COVER SHEET FOR PROPOSAL TO THE NATIONAL SCIENCE FOUNDATION

PROGRAM ANNOUNCEMENT/SOLICITATION NO./CLOSING DATE/if not in response to a program announcement/solicitation enter NSF 99-2	FOR NSF USE ONLY
99-89 07/01/99	**NSF PROPOSAL NUMBER**

FOR CONSIDERATION BY NSF ORGANIZATION UNIT(S)   (Indicate the most specific unit known, i.e. program, division, etc.)

Long-Term Ecological Research

DATE RECEIVED	NUMBER OF COPIES	DIVISION ASSIGNED	FUND CODE	DUNS# (Data Universal Numbering System)	FILE LOCATION

EMPLOYER IDENTIFICATION NUMBER (EIN) OR TAXPAYER IDENTIFICATION NUMBER (TIN)	SHOW PREVIOUS AWARD NO. IF THIS IS ☐ A RENEWAL ☐ AN ACCOMPLISHMENT-BASED RENEWAL	IS THIS PROPOSAL BEING SUBMITTED TO ANOTHER FEDERAL AGENCY? YES ☐ NO ☒ IF YES, LIST ACRONYMS(S)
581353149		

NAME OF ORGANIZATION TO WHICH AWARD SHOULD BE MADE	ADDRESS OF AWARDEE ORGANIZATION, INCLUDING 9 DIGIT ZIP CODE
University of Georgia Research Foundation Inc	**Boyd Graduate Studies Research Center** **621 Graduate Studies** **Athens, GA. 30602**

AWARDEE ORGANIZATION CODE (IF KNOWN)
0015982001

NAME OF PERFORMING ORGANIZATION, IF DIFFERENT FROM ABOVE	ADDRESS OF PERFORMING ORGANIZATION, IF DIFFERENT, INCLUDING 9 DIGIT ZIP CODE
University of Georgia	**U of Georgia** **Boyd Graduate Studies Res** **Athens, GA 30602**

PERFORMING ORGANIZATION CODE (IF KNOWN)
0015982000

IS AWARDEE ORGANIZATION (Check All That Apply)
(See GPG II.D.1 For Definitions)   ☐ FOR-PROFIT ORGANIZATION   ☐ SMALL BUSINESS   ☐ MINORITY BUSINESS   ☐ WOMAN-OWNED BUSINESS

TITLE OF PROPOSED PROJECT   **LTER - Georgia land/ocean margin ecosystem**

REQUESTED AMOUNT	PROPOSED DURATION (1-60 MONTHS)	REQUESTED STARTING DATE	SHOW RELATED PREPROPOSAL NO., IF APPLICABLE
$ **4,200,002**	**72** months	**01/01/00**	

CHECK APPROPRIATE BOX(ES) IF THIS PROPOSAL INCLUDES ANY OF THE ITEMS LISTED BELOW

☐ BEGINNING INVESTIGATOR (GPG 1.A.3)
☐ DISCLOSURE OF LOBBYING ACTIVITIES (GPG II.D.1)
☐ PROPRIETARY & PRIVILEGED INFORMATION (GPG II.D.10)
☐ NATIONAL ENVIRONMENTAL POLICY ACT (GPG II.D.10)
☐ HISTORIC PLACES (GPG II.D.10)
☐ SMALL GRANT FOR EXPLOR. RESEARCH (SGER) (GPG II.D.12)
☐ GROUP PROPOSAL (GPG II.D.12)

☐ VERTEBRATE ANIMALS (GPG II.D.12) IACUC App. Date _____
☐ HUMAN SUBJECTS (GPG II.D.12)
  Exemption Subsection _____ or IRB App. Date _____
☐ INTERNATIONAL COOPERATIVE ACTIVITIES: COUNTRY/COUNTRIES
  _____
☐ FACILITATION FOR SCIENTISTS/ENGINEERS WITH DISABILITIES (GPG V.G.)
☐ RESEARCH OPPORTUNITY AWARD (GPG V.H)

PI/PD DEPARTMENT **School of Marine Programs**	PI/PD POSTAL ADDRESS **Marine Sciences Building**
PI/PD FAX NUMBER **706-542-5888**	**Athens, GA 306023636** **United States**

NAMES (TYPED)	High Degree	Yr of Degree	Telephone Number	Electronic Mail Address
PI/PD NAME				
James T Hollibaugh	**Ph.D.**	**1977**	**706-542-3016**	**aquadoc@uga.edu**
CO-PI/PD				
Steven C Pennings	**Ph.D.**	**1990**	**912-485-2293**	**scpenn@peachnet.campuscwix.net**
CO-PI/PD				
CO-PI/PD				
CO-PI/PD				

LTER: Georgia Land/Ocean Margin Ecosystem

We propose to establish a Long Term Ecological Research site on the central Georgia coast in the vicinity of Sapelo Island. This is a barrier island and marsh complex with the Altamaha River, one of the largest and least developed rivers on the east coast of the US, as the primary source of fresh water. The proposed study would investigate the linkages between local and distant upland areas mediated by water – surface water and ground water – delivery to the coastal zone. We would explicitly examine the relationship between variability in environmental factors driven by river flow, primarily salinity because we can measure it at high frequency, and ecosystem processes and structure. We will accomplish this by comparing estuary/marsh complexes separated from the Altamaha River by one or two lagoonal estuary/marsh complexes that damp and attenuate the river signal. This spatial gradient is analogous to the temporal trend in riverine influence expected as a result of development in the watershed. We will implement a monitoring system that documents physical and biological variables and use the time trends and spatial distributions of these variables and of their variance structure to address questions about the factors controlling distributions, trophic structure, diversity, and biogeochemistry.

An existing GIS-based hydrologic model will be modified to incorporate changes in river water resulting from changes in land use patterns that can be expected as the watershed develops. This model will be linked to ecosystem models and will serve as an heuristic and management tool.

Another consequence of coastal development is that as river flow decreases, groundwater flow increases and becomes nutrified. We will compare the effects of ground water discharge from the surficial aquifer in relatively pristine (Sapelo Island) versus more urbanized (mainland) sites to assess the relative importance of fresh water versus nutrients to productivity, structure and biomass turnover rate in marshes influenced by groundwater. We will also investigate the effect of marine processes (tides, storm surge) on mixing across the fresh/salt interface in the surficial aquifer

Additional physical studies will relate the morphology of salt marsh - tidal creek channel complexes to tidal current distributions and exchange. These findings will be incorporated into a physical model that will be coupled to an existing ecosystem model.

The land/ocean margin ecosystem lies at the interface between two ecosystems in which distinctly different groups of decomposers control organic matter degradation. The terrestrial ecosystem is largely dominated by fungal decomposers, while bacterial decomposers dominate the marine ecosystem. Both groups are important in salt marsh-dominated ecosystems. Specific studies will examine, at the level of individual cells and hyphae, the relationship bacteria and fungi in the consortia that decompose standing dead Spartina and other marsh plants and examine how, or if, this changes along the salinity gradient.

TABLE OF CONTENTS

For font size and page formatting specifications, see GPG section II.C.

Section		**Total No. of Pages in Section**	**Page No.* (Optional)***
	Cover Sheet (NSF Form 1207 - Submit Page 2 with original proposal only)		
A	Project Summary (not to exceed 1 page)	1	
B	Table of Contents (NSF Form 1359)	1	
C	Project Description (including Results from Prior NSF Support) (not to exceed 15 pages) **(Exceed only if allowed by a specific program announcement/solicitation or if approved in advance by the appropriate NSF Assistant Director or designee)**	34	
D	References Cited	10	
E	Biographical Sketches (Not to exceed 2 pages each)	20	
F	Budget (NSF Form 1030, including up to 3 pages of budget justification)	44	
G	Current and Pending Support (NSF Form 1239)	26	
H	Facilities, Equipment and Other Resources (NSF Form 1363)	1	
I	Special Information/Supplementary Documentation		
J	Appendix (List below.) **(Include only if allowed by a specific program announcement/ solicitation or if approved in advance by the appropriate NSF Assistant Director or designee)**		

Appendix Items:

*Proposers may select any numbering mechanism for the proposal, however, the entire proposal must be paginated. Complete both columns only if the proposal is numbered consecutively.

NSF Form 1359 (10/98)

I. RESULTS OF PRIOR SUPPORT

James T. Hollibaugh. During the 5 year reporting period, I have been the PI/PD of 5 NSF awards: OCE 89-14921, "LMER site for the study of biogeochemical reactions in estuaries at Tomales Bay, California," 10/89-9/94, $863,139 (with Dr. S.V. Smith funded by a separate award); OCE 93-15639, "An investigation of the relationship between community composition and metabolic capabilities of coastal bacterioplankton communities," 10/93-9/96, $320,000; OPP 95-00237, "Diversity and metabolic capabilities of Arctic bacterioplankton - SCICEX 95," 1/95-12/96, $160,000; OPP 96-25131 and 97-96261, "Diversity and metabolic capabilities of Arctic bacterioplankton - SCICEX 96," 5/97-4/99, $161,000; and OPP 98-09971 "Diversity and metabolic capabilities of Arctic bacterioplankton - SCICEX 97," 4/97-5/00, $165,000. As a result of this support, I have authored or co-authored 21 peer-reviewed journal articles, 3 chapters in symposium volumes, and 3 papers in non-peer-reviewed journals. Three more papers are in review and 4 papers are in various stages of completion. In addition, 2 M.S. theses and about 50 other papers published by colleagues in peer-reviewed journals acknowledge support from these grants (see Tomales Bay LMER web page, for example). These results have also been presented at national and international meetings (see ASLO, AGU, ERF, ECSA, ISME-6 abstract volumes) and at seminars at a number of institutions. The human resources impact of the support is 5 postdocs, 6 graduate students, 3 undergraduate students, 3 graduating high school seniors and 5 technicians; most of these were women.

The data collected during these studies are available in lab notebooks kept at the Department of Marine Sciences at UGA. Survey data are available either as Excel or DBase files maintained on at least 2 computers. We are in the process of making Arctic data available on the Internet; LMER data can be accessed on the web:
http://www.mbl.edu/html/ECOSYSTEMS/lmer/tomalbay/tomalbay.html.

The Tomales Bay LMER project (BRIE, OCE 89-14921) is most relevant to this proposal, although some of the molecular techniques proposed for use below were developed in OCE 93-15639. BRIE focused on the processing and transformation of organic matter in estuaries in general, using Tomales Bay as a model, though work conducted under the auspices of this study ran the gamut from organismal biology to hydrology. Tomales Bay was chosen as a study site because its physical attributes (morphology, water residence time) made stoichiometric analysis of net ecosystem metabolism particularly tractable. Basic information on the project is contained in the web page cited above.

The results of the study are summarized in Smith and Hollibaugh (1997) which analyzed interannual variation in biogeochemical performance of Tomales Bay. We found that Tomales Bay was a net heterotrophic system (P<R, P/R<1) with about half of the excess heterotrophy driven by labile material delivered from the coastal ocean and about half driven by more recalcitrant, terrestrial organic matter. The sediment record indicated a dramatic increase in sedimentation rate coinciding with European intervention in the watershed. Increased delivery of soil organic matter probably accentuated Tomales Bay's net heterotrophy, possibly shifting it from a nutrient-limited, net autotrophic system to a net heterotrophic, light-limited system.

Steven C. Pennings. My previous NSF-supported work (OCE-9116307, "Mediation of algal-opisthobranch-predator interactions by algal secondary metabolites" 6/92-5/94, $164,995) was in an area unrelated to this proposal and therefore is described here only briefly. Dr. Valerie Paul and I investigated how algal secondary metabolites mediate interactions between algae,

herbivorous opisthobranch gastropods, and potential gastropod predators. The work produced 11 published papers, with 2 additional papers yet to be written. Five undergraduates were supported by the grant; 4 have been or will be co-authors on publications.

More recently I have been funded by the National Institute for Global Environmental Change (NIGEC) and the USEPA for work on the plant communities of coastal salt marshes. The NIGEC project was designed to examine latitudinal differences in East Coast salt marsh plant communities (CO-PI Mark Bertness, "Climate-driven process and pattern in coastal salt marsh plant communities", 7/96-6/99, $258,000). We established a series of parallel field experiments in ME, RI, GA and AL to test the general hypothesis that the factors structuring coastal salt marsh plant communities differ across latitude because of geographic differences in soil salinity, which in turn are driven by geographic differences in climate. Results to date generally support the hypothesis that geographic variation in salinity leads to geographic variation in the structure of marsh plant communities, but also suggest that evolutionary adaptations to chronic differences in salinity may counteract predictions based solely on an understanding of ecological processes at any one site. One goal of the current LTER proposal is to build on these results by examining variation in marsh plant physiology, community structure, and genetic structure on several spatial scales. The major publications from this grant are awaiting the completion of long-term experiments; but 6 publications or manuscripts acknowledge the grant to date. The grant has supported 10 students, most of whom will co-author resulting publications.

The USEPA project was designed to examine a suite of potential indicators of marsh health (CO-PI's J. Alberts, R. Kneib, S. Newell, "Health indicators for salt marsh estuaries of the South Atlantic Bight", 10/96-9/00, $786,349). My portion of the project focuses on the use of instantaneous measurements of plant gas exchange, using a portable infrared gas analyzer, as an indicator of plant health. Results to date have provided surprisingly little support for the hypothesis that pollutants depress photosynthetic rates of salt marsh plants in the field, but have indicated that gas exchange rates of salt marsh plants are highly variable in space and time. Preliminary data suggest that much of this variation may be linked to tidal stage and range, and to variation in rainfall. One goal of the current LTER proposal is to rigorously examine the relative importance of these potential sources of variation in plant production. Much of the EPA work is ongoing, but to date the award has produced 5 publications or manuscripts, and has supported 4 technicians, most of whom will co-author resulting publications.

Undergraduates are heavily involved in my research at the University of Georgia Marine Institute. Each summer I sponsor 1-2 undergraduate interns who develop and conduct research projects and co-author resulting publications. Recent interns (and their current institutional affiliations) have included Christina Richards (U. Georgia), Teresa Page (USC Wrigley Institute, Catalina Island), Ben Nomann (Peace Corps), John Flanders (UC Davis), Erin Siska (Brown U.), Greg Breed and Audra Luscher (both applying to graduate school) and Kristen Strohm (Heal the Bay, Santa Monica CA). I also employ technicians who typically are seeking additional training and experience before going on to graduate school. Technicians are treated as colleagues-in-training. They are encouraged to take primary responsibility for subsets of larger projects and to co-author resulting publications as appropriate. Recent technicians have included Ben Nomann (Peace Corps) and Kurt Reinhart (U. Montana).

Georgia Rivers LMER (GARLMER). Many of the senior investigators on the present proposal are co-PIs on the current Georgia Rivers LMER (DEB 94-12089; "LMER: A comparative study of the transport and transformation of materials from rivers through the land-

sea margin;" R.G. Wiegert PD; Co PIs: M. Alber, C. Alexander, J. Blanton, A.G. Chalmers, R.E Hodson, M.A. Moran, L. Pomeroy, and W.J. Wiebe; 10/94-9/00; $2,999,118). Results of LMER research have been the subject of 28 peer-reviewed journal articles (3 more in review), and 7 book and symposium volumes and chapters. These results have been part of 45 presentations (seminars, meetings, posters, etc.). In addition, GARLMER scientists organized or participated in 3 international workshops, symposia, or scholastic courses. A complete list of publications is given on the GARLMER web page (http://lmer.marsci.uga.edu).

To date, the project has provided support for 2 post-doctoral associates, 8 graduate students, and 11 undergraduates. Seven of these undergraduates were supported through supplementary REU funds. In addition, 3 students and 3 faculty members from several Portuguese Universities have participated in Georgia LMER research as part of a joint US-Portugal cooperative agreement sponsored by NSF, the Portuguese JNICT (Junta Nacional de Investigacao Cientifica e Tecnologica), and FLAD (Luso-American Foundation for Development).

The LMER project focuses on five Georgia rivers that transit to the Atlantic coast through a landscape of expansive freshwater and saltwater intertidal marshes linked to the river estuaries via tidally-flooded creeks and rivers (Wiegert et al. 1999). The influence of the vast salt and freshwater intertidal marshes on processes that occur within the estuarine waters and sediments serves as a focal point for GARLMER research. Coastal Georgia intertidal marshes are important sources for many materials that are transported to, or through, the estuaries, including dissolved inorganic carbon (Cai et al. 1999); inorganic nutrients (Cai et al. submitted); phytoplankton, bacteria, POM, and inorganic particles (Blanton et al. 1999, Chen et al. 1997, González et al. 1997); chromophoric dissolved organic matter (Miller & Moran 1997, Gao and Zepp 1999); and fluorescent dissolved organic matter (Sheldon & Moran, in prep.). However, in contrast to the traditional view of outwelling, the intertidal marshes do not act as sources (and may instead be sinks) for many other materials, including reduced (and biologically labile) organic carbon; dissolved oxygen; and nitrate (Cai et al. 1999, Cai et al. submitted). These estuary-marsh interactions are controlled and altered by physical processes, such as generation of irregular tidal currents (Blanton et al., in prep), tidally-driven exchange of suspended material (Blanton et al. 1999) and buoyancy-driven exchange across topographic features (Blanton et al., submitted). At the same time, resident estuarine microbial communities transform organic matter during its transit through the estuary (Moran & Sheldon 1999). Thus the five Georgia estuaries are reactors where terrestrial inputs of varying magnitude and composition are modified by, and in some cases overwhelmed by, activity in the flanking marshes. Underlying these ongoing biological and physical interactions are long-term, human-driven shifts in river discharge and flushing times, due primarily to increased freshwater withdrawals for rapidly growing domestic and industrial uses (Alber & Sheldon 1999, Alber & Sheldon, in press).

CO_2 and O_2 Flux - The low-salinity regions of the Georgia estuaries are characterized by unusually high pCO_2 values that are frequently coupled to undersaturation of oxygen (Cai et al. 1999). The observed gas concentrations cannot be explained by within-estuary processes (i.e., respiration in the estuarine water column and sediments); instead, they are driven by high biological activity in the aerobic and anaerobic subsystems of the adjacent intertidal marshes (Cai et al. 1999, Pomeroy, in prep.). Inorganic products of respiratory activity are funneled into the estuarine water from the marshes by tidal action in proportion to the ratio of marsh area:estuary area, which varies predictably within each estuary (Cai et al. 1999). The high productivity of the intertidal marshes thus affect the estuaries by exporting endproducts from

within-marsh decomposition (CO_2, HCO_3), with outwelling of organic matter to the estuaries a minor process by comparison (Cai et al. 1999, Cai et al., in press). These end products are predicted to have little influence on the adjacent coastal ocean.

Estuarine exchange- Marsh-estuarine exchange in the Georgia estuaries occurs by irregular tidal dynamics that are extremely important for moving water and sorting materials. Two distinct types of tidal current distributions characterize the Georgia estuaries and coastal marshes: tidal currents with maximum ebb and flood currents near the time of high water (typical of mouths of large tidal creeks) and currents with maximum ebb and flood currents near the time of low water (typical of shallow tidal drainage systems and flood tide deltas) (Blanton et al., in prep). One of the important consequences of this tidal current distribution is that it alters the transport of suspended materials. There are classes of suspended sediments within the Georgia estuaries that settle too slowly to reach the bed, yet others that settle within a tidal cycle and have distributions that clearly correlate with current speed. Differential transport of these particle types affects their residence time in the estuarine system and consequently their involvement in biogeochemical transformations (Blanton et al. 1999, Alber, in prep.). Cross-system exchange in the other direction, between the estuary and the ocean, occurs within a complex spatial structure surrounding individual plumes that evolve during a tidal cycle (Kapolnai et al. 1996, Blanton et al. 1997).

Bacterial communities - Who are the important bacterial players that transform estuarine- and marsh-derived organic matter in the Georgia estuaries, and can we link bacterial community structure with the critical biogeochemical functions the communities mediate? New 'in situ' molecular-based methods for targeting individual bacteria and the functional genes they carry have been developed and applied for the first time in the GARLMER estuaries (Hodson et al. 1995, Chen et al. 1997), and are being used to elucidate key steps in nitrogen and carbon transformations. Approaches based on bacterial 16S rRNA gene sequences have linked the first ecologically relevant group of marine bacterioplankton to its biogoechemical function (González & Moran 1997). The exclusively marine "Roseobacter " lineage accounts for up to 30% of the bacteria in the Georgia estuaries, and appears to play important roles in cycling of organic and inorganic forms of sulfur (González et al. 1999) and in the breakdown of naturally occurring aromatic compounds such as lignins and humic substances (Buchan, Neidle, Esham, and Moran; in prep.). Funds from NSF, Office of Naval Research, and the Department of Energy have provided essential supplemental funding for these projects.

CDOM, FDOM, and DOM photochemistry - DOM in the Georgia estuaries and other terrestrially-influenced aquatic environments is characterized by the abundance of light-absorbing or 'chromophoric' components. This CDOM influences carbon biogeochemistry in the Georgia estuaries in many ways, for example by acting as a source of biologically active photoproducts and by competing with primary producers for solar radiation (Bushaw et al. 1996, Miller & Moran 1997, Moran & Zepp 1997, Moran & Zepp 1999, Bushaw-Newton & Moran 1999). Some fraction of the light absorbed by CDOM is re-emitted as fluorescence, and thus fluorescent DOM (or FDOM) provides a sensitive measure of terrestrial DOM concentration and source (Sheldon & Moran, in prep.). FDOM fluorescence data paint a highly dynamic picture of the DOM pool in GARLMER rivers, and indicate inputs from freshwater sources, intertidal marsh sources, and even marine sources for some river estuaries, in contrast to bulk DOC measures that generally indicate simple conservative mixing of freshwater DOM through the estuaries. The GARLMER FDOM studies are currently being extended offshore through collaboration with the ONR-funded South Atlantic Bight Synoptic Offshore Observation

Network (SABSOON) to provide real-time observational data on terrestrially-derived FDOM on the U.S. southeastern continental shelf. Through the SABSOON project, CDOM fluorometers are being mounted on an offshore tower grid and will provide continuous surface and bottom monitoring of CDOM concentrations, along with a suite of other meteorological and oceanographic variables. CDOM data from riverine and coastal endmembers obtained as part of our GARLMER research will help establish the first data set on the magnitude and variability of terrestrial inputs to the land/ocean margin of the southeastern U.S.

Modeling - Modeling has been an essential tool to link physical movements of materials with biological processes in the GARLMER estuaries. Water circulation is being described through an extensive estuary-wide study of a GARLMER estuary (the Satilla River), based on moored instruments (providing data on currents, temperature, salinity, and pressure) complemented by spatial surveys emphasizing lateral as well as longitudinal variability. Calculations of salt content variability from a 3-D finite element numerical model that simulates wetting and drying of tidal marshes and channels are being compared with these empirical results. More simple models allowing a date-specific method for determining estuarine flushing times have also been developed (Alber & Sheldon, in press), and are being used to interpret distributions of particulate and dissolved materials in the estuaries. Mass balance models of O_2 and CO_2 concentrations and flux have addressed the export of gases to the coastal ocean, and predict a seasonal phase lag in CO_2 uptake and release which, extrapolated to coastal marshes worldwide, could be an important factor in global CO_2 models (Cai et al. 1999). A water transport/land use model of one GARLMER estuary that simulates river flow and material output on a daily basis predicts that nutrient output from the estuaries is the parameter likely to show the greatest impacts from anthropogenic disturbances within the watershed (Dai et al., in prep). Funds from the Georgia Coastal Zone Management (CZM) program and the State of Georgia have provided essential supplemental funding for these modeling projects.

The Human Realm - Anecdotal reports exist of historic changes in land and water use in coastal Georgia that have had an impact on the distribution of plants (e.g. wild rice) and animals (e.g. crabs), and there is concern regarding the impact that future surface water withdrawal will have on the estuaries. Historic data show significant decreases in discharge and significant increases in salinity in coastal Georgia over the 2-decade period from 1973 to 1992 (Alber & Sheldon 1999). Supplemental funds from The Nature Conservancy and the Georgia CZM program are being used to look for historic changes in vegetation on the Georgia coast, to model the effects of land use changes on runoff (and, consequently, estuarine salinity), and to produce a model of estuarine residence time that incorporates the dynamics of river discharge.

Linkages to the LTER - The study area for this proposed LTER project is in the heart of the current LMER study region. Many of the ongoing LMER projects thus provide a critical foundation for proposed LTER studies. Continued clarification of the complex patterns of water movement and resuspension within the intertidal creeks and marshes will be an important focus of the LTER studies, as will the impact of long-term trends in land use patterns and freshwater withdrawal within the LTER watershed. Fundamental data on nutrient concentrations, dissolved organic matter, particulate organic matter, heterotrophic activity, food web dynamics, sediment composition and transport, CDOM and FDOM export, dissolved gases, vegetation zones, and many other parameters are serving as the groundwork for proposed LTER activities.

II. PROJECT DESCRIPTION

INTRODUCTION

Tidal marsh/estuarine complexes occur at the margin between land and sea, and the ecological processes in this setting are driven by terrestrial and oceanic inputs that vary over many spatial and temporal scales. Terrestrial inputs include sediment, dissolved and particulate organic matter, nutrients and fresh water. These materials are delivered by rivers and groundwater seepage and are resuspended, recirculated, and deposited by tidal currents and events associated with the weather. Oceanic inputs include organic matter, nutrients and salt water delivered by tides. A final category of inputs is derived from the atmosphere and includes precipitation and nutrient deposition.

Terrestrial, oceanic, and atmospheric inputs are highly variable at multiple spatial and temporal scales. Terrestrial inputs are relatively predictable over annual scales but unpredictable over days to weeks or longer than annual time scales. Oceanic inputs are highly predictable over tidal time scales. Some of the many scales of variability interact to produce longer time-scale, predictable variation (e.g., seasonal precession of the timing and amplitude of low spring tides, which has important consequences for intertidal organisms), while other longer time scale variations (e.g., storms, upwelling events, blooms, other water quality variations) are less predictable. Atmospheric nutrient deposition varies in unpredictable ways in both space and time, particularly over time scales of days to weeks (Pearl & Fogel, 1994).

Superimposed on the scales of natural variability are the consequences of human activities. During coming decades, the magnitude and nature (riverine vs. groundwater) of terrestrial (fresh water and nutrient) inputs into Georgia marshes change because of development along the coast and global variations in weather patterns. Similarly, oceanic input into marshes may change in response to rising sea levels or large-scale perturbations to circulation as a consequence of global climate change. Atmospheric deposition patterns may change with weather patterns and air pollution in increasingly urbanized coastal counties.

Focused study of two general sets of processes is necessary to understand the multiple scales of spatial and temporal variations in coastal processes and to develop predictive models for the impact of these variations on ecosystems at the land-ocean margin: 1) *How are the effects of spatially and temporally variable patterns of terrestrial, oceanic, and atmospheric inputs propagated through coastal ecosystems?* For example, we currently have a good understanding of the processes creating these signals (e.g., variation in rainfall, tide cycles, etc.), but poor knowledge of how these signals propagate into and through these ecosystems. One of the primary impacts of development and climate change is to alter the variability of physical signals (for example, the hydrograph of rivers as watersheds are developed). 2) *How does the resulting variation in nutrients, organic matter, and salinity affect processes in coastal wetlands?* For example, we have a moderately good understanding of the correlation between long-term averages of these variables and the patterns and processes in estuarine systems and of the effects of constant levels of these variables in laboratory studies. However, we have a relatively poor understanding of how short-term (hours to days) variation in these processes affects coastal wetland function. Moreover, it remains unclear whether our current understanding of estuarine systems is adequate to predict impacts of long-term (yearly to decadal) changes in function driven by long-term changes in development, weather or sea level.

We propose to study issues related to the multiple scales of spatial and temporal variability in an LTER program sited in a barrier island/estuary/marsh complex on the central GA coast (Figure 1). The proposed study area experiences gradients in mean salinity and salinity variability (Figure 2) resulting from the influence of the Altamaha River. We hypothesize that these gradients will be reflected in ecological variables such as diversity, composition and productivity and in sediment characteristics and associated biogeochemical conditions.

GEORGIA BIGHT AS A NATURAL LABORATORY FOR LAND-OCEAN MARGIN STUDIES

The coastline of Georgia is currently among the least developed in the United States, but is projected to see rapid urbanization over the next few decades. The focus area for this LTER study encompasses a part of the central GA coast that includes the mainland, marshes, open water, and barrier islands near the mouth of the Altamaha River. The Altamaha River has an annual average flow of 380 m^3/s and its headwater tributaries drain much of central Georgia, including some piedmont near Atlanta. Atlanta currently has one of the highest population growth rates in the US, with the concomitant rapid conversion of rural woodlands and agricultural land to housing tracts and strip malls. Such urbanization has effects on surficial and groundwater hydrology and water quality and influences sediment, nutrient and contaminant loads delivered to the coastal zone. There are no reservoirs on the mainstem, however, each of its tributaries is dammed 200-300 miles upstream from the confluence.

At the same time, coastal Georgia, located in the lower reaches of the Altamaha, is also experiencing growth. The study area currently has low population density and an economy based on fishing and forestry. However, the urbanization and growth that characterize Savannah to the north and Brunswick to the south are beginning along the I-95 corridor in McIntosh County, with development of coastal waterfront property proceeding rapidly as well. While some of the impacts will be the same as those for the interior watershed, redistribution of groundwater and surface water consumption will be more important locally. For example, excessive pumping of the deep Floridan aquifer (the drinking water aquifer) in the vicinity of Savannah and Brunswick GA and Hilton Head SC has already resulted in salt water intrusion in this area. Anecdotal evidence suggests that the reduction in Altamaha river flow, the shrinking of riparian wetlands, and the cessation of artesian wells on Sapelo Island and elsewhere along the coast can also be attributed to pumping from this aquifer for municipal and industrial uses.

Once pumped to the surface, some of this water is lost through evapotransporation, and the rest returns to the coastal zone as municipal and industrial effluent, septic field leachate or irrigation runoff. A potential trajectory for the long-term effect of these activities on coastal marshes is the replacement of the vast tracts of riparian freshwater marshes along the Altamaha by saltmarsh, with freshwater marshes reduced to fringing bands supported by groundwater. This represents a significant alteration of the land/sea ecotone and a very different habitat mosaic. Oyster, shrimp and crab industries have already experienced significant declines, and coastal stakeholders have expressed concern over the impacts that further development and straining of resources may have on the fisheries, tourism, and the health of coastal systems. If the ideal for an LTER site is a pristine, idyllic, untouched coastal environment, then the Georgia coastal zone might be viewed as an unfavorable candidate. In reality, the pristine ideal no longer exists anywhere in the USA (if not the world). Because the development of the central Georgia coast has been slow compared to other coastal sites in the US, much of the intertidal
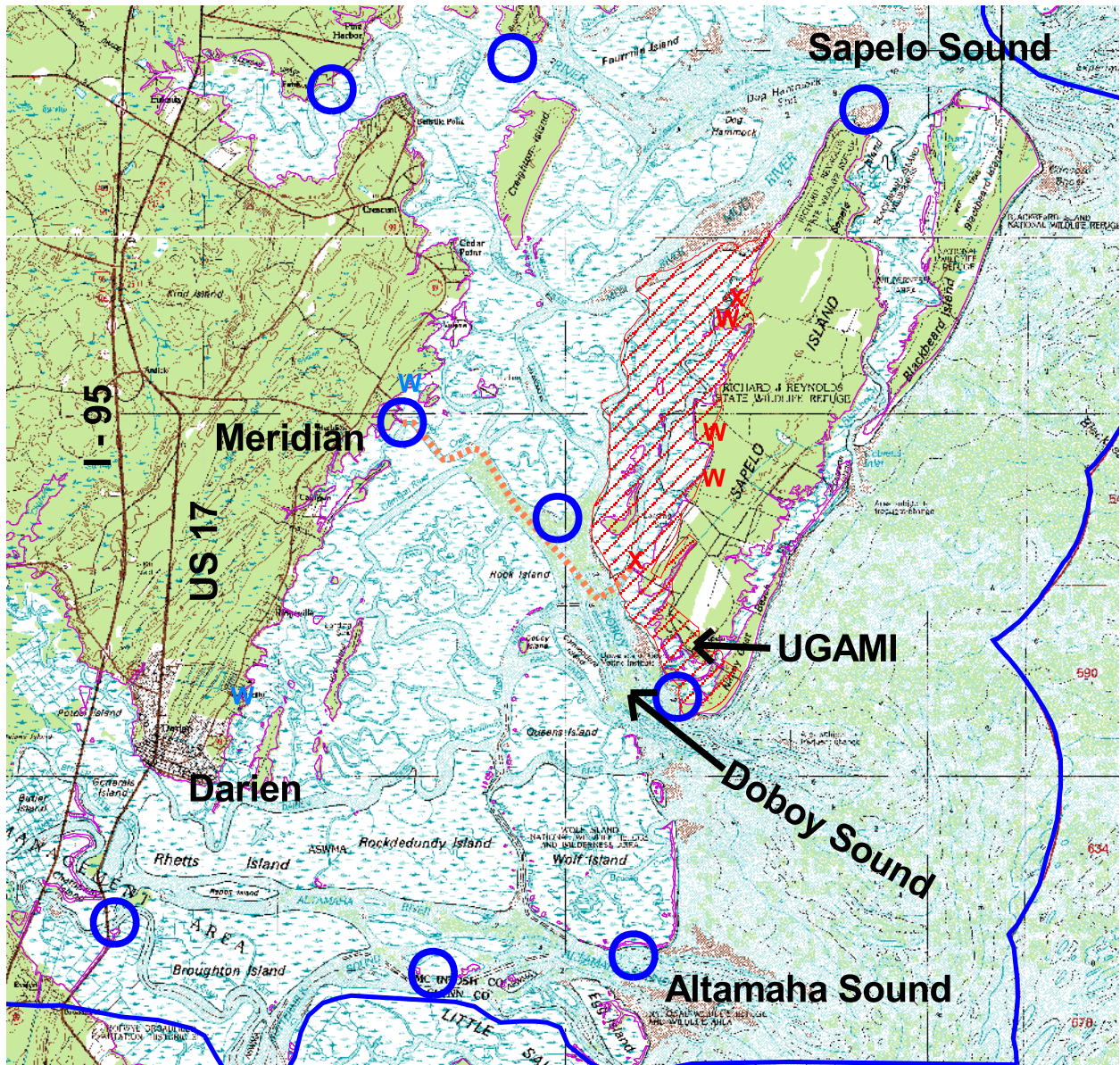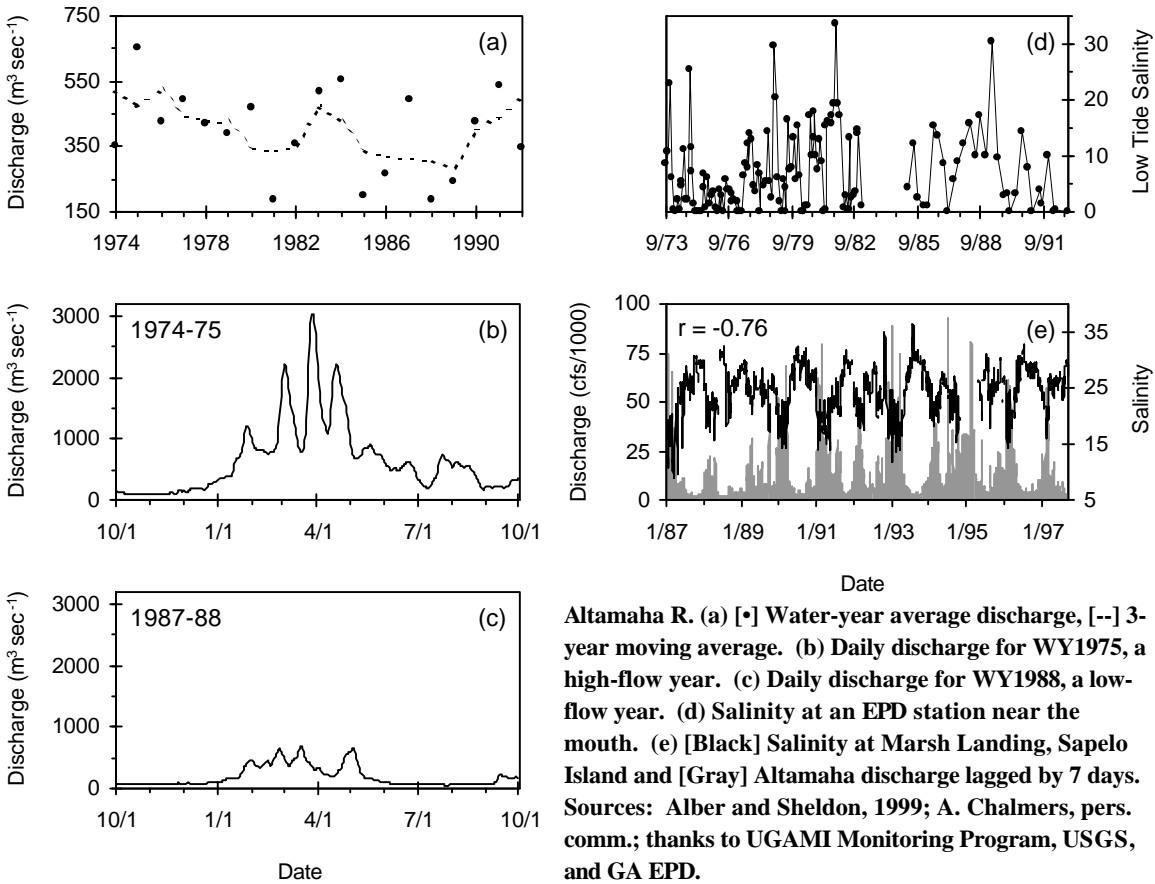
Figure 1. Proposed LTER Study Area, McIntosh County, Georgia. River water quality sampling site located at head-of-tide (54 km upstream from estuary mouth) is not shown.

Altamaha R. (a) [•] Water-year average discharge, [--] 3-year moving average. (b) Daily discharge for WY1975, a high-flow year. (c) Daily discharge for WY1988, a low-flow year. (d) Salinity at an EPD station near the mouth. (e) [Black] Salinity at Marsh Landing, Sapelo Island and [Gray] Altamaha discharge lagged by 7 days. Sources: Alber and Sheldon, 1999; A. Chalmers, pers. comm.; thanks to UGAMI Monitoring Program, USGS, and GA EPD.

marsh around Sapelo Island has been spared dredging, diking, filling, channelization and eutrophication. Thus the proposed LTER site, which contains both relatively pristine and more developed components, is ideal both for determining function of a relatively undisturbed system and for quantifying the impact of human development.

LTER Study Area

The proposed LTER study area comprises the sounds and marsh complexes surrounding Sapelo Island, Georgia. The nominal boundary is the McIntosh County line (Figure 1), including the Altamaha River and the riparian wetlands bordering it to the south. The upland-estuarine interface of the proposed LTER study area consists of (1) the riverine estuary of the Altamaha River, (2) the lagoonal estuaries bordering the mainland and Sapelo Island, and (3) the tidal marsh complexes fringing small hammocks distributed throughout the coastal area. The salinity regimes of these estuaries result from the interaction of river discharge and ocean tides. The lagoonal estuaries adjacent to upland areas are also influenced, though to a lesser and more localized extent, by local surface runoff and groundwater seepage directly to the marsh.

The most southerly estuary is <u>Altamaha Sound</u>, which lies at the mouth of the Altamaha River, the largest river in Georgia. Altamaha Sound is strongly river-dominated and constitutes a complex delta made up of low islands, marshes and tributaries.

<u>Doboy Sound</u>, located to the north of Altamaha Sound, connects to the coastal ocean via a pass between Sapelo Island and the marsh complexes of Wolf/Queen Islands. Freshwater from the

Altamaha River is transported into upper Doboy Sound through the connecting Intercoastal Waterway and marsh channels. Tidal exchange with the Altamaha's plume in the coastal ocean can also deliver low salinity water to Doboy Sound. Thus, mixing with sea water occurs under most conditions, so that water reaching Doboy Sound has low salinity but is not fresh (Figure 2).

The third estuary, <u>Sapelo Sound</u>, is at the northern edge of the study area. Like Doboy Sound, it is a lagoonal estuary with no large streams discharging directly into it. Fresh water enters as precipitation, groundwater or as small volumes of surface inflow. Although Sapelo Sound may also receive low salinity water from the Altamaha River plume via tidal exchange with the coastal ocean, the distance from the mouth of the Altamaha and the general southern trend of the Altamaha plume make this a rarer event than for Doboy Sound. Salinity data collected in the marsh complex between Sapelo Sound and the next inlet to the north (March 1967 and April 1970) confirm that little fresh water reaches this region.

The three estuaries chosen for this study clearly differ dramatically in the degree of riverine influence. Because hydrology and mixing act to damp salinity excursions, the intensity and frequency of salinity excursions decrease with distance north from the Altamaha River (Figure 2). River flow varies over annual and interannual cycles. The salinity at a station near the mouth of Doboy Sound is strongly correlated with river flow, but is less variable (CV 18%) than the salinity in the Altamaha River estuary (CV 103 %). Sapelo Sound, furthest from the Altamaha, has the most stable salinity structure (CV 10%).

A unique advantage of the study area is the long term record of scientific study and ecosystem preservation that have been established by the University of Georgia Marine Institute (UGAMI) on Sapelo Island and the Sapelo Island National Estuarine Research Reserve (SINERR). UGAMI and the SINERR lie close not only to vast tracts of undisturbed marsh, but also to a number of marshes enclosed by breached dikes, settings useful for quantifying marsh use by various organisms or for studying biogeochemical mass balances. UGAMI studies of the Sapelo Island marshes began in 1954 and have resulted in over 800 publications. These publications, LMER data, long-term SINERR monitoring records, and aerial photographs dating back to 1954 provide a perspective on long-term changes in the system and will help in interpreting data collected during the LTER project. Access to the island and surrounding areas is strictly regulated by the Georgia Department of Natural Resources, which manages much of the island. This ensures that study sites located on the island and in surrounding marshes will not be disturbed or vandalized.

ORGANIZING PRINCIPLE

We take as a general organizing principle that the structure and function of coastal ecosystems is affected by the variability of an environmental factor (e.g., salinity) as well as by the mean value experienced at a given location. While the effects of these two terms can sometimes be independent of each other and separable in space and time, they can also interact: e.g. if variation about one mean value of a variable has a different effect than the same variation around a different mean value. The hierarchy of spatial and temporal variation produces a cascade of ecological effects across multiple scales. At time scales spanning the range from hourly to annual, and spatial scales ranging from um to km, coastal ecosystems are influenced by both natural and anthropogenic perturbations (physical and chemical) that affect both the variability and the mean of important ecosystem properties (for example, hurricanes or flood control projects alter river hydrographs, which in turn affects sediment distributions and transport, estuarine salinity, etc.). We postulate that the scales of detectable change in

ecosystems and associated physical and chemical systems indicate the scales of the most critical forcing. We propose to use the existing gradient (mean and variability) of one important variable, salinity, to separate the effects of different means from the effects of different variances for key ecosystem properties with inherent spatial and temporal scales ranging from um to km and minutes to years.

Multi-scale, multi-investigators studies such as is proposed here have the structure to encourage shifting groups of scientists to set up investigations with lifetimes that may be longer than any individual scientist's participation. This cannot be accomplished by short-term grants to individuals or even to small groups of investigators. Without the focus of a long-term study and the infrastructure it provides (logistics, equipment, data management, modeling, etc.), the group fragments and the studies evolve into short-term, eclectic data sets. Such short-term studies are valuable in and of themselves, but they do not provide answers about the structure and function of the ecosystem(s) at scales that are becoming more and more necessary to predict and cope with (or at least guide) the large-scale, long-term anthropogenic impacts on the earth and its environment.

STUDY PLAN

Scope of Project

During its initial funding cycle, the LTER study will address the questions posed above by focusing primarily on marsh, estuarine, nearshore, and riparian processes that are hypothesized to be affected most directly by variations in freshwater inflow. This focus complements the nearly completed Georgia Rivers LMER project (GARLMER), which focused primarily on water column processes and exchange with the coastal ocean. GARLMER studies provide a baseline to address coupling between estuarine/marsh complexes and the coastal ocean and underscore (Cai et al. in press) the strong influence of marsh processes on estuarine water quality in this region. The proposed LTER will include monitoring across a range of space and time scales to document trajectories of ecosystem processes and ecosystem responses to perturbations. The monitoring effort will be complemented by a set of discrete directed studies that will explore specific aspects of ecosystem function. The directed studies will be of finite duration and will be phased in and out over the life of the LTER. Table 1 (Budget Justification) gives the schedule for these studies and shows their relationship to the LTER core areas.

Study Elements

Three major elements comprise the LTER study:

1. Modeling. (a) mechanistic ecological model of organism/environment interactions, (b) physical model of tidal flows and exchange of water, salt and materials between creek channels and the marsh surface, (c) GIS-based predictive model of the effects of land use change, hydrology and Altamaha River water quality, and (d) a model of bioirrigation and sediment geochemistry.
2. Monitoring. Map spatial and temporal variability and mean values of key environmental factors through the study area:

- **River.** Measure of dissolved and particulate constituents in Altamaha river water entering the study area. Examine water quality in tributaries to relate composite water quality at the head of tide to differences in geology and human activities in different areas of the watershed.
- **Groundwater.** Estimate fluxes of fresh water and dissolved constituents from the surficial aquifer into adjacent marshes and estuarine channels. Compare the quantity and water quality of freshwater emanating from developed versus undeveloped areas. Examine the effects of tidal pumping on groundwater salinity distributions.
- **Atmospheric.** Collect meteorological data, including pan evaporation and wet and dry deposition data.
- **Sounds.** Continue routine data collection begun with GARLMER. Establish and maintain continuous records of salinity and temperature at monitoring sites and on routine transects. Data analysis will focus on characterizing the distribution across the study area of mean properties and their variability spectra.
- **Marshes**. Conduct Sediment geochemistry studies and analyses of angiosperms, benthic microalgae, invertebrates, fungi.

3. Directed Studies of Marsh Structure and Function.

In addition to community ecology questions encompassed in the monitoring section (e.g. invertebrate and fungal assemblages), we will conduct additional studies focusing on spatial and temporal variability in angiosperm primary production, community composition, genetic structure and decomposition processes.

Study Element 1: Modeling.

Modeling serves as a predictive, hypothesis-generating device upon which some of the monitoring and experimental studies are based and as a mechanism for data integration, assimilation, and analysis. The LTER will use and improve 4 distinct classes of models encompassing the full spectrum of chemical, biological, and physical processes in the system.

(a) Mechanistic ecological model. (Wiegert): Mechanistic models serve to summarize and synthesize information on the LTER ecosystem(s) , thereby increasing the efficiency and utility of subsequent work. Sensitivity analysis and numerical simulation are the two most useful tools for this purpose. Secondly, because they incorporate testable statements of interaction, mechanistic models can be used in more simplified forms to develop testable theory about both populations and ecosystems (Wiegert, 1993). Finally, mechanistic models can be critical in predicting the future behavior of a system under perturbation.

Mechanistic models of the Altamaha, Doboy, Sapelo (island and sound) area will be used in this study as tools to accomplish the first two objectives described above. A combination of empirical and mechanistic models may also prove to be an important predictive tool in understanding the possible consequences of urbanization and natural system perturbations on the Georgia coast.

LTER mechanistic modeling studies will build on an existing partially spatially-explicit model of the high-salinity marshes in the Duplin River, landward of Sapelo Island. Work carried out under the auspices of the LTER will focus on rendering the model fully explicit, incorporating LTER-derived data, and modifying the model to more fully represent ecological dynamics of the three sounds, the brackish Altamaha and adjacent wetlands, and the freshwater Altamaha and adjacent riparian floodplain up to the head of tide. The mechanistic ecological

models will also be linked to hydrodynamic models of water transport in the tidal creek channels and estuaries (Blanton, Lin, Di Iorio).

(b) Modeling and measuring tidal flows and material exchange between tidal creek channels and marshes (Blanton, Lin, Di Iorio). We will implement numerical simulations of flows and fluxes in an idealized salt marsh-tidal creek channel (SM-TCC) system. This model, which is now being used in the Satilla River, will be parameterized by comparing two sites with different marsh/creek morphologies. The simulations will be used to (1) quantify the role of varying SM-TCC morphologies in the exchange of dissolved material; (2) study the propagation of source water variability into the marsh; and (3) provide steady state fields of salt and flow velocities for input to the ecological model (Wiegert). Proper modeling will allow us to predict the paths and residence times of particles and dissolved substances within marshes that are essential for models of marsh nutrient uptake, gas exchange, contaminant exposure, larval dispersion, etc. All simulations will employ the finite-element model of Lynch and Werner (1991), with the recently developed algorithm for wetting and drying (D. Greenberg, unpublished).

Combining field studies and numerical simulations in SM-TCC systems that are morphologically distinct and have different salinity regimes is necessary. Specific theoretical predictions on the effects of tidal creek morphology (Dronkers, 1986) will be simulated in the numerical model and compared to tidal current field data from SM-TCC with these morphologies. In particular, we will investigate how the exchange of material and propagation of signals between tidal channels and the marshes varies with SM-TCC morphology.

Field studies will focus on hydrodynamics and hydrology (Blanton, Di Iorio), assessment of ground water inputs (with Ruppel), and the relationship of flows and fluxes to morphology. Complementary studies will include DIC, O_2 and NO_3^- fluxes (Cai, Bronk), sediment biogeochemistry (Joye) and plant and animal community composition, density and diversity (Pennings, Craft, Alber, Bishop). Specific processes that will be addressed by field studies and numerical simulations include:

1. Influence of hydrological processes (evaporation, transpiration, groundwater input, marsh circulation) on the salt balance at different places in the creek-marsh complex,

2. Effects of forcing from water level gradients (barotropic mode) and density gradients (baroclinic mode) which reinforce and/or counteract at different stages of the tidal cycle, and

3. Tidal energy dissipation in and along the SM-TCC which provides energy for resuspension and transport sediments; dispersion of organisms; mixing and diffusion of salt and biogeochemical constituents; and controls benthic boundary layer thickness.

A series of field campaigns will define the temporal and spatial variations in tidal currents, salinity and salt and material fluxes at the mouth, middle and head waters of at least two SM-TCC complexes (for example the Duplin River and tributary TCC). The principal instrumentation will consist of high-frequency acoustic-Doppler profilers capable of resolving current profiles at <10 cm scales. Each profiler will be configured with salinity, temperature, pressure and OBS sensors for calculations of scalar transport.

(c) Effect of land-use changes on Altamaha River water quality (Chalmers, Alber, Wiegert). The impacts of human activities in the watershed are an important component of the long term variation we expect to detect in this study. Models and related studies of the impact of land use change on salinity distributions within the Altamaha estuary, freshwater runoff and river discharge were begun in GARLMER. As part of the LTER, we expand these studies to include the effects of land use changes on river water quality. The Satilla River watershed model (Dai et

al. in prep.) is being adapted to the Altamaha watershed with funds from the GA Coastal Zone Management program and the Georgia Legislature. We will add nutrient export from the Altamaha under present and past land use conditions to the runoff model. Input layers for the GIS model include land cover/land use, soils, slope and elevation, and daily precipitation. Discharge and nutrient data from LTER monitoring stations and USGS gauging stations will be compared to model output to validate the models.

(d) Biogeochemical modeling. (Joye, Van Cappellen) (Joye, Van Cappellen) Quantitative estimates of biologically-enhanced pore water exchange in Sapelo Island salt marsh sediments (first completed by Meile et al., 1999) will be obtained using an inverse model that constrains the depth distributions of pore water exchange coefficients (Boudreau, 1984; Emerson et al., 1984) using measured depth profiles of a chemical species and, if appropriate, in situ reaction rate distributions, as input. The model is based on the conservation of mass equation that accounts for molecular diffusion, advection, reaction and irrigation of the chemical species. The model iteratively determines the irrigation coefficient profile, and Monte Carlo simulations are carried out with different initial conditions to assess the uniqueness of the solution.

For the LTER study, the depth distributions of concentration-reaction rate pairs [e.g., reactive species concentration (e.g., sulfate, nitrate) and rates of reactions (e.g. sulfate reduction, denitrification)] or profiles of non-reactive species ($226Ra-222Rn$) will be measured and used as model input. The analysis will be carried out at 3 sites along the salinity gradient. This multi-species approach will permit us to obtain profiles of irrigation constants at high vertical resolution and to examine the effect of salinity fluctuation on bioirrigation. Validity of calculated irrigation coefficients will be tested by comparing irrigation coefficient profiles obtained using different input (S, N, Ra-Rn) as well as by comparing model-derived depth-integrated irrigation fluxes to those obtained from benthic chamber experiments (Joye, Cai). Irrigation constant depth profiles will be compared with depth profiles of organism distributions (Alber, Bishop) and to the mixing profiles obtained from independent radiometric methods (Craft). The data will be incorporated into a future model of system biogeochemistry.

Study Element 2. Monitoring
   A) Altamaha River. Water quality will be monitored intensively at the head-of-tide to capture seasonal variation in water quality and to develop rating curves that can be used to model the loading of various constituents to the coastal zone (e.g., Smith et al. 1996). Water samples will be collected 2-3 times per week and more frequently during floods by a local collaborator to be hired for this purpose (LTER management – Hollibaugh). A CDOM fluorometer established at the sampling station will measure and record CDOM fluorescence at 10 minute intervals. We will sample 5-10 sites at the confluence of major tributaries 4 times per year to characterize the contribution of different watersheds to Altamaha River water composition. We will also sample 4 of the small streams draining the local watershed (mainland and Sapelo Island) 4 times per year The main purpose of this sampling is to compare surface and ground water quality. After the first two years, less intensive sampling (once per week for the Altamaha mainstem and twice per year (low flow and high flow) for the confluence and local watershed sampling) will continue through the rest of the program. Variables to be measured routinely are: dissolved and particulate organic and inorganic nutrients and organic carbon, suspended sediment load, major ion composition and (CDOM) fluorescence (Bronk, Hollibaugh, Moran). Characterizing the major ion composition of the Altamaha will allow us to use ion ratios in shell material for subsequent (not funded by this proposal) reconstruction of paleosalinity distributions in the Altamaha river

estuary (cf Ingram et al. 1996). We will also collect occasional samples from the Altamaha for the US Fish and Wildlife Service to evaluate contaminant loads (Dr. Greg Masson, pers. comm.).

B) Groundwater. The surficial aquifer sustains ecosystems, controls the occurrence of some types of chemical reactions, and acts as both a reservoir (through plant uptake) and a sink (through infiltration) for nutrients, trace chemicals, pollutants, and other materials. The hydrology and geophysics component of the LTER study (Ruppel) focuses on the processes and factors that control and perturb groundwater flow and the three-dimensional distribution of freshwater, transitional water, and seawater at multiple spatial and temporal scales on both Sapelo Island and the mainland. Groundwater studies provide a fundamental link from the open water and marsh-based geochemical, biological, and physical oceanographic research to the land-based part of the system, which is the source of many of the critical freshwater and nutrient inputs. Geochemical analyses of groundwater and monitoring water level changes near human habitation will yield some of the most direct evidence for the impact of anthropogenic processes on the physics and chemistry of the land/ocean margin.

The proposed groundwater research is ongoing from a comparative study of the impact of urbanization on the surficial aquifer on Sapelo and St Simons Island (*http://hydrate.eas.gatech.edu/gms/sapelo.html*; USGS sponsorship; 1998-2000). Water level data, aquifer testing results, tidal pumping time series, and geochemical results from our existing network of 21 shallow (10-17 ft) piezometers and multilevel sampling wells located at two major well fields on the northern half of Sapelo Island will be coupled with a geophysical database containing 24 months of fine-scale and regional survey data (electrical, electromagnetic, radar, and seismic refraction) to provide guidance in the selection of LTER well sites and to place new results acquired by the LTER into a more regional framework.

Noninvasive geophysical site characterization using ground penetrating radar (50 and 100 MHz frequencies), standard and multinode DC resistivity, and seismic surveys will be used to evaluate the subsurface at each site. The initial geophysical surveys will emphasize locating potential confining layers, identifying hydrogeologic heterogeneities that could render a site less than representative of margin processes, and mapping the distribution of freshwater and more saline waters in space and time at and near the land/ocean margin. The final locations of LTER well sites will be chosen by integrating these geophysical data with existing data and with the input of other LTER researchers (for example, Blanton)

Up to 4 monitoring networks, each consisting of at least 10 and possibly as many as 15 shallow (up to 30 ft) PVC wells with a mix of piezometers and multilevel discrete samplers (Cherry et al., 1983) will be installed using a combination of hand augering and hollow stem mechanical augering. Multiport wells will be installed along the main transect and on either side of the main transect. The multiport wells can be used to obtain groundwater samples from discrete depths within the aquifer, thus providing details about vertical variations in groundwater geochemistry. These wells can also yield data about vertical variations in head (vertical flow). Finally, temporary removal of the multilevel core assembly allows the well to be used as a pumping well for determining aquifer hydraulic conductivity, with digital monitoring of drawdown carried out using transducers located in nearby mini-piezometers.

Scientific Objectives. The groundwater exchange components of the LTER study are necessarily integrative and cross all aspects of the LTER. Of particular importance are: 1) Placing bounds on the degree of saltwater intrusion at the land-estuary interface during tidal fluctuations. *Methods*: repeated EM-31 surveys over time scales of 20-30 minutes, downhole geophysical logging, groundwater geochemistry. 2) Constraining freshwater flux into the marsh

(with Blanton, Lin, Di Iorio) and its impact on marsh communities (with Pennings, Alber and Bishop). *Methods*: seepage meters, determination of vertical and horizontal flow components and mapping the potentiometric surface using head measurements, estimation of flow pathways using tracer tests, simultaneous vertical conductivity/salinity logging in tidal creeks and in monitoring wells within a few meters of tidal creeks during the tidal cycle, new kinds of EM analyses (Schultz & Ruppel 1999). 3) Characterizing vertical and horizontal distribution of freshwater, transitional water, and saltwater in the subsurface and quantifying deviations from idealized Ghyben-Herzberg lens morphology (Schultz & Ruppel, 1998). *Methods*: EM-34 surveying, direct measurement of vertical conductivity variations/salinity variations in wells, ground penetrating radar. 4) Monitoring water table fluctuations associated with tidal pumping, infiltration events, or human activities (with Alber, Chalmers). *Methods*: Dedicated water level monitoring in selected wells, periodic water level logging along well transects, seasonal EM-31 and shallow EM-34 surveys, repeated ground penetrating radar surveys. 5) Measuring hydraulic conductivity and porosity and estimating the permeability of the soils. *Methods*: Pumping tests, tracer tests, granulometric soils analyses of samples obtained during well installation (Wilson & Ruppel, in prep.). 6) Measuring groundwater fluxes of dissolved constituents. Methods: Wells will be used to collect water samples for nutrient (NH_4, $NO_2 + NO_3$, PO_4, SiO_4, total dissolved N and P); SO_4 and Cl; dissolved gas (DIC, CH_4, N_2O, O_2, N_2, and Ar); pH and alkalinity determinations using standard techniques (Joye). Groundwater seepage flux through adjacent marsh surfaces will be estimated using seepage meters (Lee 1977; Shaw & Prepas 1989; Hagerthey and Kerfoot 1998). 7) Developing numerical models for specific aspects of flow and transport processes at land-estuary margins. *Methods:* Application of modified versions of widely-accepted numerical models (e.g., SUTRA; Voss, 1984), formulation of new models that integrate variable-density flow and transport of a wide range of reactants across the land-estuary margin (e.g., Robinson & Gallagher, 1999), using specific information provided about geochemical, nutrient, and other fluxes by other LTER researchers

(C) Atmospheric. Two weather stations ("better-than-level-2", as defined in "Meteorological Observation Standards for LTER sites") located on Sapelo Island at the north and south ends of SINEER currently record photosynthetically active radiation (PAR), tide height, air temperature, relative humidity, rainfall, cumulative rainfall, wind speed, wind direction and barometric pressure at 10 minute intervals. These stations are operated and maintained by the UGAMI in collaboration with the SINEER monitoring program. A less sophisticated station is also in operation at UGAMI. We will establish another station at Meridian, a pan evaporation gauge at Marsh Landing, and wet and dry deposition collectors at both Marsh Landing and Meridian.

(D) Sounds. Continuous monitoring stations and discrete sampling will be combined to track water quality in the sounds. Continuous monitoring stations will record temperature and salinity at approximately 10-minute intervals at one depth in the water column at 3 locations in each sound (Figure 1, LTER management – Hollibaugh and Pennings with Blanton and data manager Sheldon responsible for analysis and archiving). Monitoring sites will be chosen for easy access, security, and proximity to marsh study areas and to span the salinity gradient. Through collaboration with the SINEER we will also obtain continuous records of chlorophyll fluorescence and turbidity at 2 sites in the Duplin River (D. Hurley, see attached letter). We propose to establish another of these stations at the ferry dock near the SINEER interpretative center at the head of Doboy Sound (Meridian). We will supplement this station and the SINEER

monitoring station at the mouth of the Duplin (Marsh Landing) with a fluorometer to detect CDOM fluorescence (Moran).

We propose to install a continuous underway monitoring package similar to that used by the USGS San Francisco Bay program (see USGS web site at http://sfbay.wr.usgs.gov/) on the Sapelo Island ferry. This package will record position (GPS) and monitor temperature, salinity, chlorophyll fluorescence, and OBS along the axis of Doboy Sound from the west side of Sapelo Island to the mainland (Figure 1). A UGAMI commuter will take calibration samples and oversee operation of the instrument package en route.

These continuous data will provide our best estimates of the variability in water properties experienced by sessile organisms, especially at short time scales. In addition to calculating means and variance for each site, the data will be subjected to Fourier analysis to partition the variance into temporal and/or spatial scales. Analysis of lagged correlations between records will allow us to model propagation of salinity signals across the study area.

We will occupy 9 stations in the study area (3 per sound, Figure 1) quarterly (UNOLS ship time request form for RV Bluefin attached). Conductivity, temperature, OBS, chlorophyll fluorescence, and PAR will be profiled at each station (Blanton, Hollibaugh, Sheldon). Surface and bottom samples will be taken for measurement of dissolved and particulate; organic and inorganic; C, N and P, pH, alkalinity, O_2, SPM and chlorophyll concentration (Bronk, Cai). Phytoplankton primary production will be measured using 24 hr simulated in situ incubations during years 1 and 2 (Hodson) to calibrate an empirical model based on Cloern (1987) which will be used to calculate primary production thereafter. Bacterioplankton abundance and L-leucine incorporation rate will be measured (Hodson). In addition, water column respiration will be measured (Cai) following Pomeroy et al. (1994).

(E) Marshes. We will select 9 sites (ca 4-hectare) that are adjacent to open water continuous monitoring stations and that span the mean salinity gradient in the sounds and the Altamaha River estuary, with the innermost estuarine site a tidal freshwater marsh where possible. To the greatest extent possible, these sites will also be located adjacent to the well fields used for groundwater studies. Two of the sites will be located at the heads of primary tidal creek channels used for physical studies so that they provide data to link the physical model with the mechanistic ecological model. The following paragraphs provide specifics for the marsh monitoring efforts.

Site preservation. At each site, simple boardwalks will be established during the first year of the study and maintained throughout the study to (LTER management – Pennings) simplify access and minimize trampling of sensitive marsh sites.. For some types of studies, boardwalks may cause a significant disturbance that must be accounted for in the analysis phase.

Sediment characterization. Following an initial survey during year 1 to obtain gross characterizations of sediment chemistry at the monitoring sites, detailed sediment chemistry data will be collected at each of the monitoring sites during years 4 and 5 (Joye, Craft) as follows. Pore water samples will be collected from diffusion equilibrators ("peepers") following a 4-week equilibration period. Chemical measurements will include: salinity, pH alkalinity; dissolved nutrients (NH_4^+, NO_2^-, NO_3^-, SiO_4, PO_4, TDN, TDP,); SO_4 and Cl; and reduced S and metals (Mn^{2+} and Fe^{2+}). Samples will be analyzed using standard methods (Koroleff 1983; Cline 1969; Stookey 1970; Aller and Blair 1996; Joye et al. 1996; Solaranzo and Sharp 1980).

Sediment samples will be collected from cores at 1-cm intervals and frozen under Ar for storage. Sediment analyses will use standard methods: porosity and bulk density - weight loss after drying; grain size – sieves; organic content - combustion at 500 ºC; total organic C and N – CHN analyzer,

carbonate carbon removed with 1N HCl. Solid phase P speciation will be characterized via the method of Ruttenberg (1992). Total Fe and Mn will be determined using multi-acid digests. The distribution between different solid phase reservoirs will be determined using an extraction scheme (Canfield, 1989; Lyons and Berner, 1992; Raiswell and Canfield, 1996), which distinguishes Fe fractions associated with several oxide phases, silicates and sulfides. Though these techniques were developed for Fe, Mn distribution between reservoirs can be determined on the same extracts. Rates of sediment accumulation will be measured over several different time scales using radiometric dating (^{14}C, ^{210}Pb, ^{137}Cs) and feldspar marker layers placed in each marsh (radiometric dating years 4 and 5, Craft, feldspar year 1 and monitored annually). The feldspar marker also will be used to quantify episodic inputs of sediment from floods or hurricane storm surges, should they occur, and both measures can be used to quantify the depth and intensity of bioturbation. These data will be used with measurements of angiosperm production and decomposition, to elucidate the factors controlling organic matter accumulation in fresh versus salt marsh sediment from the perspective of plant community dynamics (Craft). Because they are labor intensive, we will not be able to repeat the full suite of measurements at all stations more than once during the study, rendering analysis of short-term variability in these parameters impossible. However, selected variables (e.g., sediment oxygen demand) will be monitored more frequently as part of other LTER studies.

Angiosperms. Aboveground production (Pennings) of *Spartina alterniflora*, *S. cynosuroides, Juncus roemerianus* and other marsh plants will be estimated annually in the fall at each sampling station by harvesting 0.25 x 0.25 m plots at 3 standardized marsh zones (low, medium, and high elevations). Live and dead biomass of each species will be dried and weighed, and the height and flowering status of a subsample (10) of the shoots in each quadrat will be recorded. Although sampling peak fall biomass has known biases for estimating production, it is far less labor-intensive than more precise techniques, and the biases should be relatively similar between stations and years. N=8 quadrats/zone/sampling station.

Belowground production (Pennings, Craft) will be similarly estimated by collecting soil cores (10 cm diameter, 30 cm deep) and washing away soil to obtain living roots and rhizomes. Roots and rhizomes will be separated and sorted by species, and all samples will be dried and weighed. N=8 cores/zone/sampling station.

We will monitor angiosperm decomposition during years 4 and 5 (Craft). Decomposition of aboveground material will be determined by tagged leaves (Newell and Fallon 1989) and belowground decomposition by mass loss from root bags buried in the sediment (Blum 1993),

Since plant nitrogen status both reveals nitrogen availability to plants and predicts fungal colonization, living and standing dead leaves will be analyzed for N content using a CHN autoanalyzer. N=4 samples of live and 4 samples of dead/zone/station.

Benthic Microalgae. Production by benthic microalgae can account for more than 1/3 of total system gross production in coastal marsh-estuary complexes (Joint 1984; Reise 1985; Pickney & Zingmark 1993; Yallop et al. 1994; MacIntyre et al. 1996; Valiela et al. 1997). They are an ubiquitous component of intertidal marsh and mudflat biota (Paterson & Underwood 1992; Pinckney & Zingmark 1993; MacIntyre et al. 1996), serve as a readily available food source for fishes, invertebrates and birds, and stabilize intertidal sediments by forming barriers to erosion (Underwood & Paterson 1993; Krumbein et al. 1994; Paterson 1994, 1997).

We will document seasonal and spatial differences in the diel patterns of sediment oxygen demand, benthic chlorophyll, primary production, and denitrification during years 1 and 2. During year 3, photosynthesis-irradiance curves will be derived for two sites selected based on

results from the first two years of studies. Together, these data and will be used to develop a predictive model of benthic microalgal production (Joye) which can be used with PAR, turbidity and benthic chlorophyll data collected during routine monitoring to evaluate microalgal production across the study area. Extensive previous work by Williams (1962) on the standing crop of the benthic diatom assemblage in Sapelo Island marshes and by Darley and colleagues on aspects of primary production by benthic algae (Darley et al., 1980; Pomeroy et al., 1981; Whitney and Darley, 1983) provide valuable baseline for comparison with present-day measurements.

Net rates of benthic metabolism, primary production, sediment O_2 demand and denitrification will be determined (Joye, Cai) using light and dark benthic chambers (2 pairs per site, An & Joye submitted). Samples for dissolved gas (DIC, O_2, N_2, Ar), nutrients pH and alkalinity will be collected at the beginning and end of incubations for rate calculations. Dissolved O_2, N_2 and Ar concentration will be determined using a Dissolved Gas Analyzer (DGA; Balzers QMS 422 quadrupole mass spectrometer; Kana et al., 1994). Given the precision of the DGA (0.01%), extremely small changes in gas ratios (e.g., N_2/Ar) and concentration (e.g., $[N_2]$) can be quantified (Kana et al., 1994, 1998), permitting significant changes to be documented over short (4-8 hr.) incubation periods. Using this approach, Ar serves as a biologically inert, conservative tracer. Net rates of sediment O_2 production (net primary production, NPP) or consumption (net sediment O_2 demand, SOD) and denitrification rates can be obtained as the instrument can quantify the N_2/Ar and O_2/Ar ratios concurrently (Kana et al. 1998). PH, alkalinity and DIC concentrations (measured directly, Cai) will be determined immediately upon return to the laboratory.

Using microelectrodes, we will quantify μm scale gradients in O_2 concentration and quantify gross benthic production rates (Revsbech & Jørgensen 1986). Steady state pore water profiles of dissolved O_2 concentration will be determined using Clark-style O_2 microelectrodes (Revsbech & Jørgensen 1986) and rates of gross primary production (GPP) will be determined using the light-dark shift technique (Revsbech et al. 1989; Joye et al. 1996). Gross primary production rates will be determined at *in situ* irradiance using a fiber optic light source (Fostec[®]) that simulates the natural photosynthetically active radiation (PAR) spectrum (Joye et al. 1996). We will determine rates of metabolism (chamber measurements) and GPP concurrently.

Fungi. It is now apparent that fungal processing of standing-decaying marsh grass is key to the transfer of this material to animals (Newell & Porter 1999). Long-term measurements of fungal standing crop and rates of fungal production will enable us to link our work to several other LTER projects, including those at the terrestrial grassland LTERs. We also plan to contribute comparative data to a multi-LTER fungal-ecological working group ("LINX") which is determining impact of nitrogen subsidy upon fungal decomposition of vascular plant material.

At the time of the autumnal assay of maximum standing crop of marsh grasses, standard samples of standing-decaying leaf blades will be collected at each of the monitoring sites. These will be the first-to-third blades below the current senescent blade (yellow-green) (blades of grasses senesce and die in sequence from low to high on shoots) (Newell 1993a). Standard portions of blades will be used for the measurement of living-fungal standing crop and instantaneous rates of fungal production. Ergosterol content will be the proxy for living-fungal mass, and rate of acetate incorporation into ergosterol will be the proxy for rate of production (Newell 1993b, 2000). Rates of fungal sexual production will also be measured, as rates of expulsion of sexual propagules (ascospores) from standard leaf-blade samples (Newell & Wall 1998). This analysis also permits identification of active ascomycetous species present.

Animal Populations. The proposed animal population work (Alber, Bishop) will involve general faunal characterization and more focused work on sentinel species: pairs or suites of common marsh and estuarine organisms that may differ in life history, feeding mode, and salinity tolerance. Their relative abundances along a riverine-estuarine transect will be a useful indicator of ecosystem function, response to disturbance and health (*sensu* Rapport et al., 1998). We will: a) characterize species diversity across the study area, b) assess sentinel species, and c) use oysters as bioindicators. These studies will provide basic information on community structure within the LTER study area and will aid in discerning differences among sites and examining responses to fluctuations in freshwater inflow. Such a database will also be used in other aspects of the project, e.g. food web modeling (Wiegert), benthic biogeochemical processes (Joye, van Capellen).

Faunal assemblages. We will characterize species diversity across the study area, assess distributions of sentinel species, and use oysters as bioindicators to provide basic information on community structure, community dynamics and environmental factors affecting key species within the LTER study area. Transects will be established in each of the long-term control plots in the LTER marshes (Fig. 1), to characterize species diversity (species richness and abundance) of both resident marsh benthos and transient, intertidal nektonic fauna. All study sites will be sampled annually in April, and a subset of 4 (the 3 plots closest to the ocean and the freshwater marsh plot up the Altamaha) will be sampled quarterly. Benthic organisms will be collected at three stations along the elevational gradient at each monitoring site. Epifauna within triplicate 0.5 m^2 quadrats will be identified and counted. Infauna will be sampled with cores (10 cm dia. x 10 cm depth), sieved (0.5-mm and 63-μm mesh) and enumerated. Sample processing will follow standard methods (see Bishop & Hackney, 1987). An additional smaller core will be taken from each quadrat to assess sediment organic matter content and particle size distribution. Nekton will be sampled by the methods of Kneib (1987) in each marsh zone. Where we encounter sentinel species, we will measure their sizes and, in the first year, determine a series of regression relationships (e.g. length: wet weight, wet weight:dry weight, diameter of fiddler crab holes:fiddler crab size, etc.) to enable us to relate size information to biomass. There have been relatively few studies of the fauna of the oligohaline marshes in these systems, so we will be generating a new database. These studies will also extend our knowledge of the better-studied mesohaline fauna (Kneib, 1984, 1997). The relative contribution of various environmental factors to faunal distributions will be assessed by multiple regression and ANOVA techniques with salinity variance structure explicitly included in the analysis Non-parametric methods will be used as necessary. Although we recognize that quarterly sampling may not fully capture the variability in the distribution of motile species, Livingston (1987) demonstrated that it can be used to elucidate long-term trends for infaunal organisms (the major focus herein).

Sentinel species. Sentinel species are pairs or suites of common marsh and estuarine organisms that differ sufficiently in the <u>endpoints</u> of their physiological salinity tolerance such that we expect their relative distribution, abundance and population characteristics to vary down an estuarine gradient. Species will also be chosen to represent different feeding categories (e.g. grazers, suspension feeders, deposit feeders, predators, detritivores). For example, we will examine the relative distributions of *Penaeus setiferus* and *P. aztecus*. Although *Penaeus setiferus* (white shrimp) and *P. aztecus* (brown shrimp) coexist, they partition the estuarine habitat by salinity (Crowe 1975). Other examples of species that fit these criteria are *Uca pugnax* and *U. pugilator* versus *U. minax* (fiddler crabs); *Manayunkia aestuarina* versus

Namalycastis abiuma (polychaetes); and *Melampus bidentatus* versus *Detracia floridana* (gastropods).

Initially we will map the distributions of the sentinel species found along a transect (sampled every 2 km) down the well-defined salinity gradient of the Altamaha River estuary. Intertidal species will be sampled as described above. Subtidal species will be sampled with a small otter or beam trawl. This mapping effort will occur in July of alternate years (beginning year 2) to track long-term changes in distribution. In year 3, we will focus on the short-term response of motile species to changes in freshwater flow at different temporal scales. Over the lunar cycle, we will compare the distribution of both subtidal and intertidal species between spring and neap tide (sampled in July and August). Over the annual cycle, we will compare distributions of intertidal species within their zones of overlap (bi-monthly sampling) and try to relate these to changes in freshwater flow. Finally, we will sample intertidal species in response to stochastic events such as flood and drought conditions. These studies will also involve quantifying population parameters such as sex-ratios, mean size and abundance, reproductive condition, recruitment and, where possible, metabolic rates.

The third component of this work will focus on the oyster, *Crassostrea virginica* for intensive studies of recruitment, growth and feeding. On the Georgia coast, there is evidence that oyster distribution has shifted upstream over the last century (Linton 1968, Harris 1980), possibly as a result of long-term increases in salinity. We will assess relative growth rates, spat recruitment, and *Perkinsus marinus* infection (Ray 1963) annually in each of the three Sounds. We will compare C, N and S stable isotope signatures of oysters at each station as an indicator of changing food resources.

Study element 3. Directed Studies of Marsh Structure and Function.

(a) Angiosperm Production, Community Structure and Population Genetics. A large number of studies have explored the importance of physical stress in mediating salt marsh plant productivity and genetic structure. Two important gaps in our knowledge remain. First, few studies have systematically examined plant processes across the salinity gradient from tidal freshwater to saltwater marshes. Results from separate freshwater and salt marsh studies suggest fundamental differences in system function (Odum 1988), but these hypotheses have rarely been rigorously examined in integrated studies (but see e.g., Schubauer & Hopkinson 1984, Pezeshki & DeLaune 1991, Gough & Grace 1998). Second, most studies have focused on average conditions at particular sites, and have not examined the importance of short-term variability in physical stress on plant responses (but see Hwang & Morris 1994). Focusing on these gaps in our knowledge, we will conduct three directed studies, examining plant primary productivity, community diversity, and genetic structure.

Short-term variation in angiosperm primary production is driven by variation in tidal and freshwater forcing (Pennings). Most studies of primary production in salt marshes have focused on a monthly or yearly time scale (reviewed in Giurgevich & Dunn 1982, Dai & Wiegert 1996). For example, annual primary production of *Spartina alterniflora* in SC was positively correlated with rainfall (Morris & Haskin 1990, but see Teal & Howes 1996). Preliminary field data (Pennings unpublished) indicate that primary production may vary three-fold on a daily basis because of short-term variation in salinity and tidal range and laboratory studies confirm that *S. alterniflora* can respond to changes in salinity or flooding within hours or days (Hwang & Morris 1994, Pezeshki 1997). Numerous studies have documented negative effects of long-term exposure to high salinity (Linthurst & Seneca 1981, Ungar 1991, Drake 1989), but how plants

respond to brief periods of low salinity is not well known. Marsh plants increase in productivity following long-term fertilization (Valiela & Teal 1974**,** Gallagher 1975), but how they respond to transient nutrient pulses from river discharge or rainfall is not well known. Finally, repeated suggestions that daily tidal pulsing subsidizes plant production (Odum 1969, 1971, 1974, 1980, Odum & Fanning 1973, Odum et al. 1995) have remained largely untested because geographic correlations of productivity as a function of tidal range (Steever et al. 1976) are vulnerable to the criticism that other factors such as nutrient availability might also vary between locations (Turner 1976). By repeatedly sampling the same locations on tides of different amplitudes, and by concurrently measuring pore water chemistry, we will provide the best test to date of this long-standing and influential hypothesis. Understanding short-term variability in physical factors and plant responses may be one key to reconciling widely different estimates of *S. alterniflora* primary production and photosynthetic rates from different studies (Mitsch & Gosselink 1993, Dai & Wiegert 1997).

    Methods. Instantaneous plant productivity will be measured at several sampling stations using a portable gas exchange system with a light source (n=10 plants/ species/ station/ date). Photosynthesis will be measured before, during and after pulses of low salinity water due to high river discharge or local rainstorms, with and without experimental watering, and during tides with low and high amplitudes. Measurements will be made at midday, using light levels simulating full sun, on leaves standardized for age and position. Measurements of pore water salinity, pH, ammonia and sulfides will document edaphic variation that may explain variation in productivity. Short term (1-5 days) measurements of total leaf length of tagged plants will test the expected positive relationship between photosynthesis and short-term leaf relative growth rate.

Plant community diversity and species composition is determined not only by average levels of salinity and flooding, but also by their variability (Pennings). Marsh plant species differ in their sensitivity to salinity and flooding. Plant diversity decreases with increases in average salinity and flooding (Gough et al. 1994, Gough & Grace 1998, Odum 1988, Adam 1990). However, we do not understand how variability in flooding and salinity (as opposed to their means) affects plant communities at particular sites. At more variable sites, less tolerant plants might be eliminated by salinity extremes, thus decreasing diversity. Alternatively, greater variation in environmental conditions might give temporary competitive advantages to different species, leading to slower rates of competitive exclusion and increased diversity.

    Methods. Plant community composition (percent cover) will be measured in 0.5 x 0.5 m quadrats located at 3 elevations at multiple sites (n=60 sites, 3 zones/site, 10 quadrats/zone/site). Sites will be located along the terrestrial-oceanic gradient on all 3 estuarine systems and will include the monitoring sites. Variation in flooding will be measured by marking the low and high tide levels at each site on at least 4 tides, surveying these markers and standardizing the observed tidal ranges to a common datum at the Savannah River entrance. Variation in salinity will be measured at each site for two years, and the mean, range, and coefficient of variation of salinity at each site will be calculated. Information on edaphic variation at each site will also be used in the population genetics study (below)

    Salt Marsh Plant Population Genetics (Donovan). Tides, precipitation, riverine input, and variability in these processes, create significant spatial structuring of physical stress in the salt marsh environment, particularly along elevation gradients (tides and precipitation) and along larger-scale gradients of riverine influence related to location in the estuary. Understanding the effects of these stressors on community structure and productivity, and predicting responses to

future changes in these factors, requires an understanding of the genetic structure and diversity of each dominant plant species. In a classic study, Silander (1979, 1984, 1985) found that natural selection and other processes created genetically distinct populations of *Spartina patens* adapted to their microhabitats in coastal NC. Similarly, population genetic structure has been identified for *Hibiscus moscheutos* and *Limonium carolinianum* along estuaries (Kudoh & Whigam 1997, Hamilton 1997), although the population differences were not necessarily adaptive.

We will test the general hypothesis that spatial variation in marsh habitat drives adaptive genetic differentiation, using environmental gradients at two scales (elevation and distance-along-estuary) and two dominant clonal plants, *Spartina alterniflora* and *Distichlis spicata*. A well known example of postulated population structuring is the unresolved hypothesis that tall and short forms of *S. alterniflora* are genetically distinct populations adapted to their microhabitats (Shea et al. 1975; Gallagher et al. 1988). Our work will provide the first thorough genetic data (allozymes and RAPDs) to address this specific hypothesis. More importantly, we will test the generality of population structure and adaptation of clonal marsh plants along gradients.

Methods. Both allozymes and RAPDs will be used to ensure that there is sufficient specificity to identify genetic variation within and among populations. Techniques have been developed for these species (Shea 1975; Stiller & Denton 1995; Daehler & Strong 1997; Eppley et al. 1998; Daehler et al. 1999), and the graduate student who will do the analyses (C. Richards) is proficient in RAPD techniques. Allozyme analysis will be done in the electrophoresis lab of Dr J. Hamrick (UGA Botany) and RAPD analyses will be done in the molecular genetics core facility (UGA). We will work at the same sites as used in the study of community diversity (above) and edaphic data will be shared. To demonstrate local adaptation, we will test whether individuals perform better in their site of origin than plants collected from other sites (Pezeshki & De Laune 1995) by transplant experiments. Culms of each species will be collected from the field and grown in a greenhouse at UGAMI through several generations of rhizome production to minimize maternal effects. Culms will then be transplanted between genetically distinct populations, with controls planted back into their own population. Growth and survival will be assessed after 1 year. To determine the differential performance of populations in response to variation in salinity, ramets from different populations will be compared in greenhouse experiments. Plants will be scored for growth, ecophysiological salinity tolerance characteristics, and instantaneous plant productivity (Hester et al. 1998).

(b)Prokaryotic-Eukaryotic Decomposer Consortia

The land/ocean margin ecosystem lies at the interface between two ecosystems in which distinctly different groups of decomposers control organic matter degradation. The terrestrial ecosystem is largely dominated by fungal decomposers, while bacterial decomposers dominate the marine ecosystem. In the intertidal marshes of the Georgia coast, evidence suggests that both fungi and bacteria play critical roles in decomposition (Benner et al. 1984, Newell & Porter 1999). However, there is relatively little knowledge about decomposer community composition or the relationship between community composition and the decomposition process.

Interactions between bacteria and fungi may be strictly competitive (or even predator/prey), with factors such as water content, oxygen availability, colonization timing, sizes of openings in polymer-matrices, particle size, or nitrogen availability determining the outcome (Newell 1996, Newell & Palm 1998). Alternately, bacterial and fungal decomposers may form mixed prokaryotic-eukaryotic consortia that interact in complex, and sometimes positive, ways during

decomposition (Newell & Porter 1999). Processes such as bacterial nitrogen fixation and fungal substrate pervasion are likely to be important factors that control decomposition by both prokaryotic and eukaryotic microorganisms (Graça et al. 1999, Newell & Porter 1999). Yet despite compelling arguments in favor of an integrated approach, there has traditionally been relatively little interaction between mycologists and bacteriologists with regard to the ecology of the decomposition process (NSF/LTER web site "Why Study Microbes at LTER Sites", Benner et al. 1984, Newell 1994).

The intertidal marshes of Georgia provide an excellent opportunity to undertake a directed study of the interactions of prokaryotes and eukaryotes in marsh grass decomposition (Newell, Hodson, Hollibaugh, Moran) for three major reasons. First, there has been significant previous research over the last two decades on the separate contributions of each group to plant decomposition in these marshes (Newell & Porter 1999, Hodson et al. 1983). Second, there are now techniques available for determining activity and identity of both fungi and bacteria at equally detailed levels (Newell 1993, Kirchman et al. 1985, González & Moran 1997, Muyzer et al. 1993, Murray et al. 1996, Liu et al. 1997). Several of these methods (e.g., acetate incorporation into ergosterol as a measure of fungal productivity, leucine incorporation into protein as a measure of bacterial productivity, and in situ PCR as a measure of bacterial genetic capabilities) were conceived, developed, and ground-truthed in Georgia's intertidal marshes and estuaries (Newell 1993, Kirchman et al. 1985, Hodson et al. 1985, Newell 2000). Third, what little information we have of how bacteria and fungi interact during the decomposition of vascular plant material suggests that water saturation may be a key variable in shifting dominance between these two groups (Benner et al. 1984, Newell et al. 1995). Thus the LTER emphasis on dynamic and long-term changes in freshwater inputs to coastal communities provides an excellent framework for addressing the factors that are most likely to control decomposer community composition and activity.

We propose to simultaneously address the relative activity levels of the two decomposer groups and to identify the individual organisms that mediate this activity. This study will undertake molecular characterization of microbial assemblages, measurement of activity of each decomposer group, measurement of standing stocks of each decomposer group, determination of microscale spatial relations of specific bacteria and fungi, localization of key functional genes (for nitrogen fixation, denitrification, aromatic ring cleavage, and hydrolytic enzymes), and assessment of total system (bacterial plus fungal) respiration. Samples will be collected at the marsh monitoring sites quarterly during the first two years of the studies. Manipulation experiments (lab and field) will investigate the response of consortia to perturbations like enhanced nutrients (N and P) or moisture, salinity, anoxia, sulfide, etc.

Fungal secondary productivity and living fungal biomass will be measured by the acetate incorporation method (Newell 1993, Newell 2000), and identities of active ascomycetous fungi and sexual productivity will be determined by rate of ascospore expulsion (Newell & Wasowski 1995). Bacterial secondary productivity will be measured by the ^{3}H-leucine method (Kirchman et al. 1985). Nucleic acid-based methods will be used to provide a culture-independent (although probably not unbiased) inventory of decomposer communities by retrieval and sequencing of 16S and 18S rRNA genes (González & Moran 1997), and through fingerprinting methods for small subunit rRNA genes [denaturing gradient gel electrophoresis (DGGE: Muyzer et al. 1993; Murray et al. 1996) and terminal restriction fragment polymorphism (TRFLP: Liu et al. 1997). Identity and genetic capabilities of decomposer microorganisms at the single-cell level and

elucidation of physical associations between decomposer organisms will be carried out through whole-cell techniques (FISH and in situ PCR; Hodson et al. 1995, Chen et al. 1997).

COMPARISONS WITH OTHER SYSTEMS

Coastal salt marshes dominated by *Spartina alterniflora* are grasslands, and our site will provide an interesting comparison with other grassland-dominated LTER sites such as the Konza Prairie and the Shortgrass Steppe sites. A similarity between our proposal and existing LTER grassland sites is the emphasis on the role of variability (rainfall or fresh water flow) in driving grassland function. Major differences include the emphasis we place on tidal fluctuation, a forcing factor that is lacking in terrestrial systems but is critical in driving marsh function, and the fact that mammalian herbivores are relatively unimportant in southeastern coastal marshes but play a large role in the function of terrestrial grasslands. A long-term goal of our work will be to participate in comparative studies between other grassland LTER sites. Although salt marshes, because of their intertidal nature, will clearly be an outlier or endpoint in such comparisons, the differences in the physical environment may make comparisons all the more revealing

We have mentioned some of the LTER studies to which we can contribute (for example, LINX) above. In addition, we plan comparative studies between our site and other coastal LTER sites studying similar processes. Examples of possible collaborations include groundwater processes (Virginia Coastal), food web dynamics and detrital organic matter processing (Plum Island). Although we would be coming in late, we will also participate in the LTER global CO_2 collaborative study. We (Cai) have discussed comparison of CO_2 dynamics in coastal wetland systems and inland streams and lakes with Dr. Jon Cole, a P.I. of the LTER CO_2 project.

The Georgia coast LTER site provides a striking point of comparison with the Virginia Coast Reserve site. Both are relatively rural and have extensive intertidal marshes between a barrier island and the mainland (or Delmarva Peninsula in the case of the VCR). Sapelo Island, however, is much larger and less impacted by erosional storm events than the barrier islands of the VCR. Although the Georgia site is affected by silvicultural practices in extensive pine plantations throughout McIntosh County, it is not affected as directly by agricultural practices as the VCR. These comparisons/contrasts could lead to useful collaboration with investigators from that site.

PROJECT MANAGEMENT

Project Directors. Overall responsibility for project management will be split between Hollibaugh and Pennings with Hollibaugh assuming primary administrative responsibility and Pennings assuming primary responsibility for field logistics. Pennings and Hollibaugh will work together as co-directors and act as temporary backups for each other in the event that either of them cannot fulfill their responsibilities for some reason. They will serve as the primary contacts for LTER system activities including representing the project to the LTER Coordinating Committee (Hollibaugh) and designating appropriate project representatives for other LTER committees.

Hollibaugh will be responsible for project administration in Athens. This includes: seeing that NSF reporting requirements are met; fiscal matters; working with the Grants and Contracts office at UGA; and supervising the project data manager, W. Sheldon. Hollibaugh will be responsible for organizing the annual project workshops (see below) and the LTER-system meeting proposed to be hosted at UGA in Year 4 of the project.

Pennings will have supervisory responsibility for the LTER field technicians located at the University of Georgia Marine Institute. He will be responsible for organizing routine monitoring activities, for maintaining ongoing field experiments, boardwalks and monitoring sites, and for downloading and maintaining the continuous monitoring equipment. He will also be the primary contact for project interactions with UGAMI, the Sapelo Island National Estuarine Research Reserve and other cooperators involved in the field program.

The project co-directors will serve for 3-year terms. At the end of the third year their performance will be evaluated by the project Senior Investigators and a vote will be taken (simple majority of voting SIs) to decide whether or not to replace them. If the SIs deem it necessary to replace a co-director, or if a co-director has to relinquish the responsibility for any reason, a replacement will be selected from the project SIs by simple majority vote and will serve pending approval by the cognizant NSF program manager and the LTER steering committee.

Scientific advisory committee (SAC). We will set up an advisory committee to evaluate the project's progress and direction and provide guidance to project investigators. The committee will be composed of the project co-directors, 2 of the project SIs and 6 outside advisors, at least 3 of whom are SIs on other LTER projects. The project SIs and outside advisors will serve 6 year terms then be replaced. The SAC will meet with project personnel at an annual project workshop where results from the previous year will be presented by project PIs and students and by outside collaborators. These results will be discussed with the SAC then plans for work in the subsequent year will be refined as necessary. The workshop will be held in September so that the information can be incorporated in the annual report to NSF and taken into consideration in preparing the budget request for the subsequent year.

Investigator progress review. Individual investigators will be responsible for administration of their projects including, in consultation with Pennings, their component of the routine monitoring

program. Their progress and performance will be evaluated once per year in conjunction with the annual meeting by the SAC. If the SAC finds that a SI's progress is less than adequate, the committee will first express concern to the SI and discuss with them problems, including funding or personnel issues, that may be hindering their progress. In consultation with the SI, the committee will make recommendations to restructure the SI's responsibilities or to alter the SIs funding level to facilitate success. If the problem persists, the project director will consult the cognizant NSF program manager and the LTER Steering Committee. The monitoring responsibilities assigned to that SI may be reassigned and the directed study may be terminated or reassigned.

Student recruitment. This project will employ and train a large number of young scientists as interns, technicians, graduate students and postdocs. We will publicize the LTER program and job openings in coastal communities around the study area, with the goal of attracting potential students who are likely to take positions of environmental leadership in these communities. Particular attention will be paid to recruiting underrepresented minorities. The University System of Georgia contains several minority institutions. A number of them, like Savannah State University (SSU) are located on the Georgia Coast. SkIO has a large, NSF-funded cooperative internship program with SSU and the head of the SSU Marine Science program is an adjunct faculty member in the Department of Marine Sciences at UGA. We will build upon the existing relationships with SSU and other institutions in order to maximize our ability to provide opportunities for minority students. This approach has been used successfully in an existing multi-institutional DOE biotechnology project (see Hodson Current and Pending Support) that involves students from Jackson State University and Florida International University.

V. DATA MANAGEMENT

Information Management System and Metadata Standards

Wade Sheldon, a Research Coordinator in the Department of Marine Sciences, will be responsible for LTER data management, including internet accessibility. The foundation of our data management program will be the five years of relevant data and experience acquired on the current Georgia Rivers LMER project. Hydrographic, DOC, nutrient concentration, and other data from 16 research cruises on the Altamaha River estuary (October 1994 through March 1999) will be copied to an ODBC-compatible relational database management system. LMER GIS coverage data and results from 40 years of marsh research on Sapelo will also be incorporated in the database as possible, providing a wealth of background information on the project research area.

The database will reside on a Windows NT® file server dedicated to this purpose, and will be the primary repository for all processed data from monitoring activities and standardized periodic sampling. GIS data, model output, and experimental data from short-term or unique sampling efforts may be stored in additional database tables or as external files in standardized formats, as deemed appropriate. Information on all contributed data necessary to comply with LTER metadata exchange standards (Porter et al., 1997) will either be stored in indexed database tables or derived from the database structure itself (e.g. variable types and formats). This relational database strategy will ensure maximum flexibility by supporting the generation of formatted ASCII and HTML reports to comply with existing LTER database and display standards, while allowing us to take advantage of emerging technologies (e.g. WWW database query interfaces exploiting DHTML and XML protocols).

The integrity of the database will be protected by routing access through intermediary software on a separate computer (i.e. three-tier structure). The database will also be protected by data redundancy (RAID technology) and off-site archival of tape backups. All data submissions will be manually logged and archived in original format as well.

Data Acquisition and Quality Control

Data from monitoring studies and climatological instruments will be processed and documented by the data manager on a continuing basis. Data filtering and validation software and metadata templates already developed for the LMER project will be adapted to automate this process. These data sets will be incorporated into the database immediately and assigned provisional status. The data manager will review the calibration reports for the instrument packages at regular intervals and update the data, metadata, and status fields accordingly.

Data entry and quality control for manipulation experiments and specific investigations will be the responsibility of the individual investigators; however, the data manager will provide data entry forms and software, such as spreadsheet templates and database interface applications. Data entry software will include default values and validation logic to reduce errors and ensure submissions are complete and conform to the database structure. All LTER participants will be

given the opportunity to participate in the selection and design of data entry tools to make the process as convenient as possible and encourage timely data submission. Data contributions will be integrated into the database promptly, allowing investigators the opportunity to see their data in the context of all other site measurements, providing additional incentive.

The data manager (Sheldon) will report data submission activity to the project administrator (Hollibaugh) quarterly. LTER participants not contributing data on a timely basis will be identified and contacted by the administrator as necessary (see Program Management).

Data Access and Security

A project WWW site will be established to serve as the primary mechanism for accessing data. The four-level security protocol described by Porter and Callahan (1994) will be used, with maximum waiting periods of one year and two years for Type II and III data sets, resp. Visitors will be required to agree to a usage policy statement before viewing or downloading data. Eligible data and metadata files will be generated from the master database, uploaded to the site in HTML format, and cataloged on a monthly basis. Master catalog information will also be updated on the LTER network at this time. A database query page and graphical data display features (e.g. maps, charts) will be implemented as soon as practical.

A separate password-protected WWW page will be maintained for participants. Security time limits on Type II data will be relaxed on this page so that provisional monitoring data can be viewed as soon as it is available. Security for Type III data from individual research projects will not be relaxed except at the discretion of the investigator who contributed the data.

Integration of Data Management with Research Activities

The information management component of the project will serve several important functions in the design and implementation of research projects. In the research-planning phase, the provision of task-specific data entry forms will ensure that all necessary measurements and records are collected to interpret the results in the larger project context. The timely display of site monitoring data on the project WWW page will also serve as an important planning tool for field work. In the analysis phase, each investigator will have the opportunity to view data they have contributed alongside factors measured by other participants using database query techniques, which might yield new insights. Additionally, the planned inclusion of published manuscripts and conference presentations on the WWW site, along with a project message board, should encourage high levels of collaboration by participants.

VI. SHIPTIME REQUEST

Years 2000-2002

UNOLS Ship Time Request Form - Section ONE
==
UNOLS Request ID #: 19990624160657
Version #: 003
Valid as of: 06/25/99 05:16 PM EDT
==
P.I. Name Last: Hollibaugh First: James MI.: T
==
Institution University of Georgia Reasearch vessel required for:
Address: School of Marine Programs, UGA _ Ancillary Only
Athens, GA 30602-3636 X Principal Use
_ No Ship Required
==
Phone: 706-542-3016 Fax: 706-542-5888 E-mail: aquadoc@uga.edu
==
Co P.I. Name Institution Co P.I. Name Institution
------------ ----------- ------------ -----------
==
Proposal Title:

Georgia Land/Ocean Margin Ecosystem LTER
==
Large Program Name: Other Research Purpose: Multi-discipline

If Other, specify: LTER If Other, Specify:
==
New Proposal? Y Agency Submitted to: Foreign EEZ? N
Institution Proposal #: NSF/OCE/BIO
Amount Requested: Area(s) of Operation:
Agency Proposal #: 4,200,000 NA6
Lat/Long:
Renewal? Start Date: 01/01/00 Begin:
Grant #: End Date: 12/31/05 End:
==
Ship(s) Requested # Science
Year (Name or Size) Days Req. Optimum Dates Alternate Dates
---- ---------------- --------- ------------- ---------------
2000 Blue Fin 27 quarterly
2001 Blue Fin 33 quarterly
2002 Blue Fin 37 quarterly
==
--------------- PORTS ------------
Total Science Days: 76 Start: Intermediate: End:
in Science Party: 8 Savannah Savannah
==
Equipment Required:
_ Vans _ P-Code GPS _ MCS _ Alvin _ AMS 120
_ Dynamic Positioning _ Multibeam _ SCS _ ROV _ 680 Cond.
==
Other Special Equipment; Comments:

ADCP

Years 2003-2005

UNOLS Ship Time Request Form - Section ONE
==
UNOLS Request ID #: 19990624153706
Version #: 004
Valid as of: 06/25/99 05:17 PM EDT
==
P.I. Name Last: Hollibaugh First: James MI.: T.
==
Institution University of Georgia Reasearch vessel required for:
Address: School of Marine Programs, UGA _ Ancillary Only
Athens, GA 30602-3636 X Principal Use
_ No Ship Required
==
Phone: 706-542-3016 Fax: 706-542-5888 E-mail: aquadoc@uga.edu
==
Co P.I. Name Institution Co P.I. Name Institution
------------ ----------- ------------ -----------
==
Proposal Title:

Georgia Land/Ocean Margin Ecosystem LTER
==
Large Program Name: Other Research Purpose: Multi-discipline
If Other, specify: LTER If Other, Specify:
==
New Proposal? Y Agency Submitted to: Foreign EEZ? N
Institution Proposal #: NSF/OCE/BIO

Amount Requested: Area(s) of Operation:
Agency Proposal #: 4,200,000 NA6
Lat/Long:
Renewal? Start Date: 01/01/00 Begin:
Grant #: End Date: 12/31/05 End:
==
Ship(s) Requested # Science
Year (Name or Size) Days Req. Optimum Dates Alternate Dates
---- ----------------- --------- ------------- ---------------
2003 Blue Fin 37 quarterly
2004 Blue Fin 37 quarterly
2005 Blue Fin 32 quarterly
==
--------------- PORTS ------------
Total Science Days: 76 Start: Intermediate: End:
in Science Party: 8 Savannah Savannah
==
Equipment Required:
_ Vans _ P-Code GPS _ MCS _ Alvin _ AMS 120
_ Dynamic Positioning _ Multibeam _ SCS _ ROV _ 680 Cond.
==
Other Special Equipment; Comments:

ADCP
==

Georgia Department of Natural Resources

Wildlife Resources Division
Sapelo Island National Estuarine Research Reserve (SINERR)
Box 15, Sapelo Island, Ga. 31327
Lonice C. Barrett, Commissioner
David Waller, Director
PH (912) 485-2251

June 18, 1999

Dr. Steven C. Pennings
University of Georgia Marine Institute
Sapelo Island, GA 31327

Dorset Hurley
Sapelo Island National Estuarine Research Reserve
P. O. Box 15
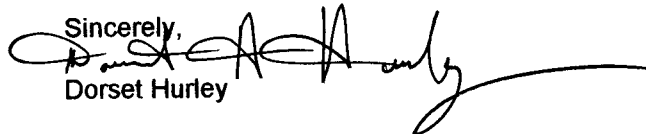Sapelo Island, GA 31327

Dear Dr. Pennings,

This communication is for my enthusiastic support of the LTER proposal for coastal Georgia that you and Dr. Hollibaugh are submitting to NSF. The long term monitoring and research efforts proposed in the study will be of significant benefit to Sapelo Island National Estuarine Research Reserve (SINERR) by increasing regional and national awareness of our developing research program and as a mechanism for enhanced collaboration among academic, federal, state and non-government organizations toward the common goal of understanding and preserving our national estuarine resources.

Currently, SINERR is funding or facilitating several research projects that will complement the LTER proposal including:

- Research Fellow Greg Schultz, "Characterization and monitoring of the spatio-temporal variations in the distribution of freshwater and saltwater in the surficial aquafer" 2 yrs @ $16,500/annually
- Research Fellow Stacy Webb, "Effect of channel complexity on residence times, growth and movements of juvenile white shrimp (*Penaeus setiferus*) within tidal marsh nursery habitats." 3 yrs @ $16,500/annually
- Research assistantship for Chip Cotton "Oyster bed distribution as a long term environmental indicator for the Sapleo Island National Estuarine Research Reserve" 1 yr @$10,000/annually
- Research assistantship for Merrilee Thorensen "Recruitment of *Crassostrea virginica* as a bioindicator of environmental stress for the Sapelo Island National Estuarine research Reserve." 2 yrs @ $17,500 annually
- Research assistantship for Dexter Sorrell "Maritime forest restoration initiative" 2 yrs. @ 18,050/annually.

SINERR is monitoring estuarine water quality in accordance to NERR protocol associated with the System Wide Monitoring Program (SWMP). We currently have two continuous monitoring stations in the Duplin River employing YSI model 6000 remote sonde units measuring: pH, DO, tidal amplitude, temperature and salinity at 30 minute intervals. We gladly make this data available to the LTER effort and will consider LTER objectives and needs as our water monitoring program expands. We enthusiastically support the LTER effort and hope you will depend upon us for any logistical assistance, expertise or local knowledge we may be able to provide your researchers.

SINERR considers the LTER effort to be an extremely beneficial initiative toward fusing collaborative research and educational directives in the much needed area of estuarine science. We are excited about the prospects of an LTER site within such close proximity of the reserve and will support the LTER in any way we can toward maximizing its success.

Sincerely,

Dorset Hurley

References:

Adam, P. 1990. Saltmarsh ecology. Cambridge University Press, Cambridge.

Alber, M., and Sheldon, J. E. In press. Use of a date-specific method to examine variability in the flushing times of Georgia estuaries. Est. Coast. Shelf Sci.

Alber, M., and Sheldon, J. E. 1999. Trends in salinities and flushing times of Georgia estuaries. In: Proceedings of the 1999 Georgia Water Resources Conference. Kathryn J. Hatcher (ed.) Institute of Ecology, University of Georgia, Athens, Georgia.

Aller, R. C., and N. E. Blair. 1996. Sulfur diagenesis and burial an the amazon shelf - major control by physical sedimentation processes. Geo-Mar. Let. 16: 3-10.

Benner, R., S. Y. Newell, A. E. Maccubbin, and R. E. Hodson. 1984. Relative contributions of bacteria and fungi to rates of degradation of lignocellulosic detritus in salt marsh sediments. Appl. Environ. Microbiol. 48: 36-40.

Bishop, T. D. and C. T. Hackney. 1987. A comparative study of the mollusc communities of two oligohaline intertidal marshes: spatial and temporal distribution of abundance and biomass. Estuaries 10:141-152.

Blanton, J. O., J. Amft and T. Tisue. 1997. Response of a small-scale bottom-attached estuarine plume to wind and tidal dissipation. J. Coastal Res., 13: 349-362.

Blanton, J., C. Alexander, M. Alber, and G. Kineke. 1999. The mobilization and deposition of mud deposits in a coastal plain estuary. Limnologica   29: 293-300.

Blum, L. K. 1993. *Spartina alterniflora* root dynamics in a Virginia marsh. Mar. Ecol. Prog. Ser. 102:169-178.

Boudreau, B. P. 1984. On the equivalence of nonlocal and radial-diffusion models for porewater irrigation, J. Mar. Res., 42, 731-735.

Bushaw, K. L., R. G. Zepp, M. A. Tarr, D. Schulz-Jander, R. A. Bourbonniere, R. E. Hodson, W. L. Miller, D. A. Bronk, and M. A. Moran. 1996. Photochemical release of biologically labile nitrogen from dissolved organic matter. Nature 381- 404-407.

Bushaw-Newton, K. and M. A. Moran. In Press. Photochemical formation of biologically available nitrogen from dissolved humic substances in coastal marine environments. Aquat. Microb. Ecol.

Cai W.-J., and Y. Wang. 1998. The chemistry, fluxes and sources of carbon dioxide in the estuarine waters of the Satilla and Altamaha Rivers, Georgia. Limnol. Oceanogr. 43:657-668.

Cai, W.-J., Y. Wang, and R. Hodson. 1998. Acid-base properties of dissolved organic matter in the estuarine waters of Georgia. Geochem. Cosmochim. Acta 62: 473-483.

Cai W.-J., L. R. Pomeroy, M. A. Moran and Y. Wang. 1999. An oxygen and carbon dioxide mass balance model of the estuarine/intertidal marsh complex of five rivers in the Southeastern U.S. Limnol. Oceanogr. 44:639-649.

Cai W.-J., W.J. Wiebe Y. Wang, and J. E. Sheldon. In press. Intertidal marsh as a source of dissolved inorganic carbon and a sink of nitrate in the Satilla River-estuarine complex in the southeastern U.S. Limnol. Oceanogr.

Canfield, D.E. 1989. Reactive iron in marine sediments. Geochim. Cosmochim. Acta 53: 619-632.

Chen, F., J. M. González, W. A. Dustman, M. A. Moran, and R. E. Hodson. 1997. *In situ* reverse transcriptase: an approach to characterize genetic diversity and activity of prokaryotes. Appl. Environ. Microbiol. 63:4907-4913.

Cherry, J. A., R. W. Gillham, E. G. Anderson, and P. E. Johnson. 1983. Migration of contaminants in groundwater at a landfill: a case study, groundwater monitoring devices. J. Hydrol. 63:31-49.

Cline, J. D. 1969. Spectrophotometric detection of hydrogen sulfide in natural waters. Limnol. Oceanogr. 14: 454-458.

Cloern J. E. 1987. Turbidity as a control on phytoplankton biomass and productivity in Ingram B. L., Ingle J. C., and Conrad M. E. 1996. Isotopic records of pre-historic salinity and river flow in San Francisco Bay estuary. pp. 35-61. In: San Francisco Bay: The Ecosystem. J. T. Hollibaugh, ed. Pacific Division, AAAS.

Crowe , A. L. 1975. Population dynamics of two species of commercial shrimp in Caminada Bay, Louisiana. Proc. La. Acad. Sci. 38:86-91.

Daehler C. C., and D. R. Strong. 1997. Hybridization between introduced smooth cordgrass (*Spartina alterniflora*: Poaceae) ands native cordgrass (*S. foliosa*) in San Franscisco Bay, California, USA. Am. J. Bot. 84: 607-611.

Daehler C. C., Anttila C. K., Ayres D. R., Strong D. R., and J. P. Bailey. 1999. Evolution of a new ecotype of *Spartina alterniflora* (Poaceae) in San Francisco Bay, California, USA. Am. J. Bot. 86: 543-546.

Dai, T. and R. G. Wiegert. 1996. Ramet population dynamics and net aerial primary productivity of *Spartina alterniflora*. Ecology 77: 276-288.

Dai, T. and R. G. Wiegert. 1997. A field study of photosynthetic capacity and its response to nitrogen fertilization in *Spartina alterniflora*. Est. Coast. Shelf Sci. 45:273-283.

Drake, B. G. 1989. Photosynthesis of salt marsh species. Aquat. Bot. 34: 167-180.

Darley, W.M., C. L. Montague, F. G. Plumley, W. W. Sage, and A. T. Psalidas. 1980. Factors limiting edaphic algal biomass and productivity in a Georgia salt marsh. J. Phycol. 17: 122-128.

Dronkers, J. 1986. Tidal asymmetry and estuarine morphology. Neth. Jour. Sea Res. 20: 117-131.

Emerson, S., Jahnke, R. and Heggie, D. 1984. Sediment-water exchange in shallow water estuarine sediments. J. Mar. Res. 42:709-730.

Eppley S. M., Stanton M. L., Grosberg R. K. 1998. Intrapopulation sex ratio variation in the salt grass *Distichlis spicata*. Am. Nat. 152: 659-670.

Gallagher, J. L. 1975. Effect of an ammonium nitrate pulse on the growth and elemental composition of natural stands of *Spartina alterniflora* and *Juncus roemerianus*. Amer. J. Bot. 62: 644-648.

Gallagher J. L., F. G. Somer, D. M. Grant, and D. M. Seliskar. 1988. Persistent differences in two forms of *Spartina alterniflora*: a common garden experiment. Ecology 69: 1005-1008.

Gao, H., and R. G. Zepp. 1998. Factors influencing photoreactions of dissolved organic matter in a coastal river of the southeastern United States. Environ. Sci. Technol. 32:2940-2946.

Giurgevich, J. R. and E. L. Dunn. 1982. Seasonal patterns of daily net photosynthesis, transpiration and net primary productivity of *Juncus roemerianus* and *Spartina alterniflora* in a Georgia salt marsh. Oecologia 52: 404-410.

González, J. M., and M. A. Moran. 1997. Numerical dominance of a group of marine bacteria in the à-subclass of the class Proteobacteria in coastal seawater. Appl. Environ. Microbiol. 63:4237-4242.

Gough, L., J. B. Grace, and K. L. Taylor. 1994. The relationship between species richness and community biomass: the importance of environmental variables. Oikos 70:271-279.

Gough, L, and J. B. Grace. 1998. Effects of flooding, salinity and herbivory on coastal plant communities, Louisiana, United States. Oecologia 117: 527-535.

Graça, M.A.S., S.Y. Newell and R.T. Kneib. 1999. Consumption rates of organic matter and fungal mass of the *Spartina alterniflora* decay system by three species of saltmarsh invertebrates. Mar Biol., in press.

Hagerthy, S. E. and W. C. Kerfoot. 1998. Groundwater flow influences on the biomass and nutrient ratios of epibenthic algae in a north temperate seepage lake. Limnol. Oceanogr. 43: 1227-1242.

Hamilton, M. B. 1997 Genetic fingerprint-inferred subdivision and spatial genetic tests for isolation by distance and adaptation in the coastal plant *Limonium carolinianum*. Evolution 51: 1457-1468.

Harris, D.C. 1980. Survey of the intertidal and subtidal oyster resources of the Georgia coast. GA Dept. of Natural Res., Coastal Res. Div., Project # 2-234-R. 44 pp.

Hester, M. W., I. A. Mendelssohn and K. L. McKee. 1998. Intraspecific variation in salt tolerance and morphology in *Panicum hemitomon* and *Spartina alterniflora* (Poaceae). Int. J. Plant Sci. 159: 127-138.

Hodson, R. E., R. Benner, and A. E. Maccubbin. 1983. Transformations and fate of lignocellulosic detritus in marine environments. pp. 185-195. In: T. A. Oxley and S. Barry, eds. Biodeterioration 5. John Wiley and Sons, NY.

Hodson R. E., W. A. Dustman, R. P. Garg, and M. A. Moran. 1995. *In situ* PCR for visualization of microscale distribution of specific genes and gene products in prokaryotic communities. Appl. Environ. Microbiol. 61:4074-4082.

Hughes, T. P. 1989. Community structure and diversity of coral reefs: the role of history. Ecology 70: 275-279.

Hwang, Y. H. and J. T. Morris. 1994. Whole-plant gas-exchange responses of *Spartina alterniflora* (Poaceae) to a range of constant and transient salinities. Am. J. Bot. 81: 659-665.

Incze, L. S., L. M. Mayer, E. B. Sherr and S. A. Macko. 1982. Carbon inputs to bivalve mollusks: A comparison of two estuaries. Can. J. Fish Aquat. Sci. 39: 1348-1352.

Ingram, B. L., J. C. Ingle, and M. E. Conrad. 1996. Isotopic records of pre-historic salinity and river flow in San Francisco Bay estuary. pp. 36-61. In: San Francisco Bay: the ecosystem. J. T. Hollibaugh, ed. Pacific Division, AAAS.

Joint, I. R. 1984. The microbial ecology of the Bristol Channel. Mar. Pollut. Bull. 15:62-66.

Joye, S., S. Smith, J. Hollibaugh, and J. Paerl. 1996. Estimating denitrification rates in estuarine sediments: A comparison of stoichiometric and acetylene based methods. Biogeochem. 33:197-215.

Kana, T. M., C. Darkangelo, M. D. Hunt, J. B. Oldham, G. E. Bennett, and J. C. Cornwell. 1994. Membrane inlet mass spectrometer for rapid high-precision determination of N_2, O_2, and Ar in environmental water samples. Anal. Chem. 66: 4166-4170.

Kana, T. M., M. B. Sullivan, J. C. Cornwell and K. Groszkowski. 1998. Denitrification in estuarine sediments determined by membrane inlet mass spectrometry. Limnol Oceanogr. 43:334-339.

Kapolnai, A., F. E. Werner and J. O. Blanton. 1996. Circulation, mixing and exchange processes in the vicinity of tidal inlets: a numerical study. J. Geophys. Res. 101: 14,253-14,268.

Kirchman, D. L., E. K'nees, and R. E. Hodson. 1985. Leucine incorporation and its potential as a measure of protein synthesis by bacteria in natural aquatic systems. Appl. Environ. Microbiol. 49: 599-607.

Kneib, R. T. 1997. The role of tidal marshes in the ecology of estuarine nekton. Oceanogr. Mar. Biol. 35: 163-220.

Kneib, R. T. 1987. Seasonal abundance, distribution and growth of postlarval and juvenile grass shrimp (*Palaemonetes pugio*) in a Georgia, USA, salt marsh. Mar. Biol. 96:215-223.

Kneib, R. T. 1984. Patterns of invertebrate distribution and abundance in the intertidal salt marsh: causes and questions. Estuaries 7:392-412.

Koroleff, F. 1983. Determination of nutrients. pp. 125-187. In: K. Grasshoff, M. Ehrhardt, and K. Kremling (eds.) Methods of Seawater Analysis. Verlag Chemie, NY.

Krumbien, W. E., D. M. Paterson, and L. J. Stal. 1994. Biostabilization of sediments. BIS Press.

Kudoh H, and D. F. Wigham. 1997. Microgeographic genetic structure and gene flow in *Hibiscus moscheutos* (Malvaceae) populations. Am. J. Bot. 84: 1285-1293.

Lee, D. R. 1977 A device for measuring seepage flux in lakes and estuaries. Limnol. Oceanogr. 22: 140-147.

Linthurst, R. A. and E. D. Seneca. 1981. Aeration, nitrogen and salinity as determinants of *Spartina alterniflora* Loisel growth response. Estuaries 4: 53-63.

Linton, T. 1968. Inventory of the intertidal oyster resources in Georgia. pp. 69-73. In: Linton, T. (ed.) Feasibility study of the methods for improving oyster production in Georgia. Completion report 2-10-R. Marine Fisheries Div., GA Game and Fish Comm. and the Univ. of GA.

Liu W.-T., Marsh T. L., Cheng H., and and L. J. Forney. 1997. Characterization of microbial diversity by determining terminal restriction fragment length polymorphisms of genes encoding for 16S rRNA. Appl. Environ. Microbiol. 63:4516-4522.

Livingston, R. J. 1987. Field sampling in estuaries: The relationship of scale to variability. Estuaries 10:194-207.

Lynch, D. R. and F. E. Werner. 1991. 3-Dimensional hydrodynamics on finite-elements: 2. Nonlinear time-stepping model. Int. J. Num. Meth. Fluids 12:507-533.

Lyons T. W. and R. A. Berner. 1992. Carbon-sulfur-iron systematics of the uppermost deep-water sediments of the Black Sea. Chem. Geol. 99:1-27.

MacIntyre, H. L., R. J. Geider and D. C. Miller. 1996. Microphytobenthos: The ecological role of the "secret garden" of unvegetated, shallow-water marine habitats. I. Distribution, abundance and primary production. Estuaries 19:186-201.

Meile, C., Koretsky, C., Van Cappellen, P. and J. Kostka. 1999. Spatial and temporal variations in bioirrigation: An inverse approach (Extended Abstract). Proc. 5th Internat. Symp. on the Geochemistry of the Earth's Surface, Aug. 16-20, 1999, Reykjavik, Iceland.

Miller, W. L., and M. A. Moran. 1997. Interaction of photochemical and microbial processes in the degradation of refractory dissolved organic matter from a coastal marine environment. Limnol. Oceanogr. 42:1317-1324.

Mitsch, W. J. and J. G. Gosselink. 1993. Wetlands. Van Nostrand Reinhold, New York.

Moran, M. A., and R. G. Zepp. 1997. Role of photoreactions in the formation of biologically labile compounds from dissolved organic matter. Limnol. Oceanogr. 42: 1307-1316.

Moran, M. A. and R. G. Zepp. 2000. UV effects on microbes and microbial processes. In: Microbial Ecology of the Oceans, D. L. Kirchman. John Wiley and Sons. In press.

Moran, M. A., Sheldon, W. M., Jr., and Sheldon, J. E. 1999. Biodegradation of riverine dissolved organic carbon in five estuaries of the southeastern United States. Estuaries 22: 55-64.

Morris, J. T. and B. Haskin. 1990. A 5-yr record of aerial primary production and stand characteristics of *Spartina alterniflora*. Ecology 71: 2209-2217.

Murray A. E., J. T. Hollibaugh, and C. Orrego. 1996. Phylogenetic composition of bacterioplankton from two California estuaries compared by denaturing gradient gel electrophoresis of 16S rDNA fragments. Appl. Environ. Microbiol. 62:2676-2680.

Muyzer G., E. C. D. Wall, and A. G. Uitterlinden. 1993. Profiling of complex microbial populations by denaturing gradient gel electrophoresis of polymerase chain reaction-amplified genes coding for 16S rDNA fragments. Appl. Environ. Microbiol. 59: 695-700.

Newell, S. Y., and R. D. Fallon. 1989. Litterbags, leaf tags, and decay of nonabscised intertidal leaves. Can. J. Bot. 67:2324-2327.

Newell, S. Y. 1993a. Decomposition of shoots of a saltmarsh grass; methodology and dynamics of microbial assemblages. Adv. Microb. Ecol. 13:301-326.

Newell, S.Y. 1993b. Membrane-containing fungal mass and fungal specific growth rate in natural samples. pp. 579-586. In: P.F. Kemp, B.F. Sherr, E.B. Sherr and J.J. Cole (eds.). Handbook of methods in aquatic microbial ecology. Lewis, Boca Raton, FL.

Newell, S. Y. 1994. Ecomethodology for organoosmotrophs, prokaryotic unicellular versus eukaryotic mycelial. Microb. Ecol. 28:151-157.

Newell, S. Y. and J. Wasowski. 1995. Sexual productivity and spring intramarsh distribution of a key salt-marsh microbial secondary producer. Estuaries 18:241-249.

Newell, S. Y., M. A. Moran, R. J. Wicks, and R. E. Hodson. 1995. Productivities of microbial decomposers during early stages of decomposition of shoots of a freshwater sedge. Freshwater Biol. 34:135-148.

Newell, S. Y. 1996. Established and potential impacts of eukaryotic mycelial decomposers in marine/terrestrial ecotones. J. Exp. Mar. Biol. Ecol. 200:187-206.

Newell, S. Y. and L. A. Palm. 1998. Responses of bacterial assemblages on standing decaying blades of smooth cordgrass to additions of water and nitrogen. Int. Rev. Hydrobiol. 83:115-122.

Newell, S. Y. and V. D. Wall. 1998. Response of saltmarsh fungi to presence of mercury and polychlorinated biphenyls at a Superfund site. Mycologia 90:777-784.

Newell, S. Y. and D. Porter. 1999. Microbial secondary production from saltmarsh-grass shoots, and its known and potential fates. in press. In: M.P. Weinstein and D.A. Kreeger. Concepts and controversies in tidal marsh ecology. Kluwer, Amsterdam.

Newell, S. Y. 2000. Methods for determining biomass and productivity of mycelial marine fungi, in press. In: K. D. Hyde and E. B. G. Jones (eds.). Techniques for the study of marine fungi. Wiley, NY.

Odum, E. P. 1969. The strategy of ecosystem development. Science 164: 262-269.

Odum, E. P. 1971. Fundamentals of Ecology. Saunders, PA.

Odum, E. P. 1974. Halophytes, energetics and ecosystems. In, Ecology of halophytes, R. J. Reimold and W. H. Queen (eds.), Academic Press, NY.

Odum, E. P. 1980. The status of three ecosystem-level hypotheses regarding salt-marsh estuaries: tidal subsidy, outwelling, and detritus-based food chains. *In* V. S. Kennedy [ed.], Estuarine Perspectives. Academic Press, NY

Odum, E. P., and Fanning, M. E. 1973. "Comparison of the productivity of *Spartina alterniflora* and *Spartina cynosuroides* in Georgia coastal marshes." Bull. GA Acad. Sci. 31:1-12.

Odum, W. E. 1988. Comparative ecology of tidal freshwater and salt marshes. Ann. Rev. Ecol. Syst. 19:147-176.

Odum, W. E., E. P. Odum and H. T. Odum. 1995. Nature's pulsing paradigm. Estuaries 18: 547-555.

Paterson, D. M. 1994. Microbiological mediation of sediment structure and behavior, p. 97-109. In: L. J. Stal and P. Caiumette (eds.). Microbial Mats. NATO ASI Ser. 35.

Paterson, D. M. 1997. Biological mediation of sediment erodibility: Ecology and physical dynamics. p. 215-229. In: Proc. 4th Nearshore and Estuarine Cohesive Sediment Transport Conf., INTERCOH '94, July 1994, Wallinford, U.K.

Paterson, D. M. and G. J. C. Underwood. 1992. The mudflat ecosystem and epipelagic diatoms. Proc. Bristol. Nat. Soc. 50: 74-82.

Paerl, H. W. and M. L. Fogel. 1994. Isotopic characterization of atmospheric nitrogen inputs as sources of enhanced primary production in coastal Atlantic Ocean waters. Mar. Biol. 119:635-645.

Pezeshki, S. R. 1997. Photosynthesis and root growth in *Spartina alterniflora* in relation to root growth aeration. Photosynthetica 34: 107-114.

Pezeshki, S. R and R. D. DeLaune. 1991. A comparative-study of aboveground productivity of dominant United-States Gulf-Coast marsh species. J. Veg. Sci. 2: 331-338.

Pezeshki, S. R and R. D. DeLaune. 1995. Variations in response of 2 US Gulf-Coast populations of *Spartina alterniflora* to hypersalinity. J. Coast. Res. 11: 89-95.

Pinckney, J. L. and R. G. Zingmark. 1993. Modeling the annual production of intertidal benthic microalgae in estuarine ecosystems. J. Phycol. 29: 396-407.

Pomeroy, L. R., W. M. Darley, E. L. Dunn, J. L. Gallagher, E. B. Haines, and D. M. Whitney. 1981. Primary production. pp.39-67. In: L. R. Pomeroy, and R. G. Wiegert. The ecology of a salt marsh. Springer-Verlag, NY.

Pomeroy, L. R., J. E. Sheldon, and W. M. Sheldon. 1994. Changes in bacterial numbers and leucine assimilation during estimations of microbial respiratory rates in seawater by the precision winkler method. Appl. Env. Microbiol. 60: 328-332.

Press, W.H., B. P. Flannery, S. A. Tenkolsky, and W. T. Uetterling. 1989. Numerical recipes. Cambridge Univ. Press, United Kingdom. 702 pp.

Raiswell, R. and D. E. Canfield. 1996. Rates of reaction between silicate iron and dissolved sulfide in Peru Margin sediments. Geochim. Cosmochim. Acta 60: 2777-2787.

Rapport, D.J., W.G. Whitford and M. Hilden. 1998. Common patterns of ecosystem breakdown under stress. Environ. Monitor. Assess. 51:171-178.

Ray, S.M. 1963. A review of the culture method for detecting *Dermocystidium marinum*, with suggested modifications and precautions. Proc. Natl. Shellfish. Assoc. 54: 389-404.

Reise, K. 1985. Tidal flat ecology: An experimental approach to species interactions. Springer, NY.

Revsbech, N. P. and B. B. Jørgensen. 1986. Microelectrodes: their use in microbial ecology. Adv. Microb. Ecol. 9: 293-352.

Revsbech, N. P., P. B. Christensen and L. P. Nielsen. 1989. Microelectrode analysis of photosynthesis and respiratory processes in microbial mats, pp. 153-163. In: Y. Cohen and H. Rosenburg (eds.), Microbial mats: Physiological ecology of benthic microbial communities. Am. Soc. Microbiol., Washington, D.C.

Robinson, M. A. and D. L. Gallagher. 1999. A model of ground water discharge from an unconfined coastal aquifer. Ground Water 37:80-87.

Ruttenberg, K. C. 1992. Development of a sequential extraction method for different forms of phosphorus in marine sediments. Limnol. Oceanogr. 37: 1460-1482.

Schubauer, J. P. and C. S. Hopkinson. 1984. Above- and belowground emergent macrophyte production and turnover in a coastal marsh ecosystem, Georgia. Limnol. Oceanogr. 29: 1052-1065.

Schultz, G. M. and C. Ruppel. 1998. Characterization of a Pleistocene-Holocene barrier island aquifer system from hydrological and noninvasive geophysical methods, Sapelo Island, Georgia, EOS Trans Amer. Geophys. Union 79: S96.

Schultz, G. M., and C. Ruppel 1999. Mapping and monitoring of the spatio-temporal variations in a tidally forced coastal aquifer system, EOS Trans. Amer. Geophys. Union, Spring Meeting.

Shaw, R. D. and E. E. Prepas. 1989. Anomalous, short-term influx of water into seepage meters. Limnol. Oceanogr. 34:1343-1351.

Silander J. A. 1979. Microevolution and clone structure in *Spartina patens*. Science 203: 658-659.

Silander J. A. 1984. The genetic basis of the ecological amplitude of *Spartina patens*. III Allozyme variation. Bot. Gaz. 145: 569-577.

Silander J. A. 1985. The genetic basis of the ecological amplitude of *Spartina patens*. II. Variance and correlation analysis. Evolution 39: 1034-1052.

Shea, M. L. 1975. Biochemical and transplant studies of the growth form of *Spartina alterniflora* on Connecticut salt marshes. Ecology 56: 461-466.

Smith, S. V., and J. T. Hollibaugh. 1997. Annual cycle and interannual variability of ecosystem metabolism in a temperate climate embayment. Ecol. Monogr. 67: 509-533.

Smith S. V., R. M. Chambers, and J. T. Hollibaugh. 1996. Dissolved and particulate nutrient transport through a coastal watershed-estuary system. J. Hydrol. 176: 181-203.

Solorzano, L. and J. H. Sharp. 1980. Determination of total dissolved phosphorus and particulate phosphorus in natural waters. Limnol. Oceanogr. 25: 754-758.

Steever, E. Z., R. S. Warren, and W. A. Niering. 1976. Tidal energy subsidy and standing crop production of *Spartina alterniflora*. Est. Coast. Mar. Sci. 4:473-478.

Stiller J. W., and A. L. Denton. 1995. 100 years of *Spartina alterniflora* (Poaceae) in Willapa Bay Washington- random amplified DNA analysis of an invasive population. Molecular Ecology 4: 355-363.

Stookey, L. L. 1970. Ferrozine – A new spectrophotometric reagent for iron. Anal. Chem. 42:779-781.

Teal, J. M. and B. L. Howes. 1996. Interannual variability of a salt-marsh ecosystem. Limnol. Oceanogr. 41:802-809.

Turner, R. E. 1976. Geographic variations in salt marsh macrophyte production: a review. Contrib. Mar. Sci. 20:47-68.

Underwood, G. J. C. and D. M. Paterson. 1993. Seasonal changes in diatom biomass, sediment stability and biogenic stabilization in the Severn Estuary, U.K. J. Mar. Biol. Assoc. U.K. 73:871-887.

Ungar, I. 1991. Ecophysiology of vascular halophytes. CRC Press, Boca Raton, FL.

Valiela, I. and J. M. Teal. 1974. Nutrient limitation in salt marsh vegetation. In, R. J. Reimold and W. H. Queen (eds.) Ecology of halophytes, Academic Press, NY.

Valiela, I., J. C. McClelland, J. Hauxwell, P. J. Behr, D. Hersh, and K. Foreman. 1997. Macroalgal blooms in shallow estuaries - controls and ecophysiological and ecosystem consequences. Limnol. Oceanogr. 42: 1105-1118.

Voss, C.I. 1984. A finite-element simulation model for saturated-unsaturated, fluid-density-dependent ground-water flow with energy transport or chemically-reactive single-species solute transport, U.S. Geol. Surv. Water-Resources Investigations Report, 84-4369, 409 pp.

Whitney, D. E. and W. M. Darley. 1983. The effect of light intensity upon salt marsh benthic microalgal photosynthesis. Mar. Biol. 75:249-252.

Wiegert, R.G. 1993. Multicompartmental models. pp. 345-384. In: J.C. Frye (ed.). Biological data analysis: A practical approach. Oxford Univ. Press.

Wiegert, R.G., M. Alber, C. Alexander, J. Blanton, A. Chalmers, R. Hodson, M. A. Moran, L. Pomeroy, and W. Wiebe. 1999. The Georgia Rivers LMER Program: A comparative study of five coastal rivers. Limnologica 29: 286-292.

Williams, R. B. 1962. The ecology of diatom populations in a Georgia salt marsh. Ph.D. Dissertation. Harvard University, Cambridge, MA.

Yallop, M. L., B. Dewinder, D. M. Paterson, and L. J. Stal. 1994. Comparative structure, primary production and biogenic stabilization of cohesive and noncohesive marine-sediments inhabited by microphytobenthos. Est. Coast. Shelf Sci. 39: 565-582.