The potential for a hemiparasitic plant to maintain species diversity during climate change: the role of warming and critical species in a salt marsh on Humboldt Bay, California, USA.

HUMBOLDT STATE UNIVERSITY

By

Marcus Dylan Jones

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The potential for a hemiparasitic plant to maintain species diversity during climate change: the role of warming and critical species in a salt marsh on Humboldt Bay, California, USA.

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By

Marcus Dylan Jones

Approved by the Master's Thesis Committee:

Erik S. Jules, Major Professor Date

Frank J. Shaughnessy, Committee Member Date

Michael R. Mesler, Committee Member Date

Sean F. Craig, Committee Member Date

Michael R. Mesler, Graduate Coordinator Date

Dr. Jená Burges, Vice Provost Date
ABSTRACT

The potential for a hemiparasitic plant to maintain species diversity during climate change: the role of warming and critical species in a salt marsh on Humboldt Bay, California, USA.

Marcus D. Jones

Salt marsh ecosystems are an extremely important part of estuarine ecosystems around the world. What might happen to these systems if predictions about climate change are realized is largely unknown. I studied the effects of warming on salt marsh plant communities in Humboldt Bay, California, USA, using open top passive warming chambers (OTCs). In addition, I subjected both the ambient and experimentally warmed plant community to the removal of a rare hemiparasitic plant. *Cordylanthus maritimus* ssp. *palustris* was previously shown to facilitate coexistence and diversity in California salt marshes by lowering soil salinity levels through an increased transpiration rate. In the event that climate change increases soil salinity through increased evaporation rates, this species could play a key role in maintaining lower salinity levels in the soil. One hundred and twenty 0.5 m$^2$ plots were arranged on a small island in Humboldt Bay. Each plot was randomly assigned to one of four treatments, Ambient, Warmed, Removal and Warmed/Removal, such that each treatment was replicated thirty times. The study lasted from April 2009 to October 2010. OTCs increased surface temperatures by 0.5-0.6 °C,
however their effect decreased over time. Warming had little effect on salinity, but it negatively affected plant species richness. Non-metric multidimensional scaling ordination (NMDS) and multiple response permutation procedure (MRPP) revealed a shift in community structure between Unwarmed and Warmed treatments from 2009 to 2010. This shift was characterized by a 40% decrease in annual plant species abundance, most likely caused by increased shading by perennial species in Warmed treatments. The results indicate that warming may significantly increase canopy height and biomass, altering richness and surface temperatures. The rare hemiparasite *Cordylanthus* was negatively affected by warming. Warmed treatments caused a 97% decrease in biomass and fruit set over a one year period. The Removal treatment significantly increased soil salinity from ambient conditions, but there was no effect of removal on plant community structure over the duration of the experiment. *Cordylanthus* is currently helping to lower salinity in Humboldt Bay’s salt marshes; however if warming increases shade and decreases evaporation in salt marshes, the effects that *Cordylanthus* has on soil salinity could be lost. A denser community that out competes annual plants could have significant impacts on biodiversity in Humboldt Bay.
I would like to say thank you to the following organizations and people. The Humboldt State University Department of Biological Sciences and Mrs. Virginia Rumble supplied financial support to this project. Humboldt State University let me use their property and Gary Krietsch helped in securing a permit through the California Coastal Commission to install experimental equipment on the island. The Humboldt Bay Harbor, Recreation and Conservation District, Army Core of Engineers and the California Department of Fish and Game all supplied jurisdictional support. Marty Reed, Lewis McCrigler and George Pease are outstanding equipment technicians, and their help in manufacturing 63 OTC’s was priceless. Frank Shaughnessy and Steve Monk let me use their kayaks and safety equipment. Frank, David Franklin, Elizabeth Wu and Kim McFarland all helped in setting up the experiment. Geoff Bale, Arthur Grupe, Andrew Weltz, Ed Sanders, Ryan Judd, Brandon Hayden, Owen Simonds and Anna Jones were all loyal field and lab assistants. The oyster farmers in the Mad River Slough were gracious enough to collect chambers that were removed from the island during the 2009-2010 winter. To Erik Jules, a trusty advisor, to my committee, my family and to my loving wife whose support and encouragement for all the days of kayaking in the bay and playing in the mud, I will never be able to repay. And thank you to anyone I may have missed; I couldn’t have finished this alone.
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INTRODUCTION

Estuarine ecosystems are the nurseries, refugia and habitat for countless aquatic and terrestrial organisms around the world, and provide many important ecosystem services (Penning and Bertness 2001). Plant communities that comprise salt marshes are critical features of these systems; by stabilizing sediments, reducing disturbance (e.g., from wave action), and supporting numerous taxa at higher trophic levels, these communities are vital habitat in coastal ecosystems. Salt marsh plants alter these habitats through nutrient deposition, habitat modification, and facilitation and competition, creating diverse communities (Bertness 1985, Unger 1992, Pennings and Callaway 1996, 1998, Jefferies 1997, Grewell 2008a, 2008b). In addition, marshes host an array of invertebrates (e.g., crabs, snails, and bivalves), serve as the nursery for fisheries (Lenanton and Potter 1987, Monaco et al. 1992), are a refuge for waterfowl and shorebird taxa during migrations (Kerbes et al. 1990), and are the nesting sites for several species of songbirds, rails, gulls and terns (Erwin et al. 2006). Changes to the structure of these communities could have both short- and long-term effects on the services they provide and to the members that inhabit them. Understanding the factors that shape the structure and diversity of salt marsh plant communities is important for conservation and restoration efforts, especially as large scale changes in climate and anthropogenic demands begin to impact estuarine ecosystems.

Threats to salt marsh communities include habitat modification, increased sedimentation, grazing pressures, non-native species and encroachment from development, as well as predicted climate changes including increased atmospheric
temperatures, sea level rise and increased CO₂ concentrations (Bertness et al. 2004). Unfortunately, the effects of climate change on salt marsh plant communities are largely unknown. The Intergovernmental Panel on Climate Change (IPCC 2002) predicts worldwide increases in sea levels and temperatures in the next few decades, both of which could have serious effects on salt marsh communities. The IPCC is predicting a worldwide increase in surface temperatures of 0.8-2.6 °C from 1990 to 2050. Some impacts caused by sea level rise could be ameliorated by natural upward shifts in communities across elevation gradients (Bertness et al. 2004) or through isostatic uplift on regional scales (Pennings and Bertness 2001). However, temperature increases may cause a more direct effect to community structure through increased evaporation rates, which could elevate soil salinity stresses and alter species diversity and coexistence between plant populations (Bertness et al. 2004). A loss in diversity at this trophic level could have serious bottom-up effects on estuarine ecosystems. Studies have shown that a loss in intraspecific diversity at the producer level impacts species interactions and diversity at higher levels (Wimp et al. 2005, Crustsinger et al. 2006, Duffy et al. 2007), and shifts trophic level interactions (Knight et al. 2005, Haddad et al 2009).

Although there is a substantial body of work documenting species interactions and community structuring within salt marsh systems (e.g., Bertness 1985, Unger 1992, Pennings and Callaway 1996, 1998, Pennings and Bertness 2001), we know relatively little about the mechanisms that govern and maintain plant diversity in these systems (Pennings and Callaway 2000, Grewell 2008a, 2008b). It was shown recently that a rare hemiparasitic plant plays a critical role in maintaining plant diversity in the salt marshes
of San Francisco Bay and Tomales Bay, California, USA. Grewell (2008b) showed that *Cordylanthus maritimus* ssp. *palustris* reduced stress caused by soil salinity and also reduced the dominant plant competitors (*Salicornia virginica* and *Distichlis spicata*) through direct parasitism. *Cordylanthus* has a parasitic or source sink relationship with host plants. *Cordylanthus* elevates its transpiration rate in order to move water and nutrients from the host, in turn pulling more water from the soil. Salts are carried in this extra water effectively lowering the salt concentration in the soil. This study implies that species diversity and coexistence is directly and indirectly facilitated by species interactions and that the absence of a key community player could reduce local biodiversity. Perhaps more importantly though, this study reveals the potential for a parasite to buffer the increase in salinity expected to accompany climate warming (Bertness et al. 2004), as well as shed light onto some of the important factors that are governing plant diversity in salt marsh communities.

The purpose of my study was to (1) assess the impacts of climate warming on diversity and structure of salt marsh plant communities in Humboldt Bay, California, USA, (2) evaluate the role of a keystone parasitic plant in the salt marsh, and (3) test whether this keystone plant has the potential to ameliorate the negative effects of warming. Warming experiments have been done in many higher latitude and terrestrial systems (Weltzin et al. 2000, de Valpine and Harte 2001, Post and Pedersen 2008), but are lacking in coastal and lower latitude systems. To my knowledge, my study is only the second to address the issue of warming on salt marsh communities (see Gedan and Bertness 2009). In addition, my study provides information about a rare plant in
Humboldt Bay, for which little information is available. The California Native Plant Society lists *Cordylanthus maritimus* ssp. *palustris* as a 1.B2 species in Humboldt County, though only basic life history work has been done on this species in the region (Bivin et al. 1991); there are no current State or Federal rankings for this species.
METHODS AND MATERIALS

I. Study Site & Experimental Design

My study was conducted in the Mad River Slough, a four mile long brackish water system on the northern end of Humboldt Bay, Humboldt County, USA. The slough experiences daily mixed semidiurnal tides and is mostly a marine environment with a small freshwater input coming from a few creeks draining agricultural lands and from rainfall events. Along its entire length, the slough is dotted with small islands and mud bars that support a diverse salt marsh community (Pickart 2009). I selected a small island (~10,000 m²) owned by Humboldt State University, near the mouth of the slough that contained a large, contiguous patch of salt marsh vegetation for this study. The study was initiated in April 2009 and terminated in October 2010.

My study site is home to a rich community of mixed annual and perennial herbaceous halophytes and has not experienced heavy invasion by the aggressive non-native cord grass, Spartina densiflora. The dominant species in this system is Distichlis spicata, although there are fifteen other angiosperms that inhabit the study site as well (Table 1). Three of these species are annual parasitic plants (C. maritimus ssp. palustris, Castilleja ambigua ssp. humboldtiensis and Cuscuta salina var. major) and two have been shown recently to facilitate coexistence and diversity in California salt marshes (C. maritimus ssp. palustris and C. salina var. major; Grewell 2008a, 2008b). The parasitic plant species of most concern for this study, C. maritimus ssp. palustris, is by far the most abundant on the island (Bivin et al. 1991; M.D. Jones, personal observation).
Canopy height on the island averages 15 cm (SD, ± 3 cm), relatively shorter than the mainland plant communities (Bivin et al. 1991, personal observations).

Table 1: Species list for Mad River Slough study site. # Annual, * Rare, threatened, or endangered in California, ^ Facultative hemiparasite, ● Obligate holoparasite.

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
<th>Family</th>
<th>Status</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distichlis spicata</td>
<td>Salt Grass</td>
<td>Poaceae</td>
<td>Native</td>
</tr>
<tr>
<td>Parapholis strigosa</td>
<td>Salt Marsh Dodder</td>
<td>Poaceae</td>
<td>Exotic</td>
</tr>
<tr>
<td>Triglochin maritima</td>
<td>Seaside Arrow-Grass</td>
<td>Juncaginaceae</td>
<td>Native</td>
</tr>
<tr>
<td>Triglochin concinna</td>
<td>Arrow-Grass</td>
<td>Juncaginaceae</td>
<td>Native</td>
</tr>
<tr>
<td>Plantago maritima var. juncoides</td>
<td>Salt Marsh Plantain</td>
<td>Plantaginaceae</td>
<td>Native</td>
</tr>
<tr>
<td>Limonium californicum</td>
<td>Sea-Lavender</td>
<td>Plumbaginaceae</td>
<td>Native</td>
</tr>
<tr>
<td>Cordylanthus maritimus ssp. palustris</td>
<td>Point Reye’s Bird’s Beak</td>
<td>Scrophulariaceae</td>
<td>Native*^#</td>
</tr>
<tr>
<td>Castilleja ambigua ssp. humboldtiensis</td>
<td>Humboldt Bay Owl’s Clover</td>
<td>Scrophulariaceae</td>
<td>Native*^#</td>
</tr>
<tr>
<td>Salicornia virginica</td>
<td>Pickleweed</td>
<td>Chenopodiaceae</td>
<td>Native</td>
</tr>
<tr>
<td>Salicornia bigelovii</td>
<td>Dwarf Pickleweed</td>
<td>Chenopodiaceae</td>
<td>Exotic</td>
</tr>
<tr>
<td>Jaumea carnosa</td>
<td>Jaumea</td>
<td>Asteraceae</td>
<td>Native</td>
</tr>
<tr>
<td>Spartina densiflora</td>
<td>Dense-Flowered Cord Grass</td>
<td>Poaceae</td>
<td>Exotic</td>
</tr>
<tr>
<td>Spergularia marina</td>
<td>Salt Marsh Sand Spurry</td>
<td>Caryophylaceae</td>
<td>Native</td>
</tr>
<tr>
<td>Grindelia stricta var. stricta</td>
<td>Gumplant</td>
<td>Asteraceae</td>
<td>Native</td>
</tr>
<tr>
<td>Cuscuta salina var. major</td>
<td>Salt Marsh Dodder</td>
<td>Convovulaceae</td>
<td>Native●#</td>
</tr>
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Study plots on the island were created using a stratified random design. An 80 x 60 m grid system was set up in a large continuous patch of salt marsh vegetation on the island and 120 points were created so that each point was four meters from an adjacent
point (Appendix, Fig. 1). At each point a 0.25 m² plot was established and randomly assigned to one of four treatments, creating four sets of plots each with thirty replicates.

The first set was assigned as unmanipulated controls (Ambient/Unwarmed). A second set was assigned as a warming treatment to assess the impacts that climate warming may have on this system (Warmed). Experimental warming was conducted using standard passive warming open-top-chambers (OTC, Fig. 1) with site-specific modifications (see below; Marion 1996, Holster and Webber 2000). The third set was treated by removing all *Cordylanthus* once during May of each field season to assess their effect on community structure (Removal). The other rare hemiparasite *Castilleja ambiguа ssp. humboltiensis* occupied roughly 1.0% of the community the first year and less than 0.01% the second, but because I do not know the effects of *Castilleja* on the community, both it and *Cordylanthus* were removed by hand during both field seasons. The fourth set was both experimentally warmed and had *Cordylanthus* removed to assess whether this species could buffer against the potential negative effects caused by increasing temperature (Warmed/Removal). The number of hemiparasites removed was recorded in 2009 and 2010.

II. Experimental Warming and Chamber Design

My passive warming chamber design mimics closely the design used in numerous other warming studies (Marion et al. 1997, Musil et al. 2005, Post and Pedersen 2008; Fig. 1). I made 378 wall panels cut from 1.22 x 3 m sheets of 6 mm Lexan Termoclear structured polycarbonate (95% transparency, AmeriLux International, DePere, WI) to construct 63 open-top-chambers. Each panel had three holes drilled along the sides that
Figure 1: Passive warming open-top-chambers (OTCs). Basic hexagon design was modeled after Marion (1996).
were connected to another panel. Panels were connected using galvanized sheet metal battens and stainless steel fasteners. Battens were hand made by sheering strips from 7.72 m² rolls of sheet metal (~ 12 m² in total) and then bent to a 120° angle down the center. Prior to bending, six holes were drilled in each to accommodate the fasteners and to fit the pre drilled holes in the panels. I used 1.5 cm long stainless steel bolts and hex nuts to fasten panels to the battens and to each other. A silicon sealant was used to seal the corners and make each panel air tight. A finished OTC stood 35 cm tall, was 50 cm wide at the top and 90.4 cm at the base (Fig. 1). Measurements are slightly smaller than Marion (1996) design due to the number of chambers needed and the cost of materials, however the size was suitable for this type of plant community and for the plot size sampled.

Marion et al. (1997) explained that all warming chamber designs in high latitude systems alter wind patterns around plants and that previous data suggests a decrease in relative humidity inside OTCs due to increasing temperatures. However, Gedan and Bertness (2009) showed in a lower latitude system that humidity increased inside the chambers due to increased transpiration by the plants. I attempted to minimize the effect of my chambers on wind and humidity by raising each OTC 9 cm off the ground by positioning it on small wooden blocks on three of the six bottom corners (eight 3 m 9 x 9 cm Douglas-fir posts cut into 9 cm³ cubes; Fig. 2). The wooden blocks were added to the anchoring system so I could minimize the amount of material on the island and also provided a way to attach the chambers to the stakes. Anchoring the OTCs was maintained by hooking a 60 cm piece of structural rebar through a pre-drilled hole in the
wooden block and pushing them into the soil. OTCs were then screwed to the wooden blocks using 5 cm galvanized screws (Figure 2).

During the winter of 2009-2010, the site received a few large tidal events, and around December 31, 2009 nearly half of my OTCs moved from their specified locations and about a dozen were washed away from the island. All chambers were recovered and relocated to their previous positions by January 3, 2010. At that date, each OTC was additionally supplied with two 1.5 m long rebar hooks for more anchorage. There was relatively no plant growth at this time of year and the OTCs that were removed from there locations were off for no more than 4-5 days.

Figure 2: a) Finished and installed OTCs on the site. b) Note the wooden blocks and their attachment to the rebar stacks; they provided additional height and air flow into the canopy. Additional anchorage added in January, 2010 is not shown (photos courtesy of Kim McFarland).
Gedan and Bertness (2009) also showed that OTCs can lose their temperature enhancing ability over time, most likely due to material degradation. In marine environments artificial structures are susceptible to fouling by the many microorganisms present in these communities. By intercepting or reflecting incoming light, fouling algae decrease the warming abilities of the chamber. To maintain an environment with higher temperatures and adequate light penetration the chambers were washed one year after installment. Cleaning was achieved by removing each OTC and scrubbing it with a kitchen sponge and sea water. Each was hand dried before it was returned to its location to minimize any new fouling that could have occurred during the wash.

III. Environmental Measurements

Temperature was measured using Thermochron® iButton temperature loggers (Maxim Integrated Products, Sunnyvale, CA). Due to budget limitations, I was able to install loggers on only a subset of plots in each treatment. Within each treatment, five randomly selected plots were used for temperature measurements. A single logger was placed at the center of each plot and positioned as low in the canopy as possible.

Temperature was measured every hour and was gathered from loggers using OneWireViewer software (Maxim Integrated Products, Sunnyvale, CA) every four to six weeks. Hourly temperatures were averaged across the five plots within each treatment to get 24 hourly averages for each day. The five loggers in each treatment were not statistically different from each other. The mean daily surface temperature for each treatment was calculated for each day. I calculated an average daily temperature in order to reduce the large amount of noise present in the hourly data.
Salt marsh ecosystems experience complete tidal inundation several times a year. During these events water temperature could be obfuscating the true effect OTCs have on ambient temperatures. Therefore, I merged my temperature data with real time tidal height data from CenCOOS (Central and Northern California Ocean Observing System; Dock B, central Humboldt Bay, CA) and removed all temperature readings when the depth of the bay from mean low-low water (MLLW) was greater than 2.0 m. Tidal heights this large cover the site and the loggers by at least 15 cm and all temperature loggers then read the temperature of the water. The CenCOOS data set was not 100% complete for the seventeen months of depth data used in the data merger. Data were merged by hour of the day and when there was more than a 24 hr period of depth data missing I used local tide books to find days and times when the island was inundated. Approximately 96 hours of temperature data was lost to tidal influx, which represents less than 1.0% of the time sampled.

Soil salinity is a major factor controlling plant growth and many other intra- and interspecific interactions throughout salt marsh ecosystems (Pennings and Bertness 2001, Bertness et al. 2004, Grewell 2008b). In my study, soil salinity was measured in each plot four times during a growing season and the average soil salinity for the year was calculated for each plot. Sampling was done on days when mean high tide was lower than 1.8 m from MLLW for four days prior to sampling. Because soil salinity is also influenced heavily by tidal inundation, my sampling technique gave the best estimate of the effect that OTC’s and Cordylanthus had on salinity. At each plot a 4 cm³ soil core was taken as close to the center of the plot as possible; rhizomes and roots in the soil
made for coring exact plot center difficult in some plots. Once a core was collected, a small sample was removed from ~5 cm below the soil surface, placed onto a small piece of coffee filter paper, and put into a 20 cc syringe. A small drop of water from each sample was placed on a Handheld Salinity Refractometor (Thermo Fisher Scientific Inc., Waltham, MA) and the soil salinity was recorded in parts per thousand.

Elevation for each plot was recorded using a simple hand surveying technique. An undergraduate and I began at a known USGS bench mark at the mouth of the Mad River Slough and used a four meter tall surveying pole and a hand held leveled monocular to transect elevation to a fixed point on the island at the edge of the study site. Since both the original elevation and the height of the monocular reader are known, simple addition and subtraction can be used to find the true elevation at each plot center. Elevation was recorded to the nearest centimeter.

The 100 year average for wind speeds on Humboldt Bay during the months of March to September is ~7 mph (National Weather Service records for Eureka, CA); and wind speeds can gust up to 60 mph on the bay. I measured wind speed in the field at one time point, using a hand held wind meter (Extech Instruments, LLC, Waltham, MA) held at the top of the canopy in the center of a chamber on a windy day in June 2010.

IV. Community Measurements

Percent cover of all vascular plants species was estimated in each plot at the end of May 2009 and 2010. All plots were sampled using a 0.25 m² quadrat with one hundred evenly spaced squares, each representing 1.0 % cover. All cover values were estimated to whole numbers, i.e. all species identified had an abundance value of at least
one percent in each plot. Using percent cover values, the proportion of the sample comprised of species \( i \) \((p_i)\) was calculated for each plot. Not all species were correctly identified the first season. During the 2009 sample, *Parapholis strigosa* was mis-identified as *Distichlis spicata*, and *Plantago maritima* var. *juncoides* and *Triglochin concinna* were mis-identified as *Triglochin maritima*. In 2010, these species were counted in the sample. However, because my analysis required assessing the change in community composition from 2009 to 2010, I grouped *Parapholis* with *Distichlis* and *Plantago* with the *Triglochin* species. Richness, evenness and diversity were all calculated to assess community response to the four treatments. Evenness was calculated using Hurlbert’s (1971) probability of an inter-specific encounter (PIE), where \( N \) is the total number of individuals sampled and \( S \) is the number of species.

\[
PIE = \frac{N}{(N-1)} \left( 1 - \sum_{i=1}^{S} p_i^2 \right)
\]

Diversity was calculated using Jost’s (2006, 2007) conversion of the Shannon index \((H)\), such that diversity is \(\exp(H)\) where \(H\):

\[
H = -\sum_{i=1}^{S} p_i \ln p_i
\]

To determine the effect of warming on the fitness of the rare hemiparasite *C. maritimus* ssp. *palustris*, up to five individuals from each plot in the Ambient and Warmed treatments were removed in August 2009 and 2010. Not every plot had five individuals each season, and I never removed every individual; thus some plots supplied fewer than five plants for fitness measurements. Shoot length, number of fruits and biomass was recorded for each individual and averaged within the plot.
Ten randomly selected plots from each treatment were selected to measure the physiological response to warming and removal within the community at the end of August 2010. Community response was estimated by using above and belowground biomass samples. At each plot all aboveground and belowground plant material was removed from a ~25 cm$^2$ patch in the center of each plot. Aboveground material was removed using garden shears; belowground material was collected using a 200 cm$^3$ volume soil corer. Soil cores were rinsed with fresh water and all material remaining in a standard USA NO. 10 soil sieve was collected. Dried biomass, as well as a root:shoot ratio was calculated for each plot sampled.

**V. Analysis**

I used separate repeated measures ANOVAs to test for a change in soil salinity, canopy height, diversity (Jost’s H’), evenness (PIE) and richness (R), with Year, Removal and Warming as factors. In addition, I ran separate two-way ANOVAs for three separate blocks of time (summer 2009, winter 09-10, and summer 2010) to determine the effect the chambers had on mean daily surface temperature over time. Because five loggers for each treatment were averaged to create a mean daily surface temperature for each day, and a day represents an independent event, a repeated measure was not used. To determine the effect of warming on *Cordylanthus* fitness each season, I ran a simple MANOVA with mean number of fruits, biomass and height as response variables and warming as the main predictor; Wilk’s test statistic was used to determine significance. To assess *Cordylanthus* abundance over time, I used repeated measures ANOVA but only with year and warming as factors. Simple two way ANOVAs were
used to test for differences in root:shoot ratios, and above and belowground biomass. All ANOVAs and their post-hoc tests were conducted using SPSS 16.0 (Levesque 2007) and Minitab 16 Statistical Software (Minitab® 2011). To assess differences in community composition among the four treatments, I conducted a non-metric multidimensional scaling ordination (NMDS) and multiple response permutation procedure (MRPP) using PC-Ord (McCune and Mefford 2006). MRPP was run for both the 2009 and 2010 sample to test for significant differences in community composition. The T-statistic manufactured by the MRPP tests the difference between the observed and the expected weighted mean within-group distance. The A statistic generated by the test describes the amount of within-group homogeneity. When A = 0 the heterogeneity within groups equals expectation by chance; when A = 1 all items are identical within the group; and when A < 0 there is less homogeneity within groups than expected by chance. The NMDS was used to visually assess differences in composition. NMDS was run with 500 iterations using PC-Ord’s “slow and thorough” mode, which uses a random starting configuration and Sørensen distances to express the community similarities. Because *Grindelia stricta* var. *stricta* and *Cuscuta salina* var. *major* occurred in only one plot each, their abundance values were not used in the NMDS or MRPP analysis in order to reduce noise caused by infrequent taxa. All data used in analysis met linear and multivariate assumptions for normality and intendance. No data transformations had to take place.
RESULTS

I. Environmental Response

Passive warming chambers influenced mean daily surface temperature, although the effect of chambers on temperature varied throughout the experiment. Mean daily surface temperature during the 2009 summer was significantly higher in Warmed treatments ($F_{1,612}=7.6$, $p=0.006$, Fig. 3a). On average, Warmed treatments were 0.5 – 0.6 °C (SD ±0.19°C) warmer than Ambient conditions. *Cordylanthus* removal had no effect on surface temperature in 2009. Surface temperature remained significantly warmer during the winter months as well ($F_{1,520}=4.6$, $p=0.032$). During summer 2010, chambers appeared to have lost their warming effect ($F_{1,612}=0.59$, $p=0.445$), however surface temperatures in plots where *Cordylanthus* was removed were significantly lower than plots where *Cordylanthus* was not removed (0.3 - 0.4 °C lower in removal plots; $F_{1,612}=3.9$, $p=0.048$, Fig. 3b). It is important to note that only surface temperatures were observed; the impact of the chambers or *Cordylanthus* removal on temperature was not directly measured above the surface (see Discussion).

![Graph](image-url)

Figure 3: Mean daily surface temperature (°C) for the months of May – September for both field seasons. Error bars represent ±1.0 standard error.
Table 2: Repeated measure ANOVA table for change in soil salinity.

### Tests of Within-Subjects Contrasts for Soil Salinity

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### Tests of Between-Subjects Effects for Soil Salinity

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</table>

Soil salinity was significantly influenced by both warming and hemiparasite removal during the study, although treatment effects were different over time (Table 2). In 2009, Warmed plots averaged 1.0-0.5 ppt (SD ± 0.36 ppt) lower in soil salinity than Unwarmed plots indifferent of removal. In 2010, average soil salinity in Warmed plots was roughly identical to Ambient conditions, but Removal plots increased significantly by 2.0-2.5 ppt (SD ±0.44 ppt; Fig. 4). The results imply that soil salinity was influenced more by removal than by warming over time (Table 2), yet both warming

![Figure 4: Mean change in soil salinity (ppt) from 2009 to 2010. Error bars represent ±1.0 standard error.](image-url)
and removal influenced soil salinity \((F_{1,116}=4.6, p=0.034, \text{Fig. 4})\). Warming appears to have caused a decrease in salinity during the first year \((F_{1,116}=6.9, p=0.010)\), but caused an increase the second year.

Wind could not be detected in any of the plots I tested. In addition, there was no difference in elevation among the four treatments. Average plot elevation was 1.95 m (SD ±0.05 m) and was not correlated with any response variable used in analysis.

II. Community Response

Canopy height was significantly higher in Warmed than in Unwarmed treatments in both 2009 and 2010 \((F_{1,116}=159.6, p<0.001)\). In 2010, canopy height increased an average of 5 cm (SD ±0.5 cm) in Warmed treatments from the previous year \((F_{1,116}=104.5, p<0.001)\) and Unwarmed treatments increased an average of 1 cm (SD ±0.3 cm, \(F_{1,116}=4.1, p=0.029\)). Warming increased aboveground biomass by the end of the experiment \((F_{1,36}=5.5, p=0.025)\), however it maintained a root:shoot ratio equivalent to Ambient plots (Fig. 5). Below ground biomass was influenced more by *Cordylanthus* removal than by warming. Removal decreased belowground biomass \((F_{1,36}=4.1, p=0.051)\) and decreased the root:shoot ratio \((F_{1,36}=5.3, p=0.028)\). When the community was warmed, and had *Cordylanthus* removed, the ratio decreases more (Fig. 5).

There was no effect of Warming or Removal on plant diversity, however, richness was significantly influenced by both treatments (Table 3). Removal alone did not significantly change richness in the community (Table 3), but richness was lower in Warmed plots at the end of the experiment. This decrease seen in Warmed plots was marginally significant \((F_{1,116}=3.1, p=0.081)\). When plots had hemiparasites removed and
were warmed, richness did not change (Fig. 6, Table 3). There was a significant three-way interaction between Warming, Removal and Year ($F_{1,116}=4.3$, $p=0.041$). Suggesting that warming alone may cause a loss to richness in salt marsh communities, but when a parasitic interaction is removed from the community, the remaining species compete equally to maintain some richness. Evenness did not change over time, but it was significantly lower in Unwarmed treatments than in Warmed treatments each year ($F_{1,116}=5.3$, $p=0.023$).

*Spergularia marina* was the only species that experienced a significant change in abundance in either the Warmed or Removal treatments (Fig. 7a). In both Warmed treatments abundance of *S. marina* decreased by 40% (SD ±5%, $F_{1,116}=4.7$, $p=0.032$). Abundance for the *Triglochin/Plantago* group was marginally increased by *Cordylanthus* removal ($F_{1,116}=3.4$, $p=0.067$), but only in Warmed treatments (Fig. 7b). All other species showed some change in abundance though none of these changes were significant.
(Fig. 7c-h). The invasive *Spartina densiflora* increased slightly in all treatments, the most in the Removal plots (Fig. 7h), however the increases were not significant ($F_{1,116}=0.53$, $p=0.467$).

### Table 3: Repeated measures ANOVA table for change in richness among treatments.

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<tr>
<td>Error</td>
<td>116</td>
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</table>

### III. Hemiparasite Response

During the 2010 growing season hemiparasite abundance fell by 50-70% in the plots that had experienced manual removal. *Cordylanthus* presence varied strongly between years ($F_{1,58}=12.8$, $p=0.001$), but was not different between Warmed and Unwarmed Removal treatments. Because there is strong inter-annual variation within this species (Bivin et al. 1991), and because the drop in abundance was seen across all plots, Removal treatments during the second field season are still relevant tests of my hypothesis. *Cordylanthus* fitness was strongly influenced by warming. In 2009, mean height, biomass and number of fruits were significantly higher in Warmed plots (MANOVA, $F_{3,56}=15.6$, $p<0.001$).
Figure 7 (a-g): Mean change in the proportion species (i) occupied in each treatment (pi) from 2009 to 2010. Error bars represent ±1.0 standard error.
Figure 8: Change in fitness measurements for *Cordylanthus maritimus* ssp. *palustris* from 2009 to 2010. a) Change in mean height (cm), b) change in mean number of fruits and c) change in mean biomass (g). White bars (Unwarmed), black bars (Warmed). Error bars represent ±1.0 standard error.

During the 2010 growing season fitness dropped dramatically in Warmed treatments (MANOVA, $F_{3,56}=4.9$, $p=0.004$, Fig. 8a-c). Warming caused a 97% decrease in mean number of fruits and biomass and a 70% decrease in mean height.

**IV. NMDS and MRPP Results**

NMDS ordination produced a two dimensional ordination for 2009 that described 90% of the variation in the data with a final stress level of 17.1 (Fig. 9a). The two dimensional ordination for 2010 described 92% of the variability with a final stress level of 15.5 (Fig. 9b). The results show a strong separation in the community between Unwarmed and Warmed treatments. Removal does not appear to have influenced community composition. MRPP results for 2010 showed a significant difference between both Warmed treatments and their respective Unwarmed counterparts (Table 4). Both Warmed treatments were significantly different from the Unwarmed Removal plots at the time I sampled in 2009, but not from Ambient plots. For the 2010 sample this difference stayed the same or increased in significance. Warmed treatments also became significantly different from ambient conditions in 2010 (Table 4, Fig. 9).
Figure 9: Ordination graphs, a) 2009 NMDS results, b) 2010 NMDS results. Axis represent the average score for the treatment. UWNR (unwarmed no removal, Ambient), UWR (unwarmed removal), WNR (warmed no removal) and WR (warmed removal). Error bars represent ±1.0 standard error.

Table 4: MRPP results for 2009 and 2010 species abundance samples. Comparison codes: UWNR (unwarmed no removal, Ambient), UWR (unwarmed removal), WNR (warmed no removal) and WR (warmed removal). Bolded values indicate P≤0.05.

### 2009 MRPP Results

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### 2010 MRPP Results

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DISCUSSION

In this study, I demonstrated the potential for climate warming to have an impact on the diversity and structure of Humboldt Bay’s salt marsh plant communities. My work suggests that an average surface temperature increase of 0.5 °C and a significantly less windy local environment, allowed the perennial plant community of Humboldt Bay had to maintain its root:shoot ratios and increase its height rapidly, whereas the annual plant community was reduced. Warming treatments effectively lowered species richness and this loss in richness could potentially alter interspecific relationships within the community. Over the two years of my study, warming had little effect on soil salinity, yet when combined with the loss of *Cordylanthus*, salinity was elevated relative to the ambient environment (Table 2, Fig. 4). The removal of *Cordylanthus* from Unwarmed treatments caused a greater spike in salinity than in the Warming/Removal treatment. This is indicating that warming is slowing or potentially buffering the increase in salinity caused by the loss of a hemiparasite from the community. Gedan and Bertness (2009) showed that salt marsh plants transpired more in warmer conditions, elevating humidity at a local scale. I was unable to measure humidity or transpiration rates in my study, but a humid environment within the chambers could have slowed evaporation causing a delayed increase in salinity. These findings are contrary to my prediction that warmer environments may increase evaporation rates.

In 2010, *Cordylanthus* experienced a strong decrease in height, biomass and mean number of fruits set in Warmed treatments. The annual *Spergularia marina* experienced a 40% drop in abundance in Warmed plots, and the non-native annual *Salicornia*
*bigelovii* had a non significant 34% decrease in abundance in Warmed treatments ($F_{1,116}=0.99$, p=0.322). This decrease in fitness and abundance among the annuals is likely attributable to an increase in canopy height within Warmed plots. Unger (1992) showed that *Spergularia marina* survival was strongly density-dependent, and that fitness of the species dropped and mortality increased in dense intraspecific groupings. During the 2009 summer, a warmer environment allowed for *Cordylanthus* to grow at the same rate as the perennial species in the community. At the start of the 2010 growing season, the perennial plant community was taller than it was at the start of the 2009 season. Because *Cordylanthus*, *Spergularia* and *S. bigelovii* are annuals, individuals had to start the 2010 season as seedlings and compete against a taller and denser community, most likely increasing seeding mortality.

My study suggests that annual plant species could be the first lost in these communities if the climate warms. If perennial plant species in these communities increase in density, biomass and stature across a local scale, density-driven mortality could increase, creating a less rich community or potentially maintaining a diverse perennial community. The results showed that diversity did not change in warmed plots. The root:shoot ratios were maintained, but richness fell, indicating that the perennial species remaining in the system are competing for resources equally. A taller community and the OTCs, would have created shade, and in salt marsh ecosystems shade plays a critical role in maintaining evaporation rates which are the key cause of salinity build-up in marsh soils (Bertness et al. 1992). By increasing shade, surface temperature may drop, decreasing evaporation rates and creating a less stressful environment for these
halophyte communities. A denser community could also favor plants that spread through vegetative means, negatively affecting nonclonal perennials like *Plantago maritima* var. *juncoides* or *Grindelia stricta* var. *stricta* that need seedling recruitment to maintain population size. I was unable to measure temperatures above the canopy so my results do not demonstrate the effects the chambers may have had on the upper canopy of the community. Warmer temperature and less wind in the canopy could have been driving canopy height increases. Shading from the OTCs may have caused some etiolation to occur among the plants within the chambers, potentially driving canopy height. However, I did not notice any chlorosis among the plants and the maintenance of the root:shoot ratio in warmed plots suggests that the whole plant was responding to warming and not just the shoots.

The rare hemiparasite *Cordylanthus maritimus* ssp. *palustris* decreases soil salinity and may influence surface temperatures in Humboldt Bay. I was not able to show that removal effected community structure, however, the ability of *Cordylanthus* to facilitate community structuring in other salt marsh ecosystems (Grewell, 2008b), and its effect on salinity in this study, it is likely to play a role in maintaining structure in Humboldt Bay salt marsh plant communities. Richness fell in Removal plots, but not significantly (Fig 6, Table 2) and the strong variation in *Cordylanthus* abundance between the two seasons may have caused unseen annual effects, such as the significant increase in canopy height observed in Unwarmed treatments.

The positive effects on biodiversity that a parasite can have are not necessarily intuitive. However, parasitic plants within salt marsh communities have been shown to
play keystone roles in influencing community structuring, diversity, coexistence and species distribution (Pennings and Callaway 1996, 1998, Grewell 2008a, 2008b). The three parasitic plants that occupy Humboldt Bay salt marshes, and their interactions within these communities, are presumably one reason for the contemporary diversity seen in these marshes. The evidence suggests that protection of the hemiparasites *Cordylanthus* and *Castilleja* is important in maintaining current diversity within the Humboldt Bay salt marsh communities. Protecting current populations of these species is cardinal and introducing them into restoration areas may help decrease soil salinity build-up, speeding up revegetation and colonization of other species.

Alterations to community structure and functions that could be caused by climate warming will not be ameliorated by one species. The negative effect of warming on *Cordylanthus* fitness indicates that climate warming may expel the species from the community before any interspecific interaction alters the growing environment. Environmental changes such as an increase in temperature or the loss of wind appears to disrupt interspecific interactions played out within this community. Implying that when climates change rapidly, a plant’s life history (i.e., annual or perennial, clonal or nonclonal) may be more important in determining their future success in the community than the interactions they may have with other species. I do not, however, have evidence to show that there were no other species interactions taking place within this community, let alone between trophic levels.

I observed that active hunting spiders seemed to be more abundant within OTCs than outside. I did not measure their abundance, but an increase in predators within the
chamber could have altered herbivory pressure, creating an unseen effect on community productivity and biomass. It was shown recently that herbivorous arthropod respond to the hunting mode of predatory spiders in a grassland ecosystem (Schmitz 2008, Barton and Schmitz 2009a, 2009b). Active hunting spiders (not “sit and wait” spiders that construct webs to catch prey) were shown to alter the diet and lower the abundance of herbivores. These hunters in the community had an indirect positive effect on grass and herb productivity. Barton and Schmitz (2009b) also showed that experimental warming can strengthen a single predator’s effect. If predator abundance increased through habitat modification in Warmed treatments, herbivory pressure may have been suppressed within OTCs. Herbivore suppression could have indirectly affected the plant community, and potentially confounded my community biomass results.

The OTCs used in this study were extremely useful for passively altering an environmental variable in the field. Still the materials used degraded rapidly in a marine environment, the chambers lost their surface warming properties after two years, they attracted active hunting spiders and they stopped wind in the upper canopy, ultimately revealing the difficulty of accurately altering just one variable in the field for any length of time. Although the OTCs I used are considered standard warming equipment (e.g., Marion et al. 1996, Hudson and Henry 2009, 2010, Kardol et al. 2010), other warming techniques using heating lamps have altered temperature effectively while not influencing other conditions, such as wind and humidity (Weltzin et al. 2000, Zavaleta et al. 2003). The chamber effects seen in this study could have been attributed to alterations in temperature, wind, humidity, or light quality making it difficult to draw strong
conclusions about the impacts of climate warming. However, the modest impacts that my OTCs had on temperature reveal the potential for even a moderate change in climate on the Pacific Northwest could lead to major impacts on salt marsh plant communities.

A large issue that arose in this study came from the results of my evenness and MRPP analyses. OTCs were installed in April 2009, two months prior to my first community abundance sample. There was no change in evenness over time, yet evenness in the Removal treatment was different from the other three treatments in 2009 and 2010. It is unclear whether the chambers began to have an immediate and permanent effect on evenness or if, by chance, evenness already varied across the plots. MRPP results confirmed a difference in community structure between Removal and Warmed plots in 2009. The difference between Warmed and Removal treatments increased by 2010, but Removal treatments did not appear to differ from ambient conditions (Table 3). These results suggest that the chamber effects strengthened over time.

Current climate change research has shown mixed results for plant community responses to experimental warming. Warming has been shown to increase plant productivity and biomass (Hudson and Henry 2009, Kardol et al. 2010, Lin et al. 2010), decrease biomass and increase dead mater (Robinson et al. 1998), increase plant mortality (Musil et al. 2005) and decrease species diversity (Gedan and Bertness 2009). In other studies, warming has had no effect on plant productivity (Barton et al. 2009a), and a high arctic plant community resisted community changes over a fifteen year warming experiment with only an increase in lichen and bryophyte abundance (Hudson and Henry 2010). Predicting the effects climate change may have on the world’s plant communities
is extremely difficult and community response will probably be strongly related to ecosystem type and functional groups occupying the area (Lin et al. 2010).

Salt marshes are relatively simple systems, with species whose distributions are controlled mainly by salt tolerance and elevation within a wave protected tidal zone (Pennings and Bertness 2001). Compared to the coasts of the eastern United States, western shorelines have relatively few estuarine systems that support salt marsh plant communities. These communities, however, play a vital role in maintaining one of the most productive ecosystems in the world (Bertness et al. 2004). Predicting threats associated with global climate change is difficult; however by conducting climate change studies, restoring degraded sites and managing the ecosystems we currently have, we may be able to determine ways to slow or even halt the potential impacts that may be associated with climate change.

Figure 10: Study site in 2010. (constructed by Marcus Jones).
LITERATURE CITED


Appendix:

Figure 1: Map of study island and plot locations; Mad River Slough, Humboldt Bay, CA. Prepared using ArcGIS.