

A COMPARISON OF TERRESTRIAL INVERTEBRATE COMMUNITIES IN
SPARTINA-INVADED AND RESTORED HUMBOLDT BAY SALT MARSHES

HUMBOLDT STATE UNIVERSITY

by

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ABSTRACT

A COMPARISON OF TERRESTRIAL INVERTEBRATE COMMUNITIES IN *SPARTINA*-INVADED AND RESTORED HUMBOLDT BAY SALT MARSHES

Matthew L. Mitchell

Despite widespread concern regarding the impacts of invasive non-native vegetation on native salt marsh ecosystems, research investigating the effects of the *Spartina densiflora* invasion in Humboldt Bay on terrestrial invertebrate assemblages is non-existent. This study compared invertebrate assemblages in *Spartina densiflora* dominated salt marsh with those found in restored salt marsh along the Mad River Slough (Humboldt County, California). Results showed significant differences in invertebrate community structure in *S. densiflora* invaded marsh when compared to samples taken in restored marsh using a multi-response permutation (MRPP) method. Richness and evenness of epibenthic and low canopy invertebrates was highest in the restored marsh. Non-metric multi-dimensional scaling (NMDS) and Dufrene-Legendre indicator analysis revealed that both the invasive snail *Myosotella myosotis* and the native snail *Littorina subrotundata* displayed a strong association with invaded sites, while the native talitrid amphipod genus *Orchestia* was associated with restored sites. In restored *Distichlis spicata* dominated salt marsh, individuals in the order Hemiptera represented nearly 100% of all invertebrates sampled, the most abundant of which was in the family Delphacidae. The long-jawed orb weaver spider family Tetragnatha was found in relatively high abundance at invaded sites, but was nearly absent from *Salicornia pacifica*

and *D. spicata* vegetation at restored sites. The taller height of *S. densiflora* (compared to native salt marsh vegetation) provides habitat niches and refugium at high tide not found in native salt marsh, and disrupts existing co-evolved relationships between invertebrates and native vegetation. Additional biotic and abiotic mechanisms can be invoked on a taxa-by-taxa basis to account for the shift in community structure between invaded and restored sites.

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INTRODUCTION

Tidal salt marshes are recognized as some of the most productive ecosystems in the world, but have been heavily degraded by human activities. In addition to reduction and fragmentation, accumulation of toxic substances such as polychlorinated biphenols (PCBs) in soil sediments and the rise of sea level are among the numerous threats to coastal salt marshes (Boorman 1999). Tidal salt marshes export organic energy to coastal ecosystems and provide food and protection for a wide variety of animals including birds, fish, crustaceans, and mammals (Mitsch & Gosselink 2000, Cain et al. 2008). Ecological integrity of these systems is important to maintain the biota found in and around them, and alterations to this habitat have repercussions throughout the system (e.g. Bortolus 2010).

Environmental stresses within salt marshes are considerable and a limited numbers of species have adapted to the large fluctuations in abiotic factors such as salinity, exposure, and temperature (Teal 1962). The extent to which vascular plants have specialized and adapted to these harsh conditions has left salt marsh habitats particularly vulnerable to invasion (Daehler & Strong 1996). Exotic species recognized as lacking regulatory mechanisms inherent in their respective systems of origin (Strong et al. 1984) are some of the most aggressive invaders.

Tidal marsh habitats in Humboldt Bay, California (Humboldt County) were drastically altered by the local railroad and agricultural activities, both of which have brought about major structural changes to salt marsh ecosystems in the area. Dikes and levees were constructed for railroad berms and to prevent inundation of agricultural areas and have severely disrupted tidal exchanges (Pickart 2001). Habitat for bird species utilizing tidal salt marsh is particularly crucial in areas where adjacent meadowlands were converted for agriculture (Boorman 1999). The areas of salt marsh habitat surrounding Humboldt Bay have been reduced by 90% since the early 1900s, from 3,642 ha (9,000 ac) to 364 ha (900 ac) (Pickart 2001).

Many of the diked areas around Humboldt Bay that still function as wetlands have been converted from estuarine to tidal palustrine (i.e. seasonally flooded freshwater and brackish water) marshes, which has resulted in a change in vegetative cover (Pickart 2001). Most of these palustrine areas are currently used as pasture for grazing. In 1999, the U.S. Fish and Wildlife Service documented the distribution of remaining native vegetation assemblages around Humboldt Bay. The results of this survey found that *Spartina densiflora*, commonly known as dense flowered cordgrass, had invaded approximately 90% of the remaining salt marsh (Pickart 2001). More recently, active removal of *S. densiflora* has taken place using mechanized methods within the Humboldt Bay National Wildlife Refuge (Pickart 2001, 2005).

Humboldt Bay salt marsh in its *S. densiflora*-invaded state is described by Eicher (1987) as consisting of three primary vegetation zones. As a result of abiotic factors such as tidal inundation and exposure, each zone is characterized by distinctly dominant vegetation. Expressed in terms of mean lower low water (MLLW) as an elevational benchmark, these zones range from 1.74 m above MMLW to 2.56 m above MMLW in the northern reaches of Humboldt Bay. In the upper elevations of the salt marsh complex, mixed marsh zones typically appear above 2.22 m MLLW. In the Eicher study, this upper salt marsh zone contained the most floristic diversity, but was most strongly dominated by *Distichlis spicata* (Figure 1, on right). The mid marsh zone, occurring between 2.10 m and 2.22 m MLLW, was characterized by Eicher (1987) as primarily consisting of *S. densiflora* (Figure 1, middle). *Salicornia pacifica* (Figure 1, on left) dominated the low marsh and typically occurred below 2.1 m MLLW, although *S. pacifica* also exists in locally abundant patches throughout the salt marsh elevational profile (Eicher 1987).

Background on *Spartina*

Spartina densiflora appears to have originated along the east coast of South America (Bortolus 2006) and at least half of the 14 members of the genus *Spartina* are known to be invasive (Daehler & Strong 1996). Extensive studies have examined members of the genus *Spartina* and their various relationships with plant communities, soil organisms and soil properties (e.g. Levin & Talley 1998, Ludlam et al. 2002, Robertson & Weiss



Figure 1. Vegetation types dominant in three salt marsh zones: *Salicornia pacifica* (low marsh) (on left), *Spartina densiflora* (mid marsh) (middle), and *Distichlis spicata* (high marsh) (on right). Photos by Britney Newby.

2005). In California, at least four *Spartina* species (*S. patens*, *S. alterniflora*, *S. anglica*, and *S. densiflora*) are recognized as actively encroaching on tidal salt marshes and estuaries, displacing native vegetation and reducing open mudflat areas available to shorebirds (Daehler & Strong 1996).

A prolific seed and rhizome producer typically occurring in densely arranged tussocks, *S. densiflora* can currently be found in vast monocultures around Humboldt Bay. The success of *S. densiflora*'s invasion in Humboldt Bay may also be partly a result of additional factors that provide a competitive advantage over native species, such as a wide salinity tolerance and the ability to colonize both low and mid marsh. Primarily expanding through year-round lateral rhizomatous tiller growth, dormant stands of *S. pacifica* are invaded and then displaced by adjacent *S. densiflora*, although this is slowed somewhat by the remaining presence of native vegetation (Kittleson & Boyd 1997). In addition to the threat of displacement, the only *Spartina* species native to California, *Spartina foliosa*, is threatened by genetic dilution. Although progeny are unable to set germinable seed, crossing with *S. densiflora* has resulted in several local hybrid populations which were discovered in San Francisco Bay in 2002 (Ayres et al. 2008).

Research that explores the effects of *S. densiflora* invasion on disturbance-sensitive terrestrial invertebrate assemblages in Humboldt Bay is virtually nonexistent. Consequently, efforts to restore native salt marsh vegetation, although widely expected to improve biodiversity and ecosystem function, have gone largely uninformed regarding

invasion and restoration impacts on community composition of lower organisms including epiphytic (on plants), benthic (within the soil matrix), and epibenthic (on soil surface) invertebrates. Due to the sensitivity of these organisms to direct and indirect disturbance and the likelihood of cascading trophic effects on vertebrate animals, the intent of this study is to characterize invertebrate communities and explore their relationship with vegetation within native-restored and *S. densiflora* invaded tidal salt marshes. It should be noted that restored, native plant communities will be examined in this study primarily because: 1) intact, uninvaded native plant assemblages no longer exist in Humboldt Bay, and 2) data is needed to understand the functionality of restored salt marshes.

The primary objectives of this study were to:

1. Describe and compare terrestrial invertebrate assemblages in *S. densiflora*-dominated salt marsh with invertebrate assemblages of native, restored salt marsh types in Humboldt Bay.
2. Explore the role of dominant salt marsh vegetation in shaping these observed invertebrate assemblages by examining the life histories of their respective invertebrate indicator taxa.

MATERIALS AND METHODS

Sampling sites were selected in two representative salt marsh habitat types: 1) those invaded by *S. densiflora* and 2) restored areas in which *S. densiflora* had been removed. Two sampling sites of each habitat type were located along the Mad River Slough north of Humboldt Bay (Figure 2). The soil series at these sites is Fluvents-Riverwash complex at all sites. This complex includes finely textured alluvial hydric soils, high in organic matter content with a typically neutral pH. Strong tidal influxes regularly flood the slough corridor and inundate the proposed study areas.

Site Descriptions

Two post-restoration sites were selected based upon their previous unrestored condition (according to FWS staff) closely emulating the invaded sites. Prior to restoration these areas consisted of heavy *S. densiflora* patches with a scattered *S. pacifica* and *D. spicata* understory. The restored sampling sites were located along the west bank of Mad River Slough (Figure 3). The Restored North (RESN) site was located just south of the U.S. Fish and Wildlife Lanphere Dunes field office, while the Restored South (RESS) site was located north of Samoa Boulevard adjacent to the Ma-l'el Dunes recreation area. At both of these sites *S. densiflora* was mechanically removed during the 2008-2011-time period, and vegetation was allowed to re-establish itself naturally.

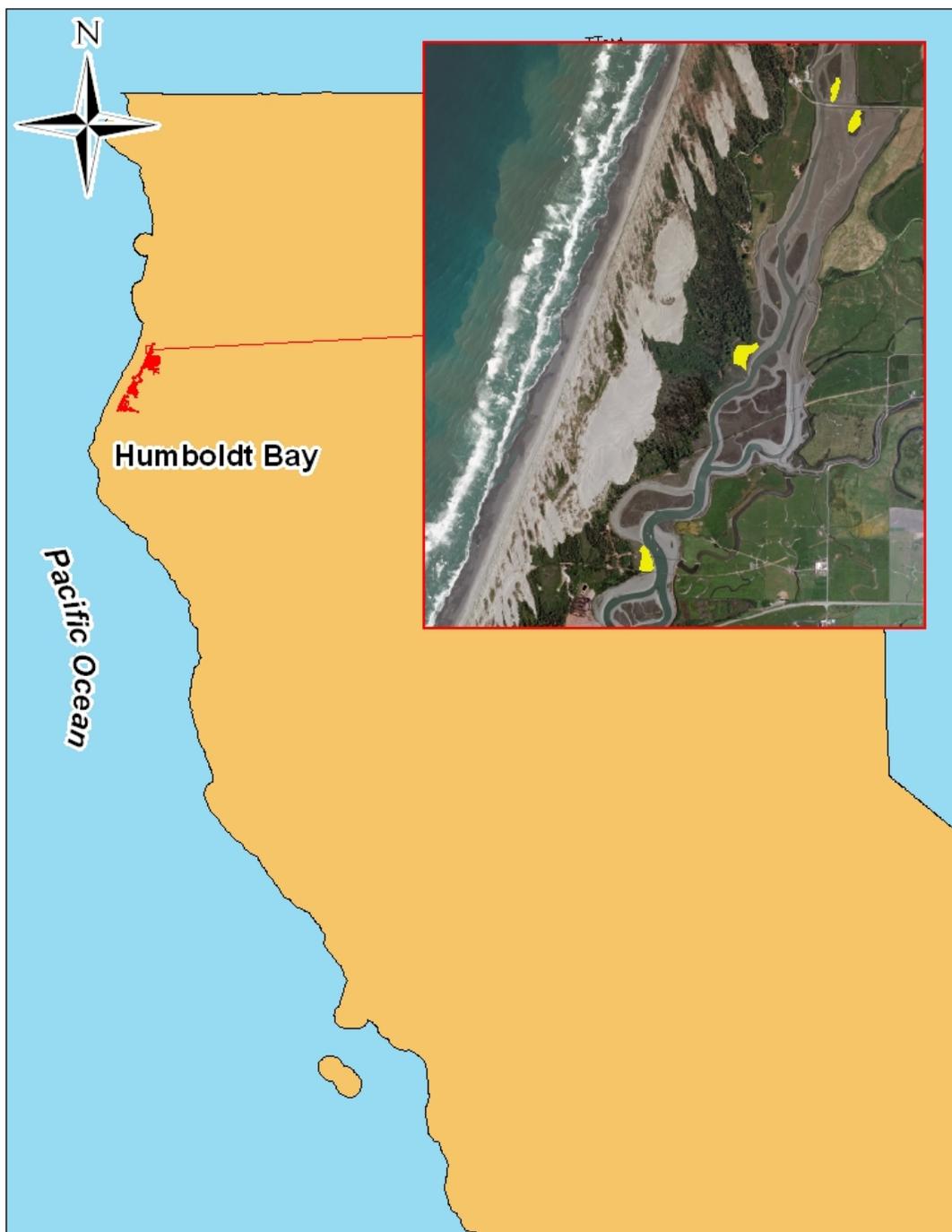


Figure 2. Location of study area and sampling sites (in yellow- see inset) along Mad River Slough north of Humboldt Bay, CA.

Restored plot locations were selected on the basis of having adequate representation of high (*D. spicata*-dominated) and low (*S. pacifica*-dominated) vegetation zones as described by Eicher (1987). Sampling areas were bounded by low marsh at the mudflat/salt marsh interface and the mid marsh habitat edge, determined by a transition in dominant plant type. *Jaumosa*, *Triglochin*, and *Cordylanthus* were found in limited abundance at both restored sites. Because the restored marshes examined in this study are still on a trajectory of recovery, they will be referred to as “post-restoration” or “restored, native” and not simply as native.

The invaded sites were located north and south of the Lanphere Road slough bridge (Figure 4). These sites were in close proximity to both the mainland and each other. Selection criteria for invaded sites included: close proximity to restored areas, vegetation similar to pre-restoration status at the restored sites, and ease of accessibility. Due to the success of past restoration efforts, no invaded sites were available on the mainland in the desired study area, therefore invaded sites were located on islands as close to the restored sites as possible. Sampling in invaded habitats was conducted in areas strongly dominated by *S. densiflora*, in addition to sampling in remnant *S. pacifica* and *D. spicata* patches.

The northern invaded site (INVN) contained exceptionally dense zones of *S. densiflora* tussocks at its southern end. This end of the island was a labyrinth of meter



Figure 3. Restored marsh sampling sites: “Restored North” (in yellow- top inset); “Restored South” (in yellow- bottom inset) with associated sample points.

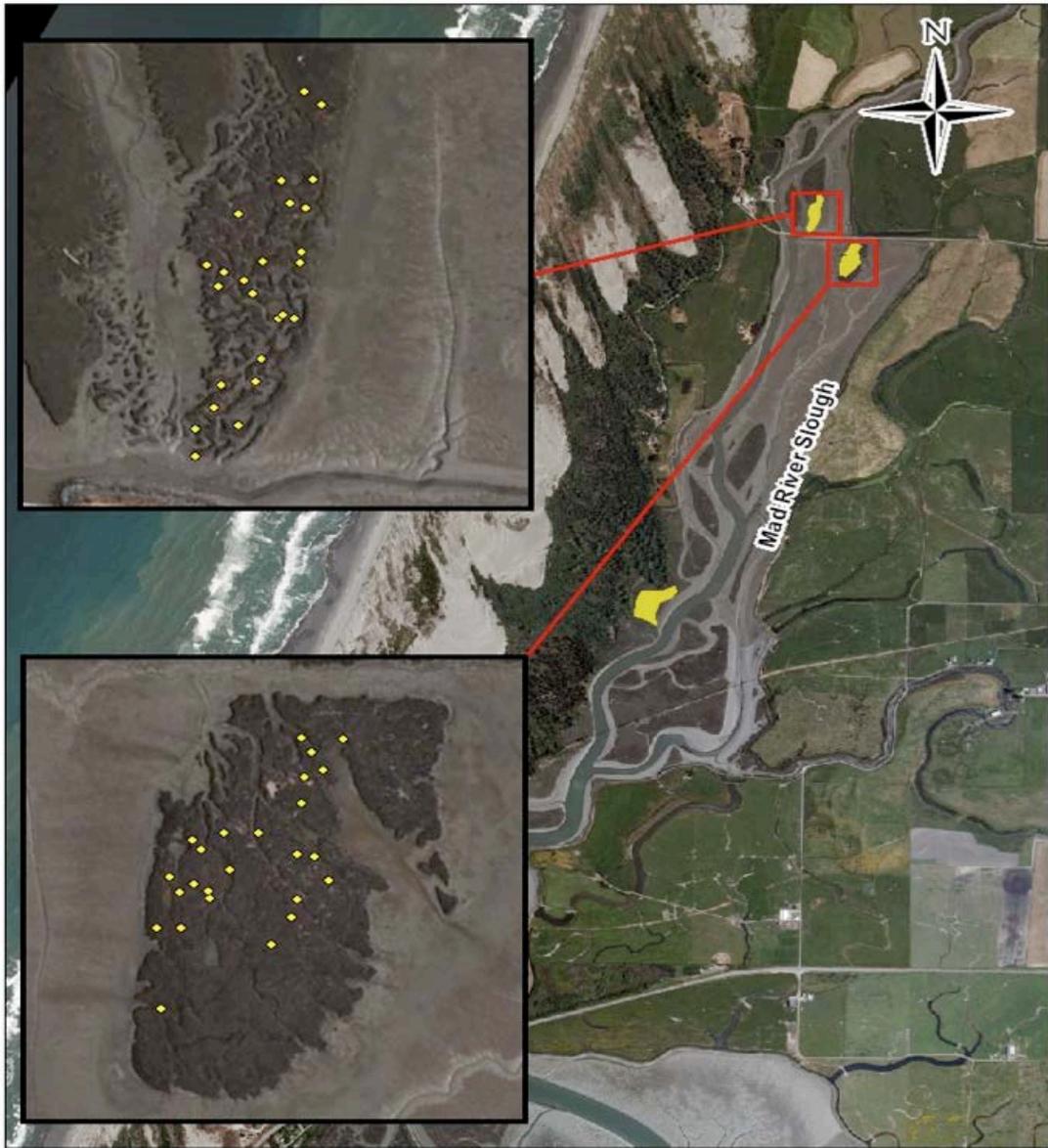


Figure 4. Invaded marsh sampling sites: “Invaded North” (in yellow- top inset); “Invaded South” (in yellow- bottom inset) with associated sample points.

deep, fine silted channels with solid interconnected banks which were one to three meters wide. *S. densiflora* individuals were packed in a monoculture on the flat, higher portions, while a thin ring of *S. pacifica* clung directly beneath the edges nearest the mudflat interface. In addition, there was a small homogenous patch of *D. spicata* lightly interspersed with *S. pacifica* dominating one small section of bank. On the north end of the island the channels gradually closed, and *S. densiflora* monocultures completely dominated. This abruptly transitioned to a thin ring of *S. pacifica*, then a mixed plain dominated by *D. spicata* with interspersed *S. densiflora*. Species such as Arrowgrass and *Jaumea* were also present in limited numbers.

The southern invaded site (INVS) was generally less heavily dissected by channelization, but remained a similar habitat. The entire island was essentially one continuous stand of *S. densiflora* with *S. pacifica* clinging to the lowest edges of the mudflat interface as characterized for INVN. There was a single small patch of *D. spicata* near the center of the island, which was the only occurrence of this species at the INVS site.

Twenty-five sample points were generated randomly throughout each site using the Hawth's tools extension in ArcMap 9.2 (ESRI, Redlands, California). If a point fell in undesirable habitat, such as a mudflat or large downed wood, it was eliminated and a new point was produced. The final number of points to be sampled was determined by the lowest remaining number of valid points of the four sites, with a minimum of 25

points. In the event that less than 25 points were viable at any one site, new random points were generated to provide 25 points.

Field Collection Methods

A garbage can with a volume of 0.12 cubic meters, height of 66 cm and surface sampling area of 0.164 m² was used as a sampling enclosure. At each sampling point the enclosure was placed with the labeled pin flag at the center. Vacuum and soil core samples were collected at each sample point, while biomass was collected only at sub-sampled points with measureable *S. densiflora*, *S. pacifica*, and *D. spicata* cover. Sweep netting was conducted between sample points within a consistent vegetation type (e.g. separate but equal efforts within *S. pacifica*, *D. spicata*, and *S. densiflora* cover). Total percent cover for the surface area within the boundaries of the sampling enclosure was assessed with the following categories: *S. densiflora*, *S. pacifica*, *D. spicata*, bare ground, algal mat, detritus, and other vegetation. Efforts were made to identify unknown vegetation if found to be present in significant quantities.

Terrestrial invertebrates were sampled using vacuum and sweep net methods similar to those described by Stewart & Wright (1995), Levin & Talley (1998), Hossain et al. (1999) and Southwood (1978), but adapted to suit site-specific conditions. This comprehensive sampling approach targets several structural components of the salt marsh habitat identified in a pilot study (Mitchell & Ascuzena 2010) and was conducted in the following sequence: (1) visual assessment of vegetation cover, ground cover, and height

- (2) vacuum collection to target the soil surface and vegetation within the enclosure, and
- (3) sweep netting to sample apical vegetation for flying invertebrates and web-spinning arachnids between sample points outside the enclosure.

Samples were collected in two sampling periods (September 9-10 and September 16-17, 2011). These sampling periods were selected for the time of year when activity levels were likely to be at their peak for the greatest number of invertebrate species. Collection at this time also facilitated proper plant identification through reproductive structures, reduced the likelihood of incident precipitation during sampling, and allowed for longer daylight hours in which to sample. Sampling was conducted at the warmest time of the day and with no significant precipitation in the previous 24 hours. Overall vegetative state of the dominant cover (e.g., actively growing, flowering, dormant) was noted.

Vacuum Method

For vacuum collection a modified Ryobi blower/vac with a 23 cc engine, a nozzle area of 81 cm², and a nozzle velocity of 89.4 meters per second (200 mph) was used. The nozzle velocity of 89.4 meters per second is significantly higher than the minimum threshold effectiveness of 40.23 meters per second (90 mph) set forth by Southwood (1978). A fine mesh nylon bag was attached inside the vacuum tube as a collector. The vacuum was then applied to the standing vegetation and soil surface within the enclosure from a vertical position. The vacuum was run for thirty seconds as evenly and thoroughly

as possible over every surface within the enclosure. In each sampling session up to a total of 25 samples were collected at each of the four sites, for a possible total of 100 vacuum samples.

Sweep Netting

The upper portion of *S. densiflora* individuals was sampled by sweep netting in a standardized manner similar to that described by Southwood (1978), Dent & Walton (1997), and New (1998). Sweep net samples are necessary to address suction trap inefficiencies, isolate organisms utilizing the upper portion of *S. densiflora* plants, and to compensate for within-plot disturbance that occurs during plot set up. Sweep net sampling was conducted by transect method, sweeping a net with a 30 cm diameter 100 times through the highest canopy 100 times while walking slowly along each transect. The length of the transect was determined by the extent of the habitat type and however many steps it took to get 100 sweeps. Identical sweep sampling efforts were conducted within the three prominent vegetation zones found in low, mid, and mixed salt marsh dominated respectively by *S. pacifica*, *S. densiflora*, and *D. spicata*.

Vegetation and Ground Cover

Several vegetation characteristics were measured at each sampling point. Height of vegetation was recorded by taking the average of several measurements within the sampling enclosure. Estimates of percentage cover by plant species within the garbage can ring was recorded for each sample while in the field. Cover by species included *S.*

densiflora, *S. pacifica*, *D. spicata*, algal mat, bare ground, and miscellaneous vegetation. Cover percentage was determined according to the Daubenmire system: 1 (0-5%) 2 (5-25%) 3 (25-50%) 4 (50-75%) 5 (75-95%) and 6 (95-100%). If any unknown vegetation was found to be in significant quantity, it was identified and given its own category.

Laboratory Procedures

Sorting methods were based on USGS protocols for processing benthic macroinvertebrates (Moulton et al. 2000) unless otherwise noted. All samples were first stored at 0 °C for 24 hours to anesthetize and preserve invertebrates. Each sample was then sorted into 3 layers of sieve trays using water to flush samples through the sieves (4 mm on top, followed by 2 mm, and then 0.25 mm). The succeeding sieve layers were then deposited into a tray and searched thoroughly. After discarding any rinsed vegetation, the water in the tray was run back through the screens a final time. After the smallest material was concentrated, it was rinsed into the bottom and flushed into a petri dish with a plastic pipette. Organisms were then separated from debris as thoroughly as possible under a dissecting microscope (magnification of 10-30x).

To feasibly characterize high-density samples, a two-stage sub-sampling technique was used. The contents of each sample dram were separated equally onto a four section divided petri dish one-quarter dram at a time. All taxa in ¼ dish search were identified and tallied. If any taxa count was greater than 100 within the first quarter, the count was multiplied by four and only the remaining taxa were tallied in the remainder of

the sample. After each quarter was processed, a large (huh?) and rare search for species not identified in the initial $\frac{1}{4}$ was conducted in the remaining sections of the petri dish until all unique taxa were accounted for. The procedure was repeated until all contents of the dram were exhausted. Previous research has shown fixed-count subsampling as generally more efficient than fixed-area sampling at thorough assemblage descriptions (eg: King & Richardson (2002). However, fixed area samples in this situation: 1) are more reasonable estimates of true sampling efficiency, 2) contained well over 200 individuals (the minimum for reliable fixed-count data), and 3) were followed by an unlimited large and rare search for organisms that might have been missed due to rarity or large size.

Analysis

Nonmetric multi-dimensional scaling (NMDS) was utilized to compare the relationship of site variables and invertebrate community structure among sites using a Bray-Curtis distance measure. Site variables included abundance of plant taxa, height, and invertebrate richness, diversity, evenness, and dominance of the top three most abundant organisms, as well as taxon abundance. P-values were reported at alpha levels of 0.05, 0.01, and 0.001. Comparisons were made between sites with differing restoration status and among vegetation types found within each site. For the purpose of community comparisons, vacuum sample data were pooled by restoration status and sweep net samples are pooled by vegetation type. *S. densiflora* sweep samples from invaded sites

were pooled for comparison to *D. spicata* and *S. pacifica* samples from restored sites, also pooled by vegetation type.

Invertebrate community composition was compared among sites using Multi Response Permutation Procedure (MRPP), again using Bray-Curtis distance. Analogous to discriminant analysis and multivariate analysis of variance, this method avoids distributional assumptions and enhances the descriptive effort of NMDS by directly testing group differences (McCune & Grace 2002).

Dufrene-Legendre indicator species analysis (ISA) was used to detect and describe the value of individual species as indicators of invaded or restored environmental conditions. This test is complimentary to the MRPP, supplementing the test of difference between groups with a description of how well each taxa separates among groups (McCune & Grace 2002). Indicator strength is based on a scale of 0-1 with 1 representing perfect fidelity of invertebrate taxa to one vegetation type. Sweep data were pooled with vacuum data for this analysis. All data were analyzed using RTM statistical software version 2.14.1 (R development core team 2008).

RESULTS

Ordination of Invertebrate Taxa by Restoration Status

Plant height and richness both differed significantly by restoration status ($p \leq .05$). Increased height was more closely associated with invaded sites than restored, while higher plant richness was correlated with restored sites ($r^2 = .37$). All ground and canopy cover types significantly differed among sites ($p \leq .05$) with the exception of algal ground cover ($p = .37$). *Spartina densiflora* was the most highly correlated plant with invaded sites, while all other types were found in higher abundance at restored sites.

Invertebrate richness was correlated with restored sites ($r^2 = .61$). Ichneumons, chalcids, and non-tetragnathan arachnids trended toward restored areas, while Molluscs, *Tetragnatha*, neobisiids, and aphids were correlated with invaded sites (Figure 5, Table 1). Of the 30 taxa included in the NMDS, populations for 21 taxa were found to differ significantly by restoration status ($p < .05$) based on 10,000 permutations (Table 1).

Diversity Measures

Invertebrate richness produced the highest r^2 value of any variable ($r^2 = .60$), correlating with NDMS axis 1 (restored) (Figure 5). Diversity, evenness, and dominance of the top three taxa differed significantly by restoration status ($p < .05$). Abundance was similar among sites ($p = .97$).

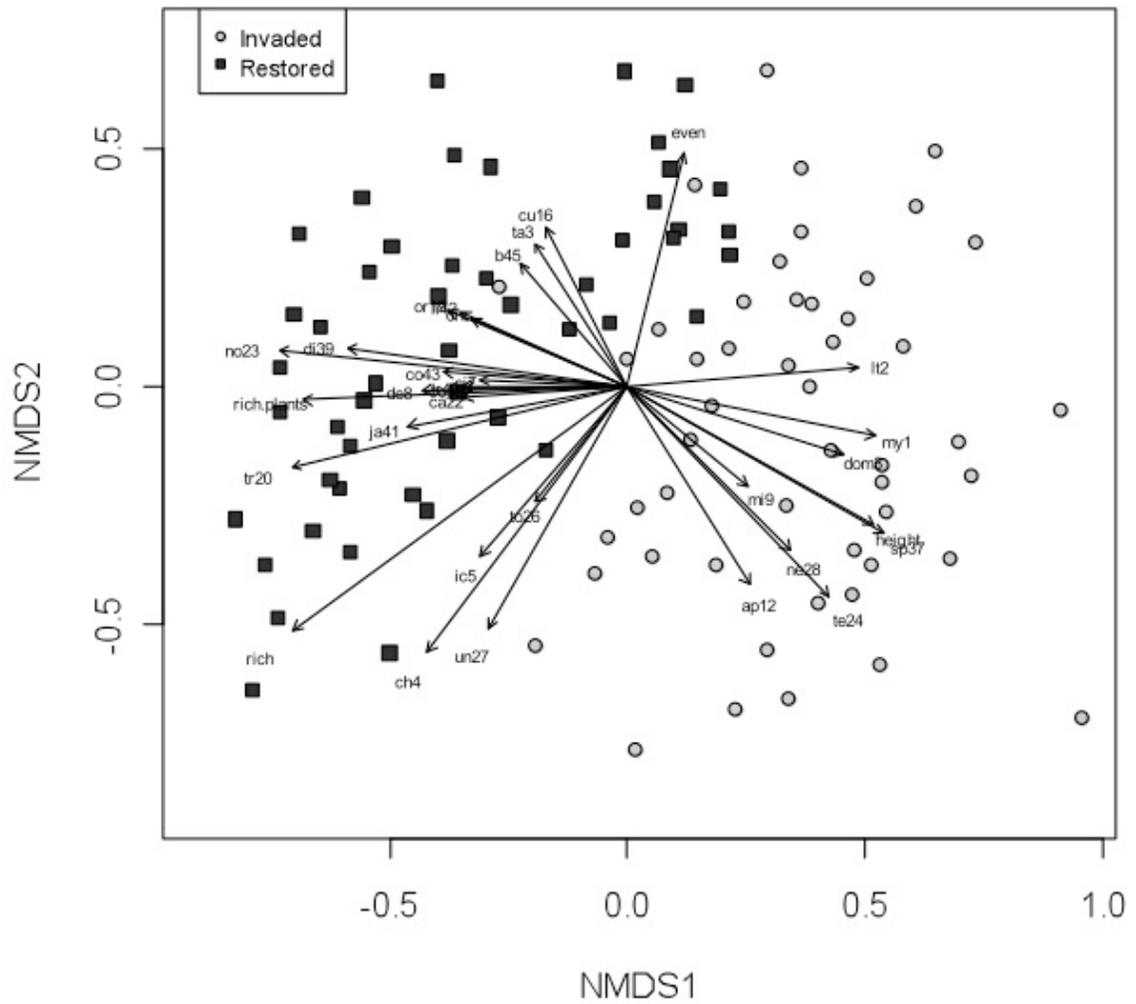


Figure 5. Ordination of invertebrates and site variables by restoration status (refer to Table 1 for taxa codes). Axis NMDS 1 = restored, axis NMDS 2 = invaded.

Table 1. Ordination of counts and variables on site restoration status.

Significance levels @ .05 (*), .01 (**), .001 (***)

Code	Taxa	Axis	r ²	p	sig. level
rich	Invertebrate richness	RESTORED	0.61	0.0001	***
no23	Non.tetragnatha	RESTORED	0.43	0.0001	***
tr20	Erythraeidae	RESTORED	0.42	0.0001	***
ch4	Chalcidoidea	RESTORED	0.39	0.0001	***
richplants	Plant richness	RESTORED	0.37	0.0001	***
di39	<i>Distichlis</i>	RESTORED	0.28	0.0001	***
un27	Lepidoptera	RESTORED	0.27	0.0001	***
even	Invertebrate evenness	RESTORED	0.20	0.0001	***
ic5	Ichneumonidae	RESTORED	0.18	0.0003	***
ja41	<i>Jaumea</i>	RESTORED	0.18	0.0002	***
de8	Delphacidae	RESTORED	0.15	0.0003	***
or19	Orbatidae	RESTORED	0.13	0.0005	***
co43	<i>Cordylanthus</i>	RESTORED	0.12	0.0013	**
li42	<i>Limonium</i>	RESTORED	0.12	0.0017	**
cu16	Culicidae	RESTORED	0.11	0.0033	**
ta3	Talitridae	RESTORED	0.10	0.0046	**
div	Invertebrate diversity	RESTORED	0.10	0.0065	**
tr40	<i>Triglochis</i>	RESTORED	0.10	0.0064	**
ca22	Carabidae	RESTORED	0.10	0.0055	**
b45	Bare ground	RESTORED	0.09	0.0105	*
co10	Coccidae	RESTORED	0.09	0.0027	**
po25	Poduridae	RESTORED	0.08	0.0118	*
ci7	Cicadidae	RESTORED	0.08	0.0102	*
sa38	<i>Salicornia</i>	RESTORED	0.08	0.0216	*
to26	Tomoceridae	RESTORED	0.08	0.0080	**
un18	Unkown Diptera	RESTORED	0.07	0.0195	*
sp37	<i>Spartina</i>	INVADED	0.31	0.0001	***
te24	Tetragnatha	INVADED	0.30	0.0001	***
ht	Plant height	INVADED	0.28	0.0001	***
my1	<i>Myosotella</i>	INVADED	0.22	0.0001	***
ap12	Aphidae	INVADED	0.19	0.0001	***
lt2	<i>Littorina</i>	INVADED	0.19	0.0001	***
ne28	Neobisiidae	INVADED	0.19	0.0001	***
dom3	Dominant 3	INVADED	0.18	0.0003	***
mi9	Miridae	INVADED	0.09	0.0055	**

Significance based on 10,000 permutations.

Richness, evenness and diversity were correlated with restored sites, while community dominance of the top three taxa was most correlated with invaded sites (see position in Figure 5).

Community Composition

A total of 30 taxa were collected by the vacuum sampling method (Table 2). The mollusks *Myosotella* and *Littorina* and armadillid isopods were the most numerous organisms observed at invaded sites, while talitrid amphipods, oribatid spiders, and delphacid planthoppers were dominant at restored sites (Figure 6). The most abundant taxonomic groups encountered among all sites regardless of restoration status were Mollusca ($n= 18,520$), Hemiptera ($n= 8,579$), and Acari ($n= 3,692$). At invaded sites, *Myosotella* outnumbered *Littorina* by a factor of 3:1 (12,117 to 3,560) (Table 2). While significantly fewer *Myosotella* and *Littorina* were observed in restored sites (1,566 *Myosotella*, 1,284 *Littorina*), the ratio between the two was closer to 1:1. Sweep sampling resulted in much lower count totals than the vacuum method for most taxa, with the exception of the Delphacidae, Ephydriidae, and an unknown Dipteran (table 3).

Multiple Response Permutation Procedure

Invertebrate communities occupying restored sites were determined to be highly dissimilar to those in invaded sites based on 10,000 permutations of class means and counts (INVADED delta 0.5082; RESTORED delta 0.6642, $p < 9.999e-05$).

Table 2. Taxa list and total counts by restoration status (vacuum method).

Taxa	Invaded	Restored
<i>Myosotella</i>	12117	1566
<i>Littorina</i>	3560	1284
Armadillidae	1293	312
Talitridae	469	1675
Orbatidae	208	3024
Delphacidae	160	7942
Saldidae	158	122
Non-tetragnatha	102	387
Ephydriidae	99	21
Poduridae	82	100
Erythraeidae	49	411
Tetragnatha	28	0
Cicadidae	24	107
Aphidae	19	3
Chalcidae	15	31
Thysanoptera	15	6
Neobisiidae	13	1
Carabidae	10	332
Culicidae	10	51
Lepidoptera	10	14
Muscidae	9	5
Miridae	6	0
Ichneumonidae	4	9
Dolichopodidae	3	1
Unk. Diptera	2	17
Chrysomelidae	2	2
Coccidae	1	39
Psocoptera	0	10
Tomoceridae	0	6
Formicidae	0	2

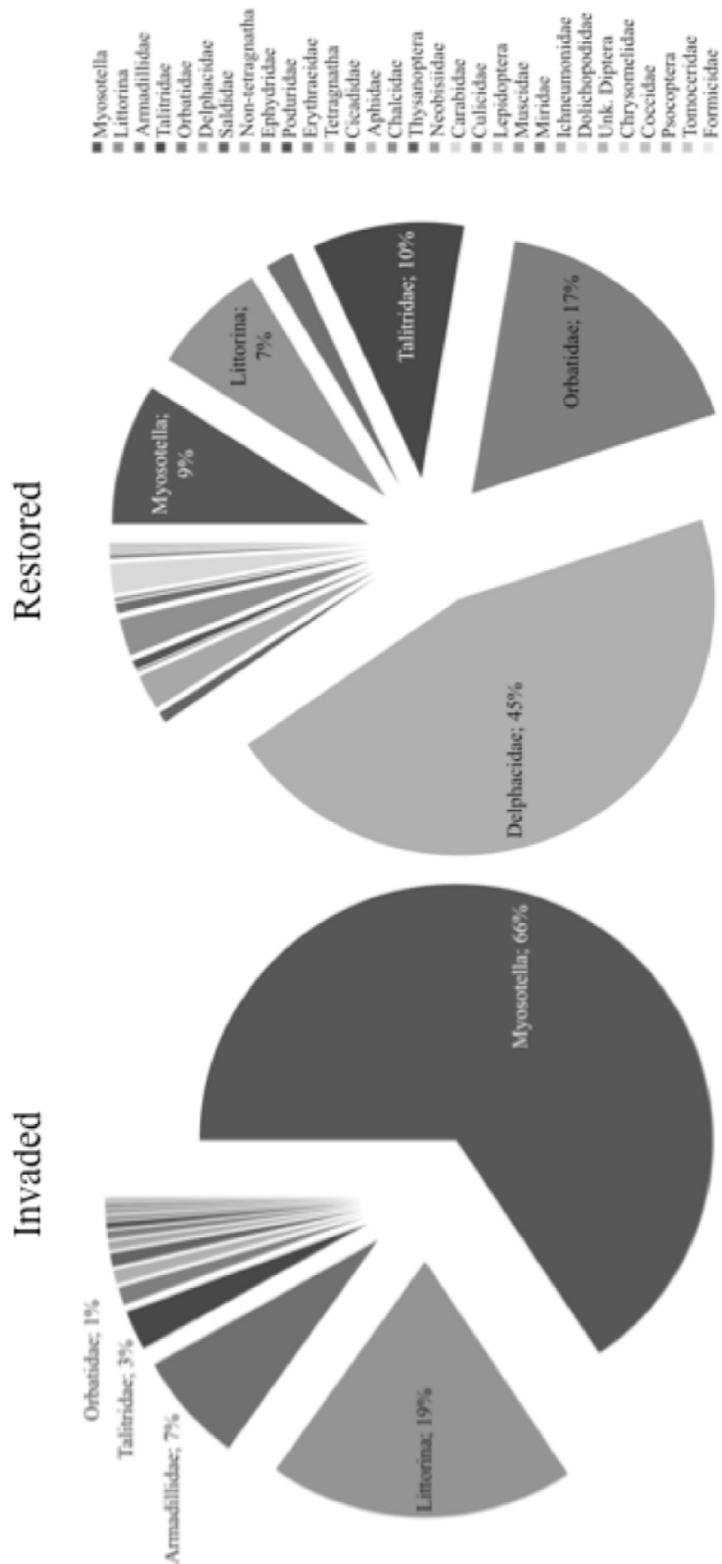


Figure 6. Distribution of invertebrate communities at invaded sites (left) and restored sites (right).

Table 3. Taxa list and total counts by vegetation type (sweep net method)

Taxa	Salicornia	Distichlis	Spartina
Delphacidae	6348	10457	1
Ephydriidae	1671	129	383
Unk. Diptera	388	22	19
Dolichopodidae	53	22	4
<i>Littorina</i>	48	29	4
Saldidae	18	11	12
Cidadidae	16	310	0
Ichneumonidae	10	10	8
Tetragnatha	9	2	25
Orbatidae	8	14	148
<i>Myosotella</i>	7	14	20
Culicidae	1	117	17
Chalcidoidea	1	9	5
Lepidoptera	1	8	0
Miridae	1	0	10
Thysanoptera	1	0	0
Psocoptera	1	0	0
Tanaid	1	0	0
Non-tetragnath:	0	8	7
Erythraeidae	0	6	0
Carabidae	0	1	19
Aphidae	0	1	10
Poduridae	0	0	1

Indicators of Restoration Status

A total of six taxa were determined as significant indicators of invaded site status, of which *Myosotella*, *Tetragnatha*, Armadillidae, and *Littorina* had the highest indicator values (table 4). Twelve taxa were significant indicators of restored status, with non-tetragnathan spiders, Talitridae, Oribatidae and Delphacidae comprising the top four (Table 3).

Indicators of Dominant Vegetation Types

Delphacid, trombilid, and non-tetragnathan taxa were significant indicators for the presence of *D. spicata* ($p < .01$) and the absence of *S. densiflora* ($p < .01$). Non-tetragnathan spiders were the sole indicators of *S. pacifica*, although less significantly so ($p = .04$) than they were for *D. spicata*. Armadillid and tetragnathan taxa strongly indicated the presence of *S. densiflora*, while *Littorina* and *Myosotella* most often indicated an absence of *D. spicata* (Table 4). Talitrids did not indicate the presence of *S. pacifica*, but were an indicator of *D. spicata* and the absence of *S. densiflora* (Table 4).

Indicators of Dominant Ground Cover

In the presence of algal cover, no taxa were significant indicators, although *Tetragnatha* and Ephydriidae indicated the absence of algal cover (indicator values = .85 and .63, respectively). Talitrids and armadillids both significantly indicated the presence of bare ground (indicator values = .63 and .58), while non-tetragnathans, delphacids, and tomocerids were indicative of detritus (indicator values = .66, .63, and .17) (table 5).

Table 4. Invertebrate indicators of restoration status (treatment) at $p = .05$

TREATMENT			
Groups (clusters): INVADED, RESTORED			
Taxa	Cluster	Indicator Value	p
Myosotella	INVADED	0.89	0.0001
Armadillidae	INVADED	0.70	0.0001
Littorina	INVADED	0.70	0.0004
Tetragnatha	INVADED	0.30	0.0012
Aphidae	INVADED	0.21	0.0097
Neobisiidae	INVADED	0.18	0.0029
Delphacidae	RESTORED	0.80	0.0001
Non. Tetragnatha	RESTORED	0.73	0.0001
Orbatidae	RESTORED	0.72	0.0005
Talitridae	RESTORED	0.69	0.0001
Erythraeidae	RESTORED	0.62	0.0001
Culicidae	RESTORED	0.45	0.0048
Cicadidae	RESTORED	0.42	0.0022
Chalcidoidea	RESTORED	0.30	0.0397
Unk. Diptera	RESTORED	0.30	0.0055
Carabidae	RESTORED	0.29	0.0251
Coccidae	RESTORED	0.24	0.0011
Ichneumonidae	RESTORED	0.20	0.0336

Number of significant indicators: 18

Table 5. Significant invertebrate indicators of primary vegetation types.

DOMINANT VEGETATION			
Groups (clusters): DISTICHLIS, SALICORNIA, SPARTINA			
Taxa	Cluster	Indicator Value	p
Delphacidae	DISTICHLIS	0.65	0.0003
Erythraeidae	DISTICHLIS	0.63	0.0001
Non.tetragnatha	DISTICHLIS	0.48	0.0029
Cicadidae	DISTICHLIS	0.40	0.0129
Aphidae	SPARTINA	0.20	0.0185
Miridae	SPARTINA	0.19	0.0007
Neobisiidae	SPARTINA	0.13	0.0423
Number of significant indicators: 7			
SPARTINA PRESENCE/ABSENCE			
Delphacidae	ABSENT	0.71	0.0001
Talitridae	ABSENT	0.69	0.0003
Non.tetragnatha	ABSENT	0.68	0.0002
Erythraeidae	ABSENT	0.66	0.0001
Orbatidae	ABSENT	0.65	0.0191
Coccidae	ABSENT	0.20	0.0319
Unk. Diptera	ABSENT	0.17	0.048
Armadillidae	PRESENT	0.55	0.0478
Tetragnathidae	PRESENT	0.26	0.0037
Aphidae	PRESENT	0.24	0.0015
Neobisiidae	PRESENT	0.18	0.0103
Miridae	PRESENT	0.09	0.0326
Number of significant indicators: 12			

Table 5. Significant invertebrate indicators of primary vegetation types.
(Continued)

SALICORNIA PRESENCE/ABSENCE

Taxa	Cluster	Indicator Value	p
Neobisiidae	ABSENT	0.26	0.012
Aphidae	ABSENT	0.22	0.0492
Miridae	ABSENT	0.15	0.0322
Non-Tetragnatha	PRESENT	0.63	0.0473

Number of significant indicators: 4

DISTICHLIS PRESENCE/ABSENCE

<i>Myosotella</i>	ABSENT	0.70	0.0067
<i>Littorina</i>	ABSENT	0.62	0.0313
Armadillidae	ABSENT	0.58	0.0143
Tetragnathidae	ABSENT	0.23	0.0063
Aphidae	ABSENT	0.22	0.0014
Neobisiidae	ABSENT	0.18	0.0055
Delphacidae	PRESENT	0.83	0.0001
Trombilidae	PRESENT	0.78	0.0001
Non.tetragnatha	PRESENT	0.70	0.0001
Orbatidae	PRESENT	0.66	0.0089
Talitridae	PRESENT	0.63	0.0016
Cicadidae	PRESENT	0.36	0.0035
Carabidae	PRESENT	0.31	0.0205
Coccidae	PRESENT	0.22	0.0077
Unk. Diptera	PRESENT	0.22	0.0058

Number of significant indicators: 15

Table 6. Significant invertebrate indicators of primary ground cover.

ALGAL COVER PRESENCE/ABSENCE

Groups (clusters): ABSENT, PRESENT

Taxa	Cluster	Indicator Value	p
Tetragnathidae	ABSENT	0.85	0.0217
Ephydriidae	ABSENT	0.63	0.0498

Number of significant indicators: 2

BARE COVER PRESENCE/ABSENCE

<i>Myosotella</i>	ABSENT	0.71	0.0049
Aphidae	ABSENT	0.24	0.0025
Neobisiidae	ABSENT	0.17	0.0175
Talitridae	PRESENT	0.63	0.0039
Armadillidae	PRESENT	0.58	0.0182

Number of significant indicators: 2

DETRITUS COVER PRESENCE/ABSENCE

<i>Myosotella</i>	ABSENT	0.85	0.001
Armadillid	ABSENT	0.67	0.0132
Non-tetragnathid	PRESENT	0.66	0.0225
Delphacidae	PRESENT	0.63	0.0044
Tomoceridae	PRESENT	0.17	0.0143

Number of significant indicators: 5

Indicator analysis based on 10,000 permutations.

DISCUSSION

According to the resource availability (O'Connor 1990) and habitat heterogeneity hypotheses (Valverde & Lobo 2007), species diversity should increase with increased habitat complexity, although this has not always been shown to be the case (Parr 2010). In general, the concept of positive habitat complexity/organism diversity relationships is commonly accepted (Bortolus 2010, Reid & Hochuli 2007). This study is in agreement with other research that implicates native habitats as supporting higher diversity and natural associations among invertebrates. Native ecosystems have consistently been identified as being structurally more complex than those that have been invaded, with invasions resulting in reductions of native diversity of invertebrates in stream substrates (O'Connor 1991), coralline algal turf (Kelaher 2002), *Spartina alterniflora* marsh (Wan et al. 2006), tropical savannah (Parr 2010), boreal wetlands (Hornung & Foote 2006) and riparian systems (Herrera & Dudley 2003) among others.

The specific biological requirements for the suite of organisms sampled in this study vary greatly. Taking this into consideration, the inconsistencies observed in invertebrate distribution between invaded and restored sites are best explained in terms of the effects of microhabitat features and resource alteration on individual taxa. Only those taxa that were demonstrated to be strong indicator species of a given habitat or occurred in significant numbers are discussed below.

Molluscs

The results of the vacuum samples revealed that *S. densiflora*-invaded sites facilitate higher densities of the invasive snail *M. myosotis* compared to the native *L. subrotundata*, and both prefer *S. densiflora* habitats to restored sites (Figure 6). Little is known of *L. subrotundata* ecology other than it is a semi-aquatic snail tolerating occasional emergence and is associated with low marsh *S. pacifica*, feeding on algae and plant material (Hinde 1954, Taylor 1981). Even less is known regarding the ecology of the invasive *M. myosotis*, although Bergman and Carlton (1991) found that it prefers higher portions of the marsh where it can remain exposed for long periods. In the Bergman and Carlton (1991) study, diets of *L. subrotundata* and *M. myosotis* (Figure 7) were identical, with both species consuming bacteria, diatoms, algae, and epithelial cells of halophytic plants. The data obtained on diets were rudimentary however, relying solely on fecal pellet examination.

My research reveals the possibility that diets could differ on a finer level based on the slight decrease in the *M. myosotis* to *L. subrotundata* ratio observed at restored sites (Table 2), which is inconsistent with the Bergman and Carlton (1991) study that found no such associations. It is possible that *M. myosotis* is better able to feed on *S. densiflora* material than *L. subrotundata* as its chemistry, toughness, and nitrogen content likely differ from *S. pacifica*, which are all important determinants of herbivore preference (Pennings & Bertness 2001).



Figure 7. *Littorina subrotundata* (top) and *Myosotella myosotis* (bottom)

In addition to a shift in forage qualities, *S. densiflora* provides *M. myosotis* with an advantageous habitat niche. Pulmonate snails such as *M. myosotis* must remain emerged at high tide or they will drown. In a cordgrass invaded marsh, the tall stems of *S. densiflora* provide a means to travel up and down with the tide, allowing them to remain emerged while consuming wetted plant material. This behavior has been previously documented for the genus *Littorina*, on *S. alterniflora* (Pennings & Bertness 2001). The question remains as to whether *L. subrotundata* would utilize *S. densiflora* to a greater extent in the absence of *M. myosotis*, although elimination of *S. densiflora* remains the best approach to *L. subrotundata* conservation. In the absence of cordgrass, marsh zones appear to be partitioned between *M. myosotis* and *L. subrotundata*, with apparently very little competition for resources (Berman & Carlton 1991).

Amphipods

As primary consumers, talitrid amphipods (Figure 8) serve a vital function in the salt marsh by converting fungi, microorganisms and detritus into animal biomass; this in turn provides forage for higher-level organisms such as fish and shorebirds. The results of this study indicate a talitrid amphipod preference for restored sites and *D. spicata* over *S. densiflora* (see Table 4 and Figure 5). This is consistent with past research. Several factors must be invoked to account for the higher ratio of the talitrids observed in restored areas: their life history, detrital processes in the salt marsh, the quality of each vegetation type as habitat and forage, and other abiotic influences.



Figure 8. Family Talitridae, order Amphipoda.

What little is known about talitrid life history in northern California bays suggests co-evolved relationships with native vegetation. A different species (*Traskorchestia traskiana*), a talitrid in the San Francisco Bay demonstrated an interaction with the local *S. pacifica* that likely reflects an analogous process in Humboldt Bay (Obrebski & Irwin, unpublished data). Preliminary results indicated that this particular species utilized the plant for both physical cover and food while providing it with nitrogen and soil aeration (from burrowing activities). During low tide as the soil dried out, talitrids burrowed into the soil among the *S. pacifica* roots, depositing urea and oxygenating the soil. *Salicornia pacifica* growth showed a linear relationship with talitrid abundance, indicating a mutualism. While the amphipods in this study were not significant indicators of *S. pacifica*, they did indicate the restored condition of the habitat, suggesting that a relationship may exist that was not detected in my study.

It has been suggested that although talitrid amphipods consume detritus, the bulk of their nutrition comes from bacteria and microorganisms, which are higher in nitrogen content, rather than the plant material (Lopez et al. 1977). Talitrids consuming only fresh marsh grasses demonstrate high mortality rates due to elevated levels of secondary metabolites such as phenols, which was especially true of *Spartina alterniflora* (Agnew et al. 2003). Conversion of *Salicornia* biomass to microbial biomass is significantly less efficient than *Spartina* (19.4% to 64.3%, respectively) (Haines & Hanson 1979), and in the Agnew et al. (2003) study growth rates for talitrids consuming year-old *D. spicata* were shown to be significantly greater than those consuming *Spartina alterniflora*.

Lopez et al. (1977) suggest that grazing and urea deposits made by talitrids encourage the presence and detrital activity of their microbial prey, creating a feedback. Although empirical data examining talitrid consumption of *Salicornia* is lacking, this feedback mechanism is complimentary to the mutualism described by Obrebski & Irwin (unpublished data). The system can be roughly summarized in three stages: 1) talitrids, attracted to native vegetation providing ideal physical habitat in which they are well hidden from predators, create additional nitrogen availability in the soil as excreted urea and in the form of increased plant biomass made possible with this additional nitrogen; 2) microbes responding to increased plant nitrogen and talitrid browsing increase their activity, breaking down plant matter and making it physically available to talitrids for consumption; 3) talitrid growth rates benefit from the consumption of decayed plant material with elevated levels of microbes, due to enhanced soil and biomass nitrogen. Evidence of any similar process between talitrids and the genus *Spartina* is absent from the literature.

Abiotic factors also likely contributed to talitrid abundances observed in restored sites. A simple explanation may be that the physical toughness of *S. densiflora* prevents adequate breakdown of the material. Another might be that at high tide, *S. pacifica*'s physical complexity provides protection from predators such as fish or shorebirds. The lower abundance of talitrids in *S. densiflora* could indicate that it is a poorer quality refuge from predators. *Spartina densiflora* is comprised of tall, homogenous vertical stems compared to the complex, overlapping thatch of the native marsh. To date there is

no literature comparing relative talitrid predation by fish in native and *S. densiflora* invaded marshes. Another possible influence is distance to shoreline. The invaded points in this study, being on islands, were closer to waterways and the water's edge in general, meaning predators would not need to travel as far to reach the prey. A predaceous fish might limit the distance it travels into the marsh in pursuit of prey depending on the depth of a particular tidal inundation or other factors (e.g. Balltz et al. 1993)

The preference of talitrids for restored over invaded marsh contrast with findings of the initial pilot study (Mitchell & Azucena 2010) that described a relatively higher number of talitrids in *S. densiflora* invaded marsh. The difference in the two studies was that the invaded sampling site in the pilot study was connected with thick vegetation to the mainland rather than separated by a mudflat, and sample points were further inland. Open to question is the role of fish predation under these circumstances and whether habitat structure, distance from the mudflat, tidal influence, or all of the above contribute to talitrid consumption.

Armadillids

Although not found in high abundance compared to other taxa, armadillids as an indicator of *S. densiflora* (see table 4) contribute an interesting aspect of the invasion story. *S. densiflora* has been shown to be a rich nitrogen source as mentioned previously; it appears that it may only be preferentially selected as live forage by a subset of the

invertebrate community. Some semi-terrestrial isopods have displayed symbiotic relationships with certain gut microbes allowing them to digest cellulose as well as phenolic compounds (Zimmer et al. 2002). This provides an advantage in that isopods can likely exploit *S. densiflora*, high in both compounds, to a greater extent than organisms such as talitrids or mollusks who cannot process much live material. The significantly higher numbers of armadillids (Figure 9) at invaded sites illustrates a forage shift that reduces invertebrate diversity through the reduction of forage quality.

Delphacids

Although the taxonomy of species in the family Delphacidae (Figure 10) is notoriously difficult (many are undescribed) and literature on specific salt marsh species is scant, individuals from Delphacidae were observed most frequently in this study and are known primarily as host plant-specific phloem feeders parasitizing grasses (Wilson et al. 1994). Because the vegetation comprising the habitats in this study are generally very limited in geographic distribution, it is easier to identify likely host plants through statistical inference and then investigate the plant's known parasites. The overwhelming majority of delphacids observed in restored areas were very strong indicators of *D. spicata* (see Table 5), suggesting this plant as the likeliest host for the local delphacid species. Extensive literature searches implicate only the genus *Megamelus* as *D. spicata*-specific (Wilson et al. 1994). The implication of a closer association with *D. spicata* over *S. densiflora* is that this is a native species, and that restoration of native grasses preserves an association between local endemics.



Figure 9. Family Armadillidae, order Isopoda.



Figure 10. Family Delphacidae, order Hemiptera.

The mechanism of extreme host plant specificity common to delphacids provides a tantalizing prospect: they can be used as bio-control agents in the control of invasive plants including *S. densiflora*'s close relative *S. alterniflora*. In Willapa Bay, Washington, the delphacid *Prokelesia marginata* was shown to reduce *S. alterniflora* biomass by 50% when high densities of the organism were maintained (Grevstad et al. 2003). In addition, no risk to non-target plants was observed. These results were limited in scale however, and long-term studies are needed to ensure that these results can be replicated. The implications of this line of thinking suggest that if a delphacid could be identified that preferentially consumes *S. densiflora* phloem over native salt marsh plants or nearby pasture grasses, a new weapon could be added to the arsenal to combat it. Although no *S. densiflora*-specific delphacids are recognized by the available data, several species are specific to the genus *Spartina* (Wilson et al. 2004), providing a starting point for future inquiry.

Tetragnatha and Non-Tetragnatha Spiders

Predation tactics in spiders have been correlated with natural enemy abundance related to habitat complexity, plant height and tidal inundation (e.g., Dobel et al. 1990, Langellotto & Denno 2004). The spiders observed in this study were broken down into non-tetragnathan (Figure 11, top) and tetragnathan (Figure 11, bottom) categories.



Figure 11. Family Lycosidae, (non-tetragnatha, top), and family Tetragnathidae (bottom), order Arachnida.

The intent of this scheme was for ease of identification, and to describe whether predation tactics change as a result of *S. densiflora* invasion. Tetragnathan spiders are classified as orb weavers, which denote a principally sedentary predatory tactic. For this type of behavior to occur, physical habitat must be available as location for a web to remain anchored. In native salt marsh, this habitat is typically uncommon, confined to scattered *Trigonchlin* stems that remain above the water at the highest tides. In a *S. densiflora*-dominated marsh, this physical attribute is readily abundant, and many closely packed stems can facilitate a great number of webs. Increasing web anchor point density is correlated with tetragnathan abundance and web placement (e.g., McNett & Rypstra 2000), consistent with the findings of this study in that tetragnatha were strong indicators of *S. densiflora* (Table 4) that is assumed to have an abundance of anchor points.

Restored areas in this study supported much fewer tetragnathan spiders, and favored of more active forms (see tables 2 and 3). Our results mirror those of Dobel et al. (1990). Short, grassy thatch was shown to support high numbers of active predators, while taller *Spartina alterniflora* stems similar in form to *S. densiflora* with multiple web attachment points supported tetragnatha and other orb weavers. Considering that native salt marshes consist of short, interweaving layers of various plants providing cover and invaded sites are typically vertical stem monocultures, it is logical that our findings are consistent with empirical data.

Oribatid and Erythraeid Mites

Several studies have indicated that aboveground interactions play the largest role in the abundance of mites in a particular sample, with soil mite diversity strongly correlating with plant diversity, soil properties, fungal abundance, precipitation, soil pH, and disturbance (Mauran & Scheu 2000, St. John et al. 2006, Nielsen et al. 2010). The observed differences in abundance between restored and invaded sites in this study may also be simply an artifact of inadequate sample size that doesn't reflect true population size. The presence of mites such as Erythraeids (Table 4, Figure 12), which are predatory as adults and an arthropod ectoparasite as larvae (personal communication, Norton, R. 2011), is suggestive that trophic processes are intact in restored salt marsh. The presence of predators in a habitat is strongly correlated with diversity, prey abundance and complex habitat (e.g. O'Connor 1990, McNett & Rypstra 2000, Valverde & Lobo 2007).

Conclusion

Knowledge of ecological impacts resulting from alien species invasion and the repercussions of restoration to native biota are invaluable for informing non-native invasive eradication efforts. Through the understanding of local co-evolved relationships and trophic processes in the salt marsh, restorationists can make informed decisions regarding best management practices intended to preserve them. This study highlights the importance of co-occurring species interactions between invertebrates and salt marsh vegetation, and these findings were consistent with past research at both the organismal and community level (e.g. Dobel et al. 1990, O'Connor 1990, McNett & Rypstra



Figure 12. Family Erythraeidae, order Prostigmata (left), and family Oribatidae, order Oribatida (right).

2000, Pennings & Bertness 2001, Valverde & Lobo 2007). This research highlights fairly broad concepts to describe the nature of the *S. densiflora* invasion while providing ample direction for future study such as the use of delphacids as an *S. densiflora* bio-control agent and the examination of talitrid predation processes.

In summary, the results of this study clearly demonstrate an invertebrate community shift resulting from the invasion of *S. densiflora* in Humboldt Bay. My results strongly suggest that *S. densiflora* removal preserves associations between native organisms and increases invertebrate richness. While *S. densiflora* was shown to encourage the presence of a threatened mollusk, an invasive *Myosotella* benefitted similarly. At restored sites however, native vegetation remained favorable to the native *L. subrotundata* while it was apparently less so to *Myosotella* (see Figure 6). The findings of this study support the notion that eradication of *S. densiflora* is necessary, and that conservation activities intended to renew salt marsh vegetation can carry the added benefit of restoring impaired invertebrate communities. The continued removal of *S. densiflora* is therefore an appropriate action to preserve the threatened *L. subrotundata*, other native biota, and related ecosystem functions in perpetuity.

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