REGIONAL ENVIRONMENTAL MONITORING AND ASSESSMENT PROGRAM

R-EMAP Region 6

Monitoring Design Criteria and Biological Indicators for Seagrass Conservation in Texas Coastal Waters

Final Report

by

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Chapter 1

An Introduction to Monitoring Design Criteria and Biological Indicators for Seagrass Conservation in Texas Coastal Waters

Recently, a Seagrass Habitat Monitoring program was proposed for Texas coastal waters in the Seagrass Conservation Plan (TPWD 1999). This document, which describes many of the potential problems facing Texas seagrass habitats, recommended monitoring of key indices to detect ecosystem changes that occur before actual loss of seagrasses. The Texas Parks & Wildlife Department (TPWD) and the Texas Commission on Environmental Quality (TCEQ) have since started a planning process with resource managers and coastal researchers in Texas to develop a statewide seagrass-monitoring plan that is based on sound scientific knowledge of the resource and links the dynamic variability in environmental parameters to changes in seagrass distribution on both temporal and spatial scales. The monitoring program developed for the Chesapeake Bay system (Dennison et al. 1993) significantly improved our knowledge of the biological and physical environment and consequently resulted in an increase in water transparency through public awareness and effective management. This R-EMAP project addresses the development of indicators and criteria that would be used in a future long-term monitoring plan for the State of Texas. It includes studies that test the effectiveness of various indicators and determination of optimum spatial and temporal sampling frequency that can be used to monitor seagrasses for management and conservation purposes.

Under a recent (2000) addition to the Texas Surface Water Quality Standards by TNRCC, seagrass propagation is a protected aquatic life use, and water quality criteria should now be defined for use as standards in regulatory applications. In order to establish quantitative criteria for healthy Texas seagrass beds, environmental parameters and ecological indicators must be surveyed as part of a sponsored sampling and monitoring program: however, a monitoring protocol has not been identified for Texas seagrass beds. An effective protocol must include appropriate parameters or indicators, and a probability-based sampling strategy. This R-EMAP project focuses on the development of a regional sampling design, the selection of specific techniques for seagrass ecological assessment, and the adoption of a geospatial database that permits rigorous data analysis.

Ecological monitoring of seagrasses requires the application of new geospatial data analysis techniques. Advances with seagrass ecosystem models based on relationships between water quality and light attenuation (Dennison et al. 1993) show great promise for interpreting field data; however, spatial analysis of seagrass dynamics should be incorporated into the monitoring process to allow better correlation of seagrass distribution data with water quality and other environmental data.

This Region 6 R-EMAP study identifies the indicators that provide the most critical information on water quality criteria that is relevant to successful maintenance and growth of seagrasses. The study allows investigators to assess the relative value of various indicators with respect to cost, inherent variability on spatial and temporal scales, and effort. The study focused on two estuarine systems, the Mission-Aransas and lower Laguna Madre (Fig. 1). The two systems are distinctly different in terms of salinity, nutrients, and freshwater inflows (Longley, 1994), yet both support extensive seagrass meadows that contain all five species of seagrasses common to the Texas coast (*Halodule wrightii, Ruppia maritima, Thalassia testudinum,* *Syringodium filiforme,* and *Halophila engelmanii*). Consequently, a monitoring program that proves successful in accounting for seagrass changes in this pilot investigation is likely to be robust in application to other systems.

One important goal of this study is to provide the underpinnings for an effective seagrass monitoring plan specific to coastal systems in Texas. Coastal systems in other areas such as Florida and the Chesapeake Bay have different environmental characteristics and anthropogenic stressors that may not be relevant to Texas seagrasses. For this reason, this report addresses the overall project results with recommendations for a seagrass monitoring program (Chapter 2) as well as two potential problems for seagrasses in Texas: nutrient loading and drift macroalgal abundance (Chapter 3).

Chapter 2

REMAP Results: The Evaluation of Several Abiotic and Biotic Parameters for a Future Seagrass Monitoring Program in Texas.

Introduction

Seagrass meadows are important because they perform a variety of ecological functions. They are highly productive and provide food for a wide range of organisms (Heck and Thoman 1984). Carbon from seagrass fuels an extensive detrital food web and supports a diverse grazer assemblage (Dawes 1998). Seagrasses provide substrate for a diverse array of epiphytes, which contribute greatly to the overall production of these systems (Penhale 1977, Morgan and Kitting 1984, Moncreiff *et al.* 1992). Seagrasses are also important because they provide protection and structure for benthic macrofauna (Stoner 1980) and support bacterial activity in the sediment (Carpenter and Lodge 1986).

Several biogeochemical processes are a function of seagrass bed dynamics, including modification of sediment and surrounding hydrodynamics. They alter sediment chemistry by releasing oxygen from roots and rhizomes (Oremland and Taylor 1977; Smith *et al.* 1984), influence nutrient concentrations (Fourqurean *et al.* 1992), and increase sediment total organic carbon (Carpenter and Lodge 1986). Furthermore, they stabilize sediment, reduce particle resuspension, and encourage settlement of fine particles by reducing water velocity, all of which lead to increased light availability (Kemp *et al.* 1984).

In addition to these ecological and biogeochemical functions, seagrass beds have enormous economic value. They serve as nurseries and habitats for a variety of commercially and recreationally important fish, crabs, and shrimp (den Hartog 1977). Commercial and recreational fishing generate significant amounts of money in coastal areas. Virnstein and Morris (1996) placed the economic value of seagrasses in Indian River Lagoon, Florida, at about $30,000 per acre for their impact on fisheries alone. Florida's Department of Environmental Protection has estimated that seagrass has an economic value of approximately $20,500 per acre each year, which adds up to over $55 billion per year (http://www.dep.state.fl.us). The value of seagrass along the Texas coast has been estimated at more than $12.6 million annually (Pulich 1998). In addition to fisheries, seagrasses beds are valued because of their role in storm protection, including their ability to reduce erosion (Pulich 1998).

Despite the positive impacts that seagrasses make on coastal ecosystems, the extent and health of seagrass beds are declining across the globe (Wyllie-Echeverria *et al.* 2002). There are many natural and anthropogenic threats to seagrass communities. Natural threats include changes in water level and hurricanes (Pulich *et al.* 1997). Changes in water level, which are typically caused by drought or storms, affect the amount of light reaching seagrasses, while hurricanes can physically remove seagrasses or bury the plants under sediment. Anthropogenic threats to seagrasses typically include physical disturbance and reduction in light. Common physical disturbances include scarring from boat propellers, physical removal by the creation of channels, and shoreline development such as piers, sea walls, and bulkheads (Pulich 1998). Anthropogenic causes of light reduction include the deposition and resuspension of dredge material (Onuf 1994) and nutrient loading, which causes blooms of phytoplankton and accumulations of epiphytes and/or macroalgae (Pulich *et al.* 1997).

Decreased light availability has been shown to be responsible for large areas of seagrass loss (Cambridge and McComb 1984, Onuf 1994, Dunton 1996, Hauxwell *et al.* 2003). One of the principal causes of reduced light availability in coastal regions worldwide is increased nutrient input (Short *et al.* 1995, Tomasko *et al.* 1996). Degradation of water quality resulting from increased nutrients leads to increased light attenuation from phytoplankton blooms, epiphyte growth, or the accumulation of drift macroalgae (Pulich *et al.* 1997). In the Laguna Madre, Texas, light was reduced by a persistent brown tide bloom (Whitledge *et al.* 1999), which caused a 50% decline in the biomass of *Halodule wrightii* over a 5-year period (Dunton 1996, Onuf 1996a). Epiphytes have also been shown to reduce photosynthesis in seagrasses by blocking light (Sand-Jensen 1977, Brush and Nixon 2003) and reducing carbon uptake (Sand-Jensen 1977).

Excess nutrients have been blamed for the decline of coastal ecosystems, including seagrass communities (Orth and Moore 1983, Tomasko *et al.* 1996). Nutrient inputs to coastal systems primarily come from anthropogenic sources (Nixon 1995, Valiela *et al.* 1997a). A large proportion of nutrients reaching estuaries are from fertilizer, livestock waste, and atmospheric deposition of nitrogen from the combustion of fossil fuels (Nixon 1995). As the population increases and more countries become industrialized, these anthropogenic inputs are likely to increase unless controls are implemented. Point and non-point sources of nutrients will increase as more land is converted to urban or agricultural land (Nixon 1995). This increase in nutrient concentrations is likely to cause further deterioration of coastal ecosystems, including seagrass beds. For this reason, it is critical to understand the full extent of effects of nutrient enrichment on seagrass beds.

Many researchers are investigating decreasing health of seagrasses, but little consensus on evaluating seagrass health has been reached. One of the main problems with assessing "health" is that researchers have different definitions of the term and different measurement approaches (Wood and Lavery 2000). Kirkman (1996) suggested that seagrass biomass, density, and productivity should be measured to assess seagrass health, while other researchers measure seagrass distribution (Dennison *et al.* 1993, Livingston *et al.* 1998, Koch 2001, Fourqurean *et al.* 2003). Both abiotic and biotic parameters have been used to explain seagrass distribution. Dennison *et al.* (1993) linked water quality to seagrass distribution. They found that light attenuation, which is critical for explaining seagrass distribution, is a direct function of factors that relate to water quality, including dissolved organic matter, total suspended solids, chlorophyll *a*, and others. Koch (2001) linked physical, geological, and geochemical parameters to seagrass distribution, in addition to traditional measurements pertaining to light availability (total suspended solids, nutrients, epiphytes, and chlorophyll concentration). Fourqurean *et al.* (2003) related the abiotic variables of salinity, light, depth, and nutrient concentrations to seagrass distribution in Florida Bay. Livingston *et al.* (1998) concluded that salinity, temperature, and depth are important for determining seagrass distribution, but when those variables are not limiting, light, sediment, and nutrients become important. Although these studies included many of the same parameters, no single set of predictors of seagrass health has emerged.

In order to develop a monitoring program for seagrasses on the Texas coast, it is critical to determine which indicators, biotic and abiotic, will give the most information about the state of seagrasses. We measured a wide array of water, sediment, and biological characteristics in two seagrass dominated Texas estuaries in order to determine which are the most critical for inclusion in a monitoring program. We also evaluated the best techniques for cost effective field sampling and laboratory sample analysis.

Materials and Methods

Study Areas

This study was conducted in two seagrass dominated estuaries along the south Texas coast, Redfish Bay (RFB) (W 97˚7'; N 27˚53') and lower Laguna Madre (LLM) (W 97˚13'; N 26˚6'). The two estuaries (Figure 1) are separated by approximately 220 km of coastline. RFB is a shallow estuary (typically <1 m) with extensive seagrass beds. *Thalassia testudinum* Banks ex König and *Halodule wrightii* Ascherson are the dominant seagrasses in RFB; however, *Syringodium filiforme* Kütz, *Halophila engelmanii* Ascherson, and *Ruppia maritima* L. are often present. Several dredged channels and spoil islands border and bisect Redfish Bay, including the Gulf Intracoastal Waterway (GIWW) along the western shore (Pulich *et al.* 1997). The Laguna Madre is a shallow hypersaline lagoon between Padre Island, a barrier island, and the mainland of Texas. It extends about 200 km from Corpus Christi Bay to the US-Mexico border. The majority (over 79%) of seagrass in Texas is found in the Laguna Madre (Pulich 1998). The Laguna Madre is divided into upper and lower sections by a land-bridge between Padre Island and the mainland (Tunnell 2002). The two sections are connected through the GIWW, which bisects the entire length of the Laguna Madre on the north-south axis. LLM is generally deeper than RFB (1-2 m) and is dominated by *T. testudinum* and *S. filiforme*.

Both RFB and LLM are connected to the Gulf of Mexico through relatively small channels. As a result, exchange with the Gulf is limited. The tidal range in both study areas is < 0.3 m. In general, RFB receives more freshwater inflow because of higher annual precipitation, and it receives freshwater inputs from the Nueces River Basin and the San Antonio/Nueces Coastal Basin via Corpus Christi Bay and Copano Bay, respectively (Figure 2). According to USGS monthy streamflow data measured from October 1989 to September 2003 at Calallen along the Nueces River, streamflow is variable, ranging from 0 ft^3s^{-1} to over 16,000 ft^3s^{-1} (http://nwis.waterdata.usgs.gov/tx/nwis/monthly). LLM receives freshwater input from the Nueces/Rio Grande Coastal Basin, which contains no major rivers (Nueces River Authority 2000). The Arroyo Colorado River, a small tributary of the Rio Grande, discharges an average of 250 ft^3s^{-1} into LLM, according to the National Stream Water Quality Accounting Network (NASQAN, http://water.usgs.gov/nasqan/progdocs/statables.html). Low freshwater input, relatively small connections with the Gulf of Mexico, and the high rate of evaporation (about 140 cm yr^{-1}) all contribute to hypersalinity in Laguna Madre (Tunnell 2002). Precipitation along the south Texas coast is irregular and unpredictable, with an average of about 70 cm yr^{-1} (Tunnell 2002). According to the National Climate Data Center, annual rainfall in Corpus Christi has ranged from 13.7 cm in 1917 to 100.1 cm in 2001 (http://lwf.ncdc.noaa.gov/oa/ncdc.html). RFB has an average salinity of 27 ppt (Longley 1994), while LLM has an average salinity of 40 ppt (Quammen and Onuf 1993).

Sampling Design

Fieldwork was conducted semiannually at 30 sampling sites within a 32 km^2 area of each estuary. Sampling commenced in July 2002 and ended in February 2004, for a total of four sampling periods. Sampling in RFB occurred over a one-month period in July/August 2002, February 2003, July/August 2003, and February 2004. Sampling in LLM occurred over a one-month period in September 2002 and over a one-week period in January 2003, September 2003, and January 2004. Multiple abiotic and biotic parameters were measured at all sites (Table 1).

In order to select sampling sites, digital geographic data of the Texas counties and water bodies were obtained from the USGS National Hydrography Dataset (NHD) (http://nhd.usgs.gov/data.html). These data were incorporated into a Geographic Information System (GIS) and were used as a basemap. A shapefile of the two study areas was created using ArcInfo 8.3.0 (ESRI, Redlands, California, 2003), and a layer of 0.66 km^2 hexagonal subunits of equal size was overlaid on each study area (Figures 3 and 4). Sampling sites were selected using a stratified-random approach developed by the US EPA's EMAP program (http://www.epa.gov/emap) to ensure a random, yet evenly distributed sampling effort. Sixty random points were created in each study area: 30 sampling sites and 30 alternate sites. Alternate sites were created in the event that initial selections were inaccessible because of ship channels, oyster reefs, or other obstructions. All random points were created using a Random Sample Generator (RSG) program from USGS. The RSG runs in ArcView and was created from several programs and scripts written in Perl, UNIX csh, ArcInfo macro language, and ArcView Avenue (ArcInfo and ArcView products from ESRI, Redlands, California) (Steve Robb, USGS, personal communication). The probability of a hexagon containing a point was proportional to the area within the hexagon covered by water. Each hexagon could only have one site and some hexagons had no sites. All hexagons and sampling sites were added to the basemap (Figures 5 and 6).

Each site was given a unique identification number and coordinates in both decimal degrees and in meters. All data points were in the North American Datum (NAD) 1927 geographic coordinate system and were projected in Transverse Mercator (UTM Zone 14N). Sampling sites were located in the field using a handheld Global Positioning System, GPSMap 76S (Garmin International Inc., Olathe, Kansas, USA) which is accurate to ± 5 m. Initially, a PVC pole was used to mark sites; however, in some cases sites were too deep to use PVC poles or the poles were lost. At deep sites and sites with missing poles, the GPS was used to locate sites.

At each site, a temporary 50-m transect was established by looping a rope marked at 1 meter intervals around a PVC pole (Figure 7). The rope was extended in a southerly direction, and the far end was secured with a temporary PVC pole and a weight if necessary. Transects were assembled in the same direction at all sites throughout all sampling periods. Seagrass percent cover was measured and drift macroalgae were collected at ten random locations along each transect. We used a random number generator to select 10 points (out of a possible 50) along each 50-m transect line. These random points were used as sampling locations on transects at all thirty sites. A new set of randomly generated points was selected each sampling period.

Drift macroalgal collections and percent cover estimates were both made directly beneath the meter marks. Percent cover of seagrasses, attached macroalgae, and bare area were visually estimated using a 0.25 m^2 quadrat subdivided into 100 5-cm x 5-cm cells held over the seagrass canopy. Visual estimates of percent cover were made using snorkeling equipment; however, SCUBA was occasionally required if water levels were unusually high. If visibility was extremely poor, such as after a rain event or during periods of high winds, percent cover was estimated by feel.

Drift Macroalgal Abundance

Drift macroalgae were collected within a 0.0625 m^2 quadrat at each random sampling point, bagged, and placed in a cooler on ice. On return to the lab, samples were refrigerated at 4 ºC. Samples were subsequently rinsed with fresh water, cleaned of any dead seagrass material, and sorted by species. Macroalgae were identified to species and dried separately in an oven at 60 ºC to a constant weight. Species dry weight and total dry weight per quadrat were calculated and expressed as dry weight m^{-2}.

Seagrass Biomass

We collected three replicate seagrass biomass cores of species found at the site. Samples were not collected along the transect to avoid disturbing areas used for percent cover estimates. *Thalassia testudinum* was collected using a 15-cm diameter core, and a 9-cm diameter core was used to estimate biomass for *Halodule wrightii*, *Syrindogium filiforme*, *Halophila engelmanii*, and *Ruppia maritima*. A larger core was used for *T. testudinum* because it has a much lower shoot density compared to the other species. We collected three replicates of each species if beds were monospecific. If beds were a mix of two species, a total of three cores were taken instead of six cores to avoid collecting six replicates of the same species. All cores were sieved using a 1-mm mesh screen to remove sediment. Sieved samples were bagged and placed in a cooler on ice. Back at the lab, samples were refrigerated at 4 ºC until they could be processed. During processing, we recorded the number of shoots per core to estimate shoot density (shoots m^{-2}). Five shoots were selected haphazardly for plant morphometric measurements (number of blades per shoot and the length and width of the longest blade on each of those shoots). All shoots were separated into above- and below-ground tissues and dried in an oven at 60 ºC to a constant weight. Final weights of above- and below-ground biomass were expressed as dry weight m^{-2}.

Seagrass Epiphytes

We collected six to ten shoots of each species to determine the biomass of seagrass epiphytes. Shoots were placed in sealable 12-oz plastic sample bags (Whirlpak, NASCO, Kansas, USA) with water to prevent sample desiccation, and bags were placed in a cooler on ice. Back at the lab, samples were refrigerated at 4 ºC. Epiphytes were gently removed with a razor blade from a 10 cm portion of three blades of *Thalassia testudinum*. Only the middle sections of blades were used because the ends were often completely covered with epiphytes, which made them extremely fragile. In addition, the middle section was used so we could compare epiphyte biomass across shoots of different sizes. Epiphytes were transferred to a pre-weighed glass fiber filter and dried in an oven at 60 ºC to a constant weight. The dry weight of epiphytes was converted to mg cm^{-2} of blade area.

C:N Blade Ratios

After epiphytes were removed from 10 cm blades of *T. testudinum*, the cleaned blades were frozen for subsequent analysis of elemental carbon and nitrogen. Blades were thawed and dried in an oven at 60 ºC. We used a Wig-L-Bug (DENTSPLY Rinn Corp., Elgin, Illinois) to pulverize the seagrass blades into a fine powder. Carbon and nitrogen content were analyzed with an automatic elemental analyzer (model NC 2500, Fison Instruments, Rodano-Milan, Italy).

Abiotic Parameters

We measured dissolved oxygen (mg L^{-1}), salinity (ppt), and temperature (ºC) with a YSI 600XLM Sonde (YSI Incorporated, Yellow Springs, Ohio, USA). Three measurements of each parameter were recorded at each site. Light attenuation (k) and percent surface irradiance (%SI) were calculated from measurements of irradiance from the water surface and at the top of the seagrass canopy (or near the sediment surface if no seagrass was present). Photosynthetically active radiation (PAR = 400 to 700 nm wavelengths) was measured in μmol photons m^{-2} s^{-1} using an LI-190SA cosine quantum sensor in conjunction with an LI-1000 data logger (LI-COR Inc., Lincoln, Nebraska, USA). Light attenuation, k, was calculated using the transformed Beer Lambert equation:

$$k = [-\ln(I_z/I_0)]/z \qquad (1)$$

where k is the attenuation coefficient (m^{-1}) and I_z and I_0 are irradiance (μmol photons m^{-2} s^{-1}) at depth z (in m) and at the surface, respectively. The following formula was used to calculate %SI:

$$\%SI = ((I_0-I_z)/z)*100 \qquad (2)$$

where I_z and I_0 represent irradiance (μmol photons m^{-2} s^{-1}) at depth z (in m) and the surface respectively.

Sediment Analysis

Sediment cores were collected for measurement of total organic carbon (TOC), porewater NH_4^+, and sediment grain size. Three 60-cm^3 cores were collected for each analysis (total nine cores per site). Cores were taken haphazardly near the transect. All cores were placed in sealable 4-oz plastic sample bags (Whirlpak, NASCO, Kansas, USA) and placed in a cooler on ice. Samples were taken back to the laboratory and stored at -70 ºC. To measure TOC, approximately 20-25 cm^3 of sediment was placed into a crucible. Crucibles were placed in an oven at 105 ºC for at least 48 hours. They were dried to a constant weight and then positioned in an Isotemp Programmable Muffle Furnace (Fisher Scientific, Fowlerville, Michigan) at 550 ºC for 4 hours (Dean 1974). Samples were allowed to cool, and we recorded a second dry weight. TOC was calculated as the percent loss on ignition (LOI) using the following formula:

$$\%\ LOI = ((DW105 - DW550)/DW105) \times 100 \qquad (3)$$

where DW105 and DW550 are the dry weights after oven drying and combustion, respectively (Dean 1974).

Sediment cores used in porewater NH_4^+ analysis were thawed, and the sediment was homogenized by hand in the plastic bag. Sediment was scooped into plastic centrifuge tubes and centrifuged at 10,000 rpm for 20 minutes to extract porewater. We removed 2.5 mL of porewater from each centrifuge tube. Concentrations of NH_4^+ (μmol) were determined using standard colorimetric technique described by Parsons *et al.* (1984).

Sediment grain size was only measured during the first and last sampling periods (summer 2002 and winter 2004). Percent contribution by weight was measured for four components following Folk (1974): clay (0.06 – 2 μm), silt (3.9 – 53 μm), sand (62.5 –250 μm), and rubble (>250 μm). After samples were thawed and homogenized, 20 cm^3 were put into a glass beaker and approximately 100 mL of 3% hydrogen peroxide were added to digest organic material. Samples were stirred daily for at least one week to ensure all organic material was digested. Samples were wet sieved through a 62.5-μm mesh stainless steel screen using a vacuum pump to separate rubble and sand from silt and clay. After drying for 24-48 hours at 110 ºC, rubble and sand were separated using a 250-μm screen. Silt and clay fractions were measured using pipette analysis. The settling velocity was used to classify the particles and to determine the percent composition of each fraction, based on weight. The amount of silt and clay were calculated using the following equations from Folk (1974):

$$\text{clay} = (\text{dry weight of clay} - 0.02)50 \tag{4}$$

$$\text{silt} = [(\text{dry weight of silt} + \text{clay}) - 0.02]50 - \text{dry weight of clay} \tag{5}$$

Water Quality Analysis

At each site, surface water was collected for analysis of total suspended solids (TSS), chlorophyll *a* concentration, and nutrient concentrations. Triplicate 1-L plastic bottles of water were collected for analysis of TSS. A known amount of water was filtered using a pre-weighed glass fiber filter (1.6 μm mesh size). Filters were dried to a constant weight in an oven at 60 ºC. TSS (mg L^{-1}) was calculated by subtracting the filter's initial weight from the final weight following filtration.

Three 500-mL bottles of water were collected for analysis of chlorophyll *a* concentration and placed in a dark cooler on ice. Immediately upon return from the field, a known volume of water was filtered in the dark on a 0.45-μm cellulose nitrate membrane. Chlorophyll *a* was extracted according to Parsons *et al*. (1984). After filtration, nitrocellulose membranes were placed in 10-mL glass tubes and 5 mL of 90% acetone was added to each tube. Chlorophyll *a* concentration was calculated using absorbance measured at wavelengths 630, 647, 664, and 750 nm on a UV-2401PC Spectrophotometer (Shimadzu, Tokyo, Japan). Absorbance values at 750 nm were subtracted from absorbance values at wavelengths 630, 647, and 664 nm to correct for turbidity. Chlorophyll *a* concentration was calculated in μg L^{-1} using the following formula:

$$\text{Chlorophyll } a = [S(11.85A_{664} - 1.54A_{647} - 0.08A_{630})]/V \tag{6}$$

where S, A, and V represent the volume of acetone used (mL), absorbance (nm), and volume of filtered water (L), respectively (Parsons *et al*. 1984).

Three 100-mL bottles of water were collected for analysis of dissolved inorganic nutrient (DIN) concentrations. Samples were immediately placed in the dark on ice and then frozen at -70 ºC. A Lachat QuikChem 8000 (Zellweger Analytics Inc., Milwaukee, Wisconsin, USA) was used to measure concentrations of NH_4^+, NO_2^-+NO_3^- and PO_4^{3-} in μM by continuous flow injection analysis using colorimetric techniques. This method of nutrient analysis was chosen because it has a minimum detection level of 0.03 μM.

Geostatistical Analysis

Each measured parameter measured at each site within each study area was displayed spatially in ArcMap (ArcInfo 8.3.0, ESRI, Redlands, California, 2003). Data were represented spatially to better detect trends. Geostatistical analysis was conducted using the Geostatistical Analyst extension in ArcMap following Johnston *et al.* (2001). First, percent cover data were added as data points on the basemap in ArcMap. Then, the statistical properties of the data were investigated by examining trends, identifying outliers, and plotting the distribution. Next, a model of the semivariogram was created, which is a function that relates semivariance of data points to the distance between them. Kriging was used to create a continuous surface. If more than one surface was created, results were compared and cross-validation was used to choose the most appropriate surface. Cross-validation (in Geostatistical Analyst) determines how well the surface predicts values in unmeasured locations. It removes a data point and predicts its value using the remaining data points. Then, the predicted point is compared to the measured value to determine whether the model is reasonable. This kriging procedure was repeated for all parameters in RFB and LLM.

Results

Abiotic Parameters

Redfish Bay was generally very shallow (<1 m) at most sites (Figure 8). In South RFB, sites 21, 23, 24, and 26 were located in the shallowest portion of RFB in an area surrounded by spoil islands. Sites 14, 22, 25, 28, 29, and 30 were relatively deep (>1 m) and unvegetated. In north RFB, sites 11, 12, 13, 15, and 16 were very shallow (< 0.5 m). On average, sites in Lower Laguna Madre were deeper than RFB, with all sites deeper than 1 m (Figure 9). Sites to the far west were the deepest and did not have seagrasses. Sites 3, 11, 14, 17, 20, 23, 26, and 29 were just west of the Gulf Intracoastal Waterway (GIWW) and had sparse seagrass cover. From the GIWW to South Padre Island depth gradually decreased.

Salinity was highest in the southeast corner of RFB (Figure 10). Average salinity in RFB ranged from 21.4 ± 1.1 ppt during winter 2003 to 35.6 ± 0.7 ppt during summer 2003 (Table 2). Salinity was higher during the summers than the winters in both RFB and LLM, but salinity was higher in LLM than RFB during each sampling period (Table 2). In LLM, salinity was higher at sites in the south, closest to the opening to the Gulf of Mexico (Figure 11). Average salinity in LLM ranged from 27.9 ± 0.6 ppt in winter 2003 to 40.7 ± 0.2 ppt in summer 2003.

In RFB, total suspended solids (TSS) were higher in sites with seagrasses than in the deeper, bare sites (Figure 12, left panel). Sites with high TSS also had higher % SI (Figure 12, right panel). Light attenuation in RFB was generally between 1.0 and 2.0 m^{-1} and was higher in shallow, seagrass dominated areas (Figure 13). In LLM, TSS were higher at sites on the west side of the Gulf Intracoastal Waterway (Figure 14, left panel). These sites were in deeper water (> 2 m) and had low light near the sediment surface (Figure 14, right panel). Sites east of the GIWW had lower TSS and higher % SI. Light attenuation in LLM was generally between 1.0 and 3.0 m^{-1} and increased from east to west (Figure 15). TSS, % SI, and light attenuation all followed the same pattern across LLM.

Chlorophyll *a* concentrations in RFB ranged from an average of 1.5 ± 0.1 $\mu g\ L^{-1}$ in winter 2004 to 6.5 ± 0.8 $\mu g\ L^{-1}$ in winter 2003 (Table 2). We did not observe any seasonal patterns in chlorophyll *a* concentrations in RFB or LLM. Overall, sites in northern RFB had higher chlorophyll *a* concentrations, especially at sites 12, 13, and 15 (Figure 16). In LLM, the seasonal average chlorophyll *a* concentration ranged from 1.0 ± 0.1 $\mu g\ L^{-1}$ in summer 2002 to 2.1 ± 0.2 $\mu g\ L^{-1}$ in winter 2004 (Table 2). Sites in the center of LLM had higher chlorophyll *a* concentrations, especially at sites 5 and 6 (Figure 17); however, variability between sites in LLM was low.

Water column nutrients (NH_4^+, $NO_3^- + NO_2^-$, PO_4^{3-}) in RFB and LLM did not vary much between seasons. In RFB, the average seasonal NH_4^+ concentration ranged from 0.76 ± 0.08 µM to 1.84 ± 0.11 µM (Table 2). The concentration of NH_4^+ generally decreased from north to south (Figure 18, left panel). This pattern was not as clear when we looked at each site during all 4 sampling periods (Figure 18, right panel). Average water column $NO_3^- + NO_2^-$ was lowest during summer 2003 at 0.09 ± 0.01 µM and highest during winter 2003 at 0.73 ± 0.21 µM (Table 2). We also observed a decreasing trend in $NO_3^- + NO_2^-$ concentration from north to south (Figure 19, left panel). Seasonal differences between sites were small, but we did observe higher concentrations at some sites during winter 2003, especially at site 4 (Figure 19, right panel). The concentration of PO_4^{3-} in RFB did not change much seasonally. The seasonal average ranged only from 0.32 ± 0.02 µM in winter 2004 to 0.54 ± 0.06 µM in summer 2002 (Table 2). The concentration of PO_4^{3-} decreased during each sampling period. We observed the same pattern of decreasing concentration from north to south across RFB (Figure 20, left panel). Decreasing seasonal concentrations of PO_4^{3-} were more evident in north RFB (Figure 20, right panel). In general, nutrient concentrations of NH_4^+, NO_3^- + NO_2^-, and PO_4^{3-} in RFB were low during all sampling periods, decreased from north to south, and did not vary much between sites.

In LLM, water column nutrient concentrations were similar to RFB (< 2 μM). The average seasonal NH_4^+ ranged from 0.49 ± 0.04 μM in winter 2003 to 1.47 ± 0.03 μM in winter 2004 (Table 2). NH_4^+ concentration was highest near Padre Island and decreased towards the south west (Figure 21, top panel). The concentration of NH_4^+ generally increased from the first sampling period to the last (Figure 21, lower panel). We did not observe a seasonal pattern in the concentration of NO_3^- + NO_2^-. The seasonal average ranged from 0.05 ± 0.01 μM to 0.62 ± 0.18 μM (Table 2). We did not find the same spatial trend in NO_3^- + NO_2^- as we did with NH_4^+ (Figure 22, top panel). Sites in the middle in the east/west direction had the lowest concentrations. During winter 2003, sites 23, 24, 26, and 29 in south LLM had much higher NO_3^- + NO_2^- concentrations than the other sites (Figure 22, lower panel). Concentrations of PO_4^{3-} did not follow a seasonal pattern and the average seasonal concentration ranged from 0.16 ± 0.01 μM to 0.61 ± 0.13 μM (Table 2). More northern sites had higher concentrations of PO_4^{3-}, with the highest concentrations at site 9 (Figure 23, top panel). These higher concentrations were present during the winter 2003 sampling period (Figure 23, lower panel).

Sediment total organic carbon (TOC) did not vary seasonally in RFB or LLM. In RFB, sites in areas with higher seagrass cover tended to have higher TOC content (Figure 24, left panel). In addition, those sites also tended to have smaller grain sizes. Sites with lower TOC tended to have sediment with a higher sand content instead of smaller silts and clays (Figure 24). This relationship was especially clear in sites in north RFB. In LLM, TOC did not vary seasonally (Table 2). TOC increased from the northwest towards the southeast (Figure 25, top panel). In addition to RFB, we also observed a relationship between sediment grain size and TOC in LLM (Figure 25). Sites with higher TOC had lower percent sand.

Sediment porewater NH_4^+ concentrations in RFB were higher in the summers than during the winters (Table 2). The average seasonal porewater NH_4^+ concentration ranged from 65.6 ± 3.1 μM to 109.6 ± 7.2 μM in RFB. Spatially, no clear trends were apparent (Figure 26). Porewater NH_4^+ concentrations at each site and between sites were highly variable. In LLM, the average seasonal porewater NH_4^+ concentrations were lower than in RFB during each sampling period. Concentrations ranged from an average of 27.9 ± 4.3 μM to 39.0 ± 3.1 μM (Table 2). We did observe a spatial trend to porewater NH_4^+ in LLM. Concentrations decreased from west to east towards Padre Island (Figure 27). The highest concentrations were found in deeper bare areas on the west side.

Biotic Parameters

Aboveground (AG) biomass of *Thalassia testudinum* in RFB was more than twice as high during the summers as the winters (Table 3). The average winter and summer aboveground biomass values were 74 ± 8 g m^{-2} and 206 ± 22 g m^{-2}, respectively. AG biomass was highest in the shallowest parts of RFB (Figure 28, left panel). In north RFB, sites 10, 12, 13, 15, and 16 had the highest *Thalassia* AG biomass. In south RFB, sites 21, 23, 24, and 26 had the highest *Thalassia* AG biomass. The most northern sites in RFB were more commonly dominated by *Halodule wrightii* instead of *Thalassia testudinum*. Root:shoot ratios were higher during the winters when AG biomass was lower (Table 3). In general, root:shoot ratios were higher in south RFB as well as at site 4 in north RFB (Figure 28, right panel). In LLM, AG biomass was approximately twice as high during the summers as the winters (Table 3). Average summer and winter AG biomass values were 139 ± 21 g m^{-2} and 68 ± 8 g m^{-2}, respectively. The highest AG biomass values were found at sites in the north east corner of our study area (Figure 29, top panel). Sites in the south west corner had the lowest AG biomass values. Similar to RFB, root:shoot ratios were also higher during winters than summers. Sites with lower AG biomass also had lower root:shoot ratios in LLM (Figure 29, lower panel).

In RFB, shoot density of *Thalassia testudinum* did not follow a clear seasonal pattern. We measured the highest average shoot density, 916 ± 59 shoots m^{-2}, during summer 2002 (Table 3). The lowest average shoot density, 688 ± 48 shoots m^{-2}, was measured during winter 2003. The highest shoot density was observed in north RFB at sites 7, 9, 10, and 12 (Figure 30). The lowest shoot density was found at sites 1-4 in north RFB; however, those sites were often dominated by species other than *T. testudinum*. In LLM, shoot density was higher during the summers than winters (Table 3). Average summer and winter values were 1006 ± 145 shoots m^{-2} and 846 ± 135 shoots m^{-2}, respectively. Variability in shoot density was higher in LLM than in RFB. Sites in LLM with higher AG biomass tended to have higher shoot density (Figure 31). Sites towards the northeast, especially sites 1 and 7, had the highest shoot density.

Epiphyte biomass on blades of *Thalassia testudinum* was generally higher in RFB than LLM (Table 3). We did not observe a seasonal pattern to epiphyte biomass in RFB. Epiphyte biomass was highest in RFB at sites 8 and 11 in north RFB and lowest at sites 1-3 and 6 in the far north (Figure 32). In LLM, epiphyte biomass was higher during the two winter sampling periods than during summer sampling periods (Table 3). Epiphyte biomass was highest at sites in the southwest corner of our study area and decreased towards the northeast (Figure 33).

C:N ratios of *Thalassia testudinum* blades from summer 2002 were not significantly different between RFB and LLM (Table 3). In RFB, the average C:N blade ratio was 12.9 ± 0.3. The lowest C:N ratios were found at sites 18-20 in south RFB (Figure 34). In LLM, the average C:N blade ratio was 13.1 ± 0.2, with higher values close to Padre Island (Figure 35). Variability between sites in C:N ratios was small in both RFB and LLM.

Discussion

Abiotic Parameters

Salinity increased towards the southeast portion of RFB due to channel openings to the Gulf of Mexico. RFB had lower salinity during each sampling period than LLM due to higher precipitation, lower evaporation, and higher fresh water inflow at RFB; however, these estuaries followed similar salinity seasonal patterns due to their close proximity and similar weather conditions.

It was surprising to find higher total suspended solids (TSS) in sites with seagrasses at RFB. This is likely because all sites with seagrasses were in depths of less than 1 m, where sediment may be easily stirred up by wind. In addition, these seagrass covered areas tended to have smaller sized particles (Figure 24), which become suspended more easily. Despite higher TSS levels, seagrasses probably survived lower light conditions because of the shallow depth. Consequently, % SI is a better indicator of the underwater light environment. Sites with high TSS still had high light at the canopy level. These results emphasize the importance of measuring both TSS and light at the surface and at depth. In LLM, TSS was higher at the bare sites west of the spoil islands from the dredged Gulf Intracoastal Waterway (GIWW). The dredged material is resuspended in the water column, creating high turbidity and low light at depth. Even though sites in RFB had high TSS, the depth was shallower, which allowed for light to penetrate. In LLM, sites on the far west were at least 2 m deep, which did not allow enough light to penetrate for seagrasses to survive (see Onuf 1994 for more).

Chlorophyll *a* concentrations did not vary seasonally and were highly variable between sites. We did not find a relationship between water column nutrients and chlorophyll *a* concentrations. Therefore, we did not find chlorophyll *a* concentrations to be very informative. It is likely that nutrient and chlorophyll concentrations vary on a daily basis. In LLM, chlorophyll *a* concentrations were very low and not highly variable between sites. We also found low water column nutrient concentrations in LLM. Our biannual sampling scheme does not adequately capture the nutrient and phytoplankton dynamics in these estuaries.

Water column nutrient concentrations were higher in RFB and LLM. This could be due to higher annual precipitation, higher freshwater inflow, and potentially higher nutrient loading to RFB (Tunnell 2002). In RFB, nutrient concentrations decreased from north to south. This corresponds to the salinity gradient across RFB (Figure 10). Sites with lower salinity also had higher nutrient concentrations. In LLM, we did not find a relationship between salinity and NH_4^+, $NO_3^- + NO_2^-$, or PO_4^{3-}. This could be due to a difference in wind direction during the seasons, which could change current directions and influence the mixing of fresh and salt water in LLM. In Laguna Madre, southeasterly winds prevail most of the time, except for some northerly winds during winter storms (Tunnell 2002). Since LLM has a larger opening with the Gulf of Mexico and it is an open lagoon without interior islands to obstruct water movement, it is probably more extensively mixed than RFB. This scenario could also explain why the variability between nutrient concentrations at sites in LLM was very small.

Sediment total organic carbon (TOC) and grain size were strongly correlated. Sites with low total organic carbon tended to have a higher percentage of sand. Bare sites tended to have low TOC and high percent sand, whereas sites with seagrasses tended to have high TOC and low percent sand.

Porewater NH_4^+ was highly variable, especially in RFB. Within and between site variability were both high. This heterogeneity is likely because of the variability in seagrass cover in RFB. At many sites, several species could be found together in addition to many bare areas. Random sampling within this heterogeneous environment could account for much of the within site variability. In LLM, porewater NH_4^+ was not as variable. We found a trend of increasing concentrations from east to west. Bare sites had higher porewater NH_4^+ concentrations than sites with seagrasses. Within site variability was less in LLM than in RFB. In LLM, seagrass cover was dominated by *Thalassia testudinum* at all vegetated sites, reducing the within site heterogeneity.

Biotic Parameters

Aboveground biomass and root:shoot ratios of *Thalassia testudinum* varied seasonally in RFB and LLM. There was more of a seasonal effect on seagrasses in RFB, which could be due to a higher temperature difference between summer and winter and colder average temperatures in winter (Tunnell 2002). In RFB, sites in the shallowest protected areas had the most seagrass biomass. This pattern is likely related to the high amount of available light in these areas. In LLM, sites with lower AG biomass also had lower BG biomass and root:shoot ratios. These sites were on the west side of the GIWW, near the spoil islands. It was not surprising to find lower above- and below-ground biomass in this area, which also has higher TSS and lower available light (Figure 14).

Shoot density of *Thalassia testudinum* did not follow a seasonal pattern in RFB, but a seasonal pattern was evident in LLM. LLM was continuously dominated by *T. testudinum* mixed with *Syringodium filiforme*. Shoot density decreased during the winters, but when it increased in the summers, new shoots of the same species reappeared. In RFB, 5 species were present. At some sites *T. testudinum* was present during some sampling periods and then absent during other sampling periods. Also, most sites in north RFB had mixed assemblages, which could influence the shoot density of *T. testudinum*.

Epiphytes were abundant on seagrasses in RFB during all sampling periods. The overall high abundance of epiphytes in RFB suggests that it is a nutrient-replete system. In LLM, epiphyte biomass was higher during winters than summers. The within and between variability of epiphyte growth was high. C:N ratios in both RFB and LLM were low (approximately 13). Low C:N ratios indicate that nitrogen is not a limiting nutrient for seagrasses in either estuary. In a study by Lee and Dunton (1999), *Thalassia testudinum* in Corpus Christi Bay (near RFB) had C:N ratios ranging from 13 – 18. In LLM, Lee and Dunton (1999) found C:N ratios of 20 – 25 for *T. testudinum*. Our study indicates that LLM may not be as nitrogen limited today as previously noted.

Potential threats to seagrasses at specific sites

In south RFB, sites 21, 23, 24, and 26 were in a shallow area surrounded by spoil islands. These sites had above average accumulations of drift macroalgae. Although seagrasses were present at these sites, we often found large bare areas covered by drift macroalgae. We do not know if the drift macroalgae created these bare areas or if the macroalgae accumulated in already bare areas. Regardless of the origin of the bare areas, if the presence of drift macroalgae prevents the re-growth of seagrasses in bare areas, the algae will have a negative impact on seagrasses. Additionally, the abundance of drift macroalgae could be an indicator of excess nutrients in this estuary and should be monitored in the future.

In LLM, sites west of the GIWW have low shoot density, low above- and below-ground biomass, and high epiphytes. Of the sites in LLM, seagrasses at these sites are the most likely to be stressed due to light conditions. The low % SI, high TSS, and increased epiphyte growth all contribute to lower light availability compared to sites east of the GIWW. As a result, the biotic parameters we measured should be measured at these vulnerable sites in the future. The large quantity of drift macroalgae is another potential threat to seagrasses in LLM. In order to fully understand this threat, drift macroalgae should be monitored in addition to seagrasses. In addition, we found the intrusion of several attached algal species, including *Halimeda incrassata*, *Caulerpa prolifera*, and *Caulerpa mexicana* at many of the vegetated sites west and south east of the GIWW. An intrusion by algae should be monitored in the event of species replacement.

Conclusions and Recommendations

This study was successful because it has given us a wealth of information about two seagrass dominated estuaries in Texas. In addition, it has allowed us to make recommendations for the development of a future seagrass monitoring program. Our in-depth study can be reduced to fit the needs of others interested in monitoring seagrasses in Texas. We can also modify our methods to make them more cost effective. Each section below addresses problems and suggestions for improvement or ways of reducing time or costs.

Nutrients

We measured nutrients in the water column at all 30 sites in both estuaries (RFB and LLM). Some of the sites were very close together (< 500 m between sites). The difference in nutrient concentrations between these sites was not significant for NH_4^+, $NO_3^- + NO_2^-$, or PO_4^{3-}. Even sites that were separated by several kilometers were not highly variable. We determined that fewer nutrient measurements are needed in these small areas. We recommend measuring nutrient concentrations at 3 – 5 sites instead of 30. Such a reduction would also reduce costs significantly. One of our main conclusions in chapter 2 is that dissolved inorganic nutrient (DIN) concentrations may not necessarily reflect nutrient loading to these estuaries. Rather than focus on DIN, we argue that integrative biological measurements including epiphyte biomass, drift macroalgal biomass, and C:N:P ratios give more information about the nutrient status of these systems. We believe that greater focus on these biological indicators may be more effective than intensive measurements of abiotic parameters.

Field sampling

We sampled twice per year and recommend the winter/summer sampling schedule. We were able to observe seasonal differences in seagrass characteristics, including changes in above- and below-ground biomass, root:shoot ratios, shoot density, percent cover, and blade length (Table 3). It was also useful to sample biannually to understand fluctuations in epiphyte and drift macroalgal biomass.

Sampling at each site required 4 people per day and we were able to sample an average of 5 sites per day. This translated into 6 field days x 2 estuaries x 2 seasons, for a total of 24 field days per year. The number of field days could be dramatically reduced by modifying some of our techniques. First, at each site we set up a 50-m transect line to measure percent cover and collect drift macroalgae ten times. Setting up the transect, collecting drift macroalgae, and measuring percent cover took the most time at each site. Using the transect also required two people to work on the transect while two others collected cores. If four people are not available for field work, setting up a transect may not be feasible. Percent cover measurements could be made by randomly throwing the 0.25 m^2 quadrat from the boat. If only a more general estimate of seagrass cover is needed, percent cover could be assessed visually from the boat; however this would not be feasible if there is dense cover of drift macroalgae. This would reduce the number of people required as well as dramatically reduce the amount of time spent at each site.

To reduce time, effort, and costs, sediment and seagrass biomass cores could be taken over the side of the boat (Onuf 1996b). In the seagrass cores, drift macroalgal biomass could be collected and assessed instead of collecting it along a transect line. This would mean a reduced number of individual samples collected which would also alleviate some of the extensive time necessary to separate, identify, and dry the drift macroalgae. There are some drawbacks to this change; however, because we found drift macroalgal biomass to be highly spatially variable. If the number of samples were reduced from 10 to 3, the assessment of algal biomass could be less accurate.

In addition to taking cores from the boat, another way to increase efficiency is to only take cores of the dominant species at each site. In order to compare sites, seagrasses of the same species must be compared. We collected cores of all seagrasses present at each site, but were only able to compare the dominant species present at all sites. Taking cores of species that are not found often, such as *Halophila engelmanii* and *Ruppia maritima* yields little additional information.

Light measurements could also be made without exiting the boat. We used a light sensor mounted to a small PVC pole that was inserted into the sediment to measure irradiance at the seagrass canopy. If the light sensor is instead mounted on a frame and lowered into the water (Onuf 1996b), the same measurements could be made faster and easier.

Most important parameters

Of the list of measured parameters (Table 1), several parameters are critical for a seagrass monitoring program. The most important seagrass parameters are above- and below-ground biomass, shoot density, blade length/width, and percent cover. In order to monitor changes in seagrasses, these measurements give the most information about physical changes in the seagrasses themselves. Other biotic parameters that are important are epiphyte biomass, drift macroalgal biomass, and blade C:N:P. These measurements can provide information about nutrient availability. In addition, changes in parameters including shoot density, seagrass cover, and epiphyte biomass could indicate potentially threatened seagrasses. Of the abiotic parameters, understanding light availability is most important. Measurements of light attenuation, % surface irradiance, chlorophyll *a*, and total suspended solids are useful for understanding the underwater light availability. In addition to light, measuring sediment porewater NH_4^+ is important for determining nutrient availability for seagrasses as well as monitoring for toxic levels of NH_4^+, which can threaten seagrasses.

Less critical parameters

While each parameter was of some value, in several instances, the contribution made to the understanding of seagrass conservation does not justify extensive sampling or inclusion in a monitoring program. For example, water column nutrient concentrations are important, but should not be a major focus. Sediment grain size and sediment total organic carbon give some information about the hydrodynamics of these systems, but are not extremely critical and can be difficult to interpret. Additionally, analysis of sediment grain size is very labor intensive, and the unique information it generates may not warrant such extensive sampling.

Modifying parameters

Dissolved oxygen (DO) measurements are considered important; however, the way we measure DO should be modified. When we measured DO at each site, the level was always acceptable (> 5 mg L^{-1}) because measurements were made during the day when photosynthesis occurs and keeps oxygen levels high. Our DO measurements were more a function of time of day than biological status of the seagrass beds. It would be more useful to measure DO at least for a 24 hour period to determine levels at night when respiration dominates.

Measuring seagrass cover is important in looking for long term trends of seagrass gain or loss; however, looking at percent cover on a very small scale only provides information specific to the sampling location. It would be useful to take concurrent aerial photographs to assess long term trends in cover on larger spatial scales. Aerial photography with accurate ground truthing may be the best method for quantifying the total extent of seagrass cover within these estuaries.

GIS and kriging

Throughout this project, we used GIS for mapping and analyzing data. We believe that GIS is an excellent tool to include in a seagrass monitoring program. It is especially useful in displaying data spatially and would be useful for observing changes over time. With the Geostatistical Analyst extension in ArcGIS, kriging can be quickly and easily done to permit interpolation between sampling sites. In this way, parameter estimates can be generated in areas where measurements are lacking, thereby lending predictive power to the data set and highlighting areas of particular interest. These techniques could easily be incorporated into a monitoring program to enhance its effectiveness.

Chapter 3

Drift Macroalgal Abundance and Distribution in Relationship to Biological Indicators in Two Seagrass Dominated Texas Estuarine Systems

Introduction

Most efforts to assess seagrass health have focused on the effects of nutrients. Tomasko and Lapointe (1991) linked seagrass biomass and productivity to water column nutrients and epiphyte biomass; however, Tomasko *et al.* (1996) found that water column nutrient levels did not clearly reflect watershed nitrogen loadings. Pulich *et al.* (1997) also suggested that nutrient levels may be poor indicators of water quality problems. Dunton (1996) found low concentrations of dissolved nitrogen in Laguna Madre during brown tide bloom conditions. This suggests that instantaneous measurements of nutrient concentrations may not reflect actual nutrient availability, which was suspected as the initial cause of the bloom (Whitledge *et al.* 1999).

Other studies have looked at the relationship between nutrients and epiphyte growth on seagrasses. Some research has indicated that increased nutrient availability results in greater epiphyte abundance on seagrasses (Cattaneo and Kalff 1980, Borum 1985, Dunton 1990). Frankovich and Fourqurean (1997) reported a positive relationship between epiphyte abundance and phosphorus availability, but suggested that epiphyte levels may not reflect nutrient enrichment as well as other seagrass parameters, including leaf nutrient content. Lin *et al.* (1996) concluded that epiphyte biomass on the seagrass *Zostera marina* was not a good indicator of nutrient input to the system or the extent of eutrophication. Further research is needed to clarify if epiphytes are reliable indicators of nutrient loading.

Despite the intensive research into declining seagrass health, relatively few studies have explored the potential problem of excessive drift macroalgal abundance and its threat to seagrasses. Drift macroalgae have been shown to compete with seagrasses for light and nutrients (Cowper 1978, Hauxwell *et al.* 2001, Hauxwell *et al.* 2003). A 20% reduction in surface irradiance by drift macroalgae has the potential to reduce the maximum rate of photosynthesis in seagrasses 50% (Cowper 1978). In conditions of high winds or increased terrestrial run-off, up to 90% of surface irradiance is attenuated in the top 10 cm of water (Conover 1964). In these poor surface conditions, drift algae may further increase seagrass stress by shading what little light is available.

Peckol and Rivers (1996) measured light attenuation through macroalgal canopies of different algal taxa. They found that irradiance was reduced by 95% within 6-8 cm from the top of the algal canopy, regardless of the algal taxon. Hersh (1996) studied macrophytes in several estuaries with different nutrient inputs in Waquiot Bay, Massachusetts. As nutrient loading increased, Hersh (1996) found that seagrass biomass decreased, biomass of drift macroalgae increased, and seagrass epiphytes decreased in abundance. Macroalgae in higher nutrient environments had a primary production to biomass ratio 8 times lower than macroalgae in lower nutrient environments. Hersh (1996) attributed this difference to self-shading because it limited photosynthesis to the top few centimeters of the algal canopy. Hauxwell *et al.* (2001) observed increasing rates of eelgrass loss as a function of algal canopy height and identified two main causes for seagrass decline: harsh sediment conditions and light limitation. Poor sediment conditions resulted from lowered redox conditions and high concentrations of NH_4^+, both which were attributed to the presence of macroalgal canopies (Hauxwell *et al.* 2001).

Increasing nutrient concentrations have the potential to change coastal ecosystems dramatically. In high nutrient environments, phytoplankton and macroalgae are superior competitors for light, which allows them to proliferate (Duarte 1995). If nutrient inputs increase, slow-growing seagrasses and large macroalgae will be replaced by fast-growing macroalgae and eventually phytoplankton (Duarte 1995, Deegan *et al.* 2002). According to McGlathery (2001), conversion of seagrasses to macroalgae can have many negative impacts on coastal ecosystems. For example, sediment resuspension increases because drifting macroalgae do not provide the same sediment stability that is provided by seagrass below-ground structures (McGlathery 2001). Conversion from seagrasses to macroalgae can lead to changes in trophic interactions and potentially a loss of species, including invertebrates and fish, that rely on seagrasses for survival (Norkko and Bonsdorff 1996).

Because of the potential effects of drift algae on seagrasses, it is essential to understand drift algal dynamics within seagrass beds. The main objective of this study was to determine the spatial and temporal variability in drift algal abundance in seagrass beds along the south Texas coast. Specifically, we tested the null hypothesis that there is no spatial or temporal variability in drift macroalgal abundance. We measured biotic and abiotic parameters to determine if spatial and temporal variability in drift algal abundance could be explained by these parameters. We examined both water column and sediment abiotic parameters, including salinity, temperature, nutrients, water column chlorophyll *a*, total suspended solids, light attenuation, % surface irradiance, depth, sediment grain size, porewater NH_4^+, and total organic carbon. Biotic parameters included seagrass measurements (above- and below-ground biomass, root:shoot ratio, shoot density, blade length, blade width, and C:N blade ratios) and epiphyte biomass.

Materials and Methods

Field sampling/laboratory analysis

See the materials and methods section of Chapter 2.

Data Analysis

A mixed model univariate analysis of variance (UNIANOVA) in SPSS (SPSS 11.5, SPSS Inc., 2002) was used to examine differences in drift macroalgal abundance between the two study areas, sampling periods, and sites within each study area. Drift macroalgal abundance was included as the dependent variable, sampling period and study area were included as fixed effects, and site within study area was the random effect (the nested variable). We examined significance of sampling period, study area, study area by sampling period, site within study area, and sampling period by site within study area.

Relationships between measured parameters were analyzed with principal components analysis (PCA) using the software package Primer 5 (version 5.2, Primer-E Ltd., United Kingdom). PC analysis transforms several variables into a smaller number of uncorrelated variables called principal components. Principal component 1 (PC1) is the linear combination of variables with maximum variance, and each subsequent component is orthogonal to the preceding with maximum variance. Abiotic and biotic parameters were included that were likely to influence drift macroalgal abundance. The variables included in PC analysis were: temperature, salinity, depth, light attenuation, percent surface irradiance or %SI, TSS, water column nutrients (NH_4^+, $NO_2^- + NO_3^-$, PO_4^{3-}), porewater NH_4^+, chlorophyll *a*, sediment TOC, percent seagrass cover, drift macroalgal abundance, epiphyte biomass, shoot density, above-ground biomass, and blade width and length. Seagrass parameters shoot density, above-ground biomass, and blade width and length were all measurements of the species *Thalassia testudinum*, which was found at almost all vegetated sites. Sediment grain size was not included because it was only measured during two of four sampling periods. Variables were log transformed when distributions were not normal. PCA ordination plots were created using the new variables PC1 vs. PC2 and PC2 vs. PC3. Other PC variables were not included because they explained very small portions of the variability in the data. The angle and length of the lines extending from the origin to each parameter illustrate the correlation of that parameter with the PC variables.

PCA was completed for each study area (RFB and LLM) separately. Sites were analyzed using data from all four sampling periods. PCA was performed first with all 30 sites per study area and then with only vegetated sites (24 in RFB and 20 in LLM). Unvegetated sites were removed because the trends in the data were probably influenced by the seagrass parameters, which had values of zero at unvegetated sites. The results of the PCA of all sites were compared to the PCA of only vegetated sites.

Results

Abiotic Parameters

We measured the water quality and sediment parameters of salinity, temperature, chlorophyll *a*, % surface irradiance, light attenuation, total suspended solids (TSS), nutrients, sediment total organic carbon (TOC), porewater NH_4^+, and sediment grain size. Redfish Bay (RFB) and lower Laguna Madre (LLM) had several similar water column and sediment characteristics, including comparable ranges of temperature, chlorophyll *a*, TSS, nutrient concentrations, and sediment grain size (Table 2).

Salinity was slightly higher in LLM than in RFB during each sampling period. Average salinity across all sampling periods was approximately 26.6 ± 0.6 ($\bar{x}$ ± SE) and 33.8 ± 0.5 ppt in RFB and LLM, respectively. Temperature was similar in both estuaries during summer sampling, but was slightly higher in LLM during winter sampling. In RFB, average temperatures ranged from 15.4 ± 0.4 ºC in winter to 30.4 ± 0.2 ºC in summer. Temperatures in LLM ranged from an average of 18.5 ± 0.1 ºC and 30.0 ± 0.2 ºC in winter and summer, respectively. Chlorophyll *a* concentrations averaged across sampling periods were not statistically different between RFB and LLM ($p > 0.05$).

In RFB, sites with seagrasses (vegetated sites) had an average depth of 61 ± 3 cm, and received approximately 64.1 ± 2.4% of surface irradiance (SI) at the top of the seagrass canopy. Only 18.2 ± 1.9% SI reached the sediment surface at unvegetated sites (depth of 270 ± 28 cm). Mean depth of vegetated sites in LLM was 125 ± 3 cm. Vegetated sites received an average of 45.0 ±2.6% SI at the top of the seagrass canopy. Approximately 24.1 ± 1.1% SI reached the sediment bottom at unvegetated sites, which had an average depth of 189 ± 4 cm. Light attenuation values were generally similar in RFB and LLM, except that LLM had a high mean value of 7.4 ±0.6 m^{-1} during the first sampling period (Table 2).

Total suspended solids were not significantly different between the two estuaries when averaged across all sampling periods ($p > 0.05$). However, we did find trends between sites. In RFB, sites with seagrasses had higher TSS than bare sites. In LLM, we found the opposite trend, with unvegetated sites having higher TSS.

Both RFB and LLM were characterized by low dissolved inorganic nutrient concentrations (Table 2). Average concentrations of NH_4^+, $NO_2^- + NO_3^-$, and PO_4^{3-} were less than 1.9, 0.8, and 0.6 µM respectively. Nutrient concentrations averaged across sampling periods were not statistically different between RFB and LLM ($p > 0.05$).

In RFB, sediment total organic carbon (TOC), expressed as percent loss on ignition (%LOI), ranged from 0.6 – 3.8% (mean 2.1 ± 0.1%). Sediment TOC was similar in LLM, ranging from 0.7 – 4.6% with a mean of 2.6 ± 0.1%. TOC tended to be higher in vegetated sites than unvegetated sites. Porewater NH_4^+ was higher in RFB than in LLM during all four sampling periods ($p < 0.02$). Average porewater NH_4^+ concentrations across all sampling periods were 82.3 ± 3.4 µM and 34.6 ± 2.2 µM for RFB and LLM, respectively.

Sediment grain size, reported as % silt + clay (Table 2), was not significantly different between the first and last sampling period for either RFB or LLM. Sediment in LLM had a slightly higher average silt + clay content than RFB (36.2 ± 2.1% and 30.0 ± 1.9%, respectively).

Seagrass Cover

Seagrasses were present at 24 of 30 sites in RFB. *Thalassia testudinum* and *Halodule wrightii* were the dominant species in RFB, but *Ruppia maritima*, *Halophila engelmanii*, and *Syringodium filiforme* were also present. Based on measurement at the thirty sampling sites, seagrass percent cover was interpolated across RFB (Figure 36). Seagrass percent cover includes the total percent cover of all species together out of a total 100%. Seagrass beds often contained several species and were somewhat patchy. Highest seagrass percent cover was found at sites in the northern half of RFB. On the south side of RFB, six sites (14, 22, 25, and 28 – 30) in deeper water (>1.5 m) were completely unvegetated.

In LLM, seagrasses were present at 20 of 30 sites. Dominant seagrass species included *Thalassia testudinum* and *Syringodium filiforme*. Seagrass percent cover was interpolated across LLM (Figure 37). Extensive seagrass cover was found on the east side of the Gulf Intracoastal Waterway (GIWW). Just west of the GIWW, near the deposited dredge material, seagrass cover generally decreased. Sites 5, 8, 10, 13, 16, 19, 22, 25, 28, and 30, located on the far west side of the study area, were unvegetated and located in water depths > 2 m.

Biotic Parameters

Biotic parameters were measured on *Thalassia testudinum* at all vegetated sites since *T. testudinum* was the species most common among all sites in RFB and LLM. Average values for each parameter for each sampling period in RFB and LLM are shown in Table 3. Percent seagrass cover includes the total % cover of all seagrass species present.

Average epiphyte biomass was significantly different between sampling periods in RFB and LLM ($p < 0.001$). Epiphyte biomass ranged from 0.87 ± 0.18 to 5.29 ± 0.61 mg cm^{-2} in RFB and from 0.33 ± 0.06 to 1.09 ± 0.14 mg cm^{-2} in LLM (Table 3). Epiphyte biomass was higher in RFB than LLM during all sampling periods. However, that difference was only significant in summer 2003 ($p = 0.004$) and winter 2004 ($p < 0.001$).

At vegetated sites, average seagrass cover was higher in LLM (81 ± 3%) than in RFB (67 ± 7%), but the difference was not significant ($p > 0.05$) because of the high variability in percent cover in RFB. Seagrass cover varied seasonally across LLM and RFB, with significantly higher cover in summer sampling periods than in winter sampling periods ($p = 0.001$). The average % seagrass cover in winter 2004 in RFB was significantly different from all other sampling periods in RFB and LLM (Figure 38), but other sampling periods were not different from each other (in RFB or LLM).

Above-ground biomass of *Thalassia testudinum* varied seasonally in both estuaries (Table 3). Biomass was generally higher in RFB than in LLM, but the difference was not significant ($p > 0.05$). In RFB and LLM, above-ground biomass was significantly higher during summer 2002 and 2003 than during winter 2003 and 2004 ($p < 0.001$). In RFB, above-ground biomass was an average of 206 ± 15 g m^{-2} during the summers and 74 ± 5 g m^{-2} during the winters. Above-ground biomass in LLM averaged 138 ± 15 and 68 ± 6 during g m^{-2} summer and winter, respectively.

In both estuaries, below-ground biomass of *Thalassia testudinum* was higher than above-ground biomass (Table 3). Below-ground biomass was significantly higher in LLM than in RFB ($p < 0.001$). There were no differences between sampling periods within either LLM or RFB ($p > 0.05$). Seagrass root:shoot ratios were higher in LLM than RFB. Root:shoot ratios were significantly higher in LLM, which ranged from 7.4 ± 0.9 to 14.2 ± 1.8, than in RFB, which ranged from 2.7 ± 0.2 to 6.8 ± 0.7 ($p < 0.001$). We found significant differences between root:shoot ratios between seasons in RFB and LLM, with higher winter values than summer values ($p < 0.001$).

Thalassia testudinum shoot density was slightly lower in RFB than in LLM, with average values of 723 and 926 shoots m^{-2}, respectively. However, the difference between RFB and LLM was not significant ($p > 0.05$), and sampling periods were not different from each other within or between study areas ($p > 0.05$). Blade length varied with season, but blade width did not significantly change seasonally ($p > 0.05$) (Table 3). Blade length and width did not differ between RFB and LLM. During summer 2002, blade C:N ratios averaged 12.9 ± 0.3 and 13.1 ± 0.2 for RFB and LLM, and were not significantly different ($p > 0.05$).

Drift Macroalgal Abundance

Drift macroalgae were collected at 24 of 30 sites in RFB and at 20 of 30 sites in LLM. No drift algae were found at unvegetated sites. We collected 17 species in RFB and 18 species in LLM (23 total species). Many species were found in both areas. The five most common species in RFB, in order of most to least common, were *Gracilaria cornea*, *Gracilaria verrucosa*, *Digenia simplex*, *Laurencia poiteaui*, and *Jania capillacea*. In LLM, the five most common species from most to least common were *Digenia simplex*, *Laurencia poiteaui*, *Dictyota cervicornis*, *Jania capillacea*, and *Agardhiella tenera*.

Drift macroalgal distribution tended to be very patchy in RFB. Within site variability was very high. At some sites, drift macroalgae was nearly knee deep along some parts of the transect while completely absent along other parts of the same transect. The largest within site variability was recorded at site 20 during the first sampling period, which ranged from 16.4 – 1970.6 g m^{-2}. The distribution was also variable between seasons. In summer 2002, drift macroalgae were found at almost 98% of the meter marks at vegetated sites (Figure 39). Drift macroalgae were only found at about 50% of the meter marks during the summer 2003 and winter 2004.

In LLM, drift macroalgal distribution was also patchy within sites. The largest within site range, 26.4 – 817.4 g m^{-2}, was found at site 4 during the third sampling period. The variability within sites was smaller in LLM than RFB, forming more of a continuous layer. Drift macroalgae were found at 85% of all randomly selected meter marks at vegetated sites (Figure 39).

There was no significant difference in average drift macroalgal abundance between RFB and LLM (90.1 ± 10.2 g m^{-2} and 72.7 ± 10.7 g m^{-2}, respectively; $p > 0.05$); however, we found significant differences between sites within each study area ($p < 0.001$) (Figures 40 and 41). Average drift macroalgal abundance in RFB and LLM is shown in Figures 42 and 43. In RFB (Figure 42), drift macroalgae tended to accumulate in shallow protected areas, especially in the southern portion of RFB. In LLM (Figure 43), we found a decreasing trend in drift macroalgal abundance going from east to west. Drift macroalgae were highly abundant near Padre Island, but west of the GIWW, vegetated sites had relatively low drift macroalgal abundance.

In both RFB and LLM, drift macroalgae were present during all four sampling periods. There was a significant difference in drift macroalgal abundance between the sampling periods ($p = 0.023$). We found a significant interaction between sampling period and study area ($p < 0.001$), indicating drift macroalgal abundance was different between the study areas during different sampling periods (Figure 44).

In both estuaries, biomass of drift macroalgae was comparable to above-ground biomass of the seagrass *T. testudinum* (Figure 45). In RFB (Figure 45, panel a), the biomass of seagrass and drift macroalgae were not statistically different during 3 of 4 sampling periods. During the summer sampling periods, seagrass above-ground biomass was higher than during winter. In summer 2002, drift macroalgae were also in greater abundance than in winter, but we did not observe an increase in drift macroalgal abundance in summer 2003. In LLM (Figure 45, panel b), drift macroalgal abundance was not statistically different than seagrass biomass during winter 2003, summer 2003, or winter 2004. Seagrass biomass was higher than drift macroalgal biomass in summer of 2002. Similar to RFB, seagrass above-ground biomass in LLM followed a seasonal pattern of higher values in summers than winters; however, drift macroalgae did not follow the same pattern.

Principal Component Analysis (PCA)

When all data from RFB were included, drift macroalgal abundance was positively associated with above-ground biomass and blade length of *Thalassia testudinum* (Figure 46, panel a). Sites with higher above-ground biomass and blade lengths tended to have more drift macroalgae. In Figure 46 (panel b) the variables epiphyte biomass and total suspended solids (TSS) were most negatively associated with drift macroalgal abundance. In this case, as TSS and epiphyte biomass increased, drift macroalgae decreased. Vegetated sites tended to have higher TSS values than bare sites. Variables PC1, PC2, and PC3 explained 27.4, 17.0, and 9.6% of the variation in the data, respectively.

When only vegetated sites were included in the PCA, different relationships emerged between drift macroalgal abundance and the other biotic and abiotic parameters (Figure 47). In Figure 47 (panel a) the parameters porewater NH_4^+, epiphyte biomass, and TSS were most closely associated with drift algal abundance. Sites with higher porewater NH_4^+ and lower TSS had more drift algal biomass. We found a negative relationship between epiphyte biomass and drift algae, with lower algal abundance at sites with higher epiphyte biomass. In Figure 47 (panel b) the variables depth and shoot density were most associated with drift algal abundance. More drift macroalgae were found at deeper sites and where shoot density was lower. PC variables 1, 2, and 3 explained 23.2, 13.7, and 10.2% of the variation, respectively.

In LLM, light was a critical factor in explaining drift macroalgal abundance. In Figure 48, drift algal abundance was most associated with the parameters % surface irradiance, and depth, when all sites were included. As depth increased and % SI decreased, drift macroalgal abundance decreased. The variables PC1, PC2, and PC3 explained 33.6, 15.4, and 11.9% of the variability.

When unvegetated sites were excluded, seagrass parameters and light were most closely associated with drift macroalgal abundance. Percent surface irradiance, depth, % seagrass cover, and shoot density were most correlated with drift algal abundance in LLM (Figure 49). Sites with higher seagrass cover and shoot density tended to have higher drift macroalgal abundance. PC variables 1, 2, and 3 explained 23.0, 18.5, and 10.0% of the variability. PCA results for RFB and LLM are summarized in Table 4.

Discussion

Drift macroalgae are a prominent feature of Redfish Bay and lower Laguna Madre. We found that the average biomass of drift macroalgae was equivalent to the above-ground biomass of the dominant seagrass, *Thalassia testudinum*, in both estuarine systems. Seagrasses and their associated fauna living in RFB and LLM are likely influenced by these large concentrations of drift macroalgae. High drift macroalgal abundance could indicate that nitrogen is not limiting in these systems.

Abiotic Parameters

Similar abiotic water column and sediment characteristics were observed in the two estuaries. Throughout the study, RFB and LLM had similar temperature ranges, dissolved inorganic nutrient concentrations, and chlorophyll *a* concentrations. In RFB, shallow vegetated sites had higher TSS than deeper, unvegetated sites. This is likely because shallow areas, with an average depth of only 0.61 m, are more easily influenced by wind, which causes sediment resuspension. Despite higher TSS values, vegetated sites received about 64% of surface irradiance. In LLM, TSS in deep unvegetated sites was higher than in shallow vegetated sites. This high TSS is likely because of the resuspension of dredge material from the Gulf Intracoastal Waterway (GIWW). Sites in LLM received a lower average % surface irradiance, 45%, at vegetated sites. This was lower than RFB because sites in LLM were deeper and several were influenced by high TSS levels. The sediment characteristics total organic carbon and sediment grain size were not different between the two estuaries. Porewater NH_4^+ was significantly higher in RFB than LLM.

Biotic Parameters

More seagrass cover was found at vegetated sites in LLM than RFB, and cover varied seasonally in both estuaries. Average above-ground biomass, blade width, blade length, blade C:N ratios, and shoot density of *Thalassia testudinum* were not different between RFB and LLM. However, below-ground biomass and root:shoot ratios were significantly higher in LLM than RFB. Higher below-ground biomass in LLM could explain why porewater NH_4^+ was lower in LLM. More nutrients could be taken up by increased below-ground biomass.

Drift Macroalgal Abundance

Drift macroalgae were in high abundance in RFB and LLM. Maximum macroalgal abundance in RFB and LLM was 1,970 and 817 g m^{-2}, respectively. In RFB, average drift algal abundance ranged from 62 ± 12 g dry weight m^{-2} in winter 2003 to 162 ± 25 g dry weight m^{-2} in summer 2002 ($\bar{x}$ ± SE, n = 30) (Table 3). During 3 of 4 sampling periods, there was no significant difference between drift macroalgal biomass and *Thalassia testudinum* above-ground biomass (Figure 45). We frequently found drift macroalgae tens of centimeters thick, and often filling in large bare patches. Sometimes drift algae were found only on the sediment surface, around the base of seagrass shoots. However, at some sites it accumulated in large patches covering seagrasses completely. In those areas, it was likely that drift macroalgae were blocking out a majority of available light. In addition, in some of the more shallow areas of RFB (< 0.5 m), seagrass shoots grew up to the surface of the water. These shoots created areas of slow water movement, which allowed for drift macroalgal accumulation.

In LLM, drift algal biomass was also high, with average values ranging from 43 ±8 g dry weight m^{-2} in summer 2002 to 104 ± 31 g dry weight m^{-2} in winter 2004 (Table 3). Similarly to RFB, during 3 of 4 sampling periods, there was no significant difference between drift macroalgal biomass and *Thalassia testudinum* above-ground biomass (Figure 45). In LLM, drift macroalgae tended to accumulate in areas of high seagrass cover. Seagrass cover was less patchy, and drift macroalgae tended to accumulate around the base of seagrass shoots. LLM sites were not as shallow, which facilitated increased water movement and prevented stagnant areas. Consequently, drift macroalgae was more evenly distributed.

The high abundance of drift algae in RFB and LLM has been previously documented. Cowper (1978) noted that drift algal accumulation was knee-deep in RFB, with an average of almost 200 g dry weight m^{-2}. Drift algae tended to accumulate in areas with minimal seagrass growth, such as in prop scars. Cowper (1978) also pointed out that RFB and a few bays in Florida are different from most Atlantic North American seagrass beds dominated by *Thalassia testudinum*. In most Atlantic systems, constant pressure from herbivores including reef fish and urchins, as well as currents associated with the trade winds, prevent high accumulations of drift macroalgae (Cowper 1978). Additionally, Onuf (1996b) noted high macroalgal biomass in the lower section of Laguna Madre, with a mean of about 50 g m^{-2}. Onuf (1996b) hypothesized that high accumulation in LLM was a result of high nutrients from agricultural runoff from the Arroyo Colorado River.

RFB and LLM have high drift algal abundance compared to seagrass beds in many other areas. In a study of Florida Bay by Zieman *et al.* (1989), the most abundant macroalgae, *Laurencia* spp., had a baywide average of only 8.9 g dry weight m^{-2}. Bell and Hall (1997) examined drift algal abundance at 12 sites in Tampa Bay, and found that average abundance ranged from nearly zero at some sites up to 150 g dry weight m^{-2} at one site, with an average of about 30 g dry weight m^{-2}. One additional estuary that has high drift macroalgal abundance is the Indian River Lagoon on the east coast of Florida. Virnstein and Carbonara (1985) reported that drift macroalgae were extremely spatially variable and tended to aggregate in high density patches. In some areas, drift algae were tens of centimeters thick while drift algae were absent in other areas. Maximum abundance averaged over a 15 ha area was 164 g dry weight m^{-2}, but several smaller patches had an average of 409 g dry weight m^{-2}.

Drift Macroalgal Spatial and Temporal Variability

We found that drift macroalgal abundance was highly variable within sites, between sites, and between seasons. Often, drift macroalgae were in high abundance along parts of the transect and not present at other parts of the transect. Within site variability was higher in RFB than in LLM, ranging from 16.4 – 1970.6 g m^{-2} in RFB and 26.4 – 817.4 g m^{-2} in LLM. Variability in drift macroalgal abundance between sites was high in both estuaries (Figures 40 and 41). At vegetated sites, drift macroalgal abundance at each site ranged from 0 to 539.9 and 0.38 – 464.6 g m^{-2} in RFB and LLM, respectively. Seasonal variability was also apparent in both estuaries (Figure 44). In RFB, drift macroalgal abundance was highest during summer 2002 (162 g m^{-2}), but ranged from 62 – 65 g m^{-2} during the other sampling periods (winter ’03, summer ’03, winter ’04). This could be related to an abnormally high freshwater inflow during July 2002. South central Texas experienced severe flooding, including the Nueces River Basin and the San Antonio/Nueces River Basin (Figure 2). Streamflow data from a USGS gauge on the Nueces

River indicated July 2002 mean streamflow was 16,170 ft^3 s^{-1}, and average monthly streamflow from 1989 to 2003 was only 412 ft^3 s^{-1} (http://nwis.waterdata.usgs.gov/tx/nwis/monthly).

In LLM, there were no seasonal trends in drift macroalgal abundance. In contrast to the Nueces River, streamflow in the Arroyo Colorado River, the primary freshwater source to LLM, was actually below average during July 2002. The average monthly streamflow from 2001 – Sept. 2004 was 270 ft^3 s^{-1}, but during July 2002 streamflow was only 170.9 ft^3 s^{-1} (data from Kenneth Rakestraw, International Boundary & Water Commission, http://www.ibwc.state.gov). Average drift macroalgal abundance values for each sampling period were not significantly different from each other.

The overall abundance of drift macroalgae in the two estuaries was not significantly different. Initially, this was surprising because RFB receives higher freshwater inflow. We hypothesized that higher levels of freshwater inflow would lead to higher nutrient availability and more drift algae. However, concentrations of NH_4^+, NO_2^- + NO_3^-, and PO_4^{3-} were low in both RFB and LLM (Table 2), and not significantly different between the estuaries. Additionally, the large quantity of drift macroalgae itself indicates that nutrients are readily available in both estuaries. This pattern is explained by several possibilities: 1) DIN concentrations do not reflect actual nutrient loading, 2) nutrient concentrations are highly variable; thus, measuring them twice a year may not give an accurate picture of DIN in the system, or 3) the nutrients are being taken up very quickly by epiphytes, seagrasses, macroalgae, or phytoplankton, so actual nutrient concentrations were higher. The idea that DIN concentrations do not reflect nutrient loading has been suggested before. Tomasko *et al.* (1996) concluded that water column nutrient concentrations are poor indicators of nutrient loading, in part because they have high turnover rates. Suttle *et al.* (1990) found that dissolved NH_4^+ may be taken up in as little as 13 minutes.

Seagrass blade C:N ratios

Several studies have suggested that seagrass blade C:N ratios may be indicators of nutrient loading. Redfield *et al.* (1963) found that oceanic phytoplankton have C:N:P ratios of 106:16:1 in optimal conditions. A deviation from this "Redfield ratio" would indicate nutrient limitation. C:N:P ratios in seagrasses have been compared to the Redfield ratio, but seagrasses have higher structural carbon content compared to phytoplankton (Atkinson and Smith 1983, Duarte 1990). Consequently, seagrasses may have higher ratios than the Redfield ratio when they are not, in fact, nutrient limited. The use of C:N:P ratios in seagrasses to infer nutrient availability has been criticized in part because nutrient ratios have been found to vary within and between species (Duarte 1990), tissue, and season (Perez-Llorens and Niell 1993).

In a study of 27 species of seagrasses, Duarte (1990) found that the median C:N:P ratio in seagrasses worldwide is 474:24:1, which is a C:N ratio of 20. Interestingly, C:N ratios of *Thalassia testudinum* in this study were approximately equal in RFB and LLM, both with an average of 13 (Table 2). A C:N ratio of 13 is lower than the C:N blade ratios of *T. testudinum* reported in other studies. In Florida Bay, C:N ratios of *T. testudinum* ranged from 16 – 23, with an average of approximately 19 (Fourqurean *et al.* 1992); Fourqurean and Zieman (2002) reported C:N blade ratios of 11.1 – 47.1, (mean 24.6). Rose and Dawes (1999) noted that C:N ratios of *T. testudinum* in Tampa Bay ranged from 18.3 – 22.1 (average of 19.6). Compared to these studies, RFB and LLM have a lower C:N ratio, which indicates that nitrogen is more available than in those systems in Florida.

The idea that nitrogen is not limiting in RFB is not a new one; however, previous studies in LLM have shown that nitrogen is limiting there. In a fertilization experiment by Lee and Dunton (1999), C:N blade ratios of *Thalassia testudinum* from LLM and Corpus Christi Bay (CCB) were compared. Seagrasses from CCB, which is adjacent to RFB, had C:N ratios from 12 – 17 and these ratios did not change with the addition of nitrogen to the sediment. However, in LLM, C:N ratios ranged from 20 – 25. Following the addition of fertilizer, C:N ratios decreased to 15 – 18. Lee and Dunton (1999) concluded that because the C:N ratio of seagrasses in LLM decreased with fertilization, nitrogen is limiting there; however, nitrogen is not limiting in CCB. In a study by Kaldy and Dunton (2000), *Thalassia testudinum* in LLM had an average C:N ratio of 20. Both of those studies suggested that nitrogen is limiting in LLM. However, low C:N ratios in this study indicate that nitrogen may not be as limiting in LLM as previously thought.

There could be several explanations for a difference in C:N ratios between previous studies (Lee and Dunton, 1999; Kaldy and Dunton, 2000) and this study. Seagrasses were collected during the mid 1990's when South Texas was under drought conditions. According to monthly streamflow data from USGS (http://nwis.waterdata.usgs.gov/tx/nwis/monthly), during the period of 1995 – 1997, average streamflow of the Nueces River (which flows into CCB), was 80 $ft^3 s^{-1}$. In 2002, the monthly average was an astonishing 3,400 $ft^3 s^{-1}$. An increase in freshwater inflow would probably mean increased nitrogen availability. More research is needed to determine if nitrogen is limiting in LLM or if it is changing to a less limited system.

In addition to C:N ratios, epiphyte biomass may be an indicator of nutrient input. Several studies have found that epiphyte biomass is linked to nutrient availability (Cattaneo and Kalff 1980, Dunton 1990). Seagrasses in RFB had more epiphyte biomass that in LLM during all sampling periods, which suggests that nutrients are more available in RFB than LLM. Although we did not find statistically significant differences in water column nutrient concentrations, it is likely that those concentrations do not reflect actual nutrient availability. Tomasko *et al.* (1996) concluded that water column nutrient levels do not accurately represent watershed nutrient loadings.

Although LLM receives less freshwater than RFB, it is likely that nutrients are not limiting in this system based on relatively low C:N ratios and high drift algal abundance. The Arroyo Colorado, which brings freshwater (and nutrients) to LLM, has been shown to have high nutrient concentrations from treated wastewater from the Brownsville/Harligen areas and runoff from local farms. According to the Texas Commission on Environmental Quality, the Arroyo Colorado contains a considerable amount of agricultural runoff because a large portion of its watershed is farm land (TCEQ 2003). Flow in the Arroyo Colorado is maintained by wastewater discharges, urban runoff, and the return flow of agricultural irrigation (TCEQ 2003).

Drift Macroalgae vs. Other Measured Parameters

In order to identify possible relationships between measured abiotic and biotic parameters and drift macroalgal abundance we used PCA. According to the PCA on all sites in both RFB (Figure 46) and LLM (Figure 47), the presence of seagrasses and light were the most important factors determining whether drift algae were present; nutrients or other water quality parameters were not indicative of macroalgal biomass. In RFB, sites with higher seagrass above-ground biomass and blade length had higher drift macroalgal abundance. Drift macroalgae, which are unattached and carried by currents, tend to become physically trapped in areas with seagrasses. We often observed large mats of drift macroalgae which had accumulated in large bare patches within seagrass beds. The drift macroalgae did not necessarily accumulate between shoots, but without seagrass boundaries drift macroalgae could not accumulate in bare areas.

To gain a better understanding of why drift macroalgae were in higher abundance in certain vegetated sites over other sites, we performed another PCA including only vegetated sites in RFB (Figure 47). Parameters with the strongest associations with drift macroalgal abundance included total suspended solids, shoot density, porewater NH_4^+, depth, and epiphyte biomass. Not surprisingly, total suspended solids were negatively associated with drift macroalgal abundance, indicating that sites with lower TSS had higher drift macroalgal abundance. When TSS are low, more light is available. TSS tend to be higher in shallow areas because sediment is resuspended by wind more easily than in deeper areas.

In RFB, shoot density was negatively associated with drift macroalgal abundance. Sites with higher shoot density had less drift macroalgae. It is not clear whether shoot density affected how much drift macroalgae was caught by the seagrass shoots or whether areas with higher drift algal abundance caused a decrease in shoot density.

Within vegetated sites, drift macroalgal abundance was positively associated with porewater NH_4^+, which indicates that areas with high porewater NH_4^+ concentrations had higher drift macroalgal abundance. Normally, when nutrients are regenerated in sediment, they diffuse into the water column, and can be an important source of nutrients for primary producers (Kemp and Boynton 1984). However, drift macroalgae at the sediment surface have been show to interrupt the movement of regenerated nutrients from the sediment to the water column, thus blocking the link between the benthos and water column (McGlathery *et al*. 1997, Valiela *et al.* 1997b). When this occurs, drift macroalgae thrive on the high nutrient concentrations. Consequently, water quality may appear high because chlorophyll and nutrient concentrations are low even though nutrient inputs to the system are high (McGlathery 2001).

Within vegetated sites, we found a positive association between drift macroalgal abundance and depth, with increasing abundance at increasing depth. In deeper water where less light is available, drift macroalgae could be out competing seagrasses for light. Another possibility is that in very shallow areas, drift macroalgae experience photoinhibition due to very high irradiances. Photoinhibition could lead to a reduction in photosynthesis and result in lower biomass.

Epiphyte biomass was negatively associated with drift algal abundance in RFB. Sites with higher drift macroalgal abundance tended to have lower epiphyte biomass. It is likely that this relationship between drift macroalgae and epiphytes is a result of competition for nutrients, light, or both. At sites with low drift macroalgal abundance, only the bottom portions of seagrass shoots were shaded. However, at sites with high drift macroalgal abundance, many shoots were mostly or almost completely shaded. Any epiphytes on the shaded shoots would probably be light limited. Irlandi *et al*. (2004) also found that the presence of drift macroalgae reduced epiphyte biomass.

PC analysis on all sites in LLM revealed a positive association between drift macroalgal abundance and % surface irradiance, with increasing abundance as light availability increased (Figure 48). There was a negative association with depth, which is related to the decrease in light availability. In LLM, dredge material from the GIWW has been shown to reduce light availability (Onuf 1994). Shallow sites west of the deposited dredge material had low seagrass cover (Figure 37) and received low irradiance (about 30% SI). These sites also had low drift macroalgal abundance, which could be attributed to the low light and/or low seagrass cover and low shoot density, which might catch less macroalgae. As depth increases towards the west, the light becomes insufficient for seagrass growth; consequently, those sites are unvegetated and do not have macroalgae. Even though the PCA points to light as the most important factor associated with drift algal abundance, it is also likely that the lack of vegetation is critical.

PCA on only vegetated sites in LLM revealed that depth, % seagrass cover, and shoot density were most associated with drift macroalgal abundance (Figure 49). Shallower sites also tended to have higher drift macroalgal abundance, due to more light availability. This was in contrast to RFB, which had the opposite trend. Sites in LLM were deeper than sites in RFB. The most shallow vegetated site in LLM and deepest vegetated in RFB have the same depth of 1 m. It is likely that the relationship between % SI and drift macroalgal abundance reflects the fact that light is a limiting factor for drift algae in LLM, more so than for RFB.

Percent seagrass cover and shoot density also had positive relationships with drift macroalgae in LLM (Figure 49, panel b). Sites with higher seagrass cover and shoot density tended to have more drift macroalgae. Areas with more seagrass cover and more shoots m^{-2} probably catch more of the drifting macroalgae. Seagrass blades also retard water movement, which could cause macroalgae to settle to the bottom. Sites with higher shoot densities would probably trap more macroalgae since the plants often get trapped among shoots and eventually settle on or near the sediment surface. It is interesting that in RFB, sites with higher shoot density had less drift algae. In RFB, we observed that seagrass cover was very patchy and drift macroalgae tended to accumulate in bare areas or areas with low seagrass cover and shoot density (Figure 50). Seagrass cover in LLM was not patchy, especially at the sites east of the GIWW. There were few bare areas, and drift macroalgae did not dominate. We believe that in LLM, drift macroalgae in bare areas tend to be pushed out by currents. LLM is a long, wide open lagoon with no islands. The sites were deeper in LLM than RFB, which allowed for more water movement. Some sites in RFB were sufficiently shallow to allow seagrass blades to reach the surface of the water, which dampened the effects of wind stress and slowed water movement. This resulted in areas with enormous accumulations of drift algae that were often a half meter thick. In LLM, higher current speeds may have prevented the accumulation of drift macroalgae in bare areas. Only drift macroalgae caught between high density shoots of seagrasses could remain on the sediment surface. We believe that because of this difference between RFB and LLM, hydrodynamics play a critical role in drift macroalgal abundance and distribution.

In general, PC analysis revealed drift macroalgal differences between RFB and LLM in response to several abiotic and biotic parameters (Table 4). When examining all sites in RFB, seagrass presence was the most important factor that determined whether drift macroalgae were present. When only sites with seagrass were considered, drift macroalgal abundance was associated with TSS, shoot density, porewater NH_4^+, depth, and epiphyte biomass. In LLM, light availability and seagrass presence were most important in determining whether or not drift macroalgae were present. Within vegetated sites, % surface irradiance, depth, % seagrass cover, and shoot density were most related to drift macroalgal abundance. In both estuaries, PC analysis identified different relationships between the measured parameters when unvegetated sites were or were not included. These differences show that those bare sites are so different from vegetated sites that they skew the analysis. We believe that it is important to examine both analyses in order to understand drift macroalgal abundance. Factors such as light and the presence of seagrasses are first important to understanding the absence/presence of drift macroalgae. Once those areas have been identified, data from only vegetated sites is useful for understanding relative amounts of drift algal cover.

Conceptual Models

We constructed two conceptual models to further clarify nutrient and drift algal dynamics in RFB and LLM (Figures 50 and 51). Figure 50 compares drift algal accumulation in the two systems. In the shallow protected areas of RFB (panels a and b), slow currents aid in the accumulation of drift algae in bare areas. At the same time, porewater NH_4^+ flux is attenuated by the presence of drift macroalgae. Over time, drift algae grows and accumulates more in these bare areas. In LLM (panels c and d), seagrasses occur in deeper, faster moving water. Drift macroalgae that may accumulate in a bare patch get transported out by currents. A higher abundance of drift macroalgae occurs in areas of high shoot density.

Figure 51 illustrates nutrient dynamics in RFB and LLM. In RFB (panel a), higher freshwater inflow is likely to result in a greater nutrient flux. Higher porewater NH_4^+ levels and lower root:shoot ratios for *Thalassia testudinum* may be related to the increased nutrient availability in RFB, which implies that less root biomass is needed to acquire nutrients. Low blade C:N ratios, high epiphyte biomass, and high drift algal abundance all indicate that RFB is a nutrient replete system. In LLM (panel b), it is likely that the nutrient flux is low because freshwater inflow is limited. In addition, porewater NH_4^+ concentrations are low. *Thalassia* root:shoot ratios are higher in LLM, which is probably a response to lower nutrient availability in the sediment and water column. Similarly, epiphyte biomass is also lower, but high drift algal abundance and low blade C:N ratios indicate that LLM may not be nitrogen limited.

Other studies on drift macroalgae have linked many abiotic and biotic factors to drift algal abundance. Zieman *et al*. (1989) linked wind to the abundance of drift macroalgae. They found more drift algae on the east side of Florida Bay and less to the west, which was attributed to predominantly easterly winds. According to Lapointe (1989), drift algae in Florida Bay has been linked to irradiance, temperature, and nutrient availability. In a study of seagrass beds in Tampa Bay, Bell and Hall (1997) observed a relationship between drift algae and hydrodynamics. They found that % silt + clay was the best predictor of drift algal abundance. Areas with higher silt + clay content were areas with lower wave action and current velocities. Bell and Hall (1997) concluded that sites which are less active hydrodynamically may accumulate drift macroalgae at a faster rate than sites with more wave energy or higher current flow. In a study by Virnstein and Carbonara (1985), drift algal abundance was related to seagrass species composition because morphological differences in seagrasses was related to drift algal biomass. While drift macroalgal growth is limited by low nutrients in some estuaries, drift macroalgae in RFB does not appear to be nitrogen limited. LLM has been shown to be nitrogen limited by previous studies (Lee and Dunton 1999, Kaldy and Dunton 2000); however, low C:N ratios and high drift macroalgal abundance indicate nitrogen may be less limiting now than during the mid 1990’s when those studies were conducted.

Conclusions and Recommendations

In RFB and LLM, drift macroalgal abundance was high and even exceeded *Thalassia testudinum* above-ground biomass in some areas. The distribution of drift macroalgae was patchy, yielding high within and between site variability. Seasonal variability was also apparent, which we attributed to changes in freshwater inflow and nutrient input to the estuaries. Although we did not find a relationship between DIN and drift macroalgal abundance, we believe that DIN measurements may not reflect actual nutrient loading. High epiphyte biomass and low *T. testudinum* blade C:N ratios also indicate that these are nutrient replete estuaries. In addition to the impacts of nutrients on drift macroalgae, we also identified several relationships with abiotic and biotic parameters. In RFB, we found relationships between drift macroalgal abundance and TSS, shoot density, porewater NH_4^+, depth, and epiphyte biomass. In LLM, % surface irradiance, depth, % seagrass cover, and shoot density were all associated with drift macroalgal abundance. It is clear that the difference in seagrass cover and hydrodynamics in these two systems affects the abundance and distribution of drift macroalgae. In RFB, patchy seagrass beds and shallow protected areas result in high abundance of drift macroalgae in bare patches and areas with slow moving currents. LLM is deeper, does not possess extremely shallow stagnant areas, and has more continuous seagrass cover, all of which limit drift macroalgae to areas of high seagrass cover and prevent it from accumulating in bare areas. Considering the high abundance of drift macroalgae already present in these systems, any increase in nutrient loading could lead to loss of seagrass cover. Nutrient enrichment could especially be a problem in parts of RFB where drift macroalgae may accumulate for long periods of time. Some of the patchiness in RFB could be a result of seagrass die-off caused by large accumulations of drift macroalgae. Further study is needed to fully understand the interaction between nutrients and drift macroalgae in these systems.

Bibliography

Atkinson, M.J. and Smith, S.V. 1983. C:N:P ratios of benthic marine plants. *Limnology and Oceanography* 28: 568-574.

Bell, S.S. and Hall, M.O. 1997. Drift macroalgal abundance in seagrass beds: Investigating large-scale associations with physical and biotic attributes. *Marine Ecology Progress Series* 147: 277-283.

Borum, J. 1985. Development of epiphytic communities on eelgrass (*Zostera marina*) along a nutrient gradient in a Danish estuary. *Marine Biology* 87: 211-218.

Brush, M.J. and Nixon, S.W. 2002. Direct measurements of light attenuation by epiphytes on eelgrass *Zostera marina*. *Marine Ecology Progress Series* 238: 73-79.

Cambridge, M.L. and McComb, A.J. 1984. The loss of seagrasses in Cockburn Sound, Australia. I. The time course and magnitude of seagrass loss in relation to industrial development. *Aquatic Botany* 20: 229-243.

Carpenter, S.R. and Lodge, D.M. 1986. Effects of submerged macrophytes on ecosystem processes. *Aquatic Botany* 26: 341-370.

Cattaneo, A. and Kalff, J. 1980. The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophyte beds. *Limnology and Oceanography* 25: 280-289.

Conover, J.T. 1964. The ecology, seasonal periodicity, and distribution of benthic plants in some Texas lagoons. *Botanica Marina* 7: 4-41.

Cowper, S.W. 1978. The drift algae community of seagrass beds in Redfish Bay, Texas. *Contributions in Marine Science* 21: 125-132.

Dawes, C.J. 1998. *Marine Botany*. 2nd edition. John Wiley & Sons, New York.

Dean, W.E.Jr. 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: Comparison with other methods. *Journal of Sedimentary Petrology* 44: 242-248.

Deegan, L.A., Wright, A., Ayvazian, S.G., Finn, J.T., Golden, H., Merson, R.R., and Harrison, J. 2002. Nitrogen loading alters seagrass ecosystem structure and support of higher trophic levels. *Aquatic Conservation: Marine and Freshwater Ecosystems* 12: 193-212.

den Hartog, C. 1977. Structure, function, and classification in seagrass communities. In: *Seagrass Ecosystems: A Scientific Perspective*. McRoy, C.P. and Helfferich, C. (Eds.). Marcel Dekker, Inc., New York.

Dennison, W.C., Orth, R.J., Moore, K.A., Stevenson, J.C., Carter, V., Kollar, S., Bergstrom, P.W., and Batiuk, R.A. 1993. Assessing water quality with submersed aquatic vegetation. *Bioscience* 43: 86-94.

Duarte, C.M. 1990. Seagrass nutrient content. *Marine Ecology Progress Series* 67: 201-207.

Duarte, C.M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. *Ophelia* 41: 87-112.

Dunton, K.H. 1990. Production ecology of *Ruppia maritima* L. s.l. and *Halodule wrightii* Aschers. in two subtropical estuaries. *Journal of Experimental Marine Biology and Ecology* 143: 147-164.

Dunton, K.H. 1996. Photosynthetic production and biomass of the subtropical seagrass *Halodule wrightii* along an estuarine gradient. *Estuaries* 19: 436-447.

Folk, R.L. 1974. *Petrology of sedimentary rocks*. Hemphill Publishing Company, Austin, Texas.

Fourqurean, J.W., Zieman, J.C., Powell, G.V.N. 1992. Relationships between porewater nutrients and seagrasses in a subtropical carbonate environment. *Marine Biology* 114: 57-65.

Fourqurean, J.W., Boyer, J.N., Durako, M.J., Hefty, L.N., and Peterson, B.J. 2003. Forecasting responses of seagrass distributions to changing water quality using monitoring data. *Ecological Applications* 13: 474-489.

Fourqurean, J.W. and Zieman, J.C. 2002. Nutrient content of the seagrass *Thalassia testudinum* reveals regional patterns of relative availability of nitrogen and phosphorus in the Florida Keys USA. *Biogeochemistry* 61: 229-245.

Frankovich, T.A. and Fourqurean, J.W. 1997. Seagrass epiphyte loads along a nutrient availability gradient, Florida Bay, USA. *Marine Ecology Progress Series* 159: 37-50.

Hauxwell, J., Cebrian, J., Furlong, C., and Valiela, I. 2001. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. *Ecology* 82: 1007-1022.

Hauxwell, J., Cebrian, J., and Valiela, I. 2003. Eelgrass *Zostera marina* loss in temperate estuaries: Relationship to land-derived nitrogen loads and effect of light limitation imposed by algae. *Marine Ecology Progress Series* 247: 59-73.

Heck K.L.Jr., and Thoman, T.A. 1984. The nursery role of seagrass meadows in the upper and lower reaches of the Chesapeake Bay. *Estuaries* 7: 70-92.

Hersh, D.A. 1996. *Abundance and distribution of intertidal and subtidal macrophytes in Cape Cod: The role of nutrient supply and other controls*. Ph.D. Dissertation. Boston University, Boston, Massachusetts, USA.

Irlandi, E.A., Orlando, B.A., and Biber, P.D. 2004. Drift algae-epiphyte-seagrass interactions in a subtropical *Thalassia testudinum* meadow. *Marine Ecology Progress Series* 279: 81-91.

Johnston, K., Ver Hoef, J.M., Krivoruchko, K., and Lucas, N. 2001. *Using ArcGIS Geostatistical Analyst*. ESRI Press, Redlands, CA.

Kaldy, J.E. and Dunton, K.H. 2000. Above- and below-ground production, biomass and reproduction ecology of *Thalassia testudinum* (turtle grass) in a subtropical coastal lagoon. *Marine Ecology Progress Series* 193: 271-283.

Kemp, W.M. and Boynton, W.R. 1984. Spatial and temporal coupling of nutrient inputs to estuarine primary production: The role of particulate transport and decomposition. *Bulletin of Marine Science* 35: 522-535.

Kirkman, H. 1996. Baseline and monitoring methods for seagrass meadows. *Journal of Environmental Management* 47: 191-201.

Koch, E.W. 2001. Beyond light: Physical, geological, and geochemical parameters and possible submersed aquatic vegetation habitat requirements. *Estuaries* 24: 1-17.

Lapointe, B.E. 1989. Macroalgal production and nutrient relations in oligotrophic areas of Florida Bay. *Bulletin of Marine Science* 44: 312-323.

Lee, K-S. and Dunton, K.H. 1999. Influence of sediment nitrogen-availability on carbon and nitrogen dynamics in the seagrass *Thalasssia testudinum*. *Marine Biology* 134: 217-226.

Lin, H.J., Nixon, S.W., Taylor, D.I., Granger, S.L., and Buckley, B.A. 1996. Responses of epiphytes on eelgrass, *Zostera marina* L., to separate and combined nitrogen and phosphorus enrichment. *Aquatic Botany* 52: 243-258.

Livingston, R.J., McGlynn, S.E., and Niu, X. 1998. Factors controlling seagrass growth in a gulf coastal system: Water and sediment quality and light. *Aquatic Botany* 60: 135-159.

Longley, W.L., ed. 1994. *Freshwater inflows to Texas bays and estuaries: Ecological relationships and methods for determination of needs*. Texas Water Development Board and Texas Parks and Wildlife Department, Austin, TX. 386pp.

McGlathery, K.J. 2001. Macroalgal blooms contribute to the decline of seagrass in nutrient-enriched coastal waters. *Journal of Phycology* 37: 453-456.

McGlathery, K.J., Krause-Jensen, D., Rysgaard, S., and Christensen, P.B. 1997. Patterns of ammonium uptake within dense mats of the filamentous macroalga *Chaetomorpha linum*. *Aquatic Botany* 59: 99-115.

Moncreiff, C.A., Sullivan, M.J., Daehnick, A.E. 1992. Primary production dynamics in seagrass beds of Mississippi Sound: The contributions of seagrass, epiphytic algae, sand microflora and phytoplankton. *Marine Ecology Progress Series* 87: 161-171.

Morgan, M.D. and Kitting, C.L. 1984. Production and utilization of the seagrass *Halodule wrightii* and its attached epiphytes. *Limnology & Oceanography* 29: 1066-1076.

Nixon, S.W. 1995. Coastal marine eutrophication: A definition, social causes and future concerns. *Ophelia* 41: 199-219.

Norkko, A. and Bonsdorff, E. 1996. Rapid zoobenthic community responses to accumulations of drift algae. *Marine Ecology Progress Series* 131: 143-157.

Nueces River Authority. 2000. *Basin Highlights Report for the Nueces River Basin and the San Antonio-Nueces and Nueces-Rio Grande Coastal Basins*. http://www.nueces-ra.org/CP/CRP/reports.

Onuf, C.P. 1994. Seagrasses, dredging and light in Laguna Madre, Texas, U.S.A. *Estuarine,Coastal and Shelf Science* 39: 75-91.

Onuf, C.P. 1996a. Seagrass responses to long-term light reduction by brown tide in upper Laguna Madre, Texas: Distribution and biomass patterns. *Marine Ecology Progress Series* 138: 219-231.

Onuf, C.P. 1996b. Biomass patterns in seagrass meadows of the Laguna Madre, Texas. *Bulletin of Marine Science* 58: 404-420.

Oremland, R.S. and Taylor, B.F. 1977. Diurnal fluctuations of O_2, N_2, and CH_4 in the rhizosphere of *Thalassia testudinum*. *Limnology and Oceanography* 22: 566-570.

Orth, R.J. and Moore, K.A. 1983. Chesapeake Bay: An unprecedented decline in submerged aquatic vegetation. *Science* 222: 51-53.

Parsons, T.R., Maita, Y., and Lalli, C.M. 1984. *A manual of chemical and biological methods for seawater analysis*. Pergamon Press, New York.

Peckol, P. and Rivers, J.S. 1996. Contribution by macroalgal mats to primary production of a shallow embayment under high and low nitrogen-loading rates. *Estuarine, Coastal, and Shelf Science* 43: 311-325.

Penhale P.A. 1977. Macrophyte-epiphyte biomass and productivity in an eelgrass *Zostera marina* L. community. *Journal of Experimental Marine Biology & Ecology* 26: 211-224.

Perez-Llorens, J.L. and Niell, F.X. 1993. Seasonal dynamics of biomass and nutrient content in the intertidal seagrass *Zostera noltii* Hornem. from Palmones River estuary, Spain. *Aquatic Botany* 46: 49-66.

Pulich, W.Jr., Blair, C, and White, W.A. 1997. *Current status and historical trends of seagrasses in the Corpus Christi Bay National Estuary Program study area*. Publication CCBNEP-20, Texas Natural Resource Conservation Commission, Austin.

Pulich, W.Jr. 1998. *Seagrass conservation plan for Texas*. Texas Parks and Wildlife Department, Austin.

Quammen, M.L. and Onuf, C.P. 1993. Laguna Madre: Seagrass changes continue decades after salinity reduction. *Estuaries* 16: 302-310.

Redfield, A.C., Ketchun, B.A., and Richards, F.A. 1963. The influence of organisms on the composition of seawater. In: *The Sea*. Hill, M.N. (Ed.). Wiley, New York.

Rose, C.D. and Dawes, C.J. 1999. Effects of community structure on the seagrass *Thalassia testudinum*. *Marine Ecology Progress Series* 184: 83-95.

Sand-Jensen, K. 1977. Effect of epiphytes on eelgrass photosynthesis. *Aquatic Botany* 3: 55-63.

Short, F.T., Burdick, D.M., and Kaldy, J.E. 1995. Mesocosm experiments quantify the effects of eutrophication on eelgrass, *Zostera marina*. *Limnology and Oceanography* 40: 740-749.

Smith, R.D., Dennison, W.C., and Alberte, R.S. 1984. Role of seagrass photosynthesis in root aerobic processes. *Plant Physiology* 74: 1055-1058.

Stoner, A.W. 1980. The role of seagrass biomass in the organization of benthic macrofaunal assemblages. *Bulletin of Marine Science* 30: 537-551.

Suttle, C.A., Fuhrman, J.A., and Capone, D.G. 1990. Rapid ammonium cycling and concentration-dependent partitioning of ammonium and phosphate: Implications for carbon transfer in planktonic communities. *Limnology and Oceanography* 35: 424-433.

Texas Commission on Environmental Quality (TCEQ). 2003. *Twelve Total Maximum Daily Loads for legacy pollutants in the Arroyo Colorado above tidal and the Donna reservoir and canal system*. http://www.tnrcc.state.tx.us/water/quality/tmdl/.

Tomasko, D.A. and Lapointe, B.E. 1991. Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability and epiphyte levels: Field observations and experimental studies. *Marine Ecology Progress Series* 75: 9-17.

Tomasko, D.A., Dawes, C.J., and Hall, M.O. 1996. The effects of anthropogenic nutrient enrichment on turtle grass (*Thalassia testudinum*) in Sarasota Bay, Florida. *Estuaries* 19: 448-456.

Tunnell, J.W.Jr. 2002. Geography, climate, and hydrography. In: *The Laguna Madre of Texas and Tamaulipas*. Tunnell, J.W.Jr. and Judd, F.W. (Eds.). Texas A&M University Press, College Station.

Valiela, I., Collins, G., Kremer, J., Lajtha, K., Geist, M., Seely, B., Brawley, J., and Sham, C.H. 1997a. Nitrogen loading from coastal watersheds to receiving estuaries: New method and application. *Ecological Applications* 7: 358-380.

Valiela, I., McClelland, J., Hauxwell, J., Behr, P.J., Hersh, D., and Foreman, K. 1997b. Macroalgal blooms in shallow estuaries: Controls and ecophysiological and ecosystem consequences. *Limnology and Oceanography* 42: 1105-1118.

Virnstein, R.W. and Carbonara, P.A. 1985. Seasonal abundance and distribution of drift algae and seagrasses in the Mid-Indian River Lagoon, Florida. *Aquatic Botany* 23: 67-82.

Virnstein, R.W., and Morris, L.J. 1996. *Seagrass preservation and restoration: A diognostic plan for the Indian River Lagoon.* Technical memorandum no. 14. St. Johns River Water Management District, Palatka, Florida.

Whitledge, T.E., Stockwell, D.A., Buskey, E.J., Dunton, K.H., Holt, G.J., Holt, S.A., and Montagna, P.A. 1999. Persistent brown tide bloom in Laguna Madre, Texas. In: *The Gulf of Mexico Large Marine Ecosystem*. K. Sherman (ed.). Blackwell Science.

Wood, N. and Lavery, P. 2000. Monitoring seagrass ecosystem health – the role of perception in defining health and indicators. *Ecosystem Health* 6: 134-148.

Wyllie-Echeverria, S., Gunnarsson, K., Mateo, M.A., Borg, J.A., Renom, P., Kuo, J., Schanz, A., Hellblom, F., Jackson, E., Pergent, G., Pergent-Martini, C., Johnson, M., Sanchez-Lizaso, J., Boudouresque, C.F., and Aioi, K. 2002. Protecting the seagrass biome: Report from the traditional seagrass knowledge working group. *Bulletin of Marine Science* 71: 1415-1417.

Zieman, J.C., Fourqurean, J.W., and Iverson, R.L. 1989. Distribution, abundance, and productivity of seagrasses and macroalgae in Florida Bay. *Bulletin of Marine Science* 44: 292-311.

Appendices

Appendix A
Tables

Table 1: Parameters measured at all sampling sites in Redfish Bay and lower Laguna Madre.

ABIOTIC PARAMETERS		BIOTIC PARAMETERS	
WATER	**SEDIMENT**	**SEAGRASS**	**ALGAE/EPIPHYTES**
Salinity and temperature	Sediment grain size	Biomass (above- & below-ground)	Drift macroalgal abundance
Dissolved oxygen	Porewater NH_4^+	Root:shoot ratio	Drift macroalgal species composition
Nutrients (NH_4^+, NO_2^-, NO_3^-, PO_4^{3-})	Total organic carbon (TOC)	Shoot density	Epiphyte biomass
Chlorophyll *a*		Blade length, width	
Total Suspended Solids (TSS)		Species composition	
%Surface Irradiance (%SI)		Maximum depth limit	
Light attenuation (k)		C:N blade ratios	

Table 2: Values are $\bar{x}$ ± SE (n = 30) for abiotic parameters at all sites in Redfish Bay and lower Laguna Madre. ND = no data.

	REDFISH BAY				**LOWER LAGUNA MADRE**			
PARAMETER	**SUMMER 2002**	**WINTER 2003**	**SUMMER 2003**	**WINTER 2004**	**SUMMER 2002**	**WINTER 2003**	**SUMMER 2003**	**WINTER 2004**
Salinity (psu)	25.2 ± 0.6	21.4 ± 1.1	35.6 ± 0.7	24.2 ± 0.4	36.1 ± 0.2	27.9 ± 0.6	40.7 ± 0.2	30.6 ± 0.5
Temperature (^{o}C)	30.9 ± 0.3	14.8 ± 0.6	30.0 ± 0.3	16.1 ± 0.5	29.3 ± 0.2	19.0 ± 0.2	30.8 ± 0.3	18.1 ± 0.2
Chlorophyll *a* (µg L^{-1})	2.0 ± 0.2	6.5 ± 0.8	1.8 ± 0.1	1.5 ± 0.1	1.0 ± 0.1	1.2 ± 0.2	1.3 ± 0.1	2.1 ± 0.2
% Surface Irradiance	64.3 ± 3.4	46.3 ± 4.7	46.0 ± 4.6	61.6 ± 5.0	38.4 ± 3.7	40.1 ± 3.0	33.2 ± 2.9	43.4 ± 2.3
Light Att. (k; m^{-1})	1.0 ± 0.1	1.8 ± 0.2	1.5 ± 0.1	1.6 ± 0.2	7.4 ± 0.6	1.1 ± 0.1	1.0 ± 0.05	0.8 ± 0.05
TSS (mg L^{-1})	7.7 ± 1.1	15.4 ± 1.4	20.9 ± 1.1	18.7 ± 0.6	12.3 ± 1.5	17.9 ± 2.9	19.6 ± 1.0	10.9 ± 0.5
NH_4^+ (µM)	0.76 ± 0.08	1.51 ± 0.19	0.86 ± 0.07	1.84 ± 0.11	0.50 ± 0.06	0.49 ± 0.04	0.93 ± 0.13	1.47 ± 0.03
$NO_2^- + NO_3^-$ (µM)	0.18 ± 0.03	0.73 ± 0.21	0.09 ± 0.01	0.10 ± 0.01	0.12 ± 0.03	0.62 ± 0.18	0.42 ± 0.05	0.05 ± 0.01
PO_4^{3-} (µM)	0.54 ± 0.06	0.50 ± 0.04	0.41 ± 0.03	0.32 ± 0.02	0.21 ± 0.04	0.61 ± 0.13	0.28 ± 0.02	0.16 ± 0.01
TOC (% LOI)	1.8 ± 0.1	1.9 ± 0.1	2.5 ± 0.1	2.1 ± 0.1	2.5 ± 0.2	2.2 ± 0.2	2.8 ± 0.2	2.8 ± 0.2
Porewater NH_4^+ (µM)	109.6 ± 7.2	65.6 ± 3.1	82.8 ± 7.4	76.2 ± 5.6	34.2 ± 4.0	39.0 ± 3.1	27.9 ± 4.3	37.5 ± 5.6
% Silt + Clay	30.4 ± 2.7	ND	ND	29.3 ± 2.8	37.4 ± 3.0	ND	ND	35.0 ± 2.9

Table 3: Values are $\bar{x}$ ± SE (n = 24) for biotic parameters at all vegetated sites in Redfish Bay and lower Laguna Madre. ND = no data. * = measurements of *Thalassia testudinum*.

	REDFISH BAY				**LOWER LAGUNA MADRE**			
PARAMETER	**SUMMER 2002**	**WINTER 2003**	**SUMMER 2003**	**WINTER 2004**	**SUMMER 2002**	**WINTER 2003**	**SUMMER 2003**	**WINTER 2004**
Drift algae (g m^{-2})	162 ± 25	62 ± 12	67 ± 16	65 ± 18	43 ± 8	71 ± 21	72 ± 18	104 ± 31
Epiphytes* (mg cm^{-2})	0.87 ± 0.18	2.33 ± 0.42	2.06 ± 0.20	5.29 ± 0.61	0.33 ± 0.06	1.09 ± 0.14	0.49 ± 0.06	0.89 ± 0.12
% Seagrass Cover	80.4 ± 5.4	71.1 ± 4.3	69.9 ± 5.2	46.9 ± 6.6	86.9 ± 5.4	73.5 ± 6.5	86.8 ± 4.4	78.1 ± 5.4
AG biomass* (g m^{-2})	197 ± 16	68 ± 6	214 ± 27	79 ± 9	135 ± 17	77 ± 9	142 ± 25	59 ± 7
BG biomass* (g m^{-2})	486 ± 36	400 ± 39	486 ± 45	416 ± 31	1255 ± 222	867 ± 162	908 ± 158	851 ± 166
Shoot density* (shoots m^{-2})	916 ± 59	688 ± 48	768 ± 79	821 ± 57	1079 ± 147	803 ± 130	933 ± 143	888 ± 140
Blade Length* (cm)	28.9 ± 0.8	13.8 ± 1.0	33.3 ± 1.7	14.8 ± 0.7	26.6 ± 1.2	16.7 ± 0.8	28.1 ± 1.4	15.5 ± 0.8
Blade Width* (mm)	6.1 ± 0.2	5.6 ± 0.3	5.5 ± 0.3	5.9 ± 0.2	6.0 ± 0.1	5.9 ± 0.2	6.2 ± 0.1	5.8 ± 0.1
Root:shoot ratio*	2.7 ± 0.2	6.8 ± 0.7	3.1 ± 0.5	6.6 ± 0.6	9.3 ± 1.0	11.5 ± 1.4	7.4 ± 0.9	14.2 ± 1.8
C:N blade ratio*	12.9 ± 0.3	ND	ND	ND	13.1 ± 0.2	ND	ND	ND

Table 4: Summary of Principal Component Analysis for sites in RFB and LLM.

Location	**sites**	**parameters most associated with drift algae**	**positive or negative association**
RFB	All	*Thalassia* above-ground biomass *Thalassia* blade length TSS	+ + –
	Only vegetated	Porewater NH_4^+ TSS Epiphyte biomass Depth Shoot density	+ – – + –
LLM	All	% Surface irradiance Depth	+ –
	Only vegetated	% Seagrass cover *Thalassia* shoot density Depth	+ + –

Appendix B
Figures

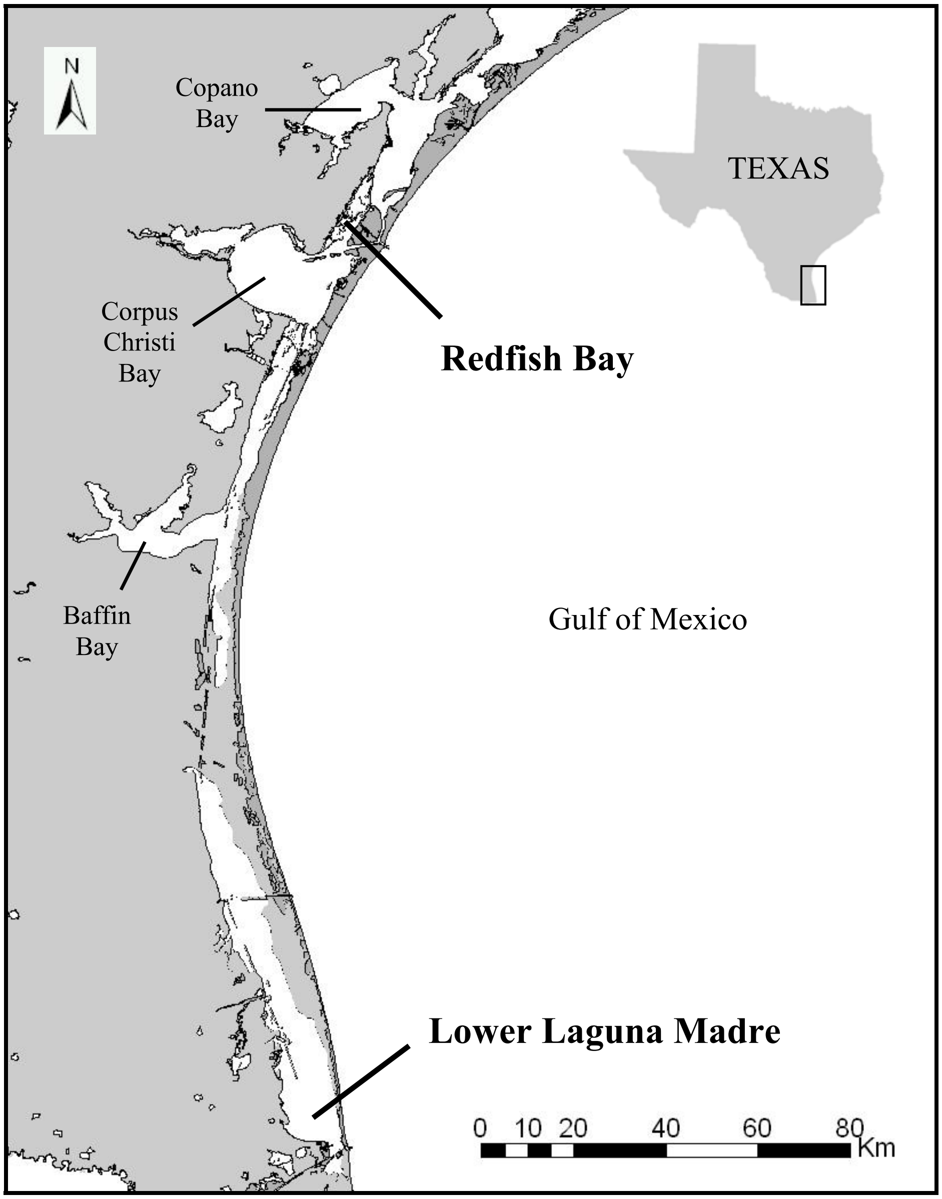

Figure 1: Location of Redfish Bay (RFB) and lower Laguna Madre (LLM) study areas on the Texas Gulf Coast.

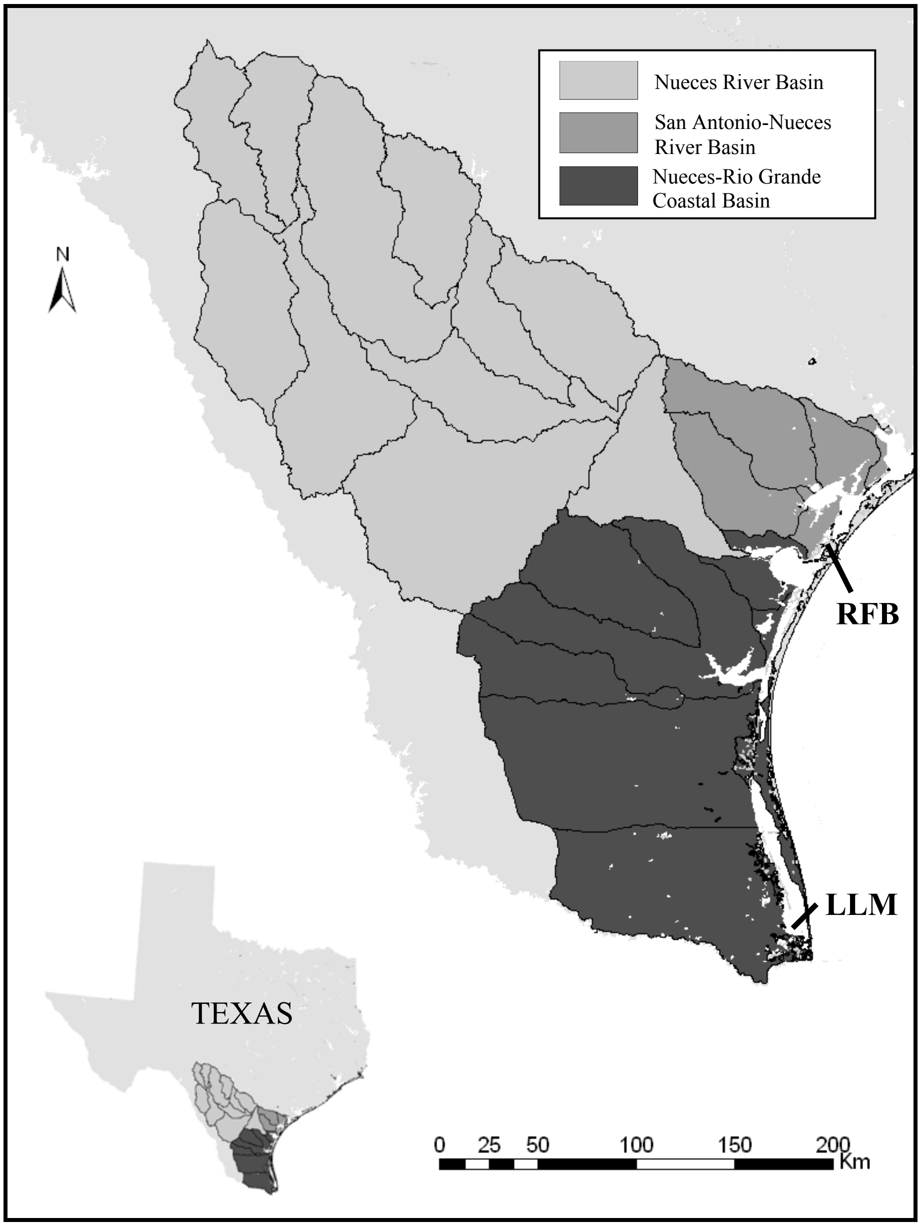

Figure 2: Watersheds delivering freshwater inputs to Laguna Madre and Redfish Bay.

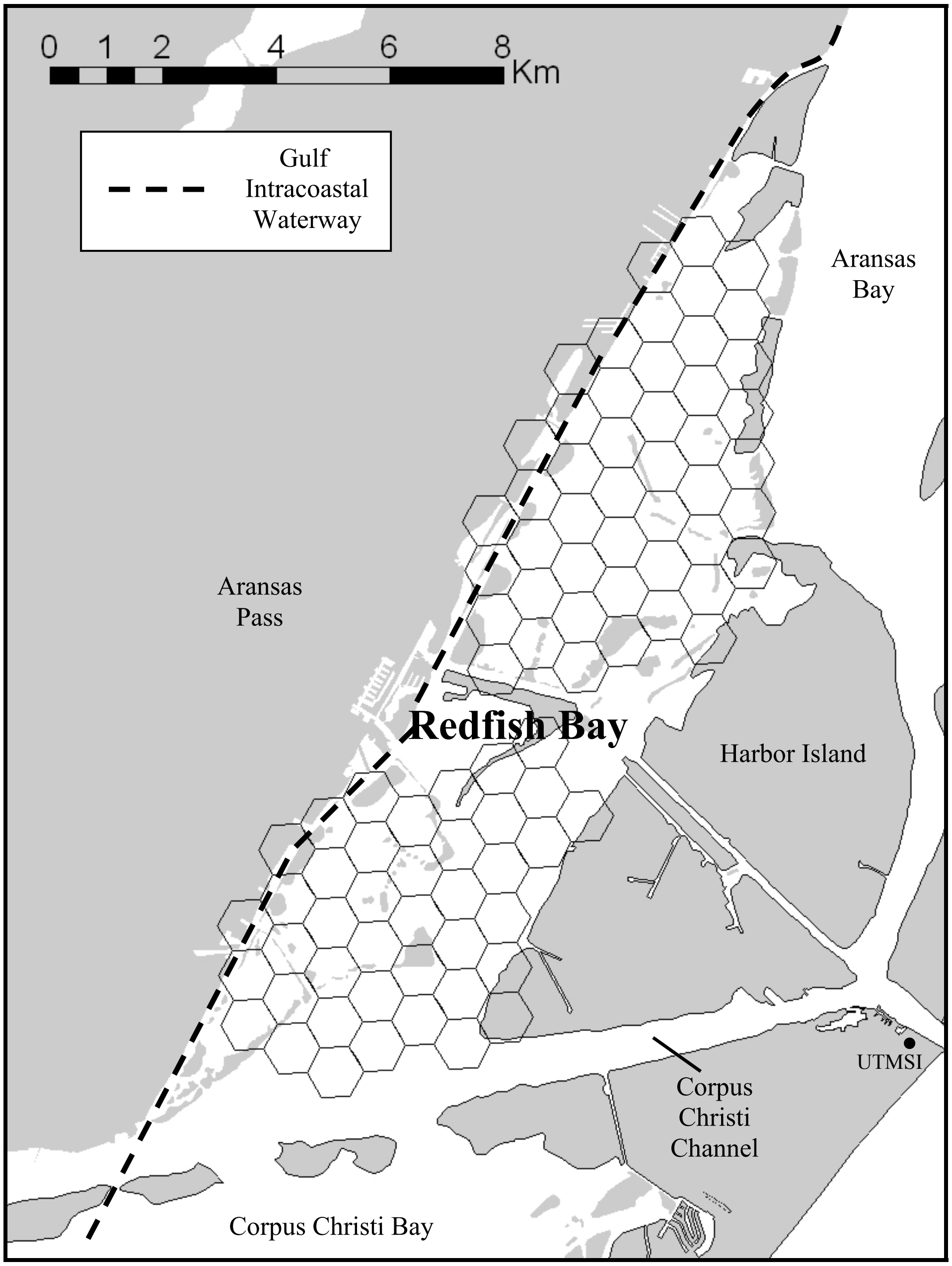

Figure 3: A hexagon layer superimposed on Redfish Bay. The 0.66-km^2 hexagons contain up to one random sampling location (see text for details).

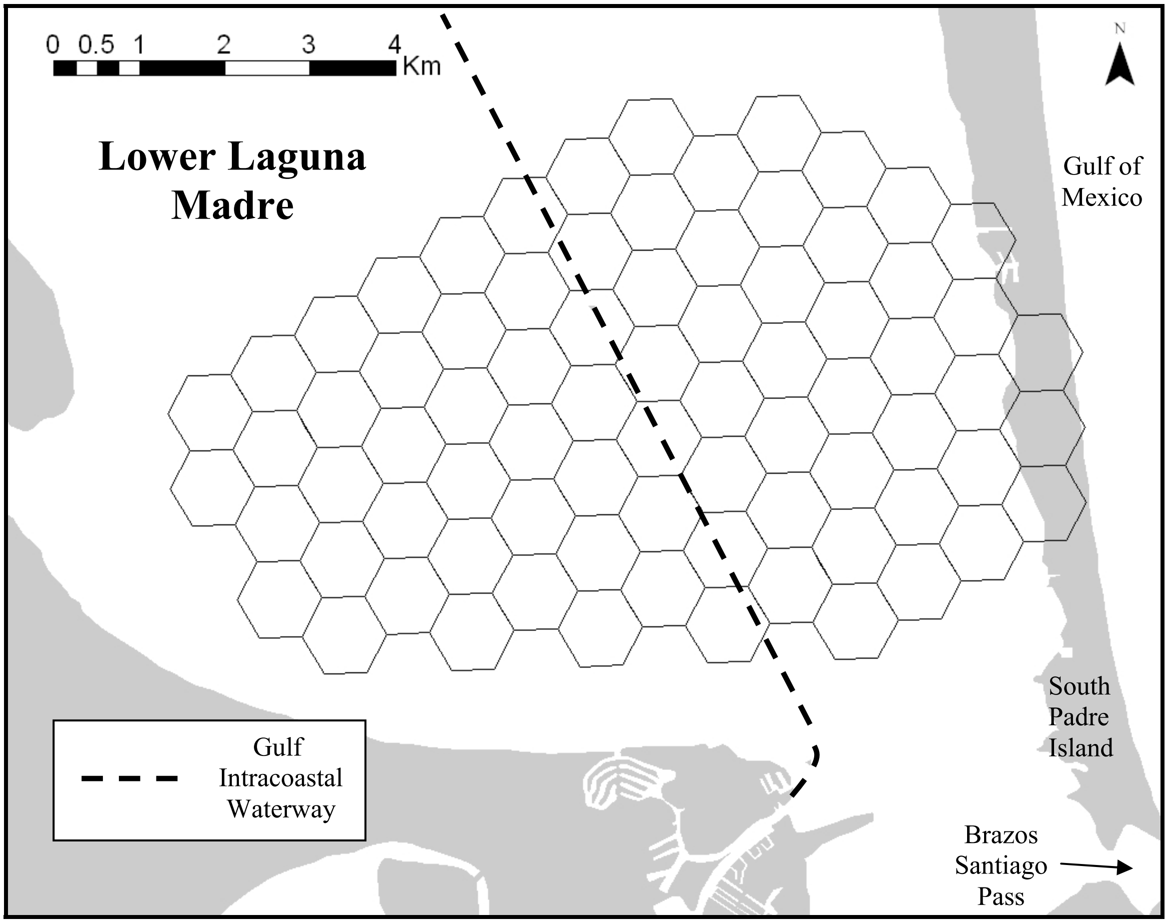

Figure 4: A hexagon layer superimposed on lower Laguna Madre. The 0.66-km^2 hexagons contain up to one random sampling location (see text for details).

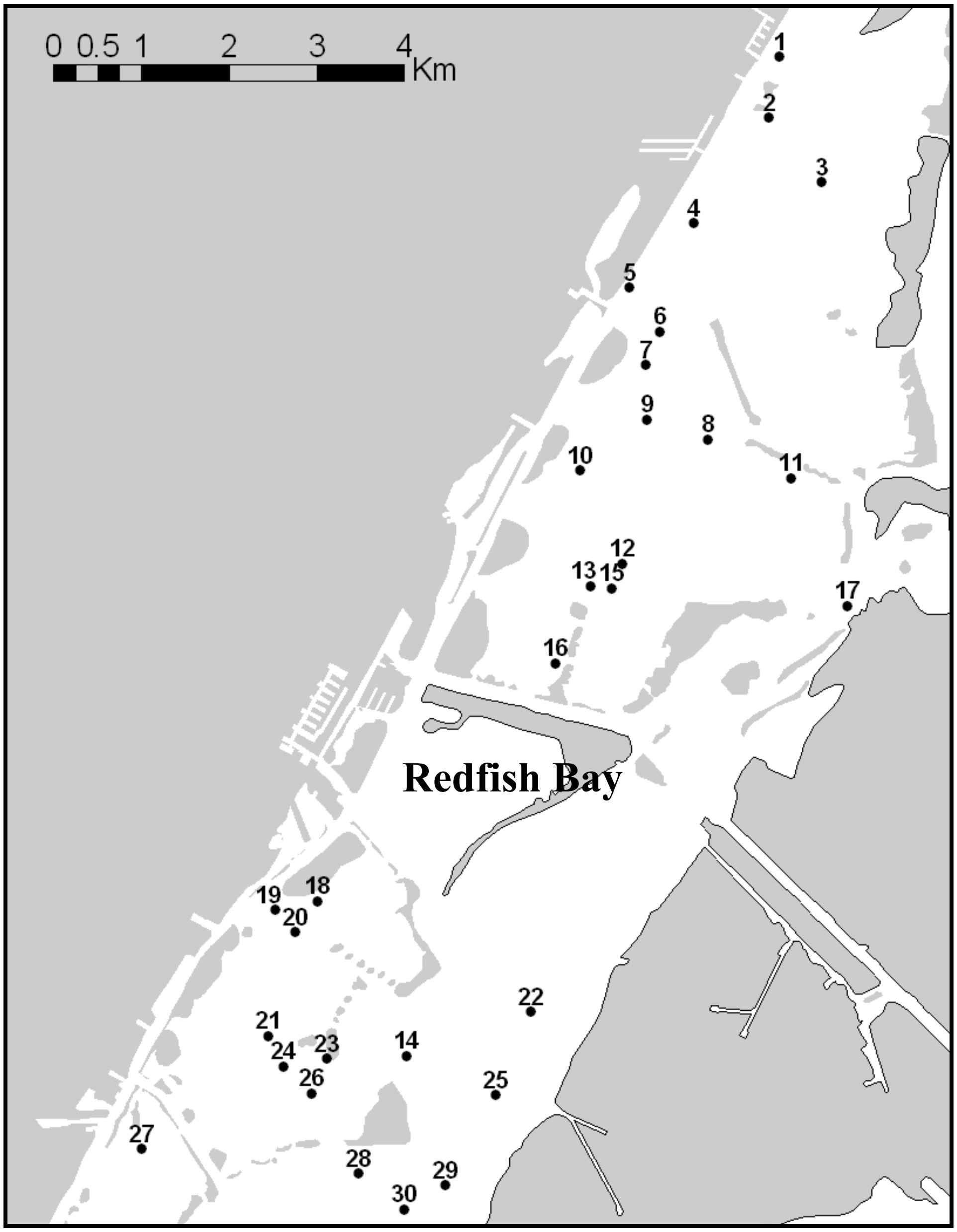

Figure 5: Location of sampling sites in Redfish Bay based on hexagonal tessellation procedures.

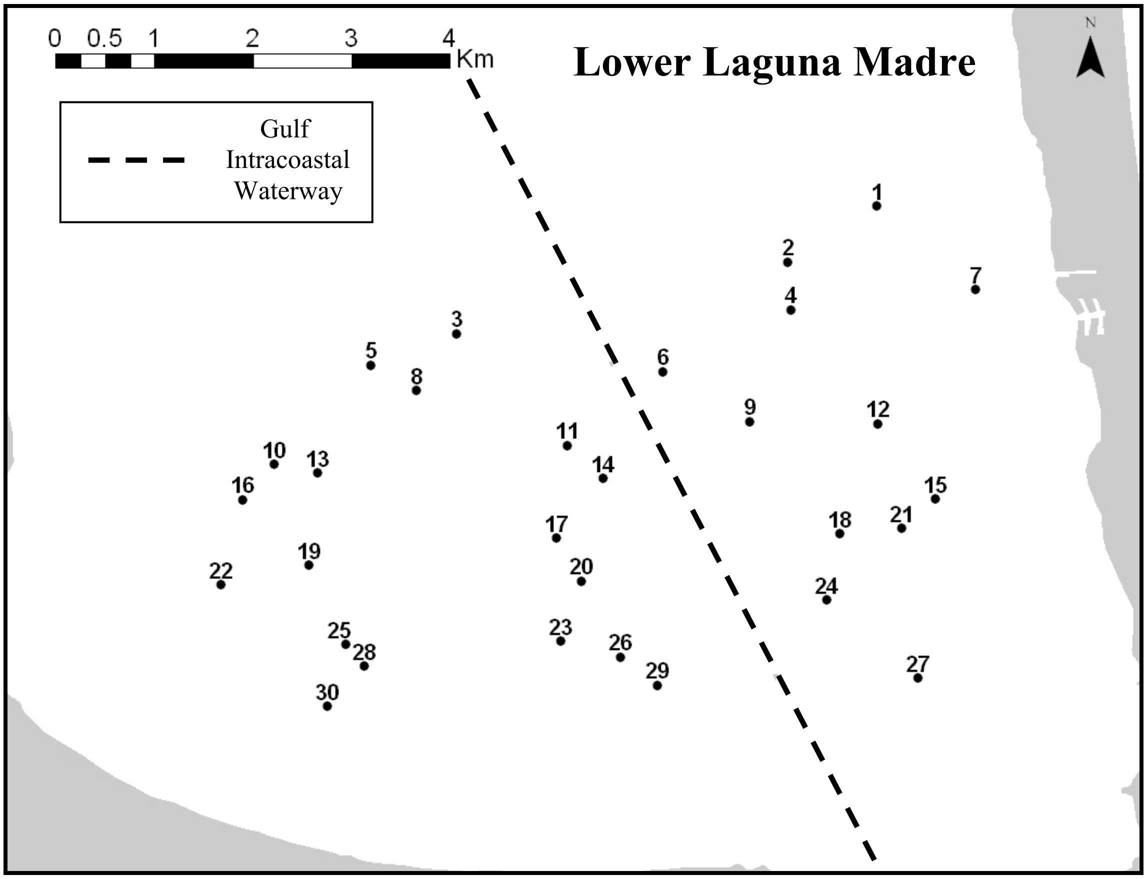

Figure 6: Location of sampling sites in lower Laguna Madre based on hexagonal tessellation procedures.

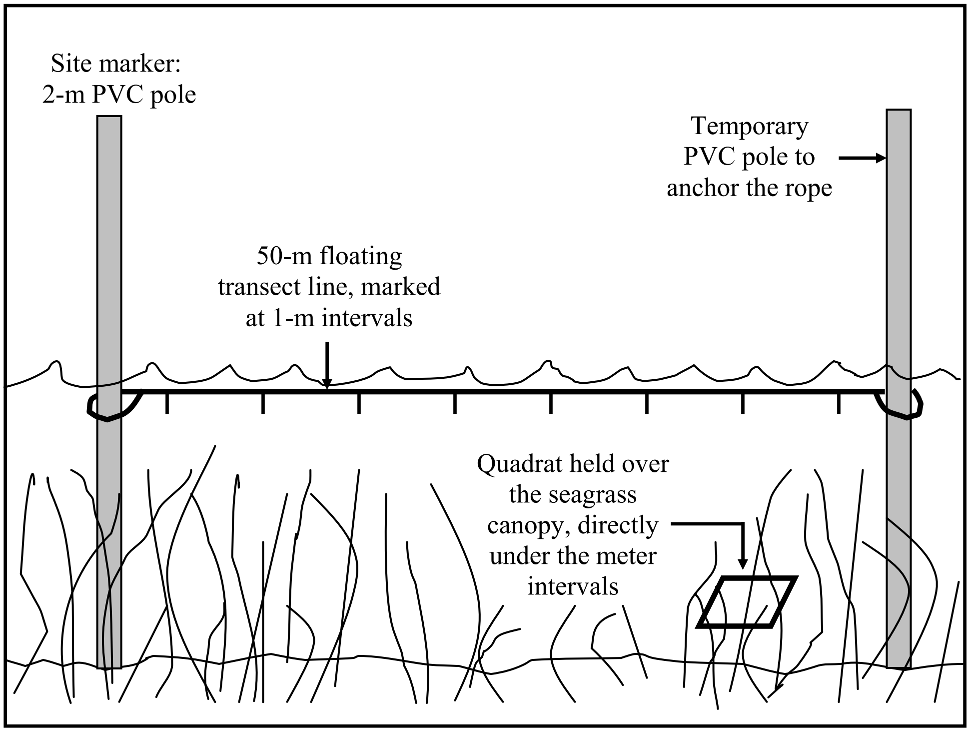

Figure 7: Temporary 50-m transect assembled at each site.

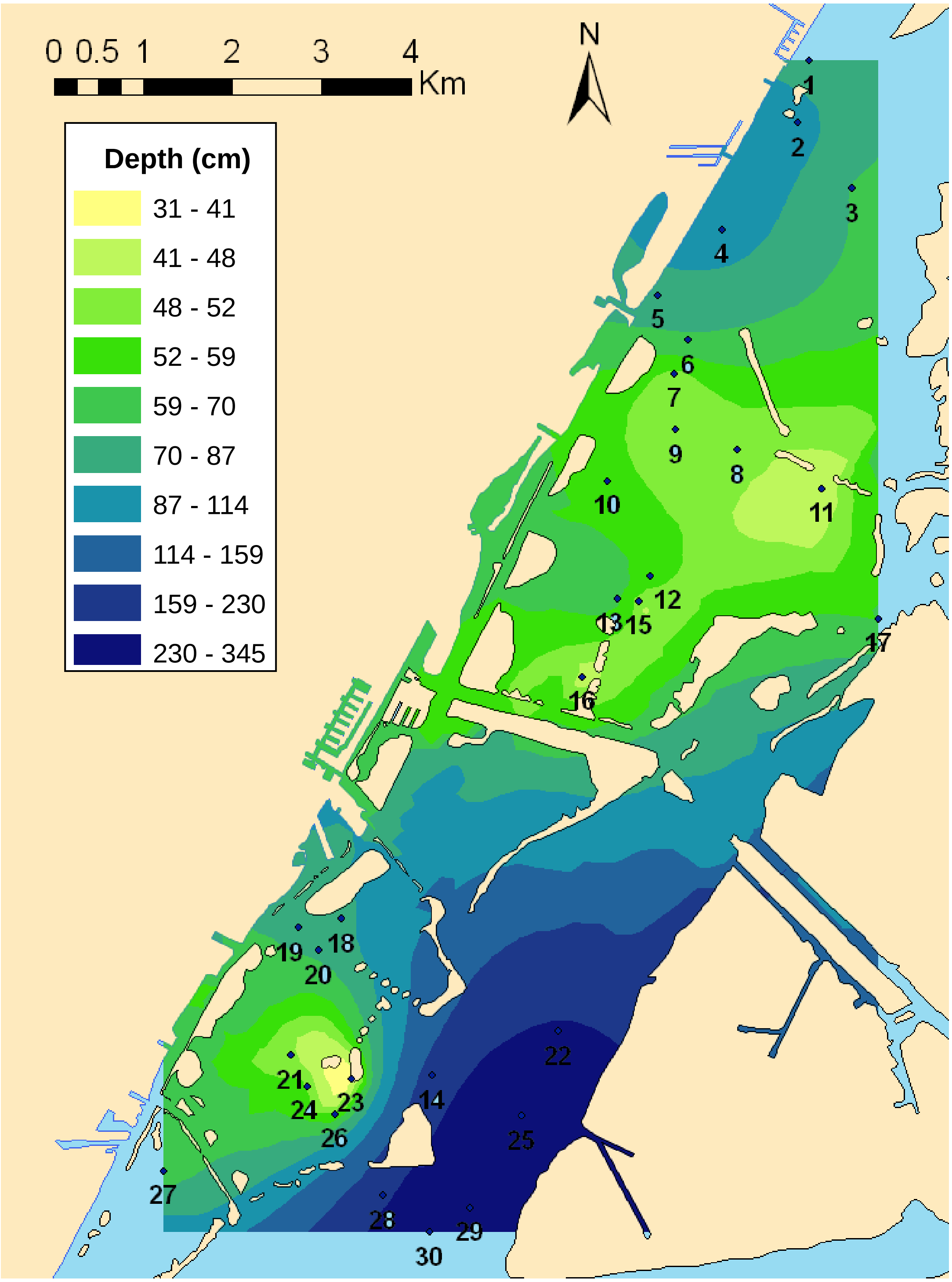

Figure 8: Interpolated average depth (cm) in Redfish Bay.

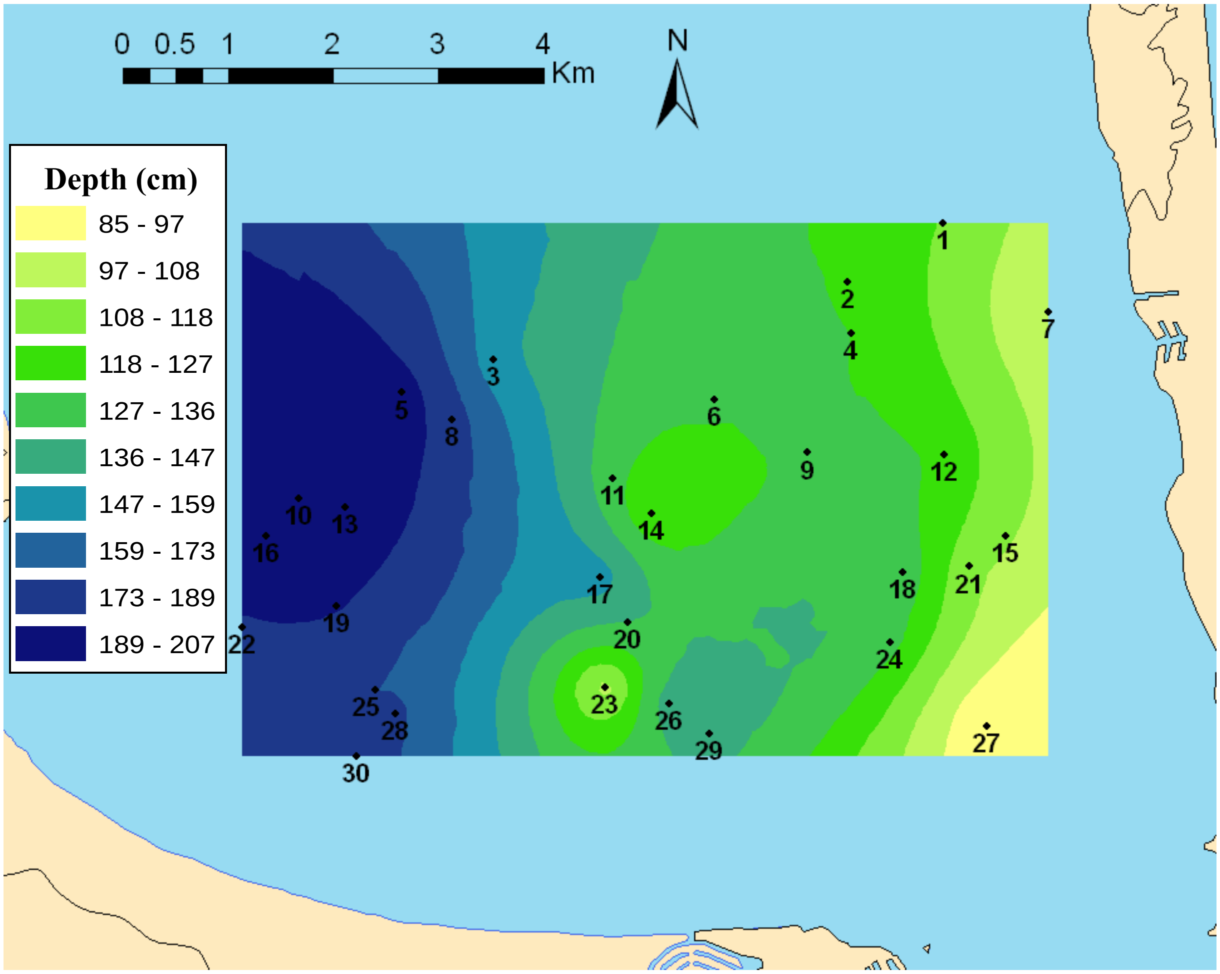

Figure 9: Interpolated average depth (cm) in lower Laguna Madre.

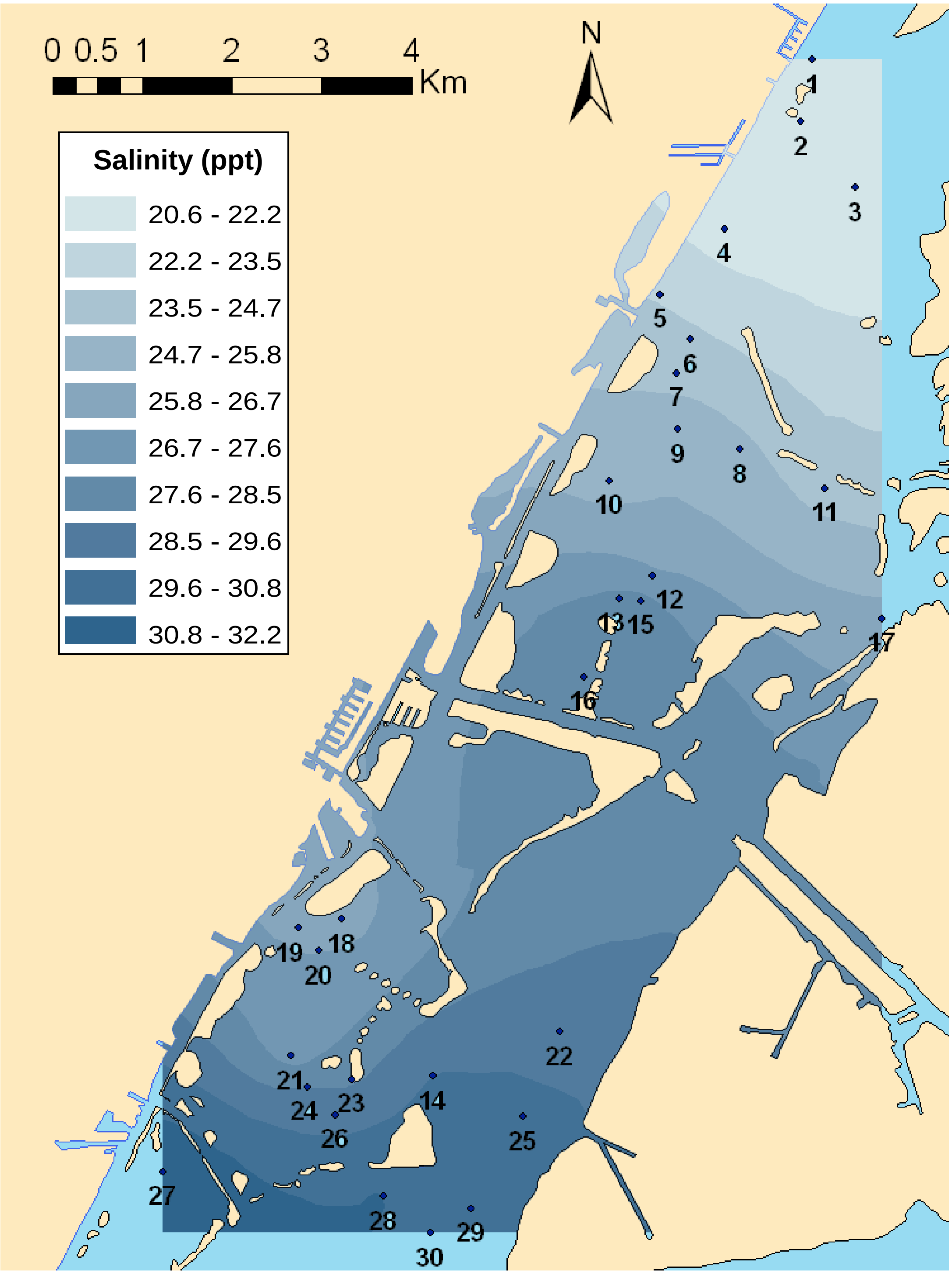

Figure 10: Interpolated average salinity in Redfish Bay.

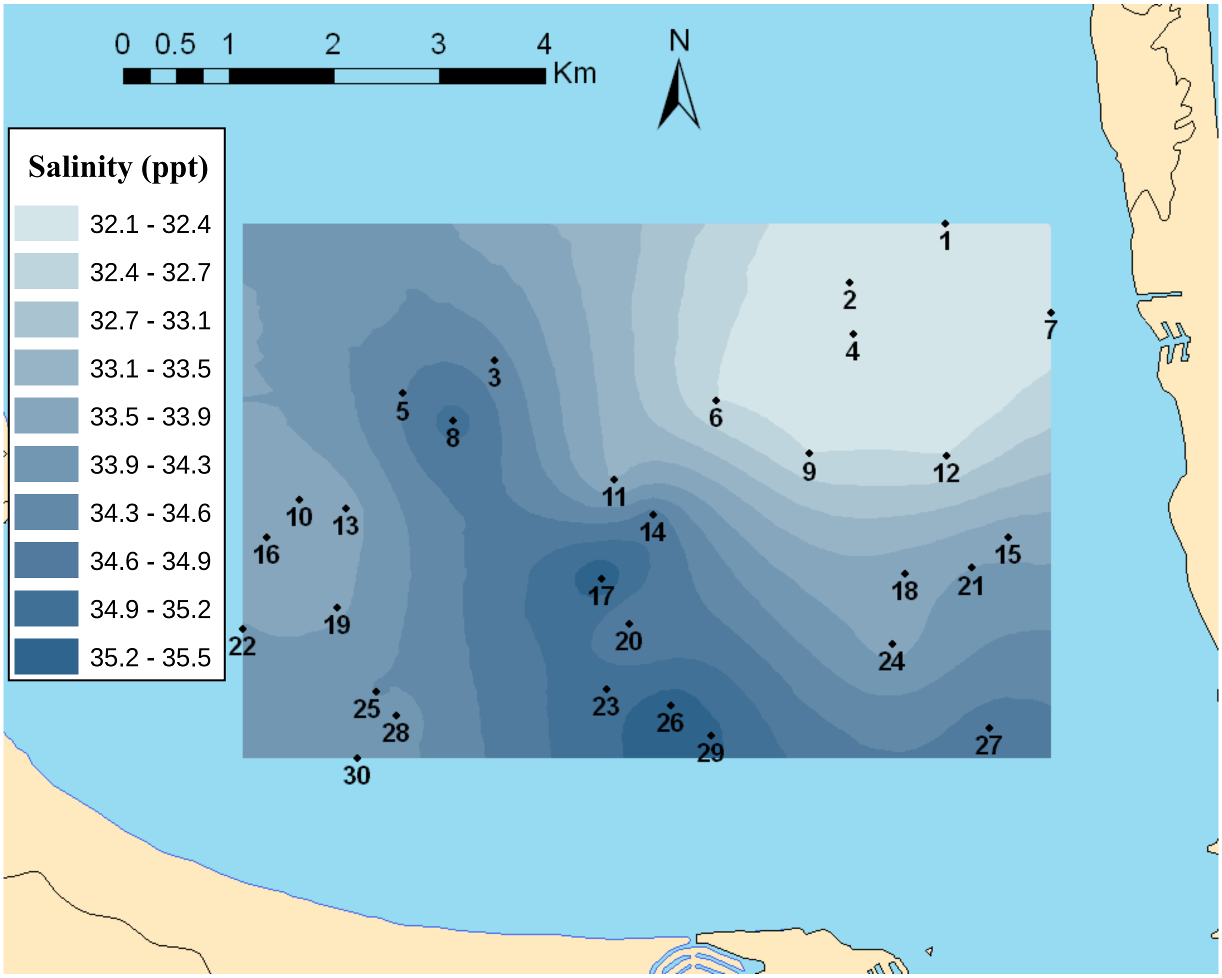

Figure 11: Interpolated average salinity in lower Laguna Madre.

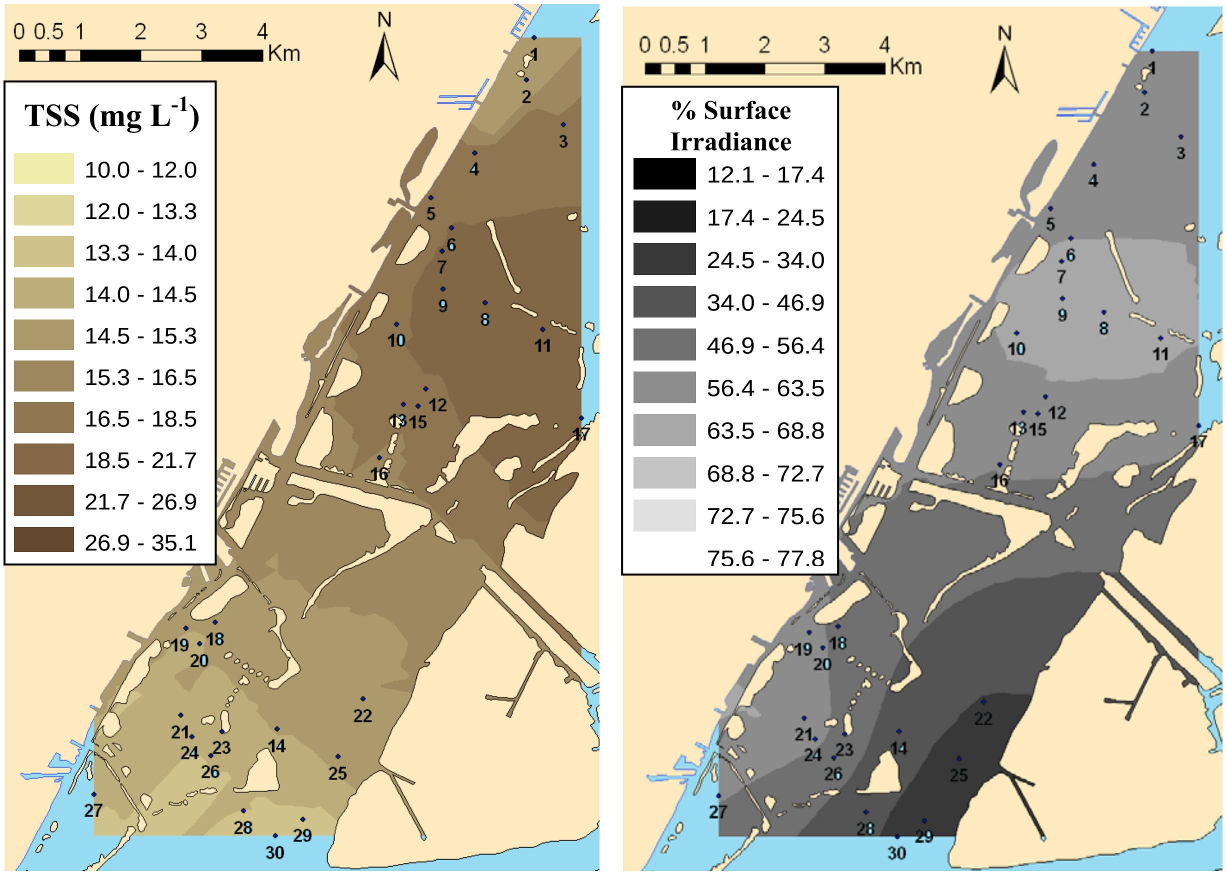

Figure 12: Left panel: interpolated average total suspended solids (TSS) in Redfish Bay. Right panel: interpolated average % surface irradiance in Redfish Bay.

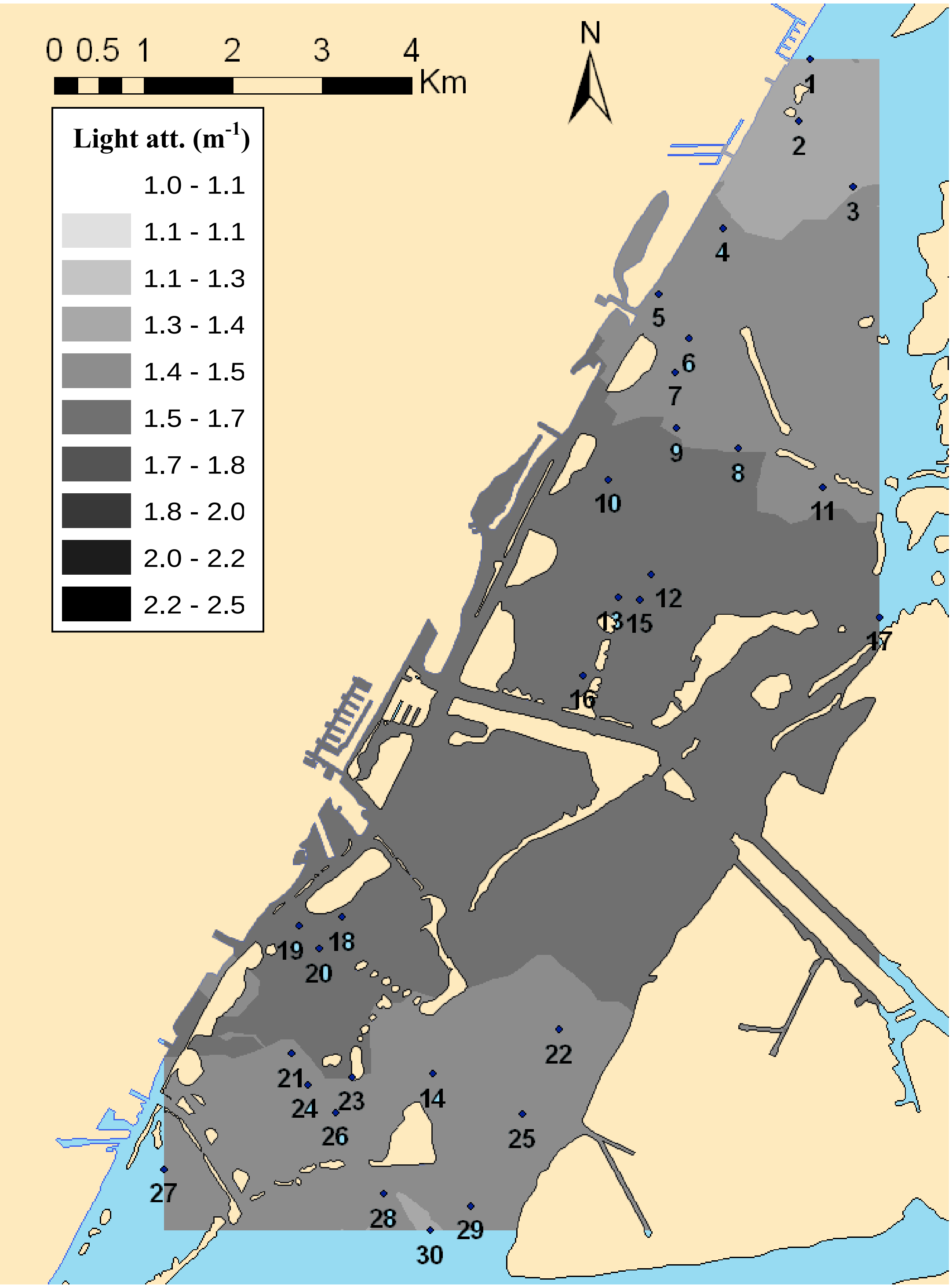

Figure 13: Interpolated average light attenuation (k) in Redfish Bay.

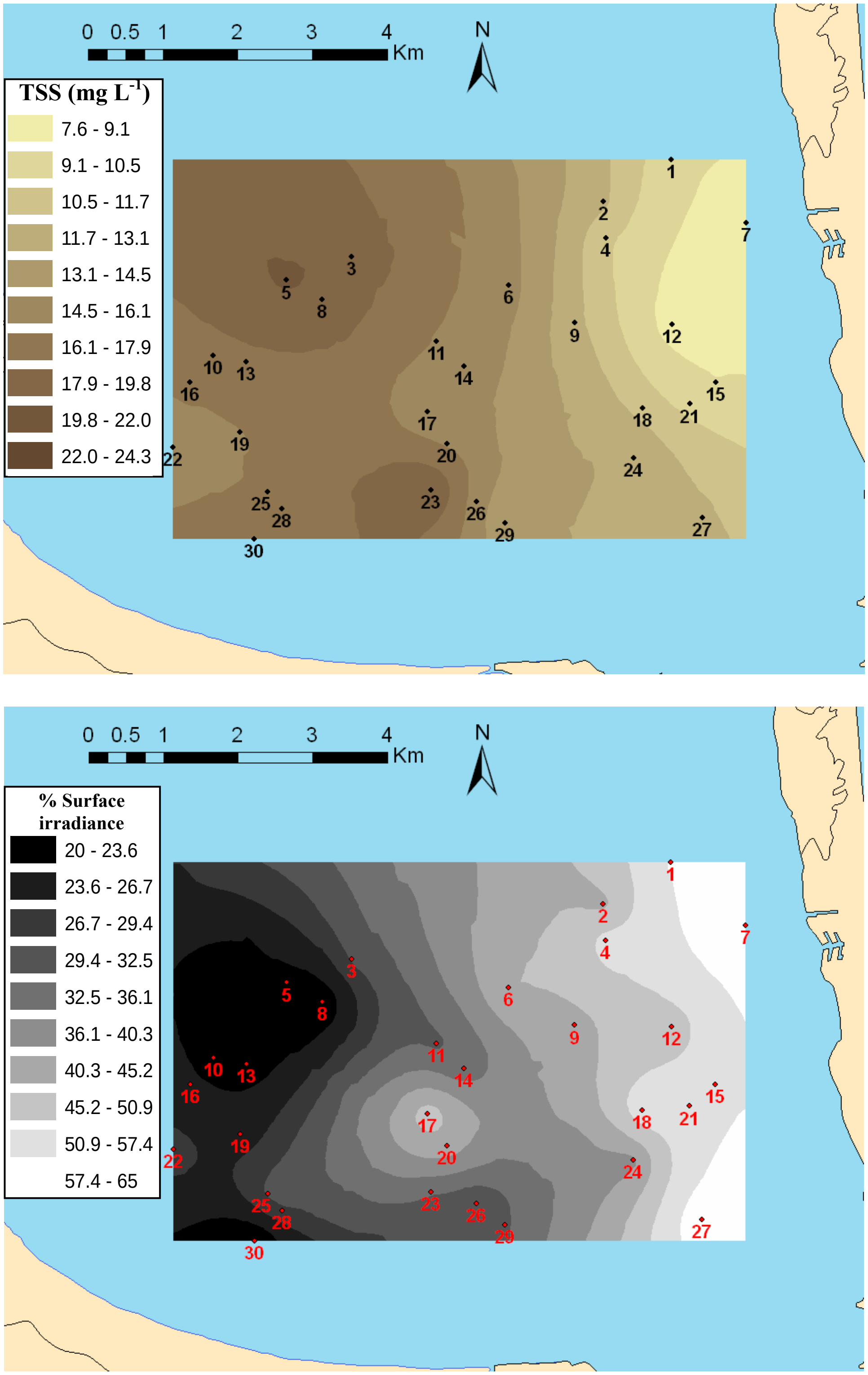

Figure 14: Top panel: interpolated average total suspended solids (TSS) in LLM. Lower panel: interpolated average % surface irradiance.

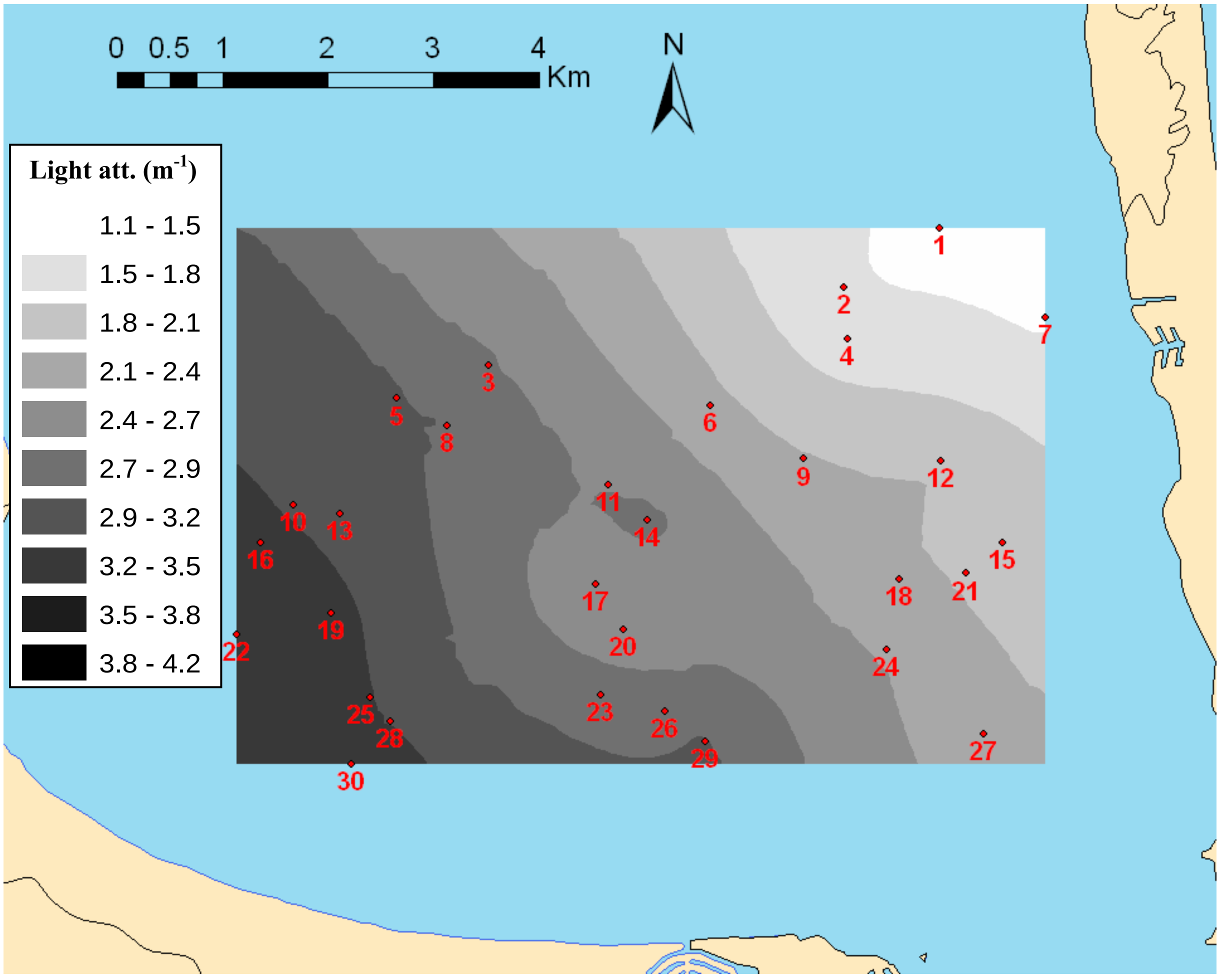

Figure 15: Interpolated average light attenuation (k) in lower Laguna Madre.

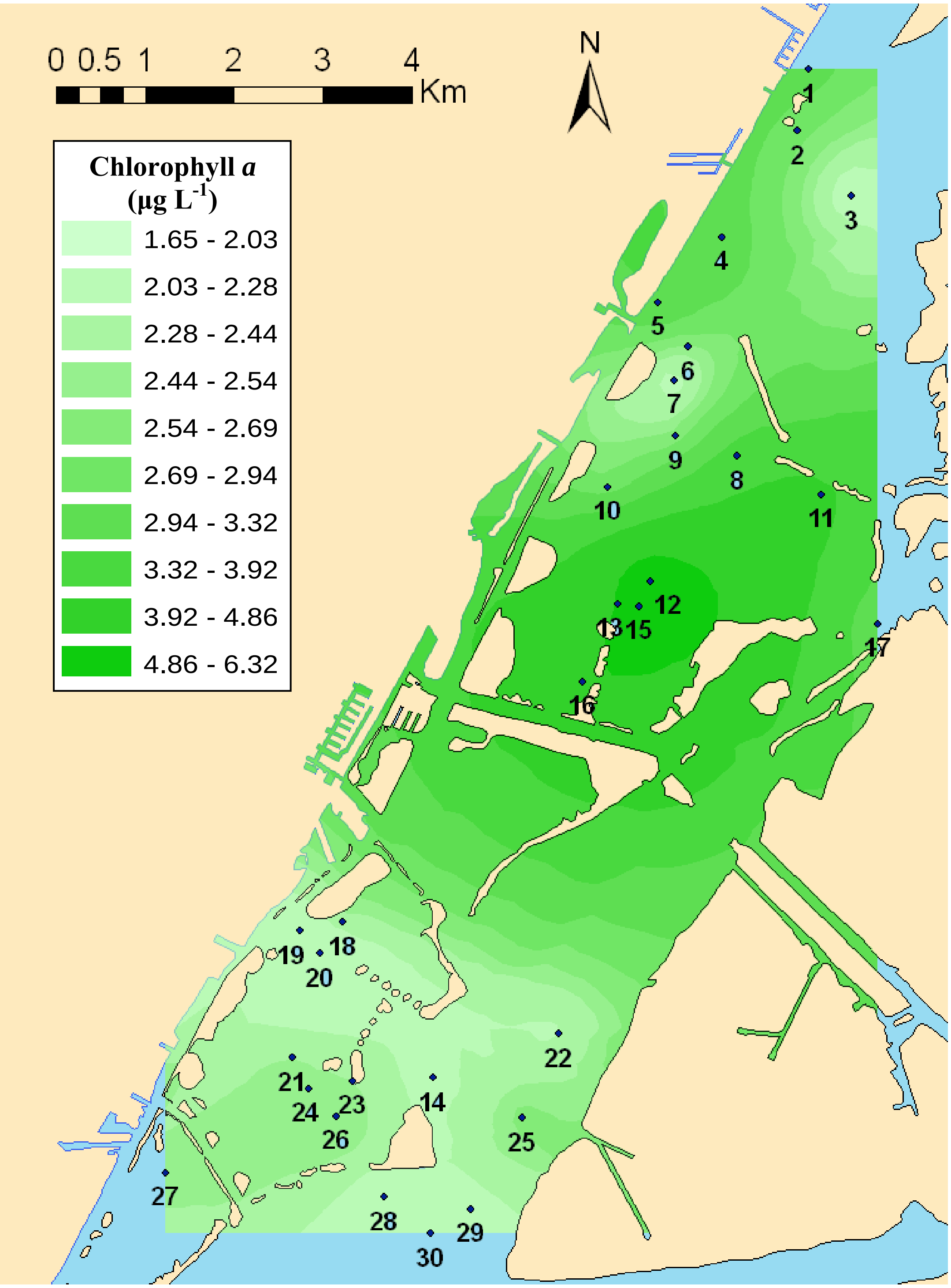

Figure 16: Interpolated average chlorophyll *a* concentration in Redfish Bay.

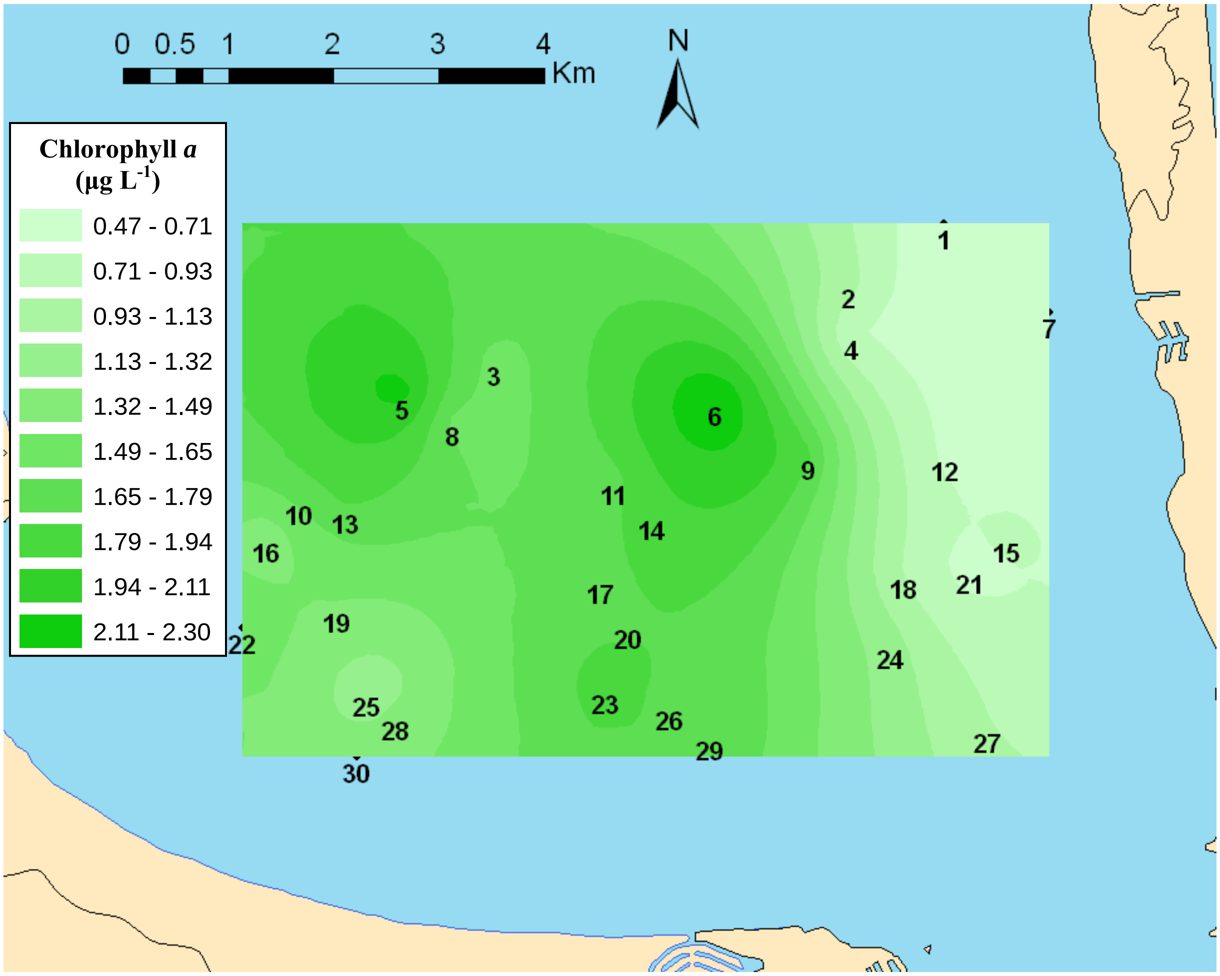

Figure 17: Interpolated average chlorophyll *a* concentration in lower Laguna Madre.

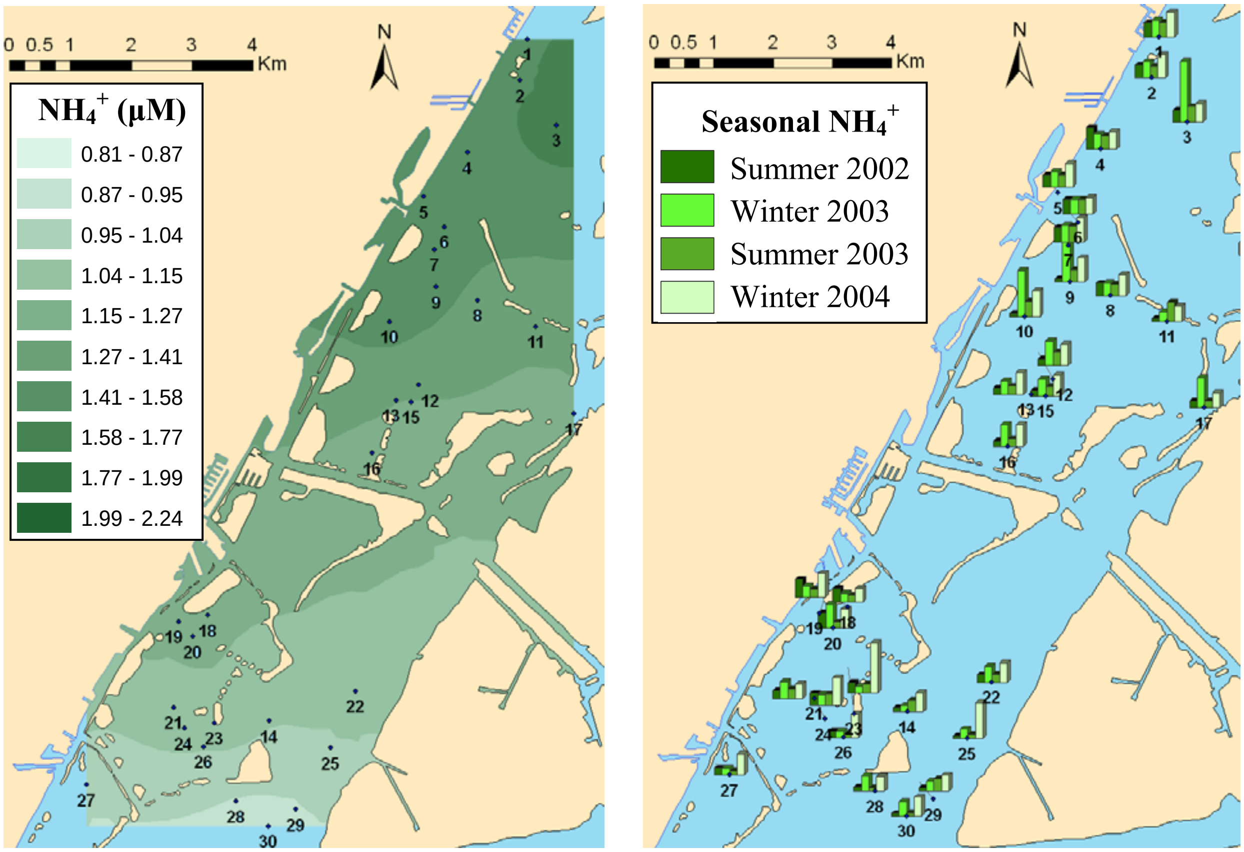

Figure 18: Left panel: interpolated average water column NH_4^+ in Redfish Bay (across all 4 sampling periods). Right panel: Average water column NH_4^+ during each sampling period. Bar height represents NH_4^+ concentration.

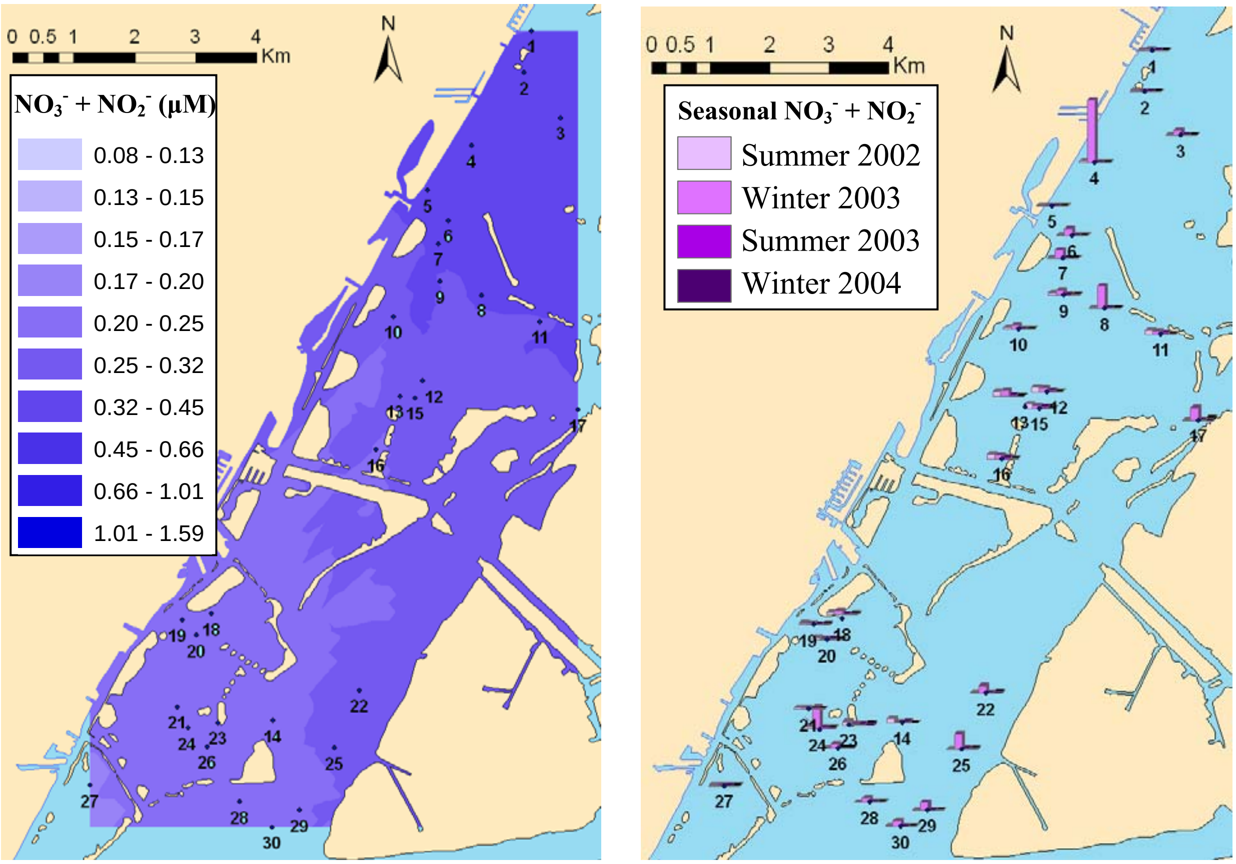

Figure 19: Left panel: interpolated average water column $NO_3^- + NO_2^-$ in Redfish Bay (across All 4 sampling periods). Right panel: Average water column $NO_3^- + NO_2^-$ during each sampling period. Bar height represents $NO_3^- + NO_2^-$ concentration.

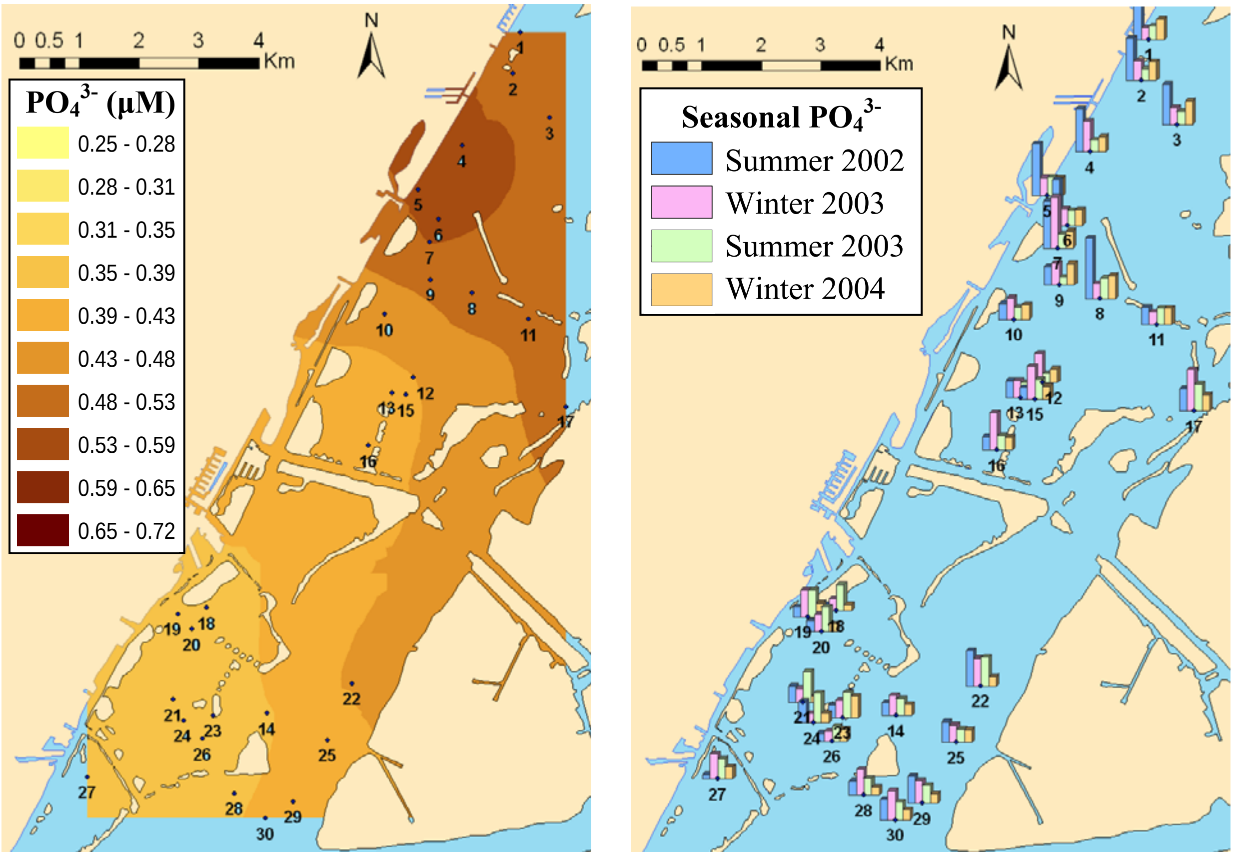

Figure 20: Left panel: interpolated average water column PO_4^{3-} in Redfish Bay (across all 4 sampling periods). Right panel: Average water column PO_4^{3-} during each sampling period. Bar height represents PO_4^{3-} concentration.

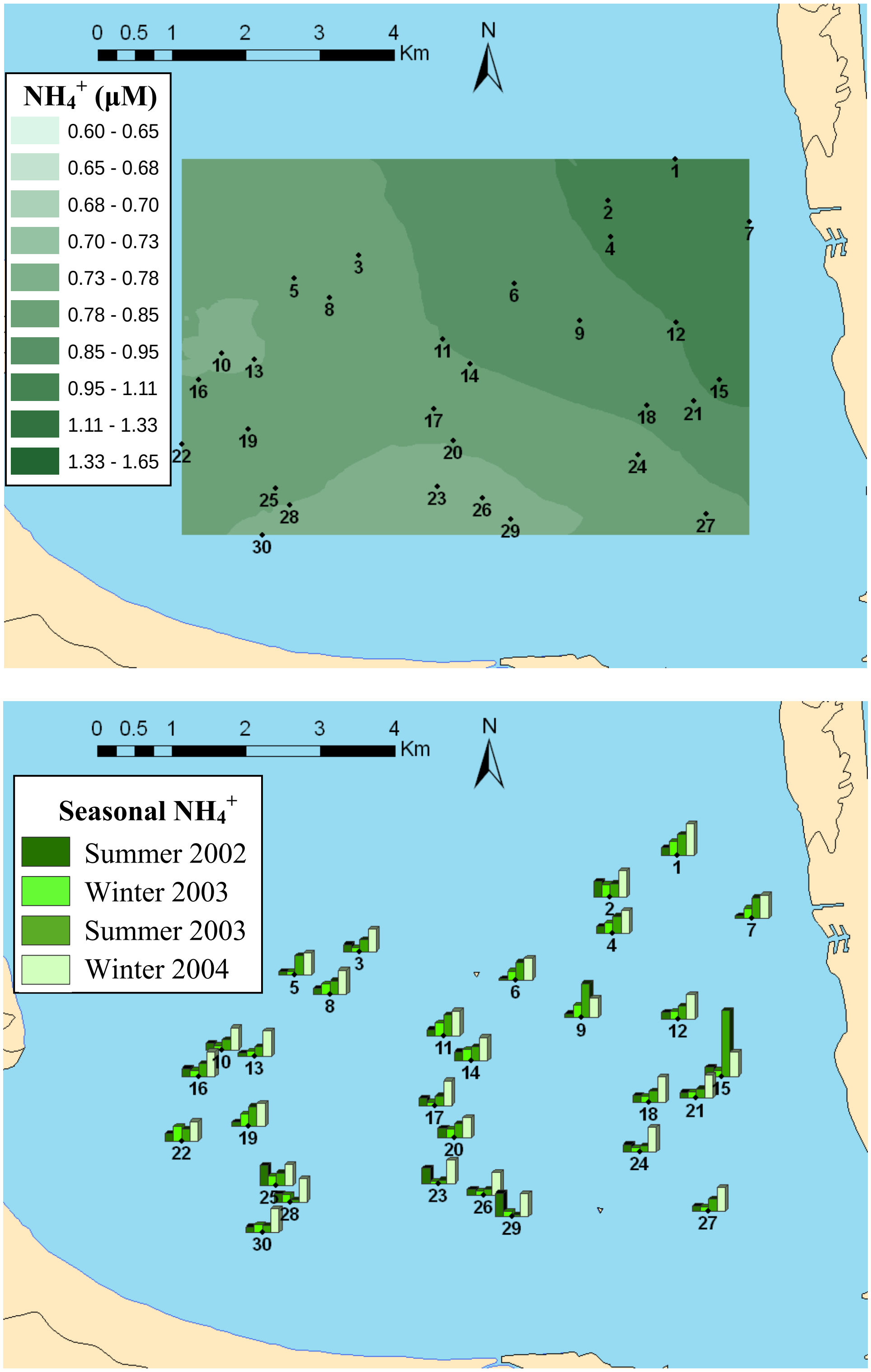

Figure 21: Top panel: interpolated average water column NH_4^+ in LLM (across all 4 sampling periods). Lower panel: Average water column NH_4^+ during each sampling period.

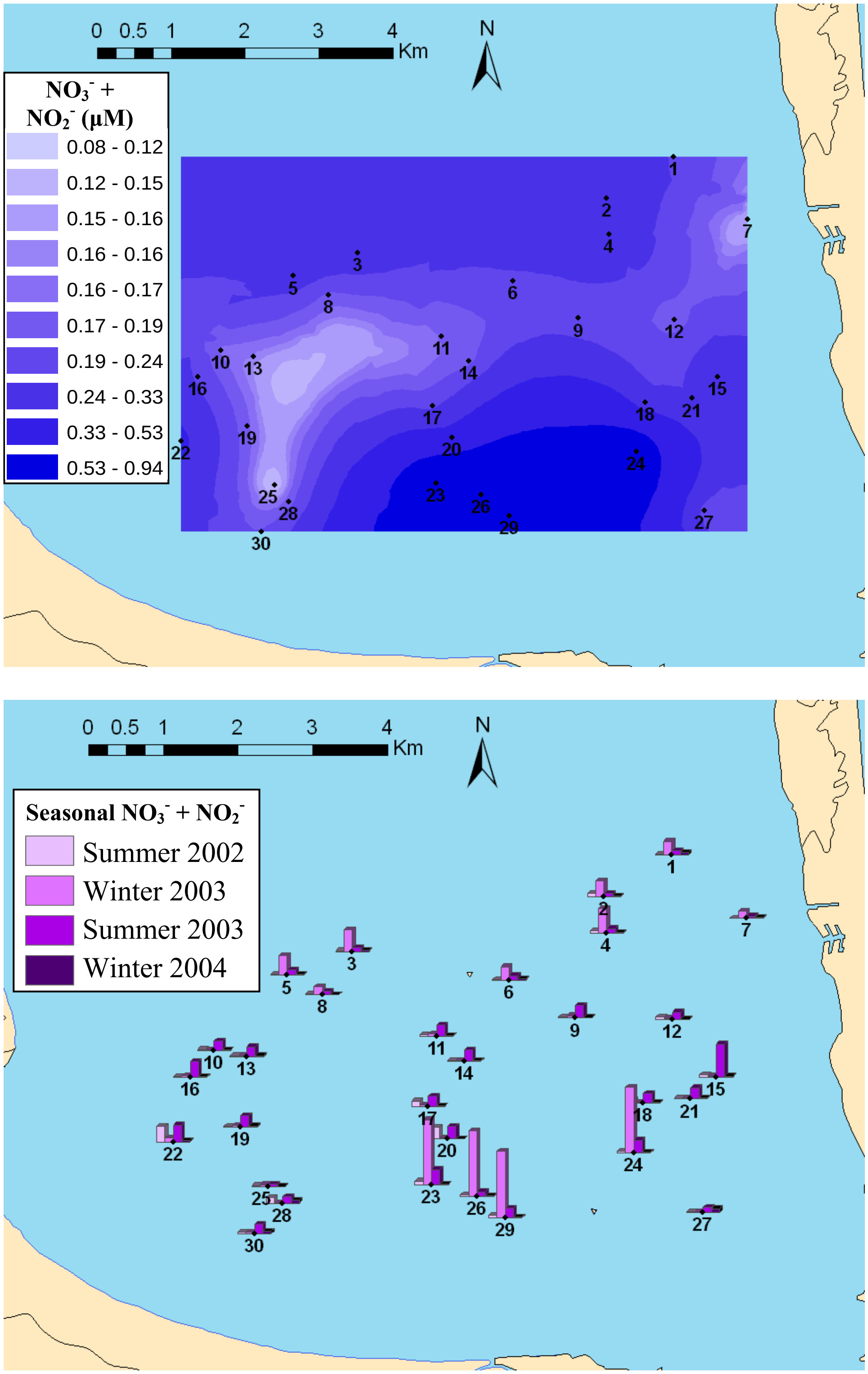

Figure 22: Top panel: interpolated average water column NO_3^- + NO_2^- in LLM (across all 4 sampling periods). Lower panel: Average water column NO_3^- + NO_2^- concentration during each sampling period.

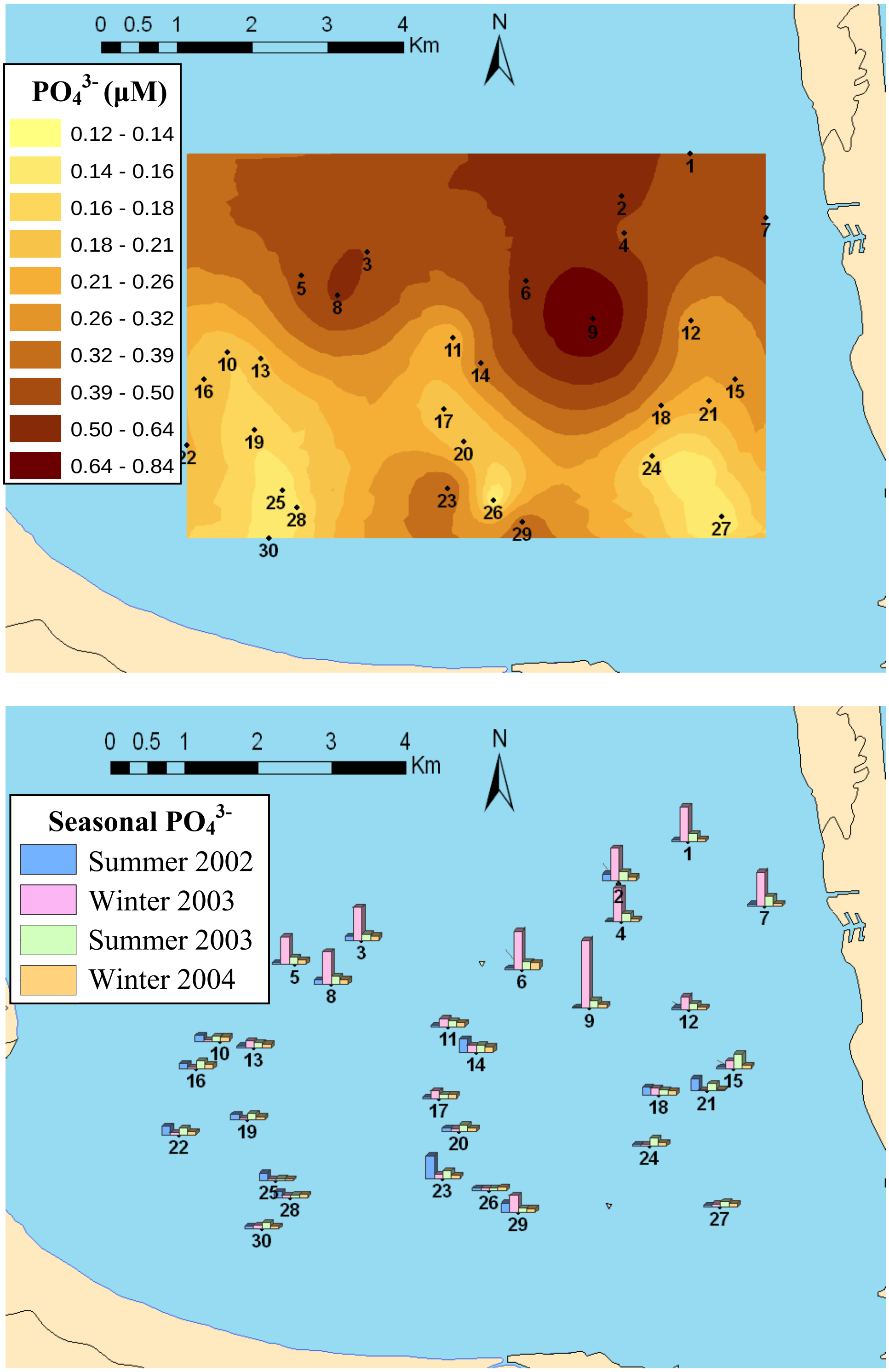

Figure 23: Top panel: interpolated average water column PO_4^{3-} in LLM (across all 4 sampling periods). Lower panel: Average water column PO_4^{3-} during each sampling period.

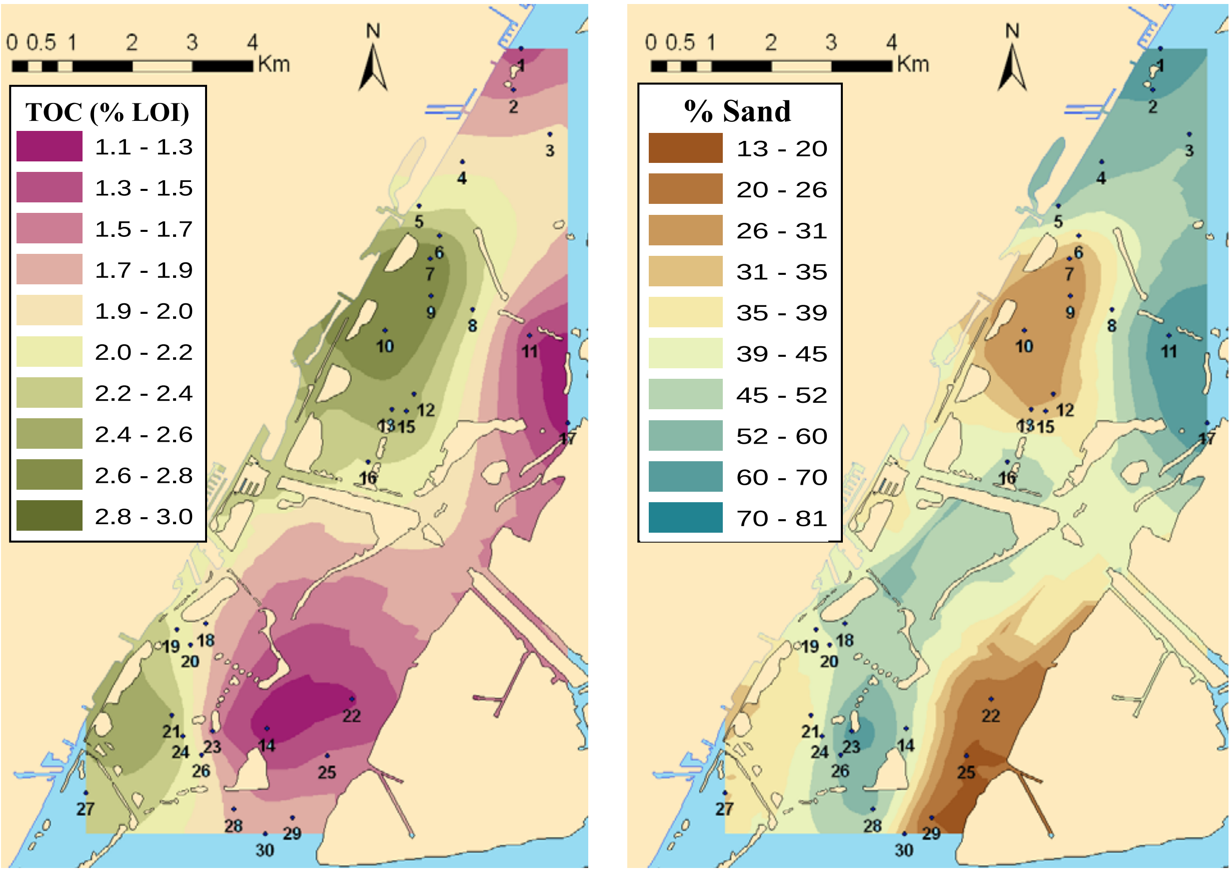

Figure 24: Left panel: Interpolated average sediment total organic carbon (% loss on ignition) in Redfish Bay. Right panel: Interpolated average % sand in Redfish Bay.

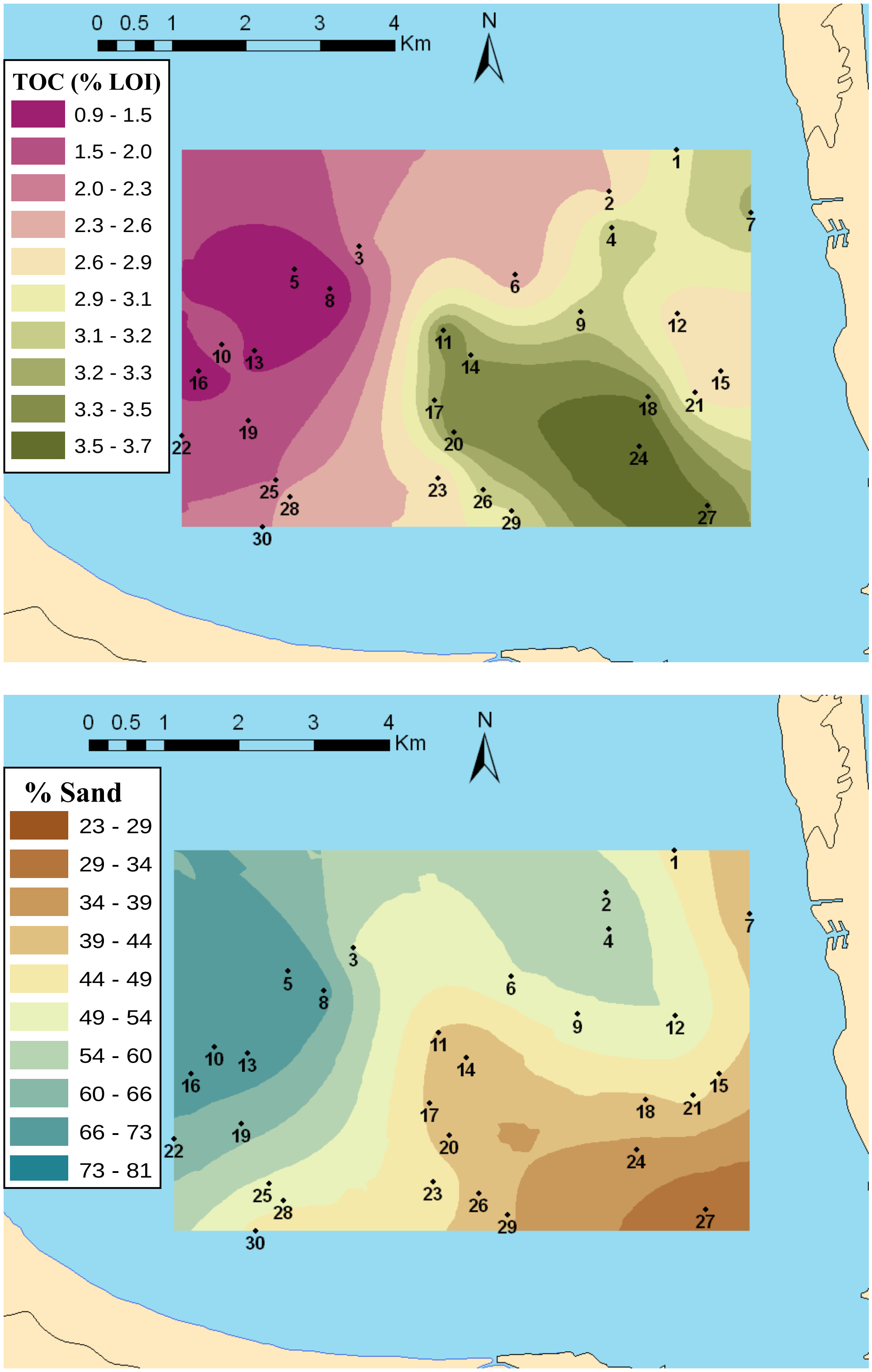

Figure 25: Top panel: Interpolated average sediment total organic carbon (TOC) in LLM. Lower panel: Interpolated average % sand in LLM.

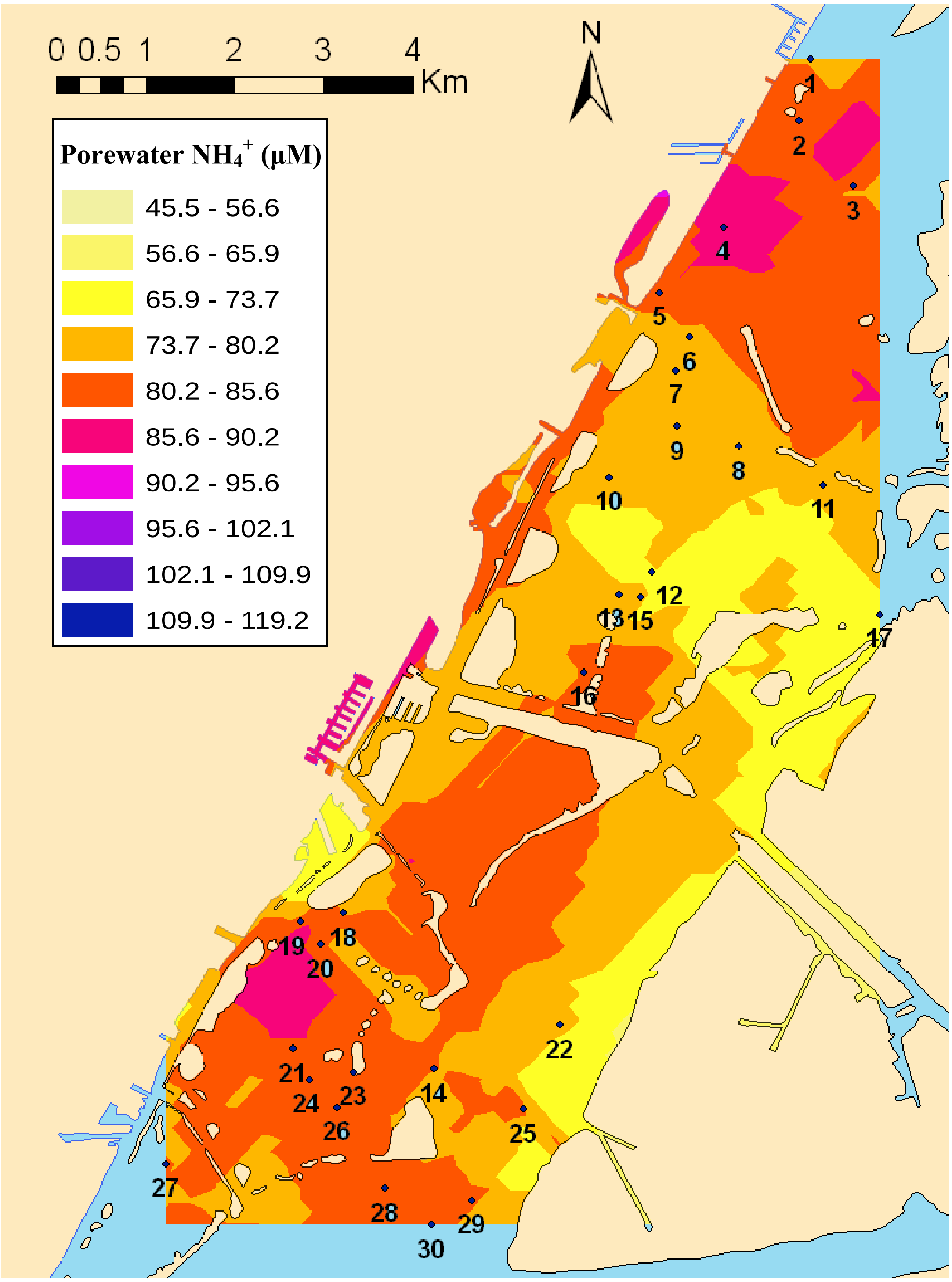

Figure 26: Interpolated average sediment porewater NH_4^+ in Redfish Bay.

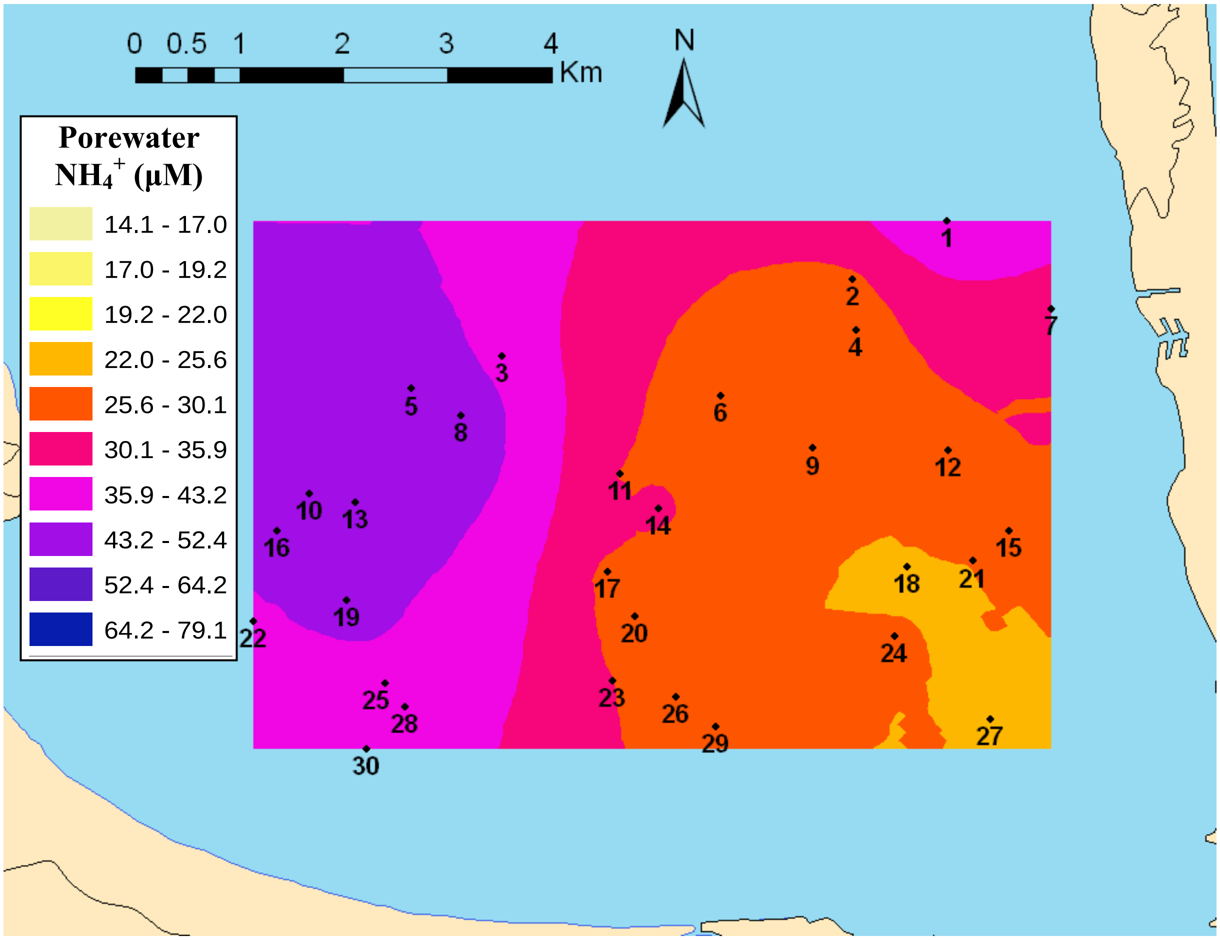

Figure 27: Interpolated average sediment porewater NH_4^+ in lower Laguna Madre.

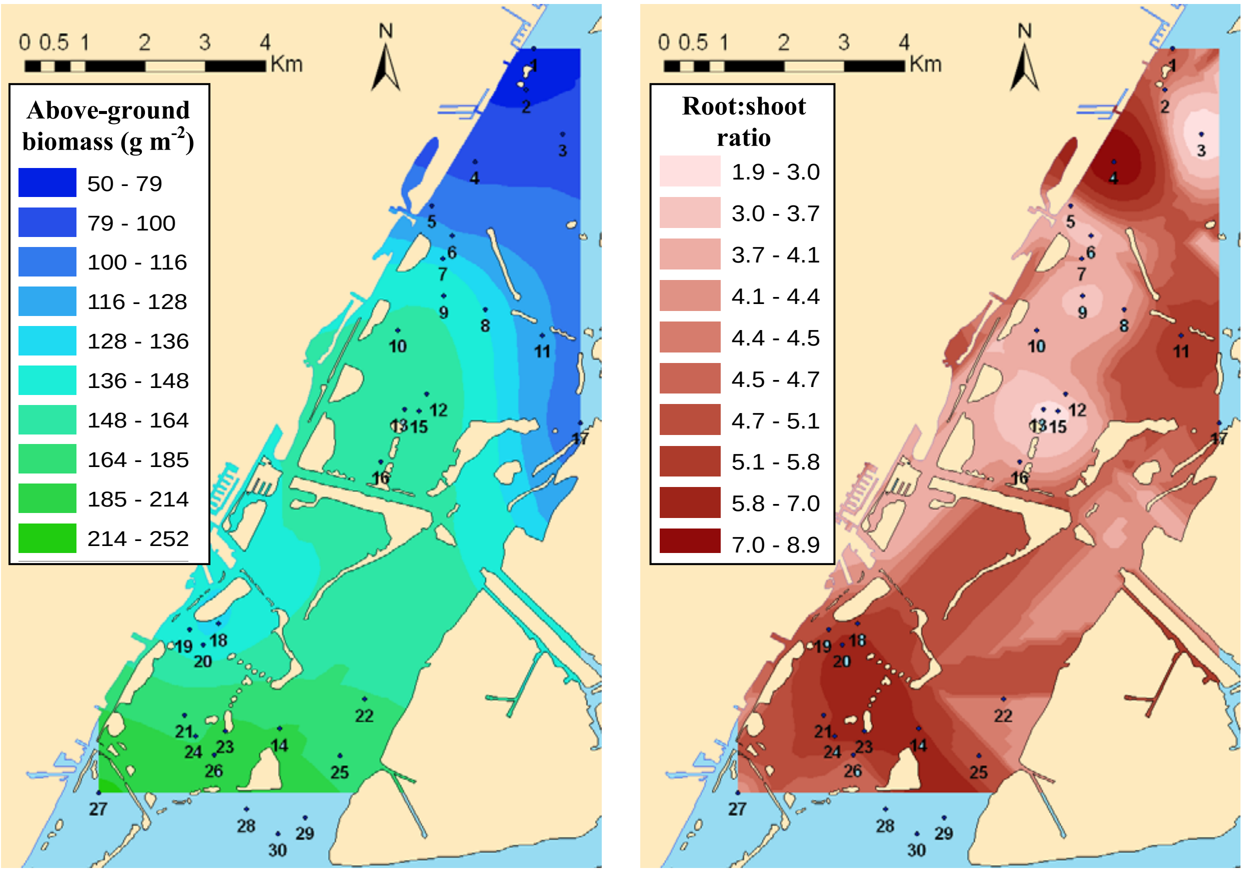

Figure 28: Left panel: interpolated average above-ground biomass of *Thalassia testudinum* in Redfish Bay. Right panel: interpolated average root:shoot ratio of *Thalassia testudinum* in Redfish Bay.

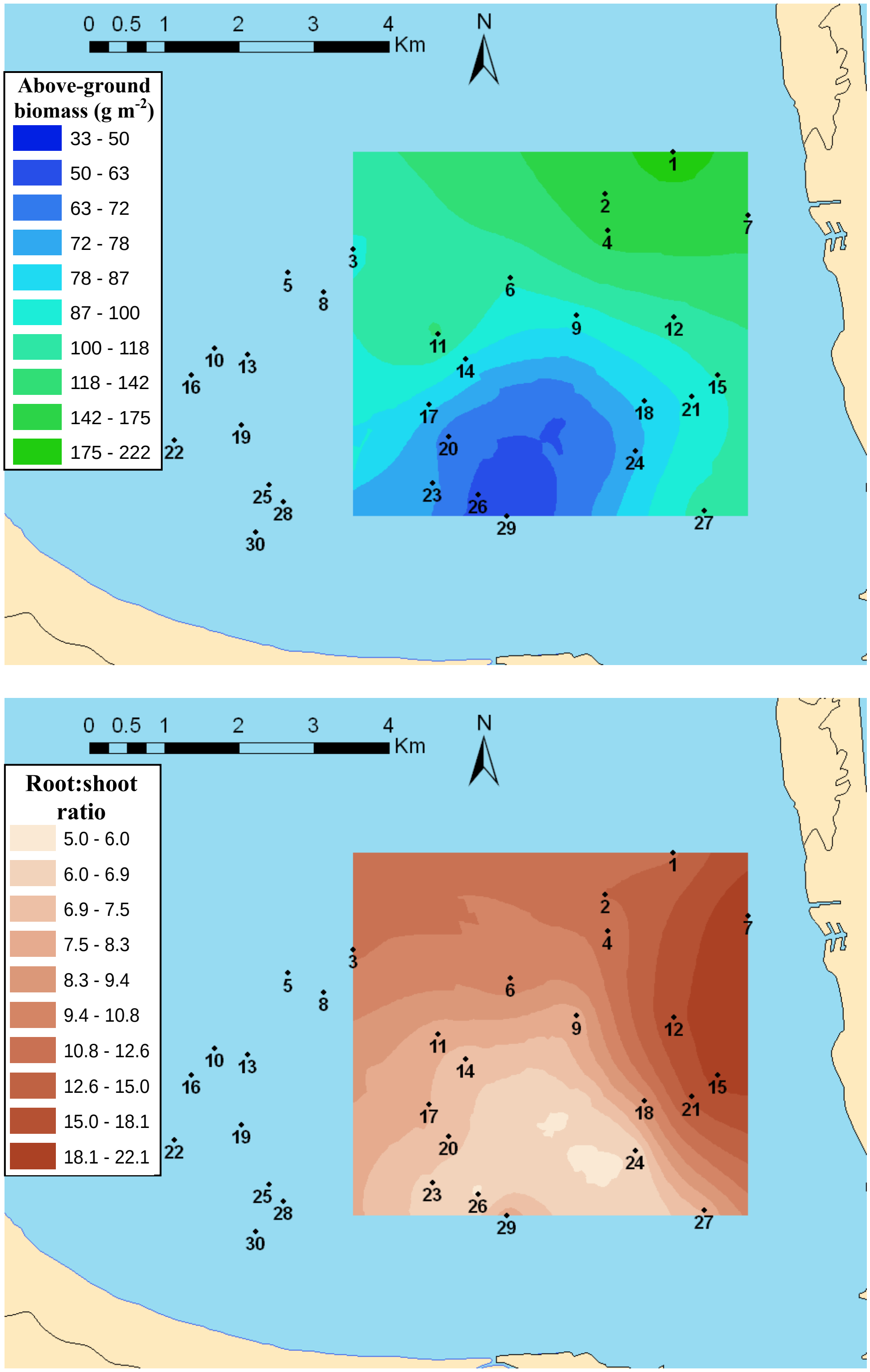

Figure 29: Top panel: interpolated average above-ground biomass of *Thalassia testudinum* in LLM. Lower panel: interpolated average root:shoot ratio of *Thalassia testudinum* in LLM.

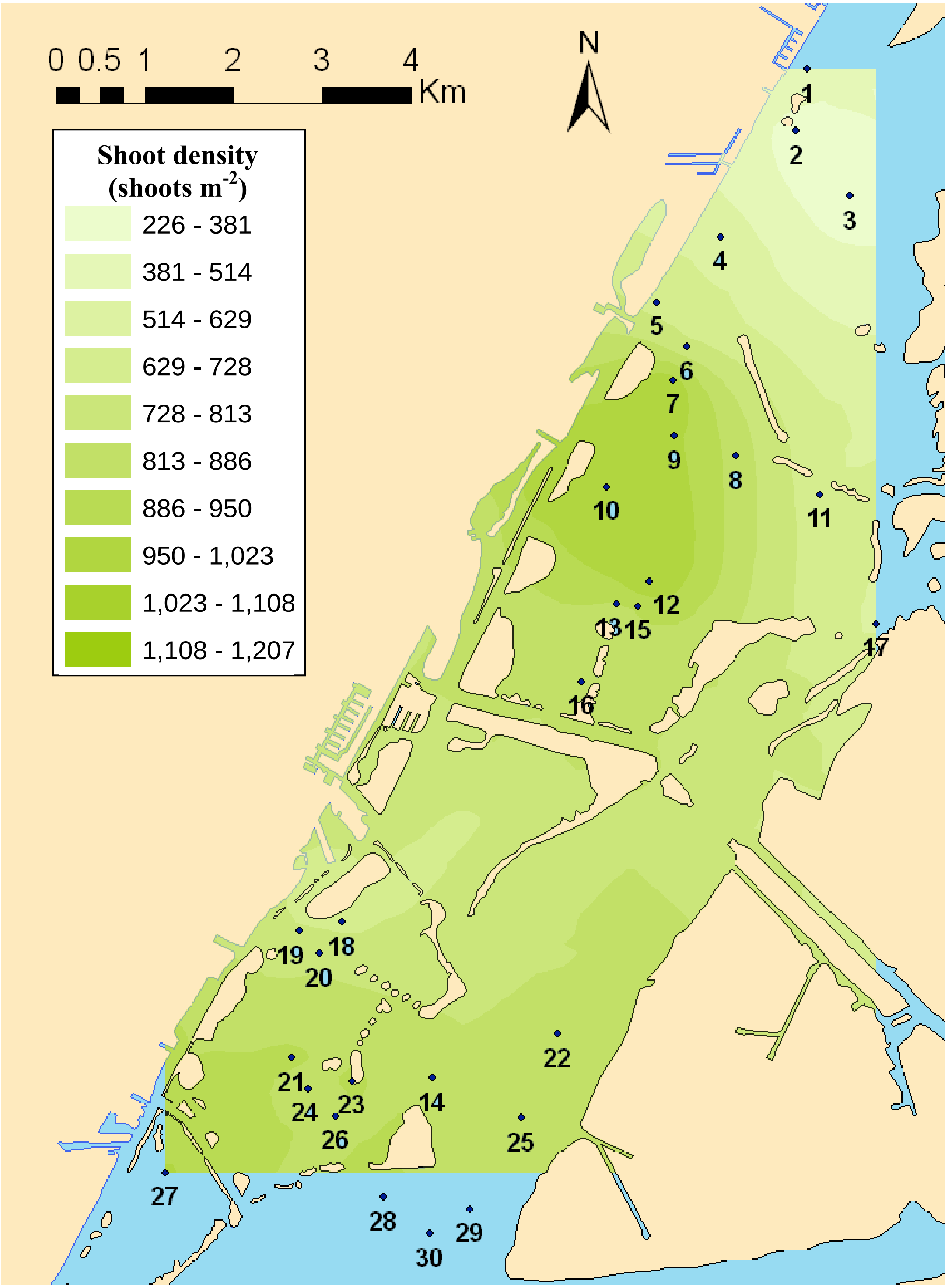

Figure 30: Interpolated average shoot density of *Thalassia testudinum* in Redfish Bay.

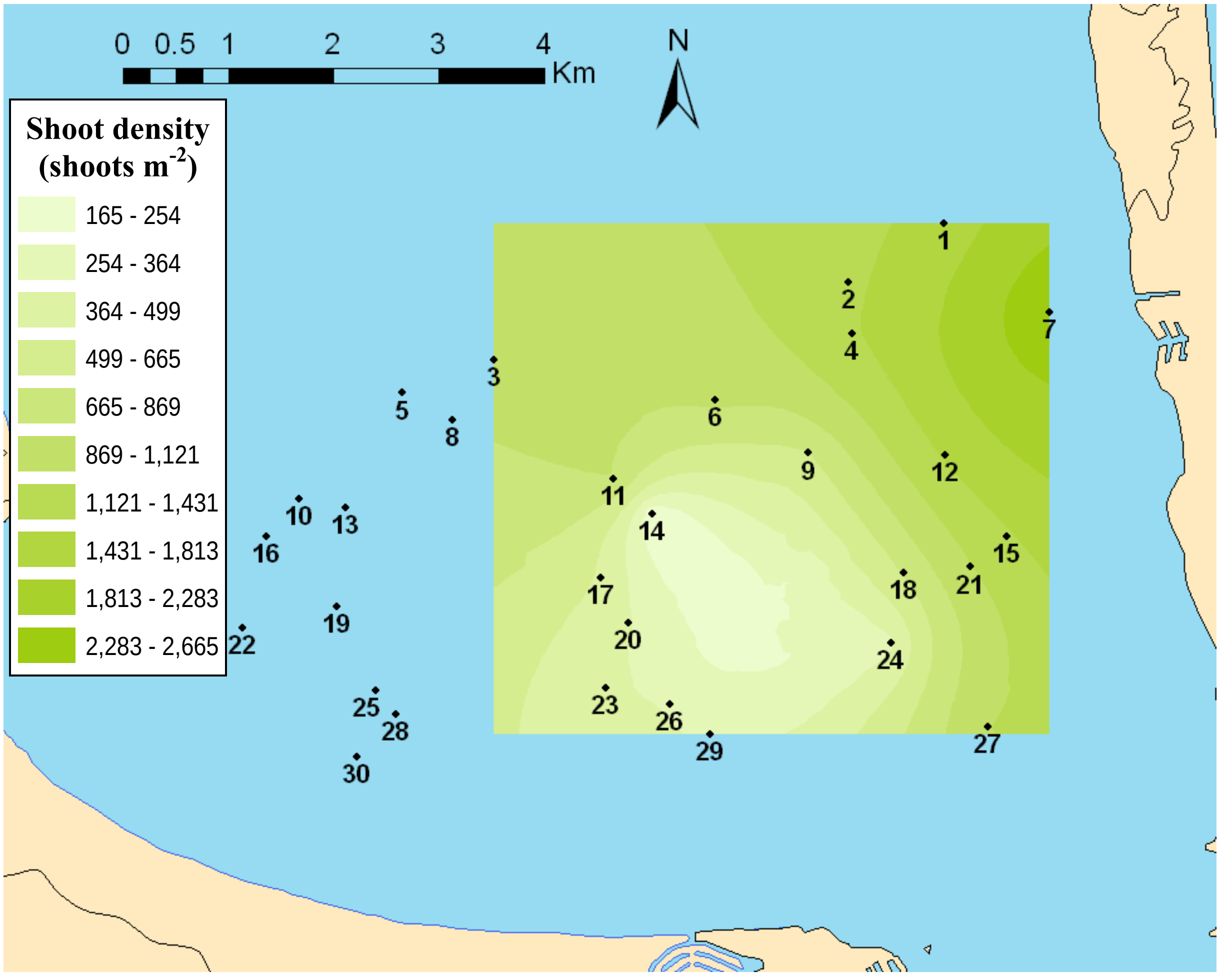

Figure 31: Interpolated average shoot density of *Thalassia testudinum* in Redfish Bay.

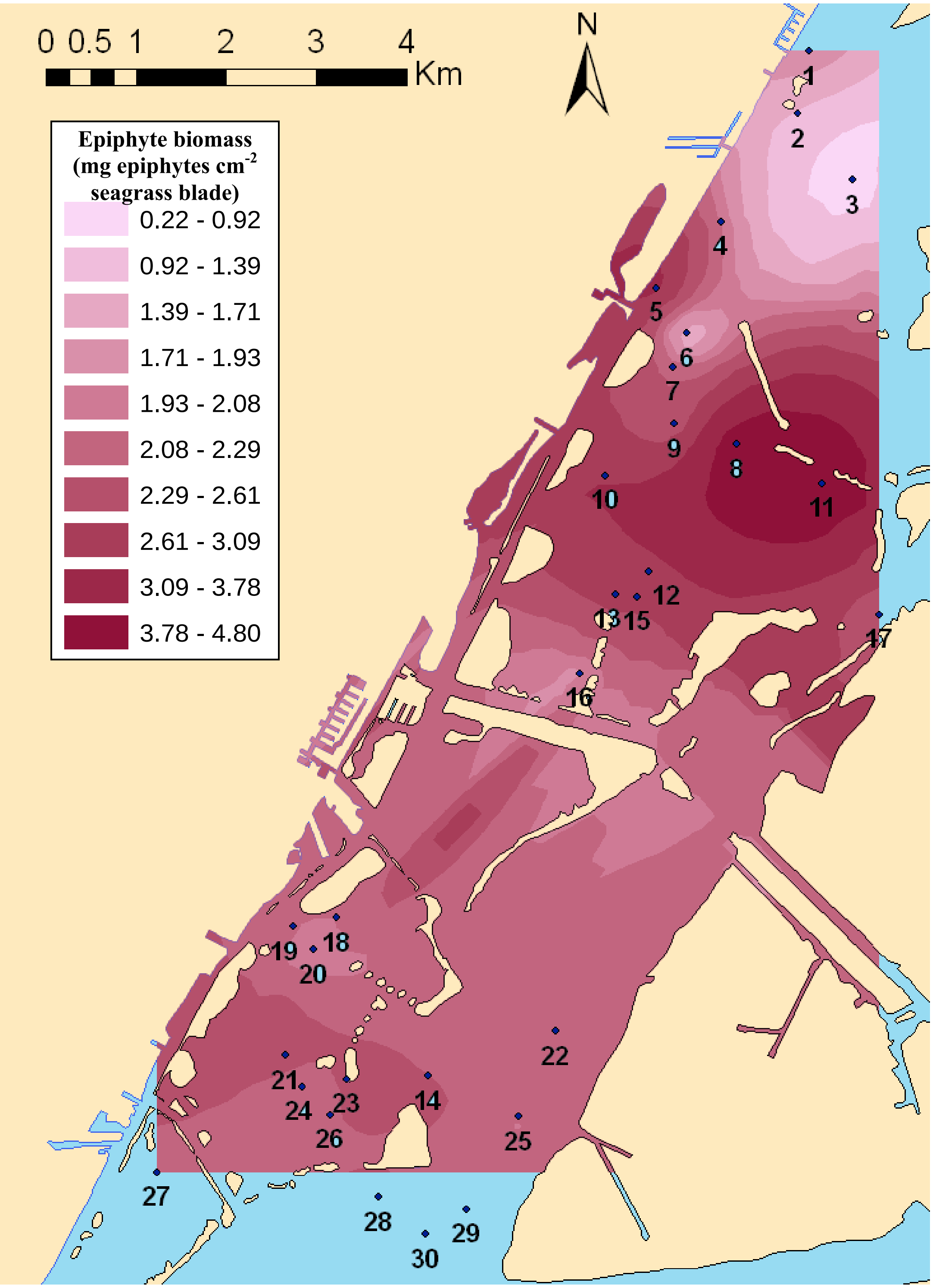

Figure 32: Interpolated average epiphyte biomass on blades of *Thalassia testudinum* in Redfish Bay.

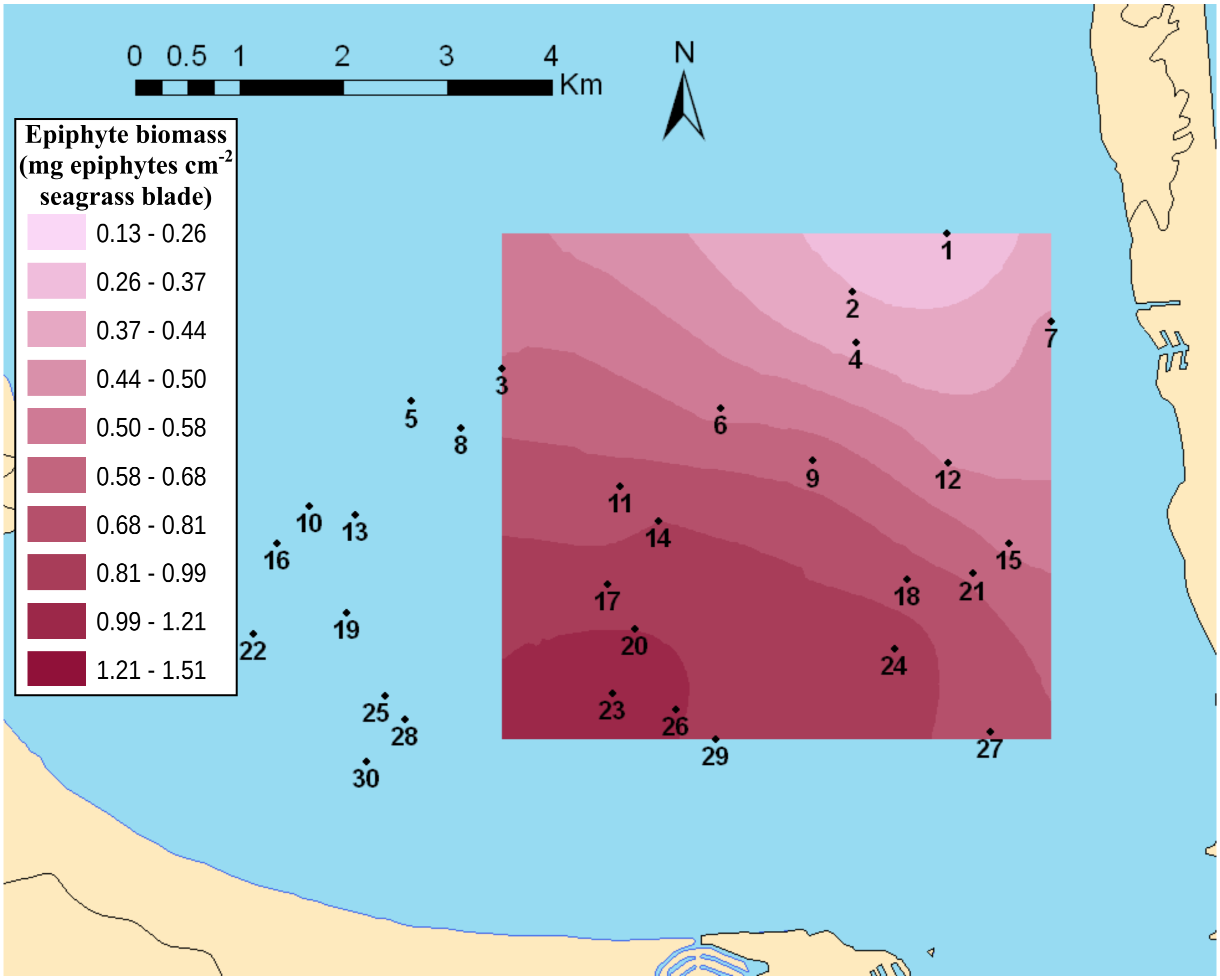

Figure 33: Interpolated average epiphyte biomass on blades of *Thalassia testudinum* in lower Laguna Madre.

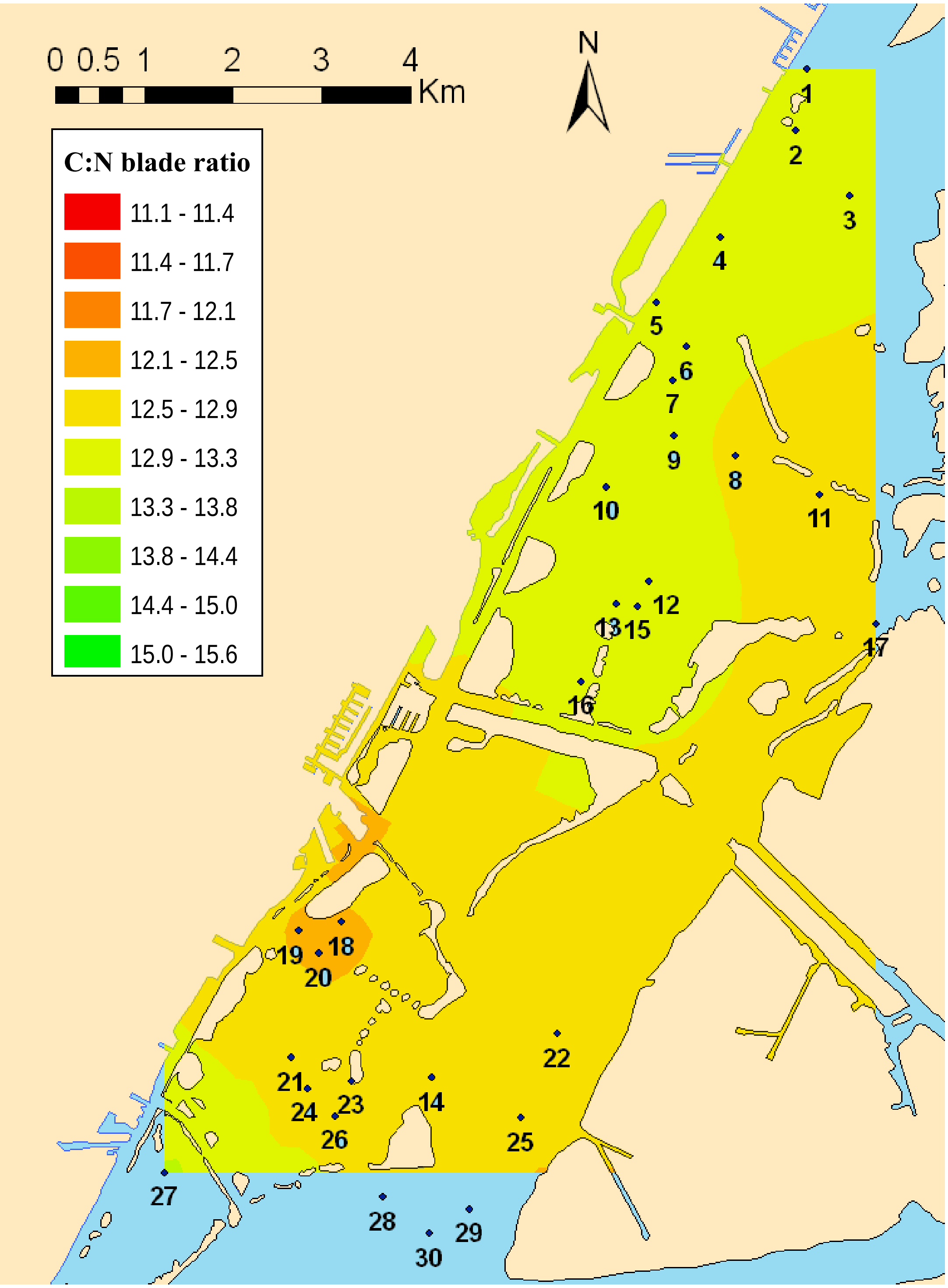

Figure 34: Interpolated blade C:N ratios of *Thalassia testudinum* in Redfish Bay from summer 2002.

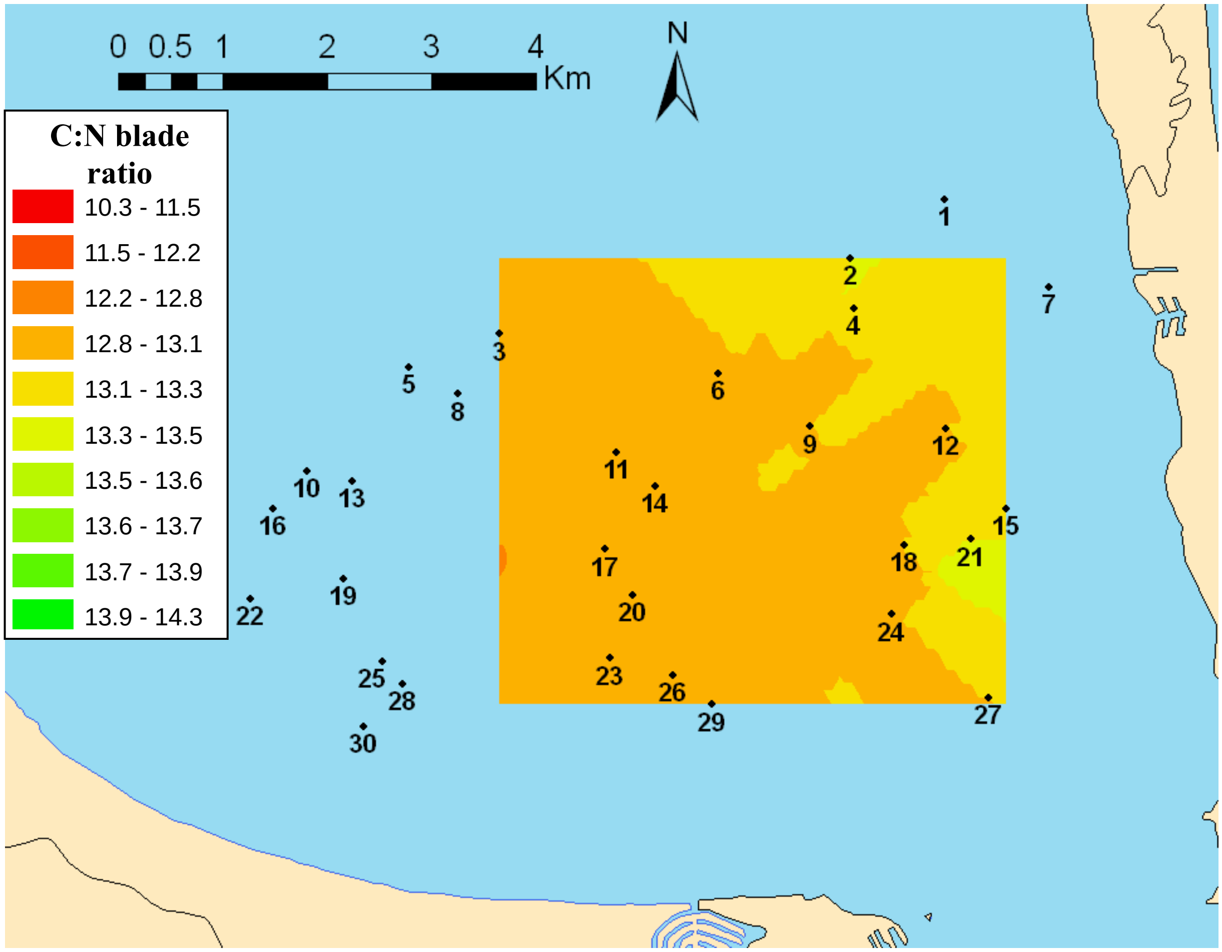

Figure 35: Interpolated blade C:N ratios of *Thalassia testudinum* in lower Laguna Madre from summer 2002.

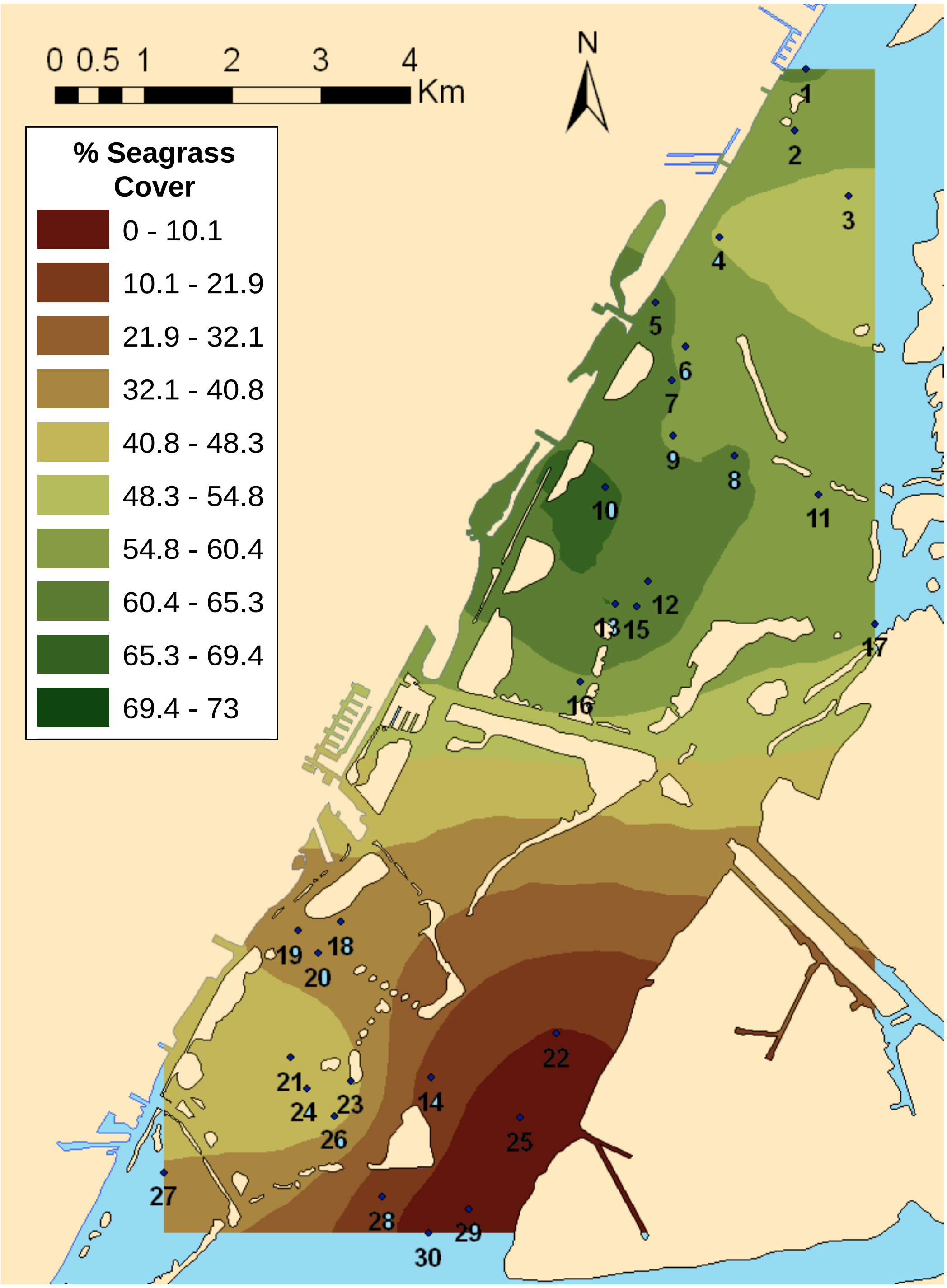

Figure 36: Interpolated average % seagrass cover in Redfish Bay.

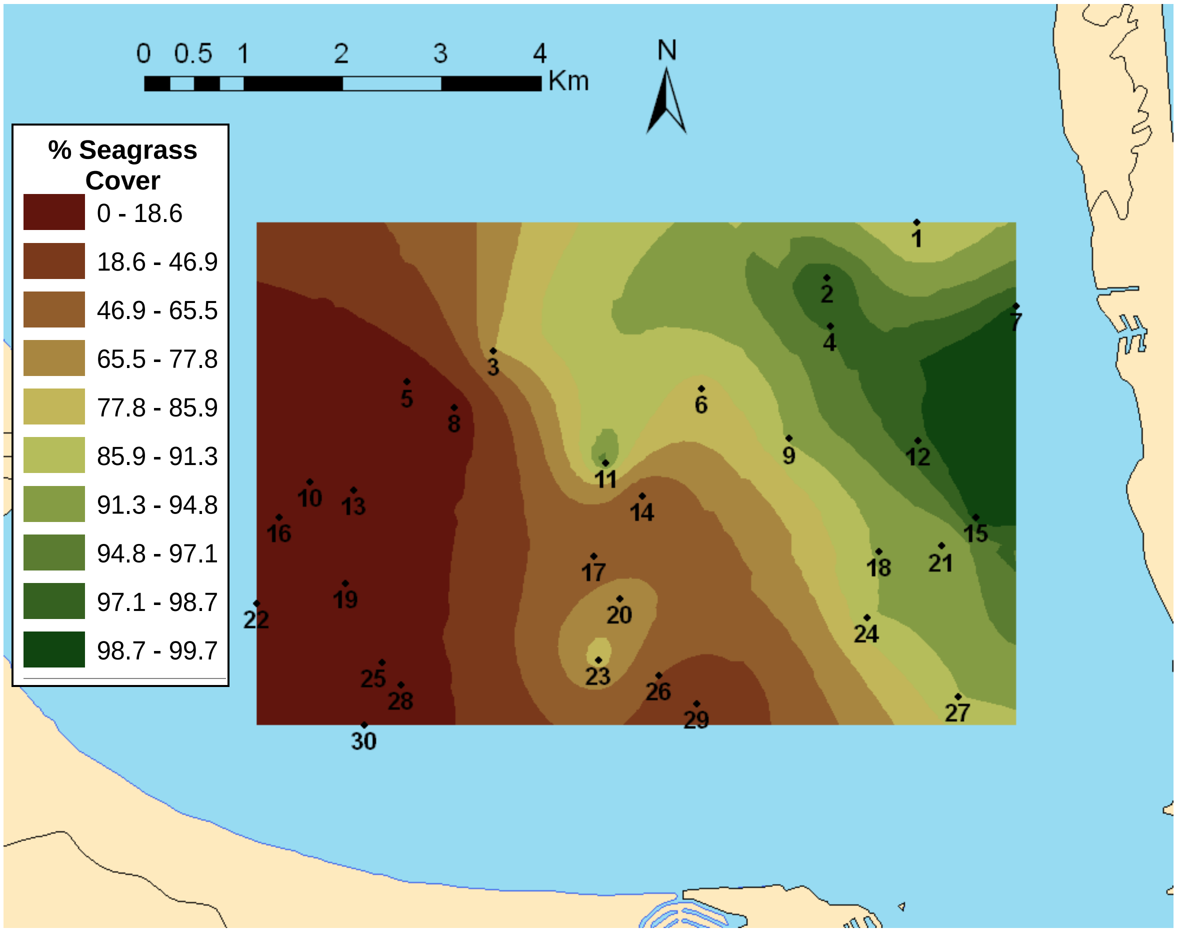

Figure 37: Interpolated average % seagrass cover in lower Laguna Madre.

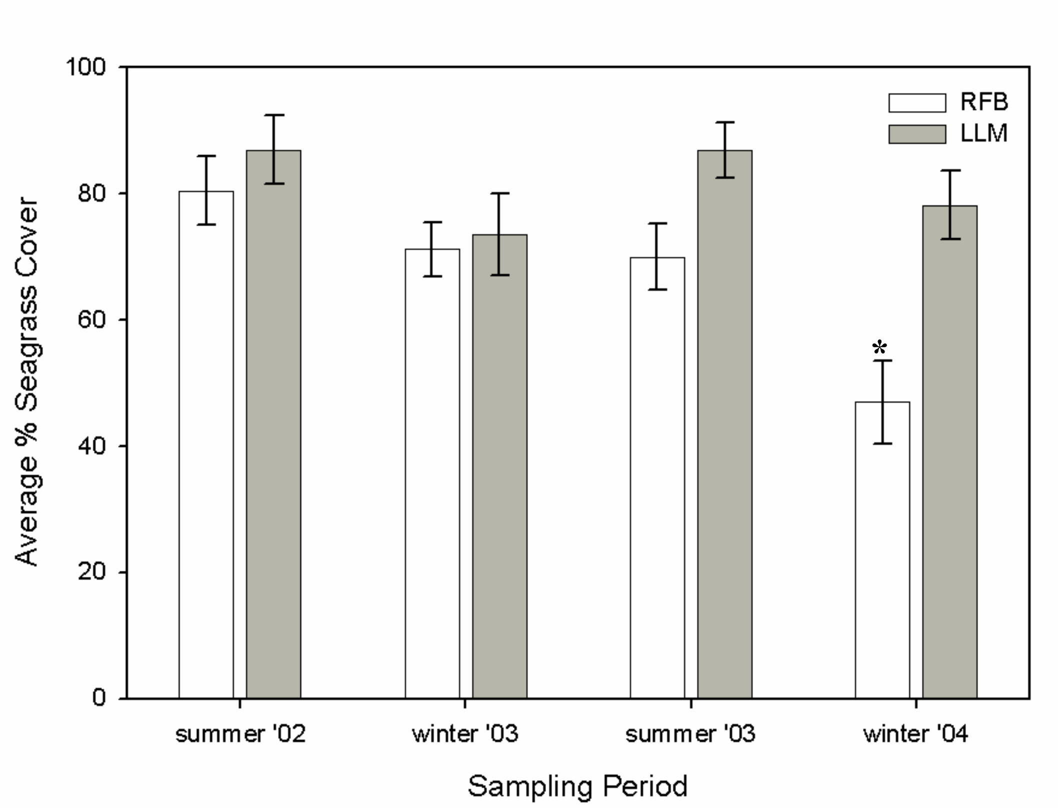

Figure 38: Average % seagrass cover in Redfish Bay and lower Laguna Madre for each sampling period. Values are $\bar{x}$ ± SE (n = 30). * = significantly different from all other bars.

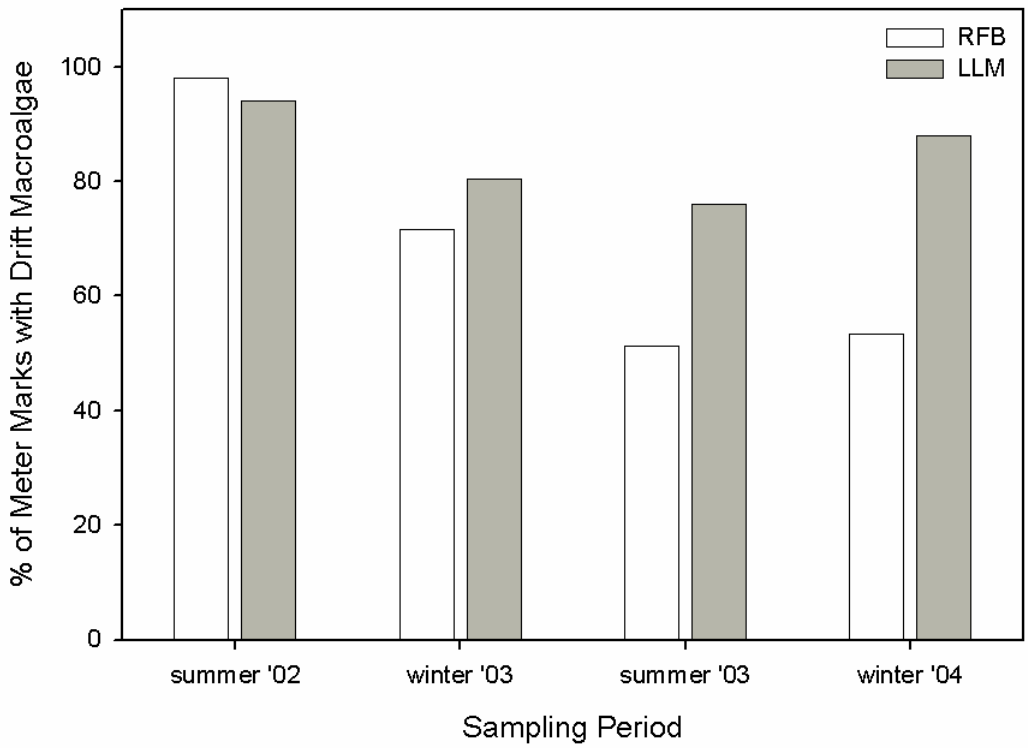

Figure 39: Frequency of occurrence of drift macroalgae in Redfish Bay and lower Laguna Madre. Bars represent the percentage of meter marks sampled that contained drift macroalgae.

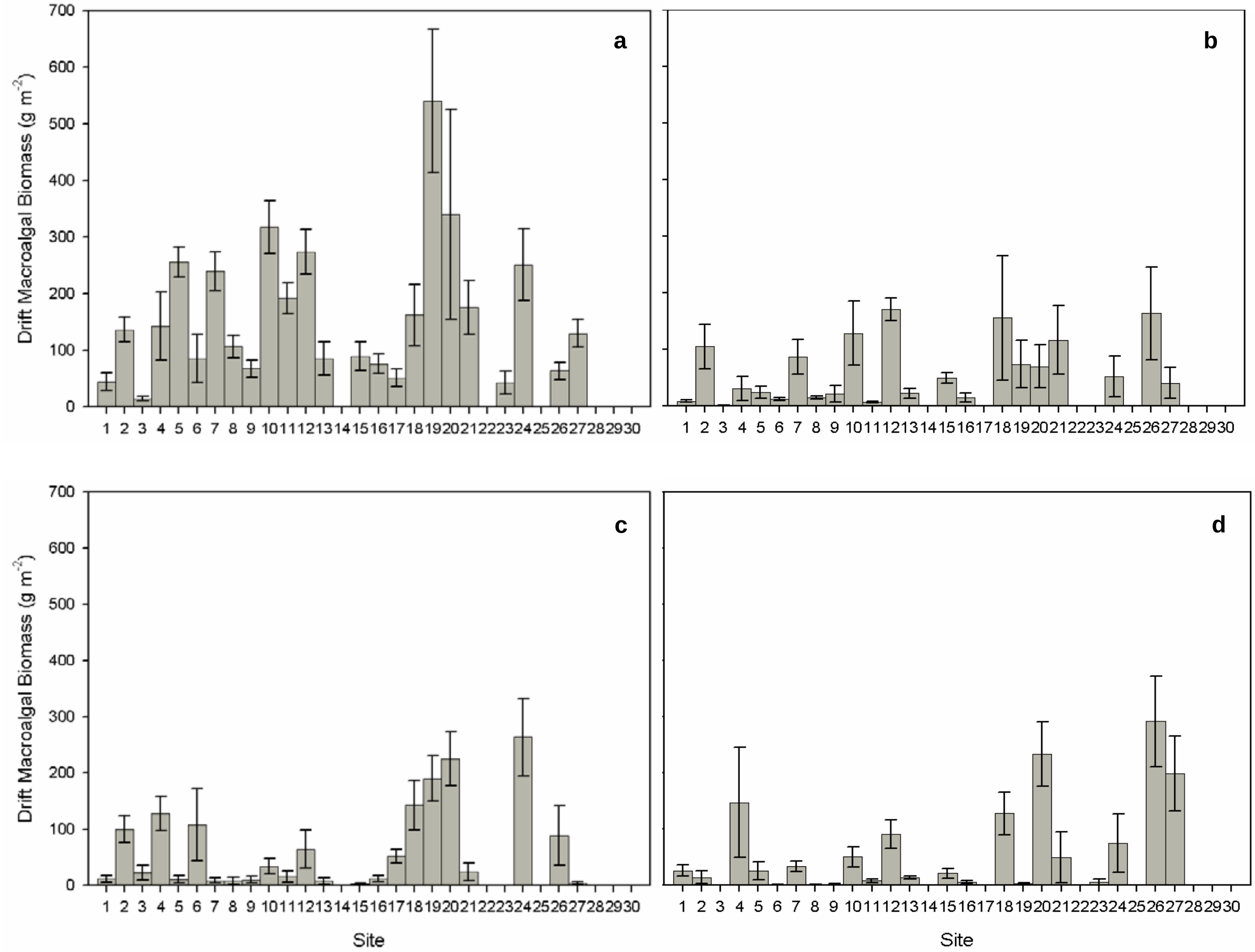

Figure 40: Average drift macroalgal abundance at sites in RFB during all four sampling periods. a = summer '02, b = winter '03, c = summer '03, and d = winter '04. Values are $\overline{x}$ ± SE (n = 10).

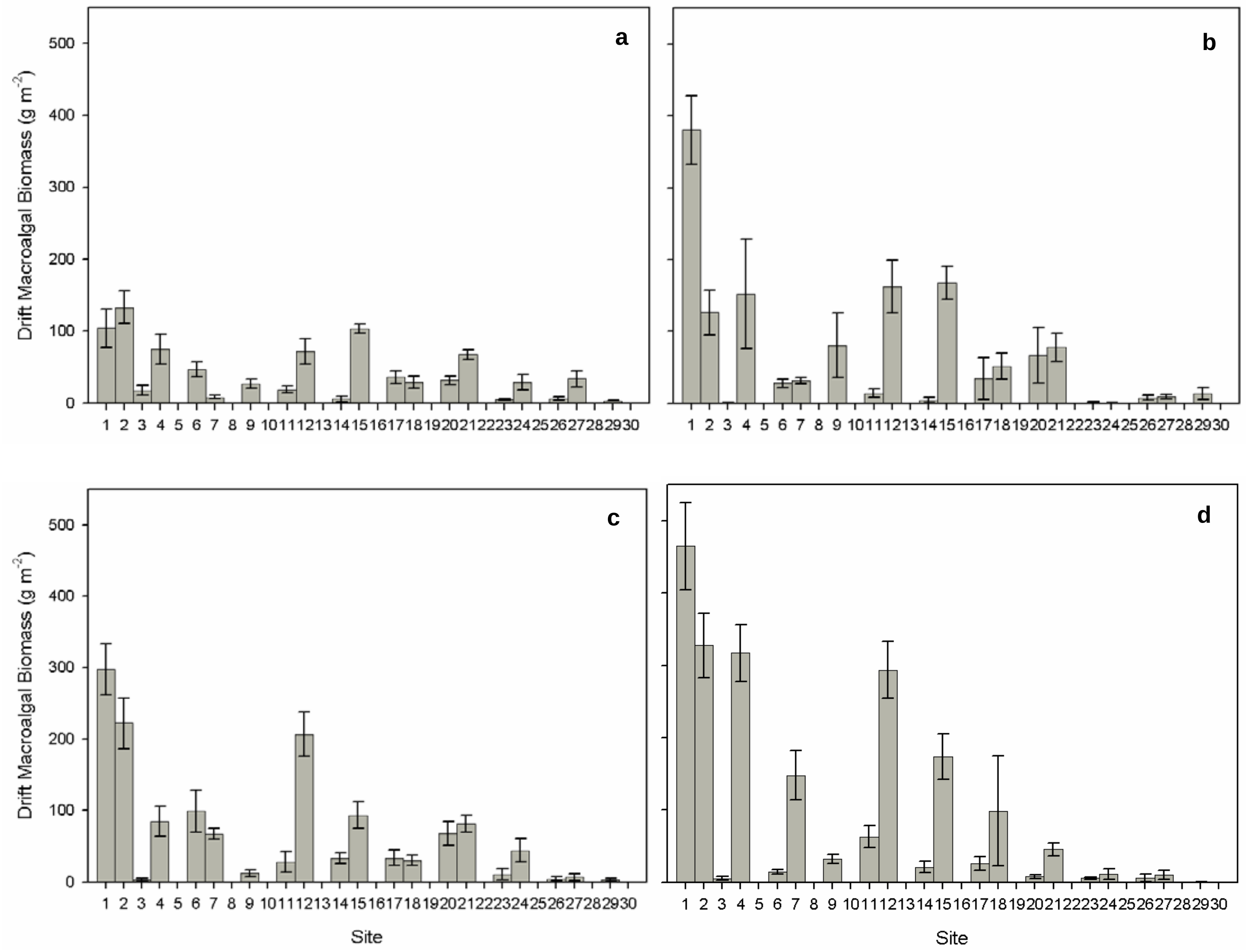

Figure 41: Average drift macroalgal abundance at sites in LLM during all four sampling periods. a = summer '02, b = winter '03, c = summer '03, and d = winter '04. Values are $\bar{x}$ ± SE (n = 10).

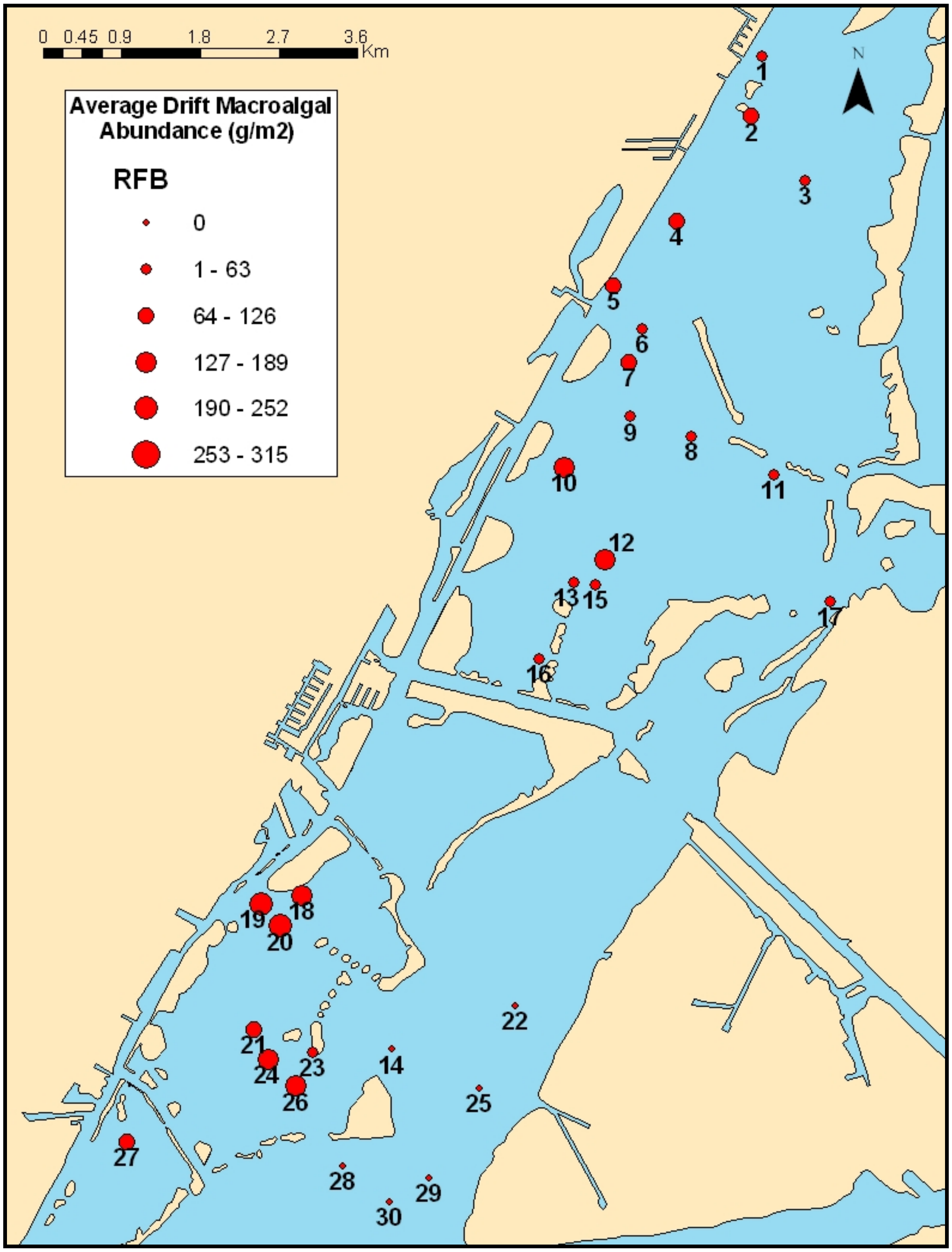

Figure 42: Average drift macroalgal abundance at each site in Redfish Bay.

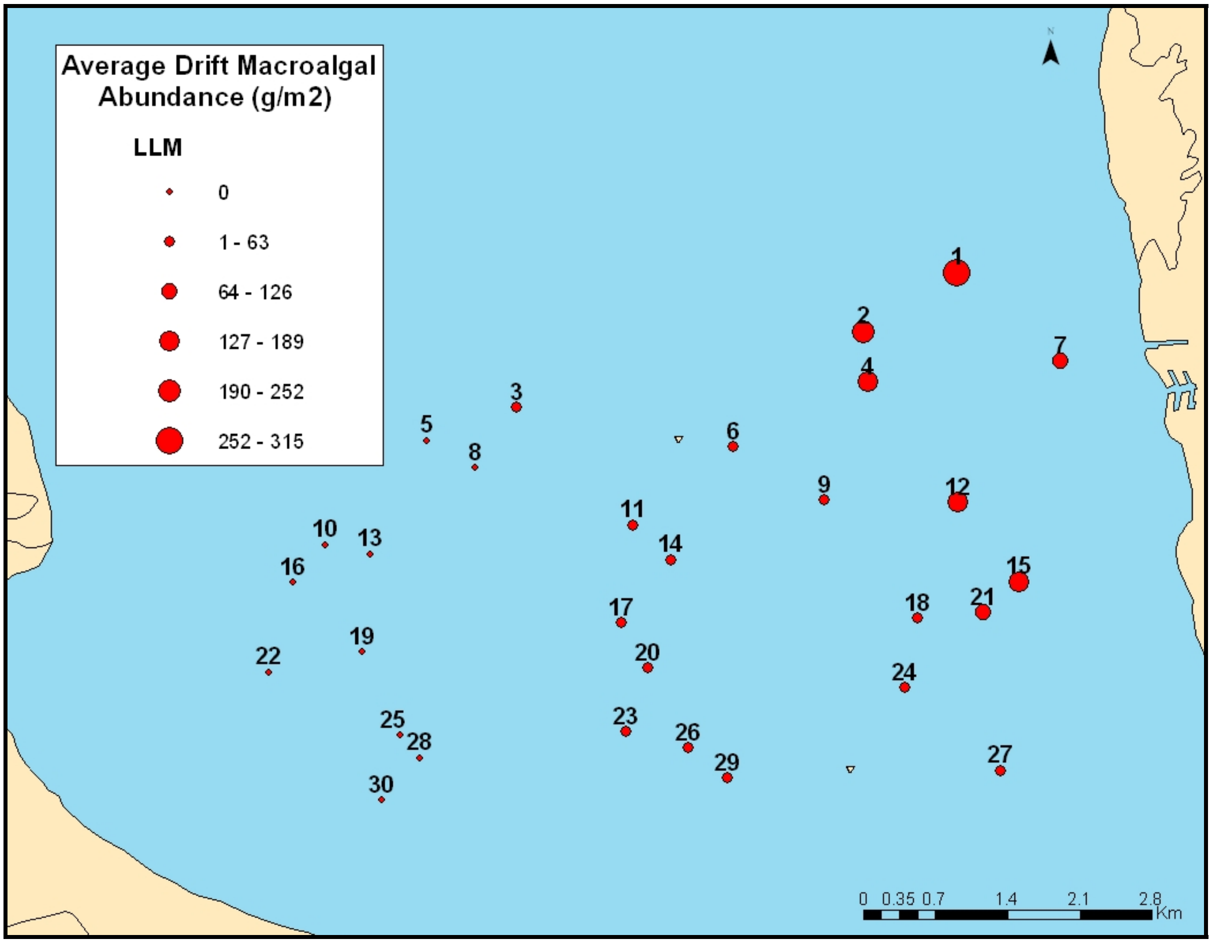

Figure 43: Average drift macroalgal abundance at each site in lower Laguna Madre.

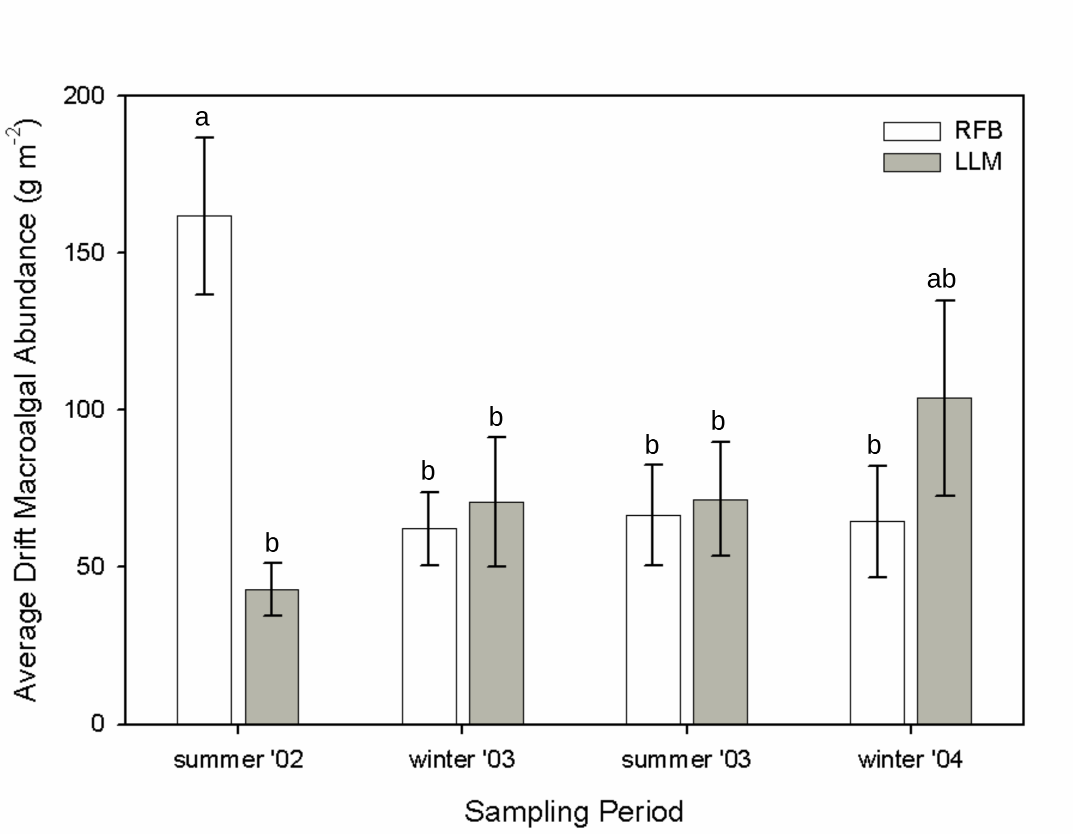

Figure 44: Average drift macroalgal abundance in Redfish Bay (RFB) and lower Laguna Madre (LLM) during the four sampling periods. Values are $\bar{x}$ ± SE (n = 24). Bars with the same letter are not significantly different.

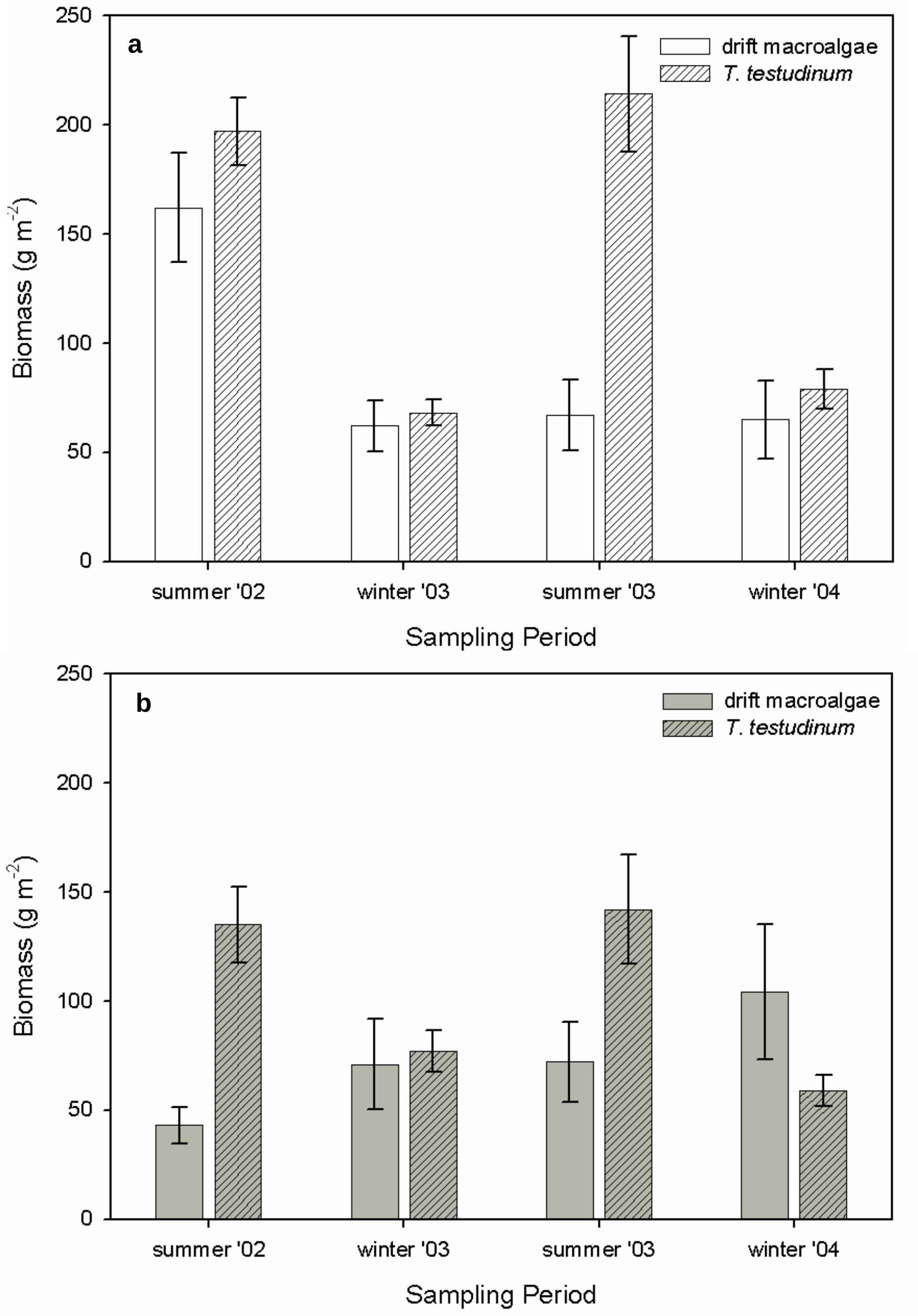

Figure 45: Average biomass (± SE) of drift macroalgae and above-ground biomass of *Thalassia testudinum* during each sampling period. Panel a = Redfish Bay, panel b = lower Laguna Madre. Values are $\bar{x}$ ± SE (n = 24).

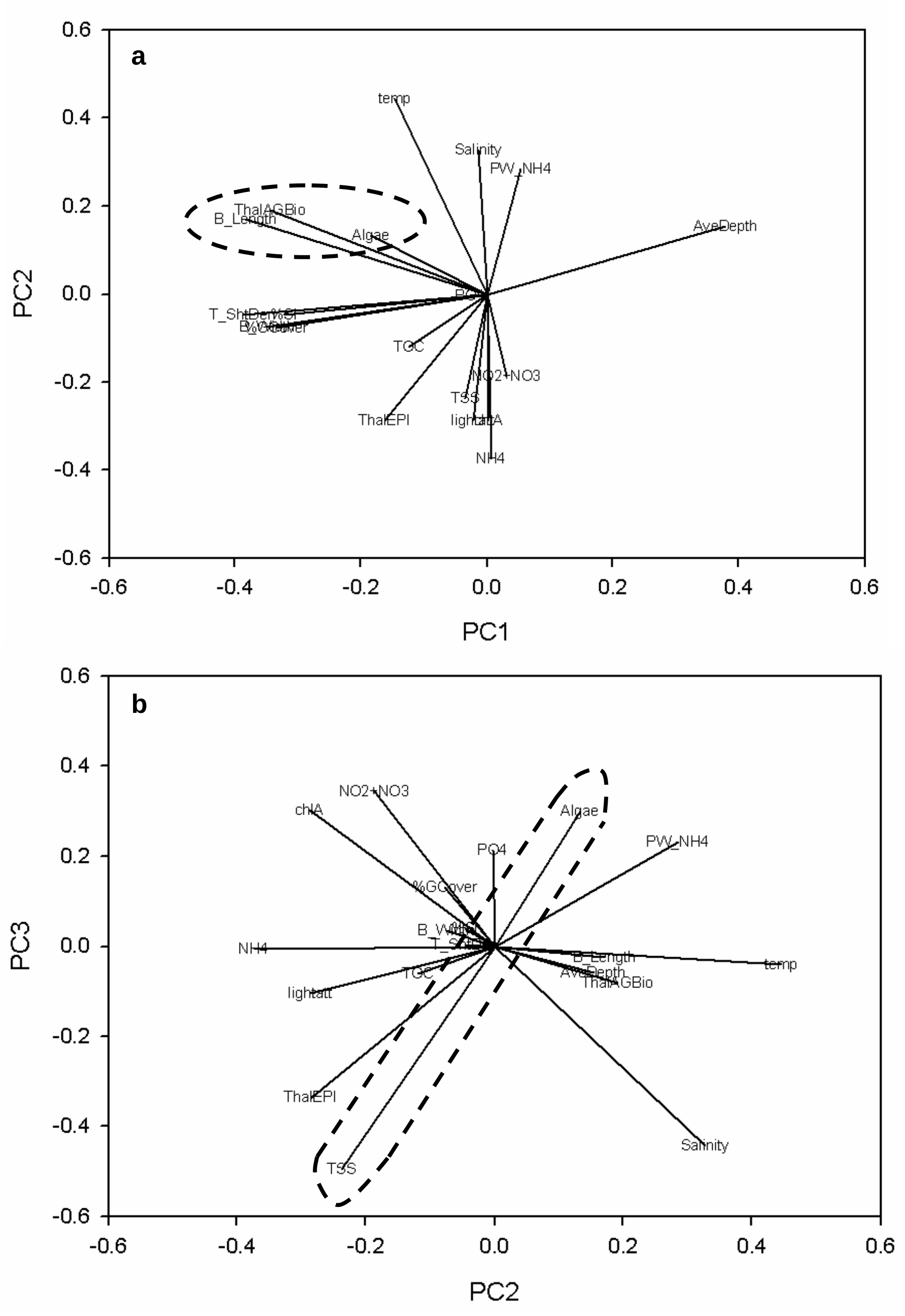

Figure 46: Results of PCA on all sites in RFB. Panels a and b illustrate principal component variables PC1 vs. PC2 and PC2 vs. PC3, respectively.

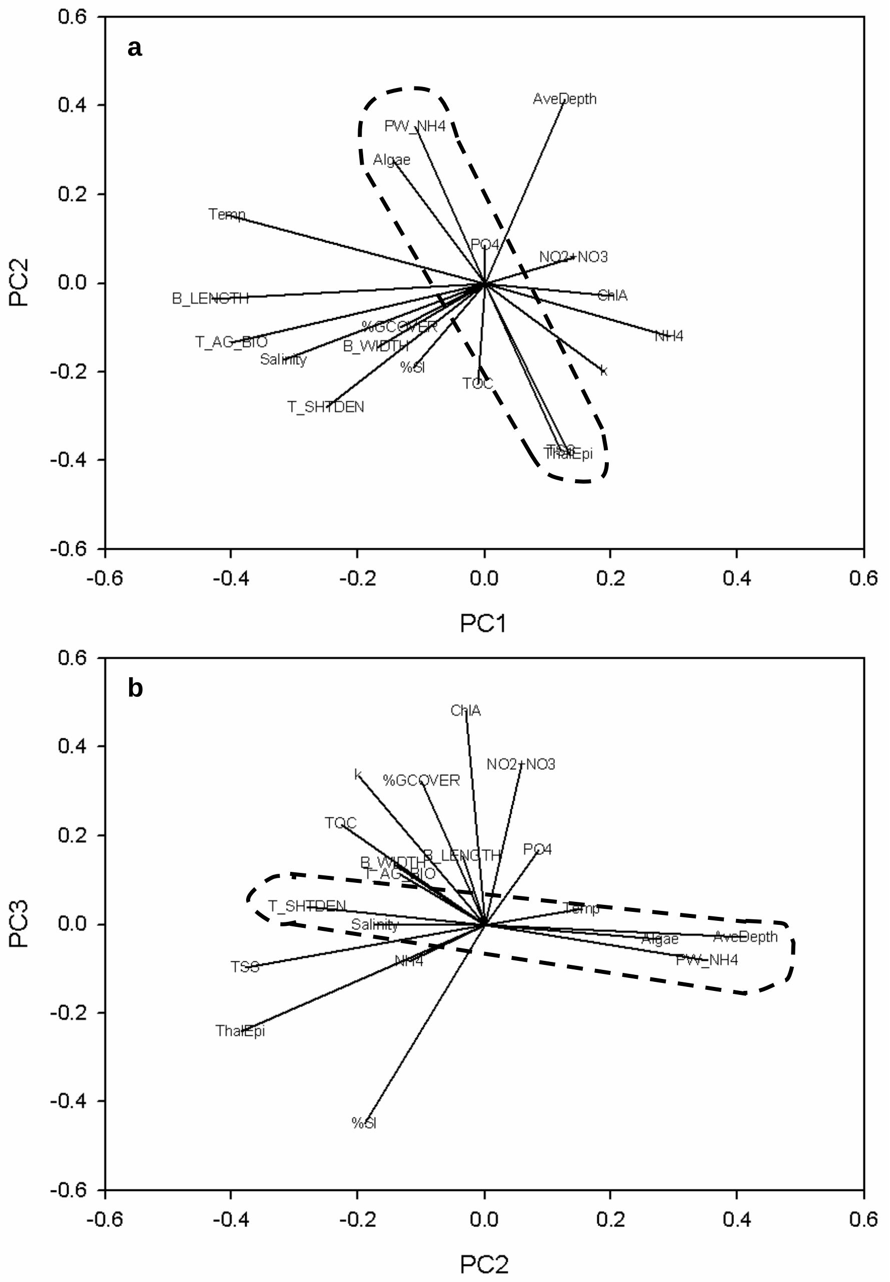

Figure 47: Results of PCA on vegetated sites in RFB. Panels a and b illustrate principal component variables PC1 vs. PC2 and PC2 vs. PC3, respectively.

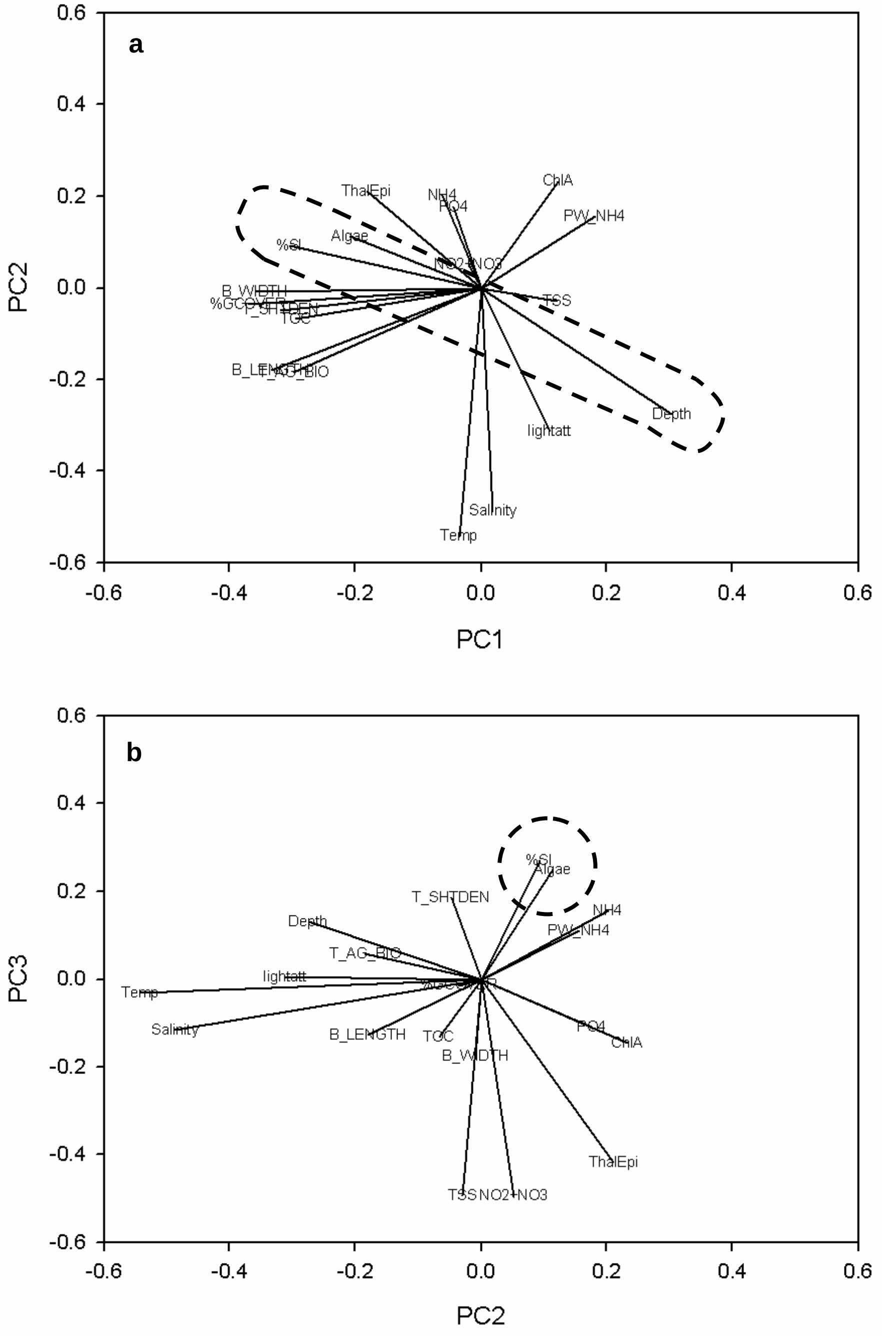

Figure 48: Results of PCA on all sites in LLM. Panels a and b illustrate principal component variables PC1 vs. PC2 and PC2 vs. PC3, respectively.

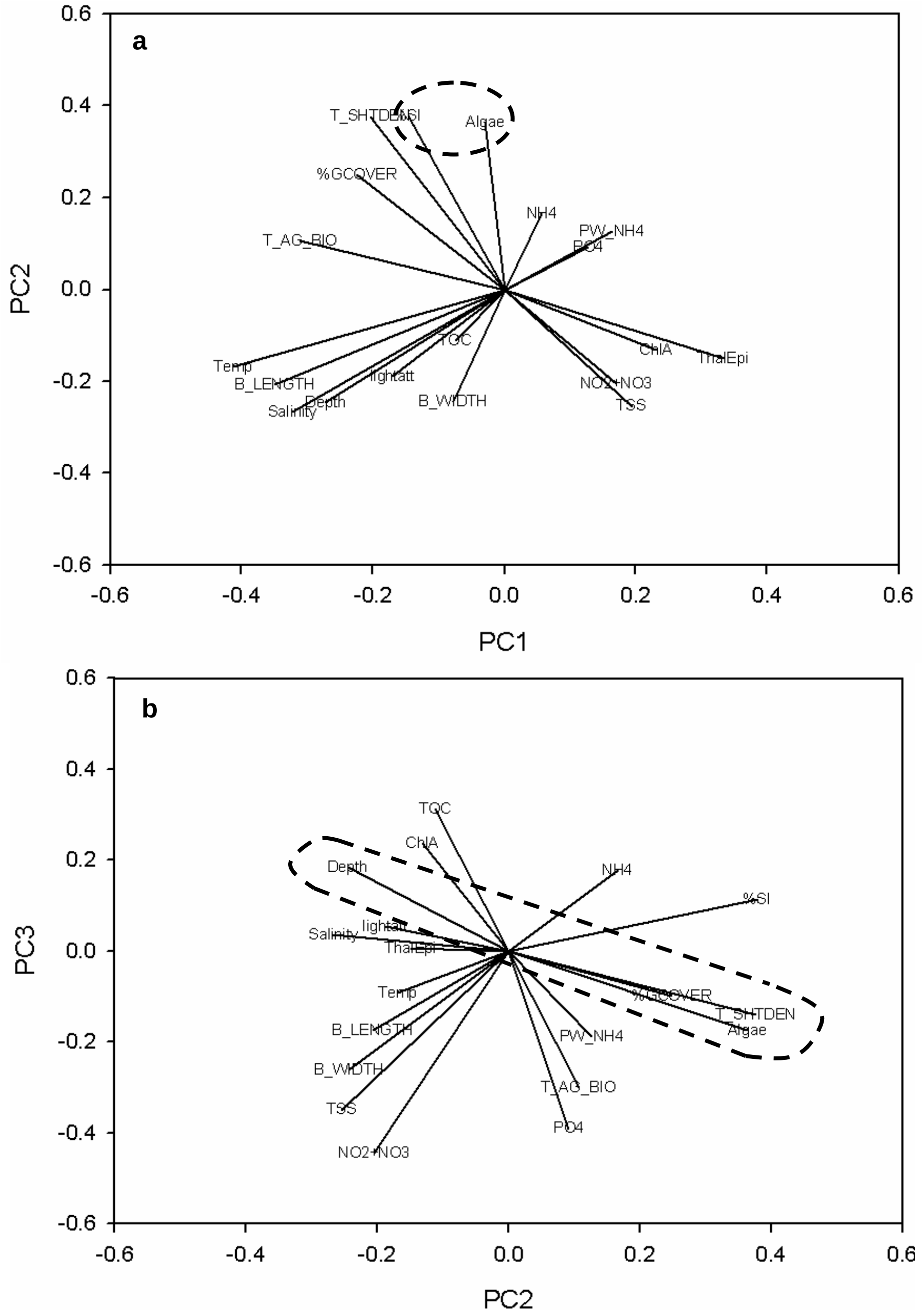

Figure 49: Results of PCA on vegetated sites in LLM. Panels a and b illustrate principal component variables PC1 vs. PC2 and PC2 vs. PC3, respectively.

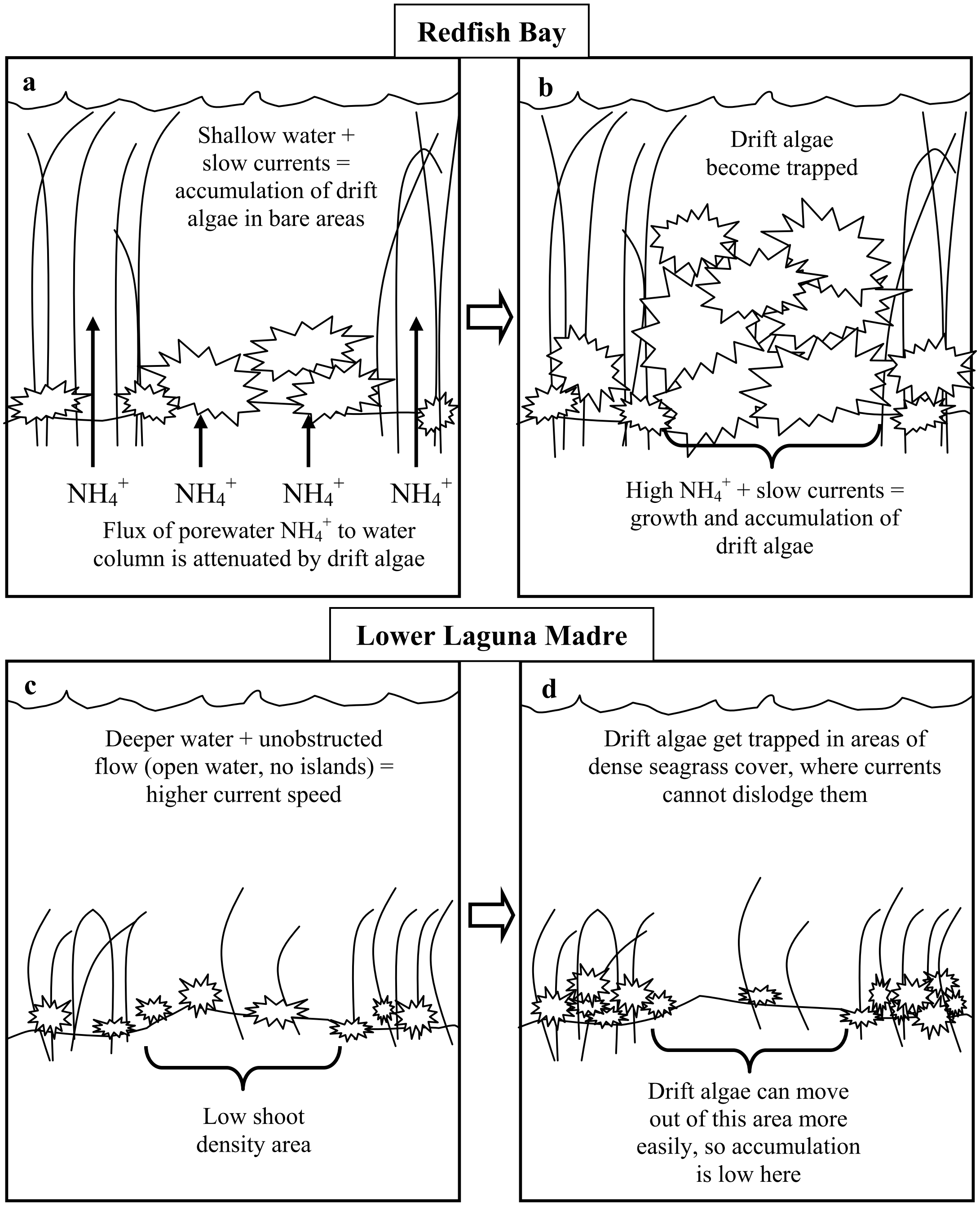

Figure 50: Schematic of drift algal accumulation in RFB (panels a and b) and LLM (panels c and d). Depth in RFB and LLM is approximately 0.5 and 1.5 m, respectively. Seagrasses in RFB and LLM are the same height. Panels on the right (b and d) represent changes over time.

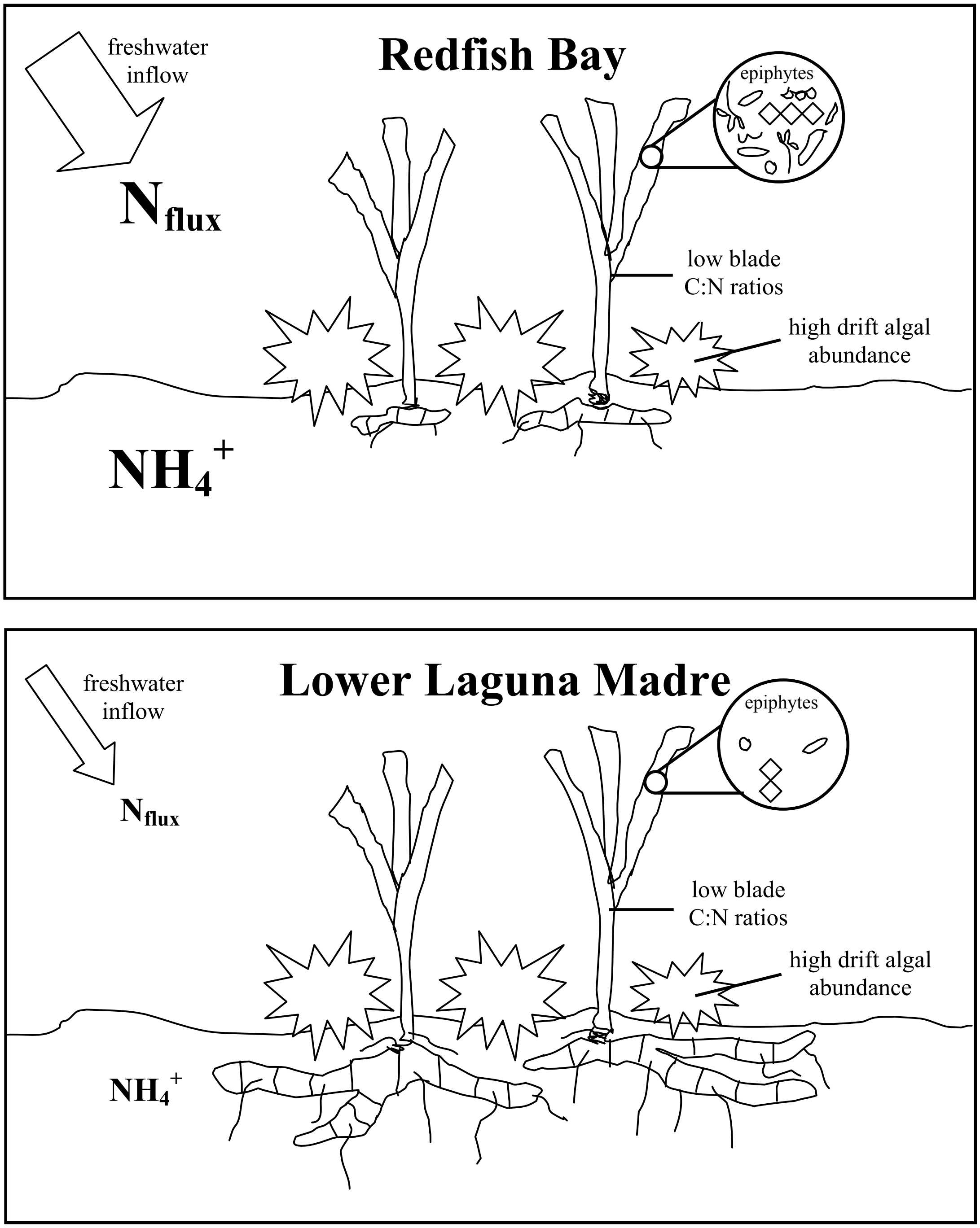

Figure 51: Conceptual diagrams of nutrient dynamics in RFB and LLM. Nutrient flux is hypothesized to be lower in LLM than RFB.