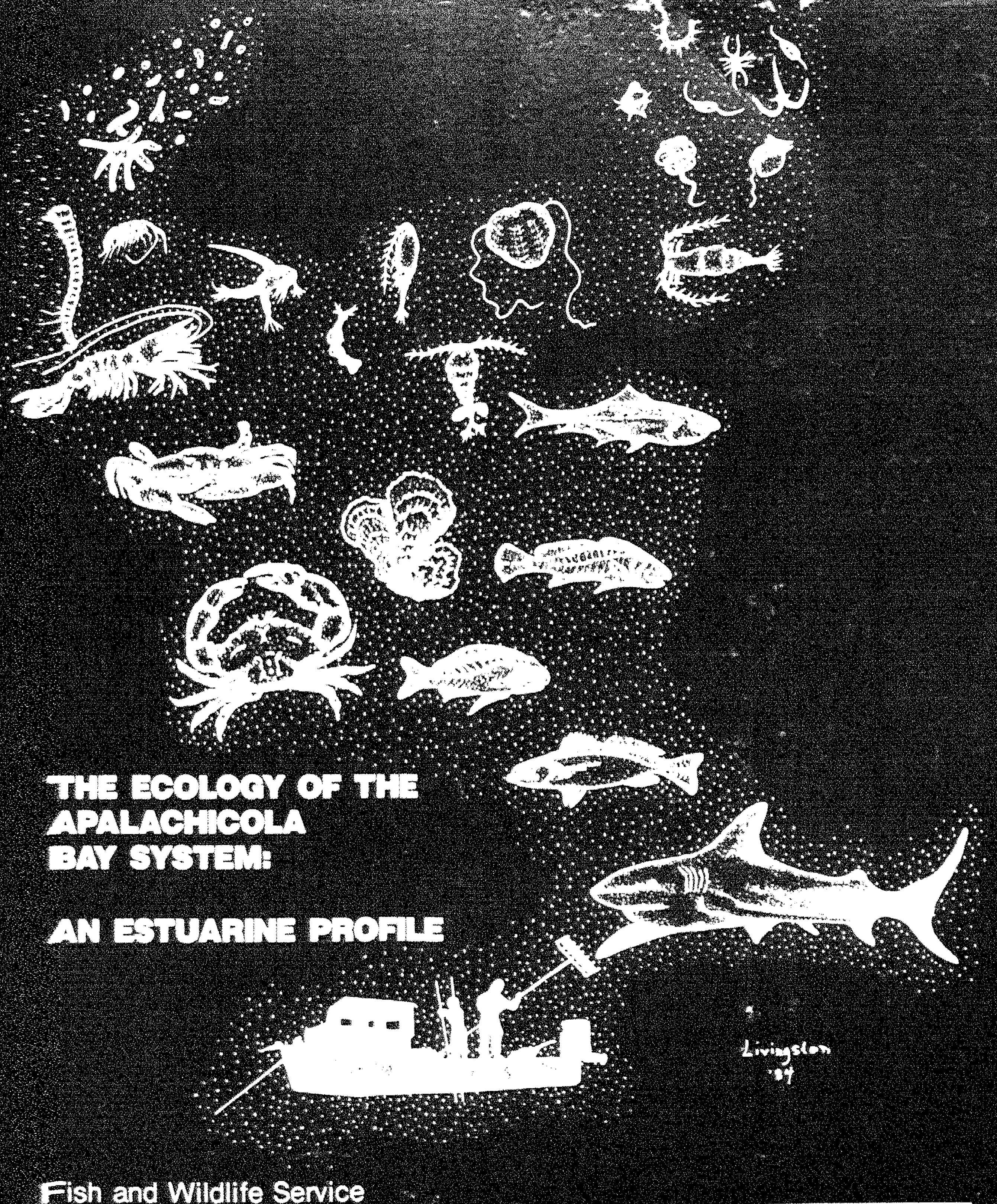
FWS/OBS-82/05
September 1984



THE ECOLOGY OF THE APALACHICOLA BAY SYSTEM:

AN ESTUARINE PROFILE

Fish and Wildlife Service
U.S. Department of the Interior

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THE ECOLOGY OF THE APALACHICOLA BAY SYSTEM: AN ESTUARINE PROFILE

by

Robert J. Livingston
Department of Biological Science
Florida State University
Tallahassee, FL 32306

Project Officer

Wiley M. Kitchens
National Coastal Ecosystems Team
U.S. Fish and Wildlife Service
1010 Gause Blvd.
Slidell, LA 70458

Prepared for

National Coastal Ecosystems Team
Division of Biological Services
Research and Development
Fish and Wildlife Service
U.S. Department of the Interior
Washington, DC 20240

Library of Congress Card No. 84-601077

This report should be cited as:

Livingston, R.J. 1984. The ecology of the Apalachicola Bay system: an estuarine profile. U.S. Fish Wildl. Serv. FWS/OBS 82/05. 148 pp.

PREFACE

This paper represents a synthesis of knowledge concerning the Apalachicola drainage system, which is located in Florida, Georgia, and Alabama. The Apalachicola Bay complex is only one part of a major drainage area that includes the Apalachicola, Chattahoochee, and Flint River systems on one side and the northeastern Gulf of Mexico on the other. The boundaries that separate various components (i.e., the river and its associated wetlands, the bay system, and the open gulf) are artificial in an ecological sense. Likewise, the traditional boundaries that have separated various scientific disciplines--such as physics, chemistry, meteorology, and biology--are somewhat arbitrary when a systems approach is used to determine the functional interactions among interacting subsystems. Thus various boundaries must be crossed when the investigator attempts to understand an entire aquatic ecosystem.

Over the past 12 years, researchers in the Apalachicola system have carried out a series of multidisciplinary and interdisciplinary studies to determine the response of the Apalachicola estuary to a series of environmental variables. Such an effort can be likened to the growth of concentric layers of a snowball as it rolls down a hill. The solution of each problem forms the foundation for a new question, which, in turn, serves as the template for new hypotheses and tests. The combination of background field analyses and experiments in the laboratory and the field have been used as the basis of this effort. Eventually, we can view the overall picture by cutting through the snowball of ideas, hypotheses, and resolutions to form models of how the ecosystem works. As of this writing, 12 years of continuous field and experimental data have been transformed into computerized files, which are now being used to develop models of how the Apalachicola Bay system works in comparison with other such systems in the southeastern United States.

The scientific work on the Apalachicola estuary is only the first step in our understanding of system functions. Increasingly, humans are having an important influence on natural aquatic systems. Urbanization, industrialization, and agricultural activities can lead to habitat destruction, pollution, and severe restrictions on productivity, which, in turn, can be translated into very real socioeconomic problems. The Apalachicola area is a multiple-use system. Accordingly, sound land planning and progressive resource management are best carried out with a comprehensive base of objective scientific and economic information. With the recent establishment of the Apalachicola River and Bay National Estuarine Sanctuary--the largest such sanctuary in the nation--the Apalachicola drainage system has been designated by law as a special area, a place of refuge and shelter for important aquatic species as well as humans as integral parts of the ecosystem. As one of the last relatively natural big river areas in the United States, the highly productive Apalachicola system is small enough to analyze in a comprehensive scientific fashion while being extensive enough to be used as a natural model for other such areas. The Apalachicola valley is currently part of a major experiment to determine whether scientific data can be translated into a comprehensive resource management program that will accommodate economic development while perpetuating the natural resources of the region.

SUMMARY

The results of 12 years of continuous field studies and experiments in the Apalachicola Bay system are reviewed and summarized in this paper. Included are data concerning the geography, hydrology, chemistry, geology, and biology of the Apalachicola drainage system with particular emphasis on the estuary and associated waters.

The Apalachicola Bay system is part of a major drainage area that includes four rivers and their associated wetlands in Georgia, Alabama, and Florida. The Bay is a shallow coastal lagoon fringed by barrier islands and dominated by wind effects and tidal currents. River bottomlands that include the channels, sloughs, swamps and backwaters, and periodically flooded lowlands are important components of the system. Principal influences on the biological processes in the estuary are the physiography of the basin, river flow, nutrient input, and salinity distribution in space and time. Water quality is affected by periodic wind and tidal influences and freshwater inflows.

Compared to most of the estuaries in the United States, the Apalachicola Bay system is in a relatively natural state, although hardly pristine. However, economic development and population growth are beginning to put pressure upon the region, threatening it with destructive changes. The economic and ecological importance of the area as a producer of food and as shelter for diverse species is such that it has inspired a movement to protect its natural resources. Broadening the economic base of the region while maintaining its biological productivity will require the development of a comprehensive management plan based on the deepest possible understanding of the basis for that productivity, supported by ongoing study, close monitoring, and continued cooperation from local interests.

Research efforts to acquire the necessary understanding are not yet complete, but have nonetheless given rise to one of the most extensive computerized data bases so far assembled on an estuarine system. Powerful programs for working with these data have also been developed; because of the extreme complexity of their interplay, computer analysis has been and will continue to be a primary tool in understanding how physical and biological processes work in the estuary.

Based upon the data obtained thus far, some efforts have been initiated to preserve and protect important freshwater and estuarine wetlands. Included in these efforts are the following:

- State and federal land-purchase programs
- Integration of local (county) land-use regulations into a comprehensive plan for new and existing development
- Creation of the Apalachicola River and Bay National Estuarine Sanctuary, the largest such sanctuary in the country.

The effort to manage the Apalachicola Bay system is an ambitious one; only time will tell whether it will be successful in its effort to protect important wildlife values as the region undergoes economic development.

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CONVERSION TABLE

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
kilometers (km)	0.6214	miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

Multiply	By	To Obtain
inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
acres	0.4047	hectares
square miles (mi^2)	2.590	square kilometers
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees	0.5556(°F - 32)	Celsius degrees

ACKNOWLEDGMENTS

The research on which this paper is based began as a modest monitoring project in Apalachicola Bay in March 1972. Since that time, more than 1000 people--scientists, research aides, graduate and undergraduate students, and professional staff people--have participated in a series of projects carried out within a broad spectrum of disciplines. The research effort has included chemistry, hydrological engineering, physical oceanography, biology, geology, geography, fisheries, computer programming, statistics, resource planning and management, and economics. Many of the data have been retained and organized into a series of computer files, which I am currently holding at the Florida State University Computer Center. A complete list of this information is given in the appendices to this paper.

Although funding for this program has come from various sources, the major contributions have been made by the Florida Sea Grant College (National Oceanic and Atmospheric Administration) and the Franklin County Board of Commissioners. Supplementary funds have been provided by private industry and state and federal agencies. The list includes local developers, forestry interests, the Florida Department of Environmental Regulation, the Florida Department of Community Affairs, the Coastal Plains Regional Commission, the U.S. Environmental Protection Agency, the National Science Foundation, the Florida Department of Natural Resources, the Northwest Florida Water Management District, the U.S. Geological Survey, the Florida Game and Fresh Water Fish Commission, the U.S. Fish and Wildlife Service, and the Man in the Biosphere Program of the U.S. Department of State. Special credit should be given to the Department of Biological Science (Florida State University) for its long-running support of the research. It is somehow consistent that the main impetus for the research effort has come from local concerns (the fishermen of Franklin County, Florida) and a federal agency (the Florida Sea Grant College, NOAA) that has always sought to apply basic scientific knowledge to practical problems. The people of Franklin County, depending on the sea for their livelihood, recognized early that, as land development accelerates in Florida, a forward-looking management program will be necessary to protect the resource that has been at the center of their way of life for generations. The combination of basic and applied science, local, state, and federal involvement, and a multidisciplinary, long-term research program has led to a series of resource management/planning actions that are unprecedented in the nation.

CHAPTER 1
INTRODUCTION (HISTORICAL PERSPECTIVE AND OVERVIEW)

1.1. GEOGRAPHIC SETTING AND CLASSIFICATION

The Apalachicola estuary (Figures 1-3) is part of a tri-river system that includes the Apalachicola River in Florida and the Chattahoochee and Flint Rivers in Georgia and Alabama. The Chattahoochee River originates at the base of the Appalachian Mountains in the Piedmont upland, and traverses three geologic provinces: the Piedmont, the Appalachian, and the Coastal Plain. The Flint River begins in the lower Piedmont Plateau just north of the fall line and flows through the Coastal Plain.

The Apalachicola-Chattahoochee-Flint (ACF) drainage basin includes an estimated 48,484 km^2 (19,200 mi^2) in western Georgia, southeastern Alabama, and northern Florida (Figure 1). The Chattahoochee River drains approximately 21,840 km^2 (8,650 mi^2) and the Flint River drains an estimated 21,444 km^2 (8,494 mi^2). The Jim Woodruff dam, which forms Lake Seminole at the confluence of the Flint and Chattahoochee rivers, constitutes the headwaters of the Apalachicola River. The Apalachicola River is approximately 171 km (108 mi) long, with a fairly uniform slope of 0.15 m/km (0.5 ft/mi); it falls approximately 12 m in its course from Lake Seminole to the Gulf of Mexico. The Apalachicola River drains an area of about 2,600 km^2 (1,030 mi^2). The Chipola River, which joins the Apalachicola River near its southern terminus (Figure 1), has a watershed equal to that of the Apalachicola. About 3% of the ACF basin is in the Blue Ridge mountains, 38% in the Piedmont Plateau, and 59% in the coastal plain below the fall line (Figure 2). The lower coastal plain is nearly flat, with extensive wetlands development.

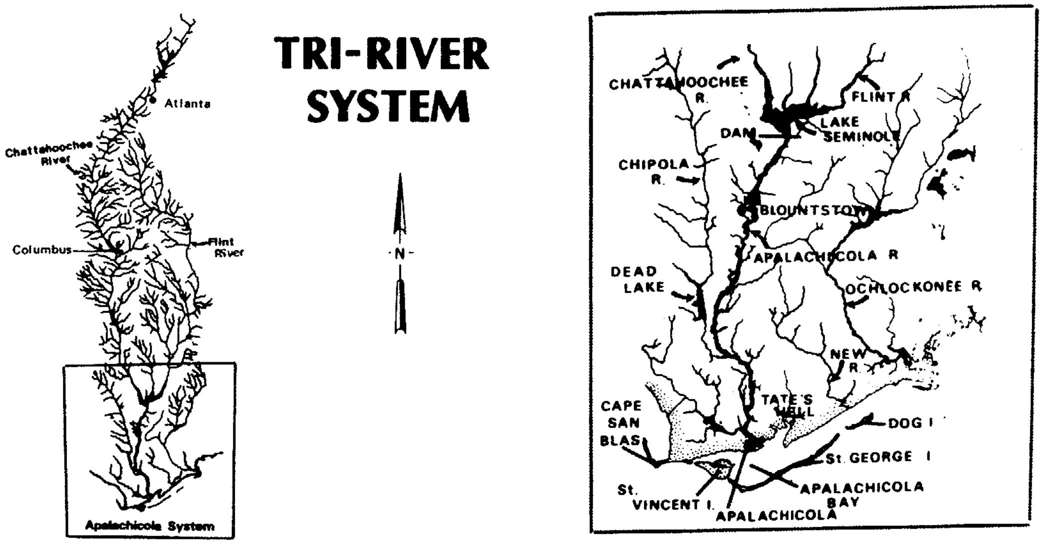


Figure 1. The tri-river (Apalachicola, Chattahoochee, Flint) drainage area showing the distribution of the important habitats and the position of key cities and municipalities within the Apalachicola-Chipola drainage system.

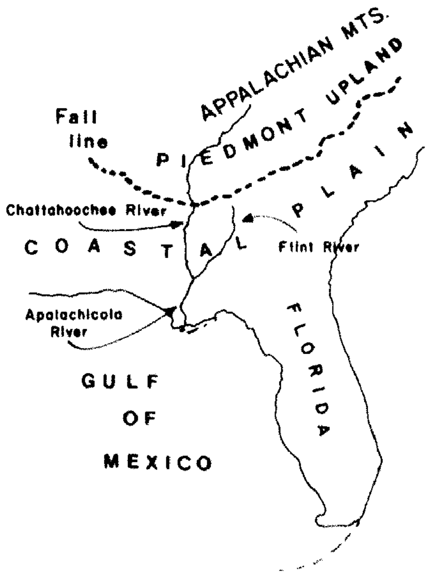


Figure 2. Location of the tri-river drainage system in the southeastern United States showing the relative positions of upland features and the Apalachicola estuary.

A detailed review of the dimensions of the Apalachicola Bay system (29°35'N to 29°55'N; 84°20'W to 85°20'W) (Figure 3) is given by Livingston (1980a). This system is composed of six major subdivisions:

East Bay	3,981 ha (9,837 acres)
Apalachicola Bay	20,959 ha (51,792 acres)
St. Vincent Sound	5,540 ha (13,689 acres)
West St. George Sound (to Dog Island)	14,747 ha (36,440 acres)
East St. George Sound	16,016 ha (39,576 acres)
Alligator Harbor	1,637 ha (4,045 acres)

The entire area totals 62,879 ha (155,374 acres). A natural shoal forms a submerged boundary between Apalachicola Bay and St. George Sound. The bay is bounded on its extreme southern end by three barrier islands: St. Vincent, St. George, and Dog Island. There are four natural openings to the gulf: Indian Pass, West Pass, East Pass, and a pass between Dog Island and Alligator Harbor. A man-made opening (Sike's Cut) was established in the western portion of St. George Island. The 3.6-m- (12-ft-) deep Intracoastal Waterway extends northwestward from St. George Sound through Apalachicola Bay, up the Apalachicola River to Lake Wimico and then along an artificial channel to St. Andrews Bay to the west.

The Apalachicola estuary is a lagoon and barrier island complex. It has been classified as a shallow coastal plain estuary oriented in an east-west direction (Dawson 1955). Because of the placement of the barrier island complex, it could be called a coastal lagoon. The average depth is between 2 and 3 m at mean low tide (Gorsline 1963).

In terms of Pritchard's (1967) estuarine classification scheme, the Apalachicola Bay system is a width-dominated estuary controlled by lunar tides and wind currents. As such, it is a type D estuary (Conner et al. 1981) in that it is dominated by physical forces (i.e., tidal currents, wind) as a function of its shallow depths. As a result, the bay system is relatively well mixed, although various portions of the estuary are periodically (seasonally) stratified (Livingston 1984a).

1.2. DRIVING FORCES AND HUMAN INFLUENCE

The principal driving forces that determine the habitat structure and biological processes of the estuary are river flow, physiography of the basin, seasonal changes of nutrients, and salinity as modified by wind, tidal influences, and freshwater inflows. Tidal influence extends approximately 40 km (25 miles) up the river. As a biological entity (Odum et al. 1974), the estuary (which includes East Bay, Apalachicola Bay, St. Vincent Sound, and western portions of St. George Sound), is characterized by upland marshes that grade into soft-sediment areas, vegetated shallow bottoms, and oyster reefs. The oligohaline East Bay merges with mesohaline and polyhaline portions of Apalachicola Bay, St. Vincent Sound, and St. George Sound.

The Apalachicola River, the largest in Florida in terms of flow, is the principal source of fresh water to the estuary. The average flow rate is about

665 m^3 sec^{-1} (23,500 ft^3 sec^{-1}) measured at Blountstown, Florida. Maximum and minimum discharges over the past 15 years are 4,600 m^3 sec^{-1} (162,500 cfs) and 178 m^3 sec^{-1} (6,280 cfs), respectively. The river and, secondarily, local rainfall determine the distribution of salinity in the estuary. The placement of the barrier islands also has a major influence on the salinity regime of the estuary (Livingston 1979, 1984a). The islands limit the outflow of the low-salinity water to the outer Gulf of Mexico.

The Apalachicola basin occupies the last sparsely inhabited and undeveloped drainage system and coastal region in Florida (Livingston 1983a, b, c). Franklin County, with a population of only 8,403 in 1979, encompasses the lower river and bay system. Forested uplands, wetlands, and aquatic habitats comprise most of the land area in Franklin County. The local economy is based largely on the sport and commercial fisheries of the Apalachicola River and Bay system. According to recent estimates (Florida Department of Administration 1977), commercial fishing, recreation, forestry and timber processing, agriculture, and light manufacturing characterize the regional economy of the entire Apalachicola basin. The human population of the six counties along the river has grown slowly since 1960, increasing only 7% (from 101,782 to 109,254) from 1969 to 1974. State government is a major employer in the region, while industrial or commercial land use is confined to only 0.2% of the basin area.

The Apalachicola drainage system is one of the least polluted in the country (Livingston 1974a, b, 1977a-d, 1978, 1979, 1980a-c; Livingston and Thompson 1975; Livingston and Duncan 1979; Livingston et al. 1974, 1976a, b, 1977, 1978). Some problems, however, have emerged in recent years (Livingston 1983d).

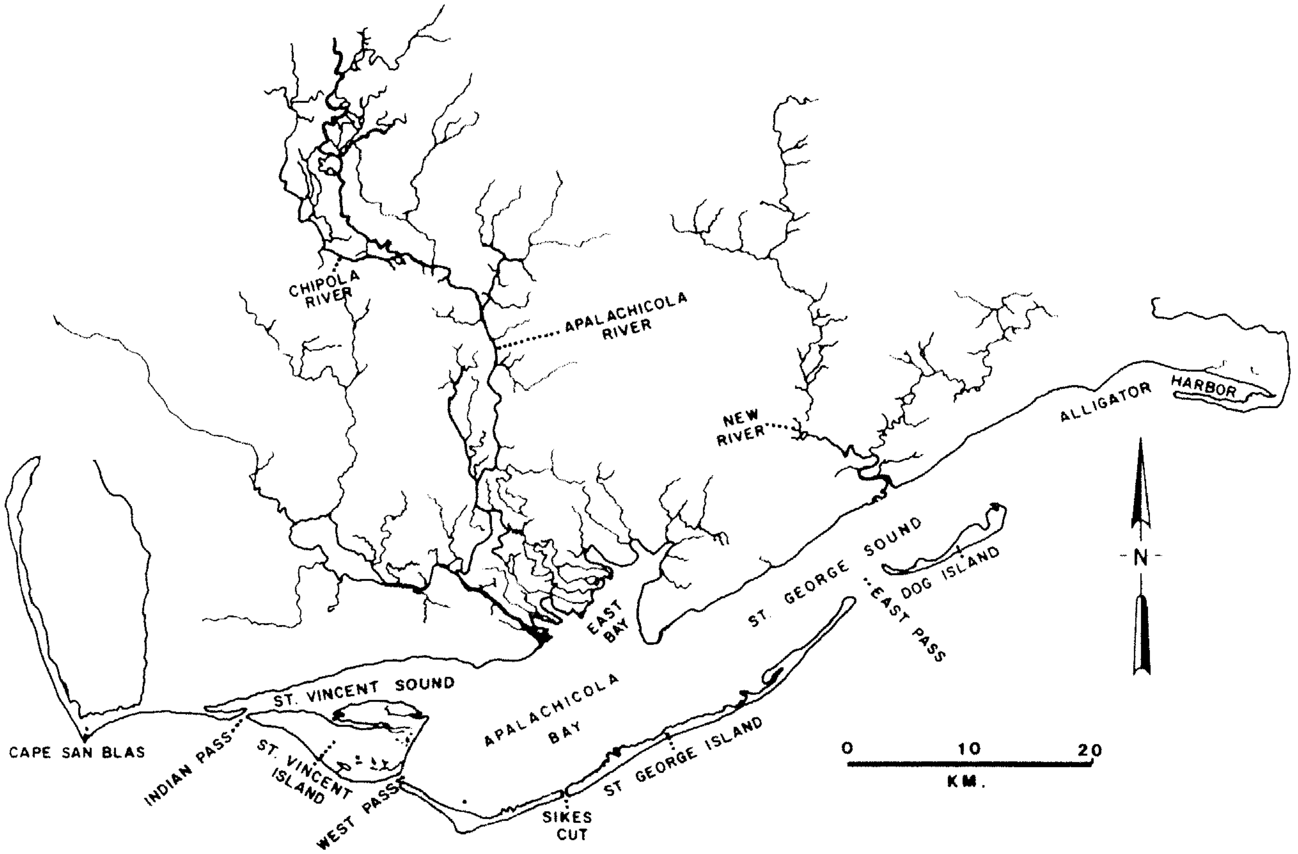


Figure 3. Detailed features of the Apalachicola Bay system including the major contributing drainages, the barrier island complex, and the major passes in the bay complex.

1. A 13,352-ha (33,000-acre) cattle ranch was established in the Apalachicola River floodplain about 9-10 km (6 mi) above the bay. Much of the area was cleared, ditched, and drained, while waste water was pumped over the dikes into the river system. The potential impact of this operation is under study and review, although farming has continued, and water quality has deteriorated in some of the upland creeks.

2. Portions of the drainage system have historically been subjected to forestry operations, which include ditching, draining, clearcutting, and reforestation. These activities have been associated with local changes in water quality and short-term adverse effects on aquatic biological associations (Livingston 1978). A long-term multidisciplinary study has just been completed by the Florida Sea Grant College (Livingston 1983c) along with proposed management practices which are designed to mitigate adverse impacts.

3. Recent population increases along the north Florida coast have stressed regional coastal counties in terms of municipal development, sewage disposal, and storm water runoff (Livingston 1983d). The recognition of such potential impact has led to the development of relatively advanced local land use plans such as that adopted by Franklin County in 1981 (Livingston 1980a, b, 1983c). Implementation of the comprehensive plan has not been carried out, however. During 1984, sewage spills closed down the Apalachicola oyster industry for prolonged periods. Meanwhile, proposals to bring high-density construction projects to coastal areas of Franklin County have proliferated.

4. A continuing problem in the region involves proposals to either channelize or dam the Apalachicola River to make a corridor for barge traffic and industrial development. These developments would serve as a north-south link between upriver ports on the Chattahoochee and Flint Rivers in Alabama and Georgia and the Gulf of Mexico. Authorization for a maintained channel (30.5 m or 100 ft wide, 2.7 m or 8.8 ft deep) by the U.S. Army Corps of Engineers (USACE) was part of the amended Rivers and Harbor Act of 1946. A system of 13 dams is already in place on the Chattahoochee River and three dams are currently in use on the Flint River (Figure 4). Associated with these activities are a series of barge terminal facilities and offloading systems. Rock outcrops in the Apalachicola River have been removed as part of ongoing, extensive dredging and channelization of the river. Superimposed over these activities is the increasing municipal water use in areas such as Atlanta, Georgia, where sustained population growth could reduce water flow in the tri-river system in the near future.

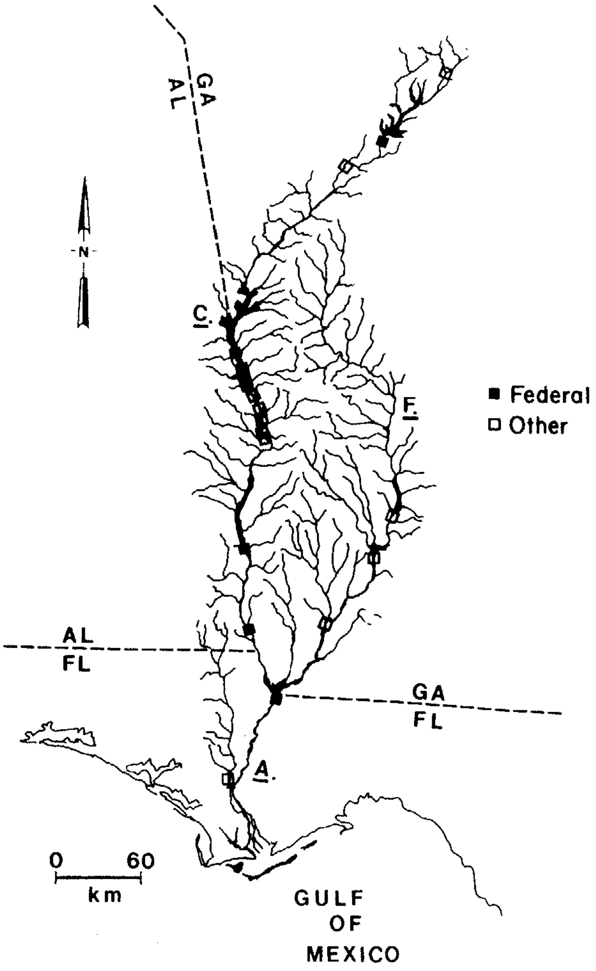


Figure 4. Distribution of impoundments along the tri-river system (after information provided by the U.S. Army Corps of Engineers).

5. Past studies on pesticide distribution in the estuary (Livingston and Thompson 1975; Livingston et al. 1978) have indicated relatively low levels of organochlorine contamination in the Apalachicola Bay system by the mid 1970's. Winger et al. (1984) found that biota from the Apalachicola River had moderately high levels of total DDT, total PCB's, and toxaphene in 1978. Animals from the upper river had higher organic residues than those taken in the lower river. Such levels exceeded recommended permissible levels for the protection of aquatic life. A recent review of the heavy-metal distribution (Livingston 1983d; Livingston et al. 1982) indicates local increases of metals in the sediments and biota of Lake Seminole, parts of the Chipola drainage, and areas in the bay system that receive municipal runoff. These increases are due to local point sources such as battery recycling operations (upper Chipola), industrial sources in Georgia, marinas, and municipal outfalls. Winger et al. (1984) found metal residues in riverine organisms generally below 1 μg g^{-1}. A recent analysis of data on long-term monitoring of the metal concentrations in oysters (Crassostrea virginica) in the estuary (Florida Department of Natural Resources, personal communication) indicates no undue increases of such metals in shellfish over the past decade.

6. Dredging and spoil placement take place in the Apalachicola River and Bay system (Livingston 1984a). These operations are being reviewed by the Florida Department of Environmental Regulation (S. Leitman et al. 1982). The immediate impact of long-term dredge and spoil activities on the estuary is given by Livingston (1984a).

In summary, the Apalachicola drainage basin is currently lightly populated with an economic system dominated by renewable natural resources. However, over the next few decades, the essentially rural economy will probably give way to more energy-dependent industrial and urban development, which might lead to increased stress on the natural system due to growing population pressure, residential development, agricultural activities, toxic waste disposal, erosion and sedimentation, and alteration of the physical structure of the drainage basin.

CHAPTER 2
ENVIRONMENTAL SETTING

2.1. ORIGIN AND EVOLUTION OF THE ESTUARY

2.1.1. Geological Time Frame

The physiographic structures of most estuaries are ephemeral in terms of geological time. Climatological forces are continuously at work shaping and reshaping the basin features. Characteristics of the Apalachicola estuary are dependent on the interaction of an upland drainage system with offshore marine conditions. The estuary is, in effect, an extension of the upland river or drainage area, and its origin and evolution are inextricably linked to the dynamic geological history of the land/sea interaction.

The Apalachicola River is the only drainage area in Florida that has its origin in the Piedmont, which, as will be explained later, is of biological importance to the region. The geological history of this area is well known in general terms. By the Cretaceous period (about 135 million years ago), most of the tri-river valley was submerged under ancient seas (Tanner 1962). The origin of the Apalachicola River or its antecedents occurred some time in the Miocene epoch about 25 million years ago (W. F. Tanner, Florida State University, pers. comm.). There has been a gradual decline in sea level through Cenozoic time (70 million years ago to present); sea level has dropped an estimated 70-100 m from the middle of the Miocene (Tanner 1968). Olsen (1968) gives evidence that the upper Apalachicola River basin (the area around Blountstown, Florida; Figure 1) was a deltaic or coastal environment during the Miocene. By the Pleistocene epoch (1 million years ago), there was evidence of an arcuate chain of barrier islands approximately 22.5 km (14 mi) northeast of Apalachicola, Florida. These islands were located in what is now the Tate's Hell Swamp (Figure 1). The general dimensions of the Apalachicola valley as we see them today were established in the Pleistocene.

The major drainages of the Florida panhandle (which includes the Apalachicola drainage system) are alluvial in that they carry sediment loads that eventually end up in the coastal estuaries (Figures 1, 5). The geological structure of the Apalachicola River estuary is of Recent and Pleistocene origin. Marine sediments comprise a major physical feature of the region. The Apalachicola estuary is bounded by well-developed beach-ridge

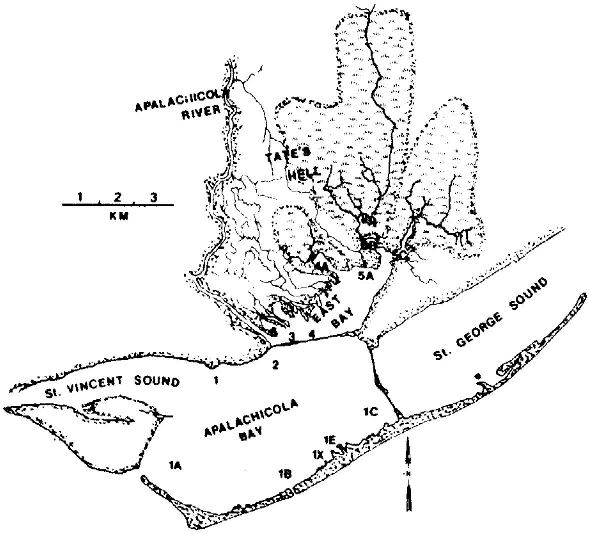


Figure 5. The Apalachicola estuary with details of upland drainage areas and the placement of permanent sampling sites for the long-term field studies of the Florida State University research team (after Livingston et al. 1974).

plains of late Holocene origin (Fernald 1981). The linear, gently curving beach ridges of the area attest to the changes in orientation of the estuary through geological time in response to wide fluctuations of sea level. The Apalachicola estuary is part of a broad, sandy shore plain, which is constantly being changed by a combination of climatological elements such as wind, rainfall and sea level alterations. The present structure of the bay is around 10,000 years old (Tanner 1983). Sea level reached its modern position about 5000 years ago when the construction of the present barrier island chain was underway. Except for the southward migration of the delta front, the general outline of the bay system was established at this time (Tanner 1983).

2.1.2. Geomorphology and Regional Geology

a. Upland areas. The major formations in the upper Chattahoochee River system are underlain by igneous rocks and crystalline schists. The area is characterized by Tertiary limestone outcroppings, which add to the habitat diversity of the region (Figure 6). The lower division of Piedmont upland, defined as the Opelika Plateau, is underlain by Archean (i.e., Precambrian) rocks. Tributaries of the Chattahoochee River have subsequently eroded these formations with some valleys cut approximately 62 m (200 ft) below the general surface. The rocks of the Appalachian province pass under the Coastal Plain formations. Along the border between the Appalachian province and the Coastal Plain, Appalachian rocks are overlain by Cretaceous formations. These rocks are more deeply buried by Tertiary and Quaternary sediments further north. The Coastal Plain is covered with a thick layer of clastic (erosion produced) sediments as well as limestone (nonclastic) sediments, some of which may be crystalline.

Adams et al. (1926) have presented a detailed account of the Paleozoic, Mesozoic, and Cenozoic formations in Alabama, which is generally applicable to the Apalachicola valley. The Cenozoic formations are confined to the Coastal Plain and represent deposits at the bottom of an ancient sea, which consist of sand, clay, mud, or calcareous ooze. Fossil marine mollusks and echinoderms are interspersed with remnants of fossil plants from flood plains, marshes, and swamps. Pleistocene marine sands and clays overlie older formations along the coast, and estuarine and fluvial deposits extend up the main river valley. Swamps immediately upland of the Apalachicola estuary are underlain by quartz sand (Brenneman and Tanner 1958).

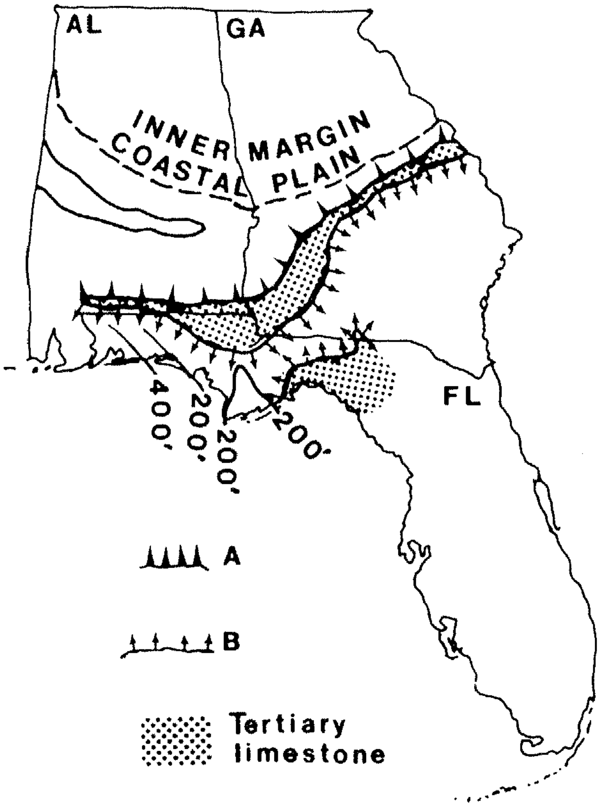


Figure 6. Geological features of the Apalachicola drainage system showing (A) a line north and west of which there are thin patches of Tertiary limestone near the land surface and (B) a line beyond which the limestone thickens and is more deeply buried. The top of the Tertiary limestone is shown in feet below sea level, while Tertiary limestone that occurs in or near the land surface is also outlined (modified from Means 1977).

The coastal geomorphology of the Apalachicola region is extremely complex; major features are developed from wind and current modified beach ridges (Clewell 1977). These formations are complicated by considerable Pleistocene sea-level fluctuations. The northern gulf coastal lowlands are dominated by Pliocene epoch marine sands. The flood plain of Holocene (recent) sediment reaches depths approximating 24.3 m (80 ft) near the river mouth and 13.7 m (45 ft) near Blountstown, Florida (Figure 1). These sediments lie directly on Miocene strata because much of the Pliocene and Pleistocene sediments were eroded during periods when sea level was lower and river flow was greater. The sea level approximately 20,000 years ago was over 125 m (410 ft) lower than that found today, and the coastline was considerably seaward of its current position.

The Florida panhandle is an uneven platform of carbonate bedrock (limestone with dolomite) overlain by one or more layers of less consolidated clastics (Figure 6, Puri and Vernon 1964; Clewell 1978). Superficial strata are of Eocene, Oligocene or early Miocene origin. Considerable solution activity has led to the formation of sinks, caves and other karst features (Means 1977). The clastics consist of Fuller's earth (primarily the clays montmorillinite and attapulgite), phosphatic matrix, sand, silt, clay, shell marl, gravel, rock fragments, and fossil remains. The clastics with shell marl are sediments of ancient shallow seas and estuaries. Various clastic strata were deposited during the early Miocene, while others were fluvial and aeolian deposits or sediments in lake bottoms. These clastics form terraces sloping toward the Gulf. Such terraces are altered by erosion and dissection by streams and rivers. In spite of various post-Pleistocene sea-level fluctuations, elevations in this area have changed less than 10 m as a result of erosion, deposition, and sedimentation. Dunes, spits, bars, and beach ridges became stranded inland as the sea receded.

b. Soils and sediments. The Apalachicola River floodplain lies wholly within the Florida Coastal Plain and is in contact with Tampa Limestone (early Miocene). The river just below the Jim Woodruff Dam flows through the Citronelle formation (Pliocene) that borders the western edge of the Pleistocene bed from 16 to 20 km below the dam to Blountstown. The eastern portion of the river is influenced by the Hawthorn formation (Fuller's earth and phosphatic limestone) and Duplin marl (sandy marine and clayey, micaceous shell marl). The clays in particular and fine sands cause considerable turbidity. The river bed is composed primarily of remnants of Pleistocene deposits (sand to coarse gravel) that are covered by fine clay sediments. The lower river valley is composed largely of Plio-Pleistocene marine sands, which lie over the Aucilla Karst Plain, the Jackson Bluff formation, and the lower part of the Citronelle formation.

Upland soil composition reflects the geological history of the Apalachicola valley. Soils in the titi swamps and savannahs of the Apalachicola National Forest are strongly acidic and low in extractable cations (Mooney and Patrick 1915; Coultas 1976, 1977, 1980). Total phosphorus is low in all soils of the basin. Cypress and gum swamps are also highly acidic and low in extractable bases, while more alluvial soils are less acidic. Estuarine marsh soils are relatively high in organic matter, especially at the river mouth. These soils are derived largely from the erosion of the northern Piedmont-Appalachian soils, which have been deposited on the sea floor and, at times, have been uplifted above sea level. Floodplain soils are composed of a broad range of textures and colors. They are predominantly clay with some silty clay and minor clay loams (Leitman, 1978). Point bars in the river bed are composed largely of fine and very fine sands.

Soils in wetlands directly associated with the Apalachicola River have been analyzed. Swamp soils are wet, moderately acidic, high in clay content, and low in salinity (Coultas in press). The principal clay-sized minerals include kaolinite, vermiculite, quartz, and mica. These areas are poorly drained and contain considerable amounts of clay and organic matter. The soils are formed from recent accumulations of sediments deposited in stream channels and estuarine meanders. The pH values range from 4.9 to 6.6.

Studies of the marshes above East Bay (Coultas 1980; Coultas and Gross 1975) indicate that the deltaic soils are slightly acidic and become alkaline with depth. The dense mats of roots and rhizomes from the predominant sawgrass (*Cladium jamaicense*) and needlerush (*Juncus roemerianus*) along the eastern portions of the estuary tend to hold the soils in place. The soils are composed of thin organic deposits mixed with clay and overlie loamy sands of fine-textured materials. Considerable amounts of silt occur in some soils, and most have poor load-bearing capacity because of the high organic content and high field moisture levels. Vegetation differences are attributed to soil salt content. Sawgrass is dominant in areas most affected by river flow (i.e., with low salinity), and needlerush is predominant in tidal areas (i.e., those with higher salinity) (Coultas 1980).

Sediments in the estuary are characterized by mixtures of sand, silt, and shell components (Livingston 1978). Present sediments are accumulating over tertiary limestones and marls that outcrop in the scoured central channels of West Pass and Indian Pass. St. Vincent Sound and northern portions of Apalachicola Bay are silty areas that grade into sand/silt and shell gravel toward St. George Island. The thickness of these sediments (10-20 m) (Gorsline 1963) may be the result of erosion of older deltaic deposits during periods of higher sea level. East Bay is composed of silty sand and sandy shell. Areas near the river mouth have varying quantities of woody debris and leaf matter, especially during winter and spring months of heavy river flooding (Livingston et al. 1976a). The floor of the bay is thus formed largely of quartz sand with a thin (but varying) cover of silt, clay, and debris depending on the proximity to land runoff.

The estuarine sediments originated in the southern Appalachians and have undergone a complex history of deposition and reworking in the coastal plain deposits, coastal marshes, beaches, and dunes. Fine sediments flow out of the bay into the Gulf of Mexico while sand is moved by tidal currents within the bay and at the mouths of the western inlets. The cusp of the Apalachicola Bay coastline has been built by river sediments deposited during Tertiary and Pleistocene times with modification by waves and long-shore drift. Puri and Vernon (1964) and Clewell (1978) have made a detailed review of the geological formations and soil distribution in the region.

2.1.3. Watershed Characterization

Numerous physiographic, geological, and biogeographic features contribute to the biotic richness of the Apalachicola drainage system (Clewell 1977; Means 1977). While the Apalachicola basin (Figure 7) lies entirely within the Coastal Plain, it is subdivided into upper and lower regions; the Marianna lowlands, New Hope Ridge, Tallahassee Hills and

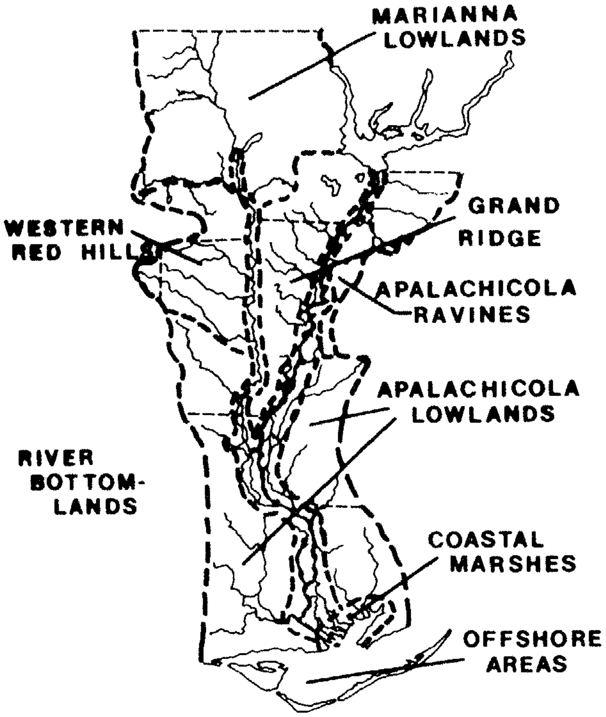


Figure 7. Natural areas of the Apalachicola basin based on the physiography, vegetation types, regional geography, and distribution of organisms (after Means 1977).

Beacon Slope are part of the Gulf-Atlantic rolling plain, while the lower coastal lowlands are part of the Gulf-Atlantic Coastal Flats (H. M. Leitman et al. 1982). The drainage system contains streams of various types, which range from first-order ravine streams (Means 1977) to the higher order low-gradient, meandering types. The latter contain high organic acid levels in the flatwoods or are calcareous and clear in the Marianna Lowlands karst plain. Extensive lake systems are lacking in the valley; Ocheesee Pond is located in an abandoned bed of the Apalachicola River, and two other natural lakes (Lake Wimico, Dean Lake) occur in the basin. The upper river region, cutting through Miocene sediments, has a flood plain 1.5-3 km (0.9-1.9 mi) wide. This floodplain widens to 3-5 km (1.9-3.1 mi) along middle portions of the river, with the lower river having the widest floodplain (7 km; 4.4 mi). The upstream tidal influence in the floodplain does not extend above km 40 (mi 25). The Chipola River joins the Apalachicola at km 45 (river mi 28). The delta is about 16 km (10 mi) wide and is surrounded by a broad marsh.

The previously described geological processes have led to high physical diversity of the land forms in the Apalachicola basin. "Steepheads" or amphitheatre-shaped valley heads with very steep walls (Means 1977) occur in small drainages that dissect the eastern escarpment between Bristol and Torreya State Park within a narrow east-to-west alignment through the Florida panhandle. These constant environments are important habitats for various species. The Apalachicola Ravines (Figure 7) (Hubbell et al. 1956) are drainages that form another unique habitat associated with the river basin. These ravines include small-order stream bottoms and steep valley slopes; the vegetation grades upward from hydric plant communities near the bottom to xeric vegetation at the top of small divides between ravines. The Marianna lowlands form a karst plain containing more vadose (i.e., above water table) cave ecosystems than any other part of the coastal plain (Means 1977). The Apalachicola lowlands, a flatwoods region with little relief, is a low, slightly inclined plain with extensive swamplands. The eastern portion of the Apalachicola lowlands contains parts of the Tate's Hell Swamp, which is undergoing extensive changes due to forestry operations. The western lowlands are part of a cattle ranch and farming operation. The Western Red Hills are separated from the other natural areas by the Chipola River valley. This area is high in elevation but not as deeply dissected as the Apalachicola Ravines. Grand Ridge (Figure 7) is a wedge-shaped area bounded by the Chipola and Apalachicola Rivers. While originally part of the same upland mass that extended from the Apalachicola Ravines westward, Grand Ridge has been eroded. This area is associated with springs, caves, and troglodyte (i.e., subterranean) fauna. The river bottomlands represent a floodplain habitat characterized by the river channel, sloughs, swamps and backwaters, and the periodically flooded lowlands. Many springs and aquatic cave systems empty directly into the river bottomlands.

2.1.4. Barrier Islands

At the mouth of the Apalachicola River is a well developed barrier-island system composed of three islands (St. Vincent, St. George, Dog) (Figure 3). These islands roughly parallel the coastline and are characterized by sets of sand dunes of differing geological ages. While the shore system is based on dunes that date back some 3000 to 6000 years, the barrier islands are no older than 3000 years. They consist of quartz sand that has been transported from the southern Appalachian Piedmont by the river system and that currently rests on an eroded Pleistocene surface (Zeh 1980). On St. Vincent Island, for example, gently curving lines of beach ridges (Figure 8) up to 1 m (3 ft) high serve as the base for small dunes; such ridges represent the geological history of sand deposition in the region, with the oldest (northernmost) ridges indicating where sea level achieved its earliest position.

St. George Island is about 48 km (30 mi) long and averages less than 0.5 km (1/3 mi) in width. It consists of 2,973 ha (7,340 acres) of land and 486 ha (1,200 acres) of marshes. The medium to fine grain sands provide for relatively poor

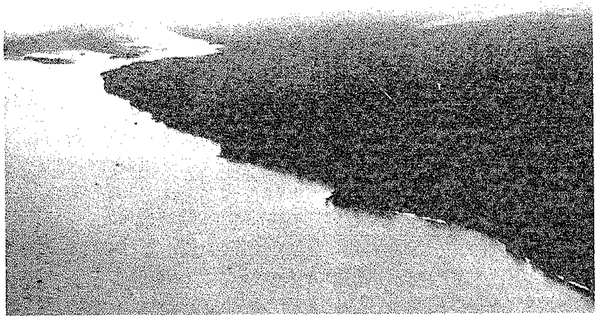


Figure 8. Aerial view of St. Vincent Island.

aquifer conditions; all fresh water is derived from rainfall. Silty clay sediments at depths between 7.6 and 9.2 m (25-30 ft) below the sandy surface create an impermeable barrier to separate rain-derived fresh water from the surrounding salt water. There is a shallow lens of fresh water beneath the island. Some of this fresh water, modified by transpiration and evaporation, is eventually discharged into the Gulf and lagoonal marine systems.

2.2. CLIMATE

2.2.1. Temperature

The climate in the Apalachicola basin is mild, with a mean annual temperature of 20° C (68° F). Temperature varies with elevation and proximity to the coast. The mean annual number of days with temperatures at or below freezing is 20 at Lake Seminole and 5 along the Gulf Coast (National Oceanic and Atmospheric Administration, unpublished data; Clewell 1977). Livingston (unpublished manuscript), working with long-term (40-year) climatological data, found that temperatures usually peak in August with lows from December to February, at which time monthly variance is maximal. While peak summer temperatures are similar from year to year, winter minima vary. A time-series (spectral) analysis indicates that there is a long-term period of recurring low winter temperatures of 118 months (9.8 yr). Periodic low winter monthly minima occurred in 1940, 1948, 1958, 1968, and 1977. Thus, in addition to a strong seasonal component, there may be a long-term periodicity to temperature fluctuations in the Apalachicola region.

2.2.2. Precipitation

Mean annual rainfall in the Apalachicola River basin is approximately 150 cm (59 inches). There are, however, considerable local differences in monthly precipitation totals. In the Apalachicola delta, areas west of the river receive almost one-third less rainfall than those east of the river (i.e., Tate's Hell Swamp). Rainfall in the Georgia portion of the watershed is 130 cm/yr (51 inches/yr).

The rainfall patterns of Florida and Georgia (Figure 9; Meeter et al. 1979) are basically similar except for the timing of rainfall peaks. Georgia rainfall has two

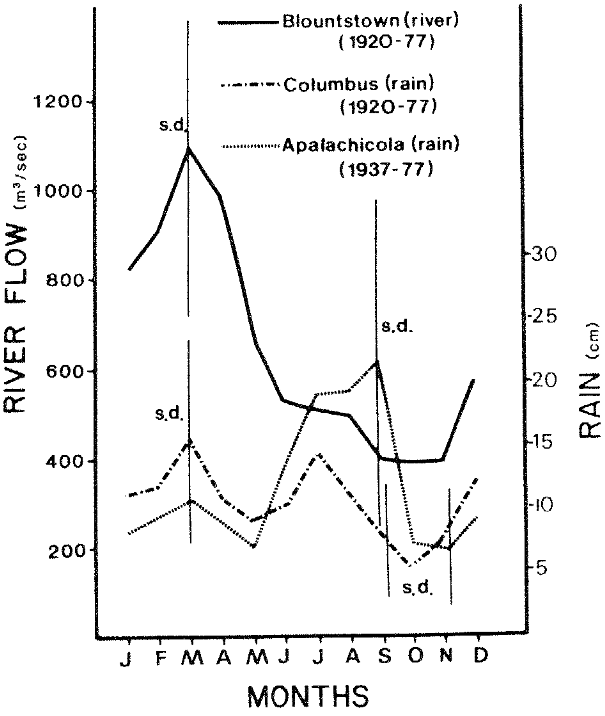


Figure 9. Seasonal averages of Apalachicola River flow (Blountstown, Fla.) and rainfall from Columbus, Georgia, and Apalachicola, Florida. Standard deviations (S.D.) are given for selected months (after Meeter et al. 1979).

peaks: one in March and another of equal magnitude in July. The Florida rainfall peak in March is not as great as that of Georgia, but the primary difference is the much larger, sustained rainfall peak in summer and early fall in Florida. In both areas, there are drought periods during mid to late fall. Spectral analysis of long-term trends (Figure 10) indicate that, while rainfall is highly variable, there are certain long-term trends. Florida (Apalachicola) rainfall has 80-month (6.7-yr) cycles in peak reoccurrence, while Georgia rainfall has a slightly different spectrum.

2.2.3. Wind

Wind direction is predominantly from the southeast during the spring (March-May) and southwest to west during the summer (June-August). Winds come from the north or northeast during the rest of the year. However, analysis of long-term wind data indicates that there is wide variability of wind velocity and direction over the Apalachicola watershed at any given time. In the shallow estuary, winds can cause rapid changes in the normal tidal current patterns. Southerly winds tend to augment astronomical tides and

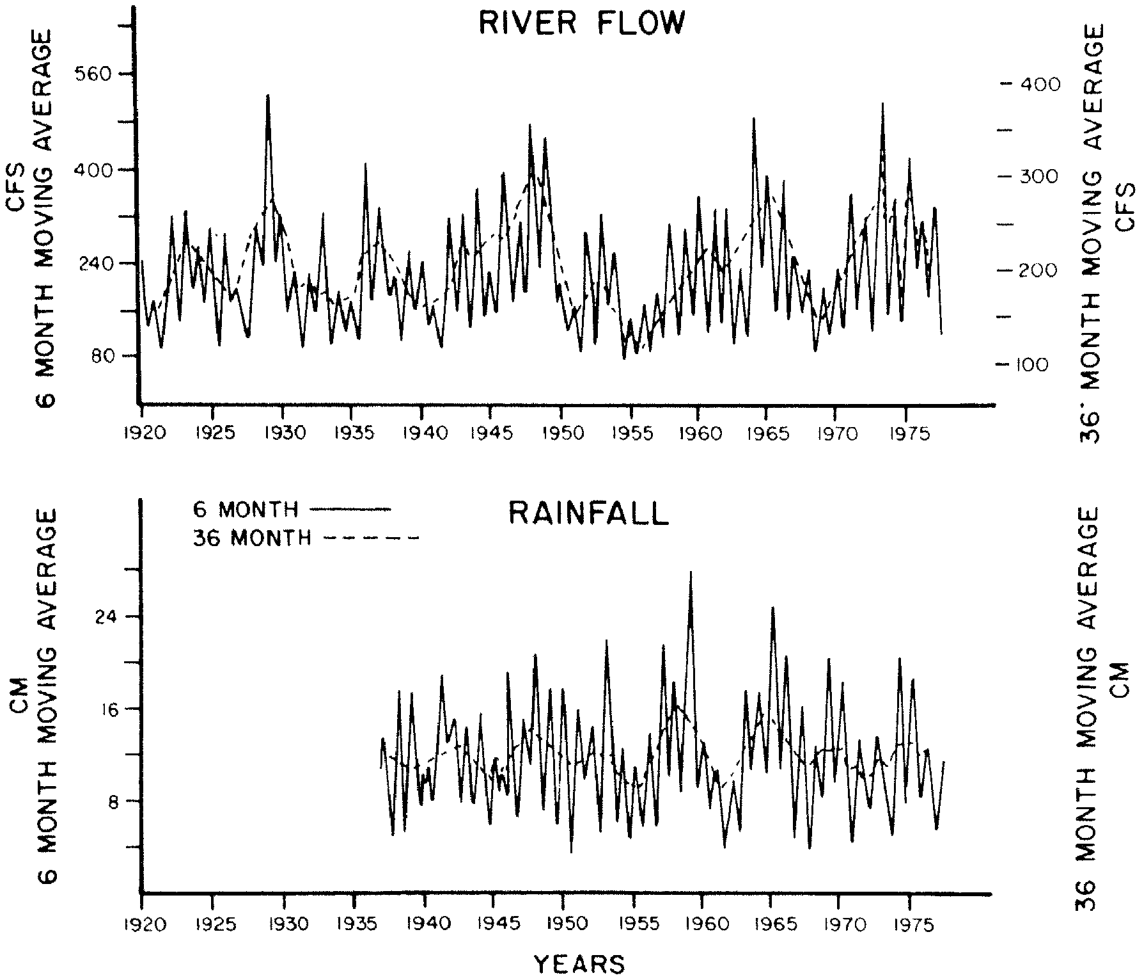


Figure 10. Six-month and 36-month moving averages of Apalachicola River flow (cfs; 1920-1977) and Apalachicola rainfall (1937-1977). Data are taken from Meeter et al. (1979).

cause abnormally high water without the usual ebb.

The air circulation over the Gulf of Mexico is primarily anticyclonic (clockwise around an atmospheric high-pressure region) during much of the year. However, strong air masses of continental origin often move through the northern Florida area, especially during the winter. From November to March, an average of 30 to 40 polar air masses penetrate the Gulf each year. Storms are usually formed along slow-moving cold fronts in winter. Tropical storms or hurricanes may occur in summer and early fall. Lesser storms often occur as extratropical cyclones, which tend to move across the Gulf from west to northeast during winter periods (Jordan 1973). Winter storms tend to be more pervasive in a geographic sense, while summer storms are often intensive, short-lived, localized events. The likelihood of the occurrence of a hurricane in the northeast Gulf is about once every 17 years with fringe effects about once every 5 years (Clewell 1978). The last hurricane to hit Apalachicola, Hurricane Agnes, occurred in June 1972. Overland (1975) showed that basin orientation (relative to wind direction, headlands, and marsh areas) can produce variations in surge heights, which are responsible for much damage. Livingston (unpublished data) found that Hurricane Agnes had no sustained effect on water quality or the biota of the Apalachicola estuary.

2.3. HYDROLOGY

2.3.1. Freshwater Input

The Apalachicola River has the highest flow rate (690 m^3 sec^{-1} at Chattahoochee, Florida; 1958-1980) and broadest flood plain (450 km^2 of bottomland hardwood and tupelo-cypress forests) of any river in Florida (H. M. Leitman et al. 1982). Apalachicola River discharge accounts for 35% of the total freshwater runoff on the west coast of Florida (McNulty et al. 1972). Seasonal variation (Figure 9) is high, with peak flows from January through April and low flows from September through November. The absence of a summer river-flow peak (despite rainfall peaks in the basin at this time) may be related to higher evapotranspiration rates in the vegetation of the watershed (Livingston and Loucks 1978). A spectral analysis using data from 1920 to 1977 (Figure 10) indicated river-flow cycles on the order of 6-7 years (Meeter et al. 1979). Indications of longer-term cycles were shown along with the abnormally low river flow during the mid-1950's.

In a cross-spectral analysis of Georgia rainfall with river flow, the two patterns were in phase (Meeter et al. 1979; Figure 9). The analysis indicated that the Apalachicola River flow patterns more closely resembled cycles of Georgia rainfall than they did those of Florida rainfall. This pattern should be expectd since only 11.6% of the drainage basin is in Florida, and the remainder is in Georgia. Stage fluctuations vary greatly from upper to lower river with the narrowest ranges (from peak to low) at downstream stations (H. M. Leitman et al. 1982). Such flooding patterns are essential to elements of the hydrology of the estuary.

Floodplain inundation varies with location on the river and reflects the influence of natural riverbank levees (H. M. Leitman et al. 1982). Natural levees within the flood plain are inundated only at high stages of river flow. The level of the water table also depends on river stage. Fluctuations are damped by water movement through floodplain soils. The levees of the upper river, where there is a greater range of water fluctuation, are higher than those in the lower river where the flood plain is quite flat. Flood depths tend to decrease from the upper to the lower river and rates of flow in the upper river floodplain are generally less than those along the middle and lower reaches of the river. The height of the natural levees and the size and distribution of breaks in the levees all control the hydrological conditions of the river flood plain. Such hydrological conditions, in turn, control the form and distribution of floodplain vegetation (H. M. Leitman et al. 1982).

2.3.2. Tides and Currents

Franklin County straddles a region of transition between the diurnal tides of west Florida and the semidiurnal tides on the Gulf peninsula. Tides at Apalachicola are diurnal to semidiurnal, with "uncertainties" concerning the selection of a "typical" tide pattern for each month (Conner et al. 1981). Tides in the Apalachicola estuary are influenced by the main entrances and smaller passes. Tidal ranges vary from 0.13 m (0.43 ft) at Dog Island near the eastern end of the estuary to 0.23 m (0.75 ft) at East Pass. Gorsline (1963) classified this estuary as "unsymmetrical and semidiurnal except during periods of strong wind effect." While currents in the Apalachicola estuary are tide-dominated, they are also dependent on local physiographic conditions and wind speed and direction (Livingston 1978). River discharge has little influence on the hydrodynamics of the partially stratified estuary (Conner et al. 1981). Shallow estuaries such as the Apalachicola are wind dominated in terms of flushing and current movement. The wind can be up to three times more important than the tidal input in the determination of current strength and direction (Conner et al. 1981).

Net flows tend to move to the west from St. George Sound; East Bay water merges with the westward flow (Figure 11). West Pass appears to be a major outlet for the discharge of estuarine water to the Gulf, especially when influenced by long-term or high velocity winds from the east. Water movement through Indian Pass also occurs in a net westward direction, although the Picoline Bar may retard passage (Dawson 1955). Estuarine currents may be affected by excessive land runoff or high velocity winds from the east or west. Strong north to northeast winds deflect water downwind and to the west.

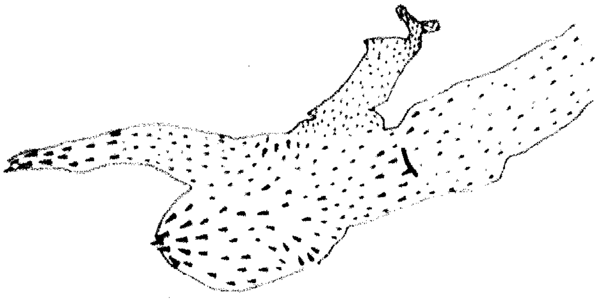


Figure 11. Net water current patterns in the Apalachicola estuary as indicated by flow models developed by B. A. Christensen and colleagues. (A detailed analysis of such currents can be found in Conner et al. (1981).)

Gorsline (1963) estimated a tidal prism equal to about 20% of the bay water volume, and he suggested that the residence time of river water in the estuary ranges from a few days to a month. The two western passes account for over 66% of the total bay discharge, even though they account for only 10% of the inlet area (Gorsline 1963). The bulk of river flow exits through these passes, and the effects of river flow on salinity can be felt 265 km (165 miles) offshore in the gulf. Tidal deltas extend seaward from Indian Pass, West Pass, and East Pass, indicating appreciable sediment transport through these areas. Current velocities in the bay rarely exceed $0.5\ m\ sec^{-1}$, while velocities in the passes may reach $2\text{-}3\ m\ sec^{-1}$.

2.4. PHYSICAL/CHEMICAL HABITAT

Important habitat features of the Apalachicola Bay system include physiographic, climatic, and river-flow conditions. While marshes (emergent vegetation), oyster beds, and grassbeds (submergent vegetation) represent important biological habitats of the estuary. the primary physical habitat in terms of areal extent is the shallow, unvegetated soft sediment bottom (Table 1). Within the myriad of rapidly changing gradients of physical and chemical features of the estuary, there are certain recurrent patterns and general trends that remain more or less constant in space and over time. Such water-quality features and nutrient distributions are important determinants of the habitat conditions in the Apalachicola Bay system.

2.4.1. Temperature and Salinity

Because of the shallowness of the bay system and wind-mixing of the water column, there is little thermal stratification in the estuary. Water temperature is highly correlated ($r = 0.90$, $p < 0.00001$) with air temperature (Livingston 1983c), which indicates rapid mixing. Summer temperature peaks are similar from year to year, with seasonal highs usually in August. Water

Table 1. Distribution and area of major bodies of water along the coast of Franklin County (north Florida) with areas of oysters, grassbeds, and contiguous marshes.

Water body	Area (ha)	Oysters (ha)	Grassbeds (ha)	Marshes (ha)
St. Vincent Sound	5,539.6	1,096.5	---	1,806.9
Bay	20,959.8	1,658.5	1,124.7	703.4
East Bay	3,980.6	66.6	1,433.5	4,606.1
St. George Sound (West)	14,746.8	1,488.8	624.3	751.9
St. George Sound (East)	16,015.5	2.6	2,767.3	810.8
Alligator Harbor	1,637.0	36.7	261.3	144.3
Total	62,879.3	4,349.7	6,211.1	8,850.4
Percent of total water area	100	7	10	14

temperature minima occur from December to February; monthly variance is highest during winter. Whereas peak summer temperatures are comparable from year to year, winter minima vary annually (Figure 12). During years of extreme cold, temperature ranged from 5° C to a maximum of 33° C over a 12-month period. In addition to strong seasonal components of changes in water temperature, periodic winter lows occurred at relatively regular (8-11 yr) intervals. In recent times, the winter of 1976-77 was particularly cold. The seasonal temperature cycles are evidently superimposed over long-term temperature trends.

The distribution of salinity in the bay at any given time is affected primarily by river flow, local rainfall, basin configuration, wind speed and direction, and water currents. The principal source of fresh water for the estuary is the Apalachicola River, although there is evidence that local runoff and ground water flows affect the habitat characteristics of the bay system in local areas (Livingston unpublished data). In terms of salinity, the bay system may be divided into two main provinces: the open Gulf waters of eastern St. George Sound and the brackish (river-diluted) portions of western St. George Sound, Apalachicola Bay, East Bay, and St. Vincent Sound.

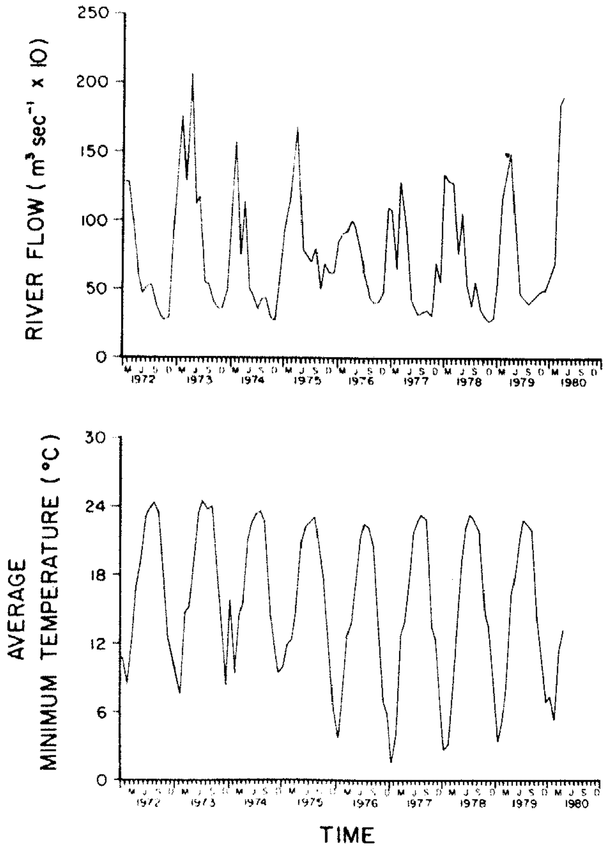
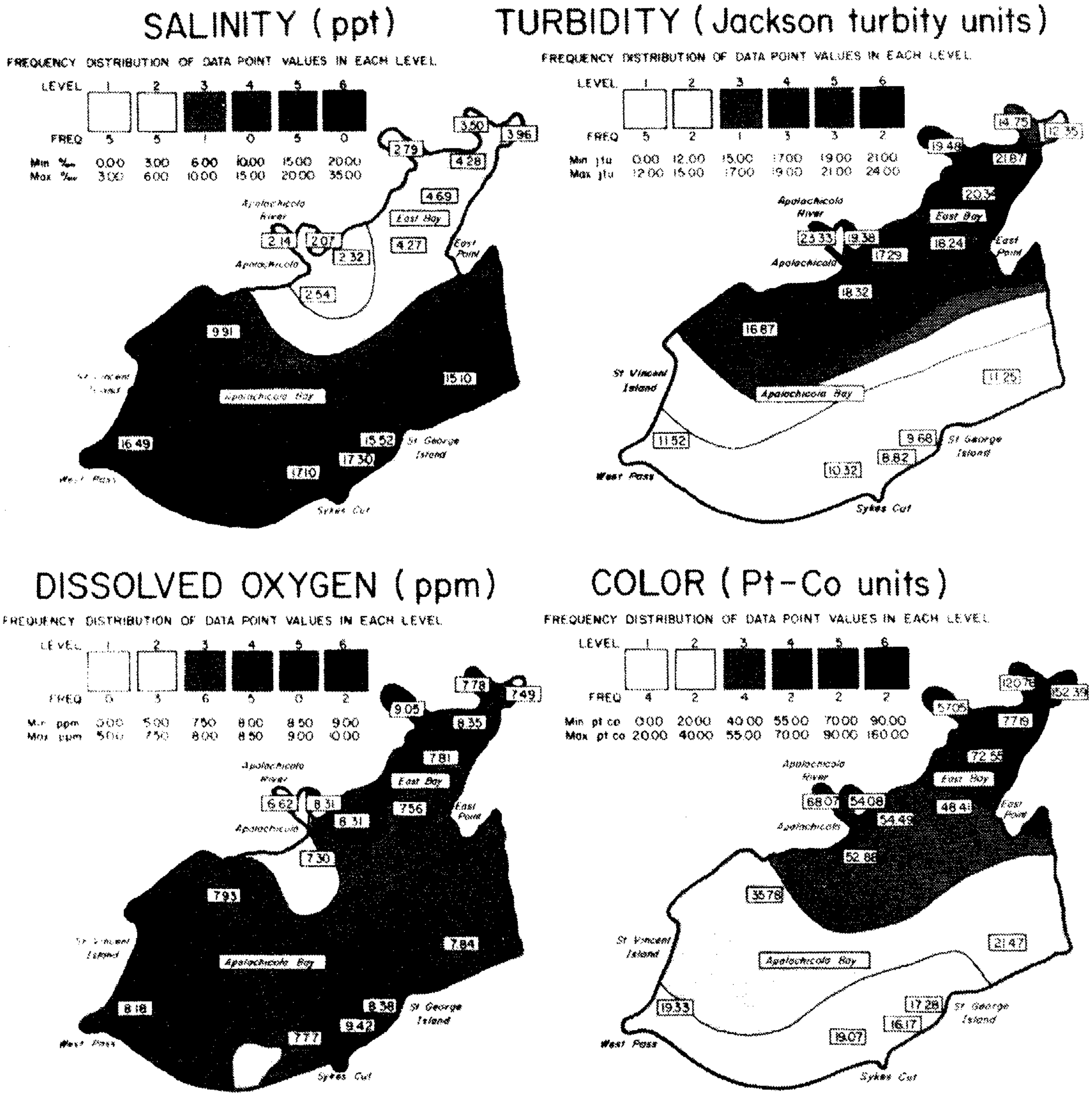


Figure 12. Apalachicola River flow and average minimum air temperature data provided by U.S. Army Corps of Engineers and the NOAA Environmental Data Service, Apalachicola, Fla.

Mean salinity values are lowest at the mouth of the river and in East Bay (Table 2, Figure 13). According to the Venice system of brackish water classification, the lower reaches of the Apalachicola River constitute the limnetic zone, with salinities reaching 0.5 parts per thousand (ppt). During periods of high river flow, the zone expands to include East Bay and considerable portions of Apalachicola Bay. Because of extreme seasonal and annual variability, there are no clear-cut zones that remain stable in the bay system. Rather, the salinity gradients move through the bay area according to upland runoff conditions. East Bay, lying northeast of the river head, is oligohaline (0.5-5.0 ppt) during most of the year (Figure 13). Apalachicola Bay, St. Vincent Sound, and western portions of St. George Sound vary between mesohaline (5-18 ppt) and polyhaline (18-30 ppt) conditions, depending on river flow and upland runoff (Livingston 1983d). Areas near the passes and in the eastern sections of St. George



SALINITY (ppt)

TURBIDITY (Jackson turbity units)

DISSOLVED OXYGEN (ppm)

COLOR (Pt-Co units)

Figure 13. SYNMAP projections of average levels of salinity, dissolved oxygen, turbidity, and color at permanent stations in the Apalachicola estuary, based on data taken monthly from 1972-1980.

Sound vary from polyhaline to euhaline (> 30 ppt) conditions. Gorsline (1963) alluded to the vertical isohaline conditions of the estuary except for areas that are deep or near the inlets. Livingston (1978, 1984a), however, has documented seasonal vertical salinity stratification in various parts of the estuary, especially in areas affected most directly by the river. Differences of surface and bottom salinities of as much as 5-10 ppt during periods of stratification further complicate the exact dimensions of the salinity regime in a given area of the bay system through time. However, by most statistical measures, river flow is the chief determinant of the salinity structure of the estuary (Meeter and Livingston 1978).

There are persistent seasonal patterns of salinity in the Apalachicola estuary, although such patterns are modified by annual variation of river flow and fluctuations of local rainfall. Low bay salinities coincide with high river flows during winter and spring periods; secondary salinity reductions occur in the bay system during late summer-early fall periods of high local precipitation (Figure 14). Salinity generally peaks during the fall drought (October-November). Long-term salinity trends follow river flow fluctuations; low salinity was noted for a prolonged period throughout the estuary during the heavy river flow conditions of the winter of 1972-73, although various factors combine to shape the long-term (multiyear) salinity trends in the estuary. Various statistical analyses (Meeter and Livingston 1978; Meeter et al. 1979) have made a strong association of Apalachicola River flow with the spatial/temporal distribution of salinity throughout the bay system.

Table 2. Bottom salinities in parts per thousand at stations in the Apalachicola estuary. All data represent 5-year means (1972-77) with maxima and minima for this period. A cluster analysis was made to group the stations according to salinity type.

	Bottom salinities (ppt)			
Apalachicola estuary areas	Station	Minimum	Maximum	5-yr mean
Outer Bay	1	0.0	33.7	15.7
	1A	3.0	35.6	22.1
	1E	6.9	31.6	15.7
	1C	1.4	33.7	20.4
	1X	0.0	32.0	17.8
River dominated	2	0.0	28.1	10.4
	3	0.0	22.0	4.8
	4	0.0	31.8	9.6
Upper (East) bay	4A	0.0	26.2	3.6
	5	0.0	28.0	7.4
	5A	0.0	27.3	5.1
	5B	0.0	25.7	3.8
	5C	0.0	27.8	4.3
	6	0.0	23.0	3.6
Sike's Cut	1B	10.6	35.5	28.6

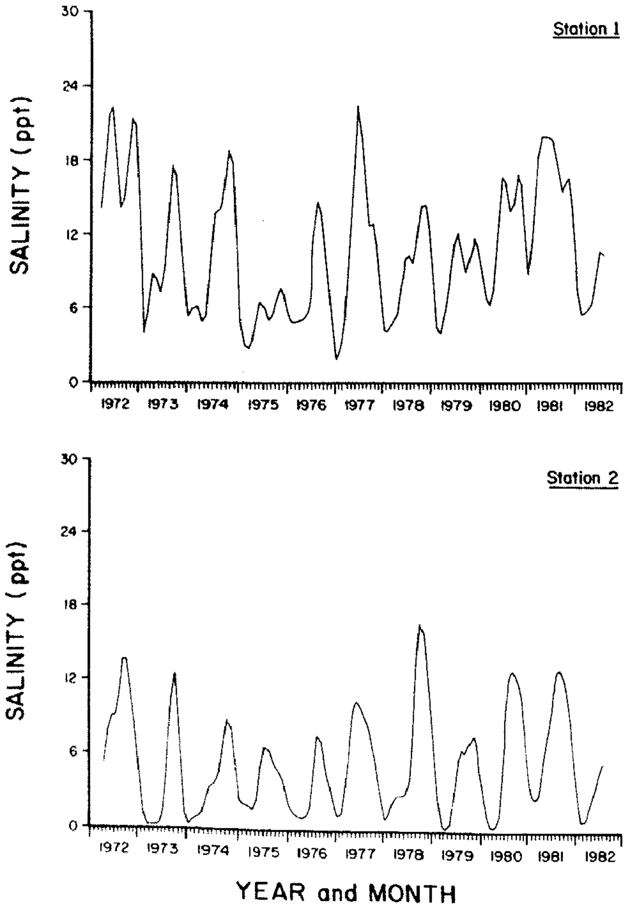


Figure 14. Surface salinity (5-month moving averages) at stations 1 and 5 (Apalachicola Bay, East Bay) taken monthly from 1972 through 1982.

2.4.2. Dissolved Oxygen

Diurnal and seasonal variations of dissolved oxygen (Figure 15) reflect biological and physical processes in the system. Maximum levels usually occur during winter and spring months because of low water temperature and, to a lesser degree, low salinity. During summer and fall periods, vertical stratification of dissolved oxygen is evident in various parts of the estuary. Spatial distribution of mean dissolved oxygen values (Figure 13) is not uniform; the highest values occur in the upper reaches of East Bay (i.e., Round Bay), just off St. George Island (i.e., Nick's Hole), and along the eastern side of St. Vincent Island. Concentrations of dissolved oxygen in most of the estuary during the 10-yr period of observation are sufficient to support most forms of estuarine biota (Figure 15). No sign of cultural eutrophication is evident. The long-term pattern of dissolved oxygen maxima followed the long-term temperature trends, with dissolved oxygen peaking during the cold winters from 1976 to 1978. Such changes represent an indirect effect of temperature on long-term habitat variation in the estuary.

2.4.3. pH

From 1972 to 1982, the pH throughout most of the bay system ranged between 6 and 9 (Livingston 1983c, unpublished data). However, relatively low pH levels (4-5) were observed in upper portions of East Bay during periods of heavy local rainfall and runoff from newly cleared lands in Tate's Hell Swamp (Livingston 1978). Such changes were temporary and, overall, the pH of the Apalachicola Bay system remains within a range that is not limiting to most life forms.

2.4.4. Water Color and Turbidity

Light transmission, as determined by color (measured in platinum-cobalt units) and turbidity (in Jackson Turbidity Units), is a key variable in the timing and distribution of primary and secondary productivity in the estuary. The spatial and temporal distributions of water color and turbidity (Figures 13, 16, 17) are related to patterns of fresh-water flow into the bay system. The highest levels of both factors are found at the mouth of the river and throughout upper East Bay with clear-cut gulfward gradients. Both color and turbidity reach seasonal high levels during winter and early spring periods of high river flow and overland runoff. During the major flooding in the winter of 1972-73, turbidity and color in the estuary reached a 10-yr high point at most stations. While the general pattern of color in the estuary follows river flow fluctuations, the highest levels occurred in eastern East Bay. The color was directly associated with forestry activities and runoff from the Tate's Hell Swamp (Livingston 1978). Various compounds such as tannins, lignins, and

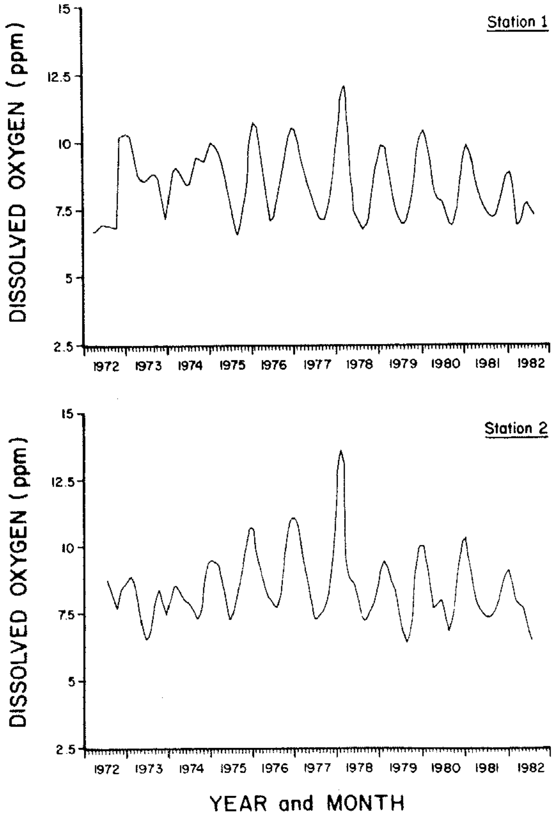


Figure 15. Surface dissolved oxygen (5-month moving averages) at stations 1 and 5 in the Apalachicola estuary taken monthly from 1972 through 1982.

fulvic acid complexes, which occur naturally in the upland swamps, are washed into the estuary during periods of high local precipitation. Such water-quality changes, associated with river flow and local rainfall, affect the biological organization of the bay system in terms of primary productivity and food web structure (Livingston 1983b-d).

2.5. BIOLOGICAL HABITATS

The Apalachicola drainage system as a whole is an almost unbroken series of natural habitats, which include upland vegetation, swamps, marshes, and flood plain wetlands. Much of the basin vegetation has the appearance of a mature forest because of rapid regrowth. Slash and longleaf pine are abundant in upland areas. Although several municipalities are located near or within the Apalachicola and Chipola flood plains, none is a major urban center; there is little industrialization in the basin. The dimensions of the biological habitats within the bay system and its associated watershed (i.e., Franklin County) are given in Tables 1 and 3. Aquatic areas, together with forested and nonforested wetlands, comprise about 42% of the total area of Franklin County. As noted previously, aquatic areas are dominated by unvegetated soft-bottom substrates.

2.5.1. Wetlands

a. Bottomland hardwoods. The Apalachicola flood plain (Figure 18) of the upper river is relatively narrow

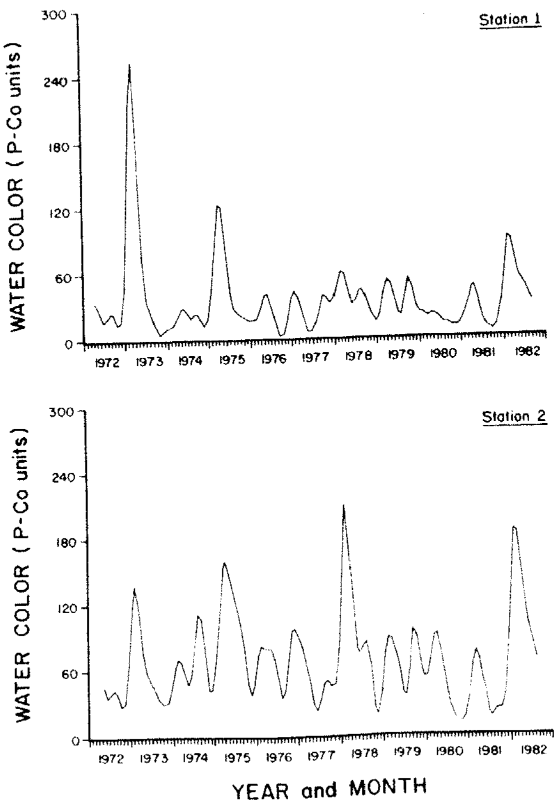


Figure 16. Color (5-month moving averages) at stations 1 and 5 in the Apalachicola estuary taken monthly from 1972 through 1982.

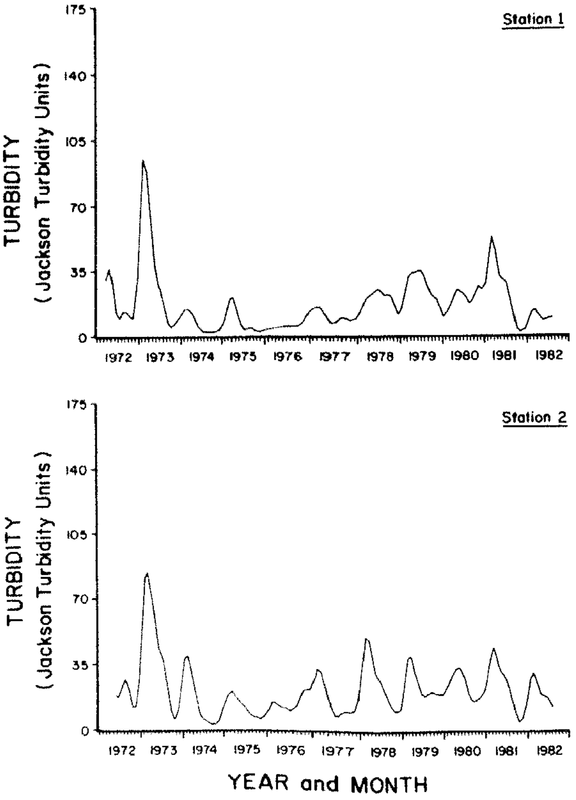


Figure 17. Turbidity (5-month moving averages) at stations 1 and 5 in the Apalachicola estuary taken monthly from 1972 through 1982.

Table 3. Terrestrial habitats and land-use patterns in the immediate watershed of the Apalachicola Bay system (Florida Bureau of Land and Water Management 1977).

Category	Total area (ha)	% of total
Residential	2,461	1.3
Commercial, services	178	0.1
Transportation, utilities	218	0.1
Mixed urban or built-up areas	27	0.0
Other urban or built-up areas	39	0.0
All urban or built-up areas	2,922	1.5
Cropland and pasture	78	0.0
Other agriculture	4	0.0
All agricultural land	82	0.0
Herbaceous rangeland	13	0.0
Rangeland	13	0.0
Evergreen forest land	68,598	35.7
Mixed forest land	36,396	18.9
All forest land	104,994	54.6
Streams and canals	1,469	0.8
Lakes	452	0.2
Reservoirs	10	0.0
Bays and estuaries	62,879	24.3
All water	64,810	25.4
Forested wetland	25,562	13.3
Nonforested wetland	8,465	4.4
All wetlands	34,027	17.7
Beaches	1,441	0.7
Quarries and pits	25	0.0
Transitional areas	110	0.1
All barren land	1,575	0.8
Total area of Franklin County:	198,398	

(1.5-3.0 km or 0.9-1.9 mi wide). The forested flood plain broadens along the lower river (up to 7 km or 11.3 mi wide), with most of the flood-plain wetlands located in the lower delta (H. M. Leitman et al. 1982). The forested flood plain of the Apalachicola basin is the largest in Florida (450 km², 173 mi²; Wharton et al. 1977), and 60 of the 211 tree species in north Florida are found there (Table 4). The predominant species in terms of cover include water tupelo, ogeechee tupelo, baldcypress, carolina ash, swamp tupelo, sweetgum, and overcup oak. These species are typical of southeastern alluvial flood plains and occur in such areas partially because of their adaptive response to restricted availability of oxygen in saturated and inundated soils. Despite continuous logging for over a century, the

Table 4. A. Tree species found in the Apalachicola floodplain (from Leitman 1983 and H. M. Leitman et al. 1982). Included is the relative basal area (in percent) of the top 25 species. B. Area, in acres, of each mapping category for five reaches of the Apalachicola River (from Leitman 1983).

A. Common name	Scientific name
Ash, Carolina	*Fraxinus caroliniana* Mill. (5.4)
Green	*Fraxinus pennsylvanica* Marsh. (2.9
Pumpkin	*Fraxinus profunda* (Bush.) Bush. (1.9)
Baldcypress	*Taxodium distichum* (L.) Rich. (10.6)
Birch, river	*Betula nigra* L. (0.8)
Box elder	*Acer negundo* L. (0.3)
Bumelia, buckthorn	*Bumelia lycioides* (L.) Pers.
Buttonbush	*Cephalanthus occidentalis* L.
Chinaberry	*Melia azedarach* L.[a]
Cottonwood, swamp	*Populus heterophylla* L. (0.4)
Cypress	see baldcypress
Dogwood, stiffcornell (swamp dogwood[b])	*Cornus foemina* Mill. (*Cornus stricta* Lam.[b])
Elm, American	*Ulmus americana* L. (2.4)
Slippery	*Ulmus rubra* Muhl.
Winged	*Ulmus alata* Michx.
Grape	*Vitis* spp.[c]
Hawthord, green	*Crataegus viridis* L.
Parsley	*Crataegus marshallii* Eggle.
Hickory, water	*Carya aquatica* (Michx. f.) Nutt. (2.9)
Hornbeam, American	*Carpinus caroliniana* Walt. (2.0)
Locust, water	*Gleditsia aquatica* Marsh.
Maple, red	*Acer rubrum* L. (1.5)
Mulberry, red	*Morus rubra* L.
Oak, cherrybark	*Quercus falcata* Michx., var. *pagodaefolia* Ell.
diamond-leaf	*Quercus laurifolia* Michx. (2.5)
laurel	*Quercus hemisphaerica* Bartr. (*Q. laurifolia* Michx.[d])
overcup	*Quercus lyrata* Walt. (3.2)
swamp chestnut	*Quercus prinus* L. (*Q. michauxii* Nutt.[b]) (0.3)
water	*Quercus nigra* L. (1.8)
Palmetto, cabbage	*Sabal palmetto* (Walt.) Lodd.
Persimmon, common	*Diospyros virginiana* L.
Pine, loblolly	*Pinus taeda* L.
spruce	*Pinus glabra* Walt.
Planertree (water-elm[b])	*Planera aquatica* Gmel. (2.9)
Possumhaw holly	*Ilex decidua* Walt. (0.8)
Silverbell, little	*Halesia tetraptera* Ellis. (*H. parviflora* Michx.[b])
Sugarberry (hackberry)	*Celtis laevigata* Willd. (2.8)
Swamp-privet	*Forestiera acuminata* (Michx.) Poir.
Sweetbay	*Magnolia virginiana* L. (1.0)
Sweetgum	*Liquidambar styraciflua* L. (4.8)
Sycamore, American	*Platanus occidentalis* L. (0.6)
Titi	*Cyrilla racemiflora* L.

(continued)

Table 4. (Concluded.)

Common name	Scientific name
Tupelo, Ogeechee	*Nyssa ogeche* Bartr. (11.0)
water	*Nyssa aquatica* L. (29.9)
swamp (blackgum)	*Nyssa biflora* Walt. (*N. sylvatica* var. *biflora* (Walt.) Sarg.[b]) (5.0)
black (sourgum)	*Nyssa sulvatica* Marsh. (*N. sylvatica* Marsh. var. *sylvatica*[b])
Viburnum, witherod	*Viburnum cassinoides* L.
Walnut, black	*Juglans nigra* L.
Willow, black	*Salix nigra* Marsh. (0.4)

[a] Introduced exotic species.
[b] According to Little (1979).
[c] Radford and others (1968).
[d] Little (1979) does not recognize *Quercus hemisphaerica* as a separate species.

B.	Acres					
Mapping category	Upper river	Middle river	Lower river from Wewahitchka to Sumatra	Lower river from Sumatra to mile 10	Lower river from mile 10 to mouth	Total
Pine	136	672	0	204	0	1,010
Sweetgum-Sugarberry-Water oak-Loblolly Pine	642	1,440	154	474	0	2,710
Water hickory-Sweetgum-Overcup oak-Green ash-Sugarberry	12,500	32,200	15,800	1,770	48.0	62,300
Tupelo-cypress with mixed hardwoods	1,170	1,860	8,310	15,800	6,920	34,100
Tupelo-cypress	2,420	2,270	6,240	10,300	456	21,700
Pioneer	0	150	19.2	0	0	169
Marsh	0	0	0	0	9,030	9,030
Open water	2,730	3,110	1,540	2,010	1,260	10,700
Unidentified	1,020	748	81.3	76.8	19.2	1,950
Total	20,600	42,500	32,100	30,600	17,700	144,000

Apalachicola flood plain remains relatively intact as a functional bottomland hardwood system.

Tupelo, gum, and cypress species are dominant in the upper flood plain (Table 4). The lower flood plain is characterized by coastal plain pine flatlands, coastal dunes (shortleaf pine, titi, and bayhead) and freshwater and brackish marshes. Various forest associations occur in different regions of the basin (Table 4) (Leitman 1983, H. M. Leitman et al. 1982): (1) The sweetgum/sugarberry/ water oak/loblolly pine association is found in dry to damp soils or wetland-toupland/transition areas. These forest types decrease in the area within the basin as the river approaches the coast. (2) The water hickory/sweetgum/overcup oak/green ash/sugarberry association covers about 78% of the floodplain mainly in the upper and middle reaches of the river basin. This association is not common in the lower reaches of the valley. (3) The water tupelo/ogeechee tupelo/baldcypress association is found in dry to saturated soils and is concentrated along waterways and relict waterways in the lower reaches of the river basin. (4) The water tupelo/baldcypress association is located in damp to saturated soils along the entire length of the river. Pioneer associations are dominated by a narrow zone of black willow in areas inundated more than 25% of the time. Marsh areas are located along the lower river. Water depth, duration of inundation and saturation, and fluctuations in water levels all contribute to the composition of the wetland forests. These conditions

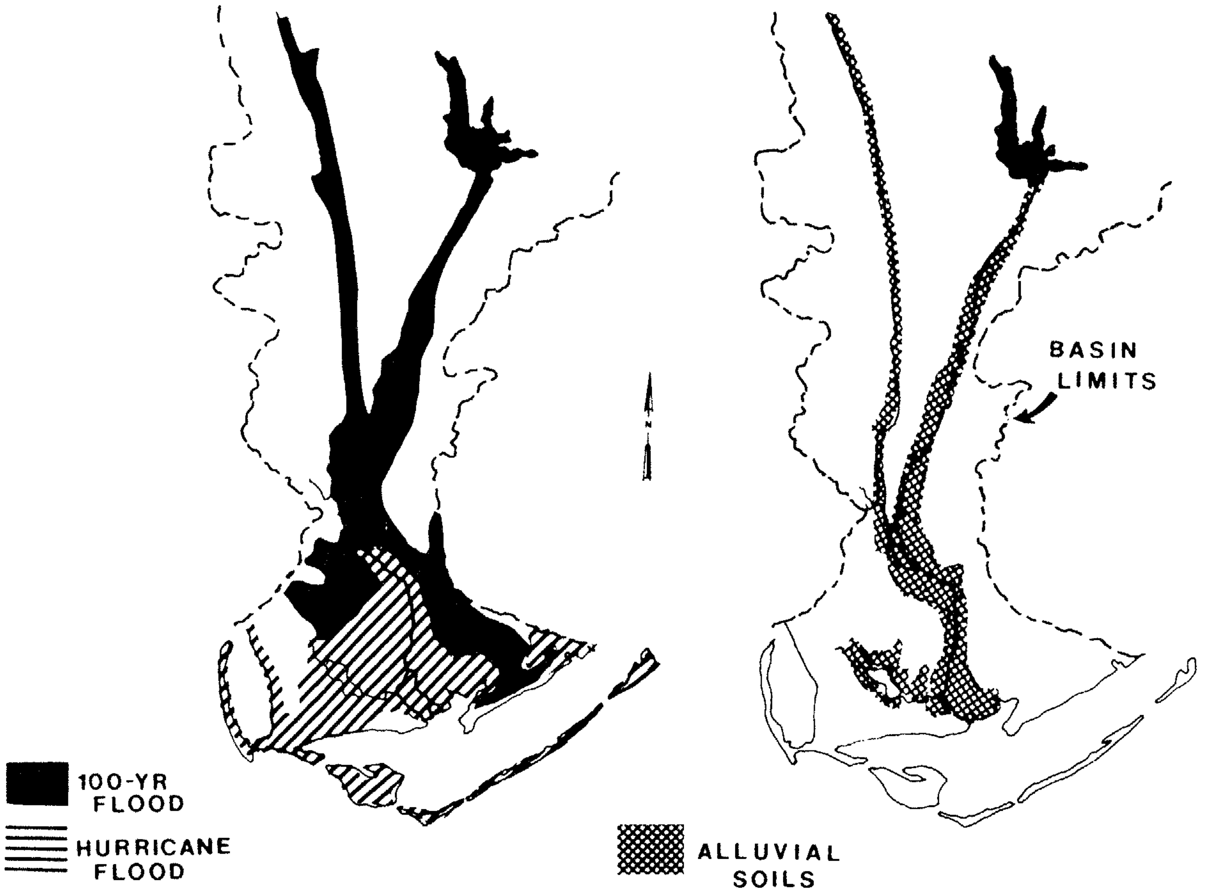


Figure 18. Frequently flooded areas and soil associations in the Apalachicola River Basin (taken from the Florida Department of Administration 1977).

are dependent to a large degree on watershed runoff, flood plain topographic relief, and drainage characteristics.

b. Marshes. Most of the intertidal areas around the estuary are surrounded by freshwater, brackish, and saltwater marshes (Figure 19). The freshwater and brackish-water marshes are characterized by bullrushes (*Scripus* spp.), cattails (*Typha* spp.), saw grasses (*Cladium* spp.), cordgrass (*Spartina* spp.), and needlerush (*Juncus roemerianus*). Salt marshes of the region are represented by black needlerush, cordgrass, *Distichlis spicata*, and *Salicornia* spp. Major marsh development is found along the lower flood plain and areas adjacent to East Bay. These marshes are dominated by mixed freshwater species. Similar marsh associations are found in the New River and Ochlochonee River drainages to the east. Narrow stands of brackish water marshes occur intermittently along the lagoonal interface of the Alligator Point peninsula (at the extreme east end of the system; Figure 3) and along the bayside portion of the barrier islands. Limited marshes are located along the mainland east and west of the Apalachicola River mouth. The East Bay marshes dominate the system by area (Table 1) with lesser marsh development along St. Vincent Sound and along the lagoonal portions of St. George Island and Dog Island. The marshes in the entire bay system comprise approximately 14% of the total water surface.

The Apalachicola marshes are significant feeding and reproductive zones for various aquatic and terrestrial species (Livingston 1983c). Vertical and lateral stratification of this habitat has provided conditions that house and feed some of the most important species (ecologically and commercially) in the river-bay system.

2.5.2. Seagrass Beds

Grassbeds in the Apalachicola estuary (Figure 19) account for about 10% of the

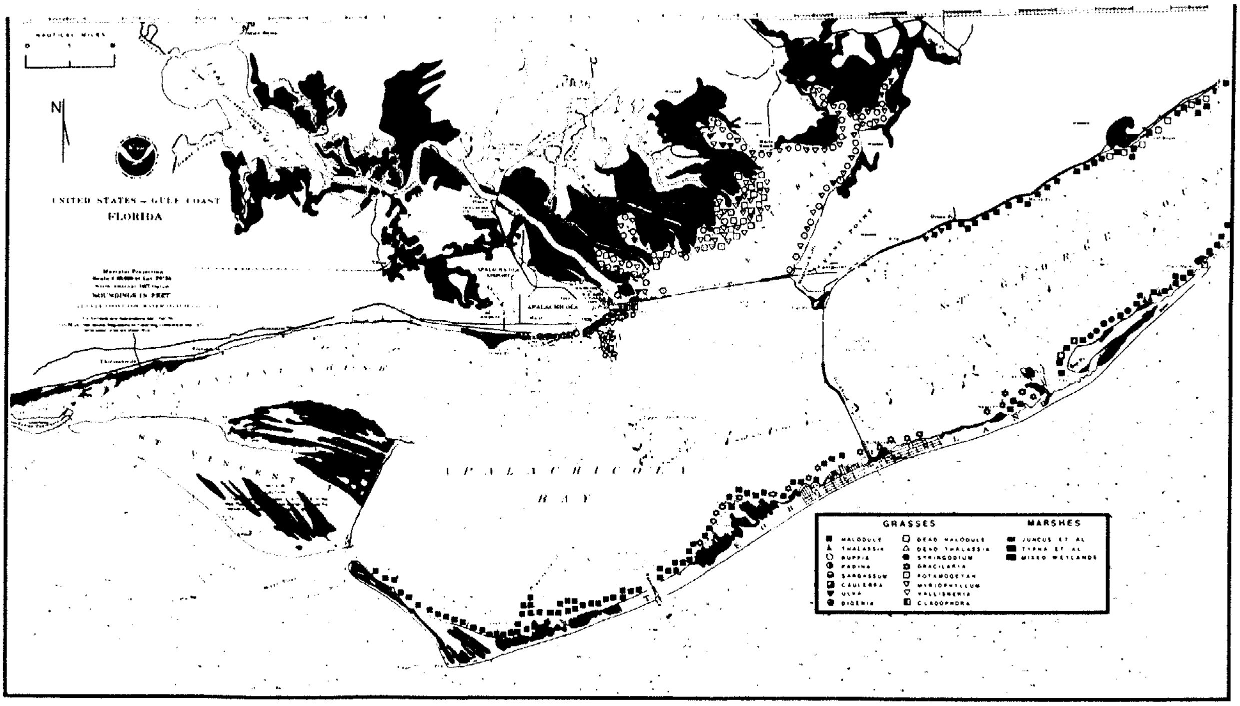


Figure 19. Distribution of the marshes and submergent vegetation in the Apalachicola estuary (data compiled from aerial photographs and ground-truth observations by divers) (see Livingston 1980a).

total water area (Table 1). Except for certain areas along the eastern portions of St. George Sound, submerged vegetation in the Apalachicola estuary is light-limited by high turbidity and water color. High sedimentation and resuspension of sediments in the estuary may also affect the seagrass bed distribution. Seagrasses and algal associations are largely confined to fringes of the estuary at depths of less than 1 m. The largest concentration of these submerged grassbeds is in eastern St. George Sound; such seagrass beds also occur in upper East Bay, inside St. George Island in Apalachicola Bay, and in western St. George Sound. In East Bay, freshwater and brackish-water species (*Vallisneria americana*, *Ruppia maritima*, and *Potamogeton* sp.) are predominant. Grass beds along the mainland east of the river are dominated by *Halodule wrightii*, *Syringodium filiforme*, and *Thalassia testudinum*. The shallow lagoonal flats of Alligator Point, Dog Island, and St. George Island are populated by *Halodule wrightii*, *Gracilaria* spp., and *Syringodium filiforme*. Few if any grassbeds are found in St. Vincent Sound.

As a habitat, seagrass beds provide organic matter and shelter for various infaunal and epibenthic invertebrates and fishes.

2.5.3. Soft-Bottom Substrates

Muddy, soft bottom substrates comprise about 78% of the open water zone of the Apalachicola Bay system and are thus the dominant habitat form in the area. The relative composition of the sand, silt, clay and shell fractions of the sediments depends on proximity to land, runoff conditions, water currents, and trends of biological productivity. Sediment type and associated water-quality conditions in the benthic habitat determine the composition of infaunal and epifaunal biological components. Recruitment and community composition of the benthic invertebrates (meiofauna and macrofauna) may depend on the distribution of flocculent resuspended sediments and bedload transport. The unvegetated, soft-bottom habitat in the Apalachicola Bay system represents the basis for important food web relationships in the estuary.

2.5.4. Oyster Bars

The Apalachicola estuary is an ideal environment for the growth and culture of the oyster (*Crassostrea virginica*). The oyster bars that cover about 7% of the aquatic area of the bay system (Table 1) are an important habitat for various assemblages of estuarine organisms. Major oyster beds are located in St. Vincent Sound, west St. George Sound, and the East Bay-Apalachicola Bay complex (Figure 20). New (constructed or artificial) oyster reefs are located in eastern portions of St. Vincent Sound. The highly productive natural oyster bars of St. Vincent Sound and western St. George Sound represent the primary concentrations of commercial oysters in the estuary. The waters of both areas are well circulated by the prevailing currents and are characterized by salinity conditions optimal for oyster propagation and growth (Livingston 1983c, d). The reefs near the seaward edge of the bay thrive when the river is high while those near the river mouth do well during conditions of low water.

Whitfield and Beaumariage (1977) estimate that about 40% of Apalachicola Bay is suitable for growing oysters but that substrate type is a major limiting factor. Rapid oyster growth due to favorable environmental conditions accounts for the fact that over 90% of Florida's oysters (8%-10% nationally) come from the Apalachicola estuary.

2.5.5. Nearshore Gulf Environment

The shallow nearshore gulf is a drowned alluvial plain grading into a limestone plateau to the east and south (McNulty et al. 1972). The eastern Gulf of Mexico is characterized by moderately high-energy sand beaches. The north gulf coast sedimentary province contains relict sand west of the Apalachicola delta. The Miocene relict sands and clays off the Apalachicola embayment grade into quartz sand and mud over limestone characteristic of the extreme eastern gulf region. Much of the water motion along the shallow West Florida Shelf is due to tides, although wind effects are evident, especially in winter when cold fronts move through the area. The high-salinity coastal waters are well mixed except during warmer months

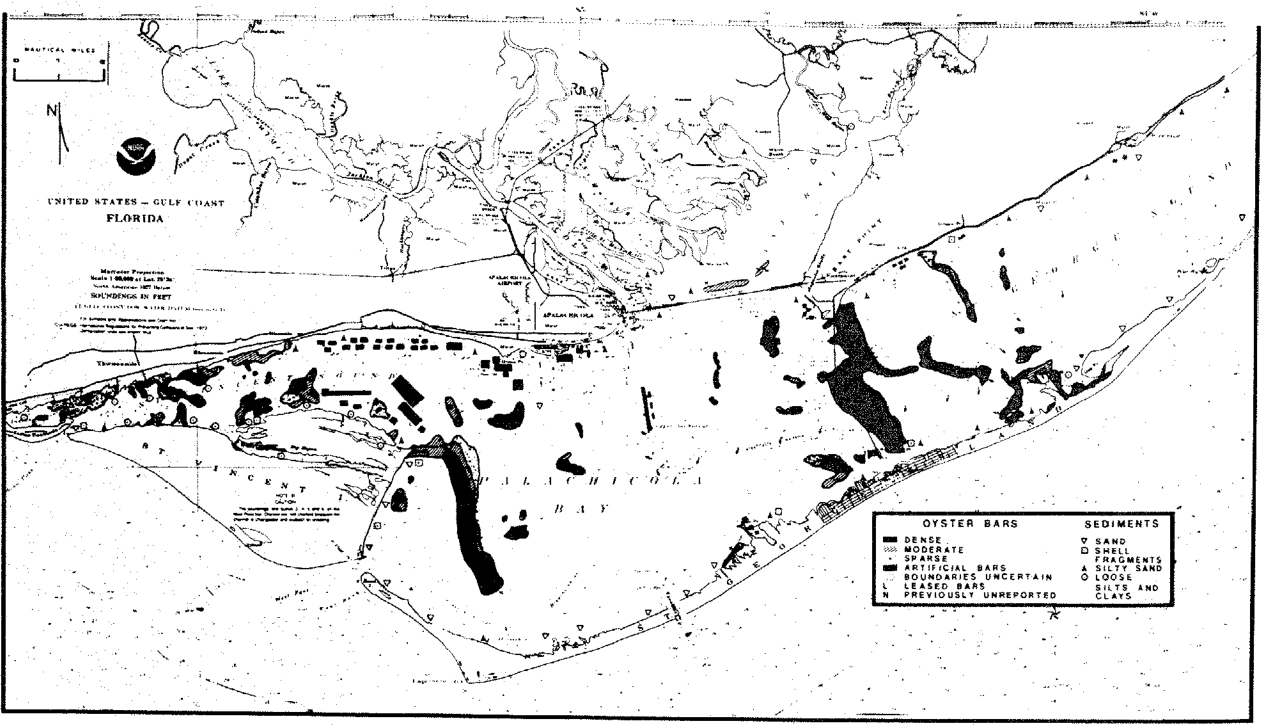


Figure 20. Distribution of oyster bars and sediments in the Apalachicola estuary (data from historic records, personal information from oyster dealers in Apalachicola, field observations by F.S.U. field personnel, and records from the Florida Department of Natural Resources) (Livingston 1980a). (This chart is currently being updated.)

when a thermocline separates the cooler bottom waters from the surface waters.

Organisms in near-shore areas are part of a temperate sand community (Jones et al. 1973; Smith 1974). The shallow (10-20 m) shelf benthos reflects the intrusion of tropical species in both sandy areas and rocky outcrop substrates. The northeastern gulf lies in the Carolina Zoogeographic Region with a warm-temperate fish fauna. Fish assemblages are characterized by high endemism and high species diversity due, in part, to a number of eurythermic tropical species. The northeastern Florida gulf coast has a relatively high fishery potential for crustaceans and finfishes (Jones et al. 1973; Smith 1974).

2.6. NATURAL RESOURCES OF THE APALACHICOLA DRAINAGE SYSTEM

There are several natural attributes of the Apalachicola drainage system that make it unique among Florida and North American river estuaries (Livingston and Joyce 1977). The strategic placement of the drainage, together with the relatively unspoiled natural components--streams, rivers, wetlands, estuary, offshore gulf--have combined to create the conditions for speciose and unique assemblages of terrestrial and aquatic organisms. In many ways, the Apalachicola system is an important dispersal route for temperate species of plants and animals from the high elevations of the southeastern United States to the Gulf of Mexico.

The following is an abbreviated summary of such attributes:

1. The Apalachicola ranks as one of the great rivers of the United States and is the largest river (in terms of flow) in Florida. It is the only river in Florida to stretch from the Piedmont to the Gulf of Mexico.

2. The area of forested floodplain is the greatest of all river systems in Florida. The densely forested, bottomland hardwood wetlands of the Apalachicola River have the highest litter-fall production rates of the worldwide warm-

temperate systems that have been studied (Mattraw and Elder 1980).

3. Nutrient levels are higher in the Apalachicola wetlands than in most comparable systems throughout the northern hemisphere. The Apalachicola wetlands contribute significant quantities of nutrients and organic matter to river and bay areas. Regular seasonal flooding by the currently free-flowing river is necessary for mobilization of particulate organic matter (POM) and nutrients out of the floodplain (Mattraw and Elder 1980).

4. The Apalachicola drainage system includes a group of ecological regions that contribute to speciose and unique plant associations. The flora comprises 117 plant species, of which 17 are endangered, 28 are threatened, and 30 are rare. Nine species are narrowly endemic while 27 are endemic to the general Apalachicola area (Means 1977).

5. The Apalachicola wetlands provide habitat for rich faunal assemblages. The basin receives biotic exchanges and input from the Piedmont, the Atlantic Coastal Plain, the Gulf Coastal Plain, and peninsular Florida. The floodplain forest, with over 250 species of vertebrates, is one of the most important animal habitats of the Southeast (Means 1977).

6. Of the drainages of the Apalachicolan and West Floridian molluscan province (from the Escambia River to the Suwannee River), the Apalachicola River contains the largest total number of species of freshwater gastropod and bivalve mollusks. The river contains the greatest proportion of endemics to the total fauna in the province, with at least six rare and endangered species (two Amblemids, four Unionids) (Heard 1977).

7. The tri-river valley is characterized by a rich fish fauna (116 species) (Yerger 1977). The Apalachicola basin contains more fish species (85) than any other Florida river. Three species (Notropis callitaenia, N. zonistius, Moxostoma sp.) are restricted to the Apalachicola River and its major tributaries, while a fourth species (the "handpaint" bluegill, Lepomis macrochirus) originated in the system. Existing freshwater sport and commercial fisheries are diverse and rich. The Apalachicola River is the only river on the Florida gulf coast that supports a striped bass (Morone saxatilis) fishery (Livingston and Joyce 1977). This fishery is based on a population that is endemic to the river and considered a separate race from the Atlantic coast striped bass.

8. Excluding fishes, the Apalachicola River system contains over 250 species of vertebrates. The highest species density of amphibians and reptiles in North America (north of Mexico) occurs in the upper Apalachicola basin (Means 1977). The abundant and diverse bird fauna is concentrated in the floodplain forests. Two species considered extinct, the ivory-billed woodpecker (Campephilus principalis) and Bachman's sparrow (Aimophila aestivalis), were last sighted in the Apalachicola system. These species are part of a growing list of approximately fifty species of amphibians, reptiles, birds, and mammals that are considered endangered, threatened, rare, of special concern, or of undetermined status.

9. The Apalachicola estuary, with its barrier islands, represents a major flyway for gulf migratory bird species. The estuary has the highest density of nesting ospreys (Pandion haliaetus) along the northeast Florida gulf coast (Eichholz 1980).

10. The Apalachicola Bay system is one of the richest and least polluted such areas in the United States. The estuary now provides over 90% of Florida's oysters and is part of a major spawning ground for blue crabs along the Florida gulf coast (Livingston and Joyce 1977). The bay serves as an important nursery for penaeid shrimp and finfishes and is characterized by some of the highest densities of infaunal invertebrates of any comparable area in the United States.

11. The highly profitable Apalachicola oyster industry and various sport and commercial fisheries directly and indirectly provide the economic and cultural basis for a high proportion of the people in the region (Livingston 1983c).

CHAPTER 3
PRIMARY PRODUCTIVITY AND NUTRIENT CYCLING

Most aquatic systems such as rivers and estuaries depend on sources of organic matter outside the system (i.e., allochthonous: dissolved and particulate organic matter from associated wetlands) and within the system (i.e., autochthonous: phytoplankton, benthic plants). Inorganic nutrients (phosphorus, nitrogen) and organic matter (dissolved, particulate) are swept into aquatic systems by rainfall, overland runoff, and river flooding. The extremely complex chemical processes involved in the transformation of nutrients into plant and animal biomass are not well understood and are intricately related to microbiological activity. One important generalization based on the long-term field studies is that the Apalachicola estuary is inextricably linked to the river in terms of freshwater input and the movement of dissolved and particulate organic material into the estuary. River input is seasonally and annually pulsed, and such influx of materials has an important influence on allochthonous and autochthonous sources of organic matter throughout the Apalachicola estuary.

Nutrient fluxes and primary productivity of the river-estuary system have been studied for over a decade; the following is a review of the available information concerning the Apalachicola system.

3.1. PRIMARY PRODUCERS

3.1.1. Allochthonous Sources

a. Freshwater wetlands. The production and decomposition of organic matter in the floodplain wetlands represents one facet of estuarine productivity (Livingston 1981a; Livingston et al. 1977; Elder and Cairns 1982; Elder and Mattraw 1982; Mattraw and Elder 1980, 1982). Over time, the Apalachicola River has meandered in broad curves through the flood plain. Erosional and depositional processes have led to the development of shoals, backswamps, channels, sloughs, levees, and oxbow lakes. The dynamics of the Apalachicola River affect the transport of dissolved and particulate substances into receiving aquatic areas. However, such transport of allochthonous substances depends on complex interactions of river flooding with factors such as wetland productivity, decomposition processes, the timing and relative heights of the flood stage, the heights of surrounding lands, soil types, and drainage characteristics of the flood plain. The unifying characteristics of the wetland inputs are the distribution and environmental functions of the bottomland hardwood forests of the Apalachicola floodplain (Figure 21).

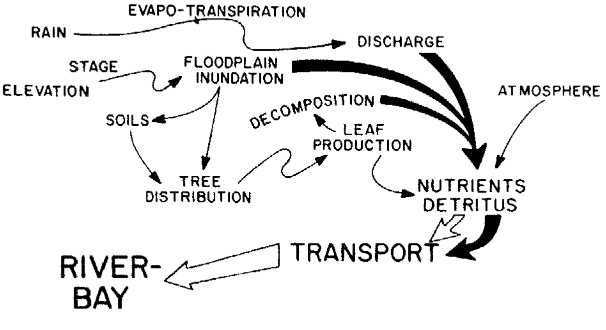


Figure 21. Nutrient/detritus transport mechanisms and long-term fluctuations in detrital yield to the Apalachicola River flow (modified from Mattraw and Elder 1980 and Livingston unpubl.).

General plant distribution in the riverine wetlands is associated with topographic features of the flood plain and surrounding forested lowlands (Clewell 1978). H. M. Leitman et al. (1982) showed that the height of natural riverbank levees and the size and distribution of levee breaks control floodplain hydrologic conditions. Vegetative composition is highly correlated with depth of water, duration of inundation and saturation, and water level. Leitman (1978, 1983) and Leitman and Sohm (1981) described in detail the distribution of floodplain trees in the Apalachicola drainage. According to these studies, pine flatwoods and loblolly pine-sweetgum associations are often found on elevated slopes while more mesic hardwoods inhabit the levees. River banks are occupied by willows and birches. Terraces or basin depressions are inhabited by hardwood swamp species. Cypress-tupelo associations are often located in sloughs. Backswamps are characterized by blackgum and sweetbay associations.

The bottomland hardwood community of the Apalachicola floodplain produces large amounts of potentially exportable material (Elder and Cairns 1982). The weighted mean of litterfall was 800 grams m^{-2} with overall annual deposition within the 454 km^2 bottomland hardwood flood plain of 360,000 metric tons (mt) (396,720 tons) of organic matter. These production levels are similar to those observed in equatorial forests but are higher than those noted in cool temperate forests and most warm-temperate forests. Levee vegetation produced more litterfall per ground surface area than did the swamp vegetation. The seasonal distribution of litterfall was characterized by a sharp late autumn peak. The three most abundant flood plain tree species (tupelo, cypress and ash) accounted for over 50% of the total leaf-fall, even though these species were the least productive of those analyzed on the basis of mass-per-stem biomass.

Annual flooding is a major factor for mobilization of substances out of the flood plain. Flooding leads to immersion of litter material, enhanced decomposition rates, and transfer of the breakdown products (nutrients and detritus) to associated aquatic systems (Cairns 1981, Elder and Cairns 1982). The river is thus closely associated with the rich productivity of the Apalachicola wetlands and is the primary agent for movement of organic matter out of the floodplain. In this way, the forested Apalachicola River flood plain is an important source of organic carbon for the estuary. Spring floods during March and April of 1980 deposited 35,000 mt (38,570 tons) of detritus derived from litterfall into the Apalachicola estuary (Mattraw and Elder 1982). During one year of observation, total organic carbon deposits in the bay amounted to 214,000 mt (235,830 tons). Total nitrogen and total phosphorus inputs to the river during the same period were 21,400 (23,593) and 1,650 mt (1,818 tons), respectively (Mattraw and Elder 1982). The annual detrital organic carbon input was 30,000 metric tons (Mattraw and Elder 1982). Mattraw and Elder (1982) estimated that an 86-day period of winter and spring flooding accounted for 53, 60, 48, and 56 percent of the annual total organic carbon, particulate organic carbon, total nitrogen, and total phosphorus transport, respectively. Flood characteristics are important determinants of the amounts and forms of transported materials. While there was an annual net export of nutrients to the estuary, it is likely that the wetland system acted as a nutrient sink during certain periods of the year. Although nutrients are released to the river by flood-plain vegetation, such compounds are subject to active recycling within the receiving aquatic systems.

The considerable export of particulate matter from the flood plain is consistent with previous findings. Livingston (1981a) and Livingston et al. (1976a) found a direct relationship between river flooding and the appearance of micro- and macroparticulate matter in the estuary. Results of long-term studies of the significance of river-derived particulate organic matter to the estuary (Livingston 1981a, b) indicate that the exact timing of the peak river flows and the seasonal changes in the productivity of wetlands vegetation are key determinants of short-term fluctuations and long-term trends of the input of allochthonous organic matter into the

Apalachicola estuary (Figure 21). A linear regression of microdetritus and river flow by season (Table 5; Figure 22) showed seasonal differences in the relationship of detrital concentration and river flow (Livingston 1981a). During summer periods, there was no direct correlation of river flow and detritus in the estuary. By the fall, there was still no significant relationship although there were occasional influxes of detritus with minor peaks in the river flow. By winter, however, a strong direct relationship was apparent between microdetrital loading and river-flow peaks. The winter regression differed from that of the spring detrital loading, which, though significantly associated with river-flow levels, required higher river levels for comparable concentrations and loading of detritus. This analysis indicates that the degree and timing of river flooding on a seasonal basis affects the level of detrital loading to the estuary.

There are various additional sources of allochthonous nutrients and detritus for the Apalachicola River and estuary

Table 5. Linear regression (log/log) of total microdetritus (ash-free dry weight) and river flow (m^3 sec^{-1}) by month/year by season (August 1975-April 1980), at station 7, located at the mouth of the Apalachicola River. Data are taken from Livingston (1981a). r = Pearson correlation coefficient.

Station/month	r	r^2	(Significance of r)
Station 7 (Surface)			
June-August	0.08	0.23	0.39863
September-November	0.48	0.23	0.03469
December-February	0.70	0.49	0.00188
March-May	0.77	0.60	0.00057
Station 7 (Mid-depth)			
June-August	0.35	0.12	0.11809
September-November	0.19	0.04	0.25542
December-February	0.64	0.40	0.00570
March-May	0.68	0.46	0.00397
Station 7 (Bottom)			
June-August	0.08	0.01	0.40243
September-November	0.21	0.04	0.22867
December-February	0.77	0.60	0.00037
March-May	0.55	0.30	0.02253

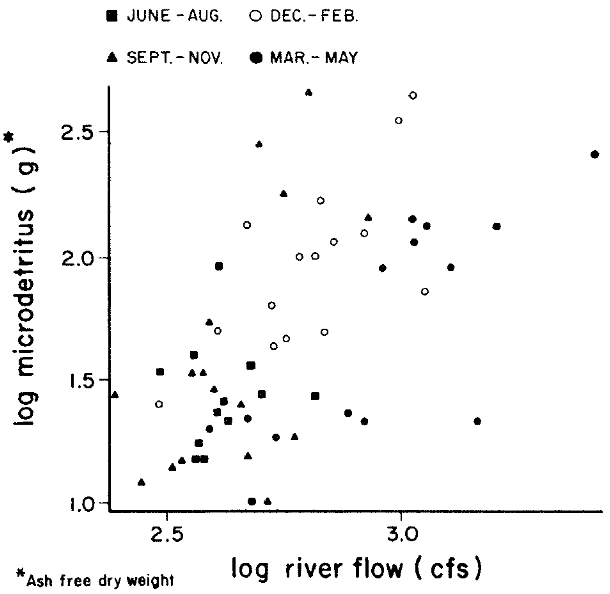


Figure 22. Regression analysis of the relationship of microdetritus to Apalachicola River flow by season (totals taken from station 7, surface) (after Livingston 1981a).

systems (Mattraw and Elder 1982). These include headwater inflow, tributary and ground-water inflow, upland productivity, atmospheric fallout, and productivity within the aquatic system itself. The hydrological characteristics of the river system influence both the type of detritus produced and the quantity transported, since the wetland distribution is determined by patterns of flooding, and the same flooding provides an energy input as a transport medium. The Jim Woodruff Dam removes practically all the particulate matter from the Flint and Chattahoochee drainages (Mattraw and Elder 1982), so the Chipola-Apalachicola wetland area is the primary contributor of organic detritus to the bay system.

b. Coastal marshes. The primary nonforested area in the bay system consists of freshwater and brackish marshes in the Apalachicola delta just above East Bay (Figure 19). In parts of East Bay, marshes are dominated by bullrushes (Scirpus spp.), cattails (Typha domingensis), and other freshwater species such as sawgrass (Cladium jamaicense). Brackish-water species such as cordgrass and needle rush are also found. The northeast section of St. Vincent Island has a well-developed brackish-water marsh.

Kruczynski (1978) and Kruczynski et al. (1978a, b) have analyzed the primary production of tidal marshes dominated by Juncus roemerianus in the St. Marks National Wildlife Refuge just east of the Apalachicola estuary. The authors considered such marshes representative of undeveloped wetlands in northwest Florida. Aboveground production was measured in each of three zones based on soil characteristics, elevation, and species assemblages. The high marsh areas were located approximately 600 m (1,969 ft) inland; middle marsh areas were located approximately 240-360 m (787-1,181 ft) from the bay; and low marsh areas were placed 0-120 m (0-394 ft) from the bay. Based on carbon-14 methods, the authors found that total aboveground production of a north Florida Juncus marsh is 8.5 t C ha^{-1} yr^{-1} (3.8 tons/acre/yr) (low marsh), 5.7 t C ha^{-1} yr^{-1} (2.5 tons/acre/yr) (upper marsh), and 1.8 t C ha^{-1} yr^{-1} (0.8 tons/acre/yr) (high marsh). Using average figures weighted by area for an extrapolated estimate of marsh productivity in the Apalachicola marshes (Table 1), there is an estimated net production of 37,714 t yr^{-1} (41,561 t/yr^{-1}) in the Apalachicola estuary (East Bay, Apalachicola Bay, St. Vincent Sound) and 46,905 t yr^{-1} (51,689 tons/year) in the entire bay system.

A comparison of these figures with those from other areas (Table 6) indicates that production of Juncus and Spartina systems along the northeast Gulf coast is comparable to that in other marsh areas. According to Kruczynski et al. (1978b), Spartina decomposes faster than Juncus, so nutrients from the former may be more readily available to associated estuarine systems.

3.1.2. Autochthonous Sources

a. Phytoplankton. Phytoplankton are ubiquitous in rivers, estuaries, and coastal systems. The phytoplankton community represents an important part of aquatic ecosystems both from the standpoint of primary production and as a key element in food webs. Diatoms are dominant in the net phytoplankton taken in the Apalachicola estuary throughout the year (Table 7) (Estabrook 1973). In East Bay, *Melosira granulata* is the dominant species; *Chaetoceros lorenzianus* is dominant in Apalachicola Bay. Species such as *Chaetoceros lorenzianus*, *Bacteriastrum delicatulum*, and *Thalassiothrix frauenfeldii* are predominant in the spring, while *Skeletonema costatum*, *Rhizosolenia alata* and *Coscinodiscus radiatus* prevail during fall and winter months. Although the phytoplankton standing crop is quite low at any given time, phytoplankton productivity is often quite high in areas such as the Apalachicola Bay system.

Table 6. Net above-ground primary production of marsh plants in various salt marshes (Kruczynski et al. 1978b).

Marsh plant and location	Net primary productivity g/m^2/yr			Authors
	LM	UM	HM	
Spartina alterniflora				
FL	700	335	130	Kruczynski et al. 1978a
NJ	---	---	300	Good 1965
DE	---	---	445	Morgan 1961
NY	827	508	---	Udell et al. 1969
GA	985	---	---	Smalley 1959
New England	800-1300	200-300	---	Shea et al. 1975
GA	1158	---	---	Teal 1962
MD	1207	---	---	Johnson 1970
NC	1296	329	---	Stroud & Cooper 1968
NC	1300	610	---	Marshall 1970
LA	1410	1005	---	Day et al. 1973
GA	2000	---	---	Schelske & Odum 1961
LA	2960	1484	---	Kirby 1971
VA	---	500	---	Keefe & Boynton 1973
DE	---	---	445	Morgan 1961
NC	---	---	650	Williams & Murdoch 1972
VA	---	---	1332	Wass & Wright 1969
GA	---	---	2883	Odum & Fanning 1973
GA	---	---	3000	Odum 1971
Juncus roemerianus				
FL†	949	595	243	Kruczynski et al. 1978a
MS	---	---	390	Gabriel & de la Cruz 197
NC	---	---	560	Foster 1968
NC	---	---	754	Williams & Murdoch 1972
NC	---	---	796	Stroud & Cooper 1968
NC	---	---	849	Heald 1969
NC	---	---	895	Waits 1967
NC	---	---	870-1900	Kuenzler & Marshall 1973
MS	---	---	2106	Willingham et al. 1975

LM = low marsh.
UM = upper marsh.
HM = high marsh.
† = estimate by change in biomass method.

Table 7. Presence/absence information for net phytoplankton taken from the Apalachicola estuary by month from October 1972 through September 1973 (Estabrook 1973). x = presence.

1 = 10/14/72
2 = 12/02/72
3 = 01/06/73
4 = 03/19/73
5 = 04/22/73
6 = 05/19/73
7 = 06/11/73
8 = 07/12/73
9 = 08/22/73
10 = 09/10/73

Phytoplankter	1	2	3	4	5	6	7	8	9	10
PHYLUM CHRYSOPHYTA										
Melosira sulcata		x	x	x						x
Melosira granulata		x	x	x	x	x	x			x
Melosira nummuloides			x							
Melosira dubia			x							
Melosira varians						x				
Skeletonema costatum		x	x	x	x					
Coscinodiscus radiatus	x	x	x	x	x	x	x	x	x	x
Coscinodiscus spp.	x		x	x			x		x	x
Coscinodiscus apiculatus			x	x					x	x
Coscinodiscus wailessi			x							x
Coscinodiscus excentricus			x	x						
Coscinodiscus marginatus			x	x	x	x			x	x
Coscinodiscus centralis				x						
Coscinodiscus oculus iridis				x						
Coscinodiscus nitidus				x						
Coscinodiscus concinnus				x			x	x	x	
Actinocyclus chrenbergii				x	x					
Actinocyclus undulatus			x	x		x				x
Biddulphia sinensis		x	x	x	x	x	x	x	x	x
Biddulphia rhombus		x	x	x	x	x			x	x
Biddulphia aurita		x								x
Biddulphia alternans		x					x			x
Biddulphia longicruris										x
Eupodiscus radiatus						x				x
Bellarochia malleus									x	
Triceratium favus		x	x	x	x	x	x	x	x	x
Triceratium reticulum			x							x
Hemiaulus hauckii									x	x
Chaetoceros spp.	x			x	x	x	x	x	x	x
Chaetoceros lorenzianum	x	x	x	x	x	x	x	x	x	x
Chaetoceros decipiens			x	x	x					
Chaetoceros didymus			x			x	x	x	x	x
Chaetoceros curvisetus			x					x		x
Chaetoceros coarctatus			x							
Chaetoceros bravis				x	x	x	x	x	x	x
Chaetoceros affinis					x				x	x
Chaetoceros compressus					x	x			x	x
Chaetoceros peruvianum						x	x	x		
Chaetoceros glandazii								x	x	x
Chaetoceros pelagicus									x	
Chaetoceros danicum									x	x
Chaetoceros constrictum										x
Bacteriastrum delicatulum	x	x	x	x	x	x	x	x	x	x

(continued)

Table 7. (Continued.)

Phytoplankter	1	2	3	4	5	6	7	8	9	10
Bacteriastrum elongatum				x						
Rhizosolenia alata	x	x	x		x	x	x		x	x
Rhizosolenia imbricata		x	x	x	x	x		x	x	x
Rhizosolenia setigera		x	x		x	x	x		x	x
Rhizosolenia bergonii			x							
Rhizosolenia spp.				x					x	
Rhizosolenia robusta					x		x	x	x	x
Rhizosolenia stotterfothii					x	x			x	x
Rhizosolenia calcar-avis					x					x
Rhizosolenia hebetata							x		x	x
Guirardia flaccida		x	x		x	x	x	x	x	x
Asterionella formosa				x			x			
Thalassiothrix frauenfeldii	x	x	x	x	x	x	x	x		
Thalassiothrix mediterranea	x	x	x		x	x	x	x		x
Thalassiothrix longissima				x						
Thalassiothrix nitzschioides	x	x	x	x	x	x	x		x	x
Licmophora abbreviata							x			
Rhabdonema adriaticum			x							
Pleurosigma spp.			x						x	x
Gyrosigma spp.		x		x				x		x
Amphiprora paludosa	x									
Navicula lyra										x
Navicula spp.	x		x	x		x	x			
Lithodesmium undulatum		x		x	x	x	x			x
Fragilaria spp.		x		x		x	x	x		
Diatoma spp.			x				x			
Nitzschia pungens	x	x	x							x
Nitzschia spp.	x		x	x	x	x	x	x		x
Nitzschia sigmoidea		x	x							
Nitzschia closterium			x							x
Nitzschia paradoxa						x	x	x	x	x
Grammatophora marina			x						x	
Cymbella tumida				x	x	x				
Cymatosira belgica				x						
Pinnularia spp.						x				
Synedra spp.						x				
Surirella fastuosa								x		
Cocooneis disculoides								x		
Schroederella delicatula										x
Eucampia cornuta										x
PHYLUM PYRROPHYTA										
Ceratium furca	x		x	x	x		x	x	x	x
Ceratium tripos	x	x	x	x	x	x	x	x	x	x
Ceratium massiliense	x	x	x	x			x	x	x	x
Ceratium fuses		x	x	x			x	x	x	x
Ceratium concilians				x						
Ceratium trichoceros										x
Peridimium spp.	x					x		x	x	
Peridimium grande(?)			x							

(continued)

Table 7. (Concluded.)

Phytoplankter	1	2	3	4	5	6	7	8	9	10
Dinophysis caudata			x		x					
Dinophysis diagenesis(?)									x	
Dinophysis tripos										x
PHYLUM CHLOROPHYTA										
Pediastrum simplex						x	x			
Pediastrum duplex						x	x			
Pediastrum tetras var. *tetraodon*							x			
Scenedesmus quadricauda							x			

Studies by R. L. Iverson and his students indicate that phytoplankton productivity is an important source of organic matter in the Apalachicola estuary. In general, phytoplankton growth depends on temperature, light, and available nutrients (nitrogen, phosphorus) (Figure 23). Temperature is the primary limiting factor for phytoplankton productivity in the estuary during the winter months. Nutrient concentrations and possibly predation pressure control phytoplankton production from late spring to the fall. The usually low levels of phytoplankton productivity during the winter give way to peaks in April. Secondary peaks are noted during summer and fall months.

The average C^{14} phytoplankton productivity (Figure 23) ranged from 63 to 1,694 mg C m^{-2} day^{-1} (Estabrook 1973; Livingston et al. 1974). The relationship of phytoplankton productivity and predation pressure from zooplankton has not been determined. However, since river discharge is strongly associated with nutrient concentrations in the estuary (Livingston et al. 1974), such factors as river flow and nutrients, together with the general ecological conditions in the estuary, combine to control the phytoplankton productivity of the bay system.

Despite considerable spatial and temporal variability of phytoplankton productivity, Eastabrook (1973) estimated an annual productivity value of 371 g C m^{-2} for the Apalachicola estuary. This figure was taken from averaged data (five bay stations) sampled monthly over a 12-month period. Based on these figures, the phytoplankton productivity from the bay system approximates 233,284 t C yr^{-1} (257,079 tons C yr^{-1}); for the immediate estuary (East Bay, Apalachicola Bay), this figure is 103,080 t C yr^{-1} (113,594 tons C yr^{-1}). When compared to production values in other estuaries of the region (Table 8), the phytoplankton productivity and chlorophyll *a* levels in the Apalachicola estuary are relatively high.

b. *Submerged vegetation*. The relatively high levels of color, turbidity, and sedimentation tend to limit submerged macrophytes to the shallowest portions of the Apalachicola estuary (Livingston 1980c, 1983c). Species composition and distribution of seagrass beds are given by Livingston (1980c, 1983c). A major concentration of seagrasses occurs in eastern St. George Sound, which remains outside of the influence of river drainage (Table 1, Figure 19). Such areas are dominated by turtle grass (*Thalassia testudinum*), shoal grass (*Halodule wrightii*), and manatee grass (*Syringodium filiforme*). Seagrass beds are also located in upper portions of East Bay. Such assemblages are dominated by tape weed (*Vallisneria americana*), widgeon grass (*Ruppia maritima*), and sago pondweed (*Potamogeton* sp.). Since the early 1980's Eurasian watermilfoil (*Myriophyllum spicatum*) has taken over

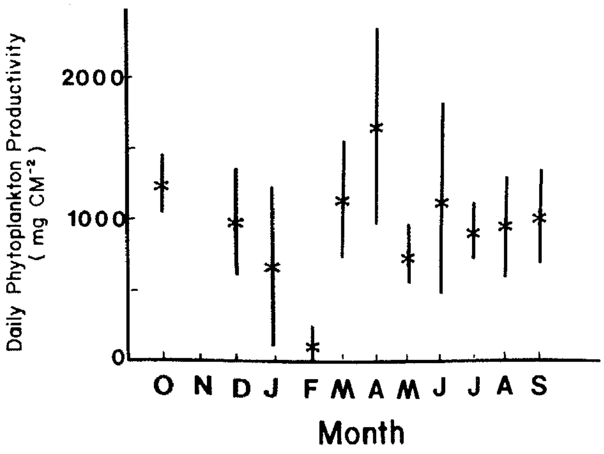


Figure 23. Average seasonal variation in daily phytoplankton productivity for the Apalachicola estuary (taken from Estabrook 1973; Livingston et al. 1974).

various bayous along the northeastern margin of the bay (Livingston, unpublished data). There is little or no submerged vegetation in St. Vincent Sound. Seagrass beds in Apalachicola Bay and western St. George Sound are restricted to shallow lagoonal portions of Dog Island and St. George Island and are dominated by Halodule wrightii, Gracilaria spp., and Syringodium filiforme. Thus the distribution of submerged vegetation generally reflects previously described depth characteristics, water-quality features, drainage and current patterns, and salinity distribution.

Seagrass beds undergo regular seasonal cycles of productivity and standing crop. The ecology of the East Bay Vallisneria beds has been well studied (Livingston and Duncan 1979; Purcell 1977; Sheridan 1978, 1979; Sheridan and Livingston 1979, 1983). Net annual production of Vallisneria varies from 320 g C m^{-2} yr^{-1} to 350 g C m^{-2} yr^{-1}. This species undergoes sharp reductions of standing crop biomass during winter months. After a period of rapid spring growth, maximum leaf development is maintained from May through July. By August, considerable degeneration of the plant standing crop occurs and is followed by new growth during September and October. Similar cycles of growth occur in the Thalassia-dominated grassbeds in areas of higher salinity (Bittaker 1975; Livingston 1982a; Zimmerman and Livingston 1976a, b, 1979). Net annual production has been estimated to be 500 g C m^{-2} yr^{-1} (Iverson unpublished data). Rapid growth occurs during spring and early summer. Standing crop biomass usually peaks during summer months with rapid degeneration as water temperature falls (November, December). During winter months, productivity and standing crop are relatively low in the various types of seagrass beds in shallow coastal areas of the northeast Gulf coast of Florida.

Based on the productivity figures and the seagrass distribution (Table 1), the grassbeds in the East Bay-Apalachicola Bay area produce 8,953 t C yr^{-1} (9,866 tons C yr^{-1}). Grassbed production in the remaining portions of the Apalachicola Bay system approximates 18,260 t C yr^{-1} (20,122 tons C yr^{-1}). Total production for the entire system is 27,213 t C y-1 (29,989 C y^{-1}).

3.2. DETRITUS FLUX AND NUTRIENT DYNAMICS

Availability of organic matter does not explain the processes involved in transformation of energy as it moves through the complex food webs of the river-estuary system. Since relatively few organisms feed directly on living macrophytes, the degradation processes, which include mechanical fragmentation, chemical leaching, autolysis, hydrolysis, oxidation, and microbial activity, are important in the dynamic transfer of estuarine nutrients from available organic matter. Input to the immediate estuary and the bay system as a whole is seasonally timed to specific meteorological factors (Table 9). Most of the river input occurs during winter and spring periods, while major phytoplankton blooms take place in the spring and fall. Input of organic matter from the seagrass beds occurs during the summer and fall. The transfer of organic materials from the coastal marshes is not as well understood as that of the other sources. In general, the contribution of plant detritus to the nutrient dynamics of the estuary is extremely complex in terms of timing and

Table 8. Physical, chemical, and productivity data taken from locations along the northwest gulf coast of Florida (from R. L. Iverson and his students, unpublished data, Myers 1977). Standard deviations () are also given.

Station	Temp.	Salin.	Turb.	Light	NO_3	NO_2	PO_4	Pri. prod.	Chl-a
	°C	°/oo	JTU	ly hr^{-1}	g atm l^{-1}			mg C m^{-3} hr^{-1}	mg m^{-3}
Econfina estuary	28.4 (1.01)	26.2 (2.48)	3.15 (0.35)	26.5 (5.60)	0.32 (0.14)	0.01 (0.03)	0.04 (0.01)	6.00 (1.25)	0.61 (0.17)
F.S.U. Marine Laboratory	27.8 (1.78)	29.7 (3.53)	3.15 (0.49)	37.8 (3.73)	0.55 (0.10)	0.02 (0.02)	0.19 (0.04)	9.20 (0.58)	0.52 (0.21)
Ochlockonee River estuary (1)	28.2 (0.90)	4.20 (1.06)	4.97 (0.78)	37.9 (7.22)	1.83 (0.37)	0.05 (0.01)	0.37 (0.07)	30.8 (2.57)	2.14 (0.41)
Ochlockonee River estuary (2)	28.2 (0.80)	10.3 (0.70)	4.93 (0.61)	37.9 (7.22)	2.24 (0.83)	0.12 (0.05)	0.36 (0.09)	26.4 (4.74)	3.00 (0.51)
Apalachicola estuary (5)	27.5 (1.19)	3.74 (2.58)	16.5 (8.96)	33.9 (9.17)	3.08 (2.63)	0.15 (0.16)	0.34 (0.08)	40.3 (10.7)	5.13 (1.12)
Apalachicola estuary (2)	27.5 (1.34)	11.7 (3.26)	11.7 (6.88)	36.9 (3.50)	3.55 (3.69)	0.21 (0.16)	0.40 (0.09)	36.7 (5.81)	4.11 (0.84)

processing (Odum and Heald 1972; Odum et al. 1979).

Among the major litter producers of the Apalachicola flood plain, Cairns (1981) and Elder and Cairns (1982) found decomposition rates of floodplain leaf matter to be species-specific. Tupelo (Nyssa spp.) and sweetgum (Liquidambar styraciflua) leaves decomposed completely in 6 months. Leaves of baldcypress (Taxodium distichum) and diamond-leaf oak (Quercus laurifolia) were more resistant. Water hickory (Carya aquatica) had intermediate decomposition rates. Rates of carbon and biomass loss were linear over a 6-month period, but phosphorus and nitrogen leaching was nearly complete within a month. Periods of river flooding were particularly important for mobilization of the litterfall into the aquatic system. Flooding immerses litter material, increases decomposition rates, and provides a transport medium. Because of the high diversity of floodplain tree species, the autumn peak of leaf fall is relatively prolonged (September-December) (Figure 24). Compared to the ACF system as a whole, the Apalachicola flood plain is extremely high in nutrient yield per unit area, especially for carbon and phosphorus (Table 10). Mattraw and Elder (1982) postulated that the upper ChattahoocheeFlint watersheds yielded fewer nutrients because the 16 reservoirs act as nutrient retention ponds. Although headwater inflow provides substantial loads of dissolved nutrients to the estuary, particulate matter delivered from the river is derived almost exclusively from the Apalachicola/Chipola wetlands. Approximately 16% of the organic carbon delivered to the estuary is derived from less than 1% of the ACF basin (Mattraw and Elder 1982).

Particulate organic matter is transferred from the river to the estuary primarily during winter/spring floods, athough there is no direct correlation between microdetritus in the estuary and river flow by season (Table 5). Microdetritus flow is generally low during summer and fall periods and highest during the first river floods of winter (Figure 22). In the estuary, surface dissolved nitrogen and phosphorus concentrations peak during periods of high river flow (Estabrook 1973; Livingston et al. 1974, 1976a; Table 11). Thus, the degree and timing of river flooding on a seasonal basis determines the form and level of nutrient fluxes into the estuary from the river wetlands.

Table 9. Total annual net productivity and net input to the Apalachicola estuary (East Bay, Apalachicola Bay, St. Vincent Sound) and the Apalachicola Bay system (Apalachicola estuary, St. George Sound, Alligator Harbor). Productivity includes (metric tons) organic carbon produced by the Apalachicola River wetlands, coastal marshes, phytoplankton, and seagrass beds.

	Apalachicola estuary		Apalachicola Bay system		
Vegetation	Net in situ productivity mt C yr^{-1}	Net input mt C yr^{-1}	Net in situ productivity mt C yr^{-1}	Net input mt C yr^{-1}	Season of maximum input
Freshwater wetlands	360,000	30,000	360,000	30,000	winter/spring
Coastal marshes	37,714	37,714(?)	46,905	46,905(?)	late summer, fall(?)
Phyto-plankton	103,080	103,080	233,284(?)	233,284(?)	spring and fall
Seagrass beds	8,953	8,953	27,213	27,213	summer-fall

A review of the phytoplankton ecology of the Apalachicola estuary (Estabrook 1973; Livingston et al. 1974, 1976a; Myers and Iverson 1977) indicates that phytoplankton productivity is relatively restricted to conditions of optimum temperature and ample (available) nutrients. Such conditions occur principally in the spring, summer, and fall. Multiple regression analysis (Myers and Iverson 1977) indicated that river discharge explained 20%-50% of the variability of chlorophyll a and phytoplankton productivity. Nutrients were positively correlated with river discharge. Temperature accounted for 26% to 49% of the variability in phytoplankton productivity. Water temperature was also positively correlated with phytoplankton productivity. Wind speed was positively correlated with suspended sediments and phosphate concentrations, increases in which were followed by increases in phytoplankton productivity. Nutrient enrichment experiments indicated that nutrients are limiting only during summer and fall (Estabrook 1973) and that phosphate is the primary nutrient that limits phytoplankton productivity in East Bay and Apalachicola Bay (Myers and Iverson 1977), although both nitrates and phosphates may be limiting in summer (Livingston et al. 1974).

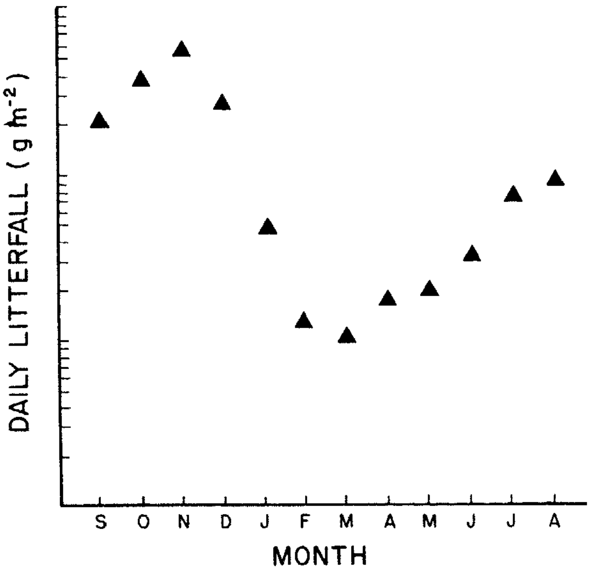


Figure 24. Monthly averages of daily litterfall on intensive transect plots across the Apalachicola wetlands (after Elder and Cairns 1982).

Recently, certain revisions have been proposed of early concepts of detritus outwelling from coastal marshes (Haines 1979). There is evidence of no net export of particulate organic matter (POM) from salt marshes under certain conditions (Woodwell et al. 1977). Odum et al. (1979) have hypothesized that net fluxes of POM from coastal marshes depend on the geomorphology of the wetland basin, the magnitude of the tidal range, and upland freshwater input. In the Apalachicola estuary, the tidal range is relatively small. Marsh distribution is limited largely to the delta area (East Bay) and lagoonal portions of the barrier islands. The considerable river runoff and the associated export of organic matter due to flooding would amplify the importance of the East Bay marshes according to the Odum model (Odum et al. 1979).

The salt marshes of the bay system contribute only a small fraction of the particulate organic loading to the bay system (Livingston et al. 1974), although such areas are important nurseries for estuarine fishes and invertebrates (Livingston 1980c). However, the marshes may play a role in the export of organic material to the bay system. Ribelin and Collier (1979) showed that local marshes export detrital aggregates or films that average 25-50 m in thickness and are produced by benthic algae rather than by microbial decomposition of the marsh plants. Tidal action lifts these films of algae out of the marshes, especially during late summer ebb flows. Thus, while the vascular tissue of the marsh grasses is decomposed beneath a layer of benthic algae, it is essentially retained within the marsh proper. Amorphous aggregates of "nanodetritus" composed of microalgae may play a more important role in the nutrient budget of the bay system than previously thought, especially during late summer and early fall periods.

The seasonal abundance and spatial distribution of nutrients and detritus in the Apalachicola Bay system result from a combination of forces, some of which are quite localized and specific in nature. For example, the timing and magnitude of localized hydrologic events such as

Table 10. Nutrient yields for various drainage areas in the Apalachicola-Chattahoochee-Flint River system. Data are presented on an areal basis (adapted from Mattraw and Elder 1982).

		Annual output minus input (metric tons)			Areal yield ($g\ m^{-2}\ yr^{-1}$)		
Drainage basin	Area (km^2)	Carbon	Nitrogen	Phos-phorus	Carbon	Nitrogen	Phos-phorus
Apalachicola-Chattahoochee-Flint	50,800	213,800	21,480	1,652	4	0.4	0.03
Chattahoochee-Flint	44,600	142,700	17,860	1.340	3	0.4	0.03
Apalachicola-Chipola	6,200	71,100	3,620	312	12	0.6	0.05
Apalachicola	3,100	41,500	1,060	237	13	0.3	0.08
Chipola	3,100	29,600	2,560	75	10	0.8	0.02
Apalachicola flood plain	393	34,300	674	206	87	1.7	0.52

passing thunderstorms, wind effects, and tidal actions are superimposed over basin characteristics such as depth and bottom morphology. These, in turn, may significantly influence larger-scale conditions such as temperature, salinity, and light penetration. The large-scale seasonal fluctuations of important climatic features, in combination with the influence of local habitat distribution and basin configuration, produce an array of processes whereby organic matter is incorporated into the estuarine food webs.

The seasonal cycle of nutrient-detritus flux in the Apalachicola estuary has been well established (Livingston et al. 1976a; Livingston and Loucks 1978). During winter and spring periods of high river flow, dissolved nutrients and particulate organic matter are washed into the estuary. The influx is concurrent with salinity reductions. Peak levels of leaf matter are present during these periods. One to two months later, wood debris and other forms of particulates appear in the bay system. In the spring, as river flow diminishes, temperature increases, and the water becomes clearer, the spring phytoplankton blooms occur. As nutrients, principally phosphorus, become limiting during summer/fall months, phytoplankton productivity becomes dependent on wind-mixed transfers of nutrients from the sediments into the water column. During the summer and early fall, local rainfall enhances nutrient enrichment. At this time, benthic macrophytes begin to die off. The peak levels of macrophyte organic debris and

Table 11. Nutrient values (winter and summer) for stations in the Apalachicola estuary (means ± one standard deviation of five stations) and River (Station 2) (Livingston et al. 1974).

		Nutrient values (g/l)	
Nutrient	Site	17 February 1973	12 July 1973
NO_3	Bay T	179.53 ± 13.11	2.25 ± 2.84
	B	186.79 ± 19.48	4.24 ± 2.25
	River	232.90	219.54
NH_4	Bay T	26.13 ± 18.53	8.05 ± 3.30
	B	38.15 ± 30.61	14.26 ± 4.40
	River	7.81	7.57
PO_4	Bay T	6.92 ± 1.17	4.03 ± .76
	B	6.93 ± 1.29	5.78 ± 1.69
	River	12.63	9.53
Silicate (SiO_4)	Bay T	2,531.80 ± 57.59	1,939.66 ± 413.15
	B	2,534.08 ± 62.88	1,216.67 ± 802.98
	River	2,632.55	3,109.12

microaggregates from the marshes occur during the fall as river flow and rainfall are minimal. By late fall (November), temperature drops and salinity coincidentally increases to an annual maximum throughout the estuary. By winter, temperature is low as river flow once again rises.

Even though the input from various sources is variable in terms of magnitude over time, the input of particulate organic matter to the estuary from all sources is fairly constant. Thus, there is a generally continuous influx of dissolved and particulate organic and inorganic matter to the estuary throughout the year; this matter is then subject to various processes, physical and biological, which are dependent on specific spatial-temporal habitat conditions.

3.3. MICROBIAL ECOLOGY

In the Apalachicola estuary, approximately 0.005% of the sediment dry weight is composed of bacterial biomass (organic carbon) and 0.09% is composed of extracellular carbohydrates (D. C. White, Florida State University; pers. comm.). Usually, these microbes are concentrated on particulate surfaces as morphologically diverse prokaryotic and microeukaryotic assemblages (White 1983). The ecological importance of microbes to the estuary is defined by microbial biomass (which forms the basis of food webs) and microbial metabolic activity (which contributes to various biogeochemical and recycling processes). White and his coworkers have quantified the biochemical "signature" components of specific microbial community associations. These components include phospholipids, adenine-containing components, muramic acid, and hydroxy fatty acids, which provide biomass estimates. Community composition has been evaluated by analysis of phospholipid alkyl fatty acids (prokaryotes microeukaryotes) and "signature" lipids (anaerobic-aerobic bacteria). Fatty acids are an excellent measure of algae, and other groups of microeukaryotes can be characterized by the polyenoic fatty acid composition (Federle et al. 1983). Nutritional status was analyzed by measurement of poly-beta-hydroxy alkonates (PHA), extracellular glycolalyn, and other microbial byproducts (White 1983). These methods were used to analyze microbial activity in the Apalachicola estuary.

A series of experiments have been carried out to learn the fate of particulate organic matter deposited in the estuary as a result of river flooding. Morrison et al. (1977) demonstrated a succession of microbiota that colonized oak leaves deposited in the estuary. Initially, colonization is by bacteria with a high ratio of muramic acid to ATP. These bacteria are succeeded by diatoms and fungal mycelia that do not contain muramic acid. Thus, initial bacterial colonization is succeeded by a community of fungi and microeukaryotes. Bobbie et al. (1978) found that microbial communities on biodegradable substrates such as leaf matter are biochemically and morphologically more diverse than those on biologically inert substrates. A 10-fold increase in biomass on the biological substrates was also noted. Grazing amphipods removed microbiota without affecting the morphology of oak leaves (Morrison and White 1980). The colonization of mixed hardwood leaves from the Apalachicola flood plain in the estuary varied more as a function of leaf surface than of location (White et al. 1977, 1979a, b). However, macroorganisms were attracted to the litter baskets as a function of location rather than microbial biomass (Livingston unpublished data).

The activities of microbes are inextricably linked with organisms at higher levels of the estuarine food web (Figure 25). Amphipod distribution was significantly correlated with concentrations of certain bacterial fatty acids (White et al. 1979a, b). Amphipods grazing at natural densities induced increases in microbial biomass, oxygen utilization, PHB synthesis, lipid synthesis, and $^{14}CO_2$ release from simple substances by microbes (Morrison and White 1980). These changes caused grazing shifts in community structure from diatom-fungal-bacterial associations to bacterially dominated ones. Within limits, grazing thus stimulates microbial growth and alters the microbial community. Indications are that organisms graze on detrital and sedimentary microbiota and substantially affect the microbial associations. Studies of microbes in the absence of their predators are not sufficient if comparisons with natural functions are intended (White 1983).

Recent studies indicate that estuarine microbial associations in polyhaline areas of the bay are actually controlled by epibenthic predators (Federle et al. 1983). Replicate areas (4 m^2) of mud-flat sediment were caged in the field to confine and exclude predators. Uncaged areas were used as controls. The microbiota of the sediments was characterized at weeks 0, 2, and 6 by measurement of the concentrations of phospholipid and analysis of the fatty acids of the microbial lipids extracted from the sediments. The data were analyzed using an analysis of variance and step-wise discriminant analysis. After 2 weeks, the microbiota of the predator-exclusion area was significantly different from that in the control and predator inclusion areas. After 6 weeks, these differences became more pronounced. There were no demonstrable caging effects that could account for the treatment differences. The results indicated that removal of predators had a profound effect on the microbial communities in estuarine sediments. Thus, we see that the intermediate trophic levels (epibenthic predators) of the estuarine food webs are part of the control mechanism that defines the structure and level of productivity of the microbial communities.

Sediments and particulate matter deposited in the estuary form a substrate for microbial productivity, which is stimulated by dissolved nutrients in various forms (Figure 25). The transformation of dissolved substances into living particulate matter produces the food of important groups of grazing organisms, which, in turn, represent the base of the detrital food webs in the estuary. Grazing and other physical disturbances enhance microbial productivity and alter the qualitative composition and succession of the microbial community. The periodic input of particulate organic matter and dissolved nutrients into a shallow bay ecosystem characterized by gradients of salinity is seen to provide the appropriate components for a highly productive system. Tidal and wind-induced currents, periodic flooding, and predation all provide a series of disturbances that, together with the periodic enrichment of the system from upland runoff, increase microbial productivity. River flow and fresh water runoff from associated wetlands, together with the shallowness of the system and tidal/wind energy subsidies, all contribute to the observed high productivity of the estuary. Considering their immense biomass and their role as processors of nutrients into biologically active material, the microbes are an important component in the energy transformations within the system.

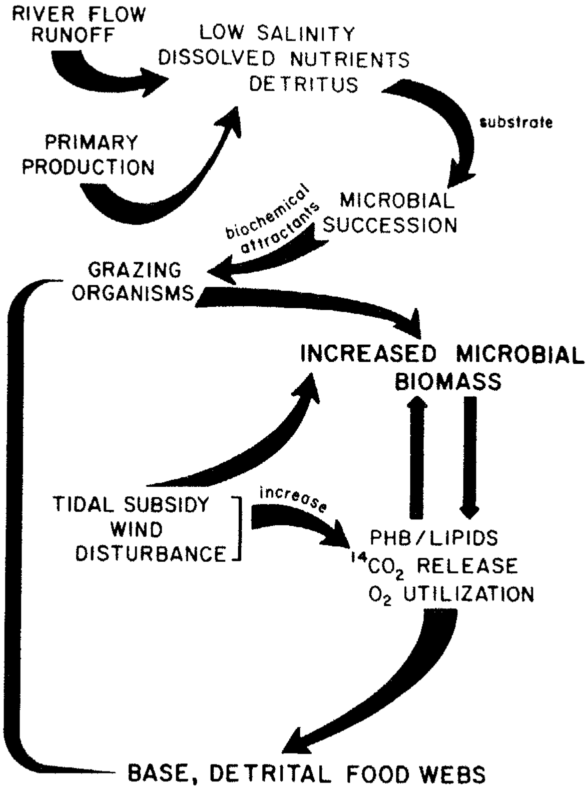


Figure 25. Tentative model of microbial interactions with various physical and biological processes in the Apalachicola River estuary (Livingston 1983c).

CHAPTER 4
SECONDARY PRODUCERS

4.1. ZOOPLANKTON

The diverse zooplankton represent an important link between the phytoplankton and higher levels of the estuarine food webs. Almost every major group of organisms is represented in the zooplankton, either as larvae or as adults; great variety is also evident in the relatively extensive size range of individuals. Zooplankton have marked differences in swimming ability and are often dispersed in patchy, somewhat irregular spatial distributions. Zooplankton repackage organic matter produced by phytoplankton into larger particles, thereby concentrating energy into forms more useful to higher predators. At the same time, they excrete nutrients that may again contribute to phytoplankton productivity.

Zooplankton (Table 12) are among the least known assemblages in the Apalachicola estuary. While the dimensions and interrelationships of the zooplankton community are relatively poorly understood in the Apalachicola estuary, certain factors such as temperature, salinity, wind, nutrients, primary (phytoplankton) productivity, and predator-prey relationships are known to contribute to processes involving this group of organisms. Net zooplankton are composed largely of holoplankton (plankton for entire life cycle; about 90%), while meroplankton (temporary plankton) constitute less than 10% of the total (Table 12; Edmisten 1979). The holoplankton are composed mainly of copepods, cladocerans, larvaceans, and chaetognaths. Copepods, notably Acartia tonsa, are dominant throughout the estuary. Apalachicola Bay supports higher numbers of copepods than any other portion of the estuary (Figure 26). Overall seasonal peaks of copepods in Apalachicola Bay are noted from March to August with minimum densities in January and February. Optimal salinities for the dominant species, Acartia tonsa, range from 16 to 22 ppt. East Bay, characterized by low but variable salinity, has the highest variability in zooplankton numbers over time. Coastal waters have been most stable in terms of seasonal changes in zooplankton abundance. Apalachicola Bay also has the highest species richness of the three areas studied. Cladocerans and chaetognaths are located primarily in coastal waters. Decapod larvae throughout the estuary are primarily crab zoeae; other zooplankton include polychaete larvae, ostracods, amphipods, isopods, mysids, echinoderms, ctenophores, and coelenterates.

The zooplankton mean standing crop (dry weight) in East Bay approximates 4.0 mg m^{-3} annually; in Apalachicola Bay, 32.1 mg m^{-3} yr^{-1}; in coastal areas, 16.7 mg m^{-3} yr^{-1}. Peak dry-weight biomass occurs in May throughout most of the study area with secondary increases during July and August (Figure 26). Zooplankton distribution is influenced by changes of temperature and salinity through time (Table 13). Edmisten (1979), using analysis of covariance with temperature and salinity as covariates for factors such as Acartia numbers, percent abundance (of Acartia), total zooplankton numbers, zooplankton biomass, and Shannon diversity, found significant station and month differences in all cases ($p < 0.02$). Temperature significantly influenced numbers of Acartia, total zooplankton numbers ($p < 0.01$), and biomass. Salinity significantly affected zooplankton numbers, biomass, and diversity ($p < 0.01$)

Table 12. Distribution of the major zooplankton groups in the Apalachicola estuary and associated coastal areas (after Edmisten, 1979). Average values are given from 1973 through 1974. The symbol (+) means 1/m^3 or less than 0.1%.

Zooplankton groups	Average 1973-1974 values					
	East Bay (1 station)		Apalachicola Bay (6 stations)		Coastal (1 station)	
	No./m^3	%	No./m^3	%	No./m^3	%
Copepods	1696	94.1	6522	80.2	2286	71.4
Acartia tonsa	1666	92.5	5546	68.2	635	19.8
Paracalanus crossirostris	2	+	352	4.3	244	7.6
Paracalanus parvus	0	0	48	0.6	342	10.7
Temora turbinata	+	+	101	1.2	567	17.7
Oithona nana	1	+	35	0.4	194	6.0
Oirhona colcarva	9	+	60	0.7	11	0.4
Pseudodiaptomus coronatus	9	+	217	2.7	17	0.5
Centropagestus	0	0	25	0.3	36	1.1
Centropagestus hamatus	0	0	15	0.2	64	2.0
Euterpina actifrons	4	0.2	25	0.3	44	1.4
Corycaeus americanus	0	0	9	0.1	28	0.8
Carycaeus amazonicus	0	0	14	0.2	17	0.5
Labidocera aestiva	0	0	60	0.7	25	0.8
Other copepods	3	0.2	21	0.3	61	1.9
Cirripedia larvae	49	2.7	949	11.7	180	5.6
Decapod larvae	50	2.8	79	1.0	26	0.8
Cladocerans	2	0.1	168	2.1	460	14.4
Molluscan larvae	+	+	166	2.1	58	1.8
Larvaceans	+	+	74	0.9	95	3.0

(continued)

Table 12. (Concluded.)

Zooplankton groups	East Bay (1 station) No./m^3	East Bay (1 station) %	Apalachicola Bay (6 stations) No./m^3	Apalachicola Bay (6 stations) %	Coastal (1 station) No./m^3	Coastal (1 station) %
	Average 1973-74 values					
Chaetognaths	0	0.0	27	0.3	52	1.6
Polychaete larvae	1	+	92	1.1	10	0.3
Fish eggs & larvae	1	+	92	1.1	10	0.3
Other zooplankton	2	0.1	35	0.4	16	0.5

(Table 13). Although direct correlations were lacking, there was a strong positive relationship between salinity and diversity. Temperature and salinity had no significant effect (at the 0.05 level) on the various dependent variables in East Bay or coastal areas.

The general lack of definitive statistical relationships between individual zooplankton indicators or indices and dominant physical variables such as temperature and salinity reflects the considerable diel, seasonal, and annual variability in the distribution of zooplankton in the estuary. Other factors are almost certainly important to such distribution during various periods of the year. Peaks of zooplankton biomass tend to be associated in some way with phytoplankton peaks, especially in Apalachicola Bay and coastal areas (Figure 26). Predator-prey relationships may play an important role in zooplankton distribution and abundance throughout the year. Such trends are obviously affected by habitat differences, however. The relatively small East Bay is characterized by low salinity and high sedimentation and turbidity. Salinity changes, derived largely from river flow and storm-water runoff, are rapid. Most of the peaks of zooplankton abundance correspond to salinity increases in this area. The copepod Acartia tonsa has a major influence on abundance curves and diversity indices in East Bay; it averages 92% of the zooplankton taken throughout the year.

Coastal areas are physically stable when compared to the estuary; salinity varies little throughout the year in the offshore systems. In such areas, zooplankton standing crop is generally higher than that in East Bay. Diversity tends to increase because Acartia averages

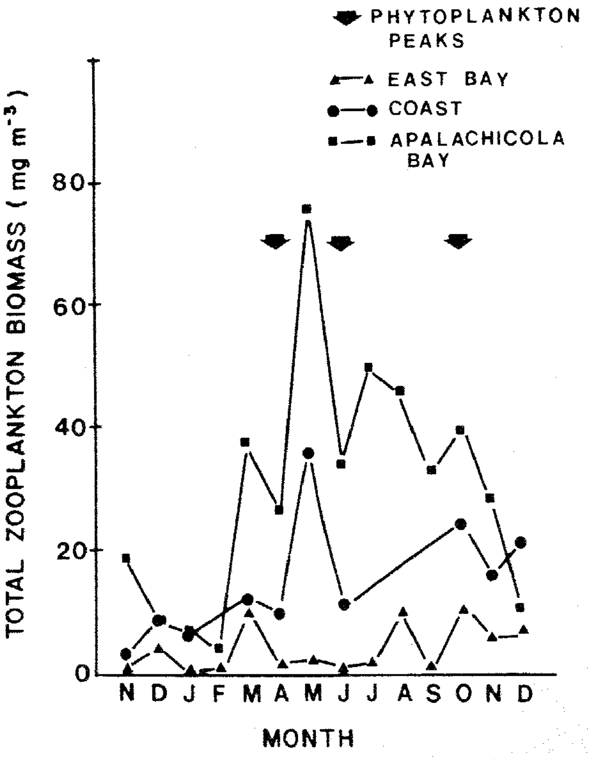


Figure 26. Seasonal distribution of zooplankton biomass in the Apalachicola estuary and associated coastal areas during 1974 (after Edmisten 1979).

Table 13. Pearson correlation coefficients (r) for significant ($p < 0.05$) zooplankton relationships in East Bay, Apalachicola Bay, and coastal areas (Edmisten 1979).

Variable	East Bay	Apalachicola Bay	Coastal areas
Temperature vs.			
Acartia tonsa	--	0.45	--
Total zooplankton	--	0.58	--
Zooplankton biomass	--	0.58	0.46[a]
Salinity vs.			
Acartia tonsa	0.45	--	--
% Acartia tonsa	--	-0.30	--
Total zooplankton	--	0.31	--
Zooplankton biomass	0.50[a]	0.40	--
Zooplankton diversity	--	0.51	--

[a] Significant at $p < 0.10$.

less than 20% of the overall abundance. The evenness factor is higher in the more stable marine environment with increased representation by cladocerans, decapod larvae, and other copepods (i.e., Temora turbinata, Paraclinus parvus, P. crassirostris, Oithona nana) (Edmisten 1979). Zooplankton biomass in coastal waters is correlated with temperature ($r = 0.46$).

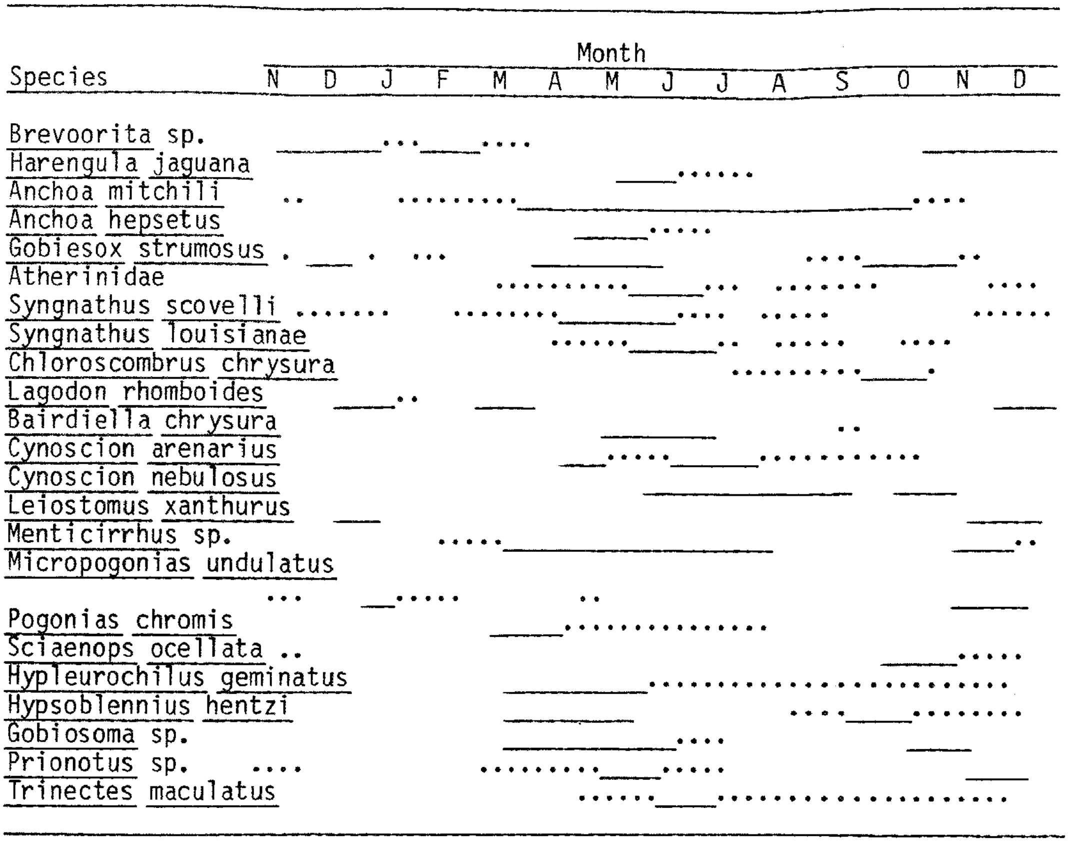
Zooplankton in Apalachicola Bay has characteristics of both the inshore and offshore components (Edmisten 1979). Overall numerical abundance was highest in Apalachicola Bay (Figure 26). Numbers of Acartia tonsa and total zooplankton abundance and biomass follow general seasonal trends of water temperature. Salinity affects the spatial distribution of zooplankton in Apalachicola Bay at any given time. Salinity increases appear to be associated with decreased relative abundance of Acartia tonsa. At low salinities, lower numbers of Acartia are taken although this species still comprise a higher percentage of the overall zooplankton assemblage at such times. Thus, while temperature influences overall trends of abundance through time, salinity is associated with the spatial distribution and relative abundances of zooplankton in Apalachicola Bay at any given time.

4.2. LARVAL FISHES

Planktonic fish larvae, derived from either demersal or planktonic eggs, are common among various marine teleost species. While it is well known that estuaries have relatively high levels of phytoplankton productivity and that such levels are necessary for feeding aggregations of zooplankton (Mann 1982), the relationship of such high productivity to developing stages of marine fishes is not quite as well known. Lasker (1975) has shown that larvae of the northern anchovy (Engraulis mordax) feed on phytoplankton and that there is a direct association between feeding activity and phytoplankton concentration. Thus, there may be close relationships between the highly productive inshore waters of the Gulf and developing stages of various teleost fishes.

The relatively high numbers of ichthyoplankton in the Apalachicola estuary indicate the importance of this system as a nursery for fishes. The most abundant planktonic form is the bay anchovy (Anchoa mitchilli), which accounts for 92% of the eggs and 75% of the larvae taken during a year-long survey (Tables 14, 15; Blanchet 1978). Other relatively abundant larvae include silversides

Table 14. Distribution of ichthyoplankton in the Apalachicola estuary as indicated by the presence of eggs and larvae. Dotted lines indicate sparse breeding activity. Solid lines indicate widespread and/or intensive breeding as indicated by large numbers of eggs or larvae. Data are taken from Blanchet (1978).



(Atherinidae), skilletfish (Gobiesox strumosus), gobies (Gobiosoma spp.), and various warm-season spawners. Winter to early spring types are dominated by Atlantic croaker (Micropogonias undulatus), spot (Leiostomus xanthurus), and Gulf menhaden (Brevoortia patronus). Various other sciaenid larvae are taken, including red drum (Sciaenops ocellatus), southern kingfish (Menticirrhus americanus), and the sand seatrout (Cynoscion arenarius). The abundance of total larvae is highest in western portions of Apalachicola Bay, largely because of the high numbers of Anchoa mitchilli.

Eggs of most species (except anchovies) are generally found offshore, indicating that few species actually spawn within the estuary. The developing stages of fishes usually appear within the bay system at different times of the year. Areas in the estuary away from the passes are characterized by the presence of species that spawn within the bay (anchovies, atherinids, blennies and gobies). Relatively large numbers of goby larvae are found at West Pass.

With the exception of the gulf pipefish (Syngnathus scovelli), which appears to breed throughout the year, most species have specific breeding seasons extending from one to several months. Anchovies have an extended breeding season although they are considered warm-season spawners. Two peaks in total larval abundance (April-May and July-September) occur (Table 15). Larval abundance and species richness are higher during spring months, however. Peak numbers of

Table 15. Numbers of ichthyoplankton with larvae and without anchovy larvae (in parenthesis) taken at various stations within the Apalachicola estuary (after Blanchet 1978).

	Station							
Date	3	1C	2	offshore	1B	Inshore Little St. George	1A	1
11/21/73	0.8 (0.8)	8.4 (8.4)	2.7 (2.7)	0.8 (0.8)	4.1 (4.1)	1.5 (1.5)	6.2 (6.2)	1.7 (1.7)
12/9		0.7 (0.7)		1.4 (1.4)	1.9 (1.9)	3.4 (3.4)	4.3 (4.3)	0.7 (0.7)
12/27	0.3 (0.3)	1.3 (1.3)	1.0 (1.0)	11.3 (11.3)	12.0 (12.0)	0.4 (0.4)	0.7 (0.7)	-- --
1/5/74	3.0 (3.0)				-- --			
1/12	-- --	0.3 (0.3)	-- --	-- --			-- --	12.3 (12.3)
2/26	6.8 (0.4)	1.2 (0.7)	4.7 (4.2)			0.4 (0.0)	3.1 (1.2)	2.2 (2.0)
2/27	0.5 (0.5)	0.8 (0.8)	0.2 (0.2)		2.5 (2.2)	7.1 (7.1)	1.4 (1.4)	0.5 (0.3)
3/28	14.3 (1.8)	61.3 (40.3)	115.1 (0.9)	10.1 (6.1)	47.7 (7.3)	265.2 (3.0)	222.6 (33.2)	298.4 (10.2)
4/20	-- --	-- --	90.4 (15.8)	-- --	-- --	-- --	-- --	241.5 (24.1)
4/26	13.4 (8.4)	163.0 (7.8)	171.0 (25.3)	2.4 (1.7)	84.0 (7.7)	2580.8 (11.5)	1010.6 (25.4)	108.0 (8.4)
5/17	98.9 (52.8)	70.5 (51.0)	8.3 (0.0)	62.8 (52.7)	241.5 (50.6)	1325.2 (31.2)	1234.5 (283.8)	54.0 (12.2)
6/18	34.7 (1.6)	3.5 (0.4)	32.4 (4.0)	55.5 (50.6)	16.1 (0.7)	136.7 (16.1)	2.3 (1.7)	5.3 (1.3)
7/18	0.5 (0.0)	-- --	-- --	3.5 (3.5)	9.5 (2.4)	20.3 (5.1)	1119.4 (38.7)	61.0 (0.0)
8/22	16.4 (9.9)	150.7 (4.1)	72.8 (23.3)	-- --	16.2 (1.6)	141.1 (9.7)	75.5 (10.3)	18.1 (0.7)
9/12	5.5 (3.7)	194.9 (92.0)	99.2 (2.1)	746.6 (738.2)	217.8 (75.1)	51.1 (6.9)	1032.6 (20.6)	46.6 (0.0)

(continued)

Table 15. (Concluded.)

	Station							
Date	3	1C	2	Offshore	1B	Inshore Little St. George	1A	1
10/17	5.1 (4.1)	4.1 (4.1)	2.5 (1.4)	7.8 (7.8)	2.4 (2.4)	4.2 (4.2)	3.5 (3.2)	3.8 (0.8)
11/7	0.6 (0.6)				0.5 (0.5)	0.2 (0.2)	0.2 (0.2)	-- --
12/3	2.8 (2.8)		0.5 (0.5)	2.5 (2.5)	0.7 (0.7)	1.6 (1.6)	7.0 (7.0)	10.1 (9.8)

ichthyoplankton (25.8 m^{-3}) are found just beyond Sike's Cut in April.

Fishes that live in a given estuary can be organized into various categories according to their life history (McHugh 1967). Estuarine-dependent forms include truly estuarine species, anadromous and catadromous species, marine species that live and often spawn offshore but use the estuary as a nursery, and marine species that enter the estuary seasonally as adults but remain offshore as juveniles. In the Apalachicola estuary, the estuarine eggs and larvae are dominated by one estuarine species, the bay anchovy. At stations that are not near the passes (3, 2, 1; Table 15) numbers of larvae of species other than anchovies are usually low. Such areas tend to be dominated by species that spawn within the estuary (i.e., atherinids, blennies, skilletfish). Blanchet (1978) attributed the low number of eggs in the estuary to the flushing of the bay system. It is also possible that the generally low salinities within the estuary prevented spawning by most species. Overall, the pattern and distribution of the fish larvae within the bay system would indicate that, while specific causative factors remain unknown, the primary function of the bay is its use as a nursery by true estuarine species and marine species that spawn offshore.

4.3. BENTHOS

Considerable information is available concerning benthic macroinvertebrates in estuarine and coastal systems (Mann 1982). Benthic infauna, which live within the sediments, are usually separated according to size into macrobenthos, meiobenthos, and microbenthos. Although there are differing opinions as to the exact dimensions of each size category, most workers agree that the macrobenthos includes those organisms taken in 250-500 micrometer (m) sieves. Meiobenthic organisms are those taken between 62 m and 250 m, and organisms smaller than 62 m are classified as microbenthos. Macroinvertebrates living just above the sediments or at the sediment-water interface are called epifauna or epibenthic invertebrates. These organisms will be treated as nekton in this review.

The relative composition of any given benthic macroinvertebrate collection depends to a considerable degree on the form of sampling gear. In the Apalachicola Bay system, benthic macroinvertebrates have been taken by cores and ponars (McLane 1980; Mahoney and Livingston 1982), leaf packs (Livingston et al. 1977), otter trawls (Livingston 1976a, b; Livingston et al. 1976b), and dredge-nets and seines (Purcell 1977). The benthic macroinvertebrates in the Apalachicola Bay system represent a diverse fauna (Table 16) with distinct patterns of temporal and spatial distribution (Livingston et al. 1977). Although considerable seasonal and year-to-year variation in species composition and relative abundance is found at any given sampling area, certain trends are

Table 16. Invertebrates taken in cores, leaf-baskets, dredge nets, and otter trawls in the Apalachicola Bay system (1975-1983). Data are derived from Livingston et al. (1976c, 1977), McLane (1980), Purcell (1977), Mahoney (1982), and Sheridan (1978, 1979). Recent taxonomic updates are noted in Livingston et al. (1983).

- Phylum - Mollusca
  - Class - Gastropoda
    - Subclass - Prosobranchia
      - Order - Archaeogastropoda
        - Family - Neritidae
          - *Neritina reclivata*
      - Order - Mesogastropoda
        - Family - Calyptraeidae
          - *Crepidula fornicata*
          - *Crepidula plana*
        - Family - Naticidae
          - *Polinices duplicatus*
        - Family - Epitoniidae
          - *Epitonium rupicola*
        - Family - Hydrobiidae
          - *Texadina sphinctostoma*
        - Family - Cerithiidae
          - *Bittium varium*
      - Order - Neogastropoda
        - Family - Fasciolariidae
          - *Fasciolaria tulipa*
        - Family - Melongenidae
          - *Busycon contrarium*
          - *Busycon spiratum*
          - *Melongena corona*
        - Family - Muricidae
          - *Urosalpinx perrugata*
        - Family - Columbellidae
          - *Anachis avara*
          - *Mitrella lunata*
        - Family - Olividae
          - *Olivella* sp.
        - Family - Thaididae
          - *Thais haemastoma*
        - Family - Marginellidae
          - *Prunum apicinum*
    - Subclass - Opisthobranchia
      - Order - Cephalaspidea
        - Family - Bullidae
          - *Bulla striata*
        - Family - Retusidae
          - *Retusa canaliculata*
        - Family - Pyramidellidae
          - *Odostomia laevigata*
      - Order - Anaspidea
        - Family - Aplysiidae
          - *Aplysia willcoxi*
      - Order - Nudibranchia
        - Nudibranch sp.
  - Class - Bivalvia
    - Bivalve sp. ?
    - Bivalve sp. x
    - Order - Mytiloida
      - Family - Mytilidae
        - *Amygdalum papyria*
        - *Brachidontes exustus*
        - *Brachidontes* sp.
    - Order - Arcacea
      - Family - Arcidae
        - *Anadara brasiliana*
        - *Anadara* sp.
        - *Anadara transversa*
    - Order - Ostreoida
      - Family - Ostreiidae
        - *Crassostrea virginica*
    - Order - Veneroida
      - Family - Cyrenoididae
        - *Pseudocyrena floridana*
      - Family - Mactridae
        - *Mactra fragilis*
        - *Mulinia lateralis*
        - *Rangia cuneata*
      - Family - Solenidae
        - *Ensis minor*
      - Family - Tellinidae
        - *Macoma balthica*
        - *Macoma mitchelli*
        - *Tellina texana*
      - Family - Semelidae
        - *Abra aequalis*
      - Family - Solecurtidae
        - *Tagelus plebeius*
      - Family - Dreissenidae
        - *Mytilopsis leucophaeta*
      - Family - Corbiculidae
        - *Polymesoda caroliniana*
      - Family - Cardiidae
        - *Dinocardium robustum*
  - Class - Cephalopoda
    - Order - Teuthoidea (= Decapoda)
      - Family - Loliginidae
        - *Lolliguncula brevis*
  - Class - Polyplacophora
    - Family - Chitonidae
      - *Chiton tuberculatus*
- Phylum - Annelida
  - Class - Polychaeta
    - Polychaete (unident.)

(continued)

Table 16. (Continued.)

- Order - Orbiniida
  - Family - Orbiniidae
    - *Haploscoloplos foliosus*
    - *Haploscoloplos fragilis*
    - *Scoloplos rubra*
  - Family - Paraonidae
    - *Paraonis* sp.
- Order - Spionida
  - Family - Spionidae
    - *Carazziella hobsonae*
    - *Paraprionospio pinnata*
    - *Spiophanes bombyx*
    - *Streblospio benedicti*
    - *Scololepis texana*
  - Family - Magelonidae
    - *Magelona polydentata*
    - *Magelona* sp.
  - Family - Cirratulidae
    - *Chaetozone* sp.
- Order - Capitellida
  - Family - Capitellidae
    - *Capitella capitata*
    - *Capitella* sp.
    - *Capitellides jonesi*
    - *Heteromastus filiformis*
    - *Mediomastus ambiseta*
    - *Notomastus hemipodus*
    - *Polydora ligni*
    - *Polydora socialis*
    - *Polydora websteri*
  - Family - Arenicolidae
    - *Arenicola cristata*
  - Family - Maldanidae
    - *Branchioasychis americana*
    - *Clymenella* sp.
- Order - Phyllodocida
  - Family - Phyllodocidae
    - *Eteone heteropoda*
    - *Paranaitis speciosa*
    - *Phyllodoce fragilis*
  - Family - Hesionidae
    - *Gyptis brevipalpa*
    - *Ophiodromus abscura*
    - *Podarke* sp.
  - Family - Pilargiidae
    - *Ancistrosyllis hartmanae*
    - *Ancistrosyllis* sp.
    - *Parandalia americana*
    - *Sigambra bassi*
  - Family - Syllidae
    - *Pionosyllis* sp.
    - *Syllidae* sp.
  - Family - Nereididae
    - *Laeonereis culveri*
    - *Nereid* sp. A
    - *Nereis succinea*
    - *Stenoninereis martini*
  - Family - Glyceridae
    - *Glycera americana*
  - Family - Goniadidae
    - *Glycinde solitaria*
- Order - Amphinomida
  - Family - Amphinomidae
    - *Amphinome rostrata*
- Order - Terebellida
  - Family - Amphictenidae
    - *Cistena gouldi*
  - Family - Ampharetidae
    - *Hobsonia florida*
    - *Melinna maculata*
- Order - Eunicida
  - Family - Onuphidae
    - *Diopatra cuprea*
  - Family - Eunicidae
    - *Marphysa sanguinea*
  - Family - Lumbrineridae
    - *Lumbrineris* sp.
    - *Lumbrineris tenuis*
- Order - Sabellida
  - Family - Sabellidae
    - *Fabricia* sp.

Class - Oligochaeta

- Oligochaeta spp.
- Order - Haplotaxida
  - Family - Tubificidae
    - *Limnodriloides* sp.
    - *Peloscolex benedeni*
    - *Phallodrilus* sp.
    - *Tubificoides heterochaetus*
    - *Tubificoides* sp.
  - Family - Naididae
    - *Paranais litoralis*

(continued)

Table 16. (Continued.)

Phylum - Arthropoda
Subphylum - Crustacea
Class - Malacostraca
Superorder - Peracarida
Order - Mysidacea
Mysidopsis almyra
Mysidopsis bahia
Mysidopsis bigelow
Taphromysis bowmani
Taphromysis louisianae
Order - Tanaidacea
Hargeria rapax
Order - Cumacea
Cumacea sp.
Order - Isopoda
Family - Anthuridae
Cyathura polita
Xenanthura brevitelson
Family - Sphaeromatidae
Cassidinidea ovalis
Sphaeroma quadridentatum
Sphaeroma terebrans
Family - Idoteidae
Edotea montosa
Edotea sp. (cf. *montosa*)
Erichsonella sp. (cf. *filiformis*)
Family - Munnidae
Munna reynoldsi
Order - Amphipoda
Suborder - Caprellidea
Family - Caprellidae
Paracaprella tenuis
Suborder - Gammaridea
Family - Haustoridae
Lepidactylus sp.
Haustoridae sp.
Family - Gammaridae
Gammarus macromucronatus
Gammarus mucronatus
Gammarus sp.
Family - Bateidae
Batea catharinensis
Carinobatea sp.

Family - Ampeliscidae
Ampelisca abdita
Ampelisca vadorum
Ampelisca verrilli
Family - Melitidae
Melita appendiculata
Melita elongata
Melita fresnelii
Melita intermedius
Melita longisetosa
Melita nitida
Melita sp.
Family - Ischyroceridae
Cerapus sp. (cf. *tubularis*)
Erichthonius brasiliensis
Erichthonius sp. 2
Family - Aoridae
Grandidierella bonnieroides
Grandidierella sp.
Lembos sp.
Microdeutopus sp.
Family - Corophiidae
Corophium louisianum
Corophium sp.
Family - Crangonyctidae
Crangonyx richmondensis
Family - Amphilochidae
Gitanopsis sp.
Family - Ampithoidae
Cymadusa compta
Cymadusa sp.
Family - Talitridae
Orchestia grillus
Orchestia uhleri

(continued)

Table 16. (Continued.)

- Superorder - Eucarida
  - Order - Decapoda
    - Family - Penaeidae
      - *Penaeus aztecus*
      - *Penaeus duorarum*
      - *Penaeus setiferus*
      - *Trachypenaeus constrictus*
      - *Trachypenaeus similis*
      - *Xiphopenaeus kroyeri*
      - *Sicyonia brevirostris*
      - *Sicyonia dorsalis*
    - Family - Sergestidae
      - *Acetes americanus*
    - Family - Palaemonidae
      - *Leander tenuicornis*
      - *Macrobrachium ohione*
      - *Palaemonetes intermedius*
      - *Palaemonetes pugio*
      - *Palaemonetes vulgaris*
      - *Periclimenes americanus*
      - *Periclimenes longicaudatus*
    - Family - Alpheidae
      - *Alpheus armillatus*
      - *Alpheus formosus*
      - *Alpheus heterochaelis*
      - *Alpheus normanni*
    - Family - Ogyrididae
      - *Ogyrides limicola*
    - Family - Hippolytidae
      - *Hippolyte zostericola*
      - *Latreutes parvulus*
      - *Lysmata wurdemanni*
      - *Thor dobkini*
      - *Tozeuma carolinense*
    - Family - Processidae
      - *Ambidexter symmetricus*
      - *Processa fimbriata*
      - *Processa hemphilli*
      - *Processa* sp.
    - Family - Cambaridae
      - *Procambarus penaensalanus*
    - Family - Callianassidae
      - *Callianassa atlantica*
      - *Callianassa jamaicense*
    - Family - Paguridae
      - *Pagurus bonairensis*
      - *Pagurus longicarpus*
      - *Pagurus pollicaris*
    - Family - Majidae
      - *Libinia dubia*
      - *Libinia emarginata*
      - *Metaporhaphis calcarata*
      - *Podochela riisei*
    - Family - Portunidae
      - *Callinectes sapidus*
      - *Callinectes similis*
      - *Ovalipes guadulpensis*
      - *Portunus gibbesii*
    - Family - Xanthidae
      - *Eurypanopeus depressus*
      - *Hexapanopeus angustifrons*
      - *Menippe mercenaria*
      - *Neopanope packardii*
      - *Neopanope texana*
      - *Panopeus herbstii*
      - *Rhithropanopeus harrisii*
    - Family - Grapsidae
      - *Sesarma cinereum*
    - Family - Ocypodidae
      - *Uca minax*

Table 16. (Concluded.)

Family - Porcellanidae
Petrolisthes armatus
Clibanarius vittatus
Family - Leucosiidae
Persephona mediterranea
Superorder - Hoplocarida
Order - Stomatopoda
Family - Squillidae
Squilla empusa
Class - Ostracoda
Ostracoda sp.
Class - Branchiura
Argulus sp.
Subphylum - Hexapoda
Class - Insecta
Insect larvae (several unident.)
Order - Diptera
Family - Chironomidae
Chironomidae
Ablabesmia sp.
Chironomus sp.
Cladotanytarsus sp.
Clinotanypus sp.
Coelotanypus sp.
Cryptochironomus fulvus
Cryptochironomus sp.
Dicrotendipes sp.
Glyptotendipes sp.
Harnischia sp.
Microtendipes sp.
Nanocladius sp.
Orthocladius sp.
Parachironomus sp.
Polypedilum sp.
Procladius sp.
Procladius sp.
Tanypus sp.
Tanytarsus sp.
Family - Heleidae
Bezzia sp.
Order - Odonata
Suborder - Anisoptera
2 unident. spp.
Suborder - Zygoptera
1 unident. sp.
Order - Ephemeroptera
Family - Caenidae
Caenis sp.
Family - Heptageniidae
1 unident. sp.
Family - Baetidae
Callibaetis sp.
Order - Plecoptera
1 unident. sp.
Order - Hemiptera
Family - Corixidae
1 unident. sp.
Order - Lepidoptera
Family - Pyralidae
Nymphula sp.

Phylum - Echinodermata
Echinarachinus parma
Echinaster sp.
Hemipholus elongata
Luidia clathrata
Ophiothrix angulata

evident. Infaunal numerical abundance and dry weight biomass (Figure 27) in East Bay, Apalachicola Bay, and St. George Sound usually peak during winter and early spring months (Mahoney and Livingston 1982; Livingston 1983b, c; Livingston et al. 1983). Numbers of infaunal species reach the highest levels during winter and spring months (Figure 27). Monthly variance follows the trends of numerical abundance and species richness. Sheridan and Livingston (1983), working in shoal grass (*Halodule wrightii*) meadows on the north shore of St. George Island, found infaunal densities exceeding 104,000 individuals m^{-2} in April 1975.

Spatial gradients of salinity, productivity, and sediment types influence the infaunal community composition (Livingston et al. 1983). While physical factors appear to predominate in the infaunal community relationships in the upper estuary near the river mouth, other factors such as predation pressure and competition may be important determinants of such interspecific interactions in polyhaline portions of the bay system (Livingston et al. 1983).

Overall, infaunal species fall into four general categories: crustaceans, polychaetes, mollusks, and a miscellaneous group that includes insect larvae and oligochaete worms. Predominant species in East Bay include *Mediomastus ambiseta*, *Steblospio benedicti*, *Heteromastus filiformis*, *Ampelisca vadorum*, *Hobsonia florida*, *Hargeria rapax*, and *Grandidierella bonnieroides*. The tanaid *Hargeria rapax* is most abundant in or near grass beds in Apalachicola Bay from February to April. Other dominant grass-bed species include *Heteromastus filiformis* and *Hobsonia florida*. The amphipod *Grandidierella bonnieroides* ranges throughout the East Bay-Apalachicola Bay complex, with peak abundances during early spring and late summer. Soft-sediment polyhaline assemblages are dominated by *Mediomastus ambiseta*, *Paraprionospio pinnata*, and immature tubificid worms (Livingston et al. 1983). The sedentary polychaete *Heteromastus filiformis* is largely restricted to grass beds and is most abundant during April. The amphipod *Ampelisca vadorum* occurs primarily in the Apalachicola Bay seagrass meadows during winter and early fall months. The polychaete *Mediomastus ambiseta* is found in fine mud bottoms throughout the bay, with peaks of abundance in March. The ubiquitous polychaete *Streblospio benedicti* utilizes a variety of habitats throughout the estuary, with peak abundance during winter months. The polychaete *Hobsonia florida* is found throughout the bay from grass beds to soft sediment (unvegetated areas). Peak abundance is noted during early fall months. In general, the polychaete species are eurythermal and euryhaline and include selective and nonselective deposit feeders. Sheridan and Livingston (1983) noted that the dominant tanaids and amphipods are detritivores and deposit feeders.

Because considerable amounts of detrital matter are usually swept into the estuary by the Apalachicola River during winter-spring periods, the organic litter forms an important habitat for various macroinvertebrates. Organisms associated with leaf litter and detritus have been described by Livingston (1978) and Livingston et al. (1976b, 1977). Litter fauna is dominated by isopods, amphipods, and decapods, which utilize particulate matter and litter-associated microbes for food and/or shelter. Dominant species in East Bay and Apalachicola Bay include *Neritina reclivata*, *Palaemonetes* spp., *Corophium louisianum*, *Gammarus* spp., *Grandidierella bonnieroides*, *Melita* spp., and *Munna reynoldsi*. Salinity appears to be an important organizing feature of litter associations (Livingston unpubl.).

Life-history strategies of dominant infaunal and litter-associated macroinvertebrate populations are dictated by substrate type, temperature, salinity, and biological factors (Table 17). Most dominant infaunal populations reach peaks of numerical abundance during late winter and spring periods of low salinity and increasing temperature. Most such species are euryhaline and eurythermal. Reproduction of some infaunal populations occurs throughout the year while others reproduce only between spring and fall. Individual species have different patterns of distribution within the estuary depending on recruitment patterns and response

Table 17. General abundance information and natural history notes for the dominant organisms (infauna, epibenthic fishes, and invertebrates) in the Apalachicola estuary. A comparison of species characteristics with observations in other gulf estuaries is also given. References for such notes are listed.

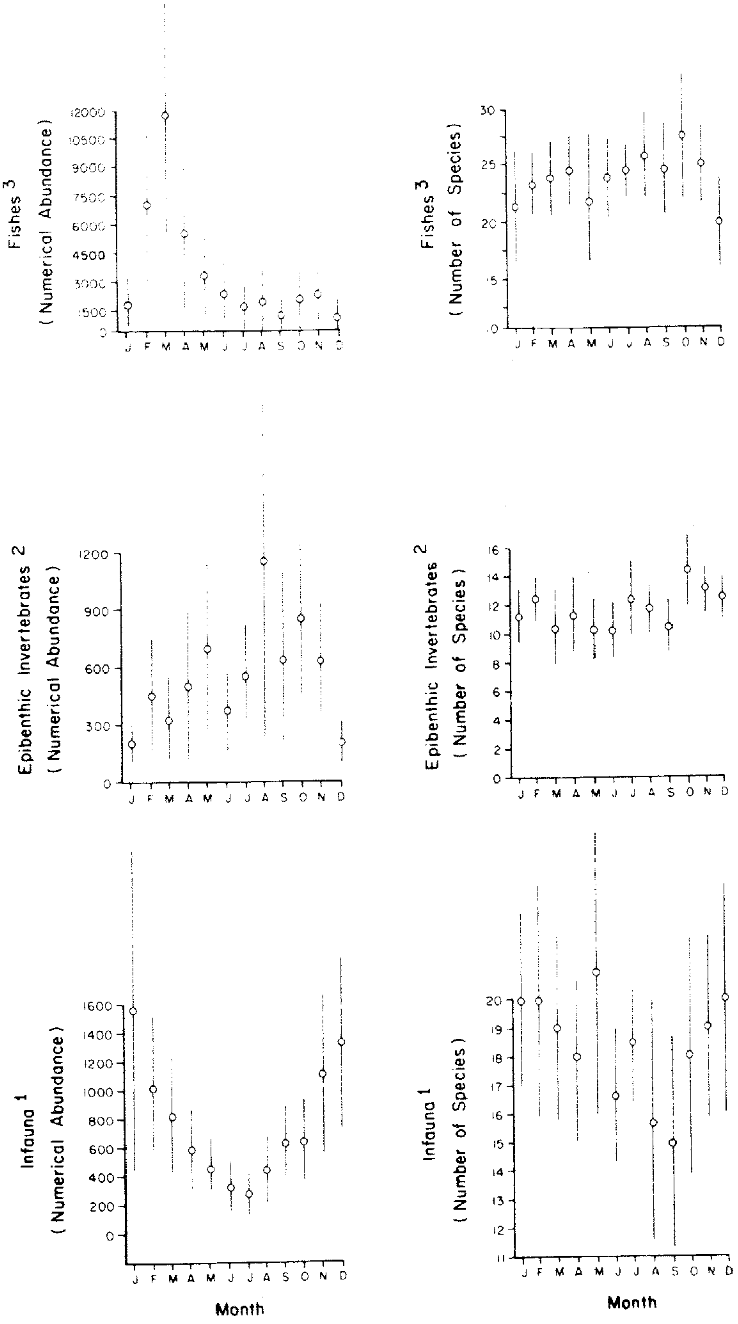
Species	Peak abundance in gulf estuaries	Peak abundance Apalachicola system	Salinity and temperature tolerance	Reproductive patterns in gulf estuaries	Reproductive patterns in Apalachicola system	References
NEKTONIC INVERTEBRATES						
Penaeus setiferus (White shrimp)	Spring and fall	Summer and fall	High; prefer low salinity. Direct relationship of size with salinity	Spawn in gulf in early spring and fall. Postlarvae and juveniles enter bays in spring	Juveniles enter bay in spring, summer	Gunter 1950; Linder and Anderson 1956; Ingle 1957; Loesch 1965; Williams 1956; Copeland and Truitt 1966; Christmas et al. 1966; Perez Farfante 1969; Perret 1971; Gaidry and White 1973; Copeland and Bechtel 1971, 1974; Stokes 1974; Swingle and Bland 1974.
Penaeus duorarum (Pink shrimp)	Late summer, fall	July - November	High; prefer high salinity, usually dominant at salnities 18 ppt	Spring and summer spawning; post larval peaks, August - September	Juvenile stages enter bay during summer	
Penaeus aztecus (Brown shrimp)	Late spring, summer	Late spring, early summer	High; prefer low salinities 10-20 ppt	Postlarvae enter bays late winter-spring; juveniles early summer	Juveniles in bay during early summer	
Palaemonetes pugio (Grass shrimp)	February, March	February - April	High; prefer low salinities 10-20 ppt	Spawn in summer and fall		Hoese and Jones 1963; Wood 1967; Rouse 1969; Perret 1971; Swingle and Bland 1974.
Callinectes sapidus	Large crabs	Winter - ?	High; direct	Spring, summer	Young enter bay	Gunter 1950; Hedgepeth 1950; Darnell 1959; Tagatz 1968; More 1969; King 1971; Lyons et al. 1971; Copeland and Bechtel 1974.
Lolliguncula brevis (Brief squid)	Varied, early spring to late	Summer, fall	Prefer high salinity, 15 ppt	Suggested estuarine spawning throughout the year		Perret 1971; Swingle 1971; Swingle and Bland 1974; Laughlin 1979; Laughlin and Livingston 1981.
BENTHIC INVERTEBRATES						
Hargeria rapax (tanaid)		February - April	Salinity range 6.3-26.8 ppt Temperature range 11.5-32.5°C	Hermaphroditic	Hermaphroditic; ovigerous females noted throughout the year	Livingston 1978; Livingston et al. 1976b, 1977; McLane 1980; Sheridan and Livingston 1983.
Grandidierella bonnieroides (amphipod)		March - August	Salinity range 0-26.8 ppt Temperature range 6.0-32.5°C .		Ovigerous females noted from November	Livingston 1978; Livingston et al. 1976b, 1977; McLane 1980; Sheridan and Livingston 1983.

Heteromastus filiformis (polychaete)	April	April	Salinity range 6.3-26.8 ppt Temperature range 11.5-32.5°C			Livingston 1978; Livingston et al. 1976b, 1977; McLane 1980; Sheridan and Livingston 1983.
Mediomastus ambiseta (polychaete)		March	Salinity range 0-18.8 ppt Temperature range 6-31°C		Ovigerous females noted all months except August with peaks in February	Livingston 1978; Livingston et al. 1976b, 1977; McLane 1980; Sheridan and Livingston 1983.
Ampelisca vadorum (amphipod)		February	Salinity range 6.3-26.8 ppt Temperature range 6-32.5°C	Year-round reproduction	Year-round reproduction	Livingston 1978; Livingston et al. 1976b, 1977; McLane 1980; Sheridan and Livingston 1983.
Streblospio benedicti (polychaete)		August - November	Salinity range 0-26.8 ppt Temperature range 6-32.5°C			Livingston 1978; Livingston et al. 1976b, 1977; McLane 1980; Sheridan and Livingston 1983.
Hypaneola florida (polychaete)		September	Salinity range 0-26.8 ppt Temperature range 6-32.5°C		Ovigerous females noted May-July	Livingston 1978; Livingston et al. 1976b, 1977; McLane 1980; Sheridan and Livingston 1983.
Cerapus sp. (amphipod)		Late spring	Salinity range 0-10 ppt Temperature range 10-30°C		Ovigerous females noted July - September	Livingston 1978; Livingston et al., 1976b 1977; McLane 1980; Sheridan and Livingston 1983; Sheridan 1979.
Dicrontendipes sp. (dipteran)		Late fall, winter	Salinity range 0-10 ppt Temperature range 6-31°C		Ovigerous females noted April, August, October	Sheridan 1979; Livingston 1978; Livingston et al. 1976b, 1977; McLane 1980; Sheridan and Livingston 1983.
					Ovigerous females noted in Spring	Sheridan 1979; Livingston 1978; Livingston et al. 1976b, 1977; McLane 1980; Sheridan and Livingston 1983.
Aricidea fragilis (polychaete)		April	Salinity range 6.3-26.8 ppt Temperature range 11.5-32.5°C		Ovigerous females noted in May, October	Sheridan 1979; Livingston 1978; Livingston et al. 1976b, 1977; McLane 1980; Sheridan and Livingston 1983.
Melita nitida (amphipod)		Late spring, early winter	Salinity range 20-33 ppt Temperature range 21-32°C		Ovigerous females noted in Spring	Sheridan 1979; Livingston 1978; Livingston et al. 1976b, 1977; McLane 1980; Sheridan and Livingston 1983.
Melita elongata (amphipod)		Spring	Salinity range 20-32 ppt Temperature range 20-32°C	Long spawning season with juvenile recruitment throughout year	Compatible with previous studies	Gunter 1945; Reid 1954; Springer and Woodburn 1960; Gunter and Hall 1965; Fox and Mock 1968; Perret 1971.

(continued)

Table 17 (Concluded.)

Species	Peak abundance in gulf estuaries	Peak abundance Apalachicola system	Salinity and temperature tolerance	Reproductive patterns in gulf estuaries	Reproductive patterns in Apalachicola system	References
Melita intermedia (amphipod)		April - June	Salinity range 0-17 ppt Temperature range 10-32°C	Spawning in passes during late fall and early winter; juveniles in estuaries October-April	Juveniles in bay around October - November. Adult migration, June to October	Gunter 1945; Reid 1954; Kilby 1955; Springer and Woodburn 1960; Bechtel and Copeland 1970; Perret 1971; Copeland and Bechtel 1974; Swingle and Bland 1974.
Corophium louisianum (amphipod)		Late summer, early fall	Salinity range 0-24 ppt Temperature range 20-32°C	Spring spawning with juveniles in estuaries April - September	Juveniles in bay April-May	Gunter 1945; Reid 1954; Kilby 1955; Springer and Woodburn 1960; Bechtel and Copeland 1970; Perret 1971; Copeland and Bechtel 1974; Swingle and Bland 1974.
FISHES						
Anchoa mitchilli (Bay anchovy)	Summer and fall	Summer, fall and early winter	High; direct relationship of size with salinity	Spawn near passes late winter, early spring; juveniles in bays December - May	Juveniles in bay January - February	Pearson 1929; Gunter 1945; Joseph and Yerger 1956; Norden 1966; Sykes and Finucane 1966; Nelson 1969; Perret 1971; Swingle and Bland 1974.
Micropogonias undulatus (Atlantic croaker)	Spring and summer	January-April	High	Spawn in estuaries April-June with juveniles appearing from May to September	Juveniles in bay summer months	Gunter 1945; Kilby 1955; Springer and Woodburn 1960; Gunter and Hall 1965; Norden 1966; Fox and Mock 1968; Perret 1971; Swingle and Bland 1974.
Cynoscion arenarius (Sand seatrout)	May-July	March-August	Even distribution over salinity; caught between 20 and 35°C			Gunter 1945; Reid 1954; Kilby 1955; Joseph and Yerger 1956; Springer and Woodburn 1960; Gunter and Hall 1965; Norden 1966; Perret and Caillouet 1974.
Leiostomus xanthurus (Spot)	April-July	January-April	High; highest catches, 10-15 ‰	Spawn near passes late winter, early spring; juveniles in bays December-May	Juveniles in bay January-February	Pearson 1929; Gunter 1945; Joseph and Yerger 1956; Norden 1966; Sykes and Finucane 1966; Nelson 1969; Perret 1971; Swingle and Bland 1974.
Bairdiella chrysura (Silver perch)	Summer-early fall	Fall-early winter	High; direct relationship of size with salinity	Spawn in estuaries April-June with juveniles appearing from May to September	Juveniles in bay summer months	Gunter 1945; Kilby 1955; Springer and Woodburn 1960; Gunter and Hall 1965; Norden 1966; Fox and Mock 1968; Perret 1971.
Chloroscombrus chrysurus (Atlantic bumper)	Summer and fall	July-October	Abundant in high salinity with direct relationship of size with salinity			Gunter 1945; Reid 1954; Kilby 1955; Joseph and Yerger 1956; Springer and Woodburn 1960; Gunter and Hall 1965; Norden 1966; Perret and Caillouet 1974.



[1] Based on 40 core samples taken monthly in East Bay 1975 - 1982

[2] Based on 48 2-min otter trawl tows taken monthly in Apalachicola Estuary 1972 - 1982

[3] Based on 48 2-min. otter trawl tows taken monthly in Apalachicola Estuary 1972 - 1982

Figure 27. Summed numerical abundance and number of species of benthic infauna and epibenthic fishes and invertebrates in East Bay and Apalachicola Bay from 1972 to 1982 (from Livingston unpubl.). Data are presented as monthly means ±1 standard deviation of the mean.

to stress. However, there is relatively little in the way of detailed life-history information concerning these invertebrate species.

4.4. OYSTERS

Oysters (Crassostrea virginica) represent an important part of the biota of the Apalachicola estuary (Figure 20). Such factors as temperature, rainfall/river flow (and hence salinity), productivity (allochthonous and autochthonous), bottom type, and predation define the life history of oysters in the Apalachicola estuary. Ingle and Dawson (1951, 1952) noted that temperature is rarely limiting and that the spawning season is one of the longest in the United States (April through November). The free-swimming larval stage persists for two weeks. Ingle and Dawson (1952) found that oyster growth in Apalachicola Bay is the fastest in the United States and is continuous throughout the year because of the relatively high year-round temperatures. Successful oyster development depends on an appropriate substrate such as oyster shells, which can be planted throughout the estuary as cultch to enhance growth. Whitfield and Beaumariage (1977) estimate that nearly 40% of Apalachicola Bay is suitable for growing oysters. The ample nutrients and primary production of the bay also enhance oyster growth.

Oyster-bar associations also include various organisms that prey on oysters (Menzel et al. 1958, 1966). These include boring sponges, polychaete worms, gastropod mollusks (such as Thais haemastoma and Melongena corona), and crustaceans (Menippe mercenaria). Salinity is the most important limiting factor for oyster populations, but it has been hypothesized that such influence is indirect in that low salinity limits predation by excluding important species such as Thais and Menippe. During periods of high salinity, oyster predation is enhanced and can be considerable. Experiments have shown that oysters over 50 mm in length are rare in unprotected areas of high salinity relative to areas where oysters are shielded from predation by baskets at similar salinities (Menzel et al. 1966).

4.5. NEKTON

Nekton are those organisms that are strong enough swimmers that they can move through the water column, even against water currents. In the Apalachicola Bay system, the nekton comprise the bulk of the sport and commercial fisheries and are among the more conspicuous biological components of the estuary. Epibenthic fishes and invertebrates in the Apalachicola marshes (Table 18) and open water areas (Table 19) are characterized by high numbers of predominant species, with the top three species of each group accounting for 70%-80% of the total numbers taken throughout the year. The relatively low number of fish and invertebrate species in the bay system at any given time, together with the high dominance of a relatively few extremely successful species, contribute to the low species diversity throughout the estuary (Livingston 1976b).

In a given year, peak numbers of fishes tend to occur from February through April (Figure 27). This situation is due largely to the presence of juvenile spot and Atlantic croaker. Species numbers, on the other hand, tend to peak during October. Epibenthic invertebrates reach abundance peaks from August through October, largely because of high numbers of penaeid shrimp and, secondarily, blue crabs (Figure 27). Seasonal patterns of invertebrate species richness tend to follow those of the fishes. The highest numbers of invertebrate species usually occur in October. The peaks of abundance and species richness of fishes and invertebrates are characterized by monthly high variances.

Various organisms appearing in the estuary may not be estuarine dependent throughout their life histories. Many such organisms are migratory. The anadromous species in the Apalachicola drainage system include the Atlantic sturgeon (Acipenser oxyrhynchus), Alabama shad (Alosa alabamae), and striped bass (Morone saxatilis) (Yerger 1977). The skipjack herring (Alosa chrysochloris) is another possible anadromous species. Other species, such as the Atlantic needlefish (Strongylura marina) may be diadromous. Catadromous species include

Table 18. Fishes and invertebrates commonly taken with seines in oligohaline (East Bay) and mesohaline (Apalachicola Bay) marshes of the Apalachicola estuary (from Livingston and Thompson 1975).

Species Scientific name	 Common name
East Bay	
Fishes	
Ictalurus natalis	yellow bullhead
Micropterus salmoides	largemouth bass
Lepomis microlophus	redear sunfish
Lepomis punctatus	spotted sunfish
Poecilia latipinna	sailfin molly
Adinia xenica	diamond killifish
Cyprinodon variegatus	sheepshead minnow
Fundulus grandis	gulf killifish
Fundulus confluentus	marsh killifish
Fundulus similis	longnose killifish
Notemigonus crysoleucas	golden shiner
Lucania parva	rainwater killifish
Lucania goodei	bluefin killifish
Notropis sp.	shiners
Lepisosteus osseus	longnose gar
Cyprinus carpio	common carp
Anguilla rostrata	American eel
Pomoxis nigromaculatus	black crappie
Menidia beryllina	inland silverside
Anchoa mitchilli	bay anchovy
Brevoortia patronus	gulf menhaden
Mugil curema	white mullet
Mugil cephalus	striped mullet
Micropogonias undulatus	Atlantic croaker
Bairdiella chrysoura	silver perch
Stellifer lanceolatus	star drum
Cynoscion arenarius	sand seatrout
Paralichthys lethostigma	southern flounder
Trinectes maculatus	hog choker
Eucinostomus gula	silver jenny
Lutjanus griseus	gray snapper
Gobiosoma bosci	naked goby
Microgobius gulosus	clown goby
Archosargus probatocephalus	sheepshead
Invertebrates	
Callinectes sapidus	blue crab
Palaemonetes pugio	grass shrimp
Penaeus setiferus	white shrimp
Penaeus aztecus	brown shrimp

(continued)

Table 18. (Concluded.)

Species	
Scientific name	Common name
Apalachicola Bay Fishes	
Anchoa mitchilli	bay anchovy
Anchoa hepsetus	striped anchovy
Menidia beryllina	inland silverside
Eucinostomus gula	silver jenny
Synodus foetens	inshore lizardfish
Strongylura marina	Atlantic needlefish
Lucania parva	rainwater killifish
Fundulus similis	longnose killifish
Syngnathus floridae	dusky pipefish
Lagodon rhomboides	pinfish
Leiostomus xanthurus	spot
Bairdiella chrysoura	silver perch
Cynoscion nebulosus	spotted seatrout
Mugil cephalus	striped mullet
Orthopristis chrysoptera	pig fish
Opsanus beta	gulf toad fish
Invertebrates	
Callinectes sapidus	blue crab
Palaemonetes pugio	grass shrimp
Palaemonetes vulgaris	grass shrimp
Palaemonetes intermedium	grass shrimp
Penaeus setiferus	white shrimp
Penaeus duorarum	pink shrimp
Penaeus aztecus	brown shrimp
Neopanope texana	mud crab

the American eel (*Anguilla rostrata*), hogchoker (*Trinectes maculatus*), and mountain mullet (*Agonostomus monitcola*). Various other freshwater species and some marine forms, such as striped mullet (*Mugil cephalus*) and the southern flounder (*Paralichthys lethostigma*), occur in the lower river and estuary although they do not make true migrations.

The estuarine dominants such as sciaenid fishes, penaeid shrimp, and blue crabs have annual migrations during which the adults spawn offshore, the larval and juvenile stages move into the estuarine nursery, and finally the subadults return to the open gulf to spawn as adults. Most such species are either marine-estuarine or estuarine. Oesterling and Evink (1977) studied migratory habits of blue crabs along the Gulf coast of Florida (Figure 28). Adult blue crabs spawn offshore and the larvae, after going through a series of zoeal (planktonic) stages, metamorphose into a single megalops stage that has both planktonic and benthic features (Figure 28). The megalops eventually molts into the first crab stage, which develops mainly within the estuarine nursery grounds. The authors found that female crabs move northward along the gulf coast of Florida, some as far as 500 km. Few males move more than 40 or 50 km. Such migrations appear to be linked to spawning within the Apalachicola offshore area (from the Ochlockonee River drainage to the Apalachicola River drainage). Large numbers of egg-bearing females are

Table 19. Epibenthic fishes and invertebrates taken in otter trawls and trammel nets at various stations in the Apalachicola estuary from 1972 through 1982 (Livingston unpublished data). Species are listed in order of numerical abundance.

Species

A. Fishes

1. *Anchoa mitchilli*
2. *Micropogonias undulatus*
3. *Cynoscion arenarius*
4. *Leiostomus xanthurus*
5. *Polydactylus octonemus*
6. *Arius felis*
7. *Chloroscombrus chrysurus*
8. *Menticirrhus americanus*
9. *Symphurus plagiusa*
10. *Bairdiella chrysura*
11. *Etropus crossotus*
12. *Trinectes maculatus*
13. *Prionotus tribulus*
14. *Stellifer lanceolatus*
15. *Anchoa hepsetus*
16. *Porichthys porosissimus*
17. *Prionotus scitulus*
18. *Eucinostomus gula*
19. *Paralichthys lethostigma*
20. *Synodus foetens*
21. *Eucinostomus argenteus*
22. *Dasyatis sabina*
23. *Cynoscion nebulosus*
24. *Microgobius thalassinus*
25. *Urophycis floridanus*
26. *Lagodon rhomboides*
27. *Gobiosoma bosci*
28. *Chaetodipterus faber*
29. *Orthopristis chrysoptera*
30. *Brevoortia patronus*
31. *Dorosoma petenense*
32. *Peprilus burti*
33. *Peprilus paru*
34. *Stephanolepis hispidus*
35. *Sphaeroides nephelus*
36. *Ophichthus gomesi*
37. *Syngnathus louisianae*
38. *Syngnathus scovelli*
39. *Gobionellus boleosoma*
40. *Harengula pensacolae*
41. *Archosargus probatocephalus*
42. *Microgobius gulosus*
43. *Bagre marinus*
44. *Menidia beryllina*
45. *Monacanthus ciliatus*
46. *Caranx hippos*
47. *Centropristis melana*
48. *Syngnathus floridae*
49. *Ancyclopsetta quadrocellata*
50. *Chilomycterus schoepfi*
51. *Diplectrum formosum*
52. *Ictalurus catus*
53. *Sciaenops ocellata*
54. *Astroscopus y-graecum*
55. *Hippocampus erectus*
56. *Lepisosteus osseus*
57. *Lucanis parva*
58. *Lutjanus griseus*
60. *Opsanus beta*
60. *Paralichthys albigutta*
61. *Ophidion beani*
62. *Aluterus schoepfi*
63. *Diplodus holbrooki*
64. *Gobionellus hastatus*
65. *Hypsoblennius hentzi*
66. *Menticirrhus saxatilis*
67. *Myrophis punctatus*
68. *Ogilbia cayorum*
69. *Oligoplites saurus*
70. *Pomatomus saltatrix*
71. *Rhinoptera bonasus*
72. *Scomberomorus maculatus*
73. *Selene vomer*
74. *Sphyraena borealis*
75. *Sphyrna tiburo*
76. *Sardinella anchovia*
77. *Caranx bartholomaei*
78. *Mugil* sp.
79. *Gymnura micrura*

B. Invertebrates

1. *Penaeus setiferus*
2. *Callinectes sapidus*
3. *Palaemonetes pugio*
4. *Penaeus duorarum*
5. *Trachypenaeus constrictus*
6. *Chrysaora quinquecirrha*

(continued)

Table 19. (Concluded.)

Species

B. Invertebrates (continued)

7. *Lolliguncula brevis*
8. *Penaeus aztecus*
9. *Palaemonetes vulgaris*
10. *Portunus gibbesii*
11. *Stomolophys meleagris*
12. *Neritina reclivata*
13. *Squilla empusa*
14. *Callinectes similis*
15. *Rhithropanopeus harrisii*
16. *Neopanope texana*
17. *Polinices duplicatus*
18. *Neopanope packardii*
19. *Mulinia lateralis*
20. *Acetes americanus*
21. *Pagurus pollicaris*
22. *Rangia cuneata*
23. *Menippe mercenaria*
24. *Xiphopeneus kroyeri*
25. *Alpheus heterochaelis*
26. *Latreutes parvulus*
27. *Palaemonetes intermedius*
28. *Metoporhaphis calcarata*
29. *Crassostrea virginica*
30. *Palaemon floridanus*
31. *Periclimenes longicaudatus*
32. *Ogyrides limicola*
33. *Trachypenaeus similis*
34. *Busycon contrarium*
35. *Branchiosychis americana*
36. *Brachiodontes exustus*
37. *Hexapanopeus angustifrons*
38. *Luidia clathrata*
39. *Persephona mediterranea*
40. *Clibanarius vittatus*
41. *Libinia dubia*
42. *Periclimenes americanus*
43. *Ambidexter symmetricus*
44. *Busycon spiratum*
45. *Procabarus paeninsulanus*
46. *Eupleura sulcidentata*
47. *Hemipholus elongata*
48. *Alpheus normanni*
49. *Eurypanopeus depressus*
50. *Lysmata wurdemanni*
51. *Pentacta* sp.
52. *Petrolisthes armatus*
53. *Podochela riisei*
54. *Tozeuma carolinense*
55. *Nudibranch* sp.
56. *Alpheus armillatus*
57. *Sesarma cinereum*
58. *Sicyonia dorsalis*
59. *Anadara brasiliana*
60. *Dinocardium robustum*
61. *Cantharus cancellaria*
62. *Urosalpinx perrugata*
63. *Ovalipes guadulpensis*
64. *Pagurus longicarpus*

concentrated in this area in winter. The authors hypothesized that larval dispersal from the Apalachicola area takes place along clockwise (Loop) currents that eventually wash onto the Florida Shelf (Figure 28). Zoea larvae then disperse along the coast, with the megalops stage settling into the coastal estuaries. Livingston et al. (1977) used daytime trawling to estimate winter populations of juvenile blue crabs in the Apalachicola estuary of approximately 30,000,000 individuals. Migration of spawning females appears to coincide with flooding of the north Florida drainage system, which makes particulate organic matter available as food to the young crabs (Laughlin 1979). Thus, the migration of blue crabs along the gulf coast could be tied to both the reproductive characteristics of the species and the trophic organization of the Apalachicola estuary.

Life-history features of the dominant epibenthic species in the Apalachicola estuary have the same patterns as elsewhere in the northern Gulf of Mexico (Table 17). Spawning and recruitment generally vary from species to species according to different combinations of seasonal physical factors. The bay anchovy is the most abundant fish and is one of the few fish species that does not show regular seasonal recruitment progressions. In contrast, the Atlantic

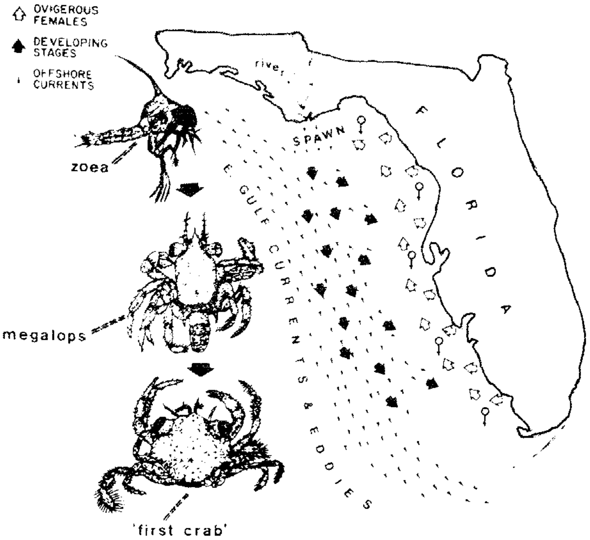


Figure 28. Life cycle of the blue crab along the gulf coast of Florida. Ovigerous females move toward the Apalachicola estuary. It is hypothesized that developing stages move back down the gulf coast of Florida with offshore currents (after Oesterling and Evink 1977).

croaker spawn near passes during fall and early winter; the juveniles occupy the estuary in peak numbers during late winter and early spring when salinities are usually less than 10-15 ppt. Spot also spawn near passes, and peaks of abundance in the estuary generally coincide with those of the Atlantic croaker. Sand seatrout are usually most abundant during summer months after spawning offshore during the spring. This species is taken at various salinities, but temperature appears to be limiting; high catches are generally taken in 20°-35°-C water.

White shrimp are dominant from August to November, with spring spawning and recruitment. Other penaeids usually reach peak numbers during late spring (brown shrimp: Penaeus aztecus) or late summer (pink shrimp: P. duorarum). The blue crab shows a bimodal annual peak of recruitment; numbers peak during winter and summer periods. Depth and specific microhabitat conditions are the principal determinants of blue crab distribution at any given time (Laughlin 1979; Livingston unpubl.). The brief squid (Lolliguncula brevis), is limited in spatial/temporal distribution by salinity (20-30 ppt) and other habitat characteristics and complex trophic relationships (Laughlin and Livingston 1982). In summary, these species-specific responses to multifactor complexes demonstrate the difficulty of trying to design linear models to explain and predict spatial/temporal patterns of occurrence.

The spatial distributions of nektonic fishes and invertebrates in the Apalachicola estuary (Table 20) tend to be associated with freshwater runoff into the system. Relative dominance at a given station varied according to salinity gradients and habitat type. Regular seasonal changes in distributions are evident for most of the dominant nektonic species. For example, anchovies are relatively uniformly distributed within the estuary during January and February (Figure 29). By the spring, anchovies are concentrated in upper portions of East Bay. During the early summer, there are minor population peaks with primary concentrations in eastern portions of East Bay. By the fall, the anchovies concentrate around the mouth of the Apalachicola River as well as in portions of East Bay, and during early winter, the anchovies become uniformly distributed throughout East Bay and Apalachicola Bay.

In January, Atlantic croaker tend to congregate at the mouth of the Apalachicola River and upper portions of East Bay (Figure 30). By February, this distribution is more uniform throughout East Bay and northern Apalachicola Bay, a situation that appears to hold during ensuing winter and spring months until, by May or June, the croakers move out of the bay.

The spatial distribution of sand seatrout through a given seasonal cycle is quite regular (Figure 31). As the young seatrout move into the bay system in May, they concentrate in upper portions of East Bay and just off the mouth of the Apalachicola River. Secondary concentrations are found throughout East Bay and northern portions of Apalachicola Bay. The distribution changes little in June,

Table 20. Epibenthic fishes and invertebrates taken in otter trawls at permanent stations in the Apalachicola estuary from June 1972 to May 1977. Stations have been ordered by cluster analysis according to relative abundance of fishes and invertebrates. Data are given concerning numbers/sample, dry weight biomass/sample, percent dominance (by numbers), and Margalef richness. Dominant species are also enumerated by station.

	Station	Number per sample	Biomass per sample (g, dry weight)	% Dominance (by numbers)	Dominant species	Margalef richness
			A. FISHES			
OUTER BAY	1	43.4	46.2	39	MICROPOGONIAS UNDULATUS ANCHOA MITCHILLI	3.77
	1A	18.0	47.5	41	ANCHOA MITCHILLI MICROPOGONIAS UNDULATUS LEIOSTOMUS XANTHURUS	3.43
	1E	55.9	53.9	77	LEIOSTOMUS XANTHURUS	3.54
	1C	51.6	75.1	43	MICROPOGONIAS UNDULATUS ANCHOA MITCHILLI	3.48
	1X	73.2	171.8	34	LAGODON RHOMBOIDES BAIRDIELLA CHRYSURA ORTHOPRISTIS CHRYSOPTERA	3.55
RIVER DOMINATED	2	96.4	65.6	46	ANCHOA MITCHILLI MICROPOGONIAS UNDULATUS	2.88
	3	44.5	31.3	44	ANCHOA MITCHILLI LEIOSTOMUS XANTHURUS	3.82
	4	100.9	46.0	49	ANCHOA MITCHILLI MICROPOGONIAS UNDULATUS BREVOORTIA PATRONUS	3.14
UPPER (EAST) BAY	4A	64.6	48.0	47	LEIOSTOMUS XANTHURUS	3.30
	5	74.3	76.6	44	ANCHOA MITCHILLI MICROPOGONIAS UNDULATUS LEIOSTOMUS XANTHURUS	3.90 3.01
	5A	101.4	60.9	47	ANCHOA MITCHILLI LEIOSTOMUS XANTHURUS MICROPOGONIAS UNDULATUS	
	5B	74.1	28.2	47	ANCHOA MITCHILLI LEIOSTOMUS XANTHURUS	2.99
	5C	90.8	27.0	47	LEIOSTOMUS XANTHURUS	3.09
	6	109.9	53.5	33	ANCHOA MITCHILLI LEIOSTOMUS XANTHURUS MICROPOGONIAS UNDULATUS BREVOORTIA PATRONUS	3.98

Table 20. (Continued.)

	Station	Number per sample	Biomass per sample (g, dry weight)	% Dominance (by numbers)	Dominant species	Margalef richness
					A. FISHES (continued)	
SIKE'S CUT	1B	20.6	129.3	36	ANCHOA MITCHILLI CYNOSCION ARENARIUS ETROPUS CROSSOTUS	4.92
					B. INVERTEBRATES	
OUTER BAY	1	7.0	7.2	47	CALLINECTES SAPIDUS PENAEUS SETIFERUS	2.58
	1A	5.5	5.3	38	PENAEUS SETIFERUS CALLINECTES SAPIDUS LOLLIGUNCULA BREVIS TRACHYPENAEUS CONSTRICTUS	1.86
	1E	10.1	11.9	48	CALLINECTES SAPIDUS PENAEUS AZTECUS	1.81
	1C	6.4	9.5	27	PENAEUS DUORARUM LOLLIGUNCULA BREVIS CALLINECTES SAPIDUS	2.82
	1X	16.3	8.8	57	ACETES AMERICANUS CALLINECTES SAPIDUS PENAEUS DUORARUM	1.86
RIVER DOMINATED	2	38.5	28.0	70	PENAEUS SETIFERUS	1.68
	3	12.2	6.2	49	CALLINECTES SAPIDUS PENAEUS SETIFERUS	1.43
	4	14.7	16.8	52	PENAEUS SETIFERUS CALLINECTES SAPIDUS	1.38

(continued)

Table 20. (Concluded.)

	Station	Number per sample	Biomass per sample (g, dry weight)	% Dominance (by numbers)	Dominant species	Margalef richness
B. INVERTEBRATES (continued)						
UPPER (EAST) BAY	4A	13.0	16.0	67	PENAEUS SETIFERUS PALAEMONETES PUGIO	1.24
	5	12.2	9.9	57	PENAEUS SETIFERUS CALLINECTES SAPIDUS	1.45
	5A	13.7	3.9	65	PENAEUS SETIFERUS CALLINECTES SAPIDUS	1.18
	5B	6.8	5.1	53	CALLINECTES SAPIDUS PENAEUS SETIFERUS	1.39
	5C	12.5	5.2	54	CALLINECTES SAPIDUS PENAEUS SETIFERUS	1.11
	6	45.8	11.1	50	PALAEMONETES PUGIO PENAEUS SETIFERUS	1.17
SIKE'S CUT	1B	10.0	8.4	41	LOLLIGUNCULA BREVIS CALLINECTES SAPIDUS PORTUNUS GIBBESI ACETES AMERICANUS	3.28

but in July, the highest concentrations of the sand seatrout are found at the mouth of the Apalachicola River. Distribution usually remains relatively unchanged during August and September. The remaining fish, dwindling in numbers during the fall months, spread out throughout East Bay and northern Apalachicola Bay. By winter or early spring, as noted above, no sand seatrout are taken.

Spot have a different pattern of distribution (Figure 32). As they move into the estuary in Jaunary, spot tend to congregate in upper East Bay and around Nick's Hole drainage off St. George Island. This distribution broadens throughout eastern portions of East Bay and Apalachicola Bay during February and March. Concentrations of spot appear in areas of the bay that receive freshwater runoff from upland areas. East Bay is a particularly important nursery area for this species. By summer, remnants of the population are found off St. George Island.

The spatial distribution of postlarval penaeid shrimp in the Apalachicola estuary illustrates the summer and fall dominance of these species (Figure 33). During early summer, they are concentrated in East Bay. However, during July and August, high numbers of penaeids are located at the mouth of the Apalachicola River. By fall, although still concentrated in East Bay, they tend to be more evenly distributed throughout the estuary as they move into the open gulf to spawn. Few shrimp are taken during the winter months. As with other dominant (and commercially important) species in the bay, the penaeids appear to

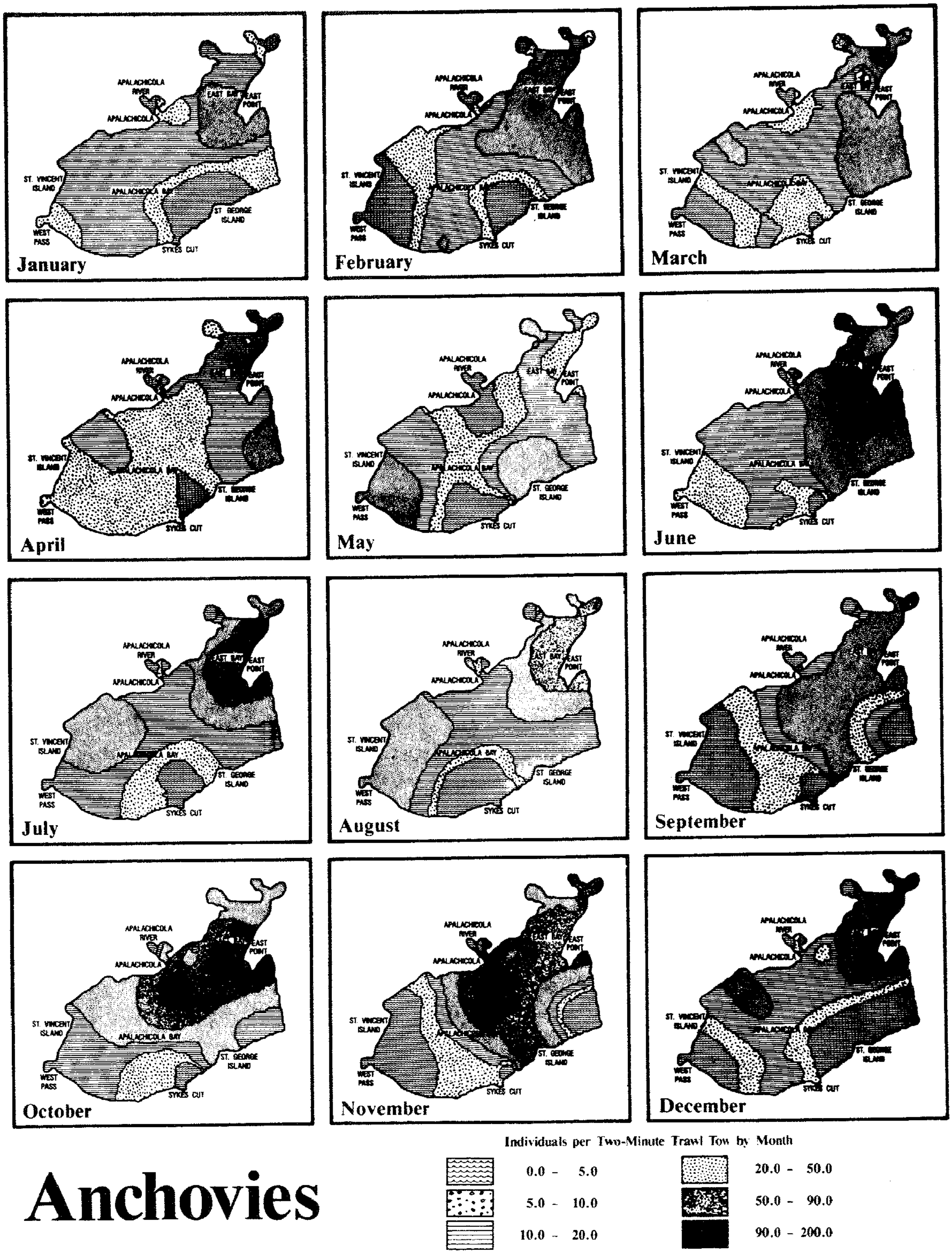


Figure 29. Average monthly distribution of anchovies (Anchoa mitchilli) in the Apalachicola estuary from 1972 to 1979.

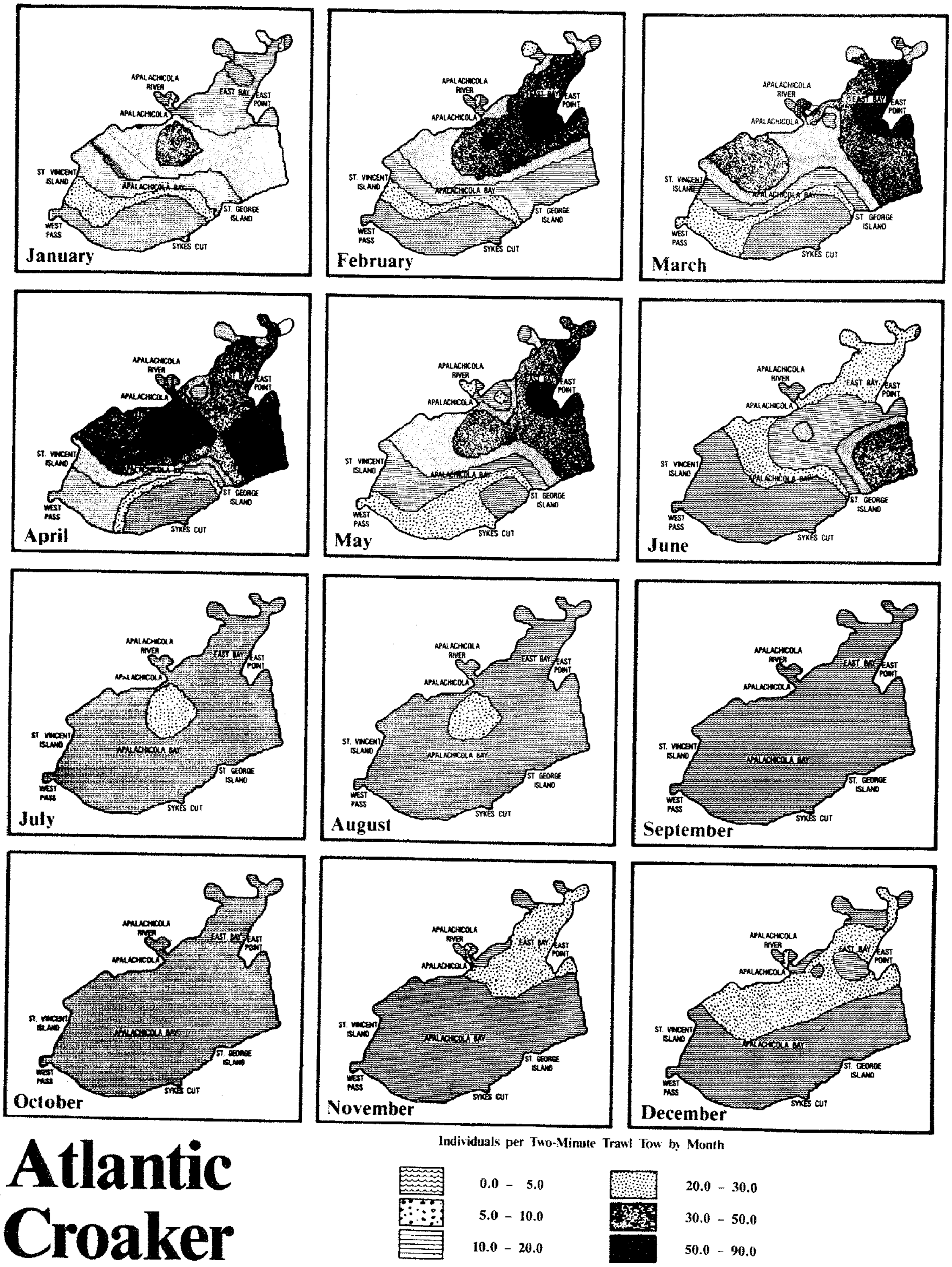


Figure 30. Average monthly distribution of Atlantic croaker (*Micropogonias undulatus*) from 1972 to 1979.

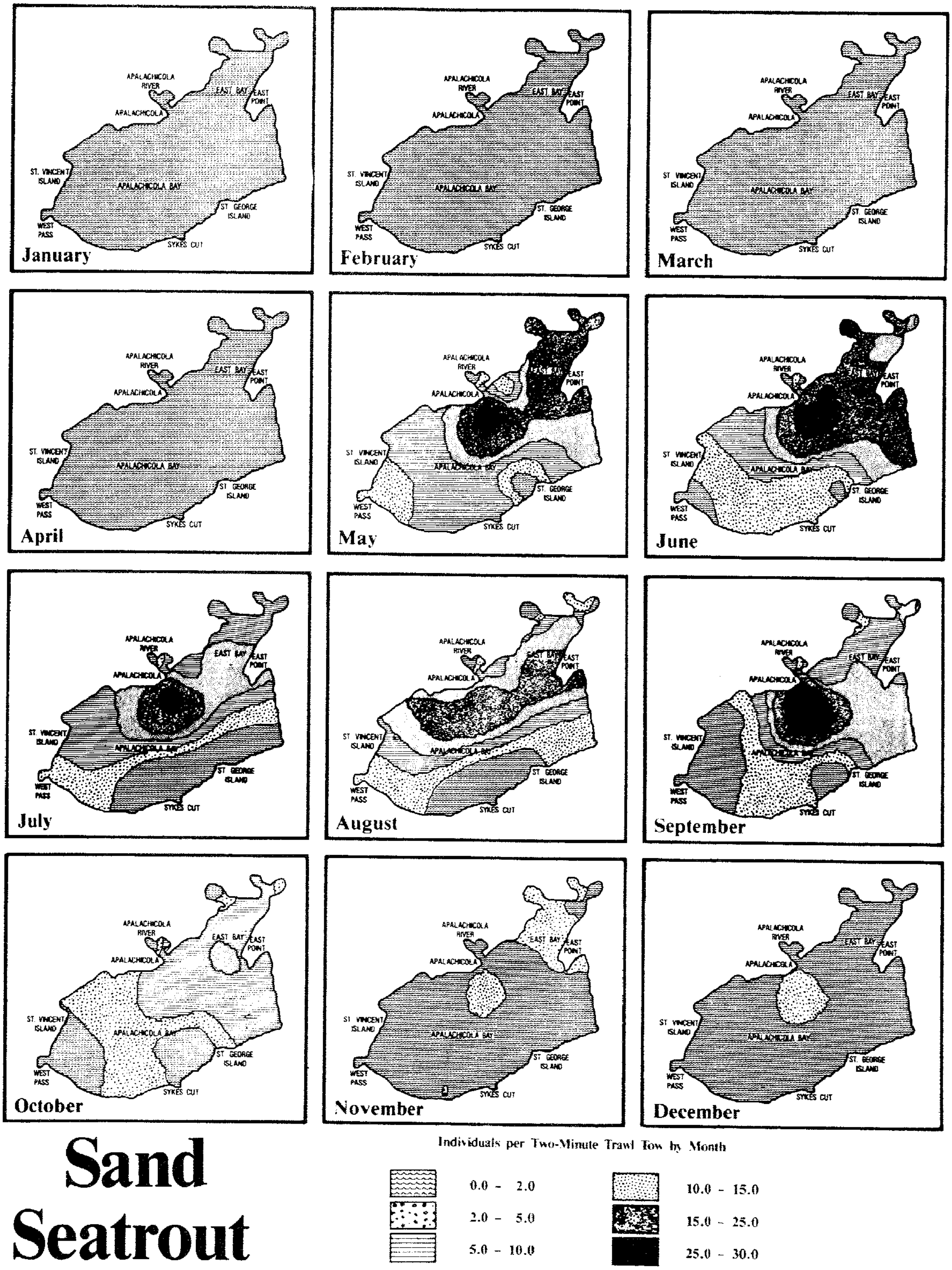


Figure 31. Average monthly distribution of sand seatrout (Cynoscion arenarius) in the Apalachicola estuary from 1972 to 1979.

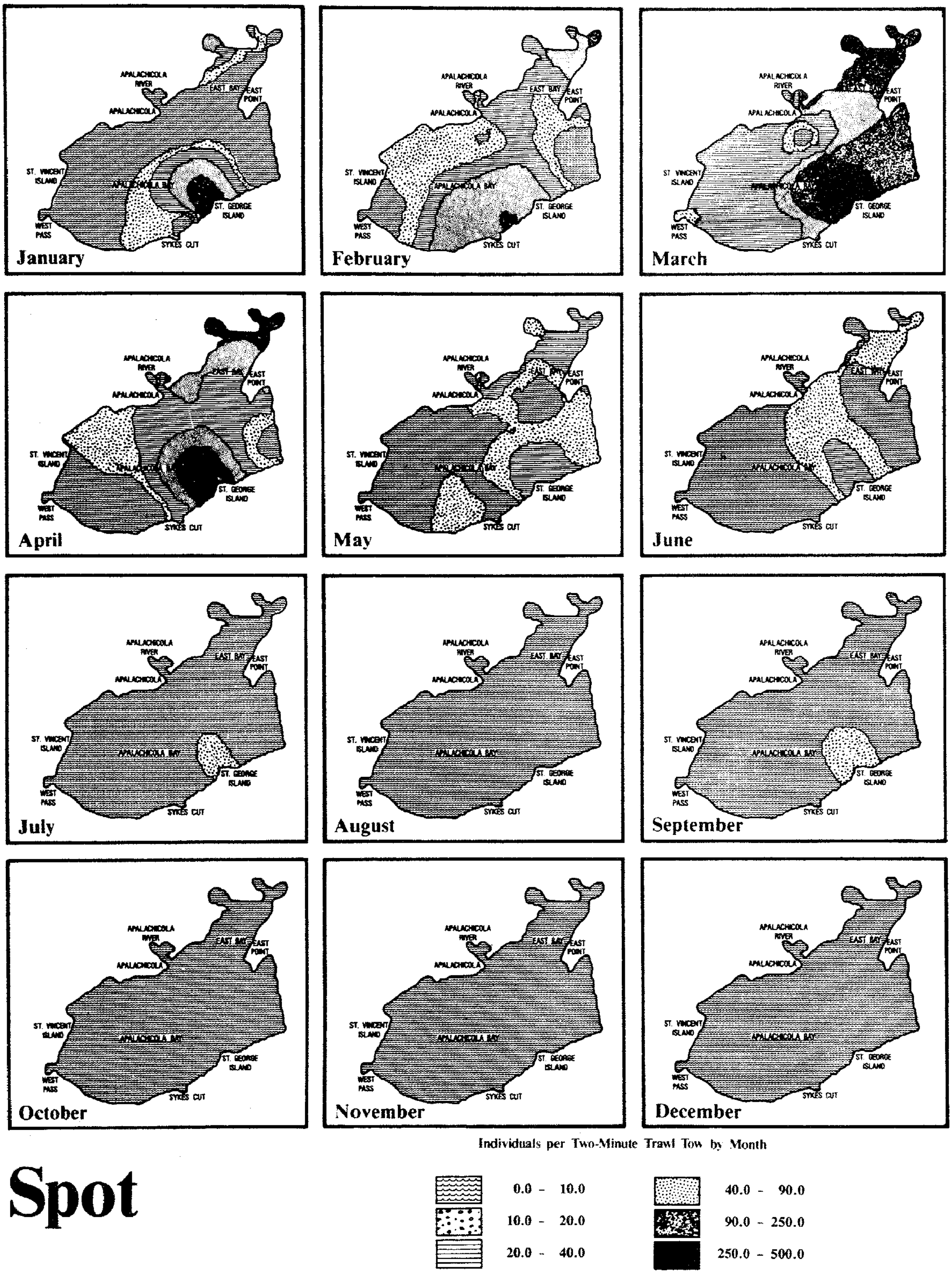


Figure 32. Average monthly distribution of spot (<u>Leiostomus xanthurus</u>) in the Apalachicola estuary from 1972 to 1979.

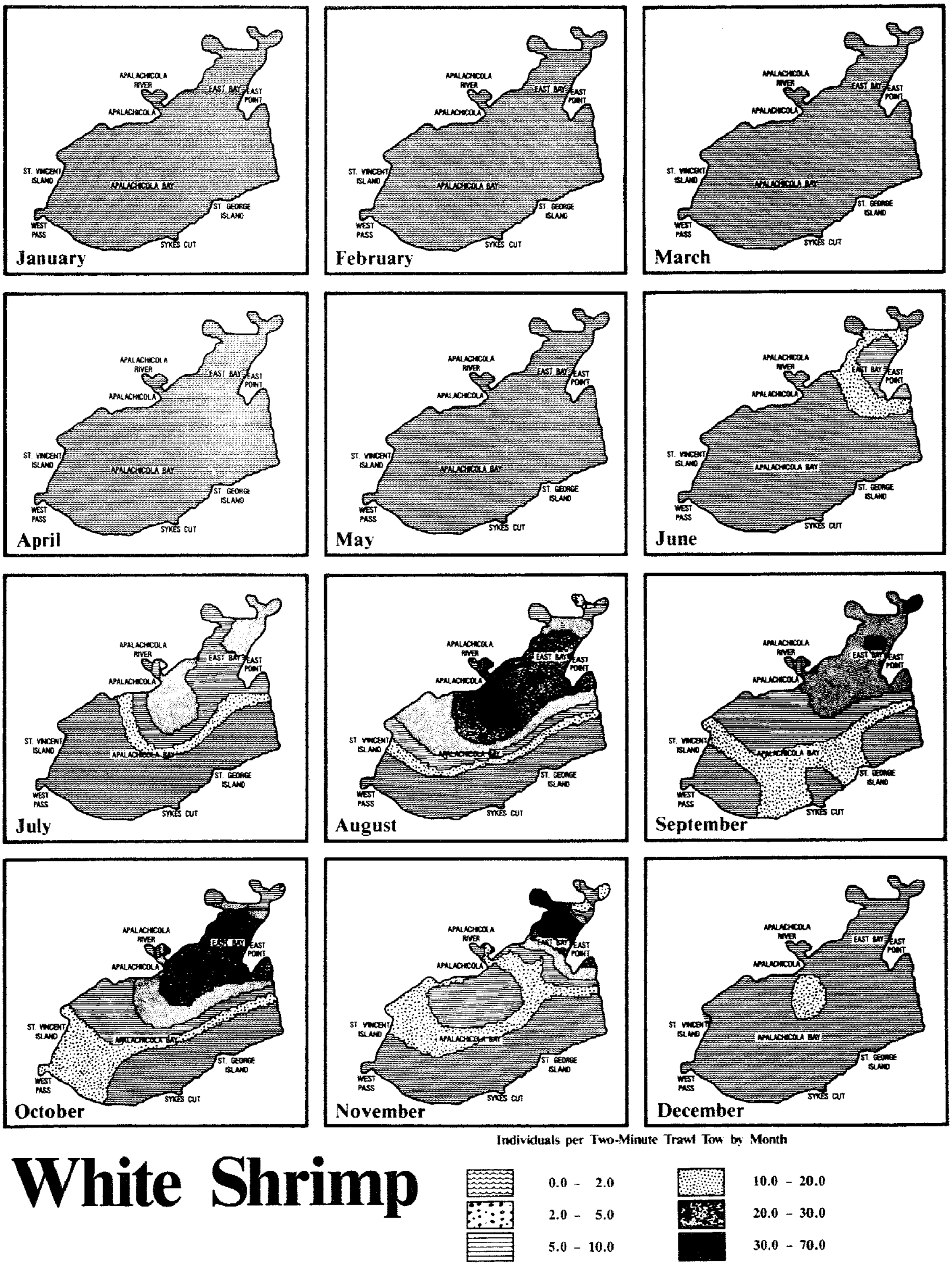


Figure 33. Average monthly distribution of penaeid shrimp (Penaeus spp.) in the Apalachicola estuary from 1972 to 1979.

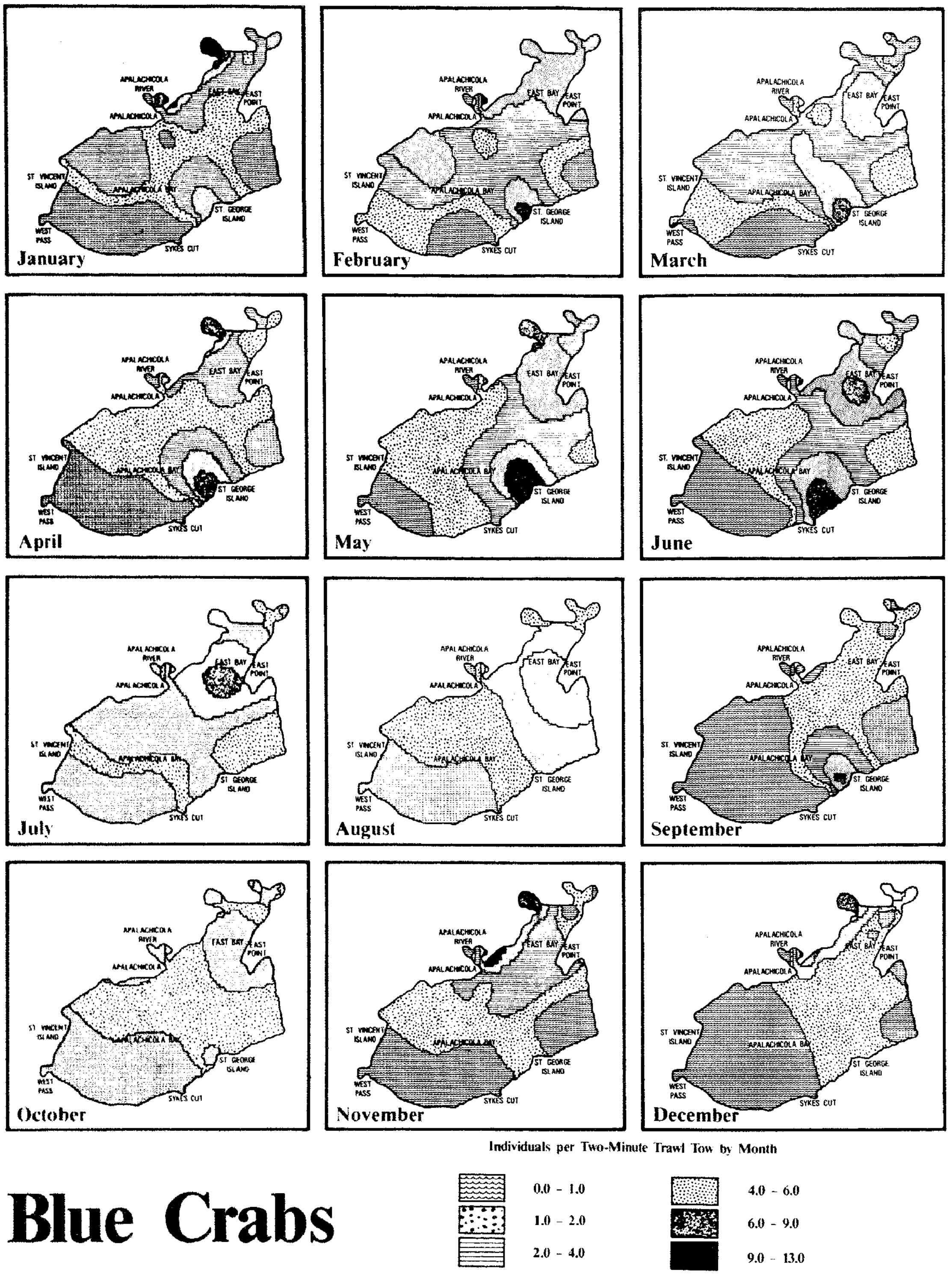


Figure 34. Average monthly distribution of blue crabs (Callinectes sapidus) in the Apalachicola estuary from 1972 to 1979.

be attracted to the upper freshwater portions in the estuary.

Although the major peaks in numbers of juvenile blue crabs occur during the winter, secondary increases are often noted during the summer and fall (Figure 34). As the young blue crabs enter the Apalachicola estuary during the winter months, they concentrate in East Bay and off the Nick's Hole drainage (St. George Island). During May and June, peaks in the number of blue crabs occur in these areas. By the summer and fall months, the blue crabs are concentrated in East Bay. Blue crabs appear to be attracted to areas that receive overland runoff although they are not attracted by direct river flow.

While there is a general pattern of concentration of the dominant epibenthic fishes and invertebrates in areas that receive direct input of freshwater runoff from upland areas, it is simplistic to assume that runoff per se is the primary factor that influences the temporal and spatial aspects of the distribution of such organisms in the estuary. There are, in fact, a complex of species-specific limiting factors that are associated with the trophic organization of the bay system.

CHAPTER 5
NICHE DIVERSITY, TROPHIC INTERACTIONS, AND COMMUNITY STRUCTURE

5.1. HABITAT-SPECIFIC ASSOCIATIONS

The Apalachicola estuary, as an ecosystem, can be defined as a series of habitats with associated assemblages of organisms. Such assemblages (or communities) live in the same general habitat, compete for space and food, and are part of the highly complex trophic structure of the river-bay system. The dimensions of a given community are difficult to define precisely because the component populations vary considerably in their distribution and community function in space and time. However, selected factors can be used to characterize the various estuarine assemblages. Sources of primary productivity, habitat features, the physical and chemical environment (including pollutants), modes of reproduction and recruitment, feeding interactions, predator-prey relations, and competition are some of the features that shape the estuarine communities.

The distribution of most of the estuarine assemblages may be partitioned into the following habitats: marshes, seagrass beds, litter associations, oyster bars, and subtidal unvegetated (soft-sediment) areas. Many of the long-term biological studies in the Apalachicola estuary have concentrated on the macroinvertebrates (benthic, epibenthic) and fishes that are found in these areas.

5.1.1. Marshes

The marshes, which include complex patterns of tidal channels and small creeks, provide food and habitat for a number of organisms in the Apalachicola estuary (Table 18). Marsh complexes include insects, mollusks, crustaceans, fishes, birds, and mammals. Topminnows of various species are dominant in such areas. Many species that are important to the sports and commercial fisheries of the region spend at least part of their life histories in the estuarine marshes. Such species include blue crabs, penaeid shrimp, large-mouth bass, lepomids, striped mullet, spotted and sand seatrout, and anchovies. Few species spend their entire lives within the marshes, however, and the marsh habitat is best characterized as a nursery for migratory species during summer and fall months.

5.1.2. Seagrass Beds

The distribution of grassbeds in the Apalachicola estuary (Figure 19) is the result of a number of environmental controlling factors. Even though it is limited to only about 10% of the aquatic area by the high turbidity and sedimentation associated with the river, this habitat's productivity is high. Grassbed productivity is also limited by water temperature, salinity, and the activity of certain invertebrates. However, grassbeds also have an effect on certain water quality indices. Various studies in East Bay (Livingston 1978; Purcell 1977) indicate that water quality factors such as dissolved oxygen and pH are higher in the grassbeds than in associated mudflats.

The oligohaline grassbeds of East Bay are dominated by tapeweed (*Valisneria americana*), a freshwater species. Other species found in conjunction with tapeweed are *Potamogeton pusillus*, *Ruppia maritima* (locally dominant in western bayous of East Bay), *Cladophora* sp., and *Halophila engelmanni*. In recent years, some parts of East Bay are being taken over by the Eurasian watermilfoil (*Myriophyllum* *spicatum*). During the period 1980-1981, this introduced species became dominant in Round Bay, one of the eastern bayous. By 1982-1983, the *Myriophyllum* had become rooted throughout the upper East Bay area (Livingston unpubl.). It is unclear how spread of Eurasian watermilfoil will affect the distribution of plants and animals in the East Bay seagrass beds.

Currently, the oligohaline seagrass beds serve as a nursery for benthic species such as the snail *Neritina reclivata* (a major dominant) and epibenthic species (*Odostomia* sp., *Gammarus macromucronatus* and *Taphromysis bowmani*). Infaunal assemblages are dominated by polychaetes (*Loandalia americana*, *Mediomastus ambiseta*), amphipods (*Grandidierella bonnieroides*) and chironomid larvae (*Dicrontendipes* sp.). Fish populations are dominated by rainwater killifish (*Lucania parva*), pipefish (*Syngnathus scovelli*), silversides (*Menidia beryllina*), gobies (*Microgobius gulosus*), and centrarchids. Many species utilize these areas (Duncan 1977; Livingston and Duncan 1979; Purcell 1977). Of the 28 dominant benthic species of fishes that comprised over 98% of the abundance in the area, most consumed detritus, small mollusks, crustaceans, epiphytes, and insect larvae. Most of the penaeid shrimp, insect larvae, and fishes that are found here are seasonally abundant at early stages of their reproductive cycles, which indicates the use of these areas as primary nursery grounds. Peaks of abundance are staggered throughout the year.

The predominant macrophyte species in mesohaline or higher-salinity areas off St. George Island in Apalachicola Bay is *Halodule wrightii* (Sheridan and Livingston 1983). Infaunal macroinvertebrates, dominated by *Hargaria rapax*, *Heteromastus filiformis*, *Ampelisca vadorum* and various oligochaetes, reach peaks of abundance during early spring. Predominant fishes include silver perch (*Bairdiella chrysoura*), pigfish (*Orthopristis chrysoptera*), pinfish (*Lagodon rhomboides*) and spotted seatrout (*Cynoscion nebulosus*). These species are abundant from May through September. Blue crabs (*Callinectes sapidus*), pink shrimp (*Penaeus duorarum*) and grass shrimp (*Palaemonetes vulgaris*) are the dominant invertebrates. Their densities are bimodal, peaking in the winter and summer months. These areas are also characterized by the year-round presence of larval and juvenile nekton.

5.1.3. Litter Associations

Leaf litter associations are dominated by omnivores and detritivores. The fraction of particulate organic matter (POM) large enough to be identified as litter is populated with gastropod mollusks (*Neritina reclivata*), amphipods (*Gammarus mucronatus*, *Melita* spp., *Grandidierella bonnieroides*, *Corophium louisianum*, *Gitanopsis* sp.), isopods (*Munna reynoldsi*), and decapods (*Palaemonetes pugio*, *P. vulgaris*, *Penaeus setiferus*, *Callinectes sapidus*).

Species richness of the litter-associated fauna in upper East Bay (station 5A), the river mouth (station 3), and the shoal grassbeds off St. George Island (station 1X) peaks during August and September (Figure 35). Such peaks are strongly associated with salinity levels at the respective study sites (Figure 36). Dominant species vary from location to location. The level and timing of peaks of abundance also vary spatially (Figure 35). Upper East Bay, which is outside of the direct influence of the Apalachicola River, appears to be the least productive part of the estuary in terms of litter-associated macroinvertebrates. Areas rich in detritus, such as station 3, are most highly populated during March and September, periods when the river is flooding or macrophytes are dying off. The highest numbers of litter-associated macroinvertebrates occur in the *Halodule* beds off St. George Island from April to June, a period of high macrophyte productivity. These data indicate that while species richness may be strongly influenced by salinity, the numerical abundance of the litter associations is more strongly aligned with the availability of detritus.

While physical factors such as salinity and temperature are important determinants of the distribution of the litter-associated organisms in the estuary, recent experiments by Florida

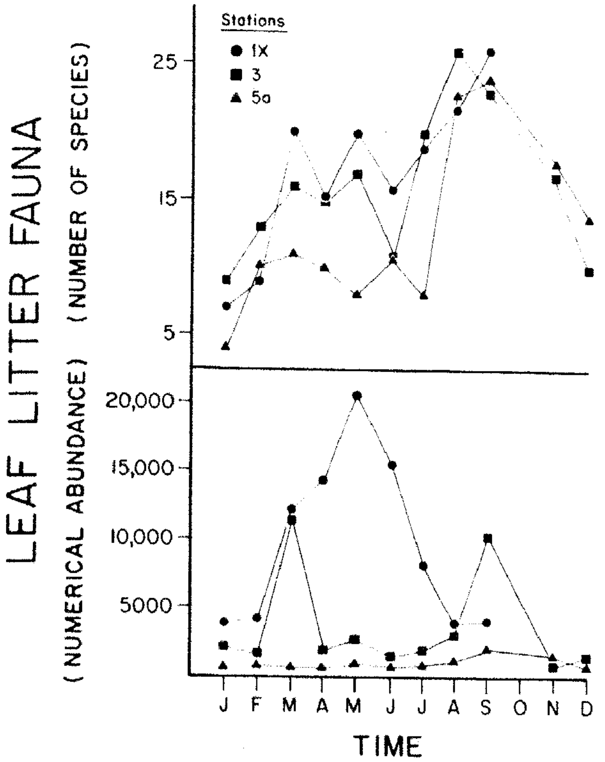


Figure 35. Numerical abundance and species richness of invertebrates taken in leaf-litter baskets at various permanent sampling sites in the Apalachicola estuary, monthly from January, 1976, through December, 1976. After Livingston (1978) and Livingston et al. (1977).

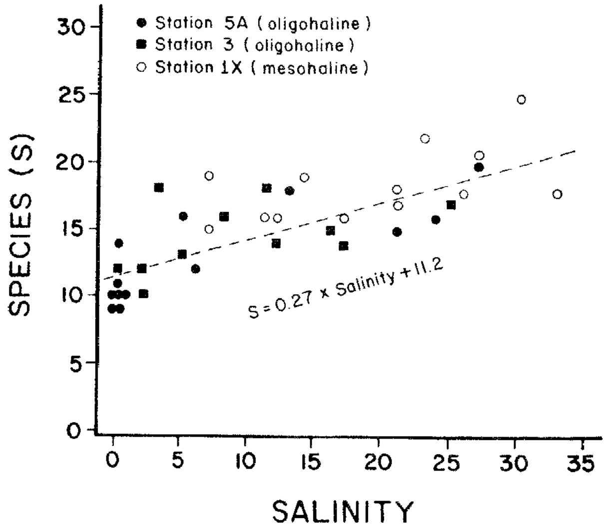


Figure 36. Regression of numbers of species of litter-associated macroinvertebrates on salinity at three stations in the Apalachicola estuary. Samples were taken over a 12-month period in oligohaline (stations 5A, 3) and mesohaline (station 1X) areas.

State University researchers indicate that biological associations are also important. Macroinvertebrates appear to utilize the detritus as shelter and a source of food (White in press). In a series of experiments with the leaf litter community, White et al. (1979a) found that, whereas the biomass (as measured by lipid phosphate and poly-beta-hydroxybutyrate), nutritional history, and respiratory activity of microbes are correlated with substrate type, the macrofaunal populations are more often associated with specific water quality features such as salinity. Numbers, biomass, and species richness of detritus-associated microfauna are associated with the mass and community structure of the macrofaunal food web. These macroinvertebrates apparently seek out microbial populations rich in anaerobic or microaerophilic bacteria. The data suggest that distinct populations may choose different microbes. The component energy linkages are poorly understood, however. Little is known concerning the protozoan components of litter associations, although preliminary analyses in East Bay indicate that ciliates constitute the dominant protozoan inhabitants of the litter assemblages (D. Cairns, pers. comm.).

In summary, physical/chemical features such as temperature and salinity influence the spatial-temporal distribution of litter-associated macroinvertebrates in the estuary. Such distribution is also determined by productivity trends and the biochemical features of the microbial communities. The detritivorous macroinvertebrates serve as a link between the microbial producers and important estuarine fishes and invertebrates that feed on these species (Laughlin 1979; Livingston et al. 1977; Sheridan 1978, 1979; Sheridan and Livingston 1979).

5.1.4. Oyster Bars

Oyster bars represent a relatively significant habitat in the estuary (Table 1). The main concentrations of oysters (*Crassostrea virginica*) (Figure 20) lie in St. Vincent Sound and western portions of St. George Sound. Oyster distribution is dependent upon substrate, temperature, salinity, and available food. Oyster bars, themselves, provide habitat and food for a variety of organisms. The oyster associated community includes sponges (*Cliona vastifica*), bryozoans (*Membranipora* sp.), flatworms (*Stylochus frontalis*), annelids (*Neanthes succinea*, *Polydora websteri*), various arthropod crustaceans (*Callinectes sapidus*, *Menippe mercenaria*, *Neopanope* spp., *Petrolisthes armatus*), gastropods (*Crepidula plana*, *Melongena corona*, *Thais haemastroma*), and pelecypods (*Brachidontes exusta*, *Chione cancellata*) (Menzel et al. 1966). Fishes include blennies (*Hypsoblennius* spp.) and toadfish (*Opsanus beta*). These organisms use the reef for shelter and/or feeding.

Salinity controls oyster-bar community organization. When salinities are high, various stenohaline gulf species are able to move into the oyster-rich areas and feed on the oysters. Low salinity limits such predation by acting as a barrier to those organisms. Species richness and diversity of the oyster-associated populations vary directly with seasonal increases in salinity. During warmer months, extensive oyster mortality in the Apalachicola estuary has been attributed to infestation by the pathogen *Perkinsus marinus* (formerly called *Dermocystidium marinum*) (Menzel 1983). Young oysters are unaffected by this disease, although up to 50% of adult oysters may be killed annually. The relatively long period of high water temperature in the gulf estuaries contributes to such mortality. A long-term study is currently under way to determine the response of the Apalachicola oyster associations to various stimuli including habitat features (water quality, substrate), predation, competition, disease, and possible over-fishing (Livingston et al., unpubl.).

5.1.5. Subtidal (Soft-Sediment) Communities

Almost 70% of the Apalachicola Bay system can be characterized as a subtidal, unvegetated, soft-sediment area (Table 1). The muddy bottom substrate is inhabited primarily by polychaetes (*Mediomastus ambiseta*, *Streblospio benedicti*) and amphipods (*Grandidierella bonnieroides*). The polychaetes are deposit and suspension feeders with a high reproductive capacity and considerable tolerance for low salinity and variable environmental conditions. Productivity trends, habitat type, and the ecological characteristics of the various populations contribute to what is a temporally variable but highly persistent assemblage of organisms in terms of species richness, relative abundance, and recruitment. In oligohaline areas of the estuary, the benthic macroinvertebrate assemblages are characterized by high dominance, low species richness, low diversity, and varying standing-crop biomass and numerical abundance (Livingston 1983c, d). Areas around the mouth of the river have much higher numbers of infaunal macroinvertebrates than areas outside of the region of general flow. Such differences have been attributed (Livingston 1983c, d) to the deposition of nutrients and detritus by the river during periods of flooding (Figure 9) and increased activity and abundance of the benthic macroinvertebrates (Figure 27).

The general community characteristics of the soft-bottom assemblages change as salinities increase temporally and spatially. In mesohaline and polyhaline portions of the system, overall numerical abundance is lower than in oligohaline areas, but species richness and diversity increase significantly (Livingston et al. 1983). Such trends are evident in the associations of epibenthic fishes and invertebrates, which are an important part of the soft-sediment communities. Dominant populations such as Atlantic croaker, spot, penaeid shrimp, and blue crabs feed extensively on organisms within the muddy bottom of the estuary.

The soft-sediment community (invertebrates and fishes) of the

Apalachicola estuary reflects the response of hundreds of species to a complex combination of physical, chemical, and biological factors. Physical control, together with productivity features, recruitment patterns, predator-prey interactions, and competition for various resources determine to a considerable degree the form and functions of the soft-sediment communities in the Apalachicola Bay system. Because the majority of the research in the Apalachicola Bay system has been carried out with the fishes and macroinvertebrates of the soft-sediment estuarine habitat, the interrelationships of the dominant features of these biological systems will be treated in a more detailed fashion below.

5.2. PHYSICAL CONTROL OF BIOLOGICAL PROCESSES

For some time, ecologists have argued about the relative importance of physical and biological control of aquatic populations and communities. Clearly, the problem is extremely complex, based on the fact that each species is a product of a given habitat while also having an input, through predation and competition, to the community. It is generally agreed that temperate estuaries such as the Apalachicola system are highly productive and physically unstable in space and time. Temperature and salinity have a major influence on the form and processes of the estuarine biota in such a system. At the same time, various populations interact with each other and their environment with almost continuous feed-back to the system as a whole.

The timed interactions of multiple physical and biological components of an estuarine system are difficult to differentiate for a variety of reasons. Individual physical events follow different temporal patterns. Often such phenomena are essentially cyclic although "cycle" does not necessarily imply that there is a complete return to a previous condition. Biological responses are not that simple and often follow nonlinear or curvilinear patterns of response to varying controlling factors. Analysis of biological responses requires the initial delineation of key dependent and independent variables. Experimental evaluation of hypotheses derived from observational data can then be used to determine the processes that define and ultimately control the observed structural components of the system.

Various attempts have been made to delineate the relationships of physical and biological variables in the Apalachicola estuary (Livingston 1975, 1976b, 1979, 1982b; Livingston and Loucks 1978; Livingston et al. 1974, 1976b, c, 1978; Mahoney and Livingston 1982; Meeter and Livingston 1978; Meeter et al. 1979). Most analyses indicate that Apalachicola River flow has a major influence on the physical and biological relationships in the estuary. For example, statistical analysis of the principal physico-chemical variables (Table 21) indicates that the main factor or component could be called "river flow." This river flow is associated with low salinity, increased color and turbidity (and reduced Secchi readings), and reduced chlorophyll _a_. River flow alone explained 32% of the total variance and about half of the variance explained by the four factors. Average bay values of major nutrients vary seasonally; high nutrient concentrations are found during high (winter) river discharge and low salinity conditions (Table 22). The Apalachicola River controls to a considerable degree various factors such as nutrient and detritus concentrations, salinity, color and turbidity, and other water quality factors. In turn, these conditions control the level and pattern of productivity fluctuations in the bay system.

Studies of temperate estuaries indicate that the combination of high primary productivity and extremely variable environmental conditions is often associated with relatively low species richness and diversity and high secondary productivity of a few dominant species. No matter which group of organisms is considered, from phytoplankton to fishes, salinity appears to be the primary regulator of species numbers at a given location in the estuary. Dominants are able to adapt to low or highly variable salinity conditions. Salinity is a major determinant of species richness (S) of

Table 21. Factor analysis of physico-chemical variables in the Apalachicola system taken monthly from March 1972 to February 1976. Color (Pt-Co units), turbidity (J.T.U.), Secchi readings (m), salinity (ppt), temperature (^{o}C), and chlorophyll a (mg l^{-1}) were noted at Station 1. Tidal data included stages of the tide on the day of collection while the wind variable was represented by two vector components (speed, direction) (from Meeter and Livingston 1978).

Variable	Factor 1 (49.0% of variance)	Factor 2 (22.3% of variance)	Factor 3 (17.9% of variance)	Factor 4 (10.8% of variance)
River flow	-0.82	-0.08	-0.07	-0.08
Local rainfall	-0.04	-0.30	-0.09	0.20
Tide (incoming or outgoing)	0.26	0.61	-0.68	0.06
Tide (high or low)	0.09	0.39	0.61	-0.37
Wind direction (E-W)	-0.02	0.09	0.36	0.37
Wind direction (N-S)	0.10	-0.20	0.22	0.31
Secchi	0.57	-0.07	-0.17	0.24
Color	-0.80	0.33	0.01	0.07
Turbidity	-0.73	0.54	0.08	0.23
Temperature	0.38	0.15	0.02	-0.18
Salinity	0.68	0.21	0.23	-0.02
Chlorophyll a	0.47	0.51	0.09	0.31

benthic macroinvertebrates taken (seasonally) in litter baskets at different stations (3, 5A, 1X) along a salinity gradient (Figure 36) ($F = 30.4$, $r^2 = 0.45$, with S as the dependent variable). Numbers of species taken during a season vary directly with salinity rather than with station-specific characteristics. Similarity coefficients of species composition at the sampled stations are closest during fall periods of high salinity. These results indicate that quantitative and qualitative species representation, regardless of location, are closely related to salinity.

Similar trends are found for phytoplankton (Estabrook 1973), zooplankton (Edmisten 1979), infaunal macroinvertebrates (Livingston unpublished data), and epibenthic fishes and invertebrates (Livingston 1979). Livingston (1979) showed that salinity is directly related to species richness and diversity of estuarine nekton. Stations characterized by low salinity are associated with high numbers of individuals, high relative dominance, and low species richness (Table 20). Outer bay stations, with higher salinities, are defined by relatively low dominance, high species richness and low numerical abundance. High densities of organisms that use the bay as a nursery, such as penaeid shrimp, blue crabs and various finfishes are not usually found in areas having stable patterns of relatively high salinity (Livingston 1984a).

Table 22. Correlation coefficients of linear regressions of nitrate, orthophosphate, silicate, and ammonia on salinity (from Livingston et al. 1974).

Date		NO_3	PO_4	SiO_3	NH_3
Oct. 14 1972	T	-0.70	-0.73		
	B	+0.12	-0.14		
Dec. 2 1972	T	-0.88	-0.20	-0.98	
	B	-0.75	-0.55	-0.85	
Jan. 6 1973	T	-0.55	-0.89	-0.99	
	B	-0.84	-0.82	-0.87	
Feb. 17 1973	T	+0.00	-0.95	-0.33	-0.02
	B	+0.58	-0.11	-0.002	-0.15
Mar. 19 1973	T	-0.95	-0.78	-0.98	-0.85
	B	-0.97	-0.60	-0.998	-0.45
Apr. 22 1973	T	-0.76	-0.77	-0.93	-0.67
	B	-0.62	-0.62	-0.80	-0.93
May 19 1973	T	-0.88	-0.54	-0.998	-0.48
	B	-0.96	-0.65	-0.99	-0.81
Jun. 11 1973	T	-0.60	-0.01	-0.995	-0.55
	B	-0.94	-0.61	-0.93	+0.06
Jul. 12 1973	T	-0.82	-0.10	-0.97	-0.82
	B	-0.80	+0.42	-0.93	+0.03
Aug. 22 1973	T	-0.90	+0.04	-0.95	-0.50
	B	-0.91	-0.84	-0.94	-0.91
Sep. 10 1973	T	-0.99	-0.29	-0.995	-0.83
	B	-0.98	+0.15	-0.99	-0.98

Species richness and diversity of nekton are directly associated with areas of high environmental stability but low secondary productivity. Infaunal macroinvertebrates show the same general response to salinity (Livingston 1983d). Within a given area of low salinity, however, species richness may increase in areas of relatively high primary productivity and detritus availability. In this way, the influence of salinity may be modified by ambient habitat conditions.

In low-salinity estuaries, species diversity indices tend to reflect the effects of salinity on recruitment of dominant populations. Within a given habitat (such as an oyster bar, unvegetated soft-sediment area, or seagrass bed), the spatial distribution of organisms at any given time may depend on gradients of productivity and salinity. The regulating features may change their relative importance through any given seasonal succession. Temperature and other physical features seasonally modify the productivity-salinity association. Among the phytoplankton, water temperature is the primary limiting factor, although river discharge, nutrients (mainly phosphorus), turbidity, and light inhibition may control phytoplankton productivity at different times of the year. Estabrook (1973) noted that grazing zooplankton also may control phytoplankton productivity since experiments removing zooplankton and net plankton enhanced nannoplankton productivity greatly. The possibility exists that competition for nutrients among various species also is an important determinant of relative phytoplankton dominance.

Among the zooplankton, copepods are dominant. The copepod *Acartia tonsa* constitutes 95.5% of total zooplankton in East Bay, 68.2% in Apalachicola Bay and 19.8% in coastal waters (Edmisten 1979). Salinity and temperature control the composition of zooplankton communities in the estuary. Populations of *Acartia* vary inversely with distance from the mouth of the Apalachicola River and are concentrated in Apalachicola Bay. Temperature is associated with significant ($p < 0.01$) differences in *Acartia* numbers. Salinity significantly ($p < 0.01$) affects the overall relative abundance of the dominant populations. Edmisten (1979) showed that temperature, salinity, station and month had a multiple r value of 0.775. In East Bay, *Acartia* numbers (as well as zooplankton numbers and biomass) peak during periods of high salinity. Thus, temperature usually determines overall numbers in the bay system, while salinity determines their spatial distribution at any given time. The response to midrange salinities explains the nonlinear (parabolic) relationship of *Acartia* with salinity,. It appears that other organisms can successfully complete with *Acartia* at higher and lower salinities.

Life history strategies of various nektonic estuarine species depend to some degree on spatial/temporal gradients of substrate type, salinity, food availability, and energy flow. The spatial distribution and abundance of brief squid (*Lolliguncula brevis*) is determined to a considerable degree by salinity and temperature (Laughlin and Livingston 1982). Optimal salinities range between 25 and 30 ppt. Squid tend to congregate near the passes during summer and fall periods of high salinity. Distribution within the estuary is associated with the distribution of zooplankton in the bay. Population trends of squid followed long-term (9-year) salinity trends that, in turn, were associated with climatic features. There were sharp decines in squid abundance during periods of low salinity.

Overall, attempts to correlate patterns of species abundance with individual physical, chemical, and productivity variables have not been entirely successful. A multiple regression analysis of individual population densities with combinations of independent variables indicates that such components accounted for less than 50% of the population variability (Table 23). No single set of physical conditions explained population variation through time. While factors such as temperature, salinity, productivity, and water quality characteristics are important determinants of general habitat availability, it is clear that other factors, presumably biological in nature, may be important to our understanding of the processes that determine the community structure of the Apalachicola Bay system.

5.3. TROPHIC RELATIONSHIPS AND FOOD-WEB STRUCTURE

Community structure is determined in part by predator-prey interactions, especially among dominant estuarine populations. Comprehensive studies of the feeding habits of dominant fishes (Sheridan 1978; Sheridan and Livingston 1979) and invertebrates (Laughlin 1979) have been carried out (Figure 37). Pelagic anchovies feed preimarily on calanoid copepods throughout their lives. Seventy percent of the diet of young anchovies (standard length (SL), 10-39 mm) is composed of these copepods. Larger fish (SL 40-69 mm) eat mysids, insect larvae and juvenile fishes. A seasonal progression of food item consumption follows trends of available prey species. The Atlantic croakers progress through a series of distinct ontogenetic trophic stages. Young fish (SL 10-30 mm) eat insect larvae, calanoid copepods, and harpacticoid copepods. Midrange fish (SL 40-99 mm) consume detritus, mysids, and isopods; larger fish (SL 100-159 mm) eat a high proportion of juvenile fishes, crabs, and infaunal shrimp. Croaker at all stages eat polychaete worms. Spot, which

Table 23. Results of a stepwise regression analysis of various independent parameters and species (numerical abundance) in the Apalachicola estuary from March 1972 to February 1975. Independent variables are listed by order of importance with R^2 expressed as a cumulative function of the given parameters (from Livingston et al. 1976b). Independent variables were run with and without lag periods of 1-3 months.

Species	Independent variables	R^2
Anchoa mitchilli	Chlorophyll *a*, Secchi	0.38
Micropogonias undulatus	River flow (lag), Secchi (lag)	0.46
Cynoscion arenarius	Chlorophyll *a*, wind, Secchi (lag) temp.	0.83
Polydactylus octonemus	Chlorophyll *a* (lag), salinity, Secchi	0.58
Arius felis	Temp., wind	0.30
Leiostomus xanthurus	Turbidity (lag), Secchi, salinity, temp.	0.85
Chloroscombrus chrysurus	Temp. (lag), temp., salinity	0.44
Menticirrhus americanus	Temp. (lag)	0.19
Symphurus plagiusa	Color (lag), color, Secchi	0.63
Bairdiella chrysura	Wind, temp., color	0.40
Penaeus setiferus	Wind, chlorophyll *a*, incoming tide, color	0.48
Palaemonetes pugio	Turbidity	0.49
Callinectes sapidus	Secchi, incoming tide	0.43
Penaeus duorarum	Chlorophyll *a*, Secchi	0.41
Lolliguncula brevis	Chlorophyll *a* (lag), temp.	0.43
Portunus gibbesii	Chlorophyll *a* (lag), Secchi	0.39
Palaemonetes vulgaris	Turbidity	0.32
Rhithropanopeus harrisii	Wind	0.18
Callinectes similis	Chlorophyll *a*, temp.	0.34

are also benthic omnivores, consume polychaetes, harpacticoid copepods, bivalves, and nematodes. Spot have a more diverse diet than croaker and do not concentrate on single prey types. Trends across size classes are not as clearcut, although there is decreased specialization with growth. The sand seatrout is a water-column predator of fishes and mysid shrimp (*Mysidopsis bahia*). Small trout (SL 10-29 mm) tend to eat mysids and calanoid copepods, while larger fish (SL 30-89 mm) consume more juvenile fishes. Anchovies (*Anchoa mitchilli*) comprise 70% of all fishes taken.

Fishes regularly undergo ontogenetic dietary shifts encompassing planktivory, carnivory, omnivory, and herbivory within the same species (Sheridan 1978; Sheridan and Livingston 1979; Livingston 1979, 1982). Sheridan and Livingston (1979) indicated that temporal differences in feeding progressions were a major factor in the lack of overlap in food types among species. Laughlin (1979) found that blue crabs also undergo trophic progressions. Juveniles, abundant during winter months, feed largely on plant matter, detritus, and bivalve mollusks such as *Rangia cuneata*, *Brachidontes exustus*, and *Crassostrea virginica*. As the crab grows, bivalves and fishes become progressively more important in the diet. Larger blue crabs feed primarily on bivalves, fishes, and crabs (i.e., blue crabs, mud crabs such as *rhithropanopeus harrisi*, and xanthid crabs of the genus *Neopanope*). Cannibalism is a significant mode of foraging in the older blue crabs. Diet generally reflects seasonal shifts of prey abundance.

Although the distinctive nutrient sources for the estuary have been identified, the rate functions of energy movement through the system are little understood. The periodic inputs of nutrients and detritus into the estuary are transformed into biological matter. Such integrative processes continuously smooth out the episodic nature of energy

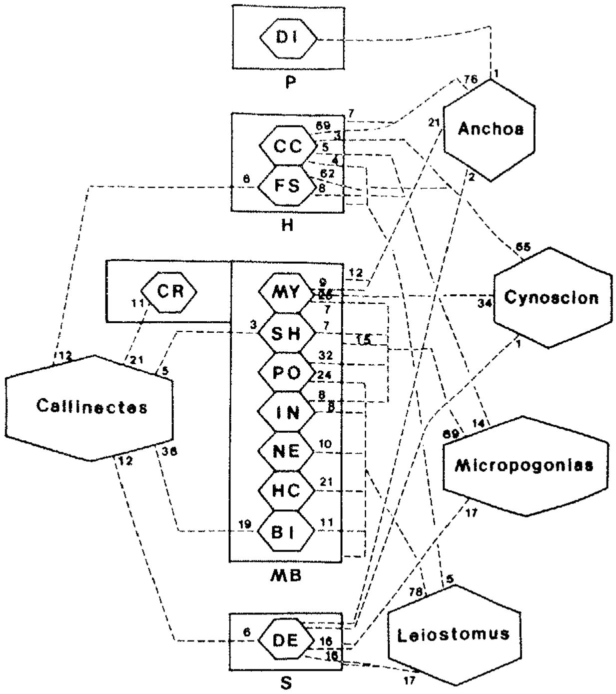


Figure 37. Simplified feeding associations of four dominant fishes--bay anchovy, sand seatrout, Atlantic croaker, spot--and blue crabs in the Apalachicola estuary. Four food compartments are shown: phytoplankton (P), holoplankton (H), meroplankton and benthos (MB), and sediments (S). Major food items in the compartments are: DE=detritus, BI=bivalves, HC=harpacticoid copepods, NE=nematodes, IN=insects, PO=polychaetes, SH=shrimp, MY=mysids, CR=crabs, FS=fishes, CC=calanoid copepods, DI=diatoms. Numbers indicate dry-weight contribution of particular food items (within boxes) and food contributions of major food compartments (after Laughlin 1979 and Sheridan 1978).

transfer from upland systems. The planktonic and detrital pathways come together at the sediment level through repackaging of fecal material and the activity of the microorganisms. The microbes transform dissolved nutrients into available particulate matter. Over 2% of the dry-weight mass of the sediments is composed of organic carbon, bacterial biomass, and extracellular polysaccharides (D. C. White personal communication). The sediment organic matrix and POM form the basis of the benthic (detrital) food webs. The grazing of detritus and its microbial populations enhances nutrient quality for subsequent microbial development by stimulating further microbial productivity and enhancing the nitrogen and phosphorus content of the POM. Physical disturbance, through wind and tidal action and active predation and biological activity, is one of the reasons why the Apalachicola estuary is such a productive system.

Seasonal relationships among the various physical and biological factors in the bay system have been developed (Figure 38). Although the biological response to a given event usually follows a nonlinear or curvilinear pattern, certain relationships have become evident after many years of observation. Seasonal variations of temperature and the pulsed river flow are usually out of phase. Local rainfall (Florida) peaks during summer months. Salinity in the estuary is highest during summer and fall months. The timing of the river flow, and the resultant loading of nutrients and POM, is critical to the seasonal biological successions in the estuary, especially during winter and early spring. During such periods of low winter temperature and salinity and high river flow and detrital movement into the estuary, benthic infaunal abundance is high. Epibenthic organisms (especially fishes) reach peak levels during late winter as temperature starts to increase and macroinvertebrates available for food are abundant. Benthic omnivores such as spot and the Atlantic croaker are favored by such conditions. Although these sciaenids overlap in their temporal distribution, food size partitioning by these two bottom-feeding fishes results in distinctive differences in prey type and size (Sheridan 1978). A larger apparatus allows croaker to penetrate deeper into the substrate and consume larger polychaetes, shrimp, and crabs. Spot tend to exploit smaller organisms, such as nematodes, harpacticoid copepods, juvenile bivalves, and smaller forms of polychaetes. There is enough dietary overlap, however, to allow the potential for competition between these two species.

Benthic macroinvertebrates occupy an important trophic link between the primary producers (and microbes) and the upper

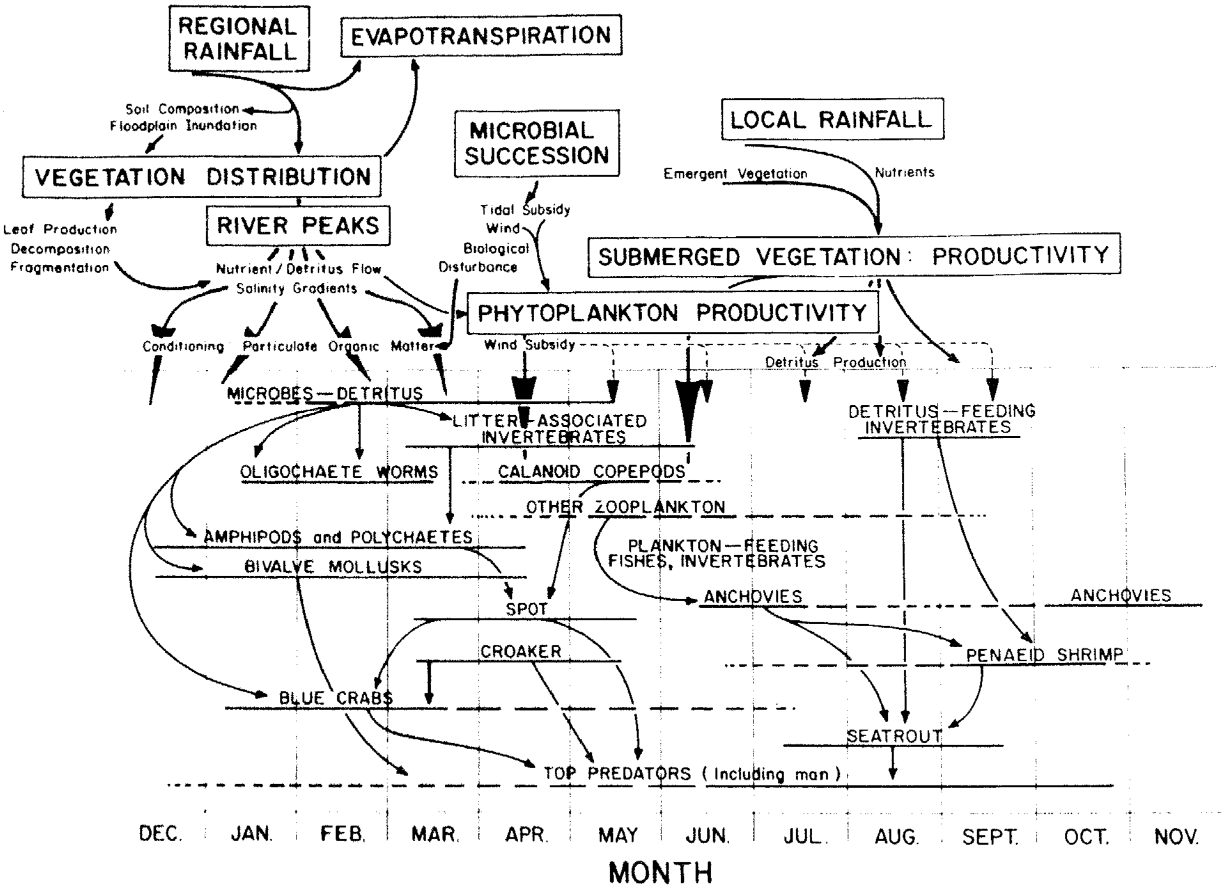


Figure 38. Generalized, simplified model of seasonal relationships of the dominant macroinvertebrates and fishes in the Apalachicola Bay system. The model associates population distribution with seasonal changes in key physical variables, productivity features, and the predator-prey relationships of the estuary.

trophic levels of the estuary. Of the 10 numerically dominant infaunal species (representing over 83% of the total number), five are detrital feeders, four are deposit feeders (surface and subsurface), and one is a filter feeder. Of the entire infaunal assemblage, there are fifteen omnivore/carnivore types, seven subsurface deposit feeders, eleven surface deposit feeders, twelve (generalized) deposit feeders, and seven filter feeders. There are high numbers of the various filter-feeding mollusks such as Rangia cuneata and Crassostrea virginica.

The important role of detritus and its associated microbial components is indicated by the predominance of the detritivore/omnivore feeders in the macroinvertebrate assemblages. Of the dominant litter-associated organisms, the polychaetes are generally omnivorous, consuming fine detritus, microalgae, copepods, and amphipods. The gastropods in the litter include omnivores, filter feeders, scavengers, suspension feeders, and carnivores. The herbivorous snail Neritina reclivata is a major species in the grassbeds of East Bay. The amphipods found among the litter assemblages include omnivores, detritus feeders (or leaf scavengers) and, in the case of some gammarids, filter feeders. A few species such as Hyalella azteca, Gammarus lacustris, and Melita spp. are known to be leaf shredders (i.e., herbivores), although other amphipods are predaceous, feeding on hydroids, bryozoans, and (possibly) zooplankton. Crustaceans such as the tanaid Hargeria rapax are generally omnivores, but some are shredders or parasites. Mysid shrimp generally feed on fine detritus and diatoms. Decapod crustaceans found in the litter associations are largely omnivores and detritus feeders, although certain dominants, such as penaeid shrimp and blue crabs, are predominately carnivorous during certain life stages.

During the spring months, river flow discharge decreases, salinity increases, and the water clears. These conditions trigger the late spring phytoplankton blooms and associated zooplankton increases. The spring plankton peaks are concurrent with increased relative abundances of planktivorous fishes such as anchovies and menhaden. As the temperature increases and river flow falls, the high numbers of infaunal macroinvertebrates fall precipitously. As a result, by the end of spring there are few spot and Atlantic croaker in the bay, and the sand seatrout, feeding on anchovies, becomes the dominant scianid. Sheridan (1978) postulated that the summer anchovy peaks are truncated by sand seatrout. There is little trophic interaction of the sand seatrout with other dominant fish predators; likewise, there is little dietary overlap of these species during their concurrent periods in the estuary (May-August). During such periods, predation pressure on penaeid shrimp and crabs is low. By fall, most of the sand seatrout have moved out of the estuary and anchovies become dominant.

As temperature peaks during the summer, the numbers of invertebrates (penaeid shrimp, blue crabs) increase (Figure 27). During this time, local rainfall reaches seasonally high levels. Benthic macrophytes attain peak productivity and standing crop. By the end of summer, macrophytes start to die off, and estuarine detritus levels increase as the temperature begins to decline and salinity increases throughout the estuary. By early fall, the numbers of species of fishes and invertebrate species reach high levels. One possible explanation for this situation is that those species limited by low salinity during most of the year are able to enter the shallow portions of the estuary at this time. Other factors that could enhance the observed high numbers of species during the fall could be falling temperatures (to optimal levels) and the availability of detritus and/or detritivorous invertebrates as food.

An overwhelming majority of the estuarine nekton is omnivorous at some life-history stage, and detritus forms an important component of stomach contents at any given time (Sheridan 1978; Sheridan and Livingston 1979; Livingston 1982b). Of the seven dominant macroinvertebrates, representing over 90% of the trawl-susceptible catch, five (Peaneus setiferus, Palaemonetes pugio, Callinectes sapidus, Penaeus aztecus and Lolliguncula brevis) are omnivore/carnivore types; Neritina reclivata is an herbivore, and Lolliguncula brevis is a zooplanktivore. While the nutritional importance of the detritus remains in doubt, omnivory appears to be an important characteristic of the predominant feeding patterns at intermediate levels of the estuarine food webs.

Top predators, feeding largely on decapod crustaceans and fishes during the fall, include spotted seatrout (Cynoscion nebulosus), flatfishes (Paralichthys spp.), adult silver perch (Bairdiella chrysoura), searobins (Prionotus spp.), and various shark types.

During November, as the temperature drops rapidly, epibenthic organisms decrease and various migratory species leave the estuary for nearshore gulf waters as part of their annual migration. Penaeid shrimp are an example of this type of population behavior. River flow starts to increase during the early winter, and salinity goes down. Benthic infaunal species richness and abundance increase as winter progresses (Figure 27).

The seasonal succession of habitat change, energy distribution, species-specific recruitment patterns, predator-prey relationships, and the resulting food web configurations contribute to the biological organization of the estuary. Infaunal macroinvertebrates reach maximum abundance from November through March, although species richness is highest in May. As indicated previously, phytoplankton and zooplankton are abundant during spring months and summer periods. Fish abundance peaks during winter and early spring although fish and invertebrate species richness indices reach their highest level in October. Epibenthic invertebrate abundance, on the other hand, is high during August when penaeid shrimp and blue crabs are prevalent. In general, the dominant fish species, while overlapping in abundance to some degree, tend to predominate during different times of the year; high croaker and spot abundance occurs in winter and early spring, sand seatrout in summer, and anchovies in the fall and early winter. Water column feeders such as anchovies are linked to plankton outbursts and predation pressure from species such as sand seatrout. Benthic feeders occur primarily during periods of detritus/macroinvertebrate abundance. Croakers and spot feed largely on polychaetes, while blue crabs concentrate on bivalves. Directly or indirectly, most such species take advantage of the detritus that is brought into the estuary by the river. The combination of low salinity, high POM, and low predation pressure contributes to the observed high relative abundance of these species.

5.4. PREDATOR-PREY INTERACTIONS AND COMMUNITY RESPONSE

Although productivity trends and habitat characteristics are important factors in the development and control of food web and community structure, biological features such as predator-prey relationships and competition for resources can be extremely important in affecting the biological organization of the estuary. Predation within aquatic associations can lead to changes in relative abundance, species diversity, and other important community indices. Peterson (1979) reviewed factors that relate the impact of predation and competitive exclusion to the response of benthic macroinvertebrates in unvegetated, soft-sediment estuarine habitats. Previous work with various marine assemblages (largely rocky intertidal communities) has indicated that isolation from predation (through manipulative processes such as caging) should lead to increased total density, increased species richness, and restriction of competitive exclusion by particular dominant species (Peterson 1979). According to this model, manipulative predator exclusion should cause simplification of the prey community as a result of enhanced competition due to increased population densities. Various authors have found that soft-bottom associations of benthic macroinvertebrates do not always follow such a paradigm (Peterson 1979). A series of tests of this basic hypothesis has been carried out in the Apalachicola Bay system over the past 3 years.

Inverse correlations between predator and prey population do exist in the Apalachicola estuary (Sheridan and Livingston 1983). Macroinfaunal abundance often declines precipitously during periods of peak abundance of the chief sciaenid predators (Mahoney and Livingston 1982). Such correlative results suggest that fishes may have a direct influence on the infaunal assemblages through predation. In grassbed areas, however, infaunal biomass is not affected because larger species (burrowing deeper in the sediments) are not influenced by such predation. Also, recent experiments indicate that macroinvertebrate assemblages in East Bay remain largely unaffected by predation pressure from fishes in the late winter and spring and by motile invertebrates (penaeid shrimp, blue crabs) in the summer/fall (Mahoney and Livingston 1982; Livingston unpubl.). Thus, predation does not appear to play a decisive role in the regulation of prey density or macroinvertebrate community structure in oligohaline portions of the estuary during periods of peak predation pressure.

One possible explanation of the apparent contradiction of the predation paradigm could lie in the recruitment potential of the dominant infaunal species. In a series of experiments with azoic sediments (i.e., devoid of macroinvertebrates), Mahoney (1982) found that infaunal larval recruitment was a deciding factor in the population dynamics of various macroinvertebrate species such as *Streblospio benedicti* and *Capitella capitata*. Such organisms are characterized by extremely short life cycles. Rapid reproduction and larval settlement could mask the impact of physical and biological disturbances, which are often important features of temperate estuaries. Heavy larval recruitment is not always followed by predominance of a given species, however. Other factors such as habitat suitability and competition could also be implicated in the determination of community structure.

At various levels of biological organization in the estuary, the dominant macroinvertebrate populations are opportunistic and are influenced to varying degrees by the high productivity and physical instability of the system. Such populations have adapted well to habitat instability and variability. Response time to disturbance remains little understood, however. Recent experiments in polyhaline portions of the bay system (Livingston et al. 1983) indicate that salinity could be a factor in the influence of predation on benthic infaunal associations. Infaunal macroinvertebrates in the field were manipulated using a series of treatments that involved exclusion cages (i.e., predators were kept out), inclusion cages (i.e., predators were returned to exclusion cages), and field controls. These treatments were compared to laboratory microcosms taken from the field. Preliminary results indicate that, over a 6-week period of observation, there were increased numbers of macroinvertebrates in the laboratory microcosms and exclusion cages. Species diversity was reduced in such treatments relative to field controls and inclusion cages. Thus predation in polyhaline areas of high macroinvertebrate diversity and low dominance may affect infaunal macroinvertebrate community structure. The influence of salinity on species diversity and relative dominance could thus be a factor in the relative influence of predation pressure on dominant populations in various portions of the estuary. In areas of low dominance, the influence of predation may be enhanced relative to oligohaline areas where dominance is naturally high. In any case, few generalizations of predation effects can be made without due consideration to local habitat conditions.

CHAPTER 6
LONG-TERM ECOLOGICAL RELATIONSHIPS

Although diurnal and seasonal changes in population and community structure in the estuary are relatively well documented (Livingston 1976b, 1977a, 1977d, 1978; Livingston et al. 1974, 1977), the long-term biological relationships, measured in decades, are still under consideration (Livingston unpublished data; Appendix A). Seasonal changes in important physical and chemical factors are relatively stable in terms of timing (Figures 9, 12); however, there is considerable annual or year-to-year variation of such factors (Figures 10, 14, 15, 16, 17). The coupling between climatological features such as river flow and long-term changes in the commercial catches of oysters, shrimp, and crabs (Meeter et al. 1979) is often complicated by socioeconomic influences on such data (Whitfield and Beaumariage 1977).

The specific short-term distribution of a given species is often associated with complex habitat variables and the availability of food. At the same time, long-term changes in a given population in the estuary may be influenced by climatological cycles. Thus, the monthly distribution of brief squid (*Lollinguncula brevis*) depends to a considerable degree on fluctuations of zooplankton abundance, but the timing and annual abundance of this species is also associated with recurrent cycles of salinity and temperature (Figure 39; Laughlin and Livingston 1982). Spring migration into the estuary has been correlated with specific changes in both temperature and salinity, while the fall emigration largely depends on temperature changes. Timing of the succession of climatological changes is important since a specific temperature has entirely different meanings to a given species in the spring and in the fall.

Long-term patterns of blue crab (*Callinectes sapidus*) recruitment cannot be determined solely by the physical and chemical environment (Figure 40; Laughlin and Livingston, unpubl.). For any given year, the winter recruitment was inversely related to blue crab population abundance and to summer recruitment levels. The variable size 1 (monthly mean frequencies of crabs of 1-30 mm; Table 24) was inversely correlated with temperature ($p < 0.01$) and with variable size 3 (monthly mean frequencies of crabs > 61 mm) ($p < 0.05$). No significant correlations were found with river flow or local rainfall, which were associated with peak recruitments at different times of the year. In a multiple regression with variable size 1 as the dependent variable (Table 25A, N = 12 months), temperature, rainfall, and variable size 2 explained about 89% of the variability of relative abundance. The variable size 2 was weakly correlated with all other variables (Table 25B). In a multiple regression with variable size 3 as the dependent variable, temperature, river flow, size 1 and size 2 explained about 70% of the variability of relative abundance (Table 25C).

Winter recruitment was below the 6-year average (59 crabs/month) in 1972-73, 1974-75 and 1975-76. A single high peak, however, occurred in 1973 and was correlated with the highest peak of river flow of the 6-year period (Figure 40). During the winter months of these years, river flow (which largely determines salinity values in the estuary) reached high (1973), intermediate (1975), and low (1976) values, whereas water temperatures deviated little (± 1° C) from the 6-year temperature mean (14.9° C). By contrast, summer recruitment for each of these years was well above the 6-year

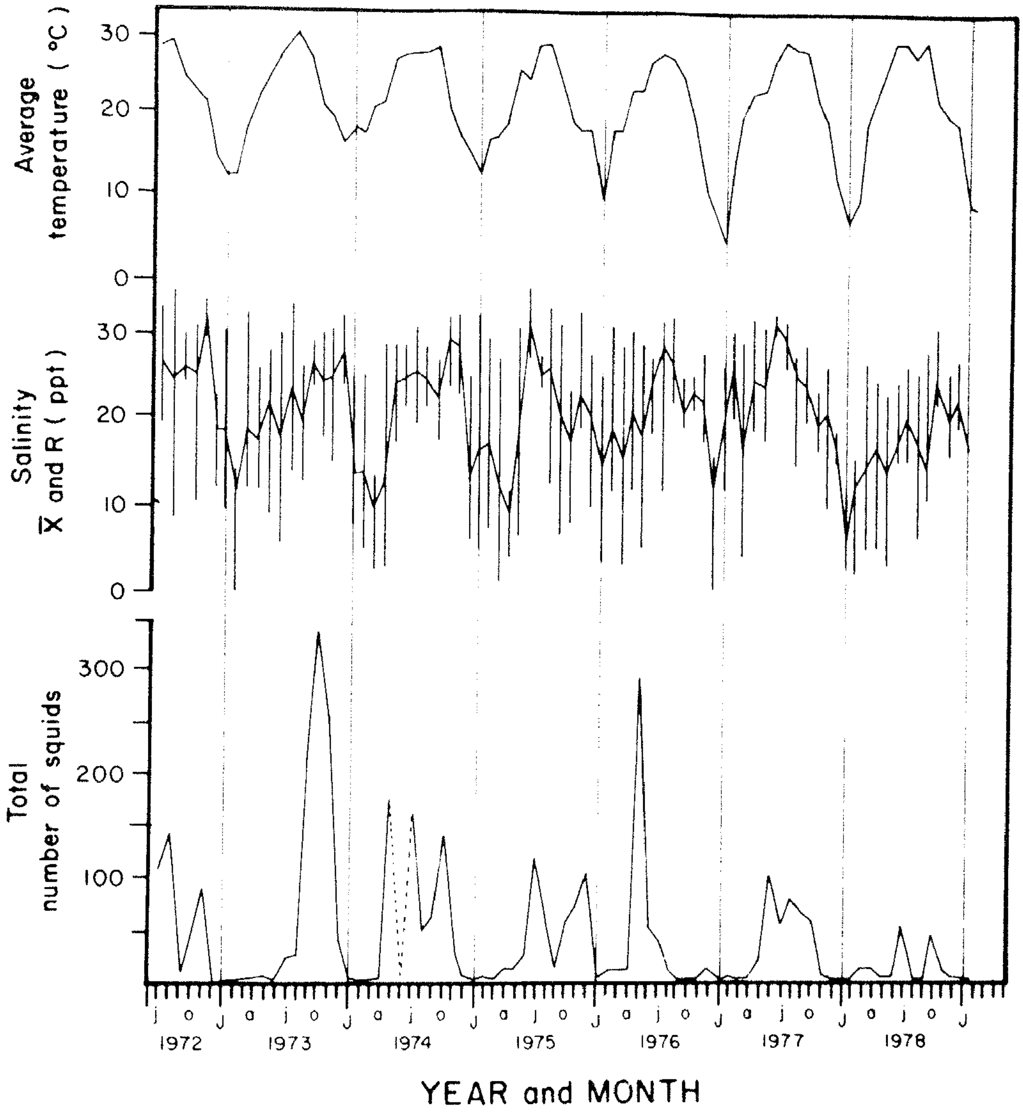


Figure 39. Long-term fluctuations of squid abundance, salinity, and temperature at stations 1A, 1B, and 1C in the Apalachicola estuary from June 1972 through March 1979 (Laughlin and Livingston 1982).

average (51 crabs/month) and was not directly correlated with abiotic or physico-chemical factors; summer rainfall varied from minimal (1976) to maximal (1975) values and temperature varied little. The total population abundance (all sizes) following the winter recruitments of 1972-73, 1974-75, and 1975-76 was above the 6-year average (59 crabs/ month). Summer recruitment values were not included in these calculations. Alternatively, winter recruitment was above the annual mean in 1973-74, 1976-77, and 1977-78, and was correlated with relatively high (1974, 1977) and low (1978) winter river flow. Water temperatures were just above the average in 1974 and markedly low in 1977 and 1978. Summer recruitment levels and total population abundance following the winters of these years were all below the 6-year average. In fact, dramatic decreases in total numbers of crabs occurred in 1974 and 1978. Again, none of these values was significantly correlated with any single abiotic factor. With the exception of

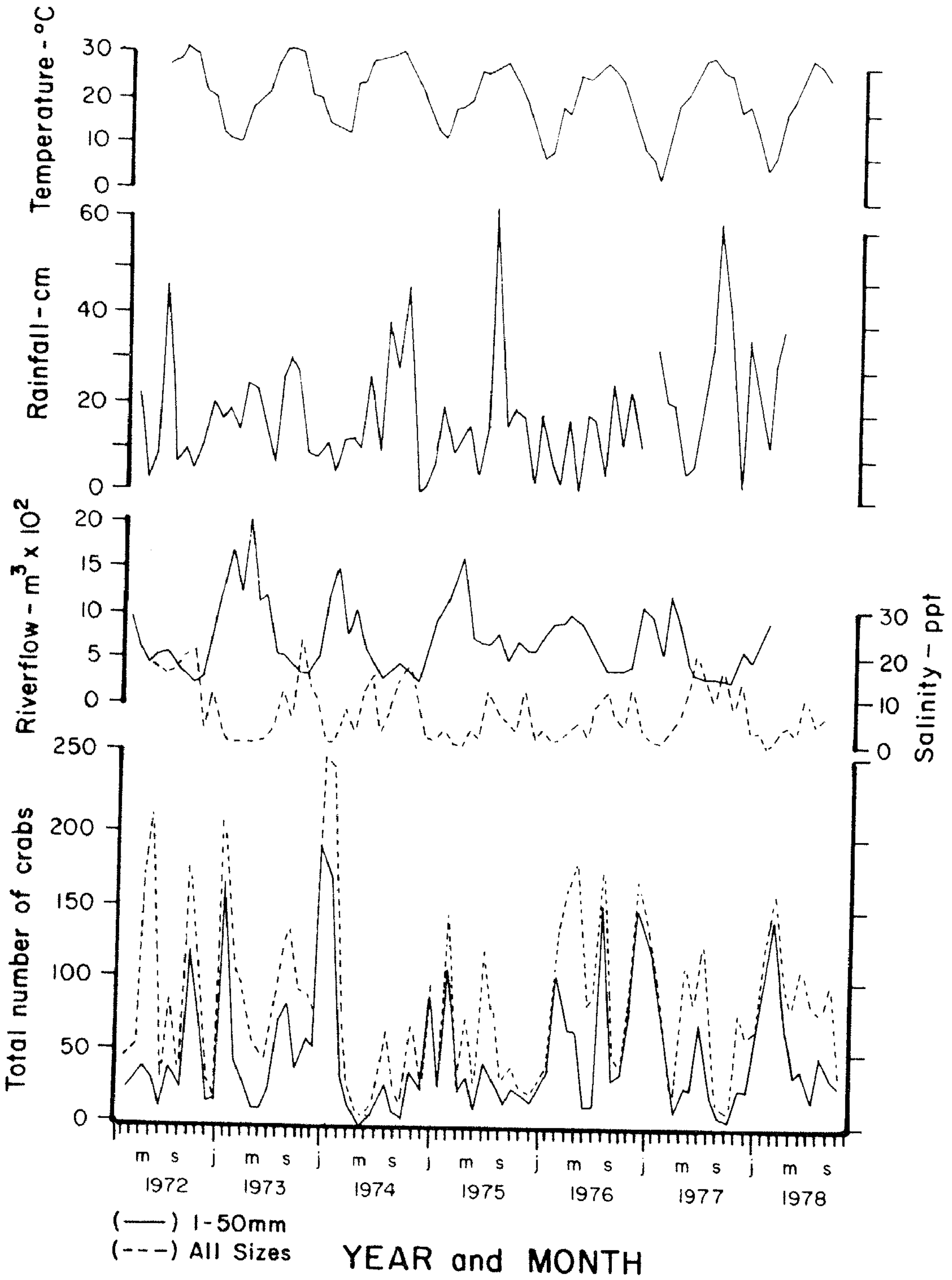


Figure 40. Monthly frequencies of blue crabs and variations in important physicochemical parameters at the 10 day-time stations in the Apalachicola estuary from March 1972 through March 1978 (Laughlin and Livingston, unpubl.).

Table 24. Parametric (r) and nonparametric (T) correlations of seasonal variations of blue crab frequencies and abiotic variables. Variables represent monthly averages of monthly data for 7 years. Salinity and temperature means are baywide over 14 stations in the Apalachicola estuary (from Laughlin and Livingston unpubl.). Correlation matrix - Seasonal variations (N = 12).

Variables		Size 2	Size 3	Salinity	Temperature	River flow	Rainfall
Size 1	r	0.323	-0.690*	-0.616*	-0.774**	-0.450	-0.070
(1-30 mm)	T	0.156	-0.554*	-0.351	-0.534**	-0.260	-0.040
Size 2	r		0.147	-0.526	-0.212	-0.570	0.340
(31-60 mm)	T		-0.015	-0.325	-0.294	-0.387*	-0.236
Size 3	r			0.172	0.690*	-0.017	0.135
(60 mm)	T				0.656**	0.040	0.108
Salinity	r				0.586*	-0.918**	0.306
	T				0.330	-0.697*	0.060

$^{*}p < 0.05$.
$^{**}p < 0.01$.

Table 25. Multiple stepwise regression of seasonal variations of frequencies of blue crabs from three size groups and abiotic variables (N=12 months). Variables represent mean monthly averages using 7-year data. Salinity and temperature means are baywide over 14 stations in the Apalachicola estuary (from Laughlin and Livingston unpubl).

A. Dependent variable — Size (< 30 mm carapace width)

Step	Variables entered	R^2	Significance
1	temperature	0.559	0.003
2	rainfall	0.800	0.001
3	size 2(31-60 mm)	0.890	0.0001
4	size 3(60 mm)	0.908	0.001

B. Dependent variable — Size 2 (31-60 mm)

Step	Variables entered	R^2	Significance
1	riverflow	0.323	0.054
2	size 3(60 mm)	0.348	0.146 (N.S)
3	size 1 (1-30 mm)	0.430	0.191 (N.S)

C. Dependent variable — Size 3 (> 60 mm)

Step	Variable entered	R^2	Significance
1	temperature	0.478	0.013
2	riverflow	0.570	0.022
3	size 1(1-30 mm)	0.650	0.028
4	size 2(31-60 mm)	0.704	0.048

1978, years with high levels of winter recruitment were preceded by years of high population abundances; however, the opposite was not true for winters of low recruitments.

Unlike the brief squid, there was no significant linear relationships between blue crab population parameters and abiotic factors. Including 1-, 2-, and 3-month time lags of the abiotic variables did not improve such linear relationships. However, for a given year, there was a significant inverse correlation between winter recruitment and the following summer recruitment ($p < 0.1$). In other words, in any given year, above-average winter recruitment was usually followed by a sharp decrease in total population and by low summer recruitment levels. Conversely, relatively high population abundances and high levels of summer recruitments followed winters of low recruitment levels. Thus, long-term population features of these dominant invertebrate species (brief squid and blue crabs) are dependent on different factors.

Temporal variability is extremely complex since, at any given instant, a natural system represents a composite of different sequences of varying periods superimposed over one another as the result of an almost infinite number of cause-and-effect reactions. Determining causality is difficult because these overlapping cycles may differ along habitat gradients and at different levels of biological organization. Consequently, the term "background noise" has become a euphemism for our inability to determine the temporal or sequential cause and effect relationships. Modeling efforts often assume that systems are in a state of equilibrium, without defining the actual extent of temporal variability. Terms such as stability, resilience, and diversity are used to give a theoretical framework to what is essentially a lack of consistent observations of organisms under field conditions.

Annual variability among dominant fish populations in the Apalachicola estuary was considerable (Figure 41). Each species followed a distinct, long-term pattern of abundance; no single aspect of the physical environment was apparent as the controlling factor of the long-term changes. Bay anchovies were most dominant during periods of high salinity. The sand seatrout population tended to follow the anchovy pattern with particularly low numbers during the year of peak flooding when anchovies were also low (1973). The Atlantic croaker followed no obvious pattern relative to temperature or salinity. Spot showed the highest year-to-year variability with relatively high numbers taken during the winter-spring months of 1981. The cold winters of 1976-77 and 1977-78 did not appear to affect any of the dominant fish populations in the Apalachicola estuary. It is clear that factors other than temperature and salinity are important in the control of long-term fluctuations of these populations.

Although generalized temperature and salinity preferences are well established for various estuarine species (Table 17), most such organisms have a relatively wide tolerance for these factors. Tolerance of this kind could explain the lack of importance of these factors in the determination of long-term population variability (Table 23). When viewed from the aspect of relative (percentage) abundance, a certain temporal regularity of the appearance of the dominant fishes and invertebrates becomes apparent (Livingston et al. 1976b; Figure 42). For example, relative occurrence of Palaemonetes pugio is high during spring while Penaeus setiferus was dominant during late summer and fall. The blue crab is abundant during winter periods. Among the fishes, sand seatrout are dominant during the spring and summer while bay anchovies (after the first year of sampling) predominate in the fall and Atlantic croaker prevail during the late winter and spring. When a comparison is made among the dominant fishes for peaks of abundance, such increases tend to be evenly distributed over a 12-month period. However, of the top invertebrates, most abundance peaks occur during fall periods (September-November) with secondary concentrations of peaks during early summer (May-June). The major dominants for both fishes and invertebrates thus

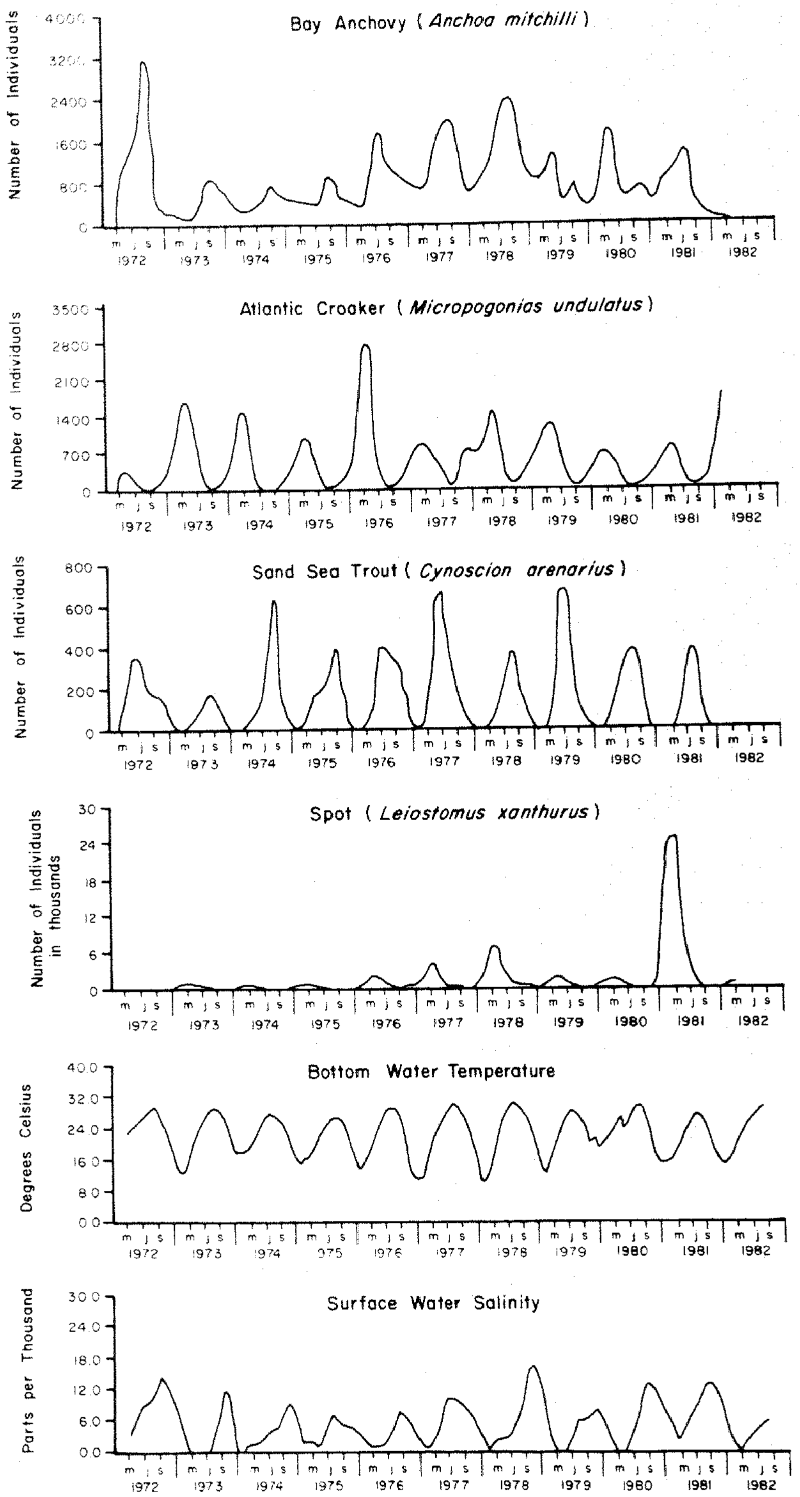


Figure 41. Long-term abundance patterns in the dominant trawlable fish populations in the Apalachicola estuary from March 1972 through February 4, 1982, with reference to temperature and salinity variations (Livingston 1983 unpubl.).

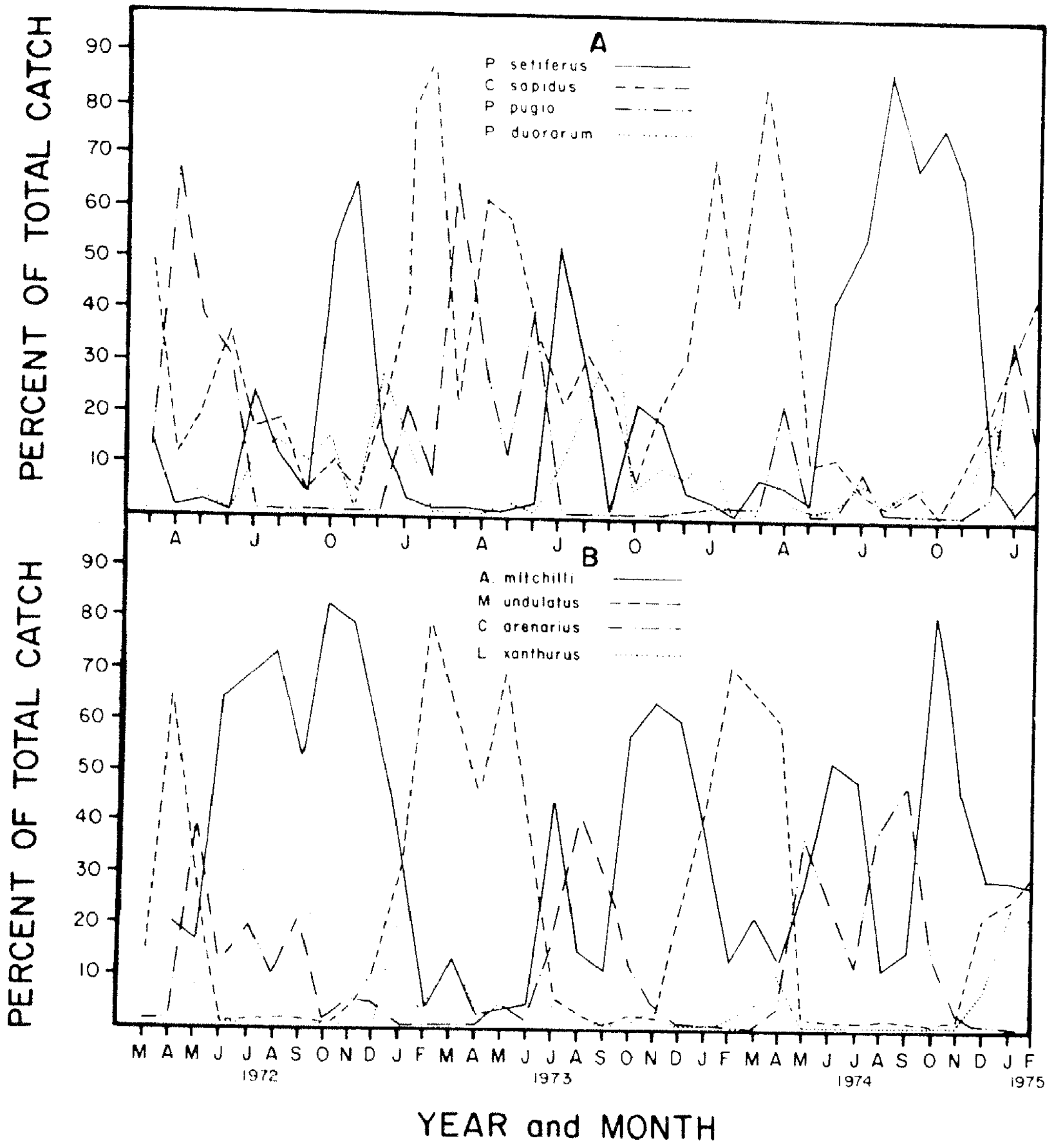


Figure 42. Relative importance of four dominant species of invertebrates and fishes taken in the Apalachicola Bay system from March 1972 through February 1975. These species represent 82.4% and 86.0% of the respective 3-yr totals (Livingston et al. 1976).

show distinct patterns of relative abundance through a given seasonal period.

Various independent ecological factors operate to determine the temporal distribution of the dominant estuarine organisms. Biological functions, such as adaptive response to the physical and trophic environment, determine distributional patterns, thereby allowing a somewhat orderly temporal succession of dominant forms within certain broad trophic spectra. Patterns of reproduction of various dominant estuarine species have evolved in such a way as to permit long-term partitioning of the estuarine environment. Superimposed on these patterns of response are varying levels of resource division based on vertical and horizontal distribution of the component species. Various microhabitat phenomena such as salinity, bottom type, currents, and the availability of detritus and food are important. Thus, no single parameter prevails in the determination of the community structure of the estuary, which itself undergoes predictable seasonal changes as part of a physically forced system.

Although there are appreciable short-term fluctuations in the numbers of individuals of different populations, the system maintains a temporal constancy which, according to a traditional view of such phenomena, could be termed stability. This does not mean that the system is not in a constantly transient state. On the contrary, through natural and unnatural mechanisms such as habitat alteration and destruction, hurricanes, cold winters, and periodic flooding, the various population equilibria continuously shift. Each population fluctuates around a specific point of equilibrium, and the fluctuations reflect the adaptive response to the specific aspects of the estuarine environment.

The Apalachicola estuary is physically unstable in time but is characterized by epibenthic populations which maintain relatively stable temporal interspecific relationships. The dominant fishes and invertebrates are temporarily partitioned in time. Particular groups of fishes tend to co-occur (Figure 43). Generally, three main clusters were arranged around the top dominants, *Anchoa mitchilli* (I), *Micropogonias undulatus* (II), and *Cynoscion arenarius* (IV). The anchovy group is abundant during the fall. The *Micropogonias* group predominates during winter and early spring periods, and the *Cynoscion* group prevails during the summer and early fall.

Studies are currently being undertaken to model the response of the major groups of fish with respect to physical stress, abundance of prey (Mahoney and Livingston 1982; Livingston et al. 1983), long-term changes of concurrent populations, and experimental manipulations of a variety of associations within the estuary (Livingston et al. 1983; Livingston, unpubl.; Appendices A, B, C). These studies will be based on occurrence patterns over a 12- to 13-year period.

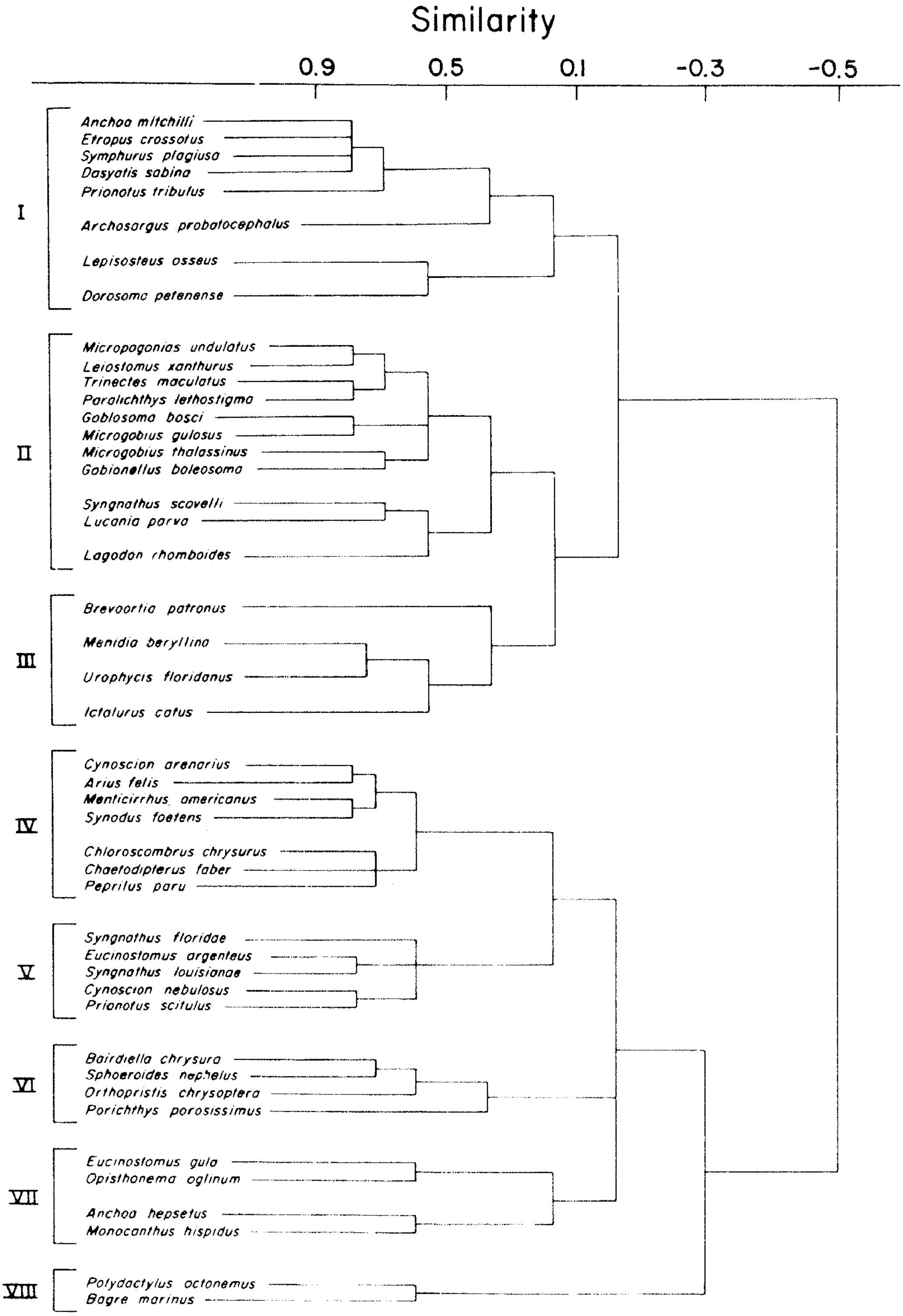


Figure 43. Temporal associations of fishes taken in Apalachicola estuary from March 1972 to February 1976. Only top 45 species in terms of total numbers of individuals are shown. Clusters represent species that occur together from one year to the next (Livingston et al. 1978).

CHAPTER 7
THE ESTUARY AS A RESOURCE

7.1. FISHERIES

There are relatively few studies of fisheries in the Apalachicola River system. Early surveys (Cox and Auth, 1970-1973) of the upper Apalachicola River noted increasing stress to various species of fishes as a result of physical alterations such as damming, dredging, and eutrophication. Studies of striped bass (Barkuloo 1967, 1970; Crateau et al. 1981) indicated that, before the construction of the Jim Woodruff Dam (1955) at the confluence of the Flint and Chattahoochee Rivers, there was a viable sport fishery for striped bass in the Apalachicola River. Since that time, the striped bass fishery has declined "drastically." The dams in Georgia (Figure 4), together with dredging and spoil deposition along the upper Apalachicola River, have eliminated spawning grounds in the Flint and Chattahoochee Rivers. Pesticides from agricultural runoff and industrial effluents (Livingston 1984b) are also suspected of reducing these populations. The native Gulf of Mexico race of striped bass, once widespread throughout the rivers of the northern gulf, is now limited to a small population in the Apalachicola River. Recent stocking of Atlantic coast striped bass has further diluted the gulf strain and has resulted in only limited success (Crateau et al. 1981). Wooley and Crateau (1983) conclude that the native Apalachicola striped bass represent the only existing remnant of a population that historically was present in numerous Gulf of Mexico drainages. For this reason, the authors recommend conservation of the existing stock as a "gene bank."

A commercial catfish fishery still exists along the Apalachicola River. However, Miller et al. (1977) cite studies that related snagging (i.e., stump removal from the river bed for navigation) to the decline of the commercial catfish harvest from the river. This activity, together with the massive excavation and maintenance activities associated with nagivation projects (Figure 44), has reduced or modified the riverine habitat substantially (Miller et al. 1977). Recent studies of the Apalachicola River (Ager et al. 1984) indicate that sand bars and spoil disposal sites are now common throughout the river; in the upper river, the gently sloping natural bank habitat has become "scarce" because of dredging activities over the past 30 years (Ager et al. 1984). It has been projected that, because of such habitat alterations, the fish species composition will continue to shift from game species (characteristic of natural habitats) to rough and forage species (characteristic of sand-bar habitats). This loss of habitat has also been associated with the recent decline of the sturgeon fishery. According to recent studies (Wooley and Crateau 1982), Florida sturgeon landings in the Apalachicola River have declined rapidly (U.S. Department of Commerce 1976 landing statistics) relative to neighboring gulf-coast rivers. The fishery effectively ended in 1970 when only five fish were taken. The Apalachicola sturgeon population appears to be in trouble, although it is believed that at least a relict sturgeon population still remains in the Apalachicola River. Recently, Wooley et al. (1982) reported the first recorded capture of a larval gulf sturgeon about 3.3 km below the Jim Woodruff Dam in May, 1977. Wooley and Crateau (1982) reported that relatively few sturgeon (35-40) were harvested by angling during 1981. An important spawning area has been

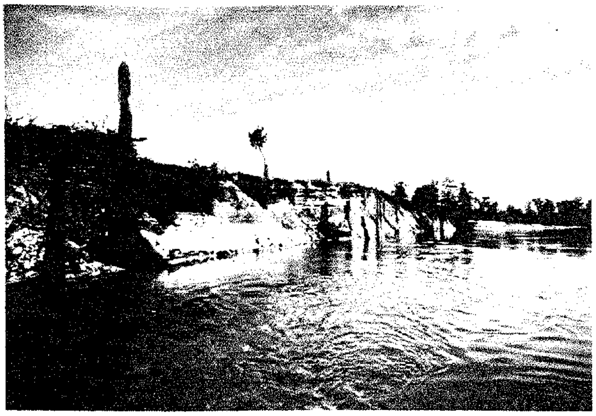


Figure 44. Dredge spoil bank along the Apalachicola River--a result of channel-maintenance efforts of the U.S. Army Corps of Engineers. Note dead trees in what was once the river floodplain.

located in the upper Apalachicola at the end of the usual spring flooding. Recent studies (Wooley and Crateau 1984 in review) indicate seasonal migrations of sturgeon between freshwater and estuarine portions of the Apalachicola system. A strong homestream tendency is apparent.

The tailwaters of the Jim Woodruff Dam still support some sport fishing in the spring, especially for the white bass (Morone chrysops) and the hybrid or sunshine bass (M. saxatilis x M. chrysops). Largemouth bass and various forms of bream and shellcrackers are also important sport fishes. The yellow perch (Perca flavescens) is taken occasionally by freshwater fishermen. The Alabama shad (Alosa alabamae) is the most abundant anadromous fish along the river. As pointed out by Miller et al. (1977), the general decline of the freshwater fisheries is inevitable if habitat destruction along the river continues. Habitats are destroyed by dredging and channelization, damming, urban and agricultural runoff, toxic substances, and other forms of river modification. There is a need for a comprehensive assessment of the current status of the Apalachicola River fisheries and the current and future effects of river modifications and habitat loss on such productivity. However, as of this writing, the channelization of the upper Apalachicola River by dredging and rock removal for navigation purposes continues, and there is little hope of a return to former levels of productivity of the once-viable freshwater fisheries.

The commercial fisheries of the Apalachicola Bay system are diverse and substantial. According to the summaries of commercial marine landings in Franklin County (Florida Department of Natural Resources, 1952-1976) and analyses of projections of commercial populations, there is considerable annual variation of such landings over the period of observation (1952-1977) (Cato and Prochaska 1977). Shrimp, together with oysters and blue crabs, provide over 80% of the annual catch by weight. Black mullet and grouper contribute almost 14% of the remaining catch. Whiting, menhaden, flounder, red snapper, and spotted seatrout all contribute to the overall landings. In terms of total value, shrimp (53.9%), oysters (33%), and blue crabs (5.1%) constitute the backbone of the commercial fishery value in Franklin County, which itself accounts for over 90% of Florida's oyster landings and the third highest catch of shrimp statewide.

The oyster fishery in the Apalachicola estuary has historical significance (Swift 1896; Ruge 1897; Danglade 1917). Many of the historic observations were similar to today's in that floods and droughts have an important impact on the viability of individual oyster bars. The present distribution of oyster bars does not differ substantially from that depicted on maps produced during the early part of this century (Whitfield and Beaumariage 1977). However, the current maps (Figure 20) need to be updated, as they are based largely on obsolete surveys. Commercially valuable oyster bars currently cover only half the area estimated to be available at the turn of the century. Shell planting with "cultch" or shucked shells has proven to be a successful management technique for encouraging oyster bar development (Whitfield 1973). Approximately 40% of the Apalachicola Bay area is suitable for growing oysters if cultched in an appropriate manner (Whitfield and Beaumariage 1977). The actual and potential productivity has been attributed to the unique geographical and physical attributes of the largely unpolluted Apalachicola drainage system. More sanitary (safe) harvesting waters for oysters exist in the Apalachicola estuary than in any other Florida estuary. Considerable support exists for this industry as a regional and statewide natural resource. This fact, added to recent information that the Apalachicola Bay system appears to be a major spawning or source area for the entire Florida Gulf blue crab fishery (Oesterling and Evink 1977), has stimulated various research investigations concerning future fishery potential.

The overall Apalachicola fishery resource has grown substantially over the past decade. During the period from 1977 to 1981, all previous oyster production records were broken on an annual basis (Joyce 1983). The record landings were due largely to an increase in the fishing effort (Prochaska and Mulkey 1983), although newly instituted programs of summer oystering (1977) and an oyster relay program (Futch 1983) have added to the annual crop. Although oyster production has increased to 41% of the total Franklin County landings, the relative value of the oyster crop has declined to 36%, partly as a result of increased county shrimp landings and considerable increases in shrimp prices (Prochaska and Mulkey 1983). Blue crabs constitute about 5% of the total value of the commercial fishery in Franklin County. Of the commercial finfish catch, striped mullet (*Mugil cephalus*) is the most important. Grouper, menhaden, and whiting are also taken, although the commercial finfish industry has declined in recent years (Livingston 1983c).

Sport fishing in the Apalachicola Bay system remains largely undeveloped, although the potential exists for a highly productive industry. Sport fisheries associated with the estuary include spotted seatrout (*Cynoscion nebulosus*), red drum (*Sciaenops ocellatus*), tarpon (*Megalops atlanticus*), sheepshead (*Archosargus probatocephlus*), black drum (*Pogonias cromis*) and flounder (*Paralichthys* spp.). Fishes taken off the barrier islands and Alligator Point include various species of sharks, cobia (*Rachycentron canadum*), bluefish (*Pomatomus saltatrix*), red snapper (*Lutjanus campechanus*), and different species of grouper. The development of artificial offshore reefs in the region could add considerably to the continued development of sport fisheries in the area.

7.2. SOCIOECONOMIC FACTORS

The Apalachicola valley depends to a considerable degree on a rather narrow economic base. A land-use inventory (Table 26) is indicative of the regional socioeconomic conditions. Forestry and agriculture account for nearly 80% of the land use in the basin. Forestry, agriculture, sport and commercial fisheries, recreation, and light manufacturing are the chief industries of the region. In Franklin and Gulf Counties, commercial and industrial land use are only 0.9% and 0.4% of the total area, respectively. In the entire river basin, the population was 109,254 in 1974, with only modest projected increases for the next 10-20 years. Per capita income is low, averaging only 65% of the state level in 1974. Despite a historic trend of emigration of workers, the natural features of the river and bay system continue to attract new residents, especially in the coastal areas. The Apalachicola system contributes an important part of the regional economy and culture, with unique sociological conditions characterized by the close relationship between the natural attributes of the drainage system and the local inhabitants. The slight investment needed to maintain the rich renewable resources of the area is an important factor in any review of the value (economic and cultural) of the natural productivity of the valley.

Franklin County, which surrounds the Apalachicola Bay System, has a relatively limited scope of employment with primary dependence on products from the aquatic resource base and tourist expenditures (Colberg et al. 1968). Commercial fisheries alone provide jobs for over 65% of the Franklin County work force. Fishing is an "export" industry for Franklin County because practically all sales are outside the region (Prochaska and Mulkey 1983). Export sales trigger a

Table 26. Land use inventory of the Apalachicola River basin (from Florida Department of Administration 1977).

Land use	County						Total (square miles)
	Gulf	Liberty	Calhoun	Jackson	Gadsden	Franklin	
Low density residential	2.50	0.25	13.50	7.00	2.00	1.00	26.25
Medium density residential	0.25	--	1.00	1.50	1.00	1.00	4.75
Commercial	1.50	0.25	4.50	2.25	0.25	0.25	11.00
Industrial	--	0.25	0.50	1.50	0.25	1.00	3.50
Recreational[a]	38.00	194.50	146.00	22.00	--	58.00	458.50
Marshes and flood lands	06.00	83.00	29.00	16.00	9.00	45.00	288.00
Agriculture	12.00	12.00	73.00	399.00	20.00	2.00	518.00
Forestry	175.00	32.00	314.00	114.00	46.00	21.00	702.00
Water	14.50	0.50	3.50	33.00	0.50	0.50	52.50
Total	349.75	322.75	586.00	596.75	79.75	129.75	2,064.50

[a] Includes Apalachicola National Forest.

chain reaction throughout the local economy because direct and indirect purchases generate income, the so-called "multiplier" effect. Recent estimates indicate that the forestry and fisheries "export" values are even more important than previous studies indicated since practically all such production is sold outside the region. The total current value of fisheries in the drainage system and associated coastal areas exceeds $23 million. Colberg et al. (1968) projected a value of $34.2 million for commercial fishing and tourism by the year 2000 if water quality and natural productivity are maintained. Value added as a "multiplier" effect would increase this estimate to almost $67 million. Thus, the as yet undiminished natural resources in the Apalachicola valley provide an important economic base for the local area, and such natural industries have a direct influence on the region through export and respending.

Rockwood et al. (1973) and Rockwood and Leitman (1977) provided an in-depth analysis of the socioeconomic basis of the Apalachicola oyster industry. The potential for oyster production has yet to be reached; greater production will be necessary if the relatively low per-capita income is to be increased and more employment is to be provided for young people in the area. In terms of general determinants of regional growth, Franklin County is rich in natural resources on which it is almost entirely dependent. Recent historic trends have contributed to the insularity of the community. The development of strong clan ties of the English and Scotch-Irish inhabitants adds to the geographic isolation of the region. Independence and individualism are hallmarks of this society and have led to the view that outside intervention by government agencies or large corporations has a negative influence on the community. The oyster industry is based on contributions of the entire family (husband and older boys as tongers, wife and older daughters as shuckers, joint management of the business). Such a family-oriented business structure has strengthened the traditional bond between the community and the industry to an extent that is not common elsewhere in today's society. Thus, family and kinship bonds underlie and strengthen the dependence of the area on the natural industries.

Some of the more important prospects for regional growth are based on residential development of areas such as St. George Island and industrialization of the river watershed. This situation has resulted in a direct confrontation between local and outside developmental interests. Future planning initiatives will have to be based on a reasonable evaluation of the natural renewable-resource base if the local industry is to be protected. The potential for destruction of these resources through environmental alterations and pollution is high. At the same time, the potential for expanding the highly profitable oyster industry with updated management of the resource is excellent.

7.3. EXISTING AND PROJECTED IMPACT BY MAN

A number of publications have addressed the problem of environmental alteration and pollution in the Apalachicola drainage system (Livingston 1974, 1975, 1976a, b, 1977a-d, 1978, 1980a-c, 1983d; Livingston and Duncan 1979; Livingston et al. 1974, 1976a, 1978). The Apalachicola estuary depends on three basic elements for its productivity: (1) the Apalachicola River system, (2) the Tate's Hell Swamp and surrounding freshwater/brackish wetlands, and (3) the barrier islands. Physical alterations of these areas or changes in water quality or quantity due to human activities could affect the natural processes that define and control the productivity of the river-bay system.

7.3.1. Physical Alterations

Darnell (1976) reviewed the effects of structural changes on a range of aquatic systems. Impoundment, channelization, dredge and spoil operations, diking, and other physical modifications have the capacity to alter natural aquatic systems. Since the early 1970's, there has been considerable controversy concerning efforts to dam and/or channelize the currently free-flowing Apalachicola River. Georgia and Alabama industrial interests want to maintain an authorized 9-ft channel so that barge traffic can move from the Gulf of Mexico to upriver cities along the Flint and Chattahoochee Rivers. Currently, this system is deep enough for barge traffic only 83% of the time (U.S. Army Corps of Engineers, 1975), which is not enough for the upriver interests. There are 13 hydroelectric dams on the Chattahoochee River and 3 dams on the Flint River, some of which are privately owned (Figure 4). Publicly owned dams and dredging and maintenance activities have cost in excess of $700 million.

According to a 1975 environmental impact statement by the U.S. Army Corps of Engineers, dredging has had adverse effects on the Apalachicola River. Livingston and Joyce (1977) point out that impoundments such as the Jim Woodruff Dam cause aquatic weed problems, water quality degradation due to the accumulation of herbicides and insecticides, continued need for dredging due to sedimentation, reduction of habitat due to spoil disposal, and restriction of the movement of nutrients and particulate matter to downriver areas. Dredging and snagging (removal of submerged stumps) operations along the Apalachicola River are blamed for habitat loss (Stevenson 1977), destruction of benthic organisms (Miller et al. 1977), loss of flood-plain vegetation (Clewell and McAninch 1977), reduction of bank overflow, blocked migrations of migratory fishes, restriction of striped bass from thermal refuges and sturgeon from former ranges, and increased pollution due to oil and chemical spills (Figure 44).

Stabilization of a river usually leads to industrialization and municipal development in the former flood plain with associated effects on water availability and quality. The development of the Apalachicola floodplain is uneconomical in terms of the cost-benefit analysis

(Rockwood and Leitman, 1977). A 1982 comparison of federal subsidies prepared by the Congressional Budget Office shows that waterways in general receive the highest level of public transportation support of all industries. On the basis of cost-per-ton mile, the Apalachicola-Chattahoochee-Flint (ACF) system is the most expensive maintenance operation in the country (45.5 mills per ton mile), being almost twice as expensive as the second highest and 41.36 times the national average. The cost to the public of moving a barge through the Jim Woodruff Dam is around $2,040. The 1981 cost for maintenance of the Jim Woodruff Dam and dredging of the Apalachicola River exceeded $6,735,000, and recent cost increases have not been offset by revenue from increased barge traffic. Despite all this information, the Corps of Engineers has recently been authorized to blast tons of rock from the river (a form of channelization) at a cost exceeding $1,000,000.

There are few available data for evaluating the environmental impact of physical alteration of the tri-river system. Cox (1970) and Cox and Auth (1971-1973) indicate that dredging (Figure 44) has contributed to local habitat destruction on the Apalachicola River along with associated simplification of the fauna and reduced productivity. As indicated above (Ager et al., 1984), the long-term dredging of the river is a significant ecological occurrence. These impacts include altered habitat, shortening of the river, and redirected natural river flow. Operations associated with these activities include construction of training dikes, maintenance dredging, spoil deposition, bendway elimination, and snag removal. The river has already been shortened by past activities, and channelization continues.

In the Apalachicola estuary, dredging of Sike's Cut has been related to increased salinity in the bay and reduced productivity due to a loss of nursery habitat (Livingston 1979). A review by state and federal agencies (Florida Department of Environmental Regulation, pers. comm.) is currently in progress (Livingston 1984a) to determine the potential impact of dredging along the Intracoastal Waterway on the salinity regime and oyster productivity in the estuary. Proven dredging effects include deterioration of water-sediment quality in dredged channels near areas of urban runoff and effects on the natural salinity regime of the estuary (Livingston 1984a).

In the lower Apalachicola valley, a 33,000-acre cattle ranch was established along the west bank of the river in the early 1970's (Figures 45, 46). This operation was accompanied by extensive clearing, ditching, and diking. Land was drained by periodic pumping of turbid, sediment-laden water over the dikes. Extensive forestry operations have been carried out in the Tate's Hell Swamp above East Bay. After clearcutting of large tracts of trees, the land was ditched, drained, plowed and replanted with pine trees. Livingston et al. (1978) found that during periods of heavy local rainfall, cleared areas caused increased levels of runoff leading to increases in color and turbidity and reductions in pH and dissolved oxygen. Analyses of the problem indicate short-term adverse impact on certain biological associations in upper East Bay. The long-term implications of forestry activities for water resources are currently being evaluated (Livingston unpubl.).

Overall, the primary wetlands of the Apalachicola valley remain intact, although dredging and associated construction activities, especially in the upper reaches of the river, are continuing. These activities include the construction of bridges across the river and development of a barge terminal facility and offloading system. Currently, state and federal agencies are attempting to purchase portions of the remaining wetlands for preservation.

7.3.2. Toxic Substances

The limited industrial and agricultural activity in the region has contributed to the relatively low levels of pollutants found in the Apalachicola drainage system. However, the water quality of the Flint and Chattahoochee Rivers has been adversely affected by waterway maintenance activity, urbanization, and the discharge of

Figure 45. Ditching and diking associated with agricultural activities in the lower Apalachicola floodplain.

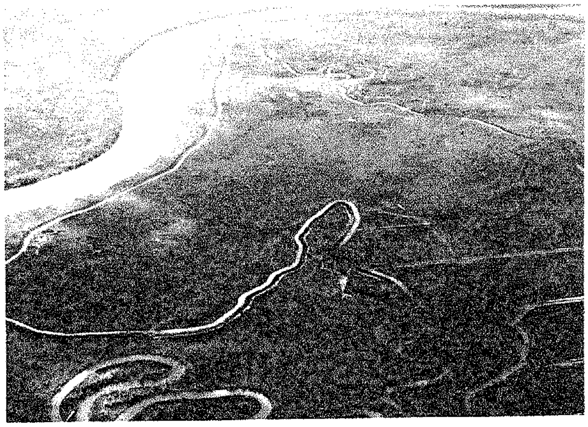


Figure 46. The extent of diking by agricultural interests along the western bank of the lower Apalachicola River.

industrial and agricultural wastes (Georgia Department of Natural Resources 1978, 1982). A thorough scientific analysis of the biological response to eutrophication and the influx of toxic substances to these rivers is lacking, however. Recent studies by the U. S. Geological Survey (H. Mattraw pers. comm.) concerning the levels of toxic substances in the Apalachicola River indicate relatively low levels of heavy metals and negligible concentrations of herbicides. In the Apalachicola estuary, from 1972-1976, there was a precipitous decrease of organochlorine residues in sediments and associated estuarine organisms. This decrease was attributed to the banning of DDT in 1972, the flushing action of the river, and the heavy sedimentation associated with the estuary (Livingston et al. 1978).

Recent studies (Winger et al. 1982) indicate that residue concentrations of organochlorine insecticides (DDT, toxaphene), polychlorinated biphenyls, and heavy metals in aquatic biota are higher in the upper Apalachicola River than in the lower river. Total organic contaminant residues, particularly from the upper river, exceeded permissible levels for the protection of wildlife. The authors considered that such moderately high residues indicated that the Apalachicola River "may be in the early stages of contamination." The highest levels of cadmium and lead in sediments and biota of the Apalachicola-Chipola drainage system are found in tributaries leading to the Chipola River below an industrial plant that discharged battery wastes into the system (Livingston et al. 1982). The pH levels of runoff water approximated 1.2 to 1.4. Concentrations of lead and cadmium in sediments of the Little Dry Creek-Dry Creek tributary to the Chipola River were particularly high. Studies are currently under way to evaluate the biological response to this contamination (R. J. Livingston unpubl.). Recent analyses indicate that this contamination has not reached the Apalachicola Bay system (Florida Department of Natural Resources, pers. comm.).

7.3.3. Municipal Development

Municipal development in Florida is concentrated along the coast. The Big Bend region, which includes the Apalachicola Bay system, remains one of the last undeveloped coastal areas in Florida. In Franklin County, urbanization is restricted to the cities of Apalachicola (approximately 3,000 people) and Carrabelle (approximately 1,000 people). A municipal waste system is currently under construction in Apalachicola to eliminate point sources of waste discharge (Scipio Creek) into surrounding areas. Nutrient, phytoplankton, and dissolved oxygen data indicate no discernible tendency for cultural eutrophication in the estuary (Livingston unpubl.). Most of the construction activity in the Apalachicola Bay system has occurred in Apalachicola and East Point and on St. George Island (Figure 47). While there is considerable pressure for construction on the island, population density is still relatively low. The outlook for future growth, however, remains uncertain, as portions of the estuary have already been contaminated with municipal and agricultural runoff and waste (Livingston 1983d).

Coastal development is often accompanied by the loss of natural vegetation, increased levels of solid waste, and enhanced effluent discharge. These activities often lead to increased runoff, erosion, physical alterations, changes in water circulation, increased deposition of sediments, and the introduction of various pollutants into the river-bay system. Such changes can have an adverse effect on the natural resources of the area. According to Bell and Canterbery (1974, 1975), "The major cause of closing of commercial shellfish areas is bacterial pollution at sublethal contamination levels." Closings of Louisiana's shellfish beds went from 5,900 acres in 1965 to 198,812 acres in 1971, a 3200% increase. In Florida, considerable areas of shellfish grounds are closed each year because of pollution. Of over 2 million acres of available shellfish areas in Florida, only 22% are approved for harvesting; 13% are prohibited, 5% are conditionally approved, and about 60% are unclassified. The national figures show over 3 million acres of clam and oyster beds closed, at a loss of over $38.4 million (Bell and Canterbery, 1975). Septic tank effluents, sewage waters, and municipal and industrial runoff account for most of these problems. Since commercial fisheries account for 65% of the Franklin County income, there is cause for concern (Florida Department of Administration 1977).

St. George Island (Figure 47) forms the gulfward perimeter of Apalachicola Bay and is of critical importance to bay productivity because its orientation determines the distribution of salinity and other water-quality features of the estuary. In 1965, a bridge was completed from the mainland to St. George Island at public expense. The bridge caused the island's value as real estate to escalate tremendously. Today, portions of St. George Island are currently under considerable pressure for municipal development (Livingston 1976a). Based on past experience in Florida and other coastal states, the outlook for St. George Island is to be the center of the growth for Franklin County. On St. George Island, as elsewhere in the drainage area, there is a real need for planned development if the natural resources of the estuary are to be maintained.

Figure 47. Portions of St. George Island showing housing development and other human activities.

Recently, there have been a number of incidents in which oystering in the bay has been closed down because of high coliform bacteria counts (Livingston et al. 1978). This situation has caused local economic problems and represents a continuing threat to the oyster industry in the Apalachicola estuary. The combination of dredging and municipal development has led to localized pollution of portions of the estuary (Livingston 1983d). Dredged channels south of Apalachicola and East Point have acted as sinks for nutrients (nitrogen and phosphorus compounds), oils and greases, and heavy metals (Livington 1983b). Such substances have been associated with the silt (i.e., fine) fractions of the sediments and have led to conditions of high biochemical oxygen demand (BOD). The degree of urban development, the heavy boat traffic, and the dredging activities have been directly associated with local destruction of near-shore grassbeds, deterioration of water and sediment quality, and the loss of biological productivity (Livingston 1983b, d).

Municipal drainages contribute significantly to the pollution burden of the Apalachicola River and Bay area (Livingston 1983d). Scipio Creek (Apalachicola), Eagle (or Indian) Creek (East Point), and runoff from East Point into near-shore areas of St. George Sound have been affected by a combination of high biochemical oxygen demand (BOD) and chemical oxygen demand (COD), low dissolved oxygen, and heavy-metal contamination of sediments. Areas of northern Apalachicola Bay that receive runoff from the city of Apalachicola also show signs of low water quality. The dredged canals of St. George Island are polluted. The boat basins at St. George Island and Apalachicola have been contaminated with organic input and heavy metals in the sediments. The lowest dissolved oxygen in the entire system occurs at the St. George boat basin (just west of the causeway as it enters the island; Figure 47) during periods of high summer rainfall and overland runoff. There are signs of organic runoff in the vicinity of St. George Sound receiving input from construction sites, although more analysis is necessary to qualify this observation. At all of the above sites, the biological indices (benthic infaunal macroinvertebrates) indicated moderate to high biological stress.

Other major sources of pollutants are located in areas receiving drainage from agricultural operations (Murphy Creek and Clark's Creek off the Jackson River; West Bayou in East Bay from the Tate's Hell Swamp). Aerial reconnaisance of the study area indicates that forestry interests have drained extensive areas of the Tate's Hell Swamp into East Bayou and West Bayou in eastern portions of East Bay. High organic input and heavy-metal contamination of the sediments have been noted in areas of the drainage system receiving agricultural runoff. Biological indices have indicated severe stress.

Various stations along the lower Apalachicola River, while having relatively low levels of pollution in the water and sediments, also appear to be biologically stressed (Livingston 1983d). These sandy areas could be naturally stressed by the heavy currents and the shifting qualities of the sandy substrate. Dredging activities along the Apalachicola River could contribute to the observed paucity of benthic macroinvertebrates noted in these areas, although the exact cause of the observed biological conditions remains unknown.

Overall, the Apalachicola River and Bay system remains relatively pollution free at this time. Some areas, such as eastern portions of St. Vincent Sound, have been characterized by relatively high levels of heavy metals in the sediments, the source of which is not immediately apparent. These areas could be points of sedimentation (such as the dredged channels in Apalachicola Bay), which naturally concentrate contaminants such as heavy metals as part of the fallout of silt/clay fractions from river input and urban runoff. Such small particles are known to adsorb chemicals such as heavy metals. The dredged channels serve as silt traps within the system. The cumulative effect of municipal and agricultural activities in the region could be especially significant to the rather sensitive oyster industry in Franklin County. It will take imaginative and progressive planning and resource management action if the fisheries potential of the Apalachicola estuary is to be preserved and enhanced.

7.4. LAND PLANNING AND RESOURCE MANAGEMENT

Resource management, based on comprehensive scientific data, depends on complex socioeconomic factors and cultural trends. The mere identification of a given natural resource does not necessarily ensure enlightened planning for its perpetuation. There have been a series of reviews of the resource problems in the Apalachicola basin. The history of resource planning and management in the Apalachicola basin has been well documented over the past decade (Livingston 1974b, 1975, 1976a, 1977a-d, 1978, 1980a-c; 1982a; Livingston and Joyce 1977). Overall, there has been a relatively good relationship between researchers, managers, and local user groups. The well-integrated (local, state, federal) planning initiatives have been based largely on preservation (land purchases) and conservation approaches. Whether such efforts will maintain the resource remains to be seen.

7.4.1. Public Land Investment

Public and private parks, designed to conserve or preserve areas in the Apalachicola Valley, are scattered throughout the area (Figure 48). The Torreya State Park includes unique plant species such as the Florida Torreya cedar and Florida yew. The Apalachicola National Forest and private wildlife management areas allow recreational and hunting opportunities. A state-owned park on St. George Island permits public beachfront recreation, and St. Vincent Island National Wildlife Refuge is used for wildlife observation, fishing, and controlled hunting activities.

One of the major land-acquisition projects, the bottomland hardwoods in the lower basin, was the result of research funded by the Florida Sea Grant College and the Franklin County Commission (Livingston et al. 1976a). In 1976, portions of the Apalachicola River floodplain were considered for purchase

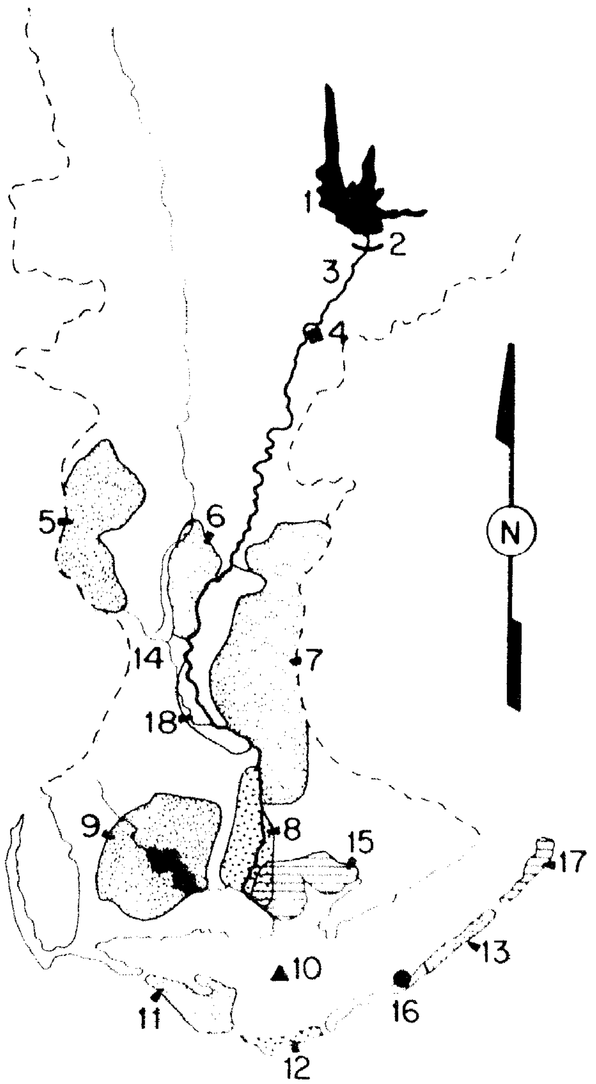


Figure 48. Major public investments and specially designated areas in the Apalachicola basin.

Legend

1. Three Rivers State Park
2. Jim Woodruff Lock and Dam
3. Jackson County Port Authority
4. Torreya State Park
5. Gaskin Wildlife Refuge (private)
6. G. U. Parker Wildlife Management Area (private)
7. Apalachicola National Forest
8. Environmentally Endangered Land Purchase
9. Ed Ball Wildlife Management Area (private)
10. Apalachicola Bay Aquatic Preserve
11. St. Vincent Island National Wildlife Refuge
12. Little St. George Island EEL Purchase
13. Dr. Julian Bruce State Park
14. Dead Lake Recreational Area
15. Proposed purchase (estuarine sanctuary)
16. Unit 4, EEL purchase
17. Dog Island, Nature Conservancy
18. Proposed bottomland hardwood purchase: Nature Conservancy and "Save Our Rivers" program (state).

through the Environmentally Endangered Lands Program (EEL) of the State of Florida. The environmental background and justification for purchase was based on data concerning the movement of nutrients and POM from floodplain areas (Livingston et al. 1977; Pearce 1977). Ecological associations were made between the hardwood forests of the lower floodplain and the productivity of the Apalachicola River-Bay system. Based on the data and the need to protect this ecologically sensitive portion of the system, the Florida Cabinet approved the purchase of 28,044 acres of the lower Apalachicola floodplain for $7,615,250 in December, 1976. While this purchase represented only a small percentage of the total floodplain and could not hope to achieve a total approach to management of the system as a whole, it provided a much needed state presence in the area.

Considerable effort has been expended in the preservation of barrier islands bordering the Apalachicola estuary. Based on information concerning the importance of the islands to the bay productivity (Livingston et al. 1976a), portions of the eastern end of St. George Island were added to the existing state park. In March 1977, the State of Florida authorized the purchase of Little St. George Island for $8,838,000. Approximately 1,300 acres of undeveloped land on Dog Island were purchased by the Nature Conservancy in 1982 for the implementation of an island conservation program. In addition, the Trust for Public Land purchased that portion of St. George Island known as Unit 4 which borders the highly productive oyster beds of East Hole. This land was recently repurchased by state agencies as part of the EEL program. The balance of St. George Island is still in private ownership. Major portions of the holdings on western portions of this island are already restricted by planning regulations to 1 unit/acre. Thus, much of the barrier island system is currently under public ownership or within the jurisdiction of the comprehensive plan of Franklin County (see below).

In summary, there has been a continuous and quite successful effort over the past decade to purchase and place in public stewardship those portions of the Apalachicola drainage system which have been identified as important for maintaining the high productivity of the area.

7.4.2. The Apalachicola Estuarine Sanctuary

After years of effort by local, state and federal agencies, the Apalachicola River and Bay Estuarine Sanctuary was established in September 1979. The sanctuary is the largest in the country and includes 192,750 acres of submerged waters and associated wetlands (Figure 49).

The approval of the Estuarine Sanctuary was the legal equivalent (Section 315, Coastal Zone Management Act; P. L. 92-583) of setting this area aside as a natural field laboratory "for long-term scientific and educational purposes." With the establishment of the Sanctuary came a federal grant of $1.8 million, to be matched by $1.95 million of Florida's EEL funds (the previous wetlands purchase on the Lower Apalachicola River) for the acquisition of the additional wetlands surrounding the East Bay system (the nursery portion of the Apalachicola estuary) (Figure 49). After the acquisition of the final 12,467 acres around East Bay and portions of the M. K. Ranch along the lower Apalachicola River by the state of Florida, the public land perimeter of the estuarine sanctuary will be nearly complete. Recently, state agencies have entered into negotiations for another tract of wetlands along the Apalachicola River. If successful, this land will become part of the "Save Our Rivers" program administered by the northwest Florida Water Management District.

Currently, in a close cooperative effort between local interests and state environmental agencies, the Apalachicola Sanctuary program is involved in the development of a resource atlas (Livingston 1983c) and management plan, several ongoing research projects, public educational programs, and continuous input into local planning problems and public interest issues. Not the least of this effort is the potential development of training programs and curricula in the Franklin County secondary school system. A group of educational films on the Apalachicola drainage system has been developed for showing throughout the valley. The close interaction of aquatic research with local and regional elements has been one of the keys to the successful development of a management program for the area. This effort will be carried out largely under the auspices of the Apalachicola Estuarine Sanctuary if an effective mode of administration can be established.

7.4.3. Local Planning Efforts and Integrated Management

A series of Florida County Commissions have been responsible for the establishment of comprehensive plans for local development and resource management. These plans have the legal status of zoning restrictions which have been upheld in recent court decisions. For some years, agencies such as the Apalachee Regional Planning Council, the Washington, D.C.-based Conservation Foundation, Florida State University, and the Florida Sea Grant College have aided local officials in the development of a comprehensive management plan for Franklin County. During the summer of 1981, the Franklin County Commission passed a plan which installed various restrictions on the level and type of construction activities in the area and established low density requirements in environmentally sensitive areas. These areas include wetlands, barrier islands, and portions of the county that drain into oyster bars and grass beds (Livingston 1983c). This plan, in conjunction with the estuarine sanctuary program and state and federal management, could eventually provide for the orderly development of the area while managing the natural resources of the region. Passage of the plan is only the first step in the planning process. Successful implementation of the Franklin County Comprehensive Plan has not yet been achieved, and the status of local resource management in the estuarine sanctuary remains in doubt.

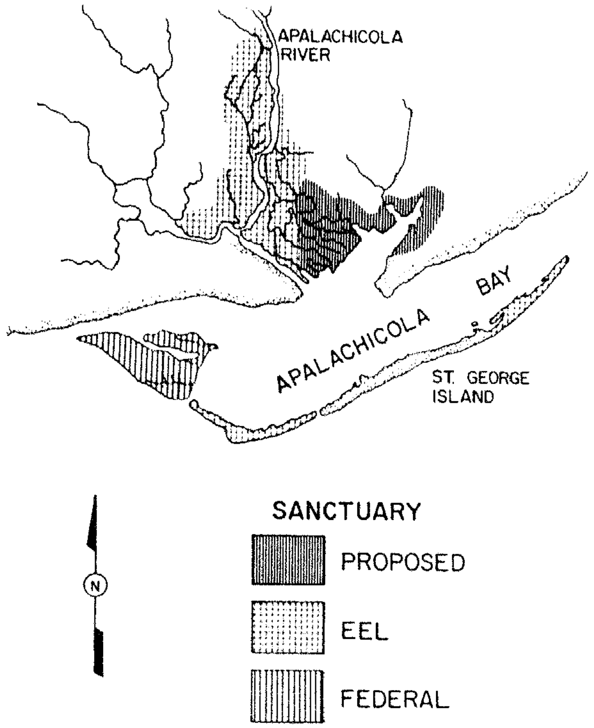


Figure 49. Boundaries of the Apalachicola River and Bay Estuarine Sanctuary, including actual and proposed purchases according to the Environmentally Endangered Lands (EEL) Program (state) and current federal holdings.

7.4.4. Integration of Management Efforts

A diverse series of management approaches coordinated through local user associations and the estuarine sanctuary could provide the key for broadening the economic base of the region while conserving the unique natural assets of the Apalachicola drainage system. This resource use will have to be subject to specific internal controls as the population grows to prevent overfishing and other problems related to the fishing industry.

Long-term scientific data have been used to address local problems such as pesticide use, aquatic weed control, shoreline development, and other aspects of human activity around the bay. Such problems have often been solved through close cooperation between researchers and local elected officials. The initial studies, funded through a series of grants administered by the Florida Sea Grant College, provided needed information concerning the ecologically sensitive points in the drainage system. These areas include the Apalachicola River, the upland wetlands (including the Tate's Hell Swamp), and the barrier islands--all features that control the hydrological regime, nutrient structure, and physico-chemical environment (salinity, water quality), which, together with other specific habitat conditions, provide the appropriate environment for the seasonal and annual progressions of prominent estuarine populations. Through contact with public officials, state and federal administrators, and leaders of private industry, researchers have been able to channel scientific information into public use. Through close cooperation with local user groups, the Apalachicola research effort is gradually being applied to regional problems.

The real test for this management effort, however, remains in the future. As of this writing, the issue is unresolved.

CHAPTER 8
COMPARISON WITH OTHER ESTUARIES

The Apalachicola estuary has been included in a comparison of 14 estuaries on the Atlantic, Gulf of Mexico, and Pacific coasts of the United States (Nixon 1983). This study indicated that Apalachicola Bay is a relatively small and shallow estuary, rapidly flushed, with a considerable watershed area (Table 27) when compared to other estuaries in the United States. The cross-sectional area of the Apalachicola estuary (18.1 x 10^3 m^2) is relatively small compared to most of the other estuaries. Because of the dimensions of the bay and the volume of freshwater input, Nixon (1983) estimates that dissolved and suspended materials are likely to remain in Apalachicola Bay for a shorter time than in many of the other estuaries in the survey. The relatively high level and strong seasonality of the rainfall in the Apalachicola drainage basin would contribute to the high river discharge rates to the estuary. Approximately 62% of the surface area of the estuary has salinities that average less than 15 ppt. Apalachicola Bay stands out, along with Mobile Bay and Northern San Fransisco Bay, as a system that responds to river discharge in "a major way" (Nixon 1983).

Because of the physical characteristics and the relatively high annual level of solar radiation, Apalachicola Bay and Kancohe Bay (Hawaii) are the only estuaries of those surveyed in which the bay bottoms fall within the euphotic zone (Nixon 1983). This fact, together with the major impact of the river on the estuary, could help to explain the apparently high productivity of the Apalachicola system. The phytoplankton productivity in the Apalachicola estuary is moderately high (Table 28). Estabrook (1973) found that such production is similar to that found in Tampa Bay. The importance of phosphorus as the limiting nutrient for phytoplankton productivity for various estuaries, including the Apalachicola system, is evident (Nixon 1983). Relatively little of the Apalachicola primary productivity is due to cultural eutrophication from input of nutrients from human wastes. The Apalachicola is the least developed of the estuaries surveyed, with an extremely low population density (Table 29). The contribution of nutrients from point source discharges to the Apalachicola estuary is extremely low (Table 30). These data indicate that the Apalachicola estuary remains in a relatively natural state compared to other such systems around the country.

A comparison of zooplankton abundance in different estuaries is difficult because distribution and abundance depend to some degree on mesh size of the nets used to take the samples. A wide variety of mesh sizes has been used in such studies. When compared with other estuaries in the gulf, Apalachicola Bay has a similar or larger zooplankton assemblage in terms of numbers and biomass (Edmisten 1979). Such numbers are comparable to those taken in various estuaries in the United States (Nixon 1983). A comparison of ichthyplankton in the other estuaries indicated that the bay anchovy (Anchoa mitchilli) as a dominant species is a common characteristic in half the estuaries surveyed (Nixon 1983). The low numbers of fish eggs in the Apalachicola system, relative to other areas such as Tampa Bay, has been attributed to the relatively low salinities in the Apalachicola estuary (Blanchet 1978). Attempts to make comparisons between the level of primary production and abundance of organisms at higher trophic levels indicate no direct or simple correlation (Nixon 1983).

Table 27. Approximate dimensions of selected estuarine systems (Nixon 1983).

Estuarine system	Watershed area (km^2)	Surface area (km^2)	Mean depth (m)	Mean tide (m)	Flushing factor (days)[a]
Narragansett Bay	4.8×10^3	265	9	1.23	27
Long Island Sound	4.2×10^4	3200	19	1.46	166
New York Bay	3.8×10^4	390	6	1.42	3
Delaware Bay[b]	3.3×10^4	1942	10	1.52	97
Chesapeake Bay	1.1×10^5	11500	7	0.73	56
Patuxent Estuary	2.2×10^3	122	5	0.43	51
Potomac Estuary	3.8×10^4	1251	6	0.46	45
Pamlico Estuary	1.1×10^4	305	3	0.15	26
Apalachicola Bay	4.4×10^4	210	2	0.55	6
Mobile Bay		1070	3	0.41	12
Barataria Bay	4.0×10^3	176	2	0.30	
San Francisco Bay[c]	1.6×10^5	1240	2	1.5	
Suisun Bay plus					107
San Pablo Bay		445	4	1.3	
South Bay		490	6	1.7	320
Kaneohe Bay	97	32	8	0.43	2

[a] Approximate annual mean hydraulic residence time. The freshwater input to Barataria Bay has not been reported.
[b] Below Smyrna River.
[c] Area includes mud flats, mean depth = 6 m excluding flats.

Table 28. Estimates of particulate primary production in various estuaries in the United States (after Nixon 1983).

Location	Primary production g C m^{-2} y^{-1}
Mid Narragansett Bay	310
Mid Long Island Sound	205
Lower New York Bay	483
Lower Delaware Bay[a]	206
Mid Chesapeake Bay[b]	445
Patuxent Estuary	210
Pamlico Estuary	200-500
Apalachicola Bay	360
Barataria Bay[c]	360
San Francicsco Bay	
Suisun Bay	95
San Pablo Bay	100-130
South Bay	150
Kaneohe Bay	165

[a] Below Leipsic River, 80% of total bay production.
[b] Four-year mean (1974-1977).
[c] Phytoplankton 165, Benthos 195.

Livingston (1981b), in a comparison of the distribution of various sciaenids in estuaries along the northeast Gulf of Mexico, found that the Apalachicola estuary is extremely productive in terms of fish populations (Table 31). Prime habitats include the mud flats of East Bay and the mouth of the Apalachicola River and the grass beds in Apalachicola Bay off St. George Island. The unpolluted, highly turbid estuary, with its high plankton productivity and abundant allochthonous detritus, presents an optimal environment for benthic omnivores (such as croaker and spot) and epibenthic carnivores (such as silver perch and sand seatrout). The Econfina estuary is a relatively clear, unpolluted system dominated by benthic plants (macrophytes), which provide the major source of productivity and habitat features for other organisms in the area. This estuary, which receives considerably less overland runoff than the Apalachicola system, is dominated by fishes associated with the extensive seagrass beds in the area. Although fish productivity is relatively high, the sciaenids are not as well represented and account for only about 20% percent of the total fish catches over the 9-year sampling period.

The Fenholloway estuary, polluted for over 20 years by pulpmill effluents, is largely devoid of benthic plants and has an increase in phytoplankton productivity and associated planktonic food webs. Relatively high levels of phytoplankton productivity (derived from anthropogenic input of nutrients) are correlated with increased representation by fishes associated with planktonic food webs. Overall fish productivity has been severely reduced because of the impact of the pulpmill effluents on the biological organization of the estuary. Although the overall abundance is low, sciaenids are well represented in terms of numbers of

Table 29. Approximate land use distribution and population density surrounding the estuarine study areas (Nixon 1983).

Study area	Developed (%)	Agriculture (%)	Other (%)	Population density (people/acre)
Narragansett Bay	37	6	57	1.5
Long Island Sound	29	3	68	1.1
New York Bay	40	--	60	3.2
Raritan Bay	39	14	47	1.5
Delaware Bay	27	35	38	0.3
Chesapeake Bay	27	24	49	1.2
Patuxent Estuary	36	21	43	0.4
Potomac Estuary	27	22	51	0.1
Pamlico Estuary	3	21	76	0.02
Apalachicola Bay	1	21	77	0.3
Mobile Bay	13	15	73	1.5
Barataria Bay	10	41	49	2.3
San Francisco Bay	18	22	60	4.6
Kaneohe Bay	32	10	58	

species in the Fenholloway estuary. This phenomenon can be attributed to the fact that the pollution altered the natural habitat in such a way as to induce a superficial resemblance to the Apalachicola estuary. This altered habitat favored plankton-feeding and mud-flat species as part of an unstable succession of adventitious populations in the polluted estuary (Livingston 1982b).

Compared with other estuaries, the Apalachicola system has relatively low finfish landings, while blue crab landings are moderately high (Nixon 1983). However, in terms of oyster yield per unit area, the Apalachicola estuary was the second highest of those systems surveyed (Nixon 1983). Although the connection between fishery yields and primary production remains largely undetermined in a quantitative sense, the importance of the response of individual species to varying sets of environmental conditions probably plays a considerable role in the form and direction of secondary production in any given system. Also, socioeconomic factors are important in the definition and use of a given fishery resource.

It is clear that relatively little has been done to compare various ecological characteristics of different estuaries. Part of the problem lies in the difficulty of carrying out simultaneous long-term studies in separate estuaries using comparable methods of data collection. The organization, funding, and execution of studies on more than one such system is difficult (Nixon 1983). It is clear that more comparative studies will be necessary if we are to understand the significance of the driving environmental features of any given estuary.

Table 30. A. Approximate annual input from land drainage and point source discharge of dissolved inorganic nitrogen (NH_4^+, NO_2^-, NO_3^-) per unit area and per unit volume in various estuaries.[a] The top number of each entry is in mmol m^{-2} y^{-1}, the bottom number is in mmol m^{-3} y^{-1} (Nixon 1983).

Estuary	Land drainage	Sewage	Total	Percent sewage
Narragansett Bay	560	390	950	41
	60	40	100	
Long Island Sound	130	270	400	67
	10	20	30	
New York Bay	5,700	26,230	31,930	82
	800	3,750	4,550	
Raritan Bay	200	1,260	1,460	86
	50	280	330	
Delaware Bay	650	650	1,300	50
	70	70	140	
Chesapeake Bay	340	170	510	33
	50	30	80	
Patuxent Estuary	310	290	600	48
	60	50	110	
Potomac Estuary	420	390	810	48
	80	60	140	
Pamlico Estuary	860	minor	860	< 1
	250	--	250	
Apalachicola Bay	550	10	560	2
	210	3	213	
Mobile Bay	1,206	80	1,280	7
	370	30	400	
Barataria Bay	570	minor	570	< 1
	290	--	290	
Northern San Francisco Bay	1,100	910	2,010	45
	160	130	290	
South San Francisco Bay	minor	1,600	1,600	100
	--	310	310	
Kaneohe Bay	50	180	230	78
	10	30	40	

(continued)

Table 30. (Concluded.)

B: Approximate annual input from land drainage and point source discharges of dissolved inorganic phosphate (PO_4^{3-}) per unit area and per unit volume in the study areas.[a] The upper entry for each estuary is area (mmol m^{-2} y^{-1}) and the lower is volume (mmol m^{-3} y^{-1}) (Nixon 1983).

Estuary	Land drainage	Sewage	Total	Percent sewage
Narragansett Bay	28 3	38 4	66 7	58
Long Island Sound	?	?	?	
New York Bay	55 8	1500 210	1555 218	96
Delaware Bay	18 2	62 6	80 8	78
Chesapeake Bay	40 1	9 1	69 2	13
Patuxent Estuary	67 12	170 32	237 44	72
Potomac Estuary	?	55 7	> 55 > 7	
Pamlico Estuary	114 34	minor	114 34	minor
Apalachicola Bay	14 5	minor	14 5	minor
Mobile Bay	240 74	9 3	250 77	3.6
Barataria Bay	?	?	?	
Northern San Francisco Bay	104 22	216 46	320 68	68
South San Francisco Bay	minor	263 50	263 50	100
Kaneohe Bay			22 3	

[a] Data rounded to the nearest 10 units, compiled and calculated for various years from different sources.

Table 31. Total numbers of fishes per trawl sample taken at permanent stations in the Apalachicola estuary (3/72-7/80), the Econfina estuary (6/71-5/79), and the Fenholloway estuary (6/71-5/79). Numbers per trawl are averaged over the entire period of study with percentages of the total number of fishes taken indicated by brackets. The 25 numerically dominant species in each estuary were used for the analysis. Sciaenids are marked with asterisks (from Livingston 1981b).

Species	Total numbers per sample (% of total)
Apalachicola estuary	
Anchoa mitchilli	2511 (30.8)
Leiostomus xanthurus*	1766 (21.6)
Micropogonias undulatus*	1513 (18.5)
Brevoortia patronus	1214 (14.9)
Cynoscion arenarius*	498 (6.1)
Harengula pensacolae	54 (0.7)
Bairdiella chrysura*	50 (0.6)
Trinectes maculatus	41 (0.5)
Arius felis	37 (0.5)
Lagodon rhomboides	37 (0.5)
Symphurus plagiusa	35 (0.4)
Chloroscombrus chrysurus	35 (0.4)
Etropus crossotus	33 (0.4)
Microgobius gulosus	32 (0.4)
Lucania parva	30 (0.4)
Polydactylus octonemus	27 (0.3)
Paralichthys lethostigma	24 (0.3)
Menticirrhus americanus*	24 (0.3)
Syngnathus scovelli	19 (0.2)
Stellifer lanceolatus*	16 (0.2)
Anchoa hepsetus	14 (0.2)
Eucinostromus argenteus	14 (0.2)
Prinotus tribulus	14 (0.2)
Menidia beryllina	13 (0.2)
Gobiosoma bosci	13 (0.2)
Econfina estuary	
Lagodon rhomboides	1418 (56.3)
Leiostomus xanthurus*	338 (13.4)
Bairdiella chrysura*	156 (6.2)
Monacanthus ciliatus	59 (2.3)
Gobiosoma robustum	53 (2.1)
Diplodus holbrooki	50 (2.0)
Orthopristis chrysoptera	47 (1.9)
Eucinostomus gula	44 (1.8)
Micrognathus crinigerus	42 (1.7)
Syngnathus floridae	40 (1.6)
Opsanus beta	32 (1.3)
Eucinostomus argenteus	28 (1.1)
Stephanolepis hispidus	23 (0.9)
Econfina estuary (continued)	
Centropristis melana	19 (0.8)
Paraclinus fasciatus	18 (0.7)
Syngnathus scoveli	18 (0.7)
Chasmodes saburrae	16 (0.6)
Cynoscion nebulosus*	13 (0.5)
Lucania parva	13 (0.5)
Microgobius gulosus	9 (0.3)
Chilomycterus schoepfi	9 (0.3)
Urophycis floridanus	8 (0.3)
Anchoa mitchilli	8 (0.3)
Haemulon plumieri	8 (0.3)
Sphoeroides nephelus	7 (0.2)
Fenholloway estuary	
Anchoa mitchilli	231 (26.3)
Leiostomus xanthurus*	228 (25.9)
Lagodon rhomboides	95 (10.8)
Bairdiella chrysura*	53 (6.1)
Anchoa hepsetus	36 (4.1)
Orthopristis chrysoptera	26 (2.9)
Eucinostomus gula	23 (2.6)
Eucinostromus argenteus	19 (2.2)
Gobiosoma robustum	15 (1.7)
Paraclinus fasciatus	12 (1.4)
Chilomyceterus schoepfi	10 (1.2)
Micropogonias undulatus*	9 (1.1)
Syngnathus scovelli	8 (1.0)
Urophycis floridanus	8 (1.0)
Cynoscion arenarius*	7 (0.9)
Opsanus beta	6 (0.7)
Stephanolepis hispidus	6 (0.7)
Micrognathus crinigerus	5 (0.6)
Sphoeroides nephelus	5 (0.6)
Polydactylus octonemus	5 (0.6)
Cynoscion nebulosus*	5 (0.6)
Monacanthus ciliatus	4 (0.5)
Centropristis melana	4 (0.5)
Syngnathus floridae	4 (0.5)
Etropus crossotus	4 (0.5)

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APPENDIX A
OVERVIEW OF SAMPLING PROGRAM IN NORTH FLORIDA COASTAL AREAS

1. Apalachicola Bay System

a. Physico-chemical measurements. (All stations, surface and bottom; March, 1972-present; minimum at monthly intervals. Temperature (air), river flow and rainfall data from Atlanta, Georgia, to Apalachicola, Florida, (monthly, 1920--present) are also on files in the data base)

temperature (^{o}C)
salinity (ppt)
dissolved oxygen (ppm)
turbidity (J.T.U.)
color (Pt-Co units)
depth (m)
pH (since 1974)
Secchi readings (m)
chlorophyll a (discontinued 9/76) (μg ℓ^{-1})
orthophosphate (discontinued 9/76) (μg P ℓ^{-1})
nitrite (discontinued 9/76) (μg N ℓ^{-1})
nitrate (discontinued 9/76) (μg N ℓ^{-1})
silicate (discontinued 9/76) (μg Si ℓ^{-1})
ammonia (discontinued 9/76) (μg NH_3 ℓ^{-1})
organochlorine compounds (pesticides, PCB's, etc.) (monthly, 1972-74)
heavy metals (1983)
B.O.D., C.O.D. (1983

b. Sediments. (representative stations, monthly intervals, 3/75-2/76)

grain size (phi units)
organic content (% dry weight)

c. Detritus. (macroparticulates: all stations, monthly from 1/75 to present). microparticulates: mouth of Apalachicola and Little St. Marks Rivers, monthly from 8/75 to present)

macroparticulates (by species or type, g dry weight)
microparticulates (sieve intervals; 45 μ, 88 μ, 125 μ, 250 μ, 500 μ, 1 mm, 2 mm; g ash-free dry weight)

d. Phytoplankton analysis (Iverson et al.). (selected stations, monthly intervals; 7/72-9/76)

qualitative (species) analysis
productivity (ng C m^{-3} hr^{-1})
limiting factor analysis

e. Grassbed (Vallisneria americana) analysis. (macrophyte samples, m^2, monthly from 11/75 to 7/77)

By species biomass (g dry weight)

f. Litter-associated assemblages. (stations 5A, 3, and 1X; quarterly and/or monthly from 4/74 to 1/77)

By species (numbers and biomass, g ash-free dry weight)

g. Benthic infauna. (stations 1, 1X, 3, 4, 4A, 5A, 5B, 6); 10 repetitive cores/station; monthly, 3/75 to present); weekly (station 3, 5A, Marine Laboratory:10/82-present)

By species (numbers and biomass g ash-free dry weight)

h. Grassbed assemblages. (stations 4A and 4B; monthly from 11/75 to 7/77)

By species (numbers and biomass in g dry weight)

i. Epibenthic fishes and invertebrates. (otter trawls; all stations, 3/72 to present. Trammel nets and seines, various stations)

By species (numbers and biomass in g dry weight)

j. Stomach contents, fishes (dominant species) and blue crabs. (all stations, monthly from 3/75 to 12/78)

By group or species according to month, size class, and station biomass (g ash-free dry weight) (Peter F. Sheridan, Roger A. Laughlin)

k. Zooplankton. (202 μ mesh nylon net; monthly from 11/73 to 12/74)

By species (numbers, biomass, g dry weight) (H. Lee Edmisten)

l. Larval fishes. (505 μ plankton net; monthly from 11/73 to 12/74)

By species (numbers) (Harry Blanchet)

m. Meroplankton. (303 μ plankton net; weekly, 10/82 to present; stations 3, 5A, Marine Laboratory)

n. Fisheries data. (key commercial species; Florida Department of Natural Resources)

(monthly from 1955 to present)

2. Apalachee Bay System

a. Physico-chemical measurements. (all stations, surface and bottom; June 1971-May 1979; at (minimum) monthly intervals)

temperature (°C)
salinity (ppt)
dissolved oxygen (ppm)
turbidity (J.T.U.)
color (Pt-Co units)
depth (m)

pH (discontinued in 1974)
Secchi readings (m)
chlorophyll *a* (discontinued in 1975) ($\mu g\ \ell^{-1}$)
orthophosphate (discontinued in 1975) ($\mu g\ P\ \ell^{-1}$)
nitrite (discontinued in 1975) ($\mu g\ N\ \ell^{-1}$)
nitrate (discontinued in 1975) ($\mu g\ N\ \ell^{-1}$)

b. Sediments. (representative stations, October 1972; November 1972; February 1973; monthly, November 1976 - December 1978)

c. Phytoplankton analysis (Iverson and Bittaker). (selected stations, monthly intervals, E10-F11, E11-F14, T21; January 1972-1975)

qualitative (species) analysis
productivity (ng C m^3 hr^{-1})

d. Benthic macrophytes: long-term changes. (monthly from March 1972 - May 1979, at certain permanent stations)

by species, m^2, g dry weight

e. Benthic infauna: seasonal variability. (same stations as sediments; 10 repetitive cores/station; monthly, 11/1976 to 12/1978)

by species (numbers and ash-free dry weight/m^2)

f. Short- and long-term variablity of epibenthic fishes and invertebrates (numbers and biomass)

Seine: marsh stations, 1972-1975
Trammel nets: Offshore stations, 1974-1975, 1976-1978
Multiple otter trawl tows (7.2 min./station) monthly, E7, E8, E10, E12; F9, F10, F11, F12; 6/72-5/79; quarterly, all stations, 6/72-5/79)

g. Trophic relationships (stomach contents) of fish assemblages in Apalachee Bay. (top 28 species, by numbers, all stations, monthly from 6/1972 to 12/1978)

biomass by group or species, according to month, size class, and station (g ash-free dry weight)

h. Trophic interactions of the pinfish (*Lagodon rhomboides*) with key biological variables such as macrophytes and benthic invertebrates in Apalachee Bay (Allan W. Stoner)

i. Nocturnal feeding habits of fish assemblages in Apalachee Bay (Joseph D. Ryan)

j. Day/night and seasonal varibility of epibenthic invertebrate distribution (Holly S. Greening)

k. Seasonal variability of larval fishes in Apalachee Bay (Kathleen Brady)

l. Trophic relationships of decapod crustaceans (K. Leber)

APPENDIX B
COMPUTER PROGRAMS FOR ANALYZING FIELD AND LABORATORY DATA

1. Special Program for Ecological Science (SPECS): System Overview

a. Introduction

Long-term field studies in which diverse habitats are regularly sampled for a variety of organisms and physical-chemical factors amass large amounts of data. Organization and presentation of such data in a useful form has been aided significantly by modern high-speed computers.

At Florida State, we have designed and developed a computer software system specifically for use with long-term biological data. Primary design criteria have been storage of a large data base, retrieval of virtually any subset of the data, and rapid access to a diverse group of biological, statistical, and graphical data.

The SPECS system has been written mostly in the FORTRAN programming language. A few subroutines are written in the Control Data Corporation (CDC) COMPASS assembly language. SPECS operates on a CDC 6500 or CYBER 74 computer under the KRONOS operating system.

b. Organization of the System

Data storage

Field and laboratory data on physical-chemical parameters and fish, invertebrate, and plant populations are assembled and punched on standard 80-column cards or entered directly via a computer terminal. Upon completion of a preliminary edit a program is executed to add the raw data to a data-base tape.

Two data base tapes are maintained, each with four files (one each for the four types of data). One tape is always the "current" data base, the other serves as a backup. Upon each addition of new information the tapes reverse roles.

Raw data information is also copied to a raw-data tape. This tape serves as an additional backup copy of information (although it is not in data-base format).

User Programs

All user programs, procedure files (predefined sets of often-used operating system commands), program libraries, and active data files reside on computer-center disk packs (for rapid access). Most of the SPECS system is stored as a single file on one of these disks.

This file contains one large program which has been structured in an overlay format having one main overlay and nine secondary overlays. Secondary overlays perform the majority of system functions, such as loading data, sorting, calculating biological indices, preparing for graphics and statistics, etc. The main overlay simply fields a SPECS system command and calls for the loading of a secondary overlay.

Library Programs

The F.S.U. Computer Center program library contains many routines accessed by the SPECS system. Among these are the Statistical Package for the Social Sciences (SPSS), the FSU plotting package, a mapping package (SYMAP), and a SORT/MERGE routine. The function of some SPECS secondary overlays is therefore to prepare data base information for input to these higher level routines.

c. Operation of the System

All programs in the system are designed to be operated from a remote teletype or CRT terminal. System operation is interactive in that there is two-way communication between the user and the program. The user guides the program through each step of analysis by entering commands or other information in response to questions displayed by the program.

Terminal Session

A terminal session with the SPECS system begins with a user call of the INIT (initiate) procedure file. This procedure first asks the user for the location of the data to be used in this run (possibly a data base tape or an active data file). It then gets the SPECS program and initiates its execution.

The main overlay of SPECS writes a "COMMAND?" message to the terminal screen. In response the user enters a SPECS system command. The LOAD (retrieve) and SORT commands are used to create an active data file from a database tape. If the user began this run with an active data file (created in a previous run), the LOAD and SORT commands are not needed. Once an active data file is available for use, the user selects from among a group of commands that initiate execution of secondary overlays which perform analyses of active data.

Upon completion of an analysis, the user may wish to load more data (create an additional active data file), request another type of analysis on the same data file, or terminate SPECS system operation. When system operation is ended file disposition is under user control. Active data files or other intermediate files may be saved if they will be used again. This option is especially valuable if an important file has taken a long time to generate (that time need not be invested again).

d. Summary

The SPECS system consists of a collection of programs written expressly for the storage, retrieval, and analysis of long-term ecological data. Some programs perform direct calculations or data manipulations while others serve as interface programs that prepare data for higher level (and widely available) program packages.

Interactive design affords a person with limited computer background immediate access to a broad-based data file. It also facilitates a rapid, relatively inexpensive yet comprehensive analysis with great flexibility of access to data and forms of analysis. All operations are carried out at the terminal; new options can be added easily; and routine periodic updates of the data base are easily made. This gives the biologist the use of a sophisticated computerized software system as a research tool.

e. Capabilities

(1) Data Storage

(a) Physical-chemical data (by area, station, date, time of day, and depth)
- -dissolved oxygen, color, turibidty, Secchi disk depth, temperature, pH, river flow, rainfall, bottom type
- -nitrate, phosphate, ammonia, water-column productivity

(b) Fish and invertebrate data (by area, station, date, and time of day):
- -genus and species, number of individuals, mean size (with standard deviation), biomass (ash-free dry wt.), sex (invertebrates only)

(c) Plant data (by area, station, date, and time of day):
- -genus and species, total wet and dry weight stems and roots (wet and dry weight), tops (wet and dry weight)

(2) Data Processing

(a) Retrieval
- -for any area, station or group of stations, date or range of dates

(b) Sorting
- -by area, date, station, time of day, or any combinaton of these
- -biological data sorted by species

(c) Calculation of biological indices (based on numbers of individuals or biomass per species for any area, station or group of stations, date or range of dates, or time of day):
- -Species Richness (number of species, Margalef Index)
- -Species Diversity (Simpson index, Brillouin Index, Shannon Index, McIntosh/indices, Hurlbert's $E(S_n)$)
- -Species equitablity (Brillouin J, Shannon J')

(3) Graphics

- -for any area, station or group of stations, range of dates, or time of day): plotted as a function of time or any other variable
- -all physical chemical variables
- -fish and invertebrates
  - a) number of individuals (single species or collective total)
  - b) average size
  - c) dry weight biomass (single species or collective total)
  - d) number of species
- -plants
  - a) dry weight biomass (single species or collective total)
  - b) number of species
- -Versatec high-resolution electrostatic plotter

(4) Statistics

- -for virtually any set(s) of numbers that can be generated by any other routine in the system

- linear regression, Student's t-tests, non-parametric correlations, discriminant analysis, factor analysis, scattergrams, analysis of variance (one, two, and three-way), multivariate ANOVA, canonical correlations, etc.

(a) Cluster analysis
- cluster by species, station, or time
- total flexibility in how species, stations, and dates are grouped prior to analysis
- selection of similarity index from among Orloci's standard distance, product moment correlation, Fager, Jaccard, Sorenson's, Webb, Kendall, Czekanowski, Canberra metric, C-lambda, rho, and tau
- selection of clustering strategy from among unweighted pair group (grp avg), weighted pair (centroid) grouping, nearest neighbor grouping, furthest neighbor grouping, median grouping, and flexible grouping (with beta)

(b) Dendrogram
- for any output from cluster analysis
- three scales available

(c) Data reduction by summary (for any area, station or group of stations, range of dates, and times of day)
- number of individuals or dry weight biomass by species, month, and year (fish, invertebrates, and plants)
- mean, standard deviation, and range of values over any specified time period (for each of 12 physical-chemical parameters)
- trophic analysis - diet summary of food items (user-defined classes)
- C-lambda (for any area, station or group of stations, date or range of dates, and times of day)

(d) Data smoothing
- moving average (number of time units optional)
- seasonal adjustment
- data tapering and trend adjustment

(e) Time-series analysis
- autoregressive moving average approach (Box-Jenkins methodology)
- spectral analysis

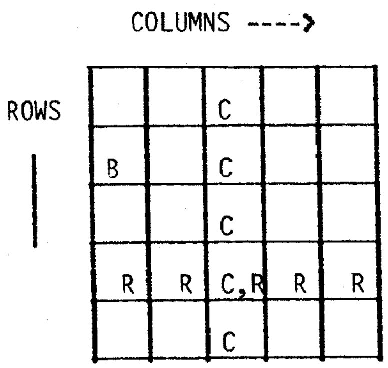
(f) Mapping
- physical-chemical data, macrophyte data, fish or invertebrate species population totals mapped for all stations in study areas (by month)

(g) Data base update
- modification of any field in a data base record or records
- deletion of data records

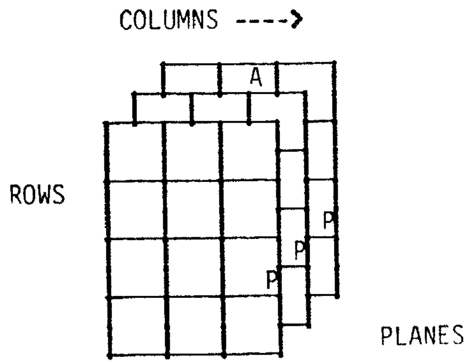
2. "MATRIX" Program System: Summary of Capabilities

a. Introduction

The term "matrix" as used here refers to a form for holding numbers. It does not have any algebraic connotations. A two-dimensional array (or table) is one very useful and frequently encountered form for the presentation of numbers. In a table (see below), basic units (cells) that contain numbers are arranged in rows and columns, where the cells of any single row or column (vector) are generally related in some way. A table of numbers can be considered a two-dimensional matrix. A three-dimensional matrix (see below) comprises a series (or set) of tables, where each table (plane) contains the same number of rows and columns. All the numbers in a single matrix plane are usually related in some way.



Matrix
two-dimensional form
(table)



Matrix
three-dimensional form

In the above diagrams, each cell in a sample column vector has been labelled with a "C", each cell of a sample row vector with an "R," and each cell of a plane vector with a "P."

An individual row, column, or plane may be referred to by a number, and numbers are, by convention, assigned in order (starting with 1) in the directions indicated by the arrows in the diagrams above. Thus all the cells labeled with "C" above are contained in column "3." An individual cell in a matrix can always be referred to by a unique set of three numbers, one each for its position by row, column, and plane. Thus the locus for the cell labelled "A" above can be described as row 1, column 2, and plane 3, or alternatively, "(1,2,3)." The three numbers can always be assigned, even if the matrix is effectively two-dimensional, as in a table, or even one-dimensional (e.g., a "matrix" might simply comprise a single cell). The point "B" above could be located by (2,1,1), where all the cells in a table would be assigned plane number 1. A cell in a single-cell "matrix" would therefore be located at (1,1,1).

b. Rationale for the MATRIX System

There are two underlying reasons for the development of the MATRIX system. First, many analytical program packages such as SPSS, BMDP, MINITAB, PLOT-10 Easy Graphing, and the SYMAP spatial mapping system require input data that is either in row and column form or in some other special form in which all data points to be utilized occur together (and sequentially). Second, many raw data files contain data points that, for a certain desired analysis, are in some way dispersed throughout the file; they must be "brought together" prior to analysis. Data points to be analyzed together might even be scattered over several raw data files. This dispersion of data points can be especially troublesome if, over a long period of time, many different kinds of data (each with a different format) are collected and entered as computer data files.

The above conditions result in what could be called a "format gap." There are two aspects of this gap: one is that the raw-data format is not suitable for direct entry of the data into an analytic routine; the other is that data points required for an analysis do not occur together. The MATRIX program system was developed as a utility (i.e., a tool) to aid an investigator in pulling together all the data required for a desired analysis and preparing the data for direct use by other analytic systems.

c. MATRIX System Design Considerations

The principal design consideration for MATRIX was flexibility in input data formats, retrieval and grouping of raw-data file values, and in manipulation and presentation of matrix file contents. Flexibility was achieved mostly through generalization of program code; MATRIX was written without any fixed input file formats so that the system could be used on a variety of input data types. Furthermore, when a matrix is produced from raw data, the user is offered a high degree of flexibility regarding which file values are retrieved, where they are positioned along a matrix dimension, and how they are "pooled" in the matrix cells. Once a matrix has been created, any of several manipulative operations can be performed on the data. Since these operations simply act on matrix rows, columns, and planes, they are effectively available for use with any MATRIX-compatible input file, regardless of the original format.

Other design considerations were adaptability and allowance for user creativity. The MATRIX system has been coded in such a way that as new higher-level package programs become available or new functions are desired of MATRIX, the changes necessary to incorporate the new features will require a minimum of programming time. There is considerable room for creativity in the use of the MATRIX system; manipulative functions currently available under MATRIX can take matrices apart, "twist" them around, change the contents, and piece them together. It is left entirely up to the user to become familiar with the power of these operations and to envision their application to specific problems.

d. Summary of MATRIX Functions

Listed below are brief descriptions of the functions performed by MATRIX system operations.

GENERATE -- Produces a numeric data matrix file of 2 or 3 dimensions from an input file containing alphanumeric storage keys and numeric data variables. The program provides for complete user definition of row, column, and plane contents, automatic insertion of missing values, and pooling of qualified retrieval values by summation or averaging. Storage keys are written along with data to serve as row, column and plane labels.

READ -- Loads the data and label information from a previously generated matrix file.

VIEW -- Displays (to the terminal) a subsection of the data points contained in the currently active matrix file. User defines the extent of row, column, and plane dimensions for a desired submatrix (which may be the entire matrix if it is 2-dimensional).

DESCRIBE -- Lists the labels assigned to rows, columns, or planes. This function is helpful in determining the contents of a matrix.

EDIT -- Allows the user to modify contents of a matrix. A user may change labels, cell values, contents of a vector (single row, column, or plane), or the missing value code assigned to a matrix. He may also add a vector to an existing matrix.

REPORT -- Similar to VIEW, but the display is written to a separate file that is suitable for printing. The display is also more informative than that of VIEW because:

(1) labels are written along with data points;
(2) an optional title is provided;
(3) the program performs report paging; and
(4) marginal totals can be reported (at user option).

SUBMATRIX -- Extracts a user-specified subsection of a larger matrix. A new matrix file (complete with labels) is created containing only the selected portion.

MERGE -- Combines two existing matrices into one, with the following restrictions:

(1) Both matrices must have the same missing-value code;
(2) At least two dimensions of the matrices must be equal (e.g., each matrix has 25 rows and 3 planes).

A new matrix file (complete with labels) is created.

TRANSPOSE -- Reorients the dimensions of a matrix in one of 2 ways:

(1) interchanging the rows, columns, or planes;
(2) making a three-dimensional matrix into two dimensions.

A new matrix file (complete with labels) is created.

STATISTICS -- Computes and (optionally) displays matrix marginal statistics including total, mean, standard deviation, number of missing points, and number of nonzero values. Statistics can be computed for either rows or columns over all planes or a selected plane. A matrix file (suitable for a MERGE operation) can also be produced if row statistics (all planes) have been selected.

TRANSFORM -- Allows a user to perform data transformation (e.g., log, square root, unit conversion) and/or standardization (i.e., to mean = 0, st. dev. = 1). Also permits computation of linear combinations of variables.

PREPARE FOR PACKAGE -- Strips a matrix file of label and header information. This function leaves a file containing data points only, which is the most convenient form of input to the BMDP, SPSS, and MINITAB statistical packages.

GRAPHICS -- Prepares matrix row or column data for the EZGRAF graphics system. A series of EZGRAF "EN"ter data commands are generated and written to a file (which is saved) suitable for EZGRAF entry with the "RUN" command.

MAPPING -- Prepares matrix data for spatial mapping with the SYMAP system. Matrix columns must correspond to predefined spatial locations (i.e., stations). The user selects which matrix rows are to be mapped.

SUBSAMPLE SPECIES -- A very specialized function, which performs "species accumulation" according to the method described by Livingston et al. (1976) and "rarefaction" according to the method of Simberloff (1978).

MENU -- Displays a "full" menu of available system operations (descriptions of options are more complete).

END -- Terminates the MATRIX program system and returns the user to interactive communication with the operating system (NOS).

e. SPECS Interfaces

The SPECS computer program system (Special Program for Ecological Science) was developed for use with the experimental and long-term biological data of Dr. Robert J. Livingston at Florida State University. While SPECS provides the capability to retrieve and sort data-base information and to calculate values of biological indices, it has only a limited ability to make these results available in a form compatible with higher-level packages such as BMDP, SPSS, EZGRAF, and MINITAB. MATRIX can act as a powerful interface between SPECS and these programs. The SPECS data base comprises the following types of data: fish, invertebrate, plant, trophic, and physical-chemical. Using the SPECS LOAD and SORT commands, these data can be retrieved for any area(s), station (or group of stations), and date (or range of dates). The resulting file is called a load/sort file and may be input to MATRIX GENERATE using one of the predefined formats described in Table A. Notice that, for each data type, there are several date options. Prudent selection of one of these can greatly reduce the user effort required for the collapse procedure specification. For example, suppose a load/sort invertebrate file is input to GENERATE and the rows of the matrix file are to be individual months from January 1978 through December 1982 (60 months). If the full date format is used, the date key values will be listed as individual days (YYMMDD). It could be tedious here to specify a monthly collapse procedure, because all the numerical assignments for the days in 01/78 would have to be entered, then all the assignments for 02/78, and so forth for possibly all of the 60 months. If the data are read with the year/month format, the day field would be skipped and the listed values would be YYMM (i.e., the monthly collapse is accomplished by the format instead of a laborious user response). The user could then simply enter 999*1 and a new row would be generated for each month. If each row were to represent one of the 12 months of the calendar year (i.e., row 1 would represent all January's, row 2 all February's, etc.), the "month only" format would be appropriate. This format causes the day and year parts of the date to be ignored, leaving only 12 possible values for the date key.

The SPECS CALC command computes ten separate diversity, richness, and evenness indices along with the total number of individuals and number of species. These variables may be calculated for any area(s), station(s), date(s), or time(s) of day or any combination thereof (see SPECS manual for details). CALC outputs two files. One (keyword OUTPUT) is suitable for printing; the other (keyword PLOTDAT) is suitable as input to MATRIX GENERATE. The use of the MATRIX program on a SPECS CALC output file is the simplest way to make these computed variables available for plotting and/or statistical analysis.

The SPECS and MATRIX systems can be run with maximum efficiency if the user gives forethought to exactly what information is needed for his analysis. A combination of LOAD, SORT, and SLECT procedures in SPECS can be used to get an input file for MATRIX with little or no extraneous data. If, for example, the fish data for all dates and stations were retrieved to a load/sort file and input to GENERATE when only the data for stations 3 and 5A from February 1978 through June 1980 were needed, two things would happen. First, MATRIX would have to read a great deal of nonrelevant data, which would result in wasted computer time and money. Second, there would be a very large number of key values listed in the collapse procedure, so more user time and effort would be required to specify the collapse correctly. The LOAD command causes an entire data base to be read. The records that match the load parameters are written to an output file. The SLECT command reads a load/sort file and writes the records that match its parameters to a smaller load/sort file. If many subanalyses are to be run on a group of data, a LOAD command should be used to retrieve all the data that will be required for all the analyses; therefore the

Table A. Predefined file formats (including lists of key and variable names) to accomplish a number of SPECS-MATRIX interfaces.

File format	Key names	Variable names
SPECS Load/Sort File -- Inverts (Full Date) -- Fish (Full Date)	AREA DATE (YYMMDD) STATION SPECIES TOD SEX (invertebrates only)	NIND (no. of indiv.) BIOMASS NSAMP (no. of samples)
SPECS Load/Sort File -- Inverts (Date is Year/Month only) -- Fish (Date is Year/Month Only)	AREA YRMON STATION SPECIES TOD SEX (invertebrates only)	NIND BIOMASS NSAMP
SPECS Load/Sort File -- Inverts (Date is Month Only)	AREA MONTH STATION SPECIES TOD SEX	NIND BIOMASS NSAMP
SPECS Load/Sort File -- Plants (Full Date)	AREA DATE (YYMMDD) STATION GENSPE TOD	DRY WT (dry weight) WET WT (wet weight) NSAMP
SPECS Load/Sort File -- Plants (Date is Year/Month Only)	AREA YRMON STATION SPECIES TOD	DRY WT WET WT NSAMP
SPECS Load/Sort File -- Phys/Chem Data (Full Date)	AREA DATE STATION TOD DEPTHCODE	DEPTH SECCHI DISSO2 COLOR TURBIDITY TEMP SALINITY pH CHL A RIVFLOW RAINFALL NITRATE PHOSPHATE PRDCTVTY AMMONIA

(continued)

Table A. (Concluded.)

File format	Key names	Variable names	
SPECS Load/Sort File -- Phys/Chem (Date is Year/ Month Only)	AREA YRMON STATION TOD DEPTHCODE	DEPTH SECCHI DISSO2 COLOR TURBIDITY TEMP SALINITY pH	CHL A RIVFLOW RAINFALL NITRATE PHOSPHATE PRDCTVTY AMMONIA
SPECS CALC Output File	AREA DATE (YYMMDD) STATION TOD	BRILL DIV SHANN DIV BRILL EVEN SHANN EVEN SIMPSON MARGALEF	DAP MAC1 MAC2 HURLBERT TOTNIND NSPECIES

large data base will only be read once. The SLECT command can then be used to create smaller load/sort files, which contain the data for specific analyses. When these smaller files are input to MATRIX, GENERATE will only have to read in relevant data points and the collapse specifications will be easy to enter.

Currently, all SPECS commands have been placed within the MATRIX operating system, and the SPECS system has been reduced to a data access system.

APPENDIX C
REVIEW OF ONGOING RESEARCH PROGRAMS OF THE CENTER FOR AQUATIC RESEARCH AND RESOURCE MANAGEMENT (FLORIDA STATE UNIVERSITY)

1. Overall Scope of Program

Since 1971, together with undergraduate and graduate students, a multidisciplinary array of scientists, and a permanent staff of post-doctoral fellows and full-time personnel, R. J. Livingston has put together a series of multidisciplinary and interdisciplinary studies concerning various aquatic systems in the southeastern United States. Simultaneous laboratory and field studies (descriptive, trophic, experimental) have been carried out, and the resulting data have been entered into a series of computerized files. Simultaneously, computer programs have been developed over the past 10 years that are designed to handle short- and long-term multidisciplinary data from various aquatic systems.

Currently, the data from the 13-year research effort are being compiled and organized for publication. These data are also being utilized to design and carry out an ongoing field experimental program in a series of freshwater, estuarine, and marine habitats.

Laboratory and Field Bioassays

A. Single-species tests (seagrasses, macroinvertebrates, fishes; fresh-water and marine animals).

B. Multiple-species tests (macroinvertebrates; freshwater and marine)

C. Seagrass microcosms

Field Surveys

A. Habitat analyses (including pollutants) and biological components (productivity, epibenthic fishes and macroinvertebrates, infaunal macroinvertebrates)

1. Spatial comparisons among rivers and associated estuaries

    a. Flint River (Georgia), Chipola River (Florida), Econfina River (Florida), Fenholloway River (Florida), Mobile River (Alabama), Escatawpa--East Pascagula Rivers (Mississippi), Pee Dee--Sampit Rivers, Winyah Bay (South Carolina)

2. Temporal comparisons (daily, weekly, and monthly intervals; 10-12 years of continuous data)

    a. Apalachicola River-estuary

    b. Econfina River-estuary

    c. Fenholloway River-estuary

B. Food-web structure of infaunal macroinvertebrates and epibenthic macroinvertebrates and fishes (freshwater and marine systems)

    1. Transformation of species-specific abundance and biomass data into trophic units by feeding mode and trophic position in food web

    2. Comparative analysis among systems by feeding mode and trophic position in food web (trophic unit)

    3. Analysis of long-term (10-12) changes of food web structure in different systems (with and without effects of pollution and habitat alteration)

    4. Interaction of habitat features, primary production, and food web features

C. Impact Analysis (freshwater, estuarine, marine)

    1. Pulp mill effluents (6 riverine and 5 estuarine systems)

    2. Storm-water runoff (Apalachicola River and Bay systems)

    3. Toxic substances (pesticides, heavy metals) (Flint River, Chipola River, Hogtown Creek, Apalachicola River and Bay systems)

    4. Dredging and spoiling (Apalachicola River and Bay system)

    5. Forestry management (Apalachicola River and Bay system)

Experimental Ecology (Laboratory and Field)

A. Validation of freshwater bioassays with field data at toxic waste sites along two rivers (Chipola River, Hogtown Creek): infaunal macroinvertebrates, epibenthic fishes and macroinvertebrates (ongoing)

B. Validation of bioassays using multi-species microcosms of soft-sediment, marine infaunal macroinvertebrates (Apalachicola Bay system and the Yorktown estuary, Virginia) (ongoing)

C. Predator-prey interactions (soft-sediment areas and seagrass beds) (ongoing)

    1. Behavioral ecology

    2. Field effects of predation on prey assemblages

    3. Influence of predator-prey relationships on community structure under varying environmental conditions (intra- and intersystem comparisons with and without pollution variables)

    4. Relation of predator-prey relationships to community structure and food web patterns

Models: time-series changes of physical, chemical, and biological variables in various aquatic systems (ongoing)

Application of research findings to resource management and public education

Development of the Apalachicola River and Bay National Estuarine Sanctuary

A. Apalachicola Atlas.

B. Continuing integration of regional research projects and a broad spectrum of educational activities (secondary, undergraduate, graduate).

C. Input of research data to local, state, and regional planning/management authorities.

2. Center for Aquatic Research and Resource Managment: Personnel (1984)

Robert J. Livingston (Director)

Glenn C. Woodsum (Associate Director)

DATA PROCESSING/ANALYSIS

Duane A. Meeter (Associate Investigator: Statistical Analysis)

Loretta E. Wolfe (Computer programming, statistical analysis)

Shelley J. Roberts (Project coordination, data transmission, formation of computer files)

FIELD OPERATIONS

Robert L. Howell IV (Field collections, epibenthic fishes/invertebrates)

BIOLOGICAL ANALYSIS

Christopher C. Koenig (Bioassay, experimental protocols, biology of fishes)

Kenneth R. Smith (Oligochaete worms, benthic invertebrates)

Gary L. Ray (Polychaete worms, benthic invertebrates)

Bruce M. Mahoney (Benthic invertebrates, experimental ecology)

William H. Clements (Benthic invertebrates, feeding habits of fishes, experimental ecology)

William R. Karsteter (Aquatic insects, benthic invertebrates, water/sediment chemistry)

John Epler (Aquatic insects)

Akshintala Prasad (Aquatic plants)

GRADUATE STUDENTS

Joseph Luczkovich (Ph.D.) (Predator-prey interactions, fish foraging, experimental ecology)

Jon Schmidt (Ph.D.) (Benthic invertebrates, experimental ecology)

David Bone (Ph.D.) (Experimental ecology, food web interactions)

Felicia Coleman (Ph.D.) (Physiological and behavioral ecology)

Kelly Custer (M.S.) (Feeding habits of decapod crustaceans, food processing by benthic invertebrates)

David Mayer (M.S.) (Ecology of penaeid shrimp, benthic invertebrates)

GRADUATE STUDENTS (continued)

Susan Mattson (M.S.) (Benthic invertebrates, experimental ecology)

Carrie Phillips (M.S.) (Benthic invertebrates, experimental ecology)

J. Michael Kuperberg (M.S.) (Interactions of benthic macrophytes and animals)

LABORATORY ANALYSIS

Kim Burton (Rough sorting, sample preparation)

Howard L. Jelks (Rough sorting, sample preparation)

Mike Hollingsworth (Sediment analysis, algal studies)

Stephen B. Holm (Rough sorting, sample preparation)

John B. Montgomery (Sample preparation)

Brenda C. Litchfield (Sample preparation)

Mike Goldman (Sample preparation)

Frank Jordan (Fish identification)

Sam Cole (Sample preparation)

Hampton Hendry (Sample preparation)

Kline Miller (Sample preparation)

Melanie Saunders (Data punching)

Joanna Greening (Sample preparation, oligochaete mounting)

Carl Felton (Sample preparation)

David Ringelberg (Sample preparation)

Sharon Solomon (Sample preparation)

Sandy Vardaman (Sample preparation)

Erica Meeter (Sample preparation)

Carol Meeter (Sample preparation)

Julia Beth Livingston (Sample preparation)

Sara Van Beck (Sample preparation)

Cathy Wallace (Data preparation)

POST-DOCTORAL ADVISORS

<u>Kenneth Leber</u> (Feeding habits of decapod crustaceans, experimental ecology)

<u>Kevan Main</u> (Predator-prey interactions, behavioral ecology)

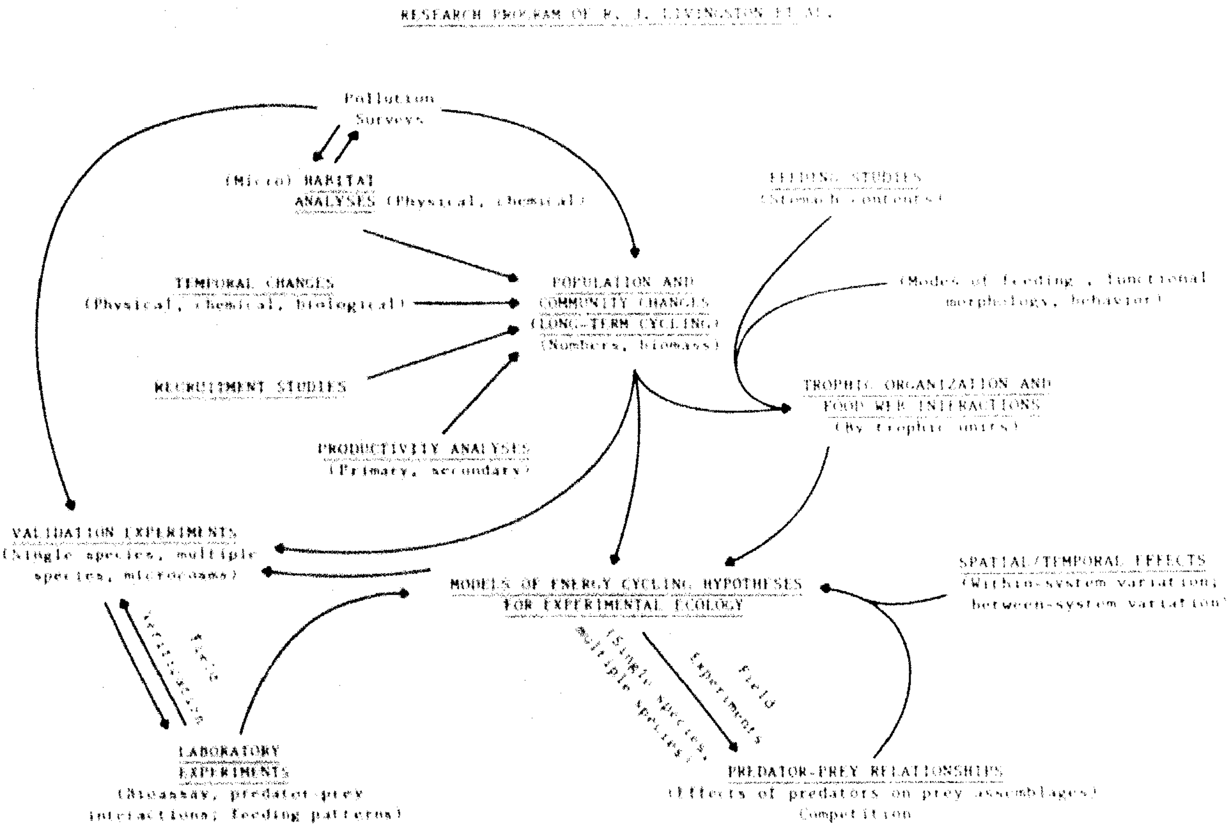


Figure A. An overview of the ongoing research program of the Florida State University Aquatic Research Group concerning long-term studies in nine river systems and six estuaries in the southeastern United States.

50272-101

REPORT DOCUMENTATION PAGE

1. REPORT NO. FWS/OBS-82/05

2.

3. Recipient's Accession No.

4. Title and Subtitle The Ecology of the Apalachicola Bay System: An Estuarine Profile

5. Report Date September 1984

6.

7. Author(s) Robert J. Livingston

8. Performing Organization Rept. No.

9. Author's Affiliation:
Department of Biological Science
Florida State University
Tallahassee, FL 32306

10. Project/Task/Work Unit No.

11. Contract(C) or Grant(G) No.
(C)
(G)

12. Sponsoring Organization Name and Address
National Coastal Ecosystems Team
Research and Development
Fish and Wildlife Service
Washington, DC 20240

13. Type of Report & Period Covered

14.

15. Supplementary Notes

16. Abstract (Limit: 200 words)

Twelve years of studies in the Apalachicola Bay system are reviewed. Included are data on geography, hydrology, chemistry, geology, and biology.

The system is part of a major drainage area including four rivers and associated wetlands in Georgia, Alabama, and Florida. It is a shallow coastal lagoon fringed by barrier islands and dominated by wind effects and tidal currents. River bottomlands (channels, sloughs, swamps, and backwater) and periodically flooded lowlands are important components. Principal influences on biological processes are basin physiography, river flow, nutrient input, and salinity. Water quality is affected by periodic wind and tidal influences and freshwater inflows.

The system is in a relatively natural state, though hardly pristine. But economic development and population growth are beginning to threaten it. The area's economic and ecological importance as a food producer and shelter for diverse species has inspired a movement to protect its natural resources, including State and Federal land-purchase programs, integration of county land-use regulations into a comprehensive development, and creation of the Apalachicola River and Bay National Estuarine Sanctuary.

Research has produced an extensive computerized data base. Computer programs for working with these data have been developed.

17. Document Analysis a. Descriptors

Geology
Hydrology
Biology
River
Estuaries
Ecology
Fisheries

b. Identifiers/Open-Ended Terms

Bottomlands
Flooded lowlands
Nutrient input
Apalachicola Bay
Florida

c. COSATI Field/Group

18. Availability Statement unlimited

19. Security Class (This Report) unclassified

20. Security Class (This Page) unclassified

21. No. of Pages 150

22. Price

(See ANSI-Z39.18)

OPTIONAL FORM 272 (4-77)
(Formerly NTIS-35)
Department of Commerce