EFFECTS OF HUMAN TRAMPLING AND CATTLE GRAZING ON SALT MARSH ASSEMBLAGES IN ELKHORN SLOUGH, CALIFORNIA

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ABSTRACT

EFFECTS OF HUMAN TRAMPLING AND CATTLE GRAZING ON SALT MARSH ASSEMBLAGES IN ELKHORN SLOUGH, CALIFORNIA

by

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The effects of human trampling on *Salicornia virginica* assemblages in Elkhorn Slough, California were experimentally tested at two sites using 9 levels of trampling intensity and frequency over 6 months, then allowing plots to recover for 1 year. Responses to cattle grazing also were examined. Human trampling at all levels decreased *S. virginica* height and flower production. Percent cover of *S. virginica* remained high (~90%) in intermediate and lightly trampled plots, but bare ground dominated in heavily trampled areas. Once trampling ceased, open space was first colonized by non-native upland plants or algae, and later, *S. virginica*. After 1 year of recovery, trampled *S. virginica* in heavily trampled areas was shorter than untrampled controls, bare patches remained in some plots, and there were significant differences between invertebrates present in heavily trampled areas and controls. Actively grazed cattle pasture was characterized by high percentages of bare ground and *Distichlis*, while ungrazed marsh was comprised of over 90% *S. virginica*. However, plants grazed by low densities of cattle responded quickly to the removal of livestock. After 15 months of recovery, *Distichlis* and bare ground declined, and *S. virginica* increased. Overall, trampling and grazing can decrease *S. virginica* abundance, lead to changes in community structure, promote invasions by introduced species, and contribute to loss of marsh habitat.

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TABLE OF CONTENTS

LIST OF TABLES

Table Page

LIST OF FIGURES

LIST OF APPENDICES

INTRODUCTION

Natural disturbances affect the structure of communities by creating open space, decreasing competition, and changing available resources (Pickett and White 1985). Variations in intensity, frequency, size and seasonality of disturbances can affect community response (Connell 1978, Sousa 1985). In salt marsh communities, common natural disturbances include debris deposition, parasites, and flooding, all of which can kill dominant plants, providing space that is then colonized by less competitive species (Bertness and Ellison 1987, Allison 1996, Pennings and Callaway 1996). In turn, these species may persist for years after the initial disturbance, creating patches of several marsh species in an otherwise monospecific habitat.

It is unclear if human disturbances have the same effect on salt marsh composition. Recent studies have attempted to compare human and natural disturbances (Allison 1995, Keough and Quinn 1998), but to date answers have been inconclusive. Investigating human impacts can contribute to the development of basic academic disturbance theory and is valuable for resource management. The question of how humans may impact estuarine lands is important because many of the world's cities are situated in or near coastal marshes. Understanding these impacts can help us manage salt marshes rationally and effectively.

Two common human impacts in salt marshes are trampling and use of the land for livestock grazing. Human trampling has been studied in a variety of systems, including grasslands, forest understories, sand dunes, and rocky shores (Duffey 1975, Hylgaard

1980, Sun and Liddle 1993, Taylor et al. 1993, Brosnan and Crumrine 1994, Keough and Quinn 1998). These and other studies have established that trampling can change the structure of natural plant assemblages. However, few studies have examined trampling in coastal salt marshes. On the other hand, studies investigating the effects of cattle grazing in salt marshes have been done (Shanholtzer 1974, Reimold et al. 1975, Bakker 1978, Jensen 1985, Turner 1987, Andresen et al. 1990), but these have focused on only the Atlantic and European coasts.

Both human and cattle trampling occur in Elkhorn Slough, an inlet of Monterey Bay and the second largest coastal wetland in California. Like many other salt marshes, it has a long history of human use. Early Native Americans hunted in the region, and the first Europeans used the land for cattle pastures. In the following years, disturbances included the diking of wetlands, the construction of a railroad, the building of salt extraction and hunting ponds, the introduction of dairies, and the opening of the harbor mouth directly west of Elkhorn Slough (Gordon 1979, King 1982). By the early 1970's, approximately 50% of the slough's marshlands were diked and altered, primarily for grazing lands (Browning 1972).

More recently there have been initiatives by several agencies to acquire and restore large portions of the slough's marshlands. As a result the area's habitat and aesthetic values have increased, drawing tourists in record numbers. Nearly 50,000 people visit the Elkhorn Slough National Estuarine Research Reserve (ESNERR) annually, up from 20,000 ten years ago, and more than 300 kayakers paddle through the slough's waters on busy summer weekends. Among others attracted to the slough are researchers, students, hunters, and fishermen. Although only a small percent of people may stray off marked trails or away from designated boat launches, the sheer number can impact marsh communities. Managers at ESNERR estimate that 1% of their visitors leave the trails (Jane Caffrey, pers. comm.), meaning almost 500 people a year may trample sensitive marshes on the Reserve alone.

In addition to being a recreation destination, Elkhorn Slough is still used to graze cattle. Although locally this business is being phased out, over 1600 cattle are still kept along the shores of the slough, and at least 500 have year-round access to marsh vegetation.

Salicornia virginica (pickleweed) dominates Elkhorn Slough's tidal salt marshes, covering approximately 3,500 ha (Barry et al. 1996). *S. virginica* is a native perennial succulent that forms extensive colonies. In Elkhorn Slough average marsh plain elevation is 1.46 m above MLLW, and S. *virginica* does not generally survive below 1.28 m above MLLW (Crampton 1994). Although it is extremely salt tolerant, *S. virginica* cannot withstand prolonged or daily inundation because it lacks air storage tissue (Purer 1942, Pestrong 1965, Barbour and Davis 1970).

Salicornia reproduces by seed, underground rhizomes, and rooting of decumbent branches (Macdonald 1977). In Elkhorn Slough, it flowers in the summer and fall, germinates January through March, disperses via water, and is an early colonist of new marsh habitat (Mayer 1987). Other plants associated with it are the perennials *Distichlis spicata* (salt grass), *Frankenia salina* (alkali heath), *Jaumea carnosa,* and the annual *Atriplex patula* (fat hen). This assemblage provides habitat for many bird species along the Pacific Flyway (Browning 1972) and invertebrates, including *Hemigrapsus oregonensis* (mud crab), *Traskorchestia traskiana* (amphipod), *Batillaria zonalis* (snail), and a variety of insects and spiders (Lane 1969, Cameron 1972, Balling and Resh 1982). Furthermore, *S. virginica* is a major source of detritus, a component of estuary production (Odum and de la Cruz 1967, Barry et al. 1996).

Although it has been established that trampling affects plant communities, there is little published information on the effects of trampling on invasions (Hobbs and Huenneke 1992). Furthermore, most studies have not accounted for variations in intensity and frequency. Those that have addressed variability in these components have often relied on natural experiments (Beauchamp and Gowing 1982, Sun and Liddle 1993, Taylor et al. 1993). Some field experiments have been used to examine the different components of disturbances, but these have been conducted primarily in rocky intertidal marine systems (Sousa 1980, De Vogelaere 1991, Povey and Keough 1991, Keough and Quinn 1998). Research using manipulative experiments is still needed to examine the effects of trampling intensity and frequency on plant communities. This type of information is critical in minimizing impacts in California salt marshes.

I studied the response of *S. virginica* assemblages in Elkhorn Slough to different levels of human trampling, and recorded its response to cattle grazing. In particular, I was interested in determining the amount of damage caused by specific levels of human trampling intensity and frequency, and subsequent recovery over at least one year. Differences between grazed and ungrazed marshes and recovery after cattle were removed from a site were also investigated. I hypothesized that different levels of human trampling would affect *S. virginica* height, reproductive ability, and percent cover in significantly different ways, and predicted that different disturbance levels would affect the abundance of invertebrates found within *S. virginica* stands. Finally, I hypothesized that these different levels would yield different rates of recovery after trampling ended. I predicted that invasive terrestrial and marsh plants or algae would colonize open space and significantly change species composition in some trampled plots.

METHODS

Study Sites

I chose two sites to investigate the effects of human trampling on *S. virginica* assemblages. The main study site was located at Whistle Stop Lagoon, on the ESNERR, Watsonville, California (Fig. 1). This saltwater "lagoon" is encircled by an approximately 3 m-wide, homogeneous zone of *S. virginica.* It is bounded by mudflats at its lower tidal edge and by upland vegetation, including *Conium maculatum* (poison hemlock), *Baccharis pilularis* (coyote bush), *Bromus diandrus (*ripgut grass), *Cirsium vulgare* (bull thistle), *Silybum marianum* (milk thistle), and *Foeniculum vulgare* (fennel) at its upper tidal limit. The Research Reserve limits access to this *S. virginica* assemblage, and it is largely undisturbed by humans. I chose this site in order to minimize confounding effects of previous or current trampling. Whistle Stop is an upper elevation marsh separated from the main channel of Elkhorn Slough by two culverts, and is rarely inundated by the slough's daily tides. Upper tidal marshes like this one are often trampled by visitors approaching the area from land. These areas tend to stay relatively dry and are more appealing to hikers than lower, wet areas.

Salicornia has different growth morphs across the marsh (Zedler 1984). It grows more erect or taller at high elevations, and is more decumbent at lower elevations (Mahall and Park 1976, Seliskar 1985, Pennings and Callaway 1992, and personal observation at Elkhorn Slough). Because *S. virginica* height is a variable in this study, I blocked my experiments at a uniform tidal elevation to remove height variability.

I used a secondary site to test the effects of trampling in another region of the slough. This marsh, designated the Northwest Marsh, is along the northwest edge of the slough's main channel (Fig. 1) and is also undisturbed, but composed of patches of *S. virginica*, *Frankenia salina*, *Distichlis spicata*, *Jaumea carnosa*, and the parasitic dodder *Cuscuta* spp. Unlike Whistle Stop, the Northwest Marsh directly flanks the main channel of the slough, is exposed to the changing tides four times a day, and occupies a wide range of tidal heights. At this location, I set up experimental units along the wrack strand line (~1.4 m above MLLW) to test the effects of trampling at a lower elevation. Lower tidal marshes are often trampled by kayakers hauling out boats, by researchers passing through to mudflats, classes visiting estuaries, or fishermen searching for clams and bait.

I chose four sites to compare grazed and ungrazed vegetation (Fig. 1): three south of the ESNERR along Parson's Slough, and the fourth along the southwestern edge of the Moro Cojo Slough, a smaller southern inlet connected to Elkhorn Slough by the Moss Landing Harbor. I used Hudson's Landing, near the northern end of Elkhorn Slough, to follow recovery once cattle were excluded from the marsh.

Experimental Design

Human Trampling Study

Trampling treatments. I tested the effects of different levels of trampling intensity and frequency on *S. virginica* using a randomized block design. I defined intensity as the number of passes over an experimental unit. A single pass was the number of steps within a unit needed to uniformly step on all the vegetation within that unit. Frequency was how often the trampling was applied. I chose levels of both factors to represent conditions that are common in Elkhorn Slough.

Nine trampling treatments varying in intensity and frequency were applied at Whistle Stop from April to September 1996. Trampling was done by adult volunteers weighing 55-85 kg wearing rubber boots. Intensities were (1) 1 pass (representing an individual researcher or volunteer on the Research Reserve), (2) 15 passes (representing a small class visiting the slough), (3) 30 passes (representing a large visiting class, or kayakers visiting popular launch areas), and (4) 0 passes (control). Frequencies were (1) once a week, (2) once a month, and (3) once every three months. One replicate of each treatment level and control were used per block, giving ten sample units per block.

Experimental unit size for each treatment was 0.56 m^2 (75 X 75 cm), but I measured only the internal 0.25 m^2 (50 X 50) cm in order to avoid edge effects. The size of disturbances may influence plant responses (Shumway and Bertness 1994), but due to time and resource constraints, I used only one experimental size. This prohibits extrapolations to larger areal disturbances, but allows for a high precision of *S. virginica* height measurements in a reasonable time.

Twenty-five cm-wide buffers separated sample units within each block. The resulting blocks were 475 cm X 175 cm (Fig. 2). The perimeter of blocks were marked with 8 upright 64 cm (length) PVC pipes, and inner treatment quadrats were marked during trampling and measuring with a temporary nylon webbing supported by the PVC markers. Ten blocks or replications were randomly placed at Whistle Stop Lagoon.

To determine if the effects of trampling were consistent in different areas and tidal elevations, I set up a smaller-scale study at the Northwest Marsh with fewer trampling treatments and replicates. Only three blocks with seven treatments were used: three levels of intensity (30, 15, and 1 passes) combined with only two frequencies (weekly and monthly), and an untrampled control. I trampled for one month in May 1997. These data were analyzed separately, but the results from both sites were compared to see if community response to trampling is different given different locations and tidal influences.

I conducted a pilot experiment in 1995 using three blocks at the southwest portion of Whistle Stop Lagoon. Nine treatments in each block were applied from April 12-May 5 1995: four levels of intensity (50, 25, 15, and 1 passes) combined with two frequencies (weekly and monthly), and one control.

Damage and post-trampling recovery measurements. Damage was defined as the amount of vegetation change that occurs as a result of trampling disturbance (Cole and Bayfield 1993) and included changes in *S. virginica* height and flower production, as well as changes in plant and invertebrate composition. Recovery was defined as the rate at which vegetation reverts to untrampled control conditions after trampling ceases.

Immediately after trampling was completed, I recorded damage once for all experiments using the variables described below. I also used the same indicators to measure recovery. At Whistle Stop recovery was measured for one year at 1, 3, 6, 8 and 12 months after trampling ended. At the Northwest site recovery was recorded at 1, 6, and 12 months. I measured the pilot project at 1, 12, 18, and 29 months.

Earlier studies have shown that vegetation height often responds significantly to grazing and trampling (Cole and Bayfield 1993). Therefore, I used *S. virginica* height as the primary indicator of immediate damage and subsequent recovery. A free-standing PVC 0.25 m^2 (50 cm X 50 cm) quadrat with 80 cm tall legs was placed over each experimental unit. Ten randomly selected height subsamples were taken within each quadrat. Height measurements were taken using a 1 m measuring tape secured to a 10 mm (diam.) 123 cm (length) wood dowel. The height of the tallest portion of *S. virginica* touching the face of the measuring dowel was recorded to the nearest mm. If no *S. virginica* touched the dowel face, a height of 0.0 cm was recorded.

I sampled the plots for percent cover of live plants and bare ground visually (Dethier et al. 1993). Visual estimates may give a more accurate representation of relative coverage than random-point-quadrats, and they can reduce overall sampling time (Dethier et al. 1993). Estimates were made using 25 small squares (10 X 10 cm each) marked off within the free-standing 0.25 m^2 quadrat frame. I documented the canopy only because *S. virginica*'s tangled woody growth cannot be easily moved aside to measure underlying layers, and other species rarely survive beneath the dense canopy. In a few plots at Whistle Stop *Conium maculatum* (poison hemlock) grew over 1 m taller than the surrounding vegetation and, in these cases, its canopy was recorded as an emergent overstory so total cover exceeded 100%. Epiphytic algae grew on some *S. virginica* at the Northwest Marsh and, in these cases, I recorded both species so total cover also exceeded 100%. Bare space was scored as any space without vegetation, and included areas covered by dead, crushed stems. Wrack, floating debris that is stranded in the marsh after high tides, was recorded at the Northwest site but did not occur at Whistle Stop.

I also used percent cover data to determine the average number of vascular plant taxa present at each trampling level. At Whistle Stop taxa were grouped by family because upland grass species were not identified to genus in the field. Because several of the species are members of the same family (i.e., *S. virginica* and *Atriplex patula* are both in Chenopodiaceae), this grouping gave only a gross measurement of plant richness. Taxa at the Northwest Marsh were identified to species and grouped accordingly.

I recorded the number of flowers on *S. virginica* measured for height in the months that flowers were present. *Salicornia* flowers May-October in Elkhorn Slough, reaching a maximum in August-September (personal observation), and flowers are often embedded in the succulent stems. Because there may be several dozen embedded flowers per spike and these could not be accurately recorded in the field, I counted only fully emergent flowers on the tallest spikes hitting the measuring dowel.

I also sampled invertebrates in treatment and control units at Whistle Stop. Although marine benthic invertebrates do occur in *S. virginica* stands, previous attempts to quantitatively study them with cores proved unsatisfactory (Mark Silberstein pers. comm.), and they are substantially less abundant than epiphytic species (de Szalay and Resh 1996). Therefore I focused on insects and arachnids, among the most abundant animals within tidal salt marshes (Lane 1969, Cameron 1972, Balling and Resh 1982).

Arthropods at Whistle Stop were sampled during late-morning on August 18 and 19, 1997 to assess recovery 11 months after trampling had stopped. I sampled only seven of the ten blocks due to limited resources and time. Invertebrates were collected using a two-cycle, air cooled vacuum (Weed Eater Blower/Vac Model 960) with a suction volume of 340 ft^3/min., fitted with a 5 cm diameter nozzle and a nylon collection bag. I collected each sample by sweeping the nozzle over the entire 0.25 m^2 sample unit. Samples were placed in an ice chest immediately after collection and, within 3 hours, placed in Berlese separation funnels for 24 hours. This method was found to extract approximately two-thirds of the arthropods caught in the collected detritus, and they represented all orders present in the detritus. Arthropods were then stored in 70% isopropyl alcohol until they could be counted and identified to order. After analyzing these data, I decided to document invertebrate densities immediately after trampling as well. Therefore, I set up 3 extra blocks and trampled them for 1 month during September 1997. Using the same vacuum, I collected arthropods from these blocks in early October 1997. Because there were fewer replicates for this sample, I separated all invertebrates from the plant material by hand using a dissecting scope at 8X magnification. This ensured that all invertebrates were extracted from the large volume of detritus.

Cattle Grazing Study

Damage. I chose four sites in Elkhorn Slough and Moro Cojo to compare vegetative cover in cattle grazed and ungrazed areas. Photo quadrat sampling was done one time, in September 1998, using 50 X 50 cm quadrats placed on either side of fences separating grazed and ungrazed vegetation. Quadrats were photographed with a Minolta 35 mm camera, a 50 mm lens, and Kodak Elite II 35 mm color slide film (ISO 200). Slides were projected onto a grid of 100 points, and the canopy species at each point were recorded. Because there were 100 points, each hit was recorded as 1 percent of the total cover.

Recovery. In the early summer of 1996, a barbed-wire fence was constructed to keep ~25 dairy cows out of the Nature Conservancy marsh at the northern end of Elkhorn Slough. I traced the recovery of marsh plants along this fence for one year, from August 1996 to August 1997, sampling the vegetation on three dates. On August 22, 1996 and February 25, 1997, plant height (for all species) and vegetative cover were sampled on the recovering side of the fence using the quadrat method described in the human trampling experiment (for both, n=5). I began sampling the still-grazed side in February 1997. Unlike the cattle-excluded area, this portion of the marsh was not accessible because it was privately owned. Therefore, I documented plant cover using the photo quadrat method, randomly placing five quadrats directly over the fence along a 21 m transect. Plant height was recorded from 30 randomly selected points along this transect.

In August 1997, I sampled a final time, recording vegetation height and percent cover in the recovering and still-grazed areas, as well as in an adjacent marsh that naturally excluded cattle. This area was separated from the others by a permanent creek too wide and deep for cattle to cross. In order to directly compare the previously- and still-trampled areas to this untrampled control marsh, I set up a 21 m long transect parallel to the fence in each section. Again, due to constraints in the still-grazed region, transects were placed within a meter of the fence. In the ungrazed marsh the transect was set up 12 m from the creek because vegetation directly flanking this border was influenced by fresh water and did not include many halophytes. As in February, I randomly chose 30 points along the transect to record plant height, and five points for photo quadrats.

Statistics

Statistically, I evaluated the effect of trampling levels on *S. virginica* height and percent cover using analyses of variance. For the main experiment at Whistle Stop, there were nine treatment groups in this 3 X 3 factorial experiment but only one control because the untrampled plots could not be classified along the frequency dimension. Therefore, I used an asymmetrical analysis to evaluate the effects of trampling intensity and frequency at the end of trampling for all experiments, and at selected recovery times. Similar analyses were used for the Northwest site and the pilot project. Trampling frequency and intensity were fixed factors, and blocks were random factors. F values for frequency, intensity and their interaction were derived by dividing by MS block*factors. Control versus all other treatments and blocks were divided by MS Error. Randomized block analyses of variance were done on invertebrate data. Factors were treatment level (high, medium, low and control) and block number. In cases where the null hypotheses were not rejected, power analyses were done (Zar 1984).

In all cases, alpha levels were set at 0.05, and the assumption of homoscedasticity was tested using Cochran's test. *Salicornia virginica* height data for Whistle Stop damage measurements were square root transformed to correct heterogeneous variances. All percent cover estimates were arcsine transformed, and when necessary, invertebrate densities were log transformed. Transformations were successful in correcting heteroscedastic data. Post hoc Tukey's tests were performed to compare treatments. Recovery was assumed to have occurred when there was no significant difference between untrampled controls and trampled treatments. ANOVA tables for each analysis are given in Appendices A-I.

For the grazing measurements, I used a t-test to compare percent *S. virginica* cover in grazed in ungrazed areas. For recovery from cattle grazing, I did not statistically analyze height or percent cover data. Only one site was excluded from grazing, thus each treatment type (grazed, recovering, and ungrazed) was unreplicated and statistics could not be legitimately used (Hurlbert 1984).

RESULTS

Human Trampling Study

Salicornia Height

Trampling at almost every treatment level significantly damaged *S. virginica* relative to untrampled plots (Fig. 3). Trampling crushed succulent stems, broke older, woody branches, and almost entirely removed vegetation in the most walked-on plots. At Whistle Stop, all trampled *S. virginica* was shorter than in controls and, in general, height of *Salicornia* declined with increasing trampling frequency. Vegetation height was damaged equally by 30 and 15 passes, and both these intensities were more destructive than 1 pass.

Results were similar at the Northwest site. However, at this site the least trampled vegetation (one time with one pass) was not significantly shorter than controls

(Fig. 3). Control heights were substantially shorter at the Northwest Marsh than at Whistle Stop, probably due to differences in tidal height.

Salicornia height did not begin to recover until the following growing season, regardless of time of disturbance. At Whistle Stop, where trampling ended in September, there was little or no regrowth during *S. virginica's* dormant months (Oct.-Mar.) (Fig 4). Once the growing season began in the spring, *Salicornia* height in all trampled plots increased, although after one year many were still significantly shorter than untrampled controls. At this point the effects of trampling frequency and intensity were still evident (frequency $F = 9.27$, $df = 2, 18$, $P = 0.003$; intensity $F = 23.36$, $df = 2, 18$, $P < 0.001$), with the most heavily trampled plots still 10 cm or more shorter than the controls. However, plots that had been trampled with only 1 pass, regardless of frequency, recovered within this time period.

At the Northwest Marsh, where trampling ended in May 1997, *S. virginica* height did not increase during the first growing season, and had not increased by the last sampling date in April 1998 (Fig. 5). A similar trend emerged in the pilot project. There, trampling ended in May 1995, and little regrowth occurred that summer. By fall 1996, after 19 months of recovery, trampled *S. virginica* had grown appreciably (Fig. 6), but significant differences between the trampled *Salicornia* and controls persisted (effect of trampling, control vs. all other treatments $F = 5.73$, $df = 1, 16$, $P < 0.05$). After 2.5 years of recovery, there were no statistically significant differences between controls and treated plots (effect of trampling, control vs. all other treatments $F = 1.96$, $df = 1, 16$, $P > 0.10$).

Percent Cover

Salicornia canopy was high year round in untrampled control plots at both sites (Figs. 7 and 8). At Whistle Stop, *S. virginica* cover in control plots ranged between 96 and 100 percent (SE ± 0-3.6%), and at the Northwest Marsh between 83 and 92% (SE ± 3.9-7.4%).

Damage to the marsh was similar at both sites. High intensities and frequencies of trampling dramatically reduced plant cover. At Whistle Stop, bare space in plots trampled with 30 and 15 passes a week exceeded 90%. At the Northwest Marsh where plots were trampled for a shorter time, bare ground cover was 45-65%. Canopy cover in plots trampled at a lower frequency also declined. At both sites, bare ground ranged between 10 and 50% in areas trampled monthly with 30 and 15 passes. At Whistle Stop, heavy trampling generally exposed dry black earth, while at the Northwest Marsh it produced thick, deep mud.

As I had hypothesized, damage was less severe at lower levels of trampling. *Salicornia* cover did not initially decline in plots trampled infrequently at Whistle Stop, (Tukey's test, treatments vs. controls $P > 0.80$ in all three cases), and areas trampled weekly with 1 pass retained S. *virginica* covers between 90 and 98%. In contrast, this level of trampling significantly reduced plant cover and increased bare mud cover at the Northwest Marsh.

Like height, *S. virginica* cover did not recover in the first months following the end of trampling. In the most severely trampled plots at Whistle Stop, bare ground did, however, decline steadily throughout the winter and spring (Fig. 7). These bare patches were initially colonized by seedlings of non-native upland species, including *Conium maculatum, Silybum marianum, Cirsium vulgare, Bromus* spp., *Geranium dissectum* (geranium), *Rumex crispus* (curly dock), *Brassica nigra* (black mustard), and *Malva* spp. (mallow), all of which occur in the nearby upland habitat. Pooled, these species peaked in March 1997, comprising ~40% of the canopy, while other marsh species made up less than 1%.

Terrestrial annuals in these highly trampled plots died back later in the summer, and *S. virginica* began to grow in from the untrampled sides, as well as from rhizomes and broken but still-rooted stems. *Salicornia* seedlings appeared in only two replicates and did not account for substantial regrowth. A year after trampling ceased, *S. virginica* cover in heavily trampled areas had increased to 70%, while upland annuals accounted for ~10%, and bare ground 15-20%. A similar trend occurred in intermediately trampled areas (Fig. 7).

Plant response was different in Whistle Stop's lightly trampled plots. Although these areas did not initially show signs of damage, *S. virginica* canopy did decline months later. By March 1997 all of these patches experienced declines of ~10% with concurrent increases in bare ground and upland species (Fig. 7). Control plots did not show similar declines. Thus, six months after trampling ended, plots that initially had been statistically identical to controls were now different (Fig 9). This trend, however, reversed itself over the spring and summer months, and by September 1997 these plots again had *S. virginica* cover similar to untrampled plots.

Recovery progressed differently at the Northwest site. As discussed above, recovery at Whistle Stop was marked by invasions of upland weeds and vegetative regrowth of *S. virginica*. There, trampling ended in September, and regrowth was followed until the next September. At the Northwest site, I stopped trampling in May and recorded regrowth through the following April. Here the percent cover of all species remained virtually unchanged through the first growing season and the following winter (Fig. 8). Only the cover of wrack increased as it washed into the marsh in June 1997. Although there were no statistically significant differences in wrack deposition by treatment ($F = 1.77$, $df = 6, 12$, $P = 0.19$, power of test < 0.30) wrack did settle in almost perfect squares, mimicking the dimensions of trampled areas. Block location was probably the most significant factor influencing deposition ($F = 8.64$, $df = 2, 12$, $P = 0.005$), but other trends were evident. In untrampled and lightly trampled plots, wrack buried 0-13% of the canopy. In all other trampled plots, wrack either did not settle at all (in 7 of the 15 damaged replicates), or covered 18-74% of the canopy (in the remaining 8 replicates). Some wrack persisted into the fall, but none remained by spring 1998.

S. virginica cover at the Northwest Marsh did not increase during the year I sampled recovery, although numerous seedlings appeared in heavily trampled plots by April 1998. At the same time, other species also began to colonize the mud (Fig. 8). *Rhizoclonium riparium*, a green filamentous alga, appeared in all treatment types and controls, and exceeded 30% of the cover in heavily trampled plots. It averaged only 2% in untrampled and lightly trampled plots. Another green alga, *Gayralia* (=Monostroma) *oxysperma*, began growing on *S. virginica*, epiphitizing ~10% of the vegetation in plots trampled with 30 or 15 passes. It covered only 1-3% in controls and plots trampled with only 1 pass.

Vascular plants other than *S. virginica* also increased in some plots by April 1998 (Fig. 8). However, unlike the green algae whose distributions were significantly affected by treatment level ($F = 3.98$, $df = 6, 12$, $P = 0.02$), these plants showed no statistically significant differences based on trampling (for example, *Atriplex patula* $F = 0.964$, $df = 6, 12$, $P = 0.49$; *Jaumea carnosa* $F = 0.547$, $df = 6, 12$, $P = 0.76$). Although ANOVAs indicated no effect of treatment level, these results are most likely due to the low number of replicates (in both cases above, power of the test < 0.30) and the early sampling date.

Despite this, patterns in species' distribution did emerge. *Jaumea carnosa* occurred in all treatment types, albeit in small numbers, while *Frankenia salina* appeared in all but the most trampled treatments. On the other hand, *Distichlis spicata* occurred more frequently in trampled plots than in untrampled ones, and *Atriplex patula* was completely absent from controls. *Cotula coronopifolia* (brass buttons—an introduced member of the sunflower family) appeared in plots trampled weekly or with 30 passes, but not in lightly or untrampled areas. No other *C. coronopifolia* occurred along this stretch of marsh, and upland species did not occur at this elevation. Algal growth into the plots did not appear to be related to wrack deposited the preceding summer, but vascular plant growth was. *Frankenia salina*, *D. spicata*, *J. carnosa*, *A. patula*, *C. coronopifolia*, and *Ruppia maritima* (ditch grass) only grew in plots that had been previously covered with more than 4% wrack.

Trampling also caused changes in distributional patterns at Whistle Stop. Upland grasses grew in both trampled and untrampled areas, but were more frequent in trampled plots. In March 1997 grasses appeared in 100% of the heavily trampled plots, but in only 30% of the controls. Thistles appeared only in plots trampled weekly or monthly with 30 or 15 passes. As at the Northwest Marsh, *A. patula*, although rare, appeared only in trampled plots. Likewise, *C. maculatum* grew in at least one replicate of all treatments at the main site, but did not occur in untrampled plots. Block location did play a statistically significant role in plant cover and composition throughout the year of recovery (effect of blocks at the end of 1 year, $F = 3.49$, $df = 9, 36$, $P = < 0.001$), but this effect was due almost entirely to one block which was much more diverse than the other nine.

These distributions were also reflected in plant richness measures, which varied by trampling level and over time. At Whistle Stop, untrampled plots averaged ~1.2 plant families year round (Table 1). Heavy trampling removed almost all plants, but as many as four or five plant families began colonizing individual plots three months after trampling ended. During the summer, most of these taxa died back while *S. virginica* regrew, causing family richness in these patches to decline. Lightly trampled plots at this site had slightly more families per area than controls, and this changed little over the year of recovery. At the Northwest Marsh, species richness did not vary dramatically among trampling levels until the last sampling date in April 1998 (Table 2). Then as many as five or six plant species appeared in heavily trampled plots, while untrampled patches averaged only 1.3 species per quadrat.

<u>Flower Production</u>

Not surprisingly, as trampling decreased the cover of *S. virginica,* it also substantially decreased the number of emergent flowers present per plot as compared to controls (Fig. 10). Based on subsamples at Whistle Stop, which recorded only a fraction of the actual number of flowers present, control plots averaged ~15 emergent flowers at the end of the trampling period. Some flowers remained in plots trampled by 1 pass or only once every three weeks, but none had as many as untrampled areas. After a year of regrowth, most treatment types had as many *Salicornia* flowers as controls, averaging 4-12 emergent flowers on sampled spikes, compared to a mean of 10 in untrampled plots. Flowering only failed to recover in plots trampled with 30 passes once a week and those trampled with just 1 pass every three months. Both of these had means less than 1 flower. Given the patchy distribution of *S. virginica* flowers at Whistle Stop, it is difficult to determine if these anomalies are a result of trampling level. Flowers did not occur at the Northwest Marsh during the months sampled.

Invertebrates

Overall, representatives from 14 invertebrate orders were collected at Whistle Stop, the most common being Homoptera, Diptera, Araneida, Hemiptera, Coleoptera and Hymenoptera. Less abundant orders included Amphipoda, Isopoda, Acarina, Thysanura, Thysanoptera, Lepidoptera and Mollusca.

Trampling level did not affect the total number of invertebrates, either immediately after trampling ended or after 11 months of recovery (damage $F = 0.61$, $df = 4, 8$, $P = 0.67$; recovery $F = 0.33$, $df = 3, 18$, $P = 0.80$). On average, I collected between 40 and 70 individuals per quadrat immediately after trampling, and 23-30 in plots allowed to recover for 11 months. Insect abundance in California salt marshes varies temporally (Lane 1969, Cameron 1972, Balling and Resh 1982), and these seasonal differences, as well as different sorting methods, probably account for the differences.

Although it did not affect total abundance, trampling did influence the distribution of some of the more abundant orders. I used one-way blocked analyses of variance on the six most common taxa, Homoptera, Diptera, Araneida, Hemiptera, Coleoptera, and Hymenoptera. Treatment level did affect Homoptera, Diptera and Araneida individually immediately after trampling ended (Homoptera $F = 4.73$, $df = 3, 6$, $P = 0.05$; Diptera $F = 13.30$, $df = 3, 6$, $P < 0.01$; Araneida $F = 10.15$, $df = 3, 6$, $P < 0.01$), and Araneida 11 months after trampling ended ($F = 4.22$, $df = 3, 18$, $P = 0.02$).

In collections made a day after trampling, Homoptera were reduced in heavily walk-on plots compared to all other levels (Fig. 11). Spiders (Araneida) followed a similar pattern—they were reduced in both heavily and intermediately trampled areas. Conversely, flies (Diptera) responded by inhabiting the most damaged quadrats and avoiding untrampled controls. Block location did play a role in the distribution of Araneida ($F = 5.39$, $df = 2, 6$, $P = 0.05$).

In plots sampled after 11 months of recovery, only spiders showed significant treatment effects. Despite the inability of the univariate ANOVAs to find significant differences within other orders (Homoptera ANOVA power = 0.40; for Diptera, Hemiptera, Coleoptera, and Hymenoptera, power < 0.20), clear trends were still distinguishable 11 months after trampling had stopped (Fig. 12). Homoptera density was still highest in lightly and untrampled areas, as were the Araneida. More flies were still found in the most damaged plots. Again, block placement played a role in density distribution, primarily for the Hemiptera.

Cattle Grazing Study

Damage

Grazed areas were characterized by high percentages of bare ground (x = 68.50%, SE ± 15.57, n = 4) and very little *S. virginica* (x = 6.25%, SE ± 6.25, n = 4). *Distichlis spicata* occurred along the grazed side of two fences, comprising 20% of the cover at one site and 3% at the other. Only two of the four fences were unbroken and completely excluded cattle. Along the cattle excluded side of the two unbroken fences, *S. virginica* cover averaged 91.50% (SE ± 8.50) and bare ground accounted for only 2.50% (SE ± 2.50). Other species did not occur. The percent cover of *S. virginica* on either side of grazed fences was significantly different (t = -7.95, df = 4, P = 0.001).

Recovery

Although cattle grazing can cause severe damage to marsh plants, its effects do not appear to be irreversible. Like other cattle trampled sites in Elkhorn Slough, the grazed pasture at Hudson's Landing was characterized by relatively high percentages of bare ground (> 50%) and *D. spicata* (17-35%), as well as very short vegetation, ranging from 0.18 cm (SE ± 0.18, n = 30) in August 1997 to 2.07 cm (SE ± 0.53, n = 30) in February 1997. However, once the Nature Conservancy's portion of this marsh was removed from grazing, plant height and composition began to change rapidly. By the first sampling date approximately 3 months after the fence was constructed, vegetation in the recovering marsh had grown to four times as tall as in the adjacent trampled pasture (x = 8.67 cm, SE ± 1.16, n = 5). Six months later, the recovering plants peaked at 14.90 cm (SE ± 2.45, n =5), more than 7 times the height of the still-grazed vegetation. A comparison done 15 months after grazing ceased showed that average plant height in the recovering pasture ($x = 14.82$ cm, SE $\pm$ 1.62, $n = 30$) was similar to the vegetation height in the ungrazed control ($x = 16.61$ cm, SE $\pm$ 1.14, $n = 30$).

Although cattle grazing greatly reduced the percent cover of vegetation, it did not remove all plants. What was not directly removed by trampling was grazed to ~2 cm high clumps. At Hudson's Landing, both *D. spicata* and *S. virginica* survived in small patches of short plants that together accounted for 45-50% cover in the grazed field. These patches responded quickly to the removal of cattle. Three months after the construction of the fence, bare ground was reduced to 15%, *D. spicata* had grown to occupy almost 50% of the space, while *S. virginica* covered 35% (Fig 13). Little new growth occurred over the dormant winter months, but by August 1997 (15 months after fence construction), *D. spicata* and bare ground had declined and were replaced by *S. virginica* that now occupied 75% of the canopy. Relative to the untrampled control marsh, however, this did not constitute a full recovery. There, *S. virginica* canopy cover was almost 100% (Fig. 14), and *D. spicata*, while present, was rare. Unlike the highly human-trampled plots, very little upland vegetation, algae, *F. salina*, *J. carnosa*, *A. patula* or *C. coronopifolia* appeared in the recovering pasture ($\leq$ 2% in any given sample).

DISCUSSION

Comparison of Treatments

This study indicates that trampling and grazing can decrease *S. virginica* abundance, lead to changes in community structure, and contribute to loss of marsh habitat. Furthermore, trampling can promote the displacement of native plants by introduced species. However, these responses vary based on differences in disturbance levels and locations.

Salicornia branches are easily broken if walked on, regardless of trampling intensity or frequency. However, at its lowest levels trampling did not lead to changes in plant composition or cover. In these cases trampling did little more than create swaths a few centimeters shorter than the surrounding vegetation and, when trampling was stopped, recovery occurred within a year. Although the number of flowers were reduced, most *S. virginica* regrowth occurred vegetatively, and this reduction in flowers appeared to have little effect on the ability of the plant to recover.

Areas trampled infrequently by many people (15-30 passes once every three months), and areas trampled weekly by 1 or 15 people, responded similarly, showing a delayed response to trampling at Whistle Stop. *S. virginica* cover declined months after trampling ended at the Whistle Stop. *Salicornia* biomass decreases naturally during the winter as succulent shoots die and are shed (Weber et al. 1977, Josselyn 1983), and this decline was much more evident in these trampled areas than in untrampled areas. The apparent delay in trampling response may be because the measurements were not sensitive enough to detect minor fluctuations in canopy cover. Indeed, these measurements failed to show seasonal declines of *S. virginica* in controls, although such declines do occur at Whistle Stop (personal observation). The threshold for detecting plant loss may not have been reached until stems lost to light trampling were joined by seasonal dieback. On the other hand, it is possible that trampling simply increased the seasonal shedding of stems relative to control plants.

Whatever the mechanism, these levels of trampling can open up bare space that can be colonized by exotic species, other marsh plants or, at low elevations, algae. However, these gaps were small relative to those created by heavy trampling, and this damage can be repaired given a year of recovery. The most dramatic damage occurred in treatments designed to mimic frequent trampling by many people. My results show that these areas are susceptible to invasions by non-native species or algae, and they can take years to recover.

Location can also affect plant response to disturbance. Although the initial response of plant assemblages to trampling were similar at both sites, recovery differed, and the Northwest Marsh did not experience an invasion of upland species. Seed dispersal may have been a factor. Upland species adjacent to the marsh at Whistle Stop needed only to disperse their seeds a few centimeters to reach most of the trampled plots, while upland species at the Northwest site were several meters away from experimental blocks. Access to the marshes may have also played a role. To reach Whistle Stop, volunteers had to walk through upland areas, where upland seeds often lodged on clothes and in boots. In these cases, we may have unwittingly acted as dispersing agents to the marsh. On the other hand, we accessed the Northwest Marsh by kayak and did not contact upland species along the way. Perhaps most importantly, environmental conditions at this lower elevation, such as high salinity and frequent inundation, presumably exclude upland plants. But these same conditions facilitate colonization by algae. It is unclear if, given more time, vascular marsh species would have accounted for more of the canopy cover in trampled plots relative to controls.

Invertebrate populations also shifted in response to different levels of trampling. These results probably arise from changes in food resources and habitat structure. Invertebrates can be divided into three types of feeding guilds—herbivores, detritivores and predators—and disturbances often influence insect and spider populations at this level of organization (Schowalter 1985). Of the insect orders I collected, only the Homoptera and Lepidoptera are exclusively herbivores in marshes (Cameron 1972). In his studies of insects in a California salt marsh, Cameron (1972) observed an increase in herbivore diversity with increasing above-ground biomass. Likewise, I discovered the largest number of Homoptera in lightly or untrampled plots where the height and percent cover of *S. virginica* were highest. Heavily trampled areas had less *S. virginica* biomass, and thus provided less food for this order. Lepidoptera was rare in all treatment types, and no effects of trampling were discernable.

Cameron (1972) found that predator diversity, consisting mostly of Araneida, increased with the number of herbivores. This, too, occurred at Whistle Stop. The density of the Araneida closely shadowed the density of the Homoptera, both immediately after trampling ended, and after 11 months of recovery. This is not to say that spiders feed only on Homoptera—that was not established by this study. The large number of spiders in lightly and untrampled plots also may be explained by differences in the structural complexity of *S. virginica*. Healthy, tall vegetation may provide more habitat for the Araneida than devegetated areas (Duffey 1975).

In contrast to the Homoptera and Araneida, many Diptera are detritivores, although some species may act as herbivores or predators. Cameron (1972) found that detritivore diversity increased with accumulation of *S. virginica* litter during the winter months. Other studies have also noted increases of Diptera in trampled areas (Duffey 1975, Liddle 1975). Most insects can apparently search for and exploit suitable feeding sites, primarily by using visual and chemical cues to determine plant suitability (Schowalter 1985). Flies may have been attracted to highly damaged plots by decaying plant matter created by trampling.

Like heavy human trampling, grazing by cattle can also decrease plant cover and plant height, removing emergent vegetation habitat during high tides. Results from Elkhorn Slough echo those from other salt marshes. Cattle grazing in a Georgia salt marsh decreased plant height and promoted the growth of *Distichlis* (Shanholtzer 1974), while simulated grazing caused declines in peak biomass and primary production of marsh vegetation (Turner 1987). Reimold et al. (1975) reported that yearly production of *S. virginica* in Georgia was seven times lower in grazed marshes than in ungrazed ones. Andresen et al. (1990) showed that grazing can change plant morphology and create bare space.

Unlike areas trampled heavily by people, marsh vegetation removed from grazing began re-growing quickly and did not include exotic upland annuals or algae. Relative to recovery from human trampling this was unexpected, but these results do agree with previous grazing studies. Reimold et al. (1975) found that overall plant production was higher in a recovering marsh than in both ungrazed and grazed areas. They also reported that, like at Hudson's Landing, *Distichlis* occurred in grazed marshes but not in ungrazed areas, and reached a maximum in recovering areas. Fifteen months after cows were excluded in Elkhorn Slough, *Distichlis* was declining as *Salicornia* increased, indicating a shift toward full recovery. This corresponds to conclusions reached by Andresen et al. (1990) who noted that marshes removed from grazing initially increase in plant richness, then decline over time as they return to monocultures.

The differences in recovery between human and cattle disturbances may be due to several factors, including disturbance intensity, frequency, size, and location. Unfortunately, I could not manipulate the number of cows grazing in the fields I studied, and I was able to document recovery from grazing at only one site. These limitations make it difficult to directly compare results from the human trampling experiments to observations from grazed fields. At Hudson's Landing, grazing by 25 cows maintained short patches of *S. virginica* and *D. spicata*, that recovered quickly after cattle were removed. However, had this field been grazed by higher densities of cattle, recovery rates may have been similar to heavily human-trampled areas. The mechanisms behind human and cattle disturbances may have also played a role in their different recovery times. Human trampling acts primarily by breaking stems, although it may serve to disperse some seeds as well. On the other hand, grazing includes not only trampling, but also deposition of wastes, uprooting of plants, and herbivory (Jensen 1985). Some researchers report that moderate herbivory or grazing, especially when combined with fertilization by deposited wastes, can increase primary production by triggering plant compensatory growth mechanisms (Owen and Wiegert 1976, Hik and Jefferies 1990), but this concept is hotly debated (McNaughton 1993, Painter and Belsky 1993).

Management Issues

These results can help managers develop strategies to protect natural resources while allowing access for visitors, researchers, and cattle. *Salicornia* assemblages are sensitive to trampling, but regulating people's presence in the marsh can minimize community shifts and habitat loss. In fact, trampling at the lowest intensities and frequencies may be sustainable, especially in higher elevation marshes. Individuals (such as researchers or maintenance workers) who visit specific sites once a month or less are unlikely to cause significant damage to marsh assemblages. Those needing access more than once a month could be encouraged to use different paths each time they walk through the marsh, or managers may prefer to concentrate these people on narrow paths, minimizing the areal extent of damage.

In terms of allowing visits by large groups, strategies adopted by managers will depend on conditions they desire to have at a given location. This approach, called the limits of acceptable change, accepts as a basic premise that change is an inevitable consequence of human use (Stankey et al. 1984) The question that needs to be addressed in this approach is "How much change is acceptable?" All areas trampled by more than 15 people are subject to some damage and are susceptible to at least a few invasive species, but areas trampled infrequently or only once retain high covers of vegetation and appear to recover within a year. If managers want groups to explore marshes that resemble undamaged areas, they may need to rotate the areas visited.

On the other hand, allowing many people to visit the same area frequently can lead to large scale and long term changes, and managers should try to minimize the number of areas used often by large numbers of people. This method is already used in Elkhorn Slough, where two designated boat launches accommodate large numbers of kayakers, especially during the summer. While causing a severe amount of damage locally, these areas serve to contain heavy trampling in a small area, reducing the overall amount of marsh that is damaged. This may be the best solution to accommodating many recreationists. However, managers probably do not want to encourage the construction of many more docks, since trampling at these elevations removes almost all *Salicornia* cover, and can promote the expansion of *C. coronopifolia*. Previous studies indicate that marsh land in Elkhorn Slough is more susceptible to erosion when *S. virginica* surface vegetation and root mass are reduced or degraded (Sliger 1982, Crampton 1994). Erosion is a major cause of salt marsh loss in Elkhorn Slough (Crampton 1994), and trampling along the lower margins of the marshes may contribute to the problem.

There may be fewer opportunities for managers to regulate grazing, particularly if private ranchers are reluctant to limit marsh access for their cattle. But cattle ranchers often apply principles of land management. A chief question of range management is "What level of grazing will maximize productivity and maintain a pasture's general character?" (Hobbs and Huenneke 1992). This study suggests that if grazing must occur, salt marshes can benefit from the rotation of cattle from one portion of a pasture to another. Allowing areas to recover for 12-15 months before re-introducing grazing may permit portions of marsh to regrow to nearly ungrazed conditions.

Comparison between Natural and Human Disturbances

In a broad sense, natural disturbance theory suggests that disturbances maintain local diversity by disrupting successional sequences (Connell 1978). This study confirms that human-caused disturbances can also increase plant richness. But although human disturbances may superficially resemble natural disturbances, they may differ in several important respects (White and Harrod 1997). Studies in California coastal marshes indicate that natural disturbances increase species richness by promoting the germination and growth of several high marsh species in *S. virginica* assemblages. Allison (1996) found that flooding increased the cover of *Distichlis spicata*, *Frankenia salina*, *Jaumea carnosa*, and *Spergularia media* relative to *S. virginica* in Bolinas Lagoon. Pennings and Callaway (1996) discovered that *Cuscuta salina*, a native parasitic plant that infects *S. virginica*, decreased *S. virginica* biomass and facilitated the rare species *Limonium californicum* and *F. salina*, thus increasing plant diversity. In Elkhorn Slough, Oliver and Reilly (1981) found that areas covered in wrack were colonized by *J. carnosa*, *F. salina*, and *Atriplex* spp.

Likewise, this study indicates that human trampling can increase the number of species occurring with *S. virginica*. However, the native species facilitated by natural disturbances are much different than those promoted by human trampling at high tidal elevations. In marshes along the transition between upland and marsh lands, heavy trampling promotes the establishment of exotic annual plants. Results in the lower marsh were less conclusive. Although not statistically significant, several high marsh species that germinated in trampled spaces did not appear in controls, and species richness was highest in heavily trampled plots allowed to recover for a year. But clearly, the short-term effect in heavily trampled plots was to change marsh to a mudflat habitat that was then overgrown by green algae. Additionally, heavy trampling promoted the invasion of *C. coronopifolia*, an exotic species that has been expanding its range throughout Elkhorn

Slough since the late 1970's.

In another study, Allison (1995) concluded that some human disturbances in salt marshes can actually reduce species diversity. He tested marsh plant response to experimental sediment deposition in Bolinas Lagoon, California and predicted that disturbed *S. virginica* patches would be colonized by less dominant marsh species. This did not occur. Instead, these disturbances reduced the cover of several marsh species, while *S. virginica* and *D. spicata* regrew vegetatively to occupy the newly created bare space.

In these cases, natural disturbances promoted native species diversity, while human disturbances facilitated invasions, changed habitat types, or even decreased diversity. These results may be partially a consequence of disturbance intensity. Both natural and human disturbances create bare space in an established canopy, but the amount of bare space may differ by perturbation type. In this study, the amount of bare ground exposed was directly a function of trampling intensity and frequency. The percent cover achieved by invasive species was also closely tied to the level of trampling. Burke and Grime (1996) found similar results when experimentally disturbing a British grassland. In their study disturbance intensity and the availability of bare space were by far the most important factors determining the cover attained by exotic plants. It may be that heavy trampling more completely removes *S. virginica* than wrack burial, parasites or flooding, releasing more resources for exotics to exploit.

Disturbance frequency may also play a role. Natural disturbances in marshes are seasonal and tend to allow months or years for recovery. In my experimental program, disturbance frequency was too high to allow plant recovery between tramplings, and plants did not begin growing until several months after disturbances ended. Even given this much time, recovery at the Northwest Marsh was minimal. Had this area been trampled again the following summer, a common pattern of recreational use in Elkhorn Slough, the disturbed areas would have presumably remained unvegetated, marking a long-term change to a mudflat habitat. In fact, this is what has occurred at popular kayak launches in the region.

Species' life-history traits may also partially account for differences in responses to natural and human disturbances. Many communities are thought to have evolved in response to the regime of natural disturbances (Sousa 1979), meaning that some species' characteristics may have been shaped by the size and seasonality of historical disturbances. For example, competition in marshes is partially shaped by the timing of seedling emergence (Bertness and Ellison 1987). Many marsh species germinate in the late winter or early spring, coinciding with bare space and fresh water input created by winter floods (Zedler and Beare 1986, Allison 1996). Competitively inferior marsh plants are also adapted to burial by wrack mats, not only because mats create bare space but also because they carry and deposit seeds (Bertness and Ellison 1987, Ellison 1987). Human alteration of these natural disturbance regimes may mean native species are no longer well adapted for recruitment or establishment, and these deviations may lead to non-native invasions (Hobbs and Huenneke 1992).

This appears to be true in Elkhorn Slough. Here exotic upland species and green algae were apparently better adapted than native marsh plants to invade open space created by trampling. At Whistle Stop, upland annuals germinated in the early winter after trampling stopped, well before native seedlings emerged or *S. virginica* broke winter dormancy. In their study of community invasibility, Burke and Grime (1996) also found that the ability of introduced species to colonize disturbed areas was determined largely by the germination characteristics of the species. Furthermore, propagule availability may have been important. Whistle Stop is rarely inundated and, therefore, probably received few marsh seeds. At the Northwest Marsh, human trampling interacted with natural wrack disturbance to determine seed dispersal and germination. Trampling initially opened bare space, but non-dominant plants were only able to colonize areas also covered in wrack, which most likely provided seeds. Although not statistically significant, my study also suggests that trampled marshes may trap more wrack than untrampled areas. If true, this interaction between human and natural disturbances may increase plant mortality above the level expected by trampling alone, and perhaps promote further changes in invertebrate populations.

Many authors have reported that disturbance level only partially determines organisms' responses to disturbances. Other factors include species' life histories, historical patterns of disturbance, seed availability, interactions with other disturbances and habitat variation (Sousa 1979, Connell and Keough 1985, Hobbs and Huenneke 1992, Brosnan and Crumrine 1994, Brewer and Bertness 1996, Keough and Quinn 1998). This study suggests that all are important to recovery in California salt marshes as well, but that their roles may differ between natural and human disturbances. However, the most convincing evidence for differences would come from manipulative experiments, perhaps directly comparing flood and wrack disturbance to trampling or deposited dredged sediments in the field.

This research shows that human trampling can have several negative impacts on coastal salt marshes, including localized loss of marsh habitat and the expansion of invasive plants. Disturbance intensity and frequency appear to be strong determinants of the amount of damage caused and the time required for recovery. Cattle grazing also causes severe damage to *S. virginica* assemblages. However, evidence from this study suggests that marshes grazed by low densities of cattle may partially recover 15 months after livestock are excluded. California marshes are sensitive to human disturbances, but effective management practices may limit the extent of damage.

Table 1. Patterns of plant richness (by family) in treated plots at Whistle Stop by trampling level. Entries are the percentages of plots with a given number of plant families. The mean number of families (± SE) per treatment type are listed in the last column, n = 10. Trampling levels are high: 30 passes/week, intermediate: 15 passes/month, low: 1 pass every 3 months, and untrampled. Trampling ended September 1996, and recovery was followed until September 1997.

Date	Trampling level	Number of families						Mean no. of families ± SE
		0	1	2	3	4	5	
September 1996	High	10	80	10	0	0	0	1.0 ± 0.1
	Intermediate	0	80	20	0	0	0	1.2 ± 0.1
	Low	0	50	40	10	0	0	1.6 ± 0.2
	Untrampled	0	80	20	0	0	0	1.2 ± 0.1
December 1996	High	0	0	30	30	30	10	3.2 ± 0.3
	Intermediate	0	0	30	50	20	0	2.9 ± 0.2
	Low	0	40	50	0	0	10	1.9 ± 0.4
	Untrampled	0	80	20	0	0	0	1.2 ± 0.1
May 1997	High	0	10	60	20	10	0	2.3 ± 0.3
	Intermediate	0	20	50	30	0	0	2.1 ± 0.2
	Low	0	50	40	30	0	0	1.6 ± 0.2
	Untrampled	0	80	20	0	0	0	1.2 ± 0.1
September 1997	High	0	30	50	20	0	0	1.9 ± 0.2
	Intermediate	0	30	50	20	0	0	1.9 ± 0.2
	Low	0	40	50	10	0	0	1.7 ± 0.2
	Untrampled	0	90	0	10	0	0	1.2 ± 0.2

Table 2. Patterns of species richness in treated plots at the Northwest Marsh by trampling level. Entries are the percentages of plots with a given number of vascular plant species. The mean number of species (± SE) per treatment type are listed in the last column, n = 3. Trampling levels are high: 30 passes/week, intermediate: 15 passes/month, low: 1 pass/month, and untrampled. Trampling ended May 1997, and recovery was followed until April 1998.

Date	Trampling level	Number of species 1	2	3	4	5	6	Mean no. of spp. ± SE
May 1997	High	66.7	33.3	0	0	0	0	1.3 ± 0.3
	Intermediate	33.3	66.7	0	0	0	0	1.7 ± 0.3
	Low	100	0	0	0	0	0	1.0 ± 0.0
	Untrampled	33.3	66.7	0	0	0	0	1.7 ± 0.3
November 1997	High	33.3	66.7	0	0	0	0	1.7 ± 0.3
	Intermediate	33.3	66.7	0	0	0	0	1.7 ± 0.3
	Low	100	0	0	0	0	0	1.0 ± 0.0
	Untrampled	33.3	66.7	0	0	0	0	1.7 ± 0.3
April 1998	High	33.3	0	0	0	33.3	33.3	4.0 ± 1.5
	Intermediate	66.7	0	0	33.3	0	0	2.0 ± 1.0
	Low	66.7	0	33.3	0	0	0	1.7 ± 0.7
	Untrampled	66.7	33.3	0	0	0	0	1.3 ± 0.3

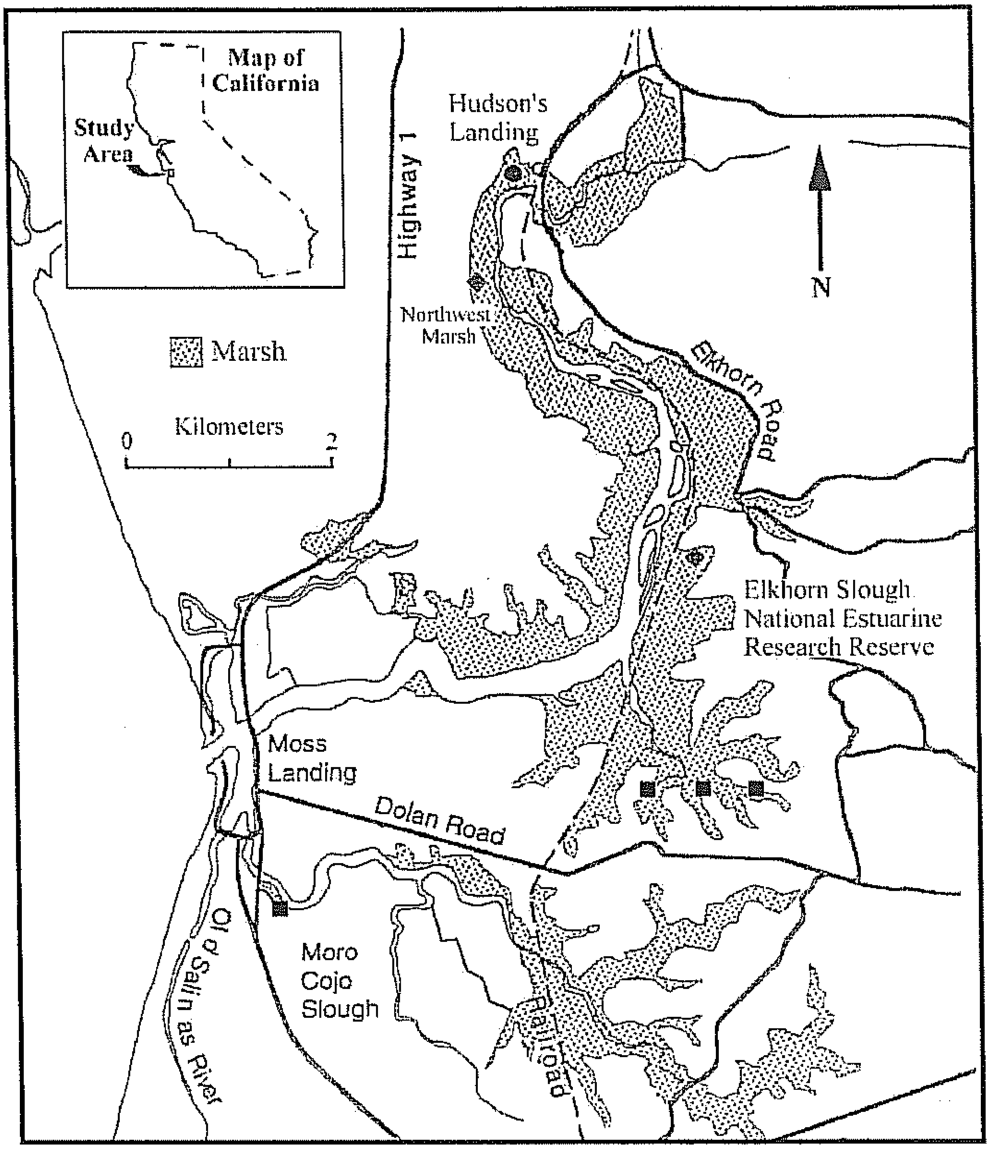

Figure 1. Location of study sites in Elkhorn Slough, California. Diamonds designate human trampling experiments, squares show grazed study sites, and the circle marks the recovering pasture at Hudson's Landing.

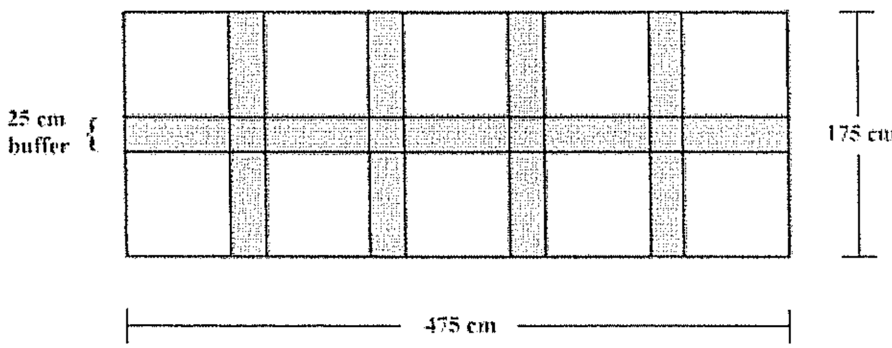

Figure 2. Diagram of block used in human trampling experiment at Whistle Stop. Each inside quadrats are 75 X 75 cm, and each block had a combination of 9 treatments and 1 control.

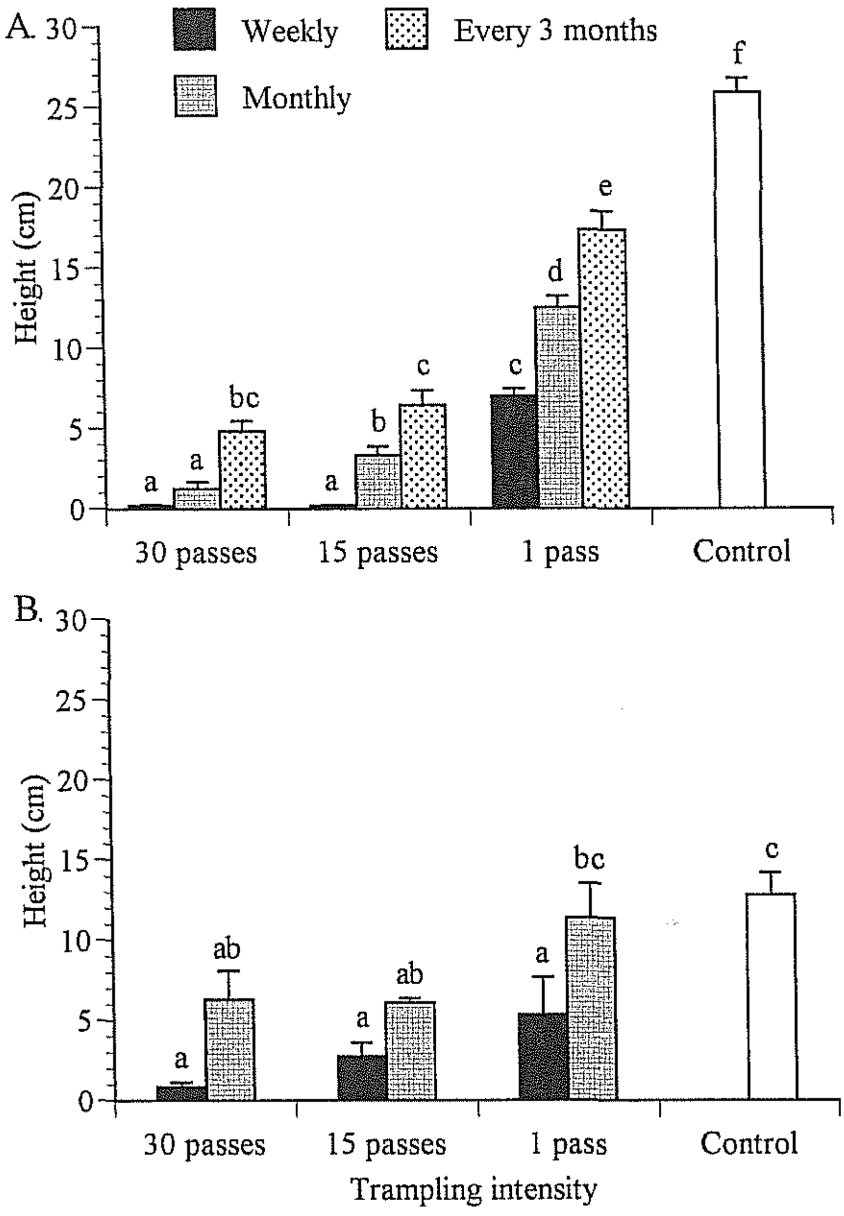

Figure 3. Damage to *S. virginica* height at (A) Whistle Stop and (B) Northwest site by trampling level. Only weekly and monthly frequencies were used at Northwest site. Vertical lines represent 1 SE, n = 10 at Whistle Stop, n = 3 at Nature Conservancy. Treatments within a site with different letters are statistically different at the $P < 0.05$ level.

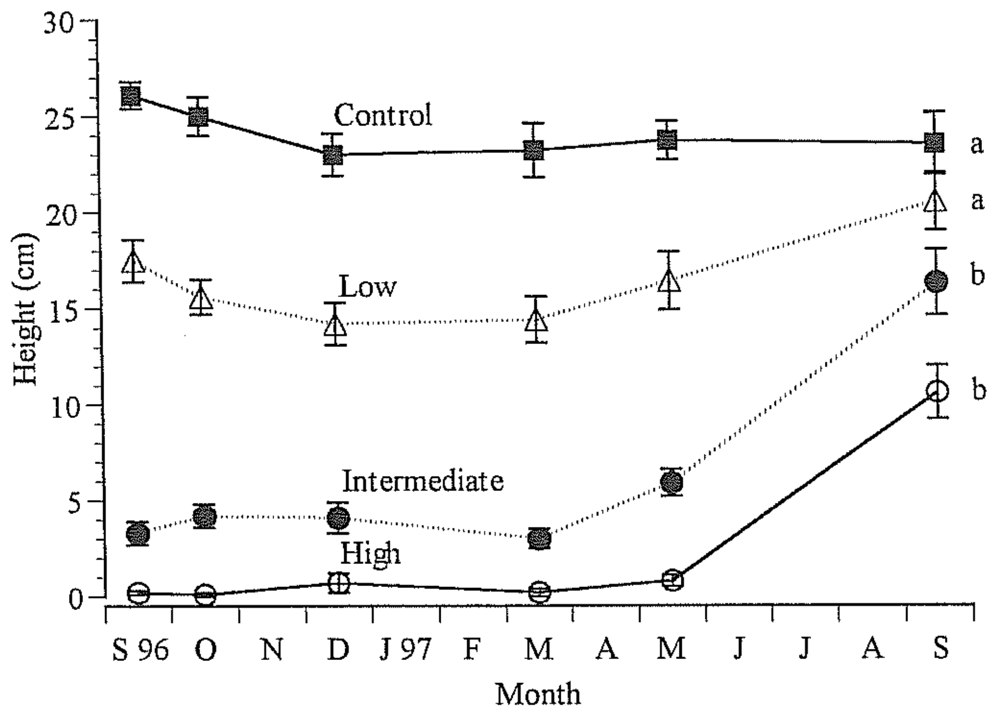

Figure 4. *Salicornia* height at Whistle Stop immediately after trampling stopped (Sept. 1996) and following one year of recovery (Sept. 1997). Trampling levels are high (30 passes a week), intermediate (15 passes a month), low (1 pass every three months), and untrampled controls. SE bars smaller than the plotted symbol are not visible on the graph, n=10. Treatments in Sept. 1997 with different letters are statistically different at the $P < 0.05$ level.

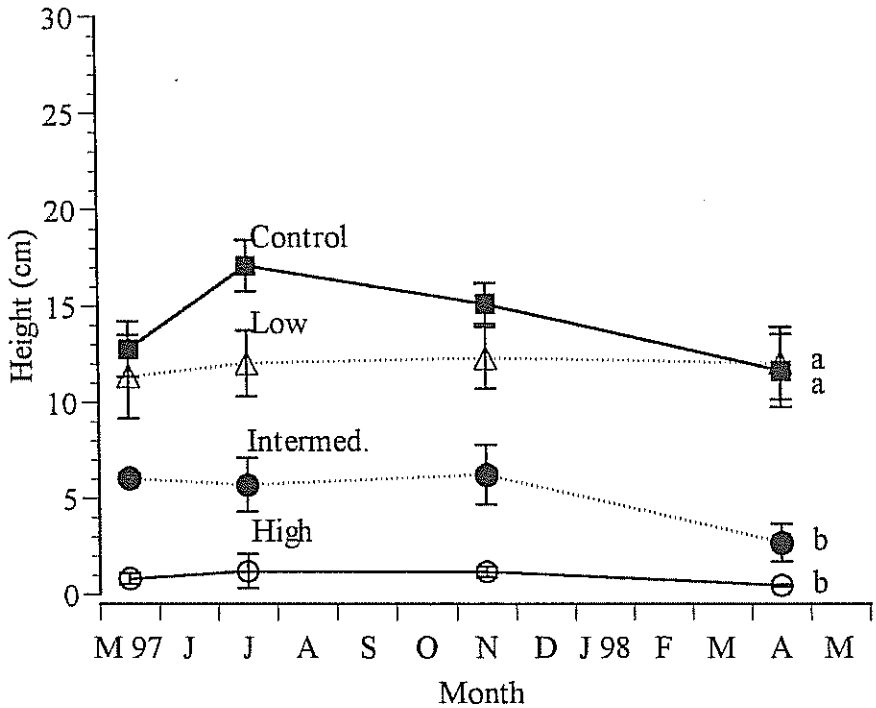

Figure 5. *Salicornia* height at Northwest site immediately after trampling stopped (May 97) and following approximately one year of recovery (April 98). Trampling levels are high (30 passes a week for four weeks), intermediate (15 passes done one time), low (1 pass done one time), and untrampled controls. SE bars smaller than the plotted symbol are not visible on the graph, n=3. Treatments in April 1998 with different letters are statistically different at the $P < 0.05$ level.

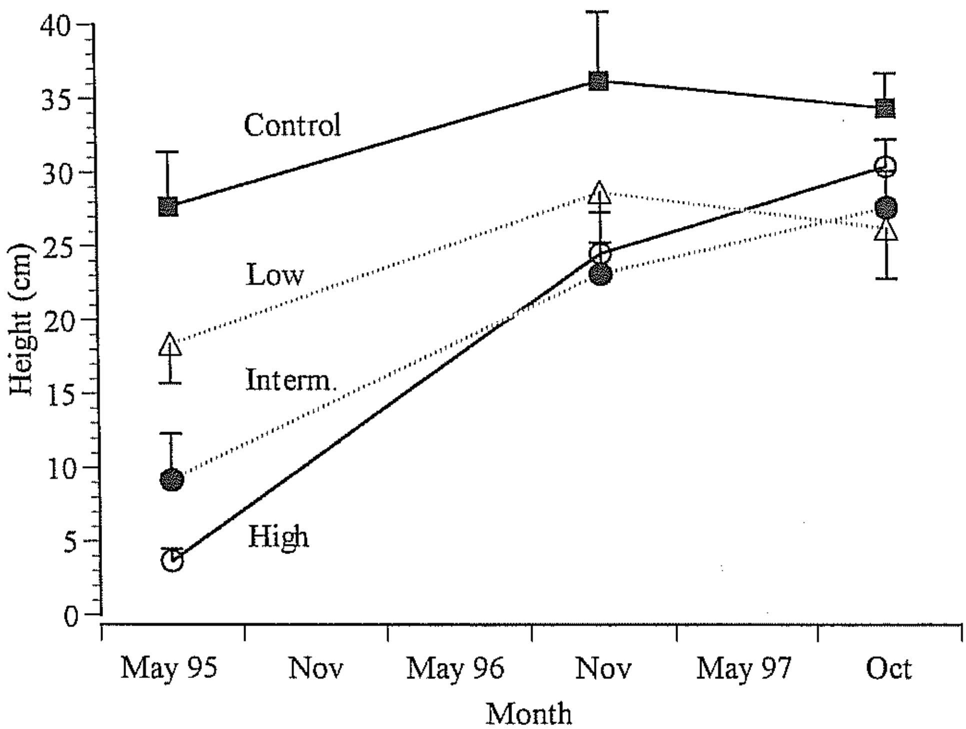

Figure 6. *Salicornia* height in pilot project immediately after trampling ended (May 1995) and following approx. 2.5 years of recovery. Trampling levels are high (50 passes a week), intermediate (15 passes done one time), low (1 pass done one time), and untrampled controls. Vertical lines represent 1 SE of the mean, n=3.

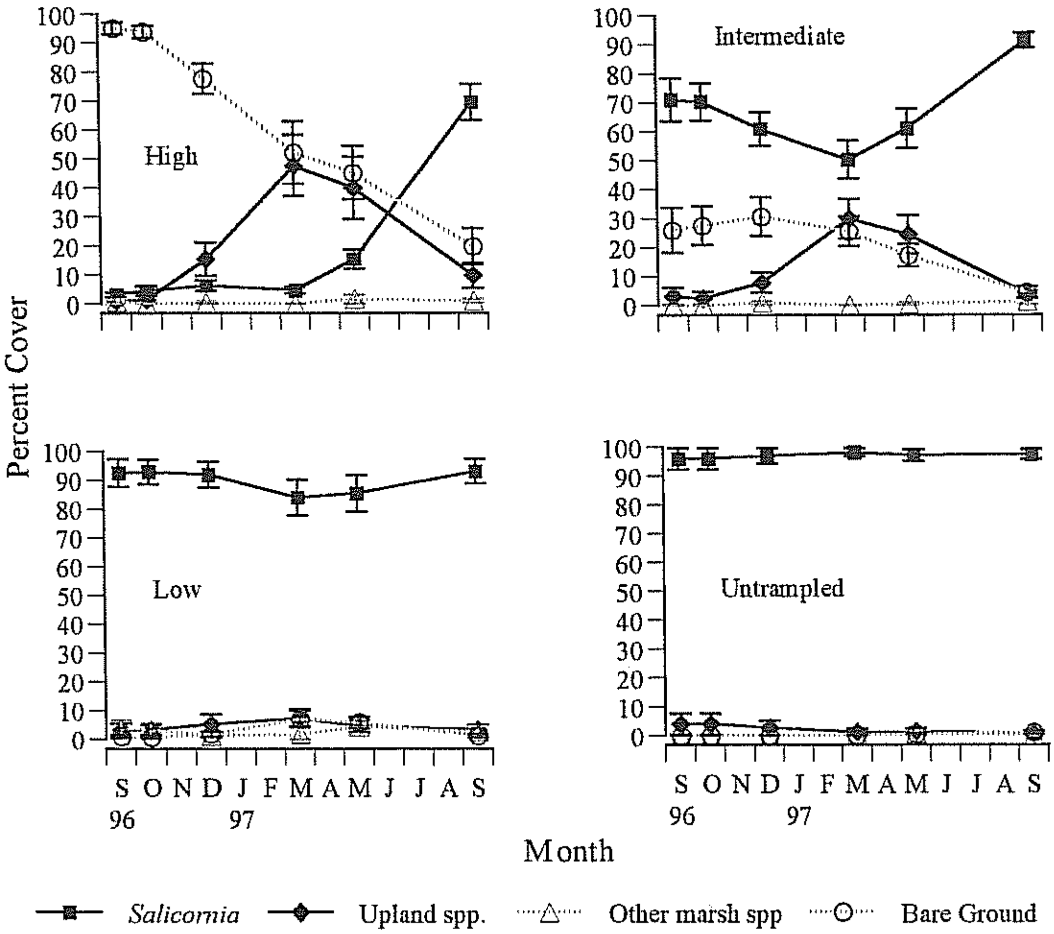

Figure 7. Changes in vegetation cover in three treatments and the untrampled controls at Whistle Stop, immediately after trampling ended (Sept. 96), and over one year of recovery (until Sept 97). High: 30 passes a week. Intermediate: 15 passes a month. Low: 1 pass once every three months. Vertical lines represent SE, n=10.

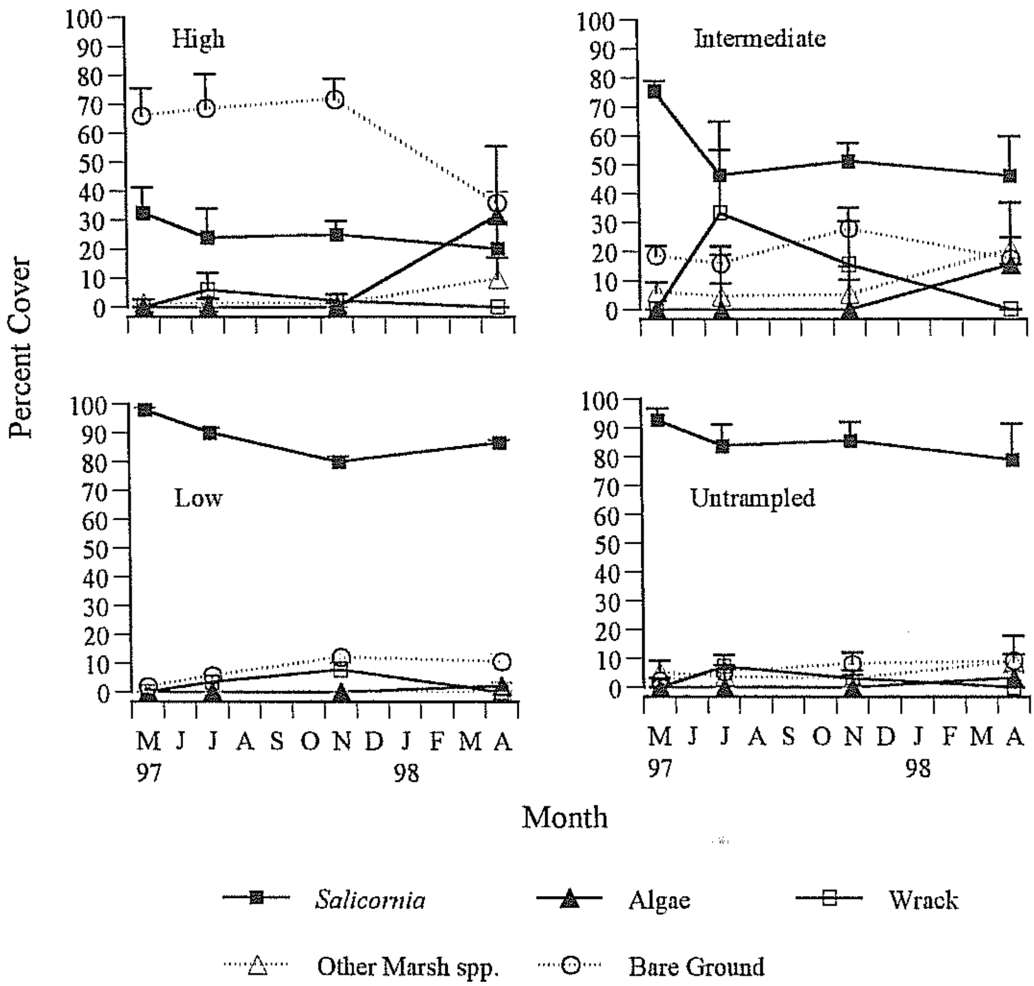

Figure 8. Changes in vegetation cover in three treatments and the untrampled controls at Northwest site, immediately after trampling stopped (May 97), and over almost one year of recovery (until April 98). High: 30 passes a week. Intermediate: 30 passes done one time. Low: 1 pass done one time. SE bars smaller than the plotted symbol are not visible on graph, n=3.

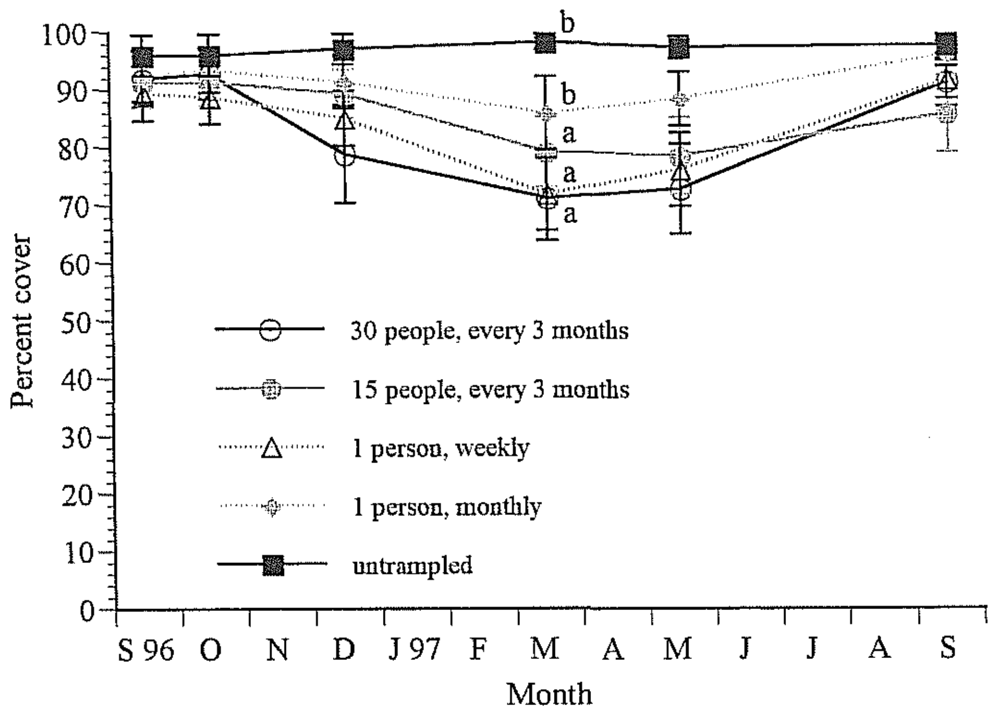

Figure 9. Changes in *Salicornia virginica* cover in lightly trampled plots and controls over time. Vertical lines represent SE, n=10. ANOVAs and Tukey's tests were done for Sept. 96, March 97, and Sept. 97. Treatments within these months with different letters are statistically different at the $P < 0.05$ level.

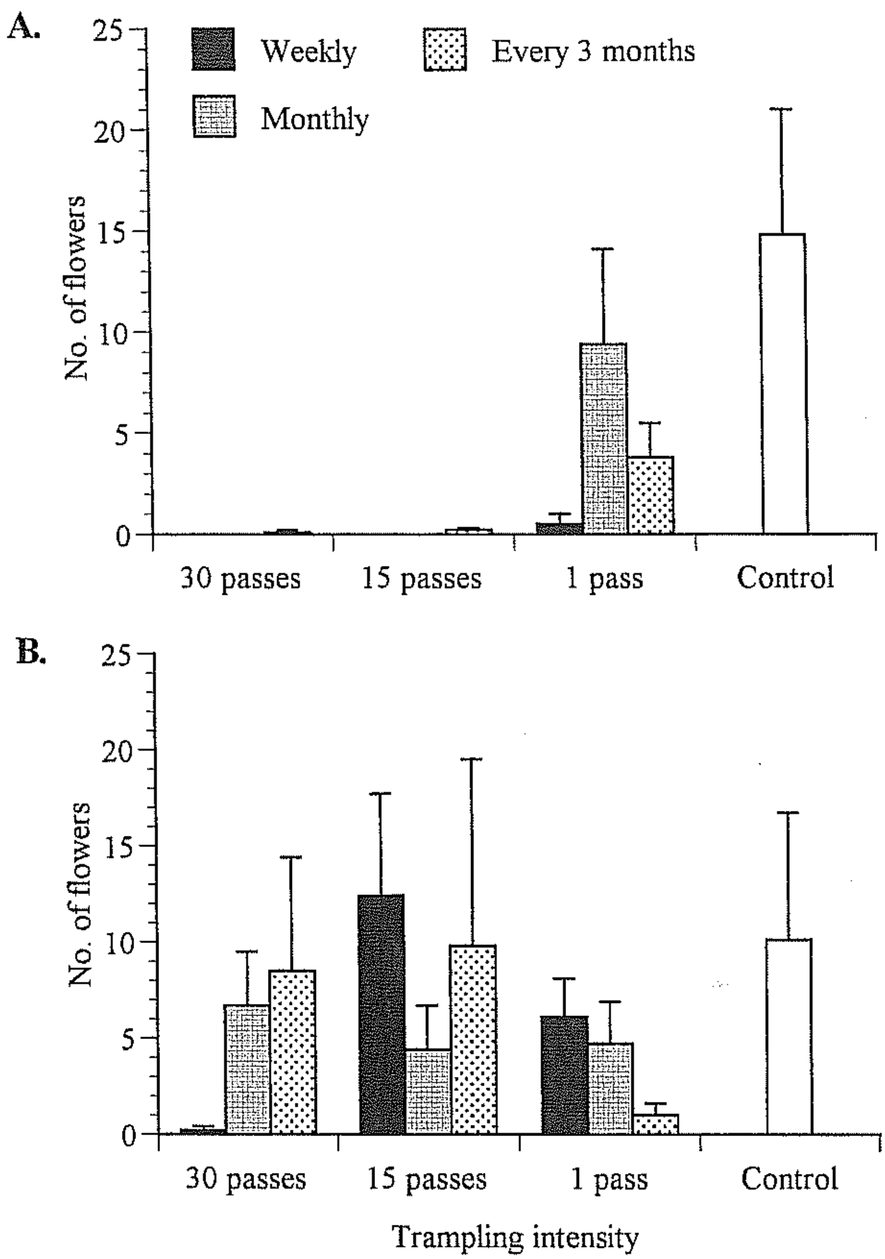

Figure 10. Mean number of *S. virginica* flowers subsampled per plot at Whistle Stop (A) immediately after end of trampling, and (B) after 1 year recovery. Vertical lines represent 1 SE, n=10.

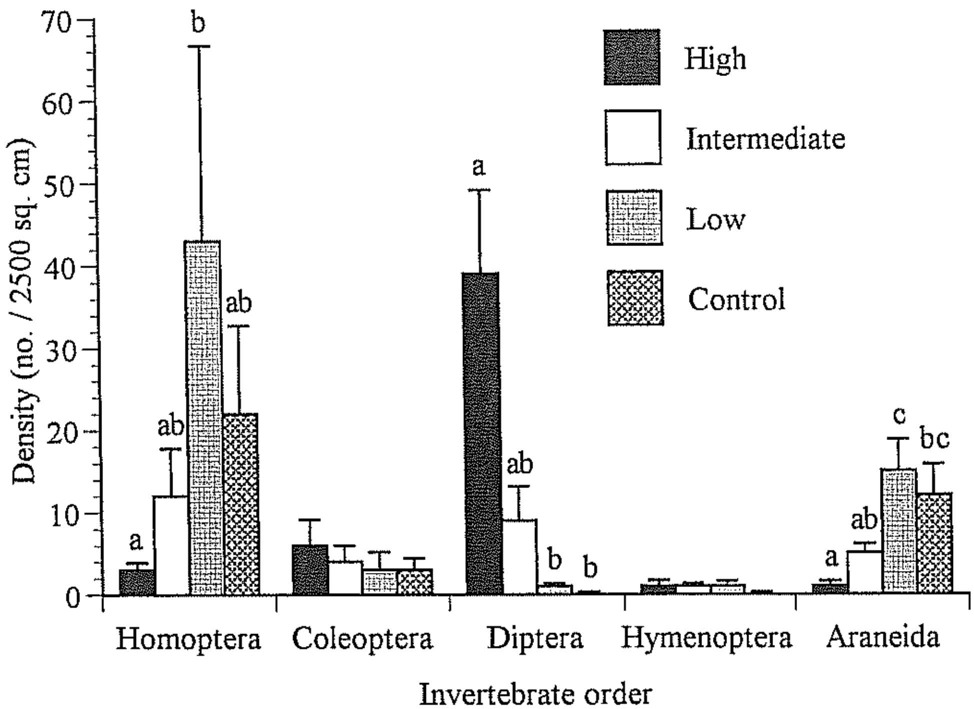

Figure 11. Density of selected invertebrates at Whistle Stop immediately after trampling ended (October 1997), by treatment level. High: 30 passes a week, intermediate: 30 passes a month, low: 1 pass a month. Vertical lines represent 1 SE, n=3. Treatments within an order with different letters are statistically different at the $P < 0.05$ level.

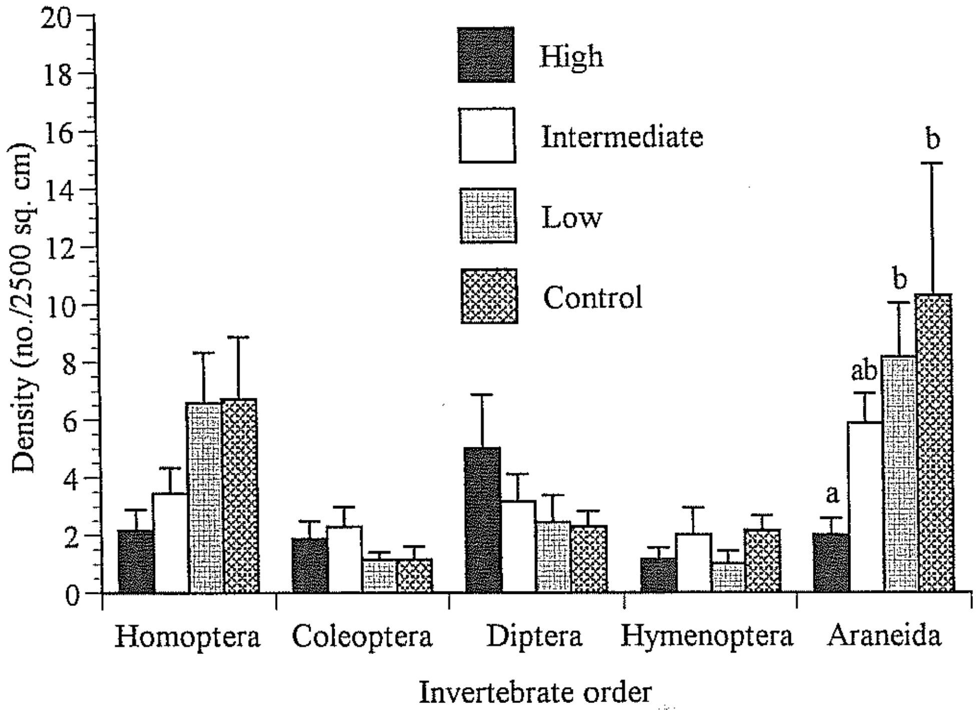

Figure 12. Density of invertebrates at Whistle Stop 11 months after trampling ended (August 1997) by treatment level. High: 30 passes a week, intermediate: 15 passes a month, low: 1 pass every 3 months. Vertical lines represent 1 SE, n=7. Treatments with different letters are statistically different at the $P < 0.05$ level.

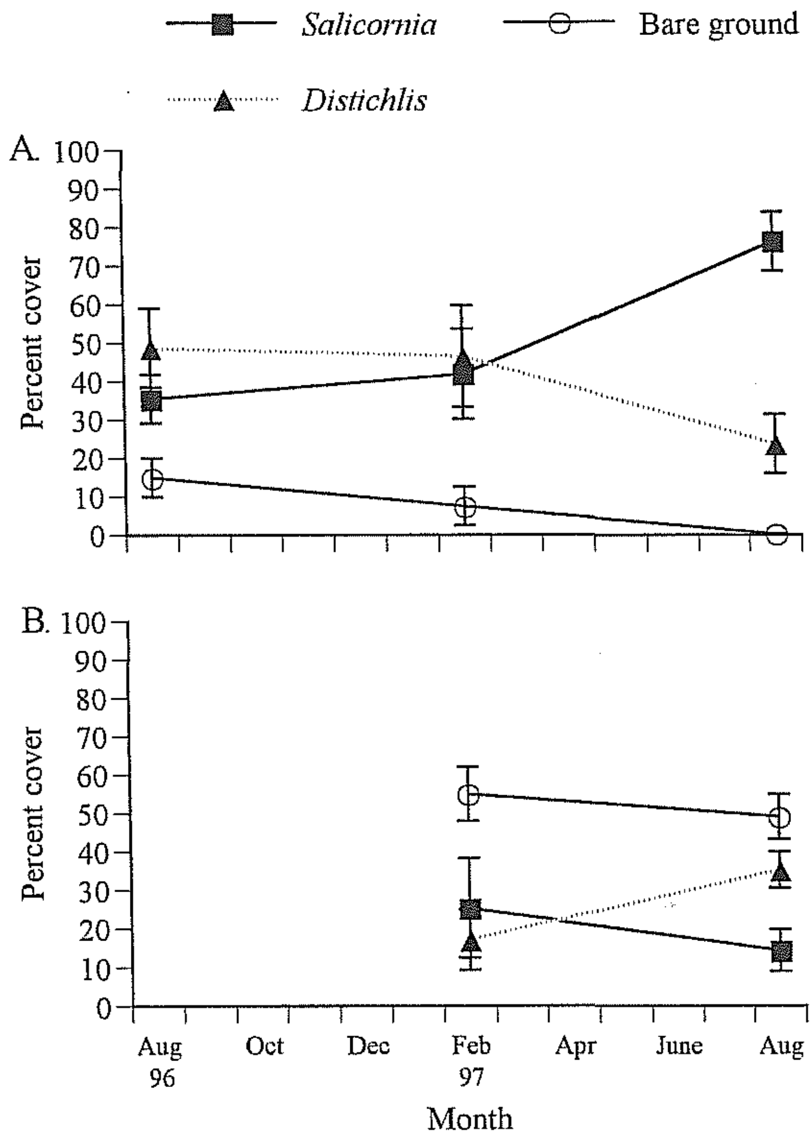

Figure 13. Changes in vegetation cover in pasture at Hudson's Landing. (A) In section where cattle were excluded in May 1996 and (B) in section still grazed by cattle. Data not available for grazed area in August 1996. Vertical lines represent SE, n=5.

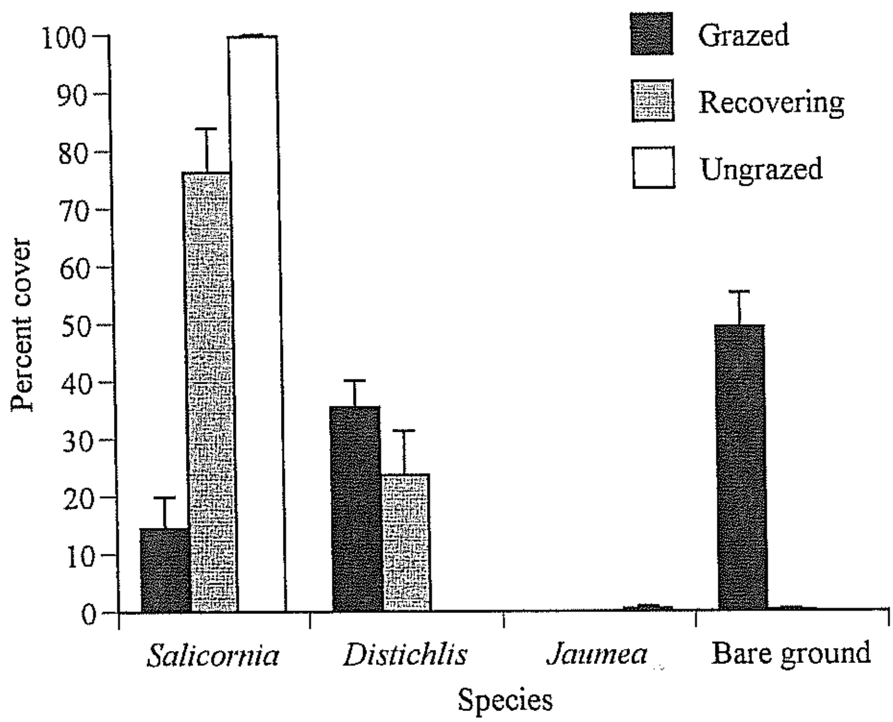

Figure 14. Comparison of vegetative cover at Hudson's Landing by section of marsh in August 1997. Vertical lines represent 1 SE, n=5.

APPENDICES

Appendix A

Effects of trampling on *Salicornia virginica* height at Whistle Stop.

a. Analysis of variance. P values <0.05 are considered significant.

Source of variation	df	MS	F	P
Frequency (F)	2	18.32	130.87	<0.0005
Intensity (I)	2	37.30	146.27	<0.0005
F*I	4	0.34	2.69	<0.05
Control vs. all others	1	75.70	493.88	<0.0005
Blocks (B)	9	0.19	1.25	>0.25
B*F	18	0.14		
B*I	18	0.26		
B*F*I	36	0.13		
Error	81	0.15		

b. Means and Tukey's tests for effects of trampling on *S. virginica* height (cm) at Whistle Stop. Inequalities indicate comparisons that are significant at P<0.05. The bottom line ranks means in descending order, and horizontal lines underlie means not different at P=0.05.

<table>
<tr><th>Intensity</th><th>30 passes</th><th></th><th>15 passes</th><th></th><th>1 pass</th></tr>
<tr><td>Frequency:</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>weekly</td><td>0.19</td><td>=</td><td>0.18</td><td><</td><td>6.97</td></tr>
<tr><td></td><td>||</td><td></td><td>^</td><td></td><td>^</td></tr>
<tr><td>monthly</td><td>1.21</td><td><</td><td>3.30</td><td><</td><td>12.74</td></tr>
<tr><td></td><td>^</td><td></td><td>^</td><td></td><td>^</td></tr>
<tr><td>every 3 months</td><td>4.83</td><td>=</td><td>6.43</td><td><</td><td>17.49</td></tr>
<tr><td></td><td></td><td></td><td></td><td></td><td>^</td></tr>
<tr><td></td><td></td><td></td><td></td><td>Control:</td><td>25.91</td></tr>
</table>

Control > 17.49 > 12.74 > 6.97 = 6.43 = 4.83 = 3.30 > 1.21 = 0.19 = 0.18

Appendix B

Effects of trampling on *Salicornia virginica* height at Northwest Marsh.

a. Analysis of variance. P values <0.05 are considered significant.

Source of variation	df	MS	F	P
Frequency (F)	1	110.01	59.76	<0.025
Intensity (I)	2	39.05	7.97	<0.05
Freq*Inten	2	3.01	0.67	>0.25
Control vs. all others	1	139.13	32.94	<0.0005
Blocks (B)	2	24.28	5.75	<0.025
B*F	2	1.84		
B*I	4	4.90		
B*F*I	4	4.50		
Error	12	4.22		

b. Means and Tukey's tests for effects of trampling on *S. virginica* height (cm). Inequalities indicate comparisons that are significant at P<0.05. The bottom line ranks means in descending order, and horizontal lines underlie means not different at P=0.05.

<table>
<tr><th>Intensity</th><th>30 passes</th><th></th><th>15 passes</th><th></th><th>1 pass</th></tr>
<tr><td>Frequency:</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>weekly</td><td>0.83</td><td>=</td><td>2.71</td><td>=</td><td>5.30</td></tr>
<tr><td></td><td>||</td><td></td><td>||</td><td></td><td>^</td></tr>
<tr><td>monthly</td><td>6.26</td><td>=</td><td>6.06</td><td>=</td><td>11.35</td></tr>
<tr><td></td><td></td><td></td><td></td><td></td><td>||</td></tr>
<tr><td></td><td></td><td></td><td></td><td>Control:</td><td>12.77</td></tr>
</table>

Control = 11.35 = 6.26 = 6.06 = 5.30 = 2.71 = 0.83

Appendix C

Effects of trampling on *Salicornia virginica* height after one year of recovery at Whistle Stop.

a. Analysis of variance. P values <0.05 are considered significant.

Source of variation	df	MS	F	P
Frequency (F)	2	170.88	9.27	<0.0025
Intensity (I)	2	267.93	23.36	<0.0005
Freq*Inten	4	14.69	0.78	>0.25
Control vs. all others	1	472.99	26.22	<0.0005
Blocks (B)	9	68.48	3.80	<0.005
B*F	18	18.43		
B*I	18	11.47		
B*F*I	36	18.89		
Error	81	18.04		

b. Means and Tukey's tests for effects of trampling on *S. virginica* height (cm) after one year of recovery. Inequalities indicate comparisons that are significant at P<0.05. The bottom line ranks means in descending order, and horizontal lines underlie means not different at P=0.05.

Intensity	30 passes		15 passes		1 pass
Frequency:					
weekly	10.62	=	13.47	=	17.70
	‖		‖		‖
monthly	12.31	=	16.30	=	19.89
	‖		‖		‖
every 3 months	17.21	=	18.43	=	20.46
					‖
					Control: 23.51

Cntrl = 20.46 = 19.89 = 18.43 = 17.70 = 17.21 = 16.30 = 13.47 = 12.31 = 10.62

Appendix D

Analysis of variance on effects of trampling on *Salicornia virginica* height in pilot project after (A) 1.5 years recovery and (B) 2.5 years recovery.

A. Source of variation	df	MS	F	P
Frequency (F)	1	15.23	0.40	>0.25
Intensity (I)	3	29.83	1.61	>0.25
Freq*Inten	3	47.98	1.24	>0.25
Control vs. all others	1	189.51	5.73	<0.05
Blocks (B)	2	49.73	1.50	>0.25
B*F	2	38.35		
B*I	6	18.51		
B*F*I	6	38.55		
Error	16	33.07		

B. Source of variation	df	MS	F	P
Frequency (F)	1	18.11	0.44	>0.25
Intensity (I)	3	61.37	1.63	>0.25
Freq*Inten	3	15.01	1.43	>0.25
Control vs. all others	1	51.62	1.96	>0.10
Blocks (B)	2	189.81	7.21	<0.01
B*F	2	40.89		
B*I	6	37.76		
B*F*I	6	10.53		
Error	16	26.34		

Appendix E

Effects of trampling on *Salicornia virginica* percent cover immediately after trampling at Whistle Stop.

a. Analysis of variance. P values <0.05 are considered significant.

Source of variation	df	MS	F	P
Frequency (F)	2	16698.04	58.24	<0.0005
Intensity (I)	2	10582.66	77.32	<0.0005
F*I	4	3805.74	39.45	<0.0005
Control vs. all others	1	7019.87	49.35	<0.0005
Blocks (B)	9	775.16	5.45	<0.0005
B*F	18	286.71		
B*I	18	136.87		
B*F*I	36	96.48		
Error	81	142.26		

b. Means and Tukey's tests for effects of trampling on *S. virginica* percent cover at Whistle Stop. Inequalities indicate comparisons that are significant at P<0.05. The bottom line ranks means in descending order, and horizontal lines underlie means not different at P=0.05.

Intensity	30 passes		15 passes		1 pass
Frequency:					
weekly	9.10	=	10.89	<	76.30
	∧		∧		‖
monthly	42.31	<	59.95	<	79.83
	∧		∧		‖
every 3 months	77.84	=	79.36	=	79.49
					‖
					Control: 85.16

Cntrl = 79.83 = 79.49 = 79.36 = 77.84 = 76.30 = 59.95 > 42.31 > 10.89 > 9.10

Appendix F

Effects of trampling on *Salicornia virginica* percent cover after 6 months of recovery at Whistle Stop.

a. Analysis of variance. P values <0.05 are considered significant.

Source of variation	df	MS	F	P
Frequency (F)	2	10225.11	49.96	<0.0005
Intensity (I)	2	9449.35	103.54	<0.0005
F*I	4	1400.84	12.35	<0.0005
Control vs. all others	1	12555.80	104.86	<0.0005
Blocks (B)	9	556.83	4.65	<0.0005
B*F	18	204.67		
B*I	18	91.27		
B*F*I	36	113.45		
Error	81	119.74		

b. Means and Tukey's tests for 6 month recovery of *S. virginica* percent cover at Whistle Stop. Inequalities indicate comparisons that are significant at P<0.05. The bottom line ranks means in descending order, and horizontal lines underlie means not different at P=0.05.

Intensity	30 passes		15 passes		1 pass
Frequency:					
weekly	11.37	=	12.95	<	60.44
	^		^		||
monthly	33.75	=	45.02	<	73.11
	^		^		||
every 3 months	58.58	=	65.44	=	70.63
					||
					Control: 85.27

Cntrl = 73.11 = 70.63 = 65.44 = 60.44 = 58.58 = 45.02 = 33.75 > 12.95 = 11.37

Appendix G

Effects of trampling on *Salicornia virginica* percent cover after 1 year of recovery at Whistle Stop.

a. Analysis of variance. P values <0.05 are considered significant.

Source of variation	df	MS	F	P
Frequency (F)	2	1185.29	6.90	<0.01
Intensity (I)	2	1397.54	11.42	<0.001
F*I	4	226.17	1.83	<0.25
Control vs. all others	1	1582.40	12.84	<0.001
Blocks (B)	9	430.11	3.49	<0.001
B*F	18	171.78		
B*I	18	122.38		
B*F*I	36	123.29		
Error	81			

b. Transformed means and Tukey's tests for 1 year recovery of *S. virginica* percent cover at Whistle Stop. Inequalities indicate comparisons that are significant at P<0.05. The bottom line ranks means in descending order, and horizontal lines underlie means not different at P=0.05.

Intensity	30 passes		15 passes		1 pass
Frequency:					
weekly	57.42	=	60.02	=	76.06
	||		||		||
monthly	65.53	=	74.70	=	82.54
	||		||		||
every 3 months	76.21	=	73.01	=	79.52
					||
					Control: 84.93

Cntrl = 82.54 = 79.52 = 76.21 = 76.06 = 74.70 = 73.01 = 65.53 = 60.02 = 57.42

Appendix H

Analyses of variance for effects of human trampling on invertebrate abundance at Whistle Stop immediately after trampling ended.

Order	effect	df	MS	F	P
Homoptera	treatment	3	0.46	4.73	0.05
	block	2	0.39	3.99	0.08
	error	6	0.10		
Diptera	treatment	3	1.06	13.30	<0.01
	block	2	0.02	0.26	0.78
	error	6	0.08		
Araneida	treatment	3	137.64	10.15	<0.01
	block	2	73.00	5.39	0.05
	error	6	13.56		
Hemiptera	treatment	3	7.42	0.83	0.52
	block	2	9.25	1.04	0.41
	error	6	8.92		
Coleoptera	treatment	3	6.75	0.49	0.71
	block	2	27.25	1.96	0.22
	error	6	13.92		
Hymenoptera	treatment	3	3.22	0.76	0.56
	block	2	1.00	0.24	0.80
	error	6	4.22		

Appendix I

Analyses of variance for effects of human trampling on invertebrate abundance after 11 months of recovery at Whistle Stop.

Order	effect	df	MS	F	P
Homoptera	treatment	3	36.67	2.52	0.09
	block	6	19.62	1.35	0.29
	error	18	14.56		
Diptera	treatment	3	0.30	0.57	0.64
	block	6	0.59	1.11	0.39
	error	18	0.53		
Araneida	treatment	3	0.34	4.22	0.02
	block	6	0.16	1.92	0.13
	error	18	0.08		
Hemiptera	treatment	3	12.43	1.60	0.23
	block	6	36.82	4.73	<0.01
	error	18	7.79		
Coleoptera	treatment	3	2.23	1.33	0.30
	block	6	2.99	1.79	0.16
	error	18	1.67		
Hymenoptera	treatment	3	2.38	1.29	0.31
	block	6	4.73	2.55	0.06
	error	18	1.85		

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