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ECOLOGY and MANAGEMENT of TIDAL MARSHES

A Model from the Gulf of Mexico

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Introduction: The Intertidal Marshes of Florida's Gulf Coast

Clay L. Montague and Howard T. Odum

The intertidal marshes of Florida's Gulf coast are exhilarating to view and exciting to explore. They are among Florida's most productive ecosystems, annually giving rise to vast quantities of both plants and animals. They exist at the water-logged fringe of land over which coastal waters inundate and recede from the force of the wind and tide. Abundant food and cover alternately attract aquatic and terrestrial animals. The marsh vegetation is highly productive, but not very diverse. A single species may dominate, forming nearly monotypic stands that from a distance look like a vast mowed playing field or pasture. Fields of corn and sugarcane are similarly productive, but their high production and low diversity depend on artificial subsidies of fuel, human labor, and pesticides. Damaging epidemics of disease and pests, common in agricultural monocultures, are virtually unknown in intertidal marshes.

Residential property in Florida with a view of intertidal marsh often sells for a far greater price than nearby property without such a view. Access to tidal creeks adds even more value. Although these benefits of intertidal marshes accrue to the fortunate owners of marsh-front property, several ecological functions hidden within the spectacular view benefit the public at large (Table I.1). Intertidal marshes, which include salt-, brackish, and freshwater marshes in fluctuating coastal waters, are one of a set of coastal ecosystems (including seagrasses, mud flats, rocky outcroppings, mangroves, plankton, and others) that together account for Florida's productive commercial and recreational fish-

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Table I.1 Known or Suspected Public Values of Intertidal Marshes

1 Shoreline protection from storm surge, winds, and waves
2 Habitat: simultaneous food and cover for numerous fishes, crustaceans, mollusks, birds, and other vertebrates and invertebrates, many of commercial or recreational importance, some threatened or endangered
3 Part of a *set* of estuarine and nearshore habitats of varying scale and location that ensure a diversity of productive fish and wildlife at all life history stages
4 Buffer of estuarine food supply
5 Buffer of estuarine water quality
6 Contributor to attractive coastal image that encourages development

eries. They provide food and cover for juvenile stages of most estuarine fish and invertebrates, including commercially valuable shrimp and blue crabs as well as sportfish such as red drum and spotted seatrout. Intertidal marshes reduce damage from storms by attenuating the energy of winds, waves, and storm surges. Furthermore, as coastal waters alternately fill and drain, materials used and produced by the marsh are exchanged, which results in a stabilizing effect both on estuarine water quality and on the food supply to the web of estuarine biota.

Intertidal marshes help trap and stabilize estuarine sediments, increasing water clarity in coastal waters. If water were to become more turbid because of the loss of intertidal marshes, seagrass beds would die because of lack of light. Seagrass also stabilizes sediments, reduces damage from storms, and is habitat for numerous aquatic animals. Intertidal marshes form part of the image of coastal Florida, which stimulates many to tour and live on Florida's coast.

Intertidal marshes are a key part of the coastal ecosystem and the coastal economy. Florida's population continues to grow by more than 1000 people per day, more than three-quarters of whom settle in Florida's coastal counties. Coastal management is required to ensure the continuation of the functions and public values of intertidal marshes. The best management practices arise from management principles derived by integrating scientific knowledge from a variety of scales and perspectives, including models of ecological and economic theoreticians, tests of hypotheses by experimentalists, and large-scale field trials by marsh managers aimed at fish and wildlife enhancement and mosquito control.

To develop sound management principles, at least three scales of ecological study must be integrated: studies of the living components of the marsh, studies that link the components to one another and with the overall environment, and studies that link the marsh ecosystem to other estuarine subsystems and the coastal economy. Information needs at larger scales depend upon knowledge at smaller scales. However, from the perspective of coastal zone management, the whole is more than (or at least different from) the sum of the parts.

Controversies often arise concerning the use and management of marshes. Scientific, economic, and legal studies have addressed such public policy questions as the economic value of marshes, the impact and need of mosquito control, the maintenance or enhancement of coastal and estuarine fisheries, enhancement of wildlife habitat, waste disposal practices, land building on marshes, canal construction, restoration to pre-Columbian conditions, and preservation of present conditions. Unfortunately, study of such management issues is often on a crisis-by-crisis basis, initiated by those with an immediate information need and ended often prematurely when a new and different crisis begins. Usually, the entire collection of management issues is not simultaneously considered when decisions are made about one.

Effective management of the expansive intertidal marshes of Florida requires an integration of scientific knowledge with legal and economic perspectives and the development of management principles. This book is a first step in that direction. Its purpose is to summarize what is known about the structure and function of intertidal marshes as well as to present varying economic, legal, and management perspectives. It is hoped that this synthesis will lead to a more informed public and more effective management of Florida's remaining intertidal marshes. Studies of management questions at several scales are included, together with various efforts to analyze and synthesize them. This collection of information forms a basis for predicting the consequences of management decisions.

Although intertidal marshes are found along both the Atlantic and Gulf coasts, conditions for their occurrence (low wave energy and relief, high tidal range) are most favorable on the Gulf coast, particularly north of Tampa, where it is too cold for mangroves. The most extensive intact intertidal marshes are in the Big Bend region of Florida where—because of their distance from urban centers—they have been relatively protected from development pressures, though perhaps not for long given the huge growth of Florida's population and the value of coastal property. Because of their extent and attractiveness, and because there is still time to manage them properly, the intertidal marshes of the Gulf coast, particularly the Big Bend coast of Florida, are the subject of this book.

An Energy Systems Diagram of the Intertidal Marsh

To begin to synthesize knowledge of intertidal marshes and as a framework for much of what is included in this book, we have constructed an energy systems diagram (Figure I.1). A full understanding of the functions of marshes in the larger coastal ecosystem and coastal economy requires integration of scales of study, from the small to the larger. Systems methods for integrating knowledge into a fuller understanding usually involve the construction of diagrams to represent those parts and the causal connections among them that investigators believe to exist from their measurements and intuitions. These diagrams represent large-scale, complex hypotheses that reflect current knowledge and ideas. Quantifying these connections allows computer simulation of the dynamics among components that result from the hypothesis. Quantified diagrams allow other analyses as well (e.g., the "EMERGY" analysis of Odum and Odum, 1987).

Simulation modeling and analysis techniques explore the system-level consequences of the hypothesis and allow experimentation with alternative ways of connecting the parts. Often the output of a computer model is surprisingly different from what was expected or known to be true. Such a result may require a change of ideas, new hypotheses, new measurements, and revised models. In the interim, the limits of our understanding at the large scale have been learned in a rigorous manner. Old ideas, some perhaps often used in management, may have been rejected. From successful simulations come "what if" experimental manipulations that can be explored. The management consequences of allowing specific alterations to some areas in an estuary and restoring others may be predictable.

The energy systems diagram is drawn according to a protocol in which small, quickly replaced items and processes are shown on the left and slower processes with components that occupy larger territories on the right (Odum, 1983; Odum and Odum, 1987). Thus, phytoplankton are on the left and larger animals are toward the right. Products from the small components flow from left to right. Material recycling and human services form feedback loops from the right over the top of the diagram. Through these feedbacks, the high-transformity items on the right side of the diagram amplify and control the lower-transformity items on the left side.

The amount of energy of one kind (e.g., plant biomass) that is transformed in the process of producing a unit of energy of another type (e.g., herbivore biomass) is defined as the "transformity" of that product. It may take 10 calories of plankton, for example, to produce each calorie of small fish. In terms of plankton, the transformity of the fish is 10:1. All components in Figure I.1 are forms of energy and each can be expressed in units of one kind of energy,

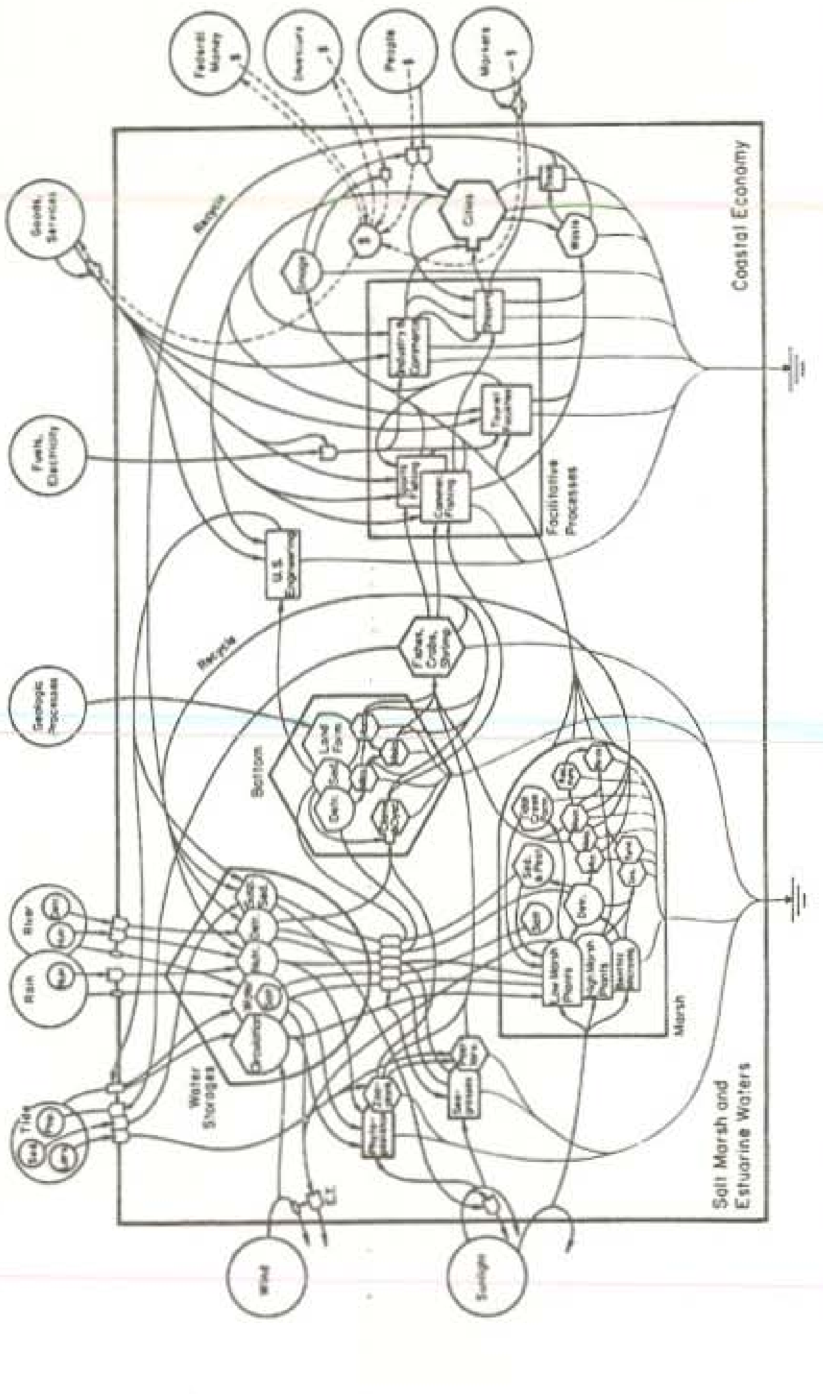

Figure I.1 The salt marsh as a component of a larger coastal ecosystem and the coastal economy as illustrated by an energy-flow network.

solar insolation, which is required both directly and indirectly to produce a unit of each component. The resulting ratios are known as "solar transformities" (Odum and Odum, 1987).

Components in the energy systems diagram are arranged from left to right in order of increasing solar transformity. Hence, basic energy sources (such as sunlight, wind, and tide) enter the diagram to the left and those which enter the system already with higher solar transformities (such as fuels, electricity, investments, and people) enter to the right. These energy sources combine at various points in the system. The flow is from left to right as the components of the system transform these energy sources into other components of higher and higher transformity. Thus, the diagram represents the natural energy hierarchy: a process in which many units of energy on the left are required to produce those to the right, which, in turn, augment or control those on the left.

Although the diagram includes many components and processes, these can be grouped into two main divisions: a natural coastal ecosystem on the left and a coastal economy on the right. Each division has a few major components and several subcomponents. The major components of the natural coastal ecosystem are the water column, the subtidal bottom, and the intertidal marsh. The main producers in these systems (indicated by bullet-shaped symbols) are phytoplankton, seagrasses, marsh plants, and microalgae. Consumers (the hexagons) include zooplankton, postlarval fish and invertebrates, microbes, meiofauna, and larger animals such as shrimp, crabs, fish, birds, and raccoons. Energy sources for the natural ecosystem (circles) include sunlight, wind, tide, rain, rivers, and long-term geologic processes that determine such things as coastal topography. Nonliving storages (the tank-shaped symbols) include circulating water (and accompanying nutrients, salts, detritus, and other dissolved and suspended materials), sediments, tidal creeks, and landforms (e.g., dunes and lowlands).

The coastal economy occupies the right third of the diagram. Cities are the main consumer. The main exogenous energy sources for this economy are fuels, electricity, goods and services, federal money (mostly defense spending), investors (many in real estate), people, and markets. Facilitative processes transform natural resources into the coastal economy. The natural ecosystem to the left produces fishes, crabs, and shrimps for commercial and recreational fisheries; contributes to an attractive coastal image that encourages tourism and development; and recycles nutrients from domestic and industrial wastes.

The diagram is the beginning of a synthesis process that will be improved by the participation of all those with specialized knowledge of its various aspects. It is hoped that this book will stimulate such a synthesis—that it will inspire research in areas where more knowledge is needed and that it will help us all, regardless of our special skills and interests, maintain a sense of the whole. Management depends on whole-system understanding.

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Setting and Functions

1

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Florida has more intertidal wetlands (salt marshes and mangroves) than Georgia, South Carolina, and North Carolina combined (Table 1.1). Over three-quarters of Florida's intertidal wetlands are on the Gulf coast, with the greatest acreage of salt marsh in the Big Bend between Tarpon Springs and Lighthouse Point at the mouth of the Ochlockonee River (Table 1.2, Figure 1.1). Extensive salt marshes are also found landward of wide bands of mangroves along the southwestern coast south of Naples.

Variations in lunar tides, topographic slope, and winter temperature account for the distribution of intertidal marshes in Florida. Sediment supply, so important to the extensive marshes of Georgia and Louisiana, is relatively insignificant along Florida's Gulf coast. Intertidal wetlands occur where coastal topographic relief is low relative to tidal range. Where coastal relief is especially low and tidal ranges high, intertidal wetlands are most expansive. A crude estimate of the inland reach of Florida's Gulf coast intertidal wetlands (in kilometers) can be obtained by dividing the predicted lunar tidal range (meters) by the change in elevation (meters/kilometers) for each region (Table 1.2).

The Gulf coast of Florida consists of a very broad continental shelf gradually rising toward land and ancient dune ridges. A little more than half of Florida's intertidal wetlands (marshes and mangroves) occur on the southwestern Gulf coast. Here, coastal topographic relief is extremely low and tidal range is higher than anywhere else along the Florida Gulf coast. In the Big Bend area, ancient dune ridges are generally well inland, nearshore topographic slope is very gradual, and predicted tidal ranges are intermediate. At the limits of the Big Bend region (Pasco County to the south and western Wakulla County to the north), geological scarps lie very near the coast and the band of marshes

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Table 1.1 Intertidal Wetland Area (Marshes and Mangroves) in the Southeastern United States

State	Marsh area (ha)	Coastline length (km)[a]
North Carolina	64,300	500
South Carolina	204,200	350
Georgia	159,000	160
Total	427,500	1,010
Florida		
Atlantic	77,800	660
Gulf	359,700	1,340
Total	437,500	2,000

[a] Measured as a boat would most likely travel if 5 km offshore.

From Montague et al., 1987a; U.S. Fish and Wildlife Service, 1984.

Table 1.2 Physical Description and Population Density Estimates for Four Regions of the Gulf Coast of Florida

Region	Area of marsh[a] (ha)	Area of mangrove[a] (ha)	Tidal range[b] (cm)	Topographic slope[c] (m/km)	Coastline length[d] (km)	1990 population density[e] (per km²)
Panhandle	16,754	97	35	10	383	50
Big Bend	66,537	6,091	100	0.4	345	37
Pinellas to Lee County	4,501	35,201	80	5	320	216
Southwest	25,345	205,142	120	0.1	290	29
Florida total	163,121	274,347	—	—	2,000	93

[a] U.S. Fish and Wildlife Service (1984).
[b] National Oceanic and Atmospheric Administration (1989).
[c] Estimate measured on 1:150,000 USGS bathymetric-topographic maps of Florida.
[d] Estimate measured on 1:500,000 USGS map of the state of Florida.
[e] Shoemyen et al. (1989).

Figure 1.1 Four regions of the Gulf coast of Florida based on environmental differences: Panhandle, Big Bend, Pinellas to Lee County coastal zone, and the southwestern coast.

narrows. The band also narrows near Cedar Key (Levy County) and between Stake Point and Rock Point in Taylor County, where ancient dune fields lie just inland (Brooks, 1981; U.S. Fish and Wildlife Service, 1985). Both southward and westward of the Big Bend region, dune ridges are close to shore and tidal ranges are lower. In the Panhandle, predicted tidal ranges are very low and coastal topography is very steep.

On the Gulf coast south of Tampa Bay, dense mangroves occupy most of the intertidal zone. Shorter marsh plants cannot survive under the shade of these trees. North of Tampa Bay, killing freezes are too frequent to allow extensive mangrove development (Table 1.3), although pockets of mangrove occur on the outer islands near Cedar Key, where the intensity of freezes is reduced by the surrounding water.

The northern extent of mangroves fluctuates with the occurrence of occasional freezes. Hard freezes in December 1983 and January 1985, for example, killed many mangroves not only at Cedar Key but also much farther south on both coasts (e.g., Indian River and Tampa Bay). At Cedar Key, where over 95% of the mangroves were killed, nonwoody salt marsh plants (mostly *Spartina alterniflora* and *Batis maritima*) have rapidly replaced mangroves in many areas. Mangrove seeds sprouted, however, during the summer of 1984 and

Table 1.3 **Climate Normals for Florida Gulf Coast**

Temperature normals (°C)

Region	*January* Max	*January* Min	*July* Max	*July* Min	*Annual* Max	*Annual* Min	*Days/year below freezing*
Panhandle	15.9	5.5	32.0	23.0	24.8	14.5	5–39
Big Bend	18.7	7.9	32.1	23.1	26.1	15.9	4–5
Pinellas to Lee County	22.7	11.2	32.6	23.3	28.3	17.7	0–1
Southwest	24.5	13.6	32.5	23.5	28.9	19.0	0–0.5

Precipitation normals (cm)

Region	*Annual mean*	*Percent from May to October*	*Monthly* Max	*Monthly* Min	*Annual range as % of mean*
Panhandle	152	58.1	20.2	8.3	7.8
Big Bend	134	63.8	20.5	6.1	10.8
Pinellas to Lee County	130	74.7	21.4	4.1	13.3
Southwest	131	79.3	22.7	3.3	14.8

Note: Computed from National Oceanic and Atmospheric Administration (1983, 1985).

young trees began to bear viable seeds by the autumn of 1987 (Montague, unpublished data).

Marshes may initially grow in a relatively narrow band of intertidal zone, but if suspended sediments are in great supply, they may expand seaward (Davis, 1940; Meade, 1982; Frey and Basan, 1985). Coasts that receive a lot of silt and clay from rivers often have extensive marsh development. In Georgia, two large rivers supply 2 million tonnes of sediment per year along only 160 km of coastline. Coastal marshes there are sediment saturated and have perhaps expanded as much as hydrodynamically possible (Meade, 1982; Meade and Parker, 1985). Additional sediment forms steep levees at the edges of marsh creeks (Frey and Basan, 1985). Likewise, in the Mississippi River Delta, the huge intertidal marsh development is attributable in large part to the (formerly) vast supply of sediments from that river, which are now largely prevented from entering marshes by dikes and levees built for channel stabilization and flood control (Turner, 1987).

Table 1.4 **Mean Total Sediment Discharge (×1000 tonnes per year) in Four Regions of the Gulf Coast of Florida**

Region	*Sediment discharge*[a]	*No. of years in mean*	*Average standard deviation*	*Ratio of standard deviation to mean*	*No. of NASQUAN stations*
Panhandle	1,459	6	36	0.41	5
Big Bend	109	6	10	0.69	8
Pinellas to Lee County	97	7	33	1.34	5
Southwest	3	7	3	1.04	1

Major sources of sediment by region:	
Percent from Apalachicola in Panhandle total	78
Percent from Suwannee in Big Bend total	67
Percent from Peace and Caloosahatchee in Pinellas to Lee County total	80
Percent from Tamiami canals in Southwest total	100

[a] Means of several years of discharge reported for all Gulf NASQUAN stations reporting in USGS Water Data for Florida, Water Years 1975–1988.

The four rivers of Florida's Big Bend (Suwannee, Steinhatchee, Sopchoppy, and Ochlockonee) supply only about 109,000 tonnes of sediment per year (Table 1.4). The Apalachicola River just to the west of marsh band supplies about 1 million tonnes per year. How much of the Apalachicola River sediment ever reaches the Big Bend coastal marshes is questionable. Sediments from the Apalachicola River tend to accumulate in shoals near the mouth and slowly drift *westward* into the very deep nearshore waters off the Panhandle (Tanner, 1960). The Big Bend is considered sediment starved, which explains why it has no barrier islands (Tanner, 1960). Because the supply of fine, marsh-building sediments from the Apalachicola River is probably also very low, these marshes have not greatly expanded seaward. Studies of the geological history of Big Bend marshes (performed by direct examination of cores) indicate little or no seaward expansion of intertidal marshes in this part of Florida over the past several thousand years (Kurz and Wagner, 1957).

Sea level along the Florida coast has been rising at a rate of about 25 cm per century and has apparently accelerated considerably in the last century, presumably due to global warming (Marmer, 1954; Wanless, 1989). As sea level rises, intertidal marshes may be expected to move inland. If nearshore conditions change so that a large supply of suspended sediment becomes available, marshes grow vertically as well, and thus the aerial extent of the intertidal zone may increase. This seems unlikely in the Big Bend area since the supply of sediment is currently so low. Furthermore, if topographic slope is steeper inland, the width of the intertidal marsh band will decrease (Mehta et al., 1989). The intertidal zone of the Big Bend area may decline considerably as the shoreline approaches the scarps and dune fields of Taylor and Levy counties. Increasing wave energy may occur with rising sea levels in some areas (Mehta et al., 1989). Whether increased wave energy will significantly reduce the loss of intertidal marsh in the Big Bend as sea level rises requires detailed hydrodynamic study.

Environment, Production, and Diversity

Abundant energy and mineral resources accumulate at the coast: rivers discharge fresh water (Table 1.5) and deposit sediments (Table 1.4) and nutrients, rain (Table 1.3) and wind (Table 1.6) are abundant, and tidal energy is discharged (Table 1.2). Together with sunlight (Table 1.7), these resources stimulate ecological production (see End-of-Chapter Note) in some intertidal marshes that is among the highest per unit area in the world. The dominant primary producer is determined largely by soil salinity and the frequency of inundation. These variables also influence the production and composition of the community of resident marsh animals and the timing of use by transient animals.

Freshwater discharges from land influence estuarine circulation and intertidal soil salinity. Surface water discharge along the Gulf coast of Florida is relatively low and decreases toward the south (Table 1.5). Low discharge of surface water usually means that saline water will extend inland for many kilometers. This is true in most regions of the Gulf coast of Florida (Table 1.8), including the large bays of the Panhandle and those of the coast from Pinellas to Lee counties. South of Lee County, very low and diffuse discharge of surface water from the Everglades allows considerable inland penetration of saline water. The Big Bend coast, however, has a surprisingly low salinity, given the low surface water discharge and the tendency of Apalachicola River water to flow westward. A significant freshwater input to this coast is groundwater. The Floridan aquifer, deep in many parts of the state, is at or near the surface throughout the Big Bend area, and flowing springs are common (Fernald and Patton, 1984). Coastal and submerged springs in the Big Bend region reduce salinity near shore.

Wind and lunar forces combine to inundate the marshes of the Gulf coast of Florida. In Gulf coast intertidal marshes, water levels are often considerably

Table 1.5 Freshwater Discharge (m^3/s) from Rivers, Streams, and Canals in Four Regions of the Gulf Coast of Florida

Region	*Mean regional discharge*	*1988[a] discharge*	*1988[a] max/mean*	*1988[a] min/max (%)*	*No. of USGS stations*	*Years of record*
Panhandle	1262	899	10	7.87	14	32
Big Bend	507	423	10	5.35	14	24
Pinellas to Lee County	163	150	29	0.21	28	19
Southwest	34	41	4	0.03	4	40

Major discharges by region	*Period of record (year)*	*Water year 1988*
Percent from Apalachicola in Panhandle total	59	56
Percent from Suwanee in Big Bend total	60	65
Percent from Peace and Caloosahatchee in Pinellas to Lee County total	50	52
Percent from Tamiami canals in southwest total	92	92

[a] Average of all stations in region.

Note: Compiled from U.S. Geological Survey Water Data for Florida, Water Year 1988.

Table 1.6 Average Wind Speed at 10 m from the Surface and Annual Storm Frequency for Four Regions of the Gulf Coast of Florida

Region	*Wind speed (m/s)[a]*	*Standard deviation[b] (12 months)*	*Probability of tropical storm or hurricane[c] (%)*	*Probability of destruction by hurricane[c] (%)*	*Mean annual days with thunderstorms[d]*
Panhandle	3.5	0.38	11–21	6–13	60–80
Big Bend	3.3	0.34	12–20	4–6	80–100
Pinellas to Lee County	3.5	0.35	9–12	4–9	100–110
Southwest	4.0	0.42	19–21	9–13	85–100

[a] Reed (1979).

[b] Computed from data in state of Florida (1983).

[c] Bradley (1972).

[d] Bryson and Hare (1974).

Table 1.7 Insolation and Cloud Cover for Four Regions of the Gulf Coast of Florida

	Insolation (Langleys)			*Cloud cover*[c] *(days/year)*	
Region	*Annual*[a]	*December*[b]	*May*[b]	*Cloudy*	*Partly cloudy*
Panhandle	408–445	225–265	565–615	120–150	110–115
Big Bend	445–453	265–300	600–615	120–125	110–140
Pinellas to Lee County	428–450	300–320	550–600	105–125	140–155
Southwest	450	300–320	550–580	100–120	155–170

[a] Bryson and Hare (1974).
[b] Bennett (1965).
[c] Conway and Liston (1974).

different than those predicted in lunar tide charts (Figure 1.2). Winds from the north and northeast, more common in the winter, may push water out of the marsh and keep it out. Winds from the south and west, which occur more often in the summer and are usually relatively gentle, may hold water on the marsh for the entire tidal cycle.

Table 1.8 Inland Extent of Saline Water in Four Regions of the Gulf Coast of Florida

	Average distance (km)[a]				
Region	*Gulf to river mouth*[b]	*Gulf to 20 ppt*	*20–5 ppt*	*5–0.5 ppt*	*No. of rivers in average*
Panhandle	32.3	15.5	18.9	12.6	7
Big Bend	1.1	0.8	4.1	10.2	12
Pinellas to Lee County	26.5	26.5	14.2	24.0	7
Southwest	1.8	21.3	8.8	4.6	4

[a] Data measured from U.S. Fish and Wildlife Service Gulf Coast Ecological Inventory Maps (see Beccasio et al., 1982).
[b] Rivers sometimes discharge into bays rather than directly into the Gulf. The number in this column reflects the prevalence of bays in each region.

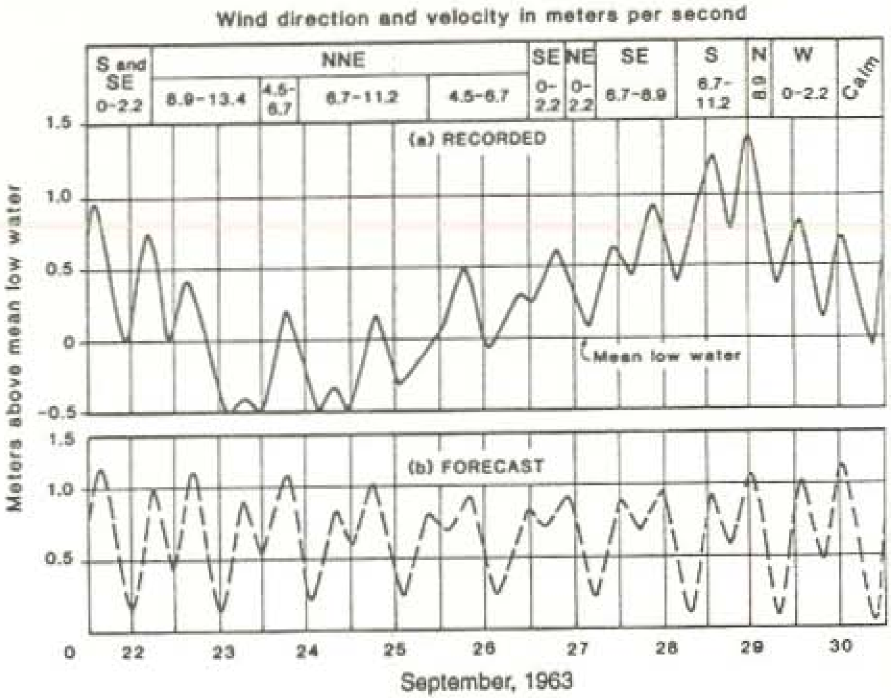

Figure 1.2 Influence of wind on the predicted tides. (Redrawn from Stelzenmuller, 1965.)

The frequency and amplitude of environmental change influence the types of animals and plants found in a coastal ecosystem. The many energies and minerals that stimulate production in coastal marshes are neither continuous nor in phase with one another. Among the most highly variable and influential factors is freshwater discharge. The most variable discharges are in the region from Pinellas to Lee County.

Intertidal marsh organisms are exposed to wide variation in oxygen, moisture, and salt. To survive, they must either avoid the many environmental extremes of the intertidal marsh or possess adaptations for withstanding them. Numerous species of rapidly growing but short-lived organisms, such as microbes, grow and die in coastal marshes in response to the high frequency of unpredictable environmental changes. Microbial "opportunists" take advantage of the abundant resources during brief periods of tolerable or favorable conditions. Patches of blue-green algae, for example, are sometimes noticeably abundant soon after rains. Few long-lived species, however, are well-adapted for withstanding all of the environmental variation in intertidal marshes. Vagile animals (i.e., animals able to move from place to place) can avoid physiologically damaging changes, but resident or sedentary animals and plants must withstand these changes or die. Fiddler crabs, mussels, salt marsh cordgrass, and other such organisms possess unique behavioral and physiological adaptations for survival. They tolerate considerable fluctuation in salinity, water level, temperature, and oxygen. Few such species exist, but resources are abundant for those few, and they are very productive.

Short-lived or vagile species occur in greater diversity. If their movement is unimpeded and changes do not occur too quickly (compared to their rate of movement), vagile animals can survive a long time in estuaries and will repeatedly revisit fringing marshes whenever suitable conditions return.

Intertidal Marsh Ecosystem Processes

Vast, complex networks of tidal creeks fill and drain the marsh except where tidal ranges are very low. The intricacies of these networks are best revealed when viewed from above (Figure 1.3). The tidal channels of Figure 1.3 are an example of "hierarchical self-organization" in which many smaller units support fewer larger ones that return some control or subsidy to the smaller supporting units. The hierarchy of tidal channels results from the mutual interaction of tidal energy, sediments, and marsh vegetation. As tidal or river waters spread into the marsh, energy dissipates and channels of various sizes are formed. Nearer to open water, the greater energy results in larger channels, but as the waters lose energy, smaller channels occur until finally the water spreads out among the grasses and very little physical energy remains. The location of the larger channels determines that of the smaller channels.

A channel hierarchy results in more productivity and diversity than would likely occur without these channels. The hydrodynamic action through the tidal channels facilitates nutrient exchange and removal of excess sulfides and salts. The energies of the wind and tide subsidize the growth of marsh vegetation in the same sense that mechanical tilling and applications of fertilizers and pesticides subsidize agricultural crops (Schelske and Odum, 1961; Odum, 1971). However, it takes some time for the sediment to accumulate, the vegetative structure to develop, and the channels to organize. The result of this process of self-organization can be viewed as the "capital" of the ecosystem, analogous to capital investment in farm buildings and machinery.

The channel hierarchy also facilitates a living hierarchy. On the outgoing tide, the products of the broad area of grass (organic matter, young animals, and rich nutrition) converge from the smaller creeks to the larger and ultimately enhance the supply of food to the larger fish and other biota of the larger channels and nearby open coastal waters. Small animals are food for larger ones that in turn regulate the populations of the smaller ones. Since the smaller tidal creeks serve as partial refuges for the smaller fish, the channels of various sizes control the spatial patterns of biota.

Figure 1.3 Aerial view of an intertidal marsh near the mouth of the Suwannee River. Note the network of tidal creeks. (From Montague and Wiegert, 1990.)

Vegetation often grows taller near the edges of the creeks, perhaps due to a combination of greater tidal energy, nutrient availability, and soil–water exchange (Kruczynski et al., 1978; Coultas and Weber, 1980; Montague and Wiegert, 1990). Fiddler crab burrows also stimulate marsh plant growth, and they are more abundant near creeks (Montague, 1982).

Tidal creeks are perhaps the key to some of the greatest values of intertidal marshland to estuarine animal life (Horlick and Subrahmanyam, 1983; Montague and Wiegert, 1990). They are access points for the ingress and egress of fish and invertebrates (Subrahmanyam and Drake, 1975; Subrahmanyam et al., 1976; Subrahmanyam and Coultas, 1980) and feeding sites of wading birds.

Salt Marsh Biota, Food Chains, and Export

The dominant intertidal marsh vegetation is black needlerush (*Juncus roemerianus*). Lesser amounts of the greener smooth cordgrass (*Spartina alterniflora*) occur nearer the water's edge, where tidal flooding and draining are more frequent and consistent. Cordgrass often forms a narrow border at the edges of creeks. Several other species of grasses and a few succulent plants occur in marsh on sediments above mean high water (high marsh) (Kurz and Wagner, 1957; Montague and Wiegert, 1990). The landward edge of the marsh may grade into maritime forest: wax myrtles, junipers (red cedars), cabbage palms, and the characteristic densely branched live oaks, or it may consist of flatwoods with pines, palmettos, gallberry, and other scrub vegetation.

Most of the plant biomass within Florida's Gulf intertidal marshes is produced by a few species of salt-tolerant vascular plants and a large number of species of soil microalgae (mostly microscopic diatoms and blue-greens). Only about 10% of the vascular plant production is eaten alive, mostly by herbivorous insects. Nevertheless, this small amount gives rise to a productive and diverse arthropod community (insects and spiders) that feeds several species of resident passerine birds as well as a variety of avian transients. Although based on only a fraction of total production, secondary (animal) production from this insect-dominated, terrestrial-like grazing food chain is comparatively high (Pfeiffer and Wiegert, 1981).

The arthropod community of the marsh is very diverse (McMahan et al., 1972), especially compared with that in other monotypic ecosystems, such as agricultural crops (Pfeiffer and Wiegert, 1981). This diversity occurs perhaps in part because the aerial portion of the plants, which is the primary habitat of this community, is less subject to the alternating levels of water, salts, temperature, and oxygen. The lack of epidemic disease in intertidal marshes may result from the complexity of the arthropod community.

Most of the vascular plants die and decay in the marsh, decompose by a productive community of bacteria and fungi, and form detritus. Along with microalgae, detritus is food for a web of consumers ranging in size from microscopic animals to snails, fiddler crabs, shrimps, minnows, oysters, and juvenile stages of some larger fish and invertebrates (Montague et al., 1981). These animals are food for a variety of mostly transient fish and birds and even a few mammals (Montague and Wiegert, 1990).

Soil microalgae contribute only about 10% of the total marsh primary production because they grow in the shade of the vascular plants or on the narrow strip of bare mud at the water's edge (Pomeroy, 1959). These algae are very nutritious, however, and contribute as much to the food web as the greater quantity of detritus (Peterson and Peterson, 1979; Montague et al., 1987a).

This detritus–algae food chain is the energy basis for early life stages of many estuarine animals of commercial and recreational importance. Only a small fraction of intertidal production is converted into this form (Montague et al., 1987a), but this portion is highly valued. Factors that control the quantity and type of aquatic animals produced in marshes are still poorly understood, but probably relate to the density of marsh creeks (Montague et al., 1987a; Montague and Wiegert, 1990).

The abundant detritus produced in intertidal marshes accumulates in sediment and decomposes slowly, while being incorporated into the soil and soil microbes and on into the detritus food chain. This accumulation creates a great oxygen demand, which results in anaerobic sediment. Anaerobic microbial processes control the supply of nitrogen and the mobility of phosphorus in marsh soils. Thus, in a dynamic coastal environment in which primary production is potentially variable from year to year, the accumulation of detritus buffers or smooths fluctuations in the supplies of food and nutrients to animals and plants and the levels of nutrients and oxygen in sediment and water (Kalber, 1959; Nixon, 1980; Simpson et al., 1983). Certain anaerobic microbial processes reduce sulfate and nitrate to gases and thus complete the cycles of these elements back to the atmosphere, thereby preventing excessive accumulation in sediment and water and contributing to global atmospheric balance (Lovelock, 1979).

Exchange Between Marshes and Coastal Waters

Intertidal marshes may buffer changes in estuarine water quality by transforming and exchanging materials with estuarine water. As the marsh becomes inundated, particulate and dissolved materials will settle or be actively extracted from water by plants, suspension-feeding animals, and microbes. Simultaneously, living organisms and advective–diffusive processes add particles and dissolved materials to the water. When the water recedes, any materials added while on the marsh become part of the pool of similar materials in adjacent waters. Whether more material leaves than enters depends upon several hydrological and biological factors, recently reviewed elsewhere (Montague et al., 1987a), including tidal range and frequency and the amount of surface and groundwater flow. As groundwater flow from the Floridan aquifer is considerable in the Big Bend marshes, an overall net export of some materials to the surrounding estuarine water may be expected. Although net export is also likely during intense rains at low tide, it is an open question whether the quantity thus exported exceeds possible imports at other times.

The ecological significance of any materials added to estuarine waters depends upon several factors. For detritus, these factors include ease of decomposition, the nutrient and oxygen demand exerted on the system when detritus decomposes, and the relative quantity of similar materials available from other sources (Nixon, 1980; Montague et al., 1987a). Whether any marshes in coastal Florida export significant quantities of useful nonliving materials is unknown. Net transport measurements are difficult and have been accomplished for fewer than 20 intertidal marsh sites worldwide with variable results (Montague et al., 1987a).

Marsh vegetation nearer to tidal creeks (e.g., *Spartina alterniflora*) regularly drops dying tissues into the tidal waters, whereas vegetative production further away from channels (e.g., *Juncus roemerianus* and high-marsh plants) tends to accumulate and may decompose for months or even years before any is washed into estuaries during a hurricane or torrential rain. This greater retention time results in less net community production and less export from such areas. As the biomass of the plants decomposes, however, it fuels a productive web of resident marsh animals; hence, secondary production should be greater within such areas. With sufficient access, transient animals from the estuary at large can still feast on the perhaps greater production of marsh residents than might occur in marshes with greater export.

Stimulation of greater production of resident animals can result from greater food supply only if the already very productive animals are food limited. Most feed on detritus and microalgae. Because detritus is especially abundant, it may be difficult to imagine how detritivores in the marsh could be food limited. Detritus, however, is not particularly nutritious and the more nutritious microalgae are not very productive. Since the consumers are so plentiful, nutrition per consumer may be relatively low (Montague, 1980a, 1980b; Montague et al., 1981; Montague et al., 1987a; Montague and Wiegert, 1990). To test whether fiddler crabs are food limited, Genoni (1985) added *S. alterniflora* detritus to a salt marsh. Significantly greater recruitment of fiddler crabs was found in plots with added detritus.

Intertidal Marshes and Coastal Development

Coastal zones in Florida are intensively used for a variety of purposes (Table 1.9). In the past, interest in the largely unquantified public values of intertidal marshes has paled within the broader context of coastal development. As development of the coastal zone continues, public policy questions involving intertidal marshes will intensify.

In 1993, over three-quarters of Florida's estimated 13.6 million people lived in coastal counties (Bureau of Economic and Business Research). Although they comprise only 57% of Florida's land area, these counties produce 80% of the state's personal income and 87% of its municipal wastes and spend 85% of the states mosquito control funds (Table 1.9). Population density along Florida's Atlantic coast (estimated to be about 300 people/km^2 in 1990) is much higher than the state average of 93 people/km^2, but along the Gulf, high densities are found only between Tampa Bay and Charlotte Harbor (Pinellas to Lee counties, see Table 1.2).

Table 1.9 Selected Economic and Environmental Statistics for Florida's Coastal Counties

Statistic	*Units*	*Coastal counties total*	*Coastal % of state total*	*Gulf % of coastal total*
Economic				
Total personal income[a]	$\times 10^{9}$ \$/year	85	80	36
Value added by manufacturing[a]	$\times 10^{9}$ \$/year	14	77	32
Defense Department expenditures[a]	$\times 10^{9}$ \$/year	7.8	73	43[c]
Recreation and tourism at beaches[b]	$\times 10^{9}$ \$/year	2.3	100	41
Fishery landings value[a,d]	$\times 10^{9}$ \$/year	0.18	100	71
Environmental				
Land area[a]	$\times 10^{3}$ km^2	79.3	57	63
1990 estimated population[a]	$\times 10^{6}$	10.2	78	41
Waste treatment discharges[a]				
Municipal	$\times 10^{6}$ m^3/day	3.7	87	34
Commercial or industrial	$\times 10^{6}$ m^3/day	0.8	74	62
State mosquito control funds[a]	$\times 10^{6}$ \$/year	2.2	85	58

[a] Shoemyen et al. (1988, 1989).

[b] Personal expenditures by residents and visitors (Bell and Leeworthy, 1986).

[c] Estimate based on distribution of number of employees in tourism-related businesses.

[d] Fishery landings values are the dockside selling price and do not include the stimulation to the economy after the dockside sale. This may be two to seven times greater than the landings value.

Florida has several major air force and naval bases along its coast. These military bases make considerable contributions to the state's economy (Table 1.9). Expenditures in coastal counties by the federal Department of Defense account for 73% of total Department of Defense expenditures in Florida. Coastal zones have also attracted heavy industry, both for waterborne shipping of raw materials and finished goods and for the abundant water for manufacturing processes, cooling of power plants, and disposal of wastes. Florida's coastal counties contribute 77% of the value added to the Florida economy by manufacturing and 74% of the commercial and industrial waste discharges (Table 1.9).

Co-occurring with heavy industrial and military uses of coastal zones are recreation, tourism, and commercial fishing. These activities depend more heavily than defense and manufacturing on a healthy coastal ecosystem that includes marshes. The contribution of these industries to the total economy is, however, considerably less than that from heavy industry and defense (see Table 1.9). Salt marshes near these more economically significant activities have been destroyed for airfields, shipping terminals, and ports.

Yet nearly three-quarters of the total personal income generated in coastal counties is not explained by manufacturing and defense expenditures. Some of this income is undoubtedly derived from the image created by the natural coastal environment, of which marshes are an integral part. On Florida's Gulf coast, this image is created by a variety of natural ecosystems including, and mutually interdependent with, intertidal marshes. The coastal image attracts not only tourists but also permanent residents who work in the heavy industries, buy residential real estate, and provide services.

Alteration of Intertidal Marshes

In Florida, the most extensive intertidal marshes are in areas of lowest population density (see Table 1.2). Lack of nearshore deep water and high ground has caused development to lag in areas where intertidal marshes are naturally most expansive. Nevertheless, activities associated with coastal development in Florida have locally eliminated a large fraction of marsh area.

Intertidal marshes have been eliminated by reducing tidal levels, increasing topographic slope, or reducing sediment supply. Restoration requires reversing these processes. Filling and bulkheading (to develop shipping terminals and residential areas) and disposal of various materials eliminated approximately 40% of the intertidal marshes around Tampa Bay between 1948 and 1978 (Estevez and Mosura, 1985).

In their natural state, marshes have considerable value to the public. They can be altered, however, to enhance habitat for certain fish and wildlife or to eliminate nuisance mosquitoes, and they can easily be eliminated by filling to create very valuable real estate. They have also been used as dump sites for trash, sediments dredged from shipping channels, wastes from phosphate ore processing, and wastewater (Montague and Wiegert, 1990).

Mosquito Control

At times, enormous populations of biting salt marsh mosquitoes make human habitation near coastal marshes almost unbearable. Salt marsh mosquitoes (*Aedes taeniorhynchus* and *A. sollicitans*) breed in temporary pools above mean high water where fishes cannot reach the mosquito larvae. Whenever heavy rains or exceptionally high tides occur, pools can remain long enough in these areas to produce another crop of mosquitoes. Any disturbance that results in greater temporary ponding of water above mean high water exacerbates the mosquito problem. Examples include roads, dikes to try to keep out tidal water, and hoof depressions of grazing livestock.

All measures to eliminate mosquitoes are controversial. Pesticides affect much of the aquatic food chain and are self-defeating because they result in selection of resistant strains of pests. By knocking out the complex, controlling, arthropod web, insecticides may also eliminate natural population controls on pest insects, thereby increasing the potential for epidemics of plant disease in salt marshes.

Ditching to drain pools at low tide and increase access of fishes at high tide has left canals with hills of spoil that interrupt marsh circulation. This can reduce the beneficial effects of the physical energy of the tide and can even *enhance* mosquito production behind the spoil piles. New efforts to improve the effectiveness of ditching and reduce negative side effects (open marsh water management) have not yet been perfected in Florida, but are being tested and should improve with sufficient trials. These techniques use very small ditches that are carefully located in mosquito-breeding hot-spots. The spoil from the ditching is spread widely over the marsh. Such ditches could even enhance marsh production if they also increase the distribution of hydraulic energy in the marsh, although too many ditches may create degradation. Quantitative determination of optimal ditch density is an open area for research.

Impounding water on the marsh is another method of mosquito control. Unlike many mosquitoes, salt marsh mosquitoes will not lay eggs on standing water. Hence, this method effectively breaks the life cycle of salt marsh mosquitoes. Impoundments also provide habitat for certain waterfowl, wading birds, alligators, and other wildlife, though perhaps at the expense of other organisms. For example, unless there are special arrangements for larvae to enter and larger animals to go back and forth between the estuary and the shallow impounded waters, the estuarine nursery functions of the marsh are lost with impoundment (Montague et al., 1985, 1987a, 1987b; Percival et al., 1987; Zale et al., 1987).

Impounding marshes for mosquito control has resulted in the alteration of 45% of the Indian River Lagoon's marshes (Atlantic coast). This mosquito control practice has not been prevalent along the Gulf coast not only because development has lagged here, but also because tidal ranges are much greater along the Gulf coast than in the Indian River Lagoon. Greater tidal range significantly reduces salt marsh mosquito-breeding area (Provost, 1973, 1974, 1976, 1977).

Other Alterations

Shallow impoundments have also been constructed in intertidal marshes solely to benefit fish and wildlife, notably ducks. Impounded marshes are successfully managed for wildlife at the Ding Darling (Sanibel Island) and the St. Marks National Wildlife Refuges.

Dams on rivers trap sediments and may reduce the sediment available for salt marsh development (Meade and Parker, 1985). In the Mississippi River delta, levees constructed to stabilize river channels and control flooding have removed the supply of sediment to intertidal marshes. These sediment-starved marshes can no longer grow vertically to keep pace with rising sea level, and large expanses of marsh are disappearing (Turner, 1987; Browder et al., 1989). Dams on the Apalachicola River may affect the future extent of coastal marshes in Apalachicola Bay and perhaps elsewhere, depending upon the future direction of transport of fine sediments as sea level rises.

In some areas where the general appearance of intertidal marshes seems unchanged, use by fish and wildlife may still be reduced by nearby disturbances (noise, distractive movement) or toxic materials (street drainage, industrial effluent, and solid wastes). These more insidious reductions in use by fish and wildlife are difficult to assess without carefully controlled studies (Odum, 1970).

Engineering Uses of Intertidal Marsh

Intertidal marshes have been successfully constructed by adjusting the elevation and slope of sediments and replanting marsh grasses or by simply awaiting natural vegetative growth on the sediments (Krone, 1982). Where the hydrological regime was suitable, marsh grasses and some associated organisms have grown in substrates of human origin such as gravel and broken pavement. One of us (HTO) has observed marsh grasses growing through road asphalt. Mitigation projects in hydraulically less suitable areas have not been as successful. The pressures of legally required mitigation (addressed in Chapter 11) require producing fully functional ecosystems in a short time, which has been difficult in many cases. Proactive ecological engineering, however, may obviate some of these concerns by providing some marsh functions, though incomplete for a time, in areas where they are needed.

Salt marsh ecosystems may be used to treat waste. Nutrient-rich waters from treated sewage stimulate and are absorbed partly by intertidal marshes. The nutrients accelerate productivity and can enhance estuarine nursery functions of marshes (Marshall, 1970). Although adding sewage to natural marshes is controversial, new intertidal marshes may be constructed as a buffer between sewage outfalls and estuaries.

A serendipitous example one of us (HTO) has observed over some years is the sewage waste outflow from a small treatment plant at Port Aransas, Texas. Wastes were released to a bare sand flat starting about 1950. As the population grew, wastes increased. Now there is an expansive marsh with a zonation of species outward from the outfall. Freshwater cattail marsh occurs immediately around the outfall. Beyond that is a salt marsh of *Spartina* and *Juncus* through which the wastewaters drain before reaching adjacent coastal waters.

Economic activities on land generate discharges. Storm runoff from streets, sewage in various degrees of treatment, and even some industrial wastes now flow directly into many coastal waters without first passing through coastal marshes. By first flowing through bands of intertidal marsh, substances in these discharges may be transformed into more innocuous and even useful forms by being bound into organic matter, buried in sediments, or converted into gases and vapors. Heavy metals can even be removed by marshes (Wolverton and Bounds, 1988).

In managing and restoring marshes and building interfaces between human settlements and estuaries, we should remember the hierarchical, branching, and tapering geometry of a system of tidal creeks, which is built by the self-organizing marsh as its own functional performance improves. For example, rather than square-cornered, bulkheaded "finger canals" for boats or for mosquito prevention, hierarchical, tapering canals with gently sloped banks provide self-flushing and an intertidal surface for the growth of some salt marsh. In this way, access is supplied for small boats, and better tidal flushing reduces the accumulation of toxic bottom-paint leachate and the depletion of dissolved oxygen. Better flushing is also a key to salt marsh mosquito control. The more geometrically natural canals have banks that are inexpensive to construct and are self-maintaining; wildlife and nursery roles are retained, and vertical bulkhead walls, which erode and are dangerous to children, are avoided.

Design and implementation of tidal creeks in constructed marshes is a new engineering challenge that can be met with appropriate consideration of the amount of hydraulic tidal energy at a site and the resistance of the marsh to erosion. Adding tidal creeks allows coastal waters to circulate through the marsh and provides essential access for fish, wading birds, and other aquatic animals.

Determining the total value of all the natural functions of intertidal marshes and effectively mitigating these values remain scientific and economic imperatives for research. Scientific as well as social controversy remains, however, over ways of evaluating nature. Several ways to quantify intertidal marsh values are presented in Chapters 8, 9, and 10. Each way yields a different value because each differs in what is measured. One method, "EMERGY synthesis" (spelled with an m, for embodied energy), estimates the public value of intertidal marsh by evaluating the work of nature and its percentage in the total work of the coastal economy (Odum and Odum, 1987). This approach estimates the marsh's indirect support of the economy through functions such as receiving and treating wastes or protecting the coast from storms. Natural processes thus contribute to the public welfare without requiring taxes.

Alternative approaches compute the economic market value, the human willingness to pay for marsh (or to pay for being assured that healthy marsh still exists), and the marginal value of marsh as it relates to the market value of a marsh-dependent product such as blue crabs. As the issue of marsh values is addressed more and more in the courts (see Chapter 11), a clear distinction in each case will be necessary between individual human rights (market value) and the welfare of the public economy (nature's direct and indirect work for the public, of which the public may not be aware).

The processes that generate each of these kinds of value are shown in the energy systems diagram in the Introduction (see Figure I.1). Market value is measured by the flow of money at the interface of the ecosystem with the coastal economy, as with the sale of fishery products. Public valuation involves the extensive environmental basis for production of wealth (on the left side of the diagram) for which no money is ever paid (money is only paid to people, but the work of the marsh is considered to be free).

Much of the history of Florida's economic development has involved intertidal marshes and their values. Perceptions on the one hand have ranged from worthless, mosquito-ridden, briny wastelands that needed to be "reclaimed" to a more modern view of marshes as a place of beauty, the basis of fisheries, real estate scenic vistas, and part of our life-support system to be protected.

Development pressures are increasing around many Gulf towns near expansive marshes as newcomers discover the natural beauty and serenity of the area (Crystal River, Cedar Key, and Steinhatchee, for example). An appreciation of the history of the effects of uncontrolled coastal development elsewhere in Florida will, it is hoped, encourage all Floridians to more effectively preserve the remaining intertidal marshes (and their investment) for the future.

Attempting a publicly acceptable balance among marsh preservation, use, and development within the economic diversity of the coastal zone is an ongoing political process that involves management agencies, businesses, citizen groups, and the courts. Teaching the naturally subsidized public values of intertidal marshes will create a more informed public as future decisions are made. It is hoped that this book will become an integral part of this educational process.

End-of-Chapter Note

Gross primary production is the formation of organic matter from raw materials (carbon dioxide, water, nutrients) using visible sunlight and aided by other energy inputs, i.e., water circulation and infrared insolation (which may aid transpiration by salt marsh plants). The net production within the marsh, however, is of special interest to those considering the organic food matter that goes into the estuary to support all aquatic food chains—ultimately the growth of many commercial species of shrimp, crabs, and fish. Because much of the gross photosynthesis is being used by the respiration of plant tissues, animals, and some microorganisms at the same time as the production is occurring, what is often measured is the difference between production and concurrent consumption. The difference between gross production and respiration is "net production." Although there are many uses of this term in this book and elsewhere, the term "net *primary* production" is only properly used when only *plant* respiration is subtracted from gross production. If respiration by unknown animal and microbial components is included, the interpretation of net production becomes difficult. Reported measurements of net production in intertidal marshes are highly variable (Montague and Wiegert, 1990). Great caution is required when comparing net production among various conditions of measurement. If net production in the same system is measured over an hour, a day, a month, a season, a year, or 10 years, entirely different results are obtained, because different amounts of consumption are included. The shorter the time, the greater the ratio of production to consumption, and thus the greater the net community production appears. Likewise, inclusion of different amounts of area also results in different results. Greater areas are more likely to include more of the larger (but rarer) consumers. Although measurements of net production may differ for other technical reasons, the time and spatial scale of measurement must be considered first in comparing measurements of net production.

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