya affinis	Lesser scaup	MW
	Branta canadensis	Canada goose	MW
Passeriformes	*Tachycineta bicolor*	Tree swallow	M
	Corvus ossifragus	Fish crow	PB
	Cistothorus palustris	Marsh wren	PB
	Cistothorus platensis	Sedge wren	W
	Agelaius phoeniceus	Red-winged blackbird	PB
	Ammodramus caudacutus	Sharp-tailed sparrow	PB
	Ammodramus maritimus	Seaside sparrow	PB

Table 23. Common mammals of Panhandle salt marshes (Stout 1984).

Species	Common name	Species	Common name
Sylvilagus palustris palustris	Marsh rabbit	*Mustela vison mink*	Southern mink
Oryzomys palustris palustris	Rice rat	*Lutra cf. canadensis*	Otter
Sigmodon hispidus	Cotton rat	*Vulpes fulva*	Red Fox
Ondatra zibethicus rivalicius	Louisiana muskrat	*Mustela frenata*	Long-tailed weasel
Myocastor coypus bonariensis	Nutria	*Lynx rufus*	Bobcat
Procyon lotor varius	Raccoon	*Odocoileus* sp.	Deer

Decomposition rates vary among the different plant species. The available detritus is usually lowest in winter months and increases through the spring and early summer to maximum values in August and September (Stout 1984).

i. Natural Impacts. Several natural factors such as sea level rise, extreme climatic events, tidal scour, and fire have affected the ability of marsh habitats to remain functional.

The current and future sea level rise (and coastal subsidence) may represent the most important potential long-range impact on salt marshes. Estimates of sea-level rise in the Panhandle (i.e., Pensacola) range from 84 to 104 cm in the next 100 years (including local subsidence rate and water-level increase) (Titus et al. 1984).

Sea-level rise will affect salt marshes in two ways: (1) increased tidal flooding and (2) wave-induced erosion (Titus et al. 1984). Since tidal flooding is an essential component of salt marsh functioning, any alteration can substantially change the system. With increased flooding, the system tends to migrate upward and landward. When insufficient organic sediment or peat is added to the marsh to keep up with the sea-level rise, the seaward zone becomes flooded so that the vegetation drowns and the soil erodes; the high marsh zone eventually becomes the low marsh or open water.

Sedimentation from rivers can offset some of the sea-level rise, but probably only for marshes in major river deltas (e.g., the Apalachicola). Other marshes will have a tendency to move inland. If there is human development just inland from the salt marshes, however, the marshes will have no room to migrate and will eventually disappear.

Sea-level rise may increase wave-induced erosion by allowing larger waves to hit the shoreline. A rise in sea level deepens bays and, depending upon bottom topography, would allow larger locally formed waves and ocean waves to strike the marsh. In addition, the protective barrier islands will rapidly erode and no longer buffer the wave energy before it strikes the coast.

j. Human Impacts. Marshes are extremely sensitive and susceptible to oil pollution. Given their location, they can be affected by oil residue running off the land as well as by oil spilled in the Gulf of Mexico and estuarine waters. Primary productivity can be severely reduced for months after a spill (Stout 1984). Contamination is usually restricted to the outer fringes of the marsh unless storms or extreme high tides drive water higher than usual. Usually, contamination will be apparent on the surface of the soil, plant stems, and leaves. The extent of an oil spill impact depends upon the amount and type of petroleum spilled, the proximity of the spill to the marsh, and other factors. The sublethal effects may be chronic or acute. The trophic effect on marsh birds and other animals higher in the food chain is not well known.

Pulp-mill effluents in the Apalachee Bay to the east of the study area have been found to severely reduce both the number of species and of individuals of marsh fishes. In addition, community structure was altered (Livingston 1975). Bird populations also exhibited reduced abundances and species numbers in pulp-mill polluted areas (Weiser 1973).

Sediment diversions such as dams, canals, and levees (e.g., fill roads) impact wetlands by decreasing the supply of fine sediment essential for the maintenance of marsh substrate. If an area is naturally subsiding, a reduced sediment supply from the land magnifies the problem.

The extraction of ground water, oil, and gas may cause subsidence of the local area. Also, impounding a marsh causes consolidation and oxidation of dewatered sediments.

Other human activities with more localized effects include: using pesticides (Tagatz et al. 1974), erosion from boat-wakes, canal dredging, using marsh buggies and other wetland transportation vehicles, and waste disposal.

k. Conclusions. The salt marsh is a critical nursery, refuge, and feeding area for many commercially important estuarine organisms such as fish and crabs. The plants protect the juvenile forms of many of the estuarine organisms against predation. They also supply the bulk of the detritus for the estuarine system. They have the important function of buffering coastal regions from the erosional effects of storms. The balance between a rising sea level and the necessary sediment supply is being upset by human encroachment in nearby habitats that directly and indirectly affects the marsh. This habitat is one that requires very stringent monitoring for future protection.

7.2.4 Intertidal Flats

a. Introduction. Intertidal flats are those portions of the unvegetated bottoms of estuaries, bays, lagoons, and river mouths that lie between the high and low tide marks as defined by the extremes of spring tides (Peterson and Peterson 1979). Intertidal flats are composed of sandy and muddy sediments in a wide range of relative proportions. Usually the distinction between intertidal "sand" flats and "mud" flats (as nearly all intertidal flats are traditionally misnamed) is made upon percentage of silt-clay in the sediment:

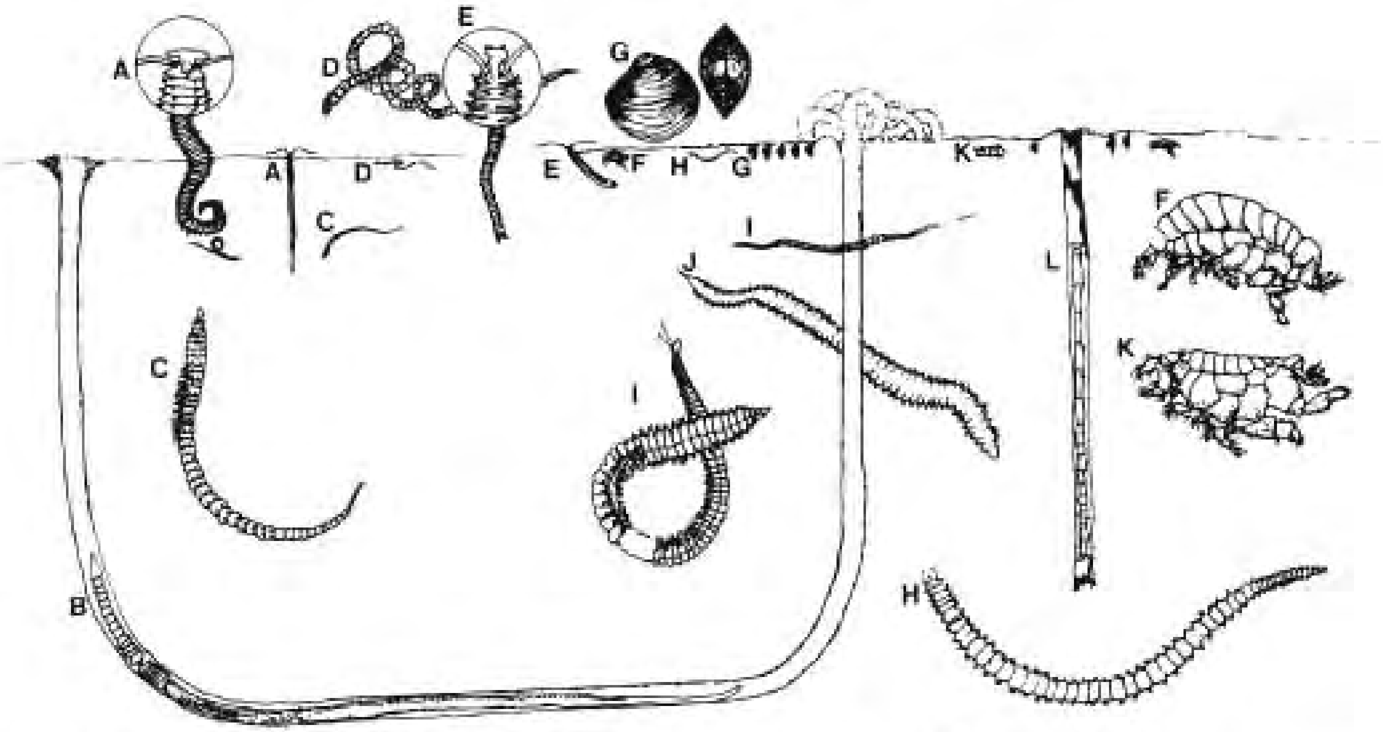
sediment	silt-clay fraction (dry wt.)
clean sands	< 5%
muddy sands	5–50%
sandy muds	50–90%
true muds	> 90%

The sediment type is indicative of the energy level of the coastline (i.e., a muddy sediment usually means a low-energy shore).

Intertidal flats appear barren and unproductive because of the absence of macrophytes such as marsh grass or seagrass. However, benthic microalgae are very abundant and productive, but do not accumulate the great biomass that, for example, marsh grasses do. Microalgae are nutritious and highly palatable to many herbivores; they are therefore rapidly used and maintain a low standing stock. Benthic microalgae generally do not go through intermediate bacterial or fungal food chains but are consumed directly by benthic invertebrates. For these reasons, intertidal flats contribute a substantial amount of primary productivity to an estuarine system which is, in turn, converted into consumer biomass. The benthic invertebrates are preyed upon by larger predators such as shorebirds, crabs, and bottom-feeding fishes. Intertidal flats play a critical role in the functioning of the entire estuarine system (Peterson 1981).

b. Flora. Microalgae, bacteria, and fungi are locally abundant on intertidal flats. The generally small sediment particles present in the intertidal habitat can support large populations of these organisms. Occasionally, the bacteria form visible purplish-red mats on the sediment surface (Heidenauer, personal observation). Bacteria are an important food source for the meiofaunal community (Carman 1984) and are the primary transformers of detritus into inorganic nutrients.

c. Faunal composition. Two groups of benthic fauna are present on the intertidal flats: epifauna (forms that live on top of the substrate) and infauna (forms that live within the substrate) (Figure 72). Mobile epifauna, such as crabs, are found most commonly during high tides. Infaunal organisms, however, are more abundant at both low and high tides.



Surface deposit feeders
A = *Spiophanes bombyx* (spionid polychaete)
B = *Ptychodera bahamensis* (protochordate)
E = *Prionospio steenstrupi* (spionid polychaete)

Suspension Feeders
F = *Protohaustorius* sp. (haustorid amphipod)
G = *Gemma gemma* (venerid bivalve)
K = *Acanthohaustorius* sp. (haustorid amphipod)

Conveyor-belt deposit feeder
L = *Clymenella torquata* (maldanid polychaete)

Burrowing deposit feeders
C = *Aricidea cerrutii* (paraonid polychaete)
D = oligochaete
H = *Exogone dispar* (syllid polychaete)
I = *Haploscoloplos* fragilis (orbiniid polychaete)
J = *Nephtys picts* (nephtyid polychaete)

Figure 72. A cross-sectional view through a typical intertidal sand-flat community in the Panhandle showing representative invertebrates (adapted from Whitlatch 1982).

The infaunal microfauna are dominated by protozoans, with foraminifera and ciliates being the dominant forms. The group has been little studied.

The meiofauna differ between sand and mud tidal flats because of the difference in interstitial space (i.e., space between sediment particles) available to the organisms in each sediment type. Sand sediments have larger interstitial spaces and the majority of the meiofauna are adapted to living within these spaces (i.e., infaunal). In muddy sediments, the meiofauna are generally restricted to living on the sediment surface (i.e., epifaunal).

The macrofauna are the most dominant group of infauna in terms of biomass present. Polychaetes, amphipods, enteropneusts, and bivalve and gastropod mollusks dominate the community (Figure 72 and Table 24).

d. Trophic dynamics and interactions. Microalgae, primarily the diatoms, dinoflagellates, filamentous greens, and blue-greens, are the primary products in the tidal flat system. Typically, these forms demonstrate a high turnover rate. Herbivores are usually deposit-feeding or grazing macroinvertebrates. Many of the common species are given in

Table 24. Commonly encountered macroinvertebrates of Panhandle intertidal flats (Abele 1970, LeBlanc 1973, Abele and Kim 1986).

Group	Species	Habitat
Crustacea	*Alpheus heterochaelis*	epifaunal
	Callianassa jamaicensis	infaunal
	Eurytium limosum	epifaunal
	Uca longisignalis	epifaunal
	Callinectes sapidus	epifaunal
Mollusca	*Mercenaria mercenaria*	infaunal
Polychaeta	*Amphicteis gunneri floridus*	infaunal
	Diopatra cuprea	infaunal
	Glycera americana	infaunal
	Glycera dibranchiata	infaunal
	Haploscoplos fragilis	infaunal
	Heteromastus filiformis	infaunal
	Laeonereis culveri	infaunal
	Notomastus latericeus	infaunal
	Onuphis eremita oculata	infaunal
	Pectinaria gouldii	infaunal
Enteropneusta	*Ptychodera bahamensis*	infaunal
Merostomata	*Limulus polyphemus*	epifaunal

Table 25. Common birds of Panhandle intertidal flats (Stout 1984).

Guild	Common name
Waders	Herons Egrets Ibises Yellowlegs
Shallow-probing, surface-searching	Sandpipers Plovers Knots
Deep-probing	Godwits Willets Curlews
Aerial-searching	Terns Gulls Skimmers Pelicans
Floating/diving	Ducks Geese Grebes Cormorants
Birds of prey	Osprey Eagles

Table 24. Shorebirds (Table 25), crabs, and fishes are the primary consumers of the herbivores.

The infauna of Panhandle intertidal flats are generally less abundant than that of adjacent salt marshes, even at similar tidal heights. The difference is usually pronounced and approaches two orders of magnitude (Stout 1984). The pattern appears to be a result of higher predation on organisms living in the flat areas (Naqvi 1968).

Large, mobile epibenthic predators are common on intertidal flats, especially during the warm summer months when most infaunal organisms are low in numbers. Predators can be divided into two general groups. One group, dominated by fiddler crabs (*Uca* spp.), roams the intertidal zone at low tide foraging for epibenthic algae and detritus. Most of the members in this group are herbivores or detritivores. The other group of predators includes organisms that forage on the flat when the tide is in. These species are mostly carnivorous. The most important species are the blue crab, *Callinectes sapidus*, the stingray, *Dasyatis sabina*, and the horseshoe crab, *Limulus polyphemus*. These species prey on bivalves and polychaetes. The tolerance of blue crabs to reduced salinities makes them effective predators under a variety of conditions. Blue crabs cannot forage efficiently for infauna in the presence of shell debris, which inhibits their digging; therefore, the abundance of many bivalves and other infauna is higher at the margins of structures such as oyster reefs. Smaller biological structures, such as *Diopatra cuprea* tubes, may also offer infaunal organisms a refuge from predation or disturbance (Woodin

1978). In addition to the invertebrate predators, birds are important predators on infaunal organisms.

In addition to removing organisms by predation, blue crabs, horseshoe crabs, and birds can be a source of infaunal mortality by disrupting the sediment surface. Blue crabs dig up to 6–8 cm deep in the sediments to forage and hide. Their pits are sites of decreased infaunal densities (Woodin 1978). Horseshoe crabs dig broad, shallower pits (less than 4 cm deep) that have slightly less impact on the infauna (Peterson and Peterson 1979). Birds disturb the infauna in a variety of ways depending on their feeding mode.

Additional food resources are supplied to the intertidal flats by grass wrack (dead fragments of seagrass and marsh grass) that are deposited on the flat during outgoing and incoming tides.

7.2.5 Hard Substrates

a. Introduction. Most of the habitat represented in this category is artificial. There is little naturally occurring hard substrate along the Panhandle coast. In addition to larger surfaces such as jetties, bridges, and pier pilings, mollusk shells and trash offer suitable microhabitats for some sessile organisms.

b. Community structure. Panhandle estuarine fouling communities demonstrate a dramatic decrease in larval settlement and population growth during the winter (November–March) (Salsman and Ciesluk 1978). The entire fouling community appears to be affected except the bacteria and associated slime film (including algae) that is usually present.

During the summer, when water temperatures are greater than approximately 20 °C, a complete biofouling community is present. The most abundant organisms are barnacles, with the species *Balanus eburneus* dominant in the upper tidal zone. Polychaetes (serpulids and spirorbids—calcareous tube builders) and bryozoans are also abundant. Later in community development, tunicates (ascidians) become important. Tunicates, or sea squirts, (e.g., *Ectenascidia turbinata* and *Styella partita*) can eventually dominate a substrate, forming a homogenous layer 30–40 mm thick.

The first macrofaunal colonizers onto a new hard substrate are usually the American oyster *Crassostrea virginica* or the barnacle *Balanus* spp. The barnacle can eventually replace the oyster.

c. Trophic dynamics and interactions. Predators on the initial colonizers of hard substrates appear quickly after settlement. Oyster predators include the American oystercatcher (*Haematopus palliatus*), the decapods—blue crab, stone crab (*Menippe mercenaria*), and mud crab (*Eurypanopeus depressus*), and the mollusk—oyster drill (*Thais haemastoma*). Barnacle predators include the decapods *Pachygrapsus transversus*, *Mithrax forceps*, and *M. pleuracanthus*. Decapods are common on Panhandle jetties (Table 26).

K. Sherman (Florida Department of Health and Rehabilitative Services, Tallahassee; pers. comm.) has investigated the epifauna of live scallop shells from St. Joseph Bay. The epifaunal assemblage is similar to the nearby *Thalassia* epifauna but is dominated by different species. There is a strong seasonality, and competition for food may be an important factor in controlling abundances (especially meiofauna). The two-dimensional nature of the hard substrate may result in spatial competition among the various residents (K. Sherman, pers. comm.).

7.2.6 Oyster Reefs

a. Introduction. The biology of the oyster has been extensively studied because of economic interests (e.g., meat and shell industries). However, the ecology of the oyster reef ecosystem, despite recognition that it is a separate community (Mobius 1877), has not been nearly as intensively investigated. Most information comes from research performed outside the Panhandle region. Oysters are typically reef organisms, growing on the shell substrate accumulated from generations of oysters (Chestnut 1974). The term oyster reef is often used interchangeably with other terms for estuarine regions inhabited by oysters, including oyster bar, oyster bed, oyster rock, oyster ground, and oyster planting. Bahr and Lanier (1981, p. 3) define oyster reefs as "the natural structure found between the tide lines that are [sic] composed of oyster shell, live oyster, and other organisms and that are discrete, contiguous, and clearly distinguishable (during the ebb tide) from scattered oysters in marshes and mud flats, and from wave-formed shell windrows."

Table 26. Common decapods found on Panhandle jetties (Abele 1970, Abele and Kim 1986).

Species name	Species name	Species name
Acanthonyx petiverii	*Hexapanopeus quinquedentatus*	*Periclemenes americanus*
Alpheus armillatus	*Hippolysmata wurdemanni*	*Portunus sayi*
Alpheus formosus	*Mithrax forceps*	*Sicyonia laevigata*
Calcinus tibicen	*Mithrax pleuracanthus*	*Stenorhynchus seticornis*
Dromidia antillensis	*Pagurus miamensis*	*Synalpheus fritzmuelleri*
Hexapanopeus paulensis		*Xantho denticulata*

Oyster reefs influence estuaries physically by removing suspended particulate matter and changing current patterns, and biologically by removing phytoplankton and other particles and producing large quantities of oyster biomass and pseudofeces. In addition, the structure of the reef provides habitats for many estuarine organisms. One square meter of a typical oyster reef actually represents approximately 50 m² of surface area or potential habitat (Bahr and Lanier 1981).

The oyster reef is a strongly heterotrophic system using tidal energy to bring in food and carry away waste material. The majority of energy or matter entering or leaving the oyster reef is surficial (filter feeders, detritus, and predator components) and not contained within complex food web networks (Dame and Patten 1981). Overall, filter feeders (e.g., the oysters) affect nutrient cycling and energy flow in the ecosystem through translocation and transformation of matter (Dame 1976).

b. Distribution. Oyster reefs are present in many of the Panhandle estuaries (Table 27). In the Apalachicola Bay system, oyster reefs cover an estimated 7% of the bottom area (Livingston 1984a). Newly constructed artificial reefs are located primarily in the eastern portions of St. Vincent Sound. The natural reefs of St. Vincent Sound and western St. George Sound represent the largest concentrations of commercial oysters in the Panhandle. It is estimated that 40% of Apalachicola Bay is suitable for growing oysters, but that substrate type is a major limiting factor (Whitfield and Beaumarriage 1977).

Table 27. Area of oyster reefs (beds) in the Florida Panhandle (from (a) McNulty et al. 1972, (b) Livingston 1984).

Area	Oyster reef coverage (ha)	Source	Area	Oyster reef coverage (ha)	Source
Ochlockonee Bay	?		East Bay (St. Andrew)	46	a
Alligator Harbor	36.7	a	St. Andrew Bay	0	a
St. George Sound (East)	2.6	b	West Bay	7	a
St. George Sound (West)	1,488.8	b	North Bay	6	a
East Bay	66.6	b	Choctawhatchee Bay	4,695	a
Apalachicola Bay	1,658.5	b	Santa Rosa Sound	0	a
St. Vincent Sound	1,096.5	b	East Bay (Pensacola)	3,395	a
St. Joseph Bay	0	a	Escambia Bay	81	a
St. Andrew Sound	0	a	Pensacola Bay	0	a

The system is characterized by very rapid oyster reproduction and growth, accounting for approximately 90% of Florida's and 8%–10% of the nation's annual oyster production.

Choctawhatchee Bay also possesses a fairly extensive coverage of oyster reefs (Burch 1983b). The oyster beds are harvested in Walton County west of the U.S. Highway 331 causeway along the southern shore of the bay.

c. Oyster autecology. The primary reef-building, commercial oyster found in the Panhandle is the Eastern or American oyster. The species *Ostrea equestris* is also present. Both species grow in a wide salinity range (10–30 ppt). Optimal growth occurs at a water temperature of approximately 25 °C.

The oyster is dioecious (i.e., having separate sexes), but once a year some members can undergo protandry (change from male to female) or protogyny (female to male). It has been postulated that under certain types of stress a population may develop a higher proportion of males than females. For instance, the harsh conditions in the higher portions of the oysters' intertidal range (the upper reef zone) may produce or regrow predominantly male colonies that would contribute little to the reproductive success of the population.

Temperature or salinity shock usually triggers the emission of sperm from mature males in a local population. The threshold temperature or salinity can vary among geographic locations. Emission of the sperm from male oysters stimulates the females in the area to release eggs via a chemical cue (protein pheromone). A mass "chain reaction" spawning can occur in dense populations. Fertilization occurs in the water column through the chance meetings of egg and sperm. This begins the planktonic, free-living phase of the oyster life cycle. When the larva first secretes a pair of shells, it reaches the veliger stage. Depending on water temperature and food availability, the larval stages usually lasts 7 to 10 days, but in some cases may last up to two months.

Hayes (1979) studied the reproductive cycle of the American oyster in intertidal areas off Turkey Point and in Alligator Harbor along the Panhandle coast. He reported that oysters 1 year of age and older undergo two major spawning periods per year with renewed gonadal development between these events. In addition, oysters that set early in the spawning season reach sexual maturity and spawn before the end of the same reproductive season.

The gonadal condition of established oyster populations depends on ambient water temperatures. In the eastern part of the Panhandle, gonadal development begins before the temperature reaches 20 °C (usually in April), probably sometime in late February or March (Hayes 1979). The majority of spawning does not occur until a minimum temperature of 25 °C is reached. Spawning can also be induced by temperature fluctuations of 5–10 °C. Gamete-containing gonads in established oysters are still present in late October and probably remain active until late November when most gonadal activity ceases (Hayes 1979).

Most of the setting occurs in the spring (late May). This peak can be attributed solely to the spawning of those oysters that attached in previous years (i.e., at least 1 year old). Setting that takes place later in the season may be due to additional spawning by older oysters and spawning of the sexually developed young-of-the-year oysters. The contribution of the young oysters to population recruitment, however, is minimal.

A number of physicochemical and biological factors influence the settlement of larval oysters. Light, salinity, temperature, and current velocity are of primary importance. In addition, oyster larvae are highly gregarious and settle in response to a waterborne pheromone or metabolite that is released by the oyster after metamorphosis. Larvae are also attracted to a protein on the surface of oyster shells. The gregariousness is critical since the reproductive scheme of the oyster requires settlement in proximity for successful fertilization.

Oyster growth occurs throughout the year in the Panhandle (Menzel et al. 1966). Maximum size (total shell length) is usually not much greater than 100 mm. Oysters reach a marketable size within 2 to 3 years after settlement.

Oysters are filter-feeders. The specific diet is not clearly known. The gills are reported to selectively retain diatoms, dinoflagellates, and graphite particles from 2 to 3 microns (Bahr and Lanier 1981). Feeding activity is highest at low food concentrations and there is a negative correlation between pumping rate and surrounding turbidity. Because they filter the water to feed, oysters can concentrate pathogenic bacteria and viruses along with food particles.

d. Oyster reef development and zonation. Oyster reefs in the Panhandle range in size from small scattered clumps to massive solid mounds of living oysters and dead shells. Reef development is usually limited to the middle portion of the intertidal zone, where minimum inundation time determines the maximum elevation of reef growth. Predation and siltation (which determines available substrate) are the main factors that often limit oyster populations in the lower intertidal and subtidal zones to scattered individuals and small clumps.

An oyster reef may begin its development with the attachment of a single oyster to some solid substrate. Succeeding generations of oysters attach to the earlier colonizers and a gradual increase in length, width, and height eventually forms a reef. In shallow intertidal water, such development can form a marsh island with a fringe of live oysters. In deeper water, a reef may form a shoal rising several feet above the bottom.

There is a difference in the size of oysters from the various parts of a reef. Individuals along the edge are usually larger (i.e., longer shell length) than those in the center (Menzel et al. 1966). This difference in growth can be as high as two-fold.

During exposure to the atmosphere (at ebb tide), the surface of a reef dries and turns gray, but, upon wetting, the thin film of algae covering the shells appears greenish-brown. Only the upper layer (5–10 cm) of oysters and dead shells actually dries out. The underlying shell layer remains moist. The reef consists of three "horizons" (Bahr and Lanier 1981): (1) pale greenish-gray (the exposed portion); (2) reddish-brown; and (3) silver-black. The reddish-brown section derives its characteristic color from the detritus covering each shell. It lacks the film of algae characteristic of the upper layer. The silver-black zone is characteristic of shells buried in an anaerobic environment high in ferrous sulfide. Mud crabs (e.g., *Panopeus herbstii* and *Eurypanopeus depressus*) graze on the organic film in the top two horizons.

A section through a typical Panhandle oyster reef shows that it has relatively distinct strata (Bahr and Lanier 1981). The moist upper portion is level, but the reef slopes steeply at the edges. The living portion of the reef is thicker at the perimeter than in the center, where mud trapped by biodeposition and sedimentation may smother oysters. This sedimentation results from suspended matter settling out as turbid water slows down while passing over the reef.

Oysters in the top (green) layer have sharper growing edges than those in the reddish-brown zone, indicating faster growth. This is a result of crowding and sediment deposition on lower oysters.

e. Associated fauna. Vertical zonation in oyster reef macrofauna is caused by the differing tolerance to desiccation of the various species rather than by their differing requirements for inundation in order to feed (Bahr and Lanier 1981). Some of the same zonation patterns are reflected on artificial pilings. In a manner similar to that of the reef, single shell or live oyster on that reef maintains a microcosm of sessile and mobile epifauna.

The reef provides a solid substrate for sessile organisms that require an attachment surface. These include algae, hydroids, bryozoans, barnacles, mussels, and polychaetes. Some forms also bore into the shell: boring sponges and mollusks, perforating algae, and burrowing polychaetes. Many organisms find refuge in the crevices of the reef. Organisms typically found on Panhandle oysters reefs are given in Table 28 (Menzel and Nichy 1958, Menzel et al. 1966, Abele 1970, Livingston 1984, Abele and Kim 1986).

The stone crab is a commercially important inhabitant of oyster reefs. Stone crab densities on oyster reefs are highest during the summer, decline over the late fall, and remain low throughout the winter (Hembree 1984) (Figure 73). Seasonal residency patterns suggest that the reefs may provide a

Table 28. Common fauna of a Panhandle oyster reef (Menzel and Nichy 1958, Menzel et al. 1966, Abele 1970, Livingston 1984, Abele and Kim 1986).

Group	Species
Microfauna/Meiofauna	
Fungus	*Perkinsus marinus*
Macrofauna	
Porifera	*Cliona vastifica*
Coelenterata	*Astrangia* spp.
Bryozoa	*Mebranipora* sp.
Platyhelminthes	*Bucephalus cuculus*
	Stylochus frontalis
Insecta	*Anurida maritima*
Annelida (Polychaeta)	*Neanthes succinea*
	Polydora websteri
	Sabellaria spp.
Arthropoda	*Balanus eburneus*
	Callinectes sapidus
	Clibinarius vittatus
	Eurypanopeus depressus
	Menippe mercenaria
	Neopanope packardi
	Neopanope texana
	Panopeus herbstii
	Petrolisthes armatus
	Synalpheus minus
Mollusca (Gastropoda)	*Anachis obesa*
	Busycon contrarium
	Crepidula plana
	Epitonium sp.
Gastropoda (cont.)	*Kurtziella* sp.
	Melongena corona
	Mitrella lunata
	Murex pomum
	Odostonia impressa
	Pleuroploca gigantea
	Polinices duplicatus
	Seila adamsi
	Thais haemastoma
	Triphura nigrocincta
Mollusca (Pelecypoda)	*Abra aequalis*
	Anadara transversa
	Anomia simplex
	Branchidontes exustus
	Branchidontes recurvus
	Chione cancellata
	Crassostrea virginica
	Corbicula sp.
	Martesia smithi
	Mulinia lateralis
	Noetia ponderosa
	Ostrea equestris
	Semele bellastriata
	Trachycardium muriacatum
Fishes	*Hypleurochilus germinatus*
	Hypsoblennius hentzi
	Hyspoblennius ianthus
	Opsanus beta
Birds	*Haematopus palliatus*

valuable site for reproductive activities. Juvenile crabs are abundant on reefs, which act as shelters from predation and offer food resources in the form of reef-associated organisms (i.e., bivalves, gastropods, and crustaceans). Hembree (1984) reported that the adult inshore residency peaked in the fall (Figure 74) and that adult heterosexual pairing of stone crabs on the oyster reefs coincides exclusively with the fall mating season, and suggested that oyster reefs provide a valuable resource for the stone crab, e.g., a high density of potential mates and suitable shelter for molting.

The stone crab fishery is concentrated in the nearshore areas of the coast. The commercial stone crab season is from October 15 to May 15. Only claws with a minimum of 7 cm propodus length or 10.8 cm overall length may be kept.

f. Commercial aspects. In the Panhandle (as well as in the entire State) oyster reefs are considered public unless yearly leases are obtained from the Department of Natural Resources. The primary advantage of leasing is the ability to designate an area and plant oyster shells or other culch material

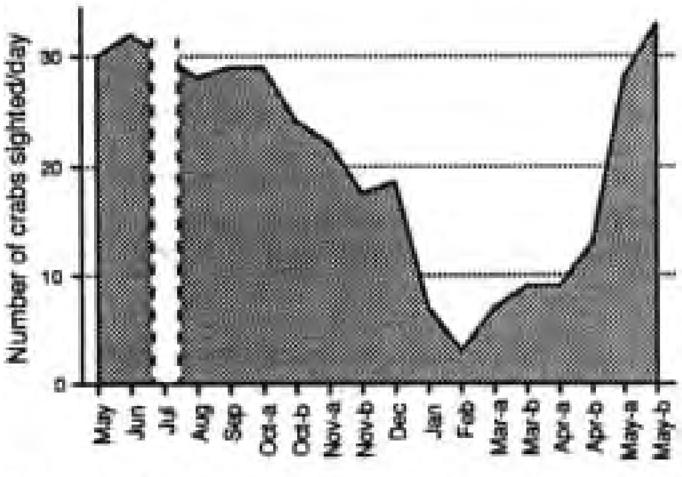


Figure 73. Seasonal stone crab densities on a Panhandle oyster reef (Hembree 1984).

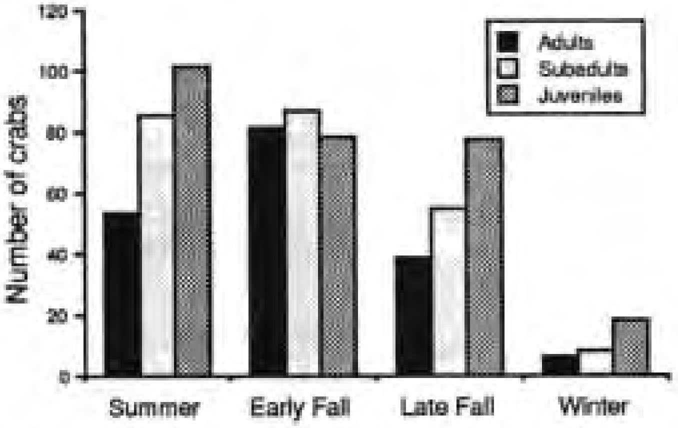


Figure 74. Stone crab age-group occurrence on a Panhandle oyster reef (Hembree 1984).

and expect that it will remain undisturbed (Burch 1983b). All leased reefs are artificial.

Potential harvest areas are classified: (1) approved; (2) conditionally approved; (3) prohibited; and (4) unclassified. Approved areas meet water-quality criteria. Conditionally approved areas normally meet water-quality standards but are subject to localized flooding or urban runoff that may temporarily lower water quality. Prohibited areas consistently do not meet water-quality standards and harvesting is prohibited. Unclassified areas are unsurveyed and unmonitored sites and are not officially approved for harvesting.

The most important oyster harvesting region in the Panhandle is the Apalachicola Bay system, which contains 83% of the State's public reefs. In 1982, 1,884,000 kg of oysters worth an estimated $4,150,366 were harvested from the system (Snell 1984). Also in 1982, Choctawhatchee Bay recorded its highest oyster landing ever (Table 29).

g. Natural Impacts. Under normal conditions, the natural environment controls population growth and regulates the distribution and density of oyster reefs.

The pathogen *Perkinsus marinus* is responsible for up to 50% of the annual mortality in adult oysters

Table 29. Oyster landings (kgs of meat) from Choctawhatchee Bay, 1965–82 (Burch 1983b).

Year	Walton County	Okaloosa County	Year	Walton County	Okaloosa County
1965	3,981	0	1974	3,529	262
1966	2,115	0	1975	1,868	799
1967	3,009	0	1976	123	0
1968	3,290	0	1977	147	0
1969	6,118	0	1978	803	0
1970	5,538	0	1979	0	1,356
1971	2,896	0	1980	36	49
1972	7,424	617	1981	0	0
1973	5,505	1,416	1982	18,196	50

in Panhandle oyster reefs. Young oysters are apparently unaffected.

Predation is a limiting factor in the growth of Panhandle oyster populations, especially in high-salinity subtidal regions (Menzel and Nichy 1958, Menzel et al. 1958). On reefs in Alligator Harbor, Menzel and Nichy (1958) found several important oyster predators. Lightning whelks, *Busycon contrarium*, are primary predators and are usually very numerous throughout the reef. These kill individual oysters by chipping away shell edges or by forcibly opening the valves to gain entry. Apple murexes, *Murex pomum*, and oyster drills, *Thais haemastoma*, are important predators of oysters below the water surface and were not found on exposed portions of reefs. In some locations, they were very abundant. They drill holes in the oyster valves to reach the meat. Another very common predator is the stone crab. Blue crabs are heavy predators of small oysters but not of large individuals. The crabs are very numerous on the reefs during incoming tides. The American oystercatcher is also a very common predator on the reef (Menzel and Nichy 1958).

There are three primary commensals associated with oysters: the boring sponge *Cliona celata*; the polychaete *Polydora websteri*, and the pea crab *Pinnotheres ostreum*. All three produce stress in the oyster. The boring sponge and polychaete induce additional shell deposition. The pea crab lives within the oyster's mantle cavity, removing food and mucus from the gills and possibly feeding on developing gametes.

Hurricane Elena (August 30–September 1, 1985) produced widespread damage to the oyster reefs in Panhandle waters. Three factors were primarily responsible for the mortality: (1) live oysters were broken from the reef and deposited onto soft-sediments where they could not feed properly; (2) increased turbidity smothered the oysters; and (3) attached oysters were crushed. Another damaging factor was decreased salinity.

Low dissolved oxygen concentrations, high temperatures (Quick 1971), excessive turbidity (sedimentation), an overabundance or shortage of appropriate food, and crowding also have an impact on oyster populations.

h. Human Impacts. Human perturbations can be lethal or sublethal for oysters but, even when sublethal, the oysters may be unfit for consumption (human or otherwise). Like most suspension feeders, oysters may concentrate suspended and dissolved constituents of the water column (including human pathogens, pesticides, and heavy metals) to levels several orders of magnitude above background concentrations. There are eight types of impacts:

(1) Physical disturbances, especially sedimentation resulting from dredging and excessive boat traffic, result in burial and anoxia of adult oysters and the reduced availability of culch for spatfall.

(2) Salinity changes caused by freshwater diversion or local hydrologic alteration increase predation and fouling.

(3) Eutrophication results in oxygen depletion in bottom water, toxic effects of blue-green algae and certain other algae, and excessive POC (Particulate Organic Carbon), which reduces clearance efficiency. A specific example is the 1971 oyster kill in Escambia Bay. Ninety percent of the commercial size oysters were destroyed by a fungus (*Perkinsus marinus = Labyrinthomyxa marina*), whose growth was promoted by increased nutrients from industrial waste discharges (Little and Quick 1976).

(4) Toxins, including pulp mill sulfites, heavy metals, chlorinated hydrocarbons, organophosphates, radionuclides, and petroleum hydrocarbons can have such sublethal effects as reduced resistance to natural stress, subtle changes in the entire community structure, and reduced gametogenesis as well as lethal effects such as increased rate of mortality.

(5) Physical impairment of feeding structures by oil contributes to eventual mortality.

(6) Thermal effluents, primarily from powerplants, contribute to decreased community diversity and enhanced oyster production.

(7) Overharvesting results in the depletion of breeding stocks, culch, and a decrease in bottom stability.

(8) Wetland loss caused by development decreases the wetland-water interface that is a prime reef habitat, and the source of primary production that contributes to oyster reef growth.

i. Conclusions. Oysters in the Panhandle represent a valuable commercial resource as well as an ecologically important habitat. Because oysters filter water to feed, they are extremely sensitive to many water quality perturbations, both natural and artificial.

7.2.7 Marine Algae

a. Introduction. There are five major phyla of algae in the Panhandle estuaries: (1) Cyanophyta—blue-greens; (2) Rhodophyta—reds; (3) Phaeophyta—browns; (4)Chlorophyta—greens; and (5) Chrysophyta—golden browns. Approximately 525 species occur in the Panhandle (Earle 1972, Humm 1973). Marine algae provide habitat for many organisms and may be found in nearly all habitats from subtidal soft bottoms to intertidal salt marshes. Hence, the habitat category was not given a strictly intertidal or subtidal designation.

Red and brown abundance is usually limited by the availability of a hard substrate for attachment. An extensive development of benthic algae can usually be found on submerged artificial structures such as jetties, seawalls, and pilings, and on natural surfaces such as oyster reefs, scattered bivalve shells, and seagrass blades.

One major group of algae is able to colonize unconsolidated sediments and may compete with seagrasses for space (Humm 1973). These algae belong to the order Siphonales, many of which have developed the ability to anchor themselves in soft sediment by means of clusters of rhizoids. Members of the genus *Caulerpa*, with their horizontal "stems," erect "leaves," and rhizoids, cover the greatest area of sandy bottom of any of the Siphonales. Other genera present include *Halimeda*, *Penicillus*, *Udotea*, and *Avrainvillea*.

b. Major algal species present. The common algal species found throughout the Panhandle are listed in Table 30. The filamentous blue-green alga *Calothrix crustacea* is a ubiquitous Panhandle species that produces a black band (often mistaken for an oil stain) high in the intertidal zone on seawalls, pilings, and other intertidal, hard surfaces. It also occurs on the basal portions of *Spartina alterniflora* and *Juncus roemerianus* in Panhandle salt marshes and is present less conspicuously in the subtidal regions.

Below the *Calothrix* band in the intertidal zone are several genera of red algae, *Bostrychia*, *Caloglossa*, *Catenella*, and *Murrayella*. The first three are nearly exclusively intertidal. The green alga *Enteromorpha* is also conspicuously abundant in the intertidal zone. Various species of *Vaucheria* are reported from the littoral sand flats on the Florida west coasts (Dawes 1974), and are probably present in the Panhandle.

In deeper water, the red algae *Digenia simplex*, *Gracilaria verrucosa*, *G. folifera*, *Acanthophora spicifera*, *Hypnea musciformis*, and *Laurencia poitei* are frequently present in large, seasonally abundant drift clumps on the bottom or in windrows on the water surface.

c. Associated fauna. The red algal clumps that occur periodically in the Panhandle contain an abundant fauna (Hooks et al. 1976). The algae provide protection from predation and the firm branches provide an attachment surface for sessile organisms. Ophiuroids and caprellid amphipods are common. Large numbers of harpacticoid copepods are usually present.

Red algae may provide refuge from predation for sediment-dwelling organisms (Hooks et al. 1976). Large numbers of the caridean shrimp *Palaemon floridanus* are occasionally present within the clumps.

7.2.8 Open Water

a. Introduction. The open water (or water column) habitat contains plankton (i.e., organisms that are passively carried by the currents) and nekton (i.e., organisms that actively swim) that cannot be associated with and assigned to particular substrate types. The habitat includes species that cover a wide size spectrum ranging from diatoms and copepods (microns in length) to fish and porpoises (meters in length). This habitat contains the phytoplankton that play a major role in the primary productivity of the estuaries.

A characteristic of the estuarine water column habitat is the extreme spatial variability present.