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 04-23	FOR NSF USE ONLY
FOR CONSIDERATION BY NSF ORGANIZATION UNIT(S) (Indicate the most specific unit known, i.e. program, division, etc.) **OCE - BIOLOGICAL OCEANOGRAPHY**	NSF PROPOSAL NUMBER **0620962**

DATE RECEIVED	NUMBER OF COPIES	DIVISION ASSIGNED	FUND CODE	DUNS# (Data Universal Numbering System)	FILE LOCATION
02/01/2006	5	06040000 OCE	1650	004315578	02/06/2006 3:52pm S

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 ACRONYM(S)
	9982133	

NAME OF ORGANIZATION TO WHICH AWARD SHOULD BE MADE **University of Georgia Research Foundation Inc**	ADDRESS OF AWARDEE ORGANIZATION, INCLUDING 9 DIGIT ZIP CODE **University of Georgia Research Foundation Inc** **616 Boyd GSRC** **Athens, GA. 306027411**
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
PERFORMING ORGANIZATION CODE (IF KNOWN)	

IS AWARDEE ORGANIZATION (Check All That Apply) (See GPG II.C For Definitions) ☐ SMALL BUSINESS ☐ FOR-PROFIT ORGANIZATION ☐ MINORITY BUSINESS ☐ WOMAN-OWNED BUSINESS ☐ IF THIS IS A PRELIMINARY PROPOSAL THEN CHECK HERE

TITLE OF PROPOSED PROJECT **LTER - Georgia Land/Ocean Margin Ecosystem**

REQUESTED AMOUNT	PROPOSED DURATION (1-60 MONTHS)	REQUESTED STARTING DATE	SHOW RELATED PRELIMINARY PROPOSAL NO. IF APPLICABLE
$ 387,450	0 months		

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

☐ BEGINNING INVESTIGATOR (GPG I.A)
☐ DISCLOSURE OF LOBBYING ACTIVITIES (GPG II.C)
☐ PROPRIETARY & PRIVILEGED INFORMATION (GPG I.B, II.C.1.d)
☐ HISTORIC PLACES (GPG II.C.2.j)
☐ SMALL GRANT FOR EXPLOR. RESEARCH (SGER) (GPG II.D.1)
☐ VERTEBRATE ANIMALS (GPG II.D.5) IACUC App. Date ________
☐ HUMAN SUBJECTS (GPG II.D.6)
Exemption Subsection ________ or IRB App. Date ________
☐ INTERNATIONAL COOPERATIVE ACTIVITIES: COUNTRY/COUNTRIES INVOLVED (GPG II.C.2.j)
____
☐ HIGH RESOLUTION GRAPHICS/OTHER GRAPHICS WHERE EXACT COLOR REPRESENTATION IS REQUIRED FOR PROPER INTERPRETATION (GPG I.G.1)

PI/PD DEPARTMENT **Department of Marine Sciences**	PI/PD POSTAL ADDRESS **Marine Sciences Bldg** **Athens, GA 306027411** **United States**
PI/PD FAX NUMBER **706-542-5888**	

NAMES (TYPED)	High Degree	Yr of Degree	Telephone Number	Electronic Mail Address
PI/PD NAME **James T Hollibaugh**	PhD	1977	706-542-3016	aquadoc@uga.edu
CO-PI/PD				
CO-PI/PD				
CO-PI/PD				
CO-PI/PD				

Electronic Signature

Project Summary

Intellectual Merit: The Georgia Coastal Ecosystems (GCE) LTER program, located on the central Georgia coast, was established in 2000. The study domain encompasses three adjacent sounds (Altamaha, Doboy, Sapelo) and includes upland (mainland, barrier islands, marsh hammocks), intertidal (fresh, brackish and salt marsh) and submerged (river, estuary, continental shelf) habitats. Patterns and processes in this complex landscape vary spatially within and between sites, and temporally on multiple scales (tidal, diurnal, seasonal, and interannual). Overlain on this spatial and temporal variation are long-term trends caused by climate change, sea level rise, and human alterations of the landscape. These long-term trends are likely to manifest in many ways, including changes in water quality, river discharge, runoff and tidal inundation patterns throughout the estuarine landscape. The overarching goal of the GCE program is **to understand the mechanisms by which variation in the quality, source and amount of both fresh and salt water create temporal and spatial variability in estuarine habitats and processes, in order to predict directional changes that will occur in response to long-term shifts in estuarine salinity patterns**.

This supplement proposal was requested by NSF to align the funding cycle of GCE with that of other LTER sites. We will pursue three major goals while transitioning from GCE-I to GCE-II during the 6.5 months covered by this supplement. These are to: 1) continue our core operations, including site management, information management, monitoring and outreach; 2) extend our directed studies in the Duplin River by completing an inundation analysis of the Duplin River watershed, obtaining remotely-sensed information on groundwater input and plant composition and productivity, and establishing a GIS framework for this information; and 3) begin to describe the population and genetic structure of plant and animal populations across the GCE domain. Goals two and three will feed directly into our research efforts during GCE-II. In addition, we will hire two new technicians (an assistant IM and a second field technician) and begin the process of leadership transition from Hollibaugh to Alber. These personnel changes will lay the administrative groundwork for implementing the research goals of our GCE-II proposal.

Broader impacts: The goal of GCE outreach is to enhance scientific understanding of Georgia coastal ecosystems by teachers and students, coastal managers, and the general public. The GCE schoolyard program is built around long-term contact and mentoring of educators, and has involved 40 teachers to date. At the college level, both undergraduate and graduate students are routinely incorporated into our work, and several investigators have integrated GCE research into the classroom. To reach coastal managers, we partner with the Georgia Coastal Research Council (GCRC) to promote science-based management of Georgia coastal resources by facilitating information transfer between scientists and managers. The GCRC has representation from 9 Universities, 6 Federal agencies, and 4 State and regional agencies. It hosts workshops, assists management agencies with scientific assessments, and distributes information on coastal issues. To reach the general public, GCE scientists routinely participate in public meetings and workshops, and we partner with non-profit organizations on the Georgia coast to address questions of public interest. Data collected by the GCE-LTER project can be accessed by other scientists and the general public via our website (http://gce-lter.marsci.uga.edu/lter/), which uses a state-of-the-art information system to manage and display information on study sites, research, taxonomy, data sets, publications, and project administration.

GCE bridge funding supplement request

This supplemental funding request is submitted at the request of Phil Taylor, director of Biological Oceanography. The purpose of the supplement is to align the GCE funding cycle with that of other LTER sites and thereby facilitate NSF administration of these long-term projects. The supplement provides funding between the ending date of the current GCE-I grant (April 30, 2006) and the proposed starting date of GCE-II (November 15, 2006). As instructed, we have budgeted for thirteen 2-week periods, pro-rated at the current GCE funding rate of $700,000/y.

Below we summarize results to-date from GCE-I, briefly introduce our general research plan for GCE-II, and then explain how the bridge supplement will be used to transition between the two projects.

Results to date from GCE-I

The Georgia Coastal Ecosystems (GCE) LTER project, located on the central Georgia coast, was established in 2000 (this is our first renewal proposal). The GCE domain is sited along three adjacent sounds (Altamaha, Doboy, Sapelo) and encompasses upland (mainland, barrier islands, marsh hammocks), intertidal (fresh, brackish and salt marsh) and submerged (river, estuary, continental shelf) habitats. Patterns and processes in this complex landscape vary on multiple scales, both spatially (within and between sites) and temporally (tidal, diurnal, seasonal, and interannual). Overlain on this spatial and temporal variation are long-term trends caused by increasing human population density, which influences land and water use patterns; climate change, which affects sea level rise and precipitation patterns; and other alterations, such as dredging or changes in fishing strategies. The goal of the GCE program is **to understand the mechanisms by which variation in the quality, source and amount of both fresh and salt water create temporal and spatial variability in estuarine habitats and processes, in order to predict directional changes that will occur in response to long-term shifts in estuarine salinity patterns**. To do this, we seek to understand how coastal processes respond to environmental forcing, and to determine which scales of variability are of primary importance.

During our first funding cycle, we developed a program of research activity addressing the five LTER core areas (primary production, populations, organic matter cycling, inorganic nutrients, disturbance), established information management and project management protocols, participated in LTER network activities, and established a strong outreach program. Since 2000, GCE researchers have produced over 100 publications, including 19 theses and dissertations. These accomplishments have created a strong foundation for the ambitious plan we propose for the next funding cycle.

1. Scientific activities. Both the monitoring and directed research activities of GCE-I were focused on evaluating temporal and spatial variation in environmental forcing and ecosystem response. Monitoring occurs at a grid of ten sites that are distributed along an onshore-offshore gradient across our domain and span the full range from tidal fresh to tidal marine habitats. The program was designed to support all GCE research areas by documenting temporal and spatial variation in key ecosystem variables, including measurements of the atmosphere, groundwater, riverine inputs, the water column within the estuaries, and intertidal areas (marsh sediments, vegetation, and invertebrates). To support this program, we installed a variety of permanent plots and instruments, often in collaboration with other organizations (Sapleo Island National Estuarine Research Reserve, United States Geological Survey, National Atmospheric Deposition Program). Monitoring data are available on our web-accessible public data catalog. We have also identified relevant long-term datasets collected by these and other agencies (National Oceanographic and Atmospheric Administration, National Weather Service) and are making these available through our data portal (http://gce-lter.marsci.uga.edu/portal/monitoring.htm).

Our research program has examined a variety of estuarine processes at temporal scales ranging from hourly (variation in turbulent mixing; Kang and Di Iorio 2005) to decadal (changes in Altamaha River discharge and chemistry; Weston et al. submitted.), and at spatial scales ranging from individual plots (plant genetics; Richards et al. 2004, 2005) to the continental shelf (carbon export; Wang and Cai 2004) to the entire Atlantic Coast (latitudinal variation in herbivory and decomposition; Newell et al. 2000; Pennings and Silliman 2005). We have worked on topics ranging from molecular taxonomy (Buchan et al. 2002) to microbial community ecology (Lyons et al. 2005) to trophic interactions (Thoresen and Alber, submitted; Zimmer et al. 2004). Here, we highlight the results of selected studies that evaluated changes in water inflow (river, ground, or ocean water) and the effects of these changes on marsh and estuarine processes, because the current proposal builds directly on these topics.

Freshwater-marine gradients. The Altamaha River is the largest source of freshwater to the GCE domain. Median flow from the Altamaha is 245 m^3s^{-1}, although flows vary considerably over both seasonal and interannual scales. On an annual scale, discharge peaks in Feb-April and is low during the summer. The early years of GCE-I encompassed most of a 4-year drought (1999-2002) that reduced median discharge to 81 m^3 s^{-1}, which was reflected in increased salinities at all GCE sites. Nutrient concentrations vary with river discharge: Nitrate + nitrite (NO_x) dominates dissolved nitrogen flux during low river discharge whereas dissolved organic nitrogen (DON) increases in importance during high flow (Weston et al. 2003).

Freshwater inflow patterns, along with tidal forces, determine salt distributions in the GCE domain. The Georgia coast has a semi-diurnal tidal regime, with a tidal height of 1.8 m (neap) to 2.4 m (spring). The tide reaches the ocean stations within 10 minutes of the same phase, and propagates to the upstream edge of the domain within about 1.5 h (Blanton unpublished). The main tidal constituent is the semi-diurnal lunar (M2), which exceeds other tidal constituents 10-fold. Frictional forces induced by bottom drag produce the quarter-diurnal M4 constituent, which distorts the tidal wave as it progresses upstream (Friedrichs and Aubrey 1988; Blanton et al. 2002). The relative phase of M4 to M2 indicates that the ebb tide is about the same length and strength as the flood in Sapelo Sound, whereas Altamaha Sound is dominated by ebb flows due to pressure gradients associated with freshwater discharge.

Differences in the magnitudes of the fresh and saltwater flows across time and space affect a variety of ecosystem processes, including water chemistry, soil accumulation, biogeochemical cycling and the ecology of multiple taxa and interactions (Alber 2002). For example, dissolved inorganic nitrogen concentrations are highest in Altamaha Sound (implying a riverine source), whereas the highest silicate concentrations are observed in Sapelo Sound with decreasing concentrations upstream (suggesting an oceanic source). Both dissolved organic carbon (DOC) concentrations and the ratio of dissolved inorganic nitrogen to phosphorus

(DIN:DIP) vary seasonally in Altamaha Sound as a result of seasonality in river discharge and within-sound biological processing. Carbon cycling is also affected by variations in salinity: Weston et al. (2006, in press) found that sulfate reduction rates in soils increased at higher salinities, resulting in doubled decomposition rates. These data help explain observed decreases in rates of soil accumulation (burial of C and N) at high salinity (and sulfate) vs. low salinity (and sulfate) sites (Craft submitted). *A major goal of GCE-II will be to separate, via experiments and modeling, the roles of salinity versus sulfate in driving longitudinal (down-estuary) patterns of biogeochemistry, soil accumulation, and species composition.*

Groundwater inflows. Groundwater enters the GCE domain via sub-marsh flow, at seepage fronts, and as baseflow to tidal creeks. During GCE-I we used a combination of geophysical and hydrological methods to determine hydraulic conductivity across the upland-marsh interface. We installed monitoring well fields at three sites (GCE 3, 4, 10), characterized sediments, and used noninvasive methods to delineate water levels and interfaces (electromagnetic data, ground-penetrating radar) (Schultz and Ruppel 2005). We found considerable heterogeneity in hydraulic conductivity both within (Fulton et al. 2001) and among sites, depending on microtopography, soil type, the morphology of the creek/marsh interface, and the degree of macropore development (Schultz and Ruppel 2002). Schultz and Ruppel (2002) concluded that a significant fraction of groundwater discharge into estuaries occurs as either baseflow into tidal creeks or as submarsh flow (although the relative importance of these two pathways has not yet been determined).

The chemistry of groundwater differs from that of surface water (Snyder et al. 2004; Joye et al. 2006, submitted). Groundwater from Sapelo Island was higher in DIP and organic C, N and P than was Altamaha River water (Porubsky et al., in prep.). The lunar cycle affected water chemistry: groundwater was more saline and reduced during neap tides and less saline and more oxidized during spring tides (Porubsky et al., in prep.). This redox switch resulted in higher concentrations of nitrate in groundwater on spring tides and higher concentrations of ammonium, phosphate, reduced iron and hydrogen sulfide on neap tides. The biogeochemical mechanisms underlying this switch are under investigation. Because groundwater flow alters porewater salinity and nutrient chemistry, it is likely to be an important factor in determining the productivity and distribution of plants and animals. *A second major goal of GCE-II will be to test hypotheses about the importance of groundwater-derived inputs of freshwater to adjacent marsh systems.*

Population and genetic responses to abiotic variation. Marsh plants respond to spatial variation in abiotic conditions at multiple scales. At the scale of individual sites, plants respond to environmental gradients through phenotypic plasticity rather than adaptation (Richards et al. 2005). Among sites, zonation patterns differed as a function of water column salinity and the nature of the marsh-upland interface (Pennings, unpublished). Along an estuary, plant community types shifted from salt to brackish to freshwater, with some evidence that these shifts correspond to high-tide (as opposed to average) salinity (Higinbotham et al. 2004). The factors structuring marsh plant communities differed between GA and New England because of geographic differences in soil salinities and salinity tolerances of the flora (Pennings et al. 2003; 2005). Photosynthesis varied as a function of the daily and monthly tidal cycles, and end-of-season biomass varied among years as a function of salinity (Pennings unpublished). The severe drought in 1999-2002 altered plant zonation patterns in individual marshes (Pennings unpublished), altered the distribution of marsh community types along the estuary (White 2004), and likely contributed to widespread marsh "dieback" (Ogburn and Alber in press).

Marsh invertebrates also show striking differences in abundance among sites and over time. Some species are more common where larval influx from the ocean is likely to be high; others are associated with low (or high) salinity habitats; and others appear to require adjacent upland habitats (Bishop and Pennings unpublished). The 1999-2002 drought sharply reduced populations of estuarine macroinvertebrates typically found in low-salinity conditions. Biomass of fungi in decomposing leaves varied little among years or marsh elevation, but peaked in winter and spring (Newell 2001). Fungal biomass did not vary within a plant species across the estuarine salinity gradient, or across latitude, but plant species typical of brackish and freshwater sites had lower fungal contents (Newell et al. 2000; Newell 2003). Plants varied in palatability to herbivores across edaphic gradients within sites (Goranson et al. 2004), and also geographically (Pennings et al. 2001; Pennings and Silliman 2005; Salgado and Pennings 2005). *A third major goal of GCE-II will be to determine the relative contributions of recruitment and post-recruitment performance in creating spatial patterns in plant and animal abundance and genetic structure across the GCE landscape.*

Long-term changes. We expect that anthropogenically-driven changes in surface flow (increased water withdrawal), decreases in groundwater infiltration (increases in overland runoff associated with development), and increases in seawater inflow (sea level rise) will combine to affect abiotic conditions (i.e. nutrient and sulfate concentrations, salinity, soil moisture), that will in turn affect estuarine resources (species composition, abundance and distribution; primary and secondary production). These predicted shifts in the quality, source and amount of both fresh and saltwater to the study domain will result in long-term directional changes in ecosystem processes. *Our monitoring program is designed to detect these long-term changes against a spatially and temporally varying background, and to support hypothesis-driven experimental work designed to unravel their mechanisms and determine their importance.*

2. Information management. Despite being a new project, we have developed an IM approach that meets the highest LTER IM standards (Section 4). We have established a comprehensive information system (GCE-IS), based on relational database and dynamic web application technology, to manage and display information on study sites, research, taxonomy, data sets, publications, and project administration. We have developed a suite of software tools for metadata-based data processing, quality control, and analysis, and coupled these tools with the GCE-IS to support dynamic metadata generation and automated data distribution via a web-based data catalog and MATLAB client applications. All LTER network standards and protocols are fully supported by the GCE-IS, and EML 2.0 metadata (exceeding Level 5 of the EML Best Practices guidelines) is automatically generated for all data sets (278 as of Dec. 2005). We have also assumed a leadership role in IM at the Network level. Our Information Manager, Wade Sheldon, formerly served on the LTER IM Executive Committee and was recently appointed to the LTER NIS Advisory Committee. He has also led a working group at LNO, served as editor of the LTER DataBits newsletter, and assisted information managers from five other LTER sites in developing EML implementations. He developed the USGS Data Harvesting Service for HydroDB (http://gce-lter.marsci.uga.edu/lter/research/tools/usgs_harvester.htm), co-authored the specification used to harvest EML documents from LTER sites, and pioneered dynamic synchronization of EML metadata with the LNO Metacat server and NBII Metadata Clearinghouse. The rapid adoption of emerging network standards at GCE has also benefited projects such as NCEAS, SEEK and NBII which use GCE metadata and data to design and test the next generation of data discovery and integration tools.

3. Program management. At the beginning of GCE-I, the program was administered by Hollibaugh and Pennings, with Project Director Hollibaugh making most administrative decisions with input from Pennings and other senior co-PIs. As the project matured, and with encouragement from the mid-term site review, we developed a formal Executive Committee (EC) and adopted formal bylaws (Section 3). The program is now governed by the EC, which has assumed responsibility for administration and oversight. The EC communicates electronically on a daily basis and meets several times per year. The full GCE membership meets once per year to review progress and plan upcoming activities. This meeting is attended by our Advisory Committee, which provides input on all aspects of project research and administration. Sub-groups of scientists meet informally throughout the year to work on joint research activities. GCE scientists have obtained more than $6,600,000 in external funding for additional projects that coordinate with the GCE program to achieve shared objectives (see GCE-II proposal Budget Justification).

4. Network participation. We have been in the forefront of network IM activities, as described above and in Sections 4 and 5. We have also participated in several cross-site research activities. Pennings is a member of the cross-site nitrogen fertilization synthesis group, which has published two papers (Pennings et al. 2005; Suding et al. 2005) with two more in preparation. Craft has participated in the working group synthesizing data on organic matter preservation in wetland soils. Research by Newell and Pennings on latitudinal gradients in fungal decomposition and plant-herbivore interactions has compared results from multiple coastal LTER and NERR sites, and Hollibaugh is involved in a similar comparison focused on ammonia oxidation. In GCE-II, we explicitly fund three cross-site comparisons (the cross-site fertilization synthesis group [see GCE-II proposal UH budget justification], the effect of upland habitats on biodiversity in coastal systems [GCE-II proposal Section 2, question 4], and large scale genetic patterns [GCE-II proposal Section 2, question 5]). Finally, several of us (Burd, Sheldon, Hollibaugh, Joye and Alber) participated in LTER Planning Grant activities, and Hollibaugh is on the organizing committee for the upcoming All Scientist's meeting. We are scheduled to host an LTER CC meeting in the spring of 2008.

5. Outreach and Human Resources. Thirty undergraduates and 38 graduate students have participated in GCE research, with 19 graduate students completing degrees. GCE-I involved scientists and students from 5 institutions (UGA, GA Tech, SKIO, IU, UH), and we continue to attract new collaborators from a variety of institutions as we move forward (Section 3). During GCE-I we developed a schoolyard program built around long-term contact and mentoring of educators that has involved 40 teachers to date. Our schoolyard coordinator, Hembree, has raised external funds to almost triple schoolyard funding, made 14 presentations at science education conferences, and co-authored the Education Handbook for system-wide SLTER programs (Section 5). We partnered with the Georgia Coastal Research Council (GCRC) to promote science-based management of Georgia coastal resources by facilitating information transfer between scientists and managers. The GCRC, which is headed by Alber, has 86 affiliated scientists, with representatives from 9 Universities, 6 Federal agencies, and 4 State and regional agencies. The GCRC hosts workshops, assists management agencies with scientific assessments, and distributes information on coastal issues (Section 5). Finally, we have developed partnerships with the Altamaha Riverkeeper, Georgia Department of Natural Resources (DNR), the National Atmospheric Deposition Program (NADP), the Sapelo Island National Estuarine Research Reserve (SINERR), the Nature Conservancy (TNC) and the United States Geological Survey (USGS) to collect data of mutual interest.

General research plan for GCE-II

1. Introduction. The GCE LTER project (**Fig. 1**) is located along three adjacent sounds on the Georgia coast (Altamaha, Doboy, Sapelo) and encompasses upland (mainland, barrier islands, marsh hammocks), intertidal (fresh, brackish and salt marsh) and submerged (river, estuary, continental shelf) habitats. The Altamaha River is the largest source of freshwater to the GCE domain and provides a natural gradient of freshwater inflow to the sites. It drains a watershed of 36,700 km^2 and is relatively unmanipulated (2 dams far upstream, free-flowing for approximately 200 km). On the ocean side, the domain is bounded by the South Atlantic Bight, which extends from Cape Hatteras, NC to West Palm Beach, FL. The broad expanse of the Continental Shelf in this area helps to protect the coast from wave and storm activity but it also serves to funnel the tides, which are semi-diurnal and range in height from 1.8 m (neap) to 2.4 m (spring).

Over the coming decades, the Georgia coast (like all coastal areas) is expected to experience substantial changes due to factors such as climate change, sea level rise, and human alterations of the landscape. In addition, the landscape likely bears legacies of several thousand years of human occupation (Thompson et al. 2004), although these have been poorly documented. These effects are likely to be manifest in many ways, including major changes in runoff and inundation patterns throughout the estuarine landscape. **The overarching goal of the GCE LTER is to understand the mechanisms by which variation in the quality, source and amount of both fresh and salt water create temporal and spatial variability in estuarine habitats and processes, in order to predict directional changes that will occur in response to long-term shifts in estuarine salinity patterns**.

Coastal areas are among the most developed regions on Earth. More than 50% of the U.S. population now lives in coastal counties, which comprise only 17% of the land area (U.S. Commission on Ocean Policy, 2004); a larger fraction of the population impacts these environments intermittently via recreational and vocational activities. Ten thousand new housing units were built in coastal Georgia from 1999 to 2001, and the coastal population is expected to double in the next 25 years (State of the Coast Report, 2004). This increase in population and accompanying land use change affects downstream water quality: over the past 18 y, Verity (2002; Verity et al., submitted) has documented significant increases in the concentrations of nutrients and chlorophyll *a* and significant decreases in oxygen concentrations in Georgia coastal waters. Humans can also affect downstream water delivery either directly, via flow diversion, channel modifications, reservoirs and dams, point source discharges; or indirectly, via changes in land cover, which affect the proportion of overland runoff versus groundwater infiltration. These types of changes are causing coastal managers throughout the world to consider water withdrawal policies that can protect estuarine environments (reviewed in Alber 2002). The state of GA is currently working to set appropriate targets for water permitting that will protect downstream resources, and one of us (Alber) is serving as a technical advisor to the Georgia Environmental Protection Division for this process.

Future climate change will also affect freshwater delivery to the coast (Boesch et al. 2000). Miller and Russell (1992) predicted that the annual average discharge of 25 of the 33 largest rivers of the world would increase under a scenario in which atmospheric CO_2 doubled. In the Altamaha River, one commonly used climate change model (the Hadley model) predicts that flow will increase by as much as 55% by the end of the century, whereas the drier, hotter Canadian model predicts that inflow will decrease (Wolock and McCabe 1999; Boesch et al. 2000). Regardless of the directional change in flow, most models agree that there will be an increase in extreme rainfall events and thus increased variability of freshwater runoff in the future. Despite the uncertainty involved in predicting future inflow changes, there is ample evidence that climate oscillations over interannual and decadal timescales affect the inflow of freshwater to coastal systems. During GCE-I, a 4-year drought (1999-2002) reduced median discharge from 245 to 81 $m^3 s^{-1}$, causing increased salinity and altered water quality throughout the GCE domain. During drought years, concentrations of DON were elevated 2-3 fold above average flow conditions, and DON exceeded DIN by a factor of 2-3. The drought also resulted in upstream shifts in the distribution of both plants and animals along the estuarine gradient (White 2004; Bishop, unpubl.) and has been tied to observations of marsh dieback (Silliman et al. 2005).

Finally, sea level is inexorably rising along the low-gradient coastal plain environments of the world. Under all model scenarios, the rate of sea-level rise is expected to increase over the coming decades as higher global temperatures accelerate both glacial melting and expansion of ocean and coastal waters (IPCC, 2001). In Georgia, sea level has been rising at a rate of 0.3 cm/y over the past 70 years (NOAA 2001). Low-lying intertidal areas are particularly sensitive to these changes, as only slight variations in vertical position can affect large parts of the landscape. Modest increases in sea level increase the productivity of marsh plants and increase rates of marsh accretion (Morris and Haskin 1990; Morris et al. 2002), but rapid rates of sea level rise will “drown“ marshes that cannot accrete fast enough to keep pace with sea level. As the land/water boundary encroaches steadily onto the upland, the increased hydraulic head will cause saltwater to intrude further into coastal aquifers (Michael et al. 2005; Schultz and Ruppel, 2002), changing the quality and quantity of potable groundwater. Rising sea levels will also drive salty surface water further inland, causing fresh and brackish marshes to convert to salt marshes, and will increase the extent of coastal flooding during storm surges from Atlantic hurricanes and Nor’eastern storms.

2. Conceptual model. During GCE-I, we began to describe the patterns of variability in estuarine processes with an emphasis on water inflow as a primary environmental forcing function. The Altamaha River exports large amounts of freshwater to Altamaha Sound. This freshwater can reach adjacent estuarine areas by flowing through the wetland complex or by tidal inputs of the Altamaha plume into other sounds. We found that 75% of the variability in salinity in the Altamaha estuary can be explained by discharge alone (Sheldon and Alber 2005). As one moves from Altamaha to Sapelo Sound the correlation of salinity with discharge has an increasing time lag, from 1 to 8 d (Di Iorio unpublished). However, at site GCE 1 (downstream from a small watershed), salinity is most strongly correlated with local precipitation with a 5.1 d lag, suggesting groundwater inputs. As a result of these differences in freshwater inflow, Altamaha Sound has low and variable salinities, whereas salinities at most sites in Sapelo and

Doboy Sounds are higher and fairly stable. We documented the marked spatial variation in freshwater inflow across the domain and put this information together into a conceptual model of the relative importance of different water flow pathways through the three sounds (**Fig. 2**). This model has allowed us to interpret broad-scale spatial patterns across the domain, such as the differences in decomposition rates between fresh, brackish and salt marshes (**Fig. 3**).

We now propose to add a more detailed understanding of the movement of water between subtidal, intertidal and terrestrial habitats to this conceptualization (**Fig 2**). This expansion takes into account not only freshwater-marine gradients along the longitudinal axis of the estuary, but also the lateral gradients that include tidal exchange on and off the marsh platform and water flow from the upland (in the form of both groundwater and overland runoff), as well as direct precipitation and evapotranspiration. Changes in the quantity or quality of water in any of these flow paths can potentially affect habitat conditions, biogeochemical cycles, and ecosystem dynamics. For example, locations with enhanced groundwater discharge near GCE-10 have higher concentrations of both N and P relative to river or sound water (Porubsky and Joye, unpublished).

During GCE-II, we will continue our focus on patterns of variability, but we will also work to elucidate the mechanisms that underlie this variation and in particular the extent to which gradients in water inflow drive landscape patterns. In so doing, we recognize the necessity of evaluating the interaction of inflow-driven changes with other factors that influence estuarine processes (i.e. geologic setting, organismal interactions, etc.). **The central paradigm of GCE-II is that variability in estuarine ecosystem processes is primarily mediated by the mixture of fresh and salt water flow across the coastal landscape.** The GCE-II proposal seeks to answer 5 main inter-related questions.

In order to be able to understand the effects of external drivers such as climate change, sea level rise, and anthropogenic alterations of the landscape, we need to document their patterns over both time and space. **Question 1 (Q1):** ***What are the long-term patterns of environmental forcing to the coastal zone?***

Variability in external forcing (documented in Q1) is manifest as environmental gradients (e.g., gradients in salinity or nutrients) within the coastal landscape. These environmental gradients cause variations in local biological, chemical, and geological processes, which in turn may feed back to affect environmental gradients. This complex set of interactions produces the observed ecosystem patterns across the landscape. In order to understand these interactions, it is necessary to describe temporal and spatial patterns of biotic and abiotic variables. The variables of interest to us span all five of the LTER core research areas. **Q2:** ***How do the spatial and temporal patterns of biogeochemical processes, primary production, community dynamics, decomposition, and disturbance vary across the estuarine landscape, and how do they relate to environmental gradients?***

The data collected to answer questions 1 and 2 can be used to describe the longitudinal salinity gradient of the estuary over time and space, and examine how well salinity correlates with observed patterns in ecosystem processes. To predict how future changes in salinity distributions might affect the ecosystem, it is necessary to understand the mechanisms that drive these patterns. In particular, we are interested in separating the effects of salt from that of sulfate on ecosystem processes, given that these factors are correlated across the estuarine gradient. **Q3:** ***What are the underlying mechanisms by which the freshwater-saltwater gradient drives ecosystem change along the longitudinal axis of an estuary?*** Similarly, data collected to answer questions 1 and 2 can be used to describe lateral gradients in the intertidal zone (from the creek edge to the marsh/upland interface) and the extent to which they are correlated with changes in groundwater discharge and/or runoff from adjacent uplands. In order to predict how future changes in these inputs might affect coastal ecosystems, it is again necessary to understand the mechanisms that drive these patterns. **Q4:** ***What are the underlying mechanisms by which proximity of marshes to upland habitat drives ecosystem change along lateral gradients in the intertidal zone?***

Populations of plants and animals vary across the estuarine landscape. Some of the variation in population density is likely driven by variations in salinity, as noted above (Questions 3 and 4). However, population density may also be affected by transport mechanisms and larval shadows that affect larval delivery, the presence of adjacent upland habitat, habitat suitability for adults, and competition. **Q5:** ***What is the relative importance of larval transport versus the conditions of the adult environment in determining community and genetic structure across both the longitudinal and lateral gradients of the estuarine landscape?***

The background, rationale and methods for these questions are described in detail in the GCE-II proposal.

Using bridge funding to transition from GCE-I to GCE-II

We will pursue three major goals while transitioning from GCE-I to GCE-II during the six and a half months covered by this bridge funding supplement. These are to: 1) continue our core operations, including site management, information management, monitoring and outreach; 2) extend our directed studies in the Duplin River by completing an inundation analysis of the Duplin River watershed, obtaining remotely-sensed information on groundwater input and plant composition and productivity, and establishing a GIS framework for this information; and 3) begin to describe the population and genetic structure of plant and animal populations across the GCE domain. Goals two and three will feed directly into our research efforts during GCE-II. In addition, we will hire two new technicians (an assistant IM and a second field technician) and begin the process of leadership transition from Hollibaugh to Alber. These personnel changes will lay the administrative groundwork for implementing the research goals of our GCE-II proposal.

First, we will continue our basic site management, information management, monitoring and outreach activities.

Site management. As described above (Results to date), the GCE program has established a formal Executive Committee (EC) and bylaws (http://gce-lter.marsci.uga.edu/lter/files/docs/GCE_Bylaws_01-Jun-2005.pdf). Early in GCE-II, Alber is expected to assume lead PI duties from Hollibaugh, and will represent the GCE project to NSF and the LTER network. Pennings will continue to serve as co-PI, and Hollibaugh will remain on the EC to ensure a smooth transition. The remaining membership of the EC (Joye, Sheldon, and Burd) will also remain stable, creating continuity between the first and second funding periods.

During the bridge funding period we will begin to operate informally under this new management structure.

Information management. As described above (Results to date), the GCE program has developed a state-of-the-art information management system that meets or exceeds all Network standards, and we have been heavily involved in IT issues on the Network level. Because our IM approach is highly automated, we have been able to achieve excellent results despite having only one IM position (Wade Sheldon). The midterm site review team, although appreciative of our IM accomplishments, suggested that we add a second IM person to aid Sheldon in this work (and serve as a backup), and also consider adding a GIS perspective to our IM approach. We agree with these suggestions. ***During the bridge funding period we will search for an assistant Information Manager with GIS skills.*** This person will provide GIS support for the project and will also assist Sheldon with routine input and QA/QC of datasets.

Monitoring. Our monitoring program supports all GCE research areas by documenting temporal and spatial variation in key ecosystem variables. The program includes measurements of the atmospheric, groundwater, and riverine inputs to the study area, the water column within the sounds, marsh sediments, marsh vegetation, and marsh invertebrates. During GCE-I, responsibility for the various elements of the monitoring program was distributed across a number of laboratories, and analyses were often done by graduate students. This allowed us to implement the best approaches for monitoring each variable, but created some operational inefficiency and concerns about continuity. In addition, it meant that we had only one full-time GCE technician at Sapelo Island, with no backup in case of emergency. ***During the bridge funding period we will search for and train an additional monitoring technician.*** Much of our monitoring effort for 2006 will take place during the bridge funding period (especially the labor-intensive population work focused on plants and invertebrates), so it will be valuable to have a second technician in place for this work. During GCE-II, the two field technicians will conduct most of the field work for the monitoring program, with training, QA/QC and data analysis provided by the appropriate PIs (**Table 1**). We believe that this approach will improve efficiency, ensure continuity of the sampling program, and provide a backup in case of emergency.

Outreach. As described above (Results to date), the most important aspects of our outreach program are graduate education, the schoolyard, and the Georgia Coastal Research Council. ***During the bridge funding period we will continue to support these outreach activities, therefore providing continuity to these programs.***

Second, we will extend our directed studies in the Duplin River by completing an inundation analysis of the Duplin River watershed, obtaining remotely-sensed information on groundwater input and plant composition and productivity, and establishing a GIS framework for this information.

Estuaries along the southeastern coast occur as a series of riverine systems with large watersheds interspersed with smaller lagoons and tidal creeks (Dame et al. 2000). The Duplin River is a well-studied example of the latter type of estuary. This 12.5 km tidal inlet is part of the Sapelo Island National Estuarine Research Reserve and at the geographic center of the GCE domain (**Fig. 4**). Early work in the Duplin described the exchange of water (and the particulate and dissolved constituents carried within it) between the inlet and the adjacent Doboy Sound (Ragotzkie and Bryson 1955; Ragotzkie and Pomeroy 1957; Imberger et al. 1983; Chalmers et al. 1985). Although we have continued research along these lines (i.e. estimates of net CO_2 exchange with the adjacent Sound, Wang and Cai 2004), we hypothesize that much of the difference in constituent concentrations is driven by the periodic flow of water over the marsh during flood tide. Water exchange occurs in a complex network of channels that alternately flood and dry large intertidal areas: approximately 80% of the watershed of the Duplin is intertidal salt marsh and mudflat (Chalmers 1997). During GCE-I, we therefore initiated a directed study of the exchange processes between subtidal and intertidal areas of the Duplin River (Blanton et al. 2005) ***During the bridge funding period, we seek to build on these efforts in several ways. We will 1) complete an inundation analysis of the Duplin, 2) obtain complementary information on groundwater input and plant production, and 3) establish a GIS framework for the area.*** All of this information will be directly useful to planned research during GCE-II on upland-marsh linkages.

Inundation analysis. During GCE-I we obtained seven sets of infrared images (1 m^2 resolution) of the Duplin River watershed at roughly one hour intervals spanning low to high tide. By categorizing individual pixels as flooded or exposed and linking this information to contemporaneous tide recordings, we are building an elevational map of much of the intertidal zone in the watershed. Two of the images have already been processed (**Fig. 4**). ***We (Blanton and collaborators at the University of Lisbon) will process the remaining five in the fall of 2006 (partially funded by the bridge supplement and partially by the first year of GCE-II).*** This analysis will allow us to compute the water area as a function of rising water elevation for the entire Duplin domain. Our initial focus will be on calculation of inundation curves for marshes adjacent to the upland areas (=hammocks) to the west of the Duplin. These areas are targeted for intensive study during GCE-II as part of our research on upland-marsh linkages.

Groundwater input and plant production. One of the major questions being pursued for GCE-II is whether (and how) freshwater from an adjacent upland controls marsh plant distributions. As a result of the analysis described above we will have good information on inundation in the watershed of the Duplin River, and so will be in a position to compare plant distribution with elevation, inundation and groundwater input. ***During the bridge funding period (summer of 2006), we will obtain both thermal IR and hyperspectral imagery of the Duplin River***. Thermal IR imaging will be used to discover sites where groundwater discharges into the marsh. This technique is most successful in summer when temperature differences between warm surface water and colder groundwater are at their maximum (Portnoy et al. 1998). Thermal IR provides visual identifications and a geospatial location of sites of groundwater inflow: white (cold) spots on images represent areas of groundwater input against the warm (black) background. In 2001, we collected 20 thermal IR images focused on GCE site 10 (Moses Hammock). Those data clearly showed multiple sites of significant groundwater inflow in the vicinity of this site (**Fig. 5**). During the summer of 2006, we will acquire a more complete set of thermal IR images of the Duplin River watershed. The georeferenced images will be entered into the GIS and used in GCE-II to select sampling sites along the Duplin River with more or less freshwater input to evaluate the effect of differential freshwater input on a variety of marsh processes.

Hyperspectral imagery provides information on plant species, biomass, and pigments.

Since 2002, the NOAA-sponsored Environmental Cooperative Science Center (ECSC) has acquired imagery at five National Estuarine Research Reserves (NERR) and adjacent areas of the Southeastern and Mid-Atlantic coastlines. In 2006, the ECSC has planned for flight missions at the Sapelo Island NERR in coordination with the GCE LTER, NERR personnel, and partner schools and NOAA laboratories of the ECSC. The imagery will be acquired with a University of Nebraska-Lincoln aircraft and AISA Eagle sensor (www.specim.fi/products-aisa.html) with 2.9 nm spectral resolution, 12 bit data precision, spectral range of 400-970 nm, and swath width of about 1000 pixels. Vegetation is normally flown at 1.0 m resolution, with a total swath of about 1 km. Dr. John Schalles, from Creighton University, will lead aerial and ground data collection and analysis at Sapelo Island (Schalles plans to spend a sabbatical leave in 2006-07 in residence at the University of Georgia Marine Institute at Sapelo Island). The GCE program will provide partial funding for the flights and Pennings will assist with ground-truthing. The end result of this effort will be maps of wetland biomass and canopy pigments for the areas (reviewed in Schalles 2006).

GIS framework. This research focus provides the ideal context for incorporating one of the suggestions of the mid-term review, which is that we develop a GIS framework for our operations. We plan to take the images and maps produced above, rectify them and import them into a GIS framework (image processing will be done by the assistant information manager). The immediate goal of this process will be to use the information described above to determine whether inundation and the presence of groundwater inputs predict plant composition and productivity at the landscape scale. In doing this, the GIS will help answer some of the basic questions about upland-marsh linkages that we will address during GCE-II. We will also work in partnership with the Sapelo Island National Estuarine Research Reserve, which has a variety of maps and historical aerial photographs of the Duplin River watershed. We will provide SINERR with access to a computing facility at the University of Georgia Marine Institute on Sapelo Island equipped with workstations, scanners and GIS software. Access to these facilities will enable SINERR to scan historical maps and photographs and provide rectified, geo-referenced images to the GCE program. We will also provide web hosting and backup for the shared GIS data and imagery on GCE servers at UGA.

We will continue to develop our GIS capabilities over time and anticipate that these will prove useful in addressing a variety of additional research questions during GCE-II and in the future. Our long-term goal is to develop integrated spatial models that combine information on landscape position, inundation, freshwater inflow, and marsh response to examine how various scenarios of changes in long-term drivers (i.e., sea level rise, changes in precipitation, water withdrawal from rivers) would affect estuarine environments.

Third, we will begin to describe the population and genetic structure of plant and animal populations across the GCE domain.

One of the major goals of GCE-II will be to evaluate the relative importance of larval transport and the conditions of the adult environment in determining community and genetic structure across both the longitudinal and lateral gradients of the estuarine landscape. ***During the bridge funding period we will begin to describe population and genetic structure of plants and animals across the GCE domain, and will initiate experiments to identify the mechanisms producing this structure.***

Ecologists working in rocky intertidal (Bertness et al. 1996, Connolly and Roughgarden 1998, Connolly et al. 2001) and coral reef (Connell et al. 1997, Hughes et al. 1999, Hughes et al. 2002) habitats have extensively addressed the roles of recruitment, competition and predation in producing population and genetic structure across the landscape (Caley et al. 1996). These processes, however, are only beginning to be addressed in soft-sediment systems (Hughes and Stachowicz 2004), and very few studies have been done in salt marsh habitats. In particular, the approach that we will take here and in GCE-II of comparing multiple species across the community will represent a major step forward for our understanding of population distributions in estuarine habitats. We will address three major questions**.** 1) What are the relative contributions of recruitment and post-recruitment survival in explaining variation in population distributions across the GCE landscape? 2) How do these processes differ among species as a function of life-history? 3) How do patterns of genetic diversity correlate with patterns of functional diversity? Addressing these questions for a range of taxa will build an understanding of the factors mediating large-scale distribution patterns of coastal species that is unmatched for any estuarine system, and will provide an interesting contrast to results from the PISCO program that is addressing similar questions in rocky intertidal systems on the Pacific Coast of the U.S. (Connolly et al. 2001).

The background and perspective to this work are described more extensively in our GCE-II proposal. The primary goal during the bridge supplement funding period will be to begin to document patterns of genetic structure. We (Wares) will use standard DNA-based molecular markers to identify patterns of genetic structure across sites, and compare these relationships among different taxa (**Table 2**). To provide a larger geographic context for this work, additional samples for genetic analysis will be collected from VCR (Virginia), PIE (Massachusetts) and the GTM NERR (Florida). We will use assignment tests and analysis of molecular variance (Excoffier et al. 1992, Excoffier et al. in press) to describe the spatial genetic structure of adult populations in order to identify sites that are likely exchanging recruits freely and sites that are isolated from others, and to identify sites with reduced genetic variation indicative of strong local selection. Detailed models of isolation and migration patterns will be developed (Hey and Nielsen 2004). To the extent that each species is a replicate analysis of the GCE sites (Wares and Cunningham 2001), we should be able to gain insights into population structure even if some species are only analyzed with a single universal mtDNA locus. We are particularly interested in comparing species with high and low dispersal ability, expecting the latter to show more population structure, and in comparing free-spawning invertebrates with those that have direct sperm transfer, expecting the former to have much higher inbreeding structure (Addison and Hart 2005). Comparisons of inbreeding structure (as measured by F_{is} statistics) may reveal otherwise unrecognized spatial population structure, variation in rates of molecular evolution in certain taxa, or high variance in reproductive success that may differ among sites in the GCE system (Turner et al. 2002).

In addition, we will conduct three other activities during the bridge supplement funding period that will provide a strong foundation for our GCE-II research program on population distributions across the estuarine landscape.

1) We (Pennings) will collect field data on plant species composition and biomass for ground-truthing the hyperspectral imagery of the Duplin River watershed described above. In collaboration with Schalles, we will utilize a stratified sampling approach to cover a range of

plant species and productivity levels within the watershed. Using standard plot-based methods, we will quantify plant species identity, height and biomass in each plot. We will collect core samples of soils from each plot to relate plant composition and biomass to soil water content, salinity, and organic content.

2) We (Bishop, Pennings) will continue our routine monitoring (including training the new field technician) and will conduct targeted sampling to document densities and sizes of taxa that are poorly sampled by our monitoring program. For example, the marsh mussel *Geukensia demissa* is poorly sampled by our monitoring protocols because it has a low density but highly aggregated distribution that needs to be sampled using plots much larger than those we routinely employ. These data will set the stage for studying recruitment and post-recruitment survival of these taxa during GCE-II.

3) We (Pennings) will initiate plant transplant studies examining the mechanisms mediating population distributions across the estuarine landscape. Salt marsh ecologists have a good understanding of the factors mediating plant distributions across elevation within single marshes (Pennings and Bertness 2001). Much less work has been done at the landscape scale, but we have a preliminary understanding of the processes that mediate plant distributions across estuaries in New England (Crain et al. 2004). This understanding needs to be evaluated with manipulative experiments in other geographic regions, because the factors mediating plant distributions in salt marsh habitats often change geographically (Pennings et al. 2003, Pennings et al. 2005). To measure post-recruitment survival and growth, we will outplant selected plant species (**Table 3**) at the 9 main GCE sites, focusing on species that are the most amenable to these experiments and that provide interesting life-history or distribution comparisons. Outplants will be done with and without competition. During GCE-II, plant experiments will continue, and parallel experiments will be conducted with invertebrates.

The funding requested here will allow us to continue the GCE program without the disruption that would be caused by a 6.5-month gap in funding. In addition to providing ongoing salary for our core staff and students, the funding will allow us to collect routine monitoring data (much of the monitoring occurs during the summer and fall period covered by this supplement request) and to gear up for the work proposed for GCE-II.

References Cited

Addison, J.A. and M.W. Hart (2005). Spawning, copulation and inbreeding coefficients in marine invertebrates. Biol. Lett. 1: 450-453.

Alber, M. (2002). A conceptual model of estuarine freshwater inflow management. Estuaries 25(6B): 1246-1261.

Bertness, M.D., S.D. Gaines and R.A. Wahle (1996). Wind-driven settlement patterns in the acorn barnacle *Semibalanus balanoides*. Marine Ecology Progress Series 137:103-110.

Blanton, J.O., G. Lin and S.A. Elston (2002). Tidal current asymmetry in shallow estuaries and tidal creeks. Continental Shelf Research 22: 1731-1743.

Blanton, J.O., J. Amft, F. Andrade, M.A. Ferreira and E. Fernandes (2005). The Duplin River Study: Exchange processes between intertidal areas and tidal creeks. LTER Network News 18(1): 11-12. (Complete color version available at < http : //www.lternet.edu/news/images/spring05/GCE Duplin River Study.pdf >.)

Boesch, D.F., J.C. Field and D. Scavia, eds. (2000). The potential consequences of climate variability and change on coastal areas and marine resources: Report of the coastal areas and marine resources sector team, U.S. National Assessment. NOAA Coastal Ocean program decision analysis series #21. NOAA Coastal Ocean Program, Silver Spring, MD. 163 pp.

Buchan, A., S.Y. Newell, J.I.L. Moreta and M.A. Moran (2002). Analysis of internal transcribed spacer (ITS) regions of rRNA genes in fungal communities in a southeastern U.S. salt marsh. Microbial Ecology 43: 329-340.

Caley, M.J., M.H. Carr, M.A. Hixon, T.P. Hughes, G.P. Jones and B.A. Menge (1996). Recruitment and the local dynamics of open marine populations. Annual Review of Ecology and Systematics 27: 477-500.

Chalmers, A.G., ed. (1997). *The Ecology of the Sapelo Island National Estuarine Research Reserve.* University of Georgia Marine Institute, Sapelo Island. 68 pp.

Chalmers, A.G., R.G. Wiegert and P.L. Wolf (1985). Carbon balance in a salt marsh: interactions of diffusive export, tidal deposition, and rainfall-caused erosion. Estuarine, Coastal and Shelf Science 21: 757-771.

Connell, J.H., T.P. Hughes and C.C. Wallace (1997). A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecological Monographs 67: 461-488.

Connolly, S.R. and J.J. Roughgarden (1998). A latitudinal gradient in northeast Pacific intertidal community structure: evidence for an oceanographically based synthesis of marine community theory. American Naturalist 151: 311-326.

Connolly, S.R., B.A. Menge and J.J. Roughgarden (2001). A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific ocean. Ecology 82(7): 1799-1813.

Craft, C.B. (submitted). Freshwater input structures soil properties, vertical accretion and nutrient accumulation of Georgia and United States (U.S.) tidal marshes. Limnol. Oceanogr..

Crain, C.M., B.R. Silliman, S.L. Bertness and M.D. Bertness (2004). Physical and biotic drivers of plant distribution across estuarine salinity gradients. Ecology 85(9): 2539-2549.

Dame, R., M. Alber, D. Allen, M. Mallin, C. Montague, A. Lewitus, A. Chalmers, R. Gardner, C. Gilman, B. Kjerfve, J. Pickney and N. Smith (2000). Estuaries of the South Atlantic coast of North America: their geographic signatures. Estuaries 23: 793-819.

Excoffier, L., P.E. Smouse and J.M. Quattro (1992). Analysis of Molecular Variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genetics 131: 479-491.

Excoffier, L., G. Laval and S. Schneider (in press). Arlequin ver. 3.0: An integrated software package for population genetics data analysis. Evolutionary Bioinformatics Online.

Friedrichs, C.T. and D.G. Aubrey (1988). Non-linear tidal distortion in shallow well-mixed estuaries: a synthesis. Estuarine, Coastal and Shelf Science 27: 521-545.

Fulton, P., G. Schultz and C. Ruppel (2001). Hydrologic and geophysical constraints on submarsh groundwater flow to an estuary in the Georgia Bight. American Geophysical Union, EOS.

Goranson, C.E., C.-K. Ho and S.C. Pennings (2004). Environmental gradients and herbivore feeding preferences in coastal salt marshes. Oecologia 140: 591-600.

Hey, J. and R. Nielsen (2004). Multilocus methods for estimating population sizes, migration rates, and divergence time, with applications to the divergence of *Drosophila pseudoobscura* and *D. persimilis*. Genetics 167: 747-760.

Higinbotham, C.B., M. Alber and A.G. Chalmers (2004). Analysis of tidal marsh vegetation patterns in two Georgia estuaries using aerial photography and GIS. Estuaries 27(4): 670-683.

Hughes, A.R. and J.J. Stachowicz (2004). Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. Proceedings of the National Academy of Science, USA 101: 8998-9002.

Hughes, T.P., A.H. Baird, E.A. Dinsdale, N.A. Moltschaniwskyj, M.S. Pratchett, J.E. Tanner and B.L. Willis (1999). Patterns of recruitment and abundance of corals along the Great Barrier Reef. Nature 397: 59-63.

Hughes, T.P., A.H. Baird, E.A. Dinsdale, V.J. Harriott, N.A. Moltschaniwskyj, M.S. Pratchett, J.E. Tanner and B.L. Willis (2002). Detecting regional variation using meta-analysis and large-scale sampling: latitudinal patterns in recruitment. Ecology 83: 436-451.

Imberger, J., T. Berman, R.R. Christian, E.B. Sherr, D.E. Whitney, L.R. Pomeroy, R.G. Wiegert and W.J. Wiebe (1983). The influence of water motion on the distribution and transport of materials in a salt marsh estuary. Limnol. Oceanogr. 28:201-214.

Intergovernmental Panel on Climate Change (IPCC) (2001). Climate Change 2001: Synthesis Report, Summary for Policymakers. Wembley, UK.

Joye, S.B., D.A. Bronk, D. Koopmans and W.S. Moore (2006, in press). Potential for groundwater-derived carbon, nitrogen and phosphorus inputs to coastal ecosystems in South Carolina and Georgia. In: Kleppel, G.S., M.R. DeVoe, & M. Rawson, eds. Implications of Land Use Change to Coastal Ecosystems. Springer Verlag.

Kang, K.R. and D. Di Iorio (2005, in revision). Variations of turbulent flow with river discharge in the Altamaha River Estuary, Georgia. Journal of Geophysical Research.

Lyons, J.I., S.Y. Newell, R.P. Brown and M.A. Moran (2005). Screening for bacterial-fungal associations in a south-eastern US salt marsh using pre-established fungal monocultures. FEMS Microbiology Ecology 54: 179-187.

Michael, H.A., A.E. Mulligan and C.F. Harvey (2005). Seasonal oscillations in water exchange between aquifers and the coastal ocean. Nature 436: 1145-1148.

Miller, J.R. and G.L. Russell (1992). The impact of global warming on river runoff. Journal of Geophysical Research 97(D3): 2757-2764.

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.

Morris J.T., P.V. Sundareshwar, C.T. Nietch, B. Kjerfve and D.R. Cahoon (2002). Responses of coastal wetlands to rising sea level. Ecology 83:2869-2877.

Newell, S.Y. (2001). Multiyear patterns of fungal biomass dynamics and productivity within naturally decaying smooth cordgrass shoots. Limnol. Oceanogr. 46: 573-583.

Newell, S.Y. (2003). Fungal content and activities in standing-decaying leaf blades of plants of the Georgia Coastal Ecosystems research area. Aquatic Microbial Ecology 32: 95-103.

Newell, S.Y., L.K. Blum, R.E. Crawford, T. Dai and M. Dionne (2000). Autumnal biomass and potential productivity of salt marsh fungi from 29º to 43º North latitude along the United States Atlantic Coast. Applied and Environmental Microbiology 66(1): 180-185.

National Oceanic and Atmospheric Administration (NOAA) (2001). Sea Level Variations of the United States 1854-1999. Technical Report NOS CO-OPS 36, Silver Spring, MD.

Ogburn, M.B. and M. Alber (2006, in press). An investigation of salt marsh dieback in Georgia using field transplants. Estuaries.

Pennings, S.C. and M.D. Bertness (2001). Salt marsh communities. In: Bertness, M.C., S.D. Gaines and M.E. Hay, eds. *Marine Community Ecology.* Sinauer Associates, Sunderland, MA. pp. 289-316.

Pennings, S.C. and B.R. Silliman (2005). Linking biogeography and community ecology: latitudinal variation in plant-herbivore interaction strength. Ecology 86(9): 2310-2319.

Pennings, S.C., E.L. Siska and M.D. Bertness (2001). Latitudinal differences in plant palatability in Atlantic Coast salt marshes. Ecology 82(5): 1344-1359.

Pennings, S.C., E.R. Selig, L.T. Houser and M.D. Bertness (2003). Geographic variation in positive and negative interactions among salt marsh plants. Ecology 84(6): 1527-1538.

Pennings, S.C., M.-B. Grant and M.D. Bertness (2005). Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity and competition. Journal of Ecology 93: 159-167.

Portnoy, J.W., B.L. Nowicki, C.T. Roman and D.W. Urish, (1998). The discharge of nitrate-contaminated groundwater from developed shoreline to marsh-fringed estuary. Wat. Resour. Res. 34: 3095-3104.

Ragotzkie, R.A. and R.A. Bryson (1955). Hydrography of the Duplin River, Sapelo Island, Georgia. Bulletin of Marine Science of the Gulf and Caribbean. 5:297-314.

Ragotzkie, R.A. and L.R. Pomeroy (1957). Life history of a dinoflagellate bloom. Limnol. Oceanogr. 2:62-69.

Richards, C.L., J.L. Hamrick, L.A. Donovan and R. Maruricio (2004). Unexpectedly high clonal diversity of two salt marsh perennials across a severe environmental gradient. Ecology Letters 7: 1155-1162.

Richards, C.L., S.C. Pennings and L.A. Donovan (2005). Habitat range and phenotypic variation in salt marsh plants. Plant Ecology 176: 263-273.

Salgado, C.S. and S.C. Pennings (2005). Latitudinal variation in palatability of salt-marsh plants: are differences constitutive? Ecology 86(6): 1571-1579.

Schalles, J.F. (2006, in press). Optical remote sensing techniques to estimate phytoplankton chlorophyll *a* concentrations in coastal waters with varying suspended matter and CDOM concentrations. In: Richardson, L. and E. Ledrew, eds. *Remote Sensing of Aquatic Coastal Ecosystem Processes: Science and Management Applications*. Springer.

Schultz, G. and C. Ruppel (2002). Constraints on hydraulic parameters and implications for groundwater flux across the upland-estuary interface. Journal of Hydrology 260**:** 255-269.

Schultz, G. and C. Ruppel (2005). Inversion of inductive electromagnetic data in high induction number terrains. Geophysics 70: G16-G28.

Sheldon, J.E. and M. Alber (2005). Comparing transport times through salinity zones in the Ogeechee and Altamaha River estuaries using SqueezeBox. 2005 Georgia Water Resources Conference, University of Georgia, Athens, Georgia.

Silliman, B.R., J. van de Koppel, M.D. Bertness, L.E. Stanton and I.A. Mendelssohn (2005). Drought, snails, and large-scale die-off of southern U.S. salt marshes. Science 310: 1803-1806.

Snyder, M., M. Taillefert and C.D. Ruppel (2004). Redox zonation at the saline-influenced boundaries of a permeable surficial aquifer: effects of physical forcing on the biogeochemical cycling of iron and manganese. Journal of Hydrology 296: 164-178.

State of the Coast Report (2004). Center for a Sustainable Coast, Works in Progress, Spring/Summer 2004 Issue, available at http://www.sustainablecoast.org/, accessed 10/01/04.

Suding, K.N., S.L. Collins, L. Gough, C. Clark, E.E. Cleland, K.L. Gross, D.G. Milchunas and S.C. Pennings (2005). Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. Proceedings of the National Academy of Science, USA 102: 4387-4392.

Thompson, V.D., M.D. Reynolds, B. Haley, R. Jefferies, J.K. Johnson and L. Humphries (2004). The Sapelo shell ring complex: shallow geophysics on a Georgia sea island. Southeastern Archaeology 23(2): 192-201.

Thoresen, M. and M. Alber (submitted). The contribution of benthic diatoms to the diets of suspension-feeding bivalves (eastern oyster, *Crassostrea virginica*).

Turner, T.F., J.P. Wares and J.R. Gold (2002). Genetic effective size is three orders of magnitude smaller than adult census size in an abundant, estuarine-dependent marine fish (*Sciaenops ocellatus*). Genetics 162: 1329-1339.

U.S. Commission on Ocean Policy (2004). An Ocean Blueprint for the 21st Century.

Verity, P.G. (2002). A decade of change in the Skidaway River estuary. I. Hydrography and nutrients. Estuaries 25: 944-960.

Verity, P.G., M. Alber and S.B. Bricker (submitted). Development of hypoxia in well-mixed estuaries. Estuaries.

Wang, A.Z. and W.-J. Cai (2004). Carbon dioxide degassing and inorganic carbon export from a marsh-dominated estuary (the Duplin River): a marsh CO_2 pump. Limnol. Oceanogr. 49(2): 341-354.

Wares, J.P. and C.W. Cunningham (2001). Phylogeography and historical ecology of the North Atlantic intertidal. Evolution 55(12): 2455-2469.

Weston, N.B., J.T. Hollibaugh, J. Sandow and S.B. Joye (2003). Nutrients and dissolved organic matter in the Altamaha River and loading to the coastal zone. 2003 Georgia Water Resource Conference. University of Georgia, Institute of Ecology, University of Georgia.

Weston, N.B., R. Dixon and S.B. Joye (2006, in press). Microbial and geochemical ramifications of salinity intrusion into tidal freshwater sediments. Journal of Geophysical Research: Biogeosciences.

Weston, N.B., J.T. Hollibaugh and S.B. Joye (submitted). The Altamaha River watershed: Thirty years of nutrient and organic carbon loading data from sub-watersheds. Water Research.

White, S.N. (2004). *Spartina* species zonation along an estuarine gradient in Georgia: Exploring mechanisms controlling distribution. Athens, GA, University of Georgia.

Wolock, D.M. and G.J. McCabe (1999). Simulated effects of climate change on mean annual runoff in the conterminous United States. Journal of the American Water Resources Association 35: 1341-1350.

Zimmer, M., S.C. Pennings, T.L. Buck and T.H. Carefoot (2004). Salt marsh litter and detritivores: a closer look at redundancy. Estuaries 27: 753-769.

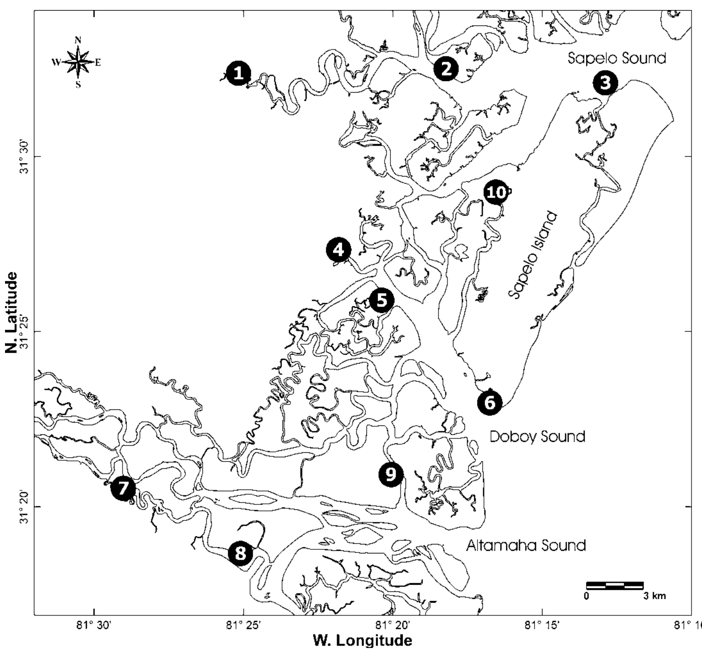

Fig. 1. GCE domain on the coast of Georgia, with core study sites marked. Sites are located on an onshore-offshore gradient on three sounds that differ in freshwater input. Altamaha sound, to the south, receives large amounts of freshwater discharge from the Altamaha River. Doboy and Sapelo sounds have no permanent river inflows. Site 10 is located on the Duplin River on the west side of Sapelo Island.

Fig. 2. Conceptual models guiding GCE research. **Left:** Longitudinal perspective showing relative contributions of river discharge, groundwater flow, oceanic influence and net flow in three coastal sounds. **Right:** Lateral movement of water among subtidal, intertidal and upland habitats; A & B: river discharge and tidal flow combine to move water up and downstream, C: tidal exchange brings water on and off the marsh platform, D: precipitation, E: precipitation leads to overland flow (runoff) if soils are saturated or impermeable, F & G: groundwater may flow directly into the marsh or may transit under the marsh to emerge sub-tidally, H: evapotranspiration. By layering this model on top of the landscape model on the left, we will gain a more sophisticated understanding of spatial variation in ecosystem processes across the GCE landscape.

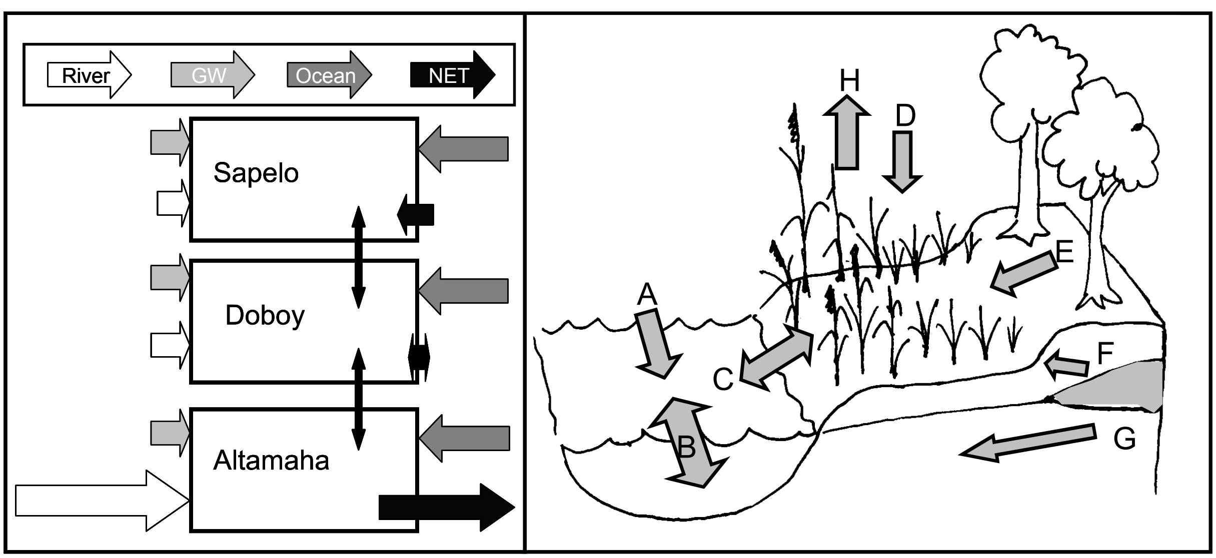

Fig. 3. Relative amounts of organic carbon (g $m^{-2}y^{-1}$) and nitrogen (g $m^{-2}y^{-1}$) accumulation across the landscape in comparison to decomposition rates (kg y^{-1}). C and N accumulation are highest in freshwater and brackish marshes (upper Altamaha Sound) whereas decomposition rates are highest in salt marshes (lower Altamaha Sound, lower Doboy Sound). ND: Not determined (Craft, submitted)

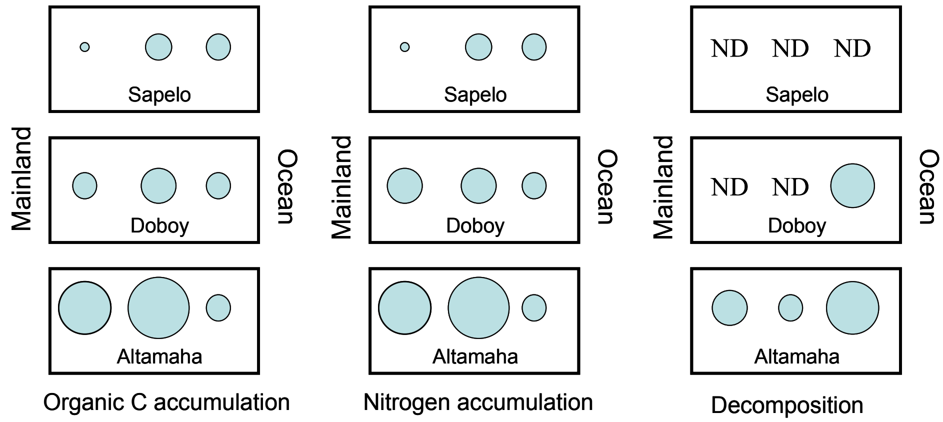

Table 1. Monitoring program for GCE-II. PIs responsible for supervising each aspect of the monitoring program are indicated in parentheses. LTER core areas are 1: primary production, 2: populations, 3:organic matter cycling, 4: inorganic nutrients, 5: disturbance.

Type	Location	Frequency	Core Area & Variables Measured
Atmospheric			
Weather stations, collaborations with SINERR, USGS (Di Iorio)	Sites 4, 6	Every 15 min	Abiotic driver of areas 1-5: > level 2 stations, measuring PAR, temperature, relative humidity, rainfall, wind speed and direction, barometric pressure
Wet deposition, collaborations with SINERR, NADP (Joye)	Site 6	Weekly	4: Hydrogen (acidity as pH), sulfate, nitrate, ammonium, chloride, base cations (such as calcium, magnesium, potassium, sodium)
Water			
Altamaha River chemistry (Joye)	Head of tide	Weekly or more often	3, 4: DIN, DIP, DSi species, organics (DOC, DON, DOP), major ions, chlorophyll, CN
Altamaha tributaries chemistry (Joye)		Quarterly	3, 4: As above
Groundwater chemistry (Joye)	Sites 4, 10	Monthly	3, 4: Dissolved nutrients (NO_2^-, NO_3^-, NH_4^+, HPO_4^{2-}, $H_2SiO_4^{2-}$), dissolved organics (DOC, TDN, DON, TDP, DOP), redox species, salts
Sound chemistry, collaborations with SINERR, USGS (Joye)	Sites 1-9	Monthly	1, 3, 4: Dissolved nutrients (NO_2^-, NO_3^-, NH_4^+, HPO_4^{2-}, $H_2SiO_4^{2-}$), dissolved organics (DOC, TDN, DON, TDP, DOP), chlorophyll *a*, total suspended sediments, particulate CN, particulate P and Fe
Sound hydrography (Di Iorio)	Sites 1-9	Every 30 min	Abiotic driver of areas 1-5: Salinity, temperature, pressure
Marshes			
Soil accretion (Craft)	Sites 1-10	Quarterly	3: Sediment accretion, elevation, compaction
Soil flooding (Craft)	Sites 1-10	Every 1 min	Abiotic driver of areas 1-5: Salinity, temperature, pressure in soils
Plant productivity (Pennings)	Sites 1-10, 2 zones	Annual	1: Stem density, height, flowering status, calculated biomass, in 2 marsh zones
Disturbance (Pennings)	Sites 1-10	Annual	5: Wrack and biotic disturbance in permanent vegetation plots
Plant distribution (Pennings)	Site 6	Annual	2: Community composition in 3 types of vegetation mixtures
Plant distribution (Alber)	Altamaha Sound stations	Every 2 y	1, 2: Stem density, height, flowering status of *Spartina alterniflora* versus *S. cynosuroides* in creekbank plots
Marsh Invertebrates (Bishop, Pennings)	Sites 1-10, 2 zones	Annual	2: Density and size of benthic macroinvertebrates in 2 marsh zones
Insects (Pennings)	Sites 3-10	Annual	2: Density of grasshoppers in transects

Fig. 4. Infrared aerial images of the Duplin River showing the distribution of low water (left) and high water (right). (Inset shows the location of the Duplin River within the GCE domain.)

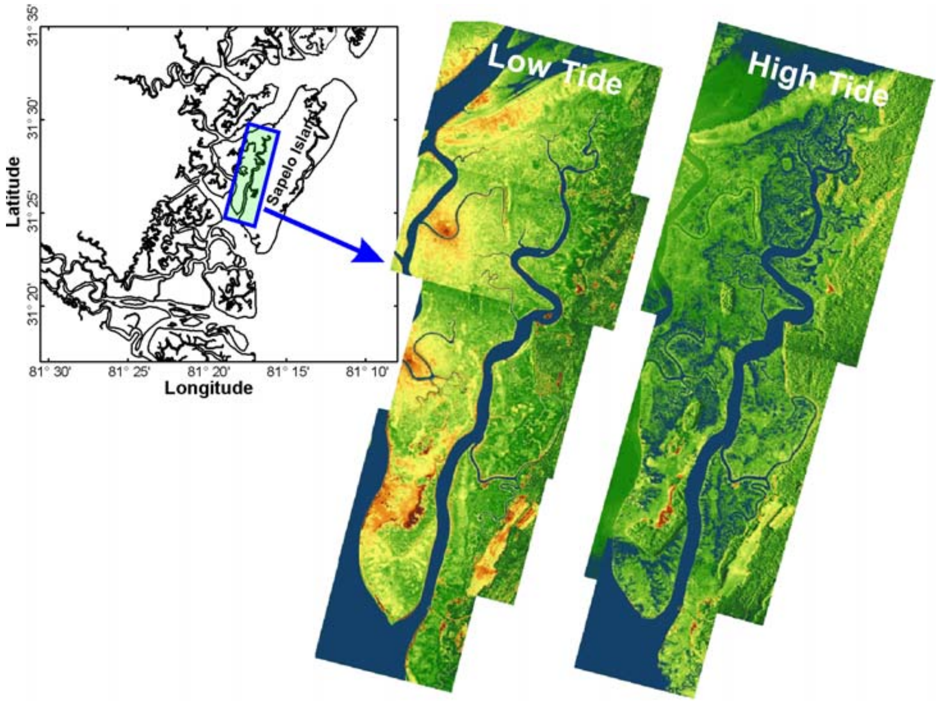

Fig. 5. Thermal images of Moses Hammock showing groundwater discharge. Freshwater appears white because it is cold. **Left:** Surficial groundwater flow at edge of Moses Hammock. **Right:** Sub-marsh groundwater inputs along the bend of a tidal creek.

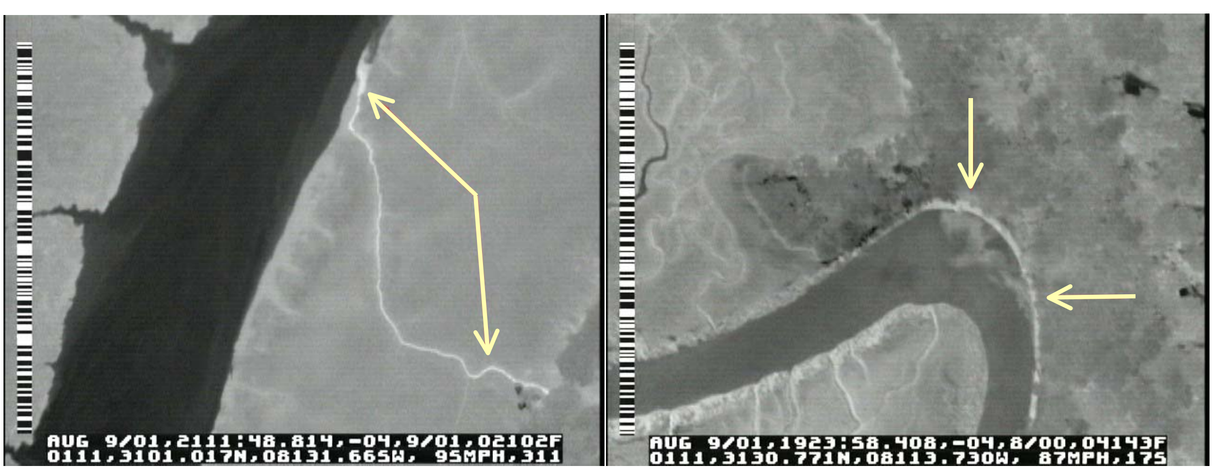

Table 2. Species for genetic analyses to be initiated during the supplement period and continued during GCE-II. We (Wares) will conduct preliminary analyses on all species (n=20/sp.), then focus in-depth work (n=60/sp.) on the species/comparisons that appear to be most tractable. Free-spawning invertebrates (Bivalvia and Polychaeta) are indicated by "FS".

Marine invertebrates	Larval planktonic period	Notes
Gastropoda		
Littoraria irrorata	6-8 wks	Abundant and important
Melampus bidentatus	2 wks	Patchy distribution
Ilyanassa obsoleta	4-8 wks	Abundant on mud banks
Urosalpinx cinerea	0	Abundant on oyster reefs
Bivalvia		
Geukensia demissa FS	5-6 wks	Abundant in marsh
Crassostrea virginica FS	2-3 wks	Commercially important, creates subtidal structure
Perna viridis FS	2 wks	Invasive species
Polymesoda caroliniana FS	2-3 wks	Patchy distribution
Crustacea		
Uca pugnax	2 wks	Abundant and important
Petrolisthes armatus	2 wks	Invasive species
Chthamalus fragilis	4-6 wk	Lives on *Spartina* stems
Cyathura polita	0	Common isopod
Orchestia grillus	0	Common amphipod
Ulorchestia spartinophylla	0	Amphipod associated with *Spartina* stems
Polychaeta		
Neanthes succinea FS	2-3 wks	Widespread
Manayunkia aesuarina FS	0	Broods larvae
Phyllodoce fragilis FS	2-4 wks	Oyster reef associate
Orthoptera	**Dispersal ability**	**Notes**
Orchelimum fidicinium	Strong flier	Abundant and important
Hesperotettix floridensis	Wingless	Patchy distribution
Conocephalus spartinae	Wingless	Patchy distribution
Plants	**Dispersal ability**	**Notes**
Spartina alterniflora (wind pollinated)	Good (floating seeds and shoots)	Most abundant salt marsh plant
Juncus roemerianus (wind pollinated)	Moderate (small seeds)	Very abundant at brackish marshes
Iva frutescens (insect pollinated)	Poor (heavy seeds)	Dominant high marsh shrub
Solidago sempervirens (insect pollinated)	Good (wind-dispersed)	Common high marsh forb

Table 3. Outplant experiments to be initiated during the supplement period and continued during GCE-II. Work will focus on the most tractable species and those that provide interesting life-history or distribution contrasts. Most experiments will be done in the mid-marsh because this habitat is the most logistically tractable, but some will target mud-flat or oyster reef species. N=10 replicates/treatment/site/species.

Species	Methods and variables	Notes
Marine invertebrates (Silliman)		
Littoraria irrorata	Caged at low and ambient densities, 6 months, shell height	Abundant marsh gastropod, varies strongly in density among sites
Melampus bidentatus	As *Littoraria*	Abundant marsh gastropod, varies strongly in density among sites
Ilyanassa obsoleta	Tagged snails released at ambient densities (caging is difficult in mudflat habitat), shell height	Abundant mudflat gastropod
Geukensia demissa	As *Littoraria*	Abundant marsh bivalve, density patchy on small and site scales
Polymesoda caroliniana	As *Littoraria*	Bivalve typical of brackish sites, range contracted during drought and expanded after
Crassostrea virginica	As *Littoraria*	Oysters
Petrolisthes armatus	Caged at low and ambient densities, 3 mo, mass and carapace width	Invasive crab on oyster reef
Chthamalus fragilis	Outplanted on PVC plates at low and high densities, 6 mo, diameter	Common barnacle, settles on plant stems
Insects (Pennings)		
Orchelimum fidicinum	Caged at low densities in areas with and without *Littoraria*, 2 wks, mass	Abundant marsh grasshopper, varies in density among sites, *Littoraria* may be a competitor
Marsh Plants (Pennings)		
Spartina alterniflora	Planted with and without competition, 6 months, height, # of shoots and flowers, biomass	Dominant at salty sites
Batis maritima	As above	Subordinate at salty sites
Aster tenuifolius	As above	Subordinate at salty, brackish sites
Limonium carolinianum	As above	Subordinate at salty, brackish sites
Juncus roemerianus	As above	Dominant at brackish sites
Scirpus americanus	As above	Subordinate at brackish sites
Zizaniopsis milacea	As above	Dominant at fresh sites
Polygonum sp.	As above	Common subordinate at fresh sites
Aster novae-angliae	As above	Common subordinate at fresh sites