UNDERSTANDING MARINE ECOSYSTEMS IN THE GULF OF MEXICO

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Robert J. Livingston

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UNDERSTANDING MARINE ECOSYSTEMS

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Robert J. Livingston[1]

Abstract. Our research group has just completed an eight-year research program in two bay systems in the northeast Gulf of Mexico. Basic processes at various levels of physical and biological organization have been analyzed to determine the basis of variability (spatial and temporal) in such areas. We have found that there is a range of functional periodicities extending from a few hours to years, and that system response is influenced by various cyclic and acyclic climatic shocks. Coastal communities are characterized by non-random progressions through time which result in a series of overlapping successions that are variable from one group of organisms to the next. There is an obvious need for further research concerning species-specific phase relationships with key physical and biological forcing functions. Without basic, long-term efforts to understand species strategies, there is relatively little hope for advances in our understanding of marine systems and the enlightened management of our coastal resources.

INTRODUCTION

It should be stated from the outset that there is currently a variety of approaches in the environmental sciences. Included are a broad range of experimental and field-oriented studies. The fact that few approaches have been universally accepted reflects both the complexity of the questions and the newness of the science if, indeed, it can be called a science. There has been a gradual evolution from simple number-gathering field studies to more precise hypothesis-testing experimental programs. In recent years, certain viewpoints have developed almost cult-like associations as a response to the extreme complexity of the questions and the urge to develop all-embracing generalizations from specific studies or groups of studies. Unfortunately, this trend has proved to be both premature and self-defeating as too few data have been available concerning actual environmental functions in most natural habitats. It has progressed to almost absurd extremes where efforts have been made to limit actual observations so as to simplify the development of elaborate, mathematically precise models for predictive purposes.

The basis of this problem and the central obstacle encountered by the ecologist is the variability of natural phenomena. This variability encompasses a range from so-called stable systems with little observed change in time to highly erratic systems which seemingly have no fundamental temporal order. Variability can be expressed in both spatial and temporal terms. Spatial variability depends entirely on the focus of one's interest and varies in range from a few microns (in microbial studies) to global dimensions. Considerable confusion could be avoided if investigators confined their hypothesis-testing approaches to the scope of the individual study area. Temporal variability is also complex. Cyclic phenomena include diurnal, lunar, seasonal, or supra-annual periodicities. Often, such progressions are superimposed over one another in a dynamic system of interacting cause and effect events. Because of the multiplicity of controlling factors and the general lack of an adequate control to measure the extent of background variability, there is simply no uniform method to describe or predict natural sequences of events. Thus, the basic problem of environmental variability in space and time has led to the present somewhat confused state of the ecological sciences where, despite a plethora of facts and figures, there are all too few basic principles available on which to build a comprehensive understanding of system function. It is clear that the present overgeneralization from specific studies reflects confusion rather than understanding.

If the above is true for ecology in general, then it is even more appropriate for the marine sciences, which deal with an environment that discourages systematic analysis. Much of the existing theoretical ecological framework has been

1/ Associate Professor, Department of Biological Sciences, Florida State University, Tallahassee, Florida 32306.

derived from relatively few studies. For example, succession has been variously embraced and distorted by marine researchers until there is no longer any meaning to the term. Productivity and food web phenomena have been oversimplified to the point where there is considerable confusion regarding the basic mechanisms of marine trophic relationships. Even the natural history of most marine organisms remains unknown despite recent considerable advances in the development of devices to test the physical, chemical, and biological features of marine ecosystems.

This paper is an attempt to describe an approach to marine ecology that has been developed by our research group at Florida State University. We have attempted to determine the source and degree of variability in two very different Gulf coastal systems. One hypothesis has led to another until the final results can be likened to an onion with a series of concentric hypotheses, each embracing the former. Various combinations of observational and experimental approaches have been developed which are designed to analyze long-term population and community interactions.

ANNUAL VARIABILITY AND "CATASTROPHIC" CHANGE

While most marine ecologists recognize the importance of short-term change in particular systems, the existence of any longer environmental patterns tends to escape critical attention. As a graduate student at the Institute of Marine and Atmospheric Sciences of the University of Miami, I engaged in a considerable number of studies, few of which went beyond two years. Most, in fact, were of relatively short duration, which happens to be close to the rule in most marine research efforts. Like others before me, I noticed incidentally that individual climatic events such as prolonged, heavy precipitation, excessively cold winters, and storms or hurricanes often had major effects on individual biological systems, and that such changes often lasted for prolonged periods. However, such observations remained enigmatic. They were usually represented in an almost anecdotal way in the scientific literature. With the exception of a handful of study programs in marine areas, the situation remains the same today.

The temporal aspects of a given study should be placed within the context of the area in question. There are several ways in which this can be done. Macrohabitat features such as climatological factors (temperature, precipitation, river flow, wind) should be evaluated with regard both to absolute extremes and to short- and long-term rates of change. The physiography, depth, and water current structure of the system should be defined. Microhabitat distribution is also an important feature, and includes substrate type, other diverse components (e.g., presence of grassbeds, corals, rocky outcrops, sediment features), and water quality parameters (e.g., salinity, dissolved oxygen, pH). The source and timing of the major inputs of energy (phytoplankton and macrophyte productivity, allochthonous or autochthonous detritus) are also important considerations. These in turn lead to questions concerning timed changes in food web phenomena and trophic relationships of various forms. When interpopulation and community characteristics, including predator-prey relationships and competition, are added, the overall complexity of the system becomes apparent. While the above ecological factors are recognized as important, relatively few (if any) marine systems have been studied where the key causative agents are understood over a prolonged period. In other words, in terms of both interdisciplinary interactions and long-term (i.e., supra-annual) changes, the inherent variability of most marine systems remains unexplained.

THE RESEARCH EFFORT AT FLORIDA STATE UNIVERSITY

What started in 1971-72 as individual projects concerning the impact of pesticides and pulp mill effluents on two bay systems (Apalachicola Bay and Apalachee Bay, respectively; fig. 1) has gradually developed into a long-term, multidisciplinary comparison of these two north Florida areas. The first phase of this comparison will be completed by the end of 1979.

The Apalachicola Estuary

The Apalachicola estuary is shown in figure 2. It is a shallow, barrier island system which is one of the most important coastal areas in Florida in terms of commercial fisheries. It serves as a major nursery for oysters, penaeid shrimp, blue crabs, and various finfishes. The key to understanding of the bay's productivity is the relative influence of three basic factors: the Apalachicola River, the Tate's Hell Swamp, and physiographic features dominated by the barrier islands.

An outline of our overall research effort is given in figure 3. Continuous measurements have been made at the permanent stations since March, 1972. They include water temperature, salinity, dissolved oxygen, pH, color, turbidity, depth, and Secchi readings. Baywide sediment characteristics (grain size, organic content) have been analyzed. Dissolved nutrients (ammonia, silicate, nitrite, nitrate, orthophosphate, organic carbon and nitrogen) have been studied (Richard L. Iverson, Florida State University) along with long-term analyses of micro-and macroparticulate matter, chlorophyll a, and total organic carbon. Phytoplankton studies (Richard L. Iverson, Florida State University), including qualitative (species) analysis, productivity, and limiting factor control, have been carried out over a four-year period. Currently, major physico-chemical features, including water mass

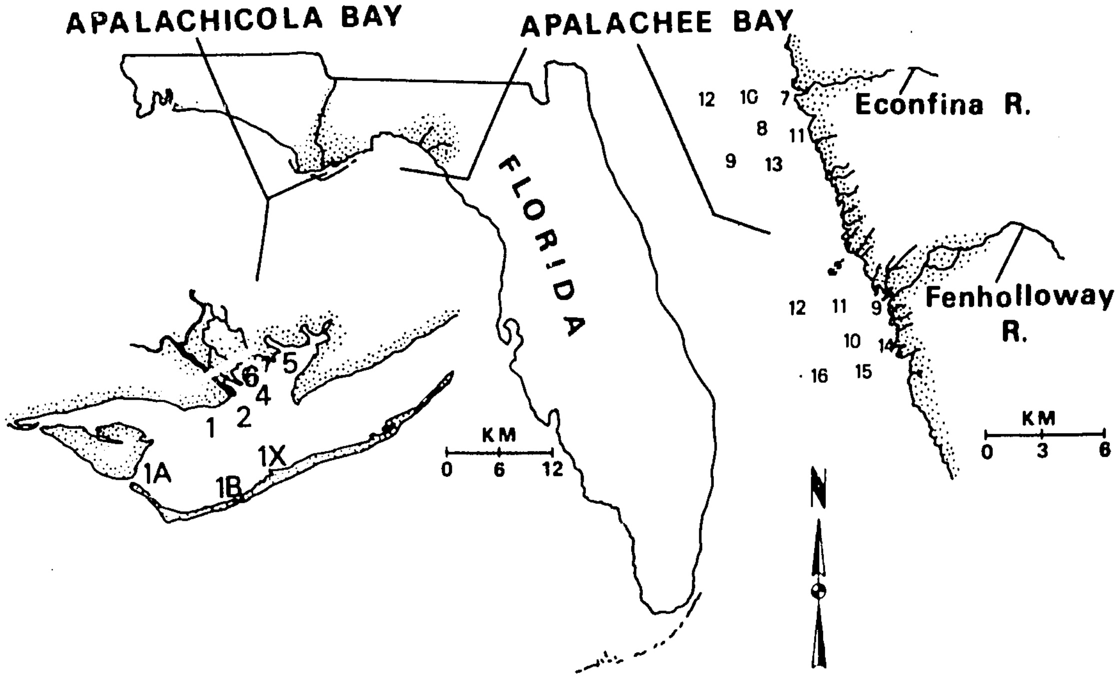


Figure 1. Two bay systems in the northeast Gulf of Mexico that have been subject to continuous study since 1971-72. Representative sets of permanent stations are also shown.

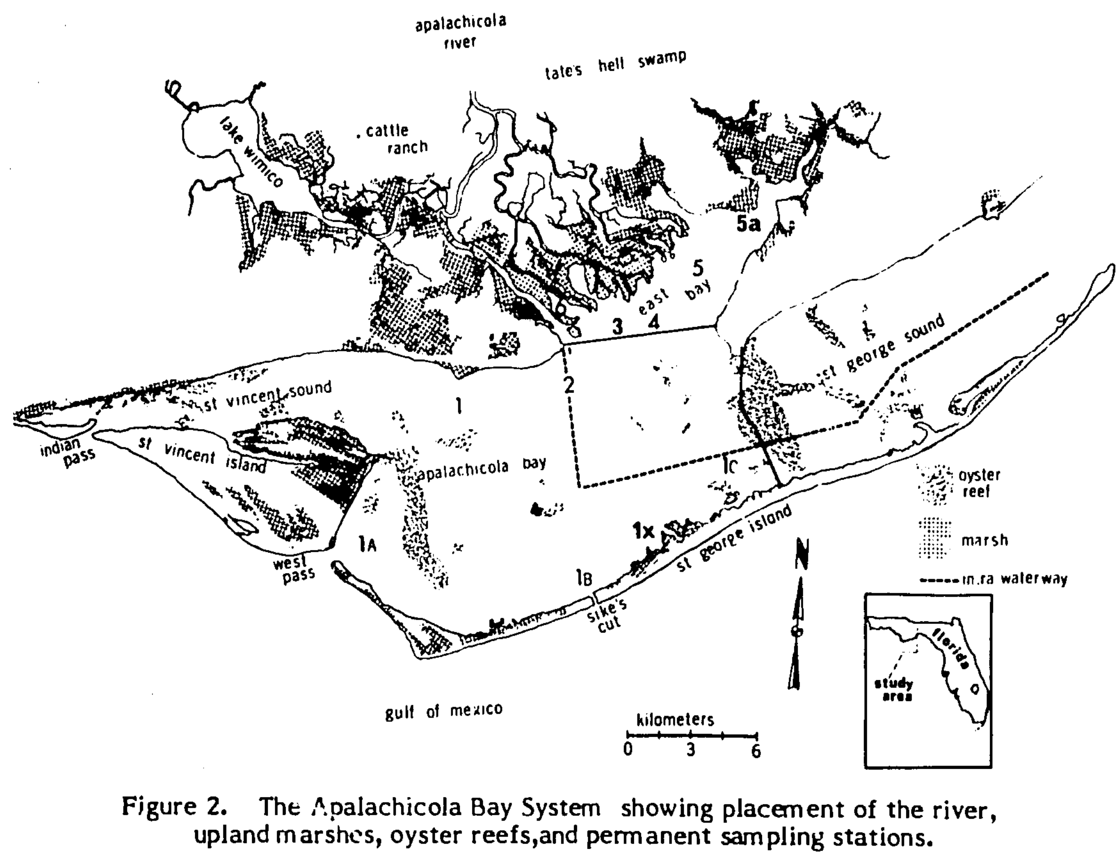
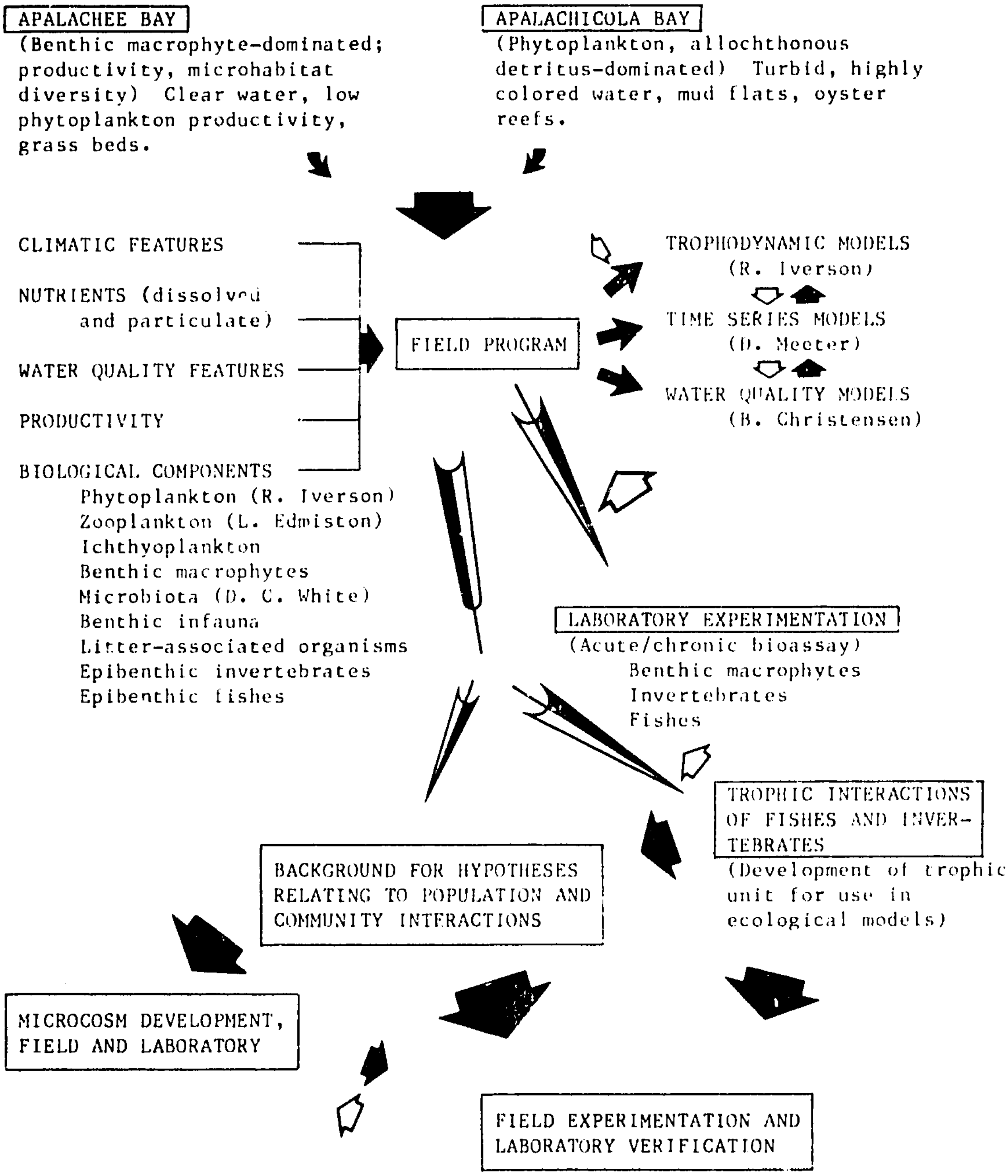


Figure 2. The Apalachicola Bay System showing placement of the river, upland marshes, oyster reefs,and permanent sampling stations.



RESEARCH PROGRAM OF R. J. LIVINGSTON, FLORIDA STATE UNIVERSITY (1970-79)

Figure 3. Comparison of Two Spatially Diverse Coastal Systems.

movement, are being modelled by Dr. T. A. Christensen (University of Florida). Various forms of time series analysis have been used to model major climatological cycles of precipitation and river flow (D. Meeter, G. C. Woodsum, Florida State University). Concurrent, long-term biological studies include analyses of grassbed (Vallisneria americana) assemblages (plant, animal) in the upper bay and baywide distribution of litter-associated groups, benthic infauna, zooplankton (Lee Edmiston, Florida State University), ichthyoplankton (Harry Blanchet, Florida State University), and epibenthic fishes and invertebrates. The microbial components of the particulates have been studied (David C. White, Florida State University) including succession, biochemical transfer mechanisms, and energy movement through the lower trophic levels of the system. Feeding habits of the dominant fish species and blue crabs (Callinectes sapidus) have also been worked out (Peter F. Sheridan, Roger A. Laughlin). The interdisciplinary effort will cover an eight-year period with four years of intensive sampling of various upland portions of East Bay to evaluate the impact of forestry activities (clearing, draining of Tate's Hell Swamp) on the estuary.

The Apalachicola estuary is a pulsed system; Apalachicola River flow physically dominates various key factors, including productivity. The data indicate that there are monthly and seasonal cycles in which monthly flow rates and the variability of daily river flow usually peak during winter-early spring months (fig. 4). At such times, high levels of dissolved nutrients and particulate matter move through the system. There are associated peaks of detritivorous organisms (benthic infauna, selected invertebrates) and their predators (blue crabs, fishes). Water temperature, which is limiting to phytoplankton productivity during winter periods, gradually increases as river flow decreases during the spring months. As the water clears, the later spring phytoplankton and zooplankton blooms occur. Again, such productivity is accompanied by sudden population increases of a series of zooplanktivorous and piscivorous species. As the summer proceeds, phosphorus becomes limiting. There is a series of lesser phytoplankton blooms as nutrients are released from sediments into the euphotic zone through wind mixing. This mixing occurs during peaks of local rainfall and the die-off of benthic macrophytes during the late summer and early fall. At this time, the bay assemblages are dominated by nurserying penaeid shrimp and blue crabs which grow at particularly rapid rates. As the fall continues, falling temperatures are a signal for various animals to migrate out of the bay. At that point numbers of anchovies peak and remain high during early winter months until increasing river flow renews the cycle.

Recent work indicates that another tier of cycles is superimposed over the seasonal progressions. Major river flood cycles, approximating periods of 6-8 years, are directly and indirectly

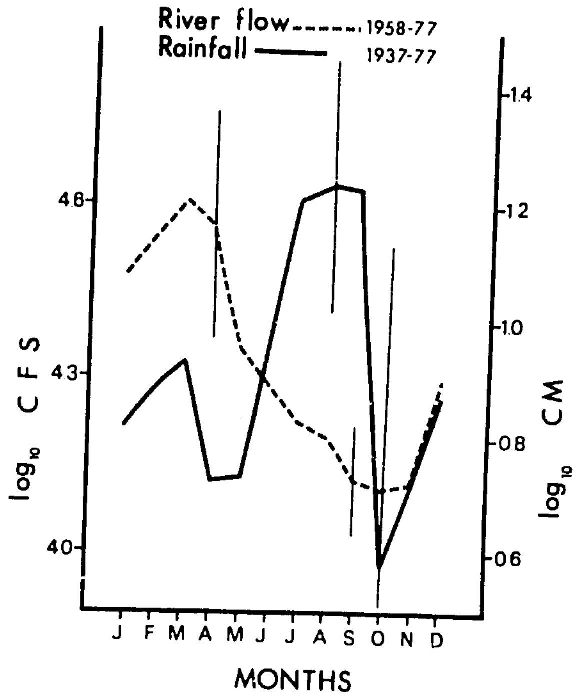


Figure 4. Monthly means of log values of Apalachicola River flow and rainfall with representative standard deviations.

related to long-term cycles of certain species, including commercial fisheries productivity. Various species tend to have particular phase angles to the long-term river-flood period depending on individual natural history and life strategies. This aspect of bay function is currently under investigation.

The timed hydrological sequences, modified by seasonal variation in wetlands functions such as evapotranspiration, play a critical role in the biotic interactions of the Apalachicola estuary. It should be noted that the north Florida Gulf coast is dominated by rainfall cycles in upland (Piedmont) areas of Georgia and Alabama. Biological reaction to inputs of nutrients and energy and modifications of the physico-chemical environment results in predictable seasonal progressions of relative species abundance in space and time. The trophic studies indicate that there is an intricate and highly efficient partitioning of resources by individual growth stages of various species.

Apalachee Bay

Most of the same sampling techniques and regimes described above have been used in this system. However, the central questions are entirely different in Apalachee Bay. The Econfina and Fenholloway Rivers are two relatively small systems which drain the same swampy upland area (fig. 5). Flow rates and water quality in upper portions of the two systems are comparable. However, from 1954 through 1973, about 50 million gallons of pulp mill effluents were dumped each day into the upper Fenholloway River, causing complex changes in the river and receiving portion of Apalachee Bay. The consequences included low dissolved oxygen, high color, turbidity, and organic matter, and generally reduced water quality conditions in an extensive portion of the bay system.

The Econfina River system was chosen as a control for a two-year study (1972-73) of the impact of the pulp mill effluents on the Fenholloway system. The Econfina area remains virtually unaffected by human activity, and this portion of the Apalachee Bay is considered one of the least polluted coastal areas in the United States. Based on the comparable flow rates and other features of the two offshore systems, cognate stations were chosen in each, equidistant from the respective river mouths (fig. 5). In this way, a field experiment could be carried out which allowed statistical testing of the null hypothesis that there was no difference in water quality or biological structure between the two systems. As a further test, a transect of permanent stations was run through the two bay areas in such a way that further comparisons could be made. Thus, because the study was developed in such a way that continuous statistical analyses could be made at a series of comparable stations, the basic hypothesis could be tested using the natural system as the experimental area.

Although most of the physical, chemical, and biological parameters were sampled in a manner similar to that described for the Apalachicola system, the emphasis was entirely different. As a source of primary productivity as well as the chief determinant of microhabitat distribution, the benthic macrophytes proved important and were continuously sampled. In addition, benthic productivity was determined (H. Bittaker and R. L. Iverson, Florida State University). By the end of the two-year period, it was found that the pulp mill discharge had affected considerable sections of Apalachee Bay, reducing species richness and biomass at all levels of biological organization. Benthic macrophyte beds were destroyed in various portions of the drainage. These effects, however, did not prove to be the most interesting aspect of the study.

Two unrelated events occurred which set up

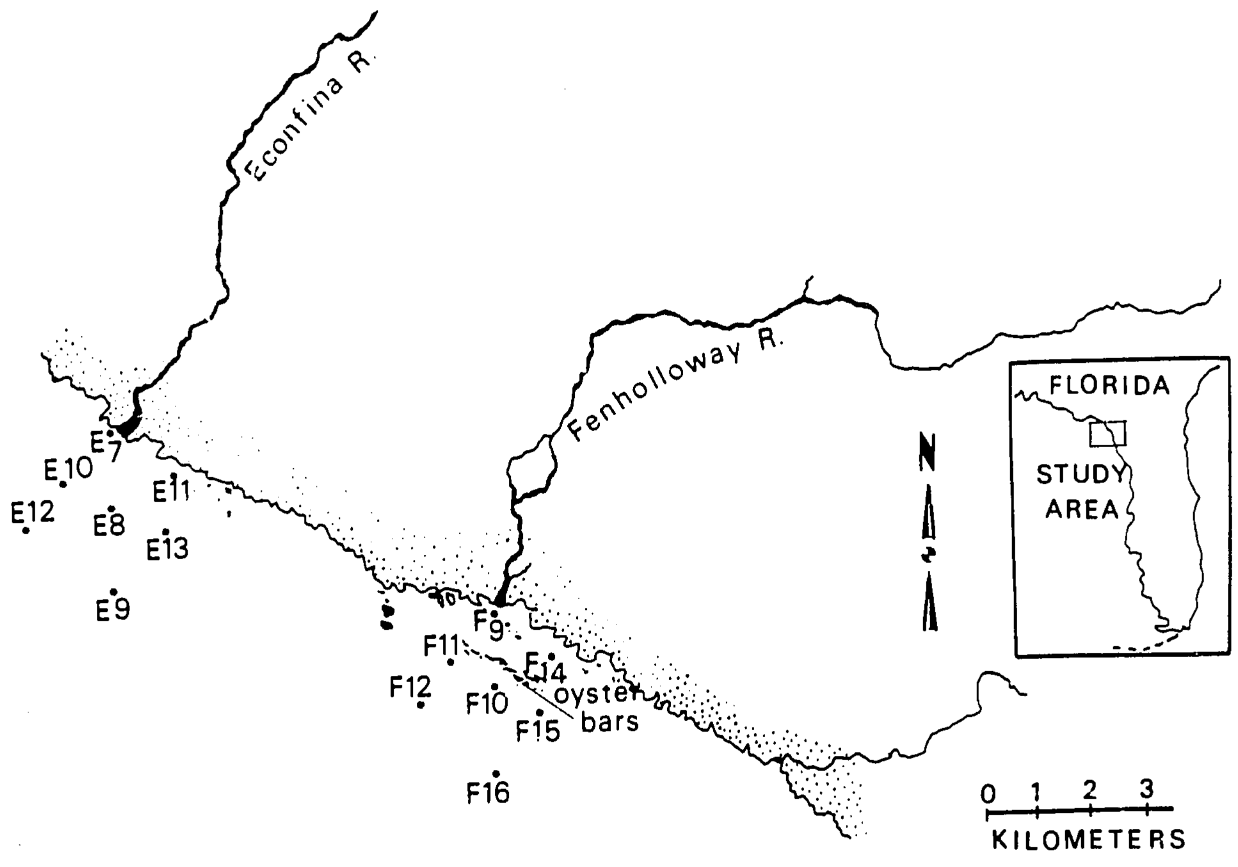


Figure 5. The Apalachee Bay system showing the Econfina and Fenholloway River drainages with associated sets of permanent sampling stations.

an entirely different sequence of studies. During the late winter and spring of 1973, heavy rainfall occurred in north Florida which caused marked changes in salinity, color, and other parameters in offshore areas along the coast. Instead of the usual spring growth, considerable portions of the grassbeds died in the study area. Although comparable amounts of local rainfall occur ordinarily in the summer and fall, upland wetlands usually buffer their effects. Evidently this buffering does not occur during winter or early spring months. High rates of land drainage resulted in massive changes in the macrophyte-dominated coastal system. Secondly, during the late fall of 1973, the pulp mill instituted a comprehensive water treatment system with the result that there were immediate improvements in various physico-chemical factors in the Fenholloway River-bay system. Consequently, a continuation of the previous study was made to determine the impact of the natural rainfall event as well as the the recovery process in the Fenholloway system. It also allowed further comparison with ongoing work in the Apalachicola estuary.

The continuation study included increased emphasis on the permanent transects as well as a major effort to determine changes in the trophic relationships of the top 20 fish species in coastal portions of Apalachee Bay from 1971 through 1977. Changes in feeding habits were measured at 5-10 mm growth intervals so that seasonal and annual variability could be worked out at all stages of development of the juvenile fishes. In addition, benthic infauna (A. Stoner) and larval fishes (K. Brady) were analyzed so that the trophic studies could be placed within the context of the long-term, comprehensive environmental survey.

A preliminary analysis of the results indicates certain definite trends. The unusual early spring rainfall of 1973 was associated with considerable decreases of macrophyte biomass during the succeeding year, due in large part to reductions in the dominant turtlegrass (Thalassia testudinum). However, total numbers of benthic macrophyte species peaked at the same time that biomass was the lowest. As Thalassia reasserted its dominance, the species richness declined. This pattern was followed in a general way by the numbers of species of fishes and invertebrates. The possibility exists that when the chief dominant plant species were reduced, other species of macrophytes took their places. That reassertion of their dominance was accompanied by reduced species richness tends to support this hypothesis. With increased microhabitat diversity, animal species richness tended to increase. The explanation of this association lies, in part, in the trophic data, which will soon be analyzed with this question in mind.

The important point is that Apalachee Bay works on different seasonal patterns than does Apalachicola Bay, and is the product of a completely different hydrological regime. The long-term, natural variability is high and affects both population variation and community structure. A natural "catastrophic" event in an unpolluted system was rate-determining over the succeeding years at various levels of biological organization. This fact means that impact analysis and management goals need to take into account annual as well as seasonal variability in the natural system with particular attention to so-called "catastrophic" events.

FUTURE RESEARCH

Until now, the field program has been linked to an ongoing laboratory program to test various questions regarding the tolerance of key species to stress (fig. 3). Currently, the entire data base is being prepared for a complete integration of the laboratory and field results in an effort to model the two systems based on observed interactions at various levels of system structure. A series of basic hypotheses have been developed with regard to long-term changes in these two disparate bay systems.

The basis for all future work rests on the comparative analysis of the Apalachicola estuary (a river-driven estuary dominated by phytoplankton productivity and allochthonous detritus) and the shallow Apalachee Bay system (dominated by benthic macrophyte productivity and autochthonous detritus). Trends in the trophic relationships of a series of key coastal species will be analyzed to establish population shifts and the relationships of individual species strategies to community structure. Short- and long-term variation of such basic biological functions will be determined in an effort to delineate potential causal relationships. There will be an emphasis on long-term variability of trophic niche dimensions relative to spatial/temporal gradients of microhabitat distribution and stress factors. This variability will also be compared to impact on and recovery of the portion of Apalachee Bay which has been affected by kraft pulpmill effluents.

The future program will be based on several approaches. In addition to the ongoing publication of previous studies, we intend to develop laboratory microcosms of microbial/macrobial systems. These will be based on our field data. Such systems will be used to test reactions of groups of co-occurring organisms to various levels of stress under controlled conditions. Also, our knowledge of the functional mechanisms of the bay systems will be used to develop a new program of field experimentation in the Apalachicola Bay system and Apalachee Bay. Various hypotheses are being developed with regard to the role of microhabitat distribution and biological interactions (competition, predation) as determinants of population dynamics and community structure. This process is already underway and within the next 1-2 years will become the focus of our next research program.

PROBLEMS AND SOLUTIONS: A FINAL PARADOX

The basic dilemma in marine ecological research today rests on the fact that too few studies are developing hypotheses that are testable within the scope of the variability of the system in question. So-called catastrophic controlling factors are dismissed as artifacts even though they may be natural, recurrent, rate-controlling features of the system. Studies are often designed within the context of short-term funding patterns or even periods determined by graduate student research projects. Most federal and state granting agencies virtually rule out any form of long-term funding programs. University patterns of limited research goals coupled with the "publish or perish" syndrome of advancement all but eliminate any sustained research effort in marine systems. Few marine biological institutions and marine laboratories can characterize even their immediate surroundings in a comprehensive (i.e., long-term, multi-disciplinary) fashion. This is not to say that all marine studies should be designed as multi-year projects; however, without at least some emphasis on long-term patterns of variability, a given research effort takes the form of uncoordinated, piecemeal projects. Ultimately, this approach is far less efficient in the long run because such studies simply cannot explain natural variability.

Our studies indicate that coastal systems function as a series of superimposed successions of populations and communities in response to cyclic or acyclic climatic shocks. There is considerable evidence that productivity and diversity may actually be enhanced by such shocks, especially within the context of long-term (supra-annual) periods. However, the fact that such successions may vary considerably from one level of biological organization to the next may also indicate that, far from the usual textbook versions of succession, coastal systems may be composed of intricate networks of non-random changes which rarely if ever reach prolonged equilibrium--hence the importance of species-specific phase relationships based on an understanding of individual strategies for survival. Unless descriptive or experimental field studies can account for a particular stage of system function relative to previous controlling events, their results will remain undecipherable with respect to a more generalized pattern of understanding. This fact has major implications for current efforts to manage our coastal resources.