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# Marsh loss in Elkhorn Slough, CA : patterns, mechanisms, and impact on shorebirds

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# MARSH LOSS IN ELKHORN SLOUGH, CA: PATTERNS, MECHANISMS, AND IMPACT ON SHOREBIRDS

A Thesis Presented to the Faculty
of
San Jose State University
through
Moss Landing Marine Laboratories

In Partial Fulfillment of the Requirements for the Degree
Master of Science in Marine Science

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# ABSTRACT

## MARSH LOSS IN ELKHORN SLOUGH, CA: PATTERNS, MECHANISMS, AND IMPACT ON SHOREBIRDS

by Patricia B. Lowe

Pickleweed (*Salicornia virginica*) marsh has declined in Elkhorn Slough, California over the last 50 years. Analysis of aerial photographs from 1931 to 1997 showed significant decreases in pickleweed cover after the opening of Moss Landing Harbor (1947) and the Loma Prieta Earthquake (1989). A transplant experiment was done to determine whether increased tidal elevation would decrease pickleweed mortality and increase growth and flowering in a deteriorated marsh 12 cm lower than a densely vegetated comparison marsh. Most plants at the lowest elevation died within two years, while those at higher elevations survived, suggesting that increased elevation decreased pickleweed mortality. Elevation surveys in dense and deteriorated marsh areas showed more densely vegetated areas were higher. Bird surveys in well-vegetated marsh, deteriorated marsh, and mud flat areas suggested that well-vegetated marsh was used by fewer species than the other habitats, but may provide important habitat at extreme high tides.

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# TABLE OF CONTENTS

Page

List of Tables viii

List of Figures ix

Chapter 1: Patterns and Potential Mechanisms of Marsh Loss 1

Introduction 1

Study Location 5

Materials and Methods 5

Data from Historic Aerial Photographs 5

Marsh Sections 1-10 Combined 6

Individual Marsh Sections 8

Pickleweed Transplants 10

Elevation Versus Cover Transects 14

Results 16

Historic Aerial Photographs 16

Pickleweed Transplants 17

Elevation Versus Cover Transects 19

Discussion 19

Chapter 2: Impact of Marsh Loss on Shorebirds 26

Introduction 26

Materials and Methods 28

Results 32

Discussion 33

Literature Cited 39

Sources of Unpublished Materials 43

Tables 45

Figures 52

Appendices 68

# LIST OF TABLES

| Table | | Page |
|---|---|---|
| 1 | Film type and scale of images used in photo transects. | 49 |
| 2 | Areas (m$^2$) of marsh sections in 1937/39 and 1994 photos and number of transects assigned to sections for the combined section analysis. | 50 |
| 3 | Percent cover of pickleweed marsh in ground versus photo transects (B&W = black and white; CIR = color infrared) for three cover classes of marsh. | 51 |
| 4 | Number of plots, survey length, and tidal period for each habitat and survey date. | 52 |
| 5 | Bird taxa observed and percent frequency of occurrence in plots over entire survey period. | 53 |
| 6 | Proportional species composition at flush for all plots surveyed February 8 & 9, 1997. | 54 |
| 7 | Mean and range of maximum shorebird density (#birds/ha) for all survey dates. | 55 |

# LIST OF FIGURES

| Figure | | Page |
|---|---|---|
| 1 | Elkhorn Slough, Moss Landing, California showing ten sections sampled in photo transects, two areas used in transplant experiment, and 22 transects surveyed in elevation versus percent cover surveys. Manipulation control treatments in transplant experiment were in Marsh $A_1$ (~97% cover). Low, Medium, and High Box treatments were in Marsh B (~23% cover). | 56 |
| 2 | Change in percent cover ( $\bar{x}$ +/- SE) of pickleweed, bare mud, and channel over time for the entire study area (n=75/year). Years with the same letter are not significantly different from each other. | 58 |
| 3 | Change in percent cover ( $\bar{x}$ +/- SE) of pickleweed over time for each of ten marsh sections (see Fig. 1). The number of samples per year (n) is indicated for each section. Years with the same letter are not significantly different from each other. | 60 |

4 Percent of branches in flower ( $\bar{x}$ +/- SE) for pickleweed treatments. Deteriorated control (deter. control) represents naturally occurring pickleweed in Marsh B. Low, Medium, and High represent the three box elevations in Marsh B. Control, Transplant, and Box/Transplant represent the three manipulation control treatments in Marsh $A_1$. Treatments with the same letter are not significantly different from each other. 62

5a Dry weight (g) of total succulent parts ( $\bar{x}$ +/- SE) for all treatments in transplant study. Treatments with the same letter are not significantly different from each other. 64

5b Dry weight (g) of succulent parts of one branch ( $\bar{x}$ +/- SE) for all treatments in transplant study area as well as naturally occurring plants in Marsh B (Control B). Treatments with the same letters are not significantly different from each other. 64

6 Cover of pickleweed marsh (%) versus elevation (m above MLLW) for surveyed transects. MHW indicates average Mean High Water in the Elkhorn Slough. Note break in x-axis. 66

7a Plots used for bird surveys. D, V, M represent deteriorated marsh, densely vegetated marsh, and mud flat, respectively. 68

7b Example of mud flat plot used in bird surveys. Center stakes were used to measure exposure of mud flat. 68

8 Tidal heights (m) and times of first arrival of birds on 4 survey dates. Arrival times for individual plots are indicated (V and circle = densely vegetated marsh plot; D and cross = deteriorated marsh plot; M and rectangle = mud flat plot). 70

# Chapter 1: Patterns and Potential Mechanisms of Marsh Loss in Elkhorn Slough

## INTRODUCTION

Tidal inundation in salt marshes affects soil aeration and chemistry and influences plant growth (Adam 1990). Rapid increases in tidal inundation may cause loss of the original plant community and/or alter plant species composition toward that characteristic of lower marsh (Beeftink 1979). Episodes of salt marsh loss related to increased tidal inundation have been reported in several studies. Hackney and Cleary (1987) suggest that human elimination of sediment sources to large areas of marsh in southeastern North Carolina has resulted in drowning of these areas due to the inability of marsh accretion to keep up with sea level rise. Similar marsh loss is taking place on the Louisiana Gulf coast where the rate of coastal submergence from sea level rise and/or land subsidence exceeds accretion rates (DeLaune et al. 1983; Wells and Coleman 1987). Interestingly, salt marsh deterioration in coastal Louisiana proceeds from the marsh interior rather than the edge: small ponds form in interior areas and widen over time (DeLaune et al. 1990).

Increased tidal inundation and subsequent drowning of vegetation has also been reported following earthquakes. During the 1960 earthquakes in Chile, coastal areas subsided approximately 2 meters, submerging farmland and trees into the intertidal zone (Plafker and Savage 1970). In 1964, the Alaskan earthquake reportedly drowned vegetation on the Portage Flats (Bartsch-Winkler and Garrow 1978). However, in this case, vegetation changes were short-lived. Within 15 years, depositional processes and/or tectonic rebound raised the surface of the flats, allowing revegetation to proceed through natural recruitment.

Edaphic conditions leading to *Spartina* spp. marsh loss have been investigated in Louisiana and Great Britain. In Louisiana, reciprocal transplant experiments resulted in an increase in standing crop for *Spartina alterniflora* plants moved from more waterlogged inland marsh to more oxygenated creekside marsh and a decrease in standing crop for those moved inland from creekside marsh (Mendelssohn and McKee 1988a). Sulfide toxicity and long periods of anaerobic metabolism were implicated. Similar findings were reported in a series of investigations of *Spartina townsendii* marsh loss in Great Britain (Goodman et al. 1959; Goodman 1960; Goodman and Williams 1961). Goodman concluded that pooling of water in pan areas resulted in waterlogged conditions, increased hydrogen sulfide concentrations, and ultimately the death of plants through soft-rotting of rhizome tips. Culture experiments suggested that plant mortality was caused by a toxic reduced inorganic ion in the substrate, potentially sulfide (Goodman and Williams 1961).

Low soil nutrient levels may also contribute to marsh deterioration. In Louisiana, nutrient deficiencies may arise where inorganic sediment is not accumulating fast enough to support growth of *Spartina alterniflora*. Sediment addition that raised deteriorating interior marsh areas by 10 cm resulted in a significant increase in tissue concentrations of Fe and Mn in *Spartina* plants and doubled above-ground biomass by the end of the second growing season (DeLaune et al. 1990).

Various investigations have suggested that pickleweed (*Salicornia virginica*) marsh has declined in Elkhorn Slough (Fig. 1). This loss has been divided into two broad categories: 1) edge recession along the main channel and tidal creeks; and 2) interior marsh thinning. Edge recession has been attributed to increased tidal scour resulting from the opening of Moss Landing Harbor in 1947 and the failing of several dikes in the 1980s (Philip Williams & Assoc. et al. 1992; Crampton 1994; Malzone and Kvitek 1995). Marsh thinning has also occurred over the last 50 years, but particularly since 1989 in the upper slough. One area northwest of Kirby Park (see Results, marsh sections 3 and 4) has thinned so severely that it now resembles high mud flat with occasional patches of pickleweed. The reason for this thinning is not well understood.

Two previous studies have addressed the deterioration of interior marsh in the Elkhorn Slough. Crampton (1994) compared the elevation of deteriorated areas of marsh to densely vegetated areas by surveying marshplain elevation along 5 transects, three of which were in "relatively dense" marsh and two where cover was "sparse to nonexistent". Average marshplain elevation among dense marsh transects ranged from 3 cm below to 6 cm above average MHW in the slough. Average elevations for the two deteriorated transects were 11 cm and 20 cm below average MHW. Crampton (1994) suggested that surface scour following the opening of Moss Landing Harbor in 1947 may have played a part in reducing the elevation of deteriorated marsh in the upper slough once vegetation died. However, it is unlikely that erosion alone caused initial pickleweed thinning in the interior marsh; water velocities over dense pickleweed marsh at high tide are very low (personal observation) and pickleweed roots form thick mats, increasing soil resistance to erosion (Sliger 1982). Current velocities are also slower in the upper slough than in the lower slough (Smith 1973). Therefore, this mechanism alone does not explain why much of the marsh in this region of the slough has deteriorated substantially while marsh elsewhere has not. While Crampton (1994) describes an interesting trend in elevation in sparsely and densely vegetated areas, further surveys are needed to establish whether this trend is significant throughout the slough.

Oliver et al. (1988) examined change in percent cover of marsh vegetation in 10 areas of the slough using 1931, 1980, and 1987 aerial photographs. Eight of these areas consistently decreased in cover over the years sampled. For these 8 areas the average decrease in vegetative cover was 23% between 1931 and 1980 and 8% between 1980 and 1987. Assuming that marsh deterioration began with the harbor opening, these decreases in cover represent rates of loss of 0.7% per year before 1980 and 1.1% per year between 1980 and 1987 (Oliver et al. 1988).

The marsh has continued to deteriorate since 1987 (Oliver personal communication). This is particularly apparent in the upper slough. There are a variety of explanations for why interior marsh thinning is more severe in the upper Elkhorn Slough. Several attribute marsh loss to increased tidal inundation following subsidence of the deteriorated areas, and differ only in the proposed mechanism(s). Potential mechanisms include: the 1989 Loma Prieta earthquake (Oliver personal communication), movement along an unmapped fault along the western side of the Gabilan Range (Stamm personal communication), groundwater extraction from the adjacent Springfield Terrace (Zembsch personal communication), and slumping of the marsh plane toward the main channel due to erosion within the channel (ABA Consultants 1989).

In this study, the author carefully reviews the extent and rate of marsh loss to 1997 and compare recent rates of marsh deterioration to historical rates. Patterns and rates of marsh deterioration are described in order to examine the hypothesis that increased tidal inundation is responsible for marsh deterioration. My objectives were:

1) to quantify marsh loss from 1931-1997 and compare pickleweed cover among periods immediately before and after the opening of Moss Landing Harbor and the 1989 Loma Prieta Earthquake; and 2) to test the hypothesis that increased tidal inundation is responsible for marsh deterioration in the slough.

## STUDY LOCATION

The Elkhorn Slough is a tidal embayment located at the apex of Monterey Bay, California (Fig. 1). The main channel is approximately 10 km long and varies in depth from approximately 6.5 m MLLW at the hwy. 1 bridge to 1.7 m MLLW near Hudson's Landing (Malzone 1999). Mean diurnal tide is approximately 1.7 m (Broenkow 1995). Mean high water varies from 1.41 m above MLLW at the hwy 1 bridge to 1.47 m above MLLW at the Elkhorn Slough railroad bridge (NOAA, 1982 &1983; See Appendix 1 for tidal benchmark locations). *Salicornia virginica* is the dominant vascular halophyte in the salt marsh (MacDonald and Barbour 1974). *Jaumea carnosa*, *Frankenia grandiflora*, and *Distichlis spicata* occur less frequently, while *Spartina foliosa* is conspicuously absent (MacDonald and Barbour 1974).

## MATERIALS AND METHODS

### Data from Historic Aerial Photographs

Percent cover of pickleweed marsh in undiked areas of the Elkhorn Slough west of the railroad tracks (sections 1-10; Fig. 1) was measured in several sets of historical aerial photographs from 1931 to 1997 (Table 1) and compared among years. In addition, cover was compared within each section over the same time period in order to examine patterns of change at a smaller scale.

### Marsh sections 1-10 combined

Cover (measured as percent of area covered by crowns of pickleweed or other vascular plants as visible in a photo) was sampled by magnifying photos to approximately 1:2,000 scale under a dissecting scope and using the ocular micrometer to create 40-m (ground length) transects of 20 evenly spaced points. A boom dissecting scope was used for photographic prints, while a standard dissecting scope was used for slides.

Each of twenty points per transect was scored as one of four classes of cover: 1) pickleweed or other vascular halophyte; 2) tidal creek; 3) mud; or 4) unknown. Pickleweed was distinguished from mud in black and white photos by its darker color. Ponded water occasionally formed dark spots in pans but could be distinguished from pickleweed by the water's darker color and by the gradual color change between the edge of the pond and the surrounding mud as compared to the sharp color change between pickleweed and mud. In addition, any areas in question could be compared in overlapping photos to see how the surface reflected light at different sun angles. A strong reflection indicated water. In color photos, pickleweed was dark green or reddish brown, while mud was gray, light brown, or light green due to algal cover. In color infrared photos, pickleweed was dark green or light brown, often with a tinge of pink, while mud was blue-gray. Channels were distinguished by their curvilinear appearance in all photos.

In order to determine the accuracy of this technique as well as sampling bias among combinations of film type and scale used in this study, areas of marsh representing a wide range in percent cover were photographed and ground sampled for percent cover on the same day. In July, 1997, the end points of forty-six 40-m marsh transects were marked and photographed using the same film types and scales sampled in this study. While in the field, percent cover of pickleweed in each transect was sampled on the ground in two ways: 1) the intercept length was used to determine "actual cover"; and 2) 20 randomly selected points per transect were sampled to imitate methods used in photo transects. The same forty-six transects were sampled in each set of photos and divided into three cover classes (low, medium, or high) based on their actual cover. The mean and standard error for each cover class were then calculated for each sampling method and compared.

Prior to sampling historical photographs, a pilot study was done to determine sample size for comparison of pickleweed cover among years for sections 1-10 combined (Fig. 1). Eight 40-m transects (ground length) were randomly assigned to each of the following sets of photos: 1937/39, 1949, 1956, 1980, 1989, and 1993. Photographs from 1937 and 1939 were combined in the 1937/39 category due to incomplete or unclear coverage of some marsh areas in each set. A power analysis (Sokal and Rohlf 1995) using $\alpha = 0.05$ and $\beta = 0.20$ indicated that 75 transects would be sufficient to detect a 10% difference in cover among years for sections 1-10 combined.

Actual sampling incorporated pilot study results. A total of 75 transects for each set of photographs was randomly placed within 10 marsh sections (Fig. 1) in proportion to the area of each section (Results Table 2, Methods below) in either 1937 or 1939, depending on which set of photos covered that section best. Transects were then sampled as described above.

Cover of pickleweed marsh for all 10 sections combined (n=75) was statistically compared among years. An arcsin transformation (Zar 1996) failed to correct non-homogenous variances and skewness. Therefore, a Kruskal-Wallis test (SYSTAT 1992) was used on the untransformed data, followed by a Games-Howell test (Day and Quinn 1989) on the arcsin-transformed data since the transformation reduced departures from normality and homogeneity of variances.

Bare mud and channel cover were also compared among years in separate analyses for each cover type. Both sets of data failed to meet assumptions of normality and homogeneity of variances despite transformation and were, therefore, analyzed using Kruskal-Wallis tests (SYSTAT1992) on untransformed data (n=75 for each test). Both tests yielded significant results and were followed by a Games-Howell test (Day and Quinn 1989) on square root-transformed data (Zar 1996) which reduced departures from normality and homogeneity of variances.

### Individual marsh sections

Additional transects were necessary to complete several of the individual section comparisons as some sections were initially sampled using only one or very few transects in the section 1-10 comparison. Pilot sampling of 5 transects per section in 1931, 1937/39, 1949, 1956, 1980, and 1989 photographs was done to estimate cover variability in each section in each year. A power analysis (Sokal and Rohlf 1995) was then used to determine sample size necessary for a minimum detectable difference of

25% cover in an ANOVA with $\beta = 0.20$ and $\alpha = 0.05$. In sections where the initial number of transects used in the section 1-10 comparison was greater than or equal to the number determined in the power analysis for that section, no transects were added or subtracted. In other sections, additional transects were randomly assigned to achieve the total number needed. Therefore, the number of transects sampled for each section comparison varied, but the minimum detectable difference in pickleweed cover was 25% or less for all sections.

Cover sampling within individual sections followed the methods used for sections 1-10 combined. For all percent cover sampling, the marsh section edge adjacent to the main channel was defined as the break in slope at the edge of the marsh plain and beginning of the channel. Frequently this was the most channelward edge of pickleweed growth. However, in marsh sections that had thinned so severely that there was no obvious pickleweed edge, the section edge was defined by other cues of break in slope such as a sharp transition in algal growth. All tidal creeks within section borders were considered part of the sampling area.

In order to determine the change in marsh section areas due to channel erosion over the time period sampled, photographs from 1937, 1980, and 1994 were scanned at 600 dots/inch and then georectified and resampled using TNTmips geographic information system software (MicroImages® 1995). The 1980 photographs were the largest scale of the three sets (1:12,000) and were used as a reference map from which to georectify the other two sets. Control points used for georectification of 1980 photographs were measured in the field with a Trimble® ProXL global positioning system with NavBeacon (horizontal accuracy +/- 0.75 m). A plane rather than affine model was used to georectify images because it more accurately fit the images, indicating there was some tilt in the photographs. Residuals were approximately equal to the cell size of 0.5 m x 0.5 m for 1980 photographs, 1 m x 1 m for 1994 photographs and 0.9 x 0.9 m for the 1937/9 photographs. Once photographs were resampled and enlarged to a 1:4,500 scale, heads-up digitizing with a planimeter was used to measure section areas in the 1937/9 and 1994 photographs. Preliminary sampling of both large and small sections showed that the error associated with tracing at 1:4,500 enlargement was less than 2% of the area of each section.

Section percent cover data that did not meet assumptions of normality and homogeneity of variances for ANOVA were transformed using an arcsin transformation (Zar 1996). Cover estimates were then compared statistically among years using ANOVA when raw or transformed data met the above assumptions and a non-parametric Kruskal-Wallis test (SYSTAT 1992) when raw data could not be successfully transformed. Significant tests were followed by one of the following unplanned multiple comparison tests: a Bonferroni test (SYSTAT 1992) if variances were equal and data were normally distributed, a Tukey's test (SYSTAT 1992) if variances were equal but data were not normally distributed, or a Games-Howell test (Day and Quinn 1989) if variances were unequal.

### Pickleweed Transplants

A large tidal creek in the northwest region of the slough divides the marsh into two areas, one with approximately 23% cover vascular halophytes (Marsh B) and the other 97% cover (Marsh A) (Fig. 1). In 1949, these areas were both >90% cover. However, Marsh B has deteriorated considerably since then (personal observation of aerial photos). Marsh A also has an extensive patch of saltgrass (*Distichlis spicata*), suggesting it might be slightly higher and less frequently inundated than the deteriorated marsh. To determine whether there was an elevation difference between the two areas, the average elevation of a 2500 $m^2$ area of each marsh was surveyed in April, 1994 using a Topcon® AT-G7 automatic level (leveling accuracy = 0.5 cm). In addition, a 25 m x 25 m subarea of Marsh A (area $A_1$) consisting of >90% cover *Salicornia* and 0% *Distichlis* was surveyed. Elevations were measured at 15 randomly selected points in each of the three areas and mean relative elevation for each area calculated. The relative elevations for these three areas were: Marsh A, +18 cm; Marsh $A_1$, +12 cm; and Marsh B, 0 cm. Mean relative elevation was found to be significantly different among all marsh areas [Kruskal-Wallis test ($p<.0001$) (SYSTAT 1992) followed by a Games-Howell unplanned multiple comparison test ($\alpha = .05$) (Day and Quinn 1989)].

To determine whether Marsh B was too low for pickleweed survival, growth, and flowering, a transplant experiment was done. *Salicornia* plants from Marsh $A_1$ were transplanted in Marsh B at low (~1.34 m MLLW), medium (~1.46 m MLLW), and high (~1.53 m MLLW) elevations created artificially using 60 cm x 60 cm wooden, open-ended boxes. Low boxes were pushed into the marsh flush with surrounding sediments. Medium boxes protruded several centimeters from the marsh surface at elevations approximately equal to the average elevation of Marsh $A_1$. High boxes protruded still further from the marsh surface at elevations approximately equal to the average elevation of Marsh A. In addition, *Salicornia* plants from Marsh $A_1$ were randomly assigned to manipulation control treatments in Marsh $A_1$ designed to test for effects of box materials and transplanting. The three manipulation control treatments were: 1) transplant treatment (~1.48 m MLLW): all existing pickleweed within a 60 cm x 60 cm area was removed and the top 15 cm of sediment excavated and replaced before transplanting pickleweed into the area; 2) transplant/box treatment (~1.46 m MLLW): same as the transplant treatment except that a box was pushed flush into the sediment around each replicate; and 3) control treatment (~1.45 m MLLW): unmanipulated pickleweed marsh.

Five replicates of each elevation treatment were randomly placed in Marsh B, and five of each manipulation control treatment in Marsh A1. From May 1-6, 1994, following a 2-week period allowing sediment within boxes to settle, four randomly selected vegetated soil blocks (7 cm x 7 cm x 15 cm) were transplanted into the center of each 60 cm x 60 cm area, with the exception of the controls.

Plants remained in treatments for approximately 16 months. During this time accumulations of drift *Enteromorpha* sp. were periodically removed from plants in Marsh B to allow adequate light penetration. Little *Enteromorpha* sp. accumulated on plants in Marsh A1 so removal was not necessary.

On August 28 & 29, 1995, approximately the middle of the flowering season for pickleweed (Mayer 1987), 20 randomly selected branches per plot were examined for flowers. A branch was defined as the portion of the plant from the tip of a distal succulent internode down the axial stem to the point where the stem was rooted in the sediment and included all side stems extending from the axial stem. The percent of 20 branches with one or more flowers was calculated for all plots and compared among treatments. In addition, five 1 $m^2$ areas of pickleweed within Marsh B were randomly selected to represent naturally occurring plants within the deteriorated marsh.

In September, 1995, aboveground growth from all treatments was harvested to compare dry weight of succulent parts (Pennings and Callaway 1992) among treatments. Pennings and Callaway (1992) found that dry weight of succulent parts was a more reliable estimate of growth than cover because *Salicornia* has different growth morphs at different tidal elevations. The control treatment did not contain transplanted plants and, therefore, was not included in this comparison. However, prior to harvest, plants within control areas were visually compared to plants within the transplant treatment to qualitatively assess whether transplanting had noticeable effects on plant growth and survival. A second, quantitative assessment of growth of the control treatment as compared to other treatments was also done. Two randomly selected branches (defined as above) from each box, including the control, were processed and weighed separately before being combined with the rest of the succulent parts. The dry weights of the two branches per plot were averaged for a single value and dry weight of branch succulent parts compared among treatments. Two randomly selected branches from naturally occurring pickleweed in Marsh B were also processed and included in the comparison.

The percent of branches in flower, dry weight of all succulent parts, and dry weight of one branch were compared among treatments in three separate tests. For all tests, the high treatment consisted of four replicates while all other treatments had five. Flowering was compared among treatments using ANOVA (SYSTAT 1992) followed by a Tukey-Kramer unplanned multiple comparison test because of unequal sample size among treatments. Dry weight of all succulent parts was compared using a Kruskal-Wallis test (SYSTAT 1992) followed by a Games-Howell unplanned multiple comparison test (Day and Quinn 1989) because transformation failed to make variances equal. Weight of succulent parts from a single branch was compared using ANOVA on log-transformed data (Zar 1996) followed by a Tukey-Kramer unplanned multiple comparison test.

### Elevation Versus Cover Transects

Between July 23, 1996 and November 4, 1996 the relationship between percent cover pickleweed and tidal elevation was examined using 22 10-m transects placed in both thinned and well-vegetated areas of marsh from Seal Bend to Kirby Park (Fig. 1). Six strata representing high (80-100%), medium (21-79%), and low (0-20%) pickleweed cover in either the upper or the lower slough were defined in a 1996 aerial photograph. In the lower slough, five, six, and six transects were randomly assigned within the low, medium and high cover areas, respectively. In the upper slough, four, one, and zero transects were randomly assigned within the low, medium and high cover areas, respectively.

Percent cover of pickleweed was determined along each transect by stretching a tape measure between the two end points and classifying cover as pickleweed or bare mud at 33 randomly assigned points. Elevation was measured with GPS along the same transects at ten points: the two end points and eight randomly assigned points. Real time kinematic (RTK) and post-processed GPS surveys were done using a Trimble™ Survey Controller™ and two 4000 Ssi™ receivers (accuracy = +/- 1.0 cm + 2 ppm). All baselines were less than 3 km and extended from a single benchmark, ELK1 (see Appendix 1 for location). Transect surveys were not repeated. However, two control points were occupied during each survey in order to check the accuracy of GPS positions.

All post-processed GPS surveys were processed using Trimble GPSurvey™ software version 2.2 (Trimble Navigation Ltd. 1996a). All RTK surveys were processed using Trimble TRIMMAP™ software version 6.00 (Trimble Navigation Ltd. 1996b). In order to translate GPS ellipsoidal heights into heights relative to NAVD 88, a fully-constrained network adjustment was done in GPSurvey. Network control consisted of 5 benchmarks surrounding the study area (see Appendix 1). Independent baselines between benchmarks were derived from 1.25 hour static surveys using two Trimble 4000 Ssi ™ dual frequency receivers to occupy two benchmarks simultaneously. Error in height estimates was less than 2.0 cm for all benchmarks after adjustment.

After elevations were established relative to NAVD 88, they were converted to NGVD 29 using NGS VERTCON software version 2.0 (National Geodetic Survey Program 1994) (accuracy = +/- 2.0 cm). Next, published 1976-1977 tidal data from two National Ocean Service tidal benchmarks in the upper and lower slough (see Appendix 1) (NOAA 1982; NOAA 1983) were used to determine the elevation of MLLW relative to NGVD 29. Because MLLW differed by 2.5 cm between the two stations, the average value, 0.83 m, was added to adjust NGVD 29 elevations to MLLW.

Assuming that the 1970s NOAA tidal data accurately describe current tidal levels in the slough, maximum error in absolute elevations (m above MLLW) is approximately 6 cm. This is the sum of: 1) error in measurement of GPS ellipsoidal heights (+/- 2.0 cm for longest baselines); 2) error in converting ellipsoidal heights to orthometric heights in NAVD 88 (+/- 2.0 cm); and 3) error in converting from NAVD 88 to NGVD 29 (+/- 2.0 cm). Since the last conversion involved adding a near constant to all points, maximum error in the relative elevation of points is only 4 cm.

Mean elevation of each transect was calculated from the 10 elevations measured. These values were then plotted against percent cover pickleweed for each transect. Two discrete clusters were apparent, one of pickleweed cover over 80% and another of less than 40%, suggesting that a regression analysis was inappropriate. Instead, the clusters were treated as two populations and their means tested for significant difference. Because these clusters differed greatly in size (16 versus 6 transects), a one-tailed Mann-Whitney U test (SYSTAT 1992) was used to test whether marsh elevation was higher in areas of over 80% cover than in areas of less 40% cover.

## RESULTS

### Historic Aerial Photographs

Marsh section areas in 1937/39 and 1994 photos are listed in Table 2. Only sections seven and eight decreased in area by more than 10% between the two dates. The total decrease in area for sections 1-10 combined was approximately 4%.

Pickleweed cover estimates from point-sampled ground transects were close to the actual cover for low, medium, and high cover classes (Table 3). Mean cover and standard error estimated from various scales and film types were also comparable within each cover class. The greatest difference, 7%, was between the Color IR estimates and actual cover values for the intermediate cover class. Differences may be in part due to the difficulty in sampling the exact same area in both the photos and on the ground. No obvious bias in marsh cover estimates was apparent among the four combinations of film type and scale.

The percent cover of pickleweed marsh in sections 1-10 combined decreased significantly during the study period (Kruskal-Wallis, $p<0.0005$) (Fig. 2). Cover remained over 90% throughout the 1930s and 1940s. This period of little or no change was followed by a significant decline in percent cover between 1949 and 1956, soon after the opening of Moss Landing Harbor (Games-Howell on arcsin-transformed data, $\alpha = 0.05$). From 1956 to 1989 marsh cover remained approximately 70-75%. The next significant decrease in cover occurred between 1989 and 1993, the period just after the Loma Prieta earthquake (Games-Howell on arcsin-transformed data, $\alpha = 0.05$). There was no significant change in percent cover between 1993 and 1997.

Percent cover of bare mud in sections 1-10 combined increased significantly between 1949 and 1956 and again between 1989 and 1993 (Kruskal-Wallis, $p<.0005$; Games-Howell on square root transformed data, $\alpha <.05$) (Fig. 2). Channel cover also increased over the study period with significant change occurring between 1949 and 1980 (Kruskal-Wallis, $p<.0005$; Games-Howell on square root-transformed data, $\alpha <.05$).

All individual sections showed a significant decrease in pickleweed cover sometime during the study period (Fig. 3; App. 2) (Note: section 7 ANOVA results were significant, but Bonferroni results were not.). Between 1931 and 1949, the only section to significantly decrease in cover was section 10. From 1949 to 1956 sections 1, 2, 3, and 10 decreased in cover. Section 1 then increased in cover between 1956 and 1980. No sections changed significantly between 1980 and 1989, although section 3 decreased significantly between 1956 and 1989. Sections 2, 3, 4, 6, and 8 decreased in cover between 1989 and 1993. No significant change occurred in any section between 1993 and 1997.

### Pickleweed transplants

The low box treatment had a significantly lower percentage of branches in flower than all other treatments in deteriorated Marsh B (ANOVA, $p<0.0005$) (Fig. 4). No significant difference was found in percent of branches in flower among manipulation controls in Marsh $A_1$, low boxes, and naturally occurring pickleweed in Marsh B (deteriorated control).

Dry weight of total succulent parts and succulent parts from a single branch tended to increase with increase in box height in Marsh B (Figs. 5a & b). The high treatment for dry weight of total succulent parts was significantly different from all other treatments in both marshes (Kruskal-Wallis, $p=0.001$; Games-Howell, $\alpha=0.05$). The high treatment for dry weight of succulent parts from a single branch was significantly different from all but the medium treatment (ANOVA on log-transformed data, $p=0.001$; Tukey-Kramer on log-transformed data, $p<0.012$ for all pairwise comparisons).

An unexpected result was that low box treatments in deteriorated Marsh B did not produce significantly lower dry weights of succulent parts than manipulation controls in densely vegetated Marsh $A_1$ (Figs. 5a & b). However, differences in plant health were apparent the following growing season: only two of the low boxes regenerated above ground growth, while all five replicates of both the box/transplant and transplant treatments did.

A second unexpected result was that the medium boxes produced greater dry weights of total succulent parts than did the box/transplant treatment in Marsh $A_1$ (Kruskal-Wallis, $p=0.001$; Games-Howell, $\alpha=0.05$) (Fig. 5a). The medium boxes were set at the same tidal elevation as the manipulation controls in Marsh $A_1$ but grew more vigorously.

Apparent differences in the water content of surface soils in the two treatments led to the hypothesis that boxes may have created artificially dry soils at the tidal elevation at which they were placed. Two mechanisms were suspected: 1) increased drainage in medium boxes from small holes (0.5 cm diameter) drilled in the sides of boxes and lined with 0.5 mm mesh; and 2) increased exposure to air due to lack of insulation by surrounding marsh soil. In order to determine whether medium boxes were drier than box/transplant treatments, gravimetric water content was determined (Rundel & Jarrell 1989) from soil cores (depth = 9 cm) taken after a daytime low tide in June of 1996. A single core was taken from each of 4 medium boxes and 4 box/transplant boxes. Soil moisture in the box/transplant treatment ( $\bar{x}$ =1.97 g $H_2O$/g dry soil; SE=0.23) was significantly higher than that in the medium treatment ( $\bar{x}$ =1.36 g $H_2O$/g dry soil; SE=0.10) [one-tailed t-test, n=4, p=0.026 (SYSTAT 1992)].

### Elevation Versus Cover Transects

Elevations measured at each of the control points among survey days were within a 2 cm vertical range, suggesting that the error in GPS observations was within the stated accuracy levels for the equipment. Average MHW was calculated from two tidal benchmarks in the upper and lower slough (NOAA 1982; NOAA 1983; see Appendix 1 for locations) and is given relative to average MLLW at the two locations.

Percent cover pickleweed for all 22 transects plotted relative to average Mean High Water (MHW) in the slough indicates two groups of points (Fig. 6). The group of six transects with percent cover values over 80% were of significantly higher elevation than those under 40% cover (Mann-Whitney U, p<.001).

## DISCUSSION

Large scale loss of pickleweed marsh in undiked areas of the Elkhorn Slough has clearly occurred over the last 50 years (Figs. 2 & 3). Although there was a significant increase in percent cover of tidal creeks (Fig. 2) and a reduction in the area of some marsh sections during the study period (Table 2), most marsh loss was due to conversion of pickleweed cover to bare mud (Fig. 2). Within the study period two episodes of more rapid loss were evident in sections 1-10 combined: after the opening of Moss Landing Harbor (1947) when pickleweed cover significantly decreased by 20%, and following the 1989 Loma Prieta Earthquake when pickleweed cover significantly decreased by 31%.

The opening of Moss Landing Harbor greatly altered the tidal regime within the Elkhorn Slough, converting a tidally restricted body of water to a more open system with a direct entrance to Monterey Bay. Following this event, the tidal prism within the Elkhorn Slough increased, resulting in more rapid tidal currents and scour within the main channel (Philip Williams & Associates et al. 1992). While erosion was likely a major cause of the reduction in marsh section areas (Table 2) and the increase in percent cover of tidal creeks over the study period (Fig. 2), it is unlikely that tidal currents were strong enough to thin pickleweed in the interior marsh. More likely, the opening of Moss Landing Harbor increased tidal amplitude (Gordon 1996; Crampton 1994), raising MHW above a critical level required for dense pickleweed in many locations. The increase in MHW was apparently large enough for local residents to observe pickleweed growing farther inland and salt water flowing farther up arroyos north of the slough (Gordon 1996). However, the researcher knows of no pre-harbor records of tidal amplitude or MHW to provide a quantitative estimate of this change.

It is possible that even a slight increase in MHW could have affected the marsh. Beeftink (1979) found that a 10 cm rise in MHW in a Netherlands salt marsh altered plant species composition toward a community typical of earlier stages of salt marsh development. In Louisiana, Mendelssohn and McKee (1988b) found that transplanting *Spartina alterniflora* 10 cm below the marsh surface significantly reduced plant height, density, and biomass relative to transplants placed at marsh level in the same marsh. Laboratory experiments by Mahall and Park (1976b) indicated that an 8-9 cm increase in maximum depth of twice daily 'tidal' flooding, together with a 35 minute increase in flood and ebb duration, was enough to decrease growth of *Salicornia virginica* seedlings by 64% and older plants by 37% over 37 days.

The results of this pickleweed transplant experiment and elevation surveys suggest that small differences in tidal elevation may also impact pickleweed growth in Elkhorn Slough. Although most of the transplant results were confounded by a box effect, one effect of elevation was clear. Most plants transplanted into low treatments in Marsh B (11 cm below MHW) died within 9 months after harvest, while those at higher elevations in both marshes survived. My elevation surveys suggest pickleweed may have difficulty growing as little as 6 cm below MHW. All but one transect below MHW had less than 40% cover pickleweed, while all those above MHW had over 80% cover pickleweed (Fig. 6). These results agree with the approximate lower limit of dense pickleweed marsh reported elsewhere in California (Hinde 1954; MacDonald and Barbour 1974; Mahall and Park 1976a). In Palo Alto, Hinde (1954) noted that where *Salicornia ambigua* (*virginica*) did occur below MHW, it was either mixed with *Spartina foliosa* or sparsely distributed and separated by muddy spaces covered with algae.

High rates of marsh loss following the 1989 Loma Prieta Earthquake suggest that this event also contributed to marsh deterioration. However, the mechanism is unclear. Sections 3, 4, and 6 in the upper slough and section 8 below Kirby Park deteriorated more than other sections after 1989. If subsidence were involved one would expect these sections to be lower in tidal elevation than those closer to the mouth where deterioration has been less severe. While this may or may not be true for these sections, it certainly is not true for the entire upper slough. According to Crampton (1994), in September, 1993, the marshplain along the west side of the main channel decreased with increasing distance from the mouth by a total of 23 cm across 4 transects. The first of his 4 transects was in the area designated marsh section 1 in the present study and the last in section 3. However, a fifth transect in marsh section 5 was higher than these four. Clearly, if the upper slough subsided during the earthquake, it either subsided different amounts in different areas, or sections 5 and 7 were higher than other areas before the earthquake.

Despite the complex patterns of marsh loss in the upper slough, the earthquake cannot be ruled out as a potential contributor. Although National Geodetic Survey (NGS) benchmarks in upland areas surrounding the slough have not been resurveyed by NGS since the earthquake (Till personal communication), levees at the Elkhorn Slough National Estuarine Research Reserve settled over 0.5 m during the earthquake and large fresh cracks were observed in the marsh north of Kirby Park (Silberstein personal communication). While pre-earthquake elevation surveys of the marshplain were done in some areas (Silberstein personal communication), they have not been repeated since the earthquake. A second survey of these areas coupled with study of surface erosion rates in denuded and densely vegetated areas of the marshplain might help clarify whether a change in marshplain elevation has actually occurred since the earthquake and whether subsidence and/or surface erosion were involved.

Another hypothesis used to explain higher marsh loss in the upper slough is that the tidal amplitude is greater there (Crampton 1994). Data for the 1960-1978 tidal epoch show a 3 cm upslough increase in MHW (relative to National Geodetic Vertical Datum-1929) between a NOAA tidal benchmark at the highway 1 bridge and one at the Elkhorn Slough railroad bridge near the head of the slough (NOAA 1982; NOAA 1983). However, if this difference has existed since at least 1978 when the tidal data were collected, why was there no sharp change in pickleweed cover in the upper slough until after 1989? This difference in MHW is, at best, only a partial explanation.

Crampton (1994) argued that accentuation of channel levees in the upper slough has led to ponding, creating waterlogged soils and marsh deterioration. However, of the two marshplain transects he surveyed in low cover areas, only one showed this feature. Also, any levee accentuation in the upper slough could as easily be the result as the cause of marsh deterioration. Levee soils are better drained and aerated than the adjacent marsh (Adam 1990) and often support more vigorous growth of marsh vegetation (Hinde 1954). In some deteriorated areas of the upper slough pickleweed exists only on levees (Crampton 1994; personal observation) and may help protect them from surface scour, resulting in slower rates of surface erosion on levees than in other areas of deteriorated marsh. Furthermore, although the researcher has often observed large puddles on the surface of deteriorated marsh, most did not appear restricted by tidal creek or main channel levees. The spatial relationship between puddles and levees and the number and size of puddles in deteriorated marsh versus well-vegetated marsh should be further investigated to determine whether deteriorated marsh areas tend to pond water more than vegetated areas, and whether puddles on the deteriorated marsh occur primarily adjacent to levees.

Another explanation for marsh loss is that marsh submergence in Elkhorn Slough is prolonged by a longer flood period (Crampton 1994). Crampton (1994) argues that because Elkhorn Slough has become more ebb-dominant due to the restoration of diked wetlands to tidal flow in the 1980s (Wong 1989) and because the difference between mean higher high water and mean sea level is greater than that between mean lower low water and sea level, pickleweed is submerged longer. However, in order for a longer flood tide to increase the time that the marsh is submerged, one needs to show that water levels are above marshplain elevation longer when the tidal curve is skewed than when it is symmetrical. Crampton (1994) did not provide any evidence of this.

Finally, ABA Consultants (1989) suggested that marsh slumping toward the eroding main channel may have aided in marsh deterioration. A crack approximately 15 m long, 15 cm wide, and up to 2.45 m deep in the upper west slough (Foster personal communication; author's measurements) may be an indication that slumping is occurring. The crack is within a band of dense marsh at the shoreward edge of a large depression devoid of pickleweed. However, to my knowledge, no other potential signs of marsh slumping have been reported. Also, since severe channel erosion occurred in the lower slough before the upper slough (Kvitek personal communication), there should have been more slumping and deterioration in the lower slough. The pattern of deterioration is just the opposite.

In summary, while the opening of Moss Landing Harbor in 1947 and the 1989 Loma Prieta Earthquake seem to have initiated periods of sharp decline in pickleweed marsh, the patterns of presently understood marsh loss in different areas of the slough do not suggest simple cause and effect relationships. Patterns of marsh change after 1956 are especially difficult to interpret. Why did the marsh recover after 1956 in section 1 but not in other sections? If the marsh surface accreted in this area, why didn't it do so throughout the slough? Next, while abundant anecdotal evidence exists regarding subsidence in the upper slough during the earthquake, there is no strong evidence of a fault to explain why the upper slough was affected more than the lower slough and why certain areas in the upper slough appeared unaffected by the event. Further geological investigation is needed. In addition, there may be other factors that could explain why the marsh has deteriorated more in the upper slough. Neither the potential impact of groundwater extraction west of the upper slough nor the effect of disease was considered. A disease affecting pickleweed morphology has been described in China Camp State Park in the San Francisco Bay area (Parker personal communication). While the author has not observed plants that have symptoms of this disease, there may be other pests or diseases of which the author is unaware. However, why would such a disease be concentrated in the upper slough?

Interestingly, the two periods of significant marsh loss for the combined sections, 1949-1956 and 1989-1993, were followed by periods of insignificant change in pickleweed cover when marsh deterioration appears to have slowed. Although it is difficult to tell whether the most recent period of marsh decline is over from only one sampling date after 1993, comparison of the significant 31% decline in marsh cover during the four year period before 1993 with the insignificant change in cover during the four year period after 1993 suggests that pickleweed cover may be stabilizing in the interior marsh.

Although marsh cover may be stabilizing within the study area, there is no strong evidence of recovery. In fact, the marsh surface in some denuded areas appears to be actively eroding (Crampton 1994; personal observation). If, as results suggest, marsh loss is in part due to low marsh elevations relative to MHW, the marsh may not recover unless slough water levels decrease and/or marsh elevation increases through accretion.

# Chapter 2: Impact of Marsh Loss on Shorebirds

## INTRODUCTION

California coastal wetlands serve as important feeding and resting grounds for several thousand shorebirds that migrate along the Pacific Flyway (Ramer et al. 1991). While shorebirds may spread out across expansive areas of suitable habitat during breeding season in the Arctic, they are restricted to much smaller patches of shore and coastal wetland during migration (Myers et al. 1987). High concentrations of birds within few sites places shorebirds at increased risk of negative impacts from wetland degradation along migration routes (Morrison 1984; Myers et al. 1987; Howe et al. 1989). In California, over 90% of wetlands have been severely altered by human activity (Dennis and Marcus 1984; Faber 1993) making protection and proper management of remaining wetlands critical to shorebird conservation.

The Elkhorn Slough in Monterey County is one of the largest coastal wetlands available to shorebirds on the Pacific Flyway (Ramer et al. 1991). Over the last 50 years pickleweed (*Salicornia virginica*) marsh within the slough has deteriorated significantly (see chapter 1). The upper slough has undergone particularly severe thinning and shows little sign of reversal. In these areas, densely vegetated marsh has been replaced by high mud flats nearly devoid of vascular plants, but seasonally covered by green algae (*Enteromorpha* spp.). The potential impact to shorebirds of this decrease in vegetated marsh and increase in deteriorated marsh is not well understood.

Shorebird use of marshes has received little attention in shorebird literature (Burger et al. 1997). In coastal California, Marbled Godwits, Willets, and Long-billed

Curlews are known to use salt marsh for roosting and feeding, particularly during mid to high tides. Gerstenberg (1979) reported that Marbled Godwits were the most frequently observed species in censuses of salt marshes near Humboldt Bay. Stenzel et al. (1976) reported that both Long-billed Curlews and Willets roosted in the salt marsh at Bolinas Lagoon during high tides. Willets fed extensively in the salt marsh during mid to high tides, while Long-billed Curlews were occasionally seen feeding there (Stenzel et al. 1976). Ramer (1985) identified pickleweed marsh in the Elkhorn Slough area as a high tide roosting and feeding area for Willets, Marbled Godwits, and Long-billed Curlews. Some Willets and Long-billed Curlews also fed in the marsh during low tides.

Two unpublished studies have examined shorebird use of deteriorated versus densely vegetated marsh in the Elkhorn Slough. Bockus (1994) compared shorebird use of a 15,000m$^2$ deteriorated marsh to an adjacent well-vegetated marsh of the same size during rising tides on 4 days in April and May, 1994. During the four rising tides observed, shorebirds tended to arrive at the deteriorated area before the vegetated area, and the number of foraging shorebirds decreased in the deteriorated marsh as it increased in the densely vegetated marsh. Shorebirds did not use either area during low tides. While this limited contrast of two marshes did not permit strong conclusions regarding habitat types, results suggest there may have been habitat selection according to tidal perameters. Benson (1994) also compared shorebird use of adjacent deteriorated and densely vegetated marsh habitats. He used three sites within Elkhorn Slough and the Old Salinas River Channel, each of which contained both deteriorated and densely vegetated marsh. Each site was surveyed at high tide on a single day between November 23 & 25, 1994. Mean shorebird density was significantly higher in the well-vegetated marshes. However, observations were carried out over a very narrow tidal range (+1.2 m - +1.4 m MLLW) and may have missed peak use times in one or both habitats.

The objective of this study was to determine potential impacts of marsh loss on shorebirds using the Elkhorn Slough. Specific objectives were to determine: 1) the tidal range during which shorebirds used each habitat over a falling tide; 2) the species that used each habitat during that time; and 3) the maximum densities that occurred within each habitat.

## MATERIALS AND METHODS

Surveys of shorebird densities in densely vegetated marsh (% aerial cover vascular plants: 96-99%, $\bar{x} = 97.2\%$), deteriorated marsh (% cover: 24-41%, $\bar{x} = 31.6\%$), and mud flat (0% cover) habitats were done on January 28 and February 26, 1995 and February 8 and 9, 1997.

Marsh areas for potential plots were selected based on several factors. All areas were near high ground that served as a good overlook and were close enough to allow observers to easily distinguish species with binoculars. Areas of at least 60 ares (1 are = 100 $m^2$) of fairly uniform cover were chosen so that plots (avg. size = 38 ares) placed within these areas would not be prone to edge effects. Areas experiencing heavy weekend kayak traffic were avoided.

Given the above restrictions, 6 areas were designated for each marsh habitat (Fig. 7a). Exact plot placement and shape within each area were based on the best possible view from the nearby overlook. In addition, all marsh plots were placed at least 25 m from the upland edge of the marsh.

Mud flat plots were 30.5 m to 45.25 m long (exposed area at a 0.0 m tide was 12 - 17 ares). This allowed the entire plot to be viewed easily from boats anchored 60 m from shore and kept the largest likely flock size observed comparable to that in the much larger marsh plots. Five plots were randomly located in mud flats north of Seal Bend adjacent to the marsh (Fig. 7a). Areas with large dips in the surface were avoided so that all birds on the mud flat would be visible.

The number of plots used during each survey is listed by habitat type in Table 4. For 1995 surveys all plots were selected randomly. For 1997 surveys plots were assigned to either February 8th or February 9th in such a way that the deteriorated and densely vegetated plots observed on the same day were not close together. This was done to avoid disturbing deteriorated plots when well-vegetated plots were flushed of all birds at the end of surveys (described below).

All surveys occurred during daylight and under low wind conditions. All surveys took place during falling tides after an extreme high tide (1.76 – 1.92 m MLLW) and began when plots were submerged. Survey length and tidal period are listed by habitat for each survey date in Table 4.

Families included in surveys were: Scolopacidae, Charadriidae, Ardeidae, and Laridae. All Dunlins, Western and Least Sandpipers were grouped as "small sandpipers". Greater and Lesser Yellowlegs were combined as were Short-billed and Long-billed Dowitchers. Species of gulls and terns were not distinguished.

Plots of each habitat were monitored by two observers using binoculars. Spotting scopes were also used in marsh plots. Number and taxa of shorebirds were recorded as arrivals and departures in 10-20 minute intervals for all habitats. In addition, observers counted all birds in the plot approximately every 30 minutes during periods of low activity.

Mud flat observers recorded tidal exposure throughout the survey period. This information was needed to calculate plot area and bird density at any given time. Mud flat observers watched a row of stakes placed 6.1 m apart in a line down the center of their plots (Fig. 7b) and reported the time at which the base of each stake became exposed. The width of the plot at any given time was the sum of: 1) the distance from the marsh edge to the last fully exposed stake; 2) the visually estimated distance from this stake to the waterline; and 3) an additional 4 m to account for submerged area available to wading shorebirds (4 m was the average distance from the waterline that shorebirds were seen wading during the surveys in those plots that contained wading birds.)

Prior to 1997 surveys, the 1995 data were analyzed for tidal height at estimated maximum density. The following procedure was used to estimate maximum density in each plot:

1) If, at the end of the survey, tallies were in agreement with counts to within +/- 2 birds, maximum density was the largest of: a) a tally; b) a count; or c) a single arrival or departure event (e.g. a departure of 110 Willets).

2) If tally and counts were not in agreement to within +/-2 birds at the end of the survey period, tally data were considered inaccurate and only counts or single arrival/departure events were used.

Next, tidal height at estimated maximum density in each plot was determined using MLML_DBASE_TIDE, a tidal height prediction program (Broenkow personal communication). For each habitat a two-way ANOVA without replication (Sokal & Rohlf 1995) was used to determine whether plot or date surveyed significantly affected tidal height of maximum density in those plots used both days. Results of the two-way ANOVAs were insignificant. Therefore, all plots were considered independent and combined in a one-way ANOVA [n=7 or 8 for each habitat (SYSTAT 1992)] to test whether tidal height at estimated maximum density was significantly different among the three habitats. ANOVA results were significant ($p<0.005$). A Kramer's modified Ryan's Q unplanned multiple comparison test (Day and Quinn 1989) revealed that significant differences existed between each habitat.

The 1997 surveys ended with a count taken as someone flushed the plot of all birds. The flush within each habitat occurred at the mean tidal height of maximum density determined from 1995 surveys which was assumed to approximate the mean tidal height of maximum density during 1997 surveys. Tidal heights at flush for each habitat were: 1.45 m for vegetated marsh, 0.88 m for deteriorated marsh, and 0.61 m for mud flat. During the flush, the two observers each took individual counts and then discussed their counts with the person flushing the plot for the final estimate of maximum density.

All 1995 and 1997 surveys were analyzed for tidal height at which birds first arrived at a plot using MLML_DBASE_TIDE (Broenkow personal communication). Time and tidal height of first arrival in each plot were then plotted for each date and visually compared to assess patterns among habitats.

Taxa use was compared among habitats using two measurements: proportional species composition at flush and frequency of occurrence of each taxa. Proportional species composition at flush was determined for February 8 & 9, 1997 data only and was equal to the percentage of birds of a particular taxa counted during the flush in all plots of a habitat over both days. Frequency of occurrence was determined using all four survey days combined and was calculated as the percentage of plots surveyed over all four days in which a particular taxa occurred. Surveys of the same plot on different days were counted as separate plots. The February 8, 1997 observation of plot M5 was not included because it was still completely underwater at the flush which may have discouraged use by nonwaders. All other mud flat plots were 21-70% as exposed as at a 0.0 m tide and were considered available to all shorebirds.

Mean and range of maximum density for each habitat were calculated for all surveys. Difference in maximum density among habitats was statistically analyzed for the February 8 & 9, 1997 surveys only, using number of birds at flush as the maximum density within a plot. The two dates were combined in a one-way ANOVA with a sample size of five or six for each treatment. Data were log-transformed prior to ANOVA in order to homogenize variances. A power analysis (Zar 1996) was done after the ANOVA because differences were insignificant and sample sizes were small.

## RESULTS

Birds appeared in vegetated marsh at tidal elevations between 1.40 m and 1.77 m, in deteriorated marsh at tidal elevations between 1.04 m and 1.55 m and on mud flats at tidal elevations between 0.55 m and 1.16 m (Fig. 8). All surveyed plots were used by shorebirds on the days surveyed with the exception of two vegetated marsh plots and one deteriorated marsh plot surveyed on February 26, 1995.

Taxa seen in each habitat over all survey dates are listed in Table 5. With the exception of Yellowlegs and Dowitchers, all taxa used mud flats more frequently than any other habitat (Table 5). Willets and Marbled Godwits were the two most frequently observed shorebirds in all habitats across all four survey dates (Table 5). In addition, during February 8 & 9, 1997, these two species represented 80% of shorebirds at flush for all deteriorated marsh plots combined and 100% of shorebirds in the vegetated marsh (Table 6). Proportional species composition at flush for mud flat plots is not presented in Table 6 due to the low total number of birds (10).

Mean maximum densities obtained during 1995 using the highest of reported counts, tallies, or arrival/departure events were generally much higher than mean densities reported at flush for Feb. 8 & 9, 1997 (Table 7). Maximum densities were not significantly different among habitats during 1997 surveys ($P < 0.217$, ANOVA on log-transformed data; power = 0.16).

## DISCUSSION

Results suggest that tide strongly influenced time of use of marsh and mud flat habitats. Although there was some overlap among habitats in tidal height of first arrival, a pattern is apparent in which birds first appeared in densely vegetated marsh, then in deteriorated marsh, and finally on mud flats over falling tides (Fig. 8). Tidal height of estimated maximum density in 1995 surveys followed the same sequence. Over rising tides, the reverse pattern has been observed. Bockus (1994) reported that the number of foraging birds in a deteriorated marsh decreased as it increased in an adjacent well-vegetated marsh over rising tides. These tidal patterns may be linked to a difference in marshplain elevation in the two habitats. Elevation surveys in densely vegetated and deteriorated marsh areas of Elkhorn Slough suggest that deteriorated marsh may be lower than well-vegetated marsh (Crampton 1994; see chapter 1).

The influence of tides on selection of habitat by shorebirds has been documented elsewhere. In Jamaica Bay, N.Y. a large pond near the estuary provided high tide roosting and feeding grounds for several species (Burger 1984). Most species flew back to the Bay at low tide, often vacating the pond within 15-20 minutes. Burger et al. (1977) also reported tidal effects on habitat selection in southern New Jersey where shorebirds used inner beaches at falling mid-tide levels, mud flats at low tide, and ocean beaches at both rising and falling mid-tide levels.

Mud flat plots were smaller than marsh plots and observed for shorter time periods (Table 4). Despite these differences, a greater variety of birds occurred at frequencies over 25% on mud flats than in either marsh habitat (Table 5), suggesting that mud flats were important habitat for more species during surveys. Vegetated marsh was used by the lowest number of taxa with only two species occurring in over 25% of plots (Table 5) This suggests that vegetated marsh was important habitat for only a few shorebird species during surveys. However, all surveys occurred during daylight and under low wind conditions. Salt marshes are known to provide nighttime roosting areas for Dowitchers, Dunlins, Least and Western Sandpipers in Bolinas Lagoon (Page et al. 1979). None of these species were seen in well-vegetated marsh during surveys. In addition, wind-sheltered feeding and roosting areas are important in maintenance of fat reserves, particularly for smaller shorebirds (Burger 1984). Therefore, densely vegetated marsh in Elkhorn Slough may provide important roosting and/or feeding areas for a greater number of species under more extreme wind conditions. Finally, the time of year of surveys may have influenced species use of all three habitats (Ramer 1985; Shuford et al., 1989). Gerstenberg (1979) reported that 16 species of shorebirds roosted in Humboldt Bay marshes over a 1.5 year census period. In Elkhorn Slough, Semipalmated Plovers and Killdeer have been seen in deteriorated marsh in spring (Bockus 1994) and late fall (Benson 1994) respectively, while Black-necked Stilts have been seen feeding and roosting in dense marsh in early fall (personal observation). None of these species were seen in any habitat during surveys.

Although small sandpipers use densely vegetated marsh in the Elkhorn Slough (personal observation), none were recorded there during surveys. It is possible that some sandpipers may have gone unnoticed in both the well-vegetated and deteriorated marsh due to the long distances between observer overlooks and marsh plots. In addition, the dark color of the densely vegetated marsh may have helped to camouflage small sandpipers as they flew by.

Mean maximum densities obtained during 1995 using the highest of reported counts, tallies, or arrival/departure events were generally much higher than mean densities reported at flush for Feb. 8 & 9, 1997 (Table 7). Although shorebird abundance may have differed between the two years, it is likely that density differences were primarily due to the differences in sampling methods. The 1995 survey results represent the highest number of birds in a plot throughout the survey while the 1997 results represent densities at a single tidal height for each habitat.

During the January 28, 1995 survey a small airplane buzzed the marsh over the entire study area during marsh observations. Birds were flushed in several areas of the marsh and flew in or out of some of the marsh plots. This may have affected the time at which maximum density was reported in individual plots and thereby the decision of when to flush plots during 1997 surveys. However, it is doubtful this disturbance greatly altered the average tidal height of maximum density in any particular direction since birds were seen to move both into and out of plots.

Although no significant difference in density existed among habitats at the estimated tidal height of peak density during February 8-9, 1997 surveys, the low power of the ANOVA for 1997 data (power = 0.16) indicates that, if there were a difference, replication may have been inadequate to detect it. In addition, flush times for determination of maximum density in 1997 surveys were based on two survey dates in 1995 and may not have predicted the exact tidal height of maximum density for each habitat. Greater abundance of shorebirds in mud flat versus marsh habitats has been reported for Cape May peninsula, New Jersey where a single mud flat area accounted for 69% of all birds surveyed in 1 mud flat, 1 beach, and 3 marsh areas of the same size ($4000m^2$) (Burger et al. 1997). The three marsh areas contained, on average, only 7-8% of all shorebirds surveyed. By dividing mean abundance in each area by plot size, mean densities of shorebirds in the marsh and mud flat areas may be compared to estimated maximum densities obtained in this study on February 8 & 9, 1997. Densities in the three Cape May marshes were 8.5 to 12/ha, while mean density in the mud flat area was 89/ha. Cape May mud flat densities were comparable to the maximum densities surveyed in the slough during February, 1997, while Cape May marsh densities were approximately half the maximum densities surveyed in the slough (Table 7). Interestingly, in Cape May the percentage of shorebirds in marsh and mud flat habitats that were feeding was approximately the same in both habitats: an average of 61% in the three marsh areas and 65% on the mud flat, suggesting that marsh was an important feeding area for the few shorebirds that used it during the surveys.

Little is known about differences in prey type and availability in vegetated and deteriorated marsh within Elkhorn Slough. Crabs (*Hemigrapsis oregonensis* and

*Pachygrapsis crassipes*) burrow in tidal creek walls (Sliger 1982) and occasionally occur on the surface of densely vegetated marsh where they may be eaten by Willets, Long-billed Curlews, and Marbled Godwits (Benson 1994; personal observation). *H.oregonensis* is important in the diets of Willets (Recher 1966; Stenzel et al. 1976; Ramer 1985), Long-billed Curlews (Stenzel et al. 1976) and Marbled Godwits (Ramer 1985) in several areas of coastal California, while *P. crassipes* has been found in Willet stomach contents from Elkhorn Slough (Ramer 1985). Other Willet prey that may come from salt marshes include the amphipod *Orchestia traskiana* and adult insects (mostly *Coleoptera*) (Stenzel et al. 1976; Ramer 1985). Insects may also provide a food source in deteriorated marsh where they occasionally occur in large numbers in small pools on the surface (personal observation) as well as in surface sediments (Bockus 1994). However, limited coring indicated that deteriorated marsh may be much lower in invertebrate infauna than adjacent mud flats (Bockus 1994).

Pickleweed thinning may increase then decrease shorebird use of the marsh. Without vegetative cover to slow surface currents over the marsh and a root mat to hold sediment, deteriorated marsh areas may erode, reducing the surface elevation. This appears to have taken place in denuded areas in the Hudson's Landing area (Crampton, 1994; personal observation) and may become more widespread. As the marsh surface is lowered it may become colonized by the rich invertebrate fauna typical of mud flats in the Elkhorn Slough (ABA Consultants 1989) and provide foraging areas for a number of species at mid to low tides. However, erosion could eventually turn these denuded areas into shallow subtidal habitats, making the gain in shorebird foraging areas only temporary. Meanwhile, loss of pickleweed marsh may reduce availability of wind-sheltered roosts for a number of species and foraging areas for Willets, Marbled

Godwits, and Long-billed Curlews. Given the wide expanse of pickleweed marsh still remaining and low densities of shorebirds in these areas, it's possible that marsh deterioration may not greatly impact most shorebirds for some time. However, if crab populations declined due to reduced cover or sediment stability provided by pickleweed marsh, larger shorebirds may be affected more rapidly.

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TABLE 1. Film type and scale of images used in photo transects.

| Year | Film type | Scale |
|---|---|---|
| 1931 | B&W Prints | 1:20,000 |
| 1937/1939* | B&W Prints | 1:20,000 |
| 1949 | B&W Prints | 1:20,000 |
| 1956 | B&W Prints | 1:24,000 |
| 1980 | Color Infrared Prints | 1:12,000 |
| 1989 | Color Slides | 1:40,000 |
| 1993 | Color Slides | 1:20,000 |
| 1997 | Color Slides | 1:20,000 |

*prints from 1937 and 1939 were combined for complete coverage of all marsh sections

TABLE 2. Areas ($m^2$) of marsh sections in 1937/39 and 1994 photos and number of transects assigned to sections for the combined section analysis.

| **Marsh section** | **1937/39 area** | **Section area (1937/39) / Total area (1937/39)** | **1994 area** | **# of transects** |
|---|---|---|---|---|
| 1 | 568,625 | 0.22 | 540,168 | 16 |
| 2 | 463,838 | 0.18 | 452,197 | 12* |
| 3 | 718,032 | 0.27 | 716,138 | 21* |
| 4 | 230,957 | 0.09 | 228,737 | 7 |
| 5 | 103,182 | 0.04 | 96,902 | 3 |
| 6 | 36,322 | 0.01 | 33,958 | 1 |
| 7 | 19,607 | 0.01 | 15,201 | 1 |
| 8 | 99,463 | 0.04 | 82,041 | 3 |
| 9 | 95,580 | 0.04 | 87,217 | 3 |
| 10 | 299,083 | 0.11 | 289,581 | 8 |
| | | | **Total # transects** | 75 |

* The number of transects per section was determined prior to georectifying photos. There was a slight difference in the areas determined, leading to the one-transect discrepancy for these two sections.

TABLE 3. Percent cover of pickleweed marsh in ground versus photo transects (B&W = black and white; CIR = color infrared) for three cover classes of marsh.

| Cover Class | Actual | | Ground sampled | | Color slides (1:40,000) | | Color slides (1:20,000) | | B&W slides (1:20,000) | | CIR (1:12,000) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | SE | Mean | SE | Mean | SE | Mean | SE | Mean | SE | Mean | SE |
| **Low Cover**<br>(5%-18%)<br>n=12 | 10 | 1.3 | 10 | 1.7 | 13 | 1.9 | 14 | 1.6 | 11 | 2.4 | 9 | 1.9 |
| **Medium Cover**<br>(22%-78%)<br>n=22 | 44 | 3.6 | 44 | 3.5 | 48 | 3.5 | 43 | 4.1 | 45 | 3.7 | 37 | 3.6 |
| **High Cover**<br>(84%-100%)<br>n=12 | 92 | 1.4 | 90 | 2.1 | 90 | 1.7 | 91 | 2.1 | 89 | 1.9 | 90 | 2.2 |

TABLE 4. Number of plots, survey length, and tidal period for each habitat and survey date.

| Survey Date | Densely Vegetated Marsh | | | Deteriorated Marsh | | | Mud Flat | | |
|---|---|---|---|---|---|---|---|---|---|
| | # plots | length (h) | tidal period (m) | # plots | length (h) | tidal period (m) | # plots | length (h) | tidal period (m) |
| 28-Jan-95 | 5 | 4.00 | 1.83 to 0.15 | 5 | 4.00 | 1.83 to 0.15 | 4 | 3.00 | 1.30 to 0.0 |
| 26-Feb-95 | 4 | 4.00 | 1.83 to 0.15 | 4 | 4.00 | 1.83 to 0.15 | 4 | 3.00 | 1.30 to 0.0 |
| 8-Feb-97 | 3 | 1.75 | 1.83 to 1.45 | 4 | 1.75 | 1.62 to 0.88 | 3 | 1.25 | 1.25 to 0.61 |
| 9-Feb-97 | 2 | 1.75 | 1.74 to 1.45 | 2 | 2.00 | 1.62 to 0.88 | 2 | 1.25 | 1.22 to 0.61 |

TABLE 5. Bird taxa observed and percent frequency of occurrence in plots over entire survey period

| Vegetated Marsh | % freq. (total plots = 14) | Deteriorated Marsh | % freq. (total plots = 15) | Mud Flat | % freq. (total plots = 12) |
|---|---|---|---|---|---|
| Willet | 86 | Willet | 80 | Willet | 100 |
| Marbled Godwit | 43 | Marbled Godwit | 67 | Marbled Godwit | 92 |
| Long-billed Curlew | 14 | Long-billed Curlew | 40 | Long-billed Curlew | 58 |
| Snowy Egret | 14 | Snowy Egret | 13 | Snowy Egret | 33 |
| American Avocet • | 7 | American Avocet | 40 | American Avocet | 58 |
| gull | 7 | gull | 13 | gull | 83 |
| Yellowlegs | 7 | Yellowlegs | 40 | Yellowlegs | 0 |
|  |  | Dowitcher | 13 | Dowitcher | 0 |
|  |  | Black-bellied Plover | 13 | Black-bellied Plover | 33 |
|  |  | small sandpiper | 7 | small sandpiper | 17 |
|  |  |  |  | Ruddy Turnstone | 8 |
|  |  |  |  | Great Egret | 8 |
|  |  |  |  | tern | 17 |
|  |  |  |  | Whimbrel | 8 |

• Observed in pan area of vegetated marsh.

TABLE 6. Proportional species composition at flush for all plots surveyed February 8 & 9, 1997

| **Vegetated Marsh** | **(5 plots combined)** | **Deteriorated Marsh** | **(6 plots combined)** |
|---|---|---|---|
| Willet | 96% | Willet | 52% |
| Marbled Godwit | 4% | Marbled Godwit | 28% |
| | | Long-billed Curlew | 11% |
| | | American Avocet | 5% |
| | | Snowy Egret | 2% |
| | | Yellowlegs | 2% |
| **Total # birds:** | **49** | **Total # birds:** | **56** |

TABLE 7. Mean and range of maximum shorebird density (#birds/ha) for all survey dates.

| | Vegetated Marsh | | | | Deteriorated Marsh | | | | Mud Flat | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | tally/count method | | flush method | | tally/count method | | flush method | | tally/count method | | flush method | |
| | 1/28/95 | 2/26/95 | 2/8/97 | 2/9/97 | 1/28/95 | 2/26/95 | 2/8/97 | 2/9/97 | 1/28/95 | 2/26/95 | 2/8/97 | 2/9/97 |
| **Mean** | 103 | 22 | 26 | 28 | 64 | 78 | 26 | 14 | 549 | 372 | 108 | 20 |
| **Range** | 2 - 297 | 0 - 64 | 0 - 78 | 13 - 44 | 4 - 180 | 0 - 230 | 0 - 59 | 5 - 24 | 66 - 1760 | 66 - 656 | 50 - 197 | 0 - 39 |
| n | 5 | 4 | 3 | 2 | 5 | 4 | 4 | 2 | 4 | 4 | 3 | 2 |

Fig. 1. Elkhorn Slough, Moss Landing, California showing ten sections sampled in photo transects, two areas used in transplant experiment, and 22 transects surveyed in elevation versus percent cover surveys. Manipulation control treatments in transplant experiment were in Marsh A1 (~97% cover). Low, Medium, and High Box treatments were in Marsh B (~23% cover).

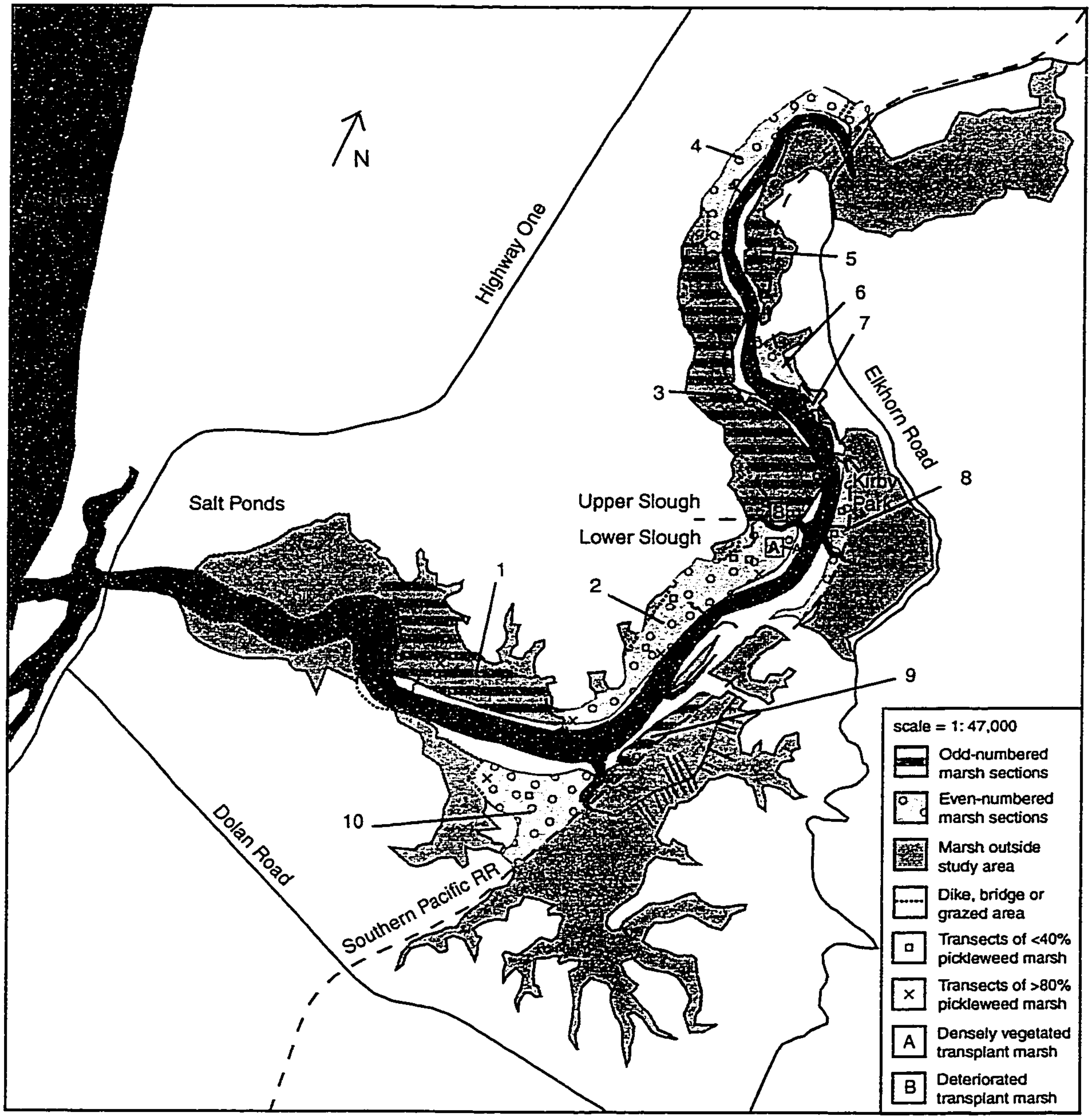

N
Highway One
Salt Ponds
Upper Slough
Lower Slough
Elkhorn Road
Kirby Park
Dolan Road
Southern Pacific RR
1
2
3
4
5
6
7
8
9
10
A
B
scale = 1: 47,000
Odd-numbered marsh sections
Even-numbered marsh sections
Marsh outside study area
Dike, bridge or grazed area
Transects of <40% pickleweed marsh
Transects of >80% pickleweed marsh
A Densely vegetated transplant marsh
B Deteriorated transplant marsh

Fig. 2. Change in percent cover ( $\bar{x}$ +/- SE) of pickleweed, bare mud, and channel over time for the entire study area (n=75/year). Years with the same letter are not significantly different from each other.

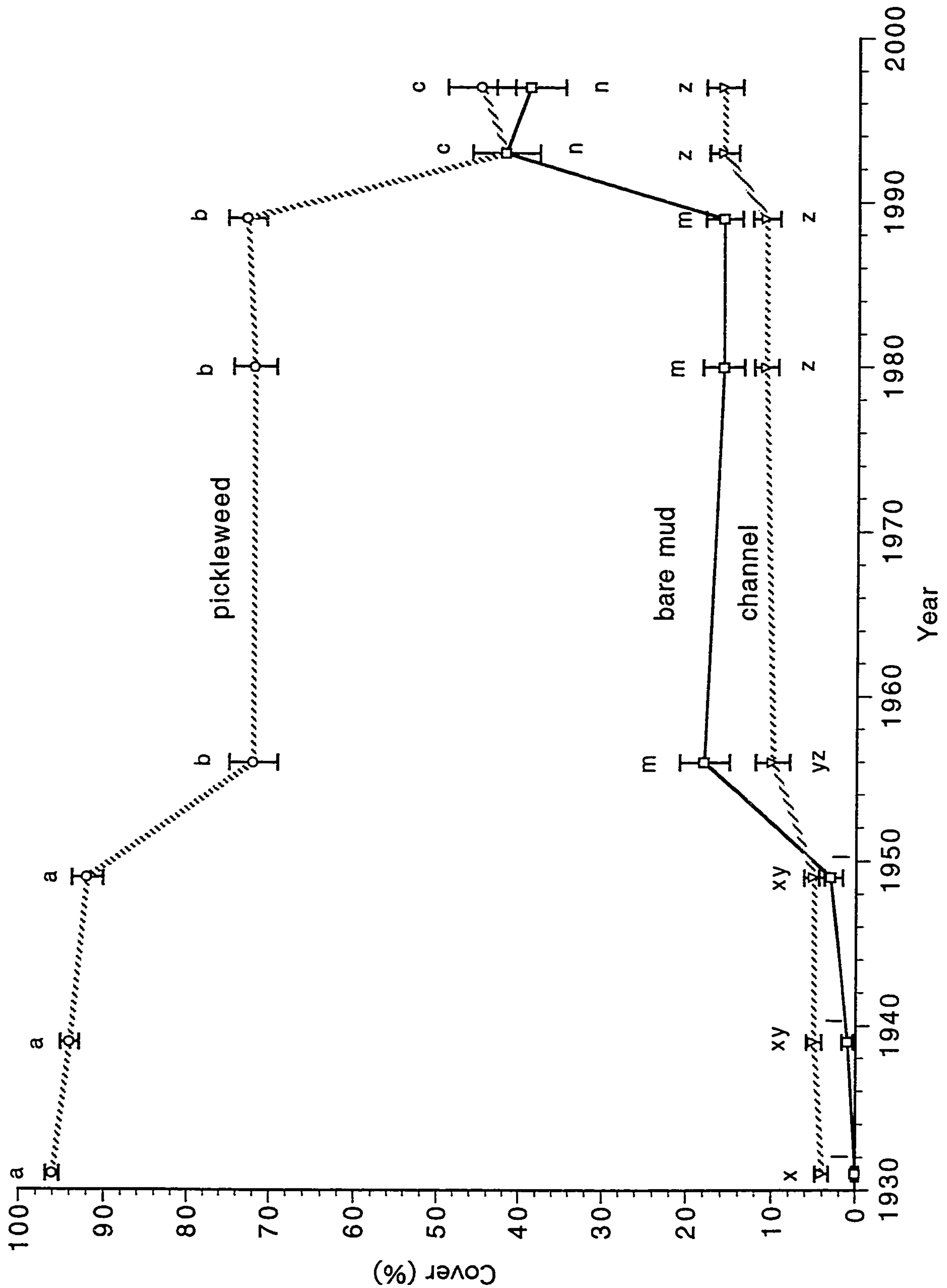

Cover (%)
100
90
80
70
60
50
40
30
20
10
0
Year
1930
1940
1950
1960
1970
1980
1990
2000
pickleweed
bare mud
channel
a
a
a
b
b
b
c
c
l
l
l
m
m
m
n
n
x
xy
xy
yz
z
z
z
z

Fig. 3. Change in percent cover ( $\bar{x}$ +/- SE) of pickleweed over time for each of ten marsh sections (see fig. 1). The number of samples per year (n) is indicated for each section. Years with the same letter are not significantly different from each other.

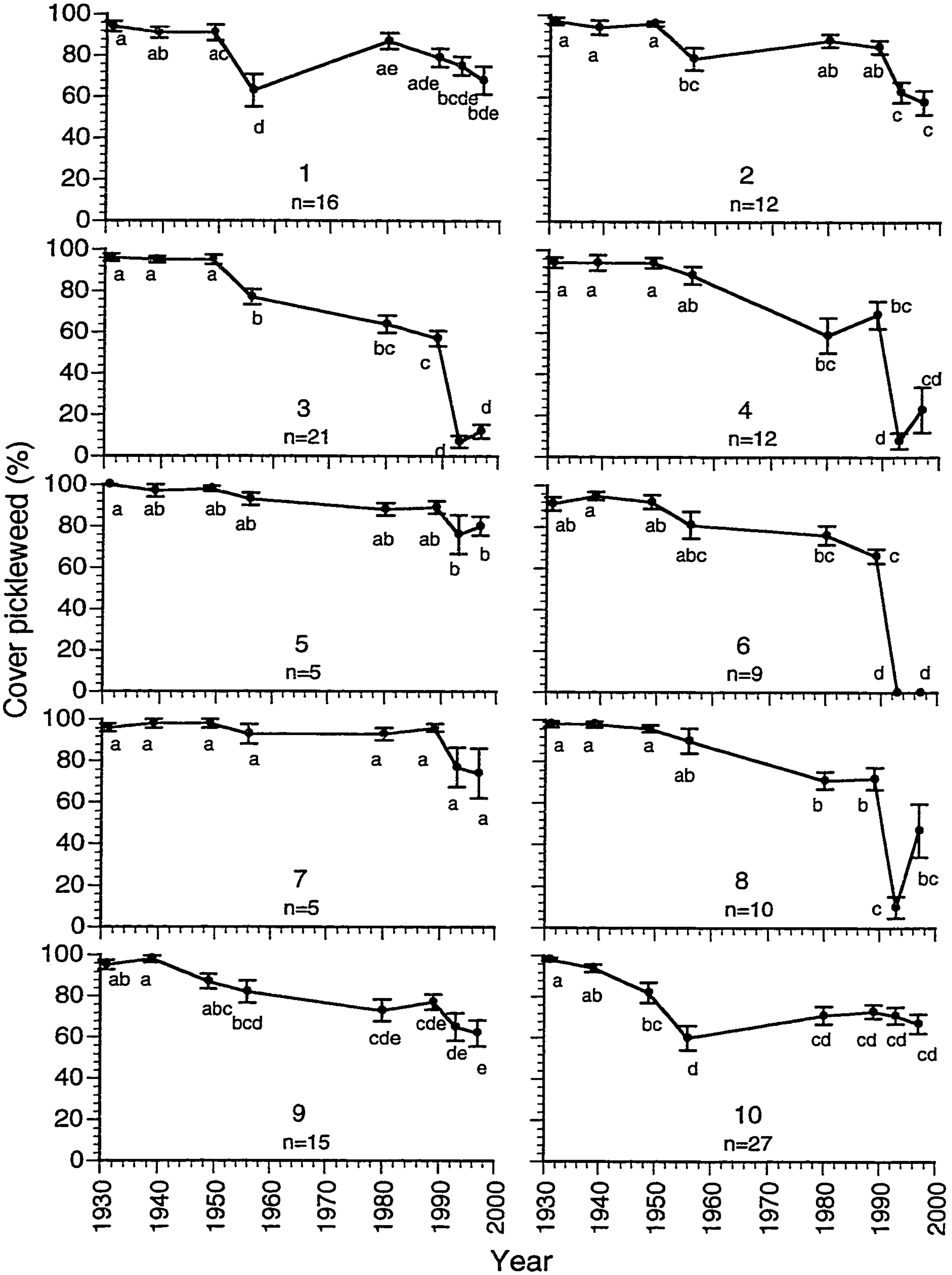

Cover pickleweed (%)
Year
0
20
40
60
80
100
1930
1940
1950
1960
1970
1980
1990
2000
1
n=16
a
ab
ac
d
ae
ade
bcde
bde
2
n=12
a
a
a
bc
ab
ab
c
c
3
n=21
a
a
a
b
bc
c
d
d
4
n=12
a
a
a
ab
bc
bc
d
cd
5
n=5
a
ab
ab
ab
ab
ab
b
b
6
n=9
ab
a
ab
abc
bc
c
d
d
7
n=5
a
a
a
a
a
a
a
a
8
n=10
a
a
a
ab
b
b
c
bc
9
n=15
ab
a
abc
bcd
cde
cde
de
e
10
n=27
a
ab
bc
d
cd
cd
cd
cd

Fig. 4. Percent of branches in flower ( $\bar{x}$ +/- SE) for pickleweed treatments. Deteriorated control (deter. control) represents naturally occurring pickleweed in Marsh B. Low, Medium, and High represent the three box elevations in Marsh B. Control, Transplant, and Box/Transplant represent the three manipulation control treatments in Marsh A1. Treatments with the same letter are not significantly different from each other.

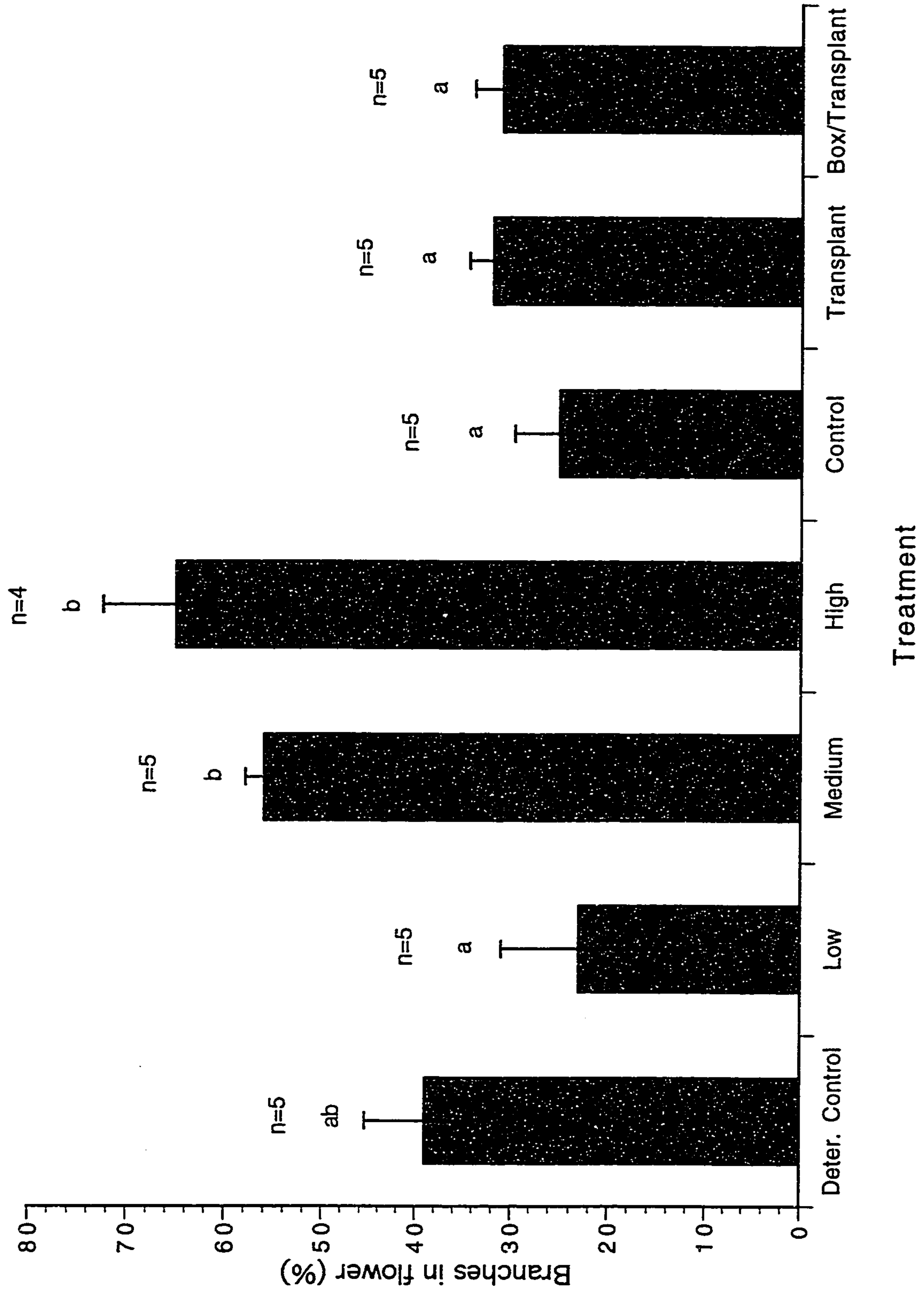
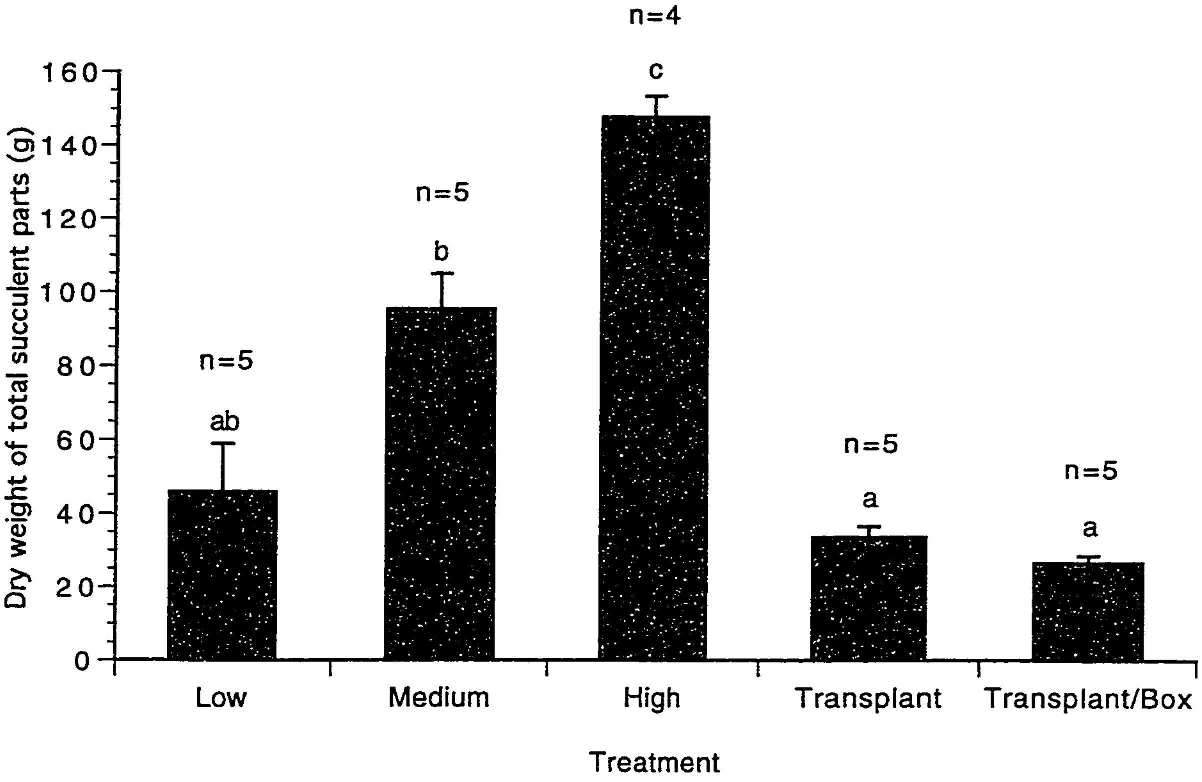

Branches in flower (%)
0
10
20
30
40
50
60
70
80
Treatment
Deter. Control
Low
Medium
High
Control
Transplant
Box/Transplant
ab
n=5
a
n=5
b
n=5
b
n=4
a
n=5
a
n=5
a
n=5

Fig. 5a. Dry weight (g) of total succulent parts ( $\bar{x}$ +/- SE) for all treatments in transplant study. Treatments with the same letter are not significantly different from each other.

Fig. 5b. Dry weight (g) of succulent parts of one branch ( $\bar{x}$ +/- SE) for all treatments in transplant study area as well as naturally occurring plants in Marsh B (Control B). Treatments with the same letters are not significantly different from each other


Dry weight of total succulent parts (g)
0
20
40
60
80
100
120
140
160
n=5
ab
n=5
b
n=4
c
n=5
a
n=5
a
Low
Medium
High
Transplant
Transplant/Box
Treatment

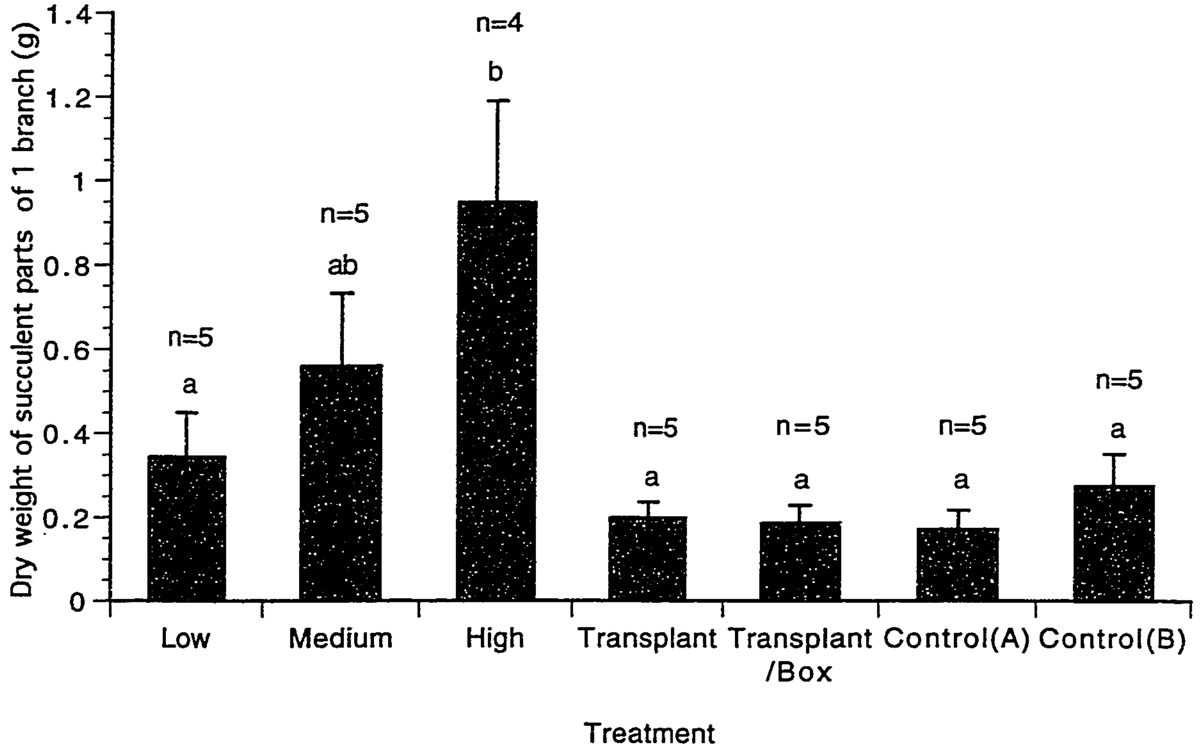

Dry weight of succulent parts of 1 branch (g)
0
0.2
0.4
0.6
0.8
1
1.2
1.4
n=5
a
n=5
ab
n=4
b
n=5
a
n=5
a
n=5
a
n=5
a
Low
Medium
High
Transplant
Transplant /Box
Control(A)
Control(B)
Treatment

Fig. 6. Cover of pickleweed marsh (%) versus elevation (m above MLLW) for surveyed transects. MHW indicates average Mean High Water in the Elkhorn Slough. Note break in x-axis.

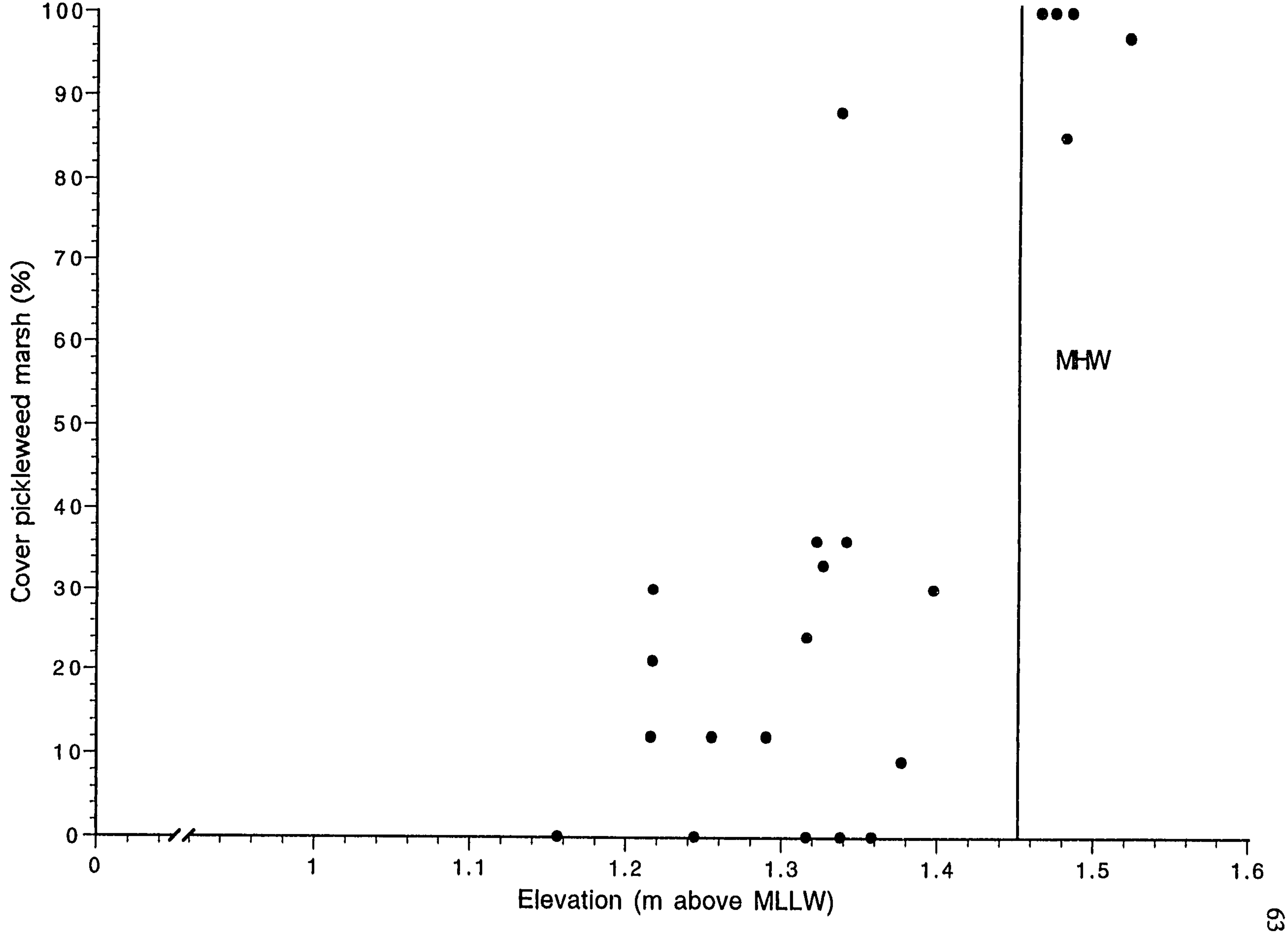

Cover pickleweed marsh (%)
100
90
80
70
60
50
40
30
20
10
0
MHW
0
1
1.1
1.2
1.3
1.4
1.5
1.6
Elevation (m above MLLW)

Fig. 7a. Plots used for bird surveys. D, V, M represent deteriorated marsh, densely vegetated marsh, and mud flat, respectively.

Fig. 7b. Example of mud flat plot used in bird surveys. Center stakes were used to measure exposure of mud flat.

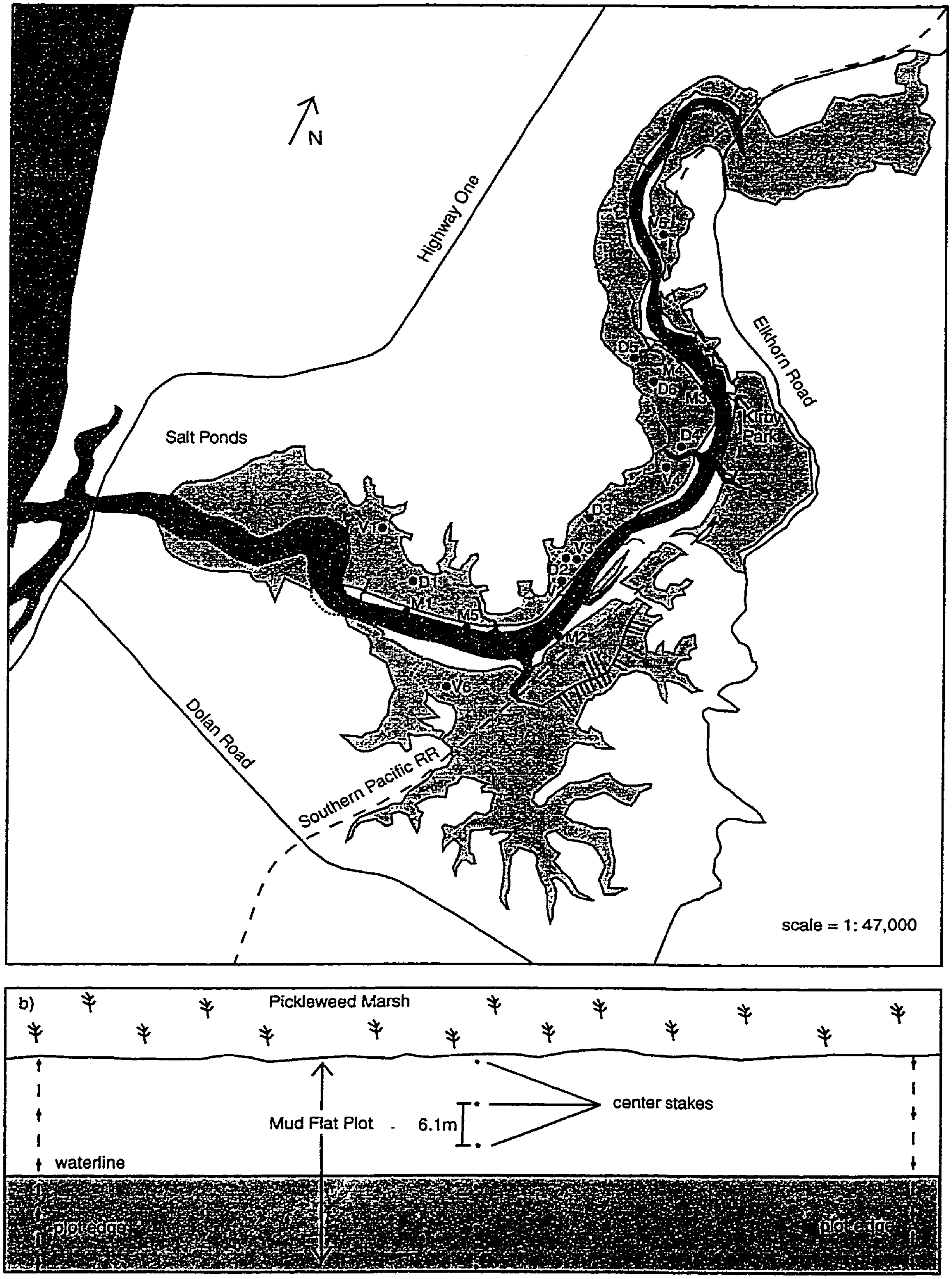
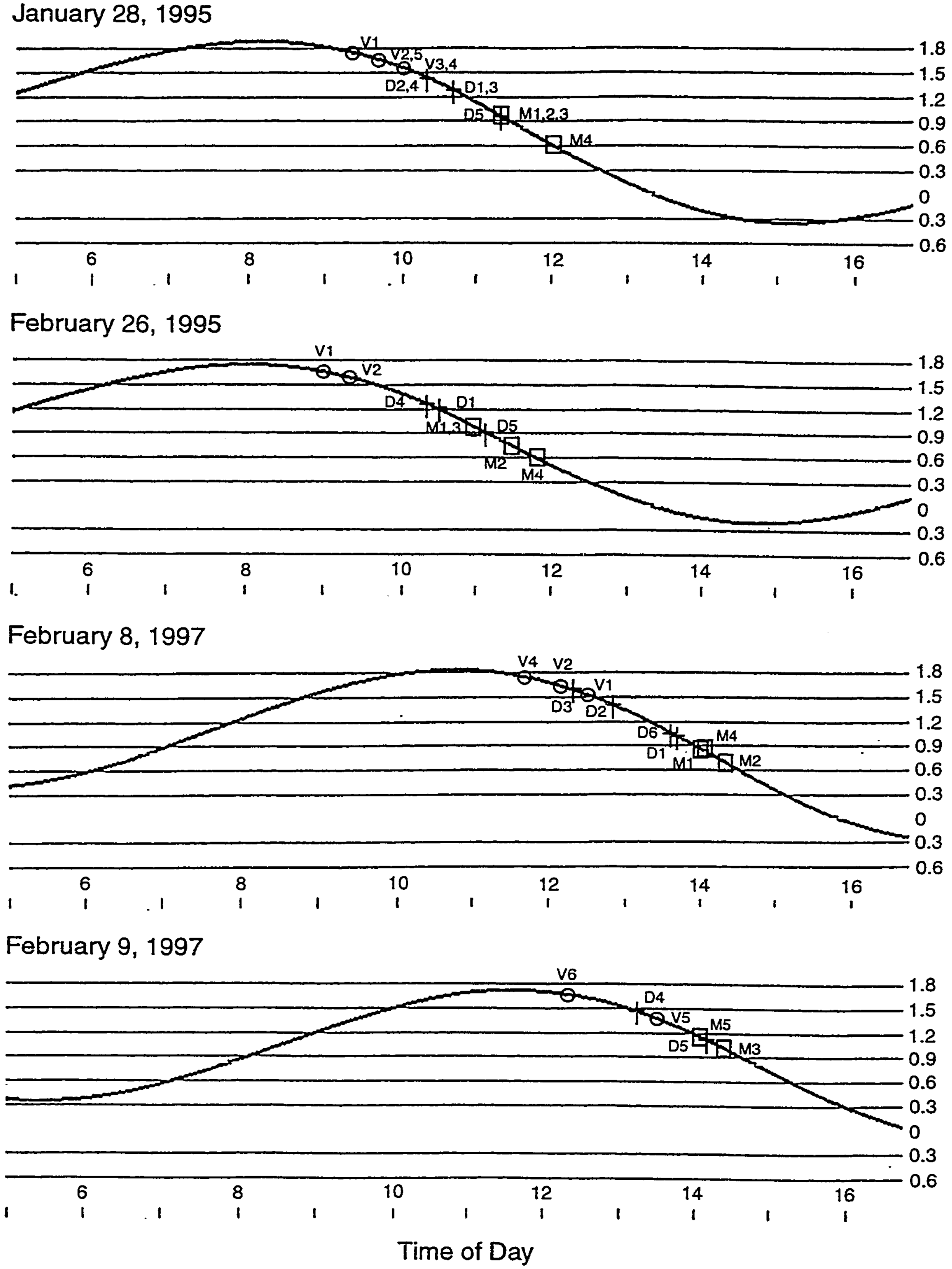

N
Highway One
Salt Ponds
Elkhorn Road
Kirby Park
V5
D5
M4
D6
M3
D4
V4
D3
V3
D2
V2
V1
D1
M1
M5
M2
V6
Dolan Road
Southern Pacific RR
scale = 1: 47,000
b)
Pickleweed Marsh
Mud Flat Plot
6.1m
center stakes
waterline
plot edge
plot edge

Fig. 8. Tidal heights (m) and times of first arrival of birds on 4 survey dates. Arrival times for individual plots are indicated (V and circle = densely vegetated marsh plot; D and cross = deteriorated marsh plot; M and rectangle = mud flat plot).


January 28, 1995
V1
V2,5
V3,4
D2,4
D1,3
D5
M1,2,3
M4
February 26, 1995
V1
V2
D4
D1
M1,3
D5
M2
M4
February 8, 1997
V4
V2
V1
D3
D2
D6
D1
M4
M1
M2
February 9, 1997
V6
D4
V5
M5
D5
M3
1.8
1.5
1.2
0.9
0.6
0.3
0
0.3
0.6
6
8
10
12
14
16
Time of Day

# APPENDIX 1. Tidal benchmarks used to calculate average MLLW and MHW in the slough and benchmarks used in GPS surveys.

## Tidal benchmarks

California 941 3623: Elkhorn Slough Highway 1 Bridge, Moss Landing

Latitude: 36° 48.6' N Longitude: 121° 47.1' W

California 941 3663: Elkhorn Slough Railroad Bridge, Watsonville

Latitude: 36° 51.4' N Longitude: 121° 45.3' W

## Benchmarks used in GPS network adjustment (datum: NAD 83)

ELK1: Elkhorn Slough National Estuarine Research Reserve overlook, Castroville.

Latitude: 36° 49' 00.18269" N Longitude: 121° 44' 00.12581" W

HPGN CA 05 13: Intersection of hwys. 156 and 183, Castroville.

Latitude: 36° 45' 45.83116" N Longitude: 121° 45' 01.26511" W

MON 1 PM 99.4: Hwy. 1 north of Moss Landing School, Moss Landing.

Latitude: 36° 50' 44.12154" N Longitude: 121° 46' 15.61331" W

A 1455: Southern Pacific RR, 5.6 km West from Salinas Rd. junction, Watsonville.

Latitude: 36° 53' 38" N Longitude: 121° 47' 59" W

V 1448: Southern Pacific RR, 3.1 km East from Watsonville Station, Watsonville.

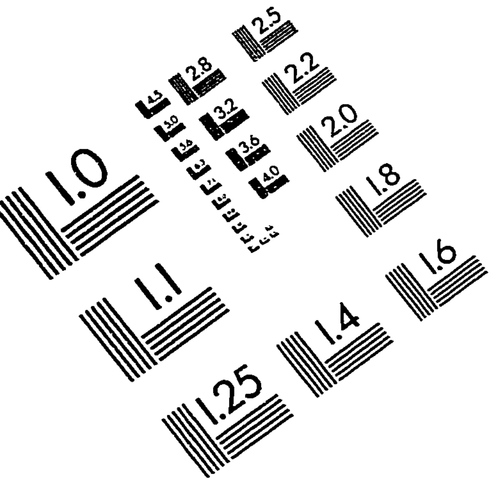
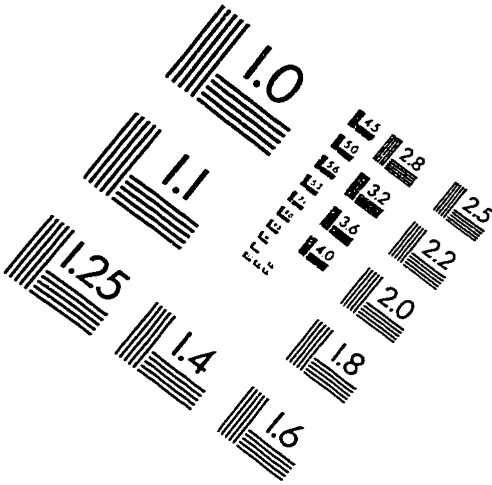
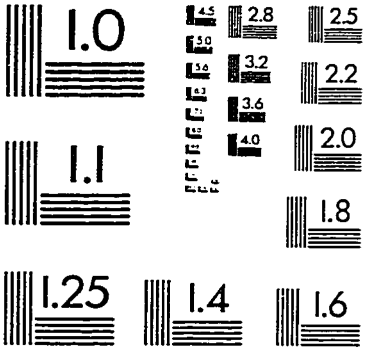
Latitude: 36° 54' 04" N Longitude: 121° 42 45" W

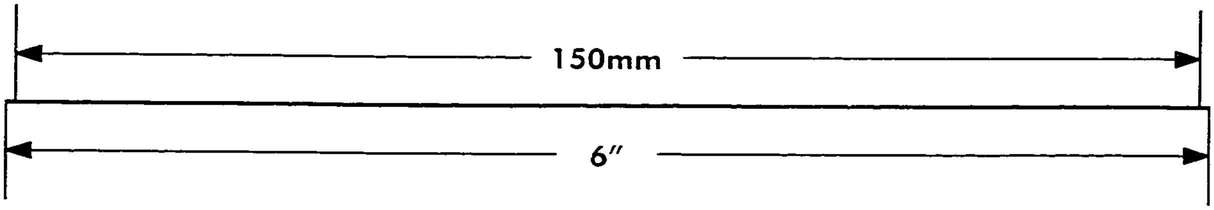
APPENDIX 2. Statistical analyses used in photo transects (figure 3) for individual sections.

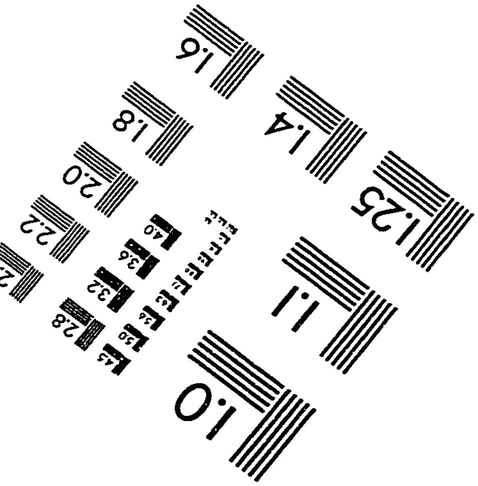
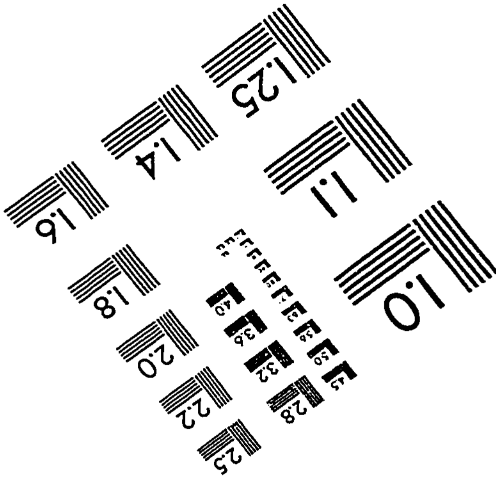
| Section | n | Transformation | ANOVA/Kruskal-Wallis | Significance (P) of ANOVA/K-W | Unplanned multiple comparison test (UMCT) |
|---|---|---|---|---|---|
| 1 | 16 | arcsin to correct unequal variances | ANOVA | <.0005 | Bonferroni* (SYSTAT, 1992) |
| 2 | 12 | arcsin to correct unequal variances and make distribution more normal | ANOVA | <.0005 | Tukey-Kramer* (SYSTAT, 1992) because data somewhat skewed |
| 3 | 21 | arcsin to correct unequal variances before UMCT. Data still severely skewed. | Kruskal-Wallis on untransformed data | <.0005 | Tukey-Kramer* because data somewhat skewed |
| 4 | 12 | arcsin to correct skewness and kurtosis; variances still unequal | Kruskal-Wallis on untransformed data | <.0005 | Games-Howell (Day & Quinn, 1989) because variances still not equal despite transformation. $\alpha<.05$ |
| 5 | 5 | arcsin to correct unequal variances | ANOVA | 0.001 | Bonferroni* |
| 6 | 9 | none successfully homogenized variances | Kruskal-Wallis on untransformed data | <.0005 | Games-Howell $\alpha<.05$ |
| 7 | 5 | arcsin to correct unequal variances | ANOVA | 0.028 | Bonferroni* |
| 8 | 10 | arcsin to correct skewness and kurtosis; variances still unequal | Kruskal-Wallis on untransformed data | <.0005 | Games-Howell $\alpha<.05$ |
| 9 | 15 | arcsin to correct unequal variances; data still skewed | Kruskal-Wallis on untransformed data | <.0005 | Tukey-Kramer* |
| 10 | 27 | arcsin to reduce heterogeneity of variances and make distribution more normal; variances still unequal | Kruskal-Wallis on untransformed data | <.0005 | Games-Howell $\alpha<.05$ |

* $P < .05$ for all significant results shown in fig. 3

# IMAGE EVALUATION
# TEST TARGET (QA-3)



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