SPARTINA DENSIFLORA, AN INVASIVE SPECIES IN THE MARSHES OF HUMBOLDT BAY

By

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ABSTRACT

SPARTINA DENSIFLORA, AN INVASIVE SPECIES IN THE MARSHES OF HUMBOLDT BAY

Heinz D. Falenski

The purpose of this study was to model the abundance of *Spartina densiflora* in Humboldt Bay. Ten marsh sites, with an average of twenty-eight plots per site, were surveyed for *Spartina* abundance and the environmental gradients that could potentially correlate to *Spartina* percent cover. Seventeen environmental covariates (gradients) were measured, and three of those covariates were found to correlate to *Spartina* abundance: available phosphorus, redox potential, and elevation. These three covariates were useful in describing and predicting *Spartina* abundance in each plot, based on the field (and lab) measurements of the covariates. It was found that differences between each site, which were not accounted for by plot covariate values, could be incorporated into the model and increase the descriptive and predictive power of the model. The covariates which describe differences between sites were calculated by taking the site average and standard deviations of the covariates phosphorus, redox potential, and elevation for each site. The phosphorus site averages for all ten sites were calculated, made into the variable PhosphorusSiteAvg., and used to create the fourth covariate. The standard deviation of elevation for all the plots at each of the ten sites was incorporated into the variable ElevNStDev, which became the fifth model covariate. The standard deviation of redox

potential for all the plots at each site became the sixth covariate, RedoxSiteStDev. The equation of the model is:

Spartina abundance = - 2.1051 + 0.0571*Phos. – 0.000352*Redox + 0.271*ElevN - 0.0493*PhosphorusSiteAvg - 1.28*ElevNStDev + 0.00676*RedoxSiteStDev

with R-squared = 0.6089.

An equation delineating *Spartina* habitat in Humboldt Bay was developed using logistic regression. The six covariates used in both the *Spartina* abundance model and habitat delineation were analyzed for both their relationships to *Spartina* abundance and their relationships to each other. This analysis was summarized as a list of site characteristics that make a salt marsh resistant or susceptible to invasion by *Spartina*.

ACKNOWLEDGMENTS

This thesis project has given me both a great joy, in carrying it out, and a great deal of frustration in getting it written and polished. First of all, I'm grateful to my committee members for guiding me through the process of creating this project, refining it, and finishing it up. Both Andrea Pickart and Dr. Howard Stauffer spent a lot of time working with me. We didn't always agree, but I learned a great deal from the process. They have helped me to learn how Science is carried out, and how I can contribute to a subject that I love.

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Finally, my faith in a God of my understanding has sustained me and helped me overcome the hurdles that I faced. At the very least, God is a great working hypothesis.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Spartina densiflora, commonly known as dense-flowered cordgrass, is a native to the coastal marshes of Argentina and Chile. In the 1870s *S. densiflora* (Botanical nomenclature follows Hickman (1993)) is thought to have been brought to Humboldt Bay by the ships transporting lumber to Chile. The cordgrass was believed to be a variety of *Spartina foliosa*, which is a native cordgrass in California. In 1984 the plant was properly identified as *S. densiflora* (Spicher 1984).

The goal of this project was to model the growth of *Spartina densiflora* in the marshes of Humboldt Bay. *Spartina densiflora* is an invasive species of cordgrass in the Humboldt area. As such, it threatens to displace native species growing in salt marshes (Kittleson and Boyd 1997). Some of the species that are being displaced are rare and may become endangered or extinct by the continued spread of *S. densiflora*. Building a model of the growth of *S. densiflora* , based on environmental requirements of the plant, may help local resource managers to make better management decisions for the rare plant species growing in the salt marshes of Humboldt Bay.

The strategy used to examine the growth of *Spartina* around Humboldt Bay was to build a multivariate linear regression model which describes the abundance of *Spartina* at any location in the salt marsh as a function of environmental variables. This model is based on samples measured in North and Central Humboldt Bay. Therefore, the model should be general enough to describe the abundance of *Spartina* anywhere in these parts of Humboldt Bay.

This study measured *Spartina* abundance (2002) at 10 marsh sites. Each plot was measured for a spectrum of environmental gradients (covariates), and those covariates which correlated to *Spartina* abundance were used to construct the models.

The environmental gradients used in describing *Spartina* abundance have a secondary value – they can be analyzed individually for their relationship to *Spartina* in the salt marsh. That knowledge can then be used to modify salt marsh landscapes so as to exclude or limit the presence of *Spartina* in those marshes.

Literature review

Spartina densiflora spreads by both vegetative and by sexual reproduction. Its main mode of propagation is vegetative reproduction (Kittleson 1993, Rogers 1981). The cordgrass grows in clumps, from 5.2 to 7.9 feet above Mean Lower Low Water (MLLW) tidal elevation (Eicher 1987). The grass is perennial, and sends out new shoots from rhizomes each year, expanding the size of the clump. In this way it eventually crowds out competitors. *Spartina* also reproduces by seed (sexual reproduction), but the seedlings are rarely able to out-compete other plants. The seedlings can become established in disturbed areas, where they are free from competition from other plants. *Spartina* produces a lot of dead foliage that is carried with the tide at the end of the growing season. This dead *Spartina* foliage (wrack) often kills the marsh plants where it has been piled up by the tide. The resulting disturbed marsh may then be populated by *Spartina* seedlings (Kittleson 1993). In these two ways, *Spartina* is slowly increasing its density around Humboldt Bay. As *Spartina* increases its density and range, it threatens to decrease the diversity of native species of plants around the bay (Clifford 2002).

In 2000, *Spartina densiflora* occurred in 94% of the salt marsh in Humboldt Bay. Of this, 38% was categorized as having sparse to moderate infestation (5-69% cover). The marsh area in the Mad River Slough had the lowest density of infestation, with 76% coverage at all levels of infestation, 91% of this area covered by densities of sparse to moderate infestation (Pickart 2001).

The frequency of *Spartina densiflora* in the Mad River was measured in macroplots located in the Lanphere Dunes unit of the Humboldt Bay National Wildlife Refuge. In 1989 measurements showed that *Spartina* had a frequency of about 4%. The same plots in 1997 showed that *Spartina* had a frequency of about 42% (Pickart 2001). Photographs of islands in the Mad River Slough show that *Spartina* is increasing in both its abundance and in its habitat-elevation range (Clifford 2002).

The growth of *Spartina densiflora* has not been modeled in Humboldt Bay or elsewhere. The relative rates of vegetative and sexual reproduction have been examined (Kittleson 1993). Greenhouse experiments have been carried out to look at germination and survival rates of seeds and seedlings, but this information has not been tied quantitatively to life stage processes of field populations. Vegetative reproduction and growth have been examined for individual genets (clumps of *Spartina*) in the field (Kittleson 1993, Rogers 1981). These studies indicate that *S. densiflora* is a clonal organism that expands by rhizomatous growth. It grows best without competition from other species, but still expands in the presence of competing species.

The congener *Spartina alterniflora* has been much more thoroughly studied (Josselyn et al. 1993). *S. alterniflora* is also a clonal grass, native to the East coast of the United States (Mobberly 1956). *S. alterniflora* invades unvegetated mudflats on the West Coast and tends to turn the habitat that it invades into a monoculture. *S. densiflora*, in contrast, usually grows at elevations already supporting saltmarsh. It invades as scattered clumps that will grade into a solid monoculture at mid-elevation ranges in the salt marsh. *S. alterniflora* colonizes areas in the tidal marsh (Spicher 1984) by seed, and then expands clonally. The invasive growth of *S. alterniflora* has been modeled at Willapa Bay, Washington by examining aerial photographs of marshes where the cordgrass was once scarce, and which are now dominated by the same cordgrass (Blake and Simonstad 2000). The rates of colonization and spread were measured by comparing photographs that spanned several years, and then taking calibrated measurements of the changes that were seen.

The success of a population can be correlated to environmental factors (Menges 1990). Many studies have suggested that the plant species in a salt marsh are limited to zones related to elevation above sea level (Pennings and Callaway 1992, Eicher 1987). The lower limit of a particular species range is controlled by physical factors, such as length of submergence and tolerance of saltwater. The upper limit is usually controlled by competition with other species. Soil character is also an important environmental factor in the success of a plant species. The amount of organic residue in the soil was found to correlate to the success of *Spartina alterniflora* (Padgett and Brown 1999). The amount of phosphorus available to the plant from the soil was found to correlate to the presence of *Spartina densiflora* in Humboldt Bay (Newby 1980). Soil salinity is a limiting factor for the success of some marsh species, particularly in the late summer when evaporation causes increases in the soil salinity of the high marsh. The anoxic soil conditions of a marsh community limit the species to only those that tolerate having their roots submerged for extended periods of time (Cronk and Fennessy 2001). Environmental factors, biotic and abiotic, are believed to limit the range of *Spartina densiflora* (Eicher 1987, Kittleson 1993). Some of these factors are known, but some are probably still unknown.

Previous studies that included *S. densiflora* around Humboldt Bay focused on various aspects of its growth including seedling survival under controlled conditions (Kittleson 1993), plant growth under natural and controlled conditions, the plant community in which *S. densiflora* can be found (Eicher 1987), its abundance relative to elevation above sea level, and the nutrients that correlate to its abundance (Newby 1980). Other factors that have been found to influence the growth of *S. alterniflora* such as soil organic content, salinity, and soil texture may apply to *S. densiflora*. This study combines all of these factors into a coherent model, to describe the growth of *S. densiflora* around Humboldt Bay.

Goals of this Study

The primary goal of this study was to model the abundance of *Spartina densiflora* in the salt marshes of Humboldt Bay, with respect to the significant environmental gradients. A population normally will have a peak density at a certain point along an environmental gradient (Whittaker 1975, Whittaker and Levin 1975, Whittaker 1967). Plant population densities are often governed by several environmental gradients (Silvertown 1993). The primary goal of this study was to find the environmental gradients that defined the habitat of *Spartina*, and then to build a model of *Spartina* abundance based on those habitat requirements.

The secondary goal was to analyze the covariates (environmental gradients) of that model for the relationship of each covariate to *Spartina* abundance, and to use that analysis to create a set of recommendations on how to plan a marsh restoration so as to minimize *Spartina* abundance.

Objectives

1. Determine the abundance of *Spartina densiflora* in seven salt marsh sites around Humboldt Bay and in three locations on the Mad River Slough.
2. Collect soil and elevation data for all sites, in order to identify the environmental gradients that correlate with *Spartina* abundance.
3. Test the following hypothesis:

H_0: the abundance of *Spartina* is not affected by soil conditions and

elevation,,

H_A : the abundance of *Spartina* is affected by soil conditions and

elevation,

4. If H_0 is rejected then I will model the relationship between the dependent variable (*Spartina* abundance) and the independent variables (elevation, soil properties).

5. Analyze the relationship between *Spartina* abundance and each significant environmental gradient, so that salt marsh restoration sites can be planned to minimize the presence of *Spartina*.

MATERIALS AND METHODS

Model overview

In this study ten salt marsh sites were surveyed for soil conditions that might correlate to the presence and density of *Spartina densiflora*. Specifically, the conditions examined were soil organic content, available phosphorus levels, soil water salinity, pH, and redox potential. In addition, several topographic variables were measured. They were slope, aspect, slope shape (convex, linear, concave, both in a horizontal and vertical direction), slope position (summit, shoulder, back slope, foot slope, plain, drainage channel, and drain-pan), distance from nearest drainage channel, and depth of that drainage channel. Some or all of these variables could potentially correlate with the success of *Spartina* in Humboldt Bay. These variables were used to create models relating the presence and abundance of *Spartina densiflora* (the dependent variable) to the measured soil conditions, elevation, and location (the independent variables).

Site Description

Humboldt Bay estuary

Humboldt Bay is located on the Northern California coast, approximately 200 miles North of San Francisco and 180 miles South of Coos Bay, Oregon. It is a large, shallow body of water with deep channels, separated from the ocean by two long, narrow sand spits (Skeesick 1963). The bay has three distinct sections – the South Bay, the North

Bay, and Entrance Bay (Figure 1). The South and North Bays consist of broad, shallow bodies of water. At low tide, they are mostly mud-flats drained by tidal channels. Entrance Bay is a deeper body of water, directly inshore of the Entrance Channel and which joins the North and South Bays. Humboldt Bay is approximately 14 miles long. Entrance Bay is 2.5 miles long and 2.0 miles wide at its widest point. South Bay is 3.7 miles long by 2.6 miles wide. North Bay, also called Arcata Bay, is 5.5 miles long by 4.2 miles wide (Thompson 1971). Humboldt Bay is unusual in that the entrance channel to the bay is at the center of the bay, rather than at one end of the bay.

Each of these three sub-bays occupies the seaward end of one or more stream valleys (Thompson 1971). Jacoby Creek and Freshwater Creek empty into the eastern edge of Arcata Bay. Elk River empties into Entrance Bay, and Salmon Creek empties into the south end of South Bay. During periods of high rainfall, the salinity of the bay water becomes somewhat diluted. The average salinity of the bay is slightly less than 34 ppt (parts per thousand). During heavy rains the bay water near Jacoby Creek has been observed to drop to 28.34 ppt. The average salinity just outside the entrance to Humboldt Bay is 33.75 ppt (Skeesick 1963), which is slightly more dilute than the median salinity of the bay waters.

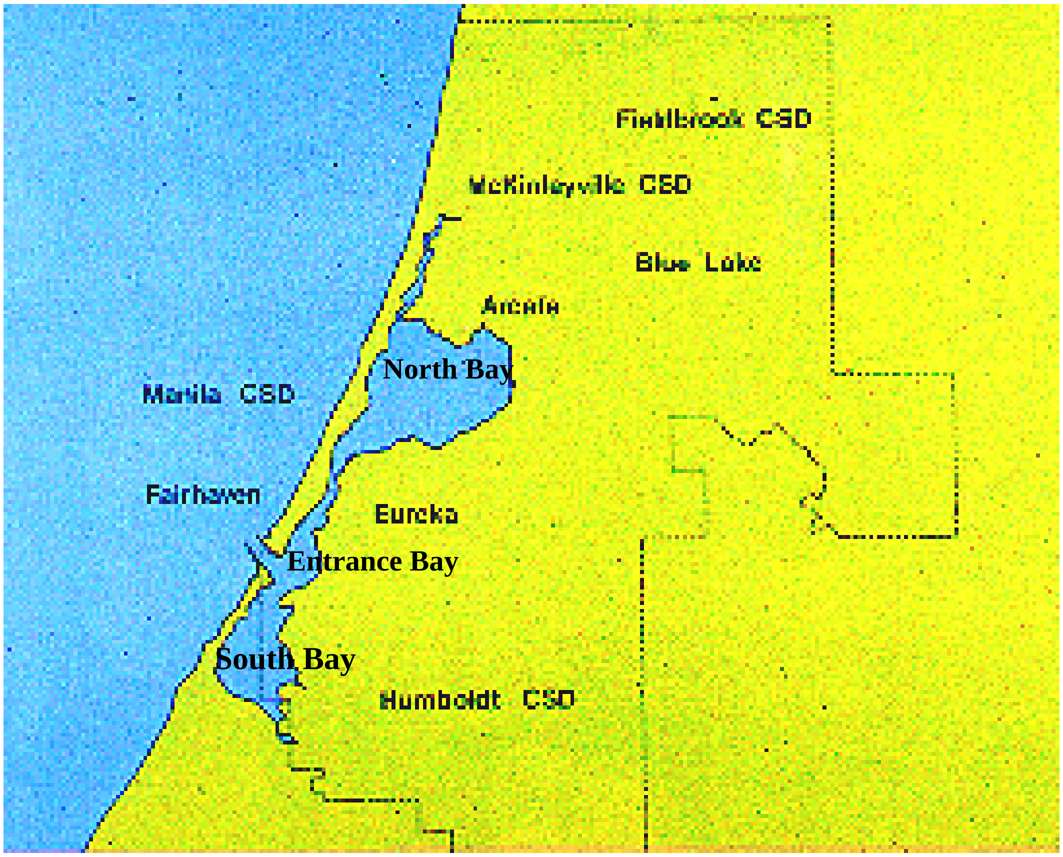


Figure 1: Map of Humboldt Bay, and surrounding areas.

The Pacific coast has two unequal low tides and two unequal high tides in a lunar day (Eicher 1987). During most of the month, the cycle follows the pattern:

- Higher High Tide (6.92 feet)
- Lower Low Tide (0.00 feet)
- Lower High Tide (5.52 feet)
- Higher Low Tide (2.50 feet)

These are the average tidal datums for the North Spit tidal station, near the mouth of Humboldt Bay (Skeesick 1963). All tidal datums are relative to Mean Lower Low Water (MLLW), which is the average of all the Lower Low Tide measurements for a given tidal station. It is assigned the value of 0.00 feet. During part of the lunar tidal cycle (about 28 days long), the tides can be more extreme (higher highs and lower lows) than average. These tides are called spring tides. In contrast, during part of the lunar tidal cycle the tides can be less extreme than average, so that the low tides are not as low and the high tides are not as high as they are on average. These tides are called neap tides. During the spring tides, the high marsh will be inundated by the salty bay waters at least once every lunar day. During the neap tides, the high marsh may not get flooded by bay waters for days at a time. During the summer when temperatures and evaporation are high, the high marsh soils during the neap tide may become very salty, up to 80 or 90 ppt in the extracted soil water, as observed during this study. The lunar tidal cycle had to be considered when collecting soil samples for salinity, pH, and redox measurements.

The Humboldt Bay area has mild, wet winters and cool, dry summers. The average yearly temperature is 52 degrees Fahrenheit, with summer months averaging 10 degrees warmer than winter months (Elford and McDonough 1974). The average yearly rainfall is 38 inches, with most of the rain occurring between October and April. The summer and early fall frequently are foggy or overcast, giving the area a moderate, cool, and damp climate. Winds are generally from the north to northwest during the dry season and from the south to southwest during the wet season (Elford and McDonough 1974).

The north wind causes ocean upwelling of nutrient rich waters (Barnhart et el. 1992). In particular, the incoming tide will carry elevated levels of phosphorus into the bay during periods of upwelling. Phosphorus has been correlated with *Spartina* productivity (Newby 1980). It has been suggested that wastewater outflow is also partly responsible for elevated phosphorus levels in the bay, relative to the levels found in ocean waters (Barnhart et al. 1992).

Humboldt Bay salt marshes

Prior to Euro-American settlement, Humboldt Bay had about 2,883 ha. of salt marshes. Beginning in about 1880, salt marshes were diked to create agricultural lands. By 1973 there were only about 393 ha (10 – 15% of the original area) of salt marsh left (Barnhart et el. 1992). The remaining salt marshes are found on Indian Island, adjacent to Eureka Slough next to highway 101, around the mouths of the Mad River Slough, McDaniel Slough, and Jacoby Creek, in Samoa off of Vance Street, on the Elk River Spit, near Salmon Creek in the South Bay, and up in the Mad River Slough. Much smaller remnants of salt marsh can be found scattered around the edge of the bay. The salt marsh plant distribution in the North Bay salt marshes is between 5.2 feet MLLW and 8.4 feet MLLW, while at Elk River Spit, the salt marsh plants grow between 3.9 and 6.1 feet MLLW (Eicher 1987). The difference in plant distribution between the Elk River Spit and the North Bay as observed by Eicher was attributed to problems in defining MLLW in this study, and not to differences in the elevation of the plants. There is a sand/mud “sill” at the mouth of the Elk River that holds back a pool of bay water when the tide goes down (NOAA tidal information glossary at http://www.weather.gov/glossary, and NOAA tidal reports for Humboldt Bay 2004-2005). The MLLW level is defined from the lowest level that this pool drops and not the lowest level that the bay waters drop. As a result, the tidal range of the Elk River Spit is about 1.8 feet less than the tidal range at Bucksport, less than 1 mile away from the mouth of the Elk River. When those problems are compensated for, the salt marsh plants at Elk River Spit grow within the same tidal range as the salt marsh plants in the North Bay.

The soils of the salt marshes are silt, clayey silt, silty clay, and clay. In most cases the marsh soils are 3-4 feet thick, and grade down to the clayey silts of the high tidal flats (Thompson 1971). The only exceptions found in this study were at the Elk River Spit salt marsh where sand could generally be found 8 inches or less below the surface of the marsh soils, and at the upper edge of the Samoa salt marsh where the boggy soils approached 70% organic content.

The upper edge of the salt marsh starts at about 8.4 feet MLLW, at the upper boundary of the extreme high tides. Above this elevation, upland or wetland glycophytic species of plants grow. Below this elevation, salt tolerant species of plants have the competitive advantage (Cronk and Fennessy 2001). The salt marsh slopes down from the high marsh to the mud flats. Most of the time the salt marsh drops off at a 2-3 foot wave cut cliff to the bay mud, but in a few places the salt marsh grades all the way to the mud in a gentle slope (Thompson 1971). The marsh is cut by meandering drainage channels which are shallow in places and unexpectedly deep in other places. These channels carry in nutrients, silt, and clay with the tide. The incoming tidal water slowly adds sediment to the marsh surface and provides nutrients to the marsh vegetation. The lower edge of the salt marsh is at about 5.2 feet MLLW.

The salt marsh is characterized by three vegetation types as described by Eicher (1987): the *Salicornia* or pickleweed plant community, the *Spartina* plant community, and the mixed marsh plant community (Eicher 1987). The *Salicornia* plant community is dominated by *Salicornia virginica*. This species is the most tolerant of the salt marsh species to long periods of salt water inundation, and sometimes grows in patches on the mud flats, as seen near the mouth of Jacoby Creek. Usually, *Salicornia* can be found growing on the sloping edges of channels. *Spartina* is found mixed in with *Salicornia* in this community, but it is more abundant slightly higher in the marsh.

The *Spartina* marsh community is dominated by *Spartina densiflora*, with *Salicornia* mixed in. *Spartina* tends to grow in clumps, but can crowd out almost all other plants, and form a virtual monoculture at about 6.7 feet MLLW (Eicher 1987), the elevation of its optimum growth. At higher elevations, *Spartina* reverts to its clumping habit, and the marsh grades into the mixed marsh community (Eicher 1987).

In the mixed marsh community, *Salicornia virginica* and *Distichilis spicata* are co-dominants, with *Jaumea carnosa*, *Triglochin concinna*., *T. maritima*, *Limonium californicum*, *and Plantago maritima* mixed in. The mixed marsh community generally appears as a low growing meadow of grasses, succulents, and small herbs, with occasional taller plants mixed in (Eicher 1987).

Study Sites

A total of 10 salt marsh sites were used in this study. The first set of marsh sites were located in central and north Humboldt Bay, and the second set of marsh sites were located in the Mad River Slough, which enters Humboldt Bay north of Manila.

Jacoby Creek salt marsh is located west of highway 101, and west of the railroad tracks, at Jacoby Creek (Figure 2). It has a gentle, consistent slope down to the bay mudflats, broken in places by small and large drainage channels. The upper and middle marsh is largely vegetated with salt grass, *Distichlis spicata*, and other mixed marsh species. Shrubby *Grindelia* is scattered most abundantly in the upper marsh areas. *Spartina* is found growing as isolated clumps throughout the upper marsh, in strip-meadows along side some of the tidal creeks of the middle marsh, and as dense meadows in the lower marsh. The bay side margin of sections of this salt marsh consists of a 4-6 foot strip of pickleweed, *Salicornia virginica*. This marsh has the best gradients of elevation and marsh community types of all the marshes examined.

The Mad River Slough site is located adjacent to the west side of the mouth of the Mad River Slough, south of Samoa Blvd (Figure 2). An old dike sits on the north-eastern edge of the salt marsh, separating the marsh from the slough. The dike supports patches of mixed marsh community vegetation, as well as solid patches of *Spartina*. The inner part of the marsh is mostly *Spartina*, but has pickleweed growing in low meadows and along the edges of most of the tidal channels.

The Samoa salt marsh is located east of Vance road, and north-west of a large island in the bay (Figure 2). Mixed marsh vegetation borders the bay side of the marsh, with a 2-3 foot bank dropping from the marsh vegetation to the bay mud. The marsh is cut by many large meandering tidal drainage channels. The lower elevation parts of the inner marsh are covered with pickleweed, while most of the rest of the marsh is dominated by *Spartina*. The upper edge of the salt marsh has fresh-water seepage where brackish marsh genera such as *Juncus* and *Carex* can be found growing.

The Eureka Slough salt marsh is located on the northern bank of the Eureka Slough, just north-west of the railroad bridge (Figure 2). This is a fairly flat marsh, cut by many tidal channels. The marsh has a 2-3 foot drop off to the bay mud flats. Mixed marsh vegetation grows along a wide channel at the northern edge of the marsh. The average *Spartina* percent cover is high, though the other vegetation types can be found in patches within the marsh.

The Elk River Spit salt marsh site is located on the Elk River Spit, along the western bank of Elk River, and about 400 yards north of the railroad bridge (Figure 2). The salt marsh slopes down from a sandy berm at the upper edge of the salt marsh, to a 2-3 foot drop off at the bank of Elk River. The marsh has a few tidal channels, but is fairly smooth and unbroken from high marsh to low marsh. Elk Spit is largely made up of sand dunes, and the salt marsh soil is a layer of silty clay about 6-8 inches deep deposited over this sandy substrate. The thick *Spartina* growth at the upper edge of the salt marsh may be due, in part, to the presence of so much sand and the resulting modified soil drainage. *Spartina* percent cover is high, over most of this part of the salt marsh. But, at the northern end of this part of the salt marsh is a meadow of arrowgrass, *Triglochin maritima*, and pickleweed. Transects were run from high marsh to low marsh, in both the *Spartina* meadows and the arrowgrass/pickleweed meadows.

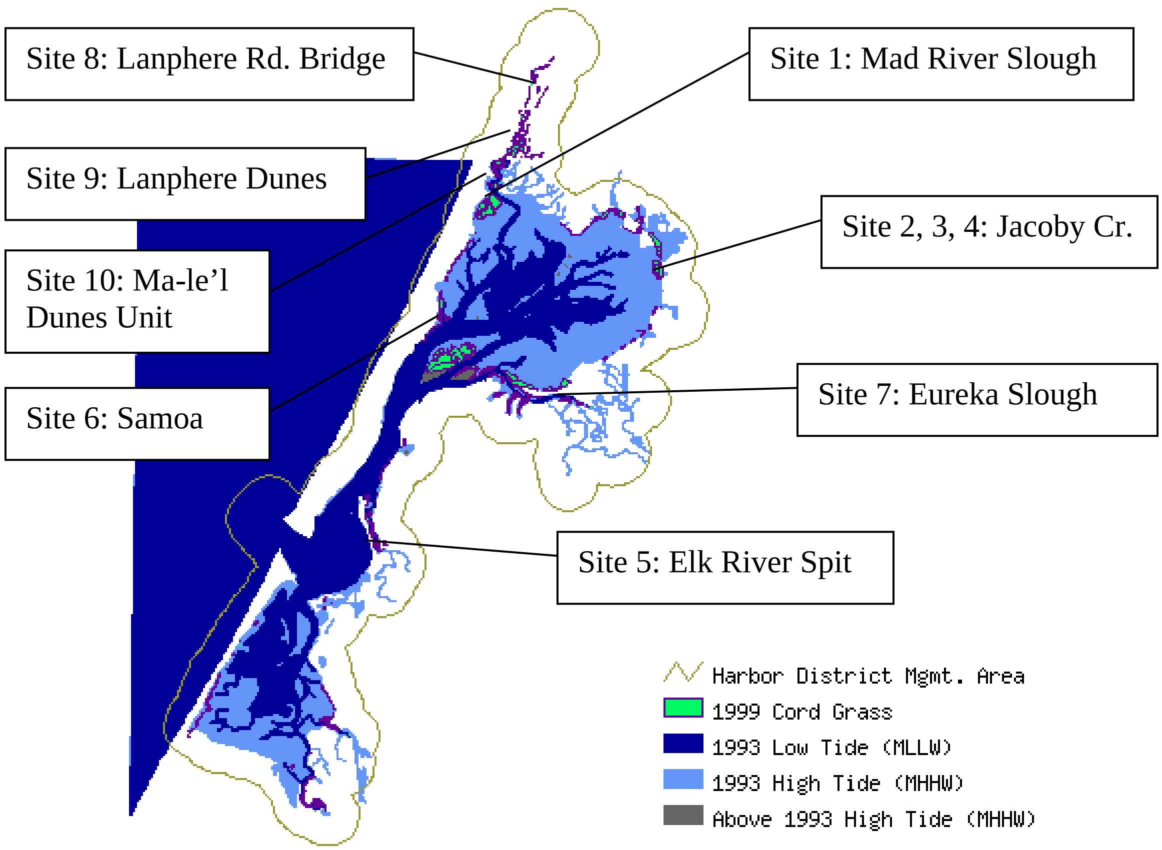


Figure 2. Humboldt Bay sites 1-7, and the Mad River Slough sites 8-10. Areas shown in green contain Spartina densiflora. Map from http://humboldtbay.org. Spartina data from Pickart 2001.

The three study sites in the Mad River Slough were located on two islands, and at the Lanphere Dunes salt marsh (Figure 2). The first of these study sites is located on a fairly flat island, Ma-le'l Dunes Unit, Humboldt Bay National Wildlife Refuge (HBNWR), 0.6 miles north of the Samoa Blvd. at the Mad River Slough bridge. The vegetation is largely of the mixed marsh type, dominated by *Distichlis spicata*. Very little *Spartina* grows on the island. The second marsh site, about 1.2 miles north of Samoa Blvd. at the Lanphere Dunes Unit of HBNWR, is protected by a long, breached dike which runs the length of the marsh along the bank of the slough. It has meadows of *Distichilis spicata*, areas of mixed marsh with clumps of *Spartina*, and areas of solid *Spartina* growth. Some large *Spartina* clumps can be found along the edges of the creek, in the middle of this marsh site. The third Mad River Slough site is located 2.5 miles north of Samoa Blvd. on an island north-east of the Lanphere Rd. bridge. The southern third of the island has the lowest elevations and a maze of tidal channels. It is covered with large clumps of *Spartina*. The northern edge of the island also has some *Spartina*. The rest of the island is of the mixed marsh vegetation type.

Variable Sampling

Transect location

The Humboldt Bay transects generally ran from high marsh to low marsh, so as to capture the variation in vegetation due to changes in elevation. The transect plots were spaced 20 meters apart, except when more plots were needed to capture large changes in vegetation and elevation. In the Mad River Slough, transects were placed to capture changes in vegetation due to changes in elevation, though not always from high marsh to low marsh. The plots were spaced 20 meters apart.

Vegetation sampling

Each plot was located by placing wooden stakes in the ground along the transect at 20 meter intervals. A 1-meter by 1-meter quadrat was placed with the stake located in the center. Each species present was identified, and a visual estimate of that species percent cover was recorded. Percent cover of bare mud or piled debris was included in the total. If a species was present but had less than 1% cover, it was given a value of 1%. Vegetation percent cover was measured in August through September of 2002 (Humboldt Bay sites), and in August through November of 2003 (Mad River Slough sites).

The volume of the *Spartina* clumps sometimes increased from the base of the clump at ground level, to the top of the clump, a meter above the ground. When this spreading of the clump shaded the underlying vegetation significantly, the *Spartina* percent cover was calculated as the area where the underlying vegetation began to thin due to shading from the *Spartina*. The result of this approach was to include most of the area shaded by *Spartina* as *Spartina* percent cover. In this way, the percent of all ground cover added up to 100 percent.

Elevation

The elevation of each plot within a marsh was surveyed using a transit and stadia. These elevation measurements were only useful for the relative elevations of each plot to all the other plots within a marsh. The elevation of each plot within a marsh site relative to the Mean Lower Low Tide (MLLW) was found by putting several poles, marked with soluble ink, next to the lowest and highest elevation plots. When the high tide came in, it washed away the ink to the high tide level. The measured high tide level was later recorded from the NOAA tidal data, and the elevation of each plot relative to MLLW was calculated. The relative elevations of all the marsh sites were verified by putting two marked poles at each of the sites on a single day, and checking the elevation values for the sites during the next low tide.

The range of the tides increases with increasing distance from the entrance to Humboldt Bay. For example, the mean diurnal range (the average range from lower low tide to higher high tide in 24 hours) of the tides at the North Spit tidal station is 6.92 feet. The North Spit station is located about 0.4 miles north of the entrance to the bay. The mean diurnal range at Samoa, 4.5 miles north of North Spit station, is 7.33 feet. The mean diurnal range at the mouth of the Mad River Slough, 8.6 miles north of the North Spit station, is 7.74 feet. As a result, when the tide rises to 6.92 feet above MLLW at the North Spit Station, it will rise to 7.74 feet above MLLW at the mouth of the Mad River Slough (Eicher 1987, Shapiro and Assoc. 1980). This affects the elevation at which a plant will be found to be growing. If a plant has a peak abundance at 6.92 feet MLLW near the North Spit tidal station, it will probably have a peak abundance at 7.74 feet MLLW at the mouth of the Mad River Slough. This difference in tidal ranges has to be taken into consideration when measuring plant abundance relative to tidal elevation, in different marsh sites around the bay. The solution is to normalize the tidal elevations, so that high tide at a North Spit (for example, 6.2 feet) on a given day will have the same high tide elevation (of 6.2 feet) at a Mad River Slough site. This problem was solved by scaling down the elevations at the Mad River Slough site by multiplying by the scaling factor 6.92/7.74. This was done for each marsh site, using that sites' mean diurnal range in the scaling factor. The result was a MLLW elevation data set, and a normalized site-elevation data set. The normalized data set was used in model calculations.

Soil

The soil was measured for bulk density, percent organic content, pH and redox potential, salinity, and available phosphorus content.

Bulk density.

A soil core was collected, from a depth of 1 to 7 cm below the soil surface. The barrel of the soil core sampler had a 5.5 cm diameter and a 6 cm height. The soil sample excluded the top 1 cm of marsh substrate, as this layer of soil and vegetation was assumed to be subject to daily and weekly changes. The next 6 cm was assumed to be less subject to change, and so more representative of the soil conditions that influence the plant community in the salt marsh. *Spartina* roots and rhizomes were observed to grow most densely from 2 to 5 cm below the marsh surface. The sample core was dried for 24 hours at 105 C, weighed, and the bulk density calculated. The formula for bulk density is:

Bulk density = sample dry weight / sample volume

Organic content.

Five grams of soil core were crushed and weighed shortly after drying. The sample was heated at 425° C for 16 hours, allowed to cool for 8 hours, and weighed within 1 hour of exposure to atmospheric moisture. The difference in the two weights divided by the original weight was the calculated organic content (Soil Survey Staff 1996).

Redox and pH.

A second sample core was collected and measured for redox potential in the field, at about 4 cm below the surface of the soil. The redox potential varied with depth, from more positive near the soil surface to more negative at depth. Each sample took about 20 minutes to measure. The measurement was recorded when the redox meter (Oakton 100 meter using AIC inc. general purpose ORP sensor (PN-6812-0000-15) for redox, and AIC inc. general purpose pH sensor for pH (PN-6031-0000-15)) held a steady value for 10 seconds, two readings in succession. The sample was then taken to the lab and measured for pH, within 24 hours of collection, using the same time/measurement protocol as was used with the redox measurements. The pH measurements went much quicker than the redox measurements.

Salinity.

A single soil core was collected, to a depth of 16 cm, at each plot. The core was sampled at 0, 5, 10, and 15 cm. Each sample was wrapped in filter paper and placed within a 35 cc syringe to extract some water. A drop of soil water was measured for salinity on a hand-held refractometer (model unknown, borrowed from the HSU Oceanography Department).

Phosphorus.

Three 16 cm deep soil cores were collected from each square-meter plot, using a split tube soil sample coring tool. The samples were air dried, crushed and combined. The soil was screened using a 2 mm soil sieve. Each plot sample was measured for available phosphorus using the Bray P-1 absorbed phosphorus test (Soil Survey Staff 1996). The test protocol was modified because phosphorus levels were high, and out of the test range. The phosphorus sample extractions were diluted to one quarter with fresh extraction solution, and then mixed with the coloring reagents. The resulting phosphorus values were then multiplied by four to obtain the correct available soil-phosphorus levels. The site air-dried soil samples were measured for average moisture content and the phosphorus values adjusted using this information.

Site topography

Site topography was measured using the standard description methods of the National Soil Survey Center (National Survey Soil Center 2002), except that the micro-topography was measured since the salt marshes are relatively flat. Each plot was measured for aspect, slope, slope shape, slope position, proximity to a drainage channel, depth of drainage channel, and the average height of any *Spartina* present in the plot. The *Spartina* height data was collected in January, so plants were probably not at their fullest height. The relative heights of the *Spartina* clumps were assumed to be similar during the whole year.

Aspect.

This was the average direction of the downhill slope. Aspect values were calculated as Sine (aspect), and Cosine (aspect).

Slope.

Two slope values were taken – the slope of the plot over the one meter length of the plot; and the slope over a three meter length of the marsh substrate, including the plot and the marsh area directly below the plot.

Slope shape.

A three meter pole was laid on the marsh surface horizontally across the plot and vertically across the plot, relative to the down-slope direction. The shape could have any of three values: convex (V), linear (L), or concave (C). A slope designation consists of two letters, the first representing the horizontal slope shape and the second representing the vertical slope shape.

Slope position.

The plot was described relative to location on the local topography. The possible plot positions were: summit (SU), shoulder (SH), back slope (BS), foot slope (FS), flat plain (PL), drainage valley (DR), or drain-pan (DP).

Proximity to channel.

This was how far away the nearest down-slope drainage channel was located. If a very deep drainage channel was located up-slope and very close relative to the down-slope channel, the upslope drainage channel was substituted for the down-slope drainage channel.

Height of *Spartina*

The average height of the *Spartina* present was measured by setting the quadrat on the plot, measuring the low and high heights of plants present in the quadrat with a tape measure, and making a visual estimate of the average plant height. The parts of the quadrat not containing *Spartina* were not included in the estimation of the average height of *Spartina*.

Mathematical analysis

Multivariate Linear Regression

Each variable (covariate) was tested for statistical significance with respect to *Spartina* percent cover. Only the data gathered from Sites 1-7 (Jacoby Creek, Eureka Slough, Elk River Spit, Samoa, and the mouth of the Mad River Slough) were used to build the model. The remaining sites were used for model validation. If the variable was statistically significant by itself, using linear regression, it was tested with other statistically significant variables using multivariate linear regression. The variables that remained statistically significant when combined in this way became part of the model.

<u>Selection of variables in multivariate linear regression</u>

Stepwise Variable Selection.

There were several distinct strategies used to select the variables for use in multivariate linear regression modeling. All of the strategies described here were used to create *Spartina* abundance models. The first strategy to finding a useful model was to run all the variables in a stepwise selection routine (Hintze 2003). This routine adds the variable with the largest R-squared value from a list of candidate variables, to the model. It then checks to see if any of the added variables have lost statistical significance in this new model. If a previously added variable has fallen below a predetermined level of significance, it is removed from the model. This process continues until none of the remaining unselected variables appreciably increases the R-squared value, or adjusted R-squared value, of the model.

A Priori Variable Selection.

The second strategy to finding a useful model is called the *A Priori* strategy of variable selection (Burnham and Anderson 1998). This is the method that probably makes the most intuitive sense to a biologist or an ecologist. It consists of thinking about the system that one wishes to model and choosing a set of independent variables that would be most likely to predict the dependent variable, and hypothesizing a priori a finite collection of models. In this case, *Spartina* abundance is the dependent variable. If *Spartina* was known to be found low in the salt marsh, but is also known to prefer a source of fresh water nearby, the predictive independent variables chosen might be

Elevation, Distance to the nearest creek, and Salinity of the soil. Several different possible models are chosen in this way, and all of them are compared to determine the best fitting models. At the very minimum, the biologist or ecologist would gain some understanding of the usefulness of the individual variables, and their possible interactions. A sub-set of the set of hypothesized models are listed in Table 5 of the Results section.

Dummy Variable Method of Variable Selection.

A third, more time consuming strategy is trial-and-error, an *ad hoc* approach. This method proved to be the most useful in my search for a model. This third method of variable selection began by taking various combinations of the significant variables, combining them into models, and keeping a record of the resulting R-squared and probability values of each model. The most useful combinations of variables can then be remixed to find those variables that consistently work well together in describing *Spartina* abundance.

The next step in this strategy is to select the most consistently significant variables that describe *Spartina* abundance at the marsh sites in Humboldt Bay, and to add a categorical variable called ‘site’. The categorical variable, ‘site’, is constructed in the following manner: for the seven sites used in building the model, six “dummy” variables were created. For example, the first dummy variable was called “Mad River Slough”. For those spreadsheet rows that contained the data for the Mad River Slough, the dummy variable was assigned a value of 1.0. All the other rows (plots not in the Mad

River Slough) were assigned a value of 0.0. This was repeated for six of the seven marsh sites. The seventh marsh site served as the reference cell, with all six dummy variables set equal to zero. These dummy variables were run with the significant variables which describe *Spartina* abundance, in a multivariate linear regression. The regression produced coefficients for all of the variables (the significant descriptive variables and dummy variables), with six of these dummy variables becoming site constants. The site constant served the purpose of filling in the gap between the prediction of the model variables for *Spartina* coverage, and the actual *Spartina* coverage at the site. In effect, the constants provided a better fit between the independent variables and the dependent variables. The full model equation is as follows:

$$\textit{Spartina}\text{ coverage} = \beta_1\text{*(first significant covariate)} + \beta_2\text{*(second significant covariate)} + \beta_3\text{*(third significant covariate)} + \beta_4\text{*site1(0 or 1)} + \beta_5\text{*site2(0 or 1)} + \beta_6\text{*site3(0 or 1)} + \beta_7\text{*site4(0 or 1)} + \beta_8\text{*site5(0 or 1)} + \beta_9\text{*site6(0 or 1)},$$

where the β_i are coefficients chosen by the multivariate regression routine.

The problem with this approach is that the dummy variables have no real ecological explanation. The solution was to make the site constant a dependent variable in a multivariate linear regression, and to find out if any of the other variables will predict this site constant for the seven marsh sites. This was done, and several sets of predictive variables were found and incorporated into models.

Residual Sum Method of Variable Selection.

This fourth method of variable selection is a modification of the Dummy Variable method. This method starts with the most consistently significant variables, as described in the first part of the ‘Dummy Variable’ method above. These variables are used to construct a multivariate regression base model of *Spartina* abundance.

This model is used to calculate *Spartina* abundance for every plot in sites 1-7, and placed in a variable column, called ‘model-abundance’. A second variable is created, called ‘residual difference’ and is calculated as follows: ‘actual *Spartina* plot abundance’ – ‘calculated model-abundance’ = ‘residual difference’. The previous Dummy Variable model, in essence, took an average of the ‘residual difference’ and turned it into a site constant. The Dummy Variable method then found variables that would predict the ‘site constant’ value. All of these variables were used to create a multivariate linear regression model. This modified approach does the same thing except it uses the ‘residual difference’ instead of the ‘site constant’ as the dependent variable, to find any variables that can accurately predict this ‘Residual Difference’. The two variable selection routines, Stepwise Selection and All Possible variable selection (Hintze 2003), were used to identify three variables that could predict the residual difference.

Mixed-Effects Modeling

Mixed-effects modeling is similar to multivariate linear regression in that it calculates a multivariate linear regression model for the entire system. But, it also calculates multivariate linear regression models for each distinct subset of the data set. In this case, each marsh site would represent a separate and distinct subset of the data set. Each sub-model should be slightly different from the others, due to site differences that were not accounted for in the model. This difference will be expressed by different coefficients on the variables of the linear regression model equation. These differences in the overall model can be described for each variable by a coefficient that has a fixed effect and a random effect. The fixed effect is the coefficient of the variable used to describe the whole system, and is the average of all the subset coefficients for a variable. The random effect term of the coefficient is generated from a normal distribution with 0 mean and estimated standard deviation of the coefficient for the given variable, across all the site sub-models. For example, suppose the linear regression equation for phosphorus at each site is:

Spartina percent cover = β_i * phosphorus

with β_i = 0.2, 0.5, 0.4, 0.6, 0.2, 0.5, 0.7, 0.1, 0.7, 0.6. Assuming that the average of all the coefficients for phosphorus is 0.45 and the standard deviation of all the coefficients is 0.22, then the mixed effect model would be:

Model equation: *Spartina* percent cover = [0.45 + ε_i]* phosphorus,

with $\varepsilon_i \sim N(\mu = 0, \sigma = 0.22)$.

The mixed-effects model serves to describe the system by estimating a system coefficient for each variable (the coefficient average) and showing the variability of the coefficients for each site sub-model in the model equation. In a multivariate system, this process can be repeated for the coefficients of all the variables used to describe the dependent variable, which is *Spartina* percent cover in this case.

Analysis of the Variables Used in the Model, for Management of the Salt Marshes

The environmental gradients useful as components to a *Spartina* abundance model have a secondary importance – they can be used in the management and restoration of salt marshes around Humboldt Bay, with the goal of minimizing *Spartina* abundance in those salt marshes. The relationships between the significant variables (environmental gradients) and *Spartina* abundance were examined and analyzed. For example, marsh topography has an influence on *Spartina* abundance. If that relationship is understood and easy to manipulate, then marsh restoration projects can be planned to encourage native plant growth and at the same time to discourage *Spartina* colonization of those newly opened sites.

The relationships between significant model variables were also examined. There are correlations between some of the environmental gradients found in the salt marsh. Changing one gradient could have the long term effect of altering several other gradients, which may support the goal of the restoration project. Those relationships need to be understood and managed, in any modification of a salt marsh with the intent of discouraging the proliferation of *Spartina*.

Actual variable values, for five *Spartina* abundance classes

When discussing the abundance of a plant in relation to environmental gradients that may control its abundance, it helps to have real and concrete values in a table to get a better understanding of the gradients being discussed. Toward that goal, five *Spartina* abundance classes were created, and the average values of the significant variables for each abundance class were tabulated.

The abundance classes are:

i) Class 1 - 00.0% to 10.0% *Spartina* present;

ii) Class 2 – 10.1% to 25.0% *Spartina* present;

iii) Class 3 – 25.1% to 50.0% *Spartina* present;

iv) Class 4 – 50.1% to 75.0% *Spartina* present; and

v) Class 5 – 75.1% to 100.0% *Spartina* present.

When the relationships between *Spartina* abundance and the significant environmental gradients are discussed, the reader can refer to the above list of abundance classes and values to clarify their understanding of the discussion. The abundance classes were selected by sorting the plot data from least to greatest *Spartina* abundance, graphing the data, and looking for significant breaks in the graphs curve. A break in the curve might represent a change in the environmental gradients that govern the presence or absence of *Spartina*, and so indicate the boundary of *Spartina* habitat. As seen in Figure 3, below this break, the abundance of *Spartina* is approximately zero. Above the break, *Spartina* abundance should rapidly increase as the environmental gradients become more favorable to *Spartina* growth. This was done, and a significant break was found at 3% to10% *Spartina* abundance (Figure 3). The remaining portion of the curve had no significant breaks, so the remaining four abundance classes were arbitrarily chosen.

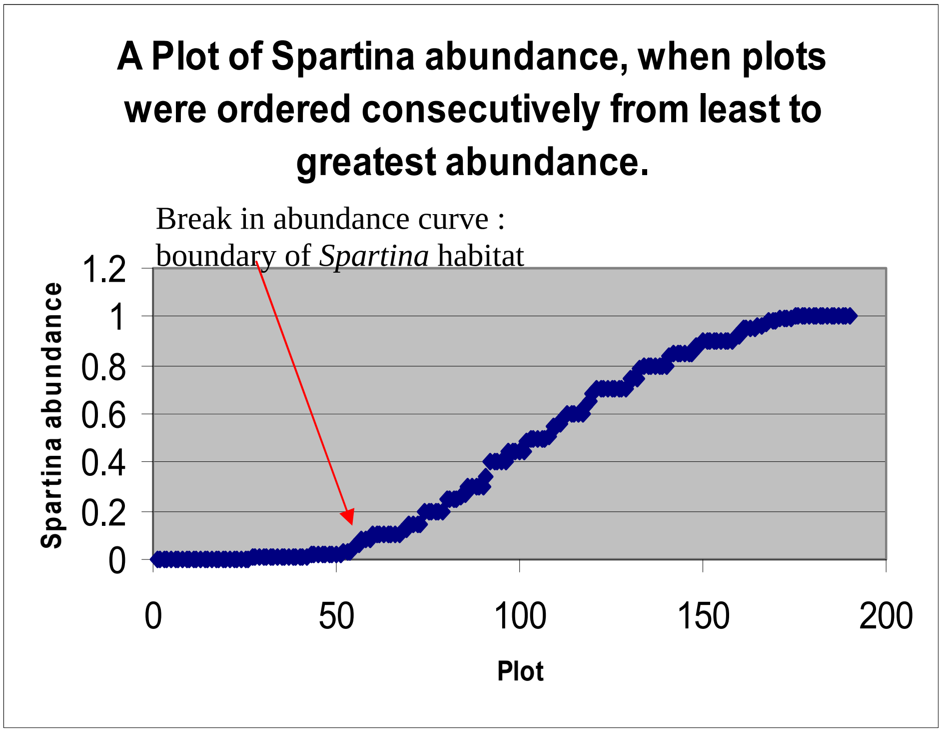


Figure 3. The plots of the initial data set were sorted from least to greatest *Spartina* abundance, in order to see if there were any natural breaks in the data, perhaps indicating a change from unfavorable to favorable *Spartina* habitat. There is a break between 0.03 and 0.10 (or between 3% and 10%) *Spartina* abundance.

Logistic Regression

An important goal of this study was to identify the environmental variables that are significant to the presence of *Spartina densiflora* in the salt marsh. Multivariate linear regression and mixed effects modeling were used to identify those variables, and to combine them in an equation to describe and predict the abundance of *Spartina* in a plot.

Another approach toward this goal was to use the environmental variables to predict the presence or absence of *Spartina* in a plot. Logistic regression is an approach that does this by predicting the probability that an individual or item belongs to one of two classes (i.e. present or absent), given the variable information.

The measured abundance of *Spartina* in the individual plots was used to separate the plots into five *Spartina* abundance classes (see previous section). Logistic regression equations were developed, using the abundance classes, and the associated environmental data. Logistic regression equations were used to classify a plot as having more or less than a boundary value of *Spartina* abundance, and creating two groupings of plots separated by the chosen boundary value. The most significant of these four logistic regression equations is the one that predicts the presence or absence of *Spartina*, using the 10% abundance value as the defined separation boundary for presence or absence of *Spartina* (for reasons of this decision see Discussion section).

Logistic regression is similar to multivariate linear regression in that multiple variables are used in a linear equation to predict the dependent variable. It differs from multivariate linear regression in that the dependent variable is binary and can have a resulting value of 0 or 1. For example, if one wanted to predict the presence (value = 1) or absence (value = 0) of *Spartina* on a plot, one would select the best predictive independent variables in a logistic regression to predict the presence or absence of *Spartina*. If phosphorus, redox, and elevation were the best independent variables that could be found, these variables would become part of a logistic regression equation. The variable values of a selected plot could be used in the equation (i.e. phosphorus, redox, elevation), and the resulting dependent value would be a probability with a value between 0.00 and 1.00 (or between 0% and 100%), that would predict the presence or absence of *Spartina* in that plot. If the resulting value was between 0.00 and 0.50, the probability is that there is no *Spartina* present in that plot. On the other hand, if the probability was between 0.50 and 1.00, the probability is that *Spartina* is present in the plot. The farther the resulting probability is from the dividing line at probability equal to 0.50, the more certain that the plot would not or would contain *Spartina*. The Logistic Regression equation has the form:

$$\text{Probability}(Y \notin \text{group}) = 1 / (1 + \text{Exp}(-(\beta_0 + \beta_1 * X_1 + \beta_2 * X_2 + \beta_3 * X_3 + \ldots)))$$

The values of β_i represent the intercept and coefficients of the logistic regression equation, and the variables X_i represent the significant variables used to predict the Probability($Y \notin$ group). In this case, ‘group’ represents those plots that contain *Spartina*.

It is an arbitrary decision whether the group ‘*Spartina* Present’ ,or $Y \notin$ group, is assigned a 0 or a 1, as long as there are two groups, each group is assigned either a 0 or a 1, and the ‘*Spartina* present’ vs. ‘*Spartina* absent’ members can be distinguished with the assignment of either a 1 or a 0. In this study, the group ‘*Spartina* absent’, or $Y \notin$ group, was defined as *Spartina* abundance ≤ 0.100 (less than or equal to 10% abundance), and ‘*Spartina* present’ was defined as *Spartina* abundance > 0.100 (or greater than 10% abundance). Three other pairs of groups were defined, based on a boundary value from the abundance classification listed below. A logistic regression equation was used to separate those pairs of groups. Finally, the resulting separations for all four of these boundary values between abundance classes were used to assign each plot to a specific abundance class. The method used to make these assignments will be discussed shortly. These pairs of groups were defined to be separated at the boundaries of *Spartina* abundance = 0.100, *Spartina* abundance = 0.250, *Spartina* abundance = 0.500, and *Spartina* abundance = 0.750. This resulted in five abundance classes, as defined below:

Spartina abundance class 1: $0.000 < $ *Spartina* abundance ≤ 0.100

Spartina abundance class 2: $0.100 < $ *Spartina* abundance ≤ 0.250

Spartina abundance class 3: $0.250 < $ *Spartina* abundance ≤ 0.500

Spartina abundance class 4: $0.500 < $ *Spartina* abundance ≤ 0.750

Spartina abundance class 5: $0.750 < $ *Spartina* abundance ≤ 1.000

The most important idea in this section of the study is the classification of *Spartina* into these five abundance classes. The logistic regression equations are useful in separating the abundance classes, given the significant environmental variable data (i.e. phosphorus, elevation, and redox for a given plot in the marsh).

The logistic regression equations were each individually used to separate the plot values of *Spartina* abundance into two groups, based on a boundary value for *Spartina* abundance. This was done for each of four boundary values. The next step was to combine the results of the four logistic regression equations into a single table of predictions of *Spartina* abundance class membership (i.e. class 1, 2, 3, 4, or 5), based on the measured values of the covariates for each plot. This was done by making a table of the probability calculations of each of the logistic regression boundary equations for each of the plots, and using those probability values to assign a plot to an abundance class. For example, if the equation for the boundary at 10% *Spartina* abundance predicts that the plot will have greater than 10% abundance, then the predictions of the equation for the boundary at 25% *Spartina* abundance is examined for that plot. If the prediction at this second boundary show that *Spartina* abundance should be less than 25%, then the plot is assigned to class two, which has a *Spartina* abundance greater than 10% and less than or equal to 25%. In this way, each plot is assigned to an abundance class. The results of the predictions are compared to the actual *Spartina* abundance of the plot, and the number of errors and the percent of correct predictions are recorded in a table.

RESULTS

Univariate Analysis: correlation of environmental variables to *Spartina* percent cover

Seventeen variables were measured in the salt marsh:

- **Soil conditions** - phosphorus, redox, pH, organic content, bulk density, and salinity;
- **Location topography** – plot elevation-normalized (referred to as elevationN, from this point on), aspect, slope shape, slope position, distance to nearest ditch, depth of the ditch, slope of plot location (1 meter baseline), and slope of plot location (3 meter baseline); and
- **Plant information** – average height of *Spartina* present, each plant species present and percent cover of each species.

Another seventeen covariates were derived from these original seventeen variables, and consist of site averages, site standard deviations, and statistically significant interactions between the variables. These covariates are:

- **Interactions** - phosphorus * elevationN, redox * salinity, elevationN * distance to ditch avg., elevationN-squared, elevationN-cubed;
- **Site averages** – phosphorus site avg., redox site avg., elevationN site avg., salinity site avg., distance to ditch avg., depth of ditch avg.; and

- **Site standard deviations** – phosphorus site StDev, redox site StDev, elevationN site StDev, salinity site StDev, distance to ditch site StDev, depth of ditch site StDev.

Even though some of these site covariates are actually site statistics, they are used as a derived covariate that is constant for all the plots at a given site, but differ between sites.

A linear regression model of each of these covariates was fitted with respect to the plot percent coverage by *Spartina*, using the seven Humboldt Bay marsh sites (not including the three Mad River Slough sites). For each model, the equation, the R-squared value, and the p-value of the coefficient and intercept, were tabulated and examined to determine that covariates' usefulness in describing *Spartina* coverage (Table 1A and 1B). Covariates were sorted first by R-squared value and then by probability, from most promising to least promising in describing *Spartina* cover. Twenty useful covariates were found in this manner.

At this point, it might be good to define what some of these statistics mean. The R-squared value of a simple regression equation describes how well the variable in the equation accounts for the variability of the data. An R-squared = 1.0 says that the data can be exactly accounted for using the variable, while R-squared = 0.7 says that 70% of the variability of the data can be accounted for with the variable of the regression equation. A multiple R-squared is similar, and indicates how well a multivariate regression accounts for the variability in the data.

In non-technical terms, the P-value is the probability that a set of data points do not belong to the proposed model, and the fit of the data to the regression model is by chance alone. A P-value = 0 indicates that there is no chance that the data and the model are unrelated. Alternately, a P-value = 1.0 indicates that there is no relationship between the data and the model. So, a P-value = 0.05 indicated that it is only 5% probable that the data set is unrelated to the model. A P-value = 0.05 is the cut-off point used here, and a regression relationship with $P \leq 0.05$ is a significant relationship.

In summary, a good regression correlation has a high R-squared value and a low P-value. A poor regression correlation has a low R-squared value and a high P-value.

Of the seventeen measured (not derived) covariates, seven were statistically significant at the 95% confidence level, from most significant to least significant: phosphorus, redox, elevationN, Cosine of aspect (north-south directions), pH, percent organic content, and one of the six slope-position sub-variables, FS (or foot slope). As the significance decreased (or probability value increased), the R-squared value also decreased. The covariates with a low R-squared value were not very useful by themselves, but sometimes became very useful in combination with other covariates, and so were included.

The measured covariates that turned out to be not significant at the 95% confidence level with respect to *Spartina* cover were: the other five slope-position sub-variables, slope shape, distance to nearest ditch, depth of that ditch, Sine of aspect (east-west directions), slope of the plot (with both a 1-meter and a 3-meter baseline), salinity, and bulk density of the soil. Some of these statistically insignificant variables became significant when combined with other variables in a multivariate linear regression, suggesting that interactions were going on between the variables when they worked

Table 1A. Regression covariates significant at greater than the 95% confidence interval, measured and derived, used to describe *Spartina* coverage in marsh plots. Covariates were considered statistically significant in model calculations if they had a probability of less than or equal to 5% of being due to chance alone ($P \leq 0.05$). Covariates are sorted from most significant to least significant. The covariates were derived (D) if they represent an interaction of variables or a site variable statistic, and not derived (ND) if they were the list of plot measurements of an environmental gradient.

Variable	**R-squared**	**Probablility**	**Regression Equation**	**Derived?**
Phos * ElevN	0.4507	< 0.00005	0.0295 + 0.00883*Phos*ElevN	D
Phosphorus	0.4088	< 0.00005	-7.23 + 0.0458*Phosphorus	ND
Redox	0.2086	< 0.00005	0.457 - 0.000896*Redox	ND
Redox * Salinity	0.1994	< 0.00005	0.462 - 0.0000211*Redox*Salinity	D
ElevN * Avg Dist to Ditch	0.1226	< 0.00005	0.702 - 0.00795*ElevN*AvgDistToDitch	D
Elev Normalized StDev	0.1186	< 0.00005	0.782 - 0.763*ElevNStDev	D
ElevN, ElevNsq, ElevNcu	0.1079	0.0001	-43.627 + 20.1849*ElevN - 2.9765*ElevNsq + 0.1491*ElevNcu	ND
Dist. to Ditch Avg	0.1059	< 0.00005	0.700-0.0518*AvgDistToDitch	ND
Salinity Site StDev	0.0908	< 0.00005	0.634 - 0.296*SalinitySiteStDev	D
Dist. To Ditch StDev	0.0772	0.0001	0.753 - 0.0572*DistToDitchStDev	ND
Phosphorus Site Avg.	0.074	0.0001	0.167 + 0.0346*PhosphorusSiteAvg	D
Elev Normalized	0.0681	0.0003	1.66 - 0.187*ElevN	ND
Elev Normalized squared	0.0662	0.0003	1.04 - 0.0139*ElevNsq	ND
Elev Normalized cubed	0.0629	0.0005	0.882 - 0.00134*ElevNcu	ND
Cosine(Aspect)	0.0491	0.0021	0.435 + 0.122*Cos(Aspect)	ND
Salinity Site Avg	0.0475	0.0025	-0.546 + 0.0238*SalinitySiteAvg	D
pH	0.0331	0.0120	-0.640 + 0.181*pH	ND
Organic Content (percent)	0.0306	0.0158	0.578 - 0.00107*OrgContent	ND
Redox Site Avg	0.0267	0.0242	0.462 - 0.00121*RedoxSiteAvg	D
Slope Position FS	0.0088	0.0477	0.5600 - 0.1784*FS (catagorical variable)	ND
Elev Normalized Avg	0.0206	0.0483	1.74 - 0.198*AvgElevN	D

Table 1B. Covariates not significant at the 95% confidence level.

Variable	R-squared	Probablility	Regression Equation	Derived?
Depth of Ditch Avg	0.016	0.0816	NS (not significant at the 95% confidence level)	D
Phosphorus Site StDev	0.015	0.0921	NS	D
Slope Position SH	0.0036	0.1205	NS	ND
Slope Position PL	0	0.1974	NS	ND
Dist. To Ditch	0.0068	0.2574	NS	ND
Slope Position BS	0	0.2679	NS	ND
Slope 1 meter	0.0053	0.3193	NS	ND
Slope Position DP	0.0011	0.3958	NS	ND
Depth of Ditch StDev	0.0035	0.4169	NS	D
Salinity	0.0031	0.4468	NS	ND
Redox Site StDev	0.0025	0.4931	NS	D
Vertical Slope Linear	0.0068	0.5457	NS	ND
Depth of Ditch	0.0008	0.6979	NS	ND
Vertical Slope Concave	0.0002	0.7869	NS	ND
Sine(Aspect)	0.0001	0.8747	NS	ND
Bulk Density	0.0001	0.8876	NS	ND
Slope Position DR	0.002	0.901	NS	ND
Slope 3 meter	0	0.9272	NS	ND
Horizontal Slope Convex	0.0094	1.0000	NS	ND
Vertical Slope Convex	0.0061	1.0000	NS	ND
Horizontal Slope Linear	0.0048	1.0000	NS	ND
Horizontal Slope Concave	0.0013	1.0000	NS	ND

together. For example, the variable, ‘slope at 1 meter’ interacted with the derived variable, ‘phosphorus site standard deviation’ in this way, causing both to become statistically significant.

Descriptive models using phosphorus, redox,
and elevationN for the marsh sites.

Multivariate linear regression for each of the 10 sites

A descriptive model for each of the ten sites around Humboldt Bay was developed to describe *Spartina* abundance, with respect to the most consistently useful variables. The variables that proved the most consistently significant in various modeling experiments were phosphorus, redox, and elevationN. ElevationN has a small R-squared value when used by itself, but it was important when used in combination with other covariates. A multivariate linear regression was run using phosphorus, redox, and elevationN to describe the *Spartina* abundance, at each site. For each of the ten sites, the intercept and the coefficients of the variables are indicated in Table 2.

Table 2. Intercept and coefficients of ten linear regression models that describe the abundance of *Spartina densiflora* with respect to the environmental gradients of available phosphorus, redox potential, and elevation-normalized.

		Coefficient Estimates		
site	Intercept	phosphorus	redox	elevationN
1	-2.6198307	0.05126060	-0.00001795	0.41066987
2	-2.5731896	0.05660038	-0.00062764	0.41050619
3	-1.9168501	0.06433906	-0.00039895	0.28114104
4	0.6825323	0.02865770	-0.00037858	-0.09188483
5	-1.2023950	0.03310614	-0.00050879	0.18646526
6	-0.0739053	0.05713280	-0.00034651	0.01164249
7	-2.2589312	0.06264749	-0.00034208	0.37701446
8	1.6713249	0.01749721	-0.00043253	-0.25180732
9	0.7273010	0.02781819	-0.00030997	-0.10206473
10	-0.6158578	-0.01317392	-0.00087817	0.12751150

For example, site 1 has the fitted regression equation:

Spartina cover = -2.62 + 0.0513*phosphorus – 0.0000180*redox

+ 0.411*elevationN.

The intercept and coefficients are rounded in this equation. These regression equations are descriptive for each site.

In the following discussions, sites 1-7 are combined into descriptive models of *Spartina* abundance. For the following discussions, sites 8-10 are used to test and validate the models, and are not used to construct the models.

Multivariate linear regression for 7 sites around Humboldt Bay

A multivariate linear regression was run, using phosphorus, redox, and elevationN as the independent variables, to describe the *Spartina* abundance when the data for the seven Humboldt Bay sites were pooled. The resulting equation combines the site data which describes the first 7 sites (Table 2). This equation will be used as written below in the Residual Sum model. It will also be used in the Dummy Variable and *A Priori* models, in slightly altered form (Table 3).

Spartina abundance = -1.7747 + 0.0571*phosphorus – 0.000352*redox

+ 0.271*elevationN.

Mixed-effects model

The variables phosphorus, redox, and elevationN were run in a Mixed-effects modeling procedure, to find the coefficients of the variables. Data for sites 1-7 were combined

Table 3. The intercept and coefficient for the multiple linear regression formula for *Spartina* abundance, using the environmental gradients of phosphorus, redox, and elevationN.

Linear Model for Sites 1-7				
Coefficients:				
site	Intercept	phosphorus	redox	elevationN
1-7	-1.7747	0.0571	-0.0004	0.271

Residual standard error: 0.2764 on 186 degrees of freedom
Multiple R-Squared: 0.4935
F-statistic: 60.4 on 3 and 186 degrees of freedom, the p-value is 0
Linear model shown in Table 3 was derived using S-Plus, 2000

carry out the modeling. As described in the Materials and Methods section, an average is found for the intercept and the coefficients, which is the "fixed effects" part of the model. The variation of the intercept and coefficients of the variables from this average value, at each site, are the "random effects" of the model. This variation, when added onto the average values or fixed effects values, results in the intercept and coefficients of the variables, or mixed effects values, for each site. The mixed effects coefficients are listed in Table 4, below. These coefficients are slightly different than the values calculated for the multivariate linear regression model, in the previous two tables. The mixed effects model coefficients are modified or shrunk, so that they are closer to the average coefficient or fixed effect value, than the coefficients of the individual site multivariate linear regression models are to their mean coefficient value.

Table 4. Intercept and coefficients of the mixed-effects models that describe *Spartina* abundance to the environmental gradients of phosphorus, redox, and elevationN, for the ten salt marsh sites used in this study.

	Coefficients			
site	Intercept	Phosphorus	Redox	Elevation-normalized
1	0.89999111	0.02251346	2.71E-05	0.312285621
2	-0.03267278	0.03916281	4.71E-05	0.455247865
3	1.19510646	0.02503849	3.01E-05	0.267029828
4	2.28257741	0.01076356	1.29E-05	0.100347194
5	1.52873542	0.01427927	1.72E-05	0.21589259
6	1.16596047	0.02796001	3.35E-05	0.271505728
7	-1.16453923	0.05377913	6.46E-05	0.628758055
8	3.4722066	-0.0061982	-7.46E-06	-0.081998827
9	2.70954393	0.00481576	5.77E-06	0.034917246
10	2.62940151	-0.00028063	-2.65E-07	0.047191749

Developing a Multivariate Linear Regression Model which describes *Spartina* abundance in Sites 1-7

Stepwise Variable Selection

The stepwise variable selection routine in the statistical package, NCSS (Hintze 2003), was used to model the seven Humboldt Bay sites. All of the significant variables and covariates were used as candidate covariates in the variable selection routine, to describe and predict the abundance of *Spartina densiflora*. Seven covariates were chosen: elevationN, average elevationN, phosphorus, phosphorus * elevationN (an interaction), redox site StDev, depth of nearest ditch, depth of nearest ditch site StDev, and distance to ditch site average. The regression model equation, and a bar graph (Figure 4) comparing the actual *Spartina* abundance with the predicted *Spartina* abundance for the 3 Mad River slough sites are shown below.

SPDE % cover = - 5.92 + 0.0108*phos.*elevN + 0.683*AvgElevN

- 0.0980*AvgDistToDitch + 1.11*StDevDepthDitch

+ 0.00420*RedoxSiteStDev + 0.102*ElevN

+ 0.109*DepthOfDitch.

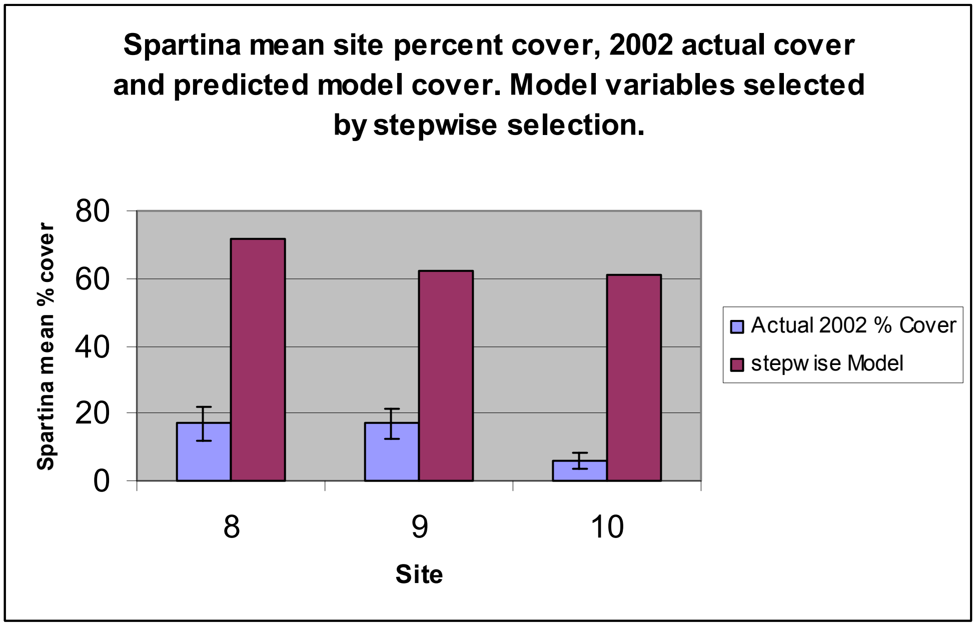


Figure 4. Bar graph comparing mean actual *Spartina* % cover to the mean predicted *Spartina* % cover in sites 8-10. The model is built using stepwise selection of variables. Error bars represent Standard Error of site sample data.

When the Stepwise selection model (constructed using the data from Sites 1-7) was used to predict *Spartina* abundance for Sites 8-10 on the Mad River Slough, the model predictions did not match the *Spartina* abundance well (Figure 4, above).

<u>*A Priori* variable selection</u>

The second method of variable selection was the *A Priori* method (Burnham and Anderson 1998), in which all the variables which might consistently correlate to *Spartina* abundance were considered. For example, the marsh sites that were very flat had a high abundance of *Spartina*, while those marsh sites that had a nice elevation gradient had large meadows that contained little or no *Spartina*. The problem was how to capture this affect, test it for significance, and incorporate it in the model. The standard deviation of the elevations of the plots in a marsh site should reflect this correlation of *Spartina* abundance to site flatness. Since there was no way to measure the flatness of a site directly, this was used as an indicator of site flatness. The standard deviation of elevation of each site became a site constant, and the collection of site constants were incorporated into the variable, 'Elev Normalized St Dev'. This variable had an R-squared of 0.1186 and a p-value < 0.0001. The variables that intuitively seemed to be predictors of *Spartina* abundance were gathered and incorporated into models. Several models were created this way (Table 5). The equation and bar graph (Figure 5) of one such model is as follows:

$$\text{SPDE \% cover} = -1.81 + 0.232*\text{ElevN} + 0.0562*\text{phos.} - 0.0522*\text{AvgPhos.} - 0.0004*\text{redox} + 0.0068*\text{RedoxSiteStDev} - 1.29*\text{ElevNStDev};$$

with R-squared = 0.6089.

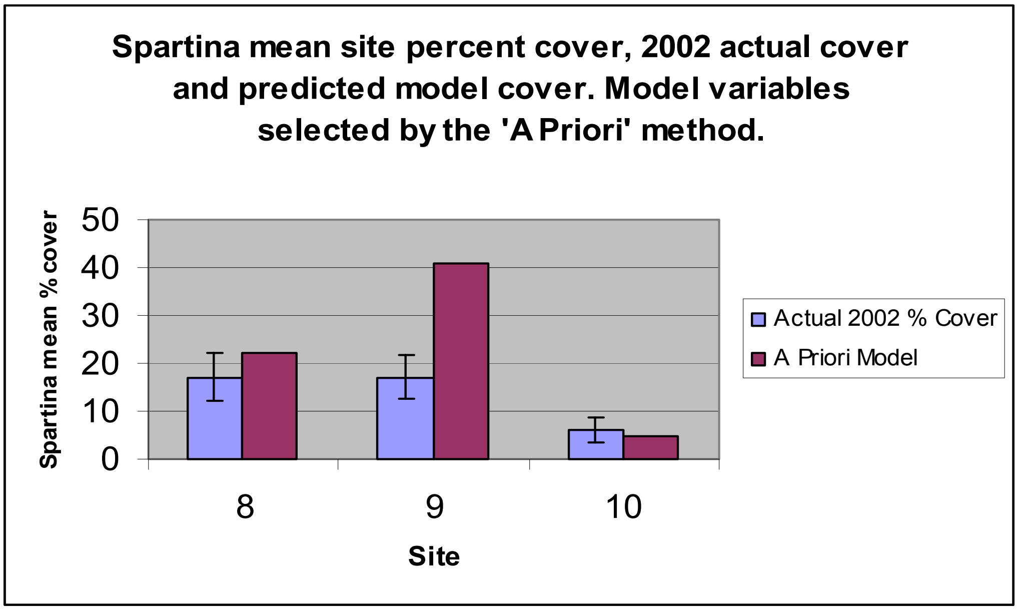


Figure 5. Bar graph comparing mean actual *Spartina* % cover to the mean predicted *Spartina* % cover in Sites 8-10. The model is built using *A Priori* selection of variables. Error bars represent Standard Error of plot sample data. Error bars are not used with the model sample data, but should be the same size as the error bars of the plot sample data.

The model (constructed from Sites 1-7) successfully predicted the average *Spartina* abundance at Site 8 and 10, but not at Site 9 (Figure 5 and Table 6). Hence, the *A Priori* model matched two of the three Mad River Slough sites.

Table 5. Listed are the first ten models developed using the *A Priori* strategy of model selection. The table lists the covariates used in each model. The calculated coefficients and intercepts are not listed, but are available from the author. Note that the table is extended into two tables, in order to list all the covariates used in these ten models.

Variables and Covariates used in models								
Model	ElevN	StDev ElevN	AvgElevN	ElevN^2	ElevN^3	Phos.	PhosAvg.	Redox
1	X	X				X	X	X
2	X	X				X	X	X
3		X		X	X	X	X	X
4	X					X		
5	X	X	X			X		X
6	X	X	X			X		X
7	X	X	X			X		
8	X	X	X			X		X
9	X			X		X		X
10	X					X		X

Model	StDev Redox	Redox Avg	Redox Transformed	AvgDist to Ditch	Depth of Ditch	R^2	P-Value
1	X					0.61	< 0.00005
2	X			X		0.63	< 0.00005
3		X				0.60	< 0.00005
4			X			0.61	< 0.00005
5	X			X		0.63	< 0.00005
6						0.57	< 0.00005
7	X					0.63	< 0.00005
8	X				X	0.64	< 0.00005
9						0.52	< 0.00005
10						0.49	< 0.00005

Table 6. Listed are the first ten *A Priori* model predictions of average *Spartina* site abundance. Model number 1 was the *A Priori* model selected for this study. The last row of abundance values are for actual measured *Spartina* abundance, to be used for comparison with model prediction values.

Model I.D.	Site 8	Site 9	Site 10
1	0.22	0.41	0.05
2	-0.11	0.23	-0.26
3	0.23	0.42	0.01
4	0.14	0.18	0.22
5	0.06	0.42	0.14
6	0.09	0.42	0.24
7	-0.001	0.43	0.27
8	0.07	0.42	0.21
9	0.24	0.32	0.51
10	0.34	0.33	0.41
Actual *Spartina* abundance	0.17	0.17	0.06

The Dummy Variable approach to variable selection

The third method of variable selection, an *ad hoc* approach, was to start by selecting the most consistently significant variables: phosphorus, redox, and elevationN, and to add a categorical variable called ‘site’. These three significant variables were discussed in the Results sub-section, ‘Multivariate linear regression for 7 sites around Humboldt Bay’, and used to describe the overall *Spartina* abundance in Humboldt Bay. The categorical variable, “site”, was constructed using dummy variables, as described in the methods section. The full model equation is as follows:

Spartina coverage = β_1*phosphorus + β_2*redox + β_3*elevationN

+ β_4*site1(0 or 1) + β_5*site2(0 or 1) + β_6*site3(0 or 1)

+ β_7*site4(0 or 1) + β_8*site5(0 or 1) + β_9*site6(0 or 1),

where the β_i are coefficients chosen by the multivariate regression routine.

The dummy site variables were represented by a constant at a given site, and a zero value at the remaining six sites. The six site constants, with a zero value for site seven, were combined into a single covariate, called ‘site’. The covariate ‘site’ was then used as the dependent variable in a multivariate linear regression, using all of the remaining variables as independent variables, to see if there were any sets of variables which could be used to predict the covariate, ‘site’. Additional derived site covariates were also used in the modeling process. The equation of the fitted model constructed in this manner was as follows:

SPDE % cover = -5.77 + 0.572*AvgElevN + 0.198*ElevN + 0.0546*phos.

- 0.000331*redox + 0.00660*RedoxSiteStDev

- 1.11*ElevNStDev

When the model predictions were examined for Sites 8, 9, and 10, and compared with the actual *Spartina* abundance found at these sites, the model predictions did not match the actual abundance (Figure 6).

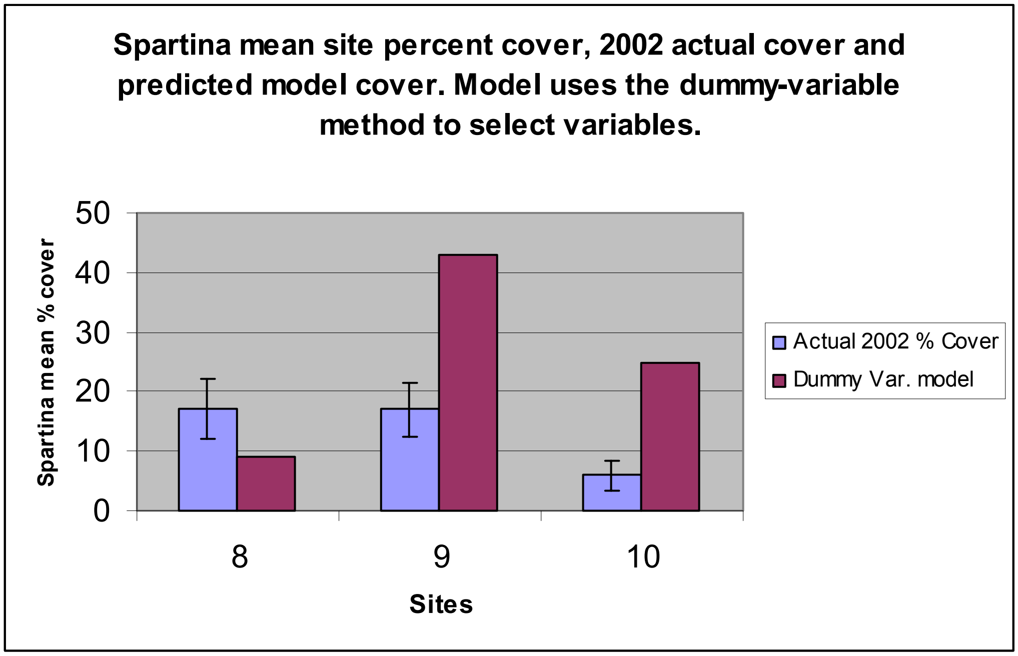


Figure 6. Bar graph comparing mean actual *Spartina* % cover to mean predicted *Spartina* % cover in sites 8-10. The model is built using the site-constant method of variable selection. Error bars represent the standard error of the plot sampling data. Error bars are not used with the model sample data, but should be the same size as the error bars of the plot sample data.

<u>Residual Sum method of variable selection</u>

This fourth method of variable selection is a modification of the Dummy Variable method, and results in a model similar to the *A Priori* model. The general strategy of this method was described in the Materials and Methods section, and is discussed in further detail here. This method starts with the three significant variables - phosphorus, redox, and elevationN. These variables are used to construct a multivariate regression base model of *Spartina* abundance. The intercept and coefficients of these variables are the same ones selected to describe the *Spartina* abundance in the seven pooled sites around Humboldt Bay, and are listed below in Table 7.

Three variables were found which would predict the difference between the site averages predicted by the *Spartina* base model, and the actual site averages of *Spartina* abundance. These variables were elevationN site StDev, redox site StDev, and phosphorus site average, the same variables identified in the '*A Priori*' method of variable selection.

Table 7. The intercept and coefficients for the linear model describing *Spartina* abundance, using the environmental gradients phosphorus, redox, and elevation-normalized.

Linear Model for Sites 1-7				
Coefficients:				
site	Intercept	phosphorus	redox	elevationN
1-7	-1.7747	0.0571	-0.0004	0.271

These six variables were used a little differently than they were in the *A Priori* model. In the *A Priori* model, all six variables were run together in the multivariate linear regression to predict *Spartina* abundance. In this case, the phosphorus, redox, and elevationN are used to create a base model for predicting *Spartina* abundance. A second model is created to predict the Residual Difference The two models are used separately to create two separate values for each plot. The first value represents the general effect of phosphorus, redox, and elevationN on *Spartina* abundance. The second value represents positive or negative site effects on *Spartina* abundance. When the two values are added together, they should predict *Spartina* abundance and account for site differences. This equation is slightly different than the equation created for the *A Priori* model, and results in slightly different predictions for mean *Spartina* site abundance.

The Residual Sum equation and a bar graph (Figure 7) of the results are shown below. The *A Priori* equation is included for comparison .

Residual Sum Equation:

SPDE % cover = - 2.1051 + 0.271*ElevN + 0.0571*phos. – 0.0493*AvgPhos.
- 0.000352*redox + 0.00676*RedoxSiteStDev
– 1.28*ElevNStDev;

A Priori Equation:

SPDE % cover = -1.81 + 0.232*ElevN + 0.0562*phos. – 0.0522*AvgPhos.
– 0.0004*redox + 0.00680*RedoxSiteStDev
– 1.29*ElevNStDev;

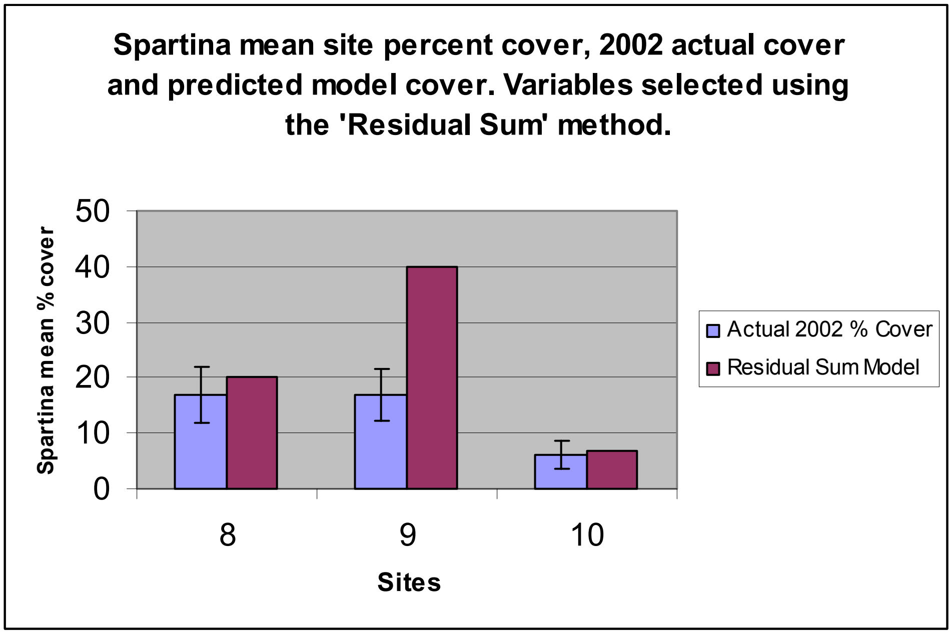


Figure 7. Bar graph comparing mean actual *Spartina* % cover to the mean predicted Spartina % cover for sites 8-10. The model is built using Residual Sum method of variable selection. Error bars represent the standard error of the plot sampling data. Error bars are not used with the model sample data, but should be the same size as the error bars of the plot sample data.

The model predictions of the Residual Sum method were compared to the actual S*partina* abundance found at Sites 8, 9, and 10 in the Mad River Slough. The model matched the site abundance for Sites 8 and 10, but did not match the site abundance for Site 9.

Summary of actual mean site *Spartina* abundance and model site predictions

Table 8 and Figure 8 show a summary of actual *Sparina* abundance and the model predictions for site average *Spartina* abundance, using all four strategies of variable selection – Stepwise variable selection, *A Priori* variable selection, the Dummy Variable selection, and the Residual Sum variable selection.

Table 8. Site averages for *Spartina* cover. The actual cover at Sites 8-10 is listed, followed by the model predictions for each of the four models described in the Results section – the Stepwise, *A Priori*, Site Constant, and Residual Sum models.

site	Actual 2002 % Cover	Stepwise Model	*A Priori* Model	Site Const. Model	Residual Sum Model
8	17	72	22	9	20
9	17	62	41	43	40
10	6	61	5	25	7

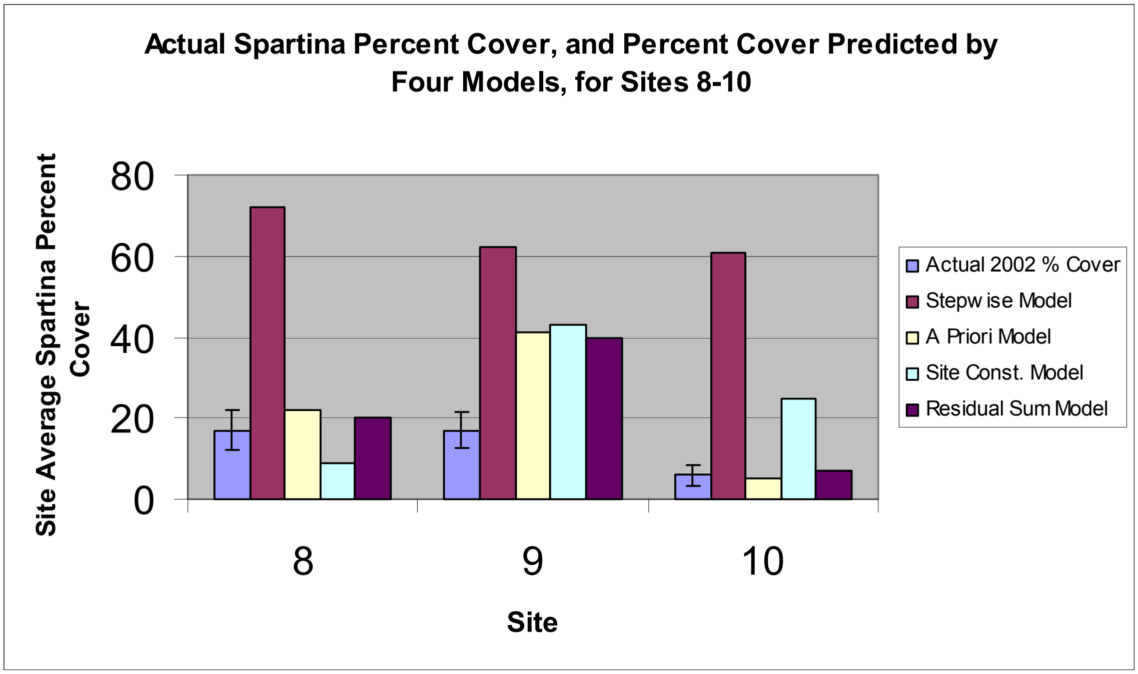


Figure 8. Site averages for *Spartina* cover in sites 8-10. The actual cover at each site in 2002 is shown as the left bar in each grouping, followed by the model predictions for each of the four models described in the Results section, developed using the Stepwise, *A Priori*, Site Constant, and Residual Sum strategies of variable selection. Each model was built using the data for Sites 1-7, and is estimating what *Spartina* abundance should be at Sites 8-10. Error bars represent the standard error of the plot sampling data. Error bars are not used with the model sample data.

Actual variable values for five *Spartina* abundance classes

Spartina plots were classified into five *Spartina* abundance classes, and the average value for each variable used in the modeling was tabulated with that abundance class. The purpose for doing this was to show the real and measurable changes in the environmental characteristics of the salt marsh that determined the abundance of *Spartina*.

A qualification is necessary. The elevation values in the table of *Spartina* abundance classes represent the average elevationN of all the plots that are included in that abundance class. So, abundance class 1 is an average of the plots at low elevations and high elevations that had contained almost no *Spartina*. ElevationN for Class 1 does not actually represent the elevation where plots without *Spartina* will be found. The elevationN value for abundance class 5 is probably most representative of the true elevationN where the highest abundance of *Spartina* will be found. The remaining variable values, for redox, phosphorus, standard deviation of elevationN, and average distance to ditch are pretty close to what will be found in the field for a given abundance class.

Table 9 shows that as the abundance of *Spartina* in a plot increases, the redox value will decrease, the amount of available phosphorus will increase, and the average distance to the nearest drainage channels will decrease. It also show that sites with a large amount of *Spartina* were also relatively flat while sites with little *Spartina* usually had a large elevation gradient, as indicated by the variable StDevElevN.

Table 9. The five *Spartina* abundance classes, and the important variable averages for each abundance class. These are actual values, and are included to give a sense of how *Spartina* abundance changes along these environmental gradients.

Mean variable values, by SPDE abundance class						
SPDE abundance class	SPDE	ElevN	Redox	Phos.	StDev ElevN	AvgDist ToDitch
Class 1: 0.000-0.100	0.024	6.63	116.9	4.21	0.530	19.78
Class 2: 0.101-0.250	0.189	6.68	66.9	5.52	0.453	15.91
Class 3: 0.251-0.500	0.400	6.41	12.2	8.9	0.418	15.88
Class 4: 0.501-0.750	0.650	6.57	-5.8	9.4	0.352	13.58
Class 5: 0.751-1.000	0.924	6.33	-103.6	12.01	0.395	13.68
Overall	0.442	6.52	16.02	7.97	0.445	16.27

Logistic Regression

Logistic Regression was used to calculate equations to separate *Spartina* abundance into five abundance classes, using the covariates phosphorus, redox, elevationN, site average phosphorus, site standard deviation of elevationN, and site standard deviation of redox. Four equations were used to separate the five abundance classes. Each equation was used to separate *Spartina* abundance into two groups at a boundary value of *Spartina* abundance. For example, the first logistic regression equation makes the separation at 0.10 or 10% *Spartina* abundance, and separates the plots with 10% or less abundance from those plots with more than 10% abundance. The percent of all plots that are correctly separated into two groups using each equation is listed in the last column, and ranges from 81% to 86% (Table 10).

Next, the probabilities calculated for each of the four logistic equations were combined into a single table. Using this table, each plot was assigned to a probable *Spartina* abundance class (see materials and methods). This predicted class membership was compared to the actual class membership, and the accuracies of the predictions were tabulated (table 11 and 12). The predictions for Class 1 *Spartina* abundance and Class 5 *Spartina* abundance were fairly high, at 77% and 62% respectively. The predictions for classes 2, 3, and 4 were poor, at 6%, 21%, and 36% respectively. Overall, separation of the plots into five abundance classes using the logistic regression equations had an accuracy of 54%.

Spartina abundance predictions were then recombined into three abundance classes, from 0 - 10%, 10.1 - 75%, and 75.1 - 100%. Classes 2, 3, and 4 were combined into a single class, which resulted in an accuracy of 59% for this combined class. Overall, separation of the plots into three abundance classes using the logistic regression equations had an accuracy of 66% (Table 11 and 12).

Table 10. Logistic regression equation coefficients used to separate the five *Spartina* abundance classes (see Table 9). Each of these equations represents the boundary separation between two classes. All those classes smaller than the boundary *Spartina* abundance value were given a binomial value of 0 and all of those classes larger than the boundary value were given a binomial value of 1. The percent of plots successfully separated into two classes using each logistical regression equation is listed in the last column on the right.

Boundary value of *Spartina* abundance	Intercept	ElevN	Phos.	Phos. Avg	Redox	Redox StDev	StDev ElevN	Percent Correct
10%	26.1282	-3.4291	-0.4665	0.0731	0.0063	-0.0324	9.1039	85.26%
25%	18.8729	-2.1602	-0.4754	0.3539	0.0042	-0.0448	10.8626	81.58%
50%	22.0958	-2.4117	-0.4468	0.5179	0.0042	-0.0640	13.0041	85.79%
75%	17.5054	-1.5331	-0.3725	0.5053	0.0031	-0.0616	10.3210	80.53%

Table 11. The abundance classes in the left column, with the number of plots found in that abundance class (Plot Count), based on collected field data of *Spartina* percent cover. The plots from each abundance class were then reclassified by using logistic regression to predict what abundance class each plot should belong to, based on the values of the covariates measured for each plot. The predicted class membership is listed to the left of the actual class membership. The percent correctly predicted is listed at the bottom of each predicted abundance class.

Actual Abundance Class		Predicted Abundance Class				
SPDE abundance class	Plot Count	Class 1	Class 2	Class 3	Class 4	Class 5
Class 1: 0-10%	67	52	7	5	3	0
Class 2: 10.1-25%	16	7	1	4	3	1
Class 3: 25.1-50%	24	4	7	5	3	5
Class 4: 50.1-75%	25	1	2	4	9	9
Class 5: 75.1-100%	58	1	2	3	16	36
Percent Correctly Predicted		77.60%	6.30%	20.80%	36.00%	62.10%

Table 12. The two following tables summarize the results of using logistic regression to precict *Spartina* abundance class membership. The column Plot Count shows the number of plots that actually belonged to the abundance class. The column Error shows the number of plots that were misclassified using the logistic regression equations. The last column shows the percent of plots correctly classified. Table (a) separates the predictions into five abundance classes. Table (b) combines abundance classes 2, 3, and 4 into a single abundance class, resulting in three abundance classes.

a)

SPDE abundance Class	Plot Count	Error	% Correct
Class 1: 0-10%	67	15	77.60%
Class 2: 10.1-25%	16	15	6.30%
Class 3: 25.1-50%	24	19	20.80%
Class 4: 50.1-75%	25	16	36.00%
Class 5: 75.1-100%	58	22	62.10%
Total of All Classes	190	87	54.00%

b)

SPDE abundance class	Plot Count	Error	% Correct
Class 1: 0-10%	67	15	77.60%
Class 2-4: 10.1-75%	65	27	58.50%
Class 5: 75.1-100%	58	22	62.10%
Total of All Classes	190	64	66.32%

DISCUSSION

Each plot at all ten sites, those around Humboldt Bay as well as those in the Mad River Slough, were measured for seventeen characteristics that became variables in the multivariate regression. Another seventeen covariates were derived from the original seventeen variables, and represent interactions between variables, site averages, or site standard deviations of measured variables. Three variables proved to be consistently useful in modeling the percent cover of *Spartina* in the plots at the seven Humboldt Bay marsh sites, in the initial stages of model building. Those variables were phosphorus, redox, and elevation-normalized.

The null hypothesis, that there was no relation between *Spartina* abundance and environmental factors, was rejected with p-value < 0.0001 (NCSS, ANOVA test for significance of the F-value of the model). The final model had an R-squared = 0.6089 and an adjusted R-squared = 0.5961. Many models were constructed (Table 5) and some had a higher R-squared value, but the models with the highest R-squared values also over-fit the data. The over-fit models usually predicted average site *Spartina* abundance in the Mad River sites with values less than 0.00, or greater than 1.00 – that is, less than 0% or greater than 100%. The three measured plot variables – phosphorus, redox, and elevation normalized – when used alone, gave reasonable plot and site *Spartina* abundance values at the seven Humboldt Bay sites used to build the models. But these three variables predicted more than twice the *Spartina* abundance at the three Mad River Slough sites than was the case. The three additional site variables – phoshorus site average, redox site standard deviation, and elevationN site standard deviation – were selected and added to the model because they resulted in reasonable average abundance values for two of the three Mad River Slough sites.

It is important to point out that many of the measured variables proved to be of little or no significance in modeling the presence and percent cover of *Spartina*. The variables that measured the topography of the immediate plot location – slope position, slope shape, slope angle to the horizon – had no correlation to *Spartina* percent cover, even though other variables that measured more general topographic characteristics, such as elevation and standard deviation of site elevation, did correlate with the presence of *Spartina*. This suggests that either those immediate topographic factors were unimportant to the presence of *Spartina*, or the way these topographic factors were defined and measured did not capture their effects on *Spartina* abundance. The slope shape and position were roughly defined using the definitions from the Soil Survey Staff of the U.S.D.A. Soil Conservation Service (National Soil Survey Center 2002). The topography of the salt marsh is different than the topography of normal terrestrial landscapes. The soil forming processes are also slightly different, so the topography and soil processes may need to be examined and more useful definitions created.

Some variables were marginally useful in predicting *Spartina* cover. Newby (1980) stated that the presence of *Spartina* seemed dependent on a nearby source of tidal waters, carrying phosphorus laden clay particles. The distance to the nearest drainage channel and the depth of that channel were significant, though not useful in constructing the model. *Spartina* does grow especially well on the edge of drainage channels. This study did not capture that effect very well, as very few plots were located on the edge of a drainage channel. The salinity of the soil was not useful in predicting *Spartina* percent cover, but it was significant in predicting the average height of *Spartina* in a plot. Kittleson (1993) noticed this effect. Bulk density and soil organic content were not useful in predicting *Spartina* cover, but they were useful in predicting the presence of other species in the salt marsh. These variables could be significant in other contexts, such as planning the topography of restored marshes so as to encourage other marsh plant species.

Validity of the models based on descriptive statistics

The model Results sections, for the Stepwise model, the *A Priori* model, the Dummy Variable model, and the Residual Sum model, each ended with a descriptive comparison of *Spartina* abundance predicted by the model to the *Spartina* abundance actually found at Sites 8-10 (see Figure 8). Table 13 summarizes these results.

Table 13 shows that the Stepwise model and the Dummy Variable model predictions did not match the actual *Spartina* site abundances at any of Sites 8-10. The table also shows that the *A Priori* model and the Residual Sum model were able to accurately predict the current *Spartina* abundance for Sites 8 and 10, while they both were unable to predict the abundance at Site 9. Based on a purely descriptive comparison, the *A Priori* model and the Residual Sum model were the best fitting models on the test Sites 8-10.

Table 13. This table shows whether each model correctly predicted the *Spartina* abundance that was found to occur at Sites 8, 9, or 10 in 2003, and summarizes the number of correct matches in the last column of the table.

Site	8	9	10	Correct matches
Stepwise model	no	No	no	0 of 3
A Priori model	yes	No	yes	2 of 3
Dummy Var. model	no	No	no	0 of 3
Resid. Sum model	yes	No	yes	2 of 3

Validity of the Models

Validity of the *A Priori* Model

Only two of the four models gave reasonable results for sites 8 and 10 in the Mad River Slough (Table 8 and Figure 9). The best models of *Spartina* abundance are the *A Priori* model and the Residual Sum model. Both models have very similar results, but the *A Priori* model has an easily calculated R-squared value, so it will be the model which is discussed first. The *A Priori* model has an R-squared value equal to 0.6081. The intercept and the coefficients of phosphorus, elevation-normalized, phosphorus site average, redox site standard deviation, and elevation site standard deviation all had a p-value less than 0.0001. The coefficient of redox had a p-value equal to 0.0035. An Analysis of Variance of the model reported the probability of the F-test had a p-value less than 0.0001.

The validity of the *A Priori* model in predicting the *Spartina* abundance at the three Mad River Slough sites is uncertain. Sites 8-10 were used as the validation sites to select the best *A Priori* model describing *Spartina* abundance. The model adequately predicts *Spartina* abundance at only Sites 8 and 10 (Table 8 and Figure 5).

Validity of the Residual Sum Model

The approach of the descriptive model is to find the best population coefficients for the most robust variables: phosphorus, redox, and elevation-normalized. These three variables were combined using multivariate linear regression, into the basic phosphorus-redox-elevation regression equation. The coefficients of these variables represent the influence that each of these environmental variables, when combined with the other two variables, has on *Spartina* abundance throughout the Humboldt Bay region, including the Mad River Slough. This model approximately describes the *Spartina* abundance in the Humboldt Bay region, but does not account for site specific differences that raise or lower the average *Spartina* abundance at a site.

The first attempt to account for these site differences was to use the Dummy Variable method, which adds or subtracts a constant to the basic phosphorus-redox-elevationN regression equation, for the seven Humboldt Bay sites. The next step was to find variables that spanned all ten sites and mimicked the site constant values for the seven Humboldt Bay sites. It was hoped that the new site constant variables would match and substitute for the site constants at the seven Humboldt Bay sites, and also accurately predict what the site constants would be at the remaining three Mad River Slough sites. A model was developed by this method, and the predictions of the Dummy Variable model are listed in Table 14.

Table 14. *Spartina* mean site cover for sites 8-10 used in this study, and mean predicted site values using the Dummy Variable Model. The actual cover was measured in 2002, and is an average of all plots measured at each site. The Dummy Variable Model was used to calculate the *Spartina* abundance for each plot at a site, and an average of all the plots at each site is presented in the table.

Site	Actual 2002 mean *Spartina* abundance	Dummy Variable Model
8	0.17	0.09
9	0.17	0.43
10	0.06	0.25

The second attempt to account for the site specific differences in *Spartina* abundance, for the basic phosphorus-redox-elevationN model, was to look at the difference between the *Spartina* abundance predicted for each plot in a marsh site, using the basic phosphorus-redox-elevationN model, and the actual *Spartina* abundance measured at each plot. This difference was listed in a new variable called ‘Residual Difference’. The Residual Difference, when averaged for a site, should produce the site constant discussed in the Dummy Variable method. A linear regression was calculated using Residual Difference as the dependent variable, and all the other variables as independent variables. The Stepwise Variable Selection method and the All Possible Variable Selection method were both used to find the variables to predict the Residual Difference for the seven Humboldt Bay sites. The equation that was found to predict the Residual Difference will be referred to as the Residual Difference Model. The variables chosen, phosphorus site average, redox site StDev, and elevationN StDev, were the same variables found using the *A Priori* method. These variables were combined in a multivariate linear regression equation, to predict the Residual Difference variable. Remember, the Residual Difference also represents the differences in average *Spartina* site abundance from the basic phosphorus-redox-elevationN model, due to site differences.

Two values were calculated for each site. The first value was calculated using the basic phosphorus-redox-elevationN model, and the result represents the average *Spartina* abundance for that site, due to the regional effects of phosphorus, redox, and elevation on *Spartina* abundance. The second value was calculated using Residual Difference Model, and represents changes from the basic model, due to site differences. These two values for each site are listed below (Table 15), as ‘Basic Model’ and ‘Residual Difference Model’. When these two values are added together, they equal the ‘Residual Sum Model’. The last three columns of the table list the values of the site variables that, when added together, make up the ‘Residual Difference Model’.

These last three variable columns in the table, containing Phosphorus Avg., Redox StDev., and ElevationN StDev., were included to show their influence on average *Spartina* site abundance, especially in the Mad River Slough. The affect of the average phosphorus in the Mad River Slough was not very influential on *Spartina* abundance. The phosphorus average was approximately the same at the three Mad River Slough sites, though the model predicted large differences in *Spartina* abundance between the three sites.

The affect of ElevationN StDev, or change in elevation at a site, had a larger influence on *Spartina* abundance than Phosphorus Average. Since the affect of ElevationN StDev was a negative one on *Spartina* site abundance, this would suggest that a site with a large elevation gradient would have decreased proportion of that marsh site covered with *Spartina*.

The most important of the three site variables was Redox StDev. A site with a large Redox StDev also had a larger proportion of plots with very saturated soils. *Spartina* generally does better in saturated soils than in unsaturated soils, so those sites with a large Redox StDev also have a greater abundance of *Spartina*. The model predicts site nine, with the largest Redox StDev, will also eventually have the highest abundance of *Spartina*.

Table 15. The 2002 actual mean *Spartina* abundance, and the results of the Residual Sum Model. The Residual Sum Model is made up of two sub-models, the Basic Model and the Residual Difference Model. The Basic Model estimates *Spartina* abundance using the environmental gradients phosphorus, redox potential, and elevation-normalized, for the Humboldt Bay region. The Residual Difference model adds or subtracts a constant to the Basic Model, to account for site differences. The three columns, Phosphorus Avg, Redox St Dev, and ElevN St Dev, list the variable values that are summed to create the Residual Difference Model, listed in the last column.

Site	Actual 2002 *Spartina* abundance	Residual Sum Model	Basic Model, first part of Residual Sum Model	Residual Difference Model, second part of Residual Sum Model	Phos Avg., component of Residual Difference Model	RedoxStDev, component of Residual Difference Model	ElevNStDev, component of Residual Difference Model
8	0.17	0.20	0.34	-0.14	-0.25	1.10	-0.65
9	0.17	0.40	0.33	0.07	-0.24	1.54	-0.90
10	0.06	0.07	0.41	-0.34	-0.28	0.82	-0.54

An important question is: when looking at the Residual Sum Model, are the results of the two sub-models reasonable? The results of the Basic Model show reasonable *Spartina* abundance values, when compared to the Actual 2002 abundance values. The average actual *Spartina* 2002 abundance for the seven Humboldt Bay sites is 0.443, or 44.3% cover in the measured plots. The Basic model averaged over the seven Humboldt bay sites, without site differences, predicts 44.2% cover. The values predicted in the Basic Model are close to actual values, and reasonable. The Residual Difference model adds 0.1% to the Basic Model, giving a predicted value of 44.3%, which is the value of the measured *Spartina* cover present.

The Residual Difference Model predicts deviations from the Basic Model, due to site specific differences. The Residual Difference Model, by using some variables and not using others, is indicating which site characteristics (or site variables) are important in describing and predicting the abundance of *Spartina*. Site ten, with a large negative Residual Difference Model value, is a good example to illustrate this point. Site ten, or Ma-le'l Island, is located in the Mad River Slough. It is a relatively flat island, covered with a low mat of salt marsh vegetation. *Spartina* is present, but it is fairly uncommon. The average elevationN of the island is 7.06 ft. This island has the highest average elevation of all the salt marsh sites. The island is well drained by many shallow drainage channels. It is sheltered from the wind by the sand dunes and the tall trees on the shore of the slough. The average soil phosphorus is low, but not the lowest of the ten sites. The question becomes: Of all the site characteristics that a person could measure, which ones will prove to be significant to the presence of *Spartina*? The Residual Difference Model indicates that the important site variables are phosphorus site average, redox site standard deviation, and elevationN site standard deviation, because these variables predict the current *Spartina* abundance of the island, and other variables failed to do so.

At Site 10, the most important of these three factors is the redox site standard deviation value. This small value may be a result of the well drained soils. Site 10 has both a large number of very shallow drainage channels and the highest average elevation of all the sites. The drainage channels are not deep enough to encourage *Spartina* colonization, but they are deep enough to carry away the tidal waters quickly. Both the high average elevation and large number of shallow drainage channels may be responsible for the well drained soils. If there had been fewer drainage channels resulting in larger areas of standing water, or the island had a lower average elevation, the redox site standard deviation might be larger and *Spartina* might be more abundant. At other sites, the average site phosphorus levels or a larger variation in elevationN (the other two site variables) could be the dominating factor that determines the increases/decreases in *Spartina* abundance due to site differences, from the Basic Model.

An important point is that these variables predict the *Spartina* abundance, but they could be proxies for other environmental processes that are going on in the marsh, and which this study failed to identify. For example, redox site standard deviation might be the result of sandy soils, high average elevation, or high soil evaporation rates. But, the variable redox site standard deviation is a good indicator or measure of these other possible site processes, and substitutes effectively for them in this model.

<u>Logistic Regression and the Habitat of *Spartina*</u>

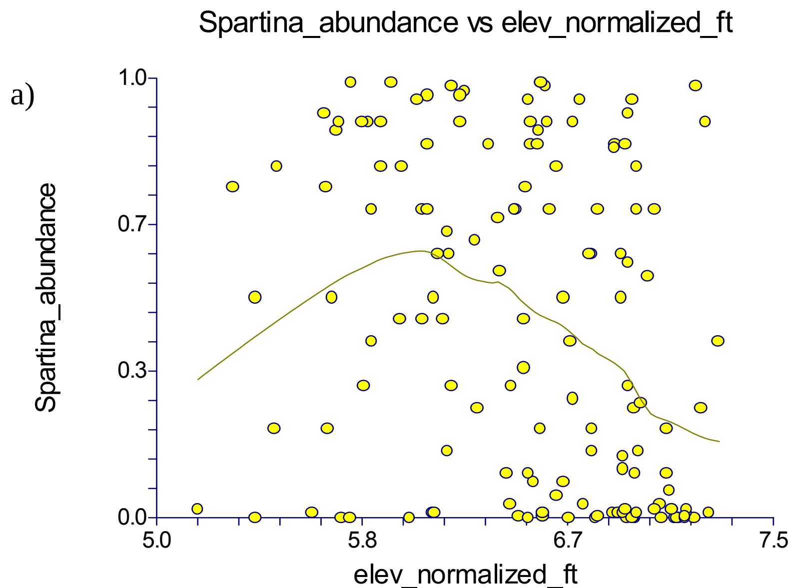
The most important logistic regression equation for this study was the equation that separated *Spartina* abundance into the classes of less than or equal to ten percent and greater than ten percent coverage. Figure 3 shows that when all of the plots were ordered from least to greatest *Spartina* abundance, there was a break in the plot curve at about ten percent *Spartina* abundance (Materials and Methods, Actual variable values for five *Spartina* abundance classes). This suggests that *Spartina* is growing outside of its optimal habitat when its abundance is less that ten percent. The clumps appear stunted and the dead stems from previous year(s) growth suggest that the plant is not increasing in size. Therefore, for the purposes of this study, *Spartina* habitat is defined as having greater than ten percent *Spartina* abundance. The habitat is bounded by the logistic regression equation for the ten percent boundary, and includes abundance classes 2-5.

The logistic regression equation that defines the ten percent boundary was 85% successful in predicting whether a plot would contain more than ten percent *Spartina* abundance, based on measured covariate values (Table 10). Since the ten percent boundary value is used to define the *Spartina* habitat, this equation is 85% successful in predicting *Spartina* habitat.

The abundance class membership predictions were less successful than the prediction for *Spartina* habitat (Table 11 and 12). When five classes were used, the predictions were correct only 54% of the time. When the middle three abundance classes were combined into one class, the remaining three class predictions were correct 66% of the time. The problem is that predicting membership to classes 2-4, or 10-75% *Spartina* abundance is unreliable.

There are several possible explanations for this. The first explanation is that disturbance in the salt marsh plant community where *Spartina* is moderately abundant makes reliable predictions impossible. Disturbance was seen and patches of the salt marsh community were killed off where piles of wrack were deposited by high tides. This was uncommon. The second explanation is that germination and colonization of *Spartina* in the salt marsh is controlled by factors not accounted for by this model. It is a reasonable hypothesis, but beyond the scope of this study. The third and most reasonable explanation is that the sampling design used in this study is responsible for inaccurately measuring the average *Spartina* abundance at a location in the salt marsh. *Spartina* grows in separate clumps, up to a meter in diameter, when it is found growing in the 10-75% abundance classes. Sampling was done by systematically placing a 1-m^2 quadrat every 20 meters and estimating the species abundance in the quadrat. If the quadrat were placed in an area where the *Spartina* had 20% abundance, it is unlikely that the quadrat would be placed to include 20-30% of a *Spartina* clump. It is much more likely that the quadrat would be place to fall between clumps, contain no *Spartina*, and underestimate the average abundance, or be placed to include 50% or more of a clump of *Spartina* and overestimate the local *Spartina* abundance. The plot of *Spartina* abundance with respect to elevationN supports this hypothesis (Figure 9). The curve of average *Spartina* abundance shows there is a maximum abundance at one point on the elevation gradient with a decreasing abundance both below and above this point of maximum abundance. A possible solution in future studies is to use a larger quadrat to get a larger area-average of *Spartina* abundance for a location in the salt marsh.

The niche of an organism includes all the environmental gradients and biological factors that determine the success of an organism in its habitat (Whittaker and Levin 1975). This study examines the environmental gradients but not the biological factors that define the place of *Spartina* in the salt marsh community. If this study had examined the role of interactions between *Spartina* and other plant or animal species, this study would be defining the possible niche of *Spartina densiflora* in Humboldt Bay. The niche is a



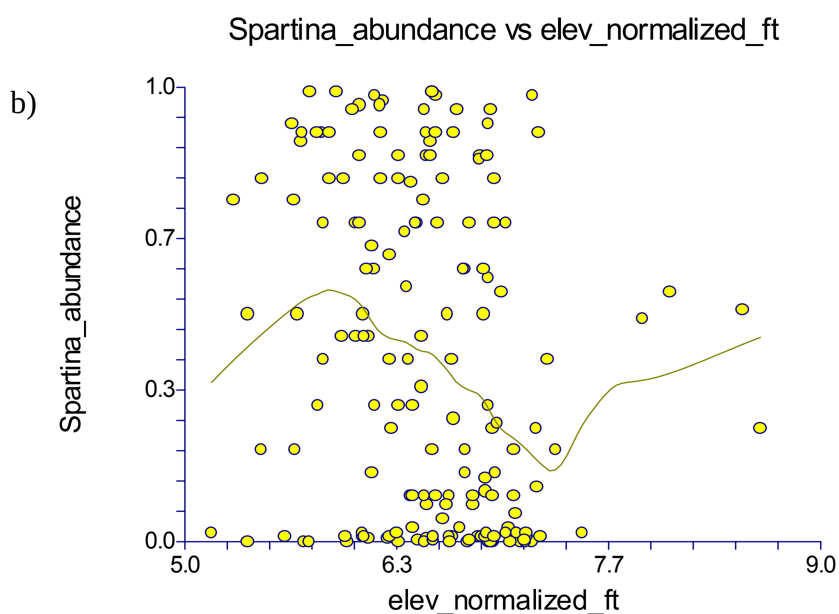


Figure 9. Scatter plot of *Spartina* abundance to elevation-normalized, of all plots at sites 1, 2, 3, 4, 6, 7 (a) and 1, 2, 3, 4, 5, 6, 7 (b). The curved line represents *Spartina* average abundance of all plots located at the given elevation, and was created using a Loess

curve. Scatter plot (a) demonstrates the normal change of *Spartina* abundance with elevation. Plot (a) shows that *Spartina* abundance reaches a peak at about 6.2 feet. Site 5 was left out of scatter plot (a) because the unusually high *Spartina* abundances at the 8.4 foot elevation at this site was anomalous to the normal change of *Spartina* abundance with elevation. Scatter plot (b) shows the Loess curve with site 5 data included.

more complete definition of the factors that might be used to control a species, and so would be more useful than the description of the habitat for *Spartina* as defined in this study. Transplant experiments in the salt marsh would be necessary to understand and quantify the effects of competition between *Spartina* and other salt marsh plant species (Bertness 1991).

The Variables Used in the Model, Describing and Predicting *Spartina* Abundance

The next question that needs attention is: How are these six variables affected by other processes going on in the salt marsh? Understanding how these variables are influenced by other processes in the marsh might give us some ideas on how to control the spread of *Spartina* at present salt marsh locations, prevent its introduction into newly created salt marshes, or reduce its abundance at locations where it is currently established.

Phosphorus

Phosphorus is the most important environmental variable correlated with the presence of *Spartina* in the salt marsh in this study. The regression of *Spartina* to phosphorus has an R-squared = 0.4088, which means that almost 41% of the variation of the presence of *Spartina* in the salt marsh can be explained by the amount of phosphorus in the soil.

The most important factor explaining the amount of phosphorus in the soil is the elevationN of the soil in the salt marsh (Table 16). The bay waters carry the phosphorus into the salt marsh on clay particles (Newby 1980), and deposit that clay in the salt marsh. The lower in elevation the soil surface is in the marsh, the longer it will be submerged by the tidal waters and have phosphorus laden clay deposited on that surface. This suggests that the graph of phosphorus to elevationN is non-linear. Rather, it should be similar to the amount of time that a plot at a given elevationN is covered by tidal waters, which is a curvilinear function. In fact, the R-squared is equal to 0.4794 for the regression of phosphorus to elevation, and the R-squared is equal to 0.5544 for the regression of phosphorus to the sum of elevation, elevationN-squared, and elevationN-cubed (Table 16). The regression relationship of phosphorus to elevationN is curvilinear, in a cubic or quadratic relationship.

The second factor correlating to the presence of phosphorus in the marsh soil is the redox measurement of the soil. The regression of phosphorus to redox has an R-squared equal to 0.3302. Redox, a reflection of the length of time that the soil stays saturated with water, correlates with elevationN, just as phosphorus does. This might suggest that phosphorus and redox are related to elevationN, but are only related to each other coincidentally. Looking at the correlation of phosphorus to redox, then phosphorus to elevation, and finally of phosphorus to redox plus elevation should help clarify this relationship. If elevation and redox are explaining the same things, then the R-squared of both of them together should not be appreciably larger than the R-squared of the larger of the two, by itself. In fact, the regression of phosphorus to elevation plus redox gives an R-squared equal to 0.5559, while the regression of phosphorus to elevation has an R-squared equal to 0.4795 and the regression of phosphorus to redox is R-squared equal to 0.3302. So, redox adds about 7% to the relationship, which cannot be explained by elevationN, and therefore this variable is important in understanding the relationships between the variables. The added effect of redox may be due to areas in the higher marsh that retain pooled water, and so add to the amount of time that phosphorus may be allowed to settle into the marsh soils. Right now, this is only speculation.

Two other variables were tested to see if they had an effect on the amount of phosphorus in the soil. These were the variables, DistanceToDitch and DepthOfDitch. Both had a minor effect on the amount of phosphorus present, but this effect was less than 1% when these variables were combined with elevationN and redox in a multivariate linear regression. So, the effect of these variables on phosphorus is virtually insignificant.

To summarize, locations in the marsh that have a low elevationN and a large, negative redox potential are also likely to have high levels of phosphorus in the soil. But, in reference to the *Spartina* abundance model, note that these three variables are not all measuring exactly the same thing. Since the effect of all three of these variables is greater than the effect any one or two of these variables, each of these three variables adds something to the model that the others do not provide, and all three are important in describing *Spartina* abundance.

Table 16. Regression relationships of covariates significant to Phosphorus, and potentially useful for clarifying relationships between covariates important to *Spartina* abundance in the salt marsh.

Dependent Var.	Independent Vars.	Coefficient	Probability	R-squared
phosphorus	Intercept	53.2393	< 0.00005	0.4794
	elevationN	-6.9408	< 0.00005	
phosphorus	Intercept	8.2290	< 0.00005	0.3302
	redox	-0.0157	< 0.00005	
phosphorus	Intercept	10.9291	< 0.00005	0.0460
	StDevElevationN	-6.6349	0.0030	
phosphorus	Intercept	73.8169	< 0.00005	0.2734
	AvgElevN	-10.0989	< 0.00005	
phosphorus	Intercept	151.2934	< 0.00005	0.5268
	elevationN	-36.7516	< 0.00005	
	elevN_squ	2.2502	< 0.00005	
phosphorus	Intercept	-400.3496	0.0156	0.5544
	elevationN	209.2030	0.0045	
	elevN_squ	-33.9515	0.0017	
	elevN_cubed	1.7585	0.0008	
phosphorus	Intercept	8.7505	< 0.00005	0.0281
	DistToDitch	-0.0447	0.0209	
phosphorus	Intercept	8.9359	< 0.00005	0.0216
	DepthDitch	-0.6420	0.0428	
phosphorus	Intercept	poor relationship		
	DistToDitch			
	DepthDitch			
phosphorus	RedoxAvgStDev	poor relationship		

<u>Phosphorus Site Average</u>

This is a site variable, measured as an average of the phosphorus values of all the plots at a marsh site. This variable, phosphorus-site-average (PhosAvg, Table 17), has less effect on the presence of *Spartina* than the variable phosphorus, with an R-squared equal to 0.3000 for the regression of *Spartina* to PhosAvg compared to an R-squared equal to 0.4088 for the regression of S*partina* to phosphorus. The main thing that can be learned from the regression relationships in the table below is that a site with a low average elevation will have a high average phosphorus level, because it is submerged in the bay waters more of the time than a site with a higher average elevation.

The last regression relationship listed in Table 17, of PhosAvg to AvgDistToDitch plus AvgElevN plus StDevElevN has an R-squared equal to 0.9229. By examining the other correlations in the table, it seems that StDevElevN probably adds about 4% to the regression of PhosAvg to AvgElevN (R-squared = 0.8610), while AvgDistToDitch adds about 2% to the regression of PhosAvg to AvgElevN plus StDevElevN. What this suggests is that a low-average-elevation marsh (small AvgElevN), that doesn't increase very much in elevation (small StDevElevN), and also contains a large number of shallow drainage channels (small AvgDistToDitch), probably contains a high *Spartina* abundance. The variable AvgDistToDitch has a strong correlation to StDevElevN (R-squared equal to 0.8111), so these two variables describe similar factors at work in the salt marsh (Table 24).

Table 17. Regression relationships of covariates significant to Phosphorus Site Average, and potentially useful for clarifying relationships between covariates important to *Spartina* abundance in the salt marsh.

Dependent Var.	Independent Vars.	Coefficient	Probability	R-squared
PhosAvg	Intercept	73.8460	0.0000	0.8610
	AvgElevN	-10.1034	0.0000	
PhosAvg	Intercept	8.5752	0.0000	0.4029
	redoxAvg	-0.0371	0.0000	
PhosAvg	Intercept	4.1362	0.0000	0.3000
	AvgSPDE	8.6756	0.0000	
PhosAvg	Intercept	10.8261	0.0000	0.2100
	AvgDistToDitch	-0.1750	0.0000	
PhosAvg	Intercept	13.1709	0.0000	0.2360
	AvgDepthDitch	-3.4899	0.0000	
PhosAvg	Intercept	13.5752	0.0000	0.3069
	AvgDepthDitch	-2.5122	0.0000	
	AvgDistToDitch	-0.1142	0.0000	
PhosAvg	Intercept	10.9321	0.0000	0.1452
	StDevElevN	-6.6423	0.0000	
PhosAvg	Intercept	-1.6440	0.3610	0.1340
	RedoxAvgStDev	0.0503	0.0000	
PhosAvg	Intercept	78.0349	0.0000	0.9229
	AvgDistToDitch	0.1421	0.0000	
	AvgElevN	-10.4735	0.0000	
	StDevElevN	-9.1935	0.0000	

Redox

Redox is related to the saturation of the soil with water, and is a measure of how oxygenated or reduced the soil is. Soil that has been under water for a long period of time has very little, if any, oxygen present. This soil is reduced and has a large, negative redox measure. The sediment found at the bottom of salt marsh drainage channels is very reduced, and has been observed in this study to have a redox measure of -250 to -370. It also usually has a rotten egg smell, due to the reduced sulfur compound hydrogen sulfide. Soil that is dry and/or well mixed with air has a redox measure of +200 to +300.

In the salt marsh, high elevation soils usually have a higher, more positive average redox measure, and lower elevation soils have a lower, more negative average redox measure. This is because the soils in the low marsh are covered with tidal waters for a longer period of time than soils in the high marsh. The regression of redox to elevationN has an R-squared equal to 0.2292 (Table 18).

The regression of redox to phosphorus is stronger than the regression of redox to elevation, with an R-squared equal to 0.3302. This suggests that soils that are saturated most of the time contain more phosphorus than soils that are better drained. Perhaps more phosphorus can enter the soil in areas where the bay waters are collected in ponds on the soil surface, after the tide waters have gone out.

From personal observations, the most highly reduced soils (large negative redox measure) are either low in the salt marsh, or on a soil shelf that contains a lot of ponded water. These soils are very mucky. This is also where *Spartina* can be found growing.

An example of both these situations can be seen in the salt marsh about 300 yards south of Jacoby Creek. The low marsh, next to the bay mudflats, contains low hummocks covered with *Spartina*. The mud between these hummocks has the consistency of wet cookie dough while the mud on the hummocks and under the *Spartina* is only slightly more firm. The soils are highly reduced (very negative) here. East, about two-thirds the distance to the railroad track and at a higher elevation in the same marsh, a large tidal channel cuts through the marsh. The western side of this tidal channel has a meadow of *Spartina* about fifteen yards deep and hundreds of yards long. The *Spartina* meadow sits on a shelf of wet soil that is re-saturated with bay waters on every high tide. Poor drainage and the natural topography of the salt marsh maintain the reduced soil conditions.

Table 18. Regression relationships of covariates significant to Redox, and potentially useful for clarifying relationships between covariates important to *Spartina* abundance in the salt marsh.

Dependent Var.	**Independent Vars.**	**Coefficient**	**Probability**	**R-squared**
Spartina	Intercept	0.4570	0.0000	0.2088
	Redox	-0.0009	0.0000	
Redox	Intercept	183.3885	0.0000	0.3302
	phosphorus	-20.9819	0.0000	
Redox	Intercept	-1128.0057	0.0000	0.2297
	elevationN	175.4313	0.0000	
Redox	Intercept	-221.4606	0.3014	0.3429
	elevationN	57.2451	0.0585	
	phosphorus	-17.0277	0.0000	
Redox	DistToDitch	no relationship		
Redox	DepthOfDitch	no relationship		
Redox	Intercept	-252.7854	0.0000	0.2496
	ElevClass	48.8732	0.0000	

Redox Site Standard Deviation

There is a strong correlation of Redox Site StDev to Redox Site Avg, with an R-squared equal to 0.6934 (Tables 19 and 20). Only ten data points are used in the regression of Redox Site StDev to Redox Site Avg, so the regression has a slightly inflated R-squared value, but the relationship is still significant and important. RedoxSiteStDev is a measure of the spread of redox values. A distribution of both very positive and very negative redox values is shown by a large Redox Site StDev. The regression of RedoxSiteStDev to RedoxSiteAvg (Tables 20 and 21) shows that as the range of redox values increase, the average redox values become more negative. Another way of looking at this is to see that when the range of redox values is small, the redox values are mostly positive because the soil is frequently drained. As the range of redox values increases, more and more negative redox values are included in the average, and so the RedoxSiteAvg drops.

This relationship would suggest that when the range of redox values is small, the average elevation (or AvgElevN) of the marsh is high. As the RedoxSiteStDev expands the average elevation of the plots should decrease because more of the plots are located at a lower elevation. The regression of RedoxSiteStDev to AvgElevN shows that a larger RedoxSiteStDev is due to a lower AvgElevN, with an R-squared equal to 0.2077 for this relationship. As the AvgElevN value decreases, the average distance to the nearest ditch should also decrease because drainage ditches are more common in the low marsh than in the high marsh (see section below on AvgElevN and Table 22). The regression of AvgElevN to AvgDistToDitch has an R-squared equal to 0.1366. Finally, as the

RedoxSiteStDev values increase, the spread of plot elevations in the marsh (StDevElevN) should also increase. This is what happens, and the relationship has an R-squared equal to 0.2877. A regression of RedoxSiteStDev to AvgDistToDitch plus AvgElevN plus StDevElevN shows this combined relationship, with an R-squared equal to 0.6891.

The RedoxSiteStDev has a positive correlation to *Spartina* abundance, so that a large RedoxSiteStDev reflects higher average *Spartina* abundance at a site. A way to decrease the RedoxSiteStDev is to increase the average elevation of the marsh site, or perhaps to increase the drainage in the lower marsh so that water does not pool and saturate the soil as much.

Table 19. Regression relationships of covariates significant to Redox Site Standard Deviation, and potentially useful for clarifying relationships between covariates important to *Spartina* abundance in the salt marsh.

Dependent Var.	**Independent Vars.**	**Coefficient**	**Probability**	**R-squared**
RedoxSiteStDev	Intercept	197.1659	0.0000	0.6934
	RedoxSiteAvg	-0.3544	0.0000	
RedoxSiteStDev	Intercept	179.4271	0.0000	0.0703
	AvgDistToDitch	0.7374	0.0002	
RedoxSiteStDev	Intercept	427.0682	0.0000	0.2077
	AvgElevN	-36.1423	0.0000	
RedoxSiteStDev	Intercept	500.2786	0.0000	0.4254
	AvgDistToDitch	1.3966	0.0000	
	AvgElevN	-50.8605	0.0000	
RedoxSiteStDev	Intercept	161.1351	0.0000	0.2839
	StDevElevN	68.1034	0.0000	
RedoxSiteStDev	Intercept	381.2946	0.0000	0.6891
	AvgDistToDitch	-1.9522	0.0000	
	AvgElevN	-35.1244	0.0000	
	StDevElevN	159.4163	0.0000	
RedoxSiteStDev	SPDE	no relationship	0.4931	0.0025

Table 20. Regression relationships of covariates significant to Redox Site Average, and potentially useful for clarifying relationships between covariates important to *Spartina* abundance in the salt marsh.

Dependent Var.	**Independent Vars.**	**Coefficient**	**Probability**	**R-squared**
RedoxSiteAvg	Intercept	390.6910	0.0000	0.6934
	RedoxSiteStDev	-1.9565	0.0000	
RedoxSiteAvg	Intercept	-768.6439	0.0000	0.4172
	AvgElevN	120.3742	0.0000	
RedoxSiteAvg	Intercept	-86.8683	0.1258	0.7830
	AvgElevN	62.6763	0.0000	
	RedoxSiteStDev	-1.5964	0.0000	
RedoxSiteAvg	Intercept	69.8308	0.0000	0.1376
	AvgSlope3ft	-16.7484	0.0000	
RedoxSiteAvg	Intercept	47.5841	0.0000	0.0561
	StDevElevN	-70.6718	0.0010	
RedoxSiteAvg	Intercept	0.4620		0.0267
	SPDE	-0.0012		
RedoxSiteAvg	AvgDistToDitch	no relationship		
RedoxSiteAvg	DistToDitch	no relationship		

ElevationN

Most of the processes occurring in the salt marsh have a significant correlation to elevationN. The elevation determines how long a location in the salt marsh will remain submerged in the tidal waters. The tidal waters bring in nutrients, and largely control the soil forming processes. Also, the length of time that a location is submerged determines the vegetation that will be present at that location (Cronk and Fennessy 2001). But the relationship between the elevation and the other variables (environmental gradients) is not 100% - elevation may be correlated to a variable such as the distance to the nearest ditch, but many factors influence where a ditch may form in the salt marsh, so the distance to the nearest ditch is also a measure of other unmeasured processes going on in the marsh. Many of the variables measured are correlated to elevation, but they are also a measure of other attributes that are important gradients to measure in the salt marsh. The regression of elevationN to one or more other variables was calculated to try and understand the relationship between elevationN and the other processes occurring in the marsh. The last relationship listed in Table 21 shows the regression of seven variables to elevationN, with an R-squared equal to 0.7386. For some of the variables listed, the R-squared of the relationship is small.

The regression of elevationN to *Spartina* abundance has an R-squared equal to 0.0681, which is small. But, the regression of elevationN to phosphorus is relatively strong, with an R-squared equal to 0.4794. The regression of elevationN to redox is moderately strong, with an R-squared equal to 0.2297. Since phosphorus and redox are the most significant variables with respect to *Spartina* abundance, this suggests that elevationN is also significant to *Spartina* abundance, but indirectly and through its effect on these two environmental gradients. ElevationN is also a measure of the effect of other environmental gradients not accounted for by phosphorus and redox, and so is important to describing *Spartina* abundance independent of phosphorus and redox.

The scatter plot of *Spartina* abundance to elevationN (Figure 9) shows this relationship. *Spartina* abundance is low at 5.2 feet elevationN, where pickleweed is the dominant species. As elevationN increases, so does the *Spartina* abundance. *Spartina* reaches a maximum abundance at about 6.2 feet elevationN, and then drops off from there as elevationN increases. At about 7.5 feet elevationN, *Spartina* is scarce in the salt marsh, and salt grass dominates the plant community. The salt marsh vegetation ends at about 8.4 feet elevation, where upland species begin to dominate.

The linear regression of *Spartina* to elevationN is so poor because *Spartina* abundance peaks in the lower-middle marsh, close to the middle of the marsh. If *Spartina* abundance had reached a maximum at the lower or upper edge of the marsh, the R-squared value of the relationship would be much stronger. A linear regression of *Spartina* to elevationN and elevationN-squared was calculated, to see if a quadratic relationship would form better regression (Table 1A, in Results). This relationship has a higher R-squared value, but decreased the R-squared value of the model when the other significant variables were included in the model, and so was not used to model *Spartina* abundance.

In summary, elevationN has a strong effect on *Spartina* abundance, but much of that effect is indirect, acting through other processes occurring in the salt marsh.

Table 21. Regression relationships of covariates significant to ElevationN, and potentially useful for clarifying relationships between covariates important to *Spartina* abundance in the salt marsh.

Dependent Var.	Independent Vars.	Coefficient	Probability	R-squared
ElevationN	StDevElevN	no relationship		
ElevationN	Intercept	6.3116	< 0.00005	0.0363
	AvgDistToDitch	0.0129	0.0085	
ElevationN	Intercept	6.3582	< 0.00005	0.1411
	DistToDitch	0.0100	< 0.00005	
ElevationN	Intercept	6.5002	< 0.00005	0.2297
	redox	0.0013	< 0.00005	
ElevationN	Intercept	7.0722	< 0.00005	0.4794
	phosphorus	-0.0691	< 0.00005	
ElevationN	Intercept	7.0133	< 0.00005	0.4893
	phosphorus	-0.0621	< 0.00005	
	redox	0.0000	< 0.00005	
ElevationN	Intercept	6.8384	< 0.00005	0.5640
	DistToDitch	0.0074	< 0.00005	
	phosphorus	-0.0057	< 0.00005	
	redox	0.0004	0.0116	
ElevationN	Intercept	6.5837	< 0.00005	0.7386
	bulk density	0.9030	< 0.00005	
	DistToDitch	0.0053	< 0.00005	
	phosphorus	-0.0525	< 0.00005	
	redox	0.0006	< 0.00005	
	SPDE	0.3603	< 0.00005	
	water content	-0.0074	0.0003	
	organic content	0.0239	< 0.00005	

AvgElevN

The variable AvgElevN is the average elevationN, of all the plots at a site. AvgElevN contains ten values, one for each site. This variable is not used in the *Spartina* models, but it is important for what it can tell us about how the salt marsh changes with respect to elevation (Table 22). The regression of AvgElevN to PhosSiteAvg, with a negative coefficient and an R-squared equal to 0.8610, tells us that as the average elevationN for a site increases, the average amount of phosphorus at that site will decrease. At a site with a high AvgElevN, the individual plots with a low elevationN will still have a high phosphorus value, but since most of the plots are at a high elevation where they receive less phosphorus, the average phosphorus value of that site will be lower. Since *Spartina* abundance is positively correlated with phosphorus, a site with a high AvgElevN will probably have a low *Spartina* abundance.

For similar reasons, a site with a high AvgElevN will have a high RedoxSiteAvg (Tables 20 and 22). The plots with a higher elevationN in the marsh will probably be better drained, and so will also have a more positive redox value than the plots with a low elevationN. Since the proportion of the well drained plots will be larger at a site with a high AvgElevN, this will increase the average redox value for that site. *Spartina* abundance is correlated with more negative redox values, so sites with a high AvgElevN and a more positive RedoxSiteAvg will probably have less *Spartina* present.

An interesting relationship is the regression of AvgElevN to AvgDistToDitch plus AvgDepthOfDitch. This relationship shows that there are fewer drainage channels at high marsh elevations than at low marsh elevations. It also shows that these few high elevation drainage channels are deeper, on average, than the lower drainage channels. This may be because the high elevation drainage channels have been around longer than the low elevation drainage channels and have been draining tidal waters from the salt marsh for a longer period of time. Also, it has been suggested that the equilibrium between sedimentation and erosion in the channel bottoms occurs at a lower elevation than the surrounding marsh, where the marsh vegetation helps to retain the sediment (Andrea Pickart 2006).

A significant exception to the relationship of fewer channels at higher elevations occurs at site 10, Ma-le'l Island. Ma-le'l Island has the highest AvgElevN (7.06 feet), but it also has the second highest average number of shallow drainage channels (AvgDistToDitch equal to 10.66 feet). Both the high AvgElevN and small AvgDistToDitch are probably responsible for the well drained soils and lowest site abundance of *Spartina*. This exception remains a mystery.

The last significant relationship in this set, the regression of AvgElevN to AvgSlope (with both a 3 foot and a 10 foot baseline) shows that sites with a higher AvgElevN are also flatter than low AvgElevN sites. This is probably because there are fewer drainage channels, and also less deposition/erosion of sediments occurring at the higher elevations, as the tidal waters cover the higher elevations proportionately less of the time.

Table 22. Regression relationships of covariates significant to Elevation Site Average, and potentially useful for clarifying relationships between covariates important to *Spartina* abundance in the salt marsh.

Dependent Var.	Independent Vars.	Coefficient	Probability	R-squared
AvgElevN	Intercept	6.3796	0.0000	0.0386
	StDevElevN	0.3144	0.0066	
AvgElevN	Intercept	4.7701	0.0000	0.2672
	ElevationN	0.2683	0.0000	
AvgElevN	Intercept	7.1993	0.0000	0.8610
	phosphSiteAvg	-0.0852	0.0000	
AvgElevN	Intercept	6.4636	0.0000	0.4172
	RedoxSiteAvg	0.0035	0.0000	
AvgElevN	Intercept	7.6195	0.0000	0.2077
	RedoxSiteStDev	-0.0057	0.0000	
AvgElevN	Intercept	6.3085	0.0000	0.1366
	AvgDistToDitch	0.0130	0.0000	
AvgElevN	Intercept	6.0297	0.0000	0.2489
	AvgDepthOfDitch	0.3291	0.0000	
AvgElevN	Intercept	6.0074	0.0000	0.2745
	AvgDepthOfDitch	0.2751	0.0000	
	AvgDistToDitch	0.0063	0.0110	
AvgElevN	Intercept	6.9448	0.0000	0.2998
	AvgSlope3feet	-0.1327	0.0000	
AvgElevN	Intercept	6.9276	0.0000	0.3726
	AvgSlope10feet	-0.2244	0.0000	
AvgElevN	StDevDistToDitch	no relationship		
AvgElevN	StDevDepthOfDitch	no relationship		
AvgElevN	phoshSiteStDev	no relationship		

Standard Deviation ElevationN

The standard deviation of elevationN is a measure of how much a marsh site changes in elevation, at least with respect to the transect plots at that site. Some of the sites change very gradually over the length of the transect(s), and some of the sites change elevation frequently over short distances. The variable, StDevElevN does not distinguish between these two salt marsh topographies.

One would expect that a site with a large StDevElevN value would also have a high AvgElevN value, since a large variation in marsh plot elevations implies a large change in overall elevation, but Table 22 shows that the correlation between these two variables is pretty weak. Some low elevation sites have a lot of topographic variation and some high elevation sites are relatively flat.

What the Table 23 does show is that sites with large changes in elevation also have a large average distance between drainage channels. One possible explanation is that sites with a relatively large change in elevation are well drained, and don't need channels to carry off the water as the tide drops, while those sites that are relatively flat and likely to hold pooled water are more likely to form drainage channels through erosion to carry away that water.

A site with a large StDevElevN, which has a relatively large change in elevation in tens of meters distance, is correlated with locally flat ground (within a 3 meter distance) at the plot location, using both a 3 foot base line (over the length of the plot quadrat) and a 10 foot base line, to measure the local ground slope. An example of this can be seen in the low growing salt marsh meadows near Jacoby Creek that gently slope toward the bay. These meadows are almost flat enough to play golf on, but have a significant drop in elevation from one end of the meadow to the other. Conversely, a site with a small StDevElevN and relatively little change in elevation within tens or hundreds of meters distance is correlated with locally uneven ground. This kind of site will have many scattered clumps of *Spartina* growing from small raised hummocks of soil, but will retain pooled water when the tidal waters have dropped because the ground is so level.

The variable StDevElevN has a negative correlation to *Spartina*. The equation developed using the Residual Sum Model method and written again below, shows the effect of the variable StDevElevN on *Spartina* abundance:

SPDE abundance = -2.1051 + 0.271*ElevN + 0.0571*phos. –0.0493*AvgPhos.

- 0.000352*redox + 0.00676*RedoxSiteStDev

- 1.28*StDevElevN.

The implication of this is that sites with a large elevation gradient (large StDevElevN and relatively large change in elevation) over the length of the site, but locally flat ground with few drainage channels, will contain little *Spartina;* while a site with a small elevation gradient, lots of pooled water and lots of locally uneven ground will contain lots of *Spartina*.

Table 23. Regression relationships of covariates significant to ElevationN Site Standard Deviation, and potentially useful for clarifying relationships between covariates important to *Spartina* abundance in the salt marsh.

Dependent Var.	Independent Vars.	Coefficient	Probability	R-squared
StDevElevN	Intercept	0.1237	0.0000	0.8111
	AvgDistToDitch	0.0197	0.0000	
StDevElevN	Intercept	-0.0243	0.0918	0.8640
	StDevDistToDitch	0.0263	0.0000	
StDevElevN	Intercept	0.0800	0.0309	0.3612
	StDevDepthDitch	0.3239	0.0002	
StDevElevN	Intercept	-0.3637	0.0001	0.2877
	RedoxSiteStDev	0.0042	0.0000	
StDevElevN	Intercept	0.6193	0.0000	0.1452
	PhosAvg	-0.0219	0.0000	
StDevElevN	Intercept	0.2889	0.0000	0.0696
	PhosSiteStDev	0.0359	0.0002	
StDevElevN	Intercept	0.5003	0.0000	0.0460
	phosphorus	-0.0069	0.0030	
StDevElevN	Intercept	0.3428	0.0000	0.0277
	AvgDepthDitch	0.0686	0.0216	
StDevElevN	redoxSiteAvg	no relationship		
StDevElevN	redox	no relationship		
StDevElevN	ElevationN	no relationship		
StDevElevN	Intercept	0.7354	0.0000	0.3584
	AvgSlope3ft	-0.0906	0.0000	
StDevElevN	Intercept	0.6907	0.0000	0.3465
	AvgSlope10ft	-0.1351	0.0000	
StDevElevN	Intercept	0.1882	0.0000	0.8183
	AvgDistToDitch	0.0184	0.0000	
	AvgSlope10ft	-0.0238	0.0072	

<u>Average distance to the nearest ditch</u>

The variable AvgDistToDitch has a positive correlation to the AvgElevN, so that low elevation sites have lots of closely spaced drainage channels and high elevation sites have fewer drainage channels (Table 24). The relationship is weak, with an R-squared equal to 0.1366, and site 10 is an exception to this trend. Sites with frequent drainage channels also have locally uneven ground. The regression of AvgDistToDitch to AvgSlope3foot (using a 3 foot base line to measure the slope) has an R-squared equal to 0.6070.

Finally, the regression of AvgDistToDitch to average *Spartina* site abundance has a negative correlation, with an R-squared equal to 0.4293. This implies that areas with large number of drainage channels are likely to have a high abundance of *Spartina*. When the effects of these three relationships are combined, it is likely that a site with a low average elevationN also has lots of drainage channels, uneven ground, and a high *Spartina* abundance.

Table 24. Regression relationships of covariates significant to Average Distance to Nearest Ditch, and potentially useful for clarifying relationships between covariates important to *Spartina* abundance in the salt marsh.

Dependent Var.	Independent Vars.	Coefficient	Probability	R-squared
AvgDistToDitch	Intercept	-52.4223	0.0000	0.1366
	AvgElevN	10.5390	0.0000	
AvgDistToDitch	Intercept	-2.0086	0.0041	0.8111
	StDevElevN	41.1180	0.0000	
AvgDistToDitch	Intercept	25.8590	0.0000	0.2100
	PhosAvg	-1.2000	0.0000	
AvgDistToDitch	Intercept	16.3100	0.0000	0.0001
	RedoxSiteAvg	-0.0014	0.8975	no relationship
AvgDistToDitch	Intercept	84.8621	0.0000	0.5381
	SalinitySiteAvg	-1.6491	0.0000	
AvgDistToDitch	Intercept	5.9041	0.4348	0.7360
	AvgElevN	12.7498	0.0000	
	SalinitySiteAvg	-1.7492	0.0000	
AvgDistToDitch	Intercept	33.5443	0.0000	0.6070
	AvgSlope3ft	-5.3832	0.0000	
AvgDistToDitch	Intercept	27.2830	0.0000	0.3327
	AvgSlope10ft	-6.0454	0.0000	
AvgDistToDitch	Intercept	-1.9645	0.6873	0.0703
	RedoxSiteStDev	0.0953	0.0002	
AvgDistToDitch	Intercept	-3.3230	0.0005	0.7238
	StDevDistToDitch	1.1009	0.0000	

<u>Summary of the effects of the variables on *Spartina* abundance</u>

Phosphorus has the strongest influence on *Spartina* abundance. *Spartina* grows in abundance where the available phosphorus concentration is greater than 5 ppm (parts per million), in the marsh soils. Phosphorus is deposited on the marsh with the clay particles found in the bay waters, and is most abundant in the low elevation marsh soils and where the bay waters can form pools when the tide has receded.

Redox is the second most important variable in influencing the abundance of *Spartina*. *Spartina* is found growing where redox values are very negative. Redox values are very negative where the soil remains saturated with water most of the time, which is either low in the marsh or in areas where the water cannot effectively drain away with the outgoing tide. These saturated soils are mucky and black, and often smell of rotten eggs.

RedoxSiteStDev is important to the average site abundance of *Spartina*. A small RedoxSiteStDev correlates to a decreased average site abundance of *Spartina*, while a large RedoxSiteStDev correlates to an increased site abundance of *Spartina*. As discussed in the analysis of the variable RedoxSiteStDev, well drained soils have a small RedoxSite StDev and mostly positive redox values. In contrast, soils with a large RedoxSiteStDev include both well drained soils and chronically wet soils, resulting in a larger range (and standard deviation) of redox values.

ElevationN has the smallest direct effect on *Spartina* abundance, when compared to the effects of phosphorus and redox. The regression or *Spartina* abundance to elevation has an R^2 = 0.0681, while the regression of *Spartina* abundance to elevation plus elevation-squared plus elevation-cubed has an R^2 equal to 0.1079 (Table 1A). *Spartina* reaches a maximum abundance at 6.2 feet, elevationN, and decreases in abundance at both lower and higher elevations in the salt marsh. While elevation has a small direct effect on *Spartina* abundance, it has a strong influence on both phosphorus and redox, with an R^2 = 0.4794 and an R^2 = 0.2297, respectively (Table 21). At the higher elevations, phosphorus decreases while redox values increase, and *Spartina* abundance decreases.

Standard deviation of elevation, StDevElevN, affects the site abundance of *Spartina*. Sites with a large StDevElevN have less *Spartina* than sites with very little variation in elevation. Ideally, a site with a gradual decrease in elevation but a large range in elevation change will not have very much *Spartina*. The *Spartina* will be located at the lowest elevations at a site with a strong elevation gradient. The two sites, sites 3 and 4, a few hundred meters south of the mouth of Jacoby creek are good examples of a marsh with a strong elevation gradient and a relatively low *Spartina* abundance.

The site average of the distance to the nearest ditch, AvgDistToDitch, is related to elevation. Sites with a low average elevation also tend to have a large number of ditches. There is a correlation of AvgDistToDitch with average *Spartina* site abundance. The *Spartina* abundance may be responsible for the large number of ditches. *Spartina* shades underlying ground. The shaded areas are mostly unvegetated, which results in a lot of bare mud that is easily eroded by tidal waters. But, the cause-and-effect in the regression of *Spartina* abundance to AvgDistToDitch is uncertain.

In summary, based on the models examined here, a marsh site resistant to *Spartina* invasion has the following characteristics:

Large elevation gradient over the length of the marsh, but locally flat,

High average elevation,

Well drained (less reduced) soils, with little pooled water or mucky spots,

Abundant, shallow, vegetated drainage channels, as found at Ma-le'l Island, but few un-vegetated, deeper channels,

Low available Phosphorus in the soil.

A site susceptible to *Spartina* invasion has the following characteristics:

Low average elevation,

Small elevation gradient over the length of the marsh site,

Lots of areas that retain pooled water when the tide recedes,

Very reduced soils,

Locally uneven ground (though this may be a result of *Spartina*),

Bare soils, easily colonized with *Spartina* seedlings,

High available phosphorus in the soil.

Actual Variable Values, for Five *Spartina* Abundance Classes

The previously discussed variable relationships to *Spartina* abundance were calculated using multivariate linear regression, and then abstracted into equations. The significance of the relationships between these environmental gradients, and to *Spartina* abundance has been previously discussed. At the end of the Results section, the average values of these significant environmental gradients were tabulated for each of five *Spartina* abundance classes. This was done because abstracted relationships (equations) may not provide the broad picture that is needed to synthesize this information into usable and practical information. This information is also presented in Table 25, below.

The information presented in Table 25, together with the plot of *Spartina* abundance vs. elevation normalized can assist in planning a marsh restoration project in which the abundance of *Spartina* will be minimized. The table and plot present real parameter values for management decision makers, although it is important to point out that the table values show the mean of each class range within the variable. For example, knowing that *Spartina* has a peak abundance at 6.33 feet elevationN (see Table 25, Class 5, ElevN), the marsh preserve can be designed to minimize the amount of area at this elevation. Alternately, the marsh can be designed with a large elevation gradient and a good drainage pattern at these elevations (i.e. large StDevElevN, positive average redox potential) in this portion of the marsh. The variation in mean gradient values for each *Spartina* abundance class is indicated in the bar graph that follows (Figure 10).

Table 25. The five *Spartina* abundance classes, and the important variable averages for each abundance class. These are actual values, and are included to give a sense of how *Spartina* abundance changes along these environmental gradients.

Mean variable values, by SPDE abundance class						
SPDE abundance class	SPDE	ElevN	Redox	Phos.	StDev ElevN	AvgDist To Ditch
Class 1: 0.000-0.100	0.024	6.63	116.9	4.21	0.530	19.78
Class 2: 0.101-0.250	0.189	6.68	66.9	5.52	0.453	15.91
Class 3: 0.251-0.500	0.400	6.41	12.2	8.9	0.418	15.88
Class 4: 0.501-0.750	0.650	6.57	-5.8	9.4	0.352	13.58
Class 5: 0.751-1.000	0.924	6.33	-103.6	12.01	0.395	13.68
Overall	0.442	6.52	16.02	7.97	0.445	16.27

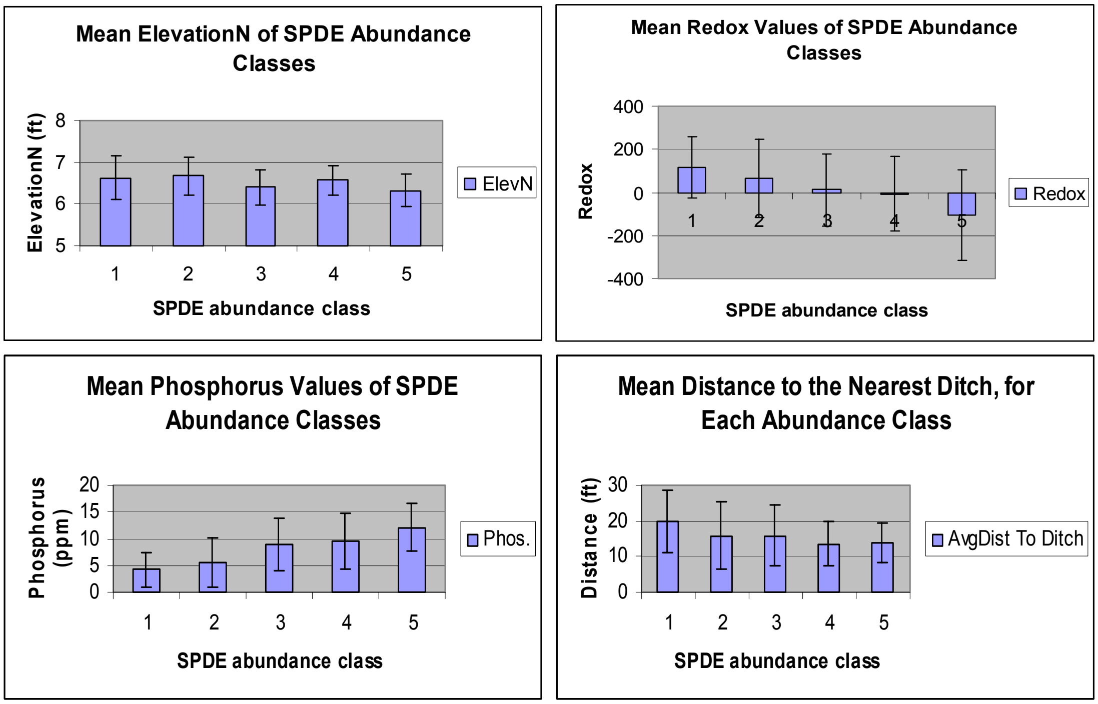


Figure 10. Bar graphs of mean variable values, by *Spartina* abundance class. The variables ElevationN, Redox, Phosphorus, and Average Distance (of plot) to Nearest Ditch show the mean value of the variable for each abundance class. The mean values are taken from Table 25, above. The error bars represent the standard deviation of each mean value.

Areas for Further Research

The rates of sedimentation and erosion in the Humboldt Bay salt marshes are unknown at this time. Thompson measured rates of sedimentation and erosion in the mudflats of Humboldt Bay (Thompson 1971). There has been some discussion recently of past tsunami events in Humboldt Bay, using sediment deposits to date those events. Those studies may lead to new knowledge in the sedimentation/erosion processes of the salt marsh. It is worth consideration and consolidation of such information, particularly with respect to salt marsh restoration projects around Humboldt Bay.

Another area for research is to determine the cause and effect in the correlation of *Spartina* abundance with available-phosphorus, redox, and elevation. It seems that phosphorus and elevationN are probably causes in *Spartina* abundance, but redox could be either a cause or an effect. Experiments could be carried out to measure the effect of adding phosphorus to a marsh site, or making it chemically unavailable for plant use. Tidal elevation experiments were carried out in San Fransisco Bay to determine the effect of elevation on seed germination and seedling success (Spicher 1984). That could be repeated for Humboldt Bay. *Spartina* may be expanding its range to lower and higher tidal elevations. Transplant experiments could shed some light on that possibility. Redox values could be experimentally changed by increasing the drainage at very saturated locations or decreasing the drainage at well drained locations.

The habitat of *Spartina* was defined using Logistic Regression with the covariates found to effectively describe *Spartina* abundance in Humboldt Bay. The habitat is defined using environmental gradients, but does not include the effects of competition between *Spartina* and other salt marsh plant species. The niche of *Spartina* could be defined when the effects of competition are added to the effects of the significant environmental gradients. The effects of competition could be quantitatively measured by carrying out transplant experiments between *Spartina* and other salt marsh species or vegetion classes (Bertness 1991, Eicher 1987). The experiment would probably require three years to complete.

With the information collected from the experiments described above, an accurate model simulation of the salt marsh, with respect to *Spartina* abundance, could be created (Berger et el. 2002, Berger and Hildenbrandt 2000). The model would serve to describe plant community changes that would occur if the environmental gradients were altered. Such a model could be expanded to include all of the salt marsh species or groupings of species.

Models that include changes in the salt marsh due to sedimentation and erosion are being constructed, and used to plan marsh restoration projects in the San Fransisco Bay Area. A new salt marsh is being formed near the mouth of Jacoby Creek due to sedimentation (Thompson 1971). Perhaps the physical changes in salt marsh due to sedimentation and erosion could be studied and coupled with a vegetation model into a larger salt marsh model.

SUMMARY AND CONCLUSION

The goal of this project was to develope a descriptive model of *Spartina densiflora* abundance, based on the environmental gradients that controlled its growth. Once that model was developed, it was expanded using logistic regression to define the habitat of *Spartina densiflora*. The covariates used in both models were analyzed to understand their relationship to *Spartina* abundance and to understand their relationship to each other. Ideally, the information learned about *Spartina* abundance could be utilized by land managers to control its further spread.

It is may be possible for the environmental gradients of phosphorus, redox, and elevationN to be manipulated to decrease *Spartina* abundance, both at current marsh sites and at future (restored) marsh sites. This possibility has not been tested. Marsh sites that have a large, relatively even elevation gradient are lower in *Spartina* abundance compared to sites with a small elevation gradient and relatively uneven marsh surface. Although site 10 was an exception to this trend, this site was within 1% of the model(s) prediction, and points to the observation that well drained and/or high elevation sites have a low abundance of *Spartina*, while sites that have very saturated and reduced soils have a high abundance of *Spartina*. Phosphorus may be the hardest environmental gradient to manipulate. Certain (volcanic) soils bind phosphorus and make it unavailable for plant use (Brady and Weil 2002). There may be chemicals that do the same thing, and can be used in the salt marsh for the management of *Spartina*.

The information collected here, combined with previous studies, constitutes an encouraging initial step in constructing an overall model of the salt marsh plant community, based on the environmental gradients found in the salt marsh. Using this model, marsh restoration projects could be simulated. The effect of alternate patterns of marsh topography, and the associated environmental gradients, on the salt marsh plant community would then be available for land managers in the planning stages of marsh restoration projects. The information collected in this study could be used to create a simple simulation of the salt marsh plant community, but such a model simulation would be greatly enhanced by field experiments testing the effects of plant competition on that community with respect to the significant environmental gradients. The effects of sedimentation and erosion in the salt marsh need to be studied, and could be incorporated into a model of the marsh community.

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